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MONOSPECIFIC STROMATOLITES FROM THE GREAT BARRIER REEF TRACT
AND THEIR PALEONTOLOGICAL SIGNIFICANCE¹

by

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(4 figures et 2 plates)

RESUME.- Des stromatolithes non calcifiés construits par l'algue bleue *Phormidium hendersonnii* poussent de nos jours sur les platiers récifaux externes de la Grande Barrière de Corail, Australie. Ils montrent une lamination noctémérale que peut compliquer l'influence exercée par les courants et les marées. Ils représentent une population stromatolithique unique et de répartition mondiale, susceptible d'aider à comprendre l'évolution des stromatolithes durant le Phanérozoïque et leur distribution limitée dans les eaux marines actuelles.

ABSTRACT.- Uncalcified stromatolites built by the blue green alga *Phormidium hendersonnii* are presently growing on the outer reef flats of the ribbon reefs, Great Barrier Reefs, Australia. They show a noctihemeral lamination which may be complicated by currents and tidal influences. They represent a unique worldwide Recent stromatolitic population which may help us understanding the Phanerozoic evolution of stromatolites and their present-day limited distribution in seawaters.

INTRODUCTION

A variety of laminated, gelatinous algal structures built by the blue-green alga *Schizothrix calcicola* have been described from various regions of the Bahamas (MONTY 1965, 1965a, 1967), Florida (GINSBURG, 1960; GEBELEIN, 1977; FROST, 1974) and Bermuda (GEBELEIN, 1969). Most of them were found in shallow lagoons, back reef tracts and tidal flats. All these structures are now recognized to result from the growth of the same blue-green alga *Phormidium hendersonnii* (GOLUBIC & FOCKE, 1978).

Up to now, no occurrences have been reported in the literature from the Pacific Ocean province. The purpose of this paper is not only to fill this gap but also describe *Phormidium* stromatolites growing on exposed reef flats together with rhodolithes and to discuss their paleontological significance.

The material described here and the field observations were collected during the 1968 Belgian Expedition on the Great Barrier Reefs, which was supported by the Ministry of Education and the National Foundation for Scientific Research.

GENERAL SETTING (fig. 1)

Fifteen to forty km off the Northeastern coast of Queensland, the outer continental shelf is fringed with elongate ribbon reefs up to a nine hundred m. wide and several km. long. These outer reefs form a true barrier facing the Pacific abysses and are separated by narrow passes. Behind these barrier reefs comes a wide "lagoon" developed on the shallow shelf, less than 35 m deep; it is floored with a variety of bioclastic carbonates and mixed terrigenous-carbonate sediments (personal observation); the shelf supports a series of variously shaped (arcuate, circular, irregular) flat-topped inner reefs.

The outer or ribbon reefs are exposed to the full ocean swell, and to strong tidal currents. The major part of the reefs remains underwater during normal low tide whereas much of it is exposed during low spring tides, mainly when the winds blow eastwards.

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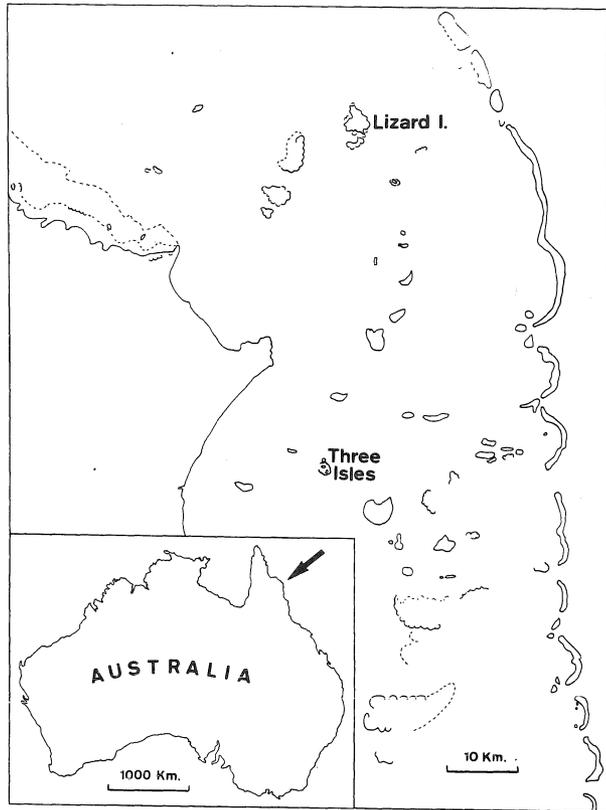


Figure 1.- Study area showing the elongate outer reefs (ribbon reefs) fringing the shelf margin to the East, and the variously shaped platform reefs growing on the shelf lagoon to the West.

OVERALL ZONATION OF THE OUTER REEFS

(fig. 2, 3)

The reef front is generally steep though its upper part shows a series of slope breaks and terrasses; it is heavily covered with corals over a depth of a least 25 m.

Behind the reef crest, comes a wide heavily cemented platform - the outer reef flat - which rises backward up to the boulder zone. The rim of this outer reef flat shows abundant encrusting *Acropora* together with short stouted branched types, solidly anchored to the substrate (*A. decipiens*, *A. digitifera*, etc...).

Behind this external coral zone, which may show some elongate moats, comes a red algal pavement which extends backward to the boulder zone. This pavement is heavily encrusted by Nullipores, bored by clams and

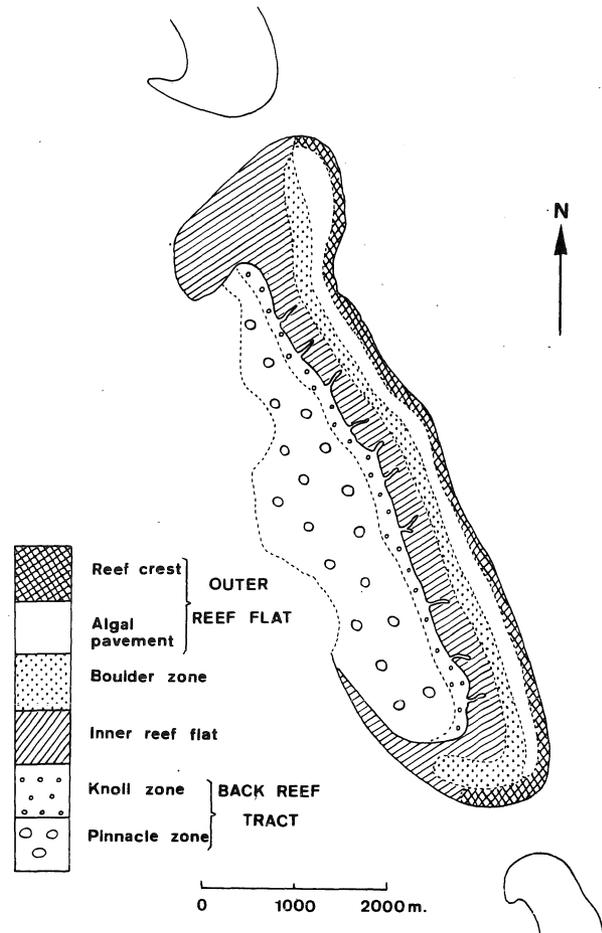


Figure 2.- Main physiographical elements of an outer ribbon reef.

sea urchins; it has a completely bare surface at places, whereas at others it is sparsely covered with *Phyllospongia* (sponges), *Aglaophelia* (hydrozoan) and *Chlorodesmis* (green alga); it may also show low, solidly anchored *Acropora* (*A. hebes*, *A. pulchra*, *A. digitifera*, etc...). The following rubble zone is also quite variable in character and may be isolated, on its wind and leeward sides by longitudinal moats; it shows here big blocks of dead coral rock, there a messy accumulation of shingle and rubble with scattered sands in the pits; most pebbles and bioclasts are heavily encrusted by nullipores forming rhodolites; at places, growths of *Caulerpa* and *Halimeda* can be found.

Leeward, that is backward from the boulder zone, comes the "inner reef flat", where the coral growth

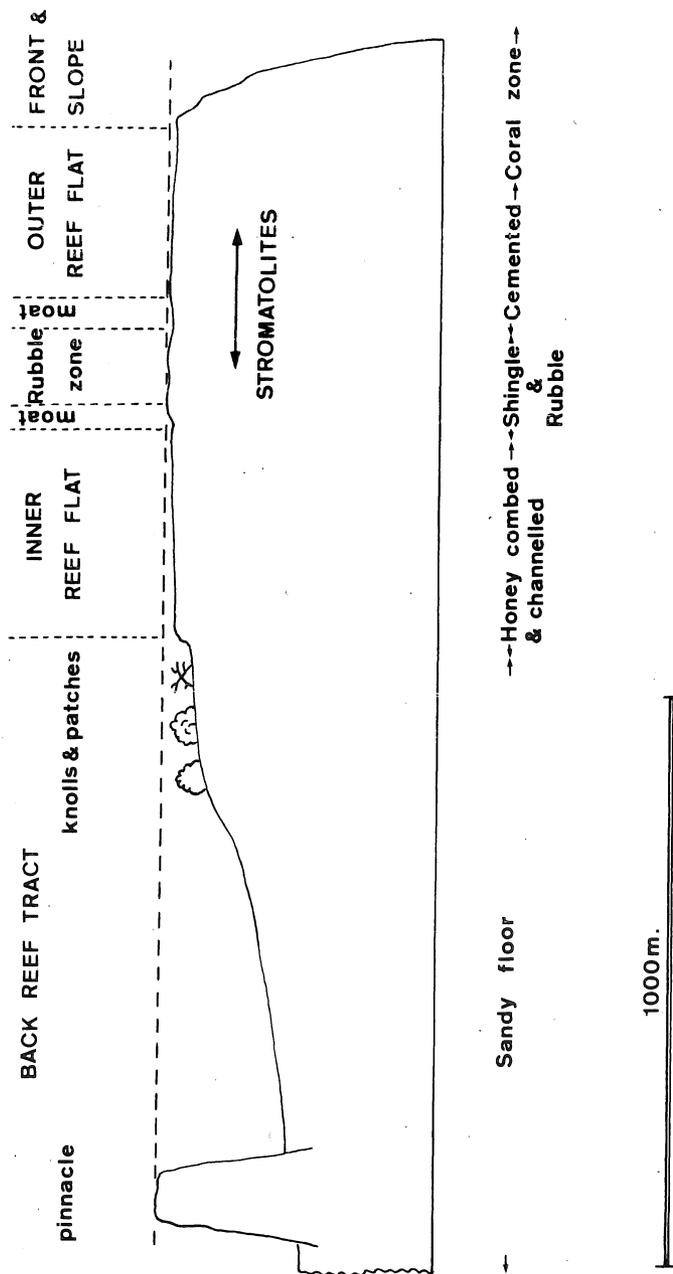


Figure 3.- Generalized cross section of an outer ribbon reef such as drawn on fig. 2. Note the areal distribution of the stromatolites.

increases. The inner reef flat is strongly pitted and honeycombed and is penetrated by the heads of sandy channels leading to the leeward rim of the reef and the shelf lagoon. It is colonized by strongly attached coral colonies of *A. palifera*, *A. hyacinthus*, *A. corymbosa*

as well as massive faviids and stretches of the soft corals *Sarcophytum* and *Lobophytum* both heavily preyed by the gastropod *Cypraea*.

The inner reef flat is limited leeward by a small vertical wall 1-2 m high which leads to the shelf floor where is found the "back reef tract". This tract shows thickets of delicately branched acropores, huge knolls of faviids, *Porites*, millepores or acropores (several meters in diameter) whereas further away, in deeper water (20 m), solid pinnacles with almost vertical flanks rise up to low water level.

In this general framework, the stromatolites have been mostly found on the inner part of the "outer reef flat" where they extend from the Rubble zone over the algal pavement (fig. 3, plate 1 : A). They grow anchored to the rock but also occur in the pits where they have probably been thrown by the waves. As a rule, this part of the reef uncovers once a month during the lowest tides.

DESCRIPTION OF THE STROMATOLITES

The *Phormidium* stromatolites appear as small brownish-grey to light brown gelatinous domes up to 2-4 cm in diameter.

They are much smaller than their Bahamian (MONTY, 1965a, 1967) and Florida (FROST, 1974) counterparts which live in shallow protected lagoons. This results from the fact that in the reef high energy environment they are easily washed away by the waves once they reach a given size and oppose too great a resistance to the currents. According, the stromatolitic population remains fairly young here.

In vertical section, they generally show a distinct lamination determined by the presence of sedimentary laminae several tens of microns thick (pl. 1 : B, C; pl. 2 : A). As described in MONTY (1965, 1965a, 1967) these layers are made of silty to finely sandy entrapped bioclastic particles. Some colonies show no entrapped material and accordingly appear rather un laminated with the naked eye. Under the binocular microscope, they however reveal a prominent "organic" or biological lamination (MONTY, 1973, 1976) resulting from the superposition of gelly layers, made of erect or oblique filaments, separated by strong physical and optical dark discontinuities (pl. 1 : D, E); these discontinuities are thin laminae (about 50 microns thick) where the filaments taper and lie parallel to the growth surface. As reported in MONTY (1965, 1965a, 1967) growth measurements were made by delicately pouring fine grained carborundum onto the domes. As was the case for

the Bahamian stromatolites, growth appeared to be mostly noctihemeral : thick organic layers (up to 700 microns) of erect filaments trapping scattered particles, are formed during the day whereas growth stops at night when a thin dark lamina is formed. When enough sedimentary particles are shifted onto the colony, they concentrate at this level originating the individualisation of a sedimentary layer. A couplet formed by an organic lamina overlain by a corpuscular lamina is thus formed over a day-night period.

Field observations revealed two exceptions to this rule, as a result of the dominant influence of tides.

During equinoxial low tides or even when the offshore winds pile away the monthly lowest tides, the stromatolites may remain exposed for such a long time that growth stops. When this occurs during the day, an extra dark biological lamina is formed. In this case two doublets of layers can be formed a day, one resulting from the tidal regime, the other resulting from the normal noctihemeral growth pattern of the alga.

Two sets of laminae per day can also form when strong incoming tides loaded with sediment invade the stromatolite field : here an extra sedimentary layer will form during the day at the tidal stillstand when the waters drop their sedimentary load over the stromatolites. Similar situations where two sets of lamina are formed per day have already been described by GEBELEIN (1977), from Cape sable where *Phormidium* stromatolites are daily submitted to significant tidal action. The normal noctihemeral laminae can generally be distinguished from the so-called storm "laminae" in that they are better and evenly sorted and show fine grained particles. The "storm laminae" are not only less well sorted but may show some tendency to developing a graded bedding. In vertical section, some stromatolites may show an asymmetrical or a symmetrical concentration of particles; this is due to particular characteristic of tidal currents or of the swell. Asymmetrical concentration (fig. 4a) occurs in areas where wind driven currents, or a strong in-coming tidal component, concentrates the particles on the lee side of the stromatolites where they are trapped in the zone of back flow to finally be binded by the algae, whereas the up current side of the stromatolite is always kept clean of particles. This deposition may also record period of storm (fig. 4b). Symmetrical concentration of particles occurs when these are mostly binded in the central part of the dome. As also observed on Bahamian samples (MONTY, 1965) this is due to oscillatory movement of the swell or waves, that is in zones of swash and backswash: during the first phase of the oscillation (fig. 4c) parti-

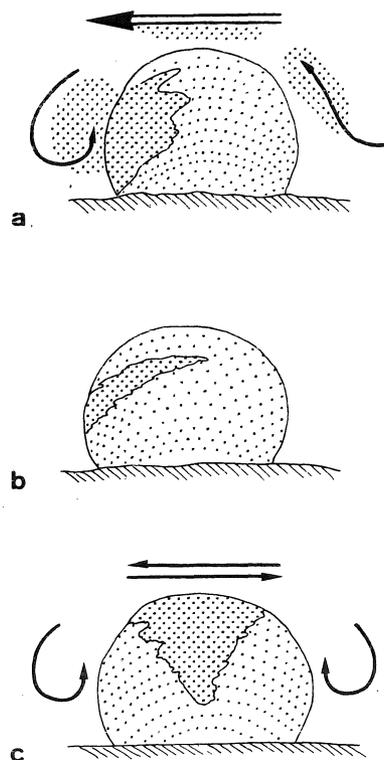


Figure 4.- Different patterns of concentration of sedimentary particles within the stromatolites due to different types of currents. See text.

- Under unidirectional flows (surface currents due to trade winds, strong in-coming tidal system), particles concentrate on the leeward side of the stromatolite where they are trapped by the backflow current component. This is accordingly the site of maximal particle binding by the algal filaments originating an asymmetrical distribution of particles in the stromatolites.
- Similar to a) but here the unidirectional flow has been temporaneous, due for instance to a storm period.
- Concentration of particles in the central part of stromatolite due to symmetrical oscillation currents which roll and hence concentrate the particles over the top of the stromatolite.

cles are carried over the dome to the leeside where they are concentrated in suspension by an eddy; during the second phase of the oscillation, the current reverses and the particles are carried back over the stromatolite where they are similarly held in suspension. Accordingly, the particles move constantly from one side of the dome to the other, but always travel along its upper part. the statistical concentration of particles is thus higher at this place and more particles will be bound there than on the flanks.

DISCUSSION

Many authors have claimed after GARETT (1970) that the Late Precambrian–Early Paleozoic decline of stromatolites was due to the rise of browsing and burrowing invertebrates. This thesis was critically opposed on ecological and evolutionary grounds by MONTY (1973, pp. 601–604) whose argumentation can be summarized as follows :

1. many blue–green algae release by–products and toxins which are highly toxic for other cyanophytes (inter-specific competitiveness) but also for protozoans, invertebrates and vertebrates.
2. although strongly calcified, Early Paleozoic stromatolites bear no trace of burrowings nor scars due to browsing.

In fact, to infest and destroy the late Precambrian–Cambrian stromatolites, the newly rising invertebrates should have had to develop very specific adaptations to accommodate the toxins and to crush the calcified stromatolites, which is highly improbable in archetypic organisms. They probably fed on non calcified and non toxic algae. Moreover, recent corals and coral reefs are heavily bored and grazed upon but this interference did not originate their extinction yet.

3. Nowadays, non marine calcified stromatolites provide an habitat for numerous invertebrates, cohabit with grazing and browsing gastropods but this does not disturb their growth or structure as a well defined ecological equilibrium exists.

The author rather believe that the Early Paleozoic decline and the Cenozoic disappearance of marine calcified stromatolites is due :

1. to the series of glaciations which occurred during Late Precambrian times; these considerably restricted the stromatolites habitats and consequently impoverished the blue–green algal communities. When sealevel finally rose again, these stromatolite building blue–green algae were faced with a new strongly competitive organic world which invaded all the available niches and habitats.
2. to severe competition for space and nutrients (calcium carbonate, nitrates, phosphates) by organisms with narrower niches, more adapted to the new Paleozoic ecosystems and which could metabolize the calcium carbonate to build rigid stony framework even against the environmental chemical gradients; on the contrary Blue–green algae had inherited a fairly large ecological niche (hence weakly competitive) and rely for their calcification either on a po-

sitive association with bacteria or/and on an abundance of CaCO_3 and free to half bound CO_2 .

The strong competition for space can still be read in Lower to Middle Paleozoic reefs where algal mats overgrow and are overgrown by tabulate corals, bryozoans, etc... (pl. 2 : c).

Furthermore, competition is also illustrated by the fact that many higher organisms are seen to replicate the very morphology of stromatolites, as was the case for Bryozoan, Stromatoporoids, or algae (*Sphaerocodium*, WRAY, 1977, fig. 19).

All these factors account for the progressive displacement of Paleozoic and Mesozoic stromatolites towards hostile perillitoral environments.

3. The decline of marine stromatolites is also due to Late Cretaceous–Cenozoic events such as :
 - a) the rise of the calcareous plankton which progressively depleted the seas in calcium carbonate below the adequate threshold for significant calcification of marine blue–green algae.
 - b) the acme of highly specialized Red algae which progressively invaded all the environments previously occupied by stromatolites, from the intertidal zone to lagoons, reefs and shelves, and definitely confined them to non marine settings. The competitiveness of Rhodophytes and their high metabolic adaptation are shown by their diversification on recent reefs and their faculty to metabolize a skeleton strongly enriched in MgCO_3 .

From the Eocene on, oncolitic beds are replaced by beds of rhodolites; the competition between encrusting organisms is now illustrated by mutual overgrowths of nullipores, encrusting foraminifera, bryozoans, serpulids, hydrozoan, etc...; this leads us to the situation described in this paper. The Great Barrier reefs show indeed the cohabitation of well defined rhodolites with blue–green algal stromatolites. The nullipores behave like many paleozoic reef stromatolites in that, in vertical section, competitive overgrowths reflects a strong competition for space (compare pl. 2 : c and d). They have clearly taken the niche of the Paleozoic stromatolites.

On the other hand, the *Phormidium* stromatolites, which have typical stromatolitic pattern and are worldwide in distribution, differ from the pre-Cenozoic fossil record in being not calcified; accordingly they are not directly competing with red algae; they have then a different niche and can cohabit as separate individuals. Moreover, as is also

observed in the subtidal occurrence of the Bahamas, Florida and Bermuda, no organism feed upon them although many gastropods and other invertebrates have accommodated required physiological and morphological adaptations to feed on spicular soft corals and even stony corals.

There is accordingly no reason to believe why Late Precambrian to Early Paleozoic invertebrates would have been able to browse on calcified stromatolites and precipitate their decline.

Finally the fact that the recent marine stromatolites are not calcified is in accordance with what has been stated above, i.e., changes in the Cenozoic to present-day chemical balance of seawater. Nowadays, the absence of stromatolitic calcification in seawater is common and has already been reported elsewhere (MONTY, 1972, MONTY & HARDIE, 1976); in the Bahamas for instance, one assists to a progressive diminution of internal primary precipitation of calcium carbonate in algal mats when they are traced from freshwaters towards marine waters.

Accordingly the *Phormidium hendersonii* stromatolites illustrate a relict situation as they appear to be about the only worldwide subtidal stromatolites (with the exception of manganese nodules, MONTY 1973a) which reflect the Cretaceous/Eocene crisis in having lost the faculty of primary marine lithification (I do not consider here the case of Shark Bay stromatolites where processes of beach rock formation and secondary cementation intervene). They cannot accordingly be fossilized and this may be another reason for the lack of stromatolites in postcretaceous marine sequences.

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PLATE 1

- A General view of the inner part of the outer reef flat where have been collected the studied stromatolites.
- B, C Vertical section in stromatolitic domes impregnated in araldite. Scale bar : 1.5 cm. Sedimentary corpuscular layers appear white.
- D General view of the noctihemeral biological lamination of stromatolites. The lower part of the photograph shows erected bundles of filaments of *Phormidium* that grew during the day and entrapped some sedimentary particles to form an hyaline lamina. The filaments then tapered at night, when growth stopped, to form a thin dark lamina. Scale bar : 100 microns.
- E Idem, close up. Scale bar : 50 microns.

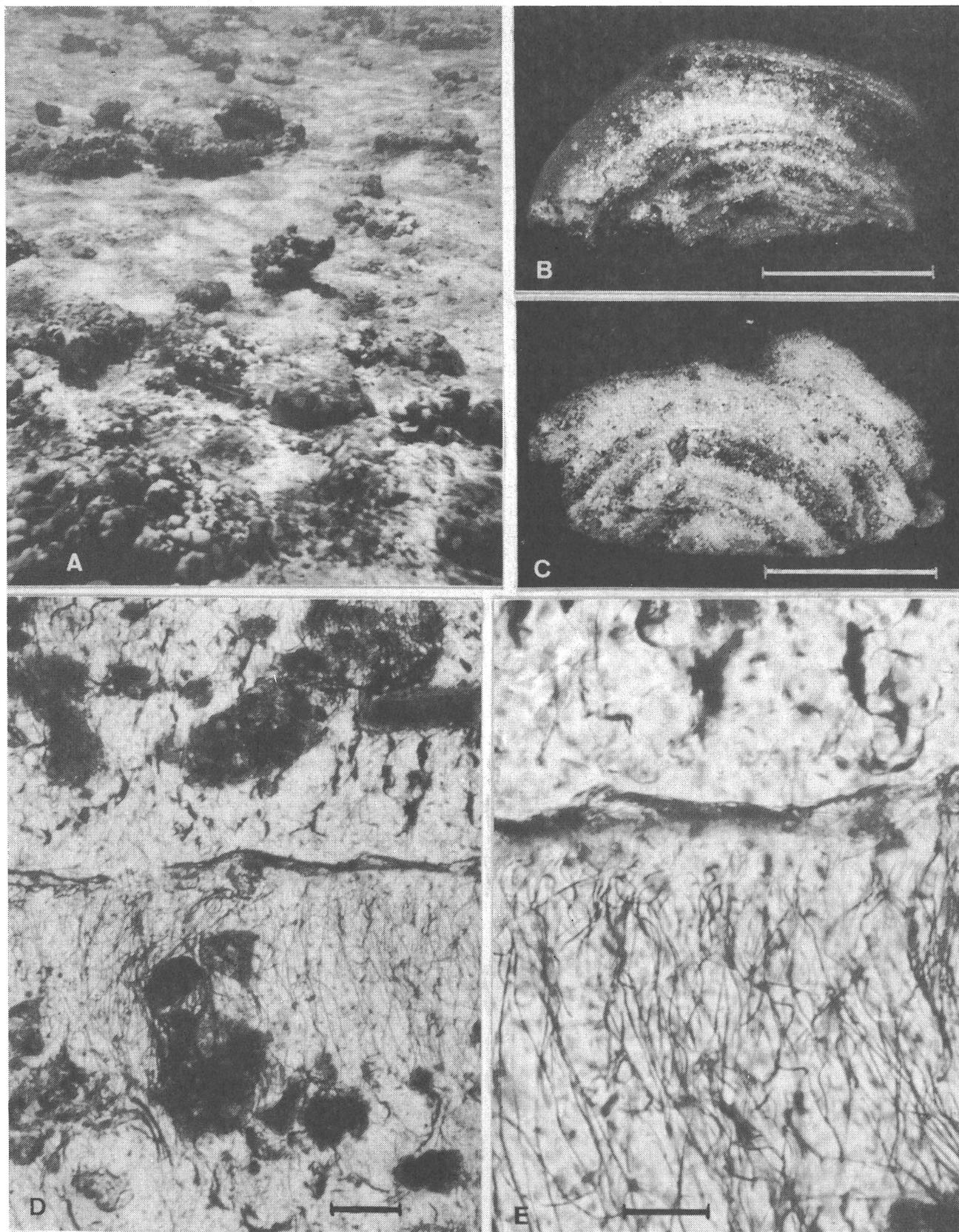


PLATE 2

- A General view of the lamination of stromatolites where detrital particles accumulated and concentrated at night over the resting filaments (dark streak of D, E, plate 1), to originate a sedimentary layer. The clear hyaline laminae are made of erected bundles of *Phormidium* that actively grew during the day. Scale bar : 100 microns.
- B Idem, close up. The nightly formed sedimentary lamina which appears in the upper third of the photograph shows that the grains become strongly binded by the filaments of *Phormidium* when they resume their growth on the following day. Scale bar : 50 microns.
- C Thin section from a Devonian (Frasnian) "reef" of Southern Belgium illustrating competition for space during reef formation : stromatolitic mats (below) are encrusted by bryozoans (upper half of photograph) which, in their turn, are overgrown by blue-green algal mats (uppermost part of photograph). Scale bar : 500 microns.
- D Thin section in organic encrustations from the outer reef flat, Ribbon Reefs of the Great Barrier of Australia illustrating present-day competition for space in reefal accretion; encrusting corals (base of photograph) are invaded by serpulid worms (middle part of photograph) overgrown in their turn by nullipores (upper third), by bryozoans (upper left) and once more by encrusting corals (uppermost part of photograph). Scale bar : 500 microns.

