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The nature and significance of microatolls

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WITH AN APPENDIX BY B. R. ROSEN

[Plates 1–4]

Microatolls, those coral colonies with dead, flat tops and living perimeters, result from a restriction of upward growth by the air/water interface. The principal growth direction is horizontal and is recorded in the internal structure, though fluctuations in water depth can influence the surface morphology producing a terraced effect. The morphology of the basal surface of the colony is controlled by the sand/water interface such that the thickness of the coral records the depth of water in which it lived.

In open water at the margin of reefs in the Northern Province of the Great Barrier Reef, tall-sided uneven-topped microatolls live, whereas, on the reef flats in rampart-bounded moats and ponds, thin flat-topped and terraced microatolls are abundant. Because water in moats can be ponded to levels as high as high water neaps (1.6 m above datum at Cairns) and still have daily water replenishment, microatolls on reef flats can grow to levels 1.1 m higher than open-water microatolls (which grow up to a maximum elevation of low water springs, i.e. 0.5 m above datum). This imposes a major constraint on the use of microatolls in establishing sea level history. The two factors controlling pond height during one sea stand (relative to the reef) are tidal range (which governs the height of high water neaps) and wave energy (which governs the height of ramparts which enclose moats).

Dating and levelling fossil microatolls exposed on the reefs show that 4000 years (a) B.P., high water neaps was at least 0.7 m higher than it is at present.

1. INTRODUCTION

(*a*) *Definition*

Early descriptions of microatolls were given by Darwin (1842), Dana (1872), Semper (1880, 1899) and Guppy (1886), using general names such as coral head or coral block. Guppy (1886) spoke of 'miniature atolls', Agassiz (1895) of 'diminutive atolls' and Krempf (1927) of 'dwarf atolls' ('*atolls nains*'). The term *micro-atoll* was first used by Krempf (1927), but without concise definition. It was widely adopted and variously defined. Kuenen (1933) used it for 'a colony of corals' with 'a raised rim, more or less completely surrounding a lower, dead surface'. MacNeil (1954) used it for 'massive colonial corals growing peripherally in shallow areas and whose dead upper surface (sometimes made concave by solution) is exposed at low tide'. Several authors, for example Newell & Rigby (1957), Hoskin (1963), Kornicker & Boyd (1962), Garrett, Smith, Wilson & Patriquin (1971) have adopted the term, inconsistent with early usage, to refer to patch reefs consisting of many corals which develop a structure having a raised growing rim and a low, commonly dead or sand-filled, centre. Scheer (1972) suggests that the term *mini-atoll* is more appropriate for such patch reefs. The term *faro* is in common use for large ring-shaped patch reefs at atoll margins. Recently Stoddart & Scoffin (1978) have reviewed the literature on microatolls.

A typical microatoll is a single coral colony, commonly massive and circular in plan, with a dead, predominantly flat, upper surface and a living lateral margin. A fossil microatoll has the same morphology and though no living polyps remain, both the internal structure and commonly the preservation of the peripheral corallites indicate that the polyps at the lateral margins lived on after those at the centre died. For microatolls to indicate the former close proximity of sea surface to their upper surfaces, their internal structure should reveal evidence of predominantly horizontal growth.

(*b*) *Corals having microatoll form*

Those colonial corals (including Scleractinia, Hydrozoa and Alcyonaria) that would, if unimpeded, grow with a dome-shaped upper surface, develop a microatoll form when upward growth is restricted. Massive corals were the most common microatolls on the Great Barrier Reefs studied, especially *Porites lutea*, but some branching corals also take on this same configuration when they reach water level. Certain corals (notably *Pavona*) encrust the lateral margins of shallow water corals and thus enhance the microatoll nature of the foundation coral.

A list of all the corals found with microatoll form on the Great Barrier Reef patch reefs and barrier reefs examined between Cairns and Cape Melville is given in the appendix. These identifications were kindly made by B. R. Rosen of the British Museum.

Although an exhaustive collection was not made it is of interest to note that in this region of the Great Barrier Reef as many as 43 species of corals (representing 23 different genera) were found growing with microatoll form. That this very limited environment should support such large numbers of coral genera all with the same general morphology suggests that growth form might carry more weight than species composition in certain environmental reconstructions.

(*c*) *Origin*

Living microatolls are all found with their tops at the lowest level of sea water for the area in which they grow; they are not found growing below lowest water level of spring tides in the open sea. This observation coupled with the nature of microatoll growth forms indicates that the dead, flat upper surface of microatolls relates to the close proximity of the water/air interface. If corals that have developed a dead surface in relation to a certain level of water break (owing to instability) such that part of the living margin is now lower in the water, this lower part will grow up to the water level and develop a new microatoll surface. This indicates that the critical effect in producing the dead surface is not a factor unrelated to water level, such as the inability of the flat parts of corals to clear raining sediment from their broad surfaces as has been proposed by some authors (Wood-Jones 1912; Krempf 1927). Also, the excessive sediment theory would not account for the existence of open-branching microatolls. Exactly what finally kills the polyps at the coral top is not known; it may be the desiccation on exposure, excessive ultraviolet radiation, or in some cases even lack of nutrients at the coral centre.

On death of part of the coral its skeleton is soon attacked by boring, grazing and encrusting organisms. The activities of this epifauna and epiflora tend to retard the recuperation of the coral growth at this site of attack. Boring organisms (filamentous algae, sponges, worms, sipunculids, bivalves) and, to an extent, grazing organisms that feed on the epiflora, all lower the dead coral skeleton and may be partly responsible for the concave nature of the tops of many microatolls. However, it is important to note that the bioerosive activities of these animals and plants are themselves not the cause of the microatoll form as defined here. This is evident from examination of the internal structure of the Great Barrier Reef microatolls. Where the dead top results principally from the bioerosion of a formerly dome-shaped coral truncation of growth lines is apparent (figure 1 *a*), whereas those skeletons showing horizontal growth lines paralleling the dead surface result from purely lateral growth during most of the coral development (figure 1 *b*). Also, the corals whose upper surfaces have been hollowed out by bioerosion generally have an irregular top in comparison with the essentially planar surface of the typical microatoll. An example of a coral with a bioeroded upper surface is shown in figure 9† where a massive colony of *Montastrea annularis* has had its upper surface extensively grazed by *Diadema antillarum* sea urchins well below low water level on a fringing reef in Barbados.

2. Growth forms and factors influencing morphology

(*a*) *Upper surface*

(i) *Steady state of lowest water level*

The most common form of microatoll on the patch reefs of the northern Great Barrier Reef is shown in figure 1 *c*. Initial growth was as a hemisphere at times t_1 and t_2 but by the time t_3 water level was reached and lateral growth commenced and continued through to the present, t_9. Upward growth is restricted by the water/air interface and downward growth by the sand/water interface. The tallness of the structure coated by living polyps and therefore the thickness of the coral skeleton are indicative of the depth of water in which the coral grew. Most reef flat microatolls are between 5 and 20 cm thick. The top dead surface is called the microatoll plane. Any bioerosion of the microatoll plane truncates the growth lines.

(ii) *Deepening of water*

Commonly the polyps at the margins grow slightly above (up to 2 cm) the microatoll plane and the lowest water level in the area in which these microatolls occur is just at the level of the uppermost living polyps (figure 1 *d*). The flexuring of the growth lines at the inner margin of the living annulus (figure 1 *d*) suggests that in these examples the corals have recently managed some upward growth indicating a recent slight increase in water depth. Of course the shape of that part of the skeleton that is covered by living polyps must result from growth. This shape cannot be accounted for by the persistent outward growth of a raised lip with concomitant erosion of the inner portion of the living annulus. Progressive development of this outer-growth/inner-erosion style would result in the structure shown in figure 1 *e*, and not the pattern observed of flexuring of growth lines inwards at the inner margin of the living annulus.

The width of the living annulus at water level was rarely more than a few centimetres before it too developed a dead centre (the secondary microatoll plane) shown in figure 1*f*. It can be seen that at this stage the polyps at the inner part of the annulus grow over, and in the opposite direction to, earlier skeletal growth that produced the primary microatoll plane (figures 1*f*, 2 and 10). Also, these polyps grow into an ever decreasing annulus and thus compete for space. As the upward growth of these two annuli also becomes restricted by water level they too

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† Figures 2–7 appear on plate 1, figures 9–14 on plate 2, figures 15–20 on plate 3 and figures 22–27 on plate 4.

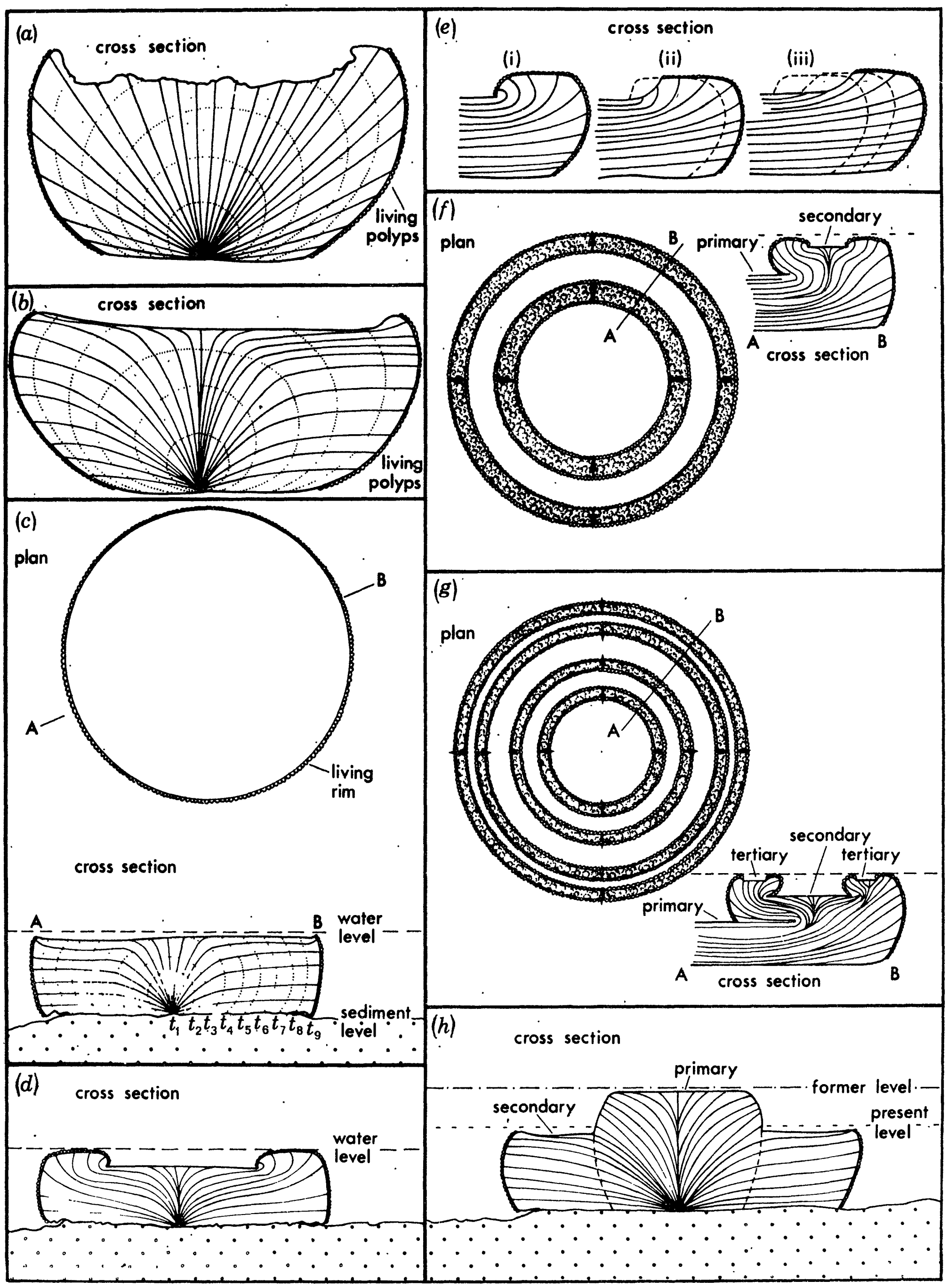


FIGURE 1. (*a*) Cross section of a coral colony with a living lateral margin and dead upper surface. The truncation of the growth lines at the top are the result of surface bioerosion. (*b*) Cross section of a coral colony, a micro-atoll, with a living lateral margin and a dead upper surface. The growth lines parallel the top surface indicating horizontal growth consequent on an upward restriction. (*c*) Microatoll in plan and cross section showing the general form and the stages of growth. Initial growth was as a hemisphere at times t_1 and t_2 but by time t_3 water level was reached and lateral growth began and continued through to the present, t_9. (*d*) Cross section of a microatoll whose living rim has grown a few centimetres higher than the dead central portion. Note the flexuring of the growth lines at the inner margin of the living annulus. (*e*) Predicted structure of the stages of development of a coral colony margin where bioerosion of the surface has progressed along with outward growth of the rim, causing the gradual removal of the flexured growth lines. (*f*) Microatoll in plan and cross section showing the development of the secondary microatoll plane. (*g*) Microatoll in plan and cross section showing the development of the tertiary microatoll plane. The arrows on the plan view illustrate the present direction of growth of the living polyps. (*h*) Cross section of a microatoll whose secondary micro-atoll plane is below the primary, indicating a shallowing of water.

bifurcate, producing a tertiary microatoll plane (figures 1*g* and 10). The maximum difference in heights recorded between a primary microatoll plane and a tertiary microatoll plane on one colony was 20 cm.

Three microatoll planes on one coral colony was the maximum number found, though theoretically, if the water is periodically deepened, there is no reason why more microatoll surfaces should not develop on the one coral colony. The surface structure becomes more convoluted with continued development of these surfaces because eventually the polyps of different annuli growing in opposing directions start to interfere with one another (figure 3).

(iii) *Shallowing of water*

The examples of microatolls with evidence of growth above the primary microatoll plane all grew in progressively deepening water. If the water shallows a new lower microatoll plane develops around the periphery of the coral (figure 1*h*). Exposure of the central part of the skeleton normally results in rapid bioerosion obscuring the earlier shape of the coral.

(*b*) *Lower surface*

Just as fluctuations in the level of the water/air interface are reflected in the morphology of the upper part of the colony and the adjacent internal structure, changes in the sand/water interface level affect the outline of the lower part of the coral and the adjacent internal structure, for the polyps tend to grow down close to the substrate level. The undersurfaces of microatolls commonly have a saw-tooth profile (figures 8*a* and 11). This shape indicates abrupt killing of lower polyps, followed, after a while, by further downward and outward growth starting from a level above the earlier lowest level. This growth pattern most probably results from the periodic piling around the microatoll base of sediment which has later been removed. Some shapes indicate that the sediment level was raised permanently (figures 8*b* and 11). The large microatoll shown in figure 11 indicates a marked raising of sand level at about the time the top reached water level. This raised sand level was maintained throughout the remaining growth with only minor fluctuations to produce the toothed base.

On reef flats normally only the small microatolls that have recently reached water surface are still connected to a solid substrate, the broad microatolls lie loosely on sand. The crevices under the lower surface provide a habitat for a range of cryptic animals, both sessile (the most common are sponges, bivalves, worms, foraminiferans, bryozoans) and motile (gastropods, fish, crustaceans, ophiuroids). These creatures help to disperse sand beneath the corals and may even bring about a lowering in the sediment under the solid skeleton. Microatoll shapes indicative of deepening water do not necessarily indicate a raising of water level, they may result from a lowering of the coral in a soft substrate.

(*c*) *Regrowth after movement or breakage*

Broad, thin microatolls are fairly easily lifted by waves; they can be moved, tilted, overturned or broken. When a microatoll is tilted, growth occurs along a new plane as shown in figure 8*c*.

Growth can continue after complete overturning (figure 8*d*) though some polyps may show a 180° change in growth direction.

If the two fragments separate when a microatoll breaks then growth becomes recurved at the edge of the break (figure 4). Lateral growth into deeper water can bring about instability of a microatoll. If the sandy substrate is removed from the periphery of a large microatoll, skeletal growth alone can be sufficient to bring about a disequilibrium causing breakage of the skeleton into segments. The margins tilt down and the polyps grow back up to the water level (figure 5).

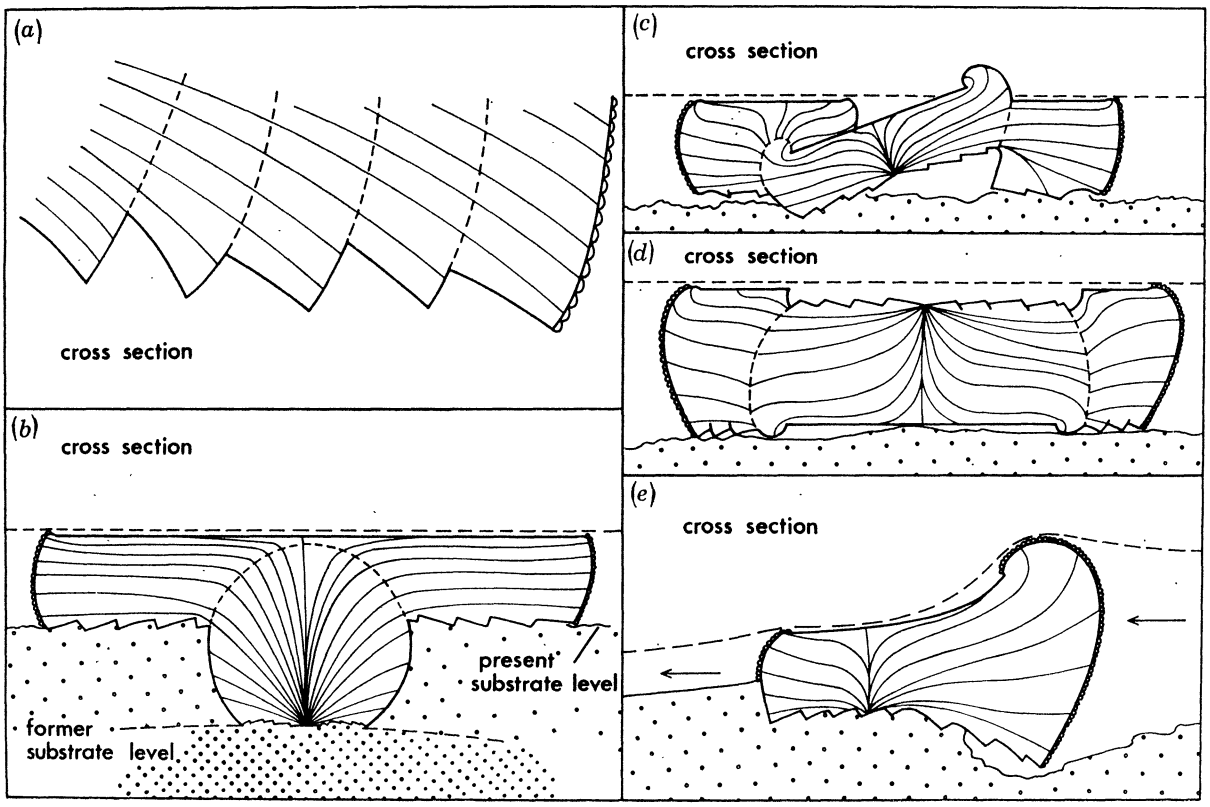


Figure 8. (*a*) Saw-tooth profile of the undersurface of a microatoll. The growth lines indicate the periodic death of the low polyps. (*b*) Cross section of a microatoll whose undersurface reveals a sharp, permanent raising of the sediment level after about a third of its development. (*c*) Cross section of a microatoll that has undergone tilting and regrowth. (*d*) Cross section of a microatoll that has been overturned and continued growth. (*e*) Cross section of an asymmetric microatoll. Dominant direction of flow of water is from right to left; this current scours the sediment away from the up-current side, piles it on the lee and at the same time, banks water high on the up-current side. Coral growth develops accordingly.

Description of plate 1

Figure 2. Cross section of the margin of a *Favites* microatoll revealing the internal growth pattern in the development of primary (a) and secondary (b) microatoll planes. Width of photograph 35 cm. Reef flat, Two Isles, Great Barrier Reef.

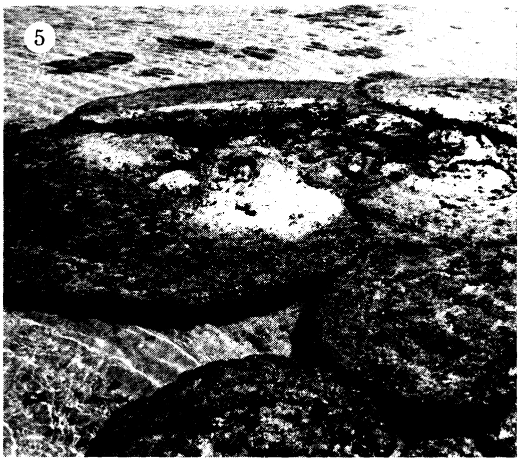
Figure 3. Convoluted growth pattern on the surface of a large *Porites* colony. Reef flat, Turtle IV, Great Barrier Reef. Hammer 30 cm long.

Figure 4. Plan view of a *Porites* microatoll that has broken along a diameter and growth at the lateral margin has continued around the broken surface. Reef flat, Two Isles, Great Barrier Reef. Hammer is 30 cm long.

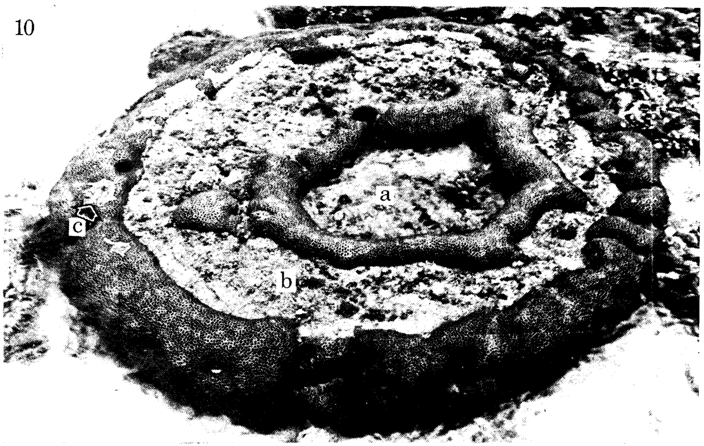
Figure 5. Large colonies of *Porites* that have split into segments on subsidence of the margins. Reef flat, Nymph Isle, Great Barrier Reef. Width of foreground in photograph 3 m.

Figure 6. Coalescing colonies of *Porites*. Note that the line of contact is at the same level as the surrounding microatolls planes suggesting a bevelling down of the former rims. Reef flat, Turtle IV, Great Barrier Reef. Width of foreground 1 m.

Figure 7. Development of a pavement of coalesced microatolls (predominantly *Porites*). Reef flat, Three Isles, Great Barrier Reef. Hammer is 30 cm long.



FIGURES 2–7. For description see opposite.



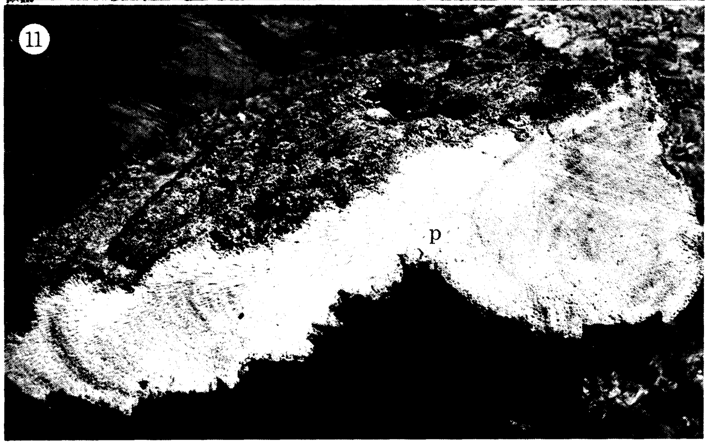


FIGURE 9. Underwater photograph of a living massive *Montastrea annularis* that has had its upper surface extensively grazed by *Diadema antillarum* sea urchins. The upper surface of this coral is at a depth of 2 m below low water level. Bellairs reef, Barbados, W.I.

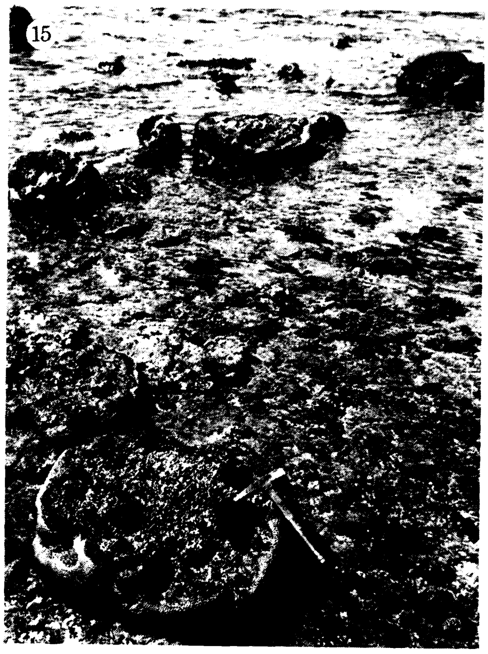
FIGURE 10. *Platygyra* microatoll 1.5 m in diameter showing development of primary (a), secondary (b) and incipient tertiary (c) microatoll planes. Reef flat, Two Isles, Great Barrier Reef.

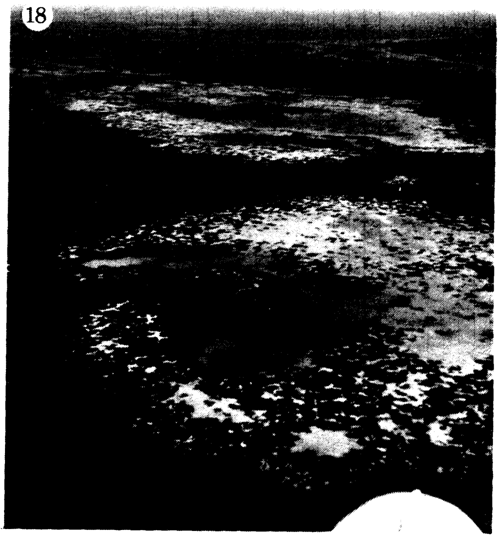
FIGURE 11. Sawed vertical section of half of a microatoll. The right side of the photograph shows the region of early development of the colony, the extreme left of the coral is the living margin. Arcuate growth bands can just be detected. The coral started growth in water about 20 cm deep but after a time (at position p) the sand level was raised to about 10 cm below the water surface. Subsequently, sand level fluctuated slightly to produce the saw-tooth profile at the base of the coral. The water level was roughly constant throughout. Reef flat, Nymph Isle, Great Barrier Reef.

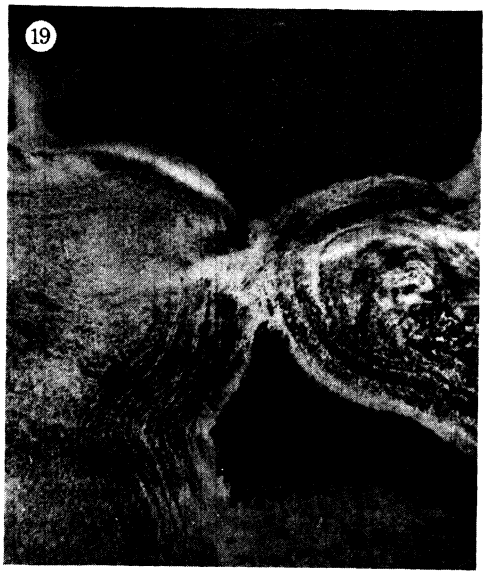
FIGURE 12. Microatolls (dominantly *Goniastrea*) with inclined upper surfaces resulting from prevailing flow of water from right to left. Photograph taken at extreme low tide leeward margin of reef flat. Low Isles, Great Barrier Reef. Foreground 3 m wide.

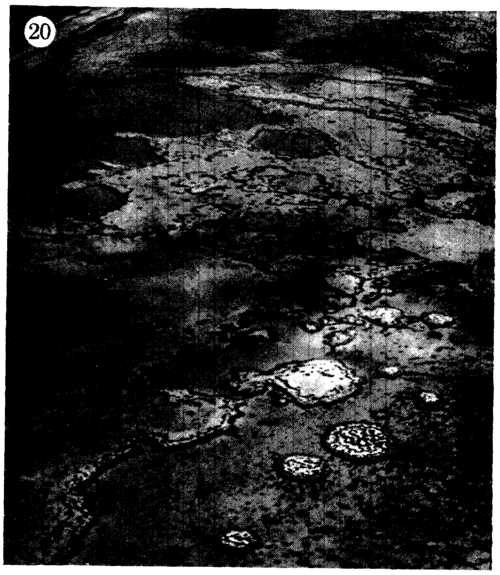
FIGURE 13. Northeast margin of reef flat at Hampton Isle, Howick Group, Great Barrier Reef, showing the broad flat pavement consisting chiefly of the surfaces of dead and living microatolls. Foreground of photograph is 5 m wide.

FIGURE 14. Underwater photograph of colony of branching *Acropora* coral that grows in open water up to the level of low water springs. At the maximum elevation for growth, branches become flattened, stubby and dense. Leeward side of East Hope Island, Great Barrier Reef.









Figures 15–20. For description see page 105.

22

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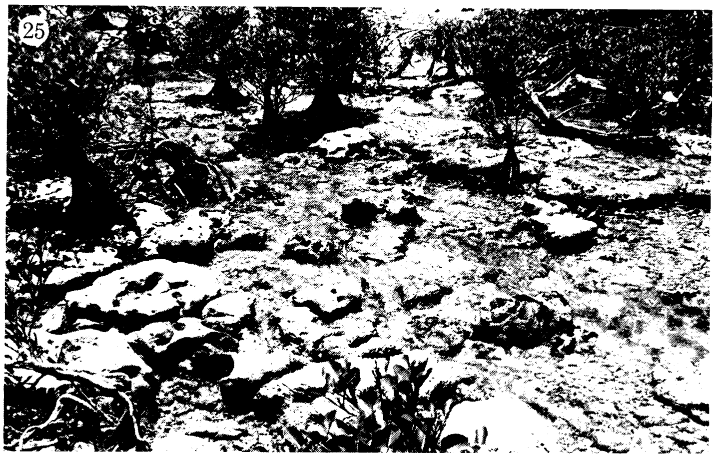

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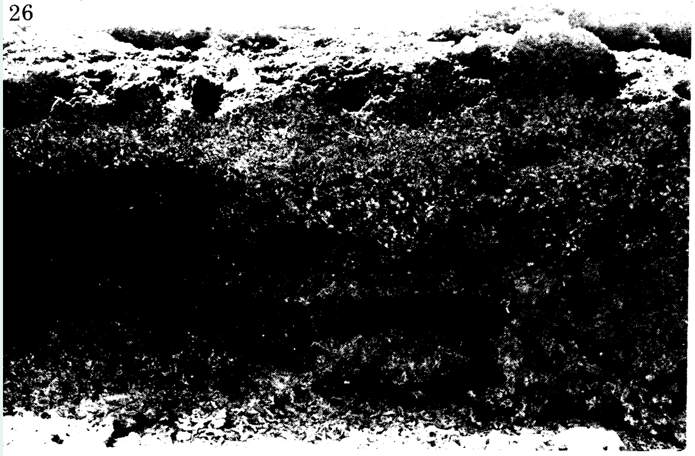

27

Figure 22. Windward margin of Watson Reef, Great Barrier Reef. The open water, at the right of the photograph, is at a lower level than the water in the moat retained by the rampart of loose coral shingle. Width of moat is about 6 m.

Figure 23. Two levels of ponded water. The higher pond, in the background, is retained by a wall of cemented shingle (the jagged projections represent eroded lithified foresets), the lower pond, in the foreground is retained by a rampart of loose coral shingle. Microatolls currently live up to the water surface in both these ponds. Windward flanks Watson Reef, Great Barrier Reef.

Figure 24. In-place dead microatolls in a drained moat. The rampart (at top of photograph) that formerly ponded water here has recently been breached. Windward margin of reef flat, Nymph, Great Barrier Reef. Foreground is 4 m wide.

Figure 25. In-place fossil microatolls exposed on the reef flat on Nymph Isle, Great Barrier Reef.

Figure 26. In-place fossil microatoll (left of the hammer) exposed in section in a cliff of cemented shingle. Upper platform, Nymph Isle, Great Barrier Reef. Hammer is 30 cm long.

Figure 27. Large dead microatoll at the leeward flanks of Low Isles. The open sea to the left was at the level of low water springs at the time of photography.

(*d*) *Asymmetric growth*

Most microatolls on reef flats show an obvious radial symmetry, but in some cases growth is uneven. The lip of the microatoll can be higher on one side than the other (figures 8*e* and 12). Microatolls of this shape grow in areas where, for the major part of the tidal cycle, water is flowing rapidly in one direction. The leeward sides of reef flats are lower than the windward. Consequently, on the flanks of the leeward sides of many reef flats, water that is draining from the windward flows steadily throughout the whole ebbing of the tide. This flow brings about scouring of sand from under the windward side of the microatoll (and some piling up of sand on the leeward) and also a banking up of water on the windward side allowing this side to grow both slightly higher and lower than it can on the leeward.

The living lip of microatolls is commonly wider on one side than the other. Though this uneven growth was commonly related to flowing water (wider side up-current, that is on the windward) this was not found to be invariably the case. In some instances it perhaps relates to slight tilting such that one side reached water level earlier than the other and therefore spread laterally earlier producing the asymmetric form.

(*e*) *Size*

Microatolls vary in size from a few centimetres to a few metres in diameter. The average diameter of reef flat microatolls is 50 cm. The tallness of the skeletons is directly related to the depth of water in which they grow. Naturally in one moat of standing water the microatolls will all grow to the same level and as the foundation is usually regular they have approximately the same thickness. Quite commonly, microatolls in one moat have a similar diameter. This suggests that conditions were suitable for coral planulae settlement in the moat for only a short time. Perhaps the moat floor became covered with sediment too fine to be conducive to planulae attachment.

(*f*) *Coalescent growth*

When polyps of the same species meet, they cause the structure to coalesce and normally to grow in the resultant direction (figure 6). The old structure decays and is shortly lowered such that the line of contact is bevelled down to the level of the microatoll plane. With time a flat pavement of coalesced microatolls develops (figure 7) revealing few or no living polyps. At the margins of reef flats many areas, several metres across, that although full of small holes were essentially flat, proved to be the surface of one or several coalesced microatolls that had suffered extensive bioerosion and encrustation (figure 13).

Description of plate 3

Figure 15. Microatoll colonies of *Goniastrea* in open water on the windward side of Three Isles, Great Barrier Reef. Hammer is 30 cm long.

Figure 16. Underwater photograph of a tall-sided *Porites* microatoll in open water on the leeward side of Low Isles, Great Barrier Reef. The coral is 80 cm tall and the top dead surface is coated with a thin layer of a soft colonial anemone that is just exposed at low water springs.

Figure 17. Mini-atolls, 'algal cup reefs'. South shore, Bermuda. Photographed from 10 m altitude.

Figure 18. Coalescing mini-atolls. North Lagoon, Bermuda. Photographed from 200 m altitude.

Figure 19. Coalescing mini-atolls (showing former concentric growth pattern on dead centres). Kaneohe Bay, Oahu, Hawaii. Photographed from 150 m altitude.

Figure 20. Coalescing mini-atolls (some showing a secondary rim development; cf. the secondary rim development in microatolls). Central Region, Great Barrier Reef. Photographed from 250 m altitude.

3. Distribution and modes of occurrence

Each shallow water location on and around the reef flats of the patch reefs is characterized by a predominance of certain species and growth forms of microatolls.

(a) *Open water*

At the peripheral margin of patch reefs, some corals are exposed at extreme low tides and develop microatoll form. The common massive coral on the windward slopes of the outer margin of the reef flat is *Goniastrea*. This coral develops an irregular or cracked surface and usually grows up to about 75 cm diameter. The windward side of reefs normally suffer heavy surf and consequently water is periodically lapping onto the exposed corals and this could be responsible for the uneven surface (figure 15). On the leeward side the massive colonies of *Porites* grow up to the level of lowest low water and develop steep sided microatolls ('bommies') commonly 1–5 m in diameter (figure 16). The microatolls in open water commonly grow in close association with other corals (commonly branched) to build a framework of skeletons, *in situ*. There is a marked change in the growth form of branched corals as they approach the maximum elevation at which they can grow. The density of branching is greater near to the low water level and the branches become flattened and stubby (figure 14).

(b) *Ponded water on reef flats*

(i) *Windward side*

Ponded water occurs in moats on the windward side of the reef flats. These moats lie between successive sets of loose or cemented shingle ramparts and are generally about 5–50 m wide (figure 22). The depth of water in moats varies according to the height of the lowest point, or sill, of the pile of sediment ponding the water above the moat floor and also according to the permeability of the ponding sediment. Most moats are between 5 and 40 cm deep at low tide.

As cemented ramparts are generally higher, more permanent and less permeable than loose ramparts, they pond the highest moats (figure 23) and consequently contain the highest living corals (see later). The microatolls contained in the more permanent moats are normally large, tabular colonies. As the water level stays fairly constant throughout the period of low water at each tide the microatolls here tend to develop a simple surface.

The migration to and fro of loose ramparts or spits that retain water brings about periodic changes in the level of pond water. These changes are reflected in the convoluted surface morphology of microatolls.

It is not uncommon for an established moat to suddenly become drained by a breach in the rampart, stranding and killing off all the contained microatolls (figure 24). In certain cases a breach in the rampart may merely lower the lowest level of the moat water and bring about the development of a lower secondary microatoll plane on the colonies. Such a case was observed at the seaward side of Third Island of the Three Isles reef (figure 21). As this reef was mapped by Spender in 1929 (Spender 1930) and again by Stoddart in 1973, it was possible to compare the positions of the ramparts. Since 1929 the rampart has moved on to the reef by about 50 m. In so doing a gap has developed, draining the ponded water over a sill. However, before the rampart was breached, part of it joined the low cliff of rampart rock on the Third Island and maintained a part of the moat. The cross section (figure 21) is drawn to scale to show the relative heights of lowest water currently in the moat and in the ponded water on the reef flat side of the sill. The corals in the moat have either an unaltered hemispherical shape or else a simple microatoll top; those behind the sill have either a simple microatoll top or a secondary microatoll plane below an exposed part of the colony indicating a lowering of lowest water level. It was also noted that through the feather edge side of the rampart were exposed round-topped dead coral skeletons that were about half the diameter of those currently living in the moat. The surface of these dead round-topped corals is considerably higher than those living in open water and they most probably grew in the moat created by the rampart in the 1929 position and were first buried then later exhumed during its subsequent advance.

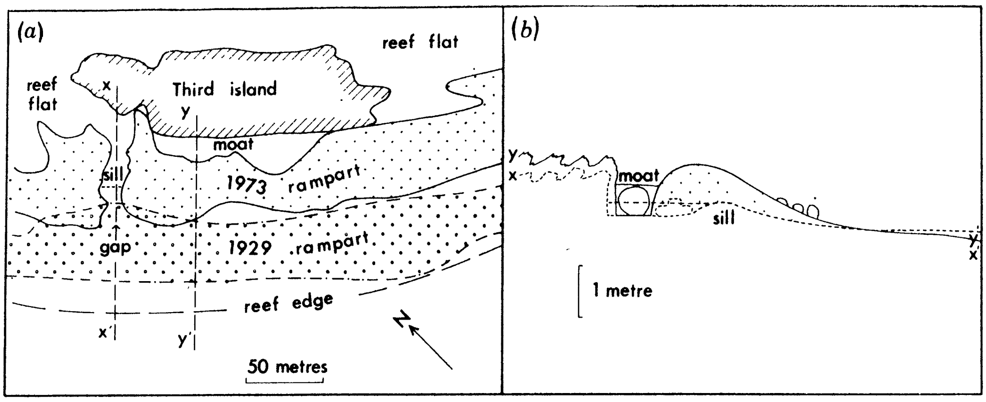

Figure 21. Plan (*a*) and cross section (*b*) of the area neighbouring Third Island on Three Isles Reef, Great Barrier Reef. The plan shows the 1929 and 1973 positions of the loose shingle rampart, indicating the positions of the present gap and moat. The cross section shows a profile through the moat superimposed on a profile along the gap over the sill.

(ii) *Leeward side*

The bulk of the draining water from the central part of the reef flat flows to leeward, the lower side of the reef flat. The water either drains freely or exits over a shallow sill at the flanks of the leeward sand cay and consequently it is rather shallow throughout low tide, supporting only thin microatolls. It is in these leeward moats that the branching coral microatolls are the most abundant. This probably relates to their greater ability to cope with the large quantities of bottom-moving sediments. Here also, asymmetric growth develops in the unidirectional currents as described earlier (figure 12). Leeward sand migration (driven by wind-induced surface currents) is common in these moats and sometimes sediment is piled up on the leeward sides of corals after strong winds. The leeward tails of sediment are ephemeral and disappear after a few days. Presumably currents, along with fish and other cavity dwellers, clear the sand.

(iii) *Central reef flat*

In the central part of the reef flat water is ponded at low tide in broad shallow pools. In these pools large thin microatolls grow and commonly coalesce to fill the pool with a flat coral pavement. Massive forms predominate and *Porites lutea* is the most common species. As the microatolls grow broad yet thin and unattached to a firm substrate they are readily broken by wave action during high tide. Both simple and convoluted upper surfaces are common.

4. Fossil microatolls

In-place fossil microatolls, up to 6000 years old, were found either exposed on the reef flats (figure 25) or in a matrix of cemented shingle in cliff exposures of limestone on the reef flats of the 'low wooded island' type of patch reefs (figure 26). The growth structure, species composition and distribution of these fossil microatolls are similar to those of the present forms living in moats and pools on reef flats.

The disposition of the fossil microatolls and the nature of the matrix and overlying sediments of the limestones indicate that these microatolls once grew in moats that were transgressed by advancing ramparts (Scoffin & McLean 1978, part A of this Discussion).

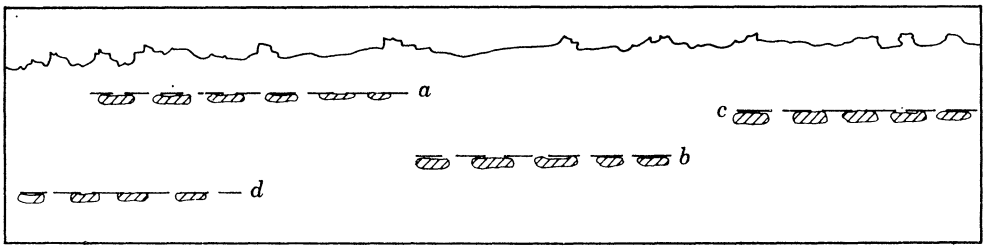

Figure 28. Cliff section view of sets of fossil microatolls. Levels *a*, *b* and *c* could be the same age but represent different moat levels. Level *d* is older than level *a*.

As the tops of living microatolls are all at the same height for one enclosed body of water, it follows that a group of fossil microatolls whose surfaces are all at the same height most possibly represent one earlier moat. Consequently layers of fossil microatolls in different strata may well be contemporaneous and just represent different heights of water in different (but neighbouring) moats (figure 28). The groups of microatolls in figure 28 at levels *a*, *b*, *c*, each represent a separate moat and they could have been (though not necessarily) contemporaneous. Field evidence for chronological difference in levels would be the existence of one group of microatolls directly under another, *a* and *d* in figure 28, not just lower and to the side.

5. Heights and ages of Northern Province microatolls

(*a*) *A note on datum*

All levelled profiles have been reduced to low water datum, which is the mean height of lower low waters at springs. Individual profiles have been related to low water datum by reference to predicted tides at Cairns: for most of the area covered by these surveys, the predicted tides do not differ significantly in amplitude or timing from those at Cairns and corrections to the Cairns curves only need to be made north of Cape Melville.

It is important to realize that there are several sources of error in these reductions and we cannot evaluate their magnitude. First, there may be actual differences in tidal curves between Cairns, the secondary stations for which predictions are available (these include several of the islands studied, notably Green Island, Hope Islands, Howick Island, Low Isles, Low Wooded Island) and the islands on which profiles were measured. Secondly, local tidal levels may have been distorted by meteorological effects: the trade winds blew strongly through most of the Expedition and it would be surprising if on some days at least tidal levels were not distorted by up to 0.3 m. Thirdly, and perhaps most importantly, all reductions to datum were made by observing a still water level at a known time on a particular profile and relating this to a predicted tide curve. Determination of a still water level is often difficult because of rough conditions, especially at middle and high waters. Relation of the still water level to the tidal curve is also more difficult on irregular low-amplitude neap tides than on springs: most of the surveys, however, were carried out on springs.

In the absence of tidal records at each of the sites surveyed, however, the height data represent the best estimate of elevations related to low water datum and enable different sections to be directly compared. The errors mentioned above are considerably reduced when the relation between one level and another is determined on one reef. All heights are given in metres. For comparison, at Cairns, mean high water springs are at 2.3 m, mean low water neaps at 1.2 m and mean low water springs at 0.5 m; these figures probably apply to all islands north to Cape Melville.

Table 1

location	elevation/m
Low Isles	0.55
Three Isles	0.25, 0.59, 0.88, 0.94
Low Wooded Island	0.63
Two Isles	0.26, 0.35, 0.44
Houghton Island	−0.07, −0.16, −0.13
Ingram	−0.47
Leggatt	0.09, 0.15

Table 2

location	elevation/m
Three Isles	0.76, 0.76, 0.85, 0.98, 0.99, 1.06, 1.09
Low Wooded Island	1.17
Two Isles	0.42
Watson	0.90
Leggatt	0.76

(*b*) *Highest living open-water corals*

The outer parts of reef flats of isolated patch reefs, seaward of the shingle ramparts, characteristically slope regularly seawards with inclinations of about 0° 40′ (about 1 : 80) and widths of 60–80 m (but sometimes over 100 m). Inclination increases rapidly about the level of low water springs and corals growing on these outer lower slopes are immersed at low spring tides. These represent the highest living open-water corals and their elevations are presumably directly related to tidal cycle and duration of immersion at different depths.

Sample elevations for living corals are given in table 1 (mean low water springs 0.5 m).

We conclude that mean low water springs represents an effective upper limit to coral growth in free-draining locations (figure 29).

(*c*) *Highest living reef-flat microatolls*

The highest uncemented rampart measured was at Watson Island and had an elevation of 3.12 m above datum. The highest cemented rampart was 3.42 m at Houghton Island. The uncemented ramparts pond water to a lower level than the cemented ramparts and this difference is reflected in the elevations of the microatolls living in the moats (figure 23).

Sample elevations of microatolls in moats of uncemented ramparts are shown in table 2.

Highest microatoll heights in moats of cemented ramparts at Watson are 1.53, 1.53, 1.54 and 1.55 m.

The highest living reef-flat microatoll (in fact the highest living coral) recorded by us on the Northern Province of the Great Barrier Reef was 1.55 m, i.e. approximately the level of mean high water neaps (1.6 m above datum). Even though it is theoretically possible for sea water to be ponded above high water neaps, it is doubtful that corals could grow in water that was not renewed every day. Thus it is concluded that the effective upper limit of growth for reef-flat microatolls is high water neaps (figure 29). Therefore, for this area, if we take present mean low water springs (0.5 m) as the effective upper limit of growing coral in open-water, free-draining localities then any fossil coral formed less than 1.1 m above this level could not be taken as evidence of any necessary change in sea level since it grew. This is so unless the fossil coral could be satisfactorily shown to be an open-water variety and not a reef-flat form.

(*d*) *Corals suitable for sea level history determinations*

When attempting to determine the earlier (low water) levels of open sea water, care should be taken in selecting those fossil corals for dating and levelling whose structures suggest that they grew up to sea level in open water rather than those characteristic of shallow pools on reef flats. Some criteria for distinguishing reef-flat from open-water forms are listed below.

(i) At low tide reef-flat pools are rarely deeper than 50 cm, for the amplitude of naturally formed ramparts of coral shingle rarely exceeds 50 cm for the *entire* perimeter of the pool. Therefore fossil microatolls having walls taller than 50 cm are likely not to have grown on reef flats.

(ii) The formation of a new rampart may seal an outflow channel and suddenly cause an increase in the level of pool water, and the new conditions continue for sufficient time to affect the coral structure; or conversely, a breaching of a rampart may rapidly lower pool level. Such changes are not uncommon on reef flats and will be reflected in the terraced structure of reef-flat microatolls. Ephemeral changes in water level of this sort do not occur in the open water and terracing of the upper surface of microatolls does not occur in this environment.

(iii) The dead surfaces of reef-flat microatolls are normally flat as a result of the stillness of the protected ponded water, whereas in the open water the waves lap onto the corals and more irregular upper dead surfaces are usual.

(iv) Reef-flat microatolls rarely form part of a contiguous coral framework. They are normally seated on cemented shingle and, with time, become enveloped in shingle and sand. The open-water microatolls grow to heights well above sediment level and are commonly part of a contiguous coral framework *in situ* which may include a variety of branching corals. It is also noted in open water that branching corals develop shorter stubby branches at the level of low water and the upper portion of the corals becomes much denser with branches (figure 14).

(*e*) *High fossil microatolls*

All the fossil microatolls that were collected for dating and whose elevations were measured were of the reef-flat type and were exposed either as isolated in-place corals on reef flats and among mangroves (figure 25) or in cliff sections where they were cemented in growth position in a matrix of coral shingle (figure 26). Sample heights of the highest of the exposed isolated types are given in table 3.

Carbon-14 dates for samples from each site are shown in table 4.

TABLE 3

location	height/m
Houghton Island	1.06, 1.16, 1.32, 1.35
Leggatt	1.08, 1.09, 1.10, 1.10, 1.11, 1.12, 1.14

(roughly the level of present mean low water neaps: 1.2 m)

TABLE 4

sample location and code	age B.P./a
Houghton Island (ANU-1287)	5850 ± 170
Leggatt Island (ANU-1286)	5800 ± 130

(determinations by H. Polach for R. McLean)

Sample heights of the highest of those cemented in shingle ramparts are as follows given in table 5 (measurements by D. Hopley marked *).

TABLE 5

location	height/m
East Pethebridge Island	0.98,* 1.44*
Turtle I	1.93, 1.99
Nymph Island	1.16,* 1.65,* 1.66* 1.76*, 1.80,* 2.10* 2.30*

Carbon-14 dates for high microatolls in cemented shingle are shown in table 6.

TABLE 6

sample location and code	age B.P./a
Turtle I (ANU-1478)	4420 ± 90
Nymph Island (ANU-1285)	3700 ± 90
Houghton Island (ANU-1595)	3250 ± 80
Three Isles (ANU-1380)	3750 ± 110

(determinations by H. Polach for R. McLean)

The only exposed fossil microatolls of reef-flat type that occur out of place with respect to present growth levels are those found above 1.6 m (present mean high water neaps). This is to say that several of the corals found exposed in different sections of cemented shingle which date about 4000 a B.P. must have grown under conditions of higher mean high water neaps than presently prevail. The highest fossil microatoll found (at Nymph) was 2.3 m above datum so mean high water neaps of about 4000 years ago here was at least 0.7 m higher than that of today. A summary of the highest levels of living and fossil microatolls in relation to tidal and moat levels is given in figure 29.

A fall of 0.7 m in the level of mean high water neaps over the last 4000 years can be accounted for by one or a combination of two processes: either sea level as a whole has lowered 0.7 m relative to the reef (i.e. eustatic or tectonic change) or sea level relative to the reef has not altered but the tidal range has changed (such an event over such a time would be accounted for most simply by a slight change in the configuration or depth of the neighbouring ocean basin). If 4000 a B.P. sea level, as a whole relative to the reef, was 0.7 m higher than it is today (but tidal ranges were similar to today's) then the highest levels of fossil open-water and reef-flat corals of this age would both now be raised 0.7 m above present highest levels; but if 4000 a B.P. sea level was as today's but tidal ranges differed such that mean high water neaps was 0.7 m higher than it is today, then the level of mean low water springs (height of open-water corals), would be *lower* than today, for when a tidal range increases the low levels are depressed while the high levels are elevated. So if the raising of the 4000 a B.P. microatolls relates only to a change in tidal range it may be expected that no evidence of fossil open-water corals higher than today's would be found.

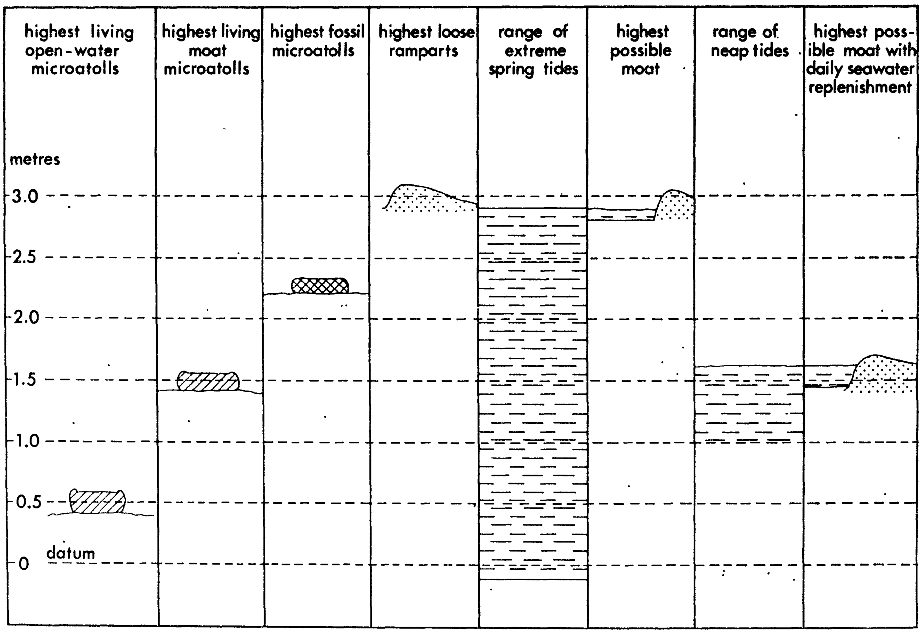

FIGURE 29. Highest levels of living and fossil microatolls shown in relation to tidal ranges and moat levels.

A thorough search of all the islands in this region between Cairns and Cape Melville revealed no exposures of cliffs or cemented platforms of in-place open-water corals. It is not impossible that such features once existed but have subsequently been eroded, though in the light of the well preserved cemented ramparts and in-place exposed microatolls as old as 6000 a B.P. it is thought unlikely that such cliffs or platforms were ever exposed. However, a 0.7 m lowering of sea level would not perhaps be expected to expose open-water reefs as cliffs and platforms similar to those produced by the intertidal deposits of ramparts that build up to 3 m elevation; rather, the open-water structures would expose to produce low broad flattish areas with very gentle seaward slopes that would soon be covered with intertidal deposits of coral shingle. If a raised open-water reef exists it should have the same relative disposition to the fossil ramparts as the present open-water reef has to present ramparts. Though no in-place fossil branching coral framework was found it is possible that some of the very large dead microatolls that occur at the leeward flanks of some reef flats (figure 27) represent examples of raised open-water microatolls ('bommies'). Unfortunately, during the Expedition no cores were taken of these corals to check their thicknesses to confirm their open-water growth form, nor were dating samples taken to indicate their age, though the elevation of the surface of one (figure 27) was measured to be 0.3 m above low water springs, i.e. 0.8 m above datum. At present all that can be stated with any degree of certainty is that between 4420 and 3250 years ago the level of mean high water neaps was at least 0.7 m higher than it is today. Whether or not the level of mean low water springs has fallen by the same amount over this time is speculation.

6. Summary of conclusions

Microatolls are coral colonies whose dead, flat upper surfaces result from a restriction in upward growth by the proximity of the air/water interface. Long fluctuations in the water level are reflected in the surface morphology and internal structure of microatolls. As the basal surfaces of many microatolls are governed by the sand/water interface the vertical thicknesses of the colonies represent the depth of the water in which they grew. The reefs of the Northern Province of the Great Barrier Reef support at least 43 species (23 different genera) of corals having microatoll growth form. Forms living at the edge of reefs in open water (up to mean low water springs, i.e. 0.5 m above datum) can be distinguished from forms living in rampart-bounded ponds and moats (up to mean high water neaps, i.e. 1.6 m above datum) on reef flats. Because of this distinction it is theoretically possible, with the aid of exposed (datable) fossil microatolls of open-water and reef-flat types, to determine not only sea level history but also tidal history of raised coral reefs. The highest fossil microatolls found in this region were 4000 years old and their elevation indicates that mean high water neaps was, at the time of their growth, at least 0.7 m higher than it is today.

7. Discussion

(*a*) *Ancient microatolls*

A microatoll shape indicates a proximity to water surface during growth and therefore would be a useful indicator of extremely shallow water deposition if found in ancient limestones. Although massive colonial organisms have been building reefs since Lower Palaeozoic times, it is surprising that there are no reports of pre-Pleistocene atoll-shaped skeletons. Possible explanations for this lack are given below.

(i) Microatolls are found growing in abundance only on reef flats that have areas of ponded water during low tide. Special conditions have to be satisfied for such reef flats to develop and these conditions may not have been met in the past. Today on the Great Barrier Reef patch reefs, reef flats are formed above low water where steady strong waves pile up branching coral sticks into ramparts around the seaward margins. If the ramparts are stabilized by cement or mangrove growth, moats are established and maintained. A wide tidal range is necessary to ensure diurnal water replenishment in the high moats. Where wave energy is very high and the reef, though shallow, is narrow (e.g. outer barrier of the Great Barrier Reef) the shingle is carried right across the reef and dumped in deeper water on the leeward side.

(ii) Microatolls grow only at the summit of reef development and are therefore the first skeletons to be destroyed on exposure of the reef.

(iii) They have not been recognized as microatolls in cross section.

(*b*) *Patch reefs of atoll shape*

A structure that grows at a uniform rate in all directions from a locus on a flat substrate will build a hemispherical shape. If this structure is confined to lateral development once water level is reached an atoll shape is produced. This structure can be a coral skeleton or a patch reef that developed from one initial coral. The chief difference between the processes operating in the production of the atoll-shaped coral and atoll-shaped patch reef is that on the reef numerous builders and reef dwellers all contribute to the supply of loose sediment which can, once sea surface is reached, choke the central areas as it cannot easily escape over the lip of actively growing corals at the margin. The central areas of patch reefs may then subside to a level of sand by a more rapid rate of bioerosion than growth. Examples of 'mini-atoll' patch reefs from Bermuda, Hawaii and Australia are shown in figures 17–20. The patch reefs coalesce (figures 18 and 19) in a similar manner to the coalescing of microatolls, except that in reefs the influence of flanking loose sediment is more important. One example of patch reefs from the Great Barrier Reef (figure 20) has the appearance of a secondary split in the coral growth of the lip producing a form similar to microatolls that have enjoyed a period of renewed growth to a higher water level, giving a secondary microatoll plane. Whether or not it is possible to interpret recent sea level changes from the surface morphology of patch reefs just as we can determine pond level changes by using the surface and internal configurations of microatolls remains to be seen.

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Appendix: Determination of a collection of coral microatoll specimens from the northern Great Barrier Reef

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1. Introduction

The following list is based on the coral collection made by T. P. Scoffin and D. R. Stoddart in the course of their investigation of microatoll growth in the Northern Great Barrier Reef during the Great Barrier Reef Expedition in 1973. The specimens are all taken from microatolls of the reef flats between Cairns and Cape Melville and are intended to be representative of the range of reef flat species observed to grow in this form, within the localities visited by the Expedition.

Table A1. Numbers of microatoll specimens collected from each locality, with species and genera data

locality	position		no. of specimens collected	no. of scleractinian genera and subgenera collected	no. of non-scleractinian genera collected	no. of scleractinian species collected	no. of non-scleractinian species collected
	lat. S	long. E					
East Hope I.	15° 00′	145° 27′	1	0	1	0	1
Larks Pass Reef	15° 08′	145° 43′	1	0	1	0	1
Nymph I. lagoon	14° 39′	145° 15′	1	1	0	1	0
Three Is	15° 07′	145° 25′	3	3	1	3	1
Turtle IV I.	14° 43′	145° 12′	38	18	1	28	1
Two Is, east side	15° 01′	145° 26′	1	1	0	1	0
Two Is, west side	15° 01′	145° 27′	12	9	0	11	0
Watson I.	14° 28′	144° 54′	13	9	1	11	1
West Hope I.	15° 45′	145° 26′	2	2	0	2	0
totals for this collection			**72**	**22**	**3**	**40**	**3**

In preparing this list, I have accepted the collectors' concept of what constitutes a microatoll, but it is useful to draw attention to the fact that, in addition to the usual massive forms, branching and foliaceous corals are also included. The diagnostic feature for microatolls formed by non-massive species is that an imaginary surface defined by the outermost growth limits of their heads should have the same form as a massive microatoll, i.e. a living lateral margin with a dead or partially dead upper surface. From this, and the species listed here, it would appear that a very wide range of reef flat corals are potential microatoll builders. Probably it is only the laminar encrusting species and the free-living fungiids that are to be excluded. For the same reason, the list cannot be regarded as a check list of all microatoll builders, as one might predict that additional species are to be found with this growth form, especially among the poritids and faviids.

In the check list I have indicated the basis of the determinations under the heading 'Reference' for each specimen. I have given a published work or works and in instances where there is relevant material in the collections of the British Museum (Natural History) I have also cited particular specimens. In this way, I have intended to convey whose species concept I have followed for each determination. I believe this to be especially helpful in the great problematic genera like *Acropora* and *Porites*. As I have not given full synonymies, it follows that concepts of authors not cited are not necessarily excluded. The classification used is that by Wells (1956). The specimen numbers throughout are register numbers of the Department of Zoology, British Museum (Natural History), where the microatoll specimens are now placed. They consist entirely of dried material.

Geographical positions of the localities given for the specimens are listed in table A1, together with the number of specimens, genera and species collected at each one. The highly selective nature of the collection makes zoogeographic comment inappropriate. None of the coral genera listed is new to the Great Barrier Reef region. All but *Goniastrea* are listed by Wells (1955), this genus having evidently been accidentally omitted. Wells listed it in his earlier table of Indo-Pacific distribution (1954). Indication of new records at species level is of doubtful value at the moment, because of the uncertain status of so many coral species names. The excellent work begun by Veron & Pichon (1976) will eventually provide a proper picture of species distribution for the whole region. Such remarks as have been made here are restricted to those genera which have been treated so far in their currently published results of this project (above). It may be inferred from the present list that unless there are remarks to the contrary, species in the genera *Psammocora* and *Pocillopora* are already known from the Cairns–Cape Melville region.

I should like to thank Ms J. G. Darrell for her assistance in this work, and Dr Michel Pichon (James Cook University of North Queensland) for checking the manuscript.

2. Determinations

class Anthozoa Ehrenberg, 1834
subclass Zoantharia de Blainville, 1830
order Scleractinia Bourne, 1900
suborder Astrocoeniina Vaughan & Wells, 1943
family Thamnasteriidae Vaughan & Wells, 1943
genus *Psammocora* Dana, 1846

Psammocora contigua (Esper)

Reference: Veron & Pichon (1976)

Material: Turtle IV I. (1976.3.1.183)

Psammocora digitata (Edwards & Haime)

Reference: Veron & Pichon (1976) and synonymy.

Remarks: Veron & Pichon regard the subgenera of *Psammocora* as recognized by previous authors as indistinguishable. This species has previously been placed in *Psammocora* (*Stephanaria*) as the synonyms *P. togianensis* and *P. exaesa*. Not previously recorded between Cairns and Cape Melville.

Material: Turtle IV I. (1976.3.1.65)

family Pocilloporidae Gray, 1842
genus *Pocillopora* Lamarck, 1816

Pocillopora damicornis (Linnaeus)

Reference: Veron & Pichon (1976)

Material: Turtle IV I. (1976.3.1.44); Two Is, west side (1976.3.1.20, 1976.3.1.30).

family Acroporidae Verrill, 1902
genus *Acropora* Oken, 1815

Acropora corymbosa (Lamarck)

Reference: Brook's (1893) *Madrepora corymbosa* specimen (1845.18.12.11)

Material: Turtle IV I. (1976.3.1.55)

Acropora cuneata (Dana)

Reference: Wells (1954)

Material: Turtle IV I. (1976.3.1.46)

Acropora cf. *cymbicyathus* (Brook)

Reference: Wells (1954)

Remarks: The present specimen differs from Wells's material probably in consequence of its habitat. There are too few well developed branches to be certain of complete identity. Brook's type is not available for examination at the B.M.(N.H.) because his species is in fact a nom.nov. for Ortmann's *Madrepora cerealis* Dana, said to be in the Strasburg Museum.

Material: Turtle IV I. (1976.3.1.43)

Acropora palifera (Lamarck)

Reference: Wells (1954)

Material: Turtle IV I. (1976.3.1.59); Two Is, west side (1976.3.1.23).

Acropora cf. *rosaria* (Dana)

References: Wells's (1954) and Crossland's (1952) specimens (1934.5.14.40 (= G.B.R.E. No. 368), 1934.5.14.357 (= G.B.R.E. No. 108)).

Remarks: The growth form of the present specimen hinders more certain determination.

Material: Turtle IV I. (1976.3.1.54)

Acropora squamosa (Brook)

Reference: Crossland's (1952) specimen (1934.5.14.361 (= G.B.R.E. No. 107)) but not necessarily other material of Crossland and Brook (1893).

Material: Two Is, west side (1976.3.1.22)

Acropora valida (Dana)

Reference: Wells (1954) and Brook's (1893) specimens of *Madrepora valida* (e.g. 1893.4.7.118).

Material: Three Is (1976.3.1.13).

genus *Montipora* de Blainville, 1830

Montipora hispida (Dana)

Reference: Bernard (1897)

Material: Turtle IV I. (1976.3.1.47)

suborder Fungiina Duncan, 1884
superfamily Agariciicae Gray, 1847
family Agariciidae Gray, 1847
genus *Pavona* Lamarck, 1801
subgenus *Pavona* Lamarck, 1801

Pavona (*Pavona*) *danai* (Edwards & Haime)

Reference: Vaughan (1918)

Material: Turtle IV I. (1976.3.1.62)

Pavona (*Pavona*) *explanulata* Lamarck

Reference: Vaughan (1918)

Remarks: See also *P. duerdeni* Vaughan and *P. diffluens* Lamarck.

Material: Turtle IV I. (1976.3.1.67)

subgenus *Polyastra* Ehrenberg, 1834

Pavona (*Polyastra*) *obtusata* (Quelch)

References: Quelch's (1886) type (1886.12.9.162) and second specimen (1886.12.9.163), and Wells (1936).

Material: Turtle IV I. (1976.3.1.32)

genus *Coeloseris* Vaughan, 1918

Coeloseris mayeri Vaughan

Reference: Vaughan (1918)

Material: Watson I. (1976.3.1.6, 1976.3.1.11)

superfamily Poriticae Gray, 1842
family Poritidae Gray, 1842
genus *Goniopora* de Blainville, 1830

Goniopora cf. *tenuidens* (Quelch)

References: Quelch's (1886) type (1886.12.9.304) and second specimen (1886.12.9.308), Vaughan (1918), and Bernard's *Goniopora* 'Great Barrier Reef (12)4' (1892.12.1.542).

Remarks: Present specimens differ from the above material in having radial wall elements which are thicker than septal elements. The corallites appear like neat 'punctures' in the corallum surface, a character not really seen in the reference specimens. Vaughan (1918) suggested that Bernard's 'Great Barrier Reef (12) 4' and '(12) 5' probably belong with Quelch's species. The first of these does; the second does not. Crossland's (1952) *G. tenuidens* (1934.5.14.498) is certainly different from the reference material, and at present should be excluded from Quelch's species. There is a great variation in corallite depth in these corals. Very shallow corallites are developed on what were the downward facing surfaces of 1976.3.1.63, as orientated in life position. This may be a regular character in this species, or even the genus.

Material: Nymph I., lagoon (1976.3.1.18); Turtle IV I. (1976.3.1.64).

genus *Porites* Link, 1807
subgenus *Porites* Link, 1807

Porites (*Porites*) *andrewsi* Vaughan

Reference: Vaughan (1918)

Material: Two Is, west side (1976.3.1.21)

Porites (*Porites*) *compressa* Dana

Reference: Vaughan (1907)

Material: Turtle IV I. (1976.3.1.39, 1976.3.1.51); Two Is, east side (1976.3.1.24).

Porites (*Porites*) *lutea* Edwards & Haime

Reference: Vaughan (1918)

Material: Turtle IV I. (1976.3.1.61, 1976.3.1.67); West Hope I. (1976.3.1.1).

Porites (*Porites*) *mayeri* Vaughan
Reference: Vaughan (1918)
Material: Watson I. (1976.3.1.4)

Porites (*Porites*) *nigrescens* Dana
Reference: Vaughan (1918)
Material: Two Is, west side (1976.3.1.25)

subgenus *Synaraea* Verrill, 1864

Porites (*Synaraea*) *iwayamaensis* Eguchi
Reference: Wells (1954)
Material: Turtle IV I. (1976.3.1.40, 1976.3.1.53)

suborder Faviina Vaughan & Wells, 1943
superfamily Faviicae Gregory, 1900
family Faviidae Gregory, 1900
subfamily Faviinae Gregory, 1900
genus *Favia* Oken, 1815

Favia favus (Forskål)
Reference: Rosen (1968)
Material: Turtle IV I. (1976.3.1.50, 1976.3.1.58, 1976.3.1.66)

Favia pallida (Dana)
Reference: Vaughan (1918)
Material: Turtle IV I. (1976.3.1.35, 1976.3.1.45); Two Is, west side (1976.3.1.16); Watson I. (1976.3.1.7, 1976.3.1.70).

genus *Favites* Link, 1807

Favites abdita (Ellis & Solander)
Reference: Wijsman-Best (1972)
Material: Three Is (1976.3.1.26); Turtle IV I. (1976.3.1.34, 1976.3.1.36, 1976.3.1.57); Two Is, west side (1976.3.1.19); Watson I. (1976.3.1.3, 1976.3.1.7).

Favites acuticollis (Ortmann)
Reference: Wijsman-Best (1972)
Material: Turtle IV I. (1976.3.1.37)

genus *Oulophyllia* Edwards & Haime, 1848

Oulophyllia crispa (Lamarck)
Reference: Wijsman-Best (1972)
Material: Watson I. (1976.3.1.69)

genus *Goniastrea* Edwards & Haime, 1848

Goniastrea australensis (Edwards & Haime)
Reference: Wijsman-Best (1972)
Material: Watson I. (1976.3.1.5)

Goniastrea palauensis (Yabe & Sugiyama)
Reference: Wijsman-Best (1972)
Material: Turtle IV I. (1976.3.1.61)

Goniastrea retiformis (Lamarck)
Reference: Wijsman-Best (1972)

Material: Three Is (1976.3.1.15); Turtle IV I. (1976.3.1.31, 1976.3.1.49); Watson I. (1976.3.1.10, 1976.3.1.68).

genus *Platygyra* Ehrenberg, 1834

Platygyra daedalea (Ellis & Solander)
Reference: Wijsman-Best (1972)
Material: Turtle IV I. (1976.3.1.33, 1976.3.1.41, 1976.3.1.48, 1976.3.1.56); Watson I. (1976.3.1.71); West Hope I. (1976.3.1.2).

Platygyra lamellina (Ehrenberg)
Reference: Wijsman-Best (1972)
Material: Two Is, west side (1976.3.1.29)

Platygyra sinensis (Edwards & Haime)
Reference: Wijsman-Best (1972)
Material: Watson I. (1976.3.1.9)

genus *Leptoria* Edwards & Haime, 1848

Leptoria phrygia (Ellis & Solander)
Reference: Wijsman-Best (1972)
Material: Turtle IV I. (1976.3.1.42)

genus *Hydnophora* Fischer de Waldheim, 1807

Hydnophora cf. *microconos* (Lamarck)
Reference: Wijsman-Best (1972)
Remarks: The character of the corallites is consistent with *H. microconos*, but the growth form is encrusting as in *H. exesa*.
Material: Two Is, west side (1976.3.1.27)

subfamily Montastreinae Vaughan & Wells, 1943

genus *Echinopora* Lamarck, 1816

Echinopora lamellosa (Esper)
Reference: Matthai (1914)
Material: Turtle IV I. (1976.3.1.60)

family Oculinidae Gray, 1847

subfamily Galaxeinae Vaughan & Wells, 1943

genus *Galaxea* Oken, 1815

Galaxea fascicularis (Linnaeus)
Reference: Matthai (1914)
Material: Turtle IV I. (1976.3.1.63)

family Mussidae Ortmann, 1890

genus *Lobophyllia* de Blainville, 1830

subgenus *Lobophyllia* de Blainville, 1830

Lobophyllia corymbosa (Forskål)
Reference: Matthai (1928)
Material: Two Is, west side (1976.3.1.17)

genus *Symphyllia* Edwards & Haime, 1848

Symphyllia nobilis (Dana)

Reference: Wells (1954)

Material: Turtle IV I. (1976.3.1.52); Two Is, west side (1976.3.1.28), Watson I. (1976.3.1.72).

suborder Dendrophylliina Vaughan & Wells, 1943
family Dendrophylliidae Gray, 1847
genus *Turbinaria* Oken, 1815

Turbinaria cf. *mesenterina* (Lamarck)

References: Bernard's (1896) specimen (1876.5.5.40), Yabe & Sugiyama (1941).

Remarks: Corallites of the present specimen are slightly smaller than in Bernard's specimen, and the coenosteum is finer and denser. Bernard's remark that *T. mesenterina* has 'very inconspicuous' septa is not correct. The above specimen of his has now been cleaned of dried soft tissue.

Material: Turtle IV I. (1976.3.1.38).

subclass Alcyonaria de Blainville, 1830
order Stolonifera Hickson, 1883
family Tubiporidae Edwards & Haime, 1857
genus *Tubipora* Linnaeus, 1758

Tubipora musica Linnaeus

Material: Larks Pass Reef (1976.3.1.14)

Order Coenothecalia Bourne, 1900
family Helioporidae Moseley, 1876
genus *Heliopora* de Blainville, 1834

Heliopora coerulea (Pallas)

Reference: Wells (1954)

Material: East Hope I. (1976.3.1.12)

class Hydrozoa Huxley, 1856
order Milleporina Hickson, 1899
family Milleporidae de Blainville, 1834
genus *Millepora* Linnaeus, 1758

Millepora platyphylla Hemprich & Ehrenberg

Reference: Wells (1954)

Material: Three Is (1976.3.1.15); Turtle IV I. (1976.3.1.67); Watson I. (1976.3.1.72).

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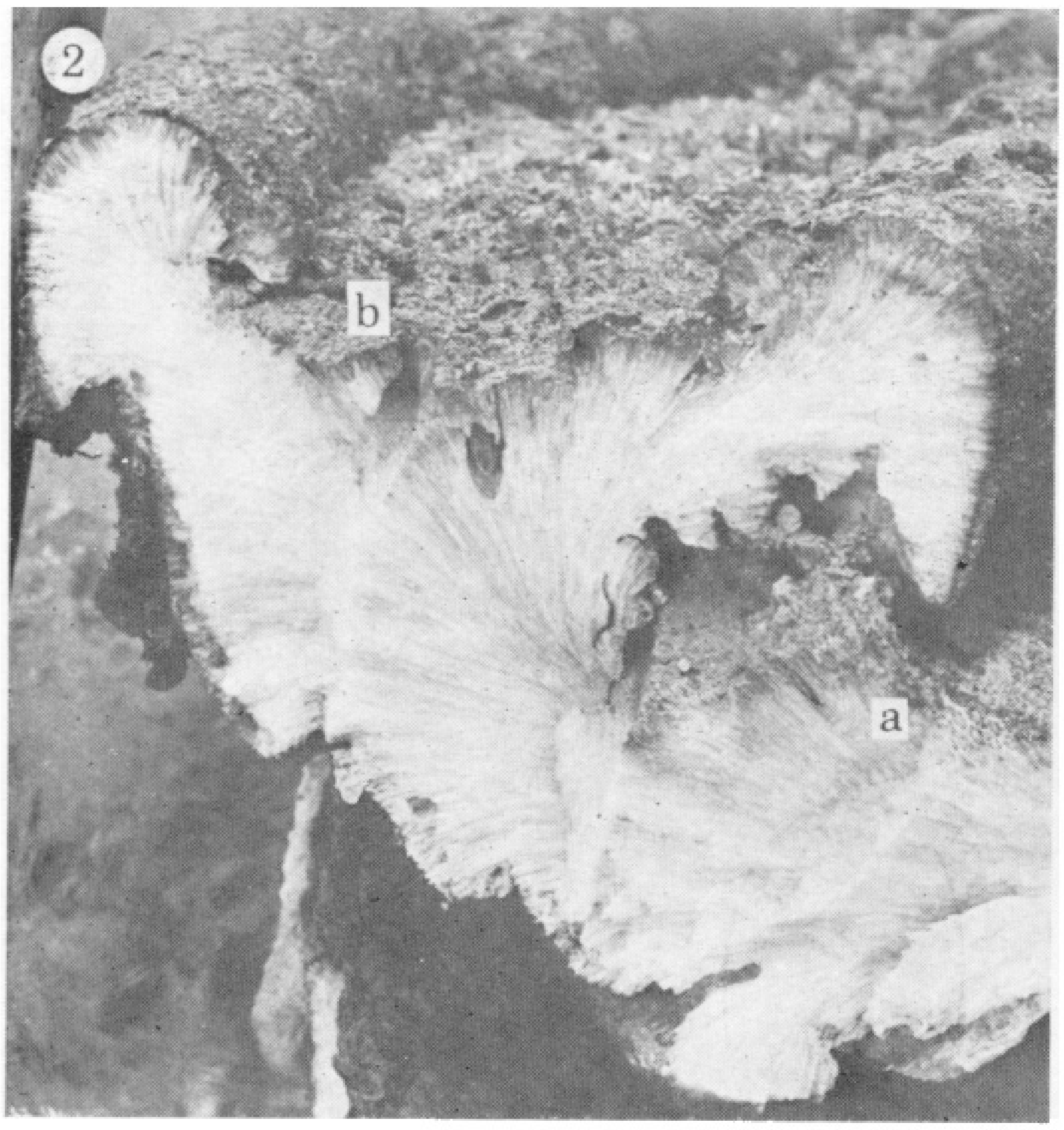
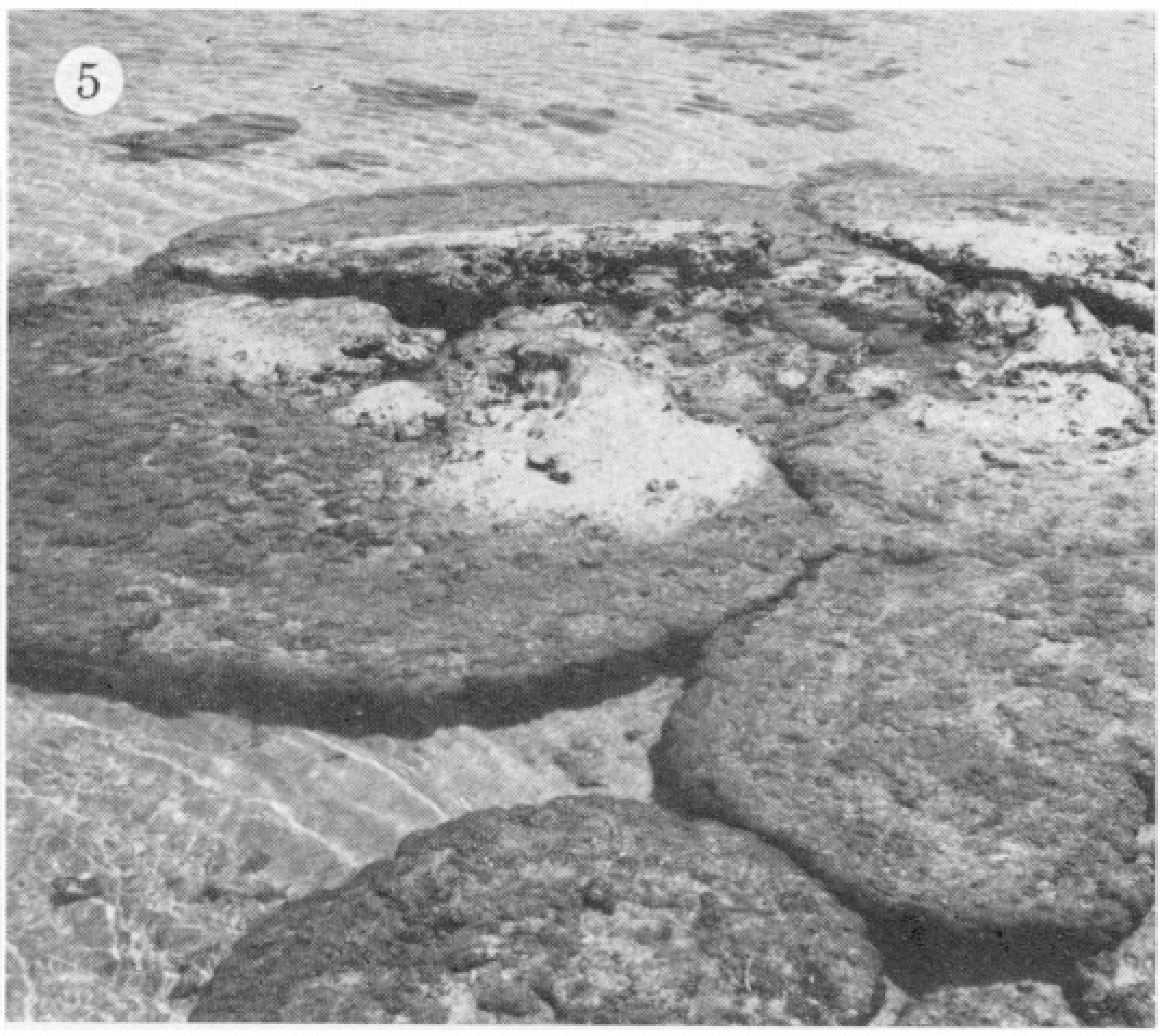
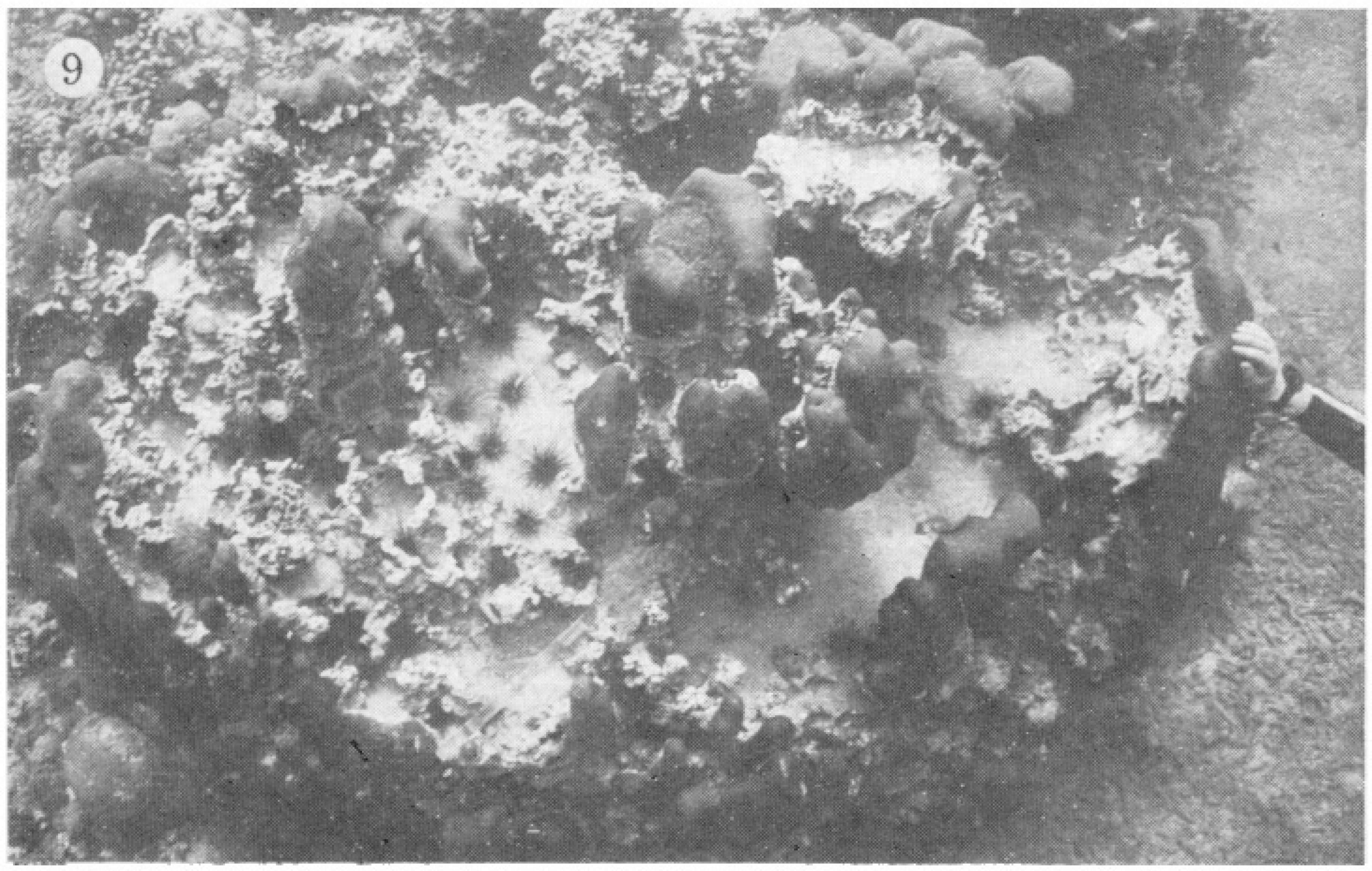
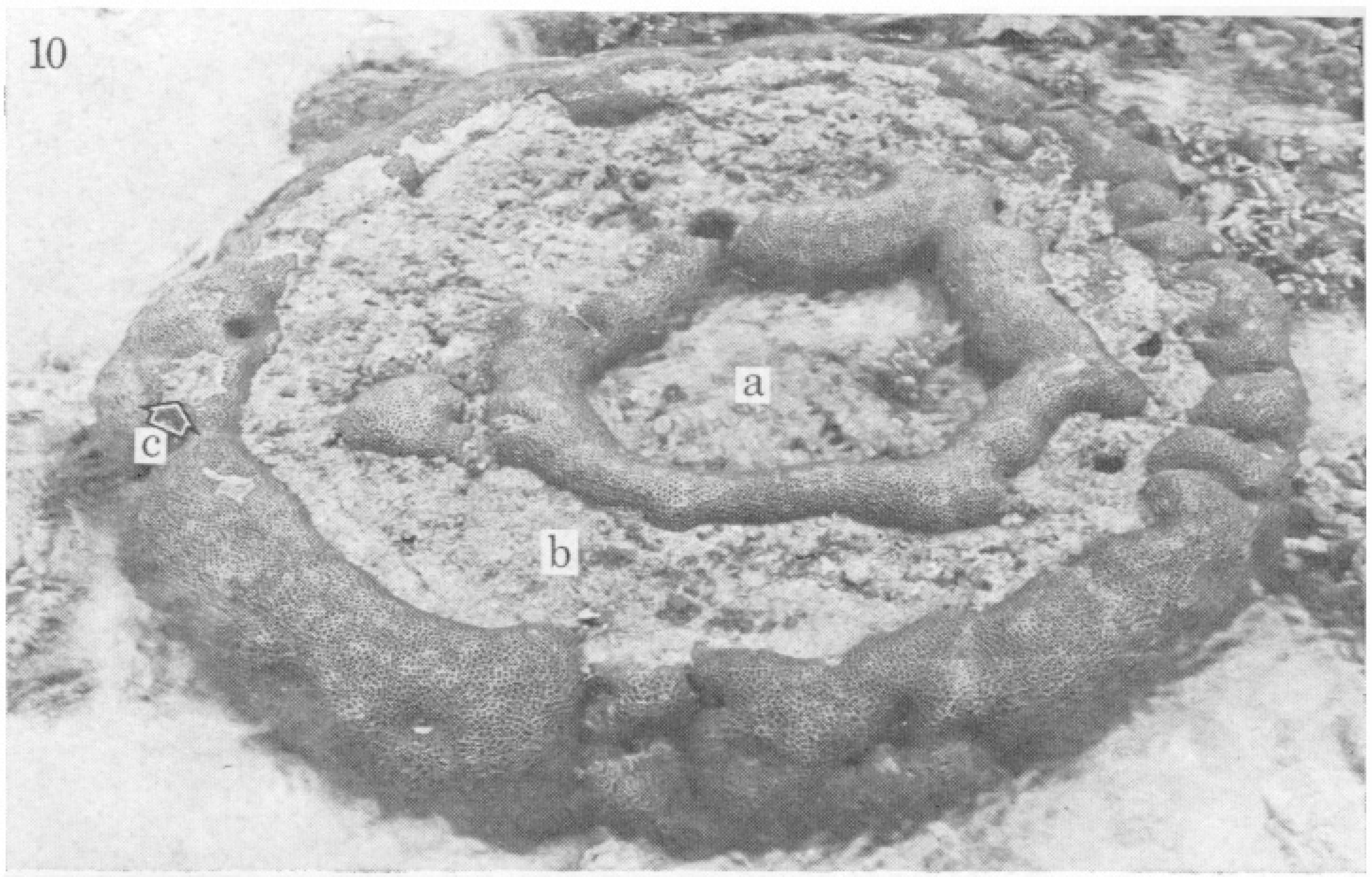
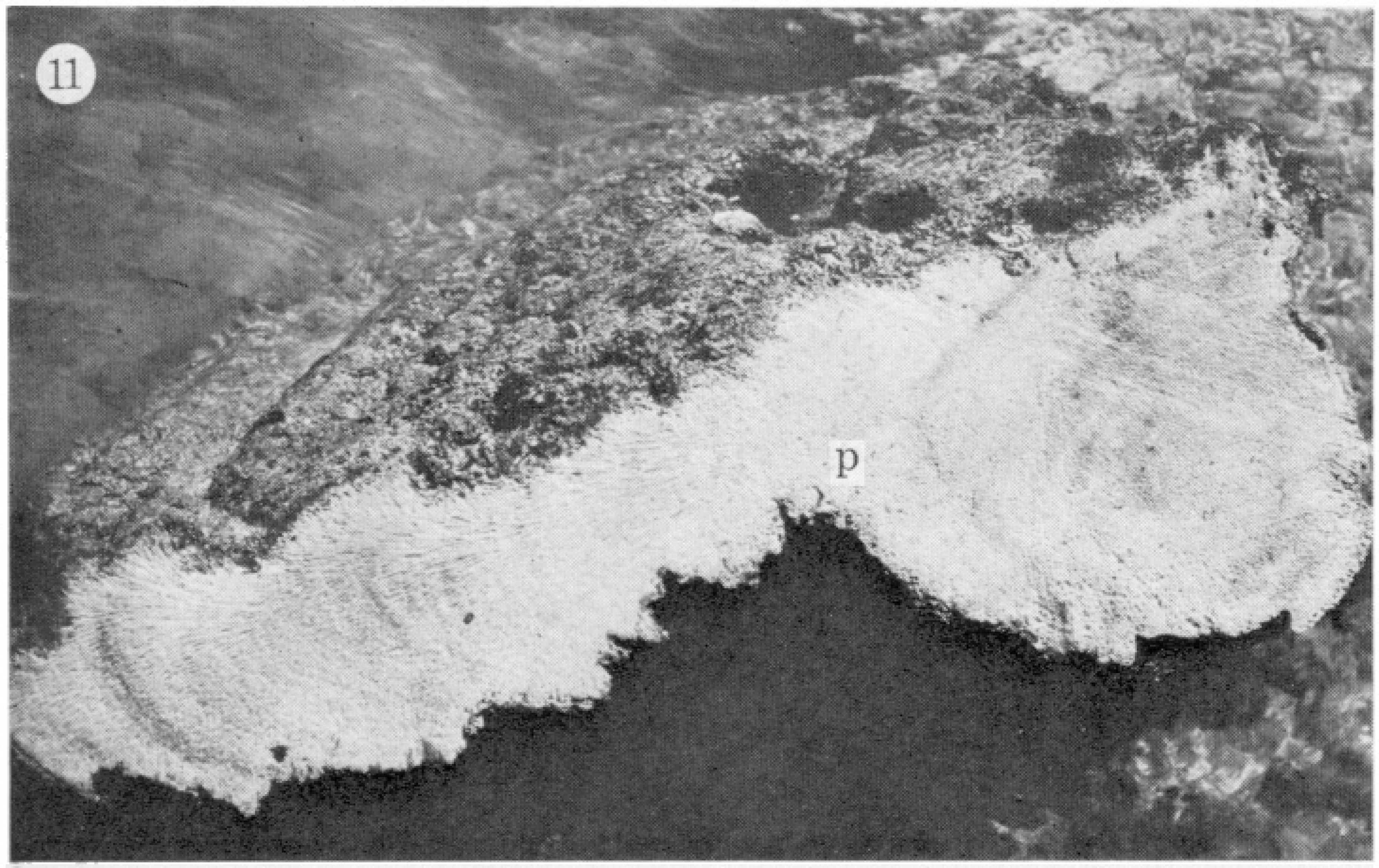


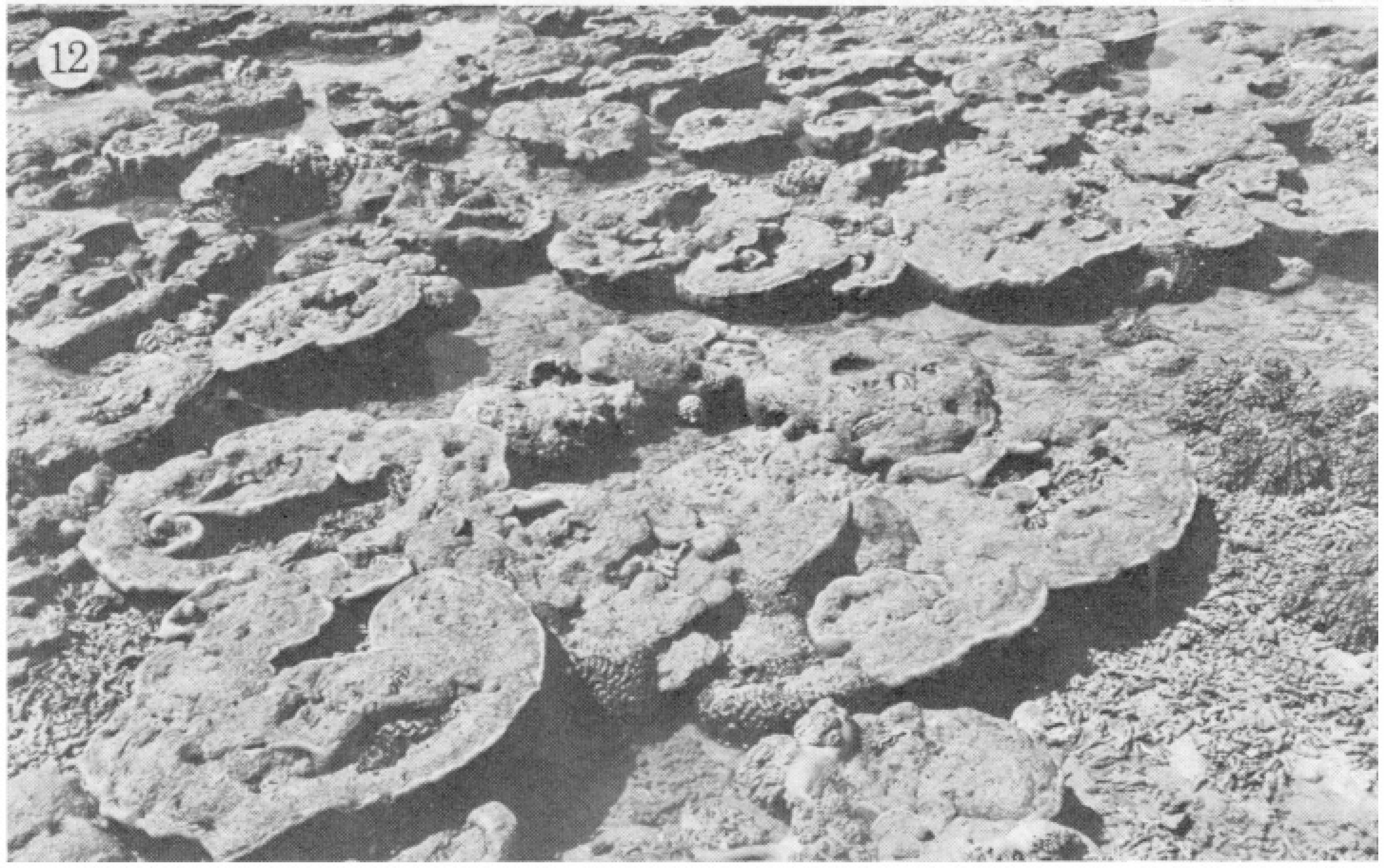


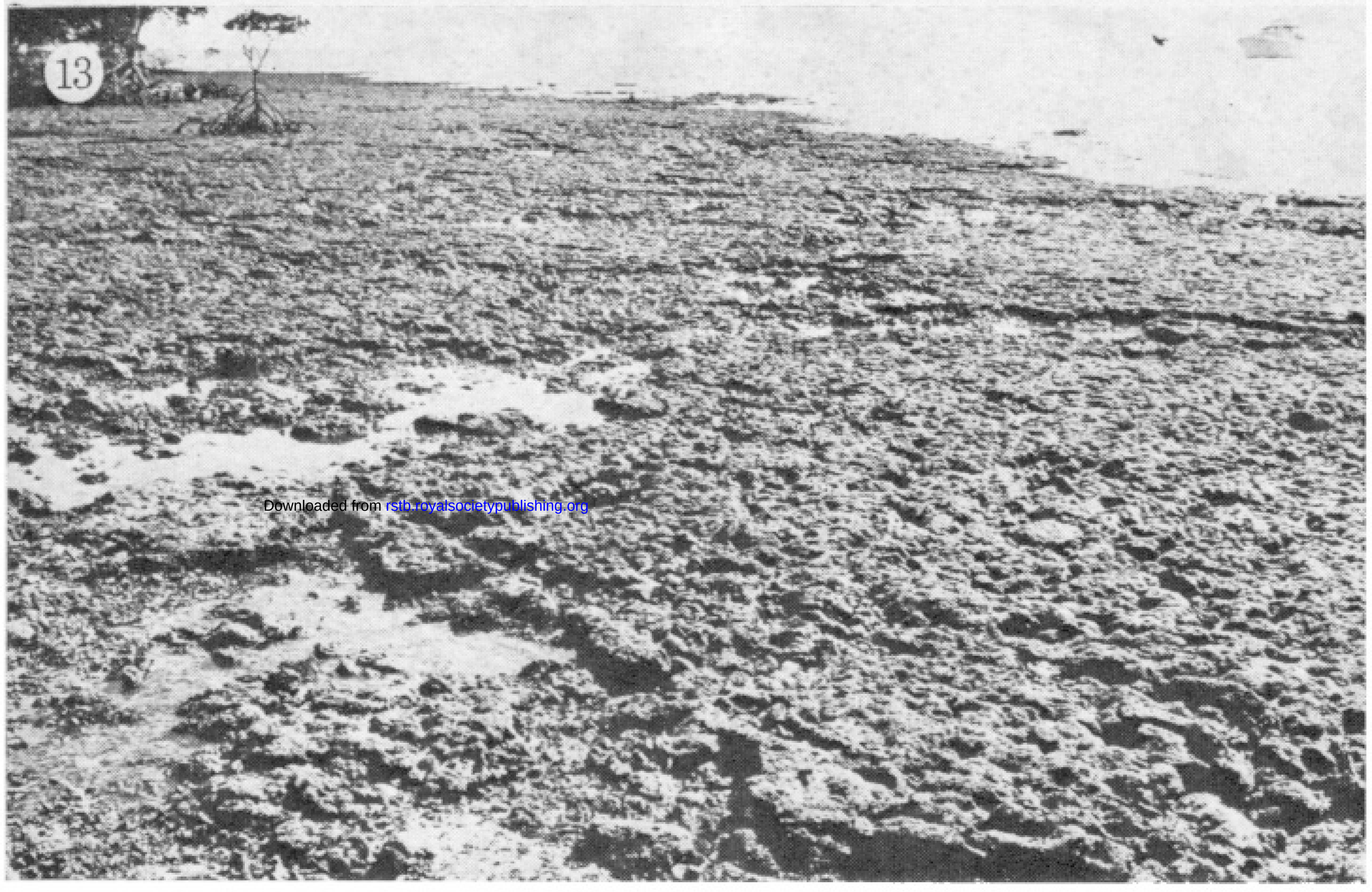
FIGURES 2–7. For description see opposite.











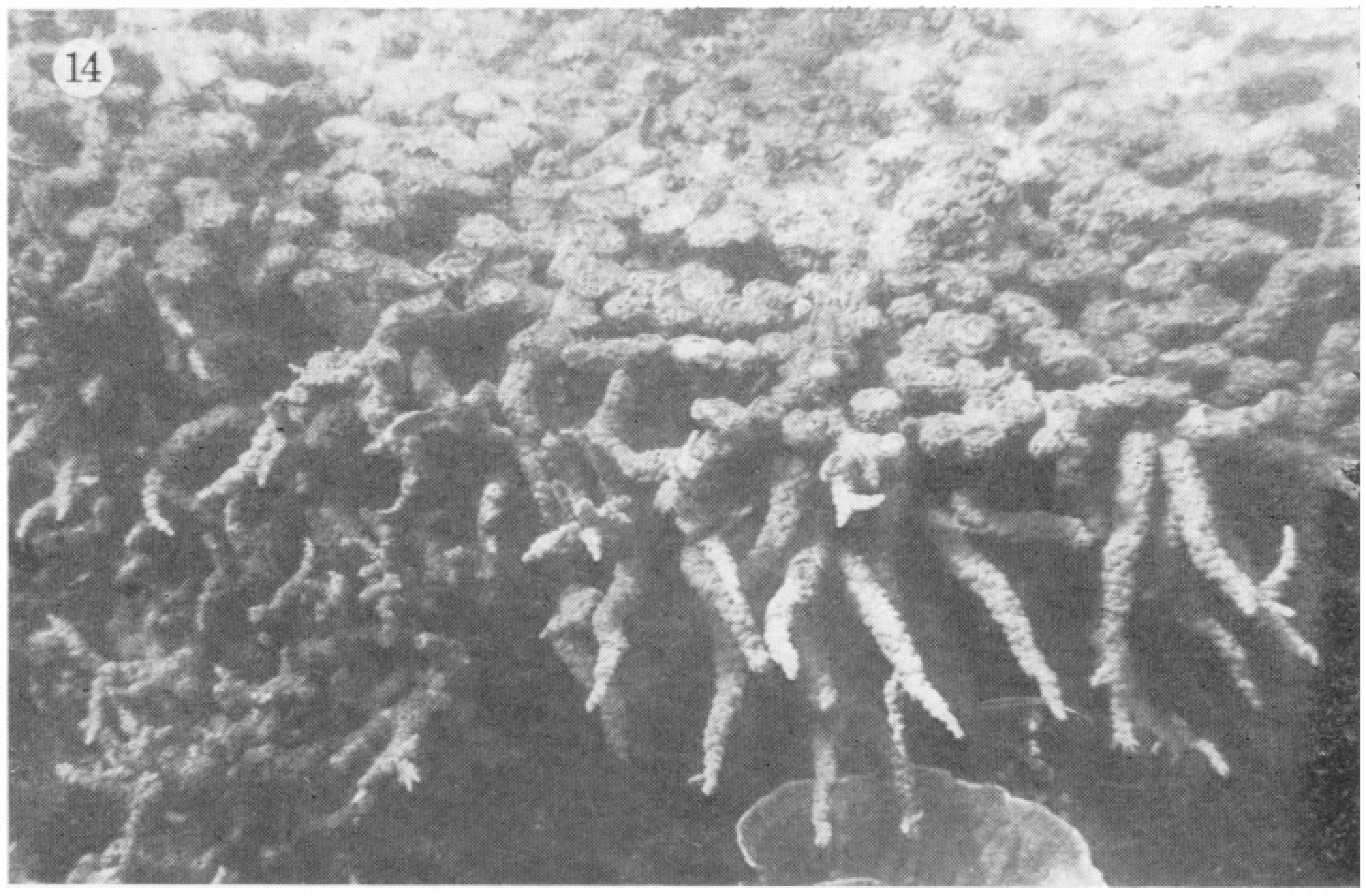


FIGURE 9. Underwater photograph of a living massive *Montastrea annularis* that has had its upper surface extensively grazed by *Diadema antillarum* sea urchins. The upper surface of this coral is at a depth of 2 m below low water level. Bellairs reef, Barbados, W.I.

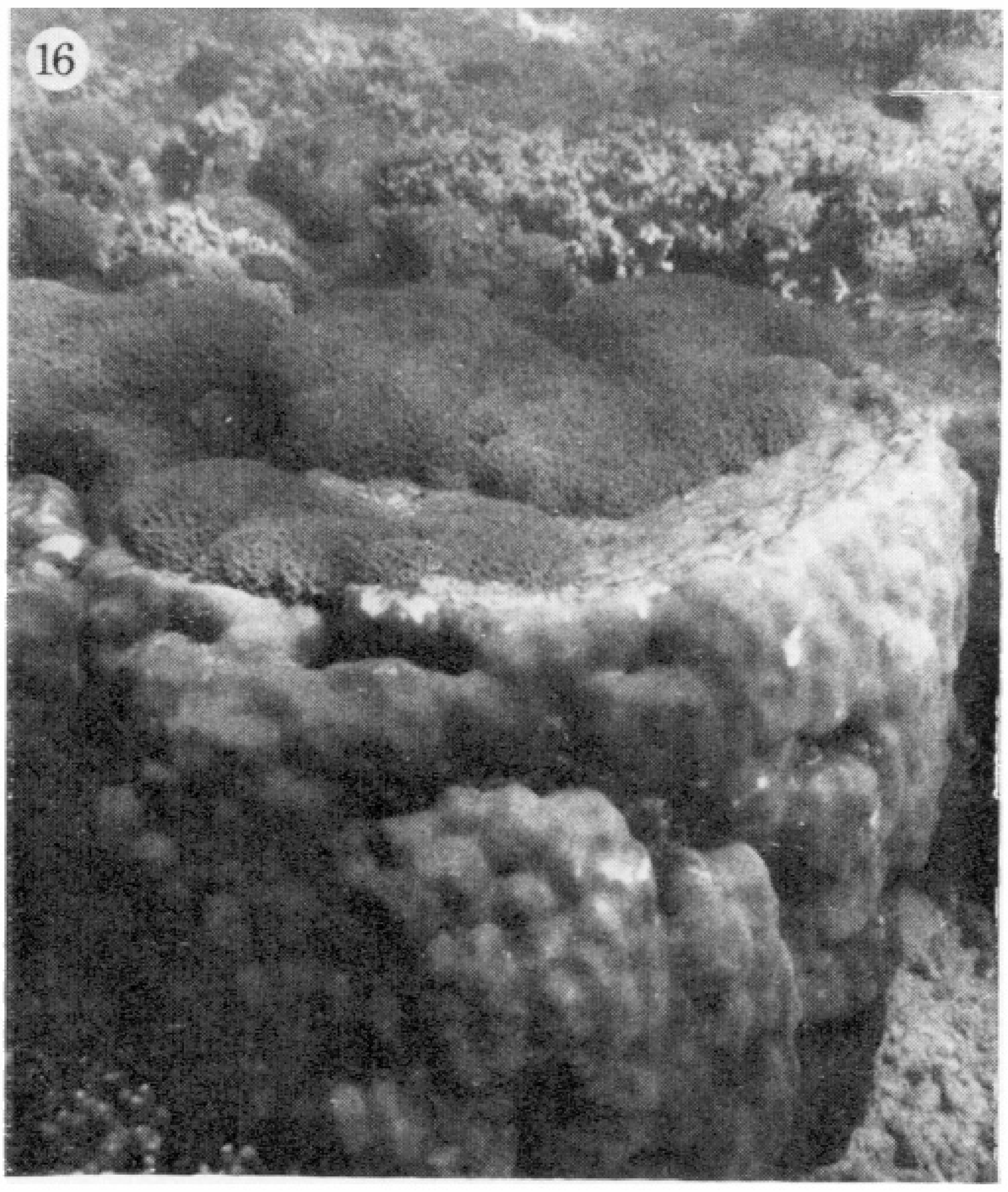
FIGURE 10. *Platygyra* microatoll 1.5 m in diameter showing development of primary (a), secondary (b) and incipient tertiary (c) microatoll planes. Reef flat, Two Isles, Great Barrier Reef.

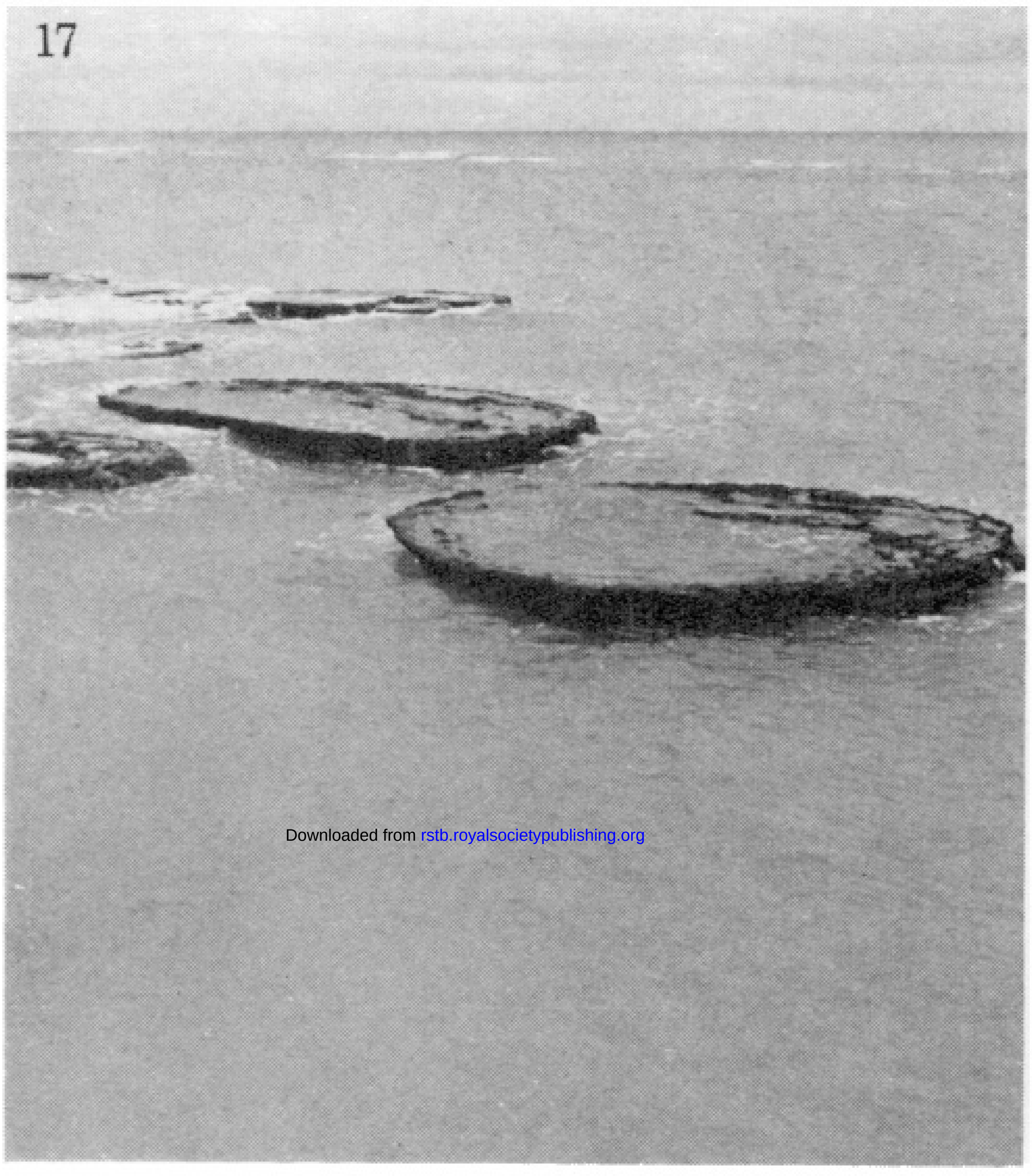
FIGURE 11. Sawed vertical section of half of a microatoll. The right side of the photograph shows the region of early development of the colony, the extreme left of the coral is the living margin. Arcuate growth bands can just be detected. The coral started growth in water about 20 cm deep but after a time (at position p) the sand level was raised to about 10 cm below the water surface. Subsequently, sand level fluctuated slightly to produce the saw-tooth profile at the base of the coral. The water level was roughly constant throughout. Reef flat, Nymph Isle, Great Barrier Reef.

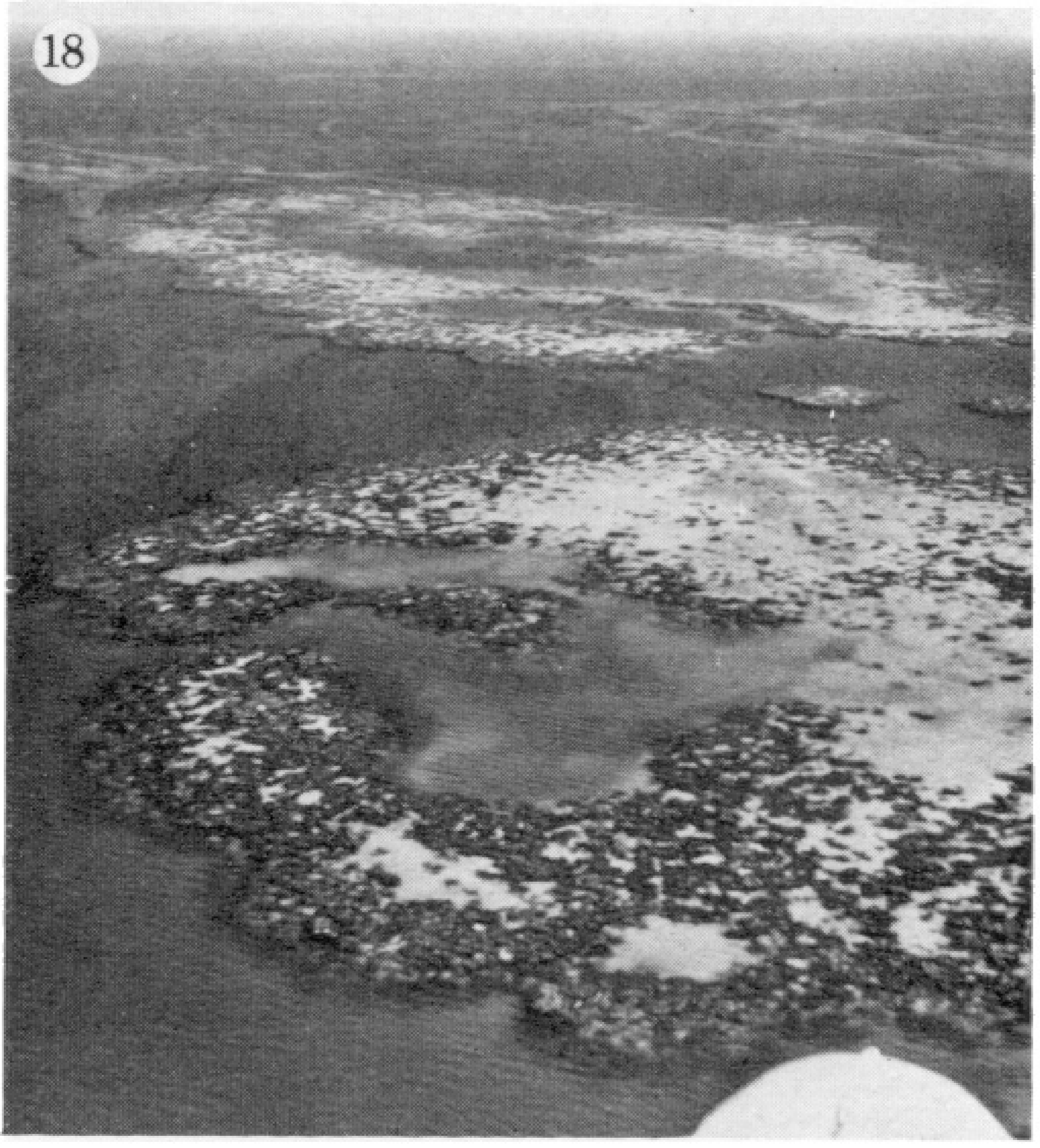
FIGURE 12. Microatolls (dominantly *Goniastrea*) with inclined upper surfaces resulting from prevailing flow of water from right to left. Photograph taken at extreme low tide leeward margin of reef flat. Low Isles, Great Barrier Reef. Foreground 3 m wide.

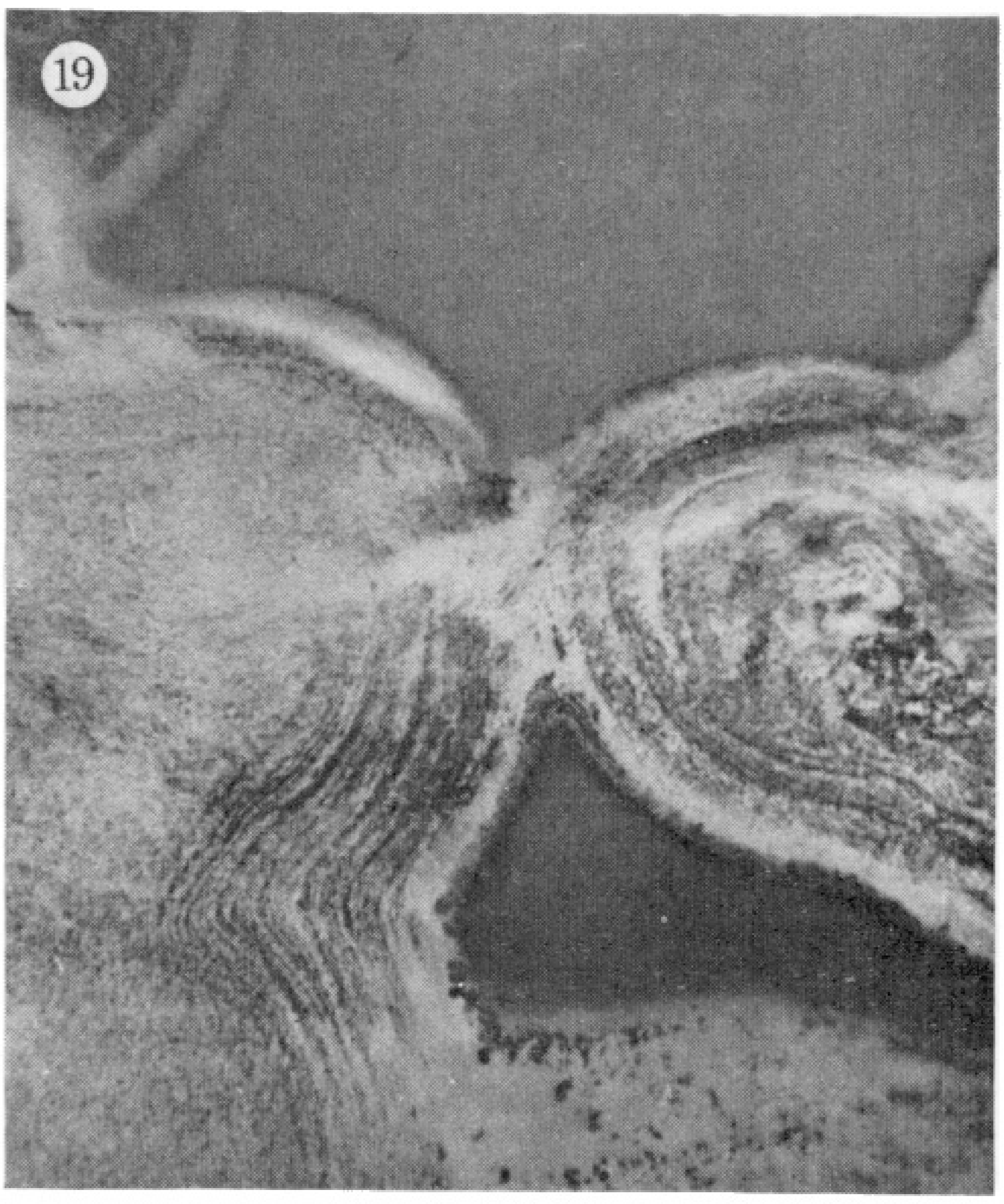
FIGURE 13. Northeast margin of reef flat at Hampton Isle, Howick Group, Great Barrier Reef, showing the broad flat pavement consisting chiefly of the surfaces of dead and living microatolls. Foreground of photograph is 5 m wide.

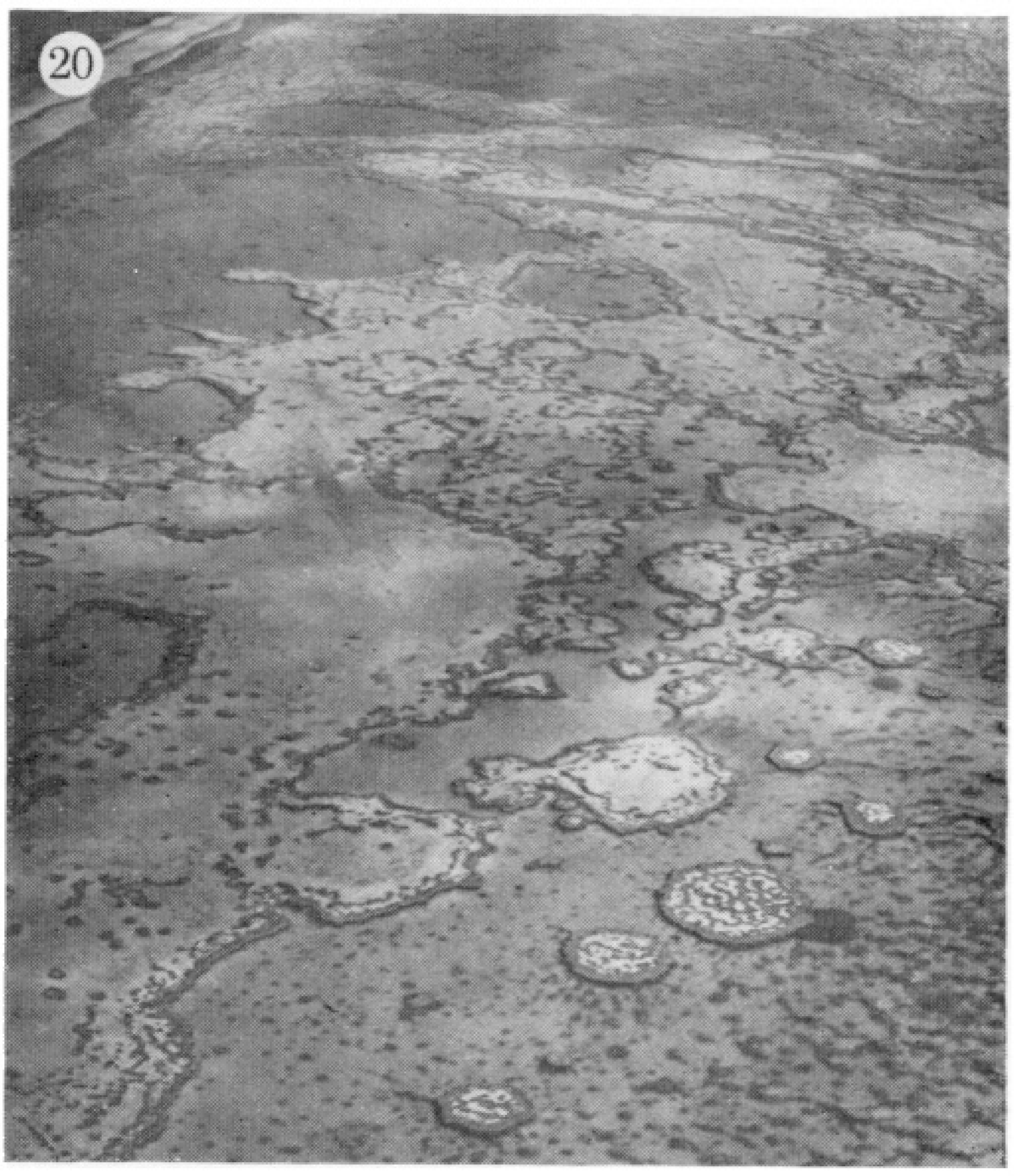
FIGURE 14. Underwater photograph of colony of branching *Acropora* coral that grows in open water up to the level of low water springs. At the maximum elevation for growth, branches become flattened, stubby and dense. Leeward side of East Hope Island, Great Barrier Reef.



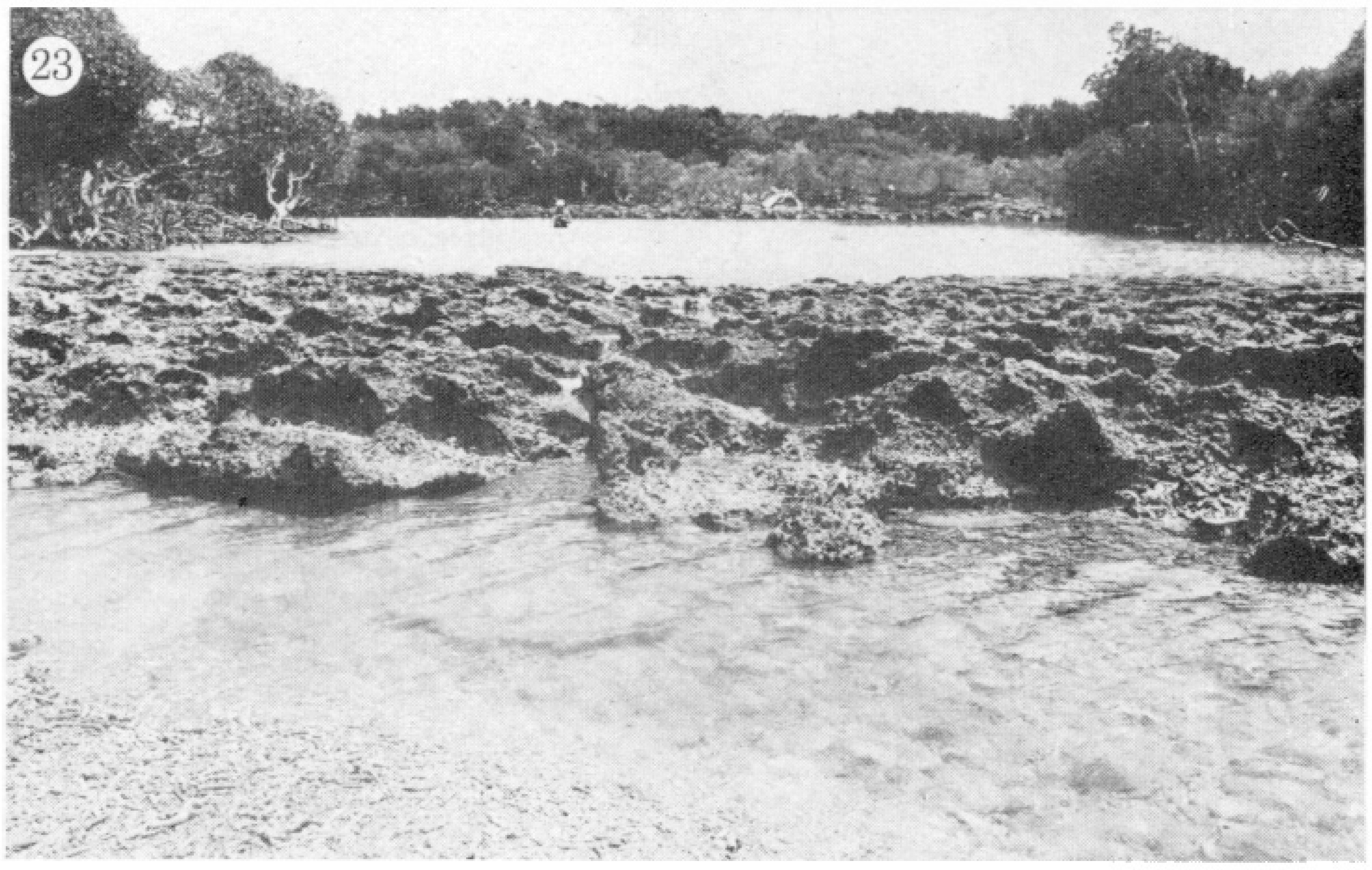


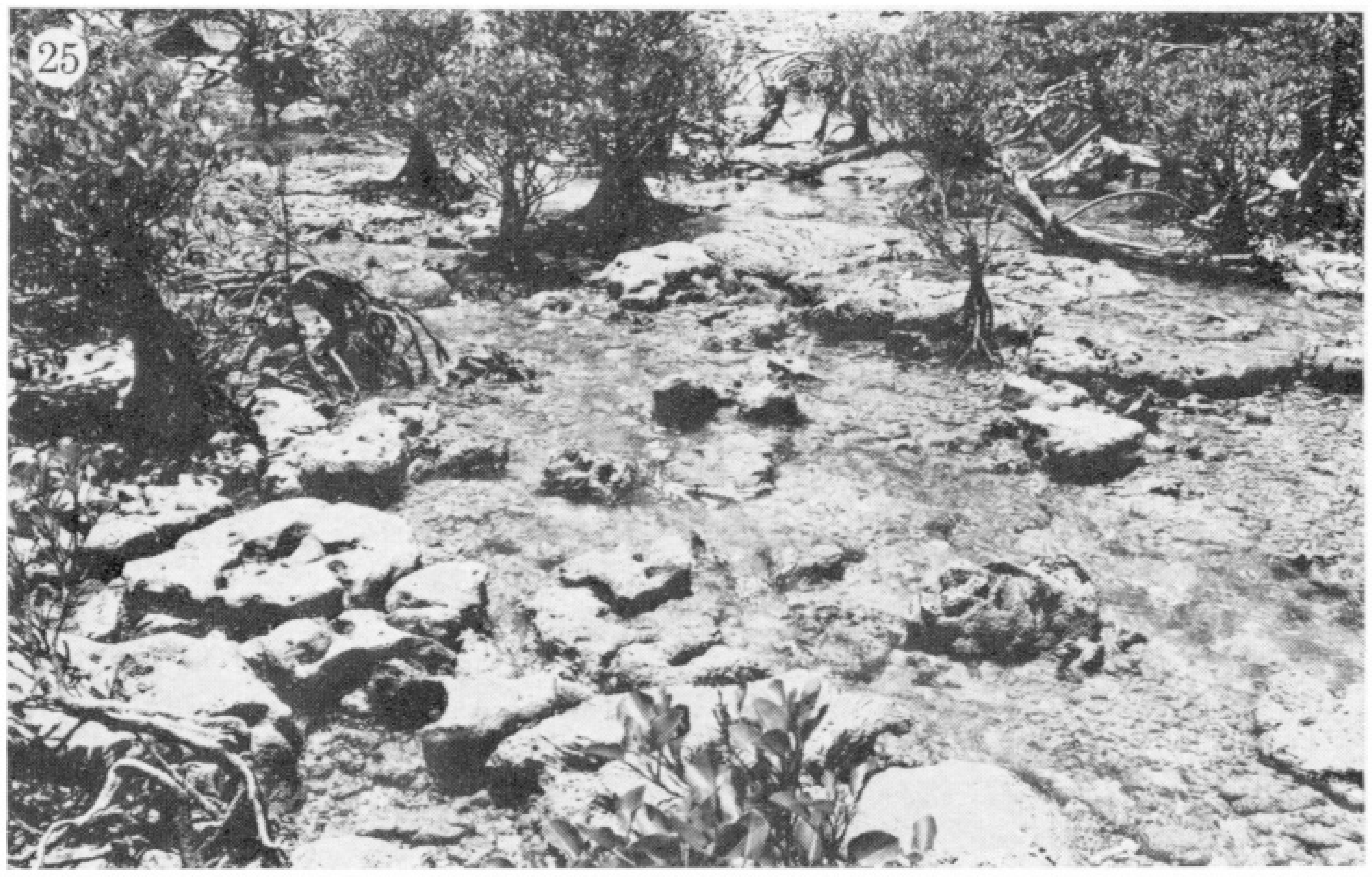


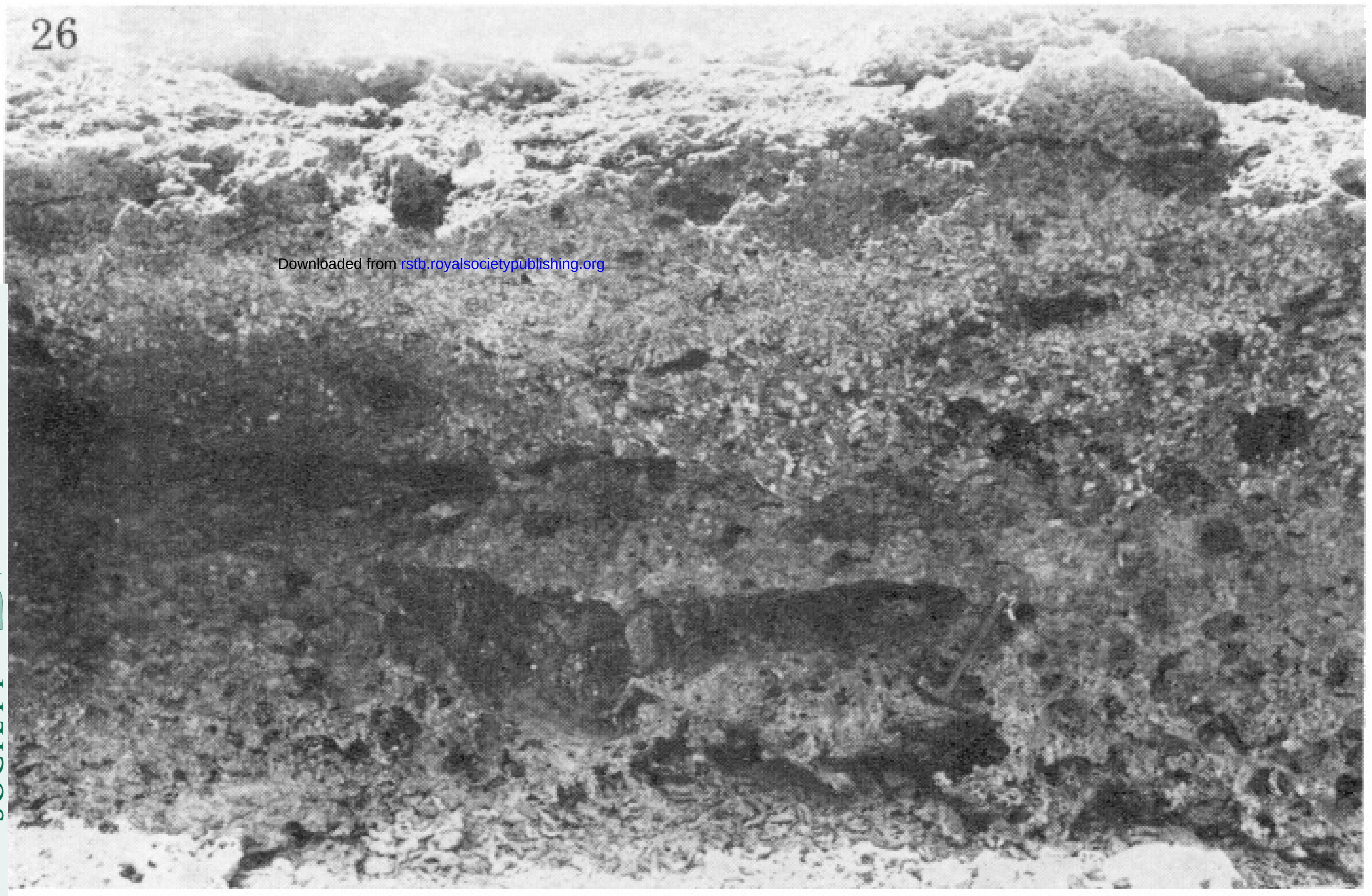




FIGURES 15–20. For description see page 105.







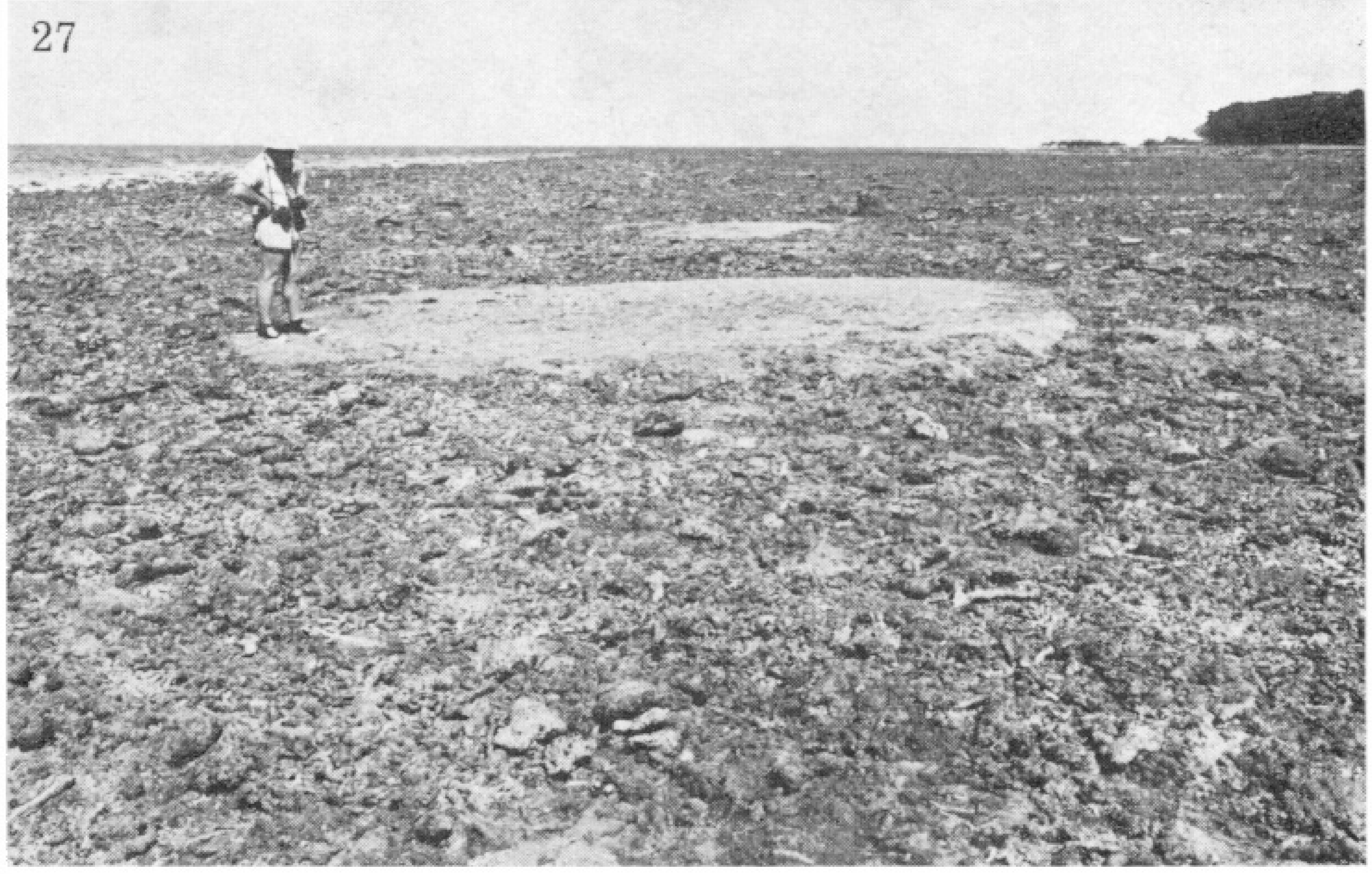


Figure 22. Windward margin of Watson Reef, Great Barrier Reef. The open water, at the right of the photograph, is at a lower level than the water in the moat retained by the rampart of loose coral shingle. Width of moat is about 6 m.

Figure 23. Two levels of ponded water. The higher pond, in the background, is retained by a wall of cemented shingle (the jagged projections represent eroded lithified foresets), the lower pond, in the foreground is retained by a rampart of loose coral shingle. Microatolls currently live up to the water surface in both these ponds. Windward flanks Watson Reef, Great Barrier Reef.

Figure 24. In-place dead microatolls in a drained moat. The rampart (at top of photograph) that formerly ponded water here has recently been breached. Windward margin of reef flat, Nymph, Great Barrier Reef. Foreground is 4 m wide.

Figure 25. In-place fossil microatolls exposed on the reef flat on Nymph Isle, Great Barrier Reef.

Figure 26. In-place fossil microatoll (left of the hammer) exposed in section in a cliff of cemented shingle. Upper platform, Nymph Isle, Great Barrier Reef. Hammer is 30 cm long.

Figure 27. Large dead microatoll at the leeward flanks of Low Isles. The open sea to the left was at the level of low water springs at the time of photography.