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Upper Devonian *Receptaculites chardini* n. sp.  
from Central Afghanistan

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INTRODUCTION

Receptaculitids have had a peripatetic taxonomic history. Zhuravleva (1970) and Zhuravleva and Miagkova (1970-1972) assigned receptaculitids together with archaeocyathids (and certain less known Paleozoic fossils) a new kingdom: Archaeata. The relationship of these two groups has been noted before (Roy, 1941, p. 59) and is based upon similarity of double-wall structure in most arachaeocyathids and in certain receptaculitids. We consider this relationship, not based upon the study of the internal morphology of receptaculitids, to be only superficial. Although some arguments that receptaculitids may be sponges have been recently proposed (Foster, 1973), the present consensus is that they are algae (Kesling and Graham, 1962; Nitecki, 1970-1972; Rietschel, 1967-1970; Byrnes, 1968; Elliot, 1972). Sushkin (1958, 1962) assigned receptaculitids into a new order of possible sponges. Rietschel (1969) considers these fossils an order of green algae. We consider receptaculitids to be an order of algae, possibly forming a complex of

\*C'est avec le regret le plus vif que le monde scientifique a reçu les nouvelles du décès de M. de Lapparent le 28 Février 1975.

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siphonous Chlorophycophyta together with the orders Siphonocladales, Siphonales, and Dasycladales.

Fossils of the genus *Receptaculites* are generally large and thus easily observed in the field. They are also relatively common and unusual in appearance; therefore, they attracted scientific attention early. In the nineteenth century, *Receptaculites* was extensively studied by Hall (1861), Billings (1865), Dames (1868), Gümbel (1876), Hinde (1884), Rauff (1892a, b), and Girty (1895); however, the concept of the genus was much broader than it is today. In this century the following writers have discussed the genus or some aspects of it: Waterlot (1932); Sushkin (1958, 1962); Kesling and Graham (1962); Byrnes (1968); Rietschel (1967-1970); Muller (1968); Nitecki (1970-1972); Foster (1973); and Mierzejewska and Mierzejewski (1973).

The genus *Receptaculites* and its included species cannot be defined on the basis of external morphology alone. Many forms from the Ordovician, Silurian, and Devonian have been assigned to this genus often only on the basis of impressions of the external surface.

Devonian receptaculitids are known from all continents except Antarctica (Nitecki, 1972b). The best known Devonian receptaculitid is *R. neptuni* from Belgium and the surrounding areas. It has been studied by Waterlot (1932), Müller (1968), and Rietschel (1969, 1970). In southwestern Asia, Devonian *Receptaculites* is known from Iran, Afghanistan, and Pakistan (fig. 1). *R. neptuni* was the first receptaculitid found in the Kuh-e Shotori, Tabas area, East Iran (Stöcklin et al., 1965). The description of the specimens was, however, published earlier by Flügel (1961). *R. neptuni* is found in red beds characterized by ferruginous oolites and pelmatozoan remains. These rocks are similar to the outcrops in Bokan, Afghanistan; however, the Iranian rocks contain abundant *Orthoceras* and goniatites, indicating Famennian age (Walliser, 1966). So far as is presently known, *Receptaculites* seems to be restricted in Iran to Kuh-e Shotori. It has not been found in the adjacent region of Shirgesht (Ruttner et al., 1968).

In northern Pakistan, an Upper Devonian fossiliferous locality without receptaculitids is known in Mastuj Valley, Chitral (Hayden, 1915; Desio, 1966); the apparent absence of receptaculitids is perhaps due to the marly and calcareous facies. A specimen and some fragments of *Receptaculites neptuni* were found by an Austrian alpine expedition to Tirish Mir (Chitral), on a ridge 4,000 m. above sea level. These have been described and figured by



FIG. 1. Map of Afghanistan and adjoining areas of Iran and Pakistan, showing the geographic distribution of Devonian receptaculitids. *Na* Dasht-e Nawar area; *Sa* Sadmarda Mountain; *Ta* Tabas area; *TM* Tirish Mir Mountain; *H* Herat; *KBL* Kabul; *Ki* Karashi; *Kn* Kandahar; *R* Rawalpindi.

Vogeltanz (1969). The mainly biosparite rock from which the fossils were obtained appears very similar to the Iranian and Afghan facies.

In Afghanistan, *Receptaculites* has been reported from central Afghanistan in the regions of Dasht-e Nawar and Sadmard (Boutière and Brice, 1966; Brice, 1970; Despament and Montemat, 1972). Durkoop et al. (1967) reported *Receptaculites neptuni* from Doni Jarchi in Afghanistan, and from Tabas in southern Iran. Many

other Devonian localities with rich coral and brachiopod faunas are known in Afghanistan, but no receptaculitids have been found (Brice, 1970). These localities appear more marly than those with receptaculitids, probably representing a different environment, and thus may have been less favorable for receptaculitid growth.

The specimens described in this paper were collected during the first and subsequent French geological expeditions to Dasht-e Nawar, Central Afghanistan, in 1961, 1963, 1965, 1966, 1971, and 1973. They were collected by Albert F. de Lapparent and André Boutière, with Nur Ahmad, Jacques de Lavigne, and Bruno Mistiaen aiding in the field.

We have had great difficulties in deciding whether our fossils are *R. neptuni* or a different species. We were concerned with the lack of good comparative material from the type locality; however, through the courtesy of Dr. Robaszynski of Mons, Belgium we received a few *R. neptuni* from the type section. These together with the fossils belonging to older (19th century) collections in various North American museums show that our specimens are indeed a different species from *R. neptuni*. The main difference lies in the nature of the digitate structure. For further comparison with *R. neptuni* see p. 47.

We do not know whether the previously described receptaculitids from Iran and Pakistan are all *R. neptuni*, nor whether they belong to our taxon. They have been described either as *R. neptuni* or as *Receptaculites* sp.

## LOCALITIES AND STRATIGRAPHIC POSITION

All the specimens described in this paper came from the vicinity of Bokan Village at 3,000 m. elevation (figs. 1, 2). The collecting area extends 1 km. east of Bokan, 3 km. northeast, and 9 km. south of the village.

Other localities where receptaculitids definitely belonging to our species have been reported are northeast of the Dasht-e Nawar region (fig. 2) along Devonian limestone outcrops; the Chaghna belt; the Ghujerak-Dewal-Kajir belt; the Saif Habib and Sar-e Karnala areas; and the Bokan-Wakak belt. The three richest localities are: east and northeast of Bokan, and Ghurjerak Pass. Other localities studied by Desparmet (Desparmet and Montemat, 1972) are situated about 100 km. farther to the north in the Sadmarda region: Spina Kada Mountain (elevation 4,300 m.), Qutun Mountain (4,000 m.), and near Badragha Village (3,000 m.).



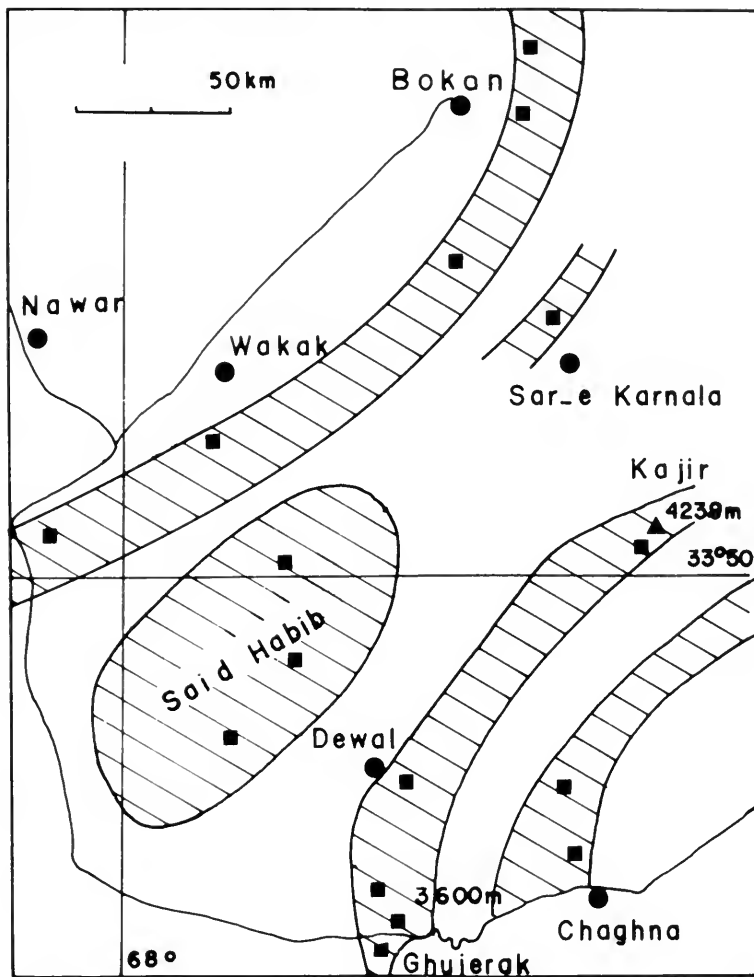


FIG. 2. Map of distribution of *Receptaculites chardini* from Central Afghanistan. Shaded areas represent Devonian outcrops and squares represent localities with *Receptaculites* (after Boutièr, unpublished).

All these localities are of Frasnian age. The age is based on a study of corals and brachiopods (Brice, 1970). At Bokan the uppermost part of the red limestone probably reaches the Famennian (fig. 3). Receptaculitids are sometimes present in massive grey limestone and are associated with corals; however, they are chiefly found in yellow or red limestones, with abundant ferruginous micronodules and pelmatozoan (mostly crinoidal) remains. The

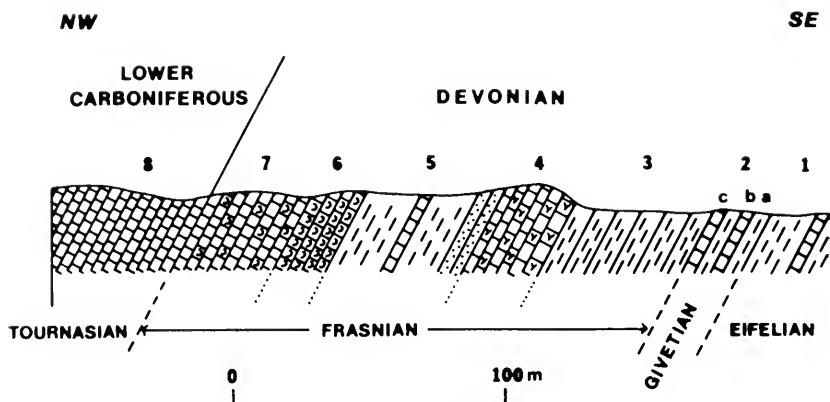


FIG. 3. Section of the Devonian fossiliferous strata, east of Bokan (Central Afghanistan).

8. Grey crinoidal limestone, with Foraminifera.
7. Red and yellow limestone with numerous scattered *Receptaculites chardini*, crinoids, stromatoporoids and brachiopods: *Whidbornella* cf. *productoides* (Murchison, 1840), *Ripidiorhynchus elburzensis* (Gaetani, 1965), *Coeloterorhynchus tabasensis* Sartenaer, 1966.
6. Purple limestone with numerous *Receptaculites chardini*, and *Atrypa* aff. *vulgaris* Liachenko, 1959.
5. Sandstone, limestone, and shale with crinoid fragments and brachiopods: *Cariniferella* aff. *iowensis* Stainbrook, 1945, *Gypidula multiplicata* (Roemer, 1854).
4. Grey limestone, with corals and stromatoporoids (biostrome).
3. Limestone with brachiopod: *Crytopirifer verneuili echinosus* Liachenko, 1958.
- 2c. Dark limestone with coral: *Phillipsastrea hennahi* (Lonsdale, 1840).
- 2b. Dark limestone with crinoid stems; brachiopods: *Gypidula multiplicata* (Roemer, 1854), *Atrypa* aff. *vulgaris* Liachenko, 1959.
- 2a. Yellow shales with brachiopods: *Cymostrophia* (?) sp., *Kransia* aff. *parallelipeda* (Bronn, 1837), *Atrypa* aff. *vulgaris* Liachenko, 1959.
1. Yellow shales and sandy limestone with spiriferids similar to *Euryspirifer intermedius* (Schlotheim, 1820).

depositional environment is interpreted as shallow marine with strong currents and high oxygenation, as suggested by the iron micronodules and the crinoids.

### TERMINOLOGY

As long as receptaculitids were considered Porifera or related organisms, the sponge terminology was used. Since they are now considered algae, however, the terminology must be changed in accordance with the algal interpretation of their anatomy. The terminology used here is that of Nitecki (1972a).

## SYSTEMATIC PALEONTOLOGY

Division: Chlorophyta (green algae)

Class: Chlorophyceae

Order: Receptaculitales Sushkin, 1962

Family: Receptaculitaceae Eichwald, 1860

Genus: **Receptaculites** Deshayes, 1828**Receptaculites chardini** n. sp.

*Name.*—The name *chardini* is in honor of Pierre Teilhard de Chardin.

*Definition.*—Large *Receptaculites*, globose; immature thallus irregular; ovoid when young, with mammillary projection in adult; sessile; calcification heaviest apically; inner wall massive with digitate structures pointing toward interior; digitate structures finger-like, fused in adult; lateral head and outer head typical of *Receptaculites*; laterals stout in adult, thin when immature; inner part of laterals thin, outer part of laterals heavily calcified; outer plates in contact; stellate structures four-rayed, regular on top, overlapping on sides of thallus.

*Stratigraphic and geographic distribution.*—Upper Devonian, Frasnian. Central Afghanistan (and possibly adjoining regions, Iran and Pakistan).

*Holotype.*—FMNH PP 18169, in collection of Field Museum of Natural History, Chicago, Illinois.

*Other Material.*—Twenty-seven specimens in Field Museum (FMNH PP) and over 80 specimens (all others) in Institut de Géologie IGAL, Paris, France.

*Comparison with Receptaculites neptuni (Defrance 1827).*—*R. chardini* is closely related to *R. neptuni* which it resembles in general body shape, in the manner of calcification, and in the shape of lateral heads. It differs from *R. neptuni* in more apico-basal flattening of the body, particularly in young organisms. *R. neptuni* appears more globose, while *R. chardini* exhibits a greater variation in the length and thickness of branches. The main character used in differentiating the two species is the presence in *R. chardini* of inward projecting fingers of digitate structures. No such structures are present in *R. neptuni*.

## PRESERVATION

All fossils are fragmentary; complete specimens have not yet been found. The most complete, apparently a young individual, is

shown in Figure 4. Specimens of *R. chardini* are very strongly recrystallized and are replaced with coarse calcite crystals. Sedimentary calcilutite mud and very abundant fragments of bryozoans and pelmatozoans are commonly found scattered within the skeletons of *R. chardini*. Occasionally calcite crystals, and less frequently quartz crystals, are noted in the matrix.

Most specimens represent only horizontal cross-sections through laterals (figs. 5-13). The laterals are best observed in thin sections cut parallel to branches (figs. 14, 15). The preserved lateral heads consist of diagonal-to-square plates (fig. 16) and stellate structures consisting of four ribs (figs. 4, 14). The inner, proximal, termination of branches is more obscure; however, the digitate terminations are clearly noted (figs. 17 and 23). Weathering effects on the head are seen in Figures 11-23, 24-25.

The branches are sometimes represented by holes (fig. 5). The preservation of branches as molds is less frequent in our material than it is in receptaculitids from other geographic and stratigraphic positions.

Most specimens are worn and only rarely are the outer plates or supporting structures preserved in their entirety. Occasionally specimens without external or internal structures are preserved and are only recognized by their general body shape. Such "molds" are common among Ordovician forms from the North American Appalachian region.

### MORPHOLOGY

*Gross morphology.*—For most receptaculitids the external morphology alone provides little taxonomic information and the shape of the thallus is often ecologically controlled (Nitecki, 1972a). The striking feature of most receptaculitids is the surficial arrangement of skeletal elements that appear as alternating spirals. These are very beautiful and regular features. In our fossils one spiral is generally better developed than the other (fig. 26). This feature is best developed on the sides of the thallus away from the apex. Just as with living Dasycladales, in many, but again not in all receptaculitids, the external and internal calcification produces two walls connected by branches (rods, columns, elements, spicules, meromes, etc. of various authors). In *R. chardini*, as in all members of the genus *Receptaculites*, both walls are well developed (figs. 17, 27B, 34B) and the branches are, relative to the size of the thallus, short and robust (figs. 14, 15, 17-19, 27B).

Only rarely are complete receptaculitid thalli preserved and the entire body is known from only a handful of species. Reconstruction of the shape of the thallus based upon incomplete specimens is very unsatisfactory. A comparison of variously curved fragments of thalli with complete American individuals of different species allows reconstruction of the general body shape (fig. 28) although with far from complete certainty. The apex of *R. chardini* ranges in shape from flat, through rarely elevated, to sometimes collapsed (fig. 30). This is characteristic of many receptaculitids. The youngest part of the body is at the apex, shown in Figures 31 and 32. By comparison with complete specimens of American "*Receptaculites*" *oweni*, the caved-in, collapsed (fig. 30) upper part is a post-mortem alteration of the body. Thus we visualize the living adult thallus as globose and bulging but definitely without concave apices (figs. 28, 29). The curvature of our fragments indicates that *R. chardini* had a closed thallus (figs. 28-30) with perhaps only a basal opening. It is not known whether the alga simply rested on the bottom or was attached by an extension of the main axis.

The largest fragment is 12.5 cm. across; therefore the organism was at least that large. The minimum size of the organism cannot be determined.

*Apex of the thallus.* — The orientation of the thallus is based upon comparisons with the complete American Silurian specimens which were collected in growth position from reef-like environments (Nitecki, 1972a). In this group of receptaculitids calcification was heaviest on the top and the lowest parts were seldom preserved.

The tip of the thallus (apex or nucleus) consists of the central area, generally elevated in adults (figs. 31, 32), and the branches appear to be almost at random. In most other receptaculitids the nuclear area is regular and symmetrical. The number of laterals in the central area is not constant, nor is the centrally positioned branch always observed. Because of the heavy pre- or post-mortem deposition of carbonates, the apex is seldom seen clearly. As in most other receptaculitids, the upper part of the thallus is more frequently preserved due to this heavy calcification.

*Laterals.* — In *Receptaculites* the branches are very short and stout. Most Devonian species are particularly noted for this character. In *R. chardini* the ratio of length to diameter of the laterals varies not only from one individual to another (table 1), but also within the same specimen. Because thalli are incomplete, the ratio of length of the laterals and the size of the thallus cannot be given.

TABLE 1. Measurements (in mm.) of length (L) and diameter (D) of branches of 14 specimens of *Receptaculites chardini*. Specimens prefixed AF.OC and NA are Institut de Géologie, IGAL, Paris, and specimens prefixed FMNH PP are Field Museum fossils.

<u>Specimen Number</u>	<u>L.</u>	<u>D.</u>	<u>L/D</u>
FMNH PP 18163	1.48	0.61	2.43
FMNH PP 18162	1.30	0.24	5.42
AF.OC.13 G10	1.55	0.36	4.30
NA 20	1.03	0.31	3.32
NA 18	1.73	0.80	2.16
NA 10	1.39	0.59	2.35
NA 8	0.87	0.40	2.17
NA 2	1.75	0.52	3.36
NA 15	1.56	0.69	2.26
NA 13	2.00	0.52	3.85
FMNH PP 18154	1.68	0.53	3.17
FMNH PP 18150	1.47	0.52	2.83
FMNH PP 18147	1.80	0.61	2.95
FMNH PP 18148	1.33	0.54	2.46

The laterals consist of a head and a shaft, and a basal part with digitate structures. Some laterals are thin and long throughout (fig. 33); others are thick (figs. 15, 17, 27B, 34B); and barrel-shaped branches (figs. 14, 17, 34A) also occur. The various shapes of laterals are shown in Figure 35.

The branches are smallest at the apex and increase in thickness and in length away from the top (figs. 31, 32). Arrangement of laterals also becomes more regular away from the nucleus. This regularity may be due to a) the increased size of heads and subsequently more regular packing; b) the apparent decrease of additions of new spirals of laterals; and c) greater resistance to destruction of older heads. Calcification also appears to increase outward away from the nucleus. Since laterals increase in length with the distance from the nucleus, the interval between two walls also increases and the fossil thickens. This has been observed on the upper part of the thallus only.

*Measurements of lateral branches.* — It is difficult to take meaningful measurements on receptaculitids. In general, measurements should provide information on growth patterns or reflect the age structure of the population. The growth curve could be based on measurements of laterals (really the only measurable elements) of a single specimen, or of the same branches of various individuals. To determine the number of populations in the sample, all the measure-

ments must also be of branches of the same age. Unfortunately, the nature of preservation of *R. chardini* does not allow for these choices to be made. Measurements of the thicknesses of branches are feasible when an entire branch is exposed. In thin-sections it is difficult to determine if the maximum thickness of the lateral is seen.

Measurements were made on length (L) and diameter (D) of laterals available for measurements (table 1). These were of necessity random samples. Ratios of L/D vary from 2.16 to 5.42. Possibly the measurements (fig. 36) show a) a very uneven growth pattern and b) variation of the individual calcification.

*Shaft of Laterals.*—The shaft consists of the outer and the inner parts (figs. 9, 10). The inner part (core) of the lateral of a very large specimen may be separated from the wall of the main axis by a partition (septum). The recrystallized core is solidly filled with calcite. The thickness of the inner part depends upon the degree of calcification of the branches. Sushkin (1958, fig. 3; 1962, fig. 122) illustrated a specimen in which an inner part is preserved independently from the branch. Thus thin branches may be inner cores preserved by accident, as a result of seasonal calcification or diagenetic alteration. Although Suskin's discovery has been neglected by subsequent workers, his demonstration of the independent preservation of inner parts implied that fossils with varied thicknesses of branches may in effect be the same species. In many Silurian receptaculitids the calcification is so weak that branches appear narrow. Certain Ordovician fossils of North America exhibit both thin and thick laterals.

In *R. chardini* the preservation shown by Sushkin is not observed; however, the core is well developed (figs. 9, 10). Adult branches are barrel-shaped and their cores are also barrel-shaped. The infrequent young, thin, elongated branches have thin and elongated cores. Thus in *R. chardini* the core represents the actual lateral and the outer part corresponds to its calcification. The calcification of branches was therefore very extensive. The thinnest calcification observed is 0.05 cm.

*Lateral head.*—The lateral head consists of the outer plate and inner, interlocking stellate structures. The shafts of laterals generally taper into heads, which are in contact and form a solid pavement (fig. 27B). The heads are flat (figs. 15-17, 27B, 31) with the stellate structures just below them (figs. 14, 24, 32, 34D).

The complete plate (figs. 16, 31-32) is quadrangular (square or rhombohedral). A worn plate (fig. 26) is tetragonal, with less regular edges that weather out into star-shaped figures (figs. 24, 32); this eventually is reduced to a small circle representing a cross-section through the lower part of a branch (figs. 5-13). When the surface is abraded, various depths of heads are exposed (figs. 24, 25, 32); the configuration of the surface changes and plates appear deformed and separate from one another. Thus variations in shape of plates result. Plates are very thin and seldom exceed 0.05 cm. in thickness (FMNH PP 18147). This is the same as the thickness of the calcified layer. The largest plate observed is 1.04 cm. across (FMNH PP 18147). Plates and the stellate structures overlap (fig. 28). The plates when complete form a solid outside pavement, with little or no space between.

Stellate structures are situated just under the plate (figs. 24, 32), and sometimes grade into it (FMNH PP 18147). They are frequently arranged like shingles and overlap one another (figs. 28, 34D). These structures consist of four arms (fig. 4) or ribs of which the longer one extends into the adjoining head (figs. 24, 25). One rib is situated higher (FMNH PP 18165) than others; the opposing arm is the lowest. The remaining two ribs are in one plane. Exceptions to this pattern are found, however, in FMNH PP 18150. Elements of the stellate structures are either in one plane or overlap in such a way that one arm fits between the stellate structures and plates of the previous head (fig. 14). This overlapping of the ribs occurs on the side of the thallus, while horizontal arms are found on the upper and lower flat surfaces of the plant. The curvature of the thallus requires that the stellate structures overlap. The proximity of stellate structures to each other also varies; in FMNH PP 18150 they are either apart or close together. Occasionally the entire head of one lateral fits between the plate and stellate structures of another. In such cases the locked-in head is lower and smaller than the locking head. Fusion of stellate structures (FMNH PP 18161) commonly produces a solid wall below the plate.

*Digitate structures.*—The basal (proximal) parts of branches in *R. chardini* are fused to form an inner wall (pavement). The inner surface of this wall has distinct, digitate structures consisting of fine, finger-like projections (figs. 17-23). Somewhat similar skeletal elements have been figured by Gumbel (1876, pl. A, fig. 18), who considered these to represent folding of the inner wall. We are not able to determine whether Gumbel's structures are diagenetic or



original. In *R. chardini* they are mostly in smaller and in medium-sized individuals. In heavily calcified fossils the fingers are fused (FMNH PP 18151) and together with the pavement form an unusually thick wall. This heavy wall is frequently detached or missing.

The digitate structures are about 2.3 times shorter than the branch and are parallel extensions of the branches. They differ from possibly analogous structures in the Belgian receptaculitids (FMNH PP 18284), in which the digitate structures are the impressions of perpendicular star-like elements. Without careful study of the Belgian material we are not able to compare these in greater detail. The number of receptaculitid taxa present in Belgium is uncertain. The Belgian fossils are currently being studied by Dr. Siegfried Rietschel of the Senckenberg Museum; therefore we will not discuss these further.

*R. chardini* can be compared with *Codium*, a living representative of Siphonales, and with the Ordovician American receptaculitids. The digitate structures of *R. chardini* are similar to the internal filaments of *Codium mamillosum* (Harvey, 1863, pl. 41; Nitecki, 1970, fig. 28) from Australia. *C. mamillosum* is a globose, nearly spherical alga, with well packed outer branches and inner, densely interwoven filaments. We assume that the branch and digitate structure of *R. chardini* is homologous to the utricle and filaments of *C. mamillosum*, and this supports the idea of taxonomic relationship of these two organisms. *R. chardini* appears to possess characters intermediate between Dasycladales and Siphonales.

In certain undescribed Ordovician receptaculitids from the Mississippi Valley, branches have long inner fingers that extend all the way to the central axis. By analogy with these forms *R. chardini* was probably not hollow, and uncalcified portions of the digitate structures may have extended deeper into the thallus. The analogy with *C. mamillosum* suggests that with age *R. chardini* may have progressively become more hollow and the fingers either disappeared, shrunk, or were heavily calcified in older individuals.

We searched our specimens for indications that the digitate structure represents an overgrowth upon the thallus. We found overgrowths (AF 7D20), particularly on the external surfaces, but all are clearly of epiphytic origin. With all epiphytic overgrowths on *R. chardini* (particularly the encrusting corals) there is a distinct demarcation line between the host and the epiphyte. We examined

the digitate structures under the scanning electron microscope (figs. 22, 23) and found them to be an integral part of the branch.

*Calcification.*—The lateral heads are well preserved because they are heavily calcified. The calcification of heads and branches in the lower part of the thallus was much thinner; hence, these structures detached easily. Shafts of laterals are preserved more often than any other parts of branches. Calcification of heads is best seen (FMNH PP 18152) when the heads are exposed on the surface; however, the bases of the laterals, even when in the matrix, are less frequently observed. We assume that heavy calcification of the heads protected outer parts of the body. The thickness of calcification of laterals appears to be correlated with the thickness of branches. The outer calcified layers of shafts of laterals are frequently observed (figs. 5-7).

#### GROWTH PATTERN

The fragmentary nature of *R. chardini* makes a study of its growth stages difficult. The reconstruction of the growth pattern is based upon a) one apparently immature specimen (fig. 37); b) one individual assumed to be young (fig. 4); and c) a number of larger and therefore presumably older organisms (figs. 16, 31-32).

In immature forms the branches are closely packed together (fig. 37A) and are thin and relatively weakly calcified (fig. 37B). The immature laterals lack the outer calcified layer characteristic of older individuals. The shape of the thallus at this stage is not well defined.

Later in young individuals, the thallus elongates into a general egg shape (fig. 4). In this stage the laterals calcify heavily and stellate structures are more or less in one plane (as seen in fig. 4). The digitate structures appear fully formed.

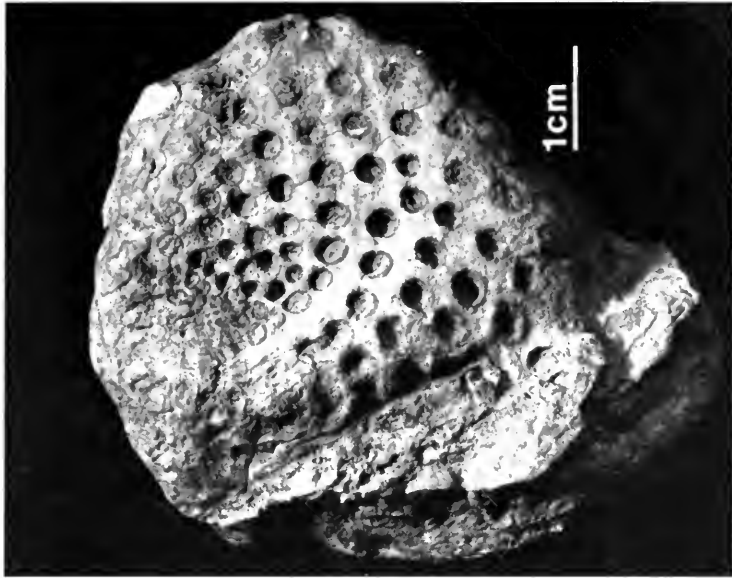
In the adult form, the uppermost part of the thallus becomes elongate and a mammillary projection forms. Branches separate and only plates and some stellate structures are in contact. The fingers of digitate structures fuse to form a heavy solid wall. The growth ceases and only a few new elements are added apically. The growth stages are shown in Figure 29.

#### ACKNOWLEDGEMENT

We thank André Boutiere and Francis Robaszynski for providing specimens for study; G. Waterlot, for helping with identifications; Denise Brice for careful determination of Devonian brachiopods and their stratigraphic meaning; our colleagues in Field Museum for reading the manuscript; and Richard Roesner, Zbigniew Jastrzebski, and Sam Silverstein for their help with illustrations.



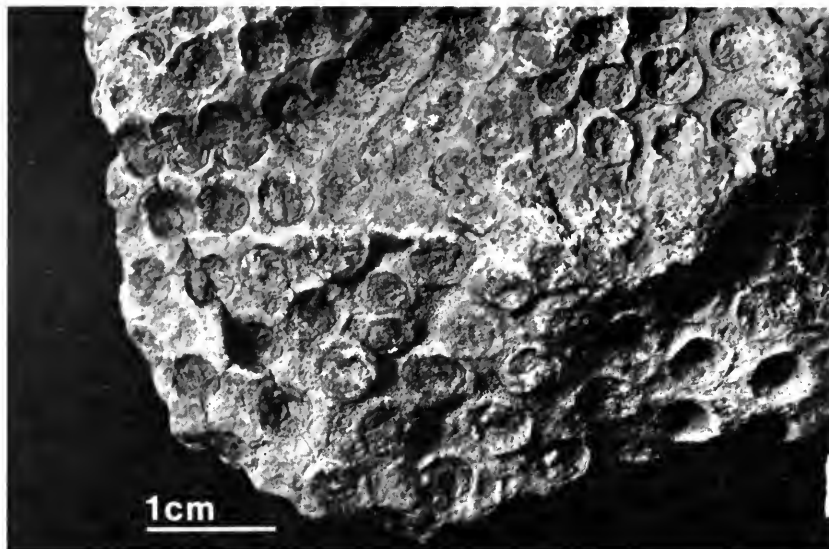
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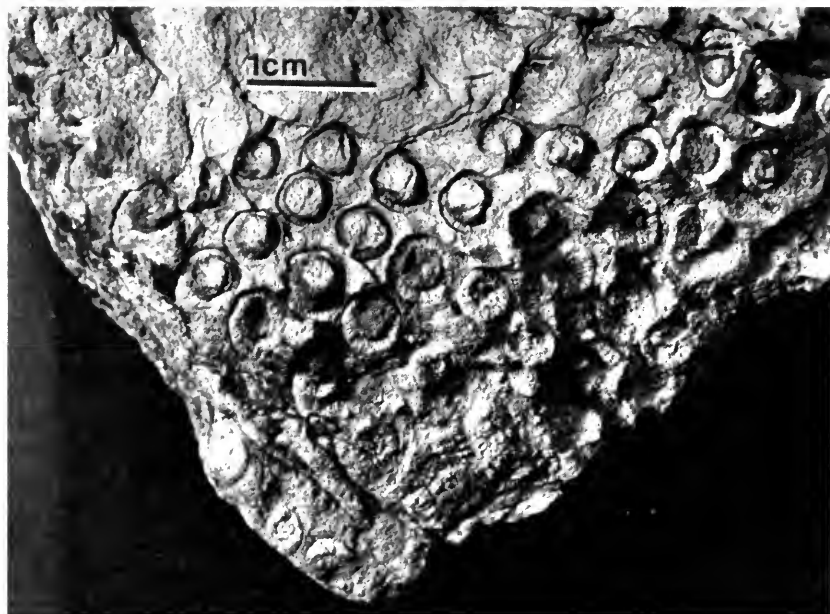
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FIGS. 4 and 5. 4. *R. chardini*, FMNH 18288. The vertical and horizontal lines represent the four ribs of stellate structures. The growth position is not suggested by the orientation of the photograph. 5. Surface of *R. chardini*, FMNH 18167, in which the branches are represented by cavities.

6



7



FIGS. 6 and 7. "Typical" preservation of the surface of *R. chardini*. The thickness of the calcified layer of laterals, is seen particularly well in Figure 7. Figure 6, FMNH PP 18168; Figure 7, FMNH PP 18163.

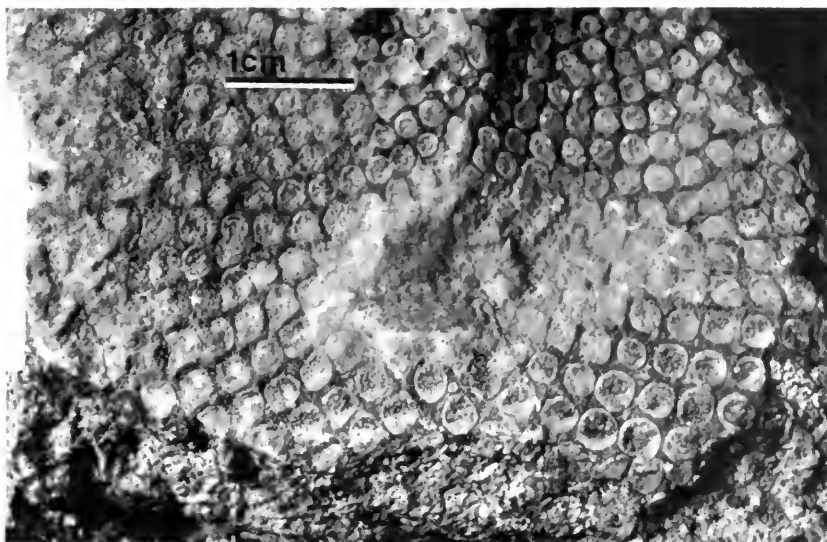


FIG. 8. Surface features of *R. chardini*, FMNH PP 18149, showing the weathering of branches.

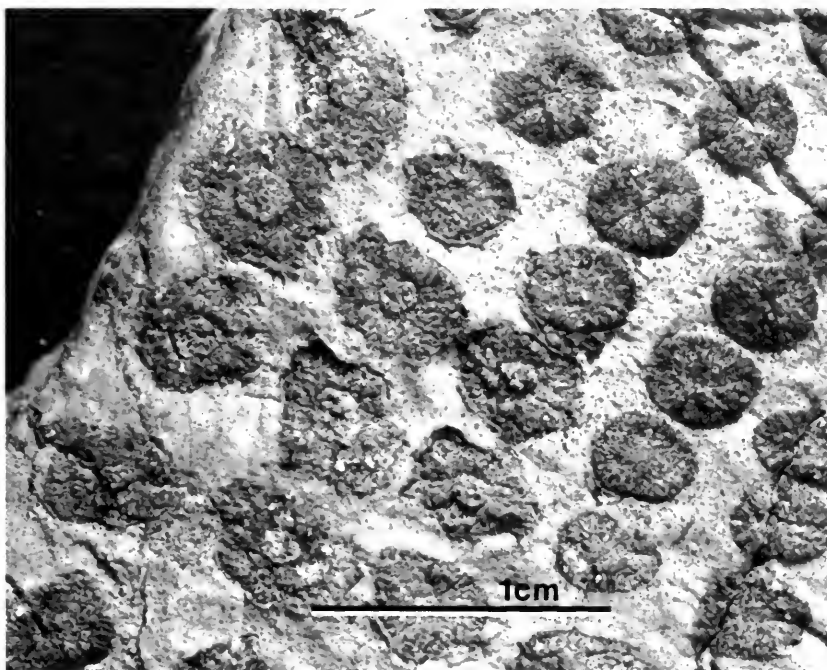


FIG. 9. Branches of *R. chardini*, FMNH PP 18150, showing the central core of laterals.

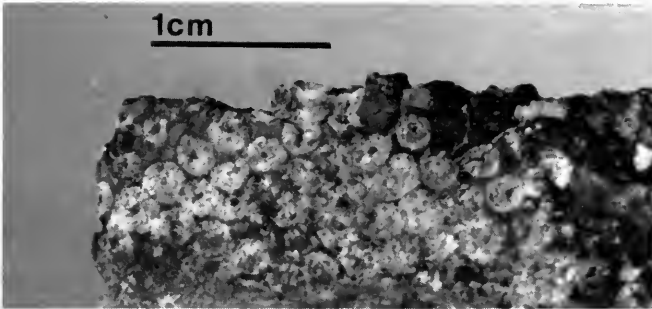


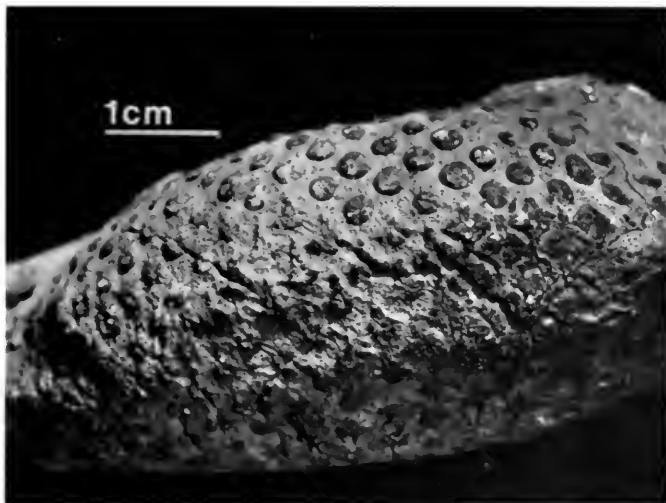
FIG. 10. Central core of laterals of *R. chardini*, FMNH PP 18153. Compare with cores in Figure 9.

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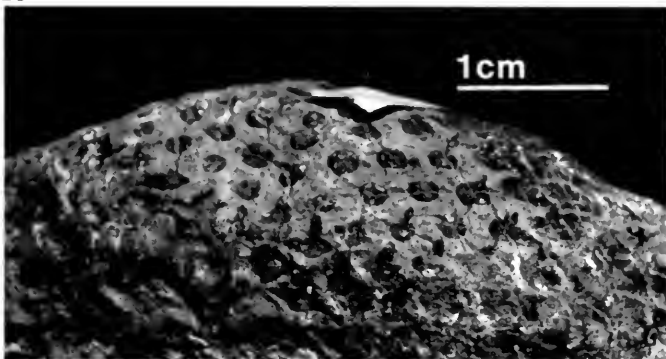


FIGS. 11-13. Holotype of *R. chardini*, FMNH PP 18169, showing various stages of weathering of branches. Round to oval cross-sections through laterals, complete plates, partial stellate and digitate structures are present.

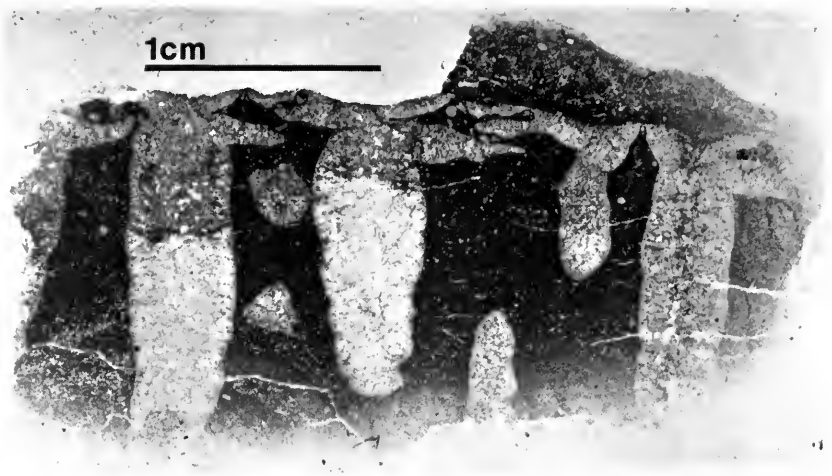
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FIGS. 14-15. Thin-sections cut parallel to the longest axis of branches of *R. charidini*. Figure 14, FMNH 18156; Figure 15, FMNH PP 18152.



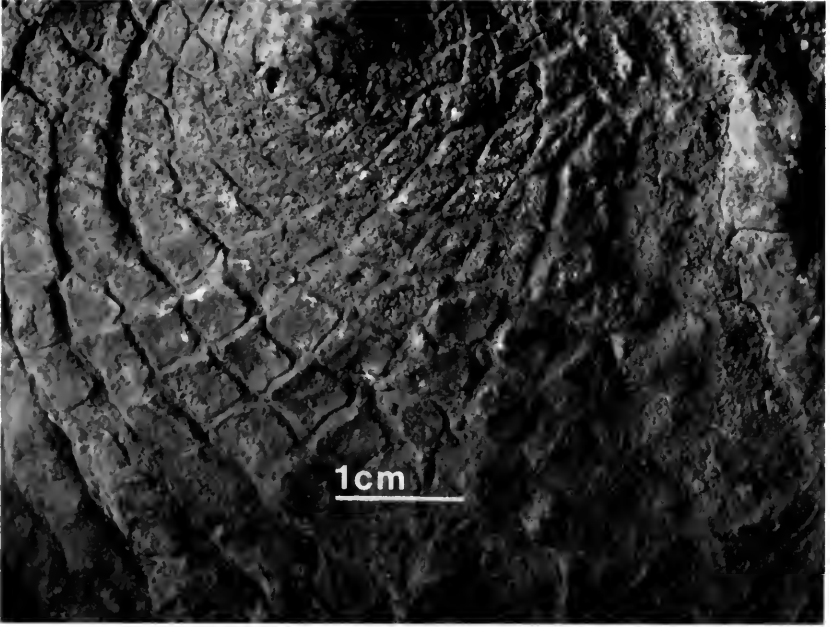
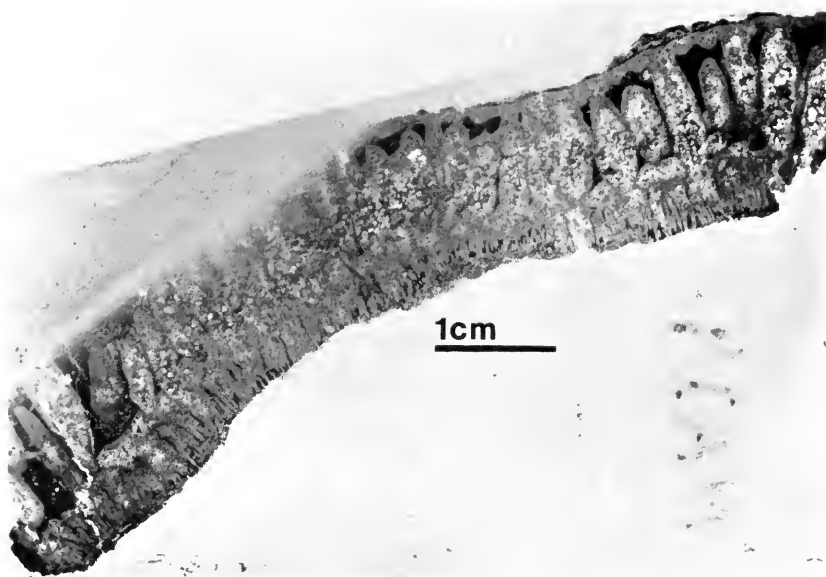
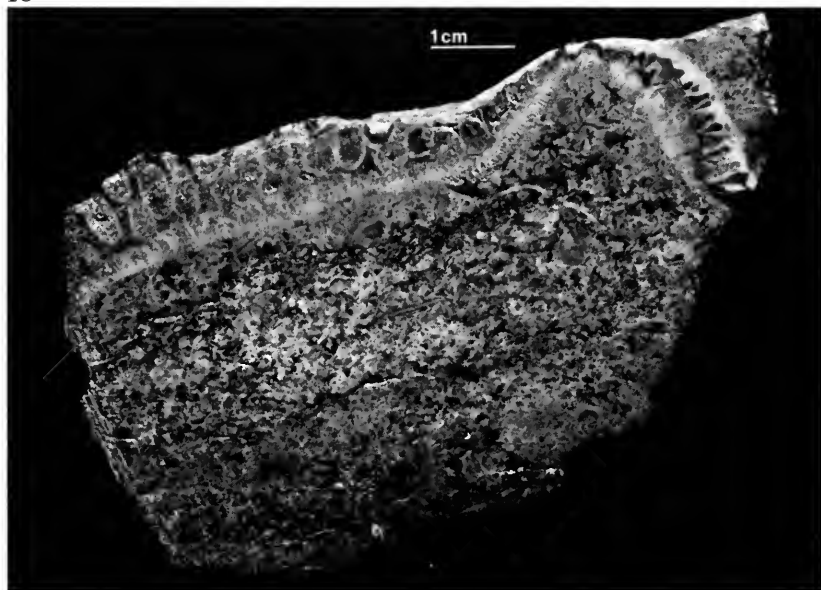


FIG. 16. Plates of the upper surface of *R. chardini*, FMNH PP 18164.

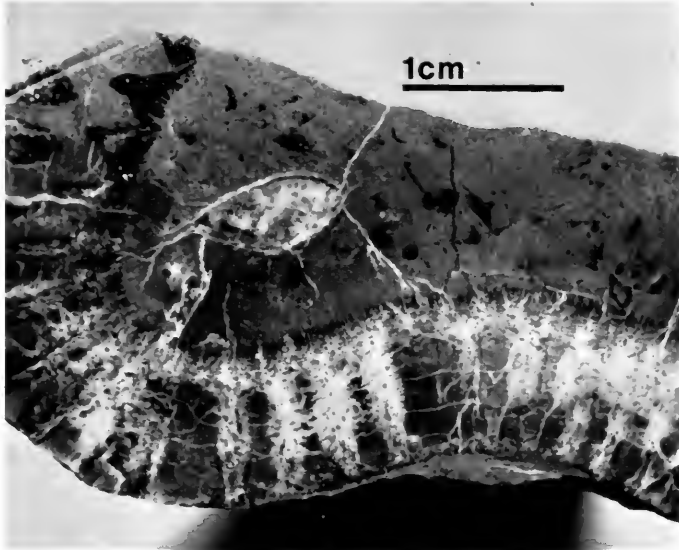
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FIGS. 17-19. Digitate structures of *R. chardini*. Figure 17, thin-section of FMNH PP 18148; Figure 18, weathered surface of FMNH PP 18292; Figure 19, polished section of FMNH PP 18169.

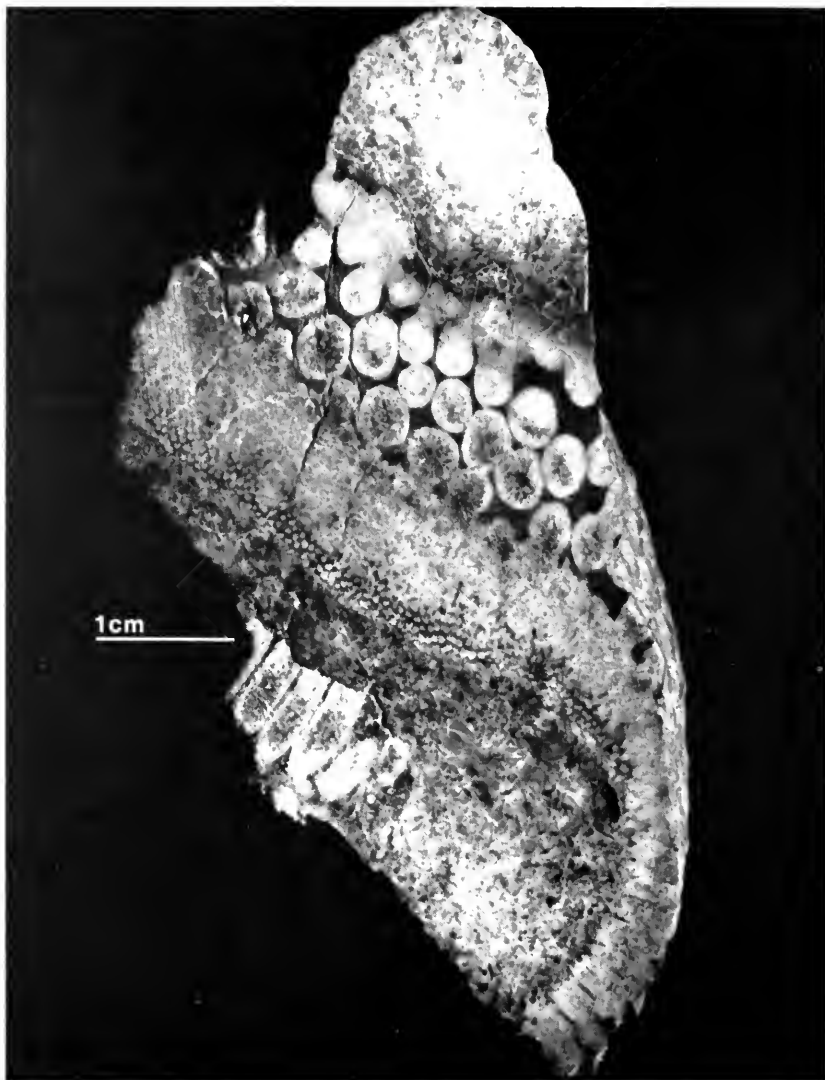


FIG. 20. Thin-section of *R. chardini*, FMNH PP 18293, showing outer and inner calcified walls and the digitate structures.

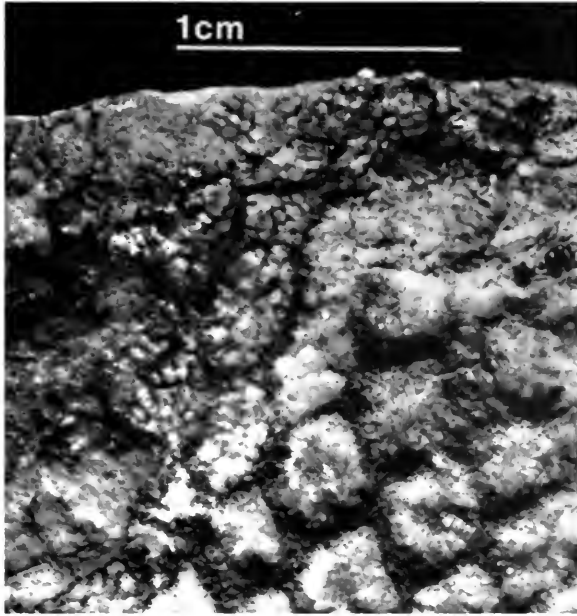


FIG. 21. Distal part of lateral of *R. chardini*, FMNH PP 18290, showing digitate structures.

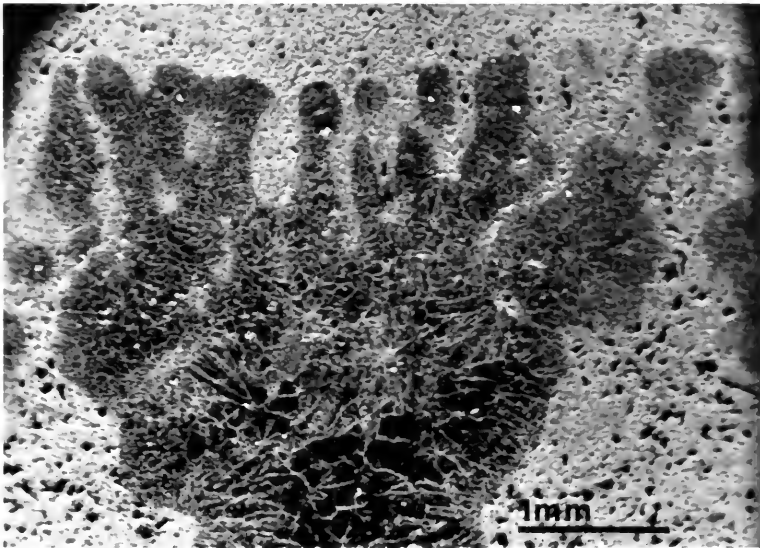


FIG. 22. *R. chardini*, FMNH PP 18169, scanning electron microscope (SEM) view of the etched surface of a digitate structure.

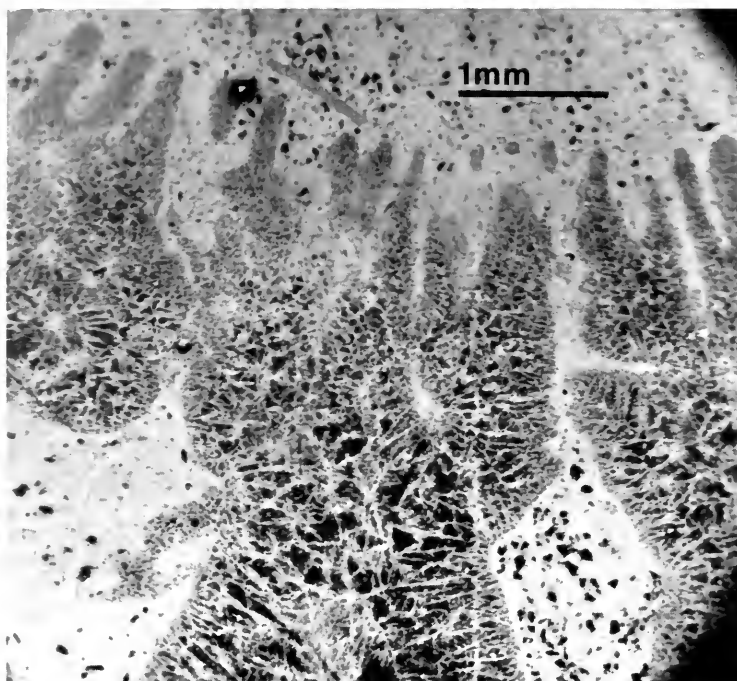


FIG. 23. *R. chardini*, FMNH PP 18169. SEM view of a digitate structure of a different branch than that shown in Figure 22.

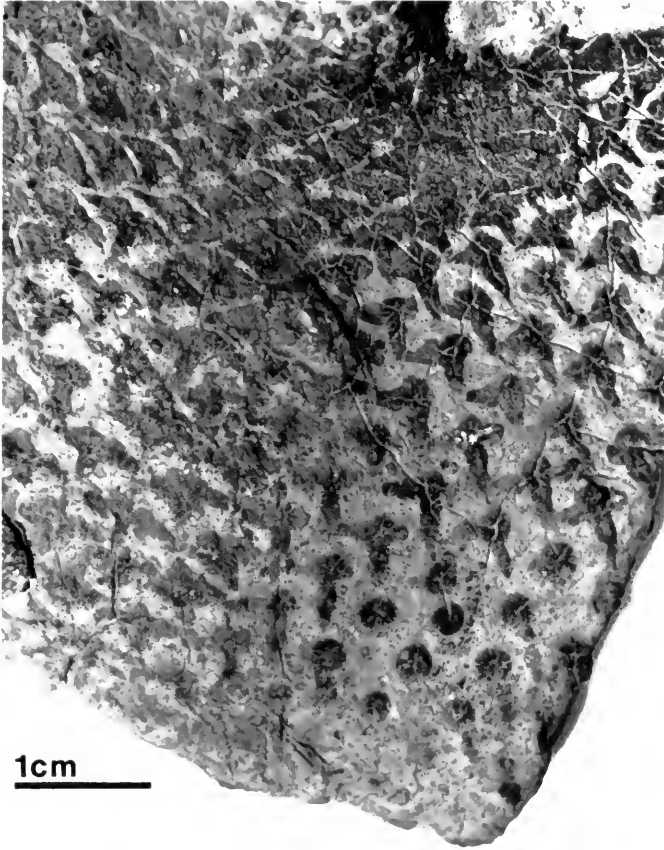


FIG. 24. Various stages of weathering effects upon the surface of *R. chardini*.  
FMNH PP 18150.

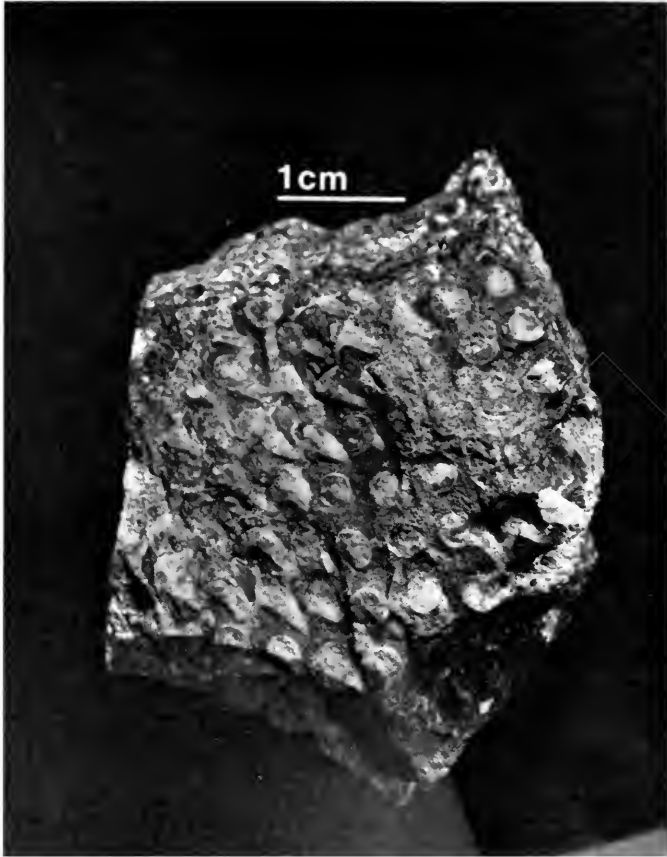


FIG. 25. Preservation of the ribs of stellate structures of *R. chardini*, FMNH PP 18165.



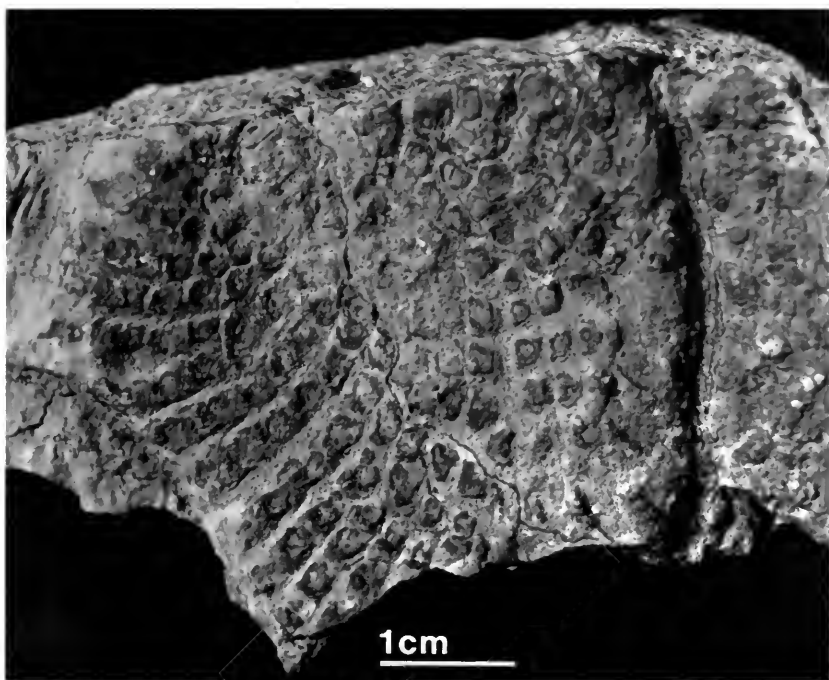


FIG. 26. Spiral arrangement of branches of *R. chardini*, FMNH PP 18161.

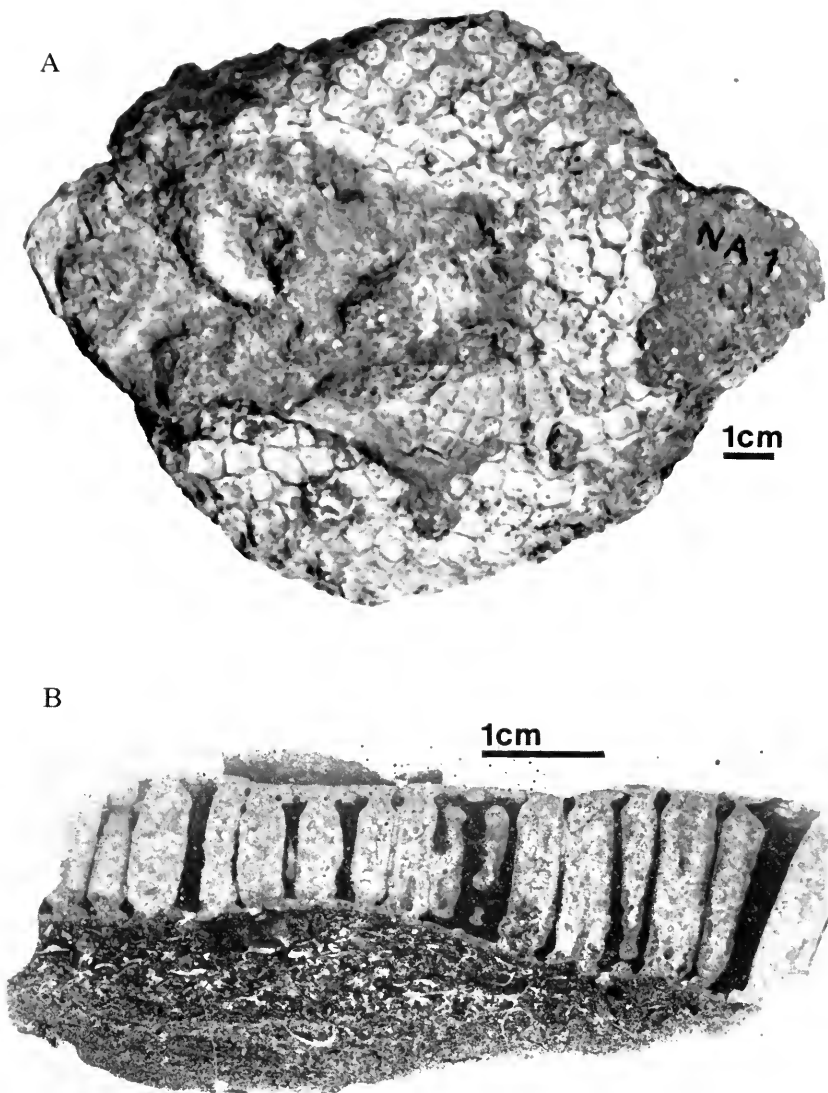


FIG. 27. *R. chardini*, FMNH PP 18147. A, apical view; B, branches in thin-section.

*Opposite:*

FIG. 28. Reconstruction of *R. chardini*. The position of individual lateral heads forming a curvature of the body on the side of the thallus is based mainly on FMNH PP 18156.

FIG. 29. Outlines of thalli of four specimens of *R. chardini* and diagrammatic reconstruction of the growth stages. Based mostly upon FMNH PP 18154 and FMNH PP 18288.

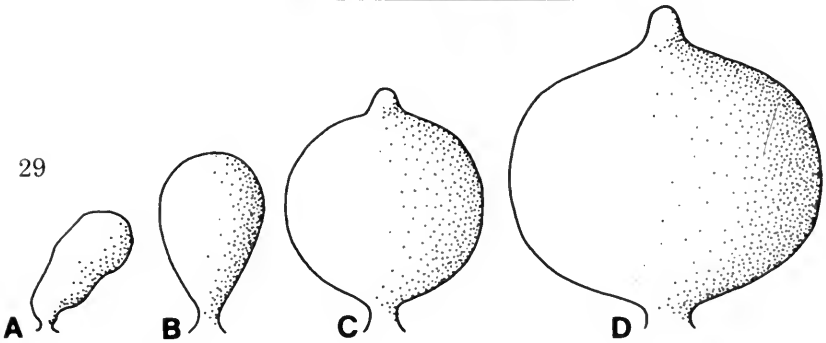
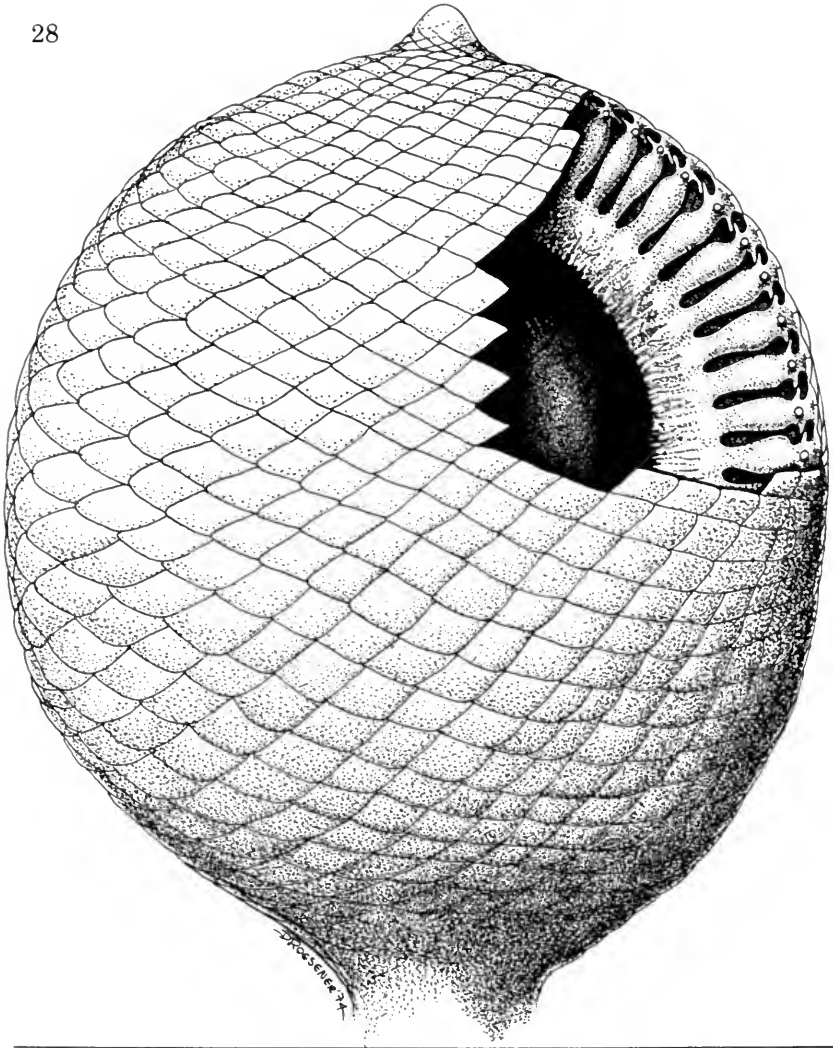






FIG. 30. A and B. Shape of three incomplete thalli of *R. chardini*, FMNH PP 18154.

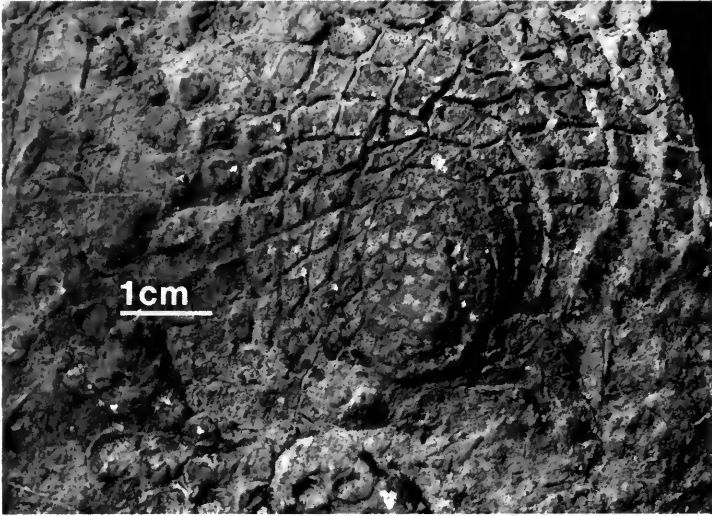


FIG. 31. Elevated apex of *R. chardini*, FMNH PP 18164.

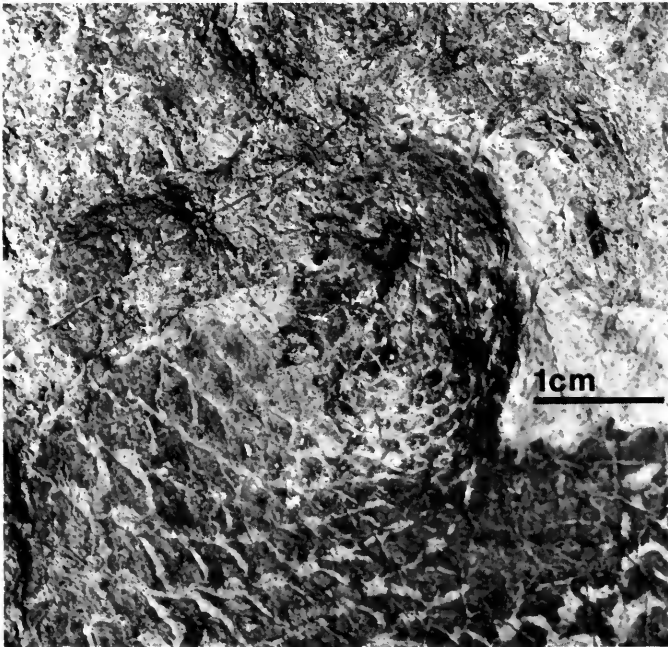


FIG. 32. Elevated apex and variously preserved plates of *R. chardini*, FMNH PP 18150.

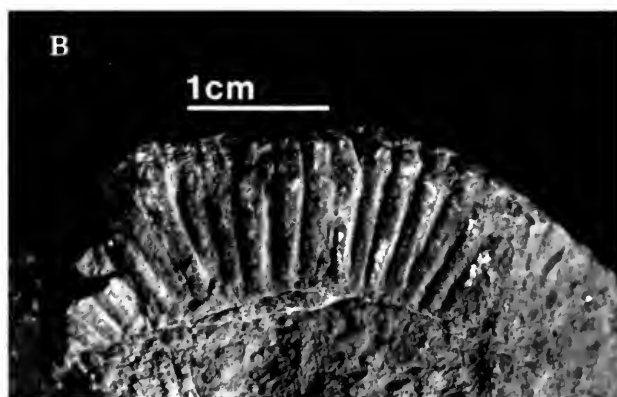
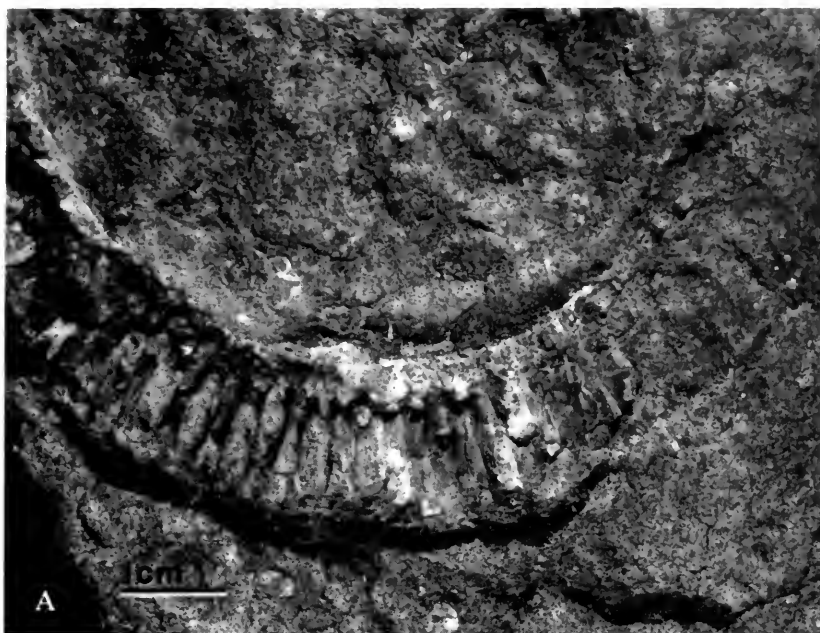
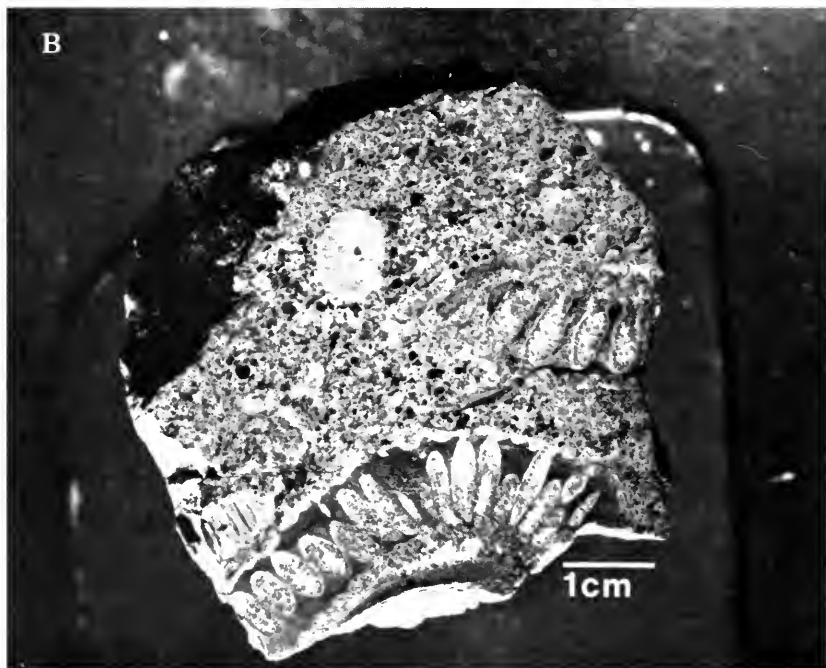
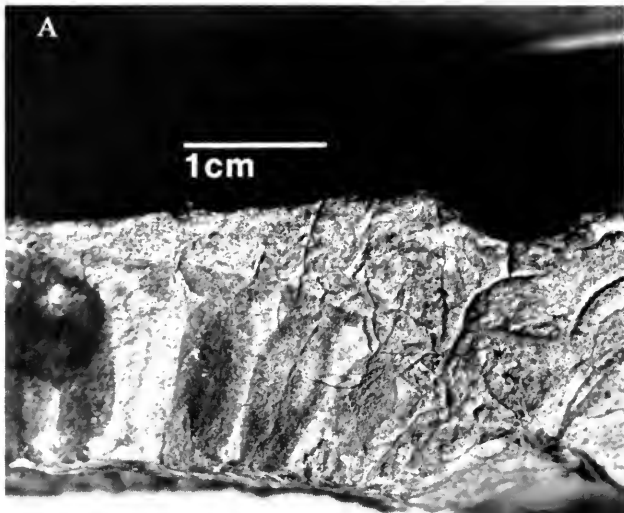


FIG. 33. Relatively thin laterals of *R. chardini*. A, FMNH PP 18289; B, FMNH PP 18162.





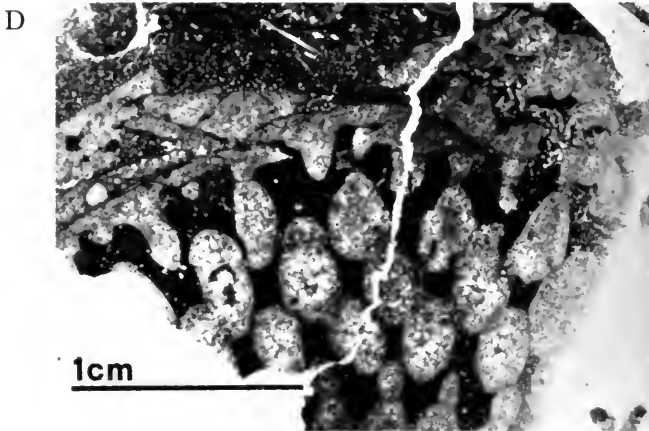
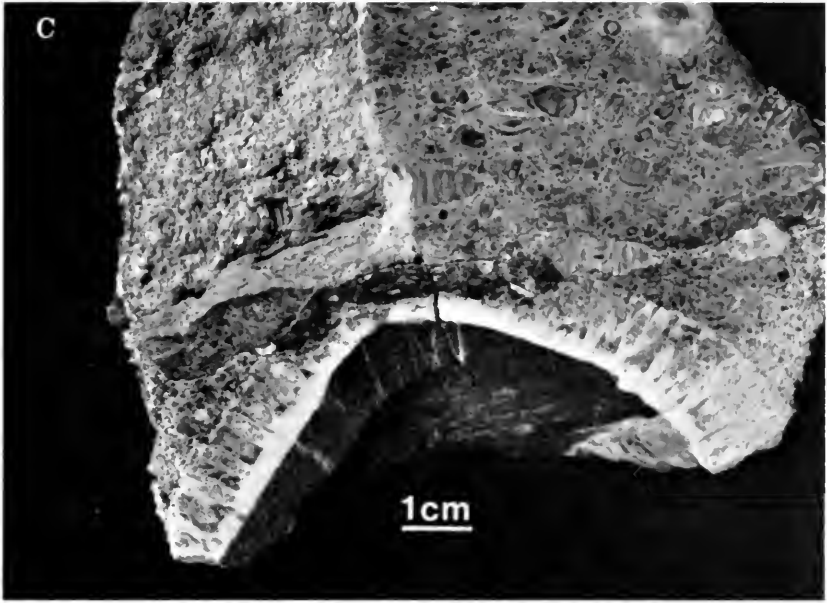


FIG. 34. Laterals of *R. chardini*. A, Barrel-shaped, etched surface, FMNH PP 18150; B, Polished section, FMNH PP 18287; C, Polished section, FMNH PP 18286; D, Thin-section, FMNH PP 18151.

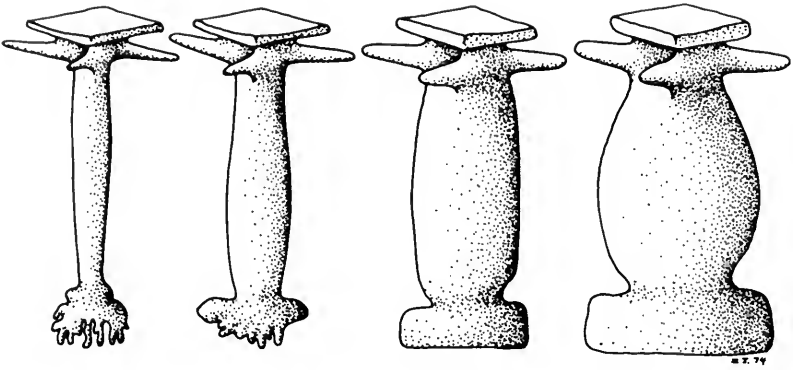


FIG. 35. Reconstruction of various shapes of branches of *R. chardini*, based mostly upon FMNH PP 18162.

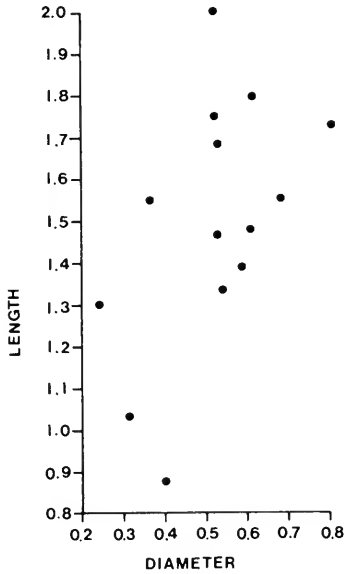


FIG. 36. Plot in mm. Length vs. diameter of 14 specimens of *R. chardini*.

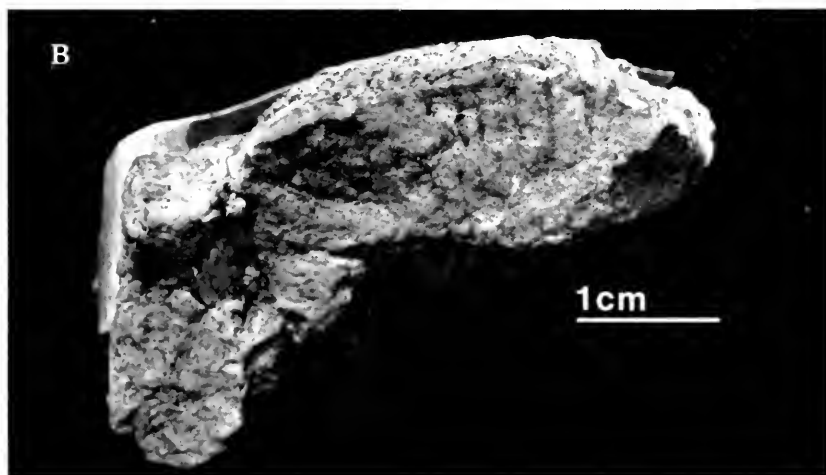
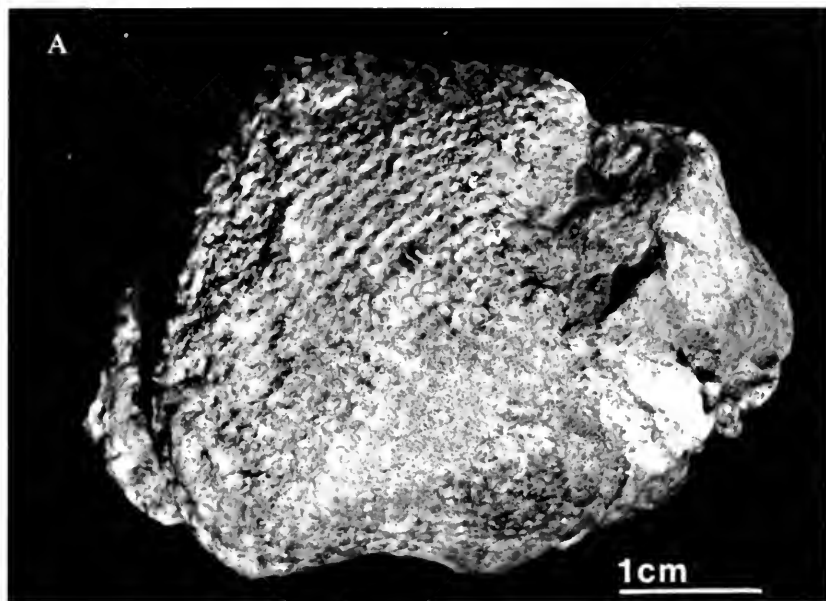


FIG. 37. Immature individual of *R. chardini*, FMNH PP 18285. A, Apical view; B, Lateral branches.

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