

THE DISTRIBUTION AND PALEOECOLOGICAL INTERPRETATION OF *CORNULITES* IN THE WAYNESVILLE FORMATION (UPPER ORDOVICIAN) OF SOUTHWESTERN OHIO

ROBERT W. MORRIS AND HAROLD B. ROLLINS

*Department of Geology, Wittenberg University, Springfield, Ohio and
Department of Earth and Planetary Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania*

ABSTRACT

Seventeen species of marine invertebrates collected from the Upper Ordovician Waynesville Formation of southwestern Ohio were found encrusted by *Cornulites*, a presumed tubicolous annelid worm. Encrustation was interpreted as symbiotic in cases where the cornulitid tubes exhibited preferred orientation upon the exoskeleton of the host. This situation may reflect cornulitid utilization of feeding currents generated or employed by the host species. Symbiotic attachments of *Cornulites* were encountered most commonly on several species of brachiopods, but were also observed on a pelecypod, a monoplacophoran, two species of bryozoa, and questionably on a gastropod and nautiloid.

Post-mortem encrustation of a host by *Cornulites* was inferred either from random orientation of the cornulitid tubes or from attachment in a manner or position incompatible with the functional morphology of the host species. *Cornulites* was found in post-mortem association with brachiopods, bryozoans, and a trilobite. In this situation the host species presumably provided, after death, a suitably hard substrate for cornulitid larval attachment.

Symmetrically positioned cornulitid clusters on a specimen of *Cyrtolites* sp. cf. *C. ornatus* Conrad supports the accepted, but unproven, interpretation of bilaterally developed mantle-cavity organs in cyclomyan monoplacophorans.

INTRODUCTION

Detailed studies of the fossil record have demonstrated that many inhabitants of early Paleozoic marine environments were epizoid on host organisms—a common situation in the modern marine environment. Epifauna-host relationships and their paleoecological interpretations are described by many authors, including Hecker (1957), Ager (1961, 1963), Fisher (1962), Hoare and Steller (1967), Schumann (1967), and Ziegler *et al.* (1968). This study concerns one such epizoid organism from the fossil record, the problematic genus *Cornulites*, a presumed tubicolous annelid.

The skeleton of *Cornulites* consists of tapering calcareous tubes, which are circular in cross-section. The tubes are usually externally smooth in juvenile stages, but are ornamented by rings or ridges in later ontogenetic stages. Cornulitids occur most commonly as single or clustered tubes attached to some object, usually the exoskeleton of an invertebrate host. Fisher (1962) suggests that cornulitid dispersal in the marine environment was by means of a free-swimming larval stage and that the usual hosts were brachiopods, gastropods, or bryozoans. He also reports that certain cornulitid species exhibited host specificity, preferring attachment to a particular species of brachiopod or gastropod. Bivalves are recorded by others as host organisms for cornulitids. *Pteronitella* sp. cf. *P. retroflexa*, a byssate suspension-feeding bivalve, is reported as a host for *Cornulites* sp. in the Silurian Cowlegh Park Beds of the Welsh borderland (Ziegler *et al.*, 1968).

Cornulitid tubes resemble the calcareous tubes secreted by marine tubicolous annelids, such as *Serpula* sp., and appear to have had a similar habit of epifaunal attachment to the shells of other marine organisms, so they are interpreted by some workers as being most closely related to marine annelids (Moore, Lalicker, and Fischer, 1952; La Rocque and Marple, 1955; Caster, Dalvé, and Pope, 1955). Fisher (1962), however, reports that cornulitid tubes possess a cellular microstructure quite different from the laminar structure of true tubicolous annelids.

We envision cornulitids as epifaunal suspension-feeding annelids or annelid-like tubicolous organisms which cemented their tubes to the shells or hard parts of other living or dead marine organisms.

Specific identification of the cornulitids collected was not attempted. *Cornulites flexuosus* (Hall) is reported from the Waynesville Formation by Dalvé (unpublished report, Department of Geology and Geography, University of Cincinnati, 1948) and undoubtedly some of the specimens studied belong to this species. However, differences in size and external morphology of the cornulitids examined suggested that several species may have been present in the fauna. It is also possible these differences in size and appearance may represent different growth stages of a single species. For this reason, and because taxonomic distinctions did not appear to be critical to the main goal of this paper, assignment to species is not attempted for *Cornulites* in this paper.

The purpose of this study was (1) to determine the diversity and frequency of organisms from the Upper Ordovician Waynesville strata which serve as hosts or substrates for cornulitids, and (2) to postulate and describe probable interactions between the cornulitids and the host organisms. In such an interpretation of the paleoecology of an epizoid fossil organism, a common problem is the recognition of criteria which suggest an interaction between the epifaunal organism and the host. Basically, one must determine if the epifaunal organism attached to a living host, thus developing a symbiotic relationship, or if attachment was to the empty shell of a dead host, which was utilized merely as a substrate for attachment. Discussion of these problems and criteria for their resolution are presented by Ager (1963), Hecker (1957), Hoare and Steller (1967), and others. These criteria, including the orientation and distribution of the epifauna on the host, resultant growth deformation of the host shell, and the sequence of epifaunal attachment, were used in this study to interpret the epizoid habits of *Cornulites*.

LOCATIONS OF COLLECTING SITES

Large samples of macrofossils were collected from the Waynesville Formation (Upper Ordovician) at several localities in the vicinity of Waynesville, Ohio. This is part of Fox's Tanners Creek Formation (1962), which, as a result of detailed stratigraphic analysis in Indiana, incorporates the Waynesville, Arnheim, and Liberty Formations. The collecting localities near Waynesville, Ohio, are as follows:

Locality A—roadcut on Route 73 approximately 0.5 miles west of the junction of Routes 42 and 73;

Locality B—roadcut on Route 42 approximately 1.5 miles north of the junction of Routes 42 and 73; and

Locality C—roadcut on Route 73 approximately 0.75 miles east of the junction of Routes 42 and 73.

All collected specimens were carefully examined for attached cornulitids, and for any evidence of symbiotic relationship of the cornulitid with the host.

CORNULITID-HOST ASSOCIATIONS IN THE WAYNESVILLE FORMATION

Specimens of *Cornulites* were found attached to seventeen species of marine invertebrates collected from the Waynesville Formation: eight brachiopods, four bryozoans, and one individual each of a pelecypod, gastropod, monoplacophoran, nautiloid, and trilobite. These host species are listed in Table 1.

SYMBIOTIC CORNULITID-HOST RELATIONSHIPS

Epizoids positioned to take advantage of feeding currents set up by a host are reported from the fossil record by several authors. Ager (1961), Hoare and Steller (1967), and Schumann (1967) note examples of Devonian spiriferid brachiopods with different attached epizoids, including the reptant tabulate coral, *Aulopora*;

TABLE 1
Host Species of Cornulites in the Waynesville Formation

	No. of Host Specimens Studied	No. of <i>Cornulites</i> Present on Host
BRACHIOPODA		
<i>Lepidocyclus capax</i> (Conrad)	1	2
<i>Leptaena richmondensis</i> Foerste	1	5
<i>Platystrophia clarksvillensis</i> Foerste	2	1,9
<i>Rafinesquina alternata</i> (Emmons)	4	1-5
<i>Onniella meeki</i> (Miller)	1	1
<i>Strophomena nulan</i> Meek	1	2
<i>Strophomena planumbona</i> (Hall)	3	1-21
<i>Zygospira</i> sp. cf. <i>Z. modesta</i> Hall	1	19
BRYOZOA		
<i>Batostoma varians</i> (James)	1	99
<i>Bythopora meeki</i> (James)	36	1-37
<i>Homotrypa dawsoni</i> Ulrich	1	72
<i>Homotrypa hospitalis</i> (Nicholson)	1	3
MOLLUSCA		
<i>Byssonychia</i> sp.	3	1-10
<i>Cyclonema bilix</i> (Conrad)	1	6
<i>Cyrtolites</i> sp. cf. <i>C. ornatus</i> Conrad	1	13
ascocerid nautiloid (fragment)	1	9
ARTHROPODA		
<i>Isotelus</i> sp. (fragment)	1	4

Hederella and other encrusting bryozoans; the worms, *Cornulites* and *Spirorbis*; and the inarticulate brachiopod, *Lingulodiscina*. Several cornulitid-host associations in the Waynesville fauna imply a similar relationship.

Cornulitid-Molluscan Associations

A specific example of a cornulitid-molluscan association is provided by an interesting, but incomplete specimen of *Byssonychia* sp. with attached *Cornulites* from the Waynesville, Ohio, area. The specimen (figs. 1-3), which preserves the articulated beak area of both valves, has attached to each valve a symmetrical cluster of *Cornulites*, both clusters of which have the tube apertures oriented directly away from the beak. One cluster contains three large tubes, and the other has seven medium-to-large tubes. Pojeta (1962) considers the equivalved clam, *Byssonychia*, to be a byssate suspension-feeder, with feeding habits which were very similar to those of the recent bivalves, *Mytilus* and *Modiolus*. On this basis, *Byssonychia* was a bivalve which lived attached to the substrate by means of byssal threads and generated inhalant and exhalant currents for suspension feeding and respiration. Because of its equivalved morphology, Pojeta (1962) suggests that *Byssonychia* did not rest on one valve, but was oriented "vertically," with the flattened portion of the anterior end apposed to the substrate for byssal attachment. Orientation of the specimen illustrated in Figures 1-3 in this presumed "living position" appears to direct the *Cornulites* clusters upward and toward the proposed feeding-current direction at the posterior end of the shell. We suggest that this unusual specimen records symmetrical clusters of *Cornulites* which were symbiotically attached to a living *Byssonychia* in order to utilize both the hard substrate and possibly the feeding currents provided by the host. Trueman (1942) describes a similar association in which several Upper Carboniferous non-marine clams had *Spirorbis* tubes attached to the shells in the region of the exhalant current. It is also possible, in the Ordovician example, that the preferred orienta-

tion of the cornulitids on both valves might be due to food being carried or settling toward the bivalve from a specific direction. Thus, cornulitids and other epizoans might orient themselves in a specific direction on the shells of living or dead hosts in order to take advantage of nutrients being carried into a local bottom community by a bottom current or by settling from a specific direction.

Cornulites could of course also utilize the shells of available dead bivalves for substrate attachment. Ziegler *et al.* (1968) report *Cornulites* attached to shells of *Pteronitella* sp. cf. *P. retroflexa*, a Silurian byssate clam, in such a way as to be interpreted as either a symbiotic or post-mortem association. However, cornulitid clusters that are symmetrically positioned on bivalves which lived attached or reclining on the bottom substrate are interpreted to reflect a life association.

A single Waynesville specimen of the cyclomyan monoplacophoran, *Cyrtolites* sp. cf. *C. ornatus* Conrad, was found with attached cornulitids at Locality C, Waynesville, Ohio (figs. 4, 5). The genus *Cyrtolites* was formerly placed in the class Gastropoda, but is now considered to belong to the separate class of molluscs, the Monoplacophora. This specimen is probably *Cyrtolites ornatus* Conrad, but as is often the case with Waynesville cyrtolitids, it is so totally encrusted with epizoic bryozoans that the shell morphology is obscured. The specimen is unusual in that it has symmetrically positioned cornulitid clusters attached to both lateral surfaces of the shell. This suggests that the clusters of *Cornulites* might have been attached in a symbiotic relationship to the living monoplacophoran. An empty cyrtolitid shell would probably lie on one side and only be colonized by cornulitids and other epizoans on the upper exposed surface.

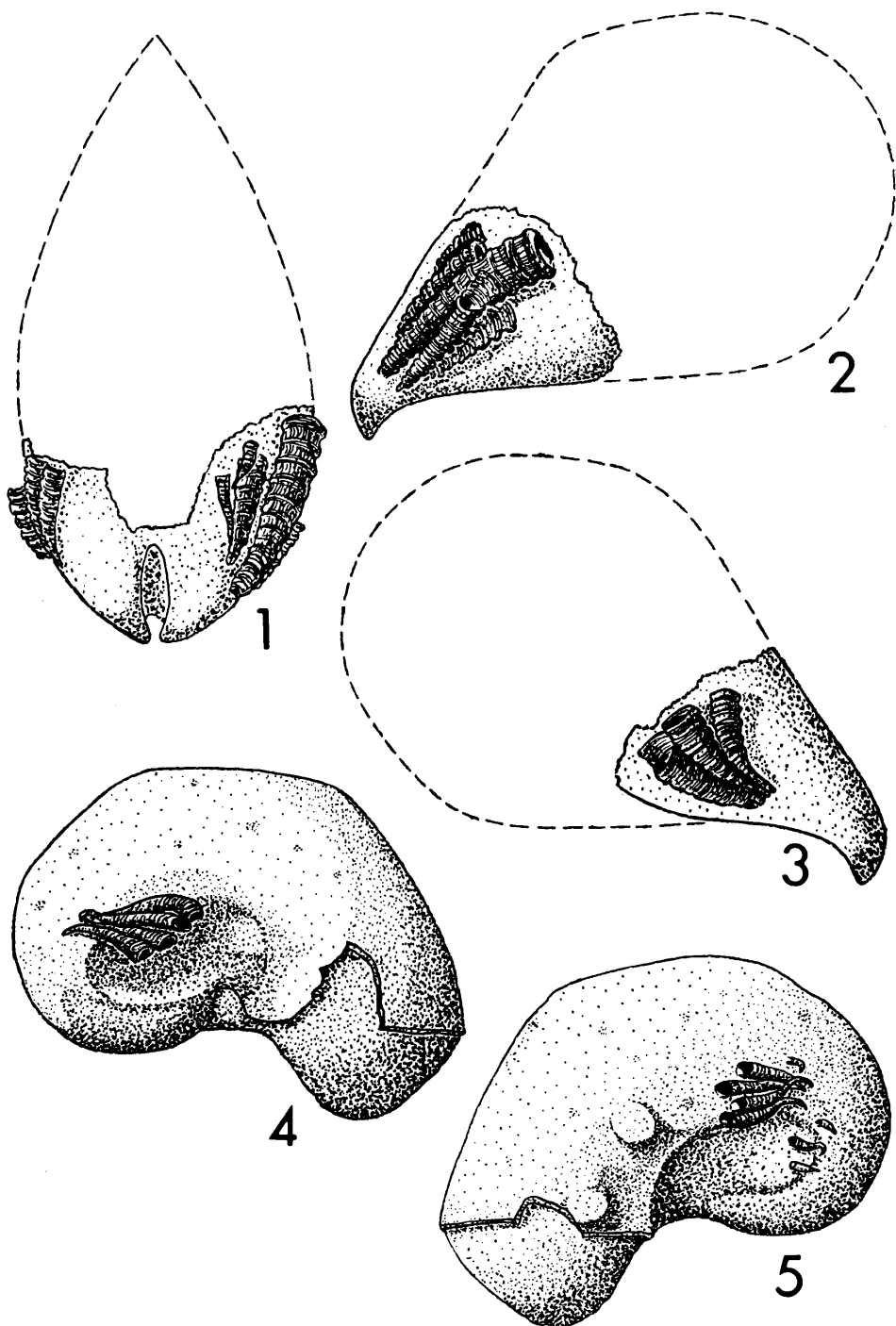
If, as suspected, cornulitids utilized respiratory or feeding currents of host organisms, the symmetrical clusters on this specimen (figs. 4, 5) suggest that *Cyrtolites* may have possessed the primitive respiratory pattern of two lateral inhalant currents and a medial exhalant current. It is possible that the lateral inhalant current on a given side may have been utilized by the cornulitid cluster on that side; however, this relationship would have been most probable when the cornulitid tube openings matched the cyrtolitid shell aperture. If this is the case, the cornulitid clusters would seem to reinforce the accepted concept of bilateral development of pallial organs in the mantle cavity of the cyclomyan Monoplacophora. Of course, the oriented cornulitid clusters may be due to the orientation of *Cyrtolites* into a directional bottom current.

One specimen of the gastropod, *Cyclonema bilix*, was also found colonized by *Cornulites* (fig. 12). It was collected from Locality B near Waynesville, Ohio. This specimen possesses six cornulitid tubes, all located on the basal whorl. Four of the tubes are oriented away from the aperture and toward the protoconch, which is covered by an encrusting bryozoan. This relationship could be interpreted

EXPLANATION OF FIGURES

- FIGURE 1. Dorsal view of articulated fragment of *Byssonychia* sp., oriented in probable growth position and illustrating symmetrically attached clusters of *Cornulites*. Note cornulitid orientation in upward direction, away from beak area. $\times 2$. Waynesville Formation, Waynesville, Ohio, A.M.N.H. # 29013.*
- FIGURES 2, 3. Left and right lateral views of same valve fragment oriented in growth position illustrating *Cornulites* clusters. Cornulitids are presumed to be in symbiotic association with host in order to utilize feeding currents. $\times 2$. Waynesville Formation, Waynesville, Ohio.
- FIGURES 4, 5. Lateral views of a specimen of *Cyrtolites* sp. cf. *C. ornatus* Conrad showing symmetrically attached *Cornulites* clusters located at the umbilical areas. Note cornulitid orientation toward aperture of monoplacophoran. $\times 2$. Waynesville Formation, Loc. C, Waynesville, Ohio, A.M.N.H. # 29014.

*All figured specimens are deposited in the Department of Invertebrate Paleontology, American Museum of Natural History.



as indicating either a symbiotic or post-mortem association. Symbiotic attachment during the life of the snail is suggested, because the colonized areas of the shell appear to have been accessible during the life of the snail. Some individuals of *Cyclonema bilix* are occasionally found attached to crinoid calices, which may indicate a coprophagous feeding habit for this snail. Ager (1963) reports an association, similar to this relationship, consisting of the Devonian gastropod *Platyceras* attached over the anal opening of a crinoid calyx. If the cornulitid-bearing Waynesville specimen was, in life, affixed to a crinoid, the cornulitid individuals would have been oriented predominantly upward (towards the protoconch) and would therefore possibly benefit from the crinoid's suspension-feeding activities.

Seilacher (1968) reports an interesting example of a probable symbiotic association between cornulitid-like epizoans and a nautiloid. He illustrates an orthoconic nautiloid from the Upper Ordovician strata of Bohemia, on which several clusters of *Conchicolites* are attached and oriented toward the anterior end of the shell, possibly to take advantage of currents set up during forward motion of the host. Sandberg (1967) illustrates an Upper Ordovician nautiloid from Ohio (locality unknown) with a cluster of cornulitid tubes. In this situation, also, the majority of the tubes are oriented with the apertures directed towards the anterior end of the cephalopod.

A single fragmented living chamber of an ascocerid nautiloid was collected from the Waynesville Formation; attached to it are nine cornulitid tubes, arranged in two clusters. Seven of the nine tubes are oriented with apertures pointing towards the anterior portion of the living chamber.

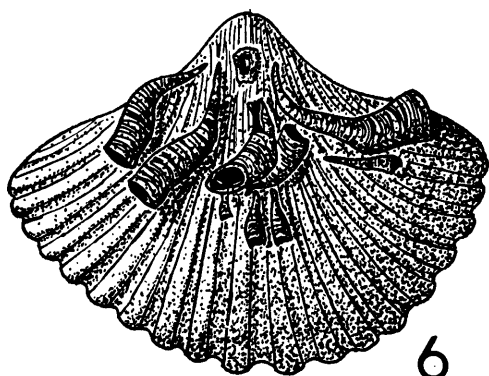
Cornulitid-Brachiopod Associations

A specimen of *Zygospira* sp. cf. *Z. modesta* (figs. 6-7) from Locality B, Waynesville, Ohio, has nineteen cornulitid tubes of varying sizes attached to the brachial and pedicle valves. Seventeen of the nineteen tubes are oriented from the pedicle-beak area towards the anterior commissure. This small brachiopod was attached to the substrate by a tiny pedicle during life; thus the orientation of the tubes suggests a symbiotic relationship in which *Cornulites* may have utilized the feeding currents set up by the host.

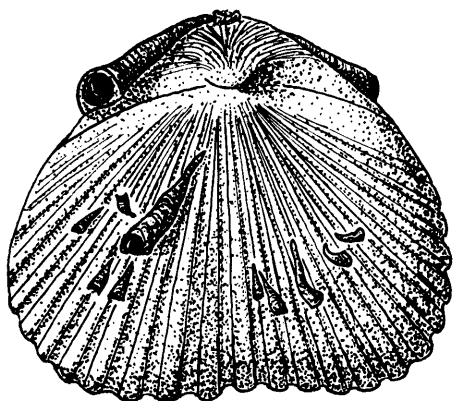
Three specimens of *Strophomena planumbona* with epifaunal *Cornulites* and colonies of reptant encrusting bryozoa were collected and studied. One specimen (fig. 9), collected from Locality A, Waynesville, Ohio, has fifteen of twenty-one cornulitid tubes oriented toward the peripheral margin of the concave (pedicle) valve. This occurrence suggests *Cornulites* had a preferred orientation on this brachiopod host to utilize the host's feeding currents. In a discussion of the life

EXPLANATION OF FIGURES

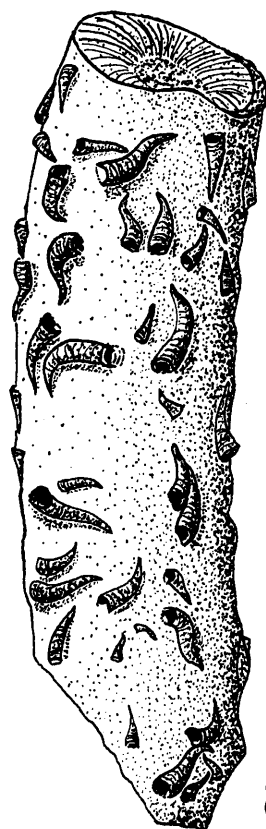
- FIGURE 6. View of pedicle valve of *Zygospira* sp. cf. *Z. modesta* Hall showing preferred orientation of cornulitid tubes away from pedicle-beak area and towards the anterior commissure. $\times 6$. Waynesville Formation, Loc. B, Waynesville, Ohio, A.M.N.H. # 29015.
- FIGURE 7. View of brachial valve of *Zygospira* sp. cf. *Z. modesta* Hall showing preferred orientation of *Cornulites*. Note size variation in cornulitid tubes. $\times 6$. Waynesville Formation, Loc. B, Waynesville, Ohio, A.M.N.H. # 29015.
- FIGURE 8. Fragment of ramose trepostome bryozoan *Batostoma varians* (James) showing heavy encrustation, but random orientation of *Cornulites*. $\times 4$. Waynesville Formation, Loc. B, Waynesville, Ohio, A.M.N.H. # 29017.
- FIGURE 9. View of concave (pedicle) valve of *Strophomena planumbona* (Hall) illustrating attached epifauna. Cornulitid tubes are partially encrusted by *Stomatopora* sp. (left half of valve) and another reptant bryozoan (species A—right half of valve). *Aspidopora* sp. encrusts across the commissure (central margin). $\times 3$. Waynesville Formation, Loc. A, Waynesville, Ohio, A.M.N.H. # 29018.



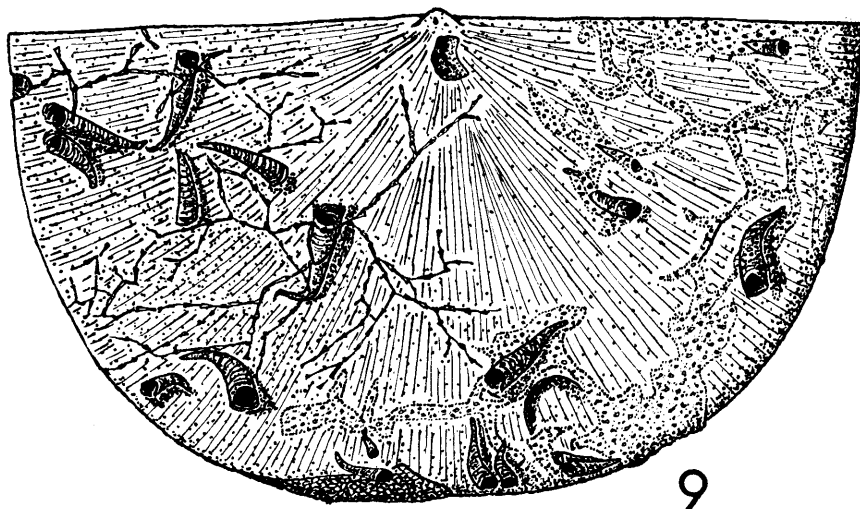
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position of *Rafinesquina alternata* from the Upper Ordovician, Richards (1969) maintains that the species lay on the posterior-median portion of the convex valve and that the concave (brachial) valve was oriented upward. If this interpretation is also applicable to *Strophomena planumbona* and the concave valve was indeed oriented upward during life, the colonization of the concave valve by *Cornulites* suggests a symbiotic association.

The same specimen of *Strophomena planumbona* presents an interesting sequence of epizoic encrustation (fig. 9). *Cornulites* was the first epizoan to become attached, followed sequentially by the reptant bryozoan *Stomatopora* sp., a second unidentified reptant bryozoan (species A), and, finally, a third species of encrusting bryozoan (*Aspidopora* sp.). Both species of reptant bryozoans encrusted the tubes of *Cornulites* on the concave valve; *Stomatopora* sp. encrusted at least three cornulitid tubes and species A encrusted seven tubes. *Aspidopora* sp. encrusted portions of both valves and extended across the commissure. Encrustation by these epizoans is interpreted as probably having taken place during the life of the host, with the exception of *Aspidopora* sp., which appears to be a post-mortem encrustation.

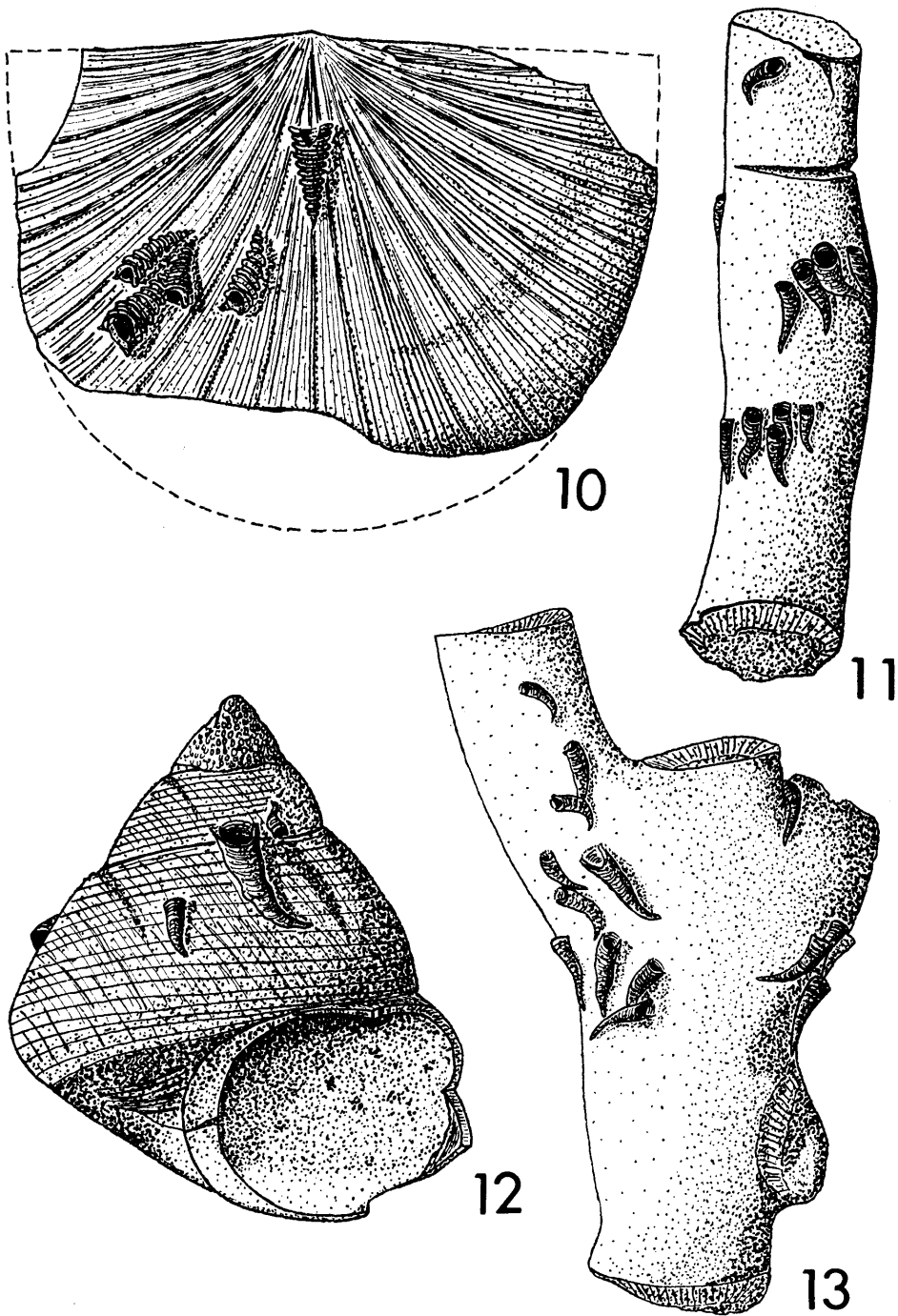
Another Waynesville brachiopod species which has been colonized by *Cornulites* is *Platystrophia clarksvillensis*. One specimen (not figured) possesses three cornulitid tubes located in the sulcus on the pedicle valve and six tubes on the surface of the brachial valve. Most tubes are located in, or parallel to, the plications on the shell exterior, similar to the position which Hoare and Steller (1967) report. Eight of nine tubes are oriented toward the anterior commissure, possibly to take advantage of the host's feeding currents. A similar pattern is evident on another specimen. Because *Platystrophia* probably lived in a vertical position with the beaks oriented downward toward the substrate, the orientation of *Cornulites* toward the commissure and feeding-currents is interpreted as evidence of a symbiotic relationship between *Cornulites* and *Platystrophia clarksvillensis*. Similar orientation of *Cornulites* on brachial valves of *Leptaena richmondensis* and *Strophomena nutans* from the Waynesville Formation also suggest a possible symbiotic relationship.

Specimens of *Lepidocyclus capax* with oriented *Cornulites* have not as yet been recovered from the Waynesville Formation; however, a specimen (not figured) with both valves articulated was recovered from the Liberty Formation near Camden, Ohio, that had attached symmetrical clusters of *Cornulites* oriented towards the anterior commissure. This relationship is interpreted as symbiotic and is similar to the types illustrated by *Byssonychia* and *Cyrtolites* with *Cornulites* discussed above.

Symbiotic relationships between *Cornulites* and brachiopods are reported by several workers. Schumann (1967) deduces the life position and feeding-current pattern of *Mucrospirifer reidfordi* Crickmay (Upper Devonian of Canada) from the orientation of attached *Cornulites* on the dorsal and ventral valves. All thirty-four cornulitid tubes on one specimen were oriented toward the anterior

EXPLANATION OF FIGURES

- FIGURE 10. Surface of convex valve of *Rafinesquina alternata* (Emmons) with attached *Cornulites*. Note that four of five cornulitid tubes are oriented toward the lateral margin of the valve. $\times 2$. Waynesville Formation, Loc. A, Waynesville, Ohio, A.M.N.H. # 29019.
- FIGURES 11, 13. Fragments of the ramose trepostome bryozoan, *Bythopora meeki* (James), showing directional orientation of *Cornulites* parallel to the growth axis and toward the growing tip of the branch. $\times 5$ and $\times 3.5$, respectively. Waynesville Formation, Loc. B, Waynesville, Ohio, A.M.N.H. # 29020 and 29016.
- FIGURE 12. Apertural view of *Cyclonema bilix* (Conrad) showing attached *Cornulites* on whorl exterior and encrusting bryozoan covering protoconch area. $\times 5$. Waynesville Formation, Loc. B, Waynesville, Ohio, A.M.N.H. # 29021.



margins of the valves, probably enabling the cornulitids to directly benefit from the feeding currents of the brachiopod. An excellent discussion of *Cornulites* and assorted epizoans attached to *Paraspirifer bownockeri* and other Devonian brachiopods is presented by Hoare and Steller (1967). They also suggest that *Cornulites* established itself in an orientation toward the anterior commissure to benefit directly from the current action of the host.

POST-MORTEM CORNULITID-HOST RELATIONSHIPS

Some elements of the Waynesville fauna were colonized after death by cornulitids. The shells of these organisms, or fragments of these shells, probably lay exposed or partially buried on the sea floor, and the larvae of *Cornulites* and other epizoans utilized these shells and broken fragments as a hard substrate on which to settle and become attached. Brachiopod valves and valve fragments, due to their abundance and availability on the Ordovician sea floor as a substrate, were common post-mortem hosts. Post-mortem attachment can be assumed if cornulitids encrusted the interior surface of a brachiopod valve. A pedicle valve of a specimen of *Lepidocyclus capax* was found with two cornulitid tubes oriented in an upward position on the valve interior and in association with a reptant bryozoan colony. This specimen is interpreted as representing a disarticulated *Lepidocyclus* valve which was available for post-mortem cornulitid encrustation.

One of the most common brachiopod species encrusted by *Cornulites* in the Waynesville fauna is *Rafinesquina alternata* (Emmons). All cornulitid tubes attached to examined specimens of this species were found on the exterior of the convex valve. Most of the cornulitids are oriented toward the anterior or lateral margins of the valve, i.e.—away from the beak or hinge area (fig. 10). If the convex valve were exposed or oriented in an upward position in a cluster or nest of *Rafinesquina* individuals, this relationship might be symbiotic; however, Richards (1969) and others conclude that living rafinesquinoid brachiopods lay on the posterior-medial portion of the convex valve on a relatively soft substrate. If the exterior of the convex valve rested directly on a mud substrate during life, *Cornulites* would almost certainly not have been able to attach and develop symbiotically on the convex valve surface. However, if the geniculation of the convex rafinesquinoid valve brought the valve above the substrate surface, colonization of that valve by epizoans might have been possible during the life of the brachiopod. Thus, this association could have been either post-mortem or symbiotic.

Ramose (branching) colonies of rigid, erect trepostome bryozoans constitute a significant portion of the Waynesville fauna and thus presumably served as firm substrates for cornulitid attachment. Criteria for absolute determination of cornulitid-bryozoan relationships are difficult to establish. Ramose bryozoans (either living or dead) probably would have been colonized on one or more exposed surfaces when in an erect position above the substrate. However, broken ramose or frondose fragments lying on the sea floor would probably have been colonized only on exposed surfaces, unless subjected to rolling or overturning by bottom currents, turbulence, or burrowing organisms. Cornulitids attached to the broken surfaces of bryozoan fragments strongly suggest post-mortem attachment, although attachment could have occurred on the broken surfaces of living erect colonies. The uniform orientation of cornulitids (all in the same direction) on the surface of a bryozoan colony might indicate directional growth of the cornulitids into a bottom current in the marine environment. Possible feeding currents set up by the bryozoan colony itself, or utilization of bottom currents by the colony, might have led to the directional orientation of *Cornulites* on parts of the surface of the bryozoan colony. Random orientation of cornulitids might be explained by food settling out from above and the absence of bottom currents carrying a food supply.

Of several hundred bryozoan fragments collected and examined in this study, four different bryozoan species comprising thirty-nine fragments were found to

be encrusted by *Cornulites* (Table 1). Thirty-six fragments of *Bythopora meeki* colonized by cornulitids were examined and found to have from one to thirty-seven cornulitids attached. The cornulitids on fifteen (42%) of these fragments of *Bythopora* were oriented in a definite direction on the fragment (figs. 11, 13); cornulitids on the other fragments were randomly oriented. On twelve (80%) of the fifteen fragments with oriented cornulitids, the directional orientation of the cornulitid tubes on the colony surface is parallel to the growth axis and toward the tip of the branch (figs. 11, 13). These data suggest that some branches of ramose *Bythopora* colonies may have maintained a direction of growth into a bottom current in the environment, and that, when cornulitids became attached, they oriented themselves and developed in this optimum direction. Twenty-eight percent of the fragments of *Bythopora* studied were encrusted on all sides; the remainder had cornulitids on only one side (surface). One specimen was found which had cornulitids encrusted on the colony surface, as well as on the broken surface of the fragment. The large number of cornulitid occurrences on *Bythopora meeki*, in comparison to occurrences on other bryozoan species, might indicate that *Cornulites* is species-selective. However, one fragment of *Batostoma varians*, a ramose trepostome similar to *Bythopora meeki*, was found at Locality B, Waynesville, Ohio, with 99 individual cornulitids in random orientation covering all surfaces of the colony (fig. 8).

Epifaunal attachment of *Cornulites* on the living surfaces of a bryozoan colony would certainly hinder growth and probably kill the zooids at the point of attachment; however, the remainder of the zooids comprising the living surface should remain undisturbed unless eventually overgrown by the cornulitids. A large flattened frondose fragment of *Homotrypa dawsoni* was found with about seventy small cornulitid tubes located on the upward oriented portion of the fragment. The closely spaced, tiny cornulitids are located on and in the relatively large autopores of this bryozoan. This suggests that larval *Cornulites* may have settled and attached in the abandoned autopores of a dead, yet still-erect, colony of *Homotrypa dawsoni*. The possibility also exists that larval cornulitids attached, overgrew, and killed this portion of the living *Homotrypa* colony. *Cornulites* was also found attached to the hemispherical bryozoan, *Homotrypella hospitalis*, itself an encrusting epizoan occurring in the Waynesville fauna. An interesting sequence of encrustation is illustrated by a single specimen in which a colony of *Homotrypella hospitalis* had encrusted the apex of a worn *Streptelasma* corallite and then had been, in turn, encrusted by three cornulitid tubes.

One specimen of a trilobite with *Cornulites* attached was found. A cluster of four cornulitid tubes is attached to a crushed fragment of an *Isotelus* cephalon and genal spine, a condition which probably represents a post-mortem association.

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