THE SHORE ECOLOGY OF UPOLU - WESTERN SAMOA

By John Morton
with Margaret Richards, Suzanne Mildner & Lui Bell

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INTRODUCTION

In August 1987, Margaret Richards, marine biologist, invited me to Apia, with the intention we should make a study, as intensive as a short trip allowed, of the biology of Upolu's coral reefs and other shores.

This booklet, owing much to her collaboration, is the outcome of that trip. Despite the shortness of time, we believe we have used it well enough in preparing an introduction to the living communities of the shores, that may be helpful to its Samoan users.

The biology of Samoan reefs has not so far been extensively written about. The chief research upon the shores have come from the earth sciences, notably the classic introduction to geology by Stearns (1944), and the bulletin on geology and hydrology by Kear and Wood (1959). Soils and land use, with brief notes on the vegetation, are dealt with by Wright (1963).

The understanding so achieved of the effects on the reef and coast of volcanic activity (none of it geologically ancient) has thus prepared the way for a biological approach to the reefs. Our project has had two important limitations. No subtidal access, by SCUBA or otherwise, was gained to outer reef front; and with minimal use of boats, the chief study was given to fringing reefs, traversable out to the edge upon foot. The virtue out of such necessity was to outline an approach to the reefs, no part of which will be beyond the ordinary competence of senior school or university students.

We begin with shores easy to reach, and to walk across as far as the seaward edge. Fringing reefs were thus mostly chosen, in preference to barrier reef. Instead of photography, every one of our illustrations was drawn in the field, or put together immediately on return. These are of a style feasible for an ordinary student to develop; and in so doing, to analyse the data to be able to capture something on paper, from each new shore visited.

The purposes of our booklet, then, - until a bigger study supersedes it - are to firstly introduce the shores in their own terms, and in relation to the other shore systems of the South Pacific. Secondly, to give to local students the advantage of some home examples. "Samoam Samoa" must be a guiding principle. If the biology of reefs and
forests is to be as attractive as it might easily be made. Thirdly, we would like to think the story contained here, could have value for administrators and elected leaders, with the problems arising from the very richness of the reef resource and the risks of its maltreatment. A final use of the booklet could be for naturalists from abroad, coming not to collect or commercially exploit the reefs, or as up-market tourists; but to see the natural things of Samoa, and needing the basic knowledge of how to get to them, and what to look for.

With such a preliminary sketch, we have tried to point some ways ahead, with continuing projects that could usefully be taken up by those with vocations or opportunities of biological research.

ACKNOWLEDGMENTS

To my friends Rhys Richards, New Zealand Deputy High Commissioner in Apia, and Margaret, I am grateful for all of their active help during my Samoan visit, and most of all warm hospitality to such a restless - but appreciative - guest. The same kind of acknowledgment I owe to Mrs Mere Roberts, of the Zoology Department, Auckland University, as my research-assistant on this and on other Pacific field trips.

Scientific assistance of a high order, in discussion as well as in the field, was given by Mr Lui Bell, Senior Marine Biologist of the Department of Agriculture, Forests and Fisheries, Apia. His special knowledge and experience will be evident in the section 'Conservation'.

Miss Nancy Helm, United States Peace Corps representative in Apia 1985-87 and Miss Suzanne Mildner, in charge of biology at the newly-founded National University of Samoa, both gave valued help and collaboration in the field.

My understanding of the coastal vegetation was helped most of all by the knowledge and good offices, of Kalati Poai, Superintendent of National Parks for Western Samoa, particularly on an instructive field trip in the O Le Pupu National Park.

This second edition owes much to the care and dedication of Andrew Jeffs, in its editing and production.
Geological structure of Upolo Island, with distribution of fringing and barrier reefs (after Stearns, 1944).
THE SHORE ECOLOGY OF UPOLU, WESTERN SAMOA... 4

GEOLOGY AND COAST FORMS

The independent state of Western Samoa consists of four inhabited islands, all volcanic in origin and lying in the central Pacific between 13° and 15°S, and between 171° and 173°W. Two of the islands, Savai‘i (1,810 km²) and Upolu (1,115 km²) are larger, with chains of coastal villages, most dense on Upolu’s north coast where the capital Apia is sited, with 21% of the total population. Only 27% live on the biggest island, Savai‘i.

The two remaining islands, the tiny Manono and Apolima lie off the western tip of Upolu.

Samoa has a tropical and maritime climate, with pronounced wet and dry seasons. Narrow coral reefs fringe most of the coastline and enclose a mainly shallow lagoon. The reef front drops rapidly into deep water.

The geology and physiography of Upolu have been well-described by Kear & Wood (1959), on whose paper most of this account is based. Stearns (1944) had already given a classic paper on the reefs, and the ways that volcanism has influenced the structures of the coastline and the living shore.

The two islands of Western Samoa are predominantly basaltic, erupted from numerous cones all over the uplands. The oldest cones are on Upolu, and the youngest on Savai‘i, but volcanism has been contemporaneous on both islands through the upper Quaternary.

The oldest basaltic rocks on Upolu are those of the Fagaloa volcanoes of upper Pliocene age, steep-sided cones (up to 25°-50° slope) along the island’s crest. They are of “a‘a” type basalts, and had become much eroded before the middle and late Pleistocene volcanics were laid down over them unconformably, flanking the older volcanics and today covering much of the island.

The island’s Pleistocene volcanic cones are aligned in a fissure along the crest of Upolu, where their lava poured from a Pliocene rift. These Pleistocene flows, of “pahoehoe” type lava, dip to about 10° near the crest, and slope gently to the sea, becoming almost horizontal near the coast.
Diagram Showing Effect of Slope on Formation of Coral Reefs

Int block shows conditions prior to a rise in sea level. Rearock shows conditions after a rapid rise in sea level, with a barrier reef developed on a gentle slope and a fringing reef on the steep slope (From Stearns, 1944).
Upolu’s several different types of coast form depend on the age and condition of the
neighbouring rocks. The island has both fringing and barrier reefs. Submergence with the
Pleistocene rise of sea level has eliminated the former barrier reefs along the Pliocene coasts (see
map on page 3). Such rise of the sea at Upolu has been too rapid for reefs to re-grow, except on coasts
with gently sloping Pleistocene lavas. Here barrier reefs have been built up to 40m thick and 3km
wide, by upgrowth from a fringing reef during continued submergence. Because the Late
Pleistocene land surfaces are very permeable, few streams of any size enter the lagoons which thus
acquire little terrigenous sediment.

Today’s principal barrier reef of Upolu lies off
Pleistocene coasts, of Salani and Mulifanua age.
From Vallele Bay on the north coast, this reef
extends all the way west, around the island’s
western tip and along the south coast to the spur
of Pliocene rock to the west of Lefaga Bay. The
eastern end of Upolu has a narrow barrier reef off
the Alipata coast.

<table>
<thead>
<tr>
<th>GEOLOGICAL STRUCTURE OF UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Geologic Age</strong></td>
</tr>
<tr>
<td>------------------</td>
</tr>
<tr>
<td>Holocene (Recent)</td>
</tr>
<tr>
<td>Puapua Volcanics</td>
</tr>
<tr>
<td>Lefaga Volcanics</td>
</tr>
<tr>
<td>Middle &amp; Late Pleistocene</td>
</tr>
<tr>
<td>Salani Volcanics</td>
</tr>
<tr>
<td>Pliocene or Earliest Pleistocene</td>
</tr>
</tbody>
</table>
The early Pleistocene Salani lavas along the south coast have formed good foundations for fringing reefs. While submergence continued too fast for barrier reefs on the steepest coasts to keep pace, the more gently sloping Pleistocene coasts allowed fringing reefs to grow up to barrier form at the breaker-exposed edge. Submergence went on until the sea reached 1.6m above present level. It then receded to the level of today, bevelling the reef where it stood above the ocean, and hastening the growth of coral living in deeper water.

The youngest (Holocene) coasts (formed of Lefaga, Puapua and Aopa volcanics) have narrow wave-cut cliff-base platforms at Lefaga, or at Puapua hardly any platform at all. On the south coast a reef is lacking immediately east of Siumu and Falealili Bays. These coasts are formed of a Puapua cliff-line: where lava spilled over the edge of a coral reef into deep water at the ends of the cliffed sections, the former reef shores have been buried. In his oft-quoted eye witness account, Jensen (1907) described the spectacular entry of Aopa volcanics into the sea. On reaching the sea the hot lava stopped flowing forward and rose by new masses being thrust under and lifting up the cooled surface. It then flowed along the coral reef and steadily widened, until it reached the seaward edge. Spilling over the edge, it preserved an almost vertical front. In this way, later flows raised the general surface by up to 15m, resulting in the sharp rocky cliffs that can be seen today.
Stages in the Development of Upolu Island

1. After erosion of the Pliocene volcanics, but prior to submergence and the eruption of Pleistocene volcanics.
2. During the eruption of Pleistocene volcanics and after submergence.
3. Present stage.
SHORE ZONATION

The living space between high and low water presents a steep 'crooking'. This is the biologist's term to recognise the great difference in conditions of life, in passing from harsh, sun-baked upper tidal rocks, down to the wave-splashed or submerged low tidal zone. Such great changes in microclimate are reflected in the species that live across the shore.

For the temperate world at large, the zonation pattern between tides is rather well known. T.A. and Anne Stephenson have shown it to have a 'universal' component. Comparable sorts of organisms - plants and mobile and sedentary animals - live at each level, though differing greatly in their particular details, planet-wide.

The Stephensons' universal scheme of intertidal zonation was first devised for temperate shores, subdividing the space between high and low water mark, together with adjacent territory above and below the tides. The same scheme works well in its essentials for tropical shores.

Its patterns are controlled not only by the semi-diurnal tidal wave, with high and low tides (as generally experienced) twice a day. On many shores, the sea waves being continually experienced may have as great or greater amplitude than the tides, constantly wetting the shore between tides by generating surge, splash and spray.

The vertical extent of a notionally 'tidal' shore may on temperate shores be much elevated. But in the tropics such vertical upreach tends to be rather short.

Tide trace recorded at Apia from 1-16 August 1987.
On sand cays and atolls, there is no rising rock face at all; and on volcanic coasts the rock-face of the inner shore is protected from strong wave action by the intervention of the off-lying reef.

The great middle expanse of the intertidal shore, the EULITTORAL ZONE, can be regarded - in the absence of strong wave action - as lying between high and low water marks of "average" tides, that is to say, the mean between springs and neaps (and with the short, metre or so tidal range of Samoa the spring-neap difference is inconsiderable). The Eulittoral zone is thus a stretch that is semidiurnally both wet and dry.

Above it will be a stretch (the LITTORAL FRINGE) that - during neap tides at least - will never be submerged; and below the eulittoral a space (the SUBLITTORAL FRINGE) that is for the same period never dry.

The boundary between the Eulittoral and the Littoral Fringe is clearly denoted upon temperate shores by the upper limit of operculate barnacles. But on the hot, often inhospitable basalt rocks of the tropics, barnacles are often lacking in the upper eulittoral, or seldom form a continuous zone.

The Stephensons' major work is presented in 'Life on Rocky Intertidal Shores' (1977) completed by Anne Stephenson, after her husband's death.
Zonation Scheme of a Sloping Rocky Shore

Relation with the tidal curve is shown for conditions of moderate exposure.
Many tropical shores, but not all, have a bivalve zone lower down in the eulittoral: oysters (Crassostrea) and below these sometimes mussels (Geukensia or Brachidontes). In Samoa, as in most Indo-Pacific shores, the small flat bivalve *Isognomon* is fixed in scattered crevices, up to and beyond the top of the eulittoral.

Over most of the world, as in Samoa, the prime denizens of the Littoral Fringe are the gastropods called periwinkles, *Littorinaidae*. In addition, within the tropics, snails of the family Neritidae play an even more dominant role in the littoral fringe, sometimes more important than periwinkles. On temperate shores, limpets (Patellidae or Acmaeidae) are familiar gastropods in the upper eulittoral, and in the fringe. In the tropics, true limpets are generally of reduced importance, being outnumbered - if present at all - by the air-breathing or amphibious pulmonate limpets of the family *Stenomelitidae*.

An aberrant pulmonate important on sunwarmed upper shores in the tropics is the naked, rubbery-skinned *Onchidium*. 
Above the Littoral Fringe, with its boundary often not very sharply defined, is the stretch called the SUPRA-LITTORAL ZONE. In the temperate, this is a broad expanse of lichens, in ascending order through black, yellow and pale green. Lichens are simple and primitive plants, best at home, on the shore, on high, spray-moistened rock faces. In the tropics such rock faces are not widespread, and the elevated effect of splash or spray is restrained by the reef edge that breaks the main wave force. Thus, behind the protection of the reef, the dense vegetation of the land mass tends to press down to abut with the littoral fringe.

The characteristic gastropods of such a zone are the primitive pulmonates of the family Ellobiidae (especially Melampus species with Pythia to landward). There are also the tropical semi-terrestrial, hermit crabs of the family Coenobitidae. A little lower down, graspid crabs appear (small Cyclograpsus under litter, and larger Grapsus scuttling about on open rock).

Lying above the Littoral Fringe, the ADLITTORAL ZONE is distinguished by the thin layer of humus that builds up in its cracks and depressions. This supports a vegetation of higher plants: trees, shrubs and scramblers, all adapted to salt spray, and forming a characteristic part of the tropical shore. Up to this level and even higher reach the thoroughly terrestrial ellobids Pythia, and hermits continue such as Coenobita rugosa.
The special peculiarity of tropical shores with coral is, however, the prolonged horizontal extension of the shore outward from just below low water neap. This is the initiation of the fringing reef, continuing from there, right out to its forward rim, at the white line of wave break. From the beginning of the littoral fringe out to that point runs a shallow, wadable moat, comparable indeed to a much prolonged intertidal pool.

Downshore, the lower boundary of the EULITTORAL stretch abuts with the SUBLITTORAL FRINGE. This will be marked by the first appearance in quantity of scattered pinkish patches of a calcareous encrusting red alga Lithothamnion or Conolithon. Sometimes white-bleached, or overfilmcd with a green algal film, this crust becomes richer pink with descending level.

The gastropods of this pink calcareous zone are typically turbinids represented in Samoa by the rather small Turbo (Lunella) cinereus. The carnivorous thaid, Morula and small mitrids (Strigatella) also become common here and reach up into the eulittoral.

On temperate shores, it is from this Fringe - rich though abbreviated - that the shore drops away.
The horizontal stretch of the reef is a shore that has been characterised for millions of years by two sorts of organism, an animal and a plant, able to extract calcium salts from the seawater, and to secrete them as skeletal deposits, from which the huge thickness of the reef has been built up. Massive and wide enough to alter the whole physiography of the tropical coastline, today’s coral reefs are a testimony to a species far older and more influential even than human-kind in shaping and transforming the margins of the land.

It is to the broad panorama of the reef - after our preliminary view of the zoned intertidal - that we must first turn our main attention: to examine its sequences of corals from land to sea, and the rich host of species that live in or upon this platform, every fragment of which is living or derived from the activities of living things.
VEGETATION: THE ADLITTORAL ZONE

Upolu has still in large proportion retained its primitive plant cover. Wright (1963) has divided this into altitudinal zones, distinguished by vegetation types, of which it is the restricted coastal zone of littoral forest and scrub we have to consider here.

Upon the narrow sandy backshore of the embayed areas, and reaching some way inward, there is a well-definable complex of species, many of them Pacific-wide. This is a flora maintained and recruited from woody seeds, able to float long distances and resist sea water.

The coconut *Cocos nucifera* - originating who knows where, in the vastness of time - is not unique, but only the largest and most universally familiar of this community. Most particularly, on the spray-drenched south-facing coasts where the trade winds drive in the waves upon the high basalt, there is a special screen of wind resistant vegetation along the coastal rim. Where the shore lies under better protection, as at the heads of bays or around stream mouths, the littoral forest becomes more diverse and complete, with its characteristic assemblage of trees and shrubs. A good selection of the following species can be found at most points along the Upolu coast.

Profile of Coastal Vegetation
<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apocynaceae</td>
<td>Orciera mangsus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nelsoschima gongyloides</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ochrosia</td>
<td></td>
</tr>
<tr>
<td>Boraginaceae</td>
<td>Masereschmidtia argentea</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neorhodotritia</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- especially where sand lies</td>
<td></td>
</tr>
<tr>
<td></td>
<td>thinly over rock</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cordia yasomota</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- occasional in littoral forest</td>
<td></td>
</tr>
<tr>
<td>Combretaceae</td>
<td>Terminalia catapua</td>
<td></td>
</tr>
<tr>
<td></td>
<td>T. samoaensis</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Indigenous to Samoa</td>
<td></td>
</tr>
<tr>
<td>Gutiferae</td>
<td>Calophyllum inophyllum</td>
<td></td>
</tr>
<tr>
<td>Hernandaceae</td>
<td>Hernandia scopora</td>
<td></td>
</tr>
<tr>
<td>Leuchnidaceae</td>
<td>Barringtonia asiatica</td>
<td></td>
</tr>
<tr>
<td>Leguminacean</td>
<td>Intisia bauca</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- reported as uncommon,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>though abundant in one area</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sophora tetraptera</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- uncommon, but locally</td>
<td></td>
</tr>
<tr>
<td></td>
<td>abundant in several sandy areas</td>
<td></td>
</tr>
<tr>
<td>Moraceae</td>
<td>Ficus scaba</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- a small fig common in</td>
<td></td>
</tr>
<tr>
<td></td>
<td>littoral scrub</td>
<td></td>
</tr>
<tr>
<td>Myrtaceae</td>
<td>Syzygium clusianifolium</td>
<td></td>
</tr>
<tr>
<td>Nyctaginaceae</td>
<td>Plinia grandidi</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- one of the superb Pacific</td>
<td></td>
</tr>
<tr>
<td></td>
<td>coastal trees, common in littoral</td>
<td></td>
</tr>
<tr>
<td></td>
<td>forest and dominant on Rose</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Island</td>
<td></td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Guettarda speciosa</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Morinda citrifolia</td>
<td></td>
</tr>
<tr>
<td>Tiliaceae</td>
<td>Grewia crenulata</td>
<td></td>
</tr>
<tr>
<td>Verbenaceae</td>
<td>Clerodendrum inerme</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- a shrub common in littoral</td>
<td></td>
</tr>
<tr>
<td></td>
<td>scrub at edge of littoral forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Premna oestrifolia</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- occasional in sandy areas</td>
<td></td>
</tr>
<tr>
<td></td>
<td>and coastal forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vitis triglifolia</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- a small tree, uncommon</td>
<td></td>
</tr>
<tr>
<td></td>
<td>in littoral forest</td>
<td></td>
</tr>
</tbody>
</table>

The immediate fringe of shore vegetation, forming the most seaward part of the Adlittoral Zone is best developed along the spray-exposed southerly coasts, constituted from a few salt-resistant and wind-robust species. Its grandest manifestation is probably along the cliff-line at O'Le 'Pupu National Park, accessible by a path out through the bush from the road's end. Still in the spray and splash zone, 20m up a sheer basal cliff-line, this is dominated by a pure thicket of strat-rooted Pandanus tectorius (fala). Where these pandanus recede, or have been cut into at the track approach, a low scrub of Scoparia faccada (to'to'ol) assumes the dominance. Common in the same strip, only a little behind the windswept front, are the trees of the littoral scrub Morinda citrifolia, Barringtonia asiatica, Calophyllum inophyllum, and a few tall, slender 'atone', Myriostica fatau.
Vines and creepers here play an important role, trailing over bare basalt surfaces or stretching tendrils forward over the sand. The purple-trumpeted *Ipomoea brasiliensis* is common enough, but not so all-dominant as on most other Pacific shorelines, where it is ubiquitous in front of *Scaevola taccada*. Samoa has two other *Ipomoea* species: *I. littoralis* (flowers white with dark red mouth), and *I. macranthus*, with its trumpets pure white. Mile-a-minute *Mikania micrantha* (family Compositae) is now a common introduced weed on the shores of Samoa.

Further back within coastal forests, the cucurbit vine *Melothria samoensis*, and the asclepiad *Hoya australis* (fue se le la) can nearly everywhere be found. The leguminosan trailing vines, prostrate or climbing over low littoral vegetation, include most commonly the yellow flowered *Vigna marina* (fue sina) and the *Canavalia* species, *C. rosea* and *C. cathartica*. Regularly met with in coastal forest is the high climbing fue'o'ona, *Derris trifoliata*.

Remarkable for its relative scarcity on Upolu (not seen at all in this study) was the common pan-Pacific *Cassytha filiformis* (fetal) (Lauraceae) a leafless parasitic vine, like a dodder.

*Scaevola taccada* and *Ipomoea brasiliensis*, common plants of the tropical Pacific strand-line.
A ground layer plant common in littoral scrub, right out to the rock face, is the yellow daisy shrub Wedelia biflora (ateate). Locally very common, creeping over coastal rocks, is the prostrate succulent Sesuvium portulacastrum. On coastal rocks in a little more shade may be the small herb Peperomia biformis, and over sun-heated sand will grow the yellow-flowered Triumfetta procumbens, Euphorbia chamissonis, and on grassy turf behind the sand Portulaca oleracea.

The commonest sedge of sandy or rocky areas is Limbrustis cymosa. We should look also for the creeping grass, Lepturus repens.

Common ferns of rocky coastal areas or coastal marshes are Acrostichum aureum (sa’ato), Asplenium nidus or "bird's nest fern" (taugapapa).
"TIDAL FORESTS" : MANGROVES

The most distinctive and discrete of coastal vegetation is that of the mangrove formation, essentially a forest growing between or just above the tides. Mangroves are thus amphibious trees forming a specialised scrub growing on landlocked shores regularly inundated by the tides. There is no single family of 'mangroves': the name belongs to a life form developed within several quite taxonomically distinct families, with convergent adaptations for a habit so physiologically difficult.

The zenith of mangrove development is in the Indo-Malaysian - North East Australian region. Their families and species thin out as we travel south and east. Their furthest southern outposts are north New Zealand and Victoria with just a single species of Avicennia. In Fiji, where Avicennia has dropped out, there are five other families with a total of some ten species.

Samoa marks one of the most easterly mangrove outposts of the Pacific, and its common species number only two, Rhizophora samoaense and Bruguiera gymnorrhiza both members of the Rhizophoraceae; while an interesting third, Xylocarpus moluccensis (Meliaceae) is uncommon and of very local occurrence.

Situation of mangroves at the shore edge, (above) with erosion.

In all the mangroves there are two basic root types, respiratory roots of various kinds taking in atmospheric air and small nutrient roots absorbing foodstuffs from the superficial layers of the soil.
All mangroves are shallow-rooted, ‘floating’ on deeper layers which are generally anoxic and may even produce methane and hydrogen sulphide. *Rhizophora* retains no proper tap-root when adult: its separate prop-roots end in knobs just below the surface, from which anchoring roots radiate, while nutritive roots come off just below the surface.

*Bruguiera* sends up hooped or knee-like cable roots covered with respiratory lenticels. In *Xylocarpus* the cable roots are raised into radial flanges, like small plank buttresses, bearing the lenticels.
The Rhizophoraceae also have the special reproductive adaptation of viviparity. The radicle grows out through the fruit until its weight points the fruit tip downward, with the cotyledons and young leaves still within the fruit. When fully developed the torpedo-shaped seedling drops into the mud beneath the tree, in Rhizophora without the fruit, but in Bruguiera with the fruit still attached. Once in the ground, the radicle does not produce a tap-root, but rapidly grows side rootlets from the seedling tip to anchor it in the ground. Xylocarpus has a hanging green fruit as large as an orange, in which large tetrahedral seeds fit together like a puzzle.

Plants and Animals of the Mangal

1. Bruguiera gymnorrhiza - leaf
2. Bruguiera gymnorrhiza - embryo
3. Bruguiera gymnorrhiza - flower
4. Rhizophora samoaensis - leaf
5. Rhizophora samoaensis - flower
6. Rhizophora samoaensis - embryo
7. Littorina seabra
8. Metopograpsus sp.
9. Sesarma erythroactyla
The mangrove areas around the coasts of Upolu are confined to a few suitable places where sand spits cut off stretches of shore and terrigenous sediments accumulate in swamps, or in sheltered rivers and stream mouths. Near Apia, there are mangroves variously disturbed and altered at the head of Vausua Bay, on the enclosed coast of Mulini'u Point, and to the east of Apia town, in a swamp enclosed by a road-bridge and a causeway at Moata'a. On the south coast, there is an extensive mangrove formation inside the long spit of Fusi, and in the river mouth at Sa'anapu; and on the Aleipata east coast at le Lepu'e near Mutiaele.

The mangroves of Samoa are of limited area, being some of the eastern-most in the Pacific, and thus of high scientific as well as environmental value. Not only do they have a flora found nowhere else in Samoa; they are also important nurseries and food-producing grounds for a wide range of fish species at some stage during life. Over the present total area, less than 1,000ha, cutting and filling is going on almost uncontrolled.

Protection of Samoa’s small extent of mangroves is being impeded by conflict of three sorts of ownership (see Bell, 1985). Today, by State law the land below high water mark is publicly owned, with right of public access. Individuals owning titles acquired during German rule, bounded by low water mark, still however consider mangroves their private domain; villages with land adjacent to mangroves will restrict outsiders from cutting mangroves, while continuing to assert such rights themselves.

MANGROVE AND SHORE-ASSOCIATED PLANTS AND A UCID CRAB

1. *Erythrina fusca*
2. *Erythrina variegata*
3. *Canavalia sericea* with seed-pod
4. *Hibiscus tiliaceus*
5. *Xylocarpus granatus*, with details of flower & fruit (in cross section)
6. The buttress breathing roots of *Xylocarpus*
7. Loop-like pneumatophores of *Xylocarpus*
8. *Uca dialisumiert* with burrow entrance, and strewn ‘ballottin’ of processed mud,
9. *Uca* crab in oblique burrow mouth
The most scenically spectacular of Upolu’s basalt coasts is the recent volcanic cliff-line of O Le Pupu-Pue National Park. Here it is hazardous and generally impossible to get down to sea level. But as strong waves course up through crevices and surge runs, we find Nerita plicata, Littorina cordina, and even big specimens (25mm) of the bivalve Isognomon acutirostris, right up at the cliff edge. The ellobid pulmonates Pythia and Marinula and the land hermits Coenobita live further back.

**THE BASALT SHORE-LINE**

Along Upolu’s south coast - and outstanding on the Lefaga and Puapua volcanics - the steep basalt shore, to landward of the reef achieves a prominence unusual on Pacific coasts. (Such volcanic shores are - of course - lacking altogether on atoll and sand-cay islands.)

**THE BASALT SHORE-LINE AT O LE PUA**

The sheer cliff drop, topped along the edge with Pandanus tectorius and Scarbola taccada.
THE SEA CLIFF OF O LE PUPU COAST

With no protective reef, waves crashing against the cliffs undercut them along the water line until in some places, the action of water and compressed air widens the vertical cracks until blow holes are created. In other places, free-standing sea stacks are cut off by wave erosion.
Beyond doubt we are finding at this raised level, the same littoral fringe as can be glimpsed at Salamumu, on the vertical front of a Lefaga volcanic flow. Here the lavas extend forwards, in successive layers of horizontal pohueheue type basalts, constantly swept by strong wave-break, as the front drops vertically to low water. Also difficult of access at low level, the black basalt reveals - as waves draw back - a white Cthamalus malayensis stretch, and - below this - a pink coralline-veneered zone, that extends higher, though without the barnacle fringe, on the shaded vertical walls inside the blowholes that periodically interrupt the horizontal bench.

THE BASALT SHORE LINE AT SALAMUMU, SOUTH UPOLU

The 'pohueheue' basalts have extended forward, over the former reef platform. At the front (to the left) is a pale Cthamalus malayensis stretch. The beach behind has Triumfetta procumbens and Euphorbia chamissonis on sand; and the tree (to the right) is Messereschmidtia argentea.
The two most prevalent molluscs on the open basalt are the ridged, pale cream *Nerita plicata*, and the periwinkle *Littorina coccinea*, smooth white, with deep apricot mouth. This is the common exposed coast litterine, throughout the tropical Pacific. On the upper bench, the pulmonates *Melampus luteus* and *Melampus fasciatus* are everywhere common under litter; they reach a good way inland towards the scrub, where the typical ellolid is the fully terrestrial *Pythia*. The land hermits, *Ceratomyia rugosa* and *C. perlata*, are common and typical.

Behind the reef at Sa'aga, the recent Puapua basalt recedes less steeply, and we can reach the shore down to where the rocky slope is cut off by sand, covering the front of the former reef that the Puapua basalt flow has largely buried. Here, below the scrambling vegetation of the Adlittoral Zone, the basalt shows three well-marked bands. The first and widest is of bare bed-rock, sometimes tinged with the dull khaki tomentum of what appears to be a *Bosfromia* species, or darkly filmed with a thin myxophycean crust. This band constitutes a littoral Fringe. *Littorina coccinea* is here scarce, but there are two pulmonate limpets in some abundance, *Siphonaria atra* and the higher built, conical *S. normals.*
At this level the shore is scattered with two important species, specialised by their flattened form, enabling them to wedge into protective crevices, and feed from intermittent splash. The first is the tiny, thin-shelled bivalve, *Isognomon acutirostris* common in this position throughout the Indo-Pacific. Attached by a byssus, and roughly comma-shaped, with its sharp curved umbones, individual shells are markedly distorted by the contour of the surrounding rock. Less dense but also regularly present is the archaic stalked barnacle, *Mitella mitella*, wedged singly or clustered in crevices. The peduncle is fore-shortened and stiff with several whorls of minute platelets, while the terminal valves, paired terga and scuta, along with rostrum and carina, are set like claws at the distal end. Well above the normal 'barnacle line' at the top of the eulittoral zone, *Mitella* can be regarded as an old barnacle, in a relict habitat for which it is specially modified. Food is collected from vigorous wave surge, passed through the passively outstretched cirri.

The second level of the basalt shore is where the Eulittoral Zone, properly so determined, begins with a scatter of the small operculate barnacle *Chthamalus malayensis*.

Over the surface, as also higher up, the high-level crab *Grapsus albinotatus* scuttles actively. The lowest level of the eulittoral zone forms a dull pink band, with a veneer of red calcareous alga, probably a *Goniothion* sp.

*Morida granulata*, a thaid snail carnivorous upon herbivorous gastropods, is common here. The small cone *Comus chalkeus* appears where the sand begins to bury the rocks at low water mark. All over the lower rock surface, little mudskipper fish, *Periophthalmus chrysoptilus* are constantly mobile over the rock surface, springing by thrusts of the muscular tail, then sitting with its chest raised aloft by the arm-like pectoral fins.
ZONATION OF BASALT AT SA'AGA

Details of trees:-
1. *Morinda curcifolia*
2. *Calophyllum inophyllum*
   The animals depicted, with their levels on the shore, are:
3. *Nerita plicata*
4. *Nodilittorina leucospica feldensia*
5. *Sphaeridia norvalia*
6. *Morida granulata*
7. *Mitrella mutella*
8. *Grapsus abclinipes*
9. *Chthamalus navicularensis*
10. *Cerastoderma greganum*
At Lotofaga and Vavau, the basalt slope is presented with different degrees of shade, as the shore recedes up a sheltered gully towards the vegetation line, or is jutted forward as smooth boulders that spill over the beach front towards the reef.

On bare basalt, *Nerita plicata* and *Littorina coccinea* are the principal gastropods, and at the base of the shore, with a cover of mixed red algal turf, the thails *Morus granulata* and *Cronia margartichola* are common. On the pink, coralline-veneered lower shore, the gastropods *Turbo cinereus* and *Strigatella scutulata* (a small yellow-striped mitrid) are regularly found.

Where the shore becomes more shaded, a formation of red *Bostrychia* and green *Rhizoclonium* covers the basalt, with a black *Heminerita* species the commonest snail. *Mitella* and operculate barnacles seemed altogether absent at Lotofaga.

ZONATION OF BASALT AT INLET BETWEEN LOTOFAGA AND VAVAU

A sun-lit surface is shown at left, with deeper shade to right.

1. Details of the shoe tree *Barringtonia asiatica* are shown, with woody fruit. Ferns in the adillitoral zone include *Asplenium nidus* and *Polypodium*, and the tree roots are of *Picus*.
2. *Nerita plicata*
3. *Cocohita rugosa*
4. *Littorina coccinea*
5. *Morus granulata*
6. *Strigatella scutulata*
7. *Turbo cinereus*
8. *Perlia scarabaeus*
9. *Melampus fasciatus*
10. *Melampus luteus*
11. *Cyclograpsus* sp.
12. *Heminerita* sp.
The south-eastern coast from Lotofaga to Saleapaga.
The stream mouth at Lepa is the source of a spill of smooth basalt boulders brought down to the shore, and distributed as a broad apron well out into the reef lagoon.

Occurring only in small local patches, the barnacle cover is made of the high-level Chthamalus intertextus. Several species of nerites are characteristic of basalt boulders smoothed by wave action: the polished Nerita polita and the hemispheric Nerita albicilla, generally under surfaces. A more pointed black nerite of the genus Clithon clusters thickly under boulders, being a species typically found near freshwater outflows. The light-coloured Planaxis lineatus with dark spiral lines is equally to be predicted in large numbers under coral rubble or basalt boulders near high water.
BOULDER STREWN SHORE AT THE
RIVER MOUTH AT LEPA

1. Clithon sp.
2. Planaxis lineatus
3. Natica polita
4. Natica albicilla
5. Chthamalus intestetus
At Si'umu, the vertical basalt face is sheltered from wave action, and rises straight from the slitted backshore of the reef. It shows a good sequence of molluscs in their individual zones. Below the rhizomes and foliage of the two polypondaceous ferns in and below a band of lichens there are ridged *Nerita plicata*. A barnacle zone of large, widespread *Chitamalus intertextus* begins the upper eulittoral. Littorines are absent, being replaced by the related *Planaxis sulcatus*, often densely massed side to side, and very typical of such shaded backshores throughout the Pacific tropics. From this level down, crowded ranks of small *Isognomon acutirostris* project edgewise from cracks and crevices. At the lowest edge of the basalt unusually large *Isognomon* grow in a level bowl, and they expand out on to the rubble on the inner reef flat. Here also may be found *Modiolus agripetus*, the only mussel species we have recorded intertidally on Samoan shores. On the pink coralline-dappled zone, the cerithid snail, *Cypraeomorus moniliferus* may be clustered in dozens in crevices or depressions.

The inner stretch of reef, where scattered pools or standing water are left behind at low tide, is a good collecting place for some large gastropods typical of slitted boulder cover. Here are to be found *Cerithium aluco*, and *Conus litteratus*, and also occasional specimens of the handsome cowry, *Cypraea tigris*.

GASTROPODS OF THE SILTY RUBBLE FLAT
AT SI'UMU

1. *Cerithium nodulosum*
2. *Conus litteratus*
3. *Cypraea tigris*
ZONATION OF BASALT AT SI'UMU

The location of the face depicted is shown on the profile of the upper slope.
The additional tree is *Manghas mangifera*.
1. Detail of *Theopsea populnea* (leaf, fruit and flower)
2. *Nerita picta*
3. *Chitharasus intertextus*
4. *Pisonomona acutirostris*
5. *Paraxiasus acutatus*
6. *Chromomorus mollilferus*
7. *Modiolus aspitetus*
Coral reefs are marine communities found only in warm shallow tropical waters. Their dominant organisms are those coelenterates which form massive calcareous skeletons: members of the Scleractinia containing zooxanthellae (i.e., 'hermatypic' or 'reef-building' corals) together with certain hydro-corals (Milleporidae). With their exceptional powers of skeleton formation, these species construct massive reefs which provide a base and shelter for innumerable other reef-associated organisms. Some of these, notably Foraminifera, and coralline algae, assist in the formation and consolidation of reefs. Other organisms such as sipunculid and polychaete worms and penetrant molluscs bore into the coral rock and promote its disintegration. Thus, a balance is struck between building and destruction. The reef will grow or recede as one or other predominates.

Corals have a prolonged fossil history dating back to the Ordovician period. Today's reefs may rest on a foundation of dead coral limestone, thousands of feet thick. The living reef is thus a relatively thin layer limited by the light intensity needed for the photosynthesis of the minute zooxanthellae living in the tissues of the coral polyps. Without these symbiotic algae, the reef-building corals cannot thrive. The reef-building corals are included with the jellyfish, fresh-water hydras, and sea anemones in the Phylum Cnidaria. Like all those animals formerly called 'coelenterates,' they have a single internal space, serving as body cavity and gut. Polyps have only two basic cell layers, separated by a non-cellular mesoglea: the external wall (epidermis) and the inner layer (gastrodermis) lining the gastrovascular or digestive cavity. A single (oral) opening is encircled by food-gathering tentacles with stinging cells (nematocysts). These can kill or numb small prey, and the tentacles then draw it into the mouth. Waste products are later ejected through the same opening.

The scleractinian or stony coral polyp is like a tiny skeleton-forming sea anemone. Most coral systems are colonial, with very small polyps, only 1 to 3 mm across. An entire colony can however become very large, reaching several metres in diameter. It grows by continued asexual division from an initial parent polyp which originated from sexual reproduction. A polyp's sex organs produce either ova or sperms. The latter are released into the sea. The ova are retained in the coelenteron,
being fertilised by sperms carried in through the mouth. Fertilised eggs develop into ‘planulae’, pear-shaped larvae, only 1mm long. These escape for a short free existence, swimming by cilia at, or near, the surface. After a few days or weeks, a successful planula attaches to its permanent base.

So established, the planula becomes a single polyp. Unlike an anemone it will secrete from its basal disc, the bottom of a skeletal cup, the theca, which will grow up to protect the polyp. First, the bottom of the cup sends up thin radiating pariuons (septa) that indent the polyp base, each lying between a pair of mesenteries, and attached to the thecal side-wall. Most corals have at the centre of the theca an axial pillar or columnella. These skeletal parts comprise the coralite (calice) of an individual polyp, and all the calices together form the corallum or exoskeleton of the whole coral colony. In colonial corals the polyps are all linked up, as tissues of the polyp wall spill over the rim of the cup to connect with adjacent polyps. This spreading fold, called the ‘coenenchyme,’ contains an extension of the gastrovascular cavity. Its lower (epidermal) layer secretes the part of the skeleton, (peritheca) that is sited between the individual polyps. The entire colonial skeleton, theca and peritheca, is thus invested with living tissue.

Elementary structure of a polyp and its secreted corallum (left). The ciliated planula, its post-settlement stage, and the rudiments of tentacles and septa.
The coral polyp itself is a column like an anemone, with an oral disk carrying the slit-like mouth. Concentric cycles of tentacles form multiples of six (hence, the other name for Scleractinian corals, Hexacorallia); one tentacle lies over each interseptal space. There may be a single marginal cycle of 6 or 12 or several alternating cycles, (6, 12, 24, etc.). The tentacles, used both for food-catching and defence, bear the stinging capsules called nematocysts. On contact with prey in the zooplankton barbed threads are shot out to paralyse the organism, which is then passed by the tentacles or cilia to the polyp mouth. Within the coelenteron, the prey is digested extracellularly by enzymes from cells in the mesenteries. With one pair to each septum these provide extra internal surface for absorption and excretion. Waste is carried outward by the circulation of water maintained by cilia.

Relation of the living parts of a polyp to the calcareous structures of the corallum (modified from Schumacher).
CLASSIFICATION

The taxonomy of the reef corals depends ultimately on the features of the dried corallum, and most of all on the fine structural details of the septa. Few students are likely to have such expertise at call, at least when corals are confronted in the field. For such reasons a taxonomic reference collection must be built up early on. This is something wholly lacking in most Pacific islands, with Western Samoa no exception. Though field notes and colour photography of the living corals will add value, species identification from the outset relies on dried and carefully cleaned hard coralla. Pieces should be large enough for recognition of calice structure and branching form, but a whole corallum need not always be sacrificed. After sun-drying and leaving outdoors to the attention of ants, specimens can be steeped for a few days in weak 'Janola' solution or other mild bleaching agent. After daily inspection to forestall erosion of delicate skeletal detail, the bleach can be thoroughly removed with fresh water, and the coralla will dry out beautifully white. To each specimen a metal or plastic tag must be tied, with a number or locality referring to field origin. Coral pieces can be stored in boxes or plastic bags to protect them from dust or grime.

With Acropora species, with delicate calice detail, branch tips should be kept with cotton wool in labelled tubes.

Without such labelling and storage, a coral collection will soon deteriorate to door-stops and bric-a-brac. Properly curated, it can open expanding horizons, towards a well-laid knowledge of the corals of the region. Along with the coral collection, literature will be needed. Still useful as a general introduction to the taxonomy and structure of the Scleractinia is the classic memoir:


Its full bibliography includes standard systematic literature up to its date of appearance.
A sumptuous work, with colour photographs and diagrams that every beginner will want to have is:


Excellent as a general reference book, its systematic detail is not really adequate to confidently identify species, especially in such prolific groups as Acropora, Montipora and the favids. For such demands, are today three monographs that supply all that could be wanted about the coral species represented in Eastern Australia. By no means all these reach east to Samoa; but of the corals found in these islands, there will be few that the Australian monographs do not include. Their titles are:


For the corals of Western Samoa, there is as yet no complete regional account or check-list. A representative coral collection from both Upolu and Savai’i could constitute at this time the single most important contribution to the marine ecology of this nation. Marine biologists, adequately equipped, should be encouraged to begin such a project, and to carry it through until well documented, and - as so far as possible - complete.
Order SCLERACTINIA

We shall bring together in this Section the stony corals likely to be found in the islands of the Samoan group, and put them in the modern classification. A regional paper that can be profitably referred to is Lamberts’ annotated checklist (1983) of the corals of American Samoa. Stony corals (Scleractinia) are divided into four orders, each with a diverse range of growth forms and habits, and distinguished ultimately (amongst other characters) by the structure of their septa, as seen in the dry coralite.

Sub-Order ASTROCOENIIDAE

This first order is probably the earliest and most generalised. Its coralites are small and numerous, with septa simple or rudimentary. Of the important families, two - the ACROPORIDAE and PORTIDAE - are lightly porous in structure, fast-growing and adaptively successful. ACROPORIDAE, with their bewilderingly large number of species, are said to account for a quarter of all the known species of reef corals.

Though there are exceptions in both families, the basic growth form of Acroporidae is of branched and re-branched fingers, while the Portidae show generally massive growth.

Family ACROPORIDAE

The lightly porous skeleton is fragile and often easily broken. The multitude of Acropora species - by their rapid growth - produce small polyps, with their calices generally tubular, and the terminal one in each branch enlarged, and often distinctively coloured (pink, mauve, blue or yellow). Growth forms of Acropora vary widely, some species showing more than one structure, in different degrees of wave exposure. They may be conveniently classified, as illustrated (see p.46)

1. ARBORESCENT: long interlaced branches, in fragile thickets, up to a metre deep, in protected lagoons and channels of leeward reef flats (common Samoan species aspera, grandis, formosa).

2. CAESPITOSE: branched growth freely developed, but shorter and more restrained.
3. CORYMBOSE: with short branches of similar length, densely re-branched and forming a wide circular bowl attached by a pedestal.

4. DIGITATE: with branches reduced to short, strong fingers, blunt or pointed, arising from spreading crust.

5. MASSIVE: branches suppressed to form ridges, flanges or low crusts, even micro-atolls.

6. TABULAR: formed of branches horizontally fused into a network forming central stalked table or side-attached bracket, covered with small vertical branchlets.

7. BOTTLE BRUSH: formed of dense, fragile and attenuate branches, with calices long and tubular. Subtidal in protected lagoons or below the level of wave energy.
Habit and Growth Range in *Acropora*, as listed on pages 44 & 45.
MONTIPORA

This second genus of Acroporidae is almost as form-variable as Acropora, though with fewer good recognition characters. Few Montipora species are branched, and they never show large terminal calices. The corallites are small, and peritheca between them is rough, granular or verrucose. Common colours are grey, khaki brown or dull green. M. tuberculosa spreads in broad plates or lamellae, upon reef flats. M. venosa, also in lagoons, has its corallites sunken into the peritheca, with a honey-comb effect.

A pedestal species of Montipora, with calice and sculpture detail.
Family SERIATIPORIDAE

A family of grossly branching corals, at once distinguished from Acropora by the lack of special apical calices. Seriatipora is scarce on Upolu. Its one Samoan species S. hystrix (found at Pakalo Deep) is easily recognised by its slender and brittle branches, tapered to points, and tiny corallites in parallel series. Pocillopora species are much more familiar, with their short and blunt branches, giving rise to small tubercles studded with corallites (with only rudimentary septa and column). The common colours are pink or green, with branches stained chocolate brown towards the base. On reef fronts will be P. verrucosa and P. brevicornis (with compact walnut-like branch systems), and P. cyclostyla in big flanges; while on the inner reef flat will be found P. damicornis, with finer, more fragile branching.
Family PORITIDAE

One of the most widespread and successful coral families, Poritidae are the first to be seen in lagoons and back-reefs. The corallites are closely united, with little coenenchyme between them. Thecal walls are porous, making the whole coral very light. Living polyps are tall and extensible, like long villi. The lightness of the skeleton allows rapid growth, and the predominant forms are massive, as big nodules or as 'helmets' (P. lutea), while P. lobata grows to 'microatolls', a metre or more across. Porites has also its bluntly branched species: P. cylindrica yellow to bluish green; P. nigrescens, dark brown, that can form micro-atolls too.
Sub-order FUNGHIDA

In this order the corallites are bigger, sometimes solitary, though generally colonial. Their septa are complex, cross-united to each other by synapticulae, and fenestrate, with margins beaded or toothed. This shows to best effect in the large corallites of the Fungidae. The familiar image is of *Fungia*, where a huge single corallite has blade-like septa radiating from the elongate mouth. The young stages are stalked like inverted mushrooms. The common Samoan species is *Fungia fungites*. The family AGARICIDAE, are familiar between tides with the common genus *Pavona* (P. variana and P. decussata), living like *Porites* in the backwaters of the reef-flat. As with *Poritidae*, there are also agaricidids (*Leptoseris* and *Pachyseris*) growing in less disturbed water on the reef-front, below wave-base level. In *Pavona* - as in the rest of this family - the polyp and its calice have become highly modified. The polyps are spread out flat, with boundaries lost, so that close-set mesenteries can be seen to run continuously between them. Tentacles are vestigial.
The small family THAMASTERIDAE is placed close to the Agaricidae, its species being massive or branched, and with the corallite walls absent. The septa form groups radiating between 'centres' (= polyp mouths). The blunt-branching *Psammocora continua* is abundant in Samoa over inner reef-flats and lagoons.
Sub-order Faviida

These corals have large corallites with laminar septa, lacking synapticulae, but carrying fine marginal denticles. The most important family, the Favidae, with its large polyps grouped in heads or massive crusts, is less commonly represented in Samoa than in the Pacific further west. The Samoan species with largest polyps and calcites are Favia rotumana, Favites abdita and Favites halicora, all to be found upon reef-flats. Of similar form are the species of Montastrea and Leptastrea. Platygyra lamellina and Leptoria phrygia are the ‘train-corals’ among the Favidae, with their calices long drawn-out, meandering and linear, each bearing a ‘system’ incorporating several mouths. Echinopora lamellosa, found in reef-edge passes, is unusual among favids in having its corallites on flat, lamellate branches.
The family MUSSIDAE, related to Favidae, has its large corallites, with strong, complex septa, marginally denticulate. They form large heads, becoming sub-meandroid, with their cups branching or separately pinched-off, as in the only Samoan mussid species, Lobophyllia costata.

The small family OCULINIDAE has one Samoan species Galaxea fascicularis, recognised by upstanding calices, with their erect septa strong and spiny.
The family MERULINIDAE, close in essentials to the favids, has a thin foliaceous corallum, with meandroid calices fanning out radially. The widespread Pacific Merulina ampliata appears to be scarce in Samoa. Recently shifted to this family is, however, Hydnophora microconos, with its calice-systems elevated into pointed ‘monticules’. This species can be locally common on reef flats.

**Sub-order DENDROPHYLLIIDA**

This is a grouping of mainly solitary corals, with large, often brightly coloured corallites. The main Samoan species belong to the family Dendrophylliidae, being generally subtidal. The bright orange Tubastrea cocinea can occur intertidally. It is occasionally found in Samoa, under coral boulders or dead rubble. Uncommon too in Samoa is Turbinaria peltata, found according to Lamberts (1981) at low water, and exceptional within this order in being colony-forming and hermatypic, possessing - that is - the symbiotic zooxanthellae that other corals of the Dendrophylliida lack.
This seaward prolongation of the shore coincides, moreover, with the level of the Sublittoral Fringe, where on temperate shores the biota becomes richest and most diversified with its freedom from the climatic constraints of the intertidal. On a temperate shore, the Sublittoral Fringe forms abrief but enriched tail-piece to the eulittoral. On coral coasts, the same Fringe is so prolonged—often to several hundred metres—that the zoned eulittoral is left as an almost forgotten prelude to the luxury and novelty of the reef beyond.

Horizontal extension is the constructive work of two important kinds of lime-secreting organisms: (i) 'stony' corals (Scleractinia) and other Cnidaria with calcified skeletons; (ii) calcareous Rhodophyceae (red algae), found also within the temperate zone, but attaining to vast biomass only in the tropics. Of the geographical distribution of corals, Dr J.W. Wells has written: "Coral reefs are scattered over an area of 190,000,000 square kilometres, wherever a suitable substratum lies within the lighted waters of the tropics, beyond the influence of continental sediments and away from the cool upwellings of the sea in the eastern part of the ocean's basins."
Distribution of Coral Reefs And Warm Seas In Relation to the Current Systems of the World.
Corals of essentially the modern sort have existed since the Triassic times (i.e., 200 million years B.P.). Reefs composed of more ancient corals are represented in strata as old as the Cambrian. Modern reef corals are geographically limited by their very special environmental needs of temperature, illumination, water movements, salinity, and turbidity. The sea temperature must not fall below 18°C and should preferably average several degrees higher. Most coral has developed in waters shallower than 30 meters; below this, massive reefs do not form. The upper limit of coral growth must be set at about low water. Above this level most polyps cannot live, being killed by a more than brief exposure to desiccation, and being susceptible to temperatures greater than 36°C.

Shallow horizontal spread with high illumination is the prime requirement of the unicellular algae, or ‘zooxanthellae,’ that are the constant symbionts of all reef-building or ‘hermatypic’ corals. Moderate water movement is most favourable to coral growth, bringing a constant supply of nutrients and oxygen. On weathered coasts with high wave action, corals are endangered by storm damage, most of all in times of hurricane. In extreme shelter, by contrast, high turbidity with silt is inimical to most corals: suspended matter clouds the water and reduces illumination; while food-collecting cilia become clogged with silt. Certain corals are adapted to this situation, removing fine particles with efficient cleansing cilia. The same corals may also tolerate lower salinity, particularly some Porites species, that have even penetrated estuaries. But the rigorous limits of salinity are between 27 and 40 parts per thousand.
REEF STRUCTURE

Every stretch of reef is different from another. Its individuality may depend on the currents that sweep its lagoon, its frontal exposure to waves, the run-off - whether with sediments or nutrients - received from the land-slope behind. Reefs will also differ in the time they have been in construction, or their age-point in the succession from young to mature.

Coral reefs are the only sort of hard shore greatly prolonged horizontally. What correspond to its zones will thus appear in a progression from the landward edge to the wave front. The full extent of the reef can be gauged from landward, even at high tide, by the line of white surge that continually breaks over the reefcrest, only shallowly submerged at high tide and well emergent during low water.

The full study of the reef involves its survey zone by zone out to that seaward margin. This will be done at low tide, preferably a low spring tide (although the tidal range in Samoa is so relatively short as to make the spring/NEAP difference for practical purposes less significant). Far more important - for the choice of a day - will be calm weather, and the absence or moderation of onshore winds.

Reefs are influenced most of all by the amount and continuity of wind impact. Running east to west, Upolu Island has its southern coast exposed to south-easterly Trades, and leeward coasts with offshore winds to the north. Every atoll or sand cay of whatever size shows such a gradient from weathered coast to shelter.

On these two sorts of coasts the reefs will show important differences. First, as can be picked up from the map, lee shore reefs are generally wider than those facing windwards. In Samoa, in addition, the coast's antecedent geology, with the flow effects of the different ages of volcanic rock mass, is of major importance in determining reef width.

Reefs of weathered coasts, with greater wave attack, and stronger currents flowing through the lagoon, will in general be cleaner of sediment and far more clear-cut in zoning. In quiet weather, they offer the best sites to begin a reef study and inspect the successive zones.

The reef chosen, at Sa'aga, is on the windward south coast of Upolu. Its approach will need a low, near-spring tide, on a calm day. No really satisfactory study can be made without being able to transect it with feet firm upon the bottom. The whole intertidal extent, from the water's edge at -
the beach, out to wave-break, is of course the "reef." A complete understanding will not be gained by striking out straight to the crest, whether by boat or swimming. Our first venture upon a reef will ideally be made by walking across its whole extent, well shod - preferably with canvas boots to protect the ankles. The right dress will also include a loose long-sleeved upper garment, and a wide-brimmed hat as sun-protection. This will be suitable attire in which to wade across stretches up to waist or even chest-deep.

But such depths should be avoided where there is any strength of current running, and when surface transparency is spoiled by ripples. To look after equipment, compare observations, and ensure safety, an ideal party is of three or four persons, keeping in reasonably close call. A good stick or staff can be a help to stability, and for trying out depth and solidity of the terrain.

In their first enthusiasm, some will want to swim straight out to the reef edge with mask and snorkel. This can add novelty of experience, and close-up perception of certain details. It can also mean less contact with the bottom, and at the end of the day, a less oriented impression of the whole reef. Snorkel swimming has immense and manifest advantages; but for the first trip methodical walking is likely to serve best. The object of a scientific visit (distinct but not always different from an aesthetic one) is to record and bring home facts. With good weather and calm water, a useful basic equipment is a clipboard, with sheets of A3 size thick cartridge paper, or the plastic, wet-proof sheets that can be written on with lead pencil. Using paper, ball-point pens in a couple of colours are preferable as they mark better than pencil. All these must of course, be kept dry, and are best carried in a plastic bag or thick envelope. Further equipment can include a plastic bucket, with small plastic pots and tubes, capped or stoppered. (It is folly to take out a complete notebook on the reef; one false step or a sudden wave could soak through all its previously accumulated results). But it is sound advice never to venture on a reef without at least a sheet of paper on a clip-board. Observations calling for record are certain to be made, on any reef walk.
TRACING THE REEF

For the first crossing of a reef, the ideal could be to take only two measurements, both straightforward and at the outset essential. Horizontal extent over the whole reef transect is measured simply by pacing: rough but adequate, knowing the length of your normal pace and keeping so far as the terrain allows a reasonably direct path to the edge. Vertical changes can be recorded against distance paced, simply by noting changes in the water depth, up to waist, knee or ankle, or the height of any emergent terrain. Periodic notes can be made of changes of terrain: whether microatolls, or coral branches, tables or rubble, or sediment with seagrass.

Nothing has yet been said about photography. This has been intentional in that all the illustrations in this booklet derive from quick field sketches made in the manner described. Hand-drawing produces, with no expense, an abundance of data instantly available for comparison and recall. For a student, it avoids the many hazards of using an expensive camera in spray and surge or at the reef’s edge. And - by far the greatest virtue of drawing - there is the conscious recognition and analysis it entrains, for the species or community.

The Use of a Viewing Box for Reef Observation
Eye and brain are engaged upon the spot, in a way the camera cannot provide. Notebook and sketch-pad - it is true - are today apt to be thought old-fashioned. So, at times, is the goodly and broad-based study of natural history. A good camera is a luxury invaluable to have at command and often to be brought into play. But for the student beginner with a slender budget, it is not yet a necessity.

A VIEWING BOX, found valuable on all reefs where wading is possible to waist depth, is shown with suitable dimensions (see page 61). Where the water surface is wind-disturbed, it allows a clear rectangular field of observation over the bottom, in places too shallow for mask and snorkel. Tilted towards the observer, it can be pushed ahead as a continuous viewing screen. Inside, the notebook can be kept dry, or a clipboard accommodated in a slot at one end. The box can also carry specimen tubes and pots, and collected pieces including portions of coral. Small space will necessarily cut down collecting to bare essentials. The viewing box is also an aid to stability; it can be leaned against by the walker, giving a tripod point as addition to the two feet. The box can be constructed from 5mm thick transparent plastic sheet. A 4cm rim helps to exclude splash and a 1cm thick transverse bar serves as a handle.

The procedure described is suited to a fringing reef, walkable or wadable out to the edge. For a barrier reef, the approach to the edge will be quite different, with its wider and deeper lagoon that will need crossing by dinghy or canoe.

The first venture should then be on a fringing reef, if possible where inspection of the large-scale map shows it drawing in conveniently close to the shore. To begin, we would recommend reefs of the windward south coast with perhaps SA’AGA as a first choice. Study can be later extended to barrier reefs and to reefs including those of the leeward north coast.

THE ZONES OF THE REEF AT SA’AGA

The zones of the reef are located on the profile illustrated at the top.

(a-b) Porites - Fragile flat
(b-c) field of live table and branched Acropora
(c-d) Towards reef summit, with rubble field of table Acropora
(d-e) Seaward slope with living mosaic of surge-swept species.

Details of (a-b), (b-c & c-d) are shown in surface view and profile.
THE REEF AT SA'AGA

The shallow lagoon begins where you step off the beach into half-knee depth, from the tilted strata of cemented beach rocks with volcanic cobbles (coquina). Close to the beach, in water relatively clear, living coral at once appears. The first will be *Porites*, of the texture of rough sandpaper, but smooth for a coral. It forms rounded nodules, helmet-shaped heads (*P. lobata*) or big circular micro-atolls of *P. lutea* (with living coral only around the margin). *Porites* are the most landward of corals, being adapted in some measure to cope with the temperature fluctuations of the shallows, and with run-off bringing sediment and fresh water. Mingled with it is the second prominent species of inshore coral, *Pavona varians*, gingery brown, and with zig-zag intersecting ridge systems. Only 20m or so from the beach the water is perceptibly cooler, disturbed by a slight current. We move here into an almost pure field of table *Acropora*: one of the finest such expanses we have anywhere seen. Fragile *Acropora* species are some of the earliest corals to appear in the ontogeny of a reef. Here we can find living all the growth forms of *Acropora* that are to be expected in sheltered stretches of the 'back reef.'

*Acropora hyacinthus* & *A. digitifera*

First, and wide-spreading are tables of *Acropora hyacinthus*. Reaching almost up to water level at low tide, the tables come closer together as we continue out over the reef. At their richest, we have to go carefully between them to avoid abrasion from their sharp edges, and so as not to damage the brittle structures themselves. Amongst the *Acropora* tables are also low heads of upright or radiating fingers, the shapes known as "corymbose" and also colonies with thicker and stronger fingers such as *Acropora digitifera*. The finest growths are those of *Acropora nana*, thickets of vertical branches pink-tipped and-
gathered in narrow clumps. Distinct again are the *Acropora* species with longer stag’s-horn branching. They form a brittle spread in the space around the tables, as the whole *Acropora* formation begins to thicken up. All these growth forms show the essential *Acropora* structure, in spite of the diversity from which John W. Wells has called *Acropora* “the protean scleractinian genus, with bewildering speciation and the reef-former par excellence.” Their basic form is of branched (and re-branched) fingers, with tubular corallites (calices) including always an enlarged atypical one, that may be brightly coloured. *Acropora* species are also light-textured, like *Porites*, and fast in growth. Their thickets or tables reach up to just below water level at low tide. They are vulnerable to burning from the sun or wind if too long emersed at an unfavourably low tide, and continue to stand out thereafter as part of the bleached and fragile dead reef; welded and consolidated by the cementation of coralline red algae. Such coral death is part of the continuing cycle of the reef. Finger rubble is formed as the branches break off into fragments and accumulate to raise the level of the reef, where the sweeping currents are least strong.

Overturned *Acropora* tables

Midway across the Sa’aga reef, we reach such an accumulation of dead coral, becoming emersed and dry as the tide recedes. Living tables and branches, side by side, are first freely invaded by rubble. Then the reef rises by a long, but quite imperceptible slope to its low summit, up to 50m inside the white line of surge and well emergent at low spring tide. A pathway towards the summit, over this “back reef slope” has to be picked out with care, chiefly to prevent damage to such corals as are still living. Their brittle, recently dead canopy-
should not be relied upon for support. New assemblages of life begin to appear among the dead corals, spaced and distributed with regard to submersion and emersion, and light and shade. Here, round the base of many pedestal Acropora still alive there are piles of overturned and broken tables that form a stable rubble. Some of these are painted with the pink alga Lithophyllum and they may shelter a wealth of species, including echinoderms beneath. Crown-of-thorns (Acanthaster) occasionally lie amongst them. At this part of the reef we should be very wary of feeling with the bare hands under rubble tables; here black needle-spined urchins Diadema lurk, painful and toxic at the slightest touch.

On the tops of overturned tables we may find little corymbose Acropora, secondarily emplaced and mostly living. These form the most recent instalement of growth. Underneath the sheltering tables there is a new dimension of diversity. This is probably the richest habitat space on the whole reef. Such assemblages can be studied by turning over the rubble slabs and tables, so long as each is conscientiously restored to its upside down position to protect its fauna from lethal effects of heat and light. One or two of the richest of these tables can permissibly be brought home for more careful study, such as their huge availability on the rubble tract of the reef. The under-rubble fauna is described in its deserved detail on page 122.

From the rubble bed, the back reef leads up the low-inclined slope, to the reef summit. Little remains here but dead coral, dull grey-brown, or pale with bleached Lithophyllum. The main contributions to this rubble are flat plaques of the short-fingered Acropora digítífera. Amongst these dead slabs we find crusts or convex mounds of the tan-brown Palythoa. Resembling at first sight a 'soft coral' it is actually a colonial zoanthid with closely massed polyps. Palythoa will become more and more frequent as we approach the seaward edge of the reef.

Outwards from the summit, the surface mosaic begins to brighten. From its profusion of colours, its cover is perceptibly living and far more diverse than we have so far seen. First to catch attention, are likely to be the salad green algae of the class Siphonales. Several species constantly present contribute their different brightness of hue. Beginning furthest back and everywhere in evidence, are the pallid green masses of Dictyosphaeria, with the thick-walled vesicles gathered together like solid spittle.
THE REEF AT SA'AGA

The seaward slope with mosaic of surge-worn species. As on section d, page 51, lower right in profile.

1) Pocillopora meandrina
2) Pocillopora brevispina
3) Pocillopora enigmatic
4) Miliciaea dayazilla
5) Acropora c.f. A. digitata
6) Cluster Acropora, A. balica
7) Chlooctesia corona
8) Jointed Amphithora sp.
9) Dactylosoma cervinum
From such first intimations of the reef edge, we walk out through surge that even on a calm day comes in with strength. A rising wall, white topped with surge, at short intervals breaking and regathering, constantly sweeps the reef edge up to waist height.

Everything that happens to seaward should now be vigilantly watched. With each wave that surges forward, an incautious venturer could be swept off his feet. This need never happen; but if it should - one would be carried in towards the reef crest. No resistance should be offered, by grabbing or clinging to coral, with risks of abrasion, that should be anyway minimised by long-sleeved clothing. The approach to the reef edge can - with a low sea - be cautiously undertaken, preferably in the company of others standing near. With such precautions one can safely venture onto the reef front at low tide.

The surface mosaic, revealed when the surge draws back, is clean, bright-coloured, and free from sediment, and far more diverse in composition than any of the surfaces yet examined.

New corals will now appear, not encountered on the landward stretch. The common feature of all these reef-edge species is their low relief, short-branched, plaque-like or even smooth, so that the currents can wash over them freely, without any raised excrescence to be broken off.

In many situations, *Acropora* species are still the main occupiers of space. At the reef edge, they are present in crusts, or plagues, welded to the rock over their whole base. Some sorts have long upright fingers, pointed in *A. humilis*, or bluntly rounded as of *A. diguita* or. Or there are some *Acropora* species with no fingers at all, like *A. palmeri*, rough brown, with its corallites flush with the surface; though occasionally a flattened branch is sent off.

Typically corals adapted to strong wave action, the *Pocillopora* species form compact clusters of short strong branches between which the surge flows. These produce smaller tubercles, studded with the corallites, with polyps usually bright pink, finely ringed in black. The branch bases are usually chocolate stained. The reef edge has as many as three *Pocillopora* species, *P. meandrina*, brown to magenta, forms massive clusters, all under high wave action, convoluted like a giant walnut. In *P. cyclostomata*, the branches are compressed into big, spatulate flanges.
POCILLOPORA MEANDRINA

ORGANISMS OF THE SEAWARD SLOPE AT SAV'AGA

1) Pocillopora meandrina
2) Pocillopora cyathus
3) Millicora phylloxilla
4) Chlorodesmis comosa

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P. brevicornis has smaller branches, than P. meandrina, generally light brown. A fourth species P. damicornis, finer branched and far more fragile, is regularly found amongst branched Acropora in the lagoon shallows.

The third regular entity, at the reef edge is the ‘fire-coral’ Millepora platyphylla. Greyish-white to mustard coloured, its parallel flanges stand up as strong lamellae, generally broken up into short spines or crests. Millepora coral has a shark-skin surface texture, smoother than in any Scleractinia. It is not a stony coral, or even an anthozoan, being classed as a calcified hydrozoan. By touching a fire coral or letting it contact the soft skin of the inner arm, a burning sensation can be felt from the action of its unusually large, virulent nematocysts.

Of the reef edge algae, the most vividly green are the tufts and tresses of Chlorodesmis comosa. By feeling amongst its filaments, the little grass green crab Caphyra can invariably be found.

The calcified green alga Halimeda opuntia is made up of branched chains of segments, loosely packed together in compressible tufts. Much softer are the creeping rhizomes of Caulerpa racemosa, carrying branchlets like little bunches of grapes. Green and blue green algal symbiots are enclosed in the tissues of the compound ascidians Diplosoma and Lissoclinum, often present in small patches on the lighted surface.

The most important algae at the reef edge are sparse are the calcareous reds, represented by encrusting and cementing lithophylla, and also by stiffly segmented Amphiroa species. These may have coarser branches, as thick as in Amphiroa crassa, spear-like as in A. foliacea, or they may form much finer tufts and bushes.

Of the brown algae normally to be expected at a reef crest, such as Sargassum and Turbinaria, none were observed at Sa’aga, though they can be found in plenty in the moats of Upolu’s leeward reefs, of the north coast.
The reefs at SA'AGA as also at SI'UMU and TAFTOALA, are some of the narrowest, from beach to wave margin, on the whole south coast, and their lagoons are easily traversable on foot. For those reasons, as well as for their different stages in development, they were chosen for first and more detailed description.

East of Lotofaga, the whole south coast of Upolu, as far as Cape Tapaga, has a narrow fringing reef, broken only by stream mouths, and drawing so close to the shore that the lagoon can easily be waded on days with a low swell. In a drive along the south coast as far as the Cape Tapaga, the reef shore can be kept in continuous view.
gauging the variations in form that correspond to physiographic features such as basalt headlands, ridges, sand-beaches and river mouths.

Access to the fringing reef lying within the strait of Nu’utele Island, off Cape Tapaga, we found hazardous, with a strong rip current even at slack water during low tide. There are safer crossings further west.

Along this straight south coast the lagoon and reef flat show some different stages of reef evolution, of which we can take the fast-growing Acropora tables at SAAGA, to denote the most youthful. Acropora species, branched or tabular, will break up into a strewn bottom rubble. On the inward extent of the flat, Porites is also fast-growing, and a zone of wide micro-atolls develops, with an important subsidiary element of Pavona decussata and - more abundant - P. varicosa, which may itself grow into micro-atolls.
SALEAPAGA REEF

In front of a strip of Tafagamanu Sand, this reef can be seen overgrown with some of the white front. Its beach boundary is of tilted beach rock conglomerate (coquina), and at middle distance across the lagoon there are massive storm blocks of old favid corals. All the principal entities of Alcyonacea are to be found here, with the exception of long-fingered Sinularia, that are on the whole confined to quieter or part-enclosed waters.

All the Alcyonacea are firmly rubbery in texture, with slippery surfaces that distinguish them at the first touch from stony corals. The 'soft corals' have a fleshy, gelatinous coenenchyme, from which only the distal parts (anthocodia) of the tubular polyps protrude. Gastrodermal tubes run right through the coenenchyme, and have cross-connections (solenia). The mesogloea is scattered throughout with discrete calcareous spicules, often protruding for defence when the polyps are withdrawn. Of the massively lobed Alcyonidae, two genera Lobophytum and Sarcophyton, are dimorphic, with two sorts of polyp flange, food-taking autozoids and small siphonozoids, the second taking in water through the tube-systems right to the colony base. Lobophytum, while also found in the raft, lives principally upon the surf edge, forming broad, rubbery sheets raised into tall transverse folds, the whole system being low streamlined for the surge. Sarcophyton colonies stand up like pedestals, S. trochelophorum undulant around the edge, and S. latum, common at Saleapaga, flat on top and smooth margined.

THE COMMON ALCYONACEA OF SAMOAN REEFS

1) Xenia
2) Sarcophyton trochelophorum
3) Sinularia (cf. polydactyla)
4) Cladiella sp.
5) Lobophytum expansum
The remaining genera are monomorphic: *Alcyonium* (blunt-lobbed and low based), often found also on temperate shores and *Sinularia*, with a variable morphology according to water movement. *S. flexibilis* has long whip-like lobes; in *S. polyactyla* these are shorter and in other species almost suppressed. There are coarse spicules stubbing the colony base. *Cardinella*, common at Salaulima, has small, stiff lobes, ashen-grey, but with the polyps picked out in dark brown. The coarse basal spicules are lacking.

The related family *Xenia*idae has soft and slippery polyps, simple and non-retractable. The tentacle circle, as always in the subfamily *Alcyonaria* is 8 in number and pinnate. In *Xenia* the soft polyps spring from a fleshy base, without massive coenenchyme or spicules. They maintain a pulsatile intake of respiratory water, and their nutrition (as in tropical *Alcyoniidae*) is almost wholly from zoanthellae, with which they are richly endowed.

**SCLERACTINIA**

Intermingled with the soft corals, the lagoon has a diversity of Scleractinia. All the main Samoan *Porites* are to be found here: *P. lutea*, in hemispheric heads or micro-atolls; *P. lobata* commonly in hemispheric mounds or helmets; and the branched *P. nigrescens*, with low convex mounds or micro-atolls beset with its short, blunt fingers. *P. cylindrica*, with a similar morphology may be cream, yellow or greenish blue.

The family *Agrariciidae*, stony corals of highly modified polyp and corallite structure, have their common genus *Pavona* between tides. In their familiar shades, tawny, or purplish brown, there are the two species are familiar in Samoa, *P. variana* and *P. decussata*.

Related to *Agrariciidae* is the small family *Thamnasteridae*, massive or branched corals, where corallite walls are likewise absent (as in *Psammocora contigua*).

The moat contains, in addition, grey *Lobophyllia costata*, and just a few occasional heads of big-cupped *Favidae* (*Favites abdita* and *Favites halicora*) as well as plaques of the meandrine *Platygyra rustica* and *Leptoria phryga*.

**THE FRINGING REEF AT SAPIAFA**

In profile (top), the zones are (a-b) tilted beach rock conglomerate (coquina); (b-c) meet with *Porites*, *Pavona* and soft corals; (c-d) zone of storms blocks and rubble; (d-e) surf swept reef summit, and seaward slope. The detailed quadrat and profiles show the main organisms of (b-c & d-e).

The chief *Acropora* are the fragile and prettily pink-tipped branch systems of *A. nana*.

The reef lagoon at Saleapaga shallows to seawards, with a large rubble zone, in which the biggest storm blocks reach two metres high, being hardly more than splashed at the highest tides. Displaced from the reef front during hurricanes, and thrown over the rim, these remain stably sited, and the largest ones, of old meandrine favid coral, have developed an intertidal vertical zonation pattern, illustrated on page 78.

Seaward of these blocks, the surge-swept slopes, on all the windward reefs of the south, come under the regular action of trade winds, carrying on to them high waves, generated over a long fetch. Powerful surge, a metre or more high, sweeps in over the seaward slope. Drawback of surge, as the wave for a few seconds subsides, allows a good appraisal of the living surface mosaic. Nearly all its species are of subdued profile, stream-lined and robustly constructed. The yellowish-grey soft coral *Lobophytum expansum* is invariably prominent, here with its transverse corrugations firm and spicule-studded. Wide plaques of encrusting stony corals are nearly always dominant: short-fingered *Acropora* (as of *A. humilis* or *A. digitifera*); or crustose species with most of the fingers suppressed, such as *Acropora palmeri*, occasionally with moose-like antlers emerging at a low angle. Crustose *Montipora* species (c.f.) (*Montipora verrilli*) will also be found, bronze green or grey, with their characteristic rough texture and rather featureless polyp form. As on all seaward reef fronts there will be fire coral, *Millepora platyphyllia*, yellowish-grey, with strong parallel lamellae, crested at the edges. *Pocillopora meandrina* is as prominent as always in strong wave action, standing out in dull magenta. Strong flanges of *P. cydonia* will also be seen.

Few favids are apparent, these being no more than a scarce subsidiary element upon Samoan reefs.

As elsewhere on the south coast, brown sargassoid algae seem un-represented. Calcareous red algae are, however, both visually and structurally important; with hedgehogs of prickly *Lithophyllum* species, and coarsely jointed tufts of *Amphiroa crassa*. The green algae of the reef edge are here in their full diversity, from the emerald green *Chlorodesmis*, through calcified *Halimeda*, and grape-like *Caulerpa*, to the stiff, pallid green pads of *Dictyosphaeria*.
ZOONATION ON A STORM-BLOCK

The vertical sequence shown in the figure on page 78 introduces the intertidal zonation pattern essentially as on a temperate shore - into the middle of the reef. Towards the top, especially facing to the landward, there are some familiar species of the Littoral Fringe (see page 12). Littorina are lacking, evidently - like operculate barnacles, preferring a hard basalt surface. The jagged coral rock has, however, many Nerita pilosa, which, towards the top of the stack there is the large aberrant pulmonate slug, Onchidiidae, reaching up to 8 cm long, and virtually terrestrial. Important high tidal limpets are the pulmonate, Siphonaria normalis and S. atra. The large chiton, Acanthozostera gemmata, with its girdle covered with flexible villi, occupies scars and crevices at high level.

The creviced coral limestone is also free, studded with the archaic barnacle, Mitella, and the small, thin-shelled bivalve, Isognomon acutirostris.

The seaward side of the storm-block, increasingly exposed to wave surge, at the return of the tide, shows a Eulittoral Zone, fitted with green algae, bleached white in sun exposure, and below this a varicoloured band, blotched with wine-red Hildenbrandia, and a pink film of calcareous red algae, probably a Goniotria species. In shaded parts of this regularly splashed zone we can detect - on a close-up view - the extroverted proboscis of rock-boring sipunculid worms (Paraspidiosiphon and Cliseiosiphon), emerging from their small holes that pit the surface, and grazing over the whole surface with the help of their rows of minute denticles. Like gastropods with radulae, the sipunculids at this level form a leading part of the grazing force (see also page 134). Their burrowing habit, and the horny opercula (in Aspidiosiphon and Cliseiosiphon) protect them from desiccation. There is also a predator force subsisting on the sipunculids, comprising the small nitrid gastropods, Strigatella, and the Drupa snails (Muricidae) that insert a long proboscis into the sipunculid holes. Drupa species largely replace Morula on the wave-exposed reef edge. Streamlined against water movement, they lie with the wide aperture flat to the surface. Each species has the shell mouth distinctly marked: violet in D. moralis, black spotted in D. rutila, orange in D. grossularia, and pink in D. clathrata.
THE ZONATION ON A STORM BLOCK AT SALEAPAGA

The location is indicated on a storm block, only briefly submerged at a high tide. (a-b) splashed littoral fringe, with Nerita plicata, Onchidium and Acanthochresta; (b-c) uppermost eulittoral, with Siphonaria, Mitella and Iasomena; (c-d) middle eulittoral, coralline pink, with spiculid borings, and Valonia; (d-e) lowest eulittoral, with zoanthids and Protasphaera; (e-f) first part of sublittoral fringe, Lithophyllum encrusted, with Chama and Spondylus. In shaded crevices (left) cowy species will cluster.

Below the dapple of coralline paint the lower part of the Eulittoral Zone becomes leaden grey, with a continuous sheet of a small, soft Zoanthus, and larger, brown Protopenythea singly inserted into the same spread. Little aggregates of the golden green vesicles of the alga Valonia ocellata are also common.

In the lower eulittoral, two species of cowry Cyprea (Mauritia) mauritiana and C. (Ravitrona) caput-serpentis, will be regularly found by searching in recesses and crevices. Both are wide-based and low built, adapted for stability under strong wave action.

In the sublittoral fringe, near the threshold where stony corals first appear, the large Turbo setosus is a common gastropod. Two bivalves (both cemented to the rock like oysters) should also be noted, being very typical members of the zoning pattern at this low level: a small Chama and the larger thorny oyster Spondylus ducalis.

**PREDATORY NEOGASTROPODA**

A) *Conus crassus* with a eunicid worm.

B) *Strigatella pumifera*, with introvert entering a sipunculid burrow.
The fringing reef at TAFTOALA is only 5 to 6km west of the rather young reef first visited at Sa’a'aga; yet in most ways the two are very unlike. Taftoala is sited at a point of the coast where the reef line is indented and pulled inwards, with its continuity broken by a river mouth. The reef owes some of its features to the influence of freshwater, carrying fine terrigenous sediment. The cross-reef transect shown, from Taftoala village, goes in part parallel to the line of the river, where the reef turns in.

As compared with Sa’a’aga, the Taftoala reef shows what could be called regressive evolution, with effects of run-off. It is somewhat impoverished in coral species; and the outer surf margin shows a dominance not of Scleractinia but of zoanthids and Palythoa, with also a large surface area covered by algae, chiefly Amphiroa and Halimeda.

The inner stretch of the reef, from the beach step out, consists of coarse coral sand and rubble admixed with silt. In water half a metre deep at a low tide, there is a surface cover of Halophila ovalis, an angiosperm related to eel grass, and at once recognisable by its pairs of thin, finely veined oval leaves. Never forming a thick sward, its long rhizomes tinge the surface with delicate green.

On the landward half of the reef flat, the stony corals are almost entirely of the Porites - Pavona assemblage. Small helmets of Porites lobata and micro-atolls of P. lutea are common, and are interspersed with clusters of upright fingers of Psammospora contigua, and a few short branched ('caespitose') clumps of Acropora that - along with Psammospora - contribute to a broken finger rubble.

From a third the way out, two sorts of algae begin to form close tufts, that in many places heavily blanket the bottom. The first is green Halimedina opuntia, with its chains of calcified segments close-packed and collecting silt in their interspaces. Coarser tangles of the sharp-pointed Amphiroa foliacea can be lifted from their loose attachments to the bottom.

The lagoon floor of silt or rubble has several very common tropic-wide echinoderms, including the familiar bright blue star, Linckia laevigata, the greenish-black holothurian Stichopus chloronotus, and a smoother black Holothuria species. There is also the small spined urchin
Echinometra mathaei, with its short, strong spines, not as in most localities - abrading the coral rock, but lying freely on the open surface.

Two thirds of the way across, the Taifoala reef rises to a rubble zone, emersed and dry from half-tide onwards. Large storm blocks, that have been thrown back by gales or hurricanes across the reef margin, now stand stable with a eulittoral zone at their higher reaches (see page 78) carrying however little encrusting fauna. These stacks are built from piles of dead Acropora brackets, strongly welded together by calcareous lithophylla. Their bases are strewn with dead Acropora pedestals and finger rubble. By comparison with Sa'aga, the sciaphilic fauna under these coral slabs is poor, but trochids (Tectus pyramis), long-spined urchins Diadema setosum, and black holothurians are regularly found. The principal sessile species are the red foraminiferan Homotrema rubrum, putty-like Didemnum spp., and the plumply rounded ascidian Corella japonica.

In shallow pools around the storm blocks, there is a small diversity of living corals. Occasional Lobophyllia are to be seen, the only species of the big-cupped Mussidae regularly found in Samoa; the sharp, shaggy fingers of Acropora (c.f. aspera), as well as the fragile branched Pocillopora damicornis, and clustered fingers of Psammocora contigua. Prominent by their pale green colour and sharp projecting septa are small colonies of Galavea fasciulata.

It is in the mosaic of the reef front where surf breaks across the margin, that differences from Sa'aga are most marked. The surface is dominated chiefly by a smooth or goose-fleshed expanse of a small Zoanthus species, leaden grey when closed, but opening out under surge to a carpet of green oral discs.

Sheets of this polyp are studded at intervals with a larger fawn-brown zoanthid, a species of Protopalystoa, with the tentacles vestigial and the oral disc only occasionally open. Polyps of Protopalystoa may regularly link up together as an irregular fawn brown reticulum, strung out over wide areas, with the grey zoanthid in the meshes.

The third important zoanthidean, Palythoa, has its polyps closely aggregated in yellowish-brown crusts or convex masses of up to fist-size. Big expanses of Palythoa reach much further in -
across the reef, to the pools and shallows around the rubble.

It will be recalled that the zoanthids are not truly 'soft corals' (see page 73), but form their own order Zoanthidea, placed alongside the Scleractinia, as a division of the sub-class Zoantharia, that includes also the large-polyped and solitary anemones. These last are typified on the reef by the big Stolichnactis species, regularly to be seen towards the margin.

Zoantharia are thus small anemone-like polyps without a skeleton. They have no pedal disc, and the oral end is stalked or wedge-like. United towards the base by stolons, Zoanthus polyps are aggregated in sheets. Their tentacles are short and reduced, arranged in a double cycle. The most widespread zoanthid across the outer half of the reef is Palythoa with polyps aggregated in convex cushions or low crusts.

Scleractinian corals are relatively scarce in the surge mosaic at Tafoaalo. Heads of Pocillopora cydonia are in places not uncommon, standing out in their dull pink or magenta.

THE COMMON ZOANTHIDEA OF SAMOAN REEFS
1) Complex of a Zoanthus species, with larger polyp of Palythoa
2,3) Zoanthus and Palythoa in surface view
4) Portion of a Palythoa cluster
5) Detail of a Palythoa polyp.
There may also be plaques of blunt fingered Acropora (c.f. digitifera), and sometimes a low crust of a meandroid favid.

The dominant algae at the reef edge are the sharply spined Amphiroa species, especially A. foliacea, forming coarse compressible mats, as well as a number of more finely segmented species. Green algae are also numerous in species. Spongy masses of Halimed a opuntia may grow as big as the Amphiroa clumps. Reaching in right to the rubble flat is the pallid green Dictyosphaer a cavernosa, always a prominent item in the mosaic. The brightest tufts are the rich green tresses of Chlorodesmis comosa. There are frequently green stolons of Caulerpa racemosa, with their small, grape-like branchlets. There are, in addition, numerous sheets and crustose patches of Lissoclinum, a turquoise coloured compound ascidian of the family Didemnidae. Unlike its relatives beneath boulders or rubble, Lissoclinum has its light-exposed tissues crowded with symbiotic zoochlorellae, giving it an important photosynthetic role on the surge-swept reef front.

At Taftoala, as at Sa’aga, the sargassoid brown algae (Sargassum and Turbinaria) are apparently absent, though generally a prominent feature of the surf swept margin.
THE FRINGING REEF AT TAFITOALA

In profile (top), the zones (a-b) salted stretch, with mainly Halophila grass; (b-c) stretch with silty finger rubble, and living Porites and Pavona; (c-d) enriched stretch with Porites and branched Acropora; (d-e) reef summit with rubble; (e-f) surge-swept seaward slope. The quadrats (lower) show details of (b-c) and (e-f).

1) Porites lutea
2) Pavona varians
3) Pavona decussata
4) Halophila ovalis
5) Echinometra mathaei
6) Liveckia laevigata
7) Amphitrite mat
8) Zoanthus sp.
9) Pocillopora brevicornis
10) Palythoa cluster
11) Propalathoa
12) Chlorodesmis comosa

ECHINODERMATA

The section following will be an introduction to the principal species of echinoderms familiar upon the reef or its lagoon, as commonly found in the tropical Pacific. Along with the Molusca and Crustacea, the echinoderms are a supremely important phylum on the reef, coming into its own in shallow tropical waters.

The shape and body design differs greatly between, and even within the five living classes of echinoderms. All, however, agree in being radially constructed, usually in five sections with a central mouth below and an anus above. They possess a unique system of locomotion by tiny suckered tube-feet, hydraulically operated by water pressure from within a system of ambulacral vessels.

The different classes express the five radial pattern in different ways. Sea urchins (ECHINOIDEA) are typically spheres, but may be hearts or flat plates. Starfishes (ASTEROIDAE) are flattened, with the arms generally five, but sometimes many more. The brittle stars or snake-stars (OPHIRUROIDEA) have a small central disc, with five jointed and sinuously moving arms. Sea cucumbers (HOLOTHUROIDEA) are stretched into long cylinders with the mouth and anus at opposite ends. The limy skeleton of other echinoderms is here reduced to microscopic spicules. Finally, the sea lilies or CRINOIDEA have a central cup or 'calyx' fastened by a permanent stalk, or temporarily attached by cirt. The margin bears flexible pinnate arms.
**ASTERIOIDEA**

The starfish or sun-stars have many representatives on the reef flat or under boulders. The largest reef species belong to the Phanerasteridae, with stiff arms kept rigid by marginal plates, and ingesting small - sometimes hard - organisms whole. Their most bizarrely shaped family is the Oreasteridae, with the marginal plates or hard framework concealed in the adult under naked areas of skin. *Proteraster nodosus*, brilliant red and cream, is studded aborally with blunt spikes. Adult *Culcita novae- guineae*, a high bush like a pentagonal loaf, *Chilaster grandilatus* is a large rubbery star, with thick blunt arms of rubbery texture. These are coral grazers. To the family Asteropidae belongs the pointed, saw-edged *Asteropsis carinata*.

The family Ophiidiasteridae includes the most conspicuous of all reef stars the vivid blue *Linckia laevigata*, with long, stiff cylindrical arms, *Linckia* lies on a sandy or rubble bottom, but the small related stars *Nardoa* and *Erythra* with a wide-spaced mosaic of smooth plates, are found under boulders.

The starfish of the order Spinulosa have no marginal plates, but carry integumentary spines. Common under boulders is the small cushion star, *Patiriella exigua*, a pentagonal disc with five points. *Echinaster*, by contrast has a small disc with five spiny cylindrical arms. Most formidably spiny of all reef stars, is the crown-of-thorns, *Acanthaster planci*, a predator of living coral. Multi-rayed and with long, needle-like spines, it can reach 25cm across.

**HOLOTHURIOIDEA**

The largest and most prominent reef holothurians are the cucumbers of the Aspidochirotida, strongly muscular, generally dorso-ventrally differentiated. They lie sluggish on sand in moats and lagoons, ingesting the soft substrate and passing large castings. Both families of aspidochirotides, the Holothuridae and the Stichopodidae push in food by the constant action of the zoal podia, with disk-like circular tips.

The genus *Holothuria* includes the fat, jet black *H. atrina*, with white sand adherent to viscid patches of its skin, *Bohadschia* species are the handsomely marbled "leopard fish," *B. argus*, and the plump, tan-coloured *B. mammata*.

The cucumbers of the family Stichopodidae, are beset with large papilae along the upper surface. As in *Holothuria*, the body is differentiated into the convex "brevium" above and a flat locomotor sole "tritium" with three rows of locomotor podia, below. Much the commonest is the small *Stichopus chloronotus*, with a greenish tinge on its jet black, and two rows of stilt papillae. The light brown *S. variabilis* has rounded mamillae and small prickly villi. The largest stichopod is *Thelepus ananas*, with large rubbery serrate papillae, lying against the surface like flexible scales. *Stichopus horridus* is stiff and inedible, with rounded mamillae.

In the Holothuroidea of the Apodida, the tube-feet, except for the oral podia, are entirely lost, and the body wall very thin, with no differentiation of its two sides. The largest is the metres long and very flaccid *Sonagita maculata*, inflatable with water, or collapsible to small volume. The skin is rough from the projection of microscopic spicules.
ECHINOIDEA

The commonest reef urchin *Echinometra mathaei* abounds in galleries in coral limestone excavated by the abrasive action of the short, strong spines. With the oval test and short spines, *Echinometra* moves regularly along the burrow or leaves it upon occasional feeding forays. Towards the seaward edge in coraline-encrusted rock lives the larger, slate-pencil urchin, *Heterocentrotus mammillatus*.

In shallow pools, part-buried in rubble, is found the very common *Tripneustes gratilla* with dark blue spineless areas on the ambulacra, and short, white or reddish spines. To the same family belongs the less common *Toxopneustes pileolus*, buff and short-spined, with large toxic pedicellariae, pink in colour.

Ledges, boulders and overhangs should be approached cautiously and never with bare hands, for they will harbour the long-spined and highly toxic *Diodon setosum* (yet black) and *D. asperius* (with banded spines). The long spines move sensitively towards the fall of a shadow.

OPHIOUROIDEA

The snake-stars or brittle stars are the most active of the echinoderms, and the most attractive in form and ornament. They all avoid light, concealing themselves in secluded places. With circular disc and jointed arms, their morphology is stereotyped. Their taxonomy is based upon their great variety of ornament, the form of shields and scales, variously sculptured with granules; arms-spines and jaw plates.

Ophiuroid feeding styles are unexpectedly diverse. One of the most versatile ophiuroids in its food collecting is the tropical *Ophiopluteus scolopendrina*. Abounding in crevices and small concavities in coral rock and rubble, it unfolds and deploys...
its arms with each return of the tide, using the flexible tips to sweep particles from beneath the water film. Mucus nets secreted between the arm-spines catch food, which is carried to the mouth by the centripetal action of the tube feet. The surface can also be directly grazed with the jaws.

The Ophiocomidae vary widely in habit, *Ophiomastix*, with the disc and slender arms covered with long spines, lives under boulders. *Ophiosthronemus*, with the disc naked and attractively patterned, has shorter arms.

The Ophiotrichidae, typified by *Macropliotrichus longicauda*, have also slender arms with long glassy spines. The Ophiuridae contain stiff, thick-armed species relatively robust and inactive. They are carnivores, and - as in *Ophioplax superba*, take large food fragments by arm-looping.

Similar habits are shown by the Ophiodermastridae, with the short-spined stars typified by *Ophiastrephes coronata*.

**CRINOIDEA**

In contrast with ophiuroids, crinoids or feather stars visibly display their ten or more pinnules. Those of tropical reefs belong to the order *CUMATULIDA* and break free early in life from the stalked attachment of the more primitive crinoids. From the margin of the calyx or cup, five basic arms spread, dividing into two, or in the comatulids frequently more. Most crinoids feed by cilia or mucus, with plankton alighting on the arm pinnules and being carried by podia into the ambulacral grooves that convey them to the central mouth. Brightly coloured crinoids are to be found commonly at the reef edge, and in the current swept spaces at the edge of boulders and coral heads.
SI'UMU

The fringing reef at Si'umu, running seawards for some 400m, is cut off from the basalt high tidal shore by a channel, floored with white sand, and reaching 2m deep at low tide. After a hundred metres or so, the bottom shallows to a virtually pure expanse of Pavona (P. varians with lesser amounts of P. decussata) no more than ankle deep. The coral closes up to a continued platform, fragile but walkable with care, until midway across the reef it gives place to a brittle canopy of the massed branches of a blunt-tipped short-antler Acropora (c.f. Acropora formosa). Mingled with these branches are the blunt-tipped, mustard-coloured fingers of Porites cylindrica, growing at knee depth. Amongst and alongside them may be found big, metre-wide micro-atolls of Pavona varians. From mid-distance outwards, until the reef crust becomes emersed at low-water, blunt-tipped Acropora holds the dominance. Passing across another stretch of small Pavona heads we ascend to a crest of coral rubble, pink-veneered with Lithophyllum. The rubble is composed of slabs and tables, welded firmly to the underlying base, with movable, recently overturned Acropora pedestals. The sciaphilic fauna underneath seemed

THE FRINGING REEF AT SI'UMU

In profile (top), the zones are (a-b) silted stretch in front of basalt shore; (b-c) deeper sand-bottom stretch; (c-d) wide zone of dominant Pavona varians; (d-e) stretch of Pavona enriched with Acropora; (e-f) reef summit with dead rubble; (f-g) surge-swept reef front.

1) Large micro-atoll of Pavona varians
2) Small heads of P. varians
3) Pavona decussata
4) Echinometra mathaei
5) Culcita novae-calediae
6) Stichopus chloronotus
7) Holothuria crispa
8) Chlorodesmis comosa
less diverse than at Sa'aga. Amongst and at the base of the rubble, the chief live elements are zoanthids, *Palythoa* and *Dictyosophera*. There are few living corals, and the impoverishment is in general reminiscent of Taftoala.

The seaward slope, over which the surge sweeps in is also like that of Taftoala. Its low incline is carpeted with close-set zoanthids and *Palythoa*, and also with the red alga *Amphiroa*. Rather little *Pocillopora* was to be seen at the points inspected.
On the north coast of Upolu, the most complete and continuous reefs lie west of Apia, fronting a coastline of Mulifanua volcanics, at a slope gentle enough for barrier reefs to have developed. The presence of a wide and relatively deep lagoon, down 5 to 10m, is the main distinction of barrier from fringing reefs. The distances across the lagoons, on north Upolu, would reach several hundred metres.

Between seaward and windward reefs there are other salient differences, clearly separating the north from the south coast.

A windward reef is built up at its seaward edge into a pronounced algal ridge, with a cement of calcareous red algae playing as great - or sometimes a greater - part than the corals themselves. The short seaward slope continues out at a low angle, to its subtidal prolongation beyond wavebreak. Heavily swept by surge, its living pavement is of crustose or plaque-like corals, streamlined to offer the waves little resistance. Flat sheets of the soft coral Lobophyllum expansum are also characteristic.

On a leeward reef the outward margin forms a parapet with a more precipitous drop to the subtidal, usually overhung by the brackets and shelves of tabular Acropora, perhaps the most typical of all coral growth forms on sheltered coasts. The reef edge is moreover quite complexly embayed or indented with narrow gullies and wave runs, having their divides just emergent at low water. Within these passes, surge constantly rises and draws back, on a calm day only just sweeping the divide at low water. Such a reef front generally allows quite a safe access at low tide, admirable for watching reef fish in their high profusion. In calm weather, the reef front and the entrances to the surge gullies are easily accessible to SCUBA observation from outside the reef.

**Some familiar reef fish**

| CHROMIS | CHAETODON | DASYCLETUS |
The barrier reefs of the north coast are difficult to access at the seaward edge, and the landward fringe is generally over-sedimented and depauperate, with little live coral to be found. To reach the barrier is best done in the Samoan way by outrigger or canoe. In a few places, where the barrier reef draws closer to the shore, it is possible in good weather to cross safely by snorkeling. Such a spot was found at Utuali, chosen for the first study of a north coast reef.

**UTUALI REEF**

The lagoon, beginning from the basalt drop-off where the main road skirts the shore, is approximately 500m across, and drops to a maximum depth of 6 to 10m. Halfway across, its colour clears to blue over clean white sand. The landward stretch is cloudy, with heavy silt run-off and supports only a diminished macro-fauna. The Mulifanua basalt of the shoreline is old and eroded, filmed or encrusted with silt up to high-water level. Neither barnacles, nor gastropods (littorines, nerites or limpets) were to be found.

From stepping off the shore, the lagoon is a dead coral expanse, filmed with grey silt in depressions between the rubble. A few live nodules of *Porites lutea* will be seen, as well as small heads of *Pavona varians*. Bright yellow fingers of *Porites cylindrica*, are also in some places conspicuous, along with a few caespitose, or moderately branched *Acropora* heads.

Beyond this landward silt cover at about halfway across the lagoon, the bottom lightens to white sand.
The seaward barrier ascends from the lagoon with a rubble of dead coral, broken Acropora fingers piling up at lower levels, and higher up a scree of dead Acropora tables, clean and increasingly veneered with pink coralline algae as we pass seaward. At the seaward edge of the lagoon, the back reef is well-washed by currents, and is constructed of strongly welded piles of living or newly dead Acropora tables, coryps and short fingers. There is also a plentiful scatter of small branching clusters of pink-pointed Acropora nana.

The reef is thus - at this level - brightly coloured and clean of sediment, with a high proportion of living coral. It bears some resemblance to the close field of Acropora tables at middle distance across Sa'aga reef (see page 64).

After the depauperate landward fringe, the crossing to the barrier will be accounted richly worthwhile. Overturned Acropora tables and broken rubble support the same abundant hypofauna as was described from Sa'aga. Just as on the south coast, sponges are never more than sparse. The ascidians are chiefly the plump rounded Corella japonica, as well as Didemnum patches, dull-white, lollipop pink, apricot or salmon. Branching Bryozoa have the high richness and cover density that seem typical of Samoa: with fine white Crisia elongata, the brittle and glassy Margaretta gracilior, as well as lattice work of Reteporella.

Hydrozoan colonies include principally Calypotheca and Sertulariidae. Sessile colonial foraminifera are abundant under every piece of rubble with the delicate ‘spun glass’ tufts of Dendrophyra, and red ‘sealing wax’ blobs of Homotrema rubrum.

Many echinoderms live amongst the rubble. The most numerous urchin is the small Echinometra mactae, while wedged into crevices are the elegant and heavy-spined slate peacock urchins, Heterocentrotus mammillatus.

The reef summit can be easily crossed to where on a calm day surge courses lightly over its edge. Inspection of the surface and collecting from it are generally easy. As on all leeward reefs, there is no straight front. Rather is the reef edge completely indented, and intricate to walk around. Old Acropora tables serve as stepping stones, as irregular as jigsaw pieces, arranged stepwise at varying levels, with surge between them, so that careful steps must be taken along the convoluted edge. Big, concave indentations can be looked-
Over all this living cover, the surge breaks constantly but rather lightly at low water. The total coral diversity can be appreciated by looking over the drop towards the sand and rubble floor. In the concave grottoes, briefly revealed as the waves draw back, are evenly spaced Acropora corymbs and tables, and short-fingered plaques. There are still Pocillopora, well apparent from its colour, and pale yellow Millepora established on the ridges and salients.

Strewn on the reef floor are also the big single corallites of Fungia fungites, with their polyps pink or pale green. Receding tiers of tabular Acropora hyacinthus can be seen further down. Deeper still are yellow fingers of Porites cylinderica, and big convex mounds of Porites lobata, common inshore, and here again seen in the less disturbed waters beyond the immediate level of wave-break.
THE ENVIRONS OF APIA, SHOWING THE REEF AND MANGROVE SWAMP
The barrier reef of the north coast, in front of the Mullifanua volcanics, extends only to Fagalii and Vailele Bay. The oldest (Fagaloa) volcanics, of Pliocene age, have lost their barrier reefs after Pleistocene submergence. A flow of recent Puapua lava emerges from a valley on a short stretch of coast at Laulii, which - like the older Fagaloa shores - is reefless in front. East of Laulii, through Leusalei’i and Luatuanu’u, to the basalt promontory of Cape Utumau’u, and then to the Namo River outfall at Vainamo Bay, there is a mere rudiment of a fringing reef, close inshore but so easily accessible from the coast road as to repay inspection.

At Cape Utumau’u, a promontory of basalt carries a wave-swept zonation pattern, with good development of algae, where the impact of waves is undiminished by any reef barrier to seaward.

From Cape Utusia to the Falefa Harbour, the intervention of Mullifanua volcanics, has made possible a wide fringing reef. Thereafter, to the eastern tip of Upolu, including Fagaloa Bay, the coast is reefless, until the reappearance of Mullifanua volcanics, along the Aleipata coast, at Upolu’s eastern end.
WEST OF LEUSOALI'I

Despite its small width and incompleteness, the fringing reef is of considerable ecological interest. Accessible across a wadable lagoon of only 200m, its outer edge has the same character as the leeward barrier reef at Utual'i, completely indentured with gullies into which the surge mounts with each wave. The edge has moreover the steep parapet dropping off to the subtidal, characteristic of leeward reefs.

At Leusoa'lli, subdued wave action makes it possible to stand at the drop-off and look over the seaward edge. The transparency is lower than for the clear blue-green water of the weather coast. But the virtual lack of white surge allows easy observation of the schools and individual reef fish, which are abundant and varied. Snorkel observation from offshore is easily possible in normal weather.

The coral species at the reef edge are few and predictable in type. The main Acropora is a small plaque-like species, (A.c.f. digitifera), without the fragile jutting tables and brackets displayed by A. hyacinthus at Utual'i. Pocillopora verrucosa, with scattered, dull magenta heads, is about as frequent as Acropora. Almost the only other coral is Millepora platyphylla with clumps of strong lamellae at the sites of greatest water movement.

Behind the margin there is no emergent reef crest or rubble zone, but a broken platform composed of horizontal shelving Acropora (c.f.) digitifera. This dead coral is chiefly interesting for the abundant bio-eroding fauna that penetrates it, and nestles in pre-existing concavities, as described at page 131.

The narrow lagoon at Luatuana'u is only knee-deep at low tide. It is impoverished of living coral, and thickly silted, the effect of terrestrial run-off. The landward half has a pale green field of the seagrass Halophila ovalis, abundant and healthy, lying upon the most silty areas. The rest of the bottom is of finger rubble of Acropora, with numerous echinoderms. Echinometra mathaei, freely living amongst rubble, rather than in deep scars, is the commonest urchin. Mespilla, Stichopus chloronotus, and Holothuria and the bright blue star Linckia laevigata also decorate the bottom.

At the upper littoral level, there are boulders of two sorts; lowest down dead coral blocks, partly-
eroded by cryptofauna, and with plentiful Siphonaria, the big spinose chiton Acanthozostera gemmata, lying in scars, and a common periwinkle, never collected by us on the south coast, Littorina undulata. At the top of the beach adjoining the roadside, large basalt boulders have both this littorine, and also the common open coast species L. coccinea. Opeculate barnacles were on this coast nowhere to be seen on the upper shore.

THE SEAWARD MARGIN OF THE FRINGING REEF AT LEUSOALI'I

The profile (top) shows: (a-b) backshore with basalt and coral boulders; (b-c) field of Halophila ovalis; (c-d) field of finger rubble; (d-e) stretch of sparse Acropora and Amphipora; (e-f) reef summit with rubble of coral plaques and boulders; (f-g) wave-washed indented reef margin.

1) Acropora digitifera
2) Millepora platyphylla
3) Pocillopora verrucosa

Details:
4) Halophila ovalis
5) Padina Procumbens
6) Sargassum sp.
7) Hydroclathrus clathrus
8) Colophenia asinata
9) Dictyota sp.
10) Littorina undulata
11) Micrasteria cavernosa
12) Mesolera sp.

Acanthozostera gemmata, a Pacific-wide tropical chiton of the upper shore.
PALOLO DEEP

The Marine Reserve at Apia, known as the Palolo Deep, the only one of its kind in Samoa and a concept virtually new in the South Pacific, is sited off Pilot Point outside Apia Harbour. It is constituted by one of the deep convolutions by which the barrier reef outer margin is turned into a grotto, or closely sheltered “deep hole.” Another such re-entrant, completely closed off, is at the tip of Muline’s Peninsula. Palolo Deep is a reef site well deserving of study, being easily accessible from the shore, and having a range of coral species characterising the most extremely sheltered lagoon situations. Especially typical are large and brittle Acropora gardens and forests, not common elsewhere on Upolu reefs.

Palolo Deep is reached at low tide by walking across the shallow flat 0.3m at low water leading seaward from the constructed observation platform. The deep hole or grotto can then be swum over with mask and snorkel. Not only can luxuriant branched corals be observed but also reef fish in their numerous diverse shoals.

From the observation platform a gentle, low angled slope proceeds seawards with a walk across a wide, close-packed field of shoreward corals Porites, Pavona, Psammocora.

Level-topped and brittle under treading, the corals of this zone are still, however, in good living state. The predominant cover is of Porites, with the yellow short-finger species, Porites (c.f. cyindrica), characteristic of sheltered water, both inshore, and on the reef front below wave action. There is also a greyish-brown Porites, with short, upright fingers truncated to flat-topped pedestals just beneath low water level. From these level tops, specimens of the sedentary coral-predating gastropod Coralliobius violaceus can be collected. The common Pavona species of Samoa, Pavona variaans and Pavona decussata, are both frequent amongst the Porites clumps. Small branched Psammocora contigua should be noted too, with its trihedral or angular, plane-topped branches reaching up to low tide water level.

PALOLO DEEP: THE SHALLOW AND THE DROP TO THE SHELTERED GROTTO

Luxuriant branched coral in the grotto include Acropora grandis and Acropora formosa, (dual of branch-tip insect). Corals illustrated are:-
1) Pavona variaans
2) Seriatopora hystrix; and some bottle-brush Acropora (in the background shown at lower left). These species have yet to be investigated for W. Samoa. Three wide-spread Pacific species are:-
3) Acropora squamosa
4) Acropora echinata
5) Acropora longicruratus.
Amongst the yellow *Porites* fingers there are also fragile bushes of *Seriatipora hystrix*, a coral not yet recorded elsewhere from Western Samoa. The slender branches taper to fine points, and the small corallites are arranged in parallel series, each living polyp outlined with a dark rim.

No Acropora were observed on the inner flat or the slope, nor any *Palythoa*. Soft corals were confined to some small, long-branched clumps of *Sinularia*.

As the slope descends, the yellow *Porites cylindrica* increases in height and its formation opens out. *Seriatipora* clumps, too, become larger and commoner.

The sheltered grotto in the deeper reaches is, however, dominated by *Acropora* species, presenting an entirely different aspect from anything seen in shallow moats, or wave-exposed reef front. These new *Acropora* range from tall, and slenderly outreaching stag's horns (as of *Acropora grandis* and *Acropora formosa*, the latter with pale blue terminal calices) to highly divided bottle-brush *Acropora* species. Here as in *Acropora echinata*, the tubular calices are long and free, slightly curved, while *Acropora* (c.f.) *squarrosa* forms branchy festoons like cake-icing, covered with calices like strong villi over the branch systems.

Prominent amongst *Acropora*, and lying broad-based at ground level, are convex heads and big helmets of *Porites lutea*. As the slope deepens, a heavy branched *Porites* occupies much of the bottom.

Not fully explored during our study, this sheltered grotto at Palolo Deep should be carefully examined for other fragile coral species, including *Acropora aspera*, *Montipora chenbergii*, *M. venosa*, *Echinopora lamellosa*, *Pocillopora damicornis*, and *Merulina ampliata*, all recorded by Lamberts (1981) in his annotated list for American Samoa.
ALGAE

The richest Samoan sites for algal collecting, and virtually the only places to find brown algae of even middling size, are along the leeward north coast. The shallow landward stretches of the lagoon on fringing or barrier reefs, sun-warmed and often cloudy with sediment, are also the habitat of *Halophila ovalis*, everywhere the principal sea-grass species of Samoa, common on both north and south coasts.

The calm lagoons of the north, as illustrated by the short fringing reef west of Leusoalii, (see page 103) are rich in brown algae. The Sargassales are represented by the tropical-Pacific-wide *Sargassum cristaefolium* recognised by its short axes, with thick, cartilaginous leaves developing a duplicated margin of spines. A second *Sargassum* species has branches of softer, slightly dentate leaves.

The alga *Turbinaria*, (not to be confused with the coral of the same name) is a modified sargassoid, with the leaves compact and peltate, forming small, flat-topped pedicels. *Turbinaria ornata* has a spiny margin, and its leaves are radially grouped, into a ball moored by a longish stalk.

Equally common as the sargassoids in warm seas is the brown alga *Padina* (order Dictyoales), daintily fan-shaped, typical of sun-warmed pools or silty rubble. The thalli are split terminally into small straps, with the edges in-rolling towards the underside. Concentric lines of hairs mark the position of the reproductive organs. *Dictyoa* species are also common, having a simple, dichotomous growth form, with its thallus composed of thin ribbons, freely branching in one plane.

Brown algae of the order Ectocarpales are well represented in lagoons. The most elementary in form are the simple unicellular brown filaments, composing the tufts of the *Ectocarpus* and *Feldmannia* species. *Colpomenia sinuata*, by contrast, has a sheet-like construction, rounded into irregular and convoluted vesticles. The related *Leathesia*, with smaller convolutions, is thick and fleshy. Both these algae are temperate-wide as well as tropical.

Their purely tropical relative, the large *Hydroclathrus clathratus* is unmistakable from its open fleshy or gelatinous network, loosely attached to the lagoon floor.
The lagoon has also its several typical green algae. Large compact hummocks of Halimeda opuntia can be frayed out to reveal the chains of calcified segments aggregated side-by-side. Rhizoids of Caulerpa racemosa with branches like small bunches of grapes, may creep over the soft bottom. On harder substrate there will be pallid green Dictyosphaeria cavernosa forming clusters of vesicles as stiff as cartilage.

**THE STRAND PLANTS AND ALGAE OF A BASALT SLOPE UNDER WAVE ATTACK AT CAPE UTUMAU’U, WITH REEF PROTECTION LACKING**

In the sublittoral zone, the creeper is Ipomoea brasiliensis (a-b); (b-c) littoral fringe with Nerita pilcata; (c-d) upper eulittoral with Ectocarpus tufts; (d-e) middle eulittoral with coralline paint; (e-f) lower eulittoral zone of Sargassum tufts with ceramidine turf; (f-g) low sublittoral fringe with general rhodophycean turf.

Detail of plants:

1. Ipomoea brasiliensis
2. Wedelia biflora
3. Halimeda opuntia
4. Caulerpa racemosa
5. Dictyosphaeria cavernosa
6. Valonia operculata
7. Sargassum cristafolium
8. Turbinaria ornata
9. Gelidium sp.
10. Cladodina sp.
11. Gelidopsis sp.
12. Chondria sp.

**ALGAE AT WAVE-BREAK**

As distinct from the calm lagoon, some rich sequences of algae are to be collected on steep basalt surfaces under direct wave-break, such as the seaward promontories and stacks of the little peninsula of Cape Utumau’u. The zonation here, under constant wave-splash is illustrated opposite.

Above the littoral fringe is an Eulittoral Zone with white flowered Ipomoea macrantha, (and less commonly I. brasiliensis) also the daisy Wedelia biflora and the creeping papilionacean, Vigna marina. The littoral fringe (devoid of barnacles here, but with plentiful Nerita pilcata) is followed by a Eulittoral Zone, at the top of which the black basalt carries spray-drenched tufts of a pale brown Ectocarpus sp.

The middle of the eulittoral is carpeted with strong sargassoid clumps, and thick tufts of red algae, which are in fact deep-brown in normal hue. Just before this turf begins there is a dappled patchwork of pink or mauve coralline algal paint.
The most conspicuous eulittoral algae are golden yellow *Sargassum cristaeolium*, with the second and softer-leafed *Sargassum* sp. and spinose *Turbinaria ornata*.

The thick rhodophycean turf is composed of springy *Laurencia* and *Chondria* species, with patches of *Acanthophora spicigera*. Lower down, upon a veneer of red algal paint are fronds of a pink dichotomous *Gigartina* sp. Amongst the turf are also found a fine green filamentary *Chlorodesmis* species, and a fine red *Gelidiopsis* or *Wurdemannia* (inseparable - August, 1987 - without fertile material).

Little pools and pans, replenished by wave action, add further algal diversity. Pools near the top have *Padina*, *Caulerpa racemosa* and *Halimeda opuntia*. Lower pools constantly awash with heavy surge have a thick turf with lanceolate-branched *Pterocladia*, or *Gelidium*, with fine lanceolate branching.

**SOME CALCIFIED RED ALGAE OF THE REEF CREST**

*Galaxaura* species are soft and flexible, not jointed but with scattered calcareous grains. *Amphiria* species are jointed fully and blunt. *Jania* is fine and dichotomously jointed, forming a soft turf. In *Lithophyllum* the branches are firmly ankylosed together.
REEF BUILDING AND CORAL DISTRIBUTION

A general account

Sometimes hundreds of metres across, the reef stretch - as we have seen - is kept close to horizontal, with its living corals no higher than the sea level at average low tide. We have referred to this whole stretch, in the world-wide zonation terminology, as a "sublittoral fringe": but with its immense scale and diversification, it will need subdivision on its own descriptive terms.

One way to begin is to notice the order in which the predominant types of corals tend to appear across the reef's horizontal extent, in relation to waves and currents, sediments and salinity.

The figure (see page 115) relating the vertical zonation of the backshore, with the coral distribution across the reef, is modified from Dr Pichon's most useful conception of a reef at Mahé, in the Seychelles. It would seem to have a universal application throughout the Indo-Pacific.

(1) In the most turbulent situations ("high-energy" environments) with strongest water movement - assemblages of Pocillopora (especially P. cydonia, P. meandrina and P. brevicornis) are the predominant corals.

These have a regular associate in the fire coral Millepora, characteristic where the surge breaks over the reef front, not only to windward but at the edge of leeward reefs as well.

(2) Where water movement is appreciably less, a wide niche spectrum will be occupied by the variant species of Acropora so widely plastic according to depth, speed of current and strength of wave attack. On leeward reefs, tabular or bracket Acropora species inter-mix with Pocillopora - Millepora right at the reef margin; whereas on windward margins, Acropora species are reduced to encrusting plaques with branches short or suppressed. Not only does Acropora assume the predominance as water movement is reduced behind the reef edge. The same transition is to be seen where water movement is appreciably diminished below wave break on the outside reef front.

(3) Furthest back on the reef, towards the beach, with decrease of water movement until wave action virtually disappears, there grows an -
assemblage of *Porites* species, almost always associated with inshore species of *Pavona* (P. varians, and *P. decussata*). Again, on the subtidal reef front, with water movement diminished at or below wave-base, *Porites* will in its turn become predominant below *Acropora*.

This sequence (*Pocillopora* + *Millepora* ... *Acropora* ... *Porites* + *Pavona*) can be found, then, associated with a gradient of diminishing water movement exemplified in these three situations:

(i) shorewards across a flat reef.
(ii) along a reef front with a transition into a more obviously sheltered situation, as from the windward (exposed) to leeward (sheltered) sides of an island.
(iii) vertically downward, from the "high energy" zone of a reef front, to the zone of reduced water movement at, or below, wave base.

**RELATION BETWEEN CORAL ASSEMBLAGES AND EXPOSURE**

The scheme represents a sublittoral continuation of the littoral zonation shown vertically in the right-hand part of the diagram.

A) Upper limit of *Littorina*
B) Upper limit of barnacles
C) Upper limit of corals and calcareous algae.

Wave action decreases in the three directions: with passage upshore, with movement towards shelter, and with increasing sublittoral depth.
CORAL DIVERSITY

We may now consider the distinctive parts played by the different stony corals in the construction and ontogeny of the reef. The REEF FRONT is generally well enough lighted for some growth of hermatypic (or symbiont-dependent) coral down to approximately 150m depth. On weathered coasts, however, two factors may reduce hermatypic coral diversity at and below the visible reef margin: the strong assault of waves and the reduction of light by its reflection from the waters at the white surge line.

On leeward coasts, tables and brackets of Acropora commonly shelf out as stacks of tables and brackets, at low water, well revealed as each wave draws back. At the reef front, and immediately behind the reef crest, corals are also adapted to strong water movement. When waves course straight up the seaward slope, the predominant Acropora are 'corymbose' with a spread of branching fingers on a short pedicel. Alternatively, Acropora with vertical branchlets may fuse directly to the ground, following its contour in heavy crusts. Some Acropora put up short points or fingers, strong enough to resist the surge. Or branches may be altogether suppressed, with their positions still marked by enlarged terminal calices flush with the surface. In much of the Pacific, though less in Samoa, hemispheric heads or low plaques are also produced near the wave-front by the faviid corals (Favia, Goniastrea and Platygyra).
For the early and post-mature windward reefs, the stages in succession are illustrated as discussed in the text.
THE LAGOON

Behind the reef front, over the landward slope, most of the corals will remain immersed even at low tide. In a young and developing reef this stretch will appear as a wadable moat or sometimes a lagoon deep enough to need a boat crossing. Such enclosed reaches and particularly the moats of fringing reefs, with a freer, more luxuriant coral growth than any other habitat, are favourite sites to explore with snorkel.

Chronologically, the first corals to appear in these quieter places are likely to be branched Acropora. The substrate will at first be of unconsolidated sediments, but with only slight water movement young corals can establish on the fragments of hard debris. Once initiated, a dense thicket of stagshorn Acropora will grow upwards, supported on their dead branches as stilts, providing space also for little solitary corals (aematypic), and also Pavona and Montipora, often with young (stalked) Fungia.

FILLING-IN

Consolidation of this branching forest comes in slow course. Cementation by calcareous red algae will progressively create a fragile canopy, between branches already dead, though sometimes with their tips still alive above the canopy. The dead branches below will gradually become colonised with a rich sciaphilic hypofauna. The canoped formation so built up will become denser and more continuous towards the outer edge of the lagoon. Corymbose Acropora of low elevation may establish on top of it. Light-avoiding (aematypic) corals will increase in number beneath. Such canoped areas will tend to open up and lose their continuity as we pass to landward. Finally only scattered pedestals will remain, with rubble or fine sediments intervening.
SECTION OF A FRINGING REEF, SHOWING STRUCTURE, WATER MOVEMENT AND ILLUMINATION
To seaward of its moat system, with consolidating and infilling of dead corals, the reef will rise to a low summit, that may broadly be one of two sorts, taking their origin in different ways. On wave-spent exposed coasts, largely free of sediment, calcareous red algae, both of the encrusting and the jointed types, may weld together a considerable thickness, softer and more friable than dead coral, yet massive enough to form the crest often known as the algal ridge. Its contribution on exposed, high-energy reef fronts has been great enough for some to advocate the term ‘biotic reef’ or ‘coral-algal’ rather than the simple term ‘coral reef.’ The algal ridge is never in evidence on leeward reefs, and it was not - in Samoa - found to be regular or conspicuous on the windward reef fronts. More often - in Samoa - as elsewhere - the reef will rise to its summit with an array of finger rubble, dead corombs and tables, or larger boulders. The most massive of these will be storm blocks that have been detached from the reef front and carried over its summit by heavy swells. Lodged stably near the edge of the flat, the biggest may stand two or three metres high, being the first parts of the reef to become visible at low tide. Their dead coral will have a rich fauna of borers and eroders, and their vertical sides may carry a zoned eulittoral and littoral fringe.

Meanwhile, the landward shallows of the lagoon have been establishing their corals too. The hardest of all the inshore corals, the species of *Porites*, have a lightly porous structure and are fast-growing. They branch only shortly, or may establish as massive heads, convex heads or ultimately flat-topped micro-atolls, elevated half a metre, and sometimes a couple of metres across.

In these quiet waters of the back-reef, *Porites* along with *Pavona* (and usually with a minor element of small *Acropora* or *Pocillopora damicornis*) are the dominant corals, especially in fluctuating temperatures or with the high turbidity and lowered salinity deriving from terrestrial run-off.
SUCCESION

The shore we have been able to examine has shown us varying stages of the development and building up of a mature reef, throughout its process of ontogeny, extending over hundreds - and often thousands - of years. The reef at Sa'aga, in front of sub-recent Puapua volcanics, shows obviously the early beginnings of a canopy formation, with living Acropora tables still luxuriant in the outer reach of the lagoon. The sheltered embayment of Palolo Deep is obviously the best example of an intricately interlaced Acropora forest, with Acropora grandis and A. formosa, with additions of brush Acropora, and the appearance of Seriatpora hystrix, elsewhere uncommon in Samoa.

Various stages of Porites and Pavona colonisation of the inward shallows have been seen at St'umu, and in the lagoon at Salaeapaga, there mingled with closed groves of soft corals, notably Sarcophyton.

The influence of transported boulders or sediment has much to do with the later stages of reef evolution, that may be called 'regressive.' What is to happen will depend much upon the balance between sediment deposits and water flow across the reef flat. Proximity to a stream mouth will ultimately inhibit reef growth altogether. A permanent stream of water with low salinity will move across the flat, and sediments of terrigenous origin will be deposited on it, or transported seaward. Where there is a strong water flow, terrigenous sediments may be swept out to sea, and only heavy boulders or rubble allowed to remain. Calcareous green alga, notably Hallimeda opuntia, or red algae, such as the Amphiroa species, may build up dense, sediment and silt-entrapping clumps; and zoanthid polyps (Zoanthus, Isaurus or Palathyra) may cover a wide extent of surface.

There are other reef flats where regressive evolution is marked by sediment accumulation, with the current flow across the flats too weak to remove it. Coral communities have generally disappeared, with the exception of small Porites nodules, on harder emergent spots. The silt deposits will carry instead sea grass beds, notably of Halophila ovalis, in Samoa. There will in addition be species of green algae well adapted to grow upon sediments, such as Caulerpa racemosa and Hallimeda species, also Cladophora and Valonia forbesi. Such a reef flat located near to a riverine passage from a stream outfall, has been described at Talitoala.
THE DARK FAUNA OF RUBBLE

Dead coral heads like other rubble blocks, carry beneath them a light-avoiding (scaphilic) fauna, one of the richest assemblages of species to be found anywhere on the reef. They are especially good collecting sites for two sorts of organisms: first, the primary crusts of sessile invertebrates (sponges, bryozoans, ascidians, foraminifera) and second, the species of carnivores... notably gastropods, opisthobranch or crabs, that feed on or associate with the sessile species.

The encrusting species form a roughly ordered sequence, according to distance beneath the boulder away from outside light. The slab from Sa'aqa illustrated opposite, shows such a species array, beginning from the lighted edge (to the right) and moving to the darkest part of the undersurface at the left.

To the outside, with low illumination still available, there are organisms needing light: a hermatypic coral (a crustose Psammocora), and a green alga Halimeda opuntia. Two encrusting red algae, both lightly calcified, occur on the threshold of shade. The dark red Hildenbrandia is hard and crustose; while a Psammocrusta coloured like burnt sienna, grows in thick flexible discs only loosely attached to the rock.

CRYPTOFAUNAS

Next away from the light, our boulder picture shows a brilliant red sponge, a dendroceratid species forming a soft crust over the surface. One of the most ancient phyla of sessile, filter-feeding invertebrates, the sponges (Porifera) divide into two rather distinct classes. The Demospongiae, often brightly coloured, have a mixture of siliceous skeletal spicules, as well as fibres of horny keratin, predominant in the example shown here. The class Calcarea, by contrast, are small tubular sponges, generally pure white and with a skeleton of minute calcareous spicules.

THE MICRO-ZONATION OF ENCRUSTING FAUNA AND FLORA OF THE UNDER-SURFACE OF A DEAD CORAL SLAB, AT SIFUMU

1) Hildenbrandia, under shade edge
2) Halimeda opuntia
3) crustose Psammocora
4) Pseossospongia rubra
5) A red dendroceratid sponge
6) Didemnum sp.
7) Corella japonica
8) Heterostyla rubrum
9) C cris longata
10) Demospongia
11) Crustose chelostome bryozoan (Palythoa)
12) A second crustose chelostome
13) Latticed bryozoan Trinema
14) Margareta gracilis
15) Erosing Aka sp.
16) Hydrocorallia Distichopora
17) A black demospongia
Ciliary feeders like the sponges, but showing a far higher level of organisation, as part of the earliest Chordata, are the ascidians (Tunicata). Two main sorts are present beneath the boulder. The first, adjacent to and sending patches into the spread of sponge, is a compound colonial ascidian, a species of Didemnum, of putty-like consistency and carrying in its tissues fine calcareous granules. Some tropical didemnids adopt bright colours, mauve or apricot, or - as in Didemnum moseleyi, common in Samoa - salmon pink. A second under-boulder tunicate illustrated below is a "sea squirt" with the large spherical test of a simple ascidian, of the rather common Pacific species, Corella japonica.

On the parts of the boulder furthest from light and strong currents, the encrusting fauna is colourless and often fragile, including some species with calcified skeleta having the appearance of spun glass.

The first are sessile colonial Foraminifera, prolific in such deeply shaded sites on every tropical reef. Delicate in structure and entirely colourless is a species of Dendrophyra, with its lightly calcified skeletal casing finely teased out into branched capitiform tubes through which the fine photoplasmic pseudopodia are extended for food-catching.

A second foraminiferan, Homotrema rubrum, is bright red, its colonies applied to the rock like spots of sealing wax, and drawn out into much shorter tubules than in Dendrophyra, which are gathered together in bundles.
**Sessile Formaminifera**
(highly magnified)

a. *Homotrema rubrum*; b. *Dendrophyra* sp;
with e.m. surface detail.

**Cyclostomatous Bryozoa**

a. part of a *Crisis* colony; b. detail of *Crisis* with brood chamber. c. Tubular zooid of a cyclostome, with tentacles expanded.
CHEIOSTOMATOUS BRYOZOA

An anascan aasid, with tentacles expanded (top right), and scanning e.m. details of (a) Rhizoporella; (b) Calyptraea; (c) Margaretia.
Notable on coral boulders in Samoa is the strong dominance of Bryozoa built up into colonies of minute chitinous and calcified boxes (zooecia). Each individual feeds by a ciliated tentacle circlet or ‘lophophore.’

Two sorts of Bryozoa are regularly to be found under boulders. The first, belonging to the class Cyclostomata, may form spreading sheets of microscopically sculptured zooecia, as exemplified by Calypotheca, at Sa’aga. Alternatively they may grow as little erect, articulated colonies, like Nella tenuis, or as prostrate colonies, glass-like and branching, such as Margareta gracilis. A common tropical growth form for chelostomes is that of an elegant calcified lattice, illustrated from Triphyllozoon and Reteporella.

The second class, the Cyclostomata, are some of the most ancient of the Bryozoa still living. The example shown here, Crisia elongata, has a fine, bushy habit, with long tubular zooecia diverging at their openings from the axis, and globular gonozoolid chambers at intervals.
Stony corals (Scleractinia) are for the most part 'hermatypic' and maintain in their tissues light-demanding zoanthellae. There are a few corals lacking these symbionts, and living in dark or shaded sites. Such are the solitary corals Caryophyllia, or the bright orange cups of Tubastraea coccinea, found under boulders in Samoa. In similar places lives the mauve or orange Distichopora violacea, not an anthozoan at all, but - like Millepora - one of the calcified Hydrozoa. The boulder (page 123) shows two small colonies, branched in a single plane. They are related to the delicate pink shade-corals of the genus Stylaster.

Boulders and coral rubble are important resorting places for a wealth of mobile species. Their communities are also vulnerable to disturbance. They should thus be handled carefully and responsibly. Any boulder lifted up should be carefully replaced in its former position, with the light-sensitive species downwards, and taking care not to damage them by abrasion.

Of all the mobile species under boulders, the most highly-prized items to collectors have probably been the small gastropods, with the finely patterned cowries (Cypraeidae) outstanding among them. All their species are today sensitive to over-collecting. In the most accessible Samoan reefs, they have already been stripped to low numbers. The commonest gastropods left under most boulders are the small yellow and black-banded Engina maculata and Caenartus plagiatus (Buccinidae) and the tiny umbrella-shaped whelks of the genus Pyrgula (Columbellidae). Larger and equally typical boulder gastropods are the top shells of which the flat-based, conical Trochus maculatus is widespread in Samoa.
In the wider space beneath the edges, boulders harbour many sorts of Echinoderma. The highly toxic black *Diadema setosum* is perhaps the commonest. The risk from its long spines should be warning enough against any incautious exploring with fingers, before turning a boulder over. Amongst boulder starfish are the small, stub-armred *Narjoe* and *Fromia* species, prettily marbled with a mosaic of coloured platelets.

**CRABS**

Final mention must be made of the crabs, exploiting one of the most ubiquitous and successful designs for life under boulders. There are far more crabs than all the rest of decapod Crustacea together, and on tropical reef flats, and in rubble, they are diverse and abundant as in no other places. The family most numerous in species is the Xanthidae, consisting of round-fronted and rather short-legged crabs, on the whole slow-moving and recognised by the black fingers of their chelae. Their genera range from the large *Carphilus*, with the big, red-spotted *C. maculatus*, through smaller and variously coloured *Xantho*, *Liomera* and *Dafra* species, to those with special habits, such as the wide arm-stretching *Trapezia*, slipping smoothly between the branches of *Pocillopora* corals.

Almost as numerous as xanthids on tropical reefs are the small, brightly coloured porcelain crabs (*Porcellana*) and stone crabs (*Petrolithes*), distinguished from true crabs by the flexible abdomen, with its tail-fan retained, the long (second) antennae, and the third maxillipeds, fringed with setae for sifting particulate food from water currents.

Swift and spider-like in its movements under boulders, is the single grapsid crab common outside the upper shore, *Percnon planissimum*, with small flat carapace, and long spineless legs.

The reefs studied on Upolu were disappointing in their yield of crab species, evidently as a result the intensive gathering of small mobile animals as food, near the villages. From the more remote places still unransacked a good range of tropical species, especially xanthids, may be expected.
The principal families of crabs represented under coral, boulders and at the reef crest.
BIO-EROADING FAUNA

Coral boulders and rubble blocks present two sorts of habitat for 'sciaphilic' species: not only as we have been describing on the encrusted undersurfaces, but also sheltered from light and desiccation by boring into the calcium carbonate substrate itself. Of these penetrant species that erode coral rock, there are two habitat groups: those that actively bore by chemical or mechanical means, and those that nestle in and enlarge the primary spaces the borers have provided.

Dead coral is eroded principally by bivalve mollusces, sipunculids and polychaete worms, mostly, as shown on page 132, boring downwards from an exposed surface. In contrast the penetrant sponge Cliona celata erodes up into the rock from the shade below. Beginning as a scatter of yellowy pustules, Cliona finally aggregates into a thick mass deeply invading the calcium carbonate.

Of the bivalves boring coral, far the largest are the 'giant clams' of the family Tridacnidae, with the moderately small Tridacna crocea common through much of the Indo-Pacific. The principal Samoan species, T. maxima has become far less abundant today as a result of food gathering.
SCHEMATIC SECTION THROUGH MARGIN OF A DEAD CORAL BLOCK, SHOWING THE BORING AND NESTLING SPECIES INVOLVED IN BIO-EROSION

1) Lithoparella zitteli
2) Hyella formosa
3) Boggonia sp.
4) Anella sp.
5) An eunicean worm
6) Penetrant and cavity-forming sponge (c.f. Chlorides)
7) A serpulid hydroid
8) Cyrculus japonicus
9) Echinasteridae
10) Lamellicol of Eucalypitidae
11) Corallim
12) A branched cheilostome bryozoan (c.f. Margeyllal)
13) An ophiuroid
14) Hydroid colony
15) A zoanthid.
Attaching by a short, strong byssus to the coral rock sediments of the lagoon floor, it can excavate a shallow burrow by rocking the strongly sculptured shell.

Far more numerous in coral rock are the small penetrating ark-shell species (Arca), beginning their boring after attachment by the byssus in a shallow concavity, and enlarging this by abrasive movements of the shell. Fully embedded, an Arca can be detected from the hinge side with the spiral umbones flush with the surface.

Generally the most abundant bivalves in coral rock are the date mussels, able to be located by the key-hole shaped openings of their vertical shafts, outnumbered only by the small holes bored by sipunculid worms, each big enough to admit a pencil’s point.

The boring mussels are some of the most specialised of the Mytilidae. The thin shell is long, narrow and parallel-sided. The mussel is secured to the wall of the burrow by a set of byssus threads, radiating fore and aft. The two pedal (= byssal) retractor muscles, alternately pull the shell forward and draw it back from the head of the boring. Mussels of the genus Botula, with stronger shell sculpture, may in this way bore mechanically in non-calcareous rock as well as coral. The Lithophaga species, the ‘date mussels,’ properly so-called, bore chemically, living only in calcareous rocks, and dissolving calcium carbonate by acid secretion from the anterior edge of the extruded mantle, as the valves gape in front. Lithophaga zitteliana, smooth with a thick white calcareous crust, is the commonest Samoan species. This bivalve has a shining brown periostracum, and the shell has a light sculpture that may augment the primarily chemical boring with mechanical erosion.
Bivalves boring in dead coral. (a) _Lebophaga zitteliana_ and (b) _Roccellaria cuneiformis_, showing schematic section, intact shell, and cross section of boring.

The burrow of a date mussel is heart-shaped in section, showing there is no shell rotation. By contrast, the boring of the small bivalve _Gastrochaena_ (= _Rocellaria_) is perfectly circular, with a narrow cylindrical neck for the siphons.

The anterior end of the shell gapes widely as with a piddock shell (Pholadidae), and the circular foot takes a hold of the burrow wall at this point, while the shell, twisted alternately in each direction, abrades the rock by its sharp sculpture.

The bivalves of the genus _Isognomon_ are nestlers rather than burrowers, like little flattened cornets clustered together, byssus attached near the apex, and distorted according to the shape of their crevice.

**SIPUNCULA**

Of all the bio-eroders, by far the most numerous are the non-segmented worms belonging to the small phylum Sipuncula. Their small circular holes increase in density from the mid-eulittoral down. Any broken section of rock will display a profusion of sipunculids in their shafts. For a proper study, the different species can be isolated by digestion of a rock sample in alcohol with 10% added hydrochloric acid, leaving the inhabitants intact.

The body of a sipunculid worm is muscular walled, rubbery in texture, with neither segments, nor limbs. The epidermis is scattered with microscopic chitinous spines, considered to have
an abrasive role. There are in addition epidermal glands whose secretions may have the role of dissolving calcium carbonate. The details of the boring mechanism are not yet, however, fully clear.

Sipunculids of the family Aspidosiphonidae are equipped with horny opercular shields. In Aspidosiphon and Paraspidosiphon, at either end, in others only at the head. In Lithacrosiphon, the operculum is a conical cap, in Cloeosiphon a complex of platelets perforated by the proboscis through its centre.
All the sipunculids are microphagous feeders, gathering particles from the surface. In Aspidosiphonidae, a tubular proboscis is rolled out from the mouth, over the burrow rim, everted like a finger in a glove. Rows of microscopic denticles on its distal part act as abraders like a mollusc’s radula. In Phascolosoma, by contrast, particles are taken up by the short ciliated tentacles that fringe the tip of the everted proboscis tip.

At the lowest shore level, rock-boring polychaete worms of the phylum Annelida, especially the Eunicidae, commingling with the sipunculids, riddling the rock mass in every direction. Eunicids are often brightly-coloured, and they include in Samoa the famous ‘palolo’ worm *Eunice (Palolo) viridis*. The numerous eunicid species are distinguished by their colour patterns, and the details of the jaw armature. The head tentacles are five in number, two pairs, with a single median.

Other polychaete worms (Phyllodocidae, Syllidae and Nereidae, also Doddoceredia (Cirratulidae)) will be found abundantly boring or nestling in coral rock.

Disused borings harbour several species of gastropods, and also the narrow-bodied chiton, *Cryptoplax japonica*, with its shell valves almost completely buried in the stiff girdle. There may too be scouring urchins, *Echinometra mathaei*, as well as ophiuroids extending serpentine arms to catch food, for example *Ophiocoma* and *Ophiactis* species.
SOFT SHORES

Accumulating shores, where fine sediments have built up beyond the capacity of the waves to carry them away, are not well-represented around the steep volcanic coasts of Samoa. We cannot yet claim to have studied the local examples thoroughly.

Of the broad, level flats of fine, silt-mixed sand, built up behind the shelter of the reef, the best and most accessible example is at Mulivai, on the south coast, in front of the Hide Away Hotel complex. This is the typical habitat of the majority of the heterodont bivalve species mentioned in this book. Digging and sieving, or searching the surface with a light at night, will also produce examples of those burrowing neogastropod and mesogastropod families recorded here. Common among them will be species of the Strombidae, Naticidae, Cymatiidae, Mitridae, Turridae, and Conidae.

On the north coast, near Apia, a still more sheltered flat is situated within the reef fringing the Muliniu’u Peninsula. Here species of Nassariidae abound, and acorn worms or balanoglossids (primitive hemichordates) may be found. A large number of the soft shore molluscs recorded in the Upolu check-list came from here. Of particular note is the smooth, thin-shelled strombid Tercebellum tercebellum, highly adapted for burrowing in sediments.

HEMICHORDATES

Coiled sand-castings crumbling into conical mounds betray the presence of hemichordates, early worm-like associates of the phylum Chordata. They are technically three-segmented, with proboscis and collar and a long, hind-body lacking any further subdivision. Hemichordates are deposit feeders from the sand surface, but can also filter a stream of particles by the passage of water through gill slits suggestive of those of chordates.

Two quite distinctive genera of hemichordates are found in the tropical Pacific. **Balanoglossus** (an ‘acorn worm’) with a short conical proboscis has the body behind the collar drawn out in yellow ‘genital wings’ with hepatic sacs emergent from the hind-body further back. **Saccoglossus** by contrast has a long cylindrical proboscis, and lacks genital wings and hepatic sacs. Much interesting work awaits a student of the biology of the Samoan hemichordates.
The location of the sand-silt intertidal flat within the protection of the reef at Mulivaal, opposite the Hide Away Hotel.
Our survey of the classification and families of molluscs must be kept to short compass; but will include most of those prominent gastropods and bivalves the ecology student will be concerned with.

**ARCHAEOGASTROPODA**

The first order of the gastropod class PROSOBRANCHIA, the ARCHAEOGASTROPODA, consists of grazing herbivores, essentially primitive in structure, belonging to hard intertidal shores. They originally had two bipectinate gills retained in the Fissurellidae and Haliotidae, (neither family common in Samoa) but reduced to one in the Trochidae, Turbinidae and Neritidae, and replaced by secondary pallial gills in patelid limpets. Fertilisation is external, with a long larval life.

Of the two largest families, the TROCHIDAE, or top-shells, are essentially conical, with horny circular operculum; and the TURBINIDAE, or turban shells, have rounded whorls, and a convex shelly operculum.

Where surge breaks over the reef front, the stream-lined archaeogastropods come into come into prominence with the limpet families, PATELLIDAE and ACMAEIDAE.

A notably important family in the tropics, on the upper shore and splash zone, is the NERITIDAE, advanced upon all other archaeogastropods in the achievement of internal fertilisation. Small egg capsules are deposited under stones.

**AMPHINEURA**

1. *Acanthoconchus gemmata* L.
2. *Cryptoplax jacksoni* L.
3. *Chiton* sp.
4. *Chiton* sp.

**GASTROPODA**

Family Patellidae
3. *Patella flexuosa* Quoy & Gaimard
4. *Cellana protaca* Powell
5. *Cellana radiata orientalis* (Plsburw)
Family Acmaeidae
Family Patellidae

A CHECKLIST OF THE COMMON INTERTIDAL AND REEF FLAT MOLLUSCA OF WESTERN SAMOA
(BASED ON A REFERENCE COLLECTION ASSEMBLED FOR FISHERIES DIVISION, DEPARTMENT OF AGRICULTURE AND FISHERIES, WESTERN SAMOA)
Family TROCHIDAE
1) Trachyrapana pricei (Lamarck)
2) Tegula hyperborea (Gmelin)
3) Tegula pristis (Gmelin)
4) Tegula maura (Gmelin)
5) Tegula gigantea (Linne)
Family STOMATELLIDAE
6) Stomatella quoyana (C.L. Adams)
Family PHASIANELLIDAE
7) Phasianella variabilis (Lamarck)
Family TURBONIDAE
8) Asreta sp. (Lamarck)
9) Turbo tectus Linné
10) Turbo pugilis Linné
11) Turbo decussatus (Linne)
12) Turbo tricinctus (Linne)
Family CYCLOSTREMATIDAE
13) Leiostoma pernix (Röder)
Family NERITIDAE
14) Nerita alba (Linne)
15) Nerita princeps (Gmelin)
16) Nerita tenuis (Gmelin)
17) Nerita nitida (Gmelin)
18) Nerita securata (Gmelin)
Family NERITOPSIDAE
19) Neritopsis sp.
Family LITTORINIDAE
Littorina (Littoraria) undulata Gray
Littorina (Littoraria) cocinea (Gmelin)
Littorina (Littoraria) scabra (L.)
Nodilittorina leucostica ferruginea (Reeve)

Family PLANAXIDAE
Planaxis lineatus (da Costa)
Planaxis sulcatus (Born)
Planaxis niger (Quoy & Gaimard)

Family MODULIDAE
Modulus testung (Gmelin)

Family CERITHIDAE
1) Cerithium abaco L.
   Cerithium abedius Hombron & Jacquinot
   Cerithium columna Sowerby
   Cerithium crinatum (Lamarck)
2) Cerithium modestulum Bruguere
3) Rhinoclavis asper (L.)
4) Rhinoclavis stenalis Gmelin
5) Clypeorarbus moniliferus (Kiener)
   Clypeorarbus trilii (Sowerby)

Family VERMETIDAE
5) Dendropoma maximum (Sowerby)

Family VANIKORIDAE
6) Vanikorana canceleata (Lamarck)

Family HIPPOCIONIDAE
7) Hippocion conicus (Schumacher)

Family CULPYTRAIDA
8) Cylindrella equitris (L.)
MESOGASTROPODA

This is the largest, most diverse, and even heterogeneous group of prosobranchs. They begin with surface-scaping herbivores, the pedinulines of the LITTORINIDAE, typical of the upper rocky shore world over. Closer allied with them are the tropical families VLANAXIDAE and MODULARIDAE.

The large, principally tropical, family CERITHIIDAE are long-spined grazers herbivores. They are represented by small Cymatium species on rocks, and in rubble by larger Cerithium. Rhinoclados includes smooth-shelled burrowing cerithids, living in sand flats.

The cowries CYPRÆIDAE, are probably the largest family of reef gastropods, and one of the most colourful and attractive. They are grazers that crop short turfing algae, or sample a wide range of sessile animal foods. A host of small species is found under boulder and coral rubble; larger cowries dwell in the lagoon, or - with broad-based streamlined form - in crevices at the reef margin.

A cropping herbivorous mode of life is shown by a second large tropical family, the STROMBIDAE. These combine a diversity of highly ornamented shell shapes, with an ability for quick hanging locomotion performed by the foot and blade-like operculum. The large, long spined peduncle, are brightly enlarged. The Sanomam genera are the cow-cow shells (Scutum), garden shells (Lambis) and the smooth, spindly-shaped Terebellum.

MICROPHAGOUS FEEDERS

Among the CALCIULACEA, several mesogastropod families have become sedentary. The VAMBRONIDAE are the least modified, with Vampyra congesta still free-living on sea grass flats. The cap-shaped HIPPOCERIDAE attach to Turba and other gastropods, and some subsist on tunicate spicules. The CALIPTERAIDAE are tunic feeders, represented in Samoa by the circular Calista squamosa.

At some distance from these is the sedentary family VERMETIDAE, consisting of tubeworm-like mesogastropods modified as mucus-trap feeders on fine particles intercepted from currents. Derbifossa minutissima is the largest species, typically embedded in tubular tubes.

The long series of carnivorous Mesogastropoda begins with the nektonic shells and moon-shells, Natica. Confined to soft and sandy flats, they prey upon bivalves and other gastropods by boring their shells with the radula aided by salivary secretion. The smooth shell is encased by a piggy parapodia, and mantle, converting the stalk to a stub-like form.

A large and widespread assemblage of tropical predators, dwelling chiefly on sandy flats and subtidal sediments is composed by the TONNACEA. Of the four families, the CYMATIDAE or trumpet shells and the BURBOSIDAE or frog shells are the least adapted for burrowing, being found more in the lagoon, and in the reef lagoon. The largest cymatid Charonia tritonis feeds on crown-of-thorns starfish.

The borer shells (CASSIDIDAE) are large and smooth-shelled, with a wide foot, predating chiefly on echinoids, especially heart urchins. The large and heavy Cassis cornuta is subtidal, but the smaller borer shell Cassis compressa is found on intertidal sand flats.

The tum-shells (TUNIDAE) large, inflated and ovate, are thin, and are chiefly predators of holothurians. Tonna perfolia is common in Samoan.
Family CYPREIDAE

1) Cypraea annulus L.
2) Cypraea arabica L.
3) Cypraea argus L.
4) Cypraea canuta L.
5) Cypraea cribraria L.
6) Cypraea croa L.
7) Cypraea helvola L.
8) Cypraea isabellia L.
9) Cypraea longa L.
10) Cypraea mauritiana L.
11) Cypraea moneta L.
12) Cypraea nucleus L.
13) Cypraea spissa L.
14) Cypraea testudinaria L.
15) Cypraea vitellus L.
Family CASSIDAE
1) Cassis cornuta (L.)
2) Casmiria erinacea (L.)

Family TONNIDAE
3) Tonna perditia L.

Family CYMATIDAE
4) Charonia tritonis L.
5) Cymatium murex (Roeding) Cymatium nihoniacum (Roeding)

Family BURSIDAE
Bursa rubra (L.)
Bursa bufoidea (Gmelin)

Cassis cornuta with heart urchin

Charonia with Acanthaster

Tonna perditia with Holothuria
NEOGASTROPODA

This third prosobranch order takes in the wide range of whelks and whelk-like predatory snails, with representatives both on rocky seashores and soft flats. The MURICIDAE - their first family - are a huge tropical group, mostly predators on molluscs, and other shelled animals, including corals, that they bore for the entry of their attenuated proboscis. The flat, or low-pitched Drupa species, each with the mouth distinctively patterned and coloured, are muricids of moving water near the reef edge. The thiads (Thais, Cronia and Moneta) are more normally shaped and typical of the middle shore. Largest and most highly ornamented is the big murex Chitonus ramosus.

Derived from near the MURICIDAE are the MAGILIDAE, that have lost the radula to become sedentary actinorhizal predators upon coelenterates. The big onion-shaped Pupa rapa embeds deep in soft corals. Coralliophila makes scars upon Porites heads, and Quoqua frequents Montipora.

The BUCCINACEA, which do not bore their prey, are smaller, more mobile roving carnivores. A large and important tropical family is the NASSARIIDAE, agile, and prolific scavengers of dead remains, on tropical flats, fast-moving with their slender, very mobile foot. The COLUMBELLIDAE are more specialist predators chiefly found under coral blocks, along with snails of the BUCCINIDAE, including the black and yellow banded Enigma mendicaria.

The family MITRIDAE is one of the largest groupings of tropical neogastropods. Its members are divided between hard and soft shores, with the small smooth and wavy patterned Striateria typically of the rocky middle shore. The larger Mitra and Vestilium species burrow in soft flats.

The VASIDAE and FASCIOLARIIDAE are large-sized and active predators living under coral boulders, or sheltering in crevices at the wave-exposed reef edge.

Exclusively dwelling in sandy flats are the olive-shells, OLVIDAE, smoothly polished and fusiform, the shell covered when living with the parapodia, preceded in front by a semicircular head shield. Similarly large-footed for sand-dwelling are the sculptured and finely patterned harp-shells, HARPIDAE, represented in Samoa by Hapla amuretta.

The TOXOGLOSSA or "arrow teeth" have become distinct from other Neogastropoda by the peculiarity of their dentition. The earliest family TURRIDAE are sculptured somewhat like mitrids, mostly in sand and living sub-tidally. Typical of sandy intertidal flats are the long-spired auger shells TEREBRIDAE, brightly coloured and regarded as some of the most attractive shells by collectors.

The Toxoglossa reach their climax development in the cone-shells CONIDAE, all active predators on live prey, which is stalked and secured by the discharge of a barbed radular tooth that conveys a neurotoxic saliva, like a poisoned harpoon. The widest mouthed and largest cones (Conus geographus, C. textilis and C. striatus) attack small fish, over sand or rubble flats. Smaller and narrow mouthed are the verrucose or worm-feeding cones, of intertidal reefs, such as C. obliquus and C. pulicaris.

Conus striatus with blenny
Family BUCCINIDAE

Cantiana fucosus Dillwyn
1) Cantiana undosa (L.)
2) Enigea mendicaria (L.)

Family NASSARIDAE

3) Nassariopsis alboconus alboconus (Dunker)
Nassariopsis auriculatus auriculatus (L.)
Nassariopsis globosa (Quoy & Gaimard)
4) Nassariopsis hornitus (Dunker)
Nassariopsis quadrafas (Hidalgo)

Family FASCIOLARIIDAE

Eiociastra (Pleurocladia) filamentosa (Roeding)
Latirus truncatus (Gmelin)
Latirus irus (Lightfoot)
5) Latirus squamosus (Reeve)
Latirus polygonus barclayi (Reeve)
6) Latirus (Galaxidea) amargatus (L.)
Peristeria nasatula (Lamarck)
Peristeria ustulata Reeve
Peristeria fastigium (Reeve)

Family VASUDEAE

7) Vasum ceramicum (L.)
8) Vasum tunbrinckii (L.)

Family COLUMBELLIDAE

9) Pyrene scripta (Lamarck)
Family MITRIDAe

Mitra glabra imperialis Roeding
Mitra mitrella mitrella (L.)
Mitra mitrella exigua (Link)
Mitra subulata eburnea Lamarck
Mitra subulata crocea Lamarck
Mitra spratula colombianus Reever
Mitra spratula truncata Lamarck
Mitra spratula spratula (L.)
Mitra spratula subulata Reever
Mitra spratula auriculata (Koenen)

Family OLYMIAe

5) Olyra auricula (Goelechi)
Olyra carinula (Roeding)
Olyra nucula Roeding

Family HAREVIDAE

6) Haresia auricula Roeding

Family TEREBRIDAE

7) Terebra albula Gray
Terebra auricula (Link)
Terebra africana L.
Terebra hypostoma L.

Family TURNIDAE

8) Lophotoma acuta (Perry)
Family CONUS

Conus catus (Hwass)
Conus coronatus Gmelin

1) Conus erinaceus L.
Conus geographicus L.
Conus imperialis L.
Conus lividus Hwass

2) Conus litteratus L.
Conus marmoreus (L.)
Conus miles L.
Conus omalius Hwass
Conus pulchraeus Hwass
Conus retius Hwass
Conus spongialis Hwass
Conus striatus L.

3) Conus textile L.
Conus tulipa L.
Conus viridus Gmelin
Conus virgo L.
OPISTHOBRANCHIA

Of the opisthobranchs or sea slugs and their shell-bearing precursors, no adequate study has yet been made in Samoa. The shelled forms include ACTINONIDAE, with Fusa sulphurea, and the AYIDAE and BULLIDAE. The APhYIDAE are known in Samoa by the heavy, high-built Dolabella auricularia, found on algae-covered rubble.

The SACOGLOSSA, sap-sucking, sap-feeders upon green algae (Chlorophyceae) have been found represented by Plagiomphalus. A search for their smaller species amongst Caulonema at the reef face could be richly rewarding.

The nudibranch slugs of the reef flat and lagoon also deserve early systematic study. Colour photography from ice and observation of habitat and habitat should form an essential part of data-collecting. The rose-coloured, intermittently swimming Hexabranchus angustifrons is the largest and most spectacular of all tropical reef slugs.

Very different reef building nudibranchs are the tropical PHYLLIDIDAE, distinguished by their stiff texture and black and yellow colour. Locking both jaws and radula, they are sap-sucking, evidently feeding on sponges.

PULMONATA

The chiefly terrestrial gastropods, the air-breathing Pulmonata, have three notable upper shore families, all important in the tropics. The SIPHONARIIDAE are secondarily converged to upper shore limpets, almost entirely replacing prosobranch true limpets on some tropical shores. The BULLIDAE, perhaps the most primitive of pulmonate families, span the shoreline from splash line (with Melanopsis) to fully terrestrial (Pyramidula). Cassidae and Ancylidae are typical under stones and rubble on mangrove flats. Entirely slug-like, with the shell lost, are the rubbery upper shore 'slugs' of the family ONCHIDIDAE.
Family ACTEONIDAE
1) Parcae subaeolata (Gmelin)

Family AXIDAE
2a pp

Family BULLIDAE
2) Bulla truncata Gould

Family APLYSIDAE
3) Aplasia auricularia (Lichtenf.)

Family PLACOBANCHIDAE
4) Placobanchus coccineus van Hasselt

Family HEXABRANCHUS
5) Hexabranchus saugus (Ruppell & Leuckard)

Family PHYLLIDAE
6) Phyllidia varicosa Lamarck

Swimming posture
PULMONATA

Family ELLOIDAE
1. Melampus parvus (Gmelin)
2. Melampus parvus (Müller)
3. Cepaea nemoralis (Gmelin)
4. Cochlicopa golosa (Quoy & Gaimard)

Family SIPHONARIIDAE
5. Siphonaria normalis Goid
6. Siphonaria atrita Quoy & Gaimard

Family ORCHIDACEAE
5. Orchidaceae sp.
BIVALVA

Family ARCIDAE
1) Anadara antiquata (L.)
   Arca ventricosa Lamarck
2) Arca sp.
   Balanites cruciata Philippi

Family ISOGONOMIDAE
3) Isognomon acutirostris (Dunker)
   Isognomon perna (L.)

Family PINNIDAE
4) Pinna muricata (L.)
5) Stroustrupia sacattata (L.)

Family MYTILIDAE
6) Modiolus arenatus Iredale
7) Lithophaga zelatiana Dunker
    Lithophaga c.f. curta (Lischke)
    Botulinia corallophila (Gmelin)
BIVALVIA

While the gastropods are most widely and diversely adapted for life on rock and coral, with rather fewer families in soft substrates, the burrowing habits of sand or silt flats, has become the leading way of life among the lamellibranchs of bivalves.

At the outset of bivalve evolution however, a number of families became specialised by attachment to rock by a byssus or cementation to hard surfaces.

Of the ancient family ARCIDAQUE, Acanthocardia longirostris burrows in muddy flats. Ustilago tripus attaches by a long byssus fringe beneath boulders, and small species of Arca with coiled umones left visible erode into burrows in dead coral.

The MYTILIDAE or mussels, not numerous in species in Samoa, have acquired an anti-sympitent condition, with the anterior adductor muscle reduced and the shell attached by byssus threads. Modiolus subtruncatus is the commonest rock-attached mussel in Samoa. The Lithophaga species, as well as Potamilla carinata, has already described burrowing into dead coral.

Superficially like mytilids are the fan mussels or PINNAEAE, with lightly calcified shells and weak hinge, opening by the hinge at the posterior end. Perna navicula burrows in and, with byssus threads attached to separate grains. Streptonicia obscides is a fragile, tubular shell, wedged into crevices.

Equally thin and fragile are the wafer-like shells of the ISOCOMONIDAE, easily distinguished by their straight, many-toothed hinge. We have seen Isocomum agullosorum as a common zonate bivalve of the upper to middle shore.

The pearly 'oysters' or PTERIIDEAE have - like the sugomenoids - reduced the adductors to a single central muscle. Pinctada species lie heavy and recumbent on the bottom, but have a small byssus issuing from a shell-notch. The same attachment is retained in the earliest scallops, the fan shells of the genera Chama and Choromytilus, not found in Samoa - has lost the byssus to become free-living and propelled by water expulsion.

The related family, the LIMIDAE or file shells, retain a byssus in which the shells often nest, and can also progress by the extrusible tongue-like foot, as well as by water jets, emitted by fast shell closure as in scallops.

The SPONDYLIDAE, including the large 'oyster' Spumellus fucalis, are pelecids that have become heavy-shelled and completely cemented to a hard base.

The true oysters OYSTERIDAE have carried cementation to an ultimate degree, with the loss in the adult of any trace of the foot. Superficially like oysters, but evolved from free-living siphonate bivalves at a somewhat higher level, are the CHAMIDAE, attached by the right valve to which the left - generally smaller - forms a lid. Chama pacifica is a common zonate species in the lower estuaries.
Family PECTINIDAE
1) Chlamys squamosa (Gmelin)
   Comptopallium podula (L.)

Family SPONDYLIDAE
2) Spondylus ducalea Roeding

Family LIMIDAE
   Lima lima vulgaris (Link)
   Lima c.f. fragilis (Gmelin)

Family OSTERIDAE
   Crassostrea sp.

Family PTERIDAE
3) Pectada margaritifera (L.)
   Pectada maculata (Coudin)
SAND-BURROWING BIVALVES

Belonging to the large assemblage of the HETERODONTA, these are the most modern of the bivalves in their style and habit, generally burrowing with a long foot, and having the posterior mantle margin produced into two siphons. Both anterior and posterior adductor muscles remain, of approximately equal size.

Clean sandy shores, in the mid-tidal zone, have two small, extremely common bivalves, smoothly wedge-shaped and rapidly burrowing in clean, waterlogged sand. To the DONACIDAE belongs the polished *Donax cuneatus* and the MESODESMATIDAE are represented by the lightly sculptured *Ataciodes striata*.

One or two families of heterodont bivalves are reef-dwellers, such as CARIDITIDAE, with *Cardita variegata*, a small "mutilised" shell, byssus-attached, and derived from ockle-like *Venericardia*. The rock-dwelling TRAPEZIIDA have become similarly modified towards a "mussel" form.

Foremost in numbers among the sand-dwelling heterodont bivalves in the tropics, are the "venus-shells" (VENERIDAE), strong and porcellaneous and generally concentric sculptured. The siphons are short and separate. The *Perigorgia* species are the largest and heaviest, rounded and strong-sculptured. *Ptilia*, *Oxyodonta* and *Lioconcha* are smoother and lighter. Of the more rectangular species, those of *Tapes* are rather smooth, while mud-dwelling *Gastrochaenidae* are strongly sculptured. Notius *macrophylus* with sharp-concentric ribs, nestsles in holes in coral rock.

With its lack of sedimentary rocks, Samoa has no pholad or piddock species; but their habit is represented by *Rocella*, (family GASTROCHAENIDAE) which we have noted already as a borer in dead coral.

The important tropical superfamily LUCINACEA exploit a very different burrowing habit from the venus shells. The LUCINIDAE, represented by *Codakia punctata* have a single (concentrically contractile) exhalant siphon, and a ventral foot, very exterhate that makes an anterior inhalant siphon leading from the surface. *Aplodonta* (family UNGULINIDAE) has a thin, smooth, spiral shell, and lacks siphons.

In the TELLINACEA, the two siphons are highly developed for the habit of deposit-feeding. The long inhalant siphon - like an animated vacuum-cleaner - sucks fine surface detritus, conveyed direct to the labial palps, with the suspension feeding role of the ctenidium greatly reduced. The *Psammobiidae*, represented by *Asaphus* and *Gari*, share this same deposit-feeding habit.

The CARDIACEAE include two sorts of tropical bivalve, superficially very unlike. The true cockles CARDIIDAE - live in sand, being short-siphoned but having a long and muscular foot. Common Samoan species are *Prangium frigum* and *Vasticardium pulcarium*.

From sand-dwelling forerunners near to the cardids the TRIDACNIDAE or giant clams have been derived. The diagrams show how their symmetry and organisation plan have been fundamentally altered, with the umbones and hinge migrating to the lower side where the foot with its byssus (in *Tridacna*) still emerges. The up-facing dorsal side has the gape, filled with highly pigmented and hypertrophied lips of the exhalant siphon, carrying in their tissues the symbiotic photosynthetic algae maintained by the tridacnids. The heavy horse-shoe clam *Hippopus* lives free with the byssus lost and its exit gape closed.
Family VENERIDAE
1) Litoconcha castrensis (L.)
2) Litoconcha fastigata (Sowerby)
3) Pilar obliquatum (Hanley)
4) Glycyodonta marica (L.)
5) Pteropoma petersery (L.)
6) Pteropoma reticulata (L.)
7) Calpurnia longicosta (Roeding)
8) Calpurnia pectinatum (L.)
9) Tapes (Diatrape) philippinarum (Adams & Reeve)
10) Natica macrocephalus (Deshayes)

Family GASTROCHAENIDAE
8) Rociobera cuneiformis (Spengler)
Family DONACIDAE
1) *Donax* latoni *cuneatus* (L.)

Family MESODESMATIDAE
2) *Ataelesca striata* (Gmelin)

Family CHAMIDAE
3) *Chama pacifica* Broderip

Family ERYCINIDAE
   *Lasaea rubra* (Montagu)

Family CARDITIDAE
4) *Cardita variegata* Bruguier

Family TRAPEZIDAE
   *Trapezium bicornatum* (Schumacher)
Family TELELIDAE
Tellina (Tellinella) staurella (Lamarck)
1) Scutacopagia scrobicata L.
2) Quinquelongus palatum Lacedale

Family PSAMMOBIIDAE
3) Asaphis violacens (Forskal)
Gari truncata (L.)

Family LUCIDAE
4) Codakia punctata (L.)

Family UNGULIDAE
5) Anodonta edentula (L.)
Family CARDIDAE
1) Frasum frasum (L.)
2) Vasicardium pulchrum (Reeve)

Family TRIDACNIDAE
3) Hippopus hippopus (L.)
   Tridacna maxima (Roeding)
   Tridacna squamosa Lamarck
4) Tridacna crocea Lamarck
REFERENCES FOR THE MOLLUSCA


What counsels can a New Zealand visitor be allowed to utter about the care of Samoan reefs and shores? Not much by citing examples from a developed world, that has palpably mis-managed its own natural environment, or in speaking to a country where the reefs and the foods gathered from them are such a traditional support for a subsistence economy.

For this is the first fact to underline: the value of the reef as a high priority resource, along with the rain forests, Samoa’s prime endowment. Today, almost everywhere on Upolu, the forests are in good shape, and largely intact. It is the reefs that have visibly suffered damage.

At one time the fish and reef fauna of Samoa was regarded as one of the richest on the globe. Kramer in 1888 could write ‘naturally, there are fishes throughout the whole year, for the seas is as inexhaustible as the land.’ Lui Bell, Senior Marine Biologist for the Samoan Government, in his informative paper “Coastal Zone Management in Western Samoa” makes it clear that this is no longer true today, and that a leading policy priority for the Samoan nation must be to protect and conserve the precious resource that is the coastal environment. To this paper, and Mr Bell’s ready help in discussion and advice upon reef conservation, I owe most of what it has been possible to write in this Section.

**TRADITION & HISTORY**

Bell (1985) has surveyed the traditional dependence on the reef, for a subsistence economy, by a people of inshore fishermen and gleaners, as well as ocean fishermen.

In the ‘Iales of the Navigators’ it was the waters within the reef that yielded the main seafoods on which a majority of the Samoan people relied for subsistence.

With the reef still a main subsistence resource today, the traditional methods of fishing, described by Buck (1938) (quoted in Bell): groping with bare hands, snares, lures, weirs, dams, fish-spears, poisoning, nets, hooks, etc, have given place to more modern procedures: diving with goggles and steel hooks, or using a mechanically propelled or hand-thrown spear, or by gill-netting and fencing using chicken wire.
Almost everything from the sea,' - it can still be said 'is taken regardless of its size. The fish catch includes lagoon and reef species but mainly mullet, small snapper, scad and surgeon-fish, while invertebrates include a variety of bivalves, snails, holothurians and jellyfish.' Seaweeds are also taken.

With Samoa's small EEZ, large-scale commercial fishing must still be of questionable feasibility. There is, however, small-scale fishing inshore, based on one or two canoes, with fence-traps or gill-nets.

Traditional wisdom must have understood pretty well at the level of the village (nu'u) how to conserve the fishing resource of the reefs. In Samoa, humankind have for long centuries been one of the species existing in and alongside the reef ecosystem: indeed one of the determinant factors of the reef's ecology. In their historic attachment to the reef, the village people (a nu'u) have pitted their skills against it in exploiting it for food. In the old days, the adjacent village owned and enjoyed customary fishing rights to all the space lying between mean high-water mark and the wave crest at the outer reef edge.

This lagoon was not only a traffic route but was the traditional fishing ground. Like all the land surface, its ownership was in either the adjoining village community or certain families and titles (suafa), and offences against the laws were punished by the local assembly. Within a village there may have been numerous fishing grounds, each with an owner.

In a paper written by W. von Bulow in 1902, it was noted that fishing rights entitled the owner to fishing on his traditional ground, and to the piling up of coral and stone heaps as hiding places for fish, as well as the setting of any number of fish and crab traps. The corresponding duties of any owner of a fishing ground included traditionally:

(i) to turn over the catches of certain large fish (and these included turtles 'laumei') to the village assembly or - in some villages - to particular chiefs.

(ii) following the orders of the village, to desist for a period from catching such fish as atule (south sea herring), so as to prepare for the catching of this fish by the large drag-net (laulos).
(iii) to observe the ritual closing of a fishing ground as forbidden (sa) as after the death of a high personage.

(iv) to allow his own or a neighbouring village to cast the large drag net, but without searching through the stone-heaps he had set up for himself.

(v) to allow the crossing of his fishing ground by anyone, by day or night, dragging a fishing lure ('pa').

Fishing rights outside the reef, records von Bulow, were open 'to the ends of the world' (eastward to Tutuila and Manua, north to Toelau, to the Uea and Viti in the west and to Faga mamo in the south), but still subject to valid rules, as in respect of shark-fishing (lepa malae) and bonito fishing (alo atu). In 1902 on the island of Savai'i, the old fishing customs still continued in their purest form, with the boundaries of fishing rights least obliterated and 'the effort and joy in fishing are still most pronounced.'

Already on Upolu, however, infringements into fishing rights were being acutely felt. Depredation and impoverishment of the reef, which traditional fishing methods had avoided, was now to come not by harvesting but from raiding and exploiting, by means no longer ecological or even rational. Like the methods of total warfare, they may wipe out everything, far beyond the target species, and may poison or disrupt a habitat into the distant future, by destroying its breeding places and its ability to reproduce.

Under old tradition, the fishing grounds - like any other valuable property - were protected by customary law. Old understanding - well down into the 20th century - vested the lagoon, and the responsibility for its conservation, in a village or a high-ranking chief. During most of this century, and particularly on Upolu, the growth of the wage economy has loosened the old and often exclusive dependence on a subsistence living from the fishing grounds.

Today's Constitution of Samoa has vested all the area below high water mark, including the reef, with its lagoon and seaward edge, in national ownership. Under Samoa's Land Ordinance (secs. 25 and 26), the Land Board - with the approval of the Minister of Lands is given a primary jurisdiction, in association with other government Departments, in any works on public land, including that below high water mark. As could -
be expected, this has loosened control by the villages, and weakened conservation initiative. What has been assumed by the state at large is no longer felt to need the particular oversight of any authority at village level.

Such disruption of traditional responsibility, with central government still ill-equipped to take it up, comes at a time when the reef environments are under heavy threat.

**PRESENT DANGERS**

In listing the exploitation pressures suffered by the reefs today, Lui Bell ranks fishing by the use of dynamite as the greatest present threat to the marine environment of Western Samoa. Reported by von Bulow from 1902 this is still widespread, as described in detail by Johannes in 1982.

Of the two methods at present used, the first involves throwing dynamite from a boat at free-ranging fish schools (notably mullet and scads) in mid-water. Three to four sticks are usually used. Matches are taped to the fuse and lit with a cigarette. Sometimes chopped up fish is used to lure schools near the boat. The second method is used for bottom fish and employs a larger charge (eight sticks), wires and a detonator cap. The charge is placed by a diver on a coral head - the wires leading from the charge 'to the boat are usually covered with sand for a distance of 10 to 20m from the charge. Four torch cells in the boat provide the power to detonate the blast.' This last type is the worse of the two because it inflicts considerable damage on the marine environment.