TERTIARY SOLENOPORACEAN ALGAE AND THE REPRODUCTIVE STRUCTURES OF THE SOLENOPORACEAE

by GRAHAM F. ELLIOTT

ABSTRACT. Knowledge of the supposed reproductive structures of the Solenoporaceae (Rhodophyta, calcareous algae, mostly Palaeozoic and Mesozoic) is reviewed, and then compared with evidence from a study of well-preserved Tertiary Solenoporaceae. Even in this material reproductive bodies cannot be identified with certainty. A suggested evolutionary history of the family relates the supposed reproductive processes to cell-structure, anatomy, and palaeoecology, comparing each with that of the related Corallinaceae.

THE Solenoporaceae are an extinct group of fossil marine organisms, nodular or encrusting in form, and formed internally of closely packed radially or vertically divergent rows of elongate cells. Occasionally referred to various animal groups, they are usually interpreted as calcareous algae related to the living Corallinaceae, which they resemble closely in growth-form and general internal structure, and to which they may have been ancestral. The cell-diameters are almost always greater than those of the corallines, but are less than those of typical members of different marine invertebrates with similar skeletal appearance, as shown by the comparison-list of Peterhans (1929): see also Oakley (1941). The solenoporaceans have thus a distinctively coarser appearance in section than the corallines. Usually taken as closely related to the latter—the two main patterns of solenoporacean structure may be paralleled in the corallines, as indicated by Lemoine (1911)—detailed classification has naturally varied: a recent summary and historical review is that of Johnson (1960).

In one important character the solenoporaceans contrast sharply with the younger group. The reproductive structures of the Corallinaceae are amongst the most conspicuous features of the family, and have proved invaluable in classification. Random sections of the fossil forms are often studded with rows of calcified sporangia like pearls, or with the larger cartouche-like conceptacles of more advanced genera, and are readily recognizable by comparison with the living algae, particularly those of the Indo-Pacific province. But in the solenoporaceans, though the vegetative tissue is similar to that of the corallines, the structures which have been interpreted as reproductive in origin are relatively uncommon and almost all doubtful and obscure. Indeed, the erection of the family Solenoporaceae by Pia (1927) was largely based on the absence of calcified reproductive elements, and he had earlier reconstructed them as external to the calcified thallus during life (Pia 1926, p. 157).

Alleged reproductive structures were reviewed by Wood (1944), who distinguished four categories. First were 'cells without regular form', a very varied group of calcite-filled cavities interpreted as remains of sporangia or conceptacles like those of the corallines: very few of these solenoporacean features are intrinsically recognizable as reproductive in origin. A second group comprised 'star-like groups of cells'; scattered stellate appearances in transverse sections apparently due to fusion or wall-failure of the

[Palaeontology, Vol. 7, Part 4, 1964, pp. 695–702, pls. 104–108.]

ordinary vegetative tissue-cells, and interpreted for the most part as connected with former reproductive structures. The third and fourth structures considered by Wood were the alleged conceptacles of Öpik and Thomson (1933) and the supposed sporangia of Rothpletz (1908). These are both calcite-filled interruptions of the normal tissue. Around the former the rows of vegetative cells are diverted, indicating growth during the life of the plant (though not necessarily that of a reproductive structure) and not to be explained as a post-mortem feature; the latter show solution of the surrounding cell-walls which Wood compared with the formation of sporangia in *Archaeolithothamnium* of the Corallinaceae. Both were discussed in the light of new material. Wood thought the latter might be sporangial but concluded: 'It will have been seen that there is a great doubt about almost all the records of organs of reproduction in the Solenoporaceae, and that no such bodies may safely be said to be present in any form.'

Subsequent to Wood's review, contributions by Garwood (1945), Rao and Varma (1953), Maslov (1956), Johnson and Konishi (1959), and others, described and figured features interpreted as solenoporacean sporangia and conceptacles, and carried on the search for understanding of this part of algal evolution.

THE SOLENOPORACEAE OF THE TERTIARY

The solenoporaceans most familar to palaeontologists are from the Palaeozoic, with subordinate occurrence in the Mesozoic. In the warm seas of Tethys, however, they survived into the early and mid Tertiary, and although limited in genera and species, they occur locally in great abundance. These forms are usually better preserved than those from older limestones. Since they are often found intimately intergrown with Tertiary corallines comparison is facilitated. They are now reviewed with especial consideration of possible reproductive structures, in an attempt to elucidate older records. The four genera concerned are *Parachaetetes*, *Solenomeris*, *Solenopora*, and *Neosolenopora*.

Parachaetetes is represented in the Tertiary by one species, *P. asvapatii* Pia, described from the Indian Danian (Pia 1936). It occurs in profusion in shallow water reefal facies of the Palaeocene–Lower Eocene of the Middle East, from the Mediterranean to the Arabian Sea (Elliott 1960). It has been recorded from the Palaeocene of the Pyrenees (Segonzac 1962) and the Danian–Montian of Cuba (Keijzer 1945), and noted by the writer in the Montian of Vigny, northern France, and as a derived form in the Eocene of Borneo. *Elianella* (Pfender and Basse 1948) appears very similar from the type description and Elliott (1955) drew attention to this; Johnson and Konishi (1960) and Segonzac (1962) agree with this probable synonymy. *Elianella*, described from the Palaeocene of Madagascar, was also recorded from Venezuela, Europe, and Anatolia (Pfender and Basse 1948); in the Carpathians it is said to appear in the Upper Cretaceous

EXPLANATION OF PLATE 104

Parachaetetes asvapatii Pia, thin-sections, ×30.

Fig. 1. Specimen showing calcite-filled post-mortem borings marked by dark marginal mineralization. Sinjar Limestone, Palaeocene–Lower Eocene; south-west Sefin Dagh, Shaqlawah, Rowanduz-Erbil, Erbil Liwa, north-east Iraq. BMNH V51231.

Fig. 2. Typical dense radiate-concentric structure. Sinjar Limestone, Palaeocene–Lower Eocene; 1 mile south-west of Sedelan, Sulemania, Sulemania Liwa, north-east Iraq. BMNH V51232.

(Schalekova 1963). *P. asvapatii* is thus a fossil with a very wide Tethyan distribution: in the writer's experience its abundant occurrence marks the Palaeocene–Lower Eocene.

The species occurs normally as compact nodules or bluntly lobed 'cauliflower-head' growths of up to several centimetres diameter, though it has been seen rarely as thinner ribbon like growths when intimately associated with other algae such as *Lithophyllum*. In vertical thin-section (Pl. 104, fig. 2) typical growths show a closely packed mass of curved radial lines of elongate cells; these are circular in cross-section, about 0·04–0·06 mm. diameter or less, and very variable in length. Pia (1936) gives the length as 'at least between 0·04 and 0·12 mm.' The tissue is characteristically uniform in appearance, though showing some concentric banding: occasionally a rudimentary distinction may be made out between hypothallic and perithallic tissue, as figured by Pia (1936, pl. 3), but this is never very clear.

Examination of several hundred thin-sections of this species from the Middle East has never revealed any structures which could be interpreted as remains of reproductive organs. Occasionally obvious non-algal features, such as holes made by boring organisms (Pl. 104, fig. 1), are to be seen. No reproductive structures have been described for the species in the literature.

Solenomeris is a coarsely cellular organism showing marked irregularity in its cells. The type-species, *S. o'gormani* (Douvillé 1924) from the Lower Eocene of the French Pyrenees, is nodular in growth like *Parachaetetes*: the cells are irregularly polygonal in transverse section, of perhaps 0·04–0·06 mm. diameter or more, showing as an irregular mesh with much better defined walls than usually seen in *Parachaetetes*. In vertical section the individual cells are seen to be polygonal also, cells in adjacent rows alternating to give a zigzag effect; they occur in horizontal zones of low cell-height (several layers of cells of about 0·065 mm. width by 0·026 mm. height) followed by similar zones of greater cell-height (0·060 mm. approx.), thus giving a characteristic banded appearance to the thallus (Pl. 105, fig. 2). This height is the equivalent of the length of more conventionally shaped solenoporacean cells. *S. douvilléi* Pfender from the Lower Eocene of the Spanish Pyrenees is an encrusting species of very similar cell-structure. Pfender (1926) compared it with certain hydrozoa, but the comparison with the Solenoporaceae seems much closer. In the Middle East both species have been recognized in local abundance in the Palaeocene–Lower Eocene of Iraq (Elliott 1960), though the specific distinction is not always easy to make. An undescribed species was recorded by Pfender (1926) from the Middle Eocene of Italy: the writer has seen a *Solenomeris*, possibly the same species, in the Middle Eocene of Qurn Behuth, Sharjah, Trucial Coast, Arabia, while Schalekova (1963) records *S. douvilléi* Pfender from the Middle Eocene of Slovakia. *S. afonensis* Maslov is from the Lower Eocene of the U.S.S.R.: Maslov (1956) compared the tissue with that of certain foraminifera as well as with stromatoporoids. *S. pakistense* Johnson and Konishi (*S.* ? *douvilléi* Rao and Varma, *non* Pfender) is from the Lower Eocene of Pakistan, and an alleged conceptacle was described from it (Rao and Varma 1953). All these species are very similar.

Examination of Middle East *Solenomeris* for reproductive structures, in contrast to *Parachaetetes*, shows many varied features. The specimen in Plate 106, fig. 1, shows what is apparently a clear vertical section of a definite conceptacle of lithophyllid type, with single central aperture. However, further examination of the same slide shows numerous entombed encrusting or adherent foraminifera (*Bullopora* sp.) overgrown and smothered by the fast-growing alga (Pl. 105, fig. 3). It is evident that this and other 'conceptacles' are in fact random cuts of buried *Bullopora*, whole or broken. The fast-growing nature of *Solenomeris* (a characteristic of modern warm-water reef Corallinaceae) is evidenced by entombed debris, larger free foraminifera such as *Alveolina* (Pl. 105, fig. 1) and even large discocyclines completely overgrown and forming the nucleus of *Solenomeris*-growths (Pl. 106, fig. 3). Clear calcite spaces with enclosed matrix sharply overgrown by the alga (Pl. 106, fig. 2) suggest other attached organisms which were smothered. Plate 107, fig. 1, shows a transverse section through the basal level of two attached specimens of *Bullopora*: it is seen that the cells beneath are slightly enlarged and globular, and there seems to be a real difference in transparency of the cell walls, relative to the ordinary *Solenomeris*-cells adjacent. In Plate 107, fig. 2, a vertical cut of an apparently similar cell-group is seen in a second section from the same rock sample. These cells occur beneath a clear calcite body representing an original attached organism or foreign body, smaller, however, than the cell-group below. The structure seems to be the same as the 'conceptacle with sporangia' figured for *S. pakistense* by Rao and Varma; their published figure is far from clear and does not show the relation between this structure and the vegetative tissue. A somewhat similar structure is seen in one of Maslov's figured sections of *S. afonense* (1956, pl. 45). It is very doubtful indeed if this is a conceptacle, and it is difficult to see why cells below such attached organisms should become enlarged: possibly it is the remains of another foraminifer. It could be argued that these enlarged cell-groups were occasioned by an external non-calcified sporangium, but there is no direct evidence of this.

Stellate cell-structures occur not uncommonly; they are seen to be sometimes connected with changes of orientation of the vegetative cell-growth. There are also various calcite inclusions connected with included reef-debris or post-mortem borings, &c.

To summarize, these growths of *Solenomeris* show an abundance of included and well-preserved structures, one of them more like a familiar pattern of coralline conceptacle than anything yet figured, yet with very little, if any, evidence of reproductive origin.

EXPLANATION OF PLATE 105

Solenomeris o'gormani Douvillé, thin-sections, ×40.

Fig. 1. Section showing horizontal (transverse) cell-structure on left, above engulfed alveoline; oblique on right. Sinjar Limestone, Lower Eocene; Mamissa, Balad Sinjar, Jabal Sinjar, Mosul Liwa, north Iraq. BMNH V51233.

Fig. 2. Vertical section to show banded growth-layers of differing cell-height. Sinjar Limestone, subsurface Palaeocene; Kirkuk Well no. 116, Kirkuk Liwa, north-east Iraq. BMNH V51234.

Fig. 3. Vertical section showing conspicuous overgrown attached foraminifer (*Bullopora* sp.) at top centre. Sinjar Limestone, subsurface Palaeocene; Kirkuk Well no. 116, Kirkuk Liwa, north-east Iraq. BMNH V51234.

EXPLANATION OF PLATE 106

Solenomeris o'gormani Douvillé, thin-sections. Sinjar Limestone, subsurface Palaeocene; Kirkuk Well no. 116, Kirkuk Liwa, north-east Iraq.

Fig. 1. Calcite-filled inclusion (top centre) in the form of a long lithophyllid conceptacle; probably oblique cut of *Bullopora* sp.; ×40. BMNH V51234.

Fig. 2. Vertical section showing sharp arching of solenomerid tissue over triangular inclusion representing original attached organism or object, ×40. BMNH V51234.

Fig. 3. Thick growth of *Solenomeris* around large discocyclinid foraminifer, with overgrown attached *Bullopora* sp., top and bottom on right; ×30. BMNH V51235.

Solenopora itself is represented in the Tertiary by a few species, e.g. *S. chiapasensis* Maldano-Koerdell from the Palaeocene–Lower Eocene of Mexico, and *S. paleocenica* Segonzac from the Thanetian (Palaeocene) of the French Pyrenees (Segonzac 1960). No reproductive structures were noted by her, and she suggested that perhaps this alga, one of the last representatives of its genus, reproduced by vegetative, non-sexual, means.

Neosolenopora is the latest of the Solenoporaceae, occurring in the Italian Helvetian (Miocene). Described originally as *Lithophyllum vinassai* (Patrini 1932, 1933), it was transferred to *Solenopora* by Mastrorilli (1955) and given the specific name *patrinii*, as it then became a synonym of the Jurassic *Solenopora vinassai* Vialli, the genus or subgenus *Neosolenopora* being erected for its reception. The species occurs also in the Vindobonian faluns of the west of France, where it has been described as a bryozoan (Canu and Lecointre 1934). As figured by Patrini, it shows a typical solenoporoid cell-structure, in which he distinguished hypothallial cells of 0·07–0·10 mm. diameter and 0·10–0·13 mm. length, and perithallial cells of 0·6–0·10 mm. diameter and 0·25–0·40 mm. length. (Many of the perithallial cells in the French specimen are very much shorter in length than this.) He also figured a specimen showing a row of clear, calcite-filled sporangia-like structures, of 0·13–0·20 mm. diameter and 0·17–0·30 mm. length, arranged on one level as in *Archaeolithothamnium*.

In the French material now figured the transverse section showed an incipient star-group of cells and one or two cavities (Pl. 108, fig. 1); the vertical section shows an incipient hypothallial basal layer, the cells turning up into the main perithallial structure (Pl. 108, fig. 2). Sporangia were not seen in the sections prepared.

THE EVOLUTION OF THE SOLENOPORACEAE

From the above account it is clear that the well-preserved Solenoporaceae of the Tertiary confirm the evidence obtained from the more abundant Palaeozoic and Mesozoic members of the group. Some show no evidence of reproductive structures at all, some show doubtful ones of varying pattern and degree of probability, and very rarely structures are seen which in a coralline would be accepted without question as sporangia or conceptacles: these do not occur in all individuals of the respective species concerned. The best of these are the conceptacles of the Silurian *Solenopora filiformis* Nicholson figured by Johnson and Konishi (1959), the sporangia of the Miocene *Neosolenopora patrinii* figured by Patrini (1932), and possibly the sporangia of *S. sardoa* (Deninger) Peterhans figured by Peterhans (1930).

This unsatisfactory picture appears well authenticated. But a little more light may be shed on it by considering also the other, non-reproductive features of the Solenoporaceae, as compared with the Corallinaceae, which appear to have replaced and surpassed the older family.

Associated with the almost invariably coarser solenoporacean cells is the very rudimentary differentiation into hypothallus and perithallus. In melobesioid corallinaceae the hypothallus is normally the creeping basal layer by which the alga spreads itself, though hypothallic tissue also occurs in upwardly directed digitations and as scar or regeneration tissue. The perithallus is the main body of subsequent vegetative tissue in which the reproductive spores will eventually be produced. In corallines hypothallus and perithallus are usually two well-defined parts of the same plant, differing in the size and arrangement of their component cells; in solenoporaceans the hypothallus, when it can be seen, is simply the basal outwardly directed portion of the cell-rows before they bend upwards. For all the evidences of rapid growth seen in *Solenomeris*, solenoporaceans lacked the specialized mechanism for this purpose seen in the corallines. Possibly because of this, too, they never (so far as is known) evolved forms with jointed or articulated thalli comparable with the branching corallines such as *Jania*, *Corallina*, &c., unless the Upper Palaeozoic *Cuneiphycus* (Johnson 1960) represents such a development.

Although solenoporaceans occur from Lower Palaeozoic to Middle Tertiary, they never occupied the same associative ecological niche with the reef-building corals which the coralline algae rapidly achieved soon after they became common. It can be argued that the Palaeozoic tetracorals and tabulates were different in reef-building properties to the later hexacorals. But throughout most of the Mesozoic, when hexacorals abounded and corallines were very rare, the solenoporaceans never grew in association with reef-corals as their successors did throughout the Tertiary and at the present day: Mesozoic corals and solenoporaceans usually occur in different beds. Indeed, not until their decline in the Tertiary are solenoporaceans found in local abundance in this environment, and then they occur intergrown with the coralline algae.

From these considerations the following evolutionary picture may be suggested. The Solenoporaceae were primitive Rhodophyta or red algae. Their cells were large enough for spore-production at the appropriate season without great individual enlargement (cf. Oakley 1941); there was thus little or no arching over of the surrounding non-sporing vegetative cells and no consequent production of calcified sporangia, and little definite trace left when the spores were shed. Occasionally a solenoporacean might have achieved reproductive structures of coralline pattern, but this advance in a single character did not occasion any marked evolutionary advantage. Not until a form with smaller cells achieved the hypothallial mechanism for spreading growth did the evolution of sporangia confer this advantage; possibly unknown factors of algal chemistry were involved too. Although the coralline *Archaeolithophyllum* has been described from the Upper Palaeozoic (Johnson 1956), it was not until the corallines of the Upper Cretaceous became

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EXPLANATION OF PLATE 107

Solenomeris o'gormani Douvillé, thin-sections. Sinjar Limestone, subsurface Palaeocene; Kirkuk Well no. 116, Kirkuk Liwa, north-east Iraq.

Fig. 1. Horizontal section through the basal layer of two attached *Bullopora* sp., showing slightly enlarged spherical solenomerid cells immediately beneath; ×40. BMNH V51234.

Fig. 2. Vertical section showing enlarged solenomerid cells immediately below calcite inclusion representing original attached organism; ×80. BMNH V51236.

EXPLANATION OF PLATE 108

Neosolenopora patrinii Mastrorilli, thin-sections, ×40. Miocene (Vindobonian; Savignean Falun); La Perchals Quarry, Tréfumel, south of Dinan, Brittany, France.

Fig. 1. Horizontal (transverse) section; stellate structure due to wall-failure or damage, top centre. BMNH V51237.

Fig. 2. Vertical section, showing incipient hypothallus at base, passing up into septate cell-rows of perithallus. BMNH V51238.

Fig. 3. *Solenomeris o'gormani* Douvillé, thin-section, ×40. Calcite-filled inclusion, origin not certain, in form of a short lithophyllid conceptacle. Sinjar Limestone, subsurface Palaeocene; Kirkuk Well no. 116, Kirkuk Liwa, north-east Iraq. BMNH V51239.

abundant that they rapidly expanded to fill the reef-associations unexploited by the solenoporaceans, and then pursued their own evolution. It should be remembered that in the evolution of other algal families, e.g. the Dasycladaceae, progressive elaboration of sexual structures has been of apparent advantage throughout geological history. In the corallines the separate sporangia of *Archaeolithothamnium*, which reached its maximum in the Eocene and now survives with limited distribution in warm seas, give place to the conceptacles of grouped sporangia seen in *Lithothamnium* and *Lithophyllum*, abundant later in the Tertiary, and even the present distribution of these two types suggests some slight differential advantage.

For a while in the early Tertiary a few Solenoporaceae such as *Solenomeris* and *Parachaetetes* grew vigorously in the same environment as the corallines, but they diminished after the optimum algal conditions of the Palaeocene, and *Neosolenopora* appears to have been the last of its tribe, unless some obscure alga living in tropical seas still represents the family.

Specimens in the collections of the British Museum (Natural History) have the prefix BMNH.

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Manuscript received 6 December 1963

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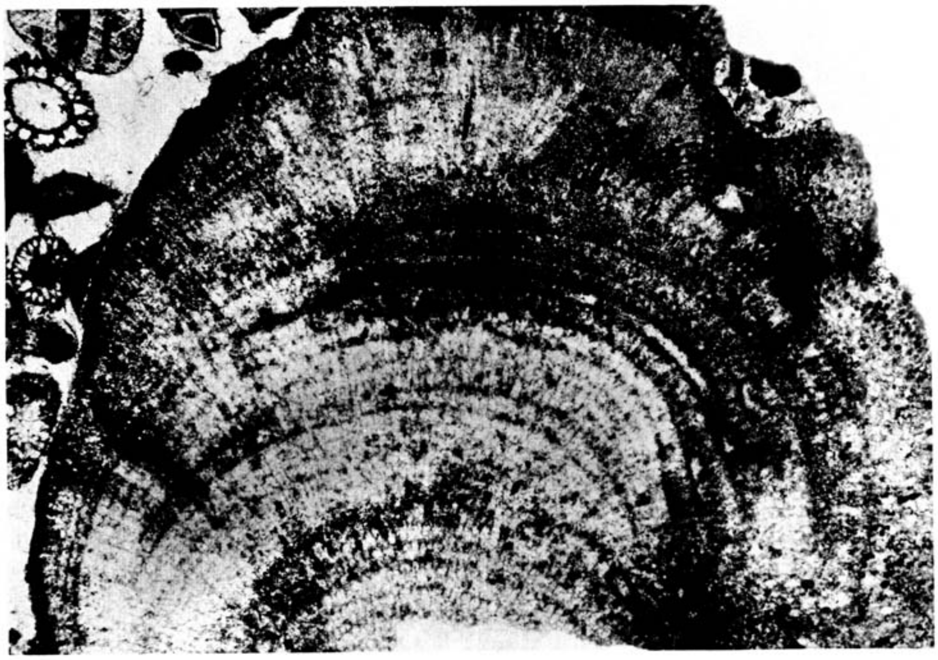

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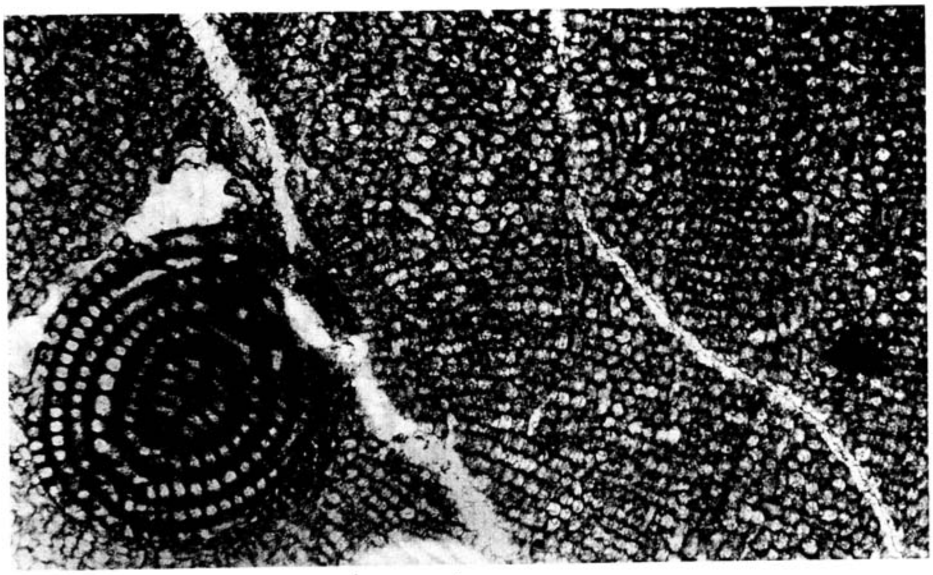

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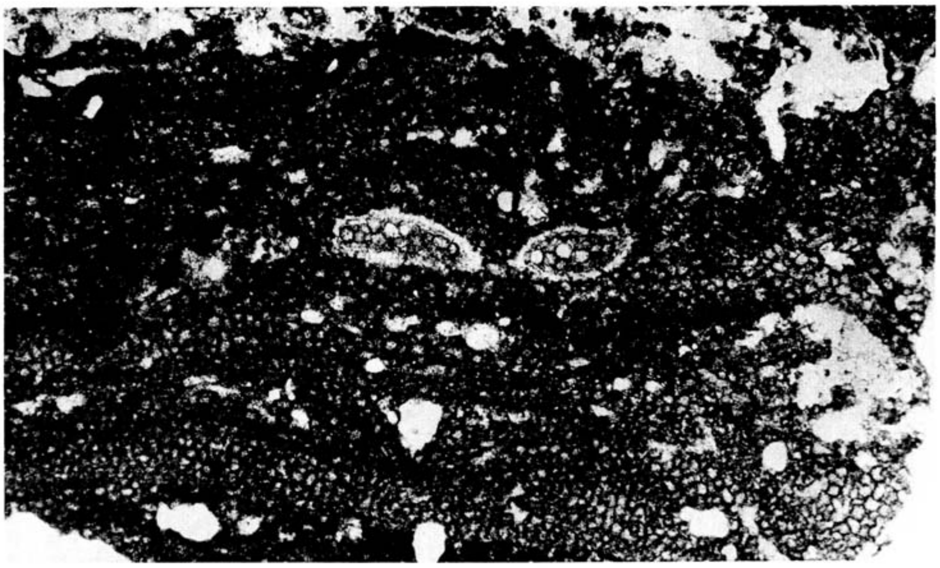

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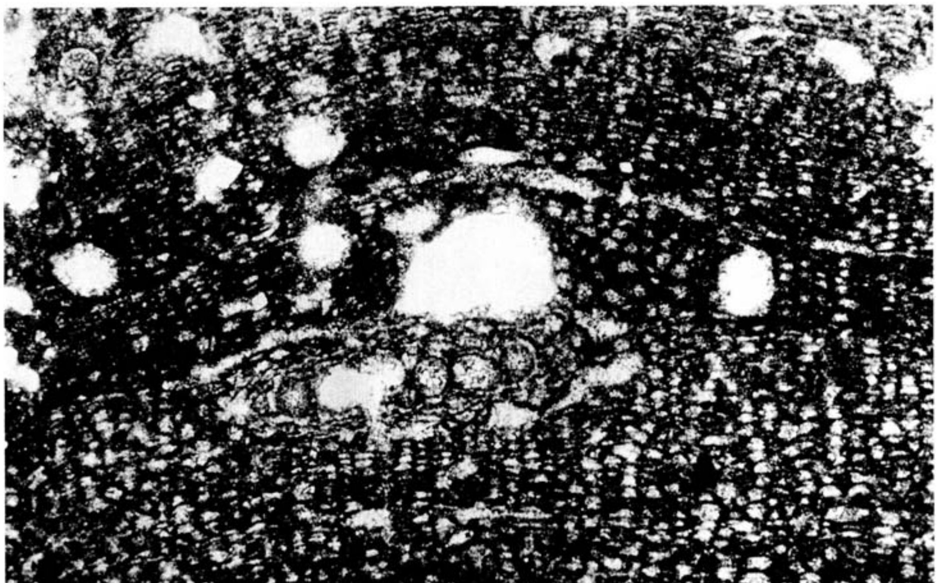

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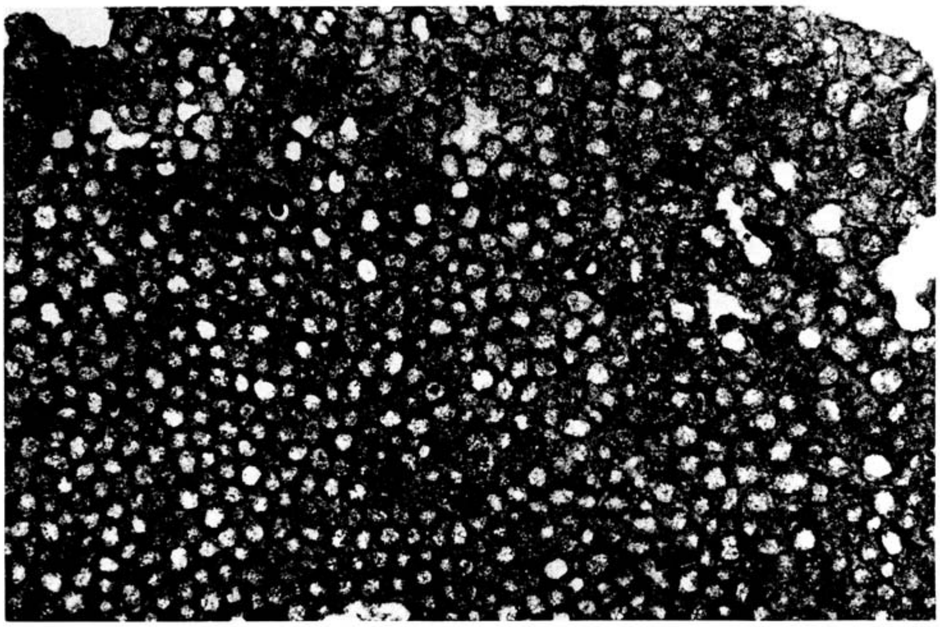

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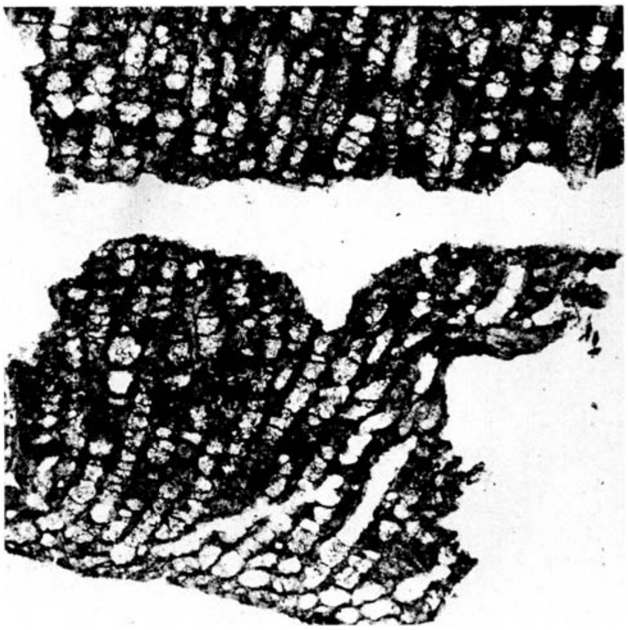

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