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GROSS STRUCTURE AND MICROSTRUCTURE OF *STROMATOPORELLA GRANULATA* (Nicholson, 1873) AND THEIR CONSEQUENCES ON THE DEFINITION OF SOME DEVONIAN STROMATOPOROID GENERA

BY

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ABSTRACT

In the abundant material of the species described in this paper great variation occurs in the form of the coenosteum, the structure of laminae and pillars and the microstructure.
The shape of the coenosteum is dependent on environmental factors such as the form of the substrate, wave action, currents and sedimentation. These factors influence the ratio between the vertical and horizontal growth rates and the formation of mamelons, astrorhizae and latilaminae.
The same ecological conditions also greatly influence the superposition of pillars and the formation of repair tissue and cyst plates. The number of laminae per mm is rather constant, it only varies between certain limits. Ring pillars are not considered as a generic character for they are associated with very different types of microstructures.
Microstructures can be changed very strongly by alterations before, during and after sedimentation. Laminae are originally composed of two or more compact layers with a clear layer or vacuoles between them. They can become transversely fibrous, flocculent and pseudocellular by recrystallization.
For these reasons great variations in the fossil material occur and are the cause that many new genera and species were created adding to the great confusion in the classification of stromatoporoids.
The following genera are probably synonyms:
Stromatoporella, *Clathrocoilona*, *Stictostroma*, *Trupetostroma* and *Taleastroma*. Many species have also erroneously been described as belonging to other genera, principally *Stromatopora*, *Syringostroma* and *Parallelopora*.

INTRODUCTION

In the course of a stratigraphic and paleoecologic study of Devonian stromatoporoids from north-western Spain (provinces León and Palencia) difficulties arose concerning the species dealt with in the present paper. The author thought at first that he was dealing with three species: one in the genus *Trupetostroma* Parks, one in the genus *Gerronostroma* Yavorsky, and one in the genus *Parallelopora* Bargatzky. It became obvious, however, when more material was collected, that only one species was present but in different states of preservation, suggesting various types of microstructure. Besides, there is a great variation in the arrangement of laminae and pillars although this is partly due to the not exactly vertical sections.
All the material was collected in the lower portion of the Portilla Formation (upper Givetian) in the northern part of the province León and in the north-western part of the province Palencia (see Comte, 1959, pp. 230, 311, 317). Specimens from other formations are not taken into account in this publication and specimens too small to be determined properly are also excluded. Evolutionary trends were not found.
The species described in this paper occurs together with *Actinostroma stellulatum*, *Stromatopora concentrica* and a very similar species but with ca. 11 lam/2 mm. Other dominant elements of the fauna are *Favosites sp.*, *Alveolites sp.*, *Chaetetes sp.*, *Thamnopora sp.* and many solitary corals.
The sediments consist of an alternation of crinoidal biosparrudites and biosparites with biomicrudites and biomicrites, in the sense of Folk (1959). They are often more or less sandy or silty and very ferruginous.
Procedure of investigation. — The material was studied in thin sections of all specimens. From the most typical examples acetate peels were made for the study of the finest structures. For this purpose a polished surface parallel to that of the thin section was etched with diluted hydrochloric acid for about 10 seconds. Photos were made with a Leitz Ortholux microscope-camera.
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DESCRIPTION OF THE SPECIES

Stromatoporella granulata (Nicholson, 1873)

1873 *Stromatopora granulata* sp. nov. — Nicholson, p. 94, Pl. IV figs. 3, 3a.

1886 *Stromatoporella granulata* (Nicholson) — Nicholson, p. 10.

1886—92 *Stromatoporella granulata* (Nicholson) — Nicholson p. 202, Pl. I figs. 4, 5, 15, Pl. IV fig. 6, Pl. VII figs. 5, 6, Pl. XXVI fig. 1.

1936 *Stromatoporella granulata* (Nicholson) — Parks, p. 95, Pl. XV figs. 6—7, Pl. XVI figs. 1—7.

1951 *Stromatoporella granulata* (Nicholson) — Lecompte p. 160, Pl. XXI fig. 1.

1957 *Stromatoporella granulata* (Nicholson) — Galloway & St. Jean, p. 131, Pl. 7 fig. 3.

Description of the material

Number of specimens: ca. 80

Coenosteum: The coenosteum is more or less laminar. There are thin laminar specimens with scarcely any mamelons, but also more compact ones with very pronounced mamelons. Generally the mamelons are rather low.

Most specimens are between 0,5 and 4 cm thick and have a lateral extension up to 20 cm. Many of them were found upside down or fragmented as bioclasts in the sediment.

About half of the specimens are more or less intergrown with *Syringopora sp.* Some specimens are overgrown by *Chaetetes sp.*, *Alveolites sp.* and other tabulate corals, while others on the contrary encrust these species.

Vertical section: The laminae are continuous, often dichotomous, typically with a white median layer in well preserved specimens. The foramina, which are often superposed, are closed by cyst plates. The laminae are more or less straight in specimens with a regular growth and irregularly undulating in specimens with a frequently disturbed growth. In 2 mm there are ca. 8—9 laminae, but within one specimen there may be a variation of 7—10 lam/2 mm. (see diagram I). A great variation is also found in the thickness of the laminae (extremes: 0,03—0,23 mm). Some specimens have strongly thickened tissue while others have a rather thin tissue, giving quite a different appearance. But all intermediate states also occur and there are even specimens which have both as latilaminae (figs. 1,4).

The pillars are spool-shaped, mostly superposed in specimens with a regular growth (figs. 2, 3), but not or scarcely superposed in specimens with an irregular growth (figs. 1,4). The pillars are not continuous; the clear layer in the laminae is not interrupted by them (figs. 1, 2, 3, 4, 8, 9, 11, 13).

The interlaminar spaces are circular or elongate, commonly between 0,10 and 0,20 mm high, the larger ones grade into astrorhizal canals. Cyst plates are common.

Astrorhizae, when present, are situated in more or less pronounced mamelons (figs. 2, 3, 4). They are formed by vertical tabulated tubes (which are only visible when the thin section cuts through the centre of a mamelon) with radiating ones in the laminae. The radiating tubes also have cyst plates; they are round in cross-section and larger than normal galleries (up to 0,40 mm at the origin). In many thin sections of laminar forms without mamelons, astrorhizae are absent.

Latilaminae are vague in specimens with regular growth. Generally they are between 4 and 6 mm thick. Apart from this some local irregularities in growth are present in many thin sections. Specimens with irregular growth show in general more marked latilaminae, due to differences of thickness in the tissue and to layers of repair tissue. Here the latilaminae are, however, only 1,5—4 mm thick.

Tangential section: The laminae are cut as concentric

Lam/2 mm	Specimen 32G	29C	128B	262C	478A	27	260F	580G	35C	580J	Total percentage
11											
10	3	1			2	1	1	1	1		10%
9	3	2	4	1	5	4	4	2	6	1	32%
8	2	3	3	4	2	4	4	5	3	7	37%
7	2	4	3	5	1	1	1	2		2	21%
6											-

Diagram I. 10 specimens with each 10 measurements. Each measurement was started from a lamina. Influence of obliqueness on measurements is obvious in some specimens.

rings if mamelons are pronounced (fig. 5). In parts of the section where the laminae and pillars are cut obliquely, an amalgamated network is visible. In parts where the section is nearly tangential to the laminae, the pillars are seen to be coalescent. Only when the pillars are cut in the interlaminar spaces are they seen as round isolated dots (fig. 6). This pattern can best be seen in well oriented tangential sections of specimens without or with scarcely developed mamelons.

The astrorhizae are visible as branched tubes, spreading radially from the centre of the mamelons. When followed for a long distance in one interlaminar space, these tubes can be seen to be very long (fig. 5). Some specimens have some structures very similar to ring pillars (fig. 7).

Microstructure: The microstructure has a very variable appearance depending on the state of preservation. There is no relation between the variation in microstructure and the variation in gross structure. The terms used for the description of microstructure are used in the sense of Stearn (1966). The term pseudocellular as defined on p. 12 and figs. 19—22 is proposed by the writer.

a) Well preserved specimens do not show any marks of alteration before, during or after sedimentation; moreover these specimens are not weathered in any way and are nearly indistinguishable in the field. For this reason there are only a few specimens of this type in the collection. Even in this state, however, the tissue is not evenly coloured, but vaguely flocculent (figs. 8, 9). This must be due to the specks which can be seen very clearly in a peel (fig. 10) from a plane in the same direction of the same specimen as fig. 9. The diameter of the specks is about 2—4 μ.
In the peel the crystal borders are also very distinct. The crystals have an irregular shape which is completely independent of the structure of the stromatoporoid, though the crystals confined to the interlaminar spaces are generally the largest. Within the tissue crystal borders often are not developed. A crystal partly situated in an interlaminar space and partly in the tissue of the stromatoporoid has only specks in the latter part; for this reason the structure of the stromatoporoid is still visible in a peel.
The laminae are multilaminar in many places (figs. 8, 9, 11, 13). Most frequently there are only two layers separated by a clear one. Thin laminae often have only one layer (figs. 1, 4). In other places the tissue is full of vacuoles (figs. 8, 9); these may lie more or less in a row. The foramina are mostly closed by a thin membrane (cyst plate).
In the writer's opinion continuous clear zones must be regarded as primary microstructures, for they occur together with ordinicellulae in one specimen, sometimes even side by side in one lamina. Moreover, tissue reversal as described by Stearn (1966, p. 84) occurs in the clear layer. This means that the clear layer was already open space during the life of the stromatoporoid or at least during sedimentation.

No traces of transverse fibers and pores or tubules are visible in the specimens of this group.

b) Other specimens have an opalescent appearance below the microscope. They look more or less leached, Fe-minerals are oxydized and crystal borders are more pronounced than in the first group; but no further alteration has occurred as vacuoles and microlamination of the tissue are clearly visible.
Many interlaminar spaces seem to have been filled with crystals starting from the border of the tissue (fig. 11), while the border between tissue and interlaminar space is rather sharp in other places.
In a peel from the same plane (fig. 12) many interlaminar spaces have one or more coarse crystals in the centre, which is surrounded by smaller ones on the border, indicating porefilling processes during fossilization. Within the crystals on the border the structure of the stromatoporoid tissue is more or less sharply defined by the specks.

c) Most specimens are more or less flocculent (figs. 2, 3, 5, 6, 7, 13, 17). This can partly be due to weathering, as the outer rim of a specimen is generally more flocculent than the centre. It seems, however, that this has already taken place, partly at least, during the life of the stromatoporoid, as in some specimens with pronounced latilaminae the uppermost part of these latilaminae is more flocculent and often even differently coloured than the rest of the coenosteum (fig. 17). Alternation before fossilization also explains the occurrence in one hand specimen of two specimens of stromatoporoids (often belonging to the same species) in very different conditions of preservation.
In a peel the same crystal pattern is visible as in the first group, but the specks are less evenly distributed and some crystals show twin lamellae (fig. 14).

d) Many specimens are more or less transversely fibrous. This is due to orientated recrystallization. Between crossed nicols an alternation of transverse clear and dark bands is visible in the thin section. Nevertheless microlamination of laminae is still present in many places (fig. 15). The microstructure of the pillars is very vague, sometimes it also looks transversely fibrous.
A peel (fig. 16) shows that twin lamellae of crystals are more or less vertical. The crystals are vertically elongated in the laminae and horizontally elongated in the pillars, causing transverse fibrosity.
Transverse fibrosity is vaguely visible in many specimens, but only in a few specimens is it really conspicuous.

e) Other specimens are quite differently altered. Their microstructure has changed to a melanospheric, "microreticulate", "pseudomaculate" or "cellular" microstructure (figs. 18, 19, 20, 22). In fig. 18 the tissue is melanospheric, giving a "microreticulate" impression, for microlamination has not disappeared

completely. Partly there is also a vague vertical arrangement of melanospheres. In figs. 19 and 20 the tissue is more coarsely melanospheric. Many melanospheres are concentrated around interlaminar spaces, leaving yellowish microlaminae with some melanospheres between them, which gives a "cellular" impression. In other places the galleries seem to have disappeared nearly completely due to infiltration of pigment specks.
In a peel (fig. 21) the interlaminar spaces are occupied by one or more coarse crystals, generally confined to this area. Laminae and pillars are full of small clear crystals, while the rest of the tissue is speckled more or less irregularly and has no distinct crystal borders.
From thin sections and peels it becomes obvious that this type of microstructure is caused by recrystallization, for crystal borders are no longer independent of the structure of the stromatoporoid. Instead there is a tendency to form clear crystals without pigment specks.
The term pseudocellular is proposed for this type of secondary microstructure.
Specimens with mainly superposed pillars look very much like *Parallelopora*. Pigment tends to concentrate along vertical walls of interlaminar spaces, while laminae between superposed interlaminar spaces tend to disappear (fig. 19). (Compare with *Stromatopora goldfussi* (Bargatzky) — Lecompte, 1952, Pl. LVII fig. 4).

Diagnosis

From the foregoing it can be seen that the material studied belongs to one species with the following diagnosis:
Coenosteum laminar to massive, often encrusting but sometimes overgrown itself by tabulate corals. Mamelons absent, low or very pronounced. Astrorhizae related to mamelons. Latilaminae present.

Diagram 2.

SPECIES	AUTHOR	COENOSTEUM
Stromatoporella socialis	Nicholson, 1886—92, p. 206, Pl. XXVI figs. 5—7.	laminar to massive, mamelons and astrorhizae well developed, with or without *Syringopora*.
Syringostroma strahlenbergi	Yavorsky, 1931, p. 1411, Pl. IV figs. 10, 11.	fragmentary specimens, *Syringopora* absent.
Trupetostroma warreni	Parks, 1936, p. 55, Pl. X figs. 1, 2 (see also Stearn, 1966, Pl. 17 figs. 1, 2).	subhemispheric? mamelons small, astrorhizae well developed, *Syringopora* absent.
Stromatoporella kayi	Parks, 1936, p. 111, Pl. XIII figs. 7, 8.	laminar, mamelons low, *Syringopora* absent.
Stromatoporella decora	Lecompte, 1951, p. 164, Pl. XXIV fig. 6.	encrusting, mamelons low, astrorhizae present, intergrown with *Syringopora*.
Stromatoporella saginata	Lecompte, 1951, p. 171, Pl. XXII figs. 5—7, Pl. XXIII figs. 1—3.	laminar, mamelons sometimes very pronounced, astrorhizae well developed; *Syringopora* absent.
Trupetostroma cellulosum	Lecompte, 1952, p. 233, Pl. XLI figs. 1, 2.	massive, mamelons very low, astrorhizae well developed, *Syringopora* absent.
Stromatoporella parasolitaria	Galloway & St. Jean, 1957, p. 137, Pl. 8 fig. 4.	laminar, mamelons low, astrorhizae small, with or without *Syringopora*.
Stromatoporella cryptoannulata	Galloway & St. Jean, 1957, p. 141, Pl. 9 fig. 2.	massive, mamelons small, astrorhizae small, *Syringopora* absent.
Stromatopora cumingsi	Galloway & St. Jean, 1957, p. 182, Pl. 15 fig. 4.	massive, no mamelons, astrorhizae small, with or without *Syringopora*.
Taleastroma lenzi	Galloway, 1960, p. 630, Pl. 75 fig. 2.	massive, neither mamelons nor astrorhizae, *Syringopora* absent.

Vertical section: 7—10 laminae in 2 mm, generally 8—9. Laminae continuous, often dichotomous. Foramina common, closed by cyst plates. Laminae consist of two or more layers with a clear layer or a row of cellulae inbetween. Thickness of laminae between 0,05 and 0,20 mm. Laminae sometimes bent up forming ring pillars. Pillars thick, spool-shaped, generally superposed in specimens with regular growth (= specimens with regular structure of laminae and pillars), but not or only scarcely superposed in specimens which were frequently disturbed in growth.
Interlaminar spaces round or laterally elongate, varying greatly in diameter. Astrorhizae in cross-section round, wider than normal galleries. In longitudinal section astrorhizae are seen as vertical tabulated canals from which horizontal, also tabulated ones, originate. The latter are bounded to one interlaminar space.
Tangential section: pillars in cross-section round, sometimes ring pillars are visible. In not perfectly tangentially cut parts of the section pillars are coalescent or may even form an amalgamated network.
Microstructure: Well preserved specimens have "tripartite" laminae. The clear layer is more or less continuous. The tissue is vacuolate in some places and finely laminar in others. By alteration the microstructure becomes flocculent, melanospheric and even pseudocellular. Other specimens become transversely fibrous and the clear layer becomes very vague by this recrystallization. Apart from this the specks can move out into the galleries, obscuring the whole structure.

Remarks

Many species have been described showing similar features in gross structure as well as in "different" microstructures. Some examples are given in diagram 2.

GROSS STRUCTURE	MICROSTRUCTURE	OCCURRENCE
pillars generally not superposed, no ring pillars, cyst plates present.	'porous but obscured by secondary crystallization'.	M. Devonian, South Devon and Eifel.
pillars generally superposed, no ring pillars, cyst plates present.	'tissue fibre finely porous'. (In fig. 10 clear layers and vacuoles are distinguishable).	M. Devonian, Kuznetsk Basin.
pillars superposed, no ring pillars, cyst plates present.	lamina with 'clear lines', 'tissue dense with vacuities'.	M. Devonian, Great Slave Lake.
pillars not superposed, cyst plates present, 'feeble development of ring-like cross sections' (not visible in figures).	'median row of minute pores in laminae'.	Hackberry shale (U. Devonian), Iowa.
laminae irregular, pillars not superposed, cyst plates common, ring pillars not visible in figures.	'microcellulaire' (In fig. 6a clear layers are visible).	Givetian, Belgium.
pillars sometimes superposed, ring pillars absent, cyst plates common.	laminae with clear layers.	Frasnian, Belgium.
pillars generally superposed, ring pillars absent, cyst plates abundant.	'poudreux, finement cellulaire, d'aspect corrodé'.	Givetian and Frasnian, Belgium.
pillars not superposed, ring pillars not visible in figures, cyst plates abundant.	'light-colored median, transversely porous layers', 'nearly identical with that of *S. granulata*'.	Jefferson limestone (M. Devonian), Indiana.
pillars generally not superposed, ring pillars 'large, obscure', cyst plates present.	'anastomosingly porous, fibrous tissue'.	lower Longasport limestone (M. Devonian), Indiana.
pillars sometimes superposed, ring pillars not visible in figures, cyst plates present.	'microlaminae', 'coarse maculae on the borders of the structures'.	lower Longasport limestone (M. Devonian), Indiana.
pillars generally superposed, no ring pillars, cyst plates scarce.	'coarsely maculate microlaminae'.	Ramparts Formation, Northwest Territories.

They all have ca. 8—9 lam/2 mm differentiating them from other species with ca. 6 lam/2 mm and from species with ca. 11 lam/2 mm. According to Flügel (1957, 1959), the number of lam/mm is rather constant in one species and seems to be a valuable specific character. Many of the species, especially the older ones, are only based on the presence or absence of cyst plates, mamelons and astrorhizae. As these features are highly variable, being very dependent on environmental factors, they cannot be considered as valuable.
Other species are based on: (a) the superposition of pillars, (b) the presence of ring pillars and (c) differences in microstructure.

a) In the writer's opinion the superposition of pillars is not a valuable character for species in this group. In the first place the pillars are not continuous but only superposed, for they do not cross the clear layer. As tissue reversal occurs in this layer (Stearn 1966, p. 84) it has probably been empty space. In the second place the superposition of pillars has been used by many authors in a rather arbitrary way. Some specimens were described as having „generally superposed pillars", while more or less similar specimens are described elsewhere with "pillars not commonly superposed". As a matter of fact many specimens can be described as well in one terminology as in the other.
In the material from Spain it can be observed that specimens with more or less superposed pillars have a tendency to more thickened tissue, broader latilaminae generally without repair tissue, and are found in generally finer sediments than specimens with an irregular growth, which can have very thin laminae, very pronounced but rather thin latilaminae, and which are mostly found in coarser sediments (see figs. 1—4).
With respect to this it is possible to explain many differences in the internal structure of the coenosteum as being due to ecological factors, mainly wave action and the presence of mud. The same has already been done by several authors in relation to the form of the coenosteum.

b) Some of the specimens with an irregular growth show some rare structures similar to ring pillars, but have no other differences.
In the writer's opinion ring pillars are simply upturns of the laminae and can occur in various genera. This opinion is based on several facts. In the first place specimens with ring pillars and specimens without ring pillars have no other differences. In the second place the amount of ring pillars is very variable from specimen to specimen and even from place to place within one specimen, which means that ring pillars are not a constant element of the structure of these stromatoporoids. In the third place many specimens with single-layered laminae and, in the opinion of the writer, belonging to quite different genera also have ring pillars.
In the Spanish material from the Santa Lucia Formation specimens occur with strongly undulating thick laminae and ring pillars. They have a true finely cellular microstructure. The cellulae are situated in rows parallel to the borders of the laminae. These specimens are found together with specimens with exactly the same microstructure but without ring pillars. Therefore the ring pillars should not be used as an exclusive feature in defining a genus. As they occur only in a few genera they nevertheless seem to be of value for determination purposes.
St. Jean (1962, p. 187) has already suggested that ring pillars can be explained satisfactorily as polymorphism. They can also be due to parasitism (or symbiosis) analogous to that of *Syringopora sp.*, but in this case by organisms without skeleton.

c) As shown earlier in this paper, the microstructure can give a highly variable impression depending on the state of preservation. Flocculency seems to be due at least partly to alterations before fossilization (see St. Jean, 1962, p. 196), while transverse fibrosity was caused by recrystallization during or after fossilization. Stearn (1966) states that transverse fibrosity may occur in all genera of stromatoporoids, and that transverse porosity too is often formed during preservation. The present writer believes, however, that all transverse fibrosity and transverse porosity are secondary features developed after the death of the organism.
Strongly recrystallized melanospheric specimens with development of clear crystals in the tissue look as if they are cellular. If melanospheres are more or less placed in vertical rows they even appear to be microreticulate. It is obvious that in a part of the material there is a strong tendency to vertical rearrangement of specks and crystals, which either causes transverse fibrosity or microreticulation, while in many specimens small more or less vertical calcite veins are found. An other striking phenomenon is the presence of yellowish microlaminae in many strongly altered specimens.
Part of the material has become almost indistinguishable by strong alteration. These specimens are not included in this species.

DESCRIPTION OF THE GENUS

Genus STROMATOPORELLA Nicholson, 1886

Type species (originally designated), *Stromatopora granulata* Nicholson, 1873, Ann. Mag. Nat. Hist. ser. 4, Vol. 12, p. 94, Pl. 4 fig. 3. (Middle Devonian, Hamilton Formation, Ontario (see Nicholson, 1886—92, p. 203)).

Stromatoporella Nicholson, 1886—92, p. 92; Parks, 1936, p. 90 (partim); Lecompte, 1951, p. 152; Lecompte, 1956, p. F 131; Galloway & St. Jean, 1957, p. 129 (partim); Galloway, 1957, p. 436 (partim); Stearn, 1966, p. 93 (partim).

Clathrocoilona Yavorsky, 1931, p. 1407; Galloway & St. Jean, 1957, p. 221; Galloway, 1957, p. 451; Stearn, 1966, p. 98.

Stictostroma Parks, 1936, p. 77 (partim); Galloway & St. Jean, 1957, p. 124 (partim); Galloway, 1957, p. 435 (partim); St. Jean, 1962, p. 185 (partim); Stearn, 1966, p. 96 (partim).

Trupetostroma Parks, 1936, p. 52; Lecompte, 1952, p. 219; Lecompte, 1956, p. F 132; Galloway & St. Jean, 1957, p. 158; Galloway, 1957, p. 439; Stearn, 1966, p. 102.
Taleastroma Galloway, 1957, p. 448; Galloway, 1960, p. 630; Stearn, 1960, p. 112.

Diagnosis

Coenosteum laminar to massive, sometimes encrusting, depending on ecological conditions. With or without prominent mamelons. Astrorhizae tabulated. Latilaminae generally present.
Vertical section: Laminae continuous, thick, typically composed of two or more layers, sometimes only one. Between these layers a clear zone or a row of cellulae is present in many places. To a varying extent laminae may be only present as cyst plates between the pillars. Ring pillars, formed by upturns of the laminae, occur in many specimens but are not a specific character. Pillars thick, spool-shaped, superposed or randomly placed depending on conditions during growth. Interlaminar spaces round, or horizontally elongate, varying in size, but smaller than astrorhizae. Cyst plates common.

Tangential section: Pillars round and isolated or coalescent. Where cut near a lamina an amalgamated network is visible. Many specimens have more or less abundant ring pillars. Mamelons visible as rings of obliquely cut laminae, generally with astrorhizae in the centre.

Microstructure: Compact, vacuolate and multilayered. By secondary alterations it becomes transversely fibrous, transversely porous, flocculent, melanospheric, pseudocellular or diffuse by migration of specks.

Discussion of the genus

The diagnosis given above includes features which have been used for the distinction of different genera. No general agreement exists about the definitions of these genera. This is shown by the large number of species from the genera mentioned in the synonimy list which have been transferred from one genus to an other. It is also striking that nearly every student of this group has found a large number of new species which have never been found again, even by himself. Thus great confusion has developed in the taxonomy of stromatoporoids and this can only be resolved by trying to establish species and genera on true differences.
There are two extremes in the structure of laminae and pillars. In some specimens the laminae are irregular and undulating, and the pillars are not superposed but arbitrarily placed. In specimens from the other extreme nearly all pillars are exactly superposed and laminae are often only represented as cyst plates. Most specimens, however, are intermediates with well developed laminae and part of the pillars superposed. In many coenostea temporary tendencies to one or the other extreme in the mode of growth are present. This is clearly visible in many figures of Lecompte (1951, 1952), because they show large areas of the sections and not only the most "typical" part of them. Many specimens have even latilaminae with repair tissue, so the soft parts could live very well in or on an irregular skeleton. Probably specimens with a fast vertical growth developed strong pillars and scarcely any laminae, while slower growing ones had time to develop thick laminae. In this light it becomes very difficult to use the superposition of pillars as a character for genera or even for species.
The main problem with this is that hardly anything is known about the soft parts of the colony and their relation to the skeleton.
Microstructure is only a valuable characteristic when in its original state. As many species and genera are based on strongly altered specimens, they will have to be reconsidered.

Stromatoporella granulata (Nicholson) has been described by many authors. All of them described specimens with rather irregular growth and with ring pillars and tripartite laminae. If ring pillars are not considered to be of value for the distinction of species and genera, there is no real difference with some specimens described in this paper (with irregular growth and a transversely fibrous and melanospheric microstructure).
Specimens with ring pillars have mainly been placed in the genus *Stromatoporella*. Many students of this group have included species that do not have a clear layer in the (thin) laminae (see Yavorsky, 1931; Parks, 1936; Galloway & St. Jean, 1957; Galloway, 1960). These species cannot be included in the present genus. For the same reason specimens with a true cellular microstructure have to be excluded. Lecompte (1951) described many specimens with rather well superposed pillars and no ring pillars in the genus *Stromatoporella*. Lecompte (1956, p. F 131) also states that pillars may have a tendency to superposition. He regards the genera *Stictostroma* and *Clathrocoilona* (probably) as synonyms of *Stromatoporella*.
Clathrocoilona abeona Yavorsky as originally described by Yavorsky (1931, p. 1407) has laminae with a clear layer and many superposed pillars as can be seen in his fig. 9 on Pl. 1 and fig. 2 on Pl. II. There is no reason to separate it from the genus *Stromatoporella* as defined in this paper.
Lecompte (1956, p. F 131) also interpreted the genus *Clathrocoilona* as being a probable synonym of *Stromatoporella*. Galloway & St. Jean (1957) and Galloway (1960) described as *Clathrocoilona* some strongly altered specimens with irregular growth which also belong to the genus *Stromatoporella*. Stearn (1966, p. 98) proposes to separate the genus *Clathrocoilona* from the genus *Stictostroma* on the basis of the proportional heights of laminae and interlaminar spaces. The present writer thinks that this is a rather subjective limit. Moreover thickness of tissue can be very variable, even within one specimen.
Stictostroma mamilliferum Galloway & St. Jean, as described by Parks (1936), St. Jean (1962) and

Stearn (1966), has laminae with ordinicellulae or a clear median layer. Galloway & St. Jean (1957, p. 126) state, however, that laminae are composed of a single, fine, transversely porous layer and that some upturns in the laminae do occur, which indicate ring pillars. If the laminae originally had a clear layer (which may have disappeared by the formation of transverse fibrosity), the species fits very well in the genus *Stromatoporella*, based on specimens with irregular growth.

The genus *Stictostroma* was created by Parks (1936, p. 77) for species with a clear layer in the laminae but no ring pillars and for species with single-layered laminae but with ring pillars. The latter group (*S. eriense* etc.) has been transferred to the genus *Stromatoporella* by Galloway & St. Jean (1957) and later authors. But species with compact thin laminae without a clear median layer cannot be included in the genus *Stromatoporella* as defined in this paper. St. Jean (1962) took into consideration the possibility that ring pillars are not a valuable character, but nevertheless maintained the genus *Stictostroma*.

Trupetostroma warreni Parks as described by Galloway & St. Jean (1957), Galloway (1960) and Stearn (1966, Pl. 16 fig. 7) is conspecific with *Stromatoporella granulata*, compared with the well preserved specimens with a regular gross structure and no ring pillars. The specimen they describe seems to have been affected by recrystallization, in such a way that part of the tissue has been replaced by clear crystals. Parks (1936, p. 55, Pl. X figs. 1, 2) figured a specimen with more conspicuously superposed pillars and more reduced laminae. The genus *Trupetostroma* has been used for specimens with generally well superposed pillars by Parks (1936). (*T. maculosum* is an *Anostylostroma* according to Stearn, 1966, p. 104). Especially Lecompte (1952) shows many specimens with conspicuously superposed strong pillars and laminae reduced to cyst plates in many places. As many species are based on strongly altered specimens, much confusion existed with the genera *Parallelopora*, *Hermatostroma* and *Gerronostroma*, and even with *Stromatopora* (see Stearn, 1966, p. 104, 105).

Taleastroma cumingsi (Galloway & St. Jean) has a gross structure similar to that of *Stromatoporella granulata* and its microstructure is similar to that of some specimens found in Spain, with a concentration of specks around interlaminar spaces.

Other species included in the genus *Taleastroma* also have a similar gross structure and are all strongly altered (see Galloway, 1960, Pl. 75, 76 and Stearn, 1966, Pl. 18 fig. 5). Most of them had originally been described as belonging to the genus *Stromatopora*.

Many strongly melanospheric specimens look indeed very much like *Stromatopora* and have been described in that genus or in *Parallelopora* and *Syringostroma*. Generally they can be distinguished, however, by their continuous laminae, with remains of the clear median layer, and spool-shaped pillars, often superposed. In the writer's opinion many of the species placed by Galloway & St. Jean (1957, p. 167) in the genus *Stromatopora* actually are altered specimens of *Stromatoporella*. Stearn (1966, p. 111) has already proposed that many of these species should be placed in the genus *Clathrocoilona*.

Reviewing the literature of stromatoporoids it is striking that identical or nearly identical forms are found in Middle and Upper Devonian Formations from North America to Australia.

CONCLUSIONS

1. Environmental conditions have a great influence on the growth habit as well as on the gross structure of stromatoporoids.
2. As the microstructure of stromatoporoids is easily affected by secondary alterations distinction should always be made between primary and secondary microstructures.
3. Therefore other genera of stromatoporoids, besides the ones mentioned above, have also to be reconsidered.
4. The order Stromatoporoidea is a relatively small group of genera and species with an almost world wide distribution.
5. The strong influence of environmental factors on their mode of growth makes stromatoporoids extremely useful for paleoecologic investigations.

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Fig. 1. (Specimen 27). Specimen showing irregular growth and some upturns in the laminae. Some pillars superposed. Latilaminae thin, marked by an alternation of thin and thick laminae. Intergrown with *Syringopora sp.* (vert. section, negative).

Fig. 2. (Specimen 260F). Specimen showing more regular growth with many superposed pillars. Tissue slightly flocculent. (vert. section, negative).

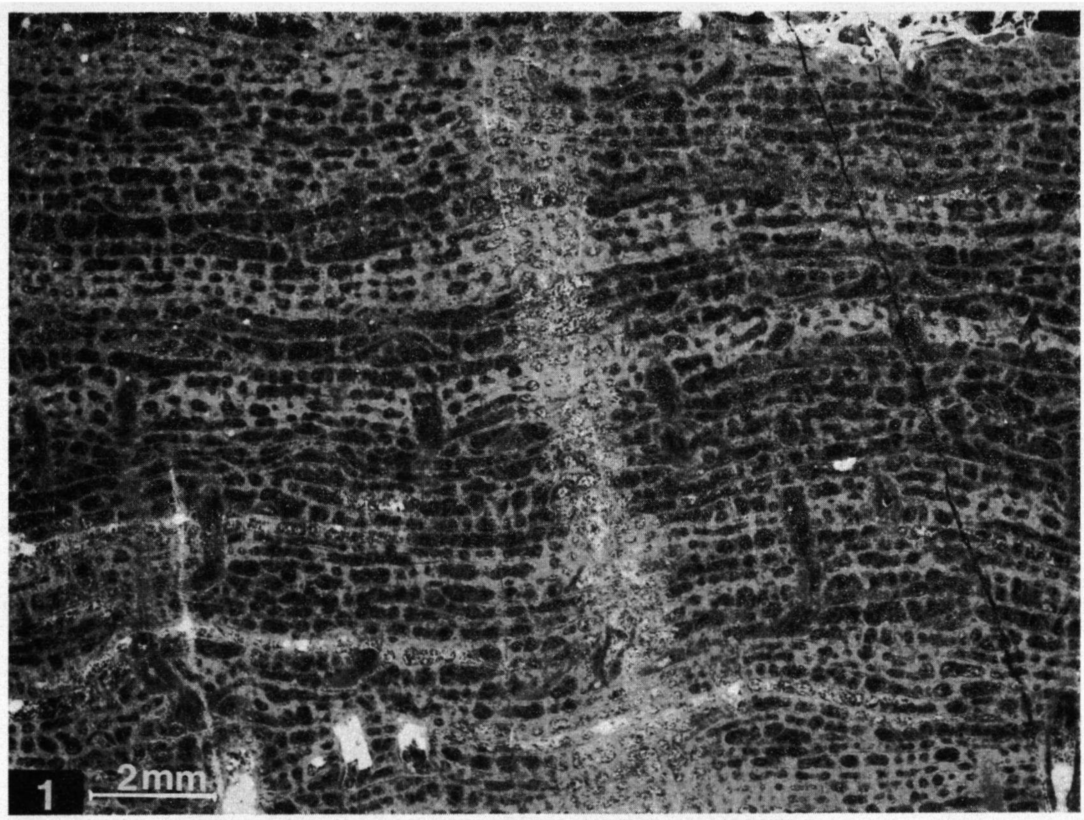
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Fig. 3. (Specimen 479E). Specimen showing regular growth, intergrown with *Syringopora sp.* Astrorhizae in the mamelons. (vert. section, negative).

Fig. 4. (Specimen 580G). Well preserved specimen showing irregular growth with latilaminae. Intergrown with *Syringopora sp.* Note astrorhizae in mamelon on the right. (vert. section, negative).

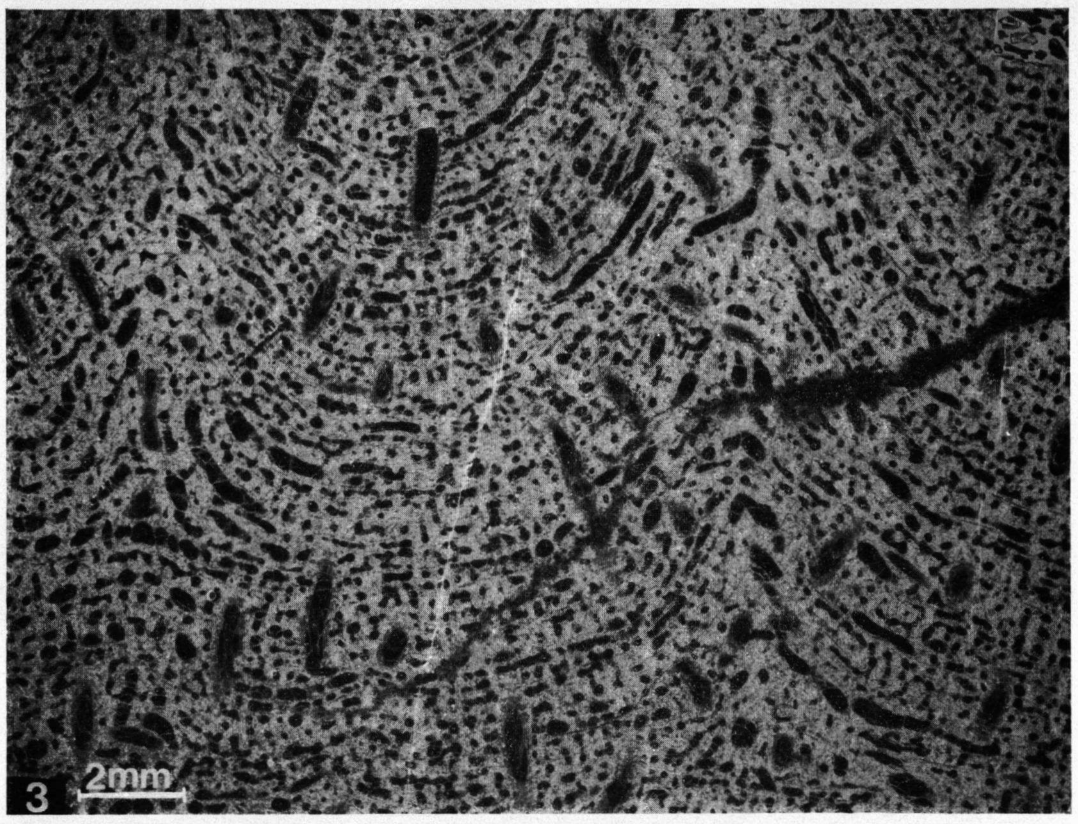
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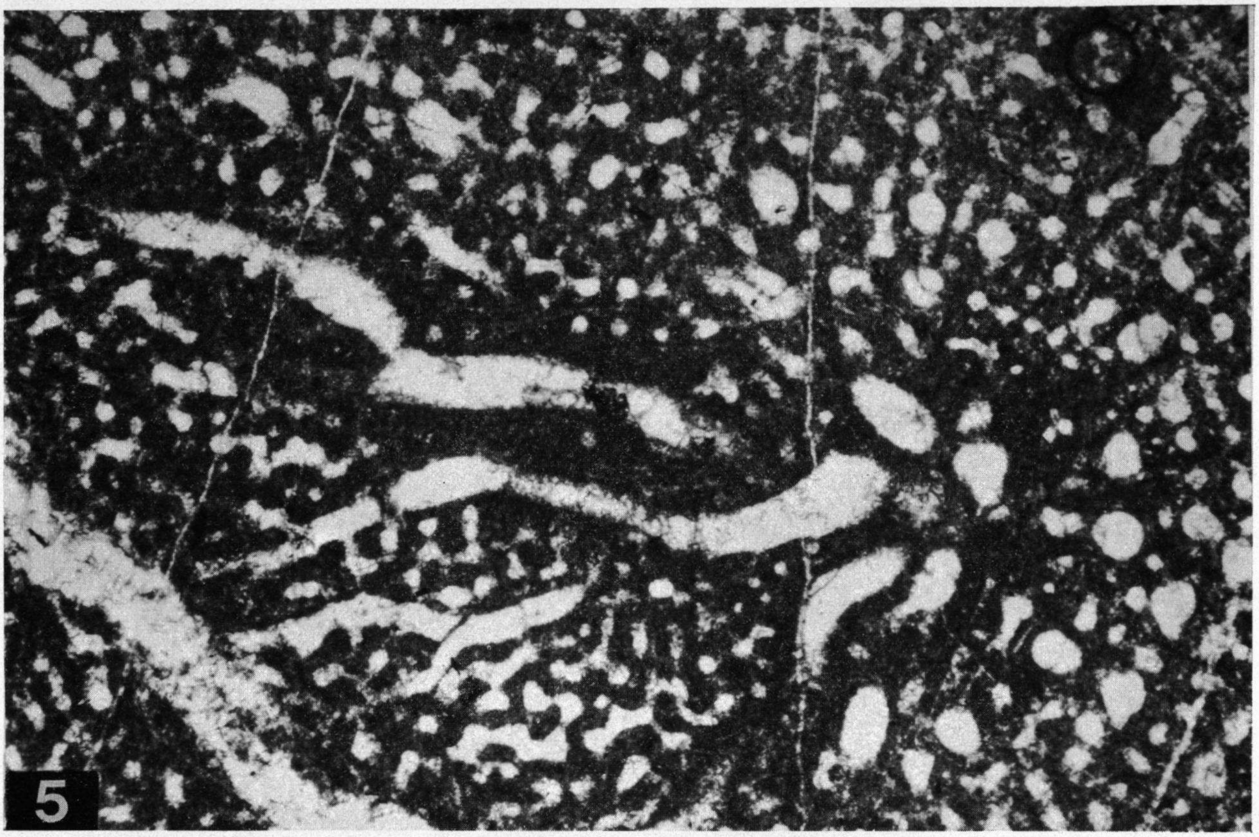
Fig. 5. (Specimen 5B). Astrorhizal canals in longitudinal section; radiating from the centre of the mamelon. Pillars coalescent. Tissue flocculent. (hor. section) × 23.

Fig. 6. (Specimen 260F). Mamelon with central canal and obliquely cut radiating astrorhizae. Pillars forming an amalgamated network, coalescent or isolated dots. Tissue flocculent. (hor. section) × 23.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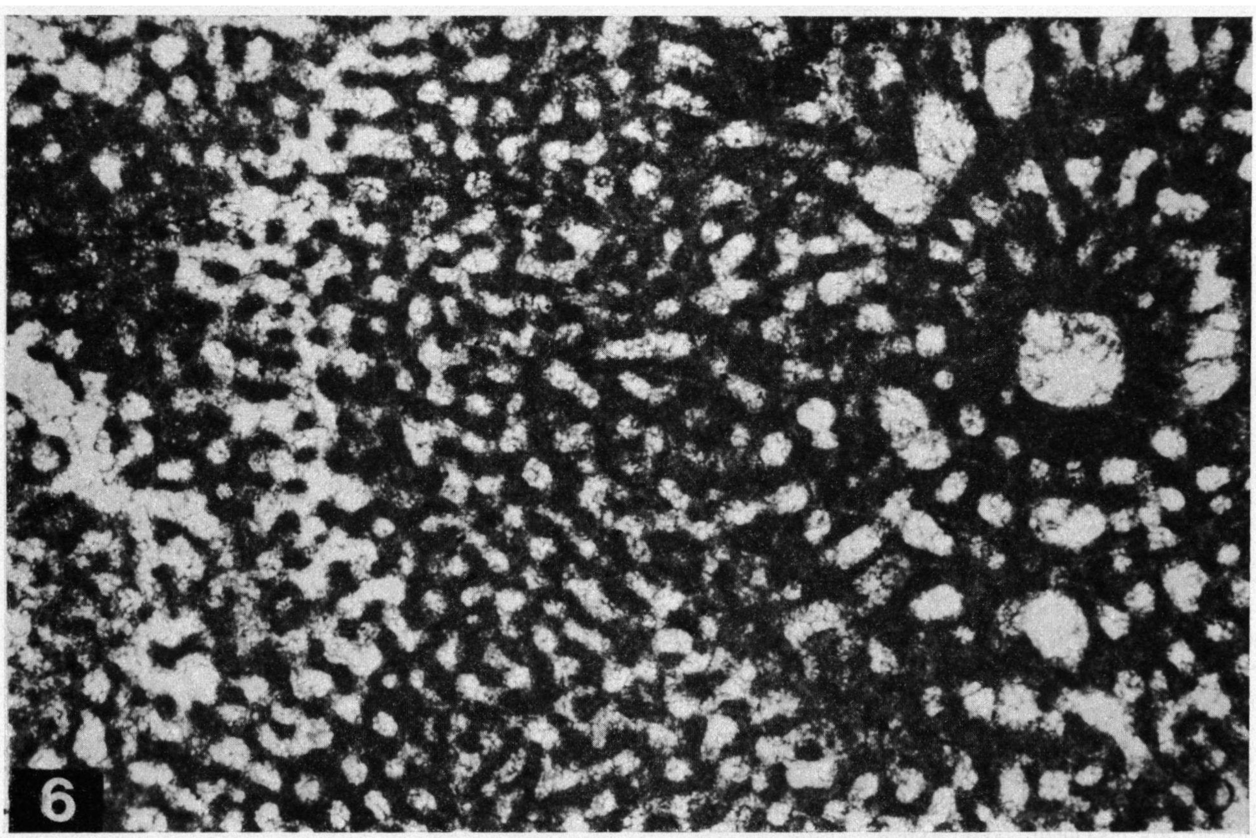
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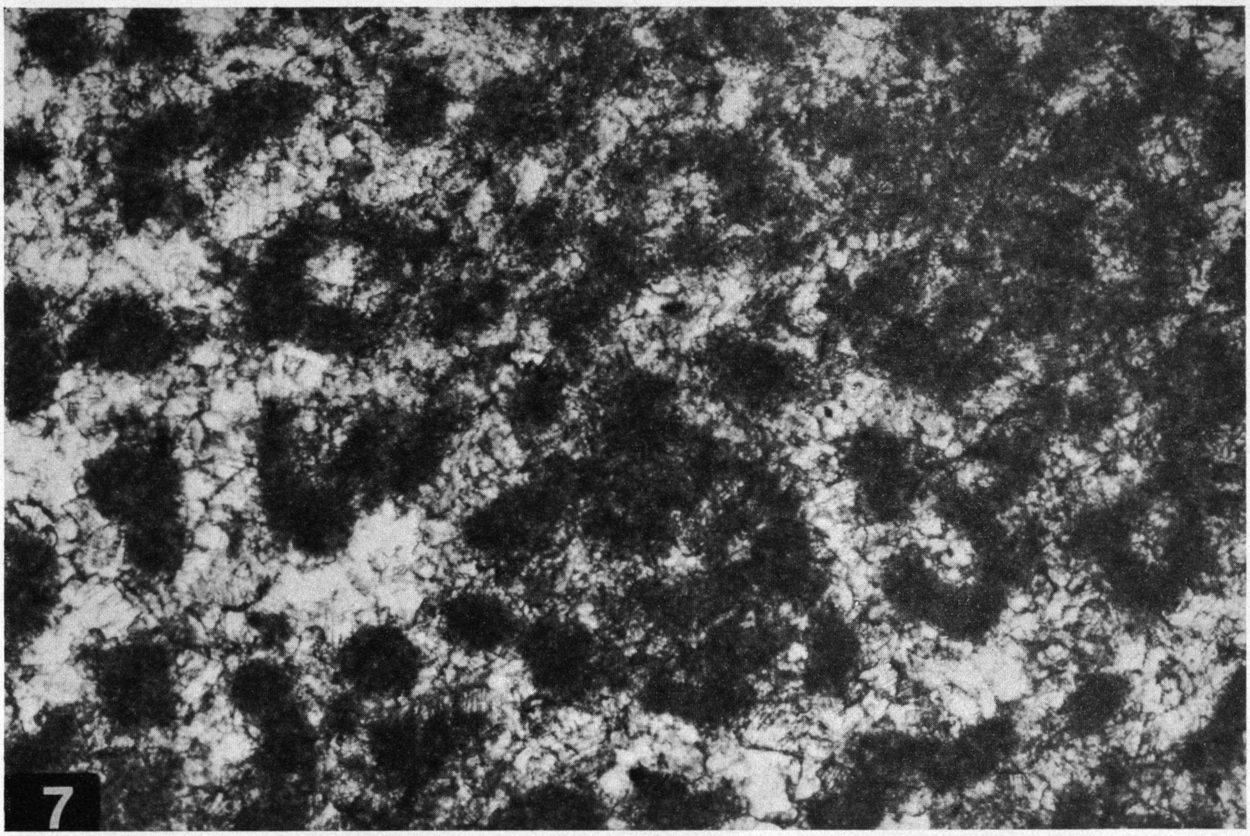
Fig. 7. (Specimen 41A). Normal isolated pillars and isolated ring pillars. Tissue flocculent. Crystals with twin lamellae due to recrystallization. (hor. section) × 57.

Fig. 8. (Specimen 32G). Well preserved specimen with multilayered laminae with ordinicellulae and clear layers. Interlaminar spaces and foramina with cyst plates. Tissue only slightly flocculent. (vert. section) × 57.



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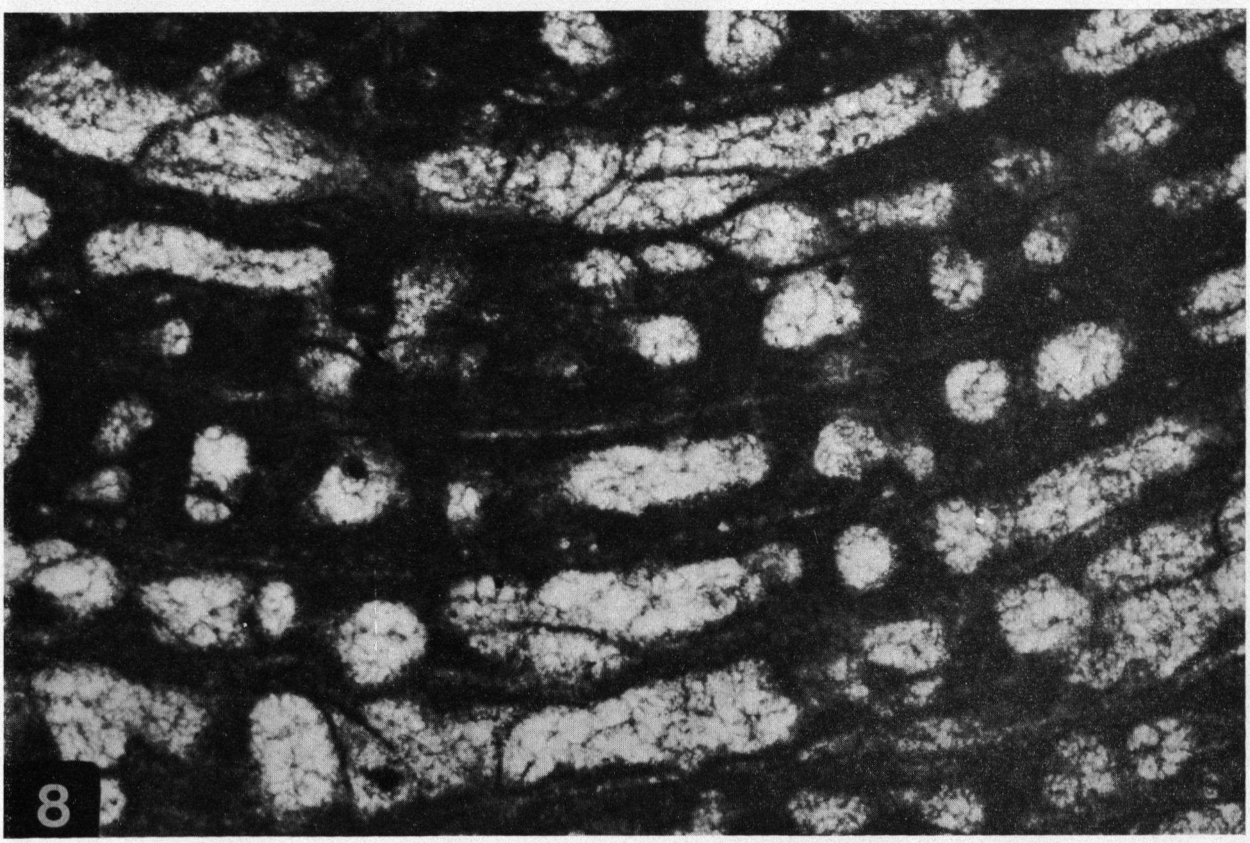

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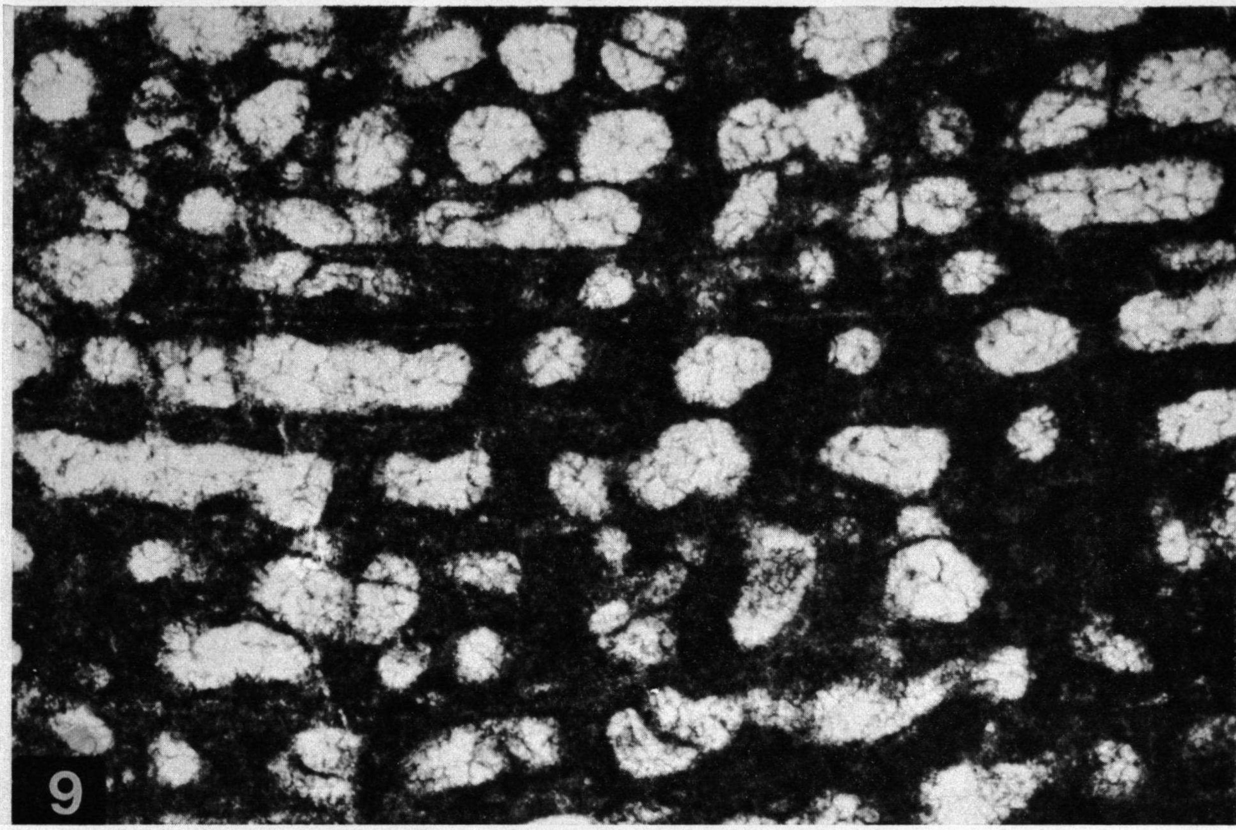
Fig. 9. (Specimen 29C). Another well preserved specimen. Laminae multilayered or thin with a single layer. In the upper part conspicuous vacuoles. Cyst plates common. Tissue slightly flocculent. (vert. section) × 57.

Fig. 10. (Specimen 29C). Peel from the same specimen as fig. 9. Crystals randomly situated. Crystal borders often vague or absent in the tissue. Specks evenly distributed in the tissue, forming a rather sharp border with the galleries. (vert. section) × 230.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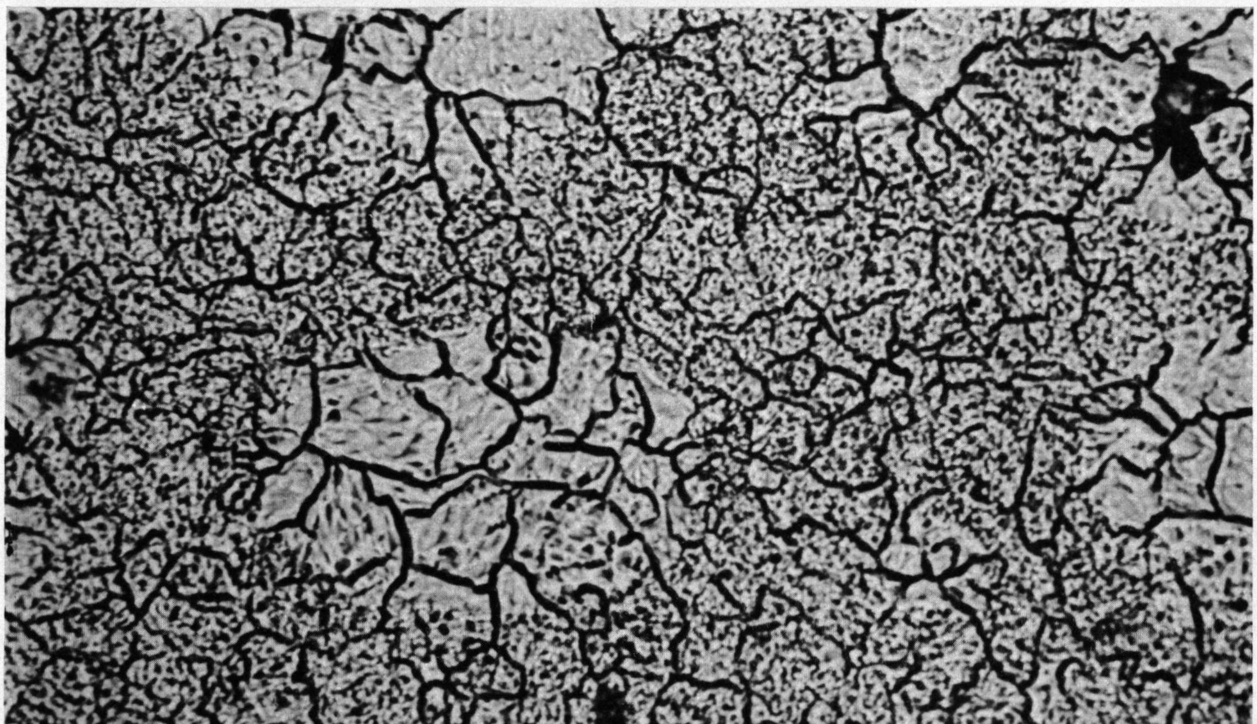
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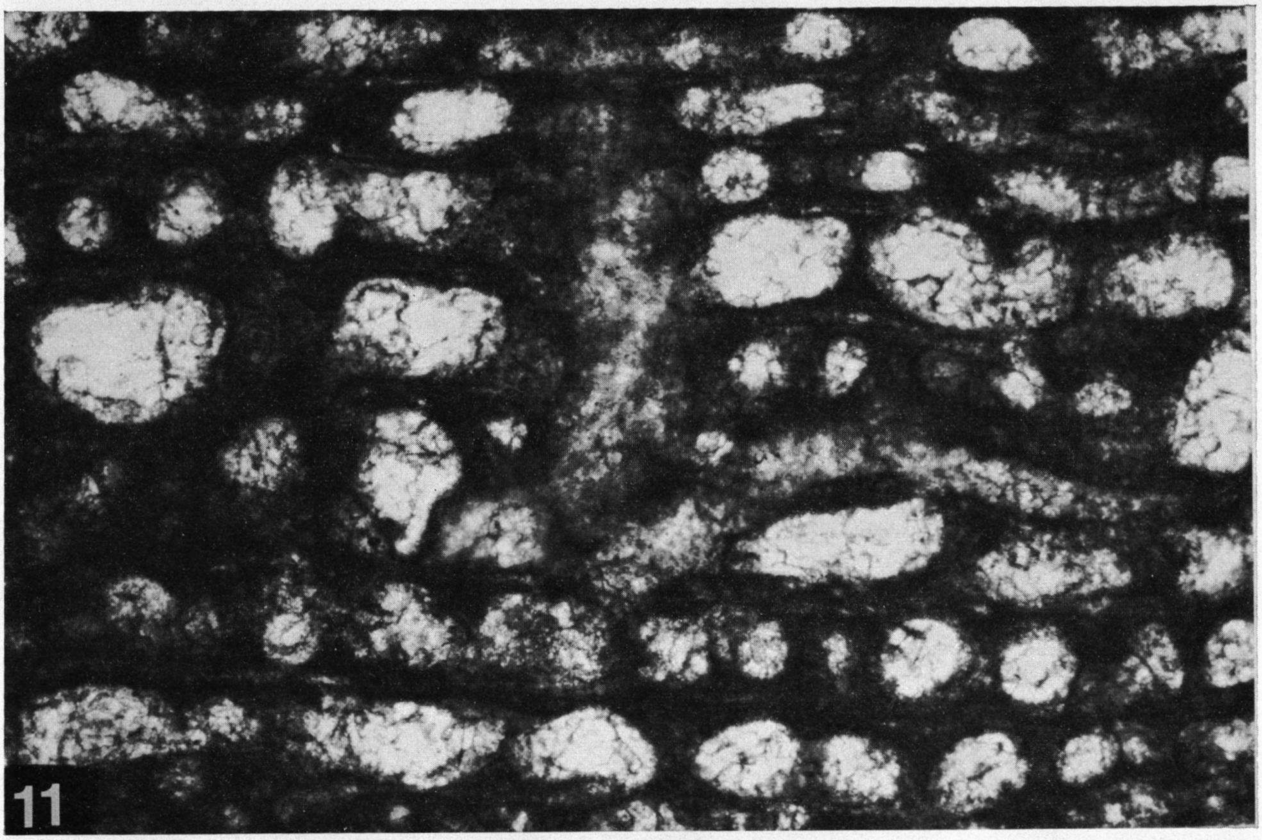
Fig. 11. (Specimen 580J). Specimen with an opalescent appearance under the microscope. Laminae microlaminated. Tissue borders sharp in some places and decayed in other ones. Galleries surrounded by crystals. Intergrown with *Syringopora sp.* (centre and to the right). (vert. section) × 57.

Fig. 12. (Specimen 580J). Peel from the same specimen as fig. 11. In centre of galleries a coarse crystal surrounded by other crystals which are partly situated in the tissue (pore-filling). Crystal borders in the tissue are vague. Tissue borders sharp only in some crystals. (vert. section) × 230.



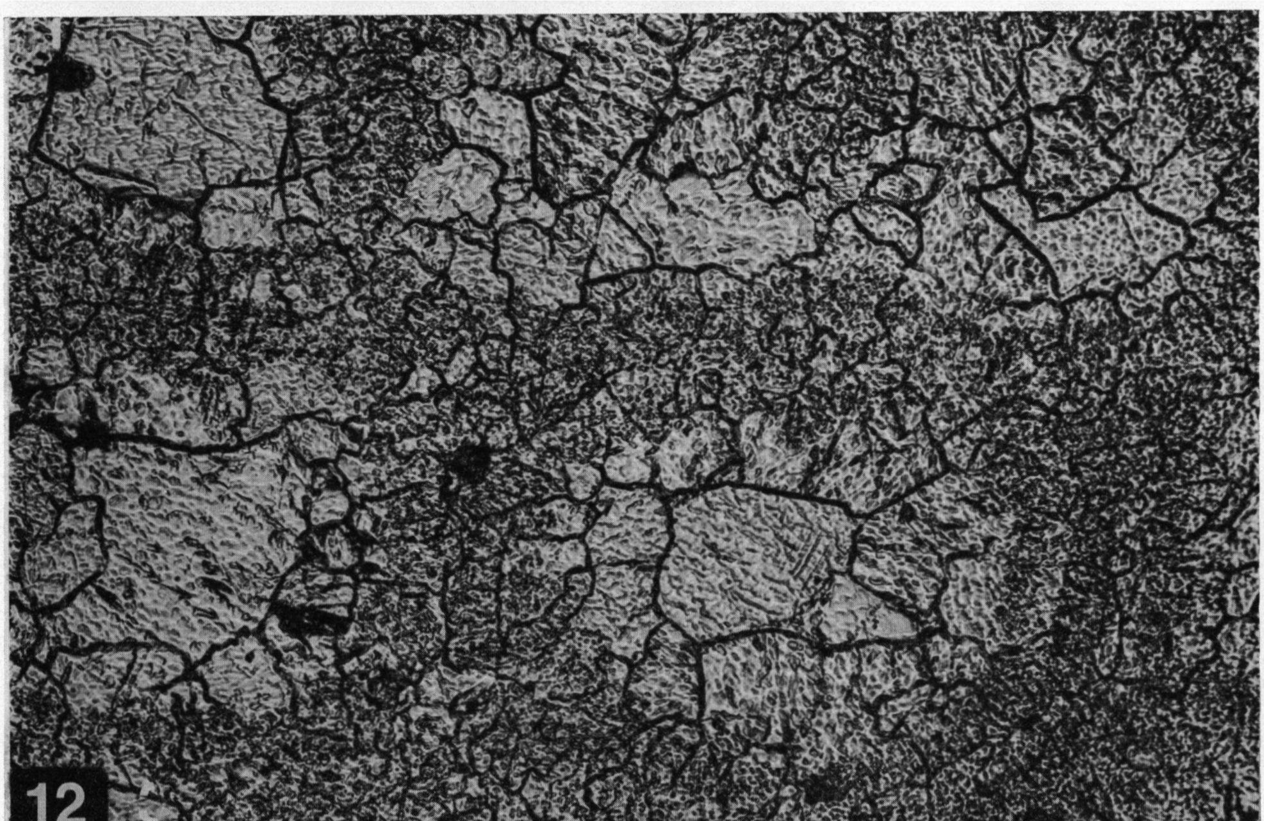
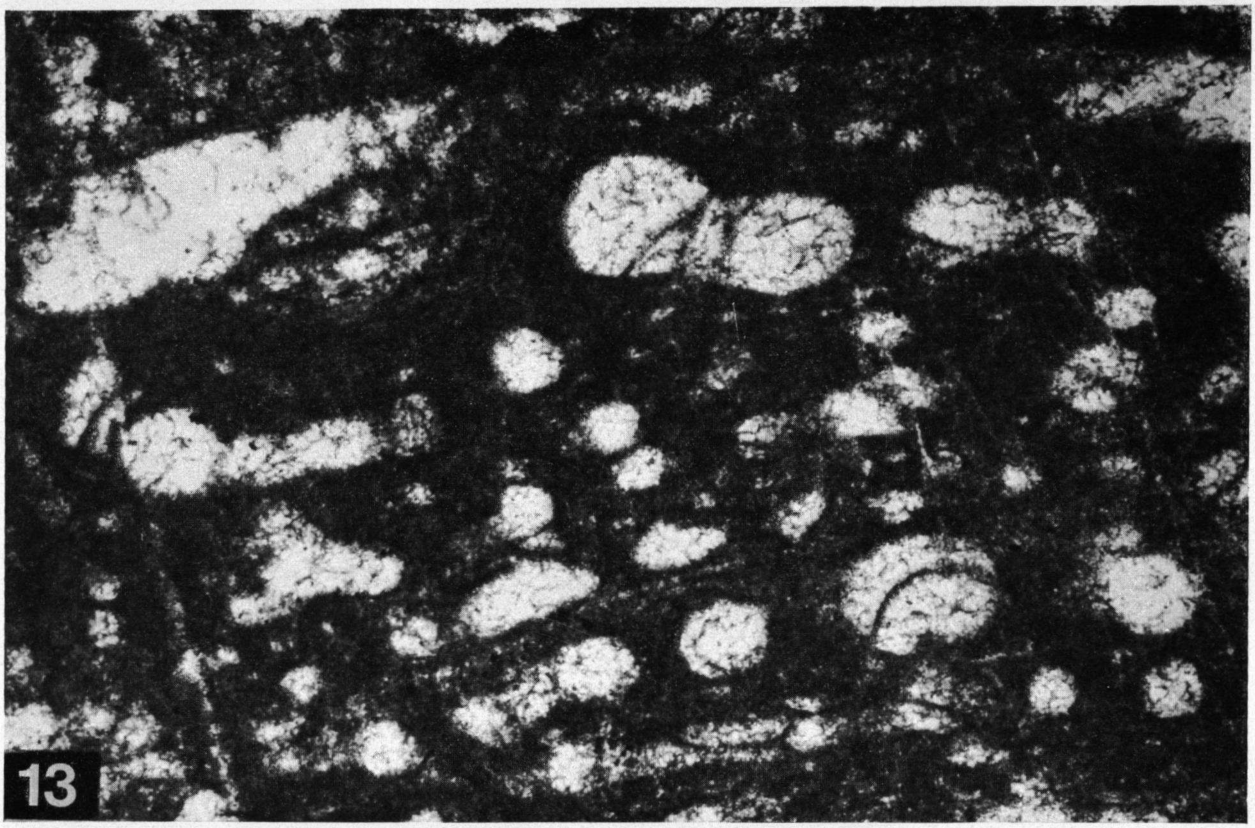


Fig. 13. (Specimen 35C). Specimen with flocculent tissue. Microlamination and cyst plates still visible. Calcite veins more or less vertical. (vert. section) × 57.

Fig. 14. (Specimen 35C). Peel from the same specimen as fig. 13. Crystals randomly situated, some with twin lamellae. Tissue borders less sharp as in fig. 10. (vert. section) × 230.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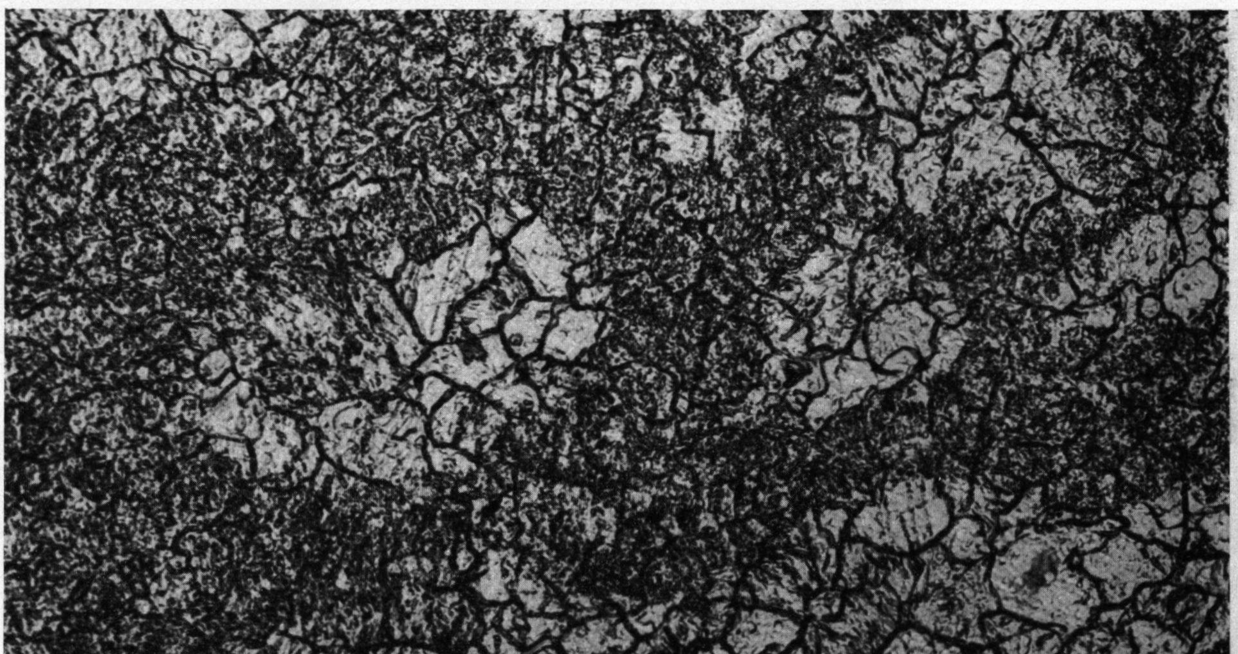
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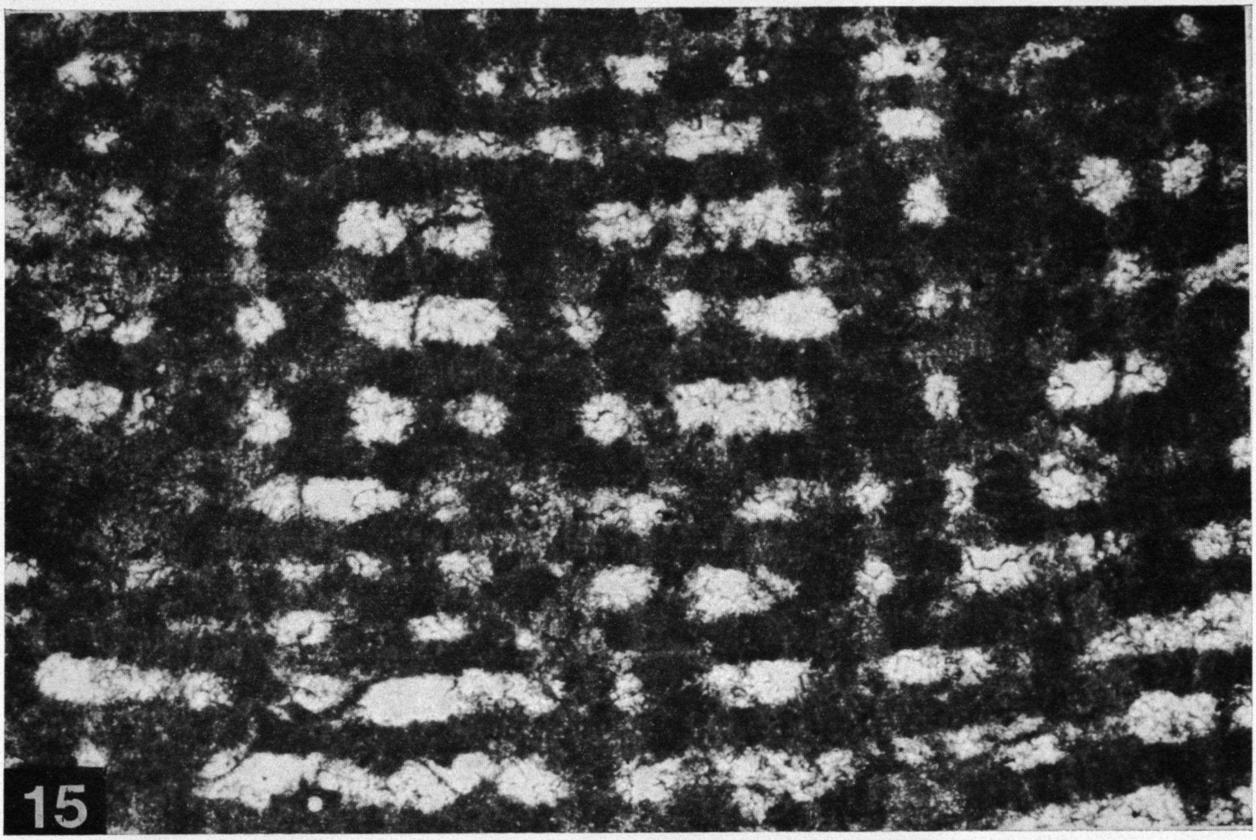
Fig. 15. (Specimen 32B). Laminar specimen with transversely fibrous tissue. Microlamination not completely disappeared. Tissue borders irregular. (vert. section) × 57.

Fig. 16. (Specimen 32B). Peel from the same specimen as fig. 15. Crystals vertically elongated in laminae and horizontally elongated in pillars. Twin lamellae vertical. Tissue borders vague. (vert. section) × 230.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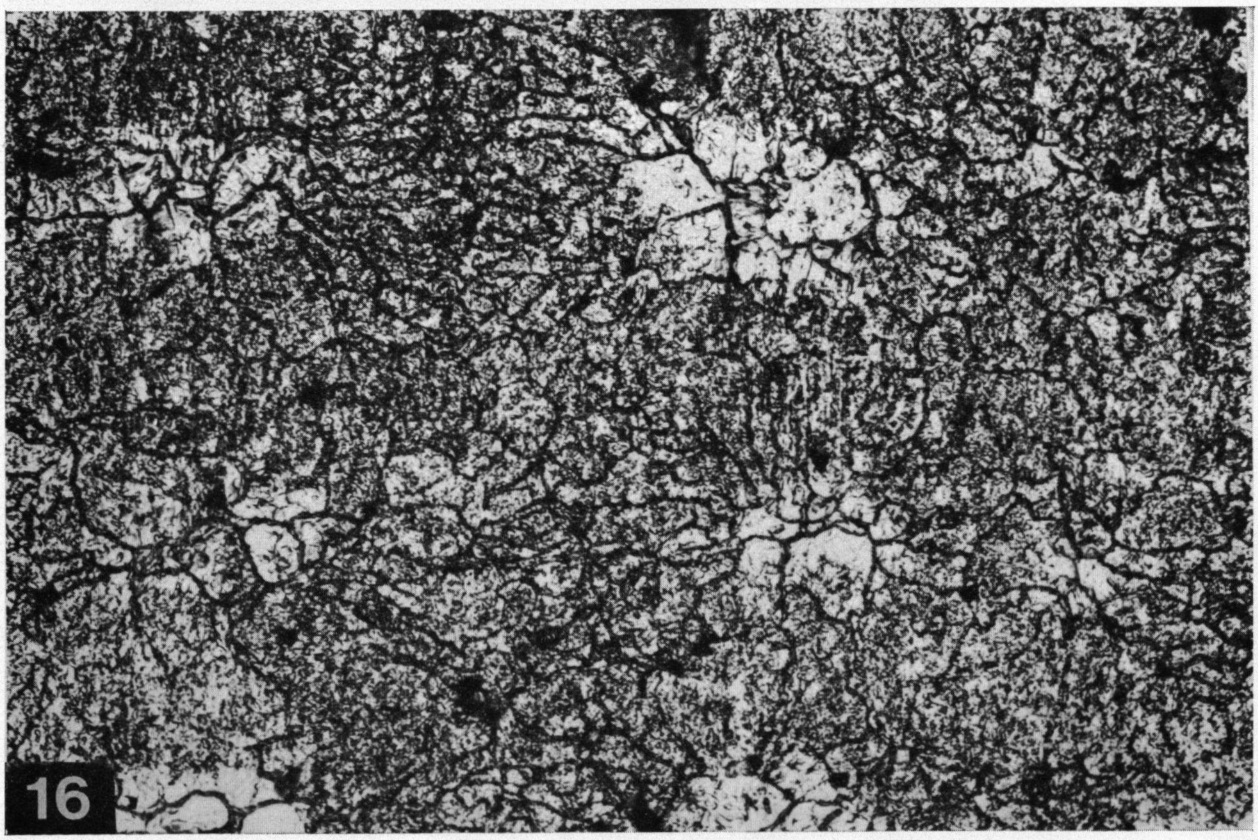
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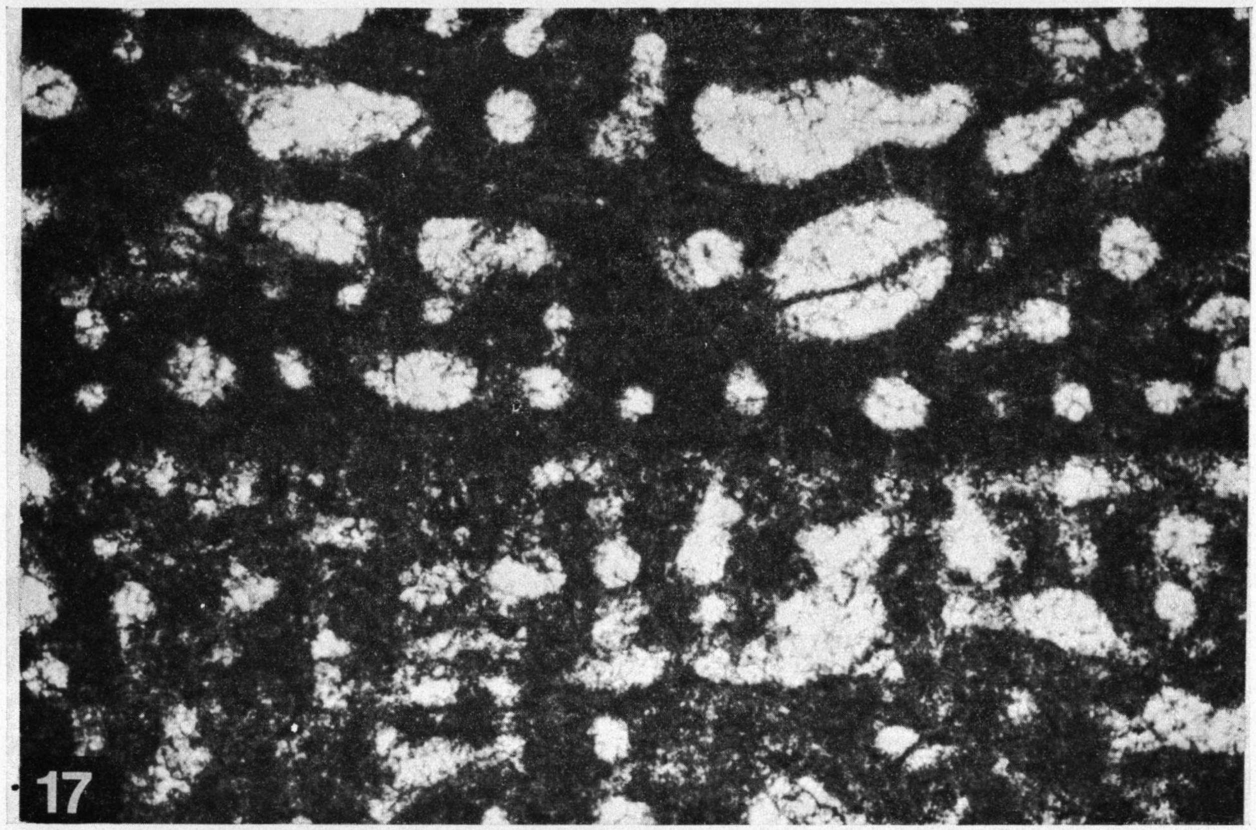
Fig. 17. (Specimen 35C). Latilaminae marked by strongly flocculent tissue below and less altered, darker coloured tissue above. (vert. section) × 57.

Fig. 18. (Specimen 478A). Specimen with melanospheric tissue. Microlamination not completely disappeared. Melanospheres more or less arranged in horizontal and vertical rows giving a microreticulate impression. (vert. section) × 57.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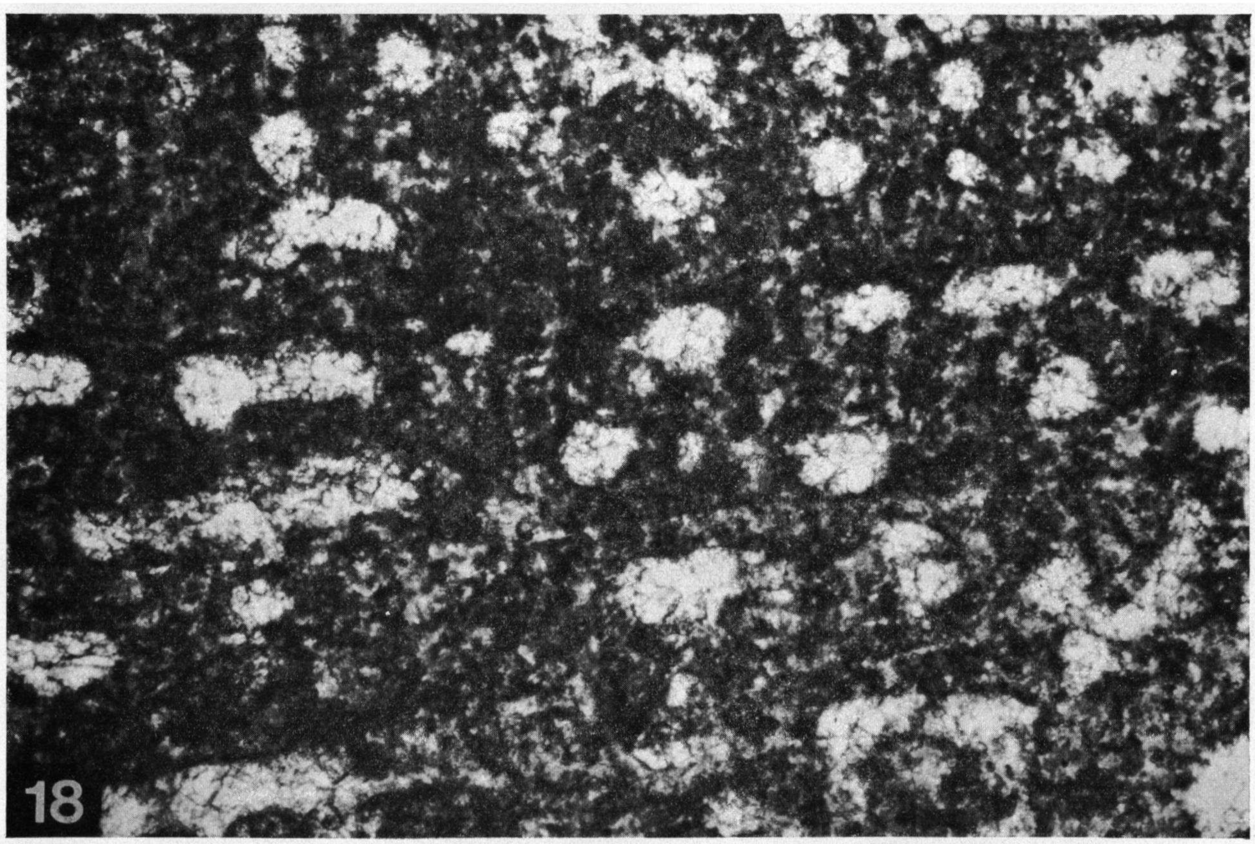
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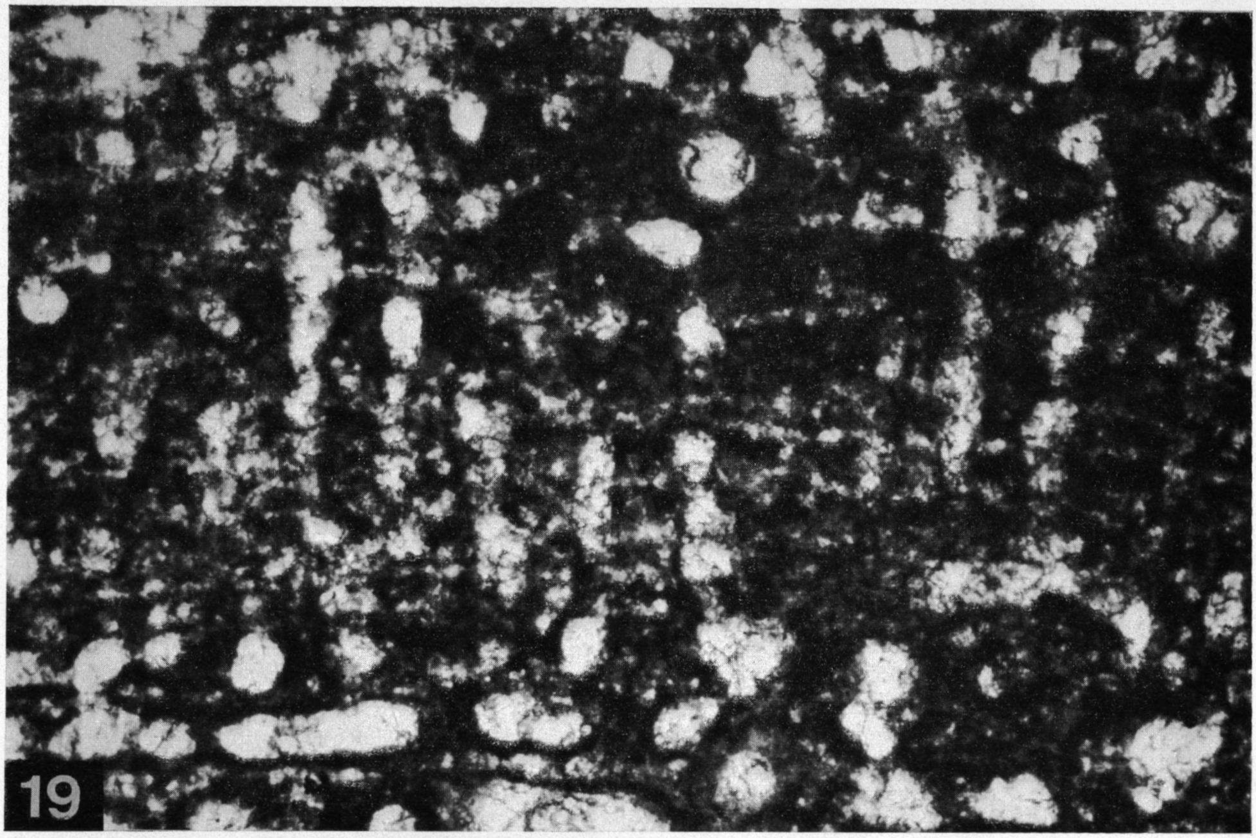
Fig. 19. (Specimen 61). Melanospheric specimen with pigment concentrated around galleries (below) or in the vertical structure elements. Some galleries are also partly or completely filled with pigment. Microlaminae visible as clear bands. Intergrown with *Syringopora sp.* (vert. section) × 57.

Fig. 20. (Specimen 582A). Extremely melanospheric specimen. Microlaminae yellowish. Structure much obscured by infiltration of specks in many galleries. Intergrown with *Syringopora sp.* (vert. section) × 57.



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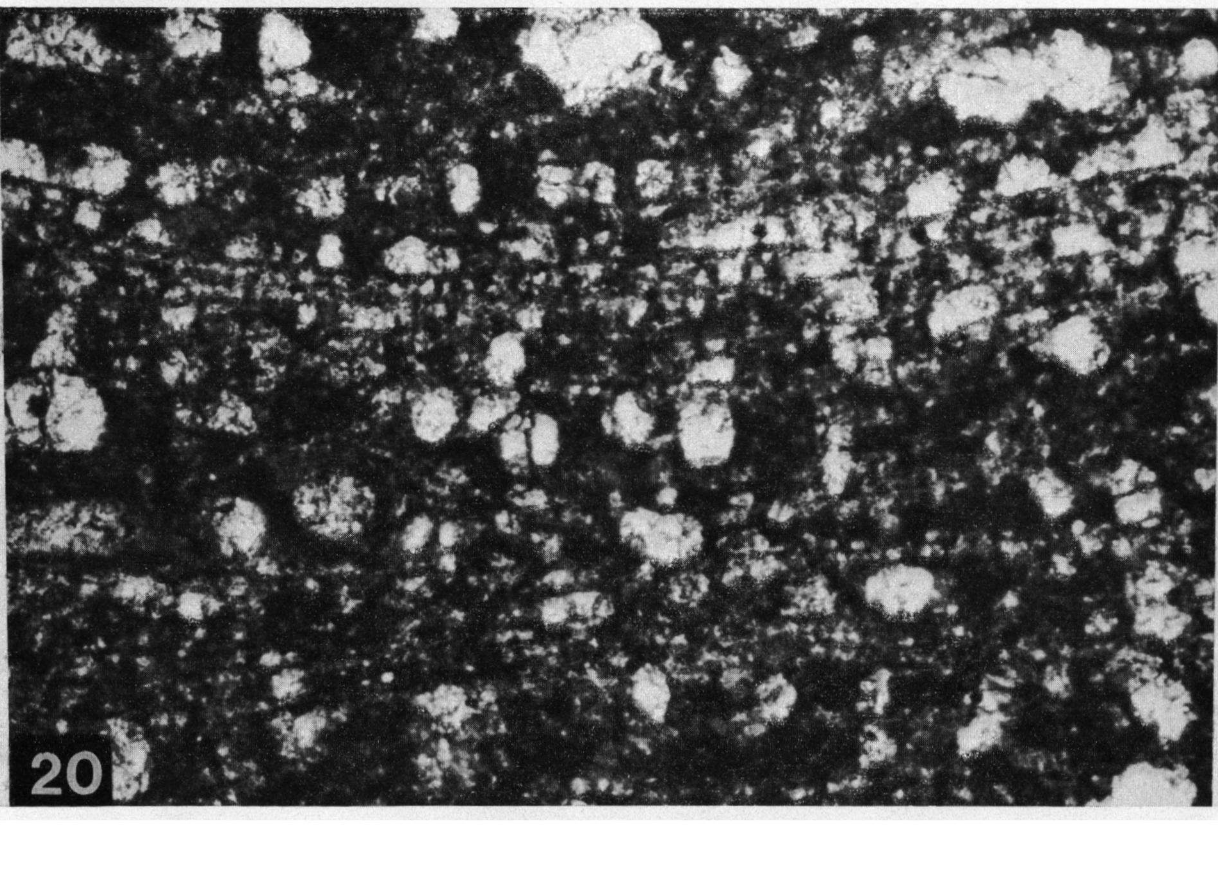

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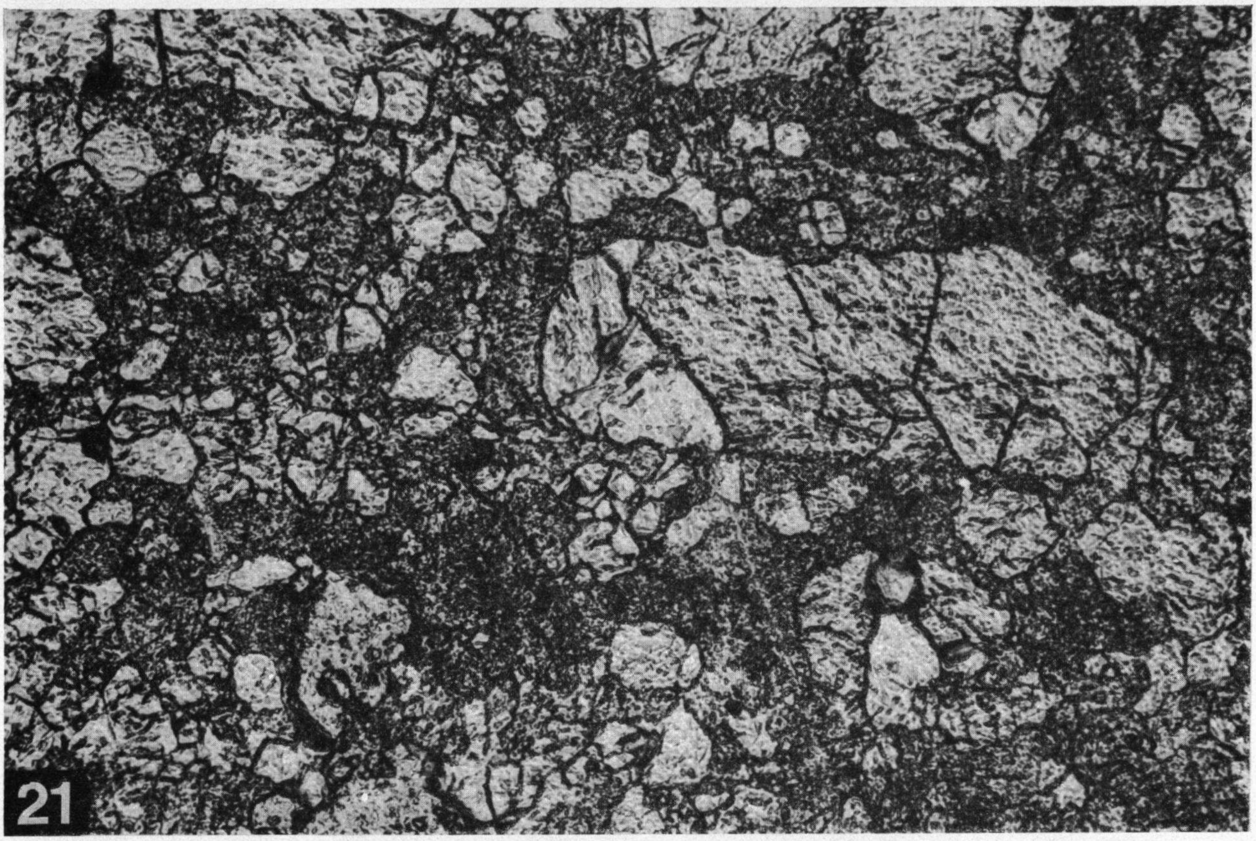
Fig. 21. (Specimen 582A). Peel from the same specimen as fig. 20. Large clear crystals limited to the galleries .Tissue recrystallized, full of small clear crystals. (vert. section) $\times 230$.

Fig. 22. (Specimen 580F). Laminar specimen intergrown with *Syringopora sp.* with a pseudocellular microstructure. (vert. section, negative).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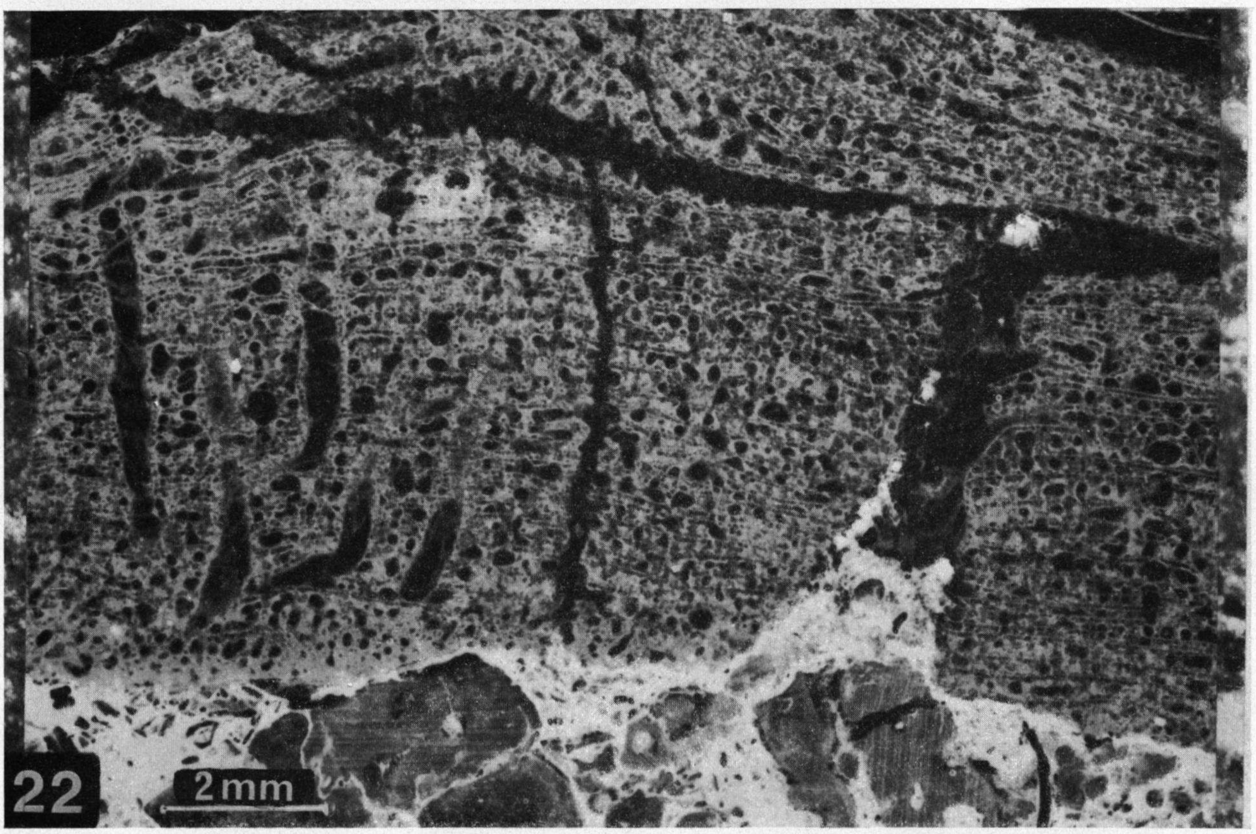
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