

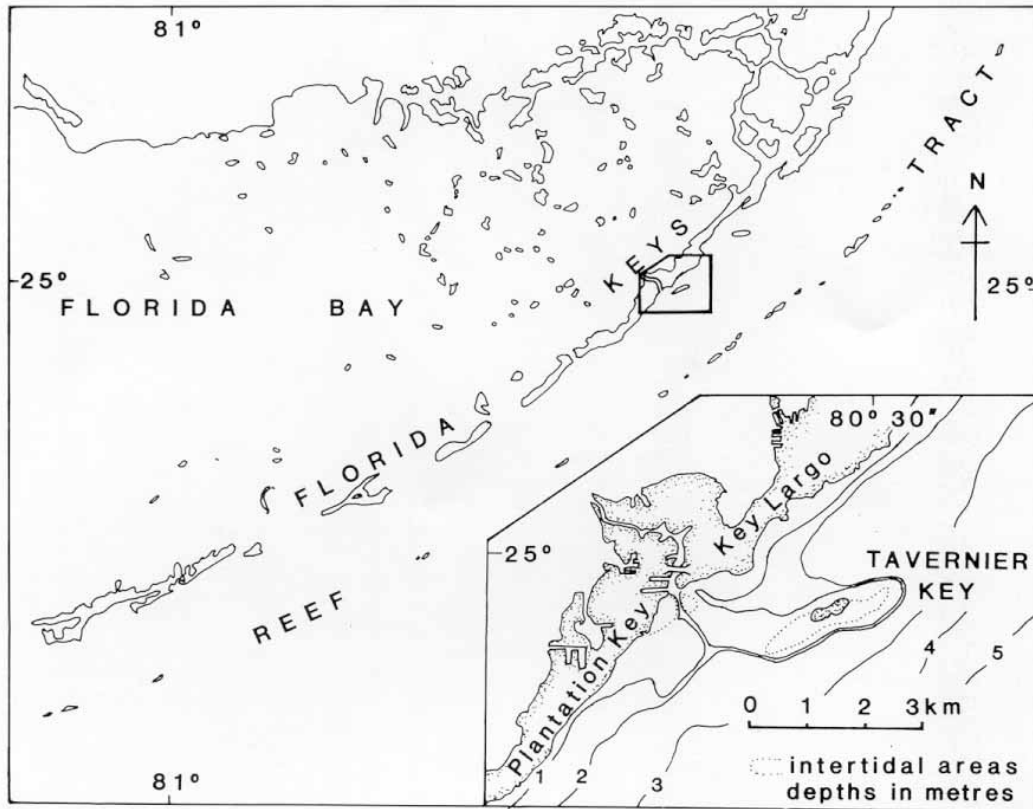
THE MORPHOLOGY AND ECOLOGY OF A MOUND-BUILDING CORALLINE ALGA (*NEOGONIOLITHON STRICTUM*) FROM THE FLORIDA KEYS

by DANIEL W. J. BOSENCE

ABSTRACT. The coralline alga *Neogoniolithon strictum* Setchell and Mason, 1943 is a major component of carbonate mound-building communities in the Florida Keys. This paper investigates the morphology, variation, and occurrence of growth forms, and the responses of this coralline alga to differing environmental conditions. Tavernier Key is an emergent back reef mound with a windward zonation of carbonate-producing communities. The windward shallow-subtidal and intertidal zones are dominated by the branching *N. strictum*. This facies is divided into three subfacies. A framework subfacies of *in situ*, branching *N. strictum* thalli occupies the sheltered shallow-subtidal areas. A rhodolith subfacies occurs in intertidal, moderately exposed parts of the mound. Rhodoliths are generated from collapsed sections of the framework and branches show increasing amounts of redirected growth as rhodoliths are transported shorewards away from the framework subfacies. Exposed areas on the north-east of the mound are characterized by a gravel patch subfacies. These gravel patches have clean, sandy gravels that migrate shorewards during storms over the muddy inshore *Thalassia* beds. The main palaeoecological conclusions arising from this work are the narrow depth range of the *Neogoniolithon* facies, the morphological response of this coralline to low-water level and hydraulic energy, and the preservation of growth forms and facies in rhodolith cores.

CORALLINE algae have been important agents in the formation of limestone since the Palaeozoic (Wray 1977). Their calcified skeletal tissue enables them to construct reefs (Ginsburg and Schroeder 1973; Bosence 1983a, 1984), rhodoliths (Bosellini and Ginsburg 1971; Bosence 1983b), and, on breakdown, coralline algal sands and gravels (Bosence 1980). In addition to their rock-forming capabilities, recent studies have shown that coralline algae are very useful palaeoenvironmental indicators for the Tertiary (Adey and MacIntyre 1973; Adey 1976; Bosence 1983a, b, c). This is a result of their strict environmental tolerances, morphological responses to hydraulic energy, and their slow rate of evolution. Similarly, the investigation of the ecology of Recent coralline algae aids in the interpretation of the abundant late Palaeozoic mound-building ancestral corallines (Wilson 1975).

This paper investigates the occurrence, ecology, and preservation of a Recent mound-building coralline alga *N. strictum* Setchell and Mason, 1943. *N. strictum* occurs as branching frameworks, rhodoliths, and mud to gravel-sized sediment. Growth forms are varied and, in particular, rhodolith morphology very closely reflects local environmental conditions. The conclusions from this work emphasize the sediment-building capabilities of coralline algae and their value in palaeoecological studies. *N. strictum* is common in many shallow water areas of the Caribbean (Foslie 1901; Setchell and Mason 1943; Adey and MacIntyre 1973; Enos and Perkins 1977; Adey pers. comm. 1984). In the Florida Keys it occurs commonly in back reef areas, on the seaward margins of carbonate mounds, and in tidal channel passes (Enos and Perkins 1977; Turmel and Swanson 1976). Adey (pers. comm. 1984) has reported a 3 km long fringing reef of *N. strictum* in a lagoon from Mayaguana, south-eastern Bahamas. The present study area of Tavernier Key is some 2 km east of southern Key Largo (text-fig. 1) and south-west of a similar mound (Rodriguez Key) described by Turmel and Swanson (1976). This paper forms part of a wider investigation to study the sediment production, deposition, and geological history of Tavernier Mound (Bosence *et al.* in press).



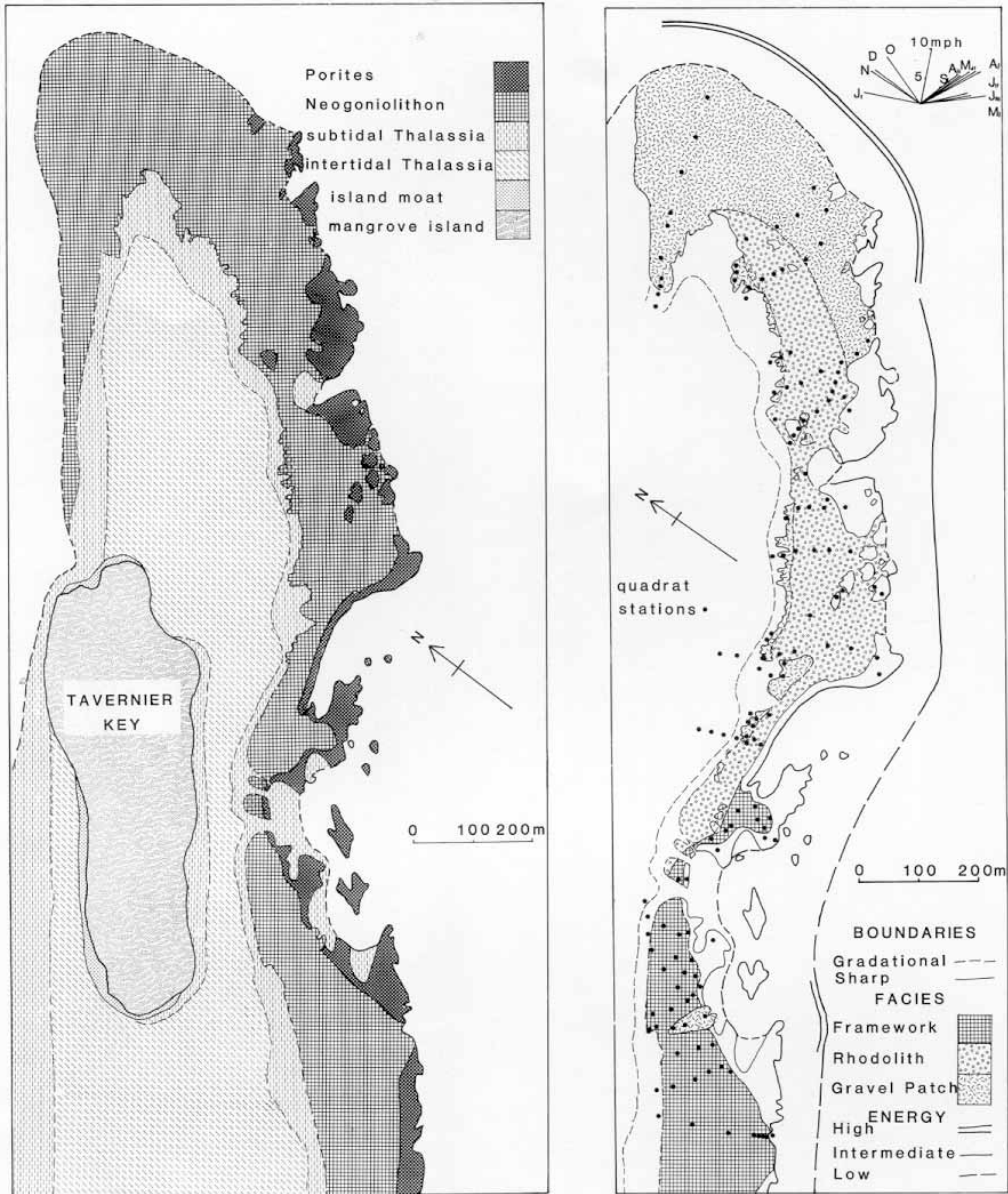
TEXT-FIG. 1. Location of Tavernier mound in the Florida Keys (after NOAA Chart 11451).

METHODS

Tavernier mound has been surveyed and mapped (text-figs. 2, 3) on a scale of 1:1500 using draughting film base maps prepared from low-altitude aerial photographs. Quadrat surveys (223 stations) were undertaken in February 1980 and August 1981 (text-fig. 3). Some 1,500 rhodoliths were collected, measured, and classified according to shape, branching density, and numbers of redirected branch growths. Shapes were estimated as being spheroidal, ellipsoidal, or discoidal. Branching densities were classified as single (I), occasional (II), common (III), or dense (IV) branching (Bosence 1976). Size was measured along the long (L), intermediate (I), and short (S) axes of rhodoliths and calculated using the volume of an ellipsoid ($\frac{4}{3}\pi LIS$) (Bosence 1976, 1983*b*). Representative rhodoliths were impregnated and sectioned to study their internal structure; some were fractured, coated with gold, and studied with a JEOL 35 scanning electron microscope operating at 25 kV. Box cores were taken to study the shallow subsurface and over fifty piston cores to the Pleistocene rock basement were collected to investigate preservation of mound facies. Data- and word-processing were carried out on a BBC microcomputer. Figured hand specimens are housed in the Marine Algal Section (box collection, BM) in the Department of Botany, British Museum (Natural History).

ENVIRONMENTAL SETTING OF CORALLINE ALGA

Tavernier Key is a Holocene (6000 BP) carbonate sediment mound built up on a basement of lithified Pleistocene Key Largo Limestone of the Floridian Plateau (Enos and Perkins 1977). The mound rises



TEXT-FIG. 2 (left). Sediment-biotic facies on Tavernier mound. The facies continue to the south-west of the map paralleling the mound margin (Pl. 21, fig. 1).

TEXT-FIG. 3 (right). Sample stations and distribution of subfacies within *Neogoniolithon* facies. Relative hydraulic energy levels were obtained from wave orthogonal study combined with exposure to strongest and most frequent winds. Wind chart indicates mean monthly direction from which wind blew (1963-1979) (NOAA 1980). The framework sub-facies continues as a parallel band to the south-eastern end of the mound.

steeply (Pl. 21, figs. 2, 3) from the surrounding 1.5–3.0 m deep sea-bed to a flat upper surface. The mound surface is largely intertidal with an emergent, central mangrove and cottonwood vegetated island (Pl. 21, fig. 1; text-fig. 2). Major currents around and on the mound are from wind-generated waves which are predominantly south-south-easterly in summer and northerly in winter (NOAA 1980). Wave refraction studies show that the windward margin of the mound can be divided into sections experiencing relatively high-energy (converging wave orthogonals and exposure to north-easterly winds), intermediate (parallel wave orthogonals), and low-energy areas (diverging wave orthogonals and shelter from north-easterly winds) (text-fig. 3). Waves of average height (0.5 m) are either reduced to very low amplitudes as they pass over the mound surface at high tide, or break within the intertidal zone. Storm and hurricane waves may, however, break on to the Key (Ball *et al.* 1967). Salinity (34–37‰) and temperature (15–32°C) of the surrounding waters are assumed to be similar to those of the reef tract (Ginsburg 1956; Enos and Perkins 1977) but increased values probably occur in local ponded areas on the mound surface. Measured tidal ranges correlated with those at Tavernier Bridge show that low-water spring tides reach the edge of the flat-topped mound surface.

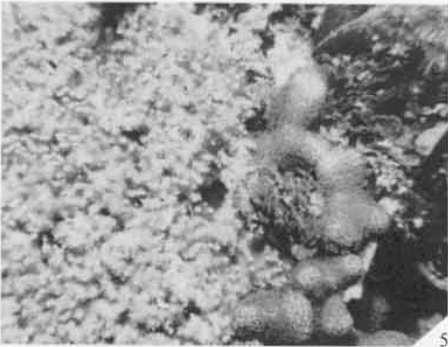
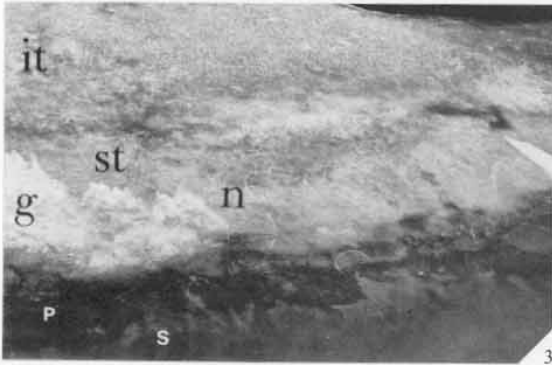
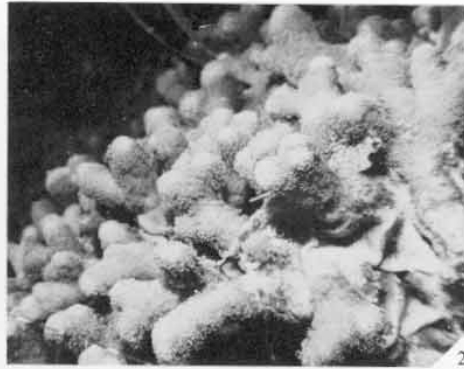
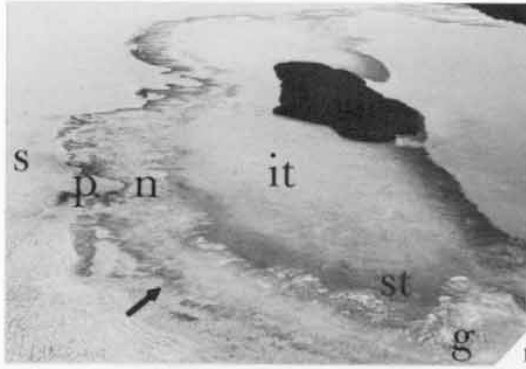
Mapping of sediments and carbonate-producing communities shows a depth related zonation (Pl. 21, figs. 1, 3; text-fig. 2) (cf. Rodriguez Bank—Turmel and Swanson 1976). The windward margin of the mound rises sharply from the surrounding *Thalassia*-covered sea floor, with slopes constructed from an *in situ* framework of branching *Porites divaricata* (Pl. 21, figs. 2, 3). This facies extends up to 0.5 m below mean low water (MLW) and gives way on the mound to the *Neogoniolithon* facies (Pl. 21, figs. 4–8; text-figs. 2, 3) which is the main subject of this paper. A small band of *Neogoniolithon* also occurs on the northern leeward side of the mound but this has not been studied in detail. The *Neogoniolithon* facies extends from 0.5 m below to 0.1 m above MLW. Shorewards the mound is covered with various *Thalassia*-dominated communities (Pl. 21, fig. 7; text-fig. 3). A deeper subtidal *Thalassia*-covered area passes shorewards into shallower, emergent *Thalassia* facies dominated by callianassid shrimp mounds. These *Thalassia* facies accumulate gravelly and sandy muds. A sand floored tidal channel surrounds the island which is fringed with mangrove swamps accumulating peat. The central part of the Key is constructed of gravel storm ridges.

GROWTH AND MORPHOLOGY OF *NEOGONIOLITHON STRICTUM*

Foslie (1901) described the typical subdichotomous and lower right-angled branching of this coralline alga; he also noted the curved tapering branches with rounded apices. Foslie gave branch cell measurements of 35–55 μm

EXPLANATION OF PLATE 21

- Fig. 1. Easterly aerial view of Tavernier mound and Key with southern tip of Key Largo visible in top right. Zonation of mound displayed by low-water spring tide and waves shoaling on dark *Porites* facies (p), *Thalassia* covered surrounding sea floor (s), *Neogoniolithon* facies (n), gravel patches (g), subtidal *Thalassia* (st), and intertidal *Thalassia* (it). Arrow indicates earlier colonized gravel patches.
- Fig. 2. Underwater photograph of *Porites* facies showing slope of mound edge and framework of *P. divaricata*, $\times 1$.
- Fig. 3. North-westerly aerial view of windward margin of Tavernier mound (letters as for fig. 1); scale from white 30–40 cm propeller scours.
- Fig. 4. Underwater photograph from junction between *Porites* and *Neogoniolithon* facies illustrating coral being overgrown by algal crusts and branches, $\times 1$.
- Fig. 5. Underwater photograph of lower part of *Neogoniolithon* facies with branching coralline overgrowing *Porites*, *Halimeda* and *Thalassia* blades to right, $\times 1$.
- Fig. 6. Underwater photograph of *Neogoniolithon* framework with intergrowing *Thalassia*; note flat-topped framework typical of thalli from the low-water level, $\times 0.25$.
- Fig. 7. Occasional large stabilized rhodoliths occur in the subtidal *Thalassia* beds inshore from the *Neogoniolithon* facies, $\times 0.5$.
- Fig. 8. Margin of intertidal pond in *Neogoniolithon* facies showing range of growth forms from the subtidal (right) to the intertidal (left); isolated domed heads in the subtidal become flat topped and grow sideways to merge with neighbouring thalli at the low-tide level (shovel 30 cm wide).



BOSENCE, Tavernier mound, Florida Keys

long and 15–25 μm broad for medullary cells, and less regular square to rounded cortical cells measuring 15–25 μm long and 15–20 μm wide; he also noted the common large heterocysts. Foslie's material was sterile and the reproductive structures have not been described (empty unipored conceptacles are illustrated in text-fig. 4E). Setchell and Mason (1943) discussed the nomenclatural problems of Foslie's *Goniolithon* and erected a new genus, *Neogoniolithon*, which included the former *G. strictum*.

N. strictum encrusts any available hard substrate in the shallow windward edge of Tavernier mound. Crusts are 170–350 μm thick (mean 288 μm , standard deviation 55 μm) and are closely applied to the substrate. The hypothallus is not well developed but when present is coaxial, one to three horizontal cells thick with rectangular cells 30–40 μm long (mean 37 μm , standard deviation 3 μm) and 11–17 μm wide (mean 13 μm , standard deviation 2 μm) (text-fig. 4C, G). The perithallus is an irregular grid (text-fig. 4C) with subsquare cells 8–24 μm long (mean 17 μm , standard deviation 5 μm) and 8–28 μm wide (mean 16 μm , standard deviation 5 μm). Heterocysts are common and are formed of one to three vertically stacked, rectangular to arched cells, the largest of each group measuring 29–40 μm high (mean 34 μm , standard deviation 6 μm) and 25–35 μm wide (mean 29 μm , standard deviation 3 μm) (text-fig. 4C, H).

The commonest growth form of *N. strictum* is branched thalli that arise from crusts (Pl. 22). Their characteristic tapered branches result in variable branch diameters from 1.3 mm in young branches to 3.5 mm in old branches. Branches have a wide, central unzoned medulla with coaxial rectangular cells (text-fig. 4B, F), 24–42 μm long (mean 33 μm , standard deviation 5 μm) and 13–20 μm wide (mean 18 μm , standard deviation 2 μm). The outer cortex is of variable width and composed of smaller, subsquare cells with a similar cell size to those of the perithallus in crusts. The tapering branches are thickened by 60–100 μm thick sheaths of cortical tissue growing up to the branch tip (text-fig. 4B). As far as I am aware this mode of branch growth has not been described in corallines previously. The common form of branch width growth is an outward growth of cortical tissue by the lateral meristem (Cabiocch 1972).

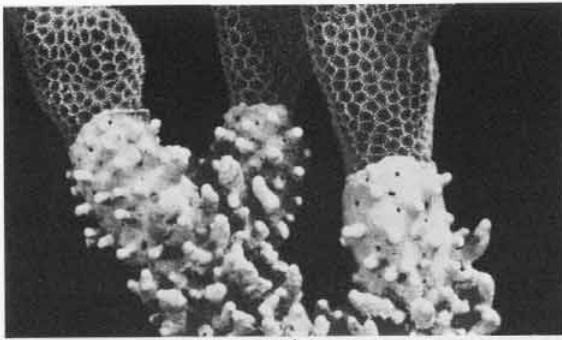
Two main processes in branch formation have been observed. Pseudodichotomous apical branching gives rise to branches diverging at low angles from each other (mean angle of divergence 41°, standard deviation 13°) (Pl. 22, fig. 5). In this case the central medullary region divides into two equal sections. Occasionally repeated apical branching occurs in one plane, giving rise to a fan-like branch arrangement (Pl. 22, fig. 5). Lateral branching results from rejuvenation of the lateral meristem and gives rise to branches that diverge at right angles to one another (mean angle of divergence 80°, standard deviation 12°) (Pl. 23, fig. 4). Similar branching types were illustrated for *Goniolithon* (*Neogoniolithon*) by Cabiocch (1972), and *Phymatolithon calcareum* and *Lithothamnium corallioides* by Bosence (1976).

FRAMEWORKS, RHODOLITHS, AND SEDIMENTS OF THE *NEOGONIOLITHON* FACIES

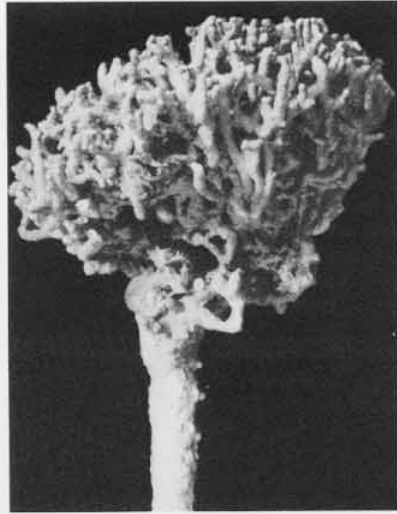
Neogoniolithon occurs in an elongate facies on the windward margin of the mound (Pl. 21, fig. 1; text-figs. 2, 3). The facies can be divided into three subfacies based on the growth forms of *N. strictum* and sediment characteristics: framework subfacies, rhodolith subfacies, and gravel patch subfacies (text-fig. 3).

EXPLANATION OF PLATE 22

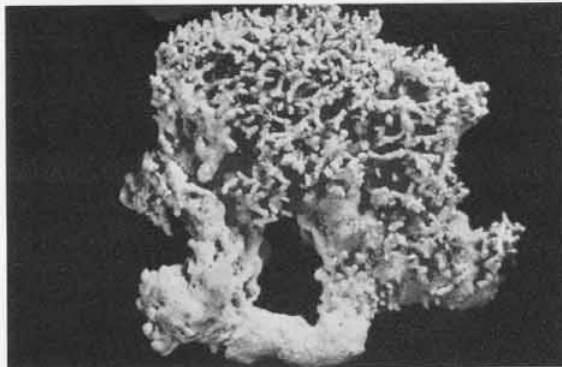
Figs. 1–7. *Neogoniolithon strictum* Setchell and Mason, 1943. 1, BM 1630, live *Porites* being overgrown upwards by crusts and branches of *N. strictum*; crusts and branches later bored by sponge, $\times 1.5$. 2, BM 1631, *Porites* branch completely overgrown by *N. strictum* to form dome-shaped thallus typical of the shallow subtidal zone, $\times 1$. 3, BM 1632, discoidal rhodolith arising from overgrowth of branched *Porites*; two growth directions are preserved, $\times 2$. 4, BM 1633, fragment of framework derived from earlier collapsed segment; note lateral branching (arrowed) with redirected growth, $\times 0.75$. 5, BM 1634, ellipsoidal rhodolith with pseudodichotomous branching (arrowed) which may be repeated in one plane to produce fan-like branches, $\times 1$. 6, BM 1635, underside of framework illustrating extensive bioerosion of thallus, $\times 1.5$. 7, BM 1636, rhodolith illustrating effects of turning on growth: (i) vertical *Porites* fragment in framework, (ii) branching framework growth of *N. strictum* (to left of figure), (iii) turning and redirected vertical growth (up figure), (iv) turning and redirected present-day growth (out of figure); note also nestling *Barbatia* in rhodolith core, $\times 0.75$.



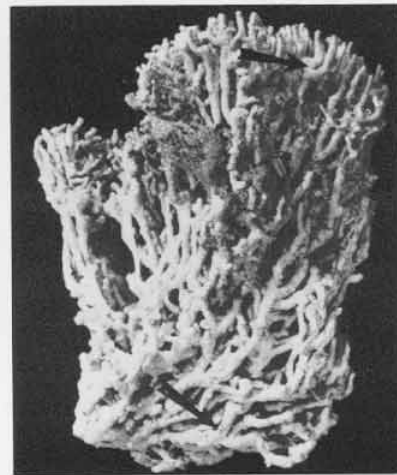
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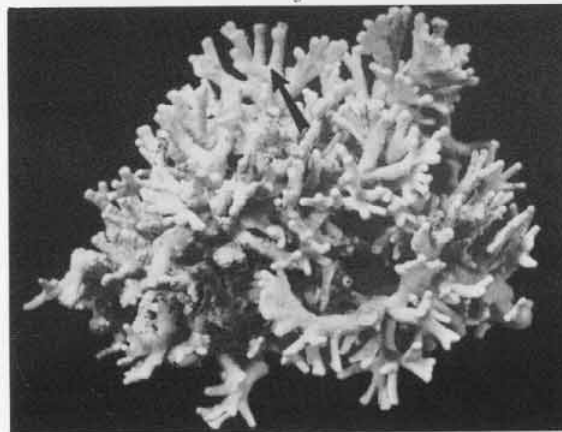
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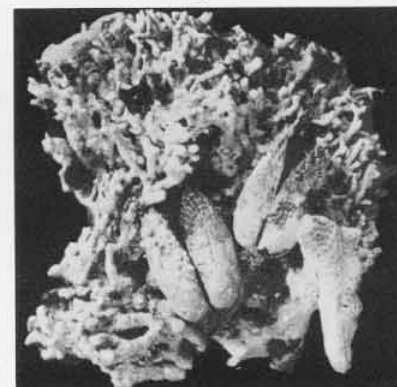
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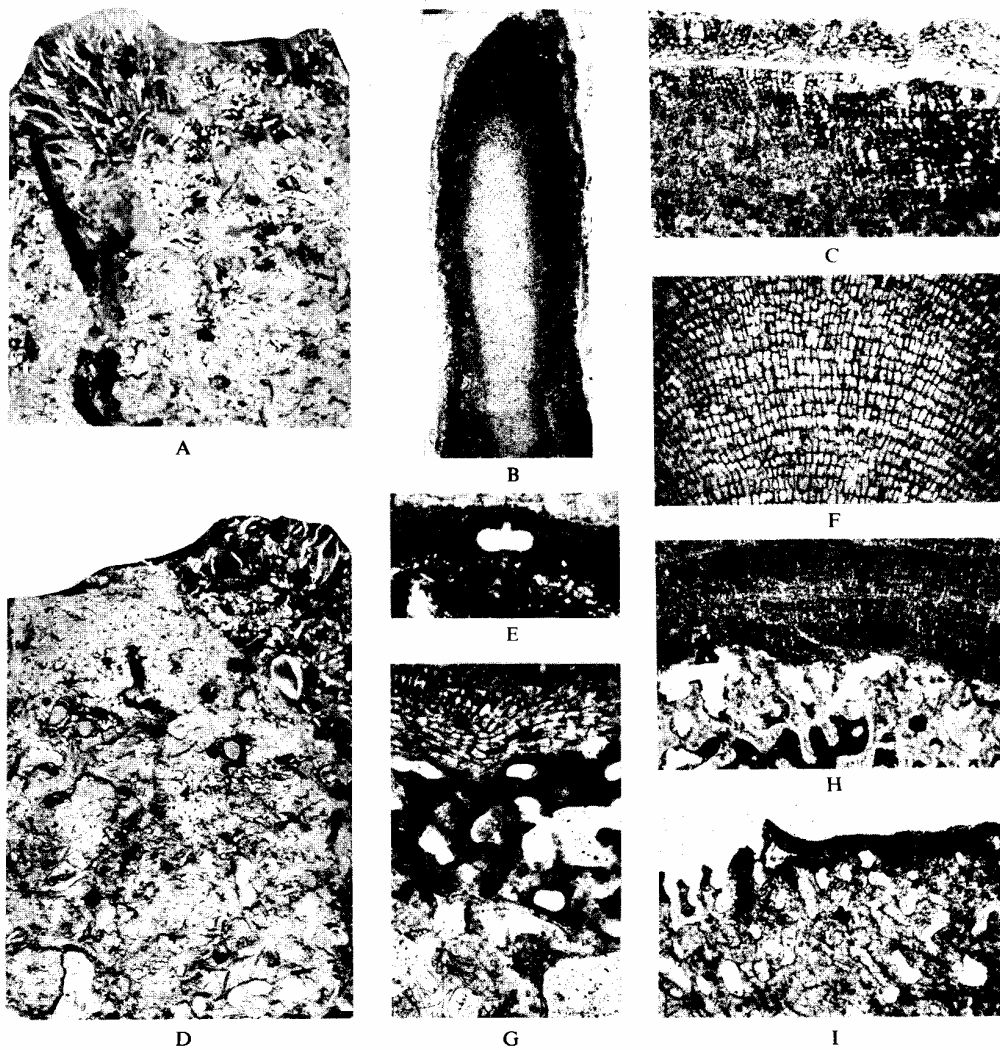


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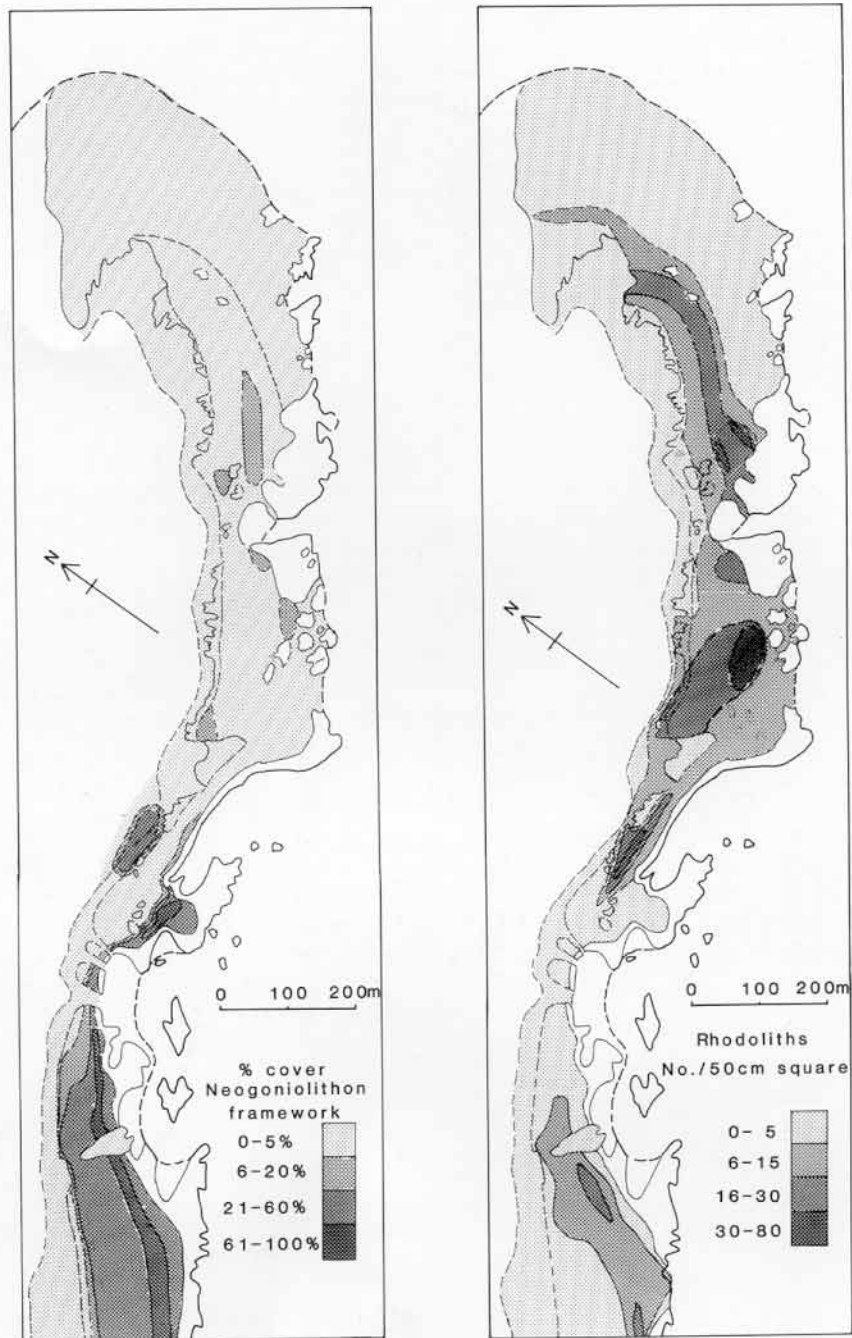


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BOSENCE, *Neogoniolithon*



TEXT-FIG. 4. A, impregnated box core illustrating *Neogoniolithon* framework and lower burrowed gravel; note *Thalassia* roots and rhizome in upper part of core, and *Porites* branches at the base, $\times 0.25$. B, longitudinal section of *N. strictum* branch illustrating inner medullary tissue and outer cortical tissue with heterocysts; note outer crustose sheath overgrowing branch, $\times 10$. C, detail of B illustrating inner partially micritized cortical tissue, with vertically arranged heterocysts overgrown by new crust with one to three cell thick hypothallus, $\times 60$. D, impregnated box core illustrating *Neogoniolithon* framework with *in situ* *Codakia*, lower burrowed muddy gravel with *Porites* and rhodolith, $\times 0.25$. E, empty unipored conceptacle of *N. strictum*, $\times 30$. F, detail of B with coaxial unzonated medullary tissue from branch centre, $\times 60$. G, lower *Porites* bored by sponges (spicules lower left) and fungae overgrown by crust of *N. strictum*, $\times 60$. H, lower fresh *Porites* overgrown by crust of *N. strictum* indicating overgrowth of live *Porites*, $\times 60$. I, *N. strictum* crust overgrowing dead fungal-bored *Porites*, $\times 60$.



TEXT-FIG. 5 (left). Abundance (estimated as percentage quadrat cover) of *Neogoniolithon* framework at sample stations shown in text-fig. 3.

TEXT-FIG. 6 (right). Abundance of rhodoliths (number per 50 cm square) at sample stations shown in text-fig. 3.

Framework subfacies

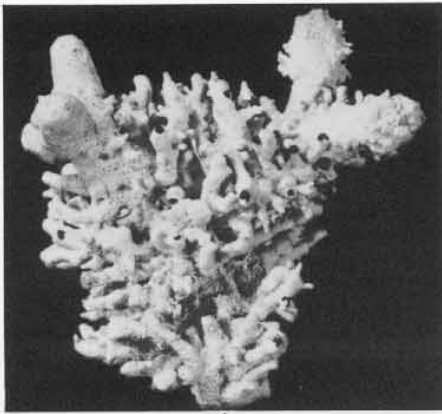
This subfacies is characterized by an *in situ* framework of *N. strictum* (text-figs. 3, 5; Pl. 21, fig. 5) covering an average 45% of the sea floor. *Porites* frameworks may persist in shallow subtidal areas with an average cover of 10%. Frameworks have a relief above the sedimentation level of up to 15 cm and extend into the shallow subsurface (text-fig. 4A, D). Sediment around the frameworks is a muddy sandy *Neogoniolithon* gravel which gives way to muddy *Neogoniolithon* gravel in the sheltered near-shore areas. The gravels are composed mainly of *N. strictum* (69%) with lesser amounts of *Halimeda* (17%), mollusc (7%), *Porites* (4%), and foraminifera (1%). *Thalassia* cover over the framework is commonly 40–50%. Text-fig. 5 illustrates the percentage cover of *Neogoniolithon* framework. The major concentrations occur in the more sheltered southern parts of the mound (cf. text-fig. 3). In addition, the framework occurs in small amounts on the windward margin of the rhodolith sub-facies adjacent to the *Porites* facies.

Shallow subtidal areas of the *Porites* facies illustrate the main way in which the *Neogoniolithon* framework is formed. Fresh crusts of *N. strictum* are found on the lower dead branches of *Porites* (Pl. 21, fig. 4). These crusts grow marginally and eventually overgrow the live upper parts of the *Porites* branches, killing off the live coral (Pl. 21, figs. 4, 5; Pl. 22, fig. 1). This can be seen in sections from live specimens, or preserved in dead specimens where crusts overgrow fresh unbored coral surfaces (text-fig. 4H). Conversely, overgrowth of dead surfaces is characterized by algal and fungal borings (text-fig. 4G, I). Branches arising from these crusts grow upwards, thicken, and rebranch to eventually form a dense interlocking framework. Branches may fuse together with the growth of additional cortical tissue. Growth begins as rounded isolated heads (Pl. 22, fig. 2); adjacent heads then coalesce to form a continuous framework. Within the framework are many nestling and crevice-dwelling bivalves (*Brachidontes*, *Barbatia*, and *Crassostrea*; Pl. 22, fig. 7; Pl. 23, fig. 3), gastropods (*Vermetus* and *Cerithium*; Pl. 23, fig. 1), echinoids (*Echinometra* and *Diadema*), ophiuroids, crustaceans (shrimps, stone crabs, lobsters, and hermit crabs), encrusting serpulids, bryozoans, and foraminifera. The framework is commonly overgrown by sponges (*Haliclona*, *Timea*, and *Spongia*) and tunicates (*Ascidea*).

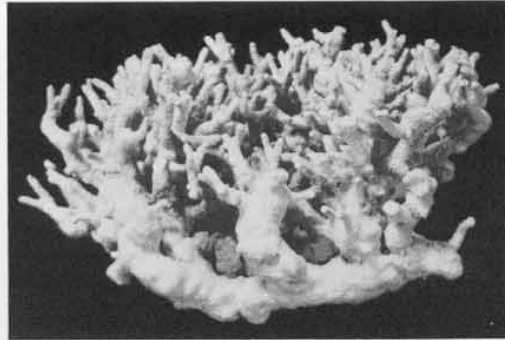
Framework growth continues to the low-water spring-tide level where upward growth is halted and the framework has a flatter top and is more densely branched (Pl. 21, fig. 6). Depressions in the mound surface are ponded at low-water spring tides with a constant tide level. Here adjacent growth heads have a common flat top and the margins of plants have large overhangs as subsequent growth is by lateral branching lower in the thallus (Pl. 21, fig. 8). The restricted upward growth and increased lateral branching results in adjacent heads coalescing with a common flat top. In this way the framework may cover up to 90% of the mound surface. Only the upper few centimetres of the framework is alive, below which occurs a band of bioerosion by sponges, algae, and fungi (Pl. 22, fig. 6). Beneath this dead zone, which is of variable height, the framework is buried by a muddy sandy *Neogoniolithon* gravel (text-fig. 4A, D). Box cores illustrate the *in situ* preservation of the framework in the shallow subsurface, but at 10–20 cm below the level of sedimentation the framework is lost, as is its original substrate. Similarly, piston cores through the mound do not penetrate areas of framework in the subsurface. There is clear evidence of the framework being weakened by small-scale bioerosion.

EXPLANATION OF PLATE 23

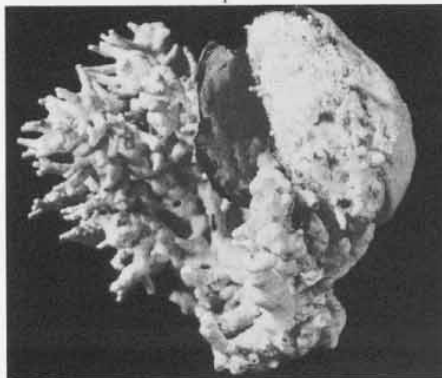
Figs. 1–8. *Neogoniolithon strictum* Setchell and Mason, 1943. 1, BM 1637, discoidal III rhodolith arising from branching *Porites*; note intergrown vermetid gastropods in coralline branches, $\times 1$. 2, BM 1638, ellipsoidal III rhodolith illustrating two directions of growth and great variation in branch thickness, $\times 1$. 3, BM 1639, rhodolith with nestling *Ostrea* and *Barbatia* later overgrown by coralline, $\times 1$. 4, BM 1640, discoidal III rhodolith illustrating two main directions of growth, $\times 1$. 5, BM 1641, spheroidal III rhodolith, $\times 1$. 6, BM 1642, ellipsoidal II rhodolith illustrating two main directions of growth, $\times 1.5$. 7, BM 1643, ellipsoidal III rhodolith illustrating three directions of growth (vertical, left to right, and out of figure), $\times 1$. 8, BM 1644, rhodolith with columnar growth and severe echinoid grazing marks over surface, $\times 1$.



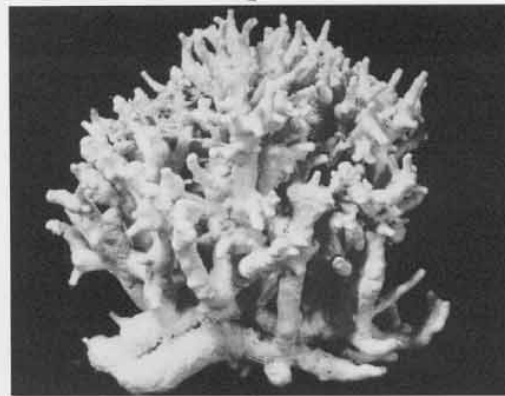
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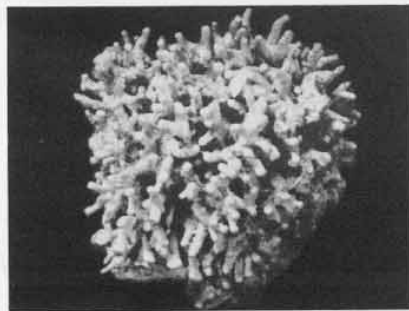
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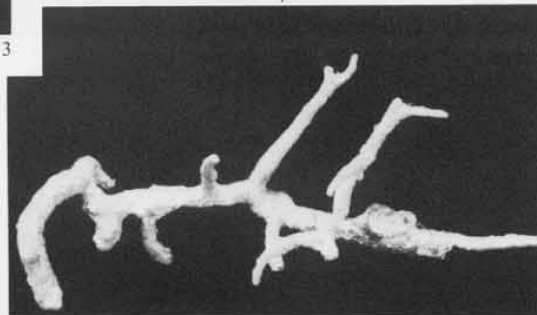
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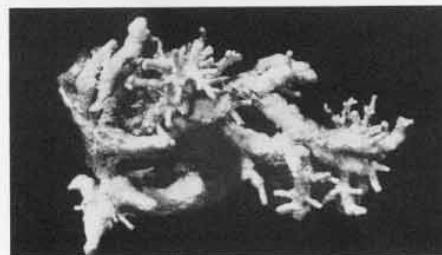
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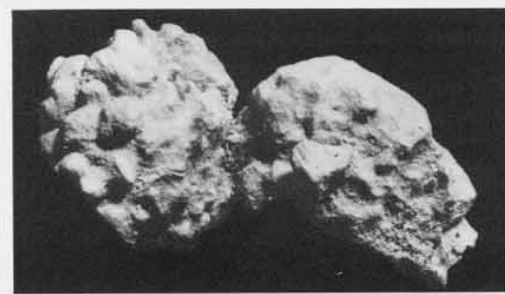
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BOSENCE, *Neogoniolithon*

No evidence for dissolution has been seen under the SEM. The most likely cause for the final breakup of the framework is the burrowing of crabs, lobsters, and shrimps (*Callinassa major*). These crustaceans are abundant on the mound and debris from their burrows shows freshly broken algal, coral, and molluscan skeletons. Box cores show burrows and bioturbation textures that could have been produced by these crustaceans. Therefore, although the framework is abundant on the mound surface and shallow subsurface, it is destroyed by bioerosion and burrowing to form mud, sand, and gravel-sized debris. These sediments are abundant over the entire surface of the present-day mound and to depths of 2 m in the subsurface.

Rhodoliths are generated from the framework by the breakage of branching segments. After falling on to the substrate, growth is either redirected vertically or new lateral branches arise from the upper surface (Pl. 22, figs. 3, 4, 7). When turned again, these rhodoliths may record a new growth direction and thus give an indication of the amount of movement involved. Rhodoliths from the framework subfacies are characterized by having only two directions of branch growth (text-fig. 8). Rhodoliths are most commonly ellipsoidal in shape (59%), less frequently discoidal (32%), while spheroidal shapes (10%) are the least abundant. Rhodoliths are common (average eight per 50 cm square) and are larger (40 cm³) than those occurring in other subfacies on the mound.

Rhodolith subfacies

This subfacies is characterized by an abundance of rhodoliths (averaging eighteen per 50 cm square; range five to ninety), sandy *Neogoniolithon* gravels, a *Thalassia* cover averaging 34%, and small patches of *Neogoniolithon* frameworks (2%). The subfacies occurs mainly to the north of the framework subfacies in the more exposed part of the mound (text-figs. 3, 6). Sediments are poorly to very poorly sorted and composed mainly of *Neogoniolithon* (68%), with lesser amounts of *Halimeda* (15%), molluscs (7%), *Porites* (6%), and foraminifera (2%). Rhodoliths are commonest in the central to windward part of the subfacies (text-fig. 6). Numbers decrease into the shoreward *Thalassia* beds where the sediments are muddier. Similarly, abundance decreases in the highest energy area of the north-eastern end of the mound. Rhodoliths are therefore most abundant in areas of intermediate hydraulic energy. Nearly all rhodoliths are of close-branching morphology and many are derived from segments of branching frameworks that have been turned so that growth is redirected (Pl. 22, fig. 7). Other rhodoliths start from *Porites* sticks (Pl. 22, fig. 3; Pl. 23, fig. 6), *Siderastrea* colonies, bivalve shells, gastropods, or artificial substrates. Initial growth on these substrates is a crust that gives rise to upward-growing branches. With occasional turning, growth is redirected (Pl. 23, figs. 2, 4). Occasional rhodoliths are found with a columnar construction. These are always found on a sandy gravel or gravel substrate. The surface of these rhodoliths is usually scoured by echinoid grazing traces (Pl. 23, fig. 8).

Rhodoliths are mainly ellipsoidal (64%) and this shape is often seen to have originated from an elongate section of *Neogoniolithon* framework. Discoidal shapes are the next most common (29%) and these are often formed from an elongate branch which has redirected its growth along one edge only. Others derive their shape from mollusc shells or *Porites* sticks with branches in one plane (Pl. 22, fig. 3; Pl. 23, fig. 1). Spheroidal rhodoliths are the least common (7%) and are characteristically densely branched (Pl. 23, fig. 5). Branching densities of rhodoliths from this subfacies are most commonly 'frequent' (70%) and least commonly 'occasional' (15%) and 'dense' (15%). The number of growth directions recognizable in rhodoliths is commonly two (33%) (Pl. 23, fig. 2), three (28%) (Pl. 23, fig. 7), or four (17%) (Pl. 22, fig. 7). This shows increased turning and transport compared with rhodoliths from the framework subfacies (text-fig. 8). Rhodoliths are slightly smaller (36 cm³) than those from the framework subfacies which suggests some breakage with transport (text-fig. 8).

Gravel patch subfacies

Oblong patches of sandy gravel or gravelly sand occur with their long axes normal to the mound edge. The patches have no coralline framework, a thin *Thalassia* cover (14%), and few rhodoliths (three per 50 cm square). Most patches of coralline gravel occur within the rhodolith subfacies, with a particularly large area to the north of the mound. In the south, however, a large patch cuts across the

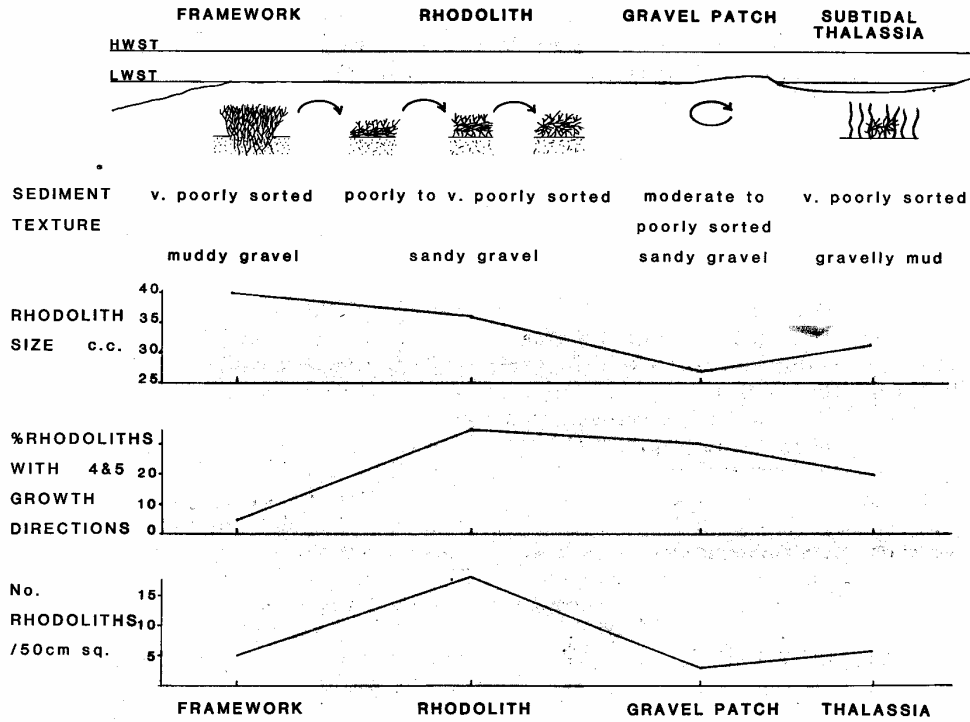
framework subfacies. The gravel patches occur in locations with the highest wave energy on the mound where wave orthogonals converge (text-fig. 3). Their long axes are orientated parallel to the direction of refracted wave approach. Sediments on the patches are moderately to very poorly sorted and of similar composition to those previously discussed (*Neogoniolithon* 62%, mollusc 14%, *Halimeda* 13%, *Porites* 4%, and foraminifera 0.5%).

Sediment is transported shorewards along the gravel patches by breaking waves. The central area of each patch may be slightly scoured and rippled, and at the shoreward crest of the patch a 10–15 cm face of gravel avalanches down into the near-shore *Thalassia* beds. The gravel patches thus mark the shoreward edge of the *Neogoniolithon* facies (Pl. 21, fig. 1). As the patches move shoreward, the seaward margin begins to be colonized by macrophytes in the following successional order: *Penicillus-Syringodium-Thalassia*, and finally an increase in *Neogoniolithon* rhodoliths. A short visit to Tavernier mound in August 1983 showed that previously mobile gravel patches seen in August 1982 (following tropical storm Dennis) had become stabilized by plants and their margins were less sharp. Old stabilized gravel patches are now preserved as bands of *Thalassia*-rich and *Thalassia*-poor areas within the rhodolith sub-facies of the northern mound (Pl. 21, fig. 1). Rhodoliths in the patches are rather scarce compared to their abundance on either side, behind, and on the front avalanche face of the patches (text-fig. 7). This is thought to be due to their rapid transport over the patches. Branching densities and numbers of growth directions of rhodoliths from the patches is similar to those from the rhodolith subfacies. This also suggests that transport is too rapid for the rhodoliths to show any growth response to the new conditions. The small size of the rhodoliths (27 cm³) suggests that some abrasion occurs with transport.

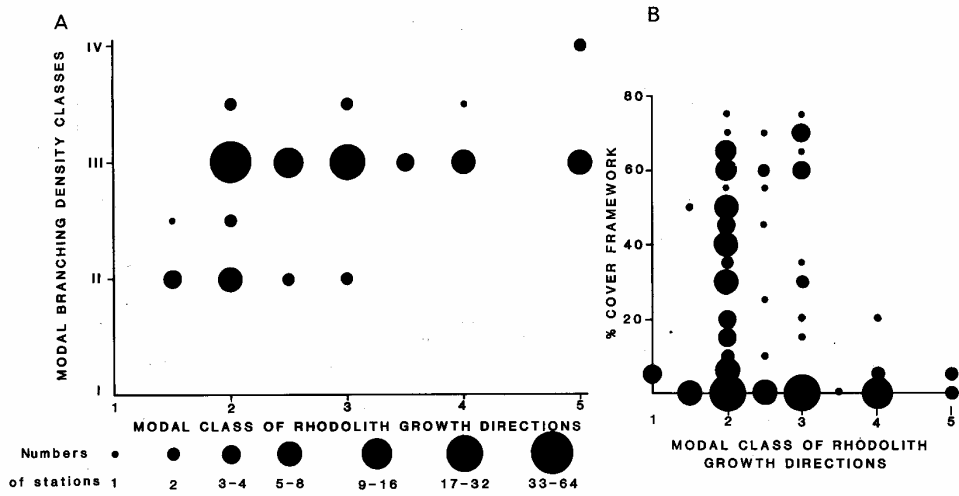
Summary and discussion

The shallow seaward margin of Tavernier mound is dominated by the branching coralline alga *N. strictum*. In shallow subtidal areas *N. strictum* overgrows *Porites*, and in sheltered parts of the mound it forms a dense branching framework up to low-tide level. Vertical growth is restricted in the intertidal zone and bushy thalli grow sideways to merge with neighbouring clumps; these clumps have a common flat top at low-water spring-tide level. The framework is weakened by bioerosion and segments are broken off to continue life as rhodoliths in the areas of intermediate wave energy on the mound (text-fig. 7). With shoreward transport, the rhodoliths are turned and growth is redirected so that two or more branch growth directions can be recognized (text-fig. 7). Eventually rhodoliths may take on their more typical radial growth habit. The majority of rhodoliths are of class III (common) branching density but classes I, II, and IV also occur. If modal classes of branching density for each station are compared with numbers of growth directions within the rhodoliths, a positive correlation can be seen (text-fig. 8). Previous workers have shown that increased branching density is a response to increased transport and apical abrasion (Bosellini and Ginsburg 1971; Bosence 1976, 1983*b, c*). This is also suggested here, with the evidence for increased transport being preserved in the lateral branching and new growth directions. One other source can be found for densely branched rhodoliths on Tavernier mound. Stations from the windward edge of the *Neogoniolithon* facies contain small numbers of densely branched rhodoliths. These rhodoliths, however, have a small number of growth directions and their close proximity to dense frameworks at the low-tide level suggests a local derivation. The occurrence of rhodoliths and their numbers of growth directions is shown in text-fig. 7. From this it can be seen that the areas of framework subfacies have rhodoliths with few growth directions (two or three) whilst areas of the rhodolith subfacies and gravel patch subfacies have higher numbers of growth directions, again indicating transport away from the frameworks. Similarly, a negative correlation exists between percentage cover of *Neogoniolithon* framework and numbers of growth directions within rhodoliths (text-fig. 8*b*), suggesting transport of rhodoliths away from frameworks.

The preservation of distinct growth directions within rhodoliths suggests fairly long periods (several years) when they are stationary, interrupted by a period or periods of transport. Transport is thought to be mainly by storms as normal wave conditions do not move rhodoliths. Observations immediately after 80 km.p.h. winds of tropical storm Dennis (August 1982) showed turned and



TEXT-FIG. 7. Summary of variation in morphology of *Neogoniolithon strictum* across subfacies on the mound surface (data from 1,500 rhodoliths from 220 stations, averaged for each subfacies).



TEXT-FIG. 8. A, modal branching density and modal growth directions of rhodoliths from stations on Tavernier mound; stations with denser branching rhodoliths also have rhodoliths with more growth directions. B, relationship between percentage cover of *Neogoniolithon* framework and number of growth directions of rhodoliths; stations with many growth directions have little *Neogoniolithon* framework (data from 1,500 rhodoliths from 220 stations).

transported rhodoliths (live, red-side down). Transport across the gravel patches is thought to be faster and is reflected in a reduction in rhodolith size. Some rhodoliths occur within the inner *Thalassia* beds. These are heavily infested with epiphytes and epizoans and are considerably weakened by bioerosion. Sediments have a similar composition throughout the three subfacies suggesting derivation from similar communities together with transport of grains over the mound surface. The only variation is in texture, which varies from the more poorly sorted and muddier sediments of the lower energy framework subfacies to the coarser better sorted gravels of the gravel patches.

COMPARISONS AND PALAEOECOLOGICAL CONCLUSIONS

Comparisons with Recent examples

N. strictum is found in environments similar to those on Tavernier mound in other areas of the Florida Keys. Turmel and Swanson (1976) have described a similar low-tide level, windward fringe of *N. strictum* on Rodriguez Bank, just to the north-east of Tavernier Key. A brief visit in 1981 confirmed their observations but there was not the same differentiation into subfacies as on Tavernier mound, and growth was less luxuriant. Other examples are known on sediment banks and channel margins from the back reef area of the Florida Keys (Enos and Perkins 1977). In all cases the environment is back reef, protected from the main ocean swell but exposed to local waves and/or tidal currents. Outside the Florida Keys, Adey (pers. comm. 1984) has observed similar occurrences at Mayaguana in the Bahamas. Here a 3 km, 0–2 m deep fringe is found in a lagoon experiencing increased temperatures (30°C) and salinities (38‰). Therefore the branching framework of *N. strictum* is found in back reef or lagoonal environments, on a soft substrate, and within a metre or so of mean low water.

Other examples of *Neogoniolithon* reef frameworks are from the Mediterranean where a 'trottoir' or pavement occurs in the intertidal zone. The leafy crustose species *N. notarisii* can be either a component of a mixed coralline community constructing the 'trottoir' (Pères and Picard 1964), or ledges, algal ridges, and microatolls may be constructed entirely by this alga (Thornton *et al.* 1978; Denizot *et al.* 1981). These reefs grow up to the intertidal zone where vertical growth is halted, lateral growth becomes important, and flat tops and overhangs develop. This is a similar response to the intertidal emergence of *N. strictum* on Tavernier mound where flat-topped and sideways-spreading clumps occur at the low-tide level. On a larger scale, coralline algal patch reefs (Ginsburg and Schroeder 1973; Adey 1975; Bosence 1984) and Pacific algal ridges (Emery *et al.* 1954) also show a similar growth response to sea level.

The branching framework of *N. strictum* may be considered intermediate in its construction between the thicker branched and early cemented branching frameworks of coralline algal ridges, and the unattached and uncemented branching frameworks of the temperate mearl (Bosence 1983a). The absence of early cementation in the *N. strictum* framework means that it is susceptible to breakage following bioerosion. Fracturing by waves and burrowing crustaceans reduces the preservation potential of the framework but leads to the formation of the associated rhodolith and gravel-patch subfacies.

Rhodoliths of *N. strictum* have not been described before but they can be compared with other detailed descriptions of rhodolith formation. Bosellini and Ginsburg (1971) described the morphological changes which take place as rhodoliths are transported from sea grass beds to channels in Whalebone Bay, Bermuda. Bosence (1976) analysed the variation in rhodolith morphology in temperate mearl beds of western Ireland. In neither of these two cases is there a similar area to that on Tavernier mound, where an *in situ* framework generates fragments to form rhodoliths. In all cases, however, a similar relationship exists between transport and branch morphology. Cessation of apical growth following abrasion leads to the growth of lateral branches and more densely branched rhodoliths. Redirected growth as a response to turning is most clearly seen in the Tavernier rhodoliths because of their derivation from the upward-branching frameworks. In ancient sequences the only evidence for the presence of former frameworks may be in the form of these unidirectionally

branched rhodolith cores. It might be expected that coralline algal patch reefs would be surrounded by rhodoliths derived from fractured frameworks, but this has not been reported (Ginsburg and Schroeder 1973). Rhodoliths occurring around patch reefs in St. Croix have crustose growths of *Tenarea*, *Porolithon*, *Neogoniolithon*, and *Homotrema* over a core of coral, shell, or pebble (Adey 1975; Bosence 1984). They are clearly not derived from the reefs that have frameworks of branching and columnar *Lithophyllum* and *Porolithon*. The reason for this apparent anomaly is probably that the coralline patch reefs are rigid and well cemented, and the greatest agents of erosion are boring organisms. These organisms release fine-grained dead material often into an environment which is not conducive to the growth of reef-building corallines.

Comparisons with ancient examples

The pattern of framework, rhodolith, and gravel-patch formation on Tavernier mound (text-fig. 7), and the leeward change to rhodoliths showing increasing amounts of transport to leeward gravels, should be preserved in ancient sequences (see below). This pattern may be applicable to and aid in the interpretation of Miocene coralline reefs from Israel (Buchbinder 1975). Here reef crests have branching frameworks of *L. prelichenoides* and *L. ghorabi*. Back-reef areas are rich in branching and crustose coralline debris of the same taxa. Buchbinder (1975) suggested that the abundance of debris is due to the presence of former branching frameworks on the back-reef platform area. A more complete picture results when this is compared with the Tavernier mound pattern. Branching debris can be related to framework breakdown and rhodolith formation and breakdown along the same transport path.

The Miocene Coralline Algal Biostrome of Malta (Bosence and Pedley 1982) also illustrates the relationship between framework, rhodoliths, and gravel, but in a deeper water setting. Crustose frameworks occur with branches arising from crusts. Within the frameworks are erosion surfaces, frequently lined with rhodoliths. The internal structure of the rhodoliths illustrates a framework-derived core with later fresh overgrowths of concentric crusts and radial branches. In this case, as with Tavernier mound, the framework was not current resistant and provided cores for rhodoliths. Shapes of the Miocene rhodoliths are similarly controlled by the nature of the framework, and the branching density by apical abrasion following transport. Thus crustose frameworks in the Miocene gave rise to discoidal rhodoliths whilst upright-branching frameworks on Tavernier mound give rise to ellipsoidal rhodoliths. Palaeocurrent directions in the Coralline Algal Biostrome are very varied and no separation of windward frameworks and leeward coralline algal gravels was detected.

Although coralline algae and algal limestones are common in the Tertiary, there are few detailed descriptions of the facies present. Therefore no further comparisons can be made at present but it is hoped that this study will help interpretation in the future.

Palaeoecological conclusions

This study provides further documentation of coralline algal facies occurring in windward reef environments. Although walled reef coralline facies are reasonably well known, coralline facies from carbonate mounds have not been previously studied in the Recent. The branching *Neogoniolithon* facies is a useful sea-level indicator as it occurs within a metre or so of low-water level. Perhaps of more use in palaeoecological studies is the growth response of this coralline alga to low-water level. Vertical growth is halted and a flat-topped framework is formed by sideways branch growth. This feature is also found in other shallow water coralline reefs and may well be applicable to other unrelated coralline algae in fossil sequences, thus giving a rare preservation of the former low-tide level. Conversely, the absence of a flat-topped framework cannot be used as an indicator of deeper water as domed frameworks may occur where there is greater tidal range, higher wave splash, or where sea-level changes are faster than coralline accretion.

The preservation potential of the *Neogoniolithon* framework is poor on Tavernier mound due to bioerosion of the algal thallus and later fragmentation by crustaceans. In ancient sequences the evidence for bioerosion and burrowing would be preserved, but careful study would have to be carried out to establish the existence of a former framework as opposed to unattached corallines

(mearl; Bosence 1976). The small core samples from Tavernier mound did not recover many segments of framework but larger exposures may contain relics of the branching frameworks with unidirectional branch growth (cf. Bosence 1984), or alternatively these may be preserved in rhodolith cores. Portions of previous frameworks were found to be preserved in this fashion in the Miocene of Malta (Bosence and Pedley 1982).

The former existence of framework, rhodolith, and gravel-patch subfacies will again depend on preservation, which in turn relates to local sedimentation and burrowing rates. These subfacies are not recognizable in the Tavernier cores. If preserved elsewhere they may give an indication of lateral energy gradients within shallow water sequences.

Rhodoliths also contain considerable palaeoecological information which can be used not only in taxonomic comparisons with Holocene and Cainozoic examples but also with unrelated corallines. Rhodolith cores may give evidence of coralline algal facies which are not otherwise preserved. The numbers of redirected branch growths in the corallines give an indication of the amount of transport away from the framework facies and possibly the frequency of storms.

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