

THE NATURE OF *ACICULELLA* PIA (CALCAREOUS ALGAE)

by GRAHAM F. ELLIOTT

ABSTRACT. The dasycladacean alga *Aciculella ogilvie-gordonae* sp. nov. is described from the Upper Permian of northern Italy: the first Permian record of a hitherto Triassic genus. Julius Pia's type-description of *Aciculella* as an originally calcified endospore stem-cell filling, and not an acicularian spicule, is examined in the light of subsequent research and of fresh evidence from the Permian fossil, and is confirmed. Records of *Aciculella*, including some possible new species, are summarized. It is concluded that the endospore stem-cell fillings referable to *Aciculella* are possibly of diverse generic origins.

Aciculella is a somewhat problematic microfossil, recognized by Julius Pia as dasycladacean in origin and named by him probably on account of resemblance to *Acicularia*. The morphology of *Aciculella* is simple and not ambiguous; the interpretation to be accorded to the structures seen, as remains of a former living alga, is difficult. Pia (1927) gave an excellent diagnosis of the genus, and somewhat characteristically named but did not describe or figure the type-species *A. bacillum*, which came from the Middle Triassic (Ladinian Stage) of the Central European Carpathians. This deficiency he remedied later (Pia 1930) when describing other problematic dasycladacean remains, in part comparable.

During a recent examination of algal limestones in the Ogilvie-Gordon collection in the British Museum (Natural History), I was surprised to find a Permian species of *Aciculella* in the Upper Permian Bellerophon Limestone from northern Italy. The preservation of this little fossil, and its association in the same rock with another problematic endospore alga, permits a re-examination and clarification of the problem. To facilitate subsequent discussion, the new species is described first.

SYSTEMATIC PALAEOLOGY

Order DASYCLADALES (Pascher) Feldmann 1938

Family DASYCLADACEAE Kützing orth. mut. Stizenberger 1860

Genus ACICULELLA Pia 1927

Diagnosis (after Pia). Cylindrical solid calcareous rod or baton, without central tubular perforation, but with numerous subperipheral globular cavities, each opening externally by a pore. Considered to be the stem-cell filling of an otherwise uncalcified endospore dasycladacean.

Type species. *A. bacillum* Pia; Middle Triassic (Ladinian) of Central Europe.

Aciculella ogilvie-gordonae sp. nov.

Plate 118, fig. 1; Plate 119, figs. 1, 2, 5

Diagnosis. *Aciculella* differing from the type-species in that the peripheral cavities are

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smaller, more numerous, crowded, and ovoid or subdeltoid, rarely spherical. These differences are summarized below.

	<i>A. bacillum</i>	<i>A. ogilvie-gordonae</i>
Length	—	2.03 mm±
Diameter	0.4–0.7 mm	0.4–0.5 mm
Diameter of cavity	0.1 mm; spherical	0.07–0.08 mm; ovoid or subdeltoid
Number of cavities on cross-section	15	24 approx.

Description. Solid cylindrical rod or baton, circular in cross-section, with length of 2.03 mm (incomplete) and diameters of 0.4–0.5 mm seen. The material forming the rod is coarse yellow-tinted crystalline calcite; the matrix of the rock outside is finely crystalline greyish calcite. Immediately within the outer periphery, as seen in both vertical and transverse section, the rod is lined with numerous closely-set ovoid bodies, often widening from within outwards (subdeltoid), and only rarely spherical. They show diameters of 0.07–0.08 mm, and are closely set, often with interstices of only 0.01 mm across. When irregular in shape they have a crowded appearance. These bodies are usually filled with very dark, very finely crystalline calcite, much finer in grain than that of the matrix. The dark colour may be due to original plant matter. Careful examination shows that the yellow calcite often extends between the peripheral bodies, but that sometimes the grey calcite of the matrix, whether due to the surface being worn originally or to later replacement, extends inwards for a short distance between them. Very rarely an occasional ovoid body is to be seen centrally in the main calcite filling; this phenomenon was also noted by Pia in *A. bacillum*.

Associated fossils are very numerous small foraminifera, rolled pieces of the codiacid alga *Tauridium*, recognizable by its distinctive thread-pattern, pieces of the dasycladacean

EXPLANATION OF PLATE 118

- Fig. 1. *Aciculella ogilvie-gordonae* sp. nov. Holotype: longitudinal thin-section, slightly oblique, $\times 48$. Marginal sporangial bodies embedded in a common mass of organic calcium carbonate. Upper Permian, Bellerophon Limestone; Plesch d'Inez, Grödener Valley, South Tirol, N. Italy. Brit. Mus. (Nat. Hist.) Dept. Palaeont., Reg. no. V.53904.
- Fig. 2. *Acicularia (Briardina)* sp. Thin-section of spicule, $\times 60$. Palaeocene-Lower Eocene, Sahil Maleh, Batinah Coast, Oman, Arabia. Reg. no. V.52033.
- Fig. 3. *Atractyliopsis darariensis* Elliott. Longitudinal thin-section of fragment, $\times 40$. In this genus the marginal sporangial bodies seen in *Aciculella* have their own individual coatings of organic calcium carbonate. Upper Permian, Darari Formation; Ora, Mosul Liwa, N. Iraq. Reg. no. V.52037.
- Fig. 4. *Acetabularia* sp. 'The Mermaid's Wine-glass', $\times 4.5$. The disc or cup is built of fused radial calcified elements, each of which is somewhat similar to the single spicule seen in fig. 2 above. Recent. Tunis, N. Africa.
- Fig. 5. *Diplopora phanerospongia* Pia. Oblique-transverse thin-section, $\times 24$. A species in which calcified sporangial bodies, marginal in the stem-cell as in *Aciculella* and *Atractyliopsis*, are encased in the calcified detail of the verticillate branches of the plant, which were not calcified in the other two genera. Upper Triassic, derived in Upper Cretaceous Hawasina Formation, Oman, Arabia.

Atractyliopsis lastensis Accordi, small rolled radiate growths of a myxophyte thread-alga, and occasional examples of the microproblematicum *Aeolisaccus dunningtoni* Elliott. This is for the most part a size- and density-sorted assemblage of small organic objects gently rolled and accumulated in shallow water not far from the place of growth of the algae. One small example of *A. dunningtoni* (Elliott 1958), now known to range from Permian to Lower Cretaceous, appears to show a tiny initial spherical structure, not seen in larger examples (Pl. 119, fig. 3). This supports the view that these ubiquitous little microfossils may have been pelagic in origin.

Holotype. The specimen figured in Pl. 118, fig. 1, from the Bellerophon Limestone, Upper Permian; Plesch d'Inez, Grödener Valley, S. Tirol, N. Italy (Ogilvie-Gordon 1927, p. 5; 1927a, p. 72 etc.). Brit. Mus. (Nat. Hist.), Dept. Palaeont., Reg. no. V.53904.

Paratypes. The specimens figured in Pl. 119, figs. 1, 5, same locality and horizon as holotype, reg. nos. V.53903, V.53905.

Other material. Several examples in thin-sections made from the same rock sample.

This species is dedicated to the late Dame M. M. Ogilvie-Gordon (1864–1939), a pioneer Scottish woman geologist, distinguished for her work on the Dolomites, and a friend of Julius Pia. The material now described has been prepared from rock specimens collected by her.

COMPARISON AND EVALUATION

Aciculella is a somewhat problematic dasycladacean fossil: it can only be evaluated by comparison with other genera now to be considered.

Acicularia is a common Tertiary micro-fossil. Species are represented by solid or occasionally hollow calcareous bodies or spicules, elongate-cuneiform longitudinally, showing various shapes in cross-section, and set with numerous small peripheral spherical cavities (Pl. 118, fig. 2). At first regarded as animal in origin, their algal origin was indicated by Munier-Chalmas (1877), who recognized them as the dissociated radial segments of the calcified terminal discs of an alga similar to the living *Acetabularia* or 'Mermaid's wine-glass' (Pl. 118, fig. 4). There is one surviving living species of *Acicularia*, and this is regarded taxonomically as a section of *Acetabularia* by botanists (Egerod 1952), but palaeontologists, with the much greater importance of *Acicularia* over *Acetabularia* in the fossil record in mind, maintain it as distinct.

Shorter spicular bodies referable to *Halicoryne* have also been described from the Tertiary (Valet and Segonzac 1969).

Associated with *Acicularia* in the Tertiary are the flattened or spherical solid calcareous sporangial bodies of *Terquemella*. These are known to have originated from dasycladacean genera of normal tubular form without reproductive discs (Morellet and Morellet 1913, 1922). In the Mesozoic, however, calcareous sporangial bodies of variably intermediate form between the two occur, and are usually referred to *Acicularia* s.l., their generic origins being quite uncertain (some may be referable to *Halicoryne*). This difference in age and morphology between *Acicularia* s. str. and *Acicularia* s.l. has led to considerable confusion amongst those not closely familiar with this problem.

In considering the Triassic *Aciculella bacillum* Pia thought it highly improbable that it came from an alga with the very specialized organization of *Acicularia* s. str. ('which seems to have developed from *Terquemella* in late Cretaceous times only'; Pia 1930, p. 180). This was a strictly morphological recognition of the nature and geological age of

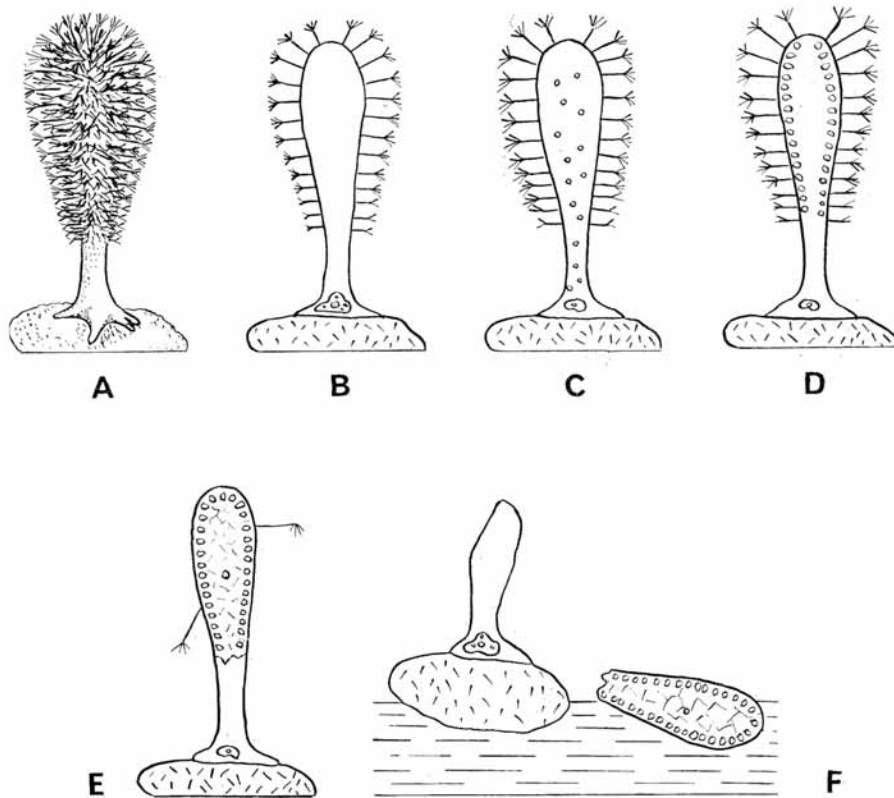
true *Acicularia* spp. However, I have since pointed out (Elliott 1968) that the reproductive disc, which in *Acetabularia* and *Acicularia* s. str. is a choristospore development, is found also in *Clypeina* (Permian-Oligocene), where it is probably a cladospore development. In other words, it is evidence of the achievement of similar morphology by an earlier, more primitive alga. Moreover, in the living species *Acetabularia clavata* Yamada and *A. tsengiana* Egerod, the lightly calcified terminal reproductive rays are not united to form a disc, but are largely separate (Egerod 1952). If heavily calcified, these would give rise to structures like *Aciculella*. Such a development may well have existed in extinct cladospore genera, and would be represented by dissociated fossil elements. If, therefore, Pia's rejection of *Aciculella* being similar in origin to *Acicularia* s. str. is to be supported, it must be on other grounds, and this is further dealt with below, as is his observation that *Aciculella* shows no pointed termination as in *Acicularia* s. str.

Holosporella (Triassic) and *Atractyliopsis* (Permian, ? Carboniferous) were interpreted by Pia (1930, 1937) as the remains of endospore dasycladaceans whose sole calcification was around the reproductive elements or sporangia (cf. text-fig. 1). These lay peripherally within the stem-cell, the exterior of the stem-cell and the outer branch-systems being uncalcified and hence quite unknown. The fossil thus consists of a hollow cylindrical arrangement of hollow spheres with calcified walls, adjacent, touching, or fused to varying degree (and with a very variable amount of secondary calcification, depending on subsequent diagenesis) (Pl. 118, fig. 3; Pl. 119, fig. 4). This apparently improbable interpretation is supported by two pieces of evidence. One is the Triassic species *Diplopore phanerospongia* Pia (Pl. 118, fig. 5), a diplopore showing normal heavy calcification of both stem-cell and detailed trichophore branch-systems, but also showing calcified peripheral sporangia within the stem-cell cavity, as postulated for *Atractyliopsis* and other genera. Due to the waxing and waning stem-cell morphology of *D. phanerospongia*, accidental post-mortem insertion of originally separate and distinct straight calcareous algal structures one within the other (cf. Elliott 1968, pl. 24, fig. 2) is impossible. The endospore nature of this diplopore is thus authenticated. This vital species, known only to Pia from a Museum specimen, has now been rediscovered in the Upper Triassic, and other new similar species described (Ott 1967, Fenninger 1969).

The second point is from the known ontogeny of living dasyclads. Here the large nucleus is housed within the holdfast or basal portion throughout most of the growth of

EXPLANATION OF PLATE 119

- Figs. 1, 2. *Aciculella ogilvie-gordonae* sp. nov. 1, Oblique-transverse thin-section, paratype, $\times 93$. 2, Longitudinal section, $\times 50$. Upper Permian, Bellerophon Limestone; Plesch d'Inez, Grödener Valley, South Tirol, N. Italy. Reg. no. V.53903.
- Fig. 3. *Aeolisaccus dunningtoni* Elliott: longitudinal thin-section, $\times 330$. Small example showing initial spherical chamber. Upper Permian, Bellerophon Limestone; Plesch d'Inez, Grödener Valley, South Tirol, N. Italy. Reg. no. V.53903.
- Fig. 4. *Atractyliopsis lastensis* Accordi. Thin-section of fragment, $\times 110$, for comparison with *Aciculella ogilvie-gordonae* in the same matrix and rock sample. Upper Permian, Bellerophon Limestone; Plesch d'Inez, Grödener Valley, South Tirol, N. Italy. Reg. no. V.53906.
- Fig. 5. *Aciculella ogilvie-gordonae* sp. nov. Transverse thin-section to show central as well as marginal sporangial bodies, paratype, $\times 160$. Upper Permian, Bellerophon Limestone; Plesch d'Inez, Grödener Valley, South Tirol, N. Italy. Reg. no. V.53905.



TEXT-FIG. 1. Reproductive ontogeny of an extinct dasycladacean leading to production of a fossil *Aciculella*.

- a. Living plant growing on stone on sea-floor.
- b. Diagrammatic section of (a) showing tall central stem-cell with lateral branches, attached by holdfast to stone, large nucleus in holdfast, no calcareous structures in green plant.
- c. Break-up of nucleus and migration of small nuclei up the stem-cell.
- d. Migration of nuclei in stem-cell to peripheral positions to form uncalcified 'sporangia'.
- e. Rapid calcification of reproductive upper part of stem-cell, shedding of side-branches.
- f. Stump of plant with regenerative nucleus on stone; calcified body with encysted gametes lying in mud of sea-floor.

the plant, but eventually breaks up into numerous smaller nuclei which migrate up the stem-cell to peripheral positions in the branches to initiate the reproductive bodies, around which calcification frequently originates (Hämmerling 1931, 1944; Egerod 1952). Pia's classification (1920) of dasycladacean reproductive structures as endospore, cladospore, and choristospore in that order approximately in geological time, suggests that the ontogeny is a recapitulation of the phylogeny, as Rezak (1959) has commented.

The existence of endospore genera, in which the sporangia are eventually distributed peripherally in the stem-cell but do not leave it for the branches (cladospore) or special reproductive outgrowths (choristospore), is thus indirectly substantiated. In abnormal living choristospore dasyclads 'endospore' sporangia are occasionally seen (cf. Valet 1969, p. 569).

In the thin-sections of Bellerophon Limestone now studied, *Atractyliopsis lastensis* and *Aciculella ogilvie-gordonae* occur together. The calcareous wall-thickness of the sporangial globules of the former is often visible, plus a varying amount of secondary calcification which may partially or wholly fill the main stem-cell cavity, which is otherwise filled with normal matrix. In one case only was the filling of yellowish calcite as in *Aciculella*, and in this instance the whole fossil was embedded in a mass of such calcite extending external to the fossil. The usual preservation of *Atractyliopsis* is thus quite different to that of *Aciculella*, embedded in the same matrix.

Pia's explanation of his Triassic *Aciculella* may now be quoted in full.

... we have to deal with the content of an 'endospore' axial cell. It must be supposed that at the time when calcification began, assimilation and circulation were stopped. The axial cell was gradually filled with lime from the growing point downward, mainly from the supply of material stored in the root-cell. When the alga died and broke to pieces, the gametes or the cysts in which they were contained, escaped from the cavities by the pores. (Pia 1930, p. 180.)

This explanation has always seemed doubtful, since it gives no reason as to why he considered the calcification original-organic in origin, and not post-mortem diagenetic filling, so necessitating an explanation like that given. Study of the new Permian species supplies evidence in support, however. In *A. ogilvie-gordonae* the peripheral cavities show no trace at all of calcareous wall thickness. If they were originally uncalcified plant-matter at the death of the alga, as this suggests, their chance of distinct preservation from the plant-matter of the surrounding stem-cell was negligible. If preserved at all, such an *Aciculella* would be matrix-filled and the outer outline alone distinguishable under favourable conditions, and subsequent diagenesis could only affect what was originally preserved. It seems likely, therefore, that the stem-cell was in fact filled by organically formed aragonitic calcium carbonate spreading around and inwards from the sporangial bodies after these had formed and were mature. Calcification in living algae has not received the study it deserves, and it is still not known why some green algae form deposits of calcium carbonate on and within their tissues whilst growing and photosynthesizing side by side in the same environment with other green algae which never calcify. Between members of the Dasycladales this calcification is extraordinarily varied, though taxonomically constant for the genera and species themselves. In the case of *Aciculella* the calcification must have been very rapid, once conditions were physiologically right, in order to preserve the occasional sporangia seen centrally in the stem-cell. The lime was not from the 'supply of material in the root-cell', as Pia supposed, though the biochemistry of its formation and timing was probably controlled from the residual nucleus in the basal holdfast (cf. Hämmerling 1953 and Brachet 1965 on living *Acetabularia*). It is probable that this calcification extended only to the fertile middle and upper parts of the stem-cell; Pia noted the absence of a proximal 'pointed end' in *Aciculella bacillum*, and *A. ogilvie-gordonae* ends irregularly proximally also. This may be due to breakage, but a ragged end to incomplete calcification is to be expected. After the calcified portion, probably containing encysted gametes in the cavities, broke

away, the nucleate holdfast and residual stump may have been capable of successive regenerations (cf. Valet (1969, p. 560) on living *Bornetella*, *Halicoryne*, *Acetabularia*, etc.). The calcareous rod, if not broken up with release of the sporangial contents, would be buried in calcareous mud. Subsequent diagenesis altered the aragonitic rod to coarse yellow calcite, the plant-filled cavities to dark finely-grained crystalline calcite, and the lime mud to lighter coloured, more coarsely-grained calcite, to give the appearances now seen in thin-section.

Pia's *Holosporella*, figured side by side with *A. bacillum* (Pia 1930, pl. 4), probably served him for discriminative comparison in the same way that *Atractyliopsis* has with *Aciculella ogilvie-gordonae*. This is not clear from his brief paper, though it probably accounts for his explanation, with which I agree.

Other records. *Aciculella ogilvae-gordonae* is the first described Permian species, so far as I know: the *Acicularia* sp. of Güvenç (1965, pl. A8), from the Turkish Permian, may be referable to *Aciculella*.

Since Pia's original paper (1930) the Triassic *A. bacillum* has been recorded from the Ladinian of Czechoslovakia by Andrusov (1939). Pia (1942) listed it again, together with undescribed *Aciculella* spp. from the Anisian and Carnic stages of central Europe. These records were repeated by Bystrický (1964), who also figured '*Acicularia* spp.' from the Ladinian. *Aciculella* sp. nov. is recorded and figured from the Moroccan Infralias by Lemoine and Raoult (1962); the same paper quotes a verbal record of J. Sigal of *A. cf. bacillum* from the Upper Triassic of Spain.

Some of the very miscellaneous bodies referred to *Acicularia* s.l. from higher Mesozoic levels may prove to be referable to *Aciculella*.

In conclusion, it must be noted that species of *Aciculella* may be the endospore stem-cell fillings from dasycladaceans of very different branch-morphology, which would certainly be referred to different genera if they had calcified more completely. *Aciculella* is thus a form-genus for Dasycladaceae *incerta sedis* in much the same way as is *Griphoporella*.

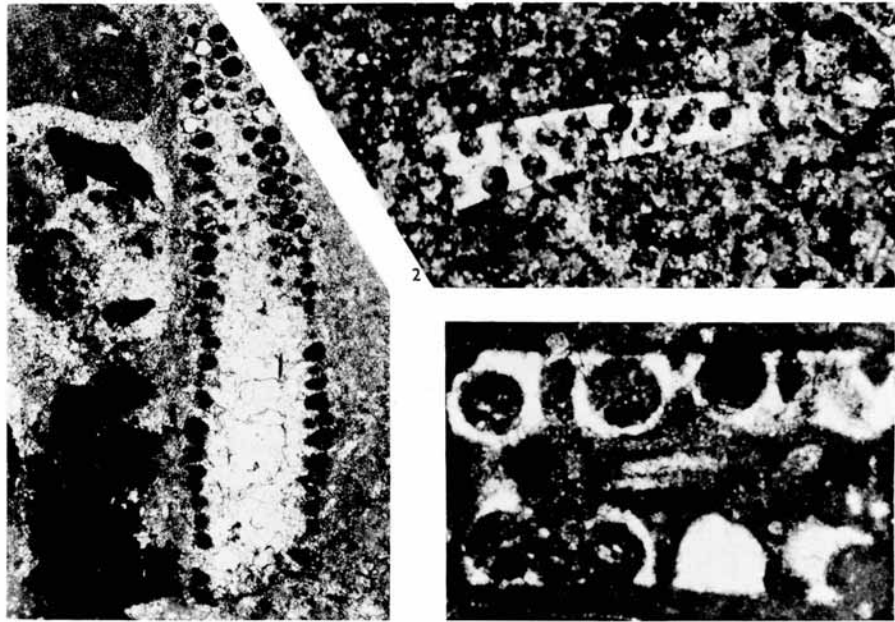
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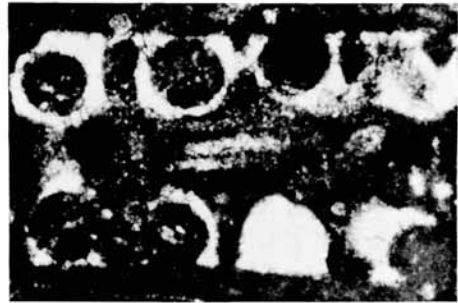
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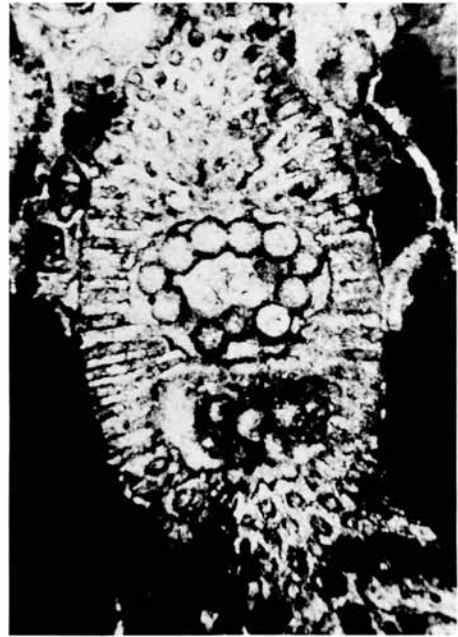
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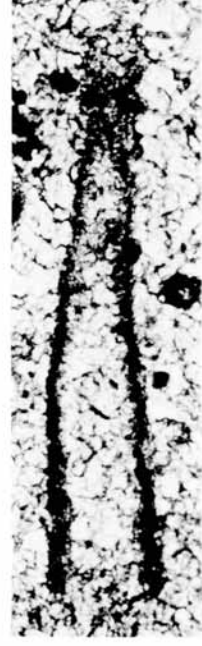
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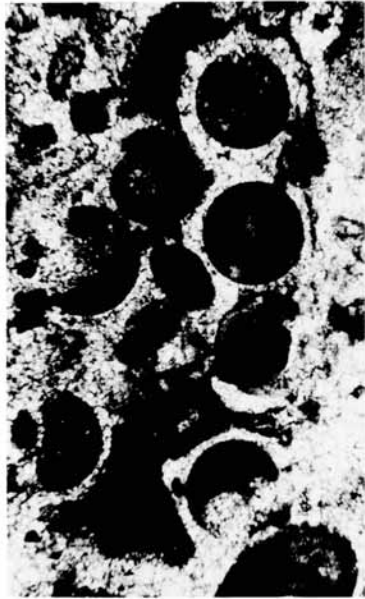
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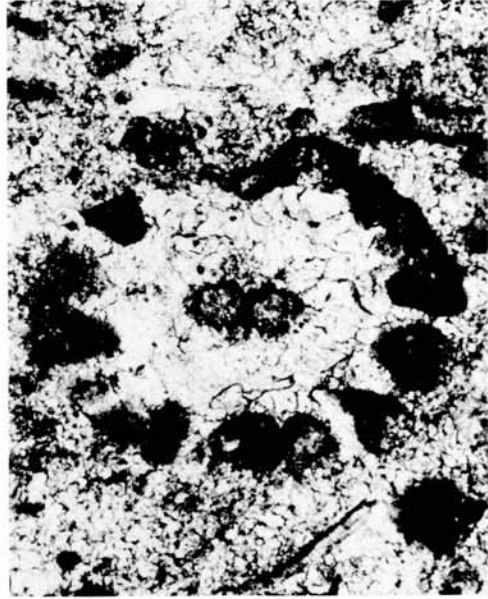
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