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The Intertidal Ecology of the British Solomon Islands: I. The Zonation Patterns of the Weather Coasts

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Phil. Trans. R. Soc. Lond. B 1973 **265**, 491-537
doi: 10.1098/rstb.1973.0034

THE INTERTIDAL ECOLOGY OF THE BRITISH SOLOMON ISLANDS

I. THE ZONATION PATTERNS OF THE WEATHER COASTS

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(*Communicated by E. J. H. Corner, F.R.S.—Received* 8 *March* 1972—
Revised 26 *March* 1973)

[Plate 57]

CONTENTS

The structure and composition of the intertidal zonation pattern on Solomon Islands exposed shores has been studied with reference to a series of transects on the south and east coasts of Banika Island, Russell Group. The generalized zonation pattern is as follows:

(1) Maritime zone with halophytes such as *Ipomea pes-caprae*, *Scaevola* and *Pemphis*.

(2) Littoral fringe characterized by littorinids and neritids.

(3) Eulittoral zone, divided into: (*a*) upper eulittoral, generally with limpets and neritids, but, except in shaded conditions, bare of a well-formed balanoid barnacle zone; (*b*) middle eulittoral, carrying attached bivalves and the barnacle *Tetraclita* in shade, but under strong insolation marked by an often white-bleached cover of *Neogoniolithon* (there is an extensive cryptofauna that has retreated below the sun-warmed surface); (*c*) lower eulittoral, with the beginning of pink and brown red algal turfs, and extensively scoured by urchins.

(4) Sublittoral fringe marked by a profusion of coral species, briefly exposed to the atmosphere under strong wave attack and also by a proliferant development of green algae (*Caulerpa*, *Chlorodesmis*, *Dictyosphaeria*, *Valonia*, *Chaetomorpha*, etc.), of the brown algae *Turbinaria* and *Sargussum* and numerous red algae, especially the calcareous *Jania* and *Amphiroa*, and *Cheilosporum* species as well as massive encrusting calcareous Rhodophyceae. The variety of corals increases with descent to

(5) Sublittoral zone, only briefly exposed at suck-back of waves.

Except in sub-maximal exposure, the corals are still outstripped in ecological importance and biomass by the encrusting and cementing red algae, especially a clathrate *Porolithon*.

Variation of intertidal topography, based upon geomorphological features of the coral limestone, was responsible for important modifications of zoning pattern. The distinctive habitat types include narrow benches with maximal wave attack and, sloping shore profiles, with freely mounting surge, as well as beaches of mobile boulders. The predominant intertidal formation is that of a bench dissected by an inner and outer moat. To the seaward of the outer moat lies a surf crest, with lavish development of calcareous and other algae. The outer moat, often breached by surge runs to the open sea, is rich in faviid corals. The inner moat, in greater shelter, has *Montipora digitata*, as well as the grass *Thalassia hemprichii*.

Detailed comparative studies were made at Titiana Point, Gizo Island; at the Spit Reef, Wickham Anchorage; Wickham Island; and at Kopiu and Waimai, South Guadalcanal.

The distribution of the Mollusca, especially the Gastropoda forms a clear-cut pattern, widely applicable in the Solomons Islands. The upper shore has a predominance of littorines, nerites and patellid limpets. The middle eulittoral supports a large series of carnivorous prosobranchs, principally subsisting upon the rock-cryptofauna (sipunculids, *Lithophaga*, *Lithotrya*, and euniciid and nereid polychaete worms) in addition to a nestling fauna occupying vacated galleries and burrows.

Where moats or shallow pools provide continuously immersed stretches between tides, a different, and much enriched, zoning pattern is evident. In the eulittoral zone, zoanthids are typical, as well as wide areas of *Padina* and – in the sublittoral fringe – *Sargassum* and *Turbinaria*, and corals, especially *Acropora*, *Porites* and faviid species. With the transition from maximal wave exposure towards increased shelter, the intertidal zonation is altered by (i) vertical and (ii) horizontal effects.

For vertical effects, less marked than on corresponding temperate shores, there is still a marked elevation of the successive zones, to occupy areas well above the nominal tide limits. With decrease of wave exposure, five distinctive types of intertidal pattern have been recognized.

The Solomon Islands intertidal pattern harmonizes well with those previously studied at the Seychelles, and shows broad general affinities with the sequence of zoning in Hawaii and with the subtropical Florida shore.

1. Introduction

During the programme of the Royal Society's Expedition to the British Solomon Islands Protectorate, from June to December in 1965, the marine party devoted much of its time to a comparative survey of communities and intertidal zonation patterns on fringing reefs and surf-exposed shores. A large range of sites was examined, necessarily often briefly, in a number of localities. An earlier report (Morton & Challis 1969) dealt with general coastal biomorphology, and gave an outline of the patterns of life between tides for the coastline as a whole. The object of this paper is to give an extended account of the 'weather shores'. These lie, for the most part, on the southern coasts of the main south-facing islands, in situations where the prevailing southeasterly winds generate continuously heavy seas over long wave fetch. The shores studied are all highly 'exposed', using the term 'exposure' to signify not emersion from water, but enhanced wave attack, with the ecological effects of heavy surge, splash and spray.

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The map of the Protectorate (figure 1) shows the location of the weather coasts principally studied by the marine party. As well as the south-facing coasts (on Banika Island in the Russell Group; on Vangunu Island, New Georgia; on Gizo Island; and on Guadalcanal) two exposed north-facing localities were visited, namely at Matiu Island, on the outer barrier of the Marovo Lagoon, New Georgia, and at Kira Kira, on the island of San Cristoval. In some respects, these two northerly shores have a simpler topographic and biological structure than the weather shores. They are referred to in this paper (p. 494) to establish a basic zonation pattern of the intertidal area.

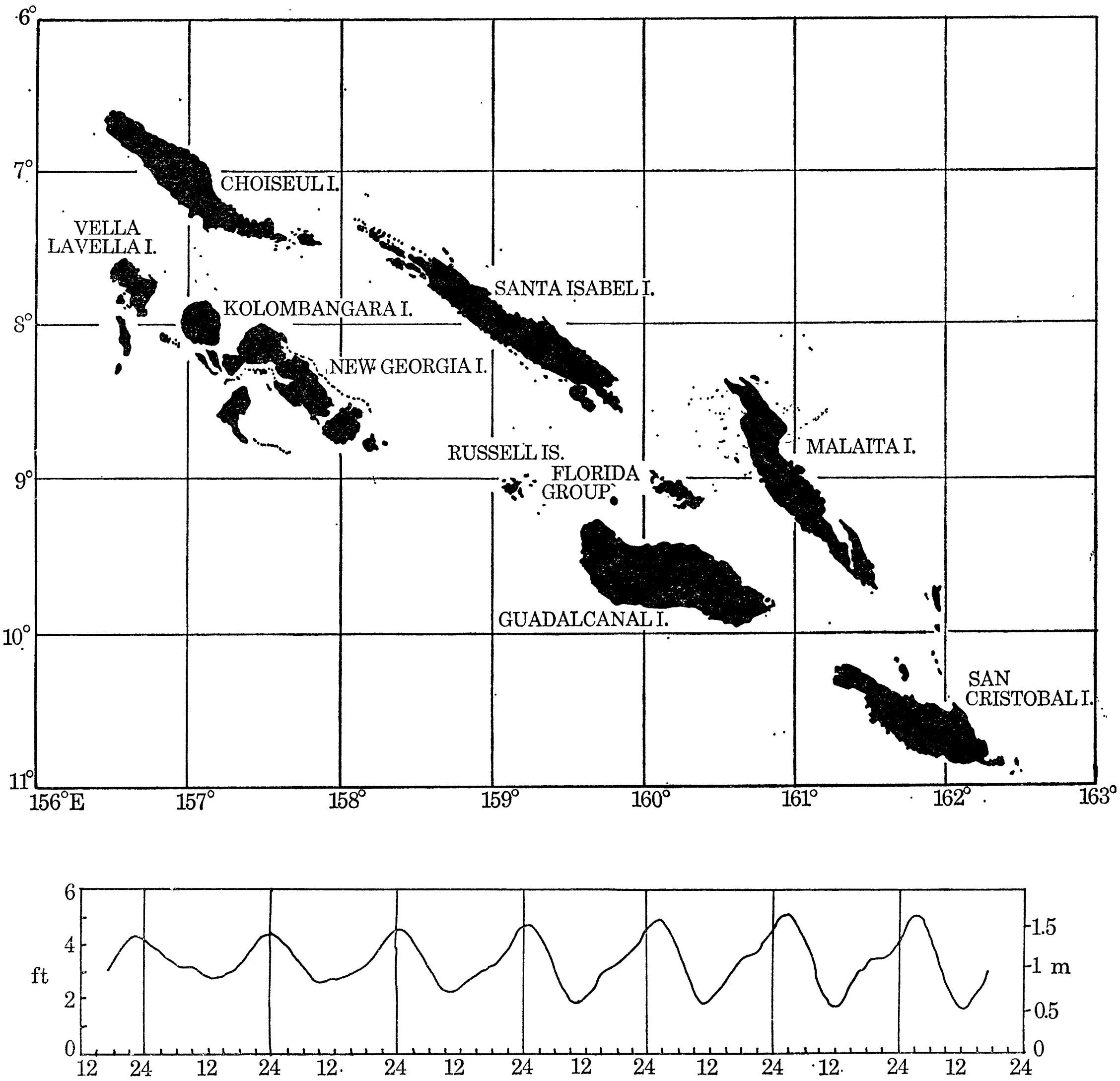

Figure 1. (Above): the British Solomon Islands Protectorate, showing the islands and localities referred to in this study; (below): tidal record from Tetel Island, Florida Group (22–29 July 1965).

(a) *Geomophology*

The coastal forms encountered in the Solomon Islands have been comprehensively dealt with by Stoddart (1969*a*), showing the general occurrence of uplifted fringing and barrier reefs, forming elevated benches of old coral rock, out of which the structures of the modern reefs and the whole coastal strip have been carved. Of great influence in the shaping of the modern terrain have been, first, the recent changes of sea level, illustrated by elevated tidal notches and platforms and drowned terraces, and, secondly, the rock forms etched by solution, both on flat and steep faces. A coastline of elevation can produce steep and often vertical gradients. The exposed rock is almost always coral limestone and sedimentary deposits are here limited to the thin mantle on the floor of the reef lagoons and flats. The development of living coral reefs is in general restricted by the prevailing conditions of uplift; this applies especially to the rougher shores we shall be considering here. Another contrast with Indo-Pacific atoll reefs is the generally slight development of the algal ridge, though calcareous Rhodophyceae are prominent as a surface veneer.

Relatively narrow intertidal benches include those studied at Kira Kira, San Cristobal, and on the south coast of Guadalcanal, as well as the surf-swept bench at Wickham Island, near Vangunu Island, New Georgia. On the outer side of Matiu Island, New Georgia, the intertidal

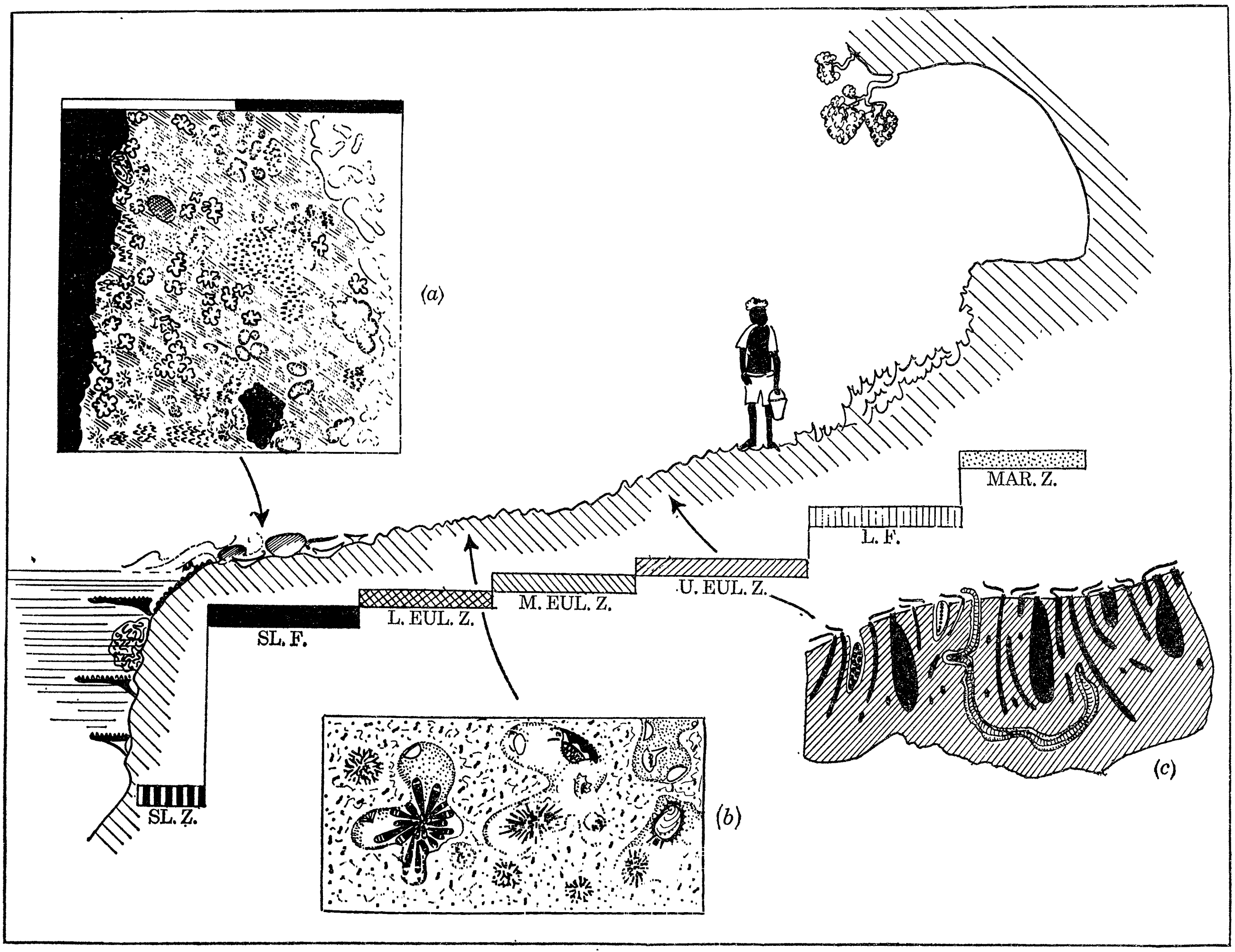

FIGURE 2. Matiu Island (outer side) Marovo Lagoon, New Georgia. Profile of intertidal bench and supra-littoral notch, showing in a simple sequence the zones referred to in this study, MAR.Z, maritime zone; L.F, littoral fringe; U.EUL.Z, upper eulittoral zone; M.EUL.Z, middle eulittoral zone; L.EUL.Z, lower eulittoral zone; SL.F, sublittoral fringe; SL.Z, sublittoral zone. Detailed insets represent: (*a*) coral and red algal cover in sublittoral fringe; (*b*) lower eulittoral zone, with echinoid excavation; (*c*) upper eulittoral zone (profile section) with worm and bivalve borings (see also figure 13).

shore (see figure 2, and Stoddart (1969c, p. 396, Fig. 83)) is marked by a deeply incised wave-cut niche above the present high-water mark, and a steep fall-off below low-water mark. On the south and east coasts of Banika Island, and the west coast of Gizo, the intertidal benches are wider and virtually level expanses, some of them more than 100 m across, characterized by one, or sometimes two, moats, the outer one divided from the inner by a residual rampart of coral limestone. In the upper part of these shores there is generally a high bench above high-water neap level.

The reef at Wickham Anchorage, New Georgia, forms a submerged coral platform with a wide moat and a low surf crest. It is attached to the land mass by a spit or cay of coarse sand and coral rubble, supporting a mangrove swamp behind. At Gizo, the shoreline inside the moat consists of black basalt. Grafted upon this land mass at the level of present mid-tide is the coral platform that floors the moat and carries a surf crest upon the seaward side.

(*b*) *The tides*

Records available for the Solomon Islands Protectorate are still no more than fragmentary. The Marine Department in Honiara kindly supplied data for two extended periods, the first from 6 January to 14 July 1962, the second from 10 November 1962 to 7 June 1963 (with 7 weeks missing). Stoddart has presented a synopsis of weekly tide levels from this information (1969*a*, p. 377, Fig. 62). The extreme range over these periods, from Point Cruz, Honiara, was 1.04 m, the greatest in any week 0.945 m. The level of weekly low tides is more variable than either the weekly mean, or weekly high-water levels.

The tidal rhythm is a diurnal one with a vestige of a second peak indicated by the tidal curve on certain days.† Broadly speaking low tides occur with some constancy around midday in winter and during the night in summer. The considerable variations in the level of weekly extreme low water (with an amplitude of 0.412 m) could have important ecological consequences, particularly in more sheltered localities, in connexion with the problem of 'dead reefs', briefly discussed by Morton & Challis (1969).

Table 1

Locality	Spring	Neap
Tetel Island	5.5′	2.2′
Paruru	3.3′	0.4′
Marovo Lagoon	2.75′	0.9′

Additional tidal data was acquired during the expedition, in the form:

(1) Of an 8-day continuous record embracing parts of a spring and neap for the Tetel Island, Florida Group, reproduced by Stoddart (1969*a*, p. 360, Fig. 50) and here shown in figure 1.

(2) A continuous record for Paruru, Marau Sound (17 September to 11 October, 1965) (Stoddart 1969*b*, Fig. 93).

(3) A record for the Marovo Lagoon (22 October to 15 November, 1965) (Stoddart 1969*a*, Fig. 78).

The extreme tidal ranges recorded for springs and neaps are shown in table 1.

The itinerary of the Marine Party involved continued moving about during a wide-ranging survey; no further continuous recording of tides was thus possible, though in all localities visited, the time of low tide hung fairly uniformly within the period 12.00 to 14.00 h. Clearly

* The semidiurnal phase was most accentuated at Paruru, Marau Sound, as found by Stoddart (1969*b*, p. 410).

the season chosen, from June to September, was the only half of the year that would have proved suitable for a study of intertidal ecology. The consensus of local tradition and fragmentary tidal data agree that the diurnal low tide shifts to around midnight in the alternate half year.

As always on outer coasts and exposed weather shores, particularly with a short vertical tidal range, the action of waves, surge and the swells raised by winds exerts a control over intertidal patterns and their vertical distribution, greatly transcending the influence of the tides (see Morton & Challis 1969, p. 462). Though we have as yet no tidal record for an exposed surf coast, observations of high and low tidal levels on calm days indicated a range typically within the limits shown for the data in table 1.

(*c*) *Zonation patterns*

As made clear both by Womersley & Bailey (1969) and by Morton & Challis (1969) the widely adopted universal pattern of intertidal zonation, first proposed by the Stephensons (1949), with modifications of terminology suggested by Lewis (1961), applies well to exposed tropical shores. A similar use of this system has been made by Endean, Stephenson & Kenny (1956) and by Taylor (1968).

The arrangement of intertidal zonation divisions may be illustrated by reference to the outer north-facing shoreline at Matiu Island, New Georgia. This locality has been previously discussed by Womersley & Bailey (1969) and by Morton & Challis (1969). The profile (figure 2) shows the sequence of zones, with a uniform hatching convention that will be used to designate comparable zones in later illustrations. Some inset detail is also introduced for the burrowing cryptofauna of the eulittoral and sublittoral fringe, an important element of every tropical limestone shore.

The first section of this paper will give a description of the reef topography and zonation on some Banika Island shores, with shorter references to other weather coasts. The second part discusses with comparative examples the important features of the patterns observed.

(*d*) *Zonation scheme*

(*As recognized between tide-marks on Solomon Islands exposed coasts*)

(See figure 2, for Matiu Island.)

(i) *Maritime zone*: never immersed and influenced only by spray and occasional splash.

(ii) *Littoral fringe*: rock surface bare, or filmed with Myxophyceae or lichen *Verrucaria*; influenced by splash. Littorinidae, e.g. *Tectarius* spp., Neritidae.

(iii) *Eulittoral zone*: fully immersed and emersed at each tide.

(*a*) Upper eulittoral: bare or with sparse algal film in shade; Littorinidae, Neritidae, patellid and siphonariid limpets.

(*b*) Mid-eulittoral: whitish bleached, or sometimes living red alga *Neogoniolithon*; sporadic barnacles *Tetraclita squamosa*; worm and lithophagid borings become dense.

(*c*) Lower eulittoral: a full cover of turfing and encrusting red algae; rock surface scoured by urchins.

(iv) *Sublittoral fringe*: emersed only briefly at lower than normal tides. A great increase in calcareous red algae, especially *Porolithon*. Numerous corals, including *Pocillopora*, *Acropora* tables, *Montipora* and *Stylophora*.

2. The weather coasts of Banika Island, Russell Group

The most extensive comparative study of shore biomorphology was made on Banika Island. Banika and Pavuvu Islands are the two largest of the Russells, consisting of volcanics dipping northwards from a faulted south coast (see Stoddart 1969*a*). The coasts are fringed by raised

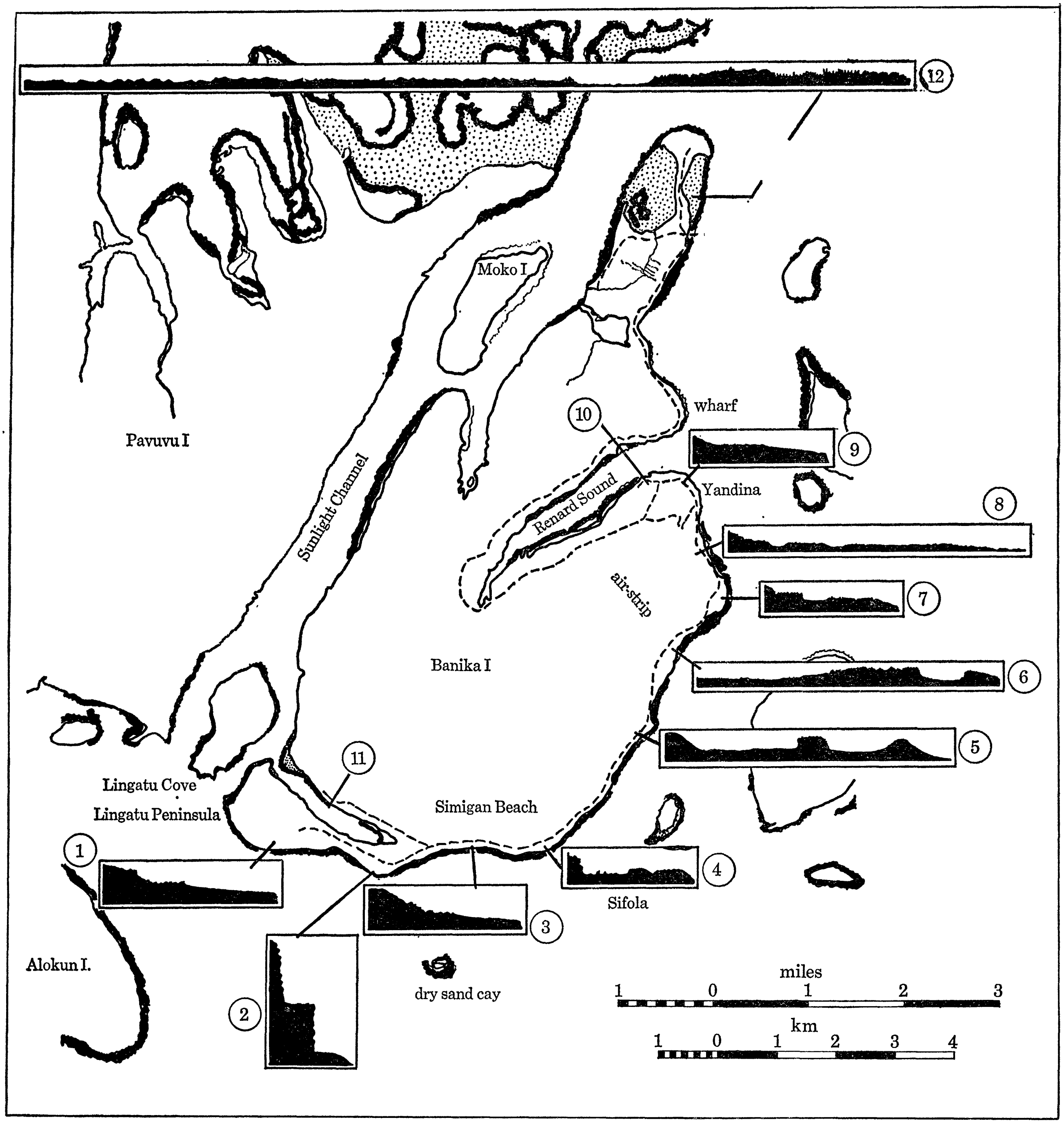

Figure 3. Banika Island, Russell Group, showing the locations and profiles of the shore sites referred to in the text. Horizontal scales are the same, except 12, which is half the scale of the rest.

limestone platforms, with a higher raised supratidal bench. The drowned northern coasts are encircled with an interrupted barrier reef. The Banika Island shores can be divided into five categories, of which only groups I comprising localities 1 to 2 and II (localities 3 to 7) are considered in detail here (see map locations, figure 3). Basically they are constructed of intertidal benches up to 50 m across, with their surface variously dissected by pools and moats.

The more sheltered shores (see profiles in figure 3) are briefly referred to in the comparative section. Group III (localities 8 and 9) have more luxuriant coral growth, their moats including branched *Acropora* species, tabular *A. surculosa*, *Porites lobata* micro-atolls, and alcyonacean soft corals. Group IV is represented by locality 12, an extensive tidal flat with sea-grass, *Thalassia*, *Montipora*, stags-horn *Acropora* and a seaward margin of *Porites lobata*. Group V (localities 10 and 11) are narrow, impoverished shorelines in land-locked inlets. With high rain and silt-run off coral is lacking and the algae depauperate.

Open sea angles for the localities studied are:

group ...	I		II					III		IV	V	
locality	1	2	3	4	5	6	7	8	9	12	11	10
angle	110	140	110	150	90	60	70	60	30	90†	—	—

† North-facing lee shore

Wind data for Banika Island are scanty and discontinuous. Observations kindly made available by Captain Douglas, Superintendent of Marine at Honiara, clearly confirm the predominance of winds in the easterly and southeasterly sector during the April to October period. In exposed situations the predominant wind in this season was reported to be SE 10 to 12 knots. In the November to March season there is considerable variability in the wind direction and strength from day to day and from one year to the next. The N–NW winds when they occur are generally much stronger than the easterly sector winds. Westerly swells (associated as they are with cyclonic disturbances) are usually higher than their easterly counterparts.

Of Banika Island, Mr J. Walton writes that for approximately the period April, May, June to October, November, December, the Sifola-Lingatu reef stretch experiences a fairly constant SE wind.

(*a*) *Banika Island: southeast coast* (*locality* 5) (*figure* 4)

This site presents typically the characteristic structures of the south Banika reef benches: a seaward reef crest, and outer moat separated by a breached rampart from an inner moat, and a raised supratidal platform. The inner moat is less than 0.3 m deep at low water, and communicates freely with the outer moat. Both are more than 0.3 m above the calm-water open sea level, and the outer moat is regularly replenished as surf breaks over the algal crusted ridge.

The biology of the successive regions can be briefly described, beginning from landward:

(i) *Supra-tidal bench and eulittoral zone*. The high bench drops vertically by a 2 m step to the inner moat. Its bare, sharply etched coral limestone supports a rich sequence of upper shore zoning molluscs. (See figure 5 for species composition and ranges.) The maritime zone, beyond the reach of splash, but strongly influenced by spray, is marked by scrambling *Ipomea pes-caprae* to the landward. In front of it grow two species of sedge, one identified as a *Fimbristylis*, and to seaward of these, the prostrate lythracean shrub, *Pemphis acidula*.

The highest occurring littorines are the *Tectarius* group. *Tectarius pagodus*, a large species, more characteristic of high vertical rock faces, as at Matiu Island, is lacking; but *T. cumingi* is found on hot, sun-baked rock near the littoral fringe step, and a smaller *T.* (*Echininus*) sp. reaches back to the maritime zone, amongst the vegetation. Immediately below the land plants,

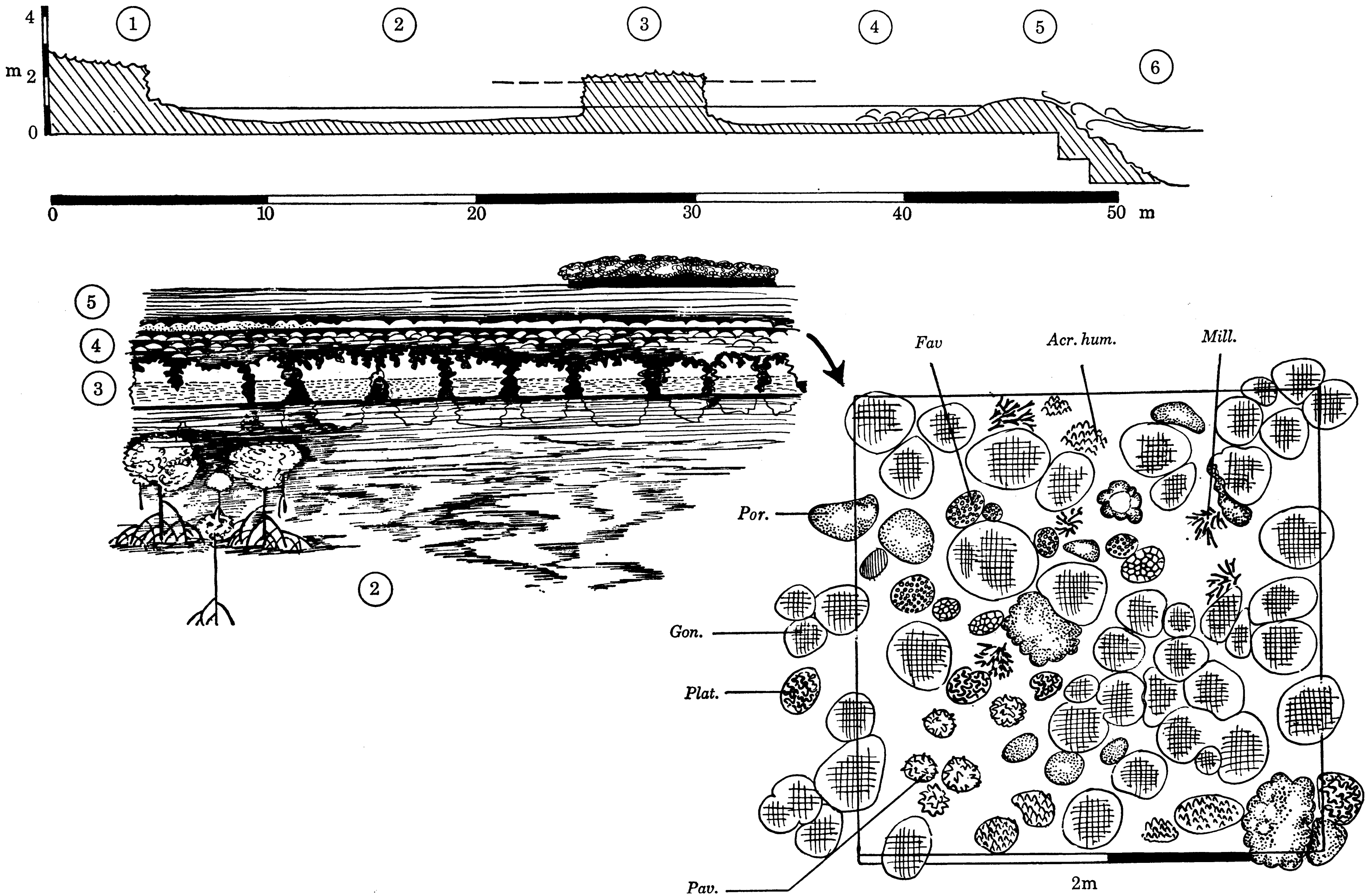

FIGURE 4. Banika Island; locality 5. (Above): profile section of the reef bench, showing the following regions mentioned in the text: (1) supratidal bench; (2) inner moat; (3) interrupted divide between the moats; (4) outer moat; (5) seaward crest; (6) surge slope. (Below left): view from the landward of the reef and moat system. (Below right): a representative quadrat (2 m square) showing the distribution of faviid and poritid heads, and other corals in the outer moat. *Acr.hum. Acropora humilis*; *Fav. Favites* head; *Gon. Goniastrea* head; *Mill. Millepora*; *Pav. Pavona*; *Plat. Platygyra*; *Por. Porites* head.

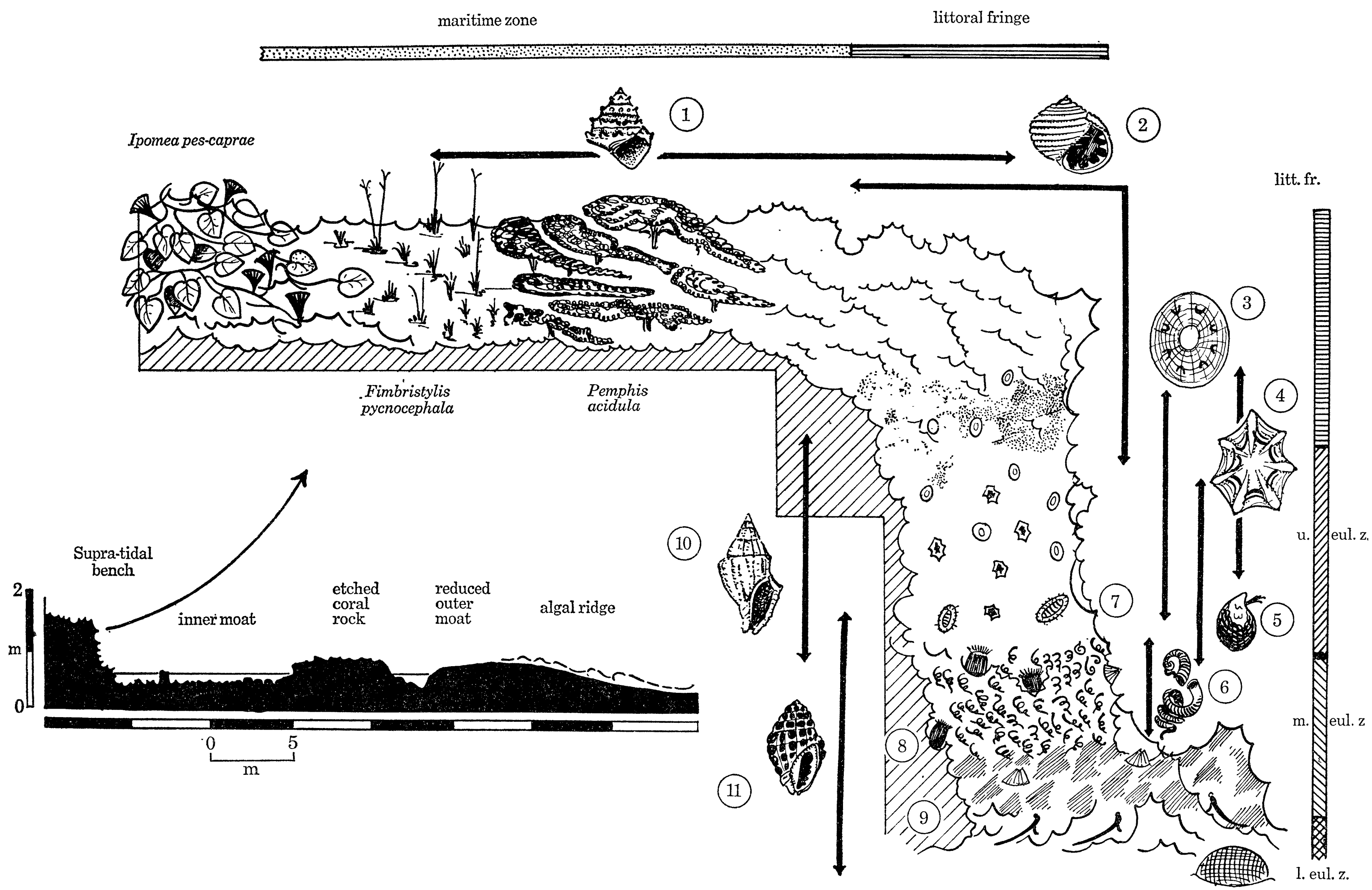

FIGURE 5. Banika Island; each of Simigan's Bay; locality 4. Detail of species distribution and zonation on the supratidal bench, and its vertical drop to the inner moat. This location is comparable with the landward formation described at locality 5. 1, *Tectarius* (*Echininus*) sp.; 2, *Nerita plicata*; 3, *Cellana rota*; 4, *Acmea saccharina*; 5, *Isognomon acutirostris*; 6, *Dendropoma* sp.; 7, (on rocks) *Acanthozostera gemmata*; 8, mid-eulittoral shade *Actinia*; 9, *Tetraclita squamosa*; 10, *Morulina fusca*; 11, *Morula granulata*.

the littoral fringe is blackened, especially in shaded concavities, with the maritime lichen, *Verrucaria* sp. The hermit *Coenobita rugosa* is common in maritime zone vegetation.

The zonation of the eulittoral zone consists of:

upper eulittoral: *Nerita plicata*, *Cellana rota*, *Acmaea saccharina*, *Acanthozostera gemmata*, *Isognomon acutirostris*, *Grapsus grapsus*

middle eulittoral: (on shaded faces) *Gelidium* sp. and *Bostrychia* sp. (in greatest shade) in a short pile; *Neogoniolithon myriocarpum*, in live or bleached patches; (in shaded concavities): *Actinia* sp.

Tetraclita squamosa (solitary or in small clusters), Vermetidae: *Petaloconchus* and *Dendropoma* (species undescribed), *Morulina fusca* (reaching to upper eulittoral and feeding on nerites)

(in concavities) small periophthalmid (near inner moat) and blennioid fish

lower-eulittoral: (bottom of vertical face) *Neogoniolithon* thickens, and thaid gastropods, especially *Morula granulata* are common; small faviid and acroporid coral heads, very sparse, mark the beginning of the inner moat

(ii) The *inner moat* is, in its shallowest places, tepid (35 °C+ at midday) and no more than ankle deep. The floor is a smooth limestone platform, much of it strewn with sediment which towards the landward edge deepens and includes much silt. Plants of the landward edge comprise: the sea-grass *Thalassia hemprichii*, thickening to a deep green sward in patches: *Rhizophora stylosa*, the only mangrove of this shore, scattered as small striplings along the inner edge of the moat; and the green alga, *Avrainvillea lacerata*, with branched upright laminae like patches of green baize.

The outer part of this moat is floored by lightly packed rubble beds of the short-branched coral *Montipora digitata*, with the live extremities of the fingers greyish brown. The dead rubble carries mauve or bleached *Neogoniolithon myriocarpum*, the most abundant calcareous alga of the inner reef. The rubble is seldom welded with *Lithophyllum*, but remains loose and mobile. Large clumps of *L. moluccense* are everywhere common, lightly attached to the bottom and often dead and bleached. They may carry ribbons of the brown alga *Dictyota friabilis* or clumps of the rhodophycean *Galaxaura fasciculata*.

Crustose corals are sparsely developed on the cleaner parts of the moat floor: strongly sculptured, yellowish brown sheets of *Pavona repens* and upstanding trabeculae of *P.* c.f. *crassa*. *Porites* is represented by small nodules of *P. lutea* and branched fingers of *P. nigrescens*. Small mounds of *Favia* or *Goniastrea* are seen only occasionally.

Molluscs of the hard moat floor, in areas clear of rubble, include the clam, *Tridacna crocea*, the large operculate vermetid *Dendropoma maximum*, and, conspicuous by its crowded siphonal openings, like small keyhole-slits, is the boring date mussel *Lithophaga curta*.

Echinodermata of the inner and outer moats comprise the following list:

Echinoidea: *Echinometra mathaei*, *Heterocentrotus mammillatus*, abrading bed-rock

Tripneustes gratilla, *Toxopneustes pileolus*, sand or silt floor of inner moat

Holothurioidea: *Stichopus* spp., *Thelonotus ananas*, *Holothuria argus*, on sandy moat floor, *H. arenicola*, in silty sand with sea-grass

	Opheodesoma griseum, a giant synaptid on silty substrates with sea-grass, esp. *Enhalus*
Asteroidea:	*Linckia laevigata*, on sandy floor or inner moat *Patiriella* spp. under faviid coral heads, in outer moat
Ophiuroidea:	*Ophiocomina scolopendrina*, in rubble or rock concavities, filter-feeding arm sweeping; (under *Porites* and faviid heads): a wide range of fragile brittle stars, including *Ophiocoma insularis*, *O. erinaceus*, *Ophiarthrum pictum*, *O. elegans*, *Ophiolepis superba*, *Ophiothrix nereidina*, *Ophiarachnella gorgonia*

(iii) The *breached rampart* dividing the inner and outer moats is vertical sided, with its coral limestone bare and sharp edged. The summit has rain-etched pools, and supports of molluscs of a littoral fringe. The shaded surface of the inner side is mauve with *Neogoniolithon myriocarpum*; on the outer side *Porolithon onkodes* to some extent protects the limestone from continued erosion.

(iv) The *outer moat* is constantly filled with moving water as the surge breaks over the reef crest or rushes through seaward channels. The run-back is never enough to deplete the moat between the arrival of waves; its water level and that of the inner moat are kept more than 0.3 m above the mean level of the open sea.

This moat is richly crowded with living corals; in particular towards the surf crest, the convex shapes of faviids and *Porites* are visible above the white surge. Tan-brown to buff in colour, they frequently compress each other to a hexagonal outline.

Short fingers of living *Montipora digitata* mingle with the serrated grey lamellae of *Millepora* cf. *forskali*. Where the tips or edges are exposed to air at low water, they are generally *Neogoniolithon*-crusted.

The principal scleractinian corals collected were:

Goniastrea pectinata	*Symphyllia recta*
G. retiformis	*Pocillopora damicornis*
Favia pallida	*Acropora humilis*
F. favus	*A. digitifera*
F. halicora	*Montipora*, a grey crustose species, unidentified
Platygyra lamellina	*Porites lobata*
P. lamellina var. *astraeiformis*	*Pavona repens*

Common green algae include *Dictyosophaeria versluysii* and *Chlorodesmis fastigiata*. Mantis shrimps (*Oratosquilla oratoria* and others) swim or somersault freely, or retreat to burrows beneath coral heads. Many species of alpheid shrimps are common; crevice-dwelling blennioids and numerous small fishes of the Pomacentridae frequent the coral heads in swarms.

(v) On the *reef-crest*, calcareous Rhodophyceae and other algae almost wholly replace the corals as the visible superficial cover. The surfaces exposed above the white surge-line show several different aspects: (*a*) the seaward face only briefly emersed from the breaking surge, (*b*) the flat tops intersected by surge channels, (*c*) the backslope from the level summit to the outer moat, (*d*) the vertical sides of the surge channels (see figure 6).

(*a*) *The seaward slope* has a massive calcareous overlay of encrusting Rhodophyceae. Though falling short of a true algal ridge, these form a chalky surface layer up to 2 cm thick, varying between mauve, pink and reddish brown, according to species. The surface at this level gives a dull sound with the hammer, in contrast to the sharp ring of the bare limestone of higher levels. The principal species is the flesh-pink *Porolithon* species, forming a strong, continuous lattice-work, with circular fenestrae. A heavier encrusting species is embossed with large, flat, grey or mauve mamillae. Massive clumps of *Lithophyllum moluccense* are occasionally found here; but this species, though common on the weather coast of Vangunu Island (see p. 509) generally flourishes best in submaximal wave exposure.

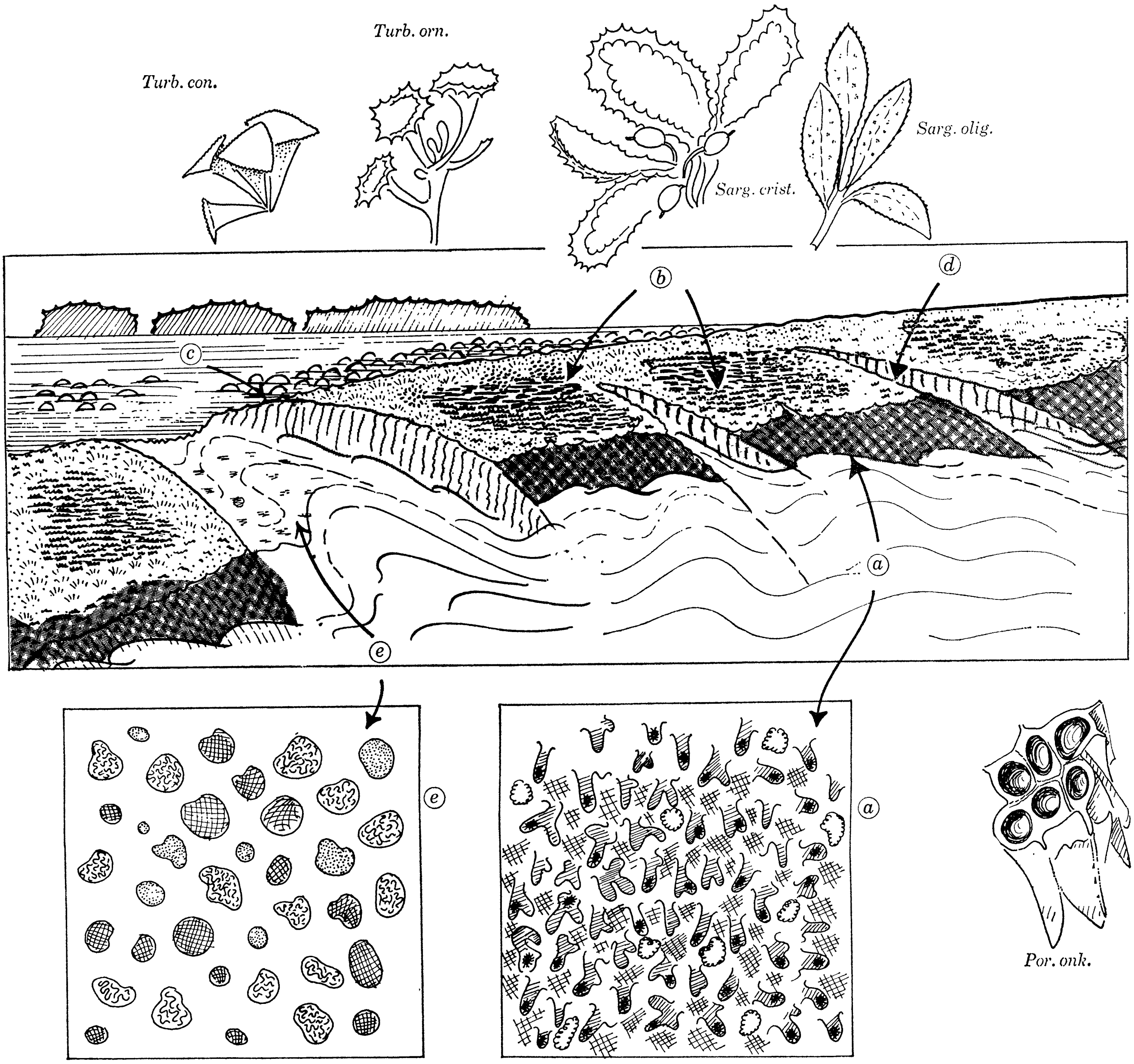

Figure 6. Banika Island: locality 5. The reef crest in schematic view, from seaward, showing the arrangement of the principal habitat types: (*a*) the surge slope to seaward; (*b*) the flat tops with *Sargassum* and *Turbinaria*; (*c*) the back-slopes to the outer moat; (*d*) the surge channels; (*e*) intersecting slope, with surge entry, with development of faviid corals. (Below): detail of the surface formation of (*a*) and (*e*). The following algae are shown inset: Por. onk., *Porolithon onkodes*; Sarg. crist., *Sargassum cristefolium*; Sarg. olig., Sargassum *oligocystum*; Turb. con., *Turbinaria conoides*; Turb. orn., *T. ornata*.

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Living corals are sparse on the seaward slope and comprise only a few species: *Acropora digitifera* and *A. humilis*, in depressed, corymbose heads, with short, strong fingers; crusts and brackets of a grey *Montipora*, *Pocillopora damicornis* and *P. verrucosa*.

(*b*) The *flat tops* have a conspicuous golden brown cover of the brown algae *Sargassum* and *Turbinaria*, growing either on the emersed, surge-swept rock face, or in shallow splash pools. As the typical fucoid algae of tropical weather coasts, species of these genera were in the Solomon Islands with few exceptions found confined to south-facing weather shores (see, however, Womesley & Bailey (1970) for scattered northern coast records). Where found in surge, both algae have a short crisp, growth, almost cartilaginous in texture; pressed stiffly against the rock, they are resistant to wave damage, and protected from desiccation by constant splash and surge.

Two *Turbinaria* species were regularly found on the south Banika coast: the common and rather variable *T. ornata*, and *T. murrayana*, lacking vesicles and showing finely dentate lateral ridges (see figure 6). For the Solomon Island *Sargassum* species, Womersley & Bailey (1970) have given clear field criteria. Three forms were found on the Sifola coast. *S. cristaefolium* is marked off by its especially crisp, compact form, and the prominently denticulate, sometimes duplicate margins of the leaves. *S. coriifolium* has the lower leaves smooth and slightly undulate, and the upper leaves strongly dentate. In *S. oligocystum*, the leaves are more slender and elongate, dark brown rather than gold, with the 'midrib' distinct to the axis and no bladders.

Of the green algae of the flat tops, most are characteristic of the surf crest under moderate to high exposure. Very numerous and chiefly confined to the pools are the diverse species of *Caulerpa; C. racemosa* var. *uvifera*, *C. cupressoides* var. *mamillosa*, *C. sertularioides*, *C. webbiana*, and *C. peltata* were all found in the present study.

Most pervasive of all green algae are the *Dictyosphaeria* species, forming small masses of stiff, cartilage-like vesicles broadly attached to the surface. *D. versluysii* is confined to the reef rim, while *D. cavernosa* extends to coral debris in the moats. In local shelter grow large stiff-walled vesicles of *Valonia ventricosa* and concealed in small crevices is *Valoniopsis pachynema*. *Boodleya composita* makes up a lacework of small tufts and cushions away from immediate surge. Stiff filaments of *Chaetomorpha antennina* grow both in pools and on surfaces wet with splash. One of the commonest green algae, on all shores except those of extreme shelter, is *Chlorodesmis fastigiata* forming green tresses up to a foot long. The small *Halimeda opuntia* was the sole species of its genus found on open shores.

Many of the algae support distinctive animal communities. Miller (1969) has discussed the cell-piercing sacoglossan slugs, associated with green algae: with *Caulerpa racemosa* are found *Oxynoe viridis*, an *Elysia* and a *Placida* species. The black and gold *Cyerce nigra* feeds on *Chlorodesmis fastigiata*. A typical faunule of *Sargassum* leaves includes a small, fast-clinging crab, *Huenia proteus*, well camouflaged by its shape and colour; a small *Pilumnus* species; an orange and white banded amphipod, *Hyale* sp.; a small ophiuroid and a tawny yellow anemone, regularly upon *Sargassum*. In feeding association with the anemone is a small, undescribed gastropod of the Pyrenidae, frequently suspended by a mucus thread secreted from the foot.

(*c*) On the *backslopes* to the outer moat, the principal cover is of turf-forming calcareous Rhodophyceae, important also on the summits. *Jania rubens* is the chief species, with the large coarsely branched *Amphiroa*: the species *A. foliacea*, *A. anastomosans* and *A. fragilissima* were all collected at Sifola. Important turf species are a small *Laurencia* and *Hypnea pannosa*. The broad, rounded laminae of *Martensia flabelliformis* are typical of temporary pools and runnels.

(*d*) The *surge channels* that intersect the main rampart are an important and typical habitat, with rapid and constant water movement. They may be V-shaped in section, or more generally square and steep-sided.

The plants and animals (figure 7) have a distinctive arrangement. Clathrate *Porolithon*, extending down the walls from tops, may be followed by sheets of *Palythoa* or of *Zoanthus confertus*. Next in order may be a brittle turf of *Amphiroa foliacea*, succeeded by pink 'Lithophyllum' paint, crustose halichondrine sponges or *Peyssonelia calcea*. On the channel floor grow corals: small *Acropora digitifera* or *A. humilis*, *Pocillopora verrucosa* and *Millepora* cf. *alcicornis*. Towards the bottom, in constantly rushing surge, grow *Amphiroa anceps*, *Cheilosporum spectabile* and *Jania rubens*.†

The distributions of the principal algae and corals across the inner and outer moats and on the reef-crest are summarized in figure 8.

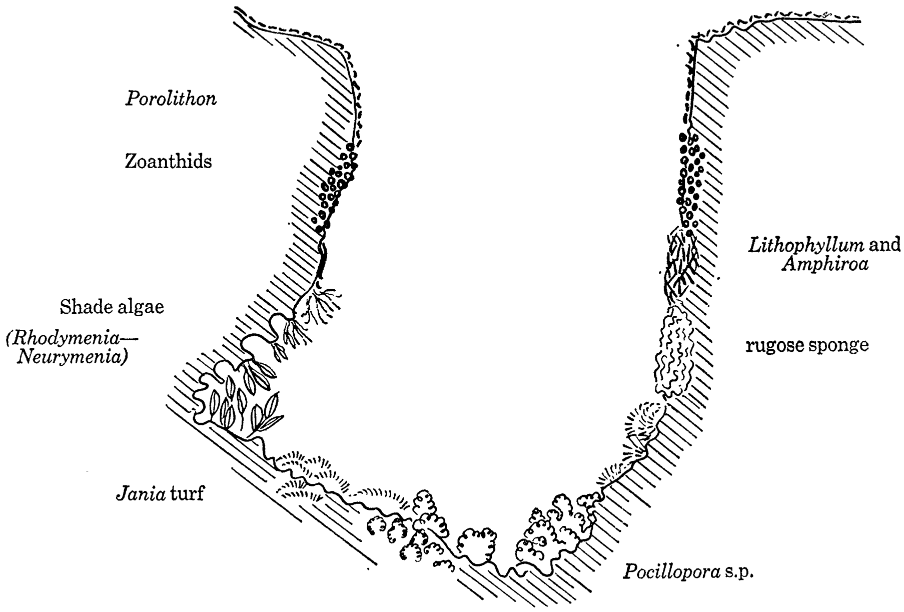

FIGURE 7. Schematic section of a surge gulley, at Kira Kira, San Cristoval, showing zonation of encrusting animals and algae.

(*b*) *Banika Island: topographic and community diversity*

The two-moated shore illustrated from the Sifola coast (locality 5) well typifies the structure and zonation pattern of the exposed parts of Banika Island. With differences of shelter, proceeding towards maximal wave exposure at Lingatu Peninsula, or into moderate shelter around the east coast of the Island, variant topographic forms are accompanied by changes in the communities:

(i) *Maximal exposure* (figure 9)

The reef benches of Lingatu Peninsula (localities 1 and 2) were the most exposed shores visited on Banika Island. At locality 1, the surf-ridge and the middle rampart have been dissected almost to vanishing, with the resultant opening up and loss of the moats. The profile of this transect is a graded seaward slope, with two steps of less than a metre high. Under the highest wave exposure, towards the extreme point of the Peninsula, the extensive intertidal

† From a similar channel at Kira Kira, San Cristoval, were collected the shade loving red algae *Rhodymenia anastomosans*, *Carpopeltis maillardi* and *Neurymenia fraxinifolia*.

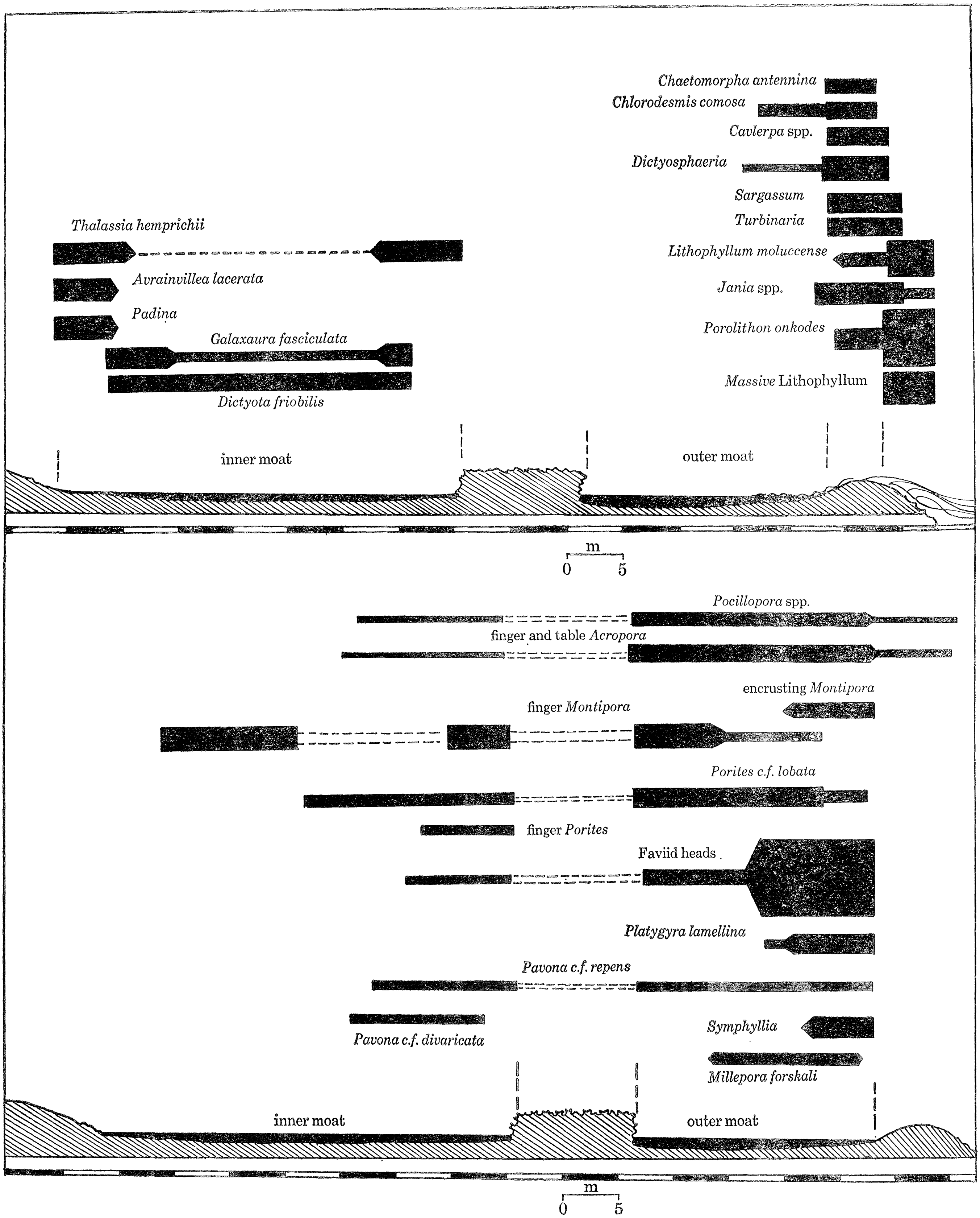

FIGURE 8. Banika Island: locality 5. (Above): the distribution of algae in the inner and outer moats and on the seaward reef crest; (below): the distribution of corals across the moats and reef crest.

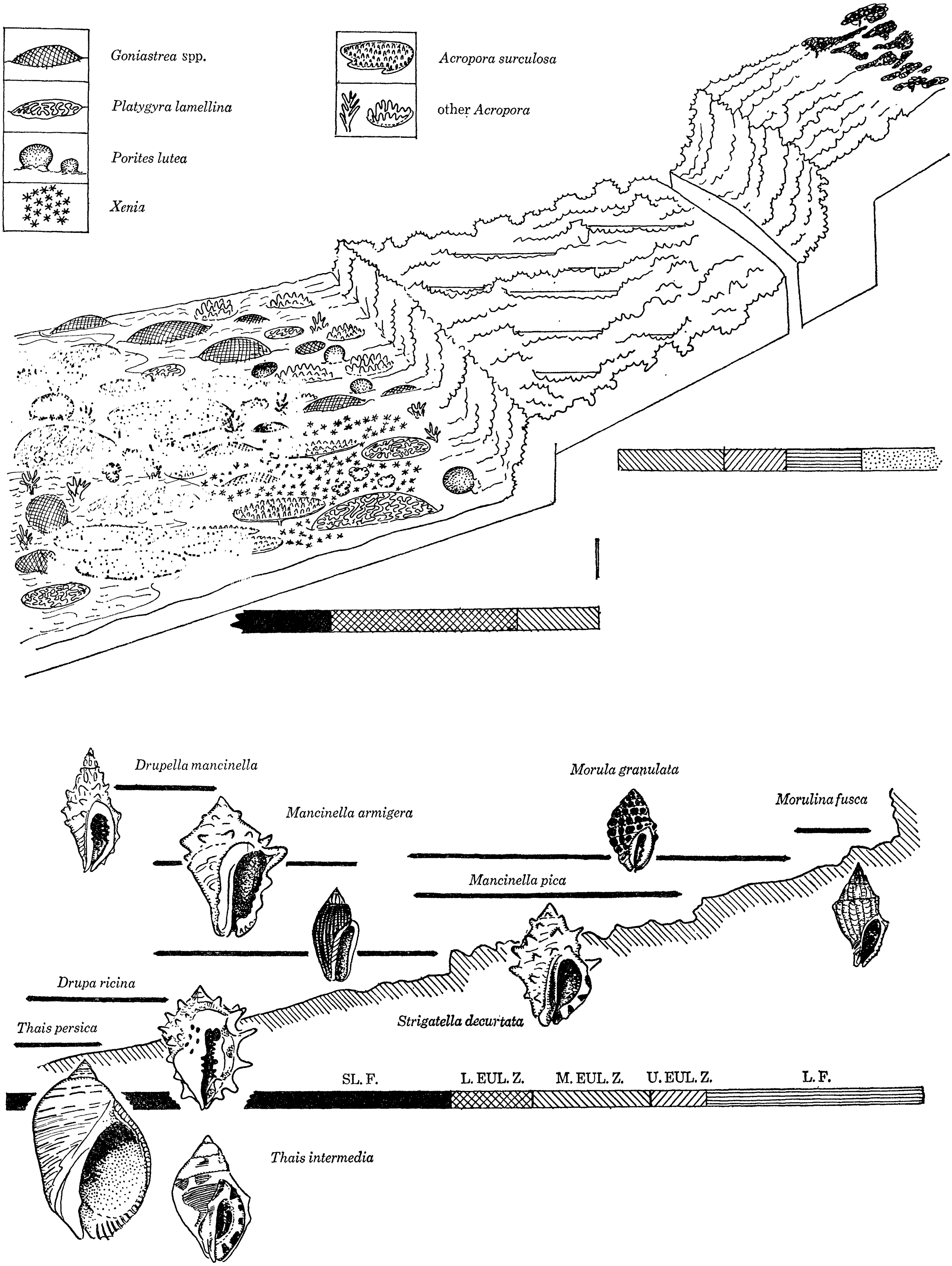

FIGURE 9. Banika Island: Lingatu Peninsula. (Above): schematic impression of the sloped bench, with its regions greatly abbreviated horizontally; (below): distribution of carnivorous gastropods across the same profile. (Zoning conventions as in Figures 2 and 15.) (locality 1.)

bench is lacking, and the much abbreviated shore consists of a cliff with an elevated high-tidal notch (described by Stoddart 1969*a*) and fronted by a narrow intertidal ledge.

At locality 1, the up-sweep of surge reaches through the whole eulittoral zone. This expanse is scattered with shallow eroded pans. At higher levels these pools become tepid during long emersion, linking up further down to a system of broad pools, increasingly pink with their lining of *Lithophyllum* paint. Towards the bottom of the eulittoral zone, corals grow in the pools, mainly crustose or convex plaques of faviids, such as *Platygra verrucosa*. *Porites lutea* also forms crusts, mingled with compact, branched clusters of *Pocillopora damicornis*. Black *Holothuria*, freckled with white sand, lie in the larger pools. *Xenia* is abundant in extensive sheets on pool bottoms and in splash.

The lower step leads to the sublittoral fringe, continuing by a gentle slope to seaward. This is an important coral zone. The disappearance of flat tops precludes the growth of *Sargassum* and *Turbinaria*, which are replaced by Scleractinia. With the free access of surge up the whole slope, the coral growth forms are well adapted, including convex mounds, compact tables, short brackets and surface crusts. The whole slope is dominated by low *Acropora* heads, and clusters of short fingered species. Ten entities of this genus were collected. The corals include:

table-forming species:	*A. squamosa*, dull-pink, with low, spreading to convex heads
	A. hyacinthus, with slender, upright fingers massed in lilac, or greyish white sheets
	A. tubicinaria, with white-tipped greyish brown fingers, anastomising in brackets
	(*A. surculosa*, a common table-former in greater shelter, is rare or lacking at Lingatu)
clusters of short, divergent fingers:	*A. digitifera*, with dull, buff to reddish branches, very abundant at Lingatu
	A. humilis, with short, conical cream-white fingers mauve-tipped
low-clusters of brittle,	*A. nasuta*, *A. nana*
upstanding branches:	(two stagshorn species, common in greater shelter, *A. grandis* and *A. formosa*, are represented by sparse and stunted specimens)
massive, club-shaped and crustose:	*A. palifera*
depressed, and thin-spreading surface crusts:	*A. palmerae*

Other important corals are Faviidae, forming convex mounds or depressed and spreading plaques. The chief species are *Favia favus*, *Favites halicora*, *Goniastrea retiformis*, *G. pectinata*. Both *Pocillopora verrucosa* and *P. damicornis* are common. *Montipora* species include surface crusts and brackets; a frequent species is *M.* c.f. *crassifolia*, with digitate or explanate lobes, grey with mauve edge.

At locality 2, Lingatu Peninsula, the abbreviated surf-beaten platform is no more than 2 m wide, and pink *Porolithon* reaches to the cliff base. Algae other than *Porolithon* are scarce: *Turbinaria ornata* in splash pools, *Sargassum oligocystum* and *Chaetomorpha antennina*. The high vertical ranges of the molluscs (see figure 20) show the striking elevation effects of high wave exposure. They are:

maritime zone:	*Tectarius cumingi*, *T. pagodus*, *T.* (*Echininus*) sp. (reaching to base of cliff-line), *Neritina* sp.
littoral fringe:	*Nerita plicata*, *N. undata*, *Melarhaphe undulata*
upper eulittoral:	*Acanthozostera gemmata*, *Acmea pallida*
middle eulittoral:	*Thais persicus*

(ii) *Boulder beaches*

The upper reaches of the sloping intertidal bench generally carry an accumulation of wave-rounded limestone boulders. These may extend into the high tidal cliff notch as it is variously represented along the Banika south coast. The hypofaunal gastropods and crabs have a wide typicality as a boulder beach faunule in the Solomon Islands (see, for comparison, p. 512, for hypofauna of boulders on silt or sand).

littoral fringe:	mobile boulders
(insolated upper surface):	*Littoraria coccinea*;
(sides):	*N. plicata*, *Nerita insculpta*,
(beneath):	*Melampus luteus*
crabs:	*Coenobita rugosa*, *Cyclograpsus* sp., *Leptograpsus* sp.
upper eulittoral zone:	
(tops and sides):	*Nerita plicata*, *Acanthozostera gemmata*, *Cellana rota*, *Siphonaria* cf. *atra*
(beneath):	*Nerita polita*, *N.* (*Thliostyra*) *albicilla*, *Lunella cinerea*, *Moneta annulus*, *Engina mendicaria*
crabs:	Grapsidae: *Grapsus grapsus*. Xanthidae: *Pilumnus*, *Ozius*. Hermit: *Calcinu shebsti*. Porcellanidae: *Petrolisthes* sp. *Pachycheles* sp.

(iii) *Surf-swept benches*

At the small Wickham islet, off Vangunu Island, south coast, a narrow surf-pounded bench under strong wave attack, was examined. Reticulated with small 'Lithophyllum' pink pools, the bench has no moat system, and falls steeply seaward in breaking surge. At each wave suck-back, a pink-brown network of *Porolithon* with occasional *Pocillopora verrucosa* was exposed for a depth of up to 2 m. The bench top, with sublittoral fringe, was situated approximately 1.5 m above low-water mark. From each breaking wave at low tide a 0.5 m wall of surge coursed powerfully across the whole platform.

The seaward pools have *Sargassum cristaefolium* and *Turbinaria ornata* along their divides, together with pads of *Hypnea nidulans*, and turfs of *Jania rubens* and *Gelidiella acerosa*. *Dictyosphaeria versluysii* is widespread and *Caulerpa peltata* and *C. serrulata* grow in the pools. Interspersed with these are sheets of large zoanthids, each 2.5 cm or more across, with tentacles light mauve, and oral disk brown, with emerald green at the centre.

Further landward, at mid-eulittoral level, the pool zoanthids continue, along with a pervasive bluish grey sponge, *Adocia caerulea*.

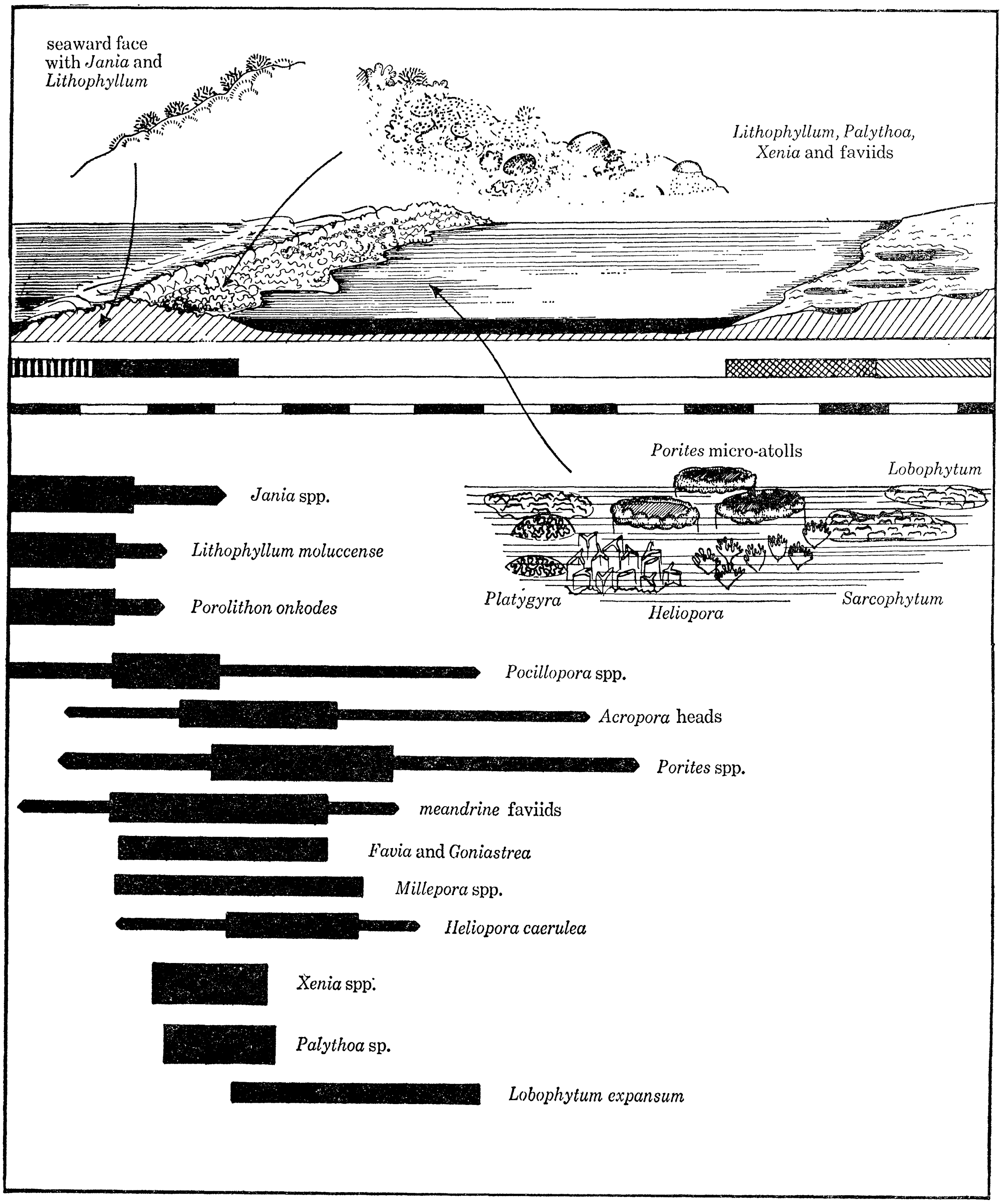

FIGURE 10. Vanganu Island: Wickham Spit. Profile section and schematic diagram of the intertidal platform with moat and surf ridge: inset diagrams: detail of wave-beaten seaward face (left); sublittoral fringe facing the moat (right); more sheltered scleractinians and soft corals of the outer part of the moat (below). The distributions of the three principal calcareous red algae, and of ten corals and soft corals, are shown below.

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3. South Guadalcanal

The south-facing weather coasts of Guadalcanal Island were visited at several points accessible from the eastern tip of the island at Marau. Stoddart (1969*a*) has described the eroded, slightly elevated reef benches of this coast, shelving seawards from the foot of basalt slopes. The reef at Waimia was the wider of the two studied, extending for some 40 m to seaward, with the surf rampart broken and highly dissected. The moat is entered by constant surge, and contains abundant living coral, including *Goniastrea pectinata*, *Platygyra lamellina*, *Acropora humilis*, *Pocillopora verrucosa* and *Porites lutea*.

At Kopiu Bay the intertidal area is a narrow surf bench, 8 to 10 m across, composed of pebble and boulder conglomerate. Its surface zonation and biology resemble that of Wickham Islet.

4. Vangunu Island: Wickham Anchorage spit (figure 10)

To the southeast of Vangunu Island extending east to Gatukai Island runs a barrier island protecting a sheltered stretch of water called Wickham Anchorage. The locality studied was the reef-flat to the outer side of the barrier's westward tip. The limestone benchrock has not been elevated but remains at intertidal level, with a wide moat bounded by a low emergent surf crest. The backshore behind the reef bench is a mangrove formation, with *Avicennia alba*, *Sonneratia griffithii* and other coastal scrub, sited upon a spit of silty coral sand.

Zones and communities

(i) A grey *littoral fringe*; increasingly darkening to landward, colonized with blue-green algal film and a black lichen (*Lichina* sp.) sun-drying to a brittle stubble.

(ii) *Upper eulittoral zone*: bare, greyish white limestone, with little surface cover, but profusely pitted lower down with sipunculid borings.

(iii) *Mid-eulittoral zone*, with mauve or pink-white overlay of *Neogoniolithon myriocarpum*.

(iv) A single *moat*, *ca*. 30 ml wide, and no more than 1 m deep. From landward most of its width is occupied by large micro-atolls of *Porites lobata*, and low, convex heads of *Platygyra lamellina* and *Goniastrea* spp. *Acropora* is represented by small tables of *A. hyacinthus*, small-branching *A. formosa*, and short clumps of *A. humilis*. Towards the reef crest the moat floor, yellow, corrugated sheets of the alcyonacean *Lobophytum expansum* occupy much area. *Platygra lamellina* increases in importance, and small clumps of the blue coral, *Heliopora caerulea*, appear as surge becomes more pronounced. *Millepora* cf. *alcicornis* mingles freely with *Heliopora*.

(v) The *surf crest* is low-pitched and gently sloped, formed not by a raised bench, but from accretions of unconsolidated rock. Its surface contour is irregular, richly encrusted with calcareous Rhodophyceae. The lack of level tops or splash pools precludes the development of *Sargassum* or *Turbinaria*. The seaward slope is notable for its large, fist-sized clumps of *Lithophyllum moluccense*, in addition to pink *Porolithon*. Especially evident on the backslope to the moat are *Palythoa* and several species of *Xenia*.

Figure 10 shows the zonation of corals, algae and gastropod molluscs across the Wickham Anchorage Spit. Their distribution can be regarded as broadly typical for all the reef-bench situations studied on the weather coasts.

5. Gizo Island: South Coast: Titiana Point (figures 11, 12)

This island is built of andesitic volcanics, tilted north, with the steeper south coast enclosed by a wide fringing reef (see Stoddart 1969*a*). The shoreline behind the reef is of steep-faced volcanic bluffs. It stretches outwards towards the reef edge in the following regions:

(i) A narrow mudflat, with fine carbonate sediments, silt and loose boulder cover.

(ii) A wide moat, half the reef width, generally no more than 0.5 m deep, resembling generally the inner moat at Sifola (p. 501).

(iii) An outer reef crest of etched and jagged coral limestone rising to a low summit (eulittoral zone) and falling seaward as a surge-face sublittoral fringe.

The regions

(*a*) *The backshore*: volcanic headlands and strewn boulder (figure 12).

The Mollusca

vertical faces:	*Tectarius cumingi*, *Melarhaphe undulata*, *Nerita plicata*, *N. insculpta* (in zoned sequence, on faces)
	Planaxis sulcatus (densely gregarious near bottom of faces); *Morulina fusca* (at same level; a predator on nerites)
	Pythia pantherina (at high levels, among leaf litter of *Avicennia alba*)
loose rocks, on sand or silt, upper eulittoral:	
upper surfaces:	*Planaxis sulcatus*, *Nerita polita*
beneath stones:	*Nerita signata*, *N. chamaeleon*, *N.* (*Thliostyra*) *albicilla*, *Clithron mertoniana*
stones in small pools:	*Siphonaria*, c.f. *atra* (above); *Clypeomorus bifasciatus*. *Lunella cinerea* (beneath); carnivorous prosobranchs: *Morula granulata*, *Engina mendicaria*, *Drupa* c.f. *pathauii*
bivalves: hard rock surfaces:	*Barbatia cruciata*, *Chama pacifica* burrowing in silty sand patches: *Asaphis dichotoma*, *Quidnipagus palatam*, *Gafrarium tumidum*, *Atrina muricata*

(*b*) *The seaward reef crest: back-slope and pools*. At the sea-ward edge the moat surface is broken by emergent stacks of sharp-edged coral limestone, with bleached *Neogoniolithon*. Farther seaward a network of shallow pans is cut off from the moat, lying at a higher level and replenished, over the low reef crest, by splash and surge. The emersed divides of the pool have a pale mauve cover of living calcareous red elgae. The pool bottoms are pink encrusted, or widely covered with the close packed, leaden grey *Zoanthus confertus*, interspersed with the larger, buff zoanthid *Isaurus elongatus*, solitary or in small clusters. Common among the zoanthids are the parchment tubes of the polychaete *Phyllochaetopterus socialis* (see figure 11). The emersed pool edges have a small undescribed vermtid, *Dendropoma* sp., densely penetrating the algal crust, and a *Stomatella* sp. grazing the moist algal surface.

The summit and seaward slope of the reef crest is highly irregular in surface contour, built above its coral basement by much calcareous algal growth. The surface is complexly welded and cemented by encrusting Rhodophyceae, forming a chalky layer, several centimetres thick, overlaid with a living algal veneer. There is an elaborate network of closed overhangs, and surge channels, through which surge rushes strongly, often spouting up through blow-holes. Living corals are sparse, being confined – along with *Zoanthus* and *Palythoa* – to the sides of surge channels. They include *Acropora surculosa* tables, pink *Pocillopora verrucosa*, *Favia pallida* and *Montipora* brackets.

Algae of the reef crest

Higher levels, well-lighted:	turfs of *Laurencia* sp. and *Hypnea pannosa*, *Jania rubens*, tufts of *Amphiroa foliacea*
in shade beneath ledges:	*Ralfsia* sp., *Peyssonelia calcea*, *Plocamium* sp., *Rhodymenia anastomosans*, *Cheilosporum spectabile*
level tops:	*Sargassum cristaefolium*, *Turbinaria ornata*, *Hypnea nidulans*, *Martensia flabelliformis*, *Champia parvula*, *Acanthophora spicifera*, *Gelidiella acerosa*, *Gelidiopsis scoparia*, *Chaetomorpha antennina*, *Dictyosphaeria versluysii*.

6. The cryptofauna: boring and nestling species (figure 13)

The species boring into the calcareous bed-rock form collectively a vast biomass, responsible for extensive biological erosion (see Carriker, Smith & Wilce (1969) and Otter (1937). They require mention in any scheme of tropical hard shore zonation, being particularly important as the food supply of gastropod predators, especially Thaisidae and Mitridae.

Exceeding all the rest in number are the sipunculoid worms. The commonest species, *Cloeosiphon aspergillus* reaches high in the upper eulittoral zone; its greatest dominance is in the middle eulittoral, where the surface is closely pitted with its apertures. The same species appears to continue as far as low water, but in the lower eulittoral is accompanied by species of *Aspidosiphon* and *Phascolosoma*. *Aspidosiphon* and *Cloeosiphon* both make vertical borings, with anterior extremity protected by a sclerified shield, serving as an operculum. Beneath this plate lies the mouth, from which a long introvert with rings of fine denticles can be rolled out to forage over the rock. Immense numbers of introverts can be detected at work on the moist rock surface, even when the tide is out. For the mechanics of sipunculid boring, see Rice (1969).

The following sipunculid species were collected from coral limestone, or dead or living corals:

Phasocolosoma nigrescens:	bed-rock in mid and lower eulittoral
Phascolosoma pacificum:	bed-rock in lower eulittoral; penetrating *Lithophyllum*, along with vermetid *Petaloconchus*
Phascolosoma albolineatum:	bed-rock at high levels in upper eulittoral
Aspidosiphon elegans:	mid-eulittoral in limestone, and in sedimentary reef platforms
Cloeosiphon aspergillus:	in *Porites lobata* heads and mid-eulittoral bed-rock
Lithacrosiphon sp.:	in mid-eulittoral bed-rock.

By the mid-eulittoral, rock boring bivalve molluscs, *Lithophaga curta*, have appeared in great numbers, along with the scarcer species, *L.* c.f. *zitteliana*. The burrow is ovoid to bottle-shaped, with a narrow keyhole-shaped aperture from the short neck. In the lower eulittoral, two associated boring bivalves are the mechanically boring species, the mytilid *Botula silicula* and

Rocellaria (*Gastrochaena*) *lamellosa*. Making short, wide-mouthed burrows amongst the bivalve borings is the specialized pedunculate barnacle *Lithotrya valentiana* (see Cannon 1935, 1946) (see figure 13).

Polychaete worms rank second only to the sipunculids as biological weathering agents. The coral-inhabiting polychaetes of a Florida reef tract were comprehensively dealt with by Ebbs (1966). In the Solomon Islands they include a number of species, chiefly of the Euniciidae and

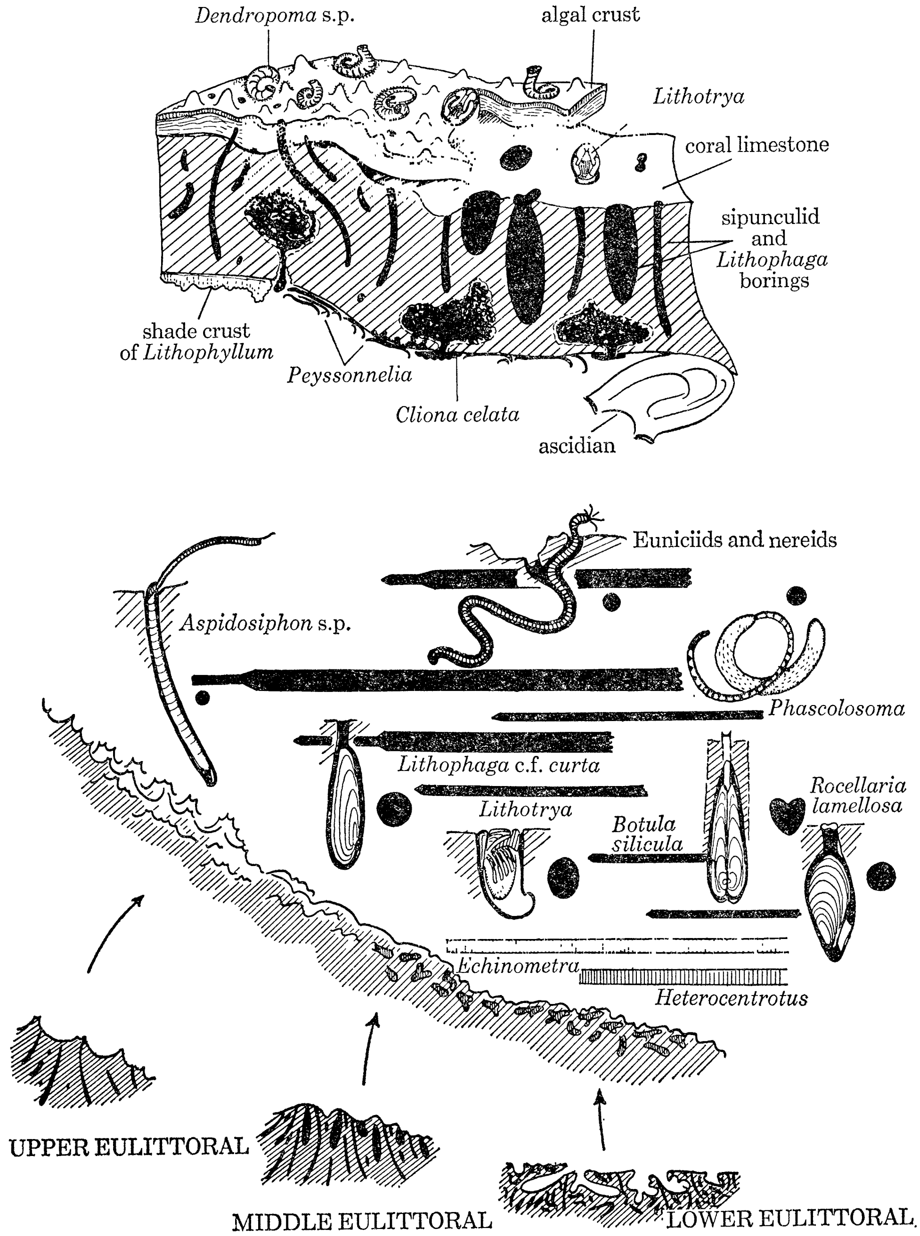
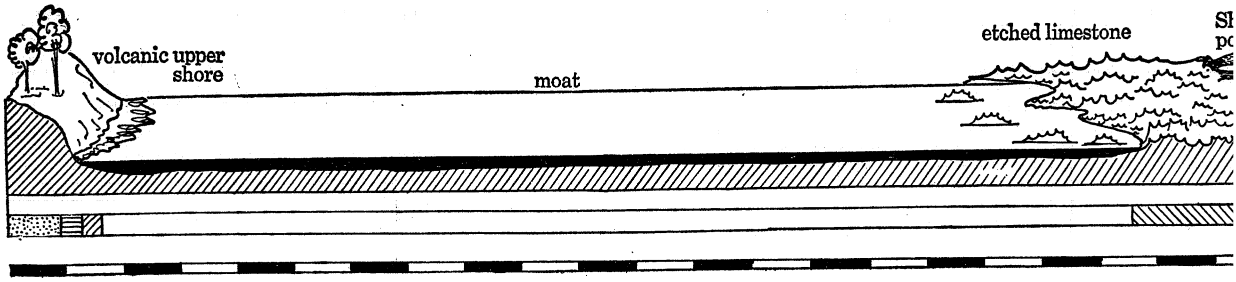
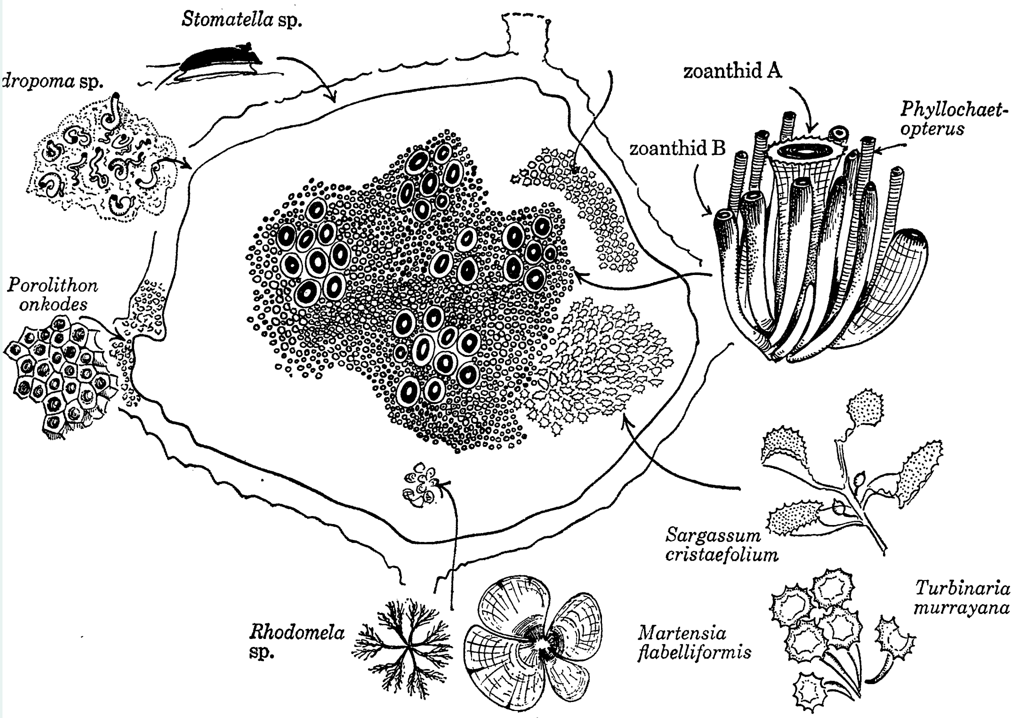
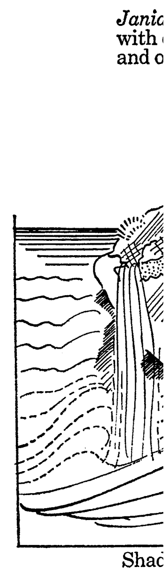
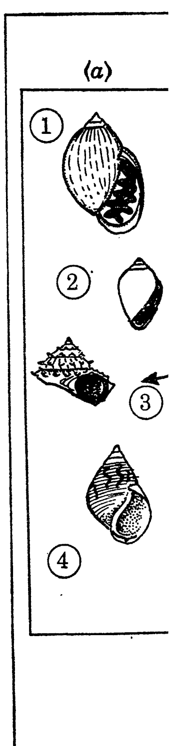


FIGURE 13. The cryptofauna of coral limestone surfaces. (Above): a shelf of rock showing its overlay of calcareous and other red algae, both above and beneath the overhang. Burrows of bivalves, sipunculids and *Lithotrya* are shown, opening above, and (below) the upward erosion of the sponge (*Cliona celata*). (Below): the ranges of the major boring organisms of the cryptobion, in the eulittoral zone of an exposed shore. Detail of burrow shape and posture is given for the bivalves, worms and *Lithotrya*, and the ranges of *Echinometra* and *Heterocentrotus* are also added (cross-hatched).









E 11. Gizo Island: Titiana Point. (Above): profile section of the reef bench, the volcanic backshore nd the pool system and surf ridge to seaward; (below left): a zoanthid-lined pool of the middle ulittoral zone, with details of the principal organisms, (below right): portion of the surf ridge, nowing the detailed distribution of the algae, Scleractinia and soft corals.

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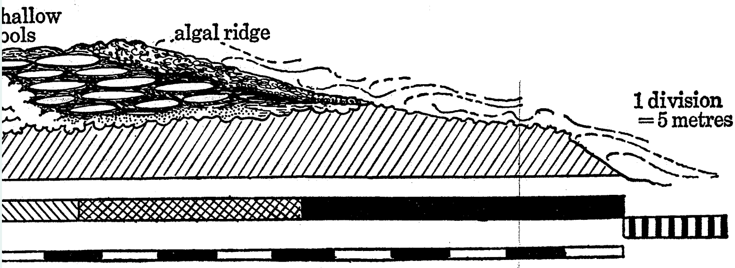
.E 12. Gizo Island: Titiana Point. The upper shore to the landward of moat, showing the arrangement of habitats and the distribution of the principal molluscs: (*a*) supratidal rock faces extending .p to terrestrial conditions; (*b*) shaded igneous faces in upper eulittoral zone and littoral fringe; *c*) under loose stones on sand or silt; (*d*) burrowing in surface layers of silty sand; (*e*) under stones esting in pools. 1, *Pythia pantherina*; 2, *Melampus* c.f. *coffeus*; 3, *Tectarius* (*Echininus*) sp.; 4, *Melarhaphe ndulata*; 5, *Nerita plicata*; 6, *Planaxis sulcatus*; 7, *Melanopsis* sp.; 8, *Nerita* (*Thliostyra*) *albicilla*; 9, *Isonomon acutirostris*; 10, *Nerita polita*; 11, *N. chamaeleon*; 12, *Clithron mertoniana*; 13, *Nerita signata*; 4, *Gafrarium tumidum*; 15, *Barbatia cruciata*; 16, *Asaphis dichotoma*; 17, *Quidnipagus palatum*; 18, *Engina nendicaria*; 19, *Conus litteratus*; 20, *Clypeomorus bifasciatus*; 21, *Morula granulata*; 22, *Lunella cinerea*.



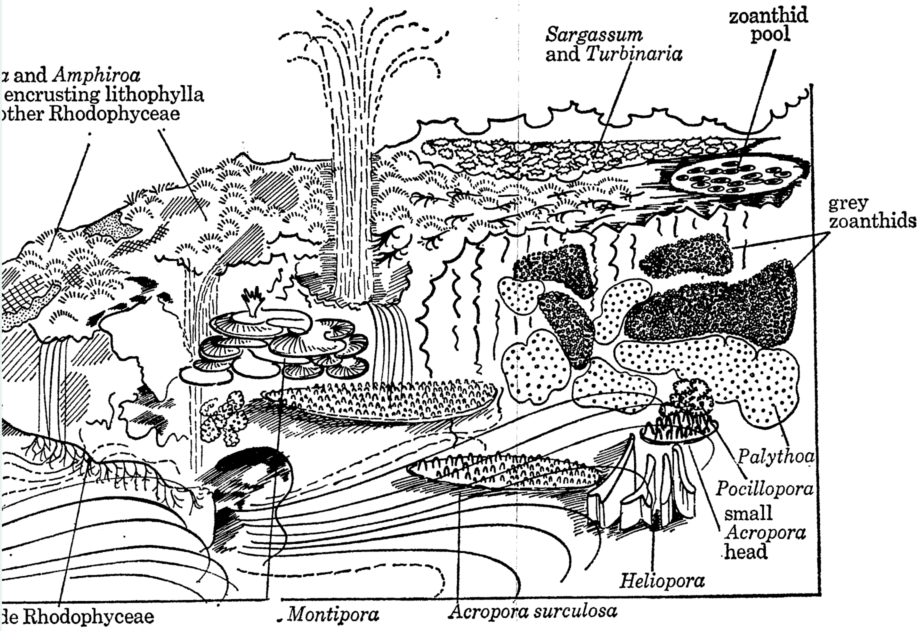


FIGURE 11

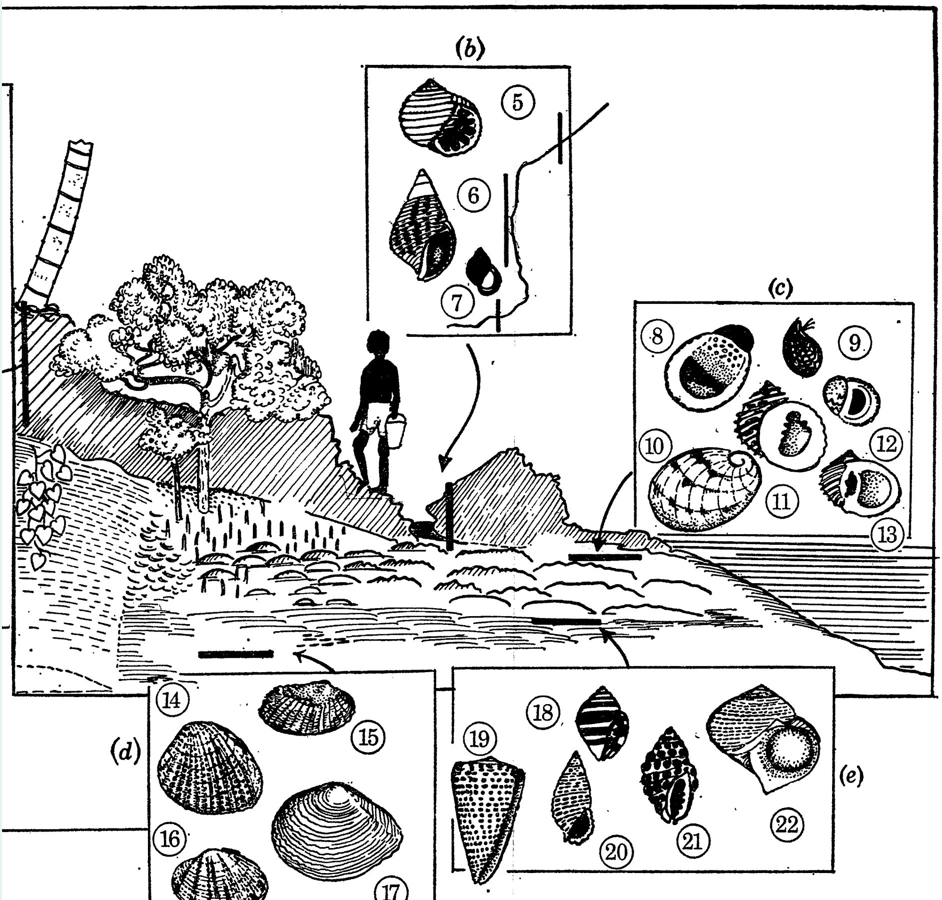


FIGURE 12

(Facing p. 514)

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Nereidae (both with hard jaws available for rock abrading). Gibbs (1969) list from beach-rock the following boring species also taken from limestone bed-rock (see also Gibbs 1971):

Nereis unifasciata	*Eunice afra*
Perinereis cultrifera	*Eunice* (*Palolo*) *siciliensis*
Perinereis nigropunctata	*Lysidice collaris*.

A leading feature of limestone tropical shores, from the mid-eulittoral downwards, is abrasion by urchins. The whole lower half of the shore is scoured with channels narrower at the mouth, and furrowing obliquely inwards to the expanded part occupied by the urchin. Widely common in the mid-eulittoral and lower eulittoral is *Echinometra mathaei*; in the lower eulittoral and the sublittoral fringe it is overlapped by the less numerous slate pencil urchin, *Heterocentrotus mamillatus*.

The galleries first opened up to sipunculids, polychaetes and bivalves are regularly occupied by non-boring species. Several phyllodocid species lodge in recent vacant worm borings, as also a jet black polynoid, a species of *Cirriformia* (Cirratulidae) and the fan-worm *Sabella fusca*. As well as several commensal *Lepidaesthenia* species, Gibbs (1969) records a palmyrid, *Bhawania goodei*, commensal in *Aspidosiphon* tubes.

Urchin furrows are the refuge of numerous gastropods, both archaeogastropods (trochids and turbinids) and the carnivorous *Drupa* species (see p. 517). Bivalve species byssus-attached include: the small ribbed mussel *Septifer bilocularis pileosus*, a second *Septifer* species, the wing-shell *Isognomon pernum* and the related *Pinctada sugillata*. Cemented in concavities of the substrate are small *Chama dunkeri*. Embedding molluscs include the clam *Tridacna crocea*, up to six inches in length, *Arca ventricosa* and the large vermetid *Dendropoma maximum*.

7. Gastropoda

A later report will give a more extended ecological account of the Mollusca of exposed and sheltered Solomon Islands shores. For the weather coasts here studied, the distribution of the leading species of prosobranch gastropods across a representative shore is indicated in figure 14. The following distinct ecological groupings of prosobranchs can be generally recognized:

(i) Deposit feeders and grazing herbivores of the open surface of the upper shore (conveniently all areas landward of the inner moat where present). Littorinidae, Neritidae, Acmeidae and Patellidae are families of high importance.

Acmeidae:	*Patelloida saccharina*
Patellidae:	*Cellana rota*
Turbinidae:	*Lunella cinerea*
Neritidae:	*Nerita polita*, *N. plicata*, *N. insculpta*, *N. undata*, *Puperita* (*Heminerita*) sp. *Neritina* sp.
Littorinidae:	*Tectarius pagodus*, *T. persicum*, *T.* (*Echinellopsis*) *cumingii*, *Littoraria scabra*, *L. coccinea*, *Melarhaphe undulata*, *Nodilittorina fijiensis* c.f. *milligrana*
Planaxidae:	*Planaxis sulcatus*

(ii) Deposit feeders and grazing hervivores living under stones, in boulder beaches or shallow pools, of the upper shore.

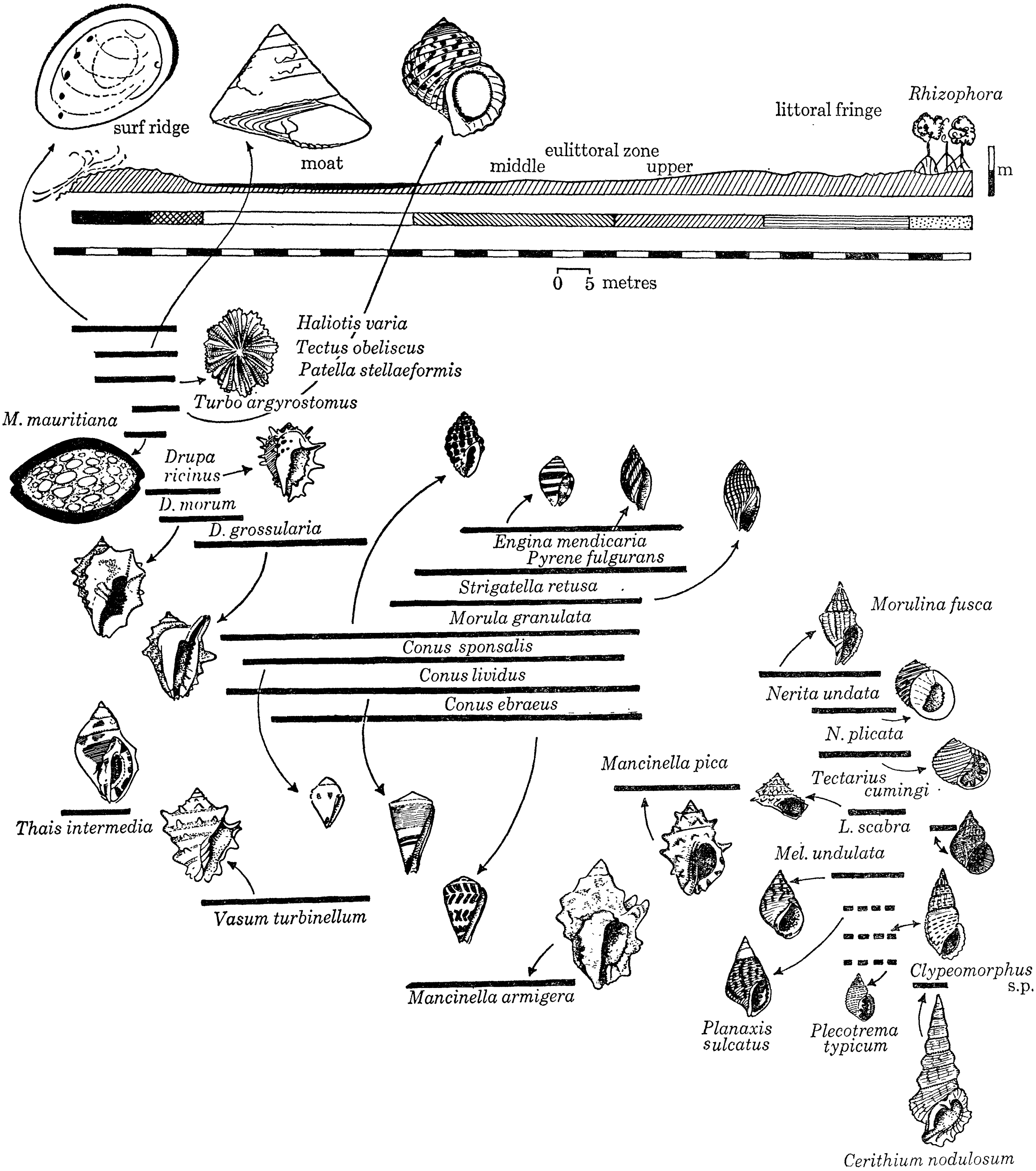

FIGURE 14. The distribution of zoning gastropods across the upper shore, most and surf-crest, from Wickham Spit, Vangunu Island (see also figure 10). The broken bars represent species under high-tidal stones.

Cerithiidae: *Cerithium fluviatilis*, *C. lemniscatum*, *C.* (*Clypeomorus*) *dorsuosum*, *C.* (*Clypeomorus*) c.f. *bifasciata*, *Semisulcospira* sp.

Neritidae: *Nerita* (*Thliosytra*) *albicilla*, *N. signata*, *N. chamaelon*, *Clithon sowerbianus*, *C. mertoniana*, *C. oulanensis*

Turbinidae: *Lunella cinerea*

Cypraeidae: *Moneta annulus*, *Monetaria moneta*

(iii) Carnivorous gastropods of the moats and eulittoral zone. This region shows a relative poverty of herbivores, but a high diversity of carnivores dependent upon burrowing and cryptofaunal prey. Predominant families are the Mitridae and Thaisidae. The Conidae, chiefly important on soft flats, have several common eulittoral hardshore species.

Muricidae: *Morula granulata*, *Morulina fusca*, *Mancinella pica*

Pyrenidae: *Engina* (*Pusiostoma*) *mendicaria*

Mitridae: *Strigatella retusa*, *S. paupercula*, *S. virgata*, *S. decurtata*, *S. litterata*.

Conidae: *Conus ebraeus*, *C. chaldeus*, *C. sponsalis*, *C. lividus*, *C. miles*

(iv) Herbivores of the reef-crest; taking green or succulent red algae, or turfing calcareous Rhodophyceae. Important families are the Fissurellidae, Trochidae, Turbinidae, Haliotidae and Cypraeidae

Fissurellidae: *Montfortula* sp. *Tugali* sp.

Haliotidae: *Haliotis varia*

Acmeidae: *Acmea pallida*

Patellidae: *Patella stellaeformis*

Trochidae: *Trochus maculatus*, *T. stellatus*, *Tectus obeliscus*, *Stomatella* sp.

Turbinidae: *Turbo argyrostomus*, *T. chrysostomus*, *T. petholatus*

red-algal and general browsers:

Cypraeidae: *Ravitrona caput-serpentis*, *Monetaria moneta*, *Palmadusta clandestina*, *Mauritia mauritiana*, *Cypraea tigris*

(v) Carnivorous prosobranchs of the reef crest, subsisting (like (ii) on cryptofaunal prey). The *Drupa* species are numerous and especially characteristics of the shores studied.

Bursidae: *Bufonella ranelloides*

Cymatiidae: *Colubrellina granularis*

Muricidae: *Drupa morum*, *D. ricina*, *D. rubuscaesius*, *D. grossularia*, *D. albolabris*, *Drupella cornus*, *D. mancinella*, *Mancinella armigera*, *Thais intermedia*, *T. persica*, *Drupa* c.f. *pathuauii*, *Morula mitosa*, *M. bruneolabrum*

Pyrenidae: *Pyrene* (*Engina*) *lauta*, *P. versicolor*

Columbellidae: *Columbella* sp.

Nassariidae: *Niotha clathrata*, *Iopas sertum*

Fasciolariidae: *Peristernia nassatula*, *Latirolagena smaragdula*,

Vasidae: *Vasum turbinellum*.

Associated with the Gastropoda may be mentioned the chitons (Amphineura) represented herbivorous by *Acanthozostera gemmata* in the upper eulittoral, and near low water, by *Anthochiton* and *Onithochiton* spp. and *Cryptoplax japonicus* in crevices and amongst encrusting coralline algae.

The feeding habits of various tropical carnivorous prosobranchs have been recently referred to by a number of authors. *Drupella mancinella*, notably found on branched *Acropora*, is regarded by Robertson (1970) as a probable coral predator. The feeding of the *Strigatella* species on eulittoral sipunculids is noted by Morton (1973), and Wu (1965) has described the cryptofaunal predation of some *Morula* species. The Conidae, as predators on errant polychaetes, and sedentary cryptofaunal worms, have been comprehensively reviewed by Kohn (1959).

The exposed hard shores support a large array of carnivorous gastropods with highly specific dietary adaptations, including the Pyramidellidae (five species recorded) and the Eulimidae, ectoparasites taking blood and body fluids of worms, crustaceans, echinoderms and other molluscs. The Eratonidae live particularly upon gorgonians, below low water. The Coralliobiidae form a specialized off-shoot of the Thaisidae. A separate paper is in preparation on their feeding morphology. Previous descriptions are given by Gohar & Soliman (1963), and Robertson (1965).

Prosobranch gastropods as sedentary predators on coelenterates. Records from Solomon Islands exposed or semi-sheltered shores.

Architectonicidae:	*Heliacus variegatus*; on *Zoanthus* sp. on finger rubble.
Ovulidae:	*Primovula coarctata*; on gorgonians, sublittoral zone
	Ovula ovum; on soft corals, sublittoral zone
Cypraeidae:	*Calpurnus verrucosus*; on *Sarcophytum* spp.
Coralliobiidae:	*Magilus antiquus*; in goniastreid coral heads
	Leptoconchus lamarcki; in faviid heads
	Coralliobia violacea; on mounds and microatolls of *Porites lobata* and *Porites* c.f. *fusca*
	Quoyula monodonta; on *Stylophora mordax* branches
	Coralliobia erosa; on *Montipora foliosa* and on branched *Acropora*
Muricidae:	*Drupella mancinella*, on branched *Acropora*.

The opisthobranchs of the exposed hard shores have been well reviewed by Miller (1969). In addition to the Sacroglossa (p. 504, above), a notable reef-rim species is the algal-cropping aplysioid *Dolabrifera dolabrifera*. *Smaragdinella calyculata*, a small surface-clinging bullomorph, is characteristic of eulittoral rock faces in submaximal exposure. Rudman (1970) has given an account of two moat-dwelling *Chelidonura* species collected by this Expedition. An important account of general gastropod ecology for Micronesian reefs is given by Demond (1957).

Other invertebrates. The sponge communities of Solomon Islands coasts, both exposed and sheltered, are discussed by Bergquist, Morton & Tizard (1971). Gibbs (1971) has completed a full taxonomic report on the polychaete worms collected by the Expedition. The echiurans and sipunculans have been determined, and will be reported upon by Dr S. J. Edmonds. Important groups awaiting taxonomic attention for the Solomon Islands are the brachyuran and anomuran crabs. Knudsen (1967) has described the host-specific relation of two coral commensal crabs, *Trapezia cymodoce* with *Pocillopora* and *Tetralia* with *Acropora*.

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8. The zones of exposed intertidal shores

An uplifted fringing reef has a wide horizontal extent. With high insolation between tides, such an expanse will in its simplest form be barren and depauperate (Morton 1973). For a visible zonation to develop, the surface must be wet between tides: with surge driven through gulleys or coursing up a long slope; waves crashing upon a narrow bench; or with still water impounded in moats. All these conditions encourage calcareous algal and coral growth.

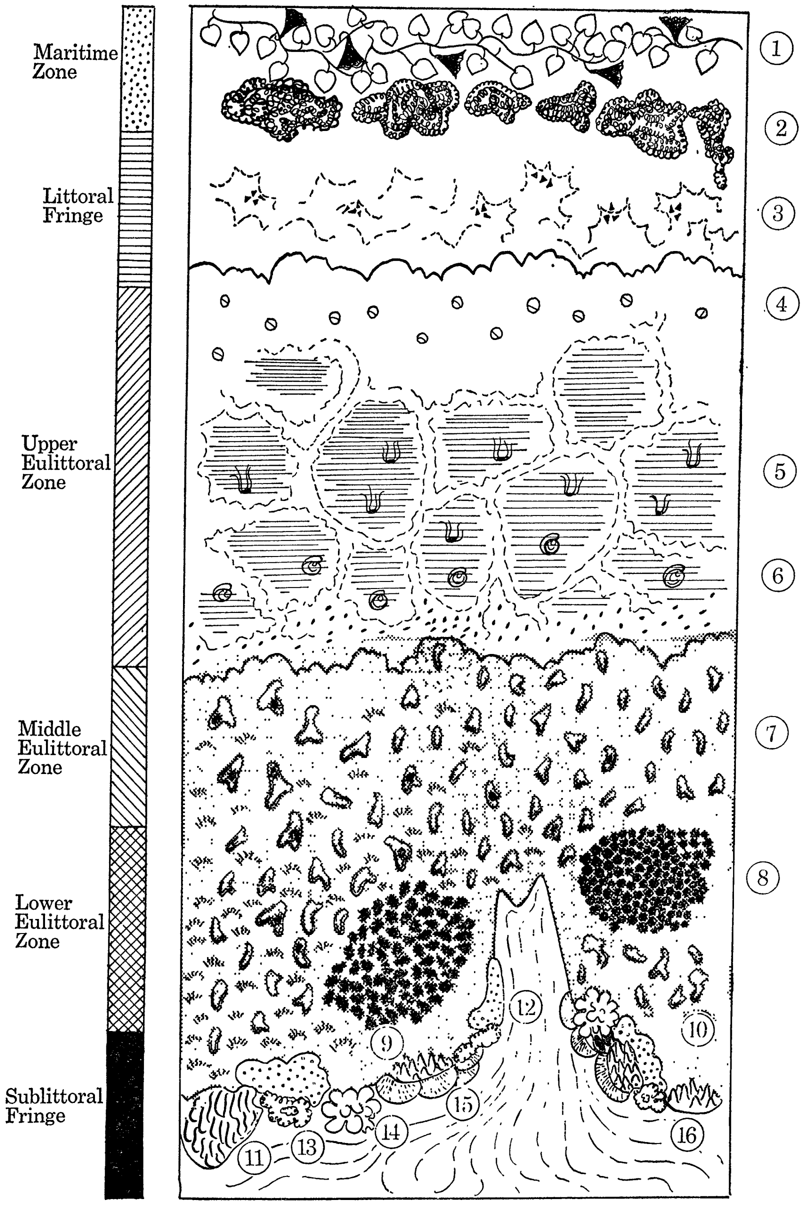

Figure 15. Schematic diagram of the general pattern of surface zonation on emersed weather coasts. The organisms represented are: 1, *Ipomea pes-caprae*; 2, *Pemphis acidula*; 3, *Tectarius* sp.; 4, *Nerita polita*; 5, pools with *Ophiocomina scolopendrina* and *Chama pacifica*; 6, openings of cryptofauna (sipunculids, polychaetes, *Lithophaga*, *Lithotrya*); 7, urchin-scoured furrows (*Echinometra* and *Heterocentrotus*); 8, *Sargassum* spp.; 9, *Turbinaria ornata*; 10, *Neogoniolithon* crust with turfing Rhodophyceae; 11, *Lobophytum expansum*; 12, *Palythoa* sp.; 13, *Pocillopora verrucosa*; 14, *Stylophora mordax*; 15, *Montipora* brackets; 16, *Acropora humilis*.

Algae flourish best on wave-swept surfaces. Corals prefer quieter conditions such as the wide shallow moats and immersed reef-flats of sheltered coasts, where virtually a whole shore may be equated to a 'sublittoral fringe pool'. It is on weather coasts, by contrast, that the zoning patterns can be harmonized most readily with those of temperate shores. Even though the surface life may sometimes be disappointingly sparse, with clear-cut zones not apparent, yet the 'universal system' of hard shore zonation (Stephenson 1958) survives an exacting test in that the complexities of the tropical shore fit well into its framework.

The chief ecological characters of the shores we have described may be summarized:

(i) the horizontal spread is very great, with maximal insolation and desiccation and drying from the sun;

(ii) the intertidal surface when fully emersed is impoverished both in algae and sessile animals;

(iii) in particular, operculate barnacles are generally absent as zone-formers;

(iv) calcareous and encrusting Rhodophyceae are well developed, as on all tropical hard shores; at the surf margin of weather shores the green algae and the brown Sargassales also achieve a high importance;

(v) with the frequent scarcity of sessile animal life-forms, gastropods are often the best-zone-markers, especially the Neritidae, Littorinidae and limpets of the upper shore;

(vi) the principal animal biomass of the intertidal shore must be looked for in the crypto-fauna eroding calcareous rock;

(vii) the algal-grazing gastropods of temperate shores tend to be out-numbered by a large contingent of carnivores feeding upon the cryptofauna;

(viii) pools and moats are a conspicuous topographic feature, and must always be considered if the zoning pattern is to be properly understood.

The basic composition of the intertidal zonation pattern on weather coasts, under moderate to high wave exposure, is summarized in the schematic diagram (figure 15).

(a) Maritime zone and littoral fringe

Both those divisions are best represented where there is a supratidal bench. The maritime zone may be defined as the first strip of the shore where humus accumulates in sufficient patches to support halophytic angiosperms. Though seldom reached by splash, it comes under strong and continuous influence of salt spray. The common vegetation includes a shrub fringe of *Scaevola taccada* to landward, followed by the familiar convulvulus *Ipomea pes-caprae*. Growing prostrate as a forward outlier on bare rock is the lythracean shrub *Pemphis acidula*.

The littoral fringe is of bare, strongly insolated rock, reaching above the highest inundated levels, but regularly affected by splash. Where coral limestone here stands out in conspicuous grey-white, its surface is jagged and rain-etched into small pools. Not only are sessile animals lacking, there is in the Solomon Islands little of the lichen cover characteristic on temperate and subtropical shores of the littoral fringe (black) and the maritime zone (yellow and greenish white). The only important shore lichen found in the Solomon Islands was a black *Verrucaria* on shaded vertical surfaces in the littoral fringe. A few species of filming blue-green algae, or in some places a mat of *Lyngbya* or shade tufts of *Bostrychia* complete the visible fringe vegetation. The productivity of the rock surface, with short-lived algal sporelings, unicellular and penetrant

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algae, and with minute wave-lodged plant cells, must however be high enough to support the considerable contingent of grazing molluscs.†

(b) *Eulittoral zone: upper and middle*

On temperate and most subtropical shores this zone clearly begins with the onset of operculate barnacles in quantity. The first third (upper eulittoral) is typically dominated by a *Chthamalus* or *Chamaesipho* species. The middle eulittoral of temperate shores is generally a zone of attached bivalves, cemented (Ostreidae) or byssus-fixed as the Mytilidae, often followed by a band of vermetid gastropods or serpulid tubeworms. The lower eulittoral is on warm temperate shores generally clad with coralline algae, with turf species predominant in shelter and encrusting 'lithophylla' in exposure.

The insolated surface of the flat or gently sloping tropical eulittoral is an impoverished one. It can be contrasted with the far more complete zonation patterns of semi-shaded vertical

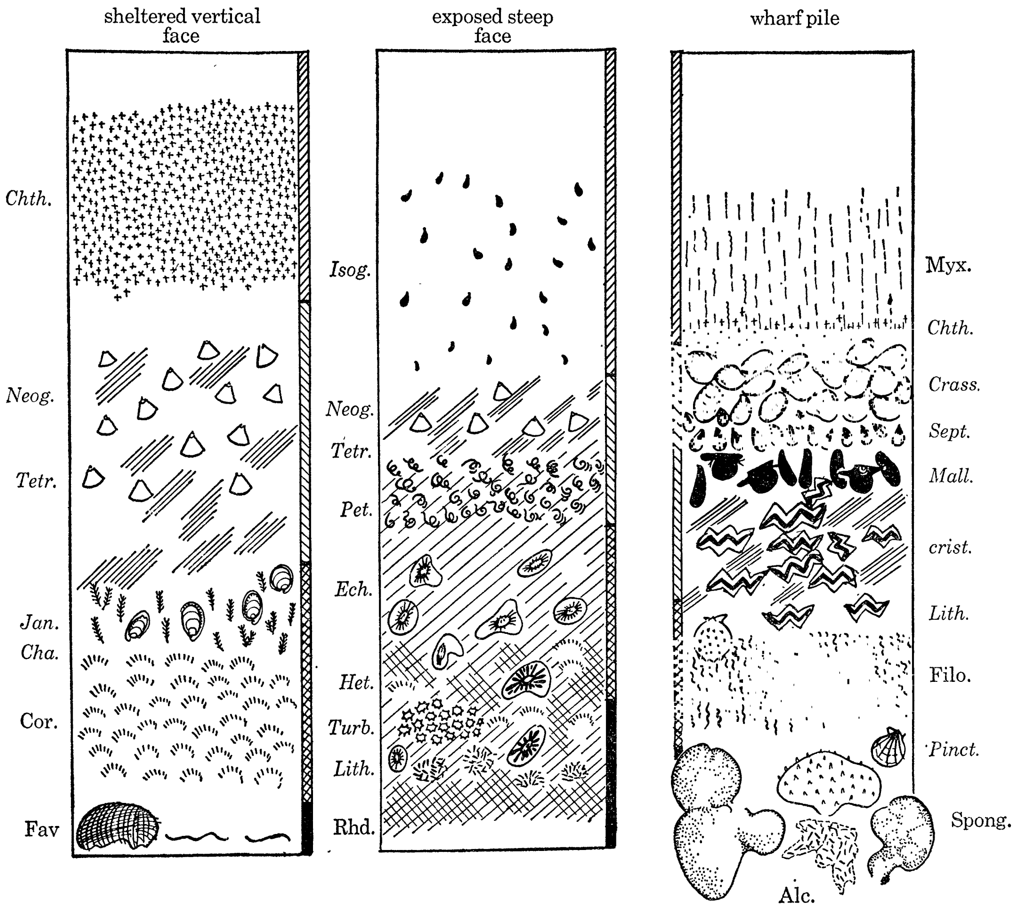

FIGURE 16. Eulittoral zonation patterns on steep or vertical surfaces. The shaded vertical face (left) is at Kukum, Guadalcanal; the exposed steep face (centre) at Banika Island; and the wharf pile (right) at Yandina, Banika Island. Alc., soft corals; Cha., *Chama dunkeri*; Chth., *Chthamalus* sp.; cor., coralline algal turf; Crass., *Crassostrea* sp.; crist., *Lopha crista-galli*; Ech., *Echinometra mathaei*; Fav., faviid coral heads; Het., *Heterocentrotus mamillatus*; Isog., *Isognomon* sp.; Jan., *Jania* spp.; Lith., mixed *Lithophyllum* spp.; Mall., *Malleus* sp.; Myx., blue-green algae; Neog., *Neogoniolithon myriocarpum*; Pet., *Petaloconchus* sp.; Pinct., *Pinctada vulgaris*; Rhd., mixed Rhodophyceae; Sept., *Septifer* c.f. *bilocularis*; Spong., mixed sponges; Tetr., *Tetraclita squamosa*; Turb., *Turbinaria murrayana*.

† Recent New Zealand studies by Beckett (1969) and Barker (1969) have provided estimates of the flora of 'bare' rock surfaces, by acetone extraction and pigment determination.

surfaces on sheltered coasts, and especially with the bivalve-dominated sequence on zoned wharf piles, with maximal shade and reduced turbulence (see figure 16 for Yandina Wharf, Banika Island). The upper eulittoral shows the barnacle *Chthamalus withersi*, and the middle eulittoral is occupied by *Crassostrea*, *Septifer*, *Malleus*, *Isognomon* and spondylids. The lower eulittoral is covered with the serpulid *Filograna* sp. and the sublittoral fringe with alcyonaceans and massive sponges (c.f. *Ancorina*).

On weather coasts, the upper eulittoral barnacles (*Chthamalus* spp.) are seldom found, but on shaded or surf-washed vertical faces in the middle eulittoral the large, conical *Tetraclita squamosa* may occur. Never found in maximal heat of the sun, this barnacle is obviously adapted against high evaporation and insolation risks: its volume to surface ratio much exceeds that of other shore barnacles, and most of its bulk is occupied by a honeycomb of cellular spaces through the whole thickness of the shell valves.

The important gastropod families of the maritime zone and littoral fringe have already been noted (prosobranchs: Littorinidae, Neritidae, Cerithiidae; pulmonates: Ellobiidae, Onchidiidae). The nerites and littorines show important species changes between exposed and sheltered shores.

Crabs are an important scavenging force of the upper shore. Where boulder and litter cover are available, small *Cyclograpsus* species abound. On the bare littoral fringe rock, agile *Grapsus* and *Leptograpsus* species are found. The most abundant hermit crab of the present level is the terrestrial *Coenobita rugosa*; under boulder cover in the upper eulittoral zone *Calcinus hebsti* is everywhere common.

At the same level as *Tetraclita*, zoning vermetid gastropods occur, with undescribed species of *Dendropoma* and *Petaloconchus*. On many subtropical shores vermetids are regular zone-formers in the middle eulittoral (see Stephenson & Stephenson 1950; Cranwell & Moore 1938). The shell tube may be deeply immersed in the coralline crust of the substratum, and unlike the species of *Serpulorbis*, characteristic of the sublittoral fringe, the eulittoral vermetids have strong protective opercula. Serpulid worms, which are important mid-littoral zone formers on southern temperate shores formed a definite zone on only one rocky shore with a *Galeolaria* species in moderate shelter at Yandina, on Banika Island (locality 8).

In small depressions in the rock face of the upper and middle eulittoral is found the very small byssus-fixed bivalve *Isognomon acutirostris*. It corresponds on weather shores to the mid-littoral *Crassostrea* or *Chama* of sheltered shores; its upward extent into a zone visited for most of the tidal interval by splash alone is a notable achievement for a ciliary feeder.

(*c*) *Lower eulittoral zone*

From mid-tide level downwards the eulittoral zone has a dull mauve or bleached crust of *Neogoniolithon myriocarpum*. In the lower eulittoral zone this is increasingly supplanted by *Porolithon* species. Short, turf-forming algae are also prominent, giving this subzone a characteristic pink or reddish brown appearance. With increasing wave action the emersed surface is always kept moist with splash. Among the turfing red algae, the *Janis rubens*, *Rhodymenia anastomosans* and species of *Laurencia* and *Hypnea* are common. In the well-replenished splash pools a great profusion of algae develops; and several coral species may be raised into this zone from their normal station in the sublittoral fringe.

(*d*) *Sublittoral fringe*

In sheltered situations, corals conspicuously dominate the sublittoral fringe. They are approached in biomass only by the calcareous red algae. On weather coasts the corals are reduced in number and their growth forms less diverse, adapted to withstand vigorous water movement. Smooth, convex mounds are common (*Porites lutea*, *Favia* and *Goniastrea* spp.), as well as depressed plaques (*Platygyra lamellina*) and surface crusts (*Montipora* spp.). Branched *Acropora* species are restricted to the short-finger *A. humilis* and *A. digitifera*, and the compact heads of *A. hyacinthus* and *A. squamosa*. Surface-spreading *Acropora* are important, including the massive, club-branched *A. palifera* and the grey to mauve crustose *A. palmeri*. Extensive flat surfaces may be apportioned between this species, calcareous rhodophycean crusts and the blue-grey sponge *Adocia caerulea*. Bracket-forming Montipora, and strongly constructed *Millepora platyphyllia*, *M. alcicornis*, *Pocillopora verrucosa* and *Stylophora mordax* are also typical.

On the reef crest of weather shores, calcareous red algae generally predominate, with crusts of heavily built rugae, strong mamillae or fenestrate networks. The chief turfing species are *Jania rubens* on wave-swept surfaces and *J. capillacea* under slighter wave action. In surge channels *Cheilosporum* and *Amphiroa* species are abundant. *Peyssonelia calcea* forms brittle crusts and scrolls in deep shade. *Lithophyllum moluccense* is widely characteristic, both in submaximal and occasionally in very heavy surf.

The sublittoral fringe of weather coasts, with constant on-shore surge, has a wealth of green and brown algae that are disappointingly sparse on open northern coasts. On level tops, and in splash pools, *Sargassum* and *Turbinaria* are conspicuous; and they can be elevated in suitable pools into the lower eulittoral. Their growth is far more restrained than is the case with temperate fucoid algae (see Morton 1973).

The green algae are an equally important element of the weather coast sublittoral fringe. Their characteristic genera are *Caulerpa*, *Chaetomorpha*, *Distyosphaeria*, *Chlorodesmis*, *Codium* and *Valonia*.

(*e*) *Does a separate sublittoral fringe exist?*

Morton & Challis (1969) have already discussed the appropriateness of a separate recognition of this level from the sublittoral zone, permanently beyond low-water mark, with which it is in many respects continuous. Since the Stephensons's designation of an 'infralittoral fringe', many, including Womersley & Edmonds (1952), Lewis (1961, 1964) (see also Womersley & Bailey 1969), and Taylor (1968) have preferred to regard this entity as a mere upward extension of the sublittoral zone. Where the term sublittoral fringe is to be locally employed they would require the presence of particular faunal and floral differences from the deeper lying zone.

Here we have chosen to give general recognition to a separate fringe, on the following grounds: first, its use is by now well-established in the literature, including papers on the temperate South Pacific. Secondly, it seems to represent a distinct ecophysiological entity, with its inhabitants adapted for brief intermittent emersion, and also for strong wave action. In particular, on weather coasts, its corals and calcareous Rhodophyceae are adapted to extreme water movement. Some entities, such as *Porolithon*, *Lithophyllum moluccense*, and the sargassoid algae do not extend farther down. By contrast, in the lower illumination of the sublittoral zone, massive sponges, gorgonians, stylasterine hydro-corals, and sessile foraminifera are increasingly dominant.

(*f*) *Pools and moats*

The existence of permanently immersed stretches of the intertidal shore introduces important modifications of the scheme of open shore zonation so far considered. A majority of the species living between tides remain in fact permanently water covered. Whereas on temperate rocky shores, often steeply sloping, rock pools could be regarded as a topographic anomaly, the pools and moats of a coral reef bench may account for most of its inhabited space. A scheme of the zonation in pools and moats discloses almost a continuous alternative pattern to that of the emersed shore.

The pool environment, increasingly at high levels, is very different from that of the surrounding surface when intermittently immersed by the tides. In confined water bodies, pH, oxygen content, salinity and temperature fluctuate widely under the influence of sun-warming evaporation and photosynthesis.

A full investigation of the physicochemical cycles of pools and moats, and their biological implications would be a valuable contribution to tropical ecology.

In a general way, as discussed by Morton & Challis (1969), the biota of a reef pool will have a biota equivalent to the emersed shore one zone further down (1969, see Table 31, p. 481). Yet, especially at upper levels, the pool biota may be strongly specialized, without equivalents on open surfaces, and adapted to meet physiological problems of a special kind.

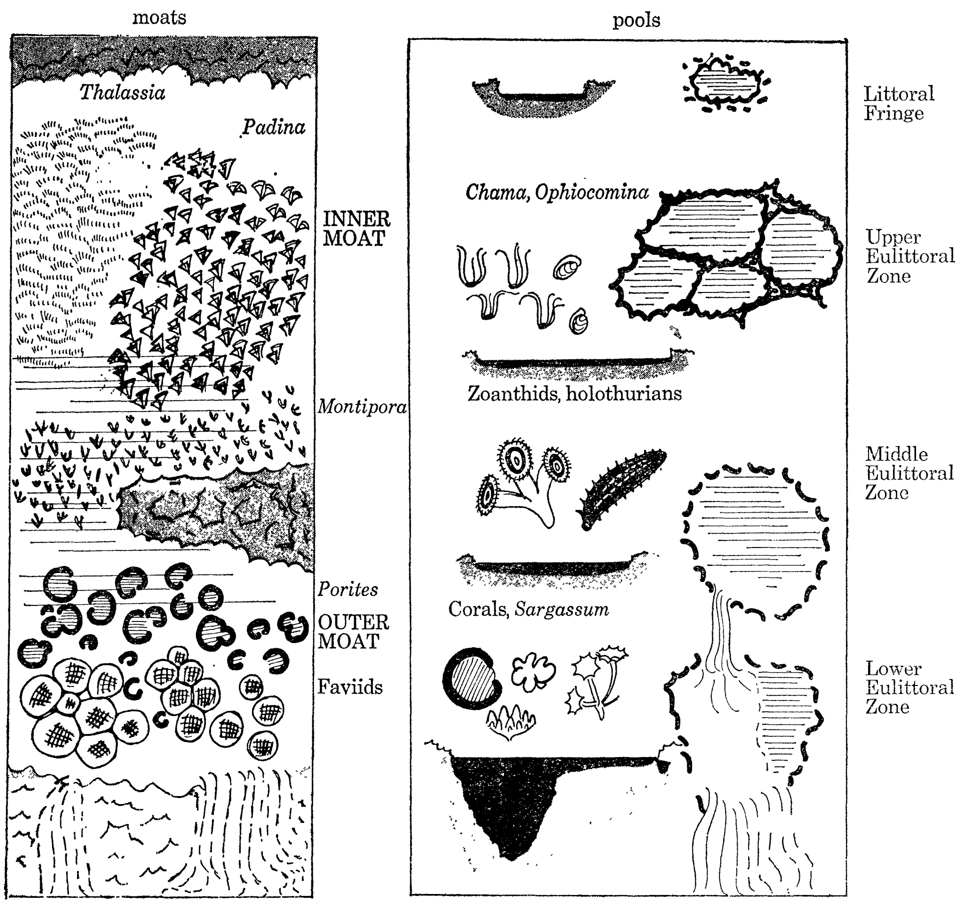

Figure 17. Zonation patterns characteristic of intertidal benches with permanent standing water: (left) moats, and (right) pools.

Moats are shallow bodies of water larger than pools and extending continuously across a considerable width of the reef (see figure 17). They intergrade in a continuous series with the shallow, immersed flats or reefs on sheltered shores. The distinction of inner and outer moats, as at Banika Island (locality 5) reflects important biological differences. The inner moats are frequently tepid at low tide, with the landward parts silted or sand-floored and carrying vegetation: sea-grasses, *Thalassia hemprichii* or, more rarely in the Solomon Islands, *Cymodoce rotundata*; green algae, *Halimeda cylindracea* or *H. opuntia*; *Padina tenuis*; *Avrainvillea lacerata*; mangroves, *Rhizophora apiculata*.

Table 2. Typical biota of intertidal pools of open coasts

zone	fauna	flora	notes
littoral fringe	Gastropoda: *Clypeomorus* spp. (*Cerithiidae*), *Clithon* spp. (Neritidae)	—	regularly tepid (40 °C+) and variously brackish or hypersaline
upper eulittoral zone	Bivalvia: *Chama* spp. Gastropoda: *Moneta annulus*. Echinodermata: *Ophiocomina scolopendrina*, *Holothuria* spp., Sponges: *Tetilla* sp. Blennioid fishes	*Gracilaria*, *Ectocarpus*, *Pylaiella*	wide temperature and salinity fluctuations
middle eulittoral zone	*Zoanthus confertus*, *Isaurus* sp., *Phyllochaetopterus socialis*. Holothurioidea: *Stichopus*, *Holothuria*, *Actinopyga* spp.	*Martensia flabelliformis*, *Caulerpa racemosa*, *Turbinaria conoides*	intermittent effects of surge and splash
lower eulittoral zone			
(*a*) shallow	*Sargassum*.and *Turbinaria* spp. *Caulerpa*, *Chaetomorpha*, *Dictyosphaeria*, *Martensia flabelliformis*, *Champia parvula*	algal-browsing herbivorous gastropods; Holothurians	regularly replenished surge pans; intertidal temperature and salinity fluctuations small
(*b*) deep and steep-sided	Scleractinia displaced from sub-littoral fringe: *Porites lutea*, small heads of *Favia* and *Goniastrea*, *Platygyra lamellina*, *Pocillopora verrucosa*, *P. damicornis*, *Acropora*, small heads	calcareous Rhodophyceae	—
sublittoral fringe	Scleractinia: *Psammocora*, *Pavona*. Hydrocorals: *Distichophora violacea*, *Stylaster roseus* sessile foraminifera: *Homotrema* and *Miniacina* spp.	*Peyssonelia* spp.	shaded pools strongly overhung, or cut off from crevices; dark and generally surge-swept; illumination reduced, as subtidally (see Morton & Challis 1969, p. 476)

Where water circulates from the outer moat, *Montipora* beds may develop: *M. digitata*, living and as finger rubble, and scrolled and explanate *M. foliosa*.

An inconspicuous but collectively rich algal flora lives upon finger rubble of moats. Womersley & Bailey (1970) have identified: (Chlorophyceae): *Valonia fastigiata*, *V. ventricosa*, *Dictyosphaeria cavernosa*, *Boodleya composita*, *Neomeris van-bossoae*; (Phaeophyceae): *Feldmannia indica*, *Dictyota friabilis*, *Lobophora variegata*.

In seaward-lying outer moats, the scleractinian fauna is greatly enriched. The moats at Banika Island, with their densely aggregated heads of Faviidae and *Porites lutea*, are fine examples of such low-tidal habitats.

(*g*) *Variation from exposure to shelter*

As previously made clear (Morton & Challis 1969), we mean by 'exposure' not emersion, but subjection to the action of moving water, surge and splash. These factors are strongest on weather coasts, and are minimal in places sheltered by the adjacent land mass or islands. There is now a considerable literature on exposure-shelter effects for temperate regions (Stephenson (1953), Lewis (1961) and Ballantine (1961) for British and Western European shores; Morton & Miller (1968) for New Zealand). As a general rule on exposed coasts, an increased vertical extent is included within the effective intertidal range with the enhanced and prolonged influence of wave action, reaching far above the notional level of high water. Where the tidal range is only narrow (see Morton & Challis 1969, p. 462, for Hawaii) waves may assume the major control of zoning. The lower reference levels, especially the line of encrusting 'lithothamnia' and (in temperate regions) of large brown algae, are elevated. At higher levels, the upper limit of operculate barnacles, marking the top of the eulittoral, may be pushed high by the effects of splash; above them the periwinkle and lichen zones are further elevated by the rise of spray, sometimes reaching 7.5 to 10 m above high-water mark.

The real physical impact of the effects we call 'exposure' is still far from understood, and must involve a complex of many separate factors. Clearly the pounding and dislodging action of moving water must have important consequences for the organisms themselves, as well as contributing to the instability and erosion of the bed-rock, to different degrees according to geological composition. Increasingly important under tropical conditions will be the constant wetting of the emersed shore, with the resulting mitigation of desiccation and insolation.

The effect of wave impact upon the biology of organisms, with methods for its measurement, has been recently discussed by Harger (1970). Jones & Demetropoulos (1968) give detailed analysis of wave exposure and its components, and Forstner & Rützler (1970) discuss general aspects of eulittoral microclimate measurements.

Indices for exposure-shelter have hitherto been based empirically on the biological composition of the zoning pattern (see Ballantine (1961) for a 'biological exposure scale'). Various suggestions have been advanced for estimating one or more of the physical components of exposure. Of obvious importance must be the direction and frequency of the prevailing winds in relation to the shore. Moore (1935) suggested for British shores, as a provisional formula for wave exposure, 'the number of days per hundred days on which the wind blows into the exposed aperture of the locality in question, this being the seaward opening measured at a distance of half a mile'. Thus on a straight shore with an aperture of 180° and with the wind direction uniformly distributed, the exposure factor would be 50. The length of fetch, i.e. the distance over which the wind has acted on the water to generate waves, is thus an important consideration, as must further be the nature of the offshore sea-bottom, a shallow sea-floor considerably modifying the wave impact received inshore.

The weather coasts of the Solomon Islands dealt with in this paper belong only to the exposed part of the shore spectrum. Enough comparative data is however available, especially from Banika Island, to show the trend with passage to regions of diminishing exposure. The effects of exposure-shelter can be classified as (i) *horizontal* and (ii) *vertical*. The first have the greater physiognomic importance on the coral shores of the tropics and may here be considered first.

(i) *Horizontal effects*

At Banika Island, reefs and reef flats are most extensive on the sheltered northern coastline. The greatest horizontal extent is found in wide but land-locked inlets, with mangrove swamps (*Bruguiera and Rhizophora* at the heads) and *Avicennia* and *Sonneratia* along sandy stretches. The seaward extent may be floored with coral rubble, especially dead and living *Montipora*, or with sea-grasses, and the outer rim of the reef is generally of massive *Porites lobata*. The narrowest enclosed channels investigated, as at Lingatu Cove and Renard Sound, Banika Island, are, however, largely depauperate, especially in places of high silt and freshwater run-off.

The variations in Indo-Pacific reef zonation from windward to leeward conditions have been well described and reviewed by Manton & Stephenson (1935), Yonge (1963) and especially in the detailed survey by Wells (1957). In the present discussion, attention will be concentrated on the sequence of shores from full exposure to close shelter, with particular reference to intertidal communities. Based primarily upon Banika Island, the examples cited apply satisfactorily to the Solomon Islands shores in general (figures 18, 19). They allow a primary division of the fringing reef shores into four classes:

I. *Wave-swept slopes or benches under constant surf attack.* Banika Island (localities 1, 2). Well-defined seaward ramparts or emergent residuals are generally lacking. Little or no structural protection is thus offered to back-lying areas and heavy surge washes the whole reef. In some places, as at Wickham Island and at Lingatu Point (locality 2), the intertidal bench is narrow and entirely swept by surf. Corals are seldom abundant and sometimes altogether lacking, replaced in general by calcareous Rhodophyceae; such corals as occur have growth forms highly resistant to surge.

II. *Exposed reefs with a seaward rampart breaking the full attack of surf.* Banika Island (localities 3 to 7); Wickham Anchorage; Gizo. On the seaward slope there is a high abundance of calcareous red algae and a reduced growth of coral. The flat-topped ramparts of bench residuals are typically clad with *Sargassum* and *Turbinaria* as well as a rich growth of red and green algae. There is typically a wide moat, sometimes divided into inner and outer parts. The outer moat contains an abundance of living coral; predominantly faviids, *Porites* micro-atolls, *Millepora*, and sometimes *Heliopora* as well as compact growth forms of *Acropora*. In the inner moat, *Montipora digitata* is typical, with silting-up, in the landward reaches, and *Padina* or sea-grass dominant.

III. *Reefs of sheltered coasts, with seaward fringe of massive living corals and reduced algal growth.* (East Banika Island.) Full consideration of these reefs lies outside the present detailed survey of exposed shores. Examples studied, as on Tetel Island and off the north-facing barrier of Matiu Island, Marovo Lagoon, will be more fully dealt with in a subsequent report.

These are wide reefs, with the seaward part (emergent at low tide) composed of *Porites lobata* or sometimes *Symphyllia recta*, micro-atolls and large faviid mounds, especially hummocks of *Goniastrea* spp. *Favia pallida* and *Platygyra lamellina*. Behind the immediate shelter of this rampart comes a luxuriant and abundant coral growth. Broad tables of *Acropora surculosa* are very typical, with compact heads of *A. squamosa* and heavy branches of *A. palifera*, *Stylophora mordax*, *Pocillopora verrucosa*, *P. meandrina* and *Seriatipora hystrix* are all typical, as well as the hydro-corals *Millepora platyphyllia*, *M. alcicornis*, and the alcyonarian coral *Heliopora caerulea*. In the quieter reaches of the moat or lagoon flat, grow the branched species of *Acropora*, e.g. *A. grandis* and *A. formosa*. A warm and shallow moat continues landwards, often more than a hundred metres

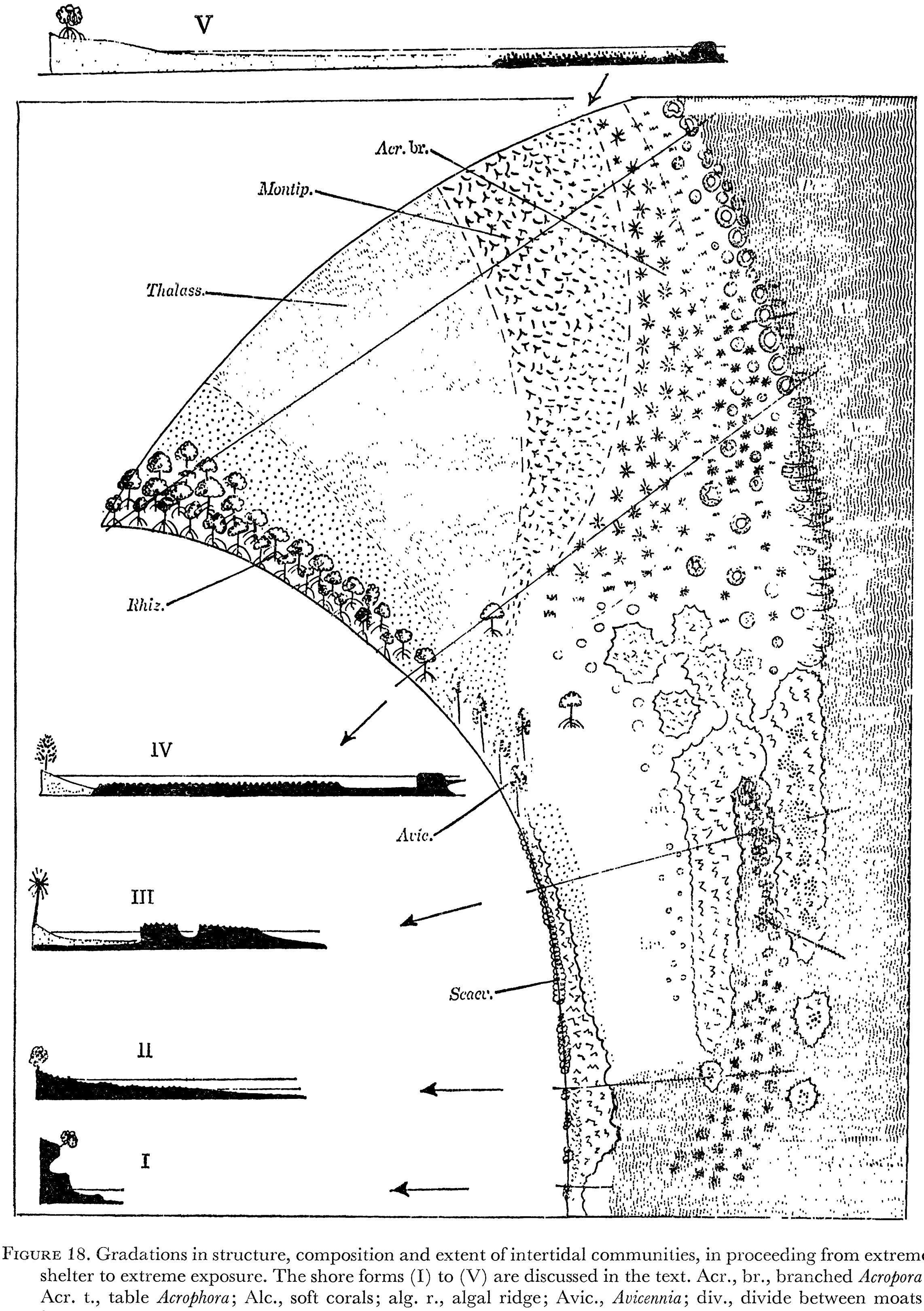

FIGURE 18. Gradations in structure, composition and extent of intertidal communities, in proceeding from extreme shelter to extreme exposure. The shore forms (I) to (V) are discussed in the text. Acr., br., branched *Acropora*; Acr. t., table *Acrophora*; Alc., soft corals; alg. r., algal ridge; Avic., *Avicennia*; div., divide between moats; i.m., inner moat; Montip., *Montipora*; o.m., outer moat; Por., *Porites*; Rhiz., *Rhizophora*; Scaev., *Scaevola*; *s.cr.*, surge crest; Thalass., *Thalassia*.

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wide. Numerous 'soft' alcyonacean corals occur here (*Sarcophytum*, *Lobophytum*, *Sinularia* spp.) and the sea-grasses *Thalassia hemprichii* and *Enhalus acoroides* are common, with several *Halimeda* species (*opuntia*, *cylindracea*, *simulans*, *macroloba*).

IV. *Wide reef-bounded shores in extreme shelter with great reduction of coral growth.* These shores comprise soft flats fringed or headed to the landward by *Rhizophora* and *Bruguiera* spp., and formed of silty sand, bare or *Thalassia*-occupied. Further to seaward may begin a coral formation usually of *Montipora digitata* sometimes with *M. foliosa* either living, or as rubble. The outer margin is generally built of massive *Porites* micro-atolls, and the water beyond is still and often turbid, with no prominent wave-break line.

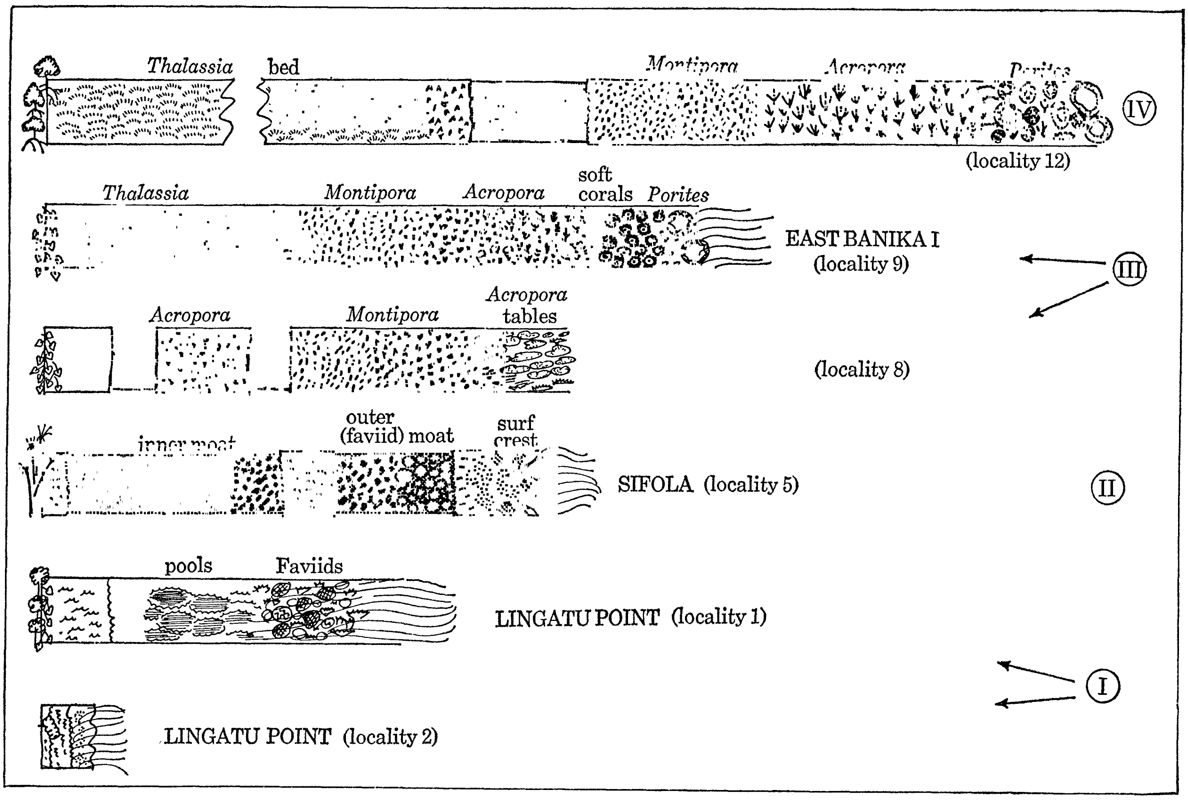

FIGURE 19. Comparison of extent and biological structure of shores ranging from extreme shelter to maximal exposure. The strips correspond to types (I) to (V) discussed in the text and illustrated in Figure 18.

(ii) *Vertical effects* (figures 20, 21)

The elevation of zonal levels with increased exposure is less widespread or pronounced in the Solomon Islands than in any of the temperate regions that are known adequately. First, it is a peculiarity of a coral shore that its main extension is horizontal. Exposure effects are thus, as we have seen, typically expressed in abbreviation of the seaward extent of the reef (see Morton & Challis 1969, p. 492). At the opposite extreme, in high shelter, the effect of turbidity from land run-off is to discourage coral growth altogether.

Further, the structure of the land mass backing a coral shore is seldom adequate for zonal elevation on an enhanced vertical scale. This is necessarily so in sand cays and atolls; and elevated benches, as in the Solomon Islands may rise only to a little above tidal range. Steep cliff faces, allowing the elevation of lichens, littorines and nerites, are a rare coast form in the Solomon Islands, though good examples were seen at Banika Island (locality 2).

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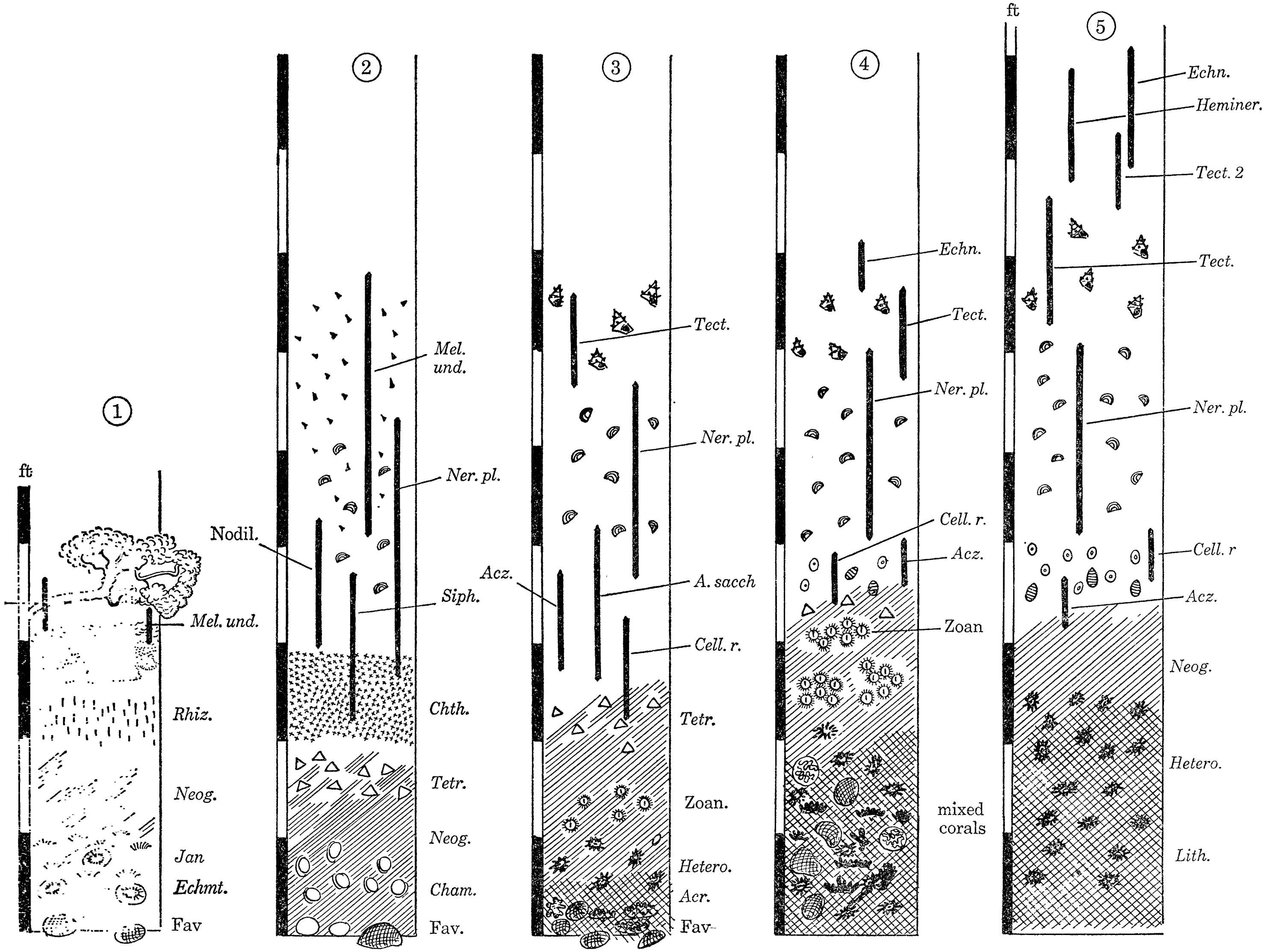


Figure 20. Changes in the vertical extent and composition of intertidal zonation with gradation from extreme shelter to maximal exposure. Vertical ranges of the principal molluscs are also shown. 1, Matiu Island, sheltered inner side; 2, Kukum, near Honiara, on vertical faces; 3, Matiu Island, exposed outer side; 4, Lingatu Peninsula, locality 1; 5, Lingatu Peninsula, locality 2. Acr., *Acropora* heads; A. sacch., *Acmea saccharina*; Acz., *Acanthozostera gemmata*; Cell. r., *Cellana rota*; Cham., *Chama* spp.; Chth., *Chthamalus withersi*; Echmt., *Echinometra mathaei*; Echn., *Tectarius* (*Echininus*) sp.; Fav., faviid heads; Heminer., *Heminerita* sp.; Hetero., *Heterocentrotus mamillatus*; Jan., *Jania* sp.; Lith., *Lithophyllum*; Mel. und., *Melarhaphe undulata*; Neog., *Neogoniolithon myriocarpum*; Ner. pl., *Nerita plicata*; Nodil., *Nodilittorina* sp.; Siph., *Siphonaria* spp.; Tetra., *Tetraclita squamosa*; Tect., *Tectarius pagodus*; Tect. 2, *Tectarius* (c.f.) *cumingi*; Zoan., Zoanthids.

Within the limits so dictated, significant exposure-elevation effects can still be found on Solomon Islands coasts. An example has already been given by Womersley & Bailey (1969), comparing the open sea coast and the nearby lagoon shore of the barrier island of Matiu, Marovo Lagoon. Figure 2 is here based on the same shore, and the exposed and sheltered zonal levels are compared in figure 21. Under close shelter, the base of the shading tree-line is reached at only 1 m above low-water reference datum. The littoral fringe is characterized by shade algae (*Rhizoclonium africanum*, *Bostrychia tenella* and, lower down, a *Cladophora*). A heavy leaf

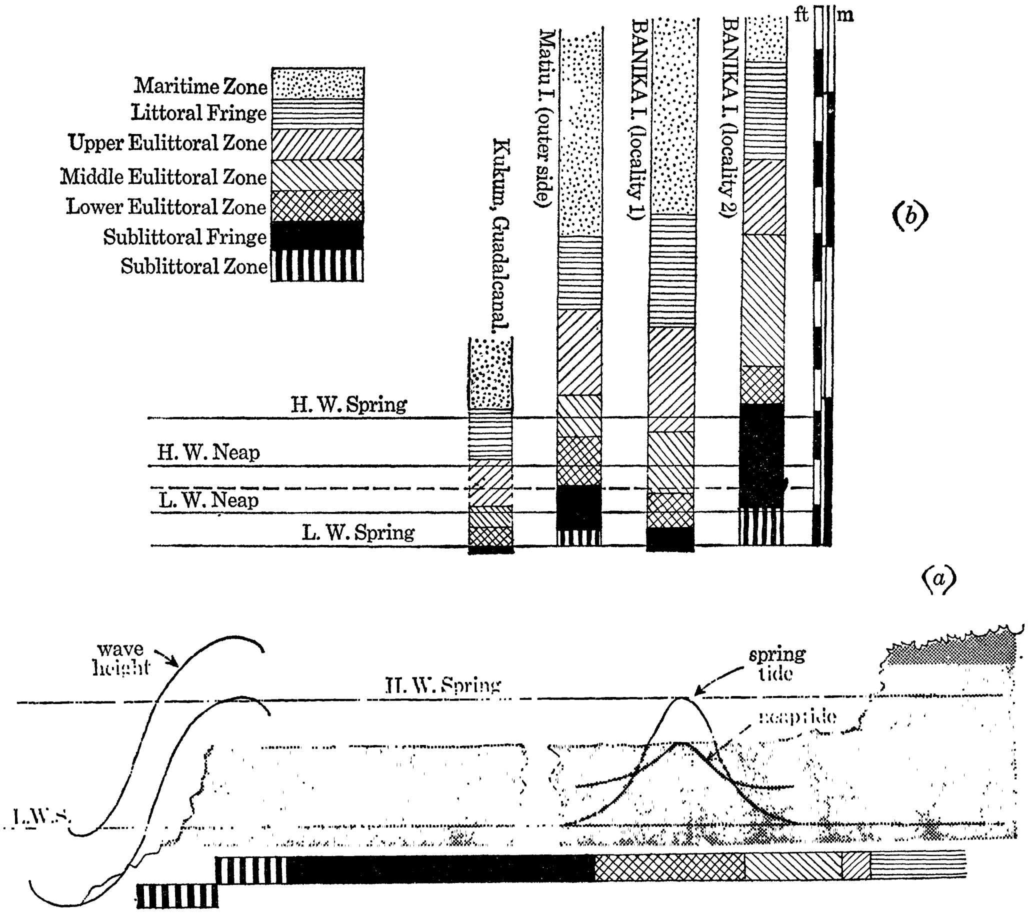


FIGURE 21. Elevation of zones with increasing wave exposure. (*a*) profile of maximally exposed surf bench at Wickham Island, with eye-estimated wave and tide levels. The curves indicate observed wave crest and trough at approximately low water and high water; (*b*) vertical extent of zones at four localities Matiu Island, inner side, in shelter; Matiu Island outer exposed side; Lingatu Peninsula, Banika Island (locality 1), sloping profile (see figure 9) with upward-coursing surge; Lingatu Peninsula (locality 2), narrow, surf-swept bench in maximal exposure.

litter supports crabs (*Cyclograpsus* spp.) and *Melampus*. *Onchidium* and *Pythia* are found at shaded supra-tidal reaches. On vertical faces under moderate shelter, but without a shading tree-line, the barnacle *Chthamalus withersi* marks the upper limit of the eulittoral. The contrast on the outer coast is very great, with high reach of splash and spray. The littorine *Tectarius pagodus* is there upward-limited, at 3 m, only by an elevated wave-cut niche.

More pronounced elevation effects were observed on the south-facing weather coasts. The eroded reef bench at Lingatu (locality 1) allows an upward sweep of surge for a vertical height of 1.9 m, across a slope covered with algae and surge-adapted corals. An extreme elevation

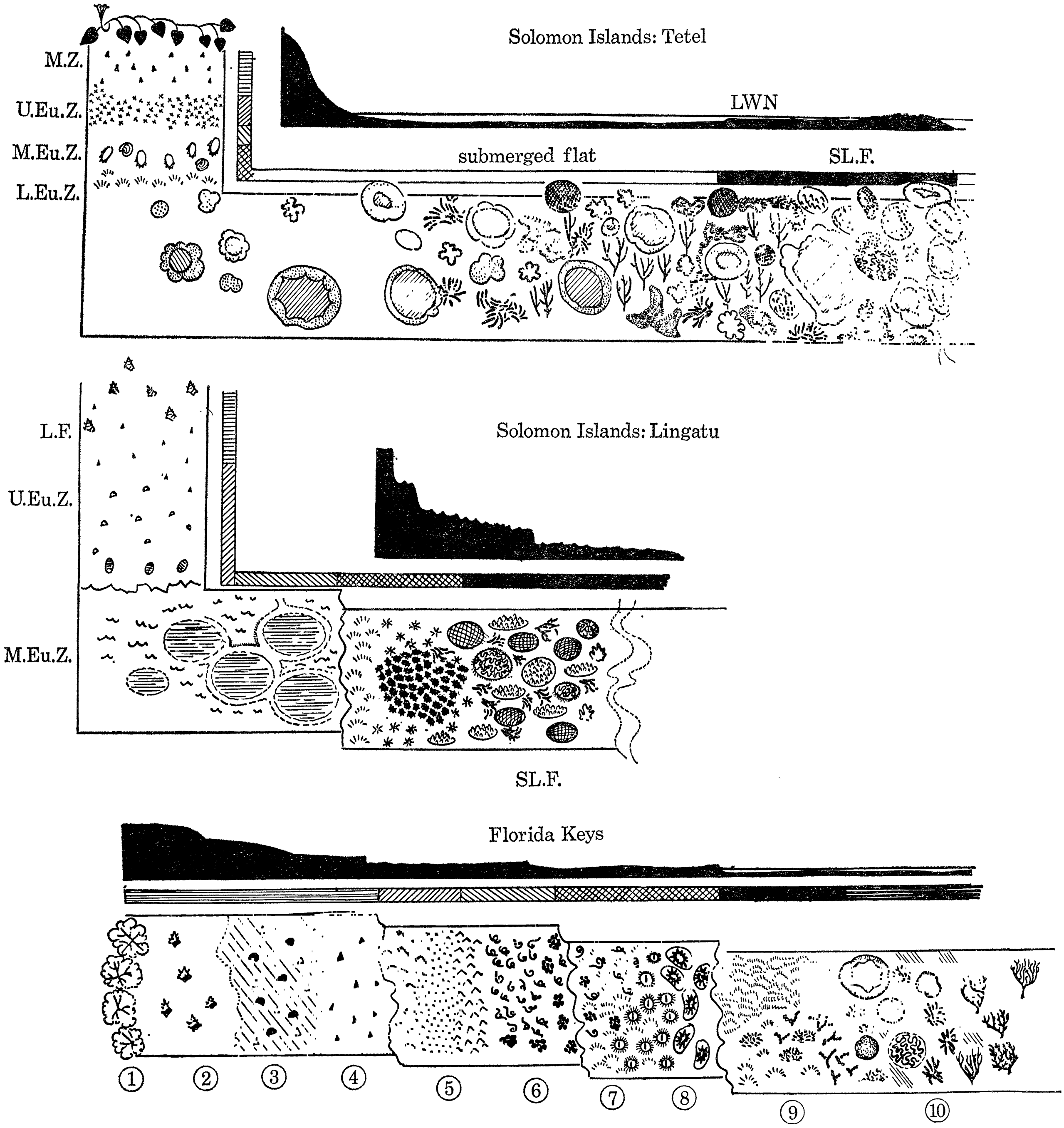
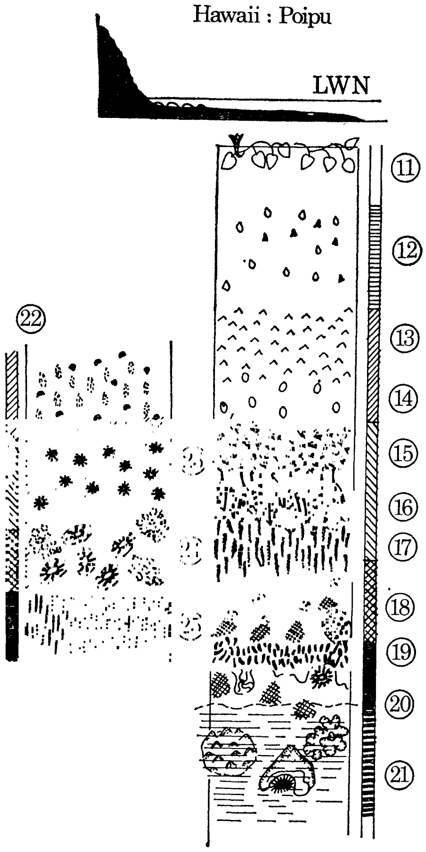


FIGURE 22. Comparison of the structure and zonation of Solomon Islands intertidal shores with Florida Keys and Hawaii. The Solomon Island data are from Morton & Challis (1969) for Tetel, and this account (p. 498 ff.) for Lingatu, locality 1. For Florida Keys, see Stephenson & Stephenson (1949) and for Hawaii, present author's unpublished observations and Morton & Challis (1969) (see facing page).

effect is to be seen at Lingatu (locality 2) with the shore platform abbreviated, and the waves making direct impact at the upper shore bench step. *Tectarius* spp., *Nerita plicata* and *Heminerita* sp. have ranges greatly prolonged. By contrast, as at Sifola (Banika Island, locality 5) where the seaward rampart breaks the major wave attack, the zone levels are not notably elevated and the corals are moat-immersed.



Organisms shown are:

(1) mangrove zone;
(2) *Tectarius bilabiatus*;
(3) *Nerita* sp. and *Littorina ziczac*;
(4) black lichen with littorine;
(5) Chthamalus *stellatus angustitergum* with *Bostrychia* and *Tetraclita squamosa* below;
(6) *Valonia ocellata* and *Spiroglyphus* sp.;
(7) *Valonia ocellata* with *Zoanthus* sp.;
(8) *Echinometra* sp.;
(9) turf of coralline and non-calcareous reds – some *Halimeda*;
(10) subtidal corals and alcyonarians;
(11) *Ipomea* sp.;
(12) *Littorina pintado*, *L. picta*;
(13) *Tetraclita purpurascens*;
(14) *Siphonaria normalis*;
(15) *Petaloconchus* sp.;
(16) *Ulva reticulata*;
(17) *Acanthophora* sp.;
(18) fine red algae; *Chaetomorpha*, *Dictyosphaeria*, *Palythoa*;
(19) *Valonia* sp.;
(20) *Lithophyllum* crusts and eroding *Echinometra* and *Heterocentrotus*;
(21) *Pocillopora* and *Porites*;
(22) *Nerita picea*, *Ectocarpus breviarticulatus*, *Morula granulata*;
(23) *Lithophyllum* paint, *Echinometra* and *Podophora*;
(24) *Sargassum polyphyllum*, *Acanthophora* and *Caulerpa*, *Heterocentrotus* eroding;
(25) *Pterocladia capillacea*, and other reds including *Gymnogongrus proliferus*, *Chnoospora pacifica*.

Weather shores under maximal exposure were seen at Kopiu, South Guadalcanal and at Wickham Island. Here there are narrow surf benches which receive direct wave impact right across their width. Zonation is under the primary control of wind-generated waves rather than tides. The sublittoral fringe is elevated by up to a metre, and may be regarded as having also a downward prolongation, as the suck-back regularly leaves its surface visible. Elevation of zonal levels is effectively limited by the height of the surf bench. A distinction between the sublittoral fringe and the lower eulittoral zone must here be drawn in horizontal terms, by the extent to which the high wall of surge can effectively advance at low-tidal wave break.

The vertical relations of sublittoral fringe and lower eulittoral zone can even in special cases be reversed at closely adjacent sites. At Titiana Point, Gizo Island, the reef crest breaks the full wave impact at low water, this must, from its biota, be designated as a sublittoral fringe. In the lee shelter of this ridge, but subject to increased insolation and dessiccation at low tide, is an area actually lower than the top of the fringe, yet from its zonation pattern, clearly constituting a lower and middle eulittoral zone.

(*h*) *Comparison: other coral shores* (figure 22)

Papers on general zonation of coral shores are not yet numerous; chief prominence is understandably given to the coral communities themselves, with neglect of the comparative patterns across a whole shore. Good accounts have however been supplied by Endean *et al.* (1956) for certain islands of the Great Barrier Reef, and more recently by Taylor (1968) on the coral reefs of the Seychelles.

From Taylor's detailed findings, the Seychelles clearly show a broad and close homology with the Solomon Islands, and probably with full coral shores throughout the Indo-Pacific region. Comparison may be made with Taylor's sequence from relative shelter to exposure (1968, p. 147, Fig. 9), on volcanic rocks above the low tidal reef flat. An upper barnacle line for a balanoid zone (*Tetrachthamalus oblitteratus*) occupying the upper eulittoral is present round all the Seychelles shores discussed. Mingled with it below is *Tetraclita squamosa*. The lower limit of the eulittoral is equated by Taylor, as here, with the upper boundary of corals and the presence on open surfaces of *Sargassum* and *Turbinaria*. A fully zoned shore, 3 m in vertical extent, under greatest exposure (Taylor's point 5) is clearly of Solomon Islands type. Differences, however, include the survival of a littoral fringe black lichen as well as an intact chthamalid zone (figure 22). The middle of the eulittoral is occupied with *Chnoospora*; below this comes a green algal turf, followed by an *Amphiroa*. *Sargassum* predominates in intermediate exposure, with *Turbinaria* exclusively holding the sublittoral fringe in highest exposure.

Of the homologies of tropical and temperate shore zonation, we may learn much from two regions on the fringe of coral status; the Florida Keys, United States, described in the important paper of the Stephensons (1950), and Hawaii, using unpublished findings by the present author. (See also, for an exposed Hawaiian shore, Morton & Challis (1969).) In both places, the intertidal bedrock is of igneous origin and a relatively small coral fauna is confined to the level below low-water spring tide.

The intertidal stretch has many features in common with the full tropical pattern. The littoral fringe is a bare rock stretch (in Hawaii bordered above with *Ipomea* and other halophytes), and having a film of blue-green algae. The Florida Keys, unlike the other shores mentioned here, retain the full temperature lichen sequence of 'grey', 'white' and 'black' zones, extending through a prolonged, low-pitched littoral fringe.

In the littoral fringe the Neritidae, Littorinidae and Ellobiidae are, in both places, predominant. The Hawaiian species are *Nerita picea*, *Littorina picta* and *L. pintado*, with several ellobiid species under loose rock cover (*Melampus castanea*, *M. semiplicata*, *Plecotrema striata*, *Pedipes sandvicensis*, *Laimodonta* sp.). The Florida Keys littoral fringe has a *Nerita* species, *Tectarius bilabiatus*, *Littorina ziczac* and an ellobiid, *Detracia* sp. On both shores, the typical crabs at this level are *Cyclograpsus* and *Coenobita*.

The eulittoral zone has a characteristic tropical facies. In the Florida Keys, the upper half is still barnacle-clad, *Chthamalus stellatus angustitergum* (mingled in shade with *Bostrychia*) at the top, and then *Tetraclita squamosa*. A lower level is dominated by the green alga *Valonia ocellata* and the vermetid gastropod *Spiroglyphus* (*Dendropoma*) sp. The Stephensons designate as their 'infralittoral fringe' (our sublittoral fringe) the lower platform corresponding in most particulars to the Solomon Islands lower eulittoral. It is marked by turfing *Laurencia*, abrading urchins (*Echinometra*) and numerous molluscs, including byssus-attached arcids. The vermetid and *Valonia* continue at this level, with patches of *Zoanthus fasciatus*.

The Hawaiian eulittoral zone has a similar composition. Under moderate shelter a barnacle cover (*Tetraclita squamosa*) persists, disappearing under full exposure. Limpets (*Cellana sandvicensis* and *Siphonaria normalis*) are common in moderate shelter, with small byssus-fixed wing-shells *Margaritifera*. The middle stretch of the eulittoral shows a vermetid (*Petaloconchus* sp.) with a sequence of zoning algae below this level. Prominent species include a first tier of *Ulva*

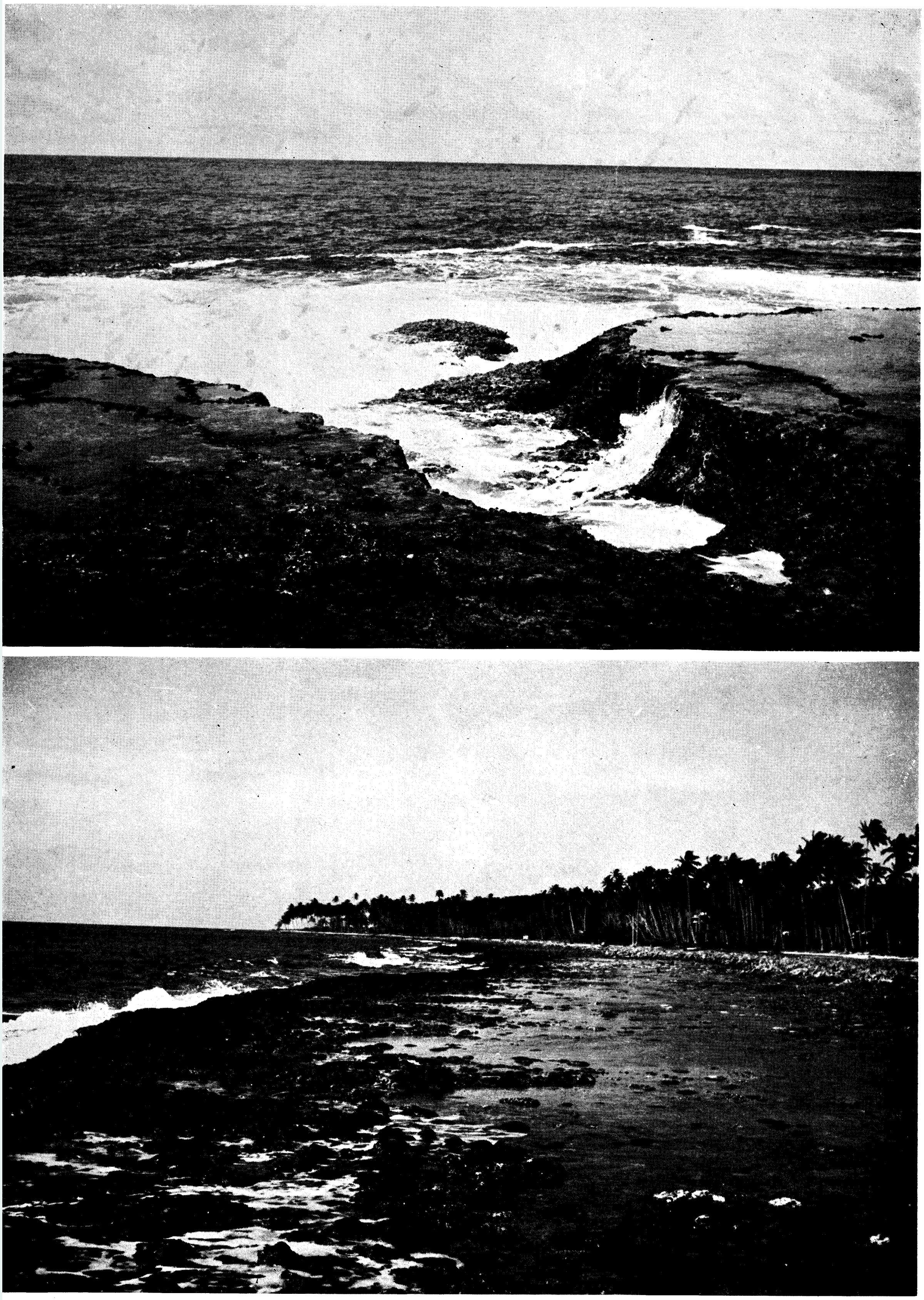


FIGURE 23. (Above): Wickham Island, off south coast of Vangunu Island. Surf exposed shallow pools at the outer edge of the intertidal bench; (below): Titiana Point, Gizo. The intertidal reef platform showing the algal ridge and the broken topography with the pools lying behind it, with the broad moat and the landward boulder fringe. (Photographs by D. R. Stoddart.)

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reticulata, then a spinulose *Acanthophora*, and species of *Corallina*, *Jania*, *Amphiroa*, *Champia*, *Hypnea* and *Laurencia*. *Dictyosphaeria* and *Caulerpa* species are the common green algae.

Morton & Challis (1969) have briefly discussed a Hawaiian shore under strong wave exposure. The broad characteristics of the upper eulittoral are the loss of the barnacle zone, and the persistence of *Nerita picea* on bare, surf-swept rock. A widespread Pacific gastropod on surf-swept faces in high exposure is the fast clinging opisthobranch *Smaragdinella calyculata*.

The lower third of the eulittoral is encrusted with calcareous red algae: in moderate shelter *Jania* and *Corallina*, in more exposure massive *Lithophyllum* species. The bed-rock is scoured by urchins, *Echinometra mathaei* and *Heterocentrotus mammillatus*. On Hawaiian exposed shores the highly adapted hemispherical urchin *Podophora atrata* clings fast to the surface. Common too in this zone are anemone patches, sheets of *Zoanthus* and *Palythoa*, and byssus-attached bivalves (Arcidae, Mytilidae, Pteriidae).

Low-tidal algae show a high variety under increasing exposure. Both in the Caribbean and the Pacific, the characteristic chlorophycean genera are *Caulerpa*, *Halimeda* and *Valonia*. *Dictyosphaeria* species are widespread. As well as coralline turfs, *Acanthophora*, *Laurencia* and *Hypnea* species are common. The principal brown algae are *Sargassum* and *Turbinaria*, present in each region discussed here, with their main emphasis in exposed conditions.

The shores above coral level have had only slight attention in most published accounts of the South Pacific. Morton & Miller (1968) give a brief mention of the zonation pattern at the Kermedec Islands; a paper on the New Hebrides is in preparation by Morton & Challis, and studies in Fiji and Samoa are in progress by Auckland workers.

In Hawaii and Florida, living coral is confined strictly to the sublittoral zone. As the Stephensons stress (1950) this is 'a different world from the intertidal'. The Scleractinia are never raised as an intermittently sublittoral fringe. Nor, in Florida or Hawaii, do we find a high sublittoral fringe development of massive calcareous Rhodophyceae. The Caribbean coral fauna is variously different from that of the Pacific. The Florida Keys have three *Porites* species, three *Siderastrea*, one *Diploria*, one *Mancina*, an inshore meandrine and a *Millepora* sp. There is a relatively huge development of sublittoral gorgonians.

The Hawaiian corals form only a small list (see Edmondson 1946). They include two common *Cyphastrea* species, a *Fungia*, a *Dendrophyllia*, two *Pavona*, three *Psammocora*, two *Pocillopora*, three encrusting *Montipora* and about four *Porites*.

Further detailed information for Pacific reefs is provided by Doty & Morrison (1954).†

As in previous reports, my debt must be acknowledged to Professor E. J. H. Corner, F.R.S., Leader of the Expedition, and to all my colleagues in the Marine Party. Of these I may be allowed to mention Dr D. R. Stoddart, for his collaboration in the studies of exposed shores, especially in discussion and interpretation of background of geomorphology; Dr B. H. S Womersley, for his guidance with the algae and the larger ecological picture; and to Mr D. A Challis who was my constant associate in almost all the studies carried out on hard shores.

Dr J. W. Wells kindly examined and identified the Expedition's whole collections of *Acropora*. A detailed systematic ecological report on the Solomon Islands corals is being prepared under the direction of Dr Stoddart and Dr Pillai. For the crustaceans and echinoderms, I relied upon

† The comprehensive symposium on reef zonation in the Indian Ocean (Stoddart & Yonge 1971) was issued too late for evaluation in this paper.

access to the collections of the British Museum (Natural History), where, during 1967, I enjoyed the help and hospitality of the late Dr W. J. Rees.

For hospitality and the generous provision of facilities and transport during a short but intense stay at Banika Island, the Marine Party were indebted to Mr J. Walton and other officials of the Leverhulme Pacific Plantations.

I am grateful to the Royal Society of London, not only for the opportunity to take part in the Expedition, but for the provision of a research assistant during six months for the curation and classifying of the ecological collections. I have thus had the advantage of Mrs Noel Gardner's experience of tropical Pacific mollusca, and of her considerable help in preparing the material for this report.

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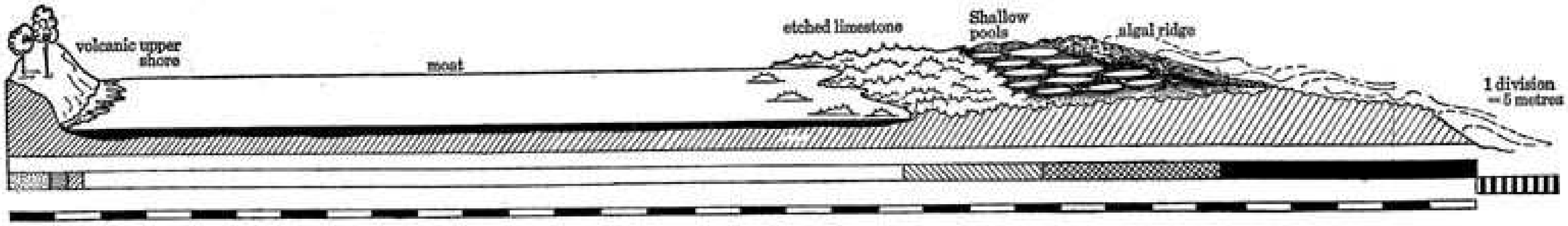
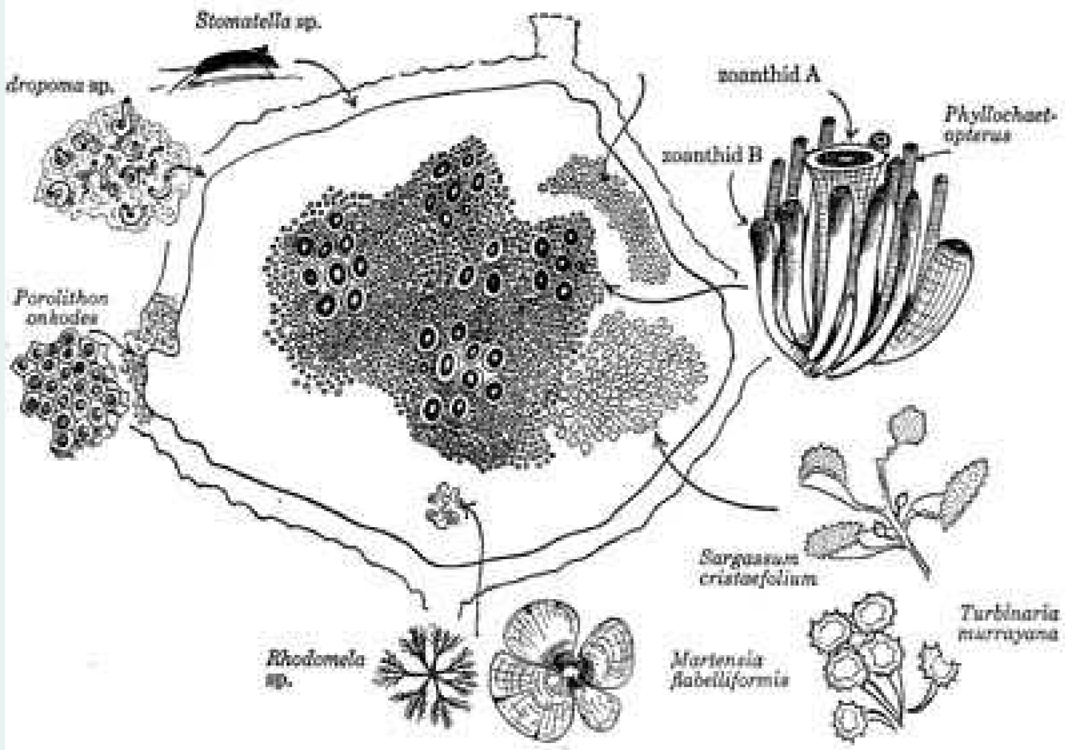
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES





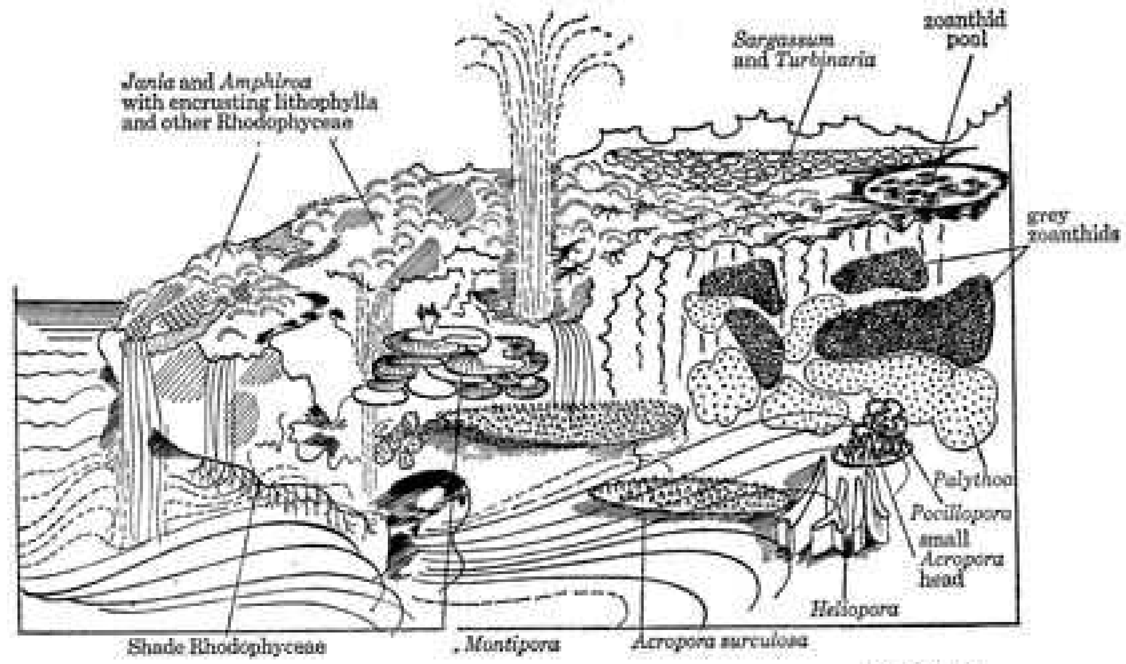


FIGURE 11

RE 11. Gizo Island: Titiana Point. (Above): profile section of the reef bench, the volcanic backshore and the pool system and surf ridge to seaward; (below left): a zoanthid-lined pool of the middle eulittoral zone, with details of the principal organisms, (below right): portion of the surf ridge, showing the detailed distribution of the algae, Scleractinia and soft corals.

RE 12. Gizo Island: Titiana Point. The upper shore to the landward of moat, showing the arrangement of habitats and the distribution of the principal molluscs: (*a*) supratidal rock faces extending up to terrestrial conditions; (*b*) shaded igneous faces in upper eulittoral zone and littoral fringe; c) under loose stones on sand or silt; (*d*) burrowing in surface layers of silty sand; (*e*) under stones resting in pools. 1, *Pythia pantherina*; 2, *Melampus* c.f. *coffeus*; 3, *Tectarius* (*Echininus*) sp.; 4, *Melarhaphe undulata*; 5, *Nerita plicata*; 6, *Planaxis sulcatus*; 7, *Melanopsis* sp.; 8, *Nerita* (*Thliostyra*) *albicilla*; 9, *Isognomon acutirostris*; 10, *Nerita polita*; 11, *N. chamaeleon*; 12, *Clithon mertoniana*; 13, *Nerita signata*; 14, *Gafrarium tumidum*; 15, *Barbatia cruciata*; 16, *Asaphis dichotoma*; 17, *Quidnipagus palatum*; 18, *Engina mendicaria*; 19, *Conus litteratus*; 20, *Clypeomorus bifasciatus*; 21, *Morula granulata*; 22, *Lunella cinerea*.

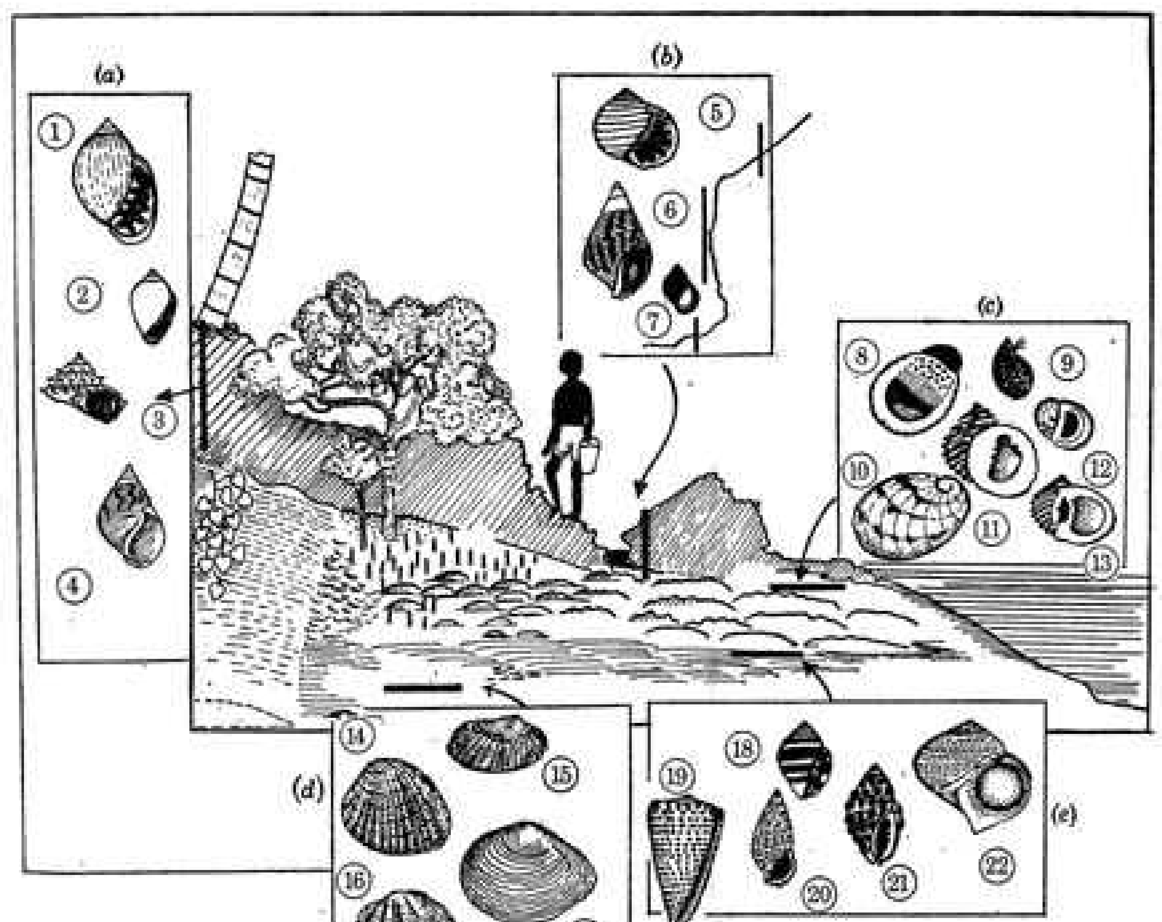


FIGURE 12

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

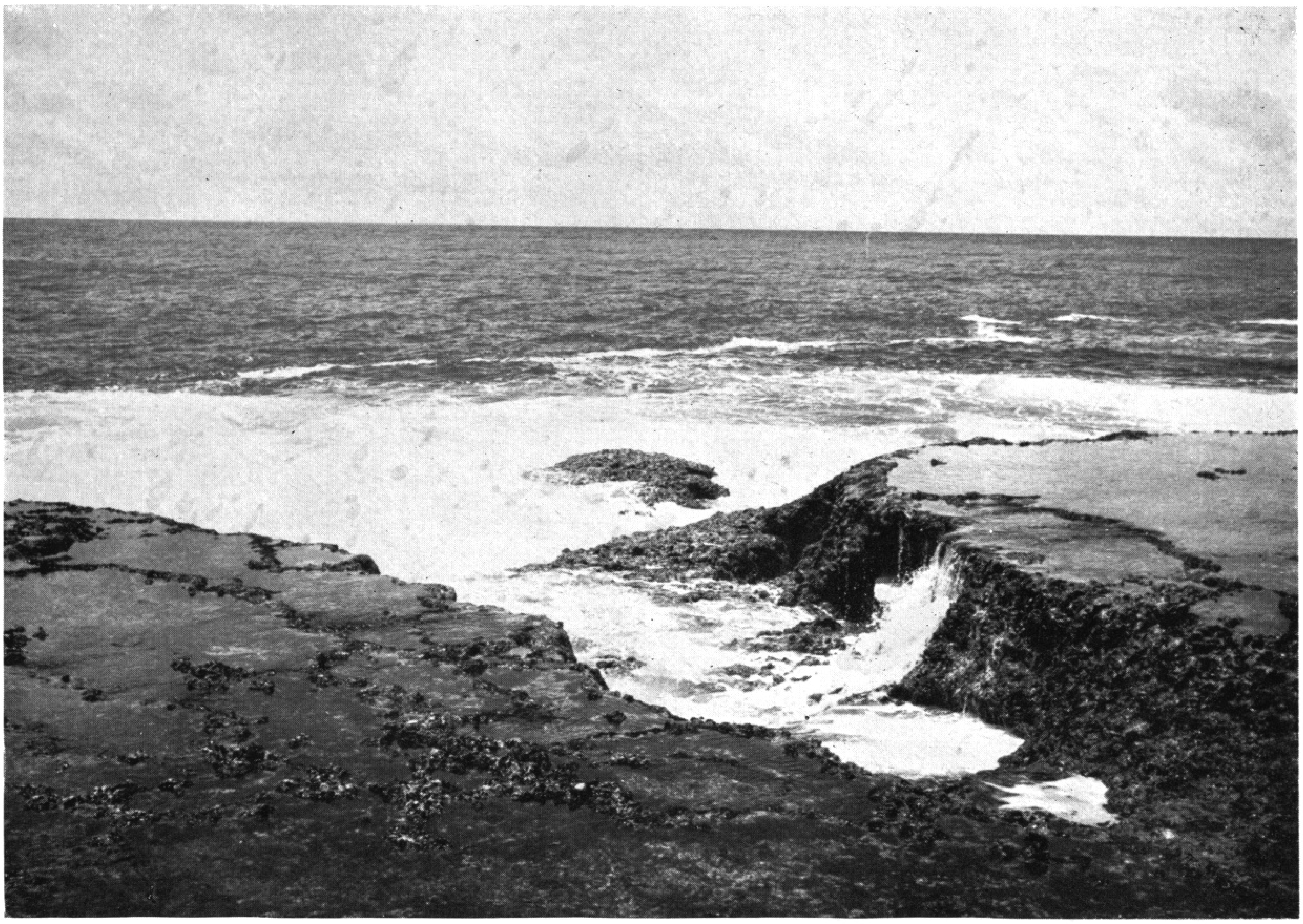


FIGURE 23. (Above): Wickham Island, off south coast of Vangunu Island. Surf exposed shallow pools at the outer edge of the intertidal bench; (below): Titiana Point, Gizo. The intertidal reef platform showing the algal ridge and the broken topography with the pools lying behind it, with the broad moat and the landward boulder fringe. (Photographs by D. R. Stoddart.)