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Surficial Pattern of Receptaculitids

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INTRODUCTION

The nature of preservation of the receptaculitid group of algae is responsible for a great variety of appearances in fossils and this in turn leads to misinterpretation and incorrect proliferation of taxonomic names. This variety of preservation is due to the degree of calcification and to the complexity of the lateral head. The degree of calcification and preservation and the complexity of the lateral head vary from taxon to taxon and are differentially imprinted upon the exterior of the thallus.

The surfaces of these fossils vary according to the degree of pre-depositional abrasion, to the preservation of skeletal elements, and to the degree of calcification that may have been seasonal and thus varied. However, in the past the identification and species description of receptaculitids has often been based only upon the character of the preserved surface. The great diversity of surfaces caused the proliferation of species and taxonomic splitting accompanied by a confusion of interpretation. In order to resolve this variety of appearances of the surface of these fossils, the receptaculitid appendage and its surficial manifestations are described.

HISTORICAL SKETCH

Although receptaculitids have been described for over a century, it was not until 1943 that their true nature as algae was explicitly described. Currie and Edwards (1943) redescribed Ordovician and Silurian cyclocrinidids from England. They illustrated certain *Mastopora* [= *Cyclocrinites*] species and demonstrated in these fossils the presence of a main axis, lateral branches, and possible sporangia. Elias (1947) described a late Permian dasycladacean alga *Permopora keenae*, and compared it with the Ordovician cyclocrinidid *Mastopora* (*Nidulites*) *pyriformis* [= *Cyclocrinites pyriformis*]. Osgood and Fischer (1960) redescribed and illustrated the North American Ordovician

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cyclocrinetid *Mastopora* [= *Cyclocrinites*] *pyriformis*. They clearly showed a dasycladacean character of the thallus and illustrated the main axis, the laterals, and supposed gametocysts.



FIG. 1. Three Ordovician cyclocrinitids from North America. A. Thallus of *Cyclocrinites darwini* (Miller) UC 8837A; B. Main axis of *C. darwini* UC 8837B; C. Thallus of *C. pyriformis* (Bassler) USNM 97372-a.

These important contributions were in turn followed by the Kesling and Graham (1962) paper that demonstrated the algal nature of the Ordovician receptaculitid *Ischadites iowensis*. In a preliminary presentation Nitecki (1968) also suggested that receptaculitids are algae, and that certain modern species of calcareous algae are so similar to the Paleozoic fossils that both can be easily included in the same family. The taxon is naturally divisible into three groups differentiated by degree of calcification and complexities of lateral branches.

Byrnes' (1968) explanation of the nature of Australian receptaculitid *Ischadites struszi* [= *Receptaculites australis*] is based upon previous papers but no reference to other algal interpretations except to that of Kesling and Graham (1962) is made. Byrnes states that "present assignments of the receptaculitaceans (receptaculitids) to the algae rests upon conclusions that these organisms grew in an orientation exactly the reverse of that which has previously been generally ascribed to them; that their secreted calcium carbonate was exoskeletal; that differential calcification was a pronounced feature of family morphology; and that they favored warm shallow marine waters" (p. 369). However, Byrnes' orientation of the thallus is exactly like that of Kesling and Graham, and of many authors even including DeFrance (1827). The recent Siphonales to which receptaculitids are assigned by Kesling and Graham (1962) and Nitecki (1967) are characterized by abundant encrustation with CaCO_3 . Therefore by definition receptaculitids are also encrusted; however, the precipitation of calcium carbonate among receptaculitids is also

found on the main axis, on laterals, and the termini of laterals, and therefore cannot be considered entirely exoskeletal. The term exoskeletal is difficult to apply to algae particularly since the precipitation of calcium carbonate in certain recent algae *inside* the cell

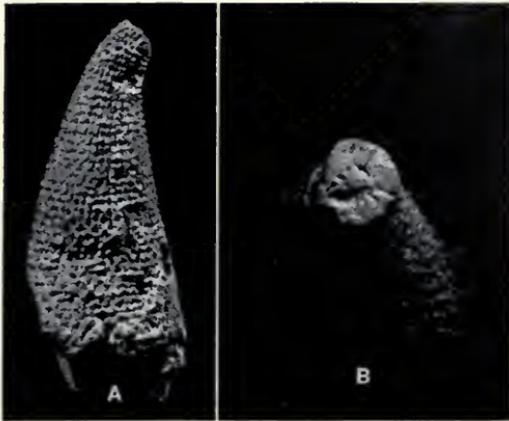


FIG. 2. Niagaran *Calathium* sp. from Joliet, Illinois. UC 4666. A. Thallus; B. Apical view of main axis and laterals.

indicates that more than surface reactions are involved (Lewin, 1962). The differential calcification is characteristic of almost all modern dasycladales. Some forms are partially calcified, some change the degree of calcification during the ontogeny, seasons, changes of salinity, and other factors (Fritsch, 1948). That the distribution of recent marine calcareous algae is correlated with the high degree of saturation of water with calcium carbonate is well known to all algal workers. Vinogradov (1953) points out that calcareous algae form reefs between 30° S and 30° N. Therefore Byrnes' assumption by analogy is correct, however, his distribution chart of receptaculitids along his Ordovician to Devonian equator is not complete. Receptaculitids have been reported from numerous areas close to his polar regions, for example, Brazil, Bolivia, West Africa, Southeastern Manchuria, Siberia, etc.

DEFINITION OF RECEPTACULITIDS

Receptaculitids are a group of marine dasycladacean algae ranging in age from the Lower Ordovician to the Lower Middle Devonian. Receptaculitids consist of three tribes: Cyclocriniteae, Calathieae, and Receptaculiteae. Cyclocriniteae are small, solitary, weakly-calcified

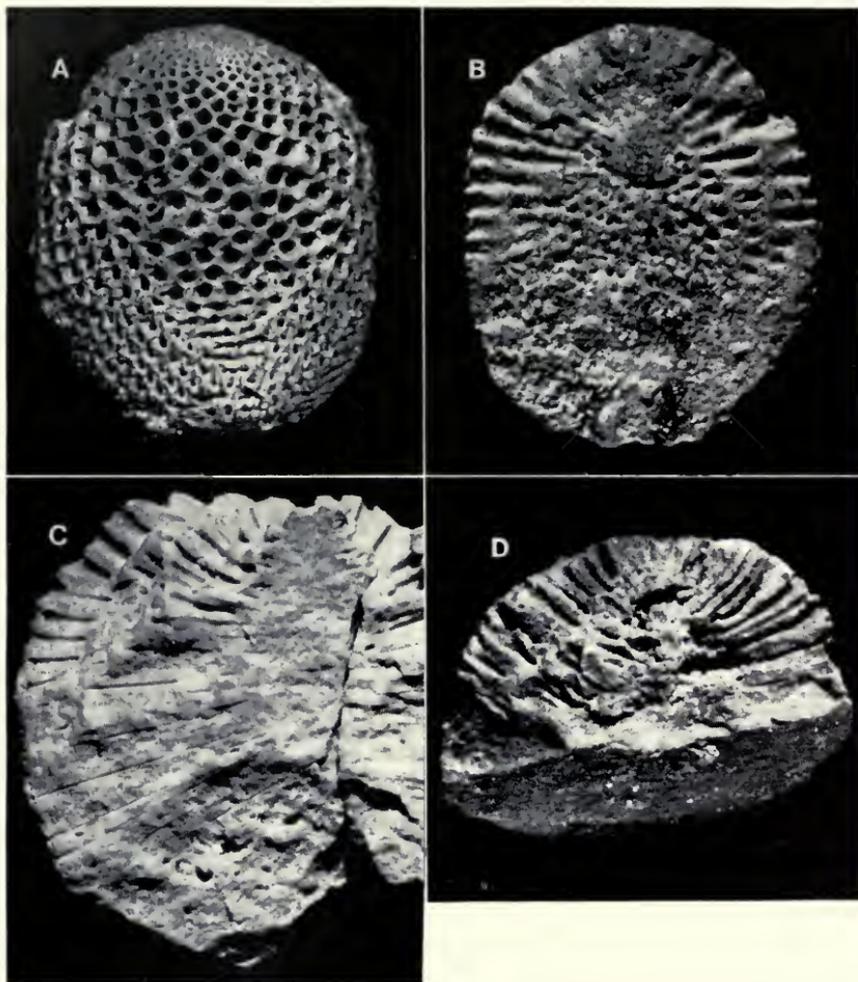


FIG. 3. Niagaran *Ischadites ohioensis* (Hall), P 11014, from Chicago, Illinois. A. Growing point, expanded lateral heads, and fragments of stellate structures, P 11014A; B. Inflated main axis and laterals, P 11014A; C. Lateral branches and main axis, P 11014B; D. Curved laterals, P 11014C.

organisms (fig. 1) with the least modified skeletons, and considered the "lowest" receptaculitid stock. The group has been monographed in German (Stolley, 1896) and in English (Nitecki, 1969a), and their laterals and the surface features have been described in detail. Calathieae are double-wall algae (fig. 2) that differ from most other receptaculitids in possession of predominantly conical thalli and very short or even absent main axes (Nitecki, 1969b). Receptaculiteae consist

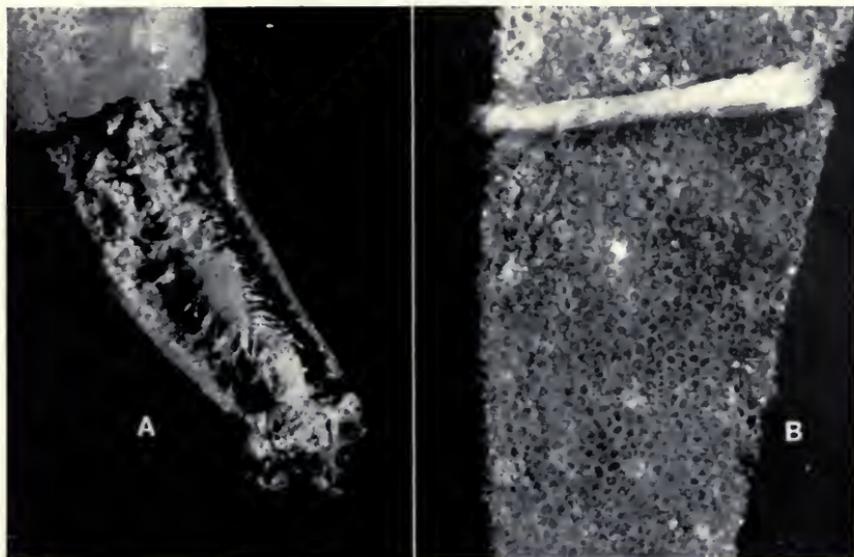


FIG. 4. Modern *Bornetella oligospora* Solms-Laubach from Philippines, FMNH 979552. A. Relation of the main axis, laterals, gametangia, and rhizoidal base; B. Six-sided nature of the cortex.

of two groups that center around the genera *Receptaculites* and *Ischadites*. The genus *Ischadites* has been redefined (Nitecki, 1969c) and is now considered a globular alga with a generally non-calcified main axis and with thin laterals borne on tightly packed whorls (fig. 3). The stellate structures consist of four ribs, and the calcification forms only one outer heavy wall. The genus *Receptaculites* has not been satisfactorily redefined. American paleontologists broadly consider it to be a two-walled organism without a main axis and with a complicated stellate structure.

In certain recent dasycladacean algae the main axis, laterals, and lateral heads may be calcified to various degrees. In *Bornetella oligospora* (fig. 4A) the main axis is elongate and rodlike. The thin laterals are arranged in whorls. The calcification occurs on the outside of the thallus. The laterals terminate with ribs that form six-sided facets (fig. 4B). The formation of facets and the calcification of their termini is discussed elsewhere (Nitecki, 1969a).

LATERAL BRANCH

The receptaculitid laterals are generally unbranched and terminate in expanded heads. The head elements commonly consist of

proximal stellate structures and variously altered distal parts. Laterals are borne in whorls, are mostly added apically and sometimes at random.

LATERAL BRANCH OF CYCLOCRINITEAE

In most cyclocrinid species the laterals are unbranched. They are borne in whorls mostly on the upper part of the main axis which



FIG. 5. *Cyclocrinites pyriformis* (Bassler), USNM 71474, from Little Oak Limestone 3 miles northeast of Pelham, Shelby County, Alabama. Termini of lateral branches and of heads are preserved.

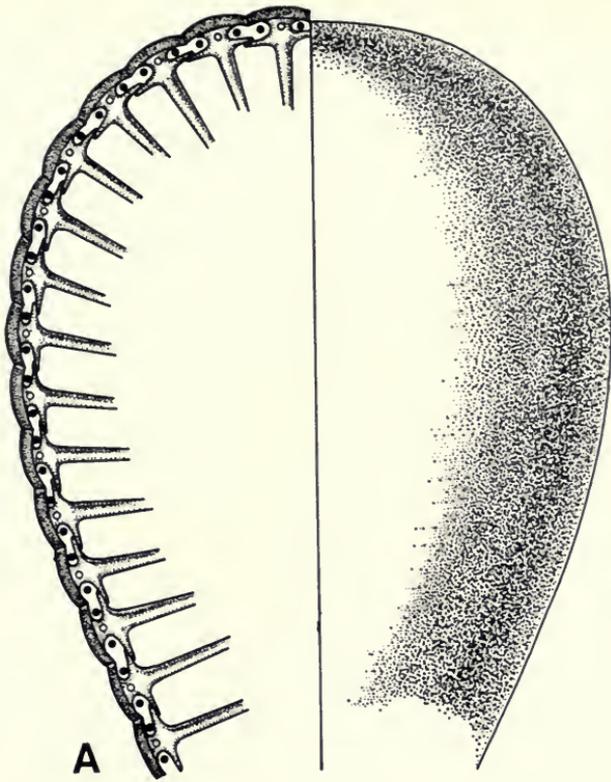
is generally inflated in the form of a bulb (fig. 1B). The laterals are mostly thin and uncalcified, and terminate in a rapidly expanding calcified head (fig. 5). The stellate structures, when present, are situated just below the head. The cyclocrinid stellate structure consists of four or more ribs and is a very thin and weakly-calcified organ. It is very similar to the ribs of recent *Bornetella oligospora*. It is analogous to the ischaditid stellate structure which, however, consists of four ribs and is heavily calcified.

LATERAL BRANCH OF CALATHIEAE

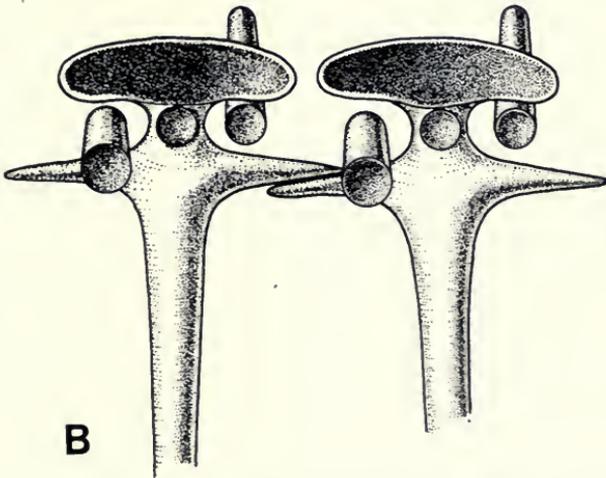
The main axis in calathiids is either absent, non-calcified, or very short. The laterals are arranged in whorls, are relatively thin and short, and are weakly calcified (fig. 2B). The laterals expand and form heads. The lateral heads are almost always heavily calcified, and their ends are often so modified as to be amorphous without the definite and regular pattern so characteristic of other receptaculitids. Stellate structures are often absent.

LATERAL BRANCH OF RECEPTACULITES

The genus *Receptaculites* in North America is understood to be an organism with laterals between a double wall. The laterals are al-



A



B

FIG. 6. *Ischadites iowensis* (Owen) based upon UMMP 30526 from Trenton rocks in Pine Ridge Quarry, 4 miles west of Escanaba, Delta County, Michigan. A. Reconstruction of the thallus; B. Reconstruction of lateral head,

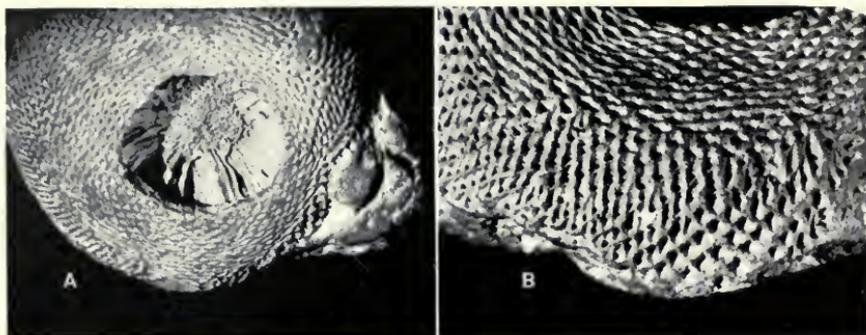


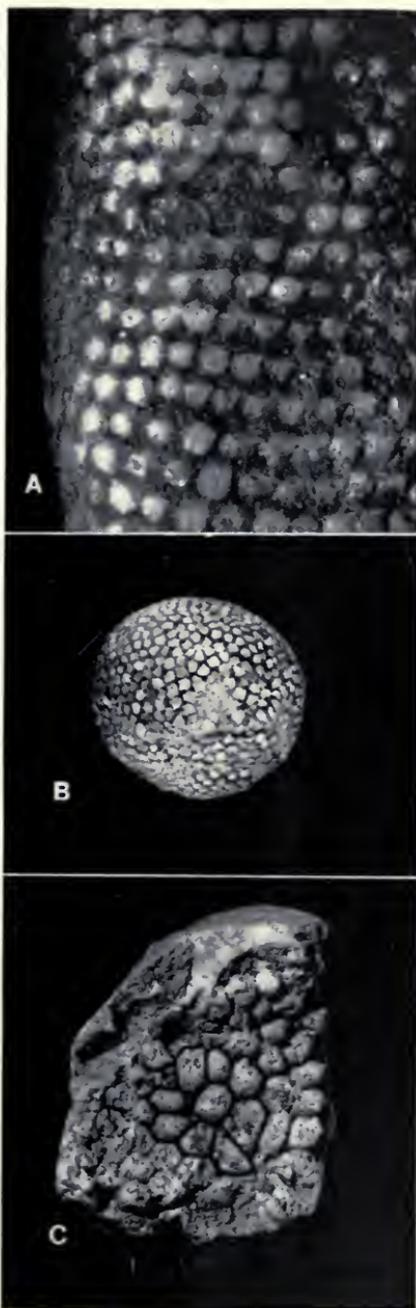
FIG. 7. *Ischadites iowensis* (Owen) from Galena Limestone, NE corner sec. 15-27N-2E Galena Quadrangle, Jo Daviess County, Illinois. Missouri School of Mines, Rolla, Mo. Geol. Dept. no. 1130. A, Apical view of the main axis and lateral branches; B, Side view of remnants of stellate structures.

ways short in proportion to the size of the thallus. The lateral head is modified into a four-ribbed stellate structure and a relatively flat plate. Commonly, the plate bears a highly ornamented radial structure presumably representing the original calcification pattern which later becomes more calcified to form a plate. When this occurs the stellate structures are very short and form one unit with the plate which they support. The plate is found only in the genus *Receptaculites*.

LATERAL BRANCH OF *ISCHADITES*

The ischaditid lateral is well known and well studied. Kesling and Graham (1962) illustrated *Ischadites iowensis* and demonstrated its algal nature. However, the inner wall and the gametocysts they illustrated represent the vertical and horizontal ribs of the stellate structure. No gametocysts or inner walls can be found on their specimen. The fossil upon which they based their interpretation is well preserved, and is diagrammatically illustrated in Figure 6. The black circles between the lateral heads (fig. 6A) are cross-sections of horizontal ribs of stellate structures that are alternate with adjacent laterals above and below the plane of the diagram (fig. 6B). In Ordovician specimens the main axis is rapidly inflated (fig. 7A) and in certain Silurian forms it is more elongate and less bulbous. The laterals are consequently shorter on these specimens that possess a bulbous main axis (fig. 7A) and longer on a main axis less inflated (fig. 3C). The uppermost laterals are often bent (fig. 3D) toward the center of the main axis.

FIG. 8. Surficial pattern of cyclo-
crinitids. A. Portion of the surface
of *Anomalooides reticulatus* Ulrich, UC
8820. Maysville Formation, Coving-
ton, Kentucky; B. *Cyclocrinites spas-
kii* Eichwald, UMMP 21104, Fremont
Formation, Canon City, Colorado;
C. *C. dactiolooides* (Owen), UC 23760,
Niagaran, Clinton, Iowa.



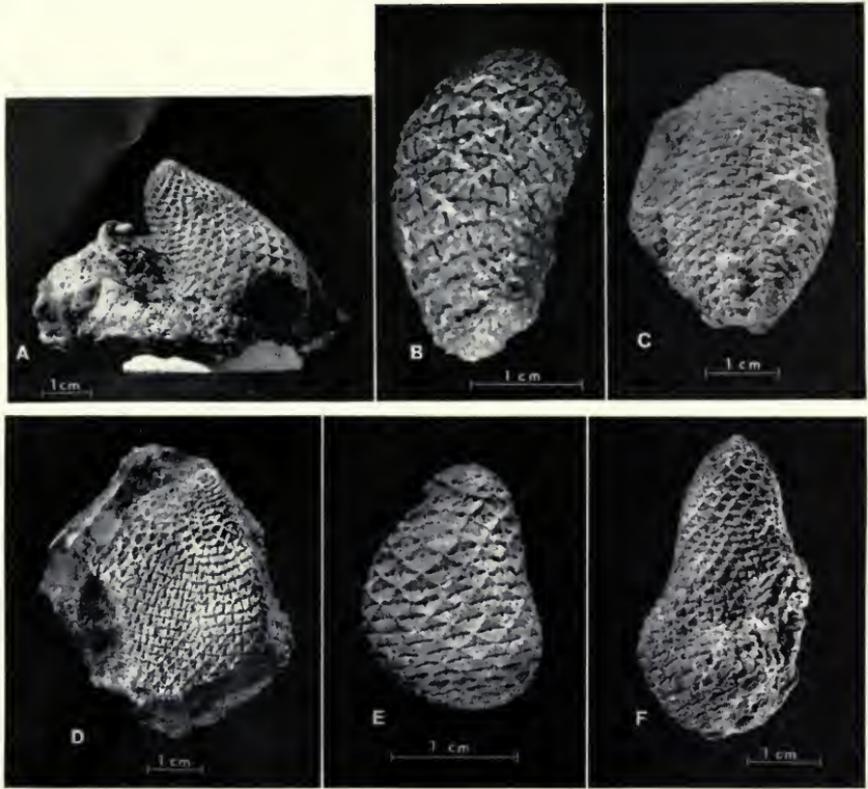


FIG. 9. *Ischadites koenigii* Murchison, Niagaran, Chicago. Field Museum of Natural History.

THE SURFICIAL PATTERN

The surface of a well-preserved receptaculitid thallus exhibits the tops of lateral heads almost always in contact. The heads and, consequently, also their facets are arranged in regular geometric pattern forming sinusoidal curves. However, this preservation is exceptional and specimens are seldom collected with their surfaces intact. Most fossils are found without lateral heads or with parts of heads only. This is due to differential calcification of the thallus, decalcification during growth or seasonal changes, to the mechanical abrasion prior to deposition, and to post-depositional alterations.

PATTERN OF CYCLOCRINITEAE

The surficial pattern of cyclocrinitids is shown in Figure 8A-C. The lateral heads are rarely preserved, and commonly only facets are

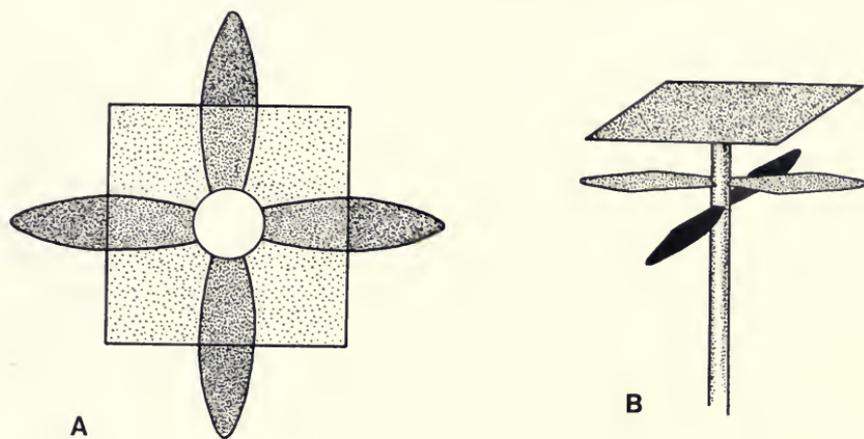


FIG. 10. Diagrammatic representation of generalized and simplified lateral head. A. Apical view; B. Lateral view.

observed. The laterals in cyclocrinids are generally in contact with six others and, therefore, their facets are six-sided. Most other receptaculitids have four-sided facets. Occasionally, the orderly pattern is disrupted by an addition of a new lateral. When this occurs the lateral head may be in contact with eight other laterals and a rosette forms (fig. 8C). In the past the rosette was interpreted as a morphological structure, or an opening.

PATTERN OF CALATHIEAE

The calathiid exterior surface is generally obscure and appears amorphous. When, however, the termini of laterals are absent the pattern is regular and similar to the ischaditid surface. This pattern is shown in Figure 2A; the area in the center of the photograph shows the facets in a rather unusual preservation for this taxon. The round knobs outside of this area are remnants of stellate structures.

PATTERN OF RECEPTACULITEAE

The surficial patterns in the genera *Ischadites* and *Receptaculites* are almost always alike. It is this similarity of the external appearance that causes difficulties in determining the generic assignment, particularly since species descriptions often have been based only upon the character of the exterior. Two Silurian and one Ordovician ischaditid species show this pattern. When the specimens of Silurian *Ischadites ohioensis* are preserved as negatives, then the dilated ter-

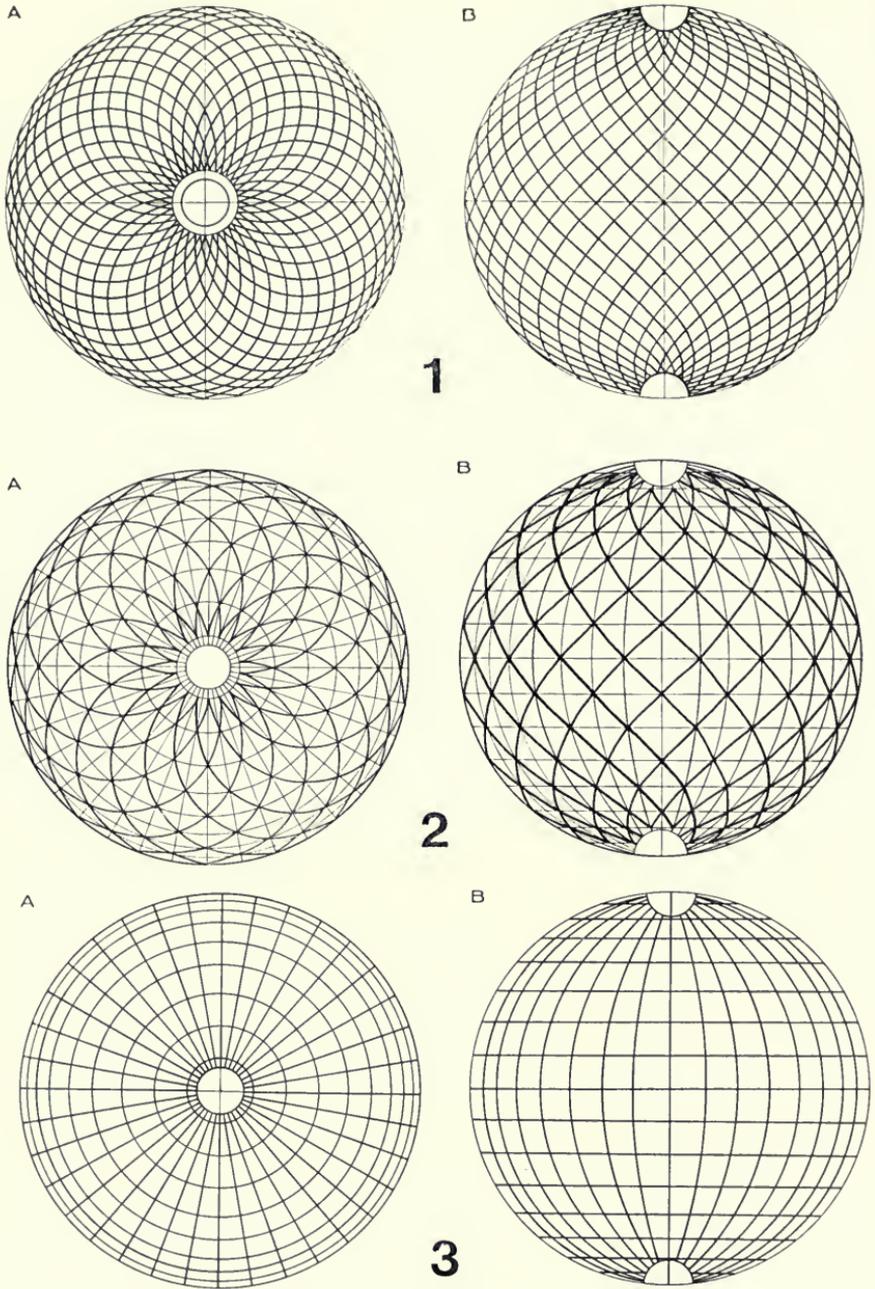


FIG. 11. Geometric representation of various levels of receptaculitid surfaces. A. Polar view of the thallus; B. Lateral view.

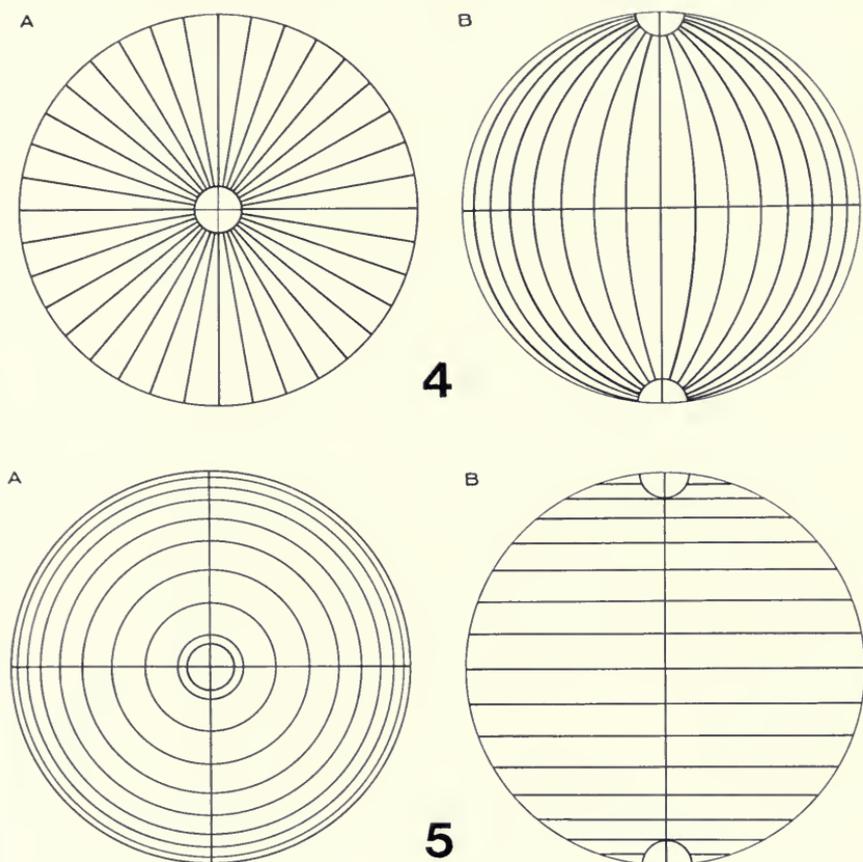


FIG. 11. (contd.) Geometric representation of various levels of receptaculitid surfaces. A, Polar view of the thallus; B, Lateral view.

mini of laterals are seen as openings in the upper part of the thallus, and the stellate structures are below (fig. 3A). The horizontal ribs are proximal and the vertical ribs are distal. In Ordovician *Ischadites iowensis* (fig. 7B) a similar arrangement is observed. The horizontal proximal ribs are in the upper part of the thallus, the vertical distal ribs are in the lower part. In the lowermost part the facets of dilated parts of laterals are seen. In Silurian *Ischadites koenigii* (fig. 9) a distinct pattern of facets and of stellate structures is clearly seen. These well-preserved, almost complete thalli, possess the stellate structures consisting of ribs at the same level and, therefore, worn out at the same time.

GENERALIZED PATTERN

The surface of most receptaculitids when preserved entirely consists of calcified lateral heads that in contact form facets (fig. 10). These facets are mostly rhomboidal, sometimes hexagonal, and their walls form two sets of diagonal spiral lines intersecting each other. The heavy calcification of stellate structures and different levels of weathering produce various patterns of lines. This is particularly evident among those species in which the stellate structures are well calcified, as in *Ischadites koenigii*. In addition, the stellate structures are often broken, misplaced, and commonly completely dissolved, thereby further complicating the appearance of the lines.

The geometric arrangement of facetal lines is represented in a series (fig. 11) of spherical geometric drawings in which the morphological complications of differences of sizes and shapes, aging, and additions of new laterals have been omitted. Each figure consists of two drawings: A—a polar view to the main axis and B—a lateral view at right angle to the axis. The scale is maintained except for the first set and the drawings are arranged from best preserved to the most destitute form. The blank areas at the top and the bottom of B set have no meaning.

Figure 11.1 represents the condition of calcified laterals preserved and forming facets whose walls represent the spiral lines. Two sets are noted, namely, two opposite edges of rhomboidal facets in contact. The biggest facets are in the equatorial region and the smallest at the "upper" and "lower" ends. This pattern is shown in Figures 6 and 8, and is common among the well-preserved material.

Figure 11.2 represents the very common preservation among *I. koenigii* in which the lateral heads are detached and the stellate structures are visible within the facets. Thus, the walls of facets form lines as in the previous figure, but in addition the horizontal and vertical lines produced by the stellate structures are clearly delineated. This preservation is particularly frequent among the Silurian specimens from the Chicago region (fig. 9) in which the stellate structures form beautiful cross-like markings within the facets. For the sake of clarity the facets in this figure have been drawn larger than in the preceding illustration (fig. 11.1).

The next illustration (fig. 11.3) represents the preservation in which the facetal walls are entirely gone and only the stellate structures are preserved. This is found on parts of many thalli of *I. koe-*

nigii and appears to have been caused by the early abrasion (fig. 9C) of the specimens. It is also common among Silurian calathiids from around Lake Winnipegosis in Canada where the entire specimens are thus preserved.

The stellate structure consists of four projections often not on the same plane but one set of two rays above the other two-ray set. Figure 11.4 shows the uppermost or vertical set. This often causes the appearance of vertical lines found most commonly on the younger, upper part of the thallus. In rare instances when only one ray is present the vertical interrupted lines form. The last condition observed is shown in Figure 11.5 where the vertical rays are eroded and only horizontal rays remain to form horizontal lines. This occurrence is infrequent among *koenigii* but is characteristically found in other species of *Ischadites*, particularly in *I. ohioensis*. If the abrasion proceeded further no recognizable receptaculitid would result.

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ABBREVIATIONS

The following abbreviations are used:

UC—University of Chicago, Walker Museum, now in Field
Museum of Natural History

USNM—United States National Museum

P—Paleontology, FMNH

FMNH—Field Museum of Natural History

UMMP—University of Michigan Museum of Paleontology

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