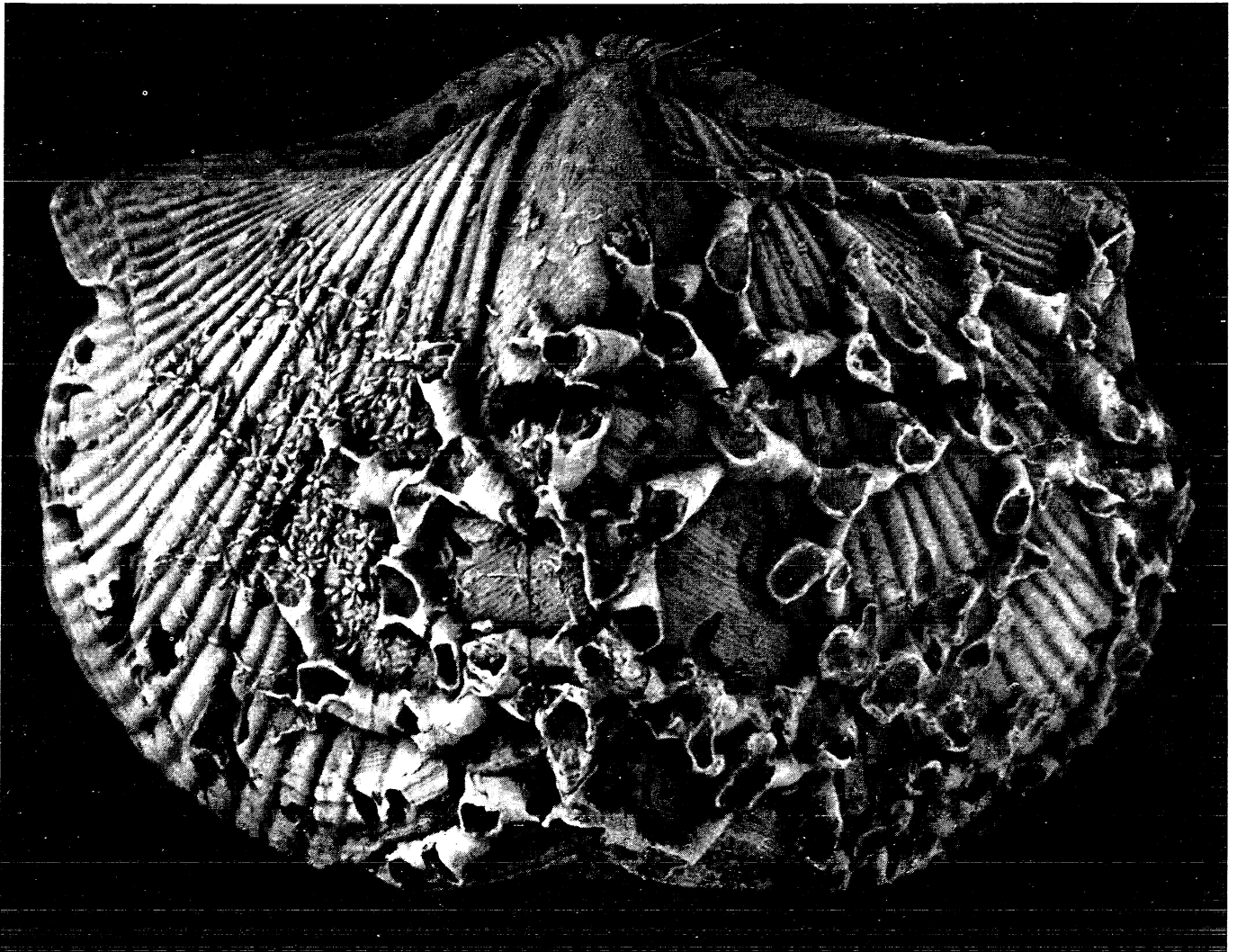


Epizoans on the Brachiopod
Paraspirifer bownockeri (Stewart)
from the Middle Devonian of Ohio

Diane K. Sparks, Richard D. Hoare, and Robert V. Kesling



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Epizoans on the Brachiopod *Paraspirifer bownockeri* (Stewart) from the Middle Devonian of Ohio

Diane K. Sparks, Richard D. Hoare, and Robert V. Kesling

ABSTRACT

During a brief interval of Middle Devonian time, the sea floor at the southeastern end of the Michigan Basin was inhabited by a remarkably diverse invertebrate fauna. Soft clay mud flats supported communities in which the large brachiopod *Paraspirifer bownockeri* thrived and served as host for 38 kinds of epizoans, most seeking the shell as available hard surface on which to settle. Our study is based on 586 excellently preserved specimens of *Paraspirifer bownockeri* from the Silica Formation in northwestern Ohio; each was studied for distribution of epizoan species in 40 grid location areas on each valve.

Bryozoans were by far the most successful epizoans, but colonial corals and other brachiopods were also present. Echinoderms, probably young crinoids, cemented holdfasts to the *Paraspirifer* valves. Periodically, swarms of larvae, presumably of sponges, bored into the leading edge of the brachiopod shell, resulting in a row of holes along a distinctive growth line where the brachiopod paused in growth to repair the damage. Some worms, *Spirorbis*, were strictly commensal, whereas others, *Cornulites*, appear to have been parasitic and injured the mantle of the host locally to produce indentations in the shell edge. Large damaged areas of the brachiopods, some exhibiting shell repair, are attributed to attacks by fish.

Epizoans are more numerous on brachial than on pedicle valves, reflecting the orientation we suppose for adult *Paraspirifer* after deterioration of the pedicle -- resting in a stable position on the pedicle valve. Distribution of epizoans is also asymmetric on each valve, being concentrated with more on one side of the brachial valve and on the diametrically opposite side of the pedicle valve. This we interpret as an indication that the currents bearing the epizoan spat and larvae approached the majority of hosts at an angle, with differential successful settling controlled by the slipstream. Coverage by bryozoans shows that colonies spread onto adjacent available areas which were less favorable for original settlement. Both life and death associations between epizoan and host and between different epizoans is amply demonstrated by the large population investigated.

INTRODUCTION

Background and scope.-- Our study is confined to those epizoans which lived upon a particular species of articulate brachiopod in a small geographic area during a brief time. In northwestern Ohio, a shaly interval of the Middle Devonian Silica Formation has yielded

numerous excellent specimens of the brachiopod *Paraspirifer bownockeri* (Stewart), many of which bear remains of other invertebrates firmly attached to their valves. These provide an exceptional opportunity to examine the relationships between particular epizoans and their host and between different epizoans occupying the same brachiopod.

During Middle Devonian time, the sea in the Michigan Basin teemed with living organisms. To date, the formation has produced 276 species of megafossils (Kesling & Chilman, 1975) and 112 species of ostracods (Kesling & Chilman, 1978). Undoubtedly, a few are yet to be discovered in this outstanding fauna.

As shown by lithologies and associated faunas, the Silica sea fluctuated in depth from agitated carbonate shallows to quiescent deeper-water mud flats. The diversity and abundance of animals increased toward deeper water (Kesling, 1978), where *Paraspirifer bownockeri* lived. The record of this crowded habitat bespeaks of intense struggles, multiple adjustments, and innovative aptitudes for the successful entrepreneurs. Competition for living space appears to have been fully as vital as the competition for food.

The brachiopod *Paraspirifer bownockeri* is found only in a few contiguous stratigraphic units in the lower part of the Silica Formation. There, it is so definitely restricted in time, so conspicuous by its size, and so common in the fauna that the units might well be termed the *Paraspirifer bownockeri* zone. Indeed, the best-preserved specimens are derived from a very thin layer in this zone; possibly, most of those used in our study came from it and hence were nearly contemporaneous.

Many contemporaries of this large and distinctive brachiopod were epizoans which settled and attached upon its surface or burrowed into its shell. We are herein concerned with the reasons why certain invertebrates chose to be epizoans on *Paraspirifer*, where they settled on the brachiopod, whether the brachiopod was alive or dead at the time of settlement, what determinable effects the epizoan had upon the host, and if certain epizoans affected the settlement of other epizoans upon the same host.

Project.-- We three authors soon reached agreement on the subject and extent of this investigation, which was used by Miss Diane Sparks for her Master of Science thesis at Bowling Green State University. Fine illustrations of epizoans on *Paraspirifer bownockeri* had just been published by Kesling & Chilman (1975, pl. 22, figs. 6-8; pl. 24, figs. 4-9; pl. 25,

figs. 1-4; pl. 31, figs. 1-4; pl. 43, figs. 14, 15; pl. 44, figs. 1, 2; pl. 46, figs. 9-11; pl. 47, figs. 8, 9; pl. 48, figs. 1, 2; pl. 107, figs. 18-20; pl. 109, figs. 7, 8; pl. 132; pl. 133; pl. 134; pl. 136; pl. 138), as well as of epizoans on other hosts in the same formation. In addition, only a decade or so earlier, Steller (1965) and Hoare & Steller (1967) studied epifauna on brachiopods of the Silica Formation.

Our first problem was collecting a significant number of excellent specimens of *Paraspirifer bownockeri* bearing epifauna, likewise well preserved. Whereas the brachiopod cannot be considered rare, the heavy toll by collectors upon the Medusa quarries has made undamaged specimens difficult to find. One might spend a day on the exposures and discover only a handful of these brachiopods with acceptable preservation. As usual in such cases we appealed to the Friends of The University of Michigan Museum of Paleontology, a dedicated group of enthusiastic workers. Almost miraculously, they soon came up with 515 fine *Paraspirifer bownockeri* with epifauna or deformities clearly discernible. Additional collecting by Hoare and Sparks brought the total to 586 good specimens.

The next problem was cleaning. All the brachiopods retained some of the soft shale matrix, obscuring (at least in part) the details of the attached epizoans. Further, some epizoans were so thin and fragile that air abrasive treatment could seriously damage them. It was discovered that prolonged boiling in a solution of one tablespoon of Quaternary-O per liter of water rendered the shale into clay, any further traces of which could (in most cases) be loosened with a soft brush and washed off at the tap. The *Paraspirifer* specimens were boiled by Kesling, five or six at a time, in this solution, dried in air, inspected, and placed in individual trays. Only rarely was additional preparation necessary, and this was done under high magnification with small picks and/or judicious application of air abrasion.

The epizoans were then ready for identification, location upon the host, and recording. Sparks, with the guidance and assistance of Hoare, proceeded with this phase. As explained below, the location of individual epizoans upon

the brachiopod host was determined with a transparent grid overlay. Thus, a record was made for each of the 582 hosts bearing epifauna, with the epizoans identified and their locations on the valves. From this data base, we counted the number of hosts bearing each kind of epizoan, the number of occurrences of each epizoan in a particular location, and the number of times one kind of epizoan occurred with another kind of epizoan on the same host.

We then studied the counts to determine for each epizoan if the frequency of occurrence, the preferred locations, and co-occurrences with other epizoans might reveal significant aspects of its growth, life habits, behavior, and interactions and interrelationships with the host and with its co-residents on an individual host. These paleoecological interpretations are the crux of this investigation and report.

The final problem was illustration to document our identifications and support our conclusions. Although each of the 586 *Paraspirifer bowmockeri* specimens used was so excellently preserved that it could have been utilized to substantiate a particular association with epifauna, we were compelled by practical economics to select only those which would depict one outstanding example of each kind of epizoan or deformity represented.

Initial photography was supervised by Karna Steelquist Orson at the Museum of Paleontology, The University of Michigan. To her we extend our sincere appreciation. For her thesis, Sparks took photographs with a 35-mm Nikon camera using a Micro-NIKKOR-P Auto 56-mm lens at a magnification of $\times 1/3$ on film; enlargements were made to natural size. It became obvious that essential characters of the very small epizoans could only be shown at higher magnifications. New negatives were made with the same equipment and procedure at selected magnifications of $\times 1/3$, $\times 2/3$, $\times 4/3$, and $\times 8/3$. Close-up shots were enlarged only three times from the negative to reproduce fine details of the epizoans.

STRATIGRAPHY

"Silica shale" was the name proposed by Stewart (1927) for Middle Devonian shales and

thin interbedded argillaceous limestones exposed by quarrying operations of the Sandusky Cement Company, now operated by the Medusa Portland Cement Company. The type locality of the Silica Formation, as it is now known, is in the abandoned South Quarry of the Medusa Portland Cement Company.

Carman (*in* Bassett, 1935) named the limestone lying between the Dundee Limestone and the "Silica shale" of Stewart the "Blue" limestone. On the basis of fauna, the "Blue" limestone correlated with the "Blue bed" of Cooper (1942). Ehlers, Stumm, & Kesling (1951) included the "Blue bed" in the overlying shales and argillaceous limestones to form the Silica Formation.

The Silica Formation has no known natural outcrops in northwestern Ohio, although it is covered by very shallow drift over appreciable acreage. It is exposed in the quarries of the Medusa Portland Cement Company, of which only the southernmost is still active. These quarries are located in Sylvania Township, Lucas County, Ohio, at about $41^{\circ}41'30''$ N Lat. and $83^{\circ}45'$ W Long. The North-north Quarry lies in $W\frac{1}{2}$ $SE\frac{1}{4}$ $NE\frac{1}{4}$ sec. 7, T 9 S, R 6 E; the North Quarry lies in $SE\frac{1}{4}$ sec. 7; the South Quarry in $NE\frac{1}{4}$ sec. 18; and the South-south Quarry in $SE\frac{1}{4}$ sec. 18. *Paraspirifer bowmockeri* (Stewart) occurs in all four quarries.

The formation consists of approximately 56 feet of limestone and alternating shale and argillaceous limestone. In northwestern Ohio, it overlies the Dundee Limestone with slight disconformity and is overlain by the Ten Mile Creek Dolomite with apparent conformity. The rocks are part of the Traverse Group and are on the northwest flank of the northeast branch of the Cincinnati Arch, dipping into the Michigan Basin in the north-south Lucas County Monocline. This structure trends $N 1^{\circ}36' W$ and the strata have dips between 8° and $3\frac{1}{2}^{\circ}$, with the dip decreasing (at least locally) toward the west and the stratigraphically higher formations (Kesling & Chilman, 1975, p. 30-33).

The Silica Formation is the time-stratigraphic equivalent of the upper part of the Delaware Limestone of north-central Ohio (Stewart, 1955). North of Ohio, it is equivalent to the

Arkona Shale of southwestern Ontario and the lower one-third of the Traverse Group in northern Michigan (Ehlers, Stumm, & Kesling, 1951; Nussmann, 1961).

Division of the Silica Formation into units by various authors has resulted in different numbering systems (Stewart, 1927; Carman in Bassett, 1935; Ehlers *et al.*, 1951; Nussmann, 1961; Mitchell, 1967). The divisions commonly used are those compiled by Kesling & Chilman (1975, p. 39-43). Of the 29 units, only units 7C through 11 contain *Paraspirifer bownockeri*; these were described by Kesling & Chilman as follows, with the thicknesses measured in the South Quarry:

- Unit 11 - Shale, calcareous, gray, marcasite concretions, weathers into angular fragments. *Devonochonetes* and *Styliolina fissurella* abundant; some ostracods; few *Paraspirifer* valves and fragments of *Rhinocaris* 2 ft. 2 in. (66 cm)
- Unit 10 - Limestone, argillaceous, gray. Abundant *Acanthoclema*, *Streblotrypa*, *Helopora*, and *Sulcoretepora* 0 ft. 4 in. (10 cm)
- Unit 9B - Shale, calcareous, blue-gray, abundant marcasite concretions. *Devonochonetes*, "*Mediospirifer audaculus*," *Phacops rana milleri*, and *Rhinocaris ehlersi* 6 ft. 10 in. (208 cm)
- Unit 9A - Limestone, argillaceous at base to very argillaceous at top, blue-gray, abundant marcasite concretions, weathers to sticky clay when wet. Very fossiliferous, produces most of the common Silica species. *Mucrospirifer prolificus*, *Phacops rana milleri*, and *Paraspirifer bownockeri* common 0 ft. 8 in. (20 cm)
- Unit 8 - Limestone, massive, argillaceous, blue-gray, abundant marcasite concretions, relatively hard. All fossils strongly pyritized. *Mucrospirifer prolificus* and *Strophodonta* abundant 0 ft. 8 to 12 in. (20 to 30 cm)
- Unit 7C - Shale, calcareous, blue-gray, many fossils worn by wave action before burial. *Megastrophia* and *Strophodonta* abundant... 0 ft. 2 to 3 in. (5 to 8 cm)

Nussmann (*in* Kesling & Chilman, 1975) divided the Silica Formation into lithologic biotopes. The section yielding *Paraspirifer bownockeri* is interpreted as:

- Unit 11 = shale with a basal smothered bottom assemblage
- Unit 10 = cryptostomate-crinoidal argillaceous limestone
- Unit 9B = shale, with minor lenses of cryptostomate-crinoidal argillaceous limestone
- Unit 9A = mucrospiriferid transition
- Unit 8 = normal argillaceous limestone
- Unit 7C = mucrospiriferid transition

Few if any of our specimens came from units 8 or 10.

The Silica Formation is exposed in two other places: a quarry in Junction, Ohio, and in Martin-Marietta Quarry, approximately 48 kilometers north-northeast of the Medusa quarries, in the southeast corner of Washtenaw County, Michigan. The latter is the only other locality where *Paraspirifer bownockeri* has been found. Although the stratigraphy there is somewhat confused by bull-dozing and quarrying operations, which have moved all the available shales out of position, the rocks at the Martin-Marietta Quarry can be correlated with the units at Medusa quarries by lithology and faunas; *Paraspirifer bownockeri* is found in units 9 and/or 11 (Chilman, 1975).

EPIZOANS ON HOSTS

What is an epizoan? -- Epizoans have been defined as animals which lived on the surface of the substrate (Raup & Stanley, 1971). As we restrict the term here, it includes only animals which attached permanently to firm surfaces. The epizoans found on *Paraspirifer bownockeri* (Stewart) appear to have attached as larvae. The bryozoans and auloporoid corals budded and branched to form colonies, but we see no sign that the settlement was ever effected after the larval stage. The attachment of many of the inarticulate brachiopods was very early in the ontogeny, inasmuch as the total area of each valve of the epizoan reflects the

underlying surface configuration of the host's shell. The time of attachment of the articulate brachiopod epizoans is less certain, but it evidently took place while the interarea of the epizoan was quite small and could accommodate to the surface features of the host *Paraspirifer*. Therefore, we use the term epizoan in this paper to mean any animal which attached firmly and permanently to a host brachiopod of the species *Paraspirifer bowmockeri*, insofar as can be determined at a very young stage in its life.

Reasons for settling on host.-- Marine organisms such as *Paraspirifer bowmockeri* have been utilized by other organisms for a variety of purposes (Ager, 1961, 1963; Hoare & Steller, 1967; Schumann, 1967). In general, these include:

(1) Substrate. The epizoan may have settled on a host shell quite incidentally because it constituted available hard surface needed for at least part of the epizoan's ontogeny; or the settlement may have been accidental or chance, with the epizoans failing to settle upon such hard surface being casualties.

(2) Protection. The shell of the host may have been a substance which could be bored into or dissolved away to provide a safe haven for the developing epizoan.

(3) Feeding advantage. Some organisms may have benefited from feeding currents generated by the host (Shou-Hsin, 1959; Ager, 1961).

(4) Source of food. Settling upon selective areas of the host's shell may have provided the epizoan with anchorage from which it could conveniently eat away at the soft tissues of its host.

EPIZOAN RELATIONSHIPS TO OTHER ANIMALS

General remarks.-- Whether or not the host was alive at the time of settlement by the epizoan is often impossible to ascertain. The reasons why some epizoans preferred or avoided the host which already bore another particular epizoan are also matters of conjecture. As more associations are studied, however, the uncertainty may decrease.

Relationships to live hosts.-- John Mason Clarke (1921) was one of the first persons to report, describe, and hypothesize the reasons for occurrences of epizoans on hosts. He stated (1921, p. 6) that he was looking for

conditions which show an actual mutual dependence of creatures upon another; that is to say, of conditions commonly known variously as symbiosis, mutualism and parasitism.

Clarke defined these terms elsewhere in his paper and numerous authors have since used them, although some have defined the terms in slightly but significantly different ways.

The classification of life relationships followed in our paper was the one proposed by G. L. Clarke (1954). He based his classification on the basis of benefit or gain (+), harm or loss (-), or no significant effect (0). The possible combinations for a host and an epizoan are as follows:

Symbiosis: a relationship between two species in which at least one species is benefited and neither species is harmed.

Mutualism (+ +): a relationship between two species in which both are benefited to some degree.

Commensalism (+ 0): a relationship between two species in which one is benefited and the other is unaffected.

Toleration (0 0): neutrality; a relationship in which neither species has an effect upon the other.

Antagonism: a relationship between two species in which at least one species is harmed.

Antibiosis (- 0): one species is harmed and the other unaffected.

Exploitation (- +): one species is harmed and the other is benefited.

Parasitism: one species derives its food from the second without killing it, at least not directly.

Predation: one species feeds upon the other and kills it in the process.

Competition (- -): a relationship between two species in which both are harmed to some degree.

Only if the host exhibits conclusive evidence of shell repair at or around sites of damage by the epizoan can we be sure that both were alive at the same time.

If a particular epizoan shows a preferred orientation with respect to the host, it may provide an indication that the host was alive and maintaining a life position relative to the substrate. On the other hand, because of its shape the host may in death assume a stable position on the substrate which duplicates its life position, in which case the orientation of the epizoans upon it bears no significance in determining life relationships. For those epizoans which themselves had no need for a particular orientation, we cannot deduce whether the host was alive or dead.

Epizoans invariably aligned at the anterior edge of the host brachiopod's shell are very strong evidence that both epizoan and host lived at the same time. Shell deformity of the host caused by an epizoan disturbing the growing edge of the mantle also indicates a life relationship.

Relationships to dead hosts.-- Steller (1965, p. 19) proposed the term epitaphism

to describe the situation in which epifauna attach onto the shell of a host that has succumbed.

We find this term useful in our study.

Epizoans which grew on the interior surface of a valve are assumed to have arrived after death of the host (Steller, 1965; Morris & Rollins, 1971). Otherwise, the epizoan would have been smothered by the living tissues of its host, or the epizoan would have by necessity caused extensive injury to the host, bringing about its quick demise. This situation is only academic for our purposes here, inasmuch as only complete shells of the host *Paraspirifer* are used.

Epizoans extending across the commissure or the hinge axis indicate at least partial death relationship, for the opening and closing of the valves by a live brachiopod would have prevented colonization or extension onto these regions.

Epizoans which show a precise orienta-

tion upon some hosts and no preferred orientation upon others may be an indication that the latter hosts were dead and came to rest on the substrate in a position other than the life position.

Relationships to other epizoans on the same individual host.-- No conclusion can be reached from examination of one individual host and its epifauna. However, study of a large sample of host shells can reveal that some pairs of epizoans occur on the same individual host more frequently or less frequently than would be occasioned by chance. We use simple mathematics, in which

A and B = two species of epizoans,

a and b = number of hosts bearing respectively specimens of species A and species B,

S = number of hosts examined, and

n = expected occurrences of species A and B together on the same individual host shell by chance.

Then, $n = \frac{a \times b}{S}$.

Now, if N = actual (observed) occurrences of species A and species B together on the same individual host,

Then, N/n = co-occurrences of species A and species B in relation to chance.

It follows that exceptionally high values of N/n indicate that species A and species B preferred settling on the same individual host or gained some advantage from their mutual presence, and that exceptionally low values of N/n indicate that the two species avoided settling on the same individual host or one epizoan eliminated the other after settlement.

We can only speculate that some pairs of epizoan species co-occurred with high frequency because one was beneficial to the other in some way, or because the condition of the particular host invited settlement by these particular epizoans. Conversely, some pairs of epizoans may have co-occurred with low frequency because one of them inhibited or precluded settlement and growth of the other, or because the condition of the particular host favored settlement of one epizoan and discouraged settlement of the other. In other words,

successful habitation of one host by one of the pair of co-occurring epizoans and not by the other may have been the end result of any one or more of the multitude of factors affecting the local environment, not necessarily a direct cause-and-effect relationship limited to the two epizoans. No explanation appears to be totally defensible; some seem more logical and likely than others.

PREVIOUS WORK ON BRACHIOPOD EPIZOANS

Cooper (1937) reported on the ecology of Recent and extinct brachiopods, compared living brachiopods with extinct forms, and discussed the modes of life of different groups of the Brachiopoda. Richards (1972) published a paper on Richmondian (Upper Ordovician) brachiopods from Indiana and Ohio, in which he concluded that the distribution of epizoans on species of brachiopods was controlled by the size and the shape of the epizoan compared to the size and shape of the brachiopod's ornamentation. More closely concerned with our investigation, Steller (1965) deduced the life position of brachiopod hosts and described life relationships of epizoans on brachiopods from the Silica Formation of Ohio.

Yakovlev (1926) and Shou-Hsin (1959) reported the occurrence of the tabulate coral *Aulopora* on *Mucrospirifer* and determined the relationship to be mutualistic. The coral presumably benefited from the food-bearing currents of the host, whereas the brachiopod gained protection by the stinging nematocysts of the epizoan. Ager (1961) described the symbiotic relationships of four epizoans on the host brachiopod *Spinocyrtia iowensis* from the Cedar Valley Limestone (Upper Devonian) of Iowa. He deduced that the epizoans attached in a distinct order and also inferred the orientation of the host from the locations of the epizoans on the valves. Schumann (1967) inferred the life position and feeding currents of *Mucrospirifer reidfordi* from the orientation of the worm (?) *Cornulites*. Hoare & Steller (1967) described parasitic and commensal relationships of epizoans to the *Paraspirifer bownockeri* host from the Silica Formation.

Although their paper did not focus on

epizoan relationships, Kesling & Chilman (1975) illustrated numerous examples of epizoans on *Paraspirifer* and other host brachiopods from the Silica Formation, and commented on them in their plate explanations.

FEATURES OF *PARASPIRIFER BOWNOCKERI* (STEWART)

External morphology.-- Shell large, very robust, and broadly oval in outline. Width consistently greater than length, although ratio variable. Greatest shell width slightly below middle. Cardinal extremities obtusely angular and distinctly auricular. Large specimen 61 mm in width, 43 mm in length, and 43 mm in thickness; small specimen 31 mm in width, 23 mm in length, and 18 mm in thickness.

Pedicle valve moderately convex, its beak slightly incurved and obtuse. Cardinal area well defined and narrow; delthyrium broadly triangular. Lateral slopes strongly convex, flattening toward cardinal ears, marked by 15 to 20 costae. Sulcus deep, troughlike, rapidly increasing in width toward anterior margin, free of costae.

Brachial valve strongly convex posteriorly with convexity decreasing toward the margins. Costae similar to those of pedicle valve on lateral surface. Fold prominent, acute, rapidly increasing in width toward anterior margin. Pedicle and brachial valve surfaces ornamented with minute teardrop-shaped granules regularly arranged in concentric rows (Stewart, 1927).

Life and death positions.-- Steller (1965) postulated life positions for brachiopod hosts from the Silica Formation. Hoare & Steller (1967, p. 291) stated:

Distribution of the epifaunal elements indicate the life position of the host to be vertical, with the beaks down, or possibly lying on the posterior portion of the pedicle valve after atrophy of the pedicle had taken place.

They further added (1967, p. 296):

Paraspirifer is a member of that group of brachiopods in which the pedicle became atrophied during latter growth stages. The incurving of the beaks,

particularly that of the pedicle valve, closed off the delthyrial region. Life position at this stage of growth was presumably with the beaks downward or possibly with the organism resting upon the pedicle valve. The scarcity of epifaunal elements attached to the pedicle valve might give strength to the latter possibility, but certainly does not preclude the former.

We would point out that the conformation of the shell permits only four positions with any degree of stability: (1) hinge down, in which case the stability is lost as soon as the shell is moved beyond either beak region, (2 and 3) resting on the rather flat surface of either the left or the right side of the brachial valve, with the apex of the fold and the lateral edge of the commissure in contact with the underlying surface (the valves are strongly tilted in both of these positions), and (4) on the pedicle valve, resting with the sides equidistant from the substrate and the hinge slightly above the center of the shell. On the soft sediment of the beds yielding *Paraspirifer*, the stability of the hinge-down position may have been considerably greater than that now seen on a firm surface. Nevertheless, the scarcity of epizoans on the pedicle valve, as pointed out by Hoare & Steller, is good evidence that this surface was not as readily available to epizoans as the brachial valve at the time of settlement. Presumably the position on the pedicle valve was the most stable one both in adult stages of life as well as in death. Even the few specimens of *Paraspirifer* with some epizoans on the pedicle valve have more epizoans on their brachial valve. With the pedicle valve down, the stability was very great; the shell has a wide concavity in the middle (the sulcus), the edges of which act as rockers, so that even with appreciable displacement, the shell returns to the same stable position.

DIAGNOSTIC FEATURES OF EPIZOANS FOUND ON *PARASPIRIFER BOWNOCKERI*

Epizoans are abundant and diverse on *Paraspirifer bownockeri*. Excellent preservation facilitates their identification. In most cases, the epizoans were identified to species; others could only be identified to order, family, genus, or group level. Some bryozoans were designat-

ed only to "groups" as defined by Bassler (1939) with assurance. No specimens were destroyed by sectioning, which might have made specific placement possible. At least six phyla are represented by 39 species or other taxa.

Phylum PORIFERA

"Clionoides" sp. Fenton & Fenton 1932
1/3,4,7,12,13; 3/3,4; 5/11; 6/4 *

A form genus of borings presumed to have been made by monactinellid sponges. The straight to slightly curved trench-like excavations may branch but do not radiate; the excavations, mostly tunnels, are primarily oriented perpendicular to the anterior edge of the host; the surface appearance is a small, nearly circular opening. On most hosts, the borings are concentrated along a particular growth line.

Phylum COELENTERATA

Subclass Rugosa
4/7; 11/6 *

A small solitary rugose coral was found. It has only part of the calyx wall and attached septa preserved. Inasmuch as it is attached by the side rather than the apex, some doubt persists as to whether it is actually part of the attached epifauna or simply adhering to the brachiopod by matrix. We here include it as an epizoan.

Subclass Tabulata

Aulopora microbuccinata Watkins
1/1,3,4,10; 2/7-12; 3/1,2; 4/1,2,7; 6/3,5; 9/2,6;
10/1,5; 11/6; 12/2; 16/3; 17/2; 22/5,6; 23/4 *

Reptant, anastomosing, trumpet-shaped corallites attached by the under surface; branching from buds originates from just below the calyx rim; colony forms fairly regular pattern, with bare pentagonal or hexagonal interspaces surrounded by a chain of corallites (normally one on each side of the polygon); corallite walls bent upward in distal part; where corallite chains meet to enclose a polygonal space, the walls of adjacent ascending tubes may unite to form a cemented pair, but the last-formed corallite remains terminal and does not send forth buds across the earlier-formed chain.

* Each plate reference has the plate number followed by a virgule (/) and the figure number(s).

Phylum BRYOZOA

Because the Bryozoa are difficult to classify without thin sections, we offer here a key which we used to make identifications. It includes only the taxa which we were able to distinguish.

Order Ctenostomata

Eliasopora stellatum (Nicholson & Etheridge)
1/12,13; 6/3,5; 9/2; 17/2,3; 20/3
Ropalonaria tenuis Ulrich & Bassler
2/1,2; 11/1,2

KEY TO EPIZOAN BRYOZOA ON *PARASPIRIFER BOWNOCKERI*

1. Zooid developed from cylindrical stalks given off by a slender tubular stolon or from one another, blister-like vesicles with generalized shapes, variable CTENOSTOMATA
Zooid with definite shape, no stolons involved in reproduction 2
2. Zoaria consisting of branched tubes forming a dendroid pattern; zooecia not in contact to form a lamellar or massive zoarium; zooecia consisting of simple calcareous tubes with plain, round, uncontracted apertures; no specialized structures such as maculae, monticules, mesopores, or acanthopores CYCLOSTOMATA
Zoaria lamellate to massive; zooecia in contact to form a continuous zoarium layer; maculae and monticules common, often regularly disposed; mesopores and/or acanthopores may be present 3
3. Zooecial tubes with few if any internal transverse partitions (diaphragms), their developmental zones not conspicuously defined, although peripheral thickening may occur CYSTOPORATA
Zooecial tubes with numerous internal diaphragms and/or cystiphragms, divided into distinct inner (immature) zone with thin walls and peripheral (mature) zone with thick walls TREPOSTOMATA

CTENOSTOMATA

1. Zoarium of fusiform internodes connected by delicate, tubular stolons; stolons partly or wholly embedded in host's shell *Ropalonaria tenuis* Ulrich & Bassler
Zoarium and stolons not embedded in host's shell 2
2. Vesicles oval, always arranged in stellar groups (radiating clusters) connected by threadlike stolons *Eliasopora stellatum* (Nicholson & Etheridge)
Vesicles elongate, pyriform to wedge-shaped, stolons (if present) not threadlike *Ascodictyon* ... 3
3. Vesicles uniformly wedge-shaped with a single row of pores along each vesicle; vesicles arranged in stellar groups, those of each group attached by their blunt ends to a central sphere *Ascodictyon radians* Nicholson & Etheridge
Vesicles not wedge shaped, no central spheres 4
4. Narrow, tubular, anastomosing stolons which may or may not radiate from a center; no bulbous vesicles *Ascodictyon (?) conferta* (Ulrich)
Distinctly inflated vesicles, with or without distinct stolons 5
5. Bulbous vesicles in flower-like groups (smaller than *Eliasopora stellatum*), connected by thin stolons *Ascodictyon floreale* Ulrich & Bassler
Elongate fusiform, minutely punctate vesicles, stolons (if present) poorly developed *Ascodictyon fusiforme* (Nicholson & Etheridge)

(continued)

(continued)

CYCLOSTOMATA

1. Zooecia branching at low angle to main axis, usually remaining in contact with it throughout most of length.. "*Hederella parallela*" group ... *Hederella bilineata* Bassler
Zooecia branching at distinct angle to separate from main axis 2
2. Zoarium robust with thick, infrequently branching tubular axis; zooecia large, varicose, alternating at close intervals "*Hederella magna*" group ... 4
Zoarium delicate with frequent branching; zooecia generally smaller, not varicose 3
3. Zoarium consisting of single narrow tubular axis with zooecia branching at fairly regular angles and distances "*Hederella canadensis*" group ... 6
Zoarium lacking central tube, with zooecia branching at such close intervals and so frequently that no central tube develops "*Hederella alpenensis*" group .. 12
4. Zooecia about 0.8 mm wide (definitely less than 1.0 mm); fairly wide angle of budding; interval of branching 4 mm *Hederella* cf. *H. michiganensis* Bassler
Zooecia large, around 1.0 mm or more wide; distinctly acute angle of budding; interval of branching 10 mm or greater 5
5. Largest *Hederella* known, zooecia 4.0 mm long; where well developed, zooecia on one side of central axis spaced 1 per 5 mm; interval of branching 10 mm
..... *Hederella reimanni* Bassler
Zooecia 2.2 mm long; where well developed, zooecia on one side of central axis spaced 2.5 per 5 mm; interval of branching 20 mm *Hederella magna* Hall
6. Old zoarium consisting of almost solid mass of radiating tubes; at about 4 mm intervals, groups of 4 or 5 short, wide tubes developed on opposite sides; zooecia about 0.7 mm wide and 2.5 mm long *Hederella thedfordensis* Bassler
Old zoaria not covering all of area, leaving distinct interareas; branching regular; zooecia about 0.35 mm wide and 1.0 mm long; where well developed, zooecia on one side of central axis spaced 4 per 5 mm 7
7. Alternate and regular arrangement of zooecia exceptionally well marked
..... *Hederella alternata* (Hall & Whitfield)
Alternation and development of zooecia somewhat irregular 8
8. Interval of branching less than 4 mm 9
Interval of branching more than 4 mm 10
9. Zooecial length 1.0 mm; angle of budding 60°; angle of branching 60°; interval of branching 2.5 mm *Hederella concinnoides* Bassler
Zooecial length 0.8 mm; angle of budding 45°; angle of branching 90°; interval of brnaching about 1.5 mm *Hederella delicatula* Hall & Simpson
10. Zooecial length 0.75 mm; angle of budding 30°; zooecial width 0.3 mm
..... *Hederella concinna* Bassler
Zooecial length 1.0 mm; angle of budding 45°; zooecial width 0.35 to 0.40 mm ..
..... 11
11. Pronounced annular ridges; interval of branching 7 mm ... *Hederella parvirugosa* Bassler
Annular ridges subdued if discernible; interval of branching 5.5 mm
..... *Hederella filiformis* (Billings)

(continued)

(continued)

12. Zooecia 0.6 to 0.7 mm wide and 2.0 mm long; where well developed, zooecia on one side of axis spaced 3 per 5 mm; angle of branching 40°; strongly rugose tubes, frequently dividing *Hederella rugosa* Bassler
- Zooecia 0.4 mm wide and 1.1 mm long; where well developed, zooecia on one side of axis spaced 4 to 5 per 5 mm; angle of branching 60°; zooecia compact, relatively smooth, each arising alternately from side of the preceding one ...
..... *Hederella alpenensis* Bassler

CYSTOPORATA

- Zoaria mound-shaped, circular, several may adjoin to cover an area; each mound rosette-like with ridges radiating from center (a macula), each ridge bearing a double row of zooecia with few diaphragms; depressed spaces between ridges with vesicles; no lunaria known *Botryllopora socialis* Nicholson
- Zoaria not mound-shaped, lamellate, commonly with regularly distributed monticules and/or maculae; apertures provided with lunaria Fistuliporoids

TREPOSTOMATA

1. Apertures petaloid; mesopores and megacanthopores common; monticules rare or absent ? *Leioclema* sp.
[Specimens included here could include the cryptostomate *Intrapora* sp., but identification is impossible without thin sections to establish the position of the aperture as peripheral or deeply recessed.]
- Apertures not petaloid, zooecia polygonal; megacanthopores not present although acanthopores may be large; monticules prominent 2
2. No mesopores; acanthopores few if present; zoarium thinly encrusting on host ...
..... *Atactotoechus* cf. *typicus* Duncan
- Mesopores few if present acanthopores well defined, commonly large; zoarium may attain considerable thickness *Leptotrypella* sp.

Ascodictyon radians Nicholson & Etheridge
1/12,13; 20/3

Ascodictyon floreale Ulrich & Bassler
1/11; 6/4; 8/5; 10/4; 17/5; 20/6

Ascodictyon (?) *conferta* (Ulrich)
6/5; 12/1,2; 18/1

Ascodictyon fusiforme (Nicholson & Etheridge)
2/7,8; 3/1,2; 4/1,2; 9/6; 16/3; 22/5,6; 23/4-6

Order Cyclostomata

Genus *Hederella* Hall

Because of poor preservation or small colony size, some specimens could only be identified as belonging to the genus, and were listed as "*Hederella* spp." Presumably, these specimens were not new species and were probably distributed among named species in approximately the proportions that those species

are represented. In other cases, the specimens could be recognized as belonging to the group called "*Hederella canadensis*" or to the group called "*Hederella magna*." Those which could not with certainty be identified to species are indicated as group names by quotation marks.

Bassler (1939) discussed this prolific genus and divided it into four form groups to aid in identification. His measurements are given in table 1; although they are useful, we find that *Hederella concinnoides* and *H. delicatula* both have zooecia which exceed the measurements given by Bassler, and attain widths of 0.35 mm, but *Hederella filiformis* is somewhat smaller than the measurements reported by Bassler, not exceeding 0.40 mm in width. Our key presents our understanding of the epizoan species of *Hederella*.

"Hederella canadensis" group*Hederella concinna* Bassler

5/9; 8/2; 15/6

Hederella parvirugosa Bassler

6/1,2,7; 8/7; 9/4; 16/1; 19/2

Hederella filiformis (Billings)

1/5; 3/5,8,9; 6/11; 7/2,3; 8/6; 14/5; 17/4; 23/1

Hederella alternata (Hall & Whitfield)

5/8; 13/6; 15/5

Hederella concinnoides Bassler

1/6; 2/3,4; 3/10; 9/1,3; 10/3; 20/5; 22/3,4

Hederella delicatula Hall & Simpson

1/5; 21/1

Hederella thedfordensis Bassler2/5,6; 3/5; 5/1-3; 6/1,2,4; 7/3,6; 8/4-6,8,9;
9/4; 13/4; 16/2,6; 17/1,6; 18/5,6; 22/2*"Hederella alpenensis"* group*Hederella alpenensis* Bassler

2/5,6; 5/4,5; 14/3; 19/5; 22/1

Hederella rugosa Bassler

3/6; 23/3

"Hederella magna" group*Hederella magna* Hall

4/6; 7/5; 21/3

Hederella cf. *H. michiganensis* Bassler

3/3,4

Hederella reimanni Bassler

5/12; 9/5; 19/3

"Hederella parallela" group*Hederella bilineata* Bassler

4/8; 12/3; 15/4

Hederella spp.

6/5; 7/9

Order Cystoporata

Botryllopora socialis Nicholson

2/7,8; 4/1,2; 5/4,5; 14/1,2; 16/4; 19/4,6; 20/1

As pointed out by Kesling & Chilman (1975), the Silica Formation yields some of the finest specimens known of this complex bryozoan.

Fistuliporoids

This is a form family as we apply it. Zoarium encrusting, bearing monticules at regular intervals; tubular zooecia, apertures generally oblique with part of proximal margin elevated into a lunarium; zooecial interspaces occupied by vesicles having convex walls on the side toward the zoarial surface.

Order Trepostomata (and/or Cryptostomata)

Without thin sections, by which the aperture can be determined to be peripheral or deeply recessed, the order cannot be certain. We think the following are correctly identified as trepostomes, but lack proof.

Atactotoechus cf. *A. typicus* Duncan

1/8,9; 7/4; 10/2; 14/6; 20/2

Leptotrypella sp.

3/5; 23/2

? *Leioclema* sp.

1/3,4; 6/5; 7/9; 10/5; 18/2-4; 21/2

Phylum BRACHIOPODA

Class Inarticulata

The accompanying key includes the essential characters of the epizoan inarticulate brachiopods.

Superfamily Discinacea

Lingulodiscina marginalis (Whitfield)

3/8,9; 12/6; 14/4

Orbiculoidea doria (Hall)

5/10; 12/4,5

Superfamily Craniacea

Petrocrania hamiltoniae (Hall)

1/10; 7/7

Philhedra crenistriata (Hall)

6/6; 8/1; 15/1

Philhedra sheldoni (White)

4/9; 11/4

Philhedra stewarti (Fenton & Fenton)

1/11; 10/4

KEY TO EPIZOAN INARTICULATE BRACHIOPODA ON *PARASPIRIFER BOWNOCKERI*

1. Shell phosphatic 2
Shell calcareous 3
2. Brachial (outer) valve suboval, strongly convex; beak near posterior margin; surface marked by closely spaced growth lines *Lingulodiscina marginalis* (Whitfield)
Brachial (outer) valve circular, moderately convex; beak located posterior to valve center; surface marked by coarse growth lines and very faint radial striae *Orbiculoidea doria* (Hall)
3. Surface of brachial (outer) valve marked by irregular concentric growth lines only *Petrocrania hamiltoniae* (Hall)
Surface of brachial (outer) valve marked by radiating costellae in addition to any growth lines *Philhedra* ... 4
4. Costellae coarse (4 to 5 per mm) *Philhedra crenistriata* (Hall)
Costellae fine (7 to 11 per mm) 5
5. Valve medium size; surface showing fine to coarse concentric growth lines; costellae radiating between adjacent pairs of growth lines, occasionally crossing over them *Philhedra sheldoni* (White)
Valve small; radiating costellae not reaching beak but continuous to valve margin, uninterrupted by growth lines *Philhedra stewarti* (Fenton & Fenton)

Class Articulata

Superfamily Spiriferacea

"Mediospirifer audaculus" (Conrad)

1/2; 2/5,6; 4/10-12; 7/1; 8/8; 13/5

Generally large, with numerous lateral plications; micro-ornamentation consisting of weak concentric growth lamellae and teardrop-shaped granules; more nearly like the genus *Spinocyrtia* than *Mediospirifer*.

Cyrtina "hamiltonensis" (Hall)

5/6,7; 13/3

Small brachiopod with hemipyramidal pedicle valve; interarea very high and triangular; lateral slopes plicated; sulcus and fold unornamented. This species may or may not be conspecific with the true *Cyrtina hamiltonensis* of New York State.

? Phylum ANNELIDA

? Class Polychaeta

Cornulites sp.1/3,4; 2/1,2; 3/7; 6/1,2; 7/8; 9/4;
11/3; 20/4; 21/4-6

More than one species may be repre-

sented in the epifauna. It is presumed to be a polychaete worm. Tubes calcareous, trumpet-shaped with transverse ridges giving way to longitudinal striae with increasing size (advancing age?); small end of tube usually bent and closed where initial attachment was made; usually oriented between costae and perpendicular to the line of commissure of the host.

Phylum ANNELIDA

Order Sedentaria

Spirorbis planum Stewart

4/1,2,7; 16/5; 19/1

Minute tube coiled in flat, low spiral; tube smooth, increasing rapidly in size; aperture circular.

Phylum ECHINODERMATA

Class Crinoidea

Holdfasts

1/1,7,12,13; 10/6; 20/3,4

Holdfasts of stemmed echinoderms, presumably crinoids, were attached to several

Table 1 -- Average measurements of species of *Hederella*. Arranged in order of increasing zooecial width. Adapted from Bassler (1939).

	Zooecial width (mm)	Zooecial length (mm)	Zooecia in 5 mm interval*	Angle of budding	Interval of branching (mm)	Angle of branching
<i>H. concinnoides</i>	0.15	1.0	5	60°	2.5	60°
<i>H. delicatula</i>	0.15	0.8	4-5	45°	1.5-6	90°
<i>H. concinna</i>	0.30	0.75	5-6	30°	5	90°
<i>H. bilineata</i>	0.30	1.0	5-6	Acute	3	60-90°
<i>H. alternata</i>	0.35	1.0	4	45°	3.5	90°
<i>H. parvirugosa</i>	0.35	1.0	4	45°	7	--
<i>H. alpenensis</i>	0.40	1.1	4-5	Acute	3.5	60°
<i>H. filiformis</i>	0.50	1.0	4	45°	5.5	90°
<i>H. rugosa</i>	0.6-0.70	2.0	3	20°	4	40°
<i>H. thedfordensis</i>	0.70	2.5	2	30°	---	60°
<i>H. michiganensis</i>	0.80	2.0	2	20°	20	90°
<i>H. magna</i>	1.00	2.2	2-2½	20°	20	60-90°
<i>H. reimanni</i>	1.00	4.0	1	Acute	10	90°

* Measured on one side of central axis where well developed.

host shells. Strangely, none of the holdfasts reached an appreciable size. Frequently, whenever one holdfast was present, it was accompanied by others on the same valve.

Phylum Uncertain - Problematica

Organic threads

Thin (around 0.05 mm wide), slightly raised or nearly flush with the surface of the host, these "threads" appear black and are composed of pyrite. They are similar in form to some stolons of *Eliasopora* but are not associated with any vesicles. Whether their original composition was organic (as we suggest) or calcareous remains uncertain; presently, the threads are all replaced by pyrite.

? Coprolites

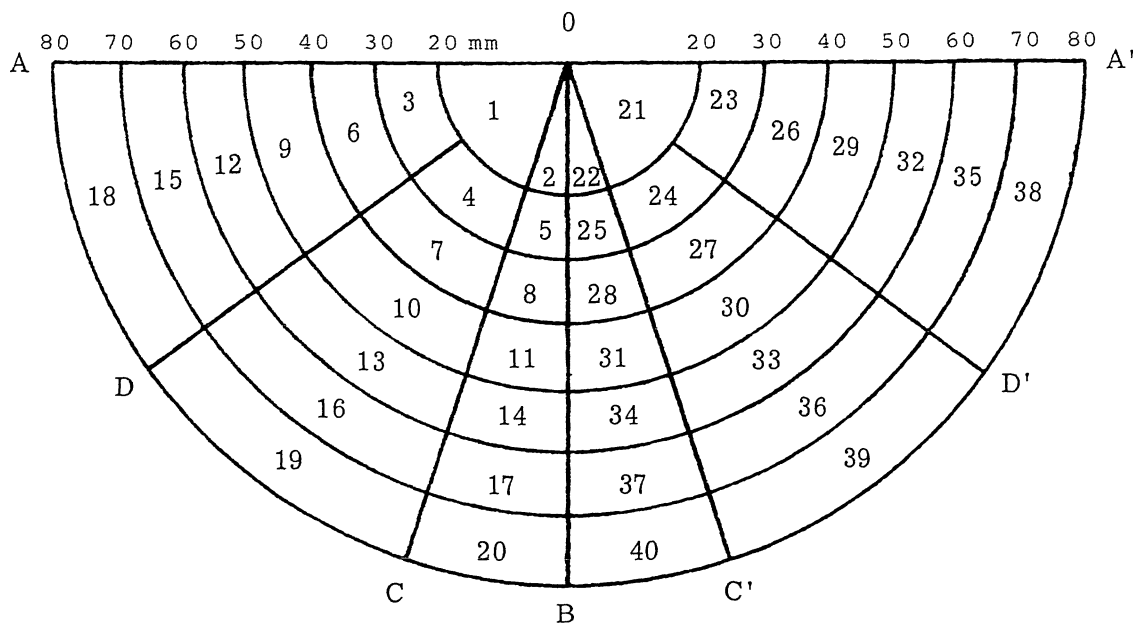
Pyritic cylindrical tubes, stringers or trails, and "heaps" have been interpreted as replaced coprolites (Nussmann, 1961, 1975). Many are free in the matrix of the formation, whereas others are attached to brachiopods and

other fossils. The pyrite is considered to have been biogenically precipitated. Because the defecating organism cannot be identified, the coprolites were not included as epizoans even though several were noted on *Paraspirifer bownockeri*.

RECORDED DATA

Brachiopod specimens.-- Each cleaned and complete *Paraspirifer bownockeri* bearing epizoans or deformities was assigned an accession number and placed in an individual tray for reference and study. All came from the Silica Formation exposed in the quarries of the Medusa Portland Cement Company in Lucas County, Ohio, and were thus collected from a narrow exposed strip no longer than 1½ miles. More precise locations were not known for most of the specimens, and none were recorded. Those in the Museum of Paleontology of The University of Michigan have been numbered 63119 through 63665.

The length, width, and thickness of each brachiopod host was measured and recorded in



TEXT-FIG. 1 -- Grid with location numbers used for designating occurrences of epifauna on *Paraspirifer bownockeri*.

the initial data.

Epizoans.-- Epizoan species were examined under magnification ranging to 70x. A micrometer ocular in the microscope was used for measuring when needed for identification. Where appropriate, the number of individuals of a particular epizoan or the estimated per cent of the valve covered by it was recorded in initial data.

In addition to the epizoans, some hosts showed extensive deformities and others had major growth lines marking positions of interrupted growth. These were also recorded for each of the 582 hosts (the other four specimens had deformities without epizoans).

Separate records were maintained for brachial and for pedicle valves.

Location of epizoans.-- The reference framework for locating epizoans on a large host is not easily designed. Objections can be found to almost any framework. For example, it may be highly significant that all specimens of a particular epizoan are found along the anterior margin of the host's valves; yet this position may lie 70 mm from the beak in a large host and

only 40 mm from the beak in a small host. On the other hand, it may be equally significant that the specimens of an epizoan are all concentrated about 40 mm from the beak; this area of habitation would be near the anterior edge of a small brachiopod host but near the middle of a large host. Hence, neither relative distance from the beak nor absolute distance will show all relationships to advantage. In the end, we opted for a grid based on absolute distances.

Our grid for location of epizoans (text-fig. 1) was devised to partition the valves of the host brachiopod into convenient and significant areas. It was constructed of transparent 2-mil plastic, which was pliable and could be molded around the valve of the host to indicate precise grid locations and, at the same time, to permit the epizoans to be seen through it. A sharp tool was used to inscribe the lines and numbers on the plastic. The design of the grid is simple. A straight edge (A-A') corresponds to the posterior edge of the lateral surface of the brachiopod valve; around a center point (0) on this edge, semicircles are drawn at radii of 20, 30, 40, 50, 60, 70, and 80 mm; from the center point, one line (corresponding to the axis of the fold or sulcus) is drawn at right angles to the straight edge (0B) and an additional

Table 2 -- Number of *Paraspirifer bownockeri* hosts with the same number of different epizoans.

Species of epizoans	Number of hosts	Per cent of hosts
1	62	10.7
2	119	20.4
3	159	27.3
4	131	22.5
5	58	10.0
6	42	7.2
7	8	1.4
8	3	0.5

Total	582	100.0

Mean number of epizoans per host = 3.3

line is drawn through the center point on each side of the perpendicular (OC and OC') to form an angle of 18° so that the two lines thus drawn lie along the edges of the fold on the brachial valve or the sulcus on the pedicle valve. Lastly, this construction leaves angles of 72° on each side; arbitrarily, these angles are bisected by lines extending between the 20-mm and 80-mm semicircles (OD and OD') to create a total of 40 grid areas. Numbers from 1 to 20 designate areas on the left half of the valve, and those from 21 to 40 designate areas on the right half; the number 0 is reserved for the interarea of the valve, situated posterior to the boundary of the lateral surface.

In use, the grid was carefully oriented with the straight edge (A-A') along the line separating interarea from lateral surface and with the perpendicular (OB) along the axis of the fold of the brachial valve or the sulcus of the pedicle valve. Lines OC and OC' were oriented along the edges of the fold on the brachial valve or sulcus on the pedicle valve. Lines OD and OD' simply divide into equal angles, the lateral slopes of the valves. Due to the differences in shapes of the specimens, the grid does not lie flat upon the specimen but must be folded in most cases, still meeting the requirements given above for determining grid locations. Thus, there are no exact areas

which can be computed for any of the grid locations.

In addition to the grid, a thin flexible paper strip marked in millimeter divisions was used to measure distances from the beak to major growth lines.

A location number was recorded each time a particular epizoan was found in that area of the brachial or pedicle valve of the host. The data base consisted, in essence, of two very wide sheets, like scrolls, of cross-ruled paper, one for the brachial valves and the other for the pedicle valves. Each sheet had horizontal rows numbered 0 through 40 for the grid locations and vertical rows for the 582 brachiopod hosts bearing epizoans. Each kind of epizoan was given a code number. Hosts were examined and their epizoans plotted one at a time. Whenever an epizoan was identified on a host, its coverage on the valve or valves was determined by the grid overlay, and its code number was entered in the appropriate square or squares on the sheet for the valve type, in the vertical row representing the particular host, and in the horizontal row or rows for grid locations. In brief, each valve of 582 *Paraspirifer* hosts was divided into grid locations, 41 being the maximum number needed to cover even the largest specimen, giving a maximum possible total of

$$2 \times 41 \times 582 = 47,724 \text{ grid locations;}$$

and since there were 38 kinds of epizoans, the maximum possible data base represented

$$47,724 \times 38 = 1,813,512$$

decisions on the presence or absence of each kind of epizoan in each of the designated grid locations of the host brachiopod sample.

From the information in the data base we constructed several tables. Rearrangement and re-combinations of the observed data do not, of course, introduce any new empirical evidence to the investigation. They do, however, focus on magnitude of differences, simplify complex relationships, and suggest support for explanatory arguments. Conversion and synthesis of cognitive factors is particularly needed when we try to interpret the community and environment of 375 million years ago by distributions of some

Table 3 -- Frequency of occurrence of epizoans on 582 *Paraspirifer bownockeri* hosts.

EPIZOAN	Number of hosts	Per cent of hosts	Areas occupied	EPIZOAN	Number of hosts	Per cent of hosts	Areas occupied
" <i>Clionoides</i> "	313	53.8	---	<i>H. cf. H. michiganensis</i>	3	0.5	68
Rugose coral	1	0.2	---	<i>H. reimanni</i>	4	0.7	42
<i>Aulopora microbuccinata</i>	84	14.4	882	<i>H. bilineata</i>	3	0.5	17
<i>Eliasopora stellatum</i>	66	11.3	1351	<i>H. spp.</i>	193	33.0	1014
<i>Ascodictyon fusiforme</i>	20	3.4	76	<i>Botryllopora socialis</i>	4	0.7	31
<i>Ascodictyon radians</i>	33	5.7	---	Fistuliporoids	3	0.5	9
<i>Ascodictyon (?) conferta</i>	1	0.2	8	<i>Atactotoechus cf. typicus</i>	18	3.1	292
<i>Ascodictyon floreale</i>	3	0.5	23	<i>Leptotrypella sp.</i>	7	1.2	13
<i>Ropalonaria tenuis</i>	12	2.1	72	? <i>Leioclema sp.</i>	11	1.9	71
" <i>Hederella canadensis</i> "	146	25.0	1078	<i>Lingulodiscina marginalis</i>	12	2.1	29
<i>H. concinna</i>	1	0.2	7	<i>Orbiculoidea doria</i>	10	1.7	24
<i>H. parvirugosa</i>	4	0.7	36	<i>Petrocrania hamiltoniae</i>	12	2.1	54
<i>H. filiformis</i>	140	24.0	918	<i>Philhedra crenistriata</i>	1	0.2	3
<i>H. alternata</i>	1	0.2	5	<i>Philhedra sheldoni</i>	2	0.3	6
<i>H. concinnoides</i>	47	8.1	574	<i>Philhedra stewarti</i>	1	0.2	2
<i>H. delicatula</i>	31	5.8	334	" <i>Mediospirifer audaculus</i> "	5	0.9	5
<i>H. thedfordensis</i>	270	46.2	4046	<i>Cyrtina "hamiltonensis"</i>	1	0.2	3
<i>H. alpenensis</i>	14	2.4	51	<i>Cornulites</i>	326	56.0	947
<i>H. rugosa</i>	1	0.2	15	<i>Spirorbis planum</i>	3	0.5	---
" <i>H. magna</i> "	4	0.7	25	Holdfasts	42	7.2	111
<i>H. magna</i>	12	2.1	149	Organic threads	23	3.9	69

38 kinds of attached fossil animals on 582 fossil brachiopods. For many questions, answers may be equivocal or even impossible. This we would expect. Nevertheless, arrangement and selection of data can lead to logical and defensible conclusions.

From the initial data base, we could readily ascertain the number of hosts having a particular number of different epizoans (table 2), the frequency of occurrence of each epizoan on the total number of brachiopod hosts (table 3), the number of times each epizoan occurred in a particular grid location on the brachial valve (table 4) or the pedicle valve (table 5), the per cent of total location occurrences for each epizoan in each grid location on the brachial valve (table 6) or the pedicle valve (table 7),

and the number of times two selected epizoans occurred together on the same brachiopod host (table 8). From these and other tables, other relationships could be shown by additional arrangements and syntheses of data.

The only exceptions to this system of recording data were the sponge borings "*Clionoides*," the bryozoan *Ascodictyon radians*, the tubes of the worm *Cornulites*, and the articulate brachiopods. Peculiarities of their form, distribution, and mode of growth could not be well expressed by a simple grid. Occurrences of the sponge borings were recorded by location area and/or concentrations along major growth lines. Calculations were based on random distribution of borings on a valve compared to the concentration of borings along major growth

Table 4 -- Number of occurrences of epizoans on grid locations of 582 *Paraspirifer bownockeri* brachial valves.

		EPIZOAN																				
		<i>Aulopora micro-</i> <i>buccinata</i>	<i>Eliasopora stel-</i> <i>latum</i>	<i>Ascodictyon fusi-</i> <i>forme</i>	<i>A. (?) conferta</i>	<i>A. floreale</i>	<i>Ropalonaria ten-</i> <i>uis</i>	" <i>Hederella can-</i> <i>adensis</i> "	<i>H. concinna</i>	<i>H. parvirugosa</i>	<i>H. filiformis</i>	<i>H. alternata</i>	<i>H. concinnoides</i>	<i>H. delicatula</i>	<i>H. thedfordensis</i>	<i>H. alpenensis</i>	<i>H. rugosa</i>	" <i>H. magna</i> "	<i>H. magna</i>	<i>H. cf. H. mich-</i> <i>iganensis</i>		
Interarea 0		5	24	1	--	1	--	5	--	--	4	--	1	--	33	--	--	--	--	1		
LEFT SIDE	Beak	18	37	1	--	2	5	25	--	3	47	--	22	8	135	3	1	1	4	2		
	Near-hinge	3	26	38	3	--	2	3	31	--	2	13	--	30	13	125	2	--	--	5	2	
		6	26	35	2	--	1	2	26	--	1	10	--	27	14	97	--	--	--	5	2	
		9	21	31	--	--	--	1	15	--	--	1	--	3	6	27	1	--	--	4	1	
		12	8	20	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	
		15	2	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	
		18	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	
		4	36	40	2	--	--	1	40	--	2	39	--	35	20	161	6	1	1	8	2	
	7	46	39	2	--	1	2	43	--	2	20	--	38	19	148	4	1	1	6	2		
	10	43	35	2	--	1	1	38	--	1	11	--	23	12	99	1	1	--	7	2		
	13	25	22	--	--	1	1	7	--	--	--	--	1	--	12	1	--	--	2	1		
	16	5	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--		
	19	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--		
	RIGHT SIDE	Beak	20	33	2	--	--	3	33	--	1	42	--	23	12	140	--	--	--	4	2	
		Near-hinge	23	26	33	1	1	--	2	39	--	1	15	--	23	13	122	--	--	--	4	3
			26	25	34	2	1	--	1	28	--	1	13	--	23	9	89	--	1	--	6	3
			29	20	32	--	1	--	1	9	--	1	3	--	1	3	25	--	--	--	4	3
			32	9	15	1	--	--	--	1	--	--	--	--	--	--	--	--	--	--	2	1
35			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
38		--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		
Near-fold		24	36	35	3	1	--	1	42	--	1	27	--	34	17	169	1	1	2	5	3	
		27	36	35	4	1	1	--	36	--	1	18	--	33	15	115	1	1	2	7	3	
		30	37	38	1	1	1	1	27	--	1	10	--	20	11	87	1	1	2	7	3	
	33	15	22	2	--	1	1	4	--	--	--	--	1	--	7	--	--	1	1	1		
	36	1	2	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1		
39	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--			
FOLD	Left	2	17	30	1	--	--	4	18	--	2	52	--	14	6	112	2	--	1	1	2	
		5	31	34	2	--	--	1	34	--	2	48	--	34	14	194	5	1	1	8	2	
		8	42	36	3	--	1	1	34	--	1	21	--	29	17	138	4	1	--	6	2	
		11	41	30	3	--	1	1	20	--	1	13	--	17	9	89	--	1	--	6	3	
		14	20	15	--	--	1	1	2	--	--	1	--	--	--	7	1	--	--	2	2	
	17	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--		
	20	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--		
	Right	22	14	24	1	--	--	3	22	--	1	43	--	20	10	104	1	1	--	1	2	
		25	25	29	1	--	--	1	37	--	1	40	--	30	12	138	1	1	1	5	3	
		28	32	30	1	--	--	--	30	--	1	22	--	33	13	128	1	1	2	6	3	
31		34	32	4	--	--	1	15	--	1	11	--	14	10	66	1	1	1	5	3		
34		17	14	--	--	--	--	2	--	--	--	--	1	--	4	--	--	--	--	2		
37	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--			
40	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--			
Totals		763	878	46	6	15	43	663	0	28	524	0	530	263	2571	37	15	16	128	62		

Table 4 -- (continued)

<i>Hederella rei-</i> <i>manni</i>	<i>H. bilineata</i>	<i>Hederella</i> spp.	<i>Botrylopora</i> <i>socialis</i>	Fistuliporoids	<i>Atactotoechus</i> cf. <i>A. typicus</i>	<i>Leptotrypella</i> sp.	? <i>Leioclema</i> sp.	<i>Lingulodiscina</i> <i>marginalis</i>	<i>Orbiculoidea</i> <i>doria</i>	<i>Petrocrania ham-</i> <i>iltoniae</i>	<i>Philhedra creni-</i> <i>striata</i>	<i>P. sheidoni</i>	<i>P. stewarti</i>	" <i>Mediospirifer</i> <i>audaculus</i> "	<i>Cyrtina "hamil-</i> <i>tonensis"</i>	<i>Cornulites</i>	Holdfasts	Organic threads	EPIZOANS
--	--	7	--	--	5	--	3	--	--	--	--	--	--	--	--	--	--	--	0
--	--	26	--	1	9	--	3	--	--	1	1	--	--	--	--	14	--	2	1
1	1	22	1	--	8	--	2	1	--	2	1	--	1	--	1	60	1	5	3
1	1	21	--	--	5	1	2	1	2	1	--	--	--	--	--	51	6	2	6
1	1	6	--	--	5	--	1	1	3	1	--	--	--	--	--	14	3	1	9
1	--	--	--	--	2	--	1	--	--	--	--	--	--	--	--	2	--	--	12
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	15
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	18
1	1	25	--	--	8	--	1	--	--	5	1	--	1	--	1	4	3	1	4
1	1	32	--	--	9	1	3	--	2	4	--	2	--	--	--	23	11	2	7
1	1	27	1	--	8	--	1	3	2	1	--	1	--	--	--	31	5	4	10
1	--	1	1	--	3	--	1	4	1	--	--	--	--	--	--	5	2	1	13
--	--	--	--	--	1	--	--	2	--	--	--	--	--	--	--	1	--	--	16
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	19
--	--	28	--	1	10	--	1	--	1	--	--	--	--	--	--	14	--	2	21
--	1	24	--	--	8	--	2	--	--	5	--	--	--	--	--	79	2	1	23
1	1	15	--	--	7	2	3	1	1	4	--	--	--	--	--	51	1	2	26
1	--	4	1	--	5	1	2	--	--	--	--	--	--	--	--	14	--	1	29
--	--	--	--	--	1	--	1	2	--	--	--	--	--	--	--	3	--	--	32
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	35
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	38
2	--	23	--	--	9	--	1	--	2	6	--	--	--	--	--	6	2	1	24
2	1	28	--	--	7	3	1	--	1	7	--	--	--	--	--	23	8	4	27
1	--	21	1	--	7	1	2	3	1	3	--	--	--	--	--	27	10	2	30
1	--	2	1	--	3	--	1	2	1	--	--	--	--	--	--	5	4	--	33
--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	36
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	39
--	--	17	--	2	9	1	1	--	--	--	--	--	--	--	--	3	1	1	2
1	1	16	--	1	10	--	1	--	--	2	--	--	--	--	--	2	3	1	5
1	1	19	--	--	8	--	2	--	1	2	--	1	--	--	--	6	1	3	8
1	1	10	1	--	8	--	1	2	1	--	--	--	--	--	--	7	3	1	11
1	--	--	1	--	3	--	1	1	1	--	--	--	--	--	--	2	--	--	14
--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	17
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	20
--	--	15	--	2	10	--	1	--	--	--	--	--	--	--	--	1	--	--	22
2	--	15	--	1	9	--	1	--	--	2	--	--	--	--	--	--	2	1	25
2	1	23	--	--	7	--	3	--	--	2	--	--	--	--	--	3	5	1	28
1	--	17	1	--	7	--	2	--	--	2	--	--	--	--	--	11	7	--	31
1	--	2	--	--	3	--	1	--	--	--	--	--	--	--	--	--	--	--	34
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	37
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	40
26	13	446	9	8	194	10	47	23	21	50	3	4	2	0	3	462	80	39	Totals

Near-hinge
LEFT SIDE

Near-hinge
RIGHT SIDE

Left
Right
FOLD

Table 5 -- Number of occurrences of epizoans on grid locations of 582 *Paraspirifer bownockeri* pedicle valves.

		EPIZOANS																				
		<i>Aulopora micro-</i> <i>buccinata</i>	<i>Eliasopora stel-</i> <i>iatum</i>	<i>Ascodictyon fusi-</i> <i>forme</i>	<i>A. (?) conferta</i>	<i>A. floreale</i>	<i>Ropalonaria ten-</i> <i>uis</i>	<i>"Hederella can-</i> <i>adensis"</i>	<i>H. concinna</i>	<i>H. parvirugosa</i>	<i>H. filiformis</i>	<i>H. alternata</i>	<i>H. concinnoides</i>	<i>H. delicatula</i>	<i>H. thedfordensis</i>	<i>H. alpenensis</i>	<i>H. rugosa</i>	<i>"H. magna"</i>	<i>H. magna</i>	<i>H. cf. H. mich-</i> <i>iganensis</i>		
LEFT SIDE	Interarea	0	2	2	2	--	--	1	8	--	1	16	--	1	--	18	1	--	--	--		
	Beak	1	2	19	2	--	--	4	14	--	1	12	--	1	--	53	--	--	--	1	--	
		3	3	22	--	1	--	1	19	--	1	12	--	3	1	71	1	--	--	1	--	
	Near-hinge	6	4	19	--	1	--	1	14	--	1	7	--	1	2	55	--	--	--	1	--	
		9	1	16	--	--	--	--	5	--	--	2	--	--	1	3	--	--	--	--	--	
		12	--	4	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	
		15	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
		18	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	
		Near-sulcus	4	--	15	--	--	--	2	12	--	1	17	--	1	1	64	2	--	--	1	--
			7	2	15	--	--	--	2	21	--	--	22	--	1	5	93	2	--	--	1	--
	10		4	20	1	--	1	2	14	--	--	17	--	1	5	70	--	--	1	--	--	
	13		4	12	1	--	1	1	3	--	--	1	--	1	2	9	--	--	--	1	--	
	16		1	3	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
	RIGHT SIDE	Beak	21	2	18	2	--	--	3	12	1	1	25	--	2	1	49	1	--	--	--	
		Near-hinge	23	3	21	--	--	--	22	1	--	10	--	2	1	68	1	--	--	--	--	
			26	2	17	--	--	--	11	--	--	7	--	1	--	25	1	--	--	--	--	
		Near-sulcus	29	1	12	--	--	--	2	--	--	1	--	--	1	1	--	--	--	--	--	
			32	--	1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	
			35	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
38			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		
Near-hinge		24	1	13	1	--	--	1	16	1	--	14	--	2	1	64	--	--	--	--		
		27	1	16	--	--	--	1	20	1	--	20	1	3	2	78	2	--	1	1	--	
		30	5	14	--	--	--	1	21	--	--	12	--	2	3	53	1	--	1	1	--	
		33	5	10	--	--	--	--	4	--	--	2	--	1	1	7	--	--	--	--	--	
		36	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
		39	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
SULCUS		Left	2	--	8	1	--	--	1	6	--	1	7	--	1	--	16	--	--	--	--	
			5	1	10	--	--	--	2	17	--	--	29	--	3	2	55	--	--	--	--	
			8	2	18	1	--	--	1	34	--	--	25	1	1	7	107	--	--	--	1	
		Right	11	8	20	3	--	1	1	32	--	--	24	1	2	9	98	1	--	1	2	1
			14	13	22	3	--	1	1	16	--	--	14	--	2	5	59	--	--	1	2	1
			17	11	19	3	--	1	--	3	--	--	4	--	1	1	18	--	--	--	2	1
	20		5	8	2	--	1	--	1	--	--	--	--	--	--	1	--	--	--	--	--	
	22		--	9	1	--	--	1	6	1	1	10	--	--	--	19	--	--	--	--	--	
	25		1	8	1	--	--	2	11	1	--	23	--	2	--	55	1	--	--	1	--	
	28		2	16	--	--	--	--	24	1	--	25	1	2	7	96	--	--	1	1	--	
	31	7	18	3	--	--	--	23	--	--	15	1	3	7	98	--	--	1	2	--		
	34	8	22	2	--	1	--	16	--	--	15	--	3	5	56	--	--	1	2	1		
	37	12	17	--	--	1	--	6	--	--	4	--	1	1	13	--	--	1	2	1		
40	5	8	--	--	--	--	1	--	--	--	--	--	--	3	--	--	--	--	--			
Totals		119	473	30	2	8	29	115	7	8	394	5	44	71	1475	14	0	9	21	6		

Table 5 -- (continued)

<i>Hederella rei-manni</i>	<i>H. bilineata</i>	<i>Hederella</i> spp.	<i>Botryllopora socialis</i>	Fistuliporoids	<i>Atactotoechus</i> cf. <i>A. typicus</i>	<i>Leptotrypella</i> sp.	? <i>Leioclema</i> sp.	<i>Lingulodiscina marginalis</i>	<i>Orbiculoidea doria</i>	<i>Petrocrania hamiltoniae</i>	<i>Philhedra crenistriata</i>	<i>P. sheidoni</i>	<i>P. stewarti</i>	" <i>Mediospirifer audaculus</i> "	<i>Cyrtina "hamiltonensis"</i>	<i>Cornulites</i>	Holdfasts	Organic threads	EPIZOANS
--	--	6	1	--	1	--	--	--	--	1	--	1	--	--	--	--	--	--	0 Interarea
1	--	26	--	--	6	--	--	--	--	--	--	--	--	--	--	12	1	--	1 Beak
--	--	26	1	1	5	--	1	--	--	--	--	--	--	--	--	71	--	2	3
--	--	21	1	--	5	1	3	1	--	--	--	--	--	--	--	36	--	1	6
--	--	3	1	--	2	--	1	--	--	--	--	--	--	--	--	1	1	--	9
--	--	--	1	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	12
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	15
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	18
1	--	30	1	--	4	--	--	--	--	--	--	--	--	--	--	8	--	--	4
--	--	32	1	--	4	1	--	--	--	--	--	--	--	--	--	31	--	4	7
--	--	25	1	--	5	--	1	--	--	--	--	--	--	--	--	35	2	3	10
--	--	7	2	--	3	--	2	--	--	--	--	--	--	--	--	5	--	1	13
--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	16
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	19
--	--	18	1	--	4	--	1	--	--	1	--	1	--	--	--	23	--	1	21 Beak
--	--	26	--	--	4	--	3	--	--	1	--	--	--	--	--	78	--	1	23
1	--	20	--	--	3	--	1	1	--	--	--	--	--	--	--	33	1	--	26
--	--	1	--	--	2	--	--	--	--	--	--	--	--	--	--	4	--	--	29
--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	32
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	35
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	38
1	--	21	--	--	4	--	--	--	--	--	--	--	--	--	--	11	--	1	24
2	1	30	1	--	3	1	1	1	1	--	--	--	--	--	--	31	1	3	27
1	1	17	--	--	3	--	1	--	--	--	--	--	--	--	--	30	2	1	30
1	--	1	--	--	1	--	1	--	--	--	--	--	--	--	--	4	--	--	33
--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	36
--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	39
1	--	12	--	--	4	--	--	--	--	--	--	--	--	--	--	--	1	--	2
1	--	24	--	--	3	--	--	--	--	--	--	--	--	--	--	2	--	1	5
1	--	25	--	--	3	--	--	--	--	--	--	--	--	--	--	4	--	2	8
--	--	40	2	--	3	--	--	1	--	1	--	--	--	1	--	15	--	2	11
--	--	20	2	--	3	--	1	1	--	--	--	--	--	1	--	11	7	3	14
--	--	9	1	--	1	--	1	--	--	--	--	--	--	1	--	2	4	2	17
--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	1	20
1	--	10	1	--	4	--	--	--	--	--	--	--	--	--	--	--	--	--	22
1	--	27	--	--	3	--	--	--	--	--	--	--	--	--	--	1	--	1	25
2	1	35	--	--	3	--	1	--	--	--	--	--	--	--	--	6	--	1	28
1	1	37	1	--	3	--	2	--	--	--	--	--	--	1	--	14	2	2	31
--	--	13	1	--	2	--	2	1	1	--	--	--	--	--	--	16	5	3	34
--	--	6	1	--	1	--	1	--	1	--	--	--	--	--	--	1	3	2	37
--	--	--	1	--	1	--	--	--	--	--	--	--	--	--	--	--	1	--	40
16	4	568	22	1	98	3	24	6	3	4	0	2	0	5	0	485	31	38	Totals

Near-hinge
Near-sulcus
Beak
Near-hinge
Near-sulcus
Beak
Near-hinge
Near-sulcus
Beak
Left
Right
SULCUS

Table 7 -- Per cent of total epizoan occurrences on grid locations of 582 *Paraspirifer bownockeri* pedicle valves.

	0	1.7	0.4	6.7	--	--	3.4	1.9	--	12.5	4.1	--	2.3	--	1.2	7.1	--	--	--
Inter	0	1.7	0.4	6.7	--	--	3.4	1.9	--	12.5	4.1	--	2.3	--	1.2	7.1	--	--	--
Beak	1	1.7	4.0	6.7	--	--	13.8	3.4	--	12.5	3.0	--	2.3	--	3.6	--	--	--	4.8
	3	2.5	4.7	--	50.0	--	3.4	4.6	--	12.5	3.0	--	6.8	1.4	4.8	7.1	--	--	4.8
	6	3.4	4.0	--	50.0	--	3.4	3.4	--	12.5	1.8	--	2.3	2.8	3.7	--	--	--	4.8
	9	0.8	3.4	--	--	--	--	1.2	--	--	0.5	--	--	1.4	0.2	--	--	--	--
	12	--	0.8	--	--	--	--	--	--	--	0.3	--	--	--	--	--	--	--	--
	15	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	18	--	--	--	--	--	--	0.2	--	--	--	--	--	--	--	--	--	--	--
LEFT SIDE	4	--	3.2	--	--	--	6.9	2.9	--	12.5	4.3	--	2.3	1.4	4.3	14.3	--	--	4.8
	7	1.7	3.2	--	--	--	6.9	5.1	--	--	5.6	--	2.3	7.0	6.3	14.3	--	--	4.8
	10	3.4	4.2	3.3	--	12.5	6.9	3.4	--	--	4.3	--	2.3	7.0	4.7	--	--	11.1	--
	13	3.4	2.5	3.3	--	12.5	3.4	0.7	--	--	0.3	--	2.3	2.8	0.6	--	--	--	4.8
	16	0.8	0.6	3.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	19	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Beak	21	1.7	3.8	6.7	--	--	10.3	2.9	14.3	12.5	6.3	--	4.5	1.4	3.3	7.1	--	--	--
	23	2.5	4.4	--	--	--	--	5.3	14.3	--	2.5	--	4.5	1.4	4.6	7.1	--	--	--
	26	1.7	3.6	--	--	--	--	2.6	--	--	1.8	--	2.3	--	1.7	7.1	--	--	--
	29	0.8	2.5	--	--	--	--	0.5	--	--	0.3	--	--	1.4	0.1	--	--	--	--
	32	--	0.2	--	--	--	--	--	--	--	0.3	--	--	--	--	--	--	--	--
	35	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	38	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
RIGHT SIDE	24	0.8	2.7	3.3	--	--	3.4	3.9	14.3	--	3.6	--	4.5	1.4	4.3	--	--	--	--
	27	0.8	3.4	--	--	--	3.4	4.8	14.3	--	5.1	20.0	6.8	2.8	5.3	14.3	--	11.1	4.8
	30	4.2	3.0	--	--	--	3.4	5.1	--	--	3.0	--	4.5	4.2	3.6	7.1	--	11.1	4.8
	33	4.2	2.1	--	--	--	--	1.0	--	--	0.5	--	2.3	1.4	0.5	--	--	--	--
	36	0.8	0.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	39	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	2	--	1.7	3.3	--	--	3.4	1.4	--	12.5	1.8	--	2.3	--	1.1	--	--	--	--
	5	0.8	2.1	--	--	--	6.9	4.1	--	--	7.4	--	6.8	2.8	3.7	--	--	--	--
	8	1.7	3.8	3.3	--	--	3.4	8.2	--	--	6.3	20.0	2.3	9.8	7.3	--	--	--	--
	11	6.8	4.2	10.0	--	12.5	3.4	7.7	--	--	6.1	20.0	4.5	12.7	6.6	7.1	--	11.1	9.5
	14	10.9	4.7	10.0	--	12.5	3.4	3.9	--	--	3.6	--	4.5	7.0	4.0	--	--	11.1	9.5
	17	9.2	4.0	10.0	--	12.5	--	0.7	--	--	1.0	--	2.3	1.4	1.2	--	--	--	9.5
	20	4.2	1.7	6.7	--	12.5	--	0.2	--	--	--	--	--	--	0.1	--	--	--	--
	22	--	1.9	3.3	--	--	3.4	1.4	14.3	12.5	2.5	--	--	--	1.3	--	--	--	--
	25	0.8	1.7	3.3	--	--	6.9	2.6	14.3	--	5.8	--	4.5	--	3.7	7.1	--	--	--
	28	1.7	3.4	--	--	--	--	5.8	14.3	--	6.3	20.0	4.5	9.8	6.5	--	--	11.1	4.8
	31	5.9	3.8	10.0	--	--	--	5.5	--	--	3.8	20.0	6.8	9.8	6.6	--	--	11.1	9.5
	34	6.8	4.7	6.7	--	12.5	--	3.9	--	--	3.8	--	6.8	7.0	3.8	--	--	11.1	9.5
	37	10.1	3.6	--	--	12.5	--	1.4	--	--	1.0	--	2.3	1.4	0.9	--	--	11.1	9.5
	40	4.2	1.7	--	--	--	--	0.2	--	--	--	--	--	--	0.2	--	--	--	--

Table 8 (continued) --

Botryllopora socialis	Fistuliporoids	Atactotoechus cf. typicus	? Leioclema sp.	Leptotrypella sp.	Lingulodiscina marginalis	Orbiculoidea doria	Petrocrania hamiltoniae	Philhedra crenistriata	Philhedra sheldoni	Philhedra stewarti	"Mediospirifer audaculus"	Cyrtina "hamiltonensis"	Cornulites	Holdfasts	Organic threads	Major growth lines	Number of occurrences	EPIZOANS
4	3	18	11	7	12	10	12	1	2	1	5	1	326	42	23	154		EPIZOANS
3	2	13	7	4	12	7	12	1	2	1	4	1	190	38	10	148	313	"Clionoides"
2	0	3	2	2	1	0	3	0	0	0	1	0	53	15	4	40	84	Aulopora microbuccinata
3	1	0	0	0	1	0	0	0	0	0	0	1	13	0	0	7	20	Ascodictyon fusiforme
1	0	2	1	1	0	0	0	1	0	0	0	0	18	3	1	12	33	Ascodictyon radians
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	Ascodictyon (?) conferta
0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	3	3	Ascodictyon floreale
1	0	1	2	2	0	1	1	1	0	0	1	0	30	10	5	22	66	Eliasopora stellatum
1	0	0	1	1	0	0	2	1	1	0	0	0	4	3	2	7	12	Ropalonaria tenuis
0	0	1	5	2	0	1	0	0	0	0	1	0	73	14	5	35	140	Hederella filiformis
1	3	8	8	5	4	6	3	1	0	0	1	0	117	15	0	66	270	H. thedfordensis
0	0	1	0	0	0	0	0	0	0	0	0	0	34	1	0	2	49	H. concinnoides
0	0	0	1	0	0	0	1	0	0	0	0	0	18	1	1	4	31	H. delicatula
0	0	0	1	0	0	0	0	0	0	0	0	0	3	1	0	2	4	H. parvirugosa
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	3	H. cf. H. michiganensis
1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	4	H. reimanni
0	1	0	0	1	0	0	0	0	0	0	0	0	5	0	0	3	12	H. magna
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	H. rugosa
3	0	0	0	1	0	0	0	0	0	0	0	0	8	0	1	3	14	H. alpenensis
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	H. bilineata
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	H. alternata
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	H. concinna
0	0	1	2	1	2	1	2	0	0	0	2	0	79	10	8	34	146	"H. canadensis"
0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	4	"H. magna"
3	0	7	1	1	6	2	5	0	0	0	0	0	122	13	4	43	193	H. spp.
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4	Botryllopora socialis
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	3	Fistuliporoids
0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	4	18	Atactotoechus cf. typicus
0	0	0	0	0	0	0	0	1	0	0	0	0	4	2	2	6	11	? Leioclema sp.
0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	7	Leptotrypella sp.
0	0	0	0	0	0	1	0	0	0	0	0	0	7	0	0	3	12	Lingulodiscina marginalis
0	0	0	0	0	0	0	1	0	0	0	0	0	4	3	0	5	10	Orbiculoidea doria
0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	0	8	12	Petrocrania hamiltoniae
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	Philhedra crenistriata
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	Philhedra sheldoni
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	Philhedra stewarti
0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	1	1	5	"Mediospirifer audaculus"
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	Cyrtina "hamiltonensis"
0	0	0	0	0	0	0	0	0	0	0	0	0	26	12	86	326	Cornulites	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	24	42	42	Holdfasts
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	23	23	Organic threads

Table 9 -- Actual occurrences (above) and expected (chance) occurrences (below) of pairs of epizoans on 582 *Paraspirifer bownockeri* hosts. Only 50 or more total co-occurrences considered significant.

								EPIZOANS	
								Number of occurrences	
<i>Aulopora microbuccinata</i>	<i>Eliasopora stellatum</i>	<i>Hederella filiformis</i>	<i>H. thedfordensis</i>	" <i>H. canadensis</i> "	<i>Cornulites</i>	Major growth line	EPIZOANS		
84	66	140	270	146	326	154			
76	54	81	133	66	190	148	313	" <i>Clionoides</i> "	
45	36	75	145	79	145	83			
--	20	13	22	16	53	40	84	<i>Aulopora microbuccinata</i>	
--	10	20	39	21	47	22			
--		13	30	11	30	22	66	<i>Eliasopora stellatum</i>	
--		16	31	17	37	17			
--			83	47	73	35	140	<i>Hederella filiformis</i>	
--			65	35	78	37			
--				66	117	66	270	<i>H. thedfordensis</i>	
--				68	151	71			
--					79	34	146	" <i>H. canadensis</i> "	
--					82	39			
--						86	326	<i>Cornulites</i>	
--						86			

lines. *Ascodictyon radians* was recorded as to the valve on which it occurred. *Cornulites* was recorded as occurring in a grid location where its tube was first attached, even though the tube frequently extended into portions of adjacent grid locations. The articulate brachiopods "*Mediospirifer audaculus*" and *Cyrtina* "*hamiltonensis*" presumably attached by a functional pedicle during or shortly after settlement; they were recorded as occurring only in a grid location in which the pedicle would have attached before their interareas were cemented onto the host brachiopod and extended by growth.

Epizoan associations.-- As discussed above, occurrences of two selected epizoans

together on the same brachiopod host can be compared with the co-occurrences to be expected by chance for the number of each epizoan, the size of the population of hosts which yielded each epizoan (582), and the sample on which co-occurrences is calculated (also 582).

Co-occurrences on the same brachiopod host (table 8) were calculated from the original data matrix. Here we restricted our study to pairs of epizoans rather than suites of epizoans numbering more than two on the same host. Epizoans having less than 50 total occurrences (8.6% of the hosts examined) were not considered significant for this purpose and were excluded in the table of actual and chance co-occurrences for selected pairs of epizoans (table 9).

Table 10 -- Actual co-occurrences of pairs of epizoans on *Paraspirifer bownockeri* in relation to expected (chance) co-occurrences. Those with ratios greater than 1.25 are enclosed in rectangles; those with ratios less than 0.80 are encircled.

<i>Aulopora microbuccinata</i>	<i>Eliasopora stellatum</i>	<i>Hederella filiformis</i>	<i>H. thedfordensis</i>	" <i>H. canadensis</i> "	Cornulites	Major growth lines	EPIZOAN
1.69	1.50	1.08	0.92	0.84	1.09	1.78	" <i>Clionoides</i> "
	2.00	0.65	0.57	0.76	1.13	1.82	<i>Aulopora microbuccinata</i>
		0.81	0.97	0.65	0.81	1.29	<i>Eliasopora stellatum</i>
			1.28	1.34	0.94	0.95	<i>Hederella filiformis</i>
				0.97	0.78	0.93	<i>H. thedfordensis</i>
					0.96	0.87	" <i>H. canadensis</i> "
						1.00	<i>Cornulites</i>

The co-occurrences of selected pairs in relation to chance (actual occurrences divided by the number expected by chance) reveals that some pairs co-occur with exceptional low frequency (less than 0.8), whereas other pairs co-occur with exceptionally high frequency (more than 1.25), as shown in table 10. These anomalies are used in our interpretations below.

OBSERVATIONS AND INTERPRETATIONS

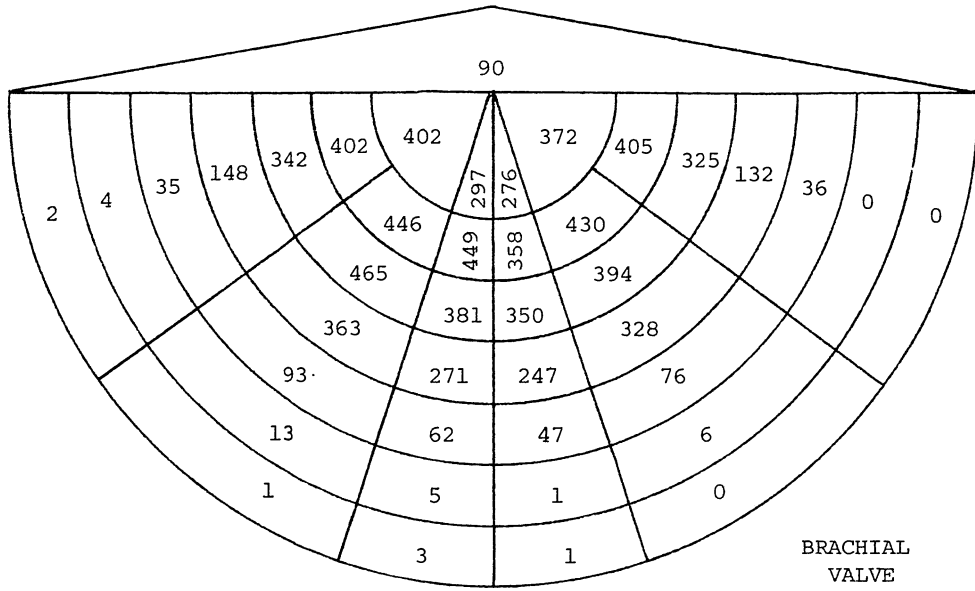
General Epizoan Relationships

Size of host.-- One might expect that the size of the host would show a direct relationship to the number of epizoans utilizing it, not only because of the larger surface area for settlement but also because of its presumed greater longevity. This appears to be substantiated by our sample. The specimens of *Paraspirifer bownockeri* examined range in length from 23 to 52 mm, with an average length of 39 mm. The three *Paraspirifer* specimens each

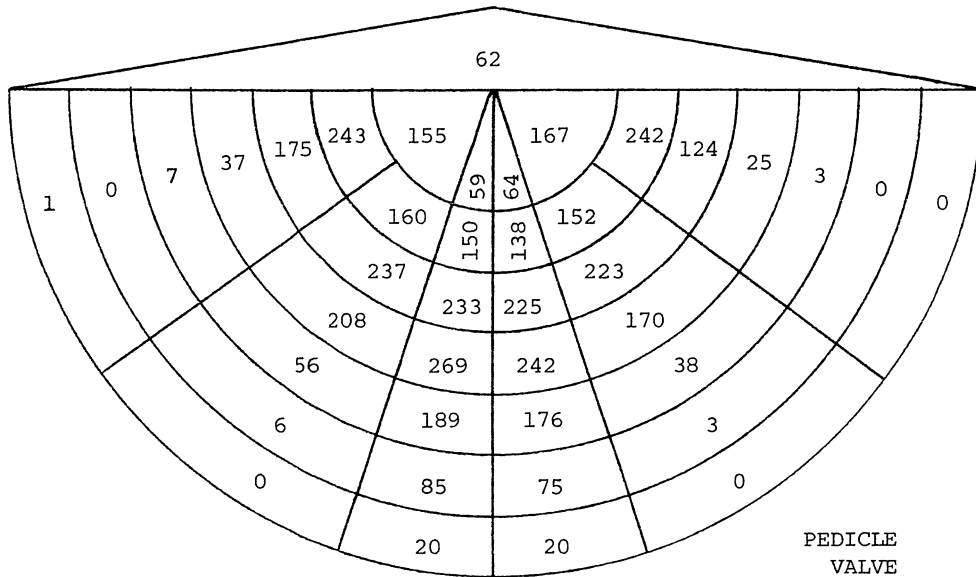
having eight kinds of epizoans (table 2) are all larger than the average. Of the 62 *Paraspirifer* hosts each bearing only one kind of epizoan, 87.1% are equal to or smaller than the average.

Utilization of host.-- It is difficult to decide which epizoans utilized *Paraspirifer* hosts to the greatest extent for two reasons. First, the size of the epizoans varies greatly whether each is measured by its total volume or by the area occupied, and second, the unit for some epizoans (such as brachiopods) is the individual, whereas the unit for other epizoans (such as bryozoans) is the colony. Hence, the successful utilization of the host could be reckoned by the number of hosts bearing the epizoan, the number of individuals of the epizoan, or the area occupied by each kind of epizoan. The number of hosts bearing each kind of epizoan (table 3) is one measure of successful settlement.

The number of areas occupied by each



TEXT-FIG. 2 -- Occurrences of epizoans on brachial valves of 582 *Paraspirifer* hosts by grid locations.



TEXT-FIG. 3 -- Occurrences of epizoans on pedicle valves of 582 *Paraspirifer* hosts by grid locations.

Table 11 -- Number of grid locations occupied by epizoans on major parts of each valve in 582 *Paraspirifer bownockeri* specimens.

	Left side	Right side	Ratio L/R
Brachial valve:			
Lateral surface	2686	2504	1.073
Near-hinge sector	1119	1084	1.032
Near-fold sector	1567	1420	1.104
Fold	1468	1280	1.147
Pedicle valve:			
Lateral surface	1285	1147	1.120
Near-hinge sector	540	477	1.132
Near-sulcus sector	745	670	1.112
Sulcus	1005	940	1.069

This table emphasizes the bilateral asymmetry in each valve. On the left side of each valve, the near-hinge sector includes grid locations 3, 6, 9, 12, 15, and 18 plus half of 1, and the near-fold or sulcus sector includes grid locations 4, 7, 10, 13, 16, and 19 plus half of 1; on the right side of each valve, the sectors include corresponding grid locations.

kind of epizoan (tables 4 and 5) is a better indicator of success in inter-specific competition for space on the host. It must be kept in mind that rarely if ever was settlement possible on an area of the host which was already occupied by a living epizoan competitor. An interesting comparison can be made of the bryozoan *Hederella magna* and the inarticulate brachiopod *Lingulodiscina marginalis*, each occurring on 12 hosts: the bryozoan colonies occupy 149 grid locations whereas the brachiopod individuals occupy only 29. The outstanding epizoan genus was the bryozoan *Hederella*, species of which had 874 occurrences on hosts and occupied 8379 grid areas.

Bilateral asymmetry of occupancy of the valves.-- Of the grid locations occupied by the epizoans on the lateral surface of the brachial valves of the host, 4154 were on the left half and 3784 on the right half (text-fig. 2). Of the grid locations occupied on the lateral surface of the pedicle valves, 2290 were on the left half and 2087 on the right half (text-fig. 3). It must be remembered that the grid is implaced with the surface of the valve upward, so that the

"left" side of the brachial valve lies immediately in contact and above the "right" side of the pedicle valve.

For comparison, each half of the valve can be divided into three sectors diverging from the beak: the sector adjacent to the hinge, the sector near the fold or sulcus, and the sector including the fold or sulcus. These divisions correspond exactly to numbered grid locations except for the small area around the beak, which can be divided in two between the near-hinge and the near-fold sectors for the brachial valve and between the near-hinge and near-sulcus sectors for the pedicle valve. Without exception, on both brachial and pedicle valves, epizoans occupy more grid locations on the left than on the right in each major sector (table 11). The asymmetry is most pronounced on the fold, which has nearly 15% more occupied areas on the left than on the right. Asymmetry is much less on the sulcus, where the left side has only 7% more occupied areas than the right. If we examine concentric zones around the beak in the brachial (text-fig. 2) or the pedicle valve (text-fig. 3), the pattern remains about the same as the overall pattern, with a distinctly greater number of epizoans on the left side.

We cannot be certain why the epizoans occupied more areas on the left sides of the two valves. It is very doubtful that the brachiopod generated asymmetric food-intake currents which influenced the settlers. We suggest a different explanation. Possibly, the members of the population of *Paraspirifer* or most of them immigrated to the Silica quarries area at about the same time, settling out from one major spat-fall or a few consecutive spat-falls. Certainly, numbers of this large brachiopod are concentrated in a very thin zone of the formation. Under such conditions, the young *Paraspirifer* individuals would have oriented their shells with respect to the prevailing current. Later, as they reached maturity and their pedicles atrophied, they lost maneuverability and all came to rest in an oriented position. If then the current direction shifted appreciably, the colonizing epizoans would not arrive in the anterior-posterior direction of the hosts, but instead from one side. The epizoan concentration on the left sides of the brachial valves and the

Table 12 -- Number and per cent of grid locations occupied by epizoans on major parts of each valve, emphasizing the differential occupancy of the two valves.

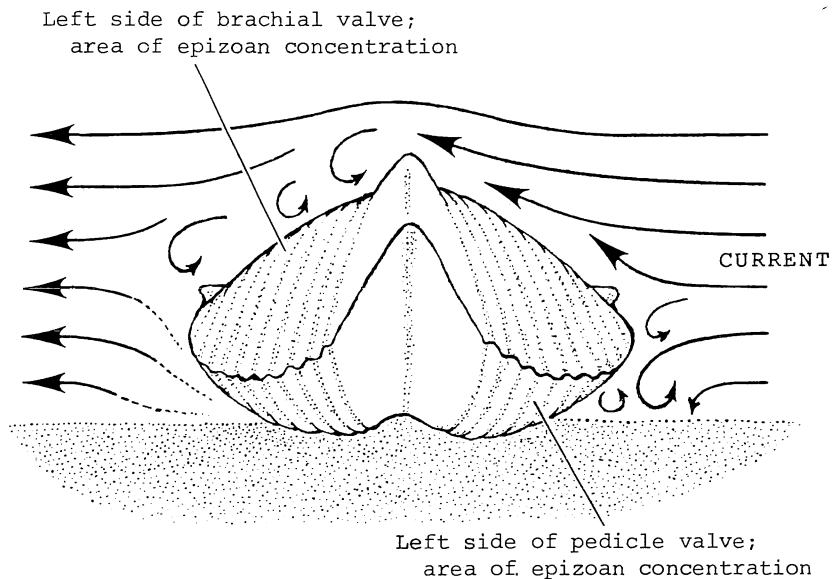
	Brachial valve		Pedicle valve		Total number	Ratio brachial/pedicle
	Number	Per cent*	Number	Per cent*		
All areas	8028	64.4	4439	35.6	12467	1.808
Lateral surfaces	5190	41.6	2432	19.5	7622	2.134
Near-hinge sectors	2203	17.7	1017	8.2	3220	2.166
Near-fold or sulcus	2987	24.0	1415	11.3	4402	2.111
Fold or sulcus	2748	22.0	1945	15.6	4693	1.413
Interarea	90	0.7	62	0.5	152	1.452

* All percentages are based on the total number of occupied grid locations on the 582 brachiopods studied.

The near-hinge and near-fold or sulcus sectors include grid locations noted in the footnote to table 11.

diagonally opposite sides of the pedicle valves might (text-fig. 4) be the result of preferential settlement of one valve on the current-facing side and settlement of the other valve on the lee side. As the *Paraspirifer* lay with its pedicle valve on the sea floor, the current slipstream

around it would have very low velocities on the current-facing side of the pedicle valve and would facilitate settlement there; at the same time, the slipstream would achieve similar low velocities across the brachial valve only on the leeward side. This might also account for the



TEXT-FIG. 4 -- Position of brachiopod in currents which could have produced the asymmetry of epizoan distributions on *Paraspirifer* hosts. Only on the left sides of the two valves did low-velocity eddies contact the host. The right side of the brachial valve was swept by strong currents, and the right side of the pedicle valve tended to be "starved" by little if any current action.

Table 13 -- Occupancy of grid locations by species of *Hederella*.

	Brachial valve			Pedicel valve		
	Left side	Right side	Ratio L/R	Left side	Right side	Ratio L/R
Interarea	51			51		
Lateral surface	1712	1579	1.084	826	726	1.138
Fold or sulcus	1051	929	1.131	749	705	1.062

greater number of grid locations occupied in the immediate lee of the fold (text-fig. 2; table 11) than farther away in the near-hinge sector.

Differential occupancy of two valves.--

The number and per cent of grid locations occupied by epizoans differs for the brachial and pedicle valves (table 12), both in total valve area and in major sectors of the valve. On the 582 brachiopod hosts examined, the brachial valves had nearly twice as many grid locations occupied as did the pedicle valves -- 8028 compared to 4439. The greater abundance of epizoans still prevails on the brachial valve when interareas, lateral surfaces, or fold portions are compared (table 12).

Epizoans on the brachial valve were concentrated on the lateral surfaces rather than on the fold: of the 12467 grid areas having epizoans on the valve, 41.6% were located on lateral surfaces and only 22.0% on the fold -- a ratio of 1.9/1, or nearly twice. In contrast, epizoans on the pedicle valve tended to be distributed more evenly across the lateral surfaces and sulcus: 19.5% of all occupied grid areas were located on the lateral surfaces of the pedicle valve and 15.6% on the sulcus -- a ratio less than 1.3/1. Perhaps the steepness of the fold sides tended to discourage settlement on that part of the brachial valve. Also, the area of the fold in relation to the lateral surfaces of the brachial valve is greater than the area of the sulcus to the pedicle valve, which may explain why the sulcus appears to have an overabundance of epizoans.

Of epizoan-occupied grid locations, the ratio of brachial/pedicel valve is greatest on lateral surfaces (exceeding 2) and lowest on the

fold/sulcus surfaces (1.413). On lateral surface of each valve, relatively more grid locations were occupied by epizoans in the sectors near the fold or sulcus than in the sectors near the hinge (table 12). At least part of the discrepancy may have been caused by inaccessibility of the near-hinge area, which would suggest that young *Paraspirifer bowmockeri* lived with the hinge set on (or even in) the soft substrate and adults lived with the hinge lower than the center of the shell.

Distribution of epizoans on small and large hosts.-- Even the largest *Paraspirifer* used in the study had some epizoans on the anterior margin of its valves. However, because size of the hosts varied greatly, and the grid was based on absolute measurements, a quantitative assessment of host size relation to epizoan distribution could not be made by our procedures. It would be possible to design a special grid for each specimen which would mark off and subdivide 10-mm wide concentric bands starting from the commissure; such individual grids would reveal whether epizoans occupied areas equidistant from the commissure equally on young and old hosts, but it would still lack in-put on the differences in the corresponding areas of the grids.

Evidence from our study is inconclusive. The epizoan counts by grid locations for brachial valves (text-fig. 2) and pedicle valves (text-fig. 3) show few occurrences on the peripheral margin of either valve for the simple reason that very few hosts attained dimensions (measured along the curve of the shell) of 160 mm in width or 80 mm in length. If the plastic grid is molded to a specimen and the position of a particular growth line is marked onto it, first for

Table 14 -- Comparison of grid locations occupied by *Hederella* with those occupied by all other epizoans.

Major parts of valves			<i>Hederella</i>	Other epizoans	Ratio
Brachial valve	Interarea		51	39	1.308
	Lateral surface	Left	1712	974	1.758
		Right	1579	925	1.707
	Fold	Left	1051	417	2.520
		Right	929	351	2.647
Pedicel valve	Interarea		51	11	4.636
	Lateral surface	Left	826	459	1.800
		Right	726	421	1.724
	Sulcus	Left	749	256	2.926
		Right	705	235	3.000

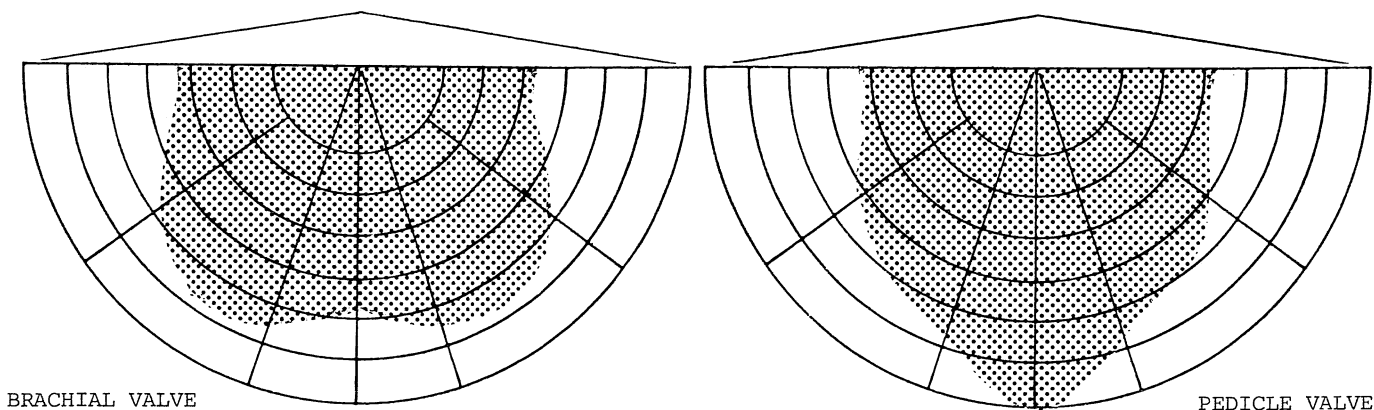
the brachial valve and then for the pedicle valve, the grid will appear as in text-figure 5 when laid flat.

Some grid location counts do differ from the overall bilateral asymmetry of epizoan distribution on both brachial and pedicle valves (text-figs. 2 and 3). Near the beak and as far as 30 mm along the near-hinge sector, the right side of the lateral surface of each valve contains as many or more occupied locations than does the left side; beyond the 30-mm radius in each valve, the asymmetry reverses and the left side has more occupied locations than the right. If the reversal has any biologic significance at all, it may be attributed to the size of *Paraspirifer* when the pedicle atrophied and the shell shifted its position with respect to the sub-

strate. On the other hand, the distributions may all result from flow and eddies in the slip-stream which transported the spat and larvae of the epizoan settlers.

Distribution of epizoans as affected by growth after settlement.-- The majority of epizoans found on *Paraspirifer* are colonial, and each extended its coverage of the host from the small spot where it settled. In investigating the modification of the distribution pattern by growth of colonial organisms, we selected the most prolific genus of the epizoans, the bryozoan *Hederella*, species of which occupy 8379 grid locations on the hosts examined, with 5322 locations on the brachial valves and 3057 on the pedicle valves. A comparison of the distribution of occupied grid locations by *Hederella* (table 13) with those by all epizoans (table 12) shows that even when extension of coverage was possible by growth after settlement, the typical colonial organism maintained about the same bilateral asymmetry of distribution on left and right sides of each valve.

If the distribution of *Hederella* is compared to that of all other epizoans (including some other colonial forms), it becomes clear (text-fig. 6) that *Hederella* occupies proportionally more grid locations on the fold and the sulcus. Evidence seems conclusive that availability of space permitted growth of established colonials into areas less favorable for settlement.



TEXT-FIG. 5 -- Appearance of a single growth line of a host when the plastic grid was unmolded from the brachiopod and laid flat.

Density of epizoans on valves.-- The shape of the high epizoan density is concentric around the beak and does not form a ring around the postulated contact area of the adult *Paraspirifer*, as one might expect if the majority of epizoans settled when the hosts had reached adulthood. A logical explanation is that these epizoans, at least the majority, settled in a ring around the beaks of young hosts, which were at the time held erect by a pedicle, and that these epizoans survived when the hosts rolled onto their pedicle valves in the adult stage. Obviously, if this hypothesis is correct, the atrophy of the pedicle and the shift of the shell must have taken place after the brachiopod had attained considerable size, for otherwise the epizoans in the spots bordering the sulcus would have been smothered in the muddy substrate. We suggest that the onset of the adult stage may have been as late in ontogeny as when the *Paraspirifer* measured about 52 mm wide, 38 mm long, 36 mm thick, and 70 mm along the sulcus; such size would ensure survival of the established epizoans into the adult stage of their host.

Our suggested hypothesis that most epizoans settled when the brachiopod was young and erect seems to conflict with the asymmetry (left vs. right) of epizoan distribution on each valve, as shown in table 11 and text-figures 2 and 3. However, the asymmetry is much weaker than the density concentration. If the process responsible for the asymmetric distribution was fully efficient in controlling settlement on the left side in preference to the right, then only 12% of the epizoan occurrences need be ascribed to it in order to produce the final pattern as we have found it.

A fully consistent and plausible history of the brachiopods and their epizoans might have involved: (1) larvae of *Paraspirifer bowmockeri* arriving in the area as current-borne immigrants, most in one fall-out, (2) young *Paraspirifer* developing shells, all held erect by pedicles burrowed into the soft bottom sediment and all oriented with respect to the currents, (3) growth of the still-upright youthful *Paraspirifer* to a size sufficient to serve as a

settling ground for larvae and spat of epizoans, (4) continued epizoan settling and colonization until the *Paraspirifer* population attained dimensions of 70 mm along the sulcus, during which time the epizoans concentrated in the horseshoe-shaped areas around the beaks (such a distribution might well have been produced by nearly vertical fall-out of epizoans onto *Paraspirifer* that were slightly inclined toward the pedicle valve, in which case the beaks would be on the underside next to or slightly into the substrate and thus unavailable for settlement), and (5) final deterioration of the pedicle as it was being pinched out between the growing beaks of the *Paraspirifer*, rocking over of the brachiopod into an equilibrium position on the pedicle valve, and currents approaching the majority of brachiopods at an angle and having sufficient velocity to form a slipstream which discouraged settlement by the epizoans on the current-facing side of the brachial valve of the host and promoted settlement on the lee side of the brachial valve and the diametrically opposite side of the pedicle valve.

Particular Epizoans

The following observations and interpretations refer to particular taxa of epizoans.

BRYOZOA Cyclostomata

Hederella.-- As pointed out, this was the most successful genus of epizoans on our *Paraspirifer bowmockeri*, having at least one colony on 502 of the 586 specimens studied. The distribution on the valves has been discussed above; in common with other epizoans, *Hederella* occupies more grid locations on the brachial valve than the pedicle valve, with more occurrences on the left than the right side in each valve (table 13). Distribution of *Hederella* shows slight differences from that of other epizoans in having greater concentrations on the fold and sulcus (table 14). These may be explained as extensions by growth after settlement into available areas.

In contrast to most other epizoans, many *Hederella* colonies on the pedicle valve were poorly preserved and generally smaller than those on the brachial valve. This we would

attribute to inferior conditions for growth on adult pedicle valves, the grid locations of which lay upon and just above the substrate.

The relationship of *Hederella* to the host appears to have been commensal, by which the bryozoan benefited from the hard surface for attachment and from the elevation above the soft substrate. A secondary benefit, enhanced food supply gained from food-bearing currents generated by the host's opening and closing of its valves, has been suggested (Ager, 1961; Hoare & Steller, 1967; Richards, 1972), but we find no convincing support for it and regard any such benefit to have been minimal.

A life association preceding the atrophy of the host's pedicle seems indicated for the bryozoan colonies occupying the edges of the sulcus near the middle of the valve, the exact areas on which the pedicle valve would rest in the stable position. A life association is also attested by *Hederella* colonies which grew to the edge of a valve and there abruptly terminated. A death relationship, epitaphism, is indicated by a few colonies which crossed over the commissure from one valve onto the other.

Hederella thedfordensis.-- This, the most common species of the genus, was present on nearly twice as many hosts as the next most common species, *H. filiformis*. It also occurred in 4046 grid locations out of a total of 12467 which had epizoans; in other words, in terms of area occupied, this one species constituted over 32% of all epizoans on *Paraspirifer bownockeri*. Distribution by valve was nearly the same ratio as for all epizoans (table 12), with 2571 grid positions on the brachial valve and 1475 on the pedicle valve -- a ratio of 1.74.

Colonies ranged in size from three or four zooids (generally the minimum necessary for specific identification) to large branching zoaria covering nearly all of a valve. No direction of growth was preferred; about as many colonies grew posteriorly as anteriorly. Most colonies grew randomly and exhibited no consistent pattern or direction.

H. thedfordensis occurred with almost every other epizoan on some host. Some colon-

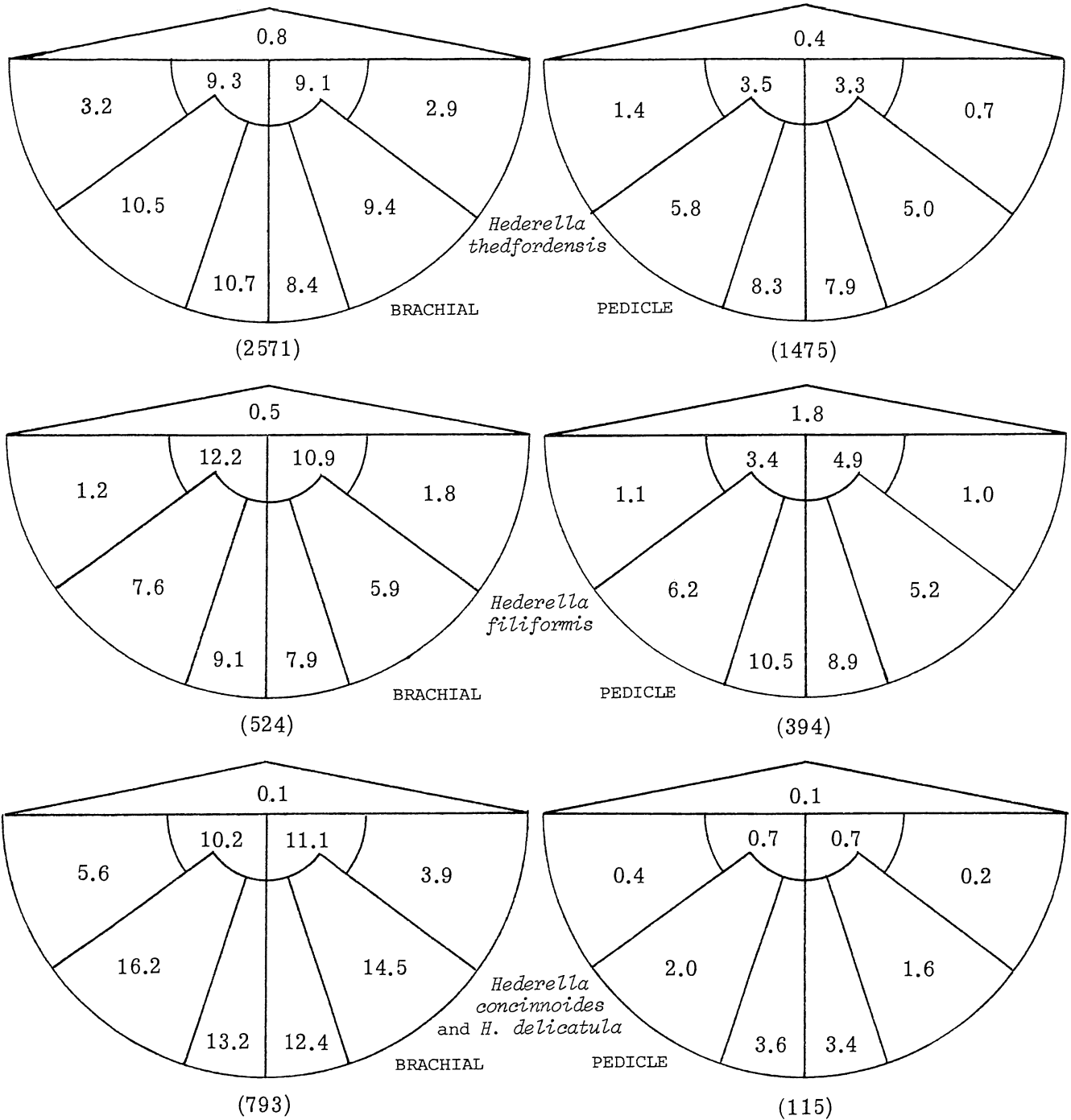
ies grew over other epizoans (including *Cornulites*, other bryozoans, and the colonial coral *Aulopora*); apparently this was epitaphism, inasmuch as we found no evidence that one epizoan disturbed the growth of another.

Hederella filiformis.-- This, the second most common species of the genus, was present on 24% of the hosts examined and occupied 918 grid locations. The colonies are most numerous in grid locations near the beaks and on the sulcus and fold (text-fig. 6). This preference for smooth areas of the host shell is borne out by the lack of colonies on the margins of those old *Paraspirifer* specimens with pronounced ornamentation. Colonies of *H. filiformis* ranged in size from a few zooids to large branching zoaria. Colonies showed no preferred orientation, although the central axis of some zoaria followed along an intercostal groove for some distance before branching off across the costae and into other locations.

Both life and death relationships were demonstrated. The latter, epitaphism, was indicated by colonies which crossed over the commissure or hinge of the host onto the opposite valve. A life relationship is clearly shown by one colony which grew toward the posterior edge of the brachial valve on one host, turned there and grew along the edge of the valve toward the cardinal extremity, then veered back toward the center of the valve, avoiding the hinge area.

Hederella concinnoides and *Hederella delicatula*.-- These two species are so similar in size and other features that rather large colonies are needed to show the differences in their angles of budding and branching. A commensal relationship is thought to have existed with the hosts, for colonies which grew to the edge of a valve extended along the margin but did not cross the commissure.

Data can be prepared from previous tables (tables 6 and 7) to show the distributions of *Hederella thedfordensis*, *H. filiformis*, and combined *H. concinnoides* and *H. delicatula*. These taxa differ in the percentages of grid locations occupied on each valve, as well as in the relative abundances on the two valves (text-fig. 6). The brachial valve has 1.7 times as many



TEXT-FIG. 6 -- Per cent of grid locations occupied by epizoan populations of *Hederella thedfordensis*, *H. filiformis*, and combined *H. concinnoides* and *H. delicatula* on selected areas of brachial and pedicle valves of 582 *Paraspirifer* hosts. Based on 4046 grid occurrences of *H. thedfordensis*, 918 of *H. filiformis*, and 908 of *H. concinnoides* and *H. delicatula* combined; numbers in parentheses indicate number of occurrences on each valve.

occupied areas as the pedicle valve in the case of *Hederella thedfordensis*, 1.3 times as many for *H. filiformis*, and a remarkable 6.9 times as many for *H. concinnoides* and *H. delicatula*. This appears to be convincing evidence that the latter pair of species shunned the under side of the host shell to a strong degree. The species *Hederella thedfordensis* occupied fewer areas around the beak on the pedicle valve than it did on the brachial valve, but otherwise it was rather evenly distributed across the lateral surface and sulcus. *Hederella filiformis* was somewhat more concentrated on the sulcus; it was slightly more often found on the sulcus than on the fold, apparently thriving equally well on the lower and upper surfaces of the shell. Although *Hederella concinnoides* and *H. delicatula* had relatively few colonies on the pedicle valve, these were concentrated on the sulcus area.

Hederella parvirugosa, *H. concinna*, and *H. alternata*. -- These species are so rare among epizoans, together occupying only 48 grid locations, that no valid conclusions can be reached on their distribution. The latter two species are here reported from the formation for the first time, each represented by a single colony.

"*Hederella alpenensis*" group.-- Only two representatives of this group were found, *Hederella alpenensis* and *H. rugosa*, the latter not previously recorded from the Silica Formation. *Hederella alpenensis* usually occurred as large colonies, but *H. rugosa* was represented on the single host by many small colonies growing in various directions.

"*Hederella magna*" group.-- This group of *Hederella* with large zoecia includes three species as epizoans on *Paraspirifer*: *Hederella magna*, *H. reimanni*, and *H. cf. H. michiganensis*, the latter not previously known from the formation. One host exhibited an epitaphic relationship with *H. cf. H. michiganensis*, the bryozoan colony extending from the brachial valve across the commissure and 20 mm onto the pedicle valve; much of the remaining surface area of this host was covered with other epizoans except for the area of the pedicle valve which,

presumably, rested on the substrate. A few colonies of this group demonstrated a life relationship, growing to the edge of the valve but not crossing it.

Hederella bilineata.-- This only species of the "*Hederella parallela*" group was present on only three hosts and occupied only 17 grid locations. No preferred orientation was evident, nor was the distribution considered significant.

In general, none of the species of the bryozoan *Hederella* showed a preferred growth direction. Some did occupy certain areas of the host more often than others. Such specific characters as size of zoecia and branching patterns have no apparent correlation with location on the host.

Ctenostomata

The ctenostomes are represented by six species: *Eliasopora stellatum*, *Ascodictyon fusiforme*, *A. radians*, *A. floreale*, *A. (?) conferta*, and *Ropalonaria tenuis*. All are difficult to distinguish. *Eliasopora* was often found without *Ascodictyon*, but only rarely did a species of *Ascodictyon* occur without another species of its genus or *Eliasopora*. Where single colonies were found on a host, they were smaller than average.

All three ctenostome genera occurred more frequently on the brachial valve than on the pedicle valve. Neither *Eliasopora* nor *Ascodictyon* displayed a distribution preference upon a valve, being rather evenly scattered. On the other hand, *Ropalonaria* concentrated within 20 mm of the beaks, perhaps finding the older and thicker portions of the host shell more suitable for embedding. Because of its embedding, *Ropalonaria* could readily be overgrown, apparently always after death, and for that reason is probably underrepresented in occurrence counts. *Ascodictyon* species and *Eliasopora stellatum* commonly grew onto and over other epizoans, which apparently presented no barrier to their growth; we find no evidence of ctenostome bryozoans competing for shell space with other epizoans, and conclude that their expansion and coverage were examples of epitaphism. Similarly, epizoans which

grew over the ctenostomes probably did so after the latter were dead. The life relationship indicated by many colonies is clearly commensal, as stated by Condra & Elias (1944).

Cystoporata

Botryllopora and *fistuliporoids*.-- All bryozoans of the Cystoporata are rare on the *Paraspirifer* specimens examined. Two hosts display distinct and different sequences of colonization by the same three epizoans: *Botryllopora socialis*, *Ascodictyon fusiforme*, and the coral *Aulopora microbuccinata*. On one specimen, *Aulopora* was first, *Botryllopora* second, and *Ascodictyon* last, having grown over both the coral and the other bryozoan. On the other specimen, *Botryllopora* was first and was partly covered in turn by *Aulopora* and then *Ascodictyon*. In both examples, epitaphism is shown with the host, inasmuch as one or more epizoans passed over the commissure. Because no preferred sequence of attachment was evident, none of the three epizoans can be considered as necessary for the success of another.

Hall & Simpson (1887, p. 282) stated long ago that for *Botryllopora socialis*,

... nearly all the specimens are parasitic on Cyathophyllid or Favositid corals.

We find, however, no support for parasitism by this species and believe the relationships were commensal or epitaphic.

The three specimens of *fistuliporoids* yield little information except that *Paraspirifer* was used as a site for attachment.

Trepostomata and/or Cryptostomata

The three species of encrusting bryozoa used *Paraspirifer* as a substrate. *Atactotoechus* occurred on 18 hosts, *Leptotrypella* on 7, and *? Leioclema* on 11. Each of these bryozoans had more occurrences on brachial than on pedicle valves. *Atactotoechus* grew to large colonies, evenly distributed upon each valve, frequently crossing hinge axis, commissure, or both; whereas the original relationship may have been symbiotic, epitaphism is certain for those col-

onies which crossed the hinge axis or commissure. There is certainly no evidence that the *Atactotoechus* harmed its host, even by colony expansion. A death relationship is also highly probable for colonies which grew over *Hederella* and *Cornulites*. A commensal relationship is exhibited by one *Atactotoechus* colony which stopped growth along a major growth line.

? Leioclema and *Leptotrypella* show no concentrations on either valve. The former appears to have had similar life and death relationships to its hosts as those of *Atactotoechus*. One *Paraspirifer* had a colony of *? Leioclema* which grew around some sponge borings near the anterior edge of the host, and barely crossed the commissure; we would assume that the original relationship was commensal, and that the bryozoan colony died soon after its host. All colonies of *Leptotrypella* are small, so that no conclusion is possible on whether the host was alive or dead as they developed.

? ANNELIDA

Cornulites.-- This is the second most abundant genus (behind *Hederella*) of the epizoans studied. At least one cornulitid tube was present on 56% of the hosts. *Cornulites* is presumed to be a tube-forming annelid, because its remains resemble the calcareous tubes secreted by known marine tubicolous annelids, as described previously (Moore *et al.*, 1952; Morris & Rollins, 1971). Their larvae were dispersed by a free-swimming stage (Fisher, 1962). Although brachiopods were among the favored hosts, some annelids settled on gastropods, bryozoans, bivalves, nautiloids, and trilobites (Morris & Rollins, 1971). In the Silica Formation, *Cornulites* selected *Paraspirifer bowmockeri* as its favorite host, although rarely it is found on *Mucrospirifer*.

Nearly all *Cornulites* are oriented postero-anteriorly with the open end toward the line of commissure; each grew in a groove between two costae or created its own groove. Orientation of *Cornulites* has been noted by Schumann (1967), Hoare & Steller (1967), Morris & Rollins (1971), Thayer (1974), Richards (1974), and Kesling & Chilman (1975). All these

authors postulated life relationships between the cornulitid and its host, but three different relationships were proposed. Symbiosis was proposed by Morris & Rollins (1971) and by Thayer (1974), without distinction between mutualism (+ +) and commensalism (+ 0). A commensal relationship was proposed by Hoare & Steller (1967) for three *Cornulites* and their *Paraspirifer bownockeri* host. An ectoparasitic relationship was proposed by Schumann (1967), Richards (1974), and Kesling & Chilman (1975). In all three relationships, *Cornulites* benefited, at least in part from the feeding currents of its host, as evidenced by the orientation and distribution of the tubes. *Cornulites* showed selectivity by choosing a site for attachment along the anterior margin in the region of the host's inhalent currents (Richards, 1974).

A truly parasitic relationship seems to be the most acceptable for the *Cornulites* observed during our study. Fisher (1962) stated that cornulitid tubes grew, at least in part, by absorption of calcium carbonate from the host. This absorption, which must weaken the host's shell, together with the probable interception of food from the host's feeding currents, points towards parasitism.

Quite likely, *Cornulites* was not content with snatching food from the currents generated by the host but actually ate pieces of the host's mantle. Strong evidence exists that the worm extended itself from the tube to feast on edges of the mantle of both valves of the *Paraspirifer*. Only rarely is only one valve scarred at the site of the *Cornulites*; in most instances, the edges of both valves failed to grow locally beyond the end of the *Cornulites* tube, often resulting in a deep (more than 10 mm) indentation of the valve bearing the cornulitid and an equally deep matching indentation of the opposite valve. We can only envisage such scars as the product of exploitation of the brachiopod by a parasite, which actually attacked the two mantle edges for food. Mantle damage caused the valve and its counterpart to cease shell formation at one spot, and that spot invariably coincides with a furrow produced by *Cornulites*, nearly always with the tube of the parasite still in its life position. In no case does the *Cornulites* tube extend beyond the commissure onto the

opposite valve; nor is a *Cornulites* ever found directed toward the beak. We have noted one *Paraspirifer*, which obviously had regenerated shell margin after the death of the *Cornulites*; the end of the worm tube marked the position of sharp indentation and confluence of growth lines, and beyond it, the brachiopod had again resumed concentric growth bands.

Kesling & Chilman (1975, p. 195) described a *Paraspirifer bownockeri* with *Cornulites*:

The brachiopod here shows the scars of damage by three *Cornulites* below one corner; each of these tube-bearing worms fastened itself to the brachiopod on one valve with the open end of the tube along the plane of the brachiopod's commissure. From this vantage point, the worm feasted on the mantle edges of both valves of its host, retarding shell secretion at that place. As the brachiopod grew forward, so did the worm's tube -- keeping its feeding station available.

ANNELIDA

Spirorbis.-- This coiled worm tube is randomly distributed on *Paraspirifer* and, also in contrast to *Cornulites*, produced no scars on its host. It is present on numerous other hosts in the Silica Formation -- bryozoans, corals, other brachiopods, and trilobites. Although on bivalves, the genus *Spirorbis* has been reported to select areas beside inhalent currents (True-man, 1942) or exhalent currents (Ager, 1963) for attachment, the few found on *Paraspirifer* do not appear to support either of these preferences. The relationship was commensal, the worm using the brachiopod as a hard substrate.

Pyritized tube? -- A thin, 0.5 mm thick pyritized tube 27 mm long curves along one valve of a *Paraspirifer*. This thoroughly pyritized tube is similar to the one suggested by Kesling & Chilman (1975) to be remains of a worm (?).

PORIFERA

Small circular borings in *Paraspirifer* are thought to have been made by sponges dissolving their way into shell material (Hoare & Steller, 1967; Kesling & Chilman, 1975). Kes-

ling & Chilman did not identify them to genus. Rodriguez & Gutschick (1975) equated *Clionoides* with *Vermiforichnus*, borings presumably made by polychaete annelids. Because the borings in our material fit the original description of the genus *Clionoides* by Fenton & Fenton (1932), who indicated that they were probably caused by sponges, we have assumed in this paper that they were produced by boring sponges.

"*Clionoides*" was the third most abundant genus of epizoans, occurring on 53.8% of the hosts (table 3). Borings occurred in practically all locations on both valves. The number of borings exceeded 70 on some brachiopods. Borings, almost without exception, penetrated the shell parallel to the host's costae. Most openings of the borings occur along or very close to a particular pair of major growth lines, one on the brachial valve and the other in a corresponding position on the pedicle valve, creating matching "dotted lines" on the host. It must be presumed that the currents once brought in a large swarm of larvae of the boring sponges and that they almost simultaneously attacked the anterior edge of the shell. That the borings were harmful is indicated by the major growth lines formed along their site, marking an interval during which growth and/or feeding of the host was curtailed or suspended; but that their damage was not fatal is attested by the further growth of the brachiopod beyond the major growth line. Clearly, the occurrence of borings and major growth lines is a case of cause-and-effect, identifying the relationship as parasitic. The few borings randomly distributed on the host and not accompanied by major growth lines may have been made after the death of the host.

COELENTERATA

Aulopora microbuccinata.-- This colonial tabulate coral was much more abundant in our collection than indicated by Steller (1965). It was found on 14.4% of our sample of the population of *Paraspirifer*, more frequently on large hosts than small. The size distribution of the brachiopods studied may account for part of this discrepancy, since small hosts are few.

Aulopora occupied 6.4 times more locations on the brachial valve than on the pedicle

valve. Obviously, this species, like most living corals, preferred well-lighted conditions for its development. The distribution on left and right sides of each valve was nearly symmetrical. The fold had slightly higher concentrations of the coral than the rest of the brachial valve; similarly, the sulcus had higher concentrations on the pedicle valve, with many colonies extending to the commissure on some of the largest hosts.

Aulopora microbuccinata ranges from a single corallite to very large colonies. Even though many colonies grew as far as the commissure, few crossed it. Presumably, those corals which stopped at the commissure were symbiotic with the host. Many workers believe that attached corals benefited from food-bearing currents of their host (Yakovlev, 1926; Hecker, 1935; Shou-Hsin, 1959; Ager, 1961). Yakovlev (1926) and Shou-Hsin (1959) further suggested the relationship may have been mutualistic, with the brachiopod acquiring some protection by the coral's nematocysts. The relationship between *Paraspirifer bownockeri* and *Aulopora microbuccinata* could have been mutualistic, but we have some doubts about the benefits acquired by a coral on the exterior of the brachiopod's shell from currents generated in the vicinity of the commissure.

Not all *Aulopora* colonies exhibit evidence of life relationships with brachiopod hosts. Ager (1961), in a report of the epifauna on *Spinocyrtia iowensis*, stated that *Aulopora* only prospered on a large, fully adult host, one whose feeding currents could support the coral. Nevertheless, we can discover no tendency of coral colonies to have grown preferentially toward the commissure, where currents of the host would have been most effective. Furthermore, many *Aulopora* colonies continued to extend across their host long after its death, crossing the stilled commissure and far onto the opposite valve, and still produced corallites fully as robust as those in earlier portions of the colony.

Very recently, Pitrat & Rogers (1978) published a study of the auloporoid coral species *Aulocystis commensalis* as an epizoan on the Middle Devonian brachiopod *Spinocyrtia clintoni*

from the Traverse Group of Michigan. They found that, with very few exceptions, the first corallite settled in a median ditch in the fold, and that the colony developed more or less symmetrically toward the commissure and along it. They also recorded that 157 specimens had the coral on the brachial valve only, and just one had the coral on the pedicle valve only. Our brachiopod species lacks any ditch or furrow along its fold, precluding this site for easy attachment.

One large colony illustrated here almost completely covered its host, but there is no evidence that the *Aulopora* was in any way responsible for the death of the brachiopod. The only parts of this host not covered were small areas where it had lain on the substrate. The coral may have begun its growth while the host was alive -- we do not know -- but it continued unabated after the host died, extending from the brachial valve toward the bald areas on the pedicle valve and stopping only when available exposed area was fully utilized. This *Aulopora* outlived other co-inhabitants of the host and clearly established a death relationship by growing over *Hederella*, *Eliasopora*, and *Botryllopora socialis*.

BRACHIOPODA
Inarticulata

Phosphatic inarticulates.-- The chitino-phosphatic inarticulate brachiopods, *Lingulodiscina marginalis* and *Orbiculoidea doria*, were difficult to identify where incompletely preserved. Slightly less than half of the 75 individuals were identifiable (23 *Lingulodiscina* and 13 *Orbiculoidea*); the remainder were fragmentary or too poorly preserved (some were mere chitino-phosphatic chips) for identification. Neither of these brachiopods, nor the unidentifiable individuals, was concentrated in a particular area of the host's valves, but the brachial valve had four times as many chitino-phosphatic brachiopods as the pedicle valve. The high concentration of *Lingulodiscina* and *Orbiculoidea* on the brachial valve may indicate that most of them settled on *Paraspirifer* after

the host assumed the mechanically stable adult position, but whether the *Paraspirifer* was living or dead at the time of settlement is not evident. The relationship would have been either commensal or epiphytic.

Both *Lingulodiscina* and *Orbiculoidea* appear to have attached by their pedicles to the host. Hoare & Steller (1967) noted a specimen of *Paraspirifer bowmockeri* in certain areas of which colonies of *Hederella* had grown around the pedicle of inarticulates and became covered by the inarticulate during the process of compaction.

Calcareous inarticulates.-- The calcareous inarticulate brachiopods *Philhedra* and *Petrocrania* have better preservation than the chitino-phosphatic forms because of their more durable and less brittle composition. As a result, they were much easier to identify. Only six of the 28 individuals of *Philhedra* and *Petrocrania* could not be placed generically with confidence.

Pedicle valves of both genera were cemented to the host. Richards (1972) reported that *Philhedra* and *Petrocrania* preferred to attach to smooth shells. On our *Paraspirifer* specimens, the two genera are found near the beak, the smoothest area of the shell. On one host, a *Philhedra* covered an area of the pedicle valve near the beak and onto the interarea, but did not cross the hinge axis. In our opinion, all calcareous inarticulates lived as commensals, doing no harm to their host. Their cementation was firm, and several show clearly the images of the underlying costae of the host, even on their brachial (outer) valves.

Articulata

"*Mediospirifer audaculus*." -- Five of these brachiopods, ranging from 10 to 33 mm in width, are attached to five different hosts. Four of these "*Mediospirifer*" epizoans are located in the sulci of large hosts and are oriented with their brachial valve uppermost (three are tilted at an angle) when the host rests on its pedicle valve. "*Mediospirifer*" may have at-

tached to a live host, preferring a position off the substrate in order to be higher in the food-bearing water currents. One individual may have inadvertently limited its own growth, and eventually its life, by attaching in the host's sulcus too close to the commissure, where the curve of the sulcus made further growth impossible; this individual grew only to 10 mm width.

We suppose the relationship to have been commensal, with the "*Mediospirifer*" gaining an advantage by attachment and the host *Paraspirifer* unaffected, although we note that the large "*Mediospirifer*" by its size and weight may have placed an extra burden on the host's operation of its valves for respiration and feeding purposes.

The only "*Mediospirifer*" not attached in a sulcus is located in a highly deformed area of its host near the commissure. This individual may have had its life curtailed by growth (repair?) of the damaged area by the host. If the *Paraspirifer* was indeed dead before the epizoan "*Mediospirifer*" settled, then the latter was limited in growth by the shape of the deformity in which it attached.

Cyrtina "hamiltonensis." -- In our sample, we have only one specimen of this epizoan, and little can be deciphered from its position. We have seen another *Paraspirifer*, not part of our collection, on which numerous small *Cyrtina* specimens are scattered over the lateral surface of the brachial valve of the *Paraspirifer* host, apparently from one spat-fall.

ECHINODERMATA

Holdfasts.-- Very small holdfasts, presumably of crinoids, are attached to 42 hosts, more on the brachial than on the pedicle valves. Those on the brachial valves are rather widely distributed with a favored spot on each side of the fold (tables 4, 6) and none on a small area around the beaks. Those on the pedicle valves are concentrated along the anterior margin of the sulcus (tables 5, 7), an area which would have been off the substrate both in young and adult hosts.

Paraspirifer with holdfasts had a greater diversity of epizoans (mean = 4.8 different epizoans per host) than those without holdfasts (mean = 3.2 different epizoans per host). In particular, holdfasts had more co-occurrences with "*Clionoides*," *Aulopora*, and *Eliasopora* than can be explained by chance. These associations are discussed below.

Why none of these holdfasts reached any greater size we do not know. One might expect that, if these are actually holdfasts, on one or more of the 42 hosts bearing them at least one holdfast would have reached a size sufficient to support a column and crown of the common crinoids present in the same beds, such as *Arthroacantha carpenteri* (Hinde). That all of the holdfasts remained small may mean that: (1) they belong to large crinoids that detached early in ontogeny and drifted out of the vicinity, (2) they belong to small micro-crinoids that have not been discovered, or (3) they belong to other kinds of invertebrates.

PROBLEMATICA

Organic threads.-- We suspect that these pyritic structures are bryozoans, perhaps of a ctenostome that either lacked vesicles or whose vesicles were not preserved. On the 23 *Paraspirifer* hosts having such structures, they occur nearly as often on the pedicle valve as on the brachial valve. Some of the threads crossed other epizoans, presumably after they were dead. These need further study.

Minute pits.-- One occurrence was found of a compact group of a few hundred minute pits, each circular to oblong in outline, within a four square millimeter area on one host. The pits may have been caused by boring sponges, an alga or fungus, sabellid worms, or hold-fast papillae of a brachiopod pedicle (Bromley & Surlyk, 1973).

Deformities.-- Although these are not epizoan in our opinion, they do show relationships of other organisms to *Paraspirifer*. We conclude that these deformities are direct evidence of predation by a fish.

At least ten *Paraspirifer* specimens have

a similar type of deformation near the interarea and involving both valves. One valve has an indentation or puncture, and the opposite valve has a corresponding bump, or sharply raised spot. Growth lines continue across the pushed-out spot and are distorted in the indented area. Inasmuch as the rest of the valve is unaffected, the deformation must have occurred elsewhere than at the margin of the growing valves. It appears that some object punctured or dented one valve with considerable force and pushed against the interior of the other valve, thrusting a section of that valve outward. Evidently, the host was alive at the time of attack and survived for a time, for the puncture has been covered by additional shell material.

The most likely candidate which could have caused this deformity in *Paraspirifer* was a large fish with a sharp pointed tooth. The rhipidist crossopterygian *Onychodus* was such a fish and has been identified in the Silica Formation from teeth and scales. Crossopterygians were basically predatory fish (Moy-Thomas, 1971). Why they would bite into a *Paraspirifer bowmockeri* is uncertain. Perhaps the pedicles of brachiopods offered available flesh, and the fish became accustomed to biting off these connections between the brachiopod shell and the substrate; whereas the biting of adult *Paraspirifer* would have soon proved to be an error, such an error would be understandable. Or perhaps the crossopterygians fed on all sorts of bottom-dwelling organisms, and the brachiopods were bitten incidentally as part of the benthos. Or perhaps the fish were actively pursuing darting prey, which dodged behind the brachiopods and the latter were punctured by accident. The presence of ten damaged specimens of *Paraspirifer* in a sample of 586 might argue against the attacks being purely accidental in nature.

Relationships Between Epizoans

Eliasopora stellatum and *Aulopora microbuccinata*.-- These species, a colonial bryozoan and a colonial coral, occurred together twice as often as they would have been associated by chance, based on the numbers of each in the total sample (table 10). This seems to us to show exceptional influence of some factor or

factors to promote the co-habitation of the same host by these species. Perhaps the factor was non-biologic, and conditions of the host shell which favored colonization by the bryozoan also favored colonization by the coral. Neither species consistently preceded the other. On some hosts, *Eliasopora* was found to have grown over *Aulopora* but on other hosts *Aulopora* was found to have grown over *Eliasopora*. Possibly, the bryozoan had greater mortality wherever it did not benefit from the protection afforded by the stinging cells of the coral, and thus had far above average association with it.

"*Clionoides*" and major growth lines of the host.-- As we interpret this greater-than-chance association, the "*Clionoides*" is the cause and the major growth line is the effect. Some hosts have so many borings along a major growth line that the shell appears to have a matched pair of perforated lines, one on each valve. At least 154 hosts had at least one or more major growth lines, and of these 148 are clearly associated with the borings. The major growth line marks an interval of cessation of growth by the brachiopod, which appears to have resulted directly from the parasitic borings. In other words, we think the cessation came immediately after the damage to the shell, rather than that the damage to the shell occurred always during a quiescent period of growth.

Hoare & Steller (1967, p. 296) reported this condition on another specimen of this brachiopod and stated that

... the host may have been secreting additional shell material internally to seal off the borings or may have been having difficulty in opening the valves for feeding.

None of the infestations by boring sponges proved fatal to the brachiopod host. All specimens of *Paraspirifer bowmockeri* we have seen possess normal shell growth beyond the line of perforations. Kesling & Chilman (1975, p. 212) in describing one example said

In early maturity, this brachiopod was the victim of a swarm of boring sponges, which left a row of perforations along the edge of its shell and drilled deeper into the shell material; the brachiopod recovered and grew to its present size.

In reference to another specimen, they remarked (1967, p. 215)

The dotted line of perforations left by the sponges outlines the edges of the two brachiopod valves at the time of the infestation. The margin of the shell shows that the brachiopod nearly ceased growth for a period of time, and then just before its death began a rejuvenated extension of the valves.

"*Clionoides*" - *Aulopora* - *Eliasopora* - major growth line associations.-- As emphasized in table 15, all possible pairings of these three species and major growth lines show a much higher number of co-occurrences than would result by chance. It would appear, therefore, that no one factor of the four was the overwhelming influence responsible for all the high values. If, as we have proposed above, the "*Clionoides*" borings were the direct cause of most (148 of 154) of the major growth lines, then we need only consider here the co-occurrences of *Aulopora microbuccinata*, *Eliasopora stellatum*, and major growth lines.

Some evidence can be arrayed to support the thesis that condition of the host brachiopod was a strong element in attracting exceptional numbers of *Aulopora* and *Eliasopora*. *Paraspirifer* specimens with major growth lines had a greater diversity of different epizoans (mean = 3.9 taxa) than those without major growth lines (mean = 3.1 taxa). For the brachiopods having "*Clionoides*" associated with the coral *Aulopora* and/or the bryozoan *Eliasopora*, we have found no way to determine the precise order of original settlement. It is possible that after an infestation of "*Clionoides*" along the shell edges, the brachiopod victim slowed or even temporarily ceased the opening-and-closing movements of its valves, and that this quiet interval of the host made settlement much easier for the epizoan larvae, including *Aulopora* and *Eliasopora*.

A different explanation concerns the breeding seasons of the epizoans. If the invertebrates of Middle Devonian time were like those of today, different animals had somewhat different breeding seasons. Hence, swarms of larvae released at one interval might have belonged to one group of species, whereas those

released later in the year might have belonged to different species. If then the young of the sponge "*Clionoides*," the coral *Aulopora microbuccinata*, and the bryozoan *Eliasopora stellatum* happened to hatch and be released into the sea water at nearly the same time, they would have been borne on the same currents and have the same opportunity to settle on the same set of hosts. Therefore, their co-occurrences on the brachiopod hosts would be much higher than by chance and much higher than their co-occurrences with species having a different reproductive season.

Hederella - *Aulopora* - *Eliasopora* - *Cornulites* associations.-- As shown in table 16, the frequently occurring species of *Hederella* have lower than chance co-occurrences with *Aulopora*, *Eliasopora*, and *Cornulites*: averages of 0.79 for the "*Hederella canadensis*" group, 0.77 for *H. thedfordensis*, and 0.80 for *H. filiformis*. Nevertheless, certain specific differences occur; "*Hederella canadensis*" particularly does not occur with *Eliasopora* (although *H. thedfordensis* does), *Hederella thedfordensis* does not occur with *Cornulites* (although the other *Hederella* taxa do), and all show low associations with *Aulopora*.

Inasmuch as *Aulopora* and *Eliasopora* have exceptionally high co-occurrences (table 15), we might suppose the reproductive climaxes came in the following series: (1) *Aulopora* and *Eliasopora*, (2) *Cornulites*, "*Clionoides*," "*Hederella canadensis*," and *Hederella filiformis*, and (3) *Hederella thedfordensis*. In this scheme, the currents of a particular season would probably bring larvae in greater numbers to a particular part of the *Paraspirifer* colony, somewhat different from the part settled by epizoans arriving in earlier or later seasons. This would explain the observed frequencies of co-occurrences.

It is within the realm of possibility that the presence of the coral *Aulopora* inhibited colonization by the bryozoan *Hederella*, perhaps because the stinging cells were lethal, or that established colonies of *Hederella* ate, attacked, or repelled the larvae of the coral. We consider the differential breeding seasons to be, at this time, a better explanation.

Table 15 -- Epizoan pairs occurring on same host with high frequency (compared to chance).

EPIZOAN	"Clionoides"	<i>Aulopora microbuccinata</i>	<i>Eliasopora stellatum</i>	Major growth lines
"Clionoides"	--	1.69	1.50	1.78
<i>Aulopora microbuccinata</i>	1.69	--	2.00	1.82
<i>Eliasopora stellatum</i>	1.50	2.00	--	1.29
Major growth lines	1.78	1.82	1.29	--
Averages	1.66	1.84	1.60	1.63

Holdfasts - "Clionoides" co-occurrences.-- A strange high association is the one between holdfasts and boring sponges. Of the 42 *Paraspirifer* specimens having holdfasts, 38 are associated with "Clionoides" (table 8). With no indication as to which was the earlier settler, we cannot explain this co-occurrence except as a possible coincidence of breeding seasons of the two.

General remarks on co-occurrences, reproduction, paleosynecology, and currents.-- We have suggested some possible explanations for co-occurrences of epizoans much more frequently than by chance or much less frequently. In general, explanations may be grouped as (1) biologic interactions of organisms in the community (paleosynecology), (2) seasonal reproductive cycles, and (3) dissemination of local epizoan populations.

First, epizoans may have affected or have been affected by the biologic processes of other epizoans on the same *Paraspirifer* host. The interactions of living organisms are very complex, wherein one factor in the physiology or ecology of one species may attract or repel another species. The interpretation of paleosynecology, dealing with extinct animals, may

have more speculation than foundation. We are dealing here with fossil records of settlement, survival, and successful development of epizoans upon both living and dead hosts. It is doubtful that we would recognize remains (if preserved) of any epizoans which died or were destroyed soon after settlement. In other words we are studying only the successful co-inhabitants of the same host, sometimes with no evidence on whether the two epizoans of a pair were alive at the same time. It becomes very difficult to affirm or deny that the life processes of one did not affect those of the other, for better or for worse. Inasmuch as every species of a co-occurring pair was also found to occur independently, we can say definitely that no epizoan studied was completely dependent upon another. The possibility remains that some epizoans may have been beneficial or harmful to others in close proximity for reasons that are not obvious from the fossil record.

Second, the co-occurrences greater or less than chance may have been the result of seasonal reproductive cycles. If larvae of two species of epizoans were released almost simultaneously from a breeding ground, they would have been carried together by the prevailing

Table 16 -- Some species of *Hederella* paired with other epizoans on same host and occurring together with low frequency (as compared to chance).

<i>Hederella</i> species or group	<i>Aulopora microbuccinata</i>	<i>Eliasopora stellatum</i>	<i>Cornulites</i>	Averages
" <i>Hederella canadensis</i> "	0.76	0.65	0.96	0.79
<i>Hederella thedfordensis</i>	0.57	0.97	0.78	0.77
<i>Hederella filiformis</i>	0.65	0.81	0.94	0.80
Averages	0.66	0.81	0.89	

currents and would have passed over parts of the *Paraspirifer* grounds in about equal concentrations. The odds of larvae of the two epizoans settling together on the same brachiopod under such conditions would have been greatly increased above chance. Similarly, the chances of the larvae of a later season being carried by the same currents to the same host in the same concentration were probably greatly diminished, for location of breeding grounds could have differed and currents could have shifted.

Third, the unusual associations may be almost entirely artifacts of original chance settlements and reproductive spread to nearby hosts. For example, if one *Paraspirifer* was settled by the coral *Aulopora* and the *Paraspirifer* adjacent to it was settled by the bryozoan *Eliasopora*, one might expect that when the coral and bryozoan matured, their offspring would colonize nearby hosts together in greater than normal numbers. Conversely, if the first *Hederella* into the area happened to settle on a *Paraspirifer* near one edge of the host colony and far away from the *Aulopora*-bearing *Paraspirifer*, then the diffusion of the two epizoan species might produce fewer co-occurrences than would be expected by chance.

CONCLUSIONS

The 586 well-preserved *Paraspirifer bowmockeri* specimens used in our study, or at least the majority, are presumed to have come from a narrow stratigraphic interval in the lower half of the Middle Devonian Silica Formation in a small quarried area in Lucas County, Ohio. Epizoans were present on 582 of these brachiopods. No crushed specimens (lacking a pyritized core) were used.

Life or death associations between epizoans and hosts can be determined only for a minority of occurrences. The only epizoan that showed possible mutualism, whereby both epizoan and host benefited, is the colonial coral *Aulopora microbuccinata*; by its stinging cells, the coral may have afforded a degree of protection to its host, while receiving anchorage for its colony. Most other epizoans appear to have had a commensal relationship with *Paraspirifer*, benefiting from the solid foundation provided by

the brachiopod host and having no effect upon it by their settlement and growth. Parasitism is exemplified by two epizoans: "*Clionoides*," presumed to have been a boring sponge, and the tubicolous worm *Cornulites*. Most borings made by the presumed sponge are located along matching major growth lines, one on each valve, indicating an infestation along the shell edges followed by an interval of slowed or halted growth by the host; none of the boring attacks proved fatal to the *Paraspirifer*, as attested by its recovery and further growth. *Cornulites* maintained the opening of its tube along the commissure edge of its host, at a spot marked by an indentation in each valve; quite evidently, the worm ate or injured the mantle edges in its proximity, causing the host to halt shell secretion at that place while the valves grew forward along the remainder of the commissure. Shell damage ascribed to bites of fish may indicate some kind of attempted predation, possibly the eating of the soft brachiopod pedicle; the exploitation was incomplete, inasmuch as the *Paraspirifer* specimens show evidence of shell repair. Numerous examples of epitaphism are noted, wherein epizoans grew across hinge and commissure after the brachiopod was dead; whether the epizoans settled before or after the death of the host is unknown.

Epizoans are unequally represented on the *Paraspirifer* sample studied, both in the number of hosts and in the areas covered. Six of every seven hosts carried at least one species of the highly successful bryozoan genus *Hederella*. The common species *Hederella thedfordensis* occupied nearly one-third of the grid locations having epizoans. Other *Hederella* species are fairly common epizoans, as are bryozoans of the Ctenostomata. The parasitic worm *Cornulites* was the second most abundant epizoan in terms of hosts affected, being present on over half of the brachiopods. Bryozoans of the Cystoporata and Trepostomata-Cryptostomata were fairly rare. Attached brachiopods, including inarticulate and articulate kinds, were present on less than 8% of all hosts.

More grid locations had epizoans on the brachial valve than on the pedicle valve, presumably because the brachial valve was uppermost in the stable adult position assumed by

Paraspirifer after atrophy of the pedicle. On each valve the left side had more occupied grid locations than the right; this we postulate may have resulted from the slipstream of currents approaching adult brachiopods from the side and bearing larvae and spat of epizoans. Colonial epizoans such as the coral *Aulopora* and the bryozoans maintained the basic bilateral asymmetry of other epizoans in their distribution, but extended onto areas of the host that were less favorable for settlement. Epizoans were concentrated in patterns which followed the shape of the anterior edge of the hosts, presumably reflecting the nearly vertical fall-out of colonizing epizoans. Density distribution of epizoans indicates that the adult stage of the *Paraspirifer* may have been delayed until the valves attained dimensions of 70 mm as measured along the sulcus.

Co-occurrences on the same host are exceptionally high for pairs of *Aulopora microbuccinata*, *Eliasopora*, and "*Clionooides*." These high numbers, far above chance values, may indicate that one or another of these epizoans could have in some way favored settlement of the others. We suggest that such associations might have been promoted by concurrences of the breeding seasons of the three epizoans, or that spread from local epizoan population centers in close proximity might have produced exceptionally high numbers of co-occurrences. Conversely, *Hederella* has exceptionally low co-occurrences with *Aulopora*, *Eliasopora*, and the worm *Cornulites*. These fewer-than-chance associations could possibly be the result of one epizoan, by some biologic action, inhibiting the settlement of others; we suggest that the infrequencies could have logically been brought about by different breeding seasons, whereby different currents distributed larvae of *Hederella* than those which carried the settlers of the colonial coral *Aulopora*, the creeping stoloniferous bryozoan *Eliasopora*, and the parasitic worm *Cornulites*.

We consider 582 *Paraspirifer bowmockeri* to be an adequate sample of its population for studying the number, coverage, and distribution of its epizoans. Interpretation of life or death associations remains unanswered or equivocal for many specimens. Nevertheless, care-

ful and accurate observations of a large number of fossils, combined with persistent curiosity and thorough understanding of the morphology, life history, and ecology of their closest living relatives -- these hold the potential of disclosing how the extinct species functioned, their population structure, their degree of dependence upon environmental factors, and their interactions with other organisms in their community.

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PLATES

EXPLANATION OF PLATE 1

[Plate 1 on page 57]

All figures natural size

- FIG. 1 -- UMMP 63138, brachial view. The right side of the brachial valve bears an irregular colony of the tabulate coral *Aulopora microbuccinata*, which extends to the commissure but does not cross over onto the pedicle valve; this indicates that the coral and brachiopod had a life relationship. On the right side of the brachial valve near the junction of the fold and lateral surface are two small holdfasts, one with tiny columnals still attached. A notch in the commissure just to the right of the holdfasts was caused by the parasitic worm *Cornulites*, whose wrinkled and finely striate tube lies there half embedded; the coral has grown over the distal part of the worm's tube, showing later occupancy of that spot. See enlargement on plate 20, fig. 4.
- FIG. 2 -- UMMP 63121, anterior view. A small specimen of the articulate brachiopod "*Mediospirifer audaculus*" is attached by its interarea to the fold area of the host's pedicle valve near the commissure. There, further growth of the epizoan appears to have been inhibited by the curvature of the fold and the proximity of the commissure. Borings of the sponge "*Clionoides*" are concentrated along a major growth line near the commissure on both valves. See enlargement of the attached brachiopod on plate 7, fig. 1.
- FIGS. 3, 4 -- UMMP 63166, posterior and brachial views. Colonies of the tabulate coral *Aulopora microbuccinata* are scattered on the brachial valve but do not extend onto the pedicle valve. The right cardinal area of the pedicle valve has a small blanket of the trepostome bryozoan ? *Leioclema*. The left side of the brachial valve and the opposing side of the pedicle valve were crushed, possibly by the bite of a crossopterygian fish. Notches just below the right cardinal corner of the brachial valve mark injuries caused by three individuals of the parasitic worm *Cornulites*, two of which left tubes on the pedicle valve and one on the brachial valve. A few scattered borings of the parasitic sponge "*Clionoides*" can be seen on the right side of the brachial valve. Small, probably aborted, colonies of an unidentified species of the cyclostome bryozoan *Hederella* are found in small patches on both valves. See enlargements on plate 10, fig. 5, and plate 21, fig. 2.
- FIG. 5 -- UMMP 63154, brachial view. Colonies of two species of the cyclostome bryozoan *Hederella* are spread on the brachial valve, *Hederella delicatula* on the right side and *Hederella filiformis* on the left. *Hederella delicatula* branches more frequently and its zooecia are thinner and somewhat shorter than those of *H. filiformis*. At the right side of this valve, a tube of the parasitic worm *Cornulites* is itself covered completely by a colony of an unidentified species of *Hederella*. Two other *Cornulites* tubes, close set at the left side, have no associated bryozoans. See enlargements on plate 7, fig. 2, and plate 21, fig. 1.
- FIG. 6 -- UMMP 63139, brachial view. A colony of the cyclostome bryozoan *Hederella concinnoidea* is attached on the left-central part of the brachial valve. In this species, the zoarium is delicate, with frequent (about 2 1/2 mm intervals) branching from a tubular axis; both budding and branching take place at angles of about 60°. Small notches at the sides mark mantle damage by young specimens of the parasitic worm *Cornulites*, some tubes of which are attached on the brachial valve and some on the pedicle valve, but all are oriented with the open end along the commissure of the host. See enlargements on plate 10, fig. 3, and plate 20, fig. 5.
- FIG. 7 -- UMMP 63175, brachial view. Two holdfasts are situated on the left side of the brachial valve. Except for a few borings of the parasitic sponge "*Clionoides*," this *Paraspirifer* is exceptionally free of other epizoans. See enlargement on plate 10, fig. 6.
- FIGS. 8, 9 -- UMMP 63128, brachial and pedicle views. A large colony of the trepostome bryozoan *Atactotoechus* cf. *typicus* blankets nearly all of the brachial valve and continues onto the pedicle valve without interruption, where it covers all except a small left-central area. On the left side of the brachial valve, *Atactotoechus* covered over an earlier occupant of the host *Paraspirifer*; the circular shape suggests that it may have been a species of the inarticulate

[Explanation of Plate 1 cont'd]

brachiopod *Philhedra*, but we cannot be certain. The pedicle valve also bears a small colony of *Hederella*, edges of which are overgrown by the *Atactotoechus*. See enlargements on plate 7, fig. 4; plate 10, fig. 2; and plate 20, fig. 2.

FIG. 10 -- UMMP 63149, brachial view. A large specimen of the inarticulate brachiopod *Petrocrania hamiltoniae* is attached on the right side of the brachial valve of this *Paraspirifer bownockeri*, its outer surface in part reflecting the configuration of the host's costae. On the *Petrocrania*, the concentric growth lines overshadow the radial costellae. On the left side of the same valve is a colony of the tabulate coral *Aulopora microbuccinata* which stopped abruptly at the commissure, an indication that the brachiopod host and the coral lived at the same time. A few small borings attributed to the sponge "*Clionoides*" are present, but their parasitic infestation did not, in this case, result in formation of a major growth line by the *Paraspirifer bownockeri*. See enlargement on plate 7, fig. 7.

FIG. 11 -- UMMP 63141, brachial view. The inarticulate brachiopod *Philhedra stewarti* is attached on the left half of the brachial valve of the host, faithfully reproducing the shapes of the costae of the *Paraspirifer* even on its outer valve. The small ctenostome bryozoan present on this valve is classified as *Ascodictyon floreale*. Some organic threads on the fold and right lateral areas are probably stolons of a ctenostome bryozoan. See enlargements on plate 10, fig. 4, and plate 20, fig. 6.

FIGS. 12, 13 -- UMMP 63133, brachial and anterior views. This large *Paraspirifer bownockeri* has colonies of the cyclostome bryozoan *Hederella* in the posterocentral and the right anterior areas of the brachial valve and along the anterior margin of the pedicle valve. Most of the left side of the brachial valve and some distal areas of the pedicle valve are thickly populated with the ctenostome bryozoan *Eliasopora stellatum*, with typical radiating clusters of vesicles connected by filamentous stolons. Here and there are a few specimens of another ctenostome bryozoan, *Ascodictyon radians*. A few borings along a major growth line near and subparallel to the commissure are attributed to the sponge "*Clionoides*." Tiny moundlike holdfasts are scattered within the area of the *Eliasopora* colony, some with a few minute columnals still attached. See enlargement on plate 20, fig. 3.

EXPLANATION OF PLATE 2

[Plate 2 on page 58]

All figures natural size

- FIGS. 1, 2 -- UMMP 63186, brachial and side views. *Paraspirifer bownockeri* specimen damaged at the left side, probably by bites of a fish, and at the right side by the parasitic worm *Cornulites*, which fed upon the mantle edges of both valves. One of the *Cornulites* tubes was itself damaged, possibly by a boring sponge. Small dark lines set at varying angles in the right side of the fold and adjacent areas are flush with the surface of the *Paraspirifer* and become invisible under a light coating of sublimated ammonium chloride; they are identified as *Ropalonaria tenuis*, a ctenostome bryozoan. A few small colonies of the cyclostome bryozoan *Hederella* are scattered on both valves. See enlargements on plate 11, figs. 1, 2, and plate 21, figs. 4-6.
- FIGS. 3, 4 -- UMMP 63200, brachial and side views. The brachial valve of this *Paraspirifer* bears a well-developed colony of the cyclostome bryozoan *Hederella concinnoides*; in contrast, the pedicle valve is completely free of bryozoans. Another colony of *Hederella concinnoides* is present on UMMP 63139, shown in plate 1, fig. 6; plate 10, fig. 3; and plate 20, fig. 5. Marginal notching of the shell in this brachiopod were made by the parasitic worm *Cornulites*, which ate on the mantle edges of both valves for an extended time. See enlargements on plate 9, fig. 3, and plate 22, fig. 3.
- FIGS. 5, 6 -- UMMP 63202, side and brachial views. This brachiopod was extensively damaged on one side of both valves, presumably by a large fish with elongate teeth, but recovered to repair the shell. In the deformed area, a young articulate brachiopod "*Mediospirifer audaculus*" attached by its interarea and appears to have grown as far as possible within the sunken and deformed area; perhaps its unfortunate settlement there predetermined its short life span. Extensive borings on and in the sulcus and adjacent areas of the pedicle valve and in the anterior area of the brachial valve were probably made by a boring sponge and are in our study attributed to the genus "*Clionoides*." However, these borings are larger and more extensive than most found in *Paraspirifer bownockeri*, and are not concentrated along a major growth line. The cyclostome bryozoan present is *Hederella thedfordensis*, one of the more robust species of its genus. See enlargements on plate 8, figs. 8, 9, and plate 22, figs. 1, 2.
- FIGS. 7, 8 -- UMMP 63276, side and brachial views. *Paraspirifer bownockeri* bearing the cystopore bryozoan *Botryllopora socialis*, the ctenostome bryozoan *Ascodictyon fusiforme*, and the tabulate coral *Aulopora microbuccinata*. On the left side of the fold near the anterior margin, the rare flower-like *Botryllopora* is partly overgrown by vesicles of the *Ascodictyon*. Some corallites of *Aulopora* also have *Ascodictyon fusiforme* on their thecal walls and even in their apertures, proof that the ctenostome bryozoan *Ascodictyon* was the last to colonize these areas and likely the last to colonize the host. At some contacts, *Botryllopora* appears to lap onto the corallites of *Aulopora microbuccinata*, indicating that the latter was the pioneer settler on this brachiopod. See enlargements on plate 22, figs. 5, 6, and plate 23, fig. 4.

[Explanation of Plate 2 cont'd]

FIGS. 9-12 -- UMMP 63146, posterior, brachial, anterior, and pedicle views. A dense colony of the tabulate coral *Aulopora microbuccinata* extended its coverage from the brachial valve onto the pedicle valve after the death of the *Paraspirifer* host, crossing both the commissure and the hinge. The coral-free central area of the pedicle valve was presumably the area of the brachio-pod in contact with the substrate in the stable adult position. See enlargement of the posterior area on plate 10, fig. 1.

EXPLANATION OF PLATE 3

[Plate 3 on page 61]

All figures natural size

FIGS. 1, 2 -- UMMP 63307, brachial and anterior views. The brachial valve bears a conspicuous colony of the tabulate coral *Aulopora microbuccinata* and an excellent settlement of the ctenostome bryozoan *Ascodictyon fusiforme*. In at least one place, vesicles of the *Ascodictyon* extend onto the corallite wall of the *Aulopora*, showing that the bryozoan was, at that spot, the later colonizer. [For epizoans which form colonies after settlement, it is seldom possible to determine which of two was the earlier settler on the host, inasmuch as both species can extend freely onto other areas. We find no evidence that any epizoan grew over another while the latter was alive.] Parasites attacked the brachiopod, including two infestations by the boring sponge "*Clionoides*" and continued mantle damage near one corner by the worm *Cornulites*. See enlargements on plate 9, fig. 6, and plate 23, figs. 5, 6.

FIGS. 3, 4 -- UMMP 63320, brachial and anterior views. Borings of the parasitic sponge "*Clionoides*" are concentrated along a major growth line on each valve of the host. Because these lines are equidistant from the commissure edge, we have presumed that the sponge infestation occurred along the shell edges when the brachiopod had attained that size. A colony of the cyclostome bryozoan *Hederella* cf. *H. michiganensis* extends from the brachial valve, over the commissure, and onto the pedicle valve, obviously concluding its extension after the death of its host.

FIG. 5 -- UMMP 63300, brachial view. On the brachial valve, the cyclostome bryozoan *Hederella* is represented by two species, *Hederella thedfordensis* at lower left and *Hederella filiformis* at center and right. The different sizes of zooecia are apparent. An area at the right anterior margin is covered by the trepostome bryozoan *Leptotrypella* sp. The *Leptotrypella* colony appears to skirt the edges of a boring by the parasitic sponge "*Clionoides*" but no part of it extends into the hole, which may be interpreted as evidence that the sponge was living when the bryozoan colony extended part way around its opening. None of the colonies extend onto the pedicle valve. See enlargements on plate 7, fig. 3; plate 16, fig. 6; and plate 23, figs. 1, 2.

FIG. 6 -- UMMP 63332, brachial view. The brachial valve shown here has well-developed colonies of the commensal cyclostome bryozoan *Hederella rugosa*, all of which terminate abruptly at the commissure. Many of the zooecia of this bryozoan show the characteristic "corrugated" rugosity of the walls. See enlargement on plate 23, fig. 3.

FIG. 7 -- UMMP 63271, brachial view. Notches along the commissure edge are scars produced by the parasitic worm *Cornulites*. As typical, the early stages of tube secretion by the worm were in radial grooves of the host, and the tube was extended in the direction of bordering costae at the same rate as the growth of the host. In this manner, the *Cornulites* maintained its opening just at the edge of the *Paraspirifer* shell, so that it could continuously feed upon the mantle of its host. See enlargement on plate 7, fig. 8.

FIGS. 8, 9 -- UMMP 63310, brachial and anterior views. This *Paraspirifer bownockeri* is slightly crushed, probably due to incomplete pyritization within the shell. Both of its valves have colonies of the cyclostome bryozoan *Hederella*, which we classify as *Hederella filiformis*, even though the development is not typical. The inarticulate brachiopod *Lingulodiscina marginalis* attached in the fold near the anterior edge of the pedicle valve when the host was nearly or quite full grown, and apparently grew beyond the commissure so that its distal margin was free. Well-developed tubes of the parasitic worm *Cornulites* extend to the commissure, filling self-deepened furrows in the host's shell. See enlargements on plate 14, figs. 4-6, and plate 6, fig. 11.

PLATE 1

[Explanation of this plate on pages 52, 53]

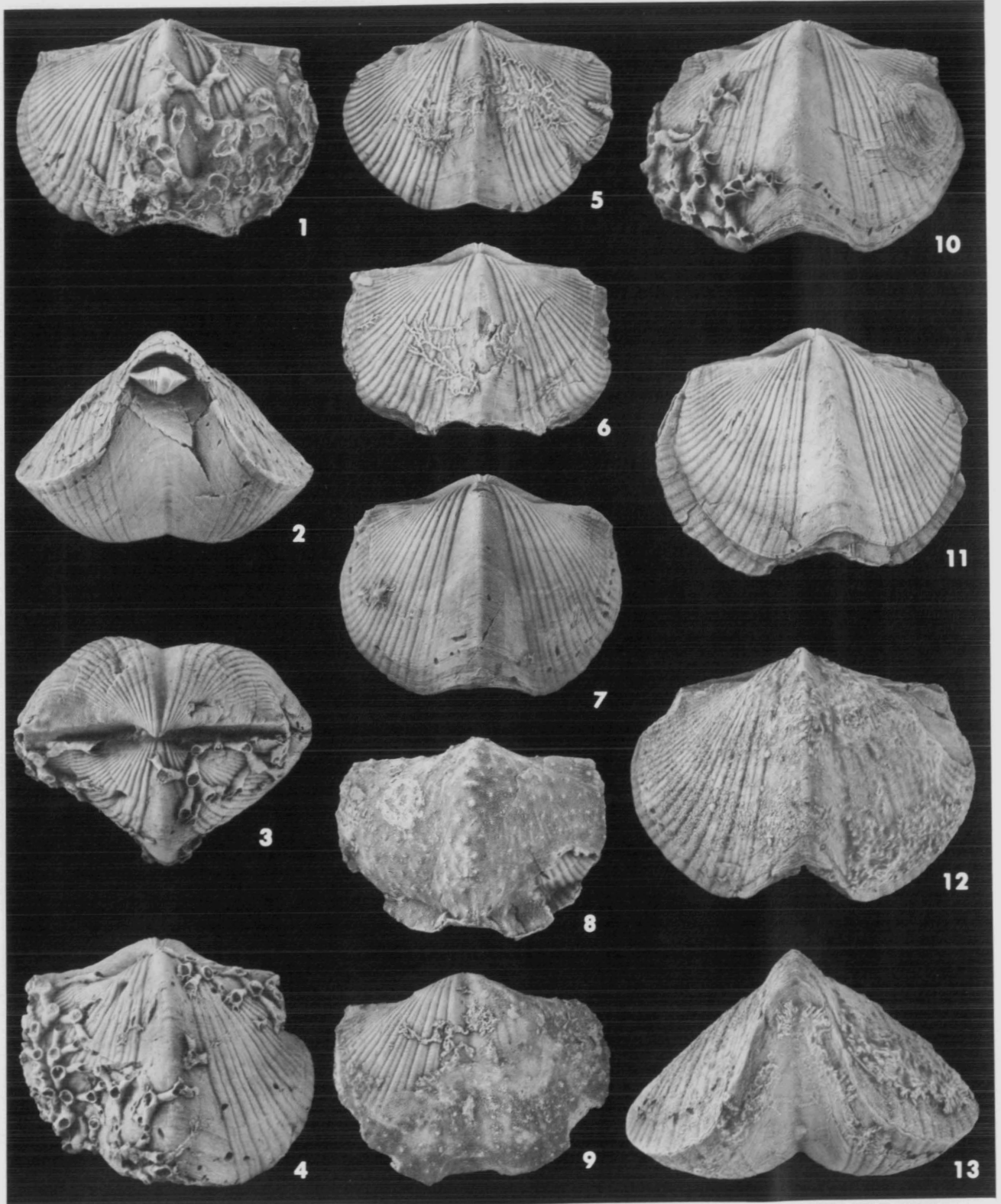
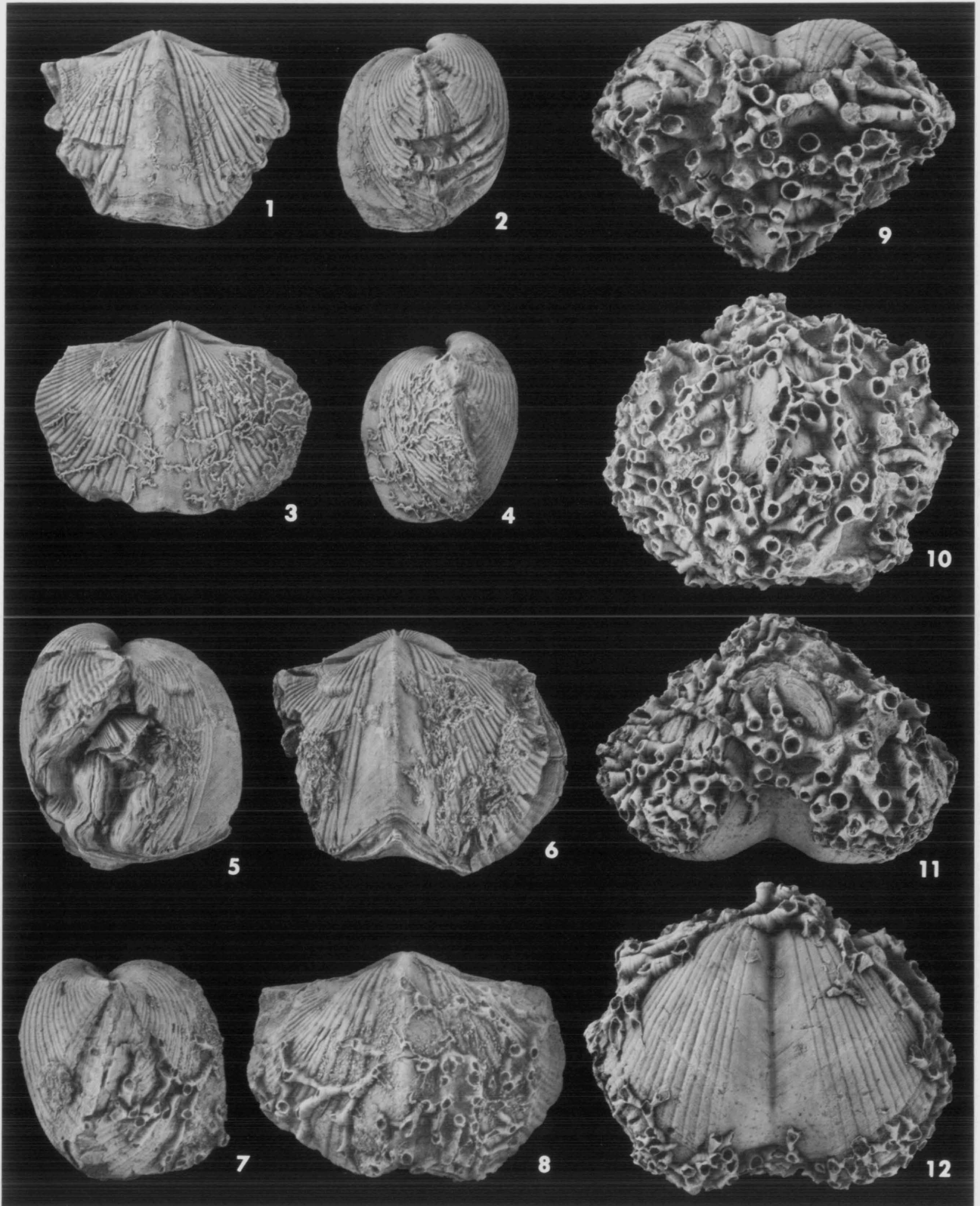


PLATE 2

[Explanation of this plate on pages 54, 55]



[Explanation of Plate 3 cont'd]

FIG. 10 -- U MMP 63188, brachial view. *Paraspirifer bownockeri* with valves slightly dislocated posteriorly, bearing an excellent colony of the cyclostome bryozoan *Hederella concinnoides* on the right side of the brachial valve. Other examples of *Hederella concinnoides* can be seen on U MMP 63139 (pl. 1, fig. 6; pl. 10, fig. 3; pl. 20, fig. 5) and U MMP 63200 (pl. 2, fig. 3; pl. 9, fig. 3; pl. 22, fig. 3). See enlargements of this specimen on plate 9, fig. 1, and plate 22, fig. 4.

FIGS. 11, 12 -- U MMP 63336, side and pedicle views. The pedicle valve has a long string-like pyritized structure which was undoubtedly organic. It may have been the tubular housing of a thin worm, or it could even have been the body itself of a very thin worm. Because part of the structure appears to have been partly embedded in the shell material of the host, one might believe that it was secreted in place, perhaps a thin-walled housing for a worm, the substance of which later dissolved away to leave a cast of the interior. It is within the realm of possibility that the structure is a preserved coprolitic casting which by its chemical corrosion caused the partial embedding. See enlargement on plate 11, fig. 5.

EXPLANATION OF PLATE 4

[Plate 4 on page 62]

All figures natural size

FIGS. 1, 2 -- U MMP 63388, brachial and side views. The brachial valve has a colony of the tabulate coral *Aulopora microbuccinata*, the ctenostome bryozoan *Eliasopora stellatum* (lower left), a colony of the cystopore bryozoan *Botryllopora socialis* (lower right) which continues across the commissure, and a small colony of the cyclostome bryozoan *Hederella* with small zooecia on the fold. The pedicle valve has *Aulopora microbuccinata* along the anterior margin, several colonies of *Botryllopora socialis* (left edge and fold), the ctenostome bryozoan *Ascodictyon fusiforme* (left anterior margin near the fold), and a coiled shell of the annelid worm *Spirorbis planum* (in the fold). The sequence of attachment as indicated by overgrowths indicates that *Botryllopora* was probably the original settler, for in places it lies below *Aulopora microbuccinata*; *Aulopora* was in turn overgrown by *Ascodictyon fusiforme* and *Eliasopora stellatum*. See enlargements on plate 16, figs. 3, 4, and plate 19, fig. 1.

FIGS. 3-5 -- U MMP 63256, brachial, posterior, and pedicle views. This *Paraspirifer bownockeri* was damaged by a bite, presumably by a long-toothed crossopterygian fish such as *Onychodus*, which punctured the brachial valve and thrust out part of the pedicle valve. The attack was not fatal, as shown by the shell repairs on both valves. The bite may have occurred a considerable time before the brachiopod expired, perhaps when it was much younger. See enlargements on plate 13, figs. 1, 2.

FIG. 6 -- U MMP 63180, brachial view. Colonies of the robust cyclostome bryozoan *Hederella magna* are present on much of the brachial valve and on a small marginal area at the left side of the pedicle valve; the two colonies are not connected. Zooecia of this species are large, reaching 1 mm wide and over 2 mm long; among Silica epizoans, they are exceeded in the genus only by *Hedereilla reimanni*. Small indentations below the prominent left cardinal corner of the brachial valve were made by the parasitic worm *Cornulites*. See enlargements on plate 7, fig. 5, and plate 21, fig. 3.

FIG. 7 -- U MMP 63412, brachial view. On the right side of the brachial valve are remains of what appears to be a small rugose coral, preserving only part of the thecal wall and traces of the septa. This is the only example we found of a rugose coral acting as an epizoan on *Paraspirifer bownockeri*. The coiled shell of a small specimen of the annelid worm *Spirorbis planum* is attached on the same side close to the edge of the fold. See enlargements on plate 11, fig. 6, and plate 16, fig. 5.

FIG. 8 -- U MMP 63634, anterior-pedicle view. The anterior region of the pedicle valve has a fine colony of the cyclostome bryozoan *Hederella bilineata*, showing typical development of the colony. The brachial valve has scattered remains of poorly preserved and unidentified *Hederella*. As in nearly all specimens of *Paraspirifer bownockeri*, epizoans cover more area on the brachial valve than on the pedicle valve. See enlargements on plate 12, fig. 3, and plate 15, fig. 4.

FIG. 9 -- U MMP 63298, posterior view. The inarticulate brachiopod *Philhedra sheldoni* settled on the posterior region of the pedicle valve of this *Paraspirifer bownockeri* and, during growth, reflected the underlying topography of its host in both its valves. The commensal inarticulate extended onto the interarea of its articulate host and stopped at the hinge. If the hinge of the *Paraspirifer* remained functional, as we believe, the relationship of the two was probably a life relationship. See enlargement on plate 11, fig. 4.

[Explanation of this plate on pages 56, 59]

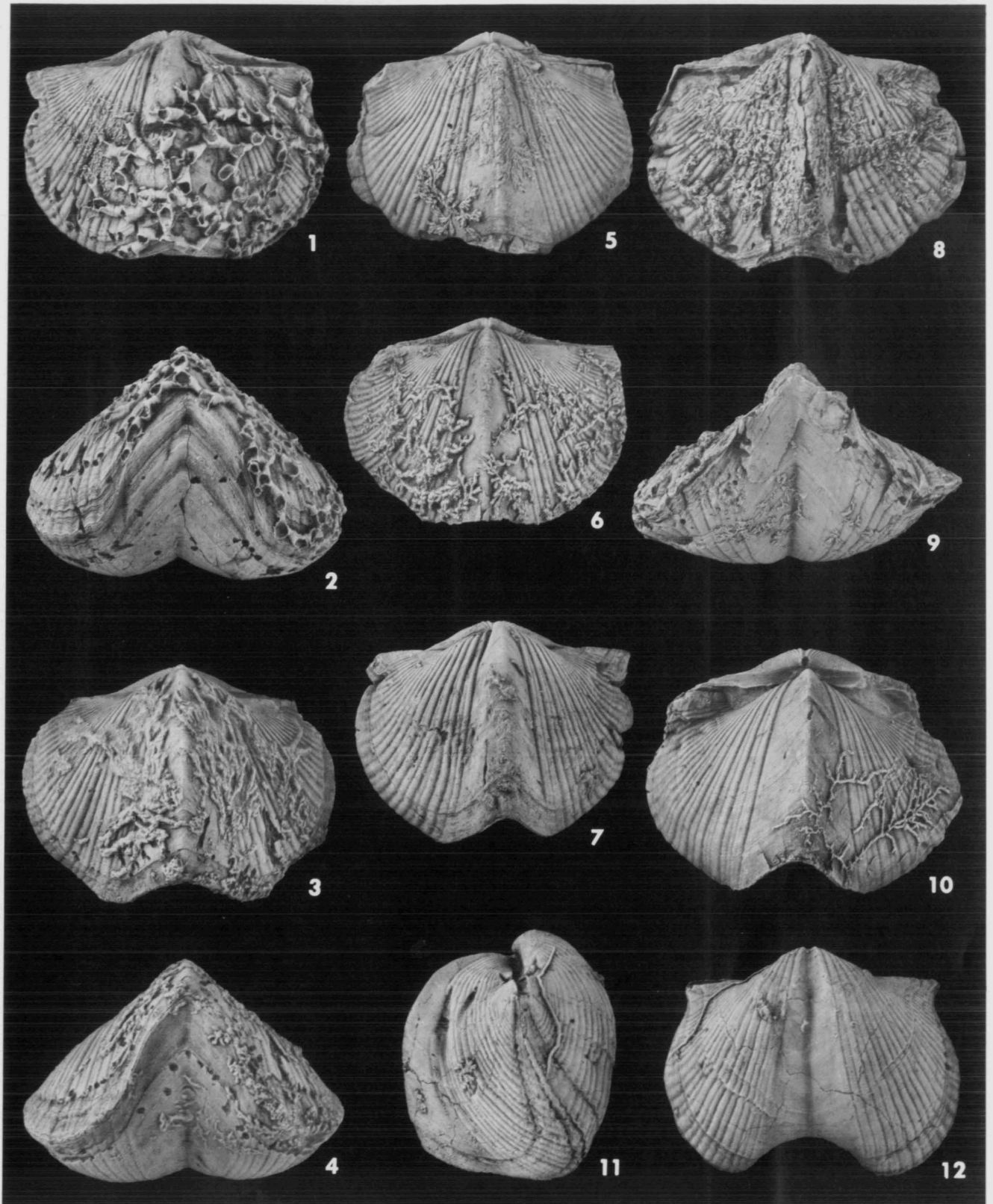
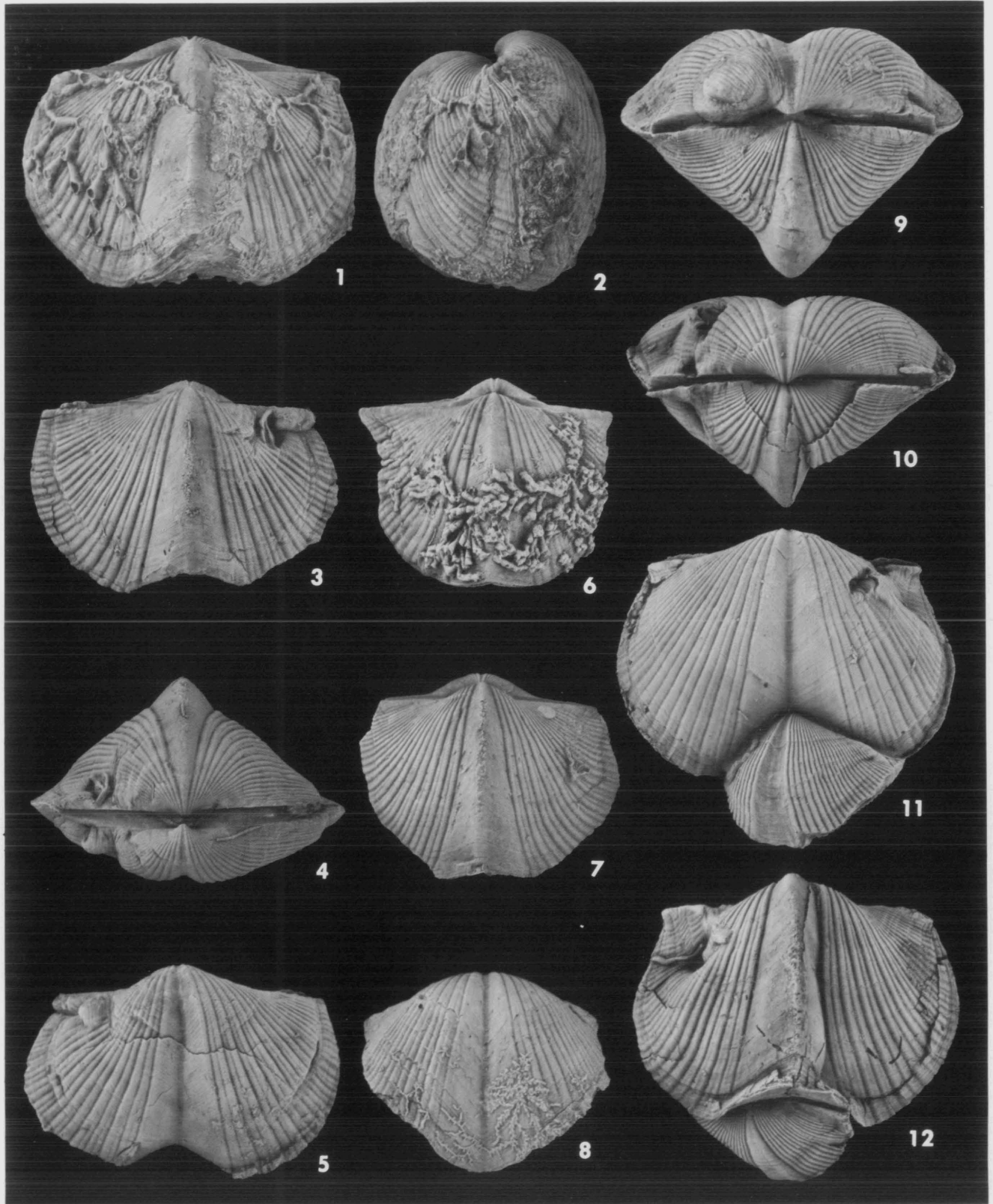


PLATE 4

[Explanation of this plate on pages 60, 63]



[Explanation of Plate 4 cont'd]

FIGS. 10-12 -- UMP 63339, posterior, pedicle, and brachial views. A very large (for an attached specimen) articulate brachiopod "*Mediospirifer audaculus*" was able by its angular position to keep its interarea attached and still occupy the fold of the host *Paraspirifer bownockeri*. The epizoan brachiopod has the same general orientation as its host, with its brachial valve facing the same direction. We do not understand why this particular "*Mediospirifer audaculus*" remained attached, when smaller specimens of its species are found free in the same unit of the Silica Formation. See enlargement on plate 13, fig. 5.

EXPLANATION OF PLATE 5

[Plate 5 on page 67]

All figures natural size

- FIG. 1 -- UMMP 63465, brachial view. The brachial valve has attached colonies of the cyclostome bryozoans *Hederella filiformis* and *Hederella thedfordensis*. The latter epizoan has larger zooecia. The pedicle valve of this host has additional colonies of *Hederella*, but they are not connected to those on the brachial valve. See enlargements on plate 8, fig. 6, and plate 17, fig. 4.
- FIGS. 2, 3 -- UMMP 63427, brachial and anterior views. The brachial valve bears two colonies of the cyclostome bryozoan *Hederella thedfordensis*, the left one continuing across the commissure and onto the pedicle valve in an obvious epitaphic relationship. See enlargements on plate 13, fig. 4, and plate 17, fig. 1.
- FIGS. 4, 5 -- UMMP 63622, brachial and anterior views. The left side of the fold supports a small colony of the cyclostome bryozoan *Hederella alpenensis*, which is rare on *Paraspirifer bownockeri* in the Silica Formation. The fold of the pedicle valve and the right side of the brachial valve are covered by a large colony of the flower-like cystopore bryozoan *Botryllopora socialis*, which effectively sealed the valves of its host and obviously developed in epitaphism. See enlargements on plate 14, figs. 1-3; plate 19, figs. 4-6; and plate 20, fig. 1.
- FIGS. 6, 7 -- UMMP 63437, brachial and inclined views. Near the left side of its hinge, this *Paraspirifer bownockeri* has a small specimen of the articulate brachiopod *Cyrtina "hamiltonensis"* fastened by its interarea. Except for a few submarginal sponge borings, this host is remarkably free of epizoans. See enlargement on plate 13, fig. 3.
- FIG. 8 -- UMMP 63640, anterior-pedicle view. A colony of the cyclostome bryozoan *Hederella alternata* developed in the fold of this host. Budding is consistently at an angle of 45° in this species of *Hederella*. See enlargements on plate 13, fig. 6, and plate 15, fig. 5.
- FIG. 9 -- UMMP 63664, pedicle view. The pedicle valve carries two species of the cyclostome bryozoan *Hederella*: *Hederella concinna* on the right and a species of the "*H. canadensis*" group on the left. Other *Hederella* colonies are attached on the brachial valve of this host, but are not illustrated. See enlargements on plate 6, fig. 10; plate 8, figs. 2, 3; and plate 15, fig. 6.
- FIG. 10 -- UMMP 63390, brachial view. The brachial valve bears two specimens of the inarticulate brachiopod *Orbiculoidea doria* on its left margin. Inasmuch as the epizoan lies near the edge of the host, it must have attached late in the life of the latter. Near the upper (posterior) specimen of *Orbiculoidea*, the edge of the *Paraspirifer* is indented by the ravages of two specimens of the parasitic worm *Cornulites*. See enlargements on plate 12, figs. 4-6.
- FIG. 11 -- UMMP 63236, anterior view. Almost at the same time, this brachiopod was infested by two parasites, the boring sponge "*Clionoides*" and the worm *Cornulites*. It survived long enough to grow an additional 1 cm. The sponges left matching "dotted lines" on the two valves to mark the edge of the shell at the time of their larval fall-out. After settlement, the sponge and the worm grew in opposite directions, the sponge boring into the shell toward the host's beak and the worm extending its tube toward the commissure. See enlargement on plate 11, fig. 3.
- FIG. 12 -- UMMP 63581, pedicle view. The pedicle valve of this brachiopod has a small colony of the cyclostome bryozoan *Hederella reimanni*, a species with exceptionally large zooecia. See enlargements on plate 9, fig. 5, and plate 19, fig. 3.

[Explanation of Plate 5 cont'd]

FIGS. 13, 14 -- UMP 63665, brachial and pedicle views. *Paraspirifer bownockeri* with repaired shell puncture. The puncture was presumably from the bite of a sharp-toothed crossopterygian fish such as *Onychodus*. The pedicle valve was punctured and shell material thrust outward on the brachial valve directly opposite. The repaired area on the pedicle valve is crossed by continuations of growth lines, and the out-thrust area on the brachial valve is crossed by deformed growth lines and costae. This brachiopod is practically free of epizoans. See enlargements on plate 15, figs. 2, 3.

EXPLANATION OF PLATE 6

[Plate 6 on page 68]

Figures natural size except as noted

- FIGS. 1, 2 -- UMMP 63385, brachial and anterior-pedicle views. The brachial valve bears colonies of two species of the cyclostome bryozoan *Hederella*. On the left is *Hederella parvirugosa* with small zooecia and wide-spaced branching and on the right *Hederella thedfordensis* with zooecia twice as large and close-set and irregular branching. The latter forms a massive colony of close-set zooecia on the pedicle valve. Two tubes of the parasitic worm *Cornulites* lie on the brachial valve, the anterior one exceptionally large. See enlargements on plate 7, fig. 6; plate 9, fig. 4; plate 16, figs. 1, 2; and plate 18, fig. 6.
- FIG. 3 -- UMMP 63428, brachial view. The brachial valve is inhabited by an incipient colony of the tabulate coral *Aulopora microbuccinata* and profuse development of the ctenostome bryozoan *Eliasopora stellatum*. Extension of vesicles onto the corallites proves that *Eliasopora* was the later colonizer of that area of the host. On the left side of the valve and on the adjacent side of the pedicle valve, the *Paraspirifer* suffered borings by the parasitic sponge "*Clionoides*" that produced a major growth line. See enlargements on plate 9, fig. 2, and plate 17, figs. 2, 3.
- FIG. 4 -- UMMP 63508, brachial view. A well-developed colony of the cyclostome bryozoan *Hederella thedfordensis* spread over the fold and left anterior area of the brachial valve, and in several places extended onto the fold of the pedicle valve after death of the host. A small isolated colony of the same species grew on the anterior margin of the brachial valve to the right of the fold. Flower-like clusters of vesicles of the ctenostome bryozoan *Ascodictyon floreale* are connected by sinuous stem-like stolons on the left side of the brachial valve. A few borings of the parasitic sponge "*Clionoides*" are associated with the submarginal major growth line. Indentations below the right cardinal ear of the brachial valve were caused by young individuals of the parasitic worm *Cornulites*. See enlargements on plate 8, figs. 4, 5; plate 17, figs. 5, 6; and plate 18, fig. 5.
- FIG. 5 -- UMMP 63501, brachial view. This *Paraspirifer bownockeri* was host for a number of epizoans. The left cardinal corner of the brachial valve and the right corner of the pedicle valve are covered by the trepostome bryozoan ?*Leioclema* sp.; although adjacent, the two colonies were not connected and do not appear to have interfered with the operation of the host's valves. On the right side of the brachial valve, the tabulate coral *Aulopora microbuccinata* grew only a few corallites before expiring. On the left side of the valve, the cyclostome bryozoan *Hederella thedfordensis* developed a colony, the edge of which grew over the ?*Leioclema*; organic matter of unknown origin settled on the *Hederella* and led to formation of a mass of pyrite. The right margin of the brachial valve has two ctenostome bryozoans, *Ascodictyon* (?) *conferta* and *Eliasopora stellatum*. Along a major growth line on each valve, equidistant from the commissure, the host bears borings made by a fall-out of larvae of the sponge "*Clionoides*." The anterior part of the pedicle valve has additional *Hederella thedfordensis*. See enlargements on plate 7, fig. 9; plate 12, figs. 1, 2; and plate 18, figs. 1-4.
- FIG. 6 -- UMMP 63653, brachial view. This robust *Paraspirifer* has the inarticulate brachiopod *Philhedra crenistriata* attached on the left side of its brachial valve. This same valve bears stolons and vesicles of a ctenostome bryozoan, particularly concentrated on the right half; the rosettes appear to belong to *Ascodictyon floreale*. Poorly preserved remains of the cyclostome bryozoan *Hederella* sp. are present on the left half of the fold and adjacent area. The host brachiopod was bored by an infestation of the burrowing sponge "*Clionoides*." See enlargements on plate 8, fig. 1, and plate 15, fig. 1.

PLATE 5

[Explanation of this plate on pages 64, 65]

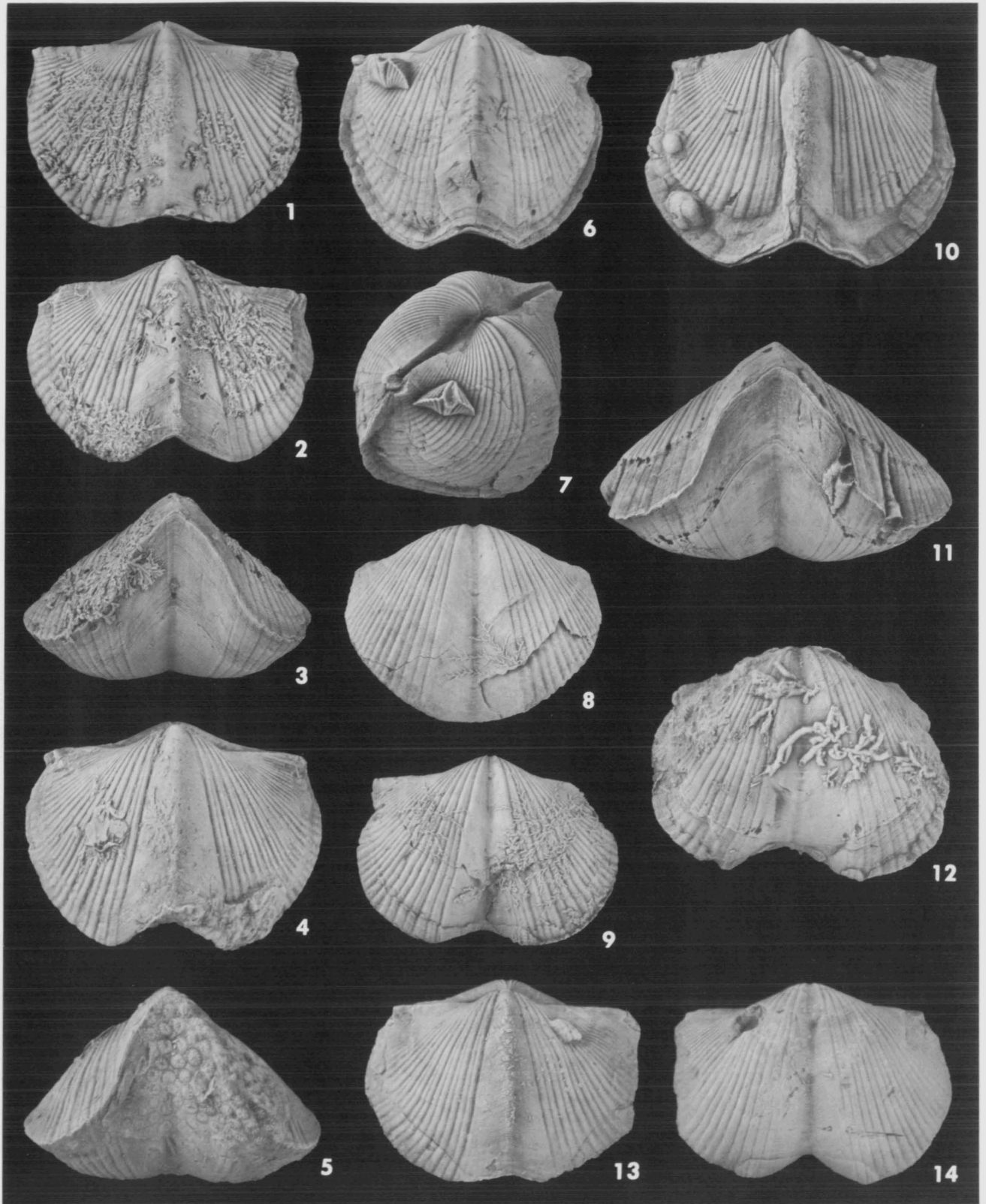
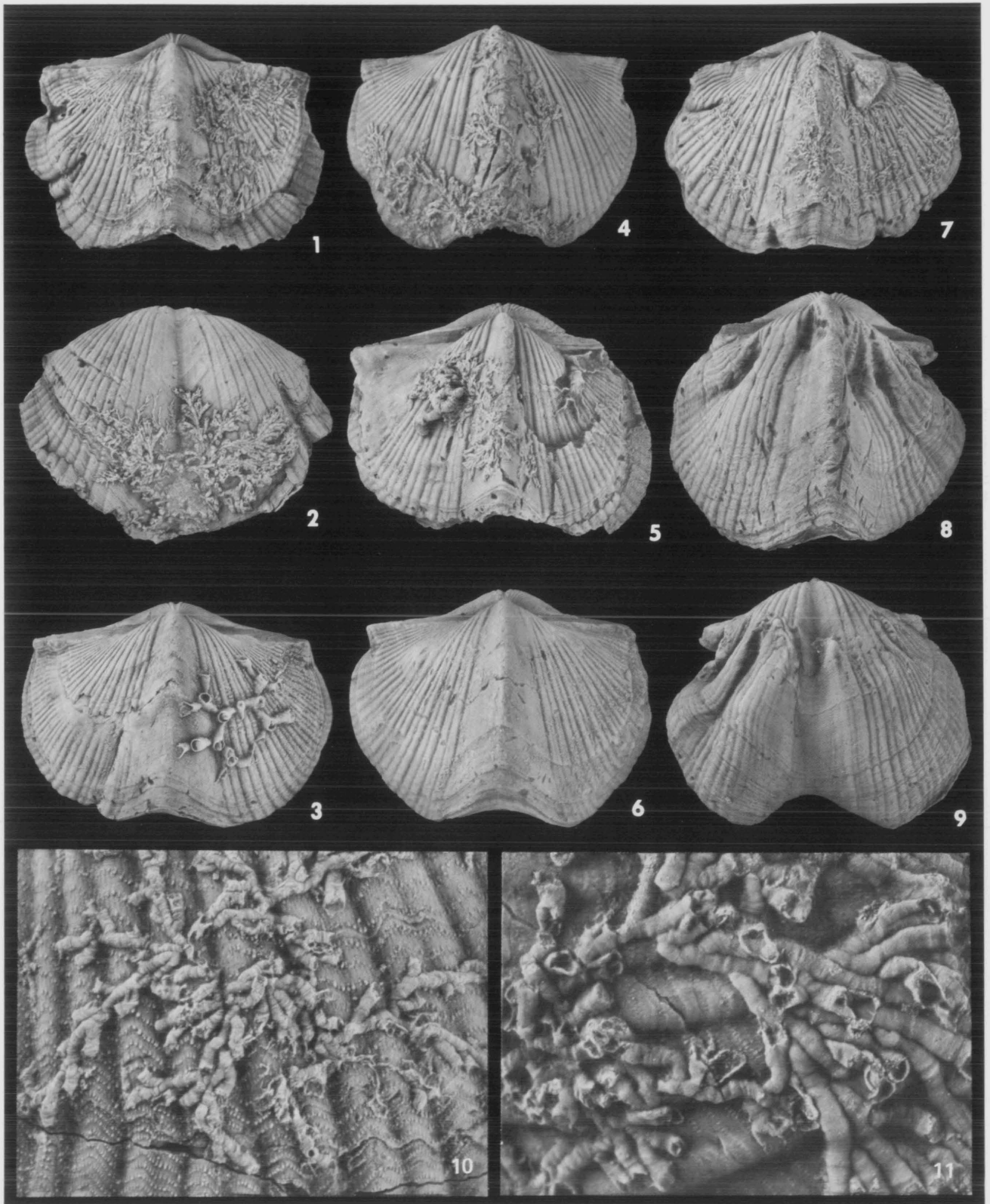


PLATE 6

[Explanation of this plate on pages 66, 69]



[Explanation of Plate 6 cont'd]

FIG. 7 -- UMMP 63579, brachial view. The brachial valve bears a colony or colonies of the cyclostome bryozoan *Hederella parvirugosa*, many zooecia of which have been abraded. A large pyrite mass to the right of the fold was initiated by organic material of unknown origin, and lies upon the *Hederella*. The margin is indented by scars of the parasitic worm *Cornulites*, one tube of which is attached on the right anterior margin. Both valves suffered borings of the parasitic sponge "*Clionoides*," most along a major growth line. The pedicle valve has a few remains of *Hederella*, but is mostly free of epizoans. See enlargements on plate 8, fig. 7, and plate 19, fig. 2.

FIGS. 8, 9 -- UMMP 63565, brachial and pedicle views. This brachiopod was badly damaged in life by punctures presumed to have been made by a crossopterygian fish. Their locations suggest that the bites occurred when the victim was much younger. The *Paraspirifer* recovered, repaired the perforations, and resumed normal shell secretion except for the marked asymmetry. Narrow open channels were probably made as borings, perhaps by the parasitic sponge "*Clionoides*"; other borings show only the circular openings. No bryozoa are present.

FIG. 10 -- UMMP 63664, x 8. "*Hederella canadensis*" group. This cyclostome bryozoan is situated on the left side of the pedicle valve. This particular species has smaller zooecia than some others of its group, such as *H. thedfordensis*; they are even smaller than those of *H. concinna*, which is present on the opposite side of this valve. Host shown natural size on plate 5, fig. 9; another enlargement of this species on plate 8, fig. 3; also on plate 15, fig. 6.

FIG. 11 -- UMMP 63310, x 8. *Hederella filiformis* (Billings). This cyclostome bryozoan is attached in the beak area of the host just to the left of the fold. Zooecia attain 1 mm in length and bud at an angle of 45°. The zooecia are unusually crowded near the terminus of the colony. Host shown natural size on plate 3, figs. 8, 9; another enlargement of this species on plate 14, fig. 5.

EXPLANATION OF PLATE 7

All figures x 2

- FIG. 1 -- UMMP 63121. "*Mediospirifer audaculus*" (Conrad). This small articulate brachiopod settled in the sulcus of the host near the commissure, attaching by its interarea. The orientation is like that of the host, with the valves facing the same directions. The selection of this site may have had the advantage of feeding currents produced by the adult host, but the configuration of the fold left little room for lateral growth and may have contributed to the epizoan's untimely demise. Host shown natural size on plate 1, fig. 2.
- FIG. 2 -- UMMP 63154. *Hederella filiformis* (Billings). This bryozoan colony is situated on the left side of the brachial valve. Despite its name, the species has neither extremely small zooecia nor elongate branches. Host shown natural size on plate 1, fig. 5.
- FIG. 3 -- UMMP 63300. *Hederella filiformis* (Billings) and *Hederella thedfordensis* Bassler. The former has smaller zooecia and the larger colony. Host shown natural size on plate 3, fig. 5; another enlargement of *H. filiformis* on plate 23, fig. 1, and of *H. thedfordensis* on plate 16, fig. 6.
- FIG. 4 -- UMMP 63128. *Atactotoechus* cf. *A. typicus* Duncan. This trepostome bryozoan blankets nearly all of its host. Diagnostic features of the species can only be seen in thin sections. Host shown natural size on plate 1, figs. 8, 9; other enlargements of this bryozoan on plate 10, fig. 2; plate 14, fig. 6; and plate 20, fig. 2.
- FIG. 5 -- UMMP 63180. *Hederella magna* Hall. This cyclostome bryozoan has very large zooecia. This colony is well developed. Host shown natural size on plate 4, fig. 6; another enlargement of this colony on plate 21, fig. 3.
- FIG. 6 -- UMMP 63385. *Hederella thedfordensis* Bassler. The species has colonies on both valves of the host. Host shown natural size on plate 6, figs. 1, 2; other enlargements of this bryozoan on plate 9, fig. 4; plate 16, fig. 2; and plate 18, fig. 6.
- FIG. 7 -- UMMP 63149. *Petrocrania hamiltoniae* (Hall). This large inarticulate brachiopod occupies the right half of the brachial valve of its articulate host. Growth lines are conspicuous, and underlying costae of the host are partly reflected in the outer valve of the epizoan. Host shown natural size on plate 1, fig. 10.
- FIG. 8 -- UMMP 63271. *Cornulites* sp. Parasitic worms of this genus have damaged the mantle of the host, retarding growth and shell secretion. One *Cornulites* has its tube on the brachial valve, and a smaller one has its tube on the pedicle valve just below the cardinal ear. Host shown natural size on plate 3, fig. 7.
- FIG. 9 -- UMMP 63501. ?*Leioclema* sp. and *Hederella* sp. The trepostome bryozoan ?*Leioclema* and the cyclostome bryozoan *Hederella*, here shown together, emphasize their different formation of colonies. Host shown natural size on plate 6, fig. 5; other enlargements of ?*Leioclema* sp. on plate 18, figs. 2-4.

PLATE 7

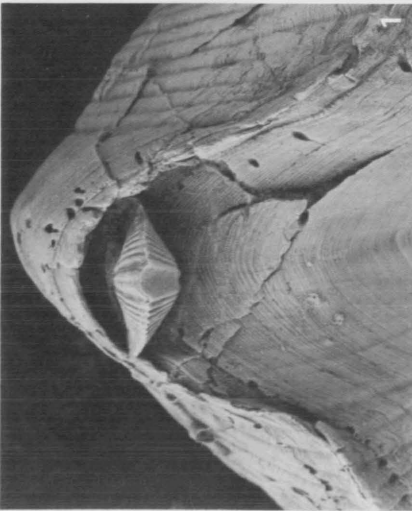
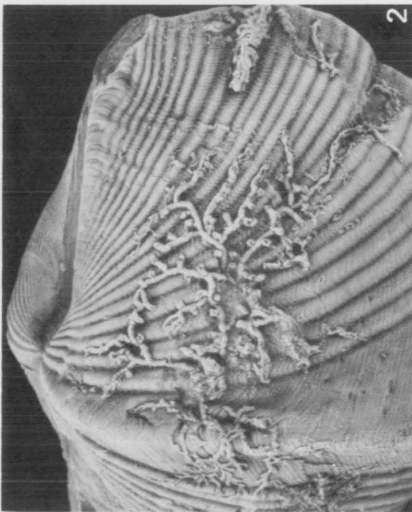
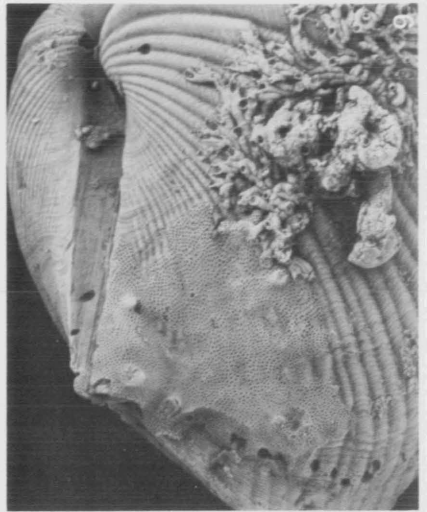
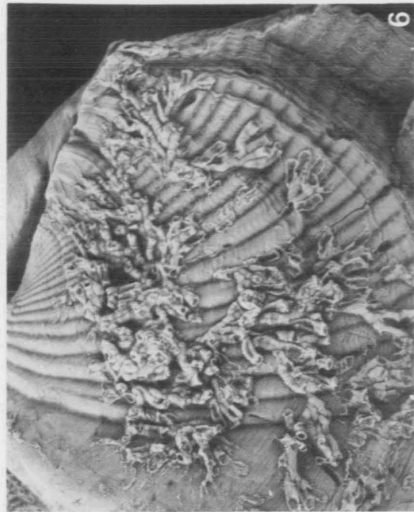
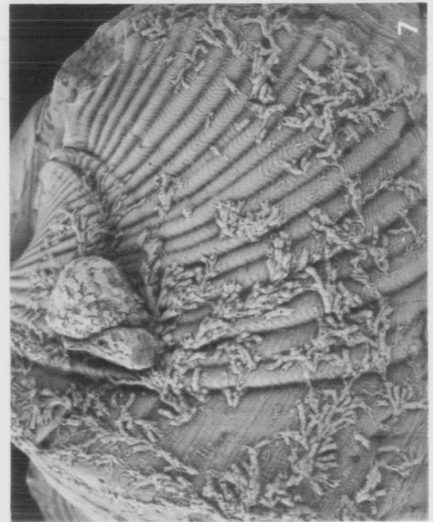
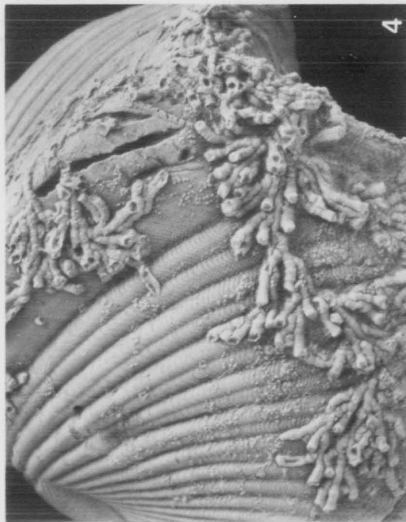
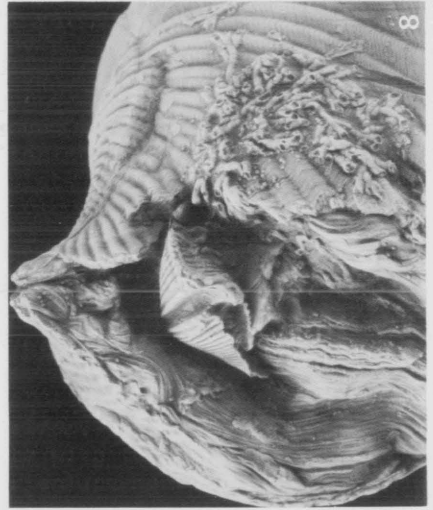
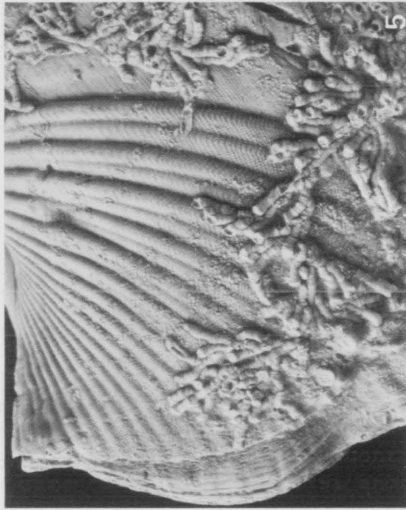
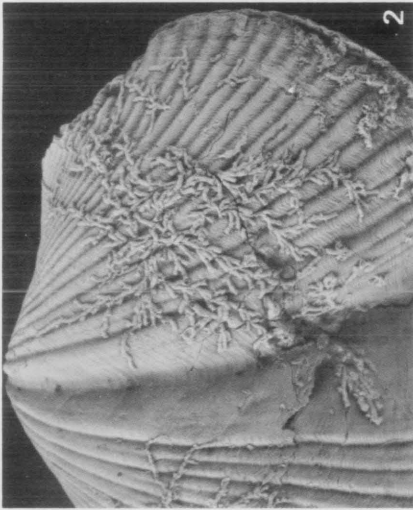
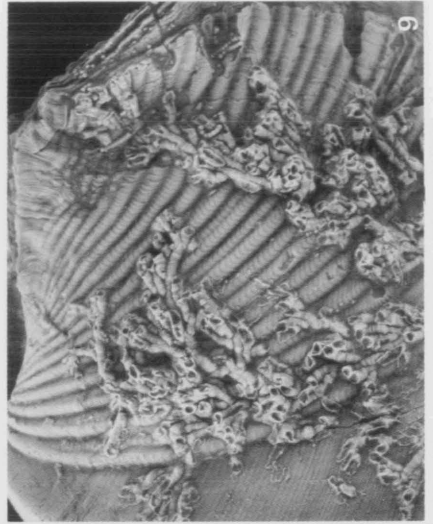


PLATE 8



EXPLANATION OF PLATE 8

All figures x 2

- FIG. 1 -- UMP 63653. *Philhedra crenistriata* (Hall). This inarticulate brachiopod, attached to the left shoulder of the brachial valve of its articulate host, shows the typical ornamentation of its species. Note that the thin valves of the epizoan reflect the underlying configuration of the host's shell. Host shown natural size on plate 6, fig. 6; another enlargement on plate 15, fig. 1.
- FIG. 2 -- UMP 63664. *Hederella concinna* Bassler. This colony of cyclostome bryozoans is situated on the right side of the pedicle valve of the *Paraspirifer*. It displays the typical patterns of budding and branching. Host shown natural size on plate 5, fig. 9; another enlargement on plate 15, fig. 6.
- FIG. 3 -- UMP 63664. "*Hederella canadensis*" group. This cyclostome bryozoan contrasts with *H. concinna* on the same valve (see fig. 2), another of this group, by its small zooecia. It may be *Hederella delicatula*, although some of the branching is atypical. Host shown natural size on plate 5, fig. 9; another enlargement on plate 6, fig. 10.
- FIGS. 4, 5 -- UMP 63508. *Hederella thedfordensis* Bassler. This well-developed colony of cyclostome bryozoans is located on the brachial valve of the host. The wide zooecia have excellent preservation. The ctenostome bryozoan *Ascodictyon floreale* Ulrich & Bassler is associated with this *Hederella* in figure 5. The host is shown natural size on plate 6, fig. 4; other enlargements of the *Hederella thedfordensis* on plate 17, fig. 6, and plate 18, fig. 5; another enlargement of this *Ascodictyon floreale* on plate 17, fig. 5.
- FIG. 6 -- UMP 63465. *Hederella filiformis* (Billings) and *Hederella thedfordensis* Bassler. The colonies of these two cyclostome bryozoans are attached on the left side of the host's brachial valve. *H. filiformis* has the larger colony and smaller zooecia. Host shown natural size on plate 5, fig. 1; another enlargement of *H. filiformis* on plate 17, fig. 4.
- FIG. 7 -- UMP 63579. *Hederella parvirugosa* Bassler. This cyclostome bryozoan is situated on the host's brachial valve. Host shown natural size on plate 6, fig. 7; another enlargement on plate 19, fig. 2.
- FIGS. 8, 9 -- UMP 63202. *Hederella thedfordensis* Bassler and "*Mediospirifer audaculus*" (Conrad). The cyclostome bryozoan appears in both figures, and the articulate brachiopod only in figure 8. The attached interarea of the "*Mediospirifer*" lies across the commissure of its host in a deformed area; it certainly grew there after the death of the host and appears to have been restricted in development to the local configuration of the deformity. Host shown natural size on plate 2, figs. 5, 6; another enlargement of the *Hederella thedfordensis* on plate 22, fig. 2.

EXPLANATION OF PLATE 9

All figures x 2

- FIG. 1 -- UMMP 63188. *Hederella concinnoides* Bassler. This colony developed with few branches in its younger stage. The 60° angle of branching is clearly exemplified. Host shown natural size on plate 3, fig. 10; another enlargement of this species on plate 22, fig. 4.
- FIG. 2 -- UMMP 63428. *Aulopora microbuccinata* Watkins and *Eliasopora stellatum* (Nicholson & Etheridge). Both the tabulate coral *Aulopora* and the ctenostome bryozoan *Eliasopora* are typically developed, the former developing its colony around polygonal spaces and the latter by clustered vesicles connected by thin stolons. Encroachment of the bryozoan onto the coral proves that it colonized later. Host shown natural size on plate 6, fig. 3; other enlargements on plate 17, figs. 2, 3.
- FIG. 3 -- UMMP 63200. *Hederella concinnoides* Bassler. The cyclostome bryozoan colony is confined to the brachial valve of the host. Host shown natural size on plate 2, figs. 3, 4; another enlargement of the colony on plate 22, fig. 3.
- FIG. 4 -- UMMP 63385. *Hederella parvirugosa* Bassler, *Hederella thedfordensis* Bassler, and *Cornulites* sp. The two species of cyclostome bryozoans can be distinguished by the smaller and more closely spaced zooecia in *H. parvirugosa*. The *Cornulites* tube, nearly 18 mm long, is one of the largest found on *Paraspirifer*. Host shown natural size on plate 6, figs. 1, 2; another enlargement of *H. parvirugosa* on plate 16, fig. 1; and another enlargement of *H. thedfordensis* on plate 7, fig. 6; plate 16, fig. 2; and plate 18, fig. 6.
- FIG. 5 -- UMMP 63581. *Hederella reimanni* Bassler. This species, on the pedicle valve of the host, contains the largest zooecia of any cyclostome bryozoan in the Silica Formation. Host shown natural size on plate 5, fig. 12; another enlargement of the colony on plate 19, fig. 3.
- FIG. 6 -- UMMP 63307. *Aulopora microbuccinata* Watkins and *Ascodictyon fusiforme* (Nicholson & Etheridge). The tabulate coral has its typical colony enclosing polygonal areas. The ctenostome bryozoan, with vesicles extending onto the corallites, was obviously the later colonizer. Host shown natural size on plate 3, figs. 1, 2; other enlargements of the *Ascodictyon fusiforme* on plate 23, figs. 5, 6.

PLATE 9

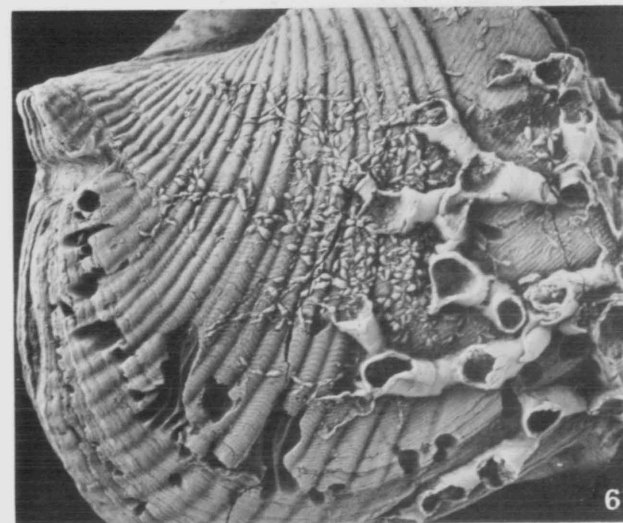
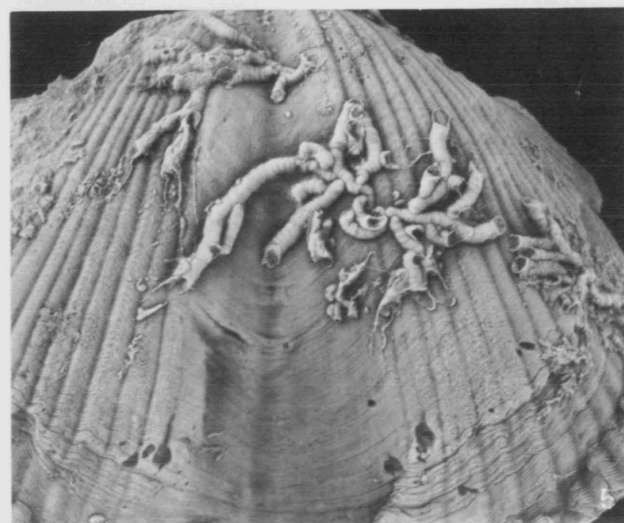
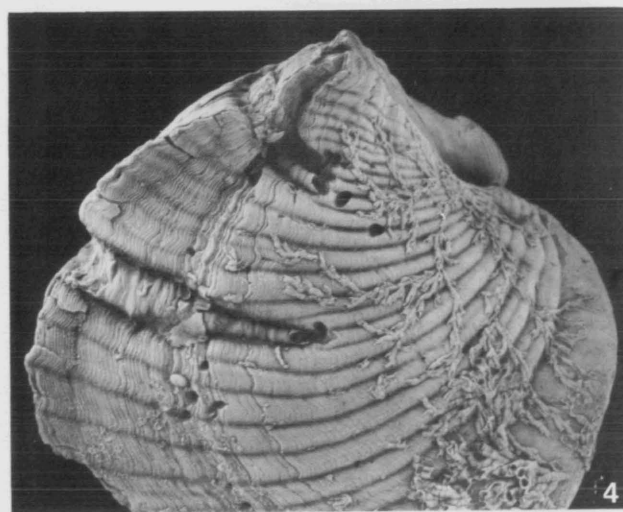
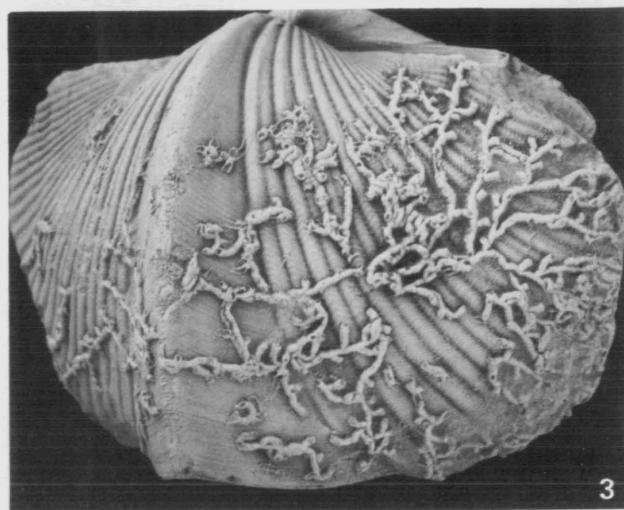
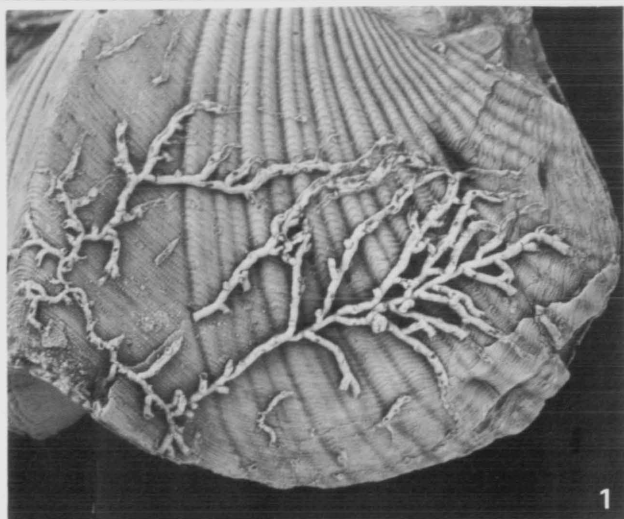
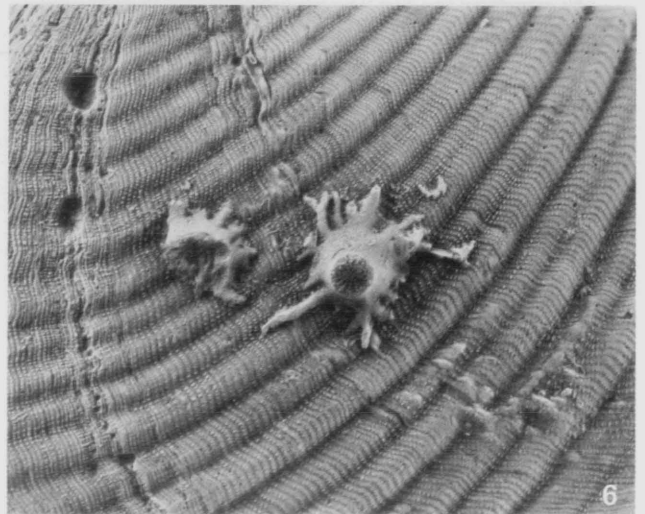
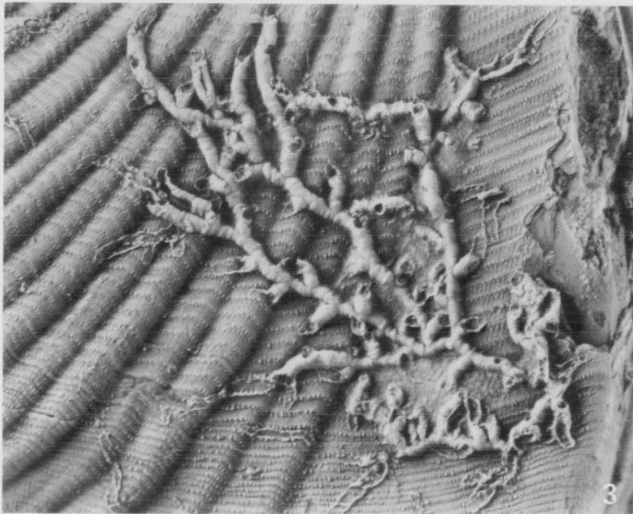
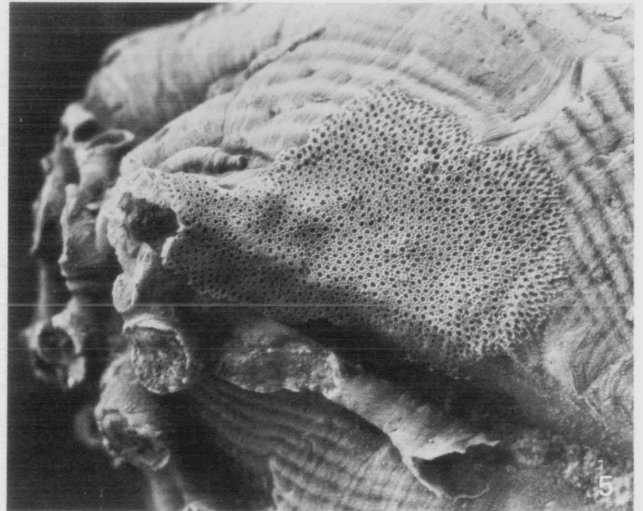
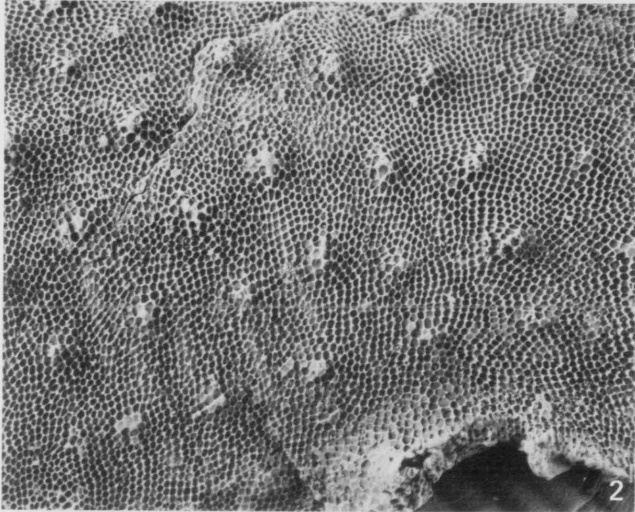
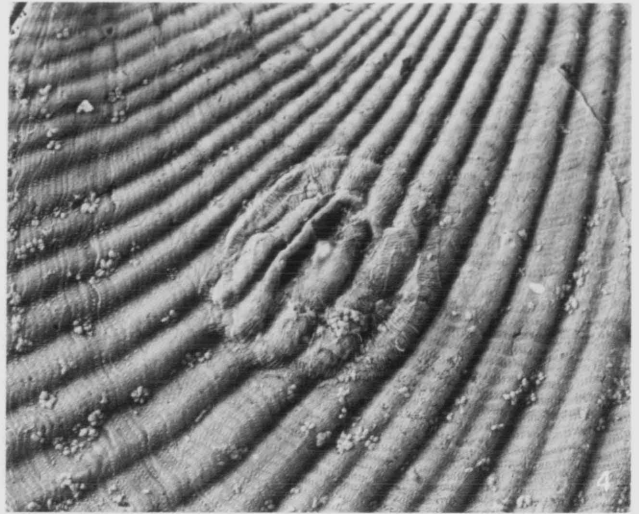
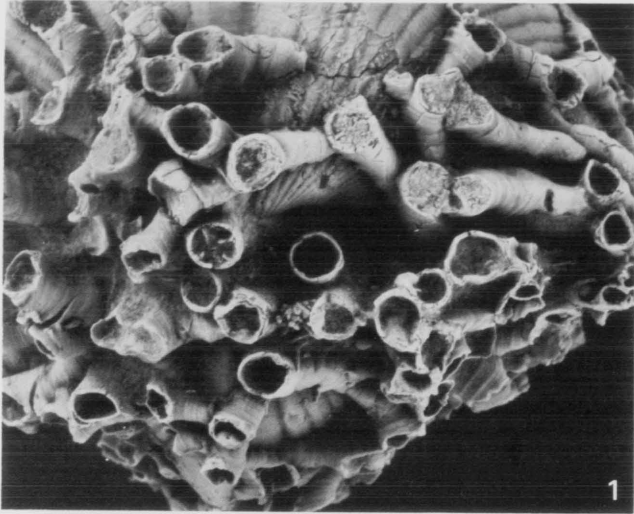


PLATE 10



EXPLANATION OF PLATE 10

Figures x 4 except as noted

- FIG. 1 -- UMMP 63146. *Aulopora microbuccinata* Watkins. Corallites crossing the hinge indicate that the brachiopod was dead at the time of this colonization, a case of epitaphy. Crowding of the corallites to fill spaces within the normal pattern appear to indicate a gerontic colony. Host shown natural size on plate 2, figs. 9-12.
- FIG. 2 -- UMMP 63128. *Atactotoechus* cf. *A. typicus* Duncan. This trepostome bryozoan blankets nearly all areas of the host, obviously colonizing across the commissure and hinge after death of the host. Host shown natural size on plate 1, figs. 8,9; other enlargements of the colony on plate 7, fig. 4; plate 14, fig. 6; and plate 20, fig. 2.
- FIG. 3 -- UMMP 63139. *Hederella concinnoides* Bassler. A young colony on the brachial valve of the host appears to have aborted; it is much smaller than most colonies on *Paraspirifer*. Host shown natural size on plate 1, fig. 6; another enlargement of this cyclostome bryozoan on plate 20, fig. 5.
- FIG. 4 -- UMMP 63141. *Philhedra stewarti* (Fenton & Fenton) and *Ascodictyon floreale* Ulrich & Bassler. The inarticulate brachiopod *Philhedra* shows the fine radiating costellae crossing growth lines. The cyclostome bryozoan has vesicles extending onto the *Philhedra*, proving it to be the later colonizer. Host shown natural size on plate 1, fig. 11; another enlargement of the *Ascodictyon floreale* on plate 20, fig. 6.
- FIG. 5 -- UMMP 63166. ? *Leioclema* sp. and *Aulopora microbuccinata* Watkins. The trepostome bryozoan ? *Leioclema* colonized as a continuous blanket, whereas the tabulate coral *Aulopora* colonized as branching corallites with open interareas. Host shown natural size on plate 1, figs. 3,4; another enlargement of the ? *Leioclema* colony on plate 21, fig. 2.
- FIG. 6 -- UMMP 63175. Holdfasts. These root-like holdfasts are presumably remains of a crinoid, one still clearly retaining the articulation with the column. We presume that the absence of larger holdfasts and columns indicates that the crinoid species detached at a young stage. Host shown natural size on plate 1, fig. 7.

EXPLANATION OF PLATE 11

All figures x 4

- FIGS. 1, 2 -- UMMP 63186. *Ropalonaria tenuis* Ulrich & Bassler. This ctenostome bryozoan embedded itself to become flush with the shell of the host. When coated with light sublimate of ammonium chloride (fig. 1), the colony is scarcely visible; but without coating (fig. 2), the straight, irregularly disposed lines are clearly discernible. Host shown natural size on plate 2, figs. 1, 2.
- FIG. 3 -- UMMP 63236. *Cornulites* sp. This parasitic worm species is common on *Paraspirifer* in the Silica Formation. These worms have secreted tubes on both the brachial and pedicle valves of the host, maintaining their openings at the commissure from which vantage point they could feed on the mantle edges of the *Paraspirifer bownockeri*. They caused notches to develop in the shell edges where the mantle was injured. Host shown natural size on plate 5, fig. 11.
- FIG. 4 -- UMMP 63298. *Philhedra sheldoni* (White). This inarticulate brachiopod, growing on the posterior margin of the host's pedicle valve, reflected the underlying topography of the host in both its valves. It stopped growing at the hinge of the host, indicating a probable life relationship. Host shown natural size on plate 4, fig. 9.
- FIG. 5 -- UMMP 63336. Worm or coprolitic casting. The long string-like pyritized structure was undoubtedly organic. It could be the body of a worm which crept over hard surfaces, or a thin tubular housing and the enclosed worm, or possibly the coprolitic casting of a long thin organism. Such structures are rare in the Silica Formation. Host shown natural size on plate 3, figs. 11, 12.
- FIG. 6 -- UMMP 63412. Rugose coral. On the right side of the host's brachial valve are remains of what we interpret as a young rugose coral, preserving the thecal wall in part and traces of the septa. The object seems to be firmly attached and therefore an epizoan, although the orientation (on its side) is exceptional. Host shown natural size on plate 4, fig. 7.

PLATE 11

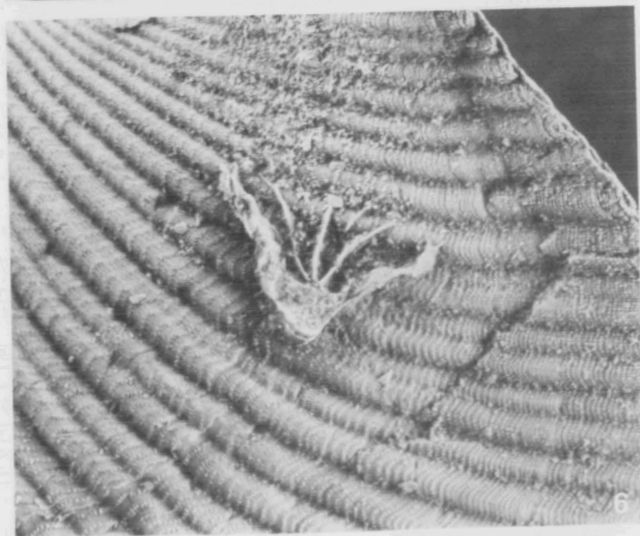
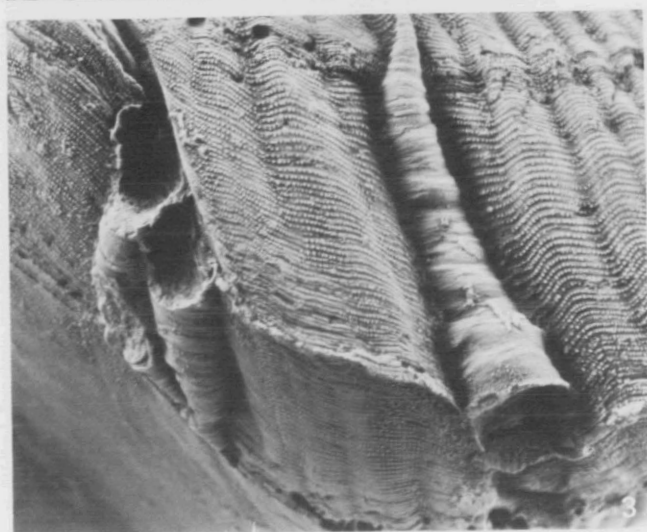
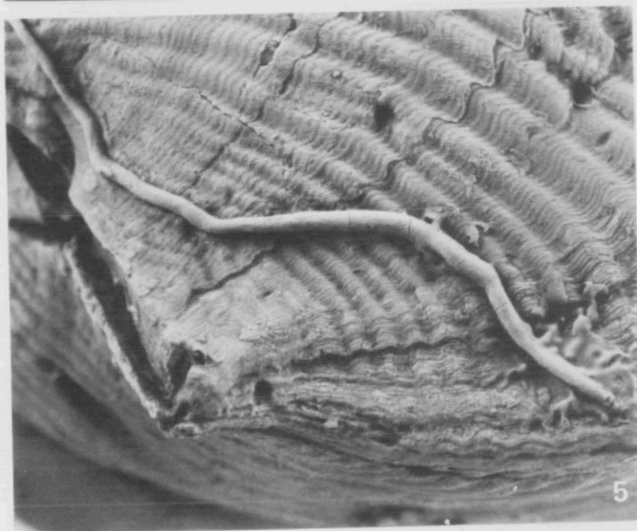
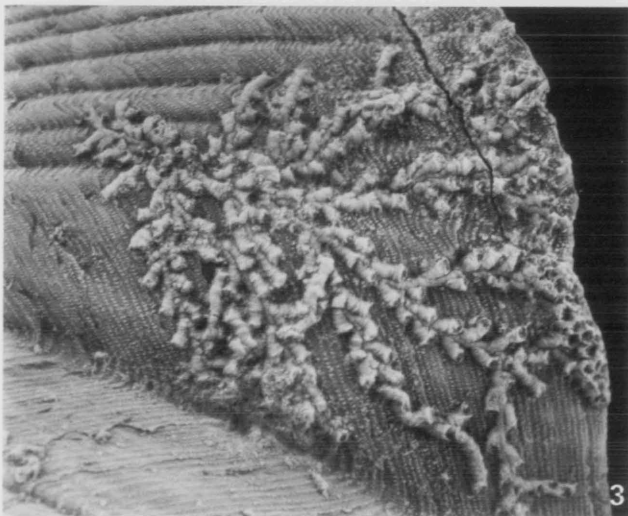
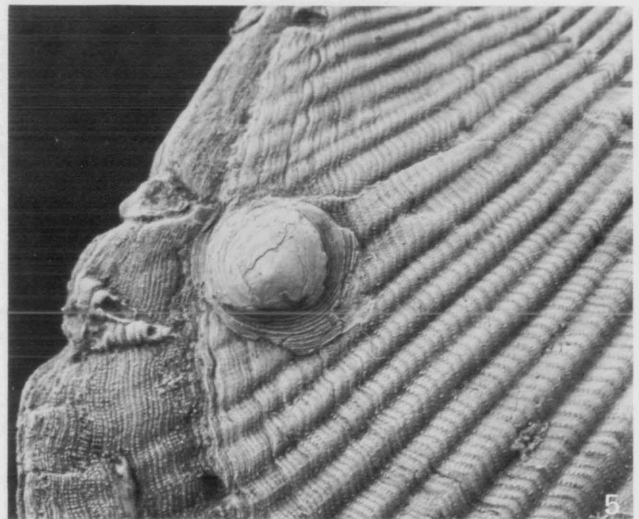
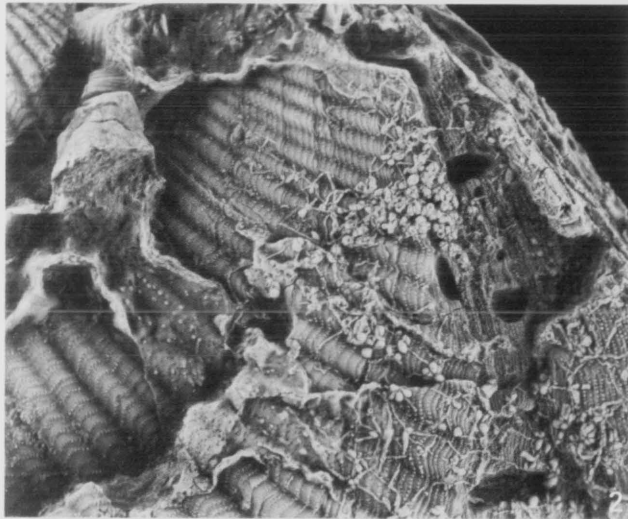
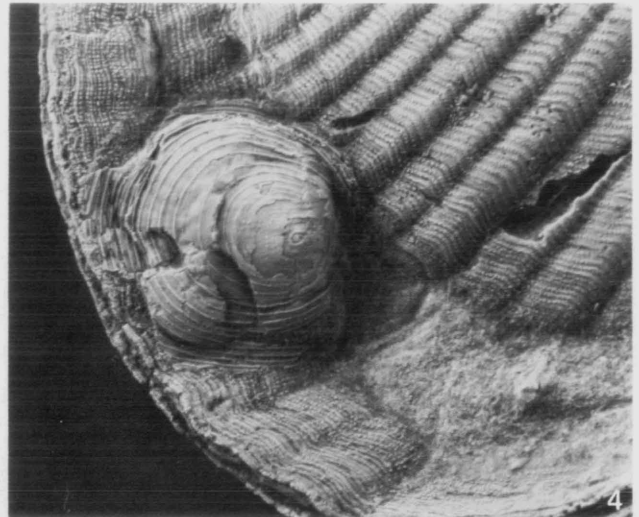
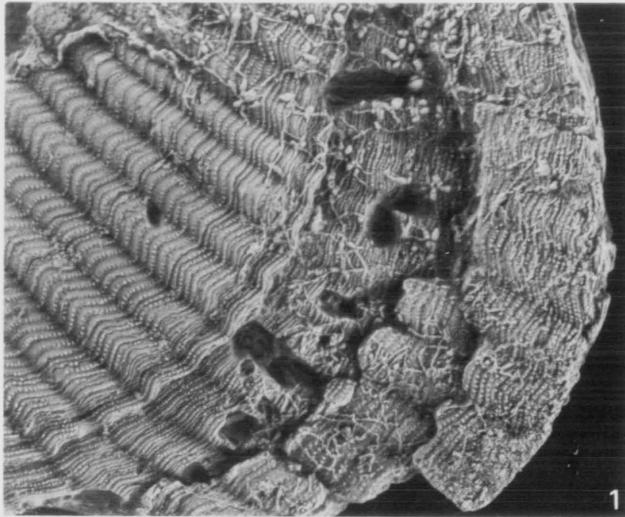


PLATE 12



EXPLANATION OF PLATE 12

All figures x 4

- FIGS. 1, 2 -- UMP 63501. *Ascodictyon (?) conferta* (Ulrich) and *Aulopora microbuccinata* Watkins. The ctenostome bryozoan *A. (?) conferta* is shown in both figures, and the tabulate coral *Aulopora* only in figure 2. Broken corallites reveal that the bryozoan colonized within the corallites after death of the coral animals. Host shown natural size on plate 6, fig. 5; another enlargement of *Ascodictyon (?) conferta* on plate 18, fig. 1.
- FIG. 3 -- UMP 63634. *Hederella bilineata* Bassler. This fine young colony of the cyclostome bryozoan developed on the anterior margin of the host's pedicle valve. Branching occurs at a high angle and budding at a low angle in this species. Host shown natural size on plate 4, fig. 8; another enlargement of this colony on plate 15, fig. 4.
- FIGS. 4, 5 -- UMP 63390. *Orbiculoidea doria* (Hall). These two inarticulate brachiopods of the superfamily Discinacea (with phosphatic shells) are situated on the left anterior margin of the host's brachial valve. Obviously, they attached when the *Paraspirifer* had reached maturity and grown to its present size. Concentric growth lines are conspicuous. Host shown natural size on plate 5, fig. 10.
- FIG. 6 -- UMP 63310. *Lingulodiscina marginalis* (Whitfield). This inarticulate brachiopod attached when its host had reached maturity. Its phosphatic shell continued to grow after the host had reached full size, so that it projected beyond the commissure of the *Paraspirifer*. Host shown natural size on plate 3, figs. 8, 9.

EXPLANATION OF PLATE 13

All figures x 4

- FIGS. 1, 2 -- UMMP 63256. Puncture. This shell damage appears to have been inflicted on the edge of the growing *Paraspirifer*, probably by the bite of a crossopterygian fish. The perforation on the brachial valve and the thrust-out shell material on the pedicle valve were both repaired and re-cemented by the brachiopod victim. The distorted growth lines and displaced costae record stages in the repairing process. *Paraspirifer* shown natural size on plate 4, figs. 3-5.
- FIG. 3 -- UMMP 63437. *Cyrtina "hamiltonensis"* (Hall). This articulate brachiopod attached by its interarea to the brachial valve of its host on the left posterior corner area. It is oriented with its brachial valve facing anterior on the host and its beak directed toward the beak of the host. The sharp-pointed beak of the epizoan leads us to believe that it is *Cyrtina hamiltonensis* as it is currently accepted, but the species needs taxonomic revision. Host shown natural size on plate 5, figs. 6, 7.
- FIG. 4 -- UMMP 63427. *Hederella thedfordensis* Bassler. Many zooecia lie in contact, probably indicative of the maturity of the colony. Host shown natural size on plate 5, figs. 2, 3; another enlargement of this species on plate 17, fig. 1.
- FIG. 5 -- UMMP63339. "*Mediospirifer audaculus*" (Conrad). Enlargement to show differences in ornamentation of the two articulate brachiopods -- one the host *Paraspirifer* and the other the epizoan "*Mediospirifer audaculus*." Host shown natural size on plate 4, figs. 10-12.
- FIG. 6 -- UMMP 63640. *Hederella alternata* (Hall & Whitfield). This excellent young colony of the cyclostome bryozoan is on the anterior region of the host's pedicle valve. Part of the colony was lost when a section of the *Paraspirifer* shell flaked off before it was found. Host shown natural size on plate 5, fig. 8; another enlargement of this colony on plate 15, fig. 5.

PLATE 13

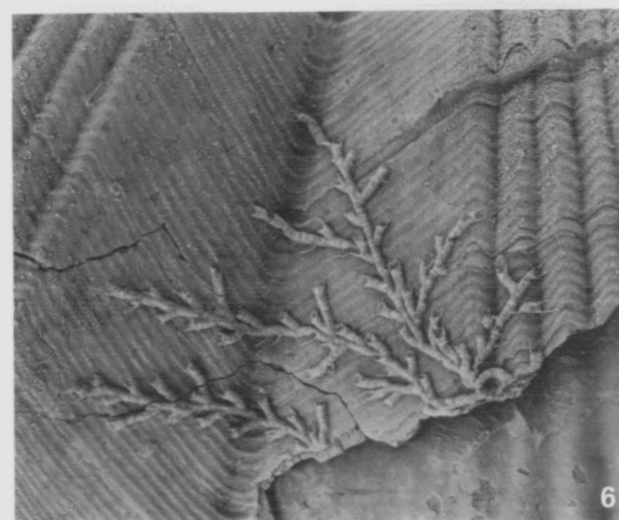
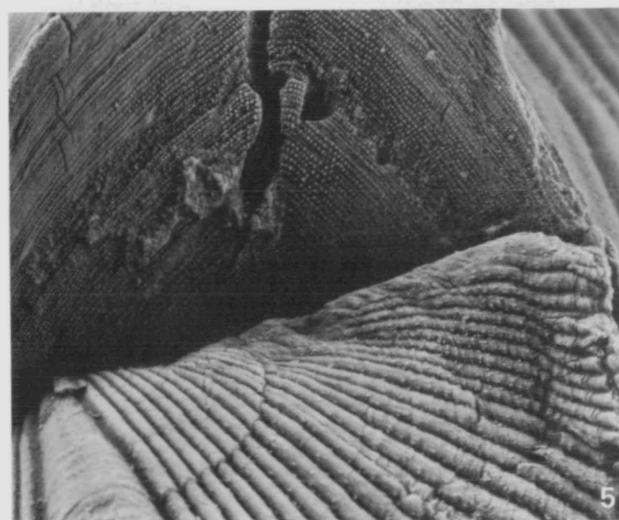
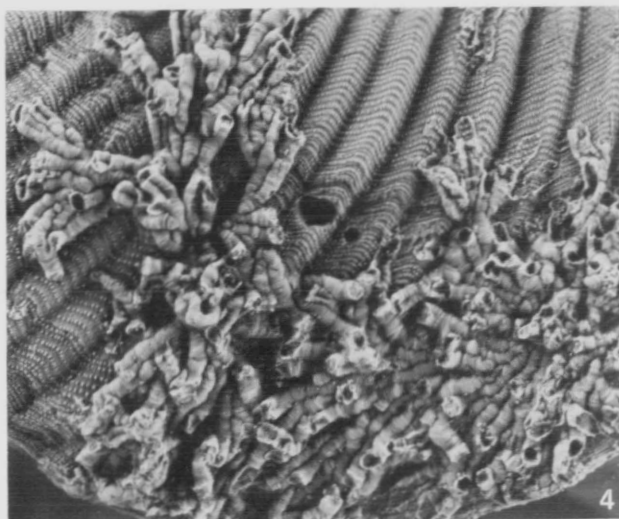
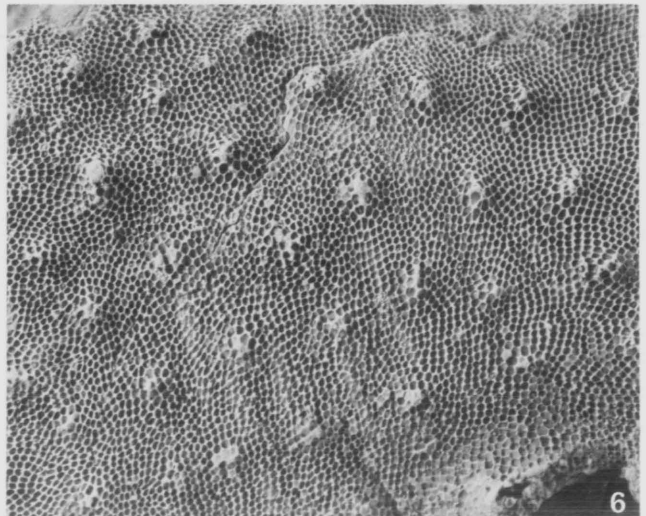
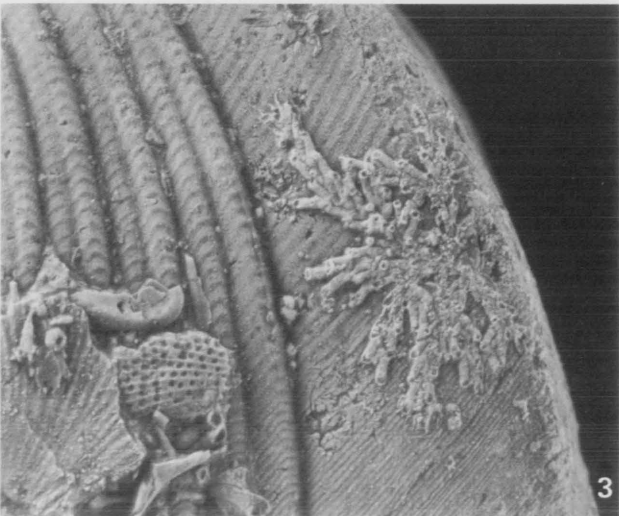
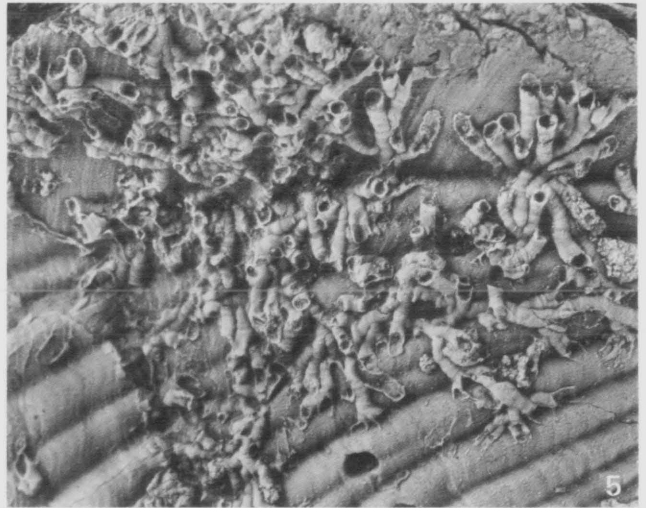
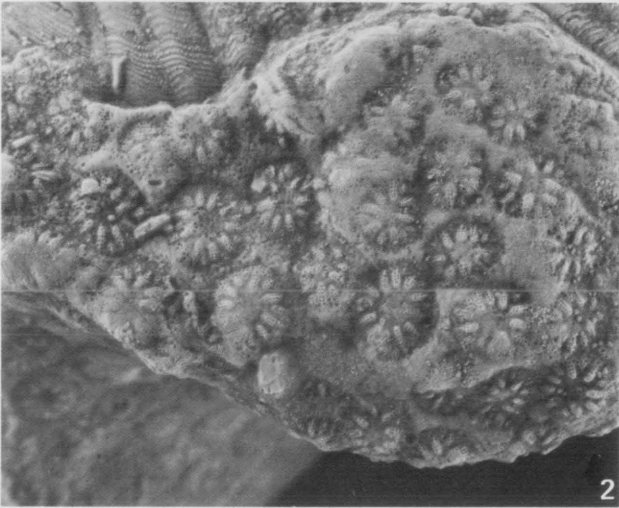
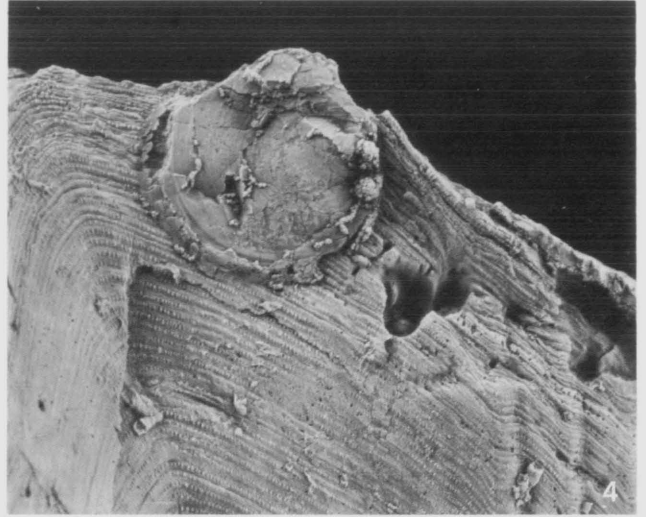
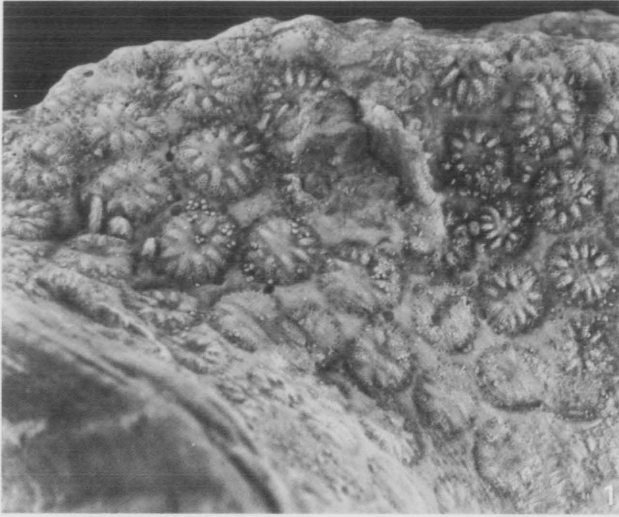


PLATE 14



EXPLANATION OF PLATE 14

All figures x 4

- FIGS. 1, 2 -- UMMP 63622. *Botryllopora socialis* Nicholson. This exceptional colony of the cystopore bryozoan spans the host's commissure. Figure 1 is on the fold of the pedicle valve and figure 2 on the anterior margin of the brachial valve. The maculae (radiating ridges) each have a double row of small zooecial pores, and vesicles fill in interareas between the clusters of maculae to form a solid mat. Host shown natural size on plate 5, figs. 4, 5.
- FIG. 3 -- UMMP 63622. *Hederella alpenensis* Bassler. A small colony of this cyclostome bryozoan lies on the fold of the host. Host shown natural size on plate 5, figs. 4, 5; another enlargement of the colony on plate 19, fig. 5.
- FIG. 4 -- UMMP 63310. *Lingulodiscina marginalis* (Whitfield). This phosphatic inarticulate brachiopod lies on the anterior edge of the host's pedicle valve. Host shown natural size on plate 3, figs. 8, 9; another enlargement of this species on plate 12, fig. 6.
- FIG. 5 -- UMMP 63310. *Hederella filiiformis* (Billings). This cyclostome bryozoan formed large mature colonies on the brachial valve of the *Paraspirifer* host. Zooecia are locally crowded. Host shown natural size on plate 3, figs. 8, 9; another enlargement of the bryozoan on plate 6, fig. 11.
- FIG. 6 -- UMMP 63128. *Atactotoechus* cf. *A. typicus* Duncan. Like other trepostome bryozoans, this species develops a blanket-like colony. This one nearly envelops its brachiopod host. Acuminate monticules are rather regularly distributed over the colony. Host shown natural size on plate 1, figs. 8, 9; other enlargements of this colony on plate 7, fig. 4; plate 10, fig. 2; and plate 20, fig. 2.

EXPLANATION OF PLATE 15

All figures x 4 except as noted

- FIG. 1 -- UMMP 63653. *Philhedra crenistriata* (Hall). This small calcareous inarticulate brachiopod shows the coarse radiate costellae. It lies on the left posterior area of the host's brachial valve. Both valves of the *Philhedra* reflect the costae of the host *Paraspirifer*. Host shown natural size on plate 6, fig. 6; another enlargement of the epizoan inarticulate brachiopod on plate 8, fig. 1.
- FIGS. 2, 3 -- UMMP 63665. Puncture. Probably the bite of a crossopterygian fish punctured the pedicle valve and thrust out shell material on the brachial valve of the living *Paraspirifer bownockeri*. The victim repaired both areas as shown by subsequent secretion of shell material. *Paraspirifer* shown natural size on plate 5, figs. 13, 14.
- FIG. 4 -- UMMP 63634, x 8. *Hederella bilineata* Bassler. This young colony, on the anterior margin of the host's pedicle valve, shows the essential characteristics of its species. The zooecia are only about 1 mm long. Host shown natural size on plate 4, fig. 8; another enlargement of this colony on plate 12, fig. 3.
- FIG. 5 -- UMMP 63640, x 8. *Hederella alternata* (Hall & Whitfield). The regular arrangement of zooecia along the tubular axis is well displayed in this young colony of the cyclostome bryozoan. The colony lies on the fold of the *Paraspirifer bownockeri*. Host shown natural size on plate 5, fig. 8; another enlargement on plate 13, fig. 6.
- FIG. 6 -- UMMP 63664, x 8. *Hederella concinna* Bassler. This cyclostome bryozoan colony is situated on the right side of the pedicle valve of the *Paraspirifer*. Zooecia vary, but average less than 1 mm long. The acute angle of budding contrasts with the steep angle of branching. Host shown natural size on plate 5, fig. 9; another enlargement of the colony on plate 8, fig. 2.

PLATE 15

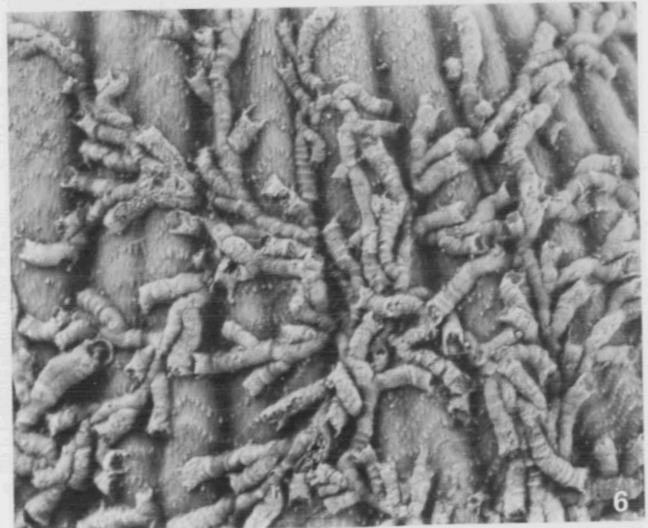
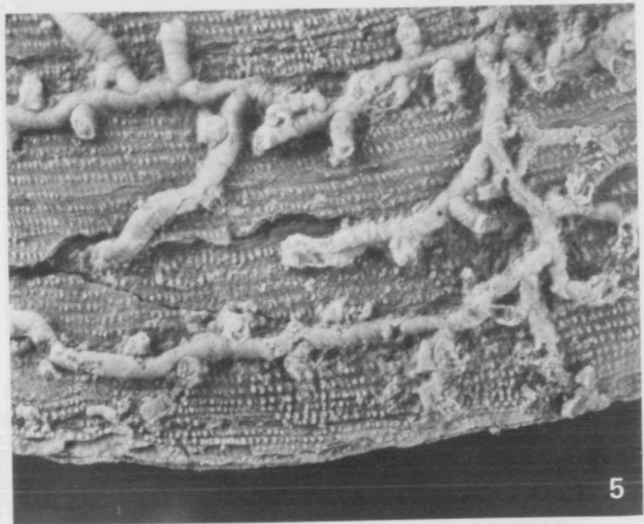
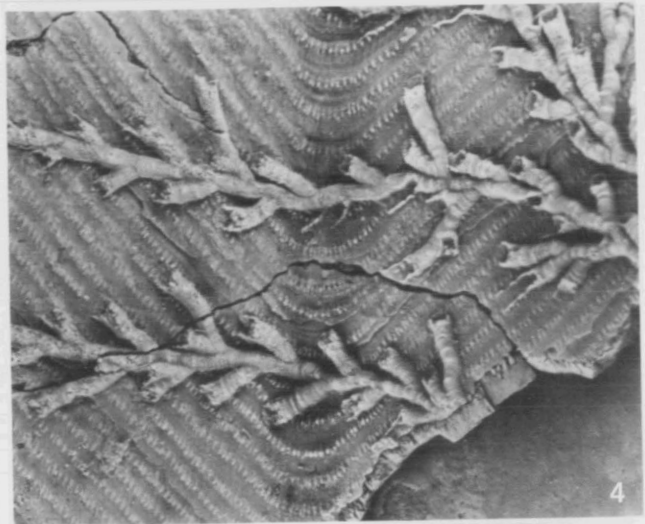
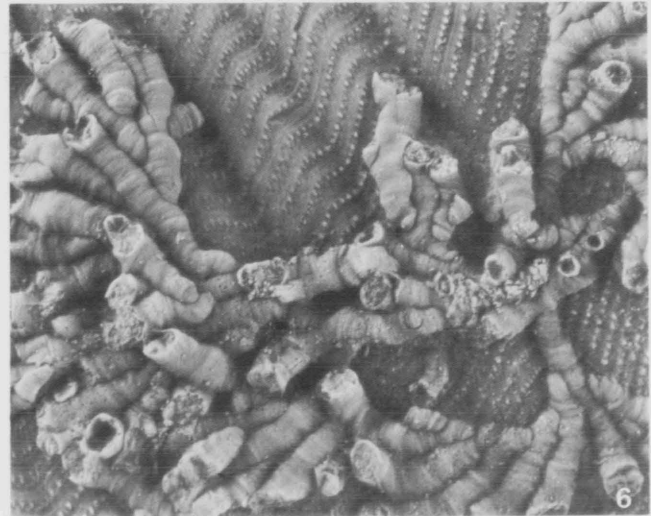
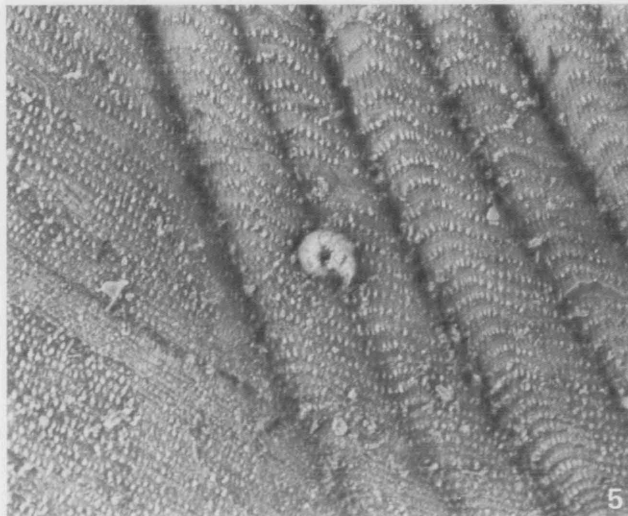
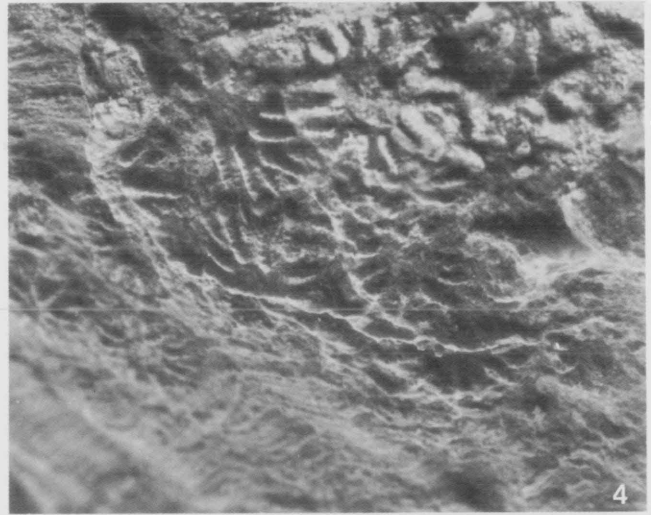
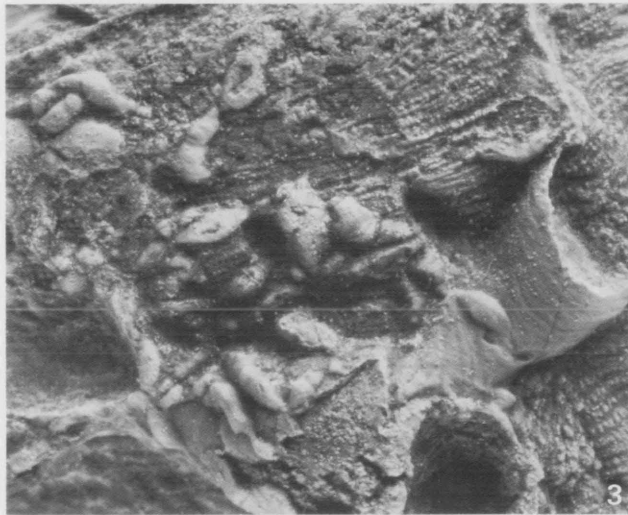
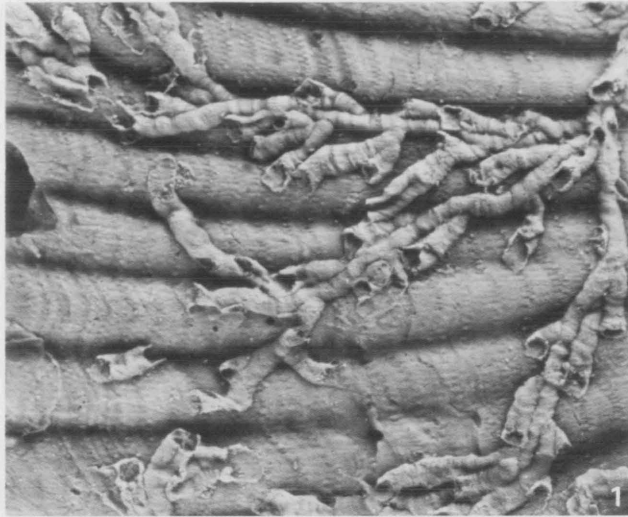


PLATE 16



EXPLANATION OF PLATE 16

All figures x 8

- FIG. 1 -- UMMP 63385. *Hederella parvirugosa* Bassler. The colony of this cyclostome bryozoan developed on the left posterior area of the brachial valve of its *Paraspirifer* host. The annular irregular ridges on the zooecial tubes are fairly prominent. Zooecial widths show exceptional variation. Host shown natural size on plate 6, figs. 1, 2; another enlargement of the colony on plate 9, fig. 4.
- FIG. 2 -- UMMP 63385. *Hederella thedfordensis* Bassler. This cyclostome bryozoan shows the close packing of zooecia in a mature colony. This part of the colony lies on the fold of the host's pedicle valve. Host shown natural size on plate 6, figs. 1, 2; other enlargements of *Hederella thedfordensis* on this *Paraspirifer* on plate 7, fig. 6; plate 9, fig. 4; and plate 18, fig. 6.
- FIG. 3 -- UMMP 63388. *Aulopora microbuccinata* Watkins and *Ascodictyon fusiforme* (Nicholson & Etheridge). On the anterior edge of the pedicle valve of the *Paraspirifer* host, near the junction of the sulcus and lateral area, these two epizoans occur together. The tabulate coral *Aulopora* was the first colonizer at this place, for it is overgrown by the ctenostome bryozoan *Ascodictyon fusiforme*. Host shown natural size on plate 4, figs. 1, 2.
- FIG. 4 -- UMMP 63388. *Botryllopora socialis* Nicholson and *Aulopora microbuccinata* Watkins. These epizoans occur together on the left margin of the pedicle valve of the host. The cystopore bryozoan *Botryllopora* and the tabulate coral *Aulopora* may at this site have lived together, but elsewhere on the host the cystopore bryozoan is overlain by the coral. Host shown natural size on plate 4, figs. 1, 2.
- FIG. 5 -- UMMP 63412. *Spirorbis planum* Stewart. A small coiled tube secreted by this annelid worm is attached in the fold of the *Paraspirifer*. Compared to other *Spirorbis planum* specimens from the formation, this one is quite small. Host shown natural size on plate 4, fig. 7.
- FIG. 6 -- UMMP 63300. *Hederella thedfordensis* Bassler. On the anterior area of the host's brachial valve, this cyclostome bryozoan has formed a colony of typically close-packed zooecia. Host shown natural size on plate 3, fig. 5; another enlargement of this colony on plate 7, fig. 3.

EXPLANATION OF PLATE 17

All figures x8

- FIG. 1 -- UMMP 63427. *Hederella thedfordensis* Bassler. Colonies of this cyclostome bryozoan, with many zooecia in contact, lie on the brachial valve of the host, with one colony extending across the commissure and proving epitaphism. This colony is on the right side of the host, and shows typical budding. Host shown natural size on plate 5, figs. 2, 3; another enlargement of the bryozoan on this host on plate 13, fig. 4.
- FIG. 2 -- UMMP 63428. *Aulopora microbuccinata* Watkins and *Eliasopora stellatum* (Nicholson & Etheridge). On the right side of the brachial valve of this *Paraspirifer bownockeri*, these two epizoans occur together. The tabulate coral, obviously the earlier colonizer, is overgrown by vesicles of the ctenostome bryozoan. The typical rosette pattern of vesicles does not always prevail; some parts of the *Eliasopora* colony have incomplete rosettes, whereas others have numerous vesicles tightly compressed so that no pattern is discernible. Host shown natural size on plate 6, fig. 3; another enlargement of the two epizoan species together on plate 9, fig. 2; another enlargement of *Eliasopora stellatum* on this host on plate 17, fig. 3.
- FIG. 3 -- UMMP 63428. *Eliasopora stellatum* (Nicholson & Etheridge). This ctenostome bryozoan occupies much of the right half of the host's brachial valve. Characteristically, its vesicles develop as a series of rosettes connected by stolons. See remarks under figure 2 above. Host shown natural size on plate 6, fig. 3; other enlargements of this *Eliasopora* on plate 9, fig. 2, and plate 17, fig. 2.
- FIG. 4 -- UMMP 63465. *Hederella filiformis* (Billings). A large colony of this cyclostome bryozoan is spread over the left side of the host's brachial valve. It differs from *H. thedfordensis*, which occurs on the same valve, by its conspicuously smaller zooecia and somewhat greater angles of budding and branching. Host shown natural size on plate 5, fig. 1; another enlargement of this colony on plate 8, fig. 6.
- FIG. 5 -- UMMP 63508. *Ascodictyon floreale* Ulrich & Bassler. Flower-like clusters of vesicles of this ctenostome bryozoan develop at points along the filamentous stolon. The species is thus very much like *Eliasopora stellatum* except that the vesicles are smaller and more elongate. Host shown natural size on plate 6, fig. 4; another enlargement of this bryozoan on plate 8, fig. 5.
- FIG. 6 -- UMMP 63508. *Hederella thedfordensis* Bassler. On the left anterior area of the *Paraspirifer bownockeri*, a colony of this cyclostome bryozoan lies close to the ctenostome bryozoan *Ascodictyon floreale* (see figure 5 on this plate); because the two are not in contact, the relative times of colonization cannot be determined. Host shown natural size on plate 6, fig. 4; other enlargements of the *Hederella thedfordensis* colony on plate 8, figs. 4, 5; and plate 18, fig. 5.

PLATE 17

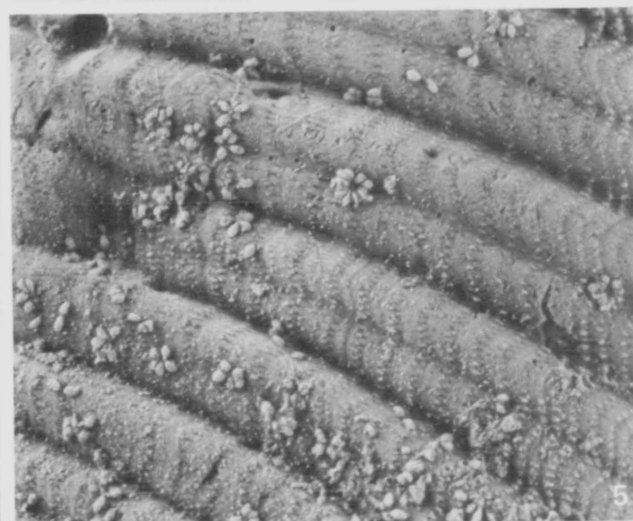
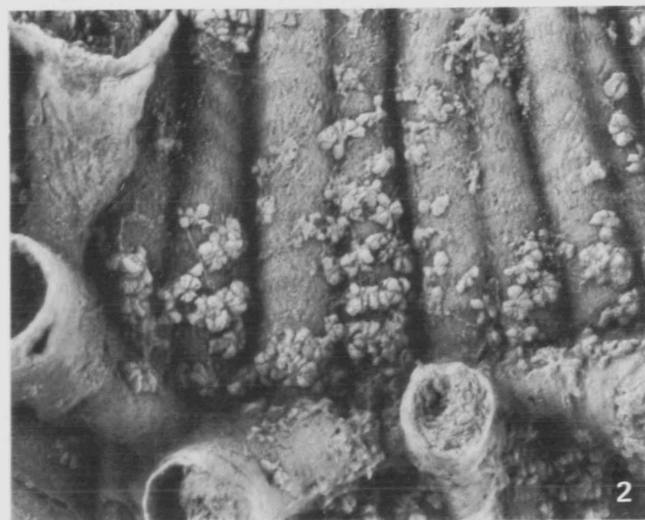
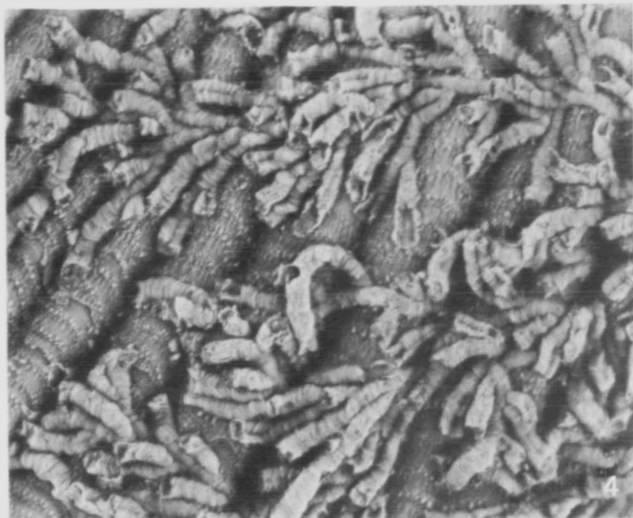
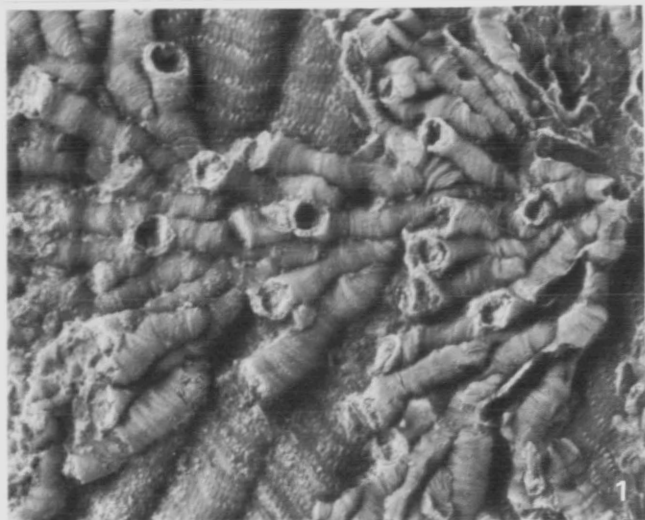
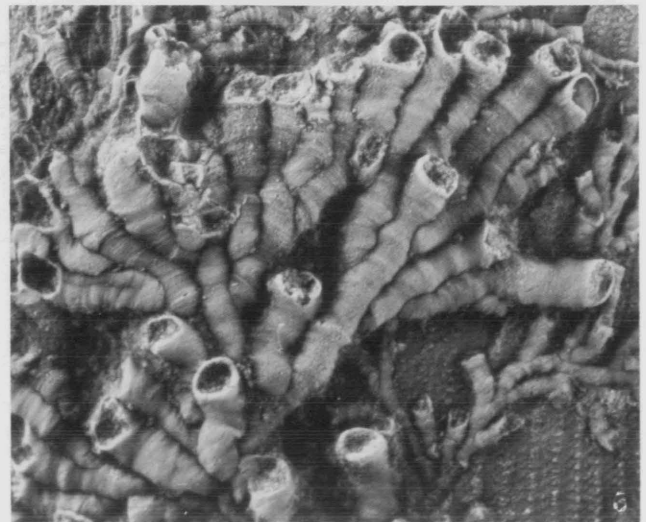
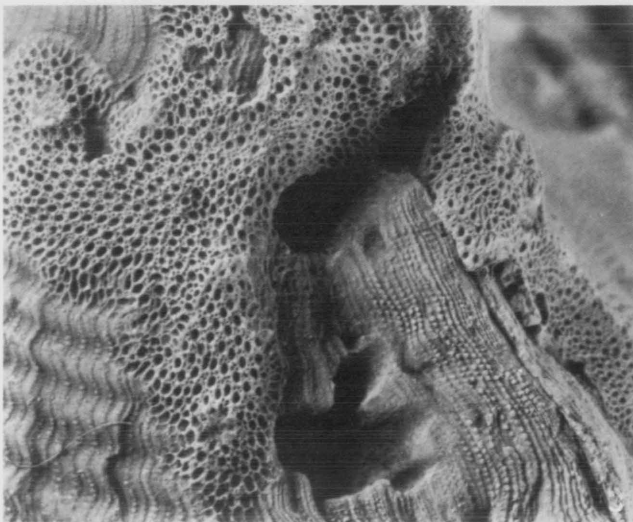
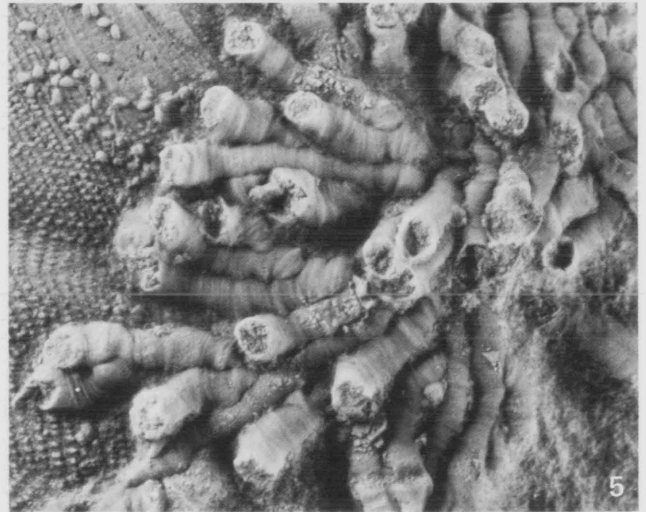
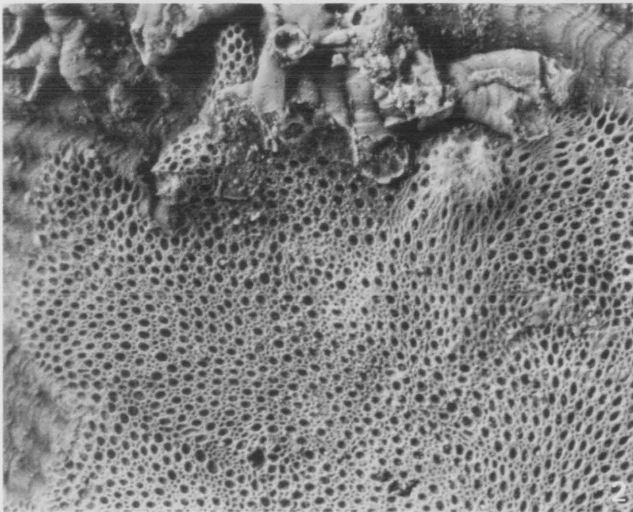
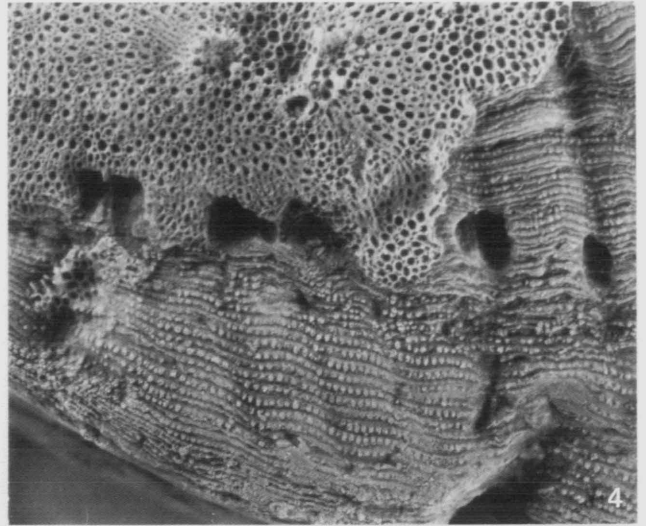
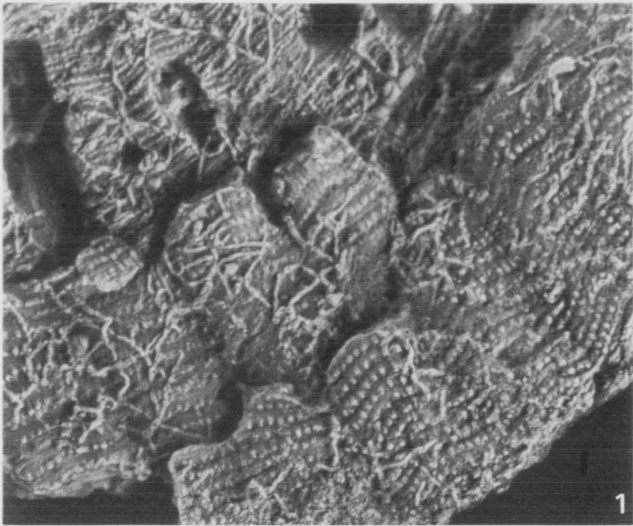


PLATE 18



EXPLANATION OF PLATE 18

All figures x8

FIG. 1 -- UMMP 63501. *Ascodictyon* (?) *conferta* (Ulrich). The absence of vesicles along this network of presumed stolons leads us to believe the ctenostome bryozoan is *Ascodictyon* (?) *conferta*, a species noted for the weak development of vesicular enlargements along the stolons. These stolons occupy an anterior right marginal area on the brachial valve. Host shown natural size on plate 6, fig. 5; other enlargements of this ctenostome bryozoan on plate 12, figs. 1, 2.

FIGS. 2-4 -- UMMP 63501. ? *Leioclema* sp. A large colony of this trepostome bryozoan forms a sheet-like cover on the left side of the brachial valve and a very small colony on the adjacent right corner of the pedicle valve of the *Paraspirifer*. Where the bryozoan colony contacts that of the cyclostome bryozoan *Hederella thedfordensis* on the brachial valve (fig. 2), the *Hederella* grew over the edges of the ? *Leioclema*, evidence of its later colonization. Where borings of the parasitic sponge "*Clionoides*" occur in contact with the ? *Leioclema* colonies on the pedicle valve (fig. 3) and the brachial valve (fig. 4), the zooecia are all complete where the bryozoan colony skirts the borings; this substantiates that the ? *Leioclema* colony spread to the contact after the sponge borings were already present. Host shown natural size on plate 6, fig. 5; another enlargement of the larger ? *Leioclema* colony on plate 7, fig. 9.

FIG. 5 -- UMMP 63508. *Hederella thedfordensis* Bassler and *Ascodictyon floreale* Ulrich & Bassler. The cyclostome bryozoan *Hederella* and the ctenostome bryozoan *Ascodictyon floreale* are shown here in association on the marginal left side of the fold and adjacent lateral area of the host's brachial valve. They are not in contact. Host shown natural size on plate 6, fig. 4; other enlargements on plate 8, fig. 5, and plate 17, fig. 6.

FIG. 6 -- UMMP 63385. *Hederella thedfordensis* Bassler. This part of the colony of the cyclostome bryozoan *H. thedfordensis* is located on the left side of the fold of the *Paraspirifer* host. It is associated with another *Hederella* species with much smaller zooecia. Host shown natural size on plate 6, figs. 1, 2; other enlargements of *H. thedfordensis* on this brachiopod on plate 7, fig. 6; plate 9, fig. 4; and plate 16, fig. 2.

EXPLANATION OF PLATE 19

All figures x8

FIG. 1 -- UMMP 63388. *Spirorbis planum* Stewart. The coiled tube of this annelid worm is attached on the fold of the host. It is rather small for its species and not well preserved. Host shown natural size on plate 4, figs. 1, 2.

FIG. 2 -- UMMP 63579. *Hederella parvirugosa* Bassler. This part of the colony of the cyclostome bryozoan *H. parvirugosa* is located on the right side of the fold of its host. The annular ridges are more pronounced on some zooecia. Host shown natural size on plate 6, fig. 7; another enlargement of this bryozoan on plate 8, fig. 7.

FIG. 3 -- UMMP 63581. *Hederella reimanni* Bassler. This cyclostome bryozoan has the largest zooecia of any species of *Hederella* in the Silica Formation. This colony is located on the pedicle valve of the *Paraspirifer*. Host shown natural size on plate 5, fig. 12; another enlargement on plate 9, fig. 5.

FIGS. 4, 6 -- UMMP 63622. *Botryllopora socialis* Nicholson. The colony of this cystopore bryozoan extended across the commissure of its deceased *Paraspirifer* host, from the brachial valve (fig. 4) to the pedicle valve (fig. 6). This unusual species has a double row of zooecial pores along each radiating ridge of the mound-like maculae and a vesicular filling of the intermaculae areas. Host shown natural size on plate 5, figs. 4, 5; other enlargements on plate 14, figs. 1, 2, and plate 20, fig. 1.

FIG. 5 -- UMMP 63622. *Hederella alpenensis* Bassler. This small colony of cyclostome bryozoans grew on the left side of the fold of the host. Each of the zooecia arises alternately from the side of its predecessor without development of an extensive central axis. Host shown natural size on plate 5, figs. 4, 5; another view of the colony on plate 14, fig. 3.

PLATE 19

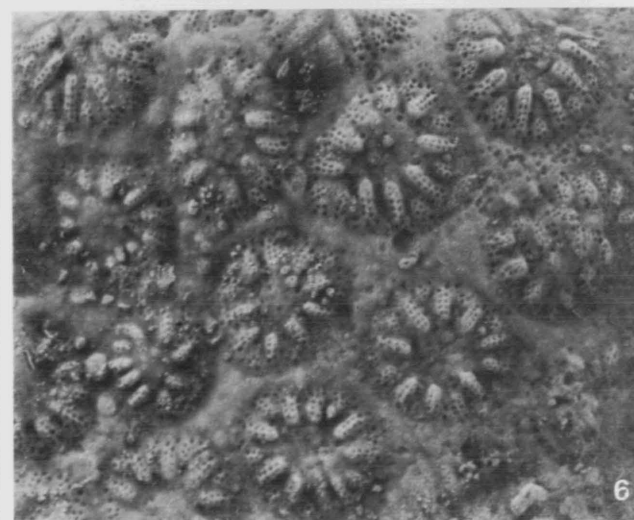
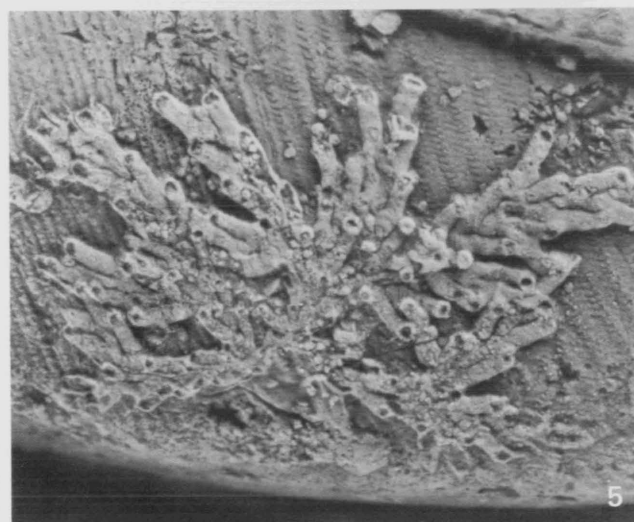
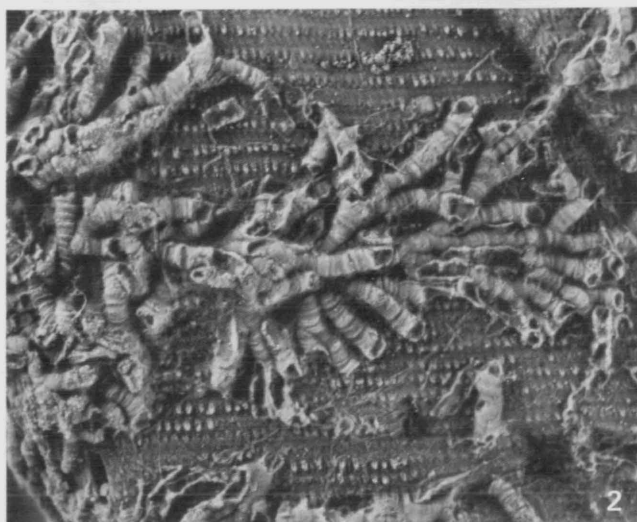
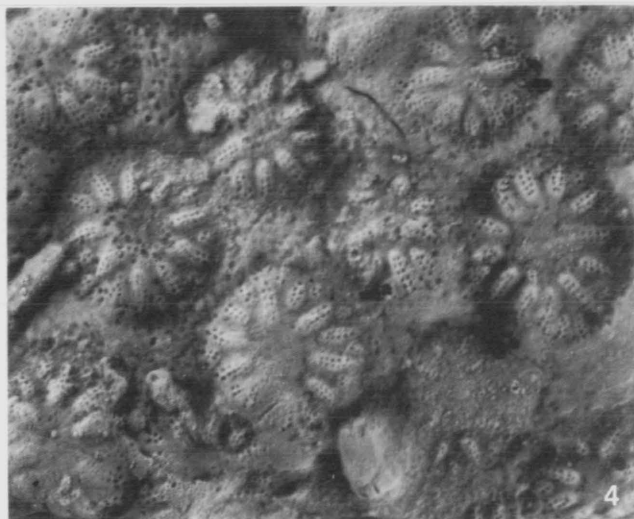
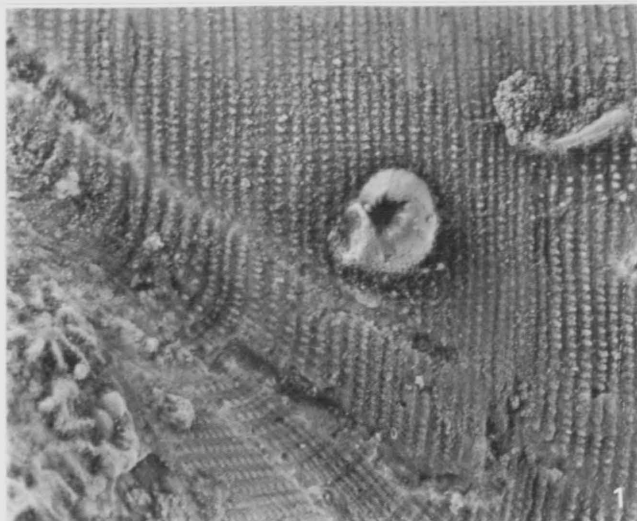
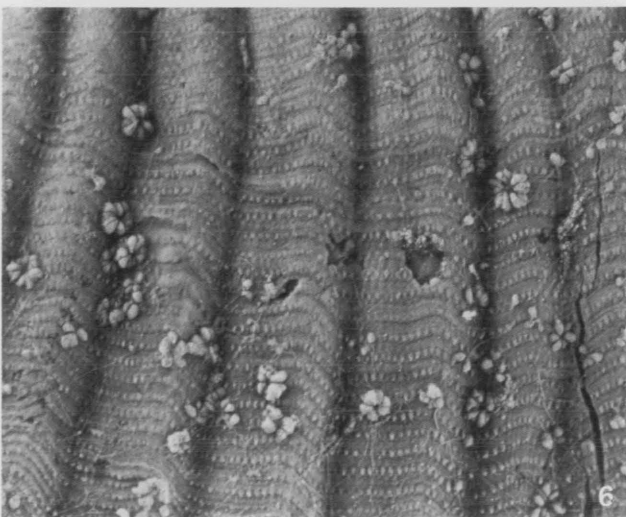
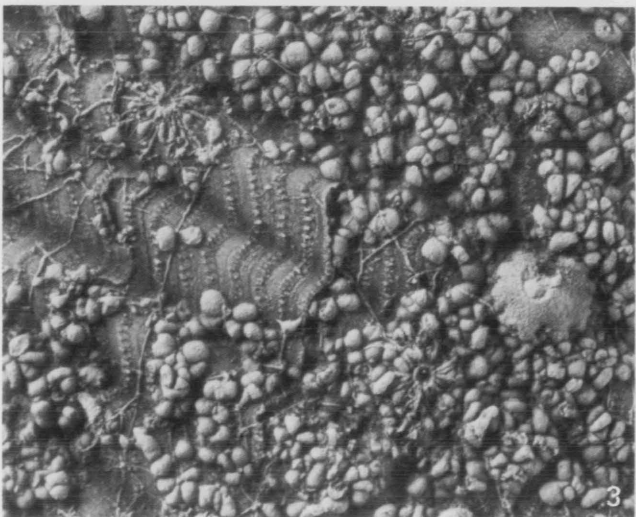
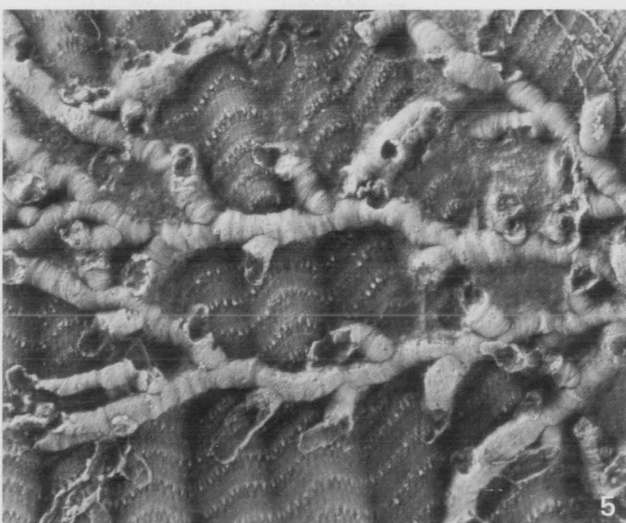
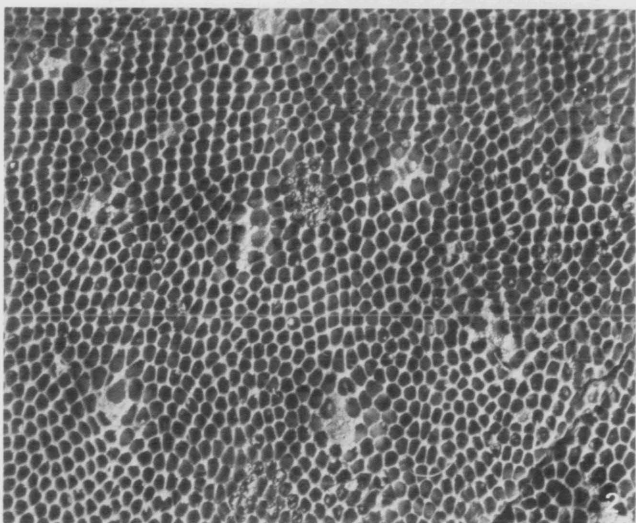


PLATE 20



EXPLANATION OF PLATE 20

All figures x8

- FIG. 1 -- UMMP 63622. *Botryllopora socialis* Nicholson. Another part of this excellent colony of the cystopore bryozoan, as seen on the anterior margin of the host's brachial valve. See remarks under explanation of plate 19, figs. 4, 6. Host shown natural size on plate 5, figs. 4, 5; other enlargements on plate 14, figs. 1, 2, and plate 19, figs. 4, 6.
- FIG. 2 -- UMMP 63128. *Atactotoechus* cf. *A. typicus* Duncan. This trepostome bryozoan blankets all but a small area on the pedicle valve of its host. Zooecia are remarkably equal in size, even those involved in the sharply elevated monticules. Host shown natural size on plate 1, figs. 8, 9; other enlargements of the *Atactotoechus* colony on plate 7, fig. 4; plate 10, fig. 2; and plate 14, fig. 6.
- FIG. 3 -- UMMP 63133. *Eliasopora stellatum* (Nicholson & Etheridge), *Ascodictyon radians* Nicholson & Etheridge, and a holdfast. The two ctenostome bryozoans are easily distinguished. Although both have clusters of radiating vesicles, *Eliasopora* lacks the central sphere in each stellar cluster and its radiating vesicles are more elevated and less elongate. The two specimens of *Ascodictyon radians* shown here seem to have deflated vesicles. The small holdfast has the cicatrix of columnar articulation, although it is not clearly exposed. Host shown natural size on plate 1, figs. 12, 13.
- FIG. 4 -- UMMP 63138. Holdfast and *Cornulites* sp. The anterior margin at the juncture of fold and right lateral surface in this *Paraspirifer bownockeri* shows a small echinoderm holdfast and the tube of the parasitic worm *Cornulites*. Associated with the holdfast is a short section of tiny column. The *Cornulites* tube has both irregular annulations and longitudinal striae. Host shown natural size on plate 1, fig. 1.
- FIG. 5 -- UMMP 63139. *Hederella concinnoides* Bassler. This cyclostome bryozoan has very small zooecia. The colony, on the left side of the brachial valve, shows the typical 60° angles of budding and branching. Host shown natural size on plate 1, fig. 6; another enlargement of the colony on plate 10, fig. 3.
- FIG. 6 -- UMMP 63141. *Ascodictyon floreale* Ulrich & Bassler. This ctenostome bryozoan has filamentous stolons connecting tiny flower-like clusters of vesicles. It is smaller than the similar *Eliasopora stellatum*. Host shown natural size on plate 1, fig. 11; another enlargement on plate 10, fig. 4.

EXPLANATION OF PLATE 21

All figures x 8

- FIG. 1 -- UMP 63154. *Hederella delicatula* Hall & Simpson. On the right side of the brachial valve of its host, this cyclostome bryozoan developed a typical colony with 90° branching. The zooecia are small for the genus. Host shown natural size on plate 1, fig. 5.
- FIG. 2 -- UMP 63166. ?*Leioclema* sp. The colony of this trepostome bryozoan died out while still covering only a small area in the right posterior sector of the host. As viewed posteriorly, the edge of the colony spans the hinge area to lie on the brachial valve; this expansion must have taken place after death of the *Paraspirifer*. Host shown natural size on plate 1, figs. 3, 4; another enlargement on plate 10, fig. 5.
- FIG. 3 -- UMP 63180. *Hederella magna* Hall. This cyclostome bryozoan settled on the right side of the brachial valve near the margin and colonized across the fold. It has very large zooecia, exceeded in the Silica Formation only by *H. reimanni*. Some zooecia extend atop others, to create locally thick parts of the colony. Host shown natural size on plate 4, fig. 6; another enlargement on plate 7, fig. 5.
- FIGS. 4-6 -- UMP 63186. *Cornulites* sp. Three individuals of this parasitic worm attached their conical tubes to the left side of the pedicle valve and grew forward at the same pace as the shell of the host. Although the open ends of two tubes are broken (figs. 5, 6), none of the tubes appears to have attained the final position of the brachiopod's commissure. From this, it may be inferred that the *Cornulites* all expired shortly before their host; this is not usually the case, and most *Cornulites* probably met death by starvation after the host expired. One of the tubes (fig. 5) was itself bored by some organism and repaired its shell. Host shown natural size on plate 2, figs. 1, 2.

PLATE 21

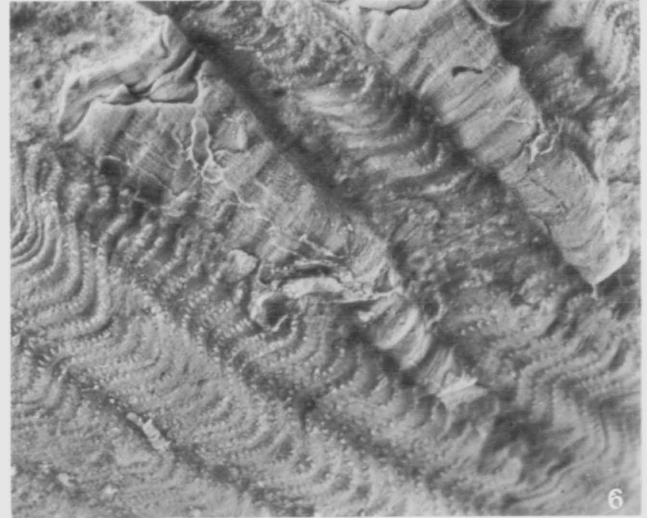
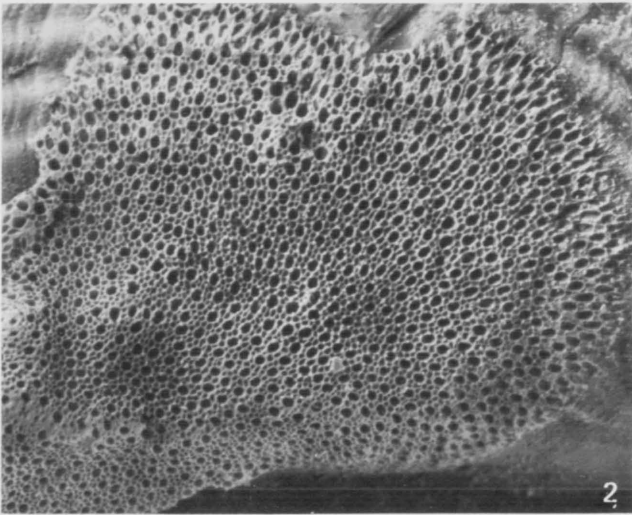
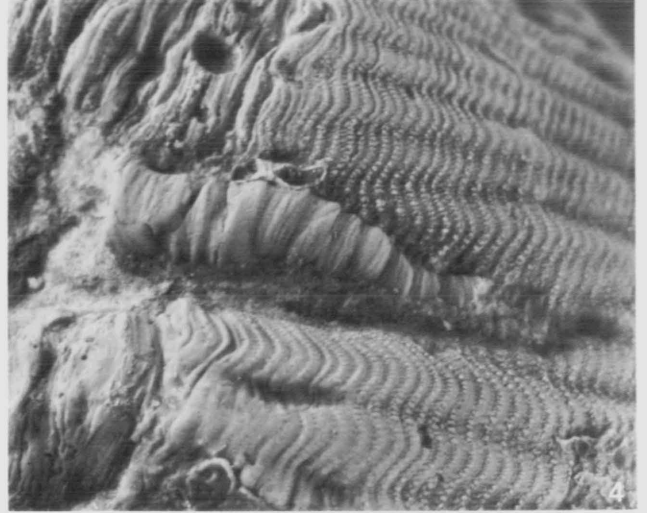
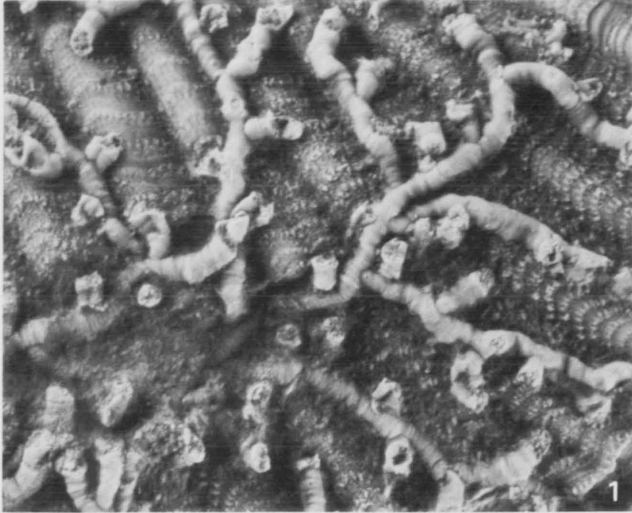
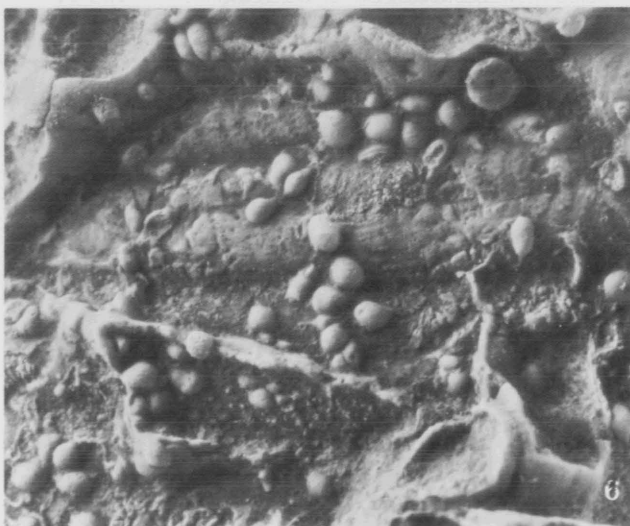
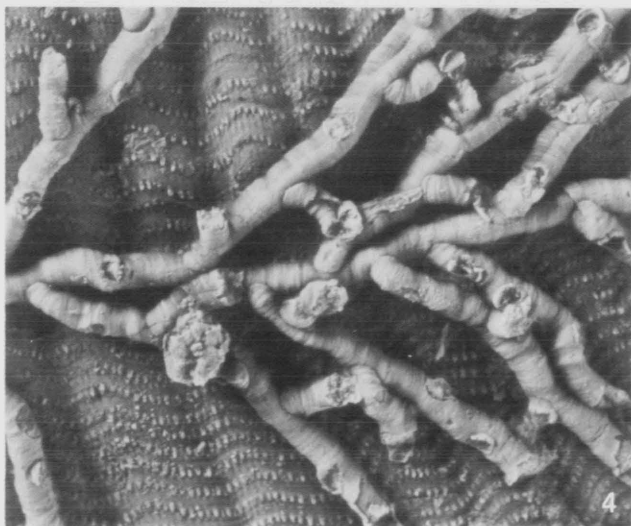
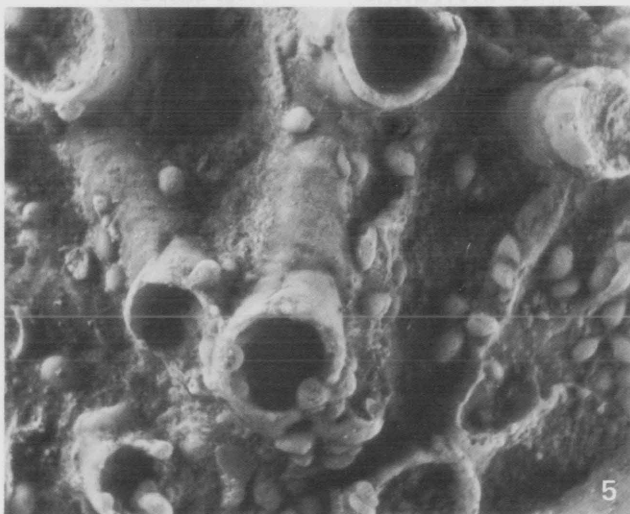
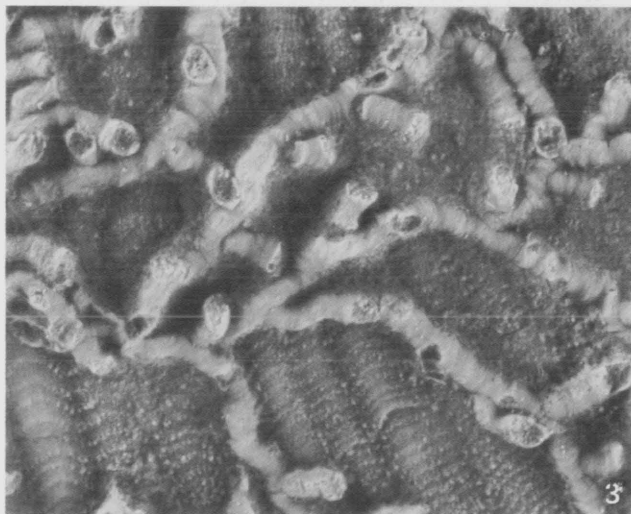
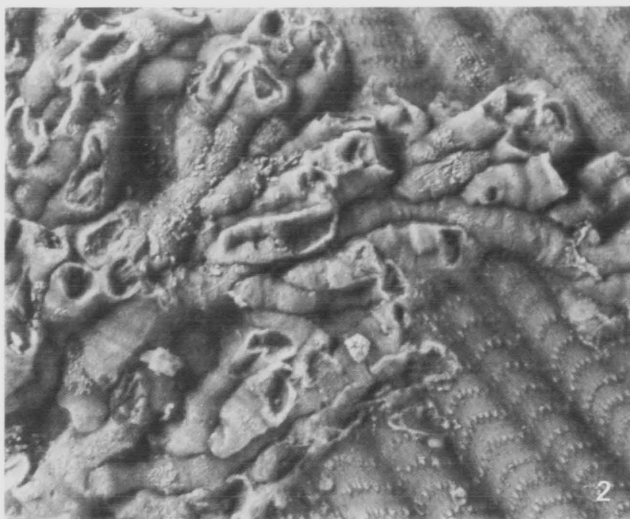
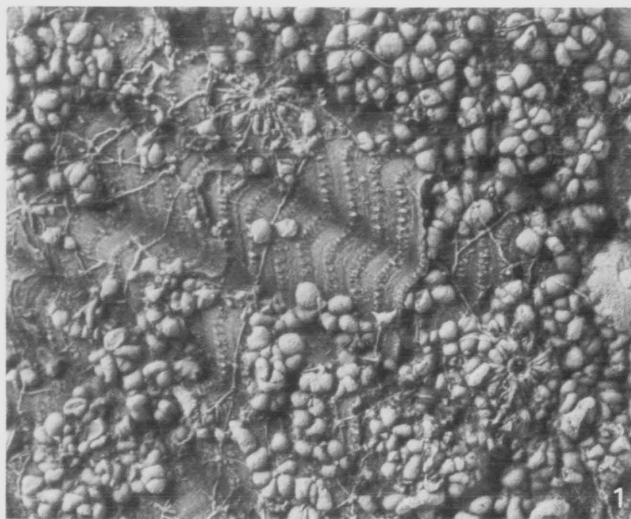


PLATE 22



EXPLANATION OF PLATE 22

All figures x 8

- FIG. 1 -- UMMP 63133. *Ascodictyon radians* Nicholson & Etheridge and *Eliasopora stellatum* (Nicholson & Etheridge). On the left side of the brachial valve of this *Paraspirifer* are two ctenostome bryozoans. The more numerous is the *Eliasopora*. *Ascodictyon radians* differs from the *Eliasopora* in having larger clusters of vesicles (rosettes), a central sphere in each rosette, and more elongate, wedge-shaped, and lower vesicles. Host shown natural size on plate 1, figs. 12, 13; another enlargement on plate 20, fig. 3.
- FIG. 2 -- UMMP 63202. *Hederella thedfordensis* Bassler. This cyclostome bryozoan lies on the right side of the host's brachial valve. Host shown natural size on plate 2, figs. 5, 6; other enlargements on plate 8, figs. 8, 9.
- FIG. 3 -- UMMP 63200. *Hederella concinnoides* Bassler. The colony of this cyclostome bryozoan has spread over the brachial valve of its host. The zooecia of this species are small for the genus, and in this colony are rather irregularly distributed along the branches. Host shown natural size on plate 2, figs. 3, 4; another enlargement of the colony on plate 9, fig. 3.
- FIG. 4 -- UMMP 63188. *Hederella concinnoides* Bassler. The colony shown here has had a unidirectional development and is probably young. The 60° branching is well shown. Host shown natural size on plate 3, fig. 10; another enlargement of the colony on plate 9, fig. 1.
- FIGS. 5, 6 -- UMMP 63276. *Ascodictyon fusiforme* (Nicholson & Etheridge) and *Aulopora microbucinata* Watkins. The tabulate coral *Aulopora* preceded the colonization by the ctenostome bryozoan *Ascodictyon*, inasmuch as vesicles of the latter lie upon some corallites. Host shown natural size on plate 2, figs. 7, 8; another enlargement on plate 23, fig. 4.

EXPLANATION OF PLATE 23

All figures x8

FIG. 1 -- UMMP 63300. *Hederella filiformis* (Billings). On the right posterior area of the brachial valve of the *Paraspirifer*, this colony of the cyclostome bryozoan extends both across costae and along them. Some sections of central axis and zooecia have collapsed, from causes unexplained. Host shown natural size on plate 3, fig. 5; another enlargement on plate 7, fig. 3.

FIG. 2 -- UMMP 63300. ?*Leptotrypella* sp. The small colony of this trepostome bryozoan is located on the right anterior margin of the host's brachial valve. For some reason, it expired before colonizing the adjacent available area. This bryozoan spread over the area after the host was bored by the parasitic sponge "*Clionoides*," as shown by the fact that the ?*Leptotrypella* colony covered over one bore hole and bordered the other with unbroken zooecia. Host shown natural size on plate 3, fig. 5.

FIG. 3 -- UMMP 63332. *Hederella rugosa* Bassler. The colony of the cyclostome bryozoan is developed on the brachial valve of the host. This section, on the right side of the fold, shows the rugosity of the axial and zooecial tubes for which the species was named. Host shown natural size on plate 3, fig. 6.

FIG. 4 -- UMMP 63276. *Aulopora microbuccinata* Watkins, *Botryllopora socialis* Nicholson, and *Ascodictyon fusiforme* (Nicholson & Etheridge). On the left side of the fold near the anterior edge of the *Paraspirifer bownockeri*, these three epizoans occur in close proximity. The tabulate coral *Aulopora* was the first to colonize the area, as shown by the cystopore bryozoan *Botryllopora* upon some of its corallites; *Botryllopora* itself is overgrown by vesicles of the ctenostome bryozoan *Ascodictyon fusiforme*. Host shown natural size on plate 2, figs. 7, 8; other enlargements of the *Ascodictyon fusiforme* on plate 22, figs. 5, 6.

FIGS. 5, 6 -- UMMP 63307. *Ascodictyon fusiforme* (Nicholson & Etheridge). These areas on the left side of the host's brachial valve contain characteristic developments of this ctenostome bryozoan. Where the colonization reaches the tabulate coral *Aulopora microbuccinata* (fig. 5), the bryozoan vesicles encroach onto the older corallites. Host shown natural size on plate 3, figs. 1, 2; another enlargement on plate 9, fig. 6.

PLATE 23

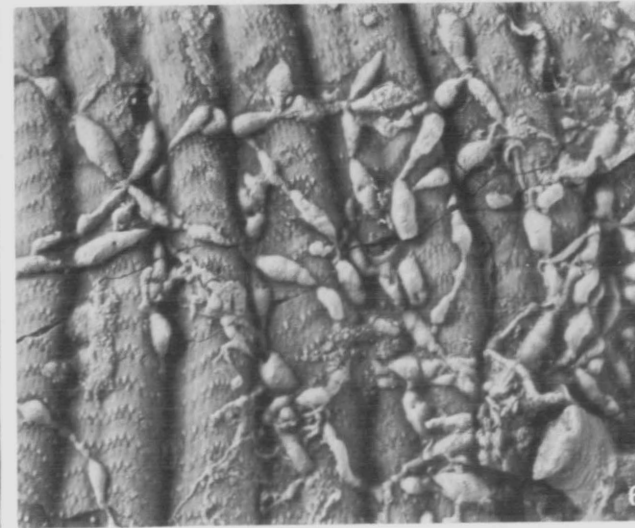
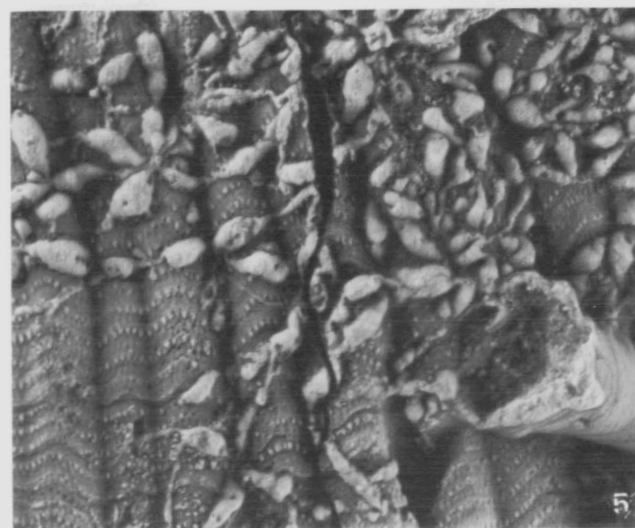
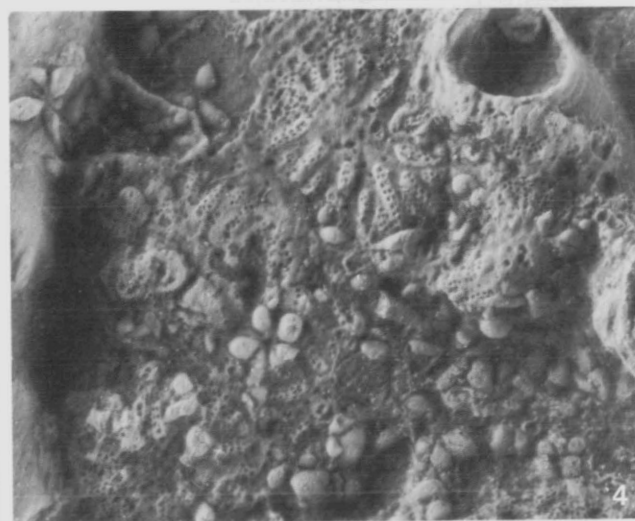
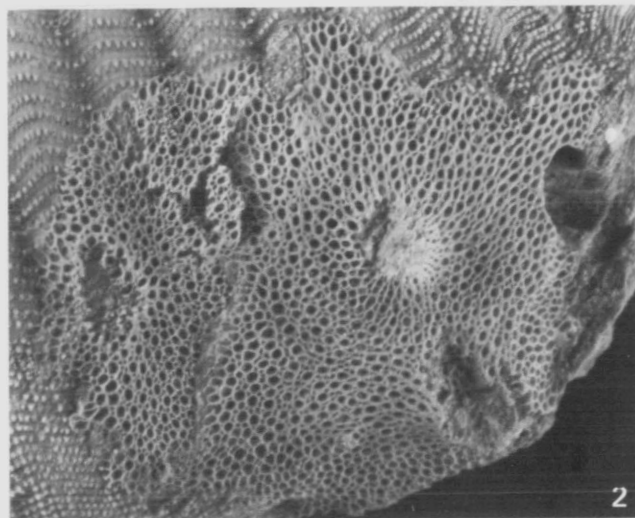
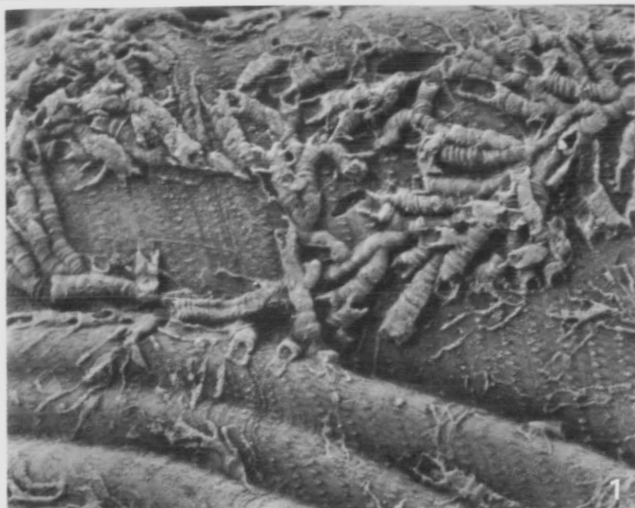


TABLE 20 -- List of illustrations of epizoans on *Paraspirifer bownockeri*.
Each plate reference consists of the plate number, a virgule (/), and the figure number or numbers.

Species	Spec. No.	x1	x2	x4	x8
<i>Ascodictyon (?) conferta</i>	63501	6/5	--	12/1,2	18/1
<i>Ascodictyon floreale</i>	63141	1/11	--	10/4	20/6
	63508	6/4	8/5	--	17/5
<i>Ascodictyon fusiforme</i>	63276	2/7,8	--	--	22/5,6; 23/4
	63307	3/1,2	9/6	--	23/5,6
	63388	4/1,2	--	--	16/3
<i>Ascodictyon radians</i>	63133	1/12,13	--	--	20/3
<i>Atactotoechus</i> cf. <i>A. typicus</i>	63128	1/8,9	7/4	10/2; 14/6	20/2
<i>Aulopora microbuccinata</i>	63138	1/1	--	--	--
	63146	2/9-12	10/1	--	--
	63149	1/10	--	--	--
	63166	1/3,4	--	10/5	--
	63276	2/7,8	--	--	22/5,6; 23/4
	63307	3/1,2	9/6	--	--
	63388	4/1,2	--	--	16/3
	63428	6/3	9/2	--	17/2
	63501	6/5	--	12/2	--
<i>Botryllopora socialis</i>	63276	2/7,8	--	--	23/4
	63388	4/1,2	--	--	16/4
	63622	5/4,5	--	14/1,2	19/4,6; 20/1
" <i>Clionoides</i> " sp.	63133	1/12,13	--	--	--
	63166	1/3,4	--	--	--
	63175	1/7	--	--	--
	63236	5/11	--	--	--
	63320	3/3,4	--	--	--
	63508	6/4	--	--	--
<i>Cornulites</i> sp.	63138	1/1	--	--	20/4
	63166	1/3,4	--	--	--
	63186	2/1,2	--	--	21/4-6
	63236	5/11	--	11/3	--
	63271	3/7	7/8	--	--
	63385	6/1,2	9/4	--	--
<i>Cyrtina "hamiltonensis"</i>	63437	5/6,7	--	13/5	--
<i>Eliasopora stellatum</i>	63133	1/12,13	--	--	20/3
	63428	6/3	9/2	--	17/2,3
	63501	6/5	--	--	--
<i>Hederella alternata</i>	63640	5/8	--	13/6	15/5
<i>Hederella bilineata</i>	63634	4/8	--	12/3	15/4
" <i>Hederella canadensis</i> " group	63664	5/9	8/3	--	6/10
<i>Hederella concinna</i>	63664	5/9	8/2	--	15/6
<i>Hederella alpenensis</i>	63202	2/5,6	--	--	--
	63622	5/4,5	--	14/3	19/5
<i>Hederella concinnoides</i>	63139	1/6	--	10/3	20/5
	63188	3/10	9/1	--	22/4
	63200	2/3,4	9/3	--	22/3
<i>Hederella delicatula</i>	63154	1/5	--	--	21/1

Table 20 continued --

Species	Spec. No.	x1	x2	x4	x8
<i>Hederella filiformis</i>	63154	1/5	7/2	--	--
	63300	3/5	7/3	--	23/1
	63310	3/8,9	--	14/5	6/11
	63465	5/1	8/6	--	17/4
<i>Hederella magna</i>	63180	4/6	7/5	--	21/3
<i>Hederella cf. H. michiganensis</i>	63320	3/3,4	--	--	--
<i>Hederella parvirugosa</i>	63385	6/1,2	9/4	--	16/1
	63579	6/7	8/7	--	19/2
<i>Hederella reimanni</i>	63581	5/12	9/5	--	19/3
<i>Hederella rugosa</i>	63332	3/6	--	--	23/3
<i>Hederella thedfordensis</i>	63202	2/5,6	8/8,9	--	22/2
	63300	3/5	7/3	--	16/6
	63385	6/1,2	7/6; 9/4	--	16/2; 18/6
	63427	5/2,3	--	13/4	17/1
	63465	5/1	8/6	--	--
	63508	6/4	8/4,5	--	17/6; 18/5
	<i>Hederella spp.</i>	63501	6/5	7/9	--
Holdfasts	63175	1/7	--	10/6	--
	63133	1/12,13	--	--	20/3
	63138	1/1	--	--	20/4
? <i>Leioclema</i> sp.	63166	1/3,4	--	10/5	21/2
	63501	6/5	7/9	--	18/2-4
<i>Leptotrypella</i> sp.	63300	3/5	--	--	23/2
<i>Lingulodiscina marginalis</i>	63310	3/8,9	--	12/6; 14/4	--
"Mediospirifer audaculus"	63121	1/2	7/1	--	--
	63202	2/5,6	8/8	--	--
	63339	4/10-12	--	13/5	--
<i>Orbiculoidea doria</i>	63390	5/10	--	12/4,5	--
<i>Petrocrania hamiltoniae</i>	63149	1/10	7/7	--	--
<i>Philhedra crenistriata</i>	63653	6/6	8/1	15/1	--
<i>Philhedra sheldoni</i>	63298	4/9	--	11/4	--
<i>Philhedra stewarti</i>	63141	1/11	--	10/4	--
Puncture	63256	4/3-5	--	13/1,2	--
	63565	6/8,9	--	--	--
	63665	5/13,14	--	15/2,3	--
<i>Ropalonaria tenuis</i>	63186	2/1,2	7/1	--	--
Rugose coral	63412	4/7	--	11/6	--
<i>Spirorbis planum</i>	63388	4/1,2	--	--	19/1
	63412	4/7	--	--	16/5
Worm	63336	3/11,12	--	11/5	--

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FRONT COVER: Brachial view of *Paraspirifer downockeri*, UMMP 63307, bearing commensal colonies of the tabulate coral *Aulopora microbuccinata* (right and center) and the ctenostome bryozoan *Ascodictyon fusiforme* (center left). Perforations of the shell near the anterior margin (left) are borings made by the parasitic sponge "*Clionoides*." The indentation below the left cardinal corner marks the position of mantle damage by the parasitic worm *Cornulites*, whose conical shell lies on the pedicle valve.

BACK COVER: All figures x 16. Upper left - *Eliasopora stellatum* and *Ascodictyon radians*, two ctenostome bryozoans, on UMMP 63133; the latter is located at the corners of the figure. Upper right - *Botryllopora socialis*, a cystopore bryozoan, on the brachial valve of UMMP 63622. Lower left - *Leptotrypella* sp., a small colony of this trepostome bryozoan, on the brachial valve of UMMP 63300. Lower right - *Hederella concinoides*, a cyclostome bryozoan, on UMMP 63188. Other enlargements of these epizoans on plate 20, fig. 3, plate 20, fig. 1, plate 23, fig. 2, and plate 22, fig. 4.

