A DEVONIAN BRACHIOPOD WITH EPIFAUNA[1]

R. D. HOARE AND D. L. STELLER
Bowling Green State University, Bowling Green, Ohio 43402

ABSTRACT

Recognition of epifauna-host relationships are difficult to ascertain in fossil material. Distribution and orientation of epifaunal elements, repair of the host shell, deformation of the host by the epifauna, and continued growth of the host provides evidence of the type of relationship.

Brachiopods in the Devonian Silica Formation of northwestern Ohio commonly have abundant epifauna. A specimen of *Paraspirifer bownockeri* Stewart, collected from this formation shows evidence of a parasitic, in part antagonistic, relationship with the boring sponge *Clionoides thomasi* Fenton and Fenton and commensal relationships with the worm *Cornulites cingulatus?* Hall, the inarticulate brachiopod *Lingulodiscina marginalis* Whitfield, and possibly the bryozoans *Hederella canadensis* (Nicholson) and *H. cirrhosa* (Hall). 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.

INTRODUCTION

Epifaunal elements, as they occur on brachiopods, have been reported by many authors in the process of describing faunas. Usually little or no indication has been made as to the relationship of the epifauna to the host or between epifaunal elements. A few authors, including Ager (1961; 1965), Clarke (1921), Fenton and Fenton (1932a), Hecker (1957), Shou-Hsin (1959), and Yakovlev (1926), have postulated various types of possible relationships between epifauna and brachiopod hosts, based upon the type of epifauna, its distribution on the host, and noticeable reactions of the host to the epifauna.

The problem of recognition of possible relationships is in part based upon knowing whether the host was alive or dead at the time of attachment and growth of the epifauna. In most instances it is impossible to make this determination from the specimens. The shell of a dead organism may serve just as favorably as a substrate for attachment as the shell of a live one. If growth of the epifauna is not controlled by growth characteristics of the host, whether the host was alive or dead may not be determinable. In cases where the host reacted to activity of the epifauna, evidence may be present which will allow interpretation, not only of whether the host was dead or alive, but also as to the relationship between epifauna and host.

Characteristics which may give evidence of some type of life relationship between epifauna and host are distribution and orientation of epifaunal elements on the host, subsequent repair of the shell by the host, deformation of the host shell by the epifauna, and evidence for continuance of growth of the host after attachment of epifauna.

When a commensal or mutualistic relationship exists between epifauna and host, such as the former benefiting from the inhalent or exhalent currents of the latter, the distribution and orientation of the epifauna on the host could be indicative of the type of relationship and whether the host was alive or dead, as postulated by Ager (1961), Hecker (1957), Shou-Hsin (1959), and others. Presumably it would be necessary to study large numbers of specimens to be certain the observations were not just a chance relationship. Statistical analysis of such populations might indicate whether the distribution and orientation of epifaunal elements were more than happenstance, as it might be if many of the hosts were dead at the time of epifaunal attachment. Individual specimens might serve as a basis for

---

[1] Manuscript received March 28, 1967.

THE OHIO JOURNAL OF SCIENCE 67(5): 291, September, 1967.

such interpretation if other characteristics of host and epifauna provide evidence to help support the relationship.

Organisms such as sponges and barnacles, which bore into and through the valves of a host shell, cause the host to secrete secondary shell material to repair the shell and thus indicate that the host was alive, as postulated by Lane (1963). In figure 2, an interior view of the pedicle valve of the Pennsylvanian brachiopod *Schizophoria texana* Girty illustrates an attempt of the brachiopod host to repair the damage to the shell by boring acrothoracic barnacles. The blister-like deposits around the holes are composed of secondary deposits of calcium carbonate which completely cover some of the smaller borings. Most of the larger borings are only partially closed off. Deposition of the blister-like coverings must have occurred while the host was still alive.

If the host had been dead, no repair could have been possible, thus giving evidence of attachment after death of the host. Figure 1 illustrates a partial specimen of the phragmacone of *Belemnitella americana* (Morton) of Cretaceous age. Borings of the sponge *Cliona cretacia* Fenton and Fenton have riddled the posterior portion of the phragmacone. The borings are preserved as internal molds with openings to the burrows located on both the internal and external surfaces of the phragmacone. No evidence of repair by deposition of secondary shell material by the host can be seen, so it is apparent that the host was dead prior to the formation of burrows by the sponges.

The effect of a predaceous or parasitic relationship such as this may also cause the host to cease growth for a period of time, resulting in the development of a pronounced growth line which may show some relationship to the distribution of the epifauna on the shell surface. If the mantle of the host has been damaged by a boring organism, the configuration during further growth of the shell may be affected, as indicated by Clarke (1921) and by Fenton and Fenton (1932b). Repair of the shell and continued growth could not take place after death of the host.

GENERAL BRACHIOPOD EPIFAUNAL RELATIONSHIPS IN THE SILICA FORMATION

Steller (1965), in a general study of brachiopod epifauna in the Silica Formation exposed in the north quarry of the Medusa Portland Cement Co. near Sylvania,

---

EXPLANATION OF PLATE 1

Belemnitella americana (Morton)

FIGURE 1. Phragmacone showing borings of the sponge *Cliona cretacica* Fenton and Fenton preserved as internal molds. Openings of burrows extend to both interior and exterior surfaces of phragmacone, indicating, because of the lack of repair of shell material that the host was dead, ×1, Upper Cretaceous, locality unknown, BGSU-3802.

Schizophoria texana Girty

FIGURE 2. Interior surface of pedicle valve with borings of acrothoracic barnacles showing deposition of secondary shell material by host in order to close off openings, ×2, Lower Pennsylvanian, Nevada, BGSU-3803.

Paraspirifer bownockeri (Stewart)

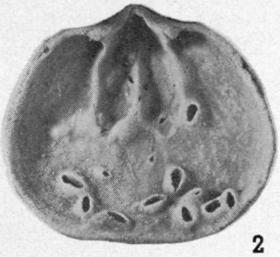
FIGURE 3. View of lateral portion of brachial value showing almost complete restriction of colony of *Hederella canadensis* (Nicholson) along major growth line, extensions of this colony onto new shell growth, distribution of species of *Lingulodiscinia marginalis* Whitfield on new shell growth, and development of groove in new shell growth inhabited by a specimen of *Cornulites cingulatus?* Hall, ×2, Silica Formation, BGSU-3765.

FIGURE 4. View of sulcus showing closely associated small specimens of *Lingulodiscina marginalis* Whitfield and *Cornulites cingulatus?* Hall near line of commissure on new shell growth, and a few of the borings of *Clionoides thomasi* Fenton and Fenton near major growth line on pedicle valve, ×2, Silica Formation, BGSU-3765.

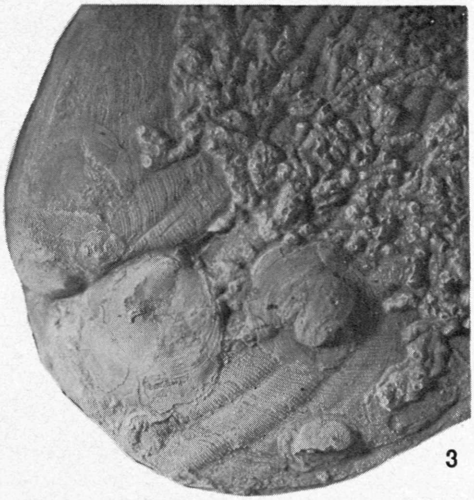
FIGURE 5. View on brachial valve showing immature specimen of *Lingulodiscinia marginalis* Whitfield at posterior margin of colony of *Hederella canadensis* (Nicholson), ×2, Silica Formation, BGSU-3765.

FIGURES 6, 7. Views of brachial value showing distribution of borings of *Clionoides thomasi* Fenton and Fenton, distribution of *Lingulodiscinia marginalis* Whitfield, and groove inhabited by *Cornulites cingulatus?* Hall, ×2, Silica Formation, BGSU-3765.

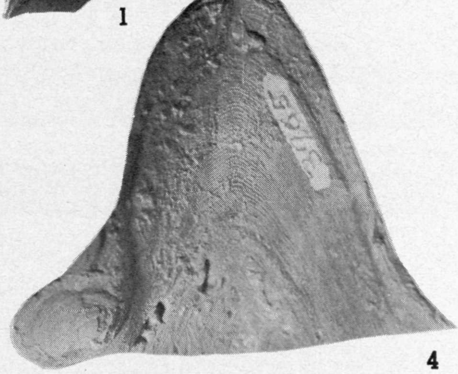
1



2



3



4

5

6

7

PLATE 1

Ohio, reports that, of the larger brachiopods, a smaller percentage of specimens of *Paraspirifer bownockeri* bear epifaunal elements. Examination of 3105 specimens of *Paraspirifer*, *Stropheodonta*, *Megastrophia*, *Protoleptostrophia*, *Spinocyrtia*, and *Brachyspirifer* shows that only 36.1 per cent of the specimens of *Paraspirifer* have epifauna, whereas the other genera listed above range from 38 to 59 per cent with epifaunal elements. Smaller forms, such as *Devonochonetes*, *Mucrospirifer*, *Atrypa*, and *Pholidostrophia*, range from 9.5 to 25.3 per cent of specimens bearing epifauna.

Epifauna found associated with *P. bownockeri* by Steller (1965) are the inarticulate brachiopods *Philhedra crenistriata* (Hall), *Petrocrania hamiltonae* (Hall), and *Lingulodiscinia marginalis* Whitfield; the bryozoans *Eliaspora stellata* (Nicholson), *Hederella cirrhosa* (Hall), *H. canadensis* (Nicholson), *Fistulipora vesiculata* (Hall and Simpson), and *Anomolotoechus tuberatus* Duncan; the coral *Aulopora serpens* Goldfuss; the worm, *Cornulites cingulatus?* Hall, and the sponge *Clionoides thomasi* Fenton and Fenton. Of these, the occurrence of the species of *Hederella* was by far the most common, being present on 78.6 per cent of the specimens of *P. bownockeri* with epifauna.

DETAILED EPIFAUNA—HOST RELATIONSHIPS

Of the specimens of *Paraspirifer bownockeri* examined, one, no. 3765 in the BGSU repository, collected at the north quarry of the Medusa Portland Cement Co., provides rather detailed information concerning the life-death relationship between the host and epifaunal elements. The specimen, illustrated on Plate 1, figs. 3–7, and Plate 2, figs. 1, 2, has associated with it two colonies of *Hederella canadensis*, one colony of *H. cirrhosa*, three specimens of *Cornulites cingulatus?*, 19 specimens of *Lingulodiscina marginalis*, and at least 29 borings made by *Clionoides thomasi*. A reconstruction of this specimen showing the arrangement of sponge borings along a major growth line is illustrated on Plate 2, figure 1. The reconstruction, on Plate 2, fig. 2, is presented to give an impression of the total epifauna which inhabited the specimen, although some of these elements, primarily the sponges, were not present during the final growth stages of the host.

The earliest elements to attach to the host specimen were either the colonies of *Hederella* or the specimens of *Clionoides*. The two colonies of *H. canadensis* are attached and concentrated on the brachial valve near mid-length, one colony being neatly restricted, except for three areas of later growth, along a major growth line (Pl. 1, fig. 3; pl. 2, fig. 1). The small colony of *H. cirrhosa* is located in the sulcus of the pedicle valve near mid-length (Pl. 2, fig. 2). The borings of the sponge *Clionoides* are concentrated on both valves along the same major growth line which practically limits antero-lateral growth of the first colony of *H. canadensis* mentioned above (Pl. 1, figs. 4, 6, 7; pl. 2, figs. 1, 2). A larger number of the borings and also the larger borings are located posterior to this growth line (Pl. 1, figs. 6, 7; pl. 2, fig. 1).

The presence of the sponges may have prevented the extension of the bryozoan colonies in an antero-lateral direction until the sponges died, were killed, or in some other manner eliminated from the host. The bryozoan colonies may have then developed in this direction, partially covering the sponge borings. The

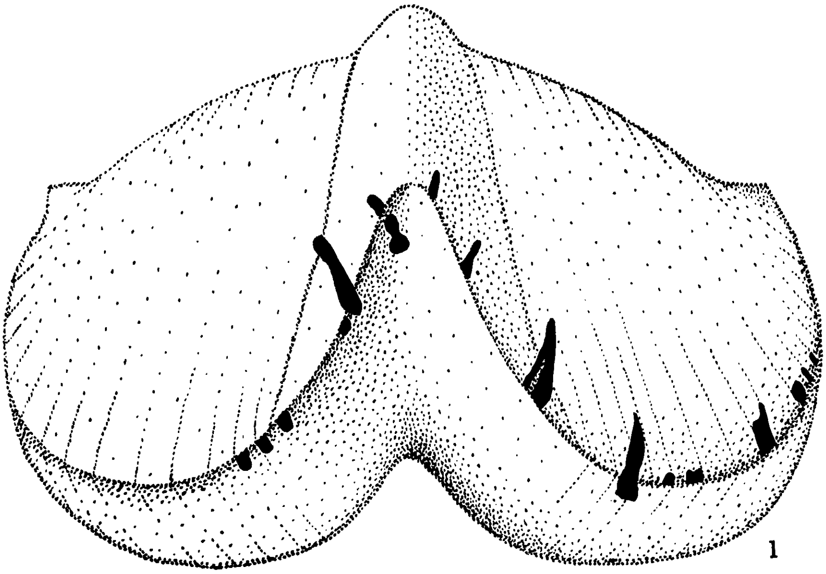
---

EXPLANATION OF PLATE 2

Paraspirifer bownockeri (Stewart)

FIGURE 1. Reconstruction of shell at major growth line illustrating distribution of borings of *Clionoides thomasi* Fenton and Fenton, ×2, Silica Formation, BGSU-3765.

FIGURE 2. Reconstruction of total epifauna. All elements not present at one time and appearance of sponges not necessarily as illustrated, ×2, Silica Formation, BGSU-3765.



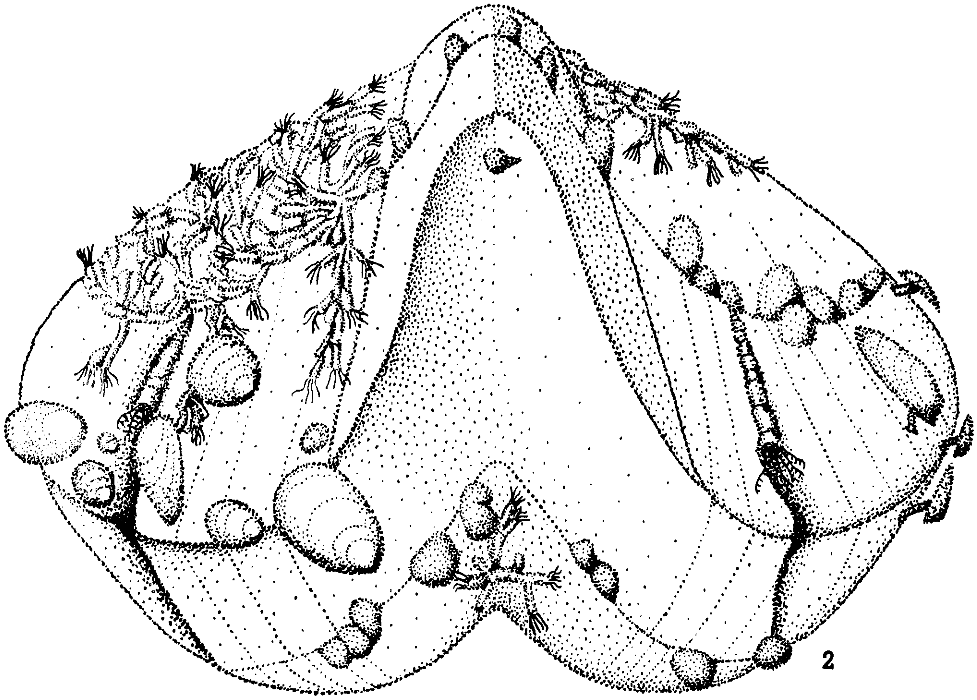


PLATE 2

action of the sponges along the line of commissure at this stage of growth appears to have been responsible for the cessation of growth by the host and consequently the development of the major growth line. 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 of the shell for feeding.

When the host resumed growth, the majority of the sponges were apparently gone, with the exception of a few indicated by borings into the new shell material (Pl. 1, fig. 7; pl. 2, fig. 2). The edge of the mantle was apparently injured at two positions by the action of the sponges, which resulted in deformations in the new shell growth in the form of major grooves, which are present on both valves (Pl. 1, figs. 3, 7; pl. 2, fig. 2). The borings which caused this injury are exposed on one side of the shell, but subsequent growth of a colony of *H. canadensis* appears to have covered them on the other side (Pl. 1, fig. 3; pl. 2, fig. 2).

Extensions of one colony of *Hederella* occurred in the area of new shell growth (Pl. 1, fig. 3; pl. 2, fig. 2). The two grooves on the brachial valve, produced by the injury to the mantle, became inhabited by specimens of *Cornulites*, with growth of these specimens in an anterior direction in relation to the host (Pl. 1, figs, 3, 7; pl. 2, fig. 2). The third specimen of *Cornulites* is located in the sulcus near the line of commissure (Pl. 1, fig. 4; pl. 2, fig. 2) and is partially obscured by an immature specimen of *L. marginalis*.

Occupancy of the host surface by the inarticulate brachiopod *Lingulodiscinia* appears to have taken place after new shell growth occurred, possibly after the full size of the specimen had been reached. Of the 19 specimens of *Lingulodiscinia* present, 18 are attached to the area of most recent growth, with most of the larger specimens located quite near the line of commissure. The one specimen not in this area is a juvenile and is located on the brachial valve at the posterior margin of a colony of *Hederella* (Pl. 1, fig. 5). Of the 18 others, the concentrations are in antero-lateral positions on both valves (Pl. 1, figs. 3, 7; pl. 2, fig. 2), with one juvenile specimen in the sulcus near the line of commissure (Pl. 1, fig. 4; pl. 2, fig. 2).

Lingulodiscinia was attached by a pedicle to the host shell. Growth of the colonies of *Hederella* occurred under the inarticulate shells and around the position of pedicle attachment of some specimens, so that compaction of the inarticulates onto the host shell caused portions of the bryozoan colonies to be covered by the inarticulates (Pl. 1, fig. 3; pl. 2, fig. 2).

Epifaunal elements are not present in the area of the hinge line, on the postero-central portion of the brachial valve, or on the posterior portion of the pedicle valve. *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.

All of the epifaunal elements may have benefited from the water-current action produced by the host. The bryozoan colonies show no preferred direction in their development, growing posteriorly, anteriorly, and laterally in relation to the host shell. The larger specimens of *Cornulites* are oriented in an anterior direction, their direction of growth controlled by the grooves in the shell. The smaller specimen, in the sulcus, has a general anterior orientation. Specimens of this genus on many other shells normally are oriented towards the line of commissure, whether they occupy grooves, intercostal spaces, or a smooth surface, and the relationship appears to be commensal, with the worms benefiting from the current action of the host.

The distribution of the inarticulate brachiopods may be significant. In relation to the size of the host shell, it seems unreasonable that chance attachment following spat fall would occur only near the line of commissure. Possibly the inhalent currents of the host were instrumental in bringing the spat to the host at this position. Other specimens of *Paraspirifer* show attachment of other genera of inarticulate brachiopods in a more haphazard arrangement. This is the only occurrence of *Lingulodiscinia* known from the Silica Formation and the position of attachment and specific association may be more than chance. In this instance the relationship is commensal, with the inarticulates benefiting from the water currents set up by the host.

The sponge *Clionoides* was parasitic on the host, weakening the shell by boring into it. The host was affected by this action, as evidenced by its cessation of growth for a period of time and by the injury to the mantle, which caused the deformation of the shell, so that the relationship was in part antagonistic and nearly became antibiotic (Ager, 1963).

ACKNOWLEDGMENTS

The authors wish to thank Mrs. Ruth Beiswenger, who collected the specimen of *Paraspirifer;* Cynthia Boyd, who collected the specimen of *Belemnitella;* and N. Gary Lane, who collected the specimen of *Schizophoria;* all of which were donated to the Department of Geology, Bowling Green State University.

REFERENCES CITED

Ager, D. V. 1961. The epifauna of a Devonian spiriferid. Quat. Jour. Geol. Soc. London 117: 1–10.

———. 1963. Principles of Paleoecology. McGraw-Hill Co., Inc. 371 p.

Clarke, J. M. 1921. Organic dependence and disease: their origin and significance. N. Y. State Mus. Bull. 221, 222, 113 p.

Fenton, C. L. and **M. A. Fenton.** 1932a. Boring sponges in the Devonian of Iowa. Amer. Midland Nat. 13: 44–54.

———. 1932b. Orientation and injury in the genus *Atrypa*. Amer. Midland Nat. 13: 63–74.

Hecker (Gekker), R. F. 1957. Introduction to Paleoecology. Amer. Elsevier Pub. Co., Inc. 166 p. (English translation, 1965).

Lane, N. G. 1963. A silicified Morrowan brachiopod faunule from the Bird Spring Formation, southern Nevada. Jour. Paleontology 37: 379–392.

Shou-Hsin, Chang. 1959. Note on the paleoecological relation between *Aulopora* and *Mucrospirifer*. Acta Paleont. Sinica 7: 502–504.

Steller, D. L. 1965. The epifaunal elements on the Brachiopoda of the Silica Formation. Unpub. M.A. thesis, Bowling Green State Univ. 79 p.

Stewart, G. A. 1927. Fauna of the Silica shale of Lucas County. Ohio Geol. Survey Bull. 32, 76 p.

Yakovlev, N. N. 1926. The phenomena of the parasitism, commensalism, and symbiosis in the Paleozoic Invertebrata. Ann. Soc. paleont, Russie 4: 113–124 (in Russian with English abstract).