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DESMIDOPORA AND NODULIPORA: MISFITS IN THE CORAL WORLD

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Skeletal morphology and its variation are described in *Desmidopora alveolaris* and in *Nodulipora acuminata*. The features of these Silurian fossils suggest sclerosponge affinities. Pores are present in both species and the surface of *Nodulipora* carries astrophorae. A comparison is made between skeletons of sclerosponges and tabulates: favositids are interpreted as the skeletons of sponges.

Key words: Sclerospongiae, morphology, taxonomy, relationships, Silurian.

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INTRODUCTION

In a study on the solenid growth habit of *Palaeofavosites* Twenhofel (Stel and Oekentorp 1976) the Nicholson (1886) pictures of *Desmidopora alveolaris* were interpreted as these of a palaeofavositid with a *Multisolenia* habitus. However, the type material proved this idea to be incorrect. As *Nodulipora* Lindström frequently is considered as a junior synonym (see Hill and Stumm 1956) of *Desmidopora* Nicholson, this monotypic genus was involved in a reconsideration.

The material was collected at Wren's Nest, Dudley (Great Britain), at Tjautet 1, Gotland (Sweden) and borrowed from the British Museum, London, the University of Birmingham and the Riksmuseet at Stockholm.

As the surface of an individual tube is more related to function of the living tissue within it than the tube diameter (according to literature the foremost characteristic at species level) both parameters were measured by means of a semi-automatic MOP-AMO 3 measuring system, placed at the authors' disposal by the firm Ahrin, The Hague, The Netherlands. For a description of this system the reader is referred to Stel (1978b). When measuring, the periphery of a tube was defined as the middle of a wall. The parameters were measured from enlarged photographs of both the surface of colonies and of thin sections/peelings. Statistic

procedures were executed by applying standardized WESP-computer programs (van der Weel 1977) on a Cyber 74—18 at the Rekenentrum of the University of Groningen.

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MORPHOLOGY OF *DESMIDOPORA ALVEOLARIS* NICHOLSON, 1886

Nicholson (1886) established the genus *Desmidopora* for a fossil he had described earlier that year as a stromatoporoid, under the name *Labechia alveolaris* Nicholson. Because of the occurrence of pores, Nicholson classified *Desmidopora* as a favositid. A possible relationship with *Alveolites* Lamarck, *Chaetetes* Fischer and *Labechia* M.-Edwards et Haime was also discussed. Fritz (1939) discussed the apparent similarity between *Desmidopora* and *Multisolenia* Fritz and considered them as different monotypic genera. Fitzgerald (1955) described *D. multitabulata* from the Silurian of New South Wales, Australia, as a tabulate coral. Hill and Stumm (1956) considered *Desmidopora* as a favositid because of the occurrence of pores. Tesakov (1960) studied some colonies of *Desmidopora*, found in Podolia, the USSR, and demonstrated the chaetetid affinities of this genus. However, this interpretation was partly based on a supposed homology of pores as small-scale-growth interruptions and gaps in the walls between neighbouring tubes. Although pores in favositids are indeed the result of localized brief growth interruptions in the wall (Stel 1978a), Tesakov's view is incorrect because even in meandroid tubes of *Desmidopora* pores, with pore plates, are found. Sokolov (1962), following Tesakov's views, ranged *Desmidopora* in the Chaetetiporinae Sokolov. Stel and Oekentorp (1976), studying the solenid growth habit of palaeofavositids, considered both *Multisolenia* and *Desmidopora* as palaeofavositids. This view was not shared by Powell and Scrutton (1978).

Desmidopora alveolaris Nicholson, 1886

1886a. *Labechia alveolaris* Nicholson: 83.

1886b. *Desmidopora alveolaris* Nicholson: 289, pl. 8: 1—8.

1939. *Desmidopora alveolaris* Nicholson; Fritz: 512, pl. 59: 1—2.

1960. *Desmidopora alveolaris* Nicholson; Tesakov: 48, pl. 4: 1—7.

Material.—A dozen colonies of *Desmidopora alveolaris*, collected from the Wenlock Limestone at Wren's Nest near Dudley, Great Britain; two colonies from the Hollcroft collection of the Geological Institute of the University of Birmingham, Great Britain; three fragments from Wren's Nest, the type material of Nicholson, stored in the British Museum in London, Great Britain; three colonies of *Desmidopora alveolaris* found by the author in the Slite Beds (unit g) at Tjautet 1, Gotland, Sweden.

Table 1

Parameters of the tubes in thin sections of five colonies of *Desmidopora* from Dudley [B 2.404.02—08]

| | Samples B2.404.02-08 Wenlock Limestone, Dudley | | | | | | | |
|------------------|--|------|-------|-------|------|------|------|------|
| | \bar{x} | S | Sk | K | min. | max. | G | N |
| Area | 0.56 | 0.40 | 2.88 | 15.10 | 0.10 | 3.70 | 0.45 | 1890 |
| D _{max} | 1.07 | 0.62 | 3.29 | 18.47 | 0.10 | 6.10 | 0.90 | 1890 |
| Δx | 0.92 | 0.49 | 3.33 | 19.67 | 0.10 | 5.70 | 0.79 | 1890 |
| Δy | 0.97 | 0.53 | 3.58 | 23.40 | 0.30 | 6.10 | 0.83 | 1890 |
| Wt | 0.12 | 0.03 | 0.80 | 3.87 | 0.06 | 0.23 | 0.11 | 556 |
| Wl | 0.12 | 0.03 | 0.85 | 3.77 | 0.05 | 0.24 | 0.12 | 211 |
| Dp | 0.14 | 0.04 | 0.97 | 4.66 | 0.04 | 0.32 | 0.13 | 427 |
| Dt | 0.47 | 0.13 | -0.14 | 3.61 | 0.08 | 1.04 | 0.49 | 300 |

Description.—The form of the colony is highly variable and ranges from an expanding sheet or successions of sheets (the Dudley material), to thick massive colonies (the Gotland material, pl. 22: 1). This difference in colony shape is probably caused by ecological factors. At the base of the colonies growth bands are frequently seen. The surface of platy colonies shows many irregularities such as small knobs (diameters up to 1.7 cm, height about 1.5 cm) and raised platforms. Small cracks are probably due to fractioning during early compaction.

In the platy colonies from Dudley, marly intercalations are frequently found. It is noteworthy that thin (the mean tabulae-distance 0.5 mm approximately) sediment covers hardly affected the organism, while thick (> 2 mm) sediment covers killed the animal. In the former situation the walls extend above the sediment cover whereas in the latter situation the silted area is usually overgrown laterally from intact parts of the organism. The variability in tube size is striking; both polygonal and meandroid tubes are found (pl. 22: 2a). The graphs shown in figure 1 were constructed from the data of 1890 area-measurements from five colonies collected at Wren's Nest, Dudley. The statistic parameters of the characters are summarized in table 1. The range of the tube area is 0.10—3.70 mm², most frequently the range is between 0.10—1.30 mm², while regularly meandroid tubes with an area of 1.70—1.90 mm² occur. The range of the tube diameter varies, but the graphs of D_{max} and Δy are almost identical and the range most frequently found is 0.40—1.60 mm. The concentration of meandroid tubes with an area of about 1.80 mm² is not reflected in the graphs of the tube diameters. The mean wall thickness is 0.12 mm, the mean diameter of the mural pores is 0.14 mm (table 1). Growth of the colony occurred by axial increase.

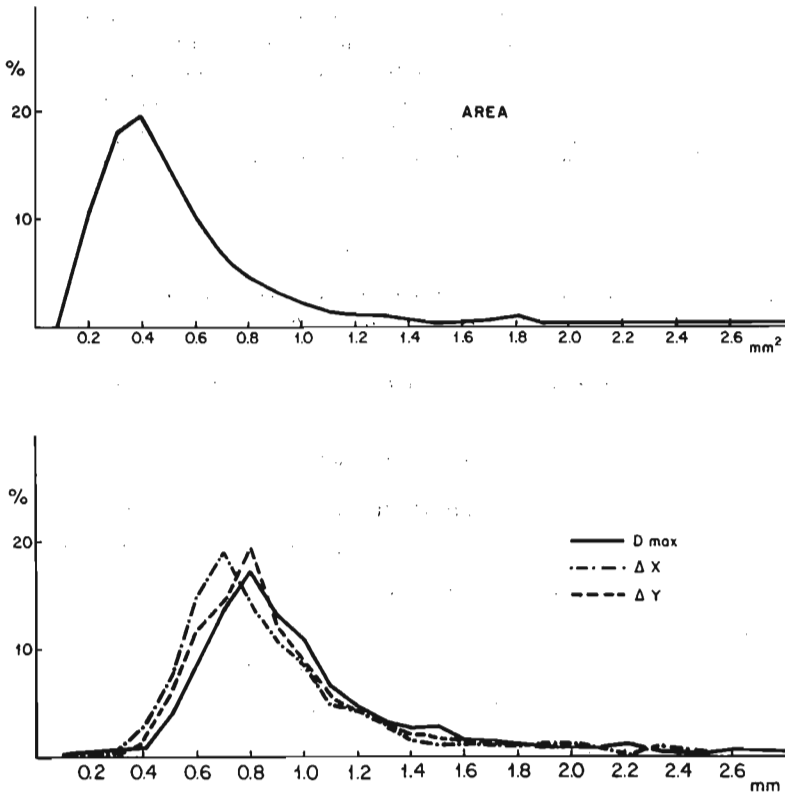


Fig. 1. Frequency distribution in 1890 measurements on thin sections from five colonies of *Desmidopora*, Wenlock Limestone, Dudley [B 2.404.02—08].

Table 2

Parameters of the tubes in a thin section of a colony of *Desmidopora* from Gotland [B 2.404.01]

| Sample B2.404.01 | Slite Beds, Tjautet 1 | | | | | | | |
|------------------|-----------------------|------|------|------|------|------|------|-----|
| | \bar{x} | S | Sk | K | min. | max. | G | N |
| Area | 0.75 | 0.44 | 1.85 | 6.51 | 0.20 | 2.70 | 0.61 | 502 |
| Dmax | 1.27 | 0.61 | 1.95 | 7.26 | 0.60 | 4.80 | 1.06 | 502 |
| Δx | 1.05 | 0.44 | 2.11 | 8.77 | 0.50 | 3.80 | 0.91 | 502 |
| Δy | 1.18 | 0.57 | 2.21 | 8.66 | 0.50 | 4.40 | 0.99 | 502 |
| Wt | 0.16 | 0.03 | 0.60 | 4.49 | 0.08 | 0.29 | 0.15 | 217 |

The graphs shown in figure 2 were constructed from the data of 502 measurements of a sample from a thin section of *D. alveolaris* found at Tjautet 1, Gotland. The statistic parameters of the characters are summarized in table 2. The range of the tube area is 0.20—2.70 mm²; most frequent are surfaces 0.20—1.20 mm². The tube diameters vary 0.60—4.80 mm, but diameters 0.60—1.80 mm predominate. The mean

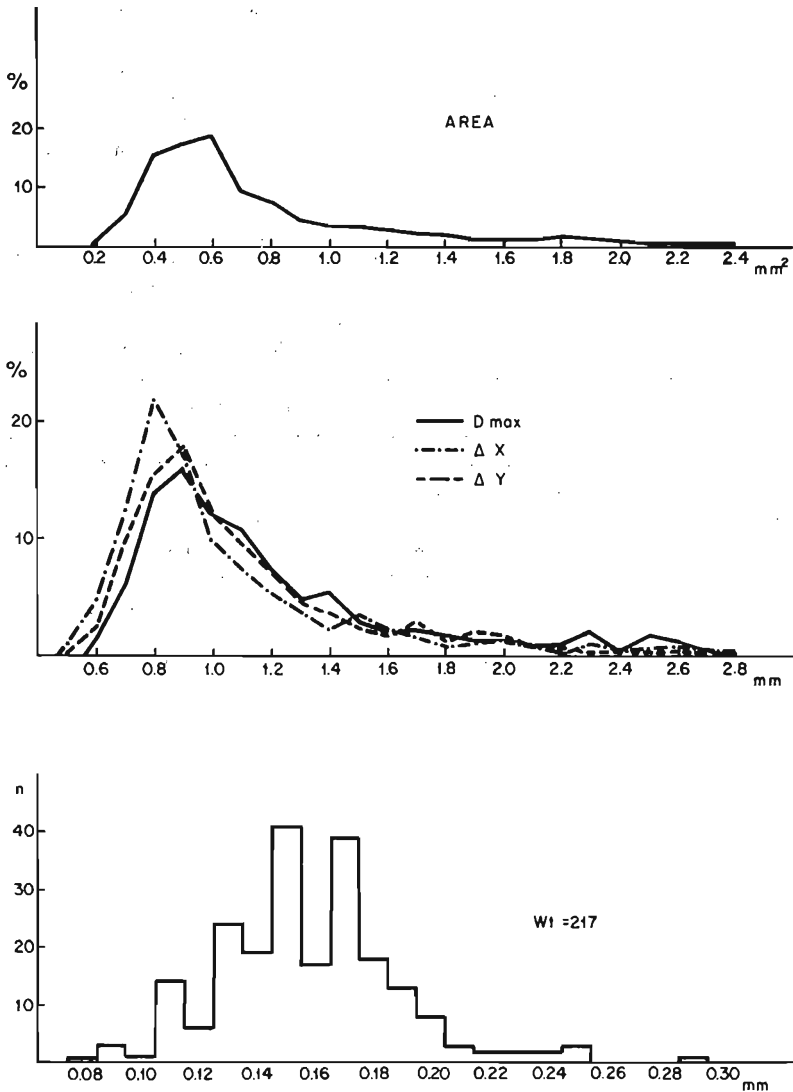


Fig. 2. Frequency distribution in 502 measurements on a thin section of a *Desmidopora* colony, Slite Beds, Tjautet 1, Gotland [B 2.404.01].

thickness of the wall is 0.16 mm. Mural pores are numerous (pl. 22: 2b). Axial increase was observed in the colony. The data of this colony are within the range of those found at Wren's Nest, although its wall thickness is larger. In all colonies of *D. alveolaris* pores are found, which are frequently closed by pore plates. However, the number of pores in the colony described above is larger than in colonies from Dudley.

Discussion.—Tesakov (1960) demonstrated the chaetetid affinities of *Desmidopora*, a view which is supported by this investigation. The morphological similarity between *Desmidopora* and chaetetids like the Palaeozoic chaetetiporids and the Mesozoic blastochaetetids is striking. Tesakov interpreted the mural pores in

Desmidopora as growth interruptions of a single trabeculum. Consequently, these pores would be homologous with large-scale growth interruptions causing the formation of meandroid tubes. In the senior author's opinion the mural pores are, just as in favositids (Stel 1978a), indeed the result of a temporary growth interruption of a part of the wall. However, this does not imply that such gaps, which lead to the formation of meandroid tubes and which indicate a complete fusion of the living tissue, are comparable to mural pores that are some hundred times smaller openings. Therefore *D. alveolaris* is either a chaetetid with pores or a favositid with a chaetetid morphology!

Hartman and Goreau (1972) made a detailed comparison between the recent sclerosponge *Ceratoporella nicholsoni* Hickson and chaetetids. The authors concluded that ceratoporellids are descendants of chaetetids, a view based on the identical increase, on the generally similar tube size, on the morphology of the tubes and on the microstructure of the wall. On the other hand, some striking differences occur as the presence of loose siliceous spicules and the infilling of the tubes by aragonite. As the absence of spicules may have been caused either because these were not entrapped in the skeleton (*Acanthochaetetes*) or because they were dissolved in early diagenesis, this feature is not difficult to explain.

In a later paper Hartman and Goreau (1975) compared the sclerosponge *Acanthochaetetes wellsi* Hartman et Goreau with Mesozoic acanthochaetetids. The acanthochaetetid affinities of this recent sclerosponge were demonstrated by both the macroscopic (astrorhizae, intermural increase, tube with tabulae and spines) and the microscopic (calcitic skeletons, lamellar microstructure) features. As a consequence chaetetids nowadays are interpreted as the skeletons of sponges *in casu* sclerosponges. Fischer (1977) distinguished the three following groups of sclerosponges:

- Chaetetida: Chaetetidae and Varioparietidae; Ordovician-Miocene;
- Tabulospingida: Acanthochaetetidae; Triassic-Recent;
- Ceratoporellida: Ceratoporellidae; Triassic-Recent.

For a detailed study of Palaeozoic chaetetids the reader is referred to Sokolov (1962) and of Mesozoic chaetetids to Fischer (1970).

Distribution — *D. alveolaris* is found in the Silurian (Wenlock) of Australia, Great Britain, Sweden and the USSR.

MORPHOLOGY OF *NODULIPORA ACUMINATA* LINDSTRÖM, 1873

Lindström (1896) described in detail a peculiar fossil from the Höglint, Slite and Halle Beds of Gotland. Although most characteristics of *Nodulipora* are also met with in *Desmidopora*, Lindström did not consider these two monotypic genera as synonyms because of differences in colony shape and the occurrence of talon-like outgrowths on *Nodulipora*. On the other hand, Lindström was convinced that skeletons of both forms probably were secreted by closely related organisms. Hill and Stumm (1956) considered *Nodulipora* as a synonym of *Desmidopora*, whereas Tesakov (1960) regarded both *Desmidopora* and *Nodulipora* as separate chaetetids. Hartman and Goreau (1975), in discussing the possible relationship between *Acanthochaetetes wellsi* and favositids, stressed the presence of astrorhiza-like patterns in *Nodulipora*, a feature also described by Lindström. According to Hartman and Goreau the presence of *Nodulipora* and *Desmidopora* might indicate the existence of several additional subgroups of sclerosponges in Palaeozoic times.

Nodulipora acuminata Lindström, 1873

1896. *Nodulipora acuminata* Lindström: 18, figs. 31—42.

1975. *Nodulipora acuminata* Lindström; Hartman and Goreau: 11, fig. 15.

Material. — A hundred colonies from the Wenlock of Gotland. Collection: Naturhistoriska Riksmuseet, Stockholm, Sweden.

Description. — The colonies are mostly small (height about 2 cm) and show a highly variable form. Scolecoïd, ceratoid, cylindrical and mushroom-shaped colonies are found with all kinds of combinations between these types. Sometimes some more or less ceratoid colonies are completely grown together. Other divide in two or more small subcolonies which develop separately but may fuse again later on (fig. 3). A striking example of this process is demonstrated by a disc-shaped colony Lindström found at Fårö.

Table 3

Parameters of the tubes in a thin section of a *Nodulipora* colony from Gotland [Cn 59685]

| | Sample Cn 59685 | | Höglint Beds, Hall sn. Vestöös Kanal | | | | | |
|------------|-----------------|------|--------------------------------------|------|------|------|------|-----|
| | \bar{x} | S | Sk | K | min. | max. | G | N |
| Area | 0.31 | 0.10 | 0.50 | 3.13 | 0.10 | 0.60 | 0.30 | 149 |
| Dmax | 0.69 | 0.11 | 0.24 | 2.92 | 0.40 | 1.00 | 0.69 | 149 |
| Δx | 0.67 | 0.12 | 0.07 | 2.80 | 0.40 | 1.00 | 0.66 | 149 |
| Δy | 0.67 | 0.12 | 0.31 | 3.11 | 0.40 | 1.00 | 0.66 | 149 |
| Wt | 0.14 | 0.04 | 0.12 | 2.58 | 0.06 | 0.24 | 0.14 | 143 |
| Wl | 0.15 | 0.03 | 0.70 | 4.47 | 0.07 | 0.27 | 0.15 | 103 |

Judging from the surface of this fossil (pl. 23: a) one would hardly be able to conjecture that the underside shows that the 'colony' is built up by at least 20 small colonies of *Nodulipora*! Although a smaller colony may sometimes have been overgrown by a large one, the colonies mostly grew together completely. This fusion is well seen in the right part of the compound colony depicted in pl. 23: b. Anyhow, this phenomenon suggests that the organisms secreting these skeletons, fuse easily and subsequently secrete a joint skeleton.

At the epitheca of the colonies growth bands are seen. The orientation of these bands helps to interpret the talon-like outgrowths (= Lindström's stolons) which are seen at the outside of a colony. In some specimens, a new subcolony develops from such a talon-like outgrowth. These structures may be homologous with the stalks by which the mushroom-shaped lamellae of the Recent demosponge *Esperiopsis challengerii* (Ridley) are attached to a peduncle (see Hartman and Reischwig 1973). However, such an interpretation is unlikely if no subcolonies were preserved. The talons sometimes grew downwards alongside or wound around the colony (fig. 4) over a distance of about one centimeter, while others formed root-like structures. Most of these structures certainly are not endobionts; they form a part of the skeleton.

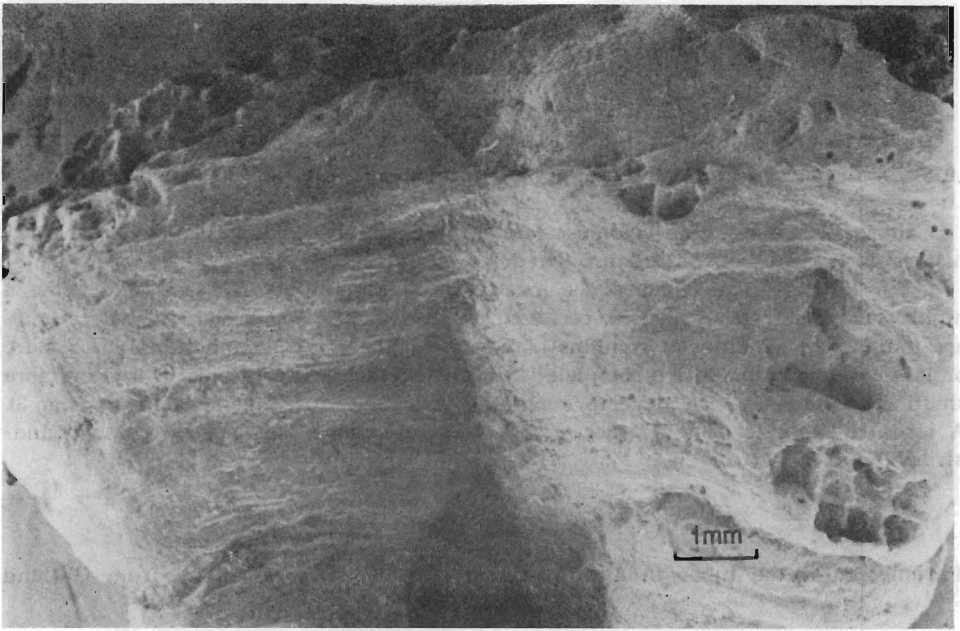


Fig. 3. Scan-micrograph of *Nodulipora acuminata* from the Högklint Beds of Gotland, showing fusion of subcolonies.

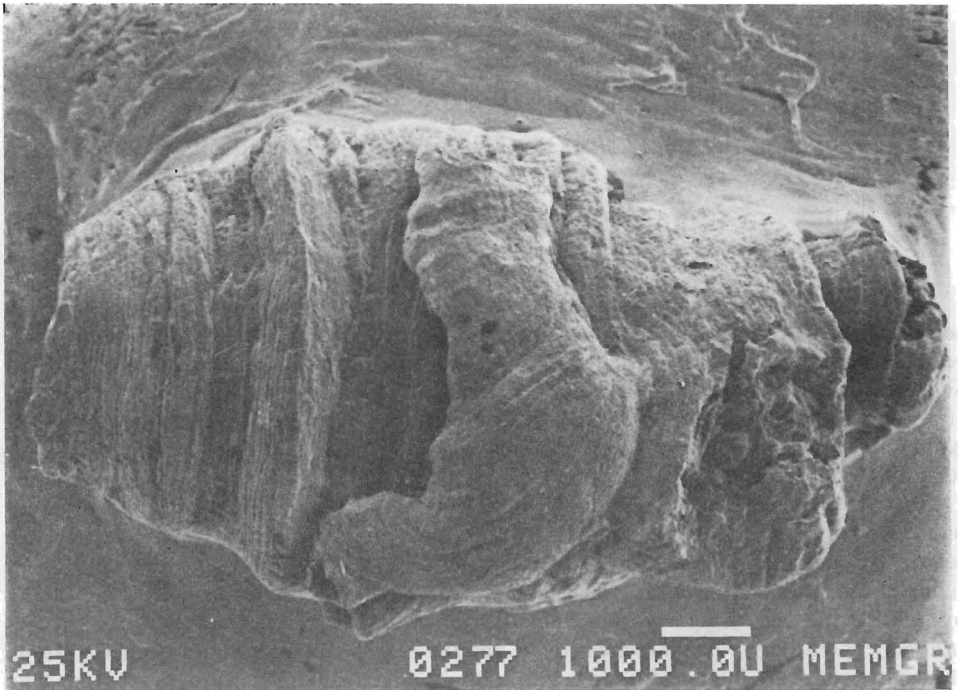


Fig. 4. Scan-micrograph of a talon-like outgrowth. Analysis of the growth rings suggests this outgrowth forms a part of the *Nodulipora* skeleton.

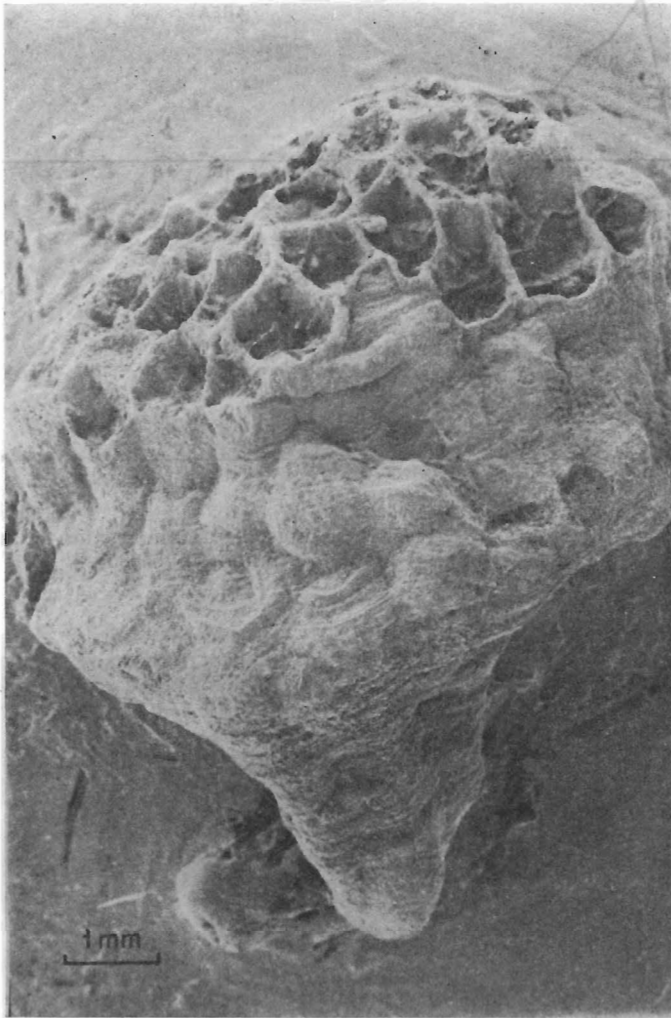


Fig. 5. Scan-micrograph of a *Nodulipora* colony showing polygonal tubes. Pores are seen in the tube walls.

The surface of the colony consists of polygonal and/or meandroid tubes (fig. 5) or of radially arranged meandroid tubes. As already stressed by Lindström (1896), astrorrhizae are sometimes found in the surface of the colony. Some specimens in the type sample show pillars (Hartman and Goreau 1975: fig. 15). These do not fit within Lindström's definition of *Nodulipora* and probably are stromatoporoids (*Lophiostroma* Nicholson?).

The graphs in figure 6 were constructed from the data of 149 measurements of a thin section (Cn 59685) from *N. acuminata*, found at Hall sn Vestöös Kanal, Gotland. The statistics parameters of the characters are summarized in table 3. The range of the tube area is 0.10–0.60 mm² and of tube diameters is 0.40–1.00 mm. It is seen that, due to the small dimensions of the tubes, the discrepancy caused by the different measuring methods is negligible. The wall thickness is about 0.15 mm; a dark line is not seen in the wall. In polygonal tubes, complete, more or less horizontal

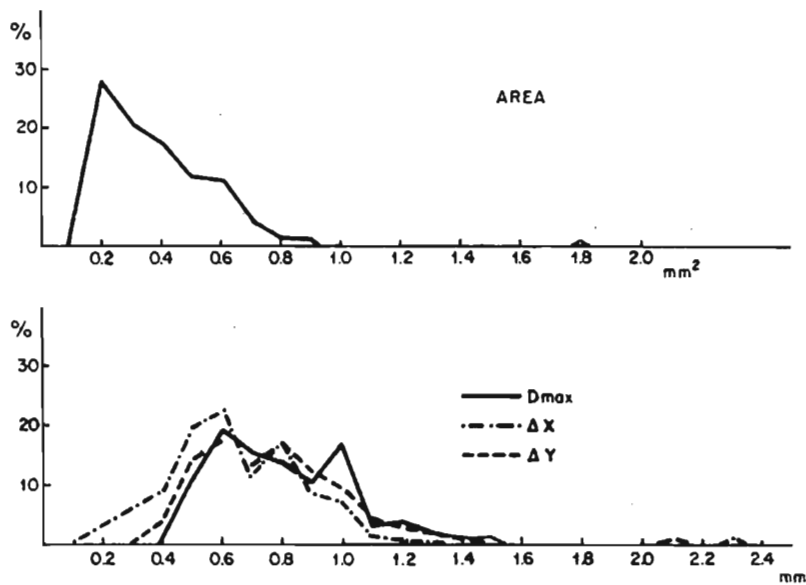


Fig. 6. Frequency distribution in 149 measurements on a thin section of a *Nodulipora* colony, Höglint Beds, Gotland [Cn 59685].

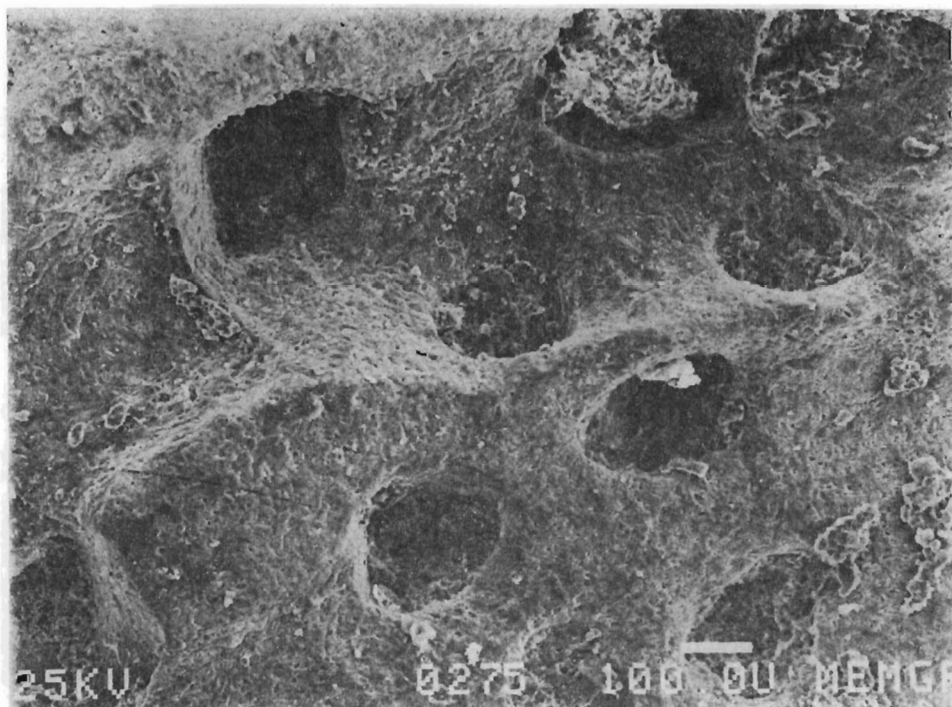


Fig. 7. Scan-micrograph of mural pores in *Nodulipora*.

tabulae are found, whereas tabellae occur in meandroid tubes. Septa or spines are not found. Growth occurred by axial increase (fission). A striking characteristic of *Nodulipora* is the presence of numerous mural pores (fig. 7), which are found in both polygonal and meandroid tubes. Just as in *Desmidopora* these pores should be distinguished from the gaps in the wall, causing meandroid tubes. In the former, pore plates occur, while in the latter such structures are not found.

Discussion. — With Lindström (1896) we think that *Nodulipora* and *Desmidopora* are closely related. These genera share the following features: 1. division of the tubes by axial increase; 2. a trabecular microstructure (Tesakov 1960); 3. presence of mural pores; 4. absence of spines; 5. occurrence of both polygonal and meandroid tubes. These similarities must be set against the different colony shape and the presence of astrorhizae in *Nodulipora*. As both *Desmidopora* and *Nodulipora* share (apart from the occurrence of pores) their morphological features with chaetetid sclerosponges, we consider these genera as the fossil relics of a group of chaetetid sclerosponges with pores. The presence of pores in chaetetids is also mentioned by Termier and Termier (1976).

Distribution. — *Nodulipora acuminata* is only known from the Silurian (Höglint, Slite and Halle Beds) of Gotland, Sweden.

RELATIONSHIP BETWEEN SCLEROSPONGES AND TABULATES

The morphology of organisms with compound skeletons, like sponges, corals and ectoprocts is defined to a high degree by physico-mathematical principles (Thompson 1917). As a consequence, the systematic place of such fossils, poor in characteristics, is not always easily established.

Edwards and Haime (1849), who introduced the name *Tabulata*, classified these fossils as an extinct suborder of the *Zoantharia* de Blainville. Later on, fossils interpreted as algae, sponges and ectoprocts were recognized amongst the *Tabulata* as defined by Edwards and Haime. Several groups, like chaetetids, heliolitids and monticuliporids, were removed from the tabulates (Nicholson and Lydeker 1889; Kirkpatrick 1911; Hill and Stumm 1956; Sokolov 1962).

However, not much doubt arose about the interpretation of tabulates *sensu* Hill and Stumm as corals. Moreover, current research on wall microstructures in Recent scleractinians (Sorauf 1970, 1972; Jell 1974), Palaeozoic rugose corals (Schouppé and Stacul 1966) and tabulates (Schouppé and Oekentorp 1974) seem to corroborate this interpretation. On the other hand, most of the recent work on tabulates is based on the hypothesis that these skeletons were formed by extinct corals. As a consequence, in analogy with scleractinians, a primary aragonitic skeleton of tabulates is postulated. Moreover, the scleractinian biocrystallisation model is also applied in the interpretation of the observed diversity in macro- and especially microstructures in tabulates. According to Stel (1978) a primary aragonitic nature of tabulates is unlikely. Although theoretically aragonitic members of the tabulates may have existed, most Palaeozoic tabulates, heliolitids, stromatoporoids and rugose corals originally were calcitic.

Due to the discovery of various demosponges with a compound basal skeleton, the systematic position of tabulates has become a matter of dispute again (Hartman

and Goreau 1972, 1975; Flügel 1976; Termier and Termier 1977a, b; Stel 1978a). In table 4, the skeletal characteristics of Recent and fossil sclerosponges and some tabulates with massive colonies are compared. The primary microstructures of these skeletons are not compared because this feature is a controversial characteristic. In calcisponges and in sclerosponges a wide spectrum of microstructures (Wendt 1978) is found.

A striking difference between favositids and sclerosponges is the presence of pores in the former. Flügel (1976) considered the formation of pores as a result of the overgrowing of an excurrent canal system, similar to the one causing the imprint of astrorhizae in some sclerosponges. This hypothesis is unlikely because of the arrangement of the pores. Nevertheless, the presence of pores in *Desmidopora* and especially *Nodulipora* (in which astrorhizae are also found) demonstrates the existence of sclerosponges with a skeleton in which pores are found. There might be a relation between the dimensions of the tubes and the presence of pores. In chaetetids, a tube diameter of 0.15–1.20 mm, but mostly less than one millimeter, is found, whereas in favositids a tube (corallite) diameter up to 5 mm occurs. However, the number of pores in the latter seems to increase in proportion to the gathering dimensions of the tubes. This view is also suggested by the dimensions of the tubes found in *Desmidopora* and *Nodulipora*, which show a mean diameter of 0.9 mm and 0.8 mm. These measures are larger than those found in most chaetetids (see Fischer 1970). On the other hand, numerous small mural pores are also found in *D. multitalulata*, which has a tube diameter of 0.3–0.5 mm (Fitzgerald 1955). Some peculiar rugose corals such as *Agetolites* Sokolov also show pores. Because of these pores Sokolov (1962) considered *Agetolites* as a tabulate.

Hartman and Goreau (1972) found that the presence of astrorhizae is determined by the thickness of the tissue layer on top of the skeleton: a thin cover of tissue leads to the imprint of astrorhizae. This is found within one and the same species as in *Ceratoporella nicholsoni*. Apparently, the morphology of the basal skeleton of the sclerosponges is highly variable; a feature, not very popular with palaeontologists who have to work with these skeletons. This feature may even become a nightmare if one realizes that due to ecological factors *Merlia normani* may even be without any basal skeleton.

From table 4 it is seen that in favositids lateral increase and in sclerosponges axial or intermural increase is found. In lateral increase (Stel 1978a) the offset is separated from a parent tube (= corallite) by the development of mural processes. Consequently, a pore-like opening, the apical pore, is found at the base of the offset. In axial increase, the parent tube is divided in two or more offsets due to the development of mural processes (pseudosepta). In this type of increase the offset completely occupies the parent tube while in lateral increase (as found in favositids) only a part of the parent tube is involved. However, basically no difference is found between these two processes: in both a part of the parent tube is partitioned off by the offset. Lateral increase is often observed in many types of colonial animals such as recent corals (Wells 1956), rugose corals (Jull 1973, 1976) and ectoprocts (Boardman and McKinney 1976). Thus, this pattern of growth is not at all

Table 4

Comparison of the skeletal characteristics of Recent and fossil sclerosponges and of some tabulates

| | <u>Merlia</u> | <u>Cerato-</u> <u>porella</u> | Tabulospongida Recent | Mesoz. | Chaetetida Mesoz. | Palaeoz. | <u>Desmido-</u> <u>pora</u> | <u>Noduli-</u> <u>pora</u> | <u>Paleof.</u> <u>asper</u> | <u>Favosites</u> <u>hisingeri</u> |
|---------------------|---------------|----------------------------------|--------------------------|--------|----------------------|----------|--------------------------------|-------------------------------|--------------------------------|--------------------------------------|
| Mineralogy | | | | | | | | | | |
| aragonite | - | + | - | - | - | - | - | - | - | - |
| calcite | + | - | + | + | + | + | + | + | + | + |
| Spicules | + | + | + | + | + | - | - | - | - | - |
| Astrorhizae | - | +/- | + | + | + | - | - | + | - | - |
| Skeletal structures | | | | | | | | | | |
| polygonal tubes | + | + | + | + | + | + | + | + | + | + |
| meandroid tubes | - | + | - | - | + | + | + | + | + | - |
| pores | - | - | - | - | - | - | + | + | + | + |
| spines | - | - | + | + | - | - | - | - | + | + |
| tabulae | + | - | + | + | + | + | + | + | + | + |
| wall with darkline | - | - | - | + | + | - | - | - | + | + |
| epitheca | - | + | + | + | + | + | + | + | + | + |
| Lateral increase | - | - | - | - | - | - | - | - | + | + |
| Axial increase | - | + | + | + | + | + | + | + | - | - |
| Intermural increase | - | - | + | + | + | - | - | - | - | - |

typical of corals and therefore the presence of lateral increase in tabulates is not *a priori* in favour of a coral interpretation of tabulates. It certainly fits in the cnidarian model, but will probably also fit in the sponge model. With intermural increase the offsets are thought to appear in the angles between the walls of adjacent tubes. Although most cases of intermural increase in tabulates actually are lateral increase, it is indeed observed in sclerosponges. This type of blastogeny fits in the sclerosponge model very well; the living tissue is restricted to the space above the uppermost tabulae and on top of the calcareous skeleton. So new offsets would be filled with living tissue from above and not necessarily by separating a part of a parent tube as is found in axial and lateral increase.

Recapitulation of the data described above indicates that the suggestive resemblance of favositids and sclerosponges (inclusive *Desmidopora* and *Nodulipora*) must be weighed against the lack of spicules and the presence of a distinct darkline in the former. The sponge interpretation of tabulates like favositids remains plausible.

Recent work of Hartman and Goreau (1966, 1972, 1975) Stearn (1975) and Hartman (1978) demonstrated that *Astrosclera* and a recently discovered *Actinostromaria*-like sclerosponge may be regarded as relics of stromatoporids. The sclerosponge affinities of chaetetids also are well demonstrated and the evidence discussed above favours the hypothesis that favositids were sponges. However, the *Merlia*-like model presented by Flügel (1976) is unlikely (Stel 1978a). Some characteristics in favositids (predominance of lateral increase, pores and a darkline) suggest a lower degree of integration as compared to chaetetid and stromatoporoid sclerosponges.

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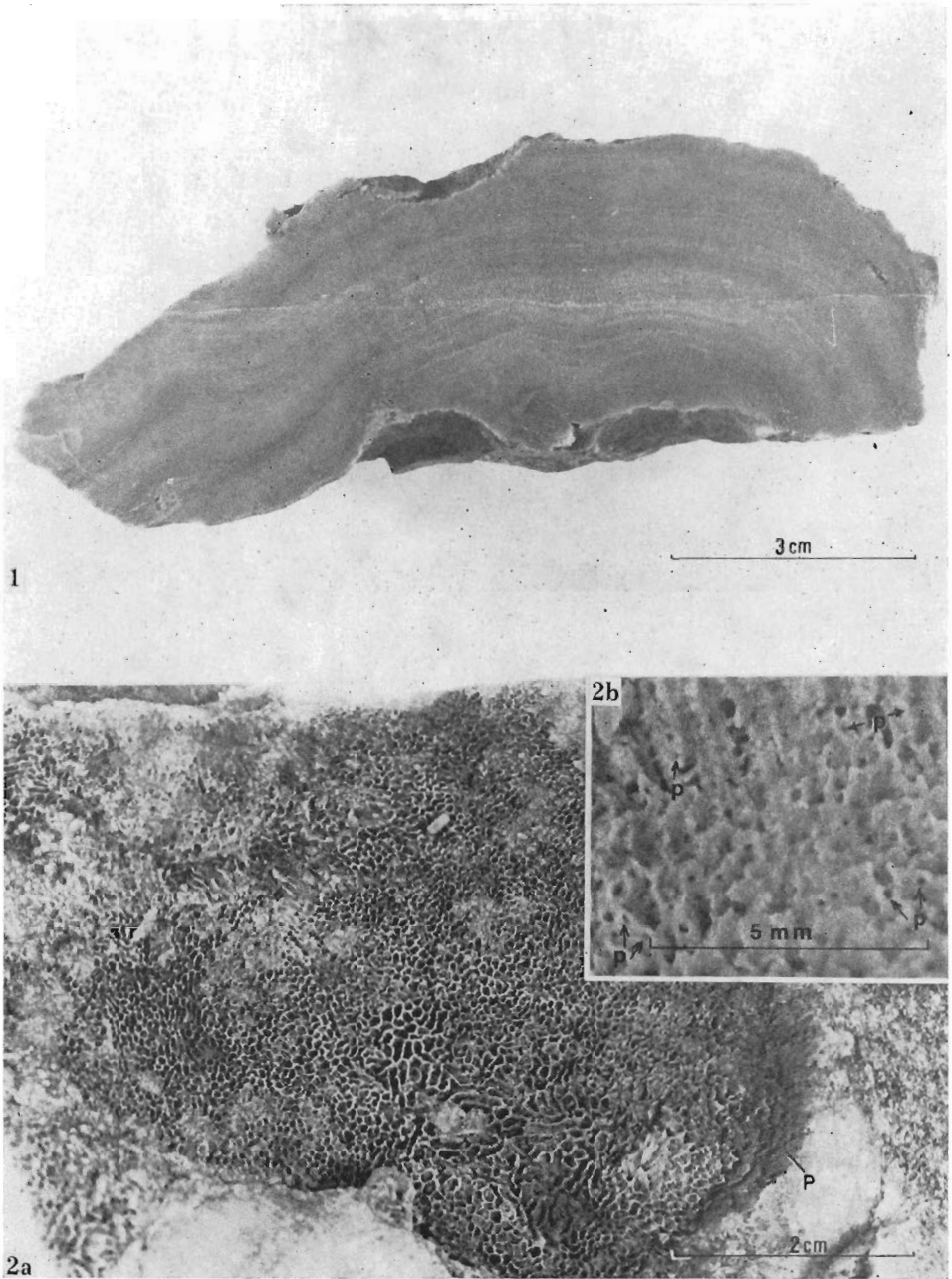
EXPLANATION OF THE PLATES 22 AND 23

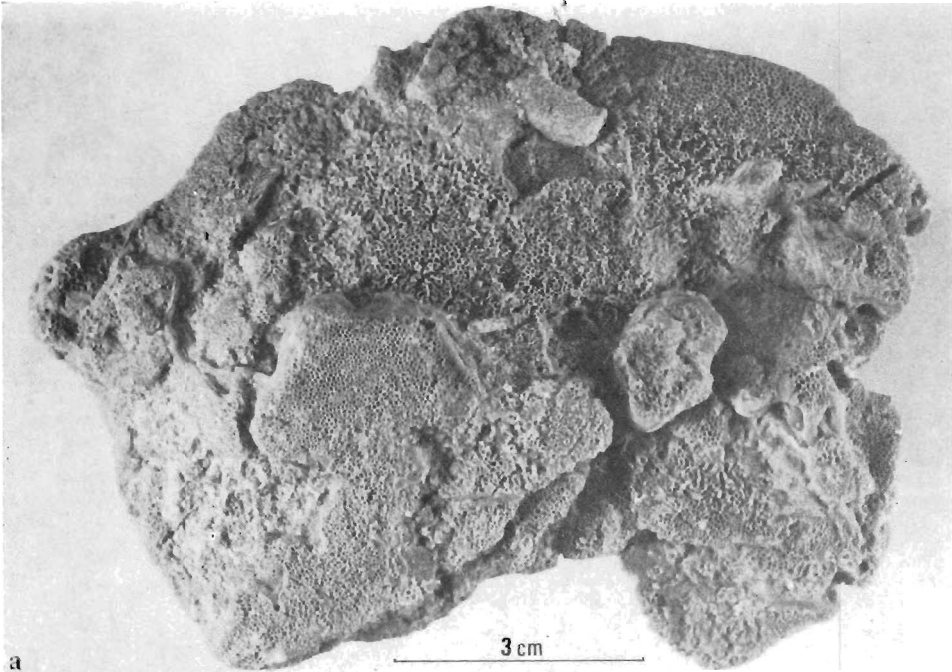
Plate 22

1. Colony of *Desmidopora alveolaris* from the Slite Beds at Tjautet 1, Gotland, Sweden [B.2.404.09]. Thin buff bands within this fossil roughly reflect morphological development during growth.
2. a, b. Details of the surface of a colony of *Desmidopora* [B.2.404.09] showing pronounced variability in the size of the polygonal and meandroid tubes, and numerous pores (p) in the tube walls.

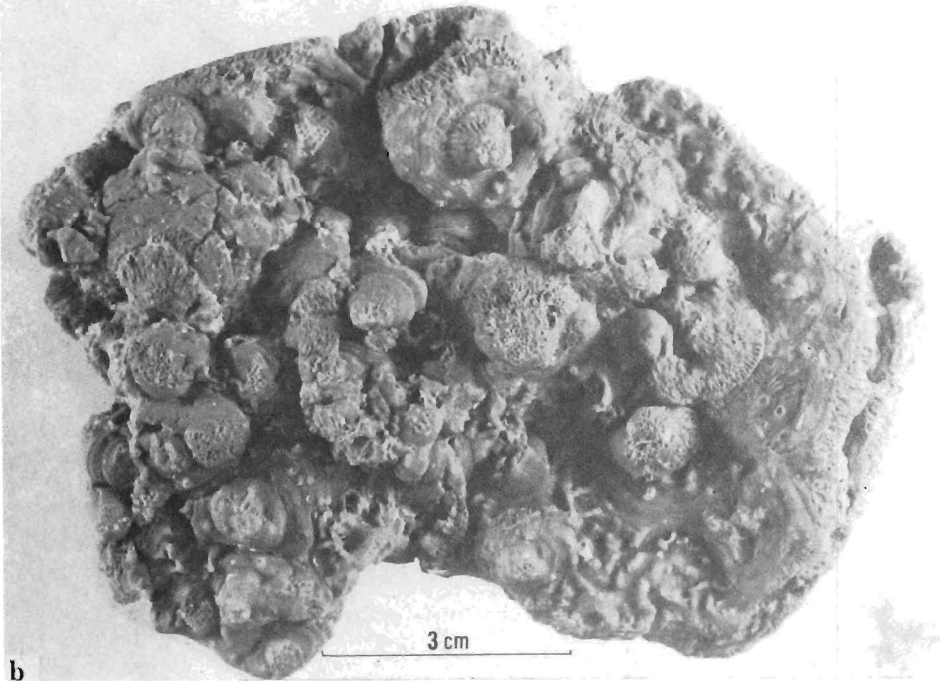
Plate 23

1. a view of the surface of a *Nodulipora* colony [Cn 59690], showing polygonal and meandroid tubes; b view of the underside of the same colony showing this colony is built up by at least 20 small colonies.





a



b