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Internal Structures of *Cyclocrinites dactioloides*, a Receptaculitid Alga from the Lower Silurian of Iowa

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ABSTRACT

Cyclocrinites dactioloides is a marine, calcareous, receptaculitid alga which occurs as a common fossil in the Lower Silurian (Llandoveryan Hopkinton Dolomite) of eastern Iowa and northwestern Illinois. The main axis and lateral branches, previously unknown in this species, are described. These internal parts, rarely known in other taxa of cyclocrinitids, were poorly calcified and hence were seldom preserved. The flattened lower parts of the thalli, previously considered resting surfaces, are now shown to result from post mortem, early diagenetic alterations. The lateral branches compare well with similar structures in both present-day dasyclads and in ischaditid receptaculitids and thus bridge the gap between these two separate orders of green algae.

INTRODUCTION

Receptaculitids constitute a large group of fossils that ranged from the Middle Cambrian to the Permian. Receptaculitids are characterized by a calcified, globose thallus consisting of a main axis bearing regularly arranged branches. The laterals (= meromes) generally terminate with a single head, below which are variously developed stellate structures. The two best-known groups of receptaculitids are ischaditids and cyclocrinitids. In ischaditids, the always-cruciform stellate structures consist of four

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elements in one plane. In cyclocrinittids the stellate structures are absent or rarely developed. When present, as, for example, in *Cyclocrinittes darwini*, they consist of four to six elements. Heads are generally the most conspicuous elements of branches and in *C. dactiolooides* they are distinct hexagonal globose structures. No stellate structures are observed in *C. dactiolooides*. In North America cyclocrinittids seem to have disappeared after the Silurian Period. The reports of the post-Silurian cyclocrinittids require further study. Typical examples of living dasyclads, fossil cyclocrinittids, and ischadittids are shown in Figures 1 through 3.

Cyclocrinittes dactiolooides, a typical cyclocrinittid, is a common fossil in the Lower Silurian (Llandovery Series) of eastern Iowa and northwestern Illinois. Although in the older American literature cyclocrinittids were considered to be either corals, sponges, protozoans, or algae, the present consensus in this country and abroad is that they are dasycladacean algae, or a group closely related to them (see, for example, Nitecki, 1970). There is little reason to doubt the similarities of cyclocrinittids to dasyclads. The arrangement and morphology of the laterals, the shape of the thallus, and the faceted surface of cyclocrinittids resemble the extant subfamily Bornetelloideae, particularly *Bornetella sphaerica* (fig. 1). However, the close relationship of cyclocrinittids to receptaculittids is not generally accepted. Rietschel (1969) and Campbell et al. (1974) do not consider cyclocrinittids to belong with receptaculittids. Nitecki (1976 and earlier) is the main proponent of the receptaculittid nature of cyclocrinittids. He assigns cyclocrinittids together with ischadittids to the receptaculittid group primarily on the basis of the presence of stellate structures in Ordovician *Cyclocrinittes darwini* and hexagonal facets in Silurian *Ischadittes koenigii*.

PREVIOUS WORK

David Dale Owen in 1839 explored the Ordovician, Silurian, and Devonian strata in Iowa, Wisconsin, and Illinois and published his findings in 1840 and 1844. The first American illustration and description of a cyclocrinittid, *Lunulittes? dactiolooides*, appeared in Owen's 1844 publication (pl. 13, fig. 4, appendix, p. 69). Owen (1844, p. 97; pl. 7, fig. 5) illustrated the fossil with corals and referred the closely related *Receptaculittes* also to corals. Eichwald (1840) was the first, shortly before Owen, to report and describe the cyclocrinittids. His fossil *Cyclocrinittes spaskii* was reported from the

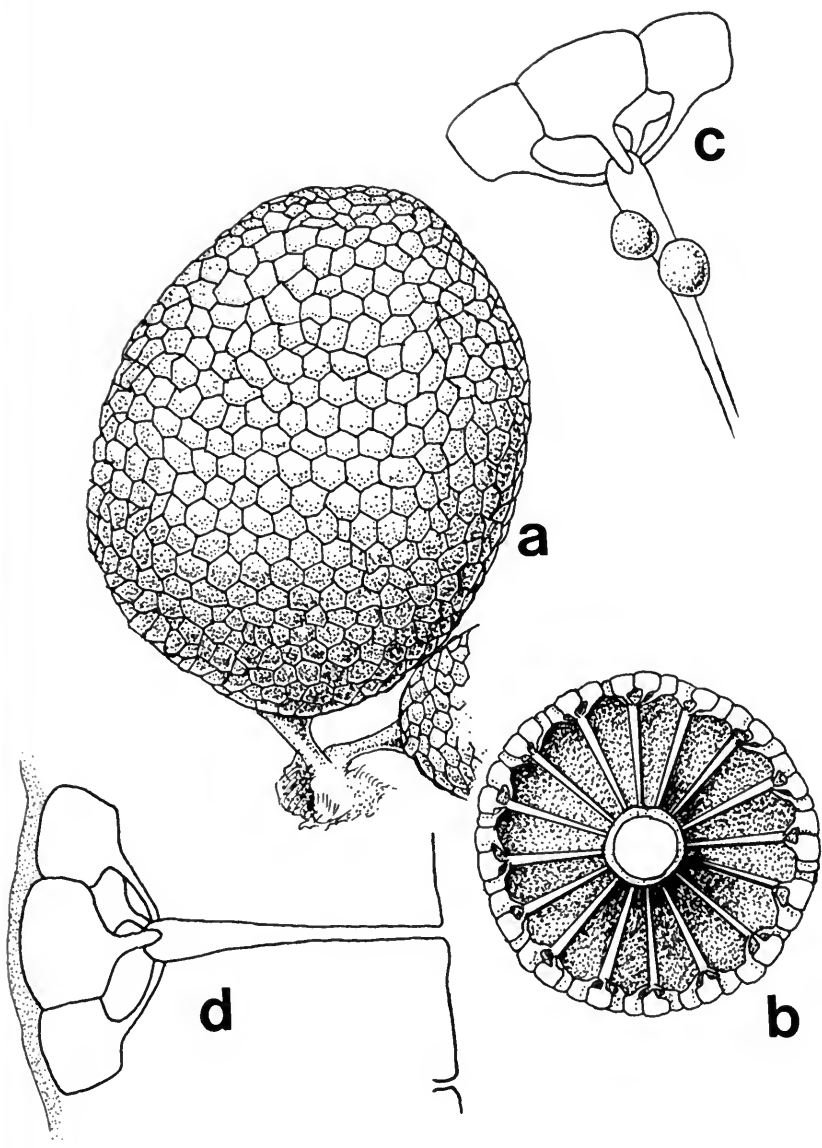


FIG. 1. Living *Bornetella sphaerica* (Zanardini, 1878) from Hawaii. a, thallus; b, cross-section through thallus; c, position of gametangia; d, lateral upon main axis and calcification (shaded). Based upon liquid preserved specimens.

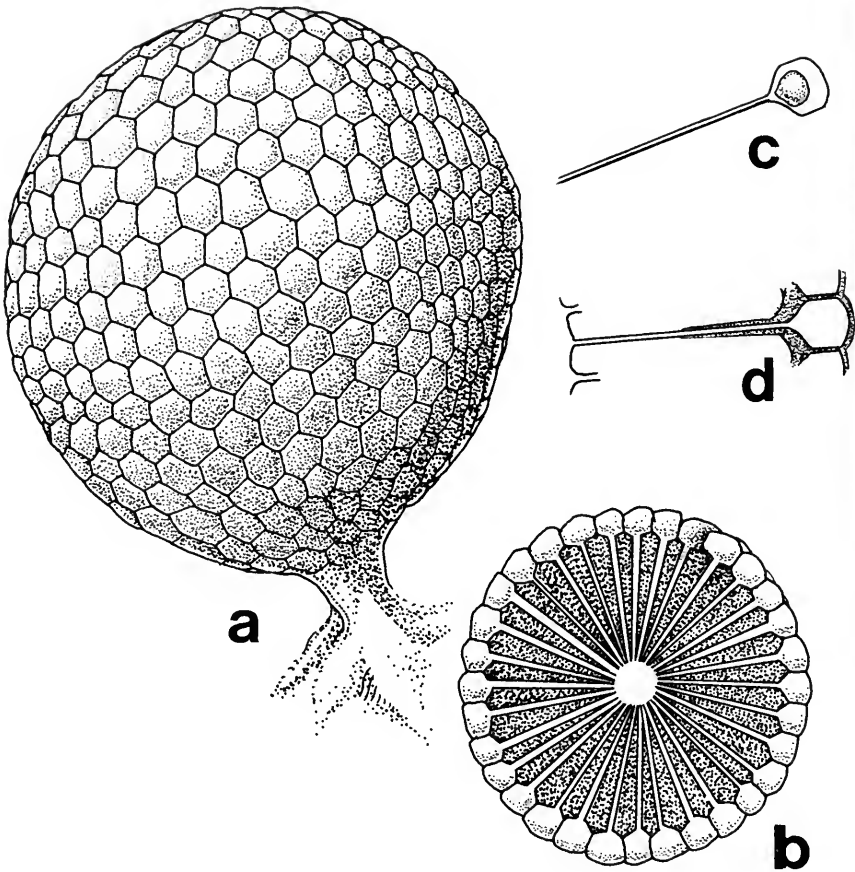


FIG. 2. Reconstruction of *Cyclocrinites gregarius* (Billings, 1866) from Gun River Formation (Silurian), Anticosti Island, Quebec. See Figure 1 for explanation.

Baltic region. Later, in Germany, Stolley (1896) monographed cyclocrinitids as algae. Samuel Calvin redescribed *Cerionites* [= *Cyclocrinites*] *dactioloides* at about the same time.

Calvin (1893, p. 15) concluded that *Cyclocrinites dactioloides* was a large, unattached protozoan colony capable of moving through the water with a "graceful rolling motion." His interpretation that *Cyclocrinites* was a protozoan was not inconsistent with the prevailing scientific opinion of his day. Protozoa in the nineteenth century included many organisms now reassigned to other groups, including sponges, and size was not a limiting factor in their definition. Thus Calvin's assignment of cyclocrinitids to the

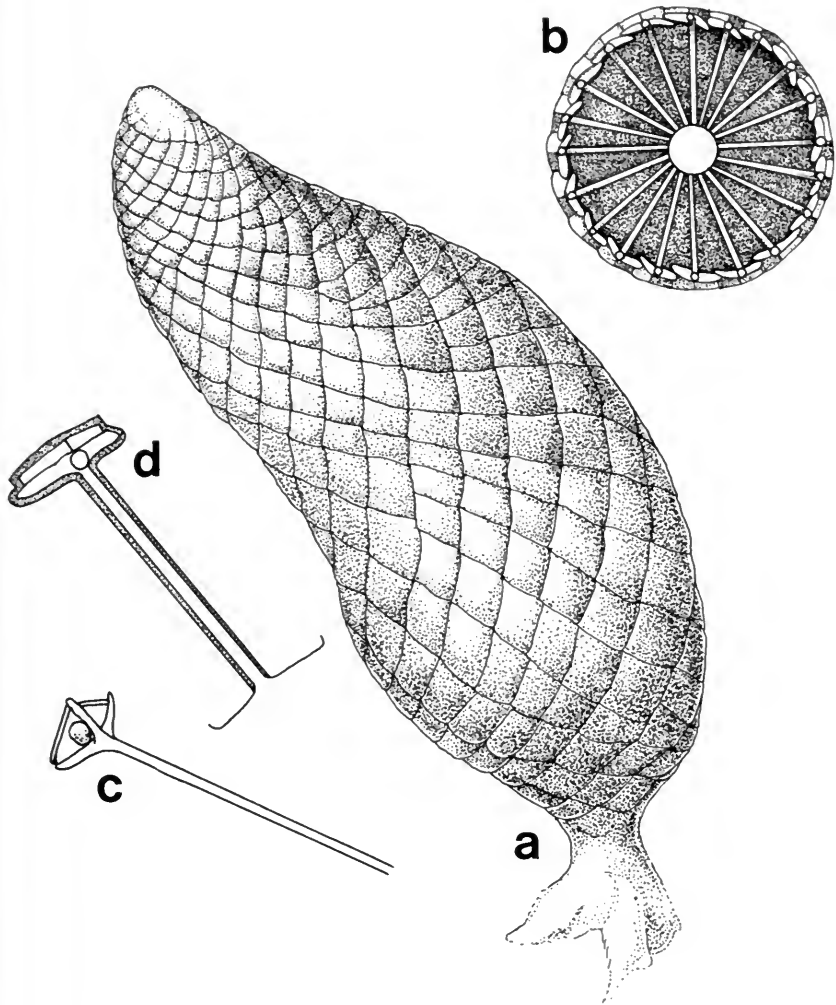


FIG. 3. Reconstruction of *Ischadites koenigii* Murchison, 1839, from Racine Dolomite (Silurian), Chicago, Illinois. See Figure 1 for explanation.

protozoa was a conservative judgement. The internal structure now recognized in this species, as well as in other cyclocrinids, can be compared with similar features in living green algae, such as *Bornetella sphaerica*. Nitecki (1970) pointed out the uncommon preservation of a main axis and lateral branches of Ordovician *Cyclocrinites welleri* and *C. pyriformis*. Evidence for attachment by a pedicle in various cyclocrinids was also discussed by Nitecki (1970, pp.

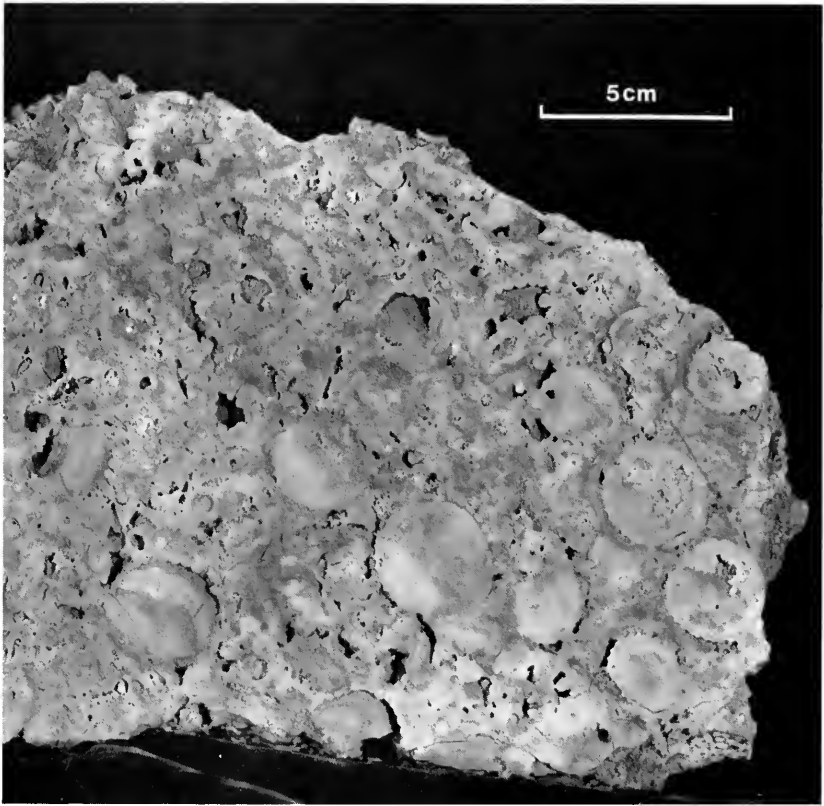


FIG. 4. Cross-sections through thalli of large numbers of "swept together" *Cyclocrinites dactiolooides* (Owen, 1844). FMNH UC 59159, from Hopkinton Dolomite (Silurian), Eastern Iowa.

18-19). In the Silurian *C. dactiolooides*, the axis and the lateral branches have not been previously demonstrated.

PALEOECOLOGY

Cyclocrinitids are found in rocks formed in the shallow seas covering midwestern North America during the Ordovician and Silurian Periods. They appear to have inhabited waters somewhat deeper than does the modern Pacific alga *Bornetella sphaerica*, which is found attached to rock fragments, shells, or corals in sheltered, shallow pools. The substrate of *C. dactiolooides* is less clearly defined and no attachment to any particular fossils or fragments has been observed. Based on the work of Johnson (1975), who recon-

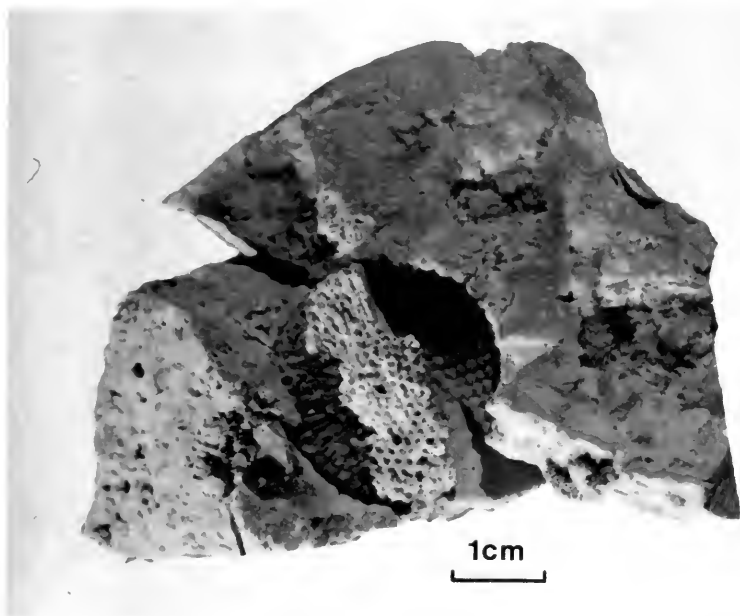


FIG. 5. Thin, disc-shaped *Cyclocrinites dactioloides* (Owen, 1844) enclosed within its complete globose mold. FMNH UC 59064, from Hopkinton Dolomite (Silurian), Eastern, Iowa.

structured three recurring communities in the Lower Silurian Hopkinton Dolomite of eastern Iowa, we believe *C. dactioloides* to have lived below the level of wave action. These communities he found to be depth associated. They are 1) a shallow coralgall community; 2) a deeper pentamerid community; and 3) an even deeper stricklandid community. *C. dactioloides* is a common element in both the pentamerid and stricklandid communities, but is absent in the shallow coralgall community where the wave base was likely to cause disturbance on the sea floor.

Even in the deeper water pentamerid community where *Cyclocrinites* thrived, individuals were sometimes detached and swept together in large numbers (fig. 4). The depth range of modern, calcareous green algae may or may not indicate the kind of tolerances experienced by *Cyclocrinites* and thus great caution needs to be exercised in assigning limits on the depth relationships of fossil communities. Taylor (1960, p. 30) states that presently, off Bermuda, calcareous green algae flourish up to a depth of 90 m. It is likely

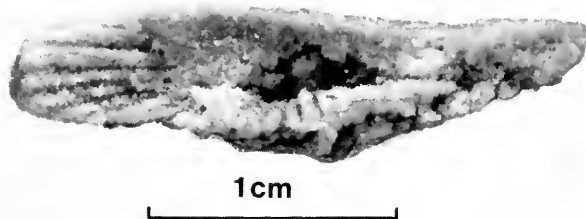


FIG. 6. Lateral view of *Cyclocrinites dactioloides* (Owen, 1844) shown in Figure 5, demonstrating lateral branches and an axis.

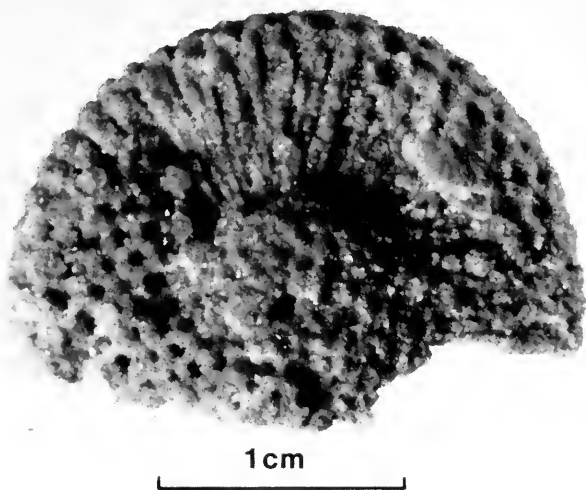


FIG. 7. Apical view of *Cyclocrinites dactioloides* (Owen, 1844) shown in Figure 5, demonstrating the branches and faceted surface.

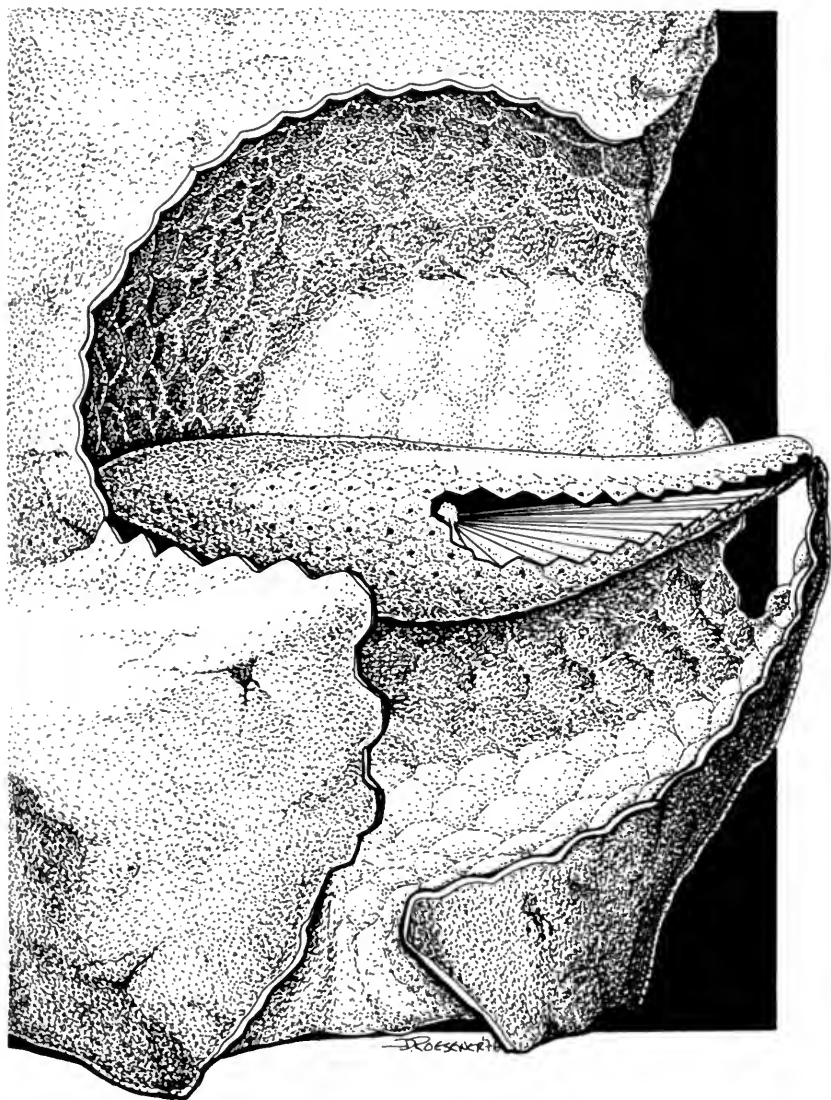


FIG. 8. Diagrammatic representation of *Cyclocrinites dactioides* (Owen, 1844) based upon the specimen shown in Figure 5.

that differences in the depth range of the Iowa communities were on the order of tens of meters and that the platform seas covering the mid-continent during the Silurian Period rarely exceeded depths of 100 m.

DISCUSSION

The internal morphology of the cyclocrinitid thallus, although rarely preserved, has greatly aided in the identification of cyclocrinitids as algae. The internal structures were undoubtedly poorly calcified in life, or at least at the time of burial, and hence had little chance of preservation. The specimens described in the present paper allow for a direct description of internal anatomy and for the confident reconstruction of missing morphological elements.

Preservation: The hard parts of many Hopkinton organisms are silicified indicating that replacement occurred early, before dolomitization removed much of the original material. However, silicified cyclocrinitids have not been collected. Like other fossils from the Hopkinton Dolomite of Iowa the cyclocrinitids are preserved as molds. The only exception is the non-silicified, calcified, preservation of the internal organs of *C. dactiolooides*, showing the main axis and lateral branches (figs. 5-8).

Body shape: *Cyclocrinites dactiolooides* and allied species have been described as completely globose or as flattened cushion-shaped organisms (Nitecki, 1970). Although intermediate shapes have been noted, as well as rare, evenly flattened, thin, disc-shaped specimens, the majority of these fossils from Illinois and Iowa are cushion-like (fig. 9). Since attachment in these has not been observed, Nitecki (1970) concluded that the flat base (almost always present in all other than globose forms) functioned as a resting surface. Now, we believe that the flattened bases of cushion-shaped specimens, the cushion-shaped forms themselves, and even the flat, disc-like fossils are not ecologically controlled, but rather are the result of post-mortem alterations. We base this conclusion upon the finding of a thin, disc-like specimen enclosed within a complete mold of a globose individual (figs. 5-8).

This remarkable find may explain shapes previously misinterpreted as representing actual life conditions. We do not know what geological processes were responsible for this preservation, which reflects a diagenetic alteration of the organism; neither are we sure whether or not the reduction in size (flattening) occurred im-

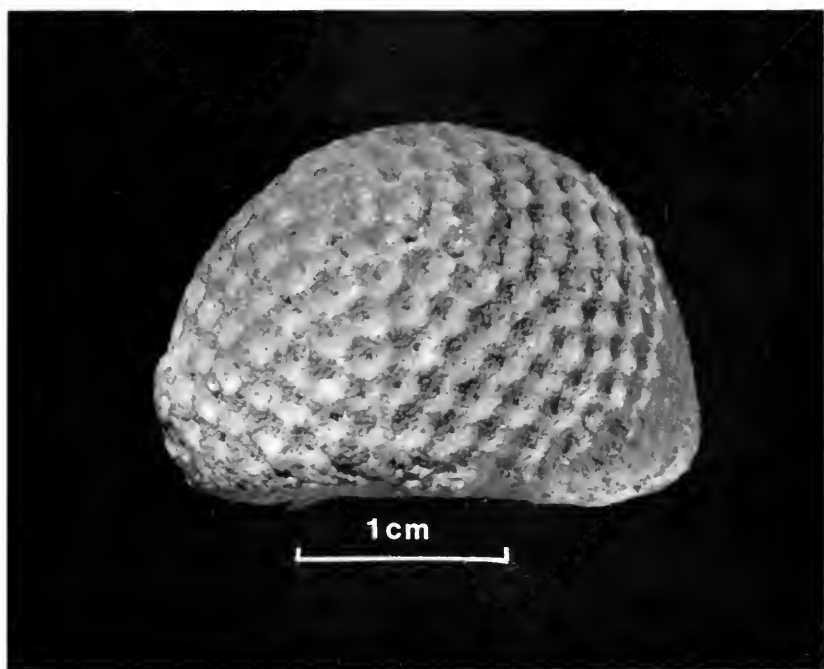


FIG. 9. Lateral view of cushion-like *Cyclocrinites dactiolooides* (Owen, 1844). FMNH PP 17709 from Hopkinton Dolomite (Silurian), Eastern Iowa. From Nitecki (1970).

mediately after burial. Although the flat fossil is found within a globose mold, the well-preserved sides of the individual are flat, while the mold is concave. Thus it is difficult to explain the reduction of the thickness of the fossil, the flattening of the surface, and the accompanying faithful reproduction of the faceted surface on the spherical mold. The shrinkage and flattening were probably due to some loss of structural cohesion of the organism, after its original globose form was preserved as a mold. Alternately, the thallus could have been open enough to receive a partial filling of lime mud. The unsupported portion could then collapse during diagenesis, while retaining the external form. The flattened base may thus represent the sedimentary interface. This evidence forces us to revise our ideas about the shape and structures of these fossils; certainly the flatness of specimens need not be ascribed to ecological factors. Cyclocrinitids appear to have been subject to post-mortem alterations uncommon among other organisms found associated with them.

Facets: The shape and arrangement of facets are observed in the free globose specimens, in cushion-shaped fossils and in molds. Although the regular arrangement of facets is characteristic of most receptaculitids, the cyclocrinitid facets are among the most uniform. They are very regular, hexagonal structures arranged in symmetrical and overlapping rows. The facets are impressions of very closely packed heads forming six-sided units. These are clearly shown in Figure 9. The tiny perforations sometimes seen at the center of the facets represent the insertion of lateral branches.

Attachment: We have not observed any attachment scars in this species. In those cyclocrinitids in which attachment scars are present, they consist of an extension of the main axis. In *C. pyriformis* and in *C. welleri* the thallus is elongated and pyriform, and the main axis may protrude in the manner of a recent dasyclad such as *Neomeris*.

In *C. darwini* and *C. spaski*, where the thallus is globose, the attachment is represented by a pronounced scar. These have been previously discussed by Nitecki (1970, figs. 12, 13).

In specimens of *C. dactiolooides* which are completely preserved a small opening is frequently found on the bottom side. This is comparable with the preservation of the recent *Bornetella sphaerica* from the Philippines and from Hawaii, where this alga is often collected without the holdfast. In the specimens from the Philippines, because the holdfast remains firmly attached to the substrate, only about one in three has a holdfast preserved (Gilbert, 1943). Egerod (1952) has pointed out that in the past, because of the ease with which the main axis is detached, there was a widespread belief that *B. sphaerica* had no holdfast at all. This belief was reinforced by examination of museum specimens, invariably without holdfasts, and frequently with the areas where the stipes may have protruded poorly preserved. We believe that in *C. dactiolooides* the lack of attachment scars is also a peculiarity of preservation. Just as the internal organs have not until now been observed (in spite of decades of collecting, yielding hundreds of specimens), so the attachment scar will eventually be recognized in this species when better preserved specimens are found.

Rosette: Our specimens, as well as those described by earlier workers, show an unusual arrangement of randomly distributed facets of the type Nitecki (1969, fig. 8c; 1970, fig. 18) has termed a rosette. The typical hexagonal cyclocrinitid head is surrounded by

only six other heads. A departure from this arrangement is an addition of one or two facets, causing a seven- or eight-sided facet or head. The eight-sided rosette, because of its regularity, is highly suggestive of an anatomical entity and we have considered that it may represent a scar of a morphological structure. The number of facets in rosettes is the same as the number of facets in the lowermost "nucleus" of other receptaculitids; however, the nuclear facets are always smaller than surrounding ones. In the rosette of *C. dactiolooides*, the facets are of various sizes and they frequently depart from the hexagonal shape. Therefore, we conclude that the rosette is only an accident of packing of branches, in which eight, instead of six, facets surround a single head.

Main axis: All our information about the central axis comes from a single specimen. A part of the internal mold is shown in two different views. A lateral view (fig. 6) illustrates lateral branches extending obliquely from a small section of the main axis. An apical view (fig. 7) shows the lateral branches radiating from the centrally located main axis. Only an upper portion of the main axis is preserved where it is very thin. The ratio of the thickness of the axis to the length of the branches is 5 to 1.

Lateral branches: Characteristically, the internal morphology of cyclocrinittids includes thin, straight branches, terminating with heads. The preservation of our specimen is not good enough to determine whether or not a constriction below the heads was present. Neither does preservation allow for the reconstruction of the exact nature of the branches, except that an internal canal appears to have been present. The branches expand gradually.

CONCLUSIONS

Cyclocrinittes dactiolooides is a typical representative of the cyclocrinittids, a group of Paleozoic algae related to dasyclads and ischaditids. The relationship of cyclocrinittids to dasyclads is well established and accepted and is based upon the similarities of the shape of the thallus, the main axis, and the branches. The facets, calcification, and reproductive structures are also comparable. Ischaditids, a small, well-defined receptaculittid group, are similar to cyclocrinittids in most respects, even in the shape of their facets and in the development of stellate structures. It seems likely, therefore, that ischaditids are also related to dasyclads. The riddle of the taxonomic placement of *all* receptaculittids is still unsolved because

it is not yet known whether the large group of receptaculitids other than ischaditids is a coherent taxon. The similarities of cyclocrinitids and ischaditids to the dasyclads warrant the assignment of cyclocrinitids and ischaditids to the complex of siphonous green algae. The differences between them, however, necessitate placing cyclocrinitids and ischaditids in a separate order from Dasycladales.

MATERIALS AND OCCURRENCES

The specimens cited in this paper are from the *Cyclocrinites* beds which occur at the middle of the Hopkinton Dolomite in eastern Iowa (see Johnson, 1975). The equivalent stratigraphic interval was called the *Cerionites* beds by Calvin and Bain (1900, p. 445). All materials are deposited at Field Museum of Natural History. FMNH UC 59064 (figs. 5-8) is from a horizon 3.75 m. below the top of the *Cyclocrinites* beds, Clarence Martins Quarries, about 7.25 km. NW of Cascade in Dubuque County (SE $\frac{1}{4}$ NE $\frac{1}{4}$ and NE $\frac{1}{4}$ SE $\frac{1}{4}$ Sec. 16, T87N, R2W). FMNH UC 59159 (fig. 4) is from the upper 4 m. of the *Cyclocrinites* beds, Krapfl Quarry, about 4 km. NW of Dyersville in Delaware Co. (SE $\frac{1}{4}$ SE $\frac{1}{4}$ Sec. 23, T89N, R3W). FMNH PP 17709 (fig. 9) was found near Clinton, Iowa, exact locality unknown.

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