

# DEVONIAN STROMATOPOROIDS OF THE CANTABRIAN MOUNTAINS (SPAIN)

BY

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## ABSTRACT

In the Cantabrian Mountains stromatoporoids only have been found up to now in Devonian formations. They occur together with tabulate and rugose corals and brachiopods. Together with these organisms they form biostromes or just biogenetic layers of brecciated and overturned colonies.

Four primary microstructures could be distinguished: compact, microlaminate, ordinicellular, and cellular. Alteration seems to begin before fossilization in many cases: the microtissue becomes flocculent by migration and/or destruction of specks. After fossilization the microstructure is altered mainly by migration of specks along slip planes and by rearrangement of the calcite crystals.

In this paper the original microstructure is used as the main character for the determination of genera. The form of the coenosteum and features of the gross structure such as superposition of pillars, absence or presence of ring pillars, spacing of laminae and pillars, and others, are strongly influenced by ecological factors. Therefore they cannot be used as characters for the definition of genera and often not even for species.

Four genera can be distinguished in the Spanish material: *Actinostroma* (compact with continuous pillars), *Stromatoporella?* (microlaminate), *Stromatoporella?* (ordinicellular) and *Stromatopora* (cellular).

The genera *Geronostroma* and *Atelodictyon* are considered to be synonyms of *Actinostroma*. The genus *Stromatoporella* should be divided into two genera: one genus with microlaminate and one genus with ordinicellular microstructure. In the microlaminate genus the genera *Clathrocoilon*, *Trupetostroma* and *Stictostroma* (partly) should also be included and perhaps *Idiostroma* (partly). The ordinicellular genus can be combined with part of the genus *Stictostroma* and some species of *Anostylostroma*. The genera *Parallelopore* and *Ferestromatopora* are considered to be synonyms of *Stromatopora*.

For the determination of species an attempt is made to establish the variability of the gross structure for each species. As this variability seems to be rather wide, species determinations are only given when sufficient material was available. The following species are described: *Actinostroma papillosum* (= *A. clathratum*), *Actinostroma verrucosum?*, *Actinostroma stellatum*, *Stromatoporella? granulata?* (microlaminate), *Stromatoporella? selwyni* (ordinicellular), *Stromatopora concentrica* and *Stromatopora huepachi?*

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## CHAPTER I

## INTRODUCTION

*Want zij die b.v. een proefschrift schrijven, dat immers alleen bestemd is om aan het oordeel van enige professoren te worden onderworpen, en die dus de strengste en meest deskundige critici niet vrezen, zijn, dunkt me, meer te beklagen dan te benijden, daar ze zich eindeloos aftobben. Ze voegen toe, veranderen, schrappen, herstellen weer, herzien, werken het weer geheel en al om, laten het graag anderen zien, houden het negen jaar in portefeuille en zijn nooit tevreden met het resultaat.*

Erasmus, 1515, p. 189  
De Lof der Zotheid

## BACKGROUND AND SCOPE OF THE WORK

The present work is a continuation of fieldwork done by the author during the summers 1962, 1963 and 1964 when a student of the University of Leiden. Then the stratigraphy, petrography and palaeontology of the Portilla Formation north of Los Barrios de Luna were studied, as part of a larger research project in the Palaeozoic of the southern Cantabrian Mountains under the general direction of Prof. A. Brouwer. Special stress was laid on the Tabulata, Stromatoporoidea and Rugosa which are the main elements of the fauna of the Portilla Formation. Later the writer

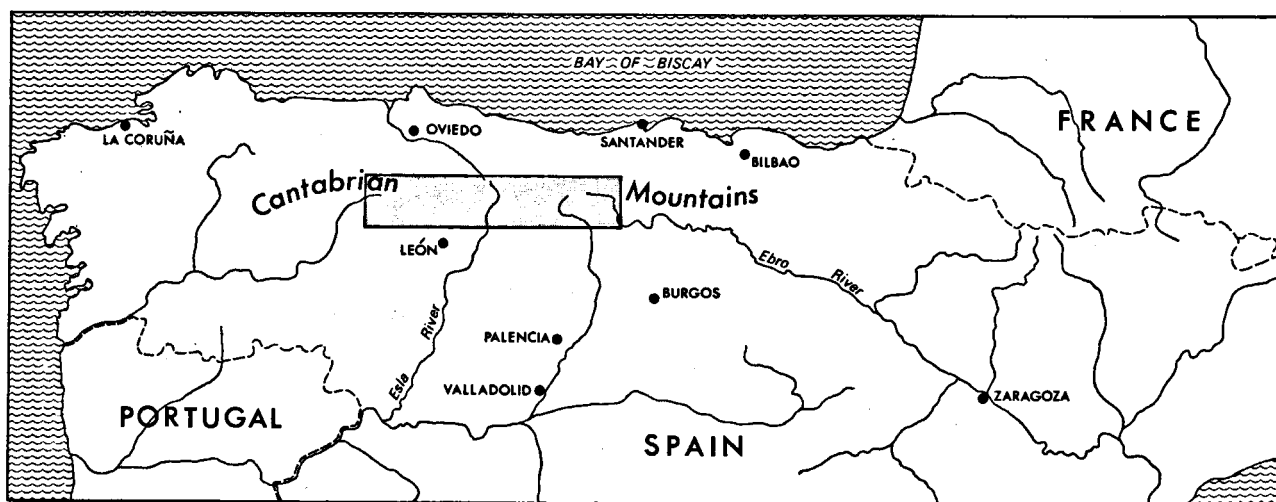
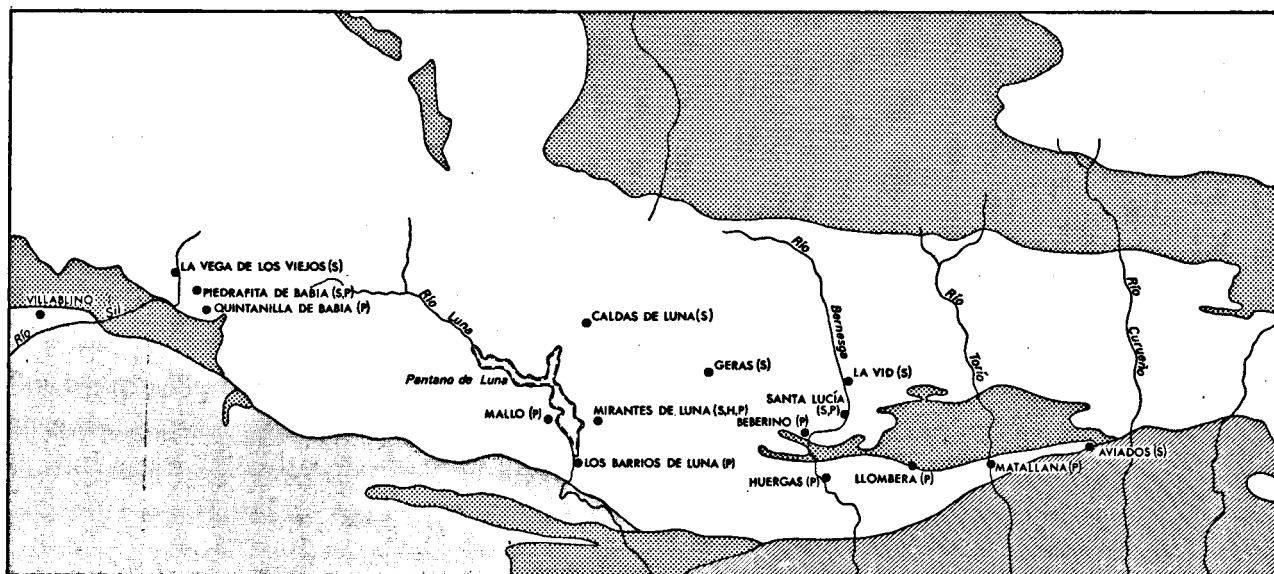


Fig. 1. Situation map, the quadrangle shows the studied area.

Fig. 2. Survey map with the most important localities.





concentrated his attention on the stromatoporoids and eventually the investigation was extended to the stromatoporoids of other Devonian limestones in the southern parts of the Cantabrian Mountains. The present publication is the result of this investigation. A preliminary paper dealing with (what by that time was considered to be) *Stromatoporella granulata* was published in June, 1968.

Little has been published up to now on the stromatoporoids of the Cantabrian Mountains. The first who mentioned them was Bargatzky (1883, presented by Barrois in a meeting in May, 1882). He recognized only two species: '*Stromatopora concentrica*' with continuous pillars and '*Stromatopora verrucosa*' with pillars generally not superposed, both from the Devonian of Asturias. The same species also are mentioned by Barrios (1882, p. 222). Grosch (1912, pp. 730, 733, list p. 749) mentioned the species *Actinostroma stellulatum* and *Stromatopora concentrica*, also from Asturias, but did not give any description. Later authors only mentioned the occurrence of stromatoporoids in Asturias as well as in León and Palencia in papers dealing mainly with stratigraphy or structural geology, e.g. Radig (1961), Comte (1959), Kanis (1956), Binnekamp (1965).

All stromatoporoids described in this paper were collected in Devonian strata. Below the Devonian formations limestones are absent in this part of the Iberian Peninsula, except the Cambrian Lancara Formation with abundant stromatolites. Silurian limestones with stromatoporoids ('*Stromatopora concentrica*', one photograph with two badly preserved colonies, no description) are reported from south-eastern Spain by Ricart & Sanchez-Paus (1963). The determination of the age of this limestone is, however, only based on this 'species'! Delgado (1908, not seen) also mentioned stromatoporoids from the 'Système Silurique' in the Sierra de la Portalegre, Portugal.

Only the stromatoporoids found on the southern slopes of the Cantabrian Mountains, that is to say the northern parts of the provinces León and Palencia, are described in this paper (fig. 1). The stromatoporoids which occur in similar limestone formations in Asturias are not dealt with. The most important outcrops where stromatoporoids occur are indicated on the locality map (fig. 2). For a detailed map of this area see de Sitter, 1962. Areal geological studies were done by van den Bosch (in press), van Staaldin (in press), Evers (1967), Rupke (1965), Koopmans (1962), van Veen (1965), and de Sitter & Boschma (1966).

#### ACKNOWLEDGEMENTS

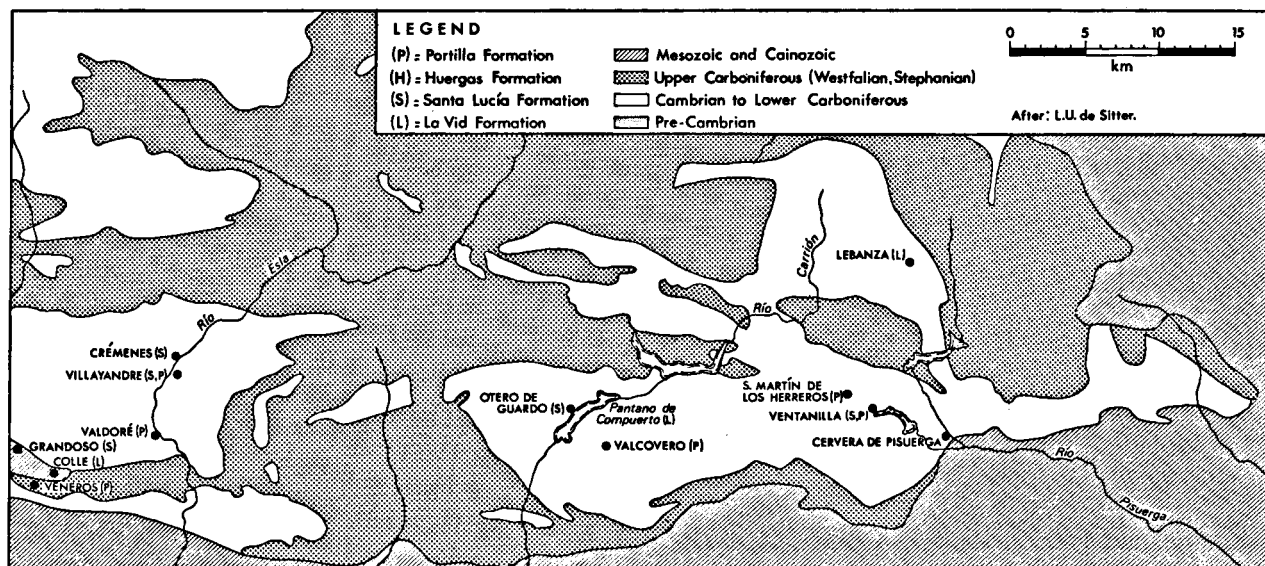
The author wants to express his special gratitude to Prof. Dr. Erik Flügel, Darmstadt, Germany. Prof. Flügel stimulated the author's work from the very beginning by discussing the material and the manuscript with him during the three visits the author made to Darmstadt. Thanks to the expert criticism and the suggestions made by Prof. Flügel the manuscript could be improved on many important points.

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Last but not least the writer wants to express his gratefulness to his wife Foyita for her constant support and help during the preparation of this thesis.

Fig. 2.



CARBON- IFEROUS		Viséan		ALBA FORMATION										griotte		
		Tournaisian								H I A T U S						
DEVONIAN		UPPER		Famennian	ERMITA FORMATION										quartzites and sandstones	
					up to 500 m											
						H I A T U S			FUEYO FORMATION					H I A T U S		
		MIDDLE <th rowspan="2">Frasnian</th> <td colspan="10">NOCEDO FORMATION</td> <td colspan="2">sandstones and shales</td>		Frasnian	NOCEDO FORMATION										sandstones and shales	
					up to 500 m											
				Givetian	PORTILLA FORMATION										coarse - grained limestones and marls	
					60 - 200 m											
				Couvinian	HUERGAS FORMATION										shales and sandstones	
					200 - 300 m											
					SANTA LUCÍA FORMATION										coarse- and fine-grained limestones	
LOWER <th>Emsian</th> <td colspan="10">150 - 280 m</td> <td colspan="2"></td>		Emsian	150 - 280 m													
		Siegenian	LA VID FORMATION										shales, dolomites and limestones			
		200 - 400 m														
SILURIAN				SAN PEDRO FORMATION										ferruginous sandstones and shales		

Table 1.

### OUTLINE OF THE STRATIGRAPHY

The stratigraphy of the southern Cantabrian Mountains was first studied in greater detail by Comte (1959). His stratigraphic division (pp. 317, 318) of the Devonian is mainly based on sections in or near the Bernesga valley. A generalized diagram is given on table 1. Apart from minor differences in thickness, composition and fossil content, the succession remains essentially the same along the whole southern border of the Cantabrian Mountains. In Asturias a similar succession is present (Radig, 1961).

The most important deviations from the Bernesga section, regarding the occurrence of stromatoporoids, can be found in the following places:

1. north of Caldas (Smits, 1965), where above the La Vid Formation the Devonian is rather incomplete,
2. east and north of Mirantes de Luna, where limestone lenses occur in the shaly Huergas Formation,
3. south of Mirantes and north of Los Barrios de Luna, where the Portilla Formation is extremely variable in thickness (0-300 m within a lateral distance of a few km; Sleumer, 1965, unpublished internal report, Mohanti, 1969, in press),
4. north-west of Colle, where some stromatoporoids occur in the La Vid Formation.

In the easternmost Devonian of the Cantabrian Mountains a different succession occurs. South of

Ventanilla bioherms are present in a mainly siliciclastic facies (Kanis, 1956). In the region north of Ventanilla stromatoporoids occur only in the Lebanza Formation; the other formations are almost exclusively siliciclastic (Binnekamp, 1965; see also Brouwer, 1964 and 1968).

The determinations of the ages of the formations mentioned above are mainly based on brachiopods (Comte, 1959; Westbroek, 1964; Mohanti (in press); Kanis, 1956; Binnekamp, 1965), microfauna (Cramer, 1964) and conodonts (van Adrichem Boogaert, 1967); the studies of trilobites and ostracods are in progress.

### REVIEW OF THE LOCALITIES

In the following pages a short description is given of the localities where stromatoporoids were collected. All localities are situated more or less in the southern part of the zone with Palaeozoic outcrops. They are described from west to east. Exact descriptive terms (after Folk, 1959) for the sediment are only used when samples for thin sections were collected.

*La Vega de los Viejos.* – North of the village the Santa Lucía Formation is exposed. Here it is ca. 380 m thick. Only in the lower part of 125 m were some layers found with silicified stromatoporoids (*H. (handspecimens) 503-506*) together with *Alveolites* sp., *Favosites* sp., *Thamnopora* sp., solitary corals, brachiopods, bryozoans and crinoid fragments. At the base the limestones are biomicruditic to biomicritic, sometimes dolomitic. Higher in the lower part they are finer grained, sometimes even bituminous. The

middle part consists mainly of laminated, fine-grained, frequently bituminous limestones with some brachiopods and crinoid fragments. The uppermost 100 m are formed by detrital ferruginous limestones intercalated with marls and shales. Many layers are rather sandy with cross-bedding. Apart from some small colonies of *Alveolites* sp. only brachiopods, solitary corals and crinoid fragments are present in this part.

*Piedrafita de Babia.* – North of the village some highly fossiliferous layers of the Portilla Formation are exposed (H. 478–479). North-east of the village the Santa Lucía Formation is also exposed but stromatoporoids are scarce and recrystallized (H. 480–482).

In the area north of Piedrafita, near La Cueta, the Portilla Formation is ca. 200 m thick and fairly fossiliferous. Stromatoporoids, however, are extremely scarce and badly preserved (H. 502). The middle part of the section is rather fine-grained (compared with the Portilla in other areas) and frequently bituminous.

*Quintanilla de Babia.* – South of the village the whole Portilla Formation is exposed:

Nocedo (sandstones and shales, decalcified).  
Portilla

- c. 35 m rather massive limestones with *Thamnopora* sp., *Alveolites* sp. and solitary corals. No stromatoporoids were found here.
- b. 50 m sandstones.
- a. 65 m biomicrudites, more or less sandy and marly at the bottom, coarse and massive at the top. With stromatoporoids, *Alveolites* sp., *Favosites* sp., *Thamnopora* sp. and solitary corals. Some colonies lie upside down (H. 507–510).

Huergas (shales).

The fossils from Piedrafita must originate from layers equivalent with member (a) in this section. More to the west according to van den Bosch (personal communication) the members (a) and (c) each measure only ca. 25 m while the sandstones (member b) measure ca. 60 m.

*Caldas de Luna.* – In the region north of Caldas de Luna the Devonian shows an aberrant development. The normally developed La Vid Formation is succeeded by the Caldas Formation which is unconformably overlain with the Ermita Formation or directly with the Alba Griotte (Carboniferous). According to Smits (1965) the following section can be measured north of Caldas (type section; along the river):

Alba (griotte).  
Caldas

- c. 37 m massive, partly ferruginous biomicrites, biopelmicrites and dismicrites (bird's eyes!); with two layers of biomicrudites containing partly fragmented stromatoporoids, *Favosites* sp., *Thamnopora* sp., solitary corals and crinoid fragments (H. 417–418, 421 and 544–545).

- b. 23 m massive bedded biomicrites, biopelmicrites, biomicrudites and biointramicrudites with stromatoporoids, *Alveolites* sp., *Favosites* sp., *Thamnopora* sp., *Chaetetes* sp., *Aulopora* sp. and solitary corals (H. 416 and 541–543).
- a. 150 m beginning with biomicrudites, biopelmicrites and biopelsparites (H. 415, 419 and 539). Upwards follows a succession of shales, marls and biomicrites, biopelmicrites and biomicrudites with *Alveolites* sp., *Aulopora* sp., *Thamnopora* sp. and mudcracks (H. 420). In the shales (only exposed on the top of the hill west of the type section and north of the village) of the uppermost part a layer of ca. 1 m impure biomicrudites occurs with stromatoporoids, *Thamnopora* sp., *Aulopora* sp. and solitary corals. Many colonies are fragmented or turned upside down (H. 540).

La Vid (crinoidal limestones and shales).

Unit (a) is called the Argillaceous Limestone Member, unit (b) and (c) form the Limestone Member. The Caldas Formation seems to be equivalent in age with the Santa Lucía Formation and the lower part of the Huergas Formation (Upper Emsian – Couvinian) according to datings from the scarce brachiopods. Apart from some minor differences this stromatoporoid and coral fauna is identical with that of the Santa Lucía Formation. Contrary to the statement by Smits (1965) no stromatoporoids were found at the base of the Caldas Formation.

*Mallo.* – North-west of the village in the Portilla Formation the following section was measured:

Nocedo (badly exposed, sandy at the beginning).  
Portilla

- d. 30 m marly and sandy, badly sorted biomicrudites, very fossiliferous and irregularly bedded in the beginning, upwards massive to well bedded and rather fine-grained. With partly silicified *Alveolites* sp. (dominant in the lower part), *Phillipsastrea* sp. (dominant in the higher part), *Chaetetes* sp., *Thamnopora* sp., solitary corals, brachiopods and bryozoans. No stromatoporoids were found (H. M421).
  - c. 20 m quartzitic sandstones, making a sharp contact with the underlying limestones but grading to the following unit.
  - b. 30 m massive, badly sorted biomicrudites and biopelsparites with partly fragmented stromatoporoids, *Alveolites* sp., *Phillipsastrea* sp., *Favosites* sp., bryozoans and crinoid fragments (H. 422–424).
  - a. 20 m impure, bedded, detrital limestones, mainly consisting of crinoid fragments.
- Huergas (sandy shales).

The Santa Lucía Formation in this region is strongly affected by tectonic influences.

*Mirantes de Luna.* – On the east side of the Pantano de Luna near the village (now abandoned), the

Mirantes anticline is situated. The Santa Lucía Formation in the core of this anticline is incomplete and badly disturbed (H. 483–485). The Huergas Formation and the Portilla Formation crop out quite normally on both sides of the anticline.

On the north flank (north-east of the village) a small limestone lens is present in the Huergas Formation:

Portilla (limestones).

Huergas

e. ca. 100 m shales.

d. 24 m biomicrudites with stromatoporoids, *Alveolites* sp., *Chaetetes* sp., *Heliotites* sp., *Phillipsastrea* sp., solitary corals, brachiopods and bryozoans; massive except for the bottom and top. Lateral extension ca. 70 m. Laterally these limestones become more and more sandy till they disappear in the surrounding shales. No tallud is present on the flanks of the lens (H. 486–487).

c. 16 m sandy shales and limestones. Lateral extension at least 150 m.

b. 11 m well bedded limestones with some solitary corals. Lateral extension ca. 60 m.

a. 10 m shales.

Santa Lucía (limestones).

The Portilla Formation to the north-west of this point is exposed as a high wall in the landscape (the lower part). It is as thick as near Mallo and similarly developed:

Carboniferous (griotte and limestones).

Nocedo (25 m sandstones).

Portilla

d. 32 m rather well sorted biomicrudites, irregularly bedded. With abundant silicified *Alveolites* sp. and further *Chaetetes* sp., *Thamnopora* sp., *Phillipsastrea* sp., solitary corals, brachiopods and crinoid fragments. Some colonies are turned upside down. The uppermost part is very impure, grading into the overlying sandstones (H. 491).

c. 24 m calcareous sandstones and sandy limestones, coarsely detrital and badly sorted. At the base with stromatoporoids, *Chaetetes* sp. (abundant), *Alveolites* sp., *Coenites* sp., *Thamnopora* sp., solitary corals, brachiopods and crinoid fragments. Upper part rather shaly. Makes a sharp contact with the underlying limestones (H. 490).

b. 18 m massive bedded biomicrudites with fragmented stromatoporoids, *Phillipsastrea* sp., *Thamnopora* sp., *Alveolites* sp., solitary corals and crinoidal debris (H. 489).

a. 32 m ferruginous fine- to coarse-grained sandy limestones with cross-bedding. Upper part less sandy and rather massive; build up by crinoidal fragments. No other fossils were found here.

Huergas (shales).



Fig. 3. Limestone lens in the Huergas Fm. SE of Mirantes. In the foreground the Santa Lucía Fm. is visible, in the background the Portilla Fm. (increasing in thickness toward the W) and the Nocedo Fm. are exposed.

On the south flank of the Mirantes anticline (north flank of the Alba syncline) a large limestone lens occurs in the Huergas Formation (see fig. 3). In the thickest part the following section was measured:

Portilla (limestones).

Huergas

h. ca. 100 m shales grading to limestones in the upper part.

g. 9 m thin bedded bituminous biomicrite with chert layers. Lateral extension unknown, probably only on top of the core of the lens.

f. 10 m impure biomicrites slightly bituminous, with chert layers and silicified fossils. The latter are concentrated in a few levels of biointramicrudites to biosparrudites: stromatoporoids, *Alveolites* sp. (dominant), *Thamnopora* sp. (abundant), *Phillipsastrea?* sp. (abundant), *Aulopora* sp., *Favosites* sp. and solitary corals (H. 325, 326, 410, 411).

The lateral extension of this member is at least 1.500 m! On the west side of the lens where a brooklet cuts through it (along a fault), cross-bedding is present in the sandy lower part. In the limestone to the west handspecimens 413 and 414 were collected.

e. 10 m calcareous sandstones, making a sharp contact with the underlying limestones. Toward the west the sandstones wedge out. Here fossiliferous biomicrites to biosparites are present with stromatoporoids, *Phillipsastrea?* sp. and *Alveolites* sp. (H. 412). On the west side of the lens the sandstones appear again. Toward the east they increase in thickness up to 15 m but after ca. 200 m (laterally) they wedge out again (below the sandstones 3 m of fossiliferous limestones are exposed here).

d. 24 m fine-grained to detrital limestones partly intercalated with marly layers, partly massive. Ex-

cept solitary corals and crinoid fragments, no fossils have been seen. Lateral extension ca. 500 m.

- c. 13 m irregularly to massive bedded biomicrudites to biosparrudites with abundant fossils, partly upside down: stromatoporoids, *Phillipsastrea*? sp., *Alveolites* sp., *Thamnopora* sp., *Chaetetes* sp., solitary corals, brachiopods and crinoid fragments. The lateral extension is ca. 150 m at the base to ca. 400 m at the top. Laterally grading into ferruginous calcareous sandstones with cross-bedding (H. 408, 409, 578).

- b. 6 m impure fine- to coarse-grained limestones with chert concretions. The lateral extension is ca. 50 m at the base to ca. 150 m at the top.

- a. 100 m shales and sandstones.

Santa Lucía Formation (limestones passing to shales).

More to the east other, but only small lenses are present in the Huergas Formation. They occur at different levels in the shales, some at the base of the formation, some in the middle and some very close to the Portilla Formation. Their fauna is similar to that of the Portilla Formation (H. 402).

The Portilla Formation ca. 2 km south-east of Mirantes has a total thickness of ca. 70 m. At the base the limestones are sandy and intercalated with shales. *Favosites* sp. is abundant. More or less in the middle a marly layer of ca. 6 m occurs with abundant fossils: stromatoporoids, *Alveolites* sp., *Chaetetes* sp., *Thamnopora* sp., *Phillipsastrea* sp., *Coenites* sp., solitary corals, brachiopods and crinoids (H. 347–356).

At one place the contact between the Portilla Formation and the Nocedo Formation is beautifully exposed. In the transitional layers between both formations *Phillipsastrea* sp. is very abundant, many colonies are turned upside down. Further there occur *Alveolites* sp., brachiopods, solitary corals, crinoids and trilobites (H. 190–192, 201–202, 309B–324, 357). Toward the west, near the nose of the Alba syncline the thickness rapidly increases to ca. 200 m. This increase is almost entirely the result of the increased thickness of the lower part of the formation which seems to be absent or scarcely developed toward the east.

*Los Barrios de Luna.* – In the south flank of the Alba syncline (on the west slope of Peña Cambrones) the Portilla Formation reaches its maximum thickness of ca. 300 m. Most specimens from the Portilla Formation were collected in this area. The following section can be measured:

Nocedo (shales with lenses of well sorted detrital limestones and calcareous limestones with cross-bedding; H. 117–119, 126, 148, 150, 344).

Portilla

- c. 90 m well bedded to massive biomicrudites and biosparrudites with stromatoporoids, *Alveolites* sp. (very abundant), *Phillipsastrea* sp. (very abundant), *Chaetetes* sp., *Thamnopora* sp. (abundant

to dominant), *Coenites* sp., solitary corals (abundant), brachiopods and other organisms.

The massive detrital limestones with fragmented colonies alternate with impure limestones, mainly built up by *Thamnopora* sp. At some levels erosion surfaces are present between them. *Phillipsastrea* sp. is also abundant in some layers. Toward the top the limestones alternate more and more with marls and shales, with abundant silicified brachiopods, *Phillipsastrea* sp., *Thamnopora* sp. and other organisms (H. 102–116, 120–125, 127, 149, 157–161, 216–222, 304, 339–343, 345, 346; from the whole south flank of the syncline).

- b. 50 m ferruginous sandy marls making a sharp contact with the underlying massive limestones. The lower part of this member is formed by marls with thin detrital limestone layers. Partly silicified *Thamnopora* sp., *Coenites* sp., *Alveolites* sp., aulopodid corals, solitary corals, brachiopods and crinoid fragments are abundant.

Toward the top more and more detrital limestone layers are intercalated with ferruginous marly layers. The latter are built up nearly exclusively by *Thamnopora* sp. and also *Coenites* sp. and solitary corals. In the limestone layers large colonies of stromatoporoids, *Phillipsastrea* sp., *Chaetetes* sp. and most of all *Alveolites* sp. occur together with *Thamnopora* sp., *Coenites* sp., aulopodid corals and solitary corals.

The bedding of this part is very irregular due to erosional features. This member is equivalent to the sandstone beds elsewhere in the Portilla Formation. Near the top of Peña Cambrones this member seems to wedge out (H. 3A, 74–101, 140–147, 210–215, 250–255, 288–303, 585, 586; from the whole south flank of the syncline).

- a. 170 m alternating thin bedded marly and massive, unsorted crinoid biosparrudites, biosparites, biomicrudites and biomicrites.

The transition between the Huergas Formation and Portilla Formation is very gradual with alternating shales, marls and sandy biomicrudites.

A rich fauna is present: stromatoporoids (very abundant), *Alveolites* sp. (3 species, dominant), *Favosites* sp. (only in the lower part), *Chaetetes* sp., *Thamnopora* sp. (abundant), *Coenites* sp., *Phillipsastrea* sp. (only in the upper part), aulopodid corals, solitary corals (very abundant), bryozoans, brachiopods and other organisms. *Heliolites* sp., *Hexagonaria* sp., *Cyathophyllum* sp. and *Eridophyllum* sp. occur only sporadically. Most fossils are fragmented or lie at random in the sediment. Even very large colonies may lie upside down. At many levels erosional surfaces occur. Many layers are rather ferruginous (H. 4–73, 128–139, 203–209, 223–233, 238–249, 256–286, 328–338, 579–584; from the whole south flank of the syncline).

Huergas (shales, H. 261).

Toward the north in a gorge cutting through the centre

of the nose of the syncline following handspecimens were collected:

member (a), 114 m: 167–176 and 305–308

member (b), 45 m: 177–182

member (c), ca. 85 m: 184.

Member (b) is here developed as well-bedded limestones. More to the north sandstones have been observed locally. Compared with the section west of Peña Cambrones it is especially member (a) which is thinner.

Toward the south-east in a distance of ca. 3 km the Portilla Formation decreases rapidly in thickness, beginning with the lower part. North of the little village of Sagüera it wedges out completely. The Huergas Formation in the south flank, which is extremely thin due to tectonical influences, also seems to disappear toward the south-east. The extremely great differences in thickness in this area must have been caused by synsedimentary tilting of the basement.

A detailed study of the petrography and the brachiopod content of the Portilla Formation in the Alba syncline is being made by M. Mohanti (University of Leiden).

*Geras.* – South of the village, the Santa Lucía Formation crops out twice due to a longitudinal fault. Because of secondary faulting in the northern zone the most complete section is found in a narrow gorge in the southern zone, south of the river Casares. The formation here is of normal thickness, i.e. ca. 240 m, and is nearly identical to the type section along the Bernesga river (see below). Unfortunately stromatoporoids are difficult to obtain along the steep slopes of the gorge and moreover rather altered. Specimens 523–529 (from bottom to top) were collected here.

*Beberino.* – North of the village the Portilla Formation crops out along the river (see also Comte, 1959, pp. 180, 181):

Nocedo (calcareous sandstones).

Portilla

- d. 5–10 m sandy, detrital limestones and marls with cross-bedding. With abundant brachiopods, *Thamnopora* sp., solitary corals, bryozoans, and crinoid fragments. These layers cover the humps of the underlying massive limestones and fill up the spaces between them (H. 388).
- c. 24 m massive bedded to massive biomicrudites interrupted by a shale layer. With stromatoporoids (abundant), *Alveolites* sp. (abundant), *Thamnopora* sp., solitary corals and bryozoans; partly fragmented. The upper surface of these limestones is erosional and shows hump-like elevations (H. 387, 513).
- b. 20 m sandy marls in the lower part, upwards irregularly bedded biomicrudites which are more or less impure. With *Alveolites* sp., *Thamnopora* sp., solitary corals and brachiopods (H. 383 and 384–386?).

- a. 43 m pelletiferous biosparrudites to biosparites and biomicrudites to pelmicrites. Well-bedded, sandy and ferruginous, with only brachiopods and solitary corals in the lowest part. Upwards massive, with stromatoporoids, *Alveolites* sp., *Phillipsastrea* sp., *Thamnopora* sp., solitary corals and crinoid fragments (H. 378–382).

Huergas (sandy shales and calcareous sandstones).

The humps result from erosion. They cannot be interpreted as bioherms as they consist of normal biomicrudites (H. 513) and not of rigid coral and stromatoporoid skeletons.

*Huergas.* – More to the south along the Bernesga river, south of the village (type locality of the Huergas Formation, see Comte, 1959, p. 185), the Portilla Formation is exposed again:

Nocedo (calcareous sandstones with brachiopods, solitary corals and crinoid fragments, grading upwards into sandy shales and then into sandstones).

Portilla

- b. 17 m very fossiliferous marls, intercalated with layers of bioturbated biomicrites and biomicrudites. With stromatoporoids, *Alveolites* sp., *Chaetetes* sp. (very abundant), *Phillipsastrea* sp., *Thamnopora* sp., *Hexagonaria* sp., *Coenites* sp., solitary corals, brachiopods, crinoids and bryozoans. Gradually changing into overlying sandstones (H. 364–376, 425).
- a. 37 m well bedded to massive, partly laminated bioturbated biosparrudites to biosparites and biomicrudites to biomicrites. The lower part is sandy with bryozoans and crinoid fragments. The upper part is partly massive, with stromatoporoids, *Alveolites* sp., *Phillipsastrea* sp., *Thamnopora* sp., *Chaetetes* sp., *Coenites* sp., solitary corals, brachiopods and crinoid fragments. Some colonies lie at random in the sediment (H. 358–363).

Huergas (sandy and calcareous shales).

The upper massive limestones are apparently absent in this section. However, the transition to the Nocedo Formation is very gradual. As in the section near Beberino the sediment seems to be better sorted and slightly finer than near Mirantes and Barrios de Luna.

*Llombera.* – 5 km to the east, near Llombera, the Portilla Formation is well exposed again on a path leading south. Due to folding the formation is exposed three times. It is followed directly by massive sandstones of the Nocedo Formation (handspecimens 428–433 have been collected here).

*Santa Lucía.* – More to the north along the Bernesga river, south of Santa Lucía, the type section of the Santa Lucía Formation is exposed along the road, it is not dolomitic as in most other places in this region:



Huergas (calcareous sandstones grading upwards into shales).

Santa Lucía

- h. 37 m ferruginous irregularly bedded crinoidal bioparrudites and biomicrudites with abundant bryozoans, alternating with shaly layers. Sandy in the upper part (H. 453).
- g. 45 m thin to thick, irregularly bedded crinoidal biomicrudites intercalated with marls and shales. With abundant stromatoporoids (laminar to massive), *Alveolites* sp., *Favosites* sp., *Chaetetes* sp., *Thamnopora* sp., solitary corals and crinoidal debris. Many colonies are brecciated, other colonies lie upside down or at random in the sediment (H. 447–452, 520–522).
- f. 6 m massive biosparites and biomicrudites with partly silicified stromatoporoids, *Favosites* sp., *Alveolites* sp. and solitary corals. Some colonies are still in the position of growth while others lie at random in the sediment (H. 446, 519).
- e. 25 m biosparites and biopelsparites gradually becoming thinner bedded toward the top. In the lower part some silicified stromatoporoids and tabulate corals occur and also local beds of washed in brachiopods. In the upper part some solitary corals and brachiopods occur, together with fossil debris (H. 445).
- d. 40 m massive, biostromal limestones. Except at the base and at the top, where *Favosites* sp. and *Alveolites* sp. are abundant, this unit is mainly built up by large laminar stromatoporoids with lateral extensions up to one metre, mostly in position of growth, especially in the lower part but fragmented colonies are also common. The matrix between the colonies is generally very coarse (bio-

sparrudites and biomicrudites, sometimes biopelsparites and biomicrites) with *Thamnopora* sp., solitary corals and crinoid fragments (H. 444, 517–518).

- c. 20 m massive biomicrudites with some shaly interruptions. With abundant partly silicified fossils: stromatoporoids (abundant; dominant in the upper layers), *Favosites* sp. (dominant, some colonies are laminar and very large, others are more or less sausage-shaped), *Alveolites* sp., *Heliolites* sp., *Thamnopora* sp. and solitary corals (H. 516).
- b. 25 m thick bedded biomicrudites intercalated with some ferruginous beds of crinoidal biomicrudites. With stromatoporoids, *Favosites* sp. (dominant), *Alveolites* sp., *Chaetetes* sp., *Thamnopora* sp., solitary corals, brachiopods and bryozoans. Most colonies are laminar, others are rather massive. Though most of them are in the position of growth, many colonies, especially in the upper part, lie at random in the sediment (H. 439–443, 514, 515).
- a. ca. 40 m partly ferruginous, crinoidal biosparudites and intraclast bearing biomicrudites intercalated with marly and shaly bioturbated biomicrites. With *Favosites* sp., *Alveolites* sp., solitary corals, bryozoans and brachiopods. The limestones mainly consist of crinoidal debris (H. 434–438).

La Vid (not exposed).

From the above a total thickness for the Santa Lucía Formation of 240 m is obtained. This is considerably more than the 132 m mentioned by Comte (1959, pp. 176–178). However, the measurements of Comte are very rough and certainly not correct in this case.

Toward the south, on the other side of the valley, the Portilla Formation is exposed as a very steep wall. The lower massive limestones do not yield many fossils, the middle part consists mainly of sandstones. The upper part is very fossiliferous (H. 426, 427). It is incomplete due to the discordant intramontane Stephanian.

**La Vid.** – Still further to the north lies the village La Vid. East of the village the type section of the La Vid Formation is exposed. The formation has a total thickness of more than 250 m (due to tectonic complications the exact thickness is not measurable).

At the base layered limestones and dolomites with brachiopods alternate with shale layers. The middle part consists mainly of shales; in the upper part the shales are intercalated with ferruginous limestones built up by crinoidal debris. Here some tabulate corals are present.

South of La Vid, along the river, the lower part of the Santa Lucía Formation is exposed (including the massive stromatoporoid limestones; H. LV510–512). As in the type section, many specimens are partly silicified. The upper part of the section is not well exposed.

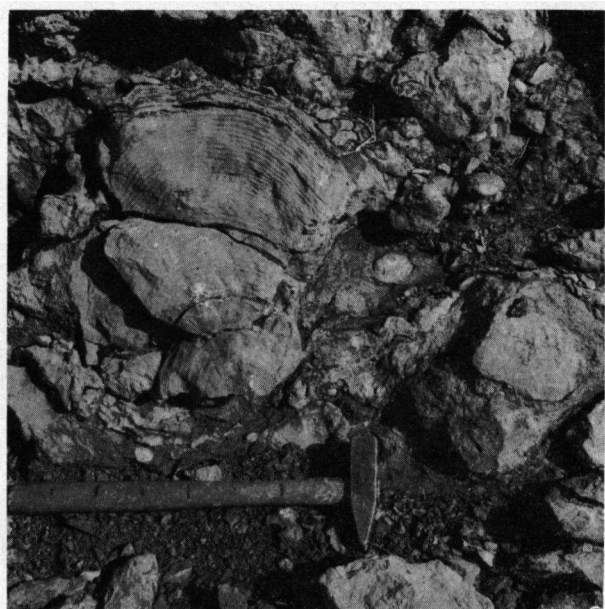


Fig. 4. Stromatoporoids, tabulate and solitary corals in bituminous marls in the Santa Lucía Fm. N of Aviaños.

*Matallana*. – In the valley of the river Torío, the Portilla Formation crops out near the village on both sides of the river. The type section of the Portilla Formation seems to be along the Arroyo de la Portilla, south of the village Orzonaga (Comte, 1959, p. 199).

Portilla outcrops occur also more to the east near Aviados. Sections have been described by Evers (1967, p. 95, Table IV). Stromatoporoids are scarce and silicified in this region.

Toward the north along the river Torío, south of Felmin, the Santa Lucía Formation is exposed. The limestones are mostly very fine-grained and laminated. At the base some desiccation cracks can be observed. There is only one place in the section where layers with stromatoporoids and tabulate corals occur. The crinoidal detrital limestones in the uppermost part of the formation are only 10 m thick.

*Aviados*. – North of the village (Peña Galicia) the Santa Lucía Formation is beautifully exposed from bottom to top and fairly fossiliferous.

Huergas (shales and sandstones).

Santa Lucía

- j. 28 m biomicrudites intercalated with marls and shales. In some layers brachiopods are abundant. More or less in the middle of this succession a layer of 1.5 m occurs with stromatoporoids, *Favosites* sp., *Thamnopora* sp., solitary corals, brachiopods and crinoid fragments (H. 538).
- i. 6 m fine-grained, bituminous to detrital, marly limestones. At the base stromatoporoids, *Favosites* sp., *Thamnopora* sp. and solitary corals are abundant. Many colonies lie at random or upside down in the sediment (H. 537).
- h. 10 m marly, thinly bedded limestones consisting of fine-grained sediment. At the top the limestone is coarser and more massive.
- g. 9 m marly pelmicrites to biointrasparrudites with fragmented stromatoporoids, *Thamnopora* sp., *Favosites* sp., solitary corals and brachiopods (H. 536).
- f. 30 m fine-grained sedimentary limestones, marly in the lower half and rather massive in the upper half. At the base chert concretions (fossils?) are abundant. At the top some strongly silicified fossils occur.
- e. 9 m fossiliferous biomicrudites and biointramicrites, marly in the beginning and massive bedded in the upper part, with silicified stromatoporoids, *Favosites* sp., *Thamnopora* sp. and solitary corals. Many colonies lie upside down in the sediment (H. 535).
- d. 47 m massive bedded limestones, sometimes marly, with cross-bedding, with chert layers at the base. The limestones and marls consist of laminated fine-grained sediment without macrofossils.
- c. 17 m biointramicrudites, well bedded to massive, partly bituminous. In the beginning without fossils, upwards with cross-bedding and then followed by 6 m of massive limestones with stromatoporoids

and *Favosites* sp. All colonies are partly silicified, some are fragmented (H. 534).

- b. 46 m predominantly massive, biomicritic, bituminous limestones with abundant large colonies of stromatoporoids, *Favosites* sp., *Alveolites* sp., *Thamnopora* sp. and solitary corals which are partly or entirely silicified. Many colonies lie at random in the sediment. The limestones are sometimes rather marly, in some layers cross-bedding is visible (H. 530–533).
- a. 23 m beginning abruptly above the La Vid Formation with detrital limestones with cross-bedding, upwards grading into fine-grained marly limestones with chert concretions (fossils?).

La Vid (crinoidal biomicrudites with cross-bedding, alternating with shales).

*Colle*. – East of Boñar in the village of Colle (below the church), the upper part of the La Vid Formation is exposed. It consists of shales with some biomicruditic limestone layers built up by solitary corals, bryozoans, brachiopods and crinoid fragments. In one of these layers which exists nearly exclusively of solitary corals, some large stromatoporoid colonies occur together with colonies of *Favosites* sp. and *Alveolites* sp. This layer can be followed in north-west direction. It lies ca. 20 m below the base of the Santa Lucía Formation (described below) and is known in this form only from this area (H. 570–572).

*Grandoso*. – Further to the west the Santa Lucía Formation is exposed in a little valley north-east from the village Grandoso. It is overlain with discordant Cretaceous conglomerates and sandstones:

Santa Lucía

Hiatus (20 m?).

- g. 20 m coarse detrital limestones intercalated with some marl and shale layers. Some layers are ferruginous.
- f. 18 m bituminous fine-grained limestones, at the base massive bedded, above marly with brachiopods and bryozoans.
- e. 40 m massive stromatoporoid limestones. The space between the colonies is filled up by bituminous biomicrudite and fragments of stromatoporoids. The colonies are very difficult to distinguish in the field! At the base *Favosites* sp. and *Thamnopora* sp. also occur (H. 576).
- d. 38 m alternating fine-grained, bituminous and rather coarse limestones and marls. The upper part is biomicruditic, bituminous. Partly silicified fossils are abundant: stromatoporoids, *Favosites* sp., *Thamnopora* sp., *Chaetetes* sp., solitary corals and brachiopods (H. 573–575).
- c. 23 m bituminous, fine-grained, massive bedded (below) to well bedded (above) limestones. The upper part contains many chert layers.
- b. 8 m beginning with massive, coarse, detrital limestones which grade into fine-grained, bituminous limestones with silicified stromatoporoids, *Favosites*



sp., *Alveolites* sp., *Thamnopora* sp. and abundant solitary corals. The highest part is rather shaly.

- a. 41 m coarse- to fine-grained, detrital limestones intercalated with marls and shales. The succession begins abruptly above the La Vid shales. In some layers cross-bedding is present. 30 m above the base some bituminous fine-grained limestones intercalated with shales occur. At the top the sediment becomes fine and bituminous again.

La Vid (shales).

*Veneros*. – In a zone, limited by the intramontaneous Stephanian of the Sabero basin in the north and by the discordant Cretaceous in the south, the Portilla Formation is exposed as a large ridge protruding in the landscape. A section was measured south of Veneros, near a coal mine. In the debris at the foot of the section specimens 454 and 569 were collected.

Nocedo (calcareous sandstones).

Postilla

- f. 18 m bioturbated fossiliferous micrites, marls and shales with brachiopods and some colonies of *Alveolites* sp. In the uppermost layers *Alveolites* sp., *Thamnopora* sp., solitary corals and brachiopods occur; one small stromatoporoid was found here (H. 568).
- e. 9 m sometimes slightly bituminous, well bedded fossiliferous microsparites and marls with chert layers and partly silicified fossils: stromatoporoids, *Alveolites* sp., *Phillipsastrea* sp., *Thamnopora* sp., solitary corals and brachiopods (H. 458).
- d. 12 m bituminous fine-grained, well bedded limestones with chert layers. Only solitary corals and brachiopods were seen.
- c. 11 m coarse- to rather fine-grained limestones with erosion surfaces. Silicified fossils are abundant: *Alveolites* sp., *Chaetetes* sp., *Thamnopora* sp., *Coenites* sp. and solitary corals. Most colonies are laminar. Stromatoporoids were not found.
- b. 21 m badly exposed marls, intercalated with some detrital limestone layers.
- a. 27 m coarse to very coarse biomicrudites, massive bedded with some marly intercalations. At some levels erosion and reworking of the sediment is evident. Fossils are especially abundant in the upper part: stromatoporoids, *Alveolites* sp. (very abundant), *Thamnopora* sp., *Phillipsastrea* sp., *Coenites* sp., solitary corals, brachiopods and bryozoans. Many colonies are fragmented (H. 455–456).

Huergas (shales and sandstones, scarcely exposed).

*Valdoré*. – North of the Sabero basin the Portilla and the Santa Lucía Formations are exposed in two structural units: one roughly on the west side of the river Esla (autochthonous) and one on the east side (Esla nappe). On the west side the Portilla Formation is well exposed along the river north of the village Valdoré. Above the last sandstone layers of the Huergas Formation there lie 125 m Portilla limestones and

marls. Only the lower 30 m (biomicrudites with burrows), which are equivalent with unit (a) of the section above, contain stromatoporoids (H. 562–563). According to Rupke (1965, p. 22) in some places of this area cross-bedding and oolites are present in this member. No stromatoporoids were seen higher in the section. The limestones and marls are mostly coarse- to fine-grained. Some limestone layers are very fine-grained and bituminous. Macrofossils in general are not abundant in these layers, but at some levels *Thamnopora* sp. is very common. At other levels solitary corals or brachiopods occur. The highest part of the formation is coarse- to very coarse-grained. It is overlain with Nocedo shales and calcareous sandstones. More to the north the Portilla Formation is partly or entirely eroded by the transgressive Ermita Formation.

*Crémenes*. – The Santa Lucía limestones west and north of Crémenes are partly converted into dolostones in which structures are no longer recognizable. Therefore the section of the Santa Lucía Formation was taken on the hill north of Crémenes, where the formation seems to be less dolomitised than in the small valley southwest of this hill. According to van Adrichem Boogaert (internal report) the following section can be measured (simplified):

Huergas (sandstones).

Santa Lucía

- e. 15 m detrital ferruginous limestones.
- d. 90 m fine-grained sedimentary limestones intercalated with marls and shales. At the base intraclasts are very common. 10 m above the base a fossiliferous layer occurs with stromatoporoids, *Alveolites* sp., *Thamnopora* sp. and solitary corals. Higher in the section no stromatoporoids and scarcely any macrofossils were found. At some levels desiccation cracks are present (H. 560–561).
- c. 200 m dolostones, tectonically thickened.
- b. 60 m middle- to coarse-grained limestones intercalated with crinoidal biomicrudites. Some small (ca. 2 m high) bioherms occur in these limestones. The abundant fossils are strongly silicified: stromatoporoids (dominant), *Favosites* sp., *Thamnopora* sp. and solitary corals. Most colonies lie at random or upside down. The uppermost layers (above the last bioherms) are finer grained with chert layers (H. 559).
- a. 57 m coarse, partly dolomitic (primary) limestones predominantly formed by crinoidal debris. The transition from La Vid to Santa Lucía is very sharp. La Vid (shales intercalated with layers of crinoidal debris).

*Villayandre*. – East of the village a section of the complete Devonian is perfectly exposed (the so called Agua Salio section, Rupke, 1965).

Huergas (200 m mostly sandstones with cross-bedding).  
Santa Lucía

- e. 35 m ferruginous, bedded biomicrudites and biopelmicrites with burrows, crinoidal debris and partly silicified fossils. Many colonies lie upside down or at random in the sediment. Sometimes very large stromatoporoids are dominant but *Favosites* sp. is also present (H. 473 and 567).
  - d. 65 m coarse-grained, massive limestones. No fossils were seen here.
  - c. 45 m well bedded, biomicrites with marly intercalations. Strongly silicified fossils are common: some stromatoporoids, *Favosites* sp. (abundant), *Thamnopora* sp. (abundant), *Alveolites* sp., solitary corals and burrows (H. 566).
  - b. 55 m thin to thick bedded, partly dolomitised biomicrudites and biosparrudites, with silicified fossils and fossil fragments: stromatoporoids, *Alveolites* sp., *Favosites* sp., *Thamnopora* sp., solitary corals and crinoidal debris. In the upper part many fossils lie upside down (H. 472 and 564–565).
  - a. 50 m grey, bedded and massive, detrital limestones (crinoidal debris), partly dolomitic.
- La Vid (uppermost layers are shales, intercalated with ferruginous detrital limestones formed by crinoidal debris).

The Portilla Formation forms very steep slopes above the softer Huergas Formation. Therefore fossils are difficult to collect. In the debris at the foot of the section specimens with number 474 were collected. According to Rupke (1965) the following section can be measured:

Nocedo (calcareous sandstones with cross-bedding).

Portilla

- d. 70 m beginning with massive biostromal limestones with silicified fossils. Upwards the limestones are well bedded, detrital.
- c. 30 m well bedded, detrital limestones with fossils and shale lenses.
- b. 55 m massive limestones. The upper part is biostromal.
- a. 45 m beginning with coarse-grained arenaceous limestones with shale lenses and cross-bedding. The upper part is oolitic. Brachiopods and corals were seen in this member.

Huergas (sandstones and shales).

It has to be borne in mind that the Agua Salio section is situated in the Esla Nappe, coming from the south. The same is true for the sections near Colle, Grandoso and Veneros, but not for the sections near Valdoré and Crémenes which are autochthonous!

Toward the east lies the intramontane Cea Basin with Stephanian. East of this basin, in the Valsurvio Dome, the Devonian is again exposed. This area has been described by Koopmans (1962). The Devonian is similar to that in the west although Koopmans used different formation names.

*North of the Pantano de Compuerto.* – Here are some small limestone lenses in the Compuerto Formation (= La Vid Formation) ca. 100 m below the top. The

limestones are fine- to coarse-grained with cross-bedding. In some layers abundant stromatoporoids occur together with *Thamnopora* sp. Specimens 555–556 were collected here. However, all the specimens are strongly recrystallized due to slight metamorphosis. As far as they are recognizable the stromatoporoids seem to belong to the same species as that in the Santa Lucía Formation.

The Otero Formation (= Santa Lucía Formation) which crops out more to the north along a side arm of the lake, is badly exposed. The limestones are also strongly recrystallized. The lowest exposed part is detrital with stromatoporoids, *Favosites* sp., *Thamnopora* sp. and solitary corals. (H. 557, indeterminate). Higher in the section the limestones are fine-grained, intercalated with marls and shales, no fossils were found here.

*Otero de Guardo.* – The type section of the Otero Formation is now covered by the lake.

*Valcovero.* – East of the village the type section of the Valcovero Formation (= Portilla Formation) is exposed. The lower part, which is well bedded, has become very slaty. The upper part is massive and mainly built up by *Thamnopora* sp. but also *Chaetetes* sp. and other species of corals are present. They are all strongly recrystallized.

North of the Valsurvio Dome, in the Cardaño Area, Devonian limestones are only developed as nodular limestones. They belong to the mainly clastic Palentian Facies (van Veen, 1965; Brouwer, 1968).

*San Martín de los Herreros.* – South of the village a limestone is exposed with a typical Portilla fauna (see also Kanis, 1965):

Lower Carboniferous (radiolarian rock)

Hiatus?

Nocedo (2.5 m quartzite beginning abruptly after the limestones).

- c. 40 m massive bedded biomicrudites. The lower part is badly sorted with stromatoporoids, *Alveolites* sp., *Heliolites* sp., *Hexagonaria* sp., *Phillipsastrea* sp., *Thamnopora* sp., solitary corals and brachiopods. In the middle of this member there occur 3 m of well sorted, thick bedded detrital limestones with few fossils. The upper part shows the same development as the lower part (H. 553–554).
  - b. 10 m massive bedded biomicrudites with stromatoporoids, *Phillipsastrea* sp., solitary corals and brachiopods. Also fragments of colonies are present. The uppermost layers are marly (H. 552).
  - a. 23 m impure biomicrudites intercalated with marls, rather massive at the base with abundant solitary corals and some stromatoporoids. Higher in the section only brachiopods are abundant (H. 551).
- Ferruginous sandstones (up to 47% Fe).

*Ventanilla.* – South-west of the village in the core of an overturned fold the Devonian is exposed down to the

Emsian. The Devonian here is very different from that to the west and also from that in the north. Unlike the biostromal limestones in the west and the mainly clastic facies in the north, only large limestone lenses are found in this area. Unfortunately, however, the fossils are badly preserved. The following section was measured (after Kanis, 1956, modified):

#### Carboniferous

Nocedo (55 m sandstones, making a sharp contact with the underlying shales).

m. 35 m shales (scarcely exposed).

- l. 3 m biomicrudites, with fragmented stromatoporoids, *Thamnopora* sp. and brachiopods in the upper part. This is also a Portilla fauna. The lateral extension could not be measured (H. 550).
- k. 17 m sandy shales (scarcely exposed).
- j. 6 m biomicrudites, marly at the base and very fossiliferous at the top, where it grades into sandy shales. The lateral extension could not be measured. A typical Portilla fauna was found: stromatoporoids, *Phillipsastrea* sp., *Thamnopora* sp., *Alveolites* sp., *Chaetetes* sp. and bryozoans (H. 463).
- i. ca. 40 m shales (scarcely exposed).
- h. 15 m very ferruginous sandstones (the same as the ones south of Ventanilla).
- g. 70 m sandstones (scarcely exposed).
- f. 60 m massive biomicrudites with abundant silicified fossils and fossil fragments: stromatoporoids (dominant), *Favosites* sp., solitary corals and bryozoans. The uppermost 20 m are mainly micritic and bituminous with large solitary corals but also with stromatoporoids (H. 464–465).
- e. 43 m bedded limestones (badly exposed).
- d. 22 m beginning with coarse biosparrudites and biomicrudites which further up contain (partly fragmented) *Favosites* sp. and *Alveolites* sp. The upper part is massive with stromatoporoids (H. 466).
- c. 90 m slates with abundant brachiopods, indicating an Emsian age. The slates gradually change to the next member.
- b. 60 m biomicrudites intercalated with marly layers. Fossils are scarce, except *Thamnopora* sp. At the top the sediment is coarser but also more shaly, with stromatoporoids, *Alveolites* sp., *Thamnopora* sp., bryozoans and crinoid fragments (H. 467 and 548–549).
- a. ca. 35 m massive biomicrudites and intrapelsparites (bituminous at the base; with stromatoporoids, *Alveolites* sp., *Favosites* sp. and *Thamnopora* sp., H. 469? This is the lowest part of the section cropping out in the distorted core of the fold). Stromatoporoids, *Favosites* sp. and *Heliolites* sp. were collected in the upper part (H. 468–470 and 547).

Members (i) to (m) are equivalent to the members (a) to (c) of the section near San Martín d.l. Herreros (Portilla). The lower limestone lenses (members a, b, d, e, f) contain the same species of stromatoporoids as

the Santa Lucía Formation. An exact correlation of these members with the Devonian in the west is not possible.

*Lebanza*. – Toward the north, in the Palentian facies, stromatoporoids were only found in the type section of the Lebanza Formation, west of the village (see Binnekamp, 1965, p. 14).

The Lebanza Formation consists of a succession of ca. 100 m bedded limestones intercalated with shales. At the base well bedded biomicrudites with fossil fragments and abundant brachiopods and cross-bedding (H. 459) are exposed. Then follow some biomicrudites with abundant solitary corals (H. 460). Above this lie ca. 15 m massive limestones. The lowest 5 m of these limestones are dolomitised biointramicrudites and intrapelsparites with cross-bedding. Generally globular stromatoporoids (all belonging to one species and lying at random in the sediment) are abundant at some levels. *Favosites* sp. and *Thamnopora* sp. also occur (H. 461–462). In the higher limestones only some beds with *Favosites* sp. occur. They are finer grained and cross-bedded. The upper part of the formation is formed again by well bedded limestones intercalated with marls and shales. Brachiopods are extremely abundant. The sediment gradually changes to shales.

South of the Pantano de Vañes the Lebanza limestones crop out again. Contrary to the statement of Binnekamp (1965, p. 16) no stromatoporoids could be found here. Only brachiopods, *Favosites* sp., solitary corals and burrows were found.

The Lebanza Formation is more or less equivalent to the lower part of the La Vid Formation (see Brouwer, 1968, pp. 39, 40).

#### SOME REMARKS ON PALAEOECOLOGY

As can be seen from the descriptions of the localities, stromatoporoids are always associated with tabulate and rugose corals and further with brachiopods, bryozoans, and crinoids. Pure stromatoporoid limestones do not occur. Although stromatoporoids are dominant in some beds in the Lebanza, Santa Lucía and Caldas Formations, they are always associated with *Favosites* sp. and *Thamnopora* sp. while solitary corals mostly are also abundant.

On the other hand stromatoporoids seem to be lacking in layers with abundant *Favosites* sp., *Alveolites* sp., *Phillipsastrea* sp., *Chaetetes* sp. and/or *Thamnopora* sp. Although in some cases these limestones are rather impure or very fine-grained, in other cases no essential petrographic differences exist with stromatoporoid bearing limestones. Moreover fine-grained, bituminous limestones are frequently biostromal with a dominant stromatoporoid fauna. Stromatoporoids are often also abundant in sandy and ferruginous marls.

From the foregoing we may conclude that in the Devonian of the Cantabrian Mountains at least the ecological differences between stromatoporoids, tabulate corals and colonial rugose corals are not very

marked. According to M. P. Michel (personal communication) in Asturias a better facies differentiation can be made in the Candas Formation (equivalent with Portilla Formation).

Below the Huer gas Formation the limestones are mainly built up of more or less impure micritic, bituminous to coarse detritic sediment, frequently with cross-bedding. Intercalated in this succession are biogenetic banks and biostromes. Locally limestone lenses may occur. The position of biogenetic limestones in the succession can probably vary from one section to another. Their occurrence and thickness seems to depend in the first place on local ecological factors (mainly supply of sediment).

On the whole the Emsian and Couvinian limestones (limestone lenses near Ventanilla, Santa Lucía Formation, Caldas Formation) have a uniform coelenterate fauna throughout the whole succession. Stromatoporoids (*Actinostroma papillosum*, *Actinostroma verrucosum*?, *Stromatoporella*? *selwyni*, *Stromatopora huepschi*?) are present from the bottom to the top. Together with *Favosites* sp., *Thamnopora* sp. and solitary corals they form the main components of the fauna. *Alveolites* sp. and *Chaetetes* sp. generally are less common but are also present from the bottom to the top. *Heliolites* sp. and some colonial rugose corals occur sporadically.

The Portilla Formation largely consists of biogenetic banks. The sediment between the fossils is composed of large to small fragments of fossils and biomicrudite. The amount of admixture of sand, clay and ironoxide is variable from layer to layer (and from place to place).

Apart from biogenetic banks also more or less detrital or fine-grained layers with few coelenterates occur in some areas. In most biogenetic banks of the Portilla Formation it is *Alveolites* sp. which is dominant but in some beds it is *Thamnopora* sp. that is dominant. *Actinostroma stellatum* and solitary corals also are very abundant through the whole formation. *Stromatopora concentrica*, *Chaetetes* sp. and *Coenites* sp. are common through the whole formation but mostly not abundant. In the lower part of the Portilla Formation *Stromatoporella*? *granulata*? is quite common, but the colonies have remained small, so it is not an important rock builder. *Favosites* sp. also occurs in the lower part but is only common north of Los Barrios de Luna. Here and in some other places *Heliolites* sp. and *Hexagonaria* sp. and other colonial rugose corals occur sporadically. *Phillipsastrea* sp. becomes more and more important toward the top of the formation, where it can even be dominant.

Further the mode of growth of stromatoporoids and tabulate corals, and to a lesser extent colonial rugose corals is very similar. The similarity between the form of the coenosteum of stromatoporoids and specimens from genera such as *Alveolites*, *Chaetetes*, *Heliolites* and *Favosites* is striking. Both stromatoporoids and tabulate corals vary from thinly laminar to very large, irregularly massive, semihemispherical or bell-shaped. Specimens belonging to one species of the genus

*Favosites* may be flat umbrella-shaped, massive or sausage-shaped. The different forms occur together within one bed! Elongated sausage-shaped forms of *Favosites* sp. are abundant in some layers both in the lower Portilla Formation near Los Barrios de Luna and the Santa Lucía Formation near Santa Lucía. Stromatoporoids with conical coenosteum are sometimes found in the Santa Lucía Formation, globular to elliptical forms are common in the Santa Lucía and in the Lebanza Formation but absent in the Portilla Formation. *Phillipsastrea* sp. is mostly flat umbrella-shaped. A fragment of *Thamnopora* sp. is frequently present at the starting point of the colony. The same can be observed below many specimens of *Alveolites* sp. found in the marly layers in the Portilla Formation north of Los Barrios. Also some specimens of *Favosites* and *Chaetetes* found in marly layers have flat umbrella-shaped coenosteum.

Apart from the variations in the coenosteum mentioned above, asymmetric growth of the colonies is common. However, the directions of principal growth are difficult to measure because in general only two dimensions of the colonies in situ are visible.

Thus it seems that the form and size of the colonies depend on the extent of lateral expansion, on the one hand, and of the time the colonies were able to grow vertically before the organisms died, on the other hand. Causes of death between others may be being buried in the sediment, being turned upside down by wave action, incrustation by other organisms and abrasion by storms. As every colony grew in a different micro-environment, it is understandable that each colony has a different form.

*Thamnopora* sp. is very common in the Devonian limestones in the Cantabrian Mountains. Except for some beds in the lower part of the Caldas Formation only fragmented coenosteum were found. On the other hand, branching stromatoporoids are extremely scarce. *Amphipora* sp. is even completely missing; probably because a back-reef facies is absent in the area.

The similarity in growth habit between stromatoporoids and corals is also reflected in their internal structures. Stromatoporoids have latilaminae caused by seasonal influences. The same feature can be observed in corals. Especially in specimens of the genera *Alveolites* and *Chaetetes* growth zones may be very conspicuous and even solitary corals frequently show them.

Stromatoporoids sometimes encrust other stromatoporoids, tabulate corals and even solitary corals and bryozoans. But in the same way stromatoporoids may themselves be overgrown by the same species of tabulate corals and bryozoans (Pl. 2 figs. 1, 2). Sometimes there are even whole sequences of successive incrustations (Pl. 1) (see also Nicholson, 1886-92, p. 28). These examples prove again that, at least in these cases, stromatoporoids were more or less equally adapted to the same ecological conditions as the tabulate corals they occur with.

Some organisms are intergrown with stromatoporoids. In the first place *Syringopora* sp. has to be men-

tioned. It occurs in the coenostea of *Stromatoporella? granulata?*, *Stromatopora concentrica* and *Stromatopora huepschi?*. However, only about half of the specimens of these species are intergrown with *Syringopora* sp. Moreover, colonies of *Syringopora* sp. have been found which are not intergrown with stromatoporoids. Thus this intergrowth seems to be neither symbiosis nor parasitism.

Other organisms intergrown with stromatoporoids are little corkscrew-like worms (Pl. 24 figs. 1, 2) (see also Lecompte, 1951, Pl. V fig. 3). The same organisms also occur in *Alveolites* sp. and *Chaetetes* sp. In other specimens cone-shaped vertical hollow tubes are present. Sometimes it can be observed that repair tissue of the stromatoporoid has grown into the opening of the tubes (Pl. 2 figs. 3, 4 and Pl. 20 fig. 3).

Common are tube-like perforations through the skeleton of the stromatoporoid by some unknown organisms (Pl. 2 fig. 5). They can also be observed in compound tabulate corals.

Occasionally stromatoporoids are found with enclosed foreign objects like crinoid fragments, brachiopods etc. in the latilaminae.

#### FACIES, PALAEOGEOGRAPHY AND COMPARISON WITH OTHER AREAS

From the descriptions of the localities one gets the impression that the Devonian limestones in the Cantabrian Mountains were formed in a predominantly shallow to very shallow environment.

During the sedimentation of the Lebanza Formation and the La Vid Formation the siliciclastic sedimentation as a whole was stronger than the sedimentation of carbonates. Only in a few places (Lebanza, north of the Pantano de Compuerto and Colle), were stromatoporoids able to live for a short time.

During the sedimentation of the Santa Lucía Formation the limestone sedimentation was dominant over the siliciclastic supply. But the amount of clastic material largely determines whether the limestones are massive or bedded. Frequently, even the supply of micrite, pellets, intraclasts and fossil fragments was so low that biostromes could develop. However, the sea was mostly so shallow that the colonies of stromatoporoids and corals did not remain in situ but were turned upside down or even fragmented by wave action. Then only biogenetic limestones were formed.

Apparently the supply of sediment increased north and eastward. Therefore the sediment near Caldas is mainly siliciclastic. Only in the higher part of the Caldas Formation are thick limestone beds present. Near Ventanilla limestones were formed only locally in a mainly siliciclastic environment. More to the north-east, in the Palentine facies, the sedimentation was almost completely siliciclastic at this time. Also in general it can be seen that toward the north the number of beds with stromatoporoids and corals decreases (compare the Santa Lucía Formation near Aviados with that near Felmín and the Santa Lucía Formation near Villayandre with that near Crémenes).

After the Santa Lucía Formation the sedimentation became siliciclastic in the whole area (Huergas Formation). Apart from some calcareous sandstones, only near Mirantes some limestone lenses are present. They are not real bioherms, as they exist of an alternation of laterally limited fine-grained, detrital, biostromal and biogenetic (when most fossils are not in situ) limestones, as in the Santa Lucía Formation and Portilla Formation. The same can be said of the limestones near Ventanilla.

The change from limestones to clastic material does not seem to have been caused by the deepening of the environment, for in nearly all places the upper part (and also the lower part!) of the Santa Lucía Formation consists of coarse crinoidal debris.

After a period with nearly exclusively clastic sedimentation the Portilla limestones were formed. In the area of the Luna Valley these limestones must have been formed in very shallow water with little supply of sediment. The layers are irregularly bedded, erosion features are frequent and fossils are fragmented or turned upside down.

In the area of the Bernesga valley the sediment is generally finer and better sorted and more toward the east, near the river Esla, even bituminous layers occur in the formation. Near Ventanilla limestones were formed only in very limited areas.

The Portilla Formation is interrupted by a period of strong siliciclastic supply. West of the river Luna sandstones are present. Near Mirantes the sandstones are fossiliferous and near Los Barrios and in the Bernesga valley fossiliferous marls were formed. More towards the east the clastic interruption is difficult to distinguish.

After the massive upper Portilla limestones, the sediment became gradually clastic again with shales and calcareous sandstones (Nocedo Formation), but locally some lenses with detrital, cross-bedded limestones developed. Near Villayandre even some fossiliferous limestones were formed (Crémenes limestones).

The Nocedo Formation is followed by the discordant Ermita Formation which towards the north eroded more and more of the underlying Devonian sediments. In the central part of the mountains the Ermita quartzites even lie upon the Ordovician Barrios Formation.

As a whole it can be stated that the Devonian limestones, described here, were formed in the Asturo-Leonese Basin. This basin begins in the east near Ventanilla and bends toward the north near Quintanilla and La Vega. In the area north of Ventanilla the deeper Palentine Basin was situated with a mainly clastic sedimentation. West of this basin and north-east of Caldas the Asturian High was situated (see Smits, 1965, van Adrichem Boogaert, 1967, Brouwer, 1968). Toward the south (now covered by Tertiary) and the south-west (Precambrian is exposed here) another high was situated (see also Llopis Lladó et al., 1968). Contrary to the Asturian High, this area was rather stable for the supply of clastic material nearly always came from the north during the whole De-

vonian (van den Bosch, personal communication). Therefore stromatoporoids and corals are far more common along the southern border than toward the north.

The Devonian can be followed up to the north coast of Asturias, where more or less the same formations (also with stromatoporoids) can be found (Radig, 1961).

A comparison with all other areas where Devonian outcrops have been found has been very much facilitated by the 'International Symposium on the Devonian System' in Calgary, Canada, 1967 (D. H. Oswald *ed.*, 1968). However, a comparison with the Devonian in North America, Europe, North Africa, Asia and Australia is beyond the scope of this work. Only a few remarks should be made:

Contrary to other areas no real bioherms and barrier

reefs have been formed in the Devonian of the Cantabrian Mountains. Therefore an obvious division in facies types with different faunal associations cannot be made. Moreover a comparison with stromatoporoid faunas from other areas is extremely difficult, if not impossible, due to the great confusion in stromatoporoid taxonomy. Nevertheless it seems that many Devonian species have a nearly world-wide distribution. Anyhow, it can be stated that, according to the figures, the fauna described by Le Maitre (1947) from Morocco is nearly identical with that of the Portilla Formation, although it was described as Eifelian.

A fauna from a single limestone bed from Lethmathe (upper Givetian, Eifel, Germany), which will be described by E. Flügel and H. Hötzl, is very similar to that of the Portilla Formation.

## CHAPTER II

## MICROSTRUCTURES AND THEIR ALTERATIONS

*The investigation of the ultimate structure of the skeletal tissue of the Stromatoporoids is a matter of great difficulty, owing to the fact that in many specimens the skeleton has undergone considerable secondary alteration, while probably none retain their original constitution unchanged.*

Nicholson, 1886-92, p. 35

## GENERAL REMARKS

As most specimens of stromatoporoids, described in literature, are more or less altered, investigation of recrystallization features is of utmost importance. Actually many of the described species and even genera are based on strongly altered material and are thus of doubtful value. Therefore a sharp distinction has to be made between primary microstructures and secondary ones due to alteration.

The finest structures of stromatoporoids are so sensitive that only in a few specimens can the microstructure be studied in more or less its original conditions. It is possible, however, that even these no longer show the original structures of the skeleton.

In most specimens the microstructure has been affected by alteration in one way or another. Some of these specimens are so altered that even the gross structure is difficult to recognize. They can only be determined by comparison with the better preserved ones and are not dealt with in this chapter. The worst preserved material had to be thrown away.

Alteration can occur before the coenosteum is covered by sediment, during diagenesis and by weathering and leaching on the surface of exposure. Due to the last many loosely found specimens do not render good thin sections, though the gross structure is very clearly visible on the surface of the specimen.

Two types of alterations of microstructure have to be distinguished:

1. those due to recrystallization of the calcite
2. those due to chemical replacement (silicification, dolomitisation, impregnation with iron oxide)

Moreover infiltration of mud has to be mentioned.

In spite of the difficulties encountered with microstructure, this remains a basic character for any classification of stromatoporoids.

For the description of the microstructures the terminology of Stearn (1966a) has been more or less applied.

In the Spanish material four primary microstructures have been found:

- a. *compact* (see Pl. 3 fig. 7). The specks are evenly distributed in the tissue and no cellulae, pores, vacuoles or microlaminae occur.
- b. *microlaminate* (= tripartite, multilayered), (see Pl. 6 fig. 3). The laminae are mostly formed by more than one layer with clear layers (empty spaces) between them. Vacuoles are common. The pillars are more or less compact.

c. *ordinicellular* (see Pl. 8 fig. 3). The laminae are formed by one or more rows of cellulae. The pillars also seem to be formed by cellulae. Stearn (1966a) used the term 'ordinicellular' only when the laminae are formed by one row of cellulae. When more than one row is present he called the microstructure 'microreticulate'. Here the term 'ordinicellular' is extended and also used for laminae with more than one row of cellulae, as the number of rows of cellulae in a lamina can vary from one to at least five, within one coenosteum.

d. *cellular* (see Pl. 10 fig. 5). Laminae and pillars are formed by a network of small cellulae. When the cellulae are rather regularly arranged, the microstructure may be called 'microreticulate', though there are no essential differences between cellular and microreticulate microstructures.

The *techniques* used for the examination of the microstructures are quite simple: thin sections for magnifications up to 50 times and acetate peels for magnifications up to 1000 times.

## ALTERATIONS DUE TO RECRYSTALLIZATION OF THE CALCITE

The preservation of the skeletal elements is not only different from outcrop to outcrop, as mentioned in chapter I, but also from specimen to specimen. Frequently even within one specimen the degree of alteration can be variable.

In all thin sections of stromatoporoids small pigment specks can be observed in the skeletal elements (Pl. 3 fig. 1) (see also Stearn, 1966a, pp. 77-78).

Peels, however, when magnified ca. 200 times or more, do not show specks but structures like little hollow rings and tubes with a diameter of ca. 2 micron (Pl. 3 fig. 2). These structures are absent or very scarce in the interlaminae spaces. Thus in a peel the structure of the stromatoporoid becomes visible due to differences in the concentration of the 'tubes'.

In specimens with many slip planes in the crystals, the 'tubes' or fragments of 'tubes' are frequently arranged along these planes (Pl. 3 fig. 3). These small structures are caused by irregularities in the etching surface due to the impurities in the crystals.

Similar hollow structures are visible on the surface of uncovered thin sections (Pl. 3 fig. 4) but then they are caused mechanically by the carborundum powder. In this case they are better visible in the clear areas than in the areas occupied by skeleton for there the section is too opaque.

Horizontal and vertical skeletal elements are formed by the same material. In the case of specimens with cellular microtissue and compact cyst plates, the cyst plates are of the same material as the walls of the cellulae. This skeletal tissue was secreted at the base and laterally by the living part of the organism in

order to support it while it was growing upward. The skeleton is constructed in such a way that an ample lateral interconnection was possible but no vertical connection through the horizontal skeletal elements.

In some specimens the skeleton is impregnated by dark organic material from the surrounding sediment. The skeletal elements become extremely dark and give a strong contrast with the transparent calcite in the galleries. This occurs especially in the specimens no. 532 and 533 from a dark bituminous marly layer in the lowermost Santa Lucía Formation north of Aviados. Here the impregnation occurs mainly along the latilaminae (Pl. 3 fig. 5). In other places impregnation occurs along the joints in the coenosteum.

The features of alteration are more or less the same for all microstructures: originally sharply defined microtissue becomes vague, flocculent, melanospheric and even pseudocellular. Other specimens develop transverse fibrosity. Moreover migration of specks into the galleries takes place (see Stearn, 1966a, p. 79). By this migration cellulae, vacuoles and clear layers between microlaminae may be filled with specks so that the tissue looks compact. In some cases even part of the galleries may be completely filled with specks while in other places clear crystals without specks are developing within the tissue, obscuring both microstructure and gross structure. Apart from this, the specimens may be affected by tectonic stress, slight metamorphosis and decoloration by leaching of the organic material.

Destruction of specks must have occurred at least partly already before fossilization. Many specimens have an altered border zone in the uppermost part of the coenosteum, even if they are overgrown by other organisms or completely covered by sediment. This feature is very distinct in some thin, encrusting forms of *Stromatoporella?* sp. 1 (Pl. 3 fig. 6) see also Sleumer, 1968, fig. 17).

Migration of specks into the galleries and/or concentration of specks in flecks or melanospheres, also seem to have taken place at a very early stage of fossilization. At a later stage of preservation, migration of specks is very much favoured by the development of slip planes in the crystals. Pillars can be more affected by alteration than the laminae and vice versa, but in most cases they are altered to the same degree.

In the following pages some examples will be given of the most frequent alterations of (a) compact, (b) microlaminate, (c) ordinicellular, (d) cellular microstructures.

#### *a. alterations in compact tissue*

(Pl. 3 fig. 7 – Pl. 6 fig. 2)

In well preserved specimens (Pl. 3 fig. 7) there is a marked contrast between tissue and interlaminar spaces and the boundary between them is sharp. The tissue is more or less evenly coloured although it may already be slightly flocculent.

In the tangential section of the same specimen (Pl. 3 fig. 8) some pillars have dark centres and dark borders but others are equally coloured or even floccu-

lent. The dark centres and borders must be due to the concentration of specks in these places. This feature is by no means common in other specimens of *Actinostroma* from Spain. It was already reported by Nicholson (1886-92, pp. 77, 132; see also Stearn, 1966a, p. 86).

The crystal pattern in the vertical section (Pl. 4 fig. 1) is random and has no relationship with the tissue of the stromatoporoid, though the largest crystals are situated in the interlaminar spaces and crystal boundaries may be vague or absent within the tissue of the stromatoporoid (see also St. Jean, 1962, p. 196 and Stearn, 1966a, p. 76). This pattern suggests that because of the specks, crystal boundaries were originally absent within the tissue and that the crystal boundaries penetrated later from the galleries into the skeleton of the stromatoporoid. This would mean that some degree of recrystallization has already taken place, even in the best preserved specimens.

In a peel of the tangential section (Pl. 4 fig. 2) some crystals are very large. The pillars are not traversed by crystal boundaries but are either included in a large crystal or form a separate crystal, generally surrounded by smaller ones.

In less well preserved specimens (Pl. 4 fig. 3) the interlaminar spaces are filled at least partly with brownish calcite. The skeletal elements, especially the pillars, are less sharply defined. That most of the pillars are vague is also caused by the fact that many pillars are cut only marginally in the section, while the horizontal elements which have two-dimensional extensions are always present through the entire thickness of a vertical section.

In a peel of the same vertical section (Pl. 4 fig. 4) the skeletal elements are marked by small crystals in contrast with the larger crystals of the interlaminar spaces (see also Stearn, 1966a, pp. 76-77). The brownish interlaminar calcite also contains many specks though there are fewer than in the skeleton. This type of preservation is quite common in specimens of the Santa Lucía Formation and the Caldas Formation.

In some specimens part of the laminae have a black central axis (Pl. 4 fig. 5); this is due to crystal boundaries resulting from recrystallization, as can be seen in a peel (Pl. 4 fig. 6). This feature also occurs in specimens with an ordinicellular microstructure. It has only been observed in specimens of the Santa Lucía Formation (see also St. Jean, 1962, p. 187).

Flocculency is extremely common in the stromatoporoids from Spain. In specimens with a flocculent microstructure the tissue is unevenly coloured due to concentration of specks in some places (see Stearn, 1966a, p. 81). Frequently it is accompanied by more or less well developed transverse fibrosity (Pl. 4 fig. 7). At the same time migration of specks into the galleries occurs. Therefore it is not possible to give exact measurements of the thickness of the skeletal elements in flocculent specimens.

In tangential sections the flocculency of the pillars is sometimes conspicuous (Pl. 4 fig. 8). The pillars are broken up into flecks of irregular shape and size,



and the outline of the pillars is completely diffused by the migration of the pigment specks. Scarcely any recrystallization has taken place in this specimen. Only there are many crystal boundaries cutting through the horizontal skeletal elements. This has caused some transverse fibrosity (compare with Sleumer, 1968, figs. 13, 14).

In extreme cases the specimens may become so flocculent that even the gross structure is hardly recognizable, especially at high magnifications.

Transverse fibrosity is very common, particularly in the Portilla Formation. It is always found in flocculent specimens and accompanied by some migration of specks. Actually it is nothing else than oriented flocculency. This orientation is caused by crystals with boundaries more or less perpendicular to the skeletal elements, see Stearn, 1966a, pp. 78, 81, 86; Sleumer, 1968, p. 11, figs. 15, 16).

In specimens with transversely fibrous laminae the microstructure of the pillars is far less distinct. Some pillars also look vaguely transversely fibrous, others have a vague water-jet fibrosity (see Stearn, 1966a, pp. 80, 86), while in still others the fibrosity seems to be parallel to the pillars.

In most cases transverse fibrosity can only be seen in some areas of a thin section but sometimes it is conspicuous in all laminae (Pl. 5 fig. 1) and looks transversely porous rather than fibrous (compare with St. Jean, 1962, Pl. 31).

In a peel from the same specimen (Pl. 5 fig. 2) the interlaminar spaces are filled with one or a few large, clear crystals, sometimes with slip planes. Many of these crystals have penetrated into the tissue. At the same time some small clear crystals have developed within the tissue, obscuring the whole gross structure. This state of preservation is similar to that shown by Sleumer (1968, figs. 19–22).

In the tangential section of the same specimen (Pl. 5 fig. 3) the pillars cut by the section in the interlaminar spaces are isolated and more or less round but the pillars cut by the (slightly oblique) section in the laminae show a more or less radial structure.

In a peel (Pl. 5 fig. 4), however, this radial structure is difficult to detect. Where the pillars are cut in the interlaminar spaces, they have an irregular outline and are bounded by rather large clear crystals. The boundaries of these crystals extend frequently from pillar to pillar but do not enter them. On the borders of the areas where the pillars are cut in the laminae, the pillars have some 'arms' of greyish tissue (due to the specks which tend to form rows perpendicular to the arms). Between these 'arms' irregularly shaped, clear crystals of variable size occur. These crystals with no specks have distinct boundaries with the greyish tissue, whereas within the latter the crystal boundaries are vague. In the central part of the areas where the laminae are cut obliquely, less clear crystals occur; here the pillars can no longer be recognized. These clear crystals, some penetrating from the interlaminar spaces and some formed within the laminae, both by secondary crystallization, as can be seen in the

peel of the vertical section, are the cause of the more or less radial structure. In parts of the laminae where pillars are situated below and above them, no crystals could penetrate the laminae vertically. Therefore in the tangential thin section in the areas (obliquely) cut through the laminae the places where pillars are situated are darker and have less clear spots than the part of the laminae between the pillars, where the laminae moreover are the thinnest due to the rounded corners of the galleries.

A similar specimen (the lectotype of *Actinostroma stellulatum*!) was described by Nicholson (1886–92, p. 141, Pl. XIV fig. 5; see also Stearn, 1966a, p. 87).

In again other specimens alteration is quite different (Pl. 5 fig. 5). The laminae are transversely fibrous and the boundary between tissue and galleries has become vague by migration of specks. Between the pillars small vertical cracks have developed.

In the peel (Pl. 5 fig. 6) the crystal boundaries are conspicuous in the interlaminar spaces and vague within the tissue of the stromatoporoid, especially in the pillars. The laminae are traversed by some crystal boundaries. Crystal boundaries and tissue are independent from each other; the outline of the laminae in particular is irregular due to migration of specks. The specks have a tendency to become arranged vertically, in the laminae as well as in the pillars. In some pillars a vague water-jet structure seems to be present.

In the tangential section the pillars seem to be the centres of crystals (Pl. 5 fig. 7). The pillars are vague, flocculent; sometimes the flocks are arranged more or less radially in the periphery of the pillars.

In the peel of the same section (Pl. 5 fig. 8) the same concentric arrangement of the crystal boundaries is visible. The pillars are, however, not situated in one large crystal, but in an agglomeration of small and large crystals. The boundaries of these crystals do not enter the tissue of the pillars. In some places the specks which have migrated out of the pillars are radially arranged. Between the pillars, in the interlaminar spaces, the crystals are rather large. The laminae are visible as greyish zones in the peel.

This type of more or less concentric crystallization around the pillars occurs in the Portilla Formation as well as in the Santa Lucía Formation.

A form of very strong alteration is common in the Portilla Formation. In the vertical section (Pl. 6 fig. 1) the interlaminar spaces are partly or nearly completely obscured by the extremely thick skeletal elements, especially the pillars. The tissue has become strongly melanospheric. Most of the melanospheres formed vertical dark lines by concentration in or along the pillars. The laminae look transversely fibrous or porous in some parts. At the same time the movement of specks caused a strong migration into the galleries. As a result the skeletal elements have become extremely thick and many galleries have disappeared completely.

In the peel of the same section (Pl. 6 fig. 2) the larger interlaminar spaces are filled with a few rather large clear crystals, the smaller galleries by one large crystal or a few smaller ones.

Many galleries are even reduced to a very small opening with one small, clear crystal. The crystals of the galleries generally do not enter the tissue of the stromatoporoid.

Slip planes are extremely common. Therefore the specks frequently lie in rows along these planes. Even the clear crystals, which remained after the secondary broadening of the tissue, show rows of specks.

*b. alterations in microlaminate (= multilayered) tissue* (Pl. 6 fig. 3 – Pl. 8 fig. 2; Pl. 12 fig. 8)

Even the best preserved specimens are already slightly flocculent. Nevertheless their microstructure is well distinguishable (Pl. 6 fig. 3) (see also Sleumer, 1968, figs. 8, 9). The thick spool-shaped pillars are compact. The laminae are extremely variable in thickness. In some places they are only present as cyst plates, in other places they consist of several compact layers. Between these layers continuous clearer zones are present. In some places vacuoles were formed. Mostly they are situated marginally and randomly but they may also occur more or less in a row in the central zone of the laminae (when the originally marginal vacuoles are covered by another layer). However, they do not form real ordincellulae in the sense of Stearn (1966a, p. 78) though the term has been used by Sleumer (1968, p. 11, explanation fig. 8).

The clear layers in the laminae, in this writer's opinion, certainly were not formed as a result of the joining of a line of cellulae as suggested by Stearn (1966a, p. 84). They are supposed to have been more or less empty spaces between two successive layers of the laminae (see also Sleumer, 1968, p. 11). This idea is supported by the tissue reversal occurring in these layers (see Stearn, 1966a, p. 84) and by the fact that clear layers and rows of vacuoles occur together in one specimen. It must be admitted, however, that in some laminae a row of holes occurs which can as well be called 'ordincellulae' as 'a row of vacuoles'.

Another explanation for the microstructure described above would be that it is tubulate (see Nicholson, 1886–92, p. 37). Continuous clear zones would be found if the tubules are cut more or less longitudinally by the section and the so called vacuoles would be nothing else than the cross sections through the tubules. This theory, however, is unlikely as in many specimens vacuoles are relatively rare compared with continuous clear layers. Moreover stromatoporoids seem to be fundamentally equal in all lateral directions.

In the peel of the same specimen (Pl. 6 fig. 4) (see also Sleumer, 1968, fig. 10) the crystal pattern is random with the largest crystals in the interlaminae spaces, the same as in the example given from a well preserved *Actinostroma*.

Other well preserved specimens are more or less opalescent (Pl. 6 fig. 5). The microstructure of these specimens is well preserved but the boundary between tissue and interlaminae spaces is not sharp in all places (see also Sleumer, 1968, figs. 11, 12). This is due

to the crystal boundaries as can be seen in the peel (Pl. 6 fig. 6). The crystals in the centre of the galleries are very large compared with the marginal crystals which are partly situated in the galleries and partly in the tissue of the stromatoporoid. Some crystals have a few slip planes and within some crystals movement of specks has taken place. This crystal pattern indicates pore-filling processes. It has been found only in a few specimens from the Portilla Formation north of Los Barrios de Luna.

Some degree of flocculency is present in all specimens. The degree to which a specimen is flocculent is different from specimen to specimen and sometimes even within one specimen lighter zones with more flocculency can be distinguished (see Pl. 3 fig. 6, Sleumer, 1968, fig. 17). This means that flocculency is caused at least partly before fossilization by disintegration of the skeletal tissue.

Part of the material has become strongly flocculent (Pl. 6 fig. 7). The tissue is unevenly coloured, transverse fibrosity has developed locally and the boundary between tissue and galleries is diffuse; nevertheless traces of microlamination are still visible.

The crystal pattern can be seen in the thin section but still better in a peel (Pl. 6 fig. 8). The crystals in the interlaminae spaces are large while in the tissue crystal boundaries are irregular and often vague. In some places it looks as if the tissue is breaking up into small crystals. The more or less vertical boundaries of these crystals are the cause of the transverse fibrosity. Some of the large crystals are more or less limited by the boundaries of the galleries but other crystals extend indiscriminately into the tissue. The transition between the speckled and the clear part of the crystals may even be very sharp. On the other hand migration of specks can be observed in many places. This specimen seems to be a typical example of a transition from a random crystal pattern to one that is determined by the gross structure of the stromatoporoid.

Though flocculency occurs in specimens without recrystallization of any importance (see Pl. 4 figs. 7, 8 and Sleumer, 1968, figs. 9, 10) it seems favourably affected by some recrystallization as it makes migration of specks easier. Migration of specks frequently occurs along the slip planes but the specks do not leave the crystals in which they are situated.

Migration of specks moreover is favoured by the development of transverse fibrosity (Pl. 7 fig. 1) (see also Sleumer, 1968, figs. 15, 16). Here movement of specks is mainly perpendicular to the laminae because the crystals are oriented in this direction. This results in a secondary thickening of the tissue and in very vague tissue boundaries. Many pillars also seem to be transversely fibrous, but as a whole the microstructure of the pillars is less distinct. In spite of the migration of specks, traces of microlamination are still visible in the laminae.

In the peel (Pl. 7 fig. 2) the most conspicuous feature is formed by the more or less vertical slip planes found in many crystals. This feature can best be seen within the tissue of the stromatoporoid. Here most

specks are aligned along the slip planes. Apart from the slip planes it can be observed that many crystal boundaries tend to be perpendicular to the boundary of the tissue. In some places they may even form a radial structure around the centre of a gallery.

Some specimens are altered in such a way that at first sight they look compact (Pl. 7 fig. 3). On closer examination a fine striation can be recognized. This striation has different directions in different places. Besides, the tissue is not uniformly coloured but tends to have a yellowish tint in many places. Traces of the original microstructure are very scarce and vague.

In the peel (Pl. 7 fig. 4) it can be observed that nearly all crystals have slip planes. Sometimes these planes seem to be curved! The specks are aligned along these planes. Contrary to the specimen figured in Pl. 7 fig. 2 the planes are randomly and not more or less vertically oriented. The crystal pattern is also rather random. Therefore no real transverse fibrosity is seen in the thin section.

In some specimens a very peculiar form of alteration occurs (Pl. 7 fig. 5) (see also Sleumer, 1968, fig. 22). The tissue has become melanospheric, moreover the specks are mainly concentrated along the boundaries of the tissue with the galleries. In some laminae straight, distinct microlaminae have remained in the centre of the laminae. By the movement of the specks toward the galleries, the latter have become relatively small, some of them even seem to be completely filled.

This combination of melanospheres and microlaminae had earlier been called 'pseudocellular' by the present author (Sleumer, 1968, pp. 11, 12). However, at that time he assumed that this microstructure was caused by the formation of clear crystals in the tissue which is by no means the case in all specimens with such a microstructure.

In a peel of the same specimen (Pl. 7 fig. 6) many laminae and pillars have a central zone with no specks or less specks which makes recognition of the gross structure of the stromatoporoid difficult. The concentration of specks around the interlaminae spaces is obvious, even the melanospheres can be recognized by differences in the concentration of specks. The boundaries between the crystals are only well developed in that part of the tissue where specks are absent or scarce, as in the galleries and the clear parts in the laminae and pillars. The crystals are, however, not limited to these clear areas. That is to say, part of a crystal may be clear while another part is full of specks. In some galleries the crystal pattern is similar to that of Pl. 6 fig. 6 with small peripheral crystals and larger ones in the centre. Some crystals have slip planes. In the areas where infiltration of specks into the galleries occurred and slip planes are present, the specks are aligned along these planes. In a similarly preserved specimen (Pl. 7 fig. 7) the gross structure is still less distinguishable because most galleries have been filled with specks. Where the interlaminae spaces are still visible as clear round openings, the pigment has concentrated around them. The central part of the laminae remains as lighter (yellowish) straight zones; some

pillars also are lighter in the central part. Contrary to the specimen discussed before (Pl. 7 figs. 5, 6), in this specimen the pigment has not been concentrated in distinct melanospheres.

The peel of this specimen (Pl. 7 fig. 8) is similar to the former one. It seems, however, that a division into rather undifferentiated speckled calcite and well defined clear crystals of calcite, is taking place in many areas within the tissue.

In a still more altered specimen (Pl. 8 fig. 1) (see also Sleumer, 1968, figs. 19–21) the original gross structure is largely obscured. The tissue has become pseudocellular; yellowish remains of the microlaminae dominate the whole structure. By migration of specks the pigment is concentrated around the galleries in some places, in other places the specks seem to have filled the galleries completely. On the other hand many interlaminae spaces are filled with large clear crystals.

In a peel of the same specimen (Pl. 8 fig. 2) it can be seen that in this specimen recrystallization is nearly complete. The interlaminae spaces are filled with large clear crystals limited to this area. In the tissue many small clear crystals occur, mostly completely surrounded by crystal boundaries. In the speckled areas the density of the specks is very variable and crystal boundaries are vague or absent (compare with Pl. 5 fig. 2).

From the last three specimens the conclusion may be drawn that this type of alteration was not caused by recrystallization as supposed by Sleumer (1968). The recrystallization is only a secondary feature accentuating the pseudocellular characteristics of the tissue. Typically this type of alteration has only been found in some layers of the Portilla Formation in a limited area north of Los Barrios de Luna.

Finally a specimen of *Stromatoporella?* sp. 3 is shown on Pl. 12 fig. 8. Though the specimen is not well preserved, distinct traces of microlamination are recognizable in the laminae.

#### c. alterations in ordinicellular tissue (Pl. 8 fig. 3 – Pl. 10 fig. 4)

Specimens with a well preserved ordinicellular microstructure are rare. Even then most of these specimens show a distinct microstructure only in limited areas in the thin sections (Pl. 8 fig. 3) (compare with Stearn, 1966a, Pl. 15 fig. 8 and St. Jean, 1967, Pl. 6 figs. 3–6). In the laminae one or more (up to five) rows (actually they are layers!) of cellulae are visible. The cellulae have a diameter of ca. 0.02 mm. This diameter is quite constant not only within a lamina but also within a specimen and even within a species. So it seems to be independent of the thickness and the spacing of the laminae.

The microstructure of the pillars in general is not easy to recognize. Some pillars, however, show vertical rows of cellulae and therefore their microstructure might be called reticulate. In the ring pillars the rows of cellulae bend up with the laminae (Pl. 8 fig. 4). The cyst plates are compact. In a peel the crystal

pattern is similar to that in Pl. 4 fig. 1 and Pl. 6 fig. 4 though it is disturbed in some places by silicification and filling of the galleries with mud.

It is evident that this microstructure is completely different from the microlaminate one. The vacuoles in the latter are rather randomly placed and larger than the cellulae, while the clear layers are continuous. Unfortunately in altered specimens the differences of microstructure are frequently no longer visible. Nevertheless it still seems to be possible to distinguish between specimens of both groups because the thickness within one lamina is more variable in microlaminate specimens and ring pillars are frequently far more conspicuous in ordinicellular specimens.

Another specimen (Pl. 8 fig. 5) which is partly well preserved has a quite different gross structure with frequently superposed pillars. The crystal pattern in this specimen (Pl. 8 fig. 6) is not random. The galleries are filled with comparatively large crystals which mostly do not enter the tissue. The latter and the margins of the galleries are made up of small crystals. Crystal boundaries are rather vague within the tissue.

The ordinicellulae are easily destroyed by alteration. A typical example is given by the next specimen (Pl. 8 fig. 7). In parts of some laminae the ordinicellulae are still recognizable. Other laminae have become completely diffuse by migration of specks. This migration has been strongly favoured by the development of randomly oriented, frequently curved slip planes as can be seen in a peel (Pl. 8 fig. 8) (compare with Pl. 7 fig. 4). The crystal pattern is rather random in this specimen. Only in the galleries are the crystal boundaries well developed.

Other specimens have some transverse fibrosity (Pl. 9 fig. 1). No traces of the original ordinicellular microstructure can be recognized any more. In the peel (Pl. 9 fig. 2) the crystal pattern is random as in the previous specimen but crystal boundaries have penetrated vertically in the laminae thus causing transverse fibrosity in the latter. Some galleries have comparatively large crystals in the centre. The orientation of the slip planes is random, some crystals even have two sets of slip planes. By migration in these planes the repartition of the specks in the tissue has become more or less equal. Therefore the laminae now look compact rather than ordinicellular.

Some specimens have become flocculent (Pl. 9 fig. 3). The original microstructure of the laminae is not completely destroyed; in some places it looks tripartite at first sight, under low magnification.

The crystal pattern (Pl. 9 fig. 4) is again random although as in the previous specimen some galleries have a large central crystal. Slip planes are scarcely developed in this specimen. As migration of specks nevertheless has taken place, it is obvious that slip planes are not the only cause of the migration of specks (see also Pl. 5 figs. 3–8, Pl. 7 figs. 5–8).

Some specimens are so altered it is no longer possible to give a definite determination (Pl. 9 fig. 5). Using a low magnification it seems, however, to be a speci-

men of *Stromatoporella? selwyni*. The skeletal elements are thickened secondarily by alteration and in some places they are so thick that they have filled the galleries entirely. The thick laminae look transversely fibrous in many places.

In the peel (Pl. 9 fig. 6) it can also be seen that some galleries are completely filled with specks. Other galleries have remained fairly large. Some of the galleries are not filled by clear calcite but by micritic and partly dolomitised material. These galleries have retained their original shape. Slip planes are strongly developed, they are randomly placed, the specks have moved along these planes. The crystal pattern is random in the interlaminae spaces and vague within the tissue.

Contrary to the specimens mentioned above the following specimen (Pl. 9 fig. 7) has been crystallized in a different manner. Many galleries, especially the larger ones do not have a random crystal pattern but large central crystals. This pattern does not look like a recrystallization feature, it seems to be due to pore filling processes. The tissue of the stromatoporoid looks compact although it is flocculent in many places.

In the peel (Pl. 9 fig. 8) it can be seen that some galleries are filled with one (or more) large central crystal. Other galleries seem to have a normal random crystal pattern. In the tissue some migration of specks has occurred, causing flocculency and destroying the cellulae. In some crystals alignment of specks along randomly oriented slip planes has occurred but migration of specks is very limited, so only the microstructure has been destroyed and not the gross structure.

Some specimens have very distinct latilaminae (Pl. 10 fig. 1). Each latilamina consists of a brownish lower zone with flocculent tissue and a black upper zone with tissue that looks compact due to concentration of specks in the centre of the laminae. Most pillars and cyst plates, however, are brownish and vague as in the lower zones.

The cause of this phenomenon can be explained by means of peels (Pl. 10 fig. 2). In the brownish flocculent zones the crystal pattern is coarse in the interlaminae spaces and fine within the tissue. Sometimes one large crystal is found in the centre of a gallery. In the black zone the laminae show a line in the centre which cuts more or less straight through the existing crystal pattern. As can be seen in thin sections, this line follows the laminae only partly when they turn up to form ring pillars, then it crosses the ring pillars where a cyst plate is present in them. Slip planes are quite insignificant. The occurrence of similar black lines in the laminae was already described in Pl. 4 figs. 5, 6. A possible explanation for the black lines is that they are minute stylolites in which the pigment has been concentrated when the calcite was dissolved.

Other specimens, on the contrary, show stylolite-like crystal boundaries just in the centre of most galleries and parallel to the laminae (Pl. 10 fig. 3). Another set of shorter cracks has developed perpendicular to the laminae. Therefore in tangential section a pattern

is seen similar to that in Pl. 5 figs. 7, 8. The microstructure of the tissue has been destroyed by the slip planes.

In the peel (Pl. 10 fig. 4) the gross structure of the stromatoporoid is difficult to recognize in many places because the specks have spread nearly over the whole area due to the slip planes. In the crystal pattern the strongly developed horizontal boundaries can be recognized in the galleries. Further vertical crystal boundaries are abundant. A tendency to such a crystal pattern is found in many specimens (see Pl. 9 figs. 5, 6) but seldom it is so strongly developed as in this specimen.

#### d. alterations in cellular tissue

(Pl. 10 fig. 5 – Pl. 12 fig. 7)

The present writer is in complete agreement with Nicholson, Lecompte, Stearn and others that the genus *Stromatopora* is characterized by a truly cellular microstructure. Unfortunately, as with other microstructures, only a few specimens are preserved well enough to show the tissue more or less in its original state, so that the cellulae are still distinguishable.

In one of the few (partly) well preserved specimens (Pl. 10 fig. 5) the cellulae are randomly arranged but they may also be situated in horizontal or vertical rows (compare with Stearn, 1966a, Pl. 18 fig. 1). In some areas they even form a rather regular reticulate pattern with horizontal as well as vertical arrangement. Therefore this author believes that there is no fundamental difference between cellular and reticulate microstructure. Even the ordinicellular microstructure does not differ essentially from the cellular one except for the fact that in the first the cellulae always are placed in regular rows parallel to the laminae, but in the pillars also a vertical arrangement may occur! The difference in gross structure is obvious, however, when the ordinicellular species e.g. *Stromatoporella? selwyni* and the cellular ones e.g. *Stromatopora concentrica* and *Stromatopora huepschi?* are compared. In the peel from specimen 570E in some parts even the cellulae are still recognizable by differences in the density of specks (Pl. 10 fig. 6). The crystal pattern is random. Crystal boundaries are well developed in the interlaminar spaces but vague within the tissue. Slip planes are absent in this part of the peel; in other parts where they are abundant, the microstructure is no longer recognizable.

The regularity of arrangement of the cellulae in the genus *Stromatopora* seems to depend mainly on the form of the skeletal elements (and the orientation of the section!). A horizontal arrangement is mostly found in the horizontal skeletal elements and a vertical arrangement in the vertical skeletal elements. In the obliquely oriented skeletal elements and also in a tangential section, the cellulae are randomly placed. Therefore the specimens from the Portilla Formation, which mostly have dominant horizontal skeletal elements, in general show a random to horizontal arrangement of cellulae. Specimens from the Santa Lucía

Formation (and the La Vid Formation), many of which have dominant vertical skeletal elements, frequently show a vertical arrangement of cellulae as well as random and horizontal arrangements.

A specimen from the Portilla Formation is shown in the next figure (Pl. 10 fig. 7). It is less well preserved than the previous specimen but nevertheless the horizontal arrangement of the cellulae is obvious (compare with Stearn, 1966a, Pl. 18 fig. 3).

In a peel of the same specimen (Pl. 10 fig. 8) the crystal pattern is similar to that shown in Pl. 6 fig. 6, Pl. 8 fig. 6 and Pl. 9 fig. 8 with large crystals in the centre of most galleries and small ones on the periphery and in the tissue. Within the tissue crystal boundaries are rather vague. Slip planes are quite common in this specimen. Nevertheless migration of specks is very limited. The boundaries of the galleries are sharp in most places and even the cellulae are discernible in some places by the irregular distribution of the specks in the tissue.

Another rather well preserved specimen (Pl. 11 fig. 1) has a different gross structure. Zones with continuous compact microlaminae alternate with zones of randomly built skeletal elements. The cellulae also are rather randomly placed, they show some horizontal arrangement only in a few places. In the peel the crystal pattern is similar to the previous specimen, though less conspicuous. Slip planes are very scarce.

The following specimen (Pl. 11 fig. 2) has a deviating gross structure and microstructure compared with other specimens of the genus *Stromatopora*. The horizontal elements are formed by straight compact microlaminae, with a very coarse cellular tissue on both sides, and by curved cyst plates when the microlaminae are farther apart. In some places it is difficult to make a distinction between coarse cellulae and small galleries.

The vertical elements are formed by rather straight, mostly superposed pillars. They seem to have a finer microtissue but this is difficult to confirm as the specimen is slightly altered.

The specimens from the Lebanza Limestone are not very well preserved. Nevertheless in some specimens the cellular microstructure is still recognizable in some places (Pl. 11 fig. 3). The cellulae in the pillars tend to be vertically arranged.

Many specimens from the Portilla Formation and the Santa Lucía Formation have become melanospheric in the sense of Stearn (1966a, pp. 81–83) as can be seen on Pl. 11 fig. 4. In some places the microstructure shows intermediate stages between cellular and melanospheric tissue as described by Stearn (1966a, p. 82, text-fig. 2).

The crystal pattern of this specimen (Pl. 11 fig. 5) shows large crystals with slip planes in the galleries; the tissue tends to be broken up into many small crystals with a varying amount of specks.

A specimen with conspicuous melanospheres is shown in the next figure (Pl. 11 fig. 6) (see also Sleumer, 1968, fig. 18; compare with Stearn, 1966a, Pl. 14 fig. 7). The gross structure is very regular for a *Stromato-*

*pore* and the cellulae also are placed in regular rows. This is still visible in the section by the quite regularly placed melanospheres. The latter tend to lie in horizontal as well as in vertical rows in some places. Continuous microlaminae, occurring at some levels in the section, make confusion with altered specimens of *Stromatoporella? granulata?* very easy.

The crystal pattern of this specimen (Pl. 11 fig. 7) shows rather large crystals in the galleries. Within the tissue crystal boundaries are only distinct in the clear areas. The specks are irregularly distributed due to concentration of specks. Slip planes are very rare.

In the same way as in specimens of other genera, the microstructure is easily destroyed by migration and alignment of specks along slip planes. A specimen with partly destroyed cellulae is shown in Pl. 11 fig. 8 (compare with Pl. 8 fig. 7).

In other specimens the microstructure is completely destroyed by the slip planes but migration of specks into the galleries is rather limited (Pl. 12 fig. 1) (compare with Pl. 7 fig. 3).

In some specimens, however, considerable migration of specks has taken place along the slip planes (Pl. 12 fig. 2). The gross structure is therefore rather vague. The state of preservation is similar to that of Pl. 6 fig. 1 though less extreme.

In the peel (Pl. 12 fig. 3) it can be seen that migration of specks along slip planes has only partly filled the galleries. Contrary to the specimen figured in Pl. 6 fig. 2 the crystal pattern is normal, that is to say crystal boundaries are random and moreover vague within the tissue while crystals are largest in the galleries.

In the following specimen (Pl. 12 fig. 4) the latilaminae are formed by alternating zones where the galleries are filled with micrite and zones where the galleries are filled with clear calcite. The microstructure looks compact in this specimen at low magnification due to destruction of the cellulae by minute slip planes. Migration of specks into the galleries was prevented by the micrite, but where the galleries are filled with clear calcite migration is also prevented in most places by very thin coatings of dark material (iron oxide?) along the tissue boundaries.

Obviously secondary crystal boundaries have been formed in some specimens (Pl. 12 fig. 5). The pillars are traversed by distinct horizontal cracks. In the specimens 456C (Pl. 5 figs. 5–8) and 521C (Pl. 10 figs. 3, 4) the cracks disappear when the thin section is wetted (Pl. 12 fig. 6). Otherwise the crystal pattern is normal, with the largest crystals in the galleries and vague crystal boundaries within the tissue. By migration of specks along slip planes the gross structure of the specimen is rather vague (compare with Pl. 10 figs. 3, 4).

A specimen with strong recrystallization is shown in the next figure (Pl. 12 fig. 7). The galleries are each filled with one large crystal, sometimes accompanied by small ones on the margins. The tissue of the stromatoporoid, however, shows only vague crystal boundaries. Slip planes are common, both in the tissue and in the galleries. The microstructure has not com-

pletely disappeared as in the previous specimen. In some places vague melanospheres can still be recognized (compare with Pl. 9 fig. 7).

#### ALTERATIONS DUE TO CHEMICAL CHANGES AND INFILTRATION OF MUD

Apart from changes in microstructure and crystal pattern caused by alteration of the calcified coenosteum, important alterations of the microstructure are brought about by impregnation with material other than calcite. Three types of alterations in this sense can be distinguished:

- A. silicification
- B. dolomitisation
- C. impregnation with iron oxide or mud

A. Especially specimens from the Santa Lucía Formation are frequently affected by silicification. The chert in most cases is concentrated only in the fossils and not in the sediment. Therefore many stromatoporoids, tabulate and rugose corals and brachiopods from the Santa Lucía Formation are partly or entirely silicified.

In the Portilla Formation fossils may be also silicified in some layers.

Silicification can affect the fossils in different ways.

In some specimens only isolated patches of chert are found in the skeleton. In other specimens whole zones are silicified. Generally these zones lie along the latilaminae (Pl. 13 fig. 1). They also are present around cavities or they are parallel to the surface of the coenosteum, even if it has been eroded before sedimentation. The transition between calcified and silicified areas may be very sharp in places where it is accompanied by stylolite-like features, in other places it is gradual. In most places ghost structures of the skeleton remain in the silicified areas. It is only when silicification is very strong that no structures remain visible.

An exceptional case of silicification is shown in the next figure (Pl. 13 fig. 2). In what probably has been a cavity, a small geode was formed. In the silicified tissue of the stromatoporoid around this geode, not only the gross structure but even the microstructure has been perfectly preserved in some places (Pl. 13 fig. 3). Also in the not silicified areas the microstructure is well preserved.

As silicification seems to be related with structures of the coenosteum like latilaminae, holes and the surface of the coenosteum before burial in the sediment, the conclusion can be drawn that silicification took place before the coenosteum was completely calcified and the surrounding sediment completely lithified.

As in most altered specimens the same type of alteration also occurs in the silicified areas (if still recognizable!), it seems that at least some types of alteration took place before silicification and thus in a very early stage of fossilization.

In another specimen (Pl. 13 fig. 4) several zones, in which the extent of silicification differs, can be recognized. In the silicified areas the circumferences of oxidized crystals of ferrodolomite are visible. Toward the periphery silicification is less intensive. In the dark area in the centre of the figure only the skeletal elements have been affected by silicification. Toward the centre of silicification the not silicified centres of the galleries become smaller and smaller until also the galleries are completely silicified. This phenomenon can be seen very well in a peel (Pl. 13 fig. 5) since the silicified areas are not etched by the acid.

In Pl. 13 fig. 5 the area in the upper part shows the not silicified tissue. The microstructure is altered. By migration of specks the tissue looks very thick and transversely fibrous. In the part of the silicified area where gross structure and microstructure are still recognizable the microstructure of the laminae is exactly the same. This means that the silicification (at least in this case) took place after alteration of the calcified coenosteum.

In many specimens, a form of silicification different to the type mentioned above occurs (see also St Jean, 1962, p. 197). In these cases calcite crystal after calcite crystal was replaced by not crystallized chert. Sometimes (Pl. 13 fig. 6) silicification occurred only or preponderantly in the interlaminar spaces which become rather transparent due to the lack of crystal boundaries. The not silicified galleries are darker and vague. Silicification has not prevented the alteration of the tissue for it is vague and flocculent everywhere.

In the peel of the same section (Pl. 13 fig. 7) it can be observed that the galleries which are silicified have a very irregular outline, according to the crystal boundaries of the not silicified calcite (compare with St. Jean, 1962, Pl. 32 figs. 3, 4).

In other specimens, on the contrary, in most places the skeleton is silicified and not the interlaminar spaces. It is also possible that, within one coenosteum, silicification occurs in some places predominantly in the skeleton, while in other places it occurs only in the galleries (Pl. 13 fig. 8, Pl. 14 figs. 1, 2). As can be seen, especially in the peels, silicification always seems to depend on the pre-existing crystal pattern in the calcite (compare with St. Jean, 1962, Pl. 32 fig. 2).

In a few cases silicification does not occur as amorphous chert but as more or less idiomorphic quartz crystals (Pl. 14 fig. 3). The crystals are formed independently of the skeletal elements of the stromatoporoid. In the peel of the same specimen (Pl. 14 fig. 4) small inclusions can be seen in the quartz crystals.

It is not clear whether the crystals originally were amorphous silica, crystallized at a later stage, or that silicification took place at once in the form of crystals.

Finally in many specimens from the Portilla Formation real idiomorphic quartz prisms occur. These crystals mostly occur along cracks in the coenosteum of the stromatoporoid, but they may also occur quite randomly (Pl. 14 fig. 5). It seems that these quartz crystals were formed very late in the process of fossilization, so they have nothing to do with the other forms of silicification.

B. Slight dolomitisation is common in both the Portilla Formation and the Santa Lucia Formation. Therefore crystals of ferrodolomite are common in the sediment as well as in the fossils.

In most cases the crystals are scattered more or less randomly throughout the coenosteum (Pl. 14 fig. 6). The crystals of ferrodolomite are nearly always more or less oxidized and therefore brownish and easy to recognize.

As can be seen in Pl. 13 figs. 2, 4 and as has also been observed in other specimens, the silicified areas enclose some dolomite crystals. This means that this kind of dolomite crystals is formed before silicification.

Apart from this type of dolomitisation, the Santa Lucia limestones in many places are irregularly affected by tectonical dolomite. No organic structures can be recognized any longer in this dolomite.

C. Impregnation with iron oxide (hematite) is common in all ferruginous layers. In the upper part of the Limestone member in the Caldas Formation in particular there are some highly ferruginous layers with stromatoporoids. In most cases iron oxide together with mud only fills up the galleries. In one case, however, even the cellulae were penetrated (Pl. 14 fig. 7).

Micrite may also fill up the galleries. This usually occurs only in the outer zone of the coenosteum. When mud occurs only locally, repair tissue overgrew laterally the part of the coenosteum which has died off. Only specimens of the genus *Stromatopora* seem to be less sensitive to mud because in some specimens the latilaminae are formed by alternating zones with and without mud in the galleries without really interrupting the growth.

In one case even some cellulae in the last skeletal elements formed by a buried-alive stromatoporoid are filled with mud (Pl. 14 fig. 8).



## CHAPTER III

## SYSTEMATIC DESCRIPTIONS

*The limitations of species and even of genera become increasingly difficult as more and more sections are examined, and numerous intermediate forms occur of which the specific reference is doubtful. It would be easy to erect a great many more species and varieties than has been attempted. (...) One conclusion is fairly certain – stromatoporoids of a given species vary greatly with the depth and the physical and chemical conditions of the water.*

Parks, 1936, p. 7

## GENERAL REMARKS

The material described in this paper was collected by the author in strata of Devonian age (middle Siegenian – lower Frasnian). Most of the material was broken out of the sediment. Loose specimens were only taken when in situ material was too scarce and if there could be no contamination with material from other formations.

Mamelons can seldom be seen on the surface of the handspecimens of stromatoporoids, due to erosion of the coenosteum before sedimentation and formation of stylolites during diagenesis.

Branching stromatoporoids are extremely scarce in the Devonian of the Cantabrian Mountains. Although special attention was paid to them, only a few small specimens could be found, most of them only visible in the thin sections. *Thamnopora* sp., on the other hand, is very common, especially in some layers of the Portilla Formation which are nearly completely built up of broken coralla of this genus.

For the description of the gross structures the terminology of Galloway & St. Jean (1957) has been more or less followed. The terms 'dissepiment', 'cyst' and 'cyst plate' are considered to be synonyms. Generally the term 'cyst plate' is used in this publication. The cyst plates in the astrorhizae are called tabulae.

In the first stage of the investigation the material was divided into species, later the different species were united in several genera. In order to avoid still further confusion in the taxonomy of stromatoporoids, no families have been distinguished in the present stage of investigation.

It soon became clear that the species have a wide range of variation in their gross structure. Even specimens belonging to one species and originating from one layer in one outcrop already show a considerable variability. That specimens with seemingly very different gross structures nevertheless belong to one species, becomes evident from the many specimens which are intermediate and from specimens in which two quite different types of gross structure alternate in the latilaminae. As no evolutionary trends could be detected within one species, these variations seem to be the result of differences in individual environmental factors (see also Lecompte, 1951, pp. 70, 159).

Some specimens could not be determined properly as they probably do not belong to the common species, and on the other hand the material is insufficient for establishing the variability of the species. From these specimens only the genus was determined. The main problem in determining the material is thus to distinguish ecological variations from true species characters. Unfortunately the problem is complicated in many cases by secondary alterations of the microstructure, as has been explained in the previous chapter.

After the range of variation of a species (that is to say of the Spanish specimens) was determined, comparable species were looked for in the literature. In nearly all cases the Spanish specimens seem to belong to species described by Nicholson and earlier authors.

As a consequence of the wide range of variation within a single species, it became necessary to give a revised definition of the genera they belong to, as some features, up to now believed to be characters of genera, seem to fall within the variability of a species. As a result the diagnoses of the species and genera given in this paper are mainly based on the Spanish material. The primary microstructure remains the most important character of the genera (see St. Jean, 1967, p. 419).

It is evident that at this stage of the investigation it is extremely difficult to compare one's own material with that described by others (according to Prof. Dr. E. Flügel, personal communication, more than half of the descriptions of new species are based on only one coenosteum).

In order to give an impression of the range of variation of the species with sufficient material, the number of laminae and pillars in 2 mm was counted, but only if the laminae or pillars are continuous enough to acquire exact numbers. In cases, where the pillars are not cut exactly longitudinally, the lacking pillars in one spot were interpolated. Of course this is only possible when the pillars are superposed or continuous. Each measurement was started with a lamina or a pillar and for each species 10 specimens were measured with 10 measurements in each specimen. For each specimen the maximum and minimum values were determined first to indicate the total range of variation within one coenosteum. The other measurements are random, if possible they are made in a series from bottom to top in the coenosteum. This implies that in the diagrams stress is laid on the extreme values.

No measurements were made in the part of the section where astrorhizae are distinguishable. The values for the spacing of laminae are very high when latilaminae are present in which the laminae are very close together. In this respect it has to be remembered that the minimal height of the galleries is zero where the laminae are dichotomous!

Thin sections, taken for measurements, are always as



correctly oriented as possible. The specimens from which they were taken are representative for the range of variation, not for the most occurring values.

When the number of laminae (or pillars) in 2 mm is measured in the way described above, especially with lower values, the inexactitude is rather great. If, for example, there were just 3 laminae in 2 mm, in 5 mm there would be only 6; but if 4 laminae would just not fit in 2 mm, in 5 mm there would be 8!

Therefore comparison with measurements of, for example, the number of laminae in 1 mm or in 5 mm is not completely correct, but taking into account the variability of most species, the error is not too significant.

The measurements would be more exact if instead of measuring the number of laminae in 2 mm, the distance between for example 5 or 10 laminae was measured, but it would be even more difficult to compare these measurements with the other ones.

The photographs for this and the first chapter were taken by putting the thin sections at once in the enlarger. Therefore they are seen as negatives.

#### ORDER STROMATOPOROIDEA Nicholson & Murie, 1878

Section Stromatoporoidea Nicholson & Murie, 1878, Linn. Soc. London, Zool. Jour., vol. 14, p. 241.

Order Stromatoporoidea: Nicholson, 1886-92, p. 73; Lecompte, 1956, p. F 127; Galloway & St. Jean, 1957, p. 86; Galloway, 1957, p. 413; Flügel, 1959, p. 223; Birkhead, 1967, p. 35.

#### Diagnosis

Marine polypoid Hydrozoa with a calcareous coenosteum secreted as a basal skeleton.

The coenosteum is laminar, massive, globular, conical, ramose or dendroid; largely depending on environmental conditions. The substratum may be formed by other organisms or mud. Generally the coenosteum has latilaminae and more or less pronounced mamelons. A typical feature of stromatoporoids, but not present in all specimens, are the astrorhizae, tabulated canals, usually branching star-like from the centres of the mamelons.

The coenosteum is composed of upwardly curved cyst plates, cyst plates and pillars, pillars with cyst plates and laminae or laminae and pillars. Pillars are confined to one interlaminar space, superposed or continuous. Laminae are irregularly undulating, straight and well differentiated from pillars or fused with pillars.

The microstructure of the tissue is compact, microlaminar, ordincellular or cellular. Most specimens, however, have a secondary altered microstructure.

#### Discussion of the order

Though Nicholson (1886a, p. 227), Parks (1936, p. 7), Lecompte (1951, p. 9) and many other authors recognized that stromatoporoid species can be very variable, they did not accept the consequences of this by trying to determine the range of variation of the

species they described. One of the few exceptions in this matter is Fagerstrom (1962, p. 425), who stated that in *Anostylostroma ponderosum* the thickness of the laminae varies from 0.04-0.15 mm, the spacing of the laminae varies from 4-15 in 2 mm, and the diameter of the pillars varies from 0.05-0.20 mm, apart from a considerable variation in the form of the coenosteum.

Most features of the coenosteum such as the form and size and the presence or absence of latilaminae, astrorhizae and mamelons are highly influenced by ecological factors, so they have hardly any taxonomical value.

The latilaminae are caused by seasonal influences. They are characterized by intercalations of sediment, differences in colour, interruptions in growth with or without repair tissue, alternating zones of coarse and fine gross structure and/or alternating zones of thin and thickened tissue. Specimens belonging to one species can have latilaminae which are formed either by one or by a combination of these types. It seems that, within the range of some species, the specimens with the most regular gross structure have the highest but least distinct latilaminae.

The function of the astrorhizae is not yet clear. They are not found (or are at least not distinguishable) in all specimens of one species. The astrorhizae are normally associated with the mamelons, but not all astrorhizae are found in mamelons and not all mamelons seem to have astrorhizae. The astrorhizae may have some taxonomical value as is believed by Bogoyavlenskaya (1968).

The mamelons are caused by relatively faster growth, with higher interlaminar spaces, in some parts of the coenosteum. After some time the mamelons generally become smoother and disappear again (sometimes they are even cut off by erosion) while in other places new mamelons are formed. The mamelons are also an ecological feature. Some specimens are completely smooth, while others of the same species, have extremely marked mamelons.

Dendroid forms can be morphologically derived from massive or laminar forms as specimens with extraordinarily strongly developed mamelons. The tissue between the mamelons is lacking and the laminae join each other on the sides of the mamelons. Therefore this writer strongly believes that nearly all genera defined as dendroid are superfluous. Several authors report intermediate forms between dendroid and massive specimens, so the dendroid forms may even fall within the variability of a species.

The size of the coenosteum largely depends on the time the soft parts of the colony remained alive before they were buried by sediment, overgrown by other organisms, destroyed by wave action or the whole coenosteum was turned upside down.

On the other hand the features of the coenosteum, described above, must have some taxonomic significance, because it seems probable that the species must have had some preference and some special adaptation to certain ecological conditions.

*Syringopora* sp. does not occur in all specimens of a species, but apparently is only intergrown with coenostea of certain species of stromatoporoids.

Concerning the gross structure, the range of variation of a species is wide but normally remains within certain limits both regarding the spacing of skeletal elements and the form of these elements.

The soft parts of the colony must have lived in and on the highest cavities of the skeleton, above the last formed lamina or cyst plate. Growing upwards and spreading laterally the organisms formed new layers below them from time to time, either more or less regular and thickened ones (laminae) or curved and thin ones (cyst plates). That the soft parts cannot have lived between the laminae becomes evident in specimens with continuous compact laminae.

As the soft parts lived on the skeleton, the gross structure of the latter was only of minor importance for them. It only served as a support for the colony. This explains too why the skeleton can be completely irregular (repair tissue) to completely regular (straight, continuous laminae and pillars) within one coenosteam. Whether laminae or cyst plates were formed depends on both the preference of the species and the circumstances at the time they were formed. In some specimens (see *A. papillosum*) intermediate forms between cyst plates and laminae occur. In other specimens (see *A. verrucosum*?) sometimes only cyst plates were formed during some period (not latilaminae!), then a continuous lamina was formed, then again cyst plates, etc. In again other specimens (see *A. stellatum*) only continuous laminae occur (except in the repair tissue!).

In other groups (see *Stromatoporella*? and *Stromatopora*) the thickening of the laminae is very variable. In some places the laminae are extremely thickened, in other places the laminae are only as thick as cyst plates. Cyst plates also occur as local intermediate stages between two laminae.

Thus a considerable interchange between laminae and cyst plates is possible. The astrorhizae also have cyst plates (then generally called tabulae). Actually the cyst plates and laminae of the stromatoporoids have the same morphological function as the tabulae of the corals.

The vertical skeletal elements are formed by the inclined sides of the cyst plates, by upturns of the laminae (sometimes as ring pillars) and by pillars. The normal pillars are randomly placed, superposed or continuous. In some specimens (see genera *Actinostroma* and *Stromatopora*) a differentiation in thick and thin pillars is present. These features too are partly dependent of the species and partly caused by the conditions of growth. The extent of superposition of pillars in particular is variable, frequently even within one coenosteam.

In extreme situations only the irregular and generally compact repair tissue was formed.

The spacing of laminae and pillars probably depends, apart from the species, also from the amount of

available food. In this way it is understandable why there is such a variation not only from specimen to specimen in one species but sometimes within one coenosteam.

Summarizing: the material (calcite?) of the skeleton could be arranged in different ways by the soft parts of the organism, depending on the particular ecological conditions at the moment the skeleton was formed. This results in different forms of the coenosteam and in various types of gross structures for specimens belonging to one species. These variations of form and gross structure do not only occur in specimens lying side by side in one layer. Even within one coenosteam alternating variations of the gross structure (latilaminae) may occur as an adaption to the cyclical changes (seasons?) of the environment.

Due to the fact that up to now most authors have paid insufficient attention to the variation within the species they describe, many 'new species' have been erected, which in the opinion of this author are based on insignificant individual differences in the gross structure. Some genera have even been proposed on the grounds of certain variations in the gross structure within one species, but as these variations can be shown to occur in all gradations with other variations of the same species, it has never been possible to indicate the limits of these 'genera'. Some examples are given later in this chapter.

The (original) microstructure on the other hand seems to be independent of ecological factors. Consequently the (original) microstructure should be the main character for the classification of the Stromatoporoidea. Unfortunately, however, the microstructure is easily affected by secondary alterations as described in chapter II and so has contributed still further to the confusion in the classification of the Stromatoporoidea. Dendroid forms in particular are nearly always affected by alteration and weathering for they have a far larger surface compared with massive forms. The genus name *Stachyodes* in general has been used for the most altered dendroid specimens in which even the gross structure is nearly unrecognizable. Some strongly altered specimens described in this genus, in the collection of Prof. Dr. E. Flügel, are overgrown by far less altered specimens of the same species. This means that alteration took place already before sedimentation. Most of these specimens seem to have had a gross structure and microstructure like that of *Stromatopora*. Other dubious genera that seem to be based on strongly altered type species are *Syringostroma* and *Taleastroma*.

*Hermatostroma schlueteri* is characterized by peripheral membranes. But the latter also occur in *Idiostroma roemeri*, from the same outcrop (see Stearn, 1966a, pp. 105, 106, Pl. 17 figs. 3-5) and have been described, among others, by Lecompte (1952, Pl. XLV fig. 2, Pl. XLVI fig. 1, Pl. XLIX figs. 1, 2) from specimens with a gross structure quite similar to that of specimens described as *Stromatopora* (see Stearn, 1966a, pp. 106, 109). Could it not be possible that these specimens show migration of specks in a way

similar to that of *Clathrodictyon striatellum* as figured by Stearn (1966a, Pl. 15 fig. 2)?

From the preceding it is evident that, in order to avoid still further confusion, specific determinations should only be made if: (1) at least part of the material is preserved with its original microstructure, (2) the material is large enough to show the variability of the species (at least ca. 50 specimens). The description should be accompanied by figures showing the microstructure as well as the most important variations in gross structure.

A classification of the Stromatoporoidea in families is extremely difficult under these circumstances. Since the number of Palaeozoic genera seems to be rather small, the number of families must be very small too, as far as natural units can be distinguished at all as families. Whether to include the Mesozoic forms in the order Stromatoporoidea or not is a problem that also remains open.

#### Genus ACTINOSTROMA Nicholson, 1886

Type species (by original designation): *Actinostroma clathratum*, Nicholson, 1886–92, Monogr. Brit. Strom., p. 77, Pl. I figs. 11–13 ('Mittel-Devon', Gerolstein, Eifel, Germany). In the author's opinion this is a synonym of *Actinostroma papillosum* (Bargatzky, 1881).

*Actinostroma* Nicholson, 1886–92, p. 75; Parks, 1936, p. 117; Lecompte, 1951, p. 67; Lecompte, 1956, p. F 127; Galloway & St. Jean, 1957, p. 148; Galloway, 1957, p. 437; Flügel, 1959, pp. 99, 123; Stearn, 1966a, p. 86; Flügel & Flügel-Kahler, 1968, pp. 522, 664.

#### Diagnosis \*

*Coenosteum*: laminar to massive.

*Vertical section*: The horizontal elements of the skeleton are formed either by irregular cyst plates between the pillars or by continuous, more or less straight laminae. Many specimens have an alternation of both. The pillars are generally continuous through many interlaminar spaces and more or less parallel. In some specimens two types of pillars are developed: large pillars and small pillars. The skeleton is not thickened in most cases, so the interlaminar spaces are quadrangular with more or less rounded corners. The astrorhizae, if present, are tabulated; they seem to be without walls.

*Tangential section*: The pillars are round, isolated or connected by cyst plates, depending on the amount of the latter and their irregularity. The laminae are seen as vague dark bands and the astrorhizae, when present, are branching.

*Microstructure*: In well preserved specimens the microstructure is compact. By alteration it easily becomes flocculent and transversely fibrous or porous. In

tangential sections of some recrystallized specimens the pillars have a radial arrangement of specks.

#### Discussion of the genus

Nicholson and subsequent authors laid great stress on what has been called 'radiating arms', 'horizontal processes' or 'hexactinellid network' in tangential sections. In the writer's opinion, however, these are cross-sections through cyst plates or laminae arching between the pillars. For that reason they can best be seen when the tangential section cuts slightly obliquely through the coenosteum, as then the possibility that cross-sections through the cyst plates will be made is greater.

Stearn (1966a, p. 86) gives a diagram of this feature where it can clearly be seen that if such a structure existed, isolated cross-sections of these 'arms' would have to be abundant and conspicuous in vertical sections of specimens belonging to the genus *Actinostroma*. However, they are not visible in any figure published so far! On the contrary, even in specimens with such a conspicuous 'hexactinellid network' as figured for example by Lecompte (1951, Pl. III fig. 1) the vertical section only shows continuous laminae arching between the pillars. Moreover, although cross-sections through cyst plates are visible in many tangential sections of specimens belonging to quite different genera, even in for example *Labechia* and *Stromatoporella*, they are never referred to as 'horizontal processes' (see Pl. 31 fig. 2).

The argument that the thin section is too thick to see the separate ends of the 'arms' in vertical sections, certainly cannot be applied in the specimens with a coarse gross structure. Moreover: if thin sections are too thick to show a gross structure, how is it possible that microstructures can be recognized? Nicholson (1886–92) correctly drew the horizontal elements of all specimens of *Actinostroma* as continuous connections between pillars.

Anyhow, it would be quite difficult to understand how such 'horizontal processes' could develop from the cyst plates of the Labechiidae (assuming that the latter are the ancestors of the other stromatoporoids), if one does not assume the morphologic identity of both.

From the above it becomes evident that there is no longer any reason to erect a special genus for specimens which lack the 'hexactinellid network'. Therefore the genus *Geronostroma* as defined by Yavorsky (1931, p. 1406; 1955, p. 34) must be considered identical with *Actinostroma* (see also Lecompte, 1956, p. F 127).

Galloway & St. Jean (1957, p. 151) and Galloway (1957, p. 438) considered *Geronostroma* to be similar to *Hermatostroma* and *Trupetostroma*. However, the paratype of *Geronostroma elegans* described by them (p. 152, Pl. 11 fig. 2; p. 438, Pl. 31 fig. 10) and on which their opinion seems to be based, looks quite different from *Geronostroma elegans*, as described by Yavorsky (1931, p. 1406, Pl. I fig. 12, Pl. II figs. 3–6).

\* This and the following diagnoses are based on a revised definition which became necessary during the investigation of the material from north-western Spain.

Flügel (1959) recognized the genus *Geronostroma* but did not transfer any specimens from *Actinostroma* to that genus. In his opinion (see Flügel, 1959, p. 123) *Geronostroma* has laminae consisting of a thin primary layer and a layer with vacuoles like *Trupetostroma*.

Stearn (1966a, pp. 87, 101) proposed transferring many specimens of Nicholson to *Geronostroma*. In his opinion *Geronostroma* has transversely porous laminae and spool-shaped pillars and is closely allied to *Stictostroma* and *Trupetostroma*.

In the writer's opinion the specimen described by Yavorsky (1931) has a compact microstructure (though on Pl. II figs. 4, 5 it shows some features similar to *Hermatostroma*) and thus belongs to the genus *Actinostroma*. The paratype of Galloway & St. Jean (see also Stearn, 1966a, Pl. 16 fig. 6), however, is not at all conspecific with the type of Yavorsky (1931) and so gave rise to much confusion. This paratype is badly preserved and according to Galloway & St. Jean (1957, p. 152) has thick coarsely porous laminae, sometimes with a clear layer and spool-shaped pillars. It looks very much like a specimen described by Sleumer (1968, figs. 15, 16).

*Atelodictyon fallax* Lecompte (1951, p. 125, Pl. XV figs. 1, 2) has superposed pillars according to the figures. It is identical with some specimens found in Spain which belong to *Actinostroma verrucosum*? in this author's opinion. As *A. fallax* is the type species of the genus *Atelodictyon*, this genus must be considered as being very doubtful.

To what extent continuous pillars can be considered as a character of the genus *Actinostroma* is very difficult to say. In some specimens of *Actinostroma verrucosum*?, as described in this paper, the pillars do not seem to be very well superposed, though this may be partly due to the sections not being completely vertical. Other authors (see for example Lecompte, 1951, Pl. VIII fig. 5, Pl. IX figs. 2, 8, Pl. X figs. 1, 2, Pl. XI figs. 1, 3, 5, Pl. XII fig. 1, Pl. XIV fig. 2) have also described specimens, in which the pillars are not very long, as *Actinostroma*. However, to place these specimens in other genera such as *Clathrodictyon* or *Anostylostroma* would not be convincing. Anyhow, there are specimens of *Actinostroma* which have two types of pillars: thick continuous pillars and small rather short pillars, for example *A. bifarium* Nicholson. So it is possible that specimens of *Actinostroma* also have short pillars!

Other genera which might be synonymous with *Actinostroma* are *Clathrostroma* Yavorsky and *Plectostroma* Nestor.

According to the description given by Flügel (1963, p. 330) and Flügel & Flügel-Kahler (1968, p. 538) the main characters of the genus *Clathrostroma* are: pillars of two types (also occurring in *Actinostroma*!) and lack of 'arms'. Moreover Flügel & Flügel-Kahler (1968, pp. 666, 667) state that Yavorsky later withdrew the genus and now considers it as identical with *Atelodictyon*. On the other hand none of the specimens called *Clathrostroma* and figured by Yavorsky (1961) show long continuous pillars or pillars of two types.

*Plectostroma* Nestor according to Stearn (1966a, p. 87) and Flügel & Flügel-Kahler (1968, p. 559) is distinguished from *Actinostroma* by the horizontal elements which are not continuous in *Plectostroma*. However, in the Spanish material many specimens have been found with cyst plates as well as continuous laminae, either in a gradual transition in the latilaminae as in *Actinostroma papillosum* or as an alternation of both occurring in what is called provisionally *Actinostroma verrucosum*?

*Actinostroma papillosum* (Bargatzky, 1881)  
(Pl. 15 fig. 1 – Pl. 18 fig. 2)

- 1881 *Stromatopora concentrica* Goldf. – Bargatzky, p. 54 (= 282).  
1881 *Stromatopora papillosum* n. sp. – Bargatzky, p. 54 (= 282).  
1951 '*Stromatopora concentrica* Bargatzky 1881, p. 54'. – Lecompte, p. 84, Pl. I fig. 10.  
1951 '*Stromatopora papillosa*' Bargatzky. – Lecompte, p. 85, Pl. I fig. 11.  
1959 *Actinostroma (Actinostroma) papillosum* (Bargatzky) 1881. – Flügel, p. 167.

For a complete synonymy see Flügel, 1959, p. 167 and Flügel & Flügel-Kahler, 1968, p. 303.

- 1886a *Actinostroma clathratum* Nich. – Nicholson, p. 226, Pl. VI figs. 1–3.  
1886–92 *Actinostroma clathratum*. – Nicholson, pp. 75, 131, Pl. I figs. 8–13, Pl. II fig. 11, Pl. XII figs. 1–5, Pl. XIII figs. 1–2.  
1951 *Actinostroma clathratum* Nicholson, emend. – Lecompte, p. 77, Pl. I figs. 1–12.  
1959 *Actinostroma (Actinostroma) clathratum* Nicholson 1886. – Flügel, p. 129, Pl. 6 fig. 3.  
1966 *Actinostroma clathratum* Nicholson. – Klován, p. 18, Pl. V figs. 2, 3.  
1966 *Actinostroma clathratum* Nicholson. – Stearn 1966b, p. 47, Pl. XIII figs. 4, 5, Pl. XVI figs. 3, 4.

For a complete synonymy see Flügel, 1959, p. 129 and Flügel & Flügel-Kahler, 1968, p. 69.

- 1886a *Actinostroma hebbornense* Nich. – Nicholson p. 228, Pl. VII figs. 7, 8.  
1886–92 *Actinostroma hebbornense* Nich. – Nicholson, p. 137, Pl. XVI figs. 9–16.  
1951 *Actinostroma hebbornense* Nicholson. – Lecompte, p. 92, Pl. III figs. 4–6.  
1959 *Actinostroma (Actinostroma) hebbornense* Nicholson 1886. – Flügel, p. 146, Pl. 6 fig. 1.

For a complete synonymy see Flügel, 1959, p. 146 and Flügel & Flügel-Kahler, 1968, p. 186.

*Lectotype*. – Bargatzky, 1881, p. 54, Lecompte, 1951, Pl. I fig. 11, Museum Geol. Pal. Inst. Bonn (chosen by E. Flügel, 1959).

*Locus typicus*. – Schlödetal Paffrath-Mulde, Germany.  
*Stratum typicum*. – 'Mittel-Devon' (probably Givetian).

*Diagnosis*

Coenosteum: form massive; mamelons absent or very small; astrorhizae very small, isolated.

Vertical section: laminae ca. 6–12/2 mm; normally 0.03–0.10 mm thick; continuous, more or less undulating, arching between pillars, cyst-like or irregular; generally thinner than pillars.

pillars ca. 7–13/2 mm; normally 0.05–0.12 mm thick; long, more or less parallel; often thickened. interlaminar spaces quadrangular or irregular.

Tangential section: pillars round, connected by cyst plates or isolated.

#### Description of the material

Number of specimens: ca. 60

Occurrence: Santa Lucía Formation, Emsian and Couvinian limestones near Ventanilla and Caldas Formation near Caldas de Luna.

*Coenosteum*: The form of the coenosteum is more or less massive with lateral extensions up to 1.10 m. The mamelons are generally absent or low. The latilaminae are very vague in some specimens while they are conspicuous in others.

*Vertical section* (Pl. 15 fig. 1 – Pl. 18 fig. 2): The

laminae are variable. They may be continuous, more or less undulating and dichotomous in part of the specimens; in others they arch between pillars, in still others they are not continuous but cyst-like and sometimes very irregular. In many specimens an alternation of more regular and more irregular zones is visible. The thickness of the laminae is also very variable. In some specimens it is ca. 0.03 mm while in others it is ca. 0.07 mm (extremes 0.01–0.13 mm). The number of laminae in 2 mm is not given in a diagram as it is not accurately measurable in specimens which have only cyst plates between the pillars. In specimens with more or less continuous laminae there can be 5–16 laminae in 2 mm but normally there are 7–12.

The pillars may be straight and very long or rather irregular and not parallel. The normal thickness of the pillars is 0.05–0.12 mm depending on the specimen (extremes 0.03–0.18 mm). Some specimens have rather thick pillars, others show a tendency to develop two types of pillars: normal pillars and thick pillars. The number of pillars in 2 mm is normally 7–13, though specimens with lower and higher values also occur. This number is highly variable not only from specimen

pillars/2 mm	specimen									
	473 L	LV510 F	520 F	522 K	530 G	532 A	533 G	536 H	540 B	542 A
18										1
17									1	
16					1				1	1
15					1				2	1
14		1							1	1
13		2			1	1			2	4
12	2	5			1	1		1	1	2
11	3	1			2	5		1	1	
10	4	1	1		1	1		4	1	
9	1		3	2	1	2		3		
8			4	5	2		3	1		
7			1	3			3			
6			1				3			
5							1			

to specimen but also within one specimen, as many specimens show alternating zones of fine and coarse tissue.

The interlaminar spaces are quadrangular in specimens with continuous laminae and very irregular in specimens which have cyst plates instead of laminae.

Astrorhizae are extremely scarce in the Spanish material. When present they are small, isolated or in vertical groups and scarcely branched.

The latilaminae are very conspicuous in some specimens, in others they are vague. Their thickness may be 0.5–1.5 mm in some specimens, while other specimens have latilaminae of ca. 2–3 mm, some even up to 5 mm. There is no relation between the thickness of the latilaminae and the fineness of the tissue, nor are there any stratigraphic tendencies.

*Tangential section* (Pl. 18 figs. 1, 2): The pillars are

connected by cyst plates or are isolated. In specimens with rather continuous laminae, these are seen as vague dark bands. The astrorhizae are very small.

#### Remarks

As can be seen, a great variation of features occurs in the material. As these individual variations show neither stratigraphic nor geographic trends, no division in subspecies can be made. On the other hand, all variations between the extreme developments of the gross structure exist, so it is not possible to make a subdivision into species either.

In the writer's opinion these variations are ecotypes due to environmental circumstances (which may be different for each coenosteum) but all belong to one population.

*Actinostroma clathratum* is considered to be a later synonym of *Actinostroma papillosum*. Flügel (1959)

separated both species and placed the specimens with a coarser gross structure in *A. papillosum* and the finer ones in *A. clathratum*, but at the same time recognized that a division into two species is highly artificial (p. 168). *A. hebbornense* as defined by Flügel (1959) is identical with the Spanish specimens with a fine and fragile gross structure. Therefore it is also considered to be a synonym. Lecompte (1951, p. 92) also mentions the fact that many specimens are transitional between *A. hebbornense* and *A. clathratum*. The specimens described by Klován (1966) and Stearn (1966b) on the contrary have a very coarse gross structure.

Because of the great variation in gross structure it may be very well possible that more species are actually only variations of *A. papillosum*, for example: *A. altum*, *A. dehornae*, *A. ligeriense* and *A. salairicum* (see Flügel, 1959).

Another possibility is a connection with *A. verrucosum*? (see below) for both have more or less the same diagram and thicknesses of laminae and pillars. The only difference is the presence of straight laminae in *A. verrucosum*?. As these laminae are not a constant feature but are interchangeable with cyst plates, it is possible that these laminae are an ecological feature caused by temporary standstills of growth. They would be a feature analogous with the paralaminae in *Plexodictyon Nestor* (see Flügel & Flügel-Kahler, 1968, p. 672). Similar features are also found in *Ferestromatopora krupennikovi* (see Yavorsky, 1955, Pl. LVIII) and *Clathrodictyon latilaminatum* (see Bogoyavlenskaya, 1965, Pl. 1 fig. 1).

*Actinostroma verrucosum* (Goldfuss, 1826)?  
(Pl. 18 fig. 3 – Pl. 20 fig. 4)

- 1826 *Ceripora verrucosa* nobis. – Goldfuss, p. 33, Pl. X fig. 6.  
1951 *Actinostroma verrucosum* (Goldfuss). – Lecompte, p. 107, Pl. IX figs. 1–8, Pl. X figs. 1–2.  
1951 *Atelodictyon fallax* nov. sp. – Lecompte, p. 125, Pl. XV figs. 1–2.  
1959 *Actinostroma* (*Actinostroma*) *verrucosum* (Goldfuss 1826). – Flügel, p. 190, Pl. 6 fig. 4.

For a complete synonymy see Flügel, 1959, p. 190 and Flügel & Flügel-Kahler, 1968, p. 465.

*Lectotype*. – Goldfuss, 1826, Pl. 10 fig. 6, Museum Geol. Pal. Inst. Bonn (chosen by Flügel, 1959).

*Locus typicus*. – Bensberg, Paffrath-Mulde, Germany.

*Stratum typicum*. – 'Mittel-Devon' (probably Givetian).

*Diagnosis*

Coenosteum: form laminar, massive or globular; mamelons very low to very pronounced; astrorhizae small, branching, in vertical groups or isolated.

Vertical section: laminae ca. 5–10/2 mm; normally 0.04–0.12 mm thick; continuous, sometimes dichotomous; thin or thickened on lower side.

pillars ca. 9–13/2 mm; normally 0.06–0.10 mm thick; generally superposed, straight to irregular; often thickened below laminae.

interlaminar spaces vertically elongated with many cyst plates to square without cyst plates; often upper corners rounded.

cyst plates generally abundant.

Tangential section: pillars isolated or connected by obliquely cut cyst plates.

*Description of the material*

Number of specimens: ca. 60

Occurrence: entire Santa Lucía Formation along the southern border of the Cantabrian Mountains, Emsian and Couvinian limestones near Ventanilla, Limestone member of Caldas Formation near Caldas de Luna.

*Coenosteum*: The form of the coenosteum can be laminar, massive up to 15 cm in diameter, globular or conical. Encrusting forms were not found. The mamelons are generally absent or very low, rather pronounced only in some specimens. Latilaminae are present in all specimens.

*Vertical section* (Pl. 18 fig. 3 – Pl. 20 fig. 2): The laminae are continuous often dichotomous. In most specimens they are straight on the upper side but very commonly thickened on the lower side, arching between pillars. When laminae are thin and very close together the upper side also arches. The thickness of the laminae is generally 0.04 to 0.10 mm (extremes 0.03–0.20 mm), it is very variable from specimen to specimen, depending whether the laminae are thickened or not, though it may also be influenced by alteration. The number of laminae in 2 mm is extremely variable as can be seen in the diagram, however, the extreme values are relatively seldom. Normally it is 5–10. The number of laminae in 2 mm greatly depends on whether the interlaminar spaces are high with many cyst plates or low without cyst plates.

lam/2 mm	specimen									
	449 B	472 D	528 A	530 C	530 H	531 A	533 F	537 K	565 B	567 G
17	1									
16	1									
15										
14									2	
13	2									
12			2							
11			3						2	
10	3		3		2		1	2	3	
9	1		1		1		4		2	2
8	2	1		2	1	1	2	2	1	4
7		2	1		1	4	2	2		2
6		4		1	4	3	1	1		
5		1		4	1	1				2
4		2		2		1		3		
3				1						

pillars/2 mm	specimen									
	449 B	472 D	528 A	530 C	530 H	531 A	533 F	537 K	565 B	567 G
14						1		1		
13		3	2			2	1	3	3	
12	1	1		5	1	2	3			
11	1	3	2	4	6	3		4	4	6
10	3	2	4		3	2	4	2	3	4
9	4	1	2	1			2			
8										
7	1									

The pillars are generally well superposed but in some specimens pillars are irregular when interlaminar spaces are high. Pillars are generally thicker below the laminae than above. The pillars generally have a thickness of 0.06–0.10 mm (extremes 0.03–0.16). The number of pillars in 2 mm is normally 9–13 and so much less variable than the number of laminae in 2 mm.

The interlaminar spaces are vertically elongated to square. Only in parts of specimens with very closely set laminae are the interlaminar spaces broader than high. The high interlaminar spaces (up to 0.9 mm!) are mostly subdivided by irregularly set cyst plates while the low ones generally lack cyst plates. The upper corners are usually more or less rounded.

Astrorhizae are rather scarce in the Spanish material. Indications of these have only been found in a few specimens and generally then in small local upturns of the laminae but some are found in vertical groups. They have tabulae, the diameter is 0.15–0.3 mm.

The latilaminae are visible by zones of fine closely set laminae or repair tissue, discontinuity of pillars or differently coloured zones. Specimens with few laminae in 2 mm have thick latilaminae (4–6 mm) while

specimens with closely set laminae have much thinner latilaminae (1–2.5 mm).

*Tangential section* (Pl. 20 figs. 3, 4): The pillars are visible as small dots. They are generally connected by a 'hexactinellid network' (max. 4 connections with other pillars) in specimens with abundant cyst plates. In specimens with few cyst plates the pillars are mostly isolated. The obliquely cut laminae are visible as vague dark bands. The astrorhizae are small, branching; the horizontal canals have a diameter of ca. 0.2 mm.

#### Remarks

Though the Spanish material shows a variability in the form of the coenosteum ranging from laminar to conical, the mamelons are not so conspicuous as in the specimen of Goldfuss. The material very much resembles that described by Lecompte (1951, pp. 107, 125) both in the form of the coenosteum as in the gross structure. Since there are some differences between the material described by Lecompte and the type specimen of Goldfuss (see Lecompte, 1951, Pl. 9 fig. 1) it is not clear whether this Spanish and Belgian

material is identical with *A. verrucosum* in the sense of Goldfuss. It is very well possible, as stated by Flügel (1959, p. 194), that *A. verrucosum* as described by various authors is a polyphyletic species due to the assignment of specimens with conspicuous mamelons, but different gross structures to one species.

The relationship of *A. verrucosum* to *A. papillosum* (= *A. clahratum*) is obvious. According to Flügel (1959) *A. verrucosum* and *A. papillosum* nearly always occur together and this is so in north-western Spain. Many specimens of *A. verrucosum* (including the type specimen) look very much like specimens of *A. papillosum* with continuous laminae, the only difference being that in *A. verrucosum* the laminae are conspicuously continuous compared with the pillars and in *A. papillosum* the reverse in the case.

The specimens described by Lecompte (1951, p. 125) as *Atelodictyon fallax* are identical to the forms with relatively high interlaminar spaces from the Spanish material. Therefore they are included in the species.

It is remarkable that specimens with high interlaminar spaces (= few lam/2 mm) also have thicker latilaminae than specimens with low interlaminar spaces (many lam/2 mm). This points to the fact that high interlaminar spaces are an indication of fast growth. Laminae are then partly replaced by thin and irregular cyst plates.

There is no connection between the number of laminae in 2 mm and stratigraphy. On the contrary, even within one specimen the spacing of the laminae is highly variable (see also Lecompte, 1951, p. 107).

*Actinostroma stellulatum* Nicholson, 1886  
(Pl. 21 fig. 1 – Pl. 22 fig. 2)

1886a *Actinostroma stellulatum*, Nich. – Nicholson, p. 231, Pl. VI figs. 8, 9.

1959 *Actinostroma* (*Actinostroma*) *stellulatum* Nicholson 1886. – Flügel, p. 179, Pl. 6 fig. 5, Pl. 7 fig. 4.

For a complete synonymy see Flügel, 1959, p. 179 and Flügel & Flügel-Kahler, 1968, p. 401.

*Lectotype*. – Nicholson, 1886a, Pl. VI figs. 8, 9 Nr. 170/5570, British Museum, London (chosen by E. Flügel, 1959).

*Locus typicus*. – Gerolstein, Eifel, Germany.

*Stratum typicum*. – 'Mittel-Devon' (probably Givetian).

*Diagnosis*

Coenosteum: form laminar to massive; mamelons low or consisting of concentric cylinders; astrorhizae small, branching, in vertical groups.

Vertical section: laminae ca. 13–16/2 mm; normally 0.04 to 0.06 mm thick; continuous, sometimes dichotomous.

pillars ca. 9–12/2 mm; normally 0.07 to 0.10 mm thick; long.

interlaminar spaces quadrangular with more or less rounded corners.

cyst plates absent.

Tangential section: pillars round, generally without radial arms.

*Description of the material*

Number of specimens: ca. 105

Occurrence: very common in limestones in the Huergas Formation near Mirantes de Luna and all Portilla outcrops along the southern border of the Cantabrian Mountains.

*Coenosteum*: The form of the coenosteum is thinly laminar (0.5–1 cm thick), free or encrusting to massive, up to 40 cm high and 60 cm in diameter, with all gradations between these extremes. Sometimes the coenosteum is arched on the lower side. The mamelons are low to very low, 6–11 mm apart or nearly absent. All specimens have latilaminae.

*Vertical section* (Pl. 21 figs. 1–4): The laminae are continuous, frequently dichotomous, in most specimens they are straight, in others rather undulated. The thickness of the laminae is generally 0.04–0.06 mm (extremes 0.02–0.11 mm). The number of laminae in 2 mm is generally 13–16 but in two specimens it is ca. 20. As these specimens have the same number of pillars in 2 mm (see diagrams) and the skeletal elements have the same thickness, they are included in the species.

lam/2 mm	specimen									
	209 A	297	384 B	408 E	410 A	414 A	423 C	426	454 J	479 G
22	1									
21	5				1					
20	1				3					
19	2				6					
18	1	1								
17						2				
16		1				4		3		3
15		5	2	1		4		2	4	2
14		2	4	5				3	5	5
13		1	4	2			4	2	1	
12				2			3			



pillars/2 mm	specimen									
	209 A	297	384 B	408 E	410 A	414 A	423 C	426	454 J	479 G
13						2				
12	1	5	3	1	1	3	2			3
11	5	3	4	2	2	5	5	6		5
10	3	2	2	5	5		3	2	2	1
9	1		1	2	2			2	5	1
8									3	

The pillars are long, superposed. They are more or less spool-shaped or only thickened at the upper corners of the interlaminar spaces. In many specimens with undulating laminae they have a tendency to thickening. The thickness of the pillars is generally 0.07–0.10 mm (extremes 0.05–0.20 mm). The number of pillars in 2 mm is generally 9–12 in well oriented sections.

The interlaminar spaces are subangular to subrounded, generally broader than high. They have no cyst plates.

The astrorhizae are situated in vertical groups, they are associated with mamelons if the latter are present. They are round in cross-section and have a diameter of 0.25 mm at a maximum. In well preserved specimens tabulae are visible in the central part of the astrorhizae. Astrorhizae are common in all specimens.

The latilaminae are generally 1.5–2 mm high (extremes 1–4 mm). They are marked by a more or less pronounced discontinuity of the skeletal elements and a closer setting of thin laminae, sometimes also by repair tissue and intercalations of foreign organisms, such as crinoid detritus and aulopord corals. In many specimens the interruptions of growth are only local.

**Tangential section** (Pl. 22 figs. 1, 2): The pillars are visible as small isolated dots with a diameter of ca. 0.10 mm. Sometimes a few 'arms' are visible in the central part of the mamelons. The astrorhizae are long, stellate.

#### Remarks

The form of the coenosteum is very variable. However, distinction in varieties as made by Heinrich (1914, see Flügel, 1959, p. 181), cannot be made in the Spanish material and specimens consisting of parallel cylinders were not found.

Considering the gross structure it is striking that the number of laminae in 2 mm is very high in some specimens. This form is identical to *A. perlaminatum* Lecompte (1951, p. 120, Pl. XII fig. 4), which according to Flügel (1959, p. 183) is probably identical with *A. stellulatum*.

Another feature which is rather variable is the regularity of gross structure. Some specimens have straight laminae and pillars perpendicular to each other, while other specimens have undulating laminae and thickened pillars which tend to occur in the highest parts of the undulating laminae.

#### *Actinostroma* sp. 1 (Pl. 22 figs. 3, 4)

#### Description of the material

Number of specimens: 9

Occurrence: lower and middle Santa Lucía Formation near Santa Lucía (Bernesga), Aviados and Villayandre (Esla).

**Coenosteum:** The form of the coenosteum is laminar to massive. Mamelons and latilaminae are well developed in all specimens.

**Vertical section** (Pl. 22 figs. 3, 4): The laminae are continuous, straight, often dichotomous. Typically they are sometimes interrupted by foraminae without cyst plates. The thickness of the laminae is generally 0.05–0.07 mm (extremes 0.02–0.15 mm). The number of laminae in 2 mm is generally 8–11, but sometimes laminae are closer to each other or more separate.

The pillars are long and straight but sometimes rather short due to irregular growth. Their thickness is generally 0.06–0.08 mm (extremes 0.03–0.15 mm). The number of pillars in 2 mm is 8–13.

The interlaminar spaces are quadrangular, mostly vertically elongated. In some zones interlaminar spaces are rather irregular. Cyst plates are very common, especially in the higher interlaminar spaces, generally they arch between the pillars.

The astrorhizae are comparatively wide (up to 0.6 mm), round in cross section, and conspicuous. They are situated in the mamelons but spread from there throughout the whole tissue.

The latilaminae are 2–4 mm high. They are mostly marked by large zones of repair tissue, which gives the whole section an irregular appearance. Sometimes the repair tissue shows an obvious direction of lateral growth.

**Tangential section:** The pillars are visible as round dots, isolated or connected by cyst plates. The astrorhizae are branching.

#### Remarks

This species is characterized by the foraminae in the laminae, sometimes looking like ring pillars, and the obvious, wide astrorhizae. Moreover in all specimens

repair tissue is obvious. As far as the measurements and the vertically elongated interlaminar spaces with abundant cyst plates are concerned it looks like *Actinostroma verrucosum*?, but the latter has very small astrorhizae, if they are present at all.

*Actinostroma* sp. 2  
(Pl. 23 figs. 1, 2)

*Description of the material*

Number of specimens: 3

Occurrence: lower Santa Lucía Formation near Santa Lucía (Bernesga) and Crémenes (Esla).

*Coenosteum*: The form of the coenosteum is massive. The mamelons are absent or rather low, latilaminae are present.

*Vertical section* (Pl. 23 fig. 1): The laminae are thin, continuous, straight and sometimes dichotomous. The thickness of the laminae is generally 0.04–0.06 mm (extremes 0.02–0.10 mm), there are 3–7 laminae in 2 mm.

The pillars are long and straight; in some local upturns of the laminae they are placed very near together (repair tissue). They are generally 0.05–0.06 mm thick (extremes 0.03–0.11 mm), so they are slightly thicker than the laminae. The number of pillars in 2 mm is 6–9.

The interlaminar spaces are mostly vertically elongated but many of them are more or less square. In some zones the galleries have rounded corners on the upper side. The cyst plates may be short, more or less diagonal but most of them form a very acute angle with the laminae and proceed through many galleries before uniting again with the same lamina or with the next one. That is to say, these horizontal elements are an intermediate form between laminae and cyst plates. Astrorhizae were not found. The latilaminae are ca. 5 mm high.

*Tangential section* (Pl. 23 fig. 2): The pillars are seen as isolated dots, the laminae as vague bands. Cyst plates are very scarce. In some places irregular repair tissue is visible. Astrorhizae were not found.

*Remarks*

The species described above bears a striking resemblance to *Actinostroma perspicuum* Pošta 1894 (see Pošta, 1894, p. 146, Pl. 18/1 figs. 3–6 and Flügel, 1959, p. 172, Pl. 7 fig. 5).

*Actinostroma* sp. 3  
(Pl. 23 figs. 3, 4)

*Description of the material*

Number of specimens: 2

Occurrence: uppermost Santa Lucía Formation near Santa Lucía (Bernesga).

*Coenosteum*: The form of the coenosteum is laminar

to massive without mamelons. Latilaminae are present. The coenosteum is full of worm tubes in the massive specimen.

*Vertical section* (Pl. 23 fig. 3) The laminae are thin, continuous, undulating between the pillars, sometimes they are dichotomous. The thickness of the laminae is generally ca. 0.04 mm (extremes 0.02–0.10 mm). The number of laminae in 2 mm is 7–14.

The pillars are of two types: (1) long and very thickened (ca. 0.20 mm thick), in the centre of upturns of the laminae (2) normal, short or irregular (ca. 0.06 mm thick). The number of pillars in 2 mm (both types) is 7–10.

The interlaminar spaces are vertically elongated, square or horizontally elongated, sometimes with irregular cyst plates. The astrorhizae are common but rather short and isolated, and are 0.4 mm wide at a maximum. The latilaminae are 1.5–2.5 mm high, marked by closely set laminae.

*Tangential section* (Pl. 23 fig. 4): The pillars are visible either as small or as large dots, isolated or connected by cyst plates. The laminae are visible as vague bands. The astrorhizae are branching.

*Remarks*

These specimens look very much like *Actinostroma bifurum* as described by Lecompte (1951, p. 104, Pl. VIII fig. 3) and less like the specimens figured by Nicholson (1886a, Pl. VI figs. 4, 5 and 1886–92, Pl. XIII figs. 3–7) and Flügel (1959, Pl. 7 fig. 2) because the latter have more irregular and discontinuous laminae.

*Actinostroma* sp. 4  
(Pl. 24 figs. 1, 2)

*Description of the material*

Number of specimens: 1

Occurrence: uppermost Santa Lucía Formation near Villayandre (Esla).

*Coenosteum*: The specimen is ca. 80 cm. high and 1 m broad, slightly arched, without conspicuous mamelons. Latilaminae are clearly visible. The specimen is infested with corkscrew-like worms.

*Vertical section* (Pl. 24 fig. 1): The laminae are continuous, sometimes dichotomous, they are straight to slightly undulating and often thickened on the lower side. The thickness of the laminae is generally ca. 0.05 mm (extremes 0.03–0.09 mm), the number of laminae in 2 mm is 7–11.

The pillars grade from thin and irregular to long and strongly thickened, but no separation can be made into two kinds of pillars for all gradations are present. Some thickened pillars are situated on top of undulations of the laminae. The thickness of the pillars is generally 0.07–0.15 mm (extremes 0.03–0.25 mm), the number of pillars in 2 mm is 7–9.

The interlaminal spaces are sometimes vertically elongated but generally square to horizontally elongated, commonly with irregular cyst plates. The astrorhizae are short, isolated and not conspicuous. The diameter is 0.3 mm at a maximum. Latilaminae are 2–3 mm high, marked by closely set laminae.

**Tangential section** (Pl. 24 fig. 2): The pillars are isolated or connected by cyst plates. They differ considerably in diameter but a separation into small and large ones cannot be made. The obliquely cut laminae are visible as vague bands. The astrorhizae are small, not conspicuous.

#### Remarks

The specimen described above is very similar to *Actinostroma sotenicum* described by Le Maitre (1934, p. 180, Pl. X figs. 4, 6) although the latter has more lam/2 mm. However, Le Maitre (1947) and Flügel (1959, p. 95) regard *A. sotenicum* and *A. verrucosum* as being synonyms while in the Spanish material a clear distinction can be made between this specimen and all variations of what has been described as *A. verrucosum*?

The specimen is also very similar to *Actinostroma septatum* var. *robustum* described by Lecompte (1951, p. 101, Pl. VII fig. 1). According to Flügel (1959, p. 132, tab. 4) this species is possibly identical to *A. clathratum*. Another rather similar species is *Actinostroma conglomeratum* also described by Lecompte (1951, p. 105, Pl. VIII fig. 4). According to Lecompte, this species (only one specimen!) resembles *A. verrucosum* and could be its ancestor. Flügel (1959, p. 113) considered it to be a *Trupetostroma*, but was not able to see the collection of Lecompte. Finally it resembles the two specimens described above, which are similar to *A. bifarium*.

#### Genus STROMATOPORELLA Nicholson, 1886?

Type species (by original designation): *Stromatopora granulata* Nicholson, 1873, Ann. Mag. Nat. Hist. ser. 4, Vol. 12, p. 94, Pl. 4 fig. 3 (Middle Devonian, Hamilton Formation, Arkona, Ontario).

*Stromatoporella* Nicholson, 1886–92, p. 92; Parks, 1936, p. 90; Lecompte, 1951, p. 152; Lecompte, 1956, p. F 131; Galloway & St. Jean, 1957, p. 129; Galloway, 1957, p. 436; Galloway & Ehlers, 1960, p. 75; Galloway, 1960, p. 622; Stearn, 1966a, p. 93; Birkhead, 1967, p. 50; St. Jean, 1967, p. 436; Flügel & Flügel-Kahler, 1968, p. 572; Sleumer, 1968, p. 14.

#### Discussion of the genus

As there is no general agreement about the type species nor about the characters of this genus, no diagnosis is given here.

According to many authors (including the present writer) the classification of stromatoporoids has to be based in the first place on microstructure. The problem with this, however, is that most species and genera are based on strongly altered type material in

which the original microstructure has often become unrecognizable.

This is especially the case with the present group. There are two completely different primary microstructures which have both been assigned to the genus *Stromatoporella*. One is microlaminate and vacuolate (see *Stromatoporella? granulata?* of this paper), the other is ordinicellular (see *Stromatoporella? selwyni* of this paper). Both microstructures are easily altered or destroyed by recrystallization and migration of specks.

Nicholson seems to have completely confused specimens with these two microstructures. Specimens described as *S. granulata*, *S. eifeliensis*, *S. curiosa* and *S. solitaria* seem to have microlaminate laminae and specimens described as *S. laminata*, *S. damnoniensis*, *S. arachnoidea*, *S. selwyni* and *S. socialis* probably have an ordinicellular microstructure.

The species mentioned above with microlaminate laminae should be put together in one genus with other species which have the same microstructure but are often described in other genera, e.g. *Clathrocoelona*, *Trupetostroma*, *Stictostroma* in particular and perhaps *Diplostroma*, *Simplexodictyon* and *Styloporella* (according to the definitions and discussion given by Flügel & Flügel-Kahler, 1968).

It is the strongly altered specimens in particular which have caused so much confusion, as they have been described as belonging to *Stromatopora*, *Syringostroma*, *Parallelopora*, *Taleastroma* and other genera. Indeed it is often extremely difficult to distinguish pseudocellular specimens from altered cellular specimens.

In the same way species with ordinicellular laminae should be put together in one genus. They have been described as belonging to *Stromatoporella*, *Stictostroma*, *Anostylostroma* and other genera. However, it is impossible to determine the original microstructure of many species judging only from their descriptions. Specimens with unrecognizable microstructure but recognizable gross structure should only be determined when found together with well preserved specimens of the same species.

The gross structure on the contrary is extremely variable in species of both groups. Not only are there strong individual differences in the amount of ring pillars, the superposition of normal pillars and the thickness of the tissue, but there is also a great variability in the spacing of the laminae. This implies that a revision of these species would yield a large number of synonyms.

As cyst plates do occur in the ring pillars, it is improbable that they were caused by parasitism as suggested by the present writer (Sleumer, 1968) but must be regarded as having been formed by the stromatoporoid itself.

An interesting problem is presented by the more or less dendroid specimens. In the Spanish material some branched specimens occur: two specimens with microlaminated laminae and two which seem to belong to *S.? selwyni*.

According to the redescription of *Idiostroma caespitosum* (Winchell) by Galloway & Ehlers (1960), based on a lectotype and 6 paralectotypes of Winchell, it appears that these specimens have partly recrystallized microlaminar laminae. Branched specimens can be considered as nothing else than specimens with extremely well developed mamelons in which vertical growth only occurred in the top of these. If these branched specimens are put together in one genus with massive and laminar specimens, also with microlaminar laminae, then the name of the genus should be *Idiostroma* on the ground of priority.

As superposition of pillars seems to have little value as a generic and even as a species character, specimens described in the genus *Dendrostroma* will also have to be revised. In the same way the genus *Stachyodes* must be reconsidered. Specimens described in the latter genus are generally characterized by an extremely altered tissue, which makes the microstructure and often even the gross structure unrecognizable. According to the type material of Bargatzky the not completely altered specimens described as *Stachyodes* have a microstructure and gross structure similar to *Stromatopora*.

It is quite understandable that dendroid forms have become so easily altered. Due to their form they have a far larger surface in comparison with more compact forms and so were more easily subject to outside influences.

A revision of the genera mentioned above is urgently needed. Specimens with microlaminar laminae should be put together in one genus and specimens with ordinicellular laminae in another genus, independent of the form of the coenosteum and variations in gross structure. In any case genera based on excessively altered type specimens will have to be abolished.

This would solve many problems of determination and would very much simplify the classification of stromatoporoids.

*Stromatoporella? granulata* (Nicholson, 1873)?  
(Pl. 24 fig. 3 – Pl. 27 fig. 2)

- 1873 *Stromatopora granulata* sp. nov. – Nicholson, p. 94 Pl. IV figs. 3, 3a.  
1874 *Stromatopora granulata*, Nicholson. – Nicholson, p. 10.  
1886b *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, (not Pl. I fig. 14).  
1936 *Stromatoporella granulata* Nicholson. – Parks, p. 95, Pl. XV figs. 6, 7, Pl. XVI figs. 1–7.  
1936 *Stromatoporella granulata distans* var. nov. – Parks, p. 100, Pl. XIV figs. 7, 8, Pl. XV fig. 8.  
1937 *Stromatoporella granulata* Nicholson. – Ripper, p. 191, Pl. IX figs. 3–5.  
1951 *Stromatoporella granulata* (Nicholson). – Lecompte, p. 160, Pl. XXI fig. 1.  
1957 *Stromatoporella granulata* (Nicholson). – Galloway & St. Jean, p. 131, Pl. 7 fig. 3.

- 1968 *granulata* Nicholson 1873, *Stromatopora*. – Flügel & Flügel-Kahler, p. 180.  
1968 *Stromatoporella granulata* (Nicholson, 1873). – Sleumer, p. 10, figs. 1–17, 19–22, (not fig. 18 = slightly altered *Stromatopora*).

*Holotype*. – Nicholson 329 (see Stearn, 1966a, Pl. 15 figs. 6, 7). British Museum of Natural History.

*Locus typicus*. – Arkona, Ontario.

*Stratum typicum*. – Hamilton Formation (Middle Devonian).

*Diagnosis*

Coenosteum: form laminar to massive; free or encrusting; mamelons absent, low or pronounced; astrorhizae generally strongly developed.

Vertical section: laminae ca. 7–12/2 mm; normally 0.05–0.20 mm thick; continuous, often dichotomous; straight to irregularly undulating; very variable in thickness, in many places only represented by cyst plates, in other places extremely thick.

ring pillars absent, scarce or common.

pillars spool-shaped, very thick, randomly placed to superposed (not continuous).

interlaminar spaces round or laterally elongated. cyst plates common.

Tangential section: pillars isolated, coalescent or forming an amalgamated network.

ring pillars absent, scarce or common.

Microstructure: microlaminar ('tripartite') and vacuolate, when diffuse or altered it looks compact or transversely fibrous, in other cases it has become flocculent, melanospheric and even pseudocellular.

*Description of the material*

Number of specimens: ca. 90

Occurrence: Limestone member of the Caldas Formation, limestones in the Huergas Formation near Mirantes de Luna, abundant in the lower part of the Portilla Formation along the southern border of the Cantabrian Mountains.

*Coenosteum*: The form of the coenosteum is thinly laminar to compact. Generally the coenosteum is rather small, with thicknesses between a few mm and a few cm and lateral extensions up to a few dm. It may be free or encrusting. The mamelons are absent, low or very pronounced. The latilaminae are conspicuous in many specimens, in others they are rather vague. About half of the specimens are intergrown with *Syringopora* sp.

*Vertical section* (Pl. 24 fig. 3 – Pl. 26 fig. 4): The laminae are continuous, often dichotomous. They are rather straight in some specimens but irregularly undulating in others. The thickness of the laminae is extremely inconstant. The laminae may be very thick, microlaminar and vacuolate in some places and cyst-platelike in others (extremes 0.02–0.23 mm). Also there are specimens with latilaminae of alternating zones of thick and thin laminae.

lam/2 mm	specimen									
	27	32 G	260 F	333	479 E	509 A	510 A	580 B	580 E	583 C
13						1				
12				3				1		
11		1		4		5		2		2
10	2	2	1	2		4	2	4	1	5
9	2	4	4	1	5		3	2	3	2
8	5	2	4		4		4	1	3	1
7	1	1	1		1		1		3	

Some specimens have a few ring pillars but these are never a dominant feature in the Spanish material. Most specimens have 7–10 laminae in 2 mm but a few have more (see diagram).

The pillars are spool-shaped. They are randomly placed or superposed in a varying degree (not continuous!), depending on the regularity of the gross structure and on the degree of development of the mamelons. They are as thick as the laminae.

The interlaminar spaces are round, subrounded, elongated, or irregular. They are extremely variable in diameter because the larger ones grade into astrorhizal canals and the smaller ones into vacuoles (where laminae are dichotomous).

Cyst plates are more or less common in the interlaminar spaces and in the astrorhizae. The foramina in the laminae are also generally closed by cyst plates. The foramina are sometimes superposed.

Astrorhizae are visible in most sections. When present they are generally very conspicuous. They originate in the centres of the mamelons, but the astrorhizal tubes spread far into the tissue. These tubes are tabulated and round in cross-section. The astrorhizae can have a diameter up to 0.5 mm.

Latilaminae are vague in specimens with a regular gross structure but higher (4–6 mm) than in specimens with an irregular gross structure (1.5–4 mm) where latilaminae are generally very conspicuous.

**Tangential section** (Pl. 27 figs. 1, 2): The pillars are isolated, coalescent or form an amalgamated network, depending on how the section cuts through the tissue. The laminae are visible as vague dark bands or as concentric rings (in the mamelons). Well oriented sections in specimens with no or only very low mamelons show many isolated pillars and very vague broad laminae. Specimens with conspicuous mamelons scarcely have isolated pillars but the distinct laminae appear as concentric rings and an amalgamated network in the flatter parts of the section. Some specimens show isolated ring pillars in tangential sections. The astrorhizae are branched; tabulated tubes spread from the mamelons throughout the tissue.

**Microstructure** (Pl. 6 fig. 3 – Pl. 8 fig. 2): The microstructure of well preserved specimens is microlaminate (multilayered) and vacuolate. Most laminae have one clear zone in the centre but there are also laminae

which have only one layer, while in some places laminae have more than two layers separated by clear zones. Some vacuoles occur randomly in the microtissue especially on the peripheries, others occur in the central part of the laminae in an irregular row simulating ordinicellulae. However, they never form such a regular and constant microstructure as that in *Stromatoporella? selwyni*. Apart from the microlaminae and vacuoles the microtissue is compact.

In altered specimens the microstructure can have become diffuse and look compact. Other specimens have become strongly flocculent, transversely fibrous, melanospheric and pseudocellular, but these are all secondary features due to destruction or migration of specks and recrystallization.

#### Remarks

The present author (Sleumer, 1968) defined the species as having 7–10 laminae in 2 mm. Assuming that the spacing of laminae is rather constant, he excluded the finer specimens with ca. 11 laminae in 2 mm. Considering, however, the great variability of the spacing of the laminae in other species and the fact that there is a complete range of coarser to finer gross structure in this species, and not a distinct difference, the writer is now convinced that the few specimens with a finer gross structure are conspecific with the other ones. Moreover the finer specimens have the same stratigraphic range as the coarser ones and occur in the same layers. As a consequence the diagram given (Sleumer, 1968) of the number of laminae in 2 mm is not representative for the Spanish material of the species.

The Spanish specimens do not have less than 7 laminae in 2 mm in places where no astrorhizal canals are visible. Nevertheless it might be possible that specimens with a wider spacing of laminae (commonly described as *Stromatoporella curiosa*, *Stromatoporella solitaria*, *Stromatoporella eifelienses* or *Clathrocoilona eifeliensis*) could also turn out to be conspecific with the present species.

As described in the previous paper (Sleumer, 1968), not only the form of the coenosteum but also the gross structure of the species is highly variable. Features such as superposition of pillars, straightness of laminae, amount of ring pillars and cyst plates and thickness of the tissue are developed differently not only in different specimens but even in different places within

one coenosteum. These variations in the gross structure were caused by differences of individual ecological factors, thus they cannot be used for taxonomic purposes. Therefore the following might be synonyms of *Stromatoporella? granulata?*: *Syringostroma strahlenbergi* (Yavorsky, 1931, p. 1411), *Trupetostroma warreni* (Parks, 1936, p. 55; Galloway & St. Jean, 1957, p. 159; Galloway, 1960, p. 625), *Stromatoporella kayi* (Parks, 1936, p. 111), *Stromatoporella saginata* (Lecompte, 1951, p. 171), *Stromatoporella parasolitaria* (Galloway & St. Jean, 1957, p. 137), *Clathrocoelona eifeliensis* (Nicholson 1886) – (Flügel & Flügel, 1961, p. 378) and *Stictostroma maclareni* (Stearn, 1966b, p. 43).

The microstructure on the contrary is very consistent in well preserved specimens. It is always compact with clear layers and vacuoles. These vacuoles may lie in a row but do not form real ordinicellulars as in *Stromatoporella? selwyni*, where the laminae are continuously ordinicellular. The microstructure of *Stromatoporella? granulata?* (as defined in this paper) is basically compact with clear layers and vacuoles, which seem to have been empty spaces in the tissue. Unfortunately most specimens are more or less altered. Some have become so diffuse by migration of specks that clear layers and vacuoles can no longer be distinguished (these specimens were not included in the material previously described (Sleumer, 1968) to avoid possible admixture of species). Other specimens on the contrary look cellular due to recrystallization.

Strongly altered specimens can be distinguished by the round interlaminar spaces, the thick spool-shaped pillars, and the laminae which are very inconsistent in thickness, but confusion with specimens of the genus *Stromatopora* is very easy.

Nicholson (1873) described *Stromatopora granulata* without mentioning any features of the microstructure. Later (1874) he stated that the material on which his original description was based were all from the Corniferous Limestone. He also included specimens from the Hamilton group but did not give any description of the gross structure or the microstructure.

Nicholson (1886b) described the microstructure of *S. granulata* as 'minutely porous' and stated that in vertical sections the well developed laminae often have a median clear line. He considered the species very similar to *S. eifeliensis*. Nicholson (1886–92) also described the microstructure as 'minutely porous or penetrated by delicate canaliculi' while the laminae commonly exhibit a median clear line. However, he split the original species into two: viz. the true *S. granulata* occurring in the Hamilton Formation and *S. selwyni* from the Corniferous Limestone without mentioning any differences in microstructure, for both are described as 'minutely porous' but he did not mention 'median clear lines' in the latter, nor are they visible in the drawings from this species (Nicholson 1886–92, Pl. XXVI fig. 4). *S. granulata* has a median clear line in Pl. I fig. 5 but not in Pl. VII fig. 6 and Pl. XXVI fig. 1b. Parks (1936) stated that the 'median clear line' consists rather of 'a row of tiny

openings', so that his specimens might have been ordinicellular in the sense of Stearn (1966a) before recrystallization. As they were also collected in the Hamilton Formation in Arkona, Ontario, it is very probably that they are indeed conspecific with *S. granulata*.

Ripper (1937) described the microstructure of the laminae as 'porous' while Lecompte (1951) stated that it is 'bifide à axe clair'. He pointed to the fact that Nicholson (1886–92) restricted *S. granulata* sensu stricto to the Hamilton Formation, although the material described in 1873 only comes from the Corniferous Limestone as Nicholson himself stated in 1874.

Galloway & St. Jean (1957) described the laminae as 'composed of a single, thick layer of tissue with a clear median line and many anastomosing tubules'.

Stearn (1966a, p. 93, Pl. 15 figs. 6, 7) interpreted the microstructure of the holotype as ordinicellular, which 'may be expressed as a continuous axial clear zone in the lamina, in others as a series of pores crossing the lamina transversely' depending on the states of preservation.

Earlier the present writer (Sleumer, 1968) described the microstructure (apart from vacuolate) as 'multilaminar', 'tripartite' and 'multilayered' but now considers that the term 'microlaminate' might be more appropriate for this feature.

From the foregoing it becomes evident that, without studying Nicholson's collection, it is impossible to decide ultimately whether the type material of *S. granulata* actually has an altered microlaminate microstructure or an altered ordinicellular microstructure. Provisionally it is considered here to be microlaminate.

*Stromatoporella? selwyni* Nicholson, 1892  
(Pl. 27 fig. 3 – Pl. 31 fig. 2)

- 1886–92 *Stromatoporella granulata*. – Nicholson, Pl. I fig. 14.
- 1886–92 *Stromatoporella Selwynii* n. sp. – Nicholson, p. 205, Pl. XXVI figs. 2–4.
- 1936 *Stromatoporella selwynii* Nicholson. – Parks, p. 101, Pl. XVI fig. 8, Pl. XVII figs. 1, 2, (? 5, 6).
- 1957 *Stromatoporella selwyni* Nicholson. – Galloway & St. Jean, p. 133, Pl. 8 fig. 1.
- 1966a *Stromatoporella selwyni*. – Stearn, p. 94, Pl. 15 fig. 8.
- 1967 *Stromatoporella selwyni* Nicholson. – St. Jean, p. 440, Pl. 6 figs. 1, 2.
- 1968 *selwyni* Nicholson 1892, *Stromatoporella*. – Flügel & Flügel-Kahler, p. 382.

*Holotype*. – Nicholson 330 (see Stearn, 1966a, Pl. 15 fig. 8), British Museum of Natural History.

*Locus typicus*. – Port Colborne, Ontario.

*Stratum typicum*. – Corniferous Limestone, Middle Devonian.

*Diagnosis*

Coenosteum: form laminar, massive, conical or dendroid, free or encrusting; mamelons absent, very

low or pronounced; astrorhizae strongly branched or absent.

Vertical section: laminae ca. 5–12/2 mm; normally 0.05–0.12 mm thick; continuous, more or less undulating; generally rather thick.

ring pillars (formed by upturns of the laminae) absent, scarce, common, abundant or dominant. pillars placed at very variable distances from each other; as thick as laminae or slightly thicker; short, confined to one interlaminar space, sometimes more or less superposed. interlaminar spaces round, subrounded or irregular.

cyst plates scarce to abundant.

Tangential section: pillars isolated or connected by cyst plates.

ring pillars absent to extremely abundant.

Microstructure: ordincellular (one or more parallel rows), when diffuse or altered it looks compact, transversely fibrous or porous, flocculent or very vaguely tripartite.

#### Description of the material

Number of specimens: ca. 105

Occurrence: very common in the entire Santa Lucía

Formation, Couvinian limestones near Ventanilla and Limestone member of the Caldas Formation.

*Coenosteum*: The form of the coenosteum is very variable; it can be laminar (a few mm thick), massive (a few dm high), conical or even dendroid; free or encrusting. The mamelons are generally low to well developed. Latilaminae are more or less conspicuous in all specimens.

*Vertical section* (Pl. 27 fig. 3 – Pl. 30 fig. 2): The laminae are continuous, sometimes dichotomous, generally undulating to a varying extent but rather straight in some specimens. Sometimes there are foramina in the laminae. In some specimens laminae form small mamelon-like upturns. Ring pillars formed by upturns of the laminae may be absent, scarce, common, abundant or extremely dominant. Many of them have cyst plates. The thickness of the laminae is very variable from specimen to specimen and sometimes within one specimen. Generally the laminae have a thickness between 0.05 and 0.10 mm (extremes 0.02–0.18 mm). The number of laminae in 2 mm also shows a strong variation. Most specimens have ca. 5–10 but a few specimens have more as can be seen in the diagram.

lam/2 mm	specimen									
	480 B	LV510 C	519 B	520 R	522 D	522 H	528 B	529 C	532 B	533 A
15	1									
14				1						
13	1			1						
12	4		1					2		
11	2	1	2	2				2		
10	2	1		3		1		3		
9		1	1	3		2	1	2		
8		4	3		6	5	1	1	1	1
7		2	2		4	1	2		1	1
6		1	1			1	5		2	5
5							1		3	3
4									2	
3									1	

The pillars are randomly placed; in many specimens there is a tendency towards alternate placing of the pillars in such a way that every two interlaminar spaces pillars are more or less superposed, in other specimens pillars have a tendency towards superposition, especially when pillars are placed very close together. In many specimens normal pillars are replaced to a varying degree by ring pillars. The pillars are generally as thick or slightly thicker than the laminae. Their normal thickness is 0.05–0.11 mm (extremes 0.03–0.40 mm (when cut through the wall of a ring pillar)).

The interlaminar spaces are mostly round to subrounded; in many specimens they tend to be horizontally elongated, in other specimens growth-zones

occur with vertically elongated interlaminar spaces with cyst plates. Some specimens have very irregular galleries with many cyst plates. In specimens with abundant ring pillars it can be seen that more than one (sometimes even 4) ring pillars originate from one laterally elongated gallery (compare with Galloway, 1960, Pl. 71 fig. 3a). As can be seen from the figures the extent of cyst plates is very variable from specimen to specimen, and from place to place within one specimen.

Astrorhizae, when present, are situated in the mamelons but canals diverge widely into the tissue. The canals are tabulated, they vary greatly in diameter (up to 0.5 mm).

Latilaminae are scarcely recognizable in some specimens, while in others they are very conspicuous due to colour differences, alternating zones of coarse and fine gross structure and layers of repair tissue. They are 2–5.5 mm high.

**Tangential section** (Pl. 30 fig. 3 – Pl. 31 fig. 2): The pillars are seen as isolated round or irregular dots sometimes connected by cyst plates, the ring pillars are visible as small circles also partly connected by cyst plates. 0–100% of the vertical elements may be ring pillars. The obliquely cut laminae are visible as vague bands. The astrorhizae are situated in the mamelons but spread from there throughout the tissue. The centres of some mamelons are filled with fine repair tissue.

**Microstructure** (Pl. 8 fig. 3 – Pl. 10 fig. 4): The original microstructure is ordinicellular, thicker layers have more than one row of cellulae. This microstructure is easily destroyed during preservation, so only a very few specimens show this feature distinctly. In many specimens a vague zonation of the laminae is still visible in some parts of the thin section. In some specimens it even looks like a clear median line due to the destruction of walls between cells (see Stearn, 1966a). Most specimens look compact, flocculent or transversely fibrous or porous because the original microstructure is no longer recognizable. The microstructure follows the curves of the ring pillars. The microstructure of the normal pillars is very vague, in some pillars there seems to be a vague vertical zonation.

#### Remarks

As can be seen from the material this species shows a great variation in the form of the coenosteum. Two specimens are even more or less dendroid, having the same gross structure as the rest of the material. Unfortunately both consist only of very small fragments of the coenosteum, so that the shape of the latter cannot be reconstructed. Galloway & Ehlers (1960, p. 77) also described dendroid forms as *Stromatoporella*.

In the same way the gross structure is very variable. The ring pillars in particular are a conspicuous and very variable feature of the gross structure. In specimens with abundant cyst plates the latter occur also in the ring pillars.

Taking into account the great variability of the gross structure, probably many species can be placed in *S.?* *selwyni*. For example: *Stromatoporella damnoniensis* (Nicholson, 1886a, p. 237; 1886–92, p. 207; Galloway, 1960, p. 623), *Stromatoporella sniatkovi* (Yavorsky, 1931, p. 1409), *Stromatoporella pankratovi* (Yavorsky, 1931, p. 1410), *Stictostroma erienne* (Parks, 1936, p. 81; Lecompte, 1951, p. 137), *Stromatoporella eriensis* (Parks) – (Galloway & St. Jean, 1957, p. 145; Galloway, 1960, p. 622), *Stictostroma huronense* (Parks, 1936, p. 83), *Stromatoporella huronensis* (Parks) – (Galloway & St. Jean, 1957, p. 139) and *Stromatoporella* sp. (St. Jean, 1967, p. 442).

Species described by Nicholson are difficult to place

for he seems to have confused specimens with a clear median layer and specimens that are ordinicellular. Moreover his figures are idealized drawings according to Stearn (1966a, p. 95) and therefore very doubtful. Apart from this the original microstructure has been destroyed in most specimens, which makes it impossible to assign them to any species judging only from the figures and descriptions.

In some specimens a tendency towards superposition of the pillars is found. In these cases pillars are placed close together so that interlaminar spaces tend to be vertically elongated and generally have cyst plates. The better preserved specimens of this type show the same microstructure as the more common specimens, some of them even have abundant ring pillars. They look very much like some species described in the genus *Anostylostroma* by Galloway & St. Jean (1957). The specimens from Spain with no ring pillars and rather straight laminae also look very much like some species described as *Anostylostroma* but they have the same typical microstructure or at least remnants of it.

#### *Stromatoporella?* sp. 1

(Pl. 31 fig. 3 – Pl. 32 fig. 2)

#### Description of the material

Number of specimens: 31

Occurrence: Santa Lucía Formation, Limestone member of the Caldas Formation, lenses in the Huergas Formation near Mirantes, Portilla Formation.

**Coenosteum:** The coenosteum forms thin crusts of a few laminae on other organisms. Mamelons are generally absent. Frequently the coenostea are intergrown with aulopodid corals and bryozoans.

**Vertical section** (Pl. 31 fig. 3 – Pl. 32 fig. 2): The laminae are generally continuous but in some places rather irregular. In some specimens the laminae undulate independently from each other leaving open spaces between them. The laminae are thick to extremely thick, varying between ca. 0.05–0.30 mm.

The pillars are spool-shaped in relatively thick specimens; they may be superposed. They are about as thick as the laminae.

The interlaminar spaces are round to irregular with rounded corners, very variable in width. Cyst plates are rather rare. Astrorhizae, when present, are round in cross section. They spread throughout the tissue.

**Tangential section:** Tangential sections are difficult to obtain from these thin crusts. In more or less tangential sections pillars are seen as round, isolated or as coalescent. The laminae form thick masses or dark bands with irregular lighter lines. The astrorhizae are branching.

**Microstructure:** The microstructure is microlaminate. Most specimens are badly preserved and have a different colour than other stromatoporoids in the same section. By alteration most specimens have become flocculent to pseudocellular.



*Remarks*

Whether these specimens form one species or not, is difficult to say. Probably some of the samples found in the Portilla Formation are the beginning stages of coenostea of *Stromatoporella? granulata?* Other specimens, however, have a very typical appearance and do not occur together with this species. They look very much like *Trupetostroma* (?) *incrustans* (Hall & Whitfield) as described by Parks (1936, Pl. XI fig. 8, Pl. XII fig. 1) and *Stromatoporella obliterated* and *Stromatoporella spissa* mut. *latitexta* as described by Lecompte (1951, Pl. XXVI fig. 2, Pl. XXVII figs. 1-4, Pl. XXVIII figs. 1, 2). Many similar specimens have been described in, or transferred to, the genus *Clathrocoelona*. Some of the Spanish specimens (Pl. 3 fig. 6, Pl. 32 fig. 2) even have some similarity with *Diplostroma yavorskyi* Nestor as described by Kei Mori (1968, p. 71, Pl. II figs. 5, 6, Pl. XXIV figs. 5, 6).

*Stromatoporella? sp. 2*  
(Pl. 32 figs. 3, 4)

*Description of the material*

Number of specimens: 4

Occurrence: upper part of the Portilla Formation near Los Barrios de Luna and Veneros, lower Portilla Formation near Quintanilla de Babia.

*Coenosteam:* The coenosteam is laminar to massive (largest specimen 40 cm wide and 8 cm high). Latilaminae are present but not conspicuous. Mamelons were not seen.

*Vertical section* (Pl. 32 fig. 3): The laminae are continuous and rather straight. They are often dichotomous and sometimes have foraminae, generally closed by cyst plates. The thickness of the laminae is ca. 0.05–0.15 mm (extremes 0.03–0.25 mm). The number of laminae in 2 mm is normally 6–10.

The pillars are mostly superposed. They are more or less spool-shaped and as thick as the laminae or slightly thicker.

The interlaminar spaces are very variable in diameter. They are round to irregular with rounded corners. Cyst plates are abundant. They are in general more or less parallel to the laminae. Astrorhizae are common but seem to be rather short. They are wider than normal galleries and round in cross section. The latilaminae are 3–5 mm high.

*Tangential section* (Pl. 32 fig. 4): The pillars are round and isolated or connected by cyst plates. The laminae are seen as vague dark zones. The astrorhizae seem to be rather short.

*Microstructure:* The laminae are microlaminate and vacuolate. In some places there are many cyst plates parallel and very near to the laminae.

*Remarks*

The skeletal elements generally are thinner than those

of *Stromatoporella? granulata?*. In some zones of the coenosteam they are, however, very thick and similar to the species mentioned above. In other zones the tissue looks very much like that of *Synthetostroma actinostromoides* Lecompte, 1951, due to its microlaminate laminae and abundant horizontal cyst plates and the superposed pillars. For this reason the specimens can be considered as intermediates between what is called *Stromatoporella* and *Synthetostroma*. Except for one specimen they do not occur together with *Stromatoporella? granulata?*.

*Stromatoporella? sp. 3*  
(Pl. 33 figs. 1, 2)

*Description of the material*

Number of specimens: 2

Occurrence: middle Santa Lucía Formation near Aviados and uppermost part of the Argillaceous Limestone member of the Caldas Formation near Caldas de Luna.

*Coenosteam:* The form of the coenosteam is dendroid. The branches are ca. 1 cm in diameter.

*Axial section* (Pl. 33 fig. 1): The laminae are curved upwards in the middle of each branch. The distance between them is generally much wider in the centre of the branches than on the border where they tend to join each other or just come to an end, but sometimes the distance is rather equal in both places. The thickness of the laminae is ca. 0.07–0.20 mm. Foramina in the laminae are common.

The pillars are spool-shaped when they are rather short. When the laminae are far apart pillars are vermicular. They are more or less as thick as the laminae.

The interlaminar spaces are round to very irregular with abundant cyst plates. The tabulated astrorhizae are abundant but rather small and scattered throughout the tissue. So they do not form axial canals.

*Cross section* (Pl. 33 fig. 2): In the outer zone of the branches the cross sections through the laminae are visible. More to the centre an amalgamated network, formed by the obliquely cut pillars and laminae, is visible. In the centre of the branches the pillars are mostly seen as round dots, isolated or connected by cyst plates, or as coalescent. In some places cross sections through the astrorhizae are visible.

*Microstructure* (Pl. 12 fig. 8): Though the specimens are very flocculent, it can be seen in many places that the original microstructure of the laminae was microlaminate and vacuolate. In some places a dark median layer (tissue reversal?) seems to be present.

*Remarks*

Most authors would undoubtedly place these two specimens in the genus *Idiostroma*. But the present writer does not see the necessity of making apart genera for dendroid forms, and is thus in agreement with Stearn (1966a, p. 106).

*Stromatoporella?* sp. 4  
(Pl. 33 figs. 3, 4)

*Description of the material*

Number of specimens: 1

Occurrence: lower Portilla Formation north of Los Barrios de Luna.

*Coenosteum*: The specimen is ca. 1.5 cm high and a few cm long. Latilaminae are present, the mamelons are not conspicuous.

*Vertical section* (Pl. 33 fig. 3): The laminae are continuous but irregularly undulating. The thickness of the laminae is ca. 0.05–0.15 mm. There are 5–8 laminae in 2 mm. Typically the laminae form a series of superposed ring pillars in some places.

The normal pillars are spool-shaped, not superposed but randomly placed. They are as thick as the laminae.

The interlaminar spaces are round to irregular with rounded corners. Cyst plates are abundant, also in the ring pillars. The astrorhizae are wide and tabulated. They are placed in local upturns of the laminae. The latilaminae are ca. 3.5 mm high, marked by some repair tissue.

*Tangential section* (Pl. 33 fig. 4): The pillars are round, isolated to coalescent. The laminae are seen as vague zones or as (abundant) ring pillars. Pillars and ring pillars often are connected by cyst plates. The astrorhizae are not very conspicuous in this specimen.

*Microstructure*: The microstructure is diffuse and looks compact, but in some places a vague zonation can be seen in the laminae, in other places they even look ordinicellular.

*Remarks*

The specimen occurs together with *Stromatoporella? granulata?*. Unfortunately only one specimen could be found. It is characterized by the superposed ring pillars and by the microstructure which probably was originally ordinicellular. It looks very much like *Stromatoporella ozoraensis* as described by Birkhead (1967, p. 37, Pl. 3 fig. 7, Pl. 9 fig. 4).

Genus STROMATOPORA Goldfuss, 1826

Type species (monotypic): *Stromatopora concentrica* Goldfuss, 1826, *Petrefacta germaniae*, p. 22, Pl. VIII fig. 5 (Middle Devonian 'Übergangskalk', Gerolstein, Eifel, Germany).

*Stromatopora* Goldfuss, 1826, p. 21; Nicholson, 1886–92, p. 91; Ripper, 1937, p. 184; Ripper, 1938, p. 229; Lecompte, 1952, p. 263; Galloway & St. Jean, 1957, p. 164; Galloway, 1957, p. 447; Galloway, 1960, p. 627; Galloway & Ehlers, 1960, p. 50; Stearn, 1966a, p. 110; Stearn, 1966b, p. 54; Stearn & Hubert, 1966, p. 40; Birkhead, 1967, p. 68; St. Jean, 1967, pp. 422, 425; Flügel & Flügel-Kahler, 1968, pp. 568, 674.

*Diagnosis*

*Coenosteum*: laminar to massive and dendroid.

*Vertical section*: The horizontal elements of the skeleton are formed by thin cyst plates or by thick tissue fused with that of the pillars. Many specimens are almost entirely, or at least zonally, built up of well differentiated straight laminae with continuous microlaminae and superposed pillars.

The pillars may be completely fused with the laminae, partly long, thick and superposed in otherwise fused tissue, be long, straight and well differentiated from laminae or long and more or less tortuous, connected only by cyst plates.

Several types of gross structure may occur as growth zones in one coenosteum or one of these types may be dominant throughout one coenosteum.

Due to the generally thick tissue the interlaminar spaces are round to irregular with rounded corners.

The astrorhizae, if present, are tabulated. Frequently they are present as irregular canals in the coenosteum and thus are not very conspicuous. In other cases they are well differentiated from normal galleries and form branching tubes diverging from the top of the mamelons.

*Tangential section*: Pillars and laminae generally form an amalgamated tissue, but especially in the specimens which have a rather regular gross structure, some pillars are isolated. The astrorhizae, when present, are stellate or form irregular canals between the amalgamated tissue.

*Microstructure*: In well preserved specimens the microstructure is cellular. The cellulae may be randomly placed or in horizontal rows, especially in the laminae. In specimens with many superposed pillars they are often also vertically arranged, thus forming a reticulate pattern.

In altered specimens the microstructure has become flocculent or melanospheric, in other specimens it has become so vague that it looks compact.

*Discussion of the genus*

As in the other genera of the Stromatoporoidea, the species in this genus show a wide range of variation, not only in the form of the coenosteum but also in their gross structure. That is to say within one species, some specimens have developed a coenosteum mainly built up of vertical skeletal elements, others have developed mainly horizontal skeletal elements, still others have developed both vertical and horizontal skeletal elements, either fused or well differentiated, and finally some specimens have more than one of these types of gross structure as zones in the latilaminae.

In the same way there is an important variation concerning features such as: form of the coenosteum, height of the mamelons, presence or absence of astrorhizae, distinctness and height of latilaminae and the spacing of laminae and pillars. The so called 'pseudozooidal tubes' are not tubes at all. They are caused simply by superposed cyst plates in specimens in which the vertical skeletal elements are dominant and the

horizontal skeletal elements are mainly formed by cyst plates.

This implies, as stated before, that a species can only be distinguished and described properly if a large number of specimens is available. It also implies that a subdivision of the genus *Stromatopora* as proposed by various authors (Ripper, 1937, 1938; Lecompte, 1952; Galloway & St. Jean, 1957) cannot be made, for these forms are only ecological variations and not species. It even means that a distinction cannot be made between the genera *Paralleloporella*, *Stromatopora* and *Ferestromatopora*.

The genus *Paralleloporella* has been used mainly for specimens with very long pillars connected by cyst plates, but also specimens with well developed laminae and thus scarcely any 'pseudozooidal tubes' have been assigned to that genus (see Stearn, 1966a, p. 118).

Nicholson (1886-92, p. 95), Lecompte (1952, pp. 266, 289, 290) and others have also emphasized the similarity between the genera *Stromatopora* and *Paralleloporella*. Lecompte moreover believes (and this writer agrees) that the type specimen of *Paralleloporella ostiolata* has a rather altered (melanospheric) microstructure.

The genus *Ferestromatopora* has been used for specimens in which horizontal skeletal elements are dominant. But many specimens with well developed horizontal skeletal elements have at the same time thick superposed pillars. This is seen frequently in specimens from the Devonian of Spain but also in specimens from Belgium (see for example Lecompte, 1952, Pl. LIV figs. 2, 3). Other specimens have compact continuous microlaminae, or laminae composed of microlaminae. The microlaminae can be regarded as continuous cyst plates formed as a sheet throughout the coenosteum. This feature was probably caused by temporary standstills in growth, not only between the latilaminae but also frequently during the growth of the latilaminae (compare with *A. verrucosum*?).

There are specimens belonging to *Stromatopora* whose gross structures show well differentiated laminae and pillars, comparable with those of *Actinostroma*, therefore the main difference between *Stromatopora* and other genera is the microstructure but even that is not so different compared for example with that of *Stromatoporella? selwyni*.

The badly preserved specimens in particular have frequently been described in such dubious genera as *Syringostroma*, *Hermatostroma* and *Taleastroma* and are often confused with altered specimens of *Stromatoporella*. This is especially the case with species from which only very small areas are figured, as many figures are too small to see the gross structure and the magnification is insufficient for the recognition of the microstructure.

*Stromatopora concentrica* Goldfuss, 1826  
(Pl. 34 fig. 1 - Pl. 35 fig. 4)

1826 *Stromatopora concentrica nobis*. - Goldfuss, p. 22, Pl. VIII figs. 5a-c.

- 1886-92 *Stromatopora concentrica*, Goldfuss. - Nicholson, p. 164, Pl. III fig. 5, Pl. XI figs. 15-18, Pl. XX figs. 10-12, Pl. XXI figs. 1-3, Pl. XXIV figs. 9, 10.  
1952 *Stromatopora concentrica* Goldfuss. - Lecompte, p. 271, Pl. LIII figs. 1-4, Pl. LIV figs. 1-5.  
1968 *concentrica* Goldfuss 1826, *Stromatopora*. - Flügel & Flügel-Kahler, p. 83.

*Holotype*. - Goldfuss, 1826, Pl. VIII fig. 5 (see also Lecompte, 1952, Pl. LIII fig. 1), Paläontologisches Institut der Universität Bonn.

*Locus typicus*. - Gerolstein, Eifel, Germany.

*Stratum typicum*. - 'Uebergangskalk' (Middle Devonian).

### Diagnosis

Coenosteum: form laminar to massive, generally free; mamelons usually absent or low, sometimes conspicuous; astrorhizae mostly rather small, inconspicuous and scarce.

Vertical section: laminae ca. 6-7/2 mm; normally 0.10-0.30 mm thick; often only present as cyst plates; more or less fused with pillars but sometimes rather straight and continuous.

pillars ca. 6/2 mm; normally 0.15-0.30 mm thick; fused with laminae to rather dominant, long and tortuous with mainly cyst plates between them; in many specimens thick and long (continuous) pillars occur in the more or less amalgamated tissue.

interlaminar spaces round to irregular, laterally elongated in specimens with well developed horizontal skeletal elements but vertically elongated in specimens with dominant vertical skeletal elements.

cyst plates common to abundant.

Tangential section: pillars and laminae form an amalgamated network, some pillars are isolated.

Microstructure: cellular, cellulae in more or less horizontal rows. In altered specimens the microstructure is flocculent, melanospheric or may even look rather compact.

### Description of the material

Number of specimens: ca. 60

Occurrence: common in the Portilla Formation, along the southern border of the Cantabrian Mountains and in the limestones in the Huergas Formation near Mirantes.

*Coenosteum*: The form of the coenosteum is mostly more or less laminar but can have very large extensions (up to 30 cm high and 100 cm long). No encrusting forms have been found. The mamelons are absent to very low. The latilaminae are conspicuous in nearly all specimens, they are 1.2 to 6 mm thick. About half of the specimens are intergrown with *Syringopora* sp.

*Vertical section* (Pl. 34 fig. 1 - Pl. 35 fig. 3): Though the horizontal and vertical skeletal elements are more

or less fused, obvious tendencies to either a more horizontal growth or a more vertical growth can be seen.

Most specimens have latilaminae of ca. 1.2 to 2 mm, which consist of layers of amalgamated tissue separated by more or less continuous horizontal layers. In many specimens the amalgamated tissue exhibits a predominance of horizontal elements, although at the same time long and thick continuous pillars may be present.

The thickness of the horizontal elements varies from 0.02 mm (cyst plates) to 0.30 mm in the more or less continuous horizontal layers. The number of laminae in 2 mm is ca. 6–8 in specimens with dominant horizontal elements.

A few specimens show a strong tendency to vertical growth with more or less parallel pillars connected by cyst plates. However, this tendency is mostly only present in zones alternating with more horizontally grown zones thus forming latilaminae. In one specimen with very thick latilaminae the pillars are extremely strongly developed.

The thickness of the vertical elements varies from ca. 0.15 to 0.30 mm. The thickest are the long prominent pillars which occur rather randomly in many specimens. The number of pillars in 2 mm is ca. 5–7 in specimens with dominant vertical elements.

The interlaminar spaces are round to irregular. Frequently they are subdivided by cyst plates. Especially in specimens with strong vertical growth, the galleries are often superposed with only cyst plates between them. But these 'pseudozooidal tubes' have never actually been tubes at all.

The astrorhizae are not conspicuous in the material. When present they are only slightly wider than normal galleries.

Latilaminae are distinct in nearly all specimens. They are marked by more or less continuous layers, colour differences, alternating zones of differently developed tissue or by zones of repair tissue.

*Tangential section* (Pl. 35 fig. 4): Pillars and laminae form an amalgamated network. Nevertheless some pillars are seen as isolated dots. The astrorhizae are visible as irregular tubes.

*Microstructure* (Pl. 10 figs. 7, 8; Pl. 12 figs. 1–3, 7): The microstructure of well preserved specimens is cellular. The cellulae are frequently arranged in horizontal layers. When it has been altered the microstructure has become flocculent and melanospheric. Often it even looks rather compact.

#### Remarks

As can be seen from the material, this species shows a considerable variation in its gross structure. This variation is analogous with the variations found in species of other genera. However, the variability of the material from the Portilla Formation is far less extreme than that of the Santa Lucía Formation. This must be due to a greater uniformity of the palaeoecological

conditions during the sedimentation of the Portilla Formation. On the other hand part of the material from the Portilla Formation is nearly identical with part of the material from the Santa Lucía Formation. This makes it very probable that both groups of specimens actually belong to one species.

The specimens from the Santa Lucía Formation (provisionally described as *Stromatopora huepschi*?) lived partly in quieter water and thus grew more vertically with fewer and/or less distinct latilaminae, while the specimens from the Portilla Formation nearly all lived in very shallow water and thus showed a greater tendency to horizontal growth and all have conspicuous latilaminae.

Nicholson (1886–92), who described specimens with well developed latilaminae but with a rather vertical arrangement of skeletal elements, also pointed to the similarity of *S. concentrica* and *S. huepschi*. According to Nicholson *S. huepschi* is different because it is coarser, has no latilaminae and has better developed pillars and 'zooidal tubes'.

Lecompte (1952) described specimens which look very much like the specimens described in this paper. He also stated that the species must have a rather great variation. Further he discussed the specimens with a gross structure of well differentiated laminae and pillars and their relation to the specimens with an amalgamated gross structure. But he doubted whether the specimens described by Nicholson belong to *S. concentrica*.

According to Galloway (1957) the Belgian specimens described by Lecompte (1952) belong to *Ferestromatopora tyrganensis* but, as stated before, the present writer believes that what has been called *Ferestromatopora* is only a growth form of *Stromatopora* due to differences in ecological conditions.

The following species, among others, might also be identical with *S. concentrica*: *Stromatopora baskuskanensis* (Yavorsky, 1955, Pl. LIII figs. 7, 8), *Stromatopora tumula* (Yavorsky, 1955, Pl. LVI figs. 1–4) and *Ferestromatopora tyrganensis* (Yavorsky, 1955, Pl. LIX figs. 2, 3).

#### *Stromatopora huepschi* (Bargatzky, 1881)?

(Pl. 36 fig. 1 – Pl. 39 fig. 4)

- 1881 *Caenopora Hüpschii* n. sp. – Bargatzky, p. 290.
- 1886–92 *Stromatopora Hüpschii*, Bargatzky sp. – Nicholson, p. 176. Pl. X figs. 8, 9, Pl. XXII figs. 3–7, text-figs. 20a, b.
- 1952 *Stromatopora hüpschii* (Bargatzky). – Lecompte, p. 268, Pl. LII figs. 1–5.
- 1960 *Stromatopora* cf. *S. hüpschi* Bargatzky. – Galloway, p. 627, Pl. 74 fig. 2.
- 1967 *Stromatopora* sp. cf. *S. huepschi* (Bargatzky). – St. Jean, p. 422, Pl. 1 figs. 1–4.
- 1968 *hüpschii* Bargatzky 1881a, *Caenopora*. – Flügel & Flügel-Kahler, p. 190.

*Holotype*. – Bargatzky, no. 16 (see Lecompte, 1952, Pl. LII fig. 2), Paläontologisches Institut der Universität Bonn.

*Locus typicus*. – Büchel bei Paffrath, Germany.

*Stratum typicum*. – Paffrather Kalke (=Bücheler Schichten, upper Givetian).

### Diagnosis

Coenosteum: form laminar to massive or globular, generally free; mamelons generally absent or low; astrorhizae generally small.

Vertical section: laminae ca. 4–8/2 mm; normally 0.10–0.30 mm thick; frequently only represented by cyst plates throughout the coenosteum; when present, more or less fused with pillars to rather distinct, straight and continuous.

pillars ca. 3–8/2 mm; normally 0.10–0.40 mm thick; more or less fused with laminae but often dominant, long and tortuous with only cyst plates between them; in many specimens very thick, continuous pillars occur in amalgamated, mainly horizontally oriented tissue.

interlaminar spaces round to irregular, laterally elongated when horizontal skeletal elements are well developed, forming 'pseudozooidal tubes' when pillars dominate.

cyst plates common to abundant.

Tangential section: pillars and laminae form an amalgamated network, some isolated cross sections of pillars may occur.

Microstructure: cellular, cellulae may be irregularly placed, in horizontal rows or may even form a more or less reticulate pattern. Altered specimens are flocculent, melanospheric or look more or less compact.

### Description of the material

Number of specimens: ca. 95

Occurrence: uppermost La Vid Formation near Colle, middle Devonian limestones near Ventanilla, Santa Lucía Formation and Limestone member of Caldas Formation.

*Coenosteum*: The form of the coenosteum is laminar to massive (up to a few dm high). Many coenosteia are globular and some even appear to be branched. Unfortunately the latter are only small fragments which cannot be studied thoroughly. Only a few specimens seem to be encrusting. Distinct mamelons are absent in nearly all specimens but in some specimens they are rather obvious. Latilaminae are differently developed in each specimen. Some have very distinct latilaminae varying between 1.5 and 7 mm in height, in other specimens the latilaminae are rather vague to absent.

Some of the specimens are intergrown with *Syringopora* sp. and these are rather small in these specimens. One specimen is intergrown with an auloporid coral, while many specimens have borings.

*Vertical section* (Pl. 36 fig. 1 – Pl. 39 fig. 1): The horizontal and vertical skeletal elements are more or less fused. Nevertheless either the vertical or the horizontal elements may be dominant.

The laminae may be straight and continuous; irregular, fused with pillars; or partly to completely replaced by cyst plates. The form of the laminae varies not only from specimen to specimen but often also within one specimen, as growth zones of the latilaminae.

The thickness of the horizontal elements varies from 0.02 mm to more than 0.30 mm in some specimens with a very coarse gross structure. The number of laminae in 2 mm is 4–8 in specimens with fairly continuous horizontal elements. One specimen seems to have thin continuous microlaminae spaced irregularly but unfortunately it is badly preserved.

Many specimens have a strong tendency to vertical growth. In these specimens the pillars are long and tortuous or straight, while the horizontal elements are only or at least preponderantly represented by cyst plates. Other specimens have an amalgamated tissue in which thick, continuous pillars are more or less developed. Some specimens have some patches of cellular tissue only connected to the rest of the coenosteum by cyst plates.

The thickness of the pillars is ca. 0.10 mm up to 0.50 mm in the very coarse specimens. The number of pillars in 2 mm in coarse specimens with more or less continuous pillars is 3–5 and ca. 8 in the finest ones.

The interlaminar spaces are round to irregular with rounded corners. In the specimens with long pillars they are superposed with only cyst plates between them, thus forming 'pseudozooidal tubes'.

The astrorhizae are visible only in a few thin sections. They are irregular and not conspicuous.

The latilaminae are distinct in most specimens due to colour differences and growth zones, but in many specimens they are vague or nearly absent.

*Tangential section* (Pl. 39 figs. 2–4): Pillars and laminae form an amalgamated network. Some pillars are visible as isolated dots. The astrorhizae are seen as irregularly branched tubes.

*Microstructure* (Pl. 10 figs. 5, 6; Pl. 11 figs. 1, 4, 5, 8; Pl. 12 figs. 4–6): Well preserved specimens are cellular. The cellulae are frequently arranged in horizontal rows but are sometimes also arranged in vertical rows, giving a reticulate impression. In altered specimens the tissue has become flocculent, melanospheric or looks rather compact.

### Remarks

From the material of this species it becomes obvious that not only the spacing of the laminae and pillars but also the construction of the gross structure is extremely variable.

However, no subdivision of the material could be made since all intermediate stages occur between the extremes, so this author was forced to consider it as belonging to one species.

Moreover, part of the material looks very much like that from the Portilla Formation described in this paper as *Stromatopora concentrica*. Actually the varia-

tion of the latter, which is less extreme, fits in rather well with the variability of this species. So it is possible if not probable that they are conspecific species.

The name *Stromatopora huepschi* has provisionally been chosen because an important part of the material is nearly identical with specimens described by other authors as *S. huepschi*.

Nicholson (1886-92) described specimens with a 'reticulate' gross structure in which the pillars mostly exist as distinct structures with mainly cyst plates between them. Latilaminae are not clearly recognizable in these specimens. He compared *S. huepschi* with *S. beuthi*. In his opinion the difference between them is that *S. beuthi* has longer and more persistent pillars which are frequently seen as isolated dots in tangential sections.

Lecompte (1952) described specimens (including the type specimen and material originally described by Bargatzky as '*Caunopora placenta*') which partly are formed by long tortuous pillars with cyst plates between them and partly of fused laminae and pillars. In some places they have rather straight laminae, in other places they have patches of cellular tissue only connected to the surrounding tissue by cyst plates. These specimens conspicuously resemble many specimens from Spain.

Lecompte (1952) also pointed to the fact that Bargatzky's material shows such a great variability in the gross structure that it is very well possible that '*Caunopora placenta*' Bargatzky is identical with *S. huepschi*. This had already been proposed by Nicholson and Heinrich. Furthermore Nicholson accentuated the resemblance with *Parallelopore bucheliensis* (Bargatzky).

*Stromatopora* cf. *S. huepschi* as described by Galloway (1960) and St. Jean (1967) has the same microstructure (called maculate by the authors) as the Spanish material. The figures, especially those given by St. Jean (1967), show considerable influence by alteration.

Klovan (1966) considers that *Stromatopora* cf. *S. huepschi* as described by Galloway (1960) belongs to *Stromatopora cygnea* Stearn.

The following Devonian species also seem to be very similar to *S. huepschi*: *Stromatopora adleri* (Yavorsky, 1955, Pl. XLIX figs. 1-4, Pl. LIX fig. 6), *Stromatopora boiarschinovi* (Yavorsky, 1961, Pl. XXV figs. 3-5), *Stromatopora bucheliensis* Bargatzky - (Nicholson, 1886-92, p. 186), *Parallelopore bucheliensis* (Bargatzky) - (Lecompte, 1952, p. 290, including the holotype), *Parallelopore catenaria* (Birkhead, 1967, p. 77), *Stromatopora florifera* (Nicholson, 1886-92, p. 182), *Stromatopora pachytexta* (Lecompte, 1952, p. 275) and *Talestroma pachytexta* (Lecompte) - (Birkhead, 1967, p. 72).

*Stromatopora* sp. 1  
(Pl. 40 figs. 1, 2)

*Description of the material*

Number of specimens: 13

Occurrence: massive limestone in the Lebanza Formation near Lebanza (Pisuerga).

*Coenosteum*: The form of the coenosteum is laminar to globular up to ca. 25 cm high. Apparently not encrusting. Mamelons are present in all specimens but are always very low, conical. The latilaminae are ca. 3-5 mm high. They are present in all specimens. In some specimens there are a few corkscrew-like worms.

*Vertical section* (Pl. 40 fig. 1): Laminae and pillars are well differentiated in this species.

The laminae are formed by continuous straight compact microlaminae thickened on both sides by cellular tissue. The distance between the microlaminae is extremely variable. They are placed very near together between the latilaminae. The thickness of the laminae varies from 0.03 mm (not thickened) to ca. 0.20 mm.

The pillars are superposed, more or less straight, built up of cellular tissue. They are 0.05-0.20 mm thick, generally slightly thicker than the laminae. There are 8-12, generally 10, pillars in 2 mm.

The interlaminae spaces are round to irregular. Due to the fine gross structure and the thickness of the skeletal elements, they are relatively small. When the laminae are rather far apart, the interlaminae spaces may be subdivided by cyst plates. The astrorhizae are small, mostly superposed, situated in the mamelons and very common. The latilaminae are generally visible by alternating zones of narrowly and widely placed microlaminae. Intercalations of sediment also occur.

*Tangential section* (Pl. 40 fig. 2): The pillars are coalescent, some are more or less free. The laminae are vague. The astrorhizae are stellate.

*Microstructure* (Pl. 11 fig. 3): The microstructure is cellular, in some pillars it looks rather reticulate due to superposition of cellulae. In the altered specimens the microstructure has become rather vague.

*Remarks*

This species is characterized by its typical gross structure of long rather straight pillars and continuous laminae and microlaminae. This is an atypical gross structure for a *Stromatopora* and is similar to the gross structure of *Actinostroma*. But the microstructure is distinctly cellular and as straight, continuous laminae and microlaminae as well as long pillars also occur in the other species of *Stromatopora*, there is no reason for not placing this species in the present genus.

As all the material has come from only one layer in one outcrop and the variation in gross structure is

minimal, the total variability of the species cannot be determined.

The species is quite similar to: *Parallelopora typicalis* (Galloway & St. Jean, 1957, p. 210; St. Jean, 1967, p. 428), *Stromatopora monticulifera* Winchell (Galloway & Ehlers, 1960, p. 51 (badly preserved)), *Parallelopora winchelli* (Galloway & Ehlers, 1960, p. 57), *Stromatopora yakovlevi* (Yavorsky, 1961, Pl. XXV figs. 6–8) and *Stromatopora* sp. (St. Jean, 1967, p. 423).

*Stromatopora* sp. 2  
(Pl. 40 fig. 3)

*Description of the material*

Number of specimens: 3

Occurrence: Portilla Formation near Los Barrios de Luna and Piedrafita de Babia.

*Coenosteum*: The form of the coenosteum is laminar (a few cm thick) with well developed mamelons but very vague latilaminae, ca. 5 mm high.

*Vertical section* (Pl. 40 fig. 3): Laminae and pillars are amalgamated in some zones of the coenosteum, but in other zones they are well differentiated. The laminae are partly fused with the pillars, partly straight, continuous and partly only represented by cyst plates. The thickness of the laminae varies from 0.02 mm (cyst plates) to ca. 0.30 mm. The number of laminae in 2 mm is 5–8.

The pillars are thick. They are superposed in the zones where they are not fused with the laminae. The thickness of the pillars is ca. 0.10–0.30 mm. The number of pillars in 2 mm is ca. 6.

The interlaminar spaces are round to irregular. Frequently the interlaminar spaces are superposed with only cyst plates between them. Astrorhizae seem to be quite common. They are rather distinct and situated in the mamelons. Latilaminae are absent or scarcely recognizable. They are marked by a discontinuity of the structures with some repair tissue.

*Tangential section*: Pillars and laminae form an amalgamated network. The astrorhizae are irregularly branched.

*Microstructure* (Pl. 11 figs. 6, 7): The microstructure is cellular. The cellulae are rather regularly arranged in some parts. Some laminae have compact continuous microlaminae.

*Remarks*

It is highly probable that these specimens belong to *Stromatopora concentrica*. They occur together with this species and the only difference is that they have a more regular gross structure and scarcely any latilaminae, which indicates that they grew in quiet, almost undisturbed conditions.

Unfortunately the present writer (Sleumer, 1968, fig. 18) confused one of the specimens (478A) with

*Stromatoporella granulata*. Actually the gross structure of this specimen is similar to that of *Stromatoporella? granulata?*, but in some parts the fused laminae and pillars form a gross structure which is typical for *Stromatopora*. Some laminae show very distinct microlaminae but nevertheless most of the tissue is slightly altered cellular to reticulate. Moreover microlaminae are not uncommon in *Stromatopora* so the writer is now convinced that the specimen belongs to this genus.

Specimens similar to those described above are: *Stromatopora cooperi* (Lecompte, 1952, Pl. LX figs. 2, 4) and *Stromatopora pachytexta* (Lecompte, 1952, Pl. LIV fig. 6).

*Stromatopora* sp. 3  
(Pl. 40 fig. 4; Pl. 41 figs. 1, 2)

*Description of the material*

Number of specimens: 2

Occurrence: middle Santa Lucía Formation north of Aviados, lower part of the Limestone member in the Caldas Formation near Caldas.

*Coenosteum*: Both specimens are laminar, ca. 2 cm thick. The mamelons are very low. The latilaminae are ca. 8 mm high in one specimen and 3–5 mm in the other one.

*Vertical section* (Pl. 40 fig. 4; Pl. 41 fig. 1): In general the skeleton is well differentiated into straight, continuous laminae and mostly long superposed pillars but where the laminae are farther apart, horizontal and vertical skeletal elements are fused in the manner typical of *Stromatopora*.

The laminae exist of a dark compact axial line, thickened by cellular tissue on both sides, especially on the lower side. In some parts, generally on the upper side, the cellular tissue is lacking. The thickness of the laminae is ca. 0.10–0.20 mm. The distance between the straight laminae is extremely variable. In some zones there are 8 laminae in 2 mm while in other zones the distance between two laminae is more than 1.5 mm.

The pillars are generally superposed, where the laminae are far apart they are tortuous. They are ca. 0.10–0.30 mm thick. There are ca. 5 pillars in 2 mm.

The interlaminar spaces are round to irregular and especially where the laminae are far apart, they are full of cyst plates, which are usually curved upwards. The astrorhizae are scarcely distinguishable from normal galleries, they are only wider. Latilaminae have been formed by alternating zones of widely and closely spaced laminae in the one specimen and by interruptions of the tissue, accompanied by intercalations of sediment, in the other specimen.

*Tangential section* (Pl. 41 fig. 2): The pillars are isolated to coalescent, partly connected by cyst plates. The laminae are visible as vague dark bands, in some of them the coarse cellulae are visible. The astrorhizae are abundant, strongly branching.

**Microstructure** (Pl. 11 fig. 3): The microstructure is coarsely cellular especially in the thickening tissue of the laminae. In many places the microstructure is diffuse due to alteration.

#### Remarks

It is obvious from the vertical sections that the continuous laminae, formed by microlaminae, irregularly thickened with cellular tissue, are not a constant feature of the coenosteum as they alternate with irregular gross structures, normal in the genus *Stromatopora*. They are in fact analogous to the continuous laminae in *Actinostroma verrucosum*? as described above.

In *Stromatopora huepschi*? also some specimens occur with zones of a rather regular gross structure and continuous microlaminae, but these have a finer microstructure. On the other hand, the microstructure of the irregular tissue in the present specimens is not coarse at all. On the contrary, in the tortuous pillars the microstructure is often scarcely recognizable. Therefore it is probable that the two specimens belong to *Stromatopora huepschi*?, they are only of a quite aberrant type.

Species which are very similar to these two specimens are: *Stromatopora dubia* (Lecompte, 1952, p. 279), *Stromatopora pellucida* (Yavorsky, 1955, Pl. XLVIII figs. 5, 6), *Stromatopora pellucida* var. *artyschtsensis* (Yavorsky, 1955, Pl. LII figs. 1, 2) and *Stromatopora flexuosa* (Yavorsky, 1955, Pl. LV figs. 1–6).

*Stromatopora* sp. 4  
(Pl. 41 figs. 3, 4)

#### Description of the material

Number of specimens: 1

Occurrence: uppermost Portilla Formation near Veneros.

**Coenosteum:** The specimen has a small coenosteum ca. 2 cm high and 3 cm wide. The mamelons are low, latilaminae are ca. 3 mm high but they are extremely vague.

**Vertical section** (Pl. 41 fig. 3): The skeleton is built up of long continuous pillars with cyst plates between them, but in some parts it is formed by an amalgamated tissue in which no vertical or horizontal skeletal elements are differentiated. The pillars are generally 0.05–0.20 mm thick. There are 7–9 pillars in 2 mm.

Interlaminar spaces are round to irregular, generally superposed and only separated vertically by cyst plates. Tabulated astrophorizae are abundant and conspicuous. Their diameter is ca. 0.3 mm. Latilaminae are difficult to recognize in thin sections.

**Tangential section** (Pl. 41 fig. 4): In the tangential section an amalgamated network can be seen. The astrophorizae diverge from the mamelons.

**Microstructure:** The tissue is cellular. The cellulae are more or less superposed. By alteration the microstructure has become melanospheric in many places.

#### Remarks

This specimen is characterized by its relatively fine gross structure with a very strong vertical growth so that horizontal skeletal elements are only represented by cyst plates. In the mean time latilaminae are nearly absent.

The specimen looks very much like *Parallelopora paucicanaliculata* (Lecompte, 1952, p. 294) and *Stromatopora dybowski* (Yavorsky, 1955, Pl. XLVII figs. 1–5).

### SAMENVATTING

In dit proefschrift worden de stromatoporen beschreven uit het Devoon in het zuidelijk deel van het Kantabrisch Gebergte. Het Devoon is hier ontsloten ongeveer van Villablino in het westen tot Cervera de Pisuerga in het oosten.

Stromatoporen worden in het Kantabrisch Gebergte alleen in het Devoon gevonden. Zij komen samen met tabulate en rugose koralen voor en verder met brachiopoden, bryozoën en crinoiden. Te zamen met deze organismen vormen zij biostromen of anders lagen die hoofdzakelijk bestaan uit brokstukken en omverworpen kolonies. Het sediment dat tussen de kolonies afgezet werd, kan variëren van zeer fijn, bitumineus tot zeer grof, maar slecht gesorteerd.

Aangezien de meeste stromatoporen min of meer omgezette structuren vertonen, werd bij het onderzoek speciaal de nadruk gelegd op de mikrostructuren en de wijze waarop zij omgezet kunnen worden. Er konden

vier primaire mikrostructuren onderscheiden worden: kompakt, mikrogelaagd, gelaagd-cellulair en cellulair. De omzetting van deze mikrostructuren begint in vele gevallen reeds voor de fossilisatie. Het weefsel wordt vlokkig door het verplaatsen en/of verdwijnen van pigmentkorrels.

Na de fossilisatie verandert de mikrostructuur vooral door migratie van pigmentkorrels langs schuifvlakken en door rekristallisatie van de calciet. Ook verkiezeling kan verandering in de mikrostructuur teweeg brengen.

De taxonomie der stromatoporen is nog uiterst vervaard. In deze publikatie werd de primaire mikrostructuur als hoofdkenmerk gebruikt bij het bepalen van genera. De uitwendige vorm van het skelet en eigenschappen van de inwendige bouw, zoals b.v. het boven elkaar staan van pilaren, het al of niet aanwezig zijn van ringpilaren, de onderlinge afstand van laminae en pilaren, werden sterk beïnvloed door ecologische



faktoren. Daarom zijn zij ongeschikt als genuskenmerk en vaak zelfs als soortkenmerk.

Bij het verzamelde materiaal konden vier genera onderscheiden worden: *Actinostroma* (kompakt met doorlopende pilaren), *Stromatoporella?* (mikrogelaagd), *Stromatoporella?* (gelaagd-cellulair) en *Stromatopora* (cellulair). *Stromatoporella?* moet gesplitst worden in twee genera. Het is niet duidelijk welke mikrostructuur het type-exemplaar van *Stromatoporella granulata*, de type soort van het genus, heeft.

*Geronostroma* en *Atelodictyon* worden beschouwd als synoniemen van *Actinostroma*. De genera *Clathrocoelona*, *Trupetostroma* en sommige soorten van *Stictostroma* en misschien *Idiostroma* kunnen verenigd worden met de mikrogelaagde soorten van het genus *Stromatoporella*. De soorten met gelaagd-cellulaire mikrostructuur kunnen ook gekombineerd worden

in één genus samen met sommige soorten van de genera *Stictostroma* en *Anostylostroma*. *Parallelopora* en *Ferestromatopora* worden beschouwd als synoniemen van *Stromatopora*.

Bij de determinatie van soorten werd een poging gedaan om, binnen elke soort, de variatiebreedte te bepalen van de inwendige bouw. Aangezien deze variatiebreedte nogal groot is, werden soortdeterminaties alleen gedaan als genoeg materiaal beschikbaar is. Wanneer dit niet het geval is werd alleen het genus bepaald.

De volgende soorten werden beschreven: *Actinostroma papillosum*, (= *A. clathratum*), *A. verrucosum?*, *A. stellulatum*, *Stromatoporella? granulata?* (mikrogelaagd), *S.? selwyni* (gelaagd-cellulair), *Stromatopora concentrica* en *Stromatopora huepschi?*.

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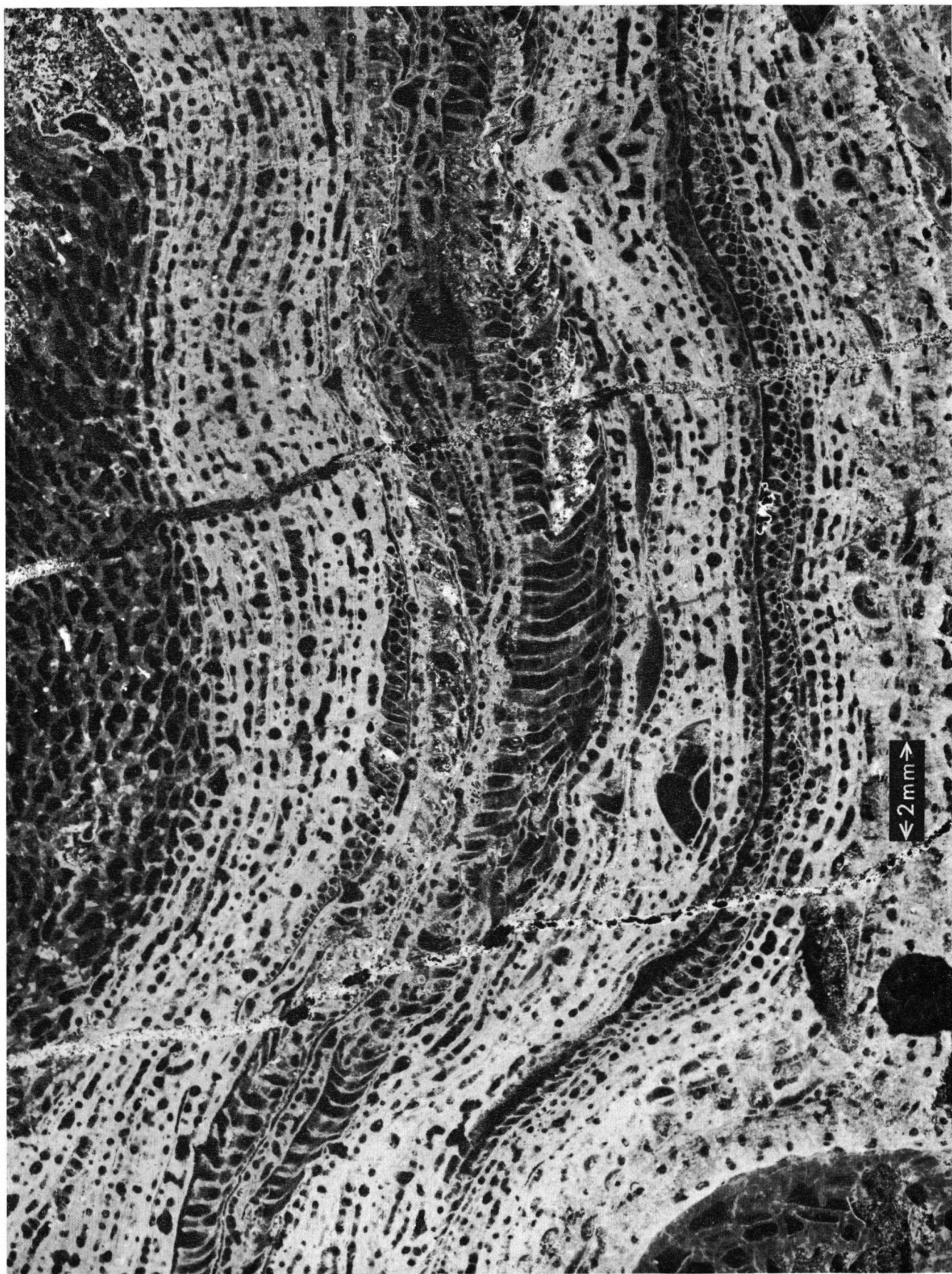
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## PLATES

PLATE 1

(Specimen 428B, Portilla Fm.). Alternate mutual encrustations of *Chaetetes* sp. and *Stromatoporella? granulata?*. The encrustations are overgrown finally by *Alveolites* sp. Vert. section, negative.



## PLATE 2

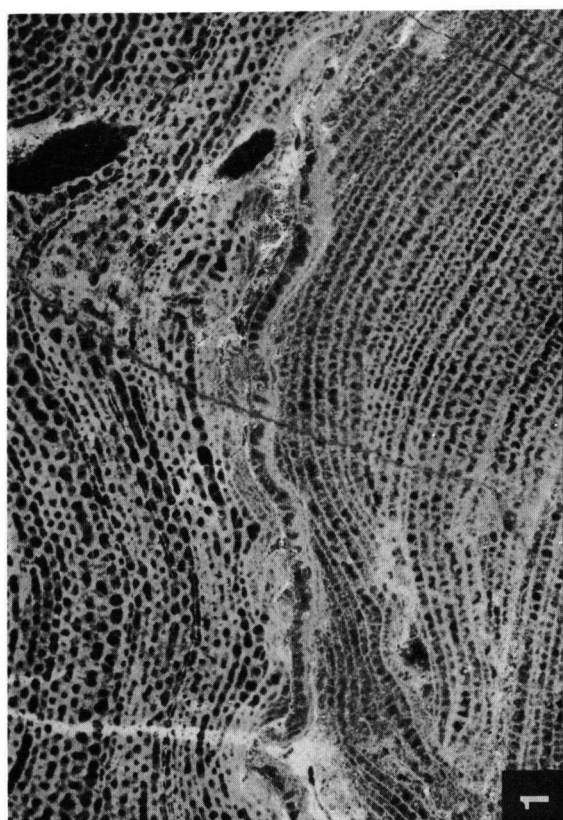
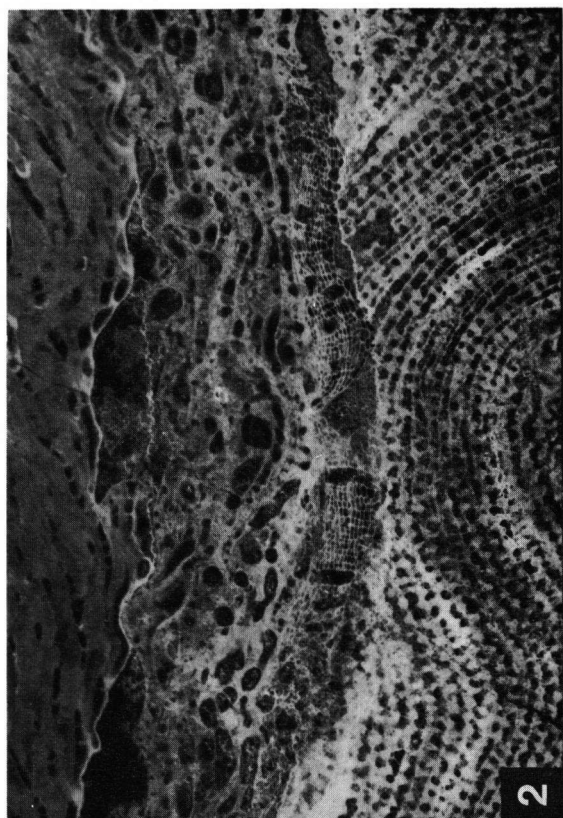
Fig. 1. (Specimen 520D, S. Lucía Fm.). The eroded surface of an *Actinostroma* sp. (obliquely cut) is encrusted by a thin layer of *Stromatoporella*? sp. 1 which is overgrown by *Stromatoporella*? *selwyni*. The latter has repair tissue at the base. Vert. section, negative, X 8.

Fig. 2. (Specimen 349, Portilla Fm.). An abraded coenosteum of *Actinostroma stellulatum* is encrusted by a bryozoan which is overgrown by *Stromatoporella*? sp. 1 which in its turn is overgrown by *Coenites* sp. Vert. section, negative, X 8.

Fig. 3. (Specimen 533G, S. Lucía Fm.). Worm tube? intergrown with *Actinostroma papillosum*. Vert. section, negative, X 8.

Fig. 4. (Specimen 533F, S. Lucía Fm.). Worm tube? intergrown with *Actinostroma verrucosum*?. See also Pl. 20 fig. 3. Note repair tissue in the opening of the tube. Vert. section, negative, X 8.

Fig. 5. (Specimen 528A, S. Lucía Fm.). Fragmented specimen of *Actinostroma verrucosum*? with boring. Many borings are partly or entirely filled up with sediment. The mud even penetrates the surrounding galleries. Note abrasion surfaces between some latilaminae. Vert. section, negative, X 8.





### PLATE 3

Fig. 1. (Specimen 32G). Pigment specks in *Stromatoporella? granulata?*. In the gallery (upper part) also some specks are present. Covered vert. thin section, X 500.

Fig. 2. (Specimen 473L). Peel of *Actinostroma papillosum* showing 'tubular network' in a pillar. The 'tubes' are caused by irregularities of the etching surface. Vert. section, X 500.

Fig. 3. (Specimen 479B). Peel of *Stromatoporella? granulata?* showing migration of 'tubes' along slip planes towards the gallery (below). Vert. section, X 500.

Fig. 4. (Specimen 32G). 'Tubes' on the surface of an uncovered thin section. The 'tubes' disappear when the section is wetted or impregnated with paraffin oil. They are caused by irregularities on the surface of the section. Same specimen as in fig. 1. Vert. section, X 500.

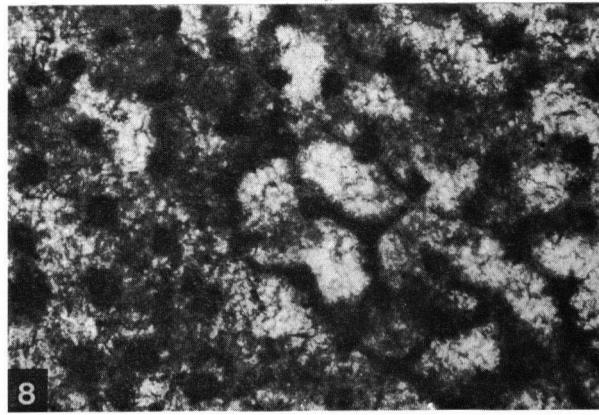
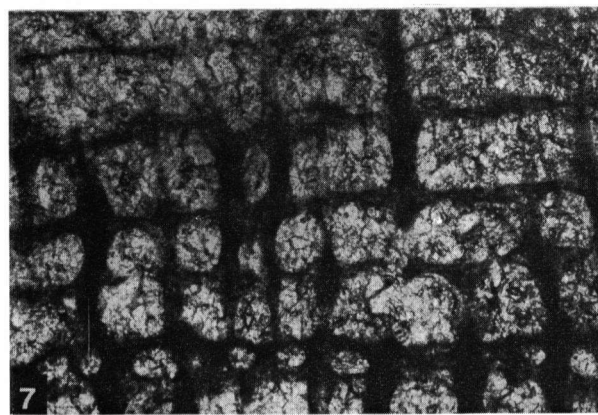
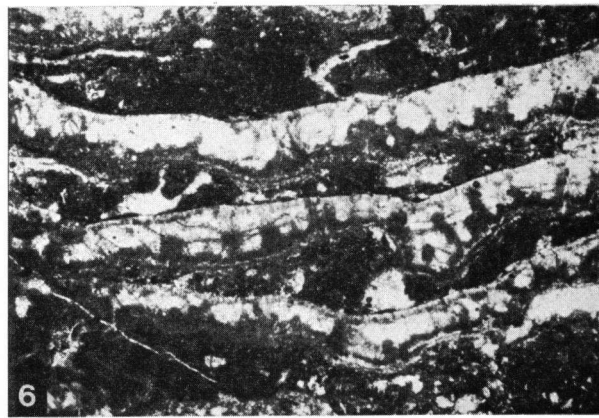
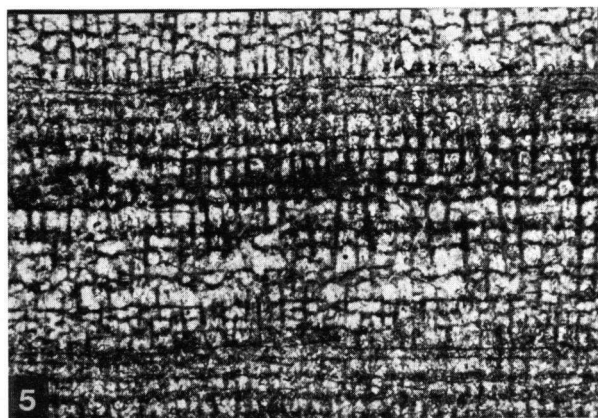
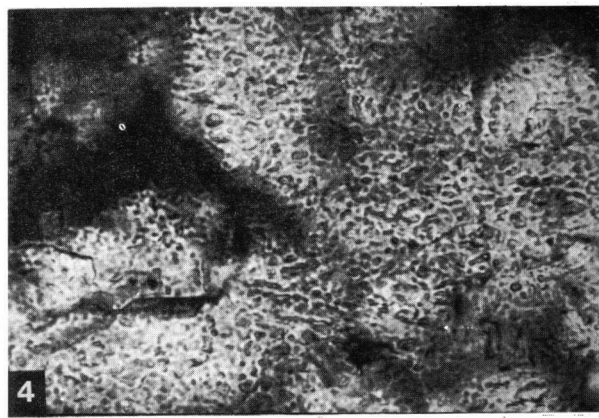
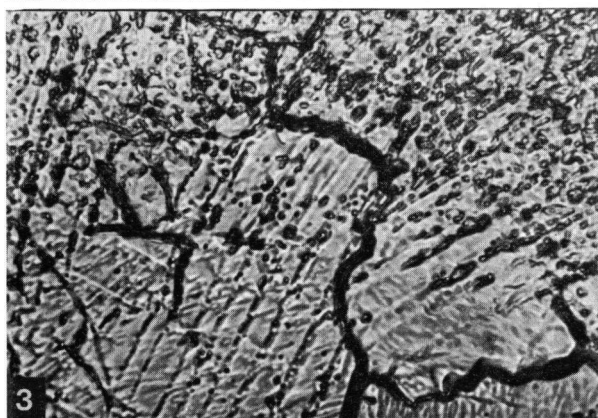
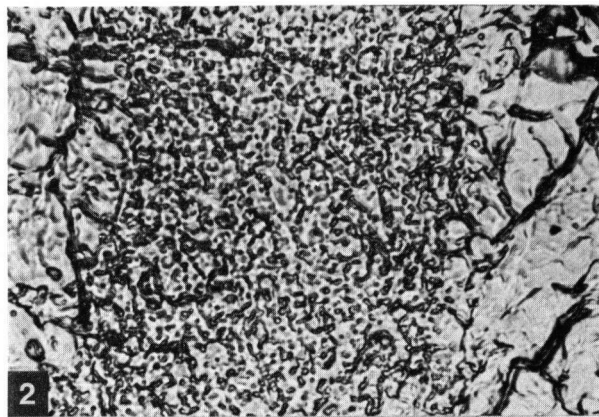
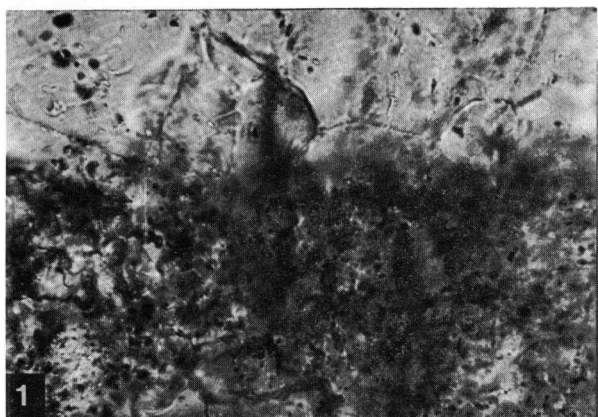
Fig. 5. (Specimen 532H). Flocculent *Actinostroma papillosum* with lighter and darker zones in the latilaminae. Vert. section, X 10.

Fig. 6. (Specimen 520D). Thin crusts of *Stromatoporella* sp. 1, leached on their upper surface before sedimentation. Vert. section, X 10.

Fig. 7. (Specimen 473L). Well preserved *Actinostroma papillosum* showing a compact microstructure, though in some places the skeleton is slightly altered. Note the thin continuous cyst plates in the upper part. Vert. section, X 40.

Fig. 8. (Specimen 473L). Tangential section of the same specimen as fig. 7. In some pillars concentration of specks along the periphery has taken place. The obliquely cut cyst plates are visible as 'arms'. When the cyst plates are nearly parallel to the section they appear broad and vague. Tang. section, X 40.





#### PLATE 4

Fig. 1. (Specimen 473L). Peel of the same specimen as in Pl. 3 fig. 7, showing the random crystal pattern. Within the tissue crystal boundaries are mostly absent or vague. Vert. section, X 100.

Fig. 2. (Specimen 473L). Tangential peel of the same specimen as in Pl. 3 fig. 7, showing the large crystals in the interlaminar spaces. Crystal boundaries generally do not enter the tissue. Tang. section, X 100.

Fig. 3. (Specimen 543D). Less well preserved *Actinostroma papillosum*. The pillars in particular are vague. The galleries are in part filled with brownish calcite. Vert. section, X 40.

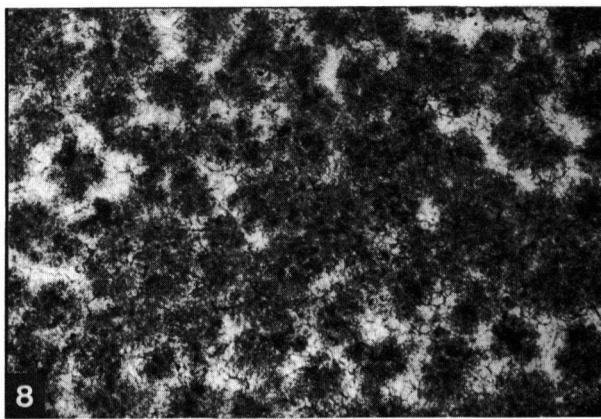
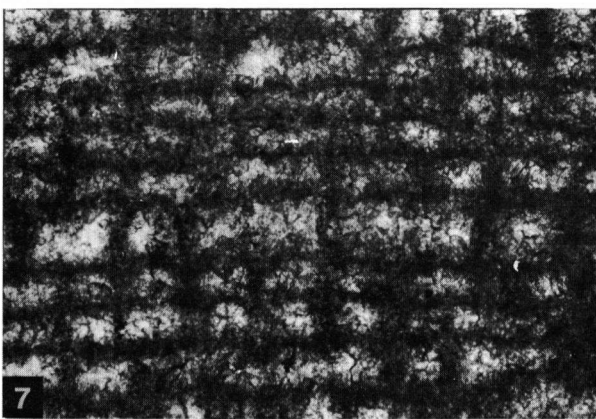
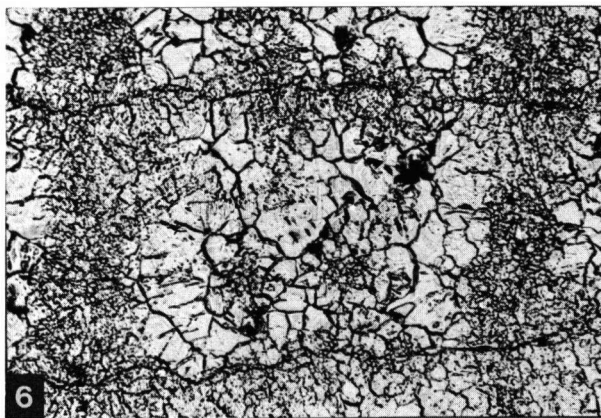
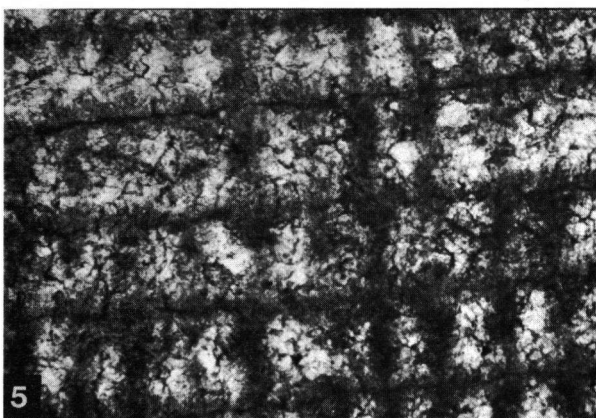
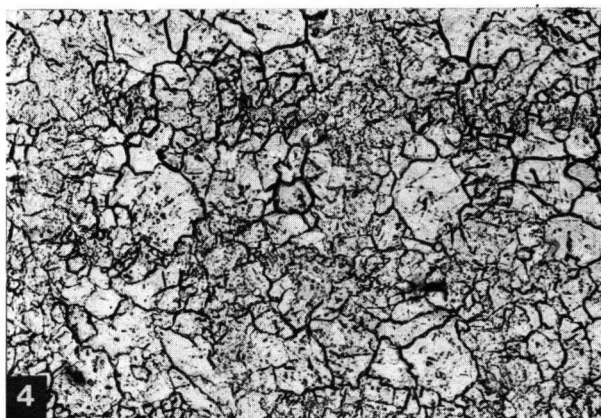
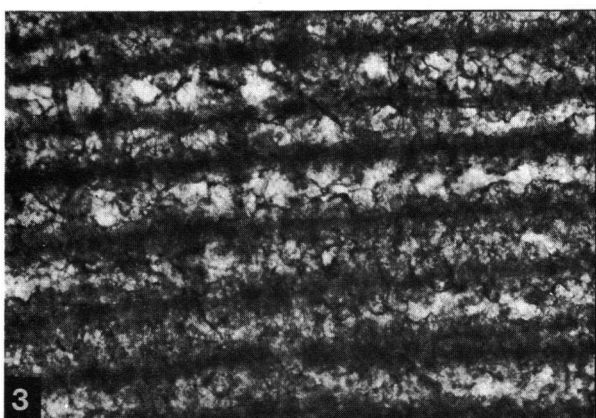
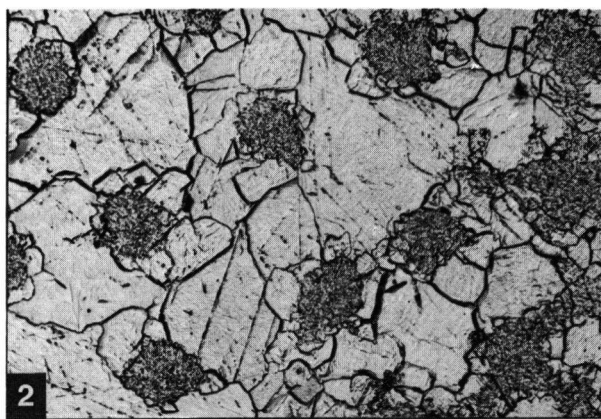
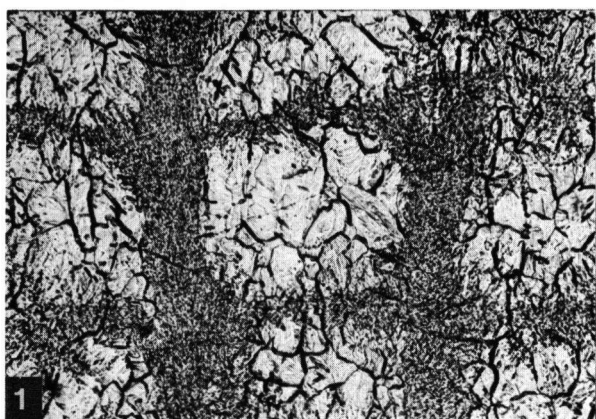
Fig. 4. (Specimen 543D). Peel of the same specimen as in fig. 3, showing a recrystallized crystal pattern. Within the tissue the crystals are small. In the galleries the crystals are larger. They contain a considerable amount of specks. Vert. section, X 100.

Fig. 5. (Specimen 532E). Slightly flocculent *Actinostroma verrucosum*?. Some laminae have a dark central axis. Vert. section, X 40.

Fig. 6. (Specimen 532E). Peel of the same specimen as in fig. 5, showing the dark lines of the laminae. Vert. section, X 100.

Fig. 7. (Specimen 532A). Strongly flocculent *Actinostroma papillosum* with some transverse fibrosity in the laminae. Vert. section, X 40.

Fig. 8. (Specimen 532A). Tangential section of the same specimen as in fig. 7, showing the flocculency in the pillars. Tang. section, X 40.



## PLATE 5

Fig. 1. (Specimen 426). Transverse porosity in *Actinostroma stellulatum*. Vert. section, X 40.

Fig. 2. (Specimen 426). Peel of the same specimen as in fig. 1. The large crystals in the galleries have partly penetrated into the tissue. In some crystals slip planes are visible. Vert. section, X 100.

Fig. 3. (Specimen 426). Tangential section of the same specimen as in fig. 1. Many pillars have more or less radial structures. The laminae are dissolved into flecks. Tang. section, X 40.

Fig. 4. (Specimen 426). Tangential peel of the same specimen as in fig. 1. In the lower part the pillars are isolated, as the section cuts through the galleries. Note the distinct crystal boundaries going from pillar to pillar without entering them. In the higher part the pillars are cut within the laminae which are penetrated by small and large clear crystals. Tang. section, X 100.

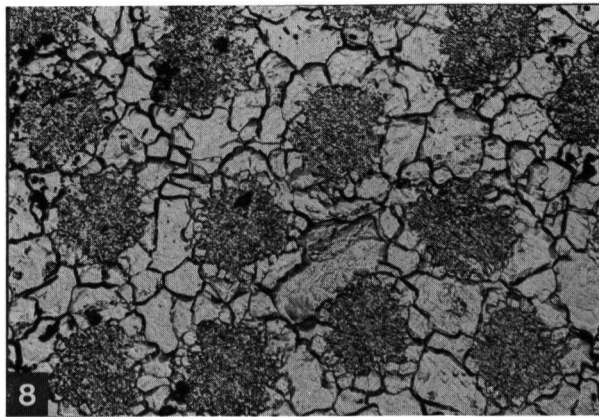
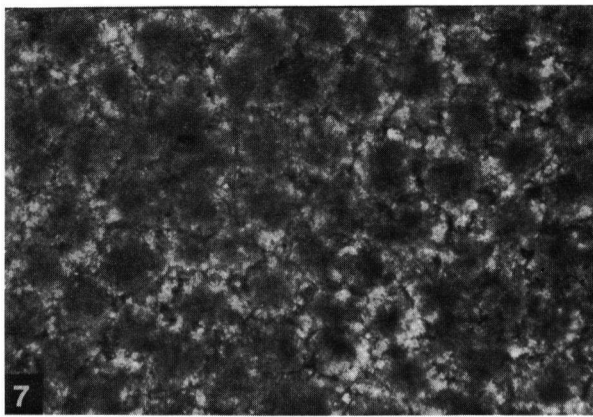
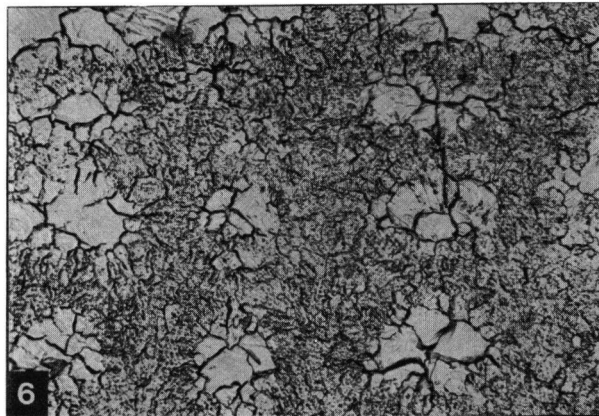
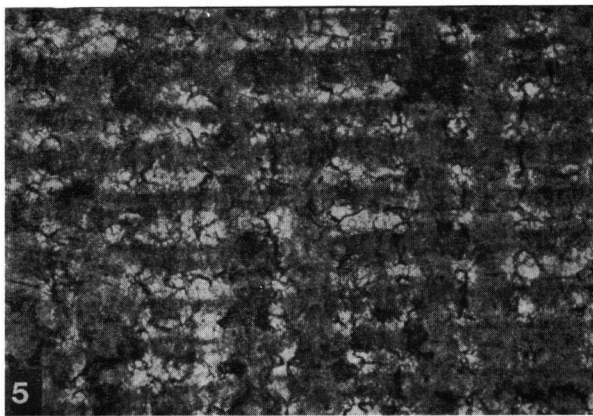
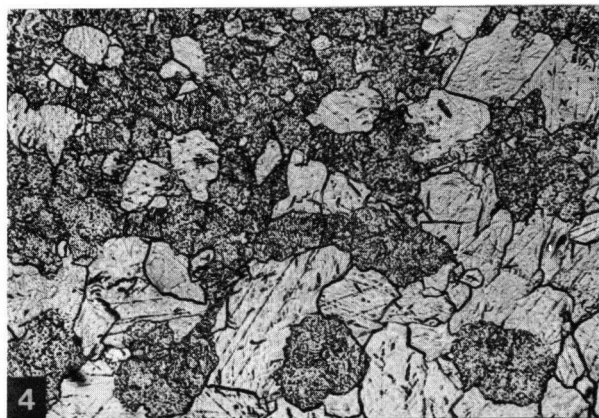
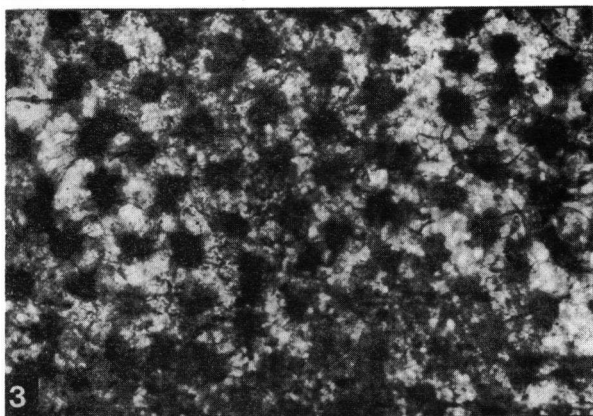
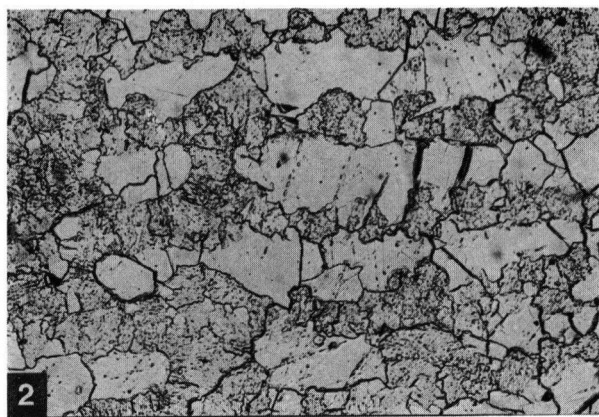
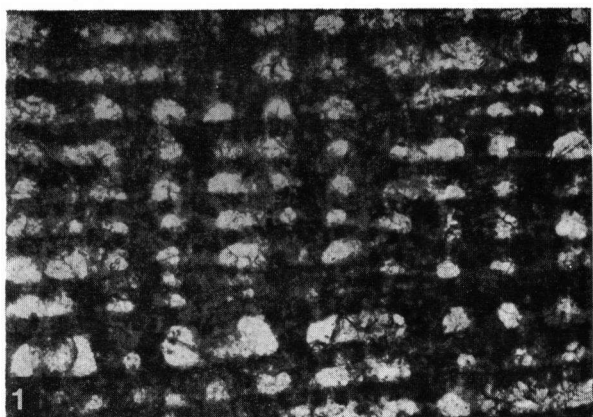
Fig. 5. (Specimen 456C). Transverse fibrosity in *Actinostroma stellulatum*. The boundaries of the tissue are vague due to migration of specks. Vertical cracks have developed between the pillars. Vert. section, X 40.

Fig. 6. (Specimen 456C). Peel of the same specimen as in fig. 5. With many, more or less vertical crystal boundaries in the laminae: the cause of the transverse fibrosity. Vert. section, X 100.

Fig. 7. (Specimen 456C). Tangential section of the same specimen as in fig. 5. The vague pillars are surrounded by crystal boundaries. Tang. section, X 40.

Fig. 8. (Specimen 456C). Tangential peel of the same specimen as in fig. 5. The pillars are concentrically surrounded by small and large crystals. Within the tissue no crystal boundaries are visible. Tang. section, X 100.





## PLATE 6

Fig. 1. (Specimen 304B). Strongly altered *Actinostroma stellulatum*. The melanospheres are mostly vertically arranged along the pillars. By migration of specks many galleries have completely disappeared. Vert. section, X 40.

Fig. 2. (Specimen 304B). Peel of the same specimen as in fig. 1. The interlaminar spaces are filled with a few large crystals or have almost or completely disappeared. By migration of specks along slip planes the tissue has broadened secondarily. Vert. section, X 100.

Fig. 3. (Specimen 32G). Well preserved *Stromatoporella? granulata?* with clear layers and vacuoles. The tissue is already slightly flocculent. Vert. section, X 40.

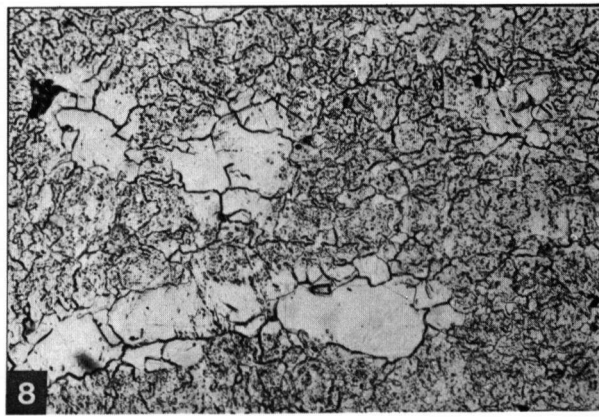
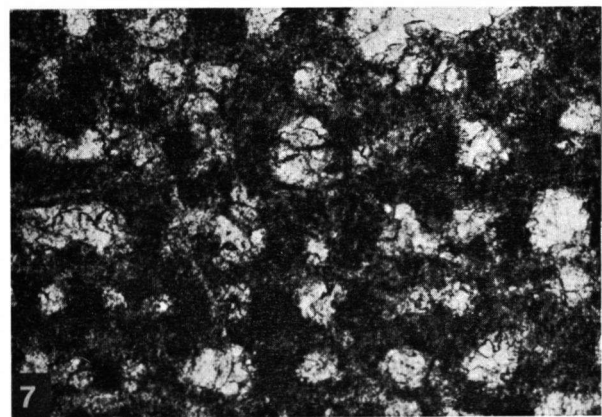
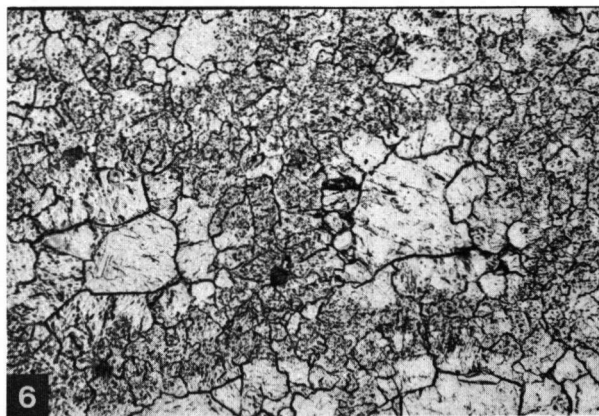
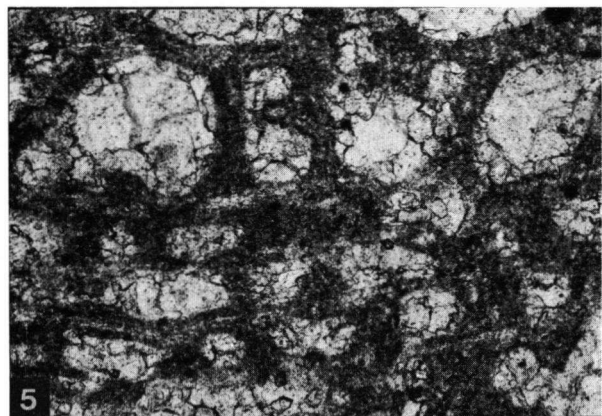
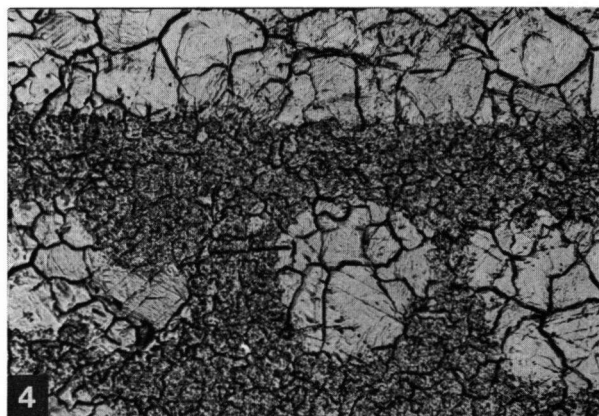
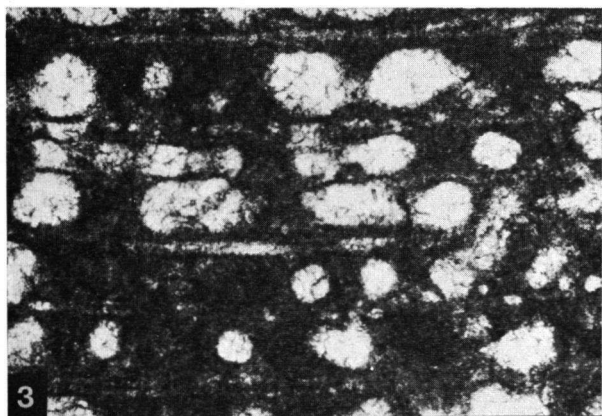
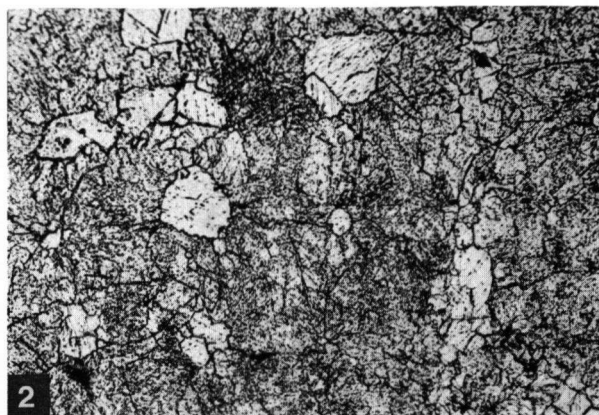
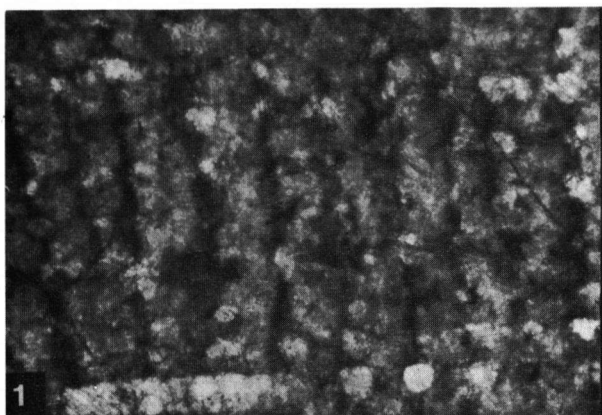
Fig. 4. (Specimen 32G). Peel of the same specimen as in fig. 3. The crystal pattern is random. The skeletal elements are sharply defined. Vert. section, X 100.

Fig. 5. (Specimen 580J). Another quite well preserved *Stromatoporella? granulata?* Vert. section, X 40.

Fig. 6. (Specimen 580J). Peel of the same specimen as in fig. 5. Large crystals occur in the centre of the galleries. Vert. section, X 100.

Fig. 7. (Specimen 583C). Flocculent tissue in *Stromatoporella? granulata?*. Traces of microlamination are still visible. In some places transverse fibrosity has developed. Vert. section, X 40.

Fig. 8. (Specimen 583C). Peel of the same specimen as in fig. 7. In many galleries large crystals are present, which are limited to these spaces. Other crystals extend into the tissue. The specks are irregularly distributed in the tissue and the boundary with the galleries is vague in most places. Vert. section, X 100.



## PLATE 7

Fig. 1. (Specimen 32B). Transverse fibrosity in *Stromatoporella? granulata?*. Traces of microlamination are still visible. Vert. section, X 40.

Fig. 2. (Specimen 32B). Peel of the same specimen as in fig. 1. In the laminae crystal boundaries tend to be vertical and in the pillars horizontal. Most slip planes are more or less vertical. Vert. section, X 100.

Fig. 3. (Specimen 479B). Compact-looking *Stromatoporella? granulata?* with very obvious slip planes. Vert. section, X 40.

Fig. 4. (Specimen 479B). Peel of the same specimen as in fig. 3. The microstructure of the skeleton is completely irreco gnizable because of migration of specks along obvious, randomly oriented slip planes. Vert. section, X 100.

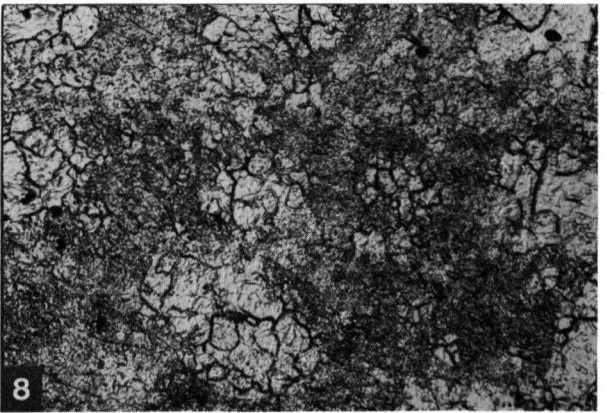
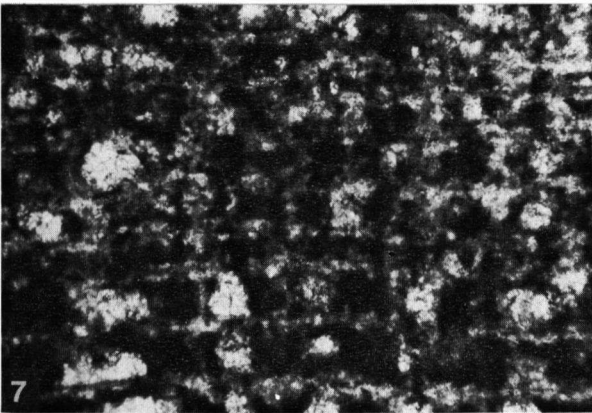
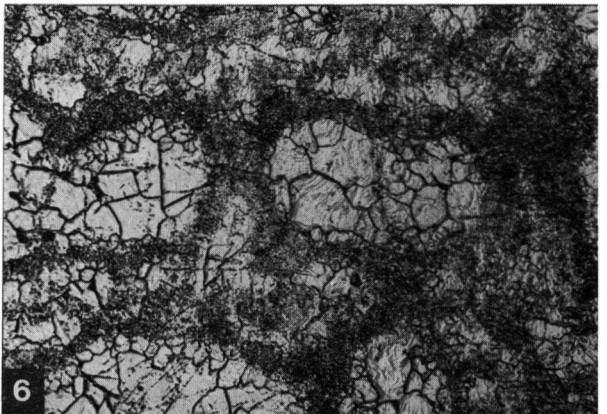
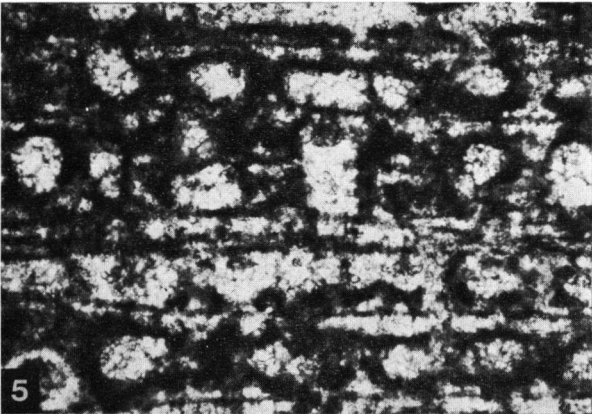
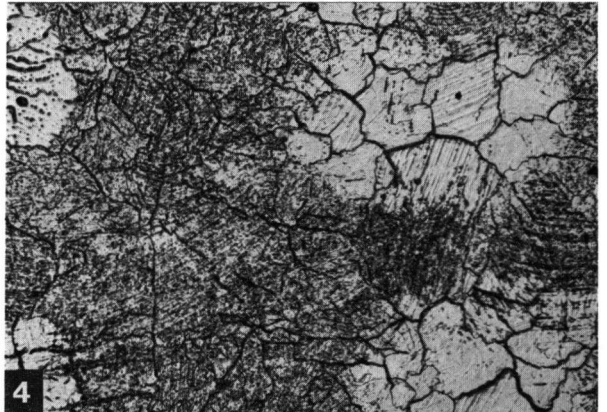
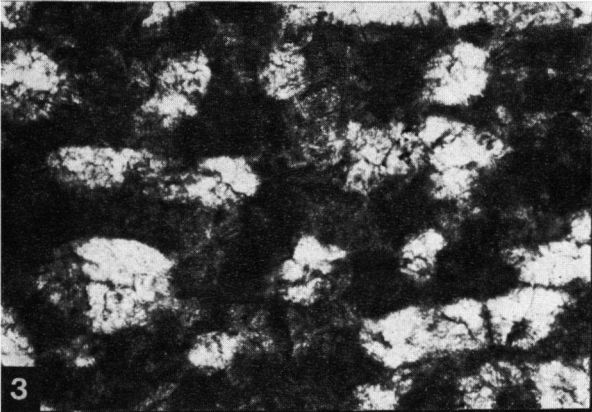
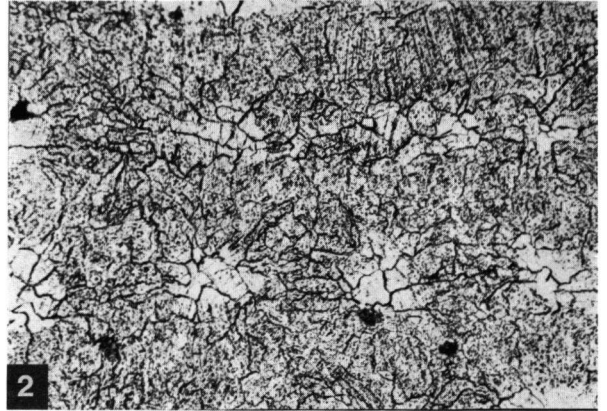
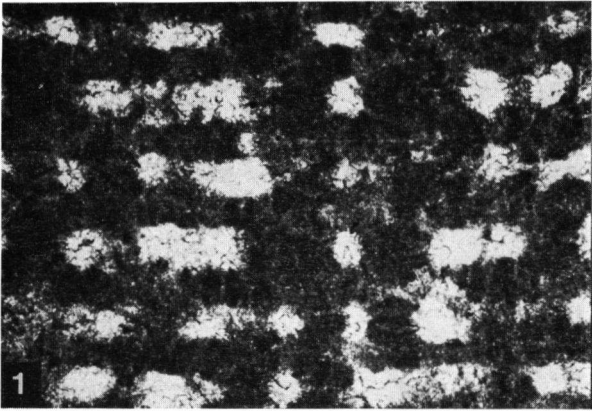
Fig. 5. (Specimen 580F). Melanospheric *Stromatoporella? granulata?*. The specks are concentrated along the boundaries of the tissue leaving microlaminae in the centres of some laminae. Vert. section, X 40.

Fig. 6. (Specimen 580F). Peel of the same specimen as in fig. 5. The specks are concentrated around the interlaminar spaces. Vert. section, X 100.

Fig. 7. (Specimen 35B). *Stromatoporella? granulata?* which has become nearly indistinguishable by infiltration of specks into the galleries. Note rest of microlaminae. Vert. section, X 40.

Fig. 8. (Specimen 35B). Peel of the same specimen as in fig. 7, showing the irregular distribution of specks. Skeletal elements are scarcely recognizable. Vert. section, X 100.





## PLATE 8

Fig. 1. (Specimen 582A). Pseudocellular *Stromatoporella? granulata?* with melanospheres and microlaminae. Some galleries are strongly infiltrated by specks. Vert. section, X 40.

Fig. 2. (Specimen 582A). Peel of the same specimen as in fig. 1. The tissue is recrystallized. The crystals are more or less limited to the speckless areas. Vert. section, X 100.

Fig. 3. (Specimen 514B). Well preserved *Stromatoporella? selwyni* with ordinicellular microstructure. Note ring pillar (left), and normal pillars (right) with vertical arrangement of cellulae. Vert. section, X 40.

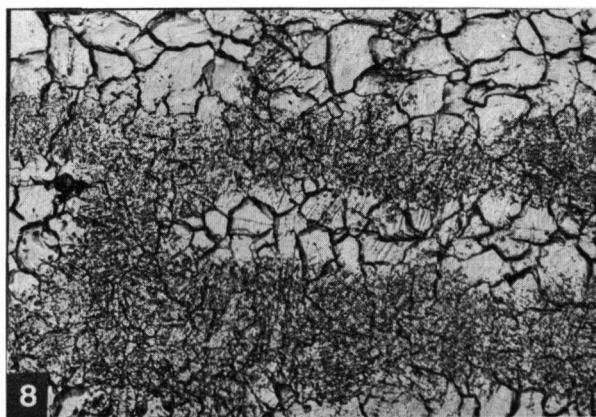
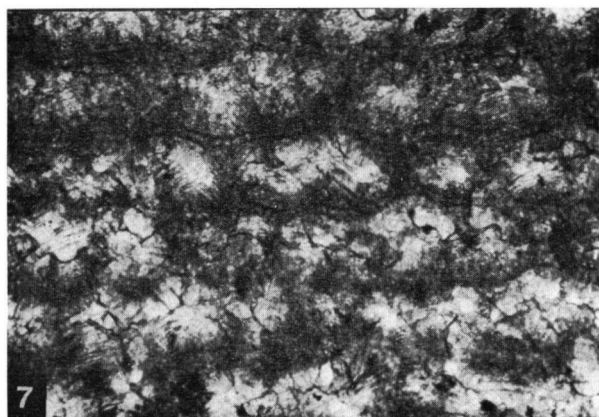
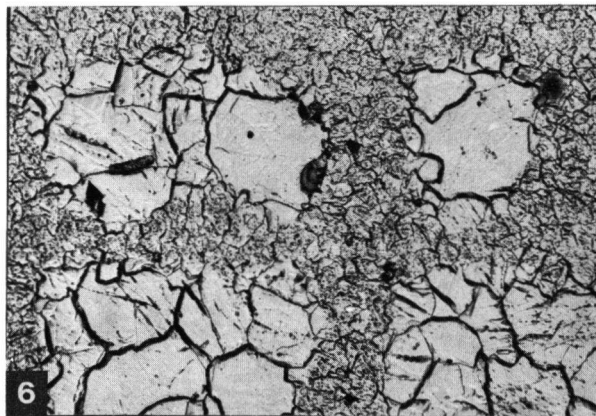
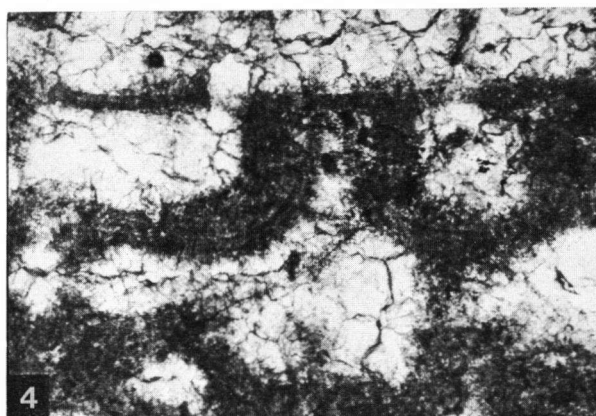
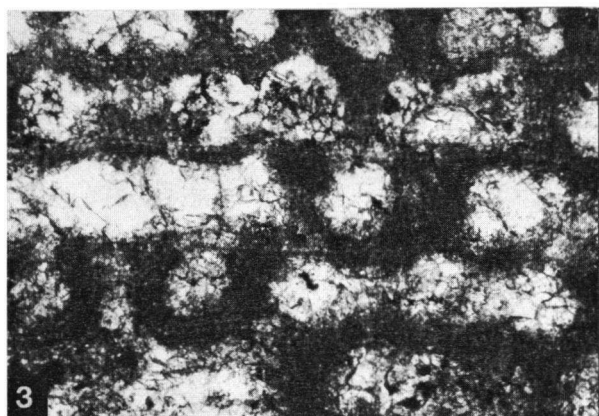
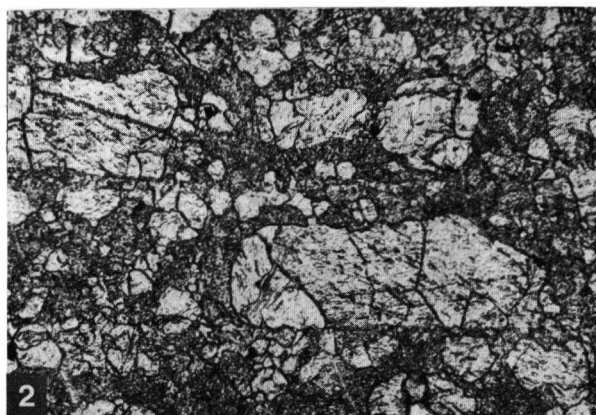
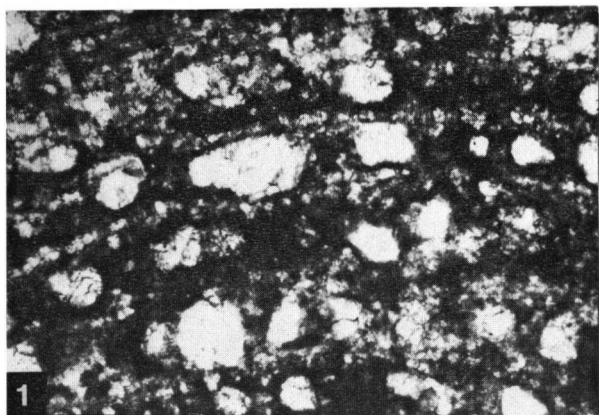
Fig. 4. (Specimen 522I). Ring pillar in *Stromatoporella? selwyni*. The thick laminae consist of several layers of cellulae. Vert. section, X 40.

Fig. 5. (Specimen LV510G). Ordinicellulae in *Stromatoporella? selwyni* with frequently superposed pillars. Vert. section, X 40.

Fig. 6. (Specimen LV510G). Peel of the same specimen as in fig. 5. The galleries are filled with large crystals. Vert. section, X 100.

Fig. 7. (Specimen 522H). *Stromatoporella? selwyni* showing destruction of the ordinicellulae by migration of specks along slip planes. Vert. section, X 40.

Fig. 8. (Specimen 522H). Peel of the same specimen as in fig. 7. Migration of specks occurs along slip planes. Vert. section, X 100.



## PLATE 9

Fig. 1. (Specimen 522D). *Stromatoporella? selwyni* with transversely fibrous laminae. Vert. section, X 40.

Fig. 2. (Specimen 522 D). Peel of the same specimen as in fig. 1. In the laminae many vertical crystal boundaries occur. The orientation of the slip planes is random. Vert. section, X 100.

Fig. 3. (Specimen 537F). Flocculent *Stromatoporella? selwyni*. The laminae look 'tripartite' in some places. Vert. section, X 40.

Fig. 4. (Specimen 537F). Peel of the same specimen as in fig. 3. In the centre of some galleries large crystals are present. Slip planes are rare. Vert. section, X 100.

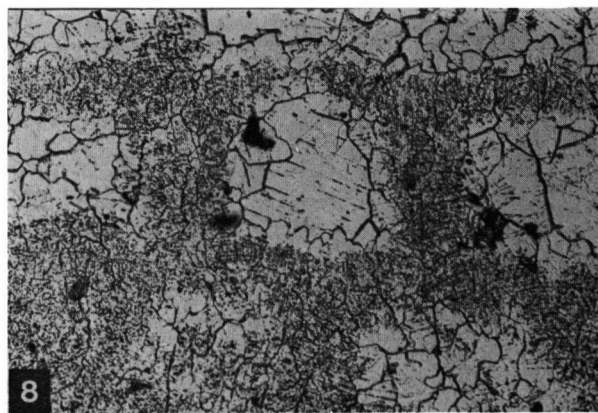
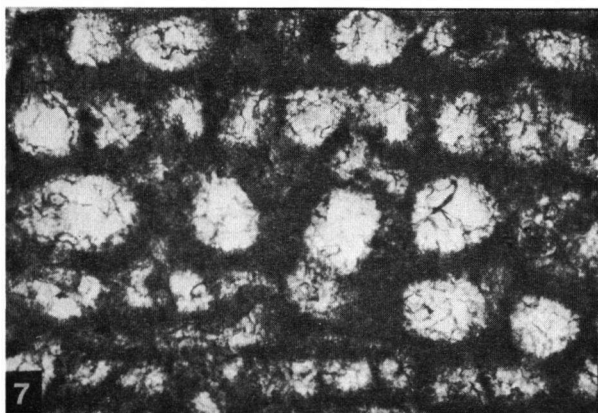
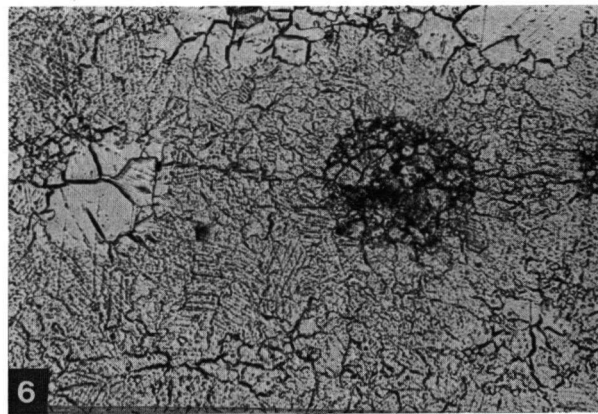
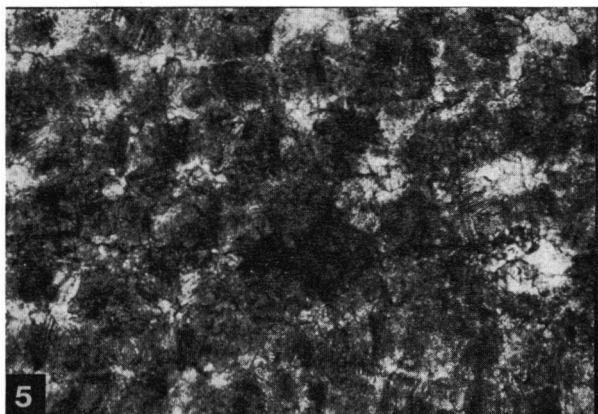
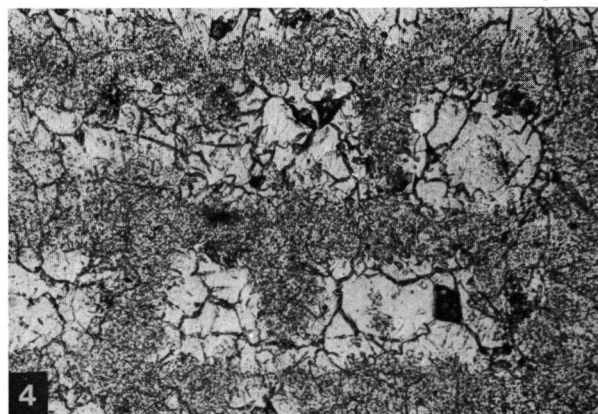
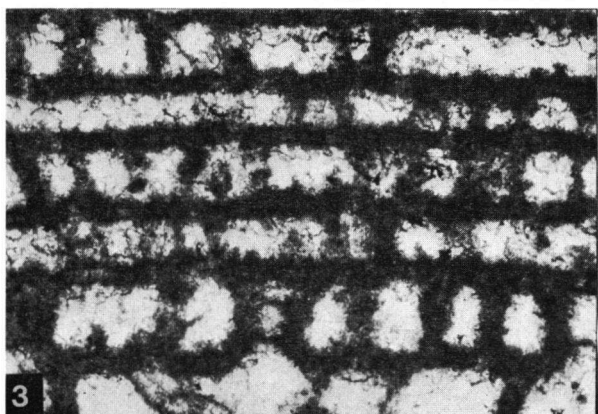
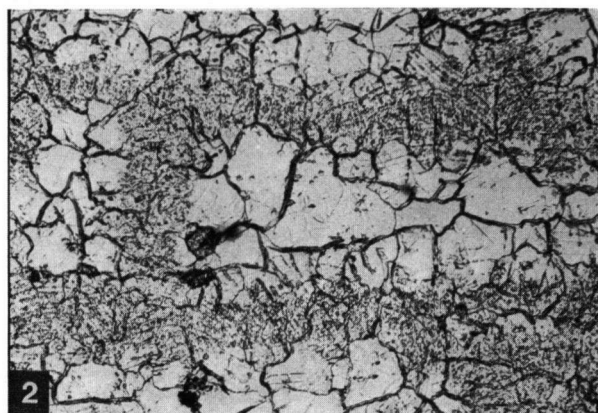
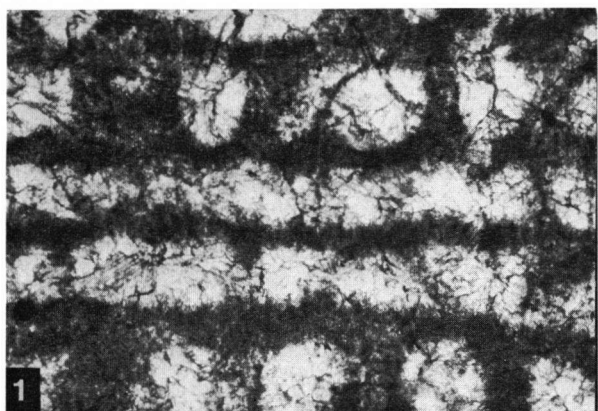
Fig. 5. (Specimen 480F). Very strongly altered specimen of *Stromatoporella? selwyni*. By migration of specks the galleries are partly or entirely filled with specks. Vert. section, X 40.

Fig. 6. (Specimen 480F). Peel of the same specimen as in fig. 5. In the lower part of the figure the galleries are nearly completely filled with specks, in the upper part they have remained fairly large. Only the gallery filled with dark material has retained its original shape. Vert. section, X 100.

Fig. 7. (Specimen 473B). *Stromatoporella? selwyni* with flocculent microstructure. In many galleries large central crystals are present. Vert. section, X 40.

Fig. 8. (Specimen 473B). Peel of the same specimen as in fig. 7. Some galleries have large central crystals. Migration of specks along slip planes is only limited. Vert. section, X 100.





## PLATE 10

Fig. 1. (Specimen 533B). *Stromatoporella? selwyni* with abundant ring pillars. In the lower part of the figure the tissue is flocculent. In the upper part the laminae look compact due to concentration of specks in the centre of the laminae. Vert. section, X 40.

Fig. 2. (Specimen 533B). Peel of the same specimen as in fig. 1. In the upper lamina a continuous line occurs. In the lower lamina concentration of specks has taken place but a continuous line is absent. Vert. section, X 100.

Fig. 3. (Specimen 521C). *Stromatoporella? selwyni* with small stylolite-like cracks between the laminae and vertical crystal boundaries crossing the laminae. Vert. section, X 40.

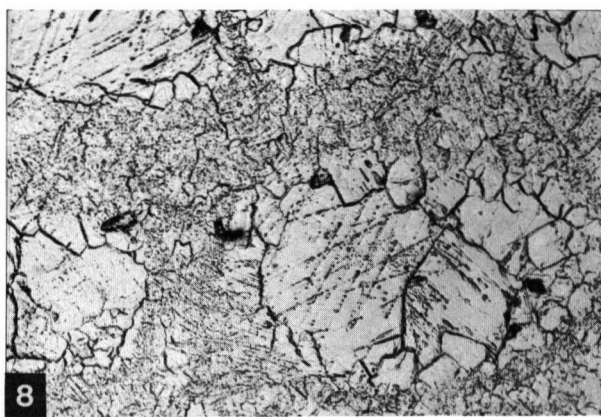
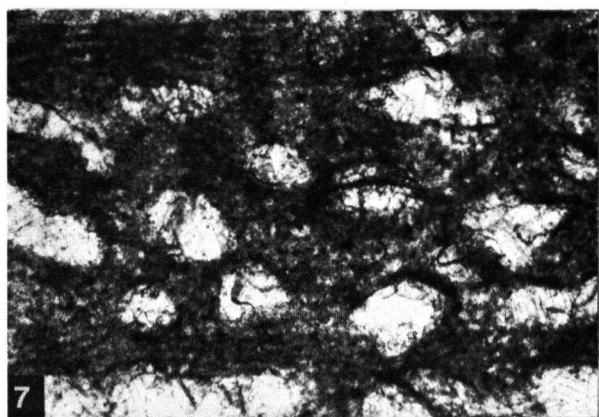
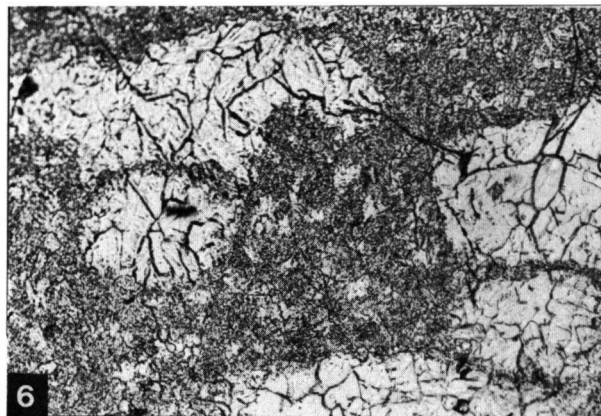
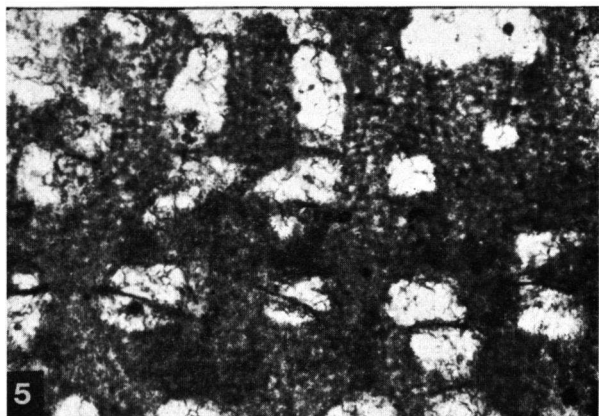
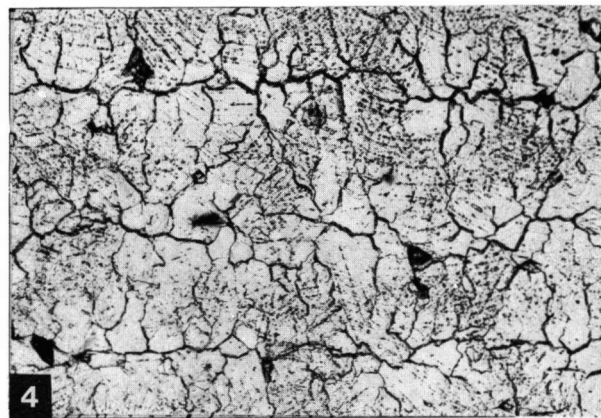
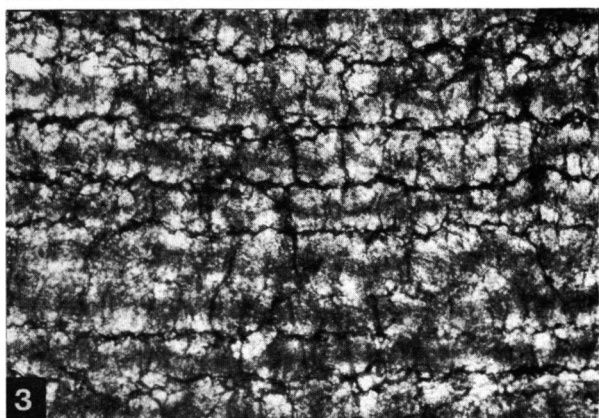
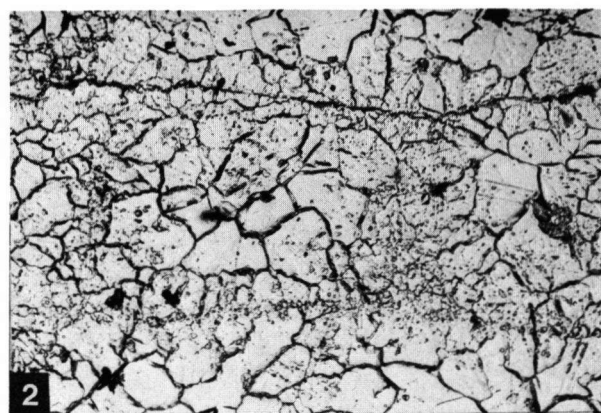
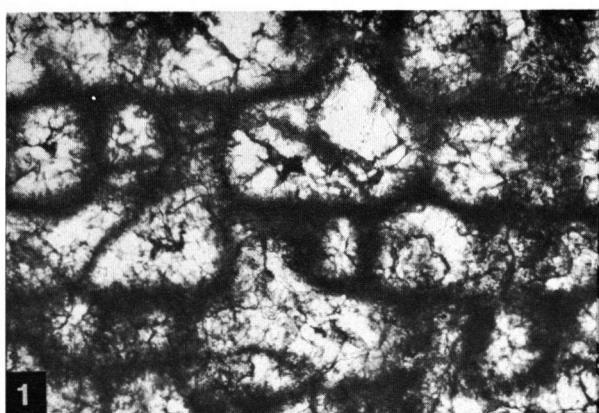
Fig. 4. (Specimen 521C). Peel of the same specimen as in fig. 3. The specks have migrated along the curved slip planes. Note the cracks in the galleries and the obvious vertical crystal boundaries. Vert. section, X 100.

Fig. 5. (Specimen 570E). *Stromatopora huepschi?* with well preserved cellular microstructure. The cyst plates are compact. Vert. section, X 40.

Fig. 6. (Specimen 570E). Peel of the same specimen as in fig. 5. The cellulae are recognizable by differences in the density of specks. The crystal pattern is random. Vert. section, X 100.

Fig. 7. (Specimen 586). *Stromatopora concentrica* with a rather horizontal arrangement of cellulae. Vert. section, X 40.

Fig. 8. (Specimen 586). Peel of the same specimen as in fig. 7. Large crystals occur in the centre of many galleries. Some slip planes occur in the crystals. Vert. section, X 100.



## PLATE 11

Fig. 1. (Specimen 537M). *Stromatopora huepschi*? with compact microlaminae and cellular tissue. Vert. section, X 40.

Fig. 2. (Specimen 536J). Slightly altered *Stromatopora* sp. 3 with compact microlaminae, cyst plates and cellular tissue. Vert. section, X 40.

Fig. 3. (Specimen 461F). Slightly altered *Stromatopora* sp. 1. The compact microlaminae and cellular tissue are still discernible. Vert. section, X 40.

Fig. 4. (Specimen 416I). *Stromatopora huepschi*? with microstructure grading from cellular to melanospheric. Vert. section, X 40.

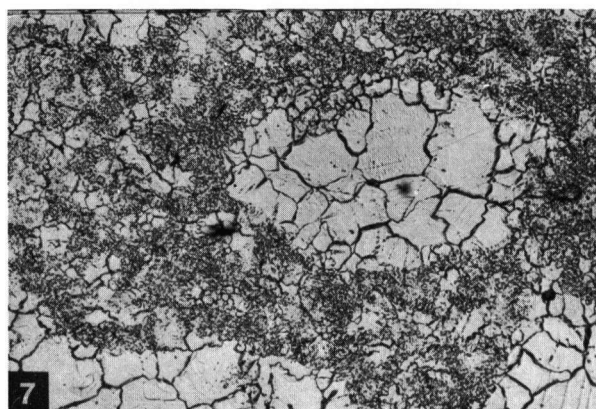
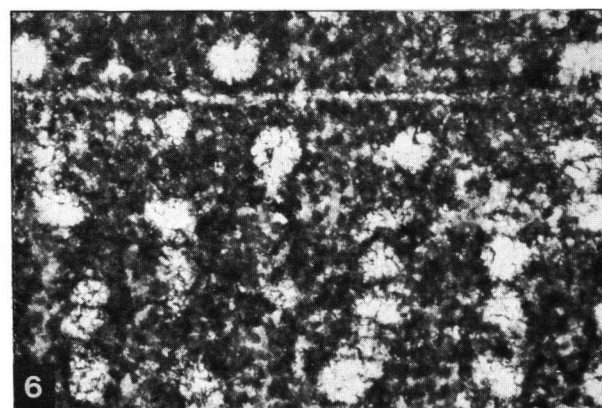
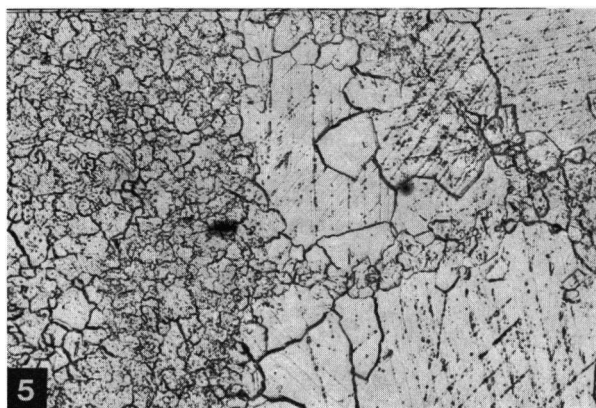
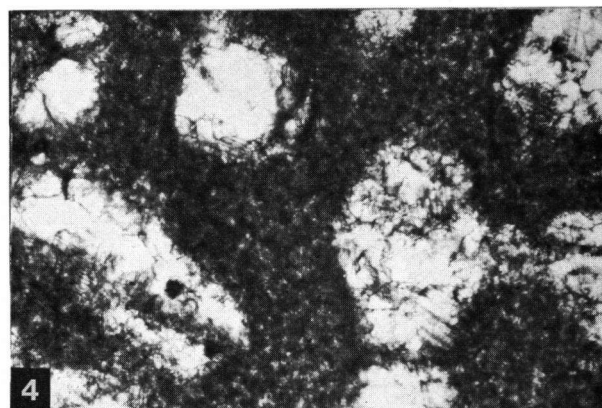
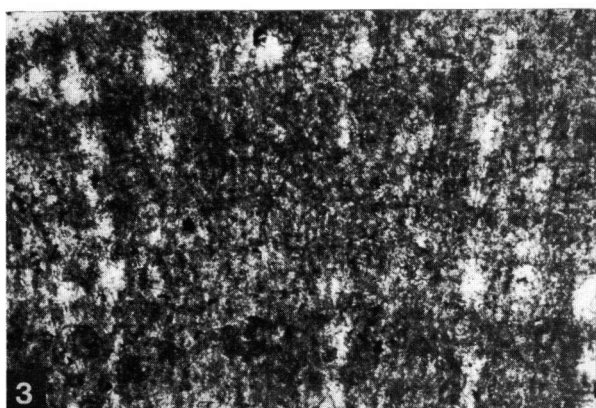
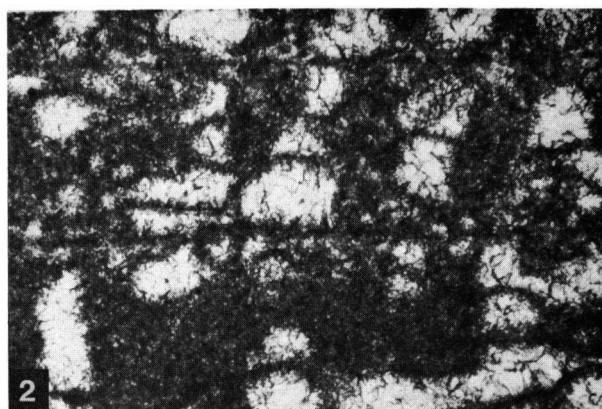
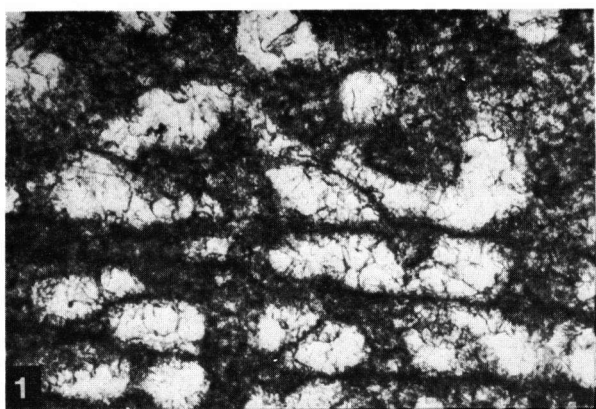
Fig. 5. (Specimen 416I). Peel of the same specimen as in fig. 4. The galleries are filled with large crystals with slip planes. The tissue is broken up into small crystals. Vert. section, X 100.

Fig. 6. (Specimen 478A). Strongly melanospheric *Stromatopora* sp. 2 with a rather regular gross structure and microlaminae. Vert. section, X 40.

Fig. 7. (Specimen 478A). Peel of the same specimen as in fig. 6. The galleries are filled with rather large crystals; within the tissue the specks are concentrated in the melanospheres. Vert. section, X 100.

Fig. 8. (Specimen 520J). *Stromatopora huepschi*? showing destruction of the microstructure by development of slip planes. Vert. section, X 40.





## PLATE 12

Fig. 1. (Specimen 510B). *Stromatopora concentrica*. The cellulae are completely destroyed by migration of specks along slip planes. Vert. section, X 40.

Fig. 2. (Specimen 486A). *Stromatopora concentrica*. By migration of specks along slip planes even the gross structure has become vague. Vert. section, X 40.

Fig. 3. (Specimen 486A). Peel of the same specimen as in fig. 2. The crystal pattern is normal. The galleries are in part filled with specks which migrated along slip planes. Vert. section, X 100.

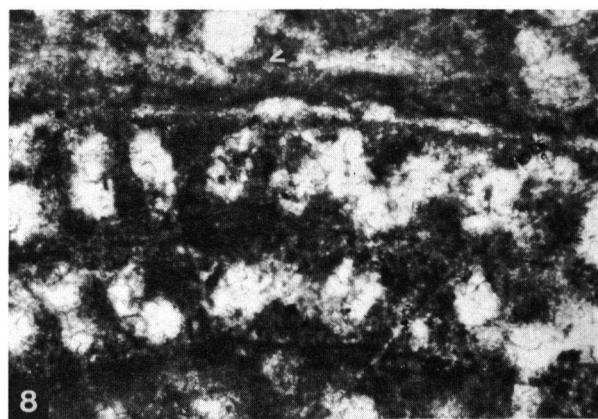
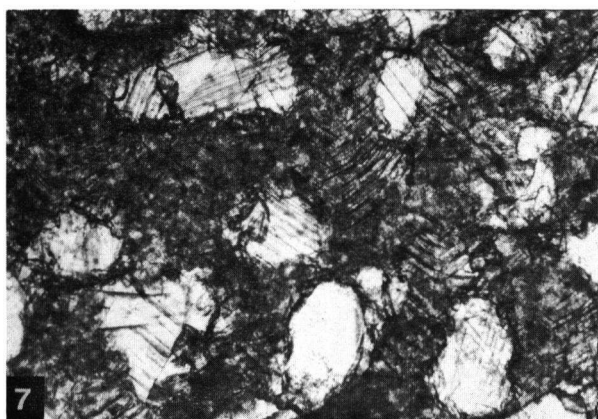
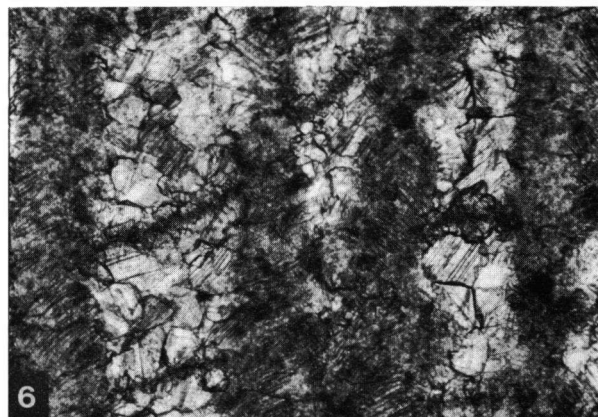
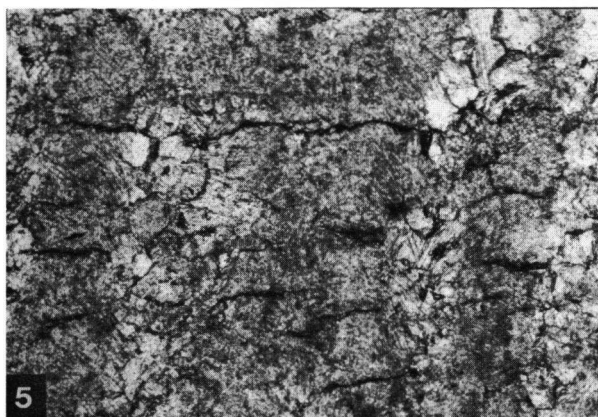
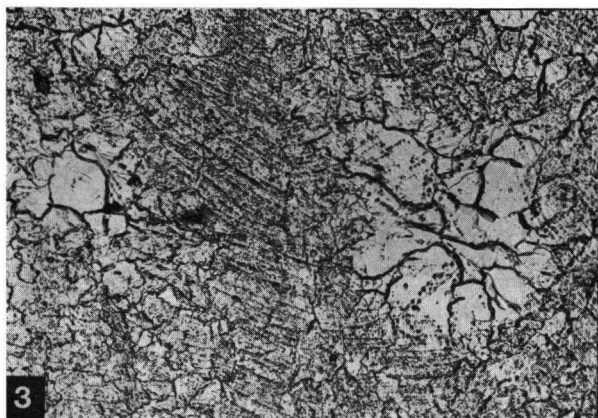
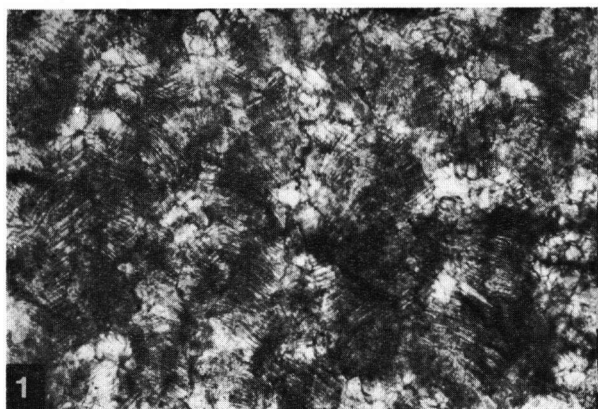
Fig. 4. (Specimen 520G). Badly preserved *Stromatopora huepschi*?. Migration of specks into the galleries was prevented by the micrite or by thin coatings along the boundary of the tissue. Where the latter is not the case, tissue boundaries are vague. Vert. section, X 40.

Fig. 5. (Specimen 517H). Horizontal cracks in badly preserved *Stromatopora huepschi*?. Vert. section, X 40.

Fig. 6. (Specimen 517H). Photograph of the same thin section as in fig. 5, but now impregnated with paraffin oil. The gross structure is now better visible but no cracks can be seen. Vert. section, X 40.

Fig. 7. (Specimen 585B) *Stromatopora concentrica* with large obvious crystals in the galleries. The microstructure is nearly completely destroyed by slip planes. Vert. section, X 40.

Fig. 8. (Specimen 540A). *Stromatoporella*? sp. 3. Though the microstructure is flocculent or even melanospheric, the microlamination in the laminae is still recognizable. Vert. section, X 40.



## PLATE 13

Fig. 1. (Specimen 442A). *Stromatoporella? selwyni* with zones of silicification parallel to latilaminae and former eroded surfaces. On the left side an incrustation by a bryozoan is visible. Vert. section, X 3.5.

Fig. 2. (Specimen 472B). *Stromatopora huepschi?* with geode and partly silicified coenostecum. Note the dolomite crystal in the upper right corner. The not silicified tissue is dark. Vert. section, X 10.

Fig. 3. (Specimen 472D). Detail of another section of the same specimen as in fig. 2. The cellulae in the silicified tissue are partly beautifully preserved. However, the microstructure is only visible in very thick thin sections. Vert. section, X 40.

Fig. 4. (Specimen 454E). *Actinostroma stellulatum* showing zones differing in extent of silicification. In the lower part no silicification has taken place. In the dark area only the skeletal elements are silicified. In the upper left corner some dolomite crystals are visible in the completely silicified area. Vert. section, X 5.5.

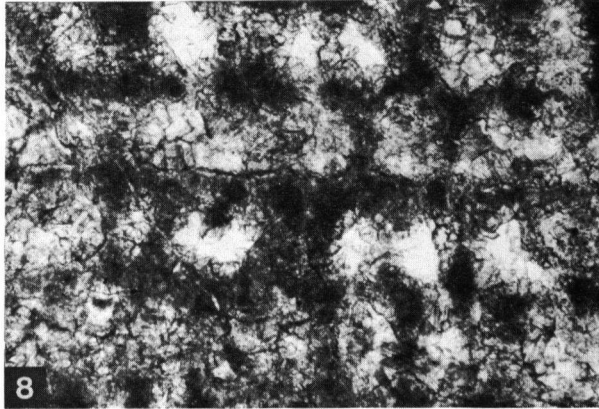
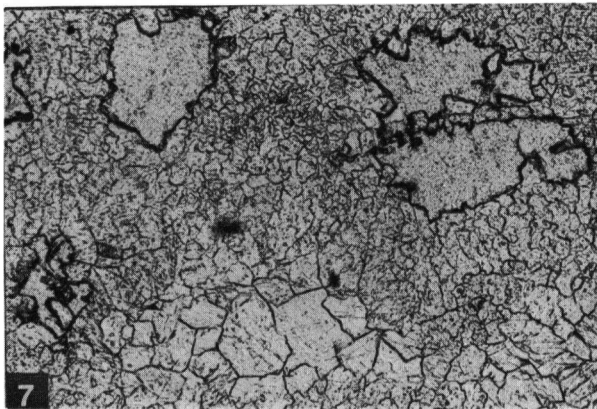
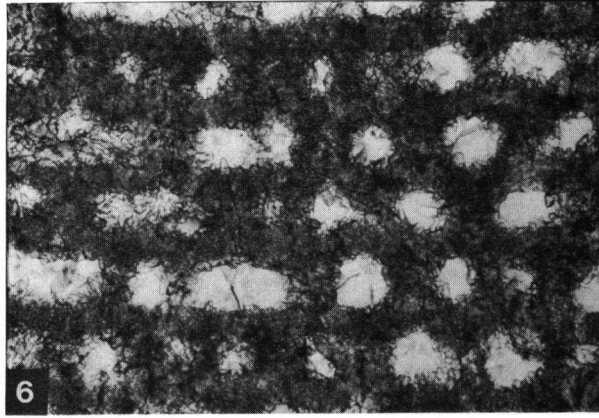
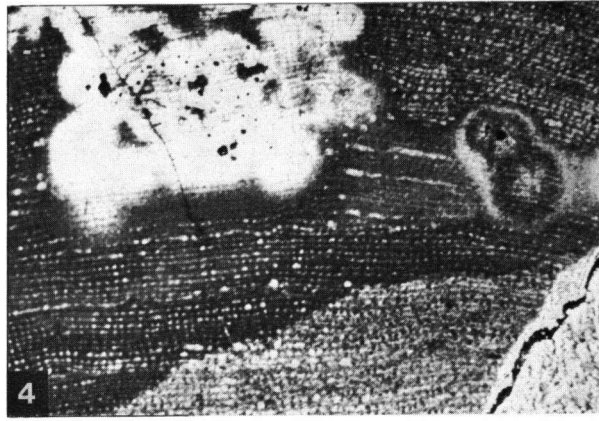
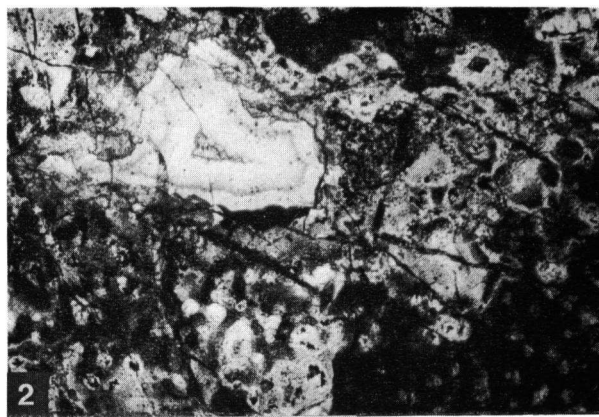
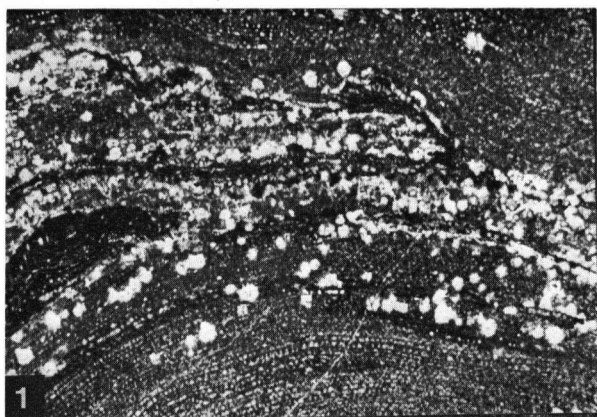
Fig. 5. (Specimen 454E). Peel of the same specimen as in fig. 4. The upper zone is not silicified, in the middle of the figure only the skeleton is silicified, while in the lower part even the calcite of the interlaminar spaces is replaced by chert. Vert. sections, X 25.

Fig. 6. (Specimen LV510D). Flocculent *Stromatoporella? selwyni*. Most, but not all, galleries are filled with chert. The alteration of the microstructure has not been influenced by silicification. Vert. section, X 40.

Fig. 7. (Specimen LV510D). Peel of the same specimen as in fig. 6, showing a not silicified gallery (below) and two galleries filled with chert (above). The silicified areas are limited by crystal boundaries of the calcite. The cyst plate on the right has not been silicified. Vert. section, X 100.

Fig. 8. (Specimen 523C). *Stromatoporella? selwyni*. In some areas silicification occurs predominantly in the galleries, in other areas predominantly in the skeletal elements. Vert. section, X 40.





#### PLATE 14

Fig. 1. (Specimen 523C). Peel of the same specimen as in Pl. 13 fig. 8. Some galleries are filled with calcite and are surrounded by silicified tissue, while other galleries are filled with chert and bounded by calcite crystals. Vert. section, X 40.

Fig. 2. (Specimen 523C). Peel of the same specimen as in Pl. 13 fig. 8, showing calcite crystals 'piercing' into the silicified galleries. The laminae are partly silicified. Vert. section, X 100.

Fig. 3. (Specimen 565A). Badly preserved *Actinostroma papillosum* with more or less idiomorphic quartz crystals. Vert. section, X 40.

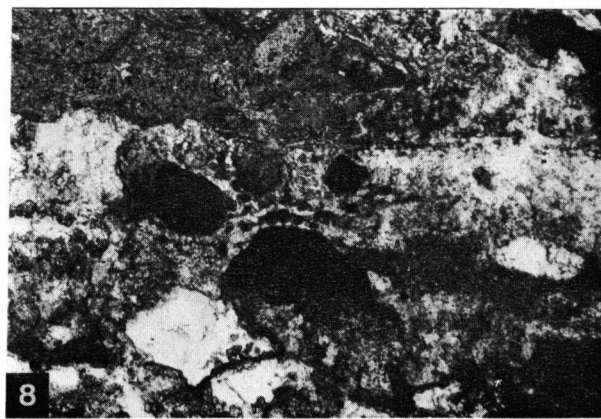
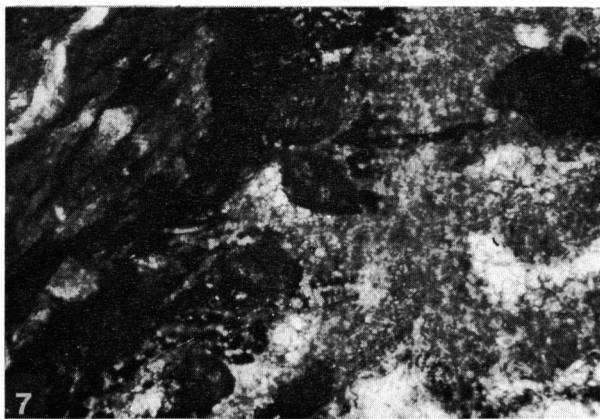
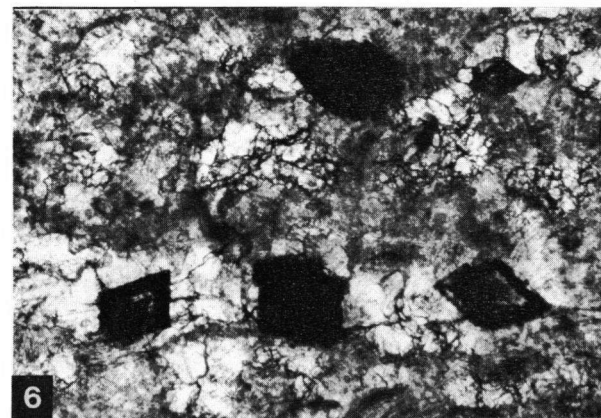
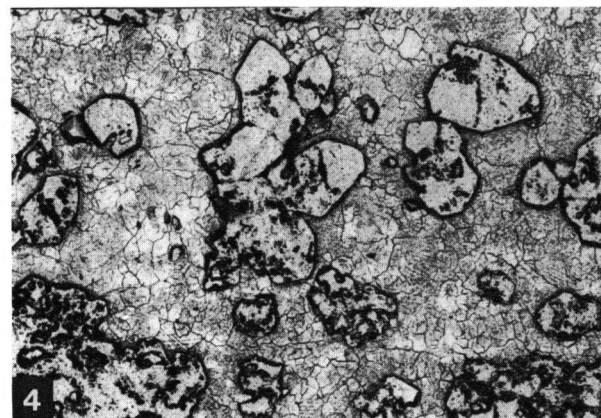
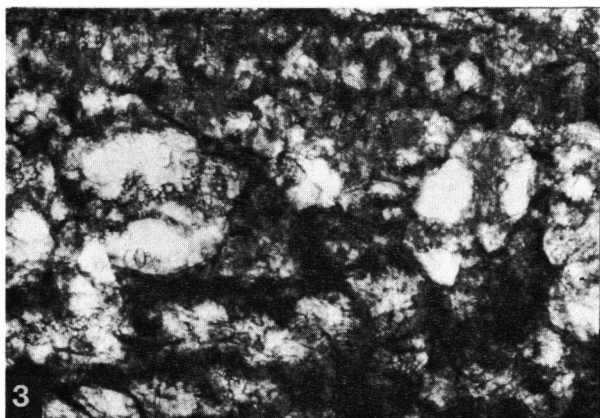
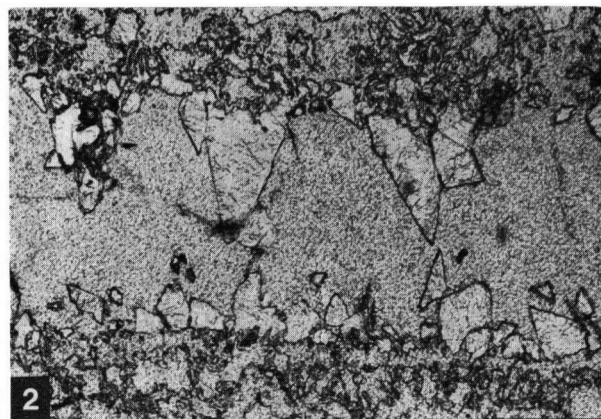
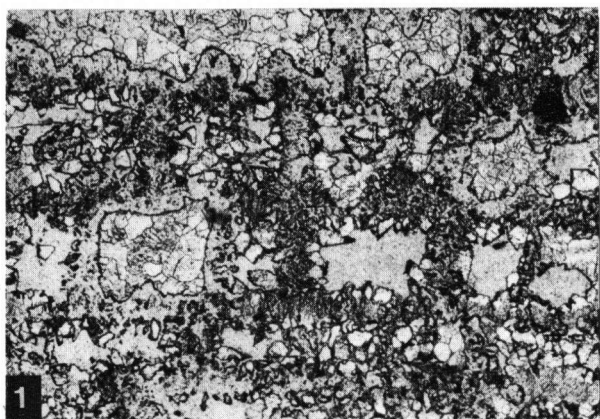
Fig. 4. (Specimen 565A). Peel of the same specimen as in fig. 3. The quartz crystals have enclosed many small calcite crystals and other impurities. Vert. section, X 40.

Fig. 5. (Specimen 581D). *Stromatopora concentrica* with idiomorphic quartz crystals. Vert. section, X 40.

Fig. 6. (Specimen 93A). Partly to entirely oxidized ferrodolomite in *Stromatopora concentrica*. Vert. section, X 40.

Fig. 7. (Specimen 260A). Badly preserved *Stromatopora concentrica*. Cellulae are only recognizable along the border where they are filled with hematite. Vert. section, X 40.

Fig. 8. (Specimen 570E). *Stromatopora huepschi?* in which some galleries and part of the cellulae are filled with micrite. Same specimen as that in Pl. 10 fig. 5. Vert. section, X 40.





#### PLATE 15

Fig. 1. (Specimen LV510F). *Actinostroma papillosum* with a regular gross structure. Vert. section, X 8.

Fig. 2. (Specimen 517O). *Actinostroma papillosum* with a regular gross structure grading from coarse to fine. Vert. section, X 8.

Fig. 3. (Specimen 473L). *Actinostroma papillosum* less regularly grown. Note the curved cyst plates. See also Pl. 3 figs. 7, 8 and Pl. 4 figs. 1, 2. Vert. section, X 8.

Fig. 4. (Specimen 530G). *Actinostroma papillosum*. The latilaminae are formed by alternations of rather regular, fine gross structure with irregular, coarse gross structure. Vert. section, X 8.

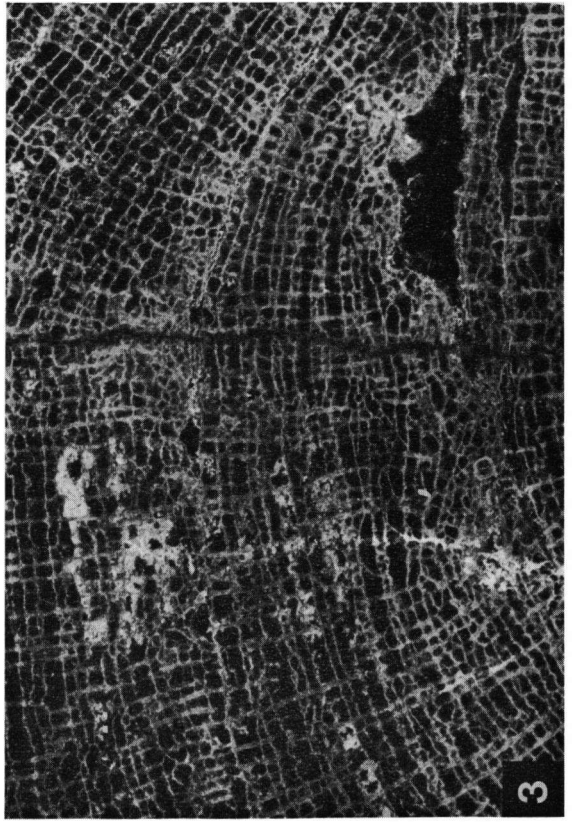
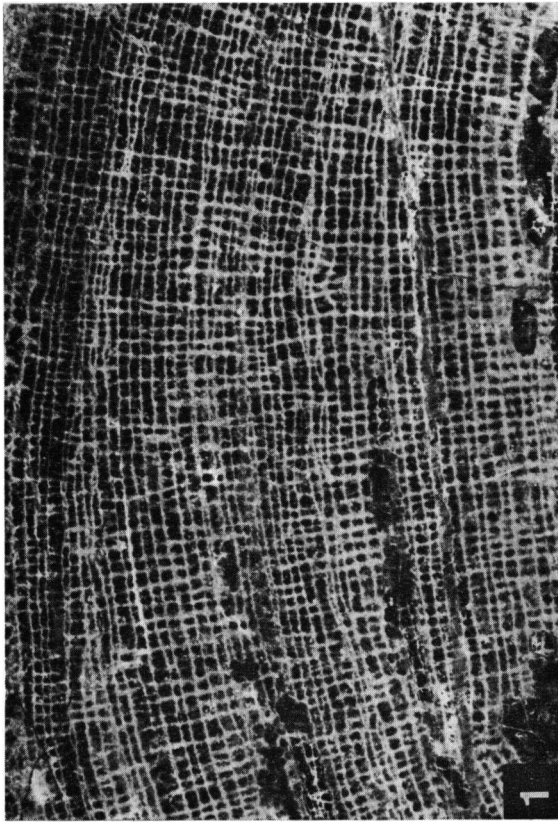
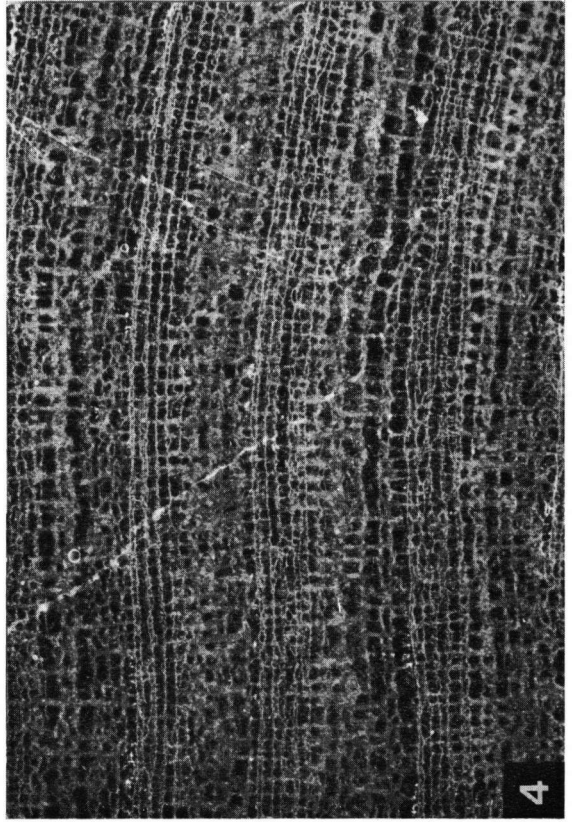


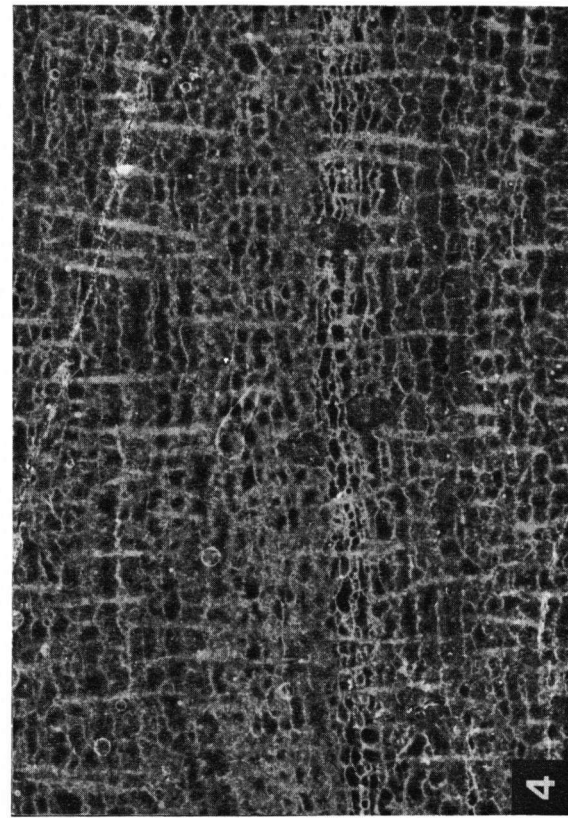
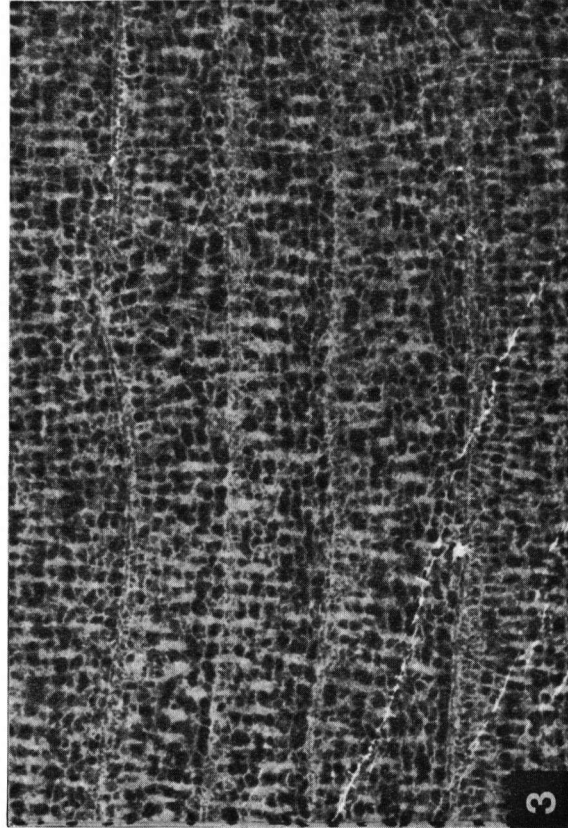
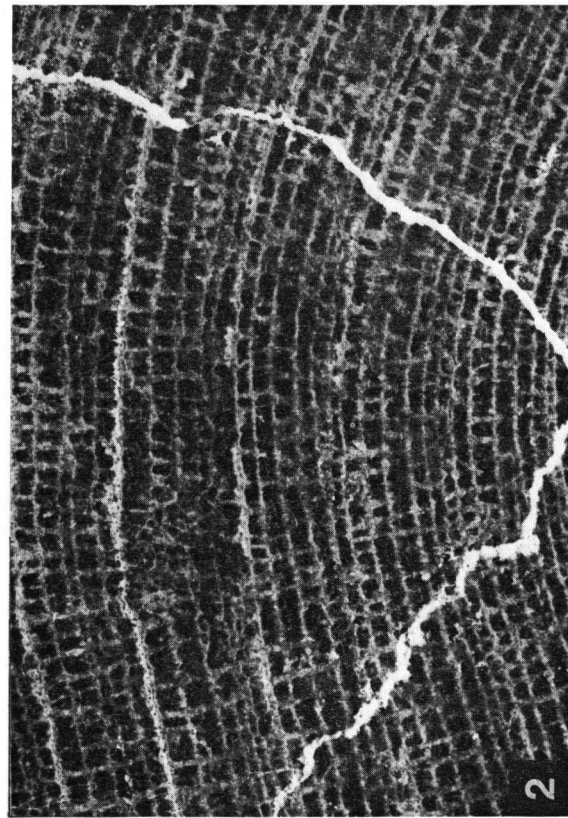
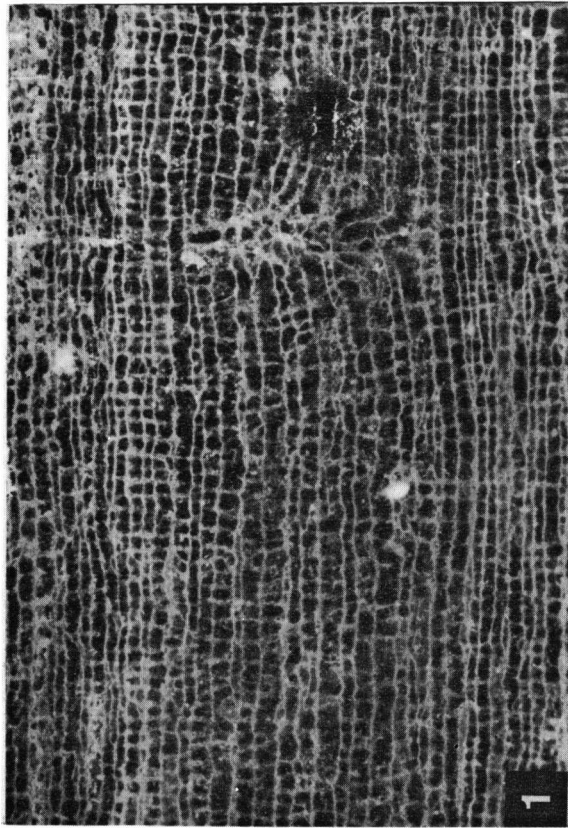
PLATE 16

Fig. 1. (Specimen 536H). *Actinostroma papillosum* with irregular but continuous laminae. Note the small astrorhizae on the right. Vert. section, X 8.

Fig. 2. (Specimen 540A). Same specimen as in fig. 1. The pillars are frequently structure. Note the form of the galleries. Vert. section, X 8.

Fig. 3. (Specimen 516D). *Actinostroma papillosum* with conspicuous latilaminae and thickened pillars. The irregular gross structure becomes very fine in the uppermost zone of each latilamina. Vert. section, X 8.

Fig. 4. (Specimen 533G). *Actinostroma papillosum* with very irregular horizontal skeletal elements and thick pillars at irregular distances from each other. Vert. section, X 8.



#### PLATE 17

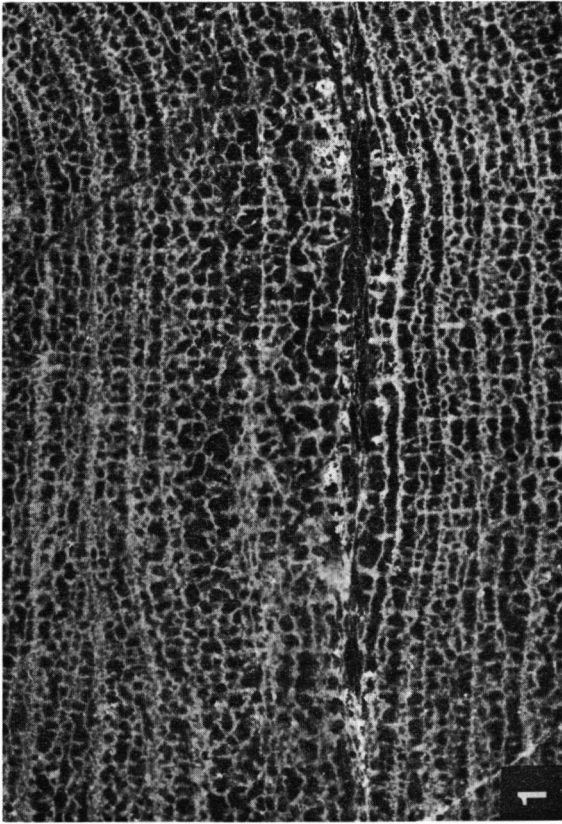
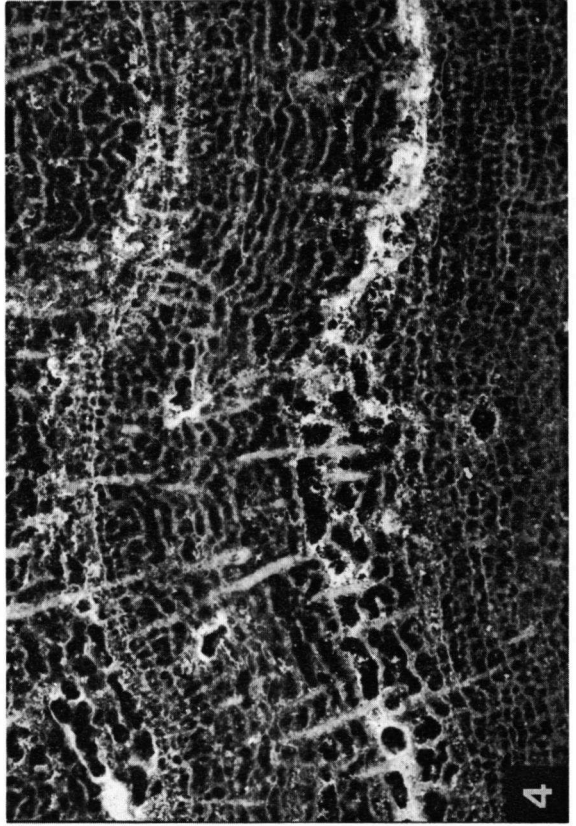
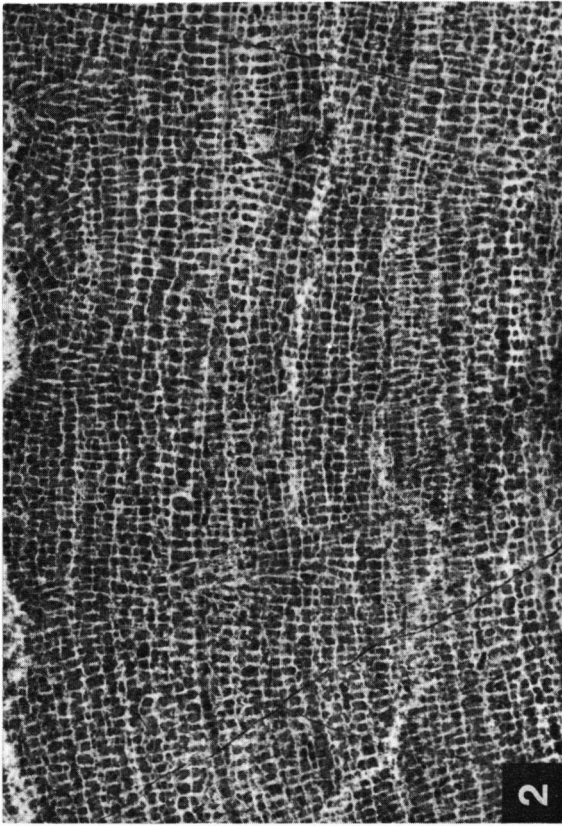
Fig. 1. (Specimen 536I). *Actinostroma papillosum*. The cyst plates form an irregular network. The pillars are not very continuous. Vert. section, X 8.

Fig. 2. (Specimen 542A). *Actinostroma papillosum* with a fine gross structure, formed by continuous pillars and cyst plates. The skeletal elements are rather fragile. Vert. section, X 8.

Fig. 3. (Specimen 540B). *Actinostroma papillosum* with a fine to extremely fine gross structure. Vert. section, X 8.

Fig. 4. (Specimen 559B). *Actinostroma papillosum* with latilaminae in which the gross structure grades from coarse, irregular to very fine. Vert. section, X 8.





# PLATE 18

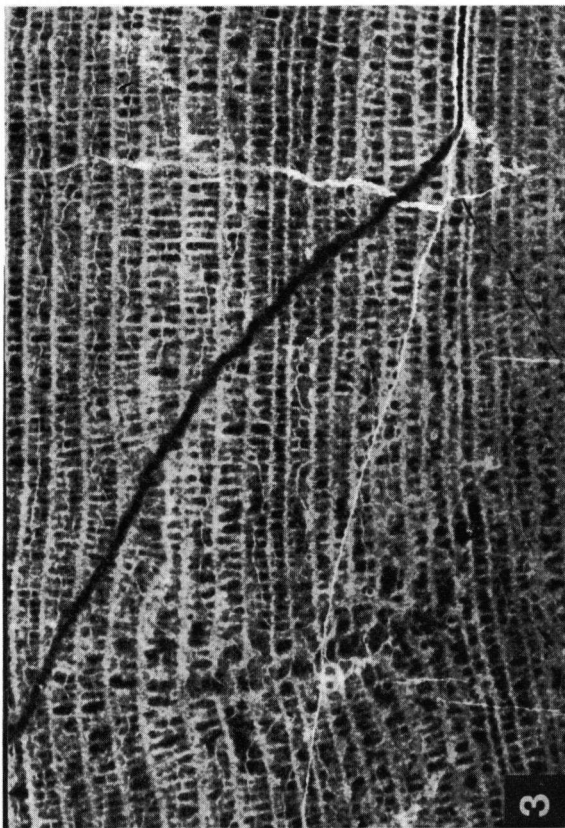
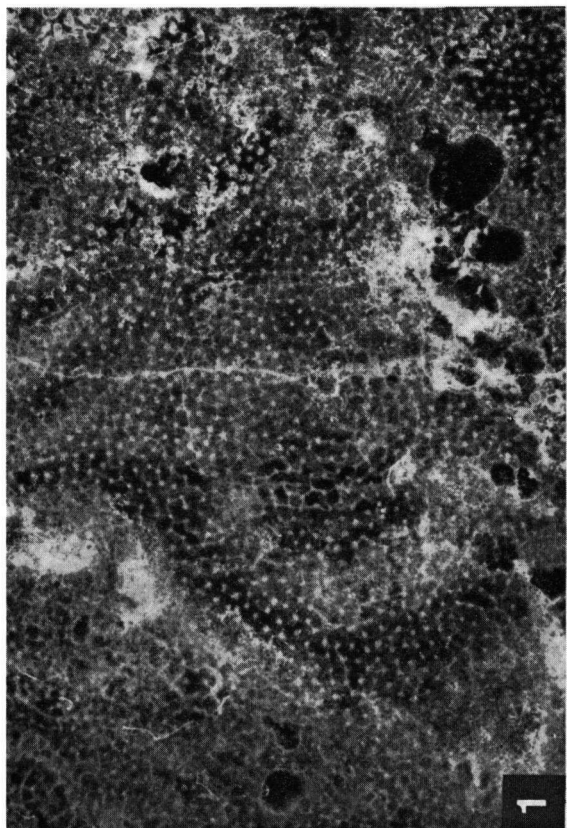
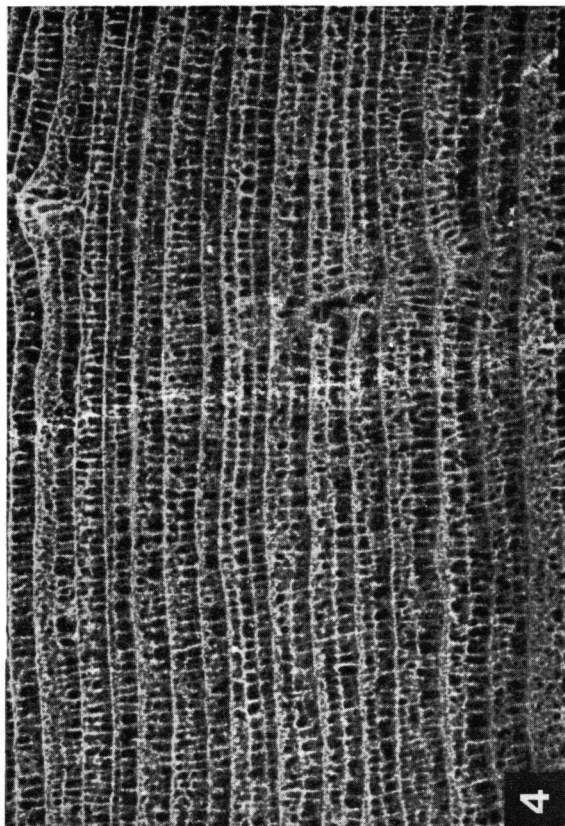
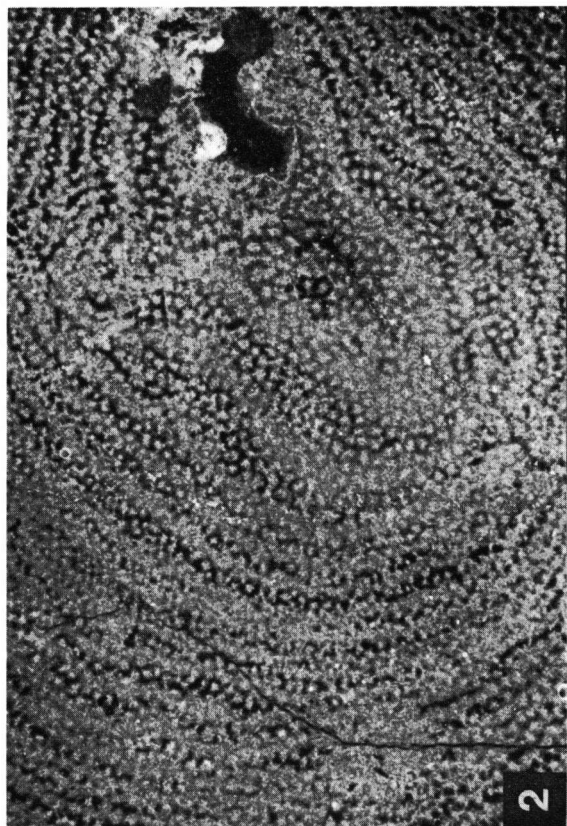
Fig. 1. (Specimen 473L). *Actinostroma papillosum*. Tangential section of the same specimen as figured in Pl. 15 fig. 3. Most pillars are isolated. Only in some areas is a vague 'hexactinellid structure' visible. Tang. section, X 8.

Fig. 2. (Specimen 532A). *Actinostroma papillosum* with flocculent tissue. Scarcely any 'arms' are visible. See also Pl. 4 figs. 7, 8. Tang. section, X 8.

Fig. 3. (Specimen 472D). *Actinostroma verrucosum*? with straight laminae intercalated with cyst plates. The pillars are mostly continuous. Note astrorhizae on the left. Vert. section, X 8.

Fig. 4. (Specimen 416F). *Actinostroma verrucosum*? with thin, straight laminae alternating with cyst plates. This and other specimens provisionally called *A. verrucosum* are actually very similar to some specimens of *A. papillosum*. Vert. section, X 8.





## PLATE 19

Fig. 1. (Specimen 530C). *Actinostroma verrucosum*?. In the upper zone the distance between the laminae is very wide and the pillars are irregular. Vert. section, X 8.

Fig. 2. (Specimen 537K). *Actinostroma verrucosum*?. In the lower part of the figure the distance between the laminae is wide, the pillars are rather irregular. In the higher part the laminae are very close together. Vert. section, X 8.

Fig. 3. (Specimen 532E). *Actinostroma verrucosum*?. In this specimen the pillars are mostly straight and continuous. Note the small astrorhizae in a local upturn of the laminae. See also Pl. 4 figs. 5, 6. Vert. section, X 8.

Fig. 4. (Specimen 533F). *Actinostroma verrucosum*? with repair tissue between latilaminae. In some parts the gross structure is quite similar to that of *A. papillosum*. The irregular lines are caused by algae according to Prof. Dr. E. Flügel (personal communication). Vert. section, X 8.

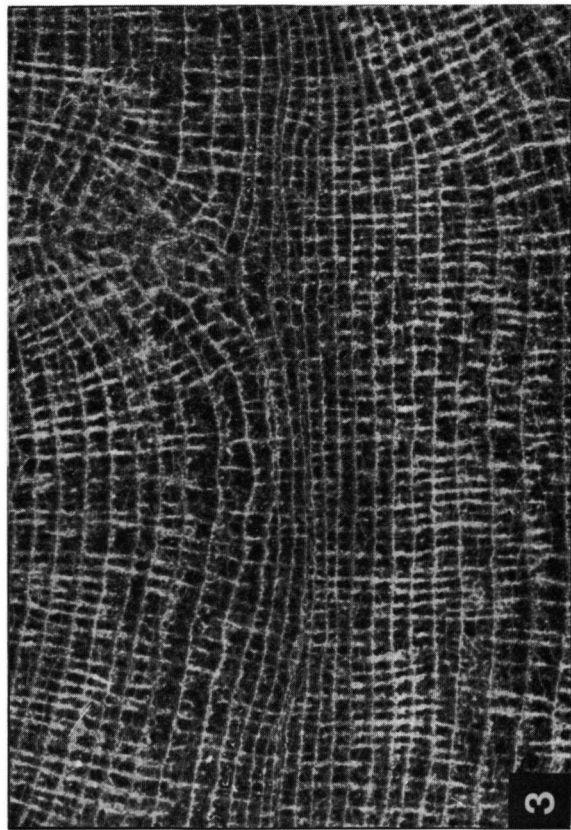
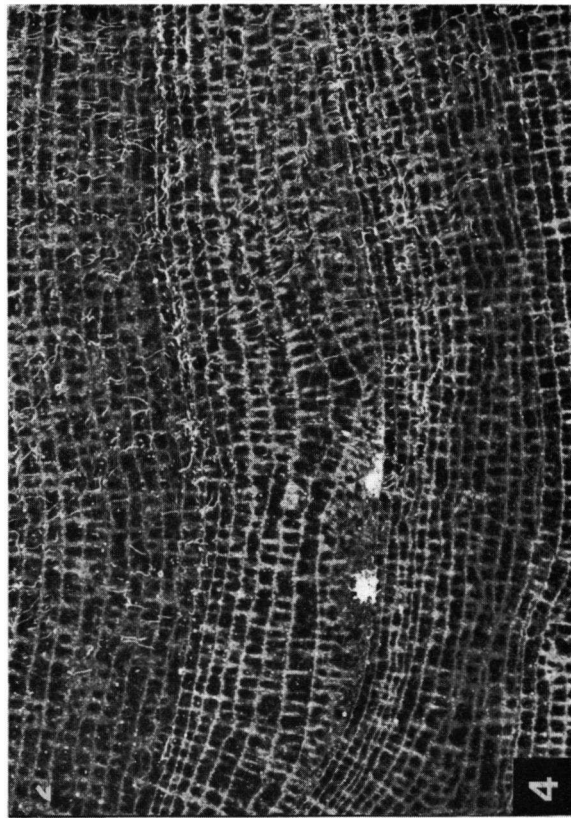
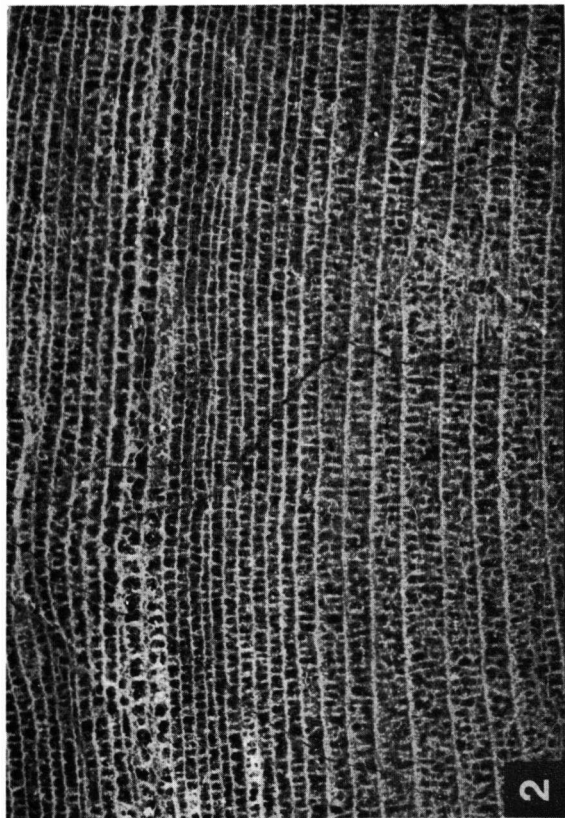


PLATE 20

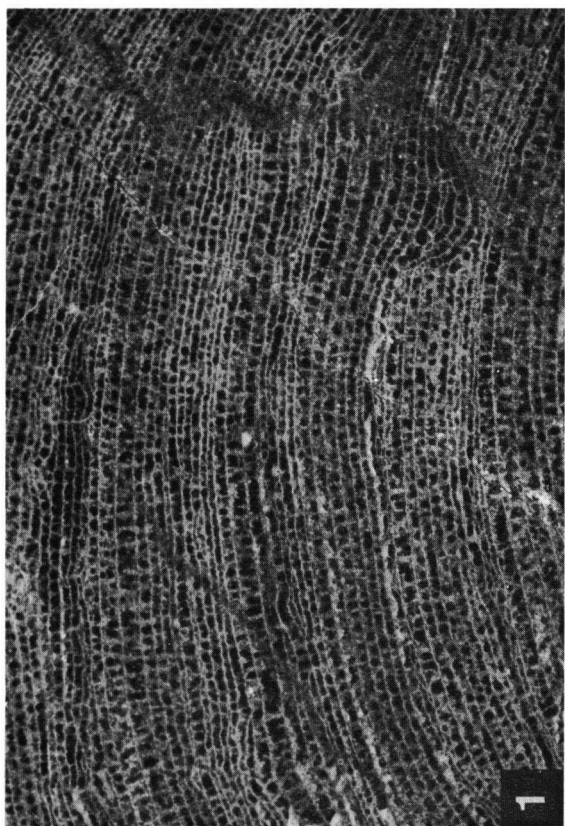
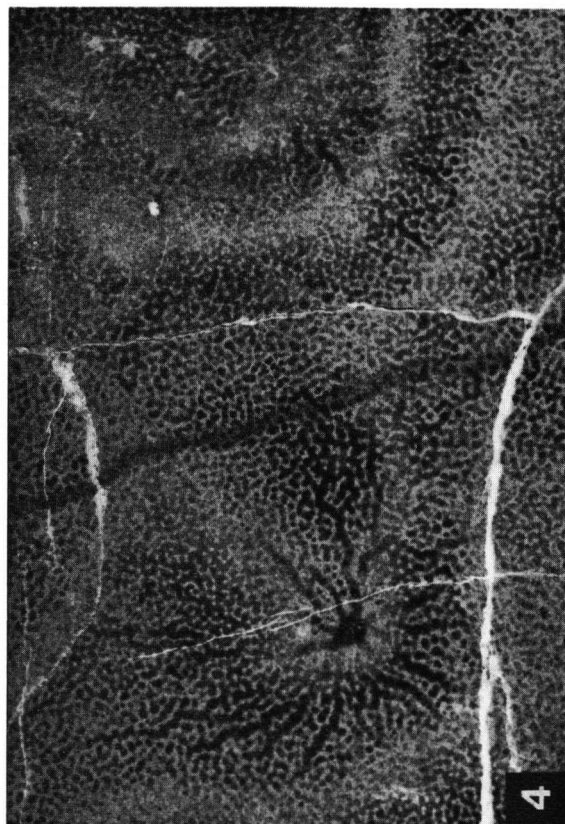
Fig. 1. (Specimen 528A). *Actinostroma verrucosum*?. The gross structure is rather irregular. Most galleries are very low without cyst plates. The latilaminae are also very low. Vert. section, X 8.

Fig. 2. (Specimen 449B). *Actinostroma verrucosum*?. In this aberrant specimen the gross structure is very irregular. The galleries are extremely low in some zones. Vert. section, X 8.

Fig. 3. (Specimen 533F). *Actinostroma verrucosum*?. Same specimen as in Pl. 19 fig. 4. Part of the pillars are isolated while others are connected by cyst plates. The laminae are seen as vague bands. In the lower left corner the cross-section through a worm tube is visible. See also Pl. 2 fig. 4. The dark spots are caused by silicification. Tang. section, X 8.

Fig. 4. (Specimen 472D). *Actinostroma verrucosum*? with astrorhizae. Tang. section, X 8.





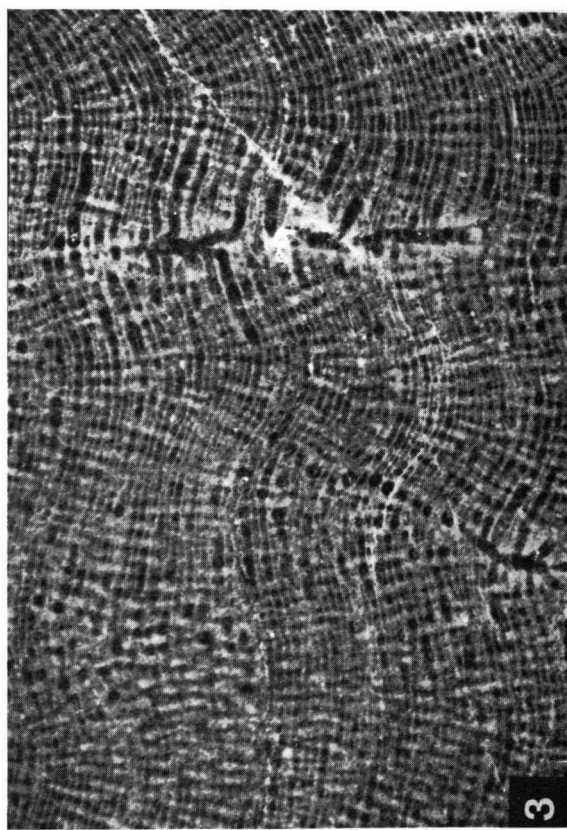
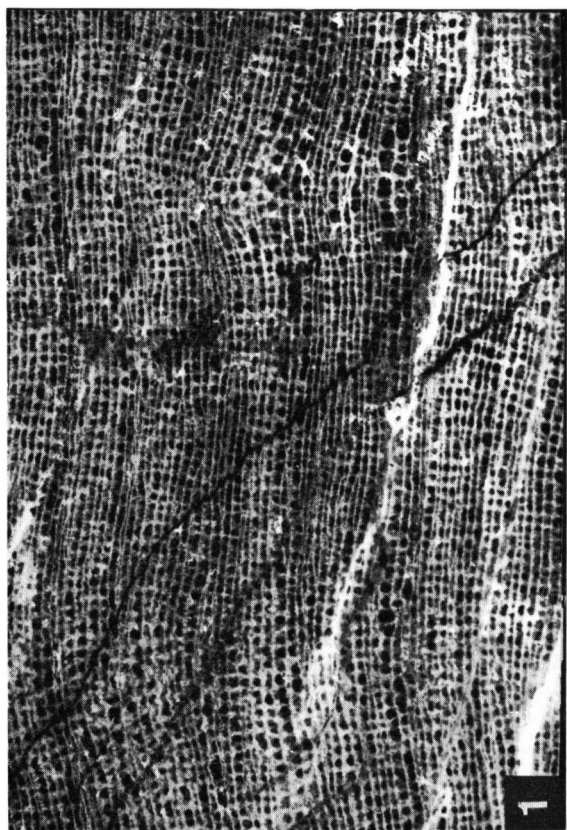
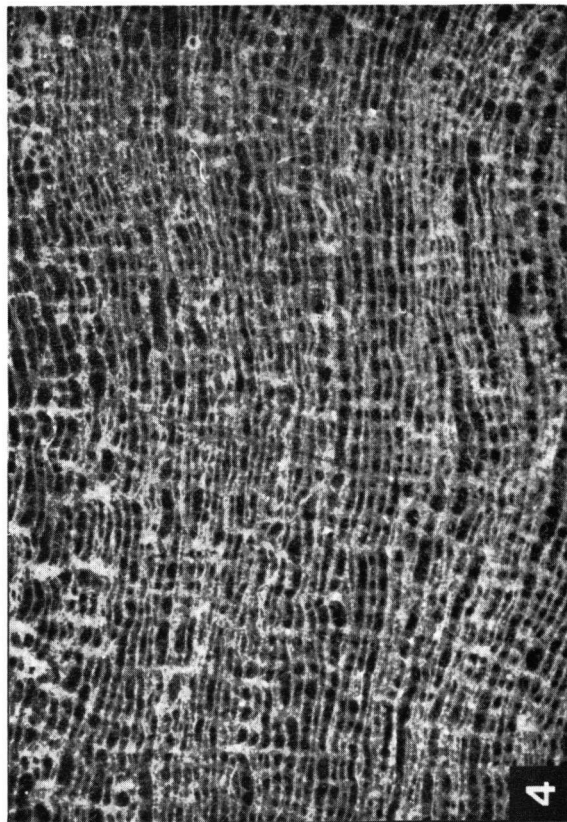
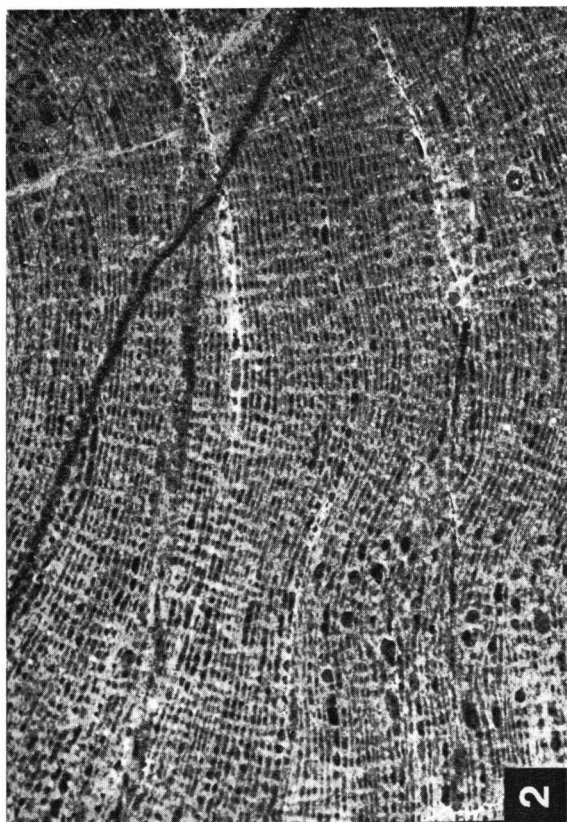
## PLATE 21

Fig. 1. (Specimen 426). *Actinostroma stellulatum* with distinct latilaminae. See also Pl. 5 figs. 1–4. Vert. section, X 8.

Fig. 2. (Specimen 410A). *Actinostroma stellulatum* with rather low interlaminar spaces. The astrorhizae are recognizable by their wider diameter. Vert. section, X 8.

Fig. 3. (Specimen 454F). *Actinostroma stellulatum* with rather thick pillars and superposed astrorhizae in a mamelon. Vert. section, X 8.

Fig. 4. (Specimen 372). *Actinostroma stellulatum* with thin laminae which undulate between the thick pillars. Vert. section, X 8.





## PLATE 22

Fig. 1. (Specimen 223). *Actinostroma stellulatum*. The pillars are isolated, the laminae are visible as vague bands. Tang. section, X 8.

Fig. 2. (Specimen 426). *Actinostroma stellulatum*. The pillars seem to have a radial structure but this is due to recrystallization. See also Pl. 5 figs. 1-4 and Pl. 21 fig. 1. Note the branching astrorhizae. Tang. section, X 8.

Fig. 3. (Specimen 517B). *Actinostroma* sp. 1 with abnormal large astrorhizae. Note the layers of repair tissue in the latilaminae. On the left a few foraminae are present in the laminae. Vert. section, X 8.

Fig. 4. (Specimen 517J). *Actinostroma* sp. 1. The gross structure is irregular, although the laminae and pillars tend to be continuous. The astrorhizae are much smaller than in the specimen of fig. 3. Vert. section, X 8.

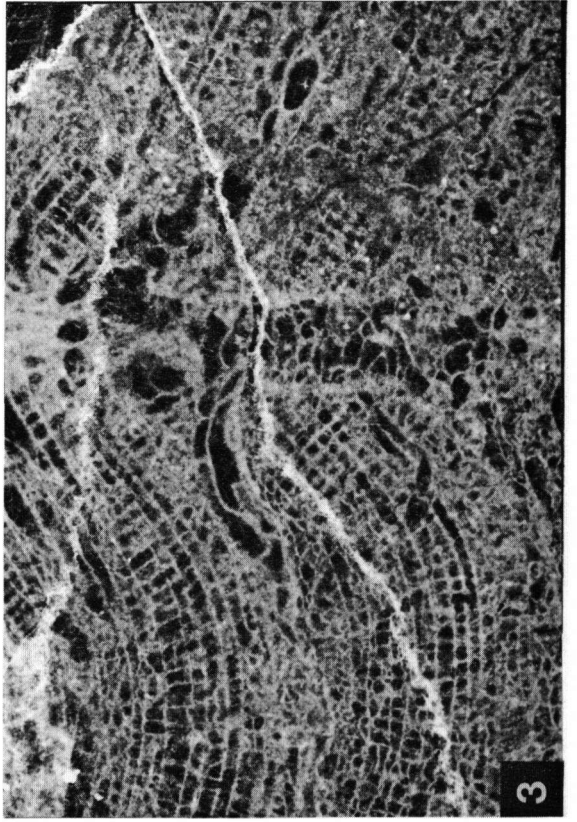
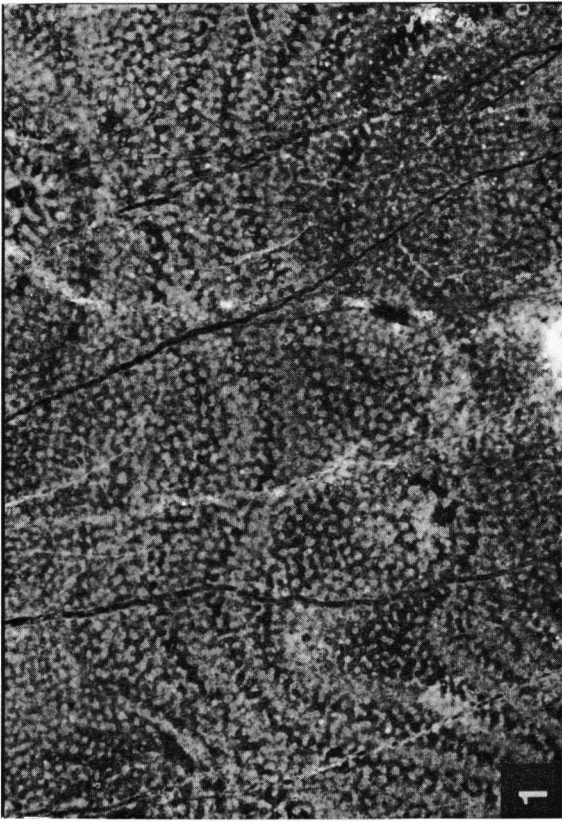


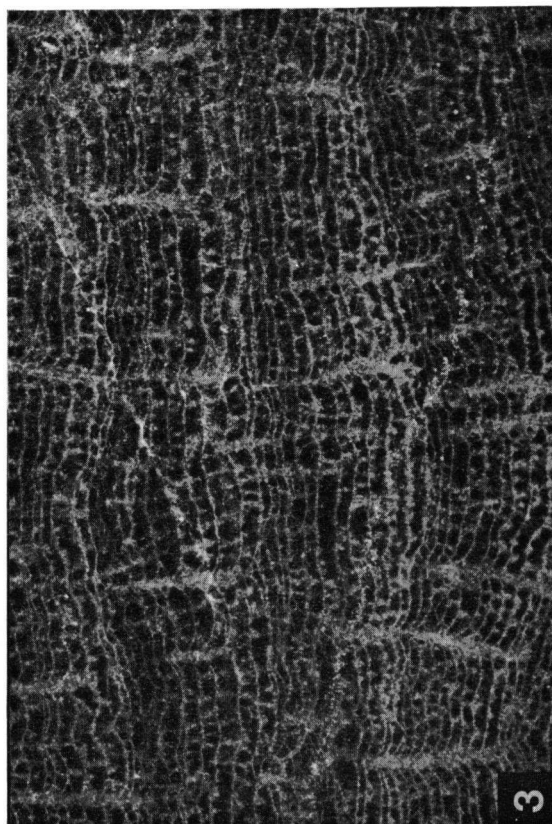
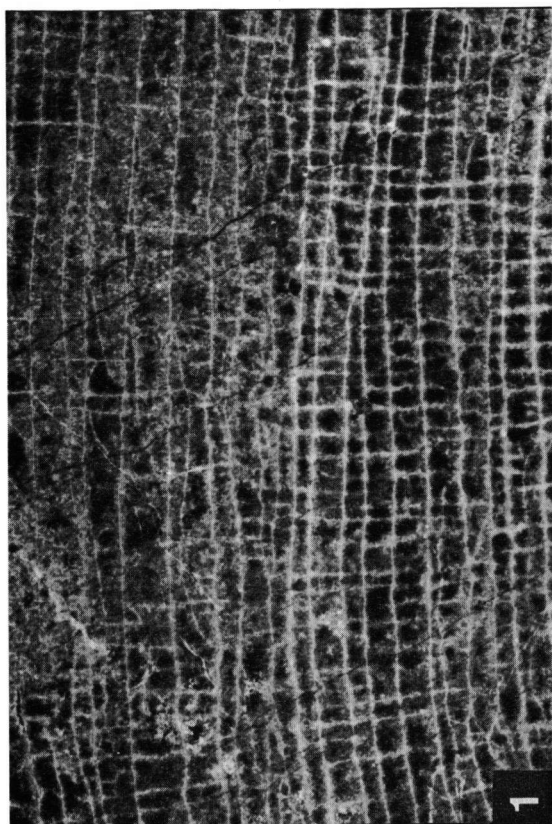
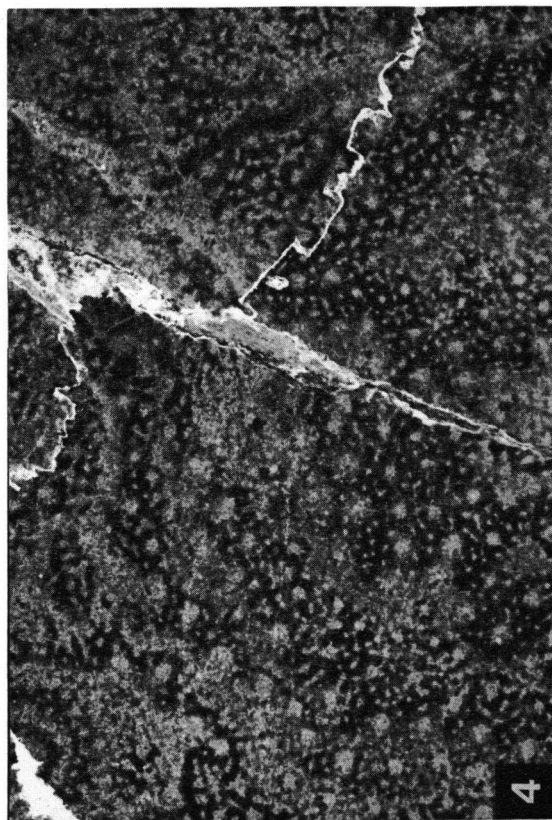
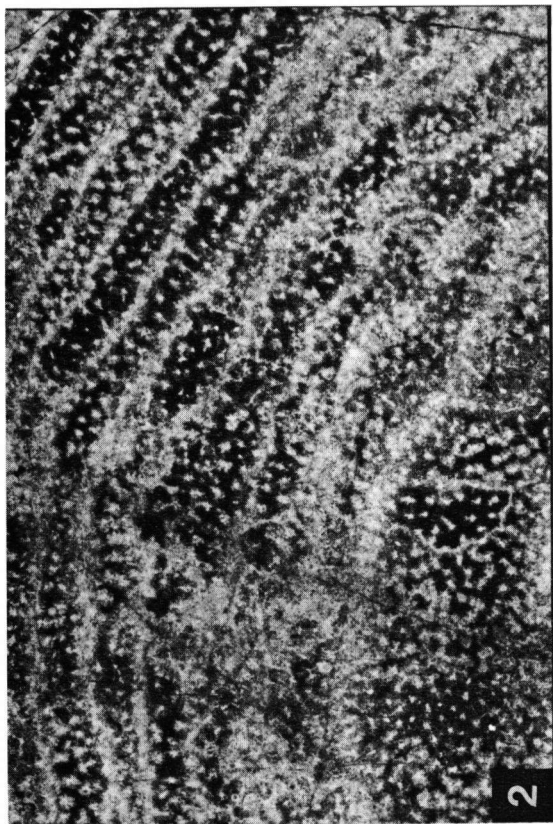
PLATE 23

Fig. 1. (Specimen 515C). *Actinostroma* sp. 2. The gross structure is rather coarse. Some of the horizontal skeletal elements are intermediate between laminae and cyst plates. Vert. section, X 8.

Fig. 2. (Specimen 515C). Tangential section of the same specimen as in fig. 1. The pillars are connected by cyst plates only in a very few places. Tang. section, X 8.

Fig. 3. (Specimen 522C). *Actinostroma* sp. 3 with pillars of two types. The continuous laminae undulate between the thick pillars. Vert. section, X 8.

Fig. 4. (Specimen 522C). Tangential section of the same specimen as in fig. 3, showing the differentiation in two types of pillars. Tang. section, X 8.



#### PLATE 24

Fig. 1. (Specimen 567A). *Actinostroma* sp. 4. The continuous pillars have a rather variable diameter. Note the corkscrew-like worm. Vert. section, X 8.

Fig. 2. (Specimen 567A). Tangential section of the same specimen as in fig. 1. The pillars may be thin or rather thick (left part of the figure). Tang. section, X 8.

Fig. 3. (Specimen 32G). *Stromatoporella? granulata?* with obvious mamelons. The microstructure is microlaminate and vacuolate. See also Pl. 6 figs. 3, 4. Vert. section, X 8.

Fig. 4. (Specimen 478A). *Stromatoporella? granulata?*. The pillars are rather superposed in this laminar specimen. (This specimen occurs in the same hand-specimen as the specimen figured in Pl. 40 fig. 3.) Vert. section, X 8.



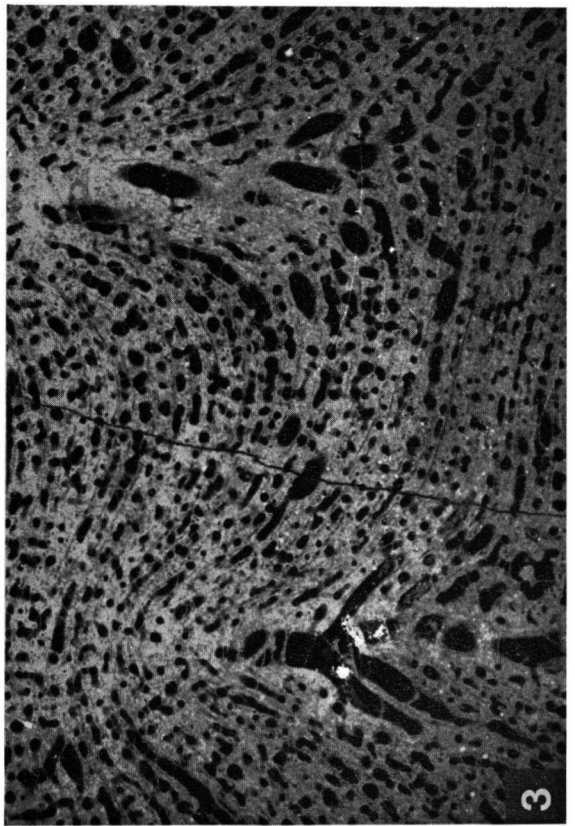
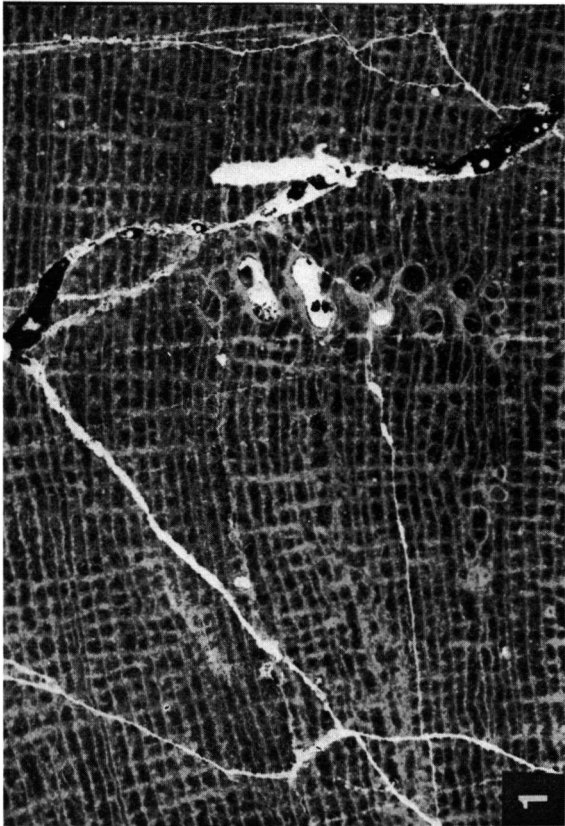
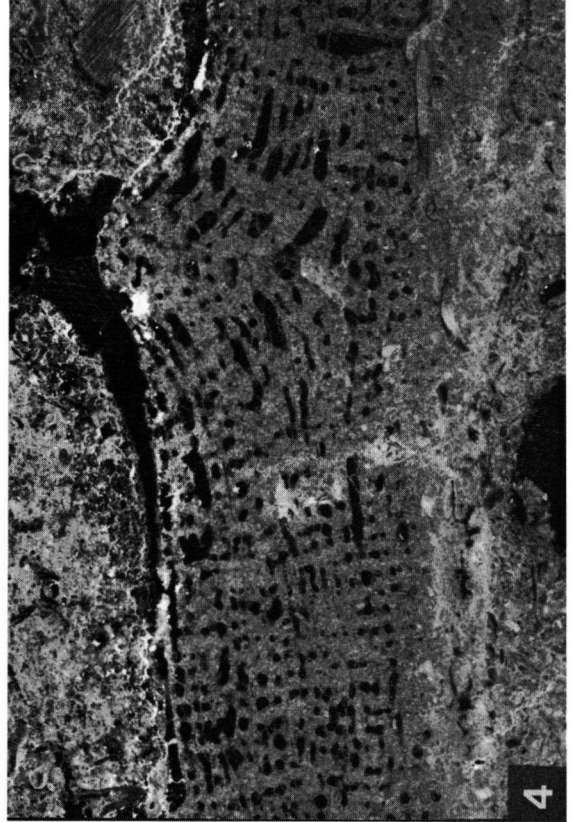
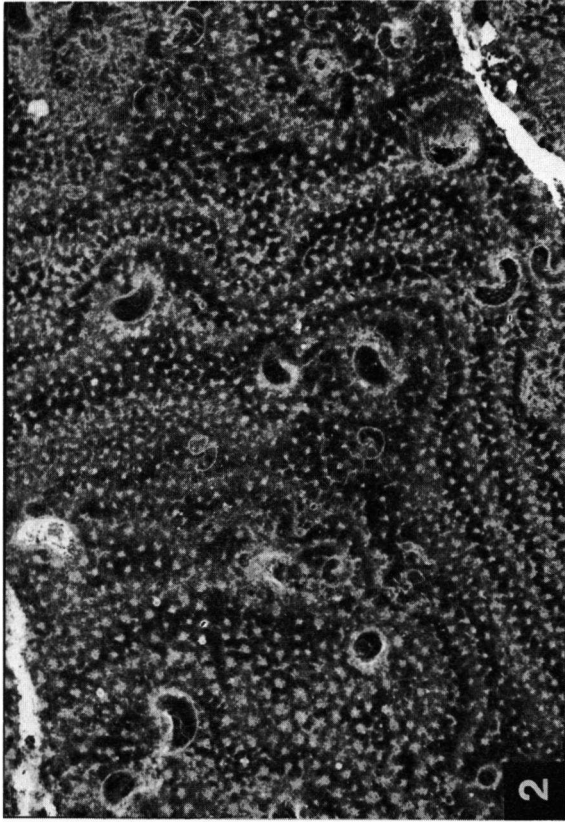




PLATE 25

Fig. 1. (Specimen 580B). *Stromatoporella? granulata?* intergrown with *Syringopora* sp. A few ring pillars are visible. Vert. section, X 8.

Fig. 2. (Specimen 580J). *Stromatoporella? granulata?* intergrown with *Syringopora* sp. Note the variability of the height of the galleries. See also Pl. 6 figs. 5, 6. Vert. section, X 8.

Fig. 3. (Specimen 580G). *Stromatoporella? granulata?* intergrown with *Syringopora* sp. Note the differences in gross structure between different zones of the same coenosteum. Vert. section, X 8.

Fig. 4. (Specimen 27). *Stromatoporella? granulata?* intergrown with *Syringopora* sp. The latilaminae are formed by alternating zones of thick and thin tissue. Vert. section, X 8.

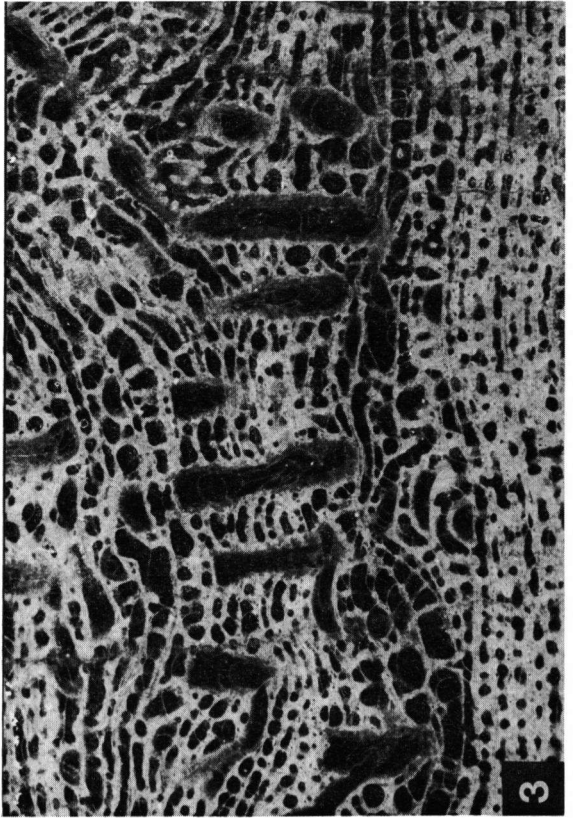
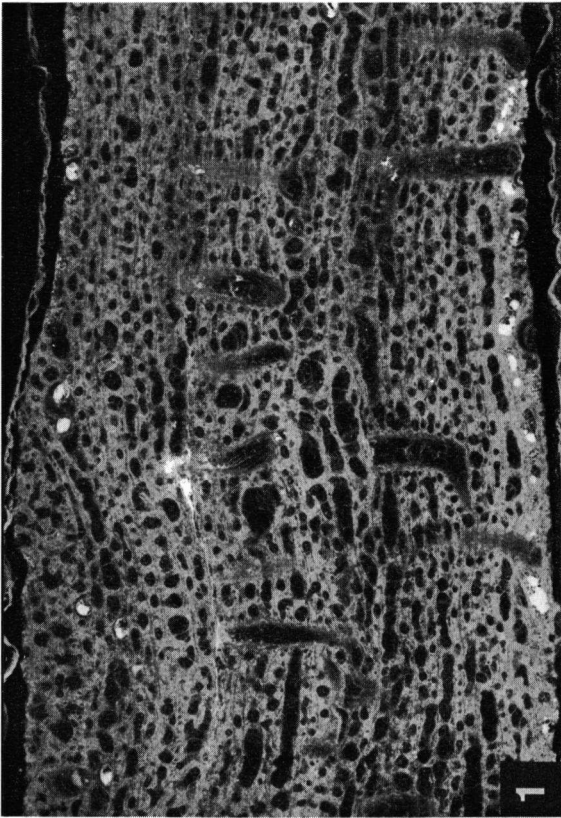
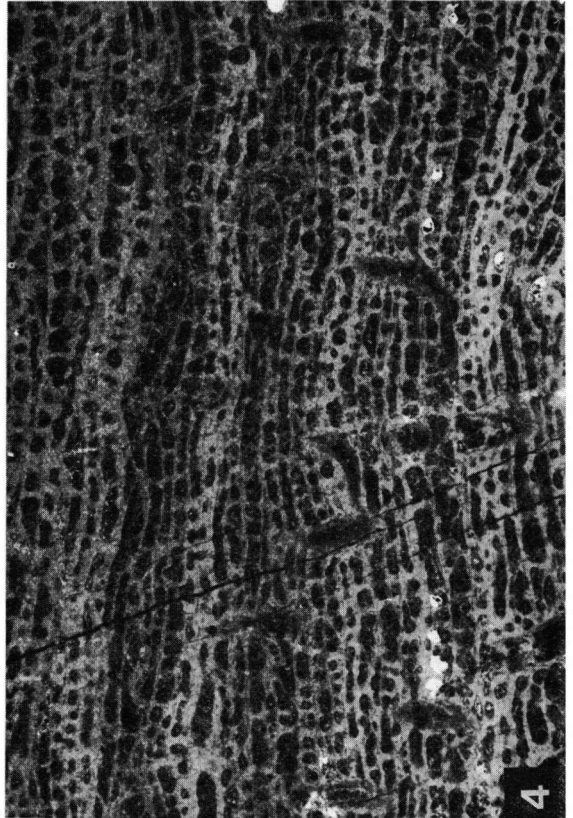
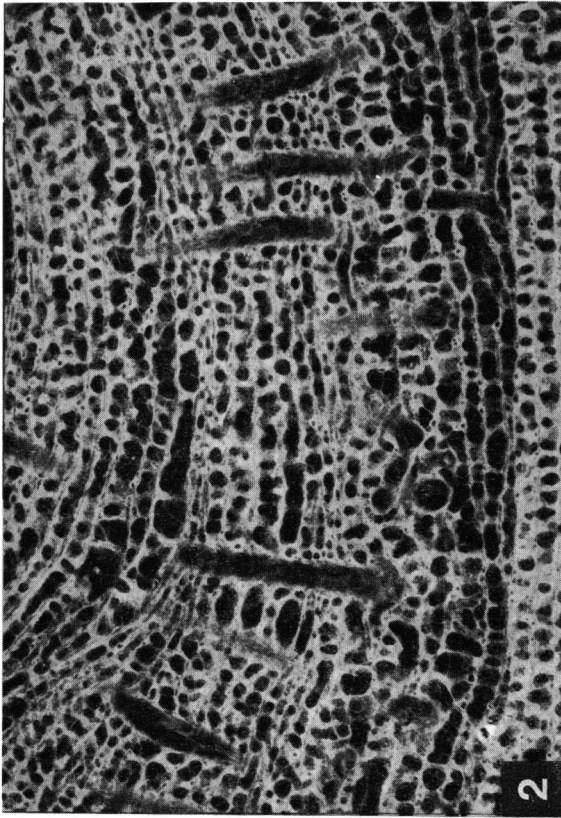


PLATE 26

Fig. 1. (Specimen 421A). *Stromatoporella? granulata?*. This rather badly preserved specimen came from the uppermost Caldas Formation. Vert. section, X 8.

Fig. 2. (Specimen 333). *Stromatoporella? granulata?* with a rather close spacing of the laminae and more or less superposed pillars. Vert. section, X 8.

Fig. 3. (Specimen 582D). *Stromatoporella? granulata?* intergrown with *Syringopora* sp. The gross structure is scarcely recognizable due to the pseudocellular microstructure. See also Pl. 8 figs. 1, 2. Vert. section, X 8.

Fig. 4. (Specimen 35B). *Stromatoporella? granulata?*. The gross structure is still recognizable although the specimen has been very strongly affected by alteration. Vert. section, X 8.

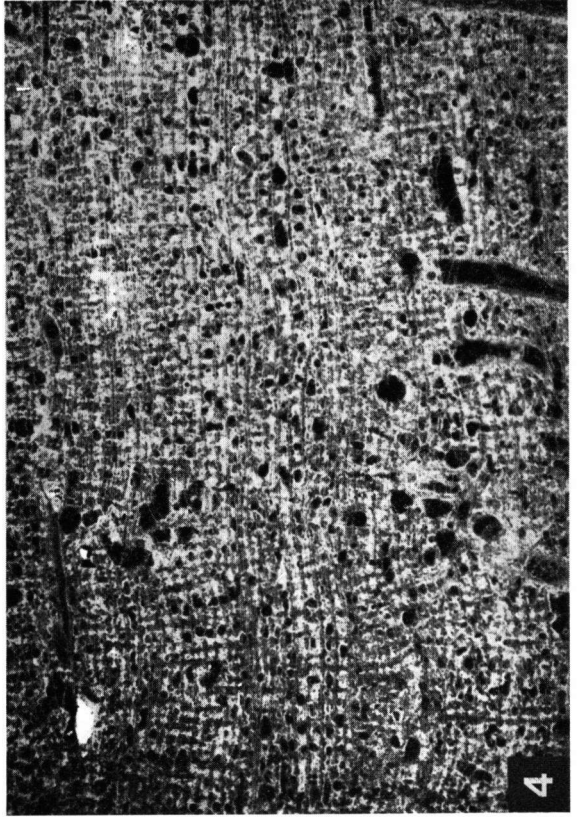
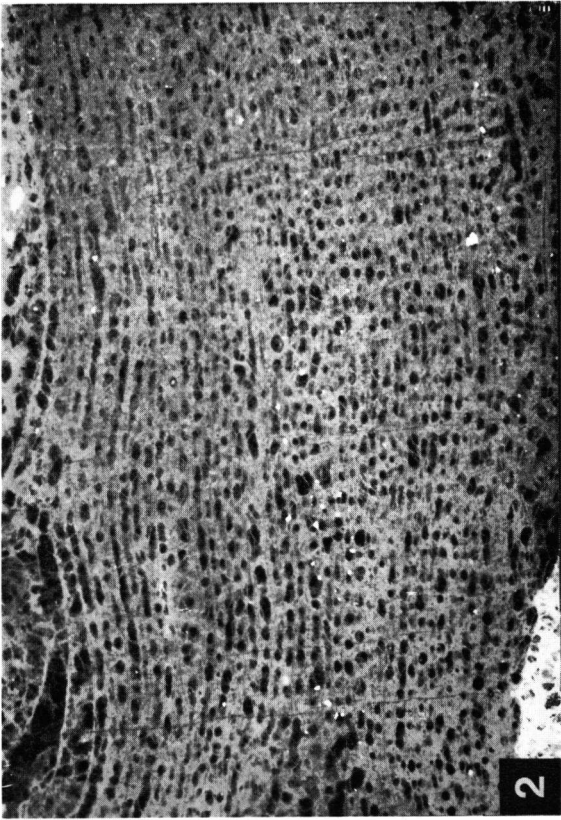


PLATE 27

Fig. 1. (Specimen 5B). *Stromatoporella? granulata?* with well developed mamelons and astrorhizae. Tang. section, X 8.

Fig. 2. (Specimen 41A). *Stromatoporella? granulata?*. Laminar specimen without mamelons. Most of the pillars are isolated. Note the presence of some ring-pillarlike structures. Tang. section, X 8.

Fig. 3. (Specimen 538E). *Stromatoporella? selwyni* with a very common type of gross structure, ring pillars are rather scarce. Vert. section, X 8.

Fig. 4. (Specimen 529C). *Stromatoporella? selwyni*. The gross structure of this specimen is similar to that of fig. 3 but finer. Vert. section, X 8.



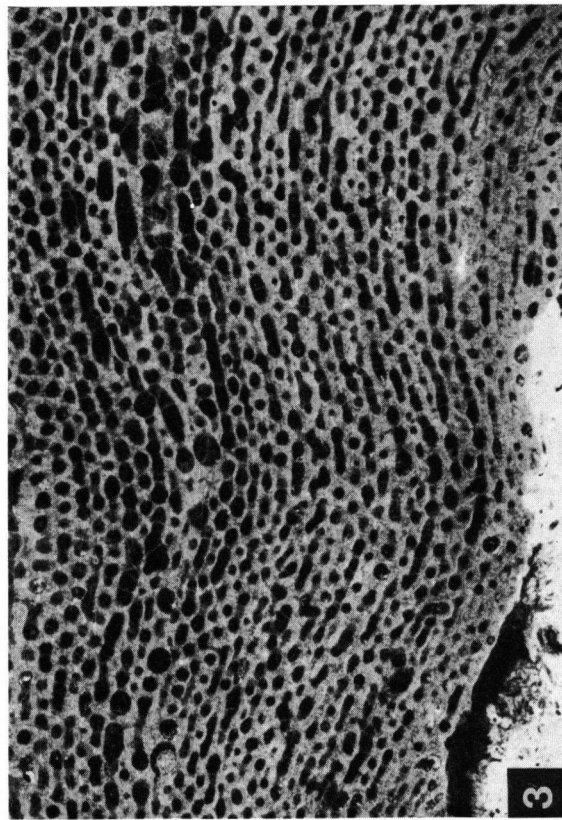
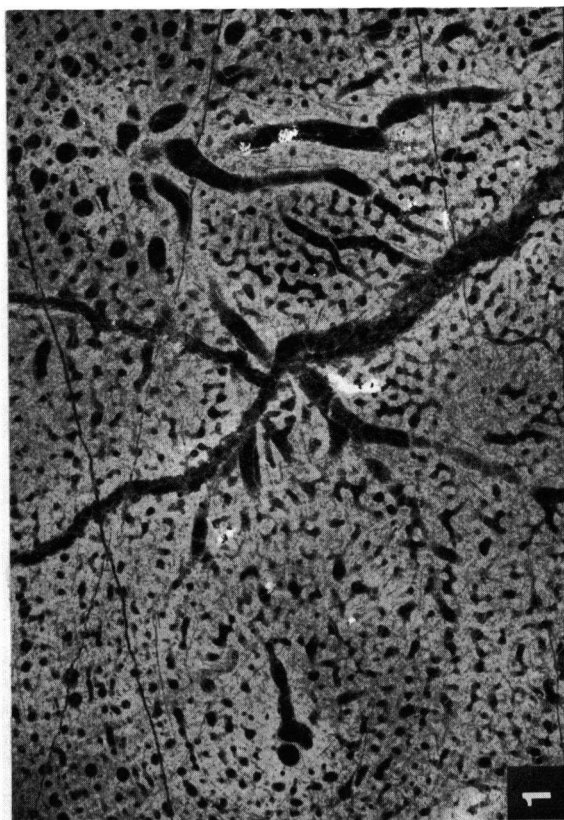
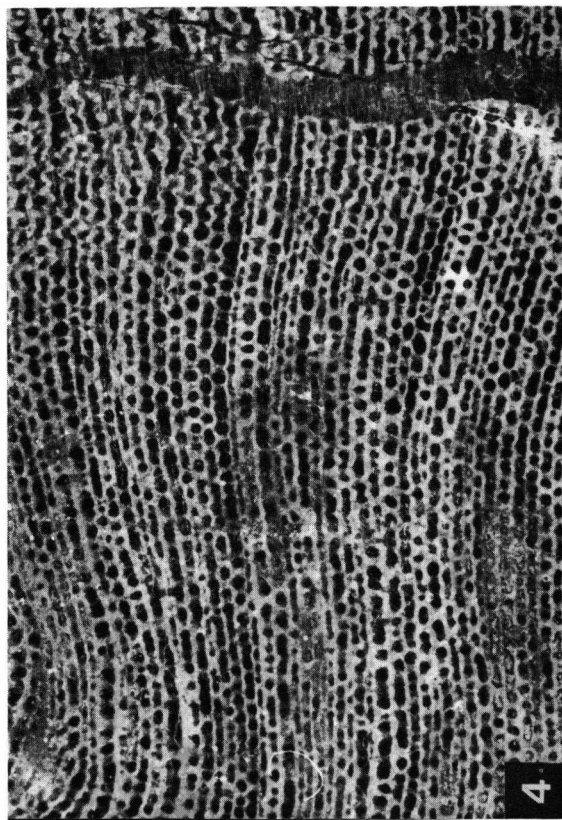
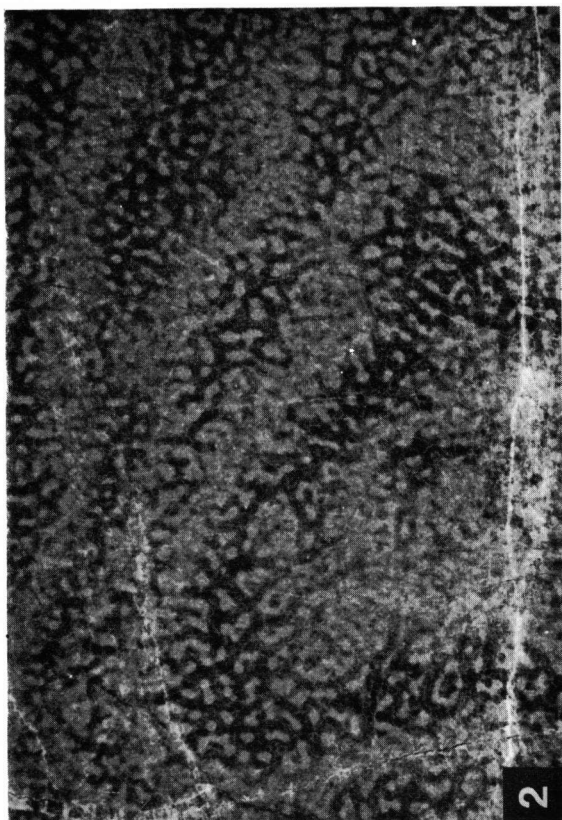




PLATE 28

Fig. 1. (Specimen 522D). *Stromatoporella? selwyni* with small columnar-like mamelons. See also Pl. 9 figs. 1, 2. Vert. section, X 8.

Fig. 2. (Specimen 537J). *Stromatoporella? selwyni* with an interruption of growth and repair tissue. Above the repair tissue, temporarily only pillars and cyst plates were formed. The dark areas are caused by silicification. Vert. section, X 8.

Fig. 3. (Specimen 532B). *Stromatoporella? selwyni* with zones of very high galleries and more or less superposed pillars. Ring pillars are also present. Vert. section, X 8.

Fig. 4. (Specimen 533A). *Stromatoporella? selwyni* with extremely abundant ring pillars. Note the occurrence of cyst plates in the ring pillars. In some galleries there are up to four ring pillars! The latilaminae are visible as alternating zones of distinct and vague tissue. The preservation of this specimen is similar to that shown in Pl. 10 figs. 1, 2. Vert. section, X 8.

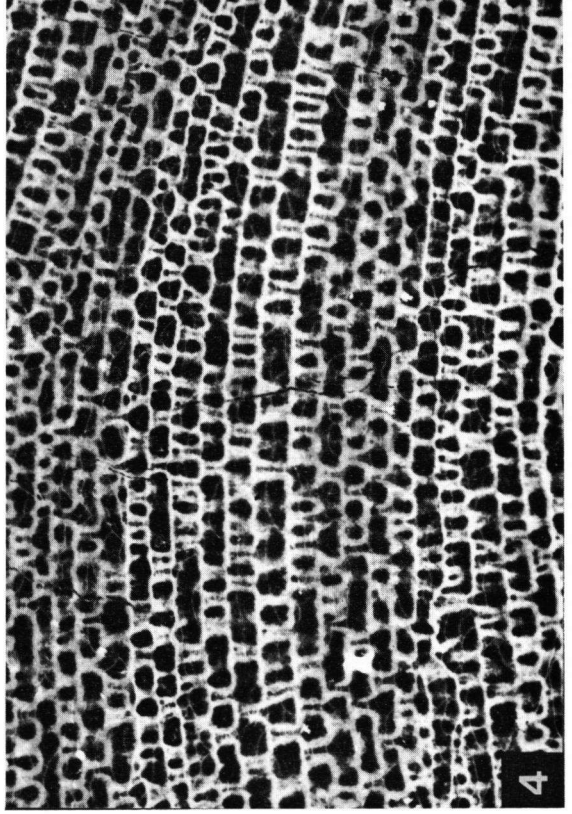
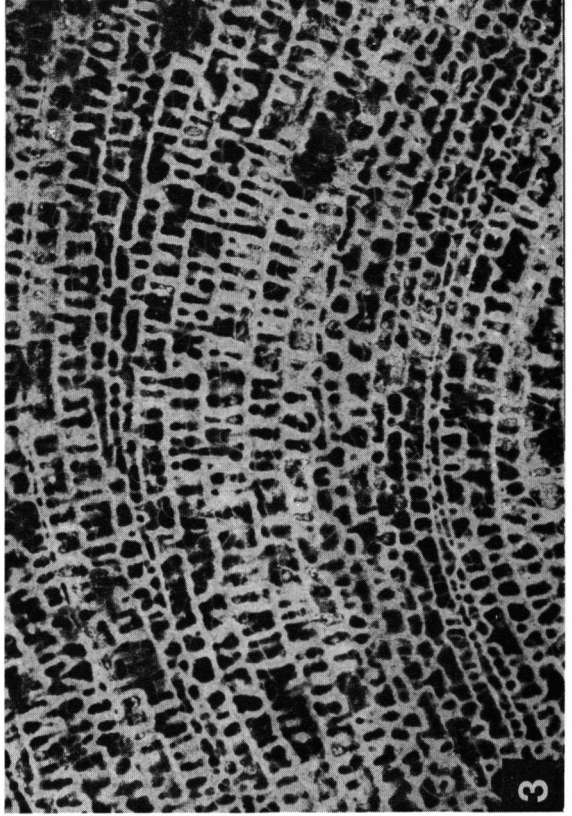
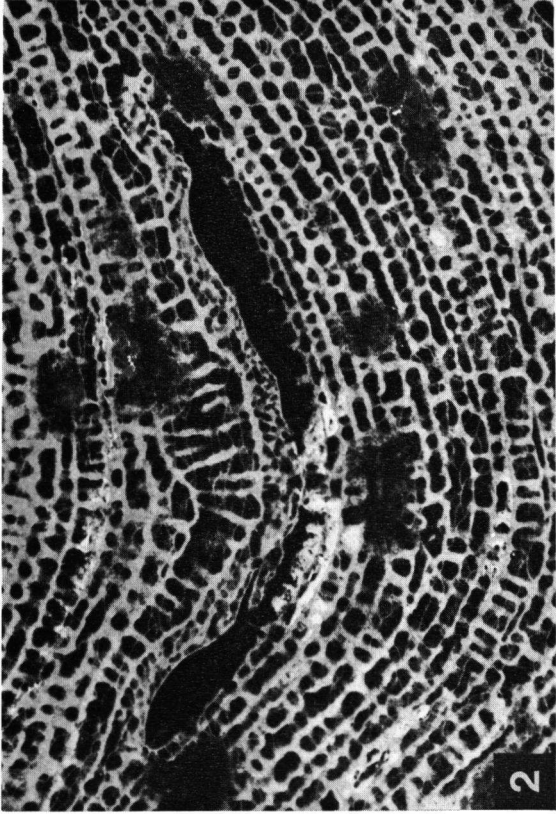
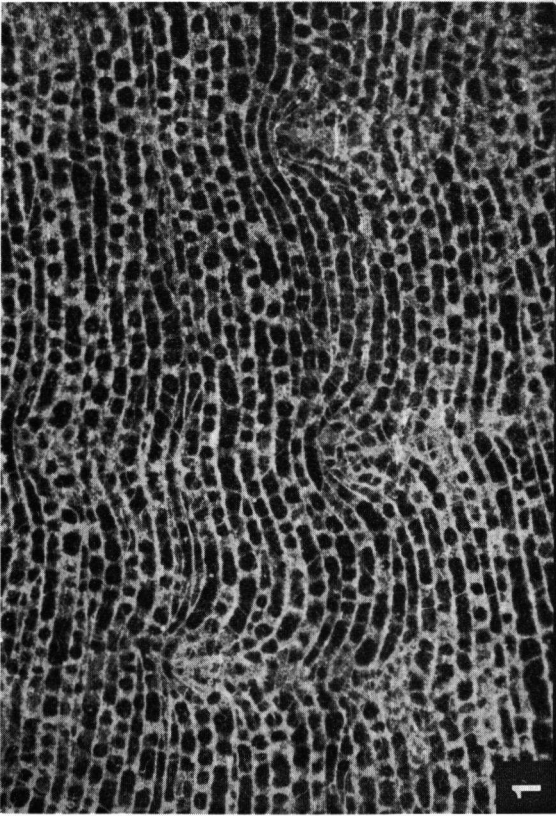


PLATE 29

Fig. 1. (Specimen 528B). *Stromatoporella? selwyni* with a well preserved micro-structure. The gross structure is rather irregular in this specimen, some pillars are superposed. Vert. section, X 8.

Fig. 2. (Specimen LV510C). *Stromatoporella? selwyni* with latilaminae formed by alternating very fine and coarse gross structures. Pillars are frequently superposed in this specimen. Vert. section, X 8.

Fig. 3. (Specimen 537I). *Stromatoporella? selwyni*. This specimen is similar to that on fig. 2 but here the pillars are not superposed. Note the *Hermatostroma*-like structures in some galleries. Vert. section, X 8.

Fig. 4. (Specimen 519B). *Stromatoporella? selwyni* with a fine to very fine gross structure and thin skeletal elements. Note the repair tissue at the base. Vert. section, X 8.

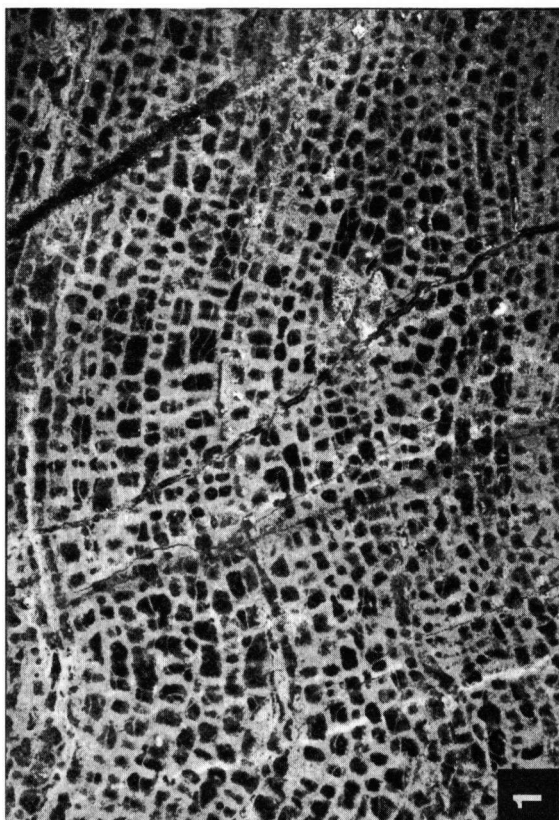


PLATE 30

Fig. 1. (Specimen 522H). *Stromatoporella? selwyni* with very fine repair tissue. On the right the section is oblique. See also Pl. 8 figs. 7, 8. Vert. section, X 8.

Fig. 2. (Specimen 522A). *Stromatoporella? selwyni* encrusting a bryozoan. Note the very fine repair tissue in the mamelon. Vert. section, X 8.

Fig. 3. (Specimen 472E). *Stromatoporella? selwyni* without ring pillars. Most pillars are isolated. Note the dolomite crystals in the silicified areas. Tang. section, X 8.

Fig. 4. (Specimen 473B). *Stromatoporella? selwyni* with normal pillars and ring pillars. In the lower part of the figure astrorhizae are visible. The gross structure is rather fine. See also Pl. 9 figs. 7, 8. Tang. section, X 8.



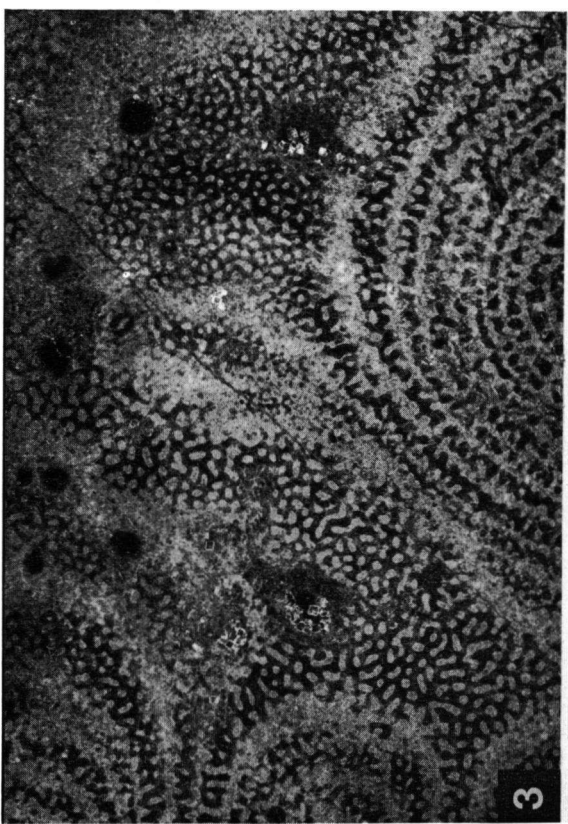
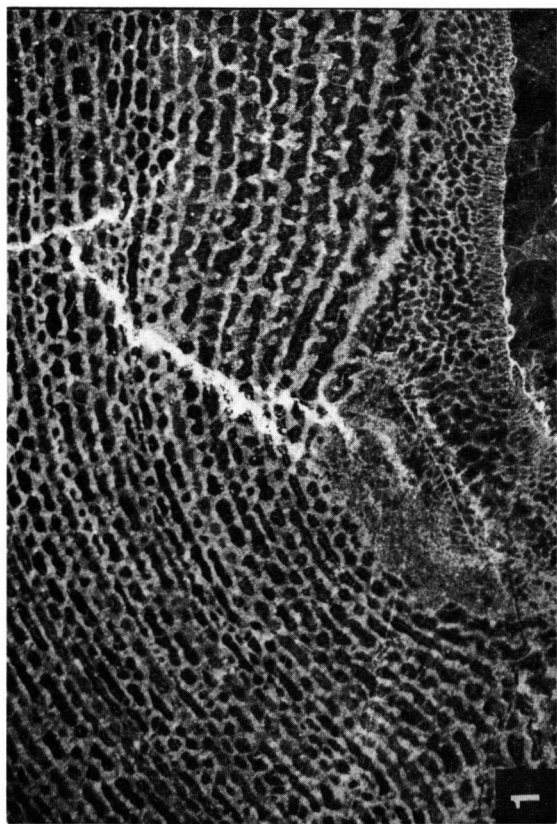
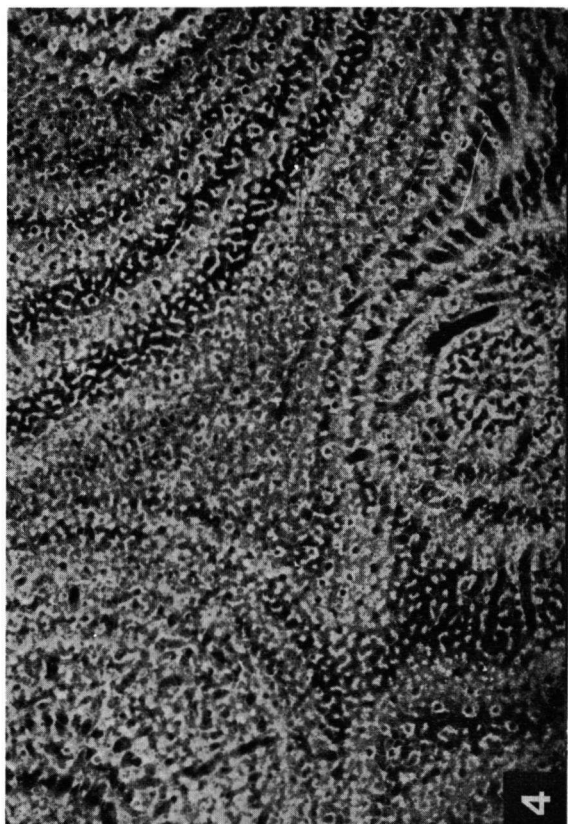
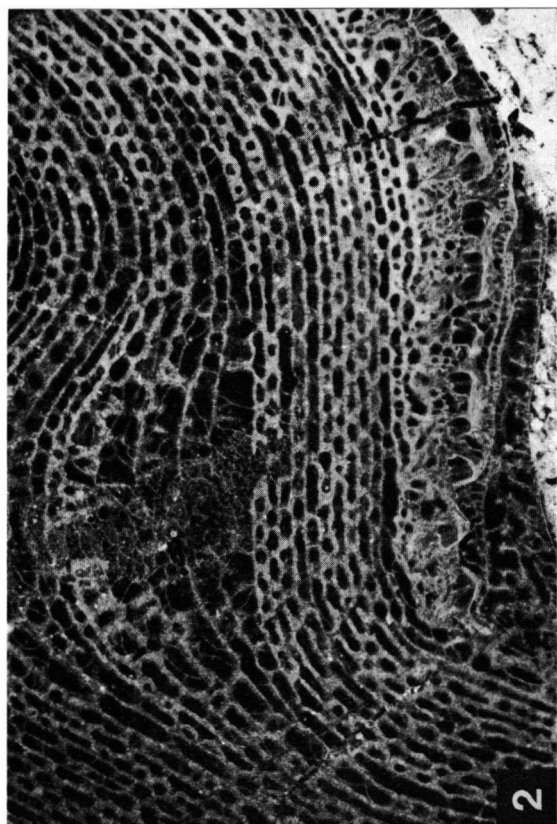




PLATE 31

Fig. 1. (Specimen 532B). *Stromatoporella? selwyni* with obvious ring pillars as well as normal pillars. Same specimen as that of Pl. 28 fig. 3. Tang. section, X 8.

Fig. 2. (Specimen 575D). *Stromatoporella? selwyni* only with ring pillars. Note the 'hexactinellid structure' between the ring pillars. Tang. section, X 8.

Fig. 3. (Specimen 355B). *Stromatoporella?* sp. 1 between *Coenites* sp. and *Alveolites* sp. with fine corallites. Vert. section, X 8.

Fig. 4. (Specimen 86A). *Stromatoporella?* sp. 1 between two coenostea of *Alveolites* sp. with coarse corallites. Vert. section, X 8.

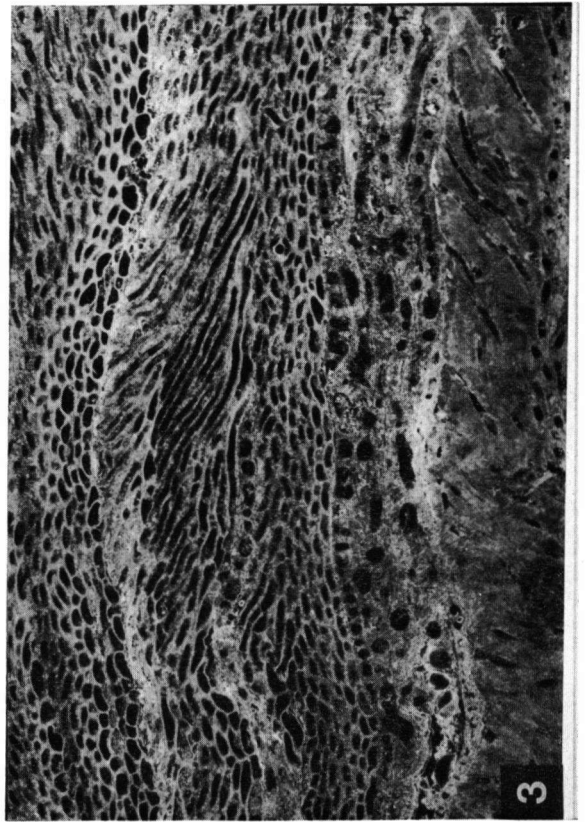
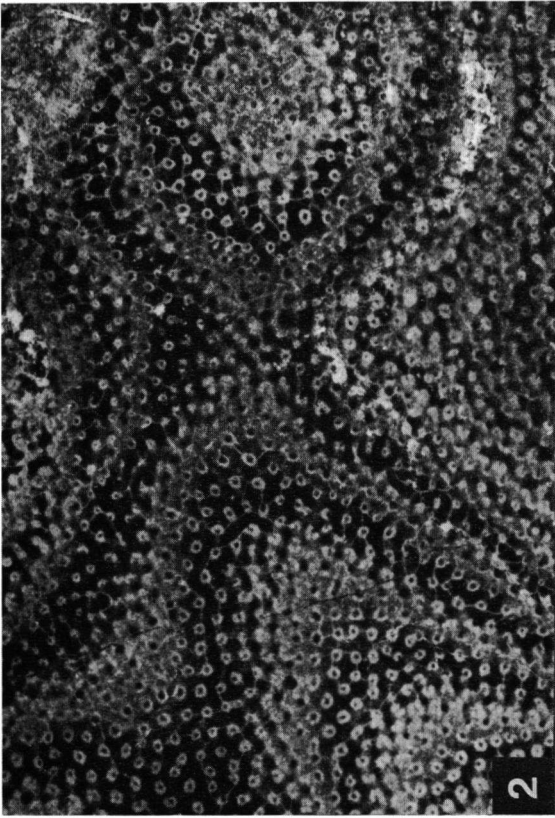


PLATE 32

Fig. 1. (Specimen 52). *Stromatoporella*? sp. 1 with very thick tissue in the upper part. Note the geopetal structure below. The specimen is encrusted by an *Alveolites* sp. with coarse corallites. Vert. section, X 8.

Fig. 2. (Specimen 451D). *Stromatoporella*? sp. 1 forming thin crusts, partly isolated from each other. This specimen is similar to that shown in Pl. 3 fig. 6. Vert. section, X 8.

Fig. 3. (Specimen 293). *Stromatoporella*? sp. 2 intergrown with *Syringopora* sp. The pillars are mostly superposed, cyst plates are extremely common. Vert. section, X 8.

Fig. 4. (Specimen 507B). *Stromatoporella*? sp. 2 intergrown with *Syringopora* sp. The pillars are generally seen as isolated. Tang. section, X 8.

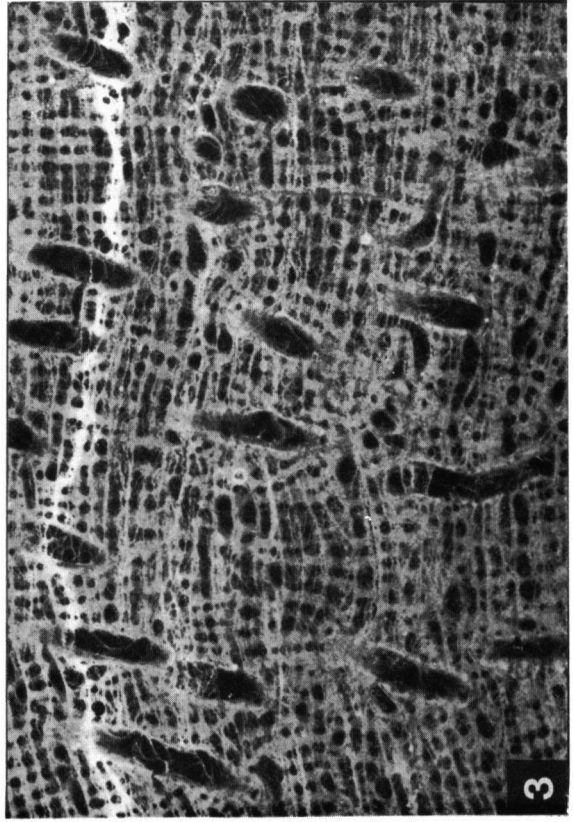
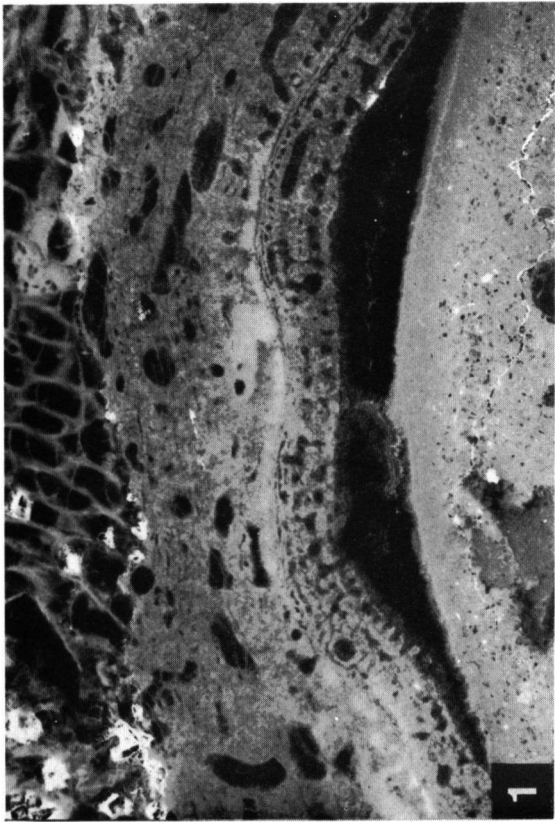
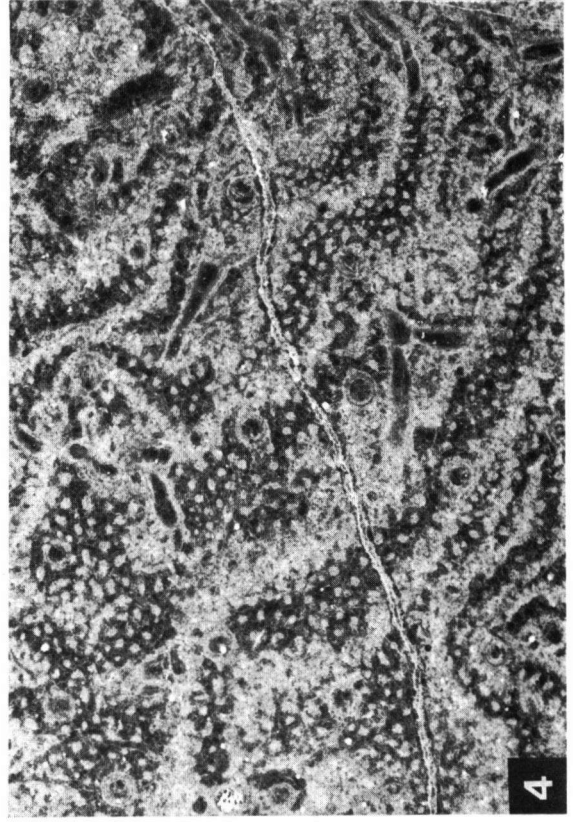
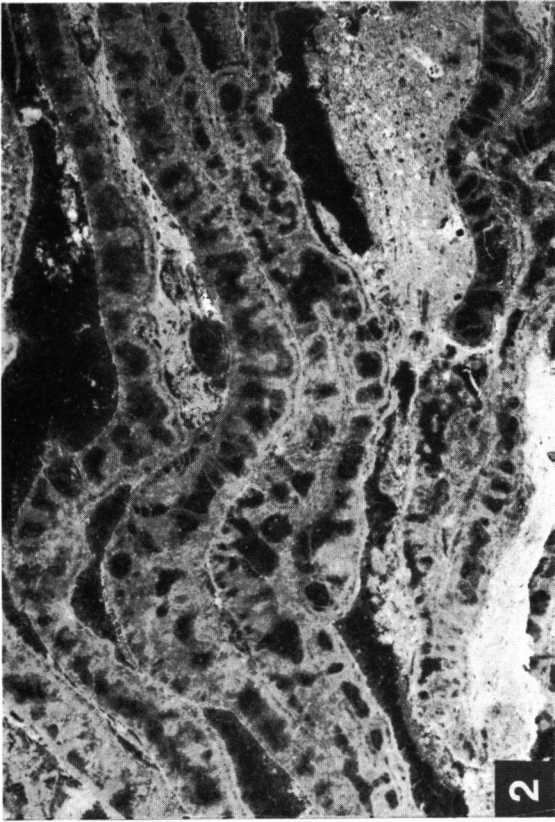


PLATE 33

Fig. 1. (Specimen 540). *Stromatoporella?* sp. 3. The distance between the laminae can be very large in the centre of the dendroid coenosteum. See also Pl. 12 fig. 8. Axial section, X 8.

Fig. 2. (Specimen 540A). Same specimens as in fig. 1. The pillars are frequently isolated. Cross section, X 8.

Fig. 3. (Specimen 56). *Stromatoporella?* sp. 4 with superposed ring pillars. Vert. section, X 8.

Fig. 4. (Specimen 56). Same specimen as in fig. 3. With ring pillars and normal pillars. The normal pillars are isolated or coalescent. Tang. section, X 8.

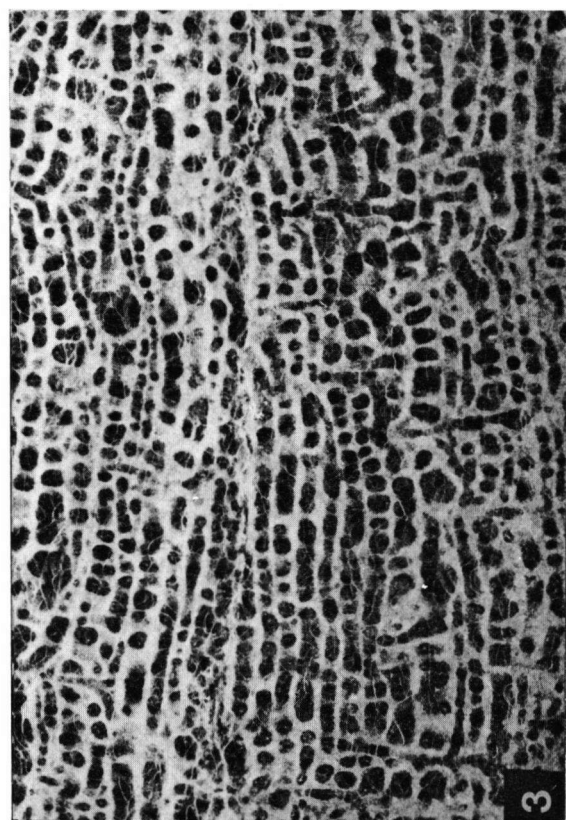
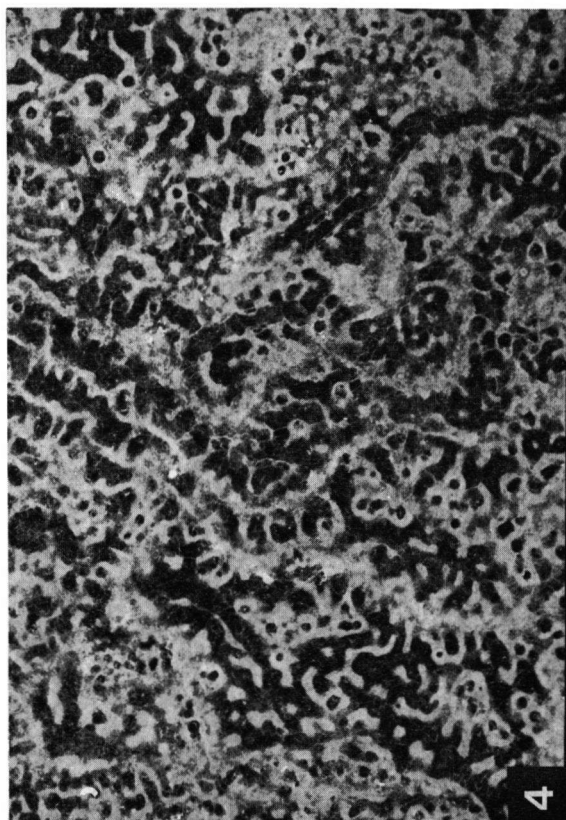
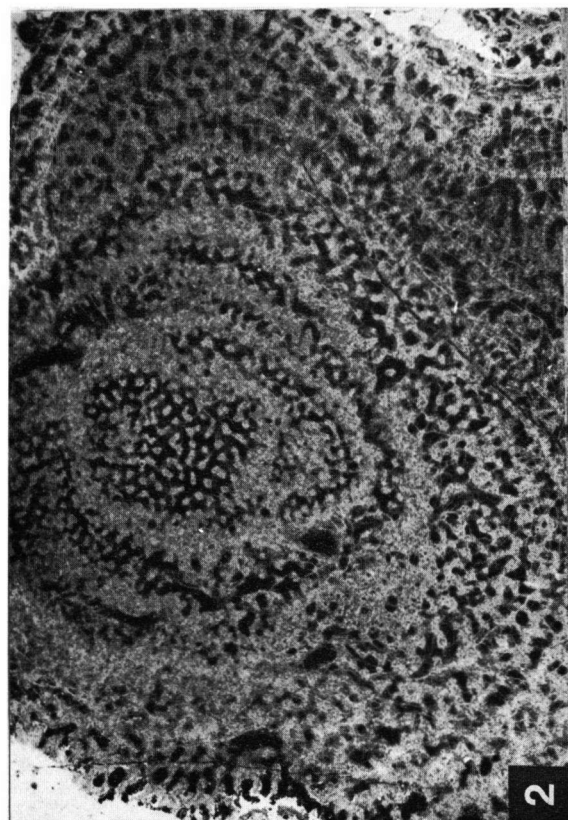




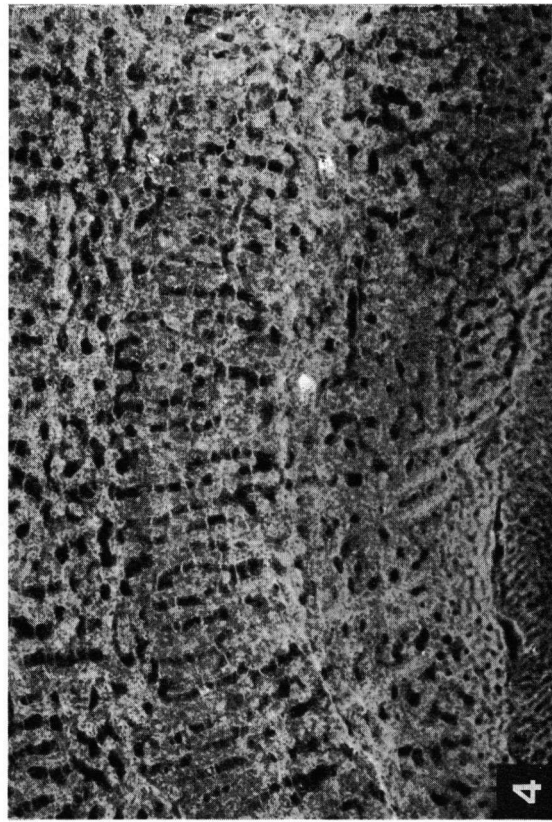
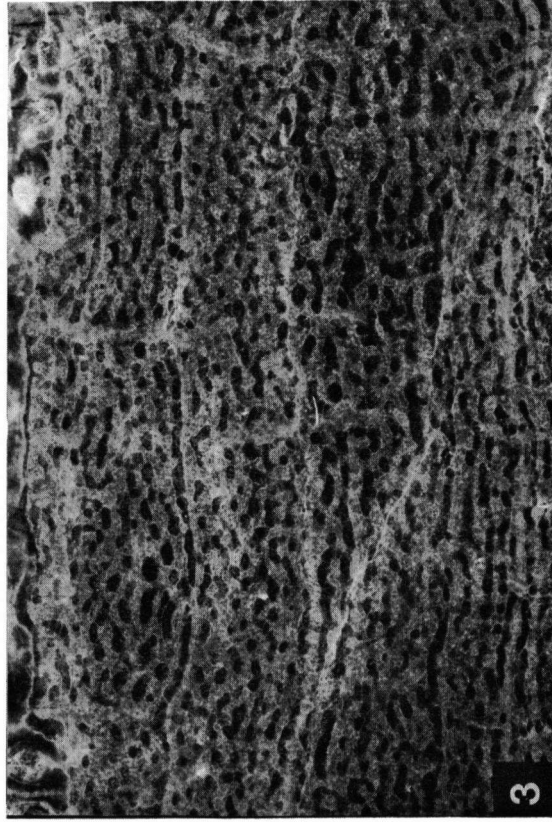
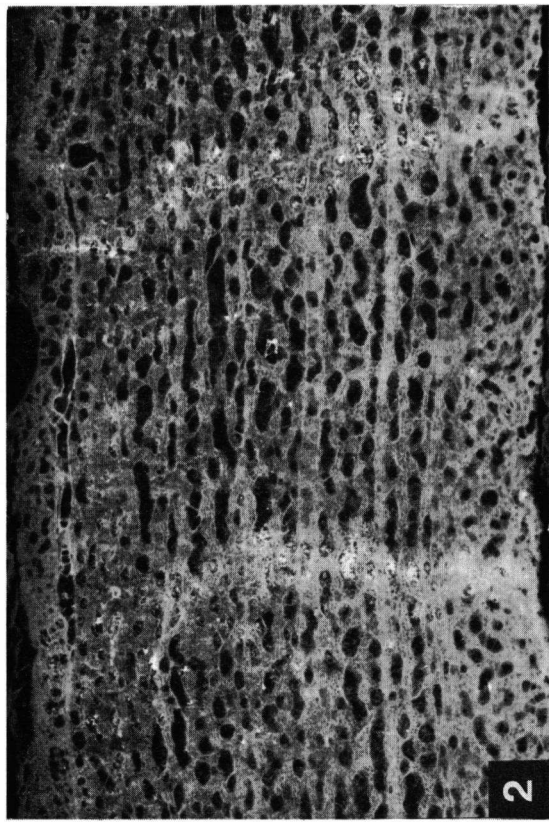
PLATE 34

Fig. 1. (Specimen 581F). *Stromatopora concentrica* intergrown with *Syringopora* sp. Both horizontal and vertical skeletal elements are well developed. Vert. section, X 8.

Fig. 2. (Specimen 586). *Stromatopora concentrica*. Laminar specimen with dominant horizontal skeletal elements. Note repair tissue at the base and top. See also Pl. 10 figs. 7, 8. Vert. section, X 8.

Fig. 3. (Specimen 348). *Stromatopora concentrica* with dominant horizontal skeletal elements and some thick continuous pillars. The laminar coenosteum is overgrown by an aulopodid coral. Vert. section, X 8.

Fig. 4. (Specimen 474T). *Stromatopora concentrica*. The latilaminae are formed by zones with dominant vertical skeletal elements alternating with zones with dominant horizontal skeletal elements. Note fine repair tissue at the base. Vert. section, X 8.



## PLATE 35

Fig. 1. (Specimen 585D). *Stromatopora concentrica* with some straight continuous pillars. The more or less dominant horizontal skeletal elements are mainly formed by cyst plates or very thin laminae. Note astrorhizal canals in the lower part of the figure. Vert. section, X 8.

Fig. 2. (Specimen 581). *Stromatopora concentrica* intergrown with *Syringopora* sp. The vertical elements are dominant in the rather fine gross structure. Vert. section, X 8.

Fig. 3. (Specimen 474D). *Stromatopora concentrica* with thick latilaminae formed by zones with a fine gross structure in which vertical elements are dominant, alternating with zones with a coarse gross structure with thick pillars and well developed horizontal elements. Vert. section, X 8.

Fig. 4. (Specimen 29A). *Stromatopora concentrica* intergrown with *Syringopora* sp. The pillars form an amalgamated network or are coalescent, some are isolated. Tang. section, X 8.

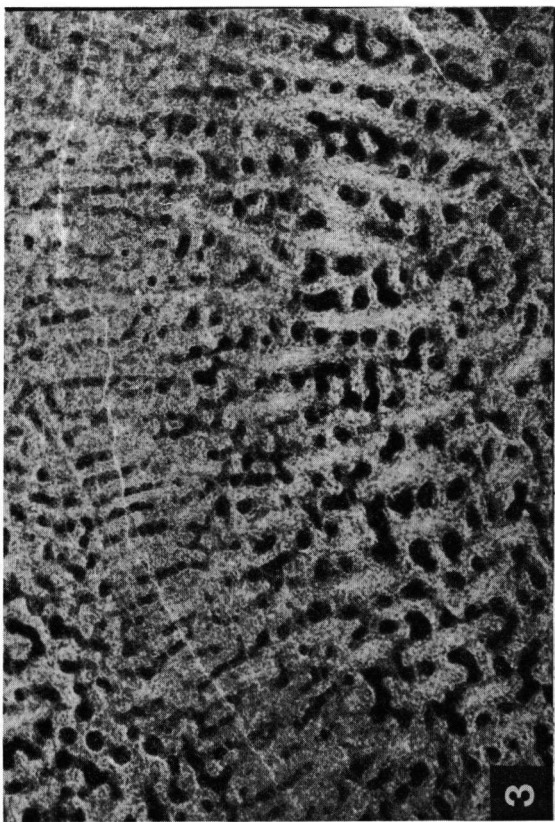
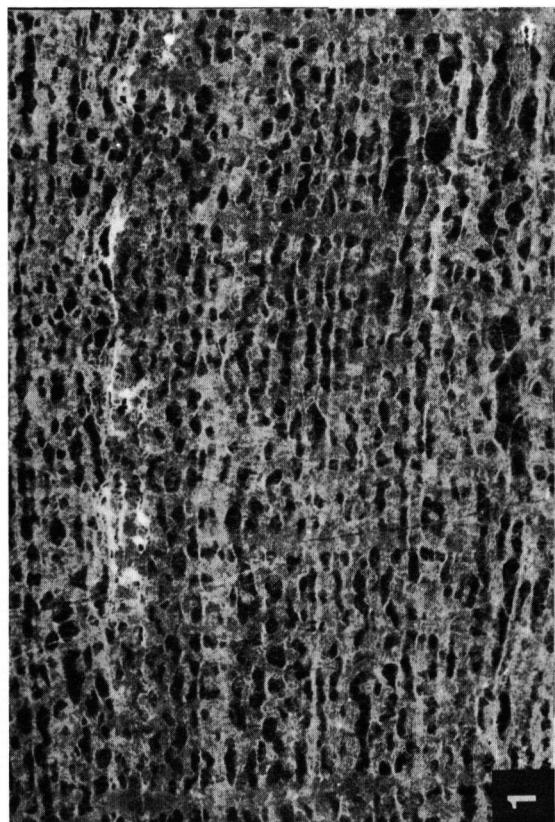
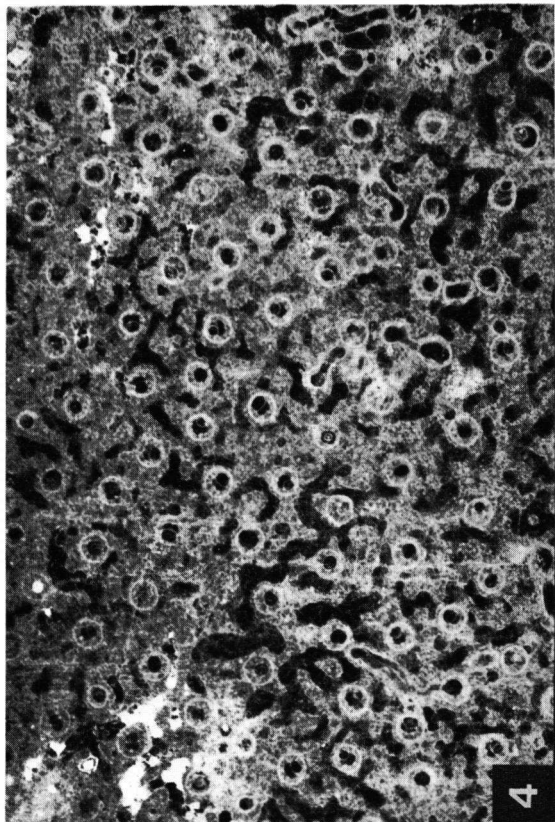


PLATE 36

Fig. 1. (Specimen 570E). *Stromatopora huepschi*?. In some zones the vertical elements are dominant, in others both horizontal and vertical elements are well developed in the skeleton. See also Pl. 10 figs. 5, 6. Vert. section, X 8.

Fig. 2. (Specimen 451B). *Stromatopora huepschi*?. In some places the vertical elements are long and rather straight, in other places the horizontal elements dominate in the skeleton. Vert. section, X 8.

Fig. 3. (Specimen 537M). *Stromatopora huepschi*? with alternate zones of irregular and regular gross structure. See also Pl. 11 fig. 1. Vert. section, X 8.

Fig. 4. (Specimen 416I). *Stromatopora huepschi*? with a coarse gross structure in which the irregular vertical elements are dominant. See also Pl. 11 figs. 4, 5. Vert. section, X 8.



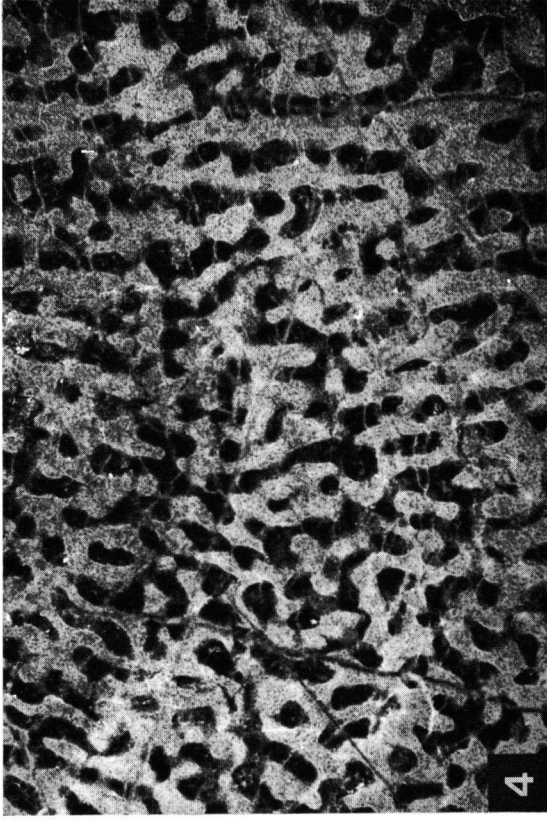
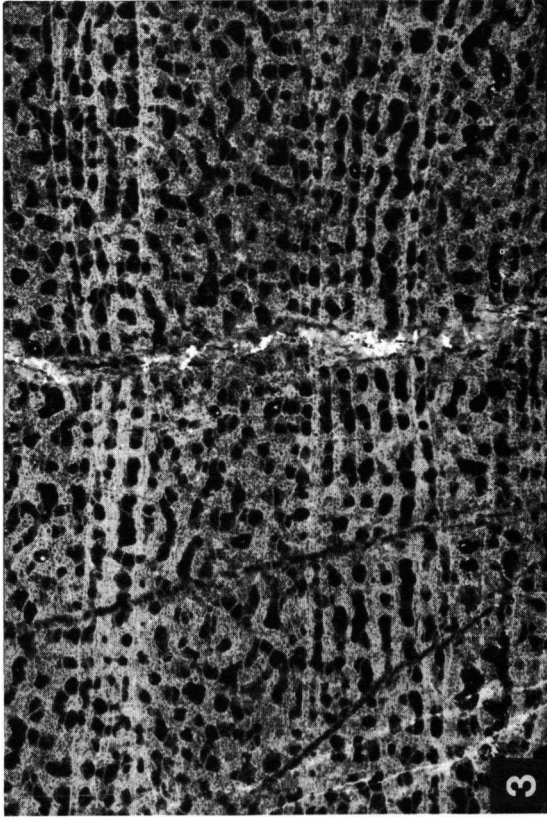
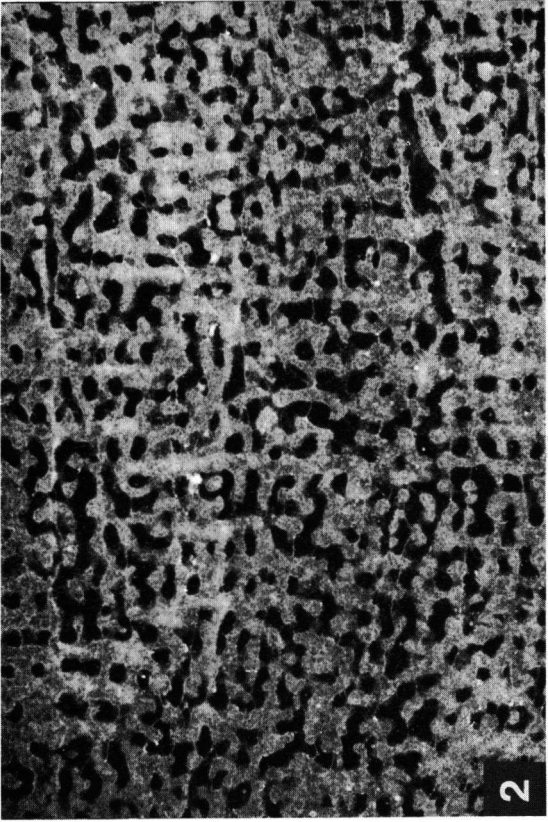
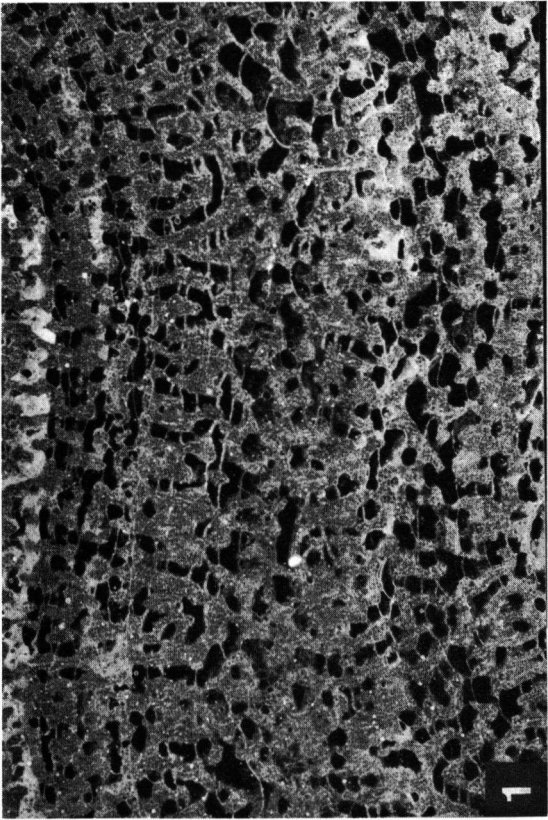




PLATE 37

Fig. 1. (Specimen 522O). *Stromatopora huepschi*? with a coarse gross structure in which the irregular horizontal elements are dominant. More or less straight pillars are present only in a few places. Vert. section, X 8.

Fig. 2. (Specimen 526A). *Stromatopora huepschi*? with straight and dominant vertical skeletal elements. Note the patches of tissue which seem to be connected only by cyst plates to the rest of the tissue. Vert. section, X 8.

Fig. 3. (Specimen 450C). *Stromatopora huepschi*? with well developed irregular horizontal elements and thick straight vertical elements. Note the fine repair tissue at the base. Vert. section, X 8.

Fig. 4. (Specimen 522E). *Stromatopora huepschi*? with a similar, but coarser, gross structure as the specimen in fig. 3. Most galleries are partly or entirely filled with sediment. Vert. section, X 8.

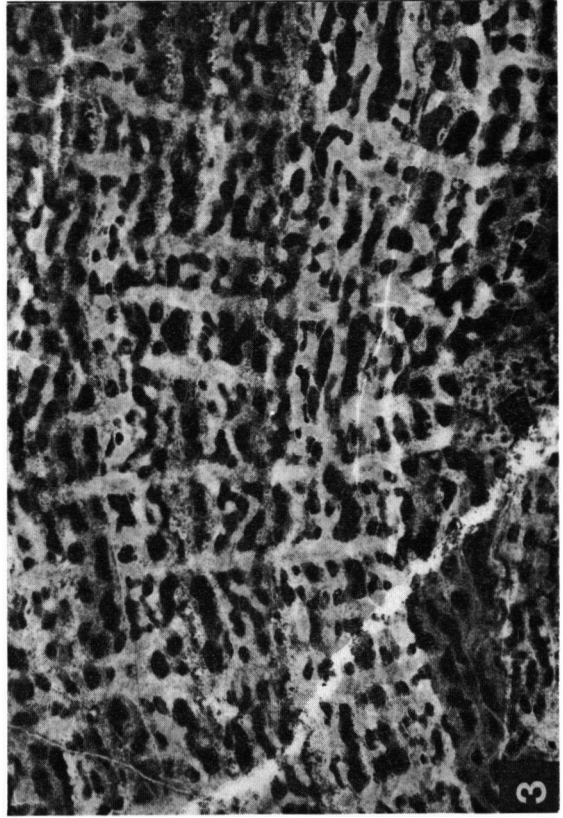
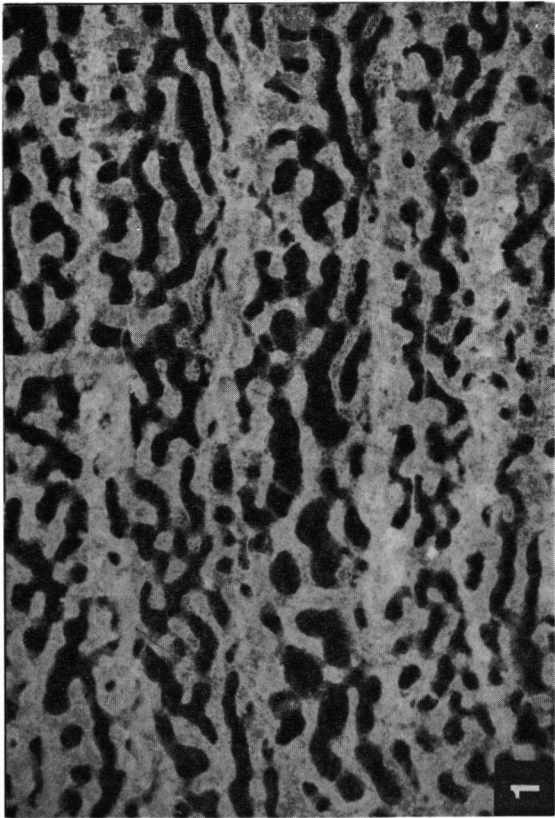


PLATE 38

Fig. 1. (Specimen 533E). *Stromatopora huepschi*? with alternate zones of fine and coarse gross structure. Vert. section, X 8.

Fig. 2. (Specimen 573B). *Stromatopora huepschi*? with a rather fine gross structure, intergrown with *Syringopora* sp. Vert. section, X 8.

Fig. 3. (Specimen 538B). *Stromatopora huepschi*? with zones of coarse and fine, completely amalgamated skeletal elements. Vert. section, X 8.

Fig. 4. (Specimen 421D). *Stromatopora huepschi*? with alternate zones of irregular and rather regular gross structure. Vert. section, X 8.

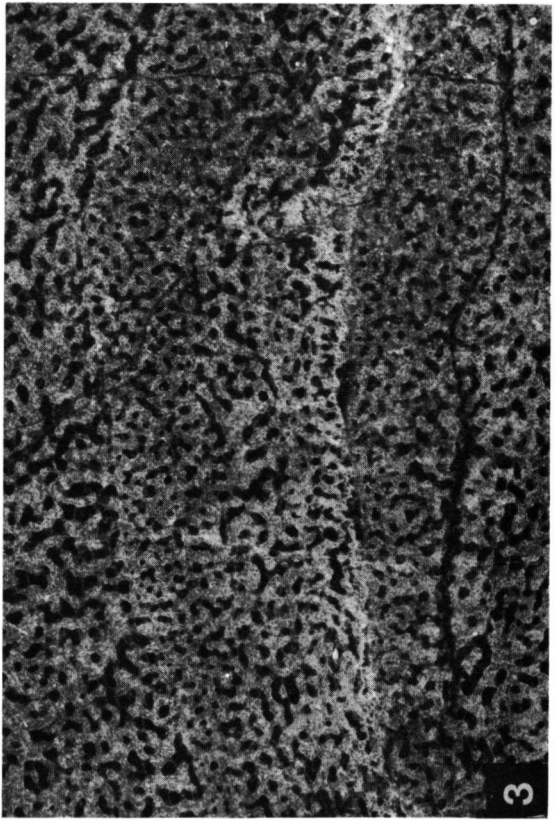


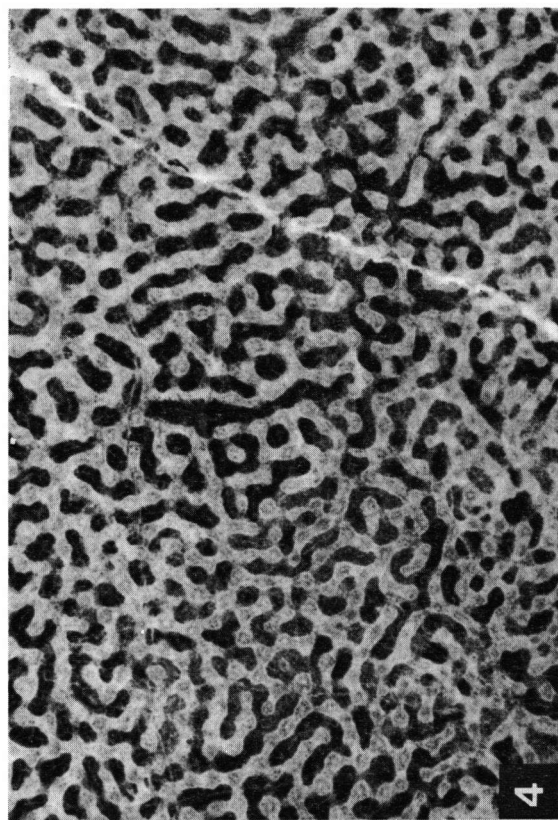
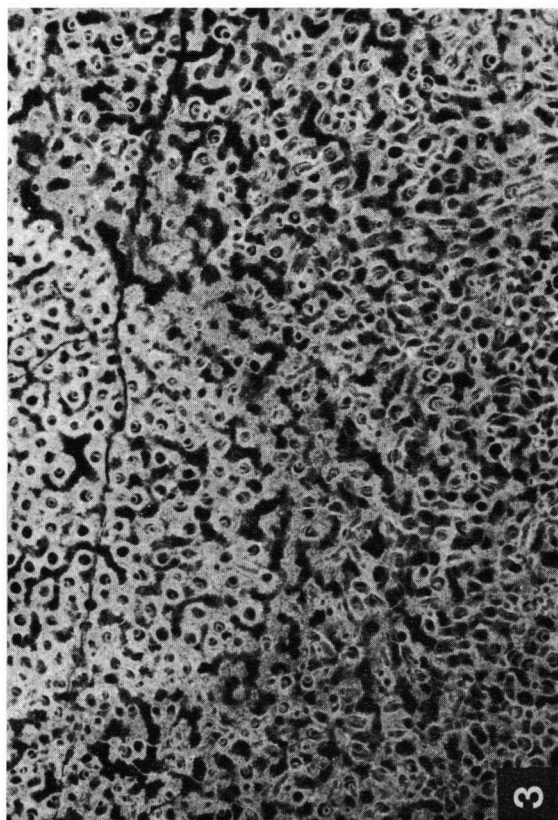
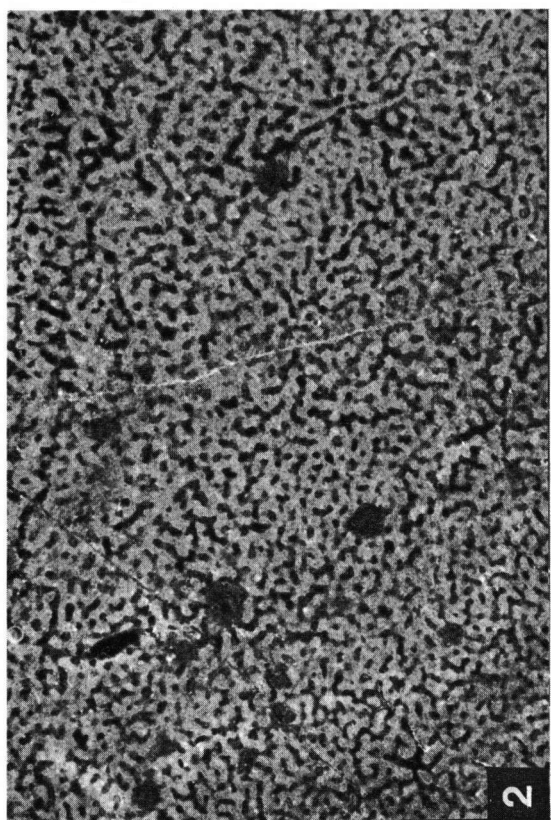
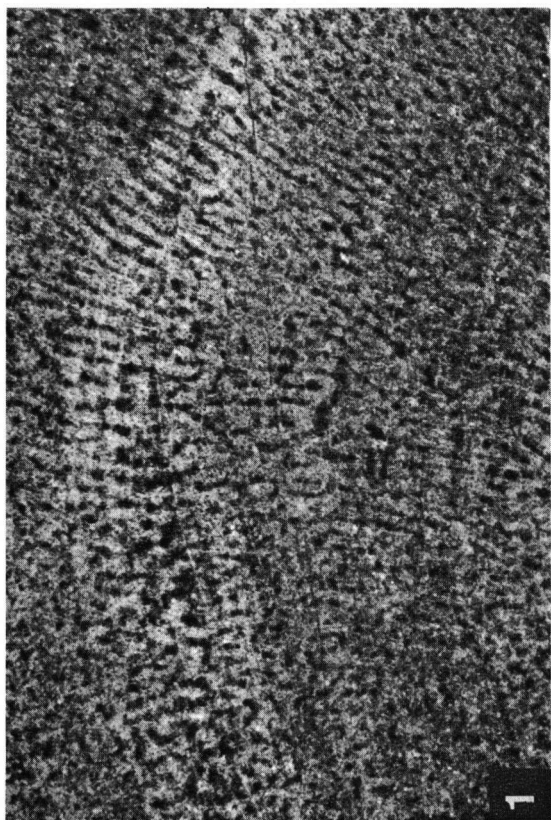
PLATE 39

Fig. 1. (Specimen 416E). *Stromatopora huepschi*? with a fine gross structure in which the vertical elements are dominant. Vert. section, X 8.

Fig. 2. (Specimen 532F). *Stromatopora huepschi*? showing amalgamated skeletal elements. The dark spots are caused by silicification. Tang. section, X 8.

Fig. 3. (Specimen 532L). *Stromatopora huepschi*? intergrown with *Syringopora* sp. Some astrorhizal canals are visible in the fused skeletal elements. The gross structure of this specimen is coarser than that of the specimen shown in fig. 2. Tang. section, X 8.

Fig. 4. (Specimen 517H). *Stromatopora huepschi*? with coarse gross structure. A few pillars are isolated. Tang. section, X 8.





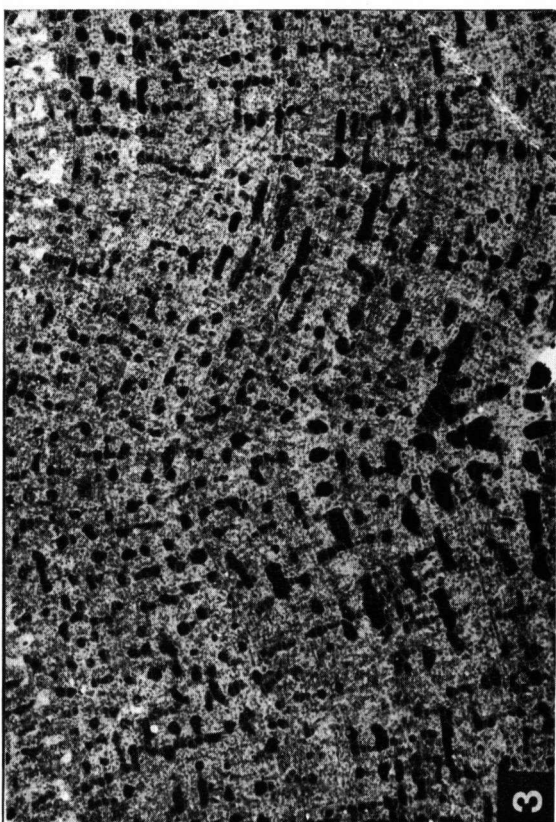
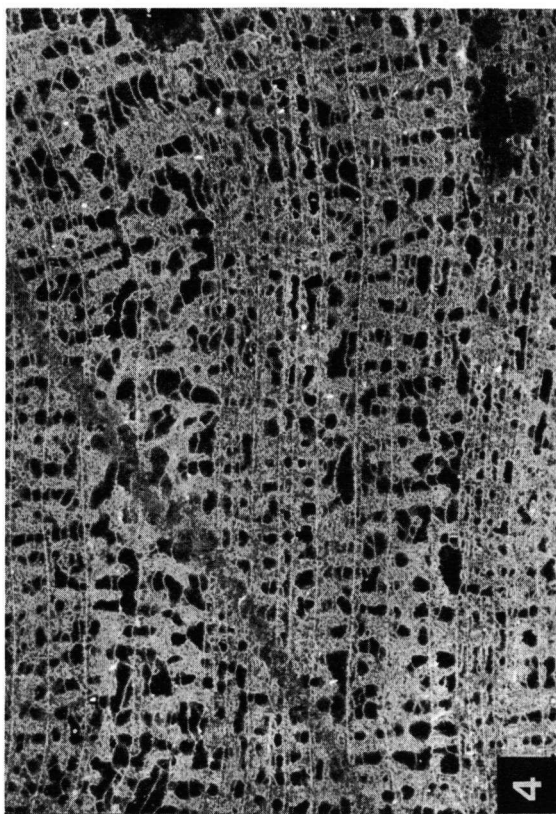
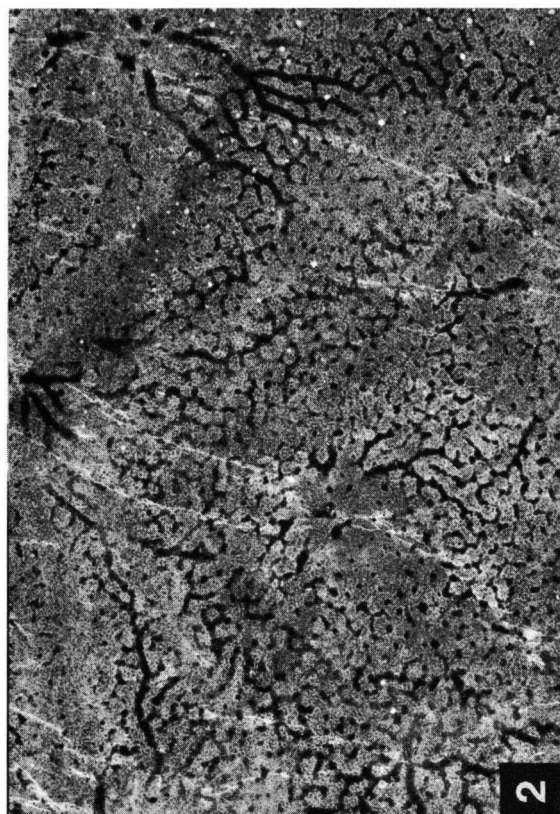
#### PLATE 40

Fig. 1. (Specimen 461A). *Stromatopora* sp. 1. The gross structure is fine and very regular for a *Stromatopora*. The astrorhizae occur in low mamelons (left). Vert. section, X 8.

Fig. 2. (Specimen 461C). *Stromatopora* sp. 1. Most pillars are coalescent. The abundant astrorhizae are stellate. Tang. section, X 8.

Fig. 3. (Specimen 478A). *Stromatopora* sp. 2. The gross structure is very regular for a *Stromatopora*. Microlaminae are present in the slightly altered tissue. See also Pl. 11 fig. 6. Vert. section, X 8.

Fig. 4. (Specimen 536J). *Stromatopora* sp. 3 with straight laminae at irregular distances and more or less superposed pillars. The cyst plates are frequently so close together that a distinction with cellulae can no longer be made. See also Pl. 11 fig. 2. Vert. section, X 8.



#### PLATE 41

Fig. 1. (Specimen 541D). *Stromatopora* sp. 3 with a gross structure similar to that of the specimen in Pl. 40 fig. 4 but less well preserved. Vert. section, X 8.

Fig. 2. (Specimen 541D). Same specimen as in fig. 1 with coalescent pillars and astrorhizae. Tang. section, X 8.

Fig. 3. (Specimen 568B). *Stromatopora* sp. 4 with a very fine gross structure with dominant vertical elements. Vert. section, X 8.

Fig. 4. (Specimen 568B). Same specimen as in fig. 3 showing amalgamated network and astrorhizae. Tang. section, X 8.

