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Anatomy, life history, and evolutionary affinities of conulariids

Van Iten, Heyo Towne, Ph.D.

The University of Michigan, 1989

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ANATOMY, LIFE HISTORY, AND EVOLUTIONARY AFFINITIES
OF CONULARIIDS

by

Heyo Van Iten

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Geology)
in The University of Michigan
1989

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To my wife, Tatiana, and my parents, Richard and Helga
(and to Gigi, Malish, Kyzya, and Bussy)

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INTRODUCTION

"The class to which this curious fossil originally belonged is not, so far as I know, determined."

David Ure, 1793

This dissertation is a report of research on the paleobiology and evolutionary affinities of conulariids, an extinct group of marine organisms currently known from the Middle Ordovician to Triassic. Conulariids are characterized by a phosphatic, finely lamellar, steeply pyramidal test that usually exhibits four sides, or faces. Specimens range from less than one centimeter long to at least 40 centimeters long (Sinclair, 1948). Viewed externally, their faces are crossed by fine, more or less sharply crested transverse ridges, or by numerous rows of small, closely spaced tubercles, also arranged in longitudinal files. In most cases, transverse ridges and tubercle rows arch toward the wide, or apertural end of the test.

Originally discovered toward the close of the eighteenth century (Sinclair, 1948), conulariids were interpreted throughout the nineteenth and early twentieth centuries as a group of molluscs, and were variously allied with cephalopods, gastropods, or pteropods (Boucek, 1939). In 1937, however, the late Helmut Kiderlen, in one of the most influential discussions of conulariids ever written (Kiderlen, 1937), proposed that conulariids are an extinct group of

scyphozoan cnidarians, ancestral to all extant members this class. His proposal was based in part on the contention that conulariids show strong evidence of tetrameral organization of their soft parts (similar to the tetrameral organization of scyphozoan soft parts), and on similarities between internal, Y-shaped carinae in the conulariid Coconularia loculata (Wiman) and the bifurcate gastric mesenteries (septa) of certain stauromedusan scyphozoans (Kiderlen, 1937). Several subsequent investigators (e.g., Boucek, 1939; Moore and Harrington, 1956; Chapman, 1966; Werner, 1966, 1967; Glaessner, 1971; Bischoff, 1978) have pursued these comparisons further, and have discovered additional similarities between conulariids and scyphozoans. Partly as a result of this and Kiderlen's (1937) work, the hypothesis of a molluscan affinity for conulariids has been abandoned, and many other paleontologists have espoused the hypothesis that conulariids were scyphozoans or an independent group of organisms most closely related to scyphozoans.

In spite of what Kiderlen (1937) and his supporters regard as compelling evidence for a scyphozoan affinity for conulariids, several investigators, most of them writing in very recent years, have rejected this hypothesis (e.g., Termier and Termier, 1949, 1953; Kozłowski, 1968; Oliver, 1984; Steul, 1984; Mortin, 1985; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986; Oliver and Coates, 1987). Interestingly, nearly all of these authors contend that conulariids represented a group of organisms distinct from cnidarians and other phyla. Feldmann and Babcock (1986) have formally elevated them to phylum rank, based on the claim that the conulariid test is fundamentally different from tests of all other taxa. Only Steul

(1984), who presented a highly intriguing analysis of relic soft parts in specimens of Comularia from the Hunsruck Slate (Middle Devonian, West Germany), has argued that conulariids can be accommodated within one of the extant non-cnidarian phyla. Steul (1984) maintains that conulariids are members of the Phylum Chordata, and are most closely related to vertebrates. Together with all other opponents of a scyphozoan affinity for conulariids, she claims that similarities thought to indicate a close relationship between conulariids and scyphozoans are superficial, and/or that conulariids and scyphozoans are characterized by fundamental dissimilarities.

The purpose of the present work is to investigate certain poorly understood, controversial aspects of conulariid anatomy, growth, and mode of life, and to apply this research to evaluating alternative interpretations of conulariid affinities. Even at the level of descriptive morphology, proponents and opponents of a scyphozoan affinity for conulariids have disagreed with one another over a variety of issues. In addition, several related, fundamental problems of interpretation, including the origin and growth of the conulariid test, the life history of conulariids, and the function of various parts of their test, have been inferred largely by analogy with extant organisms, with little attention to evidence intrinsic to conulariids themselves. The present work covers three general areas: (1) the microstructure and growth of the conulariid test; (2) the nature of specimens whose apical end terminates in a smooth, generally outwardly convex wall (the schott); and (3) the anatomy and phylogenetic significance of the corners and midlines of the conulariid test. Also covered in this dissertation is the interpretation of putative relics

of conulariid soft parts. This problem, along with test microstructure and the anatomy of corners and midlines, have been the principle focus of debate over conulariid affinities. The problem of the nature of specimens exhibiting a schott also bears on the problem of conulariid affinities, though to a lesser degree than the other general problems just enumerated. It is covered here because of the abundance of schott-bearing specimens in many taxa, and because of controversy surrounding its implications for conulariid life history.

The body of this dissertation consists of four chapters, each dealing all or in part with one of the general areas of investigation outlined above. Each chapter is written in the format of a suitable professional journal.

The first chapter, to be submitted for publication to the *Journal of Paleontology*, covers the microstructure and growth of the conulariid test. It is based on results of scanning electron microscopy of polished, transverse and longitudinal sections through members of six conulariid genera, and on analysis of patterns of malformation displayed by features interpreted by previous workers (e.g., Babcock et al., 1987) as healed conulariid injuries. The purpose of this chapter is to evaluate Werner's (1966, 1967) proposal, recently disputed by Kozlowski (1968), Mortin (1985), and Feldmann and Babcock (1986), that the conulariid test is homologous to the periderm of coronatid scyphozoans.

The second chapter, to be submitted for publication to the journal *Palaeontology*, covers the anatomy, patterns of occurrence, and origin of schott-bearing conulariids. Based in part on analysis of the anatomy of schotts and schott-bearing conulariids, and on analysis of

patterns of distribution of schott-bearing specimens with respect to sedimentary facies, it is argued that schott-bearing conulariids represent individuals that were truncated, in life, by currents. This interpretation, originally proposed by Werner (1967), runs counter to that accepted by most other advocates of a scyphozoan affinity for conulariids, namely that schott-bearing conulariids represent free-swimming, conulariid medusae. However, it will be argued that the interpretation favored in this work is consistent with a scyphozoan affinity for conulariids.

The third chapter, also to be submitted for publication to *Palaeontology*, covers the morphology and phylogenetic significance of conulariid corners and midlines. Based on examination of sectioned, etched, or broken specimens representing most conulariid genera, its purpose is to evaluate the hypothesis that conulariid midlines were sites of gastric mesenteries, or septa, homologous to the four septa of scyphozoans (Kiderlen, 1937; Moore and Harrington, 1956a; Werner, 1966, 1967; Bischoff, 1978; Grasshoff, 1984). Although opponents of a scyphozoan affinity for conulariids have not suggested an alternative hypothesis of homology, they (e.g., Kozłowski, 1968; Babcock and Feldmann, 1986a) nevertheless maintain that similarities thought to support the gastric septa hypothesis are superficial. Following a description of basic types of corner and midline anatomy, including several new types that were discovered during the course of this work, the chapter compares conulariid corners and midlines with soft-part and peridermal structures of scyphozoans. Following this, the relationship of conulariids to scyphozoans and other cnidarians is examined, based on a cladistic analysis of similarities between these taxa.

The fourth and final chapter presents a general discussion of the problem of conulariid affinities. It summarizes information presented in the preceding chapters (primarily Chapters 1 and 3), and includes an extended discussion of relic conulariid soft parts. Inclusion of such a discussion, though not called for in the research prospectus for this dissertation, was prompted by the author's recent discovery of probable relic soft parts in the test cavity of the holotype and only known specimen of Eoconularia amoena (Sinclair), collected from a Middle Ordovician limestone in Quebec, Canada. Based on comparison of these and previously described relics (Steul, 1984) with soft parts of scyphozoans and internal organs of vertebrate chordates, an interpretation of these features that is consistent with hypotheses of a scyphozoan affinity for conulariids will be offered and defended. A preliminary draft of this chapter was read at an international symposium on problematic fossil taxa and the origins of metazoans, held on March 28 - April 2, 1989, at the University of Camerino, Camerino, Italy. The final version of this paper will appear in a special symposium volume, to be published in 1990 by the University of Camerino Press.

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CHAPTER 1

MICROSTRUCTURE AND GROWTH OF THE CONULARIID TEST IMPLICATIONS FOR DISCUSSIONS OF CONULARIID AFFINITIES

Abstract

The conulariid test is built of extremely thin, alternately dense and vacuity-rich, apatitic lamellae that are concordant with the test's inner and outer surfaces. Transverse ribs and external tubercles are often characterized by accentuated mineralization, in some cases to such a high degree that lamellar boundaries within and below these features are strongly obscured. The claim that thickening of the test at transverse ribs is due to the presence of a series of discrete, solid, transverse internal rods (Feldmann and Babcock, 1986; Feldmann and Babcock, 1986a,b) is incorrect. Such thickening is actually due to localized thickening of individual lamellae.

Especially in relatively thick specimens, lamellae are often grouped in two, more or less distinct layers. The outer layer is corrugated and is characterized by accentuated mineralization and/or thickening of individual lamellae at transverse ribs and tubercles. The inner layer, though commonly also corrugated, consists of lamellae that do not thicken at transverse ribs or tubercles and do not exhibit accentuated mineralization at these sites.

Microstructural data, coupled with information present in healed

injuries and growth abnormalities, indicate that the conulariid test was an external skeleton, as has generally been thought. Growth of the test involved successive accretion of lamellae to the test's inner surface, which caused the test to thicken. Although it has generally been thought that growth of the test also involved marginal accretion, this process may have involved a set of non-mineralized lamellae that have not been preserved in conulariid fossils.

These results are consistent with interpretations of the conulariid test as a mineralized periderm, similar in microstructure and origin to the chitinous periderm of thecate scyphozoan polyps (e.g., Moore and Harrington, 1956a; Werner, 1966, 1967; Bischoff, 1978), but they contradict recent claims (Kozłowski, 1968; Mortin, 1985; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986a,b) that the conulariid test and scyphozoan periderm are fundamentally different structures.

Introduction

Recent disagreement over the biology and evolutionary affinities of conulariids has stemmed in part from conflicts in the characterization and interpretation of the microstructure of the conulariid test. Based on examination of thin sections and/or fracture surfaces using transmitted and reflected light, most previous investigators (e.g., Barrande, 1867; Boucek and Ulrich, 1929; Moore and Harrington, 1956a; Kozłowski, 1968; Bischoff, 1978) have described this test as built of microscopic, phosphatic or chitinophosphatic lamellae that parallel its surface. Kozłowski (1968) and Bischoff (1978) have

shown that these lamellae are less than 10 microns thick and are alternately dense and porous. They and several other authors (e.g., Barrande, 1867; Slater, 1907; Boucek and Ulrich, 1929) have reported that the lamellae are grouped in two layers: an outer, corrugated layer bearing transverse ridges or rows of closely spaced tubercles (the ornamental layer; Kozlowski, 1968), and an inner layer that is more or less planar (the basal layer; Kozlowski, 1968). Moore and Harrington (1956a) report that the test itself is often very thin, in some cases as little as 0.056 to 0.07 millimeters (56 to 70 microns). Several other investigators (e.g., Kowalski, 1935) document specimens that are crumpled but unbroken, or that exhibit regular, complex infolding along the aperture. This has generally been interpreted as indicating that such tests were flexible in life (e.g., Moore and Harrington, 1956a).

Based in part on gross anatomical and microstructural similarities between the conulariid test and the finely lamellar, chitinous periderm of certain polypoid, scyphozoan cnidarians, several investigators have concluded that conulariids were scyphozoans (Kiderlen, 1937; Boucek, 1939; Moore and Harrington, 1956a; Chapman, 1966; Werner, 1966, 1967; Bischoff, 1978) or that conulariids were more closely related to scyphozoans than to any other taxon of comparable rank (Glaessner, 1971). These authors interpret the conulariid test as a mineralized periderm, secreted, as in extant scyphozoans, by ectodermal tissue. Taking this interpretation still further, Werner (1966, 1967) maintains that the basal and ornamental layers of the conulariid test are homologous, respectively, to the inner and outer layers of the steeply conical, bilayered periderm of coronatid

scyphozoans. In his opinion (Werner, 1966, 1967), the coronatid periderm was inherited from a conulariid ancestor, through rounding of the corners and loss of mineralization.

The hypothesis that the conulariid test is a mineralized periderm, similar or homologous to the periderm of coronatids and/or other scyphozoans, has been directly challenged by several authors (Kozłowski, 1968; Mortin, 1985; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986a,b), all of whom have also rejected the hypothesis that conulariids are extinct members or close relatives of Scyphozoa. Although none of these authors has argued that the conulariid test is homologous to the test or periderm of a non-scyphozoan taxon, all claim that the conulariid test and scyphozoan periderm exhibit fundamental dissimilarities. Kozłowski (1968), based on examination of non-sectioned conulariid tubercles, maintains that these structures are often pierced by a small, centrally located pore (choanophyme) that opens to the exterior (Kozłowski, 1968). He interprets this feature as the former site of a minute, externally terminating sensory organ having no homolog in scyphozoans or any other extant taxon. In order to account for the fact that the external surface of many of the tubercles he examined showed no evidence of an opening (Kozłowski, 1968), he further maintains that during ontogeny, tubercles were covered by deposition of lamellae on the test's exterior surface. This leads Kozłowski (1968) to conclude that the conulariid test was secreted internally, rather than externally as in scyphozoans or other cnidarians.

Kozłowski's (1968) interpretation of conulariid tubercles as perforated structures has been refuted by Bischoff (1973, 1978), who

reports that "sections through tubercles (spikes) of well-preserved conulariid test material have. . . shown that [test lamellae] are continuous over the whole of the tubercles (and adjacent parts of the test), thus excluding the possibility of the existence of a passageway between the interior [test cavity] and the surrounding medium at any stage (Bischoff, 1978, p. 298)." Kozlowski (1968) was misled by tubercles that had been broken (Bischoff, 1978, p. 298): "There are numerous [conulariid] test fragments in my collections where tubercles, broken at various levels, occur together with unbroken tubercles on the same transverse rib." These observations nullify Kozlowski's (1968) argument for the presence of test-producing soft tissues on the conulariid test's exterior surface, which was invoked by Kozlowski (1968) in order to account for the observation that many of the tubercles he examined showed no evidence of an opening.

Echoing Kozlowski (1968), Mortin (1985), Feldmann and Babcock (1986), and Babcock and Feldmann (1986) contend that conulariids represented a group of animals distinct from cnidarians and all other phyla. Mortin (1985, p. 12), in a short abstract on conulariid test structure, proposes, without elaboration, that the conulariid test "displays various features suggestive of a reasonably complex secretory physiology, probably involving a mantle-like secretory mechanism." In his opinion (Mortin, 1985, p. 13), this "seems incompatible with a cnidarian affinity for conulariids." Feldmann and Babcock (1986, p. 469) claim that the conulariid test is built not only of fine lamellae, but also incorporates structures they call rods. They interpret the conulariid test as consisting of a thin, finely lamellar "integument," within which is a series of solid, transversely arrayed rods, spaced at

more or less regular intervals. In their opinion (Feldmann and Babcock, 1986, p. 470), "the rods and multilayered integument [together] form a style of exoskeletal construction unknown in other organisms." Based on the purported absence of rods in the genus Metaconularia Foerste and the species Conularina triangulata (Raymond), two taxa traditionally interpreted as conulariids (e.g., Sinclair, 1940, 1948; Moore and Harrington, 1956b; Van Iten, 1989), Feldmann and Babcock (1986) and Babcock et al. (1987) maintain that these taxa are not conulariids.

Objectives, material, and procedure

The purpose of this paper is to evaluate the hypothesis that the conulariid test is comparable or homologous to scyphozoan periderm by addressing recent challenges to this hypothesis by Mortin (1985), Feldmann and Babcock (1986), and Babcock and Feldmann (1986), and by making additional comparisons with the periderm of coronatid scyphozoans. A subsidiary goal of this study is to evaluate claims by Feldmann and Babcock (1986) and Babcock et al. (1987) that Metaconularia and Conularia triangulata are not conulariids. Until now, evaluation of conflicting characterizations and interpretations of conulariid test microstructure had been seriously hindered by lack of adequate documentation of disputed features. This paper supplies such documentation, in the form of scanning electron photomicrographs of sectioned conulariids. Also analyzed in this paper are the microstructure and patterns of malformation of healed conulariid injuries and growth abnormalities. These features have been recognized

by several previous authors (Babcock et al., 1987; Mapes et al., 1989) as having a potentially critical bearing on the mode of growth of the conulariid test and its relation to former soft tissues.

Conulariids examined in this study range from Ordovician to Mississippian in age and are distributed among six of the eighteen currently recognized conulariid genera. Listed alphabetically, they are Climacoconus Sinclair, Conularia Sowerby, Conularina Sinclair, Metaconularia Foerste, Paraconularia Sinclair, and Pseudoconularia Boucek. These six genera include a majority of the total number of known conulariid species, and they provide a comprehensive sample of basic types of conulariid test ornament. Two of the taxa examined here, namely Metaconularia and Conularina triangulata, are especially relevant because of the dispute over whether or not they are conulariids. Genera not examined here are known only from steinkerns (Anaconularia Sinclair, Neoconularia Sugiyama), or are extremely rare and represented by non-preparable type specimens (e.g., Conulariella Boucek), or consist of species extremely similar to and formerly included within one of the six sectioned genera (e.g., Calloconularia Sinclair, Notoconularia Thomas).

Wherever possible, specimens were chosen that were embedded in rock matrix and preserved close to the apex and aperture, though due to limited material some taxa (e.g., Conularina triangulata, Pseudoconularia) could only be examined using fragmentary specimens. Sections through specimens were cut using a Buehler Isomet serial section saw. They were ground and polished using 600 grit and 0.3 micron aluminum oxide powder. They were then cleaned ultrasonically and coated with gold or carbon. It was found that at relatively low

magnifications (100 to 800 diameters), microstructural features were best resolved using carbon-coated specimens examined in back-scattered electron mode. All sections are housed in collections of the Museum of Paleontology, the University of Michigan, Ann Arbor.

Review of conulariid gross anatomy

The steeply pyramidal conulariid test usually exhibits four (but in some cases three or six) sides, or faces (Figure 1A). The test's wide end is open and is referred to as the aperture. In most taxa, the apertural end of each of the faces projects beyond the corners, forming a subtriangular or broadly rounded lappet. At its apical end, the test may terminate in a small, circular attachment disc (Ruedemann, 1986a,b; 1897; Kozlowski, 1968), or it may be truncated some distance above the apex and terminate in a smooth, finely lamellar, usually outwardly convex transverse wall, generally referred to as a schott. This feature also extends along the inside of the test, toward the aperture (Sinclair, 1948). In nearly all conulariids, the corners of the test are furrowed by a prominent corner groove. Corner grooves of many species exhibit an internal, longitudinal carina, produced by localized inflection and thickening of the test's innermost lamellae (e.g., Knod, 1908; Boucek and Ulrich, 1929; Boucek, 1939; Van Iden, 1989). In many cases, the carinae are strongly pigmented and can be seen through the corners.

Viewed externally, the test of almost all conulariids is crossed by closely spaced transverse ridges, called transverse ribs, or by transverse rows of minute, closely spaced tubercles, which are also

arranged in longitudinal files. Tubercle rows and, in most cases, transverse ribs, arch toward the aperture as they cross the faces. As shown by longitudinal sectioning (e.g., Sinclair, 1948), transverse ribs are an external expression of trochoidal corrugation. Transverse ribs of several taxa (e.g., Comularia) exhibit regularly spaced, hemispherical swellings, similar in morphology and arrangement to tubercles in taxa lacking transverse ribs. In the former taxa, the region between two adjacent transverse ribs, the interrib area, is longitudinally corrugated. Both in ribbed taxa and taxa bearing transverse tubercle rows, transverse features may be more or less evenly spaced, or at certain latitudes they may be closely crowded, in some cases to such an extent that ribs or tubercles rows are essentially contiguous (Sinclair, 1948).

With few exceptions, the midline of each of the faces is marked by a groove or by offset or deflection of transverse ribs or tubercle rows. Internally, midlines of many taxa exhibit one of several types of longitudinal, single or paired carinae or thickenings, produced again by localized inflection and thickening of inner test lamellae (e.g., Wiman, 1895; Boucek, 1939). As in the case of corner carinae, internal structures at conulariid midlines are often strongly pigmented and visible through the faces.

Anatomy and growth of the coronatid periderm

Details of the anatomy and growth of the peridermal tubule of coronatid polyps have been discussed by Chapman (1966), Werner (1966, 1967, 1970, 1974, 1979, 1983), and Chapman and Werner (1972).

Reviewing the main points, the tubule fully covers the sides of the calyx and may be more or less straight or variably curved or torted (Figure 1B). The tubule is present throughout the polyp's life, and during ontogeny it increases in length, keeping pace with lengthening of the soft body (Werner, 1974). At its basal, or apical end, the tubule exhibits a small, plano-convex attachment disc, cemented to rocks or other firm substrates. The oral, or apertural end is open, but during periods of strobilation (during which the soft body transforms into a series of incipient medusae) the animal often closes this end by secreting a thin, circular operculum.

Examination of sections through the periderm using transmission electron microscopy (Chapman and Werner, 1972) shows that it is built of numerous, 12 nanometer-thick lamellae, separated from each other by an equally narrow gap that is bridged at short intervals by minute peridermal processes. The lamellae are grouped in two layers: a finely sculptured, outer layer, about 2 to 4 microns thick; and a non-sculptured, inner layer, locally almost 20 microns thick. The sculptured, outer layer extends the full length of the periderm and is crossed by numerous, transverse and longitudinal corrugations. The ridge-like crests of the trochoidal, transverse corrugations completely encircle the tubule and number from 10 to 20 ridges per millimeter; spanning the region between these ridges are evenly spaced, rounded, longitudinal ridges, corresponding to the crests of the longitudinal corrugations. Line drawings of longitudinal cross sections in Werner (1970) show the outer layer alternately thickening and thinning, respectively, at the crests and troughs of the transverse corrugations. Observations on specimens raised in laboratory cultures (Werner, 1974)

indicate that changes in the rate of growth of the soft body are reflected in changes in the spacing of the transverse ridges, with periods of relatively slow growth marked by localized crowding of ridges. Although not explicitly stated, it is evidently the case that the exterior surface of the outer layer (i.e., the exterior surface of the tubule) is defined by a single lamella, and that outer layer lamellae below the exterior one run parallel to it and, like it, extend the entire length of the outer layer.

In contrast to the outer, sculptured layer, the inner layer usually pinches out a short distance below the aperture. Measurements made on one specimen (Chapman and Werner, 1972), about 30 millimeters long, show the inner layer narrowing from a thickness of almost 20 microns near the basal disc to a thickness of 2 microns at a distance of 100 microns from the aperture. Within this layer, lamellae apparently parallel the inner surface of the sculptured layer. In some species, inner layer lamellae are locally inflected, forming up to six or seven whorls of eight tetramerally arranged, thorn-like protuberances, or teeth, that project into the peridermal cavity. In all whorls, four of the teeth are situated at the base of each of the four gastric septa, which together define two mutually perpendicular planes of symmetry called the interradii. The other four teeth are situated midway between the interradial teeth and lie in the two perradial symmetry planes. The perradial teeth are consistently larger (longer, wider, higher) than those at the interradii.

The two coronatid periderm layers also differ in the manner in which they are produced. The outer layer is secreted by gland cells in an adoral, collar-like zone of modified ectoderm, called the junctional

secretory band (Chapman and Werner, 1972). Werner (1979, p. 85) reports that this structure exhibits "a small transverse groove in which the soft body and rim [apertural margin] of the tubule are intimately connected." The gland cells that secrete the outer layer are situated within this rim, and it is their activity that allows the tubule margin to migrate with the lengthening soft body (Werner, 1979). Given that lamellae defining the outer layer evidently parallel the tubule's exterior surface and extend its full length, this implies that the outer layer grows by addition of peridermal material along the apertural margin, to existing lamellae.

Growth of the inner layer is mediated by gland cells in the sides of the calyx, below the junctional secretory band. Inner layer lamellae are successively accreted to the tubule's inner surface, in a direction perpendicular to lamellar boundaries. This process occurs throughout ontogeny, resulting in sequential production of whorls of peridermal teeth, with the first whorl produced near the base of the tubule and more adorally situated whorls added later, as the outer layer lengthens. Finally, damage to the tubule, including punctures in its side and breakage of the apical end, is repaired by secretion of a thin patch of inner layer lamellae (Werner, 1967).

Conulariid test microstructure

Observations

The tests of conulariids here examined are built of extremely thin, alternately dense and vacuity-rich lamellae (Figure 2A-I).

Lamellae are especially distinct in Conularia, Paraconularia, and Climacoconus (e.g., Figures 2A-F). In these and the remaining three genera (Figures 2G-I), lamellar boundaries are conformable with the test's outer surface (for reasons that are not yet understood, the inner surface is often modified by diagenetic alteration; e.g., Figure 2A). X-ray diffraction and energy dispersive elemental analysis confirm that the lamellae are apatitic, as indicated by microstructural and compositional data presented in Boucek and Ulrich (1929).

In all cases, the test is thicker at sites of transverse ribs and tubercles than at sites between these features (Figures 2A, 2C, 2E-I). This is due to localized thickening of individual lamellae. In parts of the test between transverse ribs and tubercles, lamellae are 1 or 2 microns thick (e.g., Figure 2B). Beginning in the vicinity of a transverse rib or tubercle, the outermost lamellae gradually thicken toward the rib or tubercle summit, where they attain a maximum thickness of about 5 microns (Figure 2C). The number of lamellae showing such thickening appears to vary from species to species; in specimens of Conularia cf. subulata Meek and Worthen (Figure 2A), the number of lamellae thickening at the transverse ribs is about 100.

In most species, the test is more strongly mineralized at sites of ribs or tubercles than in other parts of the test (Figures 2A, 2F). This phenomenon is restricted largely (but not exclusively) to lamellae that thicken at ribs and tubercles. (Accentuated mineralization in these lamellae also occurs in test material between ribs or tubercles, though to a lesser extent.) Lamellae below these are of uniform thickness. Because all lamellae are in continuous

contact with each other, lamellae below the zone of localized thickening and accentuated mineralization may, like lamellae within this zone, be corrugated. Depending on the thickness of the test (i.e., on the total number of lamellae present), the zone of non-thickened, non-obscured lamellae may be up to 20 times thicker than the outer zone (Figure 2E).

Finally, more or less complete tests (tests preserved close to the apex and aperture) are thinnest at their apical and apertural ends (see however Barrande (1867) for descriptions of specimens of Archaeoconularia fecunda (Barrande) whose test thickens toward the apex, in some cases to such an extent that the apical region of the test cavity is occluded). This is due to a more or less gradual decrease in the thickness of the inner layer. Since all inner layer lamellae here observed are mutually parallel and of uniform thickness, this implies that inner layer lamellae terminate at latitudes above and below the apex and aperture. Due to incomplete preservation and/or diagenetic alteration (replacement of apatite by calcium carbonate; e.g., Figure 1A), however, such terminations could not be observed. No evidence of termination was observed among lamellae in the outer zone. The number of lamellae forming this layer appears to be the same, at least at latitudes not immediately adjacent to the apex and aperture. Again, even the best preserved specimens are broken short of these features, and thus it is not clear how many lamellae were present in the basal disc or along the apertural margin.

Discussion

Traditional characterizations. For the most part, these observations agree with traditional characterizations of conulariid test microstructure (e.g., Boucek and Ulrich, 1929), which describe the test as built of microscopic, phosphatic lamellae that parallel the test's surface and are grouped in two, more or less distinct layers. The only point of disagreement concerns the characterization of the two layers. In previous studies (e.g., Kozłowski, 1968), the outer layer is described as ornamented (i.e., consisting of corrugated lamellae), while the inner layer is described as smooth (i.e., consisting of lamellae that are more or less flat) - no mention is made of differences in degree of mineralization. Results of this study suggest that a better way of characterizing the organization of conulariid test lamellae is to describe the outer layer as consisting of lamellae that are obscured and/or thicken at transverse ribs or tubercle rows, and the inner layer as defined by lamellae that neither thicken nor become obscured as they approach the summit of a rib or tubercle row. One or both of these phenomena were observed in all taxa examined here, suggesting that this way of distinguishing between inner and outer lamellae is based on more fundamental criteria. Note, too, that it takes into account the observation that expression of transverse ornamentation often extends into lamellae that do not show thickening or obscuration at sites of ribs or tubercle rows.

Later characterizations. This characterization of conulariid test microstructure conflicts with more recent characterizations offered by Feldmann and Babcock (1986) and Babcock and Feldmann (1986a,b). These

authors claim that the conulariid test possesses additional structural elements, called rods. These features are described as "solid, narrow, elongate structures" (Feldmann and Babcock, 1986, p. 469), "embedded in the [lamellar] integument" (Babcock and Feldmann, 1986b, p. 359).

According to Feldmann and Babcock (1986, p. 469), "[it] is the rods that, when covered by integument, form the prominent ridges [transverse ribs] across each face of a conulariid." This interpretation is based on results of very low magnification, reflected light and SEM imaging of non-sectioned material, particularly specimens of Paraconularia subulata from the Orangeville Member of the Cuyahoga Formation (Lower Mississippian), northeast Ohio (Feldmann and Babcock, 1986). As in many other corrugated conulariids, these specimens are substantially thicker at transverse ribs than at sites between these features, and the specimens exhibit extensive break-up along interrib areas. One of these specimens, housed in collections of the United States National Museum (USNM 395829), appears on superficial examination to consist only of transverse ribs. (Close inspection of this specimen reveals that interrib test material is actually present but is covered by matrix or broken immediately adjacent to the ribs.) In the opinion of Feldmann and Babcock (1986), these ribs represent discrete, transverse support structures, or rods, now exposed and isolated due to decomposition of the lamellar integument that purportedly covered them in life.

SEM imaging of sectioned, polished specimens of Paraconularia and other corrugated conulariids reveals that transverse ribs are not sites of a discrete, transverse internal rod. Rather, the pronounced increase in test thickness often seen at transverse ribs is due to

thickening of individual test lamellae as they pass through the ribs (e.g., Figure 2C). Although in many cases the core of the rib is more strongly mineralized than adjacent parts of the test (e.g., Figure 1A), the observation that lamellae can still be traced through this region indicates that it is part of a single, continuously laminated structure. As noted above, accentuated mineralization is exhibited not only in transverse ribs, but in tubercles as well (e.g., Figure 1H).

Healed conulariid injuries and growth abnormalities

Features interpreted in this paper as healed injuries or growth abnormalities of the conulariid test have recently been discussed by Werner (1967), Babcock et al. (1987), and Mapes et al. (1989). Based on microstructural characteristics and/or patterns of malformation of transverse ribs or tubercle rows, to be considered in this section, such features are assigned here to one of two general categories. The first category consists of features that have been interpreted as areas of repaired test breakage sustained below the apertural margin. These features are schotts, described in detail by Sinclair (1948) and Van Iten (1989), and features analogized by Babcock et al. (1987) with embayed injuries (Alexander, 1986) on fossil articulate brachiopods (Figures 3A-B). In this paper, features analogized by Babcock et al. (1987) with embayed injuries will be referred to as patches (for reasons that will be apparent in the remainder of this paragraph). Viewed externally, both schotts and patches consist of an area of smooth or finely wrinkled (in some cases concentrically) test that is surrounded by, and depressed below, transversely ornamented test that

has been broken (Figures 3A-B). At or near the center of the area of non-ornamented test there is often a small, circular or approximately quadrate dimple (Figures 3A-B). Examination of polished sections through schotts (e.g., Figure 3C) reveals that they are built of inner layer lamellae that parallel the schott surface and are concordant with lamellae in the faces. Inspection of fracture surfaces on patches (patches here examined occur on museum specimens that could not be sectioned) suggests that these features are also built of inner layer material. Schotts extend for considerable distances (up to several centimeters or more) beyond the line of test truncation, along the inside of the faces (Sinclair, 1948; Van Iten, 1989); patches, on the other hand, appear to pinch out close to this line (as indicated again by inspection of fracture surfaces).

By analogy with coronatid scyphozoans whose periderm has been broken or punctured (exposing the calyx), Werner (1966, 1967) proposes that conulariid schotts and patches were formed by deposition of new lamellae on the test's inner surface, in response to breakage of the apical end (schotts) or to formation of a hole in the side of the test (patches). Observations presented here and in Babcock et al. (1987) tend to confirm this interpretation. For example, the presence of fine wrinkles or a central dimple on patches, coupled with lack of topographic expression of transverse ribbing or tuberculation on these features, indicate that patches are not due to removal of overlying test material subsequent to death. Together with similarity to patch-like features occurring on peridermal tubules of coronatids, these attributes suggest that conulariid patches were formed, in life, in order to cover soft tissues exposed by localized removal of test

material. Sinclair (1948) and Babcock et al. (1987) suggest that the presence of concentric wrinkling and/or a central pucker also indicates that schotts and patches were secreted centripetally, i.e., along growth surfaces that were oriented at a high angle to lamellar boundaries. However, no evidence of growth increments other than lamellar boundaries was observed in this study (and no such evidence has been offered in previous papers), and for this reason it is here assumed that schotts and patches were formed by successive, inward (adaxial) accretion, along growth surfaces paralleling lamellar boundaries (which, judging from accounts in Werner (1967), is evidently the way similar features in coronatids were formed).

Schotts or patches (or both) have been documented in species of Anaconularia (schotts; e.g., Barrande, 1867), Archaeoconularia (schotts; e.g., Barrande, 1867; Boucek, 1928, 1939), Conularia (schotts and patches; e.g., Babcock and Feldmann, 1986b; Babcock et al., 1987), Paraconularia (schotts and patches; e.g., Babcock and Feldmann, 1986c; Babcock et al., 1987), and Metaconularia (schotts; Sinclair, 1940). Importantly, no instances of damage repair involving lamellae deposited on the test's exterior surface have been found in these or any other conulariids (see discussion below).

The second category consists of areas of abnormal test ornamentation that have been interpreted by Babcock et al. (1987) as areas of repaired test breakage sustained along the apertural margin. Babcock et al. (1987) recognize two such features, which they analogize with scalloped and cleft injuries (Alexander, 1986) on valves of certain fossil articulate brachiopods. Areas of scalloped ornamentation on conulariids (Figure 4A) are situated on a single face,

astride the midline, and resemble an angular unconformity. They consist of one or more transverse ribs or tubercle rows that are truncated by a rib or tubercle row situated closer to the aperture. In many cases, the truncating rib or tubercle row, together with one or more of its more adaperturally situated neighbors, arch toward the apex, instead of toward the aperture. The surface of the test shows no change in elevation across the line of unconformity (Babcock and Feldmann, 1987; Figure 4B), and sections through this line show no evidence of truncation of test lamellae (Figure 4B).

Cleft features, situated on a single face or encompassing portions of two adjacent faces, consist of a subtriangular region of non-ornamented or abnormally ornamented test that points toward the apex and is depressed below adjacent, normally ornamented test bordering the two sides of the cleft nearest the apex (Figure 4C-D). The difference in elevation between the cleft and laterally adjacent test decreases toward the cleft's adapertural end, where the cleft and normally ornamented test are coplanar. Sections through clefts (Figure 4E) show that depression of the test along the lateral cleft margins is due to downward bending of the test; individual lamellae are weakly defined but continue through the margins, without truncation. Also along the two sides of the cleft nearest the apex, ribs or pustule rows crossing the cleft are offset from laterally adjacent ribs or pustule rows crossing normally ornamented portions of the test. As in the case of scalloped injuries exhibiting abnormal, adapical rib arching, transverse ribs or pustule rows crossing the cleft, rather than arching toward the aperture, arch toward the apex. The degree of departure from normal, adapertural arching is most pronounced at the adapical end

of the cleft and decreases toward the cleft's apertural end. Despite termination of transverse ribs (or pustule rows) at the lateral margins of clefts, none of the lateral cleft margins here observed (or illustrated by Babcock et al., 1987) exhibit test material that can unambiguously be interpreted as broken. Rather, it appears that the test surface, though downwardly bent, is continuous.

Areas of abnormal shell ornamentation similar in external morphology to scalloped and cleft abnormalities on conulariids have been observed on fossil articulate brachiopods and extant molluscs (Alexander, 1986; see also references cited therein). In molluscs and, probably, fossil brachiopods as well, such features were produced in response to localized irritation of test-secreting cells in the mantle edge, possibly associated with minor chipping of shell material (Alexander, 1986). Apparently by analogy with brachiopods and molluscs, Babcock et al. (1987) interpret scalloped and cleft features in conulariids as areas of repaired test breakage. They maintain that such breakage was sustained along the apertural margin, and that repair of damage was accomplished by secretion of new test material along this margin (Babcock et al., 1987).

Consideration of other ways in which areas of scalloped and cleft ornamentation on conulariids might have formed suggests several alternative explanations, all of them consistent with the more general hypothesis (see the following section) that conulariid tests were characterized by marginal growth. Among these alternatives are: (1) localized irritation of periderm-secreting soft tissues situated along the aperture, without breakage of periderm and/or formation of a cleft or indentation but resulting in localized disruption of the transverse

ornament (cleft and scalloped features) and/or peridermal surface (cleft features); (2) localized irritation of periderm-secreting soft tissues situated along the aperture, without breakage of periderm but resulting in formation of a cleft or indentation along the aperture that was repaired by subsequent, marginal secretion; and (3) localized, marginal breakage of an exterior layer of non-mineralized periderm that is not directly preserved in conulariid fossils but whose inner surface is mirrored by the outer surface of mineralized, more adaxially situated periderm formerly lining the inner surface of the layer of non-mineralized periderm. Evaluation of these alternatives, all of them intimately associated with the more general problem of how the conulariid test grew, will be considered in the following section, which deals specifically with this problem.

Scalloped and/or cleft injuries have previously been documented on specimens of Conularia and Paraconularia (Babcock et al., 1987). In this study, they were observed on specimens of Metaconularia as well (Figure 4D).

Mode of growth of the conulariid test

Largely by analogy with extant taxa, several authors (e.g., Moore and Harrington, 1956a; Werner, 1966, 1967; Bischoff, 1978; Babcock et al., 1987) have proposed that growth of the conulariid test involved two distinct modes: secretion along the apertural margin (marginal growth); and secretion on the inner surface (thickening). By analogy with the bilayered periderm of coronatid scyphozoans, Bischoff (1978) proposes that as the conulariid's soft body lengthened,

the outer test layer (*sensu* Kozlowski, 1968) also lengthened, through addition of new material to the adapertural margin of existing lamellae. Simultaneously, parts of the test below the apertural margin were thickened through successive addition of whole lamellae to the inner test surface, producing the inner test layer (with or without longitudinal carinae at the corners and/or midlines).

At least three other hypotheses of conulariid test growth, all of them substantially different from each other and the hypothesis outlined above, could also be proposed. These are: (1) that all conulariid test lamellae were produced successively, as whole units and with each new unit added to the outer surface of its predecessor (abaxial addition); (2) that all lamellae grew by extension along their adapertural margin, through addition of new material to this margin (marginal extension); and (3) that all lamellae were produced successively, again as whole units but with each new unit added to the inner surface of its predecessor (adaxial addition). Other hypotheses, many of them involving combinations of the three alternatives just outlined, could also be offered.

The hypothesis that the conulariid test was produced through successive addition of whole lamellae to the test's exterior surface (thought by Kozlowski (1968) to account for formation of the outer test layer) implies that this surface was covered by test-secreting soft tissues. However, as discussed above in connection with healed conulariid injuries and growth abnormalities, damage to the conulariid test was repaired only by test material (schotts and patches) deposited on the test's inner surface, and never by material deposited on the test's exterior surface. Since damage repair on known internal

skeletons (e.g., the calcitic skeleton of echinoderms) occurs both on inner and outer skeletal surfaces, the lack of damage repair on the exterior surface of conulariid tests suggests that test-secreting soft tissues were not present on the exterior surface.

Results of this study are consistent with the hypothesis that growth of the conulariid test involved successive accretion of lamellae to the inner test surface. Barrande's (1867) observation that specimens of Archaeoconularia fecunda (Barrande) show occlusion of the adapical part of the test cavity, coupled with the inference that the conulariid test was an external skeleton, lead to the conclusion that formation of at least some lamellae can be attributed to accretion on the inner test surface. The fact that lamellae here observed are concordant with the outer test surface (and not inclined to this surface), suggests that thickening of the conulariid test, described by previous authors (e.g., Moore and Harrington, 1956; Bischoff, 1978) as occurring throughout the course of ontogeny, in an adapertural direction, actually began at some point relatively late in the animal's life, covering essentially all of the inner test surface at once.

The hypothesis that growth of the conulariid test also involved marginal secretion has been based on analogy with the bilayered periderm of coronatid scyphozoans (Werner, 1966, 1967), and on interpretation of healed injuries or growth abnormalities (e.g., Babcock et al., 1987). In arguing for marginal growth in conulariids, previous authors have cited the following: (1) localized crowding of conulariid transverse ribs or tubercle rows (analogized with localized, growth-related crowding of surficial costae or transverse ribs on tests or peridermal tubules that are known to be marginally secreted; e.g.,

Moore and Harrington, 1956a); and (2) presence of areas of scalloped and cleft ornament patterns (analogized with similar features on ribbed or costate shells of fossil brachiopods and extant molluscs; Babcock et al., 1987).

In agreement with interpretations implicit in Babcock et al. (1987), it is here proposed that conulariids could not have produced cleft or scalloped features had growth of their test (or periderm) only involved secretion on the inner surface. Rather, it seems there must have been an element of marginal growth. As conceived in this paper, this proposal is based on the following grounds: (1) cleft features show a consistent, adapertural decrease in degree of topographic abnormality (adapical rib deflection and depression below the surface of normally ornamented test); (2) similar patterns of abnormal ornamentation on ribbed or costate shells of fossil brachiopods and extant molluscs are produced by irritation of test-secreting mantle tissue along the edge of the shell (Alexander, 1986); and (3) similar patterns of abnormal test ornamentation are never shown by conulariid schotts or patches, which as argued above were produced by accretion perpendicular to lamellar boundaries.

Purposely omitted from the argument just outlined is an answer to a very important question: Did marginal growth involve fully mineralized lamellae? More specifically, did this process involve addition of test material to the apertural edges of existing lamellae (as would have been the case, since outer layer lamellae parallel the test's exterior surface). Implicit in previous discussions of marginal growth in conulariids (e.g., Werner, 1966, 1967; Bischoff, 1978) is the assumption that this process did occur in the manner just described.

The reason this interpretation is targeted here is that outer layer lamellae observed in this study parallel (or are concordant with) inner layer lamellae and show no evidence of possible growth increments inclined to lamellar boundaries. Given that such increments are present in shells of extent invertebrates (i.e., molluscs) exhibiting marginal shell growth, it seems difficult to imagine how marginal test growth in conulariids, which has been interpreted by some previous authors (e.g., Moore and Harrington, 1956a; Werner, 1966, 1967; Babcock et al., 1987) as a discontinuous process, could have involved fully mineralized lamellae.

So how, exactly, might this process have been accomplished? One possibility, admittedly extremely difficult to test directly, is that marginal growth in conulariids involved a set of non-mineralized, exterior lamellae that are not preserved in fossil conulariids. The presence of cleft features on mineralized tests would be explained as the result of accretion of mineralized lamellae to the inner surface of this non-mineralized layer, which, acting as a template, imparted its topography to lamellae accreted to it. This hypothesis is, it seems, consistent with test microstructure. In particular, the fact that outer layer, mineralized lamellae are concordant with the outer surface of the test suggests that all of the test's lamellae, not just those forming the inner layer, could have been formed by successive accretion, perpendicular to lamellar boundaries.

One strategy that may help resolve this problem is to conduct additional, more detailed investigations of the microstructure and growth of the coronatid periderm, and to do additional work on conulariids, in the hope of finding specimens that preserve the apex

and apertural margin. If, as implied for example by discussions in Chapman and Werner (1972) and Werner (1974, 1979), growth of the coronatid periderm's outer layer does involve addition of new material to margins of existing lamellae, and if the apertural margin of the conulariid test is defined by edges of a substantial number of lamellae, then the hypothesis that growth of the conulariid test involved addition of test material to edges of existing lamellae would be more plausible. Suffice it say, while conulariids do show features suggestive of marginal test (periderm) growth, the loci and mechanics of this process are still unclear.

Implications for the affinities of
Metaconularia and Conularina triangulata

Feldmann and Babcock (1986) and Babcock et al. (1987) have proposed that Metaconularia and Conularina triangulata be removed from Conulariida, based on the claim that the former two taxa lack rods. However, results of this study indicate that both Metaconularia and C. triangulata are extremely similar in microstructure and mode(s) of injury repair to other taxa traditionally interpreted as conulariids, and as documented in previous studies (Sinclair, 1940, 1942, 1948; Van Iten, 1989), they and other conulariids share several gross anatomical similarities that are unique to members of this group. Among the most conspicuous of these similarities are: (1) possession of transverse ribs (C. triangulata) or tubercle rows (Metaconularia) that arch toward the aperture as they cross the faces (Metaconularia) and/or exhibit offset or adapical deflection at the midlines (C. triangulata)

(Sinclair, 1940, 1942, 1948); (2) possession of sulcate corners (Metaconularia, C. triangulata) that may be either non-thickened (Metaconularia) or internally carinate (C. triangulata) (Sinclair, 1940, 1942, 1948); and (3) presence of a pair of internal, adaperturally diverging longitudinal thickenings or carinae at the midlines, with members of each pair situated on opposite sides of the midline proper (Metaconularia, C. triangulata; Van Iken, in prep.). Although C. triangulata differs from Metaconularia and other conulariids in having only three faces, rather than four, the recent discovery of a specimen of Paraconularia missouriensis (Swallow) possessing six faces (Babcock et al., 1987) indicates that conulariids sometimes departed from four-fold symmetry.

In short, there are no consistent, fundamental differences between Metaconularia, C. triangulata, and other taxa traditionally interpreted as conulariids. Given the number and complexity of similarities between these taxa, and the fact that several of these similarities are uniquely shared by members of this group, it seems wisest to continue to interpret Metaconularia, C. triangulata, and similar taxa as members of a single, monophyletic taxon.

Implications for the affinities of conulariids in general

As is evident from observations and discussion above, conulariids and coronatid polyps show a number of similarities in test (peridermal) structure and growth. In both groups, the test (periderm) is built of extremely thin, parallel lamellae that are generally concordant with the inner and outer surfaces. The innermost lamellae

may be locally inflected (inflected and thickened in conulariids), at sites interpreted on other grounds as positionally comparable (Werner, 1966, 1967; Bischoff, 1978; Van Iten, 1989), forming longitudinal structures that project into the test cavity. Again in both groups, holes in the test (periderm) are covered by smooth (non-ornamented) lamellae, deposited on the inner surface. Finally, both groups show evidence of two modes of test (peridermal) growth: accretion of lamellae to the inner test surface (in some members of these two groups forming internal teeth (coronatids) or carinae (conulariids)); and marginal growth.

At the very least, these similarities suggest that the conulariid test was a mineralized, ectodermally secreted periderm, similar, and possibly homologous (in part) to, the periderm of coronatid scyphozoans. They therefore also suggest that Mortin's (1985) description of conulariid test growth as involving a mantle-like secretory mechanism is not inconsistent with hypotheses of a cnidarian affinity for conulariids. To be sure, the conulariid test and coronatid periderm do show differences in general shape (steeply pyramidal in conulariids versus steeply conical in coronatids) and degree of mineralization (apatitic in conulariids versus non-mineralized in coronatids). These two differences figure prominently in arguments against homology presented by some of Werner's (1966, 1967) earlier opponents (Termier and Termier, 1949, 1953; Kozłowski, 1968). However, given the similarities outlined in the preceding paragraph, evolutionary transformations between these two groups involving changes in test (periderm) shape and loss or derivation of apatitic mineralization do not seem at all unreasonable. Moreover,

given that variation in degree and, even, type of mineralization is characteristic of many class-level taxa (e.g., absence of mineralization in thecate trachyline hydrozoans versus calcium carbonate mineralization in milleporine and stylasterine hydrozoans; Hyman, 1940), the fact that the conulariid test is apatitic and the periderm of coronatids and other scyphozoans is not is hardly grounds for rejecting hypotheses of phylogenetic relationship between these groups. While it remains to be evaluated whether or not similarities between the conulariid test and coronatid periderm can be interpreted as synapomorphic (which would indicate that conulariids and coronatids are more closely related to each other than either group is to non-coronatid scyphozoans), at present there seems to be no evidence that would preclude the possibility that they are.

Acknowledgements

This study forms part of a Ph.D. dissertation written in the Museum of Paleontology, University of Michigan, Ann Arbor. I thank the members of my dissertation committee (D. J. Eernisse, D. C. Fisher, K. C. Lohmann, G. R. Smith, and B. H. Wilkinson) for their comments on earlier versions of this paper. I also thank R. Titus for permission to prepare specimens of Conularia trentonensis Hall in collections of Hartwick College (Oneonta, New York), and W. F. Rice for permission to prepare a specimen of Metaconularia sp. in collections of the Department of Geology, University of Minnesota, Minneapolis. SEM analysis was conducted in the Robert B. Mitchell Electron Microbeam Analysis Laboratory (Department of Geological Sciences, University of

Michigan). Support for this study was provided in part by NSF
Research Grant BNS-8521097 to D. C Fisher.

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Figure 1A-B. A, Reconstruction of a living conulariid showing inferred apical attachment and one interpretation of the relationship of soft tissues to the test (X2). B, Living coronatid polyp (X2). Both figures taken from U. Lehmann and G. Hillmer (1983), *Fossil Invertebrates*, Cambridge University Press (Figures 38a,c).



Figure 2A. Longitudinal section through a transverse rib of *Conularia* cf. *subulata* (Hall) (Cedar Valley Limestone, Middle Devonian, Iowa; X500). The apertural end is to the right while the outer test surface faces the top of the page.



Figure 2B. Longitudinal section through part of the test between two adjacent ribs of the specimen in the previous figure (X400). The apertural end is toward the upper right-hand corner of the page, and the exterior test surface faces the upper left-hand corner.

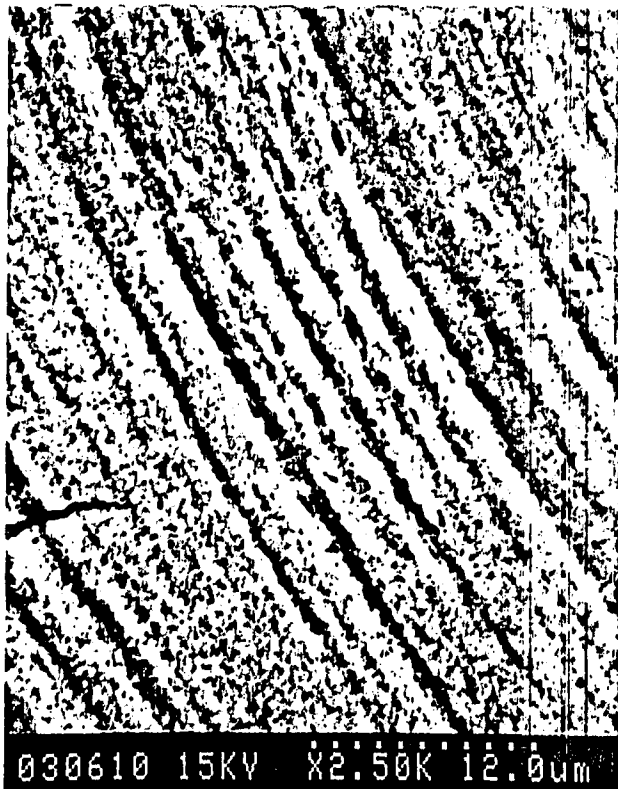
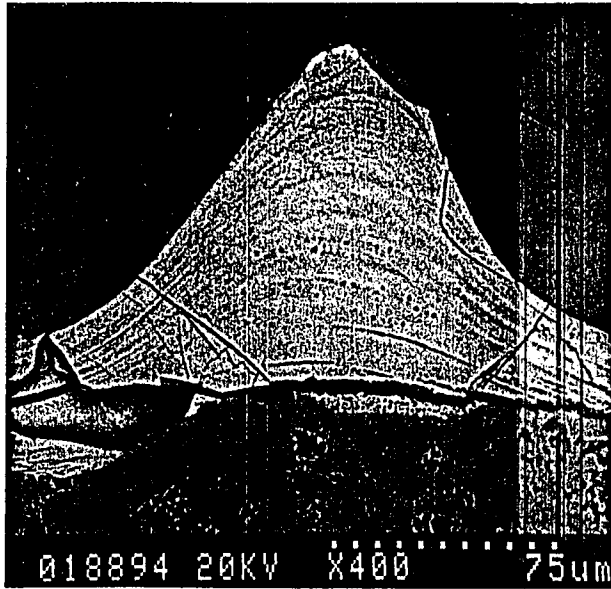


Figure 2C-D. C, Longitudinal section through a transverse rib of Paraconularia sp. (Mississippian, Illinois; X400, apertural end lies to the right); D, Detail of another part of the same specimen, near a transverse rib (X2500).



Figure 2E. Part of a longitudinal section through Paraconularia crustula (White), intersecting a midline carina (Pennsylvanian, Texas; X 100, apertural end lies to the northeast). The boundary between the inner and outer layers is marked by arrows.

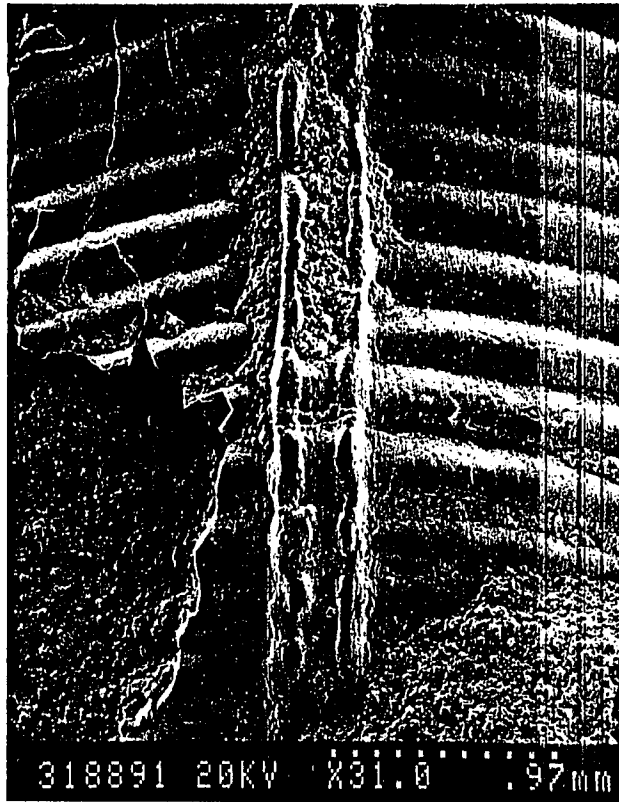


Figure 2F. Longitudinal section through a transverse rib of Climacoconus sp. (Maquoketa Formation, Upper Ordovician, Iowa; X800, aperture to the right). The boundary between the inner and outer layers is marked by arrows.

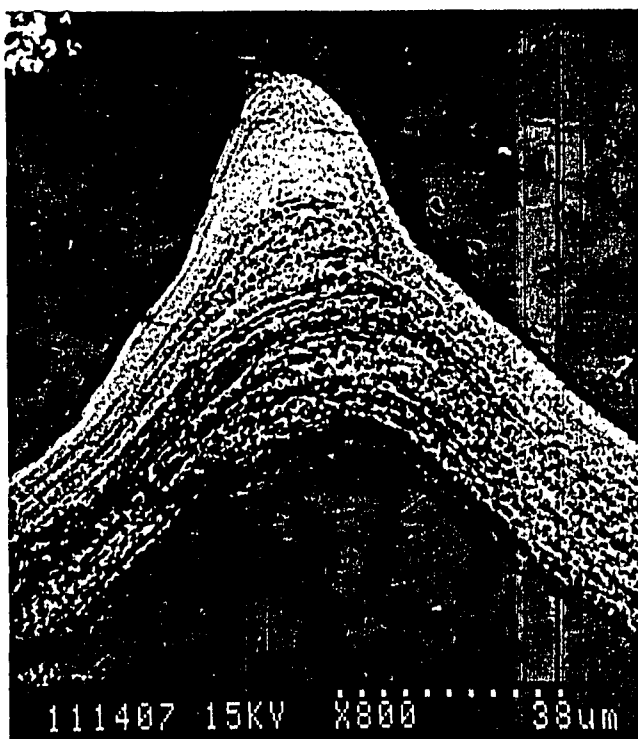


Figure 2G. Part of a longitudinal section through Pseudoconularia sp., intersecting two tubercles (Manitoulin Limestone, Lower Silurian, Michigan; X350, apertural end lies to the right).

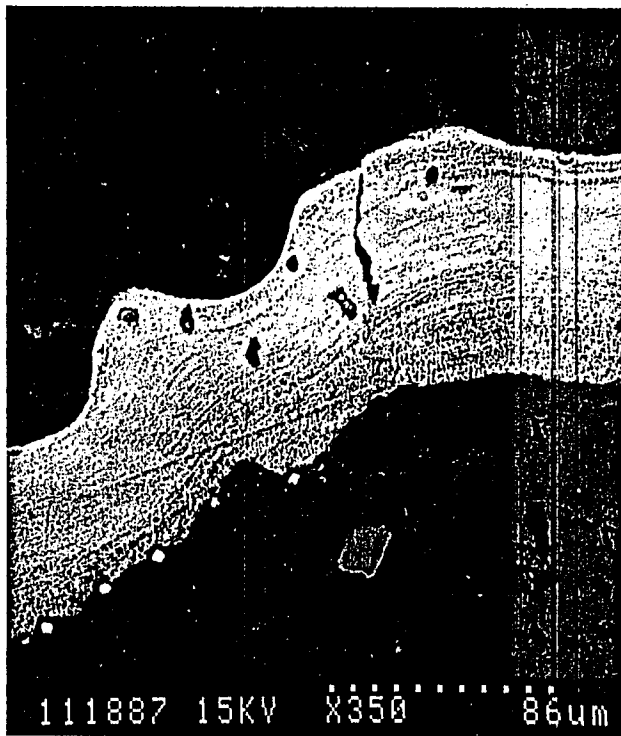


Figure 2H. Part of a longitudinal section through *Metaconularia* sp., intersecting a tubercle (Middle Ordovician, Iowa; X400, apertural end lies to the right).



Figure 2I. Part of a longitudinal section through Conularina triangulata (Raymond), intersecting several transverse ribs (Middle Ordovician, Quebec; X500, apertural end lies to the right).

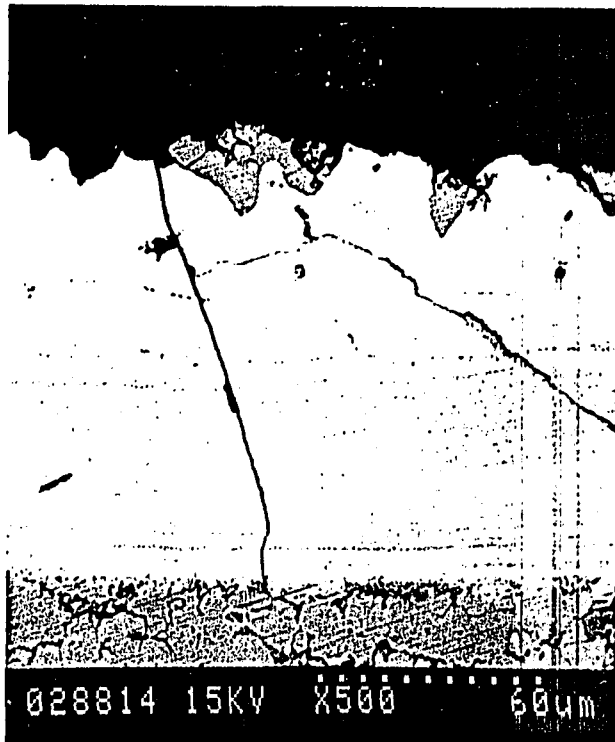


Figure 3A. Exterior view of a schott in Comularia trentonensis Hall (Trenton Group, Middle Ordovician, New York; X22).



Figure 3B. Exterior view of a patch on Comularia splendida Twenhofel (Maquoketa Formation, Late Ordovician, Iowa; X 6). The apertural end lies toward the top of the page.



Figure 3C. Part of a longitudinal section through a schott in Comularia trentonensis Hall (X250).

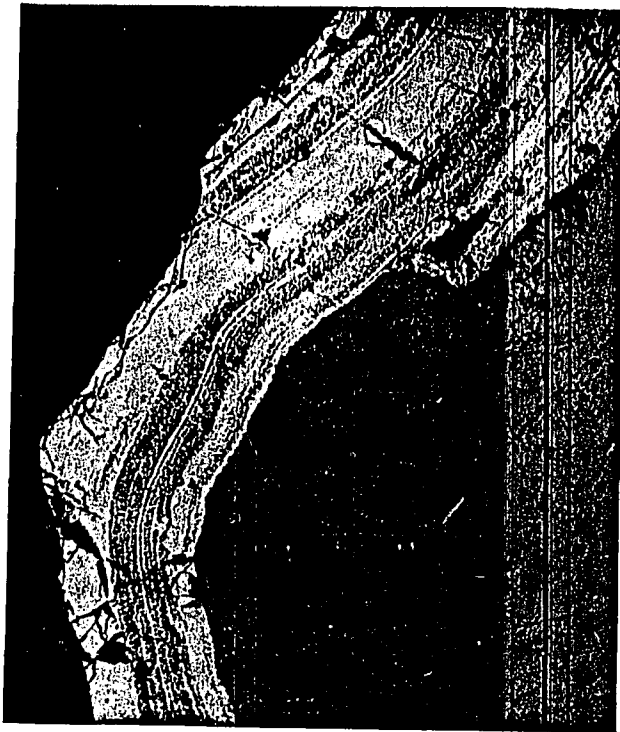


Figure 4A. Exterior view of scalloped ornament straddling a midline of *Conularia splendida* Billings (Late Ordovician, northeast Iowa), SUI 46700, X25. The specimen is oriented with its adapertural end facing the top of the page.



Figure 4B. SEM (backscattered electron mode) photomicrograph of a longitudinal section through scalloped ornament on another specimen of *C. splendida*. Arrow marks the line of unconformity (X400; apertural end lies to the left).

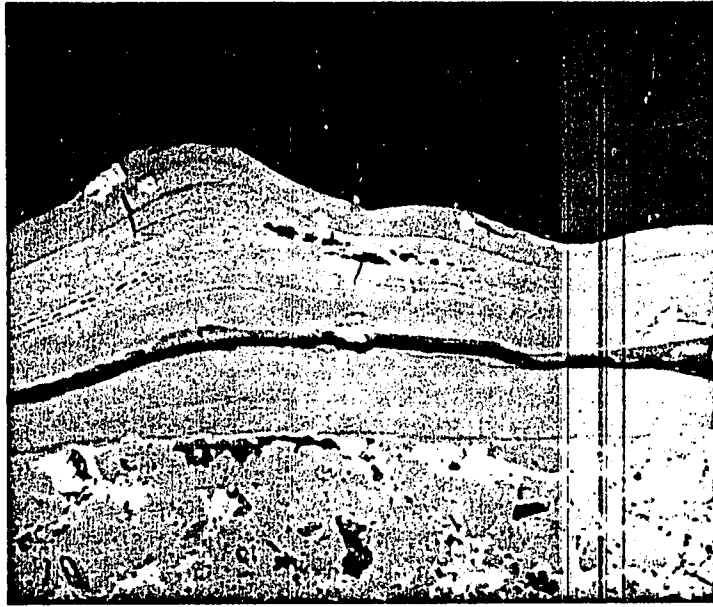


Figure 4C. Exterior view of a cleft feature straddling a midline of Conularia splendida Billings, SUI 10000, X25. The specimen is oriented with its apertural end facing the top of the page.

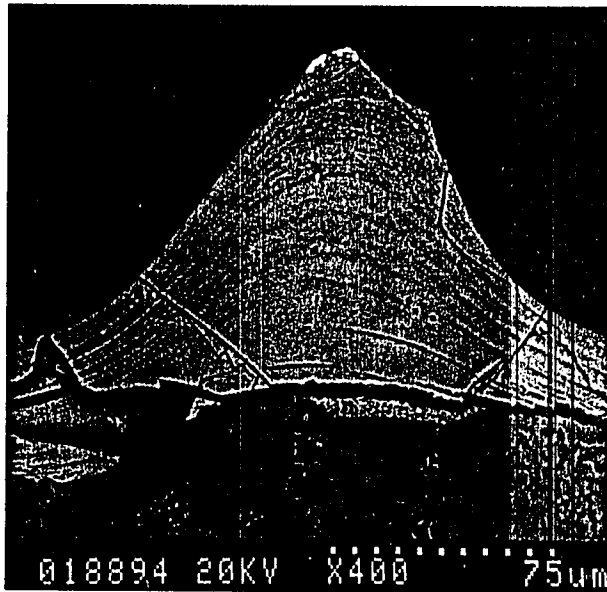


Figure 4D. Exterior view of a cleft feature straddling a midline of Metaconularia sp. (Middle Ordovician, northeast Iowa), SUI 10000, X6. The specimen is oriented with its apertural end facing the top of the page.

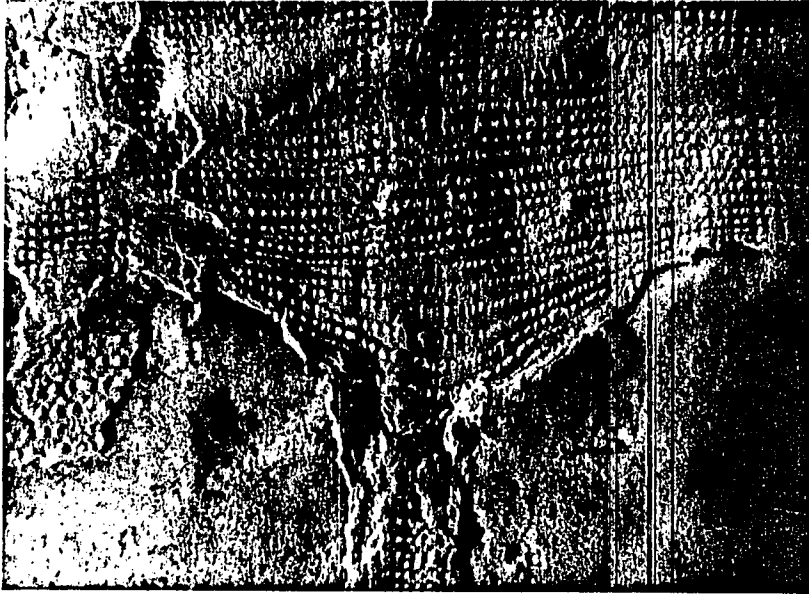


Figure 4E. SEM (backscattered electron mode) photomicrograph of a transverse section through part of a cleft on another specimen of *C. splendida*. Arrow points to zone of bending at the boundary between the cleft and laterally adjacent test (some of the outermost lamellae have been removed by exfoliation), SUI 10000, X400.



CHAPTER 2

ANATOMY, PATTERNS OF OCCURRENCE, AND ORIGIN OF THE CONULARIID SCHOTT

Abstract

Conulariid specimens terminating in a transverse apical wall, or schott, have been interpreted in several different ways. These interpretations have been based more on analogy with extant organisms than on evaluation of fossil material. Among these interpretations are (1) that schott-bearing conulariids represent individuals that were broken, in life, by currents; (2) that schott-bearing conulariids were pelagic or free-swimming individuals; and (3) that schott-bearing conulariids represent non-injured, sessile individuals that simply retracted the apical part of their soft body toward the oral end, as part of their normal life history.

Examination of the test cavity of specimens that do not terminate in a schott, and analysis of the frequency of occurrence of schott-bearing specimens in low- versus high-energy sedimentary deposits, indicate that the most likely interpretation of schott-bearing specimens is that they represent individuals that were broken, in life, by currents. Proponents of a scyphozoan affinity for conulariids have generally interpreted schott-bearing specimens as pelagic or

free-swimming, conulariid medusae, one of the alternatives not favored by this analysis. In spite of this, the interpretation of schott-bearing specimens as truncated individuals is by no means inconsistent with the hypothesis that conulariids and scyphozoans were closely related.

Introduction

Previous discussions of the mode of life and life history of conulariids have presented compelling evidence that conulariid specimens terminating in a narrow apex were sessile animals, attached at the apex to shell material (including tests of other conulariids) or directly to the sea floor (Ruedemann, 1896a,b, 1897; Rooke and Carew, 1983; Babcock et al., 1987; this paper, Appendix 1), or embedded in massive sponges or bryozoans (Sinclair, 1948; Finks, 1955, 1960; this paper, Appendix 1). Yet uncertainty persists as to the nature of conulariid specimens whose apical end, now truncated some distance above the apex, terminates in a smooth, generally outwardly convex transverse wall, or schott (Figure 1). This feature was originally interpreted as one of a series of internal septa, homologous to the septa of nautiloid cephalopods (Hall, 1847). Although rare conulariid specimens have been found that exhibit one or two additional schotts above the terminal one (Babcock and Feldmann, 1986a; see also below), it is now agreed that the conulariid schott and nautiloid septa are not homologous structures (e.g., Werner, 1966, 1967; Bischoff, 1978; Grasshoff, 1984; Babcock and Feldmann, 1986a). Among the reasons for this conclusion is the observation, reported by several previous

workers (e.g., Barrande, 1867), that conulariids whose apical end is more or less pointed apparently show no evidence of internal schotts.

More recent interpretations of the nature of the conulariid schott include the following three alternatives: (1) that the schott was a cicatrix, produced in response to truncation of the apical end by currents (Werner, 1967); (2) that the schott was an autotomy scar, produced when the adult conulariid detached from its apical end and assumed a free-swimming or pelagic mode of life (Ruedemann, 1896a,b, 1897, 1916; Kiderlen, 1937; Boucek, 1939; Moore and Harrington, 1956a; Chapman, 1966; Kozlowski, 1968; Bischoff, 1978; Grasshoff, 1984); and (3) that the schott was a regular growth feature, produced by non-truncated, apically attached specimens in association with retraction of the soft body toward the aperture (Sinclair, 1948; Babcock and Feldmann, 1986a). With the exception of Ruedemann (1896a,b, 1897, 1916) and Kozlowski (1968), advocates of the hypothesis that the conulariid schott was produced in response to assumption of a free-swimming or pelagic mode of life interpret schott-bearing conulariids as similar to medusae of scyphozoan cnidarians, a group that has been widely regarded as the most likely candidate for an extant nearest relative of conulariids (e.g., Kiderlen, 1937; Boucek, 1939; Moore and Harrington, 1956a,b; Chapman, 1966; Werner, 1966, 1967; Glaessner, 1971, 1984; Grasshoff, 1984; Van Iten, 1989). Their interpretation of the conulariid schott, here designated the medusa hypothesis, is based strictly on analogy with scyphozoans exhibiting alternating polypoid and medusoid life stages. (The basis for Ruedemann's (1896a,b, 1897, 1916) and Kozlowski's (1968) advocacy of a free-swimming or pelagic mode of life for schott-bearing conulariids was their belief that the

conulariid apex was not strong enough to support an apically attached individual much larger than a centimeter long.) Werner (1967), though himself a leading proponent of a scyphozoan affinity for conulariids, proposed that schott-bearing specimens were not medusa-like, but represent mechanically truncated polyps that survived to heal their damaged apical end as they lay on the sea floor. His interpretation, here designated the mechanical truncation hypothesis, was based on the fact that the conulariid test is often extremely thin (in some cases fewer than 100 microns thick; Moore and Harrington, 1956a), and on analogy with periderm-bearing, coronatid scyphozoan polyps whose periderm and soft parts have been truncated experimentally. As documented by Werner (1967) and Chapman and Werner (1972), such animals survive truncation and heal their injury by producing a thin, smooth sheet of periderm that is extremely similar in microstructure and gross morphology to the conulariid schott. The third alternative, here designated the apical retraction hypothesis, has been offered with essentially no supporting arguments (Sinclair, 1948; Babcock and Feldmann, 1986a). An attempt at such an argument was made by Sinclair (1948), who proposed that this interpretation is suggested by the observation, based on examination of 11 specimens of Conularia trentonensis Hall (Sinclair, 1948), that schotts occur within a relatively narrow segment of the test's total length.

The present paper seeks to evaluate the foregoing alternative interpretations of the nature of the conulariid schott through analysis of its occurrence within conulariids, and through analysis of patterns of occurrence of schott-bearing specimens with respect to sedimentary facies. As suggested by Sinclair (1948), these three hypotheses are

not necessarily mutually exclusive, i.e., it is conceivable that different instances of schott formation were sometimes brought about by different causes. (As an example, there is no a priori reason why schotts could not have been produced both in response to apical truncation and to adapertural retraction without injury.) In addition, it is by no means certain that these hypotheses exhaust all possible explanations. The reasons these (and no other hypotheses) are considered here are that they have been suggested by previous authors, and that each of them can be tested, using presently recoverable anatomical and/or taphonomic data.

The tests to be conducted in this study are as follows. A key prediction of the hypothesis that the conulariid schott was a regular growth feature, produced in association with adapertural retraction of non-injured soft parts (apical retraction hypothesis), is that specimens that preserve their apex (pointed specimens) and belong to taxa that have yielded schott-bearing specimens should exhibit one or more internal schotts (i.e., transverse walls situated within the test cavity). With the exception of Barrande's (1867) observation that flattened, pointed conulariid specimens from Bohemia show no evidence of crushed, internal schotts, data bearing on conditions of the test cavity of pointed conulariid specimens have not previously been gathered.

Two key predictions of the mechanical truncation hypothesis are (1) that specimens that preserve the apex (and therefore show no evidence of mechanical truncation) should not exhibit internal schotts; and (2) that the percentage of schott-bearing specimens in a given sample of conulariids should be dependent on original levels of

physical energy of the deposit hosting the sample. As noted by previous workers (e.g., Barrande, 1867; Boucek, 1928; Sinclair, 1948), conulariids occur in large numbers in a variety of marine strata. Among these are strata that were deposited under conditions of extremely low physical energy (e.g., dark, laminated, deep-shelf shales and lime mudstones), and strata deposited under conditions of moderate to high physical energy (e.g., shallow-shelf quartz sandstones and lime grainstones). If schott formation was associated with mechanical truncation, then not only should schotts be absent in the test cavity of specimens that have not been truncated in life, but proportions of schott-bearing specimens should be significantly higher in samples from moderate- to high-energy deposits than in samples from low-energy deposits (since the chances of a conulariid being truncated would have been higher in turbulent waters than in waters that were quiet).

This facies-dependent pattern of occurrence would not be expected were schott formation associated with assumption of a free-swimming or pelagic mode of life. This is because schott formation would have been mediated principally by the life history of the developing organism, rather than by physical characteristics of the surrounding water, and because the chances of a pelagic or free-swimming conulariid being preserved in fine grained, low energy deposits, where conulariids commonly occur in great abundance (Moore et al., 1952; Sinclair, 1948) and have been found preserved in situ (Appendix 1), would presumably have been at least as good as the chances of their being preserved in relatively coarse grained, moderate- to high-energy deposits. In short, the medusa hypothesis predicts that proportions of schott-bearing specimens in low- versus moderate- or high-energy deposits

should not be significantly different.

Although details of the anatomy of the conulariid schott and schott-bearing conulariids are covered in a Ph.D. dissertation by Sinclair (1948), this work has never been published. To rectify this deficiency in the conulariid literature, and to present additional information having a potential bearing on alternative interpretations of the cause(s) of schott formation, data on the anatomy of the conulariid schott will be presented below.

Material

The present study is based on examination of nearly 1300 conulariid specimens, and on published data on approximately 500 additional specimens. Examined specimens are housed in collections of the following institutions: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York City; BMNH, British Museum (Natural History), London; EM-UW, Burke Museum, University of Washington, Seattle; EMS, Buffalo Museum of Science, Buffalo, New York; BUGM, Birmingham University Geology Museum, Birmingham, England; CM, Carnegie Museum of Natural History, Pittsburgh; CMNH, Cleveland Museum of Natural History, Cleveland; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; HC, Hartwick College, Oneonta, New York; NYSM, New York State Museum and Science Service, Albany; SUI, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMMP*, University of Montana Museum of Paleontology, Missoula; USNM, United States National Museum, Washington, D. C.; UWGM,

University of Wisconsin Geological Museum, Madison.

Schott anatomy

The conulariid schott ranges from about 100 microns to 1 millimeter thick and is built of extremely thin (1 to 10 microns), apatitic lamellae, alternately dense and vacuity-rich, that generally parallel its inner and outer surfaces (Figure 2A). It consists of a transverse portion, or wall, extending across and partitioning the test cavity, and a longitudinal portion, or sleeve, running along the inner surface of the test, toward the aperture (Figure 2A). Although none of the schott-bearing specimens here examined preserve their aperture, the sleeve was observed to extend all the way to the broken apertural end, situated in some cases several centimeters above the wall. The wall may be adapically convex, more or less planar, or adaperturally convex. It may be smooth or crossed externally by low, short, wrinkle-like ridges, usually concentrated along the wall/sleeve boundary and oriented at various angles to it (Figure 2B). In some cases, the wall's central region is distinctly protuberant or is provided with a small, circular or approximately quadrate pucker (Figure 2B).

As determined by examination of the test cavity of nearly 200 individuals terminating in a schott (Appendix 2), schott-bearing specimens almost always exhibit no more than one such feature. Only two specimens, USNM 373992 (Conularia quichua Ulrich) and AMNH 42316 (Conularia trentonensis Hall), were found to exhibit a second schott (in both cases situated several millimeters above the terminal one). Although additional specimens bearing multiple schotts have been

reported by previous authors, each of these reports involves only one (Eichwald, 1860; Steinmann and Doderlein, 1890; Slater, 1907) or two such specimens (Sinclair, 1948). Most of these specimens possess a total of two schotts (two of them exhibit a total of three schotts; Slater, 1907; Sinclair, 1948), again with the second schott situated several millimeters above the terminal one.

As demonstrated by Sinclair (1948), the sleeve of the second schott rests on the inner surface of the sleeve of the terminal one. Together with the fact that the microstructure of schotts is lamellar, this suggests that the sequence of formation of multiple schotts was adapertural in direction, and that growth of each schott involved accretionary addition of new, entire lamellae to the inside of the test.

The distance between the schott and the former apex is variable. In Conularia trentonensis Hall (Middle to Late Ordovician, North America), characterized in life by a test length of up to about 10 cm, schotts occur at facial widths ranging from 1.5 to 6.0 mm (N = 29, ave. = 3.6 mm, std. dev. = 1.1 mm), indicating a minimum distance to the site of the former apex ranging from roughly 5 to 30 mm (as determined by extension of the corners to their point of intersection). In C. subcarbonaria Meek and Worthen (Mississippian, North America), a larger species whose test exceeded 20 cm in length, schotts occur at facial widths ranging from 15 to 25 mm (N = 7, ave. = 21 mm, std. dev. = 3 mm). Schotts in Metaconularia Foerste occur at facial widths ranging from 5 to 20 mm (N = 8, ave. = 15 mm, std. dev. = 3 mm), and in Archaeoconularia pyramidata (Hoeningsmoen) (Late Ordovician, France and Bohemia) they occur at facial widths ranging from 10 to 25 mm (N = 18,

ave. = 19 mm, std. dev. = 4 mm). Finally, in Paraconularia Sinclair, schotts occur at facial widths ranging from 10 to 18 mm (N = 3). (The small size of the Paraconularia sample is a reflection of the extreme rarity of schott-bearing Paraconularia from North America, where nearly all Paraconularia here examined were collected.)

As is commonly the case in specimens lacking schotts, schott-bearing specimens often exhibit a strongly rhombic transverse cross section, rather than one that is rectangular (Figure 2C). In many such specimens, the schott itself is smoothly curved and shows no evidence of compactional distortion (Figure 2D). This suggests that rhombic specimens terminating in a non-compacted schott exhibited a rhombic cross sectional geometry while alive.

Taxonomic distribution of conulariid schotts

Schott-bearing specimens are known from five of the eighteen currently recognized conulariid genera. These are Anaconularia Sinclair, Archaeoconularia Boucek (= Exoconularia Sinclair), Conularia Sowerby, Metaconularia Foerste, and Paraconularia Sinclair.

The absence of schott-bearing specimens in other conulariid taxa may, in some instances, be an artifact of sampling. This could be the case for taxa such as Conulariella Boucek, Flectoconularia Parfrey, Glyptoconularia Sinclair, Malvinoconularia Babcock et al., and Neoconularia Sugiyama, each of which is represented by fewer than 10 known specimens. Other taxa, including the genera Climacoconus Sinclair and Pseudoconularia Boucek, and the species Archaeoconularia fecunda (Barrande) and Paraconularia crustula (White), are represented

by no fewer than 200 (and, in the case of P. crustula, as many as several thousand) known specimens, many of them with the apical end broken a very short distance above the apex. In these cases, it is not likely that the absence of schott-bearing specimens is an artifact of small sample size (see also discussion at the end of this paper).

Occurrence of schotts within the test cavity of pointed specimens

To determine if schotts occur in the test cavity of specimens whose apical end is more or less intact and does not terminate in a schott, observations were made on sectioned or extensively exfoliated specimens of Archaeoconularia granulata (Hall) (N = 2; all exfoliated), Metaconularia manni (Roy) (N = 12; all exfoliated), Conularia trentonensis (Hall) (N = 151; all exfoliated), C. splendida Billings (N = 8; 7 sectioned, 1 exfoliated), and Paraconularia (N = 11; all exfoliated) (Appendix 2). Except for Paraconularia, all of these specimens terminate at facial widths of 1 millimeter or less. The Paraconularia terminate at facial widths of up to 5 millimeters, still well below the level of occurrence of schotts in schott-bearing Paraconularia specimens here examined (see above). Although small, the A. granulata and M. manni samples include all or nearly all (12 of 13 M. manni) known specimens of these two taxa, and the C. splendida sample includes all known pointed specimens of this taxon (nearly all of which were found by the author). All of the specimens in the sample allow examination of the test cavity at latitudes where terminal schotts occur in conspecific or congeneric, schott-bearing specimens (see above), and also at latitudes extending well above (up to several

centimeters in the case of Paraconularia) those where the most adaperturally situated terminal schotts occur.

None of the specimens in this sample exhibit an internal schott. Together with the observation that many conulariid taxa, some represented by 200 or more known specimens, have not yielded schott-bearing specimens, this result suggests that schotts were not a regular feature of the conulariid test cavity.

Distribution of schott-bearing specimens relative to sedimentary facies

Background. As indicated by studies of the stratigraphy and/or sedimentology of conulariid-bearing strata (e.g., Branson, 1944; Svoboda, 1966; Belt et al., 1967; Scoffin, 1971; Lane, 1973; Ramsbottom, 1973; Bender, 1974; Babin et al., 1976; Titus and Cameron, 1976; Watkins, 1978; Harland and Pickerill, 1982; Harper, 1982; Brett and Brookfield, 1984; Mikulic et al., 1985a,b; Titus and Cameron, 1976; Titus, 1982, 1986; Bakush and Carozzi, 1986; Waterhouse and Briggs, 1986), conulariids occur in marine deposits spanning a more or less continuous spectrum of shallow nearshore to deep offshore facies. Based on inferred levels of physical energy at the time of deposition, these facies can be interpreted as belonging to one of three general depositional regimes. Arranged in order of increasing energy, these are: (1) sheltered nearshore or deep, distal shelf or basinal waters that were characterized, over prolonged periods of time, by extremely low physical energy; (2) moderately deep, mesial shelf waters, situated below fair-weather wave base but subject to episodes of moderate to high current energy during storms; and (3) shallow, proximal shelf

waters, situated at or near fair-weather wave base and subject to more frequent and/or intense episodes of bottom turbulence than characterized Regime 2.

Depositional Regime 1 is represented primarily by dark (gray to black), finely laminated shales, lime mudstones, and muddy siltstones, generally with benthic macrofaunas that are sparse and of low diversity. As indicated by faunal and sedimentological evidence and by stratigraphic relationships (e.g., Belt et al., 1967; Lane, 1973; Titus and Cameron, 1976; Watkins, 1978; Harland and Pickerill, 1982), Regime 1 sediments accumulated in situ (carbonate muds) or were deposited from suspension (clastic muds and silts), generally in sheltered lagoons or embayments, or on the distalmost, deepest-water portions of cratonic shelves or on laterally adjacent portions of cratonic shale basins, below storm-weather wave base. Examples of lagoonal deposits include laminated lime mudstones in the Cementstone Facies of the Calciferous Sandstone Group (Lower Carboniferous), southern Scotland (Belt et al., 1967). Examples of distal shelf or shale basin deposits include the Tetreauville Limestone (Middle Ordovician), Quebec (distal shelf; Harland and Pickerill, 1982), and the lower Ludlow Shale (Late Silurian), Wales and England (shale basin; Watkins, 1978). Not surprisingly, conulariids in Regime 1 deposits often occur in what are here interpreted as non-disturbed (non-transported) life clusters. Such clusters consist of 2 to 20 specimens, all disposed in radial fashion, with their apical ends in apparent mutual contact or pointing more or less toward the cluster's center (Figure 3; see also illustrations in Slater, 1907; Ruedemann, 1925; Sinclair, 1940; Lane, 1973). In the remainder of this text, such clusters will be referred

to as radial clusters.

Depositional Regime 2 is represented primarily by light- to dark colored, variably bioclastic shelf limestones with abundant and diverse macrobenthos, and by fine-grained, muddy shelf sandstones and sandy shales, likewise with abundant and diverse benthic fossils. Examples of Regime 2 carbonate deposits include shallow shelf limestones of the Kings Falls, Denley, Steuben, and Hillier Formations of the Trenton Group (Middle Ordovician) of New York (Titus and Cameron, 1976; Titus, 1982, 1986), and the Verulam (Cobourg) Formation (Middle Ordovician) of Ontario (Brett and Brookfield, 1984). These and similar deposits in other areas exhibit alternating thin mudstone and packstone/grainstone layers, with the packstone/grainstone layers commonly showing one or more of the following features: (a) sharp lower contacts, (b) graded bedding, (c) abrasion (and/or fragmentation) and preferred orientation of skeletal grains, and (d) cross stratification. The mudstone and packstone/grainstone couplets are interpreted as moderate- to high-energy storm deposits (tempestites), formed by differential settling of mud and skeletal debris on a scoured surface (e.g., Bakush and Carozzi, 1986). Clastic analogues of these deposits are characterized by alternating thin shales and fine- to medium-grained, clean to argillaceous sandstones, with the sandstones generally showing sharp lower contacts and cross stratification. Examples of such deposits include strata transitional between the Liben shales and the Revnice quartzites (Middle Ordovician) of Bohemia (Svoboda, 1966), and the "Comularia" Sandstone (Late Ordovician) of southern Jordan (Bender, 1974).

Depositional Regime 3 is represented in part by thick, laterally

extensive deposits of clean, fine- to coarse-grained quartz sandstone or protoquartzite, and by bodies of skeletal lime grainstone of similar extent. Examples of clastic deposits include the Drabov Quartzite (Middle Ordovician) of Czechoslovakia (Svoboda, 1966), and the Upper May ("Conularia") Sandstone (Late Ordovician) of Brittany, France (Babin et al., 1986). Examples of carbonate analogues include thick, laterally persistent grainstone beds in the Burlington Formation (Mississippian) of the Upper Mississippi Valley, USA, and grainstone facies of the Carboniferous Limestone of England (Ramsbottom, 1973). As indicated again by faunal and sedimentological evidence and by stratigraphic relationships (Johnson, 1980), Regime 3 sediments consist of current winnowed, clastic or skeletal sands that were deposited in shallow, proximal shelf waters characterized by periods of moderate to strong bottom turbulence.

As suggested by the foregoing sedimentological considerations, the chances of a live conulariid being subjected to current energy of sufficient magnitude to cause breakage would have been greater in Regime 2 or 3 environments than in Regime 1 environments (assuming of course that live conulariids could have been broken by currents, an assumption that no one has yet disputed). Thus, if schott formation was associated with repair of a truncated apex, one might expect to observe significantly greater proportions of schott-bearing specimens in Regime 2 and 3 samples than in samples from Regime 1. Since Regimes 2 and 3 were both characterized by episodes of moderate to high physical energy (the distinction between these two regimes involving the frequency and intensity of such episodes), differences in the proportion of schott-bearing specimens between samples from Regimes 2

and 3 might not be significant.

Observations. Data on the frequency of occurrence of schott-bearing conulariids in samples from the three depositional regimes just outlined are presented in Table 1. As shown in this table, specimens in Regime 1 samples almost never terminate in a schott. Instead, nearly all specimens whose apical end has not been broken (due to vagaries of weathering or collecting, or to post-mortem, pre-burial breakage) taper to a facial width of 1 mm or less (Table 1). In contrast to conulariids in Regime 1 samples, conulariids in Regime 2 and 3 samples commonly terminate in a schott.

Statistical analysis of data for particular species or genera indicates that the differences in proportions just summarized are almost always significant. For nearly all comparisons involving samples from Regime 1 versus samples from Regimes 2 or 3, the probability that observed differences in the proportion of schott-bearing specimens is due to chance is less than 0.01 (as indicated by application of Fisher's Exact Test; Sokal and Rohlf, 1981). In those cases where the difference is not significant (comparison of Paraconularia from Depositional Regimes 1 and 3, and comparison of Conularia trentonensis from Depositional Regimes 1 and 3), statistical insignificance can be attributed to small sample size.

These conclusions are reinforced by semi-quantitative observations on additional samples in the conulariid literature. Kowalski (1935, p. 291), discussing a sample of approximately 20 specimens of Archaeoconularia pyramidata (Hoeningmoen) from the Upper May ("Conularia") Sandstone (Late Ordovician) of northwest France, states that "many specimens" terminate in a schott (translated from the

original French). Boucek (1928, p. 78), who examined approximately 200 specimens of A. consobrina (Barrande) from the Drabov Quartzite (Middle Ordovician) of Bohemia, reports that "the apex of the shell is almost always missing, and one finds in its place a hemispherical schott" (translated from the original French). Barrande (1867, p. 15), commenting on Bohemian (Barrandian Basin) conulariids in general (a sample consisting of several thousand specimens), notes that "in most species, especially those that [occur] in shales, we see conulariids terminating in a fine point. . . [but] 5 of our species, preserved in quartzite. . . , show, in many cases, a [schott]" (translated from the original French). A similar generalization is suggested by Slater's (1907) data on the anatomy of British conulariids, which indicate that whereas conulariids from shallow-water, open shelf limestones (the Silurian Wenlock Limestone (Scoffin 1971) and the Carboniferous Limestone (Ramsbottom 1973)) often terminate in a schott, conulariids from dark shales and slates do not terminate in a schott but end in a sharp point. Slater's (1907) observations also indicate that at least some schott-bearing Carboniferous Limestone specimens (e.g., specimens of Conularia quadrisulcata Sowerby) are from coarse, bioclastic limestones (Regimes 2 or 3).

Discussion. These results suggest that the frequency of occurrence of schott-bearing specimens in samples of conulariids from a particular sedimentary deposit is a function of former levels of current energy represented by that deposit. Interestingly, the one Regime 1 sample here encountered that does contain schott-bearing specimens (Conularia trentonensis Hall, Collingwood Shale, Ns = 2/40) differs from many other Regime 1 deposits in lacking radial (non-

disturbed) clusters. This suggests that Collingwood conulariids were subjected to some degree of disturbance, possibly associated with storm events affecting adjacent, shallower-water shelf environments (Brett and Brookfield, 1984).

Evidence of disturbance is commonly exhibited by conulariids in Regime 2 and 3 samples. In the case of specimens collected from quartz sandstones, the grain size of the host matrix is often medium to coarse (see also Kowalski, 1935), suggesting that the horizons that yielded these specimens were deposited under conditions of relatively high energy. Similarly, most of the schott-bearing specimens in Regime 2 samples occur in a packstone/grainstone matrix rich in disarticulated echinoderm ossicles and disarticulated and/or broken trilobites and brachiopods, suggesting that they originally occurred in tempestite layers. One such specimen, a member of a cluster of three specimens (Conularia trentonensis Hall; Sherwood Member, Dunleith Formation, Iowa; SUI 55079), occurs with its two companions immediately above a scour surface, in matrix containing lime mud intraclasts (Figure 4A). Although clustered, these specimens do not exhibit a radial arrangement, further suggesting that they were disturbed or transported prior to burial. Similarly, of a total of three schott-bearing specimens of C. splendida Billings collected thus far from the Elgin Member of the Maquoketa Formation (Late Ordovician), northeast Iowa, two (SUI 55080, 55081) specimens occur as members of non-radial, presumably disturbed clusters. Yet another non-radial cluster, consisting of three specimens of C. trentonensis and preserved in coarse, skeletal lime grainstone (assigned here to Regime 3; EMS 10807), includes two schott-bearing specimens (Figure 4B). In contrast

to specimens in these non-radial, Regime 2 (or 3) clusters, none of the specimens in currently known radial clusters (total number of specimens = 89; Appendix 5), interpreted as non-disturbed and nearly all from Regime 1 deposits, terminates in a schott (e.g., Figure 3).

These observations suggest that it is unlikely that observed proportions of schott-bearing specimens reflect factors other than physical energy, in particular mass mortality of very young conulariids (i.e., individuals that were killed before they had a chance to form a schott) or inhibition of schott formation by unfavorable water chemistry (low dissolved oxygen content, etc.). Low likelihood of mass mortality of juvenile conulariids is further suggested, in some cases, by data on specimen sizes (since conulariids are often broken below the aperture, it is difficult, in many cases, to determine their full original length). As indicated by data in Barrande (1867) on sizes of Bohemian Archaeoconularia (Table 1), specimens from dark, laminated shales (Regime 1) are at least as large as morphologically similar specimens from quartz sandstones (Regimes 2 and 3).

Inhibition of schott formation by unfavorable water chemistry is further weakened by the observation that many of the most common conulariids (e.g., Paraconularia crustula (White)) are known only from dark shales or lime mudstones (Moore et al., 1952; Sinclair, 1948), and by the fact that these and other conulariids from Regime 1 deposits show no obvious evidence of anatomical abnormalities (e.g., deviations from patterns of test ornament exhibited by conspecific or congeneric specimens from Regime 2 or 3 deposits).

Implications for alternative interpretations of
schott-bearing conulariids

Apical retraction. As outlined above, this hypothesis suggests that at some point(s) in their life, conulariids retracted the apical part of their body toward the aperture, sealing off the portion of the test cavity just evacuated with a transverse partition. Presumably, the occurrence of conulariids terminating in a schott could be attributed to breakage of the test after the schott was formed. Again, a critical prediction of this hypothesis is that some non-trivial proportion of conulariid specimens that preserve the apex, and that belong to taxa that have yielded specimens terminating in a schott, should exhibit one or more schotts within the test cavity. As discussed above, none of the over 150 pointed specimens of Archaeoconularia, Conularia, Metaconularia, and Paraconularia here examined were found to exhibit internal schotts. This result makes it unlikely that schott formation can be explained as a regular feature of ontogeny.

Alternation of generations. As suggested by Brood (1979), the interpretation of schott-bearing conulariids as pelagic or free-swimming individuals, comparable in life orientation and swimming (or floating) dynamics to cnidarian medusae, is suspect in light of conulariid test anatomy. In particular, whereas cnidarian medusae are invariably naked or provided with non-mineralized, vacuity-rich peridermal structures that are less dense than water (e.g., the hydrozoan Velella), conulariids were provided with a mineralized test composed of more or less solid apatite (Van Iken, 1989). Granted, the

test of many conulariids is extremely thin (as few as thirty or so microns), but in other cases, including schott-bearing specimens with unusually thick schotts (e.g., Metaconularia calderi Sinclair), the test is up to 2 or 3 mm thick. Such thick-shelled conulariids would almost certainly have had a fairly substantial negative buoyancy.

Interpretations of schott-bearing specimens as medusa-like are also difficult to reconcile with their observed patterns of occurrence. Coupled with the occurrence of known fossil medusae in mud rocks representing both shallow nearshore and deep offshore facies (e.g., the Solnhofen Limestone and the Burgess Shale; Walcott, 1898), the occurrence of abundant pointed conulariids (some of them preserved in undisturbed, radial clusters) in similar deposits suggests that settling of conulariid medusae onto low-energy shelf bottoms would have been no less likely than their settling onto moderate- or high-energy shelf bottoms. Moreover, whereas both Recent and fossil medusae are often found in sandstones deposited on intertidal flats, but evidently not in subtidal sandstones (Glaessner, 1984), currently known conulariid-bearing sandstones represent subtidal deposits only (e.g., Svoboda, 1966; Thomas, 1969; Bender, 1974; Babin et al., 1986; Waterhouse and Briggs, 1986). Together with the relatively great test thickness of many schott-bearing conulariids, these occurrence patterns suggest that schott-bearing conulariids were not medusa-like, but rather that they, like other fossils exhibiting facies-dependent occurrence patterns, lived on the sea bottom.

Mechanical truncation. As discussed above, Werner (1967) has proposed that living conulariids, especially large forms with extremely thin tests (e.g., many species of Archaeoconularia and Metaconularia),

were susceptible to truncation by currents. By analogy with experimentally truncated, periderm-bearing coronatid polyps, he argues that the conulariid schott was a truncation scar, produced by the injured animal as it lay on its side. Again, if schott formation was induced by truncation, one might expect to find (1) that schotts do not occur in the test cavity of specimens that do not terminate in a schott; and (2) that schott-bearing specimens occur in significantly higher proportions in samples from moderate- to high-energy deposits than in samples from low-energy deposits. Both of these predictions are satisfied by observations presented here. As discussed above in connection with the apical retraction hypothesis, conulariids that preserve their apex more or less intact do not exhibit internal schotts. Also, whereas schott-bearing specimens are extremely rare or absent in fine-grained, low energy deposits, they are common in relatively coarse grained, moderate- to high-energy deposits.

Although some schott-bearing conulariid specimens exhibit more than one schott, this does not necessarily mean that their apicalmost schott could not have formed in response to truncation. The observation that specimens that are more or less pointed do not exhibit internal schotts suggests that formation of multiple schotts was actually prompted by apical truncation, which may well have left the animal susceptible to subsequent infection or necrosis.

Mechanical truncation is also supported by other observations, none of which would necessarily be expected were schott formation a regular feature of ontogeny or associated with transformation into a medusoid individual. As noted above, several conulariid taxa, all of them represented by 200 or more known specimens, have not yielded

schott-bearing specimens. Although it is conceivable that some conulariids did not transform into medusae, or that not all conulariids were characterized by life histories involving adapertural retraction (followed by schott formation), currently available anatomical and distributional data suggest that the absence of schotts in some conulariid taxa is due to factors that acted to decrease the probability of these taxa being subjected to currents of sufficient strength to break them in life. Some of these taxa, including the genus Pseudoconularia Boucek, and the species Archaeoconularia fecunda (Barrande) and Paraconularia crustula (White), are known exclusively or predominantly from dark, laminated mud rocks (Barrande, 1867; Boucek, 1928; Sinclair, 1940), originally deposited in waters of extremely low physical energy. The latter two taxa are further characterized by tests that are unusually thick. As reported by Barrande (1867), the test of Archaeoconularia fecunda is often so thick that the apical region is fully occluded. Similarly, tests of Paraconularia crustula may be up to 2 mm thick at the corners and midlines (Sinclair, 1948; Van Iten, 1989). Finally, as discussed above in the section on schott anatomy, many schott-bearing specimens exhibit a strongly rhombic (as opposed to rectangular) transverse cross section, but the schott itself shows no evidence of compaction. Again, this suggests that such specimens exhibited a rhombic cross section while they were alive. Since it has generally been agreed that the cross sectional geometry of living conulariids was normally rectangular (Boucek, 1928; Sinclair, 1948; Moore and Harrington, 1956a; Babcock and Feldmann, 1986b), this suggests that rhombic specimens with a non-compacted schott represent individuals that underwent distortion, in life and prior to schott

formation, from an original rectangular cross section. While it is difficult to imagine how this could have occurred were schott formation a regular feature of ontogeny or associated with transformation into a medusa, it is conceivable that a truncated individual, lying on its side, could have been distorted under the weight of its body.

Conclusion

Analyses of the anatomy and patterns of occurrence of the conulariid schott show that schotts do not occur in the test cavity of specimens whose apex is more or less pointed, and that schott-bearing conulariids are common in samples from moderate- to high-energy deposits but extremely rare or absent in samples from low-energy deposits. These results corroborate the hypothesis that conulariids terminating in a schott represent individuals that were broken, in life, by currents, but they are inconsistent with other proposed hypotheses of the circumstances prompting schott formation. Although schott-bearing specimens probably were not medusa-like, as suggested by Kiderlen (1937) and several other proponents of a scyphozoan affinity for conulariids, this does not necessarily mean that conulariids did not produce medusae (through means other than direct transformation of test-bearing, polypoid individuals). Moreover, even if conulariids did not produce medusae, this alone would not mean that conulariids and scyphozoans can not be closely related to each other, since some scyphozoans (members of the Order Stauromedusida) do not produce medusae (Hyman, 1940). As noted earlier by Werner (1967), schott-bearing conulariids are similar to coronatid polyps that have been

truncated and have lived to heal their injury by producing a schott-like apical wall. At present, the only circumstance known to cause formation of this feature in coronatids is breakage (Werner, 1967, 1979; Chapman and Werner, 1972), and results of the present study indicate that mechanical truncation was the predominant cause of schott formation in conulariids.

Acknowledgements

This study forms part of a Ph.D. dissertation written in the Museum of Paleontology, the University of Michigan, Ann Arbor. I thank the members of my dissertation committee (D. J. Eernisse, D. C. Fisher, K. C. Lohmann, G. R. Smith, and B. H. Wilkinson) for comments on earlier versions of the manuscript. Permission to borrow museum specimens was given by T. E. Bolton, F. J. Collier, R. C. Eng, J. Golden, E. Landing, R. Laub, R. Titus, and K. Westphal. Data on the anatomy of conulariids in collections of the British Museum of Natural History and the University of Birmingham were graciously obtained by B. S. Beall, and R. S. Cox. Finally, I gratefully acknowledge financial assistance of a Grant-in-Aid-of-Research from Sigma Xi.

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Table 1. Frequency of occurrence of conulariid specimens terminating in a schott in samples from the three depositional regimes outlined in the text. Lettered symbols are as follows: N = total number of specimens in sample, Ns = number of specimens terminating in a schott, Np = number of pointed specimens (specimens tapering to a facial width of 1 mm or less and lacking a terminal schott). Sources of numerical data taken from the literature are as follows: ** = Boucek (1928), ++ = Sinclair (1948), * = Lane (1973), + = Slater (1907). An asterisk following a question mark in the Np column indicates that the percentage of pointed specimens is reported to be large. Numbers following the geologic age of the host rock unit refer to one of the following sedimentological and/or stratigraphic studies: (1) Svoboda (1966), (2) Titus and Cameron (1986), (3) Ruedemann (1925), (4) Brett and Brookfield (1984), (5) Harland and Pikerill (1982), (6) Mikulic et al. (1985a,b), (7) Watkins (1978), (8) Lane (1973), (9) Belt et al. (1967), (10) Scoffin (1971), (11) Bakush and Carozzi (1986), (12) Williams and Telford (1986), (13) Babin et al. (1976). See Appendix 4 for information on specimen locations.

Taxon	Unit and Age	Locality	Unit Lithology	N	Ns	Np
Depositional Regime 1						
Archaeoconularia						
<i>A. exquisita</i> **	Liben Shale (M. Ordo., 1)	Bohemia	Black, laminated shale	300	0	? (*)
<i>A. granulata</i>	Dolgeville Fm. (M. Ordo., 2)	New York	Black, laminated lime mudstone	2	0	2
Conularia						
<i>C. tenuicosta</i>	Gasport lens, Lockport Fm. (Silur., 3)	New York	Dark brown, laminated shale	5	0	4
<i>C. trentonensis</i>	Collingwood Shale (U. Ordo., 4)	Ontario	Black, laminated shale	40	2	38
<i>C. trentonensis</i> **	Tetreauville Fm. (M. Ordo., 5)	Quebec	Black, laminated lime mudstone	100	0	? (*)
<i>C. trentonensis</i>	Brandon Bridge Fm. (Silur., 6)	Wisconsin	Gray, laminated shale	159	0	113
Metaconularia						
<i>M. aspersa</i>	Lower Ludlow Shale (Silur., 7)	England	Gray-brown, laminated shale	20	0	20
<i>M. bilineata</i> **	Liben Shale (M. Ordo., 1)	Bohemia	Black, laminated shale	17	0	? (*)
<i>M. manni</i>	Lecthaylus Shale (Silur.)	Illinois	Gray, laminated shale	13	0	12
Paraconularia						
<i>P. chagrinenensis</i>	Chagrin Shale (U. Devon.)	Ohio	Gray, laminated shale	13	0	2
<i>P. chesterensis</i> *	Edwardsville Mbr., Muldraugh Fm. (L. Miss., 8)	Indiana	Gray, laminated shaley siltstone	53	0	? (*)
<i>P. tenuis</i> †	Cementstone Facies, Calceiferous Sandstone Gp. (Miss., 9)	Scotland	Gray, laminated lime mudstone	70	0	? (*)
Depositional Regime 2						
Conularia						
<i>C. sowerbyi</i>	Wenlock Limestone (Silur., 10)	England	Lime mudstone/wackestone/packstone	25	17	0

<i>C. splendida</i>	Unit 2, Elgin Mbr., Maquoketa Fm. (U. Ordo.)	Iowa	Lime mudstone/wackestone/packstone	24	3	5
<i>C. subcarbonaria</i>	Keokuk Limestone (L. Miss.)	Illinois	Lime wackestone/packstone/grainstone	8	4	0
<i>C. trentonensis</i>	Verulam Fm. (M. Ordo., 4)	Ontario	Lime wackestone/packstone/grainstone	11	5	0
<i>C. trentonensis</i>	Denley, Kings Falls, Sugar River Fms. (M. Ordo., 2)	New York	Lime wackestone/packstone/grainstone	11	7	0
<i>C. trentonensis</i>	Sherwood Mbr., Dunleith Fm. (M. Ordo., 11)	Iowa	Lime wackestone/packstone/grainstone	8	2	0
Metaconularia						
<i>M. calderi</i>	Verulam (Cobourg) Fm. (M. Ordo., 4)	Ontario	Lime wackestone/packstone/grainstone	3	3	0
<i>M. divisa</i>	Dubuque Fm. (M. Ordo., 11)	Iowa	Lime wackestone/packstone	5	5	0
<i>M. sp.</i>	Lower Lindsay Fm. (M. Ordo., 12)	Ontario	Lime wackestone/packstone	1	1	0
Depositional Regime 3						
Anaconularia						
<i>A. anomala</i>	Drabov Quartzite (M. Ordo., 1)	Bohemia	Fine to medium quartz sandstone	760	140	0
Archaeoconularia						
<i>A. consobrina</i>	Drabov Quartzite (M. Ordo., 1)	Bohemia	Fine to medium quartz sandstone	47	35	0
<i>A. pyramidata</i>	Upper May (Conularia) Sandstone (U. Ordo., 13)	Brittany	Fine to coarse quartz sandstone	20	10	0
Conularia						
<i>C. subcarbonaria</i>	Burlington Limestone (L. Miss.)	Missouri	Coarse, skeletal lime grainstone	11	3	0
<i>C. trentonensis</i>	Ordovician	New York	Coarse, skeletal lime grainstone	3	2	0
Paraconularia						
<i>P. sp.</i>	Burlington Limestone (L. Miss.)	Iowa	Coarse, skeletal lime grainstone	4	2	0

APPENDIX 1

SUMMARY OF EVIDENCE INDICATING
A SESSILE MODE OF LIFE FOR CONULARIIDS

Evidence of a sessile mode of life for conulariids was first discovered by Ruedemann (1896a,b, 1897), who collected minute specimens of Glyptoconularia gracile (Hall) (Middle Ordovician Utica Shale, New York) attached at their apex to tests of other G. gracile. Although several subsequent workers (Sinclair 1948; Feldmann et al. 1986; Babcock and Feldmann 1986; Babcock et al. 1987) have claimed that Ruedemann's specimens are not conulariids, but individuals of the problematic taxon Sphenothallus, reinspection of Ruedemann's G. gracile specimens, currently housed in collections of the New York State Museum (Albany), indicates that they are identical to larger specimens of this species (including the holotype) in collections of the American Museum of Natural History and the Geological Survey of Canada (Van Iten, 1989). The only difference between these specimens is their size.

Since Ruedemann's time several additional lines of evidence of sessility in conulariids have also been reported. One line of evidence is the occurrence of erect Paraconularia in the Colony Creek Formation (Pennsylvanian), north-central Texas (Rooke and Carew 1983). Found in a black shale horizon yielding no macrofossils other than conulariids, the specimens (since removed from the outcrop) formed two clusters, each consisting of one large individual surrounded by several smaller ones and with the apex of all specimens lying on a common bedding plane (J. L. Carew, personal communication, 1984). As suggested by Rooke and

Carew (1983), the erect posture of these conulariids is difficult to reconcile with any interpretation other than that it represented their original life orientation. The fact that their apices were situated on a common bedding plane suggests that the specimens stood on their apex, with the apex either cemented to a hard depositional surface or anchored in soft sediment by means of rootlets or stolons.

Evidence of apical attachment is also provided by specimens whose apex is preserved in extremely close proximity to non-conulariid shell material and whose long axis is oriented at a high angle to it. At least four such specimens have been discovered thus far. Babcock et al. (1987) have documented two specimens of Conularia quichua Ulrich, both from the Devonian of Bolivia, that are preserved with their apex situated immediately adjacent to a mold of a hyolith shell and with their long axis oriented perpendicular to it. The specimens, currently housed in collections of the United States National Museum (USNM 409840, 409837), are about 2.5 cm and 3.5 cm long, respectively. Although neither of them show actual contact of original test material with shell material of the putative substrate, the fact that in both cases the apex lies immediately adjacent to the substrate, with the long axis oriented perpendicular to it, argues very strongly for the conulariids having been attached. A similar case can be made for the two remaining specimens, which have not figured in previous discussions of the mode of life of conulariids. These specimens are types of Archaeoconularia granulata (Hall), collected from the upper part of the Trenton Group (Middle Ordovician) near Middleburry, New York. The specimens, currently housed in collections of the American Museum of Natural History (AMNH 789), occur together on a single slab of black

lime mudstone and are preserved next to a cephalopod phragmocone, probably of Endoceras proteiforme Hall. They are about 4.5 and 5.5 cm long. The apex of each conulariid, broken just above the tip, lies immediately adjacent to the cephalopod, and the two conulariids are oriented parallel to each other and at a high angle to the cephalopod. This disposition, with its multiple, spatial "coincidences," is extremely unlikely to be fortuitous. Rather, it indicates that the conulariids probably were originally attached to the cephalopod.

Another line of evidence indicating apical attachment consists of conulariids that have been overgrown by sponges or bryozoans, in such a way as to indicate that overgrowth took place on all four faces simultaneously and with the apex embedded within the encruster. One such example, discovered and illustrated by Finks (1955, 1960; Plate 12, Figures 3-6), consists of two conulariid molds in the holotype (USNM 127604i) of the lithistid sponge Defordia defuncta Finks (Permian, West Texas). Reexamination of the sponge reveals that the sides of the molds are strongly recrystallized and do not preserve transverse ribbing, characteristic of the only known conulariid (Paraconularia leonardensis (Finks)) from the deposit that yielded the sponge (Finks 1955). Nevertheless, the molds are four-sided and steeply pyramidal, thus indicating that they do not represent part of the sponge's canal system or molds of some non-conulariid organism. The molds are oriented perpendicular to successive growth surfaces of the sponge, and their apical end is embedded within the sponge. This indicates that the conulariids that originally occupied the molds must have been overgrown in an upright posture, with the apex presumably resting on a former growth surface of the sponge. Again, it seems

extremely unlikely that an accidental relationship (e.g., chance lodging of the conulariids within oscula of the sponge) could explain the similar disposition of both conulariids. Rather, this disposition appears to indicate that the conulariid specimens had a primary, apical attachment to the sponge. A similar occurrence, not previously published, is represented by molds of three conulariids in another lithistid sponge, likewise from the Permian of West Texas and currently housed in collections of the Geological Survey of Canada (GSC 87185). The largest of these molds exhibits clear impressions of the transverse ribs.

As indicated by Finks (personal communication, 1987), occurrences of the sort just outlined are known among extant invertebrates. For example, certain species of tubicolous marine annelids settle upon and are encrusted in life by demosponges, resulting in encasement of the basal portion of the tubules within sponge material.

Other occurrences of overgrown conulariids, similar to the ones just described but with the apical end of the conulariids missing, have also been noted. Bryozoan-encrusted specimens of Conularina triangulata (Raymond) have been reported by Sinclair (1948) from Middle Ordovician (Chazyan) limestones near Montreal, Quebec. According to Sinclair (1948, p. 57), the conulariids are surrounded on all four sides by a single bryozoan colony, thus indicating that "[the] only way in which [the bryozoans] could have grown is around an erect conulariid." Unfortunately, Sinclair (1948) does not illustrate these specimens or indicate where they are repositied. Fragmentary specimens, encrusted by bryozoans and apparently from the same horizon, are in collections of the Geological Survey of Canada. At least three

bryozoan-encrusted conulariids from localities in the United States, none of them previously discussed, are housed in collections of the United States National Museum (USNM 721u, 40818, 50137). The largest and best preserved specimen (USNM 50137), found in the Cincinnati Group (Late Ordovician) of southern Ohio, consists of an incomplete Peronopora colony enveloping a partial specimen of Conularia cf. trentonensis Hall. When complete, the conulariid was at least 10 cm long (as indicated by extension of the corners to their point of intersection). It is clear from the morphology of the bryozoan that the encrusted conulariid must have been overgrown on all four sides simultaneously. That the apical end of the conulariid, now missing, originally pointed downward is suggested by the geometry of the Peronopora zooecia. Near their contact with the faces of the conulariid, the zooecia show a tendency to bend slightly toward the conulariid's apical end. Inspection of USNM specimens of Peronopora that exhibit a similar growth form and that preserve their base indicates that the proximal ends of the zooecia bend toward the base.

APPENDIX 2

Listing of specimens terminating in a schott and allowing direct examination of all or substantial portions of the test cavity. Species followed by an asterisk are preserved as sandstone steinkerns. See text for explanation of repository abbreviations.

Species	Repository	N
<u>Anaconularia anomala</u> * (Barrande)	MCZ 113, 114	144
<u>Archaeoconularia consobrina</u> * (Barrande)	MCZ 10000	5
<u>A. dubia</u> (Sinclair)	ROM 18889	1
<u>A. pyramidata</u> * (Hoeningsmoen)	FMNH PE294, PE379-382; GSC 87183; ROM 22289, 22532	9
<u>Conularia</u> sp.	UMMP 2167	1
<u>C. trentonensis</u> Hall	HC 10000-10000; ROM 67, 23278, 23737, 23738, 24007, 28324, 24917; SUI 10000	20
<u>Metaconularia calderi</u> Sinclair	GSC 9794-9795	2
<u>M.</u> sp.	ROM 87DR	1
<u>M.</u> sp.	SUI 53089	1
<u>Paraconularia byblis</u> (White)	UMMP 259	2

APPENDIX 3

Listing of specimens not terminating in a schott and allowing direct examination of all or substantial portions of the test cavity. See text for institutional abbreviations. The letter P following a specimen number or numbers indicates that the corresponding specimen or specimens taper to a facial width of 1 mm or less.

Taxon	Specimen numbers
<u>Archaeoconularia granulata</u> (Hall) <u>Conularia trentonensis</u> Hall	AMNH 791 (P, 2 specimens) AMNH 29649(P), 42316(P), HC 1(P) (3 specimens); ROM 27274(P) (38 specimens); UWGM WW4001(P) (113 specimens)
<u>Conularia splendida</u> Billings <u>Metaconularia manni</u> (Roy)	SUI 10000-10000 (8 specimens) FMNH PE6252-6256(P), PE10132(P), PE23674-23675(P), unnumbered(P) (12 specimens)
<u>Metaconularia</u> sp. <u>Paraconularia chagrinensis</u> Babcock	SUI 10000(P) (1 specimen) CMNH 1788(P), 6633 (3 specimens)
<u>Paraconularia chesterensis</u> (Worthen)	GSC 49383 (1 specimen); UMMP 802 (1 specimen)
<u>Paraconularia recurvatus</u> Babcock and Feldmann	USNM 409806 (1 specimen)
<u>Paraconularia subulata</u> (Hall)	CM 34521, 34524 (2 specimens); CMNH 1788, 6633 (3 specimens); UMMP* 5613A/I7106, 5628NC/MI7106 (2 specimens)
<u>Paraconularia yochelsoni</u> Babcock and Feldmann	UMMP 45499(P) (1 specimen)

APPENDIX 4

Specimen numbers for samples listed in Table 1. See text for institutional abbreviations.

Taxon	Specimen Numbers
<u>Depositional Setting 1</u>	
Archaeoconularia	
A. <u>granulata</u> (Hall)	AMNH 791 (2 specimens)
Conularia	
C. <u>tenuicosta</u> Ruedemann	NYSM 9415-17, 11531 (5 specimens)
C. <u>trentonensis</u> Hall (Collingwood)	ROM 27274 (40+ specimens on 15 slabs)
C. <u>trentonensis</u> Hall (Brandon Bridge)	UWGM WW4001 (159+ specimens on slabs)
Metaconularia	
M. <u>manni</u> (Roy)	FMNH PE6252-6256, PE10132, PE23674- 23975, FMNH unnumbered (13 specimens)
Paraconularia	
P. <u>chagrinsensis</u> Babcock and Feldmann	CMNH 1247, 1272, 1427, 1622, 1674, 1788, 1818, 4030, 4292, 6633, 6717, 6807-6808 (13 specimens)
<u>Depositional Setting 2</u>	
Conularia	
C. <u>sowerbyii</u> (Slater)	BMNH 6275, 6327, 10043, 11795, 17500-17505, unnumbered (10 specimens); UBGW 1000-1000 (10 specimens)
C. <u>splendida</u> Twenhofel	AC I-1448; SUI 1000-1000 (24 specimens)
C. <u>subcarbonaria</u> (Meek and Worthen)	FMNH UC18494, UC19647, FMNH unnumbered (8 specimens); MCZ 27946-27956 (11 specimens)
C. <u>trentonensis</u> Hall (Verulam Fm.)	ROM 67, 23738(512T), 24917(240U) (9 specimens); GSC 1725-1726 (2 specimens)
C. <u>trentonensis</u> Hall (Denley Fm.)	HC 1000-1000 (11 specimens)
C. <u>trentonensis</u> Hall (Sherwood Mbr.)	SUI 10000-10000 (8 specimens)
Metaconularia	
M. <u>calderi</u> Sinclair	GSC 9794-9795 (3 specimens)
M. <u>divisa</u> Sinclair	SUI 53089; UMPC W1994; UW-EM 1000-1000 (5 specimens)
M. sp.	ROM 87DR

APPENDIX 4 (continued)

Depositional Regime 3

Anaconularia

A. anomala (Barrande)

MCZ 113,114 (760 specimens)

Archaeoconularia

A. consobrina (Barrande)BMNH 80215, 80219, 80386-
80389 (37 specimens); MCZ
unnumbered (10 specimens)A. pyramidata (Hoeningshaus)BMNH 340909, unnumbered (9
specimens); FMNH PE294, PE379-
382, FMNH unnumbered (7
specimens); GSC 87180 (1
specimen); ROM 22289, 22532 (3
specimens)

Conularia

C. trentonensis Hall

BMS E10807 (3 specimens)

Paraconularia

P. sp.

USNM 57164, 99502 (4
specimens)

APPENDIX 5

Listing of radial conulariid clusters examined in the present study (total number of clusters = 13, total number of individual specimens = at least 93; N = number of specimens comprising a cluster). See text for symbols for host institutions. All of the clusters listed here are preserved in shale or lime mudstone.

Repository	Host Unit	Taxon	N
SUI 49979	Unit 1, Elgin Mbr., Maquoketa Fm. (Ordo., Iowa)	<u>Conularia splendida</u>	8
SUI 00001	Unit 2, Elgin Mbr., Maquoketa Fm. (Ordo., Iowa)	" "	6
SUI 00002	" "	" "	2
NYSM 9417	Gasport Lens, Lockport Fm. (Silur., New York)	<u>C. tenuicosta</u>	2
BMS E12301	" "	<u>Metaconularia nuda</u>	4
SUI 37414	Brainard Shale Mbr.?, Maquoketa Fm. (Ordo., Iowa)	<u>M. sp.</u>	4
USNM 50145	Pennsylvanian shale, Missouri	<u>Paraconularia crustula</u>	3
USNM 50148	Pennsylvanian shale, Illinois	" "	3
CMNH 1788	Chagrin Shale (Dev., Ohio)	<u>P. chagrinensis</u>	2
USNM 50150	Borden Gp. (Miss., Indiana)	<u>P. chesterensis</u>	20
EMNH G11798	Cementstone Gp. (L. Carb., Scotland)	<u>P. tenuis</u>	17
EMNH 17664	" "	" "	7
EMNH 17662	" "	" "	4

Figure 1. Schott-bearing specimen of Conularia sp. The specimen is preserved in fine sandstone and is from the English River Formation (Upper Mississippian) near Keokuk, Iowa (UMMP 259; X1.5).



Figure 2A. Longitudinal section through part of a terminal schott of Conularia trentonensis Hall., showing portions of the wall (W) and sleeve (S) (HC 4010; X250).



Figure 2B. Oblique view of part of the external surface of a terminal schott (wall) of another specimen of the same species (HC 4011; X25).



Figure 2C. Side view of the apical end of a strongly rhombic, schott-bearing specimen of Conularia trentonensis Hall (ROM 67a; X6).



Figure 2D. Apical view of the same specimen, showing the non-distorted condition of the schott (X6).



Figure 3. Radial cluster of 8 specimens of Conularia splendida Billings, collected from dark blue-gray, trilobite lime mudstones in Unit 1 of the Elgin Member of the Maquoketa Formation (Late Ordovician), northeast Iowa, USA (SUI 49979, X0.8).

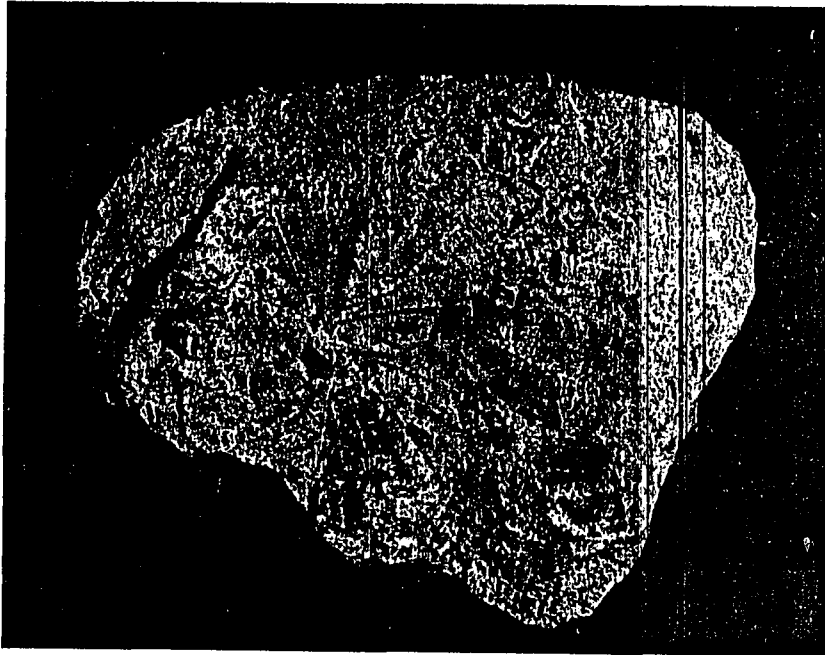
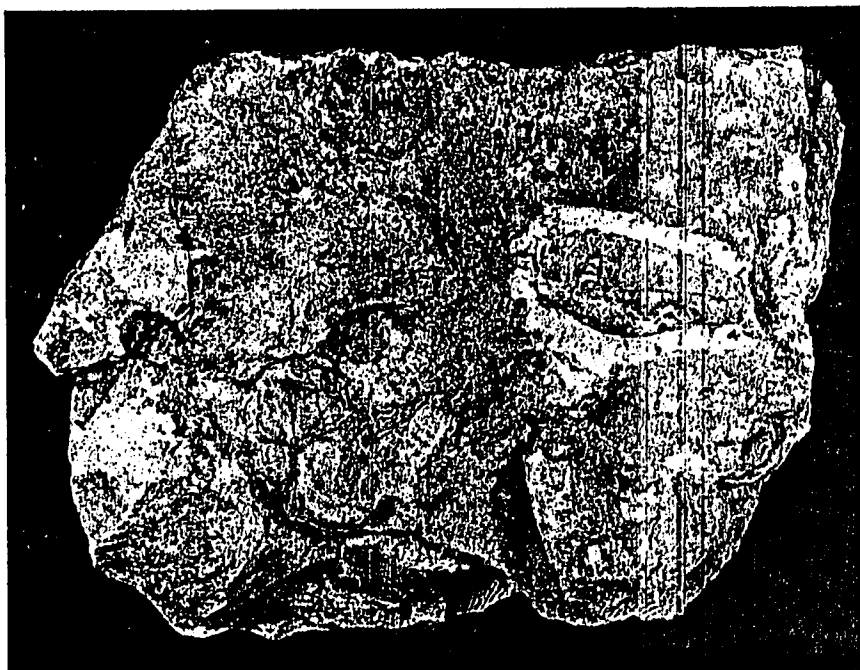


Figure 4. Examples of disturbed (non-radial) conulariid clusters containing one or more schott-bearing specimens. A, polished section through a small limestone slab hosting a cluster of three Conularia trentonensis (Hall) (Ns = 1), showing scour surface (large arrow) overlain by biomicrite containing abundant shell fragments and a lime mud intraclast (small arrow); the three conulariids (not pictured) lie within several mm of each other and occur immediately above the scour surface (Sherwood Member, Dunleith Formation (Middle Ordovician), northeast Iowa; SUI 55080, X2). B, cluster of three C. trentonensis (arrows) on a small slab of coarse, skeletal lime grainstone; two of the specimens (large arrows) terminate in a schott (Ordovician, New York, EMS 10807; X0.75)



CHAPTER 3

MORPHOLOGY AND PHYLOGENETIC SIGNIFICANCE OF THE CORNERS AND MIDLINES OF THE CONULARIID TEST

Abstract

The hypothesis that conulariids were closely related to scyphozoan cnidarians is based to a large extent on interpretations of the morphology of the corners and midlines of the conulariid test. Until now, however, the corner and midline anatomy of most conulariids had not been adequately studied. Corners and/or midlines of some or all species of at least nine of the 18 currently recognized conulariid genera exhibit some form of internal, generally carinate longitudinal thickening. Internal midline structures of some or all species of five conulariid genera are paired or longitudinally bifid. Some or all species of five conulariid genera exhibit internal structures both at the corners and the midlines. Almost without exception, internal structures at the corners are broader and/or higher than associated midline structures. Finally, internal corner and/or midline structures of some members of at least two conulariid genera are seriated.

Comparison of internal structures at conulariid corners and midlines with soft-part and peridermal structures defining the scyphozoan perradii and interradii reveals a number of similarities.

These similarities indicate that conulariid midlines are former sites of a set of four gastric septa, homologous to the four gastric septa of scyphozoans. Cladistic analysis of the relationship of conulariids to scyphozoans and other extant cnidarians suggests that conulariids and scyphozoans are nearest relatives, and that together these two groups are more closely related to anthozoans than either they or anthozoans are to hydrozoans.

Introduction

Much of the controversy surrounding the analysis of conulariid affinities can be traced to conflicting interpretations of the gross anatomy of the steeply pyramidal, generally four-sided conulariid test. In many conulariids, the corners of this test, and/or the midline of each of its faces, exhibit some form of internal longitudinal thickening, produced by localized inflection and thickening of the test's inner lamellae (e.g., Wiman, 1895; Ruedemann, 1897; Knod, 1908; Sinclair, 1940, 1948; Bischoff, 1978; Van Iten, 1989a). Based on comparisons of these features with soft-part and peridermal structures of scyphozoan cnidarians, conulariid midlines have been interpreted as former sites of longitudinal gastric septa, homologous to the gastric septa of scyphozoans (Kiderlen, 1937; Werner, 1966a, 1967; Bischoff, 1978; Van Iten, 1989a). The septa of scyphozoans are almost always four in number and lie within one of two mutually perpendicular planes of symmetry, called the interradii. Bisecting the angles between the interradii are two additional symmetry planes, the perradii, which intersect the corners of the rectangular scyphozoan mouth. Conulariid

corners, situated along two planes that lie more or less midway between the two planes containing the midlines, have been interpreted as comparable in position to the scyphozoan perradii (Kiderlen, 1937; Werner, 1966a, 1967; Bischoff, 1978). These anatomical relationships are illustrated in Figure 1.

Especially in recent years, this and other hypotheses of homology between conulariids and scyphozoan cnidarians have been rejected by several authors (Termier and Termier, 1949, 1953; Kozłowski, 1968; Oliver, 1984; Steul, 1984; Mortin, 1985; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986a,b; Oliver and Coates, 1987). Yet none of these authors has proposed that conulariid corners and midlines exhibit more compelling similarities to test or soft-part structures of any non-scyphozoan group. Their rejection of the hypothesis that conulariid midlines were sites of gastric septa is based instead on claims that (1) conulariids and scyphozoans exhibit fundamental anatomical dissimilarities (Termier and Termier, 1949, 1953; Kozłowski, 1968; Steul, 1984; Mortin, 1985; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986a,b); and that (2) similarities between conulariid corners and midlines and features at the scyphozoan perradii and interradii are superficial (Termier and Termier, 1949, 1953; Kozłowski, 1968; Oliver, 1984; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986a,b; Oliver and Coates, 1987). The first of these two claims has recently been treated by Bischoff (1978) and by Van Iten (1989a), who argue that dissimilarities between conulariids and scyphozoans do not allow one to reject the hypothesis that these two taxa are closely related. The second claim, that similarities between conulariid corners and midlines and scyphozoan perradii and interradii

are superficial, is examined in this paper.

The present analysis of conulariid corners and midlines is based in part on new information on the anatomy and occurrence of internal test structures at these sites. In order to better organize our knowledge of this critical aspect of conulariid anatomy, new data on corners and midlines are presented in the context of a general review of conulariid cross sectional geometry and internal anatomy. This investigation builds on observations of several previous studies. Among the most important of these are Wiman's (1895) work on Euconularia loculata (Wiman), Sinclair's (1940) work on Metaconularia Foerste, Werner's (1966a,b 1967, 1970, 1974, 1983) work on the periderm of coronatid scyphozoans, and Bischoff's (1978) work on circonulariids, a group of steeply conical (as opposed to steeply pyramidal) Problematica that are similar to conulariids and are probably closely related to them. Together with information gathered by previous investigators, results of this study reveal that conulariid corners and midlines are more complex anatomically than has hitherto been realized. Now that our knowledge of this complexity is more complete, we are in a better position to evaluate whether or not anatomical similarities between conulariids and scyphozoans are best interpreted as indicative of a close phylogenetic relationship.

Material and methods

The present study is based on examination of some or all known species of 12 of the 18 currently recognized conulariid genera, supplemented by data presented in previous papers (Barrande, 1967;

Wiman, 1895; Knod, 1908; Boucek, 1928, 1939; Sinclair, 1940, 1941, 1942, 1944, 1948; Sugiyama, 1942; Bischoff, 1978) on members of these and three other genera. Specimens from the following genera have been studied: Anaconularia Sinclair, Archaeoconularia Boucek (=Exoconularia Sinclair), Climacoconus Sinclair, Conularia Miller, Conularina Sinclair, Ctenoconularia Sinclair, Eoconularia Sinclair, Glyptoconularia Sinclair, Metaconularia Foerste, Notoconularia Thomas, Paraconularia Sinclair, and Pseudoconularia Boucek. Information on the identity and location of these specimens is provided in the Appendix. Availability of specimens varies widely from genus to genus, with some genera (e.g., Ctenoconularia and Eoconularia) known only from a handful of specimens, mostly non-preparable types, and others (e.g., Conularia and Paraconularia) represented by hundreds or even thousands of specimens. Fortunately, type specimens of some of the rare taxa are often broken or exfoliated in such a way as to permit inspection of the test's inner surface.

Depending on the nature of the host matrix, specimens were prepared in one of two ways. Specimens embedded in acid resistant, non-calcareous matrix were serially sectioned. Sections were cut perpendicular to the specimen's long axis, or parallel to it, along a pair of opposite corners or midlines. Other specimens, preserved in limestone, were embedded in casting resin and then cut in half longitudinally. The two halves were immersed in 10% formic acid until the internal matrix was dissolved, thus revealing the test's inner surface. Wherever possible, specimens were chosen that preserved or were broken near the apertural margin and that tapered to within a few millimeters or less of the apex.

Repositories

Abbreviations of repositories containing material examined in this study are as follows: American Museum of Natural History, New York (AMNH); Buffalo Museum of Science, Buffalo (BMS); Burke Museum, University of Washington, Seattle (BM-UW); Carnegie Museum, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Geological Survey of Canada, Ottawa (GSC); Museum of Comparative Zoology, Harvard University (MCZ); Peabody Museum of Natural History, Yale University (PMNH); Peter Redpath Museum, Montreal (PRM); Royal Ontario Museum, Toronto (ROM); State University of Iowa, Iowa City (SUI); University of Michigan Museum of Paleontology, Ann Arbor (UMMP); University of Illinois, Champaign-Urbana (UI); University of Minnesota, Minneapolis (UMPC); and the United States National Museum, Washington, D. C. (USNM).

Conulariid corners and midlines

Conditions of conulariid corners

Non-Sulcate (NS) (Figure 2A). Corners of a small number of conulariids are characterized by direct abutment of adjoining faces of the test pyramid, with no suggestion of a longitudinal groove. This condition was originally detected in Anacomularia (Middle Ordovician, Bohemia), a monospecific genus currently known only from sandstone steinkerns (Barrande, 1867; Boucek, 1928; Sinclair, 1948, 1952). As indicated by present observations and those of previous studies

(Barrande, 1867; Boucek, 1928), the corners of all of the 2000 or so steinkerns collected thus far are rounded and show no evidence of internal thickening of the original test. As reported by Sugiyama (1942), non-sulcate corners also characterize Comulariopsis Sugiyama, a monospecific genus from the Lower Triassic of Japan.

Simple Groove (SG) (Figure 2B). Except in the two taxa just mentioned, corners of all conulariids are furrowed by a broad, angular or rounded groove. In many taxa, this groove is not accompanied by noticeable test thickening. As indicated by present observations and those of previous studies (Barrande, 1867; Boucek, 1928; Sinclair, 1940, 1941, 1948), this condition characterizes all known species of Conularia, Metaconularia, and Pseudoconularia. It also characterizes some species of Ctenoconularia and Paraconularia (see Appendix). Judging from illustrations in Boucek (1928, Plate III, figure 14; 1939, figure 10), corner grooves of Conulariella Boucek (Middle Ordovician, Bohemia) are probably non-thickened as well.

Corners of certain Conularia subcarbonaria Meek and Worthen, collected from the Cedar Valley Formation of east-central Iowa, USA (see Appendix), exhibit a narrow, sharply delineated band of dark pigmentation running along the center of the corner groove. In other conulariids, such pigmentation is usually associated with an internal carina (see below).

Mesially Folded Groove (MFG) (Figure 2C). This condition constitutes the sole diagnostic feature of Notoconularia, erected by Thomas (1969) to receive three Permo-Triassic species formerly assigned to Paraconularia. Although not accompanied by internal test thickening, corner grooves of Notoconularia differ from simple grooves

in exhibiting an outwardly directed, mesial fold.

Carinate Groove (CG) (Figures 2D, 3). Corners of a large number of sulcate conulariids exhibit a broadly rounded or keel-like internal carina, produced by inflection and thickening of the test's inner lamellae (Figure 2D). This condition, previously detected in Ctenoconularia (Sinclair 1948, 1952), also characterizes species of Archaeoconularia, Climacoconus, Conularina, Coconularia, Glyptoconularia, and Paraconularia (see Appendix). Corner carinae usually exhibit a gradual, more or less continuous increase in height and width toward the aperture, and they project from about 1/20 to 1/10 of the distance to the opposite corner. In many cases (e.g., carinate Climacoconus), corner carinae are strongly pigmented and are manifested externally as a narrow, dark-colored band. Inspection of longitudinally sectioned and exfoliated carinae reveals that lamellar boundaries within the carinae parallel their inner surface.

An interesting and potentially highly significant feature characterizes at least some carinate Climacoconus. In two of four specimens here prepared using acid, corner carinae exhibit regular variation in height and width (corner carinae of the other two specimens also vary in height and width but are not complete enough to allow evaluation of regularity). This variation is most pronounced in a specimen collected from the Maquoketa Formation (Late Ordovician) of northeast Iowa, USA (Figure 3). Each of this specimen's three preserved carinae displays a series of three long segments. Consecutive segments along the same carina are separated by a short stretch of non-carinate test, and isolatitudinal segments on different carinae begin and end at the same distance from the apical end of the

specimen. Each segment increases in height and width relatively rapidly, near its adapical end, then rises more gradually to a maximum height, after which it falls gradually, and then more abruptly, toward the adapertural end. Segments vary in length from 12 to 18 millimeters, which corresponds to 10 to 15 of the transverse corrugations on each face. The symmetry and relative constancy in size of these segments, coupled with the smoothness of their surfaces, indicates that they are not simply the result of breakage or incomplete preservation. The specimen displaying these structures shows no signs of injury or malformation; its transverse ornament is normal, and its corners diverge more or less continuously, with no apparent constriction at the ends of carina segments. Together with the presence of similar (albeit less pronounced) variation in corner carinae of at least one other specimen, this suggests that the carina anatomy displayed by this specimen is not accidental, but a type of seriation.

Conditions of conulariid midlines

Simple (S) (Figure 4A). Midlines of many conulariids are furrowed by a groove and/or exhibit inflection and thickening of inner test lamellae. Midlines that exhibit neither of these two attributes are referred to here as simple. Simple midlines characterize some species of Conularia, Climacoconus, Ctenoconularia, Notoconularia, and Paraconularia. Judging again from illustrations in Boucek (1928, Plate III, figure 14; 1939, figure 10), simple midlines probably characterize Conulariella as well.

Outwardly Folded (OF). This condition is diagnostic of the genus Pseudoconularia (Boucek, 1939; Sinclair, 1941, 1948). In this taxon, each midline is marked by a low, broad, outwardly-projecting longitudinal fold. As indicated by inspection of figures in Barrande (1867, Plates 3-7) and exfoliated areas on the only known North American specimen of this genus (see Appendix), portions of the test comprised by the fold are non-thickened.

Single Carina (SC) (Figures 4B, 5A-B). Midlines of a number of conulariids exhibit a single, broadly rounded or keel-like carina, produced by localized inflection and thickening of inner test lamellae. Such a condition characterizes some species of Climacoconus, Conularia, Eoconularia, and Paraconularia (see Appendix). Like corner carinae, midline carinae generally show a more or less continuous increase in height and width toward the aperture, and they may also be strongly pigmented. Inspection of exfoliated and longitudinally sectioned carinae indicates that lamellar boundaries within carinae are concordant with their inner surface.

In addition to having carinate midlines, the North American species Eoconularia forensis Sinclair and Paraconularia crustula (White) also possess carinate corners. In E. forensis, currently represented by three known specimens (see Appendix), the corner carinae are about 10 times higher and eight times wider than the midline carinae (Figure 5A). In P. crustula, the corner carinae are from 1.1 to two times higher than the midline carinae (Figure 5B).

Thickening of corners and midlines of the same specimen has also been documented by Knod (1908), in a Ctenoconularia (?) from the Devonian of Brazil (Figure 5D). However, Knod's (1908) single

transverse section through this specimen shows the midline thickenings to be stronger than those at the corners. Because Knod (1908) apparently prepared only one section, it is not clear whether this size relationship is exhibited at other latitudes on this specimen.

Groove with seriated carina (GSC) (Figures 4C-D, 5C). Midlines of all Archaeoconularia and Glyptoconularia are furrowed by a sharp, longitudinal inflection (Barrande 1867; Boucek 1928; Sinclair 1944, 1948). In the North American species A. membranacea (Ringueberg), currently represented by two incomplete specimens (see Appendix), the midlines are also sites of internal thickening. Viewed internally, preserved portions of two midlines of the holotype and most complete specimen (the inner surface of the other two midlines of this specimen can not be seen) exhibit a series of extremely low, narrow, closely spaced ridges, running along the crest of the midline groove (Figure 4C-D). The ridges range from about 0.4 to 0.8 millimeters long and are about 0.05 millimeters wide. They may be more or less contiguous or spaced up to 0.8 millimeters apart. Each ridge exhibits a gently arcuate longitudinal profile, with a maximum height near the center of the ridge of about 0.05 millimeters. As in the case of seriated corner carinae in Climacoconus, the symmetry and relative constancy in size of midline ridges in A. membranacea, together with the smoothness of these structures, indicate that they are not artifacts of breakage or incomplete preservation. The specimen exhibiting these ridges shows no sign of injury or malformation. For these reasons, the ridges are interpreted as members of a low, seriated internal carina.

A similar structure may be present in the European species A. fecunda (Barrande). As illustrated in a single transverse section in

Boucek (1939), reproduced here in Figure 5C, midlines of A. fecunda are internally thickened. Because only one section is given, however, it is not clear whether this thickening is continuous or seriated.

The corners of the aforementioned Archaeoconularia are also thickened. In both cases, the corners are more strongly thickened than the midlines (e.g., Figure 5C).

Paired Carinae (PC) (Figures 4E-G, 5D). This condition characterizes all known species of Metaconularia (Sinclair, 1940b, 1948), and at least one species of Conularina as well (see below). It is defined by a pair of low, broadly rounded or keel-like carinae, with members of each pair situated on opposite sides of the midline proper. Paired midline carinae of Metaconularia (Figure 4E-F) show a gradual, more or less continuous increase in height and width toward the aperture. They generally project about 1/25 of the distance to the opposite midline. Members of the same pair of carinae are separated by a narrow band of non-thickened test and gradually diverge toward the aperture, at between 1 and 2 degrees. Examination of exceptionally well preserved specimens of Metaconularia manni (Roy) (e.g., Figure 4E) shows that even at a facial width of 0.5 mm, or about 2 mm above the original apex, members of a given pair of carinae are discrete. As in the case of single carinae in other conulariids, paired carinae in Metaconularia are often strongly pigmented and can be seen through the faces (e.g., Figure 4E). Inspection of exfoliated carinae (e.g., Figure 4F) reveals that lamellar boundaries within these structures are concordant with their inner surface.

As noted by Sinclair (1940), some species of Metaconularia, for example M. papillata (Hall), exhibit a groove along the midline proper.

Although present observations suggest that this condition characterizes only some individuals of these species, observations presented in Barrande (1867) suggest that a grooved midline is found consistently in Metaconularia? modesta (Barrande), a species from the Ordovician of Bohemia.

In addition to characterizing Metaconularia, paired midline carinae also occur in Conularina narrawayi Sinclair, currently represented by a single, strongly exfoliated partial specimen from the Middle Ordovician of Quebec. Paired midline carinae on this specimen are extremely low and narrow (Figure 4G). The corners of this specimen are also carinate, but the corner carinae are about eight times wider and 10 times higher than those at the midlines (Figure 5D).

Low Carina, Longitudinally Bifid (IBC) (Figure 4H-I). This condition characterizes Conularia splendida Billings, currently known from Late Ordovician strata of Anticosti Island (English Head Formation; Twenhofel, 1927) and northeast Iowa (Elgin Member, Maquoketa Formation; Van Iten, 1981). Midlines of this species exhibit a low, broadly rounded or carinate thickening, all or portions of which are longitudinally bifid (Figure 4H). Although this is similar to paired midline carinae of Metaconularia and Conularina triangulata, the paired crests of longitudinally bifid carinae are parts of a single thickening situated on the midline proper, rather than a pair of separate thickenings straddling the midline (Figure 4I). Another difference between these structures is that whereas paired midline carinae are continuous and discrete throughout their length, the midline carina of Conularia splendida is commonly discontinuous (Figure 4H).

Midlines of Euconularia amoena Sinclair, currently represented by a single known specimen from the Middle Ordovician of Quebec (Sinclair, 1944; see also Appendix), exhibit internal structures that are similar to those of Conularia splendida. At the specimen's apical end, now broken, the narrowest face (the specimen exhibits a trapezoidal transverse cross section) exhibits a low, rounded thickening, visible in cross section (Figure 5E). At the opposite end, the widest face exhibits cross sections through a pair of thickenings, one on either side of the midline proper. Preparation of this and/or additional specimens is needed in order to determine whether these features are parts of a carina that is discontinuously bifid, or parts of a carina that bifurcates adaperturally.

As noted in the preceding section, the corners of Euconularia are strongly carinate. In E. amoena, the corner carinae are about four times higher and three times wider than the midline carinae (Figure 5E).

Paired Thickenings (PT) (Figures 4J-K, 5F). This condition characterizes most species of Conularina Sinclair, including the unusual form C. triangulata (Raymond), which has three (rather than four) faces (Sinclair, 1942, 1948). It consists of a pair of broad, very low, continuous thickenings, one on either side of the midline proper. Although similar to paired carinae, paired thickenings differ from the latter in being substantially broader and lower, and in being marked on the test's exterior by a pair of very shallow depressions, each corresponding to one of the thickenings. Because known specimens of Conularina are broken well above the apex, it is not yet clear whether the thickenings continue as a discrete pair throughout their

length or merge adapically to form a single thickening.

As noted in the preceding section, the corners of Conularina are also thickened. In all specimens examined here, the corner thickenings are from two to three times higher than those at the midlines (Figure 5F).

Paired Seriated Carinae (PSC) (Figures 4L-N, 5G). This condition was observed in 10 specimens of Climacoconus, all collected from Middle or Late Ordovician strata of the Upper Mississippi Valley and assigned by Sinclair (1948) to one of three species. The midlines of these specimens are flanked along most of their length by two files of short, closely spaced, bar-like ridges (Figure 4L). The ridges are expanded at their ends, making them I-shaped in internal aspect, and they consistently extend between the crests of two adjacent transverse ribs. In most specimens, the ridges are strongly pigmented and can be seen through the faces. Along a given midline, the two files of ridges gradually diverge toward the aperture, terminating several corrugations below it. Test material between the two files is thickened. In all four pairs of files, the height and width of the ridges gradually increase toward the aperture. Inspection of exfoliated ridges (e.g., Figure 4M) indicates that lamellar boundaries within the ridges parallel their inner surface.

Inspection of the adapical end of one of these Climacoconus (GSC 93407), prepared using acid, has revealed an extremely interesting feature. At a facial width of about 2 millimeters (or roughly 10 millimeters above the apex, now missing), paired ridge files on two faces stop (the other two faces are not preserved at this level). Not far below this point, both of these midlines exhibit a continuous,

single carina, situated on the midline proper (Figure 4N). (Due to poor preservation, the geometry of the adapertural end of this carina is unclear.) A single face of another specimen (GSC 93408), likewise preserved close to the apex, shows the same feature (faces of other specimens examined here have been broken further above the apex). This suggests that an adapically situated, single midline carina originally characterized all Climacoconus showing paired seriated carinae straddling more adaperturally situated parts of the midlines.

All Climacoconus with paired, seriated midline carinae also exhibit carinate corners. (Not all Climacoconus with carinate corners, however, exhibit paired midline carinae.) At a given latitude, the corner carinae are two to three times higher than the midline ridges (Figure 5G).

High Bifid Carina (Figure 6A-B). This condition was discovered by Wiman (1895) in a specimen of Eoconularia loculata (Wiman), a rare species from the Middle Silurian of Norway. Wiman's (1895) transverse sections through this specimen show four high, variably broken carinae whose inner (adaxial) margin is strongly bifid (Figure 6A). The non-bifid portion of each carina extends about one-third of the way to the center of the test cavity. From the branching point, the two arms diverge at between 45 and 70 degrees and then bend abruptly toward the face. The ends of the arms apparently were free.

Recently, Babcock and Feldmann (1986b) have proposed that Wiman (1895) misinterpreted the midline anatomy of E. loculata (Wiman), and that high bifid carinae are not actually present in this species. This opinion appears to be based, in part at least, on the fact that identical structures have not been found in other conulariids (Babcock

and Feldmann, 1986b). Unfortunately, material examined by Wiman (1895), consisting of one sectioned and one non-sectioned specimen, now appears to be missing (Babcock and Feldmann, 1986a). Nevertheless, it is clear from Wiman's (1895) line drawings that the sectioned specimen, at least, did possess high bifid carinae. As shown in Figure 6B, the carinae are built of locally inflected, inner test lamellae. Viewed externally, the midlines were marked by a broad, longitudinal band of accentuated pigmentation (Wiman, 1895). Both of these features are exactly what one sees in other conulariids bearing internal carinae, and thus tend to corroborate Wiman's (1895) description of the carinae themselves. Under these circumstances, it seems unwise to disregard Wiman's (1895) illustrations of their cross sectional geometry.

Further support for this conclusion is provided by observations of this study on internal midline structures of other conulariid taxa. High bifid carinae, though distinctive in their large size and strongly bifid cross sectional geometry, are fundamentally similar to low bifid carinae detected here in Conularia splendida (Figure 4J). As indicated by the geometry of test lamellae within the latter structures, amplification of growth processes leading to the formation of a low carinae with subdued arms would lead to the production of a high carina with elongate arms, like that in E. loculata.

High Carina with Surficial Pustules (Figure 7). This condition was detected by Bischoff (1978) in specimens of a Paraconularia-like conulariid from the Silurian of Australia. Midlines of this conulariid are marked by a strong, angular groove that is associated internally with a high, carinate thickening that extends about two-fifths of the way to the central axis of the test cavity. This carina differs from

those discussed above in being covered by small, broadly conical pustules. The pustules, arranged in irregular fashion on the carina's two flanks, range from about 0.02 to 0.13 mm wide (as measured at their base) and 0.03 to 0.17 mm high.

Midline conditions of circonulariids

Circonulariids are represented by abundant but fragmentary material collected from Silurian and Devonian strata of south-central Australia (Bischoff, 1978). Except for their steeply conical (as opposed to steeply pyramidal) shape, circonulariids are extremely similar to conulariids, consisting of an apatitic, finely lamellar test that is transversely corrugated or ornamented externally by transverse rows of small, closely spaced tubercles. In most species, the corrugations or tubercle rows arch toward the aperture, in such a way as to define eight longitudinal tracts spaced around the test at 45 degree intervals. Four of these tracts, spaced at 90 degree intervals, are defined by the summits of segments arching toward the aperture and are interpreted by Bischoff (1978) as homologous to the midlines of conulariids.

Bischoff (1978) has documented five types of internal structures at circonulariid midlines. Two of these, termed septal ridges and paired septal ridges, are extremely similar, respectively, to single and paired midline carinae of conulariids such as Paraconularia and Metaconularia. The remaining three midline structures, though similar in many ways to other kinds of conulariid midline structures, are unique to circonulariids. One of these, termed an adaperturally

bifurcating low septum, is a low carina that splits adaperturally, forming two short branches that diverge at between 15 and 30 degrees. The flanks of the carina (including both single and forked portions) may be smooth or covered by small pustules, similar to pustules on the flanks of midline carinae of the Paraconularia-like conulariid described above. In many cases, a given midline shows multiple bifurcating septa, arranged in series and with the adapical end of each member of a series situated immediately above the adapertural end of the member below it. The second uniquely circonulariid midline structure, similar to multiple bifurcating septa, consists of a series of low, stout, v-shaped ridges, called funnel-shaped septa, whose pointed end is directed toward the apex. Individual ridges exhibit a small hole in their apical end, apparently providing continuous communication between the triangular regions bounded by the two arms of the ridges. Finally, the third uniquely circonulariid midline structure, termed a septal apparatus, consists of four massive septa that join at the center of the test cavity, forming a single continuous unit. The sides of each septum exhibit a single longitudinal row of pustules or a coarsely pustulose longitudinal ridge.

Summary of conulariid corner and midline anatomy

Corners and/or midlines of some or all species of at least nine conulariid genera consistently display some form of internal longitudinal thickening, produced by localized inflection and thickening of inner test lamellae. Although internal corner and midline thickenings of most conulariids exhibit a smooth (non-

pustulose) inner surface, midline carinae of at least one Australian conulariid, similar to Paraconularia, are covered by small nodes or pustules.

Internal midline structures of some or all species of at least five conulariid genera - Climacoconus, Conularia, Conularina, Eoconularia, and Metaconularia - are paired or longitudinally bifid. In many cases (e.g., Metaconularia), members of paired midline structures are discrete throughout their length; however, midlines of some Climacoconus, flanked by a pair of seriated carinae that begins several millimeters or more above the apex, exhibit a mesially situated, single carina below this point. Among conulariids showing longitudinally bifid midline structures, one species, Eoconularia loculata (Wiman), exhibits an unusually high carina whose cross sectional geometry is more or less Y-shaped.

Some or all species of five genera - Archaeoconularia, Climacoconus, Conularina, Eoconularia, and Paraconularia - exhibit midlines and corners that are both thickened. Almost without exception, the corners are more strongly thickened than the midlines. The exception to this rule, documented by Knod (1908), consists of a single section through one specimen. Given that internal structures of some conulariids are seriated and/or exhibit variation in height and width, it may be the case that corners of Knod's specimen are more strongly thickened than the midlines at latitudes other than the one intersected by his single section.

Some species of at least two genera - Archaeoconularia and Climacoconus - exhibit internal corner and/or midline thickenings that are seriated. In Climacoconus, where seriation has been found

both in midline and corner structures, members of a series of corner carinae are longer and higher than members of midline series.

Conulariid midline structures show a number of similarities to midline structures of circonulariids. In both groups, these structures represent localized inflections of inner test lamellae, and their inner surface may be smooth or covered by small pustules. Two types of structures, namely single and paired carinae, occur in members of both groups. One type of uniquely circonulariid structure, the adaperturally bifurcating low septum, is comparable to internal midline structures of certain Climacoconus, which as discussed above exhibit an adapically situated single carina that gives way adaperturally to a pair of seriated carinae that gradually diverge toward the aperture. A similar geometry may also be exhibited by midline structures of Eoconularia amoena (though again this needs to be verified by sectioning or acid preparation).

These similarities reinforce Bischoff's (1978) contention that conulariids and circonulariids are closely related. In view of the fact that these similarities are uniquely shared by these two taxa, it seems reasonable to interpret them as members of a single, higher level monophyletic group. For this reason, observed conditions of circonulariid midlines are regarded here as having a bearing on the interpretation of conulariid anatomy.

Scyphozoan perradial and interrarial anatomy

General. The Class Scyphozoa includes five extant orders (Hyman, 1940), three of which (Coronatida, Carybdeida, Stauromedusida) are

characterized by the presence of gastric mesenteries, or septa, throughout their life history. In the remaining two orders (Semaestomatida, Rhizostomatida), septa are limited to the polypoid stage. Although members of most scyphozoan orders are naked, polyps of the Order Coronatida are sheathed in a steeply conical, finely lamellar chitinous periderm. Moreover, in some coronatids, the inner peridermal lamellae are locally inflected at the perradii and interradii (e.g., Werner, 1966a,b, 1967, 1983; Chapman and Werner, 1972).

Septa. Details of the anatomy of scyphozoan septa have been reviewed by Hyman (1940). Summarizing the main points, scyphozoans almost always exhibit four septa, though certain rare species are characterized by six septa, and aberrant individuals of species that normally produce four septa may exhibit three, five, or six septa. Where four septa are present, the septa divide the enteron into a central stomach and four peripheral cavities, the gastric pockets, that are bisected by the perradii (Figure 8). At its oral end, each septum is penetrated by a funnel-shaped, adapically directed invagination, the peristomial funnel, that causes the septum to bulge laterally. Along its free inner edge, the septum is provided with numerous, nematocyst-laden gastric filaments. These structures are arranged in two longitudinal rows, or phacellae, one on either side of the interradius. Situated nearer the abaxial or fixed edge of the septum is a pair of elongate, laterally situated entodermal gonads. Located still closer to the septum's fixed edge is a longitudinal retractor muscle, derived from the ectoderm.

Important variations on this basic design are shown by septa of the Order Stauromedusida, a group of exclusively polypoid scyphozoans

(Figure 8). Near the polyp's apical end, the septa merge to form a single continuous structure, eliminating the central stomach. In some stauromedusans, portions of the septa above this zone exhibit a pair of lateral outgrowths, called claustra. Near their apical ends, the claustra exhibit free edges, but above this they merge with claustra of adjacent septa to form a continuous wall that separates the gastric pockets from the central stomach. In most stauromedusans, as in other scyphozoans, the septal retractor muscle consists of a single tissue bundle. However, in Craterolophus the retractor muscle splits near the base of the peristomial funnel (Gross, 1900), forming two closely spaced bundles that diverge toward the apertural end, at about 1 to 2 degrees. Similarly, the retractor muscle of Lucernaria splits in the vicinity of the mouth, forming two bundles that diverge at an angle of about 20 degrees (Antipa, 1892).

Coronatid peridermal structures. Details of the anatomy and growth of the steeply conical, chitinous periderm of coronatid scyphozoans have been discussed by Werner (1966a,b, 1967, 1970, 1974, 1979, 1983) and Chapman and Werner (1972). Reviewing the main points, the periderm is present throughout the polyp's life and extends the entire length of its calyx. At the periderm's narrow, or basal end is a small attachment disc, fastened in life to rocks or other hard substrates. The oral end is open and exhibits a circular margin. Transmission electron microscopy shows that the periderm is built of numerous, 12-nanometer-thick lamellae, separated from each other by an equally narrow gap that is spanned at short intervals by small processes. The lamellae are arranged in two layers: a transversely corrugated, outer layer, about 2 to 4 microns thick, and a non-

corrugated, inner layer, up to about 20 microns thick. The outer layer extends the entire length of the periderm and is secreted by gland cells in a circular band of ectoderm, the junctional secretory band, that overlaps the apertural margin. Secretion of peridermal material along this margin causes the outer layer to lengthen, keeping pace with lengthening of the soft body. In contrast to the outer layer, the inner layer commonly pinches out well below the apertural margin. Moreover, it is secreted by gland cells along the side of the calyx and grows by successive accretion of lamellae to the periderm's inner surface.

In coronatids such as Atorella, lamellae of the inner layer are locally inflected at the interradii and perradii, forming eight longitudinal files of thorn-like projections that are also arranged in whorls or circlets (Figure 9). Projections of the four interradii files, located within the septa, are substantially smaller (lower, narrower, shorter) than projections of the four perradii files. The interradii projections are situated between two adjacent crests of the transverse outer ornament and are separated from members of the same file by seven to twelve corrugations. The perradii projections span from two to four corrugation crests. Within a given circlet, the aboral end of each perradii projection is situated at about the same level (latitude) as the aboral end of each of the associated interradii projections. Within a given file, both perradii and interradii projections increase in size toward the aperture. In most species, the inner surface of the projections is smooth; in some species, however, the inner surface of the perradii projections has numerous small, broadly conical pustules. Although the interradii

projections occur within the septa, adjacent to the retractor muscle, they apparently are not sites of muscle attachment (Werner, 1967).

Comparisons between scyphozoans and conulariids

As is evident from the descriptions above, conulariid corners and midlines exhibit a number of similarities to soft-part and peridermal structures located along scyphozoan perradii and interradii. Some of these similarities involve directly comparable anatomical entities such as the conulariid test and the periderm of coronatid scyphozoans. Other similarities involve comparisons of the conulariid test with scyphozoan periderm and soft tissues, or with scyphozoan soft tissues alone. This has led to some confusion on the part of critics of previous comparisons of conulariids and scyphozoans. Babcock and Feldmann (1986a), for example, characterize these comparisons as though they involve simplistic identifications of conulariid test structures with scyphozoan soft parts. That this is not the case will be made clear in the rest of this section.

As noted by Kiderlen (1937), high, adaxially bifid midline carinae of Euconularia loculata (Wiman) are similar to claustra-bearing stauromedusan septa. The two features are identical in number and arrangement, and show resemblances in cross sectional form and size (both absolute and relative to the body, or test, cavity). Previous work (Bischoff, 1978) has shown that the test of E. loculata and other conulariids was an exoskeleton, secreted by soft tissues covering its inner surface. This means that the geometry of midline carinae in E. loculata is an indirect, and minimal, indication of the configuration

of soft tissues within the test cavity of this species. Together with the aforementioned gross anatomical similarities between E. loculata and stauromedusans, this suggests that high, bifid midline carinae were originally covered by an adaxially expanded, gastric septum.

This inference is further supported by configurations of low midline carinae in other conulariids. As noted above, such structures may be either single, paired, or longitudinally bifid. These conditions are similar to the single-stranded and adorally bifurcate conditions of the stauromedusan retractor muscle. Paired midline carinae in the conulariids Climacoconus, Conularia, Conularina, and Metaconularia are comparable in spacing and angle of divergence to the paired muscle strands of the bifurcate retractor muscle of Craterolophus. Although paired carinae here observed are generally discrete throughout their length, rather than bifurcate, bifurcation of internal midline structures does characterize at least some Climacoconus and, possibly, Eoconularia amoena as well. Moreover, bifurcate midline carinae of the circonulariid Garraconularia are similar to the retractor muscle of Lucernaria, a species in which the paired strands of the muscle's bifurcate portion diverge more rapidly than in Craterolophus. Like the conulariid (and circonulariid) test, scyphozoan retractor muscle is derived from ectoderm, and thus it is reasonable to suppose that similarities between internal midline structures of conulariid tests and the scyphozoan retractor muscle is indicative of similarity at a more general level of comparison. Thus, while test structures at conulariid midlines are not directly homologous to scyphozoan septal muscle, similarities in the configuration of these two features can be interpreted as further

evidence of the former presence of soft part features similar to scyphozoan septa at conulariid midlines. More specifically (and as proposed earlier by Bischoff (1978)), these similarities suggest that the presence of single, paired, and adaperaturally bifurcate midline carinae in conulariids (and circomulariids) is a reflection of corresponding conditions of a septal retractor muscle, situated in life above each of the midlines.

Still more evidence of similarities in soft part anatomy is provided by other comparisons. As noted above, some rare scyphozoan species are characterized by six septa, and individuals of species that normally exhibit four septa are known to produce three, five, or six septa. Similarly, the conulariid Conularina triangulata (Raymond) exhibits only three faces (and hence three midlines), and Babcock et al. (1987a) have documented a specimen of Paraconularia missouriensis (Swallow) possessing six faces. (It should be noted here that Babcock et al. (1987b) have recently removed Conularia triangulata from the Conulariida, based on putative microstructural differences between this species and other conulariids; however, more recent work by Van Iten (1989) has shown that C. triangulata is in fact identical microstructurally to other taxa traditionally interpreted as conulariids.) The only other organisms known to exhibit tetrameral, trimeral, pentameral, or hexagonal symmetry, and that can reasonably be considered as possible candidates for a close extant relative of conulariids, are hydrozoan cnidarians (Hyman, 1940).

Finally, internal structures at conulariid corners and midlines show several similarities to internal peridermal projections of coronatid scyphozoans. Both sets of features represent localized

inflections of an inner set of fine, parallel lamellae, and their inner surface (the one in former contact with soft tissue) may be either smooth or covered by low pustules. Just as coronatid perradial projections are consistently larger (higher, longer, broader) than projections at the interradii, in conulariids exhibiting internal structures at both the corners and the midlines, the corner structures, interpreted as perradial in position, are almost always larger than associated midline structures. Although internal thickenings of most conulariids are more or less continuous, internal test structures of some conulariids are seriated, in a manner similar to seriation shown by coronatid projections. Like coronatid interradiial projections, paired files of I-shaped ridges flanking the midlines of the conulariid Climacoconus consistently extend between two adjacent transverse corrugations and show a gradual increase in height and robustness toward the oral end. Seriated carinae at Climacoconus corners are no fewer than several corrugations long, substantially longer than members of observed midline series. Based on a smaller set of similarities than this one, Werner (1966, 1967) maintains that internal structures at conulariid corners and midlines are directly homologous to peridermal projections at coronatid perradii and interradii, respectively. This hypothesis has been questioned by Bischoff (1978) (himself a leading advocate of a scyphozoan affinity for conulariids), and it is not within the scope of the present study to attempt a detailed evaluation of it. Nevertheless, the similarities just outlined involve a relatively complex set of anatomical structures, uniquely present in conulariids and coronatid scyphozoans, and thus at the very least they tend to reinforce the contention that conulariids

and scyphozoan in general were characterized by fundamental similarities in soft part anatomy.

Discussion

Opponents of a scyphozoan affinity for conulariids have yet to offer an alternative hypothesis of homology that is more strongly supported than the hypothesis that conulariid midlines were sites of gastric septa. Nearly all of the similarities outlined in the previous section are uniquely shared by conulariids and scyphozoans, and as indicated by discussions of invertebrate and chordate anatomy in Barnes (1987) and Jollie (1962) there is no evidence of greater similarity between conulariid corners and midlines and soft- or hard-part features of any non-scyphozoan taxon. Although the presence of internal structures at conulariid corners and midlines probably strengthened the test, as suggested by Babcock et al. (1987), a strictly functional explanation for the occurrence of these features in conulariids does not account for similarities between details of their anatomy and details of the anatomy of scyphozoan septa and internal peridermal structures. For these reasons, the interpretation of conulariid corner and midline anatomy favored here is that conulariid midlines were sites of gastric septa, homologous to the gastric septa of scyphozoan cnidarians.

This hypothesis is consistent with current understanding of other aspects of conulariid paleobiology. Evidence reported by Ruedemann (1896a,b, 1897), Sinclair (1948), Finks (1955, 1960), Rooke and Carew (1983), Babcock et al. (1987b), and Van Iten (1989) indicates

that conulariids were sessile organisms, attached at their apical end and thus comparable in mode of life and life orientation to scyphozoan polyps. Known sizes of conulariids, which range from about one to 40 centimeters long (Sinclair, 1948), are comparable to sizes of stauromedusans, some of which (e.g., Ctraterolophus) are up to 20 centimeters long (Hyman, 1940). As shown by Werner (1966a,b, 1967), Bischoff (1978), and Van Iten (1989), the conulariid test is similar in microstructure and mode of growth and damage repair to the coronatid periderm, suggesting that these two structures are homologous (Werner, 1966, 1967; Van Iten, 1989). There is evidence that conulariids formed colonies of mutually connected, apically budded clones (Kozlowski, 1968), similar to polyp colonies of certain coronatid scyphozoans (Werner, 1979). Finally, ongoing analysis of relic conulariid soft parts (Van Iten, 1989a,b) suggests that conulariids underwent polydisc strobilation (Barnes, 1987), a mode of medusa formation previously known only in certain groups of extant scyphozoans.

To be sure, conulariids and scyphozoans do show certain differences. One of these differences, namely the presence of an apatitic test (periderm) in conulariids versus the absence of peridermal mineralization in thecate scyphozoans, has been interpreted by some authors (e.g., Termier and Termier, 1949) as grounds for rejecting the hypothesis that conulariids and scyphozoans exhibit homologous gastric septa. However, given that many higher-level taxa (e.g., hydrozoan cnidarians) include both mineralized and non-mineralized members (Barnes, 1987), the observation that conulariids are apatitic and scyphozoans are not can be interpreted as a significant but not fundamental variation on the pattern of anatomical

organization shown by scyphozoans.

Implications for conulariid affinities

Proponents of the hypothesis that conulariid midlines were sites of gastric septa interpret conulariids as extinct members of the Phylum Cnidaria, now generally regarded as a monophyletic taxon whose extant members include the Classes Anthozoa, Hydrozoa, and Scyphozoa (Barnes, 1987). Although there is still a great deal about conulariids that is poorly understood, results of this and other studies (Kiderlen, 1937; Werner, 1966a,b, 1967; Bischoff, 1978) suggest that conulariids and circomulariids are more closely related to extant cnidarians than they are to any other group of organisms. Relationships among taxa within Cnidaria have been subject to divergent interpretations (e.g., Hyman, 1940; Hadzi, 1963; Thiel, 1966; Werner, 1973), and at present there appears to be no consensus on this problem (Oliver and Coates, 1987). Nevertheless, the presence of four gastric septa in conulariids and scyphozoans indicates that these two groups may be more closely related to each other than either group is to anthozoans or hydrozoans.

In order to conclude that conulariids and scyphozoans are nearest relatives, it is necessary to argue not only that the presence of four gastric septa is homologous, but also that it is derived relative to the absence of gastric septa in hydrozoans, and either derived or independently derived relative to the more numerous gastric septa of anthozoans. If the presence of four gastric septa is not homologous and derived, then either conulariids or scyphozoans could have a more recent common ancestry with hydrozoans or anthozoans. To determine if

conulariids and scyphozoans are best interpreted as nearest relatives, relationships between conulariids, circonulariids, and extant cnidarians were analyzed cladistically, using the Phylogenetic Analysis Using Parsimony (PAUP) algorithm by David Swofford. Also included in the analysis were the Phyla Platyhelminthes and Ctenophora, traditionally regarded as the two most likely candidates for a nearest extant relative of cnidarians (Harbison, 1985). A total of 21 anatomical characters (Table 1), most of them involving soft part features whose states in conulariids and circonulariids are uncertain, were scored. Character state data for extant cnidarians, ctenophorans, and platyhelminthes were obtained from discussions of these groups in Hyman (1940) and/or Barnes (1987), while character state data for conulariids and circonulariids were taken from the present paper and from discussion in Bischoff (1978).

Using the Beta-3 version of PAUP (run using the exhaustive search option and with character states unordered and coded to allow for polymorphism), it was found that the most parsimonious hypothesis of relationships between conulariids+circonulariids and extant cnidarians is that conulariids+circonulariids and scyphozoans are nearest relatives, and that together these three groups and anthozoans form a monophyletic group within Cnidaria that excludes hydrozoans. (This result was confirmed using an earlier version of PAUP that does not allow coding for polymorphism.) This hypothesis of relationships, summarized in the cladogram in Figure 10A, requires a total of 25 evolutionary steps (particular instances of derivation of a character state). It is consistent with interpretations of ancestor-descendant relationships among extant cnidarians advocated by authors such as

Hyman (1940), Hill and Wells (1956), and Hand (1963), who hold that hydrozoans are directly ancestral to scyphozoans, and that scyphozoans in turn are directly ancestral to anthozoans.

Two other hypotheses of relationship, each requiring 26 evolutionary steps (one more than the most parsimonious hypothesis), were also found. Both of these hypotheses agree with the most parsimonious one (Figure 10A) in suggesting that septate cnidarians form a monophyletic group within Cnidaria that excludes hydrozoans (differing only in their interpretations of relationships within this monophyletic group), and that conulariids+circonulariids and scyphozoans are nearest relatives.

The next most parsimonious hypotheses of relationship, totalling four in number, each require 27 evolutionary steps. Two of these hypotheses suggest that conulariids+circonulariids and scyphozoans are nearest relatives (the two that do not hypothesize that conulariids or circonulariids are more closely related to anthozoans). One of these hypotheses, summarized in the cladogram in Figure 10B, differs from all of the aforementioned hypotheses in suggesting that hydrozoans and scyphozoans are more closely related to each other than either group is to anthozoans. This interpretation of relationships among extant cnidarians is consistent with interpretations of ancestor-descendant relationships advocated by authors such as Remane (1954), Jagersten (1955, 1959), Marcus (1958), and Hadzi (1958, 1963). These authors hold that anthozoans are directly ancestral to scyphozoans, and that scyphozoans in turn are directly ancestral to hydrozoans.

The remaining hypotheses of cladistic relationship (total number approximately 400) recovered in this analysis require from 28 to 34

evolutionary steps. Many of these hypotheses conflict with currently accepted interpretations of relationship among taxa within Cnidaria and/or between members of Cnidaria and taxa outside this group.

In sum, results of cladistic parsimony analysis of relationships among conulariids and extant cnidarians tend to favor the hypothesis that conulariids+circonulariids and scyphozoans are nearest relatives, and that they and anthozoan cnidarians are more closely related to each other than any one of these groups is to hydrozoan cnidarians. The interpretation of anthozoans and scyphozoans as more closely related to each other than either group is to hydrozoans is controversial, and some of the hypotheses of homology and polarity implied by it have been directly challenged by advocates (e.g., Salvini-Plawen, 1978) of its most popular rival, namely that scyphozoans and hydrozoans are nearest extant relatives. The difference in degree of cladistic support between these two interpretations is by no means large (25 evolutionary steps for monophyly of septate cnidarians versus 27 evolutionary steps for monophyly of the group containing Hydrozoa and Scyphozoa), and thus it would be desirable to analyze additional characters (e.g., molecular or biochemical characters). Needless to say, more work is also needed on conulariids (and circonulariids), particularly on details (Table 1) of their life history and soft part anatomy. As indicated above, such work is currently being conducted by the present author, using data in Steul (1984) on pyritized soft parts in specimens of Conularia from the Hunsruck Slate (Middle Devonian, West Germany) and information obtained through examination of soft part relics in the holotype of Eoconularia amoena (Sinclair) (Middle Ordovician, Quebec) (Van Iten, 1989a,b).

Acknowledgements

This study forms part of a Ph.D. dissertation written at the University of Michigan, Ann Arbor. I thank the members of my dissertation committee, Douglas J. Eernisse (Department of Biology, University of Michigan), Daniel C. Fisher, Kyger C Lohmann, Gerald R. Smith, and Bruce H. Wilkinson (Department of Geological Sciences, University of Michigan) for their advice and for discussions of earlier versions of the manuscript. I am particularly grateful to Douglas J. Eernisse for his advice on cladistics and for help in running PAUP. I also thank Robert Titus (Hartwick College, Oneonta, New York) for permission to section specimens of Conularia trentonensis in collections of Hartwick College, and Tatiana Van Iten for help in preparing the plates and figures. Permission to borrow or examine museum specimens was provided by Thomas E. Bolton (Geological Survey of Canada, Ottawa), Mary Carmen (Field Museum of Natural History, Chicago), Frederick J. Collier (United States National Museum, Washington, D. C.), Niles Eldredge (American Museum of Natural History, New York), Ronald Eng (Museum of Comparative Zoology, Harvard University), Julia Golden (State University of Iowa, Iowa City), Terry Frest (Burke Museum, University of Washington, Seattle), Richard Laub (Buffalo Museum of Science, Buffalo), and Janet Waddington (Royal Ontario Museum, Toronto). Their assistance is much appreciated. Financial support for this study was provided in part by a Grant-In-Aid of Research from Sigma Xi to the author, and by NSF Research Grant BNS-8521097 to D. C. Fisher.

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Table 1. Character state data used in analyzing phylogenetic relationships between conulariids, circonulariids, and the extant cnidarian classes. Data for the Phyla Platyhelminthes and Ctenophora, traditionally regarded as the two most likely candidates for a nearest extant relative of cnidarians, are also included. The 21 characters and their states are listed below the data matrix. In the matrix, the letter P indicates that a taxon is polymorphic for the corresponding character, while a question mark indicates that the state is undetermined. Six of the characters used here pertain only to taxa having medusae (characters 5 through 9) or intrinsic nematocysts (character 13). For taxa lacking medusae or nematocysts (Platyhelminthes, Ctenophora, Anthozoa), states of these six characters are coded as undetermined.

<u>Taxon</u>	<u>Character</u>																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Platyhelminthes	0	0	0	0	?	?	?	?	?	0	0	0	?	0	0	0	0	0	0	0	0
Ctenophora	1	P	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Hydrozoa	1	1	1	1	1	1	1	P	1	1	1	P	1	P	1	1	1	0	0	0	0
Anthozoa	1	1	1	0	?	?	?	?	?	1	1	0	0	P	0	0	1	1	0	1	0
Scyphozoa	1	1	1	1	P	P	P	1	1	1	1	1	1	P	P	0	1	1	1	1	0
Circonulariida	1	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	1	?	1
Conulariida	1	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	1	?	1

- Character 1 - Symmetry: radial (1); non-radial (0)
 Character 2 - Ectodermal tentacles: present (1); absent (0)
 Character 3 - Cnidocytes or colloblasts: present (1); absent (0)
 Character 4 - Medusa or medusa-like form: present (1); absent (0)
 Character 5 - Ring canal: present (1); absent (0)
 Character 6 - Marginal ocelli: present (1); absent (0)
 Character 7 - Velum or velarium: present (1); absent (0)
 Character 8 - Marginal lappets: present (1); absent (0)
 Character 9 - Marginal statocysts: present (1); absent (0)
 Character 10 - Planula larva: present (1); absent (0)
 Character 11 - Polyp and/or actinula larva: present (1); absent (0)
 Character 12 - Tetraradial symmetry: present (1); absent (0)
 Character 13 - Cnidocil-bearing cnidocytes - present (1); absent (0)
 Character 14 - Coloniality: present (1); absent (0)
 Character 15 - Mesogleal or mesenchymal cells: present (0); absent (1)
 Character 16 - Sex cells ripening in: entoderm (0); ectoderm (1)
 Character 17 - Circumoral tentacles: present (1); absent (0)
 Character 18 - Enteron: septate (1); non-septate (0)
 Character 19 - Number of septa: four (1); other (0)
 Character 20 - Gastric filaments: present (1); absent (0)
 Character 21 - Apatitic periderm: present (1); absent (0)

APPENDIX

Listing of conulariid species examined in the present study, with information on specimen locations and numbers. An asterisk following a genus name indicates that the genus is monospecific. Letters in parentheses following species names indicate observed or inferred condition of the corners and midlines (see text for explanations of the letter code).

Taxon	Repository
<u>Anaconularia</u> * Sinclair, 1952	
<u>A. anomala</u> (NS, ?)	MCZ unnumbered (760 specimens)
<u>Archaeoconularia</u> Boucek, 1939	
<u>A. attenuata</u> (SC, ?)	ROM 23280 (Holotype)
<u>A. membranacea</u> (SC, GSC)	BMS E10071, E10791
<u>A. dubia</u> (SC, ?)	ROM 18889 (Holotype)
<u>Climacoconus</u> Sinclair, 1942	
<u>C. batteryensis</u> (SG, SC)	GSC 29594; PMNH 10367 (Holotype)
<u>C. quadratus</u> (CG, S)	GSC 17710-17712
<u>C. rallus</u> (CG, S)	GSC 17713
<u>C. sp. 1</u> (CG, PSC)	GSC 93407-93415
<u>C. sp. 2</u> (CG, PSC)	SUI 55070
<u>Conularia</u> Sowerby, 1821	
<u>C. albertensis</u> (SG, SC)	USNM 409813-409814
<u>C. cf. splendida</u> (SG, LBC)	SUI 56001-56015; UW-BM 23023
<u>C. subcarbonaria</u> (SG, S)	SUI 55080
<u>C. trentonensis</u> (SG, S)	GSC; HC; NYSM; ROM; SUI; USNM
<u>Comularina</u> Sinclair, 1942	
<u>C. irrasa</u> (CG, PT)	GSC 17714
<u>C. narrawayi</u> (CG, PC)	ROM 18905 (Holotype)
<u>C. raymondi</u> (CG, PT)	GSC 17715
<u>C. triangulata</u> (CG, PT)	CM 2099 (Holotype); GSC 17715-17717; UMMP 65988
<u>Ctenoconularia</u> Sinclair, 1952	
<u>C. obex</u> (SG, S)	UMPC 3211
<u>C. tibialis</u> (SG, S)	GSC 94784
<u>Eoconularia</u> Sinclair, 1944	
<u>E. amoena</u> (CG, LBC?)	ROM 23297
<u>E. forensis</u> (CG, SC)	GSC 1712-1713
<u>Glyptoconularia</u> Sinclair, 1952	
<u>G. gracile</u> (CG, ?)	AMNH 789 (Holotype); GSC 94782-94783 SUI 55065-55066

APPENDIX (continued)

Metaconularia Foerste, 1928

<u>M. calderi</u> (SG, PC)	GSC 9794, 9795
<u>M. delicatula</u> (SG, PC)	UIPC X-614
<u>M. gibraltarensis</u> (SG, PC)	ROM 7537 (Holotype); UMMP 65989
<u>M. heymanni</u> (SG, PC)	USNM 78433, 78430
<u>M. manni</u> (SG, PC)	FMNH P23674 (Holotype), PE 6252- 6256, PE 10132, PE 25975, PE 40268
<u>M. papillata</u> (SG, PC)	AMNH 790; MCZ 27809
<u>M. sp.</u> (SG, PC)	SUI 37414, 36986
<u>M. sp.</u> (SG, PC)	ROM 87DR
<u>M. ulrichi</u> (SG, PC)	USNM 43087

Notoconularia Thomas, 1969

<u>N. laevigata</u> (MFG, S)	UMMP 9299
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Paraconularia Sinclair, 1940a

<u>P. crustula</u> (OG, SC)	UMMP 65990 (4 specimens)
<u>P. planicostata</u> (SG, SC)	ROM 29823 (14 specimens)
<u>P. ulrichiana</u> (SG, SC)	USNM 409842-409843
<u>P. yochelsoni</u> (SG, S)	UMMP 45499 (Holotype), 45500, 65509

Pseudoconularia Boucek, 1939

<u>P. magnifica</u> (SG, OF)	PRM 1019
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Figure 1. Diagrammatic transverse cross sections through (A) a comulariid and (B) a scyphozoan. Letter symbols are as follows: M = midline, C = corner, IR = interradius, PR = perradius.

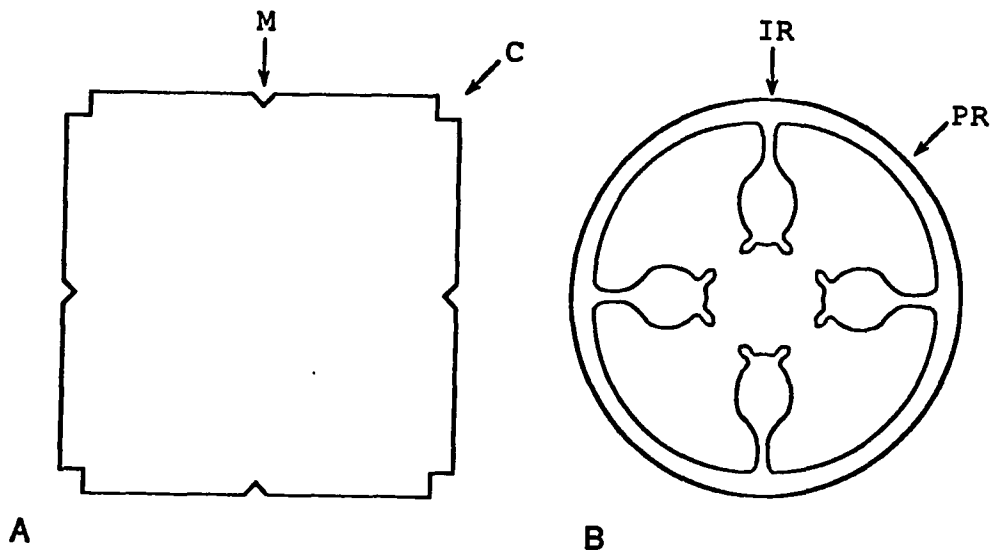


Figure 2A-B. Examples of the some of the four basic conditions of conulariid corner anatomy recognized in the present study. A, non-sulcate (NS), SEM photomicrograph of a transverse section through a corner of Anaconularia anomala (Barrande) (Middle Ordovician, Bohemia), UMP 10000; B, simple groove (SG), SEM photomicrograph of the inner surface of part of a corner of Conularia splendida Billings (Late Ordovician, Iowa), SUI 10000.

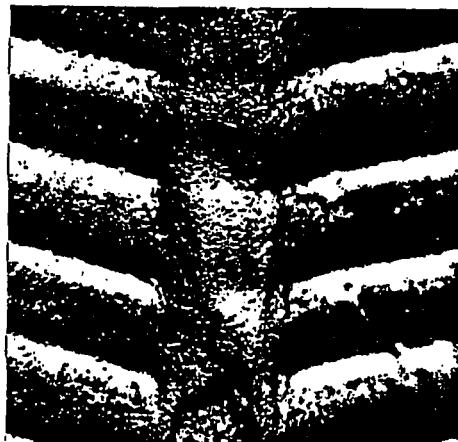
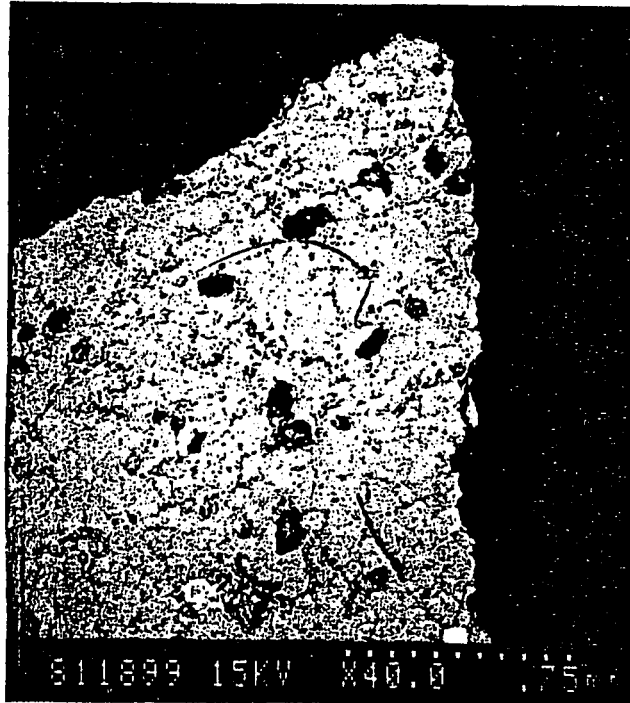


Figure 2C-D. Examples of some of the four basic conditions of conulariid corner anatomy recognized in the present study. C, mesially folded groove (MFG), SEM photomicrograph of a transverse section through a corner of Notoconularia laevigata (Morris) (Permian, Tasmania), UMP 9299; D, carinate groove (CG), SEM photomicrograph of a transverse section through a corner of Paraconularia crustula (White) (Pennsylvanian, midcontinental USA), UMP 10000.

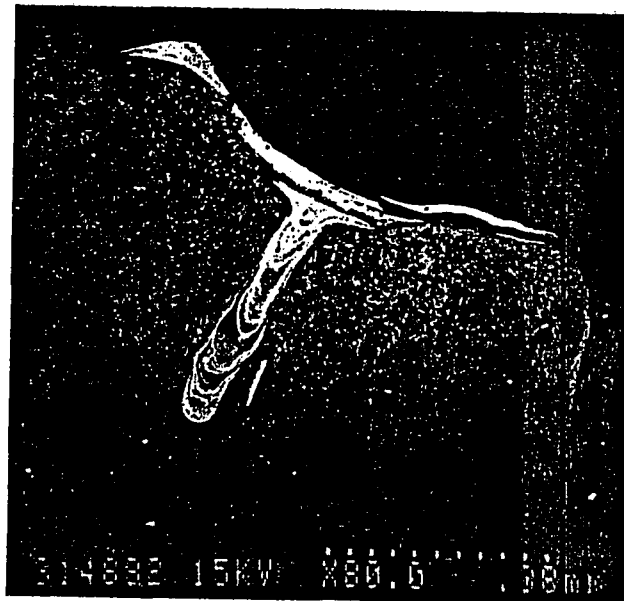


Figure 3. Line drawings of longitudinal profiles of three corners of a specimen of an undetermined species of Climacoconus, collected from the Elgin Member of the Maquoketa Formation (Late Ordovician), northeast Iowa, USA (UMMP 65994, X3).

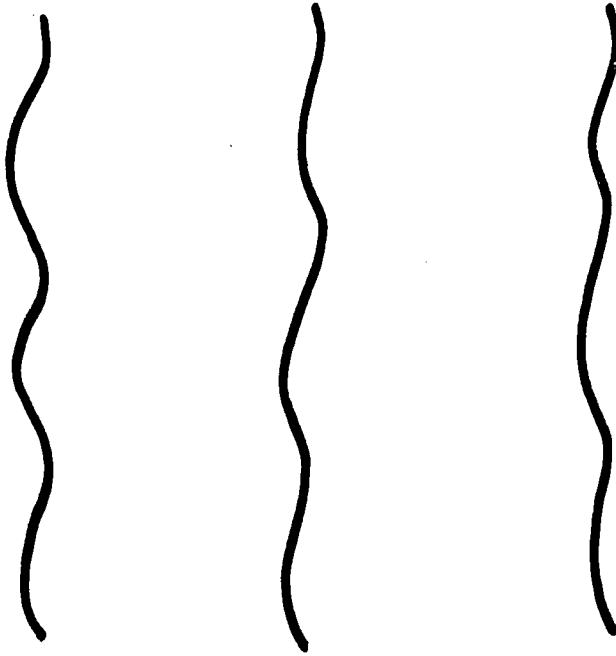


Figure 4A-B. Examples of some of the nine conditions of conulariid
midline anatomy recognized in the present study. A, simple midline (S),
inner surface of part of a midline (arrow) of Conularia trentonensis
Hall (Middle Ordovician, Iowa; SUI 10000, X12). B, single carina (SC),
transverse section through a midline of Paraconularia crustula (White)
(Pennsylvanian, midcontinental USA; UMPF 10000, X100).

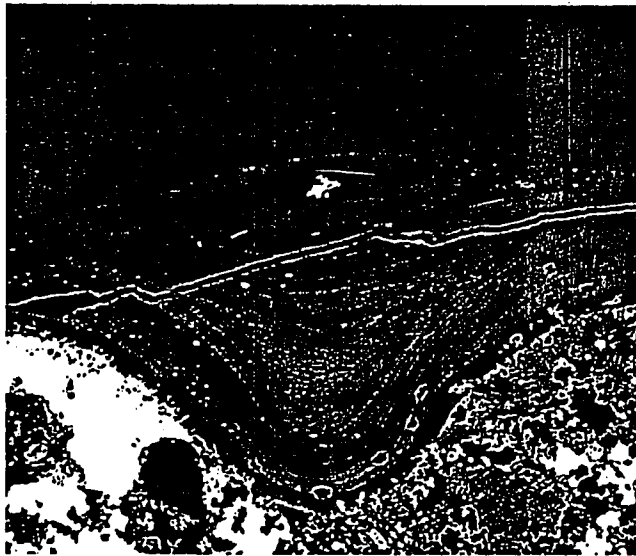


Figure 4C-D. Grooved midline with seriated carina (GSC). C, interior view of part of a midline of A. membranacea Sinclair, showing a series of low, carinate ridges (small arrows) along the crest of the groove (Silurian, New York; EMS E10791, X40); D, portion of another midline of the same specimen, showing parts of two ridges (arrows) (X40).

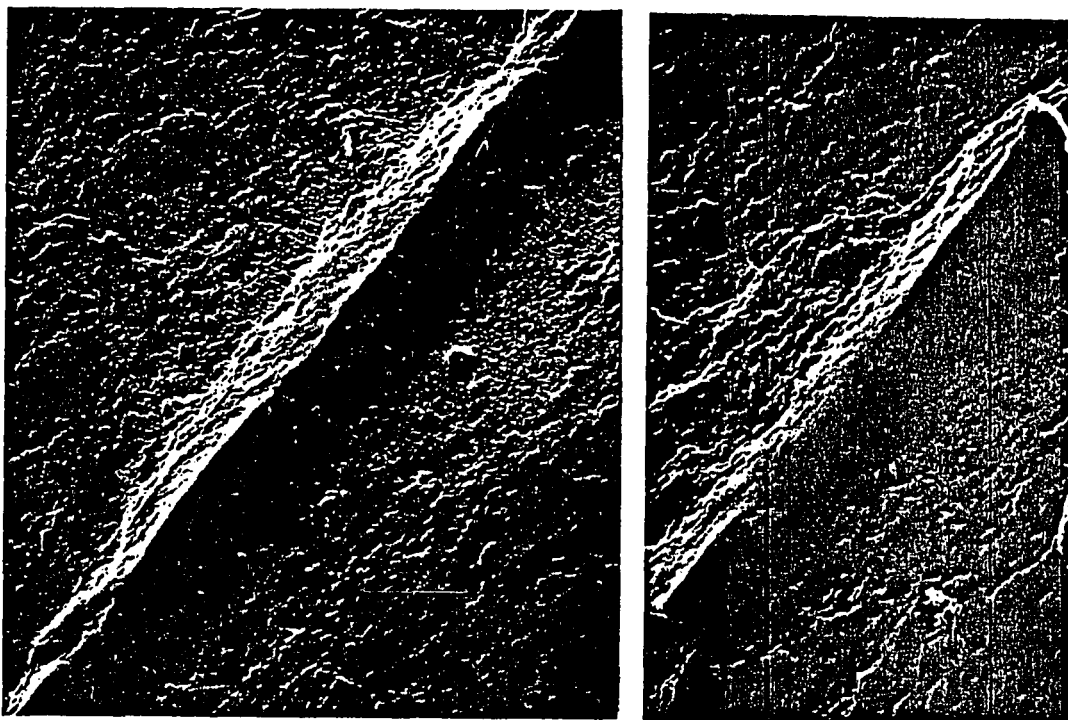


Figure 4E-F. Paired carinae (PC). E, exterior view of a face of Metaconularia manni (Roy) (Silurian, Illinois; FMNH PE 6255, X6); F, inner surface of part of a midline of Metaconularia sp. (Middle Ordovician, Iowa; SUI 10000, X 30).

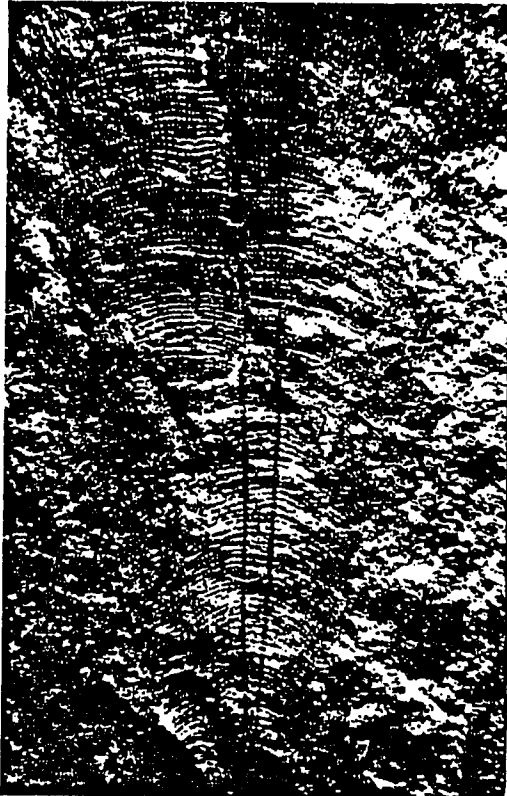


Figure 4G. Paired carinae (PC). Exterior view of part of a midline of the holotype of Conularina narrawayi Sinclair, showing fragments (arrows) of paired carinae (Middle Ordovician, Quebec; ROM 18905, X30).

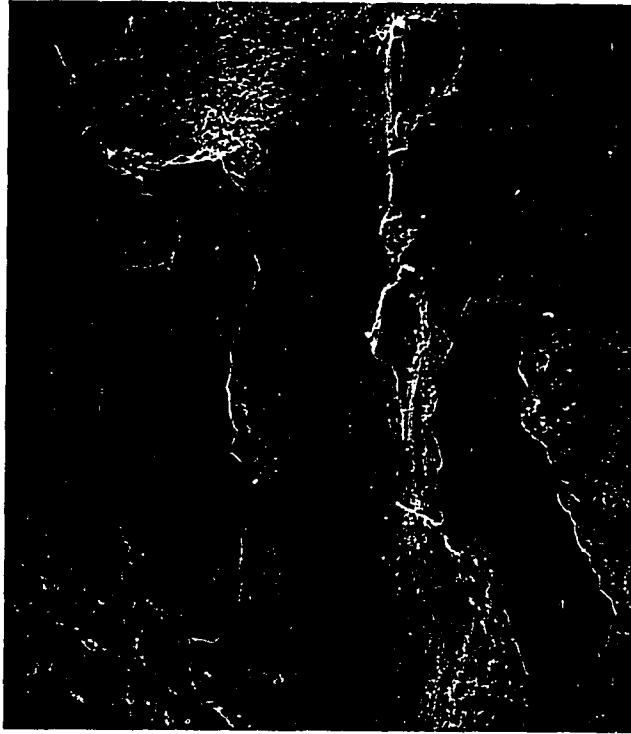


Figure 4H-I. Low carina, longitudinally bifid (LBC). H, inner surface of part of a midline of Conularia splendida Billings (Late Ordovician, Iowa; UW-EM 10000, X6); I, detail of the adapical end of the same midline (X50).



Figure 4J-K. Paired thickenings (PT). J, inner surface of part of a midline of Comularina triangulata (Raymond) (Middle Ordovician, Quebec; SUI 10000, X30); K, transverse section through a midline of another specimen of the same species (SUI 10000, X50).

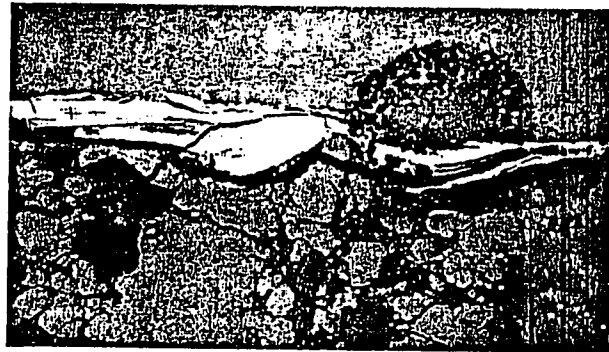


Figure 4L-N. Paired seriated carinae (PSC). L, inner surface of part of a midline of an undetermined species of Climacoconus (Middle Ordovician, Minnesota; GSC 10000, X30); M, morphology of one of the midline ridges in another Climacoconus specimen, apparently from the same locality (Middle Ordovician, Minnesota; GSC 10000, X50); N, adapical end of another specimen, showing the presence at the midline of a single carina (Middle Ordovician, Minnesota; GSC 10000, X40).



Figure 5. Camera lucida drawings of transverse sections through conulariids possessing internal structures at both the corners (C) and the midlines (M) (scale bars = 1 mm). A, Archaeoconularia fecunda (Barrande) (modified from Boucek 1939, figure 2a); B, Eoconularia amoena Sinclair (GSC 1753); C, Paraconularia crustula (White) (UMMP 10000); D, ?Ctenoconularia sp. (modified from Moore and Harrington 1956a, figure 26a); E, Conularina narrawayi Sinclair (ROM 18905); Eoconularia amoena Sinclair (ROM 23297); F, Conularina triangulata (Raymond) (SUI 10000); G, Climacoconus sp. (SUI 10000).

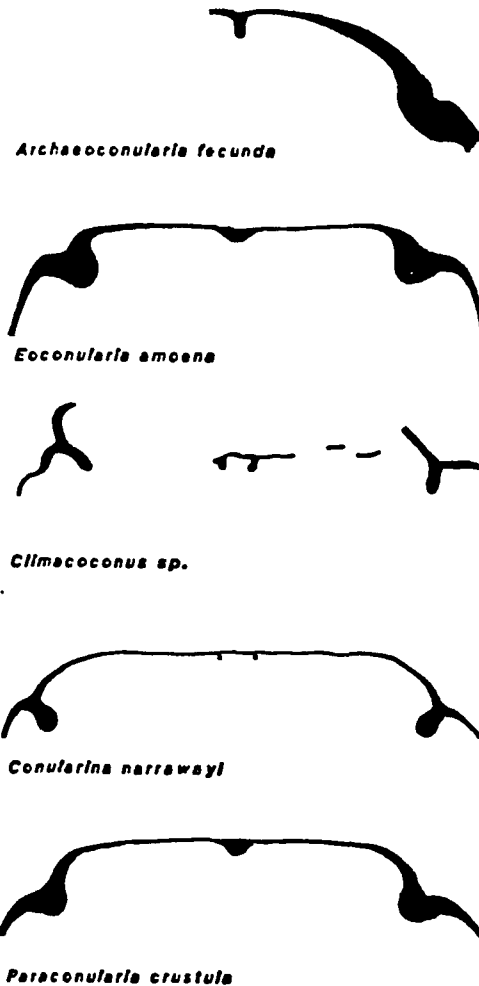


Figure 6. Line drawing of a transverse section through a fragment of a Paraconularia-like conulariid with a high midline carina covered by small pustules (Borenore Limestone (Silurian), New South Wales, Australia; drawing modified from Bischoff (1978), Text-figure 15; X6).



Figure 7. Wiman's (1896) line drawings of three transverse serial sections through a specimen of *Coconularia loculata* (Wiman), showing (A) the presence at each of the four midlines of a high, adaxially bifid longitudinal carina, and (B) inflection and thickening of inner test lamellae at the base of one of the carinae.

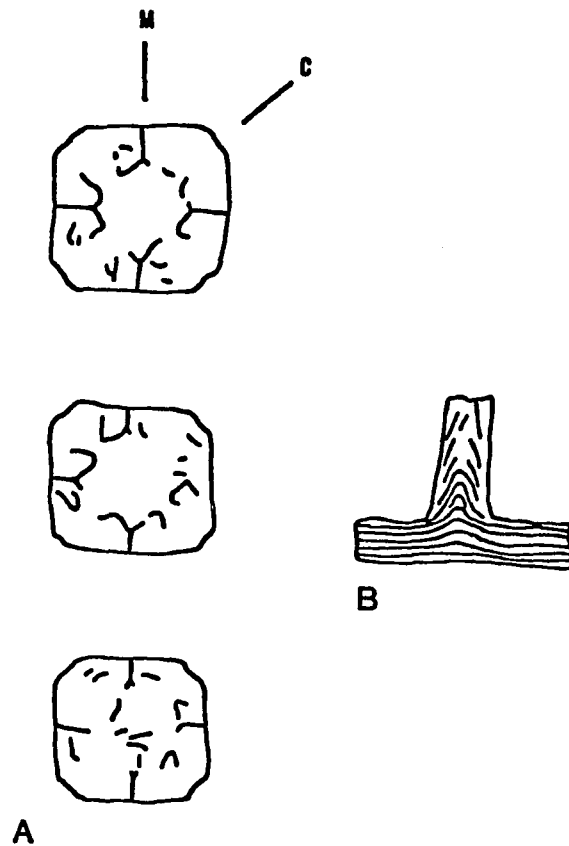


Figure 8. Diagrammatic transverse cross section through Craterolophus, a polypoid scyphozoan of the Order Stauromedusae. Numbers refer to the following anatomical features: (1) septum, (2) central stomach, (3) gastric pouch, (4) claustrum, (5) phacellae, (6) peristomial funnel, (7) gonads, (8) retractor muscle. Letters I and P stand for interradius and perradius, respectively.

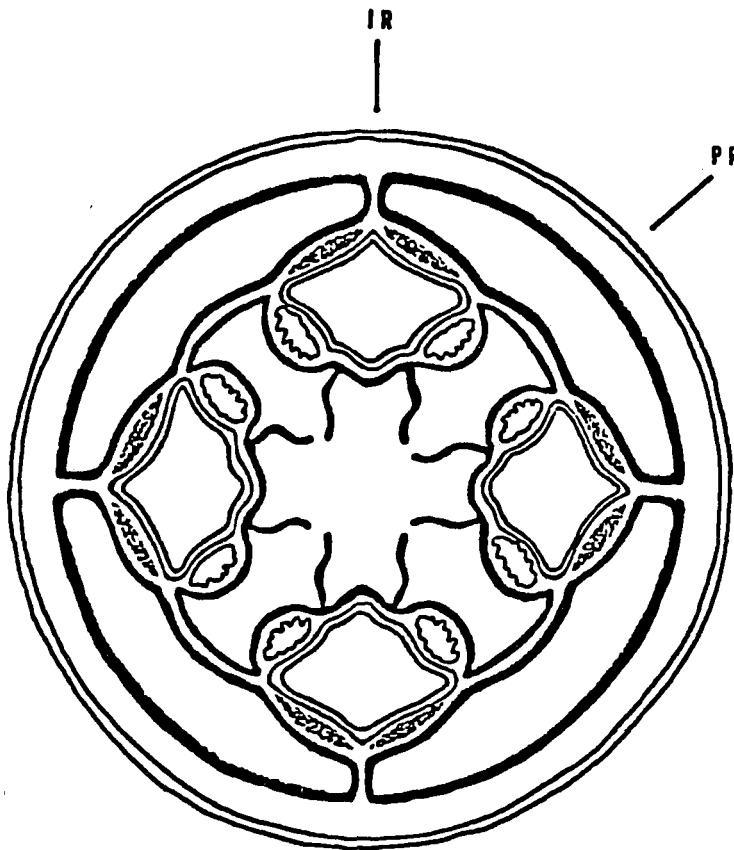


Figure 9. Diagrammatic line drawings of seriated internal projections at the perradii (P) and interradii (I) of the periderm of coronatid scyphozoans (drawings modified from Werner 1967, figure 6b). A, transverse section through a single whorl; B, side view of parts of one perradial and two interradial files.

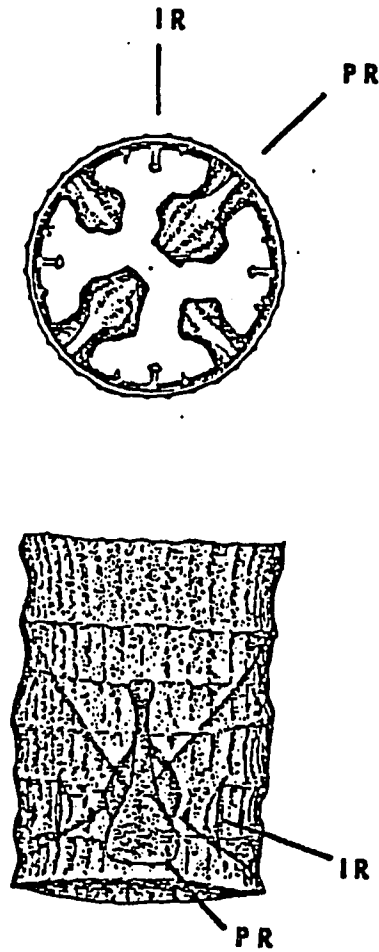
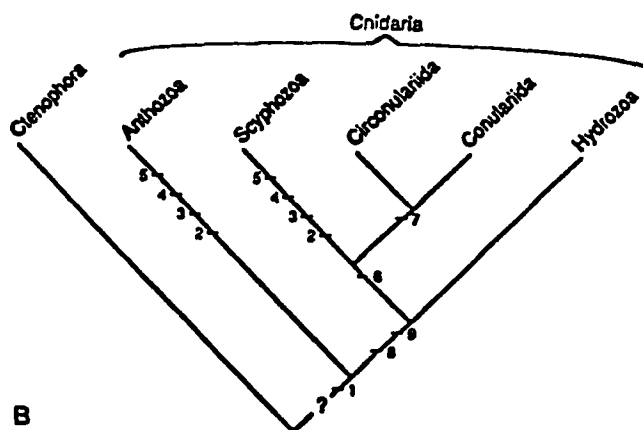
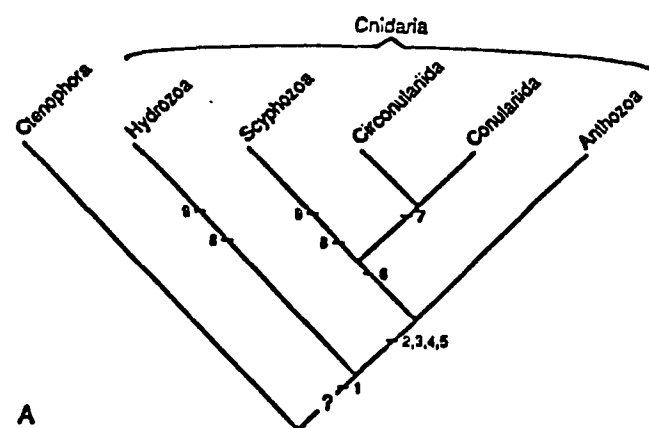


Figure 10. Cladograms summarizing rival alternative interpretations of phylogenetic relationships between major taxa within Cnidaria. A, cladogram hypothesizing monophyly of septate cnidarians; B, cladogram hypothesizing monophyly of the group containing Hydrozoa and Scyphozoa (the two cnidarian classes known to exhibit alternation of generations). Putative synapomorphies discussed in the text are as follows: (1) presence of nematocysts, (2) mesoglea containing cells, (3) sex cells originating in the entoderm, (4) nematocysts present in the entoderm, (5) enteron septate, (6) enteron with four septa, (7) body with an astatic periderm, (8) presence of eurytele nematocysts, (9) alternation of generations. The relationship between Cnidaria and Ctenophora here suggested is problematic, and the reader should refer to the text for discussion of interpretation of character state polarities.



CHAPTER 4

EVOLUTIONARY AFFINITIES OF CONULARIIDS

Abstract

The hypothesis that conulariids were closely related to scyphozoan cnidarians, once widely regarded as the most likely interpretation of conulariid affinities, has recently come under attack. However, most challenges to this hypothesis have been refuted by results of subsequent, more detailed microstructural and gross anatomical analyses (e.g., Bischoff, 1978; Van Iten, 1989). This work has shown that steeply pyramidal, generally four-sided conulariid tests shows numerous similarities to scyphozoan periderm and soft parts. These similarities, nearly all of them uniquely shared by conulariids and scyphozoans, constitute evidence that conulariids were a group of septate cnidarians most closely related to scyphozoans.

Based on analysis of relic conulariid soft parts, Steul (1984) and Babcock and Feldmann (1986) have recently claimed that conulariids could not have been cnidarians. As argued in the present contribution, however, relic soft parts documented by Steul (1984) in specimens of Conularia from the Hunsruck Slate (Middle Devonian, West Germany), and similar relics in the holotype of Eoconularia amoena (Sinclair), show evidence of homology to soft parts of scyphozoan polyps undergoing

polydisc strobilation, a mode of medusa formation previously known only in certain extant scyphozoans.

Introduction

Previous comparisons of conulariids and scyphozoan cnidarians have revealed intriguing similarities in gross morphology, test microstructure and growth, and mode of life and life history (Kiderlen, 1937; Moore and Harrington, 1956a; Werner, 1966, 1967a; Bischoff, 1978; Van Iten, 1987a,b, 1988, 1989). These similarities have been interpreted as evidence that conulariids were scyphozoans (Kiderlen, 1937; Moore and Harrington, 1956a; Werner, 1966, 1967a; Bischoff, 1978) or that they were more closely related to scyphozoans than to any other currently recognized taxon of comparable rank (Glaessner, 1971; Van Iten, 1989). Recently, these interpretations of conulariid affinities have been rejected by several authors (Kozłowski, 1968; Oliver, 1984; Steul, 1984; Mortin, 1985; Feldmann and Babcock, 1986; Babcock and Feldmann, 1986a,b). With the exception of Steul (1984), none of these authors has interpreted conulariids as members or close relatives of a non-scyphozoan group. All have claimed that similarities thought to indicate a close relationship between conulariids and scyphozoans are superficial, and/or that conulariids and scyphozoans are characterized by fundamental dissimilarities.

The present contribution seeks to evaluate these conflicting interpretations of conulariid affinities by addressing three critical areas of disagreement. Two of these concern the interpretation of the anatomy of the steeply pyramidal, generally four-sided conulariid test.

Based on analyses of the gross anatomy, microstructure, and mode of growth and injury repair of this test, proponents of a scyphozoan affinity for conulariids have proposed (1) that the midline of each of the test's sides (faces) was the site of a gastric mesentery, or septum, homologous to gastric septa of extant scyphozoans (Kiderlen, 1937; Chapman, 1966; Werner, 1966, 1967a; Bischoff, 1978; Van Iten, 1989); and (2) that the conulariid test is a mineralized, ectodermally secreted periderm, homologous to the periderm of polypoid scyphozoans of the Order Coronatida (Werner, 1966, 1967a). Opponents of these interpretations have claimed that similarities thought to corroborate the first hypothesis of homology are superficial or based on misidentification of features present in the test cavity of certain conulariids (Kozłowski, 1968; Oliver, 1984; Babcock and Feldmann, 1986a,b), and that the second hypothesis of homology is precluded by fundamental dissimilarities in test (peridermal) microstructure (Kozłowski, 1968; Feldmann and Babcock, 1986). As will be discussed below, these claims have been refuted by results of subsequent anatomical and microstructural analyses (e.g., Bischoff, 1978; Van Iten, 1988, 1989). The third area of disagreement centers on the interpretation of putative relics of conulariid soft parts. Such features have recently been documented by Steul (1984) and Babcock and Feldmann (1986a), who claim that they exhibit a higher level of anatomical organization than that shown by soft parts of scyphozoans or other cnidarians. As will be argued in this paper, comparison of Steul's (1984) relics with scyphozoan soft parts, and analysis of a possible additional occurrence of relic conulariid soft parts, discovered by the present author and documented here, suggest that

features reported by Steul (1984) can be homologized with soft parts of scyphozoans.

Homology of conulariid corners and midlines

Anatomical Background

Scyphozoans. Proponents of a scyphozoan affinity for conulariids have placed particular emphasis on similarities between conulariid corners and midlines and soft-part and peridermal structures located at the scyphozoan perradii and interradii. Except in medusae of the Orders Rhizostomatida and Semaestomatida, the digestive cavity (enteron) of all scyphozoans is subdivided by radially disposed, entodermal septa (Hyman, 1940). Usually there are four such structures, but certain rare species produce six septa, and aberrant individuals of species that normally exhibit four septa are known to produce three, five, or six septa (Hyman, 1940). Where four septa are present, the septa define two mutually perpendicular planes of symmetry, called the interradii. The angles formed by the interradii are bisected by two additional symmetry planes, the perradii, which intersect the corners of the rectangular mouth. Each septum is penetrated adorally by a deep, ectoderm-lined, funnel-shaped invagination, the peristomial funnel, that causes the septum to bulge laterally. In some members of the Order Stauromedusida, each of the two sides of the septum exhibits a sheet-like longitudinal outgrowth, called a claustrum, that is fused along most of its length with a claustrum of the laterally adjacent septum. In all taxa, the septum's

free or adaxial edge exhibits two longitudinal rows, or phacellae, of nematocyst-laden gastric filaments. Nearer the septum's fixed, or abaxial edge is a pair of longitudinal gonads, situated within the mesoglea or along the septum's sides. Below the gonads, the septum exhibits a longitudinal, ectodermally derived retractor muscle. In most scyphozoans, this muscle consists of a single tissue bundle; however, in the stauromedusans Craterolophus and Lucernaria, the septal muscle is adorally bifurcate (Antipa, 1892; Gross, 1900). In Lucernaria, the paired bundles originate near the polyp's oral end and diverge at about 20 degrees; in Craterolophus, they originate nearer the basal end, at the apex of the peristomial funnel, and diverge at about 1 to 2 degrees.

Polyps of the Order Coronatida are sheathed in a chitinous, steeply conical periderm that in some species exhibits internal projections at the interradii and perradii (Werner, 1966, 1967a,b, 1970, 1974, 1979, 1983; Chapman and Werner, 1972). The periderm itself is built of numerous, extremely thin (12 nanometers) lamellae that are grouped in two layers. In species exhibiting internal peridermal structures, lamellae of the inner layer are locally invaginated at the perradii and interradii, forming eight longitudinal series of tooth- or thorn-like projections. These projections are also arranged in whorls or circlets, with each circlet consisting of a set of four perradial and four interradiial projections. In all cases, projections at the perradii are larger (longer, wider, higher) than projections at the interradii, extending in some cases nearly all the way to the body's longitudinal axis. In most species, both sets of projections are smooth; in other species, however, the perradial projections exhibit

small pustules.

Conulariids. Conulariids are characterized by an apatitic, finely lamellar, steeply pyramidal test that usually exhibits four sides, or faces. Some conulariids exhibit only three faces (Sinclair, 1942, 1948; Van Iten, 1989), and Babcock et al. (1987) have documented a specimen exhibiting six faces. As seen in transverse section, non-distorted, four-sided tests may be trapezoidal, square, or rectangular. The corners of the test are usually furrowed by a longitudinal groove, and the midline of each of the faces may also be grooved, or it may be marked by a narrow longitudinal ridge or fold. The test is built of extremely thin (1-5 microns), alternately dense and vacuity-rich lamellae that are concordant with its inner and outer surface (Van Iten, 1987a, 1989). In many conulariids, the test's innermost lamellae are inflected and thickened at the corners and/or midlines, producing a longitudinal structure that projects into the test cavity.

As indicated by observations from several previous studies (e.g., Wiman 1895; Boucek, 1939; Sinclair, 1940, 1942, 1948; Bischoff, 1978; Babcock et al., 1987; Babcock, 1988; Van Iten, 1988, 1989), corners of some or all species of at least six conulariid genera - Archaeoconularia Boucek (= Exoconularia Sinclair), Climacoconus Sinclair, Conularina Sinclair, Eoconularia Sinclair, Glyptoconularia Sinclair, and Paraconularia Sinclair - exhibit a smooth, broadly rounded or keel-like carina. In some taxa (e.g., species of Climacoconus), this carina projects up to one-tenth of the way to the opposite corner. Corner carinae are usually continuous structures, but in some Climacoconus they are seriated (Van Iten, 1989).

A substantially more varied array of internal structures

occurs at conulariid midlines. Among the structures documented thus far are: (1) a low, smooth, broadly rounded or keel-like carina (present in some species of Archaeoconularia, Climacoconus, Conularia, and Paraconularia; Boucek, 1939; Sinclair, 1948; Babcock et al., 1987; Babcock, 1988; Van Iten, 1989); (2) a pair of carinae, with members of each pair situated on opposite sides of the midline proper and gradually diverging toward the aperture (present in Metaconularia and Conularina narrawayi Sinclair; Sinclair, 1940, 1948; Van Iten, 1989); (3) a pair of broad, very low thickenings, likewise with members of each pair situated on opposite sides of the midline proper and gradually diverging toward the aperture (present in other North American species of Conularina; Van Iten, 1989); (4) a low carina that is adaxially bifid (present in Conularia splendida Billings; Van Iten, 1989); (5) a high, adaxially bifid carina exhibiting a more or less Y-shaped transverse cross section (present in Eoconularia loculata (Wiman); Wiman, 1895); (6) a high, non-bifid carina that projects about one-third of the way to the opposite midline and is covered by small pustules (present in specimens of Paraconularia? sp. from the Devonian of Australia; Bischoff, 1978); (7) a series of low, narrow, elongate ridges running along the midline proper (present in Archaeoconularia membranacea (Ringueberg); Van Iten, 1989); and (8) paired series of short, closely spaced, I-shaped ridges, with members of each pair of series situated on opposite sides of the midline proper and gradually diverging toward the aperture (present in certain species of Climacoconus; Van Iten, 1989). Certain species of Archaeoconularia, Climacoconus, Conularina, Eoconularia, and Paraconularia exhibit internal structures both at the corners and the midlines (Van Iten,

1989). Almost without exception, internal structures at the corners are higher and/or wider than internal structures at the midlines. In Climacoconus, where seriation of internal structures has been observed both at corners and midlines, ridges in observed corner series are several times longer and two to three times higher than ridges in observed midline series (Van Iten, 1989).

Recently, the existence of high, adaxially bifid midline carinae in Euconularia loculata has been questioned (Babcock and Feldmann, 1986a,b), due in part to the fact that identical structures have not been found in other conulariids. Unfortunately, the two E. loculata specimens figured by Wiman (1895) have been lost or misplaced (Babcock and Feldmann, 1986a). However, it is clear from his line drawings of transverse sections through one of these specimens, shown here in Figure 1, that this specimen, at least, did possess high, adaxially bifid internal carinae. For example, as shown in a detail of one of these sections (Figure 1B), the four Y-shaped features depicted at the midlines are built of thickened, inwardly deflected lamellae that continue into the faces. Since this is exactly what one sees in carinae of other conulariids, there seems to be little question but that the Y-shaped features are bifid carinae. This conclusion is further supported by the observation, noted above, that longitudinal bifurcation characterizes the low carina seen at midlines of Conularia splendida (Billings) (Figure 2). Accentuation of growth processes leading to the formation of these carinae could easily have led to the formation of higher, more strongly bifid carinae like those in E. loculata.

Comparisons of conulariids and scyphozoans

As is evident from the foregoing characterizations, conulariid corners and midlines exhibit a number of similarities to soft parts and peridermal structures located at scyphozoan perradii and interradii. Many of these similarities were discovered subsequent to publication of papers rejecting a scyphozoan affinity for conulariids, and nearly all of them are uniquely shared by conulariids and scyphozoans. As originally formulated (Kiderlen, 1937), the hypothesis that conulariid midlines were sites of gastric septa, homologous to scyphozoan septa, was based in large part on comparisons of high, adaxially bifid midline carinae of Coconularia loculata (Wiman) and claustra-bearing septa of stauromedusans such as Craterolophus. Both sets of structures are identical in number and arrangement, and show resemblances in size (both absolute and relative to the body, or test, cavity) and cross sectional form. Coupled with evidence indicating that the conulariid test was secreted by soft tissues lining the test's inner surface (Bischoff, 1978; Van Iten, 1989; see also the following major section), these gross anatomical similarities suggest that each of E. loculata's four carinae was covered in life by a large, distally expanded gastric septum.

This interpretation is further supported by similarities between stauromedusans and other conulariids. As noted above, stauromedusan retractor muscles, situated near the base of each septum, consist either of a single strand, or are adorally bifurcate. Similarly, midlines of many conulariids exhibit either a single carina, or a pair of carinae, similar in spacing and angle of divergence to paired

retractor muscle strands of Craterolophus. Given that the conulariid test, like scyphozoan retractor muscles, was derived from ectoderm (Bischoff, 1978; Van Iten, 1989), these similarities suggest that conulariids, like stauromedusans, possessed interradial retractor muscles that could be either single or paired.

Additional support for these interpretations is provided by similarities between internal structures at conulariid corners and midlines and internal peridermal structures at the perradii and interradia of coronatid scyphozoans. Both sets of structures represent localized inflexions of inner test (peridermal) lamellae and may be smooth or covered by small pustules. Just as coronatid perradial projections are consistently larger (higher, broader, longer) than projections at the interradia, in those conulariids whose corners and midlines are both thickened, it is nearly always the case that the corners, interpreted as perradial in position, are more strongly thickened than the midlines (Van Iten, 1989). Although internal corner and midline thickenings of conulariids are generally continuous, not seriated, internal structures at midlines of Archaeoconularia membranacea (Ringueberg), and at corners and/or midlines of some Climacoconus, are seriated. Like the perradial projections of coronatids, individual segments of seriated Climacoconus corner structures are several times longer and higher than segments of seriated midline structures. Taken together, these similarities suggest that internal structures at conulariid corners and midlines and internal structures at the perradii and interradia of the coronatid periderm may be mutually homologous. This hypothesis was originally proposed by Werner (1966, 1967a), on the basis of a smaller set of

similarities than that outlined here, but was subsequently questioned by Bischoff (1978). Even if we do not accept Werner's (1966, 1967a) interpretation of homology (i.e., if we allow that the most recent common ancestor of conulariids and coronatid scyphozoans lacked internal test (peridermal) structures), the fact that the similarities just outlined are uniquely shared by conulariids and coronatid scyphozoans (Van Iten, 1989) reinforces the contention that conulariids and scyphozoans in general were characterized by fundamental similarities in soft tissue anatomy.

Finally, just as some conulariids exhibit three or six corners, and not four, some scyphozoans exhibit hexamerous symmetry, and aberrant specimens of tetramerous species may be hexamerous, pentamerous, or trimerous. The only other metazoans resembling conulariids and known to exhibit this array of alternate symmetries are hydrozoan cnidarians (which, for example, show variation in the number of primary branches of the medusa's radial canal system; Hyman, 1940; Werner, 1973).

In sum, the hypothesis that conulariid midlines were sites of gastric septa, homologous to the gastric septa of scyphozoan cnidarians, is supported by a number of similarities, most of them uniquely shared by conulariids and scyphozoans (Van Iten, 1989). In view of the complexity of the features being compared here, it is unlikely that these similarities are due to chance or to independent derivation of similar solutions to shared functional problems. For these reasons, the interpretation of conulariid/scyphozoan similarities favored here is that conulariids possessed gastric septa, homologous to those of scyphozoans.

Homology of the conulariid test

Background

Coronatid scyphozoans. As noted in the introduction, similarities between the conulariid test and the periderm of coronatid scyphozoans have also been interpreted as evidence that these structures are themselves homologous (Werner, 1966, 1967a). Additional aspects of the anatomy and growth of the coronatid periderm have been discussed by Werner (1966, 1967a,b, 1970, 1974, 1979, 1983) and Chapman and Werner (1972). Briefly, the periderm is steeply conical and possesses a small, disc-like holdfast, floored by a basal membrane and attached in life to rocks or other hard substrates. The periderm's numerous, parallel lamellae are arranged in two layers: a thin, outer layer that is crossed by fine, closely spaced transverse and longitudinal corrugations, and a thicker, non-corrugated, inner layer. The outer, corrugated layer ranges from about 2 to 4 microns thick and is produced by secretion along the apertural margin. The inner layer, locally almost 20 microns thick, is secreted by ectoderm of the body wall and is produced by addition of lamellae to the inner test surface. Holes in the periderm, produced by puncturing or by truncation a short distance above the apex, are repaired by secretion of a thin sheet of non-ornamented, inner-layer lamellae.

Conulariids. The steeply pyramidal, finely lamellar conulariid test is apatitic and usually exhibits four faces. In nearly all conulariids, the faces are crossed by closely spaced, aperturally arching transverse ridges (transverse ribs), or they are covered by

minute, closely spaced tubercles, arranged in transverse rows and longitudinal files. As seen in longitudinal section, conulariid tests are thicker at transverse ribs and tubercles than at sites between these features. This is due to localized thickening of individual lamellae (Van Iten, 1989; see also below). The margin of the test aperture may be simple, or each of the faces may project beyond the ends of the corners, forming a broadly rounded extension traditionally referred to as a lappet (Moore and Harrington, 1956a,b). The apex, attached in life to shell material (including tests of other conulariids) or directly to the substratum (Van Iten, 1989), terminates in a minute, circular, collar-like feature that probably served as a holdfast (Kozlowski, 1968).

As noted above in connection with internal structures at the corners and midlines, the test is built of numerous, very thin lamellae, alternatively dense and vacuity-rich, that are concordant with its inner and outer surfaces. Growth of the test involved two distinct modes: accretion of lamellae to the test's inner surface, perpendicular to lamellar boundaries; and secretion along the apertural margin, possibly involving an outer set of non-mineralized lamellae (Van Iten, 1989). Holes in the side of the test or truncation of its apical end were repaired by production of a thin sheet of non-ornamented test material laid down on the test's inner surface (Werner, 1966, 1967a; Bischoff, 1978; Babcock et al., 1987a; Van Iten, 1989). Damage repair by material laid down on the test's exterior surface has not been observed, indicating that the test was most likely an external skeleton (Van Iten, 1989).

Discussion

Opponents of the hypothesis that the conulariid test and the coronatid periderm are homologous structures have offered various reasons in defense of their opinion, including the fact that unlike the steeply conical, non-mineralized coronatid periderm, the conulariid test is mineralized and generally more or less quadrangular in cross section (Termier and Termier, 1949, 1953; Kozlowski, 1968; Scrutton, 1979). Other objections that have been put forth include the following two claims: (1) that the conulariid test was secreted internally, not externally as is the case in scyphozoans (Kozlowski, 1968); and (2) that thickening of the conulariid test at transverse ribs reflects the existence of a series of discrete, transverse internal rods, features unique to conulariids and with no homologue in extant groups (Feldmann and Babcock, 1986). The first of these claims, that the conulariid test was secreted internally, is based on the claim that conulariid tubercles are perforate structures that, in life, housed a special sense organ (Kozlowski, 1968). However, as demonstrated by Bischoff (1978), putative tubercle pores are artifacts of tubercle breakage; sections through tubercles show that they are solid. Moreover, as noted above, holes in the conulariid test were covered by material laid down on the test's inner surface, but they were never covered by material laid down on the outer surface, as might be expected were the test an internal skeleton.

The second claim, that thickening of the test at transverse ribs is due to the presence of a series of discrete, transverse internal rods, has been refuted by results of SEM analysis of polished sections

through transversely corrugated conulariids (Van Iten, 1989). This work shows that thickening at transverse ribs is not due to the presence of internal rods, but to localized thickening of individual lamellae (Figure 3). To be sure, test material within and immediately below transverse ribs is often more strongly mineralized than adjacent regions of the test, and the distinction between individual lamellae is obscured (Van Iten, 1989); nevertheless, lamellae can still be traced through the ribs, indicating that they are part of a single, continuously laminated structure.

The conulariid test and the coronatid periderm exhibit similarities in gross anatomy, microstructure, and mode of growth and damage repair. Some of these similarities, for example the presence of seriated inflections of the innermost lamellae, are uniquely shared by conulariids and coronates. The fact that the conulariid test differs from the coronatid periderm in being mineralized and generally quadrangular in cross section, while indicating that conulariids may not have been coronatids, is interpretable as a significant but not fundamental variation on the pattern of anatomical organization shown by scyphozoans. To be sure, the absence of a periderm in polyps of many non-coronatid scyphozoans raises the possibility that the most recent common ancestor of conulariids and coronatids was naked. Clearly, it would be desirable to test this possibility in the context of a phylogenetic analysis of conulariids and all of their putative scyphozoan relatives (together with one or more outgroups), using both hard- and soft-part characters.

Relic conulariid soft parts

Background

Previous discoveries. Possible relics of conulariid soft parts have previously been documented by Steul (1984) and Babcock and Feldmann (1986a,b). Steul (1984), using x-radiography to examine pyritized specimens of Conularia from the Hunsrueck Slate (Middle Devonian, West Germany), discovered various types of dense, localized, more or less regular aggregations of pyritic material inside the test cavity. One of the features documented by Steul (1984), in at least four specimens, consists of a slender, elongate band of segment-like aggregations, apparently more or less coincident with the test's longitudinal axis. This feature, called the axial element (Steul, 1984), is associated near the aperture with a band of pyritic material that extends across the test cavity, at right angles to the axial element. Interestingly, Steul (1984) concludes that the Hunsrueck specimens show no evidence of circumoral tentacles, featured in reconstructions of the conulariid organism made by Kiderlen (1937).

Steul (1984) interprets the axial element as remains of an internal skeleton, with components homologous to the spinal muscles, vertebrae, and notochord of vertebrates; she interprets the transverse band of pyritic material at the axial element's adapertural end as relics of a pair of eyes. Although these interpretations have been challenged by Babcock and Feldmann (1986b; see also below), the fact that the features in question occur in several specimens, at the same site within the test cavity, suggests that, whatever their homology,

they are relics of original anatomical structures.

Babcock and Feldmann (1986b, p. 365), examining two specimens of Paraconularia subulata (Hall) (Early Mississippian, USA) preserved in fine grained, phosphatic concretions, have illustrated what they describe as a "single elongate tube that extends the length of the central cavity and a large globular structure near the aperture." In their opinion (Babcock and Feldmann, 1986b), the elongate tube corresponds to Steul's (1984) axial element. In contrast to Steul (1984), however, Babcock and Feldmann (1986b) interpret the axial element as a relic intestine or alimentary tract.

Additional material. Inspection of the holotype and only known specimen of Eoconularia amoena Sinclair, a conulariid from the Trenton Group (Middle Ordovician) of Quebec, Canada (Sinclair, 1944, 1948), revealed the presence of a small, circular feature located in a position corresponding to that of Steul's (1984) axial element (Figure 4). This feature, here designated the circular feature, is situated at the approximate center of the specimen's broken apical end, about 2 centimeters above the former apex. The surface on which the circular feature occurs is planar and is oriented approximately perpendicular to the specimens's long axis. The circular feature is about 0.25 millimeters in diameter and is preserved in a dark gray, micritic matrix. It consists mostly of extremely fine grained (less than one micron) micrite that shows a lamellar fabric (Figures 4B,D), concordant with the circular feature's outer margin, which is strongly scalloped (Figures 4B, D). Disposed about the center of the circular feature are three broadly triangular regions of relatively coarse micrite that shows a centripetal fabric (Figures 4B-D). The circular feature's

scalloped outer margin exhibits 16 broadly rounded lobes, arranged in such a manner that four lobes occur in each of four quadrants defined by planes containing the midlines (Figure 4B, D). The centrally located triangular regions of coarser micrite are separated from one another by two mutually perpendicular, thin bands of extremely fine-grained micrite, and they are more or less bisected by planes defined by the corners (Figure 4A, C).

Although additional work is needed to establish whether or not the circular feature extends along the test cavity's central axis, the geometry and orientation of this feature relative to the corners and midlines suggest that it is not a diagenetic artifact or the remains of some non-conulariid fossil accidentally preserved inside the conulariid. Rather, it appears to be a relic of something originally present in the animal, possibly a transverse section through Steul's (1984) axial element.

Discussion

Steul's (1984) interpretation of the axial element as remains of an internal skeleton, comparable to the vertebral column of vertebrate chordates, is based in part on analysis of a single feature (Steul, 1984, Figure 17) resembling an axial element and that, like vertebrate bone, is characterized by phosphatic mineralization (as demonstrated by x-ray fluorescence). However, Steul (1984) presents no evidence of phosphatic mineralization in any of the other features she interprets as axial elements, and inspection of her photographs of these features (Steul, 1984, Figures 11a, 12a, 14a, 15a, 16a) suggests

that they consist of pyritic material only.

An alternative interpretation of the axial element is suggested by comparisons of this feature with scyphozoan polyps that are undergoing polydisc strobilation, a process of medusa formation characteristic of many scyphozoans and documented in detail by Werner (1966b, 1974) and Werner and Hentschel (1983). During this process, the polyp's septa and tentacles degenerate, and the bulk of its soft body transforms into a slender series of incipient medusae, or ephyrae, stacked like plates one on top of the other. The ephyrae are similar in many respects to adult medusae; in some taxa they are provided with fully developed gonads, which usually appear only after the ephyrae have been liberated from the polyp (Werner, 1973). In strobilating coronatids, the adoral end of the ephyra series is attached to the periderm by means of a narrow, disc-like mass of soft tissue extending at right angles to the polyp's long axis.

Photographs of soft parts of strobilating scyphozoan polyps in Werner (1966a, 1974) and Werner and Hentschel (1983) are similar to photographs of Conularia axial elements in Steul (1984). An example of this is shown here in Figure 5. As is evident from this figure, the axial element could be interpreted as a string of conulariid ephyrae, attached to the inside of the test at its apertural end by means of the narrow band of relic soft tissue interpreted by Steul (1984) as remains of a pair of eyes. This interpretation accounts for the apparent absence of circumoral tentacles in Hunsruck Conularia (Steul, 1984), thought by Steul (1984) and Babcock and Feldmann (1986a,b) to constitute a serious problem for hypotheses of a scyphozoan affinity for conulariids. As noted above, strobilating scyphopolyps lack

tentacles.

Additional evidence of homology with soft parts of strobilating scyphozoans may be provided by the circular feature inside the test cavity of Coconularia amoena Sinclair (Figure 4). This feature, interpreted above as originally belonging to the conulariid, exhibits strong tetrameral symmetry and appears to be situated in the same position as the axial element in Hunsruck Conularia. The geometry of the circular feature is in very poor agreement with transverse sections through the vertebrate notochord and vertebral column (see for example Jollie, 1962), interpreted by Steul (1984) as homologs of the conulariid axial element, and it is also in poor agreement with transverse sections through vertebrate and invertebrate alimentary tracts (see for example Barnes, 1987), interpreted by Babcock and Feldmann's (1986a,b) as possible axial element homologs. The geometry of the circular feature agrees in several respects with the anatomy of scyphozoan ephyrae and medusae, particularly medusae of the Order Samaeostomatida (Figure 6). Together with the occurrence of the circular feature at the center of the conulariid's test cavity, this suggests that the circular feature is a relic of soft part structures homologous to those in scyphozoan ephyrae and medusae. More specifically, the circular feature's scalloped outer margin, with its 16 broadly rounded lobes arranged in four quadrants, could be interpreted as comparable to the lappet-bearing scyphomedusan bell margin. The three broadly triangular regions disposed about the circular feature's center and bisected by planes containing the corners (interpreted by proponents of a scyphozoan affinity for conulariids as perradial in position) could be interpreted as relics of a set of four

gonads (one of which has not been preserved), similar in position to the gonads of sameostome medusae. These interpretations are supported by congruencies in number, geometry, and arrangement between components of the circular feature and structures of scyphozoan ephyrae and medusae (Figure 6).

The interpretation of the circular feature in Eoconularia amoena as a relic conulariid ephyra is further supported by the recent discovery of polyp soft parts preserved as calcite in a specimen of the tabulate coral Favosites from the Jupiter Formation (Lower Silurian) of Anticosti Island, Quebec (Copper, 1985). Many of this specimens's calices contain beautifully preserved relics of the polyps, complete with gut cavity (evidently filled with argillaceous sediment) and circumoral tentacles. How these polyps came to be preserved as calcite is not yet clear (Copper, 1985). Copper (1985, p. 144) suggests that this unusual form of preservation was facilitated by the presence of algal symbionts that "may have initiated precipitation of calcite nuclei or spicules inside the polyp[s]." The mode of preservation of the circular feature in Eoconularia amoena is also unclear. One possibility, casting of a conulariid ephyra by lime mud sediment (and/or cement), is suggested by results of Walcott's (1898) taphonomic experiments on extant scyphozoan medusae. Walcott (1898) demonstrated that the digestive cavity and gonads of Aurelia medusae buried in wet plaster are readily cast, with outstanding preservation of their original three-dimensional geometry. In light of published discussions of the mechanical properties of jellyfish membranes (e.g., Walcott, 1898; Glaessner, 1984), it is conceivable that, shortly after the death of the E. amoena, one or more tears or punctures developed in

the external skin or in the lining of the digestive cavity or gonads of one of its ephyrae, allowing fine sediment to enter the ephyra as its original watery contents leaked out. Admittedly, this and other possible preservational scenarios are in serious need of additional testing. Nevertheless, comparative anatomical evidence suggests that the circular feature in Coconularia amoena is best interpreted as a relic soft part feature, most similar to ephyrae and medusae of scyphozoan cnidarians.

Additional evidence

This paper has not attempted to address all problems in the interpretation of conulariid paleobiology, but rather has focused on those issues that are generally thought to have a particularly critical bearing on the problem of conulariid affinities. Current understanding of other aspects of conulariid paleobiology is consistent with the interpretations of homology advocated above (Werner, 1966, 1967a; Bischoff, 1978; Van Iten, 1987a,b, 1989). As indicated by evidence reported by Ruedemann (1896a,b, 1897), Sinclair (1948), Finks (1955, 1960), Kozlowski (1968), Rooke and Carew (1983), Babcock et al. (1987b), and Van Iten (1989), conulariids were sessile organisms, similar in life orientation and mode of attachment to scyphozoan polyps. Observed size ranges of conulariids (Barrande, 1867; Babcock and Feldmann, 1986b) are comparable to size ranges reported for stauromedusans (Hyman, 1940). Conulariids preserved in fine-grained sediments often occur in monospecific clusters bearing remarkable similarities to colonies of clonally budded polyps (Slater, 1907;

Ruedemann, 1925; Kozłowski, 1968). Finally, the known geologic range of conulariids, from Early Ordovician to Late Triassic (Babcock and Feldmann, 1986b), is well within the range of scyphozoans, which have a fossil record extending as far back as the Vendian (Glaessner, 1984).

The question of relationship

Proponents of hypotheses of homology advocated here interpret conulariids as extinct members of the Phylum Cnidaria. Relationships among extant cnidarians have been subject to conflicting interpretations (e.g., Hyman, 1940; Hand, 1959; Hadzi, 1963; Werner, 1973; Grasshoff, 1984), and at present there appears to be no consensus on this problem. However, cladistic analysis of relationships among conulariids and the extant cnidarians classes (Van Iken, 1989) suggests that conulariids and scyphozoans are more closely related to each other than either group is to anthozoans or hydrozoans, and that together they and anthozoans form a monophyletic taxon within Cnidaria that excludes hydrozoans. This interpretation of relationships, along with shared character states thought to support it, is shown in the cladogram in Figure 7.

Acknowledgements

The author wishes to thank Simon Conway Morris (Cambridge University, Cambridge, England) and Alberto M. Simonetta (University of Camerino, Camerino, Italy) for inviting him to participate in the Camerino Symposium on problematic fossil taxa and the origins of

Metazoa. The author also thanks his colleagues in the Museum of Paleontology, University of Michigan, for helpful discussions of his work on conulariid biology and affinities. Much of the monetary support for this work was provided by funds from NSF Research Grant ENS 8521097 to Daniel C. Fisher (Museum of Paleontology, The University of Michigan, Ann Arbor), the author's senior advisor. Preparation of illustrations for the paper was done with the assistance of the author's wife, Tatiana Van Iten. Finally, the author is grateful to David Rudkin (Royal Ontario Museum, Toronto) for permission to examine the holotype of Euconularia amoena (Sinclair).

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Figure 1. Winan's (1896) line drawings of three transverse serial sections through a specimen of *Euconularia loculata* (Winan), showing the presence at each of the midlines of a high, strongly bifid internal carina (A), and details of the organization of test lamellae in the base of one of the carinae (B).

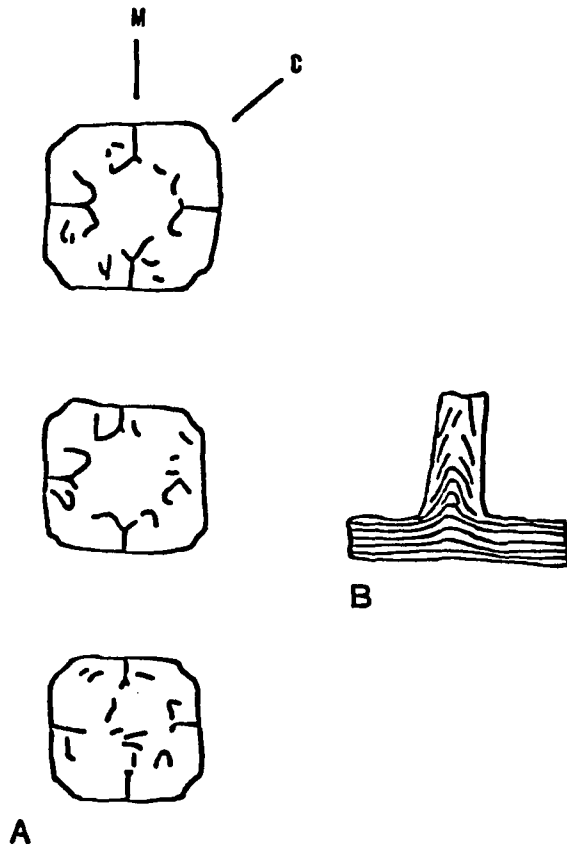


Figure 2. Conularia splendida Billings. SEM photomicrograph of a portion of the interior of one midline, showing the presence there of a low, longitudinally bifid carina, similar to the high bifid carina seen at midlines of E. loculata (scale bar = 100 microns). The specimen is repositied in collections of the Burke Museum, University of Washington, Seattle (BM-UW 1155).



Figure 3. *Paraconularia* sp. SEM photomicrograph (backscattered electron mode) of a polished longitudinal section through a thickened transverse rib, showing accentuated mineralization in the core of the rib (scale bar = 10 microns). Note that in spite of accentuated mineralization of the rib core, lamellae on either side of this region can be traced through it. The thin section of this specimen is deposited in collections of the University of Michigan, Ann Arbor (UMMP 1000).



Figure 4A-B. SEM photomicrographs of probable relic soft parts in the test cavity of *Eoconularia amoena* (Sinclair). A, photomicrograph of the specimen's broken apical end, showing the central location (arrow) of the circular feature (X30); B, close-up of the circular feature, showing its scalloped outer margin and the three broadly triangular regions surrounding its center (X250).

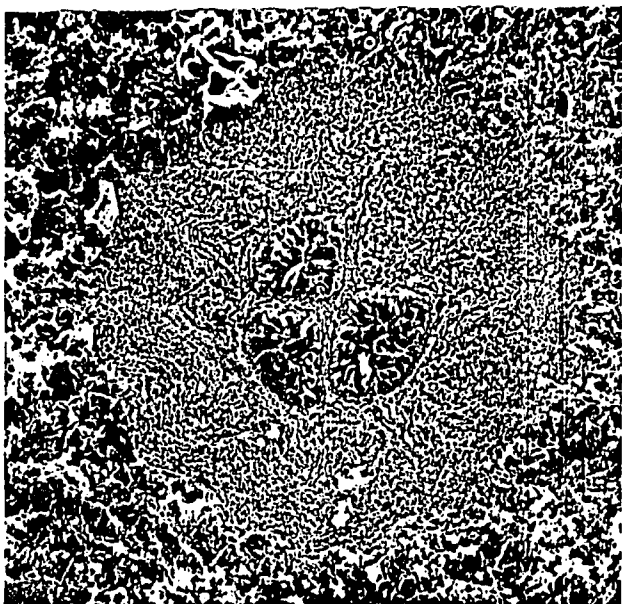


Figure 4C-D. Close-ups of specific parts of the circular feature in *E. amoena*. C, the centrally located, triangular regions of coarse micrite (X700); D, the circular feature's southwest quadrant, showing four marginal lobes (X600).

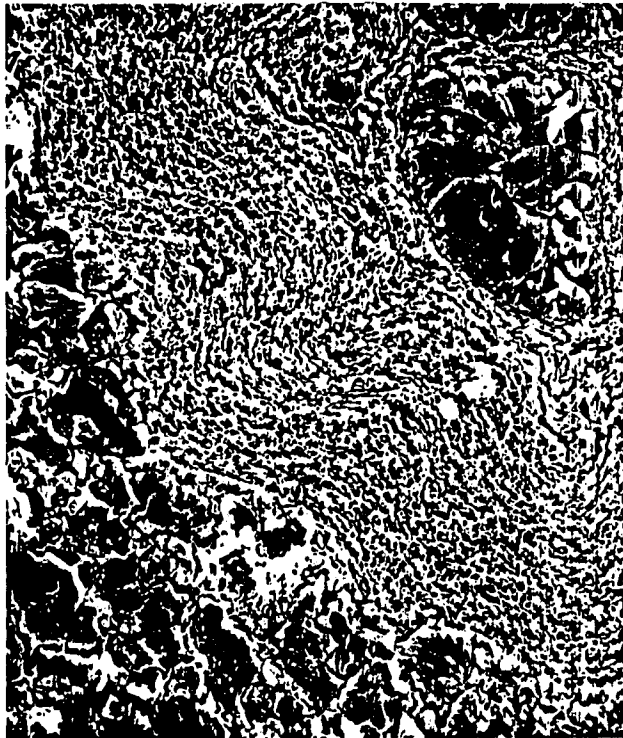
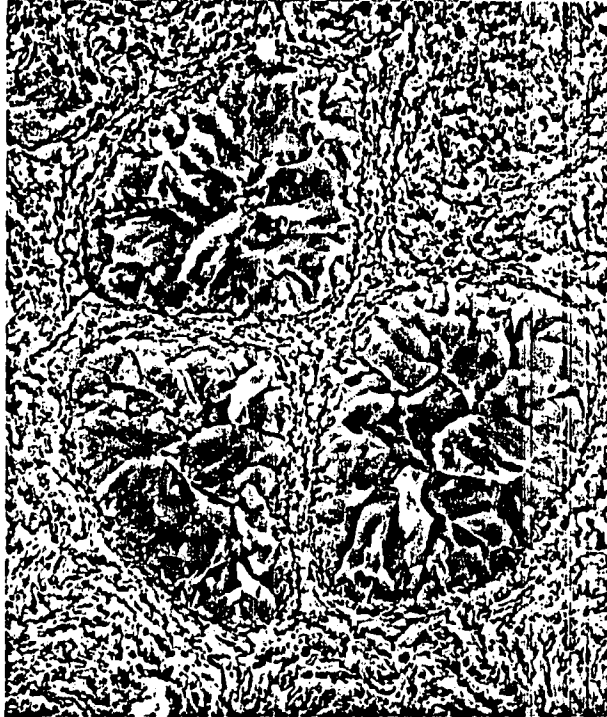


Figure 5. Comparison of (A) an axial element in a specimen of Conularia sp. (Hunsruck Slate, West Germany) and (B) a strobilating polyp of the extant, coronatid scyphozoan Nausithoe punctata. Both photographs are oriented with the oral end at the top. Scale bar in Figure 5A = 1 mm; scale bar in Figure 5B = 1 cm. (Figure 5A taken from Steul, 1984, Figure 10a; Figure 5B taken from Werner, 1966, Figure 6.)

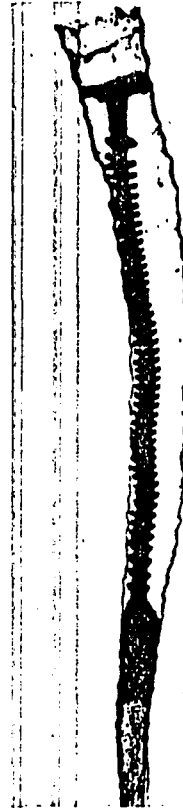


Figure 6. Comparison of (A) the circular feature in the test cavity of the holotype of *Euconularia amoena* (Middle Ordovician, Quebec, Royal Ontario Museum (Toronto, Canada) 23297) and (B) a medusa of the extant, sennaeostome scyphozoan *Aurelia*. Scale bar in Figure 6A = 1 mm; scale bar in Figure 6B = 1 cm. (Figure 6A taken from Barnes, 1987, Figure 5-27B.)

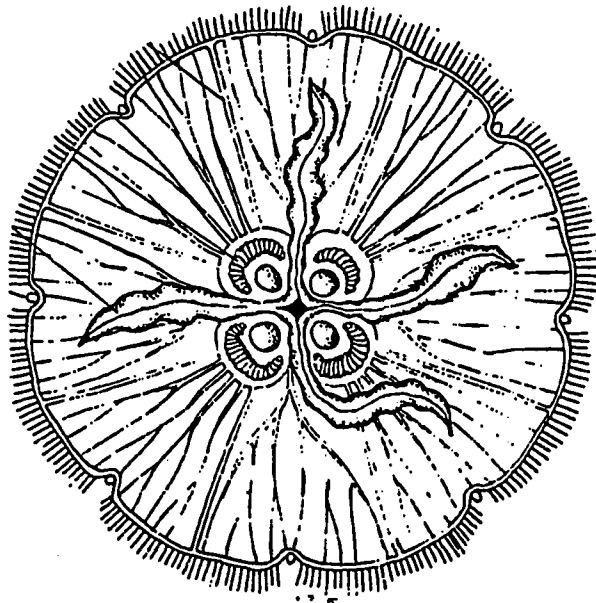
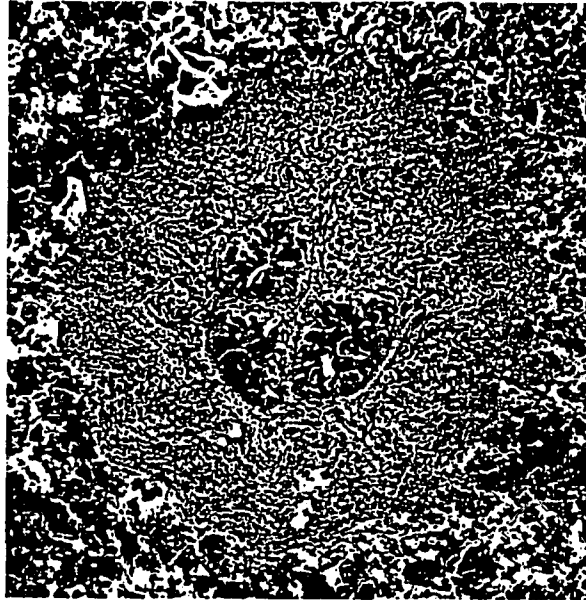
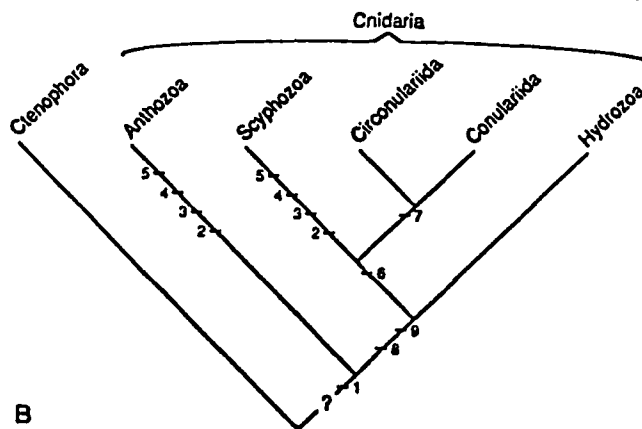
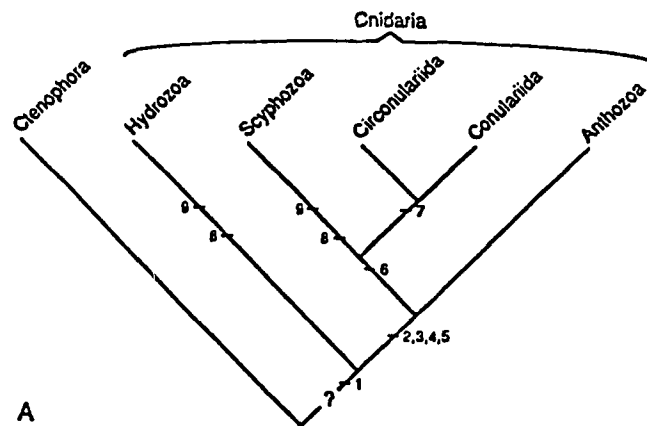


Figure 7. Cladograms summarizing rival alternative interpretations of phylogenetic relationships between major taxa within Cnidaria. A, cladogram hypothesizing monophyly of septate cnidarians; B, cladogram hypothesizing monophyly of the group containing Hydrozoa and Scyphozoa (the two cnidarian classes known to exhibit alternation of generations). Putative synapomorphies discussed in the text are as follows: (1) presence of nematocysts, (2) mesoglea containing cells, (3) sex cells originating in the entoderm, (4) nematocysts present in the entoderm, (5) enteron septate, (6) enteron with four septa, (7) body with an apatitic periderm, (8) presence of eurytele nematocysts, (9) alternation of generations. Character data are from Hyman (1940) and Barnes (1987). The relationship between Cnidaria and Ctenophora is problematic, and the reader should refer to Van Iten (1989) for discussion of inferred character state polarities.



CONCLUSION

Conulariids were a group of polypoid, septate cnidarians whose soft body was sheathed in a mineralized, finely lamellar periderm. This periderm was similar in many respects to the non-mineralized, chitinous periderm of polypoid coronatid scyphozoans. These similarities suggest that conulariids and coronatids may have inherited their periderm from a thecate common ancestor.

Conulariids living on parts of the sea floor subject to episodes of relatively high current energy were sometimes truncated, in life, by currents. Such conulariids often survived truncation, covering exposed soft parts with a finely lamellar, mineralized schott, accreted to the test's inner surface. In some cases, formation of this terminal schott was followed by production of one or two more schotts, possibly due to infection or irritation associated with truncation.

Conulariids usually exhibited four septa, one at each midline. Individuals exhibiting three or six faces presumably had three or six septa. Conulariid septa were similar to septa of scyphozoans, showing expansion of the adaxial portion and possessing a longitudinal retractor muscle that could be either single, paired, or adorally bifurcate. Conulariids and scyphozoans probably inherited their septa from a septate common ancestor that was uniquely shared by these two taxa. Together, they and the septate anthozoan cnidarians are more closely related to each other than any of one of these three groups is

to hydrozoan cnidarians.

Finally, comulariids may have exhibited a medusoid life stage, producing their medusae through polydisc strobilation.