

The shallow sublittoral marine ecology of Aldabra

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[Plates 11 to 14]

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The paper represents a preliminary treatment of the marine ecology of certain areas of the shallow sublittoral, mostly on West Island, on Aldabra. Seaward reefs on West Island are, for this island group, calm water localities. Detailed examinations of profiles, and additional observations, indicate that 'zones' can be recognized in the shallow sublittoral, but these 'zones' are more a function of the nature and physiography of the substrate and of the presence and density of marine Angiosperm vegetation than of the marine algae. Luxuriant marine algal flora is, on the reef-flat, found only in deep pools or channels landward of the 'reef-ridge', most commonly in the inner ridge/pool area. These circumstances seem to provide protection from direct wave action, together with adequate depth of water at all times. Similar conditions apparently apply in the area immediately lagoonward of Western Channels, where a most luxuriant 'turf' of marine algae and marine angiosperms was located. The biomass of marine vegetation there was quite outstanding for Aldabra, representing a cover of virtually 100%, with much additional growth of one species over another throughout most of the 'turf' area.

1. INTRODUCTION

The chief features of tropical shores are reef formations, mangrove and marine angiosperms. Although the present form of any particular reef may be as much a result of physical environmental (i.e. chiefly erosional) processes as of biological (i.e. chiefly accretionary) processes, the major determinant of the actual *presence* of the reef is clearly the primary biological processes involved in its existence. Therefore the chief features of tropical shores are the result of organic, rather than physical, processes, albeit in the case of reef formations in the possibly rather distant past. By definition the term 'fringing reef' should only be applied when the reef concerned is in process of active growth through abundant live corals, Lithothamnium and any other organisms the presence of which may be contributory to that growth. Thus a true fringing reef is in an active phase in which growth at least maintains the level relative to wave base. Such a reef generally possesses a clear reef-ridge marking its seaward boundary, not as is the case of the seaward reefs of Aldabra, a mass of shattered boulders or blocks of dead coral, with a zone of relatively sparse living coral seaward of it. Strictly, therefore, Aldabra fringing reefs are erosional features more accurately described as 'platforms' than as 'fringing reefs'. However, since 'reef' is such a widely used term for this type of tropical shores, whether the land is atoll in form or not, and since recent authors (see, for example, Isaac & Isaac 1968, pp. 16-17, etc.) have continued to employ the term for coastal areas of inactive coral formations such as those in Kenya, its use is maintained here on the understanding that it does not imply active accretional processes occurring at this time, or in the geologically recent past, on any large scale.

Shores on Aldabra exhibit all three chief features of tropical shores at locations on both the seaward and lagoon coasts. Reefs of widely varying widths are almost continuous along the shores, except where interrupted by mangrove (in the lagoon) or by drainage channels from the lagoon. In the case of the latter, there are associated sand spits, areas of outfall scour (and therefore of more or less bare coral rock), areas of deposit of coral detritus of varying size and areas of retention of sand/mud mixtures. Of necessity, and because a great deal of work, both taxonomic and ecological, remains to be completed, this present account is chiefly concerned with aspects of the seaward shores where reefs are present, although certain comments are made on lagoon drainage channels. Most of the presently available detailed work was carried out on West Island and much of the factual basis of this paper is therefore derived from that work. However, where apposite, comments on other parts of the atoll are made throughout, as data are available. Since my own work on the atoll was carried out in a restricted period during August and September 1967, it has been necessary to take advantage of collections and observations made by colleagues who were on the atoll at the same time but working in different areas, or whose work was carried out over longer periods there. Details of the help received are given at the end of this paper.

Tropical marine algae are very poorly known; few general and even fewer monographic treatments of genera or of groups are available. There is a strong likelihood that many tropical species are widely distributed, but this remains in doubt. Ideally, all genera reported from the Indian Ocean, the Indo-Pacific area, the Pacific Ocean and the tropical Atlantic Ocean need monographing on a pan-tropical basis before determination of Aldabra material is attempted, but this is clearly impracticable. Consequently, no attempt at biogeographic comparisons has been made, and even determinations of species named in this paper must be regarded only as an assessment, subsequently to be confirmed or corrected as additional data become available.

At present, 39 green, 15 brown, 64 red and 8 blue-green species are recognized, but this number should at least double as work proceeds.

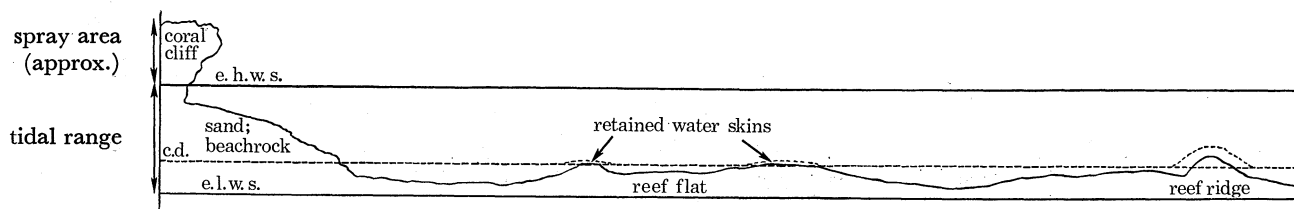


FIGURE 1. Aldabra: schematic representation of the morphology of the reef-flat and the relation of tidal levels to that morphology. Not scaled: broadly based on West Channels transect area, with additions from other West Island seaward reefs. All that area *below* dashed line is here considered sublittoral. Reef ridge height has been exaggerated for clarity. e.h.w.s., extreme high-water mark of spring tides; e.l.w.s., extreme low-water mark of spring tides (real e.l.w.s. outside reef ridge); c.d., chart datum for area and schematic water retention level (effective e.l.w.s. inside reef ridge).

2. DELIMITATION OF 'INTERTIDAL' (= EULITTORAL) AND 'SUBLITTORAL' (= INFRALITTORAL) ON TROPICAL SHORES, WITH PARTICULAR REFERENCE TO ALDABRA

On tropical shores in general it is possible to take two different but both logically defensible, views on the delimitation of the eulittoral. One of these viewpoints is advanced by Isaac & Isaac (1968, pp. 16–17). In essence, the intertidal (eulittoral) is considered in the widest possible terms as that area of shore which lies between extreme low-water mark of spring tides and extreme high-water mark of spring tides, plus that area above the latter which remains, through the medium of spray, wave-wash and so forth, within the sphere of marine influence. On the basis of vertical tidal levels only (relative to a datum) there is clearly a strong case for considering the raised ridge area (though on Aldabra only a shattered depositary vestige) generally as part of the intertidal rather than of the shallow sublittoral. On Aldabra, however, this seems defensible only on the basis of physical levels, since if an attempt is made to correlate the distribution patterns and floristics of the algae of the ridge area with those of the intertidal *sensu stricto*, here only the coral cliffs and beach-rock, very little correspondence can be found, either in species or in growth forms. Since the coral cliffs generally are undercut to some degree, the algae there present, few in number of species, are predominantly sciaphilous forms, or at very least shade tolerant. In the ridge area, even those algae found only on the undercut undersides or other shaded surfaces of boulders are predominantly tolerant of strong insolation, to which they will generally be subject at least at some stage of the day. Hence, there is more correspondence between the flora present in pools retained in hollows in the beach-rock (and even on occasion the flora of the wet beach-rock itself) and that of the reef-ridge than ever there is between the flora of the undercut coral cliffs and that of the reef-ridge. For these reasons, 'intertidal' is taken to refer only to the coral cliffs, where present, and beach-rock, again where present, unless the conditions on that beach-rock are sufficiently moist (as pools or water skins) to support selective up-carry of organisms from the shallow sublittoral (see figure 1). The intertidal is not here considered, in view of the paper being presented on that subject by J. D. Taylor, save that comments on the part involving beach-rock are made at intervals where the floristic overlap mentioned above between beach-rock and shallow sublittoral is relevant.

In view of the presence under boulders or blocks in the reef-ridge of even a few forms often

found under coral cliff overhangs in the eulittoral *sensu stricto*, it would be possible to consider that the reef-ridge blocks constitute a *sublittoral fringe*. However, all aspects of the situation on calm water shores of West Island seem to indicate that this would merely obscure rather than clarify the matter. Therefore, as an alternative to attempting recognition of any part of the reef-ridge as fringe to anything, it aids understanding further if the reef-ridge on Aldabra is considered on biological grounds to be effectively and wholly of the shallow sublittoral, while maintaining recognition that undercut coral cliffs (eulittoral) and undersides of the ridge blocks/boulders (shallow sublittoral) may occasionally have floristic elements in common. This is by virtue not of the fringe nature of the reef-ridge, but solely because of the sciaphilous nature of the floristic elements involved (e.g. *Botryocladia*, *Pocockiella*) and the fact that adequate shade exists in both locations.

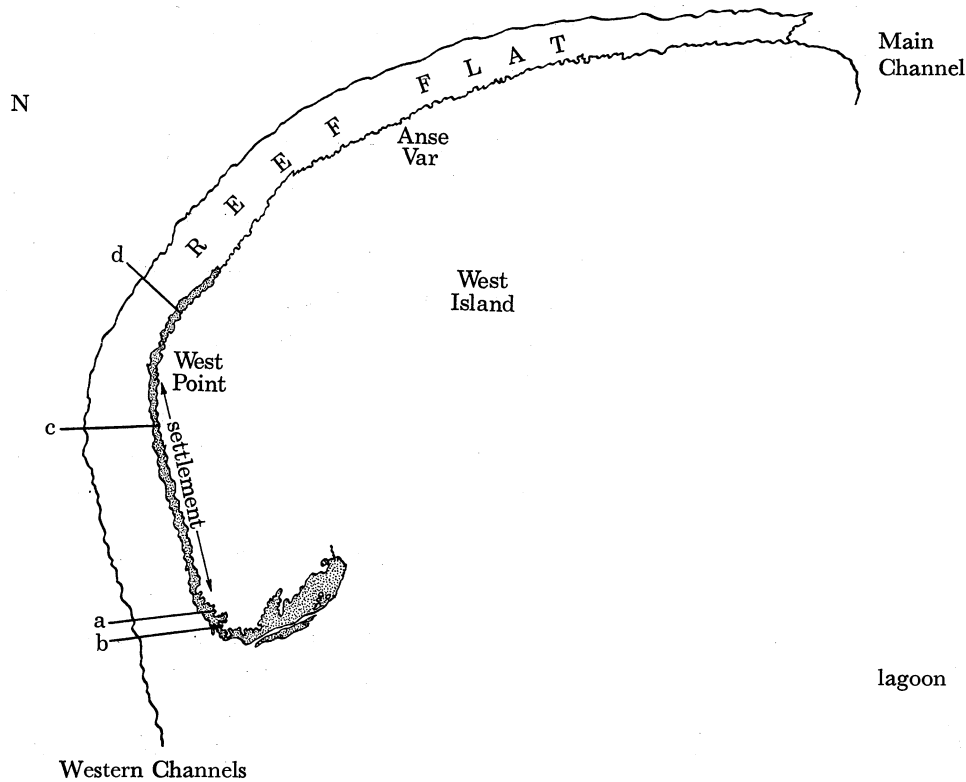


FIGURE 2. Aldabra: West Island Seaward coasts, showing reef-flat width (approximate only) occurrence of eulittoral beach-rock and sand (dotted area), and position of Settlement. Reef-flat width is as at mean low water. Lines of profiles appearing as figure 3 are also given. Absolute numerical scale 1 = 56320.

3. THE SEAWARD REEFS OF WEST ISLAND, WITH OCCASIONAL COMMENTS ON OTHER SEAWARD REEFS OF ALDABRA

The seaward reefs of West Island are essentially calm water localities and the reef-flat and offshore shattered 'ridge' are consistently present around the whole of the seaward coast. The latter coast varies in aspect from northerly (at Main Channel) round to slightly south of west (at Western Channels) (see figure 2). Near the latter, the extent of the reef-flat is probably at its greatest for the whole island group (about 450 m; $\frac{1}{3}$ mile), but in the north, near Main Channel, the reef-flat is as little as 130 to 140 m wide. The customary beach-rock in sand, and

more or less undercut coral cliff, are also commonly present in the eulittoral, but this is not so, as far as coral cliff is concerned, in the area of the Settlement. For a stretch of some 1600 m, from West Point south along the Settlement sea frontage to a point about 200 m north of the southern tip of West Island in Passe Femme, coral cliff formations are absent, being replaced by a relatively shallowly sloping sandy beach lying over beach-rock. The latter is emergent at intervals, generally as a mixed slab-shallow ridge-pool system towards the base of the eulittoral.

As in most reef areas, regardless of the nature of the reef, the reef-flat/ridge portions retain at least a skin, and usually very much more, of overlying water even at extreme low water of spring tides. Since the ridge here is only an erosional feature consisting of variably shattered, movable and distributed blocks of consolidated coral debris, the water coverage tends to be continuous with the tide front, through the many anastomosing channels 7 to 20 cm or more in depth traversing the 'ridge' between blocks (see figure 14*a*, plate 11). This is rendered possible by the very gentle initial slope of the shallow sublittoral seaward of the reef-ridge area (see figure 14*b*, plate 11). This feature, with: (i) the depth, in places near Western Channels, of the inshore ridge and pool system, (ii) the presence of two probably artificially-maintained navigation channels for use through the reef at full tide, opposite Settlement, and (iii) the existence of a good many natural breaks in the seaward reef edge seems to maintain water-level equilibrium on descending tides in the reef-flat area immediately north of Western Channels. There, a continuous flow of fairly deep water (up to a metre deep in places) passes over much of the inshore part of the reef-flat, particularly (in the major transect area, mentioned later) that portion bearing the vertical 'zonation' pattern of marine phanerogams *Halodule-Thalassia-Cymodocea*. Since the flow is generally angled SE to NW, the water also passes over and maintains depth in similar portions of the reef-flat with a similar 'zonation' pattern, but with greater density of *Cymodocea*, which exist immediately seaward of the southern tip of Settlement. These portions are of much greater width and rather farther out on the reef-flat than is the case immediately north of Western Channels (see figures 15*a* and 16, plates 11 and 12). Presence of this flow probably accounts for some of the differences in reef profile commented on later.

A number of profiles were studied in varying detail and observations of distribution patterns were made at localities on the sheltered west-facing ocean coast of West Island, and indeed at a number of locations with very different exposure (to wave action) characteristics elsewhere on the island group. Profiles for West Island reefs appear in figure 3, distribution diagrams in figures 4 to 6. One particularly detailed line transect was established, levelled and marked, just north of Passe Femme, Western Channels; the exact location is marked on figure 2 and figures 15*a* and 16, plates 11 and 12. Despite the mosaic distribution of species over much of the reef-flat area (see later) a transect with this degree of detail was still considered to be the most effective way of ensuring careful examination of all parts of the shallow sublittoral. The generalized 'zonation' scheme which appears as figure 7, therefore, is founded largely on data from this detailed transect; however, in view of the mosaic variation over the reef-flat surface and the variability in the presence and extent of intertidal beach-rock and coral cliff, additional data have been added, where relatively consistently true, from profiles other than the detailed transect. Detailed consideration of sample areas or quadrats from the major transect and elsewhere appears later, but several general points emerge from the semi-schematic 'zonation' figure:

- (1) 'Zones' or 'bands' are more or less recognizable very locally, but their presence, form,

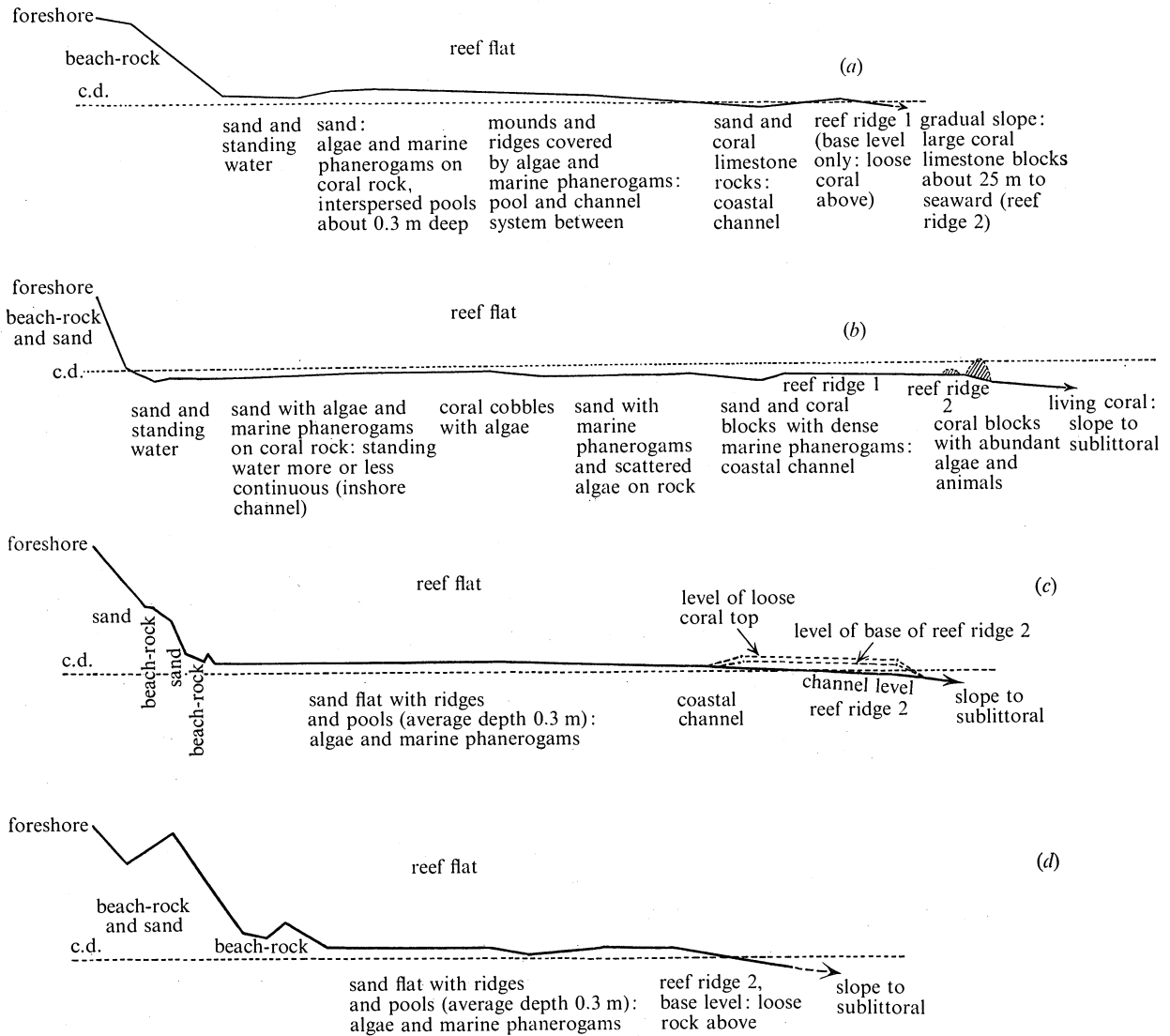


FIGURE 3. Seaward reef profile at extreme low water: West Island. Vertical scale (a), (b), 1 = 360 (c), (d), 1 = 280; horizontal (a), (b), 1 = 3600 (c), (d), 1 = 2800. Positions of the profile lines appear in figure 2. Profiles are based only on levelled heights of markers, not on detailed configuration changes. (a) Section of south of Settlement, about 80 m north of West Channels transect. Length 400 m. (b) West Channels transect. Length 482 m. (c) Section from northern steps of guest house. Length 342 m including 12 m seaward of reef-ridge, examined but not profiled. (d) Section north of Settlement, midway between Settlement and Anse Var. Length 268 m.

width and position are recognizable more on the basis of the depth and movement of water and the nature of the substrata (particularly) and of the marine phanerogam communities (to a lesser extent) than of the rest of the marine flora. The 'bands' are generally very wide in areas of their optimum development on the median reef-flat, due to the vast extent of the latter in shelter from strong wave action. However, the 'bands' sometimes vary widely within short distances and in extreme instances, by no means uncommon, the situation is so mosaic, even in aerial view, that it is virtually impossible to recognize any pattern even on the largest scale.

(2) Except locally in standing deep water in the 'moat', specimens of algae tend to be smaller than those of the lagoon channel areas and of oceanic temperate shores.

- (3) In addition to the size limitation, the algal flora (but *not* the marine phanerogam flora and excluding the crustose corallines) cannot be called dense except in standing water, and even then only rarely (usually in not less than 45 cm of water).
- (4) Most of the water drains from the blocks and boulders in the shattered ridge areas

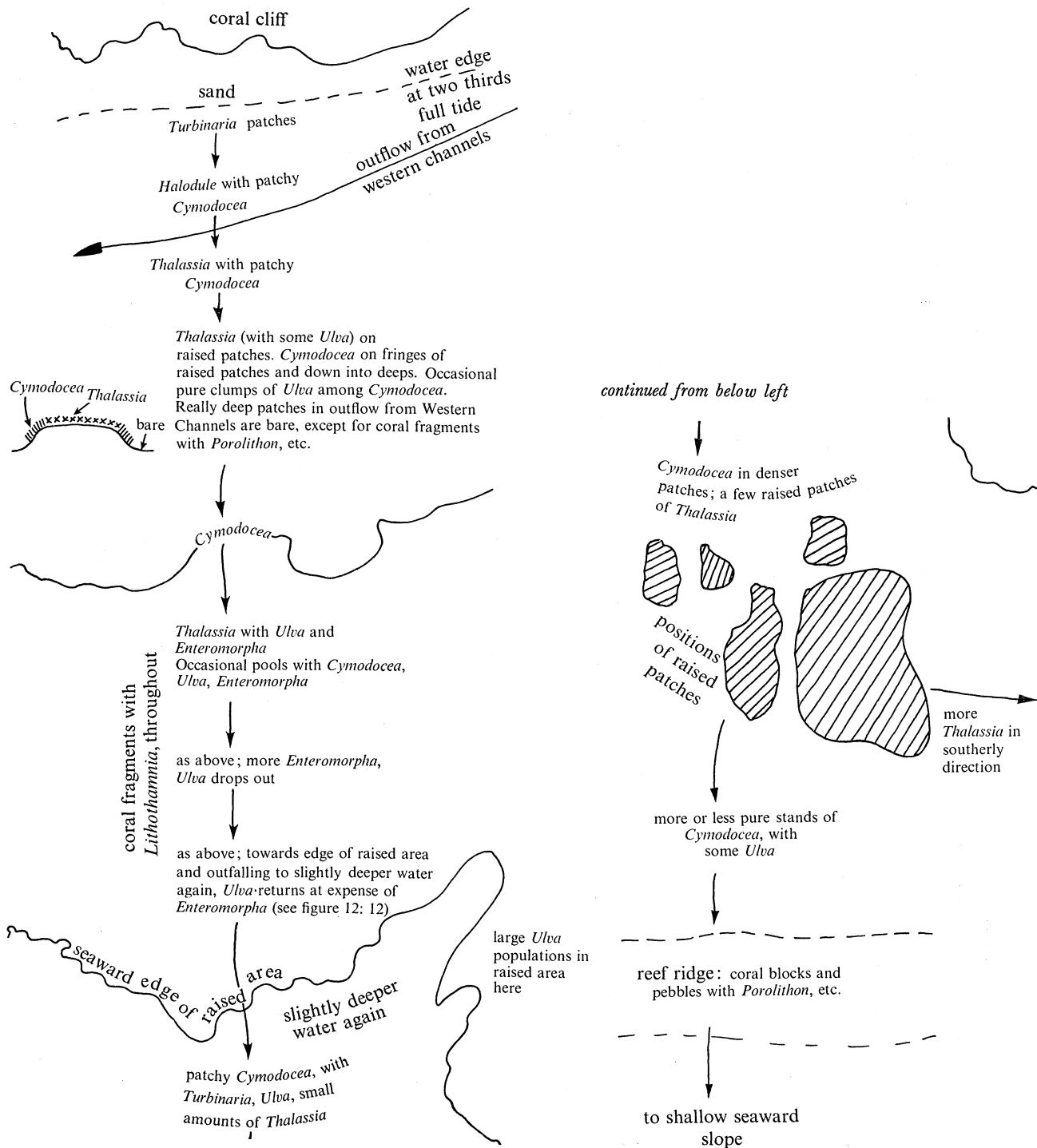


FIGURE 4. Distribution diagrams, West Island seaward reefs. General sketch of 'zonation' on reef-flat just to north of Western Channels, around Western Channels transect. Not to scale.

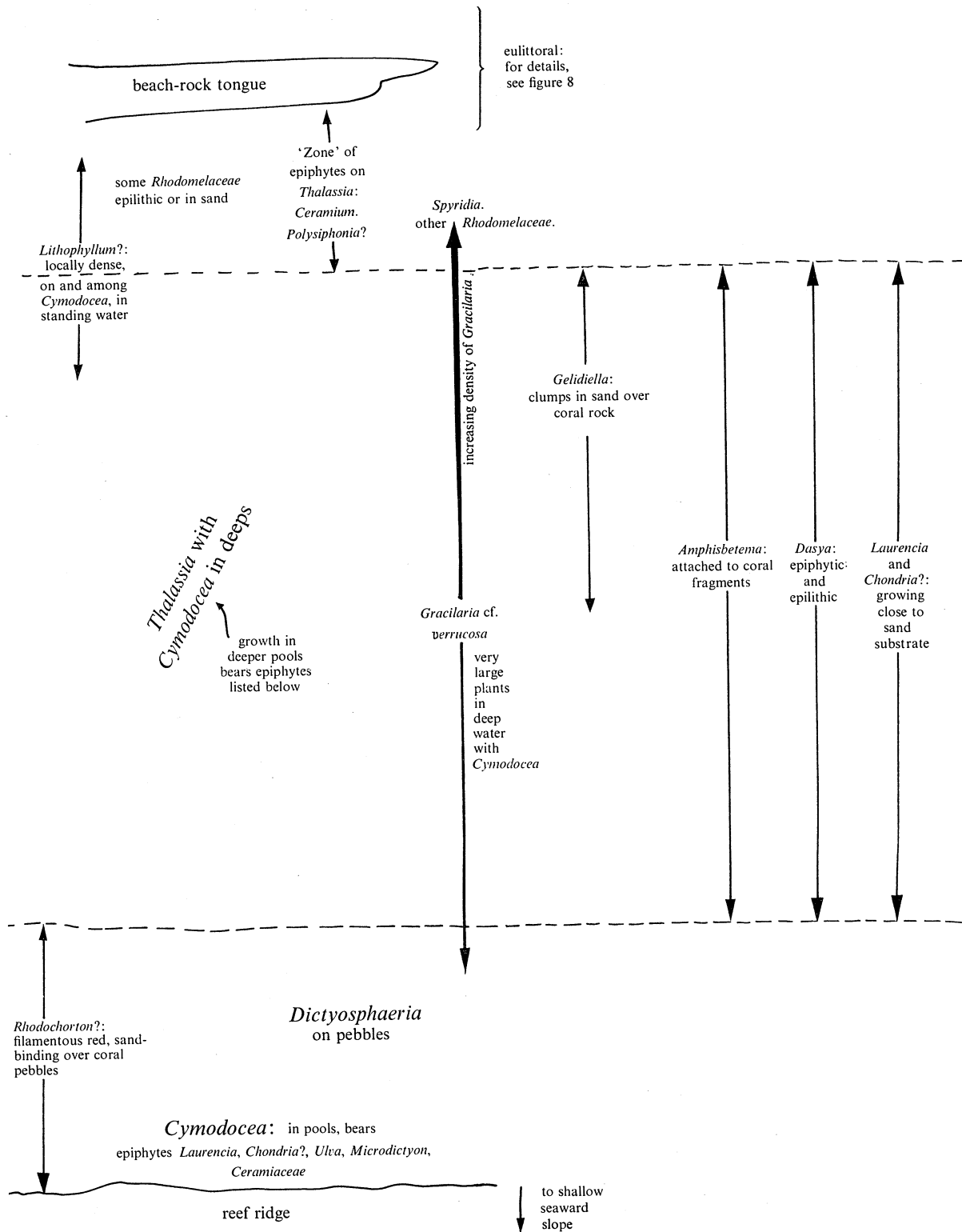


FIGURE 5. Distribution diagrams, West Island seaward reefs. General sketch of 'zonation' on reef-flat half way between fish drying shed (north end of Settlement) and Western Channels, north shore. Not to scale.

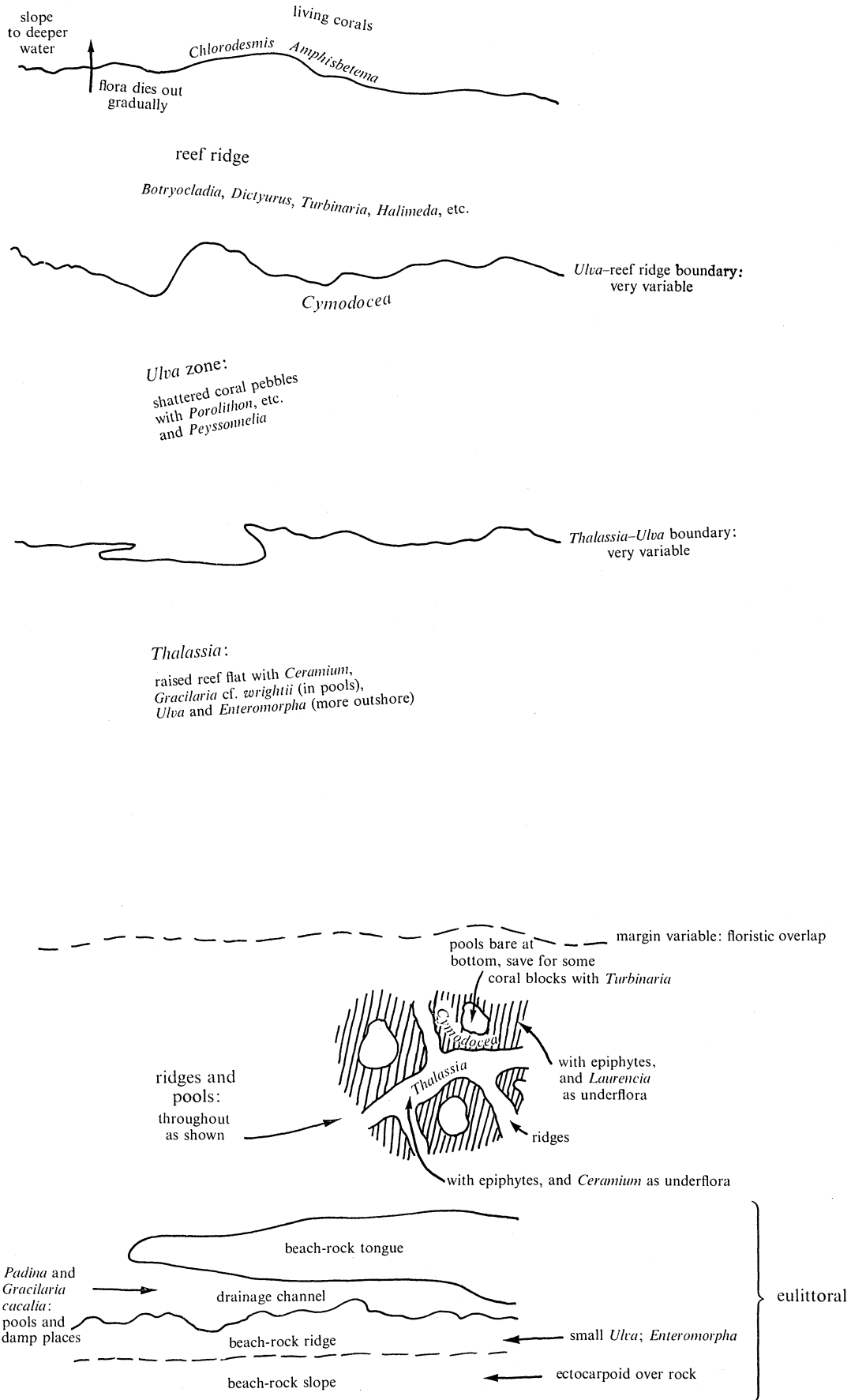


FIGURE 6. Distribution diagrams, West Island seaward reefs. General sketch of 'zonation' on reef-flat on North Steps transect, guest house, Settlement, West Island. Not to scale.

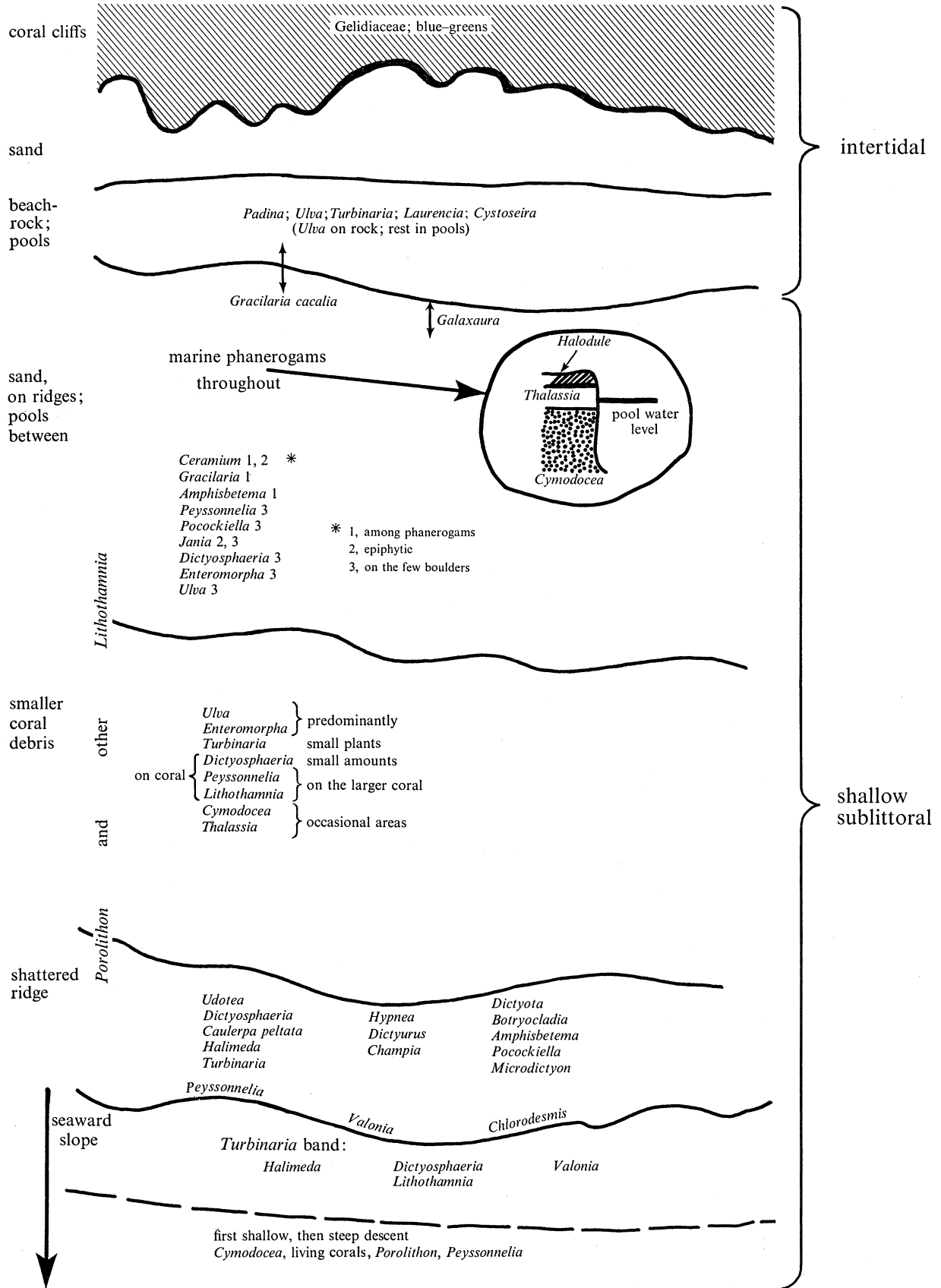


FIGURE 7. Schematic presentation of generalized zonation based on substrate nature and configuration and marine angiosperms present. Composite of data derived from all West Island reef observations available. Not to scale.

(see figure 14*a*, plate 11), and here almost all the algae occur in periodic shade conditions or standing in shallow water between or under blocks. Any algae actually on the boulder/block sides or tops tend to show an even more extreme size-reduction than those of the rest of the reef-flat area (figure 17*a*, plate 11).

Points 2 to 4 above tend to suggest the general effects of strong insolation, and possibly high temperatures, on growth, as does the bleaching of some of the species involved, for example the *Turbinaria* of the ridge blocks (see figure 17*a*, plate 11) and of the *Turbinaria* belt beyond it (figure 17*b*, plate 11), in the latter of which the bleaching is much less obvious.

(*a*) MARINE FLORA OF THE OPEN BEACH-ROCK AND POOLS

There appears to be a certain element of the otherwise sublittoral flora which is capable of tolerating that near approach to the physical parameters of the true sublittoral environment which obtains in pools that occur (with a high degree of permanence) in eulittoral beach-rock formations. Therefore, although treatment of this habitat falls, in a purely spatial sense, within the confines of J. D. Taylor's paper (this volume, p. 173), the flora forming that element has been considered here. Immediately adjacent parts of the beach-rock surface, particularly those in the path of any downflow from the pools, tend to have certain genera in common with the higher parts of open reef-flat; this is especially true of lower parts of the beach-rock whose configuration results in retention of a water-skin for at least the major part of their period of emersion. Therefore, additional comments have been made on beach-rock flora of this type.

A particular example of the situation on one stretch of beach-rock and pools between Settlement and Western Channels is presented in figure 8. A number of the species involved do not seem to appear elsewhere in calm water reef areas than on beach-rock in wet conditions in the eulittoral; where conditions are even more sheltered from wave action and where there is considerable mud or sand/mud mixtures available as substrata, these species tend to occur perhaps in no greater abundance but certainly in very considerably more luxuriant growth. An example of such circumstances is provided by muddy areas peripheral to and out of the main water flow through Western Channels. Elsewhere in more exposed circumstances, for instance on the south shore of South Island, Aldabra, some of the species may occur in deeper water in the sublittoral, rather than being eulittoral. *Padina commersonii*, for instance, occurs in these circumstances. The species of this restricted element, then, which are named in figure 8, are *Cystoseira myrica*, *Padina commersonii* and ectocarpoid species. The influence of these few species on the appearance of this pool and open beach-rock flora is rather greater than the numerical proportion which they form of the total eulittoral flora in these circumstances would seem to indicate. This is even more emphatically true if there is also taken into consideration a further species or species complex, *Gracilaria cacalia*, which overlaps from the very base of the true eulittoral into the immediately adjacent areas only of the shallow sublittoral. The species was not, unfortunately, present in the local small area represented in figure 8; had *G. cacalia* been present in the position in which it is commonly found, it would have spread on and in sand immediately below the seaward fringe of pools with *Padina*, among the boulder-attached *Enteromorpha*, and into the upper fringe of the standing water to seaward, perhaps reappearing on the seaward flange of the beach-rock tongue, if sand was present overlying that flange. (See §3*b* (ii) (2-4) for further data on *G. cacalia*.) The three species which are present in the position detailed cover much surface area there: the ectocarpoid forms a definite if discontinuous

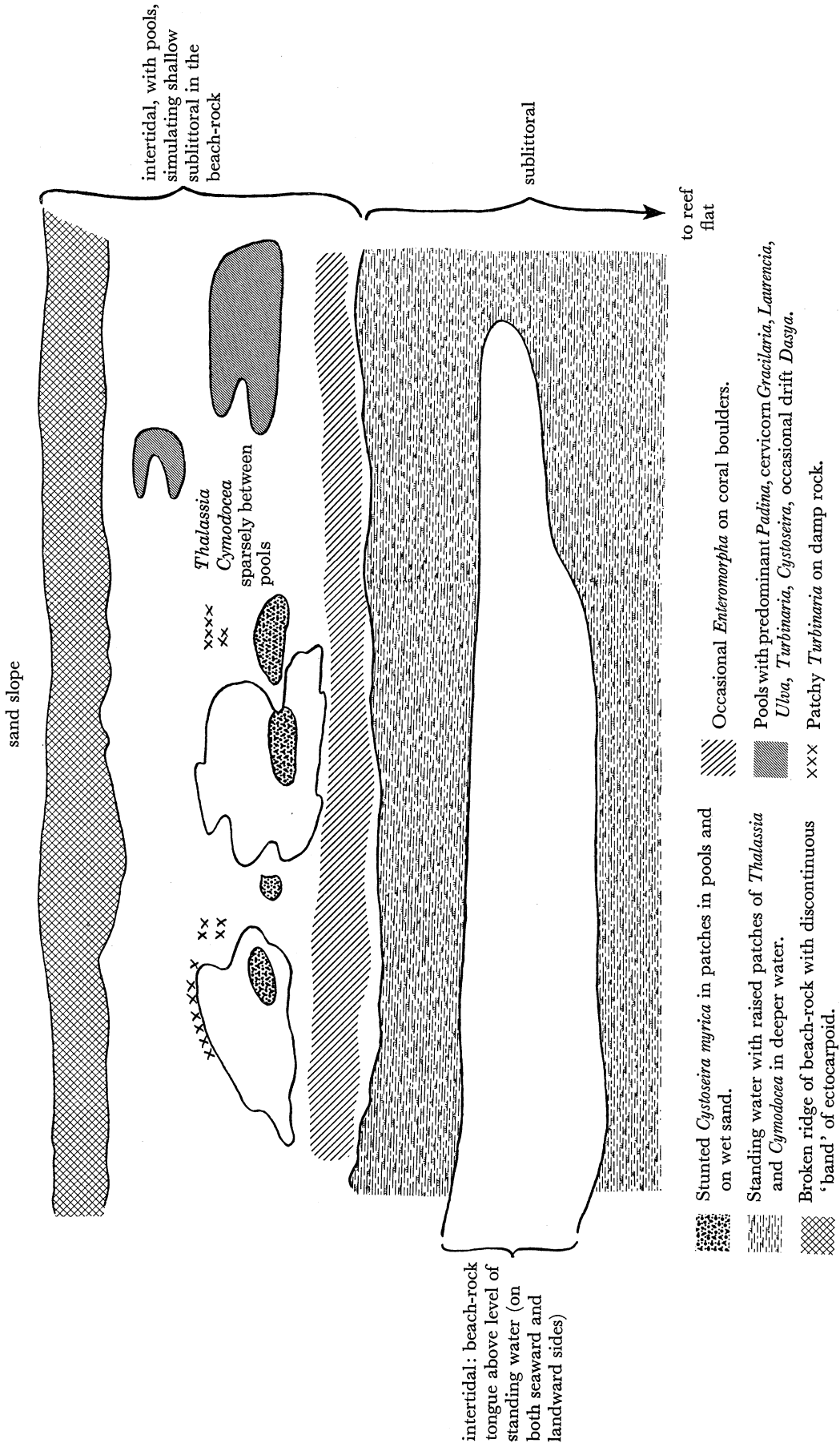


FIGURE 8. Example of the beach-rock/pool situation at one location half way between Settlement and Western Channels. With key to symbols used. Semi-schematic; not to scale.

band of algal growth in a position where no other macroalgae are attached and forms a sometimes dense cover immediately below the sand slope. *Padina*, admittedly even there rather scattered in distribution, is still more or less dominant in most of the pools. *Cystoseira* occurs in damp sand around the pools and in the pools themselves; although it is present only sporadically and is sometimes stunted in growth, it is nevertheless generally in a healthy, deeply pigmented condition and forms a very obvious facet of the beach-rock flora.

That element in the open beach-rock and pool flora which does represent an apparent up-carry from the sublittoral reef-flat consists of the remainder of the species named in figure 8. *Turbinaria (ornata)*, as elsewhere in the reef-flat, occurs on firm rock surfaces, both on the open face, where the plants are small, and in the deeper pools, where the plants reach a similar height to those in deep water on the reef-flat. *Thalassia* is sparsely present on open rock between pools, but only significantly so where a water film exists; a few stunted *Cymodocea* plants occur among the *Thalassia*. *Enteromorpha* grows on coral boulders in those areas in the lower portion of the beach-rock where no more than a water-skin exists, at rather similar levels, relative to Chart Datum, as it grows elsewhere in the reef-flat. *Enteromorpha* as a genus commonly does seem able to withstand the sequence of immersion/emersion to which it is subject on open rock surfaces in the eulittoral, in which position it is found on many shores of the world. Therefore it is not surprising that, occasionally on Aldabra, the ectocarpoid cover mentioned above and shown in figure 8 is replaced by a short band or series of patches which are predominantly *Enteromorpha*. An example of this, near Settlement, appears in figure 18a, plate 11. *Ulva*, by contrast but in complete accord with its distribution largely in deeper water in *Enteromorpha/Ulva* areas in the shallow sublittoral, is usually present only in the deeper pools on the open beach-rock (see §3b(ii) (3)). These deeper pools may occasionally retain a depth of 0.6 to 0.7 m at low water and therefore, as could reasonably be expected, carry some floristic elements characteristic of the pools from the ridge/pool phanerogam zonation areas of the reef-flat and of the 'algal turf' areas of the Western Channels (see later sections). *Ulva* is, of course, one of these elements and the others commonly present are *Gracilaria* sp. (? *wrightii*, cervicornly branched) and *Laurencia* spp. *Dasya*, which is also widely present in deep pools (both epiphytically on *Cymodocea* and epilithically) in the ridge/pool area of the reef-flat, was not here found attached but only as drift; a few rare cases of attached specimens in pools on beach-rock have been observed.

(b) MARINE BIOTA OF THE SUBLITTORAL PROPER

(i) Marine angiosperms

(1) Introduction

Marine phanerogams are characteristic of the reef-flats of calm shores of West Island and occur also in the lagoon, commonly in areas directly affected by drainage channel water-movements.

The most characteristic and immediately evident taxa on Aldabra are *Thalassia hemprichii*, *Cymodocea rotundata* and *C. ciliata*, although *Halodule uninervis*, *H. wrightii* and *Syringodium isoetifolium* are all, in their respective locales, equally distinctive and obvious. The genera *Halophila*, *Enhalus* and *Zostera*, however, are not at all obvious. Considering the general luxuriance of their development in areas surrounding Aldabra, it is astonishing that *Halophila* should have been found but very few times on Aldabra, while *Enhalus* is apparently entirely absent. The distribution and ecology of those species which are known to be present on Aldabra are

commented on in the text which follows, but it is appropriate here to consider in more detail the situation regarding the less well represented forms.

Zostera is mostly a genus of cold or cool temperate regions, but it has been reported (as *Zostera capensis*) from South Africa, Seychelles (on Praslin, collected by Gardiner), Mozambique, Dar-es-Salaam (Tanzania) and, more recently, Lamu, Mombasa and Gazi, all ports in Kenya (Isaac 1968, p. 32 and figure 2). Its occurrence in East African tropical waters is of great interest, but all the ports concerned are said to be of long standing, especially Gazi, which is really ancient, so that *Zostera* could well have been carried in by ships and established only locally. No specimens of this genus were located on Aldabra.

Enhalus acoroides is said by Isaac (1968, pp. 45–47) to occur in the tropical Indian Ocean and western Pacific, with a reported distribution of Madagascar, Seychelles, Red Sea, Ceylon, Nicobar Is., Andaman Is., Malaysia, Queensland, Solomon Is. and New Caledonia. Although it has only recently been recorded on the East African coast (Kenya and Tanzania) by, among others, Isaac (1968), the latter worker found it in dense pure stands in at least two places, while Isaac & Isaac (1968, p. 21) noted a bed of stunted plants on an old coral platform. Its absence from Aldabra, if real as well as apparent, is therefore very curious.

Halophila has been found only very rarely on Aldabra; F. R. Fosberg, who has seen the material, reports that it is probably *H. minor*. J. D. Taylor, who made all four collections, found

DESCRIPTION OF PLATE 11

FIGURE 14. (a) 'Reef-ridge' showing the variably shattered, movable and distributed blocks of consolidated coral which form the so-called ridge on Aldabra. Darker patches on either side of the ridge as it passes into the distance are of *Cymodocea*. (b) Very gentle initial slope of the shallow sublittoral seaward of the 'reef-ridge'. Foreground shows living corals, and a small patch of *Cymodocea*. Top diagonal, from left to right along seaward fringe of the reef-ridge, shows a line of more or less anastomosing patches of *Cymodocea*. Top left passing off the photograph to left is the entrance to Western Channels.

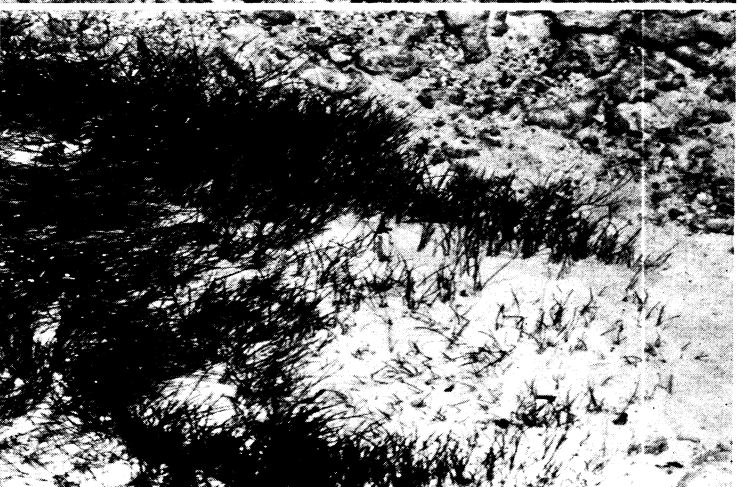
FIGURE 15. (a) Aerial view of West Island seaward reef in the vicinity of Settlement and Western Channels entrance. Settlement along sand fringe to left, Western Channels, with islands, to right. Line of major transect dotted; widening effect of flow from La Passe Femme (the northern channel) clearly visible as expanded (dark) *Cymodocea* vegetation to left (north) of transect line. Deeper water, from the flow, just inside the 'reef-ridge' to left again of darker patches, clearly visible. Western Channels angiosperm/algal 'turf' area is the darker patch behind the two islands in Western Channels. (b) *Thalassia/Cymodocea* ridge/pool vegetation of the inner reef-flat. Location of the photograph is about half way between the line of the transect and the left-hand edge of (a). Bucket gives some idea of the scale. House of southern end of Settlement in rear. *Thalassia* in shallow water; *Cymodocea* (darker) in centres and deeper parts of pools. Sand with very little emergent beach-rock in rear.

FIGURE 17. (a) Block top from the inshore fringe of the reef-ridge near Settlement (guest house) profile. *Cymodocea cilata*, top left; *Ulva* to upper left and upper right of photo; *Turbinaria*, stunted but obvious, is scattered around the periphery of the block, with a few small patches centrally; *Dictyosphaeria*, both solid and hollow forms, is present as dark or light cushions over much of the block surface; *Cladophoropsis* is present in niches and declivities at middle right, below *Ulva* and *Turbinaria*, and central front, to left of *Dictyosphaeria* cushion. The remainder of the surface is largely covered by *Porolithon* (mostly) and *Peyssonnelia* (less). (b) *Turbinaria* band, with seaward fringe of reef-ridge, Western Channels transect. Almost the whole of the visible area is covered, as can be clearly seen from the immediate foreground, with a dense growth of *Turbinaria*. Small patch of *Cymodocea* central left, with, diagonal upper right along the advancing tide front, anastomosing patches forming the *Cymodocea* band.

FIGURE 18. (a) Beach-rock on West Island, near Settlement, showing a patch of high-level greens, mostly *Enteromorpha*, in the eulittoral. *Enteromorpha* is shown as a darkening of the beach-rock surface, wide in foreground and narrowing with perspective in the distance. Central left, near the edge of the photograph, can be seen eulittoral pools in the beach-rock. Left again is the edge of the reef-flat with standing water. The patches of darker vegetation in hollows are detritus of marine angiosperms, thrown up as drift, here largely of *Cymodocea*. (b) *Halodule*, edge of sublittoral West Island. Buried in, and retaining, sand over coral cobbles and consolidated coral debris.

(a)

(b)



FIGURES 14, 15, 17 AND 18. For legends see facing page.

(Facing p. 136)

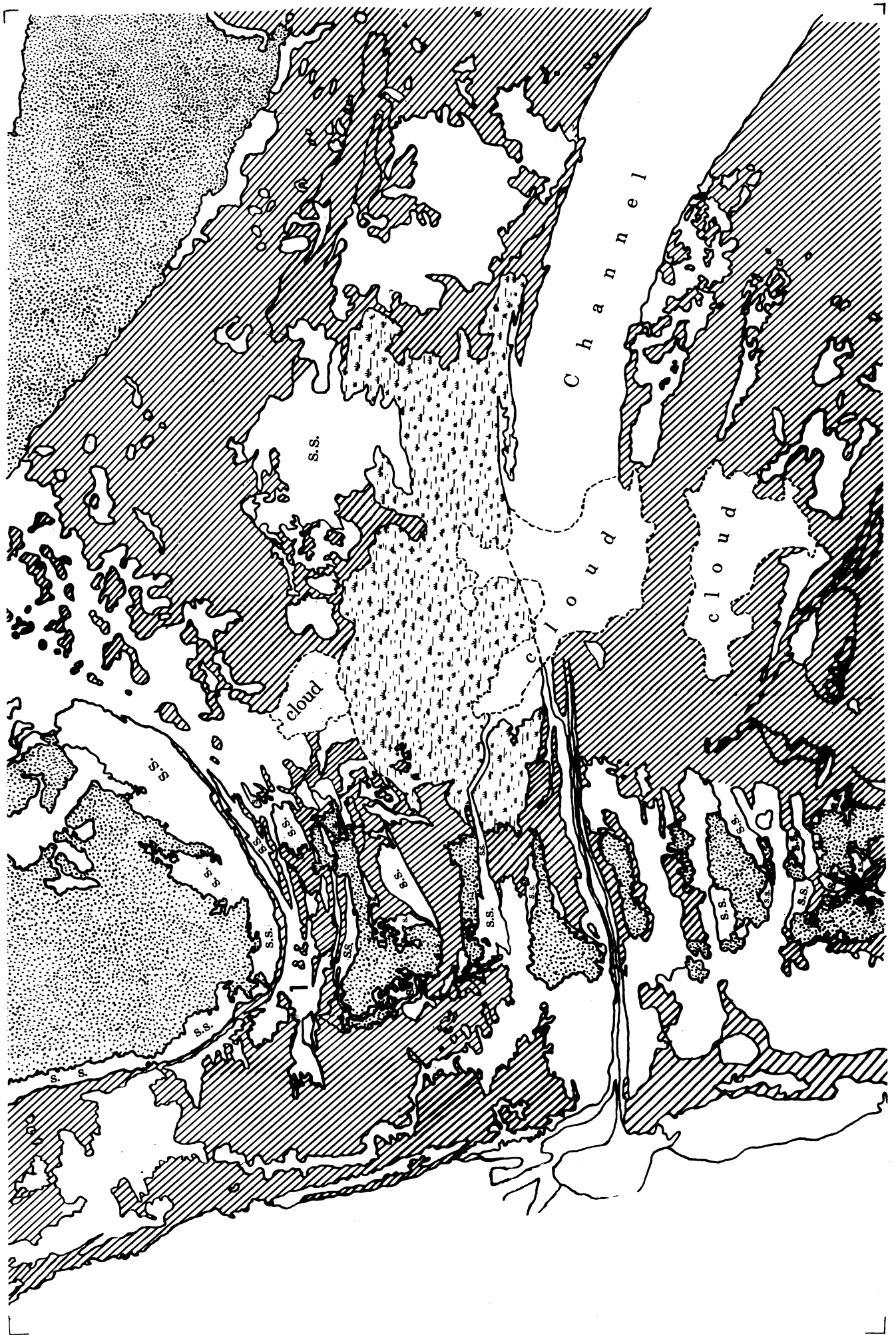




FIGURE 16. For legend see facing page.



FIGURE 16. For legend see facing page.





the plants growing in very small and sparse amounts at the South end of Passe Gionnet, near Gros Ilot (two different patches); at Bras Takamaka; and on the eastern lagoon coast of Middle Island. Neither W. Macnae, Fosberg nor I saw any *Halophila* at all on Aldabra; Den Hartog, who determined all marine phanerogams collected by S. Renvoize during phase III of the Expedition, states (verbal communication) that no *Halophila* specimens are included among those either. Clearly, aspects of the presence, or absence, and distribution of *Zostera*, *Enhalus* and *Halophila* on Aldabra need further investigation.

The detailed mapping of marine phanerogam distribution on reef-flats, other than in very local habitat studies, is an extremely arduous and possibly rather pointless business, even when aerial photographs are utilized (see, for example, Chassé 1962). Therefore, for the present paper, this mapping has been attempted in only one area, Western Channels, in connexion with the detailed studies of transect and algal 'turf'. Even there, only a gross indication of probable *Cymodocea*/*Thalassia* dominance could be given and this appears as figure 16, plate 12, which is an aerial photograph with a keyed overlay. Indications of the detailed distribution of *Halodule*, *Syringodium* and *Halophila* are not given on any diagrams, but comments on these occur in the text which follows. No attempt has been made to map separately the species of *Cymodocea* present, for reasons similar to those given at the beginning of this paragraph.

(2) *Halodule*

Halodule uninervis and *H. wrightii* are both found on the inner portions of the calm water reef-flats of West Island. The latter species seems to be the more frequent. The area occupied by *Halodule* in the transect area near Western Channels takes the form of a ridge rising between 25 and 30 cm above the sand and boulders of the adjacent inter-tidal and grading gently seaward into areas of *Thalassia* over sand. The existence of this ridge is probably a function of the presence of *Halodule*, which appears strongly and firmly to fix otherwise shifting sand over beach-rock/consolidated coral (figure 18*b*, plate 11). Figure 9 gives a detailed drawing, to scale, of the area of *Halodule* in Western Channels transect; immediately adjacent areas do not differ radically from those of the transect, but elsewhere on West Island certain variations occur. The distribution of *Halodule* near Western Channels may once again be a facet of the strong, angled outflow which crosses the inner reef-flat at or just below this *Halodule* area. The greater depth of water thus created compared with other areas of the reef-flat analogous in position but farther north, near Settlement, may well be instrumental in causing pattern differences, as may the consistent water movement and possible consequent detrital scour near Western Channels, referred to earlier. The outstanding pattern difference lies in the virtual restriction

DESCRIPTION OF PLATE 12

FIGURE 16. Vertical aerial photograph of northern half of Western Channels and southern tip of West Island. Passe Femme and Passe du Bois clearly visible. Line of Western Channels transect drawn in. Wider *Cymodocea* occurrence north of transect line clearly visible. Gives keyed overlay with accompanying legend on facing sheet. Cloud obscures some parts of photograph bottom centre. , Main area of algal turf; , *Thalassia* areas (among these are some probable stretches of clear sand. Clear sand spits actually in Western Channels are otherwise indicated); , land above tidal levels, with terrestrial vegetation; s. and s.s., sand (spits) indicated where there is space so to do: in restricted space, s. may be used where s.s. is more correct; , *Cymodocea* areas (near the mouth of Passe du Bois, and elsewhere, when reasonable identification of vegetation type is not possible, also left blank); 1, entrance to Passe Femme (Western Channel); 2, entrance to Passe du Bois (Western Channel).

of *Halodule* in Western Channels area to the narrow, discontinuous band of ridges formed by its fixing sand immediately seaward of the beach-rock, compared with a much wider lateral spread over a great deal of the ridge/pool inner reef-flat area elsewhere, for example north of Settlement. There, *Halodule* occurs generally as the upper band in a pattern of 'zonation' beginning on ridge apices and extending down the sides into the adjacent pools. The sequence *Halodule* → *Thalassia* → *Cymodocea*, from ridge apex to pool depth, is usually adhered to, although minor small local variations occur. A schematic representation of the band positions relative to pool water-level and of the relative sand widths appears as an inset to the generalized zonation diagram, figure 7, and photographs illustrating the superficial appearance of shore areas with the ridge-pool system appear as figures 15*b* and 19*a*, plates 11 and 13.

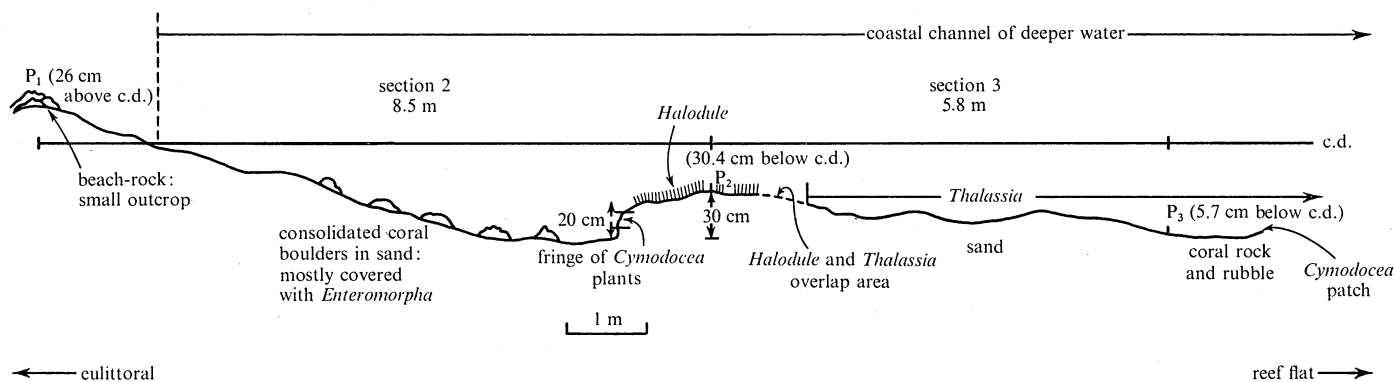


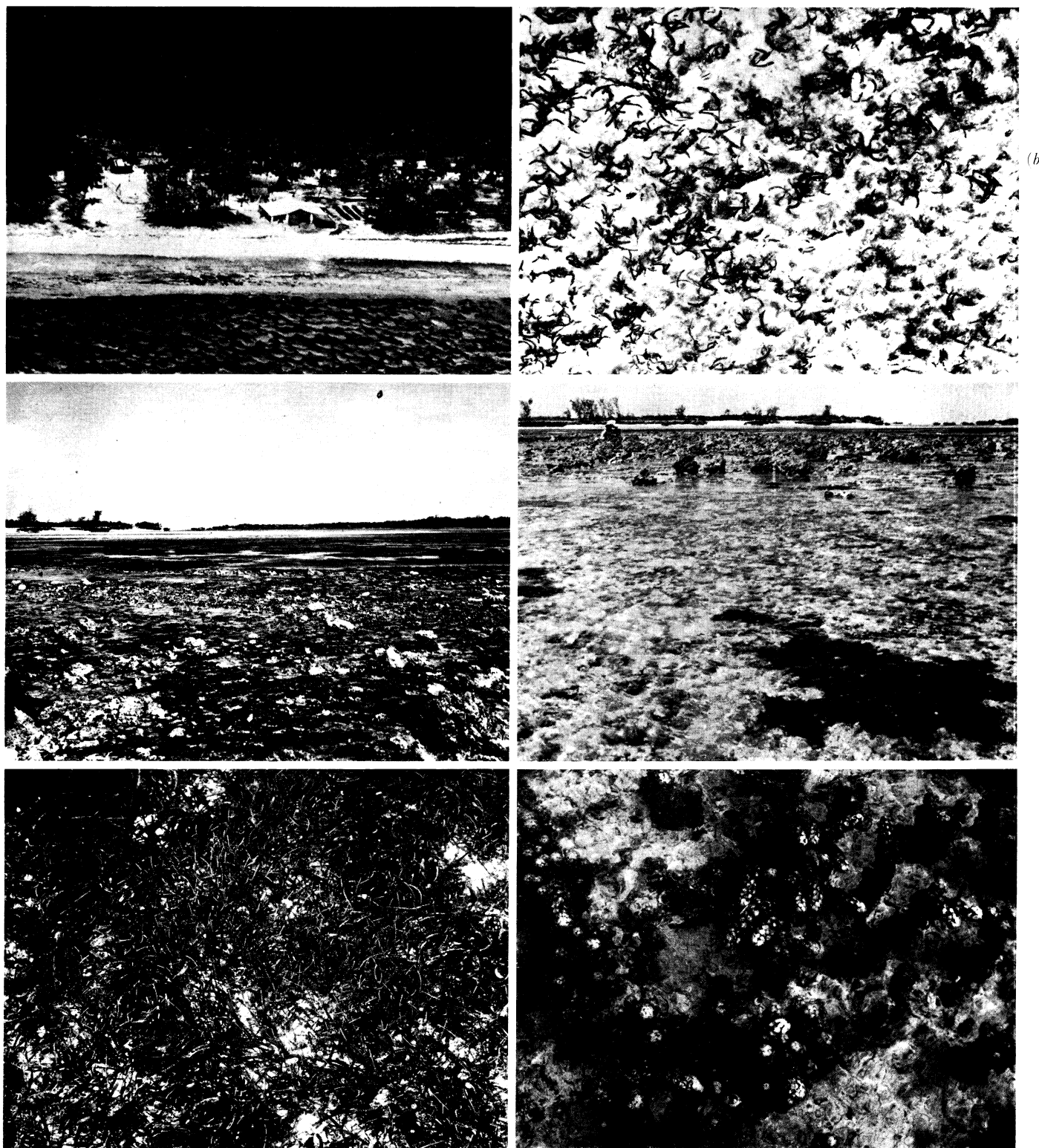
FIGURE 9. Profile of transect and distribution of main growth of *Halodule*, inshore fringe of sublittoral, Western Channels transect. Represents sections 2 and 3 of transect, piton positions indicated. Semi-diagrammatic. Vertical emphasis over horizontal: 2 to 1.

(3) *Thalassia* and *Cymodocea*

As already indicated, by far the most widespread and important genera on the seaward calm water reef-flats of West Island are *Thalassia* and *Cymodocea*. These genera have to some extent an interrelated distribution on at least those portions of reef-flat lying between the lower beach-rock (i.e. lower limit of eulittoral) and the 'reef-ridge', and for this reason they are here dealt with in one section. Both genera are equally widespread over the reef-flat, but there are two major differences in their distribution:

(i) Whereas *Thalassia* generally shows its optimum development on inner reef-flat areas immediately seaward of the *Halodule* fringe, *Cymodocea* is more luxuriant and dense in lower, outer, areas of reef-flat on either side of, and in channels within, the 'reef-ridge', that is in deeper water than *Thalassia* (see figures 14, 17*b*, 19*b* and 20, plates 11 and 13). This agrees well with the observed fact that *Cymodocea*, when present in the ridge-pool zonal patterns of the inner reef-flat, is found predominantly and most luxuriantly in the lower parts of the ridges, deep into the standing water of the pools (figure 15*b*, plate 11). Clearly, *Cymodocea* requires greater depth of water, possibly as an insolation barrier, than does *Thalassia*; the latter, in the zonal pattern mentioned above, always occupies the ridge immediately above *Cymodocea*, sometimes encroaching on the apices of the ridges when *Halodule* is not present.

(ii) *Thalassia* is represented here only by the species *T. hemprichii*. *Cymodocea*, on the other hand, is here represented by at least two, possibly three, species. Of these, *C. ciliata* appears



(b)

FIGURE 19. (a) West Island, low aerial shot of shore off Settlement, showing sand above beach-rock, the latter with variable distribution of flora, and the dappling effect given to the inner reef-flat (sublittoral) by the presence of pools with *Halodule* → *Thalassia* → *Cymodocea* zonation from ridges of sand down into adjacent pools. Bottoms of the pools are here largely free of vegetation, and the widths of individual parts of the ridge system vary, as does the density of the flora carried. (b) *Thalassia* and, predominant of the algae present, *Ceramium*, in shallow water on sand. Near mushroom islet in Western Channels near lagoon. Ground cover of the two main constituents is about equal. Standing water is here merely a skin about 2–5 cm deep.

FIGURE 20. (a) *Cymodocea* deeps just inshore of the reef-ridge, the fringe of which is seen in foreground. Raised coral cobble/*Thalassia*/*Ulva* and *Enteromorpha* flat visible as lighter area in far background. La Passe Femme in rear, undercut coral cliffs rising out of sand to left of it. Very near line of Western Channels transect. (b) Seaward side of reef-ridge, looking back along line of Western Channels transect. Small changes in level on seaward slope initially can be clearly seen. Darker areas immediately behind reef-ridge are *Cymodocea*, as are the dark patches in front. These latter patches form part of the discontinuous band of *Cymodocea* seaward of the ridge. Between it and the ridge, overlapping the fringe of the latter, can be seen the *Turbinaria* band.

FIGURE 21. (a) *Syringodium* (centrally), on raised area, and *Cymodocea* (on both sides), in deeps adjacent. Passe du Bois, Western Channels, in shade and deeps along small islet. (b) *Turbinaria* from deeper water in Western Channels area. Illustrates the longer more luxuriant growth in deeper water when compared with growth in the intertidal or on the reef-ridge.

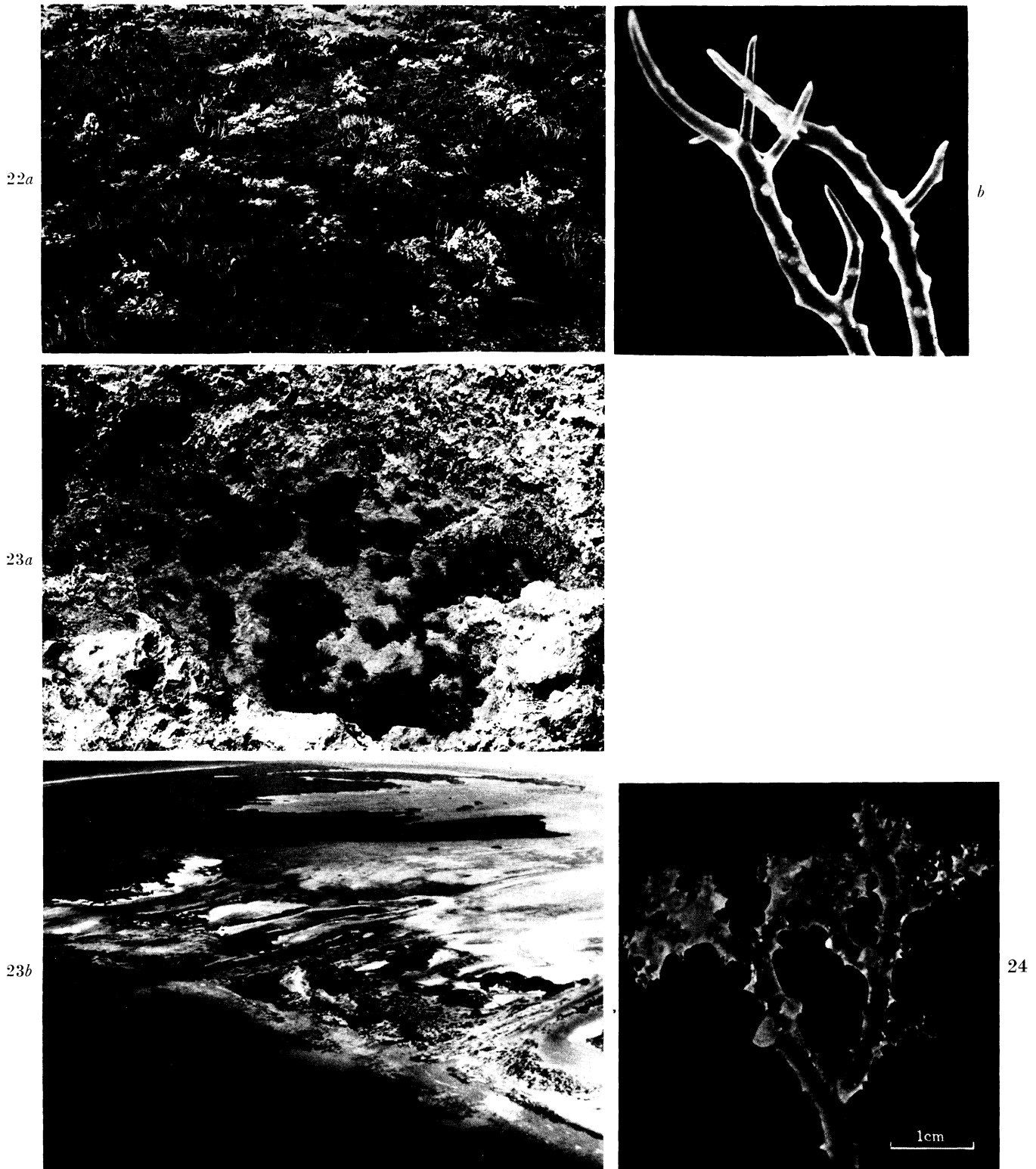


FIGURE 22. (a) Algal and angiosperm 'turf area', Western Channels, at low water of spring tide. The main genera visible are: *Halimeda*: bleached and clearly visible, large- and small-segmented forms. *Gracilaria* cf. *wrightii*: the cervicornly-branched form present, standing stiffly upright in much of the photograph. *Laurencia papillosa*: clumps of dark material, centre foreground, against the darker, widespread *Cymodocea*. *Cymodocea*: forms much of the general background to the rest of the vegetation. Bears vast amount of *Melobesia* and Spirorbidae on the leaves. *Hydroclathrus clathratus*: a clump of this net-forming species appears top right, to the left of the upper right large clump of *Halimeda*. (b) Close-up of cystocarpic material of *Gracilaria* cf. *wrightii* from the deeps of the inner reef-flat, north of Western Channels transect.

FIGURE 23. (a) *Chlorodesmis*: shallow pool with small amount of sand detritus, seaward side of reef-ridge near Settlement. More usually found in shallow water-skins and retaining much more sand than here. (b) Oblique aerial photograph showing whole of Western Channels and much of West Island. The larger channels are La Passe Femme (left, to north); La Passe du Bois (centrally); La Passe Magnan and La Passe Grabeau, which are confluent and outfall together (to right, south). Position of algal 'turf' is easily seen as large black patch centrally, behind and slightly to north of lagoon end of La Passe du Bois. Comparison with the overlay of figure 16 will identify it more firmly, if needed.

FIGURE 24. Close up, magnified $\times 1.5$, of apical portion of the (?) new *Acanthophora* sp. widespread in the algal turf area. The plants seem to be nearer to *A. muscoides* than to *A. spicifera* but do not tally well with any material of the former seen so far.

to be the most widespread over the reef-flat surface, being found as smaller plants in pools or on wet shaded surfaces adjacent to the *Halodule* 'zone' and thence right out through the reef-flat and ridge to deeper water beyond the ridge. On the basis of the amount of debris thrown up, the biomass of *Cymodocea* is largely of *C. ciliata* and far exceeds the total biomass of all other marine phanerogams on Aldabra. Not all such *C. ciliata* debris is derived from seaward reefs, however, for *C. ciliata* exists in luxuriant growth on both lagoon and seaward sides of Western Channels and probably elsewhere in the lagoon and in drainage channels. *C. rotundata* appears to be largely a plant of standing water inside the reef-ridge, but present in very much smaller amounts than *C. ciliata*. It is possible that the flora of standing waters inside the 'reef-ridge' also includes the species *C. serrulata*, but this remains to be checked further.

A distribution diagram covering all the marine phanerogams present in Western Channels transect area appears in figure 10. Although *Halodule* forms a small part of the marine phanerogamic flora of the transect area, this distribution diagram is tantamount to being that for *Thalassia* and *Cymodocea* only. The distributions there shown illustrate clearly point (i) outlined above. *Cymodocea* is shown to grow luxuriantly and predominantly in areas of deeper water in the outer reef and its distribution pattern also reflects the presence of deeper water in the inshore channel area. *Thalassia* clearly grows predominantly in the central raised areas of the reef-flat, but is also present in large amounts in the inshore ridge-pool area. Where areas of slightly shallower water exist in otherwise deep water areas in the outer half of the reef-flat, there is no reason to suppose that *Thalassia* could not grow in those circumstances. This again is reflected in the sporadic appearance of *Thalassia* in the coastal channel and reef-ridge areas of the outer reef-flat. Examination of the data derived from the North Steps (guest house) transect, from all other available profiles on West Island, from observations made by Rhyne and J. D. Taylor on West Island, and from additional observations by all of us in different parts of the island group, lagoon or seaward shores, showed no essential disagreement with any of the *Thalassia/Cymodocea* distributional data outlined above.

(4) *Syringodium*

S. isoetifolium is the exception among those marine phanerogams found commonly on Aldabra, in that it does not appear to grow on seaward reefs at all but seems to be confined to areas associated with lagoon drainage channels, particularly Western Channels, and there particularly in connexion with the 'mushroom islets', described more fully in the lagoon flora section later.

Reference to figure 11 will show a diagrammatic representation of the circumstances in which *Syringodium* is most often found in Western Channels area, in connexion with 'mushroom islets'. Similar isolated islands actually standing in the deeper parts of channels, for example in Passe Femme, Western Channels, are surrounded by rather deeper water areas, fringed by *Cymodocea*, than is the case with the mushroom islets farther back into the lagoon. The projecting ledges caused by undercutting of these islands in deep water provide a shaded environment in which *Syringodium* also occurs, thus bringing the latter into direct juxtaposition with the fringing *Cymodocea*. An example of this juxtapositioning is illustrated by the photograph in figure 21a, plate 13.

Isaac (1968, p. 39) comments that, in Kenya, *Syringodium* is found in inshore fringing pools, seldom in dense beds; this agrees in principle with the situation found in Western Channels. She goes on to say, however, '... there must be much denser growths in deeper water since, at times, large quantities of leaves and stems are washed up on the beaches...'. No evidence of

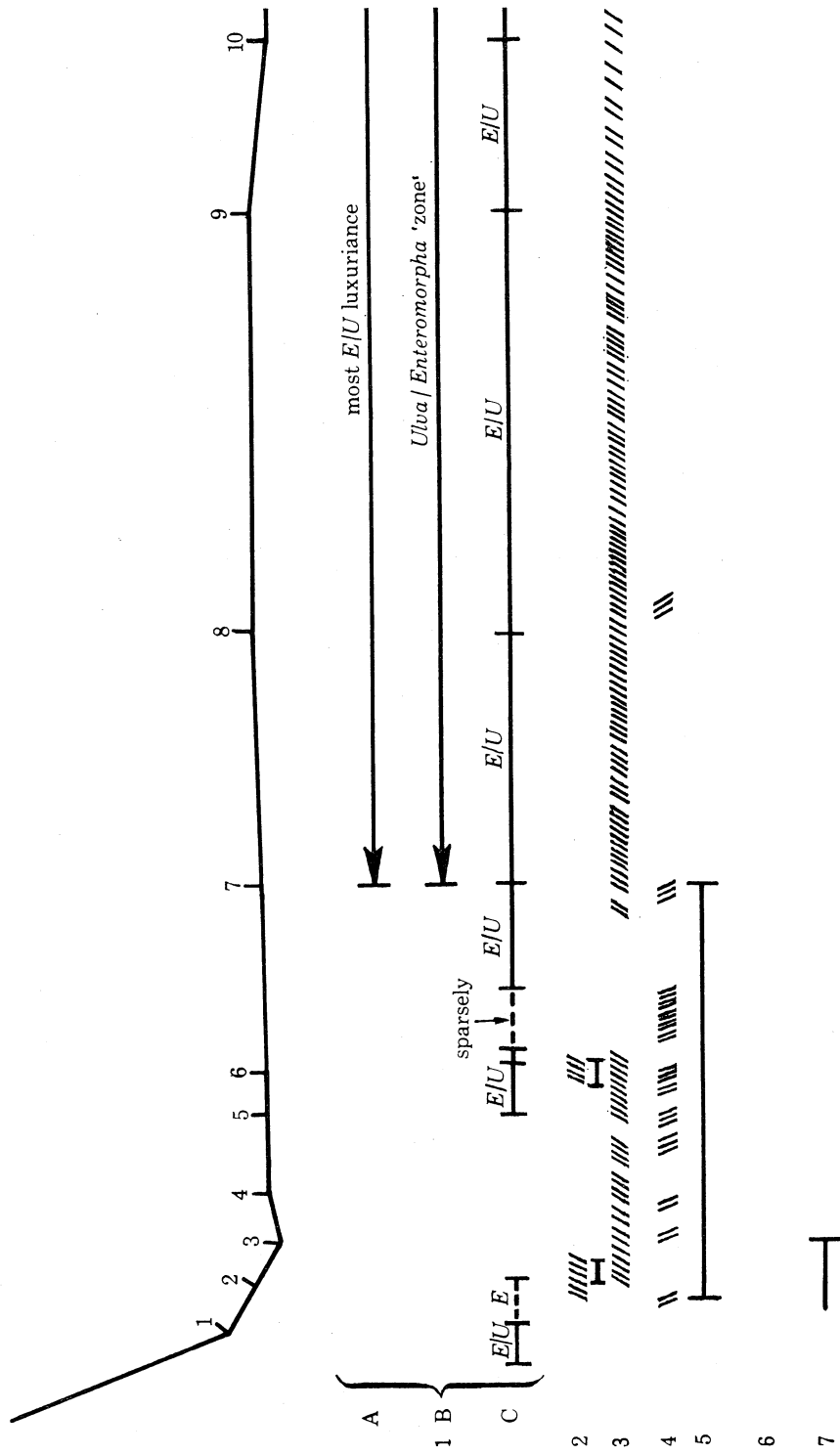


FIGURE 10. For legend see facing page.

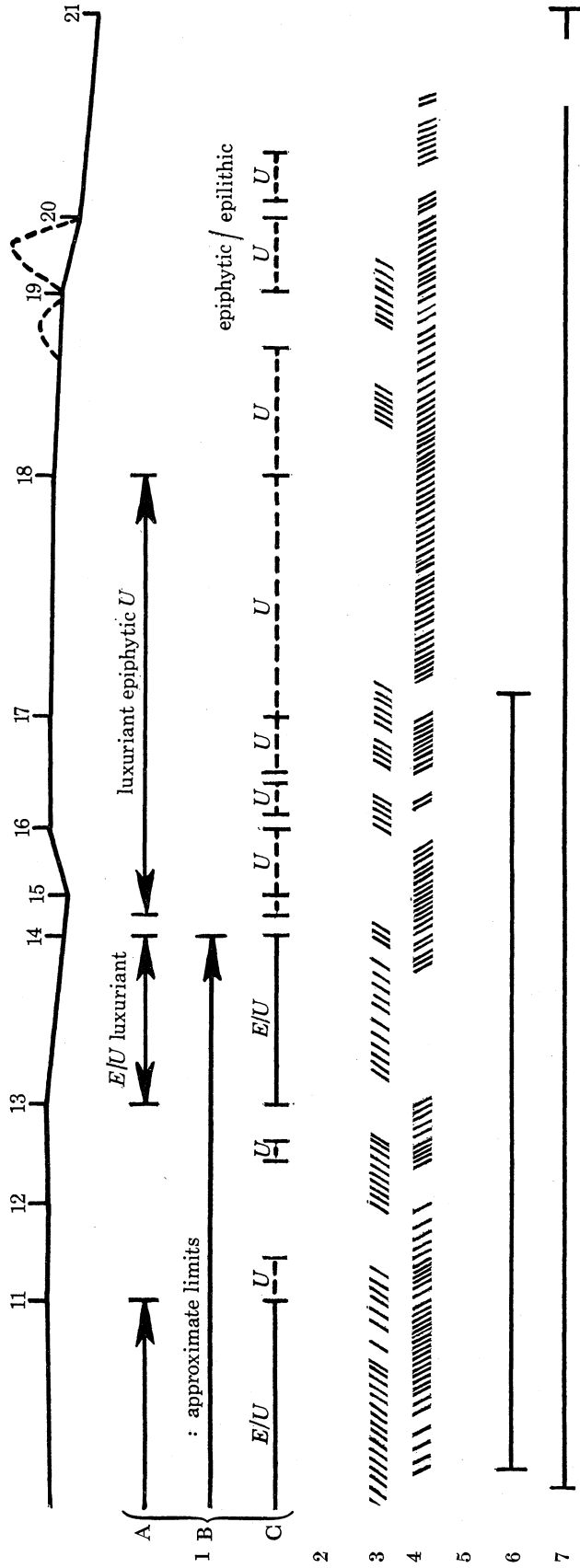


FIGURE 10. Profile of Western Channels transect, to scale of vertical 1:120, horizontal 1:1200. Shows distribution of *Halodule*, *Thalassia*, *Cymodocea*, *Ulva* and the *Ulva/Enteromorpha* zone. Numbers on profile indicate marker positions. Distribution numbers:

- (1) *Ulva/Enteromorpha*: throughout, *E/U* indicates both present; *U*, *Ulva* only; *E*, *Enteromorpha* only. A, areas of luxuriant development of either or both. Between markers 7 and 11, *E/U* balance changes locally and continually; B, limits of *Ulva/Enteromorpha* zone; C, detailed distribution from which A and B are derived.
- (2) *Halodule* } Distance between sloped lines is measure of density of growth.
- (3) *Thalassia* } Breaks indicate absence at that point. Lines between 2 and 3 show overlap areas
- (4) *Cymodocea* }
- (5) Area of ridges and deep pools, with inshore channel. Indicated by *Thalassia/Cymodocea* overlap there.
- (6) Area of *Thalassia/Cymodocea* overlap, in lower areas seaward of raised reef-flat.
- (7) *Turbinaria* distribution (see figure 13 for more details of 'reef-ridge' area).

such massive drift has been seen in the course of the present study, so that the existence of dense sublittoral growths of *Syringodium* on Aldabra must be viewed with doubt.

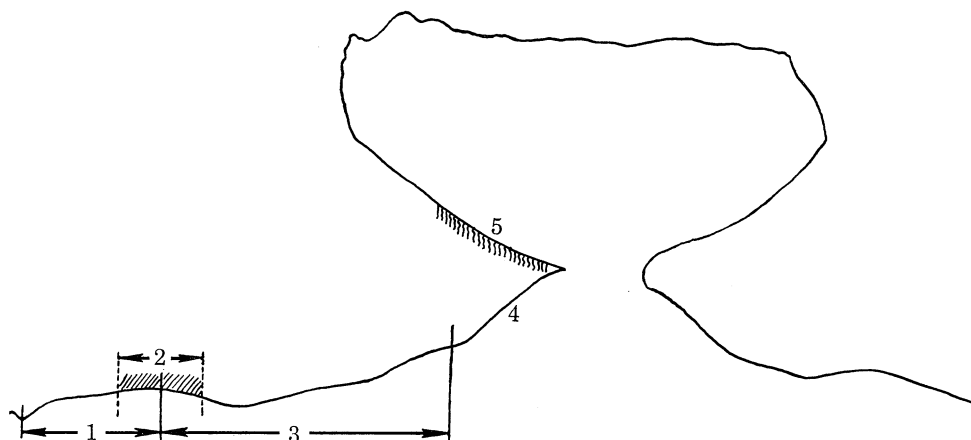


FIGURE 11. Schematic plan of the zonation around and under one of the 'mushroom islets' in the lagoon side of Western Channels. The drawing is not to scale. 1, *Ceramium*: near pure population (ground cover 50%); 2, *Thalassia* and *Syringodium*: in raised overlap area (ground cover 50%); 3, *Halimeda*; *Caulerpa taxifolia*; *Dictyota*; ?*Lithophyllum*; large orange hydroid (ground cover 25%); 4, *Halimeda* and hydroid, more sparsely; filamentous red (ground cover about 20%); 5, Pendent clumps of the filamentous red (ground cover less than 10%).

(ii) *Marine algae, with comments on the marine fauna and its distribution*

(1) *Halodule areas*

Generally speaking, the algal flora in areas dominated by *Halodule*, whether of ridge-form situation such as near Western Channels or of ridge-pool 'zonation' situations as on the reef-flat farther north, is somewhat sparse. Examination in some detail, not only of the transect area itself but also of adjacent stretches of *Halodule*, revealed no algae attached to grains of, or buried within, the sand apparently bound by the rhizomatous system of *Halodule*. The few genera involved were all epiphytic upon the basal parts of *Halodule*. *Enteromorpha*, *Laurencia* and *Gelidium* were present, only the first-named being at all frequent. *Cymodocea rotundata* and *C. ciliata* debris was intermeshed with *Halodule* basal rhizomes but, as already indicated in the section on marine phanerogams, no really attached material was present. The rhizome systems provided shelter for many amphipods and the gastropod *Columbella turturina* was also present.

(2) *Areas dominated to a greater or lesser extent by the presence of Cymodocea and/or Thalassia*

(i) *Introduction*

The distribution of the characterizing *Cymodocea* and *Thalassia* has already been discussed and that of the other 'zonal indicators' within *Thalassia*/*Cymodocea* areas, *Ulva* and *Enteromorpha*, is discussed in the next section. Only the distribution of other marine algae, therefore, is the concern of this present section. Detailed lists of algae within different transect sections falling in the *Cymodocea* and *Thalassia* areas, while illuminating, would be somewhat repetitive. Therefore, an attempt has been made to recognize algal and faunal groups on the basis of the habitat or habitat-type in which, most commonly, the groups appeared. Several algae are not distinguishable as occurring within any particular habitat or habitat-type and it is clear that the

provision of any adequately firm and/or long-lasting substratum is likely to be all that is demanded in these cases. With this latter reservation firmly noted, the basis for an attempted system of separation may be stated as follows:

(1) *Epilithic flora/fauna*. All elements attached or living on inorganic substrata and therefore including those apparently attached to ('epipsammon'), or buried in, sand.

(a) Species found only in shallow water, or in water-skins.

(b) Species found only in deeper water.

(c) Shade flora/fauna from crevices, under live or dead coral or coral blocks, or under dense stands of marine phanerogams only.

(d) Boring biota in live corals, live calcareous algae, consolidated or unconsolidated coral or calcareous algal debris, or in shells.

(2) *Epiphytic, endophytic, or epizoic biota*

(a) Species found on or in *Thalassia*.

(b) Species found on or in *Cymodocea*.

(c) Species found on or in other larger flora, such as *Halimeda*, or animals.

As with all attempts at classification at all levels, it is not possible easily to fit all situations into this system. Occasionally, particularly on the surfaces of consolidated coral blocks (and therefore predominantly applying in the 'reef-ridge' area—see that section for further data), it is very difficult to decide whether a form is epiphytic or epilithic. This is the case when, as is usual on blocks or boulders, the flora consists of a more or less continuous, completely mosaic 'mat' or 'turf' composed of many intermeshed algal genera and species; this intermeshing takes the form not only of lateral involvement but also of multi-level growth, over-growth and re-over-growth, so that the situation with regard to what is growing on what becomes exceedingly difficult to resolve. It is not uncommon to detach a luxuriant specimen of *Pocockiella* from the shaded side or underside of a boulder or block, only to find that there exists beneath a complex turf of *Cladophoropsis*, *Gracilaria ?eucheumoides* and other *Gracilaria* spp., *Champia*, occasional *Botryocladia*, *Caulerpa racemosa* var. *peltata*, young *Dictyosphaeria*, and so forth, from which it is not at all clear what was first growing where. Detaching this turf in turn not uncommonly leaves behind parts of the stolon system of *Caulerpa*, which is found at least partially to be attached to an underlying covering of *Peyssonnelia* and not unhealthy looking *Porolithon*. Some pale idea of the superficial aspects of this situation can be gained from figure 17a, plate 11.

Similarly, although it is possible relatively easily to decide whether an intermeshed assemblage of plants, say in the drift, was derived from shaded or open conditions, it is never very easy to be absolutely certain about particular drift specimens of a species known to be found both in strong insolation and in shaded conditions. The density of pigmentation is some indication, but individual specimens tend to be so variable in this respect anyway, that certainty is not possible unless attached material is collected. The presence in shade conditions of specimens of such widely tolerant species is probably largely a matter of chance rather than of preference; for this reason, and because tolerance limits of species generally are so poorly known and assessment of total diurnal sequence of illumination in any location but open shore so difficult, *shade flora* in this system includes only those species apparently never found elsewhere.

(ii) *Epilithic biota*

(a) *Species found in shallow water or water-skins.* Generally, shallow waters over sand result in the presence of a flora dominated by *Thalassia* since, as already stated, *Cymodocea* seems to occur only or much more widely in deeper water. The limiting maximum depth of sand in which *Thalassia* and *Cymodocea* will still root down to the consistently underlying beach-rock or consolidated coral is not known, but it does seem that in sheltered areas *Thalassia* at least will tolerate considerable depth of sand. However, both genera appear to require the presence of underlying firm rock at some depth attainable by their rooting systems, for attachment to such an underlying stratum seems always to be achieved. Those few algae which are commonly epilithic in or on sand, by contrast, do not seem always to penetrate down to bed-rock for attachment. Where there are forms which often occur partially buried in sand but with a relatively uncomplicated holdfast region attached to rock beneath, it seems always to be the case that elsewhere there are luxuriant growths without much sand overlying the substratum to which they are attached. Thus it seems that the complexity of the holdfast and proximal region of a large plant can be taken as an indication of whether it commonly occurs in sand and happens to have penetrated it down to the firm rock underneath, or whether it requires firm rock and happens to tolerate being occasionally or semi-permanently swamped by sand to some depth or other. In the former case, the whole growth form of the plant tends to be recumbent or prostrate, and the holdfasts and lower parts of the branching systems tend to be elaborated into a complex intertwining mass of branches; the plant is normally found in turfs or mats, often of large extent. In the latter case, the holdfast is usually simple, often discoid, and even when fibrous seems to be of limited extent and rarely to support more than a few upright axes; the latter are often unbranched for some centimetres above holdfast level. An alternative plant form occasionally found extensively attached on or in sand is that of the delicate filamentous red algae which presumably are not of sufficient bulk to become entirely detached under wave-wash, unless, that is, a good deal of sand happens to be moved bodily at one time.

The *Gracilaria cacalia* aggregate, which occurs overlapping the eulittoral-sublittoral boundary, and which has already been referred to in the section on beach-rock and pool flora, provides a good example of the recumbent ramified growth form seemingly associated with consistent growth in sand or other soft substrata. On Aldabra, this species group has not been observed growing in any conditions other than buried deeply in sand or mud, and it has also been so reported from elsewhere by Isaac & Isaac (1968, p. 21). These authors comment that although sandy and muddy areas in Kenya do not have an extensive algal flora, locally certain species may be common. *G. cacalia* is recorded as being so at Mokowe, in soft mud, in March 1967. Isaac & Isaac go on to say that plants of species which grow both on the reef and in areas to seaward of mangrove may be fewer in number in mangrove mud but tend to be individually larger and more luxuriant there; they include *G. cacalia* in this. In general terms, this statement is true but, compared with its frequency in sandy areas of reef-flat and lagoon shores, *G. cacalia* has only rarely been found in mangrove mud on Aldabra. Although *G. cacalia* has occasionally been found with definite attachment to underlying beach-rock on West Island shores, much of most mats of the alga seems only to be buried in and perhaps attached to compacted portions of the sand. It is possible that after its initial attachment to beach-rock on primary growth, the alga then ramifies throughout the overlying sand, deepening it by enmeshment, without the need for further firm basal attachment, and even that the primary basal attachment is then

secondarily lost. These points have not been investigated further. It is of interest that Isaac & Isaac (1968, p. 23) later state that both *G. cacalia* and *G. crassa*, which, it seems, may be another form within the same species aggregate or group, are common in places on rocky platforms in the intertidal (*sensu* Isaac, see p. 125 above) and that *G. crassa*, especially, may be found uncovered at low water. No mention is made of a sand substrate overlying rock to which these algae are, by implication, attached. Dawson (1954), for the Nha Trang area, similarly states that *G. crassa* forms a multitude of attachment organs at intervals by which it adheres to the rock substrate over which it ramifies, but fails to mention sand or soft overlying detritus. It is clear that the taxonomy of this group of species or species aggregate, together with the detailed ecology of its constituent forms, needs much further study.

Some observations seem to indicate that *Ceramium*, *Centroceras*, *Polysiphonia*, and other genera with similar delicate filamentous growth forms actually do attach to and presumably aggregate, sand particles as their only attachment to an inorganic substrate; the detachment and loss ratio in these cases must be presumed to be rather high. Figure 19*b*, plate 13 illustrates an example of a commonly occurring association (*sensu lato*) of *Thalassia* both with epiphytic *Ceramium* and with clumps of what is predominantly *Ceramium*, but includes some *Polysiphonia* also, at about the same distribution density as the *Thalassia*, between plants of the latter. This type of association also commonly occurs as part of the zonation pattern around mushroom islets in Western Channels area of the lagoon (see figure 11). It is true that much of the *Ceramium* in these circumstances is attached to coral fragments which are still small but much larger than the sand particles in which they occur; nevertheless, a proportion of the clumps seem only to be attached to compacted sand grains which the holdfast regions themselves must be presumed to have aggregated initially.

The distribution of other shallow-water epilithic forms is largely a function of chance and the presence at adequate depths of cobbles or consolidated block substrata. Reference to figure 7, figures 15*a* and 20*a*, plates 11 and 13, and figures 3*a* to 3*d* will indicate something of the distribution of shallow and deep waters on the reef-flat areas studied, as well as giving further emphasis to the local variability. Because of this variability, the major facets of the distribution of particular genera have been summarized for all known areas of West Island seaward reefs. *Ulva* and *Enteromorpha* are omitted from this summary list, since they are dealt with in considerable detail in the next section. Aside from that, the list is by no means exhaustive and merely covers the genera for which most data are available at present.

Lithothamnia (*chiefly* Porolithon)

Plants occur on coral cobbles and blocks, when present, under *Thalassia*, in open/bare areas, in the *Ulva/Enteromorpha* 'zones', in *Thalassia/Cymodocea* overlap areas and in areas of dense *Cymodocea* growth. Usually *Porolithon* is not present in the deepest pools, unless these latter contain (atypically) coral cobbles or (more usually) coral blocks. It is supremely important in reef-binding or consolidation over the whole reef-flat, apparently, not only in *Thalassia/Cymodocea* dominated areas, but throughout the reef-ridge and seaward reef slopes as well. Some of the material from calm waters in mid-reef-flat may prove to be *Neogoniolithon*.

Peyssonnelia

The distribution of this alga is very much the same as that given for *Porolithon* above. Probably, this genus, being non-calcareous, has little or no lasting function in reef-consolidation. The plant is present also more or less throughout the reef-ridge and seaward reef slopes. Other genera may be here also included under this name.

Turbinaria

Seems to occur wherever on the reef-flat firm 'rock' surface is available for colonization. This is the case irrespective of whether standing water is present or not, but the plants grow more luxuriantly in the deeps (see figure 21 *b*, plate 13). In water-skins or on emergent boulders (see figure 17 *a*, plate 11) *Turbinaria* tends to be small in size and/or stunted. It is possible that a number of different species are here involved, but all those specimens examined in detail seem to fall within the species *T. ornata*, as recognized by Taylor (1964). See also Taylor (1966) for additional data. After dying out at the seaward edge of the eulittoral beach-rock pools, *Turbinaria* tends not to reappear in the inner half of the reef-flat, since substrata there are largely sand of some depth and/or mobile coral cobbles. In the West Channels transect area, no *Turbinaria* reappears in the reef-flat until deeps with coral blocks begin at the landward fringe of the *Thalassia/Cymodocea* overlap area; sublittoral reef-flat distribution in the transect area is therefore coincident with the outer half of the flat, and extends through the reef-ridge, the *Turbinaria* belt beyond and, more sparsely, into the seaward slopes (see figure 17 *b*, plate 11).

Dictyosphaeria

More or less consistently present in shallow depths, in water-skins, or occasionally emergent. Occurs on coral cobbles and coral blocks over much of the reef-flat from the seaward limit of the ridge/pool area out to the limit examined of the seaward slope beyond the reef-ridge. Only occurs in deep water on coral blocks rising to a height which brings the plant into shallow depths. Not infrequently, *Dictyosphaeria* is very common on blocks or boulders in areas of dense *Cymodocea* just inshore of the reef-ridge; sometimes then it is one of the most obvious algae, with *Ulva* and *Turbinaria*, after the dominant *Porolithon*.

Jania

This genus is more or less consistently present in shallow depths, in water-skins, or occasionally emergent. It occurs on coral cobbles and coral blocks over much of the reef-flat from the seaward limit of the ridge/pool area out to the seaward edge of the reef-ridge. Occasionally, it is present farther out in the seaward slope, but only as an epiphyte on *Cymodocea* (see the section on epiphytic algae). In the Western Channels transect area, *Jania* does not seem very much in evidence on the cobbles, dominated by *Ulva* and *Enteromorpha*, within the *Thalassia* and *Thalassia/Cymodocea* overlap areas. Occasionally, as on the reef-flat near the point where coral cliffs begin north of Settlement, the plants form a definite 'zone' of tufts on cobbles just within the raised *Thalassia* area peripheral to the *Thalassia-Cymodocea* ridge/pool zonation. *Jania* occurs also in *Cymodocea* areas just inshore of the reef-ridge, but only on boulder surfaces which rise near to or above the water surface, thus creating shallow-water conditions. To some extent, this provides a contrast with the *Jania* distributions noted on boulders in the reef-ridge itself. See that section for data.

Gelidiaceae

A number of forms, including the rather widespread *Gelidiella acerosa*, are present on the reef-flat or under *Thalassia*; less often, when *Cymodocea* is present in rather shallower water than seems usual for it, Gelidiaceans occur on coral pebbles beneath it. Generally, all these forms grow in mats more or less closely appressed to sand substrata, over consolidated or unconsolidated coral rock or pebbles, in shallow water or water-skins. Less often, these mats of varying size may occur on shaded situations in the reef, such as block undersides. The growth form of *Gelidiella* consists mostly of prostrate axes appressed to the substrate; from these axes arise spiky laterals of a very even length, commonly, developed more or less alternately on either side of the axis, but directed in straight or upcurving fashion upwards at 45° or more to the horizontal. *Gelidiella* is thus a rather distinctive plant, when present; it is not uncommon in clumps or mats on the inner part of the raised *Thalassia* flat, both north and south of Settlement.

Acrochaetoid red algae

These forms occur largely as epiphytes on the marine phanerogams and therefore are dealt with more fully in the section on epiphytic algae which follows. However, on the outer part of the reef-flat, Acrochaetoids are found growing and binding sand over many pebbles and rocks in water-skins or shallow water, as well as less frequently on the upper parts of coral blocks in deeper water.

Galaxaura

Occurs occasionally in similar circumstances to those described earlier for *Gracilaria cacalia*, but generally where less sand overlies coral pebbles. Commonly this is in the fringe of the sublittoral at the point between lower eulittoral and inner ridge/pool area, but occasionally *Galaxaura* is found, as at Anse Var, north of Settlement, in the inner part of the raised *Thalassia* flat, in bare areas with overlying water-skins. Less often, *Galaxaura* also occurs on the seaward side of the reef-ridge, in channels between boulders.

Udotea

Udotea is commonly a plant of the reef-ridge area, not of the reef-flat itself. Even in the former it is rare for large numbers of plants to be found together. However, a few plants were found in the mid-reef-flat raised area, in the offshore edge of the *Ulva/Enteromorpha* 'zone', in sand over boulders.

Since all the fauna observed was generally rather variable in the depths in which it was found, a single list with details of habitat is presented at the end of the section on algae from deeper waters.

(b) *Species found in deeper water.* Aside from purely local occurrences, deeper water in the *Thalassia* and *Cymodocea* dominated reef-flat areas largely existed only in the ridge/pool areas inshore and the *Cymodocea* deeps inshore of the reef-ridge. Where unusual factors entered, such as the presence of the inshore drainage channel flowing over the inner reef-flat of Western Channels area, rather more deep water was sometimes available. In the area immediately north of the Western Channels transect, this deeper area has produced thick *Cymodocea* beds with a varied, rich and quite luxuriant algal flora most nearly resembling that found in the

algal turf area, and to some extent in the shallower channels, of Western Channels. The more obviously important of the algae from deeper waters in the reef-flat were:

Halimeda

This genus was rarely found elsewhere than in standing water of some depth (more than 0.3 m), unless shielded by dense overgrowth of *Cymodocea*, in the reef-flat. It was consistently attached to cobbles or coral blocks, the former sometimes buried in sand in deeps. In Western Channels transect area, its distribution seems to reflect the presence of the deeper water of the inshore outflow channel, with a few plants occurring under *Cymodocea* patches farther out on the reef-flat; *Halimeda* does not appear again in any amount until deeper water and dense *Cymodocea* occur in the coastal channel. Then and outwards to the limits of the examined seaward slope, the plants were mostly attached to firm coral blocks. Some apparent correlation, by no means absolute, exists in the apparent distribution of segment sizes. Plants with larger segments seem to be much the more frequent in the reef-flat and on the landward sides of the reef-ridge. Plants with smaller segments mostly occupy the outer, seaward portions of the reef-ridge and the seaward slope beyond. The need for consistent standing water seems to be borne out by figure 22a, plate 14, where the whitened *Halimeda*, after an especially low tide in the Western Channels turf area, stands out very clearly. Growth of *Halimeda* in that area, as more fully indicated in a later section, is very dense and luxuriant. Similar, but less luxuriant, growth occurs peripheral to the Main Channel coast of West Island.

Laurencia

This genus is relatively rare and reduced in size, creeping over the substrate, on the reef-flat of West Island seaward shores. Large plants only occur in really deep pools in the ridge/pool areas of the inner reef-flat. Even there, there were but few specimens (mostly in the deeper water of the coastal channel just north of Western Channels) when compared with the situation in lagoon channels. Western Channels show luxuriant *Laurencia* (*papillosa*) in masses in the turf flora and in the shallower channels (the darker, indistinct patches in figure 22a are mostly of *Laurencia*); to a somewhat lesser extent, such growth also occurs on West Island seaward fringes of Main Channel. In view of the luxuriant *Laurencia* high on intertidal rock on shores exposed to strong wave-action and consistent water-movement at the eastern end of the 'atoll', the genus seems to need such consistent water-movement and interchange, together mostly with a certain depth of water, for good growth to occur.

Pocockiella (= Lobophora)

This genus does not occur often or very widely in the reef-flat area, but occasional plants were found on cobbles, under or associated with *Cymodocea*, in deeper pools in the inshore coastal channel area of Western Channels transect. Where occasional deeps occur in the *Thalassia/Cymodocea* overlap area and coral blocks are present, *Pocockiella* also grows, not uncommonly, in crannies on the sides of those blocks. These latter conditions mirror those in which *Pocockiella* occurs most luxuriantly, in shade conditions in the reef-ridge area. See the reef-ridge section.

Gracilaria

At least two species of this genus occur quite frequently on the inner reef-flat in water of depths greater than 0.3 m, commonly associated with *Cymodocea* though growing epilithically.

Both forms have especially been found in the deeper pools of the ridge/pool, inner *Thalassia/Cymodocea* zonation areas between Settlement and Western Channels, where they are both widespread and luxuriant. One species, *G. verrucosa* or a near relative, occurred as fantastically large individuals, specimens from single holdfasts requiring two large (1.1 l) collecting bottles for accommodation of the whole plant. This species was noted along the profiles given as (a) and (c) in figure 3. The second species, *G. wrightii* or a near relative, but one on which much work remains to be done, was usually present in larger numbers of specimens than *G. cf. verrucosa*. A species of rather lower growth than the latter, *G. cf. wrightii* was nevertheless the more obvious in lower tidal conditions as it was of decidedly firmer growth, projecting above the water surface at times (see figure 22a). Both species formed an important part of the algal constituents of the 'turf' in Western Channels area, as is obvious from figure 22a, and clearly require a considerable depth of water (and perhaps associated dense plant biomass as shade) for settlement and growth at all. No occurrence of either species in stunted form in other habitat conditions was observed. The firm, terete, more or less cervicorn *G. cf. wrightii* was found richly in fruit in parts of the reef-flat near the guest house profile line; an example of this appears as figure 22b. On less frequent occasions, the pools in eulittoral beach-rock were deep enough to support growth of this sublittoral species, sparsely, in that milieu.

Amphisbetema indica

This red alga of the Rhodomelaceae is of common occurrence in sheltered seaward flats of West Island in precisely similar conditions to those described for *Gracilaria*. The genus is apparently restricted to Aldabra and Diego Garcia, both in the Indian Ocean, although much taxonomic work remains to be done (Weber-van Bosse 1914, pp. 297-299). The material collected from *Cymodocea* pools in the deep-water areas of the inner reef-flat just north of Western Channels was luxuriant in size and growth and present in large amounts; the genus does not seem to be so restricted to these conditions as are the *Gracilaria* species, however, for rather infrequent small clumps of the plant were found near the inshore fringe of the reef-ridge in Western Channels area and on the seaward slope beyond the reef-ridge in the guest house profile area. Curiously enough, no evidence could be found of the presence of *Amphisbetema* in the algal turf areas of Western Channels. In view of the strong similarity in habitat conditions between these areas (as witnessed by the presence in both of the *Gracilaria* spp., although these latter were generally more widespread in the Western Channels turf), this problem needs further investigation.

Dictyurus purpurascens

This red alga of the Dasyaceae was occasionally found in shaded conditions on the undersides and sides of blocks in the reef-ridge area. However, it was relatively rarely in good growth in these conditions. Good growth was most often found in deeper waters in the inner reef-flat, where plants up to 15 cm in length in luxuriant masses were found; collections of this type were made at Anse Var, north of Settlement by J. D. Taylor.

Dasya

Plants probably to be referred to this genus were quite widespread in the middle and outer reef-flat. In the areas near Western Channels transect, large amounts of luxuriant specimens growing in thick tufts up to 15 cm across were present in the middle parts of the reef-flat;

mostly, these grew in association with *Cymodocea ciliata* in deeper pools of 45 cm or more in depth. However, material of the same species was present somewhat farther out towards the reef-ridge, though not on the latter, in water of rather shallower depth. Specimens in deeper water, associated with *C. ciliata*, were both epilithic on the larger coral fragments and epiphytic on distal parts of *C. ciliata*.

FAUNA, FREE-LIVING OR EPILITHIC, FROM SHALLOW AND DEEP WATERS
IN *THALASSIA/CYMODOCEA* DOMINATED AREAS

EPILITHIC

Coelenterata

Pocillopora

rare; underneath boulders, in deeps, *Thalassia-Cymodocea* overlap area

Favia

rare; small colonies underneath boulders, in deeps, *Thalassia-Cymodocea* overlap area

Stylocoeniella

not common; on coral blocks in deeps, *Cymodocea* area just inshore of reef-ridge

Acropora digitifera

not common; on coral blocks in deeps, *Cymodocea* area just inshore of reef-ridge

sponges

red sponge

on stones under *Cymodocea*, deeps in ridge/pool area

orange encrusting sponges

underneath boulders in deeps in *Thalassia/Cymodocea* overlap areas and on coral blocks in deeps with dense *Cymodocea* just inshore of reef-ridge

brown sponges

on stones under *Cymodocea*, deeps in ridge/pool area

ascidians

meandrine ascidian

underneath boulders in deeps in *Thalassia/Cymodocea* overlap areas

black ascidian

on coral blocks in deeps, dense *Cymodocea* areas just inshore of reef-ridge

pink/white ascidian

on coral blocks in deeps, under *Cymodocea* in ridge/pool area and in the dense *Cymodocea* areas just inshore of reef/ridge

Gastropoda

Tectus mauritianus

on coral boulder in the *Ulva/Enteromorpha* outfall area, *Thalassia/Cymodocea* overlap area

Cerithium rostratum

on coral cobbles under *Cymodocea* and in bare areas, ridge/pool areas

Foraminifera

Homotrema rubrum

on cobbles under *Thalassia*, and under *Cymodocea*, in ridge/pool area; also on coral blocks in deeps in dense *Cymodocea* areas just inshore of reef-ridge

Marginopora

very widely distributed in varying depths from water-skins to *Cymodocea* deeps throughout much of the reef-flat

worms

Spirorbidae, brown

under stones at the seaward fringe of the raised coral cobble area, *Thalassia* areas

Serpulid worms

dead only, on cobbles in inshore fringe of the ridge/pool *Thalassia/Cymodocea* area

Sabellid worms

on cobbles on raised flat and in deeper water under *Cymodocea*, *Thalassia/Cymodocea* ridge/pool area; also rather rarely on coral blocks in deeper water just seaward of the outfall edge, raised flat area

other animals

Schizoporellid polyzoans

underneath boulders and on coral blocks, in deeps; throughout much of reef-flat from ridge/pool area to *Cymodocea* deeps just inshore of reef-ridge, but rather sparsely distributed

hydroids

on stones under *Cymodocea* in the ridge/pool area and on and underneath blocks in the deeps in *Thalassia/Cymodocea* overlap areas.

anemones, green, striped with white

underside of large coral pebbles, seaward edge of raised *Thalassia* flat

FREE-LIVING

Bivalvia

Chama asperella

underneath boulders, in deeps in *Cymodocea/Thalassia* overlap areas

Ostrea numisma

crannies in sides of coral blocks in deeps in *Cymodocea/Thalassia* overlap areas

Gastropoda

<i>Cypraea helvola</i>	on coral blocks in deeps in dense <i>Cymodocea</i> area inshore of reef-ridge
<i>Triphora monilifera</i>	on cobbles under <i>Cymodocea</i> , ridge/pool area of inner reef-flat
<i>Morula wa</i>	juvenile forms on cobbles under <i>Cymodocea</i> , ridge/pool deeps in inner reef-flat. Also on cobbles at seaward fringe of <i>Thalassia</i> raised flat area

Crustacea

galatheid crab	on cobbles under <i>Cymodocea</i> , in ridge/pool area of inner reef-flat
small crab	in <i>Jania</i> , epilithic on cobbles under <i>Cymodocea</i> , in ridge/pool area of inner reef-flat
Pagurid (hermit) crab	on cobbles at seaward fringe of <i>Thalassia</i> raised flat area
shrimps	in crevices underneath boulders, in deeps, <i>Thalassia/Cymodocea</i> overlap areas

J. D. Taylor (unpublished) has made many more detailed faunal observations elsewhere on West Island reef-flats in the course of his subsequent independent work on Aldabra. The determinations and distributions noted above are those derived mainly from joint work on the Western Channels transect area, with a few additional observations made elsewhere on the reef-flats.

(c) *Shade flora and fauna from various habitats.* Although ideally it should have been possible to consider these species in a separate section, in practice it proved more practicable and meaningful to relate their occurrence to the depths of water apparently required for, or providing optimum circumstances for, particular groups or associations (*sensu lato*) of the shade biota. Thus, shade habitats in the *Thalassia/Cymodocea* dominated areas have been covered as appropriate in the above text, whilst similar habitat conditions in the reef-ridge area, and their relation floristically to illuminated surfaces in the reef-ridge, are considered in the sections which follow concerning the reef-ridge.

(d) *Boring flora and fauna, in various calcareous substrata.* Insufficient data are as yet available from the work done to permit meaningful habitat comparisons to be made. It is intended to present such data in later, more detailed, ecological work.

(iii) *Epiphytic and epizoic biota:*(a) *Thalassia-borne flora and fauna**Flora*

The following list summarizes data on those epiphytes which have been observed on *T. hemprichii*:

Melobesia

On leaves in the inner ridge/pool area, very frequent, especially apparently on dead leaves.
Less frequent, but still common, further out in the ridge/pool area.

Gelidiaceae

On bases of *Thalassia* in the inner fringe of the ridge/pool area.

Ceramium

Epiphytic on and epilithic under and among *Thalassia* leaves, on sandy raised area in 2 to 12 cm of water, virtually throughout the reef-flat but predominantly in the middle third between the eulittoral and reef-ridge. See also the following entry.

Other Ceramiaceae, *Polysiphonia* and other Rhodomelaceae

In the Western Channels transect area, epiphytic on *Thalassia* leaves virtually throughout the reef-flat, but predominantly in the middle third as with *Ceramium*. Mostly occurring in slightly deepening water on the edge of pools, in about 15 cm depth. Usually in straggling clumps either very lightly pigmented throughout (as in *Polysiphonia*) or very lightly pigmented, often appearing translucent, apically (as in most other genera). Elsewhere, in the profile about 80 m north of the Western Channels transect area, a variety of Ceramiaceae and Rhodomelaceae occur epiphytic on *Thalassia*. In this area of the West Island seaward reefs, a definite 'zone' of predominant epiphytism on *Thalassia* occurs in the inner half of the area of *Thalassia* dominance (see figure 5). This zone of epiphytism involves mainly *Ceramium*, *Spyridia*, *Polysiphonia*, and some specimens, particularly of Rhodomelaceae, seem to be epilithic amongst *Thalassia*, or in sand over the coral.

Acrochaetioids

On leaves in the inshore fringe of the ridge/pool area.

*Fauna**Cerithium rostratum* (Gastropoda)

On *Thalassia* leaves, middle ridge/pool zonation area.

Smaragdia rangiana (Gastropoda)

On *Thalassia* leaves, inshore fringe of ridge/pool zonation area.

Marginopora (Foraminifera)

Widely distributed on *Thalassia* leaves over the whole reef-flat from inshore fringe of the ridge/pool zonation area out to and beyond the reef-ridge area. Also, equally widely present on all other living plant substrata, phanerogamic or algal.

Ophiuroids, small (Echinodermata)

On *Thalassia* leaves, in the ridge/pool zonation area.

Spirorbid worms

On *Thalassia* leaves in the midpart of ridge/pool zonation area.

(b) *Cymodocea*-borne flora and fauna

Flora: mainly on *Cymodocea ciliata*.

Melobesia

On *Cymodocea* stems and leaves in deeper waters over the whole of the ridge/pool zonation area.

Ulva

The epiphytic distribution is considered in full in the separate section on *Ulva* and *Enteromorpha*. A summarized diagrammatic representation appears in figure 10.

Gelidiaceae

On *Cymodocea* stems in the ridge/pool zonation area of the reef flat, but rather sparsely.

Ceramiales, mainly *Ceramium*

Epiphytic on *Cymodocea* in pools in the deeps, outer reef-flat just inshore of the reef-ridge; also in deeper pools in the inner half of the reef-flat.

Acrochaetoids (probably mixed with *Polysiphonia*)

On *Cymodocea* stems, in most deeper water areas of the reef-flat, but only locally common.

Laurencia

Relatively rare as an epiphyte, but not uncommon on *Cymodocea* stems in deeper pools both in the outer reef-flat inshore of the reef-ridge and in the deeper areas of the inner half of the reef-flat.

Peyssonnelia

On *Cymodocea* stems in deeper waters in the ridge/pool zonation area; fairly rare.

Dasya

See the note on *Dasya* in the section on epilithic algae. Luxuriant material growing in thick tufts up to 15 cm across grew attached to *Cymodocea ciliata*, mostly to stems, in deeper pools 45 cm or more deep on the middle reef-flat area.

Lithophyllum

This material has yet to be examined in any detail. Massive, very brittle, thin-lobed colonies, with lobes sometimes upright and fluted, sometimes recumbent, were locally dense, growing on and among *Cymodocea ciliata* in deep water, inner third of the reef-flat north of the Western Channels transect area.

Microdictyon

Epiphytic on *Cymodocea*, mostly on stems, in pools in the outer reef-flat, inshore of the reef-ridge; also occurs in deeper pools in the inner half of the reef-flat.

Champia

Occasionally epiphytic on stems of *Cymodocea ciliata* in deeper water just north of the Western Channels transect area. Not common.

Fauna

Columbella turturina (Gastropoda)

On *Cymodocea*, in mid-reef, on coral blocks in deep water just seaward of the outfall from the *Thalassia* raised flat.

Smaragdia rangiana (Gastropoda)

Distribution exactly as for *Columbella*.

Sertularioid hydroids

Distribution exactly as for *Columbella*.

Spirorbis worms

On leaves of *Cymodocea ciliata* in deeper pools of the ridge/pool zonation area of the inner reef-flat.

Marginopora (Foraminifera)

Widely distributed on *Cymodocea* leaves, and rather rarely stems, over the whole reef-flat from inshore fringe of the ridge/pool zonation area out to and beyond the reef-ridge. Also equally widely present on all other living plant substrata, phanerogamic or algal.

(c) *Species borne on other larger flora or fauna.* The most obvious of the remaining larger plants as a substrate for epiphytic flora and fauna was the green calcareous alga *Halimeda*. Both large and small segmented forms of this genus bore various epiphytes in varying numbers and, of these, the commonest seemed to be:

*Peyssonnelia**Jania**Melobesia*

Fine filamentous reds, probably mostly Acrochaetioids mixed with *Polysiphonia*. These latter plants also occurred in some areas epiphytic on *Gelidiella*.

In deep waters in the ridge/pool area, *Halimeda* occurred both under dense *Cymodocea* (rarely) and attached to coral cobbles in bare patches between *Cymodocea* plants or groups (more frequently). In the latter case, the following were associated at times (rarely) basally or epiphytically with the *Halimeda*:

Laurencia (basally associated or epiphytic)

Jania (epiphytic)

Peyssonnelia (epiphytic)

Hypoglossum (epiphytic)

Occasionally as at Anse Var, north of Settlement, *Halimeda* bore rather unusual epiphytes. Observed were a dichotomous plant of *Codium* and various small plants of *Ulva*.

Animals were rather rarely borne epiphytic on *Halimeda* or, indeed, on any of the algae. The exception to this statement is the foraminiferan *Marginopora*, which was widely distributed on all larger algae over much of the reef-flat.

The presence epizoically of algae on animals seemed a relatively unusual occurrence, though the coating of such fauna as *Conus* and other gastropod shells by *Porolithon* and *Peyssonnelia* did not seem so rare an event.

(3) *Ulva/Enteromorpha areas within Cymodocea/Thalassia dominance*

Ulva and *Enteromorpha* are present over much of the reef-flat area in Western Channel transect area and this is also true of other areas of West Island seaward reefs. Both genera also figure strongly in both eulittoral areas on beach-rock and the 'algal turf' areas associated with Western Channels. Both genera, but more especially *Enteromorpha*, are also present in massive amounts as almost the whole flora of certain lagoon shores of South Island. All these additional aspects are dealt with either elsewhere in this paper or in the paper of J. D. Taylor (this volume, p. 173).

From the Western Channels transect data and other observations, there seem to be several recognizable functional limitations in distribution of the genera (see figure 10):

(i) Until one reaches the inshore edge of the *Cymodocea*-dominated outer reef-flat areas, the only substrate on which either of the genera appears is smaller coral cobbles buried in sand or otherwise more or less fixed.

(ii) In every case in these inner flat areas, only very shallow pools, or more often only water-skins, are involved. Both genera are absent from the deeper standing or moving waters of the inshore channel area.

(iii) At the onset of *Cymodocea* domination, and therefore of deeper water, in the outer flat areas, two things happen. *Enteromorpha* dies out entirely and can be taken to be unable to tolerate continued submersion in more than a very few centimetres of water under these general conditions. *Ulva*, on the other hand, remains a very noticeable, though more sparsely distributed, feature of the flora, only becoming rare and then dying out beyond the reef-ridge, in the *Cymodocea* band there. Except where, in the region of the reef-ridge particularly, boulders in shallow water or with shaded sides exist, when it remains to some extent epilithic, however, *Ulva* now becomes epiphytic on the upper parts, generally the leaves, of *Cymodocea ciliata*. Thus, it seems to be tolerating a different substrate but adopting a similar position relative to the prevalent water depth in these deeper areas as it did in shallow water-skins in the inner reef-flat.

In all the areas examined in sufficient detail on West Island seaward reefs, it was possible to recognize a definite 'zone', in approximately the same position on the flat, the most immediately striking and predominant feature of which was the green, cobble-attached sward of *Ulva* and *Enteromorpha*. Throughout such areas, the balance between the two genera seems continually to be variable according to the local conditions. While this is probably in detail a highly complex matter involving many aspects of physical environment and biology of the species concerned, it does seem to correlate to some extent with an apparently greater ability of *Ulva* to tolerate consistently moving water, and presumably therefore better aeration and slightly lower temperatures, than is the case with *Enteromorpha*. In Western Channels area, the recognizable 'zone' seemed to extend from about marker 7 to marker 14, a distance of about 230 m in which the vertical level relative to Chart Datum varies only from 0.28 m (0.92 ft) below down to 0.72 m (2.37 ft) below.

A detailed illustration of the differential distribution of *Ulva* and *Enteromorpha* is provided by figure 12, which represents the situation around marker 10 on the West Channel transect. There, an uneven fall of some 30 to 35 cm occurs in the level of the reef-flat which, at low water, produces a draining edge; this edge is funnelled along the line of the transect, there forming a definite outrun channel with an appreciably strong downflow of water. The higher, coral cobble area inshore is largely covered by *Thalassia* which, however, becomes sparse in the last 6 to 7 m before the outrun channel, giving way to a cover of *Enteromorpha* attached to coral cobbles. The area immediately above and below the tidal water level at low water of spring tides is covered, quite densely, by an 'Ulva-fringe'; this consists mainly of *Ulva*, but in the upper part there persist patches of locally dominant *Enteromorpha*. Below, the outfall gives way to deeper water over sand-tongues, with sand of variable level lying over coral rock. In the shallower portions of this lower area, *Thalassia* plants grow in quite large clumps and appear to hold sand to the extent of clearly raising the area around where they are growing by up to 8 to 10 cm over the uncolonized surrounding sand. A few small *Cymodocea* clumps grow in deeper water, and cobbles, where present in shallower areas, bear a flora largely of *Ulva*, but with occasional *Enteromorpha*. The situation illustrates clearly the apparent preference of *Enteromorpha* for water conditions which do not involve a great deal of water movement, since all that area down which outfall water consistently drains is covered by the *Ulva* fringe.

(4) Shattered 'reef-ridge' area

(i) *Details of the Western Channels transect 'reef-ridge'*. Over the whole stretch of the seaward calm water reefs of West Island, the 'reef-ridge' consists only of irregularly distributed, sometimes aggregated, blocks of dead coral. These blocks are individually cemented with varying firmness by living and dead *Lithothamnia*, chiefly *Porolithon*. Similarly, individual blocks or groups of blocks are sometimes merely lying on the reef-flat surface, sometimes partially cemented thereto by *Lithothamnia*, sometimes immovably fixed thereto. Grouped blocks are similarly cemented to a variable extent to each other. As will be seen from figure 13a and figure 17b, plate 11, the blocks do not usually stand particularly high above the reef-flat surface; for the most part the biggest are not more than 0.5 to 0.6 m high but some few reach about 1 m high.

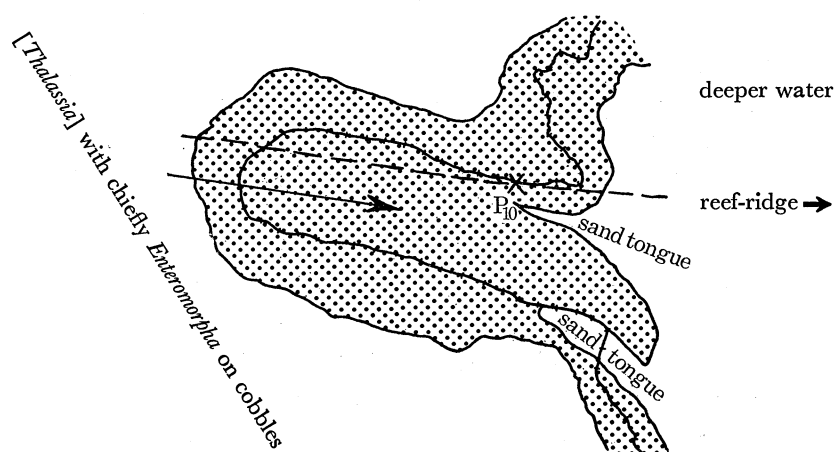


FIGURE 12. Distribution of *Ulva* and *Enteromorpha* in gently sloping outrun channel from reef-flat to deeper standing water around marker 10 on Western Channels transect. (Semi-diagrammatic: not to scale.) P₁₀, Piton 10 of Western Channels transect; ~~~, water edge at near low water, spring tides; →, direction of outrun, level drop 30–35 cm maximum; ---, line of transect; ▨, *Ulva* fringe: mainly *Ulva*, with patches of locally dominant *Enteromorpha*. [], indicates *Thalassia* sparse in last 6 m before P₁₀.

All the blocks stand in a continuous skin of water connecting the reef-flat pools and skins, continuously, with the tide front, even at extreme low water of spring tides. In the ridge area, this skin is usually of the order of 7 to 30 cm deep, most commonly 7 to 20 cm. The boulders or boulder groups are distributed over the reef-flat area which they occupy, but the width of this area, in parallel to the true eulittoral beach line or to the tide front, is very variable along the seaward reef. It is at what appears to be its widest at and near the West Channel transect line, where it reaches 31.3 m; elsewhere along West Island seaward coasts it is often no wider than 3 to 7.5 m.

The shattered reef-ridge morphology in West Channels area is further complicated by the existence of a discontinuous outlier group of blocks lying some 15 m to landward of the main block area. The outlier is separated from the main 'ridge' by an area overlain by small coral pebbles and carrying a flora, chiefly of *Cymodocea*, with a little *Thalassia*, functionally identical with that of the other adjacent landward areas of reef-flat.

As is evident from figure 17b, plate 11, boulder or block or block-aggregate undersides, even

when firmly cemented to the reef-flat substrate surface, rarely fit flush in a smooth concave curve to that surface. This is true in both main ridge and outlier. Merely by nature of the erosive power of sea water on coralline rocks, it is usual to find more or less deeply incut undersides which provide a shade microniche or set of microniches. In these latter, the flora and fauna differ at least in density, more usually at least partially in kind, from those of the sides and tops of the boulders or blocks. The intrusive element in both flora and fauna is largely sciaphilous and, although this is not true of the Western Channels transect area, there is occasionally some correspondence floristically with the sciaphilous element on the lower portions of the eulittoral undercut cliffs.

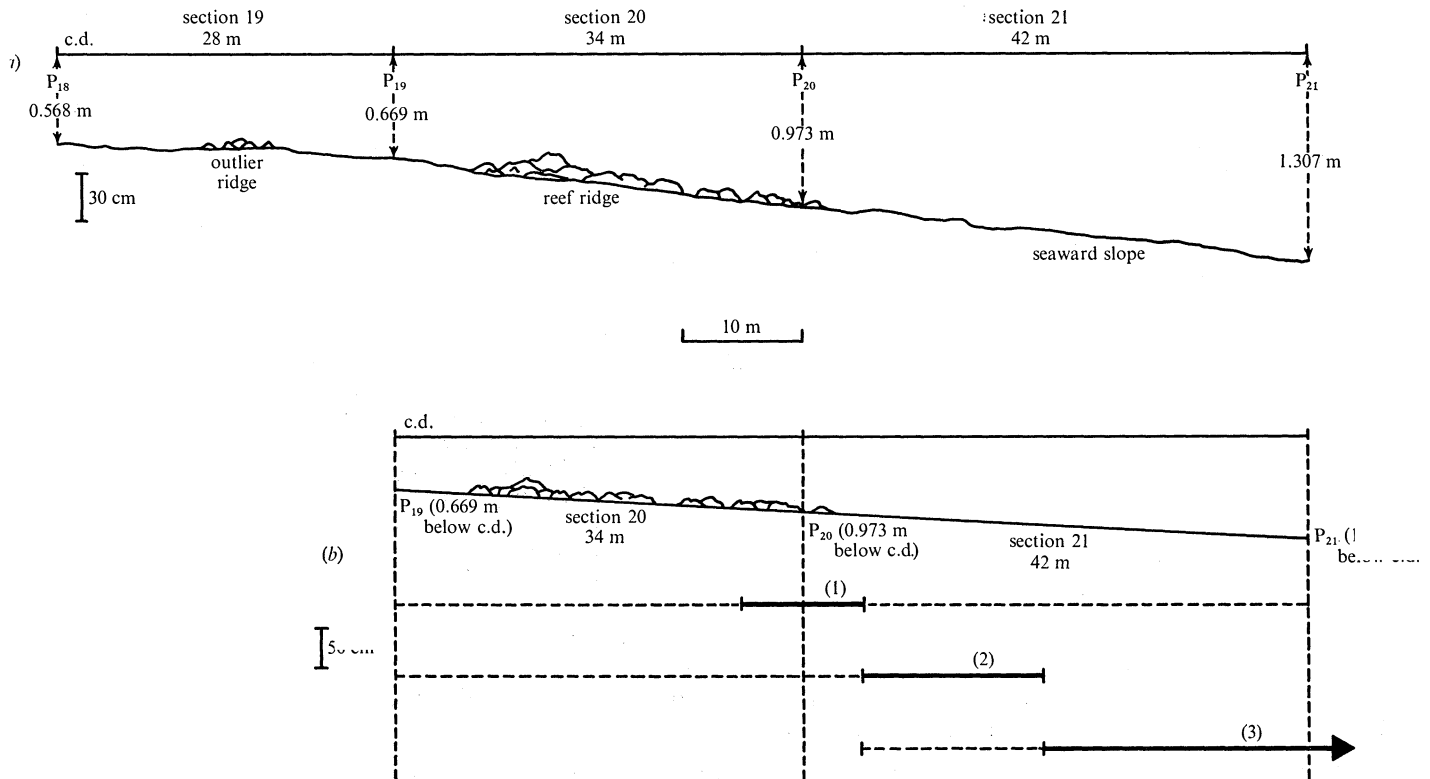


FIGURE 13. Area around Western Channels transect sections 19, 20 and 21 showing reef-ridge and outlier ridge. (a) Outline profile, with notes. (b) Semi-diagrammatic profile slope of the area, lacking detailed changes in configuration but showing the linear distribution of (1) *Turbinaria* band; (2) *Cymodocea* band, discontinuous patches; (3) living corals (with *Porolithon*, *Peyssonnelia*, occasional *Turbinaria*). Broken horizontal lines show possible occurrence of species, but not continuously, nor in band form; thick horizontal lines indicate 'bands' or 'zones' of species concerned; c.d., throughout, indicates chart datum.

Figure 13 gives an outline profile, with notes, of the area around Western Channels transect reef-ridge and outlier. This area embraces part or the whole of sections 19, 20 and 21 of the transect profile; since the total combined lengths of those sections is about 105 m (346 ft), it was clearly not possible to examine every boulder/block along even a belt transect through this distance. Therefore the observations which follow are derived from detailed study of certain arbitrarily selected sample blocks with additional data more cursorily derived from other blocks on which obvious differences existed. Sample blocks from section 19, representing the outlier ridge area, bore the following flora and fauna:

plants	animals
BLOCK TOPS	
<i>Turbinaria ornata</i> (few adults only, with some juveniles)	<i>Carpentaria raphidodendron</i>
<i>Cladophoropsis</i> (dominant; turf forming)	
Lithothamnium (probably largely <i>Porolithon</i> ; dominant but crust-forming)	
<i>Peyssonnelia</i>	
<i>Jania</i>	
<i>Dictyosphaeria</i> (solid and hollow forms, but rare)	
<i>Hypnea</i> (few only)	
Acrochaetoid? red	
BLOCK SIDES	
<i>Dictyosphaeria</i> (solid and hollow forms; large amounts on some blocks)	<i>Marginopora</i> (Foraminifera)
<i>Ulva</i>	
<i>Jania</i>	
<i>Microdictyon</i>	
Lithothamnium (abundant; largely <i>Porolithon</i>)	
<i>Peyssonnelia</i>	
<i>Laurencia</i> (three species)	
Gelidiaceae (prob. <i>Gelidiella</i>)	} (rare; in the continuous 'turf')
? <i>Gracilaria eucheumoides</i>	
? <i>Boodlea</i>	
BLOCK UNDERNEATH/UNDERSIDES	
?blue-green algae covering, blackening and penetrating into rock	<i>Homotrema rubrum</i> (abundant)
	Sertularioid hydroids (abundant)
	<i>Cypraea kieneri</i> (juvenile only)
	<i>Conus rattus</i> (rare)
	<i>Peristernia nassatula</i> (gastropod)
	<i>Cymatium pileare</i> (gastropod)
	sponge (orange; in small amounts)
	ascidian (pink; in small amounts)
	nudibranch (single specimen, not possible to determine)
	polyzoan (branching)

This smaller outlier area of coral blocks covered an area which at right angles to the shoreline was about 8 m wide and graded gently seaward into a slightly lower flatter area before the 'reef-ridge' proper. Since approaching the outlier from the inner reef-flat also involved a rise of some 0.2 m to the boulder-bearing area, it may be that the presence of the boulders has reduced wave erosion and slowed the rate of debris removal. To a degree, this is speculative, since the matter has not been checked in detail over the whole area on which the outlier is present.

The area immediately seaward of the outlier supports a relatively dense flora of *Cymodocea* with an admixture of some smaller amounts of *Thalassia* (in raised patches) (see figure 20a, plate 13 for a similar area.) Small coral pebbles cover a good deal of the area not occupied by marine phanerogams, and these pebbles bear *Porolithon*, *Peyssonnelia*, stunted *Turbinaria*, a few *Dictyosphaeria*, a few *Halimeda* and, more rarely, Hypneoid reds. The *Cymodocea* itself bears considerable numbers of leaf and stem epiphytes, many of which are common to other substrata, either in the immediate vicinity only or over much of the reef-flat. These widely distributed forms seem to attach to any substrate which is available and consequently appear wherever the load-bearing capacity of the substrate is adequate. In the present area, epiphytes noted widely in section 19 included:

stems	leaves
<i>Chondria?</i>	<i>Melobesia</i> (widespread)
<i>Microdictyon</i>	<i>Ulva</i> (occasional)
Acrochaetioid reds	
<i>Jania</i> (rare only)	
<i>Peyssonnelia</i>	

In addition, the leaves bore epiphytic hydroids in some profusion. The *Cymodocea* area lacking blocks or boulders in turn grades into the main 'ridge' area to seaward, but the reef-flat area on which the boulders and blocks of both outlier and main ridge rested was at much the same level throughout, therefore bearing a very similar flora, although there was almost no *Thalassia* in the channels between boulders of the main ridge, nor indeed to seaward of the main ridge area. Although coral pebbles bearing the flora previously detailed exist in the main ridge channels, the most conspicuous elements present as reef-flat surface flora throughout the whole of sections 19, 20 and 21 are *Cymodocea*, *Ulva* and *Dictyosphaeria*.

The main ridge area of Western Channels transect largely concerns section 20 profile, though its residual seaward portions run over into section 21. Sample boulders were again arbitrarily chosen and additional observations made from other blocks or boulders. Distributions noted on the main ridge were as follows:

plants	animals
BLOCK TOPS	
<i>Valonia</i> sp.?	<i>Tetraclita squamosa</i> (barnacle)
<i>Gelidella acerosa</i> and other Gelidiaceae	<i>Morula granulata</i> (gastropod)
<i>Microdictyon</i>	<i>Drupa ricinus</i> (gastropod)
<i>Dictyosphaeria</i> (solid and hollow)	
<i>Ulva</i>	
<i>Cladophoropsis</i> (dominant)	
? <i>Gracilaria eucheumoides</i> (juvenile?) (in niches)	
<i>Porolithon</i> (dominant crustose form)	
<i>Peyssonnelia</i>	
<i>Jania</i>	
mixed (brown/red) short filamentous turf	
<i>Turbinaria ornata</i> (stunted and juvenile)	
BLOCK SIDES	
much as top but sparser distribution and some species, such as <i>Turbinaria</i> absent	<i>Homotrema rubrum</i>
	<i>Carpentaria</i>
	<i>Sporadotrema</i>
	Sertularioid hydroids
	Schizoporellid encrusting Polyzoan
	various sponges (orange; red; brown)
	pink encrusting ascidian
BLOCK UNDERSIDES	
<i>Botryocladia</i>	Venerid bivalve (? <i>Timoclea</i>)
<i>Valonia</i> sp?	starfish (? <i>Mithrodia</i>)
mixed green short filamentous turf	<i>Echinoneus</i> (Echinoderm)
<i>Peyssonnelia</i>	several small crabs
<i>Cladophoropsis</i>	
<i>Ulva</i> (stunted material)	
<i>Microdictyon</i> (stunted material)	
<i>Caulerpa racemosa</i> var. <i>peltata</i>	
<i>Dictyota</i>	
young flabellate red (? <i>Gracilaria</i>)	
BORING INTO BLOCK SURFACES	
boring flora of greens/blue-greens	<i>Lithophaga nasuta</i>
	Lithotryid barnacle
CREVICE FAUNA IN BLOCKS	
	<i>Diadema setosum</i> (Echinoid)
	<i>Actaea tomentosa</i> (Xanthid crab)

BLOCK FLORA/FAUNA SUMMARY

	outliers	main ridge
blocks		
tops		
plants	9 spp.	> 15 spp.
animals	1 sp.	3 spp.
sides		
plants	13 spp.	> 13 spp.
animals	1 sp.	> 10 spp.
undersides/underneath		
plants	?1 sp.	11 spp.
animals	> 10 spp.	6 spp.
boring into surface		
plants (not noted)		> 3 spp.
animals (not noted)		2 spp.
crevices in blocks		
plants (not noted)		—
animals (not noted)		2 spp.

The summary chart above indicates the comparative numerical position with regard to different positions or faces of the sample blocks and fauna/flora there borne. What it cannot indicate, of course, are (i) the mosaic conditions in distribution on those faces; (ii) The floral/faunal density, or the extent of cover, on those faces; (iii) save in a minor way by parenthetic notes, the extent of stunting/luxuriance of individual specimens or clumps of plants; (iv) to what extent it is typical of blocks in the ridge. In fact, generally speaking, the undersides of those blocks in the main ridge are far more deeply incut than those of the outlier, perhaps because the main tidal effect is exerted upon the outer 'ridge', and this tends to be reflected in the presence of many more species on block undersides in the main ridge than exist in the outlier. Specimens on the undersides of blocks, as is to be expected, tend to be much more deeply pigmented and generally larger than similar specimens on block sides or block tops. Bleaching and size reduction are both manifest by plants occurring on sides and tops, although this varies a little in degree with the habit of the plant. Open growth forms such as *Turbinaria* tend to show most manifestation of this reduction in size and bleaching, whereas clumped growth forms like the Gelidiaceae and, especially, *Cladophoropsis*, both of which occur in intermixed or continuous mats, may show bleaching apically but are deeply pigmented below the bleached apical regions. Cushion growth forms like *Dictyosphaeria cavernosa* and *D. versluysii* do not seem so much affected by pigment loss under these circumstances, even when growing in positions on block tops which would seem to give the strongest possible insolation effects. However, even in such growth forms, rather more luxuriant specimens exist in standing water in inter-block channels in the ridges than are found on the blocks. The matter of micro-aspect relative to the path of the Sun has not here been discussed, but may well be of considerable importance in determining size of specimens growing on block sides and tops, as well as possibly being effective in the determination of mosaic patterns of the flora. In regard to those algae which normally are found growing happily in full sunlight conditions on the reef-flat, it is noticeable that the opposite tendency to the above is manifest. That is, when they are found underneath reef-ridge boulders, as is the case with *Ulva* and *Microdictyon* on occasions, specimens are much less luxuriant

than they appear on open reef-flat in water-skins, or, more particularly, in channels between boulders in the ridge, in pools in the inner reef-flat ridge/pool system, or in the luxuriant algal turf of Western Channels. This leads one to the conclusion that, on the whole, the most luxuriant growth of individual specimens or clumps in the reef-ridge areas exists in standing water within the channels, although the number of species present is generally greater when the whole assemblage of microniches constituted by a particular boulder, boulder clump, or boulders in a ridge area is taken into consideration.

These reservations aside, the numerical summary presentation does indicate that the proportion of the floral constituents to the faunal ones in the boulder micro-ecosystem is on the whole greater on open block sides or block tops, while the faunal contribution is greater on the shaded parts represented by incut bases of boulder sides and by the true undersides of the boulders. This statement has to be tempered by the knowledge that there is a not inconsiderable scia-philous floral element in the ridge flora, the species of which element appear only on the more shaded surfaces, such as boulder undersides. Examples of this element are *Botryocladia*, *Dictyota* and *Caulerpa racemosa* var. *peltata*.

(ii) *Comparison with the guest house (Settlement) profile and with areas adjacent to Western Channels transect.* The general morphology of the shattered reef-ridge area does not vary overmuch along the whole seaward coast of West Island. Dimensionally, there is clear variation but this does not significantly affect the variety of species present. However, the whole of the above main section was based floristically and faunistically on the Western Channels transect itself. It is the purpose of the second portion of this section to compare the floristics of the Western Channels (W.Ch.) transect area reef-ridge with that of the ridge on either side of the transect position and, in turn, with that in the Settlement (guest house) profile area. The conclusion, which will become evident as the section is examined in detail, can only be that the variations in pattern of distribution of the algae in, on, underneath, amongst, or between blocks of the reef-ridge are very considerable and are as legitimately described as 'mosaic' as are the distribution patterns over the whole reef-flat.

species	W.Ch. transect main ridge	W.Ch. transect outlier	adjacent W.Ch. transect (stn 8)	Settlement profile (stn 10)	adjacent Settlement profile (stn 11)
block/boulder uppersides					
<i>Jania</i>	+	+	.	.	.
<i>Porolithon</i>	+	+	+	+	.
<i>Polysiphonia?</i>	.	.	+	.	.
<i>Dictyosphaeria</i> spp.	+	+	+	+	.
<i>Amphisbetema</i>	.	.	+	.	.
<i>Caulerpa racemosa</i> var. <i>peltata</i>	.	.	.	+	.
<i>Champia</i>	.	.	+	+	.
<i>Cladophoropsis</i>	+	+	+	+	.
<i>Valonia</i> spp.	+	.	+	.	.
<i>Dictyota</i> ? <i>dichotoma</i>	.	.	+	.	.
Ceramiaceae	+	.	+	.	.
Rhodomelaceae	+	.	+	.	.
Acrochaetioids	+	+	+	.	.
<i>Udotea</i>	.	.	.	+	.
<i>Pocockiella</i>	.	.	.	+	.
<i>Lithophyllum?</i>	.	.	.	+	.
<i>Peyssonnelia</i>	+	+	.	+	.
<i>Boodlea?</i>	.	.	.	+	.
<i>Chondria?</i>	.	.	.	+	.

species	W.Ch. transect main ridge	W.Ch. transect outlier	adjacent W.Ch. transect (stn 8)	Settlement profile (stn 10)	adjacent Settlement profile (stn 11)
block/boulder uppersides (cont.)					
<i>Chlorodesmis</i>	+
<i>Halimeda</i> spp.	+
<i>Turbinaria ornata</i>	+	+	.	.	.
<i>Hypnea</i>	.	+	.	.	.
<i>Gelidiella acerosa</i>	+
Gelidiaceae (other)	+
<i>Microdictyon</i>	+
<i>Ulva</i>	+
block/boulder sides					
<i>Valonia</i> spp.	+	.	} none noted	.	} none noted
<i>Gelidiella acerosa</i>	+	+		.	
Gelidiaceae	+	.		.	
<i>Microdictyon</i>	+	+		+	
<i>Dictyosphaeria</i> spp.	+	+		+	
<i>Ulva</i>	+	+		.	
<i>Cladophoropsis</i>	+	.		+	
<i>Porolithon</i>	+	+		.	
<i>Peyssonnelia</i>	+	+		.	
<i>Jania</i>	+	+		+	
Ceremiaceae as red	+	.		.	
Rhodomelaceae filamentous	+	.		.	
Acrochaetioids turf	+	.		.	
<i>Laurencia</i> spp.	.	+		.	
<i>Boodlea?</i>	.	+		+	
<i>Dictyurus</i>	.	.	+		
<i>Dictyota</i> sp.	.	.	+		
<i>Champia</i> spp.	.	.	+		
<i>Chondria?</i>	.	.	+		
block/boulder undersides/underneath					
<i>Udotea</i>	.	.	.	+	.
<i>Gracilaria ?eucheumoides</i>	+	.	.	+	+
<i>Caulerpa taxifolia</i>	.	.	.	+	.
<i>Pocockiella</i>	.	.	+	+	+
<i>Halimeda</i> spp.	.	.	.	+	.
<i>Jania</i>	.	.	+	+	+
<i>Porolithon</i>	.	.	+	+	+
<i>Hypnea</i>	.	.	.	+	.
<i>Dictyota ?dichotoma</i>	+	.	.	+	+
<i>Microdictyon</i>	+	.	.	+	.
<i>Dictyosphaeria</i>	.	.	+	+	+
<i>Boodlea?</i>	.	.	.	+	.
<i>Cladophoropsis</i>	+	.	.	+	+
<i>Champia</i> spp.	.	.	.	+	+
<i>Chondria?</i>	.	.	.	+	.
<i>Valonia</i> spp.	+	.	.	.	+
<i>Lithophyllum?</i>	+
<i>Caulerpa racemosa</i> var. <i>clavifera</i>	+
<i>C. racemosa</i> var. <i>peltata</i>	+	.	.	.	+
<i>C. racemosa</i> var. <i>racemosa</i>	+
<i>Turbinaria</i> (juvenile)	+
<i>Gelidiella acerosa</i>	+
Gelidiaceae (other)	+
<i>Peyssonnelia</i>	+	.	+	.	+
<i>Dictyurus</i>	.	.	+	.	.
blackening ?blue-greens	.	+	.	.	.

species	W.Ch. transect main ridge	W.Ch. transect outlier	adjacent W.Ch. transect (stn 8)	Settlement profile (stn 10)	adjacent Settlement profile (stn 11)
block/boulder undersides/underneath (<i>cont.</i>)					
<i>Botryocladia ?skottsbergii</i>	+
green filamentous turf	+
<i>Ulva</i>	+
block/boulder shaded niches/crevices, all sides					
<i>Gracilaria ?eucheumoides</i>	+	} recorded, but nil return	.	.	.
<i>Caulerpa racemosa</i> var. <i>peltata</i>	.		+	.	.
<i>Caulerpa taxifolia</i>	.		.	+	.
<i>Botryocladia ?skottsbergii</i>	.		.	+	.
<i>Valonia</i> sp.	.		.	+	.
<i>Tapinodasya?</i>	.	.	.	+	.

Despite the justifiable description of the patterns of distribution in different areas as mosaic, it is evident that a number of genera consistently appear in the reef-ridge area, wherever examined. On the upper sides of blocks or boulders, these are *Porolithon* spp., *Dictyosphaeria* spp., *Cladophoropsis*, *Peyssonnelia* and turf-forming filamentous reds. Very much the same genera occur on the sides, shaded and otherwise, of blocks and boulders, with the addition of *Microdictyon*, *Jania* and, in some situations, *Gelidiella acerosa* and *Ulva*. None of the genera found on the undersides of or underneath boulders and blocks appears to be quite as consistently likely to be found as those mentioned above for block sides and tops. However, a number most usually occur and these are: *Gracilaria ?eucheumoides* (which also is not uncommon in shaded niches elsewhere), *Porolithon*, *Pocockiella variegata*, *Jania*, *Dictyota ?dichotoma*, *Dictyosphaeria*, *Cladophoropsis* and *Peyssonnelia*.

Such a presentation as that above does not, of course, give any idea of the relative luxuriance of specimens found in the different niches or micro-niches and it is just that aspect of the flora which is very often the most characterizing or distinctive, rather than whether a particular genus or species is or is not present.

As is evident from figure 17a, plate 11, there is a fair degree of correlation, on block tops, between the genera which are most frequently present and those which form the most distinctive elements of the flora; this is largely because none of the genera concerned is of an inconspicuous growth form. On the sides of and beneath blocks or boulders, however, *Jania*, despite its frequency of occurrence, is only rarely a really obvious facet of the flora there. Often, it occurs only as a member of the turf largely overgrown by *Pocockiella* and is only to be seen as emergent distal parts of plants at infrequent intervals. To a lesser degree, this also applies to *Dictyota* and to *Cladophoropsis*, which latter is in any case very much more luxuriantly developed on upper, or at least more illuminated, surfaces.

The other aspect of this comparative matter, the relative luxuriance of species or genera which are commonly present on all surfaces of the blocks or boulders, is another possible obscurant of the numerical aspects of the situation. The case of *Cladophoropsis* has already been mentioned above. Without listing every possible variation of this kind, a number of other outstandingly obvious cases spring to mind. *Pocockiella variegata* is a plant essentially of shaded circumstances, in this case of the undersides of boulders. In these circumstances it occasionally, as in the reef-ridge area of the Settlement (guest house) profile, reaches magnificent dimensions. Plants are so luxuriant that whole undersides of large coral blocks are more or less completely

overgrown by what seems clearly to be a single or very few confluent plants. This, of course, obscures the whole of the underlying flora so that there is only one aspect to it, that of *Pocockiella*; growth of the latter is not uncommonly so vigorous that the plant or plants extend around knobs of rock out onto the illuminated surfaces where, normally, the species is not found. *Dictyosphaeria*, *Peyssonnelia* and *Porolithon* provide good examples of genera which occur over the whole surface of boulders or blocks, but which are generally present in more luxuriant growths on the illuminated surfaces. The *Caulerpa racemosa* group provides a contrast in growth luxuriance, between surfaces, of a rather different kind. All plants of this species group which appear on the reef ridge boulders could well be referred to as stunted, when compared with material from lagoon areas. Generally, the ridge plants grow closely appressed to the substratum and show relatively strong development of the stolon and rhizoidal systems; the upright assimilators, however, are so reduced that they appear to consist of little more than the clavate lateral branches or the peltate disks on a stalk which is almost non-existent and is sometimes so difficult to distinguish that the laterals, particularly in var. *peltata*, appear as though directly attached to the stolon system. The contrast here between surfaces is one largely of the circumstances in which the plants grow. All appear generally only in the shade, which means that while on the underside of boulders or blocks the stolon system spreads quite happily throughout the whole surface, on open sides and more especially tops the plant seems to be confined to shallow declivities and niches, presumably affording some shade, from which rare cases of the stolon system spreading up onto the adjacent illuminated surfaces have been noted.

(5) *Seaward slope beyond the 'reef-ridge', including the Turbinaria band and Cymodocea band*

Immediately seaward of the shattered main 'reef-ridge', boulders or blocks thin out rapidly; also detritus is here at a minimum, which presumably is due to the consistent wave action at this point, even in these calm water localities. A water-layer of variable depth covers all but the few residual coral boulders and the larger living corals even at extreme low-water mark of spring tides. The profile associated with this area on Western Channel transect appears as figure 13*b* and this profile also illustrates the main zonal features of the whole area between the seaward reef edge and the edge of deeper water at low water of spring tides.

These features are:

(1) *Turbinaria ornata* band (figure 17*b*, plate 11). Strictly speaking overlapping from section 20 (reef-ridge area) into section 21 (seaward slope) of the transect, this band is an outstandingly clear feature of the inshore edges of this seaward slope (figure 13). Variable in width, the band is about 10 to 12 m at its maximum in the Western Channels transect area but commonly is about 5 m wide. It is not generally quite so strongly marked elsewhere on West Island seaward reefs. *Turbinaria* here appears to be in much better condition than anywhere else on the West Island seaward reefs, being more deeply and strongly pigmented and in good luxuriant growth. However, presumably as a result of the consistent wave action in water which is relatively shallow at many states of the tide, the specimens still do not reach anything like the length of plants growing in the shallow sublittoral of more exposed coasts on, say, the South Island southern facing shores, where depth of water is much greater due to shore configurations and exposure to tidal effects. The maximum noted height in this area of *Turbinaria* was 22 cm, but mostly plants were of the order of 15 cm high.

(2) *Cymodocea* band (figures 14*b*, 17*b* and 20*b*). Although patches, mostly rather small, of *Cymodocea*, occur in channels within the main reef-ridge area, and even rarely within the

Turbinaria band itself, there exists just to seaward of the latter an area of variable width and continuity which can be justifiably referred to as the *Cymodocea* band. This band strictly appears to be derived from confluent patches of *Cymodocea*, for many parts of the band remain a patchwork 'quilt', interspersed with patches in which the flora and fauna are those of the living coral area which follows to seaward. The surface distribution of the patches appears in large part to be a function of the presence of slightly deeper water, in which the *Cymodocea* occurs more luxuriantly, alongside rather shallower areas in which whatever *Cymodocea* exists is more restricted in spread and less luxuriant, and where the living coral area flora and fauna is much the more evident. The existence and development of this band is variable along the West Island seaward reefs; its position and width can be to some extent appreciated by tracing on figure 16 (Western Channels area) the darker line of variable extent near, at, or just below tidal water-edge level at the time of taking the aerial photograph. (See the overlay for ease of appreciation of what is here referred to.)

(3) *Living coral area* (figure 14*b*). Interspersed with parts of and immediately to seaward of the *Cymodocea* band there exists an area in which living corals are first found on these calm water seaward reefs. Generally speaking, this area carries a very sparse flora, the only really conspicuous element being provided by the Lithothamnia, particularly *Porolithon*. The substratum here is the most firm, for very little debris exists in this area. It is possibly significant that there seems to be rather less bleaching of the Lithothamnia crust than is the case on open faces of blocks and boulders in the reef-ridge area.

The details given above only cover the major 'zonal' determinants in the area concerned; the picture is, of course, a good deal more complex when the lesser floral constituents and the other fauna are taken into consideration.

In the area of residual blocks around marker 20 on the Western Channels transect, that is, largely within the *Turbinaria* band, certain marine algae are much more strongly evident than within the main ridge area itself, although the fauna in the marker 20 area is relatively sparse and inconspicuous. These algae are: *Halimeda* spp. (mostly rather brittle and thinly-segmented), *Dictyosphaeria* (solid and hollow forms), *Valonia* spp., Lithothamnia.

Although some of these species which appear strongly in the *Turbinaria* band have much less luxuriant representation in the *Cymodocea* area immediately to seaward (e.g. *Halimeda*; *Dictyosphaeria*; *Valonia* spp.), it is true that the number of species present in at least the *Cymodocea*/living coral area flora/fauna is rather larger again than that in the *Turbinaria* band. As already indicated, this is not true of the living coral area once one moves seaward beyond the occurrence of *Cymodocea* patches, for the flora then is rather sparse and restricted. From a point at the inner fringe of the *Cymodocea* area, about 4.5 m seaward of marker 20, to a point well below the level of extreme low water of spring tides, the following is a list of the flora and fauna observed during detailed examination of the area:

PLANTS:

<i>Dictyosphaeria</i>	solid and hollow species; relatively few specimens, on boulders
<i>Cymodocea</i>	occasional, relatively isolated patches
<i>Jania</i>	epiphytic on <i>Cymodocea</i>
<i>Dictyurus purpurascens</i>	somewhat rare patches present; only one patch observed
<i>Chlorodesmis</i> (see figure 23 <i>a</i> , plate 14)	a sand-binding form, always anchored in niches of sand and shell debris; brilliant green filaments in a few rare patches
<i>Cladophoropsis</i>	rare clumps, on boulders
<i>Caulerpa racemosa</i> var. <i>peltata</i>	rare clumps, on boulders

<i>Ulva</i>	rare specimens, in the <i>Cymodocea</i> patches
<i>Halimeda</i> sp.	large, but widely scattered, rather thin-segmented clumps in hollows
<i>Pocockiella variegata</i>	occasional plants on boulders
<i>Amphisbetema indica</i>	isolated plants in shallow standing water
<i>Peyssonnelia</i>	on rocks generally, but mainly in the living coral area
Lithothamnium	probably mainly <i>Porolithon</i> ; on rocks generally, but most luxuriantly in the living coral area. Usually on apices of knolls and corals, perhaps present throughout area, but covered elsewhere by <i>Cymodocea</i> , algae, and so on
<i>Turbinaria ornata</i>	scattered plants, well spaced and patchy; not in as good condition as plants in the band
Gelidiaceae	a few patches associated with <i>Porolithon</i>
(probably	
<i>Gelidiella acerosa</i>)	
<i>Valonia</i> sp.	rare specimens, only in the <i>Cymodocea</i> band
<i>Dictyota</i> sp.	small plants in shaded situations, only in <i>Cymodocea</i> band
Acrochaetoid reds	at least two species; one, a purple-red form, sand-binding at the fringe of the <i>Turbinaria</i> band, the other, mostly sciaphilous, on boulder undersides

A number of other undetermined reds, some sciaphilous, are also present in this flora.

ANIMALS:

Corals	Other animals
<i>Porites lutea</i>	crangonid shrimp, green
<i>Lobophytum</i>	<i>Crangon cymodoceae</i>
<i>Acropora irregularis</i>	sponges (orange form; green flaccid form)
<i>Millepora</i> sp. (platy form)	parasitic barnacles (on platy <i>Millepora</i> sp.)
<i>Pocillopora</i> cf. <i>danae</i>	<i>Hapalocarcinus</i> sp. (parasitic crab, on <i>Stylophora</i> sp.)
<i>Porites</i> sp.	Mollusca, many species as yet undetermined.
<i>Platygyra</i> sp.	polyzoan, Schizoporellid type
<i>Leptoria</i> sp.	<i>Cypraea lamarckii</i>
<i>Favia</i> spp. (at least two forms)	<i>Leucozonia smaragdula</i>
<i>Acropora</i> cf. <i>cuneatus</i>	<i>Trapezia cymodoceae</i>
<i>Acanthastrea</i> sp.	<i>Trapezia trapezia</i>
<i>Stylophora</i> sp.	<i>Conus catus</i>
<i>Goniastrea pectinata</i>	<i>Ophiocoma scolopendrina</i>
<i>Acropora</i> cf. <i>digitifera</i>	<i>Homotrema rubrum</i>
<i>Hydnophora microconos</i>	<i>Chama asperella</i>
	<i>Echinometra</i> sp.
	<i>Stichopus coronopus</i>
	<i>Marginopora</i> sp.

4. SOME ASPECTS OF THE MARINE ECOLOGY OF THE LAGOON AREAS, WITH PARTICULAR REFERENCE TO WESTERN CHANNELS

The only areas on Aldabra bearing really luxuriant marine algal flora, both in number of species and ground cover, as well as size of individuals, were in the lagoon, particularly associated with the lagoon sides of drainage channels. Figures 16 (vertical aerial photo and overlay) and 23*b* (oblique aerial photograph showing whole of Western Channels and most of West Island) illustrate, *inter alia*, the position of the major marine algal/phanerogam 'turf' area in Western Channels. Considering Western Channels as an example, it is possible that the presence of luxuriant vegetation inside these channels is a function of the combination of regular massive interchange of water between lagoon and open sea and of the predominance of shallow, more or less consolidated coral debris, sand and mangrove mud available for colonization in the area. The only really deep interchange channel is that through Passe du Bois, but occasional deeper sections with strong currents exist locally in all the channels. These deeper, faster-flowing sections or channels commonly support heavy growths of living coral, though not to the same extent as that found peripheral to Main Channel.

The 'turf' area, in its southern two-thirds at least, amounts to a ground cover of virtually 100 %, with a great deal of over-clumping or multi-layering of one entity with another (figure 22a, plate 14). The main plant genera in this turf are:

<i>Acanthophora</i>	at least two species, possibly three, of which the third may well be new (figure 24)
<i>Laurencia</i>	three, possibly four species, including <i>Laurencia papillosa</i> (figure 22a)
<i>Hypnea</i>	several species or growth forms
<i>Gracilaria</i> cf. <i>wrightii</i>	(cervicornly branched species): a large turf constituent, with occasional fruiting specimens (figures 22a, b)
<i>Gracilaria</i> cf. <i>verrucosa</i>	large specimens of this terete, rather lax and open-branched form were present, but not quite as obvious a constituent of the turf as <i>G.</i> cf. <i>wrightii</i>
<i>Halimeda</i>	three or four species, both large- and small-segmented forms, with many epiphytes of the filamentous red Ceramiaceae and parenchymatous red Gelidiaceae (figure 22a)
<i>Hydroclathrus</i> <i>clathratus</i>	large and small, probably young, plants present, but very rarely
<i>Dictyosphaeria</i>	both cavernose (<i>D. cavernosa</i>) and solid forms (<i>D. versluysii</i>) present in about equal amounts, on cobbles where the turf thinned a little
<i>Ulva</i>	patchily distributed, but locally in large amounts
<i>Thalassia</i>	relatively few plants
<i>Cymodocea</i>	by far the most widespread genus of marine phanerogams here (figure 22a)

Of the 100 % cover in the denser turf areas, the marine algae in total make up about 65 %, whereas the marine angiosperms form the remaining 35 %; this balance changes, not only locally, but as one moves north, south or west from the main turf area. The genera *Laurencia*, *Acanthophora*, *Gracilaria* and *Halimeda* form probably 80 % of the total algal cover; *Cymodocea* forms probably 70 % of the marine angiosperm cover.

As one moves northward from the dense turf area, this turf tails off to become, gradually, an open, typical *Thalassia* and *Ceramium* flora on the more sandy substrates (see figure 19b, plate 13) particularly around the undercut small 'mushroom' islets, whereunder definite 'zonation' patterns exist (see figure 11).

The filamentous red algae present seem to include *Centroceras*, ?*Polysiphonia* and other Rhodomelaceae in varying amounts, but *Ceramium* is the most obvious and frequent constituent and has therefore been used here to characterize the situation. The zonation patterns around mushroom islets merit further consideration. Figure 11 shows that, as well as leading to floristic changes from the situations holding on adjacent open shores, the presence of the islet overhangs so reduces the available light that concomitant reduction in ground cover occurs. In the areas where mushroom islets exist, the sand substrata bear the pure *Ceramium* flora at about a ground cover of 50 %, although it is easy to mis-estimate this coverage because of the lightly-pigmented plants concerned, against a not dissimilarly coloured background. Where *Thalassia* and *Syringodium* are present, visual estimates of the ground cover are likely to be at least potentially more accurate, since contrasting pigmentation makes assessment rather easier. Figure 19b (*Thalassia*/*Ceramium* photo) shows in close-up the situation at the margins of raised overlap areas like 2 in the zonation scheme presented here. From these data above, it can be appreciated that ground coverage in areas 1 and 2 is very much like that of the open ground flora around the islets, despite the relative proximity of the shading effect of the overhang. The remaining areas, 3, 4 and 5, whilst reflecting the effects, floristically, of shading, also show a visually appreciable reduction in ground cover by virtue of the growth forms of the algae present. *Halimeda* and *Dictyota* both tend to be bushy or spreading in growth from single holdfasts, and this restricts the density or numbers of individuals per unit area and gives an open effect to the flora. *Caulerpa taxifolia* here consists of two very large stolon systems spreading widely

and with luxuriant upright assimilators; however, since these almost never seemed to arise from the stolon less than 3–4 cm apart, a similar open effect upon the flora resulted.

Zonations on or around two other examples of mushroom islet in the same area reflected differences in details from the example outlined above. Largely, these consisted of the presence, in the outer parts of deep overhangs, of large numbers of quite sizeable chitons, while under the overhang there were patches of *Peyssonnelia* where the shading was rather less deep. Upper parts of the overhang and exposed surfaces of the rock itself were almost entirely bare of macroalgae, save for a few clumps of blackish, very discoloured *Valonia*.

Southward from the dense areas of turf coverage lies the draining lip of the slightly raised area on which the turf is developed. Between this draining lip and the edge of the deep channel of Passe du Bois is an area of slightly deeper standing water colonized by dense *Cymodocea* beds with a little *Thalassia* at intervals. Algae present in that deeper standing water included *Ceramium* (epiphytic), *Laurencia* (sparse), *Ulva* (very occasionally) and *Turbinaria* (in deeper patches).

The deeper patches increase in number as one moves east and there are finally almost no raised areas. The biota then consisted largely of *Turbinaria* and scattered clumps of *Halimeda* on coral blocks; few *Ulva*; isolated plants of *Thalassia* and *Cymodocea*; occasional chunks of coral debris and sand bound by *Chlorodesmis*; and scattered living corals.

Westward from the area of dense algal and angiosperm turf, there develops a *Thalassia*/*Cymodocea* sward in which *Thalassia* is dominant over the level surfaces of the sandy bottom, emersed at low spring tides. *Cymodocea* is thickest at the edges of deeper pools and along the bottoms of shallower pools. *Laurencia*, which is common in *Thalassia* beds, *Enteromorpha* in very still and shallow water habitats, and *Ulva* in similar circumstances to *Enteromorpha*, though generally deeper in the water, are the more obvious of the algae. The *Thalassia*/*Cymodocea* sward finally tails off to give way to areas of mangrove rhizophores in mud, along island fringes between and lagoonward of channels. Here, impressively luxuriant specimens of certain algae were present, mostly in mud or attached to coral pebbles buried in the mud; these include:

<i>Cystoseira myrica</i>	rather stunted; along fringes of channel mud
<i>Hydroclathrus clathratus</i>	very large plants (see figure 22a)
<i>Gracilaria</i> cf. <i>wrightii</i>	the cervicorn form, present in masses
<i>Padina</i>	along the fringes of channel mud
<i>Microdictyon</i>	very large plants
<i>Gracilaria</i> cf. <i>verrucosa</i>	patchy in distribution, but very large plants
<i>Ulva</i>	large plants on mud and epiphytic on rhizophores
<i>Enteromorpha</i>	masses of the plant, apparently mostly drift, entangled in rhizophores and lower branches of mangrove

A few *Cymodocea* plants and rather more *Thalassia* plants also remained. Where residual undercut islets are present actually within the channels, scour effects around them seem to have produced deep and shaded environments for attached benthic algae. Here, *Peyssonnelia*, *Pocockiella*, *Halimeda* and *Oscillatoria submembranacea* have been found.

Turf areas essentially similar to those described above, although of rather lesser extent, exist adjacent to the shore of South Island at East Channel, where thick beds of *Cymodocea* and fleshy, matted or erect algae stand in 30 to 60 cm of water or even with their distal parts emergent at low spring tides. *Hypnea?* and *Martensia* were commonly the most prolific genera present, but the other marine algae noted for Western Channels area also contributed to the flora

here. *Cymodocea*, particularly, bore the usual epiphytes and was associated with similar epilithic genera. Towards the edges of the deep channel of East Channel, over which edges rushing water pours on falling tides, the flora thinned and *Halimeda*, certain Rhodomelaceae and *Turbinaria ornata* of very low habit were the only really conspicuous algae.

The fauna of the dense turf areas of Western Channels were studied by J. D. Taylor both during our joint work and subsequently; I am indebted to him for the information which follows. The sand and organic detritus underlying the vegetation were not particularly productive; a sipunculid worm, a holothurian not found previously, and occasional polychaetes were the limited fauna observed. However, particularly associated with and beneath the genera *Gracilaria* and *Laurencia*, were found these animals:

Echinodermata	<i>L. crocata</i>
Ophiuroidea	<i>Conus catus</i>
<i>Ophiocoma erinaceus</i>	<i>C. arenatus</i>
<i>Ophioplocus imbricata</i>	<i>C. virgo</i>
blue/green Ophiuroid species, common	<i>C. tessulatus</i>
Echinoidea	<i>Coralliophilia violacea</i>
<i>Prionocidaris verticillata</i>	<i>Vasum turbinellus</i>
<i>Diadema setosum</i>	<i>Oliva</i> sp.
<i>Echinometra matthaei</i>	<i>Nassa sertium</i>
<i>Tripneustes pileolus</i>	<i>Amathea conica</i>
<i>Pseudomaretia alta</i>	<i>Bursa rubeta</i>
Asteroidea	<i>Stomatia</i> sp.
<i>Nardoa</i> sp.	<i>Triphora</i> sp.
<i>Asterina burtoni</i>	<i>Mitrella</i> sp.
Mollusca	<i>Strombus gibberulus</i>
Bivalvia	<i>Terebra guttata</i>
<i>Pinna muricata</i>	<i>T. affinis</i>
<i>Chlamys</i> sp.	<i>Smaragdia rangiana</i>
<i>Chama isostoma</i>	Nudibranchia, common
<i>C. aspersa</i>	
Gastropoda	Coelenterata
<i>Cypraea carneola</i>	Anthozoa
<i>C. vitellus</i>	<i>Porites lutea</i>
<i>C. lamarckii</i>	Hydrozoa
<i>C. tigris</i>	<i>Millepora</i> sp. (on <i>Cymodocea</i> stems)
<i>C. annulus</i>	Crustacea
<i>Lambis lambis</i>	<i>Thalamita</i> sp.
	Xanthid crabs
	Oxyrhynchid (green) crabs
	Hermit crabs (common amongst the marine algae)

Elsewhere on lagoon shores, on the southern side, there are wide, partly intertidal, flats of unstable sand/mud mixtures over coral rock pavement; these bear only relatively stunted algal growths, *Enteromorpha* being the most frequent genus. Other genera present included *Hydroclathrus*, *Hypnea*, *Laurencia*, *Valonia*, *Centroceras*, and the blue-green *Microcoleus lyngbyaceus*. The poor algal growth is perhaps due to the effects of high insolation at low tide and of an unstable substratum, giving very turbid water at flood tide.

The central lagoon basin, a shallow rocky area mostly 3–6 m deep with relatively little sediment, has a rather uniform flora, somewhat unimpressive because of that uniformity. The major constituents are *Cystoseira myrica*, *Laurencia* spp., *Caulerpa* spp., *Gracilaria* spp. and *Dictyota* spp.

The northern shore of the lagoon (that is, the south shore of Middle Island) is generally deeper and has a narrow intertidal area. Around the southeastern end of Middle Island, however, is a maze of small islets with anastomosing channels running between them. The bottoms of these channels and their associated embayments are mostly covered by *Microdictyon* and *Gracilaria* cf. *wrightii* (the cervicornly branched form); elsewhere, *Laurencia* spp. and *Halimeda* spp. are abundant. These four genera make up 90% of the flora in these calmer areas between mangrove-dominated islets, but in the faster-running channel waters, *Lithothamnium* and, especially, *Halimeda* become dominant. Here, and even more obviously slightly farther west, a conspicuous feature of the shore-line is the presence of abundant and luxuriant algae. *Cystoseira myrica*, *Halimeda*, several bilateral species of *Caulerpa* (*C. brachypus*, *C. taxifolia*, *C. scalpelliformis*), various forms of the radial *C. racemosa*, and *Sargassum* occur particularly widely. Some of the marine algae, especially *Chaetomorpha crassa*, *Hydroclathrus clathratus*, *Caulerpa racemosa*, and *Microdictyon* spp. occur in spectacular masses up to 5 m across.

The Main Channel area of the lagoon, which is continuous with the northern shores of West Island, already commented on at intervals throughout the foregoing text, supports abundant living corals as virtually nowhere else in the lagoon. Marine algae present here essentially mirror those reported above, from elsewhere, in similar circumstances and therefore need not be listed.

A number of colleagues in all disciplines have provided data additional to my own collections and observations on the marine algae of Aldabra. These data were derived, either from locations which I was never able to visit, or over periods longer than my own stay on Aldabra. In this context, it is with great pleasure that I acknowledge help from the following workers: J. D. Taylor and K. R. Mackenzie of the British Museum (Natural History), and C. F. Rhyne and F. R. Fosberg of the Smithsonian Institution, Washington, U.S.A.

The levelling which was carried out on transects across the West Island reefs was mainly the work of G. Brookfield of the B.B.C., whose surveying expertise made certain aspects of transect work very much easier than it would otherwise have been and to whom thanks are expressed.

All determinations of fauna given throughout the foregoing text are by J. D. Taylor; these determinations were made either in the course of joint transect work which we carried out at Western Channels, West Island, or subsequently, and I am very grateful for permission to use the names in the present work.

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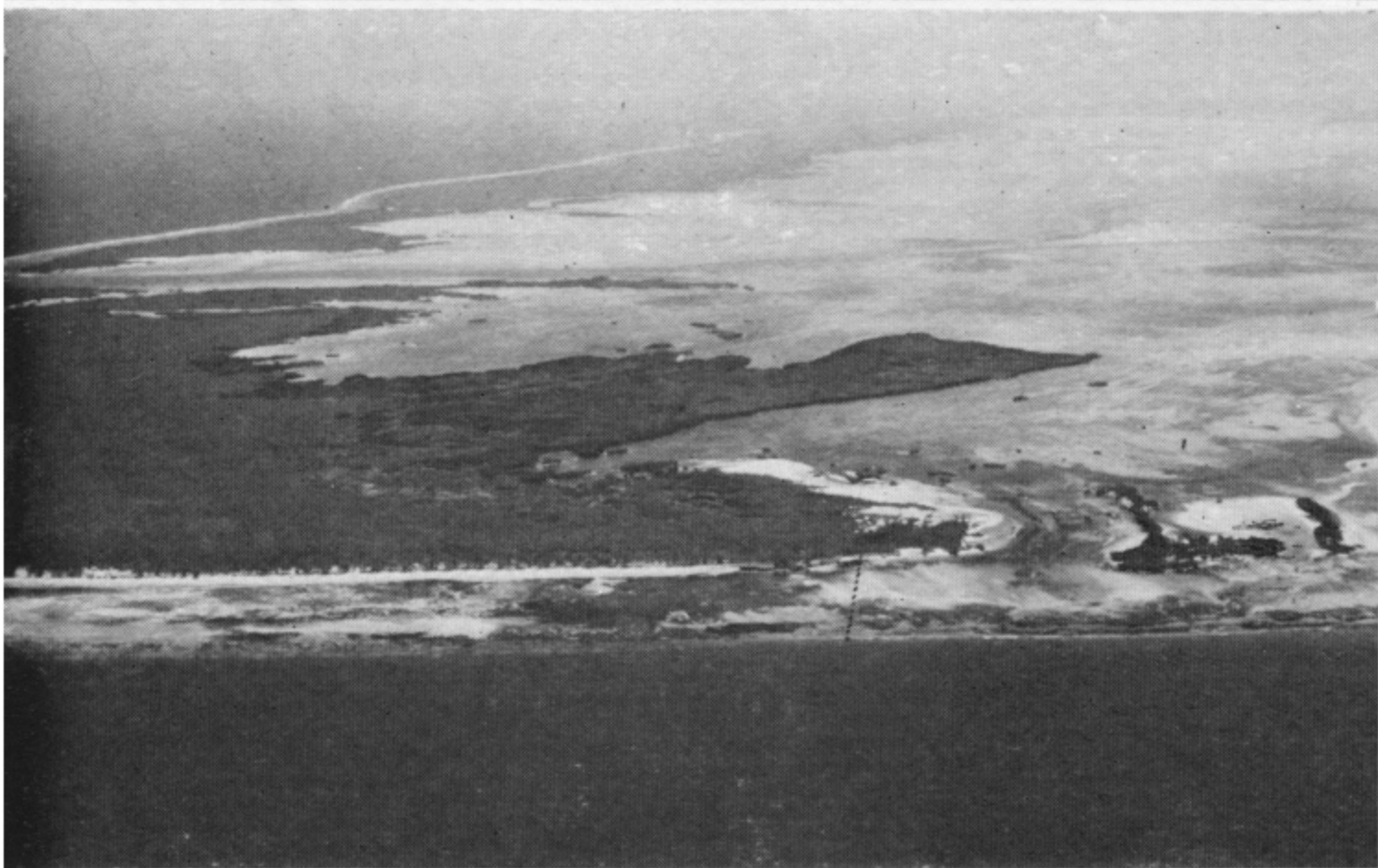
(a)

(b)

14



15



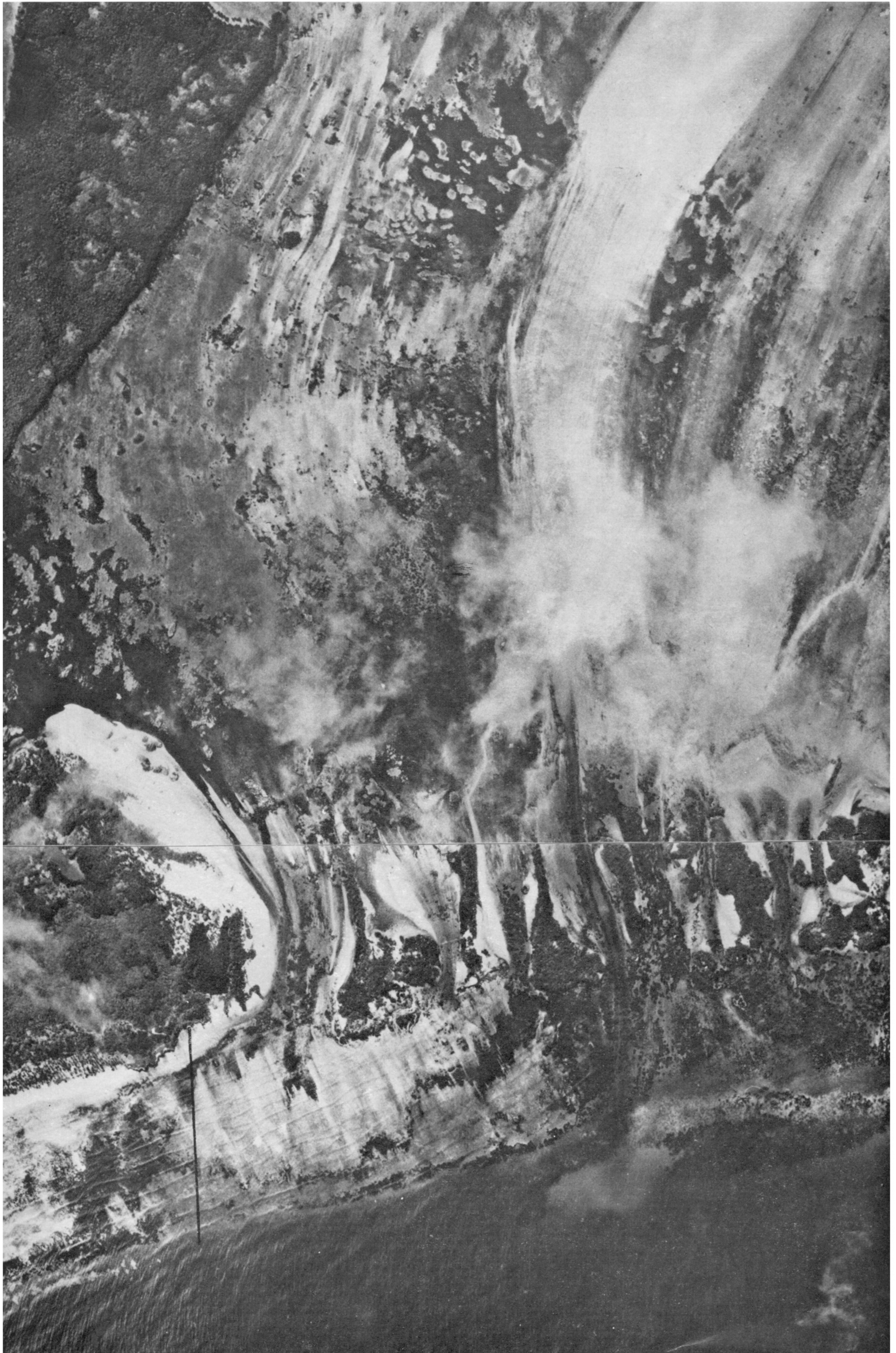
17



18



FIGURES 14, 15, 17 AND 18. For legends see facing page.



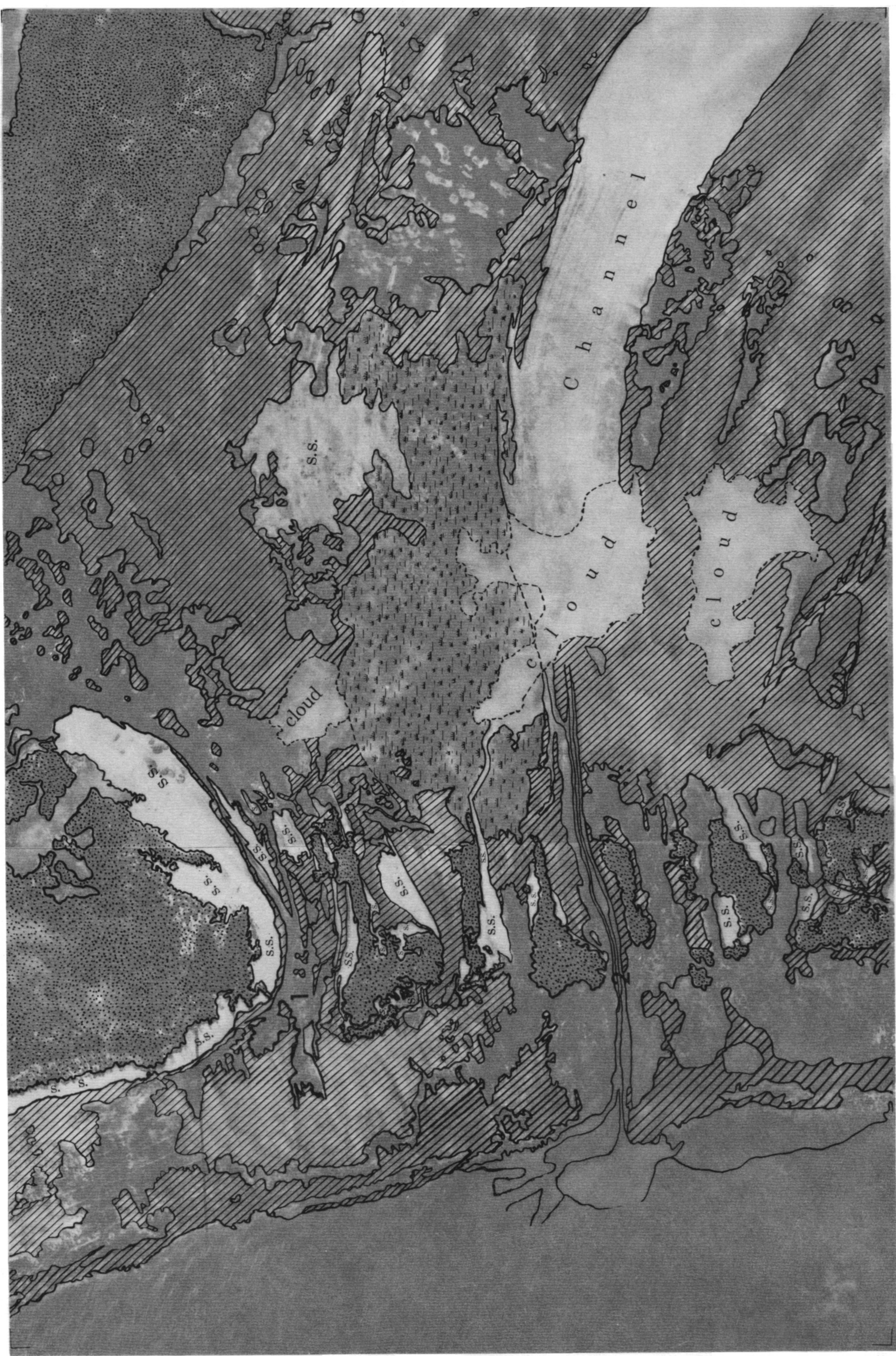
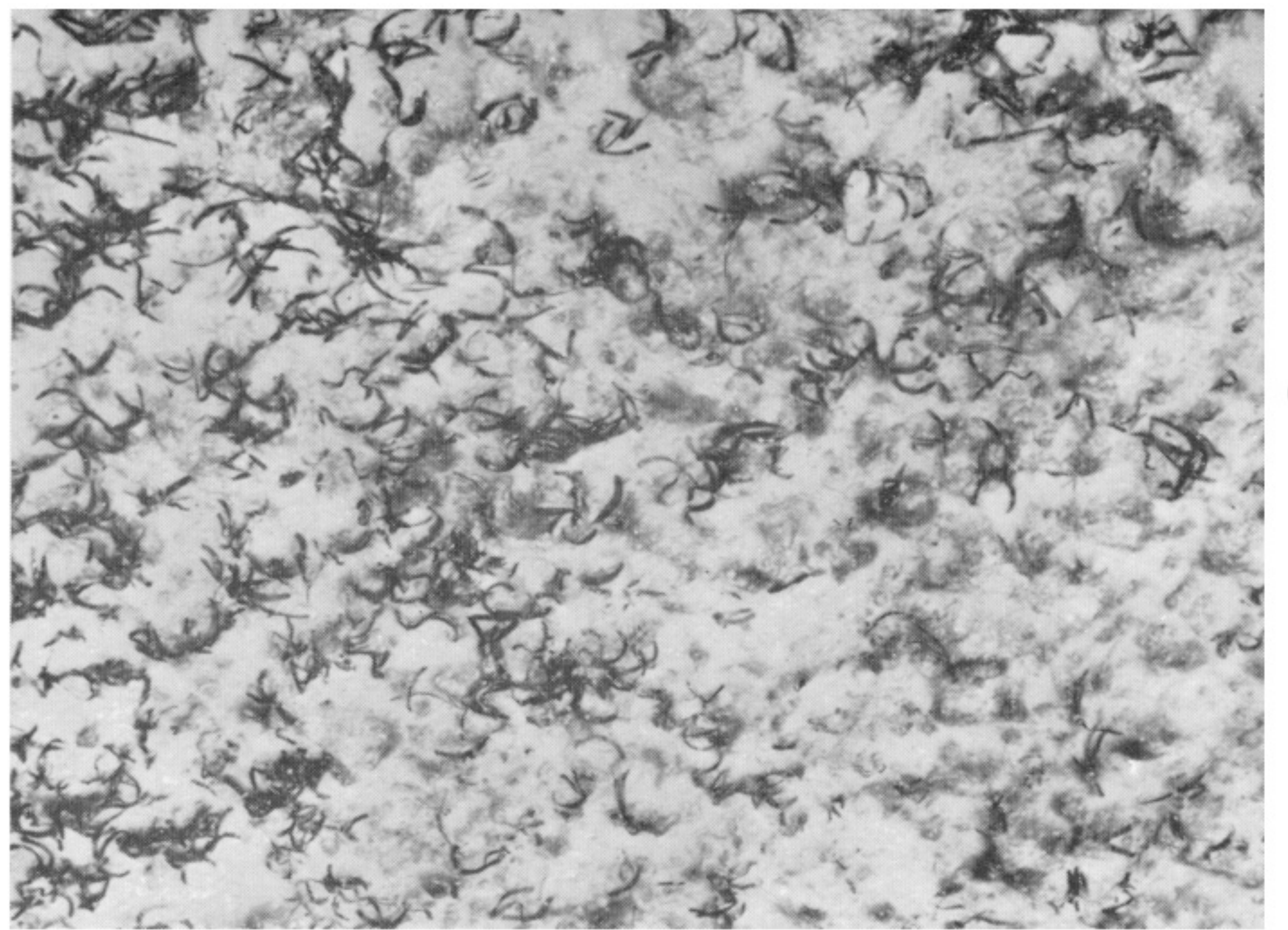
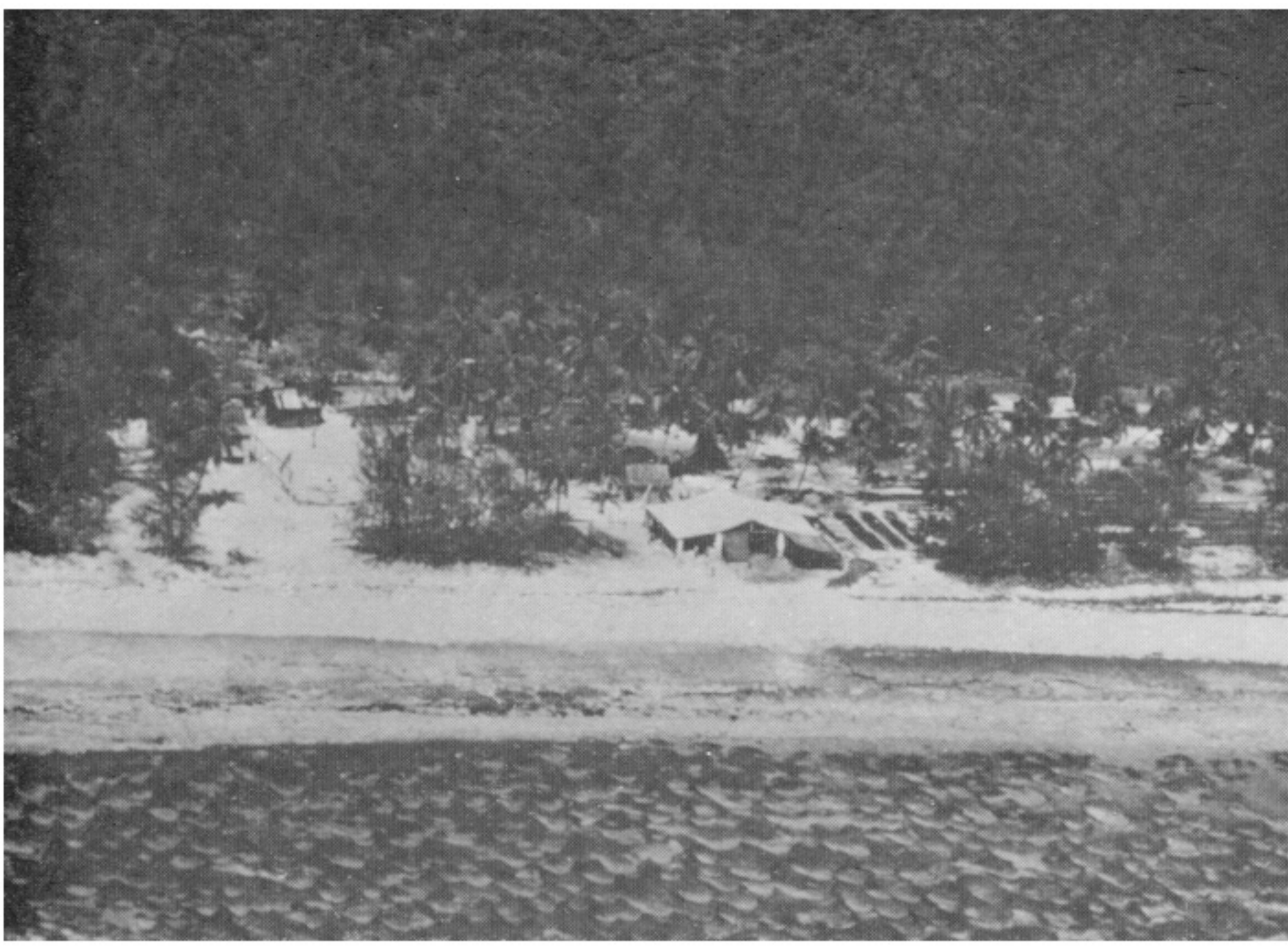


FIGURE 16. For legend see facing page.

(a)
19



(b)

20



21

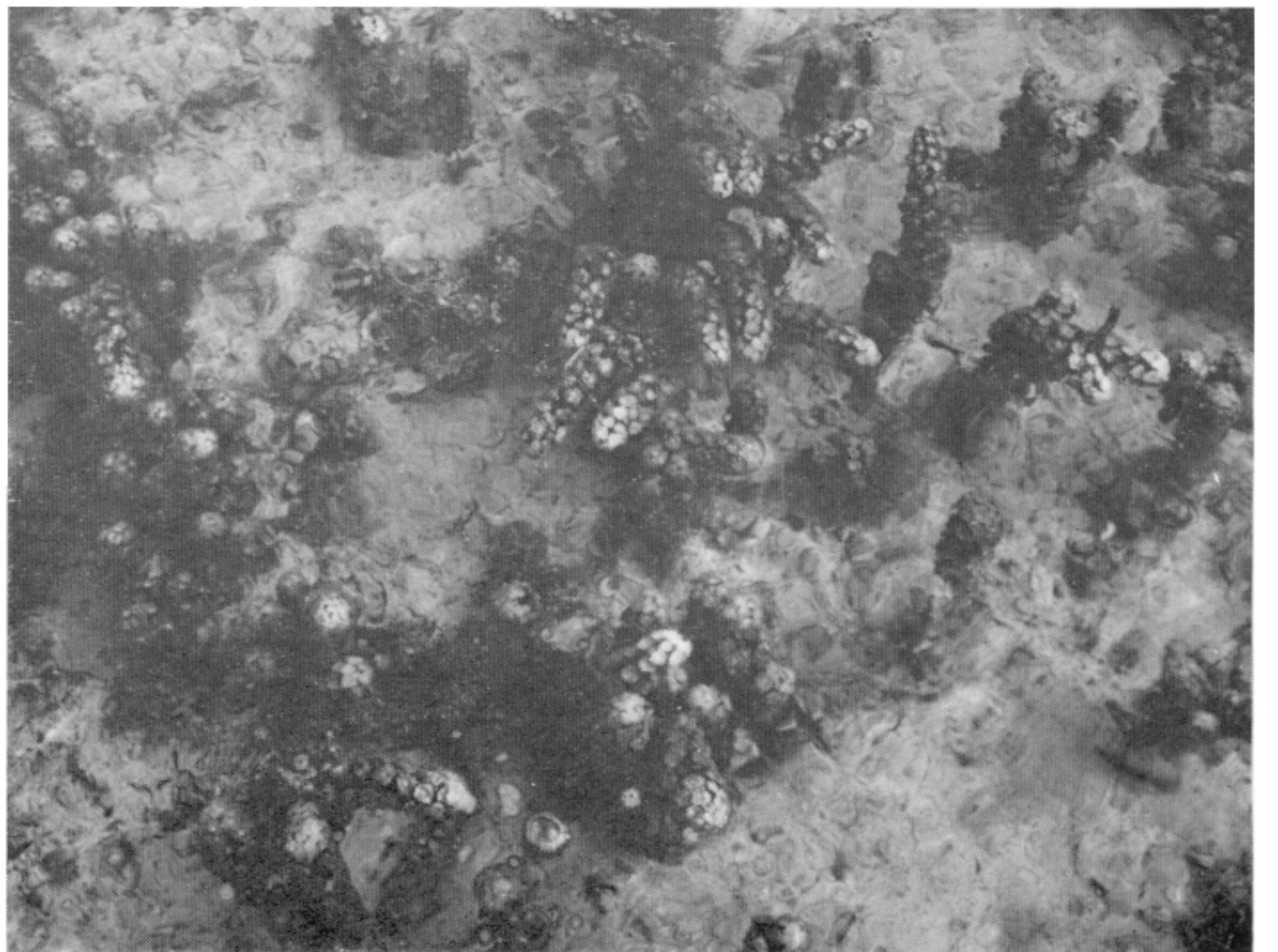
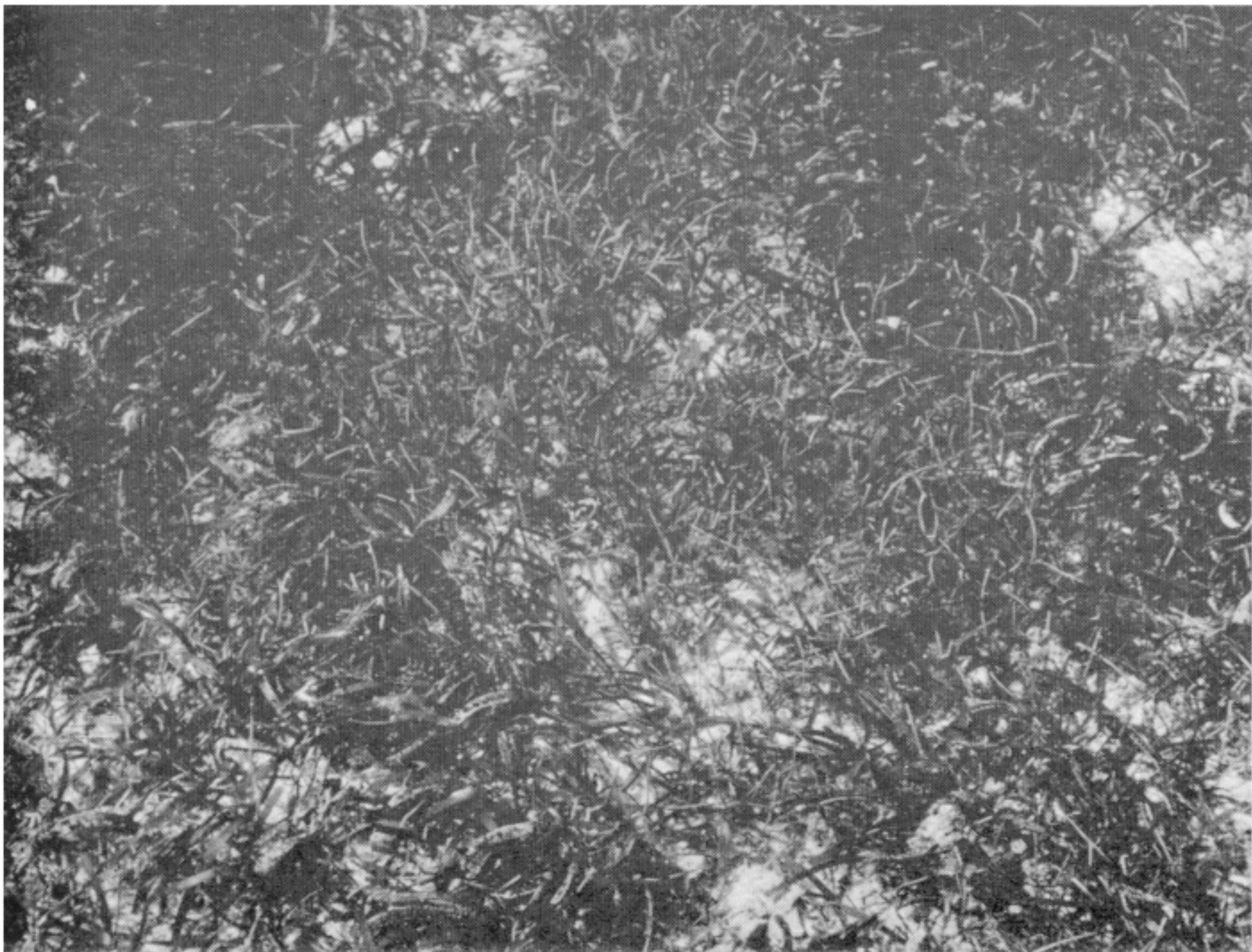
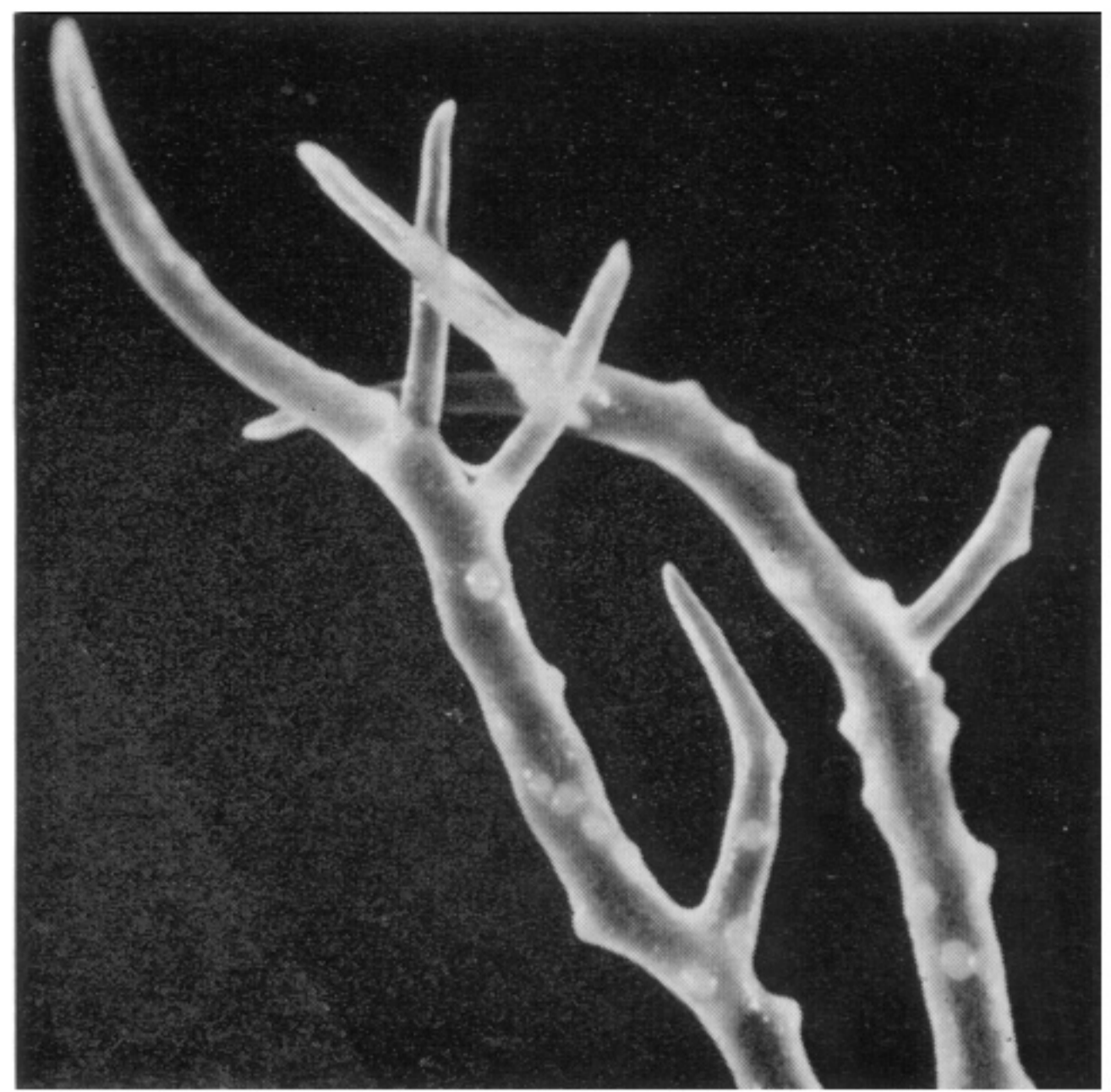
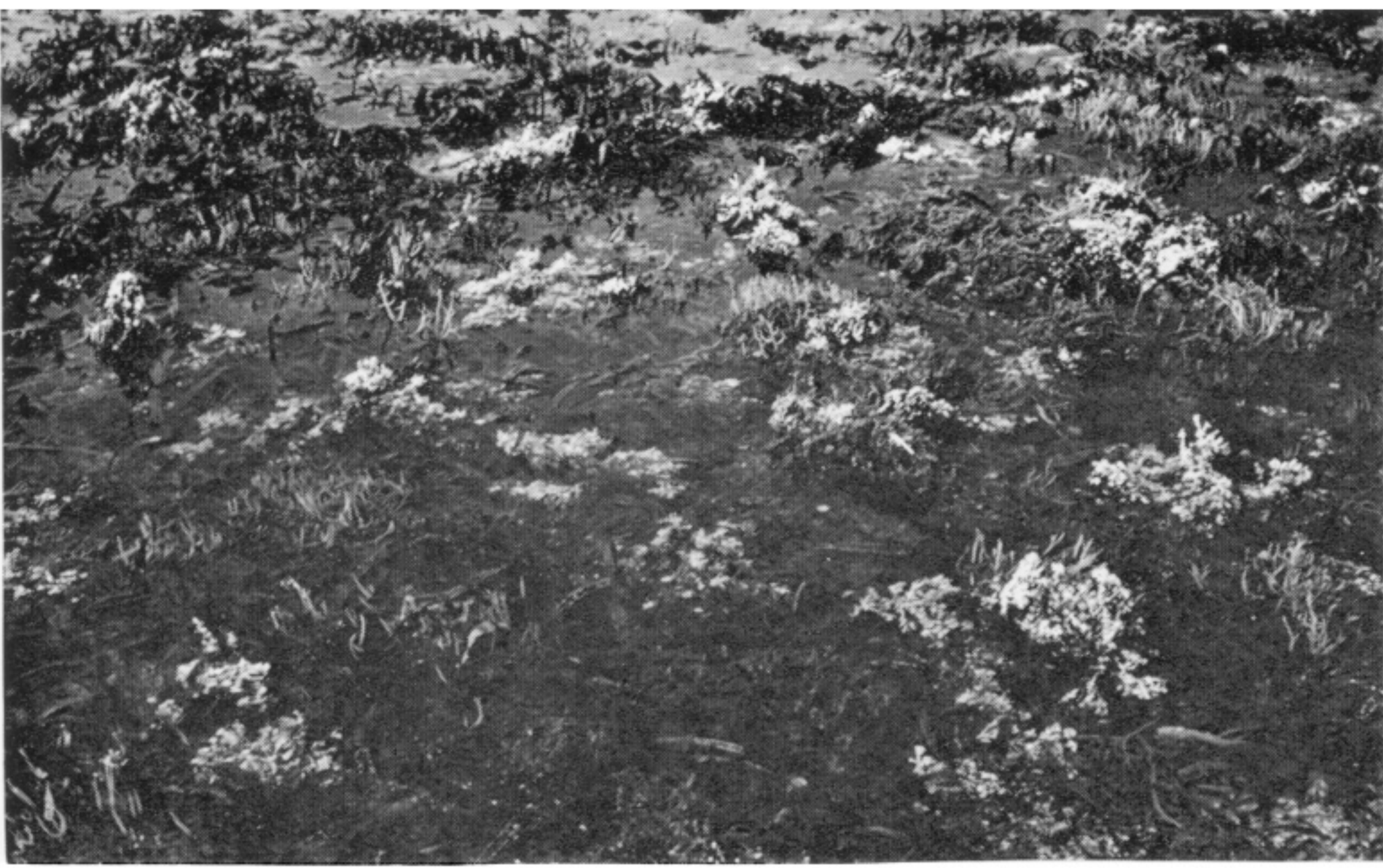


FIGURE 19. (a) West Island, low aerial shot of shore off Settlement, showing sand above beach-rock, the latter with variable distribution of flora, and the dappling effect given to the inner reef-flat (sublittoral) by the presence of pools with *Halodule* → *Thalassia* → *Cymodocea* zonation from ridges of sand down into adjacent pools. Bottoms of the pools are here largely free of vegetation, and the widths of individual parts of the ridge system vary, as does the density of the flora carried. (b) *Thalassia* and, predominant of the algae present, *Ceramium*, in shallow water on sand. Near mushroom islet in Western Channels near lagoon. Ground cover of the two main constituents is about equal. Standing water is here merely a skin about 2–5 cm deep.

FIGURE 20. (a) *Cymodocea* deeps just inshore of the reef-ridge, the fringe of which is seen in foreground. Raised coral cobble/*Thalassia*/*Ulva* and *Enteromorpha* flat visible as lighter area in far background. La Passe Femme in rear, undercut coral cliffs rising out of sand to left of it. Very near line of Western Channels transect. (b) Seaward side of reef-ridge, looking back along line of Western Channels transect. Small changes in level on seaward slope initially can be clearly seen. Darker areas immediately behind reef-ridge are *Cymodocea*, as are the dark patches in front. These latter patches form part of the discontinuous band of *Cymodocea* seaward of the ridge. Between it and the ridge, overlapping the fringe of the latter, can be seen the *Turbinaria* band.

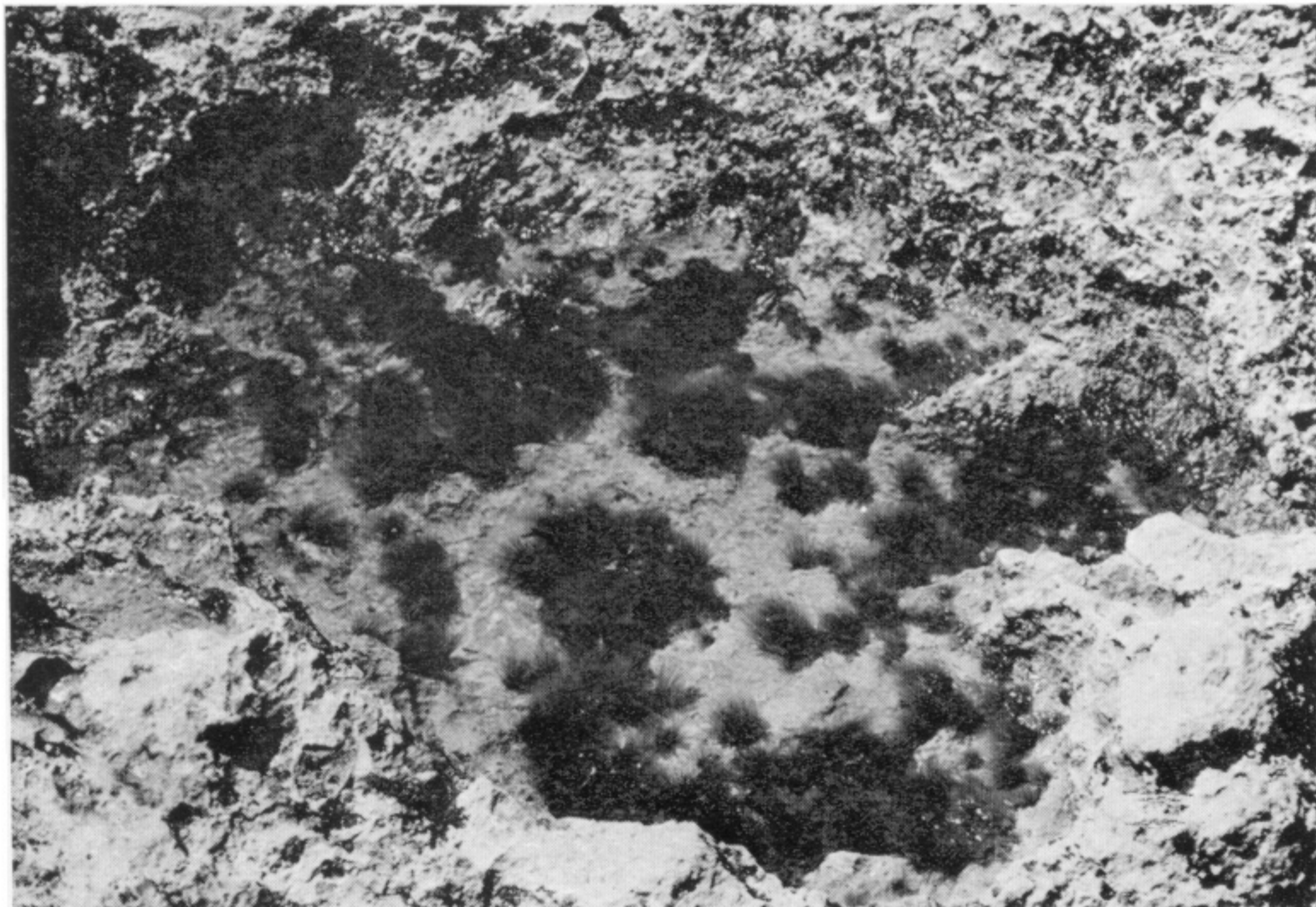
FIGURE 21. (a) *Syringodium* (centrally), on raised area, and *Cymodocea* (on both sides), in deeps adjacent. Passe du Bois, Western Channels, in shade and deeps along small islet. (b) *Turbinaria* from deeper water in Western Channels area. Illustrates the longer more luxuriant growth in deeper water when compared with growth in the intertidal or on the reef-ridge.

22a

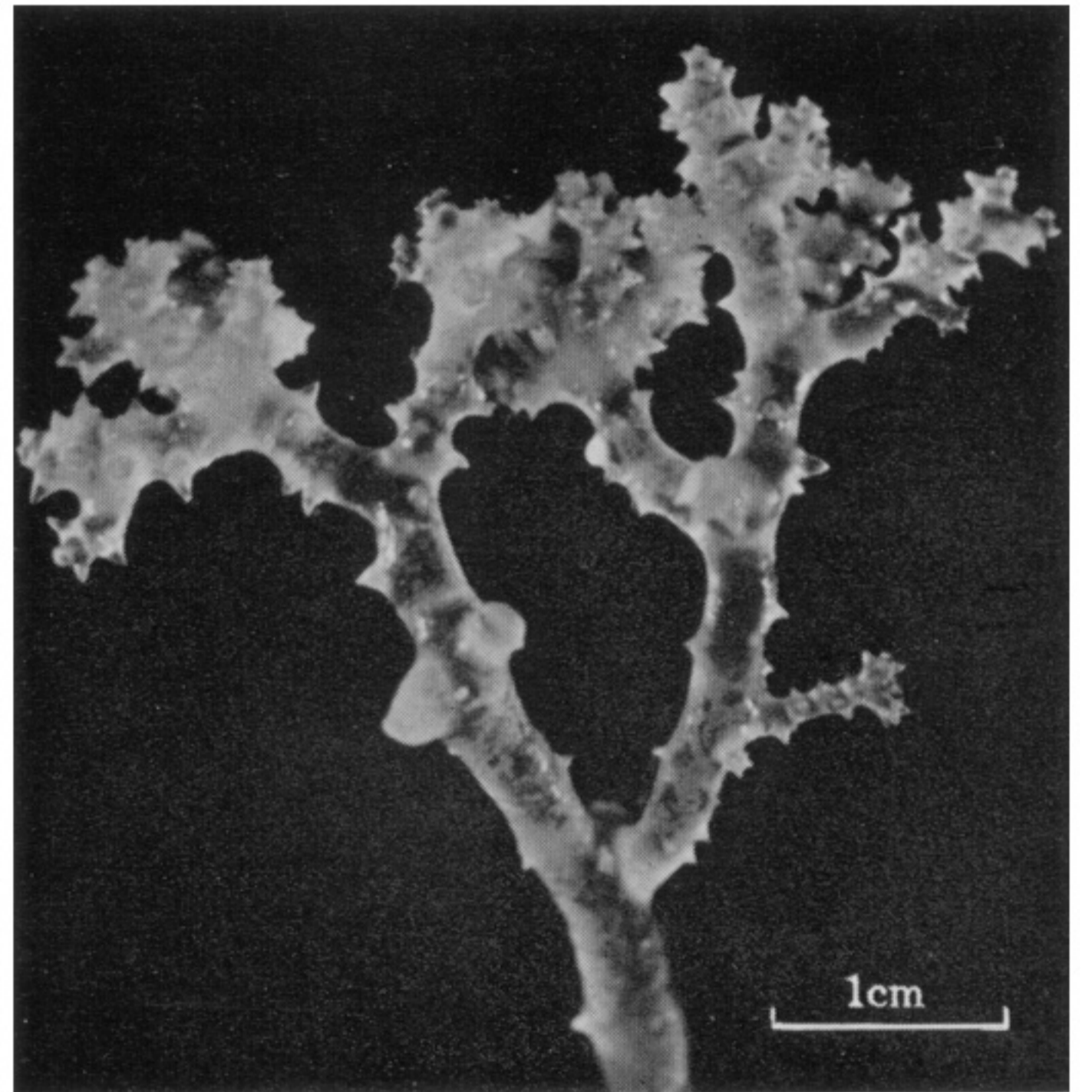


b

23a



23b



24

FIGURE 22. (a) Algal and angiosperm 'turf area', Western Channels, at low water of spring tide. The main genera visible are: *Halimeda*: bleached and clearly visible, large- and small-segmented forms. *Gracilaria* cf. *wrightii*: the cervicornly-branched form present, standing stiffly upright in much of the photograph. *Laurencia papillosa*: clumps of dark material, centre foreground, against the darker, widespread *Cymodocea*. *Cymodocea*: forms much of the general background to the rest of the vegetation. Bears vast amount of *Melobesia* and *Spirorbidae* on the leaves. *Hydroclathrus clathratus*: a clump of this net-forming species appears top right, to the left of the upper right large clump of *Halimeda*. (b) Close-up of cystocarpic material of *Gracilaria* cf. *wrightii* from the deeps of the inner reef-flat, north of Western Channels transect.

FIGURE 23. (a) *Chlorodesmis*: shallow pool with small amount of sand detritus, seaward side of reef-ridge near Settlement. More usually found in shallow water-skins and retaining much more sand than here. (b) Oblique aerial photograph showing whole of Western Channels and much of West Island. The larger channels are La Passe Femme (left, to north); La Passe du Bois (centrally); La Passe Magnan and La Passe Grabeau, which are confluent and outfall together (to right, south). Position of algal 'turf' is easily seen as large black patch centrally, behind and slightly to north of lagoon end of La Passe du Bois. Comparison with the overlay of figure 16 will identify it more firmly, if needed.

FIGURE 24. Close up, magnified $\times 1.5$, of apical portion of the (?) new *Acanthophora* sp. widespread in the algal turf area. The plants seem to be nearer to *A. muscoides* than to *A. spicifera* but do not tally well with any material of the former seen so far.