

“Hitchhiking” epizoans on orthoconic cephalopods: preliminary review of the evidence and its implications.

With 7 text figures and 4 plates.

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Abstract.

Epizoans, particularly bryozoans, commonly display conspicuously oriented growth on shell exteriors of extinct orthoconic nautiloid shells. Such patterns, including monticules and maculae aligned and streamlined with the long axes of orthocone shells, as well as preferred, one-way orientation of component zooecia and/or corallites, are strongly suggestive of epizoan settlement and growth on live cephalopod hosts. Although aligned monticules (as in *Spatiopora*) and reptate zoaria (*Reptaria*) have been thought by many to denote a “parasitic” or “commensal” mode of life on orthocones for more than a century, little critical study of this putative interaction has yet been done. Ongoing study of various encrusters, including: several Ordovician bryozoan genera (*Spatiopora*, *Atactoporella*, *Paleschara*), a Devonian tubuliporate (*Reptaria*), and a Devonian tabulate coral (*Alveolites*) has led to establishment of criteria for distinguishing growth on live cephalopods, empty drifting shells, and stable, partially buried shells. Discovery of consistent unidirectional, apertureward orientation and growth of zooecia in *Spatiopora* and a dominantly apertureward direction of zoarial growth in *Reptaria* appear to argue against epizoan growth on a drifting (vacant) nautiloid shell, and they clearly exclude growth on a stationary shell. Preliminary mapping of these alignment and orientation patterns relative to the presumed vertical “up-down” axis of cephalopod shell symmetry suggests the presence of a crude, bilateral symmetry in encrustation patterns indicative of co-biosis. Confirmation of this co-biosis should provide additional clues as to the inferred swimming behavior of orthoconic cephalopods.

Kurzfassung.

[„Hitchhiker“- (Anhalter-) Epizoen auf orthoconen Cephalopoden: erste Sichtung des Materials und Folgerungen.]

Epizoen, insbesondere Bryozoen als Oberflächen-Bewuchs von ausgestorbenen, orthoconen Nautiloideen zeigen gewöhnlich eine auffällige Orientierung. Solche Anordnungsmuster,

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of the nautiloid strongly suggest epizoan growth upon a partially buried shell (pl. 1 fig. 1). However, episodic reorientation of nautiloid shells by successive storms could have produced holoperipheral massive overgrowths with complex internal patterns of growth similar to those observed in oncolitic cheilostome zoaria which form in a variety of modern nearshore habitats and which are well represented in the fossil record (RIDER & COWEN 1977; RIDER & ENRICO 1979; DADE & CUFFEY 1984). Encrustation of cephalopod fragments constitutes clear-cut evidence of stationary substrate conditions (pl. 1 fig. 2), provided that shell breakage did not occur after overgrowth had already taken place.

Not all overgrowths on stationary shells can be recognized as such with certainty. Small, circular encrusting organisms (pl. 1 fig. 5) and thin crustose, non-monticulate zoaria covering large exterior surfaces of cephalopod conchs may have encrusted either moving or nonmoving shells. Directional orientation of zooecia, and/or corallites, however, can sometimes be identified by sectioning of zoaria to determine if zooecia show a preferred orientation or a random growth pattern with respect to the shell axis.

Growth on moving shells: Ordovician epizoans.

Late Ordovician orthoconic cephalopods, including orthocerids and some endocerids, are commonly holoperipherally encrusted by bryozoan zoaria displaying conspicuously aligned ("streamlined") monticules and maculae as well as unidirectionally oriented zoaria (pl. 1 fig. 3; pl. 2 figs. 7-8, 10, 12; pl. 3 figs. 13-14). Most notable among several genera that show this effect, is the trepostome genus *Spatiopora* ULRICH 1882 which is common at certain stratigraphic levels in the Waynesville Formation (Upper Ordovician, Richmondian) in southwest Ohio and southeast Indiana (pl. 1 fig. 3; pl. 2 figs. 7-8, 10, 12). The genus *Atactoporella* ULRICH 1883 (pl. 3 figs. 13-14) also typically displays aligned maculae; preliminary evidence indicates that this taxon occurs mainly in upper Kope and lower Fairview strata (upper Edenian—Lower Maysvillian stages) in the region around Cincinnati. A third bryozoan, *Paleschara* HALL 1874, also closely associated with cephalopod shells, lacks monticules and maculae, but around conchs forms a thin, holoperipheral mat, characterized by diamond-shaped or elongated zooecia that radiate from several ancestrulas to form a coalescent zoarial sheet. A fourth, as yet unidentified bryozoan (pl. 1 fig. 4; pl. 2 fig. 9) occurs as a one-zooecium-thick mat around numerous orthocones in the upper Kope Formation near Cincinnati.

The alignment of monticules in *Spatiopora* is striking; each monticule is conspicuously elongated ("streamlined") coaxially with the long axes of encrusted phragmocones (pl. 1 fig. 3; pl. 2 figs. 7-8, 10), and *Spatiopora* monticules are frequently arranged in rows which are slightly oblique to the cephalopod shell axis (pl. 2 figs. 8, 10). Zoaria encrust the shells almost completely and holoperipherally, not only around the chambered phragmocone but also forward around the living chambers and backward to the apical ends of phragmocones (pl. 2 figs. 7-10; pl. 3 figs. 15-16). Furthermore, several encrusted phragmocones have been found with the apical ends truncated prior to burial and the exposed septal face and siphuncle opening encrusted by the bryozoans as well (pl. 2 figs. 8-9; pl. 3 figs. 15-16).

One species, *Spatiopora corticans* ULRICH 1882, has spectacular monticules which take the form of straight ridges that extend one to two millimeters above the

surrounding zoarium surface (pl. 2 fig. 7). Within a single colony, the morphology of *Spatiopora* monticules sometimes changes along the length of the cephalopod. The elongation of monticules appears to be critically related to the diameter of the host shell; elongation decreases from the apical end forward with the monticules becoming nearly circular at the incomplete anterior end of one well preserved specimen (pl. 2 fig. 10). This pattern suggests that zooids "perceived" variations in hydrodynamic conditions along this shell and that the monticule growth program varied spatially across zoaria in response to this change. Species differences in this genus have been based on variations in monticule morphology and degree to which zooecia form parallel rows on zoarial sheets; however, there appears to be considerable variation in these parameters both across zoaria and stratigraphically. Thus, a need exists for a detailed systematic treatment of this and other cephalopod-encrusting genera. In this paper we avoid species designations for *Spatiopora* and *Atactoporella* except for certain identified museum specimens.

Large specimens identified as *Atactoporella maculata* ULRICH 1883 show spatial variations in the degree of linearity of maculae and also some minor local deviations in the directions of alignments over cephalopod surfaces (pl. 3 figs. 13-14). Where we have observed such variations, we also observed non-encrusted areas which are "walled off" by calcareous meniscus borders along the zoarium margin (pl. 3 fig. 14), suggesting that soft-bodied encrusters may have competed for space on conch exteriors and, additionally, may have affected water flow patterns over such surfaces.

Encrusting bryozoans which display elongated monticules or maculae contain zooecia that display consistent growth orientation towards the apertural end of the cephalopod, as is particularly shown by a species of *Spatiopora* from the Upper Ordovician Collingwood Shale Member in southern Ontario (pl. 2 fig. 12). This pattern is also observed for most thin, nonmonticulate, holoperipheral zoaria found with *Spatiopora* in the Waynesville Formation, suggesting that these later species also grew under conditions similar to those effecting *Spatiopora*. Close examination of zoaria seen in longitudinal (sagittal) cut sections of orthocones shows that these crusts are seldom more than one zooecium thick except in monticules and that, in most, zooecial walls initially bend toward the aperture of the nautiloid shell before changing to a near-vertical orientation (pl. 2 fig. 11). For extremely thin, crustose *Spatiopora* zoaria from the upper Waynesville claystone beds near Liberty, Indiana, the abbreviated zooecial walls are entirely slanted towards the aperture. Transverse cephalopod sections show no significant orientation of zooecia in lateral directions; zooecial walls are usually vertical in sections, except where compaction has sheared zoarial crusts. Along with adapertural zooecium orientation, we have also observed zooecia in some *Spatiopora* arranged in parallel rows that are usually, but not always, aligned coaxially with the cephalopod (pl. 2 fig. 12); where observable, these can be mapped in order to document the growth history of the zoarium.

In addition to the alignment and orientation of zoarial features on the Ordovician cephalopods, there is also evidence for the orientation of other associated organisms on conchs. Several cephalopods coated by *Spatiopora*, *Atactoporella* or *Paleschara* are further encrusted by *Cornulites flexuosus* HALL 1847 which commonly occurs on zoarium surfaces but is also found complexly intergrown within or under the bryozoan zoaria. Normally, the cornulitid tubes radiate as a cluster from a common area of origin, but, when found on orthocones, the tubes are often

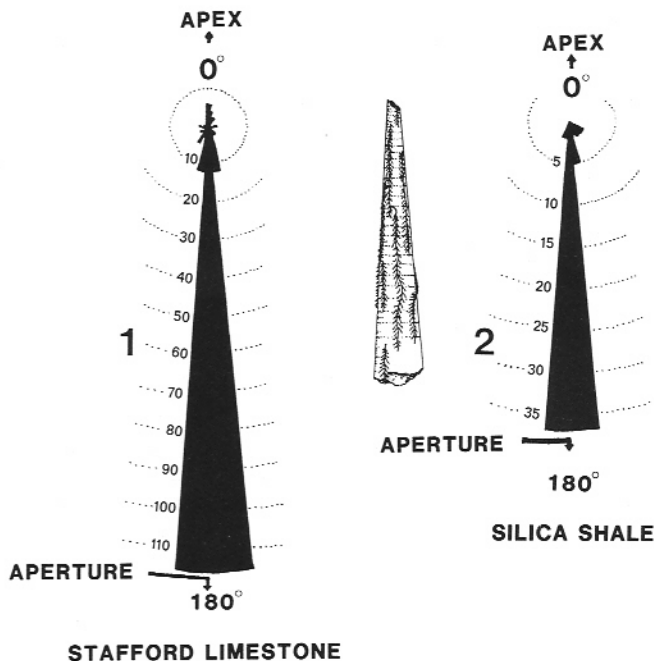
distinctly oriented in the adapical direction. One cephalopod from the Waynesville Formation displays not only the distinctive zoarium of *Spatiopora*, but also oriented cornulitid tubes which were overgrown by the bryozoan (pl. 3 fig. 18). These tubes varied in initial orientations but those originally oriented adaperturally bend around to face adapically such that these tubes are recurved. It is notable that these cornulitids are oriented in the opposite direction to those figured by SEILACHER (1968; taken from an earlier paper by PRANTL). All the more significant is the fact that *Spatiopora* sometimes overgrows worm tubes while superimposing the elongated monticule pattern directly upon these irregularities. This suggests that the tendency to produce such monticules may be a locally-induced response to rheotropic conditions.

Finally, FRITZ (1925) reports the occurrence of a stromatoporoid *Dermatostroma scabrum* JAMES 1879, as a holoperipheral encruster on cephalopods, particularly endocerids, from Upper Ordovician deposits (presently Georgian Bay Formation) in the vicinity of Toronto, Ontario. These coenostea are thin and bear papillae that sometimes display a weak linearity which is coaxial with the orthocone axis similar to *Spatiopora* and *Atactoporella* (pl. 3 fig. 17). Only a few good specimens exist in collections at the Royal Ontario Museum, Toronto, and the present authors have turned up none at Georgian Bay Formation exposures, thus precluding extensive study of this organism at this stage. However, one orthocone specimen bearing *Dermatostroma* PARKS 1910 with weakly aligned papillae has recently been found in the Upper Ordovician Kope Shale deposits west of Cincinnati. These specimens show that stromatoporoids with a fundamentally different growth program from tabulates and bryozoans could mimic very closely the exterior growth morphology of these latter groups when found on orthocone exteriors.

Growth on moving shells: Middle Devonian epizoans.

At several stratigraphic levels in the Middle Devonian Hamilton Group of New York and stratigraphic equivalents in southern Ontario and Ohio, many orthoconic nautiloids are conspicuously encrusted by the tubuliporate bryozoan *Reptaria stolonifera* ROLLE 1851. This bryozoan rarely encrusts other cephalopods, including an ammonoid and the coiled nautiloid *Nephriticeras* HYATT 1884. Smooth longicone nautiloids, largely assignable to the order Michelinoceratida, display the distinctive reptate zoarium of *Reptaria* usually aligned with the long axes of host conchs (pl. 4 figs. 1-5). Since *Reptaria* zooids are oriented in the same direction as that of the advancing zoarium, one can record both alignment and orientation information from these growths (text figs. 1-2).

Examination of museum specimens, as well as a large number of encrusted cephalopods collected in the outcrop, shows that the overwhelming majority of *Reptaria* zoaria are aligned coaxially with their cephalopod hosts (text figs. 1-2). The vast majority of aligned zoaria show evidence of growth towards the cephalopod aperture. A few specimens have been found in which most, or all, of these pinnate zoaria grow toward the apical end of the shell. Adapical orientation and growth of *Reptaria* is also reported by TUREK (1987), from the Silurian of Czechoslovakia, but it is not known if this is the predominant condition in those deposits.



Text figs. 1-2. Orientation of fronds and zoecia of *Reptaria stolonifera* ROLLE 1851 relative to the apical end (0°) and the aperture (180°) of Middle Devonian orthoconic nautiloids (*Michelinoceras* sp.).

1. Azimuths of 187 fronds on 51 orthoconic nautiloids. — Stafford Limestone Member; western New York State, USA.
2. Azimuths of 54 fronds of 5 cephalopods. Each recorded degree value is the direction in which a given frond was advancing. Note the great preponderance of fronds advancing apertureward as well as a few growing towards apices. — Silica Shale Formation; Sylvania, Ohio, USA.

The most striking *Reptaria* specimens come from the Middle Devonian Silica Shale Member near Toledo, Ohio. On phragmocones, virtually all zoarial branches bud and bifurcate in the adapertural direction (pl. 4 figs. 19-23). KESLING & CHILMAN (1975) argued that these bryozoans encrusted the interiors of living chambers and, thus, displayed only the ventral zoarium surface on cephalopod fossils. The present authors, having examined this same material, believe that *Reptaria* encrusted only phragmocone exteriors. Where bryozoan underside detail is observed (pl. 4 fig. 22), the cephalopod is preserved as a composite mold or the bryozoan is visible on the concave surface of the exterior mold. These preservational patterns are consistent for all localities and all specimens examined.

Some remarkable specimens from the Silica Shale have zoecia on opposing parallel fronds growing edge-to-edge in an alternating "tooth-and-socket" spacing (pl. 4 fig. 21). Unlike the Ordovician bryozoans which have zoecia packed tightly

together, there is commonly space between the frondose *Reptaria* zoaria so that fronds can both bifurcate and change directions. Thus, on many cephalopod molds, some fronds "wander" and others may even turn 180° (pl. 4 fig. 23). Two fronds generally bud from a single ancestrula, one adaperturally, the other adapically; generally the adapical bud is shorter, but if it is able to reroute adaperturally it may survive to produce a long front or bifurcate. Numerous small budded fronds extend in directions subnormal to the cephalopod long axis. Usually, these are abortive growths which are blocked by fronds already present.

A few specimens show several fronds oriented and aligned adaperturally but with one or several which diverge at right angles to this trend, advancing towards the opposite side of the cephalopod. Sometimes a frond will "crawl" over sister fronds in doing this (pl. 4 figs. 19b, 23). We interpret such patterns as evidence for descent of the conch to the seafloor to a recumbent, stationary position.

One specimen of an orthoconic nautiloid was found within a sparsely fossiliferous, dark gray shale sequence in the Ludlowville Formation (Givetian) of western New York which was encrusted by the tabulate coral *Alveolites goldfussi* BILLINGS 1859 (pl. 4 fig. 23). Although it is on a poorly preserved, fragmentary part of the phragmocone, the coral shows a distinct adapertural orientation of the corallites.

The case for a moving shell substrate.

Evidence for bryozoan growth on a mobile cephalopod shell substrate, which includes the alternative conditions of co-biosis with a live cephalopod host and necroplanktonic drift, is certain. The aforementioned examples of aligned monticules and frondose zoaria, as well as the one-way orientation of zoaria, worm tubes, and corallites are suggestive of a largely unidirectional current along the axis of the cephalopod shell.

The apertureward orientation of *Reptaria* zooecia (pl. 4) provides an excellent example of direct response of bryozoan zooids to a unidirectional flow. Our initial reaction to the orientation of the Ordovician *Spatiopora* zooecia was that it was also a direct response to currents. Subsequent examination of longitudinal cross-sections of those zoaria shows that growing zooecia gradually revert to a nearly vertical orientation (pl. 2 fig. 12). Thus, although zooids may have been influenced by current flow regime, their initial orientation may merely reflect constructional growth constraints imposed by the budding process. The response of the bryozoan to its environment probably must be viewed at the zoarial level as well as that of individual zooids. This caveat does not diminish the significance of the directional zoarial growth and monticule alignment on orthocone exteriors. The aforementioned orientation of cornulitids (pl. 3 fig. 18) clearly indicates that some encrusters on these cephalopods did orient their apertures to unidirectional current flow. The conspicuous association of this growth pattern with cephalopod substrates further strengthens the argument that the epizoans were responding to current flow parallel to the cephalopod long axis. This idea is supported by ANSTEY (1981) who, noting the conspicuous alignment of *Spatiopora* monticules, refers to these structures as current bypass monticules, implying that the component zooecia were passively responding to the current generated by movement of the host cephalopod rather than actively generating incurrent or excurrent flow systems above the zoarium.

uniform, ordered appearance of the extensive *Spatiopora* crusts. This process could explain the absence of other epizoans on most *Spatiopora*-covered phragmocones; coordinated advance of the zoarium with the receding mantle may have been an important strategy because it would have excluded larvae of competing epizoans from establishing a foothold on these shells. Relevant to this same problem is the question of whether the living cephalopod was capable of removing fouling organisms from the phragmocone surface. Preliminary searches for discontinuities in zoarium growth, particularly around the living chamber have not yielded conclusive evidence of such activity.

Multiple overgrowths and intergrowths of encrusters are observed. We have already noted synchronous growth of cornulitids and bryozoans, apertures of which are oriented in opposite directions (pl. 3 fig. 18), as well as bryozoan structures indicating antagonistic competition for space against unpreserved soft-bodied organisms (pl. 3 fig. 14).

A further outcome of the present study is evidence that apical portions of the phragmocone could be lost without fatal results to the living cephalopod. Several truncated orthoconic shells lacking the first several camerae have been recovered from Cincinnati-area Ordovician deposits. This breakage occurred prior to burial as indicated by overgrowth of the break surfaces by *Spatiopora* (pl. 2 figs. 8-9; pl. 3 figs. 15-16). Exposed septal faces are observed to be coated by the same bryozoans which produced aligned monticules on the phragmocone exterior. Moreover, these crusts appear to include the ancestrulas of some colonies (pl. 3 fig. 3). This suggests that these cephalopods could have lost apices due to collisions or predation without the camerae being flooded, perhaps because of pre-emptive closure of distal parts of the siphuncle by the cephalopod during life.

Elucidation of many remaining questions and problems requires extensive systematic work on the various bryozoan taxa involved in these interactions. Basic taxonomy of the Ordovician bryozoans is sketchy and antiquated; we are currently examining the various species (and perhaps genera) which may be masquerading under the names *Spatiopora*, *Atactoporella*, *Leptotrypa* ULRICH 1883, and *Pal-eschara* to see if one, several, or many additional genera are involved. Such work should lead to clues as to the amount of ecophenotypic plasticity that may have existed in Ordovician bryozoan taxa. It should also enable us to determine if one or more of these epizoans was truly an obligate encruster ecologically linked to particular cephalopod host taxa. The importance of this question is underscored by the observations of one of us (FREY) on Waynesville *Treptoceras* and associated bryozoans (see FREY 1983). He observes that there is an increase in monticule and zooecial astogenetic linearity in *Spatiopora* as one moves stratigraphically upsection. This pattern suggests that selective coevolution of *Treptoceras* and *Spatiopora* may have led to an increasingly refined host-encruster relationship through time.

Conclusions.

Preliminary studies of Late Ordovician and Middle Devonian epizoans encrusting orthoconic nautiloids reveal numerous examples of bryozoans on a mobile cephalopod substrate. A smaller subset of these examples display features strongly suggestive of bryozoan encrustation on the ectocoellear phragmocone of a

cephalopod during life. Key epizoan features, such as thin, holoperipheral zoaria bearing aligned monticules and maculae, suggest that encrustation most likely occurred on a partially buoyant, mobile shell while apertureward growth of holoperipheral zoaria originating near the apical end of the phragmocones suggest that the bryozoans "hitchhiked" on the shell of a live orthoconic host.

These results are significant because considerable information can be obtained about the life activities and growth strategies of these interacting organisms. Firstly, patterns of epibiont encrustation may yield information concerning the swimming behaviour of and growth of the host cephalopod. Observations strongly suggest a dominant forward motion in many orthoconic nautiloids; it is also evident that nautiloids frequently lived with the apical end of the phragmocone removed. Secondly, observations indicate rheophilic responses of bryozoans, tabulates, and cornulitids to prevailing uni- or bi-directional currents. Thirdly, a potentially important interaction between bryozoan astogeny and cephalopod growth can be documented and explained. Finally, systematic study of the distinctive *Spatiopora* and other Ordovician orthocone-encrusting bryozoans may yield evidence of host-epizoan coevolution through extensive timespans.

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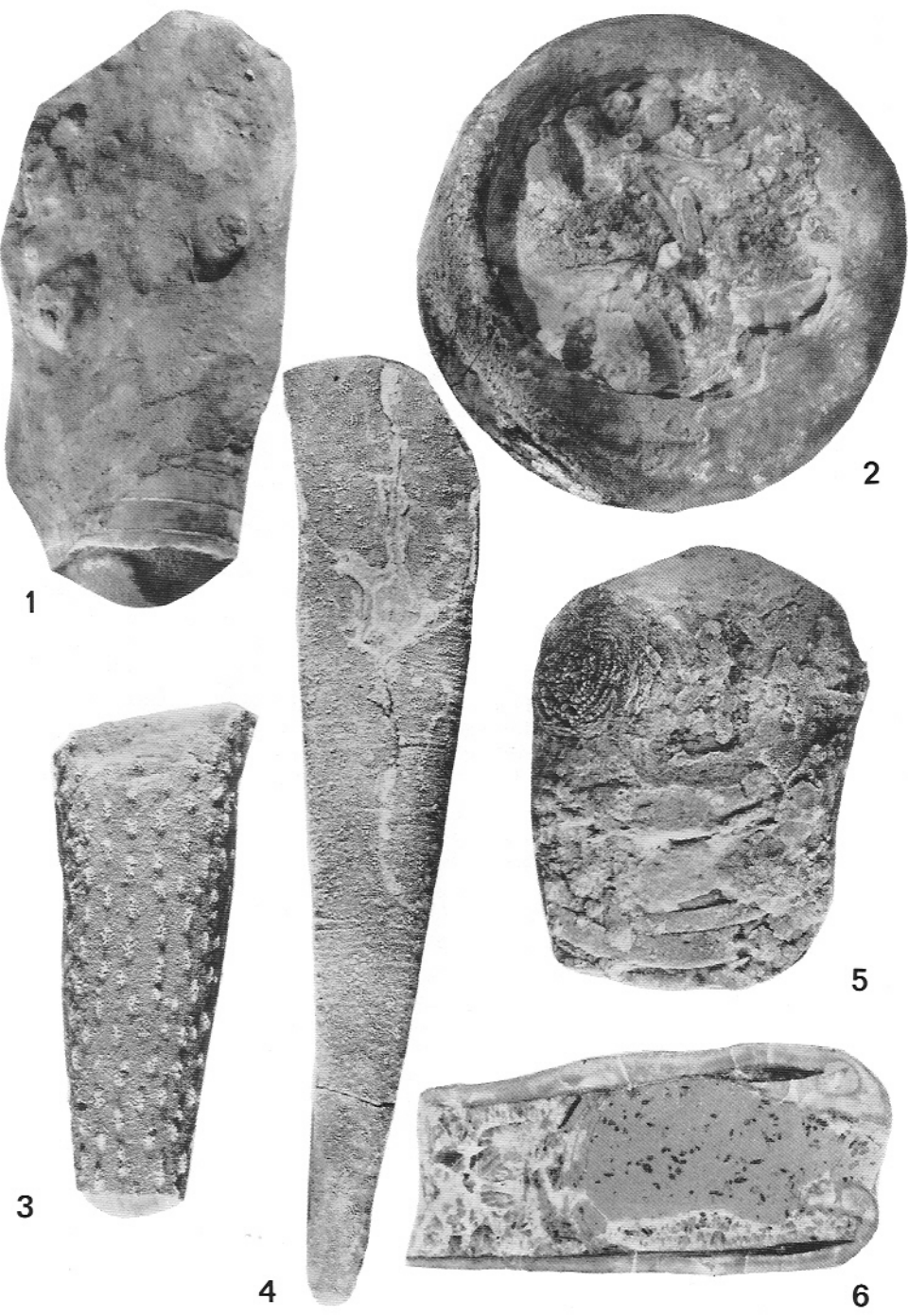
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Plate 1.

Encrustation patterns on stationary versus moving cephalopod shells. — Upper Ordovician (Cincinnatian). — All specimens are deposited in paleontological collections of the University of Rochester.

- Fig. 1. Encrusting trepostome bryozoan on an orthoconic nautiloid. Note conspicuous irregular overgrowth on one, presumably uppermost, side of a stationary shell. — $\times 0.9$. — *Treptoceras dusei* shale unit in Fort Ancient Member of Waynesville Formation; north branch of Harper's Run on G. S. A. Camp Whip-Poor-Will near Roachester, Warren Co., Ohio, USA.
- Fig. 2. Cylindrical segment of large (endocerid ?) phragmocone which is encrusted both inside and outside by a thick, trepostome zoarium. — $\times 0.8$. — Waynesville Formation; stream bed exposure 0.8 km north of Brookville, Franklin Co., Indiana, USA.
- Fig. 3. Zoarium of *Spatiopora* sp. which encrusts an orthoconic phragmocone (probably *Treptoceras*). Note conspicuous linearity of monticules which is coaxial with orthocone long axis. — $\times 1.1$. — Upper Ordovician strata of Upper Waynesville Formation; Clifton Creek, 1.1 km west of Clifton, Union Co., Indiana, USA.
- Fig. 4. Zoarium of undetermined trepostome bryozoan encrusting orthoconic nautiloid; note reflection of nautiloid growth lines in bryozoan. — $\times 1.0$. — Upper Ordovician, uppermost Kope Formation; roadcut at abandoned rest stop on I-275 near Mt. Carmel, Clermont Co., Ohio, USA.
- Fig. 5. Edrioasteroid *Streptaster* sp. on orthoconic nautiloid. This echinoderm could have encrusted either a moving or stationary cephalopod shell. — $\times 1.1$. — Upper Ordovician Corryville Formation; Stonelick Creek near Newtonsville, Clermont Co., Ohio, USA.
- Fig. 6. Polished sagittal cut section of an orthoconic nautiloid showing a thick trepostome encrustation which overgrows the anterior shell margin and extends partly into the living chamber. — $\times 1.1$. — Manchester, Adams Co., Ohio, USA.



G. C. BAIRD & C. E. BRETT & R. C. FREY: "Hitchhiking" epizoans on orthoconic cephalopods.

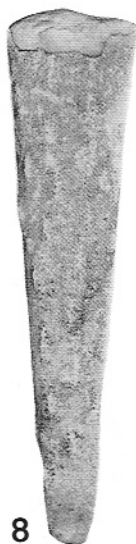
Plate 2.

Trepustome encrustations on moving orthoconic cephalopod shells. — Upper Ordovician (Cincinnatian). — Unnumbered specimens repositied in paleontology collections of the University of Rochester.

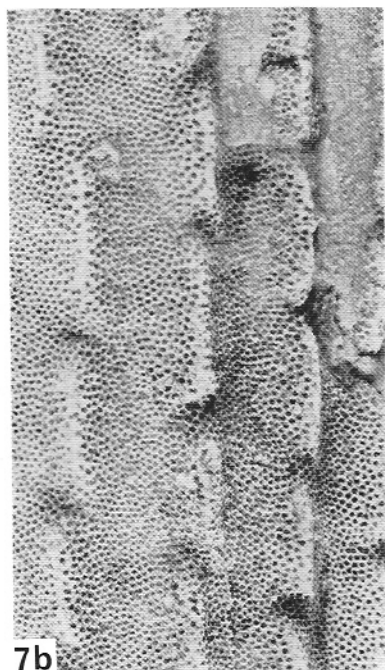
- Fig. 7. Zoarium of *Spatiopora corticans* (NICHOLSON 1875). Note conspicuous blade-like monticules. — UCM 23156 [UCM = University of Cincinnati Geological Museum]. — Upper Ordovician, Liberty Formation; Flat Fork Creek, Oregonia, Warren Co., Ohio, USA. — a) Specimen $\times 1.0$. — b) Detail $\times 3.0$.
- Fig. 8. Small orthoconic phragmocone, possessing intact apical end, which is holoperipherally encrusted by *Spatiopora montifera* ULRICH 1882. Purchased specimen. — $\times 1.5$. — Lower Waynesville Formation (probably collected from *Treptoceras duseri* shale unit); Fort Ancient area, Warren Co., Ohio, USA.
- Fig. 9. Unidentified non-monticulate trepustome coating both shell exterior and truncation surface (exposed septal face) of a damaged orthoconic phragmocone. Encrustation certainly preceded shell burial and it presumably grew on a moving shell substrate (see text). This zoarium is a uniform holoperipheral sheet no more than one zooecium thick. — $\times 2.0$. — Uppermost Kope Formation; abandoned rest stop on I-275 near Mt. Carmel, Clermont Co., Ohio, USA.
- Fig. 10. Zoarium of *Spatiopora* sp. showing a conspicuous decrease in the degree of linearity of the monticules toward aperture of nautiloid. As with previous figured specimen, this zoarium is a one-zooecium-thick holoperipheral crust. — $\times 1.2$. — *Treptoceras duseri* shale unit in Fort Ancient Member of Waynesville Formation; south branch of Harper's Run, G. S. A. Camp Whip-Poor-Will near Roachester, Warren Co., Ohio, USA.
- Fig. 11. Photomicrograph of *Spatiopora* zoarium sectioned parallel to long axis of nautiloid shell. Note convexity of zooecial walls indicative of apertureward zoarial advance (to left). Zoarium is typically one zooecium-thick except where monticules are developed. — $\times 15.0$. — Upper Waynesville Formation; Clifton Creek, 1.1 km west of Clifton, Union Co., Indiana, USA.
- Fig. 12. Lower surface of *Spatiopora delicatula* FRITZ 1928 encrusting small, highly compressed orthoconic nautiloid which has been exfoliated; note orientation of zooecia toward aperture of nautiloid shell. ROM 26472 [ROM = Royal Ontario Museum Invertebrate Palaeontology Collections]. — $\times 8.0$. — Upper Ordovician, Collingwood Shale; Craighleith, Ontario, Canada.



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7b



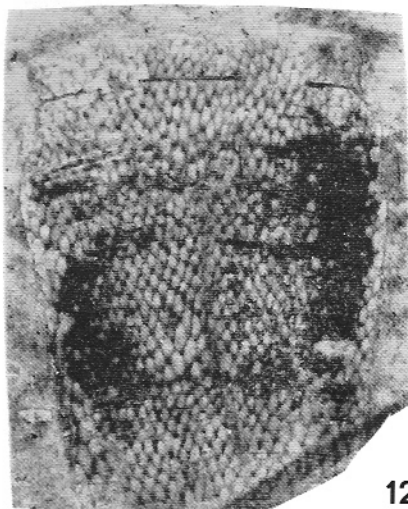
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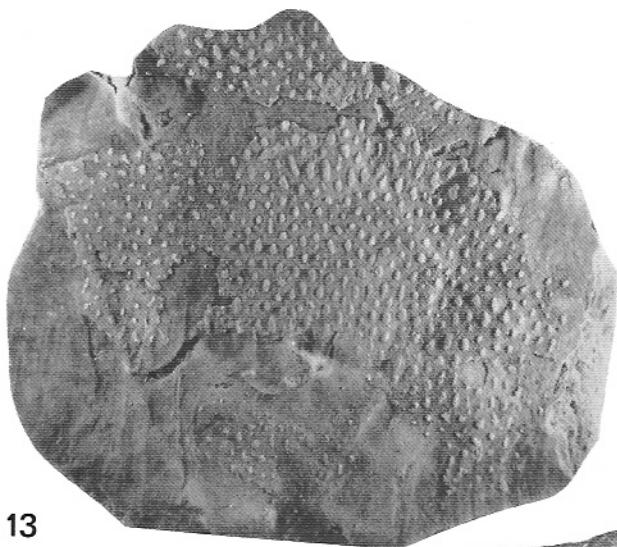


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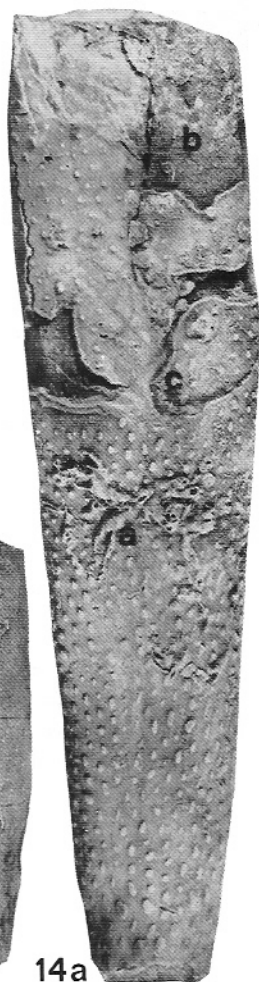
Plate 3.

Epizoan encrustation patterns on orthoconic cephalopods. — Upper Ordovician (Cincinnatian). — Unnumbered specimens are deposited in paleontology collections of the University of Rochester.

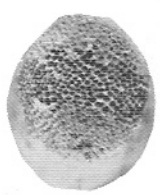
- Fig. 13. Zoarium of *Atactoporella maculata* ULRICH 1883 on fragment of very large (endocerid ?) cephalopod. Note spatial variation in linearity of maculae across zoarium surface. Zoarium is partly abraded from shell surface. UCWM 1237 [UCWM = University of Chicago Walker Collection; now part of Field Museum Invertebrate Paleontology Collection]. — $\times 0.8$. — Fairmount beds; Cincinnati area, Hamilton Co., Ohio, USA.
- Fig. 14. Zoarium of *Atactoporella maculata* ULRICH 1883 with associated cornulitid tubes, later patchy trepostome overgrowths, and a gap in the *Atactoporella* mat bounded by raised rims along edge of *Atactoporella* zoarium. An earlier *Atactoporella* zoarium underlies this zoarial mat. — UCM 20400. — Maysville-Fairmount strata; Cincinnati, Hamilton Co., Ohio, USA. — a) General view; $\times 1.4$. — b) Close-up view of the gap in the *Atactoporella* mat, the shape and associated rim of which suggest the presence of a soft-bodied encruster which competed with the bryozoan for surface space; this cephalopod specimen illustrates the spatial and temporal complexity of encrustation events observed; $\times 2.8$.
- Fig. 15. Close-up view of bryozoan-encrusted septal face of *Treptoceras*. Knot of closely-packed zooecia in center is either an ancestrula or the focus of converging zooecia which grow from the broken edge of the parent zoarium following shell truncation. — $\times 5.0$. — Fort Ancient Member of Waynesville Formation; south branch, of Harper's Run, G. S. A. Camp Whip-Poor-Will near Roachester, Warren Co., Ohio, USA.
- Fig. 16. Another specimen showing seame features. — $\times 5.0$. — Stratigraphy and locality as in fig. 15.
- Fig. 17. Coenosteum of stromatoporoid *Dermatostroma scabrum* JAMES 1879 showing slightly aligned papillae; also note circular and irregular depressions with raised rims in the coenosteum (base and upper left of view), probably similar to that shown in fig. 14b. ROM 17732 [ROM = Royal Ontario Museum Invertebrate Palaeontology Collection]. — $\times 1.5$. — Upper Ordovician, Georgian Bay Formation; Toronto, Ontario, Canada.
- Fig. 18. Tubes of *Cornulites flexuosus* (HALL 1847) which are overgrown by zoarium of *Spatiopora corticans* (NICHOLSON 1875) with exception of tube apertures. Note that linear *Spatiopora* monticule is juxtaposed on cornulitid irregularities. Cornulitid tubes initially radiate from point of origin but then flex such that most apertures face adapically (to right). UCM 12893. — $\times 2.3$. — Waynesville Formation; Weisburg, Dearborn Co., Indiana, USA.



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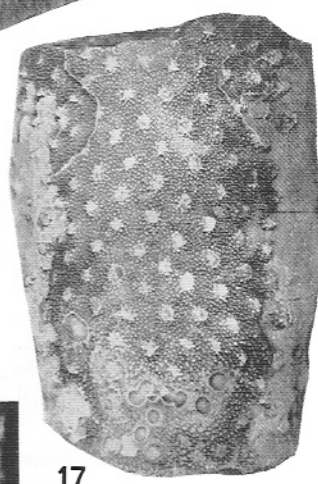
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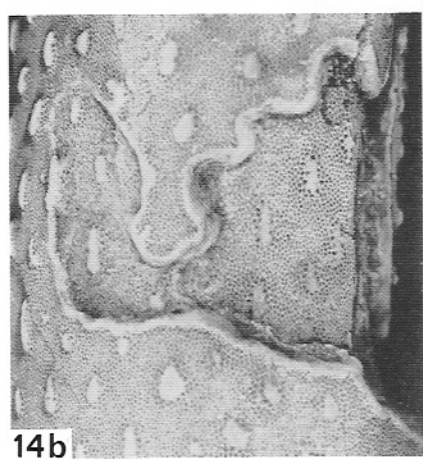
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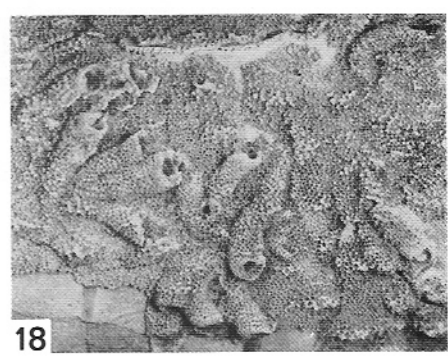
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G. C. BAIRD & C. E. BRETT & R. C. FREY: "Hitchhiking" epizoans on orthoconic cephalopods.

Plate 4.

Epizoans on orthoconic cephalopod shells. — Middle Devonian. — Unnumbered specimens are repositied in paleontological collections of the University of Rochester.

- Fig. 19. *Michelinoceras* phragmocone encrusted by frondose zoaria of the tubuliporate bryozoan *Reptaria stolonifera* ROLLE 1851. Note conspicuous adaperatural growth and orientation of fronds. — UMMP 61186 [UMMP = University of Michigan Museum of Paleontology Collection], hypotype. — Silica Shale Formation, north pit of Medusa Portland Cement (now France Stone Corporation) Quarry, Sylvania, Lucas Co., Ohio, USA. — a) General view; $\times 2.0$. — b) Close up view; $\times 3.9$. Note *Reptaria* zoarial frond which crosses several aligned oriented fronds. Errant frond is clearly younger than portions of fronds which are overgrown. This pattern suggests that the cephalopod shell came to a stationary resting position, forcing a change in the behaviour of the bryozoan.
- Fig. 20. Orthoconic cephalopod encrusted by numerous fronds of *Reptaria stolonifera* ROLLE 1851. More than 25 fronds are observed to grow adaperaturaly on the front and back side surfaces of this compressed living chamber. UMMP collection (uncatalogued). — $\times 1.6$. — Silica Shale Formation; north pit of Medusa Portland Cement (now France Stone Corporation) Quarry, Sylvania, Lucas Co., Ohio, USA.
- Fig. 21. Tightly packed interlocking *Reptaria* zooecia on parallel zoarial fronds. Note ornamentation on outer walls of zooecial tubes and alternating "tooth-and-socket" close fit of zooecial apertures on opposing fronds. UMMP 61148, hypotype. — $\times 2.0$. — Silica Shale Formation; Medusa Portland Cement (now France Stone Corporation) Quarry, Sylvania, Lucas Co., Ohio, USA.
- Fig. 22. External mold of orthocone showing fronds of *Reptaria stolonifera* ROLLE 1851 as they appear from an underside view; zooecial walls are visible on-edge only with the ornamented surfaces of zooecia facing away from the observer. — $\times 3.0$. — Lowermost bed of Stafford Limestone Member; Lancaster, Erie Co., New York, USA.
- Fig. 23. Living chamber of nautiloid encrusted by several fronds of *Reptaria*; note bifurcation of fronds and opposite longitudinal (adaperatural, adapical) as well as transverse growth directions. Also note overlap of one frond onto another. This specimen clearly indicates the encrustation of an empty shell on the seafloor. — $\times 1.0$. — Kashong Shale Member; Mentceth Gully, Canandaigua, Ontario Co., New York, USA.
- Fig. 24. Tabulate coral *Alveolites goldfussi* BILLINGS 1859 on orthoconic cephalopod. Note oriented pattern of corallites. — $\times 1.0$. — Wanakah Shale Member; Benton Run, Ontario Co., New York, USA.

