

Geology of Saipan

Mariana Islands

Part 4. Submarine Topography and Shoal-
Water Ecology

GEOLOGICAL SURVEY PROFESSIONAL PAPER 280-K



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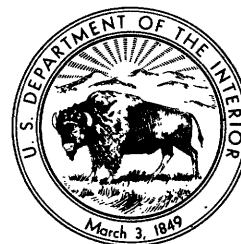
Mariana Islands

Part 4. Submarine Topography and Shoal-Water Ecology

By PRESTON E. CLOUD, Jr.

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Description and interpretation of the submarine topography and of the sediments, biotas, and morphology of the reef complex adjacent to a geologically diverse tropical island



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Geology of Saipan, Mariana Islands

Part 1. General Geology

A. General Geology

By PRESTON E. CLOUD, Jr., ROBERT GEORGE SCHMIDT, and HAROLD W. BURKE

Part 2. Petrology and Soils

B. Petrology of the Volcanic Rocks

By ROBERT GEORGE SCHMIDT

C. Petrography of the Limestones

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Part 4. Submarine Topography and Shoal-Water Ecology

K. Submarine Topography and Shoal-Water Ecology

By PRESTON E. CLOUD, Jr.

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GEOLOGY OF SAIPAN, MARIANA ISLANDS

SUBMARINE TOPOGRAPHY AND SHOAL-WATER ECOLOGY

By PRESTON E. CLOUD, JR.

ABSTRACT

The topography of the sea floor within 10 miles of Saipan broadly resembles that of the land. Eastward, toward the Mariana trench, slopes are about 6°, without prominent benches or scarps. This is inferred to indicate easterly continuation of generally pyroclastic bedrock. The westward slope averages 2° to 3° and consists mainly of nearly flat benches and west-facing scarps. This is taken to imply westward continuation of a limestone bench-and-fault-scarp topography. Projection of known faults to sea and through Tinian, on the basis of topographic trends, suggests a pattern of west-dipping normal faults that parallel the strike of the Mariana ridge and affect the shape and position of islands at the crest of the ridge.

Effects possibly attributable to gravity slides and density currents are briefly discussed. Laulau bay may be the scar of a sea slide (or slides) that dispersed a large fraction of its load through translation to a density current at depth.

The broad subdivisions of the local marine environment include shoreline, barrier reef lagoon and contiguous fringing reef moats of the western shore, organic reefs, and sea floor beyond the peripheral reefs. The organic reefs are especially important because their biota and the sediments derived from them strongly affect all adjacent habitats. The principal organic communities are those of rocky shores, sandy beaches, bare to sparsely vegetated sandy bottom, sandy bottom with abundant seaweed, gravelly bottom, and submerged organic reefs and coral-algal rock. Intergrading and interspersal of these communities and habitats result in a variety of associations that are described as 16 shoal-water biotopes and several shoreline environments of comparable status.

The average median diameter of 64 random samples of mainly calcium carbonate sediments is 0.63 mm, and the average Trask coefficient of sorting (S_o) is 1.7. Half of the samples have S_o between 1.5 and 2.0, with nearly symmetrical regression. The finest grained and best sorted sands include bar sands, and one sample just below the reef front. The coarsest grained and poorest sorted sediments sampled are very shallow-water sand and gravel. Other relatively coarse sands, principally of *Halimeda* joints, are concentrated in the deep part of the lagoon entrance.

Depth of water and physical nature of the bottom controls seaweed growth, which is important in the general nutrient system.

The reef complex can be described in various ways, which find a common denominator in terms of its nutrient chains and their disintegration products. This leads to review of some distinctive organic associations and adaptations, and to consideration of some problems of biotal distribution. The wide range of many benthonic species, even across great oceanic depths, invalidates geographic distance as a guide to specific distinction and emphasizes the need for care in the analysis

of barriers and migration routes. The common association of several morphologic species of the same genus under generally similar habitat conditions is also considered. The implied absence or low level of competition is probably explained by different food (energy) sources or different feeding habits between otherwise prospectively serious competitors. In addition, the magnitude of the habitat variations that may provide suitable niches for specific differentiation is directly related to the size and motility of the organism. Microenvironments of importance in the speciation of small organisms may be much too refined to map or even to detect by the field methods employed.

The lagoonal sediments and those that come to rest on the outer slopes of the reef are properly a part of the reef complex. These sediments consist preponderantly of biogenic calcium carbonate that owes its particulate nature to a variety of factors. A prominent fraction is of direct organic origin, *Halimeda* joints and Foraminifera being conspicuous contributors. Much detrital sediment results from impact, abrasion, and hydraulic pressure, factors which are especially effective at times of storm and against reefs and sea level benches that have been weakened in advance of mechanical attrition by boring organisms. The mechanical sediments accumulate mainly on the outer slopes. It is estimated that on the order of 1100 to 1600 tons of calcareous detritus per square mile is added annually to the sediments of the principal lagoon area of Saipan from the excrement of fish that browse on filamentous algae on coral-algal rock or on living calcareous algae or coral—a rate of accretion, assuming no transport, of perhaps 0.2 to 0.3 mm per year. Total fall of sediments in the shoal areas from all causes is probably three or more times this rate, but actual sedimentary accretion depends on entrapment or subsidence, and much of the sediment that falls is probably moved seaward to deeper waters.

Orientation of sediment trains and of growth features parallel to current flow is characteristic of the reef environment, especially adjacent to and across the crests of peripheral reefs.

Erosion in the intertidal zone is complex. The product is a nearly flat surface that terminates seaward at or near low tide level and implies processes mainly limited to the intertidal zone. Factors involved appear to include organic attrition and as yet not well understood solution effects. Organic growth at the reef edge sharpens the effect of abrupt cutoff at low tide level. Precipitation of calcium carbonate takes place in the intertidal and spray zones, causing local induration of beach deposits and cliff faces, cementing larger blocks to the reef flat, and probably contributing to the development of horizontal rims on paddy-like tidepool systems.

Variations in the characteristics of the reef flat and reef front depend on whether the surface is one of organic growth or erosion, whether it is backed by land or a lagoon, on the distribution and origin of radial grooves and spurs, on the kinds

of local reef-building organisms, and on local conditions of wind, tide, and current. The origin of some of the reef flat and reef front features is briefly discussed. Stress is placed on the significance of erosion in the primary origin of patterns seen. Inhibition of organic growth by outward moving sediment trains is also considered important, especially in maintaining and extending initially erosional patterns. Organic overgrowth has a conspicuous masking effect and at places has obliterated or supplanted erosional patterns.

In general terms the existing reef complex at Saipan between the shore and the outer slope is divisible into eight broad concentric zones that may be correlated in part with similar zones of other areas. In sequence from the sea shoreward these are reef front, peripheral reef flat, lagoon fringe of peripheral reef (or *Acropora palifera* zone), staghorn *Acropora* zone, offshore zone of accreting limesands with seaweed, lagoon proper, nearshore zone of reef clusters, and nearshore zone of limesands with seaweed.

The existing pattern is the temporary expression of a reef complex that appears to have persisted through much or all of Pleistocene time. The complexity of the whole can best be imagined in terms of probable fluctuations of facies boundaries that accompanied isostatic and tectonic shifts of sea level during that interval.

The basically erosional nature of most fringing reef surfaces is stressed. Over the reef complex as a whole, however, lateral growth of reefs and sedimentation in the interareas and beyond the reef front results in long-term accretion of the total constructional-sedimentary mass.

INTRODUCTION

PURPOSE AND SCOPE OF THE WORK

The Mariana ridge is scantily known from the few bits of it that extend as islands above the sea. Information about the adjacent submerged areas is even scarcer. Besides general bathymetry and occasional notes on the nature of the bottom, there are only a few preliminary gravity observations by Vening Meinesz and by Matuyama, as noted under "Regional geology" (Chap. A, p. 15-20). Extension of the regional deep-sea studies, and especially their geophysical aspects, although of great interest, requires special equipment and staff that was not available to the Saipan field party. There were, however, related investigations that could be made during the geological survey of Saipan because of the interest and cooperation of the U. S. Navy. The aim was to project the gross structural and lithic pattern of the island as far offshore as reasonable with the facilities available, and to study biologic and sedimentary processes and patterns that would aid interpretation of the paleoecology and evaluation of the sedimentary rocks ashore.

One part of this work involved study of the submarine topography within a radius of 10 miles of Saipan, and its interpretation in terms of the structural pattern revealed by detailed mapping ashore, and by analogy with subaerial land forms. The principal task, however, was an ecological and sedimentary survey of

the immediate shoal waters. The results of this work were applied to the interpretation of the elevated constructional and detrital limestones of organic origin in chapter A (General geology). They are described in the present chapter both because of their bearing on similar problems elsewhere, and in anticipation of a possible broader interest for ecology and paleoecology.

FIELD METHODS AND ACKNOWLEDGMENTS

For bathymetric studies Rear Admiral C. A. Pownall, then Commander Naval Forces Marianas, assigned Patrol Craft Escort 899, under the command of then Lt. J. F. Butler, to conduct a series of bathymetric traverses around Saipan in June 1949. This was done with a continuously recording echo-sounding fathometer, having a maximum sensitivity range of 2,000 fathoms. Traverses were made at a fixed speed along a selected straight line from or toward a point on shore. Fixes along these lines were taken by resection at regular intervals with an open-sight pelorus, the fathogram strip being marked the instant a fix was made. Skill and caution were called for on the part of Lt. Butler and his crew in approaching the reef and shore as closely as possible without running off-course or aground. The result was a series of sounding strips from which were plotted the eleven profiles illustrated in plate 120. Plate 121, the bathymetric chart, was prepared from the sounding strips along and between profiles, supplemented by hundreds of spot soundings and other data from all available hydrographic charts of the area. No bottom samples or hydrologic data were obtained in this part of the work.

Shoal-water studies were conducted at intervals between October 1948 and July 1949 from small craft of the U. S. Navy's boat pool at Saipan, on authorization of then Capt. G. M. Compo, Island Commander Saipan. Chief Bosn. F. X. Jozwick, in charge of the boat pool, assigned equipment and personnel for the work, instructed me in the use of diving apparatus, and personally directed operations whenever he could. A wherry equipped with plexiglass bottom ports was used for dry reconnaissance. A 40-foot, flat-bottomed personnel boat was generally employed for diving operations or for towline traverses where the observer, equipped with a glass face plate, was pulled slowly behind the boat at the end of a length of line. A radio-equipped crash boat was employed for binocular observation of cliff-coasts around Saipan and Tinian.

The direct observations in the shoal-water areas combined a series of reconnaissance runs with more closely located traverse lines and stations as plotted on plate 122. Reconnaissance runs were conducted either by the towing technique or from the glass-bottomed wherry.

The first method allowed wider and more selective coverage, the second was resorted to mainly for relief from salt-water exposure.

Lines of detailed traverse were selected on the basis of reconnaissance study. Such traverses were conducted from beach to peripheral reef by a combination of swimming and towing with face mask, skin diving, and diving with air-hose and light weights. Observations were made continuously for short stretches between convenient, characteristic, or especially interesting stopping points. Notes were dictated from the water to an assistant. Location was by Brunton-compass resection. At anchor points the bottom sediments were sampled and biologic collections were made from any masses or loose pieces of coral-algal rock nearby. Dredging was tried with locally constructed gear but abandoned as inferior to direct sampling by hand, using suitable equipment and containers.

Besides the readily visible and obtainable elements of the biota, records of the presence and associations of many secretive and inconspicuous animals were obtained by hauling aboard and breaking up large chunks of the living and dead coral-algal rock. A geologist's pick is excellent both for wedging such rock free and for breaking it up, and the samples are easily hauled to the surface by means of a perforated canvas bucket. The amount of work accomplished was greatly increased by the fact that Bosn. Jozwick took turn-about at diving, as well as by the assistance of volunteers in extracting, bottling, and labeling the biologic samples. The area of sampling and direct observation was limited to depths less than 60 feet.

SYSTEMATIC IDENTIFICATIONS AND OTHER RESEARCH AID

Study and accurate identification of collections by specialists is an indispensable part of ecology. In the present instance this was made possible by the generosity of individual systematists who donated their help, by the farsighted policy of the Office of Naval Research, whose supplemental grant to the Pacific Science Board paid for contractual services of others, and through the unfailing cooperation of the U. S. National Museum. Most of the material collected has been identified and is listed in: "Tabulation of animals and plants found in the shoal marine habitats of Saipan" (p. 416-441).

Names of the identifying specialists are given at the appropriate places, but it is emphasized that this report would not have been possible in anything like its present form without the work of these scholars. I mention with special gratitude the name of Frederick M. Bayer—an unstinting source of information on ecological oddities and unusual organisms.

The mechanical analyses of the sediments were made by standard methods—in a ro-tap machine nesting Tyler sieves, and employing Tyler's cumulative logarithmic diagram paper for records. Samples were run whole or quartered to the desired size and shaken for 20 minutes. Erratic large fragments were removed before sieving. Mrs. Esther Russell ran the mechanical analyses and prepared the cumulative diagrams, and Mr. R. E. DeMar computed the statistics for sizing, sorting, and skewness. The methods employed, and the significance of the data, are described by Twenhofel and Tyler (1941, especially p. 110-112) and by Trask, Hammar, and Wu (1932, p. 69-73).

For critical reading of various sections in draft I am indebted to Frederick M. Bayer, Fenner A. Chace, W. Storrs Cole, Robert M. Garrels, Joel W. Hedgpeth, conclusions reached are summarized in plates 120 and Wendell P. Woodring.

INTERPRETATION OF THE SUBMARINE TOPOGRAPHY

This section deals with the gross features of the marine geology along the crest of the Mariana ridge from Saipan to Aguijan, insofar as these may be inferred from submarine topography and observed features ashore. The data obtained and provisional conclusions reached are summarized in plates 120 and 121.

SIGNIFICANCE OF TOPOGRAPHIC CRITERIA

Although marine geology in the fullest sense employs all the available techniques of geomorphology, geophysics, and oceanography, only bathymetric data were obtained below depths of about 60 feet during these field studies. By analogy with land forms of known origin, however, reasonable deductions may be reached about probable relationships within the local range of structure and rock types.

Thus the two profiles off the east coast (pl. 120, profiles 10 and 11) slope rather uniformly 6°-7° eastward. In contrast the slopes of the western profiles average only about 3° westward, and they are interrupted both by abrupt scarps and by broad almost horizontal surfaces (pl. 120, profiles 1-8). The scarp positions tend to line up from one profile to another in a north-south to northeast-southwest direction.

This arrangement suggests that the submarine slopes to the east from Saipan are mainly pyroclastic sediments, which tend to assume an even and moderate slope under prevailing erosional processes. The alinement of scarp nicks toward the offshore ends of profiles 10 and 11 is the only suggestion of offshore faulting on the east side of the island. That this possible fault, if present, drops beds to the east is consistent with the

inferred coincidence between topographic and structural axes of the Mariana ridge.

The western slope, in turn, is so similar to the limestone terrain ashore that little imagination is required to visualize it as primarily an area of almost horizontal limestone benches, offset by fault scarps that have dropped bench segments mainly downward to the west. The generally gentle slopes and great width between the 300-foot elevation line and the 50-fathom depth line (pl. 121) in particular suggests origin through intertidal erosion, construction, or subaerial bench cutting for the several broad surfaces within this 600-foot interval.

Conspicuous channeling of the bottom to depths of 250 to 300 fathoms indicates the possibility of former subaerial erosion to such depths. However, some of the bottom irregularity may be the result of gravity slides and density currents, which would probably be favored in areas underlain by volcanic sediments. Volcanic bottoms in Saipan and Tinian channels and Laulau bay are implied by volcanic inclusions in beach rock and reef-rock adjacent to Saipan channel, and by volcanic outcrops adjacent to both Saipan channel and Laulau bay. Channel scouring or sliding of the volcanic materials may explain why there are no obvious places to project known and inferred faults across these areas. The absence of scarps and the presence of well-defined erosion channels at other places may also indicate volcanic bottom.

The differences in submarine slope from east to west sides of Saipan, although small, are apparently consistent. Thus only 10 miles offshore to the east the bottom is 1,000 to 1,100 fathoms deep, while at the same distance westward from shore the depth is only 550 to 700 fathoms. As the deep Mariana trench lies to the east of the island, it is not surprising that its eastern submarine slope is the steeper. At the same time, the differences in slope may result from differences in resistance to erosion of the rocks or sediments beneath.

INFERRED STRUCTURAL PATTERN

On plate 121 the inferred submarine fault scarps are shown, together with the known and inferred faults ashore; the latter are projected as far as there is reasonable topographic basis for their extension. The pattern so delineated is surely inaccurate in detail. Its broad validity, however, is supported by the general prevalence of westward downstepping along fairly straight lines that are approximately parallel to the northeasterly trending long axis of the submarine ridge from which the islands rise.

It seems probable that the location and gross morphology of the islands along this part of the Mariana

ridge is strongly affected, if not controlled, by a plexus of mainly west-dipping, high-angle normal faults and cross faults. The Matansa fault on the west may be a major structure along which both Saipan and Tinian moved upward to their present position. Only a short projection from its most southerly known position takes this fault southwestward along the abruptly straight stretch of reef south of the channel into Garapan lagoon, and this lines up with the straight and precipitous northwestern shore of Tinian. Northeastward the Matansa fault may be continuous with the Kalabera fault, but, as an alternative, it may trend along the northwest coast to follow the western crest of the Mariana ridge. Probably either the Achugau fault, or a branch of the Matansa fault does extend north of the Matansa-Kalabera fault junction.

The various other faults southeastward from the Matansa fault and its inferred extensions do not appear to have resulted in significant upstepping. They probably define blocks that have moved mainly by eastward rotation. Projection of two of these faults across Tinian is based on stratigraphy (Miocene and Eocene rocks stand above Pleistocene in the southeast peninsula of Tinian) and topography, but their movement may have been largely pre-Pleistocene and their actual traces are apparently in large part concealed beneath limestones of Pleistocene age. The Laulau bay fault marks the approximate eastern limit of the structural ridge-crest. Probably sliding has obscured the trace of this fault across the bay. The problematical east-facing fault 900 fathoms downslope could be extended southwestward along the southeast sides of Tatsumi reef and Aguijan to pair up with another hypothetical fault downthrown in the opposite direction. On the whole, though, the probability of a mainly pyroclastic bottom along the eastern slope severely limits the amount of structural detail that can reasonably be inferred for this area from geomorphic evidence.

Because the Mariana ridge is a volcanically and seismically active linear topographic high, it has been inferred to be geanticlinal by several geologists, including myself. Special note should be made, therefore, of the fact that there is nothing about the demonstrable local structure which, in itself, implies an anticlinal nature for the immediate environs of Saipan.

GRAVITY SLIDES AND DENSITY CURRENTS

It seems likely that gravity slides and density currents have been instrumental in transporting sedimentary materials and in shaping the bottom morphology about Saipan and Tinian, especially in the areas of pyroclastic sediments. Channel and spur topography in particular was studied for evidence that might indi-

cate such origin. However, above 30 fathoms, most of the submarine topography revealed by the depth interval at which contouring was practicable resembles that produced by normal subaerial agencies. To be sure, it may not have been subaerially produced, but there is no evidence to the contrary. At greater depths the information available suggests little topographic variety.

Although most of the shallow submarine topography probably results from drowning of subaerially produced features, one conspicuous feature may be in large part a seaslide scar. This is Laulau bay. The broad, crescent-shaped scar of the bay itself has the scooped-out appearance of a slide area, and geologic mapping ashore indicates that the upper bay-bottom is very near an eastward-dipping contact between the pyroclastic island-core beneath and overlapping limestones above—an excellent sliding surface. The large bottom depression surrounded by the 450-fathom (2,700-foot) contour interval at the entrance to Laulau bay suggests the unfilled remnant of an area in front of which sliding debris could have piled up. Relations to described geologic features indicate a pre-late Pleistocene age, but the preservation of the depression suggests more recent origin, and movement may have been recurrent. Evidence against the inferred slide, or for older age, consists of the fact that contouring (believed to be accurate at the scale used) has not revealed a large enough pile of debris in front of the 450-fathom depression to account for the total volume of the bay above this point. If this is not the result of inadequate bathymetry, it may indicate that high energy and low friction resulted in the slide being translated finally into a density current that spread its load thinly and widely downslope.

A comparable origin for other bottom indentations is not here argued, although any broad-headed submarine valley might have originated in this way.

SHOAL-WATER AND SHORELINE ECOLOGY AND SEDIMENTS

GENERAL SETTING, PROCEDURE, AND LIMITATIONS

In a general way Saipan exemplifies the isolated high islands of the tropical Pacific. Adjacent to it may be seen examples of a number of distinctive marine environments such as recur widely around such islands. A significant fraction of the distinctive species of plants and animals that live in these waters retain their identity from eastern Africa and the Red Sea to Hawaii, and across the deep water between (Ekman, 1953, p. 13-15), and a few are circumtropical (Ekman, 1953, p. 3-4, 41-42, 74).

Saipan itself lies in the belt of seasonal northeast trade winds and moderately high rainfall. Its narrow north end points obliquely into the north equatorial

drift current. Thus the local currents run from north-northeast to south-southwest on both sides of the island, and ordinarily southeast through Saipan channel at the south end. Climatic influence, insular and submarine topography and geology, currents, and tides affect the sedimentary characteristics, coastal morphology, and basic nutrient supply which determine the nature of the local ecologic complex.

Within this local complex the marine environment between the 10-fathom line and the coast is of special interest, for this is the site of most active reef-building and formation of reef-associated sediments. It is also easily accessible to direct inspection with modest equipment. Observations of shoal-water biotas and sediments offshore from Saipan were, therefore, carried out as opportunity arose. Physical and chemical characteristics of the water itself were noted only in the most general terms, however, and neither time nor facilities were available to attempt specific life-history or nutrition studies.

Aerial photographs of the barrier reef lagoon and the wide fringing reef moats revealed bottom patterns believed to have sedimentary and ecologic significance, and reconnaissance indicated this to be true. Traverse lines were laid out to cross the boundaries that appeared on the aerial photographs, and the distribution of observation and sample stations was planned to permit analysis and definition of the units recognized. These traverses were coordinated with shoreline studies. For reasons beyond control the studies were never fully completed; but most of the area was covered, and in time this led to the recognition of a number of ecologic sedimentary units of different orders of magnitude.

The units recognized, and their characteristics as observed in the field or determined from later laboratory studies, will be described in a following section. It seemed worth while in the field, for analytical purposes, to differentiate as facies of the principal ecologic units or biotopes a large number of minor local and probably to some extent temporary subdivisions. Although it now seems doubtful that these facies are of any great importance, their approximate limits are shown on plate 122 and their characteristics are summarized in tables 3 and 6—partly to show the range and pattern of variation within biotopes and partly with the thought that it would be of interest, should it be possible to restudy the area in the future, to see in some detail what changes have taken place. An effort has been made to organize the report and illustrations in such a way, however, that the reader who is interested only in the larger and more permanent habitats can conveniently bypass the details.

The studies described resulted in a fair amount of

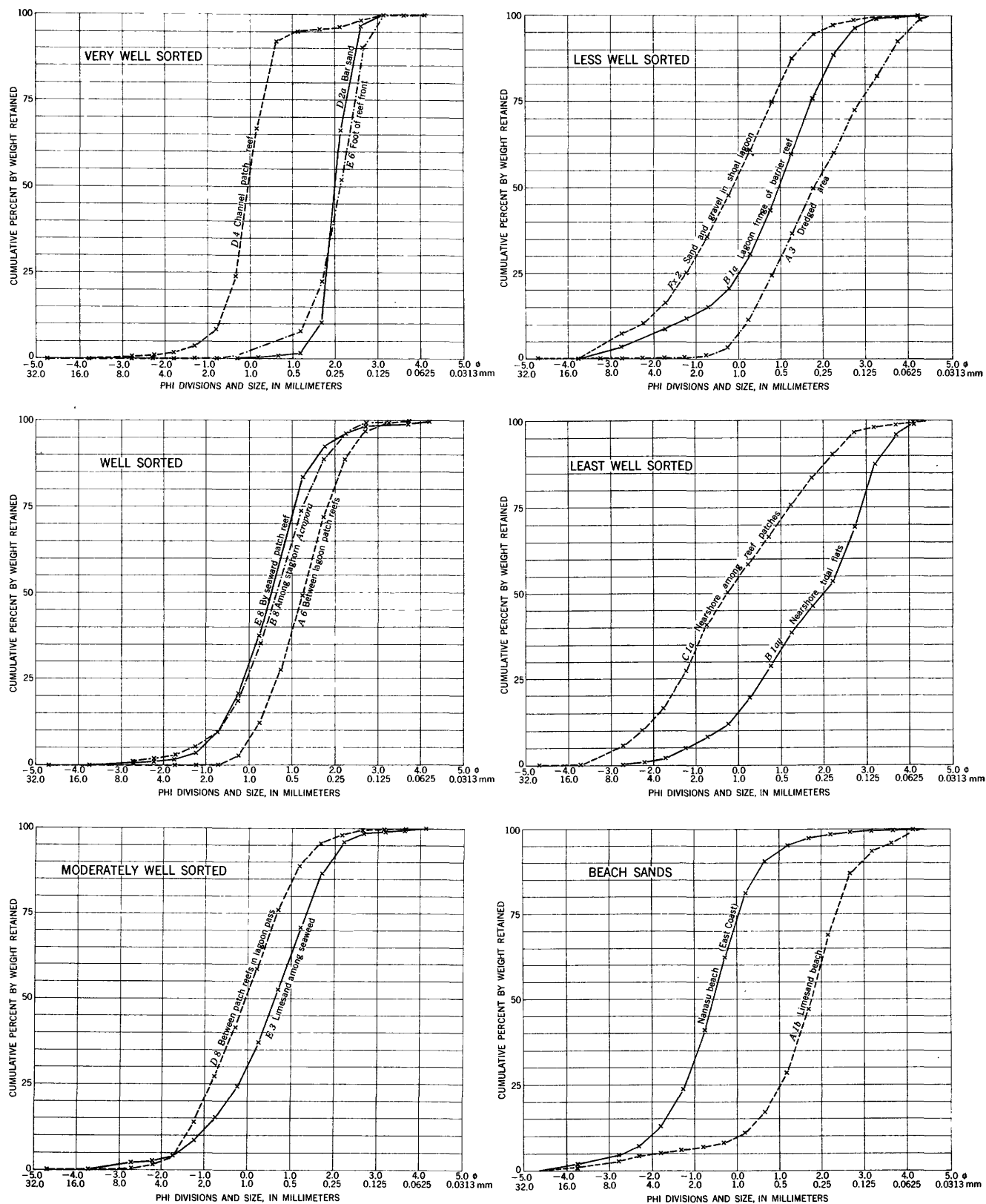


FIGURE 36.—Cumulative semilogarithmic screen analyses of representative shoal marine sediments of Saipan. (See pl. 122 and table 3 for location and further description. ϕ -millimeter conversions from Page, 1955.)

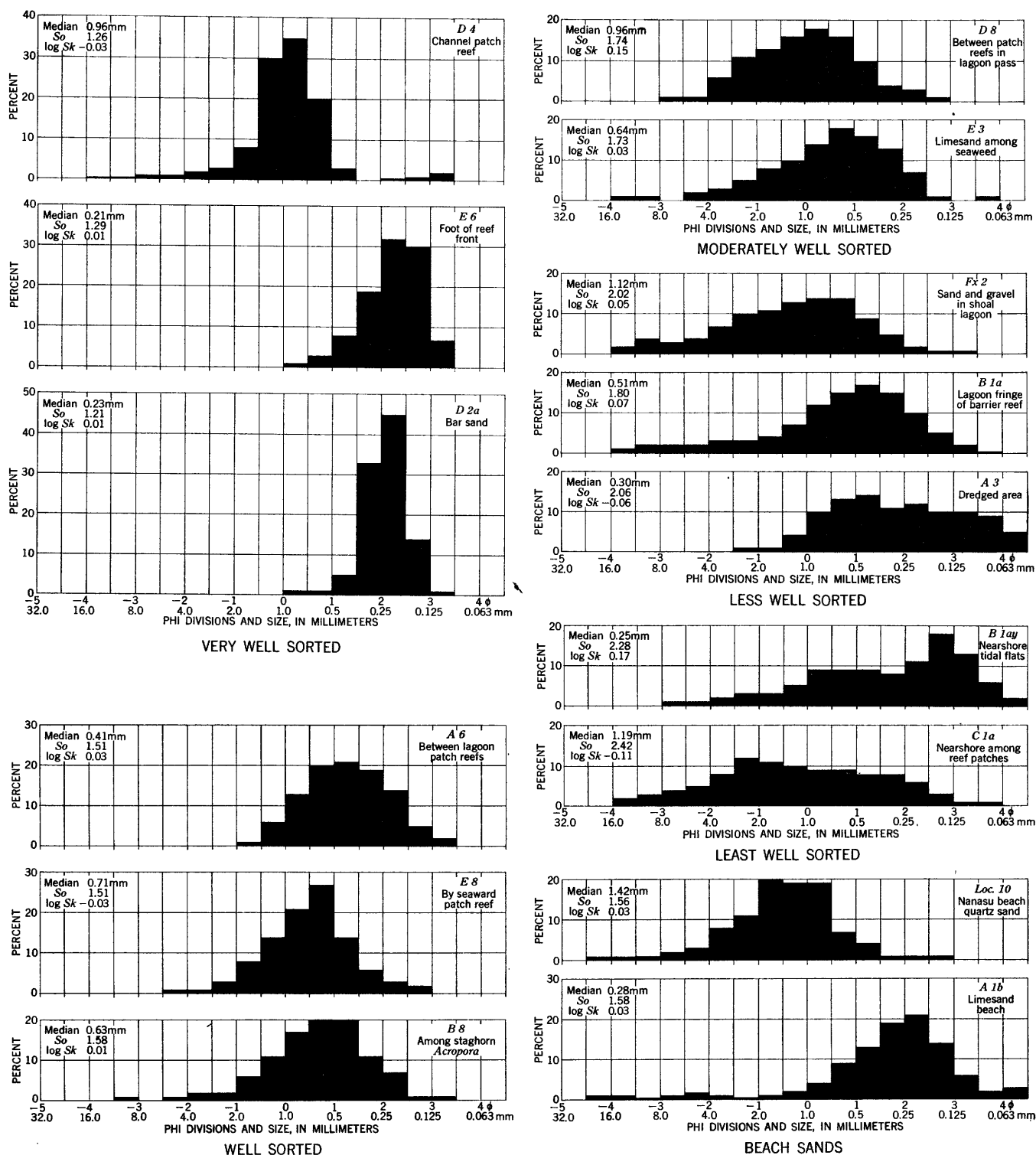


FIGURE 37.—Histograms of grain size of representative shoal marine sediments of Saipan.

information on ecologic and sedimentary associations and biogeologic processes. Biological collections, however, suffered from limitations of facilities, supplies, and time. Because of a shortage of suitable containers and preservative fluid few large animals except corals were collected. No holothurians and few alcyonarians, actinarians, ophiuroids, echinoids, starfish, and sponges were collected, although all were plentiful. Almost the only fish taken were little ones that could be shaken out of coral heads into which they had retreated for shelter. Encrusting and frondose byozoans were noticed at several places, but they were not common, and the only collecting record was accidental. Mollusks were not especially sought for, although more than 150 species were recorded from incidental collecting. As very little digging into sand bottoms was undertaken, little is recorded about the burrowing inhabitants of such locales. Unfortunately no wet samples were preserved for Foraminifera, so it is not known exactly where most of the 200 or so modern species recorded actually live. No plankton samples were taken at all. Plants were not systematically collected, but samples of three conspicuous local species of marine angiosperms were obtained, as well as of representative common algae. Every crinoid seen was collected, however. The scleractinian collections also ought to be fairly representative. Because many collections were obtained from the random breaking up of coral rock, it is probable that the collections of decapods, sipunculoids, polychaete annelids, and mollusks from this habitat are fairly representative.

To avoid repetition, names of the authors of species tabulated in the appendix are not repeated in text. Also in the interest of condensation detailed descriptions of the individual documentary traverses and stations shown on plate 122 are not here published. Instead, copies have been placed on file with the Division of Mollusks and the Division of Marine Invertebrates of the U. S. National Museum where they are available to the interested readers. The basic data are summarized in tables 3 and 6 and appendix.

Locality reference in the discussions that follow is to traverse letters and station or locality numbers shown on plate 122. Thus, station *E4* refers to station 4 along traverse *E*. Localities referred to by number only (as, *loc. 13*) are isolated sites not situated along traverse lines. Occasionally a field station was subdivided one or more times. Such subdivisions are indicated by lower case letters following primary station designation and producing combinations such as *B1ay*, for *y* part of *a* subdivision of station 1, traverse *B*.

SUBSTRATE CHARACTERISTICS AND SEDIMENT DISTRIBUTION

DESCRIPTION

The principal substrates to be considered are loose limesand (calcium carbonate sand), gravelly sand and gravel, and cavernous coral-algal rock and reef. The coral-algal rock and reef originates through direct but discontinuous growth, leading to the production of a cavernous structure that provides excellent shelter for a host of small organisms and easy burrowing for a variety of others (pl. 129). Destruction of this rock and reef material through biologic and physical processes discussed elsewhere provides a large part of the debris of which the limesands and calcareous gravels are comprised. The remainder consists mostly of the tests of micro-organisms and the separate joints or broken pieces of branching calcareous algae. The nature of the rocky and reefy bottom requires no further discussion at this place, but the loose sediments call for analysis.

In an average sediment sample, fragments of coral, algae, or coral-algal rock preponderate, with the articulate coralline algae or *Halimeda* most likely to lead in abundance among the algal detritus. Next in order of bulk are the tests of Foraminifera, and then pieces and small whole shells of mollusks. Echinoid spine fragments and plates are common in many samples, although they do not bulk large. A distinctive element of many samples is the 1.5 to 4 mm long, slightly curved and papillose, spindle-shaped, calcareous spicules of the alcyonarian *Sinularia* (pl. 131A, B). Crustacean fragments, sponge spicules, and bits of calcareous dasycladacean algae are occasionally noted, and the dermal elements of holothurians may be observed in the fine fraction of some samples at high magnification.

The loose deposits probably in large part only thinly cover cavernous substrates of coral-algal or algal rock. At most places, however, sedimentary thicknesses are unknown and they may locally be considerable. The gravels are largely concentrated just lagoonward from the southern part of the western peripheral reef flats, but the sands are widely distributed.

As clastic deposits are measured, the average grain size is coarse and sorting good to fair. The grain diameters and sorting characteristics of 63 random samples of sand and one of fine gravel were determined by mechanical sieving, the plotting of cumulative logarithmic curves, and standard computations. These are listed in table 3 at the end of this section. Tables 1 and 2 give the averages of these figures for samples from similar situations arranged in order of coarseness and sorting. A representative selection of original cumulative curves comprises figure 36; the corresponding histograms

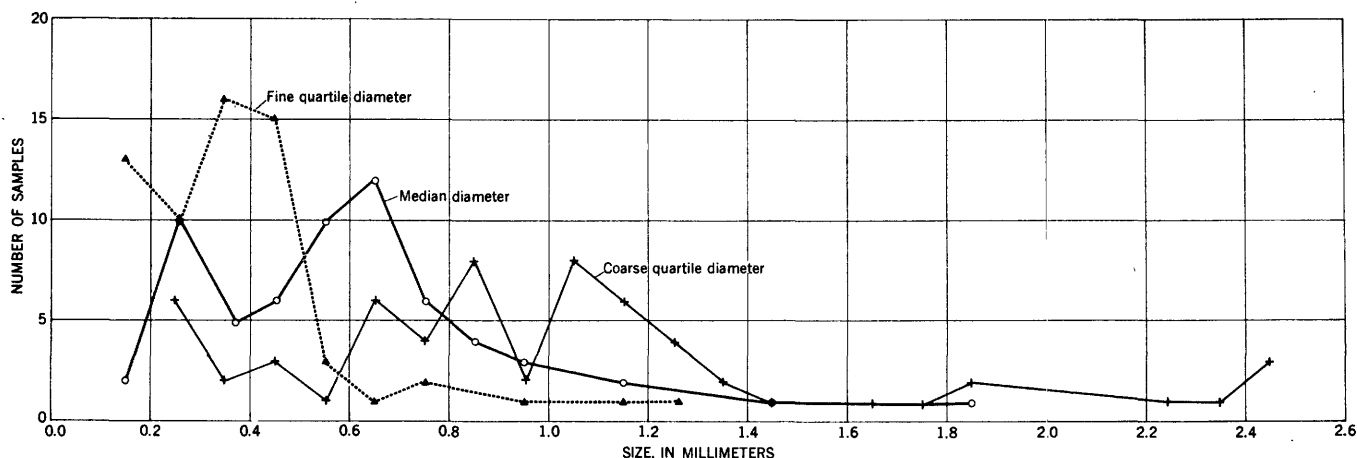


FIGURE 38.—Size-frequency distribution of 63 shoal sands from Saipan.

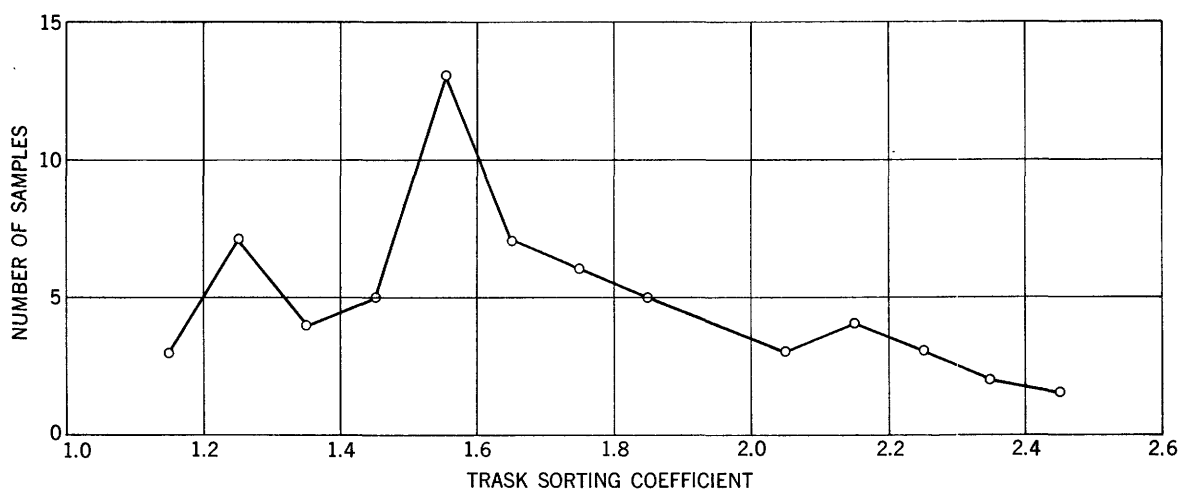


FIGURE 39.—Sorting-frequency distribution of 64 shoal sediments from Saipan.

showing grain size distribution are given in figure 37. Figures 38 and 39 summarize the size-frequency and sorting-frequency distribution of all samples taken.

In tables 1-3, and in this discussion, the definitions of Trask, Hammar, and Wu (1932, p. 69-73) are followed. The median diameter provides a simple approximation of central grain-size tendencies, and the coarse and fine quartile diameters are the range limits within which 50 percent of the sample falls. The Trask coefficient of sorting (So), a measure of the abundance of particles of median dimensions, expresses the relative efficiency of local sorting factors or size range of source materials. The coefficient of skewness (S_k) indicates the position of the mode, which may be controlled by source materials, or by selective sorting. The logarithm of the coefficient of skewness ($\log S_k$) provides a more direct comparison than the simple coefficient, and $\log S_k$ is here employed in place of S_k . A $\log S_k$ of zero indicates coincidence of the median diameter and the

mode. A negative $\log S_k$ indicates the mode to be on the coarse side of the median diameter, and a positive $\log S_k$ shows the mode to be toward the fine faction. The divergence of the $\log S_k$ from zero, plus or minus, measures the absolute median divergence of the mode from the median and permits simultaneous comparison of both degree and direction of skewness.

The average median diameter of all samples analyzed is 0.63 mm and the average coefficient of sorting is 1.7. These are not true averages for all shoal marine sediments of Saipan, but they give the order of magnitude for sands between the back beach and 5 fathoms depth.

According to the most commonly employed grain-size scales in use for clastic sediments, more than half of the sands analyzed are coarse grained—35 out of 64 samples having median diameters between 0.5 and 1.0 mm. Of the remainder 15 are medium grained (0.25 to 0.5 mm), 9 are fine grained (less than 0.25 mm), and 4 are very coarse grained (1.0 to 2.0 mm). One sample (from station *E4*) is fine gravel with a median diameter

of 3.05 mm. According to this classification, the average median diameter of 0.63 mm is at the lower margin of the coarse grained size range.

Exactly half of the 64 samples studied have coefficients of sorting between 1.5 and 2.0, with a nearly symmetrical falling away from this central grouping to 18 samples with So less than 1.5 and 14 samples with So greater than 2.0. The total range, between So 1.1 and So 2.4, is well sorted according to the definitions of Trask, Hammar, and Wu (1932, p. 71-72). For present purposes sorting is considered very good at So 1-1.3, good at So 1.3-1.8, fair at 1.8-2.5. In 8 of the 64 samples the median and modal diameters coincide and sorting is not skewed.

The ranges of average and specific figures for all samples and sample groups are as follows:

Range of average median diameter for sample groups-----	0.21 to 1.41 mm
Range of average So for sample groups-----	1.21 to 2.28
Range of average log Sk for sample groups-----	-.09 to +.17
Measured median diameter, individual sample-----	.19 to 3.05 mm
Measured coarse quartile diameter, individual sample-----	.22 to 5.59 mm
Measured fine quartile diameter, individual sample-----	.13 to 1.27 mm
Computed So of specific sample-----	1.11 to 2.42
Computed log Sk of specific sample-----	-.17 to +.30

Analysis of the data for individual samples and sample groups brings out that the finest grained and best sorted sands are from the bar or spit off Muchot point (pl. 123) and immediately seaward of the reef front in traverse E (pl. 125B). The individually finest grained and best sorted sample of all ($D3$, median diameter 0.19 mm) is on the outer down-current side of the Muchot point sandbar behind an algal reef patch. The coarsest and most poorly sorted sands sampled are from the shoal lagoon sand and gravel along traverses E and F . One of the finest grained units is also one of the most poorly sorted—organic rich limesand from a tidal flat adjacent to the lagoon beach at Flores point (pl. 126A; sta. $B1ay$).

The location of the very fine grained and very well sorted sands on the Muchot point bar and immediately seaward from the reef front suggest different sorting mechanics. The current that built this bar and the spit of land behind it presumably was a longshore current that tended to winnow out the finer material from the beach sands as it moved along, and to deposit as it eddied around the point. The fine limesand at the reef front along traverse E probably owes its nature to its location at the end of a long sorting line. Along the

reef also coarse debris that does not slump downslope tends to be moved selectively lagoonward in the surf zone, while fine material is winnowed seaward by weaker return flow and channel currents. The greater fineness of well-sorted sand at station $D3$ may result from eddy sorting between bar and reef.

The relatively poorly sorted nature of the fine-grained sands on the tide flat around station $B1ay$ may be due to the fact that the longshore drift which brings material below a certain grain size into this area is dispersed and retarded across the tidal flats so as to reduce its carrying competence and cause the bulk of the unsorted debris to be dropped here. Retention of this range of poorly sorted material is probably aided by the seaweed that grows here, tending to retard currents and to add organic slime and fine algal precipitates to the sediments.

The location of the coarsest sands and gravels on the shoreward side of the western peripheral reef, and in the shallow lagoon itself seems to be mainly surf controlled and corollary to the local concentration of fine sand at the seaward foot of the reef, as discussed above. It seems also in part to be a factor of concentration of shells and joints of large jointed *Halimeda*.

The high degree of apparent sorting displayed by the relatively coarse limesands in a re-entrant channel of an algal reef patch off Muchot point ($D4$, median diameter 0.97, So 1.26) suggests relation to source material, rather than physical selection. The relatively poor apparent sorting of sediments from the dredged part of the harbor area may be the result of artificial mixing. Other differences in sorting are probably controlled by the presence or absence of bottom-stabilizing seaweed and eddy-creating patches, bosses, and mounds of coral and coral-algal rock.

The relative coarseness of the east coast beaches probably reflects their content of quartz sand.

The mainly coarse sediment between reef patches in the main lagoon pass ($D8$, $D9$; group 15 of table 1; group 9 of table 2) consists dominantly of *Halimeda* joints. Whether these are derived from the immediate locale or transported from the inner lagoon is not surely known, but because little living *Halimeda* was seen nearby the latter circumstance is believed likely. The *Halimeda* joints are incompletely and unevenly calcified, and their porosity is high and bulk specific gravity relatively low as compared with associated sedimentary materials except Foraminifera (Emery and others, 1954, pp. 64-65). Such material is probably winnowed seaward together with the very fine materials from sediments of which the untransported parts are generally finer grained and better sorted than the *Halimeda* frac-

tion. Whether this is so needs to be confirmed or disproved by further study—but the mechanics suggested work in a simple flume and would explain apparent anomalies in both present and past distribution of *Hali-medea* debris, as discussed under Mariana limestone in chapter A.

Tables 1 and 2 summarize the sizing and sorting of the several recognizable sediment groups, and table 3 gives data for specific samples.

COMPARISON OF SEDIMENTS WITH THOSE OF OTHER AREAS

The sediments from Saipan (figs. 36, 37; pl. 122) have median diameters, sorting coefficients, skewness, and histogram patterns of about the same range as those from the beach and reef flats around Bikini, and they are of broadly similar biologic composition (Emery and others, 1954, p. 38-40, 56-68, especially fig. 10). They differ from the Bikini sediments in being gen-

TABLE 1.—*Shoal marine limesands of Saipan, in order of increasing average coarseness*

	Median diameter (mm)	So	Log Sk
FINE			
1. Bottom immediately seaward from reef front (1 sample).....	0.21	1.29	+0.01
2. Bar against shore (2 samples).....	.24	1.21	-.02
3. Tidal flat adjacent to lagoon beach (1 sample)....	.25	2.28	+1.17
MEDIUM			
4. Dredged part of harbor area (3 samples).....	.44	2.11	-.02
5. Lagoon beaches of west coast and Mañagaha islet (6 samples).....	.46	1.52	+0.01
6. Offshore between scattered lagoonal reef patches (14 samples).....	.49	1.49	+0.03
MODERATELY COARSE			
7. Lagoon bottom with sparse to abundant seaweed (16 samples).....	.54	1.77	+0.02
8. Between reef rock in lagoon fringe of barrier reef (3 samples).....	.58	1.96	+0.10
9. Offshore lagoon bottom with sparse to abundant living <i>Acropora</i> (3 samples).....	.62	1.59	.00
10. Between reef patches well seaward from reef front (2 samples).....	.67	1.45	-.02
COARSE			
11. East coast beach sands with high proportion of quartz (3 samples).....	.94	1.50	+0.05
12. Nearshore between clustered lagoonal reef patches (2 samples).....	.94	2.00	-.09
13. Reentrant channel in larger reef patch at south harbor margin (1 sample).....	.96	1.26	-.03
VERY COARSE			
14. Sand and fine gravel from shoal lagoon bottom of gravel and coarse sand (5 samples).....	1.24	2.03	+0.04
15. Between scattered reef patches of main lagoon pass (2 samples).....	1.41	1.60	+0.10

TABLE 2.—*Shoal marine limesands of Saipan, in order of average sorting*

	Median diameter (mm)	So	Log Sk
VERY GOOD			
1. Bar against shore (2 samples).....	0.24	1.21	-0.02
2. Reentrant channel in larger reef patch at south harbor margin (1 sample).....	.96	1.26	-.03
3. Bottom immediately seaward from reef front (1 sample).....	.21	1.29	+0.01
GOOD			
4. Between reef patches well seaward from reef front (2 samples).....	.67	1.45	-.02
5. Offshore between scattered lagoonal reef patches (14 samples).....	.49	1.49	+0.03
6. East coast beach sands with high proportion of quartz (3 samples).....	.94	1.50	+0.05
7. Lagoon beaches of west coast lagoon and Mañagaha islet (6 samples).....	.46	1.52	+0.01
8. Offshore lagoon bottom with sparse to abundant living <i>Acropora</i> (3 samples).....	.62	1.59	.00
9. Between scattered reef patches of main lagoon pass (2 samples).....	1.41	1.60	+0.10
10. Lagoon bottom with sparse to abundant seaweed (16 samples).....	.54	1.77	+0.02
FAIR			
11. Between reef rock in lagoon fringe of barrier reef (3 samples).....	.58	1.96	+0.10
12. Nearshore between clustered lagoonal reef patches (2 samples).....	.94	2.00	-.09
13. Sand and fine gravel from shoal lagoon bottom of gravel and coarse sand (5 samples).....	1.24	2.03	+0.04
14. Dredged part of harbor area (3 samples).....	.44	2.11	-.02
15. Tidal flat adjacent to lagoon beach (1 sample)....	.25	2.28	+0.17

TABLE 3.—*Grain diameter and sorting characteristics of samples of shoal marine limesands from Saipan, arranged in approximate order of distance from shore*

[Collecting station (A1b), biotope, and facies are shown in plate 122]

	Median diameter (mm)	Coarse quartile diameter (mm)	Fine quartile diameter (mm)	So	Log Sk
East coast beach sands with high proportion of quartz:					
Nanasu beach.....	1.42	2.29	0.94	1.56	+0.03
Fahang beach 1.....	.71	.96	.58	1.29	+0.05
Fahang beach 2.....	.69	1.24	.46	1.65	+0.08
Average.....	.94	1.50	.66	1.50	+0.05
Lagoon beaches:					
West coast of main island:					
A1b.....	.28	.46	.18	1.58	+0.03
B1ax.....	.43	.71	.21	1.86	-.11
C1b.....	.89	1.14	.64	1.34	-.04
D1.....	.33	.84	.24	1.86	+0.27
E1.....	.24	.28	.20	1.19	-.02
Mañagaha islet.....	.58	.71	.43	1.28	-.05
Average.....	.46	.69	.32	1.52	+0.01
Bar against shore (biotope VIII, part):					
Facies 22 D2a.....	.23	.28	.19	1.21	+0.01
D2.....	.24	.28	.19	1.21	-.04
Average.....	.24	.28	.19	1.21	-.02
Tidal flat adjacent to lagoon beach (biotope VIII, part):					
Facies 20, B1ay.....	.25	.69	.13	2.28	+0.17

TABLE 3.—Grain diameter and sorting characteristics of samples of shoal marine limesands from Saipan, arranged in approximate order of distance from shore—Continued

[Collecting station (A1b), biotope, and facies are shown in plate 122]

	Median diameter (mm)	Coarse quartile diameter (mm)	Fine quartile diameter (mm)	So	Log Sk
Lagoon bottom with sparse to abundant seaweed (biotope I):					
Facies 2, A1.....	0.25	0.81	0.16	02.25	+0.30
D3.....	.18	.22	.16	1.16	+ .01
Facies 3, E1a.....	.43	.66	.28	1.54	.00
A1a.....	.61	1.32	.24	2.34	-.17
E2a.....	.86	1.85	.36	2.28	-.05
E2.....	.51	1.09	.25	2.07	+ .03
E3.....	.64	1.14	.38	1.73	+ .03
Loc. 3.....	.89	1.65	.48	1.85	.00
Facies 4, B1b.....	.74	1.24	.43	1.69	.00
B1.....	.56	1.30	.28	2.15	+ .06
B3.....	.20	.28	.15	1.37	+ .04
C3.....	.56	.87	.36	1.56	-.01
Facies 5, B2.....	.43	.64	.33	1.39	+ .05
B7.....	.53	.81	.33	1.67	-.03
C4.....	.64	1.07	.38	1.67	.00
C5.....	.69	1.14	.41	1.68	-.01
Average.....	.54	1.01	.31	1.77	+ .02
Fine fraction from shoal lagoon bottom of gravel and coarse sand (biotopes II, IX):					
Facies 6, E4a.....	.71	1.27	.41	1.77	+ .01
E4b.....	3.05	5.59	1.27	2.10	-.12
E5.....	.84	2.54	.43	2.42	+ .19
Facies 23, FX1.....	.51	1.02	.30	1.82	+ .08
FX2.....	1.12	2.39	.58	2.02	+ .05
Average.....	1.24	2.56	.60	2.03	+ .04
Nearshore between clustered lagoonal reef patches (biotope X, part):					
Facies 25, C1.....	.69	1.02	.41	1.58	-.06
Facies 26, C1a.....	1.19	2.54	.43	2.42	-.11
Average.....	.94	1.78	.42	2.00	-.09
Offshore lagoon bottom with sparse to abundant living <i>Acropora</i> (biotope III):					
Facies 7, C2.....	.69	1.14	.41	1.68	-.01
B8.....	.64	1.02	.41	1.58	+ .01
Facies 8, B9.....	.53	.81	.36	1.51	+ .01
Average.....	.62	.99	.39	1.59	.00
Reentrant channel in larger reef patch at south harbor margin (biotope X, part):					
Facies 28, D4.....	.96	1.17	.74	1.26	-.03
Offshore between scattered lagoonal reef patches (biotope IV, part):					
Facies 10, B4.....	.36	.41	.33	1.11	+ .03
B5.....	.46	.66	.33	1.41	+ .02
B6.....	.23	.38	.17	1.51	+ .09
A5a.....	.22	.41	.16	1.62	+ .10
A9.....	.99	1.40	.71	1.40	.00
Facies 11, A5.....	.66	1.14	.38	1.73	.00
A6.....	.41	.64	.28	1.51	+ .03
A7.....	.61	.89	.41	1.48	-.01
A8.....	.33	.38	.25	1.22	-.05
D7.....	.79	1.04	.46	1.51	-.11
D7a.....	.38	.71	.25	1.67	+ .10
Facies 12, D5.....	.38	.81	.25	1.79	+ .15
Facies 13, A10.....	.58	.84	.41	1.44	.00
A11.....	.46	.76	.30	1.58	+ .05
Average.....	.49	.75	.34	1.49	+ .03
Between scattered reef patches of the main lagoon pass (biotope IV, part):					
Facies 12, D8.....	.97	1.78	.58	1.74	+ .15
(part) D9.....	1.85	2.54	1.19	1.46	-.05
Average.....	1.41	2.16	.89	1.60	+ .10

TABLE 3.—Grain diameter and sorting characteristics of samples of shoal marine limesands from Saipan, arranged in approximate order of distance from shore—Continued

[Collecting station (A1b), biotope, and facies are shown in plate 122]

	Median diameter (mm)	Coarse quartile diameter (mm)	Fine quartile diameter (mm)	So	Log Sk
Between living coral-algal masses in lagoon fringe of barrier reef (biotope XI):					
Facies 31, C6.....	0.58	1.07	0.36	1.73	+0.05
C7a.....	.64	1.83	.33	2.35	+ .18
B10.....	.51	.99	.30	1.80	+ .07
Average.....	.58	1.30	.33	1.96	+ .10
Bottom immediately seaward from reef front (biotope XV):					
Facies 49, E6.....	.21	.28	.17	1.29	+ .01
Between reef patches well seaward from reef front (biotope XVI):					
Facies 52, E7.....	.64	.89	.46	1.39	.00
E8.....	.71	1.04	.46	1.51	-.03
Average.....	.67	.96	.46	1.45	-.02
Dredged part of harbor area (biotope V):					
Facies 14, A2.....	.74	1.50	.33	2.13	-.04
A3.....	.30	.58	.14	2.06	-.06
A4.....	.28	.64	.14	2.15	+ .05
Average.....	.44	.91	.20	2.11	-.02

erally somewhat finer grained and in having significant weight fractions over a wider grain-size range. The samples from Saipan are also similar in the range of sedimentary components to limesands of the lagoon and beaches at Onotoa, Gilbert Islands, not as yet described in detail (Cloud, 1952), and to sediments described by Byrne (*in* Newell, 1956, p. 361-363) from Raroia, in the Tuamotus. The average median diameter of the 15 samples studied from Raroia, however, is only 0.36 mm, which is finer grained than those from Saipan.

In contrast with limesand samples from Aua reef, at the north side of Pago Pago Bay, Samoa (Bramlette, 1926), the limesands from Saipan present unimodal size histograms with peaks from 1.0 mm to 0.25 mm or as fine as 0.12 mm. The Samoan samples are distinctively polymodal, with peaks from 2 to 4 mm down to 0.1 mm, probably representing local associations of Foraminifera, shells or shell fragments, and joints of algae of different sizes. This striking difference might be due to the fact that none of the Saipan sands are from reef flats. However, Bikini reef flat sands are mechanically comparable to the Saipan sediments, and show similar differences from the Samoan materials.

More distantly located tropical and subtropical calcareous sediments with which those from Saipan may be compared were described by Vaughan (1918b), Thorp (1936), and Illing (1954). These are from the reefs at Murray Island, Australia; from the Bahama

Banks; and lagoon and beach deposits from the Florida Keys.

The Murray Island samples (Vaughan, 1918b, pl. 94) have median diameters generally between 0.5 and 2.0 mm. They are, thus, preponderantly coarser than sediments from Saipan, which average 0.63 mm, have a range of averages for sample groups from 0.21 to 1.41 mm, and show an extreme range from 0.18 to 3.05 mm.

Bahaman shoal sediments studied by Thorp and Vaughan include three batches of samples from rather widely separated areas around Andros Island, but closely spaced within batches. Those from the western side of South Bight are very fine grained aragonite muds not at all like the limesands of Saipan. Those from the eastern side of South Bight (Thorp, 1936, p. 86, 110, fig. 6, especially samples B. S. 144-148), and around Cocconut Point at the northeast corner of Andros Island (Thorp, 1936, p. 112, fig. 7, especially B. S. 184A, 189, and 192) are more nearly comparable to the sediments at Saipan in their mechanical characteristics, and of broadly similar skeletal composition. However, they tend to be finer grained (0.1 to 1.0 mm median) and some show bimodal size-distribution patterns.

The Floridian limesands of Vaughan and Thorp are also from widely separated sites. A few are beach sands but most are lagoon deposits, and they came from Dry Tortugas, Marquesas Lagoon, and the area near Key West. They are preponderantly finer grained than the samples from Saipan. When the Floridian and Bahaman samples studied by Vaughan and Thorp are taken as a group (Thorp, 1936, p. 86-91, figs. 6-10), their histograms peak at about 0.25 mm or finer, and about 1 in 5 (18 of 92) is conspicuously bimodal (one is trimodal). By contrast, samples from Saipan all have unimodal size distribution patterns and average more than twice as coarse. From field observation of Floridian and Bahaman limesands, however, it seems probable that this generalization is biased by the material selected for study. Some limesands which I have seen behind the reefs of eastern Andros Island¹ and southeastern Florida seemed much like those at Saipan except in the specific nomenclature of the skeletal components.

Bahama Bank sediments were most recently reported on by Illing who systematically studied deposits in the southeastern part of this region. His mechanical analyses and averages (Illing, 1954, p. 11-13, 17) show a general similarity with those for Saipan sediments. Illing's Bahaman samples, however, fall into two strikingly different groups as regards the composition of

individual grains. The material within the bank proper is mainly nonskeletal and thereby different from the sediments at Saipan. Samples from the bank edges, however, including his own and Thorp's samples, have skeletal fractions of 86 to 87 percent, median diameter near 0.5 to 0.6 mm, *So* near 1.5 and are generally comparable to the limesands from Saipan and Bikini.

Illing's line of traverse No. V (Illing, 1954, p. 17, 59-66, figs. 4, 7) gives a good view of the change from nonskeletal on the bank proper to skeletal on the bank edge, where the sediments generally resemble the lagoonal limesands of Saipan except that mollusks dominate the skeletal fraction instead of coral-algal debris as at Saipan.

Subtropical limesands also have been described as thinly veneering, probably drowned sediments offshore from western Florida (Gould and Stewart, 1955, p. 11-13). These have a broad mechanical resemblance to the shoal sediments of Saipan, but are mainly nonskeletal.

Thus there are specifiable similarities and differences between the limesands now forming at Saipan and those described from other areas. It would be possible too, to describe these resemblances and differences much more precisely. This, however, gets out of sedimentation, and into systematic biology, which makes possible much refinement in ecologic and geographic comparison, but which is better done on whole specimens than on fragments.

APPROACH TO ECOLOGIC ANALYSIS

The reef environment is the scene of active biogenic rock and sediment formation. Nowhere is it more apparent that a good appreciation of either environment or products requires a fully detailed assessment of the total habitat and the interrelations of everything that lives in it, every process that affects it. Only a fraction of the job is done when the geologic products are described.

Yet it is rarely, if ever, possible to attain all ends at once, and useful ecologic interpretations can result from different methods. Primary emphasis may be placed on the systematic associations of organisms with one another and the physical environment, on food chains and organic succession, on chemical or physical processes alone, or on some combination of these approaches. The limitations of the present study are such as to highlight the associations themselves. As far as practicable, however, these are considered in dynamic terms.

In following this approach we start with the primary ecologic unit, the biotope (Hesse, Allee, and Schmidt,

¹ Their characteristics are discussed in detail in a paper that appeared while this was in press: Newell, N. D., and Rigby, J. K., 1957, Geological studies on the Great Bahama Bank: Soc. Econ. Paleontologists and Mineralogists, Special Pub. No. 5, p. 14-72, pls. 1-21.

1951, p. 165). This embraces the entire complex of habitat conditions in the area defined, including substrate, accretional and erosional processes, hydrologic factors, and life associations. The biotope is not to be interpreted as limited either to the biota itself or to the physical features of the habitat. Nor is it to be confused with the niche, which is the sum of the environmental factors governing the occurrence of a species—whether this be the whole of the ocean or a small part of another organism.

Particular modifications of a biotope are known to the ecologist as facies in somewhat the same sense as sedimentary-paleoecologic facies are known to the geologist, although generally on a smaller scale. Biotopes may also be combined into a succession of larger categories according to the objectives and preferences of the writer.

By appropriate combination of habitat distinctions and associated characteristics of the organic communities it is possible to sharpen understanding of the relationships within and between the physical and organic environments, and to screen out the transient (facies) from the more enduring (biotope) characteristics. The biotic community as a separate organic complex, may, of course, and usually does overlap biotope boundaries to some degree.

BROAD ECOLOGIC PATTERN

From the shoreline outward to the 10-fathom line, the principal marine environments of Saipan are: 1. the shoreline itself; 2. the barrier reef lagoon and contiguous fringing reef moats of the western shore; 3. the various sorts of organic reefs; and 4. the sea floor beyond the peripheral reefs that fringe the land and define the lagoon. Of these broad habitat subdivisions, that of the organic reefs is the most significant, in that its unique biota and the sediments which it yields exercise a far reaching or even controlling effect on all adjacent portions of the tropical marine domain. It is at once the frame within which the scene is set and the source of its most distinctive characteristics. The barrier reef lagoon and adjacent fringing reef moats of the western shore, however, are the most extensive and most intensively studied of the habitat divisions described. A general shore-to-sea progression will be followed in the descriptions below, which should be read with plate 122 at hand.

1. The shoreline of Saipan is mainly an aggrading beach on the normally leeward (western) side of the island, and an eroding coast of high to low bluffs along the eastern, southern, and northern shores. Aggrading beach, however, is found not only along the lagoon shore of the western coast, but also behind areas of fringing

reef that are wide enough to protect parts of the generally precipitous eastern and southern shores from wave attack. These beaches are of very well sorted, medium-to coarse-grained limesand, with coarse sand and gravel fractions locally. The only animal life observed on the beaches consisted of burrowing crabs (*Ocypode*), beach hoppers, and birds. Commonly, however, the sands are almost made up of the empty tests of the reef-dwelling foraminifer *Baculogypsina sphaerulata*, at places associated with its ecologic twin *Calcarina spengleri*. At other places the dead shells of the triangular *Fragum fragum* or a small oval *Cardium* are abundant in the beach sands, along with other mollusks and Foraminifera. The bluff-lined eroding coast has a larger but still relatively impoverished life assemblage of scavenging crabs, spray-zone gastropods, and algae, characteristic of rocky shores elsewhere in the insular tropical Pacific. Flourishing intertidal biotas are found on the various reef flats and sea level benches.

2. The barrier reef lagoon and contiguous fringing reef moats of the leeward side include a number of lesser habitat subdivisions which are later grouped into nine biotopes and a number of facies.

Five of these biotopes (I-V) are distinctively lagoonal areas of limesand and minor amounts of gravel, with sparse to abundant growth of green algae and eel grass, and with locally scattered to abundant reef patches. They occupy the greater part of the lagoon, including sections that have been dredged, and in part they also extend into the adjoining fringing reef moat at the north. Depths range from a few feet to about 50 feet, and the biota is highly varied, with numerous microenvironments. Sparsely vegetated to nearly bare limesand plains apparently inhabited mainly by innumerable annelids and holothurians grade to meadow-like areas of marine angiosperms and algae that support a teeming community of their own and also help to nourish the adjacent parts with their organic detritus. The associated mounds, pinnacles, and other minor prominences that constitute the reef patches (in part biotope X) are microenvironmental complexes on and in which the highly varied and complexly interrelated building, boring, and browsing populations maintain a sometimes precarious balance between growth and destruction. These small reef structures contribute a wide size-range of skeletal and clastic debris to the sedimentary lagoon floor around them.

Two biotopes (VI-VII) are almost limited to the contiguous western moat environment, with bottoms generally less than 6 feet deep. One of these bottom areas is matted with mainly living calcareous algae and the other consists of dead and living coral-algal masses surrounded by coarse sand and gravel. The life assem-

blages in these habitats are not so highly varied as those of the lagoon proper, but they are by no means impoverished. Besides the lime-secreting coralline algae and sparse coral growth, soft red and green algae are abundant, and small fishes cluster around or in the coral-algal masses or live in holes on the bottom. Here also are found the usual complement of shoal-water mollusks, holothurians, brittle stars, urchins, and sand- and rock-dwelling annelids, echiuroids, and sipunculoids.

Two other biotopes (VIII and IX) overlap broadly from lagoon to moat environment without being distinctive of either. One of these includes all of the seemingly barren limesand bottom. The other comprises areas of coarse limesand and calcareous gravel generally less than 5 feet deep and lying immediately behind the flat surface of the outer reef. Its biota generally resembles that of the moat environment, although it is somewhat less varied.

3. Reefs that have been built mainly by corals and algae (biotopes X-XIV) skirt the island, outline its western lagoon, and dot the protected waters of the lagoon and offshore shelf to the west. The wave-breaking surfaces of the peripheral reefs (biotopes XII-XIII) are at places nearly barren except for a crust of coralline algae, a soft algal and foraminiferal association, and the usual crevice dwellers and borers. Elsewhere, however, such flats are submerged enough to support a sparse to moderate growth of corals, especially of stubby-branched *Acropora* (*A. humilis*). At such places the rest of the biota is also more varied.

The lagoon fringe of the barrier reef (biotope XI) is in important part a zone of rich coral-algal growth that occurs as low irregular stacks and masses interspersed over limesand at depths of 7 to 8 feet. The overwhelmingly conspicuous organisms are the crudely palmate coral *Acropora palifera* and *Porites lutea*, the latter occurring both in great greenish, yellowish, and bluish discrete hemispherical heads and also associated with *A. palifera* and other corals and algae in more complex masses. This area also supports a highly varied subordinate fauna that includes the only living crinoids observed at Saipan.

The irregular reef front itself (biotope XIV), immediately below the surf zone, also supports locally vigorous growths of massive and stubby branched coral and algae and a highly varied fish fauna. Many of these fishes are bottom browsers and thus an essential part of the benthic environment, but some are higher in the food chain and strictly nektonic.

The fringing reefs of the east, south, and north coasts (biotope XIII) are primarily narrow erosional benches in limestone and volcanic rocks. They have only a thin

veneer of calcium carbonate-secreting organisms on their surfaces, and active reef building is restricted to their subtidal fronts. Others are terraced ramps or pedestals owing their characteristics in large part to physical factors, but with a moderately varied biota of vermetid gastropods, mobile intertidal mollusks, borers of various sorts, and algae.

4. Beyond the southwestern reef front and lagoon passage are banks of limesand (biotope XV) and interspersed limesand and reef patches (biotope XVI). The shallow waters and broad lateral extent of this area suggests local coral-algal construction westward across the area called Saipan Bank on plate 121. Lack of time prevented study of these banks.

ORGANIC COMMUNITY

In a marine environment as varied as an area of organic reefs, the plant and animal communities rarely coincide exactly with the ecologic subdivisions that can be indicated on a map. The principal marine organic communities of Saipan, in the order of increasing variety of their biota, are those of (1) sandy beaches, (2) rocky shores, (3) bare to sparsely vegetated sandy bottom below tide, (4) gravelly bottom, (5) sandy bottom with abundant seaweed, and (6) submerged organic reefs and coral-algal rock. The intergrading and interspersal of these communities and habitats leads to the variety of associations in the biotopes to be described. Collectively their biotas make up the total organic community of this particular reef complex.

The invertebrates actually collected and identified in the laboratory by specialists include about 660 species in 380 genera, of which most have hard parts that could become fossils. This census does not include any microscopic forms except Foraminifera and ostracods. Twenty-eight species representing 26 genera of fish were collected merely by shaking these animals out of branching coral heads, removing them from an old ammunition can, and dissecting them from the insides of the starfish *Culoita*. Four other genera and species of fish were incidentally recorded. The vertebrate record does not include the large predaceous fish, the green sea turtle, or most of the probably hundreds of species of reef fish observed in the lagoon and along the reef front. Only a few distinctive or unusually abundant marine plants were collected—31 species in 21 genera. Three genera and species were angiosperms ("pondweeds") and the rest were algae.

A summary listing of the recorded biota is given in table 4, and the appendix gives the detailed distribution of plants and animals in the shoal marine habitats of Saipan as known from present studies. Both of these include sight records of common and important in-

vertebrates, as well as laboratory identifications. The range in estimated numbers of species and subspecies is from a minimum of confidently determined forms to a maximum probable number which includes uncertain and doubtful determinations.

TABLE 4.—Summary of the identified marine organisms of Saipan

Larger systematic group	Families	Genera	Species and sub-species
Algae.....	10	18	28
Flowering plants.....	2	3	3
Total plants.....	12	21	31
Foraminifera.....	27	91	200
Sponges.....	9	9	10-11
Corals.....	19	33	63-75
Scleractinians (true stony corals).....	12	26	56-68
Alcyonarians (spicular corals).....	4+	4+	4+
Actinarians and zoanthids (soft corals).....	3	3	3
Hydrozoans.....	1	1	1
Flatworms.....	2+	4	4
Brachiopods.....	1	1	1
Bryozoans.....	1	1	1
Sipunculoids.....	1+?	4	9
Echiuroids.....	1	1	1
Polychaete annelids.....	20	35	38
Mollusks.....	58	98	164-174
Amphineurans.....	1	2	2
Gastropods.....	35	60	116-122
Pelecypods.....	20	34	44-48
Scaphopods.....	1	1	1
Cephalopods.....	1	1	1
Crustaceans.....	27	87	140
Ostracods.....	3+	14+	17+
Cirripedes.....	2	2	2
Malacostracans.....	22	71	121
Stomatopods.....	1	2	4
Amphipods.....	1+	4	4
Decapods.....	20	65	113
Brachyurans.....	10	38	61
Anomurans.....	2	5	6
Macrurans.....	8	22	46
Echinoderms.....	13	24+	30+
Crinoids.....	1	2	3
Echinoids.....	2	6	6
Asterooids.....	3	5	7
Ophiuroids.....	5	8	11
Holothurians.....	2	3+	3+
Total of invertebrates.....	179	389	662-685
Fish.....	19	30	32-33
Total animals.....	198	419	694-718

The table shows that the greater number of species of invertebrates recorded from the Saipan shoal waters are Foraminifera (200 species in 91 genera), shell-bearing mollusks (164 to 174 species in 98 genera), and decapod crustaceans (113 species in 65 genera). Only 60 to 70 species and fewer than 30 genera of reef-building corals are represented (counting *Heliopora*), in contrast to the highly varied faunas of truly flourishing reef communities; and of these only a handful join with the coralline algae in actively building the organic reefs of the area. These corals, nevertheless, are the dominating faunal element, and nearly all other parts of the biota are conditioned by their presence and the detritus

that they yield to the surrounding sea floor. The species are illustrated by Wells (1954) and Vaughan (1918a). The sipunculoids and some of the polychaete annelids also are more important than is brought out by numbers of species, for these soft-bodied but effective borers swarm throughout the dead and dying parts of the reef rock everywhere, preparing it for clastic breakdown by other agencies. The total effect of the many fish that browse on coral-algal rock and coral is also significant in reef destruction, sediment production, and habitat variation.

HABITAT DESCRIPTIONS

The following pages present details about the various habitat subdivisions that fall beyond the scope of the foregoing summary discussion. They concern primarily the shoal marine habitats. The shore zone biotopes are first described for the sake of completeness, but these are left off the ecologic map (plate 122) and the summary habitat table (table 6) to avoid clutter and distraction. The shoal water habitats themselves are then arranged in hierarchical order and described, except for the facies whose distinctive features are summarized in table 6. For convenience in cross reference, biotopes are numbered in the roman system and the facies in arabic.

SHORELINE

The shoreline includes two principal ecologic subdivisions, aggrading beach and eroding coast. The characteristics of these habitats and their conspicuous organisms are described below.

AGGRADING BEACH

WESTERN BEACHES

The beaches that extend almost continuously along the west coast (pls. 124A, 125, 126A) are mainly of loose limesand, with subordinate calcareous gravel and indurated limesand or beach rock. These sands are preponderantly medium- to coarse-grained and well sorted to very well sorted. Maximum sorting is in the coarse fraction in 4 out of 6 samples tested.

Beach sandstone is found along short stretches of Sadog Tase beach in the harbor area, along Matuis beach and Magpi beach northeast beyond the western barrier reef, and around Mañagaha islet (pl. 124B).

Minor proportions of calcareous gravel are mixed with the beach limesands over a stretch of somewhat less than a mile opposite the outward bend in the reef about midlength of Garapan lagoon, and somewhat more than a mile at the south end of the western shore. Such patches of gravelly limesand locally contain scattered

large boulders, and where they do so in abundance short spits are commonly formed. The small patch of phosphatic gravel on the reef-islet at Agingan point (pl. 125D) was made up largely of human bones from the 1944 military campaign.

SOUTHERN AND EASTERN BEACHES

The small beaches along the south and east coasts show considerable diversity. Limesands closely similar to those of the western beaches are found only along the north side of Laulau bay—at the eastern end of Laulau beach and along Bapot beach (pl. 133B). The other eastern and southern beaches are all gravelly to some extent, and some of the small cove beaches toward the north end of the east coast contain large fractions of quartz sand and volcanic gravel.

Beaches that consist of abundant calcareous gravel and less conspicuous limesand are found intermittently along the south coast between Agingan and Obyan points (pl. 132A), along Obyan beach proper, and at tiny Peo beach. Similar gravels and sands occur sporadically northward along the eastern coast at western Laulau and Tutturam beaches along Laulau bay, at North Laulau and Halaihai (pl. 133C) beaches along the northeast side of the Chacha peninsula, and at Hasngot (pl. 134F) and north Fafunchuluyan (pl. 132B) beaches to the north.

Both calcareous and volcanic gravel are mixed with the beach limesands at south Fafunchuluyan and Hagman beaches (pls. 132B, 135A). The same association of sand with subordinate calcareous and volcanic gravel occurs at the small cove beaches of Talofoto (pl. 138B), Fahang, and Nanasu, together with a dominance of quartz (50 to 80 percent) in the sand fraction. In addition to the commonly euhedral quartz grains, local concentrations of magnetite occur on the last three beaches mentioned. These sands are coarse grained to very coarse grained and very well sorted, with maximum sorting in the fine fraction.

Beach rock that consists of indurated gravelly limesands or gravels is found along the outer beach fringe at Halaihai and North Laulau beaches, at Obyan and Peo beaches on the south coast, and at tiny Dandan beach on the southwest coast of Laulau bay.

BIOTA OF THE BEACHES

Few living organisms are found on the beaches. Gray and mainly nocturnal ghost crabs of the air-breathing genus *Ocypode* burrow in great numbers where the sands are deep and clean. The little whitish box crab *Calappa* is occasionally found in the water along the lower edge of the beach nearly buried in the

sand except for eyes and exhalant tubes. Unidentified springing amphipods (beach hoppers) are very abundant locally. Hermit (coenobitid) crabs scrawl inadvertent hieroglyphics with the help of pilfered shells. And birds come here to feed on the living and dead. Empty shells, of course, are common: on the lagoon shores *Fragum fragum* is the commonest beach shell, and a little oval *Cardium* and shells of the high-spired vegetarian and detritus-feeding snail *Cerithium* are also locally abundant. Abandoned and generally worn tests of Foraminifera are common in the beach sands. At places these sands contain a high proportion of the pink, stellately spinose tests of *Baculogypsina sphaerulata* and associated *Calcarina spengleri*, neither of which has been found alive except among soft algae on reef surfaces.

ERODING COAST

BLUFFS

The greater part of the eroding coastline consists of nearly vertical bluffs that rise above the ordinary range of spray and rarely support spray or splash pools. Such bluffs range from 20 feet to more than 100 feet high. Clockwise from the northwest side of the island they occur north from Magpi point to the south end of Sabaneta, at the coastal reentrant in the north tip between Sabaneta and north Laguna point, from I Madog along most of the east coast to the southeast tip of the island, and from there west to Obyan point.

Bluffs lower than 20 feet are almost continuously within the range of spray and support temporary spray pools, commonly with a growth of filamentous green algae (pl. 138E). They occur along the south coast from Obyan to Agingan points, in four short stretches along the west coast between Dogas and Magpi points, almost completely around the north "head" of the island, at and south of Tanke point, between Halaihai and north Laulau beaches, and around Trinchera and the west end of Laulau beach.

RUBBLE COAST

Accumulations of massive blocky rubble fringe short stretches of the coastline, mostly where volcanic sediments at sea level are being undercut beneath limestone bluffs above. Such rubble shores are found southwest from Fafunchuluyan point to Tanke point, at several small coves south to Gloria point, south from North Laulau point around Hagman point, and at and south of the coastal reentrant at the east side of Naftan peninsula. The rubble is everywhere preponderantly of limestone except at the center of Hagman bay where many boulders are andesite.

EROSION SURFACES

At a few places along the east coast of Saipan, limestone surfaces that slope 7° to 10° seaward characterize the intertidal zone where a beach would normally be. Such surfaces not only have the normal slope of sea-facing beaches, they are actually the sites of temporary beaches that come and go according to local storm conditions. They occur in several small coves along the southwest shore of Laulau bay, and at Laguna "beach" at the northwest end of the island.

Other erosion surfaces—nearly horizontal benches across volcanic bedrock—occur north and south from Hagman bay, at the north edge of the coastal reentrant on the east side of I Naftan, and at the tip of Naftan point. Such benches are backed by bluffs or steep slopes of volcanic rock or limestone and are fronted seaward by a fringe of living coralline algae and fewer corals. The distinction between such benches (right margin pl. 135A, center pl. 132B) and similar benches that are included among fringing reef surfaces (most of pl. 135A) is vague; the latter are in large part permanently awash, the former are swept by only the occasional wave even at high tide. Cementation of these rubbly porous pyroclastic surfaces by precipitation of calcium carbonate goes on concurrently with abrasive wave action and probably solution, welding the larger cobbles and boulders to the surface and retarding erosion.

BIOTA OF THE ERODING COAST

The eroding coastline has the distinctive if little varied biota of rocky tropical Pacific shores. Along the rocky surfaces within the spray zone the common gray-green scavenging crab *Grapsus* cf. *G. tenuicrustatus* (an airbreather) is conspicuous and abundant. Limpets of the genus *Patella* (and less commonly *Cellana*), as well as chitons, are abundant in the lower spray zone and upper intertidal zone in small, constantly wet, indentations which they fit precisely. The Pacific periwinkle *Littorina coccinea* is generally found in the upper spray zone, while *L. (Melaraphe) pintado* stays mostly in the lower spray zone, but the two overlap in their range. *Littorina undulata* is less common in this habitat. *Nerita plicata* is common in the upper intertidal and lowest spray zone, crawling actively about and feeding on the surface film of algae in the shade or at night. *Nerita polita* remains buried in sand between rocks in the intertidal zone except when foraging at night. The spray zone algae are encrusting or imbedding blue-greens, such as *Entophyalis* (Newhouse, 1954, p. 45-46), which give subaerially exposed limestone surfaces a black color and contribute to their disintegration by filamentous

penetration and solution. Long-lived spray pools also support growths of filamentous green algae.

The erosion surfaces, which are intertidal or near high tide level, have biotic characteristics in common with the narrow fringing reef surfaces elsewhere along the east coast of Saipan. These include articulate coralline algae and soft red and green algae on which browse Foraminifera such as *Baculogypsina* and *Marginopora*; the common intertidal cone shells and occasional cowries; occasional *Cantharus (Polia) undosus*; and knobby thick-shelled gastropods of the genera *Vasum*, *Bursa*, and the muricids *Drupa*, *Morula*, and *Thais*. Spiny sea-urchins; small masses or clumps of the corals *Porites* (pl. 134H), *Acropora*, and *Pocillopora*; and nodulose or branching coralline algae occur in deeper pools and at the bench front. Eels and small fish are also common in the standing pools on such benches. Indeed the Hagman area was named from the abundance of eels in the pools of its fringing volcanic benches (*hagman* being the Chamorro word for eel).

THE BARRIER REEF LAGOON AND CONTIGUOUS FRINGING REEF MOATS

The greatest variety of environments and organisms to be found in the shoal waters of Saipan is in the lagoon and contiguous moats of its leeward shore. Because the water of this area is constantly interchanged with the sea beyond, however; its hydrologic variations involve only slight changes in depth and chemistry and a somewhat wider temperature fluctuation. The organic productivity, chemical nutrients, and oxygen balance of parts of the Great Barrier Reef waters (Orr, 1933; Orr and Moorhouse, 1933) and of the Marshall Islands reefs and lagoons (Sargent and Austin, 1954) have been discussed and compared with other reef complexes in a way that suggests broad similarity in these features between reef-encircled waters. Orr (1933, p. 50-52) emphasizes the very slight year-round variation in phosphate and nitrate content of the Great Barrier Reef waters, resulting in absence of phytoplankton blooms but year-round steady numbers. All authors agree on daytime supersaturation with oxygen of water adjacent to reefs, and Sargent and Austin indicate that a vigorous reef complex produces more organic matter than it consumes!

Hydrogen ion concentration at Saipan averages about 8.0 in the nearshore lagoon according to rough colorimetric field tests through one diurnal cycle. This seems low. On the other hand, a pH of 8.39 is recorded for the surface waters of the surrounding sea (Ito, 1929), which seems high. The pH of the lagoon waters probably is lower than that of the surrounding sea, however; because the high respiratory activity of the large reef-lagoon biota would tend to increase the carbon dioxide

content of the lagoon waters. A slight apparent diurnal variation in pH from somewhat above 8 during the day to somewhat less than 8 at night probably results from nighttime cessation of photosynthesis by algae, angiospermous seaweeds, and phytoplankton.

Temperature of the lagoon and moat waters fluctuates from about 22° C on a cool night to the upper thirties in rarely flushed tide pools exposed to the sun. Temperature fluctuations and evaporation affect the chemistry and life of the tide-pool waters according to frequency of flushing.

The maximum depth is 9 fathoms (in the harbor area) but is generally less than 5 fathoms. Datum for all depth figures given is approximate mean low tide, and tide-range averages 2 to 2½ feet.

Current pattern strongly influences the distribution and orientation of the bottom sediments. As has been mentioned, the prevailing surface current around the island seems to be from north-northeast to south-southwest, but the current system of the lagoon and moats is also affected by the inflow of water across the reef and its outward transit through passes in the reef. The orientation of the reefs in relation to prevailing surface currents and passes is such that a southwesterly direction of flow characterizes all levels of Tanapag lagoon and the northern moat. Yet, the bottom flow in Garapan lagoon south from the harbor entrance is generally northward except for short stretches immediately north of several small passes. These current trends result in a pattern of hooked sediment lines that run straight across the reef for a short way and then curve north or south toward the nearest principal outlet. It is evident from these lines (pls. 123B, 124A) and from their encroachment on dredged channels (125B), that sediment is in almost continuous transport, first to the lagoon centers and thence seaward along the bottom. The aerial photographs also show that the distribution and orientation of green plant growth and reef patches is affected either by this sediment flow or by the bottom currents which induce it.

The different habitat variations of this area are arranged in nine biotopes grouped in three larger subdivisions: the lagoon proper, the contiguous moats, and intermediate biotopes. The characteristics of these and other subdivisions of the shoal marine habitats are summarized and compared in table 6.

LAGOON PROPER AND MARGINAL LIMESAND SHELVES

The lagoon proper, together with its marginal lime-sand-covered shelves, includes an area of mainly sandy bottom between low tide and a little more than 50 feet deep, above which in certain areas rise coral-algal masses of various shapes and sizes (biotopes I–V, facies

1–15). Areas of relatively stable sandy bottom support meadows of marine angiosperms and the algae *Caulerpa* and *Halimeda*, while sands that are kept in constant or repeated strong movement by wave or current action are generally bare or relatively thinly vegetated. Where current effects are pronounced the bottom is commonly gravelly or may be covered only by a cavernous crust of algae or coral-algal rock.

Aside from those substances that are carried in solution or suspension from the sea beyond or provided by the photosynthesis of the zooxanthellae, the principal nutrient source and oxygen supply of the lagoon is in the areas of thriving seaweed on limesand bottom. As might be expected, the fauna of such areas is relatively abundant and varied, although mainly of small species. An even denser and more varied fauna is found on and in the reef patches that reach above the bottom at various places. The areas of bare or thinly vegetated lime-sand support mostly holothurians and myriads of plumose tube-dwelling annelids.

Descriptions by Hiro (1936) of his coral zone and sandy zone and by Abe (1937) of several environments in the shallow waters adjacent to Koror in the Palau group indicate features in common with the lagoon at Saipan. However, the environments of the lagoon and leeward shelf at Onotoa, Gilbert Islands (Cloud, 1952, p. 25–27, 69–70), seem more nearly comparable with the situation at Saipan, probably because of the strong influence of reworked volcanic materials in the areas studied at Palau. The shallower areas of the Saipan lagoon environment, which also extend into the moats, are broadly similar to the very shoal lagoon behind the barrier reef of eastern Andros Island, Bahamas (Newell and others, 1951, p. 20–21, fig. 5, pl. 3, figs. 3–6). In fact, the algae, the marine angiosperms, the bare sand and rarer rock patches, the long spined black *Centrichinus*, the common black *Holothuria*, the boring *Echinometra*, and the short spined *Tripneustes* are so characteristic and so generally similar between the shoal lagoon environments of western Saipan and eastern Andros that, if it were not for the striking differences in their alcyonarian faunas it would be hard to believe on casual inspection that they are in different oceans!

BIOTOPE I. MARGINAL LIMESAND BOTTOM WITH SEAWEED

Biotope I, comprised of facies 1 to 5, includes those parts of the sandy marginal lagoon bottom at depths less than 18 feet that are sparsely to thickly vegetated with marine angiosperms and soft green algae. This biotope supports a distinctive and varied fauna that derives its substance either directly from the living or triturated seaweed, or through intermediary organisms.

The floristic components and degree of concentration of the seaweed vary from place to place, with concordant changes in the nature and abundance of the fauna.

Where vegetation is sparse the fauna is characterized by burrowing nereid, spionid, and terebellid annelids, and by sediment-ingesting but surface-dwelling holothurians. Among the latter, the familiar black circumtropical (or at least Indopacific) *Holothuria atra* is by far the most abundant, but probably at least five other species of slug-like holothurians and a large snakelike synaptid (cf. *Opheodesoma*) are local inhabitants of the sparsely vegetated limesands. The widely distributed blue starfish *Linckia laevigata* is another common sand-dweller. Other starfish, echinoids, and brittlestars are found locally. The short-spined, surface-dwelling bun-shaped urchin *Tripneustes gratilla* is most frequent in areas of abundant but not densest seaweed growth.

Strombid gastropods and sponges are found locally on or in such sand, whether thinly or thickly vegetated, and sand-dwelling pelecypods probably live shallowly buried in it at places.

The sands of the moderately to thickly vegetated areas are like those of the sandy substrates with only sparse seaweed, except for the general rarity of the Foraminifera *Textularia* and *Heterostegina*, and the abundance of the small shells of slime- and detritus-feeding gastropods in the areas of lush seaweed growth. This type of bottom supports the same species as occur in areas of thinly vegetated sandy bottom, but *Tripneustes gratilla* is much commoner, and holothurians and sand-dwelling annelids are noticeably less abundant. In addition, such areas support large numbers of the little high-spired gastropod *Cerithium morum*, a tiny unidentified species of the widespread seaweed-browsing genus *Tricolia* (Abbott, 1954, p. 127), and other small gastropods that are ectoparasitic on pelecypods and tube-dwelling polychaetes. A great number of small fishes and small scavenging crustaceans also live among and on the seaweed, and probably a multitude of Foraminifera and other microorganisms as well. As a result of the trituration of the marine angiosperms and algae, and through the life activities and relation of the total associated community, such areas probably function as a primary source of nutrients and oxygen in the lagoon-reef economy.

It should be possible for the geologist to infer the existence of such areas of lush seaweed growth in elevated deposits that preserve no seaweed. His clue is the presence of abundant fresh or little-worn cerithiid, phasianellid, or other seaweed-associated (and detritus-feeding) snails in sediments that show a lesser degree of sorting and structures associated with sediment

movement than adjacent deposits. Where the seaweed on which such gastropods lived happened to include *Halimeda*, the calcified joints of this alga may be mixed abundantly with the other sediments. However, as noted elsewhere, geologic concentrations of *Halimeda* joints are not in themselves evidence of its abundant growth at the place of accumulation, and the characteristic snails are not invariably restricted to areas of seaweed growth. The Termiers (1951) have also emphasized that pyrite and relatively high organic content may characterize the sediments formed in areas of lush marine angiosperm growth (if iron is present, and if the sediments are fine and adherent so as to retard flushing from above, favor bacteria, and produce negative oxidation-reduction potential).

Areas mapped as facies 3 and 4 are those of lushest seaweed growth, although facies 4 includes few or no exposures of rocky substrate. The characteristic plants of both facies include *Zostera nana*, *Caulerpa* (especially *C. taxifolia*), and small- and large-jointed *Halimeda* (*H. tuna* and *H. opuntia*). At a few places the tall straplike marine angiosperm *Enhalus acoroides* is common and tends to grow in circular patches. Locally *Zostera* and the feathery green alga *Caulerpa* grow in great profusion on an undermat of *Halimeda*. Other seaweeds include the oval-leaved stoloniferous angiosperm *Halophila ovalis*, and such noncoralline algae as *Padina commersoni*, *Hydroclathrus clathratus*, and *Turbinaria ornata*.

Partially comparable habitats at Koror in the Palau Islands are the sandy flat zone of Hiro (1936) and the muddy zone (?), *Enhalus acoroides* or "*Zostera*" zone, and *Halimeda* zone of Abe (1937, especially p. 250-251, 315, 321). I have also described very briefly a grossly similar biotype at Onotoa in the Gilbert Islands as *Thalassia* flats and shoals (Cloud, 1952, p. 25, 68).

BIOTOPE II. SHALLOW AREA OF GRAVEL TRAINS WITH SCATTERED LIVING CORAL AND ALGAE

Biotope II, including only facies 6, comprises bottom of pebble- to cobble-gravel and mostly coarse limesand at depths of 3 to 13 feet, behind the southern barrier reef. Locally this includes or grades to areas of abundantly scattered patches and bosses of living and dead crustose coralline algae and corals. Such material tends to be oriented in strips parallel to the direction of current movement and the shore, with most vigorous coral growth between the moving sediment trains of the intervening lower strips. The coralline algae are branching types, and the coral includes both staghorn *Acropora* and more massive head-forming sorts.

The coral-algal masses and dead coral-algal rock contain an impoverished reef biota and the gravelly bottom

itself supports a distinctly limited community of organisms. Seaweed growth is retarded by frequently repeated and long continuing intervals of vigorous northward streaming and scouring of sediment along the bottom. Except where sand predominates over gravel, holothurians are inconspicuous. The gravel itself, however, offers haven to a variety of polychaetes, small crustaceans, brittle stars, and fish that live under and between stones.

Nothing quite comparable to this biotope has been described elsewhere in the Pacific, so far as I know, although it seems a not unusual sort of habitat.

BIOTOPE III. STAGHORN *ACROPORA* ZONE OF OUTER LAGOON SHELF

Immediately shoreward from the lagoon fringe of the barrier reef are generally current-swept, coarse-grained, well-sorted limesands at depths of 4 to 13 feet which support a scattered to abundant growth of staghorn *Acropora*. This is biotope III, consisting of facies 7 to 9. Both *A. arbuscula* and the stouter branched *A. nobilis* have been identified as locally preponderating species, and the type is so distinctive and so limited in abundant occurrence that this is called the zone of staghorn *Acropora*.

The limesand above which the *Acropora* wisps and thickets rise is almost barren of vegetation, presumably because of its nearly constant fairly vigorous drift. The most abundant organisms on or in the limesands are unidentified sand-tube agglutinating annelids (possibly *Nematonereis unicornis*) whose myriad pale plumes are noticed only on very close inspection of the bottom. Holothurians of several sorts are locally abundant, *Tripneustes gratilla* is occasionally seen, and the yellow-green box starfish *Culcita* is distinctive but not common. A snakelike brownish-black synaptid with parallel longitudinal rows of pale yellowish markings (cf. *Opheodesoma*) is common on the sands beneath the *Acropora* thickets of this biotope, and the thickets also provide refuge for numerous small brightly colored pomacentrid, chaetodontid, and acanthurid fish. The solitary corals *Fungia* and *Herpolitha* are locally common on the loose sand between *Acropora* growths, and colonial sponges are found locally.

One of the largest collections of living organisms from Saipan was made from scattered coral-algal bosses toward the southwestern limits of this biotope, simply because it was convenient to collect there (pl. 127A). The fauna obtained from this locality includes several species that are not recorded elsewhere, but these are not considered especially distinctive. The corals and crustaceans in particular are of the same sorts and occur in the same manner and associations as those of the lagoon fringe of the barrier reef—except, of course,

for the distinctive concentrations of staghorn *Acropora*.

Acropora thickets and areas of more thinly dispersed *Acropora* growth on a limesand base are known from virtually all coral seas. They are one of the most conspicuous, most widely uniform, and most frequently described of reef-associated habitats.

BIOTOPE IV. INTERSPERSED REEF PATCHES AND LIMESAND OF LAGOON PROPER

Biotope IV, comprising facies 10–13, includes the mostly deeper, central and outer part of the principal barrier reef lagoon (Tanapag lagoon), characterized by interspersed mounds, knolls, pinnacles, and flat-topped to mushroom-shaped masses of commonly dead and lesser living coral and coralline algae that rise above surrounding limesands. The depth of the bottom, except on top of the mostly small and variously shaped reef patches, is almost everywhere greater than 10 feet, and exceeds 40 feet in the outer lagoon pass.

This biotope is a mixture of limesand habitat and reef patch habitat, so intimate that the parts cannot be usefully delineated on a map. At the same time it has distinctive characteristics of its own. The medium- to coarse-grained and rather well-sorted limesands seem to be mainly in movement, as they are commonly current-rippled (pl. 124B) and striped and support only the sparsest local seaweed growth. The fauna of such places is rather like, but even sparser than, the poorer areas of biotope I.

Except in the relatively shallow area of facies 13, the reef patches themselves differ from those in the areas of mapped concentration in consisting largely of dead coral-algal rock and dull-colored pavement algae (pl. 127B) as contrasted to living coral. This impoverished living coral fauna is associated with relatively large expanses of dead and cavernous coral-algal rock with a highly abundant and varied fauna of borers and crevice dwellers. These include boring sipunculoids and clams; a variety of polynoid, eunicid (palolo worms), and other rock-dwelling polychaetes; and crevice-dwelling clams, snails, decapod crustaceans, starfish, and brittle stars of great variety. Bright yellow and red sponges are common on the dead coral-algal rock in this area, and most of the sponges collected on Saipan were obtained here. A tube-agglutinating annelid (cf. *Nematonereis*) is locally very abundant in the sands surrounding the reef patches. The only living brachiopods obtained at Saipan were adherent on dead coral-algal rock from this biotope (facies 11, sta. A5, *Thecidellina*).

Explanation for the differences between the poorly growing coral-algal surfaces and minor reef prominences of much of this biotope and the relatively vig-

orous coral growth of shallower lagoonal reef patches is not obvious. Sedimentary suffocation will not account for these differences, for equally vigorous sedimentary movement is found in areas of healthy coral growth (as in the lagoon fringe of the northern barrier reef). General reduction of light below about 2 fathoms is a possible explanation, for many corals are sensitive to relatively inconspicuous differences in illumination (pl. 127*F*). In contrast to the bright sunlight that floods the lagoon fringe of the northern barrier reef, for instance, the bottom of biotope IV is in great part not really well lighted—probably in large degree because of dispersion by suspended sediments that are not intrinsically injurious, but also because of slightly greater depth. It is consistent with this suggestion that coral growth is relatively vigorous in the shallower and better lighted parts even of biotope IV (facies 13, pl. 124*B*).

An area of reef patches apparently somewhat similar to this is described briefly by Stephenson and others (1931, p. 87–88, fig. 6)² south from Lizard Island, behind the Great Barrier Reef, and I have described a comparable environment at Onotoa, Gilbert Islands (Cloud, 1952, p. 25–27, 69–70). It is a very common type of habitat in the quieter waters of reef lagoons and banks but is not ordinarily described in detail.

BIOTOPE V. DREDGED AREAS, MAINLY OF LAGOON PROPER

Biotope V includes facies 14, accounting for most of the dredged areas, and facies 15, which segregates several unimportant shallow artificial channels and basins. Most of biotope V consists of a sporadically dredged harbor area between 25 and 45 feet deep, but shoaling to less than 10 feet and attaining a depth of slightly more than 50 feet. Although only parts have been dredged, the whole area represents a modified and disturbed environment of a type not infrequent in and adjacent to tropical harbors.

Unfortunately the bottom in this area could not be observed extensively. The principal lagoonal currents sweep southwestward through the center of the lagoon beyond it, and the water is for the most part murky with suspended debris. Bottom observations at a few places suggest the undredged parts to be mostly of limesand, with little or no living coral and with little loose coral debris. However, an east-to-west fathometer traverse through the middle of the area revealed scattered low mounds of presumably dead coral-algal rock rising to within 30 feet of the surface above a presum-

ably limesand bottom that averages more than 40 feet deep.

The molluscan fauna of the nearer shore limesands is probably fairly well illustrated by the empty shells collected from dredgings at locality P. Most of these are excellently preserved; the bivalves are paired and include distinctive sand-burrowing forms. The abundance of Foraminifera (see chapter H) from the bottom samples in this area is also unusual and suggests that many of them actually live here. Their existence may be favored by poor lighting and disturbed bottom, tending to screen out both competitors and predators.

THE CONTIGUOUS MOATS

Although the western peripheral reef has all the characteristics of a barrier reef in its middle part, it grades to a fringing reef at its north and south ends. Thus, to the north and south, the constantly inundated strip between the reef flat and the shore becomes a moat instead of a lagoon (biotopes VI and VII, facies 16–19). These moat areas differ from the lagoon proper in being everywhere less than 1 fathom deep at low tide, and in possessing a proportionately greater area of hard bottom and gravel. They are comparable in their location and general habitat characteristics to the moats of Low Isles of the Great Barrier Reef, as described and illustrated by Stephenson and others (1931, p. 45–50, fig. 2, pl. 1, photographs on pls. 4–10). Some parts of the moat bottoms of western Saipan, however, are so like those of the contiguous lagoon that they are classified with lagoonal biotopes and facies, and others are grouped with the intermediate biotopes to be described. No particular brief is held for the exact points at which transition is indicated to take place from moat to lagoon. However, the preference is not entirely arbitrary, being based on small boat navigability.

As the physical transition from lagoon to moat is gradual, so also is that in biotic characteristics. Thus, the general physical and biotic descriptions of sandy lagoon bottom and coral-algal reef rock that have already been made apply in a general way to the contiguous moats of western Saipan, except for depth. The moat areas here included, however, are different from those on the landward parts of the fringing reef surfaces at south Saipan and Fañunchuluyan bay in that they are less intimately related to the fringing reef flat. Still different moat-like characteristics are described by Hiro (1936, fig. 3 and text) for a permanently inundated fringing reef flat on the eastern shore of Palau, although his *Diplanthera* and *Acropora* zones suggest the patches of angiosperm and staghorn coral such as are found in the moats of both Saipan and Low Isles (Stephenson and others, 1931, p. 49).

² The expression "reef patch" is used as employed by Stephenson and others as alternative to patch reef, elsewhere considered as a general designation for minor reef prominences (Tracey, Cloud, and Emery 1955, p. 3, fig. 1).

BIOTOPE VI. OUTER MOAT FLOOR OF INTERSPERSED CORAL-ALGAL BOSSES WITH GRAVEL AND SAND

Biotope VI includes intergrading facies (16 and 17) which differ slightly in the proportions of their coral faunas and bottom characteristics. The bottom, which is everywhere less than 6 feet deep, consists of patches and small irregular bosses of dead and living coral and coralline algae interspersed with patches of calcareous gravel and limestand. It might be called the zone of *Pocillopora damicornis caespitosa*, for that subspecies is the most abundant coral found here. *Acropora pali-fera* is also common, as in the lagoon fringe of the barrier reef, which this area somewhat resembles; but the relative abundance of the two species is reversed in the two biotopes, and *Porites lutea* is much less conspicuous here than in the lagoon fringe of the barrier reef. Calcareous gravel preponderates over limesand in this moat biotope also, a general distinction from other coral-liferous areas in the western shoal waters. Generally similar habitat conditions and associations are described for the outer fringing reef moat at Murray Island, Great Barrier Reef by Mayor (1918, p. 20-30).

BIOTOPE VII. BOTTOM MATTED WITH LIVING CORALLINE ALGAE

Biotope VII, consisting of facies 18 and 19, is only 1 to 3 feet deep at low tide. It is almost continuously matted with coralline algae, but also includes sparse to abundant growth of *Halimeda* and other green seaweed. Locally it also includes scattered calcareous pebbles and cobbles and minor patches of limesand. At a few places small algal heads rise above the surrounding shallow bottom.

HABITATS COMMON TO LAGOON AND MOAT

The habitats here described are transitional from lagoon to moat. They include bottom of nonvegetated limesand and calcareous gravel at depths less than 8 feet (biotopes VIII and IX, facies 20-24).

BIOTOPE VIII. CLEAN LIMESAND WITH LITTLE OR NO SEAWEED

Biotope VIII, represented by facies 20 to 22, includes constantly shifting limesands at depths less than 8 feet. Almost the only inhabitants found are *Holothuria atra* (which is very abundant locally), the little black and white crab *Lissocarcinus orbicularis* which inhabits the cloaca of *H. atra*, a scattering of *Linckia laevigata*, occasional hermit crabs, and locally abundant tube-aggregating annelids. Such impoverished habitats are very common in the lagoon and bank environments of the coral seas everywhere.

BIOTOPE IX. MIXED LIMESAND AND CALCAREOUS GRAVEL AT REEF FRINGE OF VERY SHALLOW LAGOON OR MOAT

The southern third of the western reef flat is fringed at its lagoon or moat margin by a strip of gravel and coarse limesand bottom less than 5 feet deep. It comprises biotope IX, facies 23 and 24. Such bottom is found at the landward edge of both barrier and fringing reef. Although it consists mainly of coarse detrital sediments and associated living organisms, this biotope includes irregular patches of living coral at some places.

ORGANIC REEFS AND REEF BENCHES

Organic reefs and coral-algal rock are the unifying elements of the composite shoal-water habitat of Saipan. The community that makes and inhabits the areas of reef and reef rock includes not only all of the corals and coralline algae, however. It also takes in the great bulk of the hydrozoans, gastropods, pelecypods, decapod crustaceans, echinoderms, sponges, polychaete annelids, and sipunculoids, which are limited to or found in or on the reef rock. Some of the unusual living habits of these organisms will be reviewed later, and the recorded biota is listed in full in the appendix. Here it is sufficient to note that, leaving aside the holothurians and Foraminifera, a very large proportion of the total fauna is found on the reefs and that such reefs are widely scattered among or near all other habitats.

The peripheral reef complex that surrounds the island includes a barrier reef off a good part of the western side, and a fringing reef around much of the remaining coast. Some fringing reef benches are awash all the way to the shore, but others have shallow moats between reef front and shore which are not here separated from the reef flat proper.

The conspicuous builders of the barrier reef are the true reef corals, algae, the stony alcyonarian *Heliopora*, and millepores. These calcareous organisms and subsidiary associates construct a wave-resistant frame within which sediments of various sorts are trapped and become a part of the total reef mass.

The fringing reefs of the east, north, and south coasts support a larger variety of algae and seemingly a smaller variety of different sorts of invertebrates than does the western barrier reef with its associated structures. This may result from wind, current, and surf conditions; from the fact that the fringing reefs are erosional benches with but a thin living film; or from a combination of reasons. The conspicuous veneering organisms of the present fringing reef surfaces are calcareous algae, vermetid gastropods (pl. 139), and at places corals and millepores. A volumetrically much

more important reef-building biota of algae and corals lives on the fringing reef fronts beneath the surf line.

Narrow stretches of intricately terraced fringing reef extend to the height of normal high tide splash level. Where they tend to step upward from the reef edge toward the shore (as they commonly do) they are called terraced ramps, and isolated pinnacles oceanward from the reef edge are terraced pedestals. The paddylike or hot-spring-like pools or basins of such areas owe their distinctive form to combined erosion and construction. While the margins are being built up or maintained at a level by organic growth, the individual basin floors are being lowered, probably by a combination of solution resulting from diurnal and other changes in pH caused by organic processes, organic solution, and the abrasive effects of algal-browsing snails and chitons.

Besides the peripheral reefs, the broad habitat category of organic reefs includes the smaller moundlike, platformlike, and irregular masses inclusively referred to as reef patches. These are intermixed with various lagoonal biotopes, but separate larger reef patches and reef clusters are here grouped as a distinctive category of organic reef.

The three principal habitat subdivisions included under the heading of organic reefs are: reef patches, peripheral reef surfaces, and the reef front. Peripheral reef surfaces have been much described and are generally divisible into flourishing and truncated, while the truncated surfaces in turn are divided into rocky surfaces and sediment-mantled surfaces. Reef patches are less commonly described. Descriptions of the reef front have emphasized especially the striking configurations along the reef edge.

MINOR REEF STRUCTURES

Many reef patches are included with or constitute the distinctive factor in lagoonal biotopes, as discussed earlier (pl. 135*B*). Only those individual reefs or reef-clusters large enough or isolated enough to be mapped separately are considered under the single biotope described below (biotope X, facies 25-30).

BIOTOPE X. LARGER REEF PATCHES AND REEF CLUSTERS OF LAGOON AND OFFSHORE SHELF

The various irregular to subequidimensional mounds, small platforms, pinnacles, and clusters of living and dead coral-algal rock, included under biotope X are subdivided into 6 facies on the basis of structure, dominant reef-building organisms, and broad habitat setting. All reefs and reef clusters here included rise above deeper surrounding bottom to or very near the surface of the sea. Most are within the barrier reef lagoon, but some reach above the offshore shelf that lies

seaward from the barrier reef, and those off Muchot point occupy a position corresponding to that of the barrier reef itself. Reef patches occur in most of the lagoon and bank waters of the tropic seas, and their characteristics have been described for parts of the Great Barrier Reef (Stephenson and others, 1931, p. 87-88), the Gilbert Islands (Cloud, 1952, p. 25-27, 69-70), and other areas. Those of the Gilbert Islands are structurally similar to the reef patches at Saipan, although for the most part proportionally taller and narrower and thus better designated pinnacles than patches. *Heliopora* patches are apparently common in many parts of the Pacific. The "coral knolls" of Emery, Tracey, and Ladd (1954, p. 147) and of Wells (1954, p. 401) are apparently much larger and taller than the reef patches of the present report and do not as a rule reach so close to the surface.

PERIPHERAL REEF SURFACES

The peripheral reefs are the island's first line of defense against the ever-attacking sea (biotopes XI-XIII, facies 31-43). The surfaces of these distinctively linear structures are rhythmically exposed to the pounding of the surf; the corrosive and abrasive effects of the currents that flow reversibly across them; and the desiccation and abrupt fluctuations in light, temperature, and salinity that result from periodic exposure to a changing atmosphere. That they hold their own and even built outward against the sea to some extent is proof enough of their ability to damp the pounding waves and extract energy from them in the form of oxygen and nutrients.

This building outward, however, is accomplished mainly by the organic complex of the reef front. The organisms of the reef flat themselves are mainly streamlined, cranny dwelling, or yielding forms that manage to survive, patch over breaks, and by various devices cement or anchor some of the detritus that lodges against and around them. Here are found stubbily branching corals like *Acropora humilis* (*A. leptocyathus* of some authors); encrusting corals like *Montipora*; pavement-type coralline algae; articulated and flexible algae that yield to the waves and add to the sediments; innumerable *Baculogypsina*, *Calcarina*, *Marginopora* and other microorganisms that live on the algae; and a great abundance of brittle stars and soft-bodied nestlers of various sorts in every available crack and cranny.

The life that exists here maintains the surface of the reef at the low tide level of a rising sea, if it does not rise too fast; and it creates a structure that yields way stubbornly under conditions of falling sea level.

Besides the two biotopes that closely fit the descrip-

tion given (XII and XIII), a third biotope of the peripheral reef surfaces includes a lagoonward fringe of vigorously growing coral that is classified here for reasons that follow:

BIOTOPE XI. LAGOON FRINGE OF NORTHERN BARRIER REEF

Biotope XI, comprised of facies 31 and 32, includes a concentric belt of varied and vigorous coral growth at the lagoon fringe of the barrier reef. It occupies a position relative to the reef flat itself comparable to that of biotopes VI and IX, but with a much greater abundance and variety of corals than VI and with almost no physical resemblance to the mainly gravel and sand bottom of IX. Its characteristics are in large degree intermediate between those of the lagoon and the reef proper. The lagoon fringe is regarded as a proper part of the peripheral reef, however, not only because the growth of frame-building organisms here exceeds sedimentation, but also because the corresponding area southwest from Mañagaha islet (pl. 124B) is firmly annexed to the reef and even appears to be expanding lagoonward to take in other reef patches.

Of the two facies included, one is but a small and somewhat aberrant prong at the northeast end that consists of a dense thicket of staghorn *Acropora* assigned here mainly for convenience.

The biotope at large is an area of very abundant and varied coral growth in which the greatly preponderating species are *Acropora palifera* and *Porites lutea*. *Acropora palifera* is tan colored in life and occurs in rough encrustations and palmate clumps; *Porites lutea* is greenish, yellowish, or blue, and grows as massive individual hemispheres or as parts of other coral-algal masses. Between the closely spaced coral-algal masses the mainly limesand bottom reaches depths of 7 or 8 feet. This *A. palifera*-*P. lutea* zone is also inhabited by a rich variety of other forms of life that are indicated under appropriate stations in the appendix. Besides the corals mentioned, *Heliopora* and various astreiform and meandriiform corals and crustose coral-line algae are locally common. At places there also seems to be a somewhat greater concentration of *Porites* toward the reef and *A. palifera* toward the lagoon. The coral-algal bosses to whose construction *A. palifera* contributes so conspicuously are highly irregular and full of crannies and overhangs which are locally inhabited by comatulid crinoids and other organisms (pl. 127D). Much of the surface of such bosses is dead, and large areas of both the bosses and *Porites* heads are gnawed bare by scarids and other browsing fish (pls. 130, 131).

Among habitats described elsewhere the so-called anchorage coral zone at Low Isles of the Great Barrier

Reef (Stephenson and others, 1931, p. 85, pl. 17; Mantton, 1935, p. 306, pl. 15) seems most like biotope XI.

BIOTOPE XII. REEF FLAT OF BARRIER REEF AND CONTIGUOUS FRINGING REEF

Biotope XII, consisting of facies 33 to 37, includes the surfaces of the western offshore reefs—typical truncated reef flats that are for the most part barely awash at low tide. Intertidal erosion has reduced them to pavementlike surfaces that are patchily veneered by renewed growth of coralline algae and, in lower places, by stubbily branching, encrusting, or otherwise streamlined corals. Foraminifera of several sorts and the soft algae on which they live, thick-shelled reef-dwelling gastropods, and an abundance of the brittle star *Ophionereis porrecta* and other crevice-dwelling organisms round out the biota. The five facies into which this biotope is subdivided are based on variations in dominant veneering organisms. Reef flats at many places are similar, but differ in detail. Wells (1954, p. 401-406, figs. 119-120) has summarized the common features for several widely separated areas.

BIOTOPE XIII. NARROW FRINGING REEF OF EAST, NORTH, AND SOUTH COASTS

Facies 38 to 43, which comprise biotope XIII, show some rather broad variations, but are grouped together because they are all fringing reefs of one sort or another. They comprise intertidal to very shallow shore benches that are subject to nearly similar conditions of heavy surf and to abrupt and extreme variations of temperature and salinity. These surfaces are largely erosional rather than growth features, and their near levelness or very gentle slope points to leveling processes such as solution and organic abrasion as the controlling factors.

The fringing reef habitat around Saipan is a zone of richly veneering algae, both soft and coralline, but with generally sparse and little varied coral growth except locally at the reef edge and generally down the reef front. It is also characterized by a rich and distinctive gastropod fauna of cones, cypraeids, muricids, cymatiids, and vermetids that contrasts with that of other habitats in the area and particularly with those not classified as organic reefs. Strombids, which are characteristically lagoon and limesand dwellers, appear to be very rare or absent. The decapod, annelid, and sipunculoid fauna that is so abundant in the living and recently dead coral-algal rock of the lagoonal reefs and the lagoon fringe of the barrier reef was not collected here only because little rock-breaking was done at collecting sites in biotope XIII. However, it seems from inspection that these organisms may be in part

supplanted here by the abundant gastropods which seem to have taken over many of the scavenging niches in this area, perhaps because boring is more difficult and natural crannies and pinnacles fewer.

The preceding paragraphs cover the general features of biotope XIII, and the characteristics of comparable reef flats elsewhere are discussed by Wells (1954) as mentioned under biotope XII. A few unusual features of the facies that constitute biotope XIII deserve brief elaboration, however.

The only occurrence on Saipan of a good development of the distinctive purplish-red algal ridge so common to the outer edge of many Pacific reefs is in facies 38 at Fafiunchuluyan. The reason for this is not apparent. The usual ridge builder, the crustose coralline alga *Porolithon oncodes*, is found at other localities on Saipan (pl. 128C) but for some reason fails to form a well-defined reef-edge ridge at such places. At some places also facies 38 and 39 show a concentric zonation reminiscent of that described by Tokioka (1953) for the Tokara Islands at the north limit of reef formation (29°–30° N.).

The benches included in biotope XIII in part cut across former surfaces of growth or erosion and in part into Pleistocene and Tertiary limestone and even volcanic rock. Facies 38 has a well-defined reef edge and moat. Holes and shallow channels such as locally indent the surfaces of facies 39 and 40 appear to be the result of solution or abrasion or both, and are commonly in part roughened by renewed organic growth. Such holes and channels are characteristically floored with thin patches of calcium carbonate gravel and sand, and at places support sparse to even abundant living coral such as *Porites* and occasional faviids. Facies 41, 42, and 43 are mostly upper intertidal features that are either building up or holding a level through the work especially of vermetid gastropods at the surface and algae at the reef front.

The stretch of reef referred to facies 42 was not examined closely, but it appears to represent an unusual and probably biotically rich environment. Whether the holes described are solution features or simply residual between a constructional gridwork is unknown, although reduction by solution in the past is strongly suggested by the many pinnacles that rise well above high tide level as if residual from reduction of a once subaerial bench. A large blowhole well back on this bench (pl. 137D, E) indicates the local presence of channels beneath it.

Facies 43 is a striking but sporadically occurring sequence of narrow terraced-ramps, pedestals, buttresses and various combinations of shallow rimmed-pools and basins (pls. 137F, 138, 139B). The latter appear to

result from a combination of rim veneering and construction to uniform levels by vermetid gastropods and algae, and deepening of the pools and basins through the concurrent effects of solution and the algae-browsing activities of gastropods and chitons. This facies extends above high tide toward the limit of constant wetting by heavy spray and splash. The microtopography is like that of hot-spring deposits or terraced rice paddies, and the biota consists of varied soft ("fleshy") and coralline algae, vermetid gastropods, occasional boring sipunculoids and pelecypods, and a sparse fauna of corals (especially *Porites*), crustaceans, and fish. The general structure and organic composition recalls the "serpentine reefs" of south Bermuda (Agassiz, 1895, p. 253–269, pls. 22–25).

REEF FRONT

BIOTOPE XIV. REEF FRONT OF BARRIER AND FRINGING REEFS

The important habitat of the reef front reaches downward from the reef edge to the dwindle point of living coral and coralline algae between 5 and 10 fathoms or so. It comprises a single biotope (XIV), divisible on Saipan into 5 intergrading facies (44–48) according to the abundance and nature of the radial reef front grooves, the balance between constructional and erosional factors, and the nature of the rocky substrate. The characteristics of the reef front biotope at Saipan are similar to those of reef fronts at many other places, as described by authors of references cited under a later discussion of the groove and spur system (p. 406–410).

SHALLOW SEA BEYOND THE BARRIER REEF

The last major habitat category to be considered (biotopes XV and XVI, facies 49–52) has a general resemblance to the lagoon environment. The sediments of the shallow sea immediately beyond the southwestern barrier reef, however, tend to be better sorted and locally finer grained than those of the lagoon habitats, and there are a number of differences in the details of their respective biotas. Neither sedimentary nor biotic differences can be fairly evaluated on the basis of the few stations available from beyond the reef, to be sure; but it does seem that there is a general reduction in the abundance and variety of corals, particularly among the faviids, acroporids, and seriatoporids, which are so common among the lagoon reefs and associated with the barrier reef itself. Concurrently the common mollusks, crustaceans, and sipunculoids of the latter environments tend to be rare or absent in the reef rock beyond the barrier reef, and different species of polychaetes are found (table 6). Other differences between the lagoonal and off-reef environments include the more

uniform chemical and physical characteristics of the off-reef waters and the distinctive pelagic fauna that patrols them.

As the fronts of ocean reefs for the most part pitch steeply to great depths, few described areas compare with the shallow sea biotopes at Saipan. The seaward reef slope around Low Isles of the Great Barrier Reef (Stephenson and others, 1931, p. 64-67, 93; Manton, 1935, p. 286-290, 293-299, pls. 1-18) is a composite of reef front and very shallow sea environment with generally gentler slope, much richer coral growth, and much less sand than the shallow sea environment at Saipan. The leeward shelf in the anchorage area beyond the reef at Onotoa in the Gilbert Islands (Cloud, 1952, p. 25, 69-70, fig. 2) is much more like Saipan, and probably a good part of the shallow waters around reefs that set in from the edges of their platforms will be found to show the same characteristics.

BIOTOPE XV. LIMESAND BOTTOM

Biotope XV includes the essentially clean limesand bottom that reaches seaward from the barrier reef and adjacent fringing reef. It appears to be an area of sparse and little varied life, but observation was limited and details are not well understood. Two facies (49 and 50) are differentiated on the basis of the distribution of reef patches.

BIOTOPE XVI. INTERSPERSED REEF PATCHES AND LIMESAND

Biotope XVI includes those two facies (51 and 52) of shelflike seaward-extending bottom that are characterized by scattered mounds and patches of dead and living coral-algal rock surrounded by limesand. A small fauna of boring and crevice-dwelling mollusks, sipunculoids, crustaceans, and ophiuroids was obtained from the dead coral-algal rock at station E7 in facies 52 (table 6). According to Austin Clark, the asterinid starfish *Disasterina spinulifera*, which was obtained here, was previously known only from the holotype, obtained at Broome, West Australia.

NATURE OF THE ORGANIC REEF COMPLEX

BASIC FEATURES

Geologically the reef complex is an aggregate of calcium carbonate secreting and frame-building organisms, associated biota, and mainly biogenic sediments. Ecologically it is an essentially steady state oasis of organic productivity featured by high population-density, intense calcium metabolism, and complex nutrient chains, and generally surrounded by waters of relatively low mineral nutrient and plankton content. Any reef

complex at any given time is the resultant of its nutrient chains and their disintegration products. The reef environment, therefore, cannot be considered well understood until the organic interdependencies and the life histories of at least the principal interdependent organisms are worked out in detail. The perspective of any reef study is improved, however, by review of the broader linkages in the chain as they are understood at the time.

The first step in the nutrient chain is photosynthetic elaboration of basic foodstuffs and oxygen by both macroscopic and microscopic plants, which receive their nutrient salts in solution or from a symbiotic associate. These elemental plant foodstuffs, the microfauna which they support, and other organic particles in suspension or saltant motion support various ciliary-, filter-, and tentacular-feeders, including the corals. Because of their sessile nature these organisms require a constant flow of water to carry their food to them (except insofar as it may be formed within their tissues). This water, moreover, may not contain too much undigestible sediment in suspension, and it must also be well oxygenated.

Consideration of oxygenation and nutrient relations invariably leads to review of the symbiotic algal associates of corals and other reef-dwelling animals. Besides the minute zooxanthellae, these algal symbionts in a much broader sense include also the filamentous greens that ramify the calcareous skeleton in layers in and below the polyp zone, and may outbulk the zooxanthellae as much as 16 to 1 (Odum and Odum, 1955, p. 297-302). The oxygen produced photosynthetically by these two groups of algae almost meets respiratory needs in the usual coral-algal association over a 24 hour period (Odum and Odum, 1955, p. 297), and their dependence on light narrowly limits the depth range of reef-building coral growth. There is, however, wide and vigorous disagreement about the primary function and relations of the zooxanthellae in particular, which live within and color the fleshy tissue of their host and which are widely distributed among the sedentary reef fauna. An internal microflora of these algae is maintained by all true reef-building corals; many alcyonarians, gorgonids, actinarians, and zoanthids; the hydrozoan *Millepora*; some hydroids; the giant-clams *Tridacna* and *Hippopus*; and even some Foraminifera, flatworms and ascidians (Yonge and Nichols 1931a, especially p. 173; Yonge 1940, p. 365-369; Yonge, Yonge, and Nichols 1932; Pratt, 1905, p. 347-349; Gohar, 1940, p. 41-48, 1948a, p. 19-21; Allee, and others, 1949, p. 246, 712-713). What the several partners to such association derive from and contribute to their particular symbionts is the question.

Although Yonge believed unequivocally (1936, p. 318-319) that the tridacnids "farm" and feed upon their zooxanthellae, he denied with equal emphasis that corals get any nutriment from their zooxanthellae except possibly in very unusual circumstances. This conclusion, moreover, was based on exhaustive physiologic and experimental studies of 40 scleractinian genera (Yonge, 1930a, 1930b, 1931, 1940; Yonge and Nichols, 1931a, 1931b). As a result of these studies Yonge was convinced that the algae are important to reef corals in supplementing their oxygen supply and speeding up metabolism by rapid removal of their nitrogenous and phosphatic waste products, but that the corals feed almost exclusively on zooplankton and mostly at night (confirming Murray, 1889, p. 425; Vaughan, 1912, p. 159-161; and Vaughan, 1916, p. 96-97). In his summary paper, Yonge (1940, p. 356) reaffirmed not only that the tentacles of corals never accept and their mouths never swallow vegetable matter, but also that the digestive enzymes are those of a specialized carnivore (mainly protease, weak lipase and glycogenase; amylase in zooxanthellae only: Yonge, 1930).

It might seem that this should have settled the question, but only a few years later Vaughan and Wells (1943, p. 58-59) were willing to allow some likelihood that the zooxanthellae of corals might be a secondary food supply—a possibility suggested by the fact that reef-building corals remain alive in darkness after excreting their zooxanthellae if fed, but eventually die unless fed. More recent and stronger support for a nutritional relationship between corals and zooxanthellae comes from Sargent and Austin (1954, p. 299) based on their own work in combination with that of Kawaguti (1937), Verwey (1931), Yonge (1940) and Yonge, Yonge, and Nichols (1932), on nutrient and oxygen production and exchange. They conclude (1) that the photosynthetic products appear to "remain within the coral colony"; (2) that "the external supply of organic nutrient is inadequate to support a coral colony on the reef, but the daily production of organic matter by its contained zooxanthellae can be sufficient"; and (3) that under certain conditions observed in nature "the corals must derive organic matter from the algae or die." Gardiner (1903, p. 206), as is well known, had much earlier concluded on more casual evidence that most reef corals derive nutriment from, and some subsist upon, their zooxanthellae.

That some cnidarian coelenterates are in fact nutritionally dependent upon their zooxanthellae seems to be shown conclusively by the experiments of Gohar (1940, p. 43-48; 1948a, p. 19-21) on certain alcyonarians that cannot feed at all in the usual sense and die in darkness even if food is provided. Gohar's work gives strong

support to the conclusion earlier reached by Edith Pratt (1905, p. 347-348, 351) that the development of the digestive surfaces and abundance of zooxanthellae vary inversely. He thus arrives at the eminently reasonable view that there is probably "a complete chain of conditions in the Coelenterata from animals feeding exclusively on animal diet to animals depending, more or less, completely on their harboured algae for their food supply" (Gohar, 1940, p. 42). This is supported by F. M. Bayer of the U. S. National Museum who informs me that certain gorgonians with few or no zooxanthellae have numerous nematocysts, strongly developed digestive tissue and polyps that are frequently found to contain food material, whereas others, living closely associated with them, have abundant zooxanthellae, no nematocysts, reduced digestive tissue, and polyps that are never found to contain food. It is apparently established then that not only *Tridacna* and adult *Convolvuta* but also some cnidarians subsist on their zooxanthellae; while, as Hickson (1909, p. 339, 374) has observed, it seems most improbable that the coral polyp with a complete set of organs and enzymes for catching, swallowing, and digesting animal food never uses this equipment.

From the experiments and observations that have been so briefly reviewed it seems that the relationship between zooxanthellae and host is mutually trophic, with a very wide range of dependency. Besides the soluble or solid nutrients that each may receive from the other, the zooxanthellae, like other plants, presumably also manufacture an oxygen surplus. Together with that produced by the much larger bulk of filamentous algae at the same and lower levels, this appears to fall just short of balancing total respiration within a given coral-algal mass over a 24-hour period.

Whether their dependence on their algal associates be primarily nutritional, primarily respirational, or partly both, in nature reef-building animals (as well as plants) dwindle abruptly in variety and numbers below the well-lighted, well-oxygenated surface waters³ (Verwey, 1931). This effect of varying light intensity is graphically illustrated by the uneven coral growth on the piers of the landing wharf at Fort Jefferson, Dry Tortugas (pl. 127F; Vaughan, 1916, p. 97).

Given ample food, and oxygen to convert it to energy, the existence of a flourishing reef fauna depends on a warm average temperature and a low enough content of

³ A good example of the limiting effects of the zooxanthellae with regard to light is furnished by the strikingly different living habits of two well known calcium carbonate secreting hydrozoans, *Millepora* with zooxanthellae and *Stylaster* without (Yonge, 1940, p. 369). *Millepora* lives in exposed locations in relatively shallow water; *Stylaster* has a great depth range and in shoal waters is found only in recesses and beneath overhanging surfaces where its permanently red arborescent clusters are suspended in inverted position.

suspended sediment for the living coral polyps easily to reject (or assimilate) what settles on them. Among other influences of temperature it probably affects the availability of calcium carbonate for skeletal increment, an essential factor in reef nutrition.

Most of the crustose coralline algae, appear to be favored by conditions broadly similar to those that favor the corals themselves, although they make their own food. They seem to grow with greatest vigor, however, at sites of very strong or relatively weak current movement where corals are subordinate.

Fleshy and filamentous algae (hereafter called soft algae) of considerable variety also grow vigorously on rocky bottom in areas of turbulence and constant flow. However, some noncoralline algae (*Halimeda* and *Caulerpa*) seem to be most favored by relatively stable detrital bottom and slight but appreciable depth, such as favor especially the growth of the marine angiosperms (*Enhalus*, *Zostera*, *Halophila*, *Posidonia*, *Cymodocea*, and others; Moldenke, 1940).

Depending, then, on the extent and duration of relatively stable sediments in which flowering plants can take root, the depth of water between peripheral reef and shore, and latitude,⁴ the lagoon and moat areas are likely to support marine "meadows" of sessile green plants (pls. 123B, 125B, C, 126B) on which flourish numerous scum- and diatom-browsing and detritus-feeding snails, vegetarian fish, and microorganisms. Because of their importance in the biologic economy of the reef complex and their poorly understood relations to its structure, it is desirable to consider briefly the distribution and hydrodynamic properties of such areas. Toward the beach where the current is not strong such growths simply spread out or recur in no very consistent pattern (pl. 125B). Where exposed to the strong currents that flow across the reef, however, the angiosperms in particular flourish at some distance inshore from the reef front, down current from the area of most vigorous movement of the detritus that is swept lagoonward beyond the reef (pls. 123B, 125C). In plate 123B particularly can be seen the linear distribution of dense *Zostera* and *Caulerpa* (a green alga), which has retarded the flow of sediment from the reef into the deeper part of the lagoon as a sort of antibarrier reef.

Molinier and Picard (1952; also Aleem, 1955) have described how the marine angiosperms may invade loose sediments at depths shallower than 35 to 70 meters, or even rocky surfaces following the fixation of a thin layer of sediments within an algal mat. Once rooted, the continued growth of such an angiosperm cover may

provide a baffle that extracts mineral particles from passing currents and builds up the bottom concurrently with upward growth of the grasslike plants. In the French Mediterranean such areas have built up accumulations of sand as much as 6 meters thick, with continuity of rhizomes from base to summit indicating about 600 years accumulation and forming a barrier-reef-like structure on the shoreward side of which coarser sediments accumulate. With reference to direction of current movement, this is comparable to the function of the linear vegetation baffles that retard sediment flow lagoonward (shoreward) from the barrier reef as shown in plates 123B and 125C of the present report. H. and G. Termier (1951) have discussed such habitats in coastal areas with special reference to their possible counterparts in the past. Although this useful summary deals with a nearly opposite variant of the habitat from that discussed here it includes pertinent detail on commonly associated organisms (Termier and Termier, 1951, p. 17-18) and possible geologic counterparts.

The triturated plant matter and other organic debris that is left over from the primary trophic activities of the meadowlike areas is partly eaten by ingestors of bottom sediment, such as holothurians, and some polychaete annelids and fish, and partly taken up by sedentary feeders and burrowers, such as other polychaetes, certain pelecypods, and some gastropods. Predaceous and ectoparasitic gastropods, starfish, and some true fish feed on the pelecypods and annelids. Other fish browse on coral or on algal tufts on coral-algal rock in the area, and crustaceans of varied feeding habits are found throughout.

Big fish eat little fish, and eventually the scavengers get a share of their remains and those of the other organisms that die natural deaths. Included among the scavengers are various polychaetes, crustaceans, gastropods, ophiuroids, and fish. What they miss is eventually returned to the nutrient cycle in chemical form by bacteria, except for the hard parts, which constitute a continuously accumulating sedimentary byproduct of considerable geologic and ecologic importance.

An individual reef can be comprehended only insofar as the effects of these basic processes in constructional-sedimentary terms are interpreted in the perspective of local geologic history.

SYMBIOSIS AND COMPARABLE ASSOCIATIONS

Symbiosis is the term applied to the habitually intimate living together of specific organisms, without regard to benefit or harm from the association (Allee and others, 1949, p. 253, 710). It includes mutualism, from which the partners enjoy reciprocal benefits; para-

⁴ *Halimeda*, for instance, may become overcalcified in direct bright sun, for it seems to flourish best at increasing depths or shadowed locations equatorward.

sitism, in which one of the associates is adversely affected; and commensalism wherein neither associate is harmed and one may benefit. Purely fortuitous association of organisms, as of encrustations of coral, coralline algae, bryozoa, and Foraminifera on one another or on other organisms (pl. 129C) is a matter of tolerance or competition, not regarded as a category of symbiosis.

The prime example of mutualism in the reef complex is the association of the flagellate microscopic algae known as zooxanthellae with reef-building corals and other members of the reef community, discussed above. Other long-known (Sluiter, 1888), and much discussed examples of mutualism are found between species of the little pomacentrid *Amphiprion* (and related fish) and various large anemones, commonly of the genus *Stoichactis*.

Amphiprion is characteristically found in oppositely sexed pairs (rarely as many as 7 or more individuals) among the stinging tentacles of its hosts, which afford it protection and perhaps some nutrient in exchange for services which may include oxygenation and food supply (Verwey, 1930, p. 307-308, 320-332; Gohar, 1948b, p. 36). Verwey records revival of drooping anemones supposedly accomplished through the stirring of a water current by the large pectoral fins of the fish. He interprets this as a deliberate act like the bringing of food, which Gohar describes as sometimes involving the dragging to the anemone by *Amphiprion* of "living fish almost their own size." In other circumstances, the little pomacentrids may help their host anemone by removing the debris from it after a big meal. As described by Gohar the anemone at such time "opens its mouth very wide. * * * The remains of the meal can be easily seen in the exposed coelenteron and the fish cleans them out, devouring whatever it may find edible and removing the rest." Verwey and Gohar both deny that the fish either leads prey to the anemone or seeks refuge in its coelenteric cavity, as is sometimes stated (Saville-Kent, 1893, p. 32-33, 145; Weber, 1913, p. 335; Roughly, 1947, p. 51-53). An easy prey to predators away from its host anemone, *Amphiprion* is ordinarily "protected" by the latter. Gohar (1948b, p. 38-39), however, states that the anemone does occasionally kill and devour fish of the same species as its associate, and that even accepted fish are eaten when dead or moribund—a situation which strongly implies that immunity is voluntary and probably tactile or physiological. Experimental work is needed to determine which and how; but scientists seem to be as easily bewitched as anemones by this gaudy little fish, with the result that their accounts of its behavior so far have been more romantic than analytical.

In any event, it seems unlikely that oxygenation can be of general importance because the anemone-fish association occurs in strongly flowing waters as well as calm ones. Also because the association is not restricted to particular species or genera of anemone, it is presumably "learned" rather than instinctive. Thus Red Sea *Amphiprion* are accepted by Mediterranean anemones in the aquarium at Monaco (personal demonstration by J. Garnaud), and in the Danemarks Aquarium at Charlottenlund Dr. George Mandahl-Barth showed me amphiprions in good health after 20 years without anemones. Excellent photographs of associated fish and anemones are those of Marden (1956, p. 174-175).

Only one example of known parasitism among the reef community at Saipan can be cited, although endoparasites will surely be found when looked for, and the tiny pyramidellid gastropods which are abundant in the sediments at some localities are common ectoparasites of tubicolous annelids and pelecypods in other areas (Abbott, 1954, p. 288-289). The association referred to as known parasitism is that between the pearl fish or fierasfer, *Carapus*, and certain echinoderms; an association which in some ways approaches predation on the part of the fish. Arnold (1953) has described in detail the ontogeny, habits, and associations of *Carapus acus* (Brunnich) which feeds on the gonads and brachial trees of three species of Mediterranean sea-cucumbers. At a prejuvenile stage the then completely dependent fish dies without effort to relocate when removed from its host, but juveniles and adults are able to resettle when removed or discharged by evisceration of the host (or perhaps to come and go). At Saipan, during April through mid-May of 1949, *Carapus mourlani* was obtained from the body cavity of every one of a half-dozen specimens of the box starfish *Culcita novae-guinæ* (pl. 127A) that was opened, and the starfish gonads at this time were scarcely visible. In June and early July the gonadal clusters of the starfish then opened were well developed, but none of the culcitas contained *Carapus*. Different localities were involved, but at the time a seasonal difference was inferred. During collecting in July and August 1951 at Onotoa, at 2° south in the Gilbert Islands, another species of *Carapus* was obtained from holothurians and even an echinoid (*Echinothrix*),⁵ but not to my recollection in *Culcita*. At Bikini the host is *Culcita* and the incidence is about 50 percent (Schultz, 1948, p. 305). Whether the variation of the host is a matter of species preference, season, or geographic locality remains to be settled. Photographs by Marden (1956, p. 198) show the pearl fish and a holothurian host.

⁵ The fish was found in the same dish with the echinoid after it had been left standing for several minutes. It was not taken from or seen to come out of the echinoid.

The small, black and white spotted portunid crab *Lissocarcinus orbicularis* lives inside the common black *Holothuria atra* apparently somewhat as a pea crab of the California coast lives within *Stichopus* (Ricketts and Calvin, 1952, p. 62). Of 100 *H. atra* opened on December 19, 1948, 5 were so infested, and no more than 1 *Lissocarcinus* was found in 1 holothurian. Two of the crabs proved to be males and 2 females (1 is missing); so mating evidently involves accidental contact or departure from the host. The crab was taken nowhere else except from the cloaca of holothurians. Very likely *Lissocarcinus* obtains food, oxygen, and fairly uniform habitat conditions in its dark and circumscribed niche, but it is hard to see what the holothurian gets out of the association, and commensalism (or parasitism) is probably involved.

Crabs were found, mostly as cranny dwellers or nestlers, in literally all coral that was broken up. The female of *Haplocarcinus marsupialis*, however, actually produces a confining gall at the growing tips of branching corals (Semper, 1881, p. 216-224; Potts, 1915a; Hiro, 1937; Edmondson, 1946, p. 39, 273), and specimens probably of this species were observed in living *Pocillopora* and *Seriatopora* at Saipan. As long as the crab remains alive within her distinctively purse-like gall she apparently remains in communication with the surrounding water through a row of small pores at the gap of the "purse," death and complete closure of her cell being roughly coincident. A related genus, *Cryptochirus*, lives within massive rather than branching corals (Semper, 1881, p. 216-224; Potts, 1915a). Hiro (1937) discusses the association of these two unusual crabs from direct observation and the records of many previous authors, and provides good illustrations of crabs, hosts, and habitat. He notes that *Haplocarcinus* is fertilized within her gall by a short-lived pygmy male, whereas *Cryptochirus* males form separate pits of their own and the female is fertilized when she leaves her cell to moult.

Commensalism, or possibly mutualism, is exemplified by small paleomonid shrimp found on the tegmen within the brachial arms of the comatulid crinoids at station C7a, colored in tones and patterns so like those of their host crinoids that they are hardly noticeable. The one specimen identified was an ovigerous female of *Pontoniopsis comanthi*, but my recollection of their occurrence is that they came in pairs, and later observations at Onotoa in the Gilbert Islands and Kwajalein in the Marshalls confirm that shrimp of similar habits do occur in pairs. Galatheid crabs were also observed in this association at Onotoa, and Potts (1915b, p. 75) reports similar adaptations for 6 genera and 15 species of crustacea as well as 5 genera and 6 species of

ophiuroids, myzostomid and polychaete annelids, and 1 gastropod. Potts (1915b, p. 78) also records that the alpheid shrimp observed by him ordinarily occur in oppositely sexed pairs. Like the platyceratid gastropods of the Paleozoic these small crustaceans apparently feed on the waste products of the crinoids—an arrangement that may well both feed the shrimp and reduce recirculation of previously rejected material through the comatulids' food-gathering system.

Not only the crinoids tolerate crustacean commensals, however; Morrison (1954, p. 6, 13-16) reports commensal shrimp on several echinoids and a crab on one (*Echinothrix*), shrimp associated with the pearl oyster and spiny oyster, and barnacles in zooanthid anemones and on the mouth appendages of the slipper lobster (*Parribacus*), as well as clams with boring snails, and snails on other snails.

Possible parasitism that may be commensalism is illustrated by the occurrence of abundant specimens of the syllid polychaete *Haplosyllis spongicola* in seemingly healthy examples of the sponge *Jaspis stellifera* at station D5.

A form of tenancy that may in some instances be commensalism or even parasitism is found among the various mollusks, crustaceans, sipunculoids, and polychaetes not already mentioned that inhabit living coral and sponges. Although individual corallites or cells are commonly destroyed in the process, the corallum or sponge as a whole ordinarily shows no ill effects from its function as an apartment house, and many of the tenants are merely "nestlers" that show no special preference for living coral over dead coral-algal rock.

BORING AND IMBEDDING ORGANISMS

Gardiner (1903, p. 333-341; 1931, p. 104-109), Otter (1937), and Ginsburg (1953b) have paid special attention to the ubiquitous boring and imbedding organisms, which play so important a part in tropical rock destruction. Their remarks need to be supplemented only by the addition of information not recorded by them and by discussion of some unsettled matters.

Shells of the gastropod *Magilopsis lamarchi* were found in living *Goniastrea retiformis* at locality 4—one specimen apex down in a short closed-over pit just beneath the growing surface, and another in a long boring that was also closed over at the living surface of the coral (pl. 129D, E). These gastropods can in some instances be located by the dead-looking depressions at the surface of living coral. They apparently seek only shelter, but only within living coralla, contrary, as is much that follows, to Otter's report (1937, p. 347) that "Coral polyps appear to form a protection against almost all burrowing organisms except certain algae"

(see also Odum and Odum, 1955, p. 297-302). Specimens of the similar genus *Rapa* were shown me by the very fine local naturalist Bert Bronson in the spicular bases of living alcyonarians at Guam, where they are common. They are not recorded from Saipan probably only because I had no occasion to tear up an alcyonarian there and never thought of looking for snails in such an "unlikely" place. Previous records (Abbott, 1950, p. 81) indicate the genus *Rapa* to be uncommon and its habitat unknown.

Magilus antiquus, another coralliophilid gastropod which grows encased by living coral, was also found at *loc. 4*. Unlike *Magilopsis*, however, which keeps its burrow open by chemical or abrasive means, *Magilus* merely secretes a stout calcareous tube (pl. 129A, B) that keeps pace with growth of the coral. Such tubes ordinarily become solidly filled in their lower parts as the gastropod moves upward and secretes a pedestal behind itself, but they may remain open for distances of several centimeters. Specimens collected were as much as 6 cm long and 1.5 cm in diameter, coiled like an ordinary naticid at the base, but changing upward to a somewhat irregular heavy tube or cylinder of calcium carbonate, with closely spaced concentric growth varices and faint, widely spaced, subradial ridges.

The coral-imbedding barnacle *Pyrgoma* or *Creusia* (Darwin, 1854, p. 354-382; Hiro, 1938) was observed as small pinkish oval blisters on the surfaces of living faviid and acroporid corals and millepores in the shoal waters of the northern moat (*locs. 7 and 8*). According to Hiro (1938, p. 415) all of the cirripedes inhabiting *Acropora* and some other genera belong to *Creusia* and not *Pyrgoma*, but Darwin (1854, p. 375) doubts the generic distinction of these barnacles. Whatever the genus, some corallites must die to make space for it, although it does no evident permanent injury to the colony which provides it a place to imbed itself but apparently nothing else. To the paleoecologist barnacles of this sort are of special interest as organisms that appear to live exclusively in growing corals of the shallowest part of the reef and are unlikely to be transported from their living place. Also because they consist of calcite instead of aragonite, they are commonly preserved even when the host coral weathers away or is unrecognizably altered (H. S. Ladd oral communication).

The date-mussel *Lithophaga teres*, common in most masses of living coral or dead coral-algal rock that were broken up, bores a neat cylindrical hole inches downward into the rock or coral by unknown means which have been assumed to be chemical (Roughley, 1947, p. 105; Ricketts and Calvin, 1952, p. 231). Otter

(1937, p. 327-328), however, observes that no definite acid has been identified among the supposed chemical burrowers (including various pelecypods, sponges, polychaetes, and algae) and that "many rock-burrowing animals are placed under this heading on no other evidence than restriction to calcareous rocks, and the absence of any of the specialization characteristic of mechanical borers." Joel Hedgpeth has suggested to me a third possibility that has as yet received little attention; namely, chelation. This would require neither acid nor mechanical adaptations, but only expectable chelate organic compounds that might affect breakdown of calcium carbonate through removal of the metal ion (Martell and Calvin, 1952, p. 433-470).

In addition to the burrow-formers various nonburrowing pelecypods are ordinarily common in and perhaps restricted to natural or preformed cavities in the coral and coral-algal rock. These nestlers include *Arcinella variegata*, *Arca ventricosa*, *Acar reticulata*, *Barbatia fusca*, and *Barbatia decussata*.

All of the sipunculoids that are cited in the appendix and a good many of the polychaetes were obtained from cavities in coral and rock, on which they have an important destructive effect. All of the sipunculoids ("peanut worms"), moreover, and several of the polychaetes are habitually found in fresh round borings that fit them exactly and are presumably of their own making. *Cloeosiphon aspergillum* is the principal sipunculoid borer; and several of the eunicids or palolo worms (Mayer, 1908), *Pseudonereis gallapagensis*, and *Aglaurides fulgida*, have been identified by Hartman (1954, p. 621) and Gardiner (1903, p. 336-337) as important polychaete borers. Although Otter (1937, p. 327-328, 332) has inferred that acid secretion may play a part in the boring activities of both sipunculoids and polychaetes, he recognizes from the work of others that both may also bore mechanically—the sipunculoids by means of a hard, longitudinally ribbed band "of a chitin-like substance" and the polychaetes by means of their jaws, or bristles on the parapodia. Gardiner (1903, p. 336) had early stated of the sipunculoids that the "bodies of none have any acid secretion, so that their holes are presumably made by friction," and he cites Cyril Crossland as authority for the belief that some polychaetes bore with their lower jaws (Gardiner, 1931, p. 105). Hartman (1954, p. 621) asserts that some of the polychaete species "are provided with hard pharyngeal structures that can rasp away even the hardest coralline or coral rocks," while others that have no such pharyngeal armature "may perform the same function with the aid of modified setae." Boring annelids that lack such chitinized structures (for instance,

the sabellid *Hypsicomus*) are thought by Hartman to penetrate by chemical action, while others merely nestle in natural cavities.

As for the advantages of their boring habits, both sipunculoids and annelids obtain a secure shelter for their succulent bodies, where they can wait for food to be transported to them. Because those that do bore living coral (pl. 127E) show no obvious preference for particular species, and most appear to favor dead rock over living coral, it would seem that their "host" derives no special profit from the association. The apparently unusual specific association described by Gohar (1948a, p. 6, fig. 2) between the sabellid *Branchioma* and the alcyonarian *Clavularia* is commensal and not burrowing.

OTHER DISTINCTIVE ADAPTATIONS

Many of the curious and ingenious adaptations of the reef community have been described so frequently that they are common knowledge. The pelecypod *Tridacna*, which mechanically imbeds itself in reef rock with curious distortion of its soft parts and shell (Yonge, 1936), and which grows to large size, is familiar as the giant or "man-eating" clam. That it also contributes significantly to the bulk of the reef frame at places is perhaps not so generally known. The xenophorid gastropods that permanently decorate themselves with bits of shell and stone, the spider crabs that carry about their own algal gardens on carapace and claws, and other crabs that arm themselves with stinging anemones or camouflage with ascidians, bits of sponge, or other objects (Gardiner, 1931, p. 98; Carlisle, 1953) are common in other habitats besides the tropical organic reefs. Among the usually sessile pelecypods the pectens have a remarkable mobility, made practicable in large part by their rudimentary but remarkably synchronized "eyes," ranged along the mantle edge (Buddenbrock and Moller-Racke, 1953). The limpet urchins (*Colobocentrotus*), on the other hand, have given up much of the limited mobility of their brother echinoids for a voluntary sessility, and the evolution of tightly shingled spines and a streamlined form enables them to live on exposed surfaces in the most turbulent surf. Color patterns that blend against and change with the background serve for protection or ambush among a variety of fish and cephalopods, on the reef as elsewhere. Flat-fish and rays improve their concealment by stirring up the bottom sediment and allowing it to settle around their resting bodies. Many fish appear to communicate by means of audible sounds produced by scraping parts of the skeleton or movements of the swim bladder (Frisch, 1929; Stetter, 1929). The graceful speed with which a clumsy looking octopus

disappears behind his own ink burst when threatened will never be forgotten by one who has seen it, and the vision he shares with other cephalopods is marvelous among the invertebrates.

Perhaps the most fascinating of all the well-known wonders of the tropic reefs, however, is the rhythmic and curious mating behavior of certain eunicid worms—the palolo worms—whose reproductive parts once or twice yearly swarm, breed and die in the open water while the worm itself continues its routine predaceous life in the dark reef rock (Hesse and others, 1951, p. 261–262; Mayer, 1908). The Pacific palolo appears only on or near the last quarter of the moon in October and November, "whereas the Atlantic palolo swarms within three days of the day of the last quarter of the moon between June 29 and July 28" (Mayer, 1908, p. 107).

There is really nothing to add to the accounts that have already been published of the adaptations mentioned, but a few comments seem called for on the curious behavior of certain holothurians and echinoids that apparently coat themselves with debris, on the various internal materials that are expelled by holothurians under different circumstances, and on the burrowing activities of echinoids.

The echinoid *Tripneustes gratilla* and several kinds of holothurians are commonly spotted with bits of broken shell, thin gravel, *Halimeda* joints, sand, and even strings of seaweed to which they cling with pedicellaria or tube feet. Other holothurians, notably *Holothuria atra*, come to be covered with a film of fine sand so that they look like flour-rolled sausages (pl. 126B). Coating probably results from interception of bypassing sediments and presumably is voluntary if not selective. This habit may serve to some degree both for camouflage and for protection from undue absorption of solar heat by the dark bodies of the animals that so coat themselves. That they are not invariably coated may be associated with location or nonuniform distribution of the reaction among the populations concerned. It would be of interest to determine whether there were depth or areal trends in the habit, and what correlation might be found between coated and noncoated organisms, their respective internal temperature ranges, and survival.

As the expulsion of various materials from the holothurian interior is a subject that seems to be widely misunderstood among paleontologists in particular (Shrock and Twenhofel, 1953, p. 723) some first-hand observations of the matter are here recorded.

Holothurians feed by ingesting sediments which then pass through a copious alimentary canal to be discharged from the anus as a weakly bonded cylindrical

mass of relatively large diameter that coils in a loose heap or breaks up on discharge. Among thousands of holothurians noticed and many that were watched closely for a long time, none was ever observed to discharge hard excrement, to discharge it violently as is sometimes reported, or to possess any unusual habits connected with excretion in the ordinary sense.

Holothurians are unusual, however, in the development of extensive respiratory trees that lie within a large coelomic cavity and open to the cloaca. In some genera, the lower branches of these respiratory trees give way to remarkable defensive structures, the Cuvieran organs (Borradaile and Potts, 1935, p. 650). These Cuvieran organs consist of spirally coiled fibrous tissue that rapidly expands on exposure to sea water to form white sticky threads. The ejection of such threads in my experience is invariably abrupt, and invariably the result of disturbance to the animal. Contrary to Shrock and Twenhofel, the Cuvieran organs have nothing to do with food gathering, which seems to be accomplished exclusively by sweeping with the oral tentacles. The sticky mess may immobilize the fingers of a would-be human captor and commonly spews over so wide an area that an arm may have to be shaved well above the wrist to work it free. Even granting sufficient selectivity and aim on the part of the holothurian to entangle his desired food with these threads, ingestion would appear to require engulfment of the whole tangled skein—a problem of no mean proportions for a sediment ingesting holothurian, as well as a grossly inefficient and improbable feeding method. On the contrary, the entanglement of “attacking crabs and other predators” by these sticky threads is common zoological knowledge (MacGinitie and MacGinitie, 1949, p. 250).

In some instances the Cuvieran organs may be expelled so violently that some or most of the other internal organs go along with them. Actual evisceration, however, takes place in response to a variety of chemical and mechanical stimuli, rather than being specifically (if ever) a defense against attack. The only holothurians which I have seen eviscerate did so when they had been left dry in the sun, kept in water that had been allowed to get unduly warm and stale, put in epsom salts to relax them for preservation, or treated with weak ammonia for the specific purpose of causing evisceration. F. M. Bayer informs me that some species or individuals also eviscerate on moderate mechanical stimulus without dessication, heat, anoxia, or chemical stimulus.

It is not unusual to see clusters of naturally eviscerated holothurians in tide pools; this is consistent with the interpretation, made earlier, that the coating of the exterior by light-colored debris particles might be pro-

TECTIVE against overheating (and evisceration). Natural evisceration might also be due to changes in tonicity of surrounding waters, causing rupture of the body membranes as a result of osmotic differences or plain chemical irritation. If restored to its former environment the eviscerated animal undergoes no permanent damage. Experiments with the common *Thyone* at Woods Hole, Mass., showed extensive regeneration in a month's time of a specimen that had lost its entire intestinal tract, all tentacles, its lantern and lantern retractor muscles, madreporite and stone canal, parts of the radial and tentacular canals, polian vesicles, and inner coelomic wall. After evisceration this specimen had retained its cloaca, respiratory trees, gonads, muscles except lantern retractors, main radial canals, ampullae and tube feet, outer coelomic wall, and main body wall and nervous system. Some specimens which showed almost as rapid recovery had also lost their gonads and one respiratory tree!

Mention at least should be made of the boring activities of echinoids. Although many of these animals live in natural crannies or in the open on sandy or rocky bottom, still others live in holes or almost tunnelloid grooves that fit them closely and were apparently made by them. Some of these holes are round, are occupied by regular echinoids, and have been seen in both limestones and volcanic rocks. The commonest kind at Saipan is a slightly curved sausage-shaped groove that is found in water from just below the intertidal zone to 2 or 3 fathoms deep both behind the reef and down its front. Such grooves are commonly occupied by an elongated echinoid that is similar to and probably conspecific with *Echinometra mathaei* (although this species is also found in natural crannies). At Raroia, in the Tuamotus, *E. mathaei* was common in similar grooves (Morrison 1954, p. 2), and a related species is common on the Floridian and Bahaman reefs.

The grooves in question are subcircular in transverse section, with overhanging upper edges, so that they just fit the echinoid with spines extended but are too small at the top for convenient egress. According to Otter (1937, p. 333) both *Echinometra* and *Echinostrephus* form such grooves and holes by the mechanical action of their spines and teeth; and I can confirm from personal observation that the grinding teeth of the Aristotle's lantern are effective abrasive tools, whether for algal browsing or for the specific purpose of creating a hole to live in. Solution seems improbable from the fact that some occupied holes observed in volcanic rocks on Kauai were encrusted with a thin film of calcareous algae. The fact that many such holes are unoccupied, that echinoids were not found in some extensively grooved areas, and that the outlet from the groove is commonly

smaller than the echinoid beneath it, suggests that the individual echinoid ordinarily prepares its own groove and spends its entire life there. However, F. M. Bayer has informed me of his impression that *Echinometra* lives in holes already made, whereas *Echinostrephus* makes its own. That *Echinometra* may secondarily enlarge some convenient cavity is suggested by its common occurrence in natural crannies.

BIOGEOGRAPHY

Many members of the marine communities at Saipan (appendix) are widely distributed in shallow tropical seas. Instances are also common of closely related species living together under essentially similar habitat conditions. Both of these situations have a bearing on geographic and competitive aspects of speciation that deserve elaboration.

Vast expanses of deep water separate benthonic communities that include many identical elements. Under water at Saipan in the Marianas, Zamboanga in the Philippines, Arno in the Marshalls, Onotoa in the Gilberts, and Tutuila in Samoa one sees many of the same familiar things. Commonplace forms include the blue starfish *Linckia laevigata*; the short-spined echinoid *Tripneustes gratilla*; the long-spined poisonous echinoids *Echinothrix diadema* and *Centrechinus [Diadema] setosus*; many cowries and cone shells, such as *Cypraea mauritiana*, *C. tigris*, *Conus ebraeus*, and *C. lividus*; *Trochus niloticus*, *Turbo setosus*, and the common neritids, muricids, strombids, and littorinids; the tube worm *Spirobranchus giganteus* (pl. 127E) and the nettle worm *Eurythoe complanata*; the common reef-building corals and their algal and hydrozoan associates; *Holothuria atra* and other familiar holothurians; and, of course, many fishes. Then a survey of the published record and museum collections shows a good many of the same species across thousands of additional miles of deep ocean on the Great Barrier Reef; at Cocos-Keeling, where Darwin touched; and even clear across the Indian Ocean at Mauritius and along the eastern coast of Africa. This is illustrated by a partial analysis (table 5) of papers in which identifica-

tions were made by the same specialists who identified all or many of the similar forms from Saipan.

Much more detail, indicating the high degree of similarity throughout the modern Indopacific realm, has been assembled for the gastropods by Joan Demond in a study sponsored by the National Science Foundation and now awaiting publication. Extensive supporting data is also included in Holthius' (1953) enumeration of Pacific decapod and stomatopod crustacea collected by Pacific Science Board and U. S. Geological Survey parties, although not as yet precisely quantified. Even the sparse assemblage of 10 or 11 species of sponges found on Saipan (de Laubenfels, 1954, p. 274-276) includes 9 that occur also in the Marshalls or the Caroline Islands or both, 5 that are found in Australian waters, and 2 that are said to range into the tropical Atlantic. Indeed analysis of the data from recent collecting in the Pacific has so far provided only the strongest substantiation to the familiar concept of a broadly uniform benthonic Indopacific biota.

The general shape of these things is, of course, well known to zoogeographers, and Ekman (1953, p. 11-62) succinctly summarizes the biotic features of the zoogeographic region which he calls the "Indo-West-Pacific" and differentiates it from the "Atlanto-East-Pacific." Within both regions planktonic transportation is presumably responsible for movement from one shoal area to another (Thorson, 1950). Biotic distinction is maintained by the very wide and island-free "East Pacific Barrier" (Ekman, 1953, p. 72-77) across which migration of the warm water fauna is limited, both by the great distance between shoals as compared to length of larval stage, and perhaps by the general presence of north- and south-flowing cold water currents near the American coast. From Africa and the Red Sea to Hawaii, however, and from Australia to southern Japan, an impressive fraction of the shoal water benthos is represented by identical species. According to Ekman (1953, p. 14-15) "no fewer than 30%" of the Red Sea crabs are found also in Hawaii, while, at the minimum extreme, 38 of the 550 tropical echinoderm species of the "Indo-West-Pacific" region inhabit the whole of it.

A by no means insignificant number of other benthonic species also cross the "East Pacific Barrier" and are even believed to attain a circumtropical distribution. Ekman (1953, p. 3-4, 14-15, 42, 74) mentions a number of the common ones, and Hartman (1954b, p. 622-623) indicates the truly amazing ratio of 22 out of 83 named species of polychaetes from the Marshall Islands as "circummundane" or "circummundane in warm seas". The same proportion (26 percent) of supposed world-

TABLE 5.—Numbers of mollusk and annelid species common to Saipan, Cocos-Keeling, and the Marshall Islands

Faunal group	Number of named species				Percent of species common in smaller assemblage
	Saipan	Cocos-Keeling (Abbott, 1950)	Marshall Islands (Hartman, 1954b)	Number common	
Mollusks.....	140	154	-----	56	40
Pelecypods.....	40	27	-----	11	40
Gastropods.....	100	127	-----	45	45
<i>Cypraea</i>	13	18	-----	9	69
<i>Conus</i>	19	17	-----	13	76
Muricidae.....	10	12	-----	6	60
Annelids.....	34	-----	83	21	62

girdling forms is found among the 34 named species of polychaetes collected at Saipan. In fact, polychaetes are unusual in their wide distribution of identical species, owing to the remarkable lability of reproductive and developmental mode of individual species with varying ecologic conditions. Thorson (1950, p. 30-33, 38) found that 28.4 percent of West European species also occur in the Indian Ocean and 18 percent along the California coast, while less than 2 percent of echinoderm and mollusk species had the same distribution. He also found the Persian Gulf to share polychaete species with East Greenland, but no echinoderms, mollusks, or crustaceans are common to these areas. Not only is it apparent therefore, that wide distribution of common benthonic forms occurs, but also that normal barriers to marine migration can be surmounted by suitable embryonic adaptations. Considering endemism as normal across north to south land barriers, however, the close similarity of the related tropical Atlantic and Pacific forms strongly suggests general faunal intermixing up to the instant of geographic separation.

A generally radial migration from a roughly Indonesian center, and increasing filtration outward, is suggested by the less varied sedentary faunas and smaller number of identities in Hawaii, the Line Islands, and the Tuamotus; and this is graphically demonstrated at the generic level for the corals by Wells (1954, pl. 186). At the same time, more or less continuous remigration in the embryonic stages at least to some fairly recent date would seem called for to maintain gene exchange sufficient to retard the evolution of endemic species. Twin species (Ekman, 1953, p. 30, 35) are to be looked for where such gene flow has been prevented for long intervals.

Our deep oceanic "barriers" are thus more aptly designated (after Simpson, 1953) as filters and sweepstakes routes, the characteristics of which are so aptly implied by their names. With regard to the past distribution of organisms, there is the suggestion that the general direction of favored migration may be inferred from similarity gradients between fossil biotas that have been intensively studied. In the same manner climatic or land barriers may be drawn on the basis of truly abrupt biotal changes that are not related to gross lithic facies. It may even be reasonable to conclude from historical biogeography something about the breeding and larval habits of ancient biotas, for, among the benthonic organisms that do not attach to floating or swimming objects, only those with relatively long planktonic or free-swimming early stages can be dispersed widely by means of currents. Caution must be employed in such interpretations, to be sure, for current maps of the existing oceans are not reflected in detail

by biogeographic patterns. Either current movements have changed recently, or are very complex and round-about in detail, or wind-induced surface movements that run counter to or across main trends are more important than deep flow in some plankton movement. Depending on breeding seasons and wind patterns, wind-driven surface flow could be of major importance in dispersal of marine biotas.

The facts of biogeography, in any event, make untenable the position sometimes adopted that great geographic separation alone is sufficient basis for the taxonomic separation of apparently conspecific fossils. To be sure it may well put one on the lookout for real distinctions, but it would seem mandatory to recognize close morphologic and physiologic similarity with identical systematic nomenclature regardless of geography, until and unless objective and consistent differences can be established—and similar morphology implies similar physiology in the absence of contrary evidence.

The biotic associations tabulated in the appendix lead to consideration of another commonly cited generalization, known as Gause's hypothesis, about which there are also variant points of view. To follow the general sense of a recent discussion by Gilbert, Reynoldson, and Hobart (1952), this hypothesis is perhaps best stated as the view that competing species cannot persist in the same area. The observations of Gause (1934a; 1934b) himself related primarily to competition for energy (food) supply between microorganisms, which led to rigorously mathematical elimination of one of the two competing species whenever available energy was either kept at a specific level or limited to a fixed amount. Gause did observe (1934b, p. 19) that "as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor." At the same place he stated that "the intensity of competition is determined not by systematic likeness, but by the similarity of the demands of the competitor upon the environment." He illustrates the point most specifically through the unpublished work of A. N. Formosev on four species of terns that breed and live together on the small island of Jorilgatch in the Black Sea, but which have different prey and hunting grounds (Gause, 1934b, p. 20).⁶

The broad concept implied is surely valid if persistence as well as competition in some critical phase

⁶ A similar circumstance is found on the tiny island of Mindsener Oldeog of the eastern Frisians in the North Sea, where the 1956 census of the Wilhelmshaven Vogelwarten showed 270 nesting pairs of *Sterna hirundo*, 106 of *S. albifrons*, 27 of *S. sandvicensis*, and 12 of *S. macrura* (Dr. Rudolf Drost, written communication).

of existence is emphasized. Closely related species, as Gause has shown, can certainly persist together if they neither compete nor interbreed, or if the populations are prevented from coming into effective competition by some external factor such as predation or fluctuation of environment (Hutchinson, 1948, p. 239). It is also true that if species are to compete they must live at least part of the time together until the successful competitor prevails or blending takes place. Cyclical recurrences do not imply competition in the ordinary sense, although the remains of organisms involved may accumulate in the same places (Rapson, 1954). On the other hand, there is some burden of proof on the part of systematists (including paleontologists) to establish persistent differences between closely similar species from the same area and presumed similar habitat, and to do so on the basis of statistically significant samples. Competition in any limiting phase of existence should also lead eventually to extermination of unsuccessful competing organisms even where competition is not for exactly the same environmental niche.

The frequent occurrence of several related species of the same genus in the same biotope or facies is perhaps most generally explained by differences in food, feeding habits, and microhabitats. A habitat that might offer only one niche so far as the octopus or eel population was concerned might offer dozens of niches for annelids and crabs, scores for Foraminifera, and hundreds for the smallest microorganisms. As with the pieces of a masonry wall, the various organisms that live in a complex habitat like a reef include a variety of sizes and forms that fit or are fitted together, with an increasing number of individual units and places for them to fit as the building blocks decrease in size.

Most of the habitat subdivisions recognized in this study, and even the individual collecting sites, include a range of both substrate conditions and depth. It seems a safe conclusion that they also include enough of a variety of microhabitats and feeding patterns to provide for differentiation and persistence of more than one local species of many genera.

ORIGIN OF SEDIMENTS

The sediments studied are mainly biogenic, or bioclastic⁷ in the general accepted sense of sedimentary petrologists—that is, they are made up of particles of organic origin, mostly worn or broken. Three principal particle types are recognized. (1) Some of the particles are whole organisms or discrete pieces of organisms that are only slightly worn or not worn at all. (2) Other clastic grains result from the breaking up

⁷ Grabau (1913, p. 296), who originated the term did so half-humorously for "the clastic rocks which owe their essential character to organisms," such as "plaster, concrete, cement, etc."

of living or dead coral-algal rock or other organisms, or modification of preexisting clastic particles through organic agencies. (3) Still other fragments result from the mechanical breakup of rock weakened by organic activities. These strictly mechanical processes, however, contribute most significantly to the reef talus of the outer slope, probably being no more important than other factors mentioned insofar as the lagoon sediments themselves are concerned.

All three of these kinds of sediments are clastic and ultimately of organic origin, and all except the first are strictly mechanical and detrital in the sense of resulting from the breakup of preexisting materials. They all get mixed to some degree, and although effort is made to maintain a distinction in the following discussion, it may become largely academic insofar as any given sample is concerned. Materials of volcanic and terrestrial origin are common enough along the eastern coast, but occur only in small proportion, and that locally, among the western beach and shoal-water sediments. As only the western lagoonal and reef-complex sediments were studied and sampled extensively the following discussion will be limited to them.

The effective rate of bottom accretion at any given place is related to rate of transportation of sediments to and through such place, as well as to supply and compactibility of these sediments. Transportation, in turn, is related to wave base, bottom currents, and rate of subsidence or emergence. If we accept the later computed rate of fall of roughly 0.2 to 0.3 mm per year for sediments of organic attrition, and assume approximately equal rates for the two other principal factors, the total rate of sedimentary accretion in the shoal areas, were there no transport, would be about 1 meter per 1,000 to 1,700 years. The actual rate of accretion is necessarily less, and probably much less than the rate of original sedimentary fall, because of the seaward movement of sediments. Thus the shoal sediments at Eniwetok (Ladd and others, 1953), for instance, accumulated on the long-term average at only about one-twentieth to one-thirtieth the rate inferred, because accumulation in persistently shoal areas cannot exceed total subsidence (or rise of sea level) during the time interval considered.

SEDIMENTS OF DIRECT ORGANIC ORIGIN

The principal sediments of direct organic origin are *Halimeda* limesands, coralline algal limesands, and foraminiferal limesands. All of these, of course, as well as other sediments with which they mingle, contain elements other than the dominating or distinctive fraction.

The *Halimeda* limesands at Saipan are concentrated

near the entrance to the principal lagoon pass and are well illustrated by the sample from station B8. Such limesands consist of the discrete calcified joints of the green alga *Halimeda* (pl. 128E) which are transported to their present position from nearby, and probably also from the shallower parts of the lagoon where this alga seems to grow in greatest abundance. Such sediments may be thick and areally extensive, as is known from observation of *Halimeda* limestones of Pleistocene age on Saipan, Tinian, and Guam, as well as from two borings in the Funafuti lagoon, where *Halimeda* limesands 180 to 190 feet thick were penetrated (Halligan, 1904).

Limesands that consist mainly of fragments of coralline algae are found off Muchot point, where they are well exemplified by the coarse grained but very well sorted sediment sample from station D4. Although this particular sample consists of fragments of branching crustose coralline algae, the articulate corallines provide better source material, and local deposits that consist mainly of the joints of articulate corallines are to be expected. Indeed such deposits were fairly common about Saipan during Tertiary times, to judge from the concentration of articulate coralline algae in many thin sections of the Tertiary limestones.

Foraminiferal limesands of present day Saipan are mainly beach limesands that consist of *Baculogypsina* concentrations. This salmon-pink foraminifer and its close homeomorph *Calcarina*, with their stellately arranged peripheral spines, both appear to live exclusively on the reef surfaces, but their worn tests are concentrated on the beaches by wave and current action. Some of the recently emerged limesands of the western coastal plain consist mainly of *Baculogypsina* or *Calcarina*, together with the fragments or whole shells of small strombids, cardids, and other mollusks. The foraminiferal limestones of Tertiary age consist mainly of larger Foraminifera that presumably lived and died at depths of 10 to 40 fathoms. Percentage composition of modern beach, lagoon, and deepwater foraminiferal assemblages in regions where all have been well sampled is distinctive (Cushman, Todd, and Post, 1954, p. 325-326) and importantly supplements the local data in interpreting past conditions.

Fragments and whole shells of gastropods and pelecypods were noted in many of the sediment samples. A further increment includes the spicules of sponges and alcyonarians, the dermal sclerites of holothurians, the discrete elements of other echinoderms and of fish that disintegrate on death, and minute organisms or organic objects such as tunicate spicules. Of these only the spicules of the alcyonarian *Simularia* seem to be volumetrically significant. They were observed in most

sediment samples, and were abundant in some, as slender, curved, terminally tapering granulose and spindle-shaped rods as long as several millimeters (pl. 131A). They also resemble the spicules of some gorgonids like *Muricella* or one of the related forms illustrated by Stiasny (1940), but the local gorgonid fauna is too sparse to account for a significant volume of spicules and apparently does not produce spicules of this type. The importance of alcyonarian spicules in sediments elsewhere was emphasized by Carey (1918; 1931). Holothurian plates are found only in the finest grained fraction.

DETRITAL SEDIMENTS PRODUCED OR MODIFIED BY ORGANISMS

This section is particularly concerned with the activities of fish, echinoids, and holothurians.

The coral and rock browsing activities of fish (pls. 130, 131) were observed by Darwin (1845, p. 500) at Cocos-Keeling and subsequently have been both confirmed and denied by later authors. Forbes (1885, p. 21), like Darwin, describes the feeding of scarids (parrot fish) on coral at Cocos-Keeling. Wood-Jones (1910, p. 130, 164-165, 264-266) concluded from studies at the same place that the importance of scarids as sediment makers consists in the scraping of fine debris from the dead coral-algal rock in the course of algal browsing, and not from the deliberate ingestion of coral. During his underwater work in the Bay of Batavia, Verwey (1931, p. 175) identified four species of *Pseudoscarus* as rock browsers. Motoda (1940, p. 100-101) observed that pieces of the living coral were commonly ingested by fishes at Palau. Hesse and others (1951, p. 263) state that pomacentrids, scarids, trunk fishes, and puffers bite off pieces of coral, and that as much as 1 kilogram of coral in rather large pieces has been found in the stomach of the puffer *Diodon*. In a preliminary summary of this matter (Cloud, 1952, p. 26-27) I have made reference to the observations and views of several other earlier workers, and have confirmed the importance of fish as sediment makers.

The French underwater explorer Jacques-Yves Cousteau (1952, p. 454) not only confirms that scarids (and other fish) do bite off and grind up reef rock to make sediment, but he has also emphasized graphically what Grabau knew 40 years earlier (Grabau, 1913, p. 414), that fish are truly important sedimentary agents. Both by scraping off a film of the dead coral-algal rock as they clip its living algal felt, and by ingesting living coral, coralline algae, and even the powerfully stinging millepores, they account for an abundance of mainly fine and some coarse sediment. The scarids do this partly by scraping or biting with their strong parrot-

like beaks (pl. 130A, *B*) and partly by grinding up larger pieces as these pass the pharyngeal teeth (pl. 130F) enroute to the gut and the sea floor (pl. 131A, *B*). Most recent confirmation of the essential facts comes from the work of Nesteroff (1955, p. 29), and Newell (1956, p. 360, pl. 43).

There is no further room for doubt, it would seem, that fish are important in the origin of the clastic sediments about organic reefs. By trituration of algae, corals, or rock, they contribute many hundreds of tons of sand and some fine gravel each year to the sediments about Saipan, and are probably about as significant as any other sedimentary agent in the area.

To get even a roughly quantitative idea of the importance of this factor in the sedimentary regimen of the reef complex, it is necessary to make some assumptions. My own observations of the fish and analysis of their gut contents, and discussions with Leonard Schultz of the U. S. National Museum, lead to the guess that the average fish population per square mile of the mixed sandy bottom and reef patches west of Saipan includes on the order of 100,000 to 150,000 individuals that might pass an individual average of about 30 grams per day (dry weight) of new sediment derived from browsing on coral-algal rock or eating of coral. If this assumption is of the right order of magnitude (and the later independent estimates of Odum and Odum, 1955, p. 307-309, suggest it is), the fish population of the principal lagoon areas and similar shoal bottom might contribute something like 1,100 to 1,600 metric tons of sand and fine gravel per square mile annually to the shoal bottom sediments. Assuming no transport from the area of first deposition and taking an average specific gravity of 2.5 for the sand (Gardiner, 1903, p. 330-331; Emery and others, 1954, p. 65), this would approximate an annual rate of sedimentary accretion from the activities of fish in the lagoon area of 0.17 to 0.24 mm per year. If we reduce the specific gravity, to say 2.0, to allow for interstitial porosity, the resulting figures are 0.2 to 0.3 mm per year.

The importance of echinoids and holothurians as sediment makers, has probably been overemphasized (Gardiner, 1931, p. 101-104). A large echinoid population would undoubtedly grind up much sediment in the course of algal browsing and groove formation over a long period of time, but their year-to-year importance in sediment making is probably greatly subordinate to that of fish.

Holothurians not only appear not to exercise an important short-term accretional effect on the detrital sediments, but their long-term effect is probably negative. It is well known that most reef complexes support large

populations of holothurians that industriously ingest sediment and pass it through their alimentary canals for whatever nourishment it may contain. Counts of holothurians on the bottom within a 50-foot square roped grid were made for me on Saipan by Jarvis O'Mara at two places where they were uncommonly abundant. On sparsely vegetated limesand under 3 to 5 feet of water in the general area of *loc. 8a*, 206 specimens of *Holothuria atra* and 3 of another species were counted—about 1 holothurian per 12 square feet of lagoon bottom. The second site, on sparsely vegetated limesand beneath 5 to 8 feet of water toward the shore end of *traverse E*, yielded 109 specimens of *Holothuria atra*, and 16 other specimens—or 1 holothurian per 20 square feet. Based on these counts and the general impression from tow traverses, the holothurian population is probably on the order of 1 per every 50 to 100 square feet of lagoon and moat bottom. Considering their intensive feeding activities and high rate of excretion, an enormous volume of sediment necessarily passes through them in the course of a year—perhaps several times the yearly addition of new shoal sediment from all sources.

The question is, what is the effect of this on the sediments? Certainly the holothurians add nothing to the total volume beyond the infinitesimal measure of their own tiny dermal plates following death. Samples and data were obtained to see whether any sort of size reduction factor could be worked out, but the notes were lost and the discussion falls back on general impressions and the published results of similar studies at Palau by Yamanouti (1939; 1941). Mechanical analyses by Yamanouti indicate no immediately detectable effect on sediments passed through holothurians, and this accords with my opinion of what our results would have given. This, naturally, does not mean that there is no effect, but merely that if there is one, it is small and would require a long time to cause detectable differences. It does seem doubtful that any really significant trituration would occur. However, because the pH of holothurian gut fluids is only 4.8 to 7.0 (Mayer, 1924, p. 34-35; Yamanouti, 1941, p. 39), the chemical effects of continuous passing of calcareous sediments should lead to reduction in individual grain size and partial elimination of the finest fraction. Over a very long period of time this should both lower the median diameter and move sorting skewness toward the coarse fraction. As the samples analyzed are preponderantly skewed toward the fine fraction, this suggests that the primary sediment was even more strongly skewed toward the fine side. This, if true, could be interpreted as supporting the importance of fine grinding by scarid fish and other browsers. Despite reports to the contrary (as by

Gardiner, 1903, p. 334), holothurians apparently do not themselves produce new sediments or mechanically triturate old ones.

That effects such as suggested do actually occur is rendered plausible by the size of the holothurian population and the amount of sand it passes. Yamanouti (1941, p. 41) estimates one holothurian per 20 square feet or less in the area studied by him, with an ingestion rate of about 16 kilograms of sand per square meter per year. These orders of magnitude seem a little high for Saipan, but realistic effects for any area could only be estimated by controlled experiments of long duration.

Thus the effect of the holothurians on sediment accretion probably tends to cancel out that of the echinoids and other invertebrate browsers, such as many gastropods and chitons. The total new sediments produced by the triturating activities of the invertebrates probably does not add more than a few hundredths of a millimeter to that produced by the fish—not enough to warrant raising the general total for organic attrition from the 0.2 to 0.3 mm per year suggested above.

MECHANICAL BREAKUP OF ROCK WEAKENED BY ORGANIC AGENCIES AND SOLUTION

Probably the greatest bulk of sediments that finally undergo mechanical breakdown on the reef are prepared for mechanical attack through being weakened by boring or burrowing organisms or by solution.

In the shore zone (as above tide) the CaCO_3 dissolving filaments of the blue-green alga *Entophysalis* (Newhouse, 1954, p. 45–46) ramify the surface of the rock, dissolving some of it and weakening the remainder so that it is more susceptible to abrasion. Chitons and patellids dissolve small pits in the rock, neritids and other algal browsers rasp its surface, and solution resulting from the high CO_2 content of rain water and daily pH fluctuations in the intertidal zone contribute to the development of an irregular surface whose projections are susceptible to breakage and organic attack. Sipunculoids in particular, but also mollusks and polychaetes, bore into the coral-algal and even detrital rock, by chemical or mechanical means. Such activities themselves provide little new sediment, but they commonly render the rock so weak and punky that it crushes or breaks with the lightest tap of a hammer. In this state it is, of course, easily broken by hydraulic wedging or by the impact of loose fragments of rock or broken coral masses that may be rolled or bounced across it at time of storm.

SEDIMENTS RESULTING FROM MECHANICAL FACTORS ALONE

Sediments that result from mechanical breakage and abrasion alone are formed principally at times of storm. To a lesser degree they are also formed regularly as a result of brushing by finer debris in regular transit across the reef. Naturally it is impossible to make a clear distinction between such sediments and those formed from mechanical breakup of previously weakened rock, and the following remarks apply to both.

At time of storm whole segments of the reef front may be hydraulically dislodged and cast up on its surface, rolled down its outer slope, or battered to pieces. Whole coral heads and fragments of brittle corals and algae are broken loose and rolled or bounced back and forth across the reef surface where they are further fragmented and may cause great destruction in the process. During great storms such debris is sometimes heaped up on the reef surface as extensive tracts or ridges of rubble that may subsequently be indurated through intertidal cementation or may create eddies and local currents that lead to the deposition of additional sediments and the growth of islands. The vigorous grinding and bouncing of rock against rock at times of great storm, the distances to which large blocks may be transported, and the sweeping changes of reef surface and beach features that commonly ensue must be experienced to be appreciated.

The great bulk of the mainly coarse debris that results from such storms, however, is probably worked down the outer slope of the reef to contribute to the growing talus pile on which the reef may eventually grow outward.

In review, it appears that debris of purely mechanical origin is most important in building up the outer slope of the reef and in laying the base for some reef islands. Sediments of direct organic origin and those produced by the browsing activities of reef fish are believed to be most conspicuous in lagoons and shoals, where the force of the waves is less and where habitat conditions favor large populations of the sediment-making organisms and bottom-feeding fish.

ORIENTATION OF SEDIMENT TRAINS AND GROWTH FEATURES PARALLEL TO CURRENT FLOW

One of the striking features of the reef front and lagoon bottom at many places is the manner in which both sediment trains and growth features tend to line up with the direction of flow of bottom currents. Around

the reef front and across the reef this leads toward a commonly well-defined pattern of radial stripes.⁸ In the lagoon areas behind the reef flat, the lines of sediment flow, and to a lesser degree the trends of organic growth, curve with the current paths toward the nearest pass or channel through the reef.

Radial patterns of the reef front are well exhibited by plates 125A, 132A, 133, 134G, 135A, B, 136, and 137A, B. Sediment paths that radiate behind the reef and eventually curve with the bottom currents toward the nearest lagoon outlet are shown by plates 123, 124A, and 125B. The general alinement of reef patches and current paths parallel to the outflow axis of the main channel is hinted at in the right middle- and background of plate 124B, and is well brought out by aerial photographs of the area.

A fairly high rate of movement of sediments along the lagoon bottom and seaward through available passes is suggested by plate 125B. This shows strong sedimentary encroachment from the south (right) by gravel and sand of biotope II across a dredged channel. The photograph was taken in the spring of 1949 and the channel had been dredged at least as recently as the fall of 1944.

The essential points are (1) that moving sediment trains are commonly developed in a direction parallel to the flow of strong bottom currents; (2) that the sediments of such trains move generally seaward, even if by a roundabout route; (3) that the individual trains are relatively narrow and are separated from one another by relatively stable intervening strips of heaped-up coarser sediment or by solid rock; (4) that the constant or frequently repeated seaward movement of such sediment inhibits organic growth in the areas of maximum movement and erodes the bottom where the flowing debris is in contact with a rock surface.

This results in a similar orientation of growth features parallel to current flow. Such orientation is brought about by the fact that the sediments move as trains instead of sheets, that they tend to follow the lowest available track and to deepen that track where movement is vigorous enough, and that the intervening high areas are the most favorable places for organic

growth to take hold and flourish. In certain areas, as along reef fronts that were once emerged benches, the effect is exaggerated by the fact that radial solution rills characteristically develop on the slopes and edges of limestone surfaces across which undersaturated water flows, and that such rills have been deepened or kept open by moving sediment while organic growth has masked the intervening areas or even bridged the grooves (Cloud, 1954, p. 201-203).

EROSION AND PRECIPITATION OF CALCIUM CARBONATE IN THE INTERTIDAL ZONE

CHEMICAL FACTORS

The problem of intertidal erosion is complicated by apparently conflicting evidence concerning likelihood of calcium carbonate solution by shoal marine waters. Much disagreement has arisen about this. Evidence that seems to indicate prevailing high supersaturation with the combining ions of CaCO_3 in the surface waters of the sea is commonly invoked as precluding the probability of solution of CaCO_3 by such waters. Others consider it unlikely that such supersaturation could persist generally in the sea, and believe that physical indications of solution will find a chemical explanation not now apparent. Still others suggest that the explanation is to be found in abrasive and chemical attrition by organisms.

The latter view, effectively presented by Abe (1937, p. 303), Ginsburg (1953a, 1953b), Newell (1954, p. 20-23; 1956, p. 357-360), and others, certainly accounts for much of the shoal water erosion seen. Other evidence (see pl. 125E) suggests physiochemical effects.

Before considering the field evidence bearing on this question, it seems well to have in mind some of the relationships of hydrogen ion activity (expressed as negative log pH) to the concentrations and activities of the carbonate ion (CO_3^{--}), the calcium ion (Ca^{++}), and the ionic product $\text{Ca}^{++} \times \text{CO}_3^{--}$ at which equilibrium exists. When the product of these two ions exceeds a certain level, their solubility product constant, precipitation or supersaturation occurs. If it falls to a lower value in the presence of solid CaCO_3 , solution should take place. The true solubility product constant (which differs by a factor of about 2 from calcite to aragonite) is not surely known because of uncertainty about other thermodynamic constants involved, but an approximate value can be computed from empirical and stoichiometric relationships. This value, the apparent solubility product constant (K') or K'_{CaCO_3} , increases as pH increases (Sverdrup and others, 1946, p. 206),⁹

⁸ It is of incidental interest that the growth of trees along the coast also tends toward a pattern of radial lines (pls. 133A, C, 136). Whether this is because they were planted that way, or because they orient themselves parallel to wind currents, radial to slopes, or in conformity with the emerged radial patterns of former reefs and erosional benches, is a matter for further study, though probably all factors are involved. A similar pattern has been observed in casuarina growth on presumably undisturbed beach in other areas, probably either because the waves that tossed the casuarina cones ashore also swept them into radial orientation on the backwash or because later rains or winds had the same effect. Along shore, of course, everything tends toward a radial orientation—beach cusps, gravel trains, solution rills; even accumulations of empty cartridge cases in shallow shoreline water are washed into radial orientation, with the heavy ends downslope.

⁹ Sverdrup and others do not actually say that K' increases, but their graph shows that the apparent equilibrium product $\text{Ca} \times \text{CO}_3$ increases; this amounts to the same thing.

and so does the proportion of CO_3^{--} in the total complex of weak anions called alkalinity (fig. 40).

As Garrels and Dreyer (1952, p. 332-336) have shown, however, it is inconceivable that K'_{CaCO_3} should increase with pH, concurrently with increasing CO_3^{--} , in a solution of constant ionic strength unless the proportion of ionic to total calcium decreases at the same time. This presumably means that the calcium referred to under K'_{CaCO_3} is also a complex, that includes not only free calcium ion (Ca^{++}) but also other molecular or ionic species that cannot combine as they are with CO_3^{--} to precipitate CaCO_3 . If this other Ca were all dissolved solid CaCO_3 , it theoretically would not seriously affect the practical considerations involved, for it would probably be far more mobile than solid surfaces of CaCO_3 and would move to satisfy ionic imbalances before calcium carbonate rock could be dissolved. On the other hand, if some of it were bound in chelate complexes (Martell and Calvin, 1952, p. 433-470), it might, while in such state, be essentially unavailable to enter normal solution-precipitation reactions in sea water, yet show in usual chemical analyses where calcium is separated by stronger chelating agents or acidometrically. At least there is reason for reserving judgement on the validity of the supposed high supersaturation of surface sea water with respect to CaCO_3 .

Another factor to be considered is the pH itself, and its affect on CO_3^{--} concentration. The occurrence of

marked diurnal variation in the hydrogen ion concentration of intertidal to very shoal waters with abundant plant growth is well documented (Orr, 1933, p. 53; Orr and Moorhouse, 1933, p. 87-91, 98; Manton, 1935, p. 281-298; Emery, 1946; Cloud, 1952, p. 34-41). This pH cycle, from afternoon peak to nighttime or early morning low, is brought about by corresponding variation in carbon dioxide content, related to the photosynthetic cycle. Although important changes involving precipitation or solution of CaCO_3 may take place without change of pH, if all is in balance, significant pH changes in the range found in sea water necessarily mean significant variation in the concentration of CO_3^{--} and hence of the ionic product $\text{Ca}^{++} \times \text{CO}_3^{--}$.

This is apparent from inspection of figure 40, and the approximate quantities can be calculated from standard equations in this way: Take a common version of the equation for combining CO_3^{--} (Harvey, 1955, p. 173):

$$C_{\text{CO}_3^{--}} = \frac{\text{carbonate alkalinity} \cdot K'_2}{2K'_2 + a_{\text{H}}}$$

in which pH is converted to a_{H} (hydrogen ion activity). Introduce into this the fairly normal values of 2.4 in milliequivalents per liter for "carbonate alkalinity" and 1.1×10^{-9} for the apparent second dissociation constant of carbonic acid (K'_2). With these values constant, compute the approximate carbonate concentration for diurnal pH variation from 7.7 to 8.3, which is apparently not unusual in shallow tropical waters.

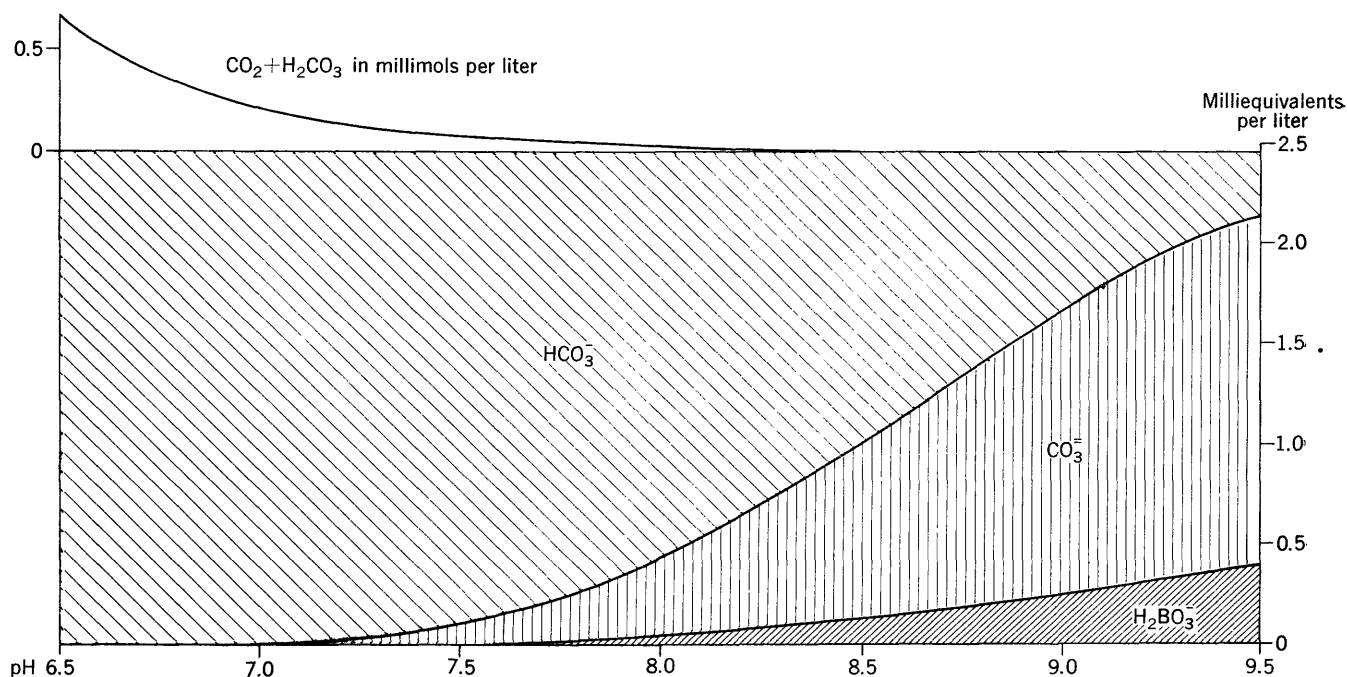


FIGURE 40.—Change in alkalinity components of sea water with changing pH (temperature 16° C, salinity 36 ‰, alkalinity 2.46 milliequivalents per liter (after Harvey, 1955, fig. 63).

The result is 0.37 millimols per liter of CO_3^{--} at pH 8.3 and only 0.12 at pH 7.7 (the temperature effect is negligible). If seawater is even near balance in $\text{Ca}^{++} \times \text{CO}_3^{--}$ the apparent threefold range of CO_3^{--} concentration offers prospect of solution at the low nighttime pH and CO_3^{--} concentration and precipitation at the higher daytime values.

Consideration needs now to be given to the pH of apparent saturation. This may be computed for a given value of K'_{CaCO_3} , temperature, and salinity from an empirical equation derived by Hindman:¹⁰ pH saturation = $-pK'_{\text{CaCO}_3} + pK'_2 + 4.69$, where pK'_2 is the second dissociation constant of carbonic acid and a correction of +0.02 is made for each °C decrease.

Let us take the K'_{CaCO_3} values of 0.53×10^{-6} for calcite and 0.99×10^{-6} for aragonite¹¹ at 36 ‰ salinity and 30° C, and compute pH saturation for this salinity and temperature and also for 25° C. The results are: at 30°, pH saturation = 7.2 for calcite and 7.6 for aragonite; at 25°, pH saturation = 7.4 for calcite and 7.7 for aragonite.

This implies that aragonite, but not calcite, might dissolve at the lower pH range of the diurnal cycle in tropical shoal waters. Taken at face value, this seriously weakens the likelihood of important solution effects by normal sea water on the majority of Pleistocene and older limestone shores. On the other hand, no allowance is made for analytical calcium possibly inactive in chelate complexes, or for expectable local variations should such a factor prove important. The face values for K'_{CaCO_3} also imply a general supersaturation of tropical surface waters of about 3 times for aragonite and 5- to 6-fold for calcite, which is hard to take seriously. Until the thermodynamic constants are better understood, therefore, and the possible elements of the calcium complex thoroughly explored, this evidence remains equivocal.

If sea water is even approximately at equilibrium with regard to CaCO_3 the occurrence of pH changes of several tenths of a unit above and below pH 8 in the presence of solid CaCO_3 should signify precipitation or solution, according to direction of change. Should this occur, the directions of change would indicate precipitation of CaCO_3 during the day and its solution at night. Solution effects would presumably predominate in the intertidal zone, because the fine precipitation product is here easily flushed away with each receding

tide (or wave), except where it is interstitial to stable sediments or is anchored by sediment entrapping organic structures, such as certain algae, mats of vermetid gastropods, or the reef frame. The prospects of such effects are heightened as a result of both organic and physiochemical withdrawal of CaCO_3 in the agitated waters of the reef front and outer reef flat. By lowering the ionic product this necessarily improves the chances of solution by the inshore waters. The likelihood of solution is also favored by experimental evidence indicating that approach to equilibrium for CaCO_3 in sea water is slow from supersaturation and rapid from undersaturation.

There is finally, the prospect of possibly important surface film effects due to gaseous exchange with the air and to floating rainwater, as well as to rain that falls on the intertidal surfaces. If all these factors mentioned should happen to work generally in the same direction, even in slight degree, cumulative effects could be large because of the large total volumes and constant renewal of the water involved. If the greatest effects are surficial, the principal results would be intertidal.

ORGANIC EFFECTS

Solution is known to result from penetration of rock surfaces by algal filaments, sponges, and other organisms; and it may be simulated by the abrasive activities of many surface-browsing invertebrates, as Abe (1937, p. 303), Ginsburg (1953), Newell (1954, p. 20-23), and others have emphasized. The effects of the browsing invertebrates increase in importance toward and below low tide level, as also observed by Ginsburg (1953b, p. 65, 68). Algae also grow most vigorously where constantly wetted, but the thick mats that they form on surfaces reduced toward low tide level appear to be more protective than destructive, especially where coralline algae preponderate (although Gardiner, 1931, p. 143, thought the reverse). The important destructive alga, *Entophyalis*, works also above high tide level, where it accounts for the black color and much irregular surface pitting of limestone surfaces. The importance of organisms in intertidal erosion in any case is well established, even though emphasis is here placed on the probable complexity of the process. Ginsburg's thoughtful and convincing résumé, however, covers this subject so well that it would be merely repetitious to dwell on it here.

PHYSICAL SUGGESTIONS OF INTERTIDAL SOLUTION

Although many of the supposed physical evidences of solution in the shore zone might also be explained as the work of organisms, it is difficult to explain by any agency other than physiochemical solution the features

¹⁰ J. C. Hindman, 1943, Properties of the system $\text{CaCO}_3\text{--CO}_2\text{--H}_2\text{O}$ in sea water and sodium chloride solutions: Univ. Calif. Los Angeles, Ph. D. thesis GC 3.U3, 534d no. 20609, 153 p. (see p. 40).

¹¹ The calcite value is that of Hindman and of Wattenberg and Timmerman (Hindman, p. 128, 131) converted to a volume basis. The aragonite value is that of Smith (1941) corrected for new constant relationships derived by Hindman (p. 131). The same value for aragonite was derived independently, and from yet unpublished evidence by Cloud.

of the jetty face illustrated in plate 125*E*. Since this structure was built at Key West, Fla., in 1919 or 1920, pebbles of oölitic limestone aggregate have been etched out intertidally to depths between $\frac{1}{2}$ inch and 2 inches below the original surface, leaving the portland cement matrix in positive relief. Surface reduction follows the outlines of the aggregate pebbles, without significantly affecting the matrix, and without the observed assistance of organisms. Immediately beneath the low tide level (bottom of photograph) a vigorous growth of rock-abrading and rock-dissolving invertebrates and algae has nonselectively undercut the face of the jetty, with equal effects on aggregate and matrix portions.

The undercut notch that is so characteristic of tropical Pacific limestone shores is so faithfully related to sea level (pls. 133*A*, 139*A*; chap. A, pls. 13, 15) and the intertidal benches below it are so nearly horizontal (pls. 133–136) that they are both presumably related to factors that act toward a constant level at or above low tide. This in effect rules out purely mechanical abrasion, general solution by marine water, or general biologic processes as controlling factors (though not as contributors). It remains possible that the basic cause could be the direct activities of organisms with strictly limited vertical range, or chemical solution that applies only or mainly in the intertidal area. The latter might involve a combination of effects such as high CO_2 absorption and floating rain in the surface film of sea water, direct rainfall on exposed surfaces, and local depletion of intertidal sea water in CaCO_3 after flow across a front of lime-secreting organisms.

It has been considered (Newell, 1954, p. 23) that the sea level notch cannot be primarily the result of intertidal solution, because its point of maximum indentation is about at high tide level, whereas the intertidal waters lie longest in contact with the rock at the low tide position. The notch at high tide level, however, is logically considered as the approximate upper point of a generally seaward-sloping surface of erosion that extends all the way across the adjacent sea level bench (and around its mushroom pedestals) to the low tide line—a surface that undergoes maximum reduction toward the low tide level until equilibrium is reached between erosion and organic construction. Such a surface would incise the cliffs at high tide simply because the factors involved have little or no effect at higher levels. It could work into the cliff through removal of a series of seaward-sloping slices that grow progressively shorter as they are reduced to or below low tide level at the seaward end. Where the tide ebbs and falls gently, as in the quiet coves of the southern Palau Islands, the notch is sharp, its lower slope relatively even, and the undersurface of its capping visor nearly horizontal.

On coasts that face the buffeting waves with only a narrow marginal bench to break their splash, as along much of eastern Saipan, the notch has relatively large vertical spread and frequently poor definition. Mechanical erosion by formation and collapse of air bubbles (cavitation) or vigorous growth of spray zone browsing organisms may help to explain this vertical spread. None of the foregoing characteristics, however, have any bearing on the nature of the factors or balance of factors that produce the erosion seen beyond requiring that they be primarily intertidal.

The spray- and tide-pools are next to be considered, as well as irregularly etched coastal surfaces above high tide line. The terraced pools of some narrow fringing reef surfaces (pls. 137*F*, 139*B*), both between and above tides, display such vigorous organic growth as to suggest probably larger than usual diurnal variation in pH and deepening by organic and chemical erosion. Concurrently they build up their even rims by organic growth and entrapment of fine debris at the margins. The highly irregular surfaces wholly above the intertidal zone (pls. 137*B*, 138*E*) are introduced because their general similarity to but particular differences from parts of many intertidal surfaces are sometimes used as evidence for, sometimes against, an origin by solution for the latter. The smoother intertidal surfaces may reflect more continuously and generally acting processes. On the other hand the irregular supratidal surfaces are also of complex origin, reflecting the results of solution both by the alga *Entophyalis* and by rainfall, as well as some mechanical removal by browsing gastropods.

The physical evidence is hardly compelling. Without belittling the importance of organic factors, some of it seems to show that solution not directly caused by organisms can be an influential factor in intertidal erosion. That the process is complex seems established. The precise levels of the eroded surfaces, showing limitation to the intertidal range, indicate the need for continuing effort to quantify to what extent that control may reside in inherent properties of the water itself and how this may vary locally and with time.

PRECIPITATION

The most conspicuous result of intertidal precipitation of CaCO_3 is beach rock, such as was early noted, described, and perhaps first named at Bermuda by Agassiz (1895, p. 223–228). Beach rock is sporadically distributed at favorable sites around Saipan (pl. 124*B*; chap. A, pls. 15*C*, *D*), as it is on many tropic beaches. Thin sections of such rock show radial fibers of aragonite or mosaics of clear calcite fringing the individual clastic grains and interstitial to them. The formation

of beach rock is believed to be favored where beach sediments remain stable long enough for such precipitation to bond their elastic particles firmly enough to prevent separation in the next interval of vigorous wave action (Cloud, 1952, p. 28-29; Newhouse, 1954, p. 53; Newell, 1954, p. 33), or below any surficial movement of the sands. Nesteroff (1955, p. 36) attributes the formation of beach rock to the activity of living organisms, perhaps bacteria; and a frequently cited explanation that was apparently first suggested by Crossland (1905, p. 186) is that formation is the effect of outflowing fresh waters at the beach margin. In a still earlier account, Gardiner (1903, p. 341-346) attributed formation of beach rock to precipitation of CaCO_3 from interstitial sea water, with clear implication of a physicochemical mechanism. He repeated this in 1931 (p. 40-43), then calling upon Crossland's fresh-water cementation for interim stabilization of the beach. Gardiner's original explanation still seems an eminently likely one to me; as it apparently does to Ginsburg (1953); to Emery, Tracey, and Ladd (1954, p. 44-45); and to Newell (1954, p. 133). It seems, further, that such induration could work either upward from below or downward from above, depending on the stability of the beach, the chemistry of the water and equilibrium factors, and the direction or directions of water movement.

Finely particulate and probably at least in part precipitated CaCO_3 is retained on the rims and slopes of terraced pools (pls. 137*F*, 139) and partly along the pendants or septa between other pools or parts of stepped surfaces (pls. 134*C*, 137*D*, *E*, 139). Here aeration and precipitation are accelerated, and algae and serpulid gastropods (pl. 139) provide good baffles for the entrapment and retention of fine particles.

Precipitation also is probably responsible for some of the conglomerates where rubble is cemented in the intertidal zone, and for welding larger blocks firmly to the bench surfaces on which they have dropped (pls. 134*F*, 135*C*, 138*A*, *B*). Walls of rock-ring fish traps built over reef flats are commonly welded into a solid structure by algal growth and interstitial bonding of fine debris that lodges in openings between blocks. The same factor probably plays a part in stabilizing conglomeratic bench surfaces such as those of plate 135 so as to retard abrasion and result in a nearly flat instead of strongly sloping surface.

VARIATION IN CHARACTERISTICS OF THE PERIPHERAL REEF FLAT AND REEF FRONT

Almost everyone who has written about reefs has noted the prevailing concentric or parallel zonation of the reef flat and reef front, and many fine descriptions of individual reefs discuss and illustrate the local char-

acteristics and regional variation of this zonation (Odum and Odum, 1955, p. 293-297; Wells, 1954, p. 396-398, 401-406, pl. 187 and 1951, p. 10-12, figs. 2-5, 8-14; Emery, Tracey, and Ladd, 1954, p. 23-34, 91-93, 158-202; Newell, 1954, p. 2-15 and 1956, p. 340-351; Doty and Morrison, 1954; Abe, 1937, p. 314-315; Hiro, 1936; Manton, 1935; Stephenson and others, 1931, p. 37-68, pls. 1, 17; Tokioka, 1953).

The principal variations in the appearance of a reef flat depend on whether the surface is one of organic growth or erosional truncation, on whether it is backed by land or a lagoon, and on whether it is broad or narrow. If the surface is one of organic growth, its nature further depends on geographic location and the nature of the organisms that are available to build reefs under local conditions of temperature, wind, tide, and current. If an erosional bench, its ultimate characteristics are also conditioned by the kind of rocks across which it is cut and the times and amounts of recent fluctuations in relative sea level.

Variations of the reef front involve the presence or absence and relative frequency of radial grooves and spurs or buttresses; whether these features are due primarily to growth, erosion, or a balance of factors; the angle of offshore slope; and of course the kinds of constructional organisms.

I have discussed the general problem elsewhere (Cloud, 1954), and the conspicuous features of organic reefs that appear to be generally present are briefly summarized by Tracey, Cloud, and Emery (1955). Particular local variations of the reef flat and reef front around Saipan are set forth under the habitat descriptions in an earlier part of the present report. The remarks that follow are intended to elaborate some of the local evidence insofar as it relates to general problems.

REEF FLAT PROPER

The reef flats of Saipan are probably all truncated to some degree. However, those of the east, north, and south coasts are in large part cut into old rock benches, whereas those that circumscribe the western lagoon-moat system seem mainly to follow rather closely antecedent reef surfaces. Subdivision into inner and outer reef flats is not particularly applicable to most of the reefs around Saipan, although the outer parts generally tend to have more coral and crustose coralline algal growth (pl. 132*C*, *D*), while the inner part is likely to be richer in soft algae and articulate corallines or to be a belt of sand or of bare rock and shallow tide pools. The surfaces of some fringing reefs of the south and northeast shores (facies 38) are divisible into relatively elevated reef edges of rich organic growth and relatively depressed inner moat surface veneered by

gravel and sand, and with only patchy organic growth.

A remarkable reef flat on the northwest coast (facies 42, pl. 137C-E) is beset with deep holes and high pinnacles. Between the deep holes is a rich growth of soft algae, and parts of the reef are ridged with narrow, irregularly intersecting walls whose surficial parts probably consist of coralline algae, perhaps vermetid gastropods, and precipitated CaCO_3 . The limestone pinnacles that rise above the general level of this reef flat are surrounded at their bases with rings of presumed organic growth and precipitated CaCO_3 like miniature fringing and barrier reefs. Although circumstances did not permit a close study of this surface, it very strongly suggests organic veneering of a bench that was earlier subaerially etched to a pinnacled surface of high relief.

The narrow terraced benches and rimmed pools that fringe so much of the coast (facies 43, pls. 137F, 138, 139) apparently owe their distinctive features to the combined effects of buildup by vermetid gastropods and algae at the rims of depressed areas concurrently with enlargement of the depressions as a result of combined solution and abrasion by browsing organisms,

GROOVE AND SPUR SYSTEM

The concentration of offshore grooves and spurs at the north and south ends of the western barrier-fringing reef complex (pl. 125A, D), where it approaches the land, and their rarity or absence in intervening areas (pl. 124), where it is backed only by lagoon waters, is of special interest. This pattern supports the thesis earlier set forth (Cloud, 1954, p. 201-202) that return current flow induced by a back reef land barrier is a critical factor in groove origin.¹² Figures 41-43 are drawn from field sketches of features observed (dimensions estimated) by swimming in and over grooves along the reef front near the southwest corner of Saipan. The undercut groove bottoms (similar to pl. 125F) that are veneered with gravel and sand, and their local association with or relation to erosional pits or marine potholes, are considered evidence that erosion has played an essential part in the origin of these grooves, regardless of the degree of algal masking of the spurs between.

Abrasion alone has probably been an effective erosional tool especially in the lower parts of these grooves. However, the channeling of abrasive tools may have been facilitated by solution rill patterns formed sub-

aerially along the edges and sloping surfaces of once emerged benches.

Aerial photographs along the northeast coast of Saipan show the tiered pattern of some of these groove and spur systems. Two tiers of grooves below sea level are clearly marked off by the lighter strip that cuts across the radial pattern parallel to and offshore from the white surf line of plate 136A. The serrated fringes of elevated groove and spur systems run all around the inshore strip of plate 136A, but are better shown in the enlarged view of plate 136B, and better yet by the irregularly scalloped shoreline fringe at the left side of plate 137A. Inspection of either aerial photographs or the surfaces of the intervening buttresses suggests a strong masking effect by veneering algal growth of the now active groove and spur system.

Plates 132A and 133A show highly irregular groove and spur systems along the south shore where construction strongly predominates over erosion. Here it seems that outflow of sediment is at places not even strong enough to maintain very regular radial orientation through inhibition of growth along well defined sediment paths. Coral growth is unusually vigorous along the reef edge (pl. 132C, D) and neither abrasion nor solution is now conspicuous there or, presumably, down the reef front. No underwater observations were made along this reef front and therefore no specific local evidence was found to prevent considering the entire groove and spur system of the south shore to be a growth phenomenon, whose orientation alone is due to outflow currents. In quiet waters no readily definable grooves and spurs form at all even though irregular algal growth may occur all along the reef front (pl. 125B).

Finally there is the unusual situation around Hagman bay (pl. 135A) where a system of grooves and spurs fringes a sea level bench that cuts across andesitic conglomerate. At the north edge of the bay (pl. 135B) this pattern is clearly erosional in the conglomerates of the surf zone. However, to judge from aerial photographs, the more coarsely spaced parts below the intertidal zone could easily represent outgrowth of algal buttresses over the volcanic substrate without indentation of the latter. The interpretation favored here is extension by algal veneering and outgrowth of an initially erosional pattern.

In summary, the evidence from Saipan is interpreted to favor the conclusion that relatively regular groove and spur systems are likely to be of basically erosional origin, although commonly with a veneer of organic overgrowth that masks or obliterates the erosional features. Doty and Morrison (1954, p. 5), as well as New-

¹² To be sure there is also a conspicuous coincidence of groove concentration with prevailing wind and surface current directions (Munk and Sargent, 1954; Emery, Tracey, and Ladd, 1954, p. 142), but this may be because these factors have also favored the formation of islands, today or in the past.

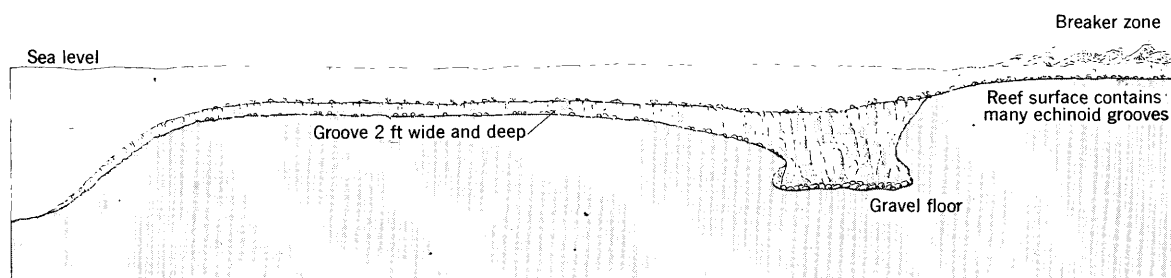
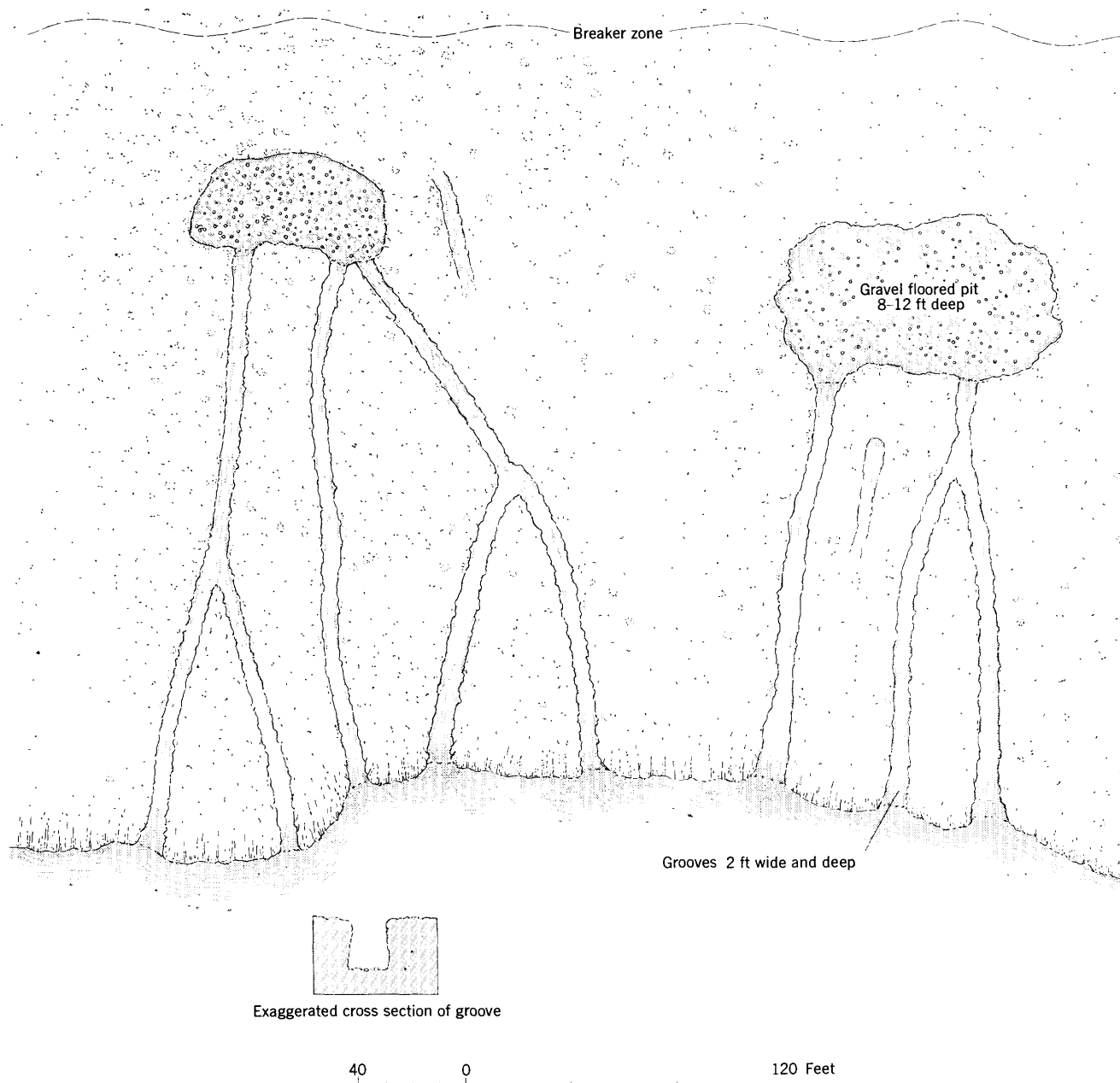


FIGURE 41.—Reef front grooves and pits near station G2.

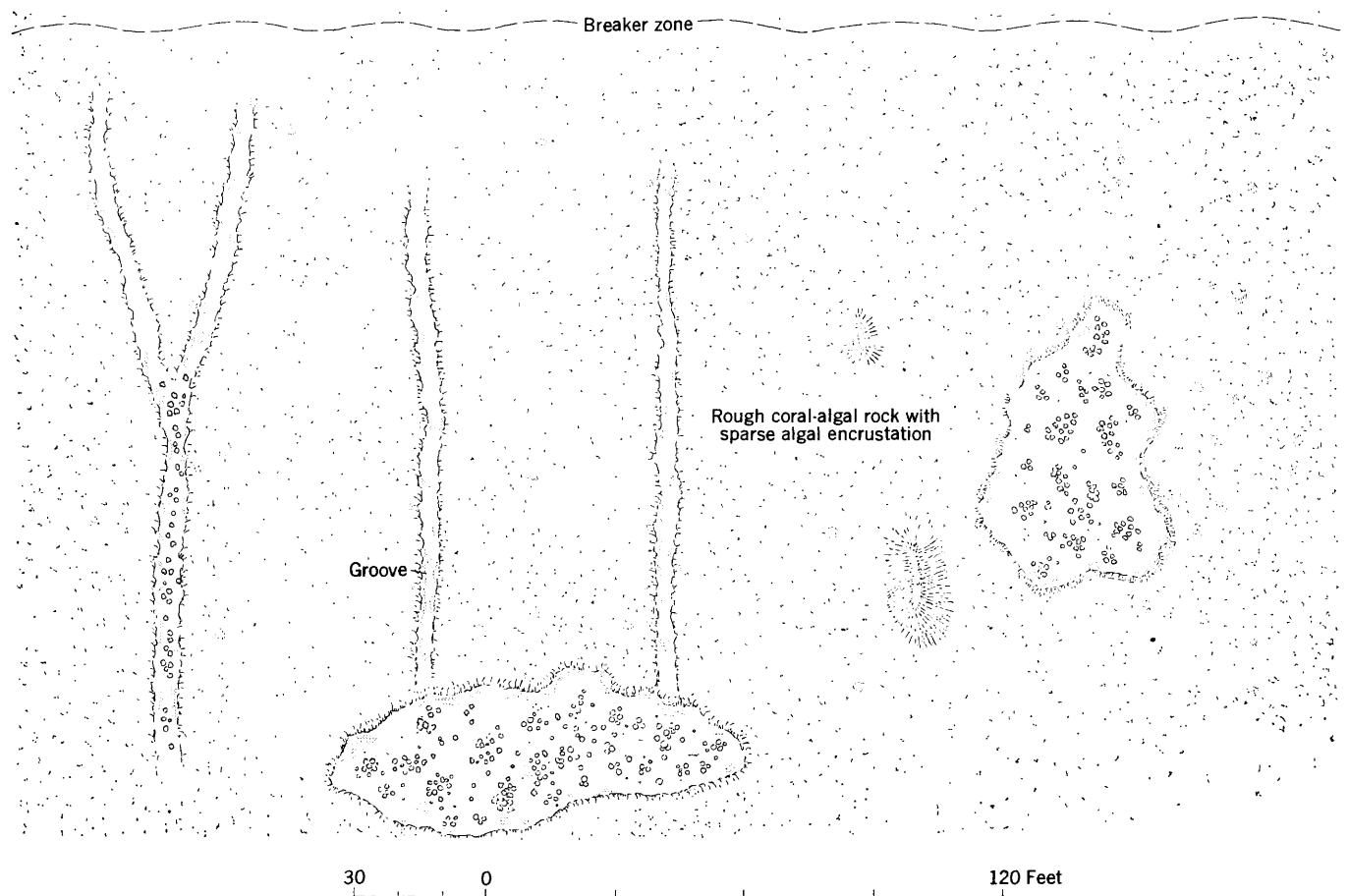
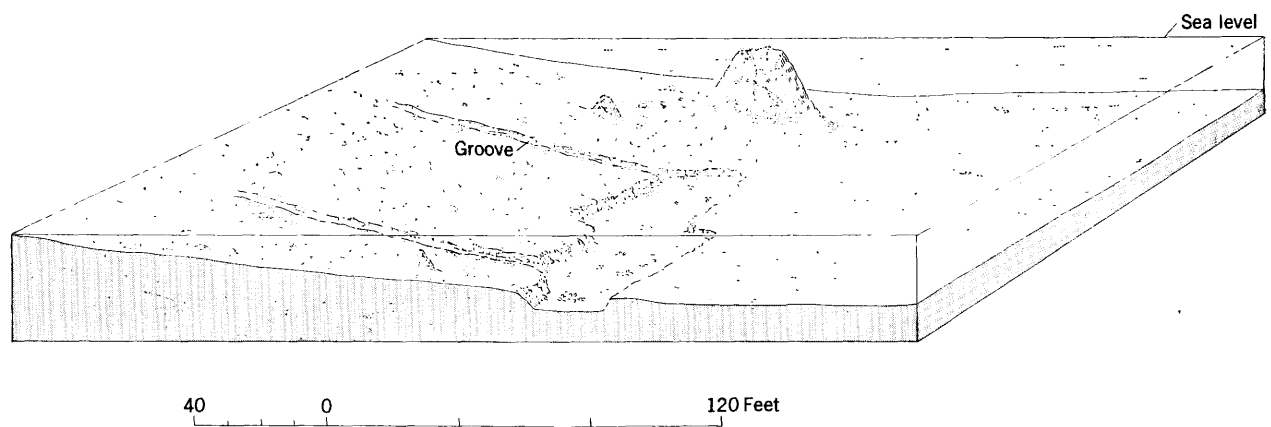


FIGURE 42.—Reef front grooves, spurs, and pits between Susupe and Afetña points.

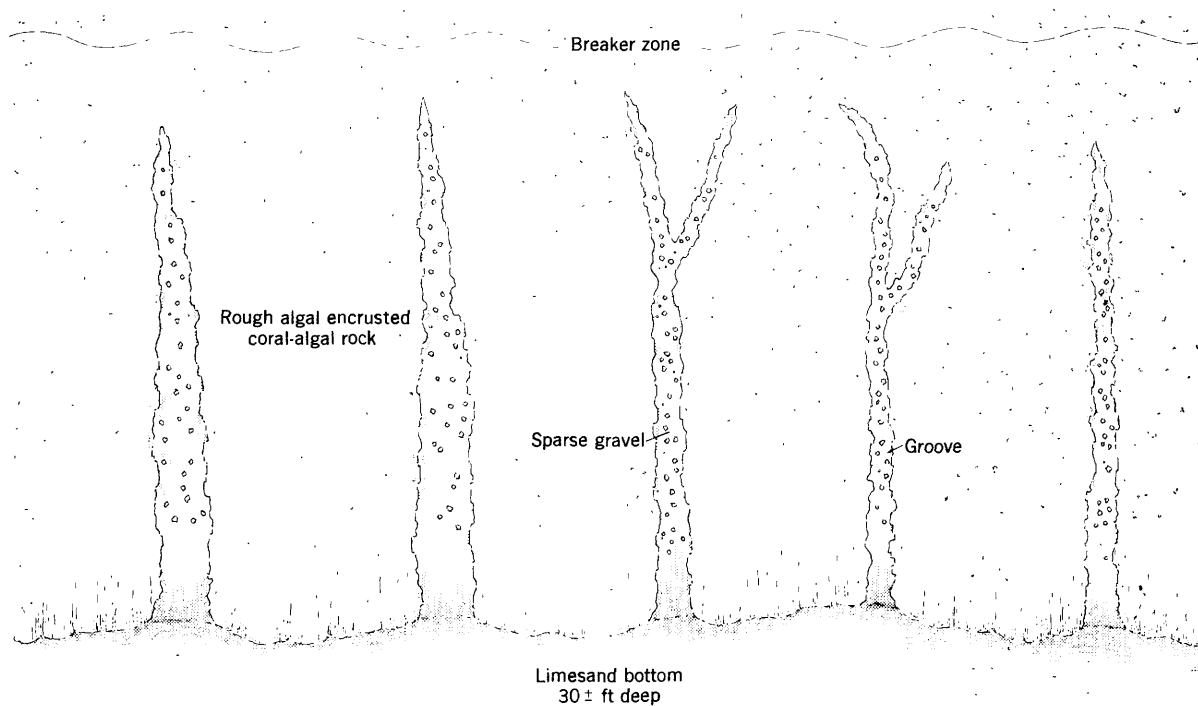
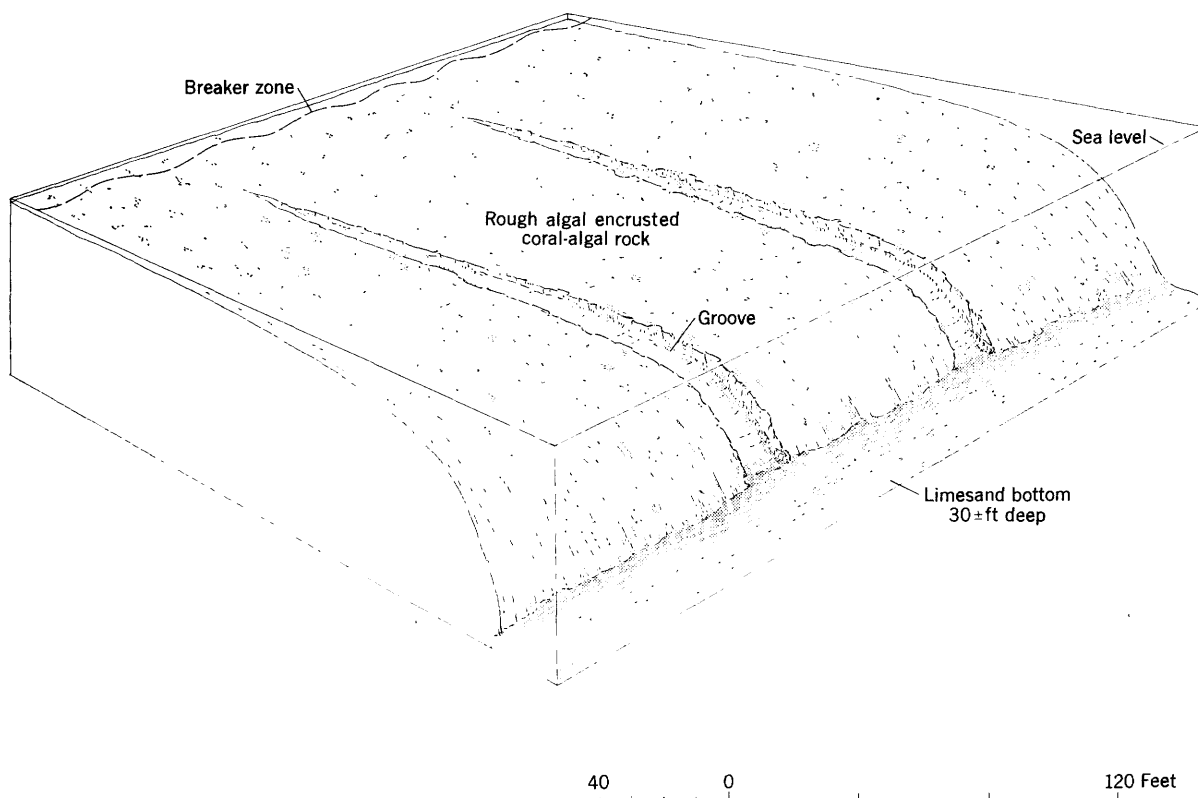


FIGURE 43.—Reef front grooves and spurs between Afetña and Agingan points.

ell (1954, p. 4), also favor a mainly erosional origin for groove and spur systems studied by them, although attributing somewhat less importance to constructional factors than is here suggested. In fact, some very irregular systems may be mainly constructional, as Emery, Tracey, and Ladd (1954, p. 145-146) have convincingly argued; and Crossland (1928, p. 584) long ago recognized that in areas familiar to him some grooves were erosional and some residual between outgrowing organic spurs. All evidence considered, it seems apparent that both erosion and construction play some part in shaping the features observed in most groove and spur systems—be it only as a partial constructional veneer on an abandoned erosional surface, or through the inhibition of organic growth in parts of dominantly constructional areas by the constant or frequently repeated movement of outflowing sediment trains.

ALGAL RIDGE AND SURGE CHANNELS

A surge channel is any minor indentation of the reef edge in the surf zone. The commonest sorts of surge channels are formed by the upper parts of reef front grooves where they cross the surf line. Other surge channels may be places where blocks have fallen or been wedged out of the reef front, or the indentations of an irregular growth line.

The algal ridge is a linear elevation at the reef edge caused by the marked upward growth of crustose coral-line algae. The principal and perhaps conditioning alga is *Porolithon oncodes* (Doty and Morrison, 1954, p. 7). A well-defined algal ridge was observed on Saipan only at the edge of the northern half of the reef at Fañunchuluyan bay (right side pl. 132B). Such ridges, however, are common along the windward reef edges of atolls in the open Pacific.

GROSS MORPHOLOGY AND EVOLUTION OF THE REEF COMPLEX

CONCENTRIC ZONATION

The shoal parts of the reef complex can be grouped in eight roughly concentric zones (pls. 123, 124). Although related to the more circumscribed ecologic units already described, these zones have a probably broader natural significance in terms of correlation with comparable living and fossil reef complexes elsewhere. The beach, of course, limits the sequence shoreward, just as the dwindle point of flourishing organic growth limits it seaward. The following paragraphs describe the main features of these eight zones in order from the sea shoreward.

1. Farthest seaward is the *reef front* itself (biotope XIV), which pitches downward from the reef flat to

the dwindle point of vigorous organic growth at 5 to 10 fathoms (Tracy, Cloud, and Emery, 1955; Cloud, 1952, p. 2130-2131). The reef front commonly is indented by a radial system of grooves and spurs, which are oriented parallel to outflow current lines as already described in this and other papers.

2. The *peripheral reef flat* (biotopes XII and XIII) is the most conspicuous of these concentric belts. It extends as a surf-laced ribbon around most of the island, defining the outer margin of the barrier reef lagoon along a large part of the western shore, and fringing the coast the rest of the way around. The moats, regardless of their own somewhat varied characteristics, are considered properly a part of the peripheral reef flat, in the broad zonation here defined. The varying characteristics of reef flats at other places are described in detail by many authors and are summed up for a number of areas by Wells (1954, p. 401-406, figs. 119-120). Odum and Odum (1955, p. 293-297) emphasize the contrasts between interisland reefs and reefs backed by islands, although their encrusting zone is very similar to the reef flat proper of other than sand-covered reefs, including those of Saipan, and regardless of whether backed by land or lagoon.

3. The *lagoon fringe of the peripheral reef* along the outer part of Tanapag lagoon east of Mañagaha islet (biotope XI; pls. 123, 124A) corresponds with the *Acropora palifera* zone of other areas. It might also be called the zone of *A. palifera* and *Porites lutea*. Its continuation southwestward from Mañagaha toward the main lagoon pass is so closely amalgamated with the reef flat proper (pls. 123A, 124B) that they are grouped for ecologic purposes; yet the preponderant corals of the lagoon fringe are unchanged. In this area also the consolidated lagoon fringe actually seems to be in the process of annexing adjacent reef patches by continued lagoonward growth. Northeastward the zone is represented by coral-algal bosses interspersed with sand and gravel along the outer moat margin (biotope VI). Southward from the main pass the growth characteristics of the lagoon fringe are supplanted by a belt of gravel (biotope IX) and lesser sand (facies 20) at the lagoon or moat margin of the reef flat.

Wells (1954, p. 397, figs. 119-120) compares the zone of *Acropora palifera* as developed at Bikini in the Marshalls, Maer Island in Torres Strait, and Yonge Reef of the Great Barrier Reef. At the first two places it is but a minor subdivision of reef flats backed by islands. At Yonge Reef, however, where it has been called the "anchorage coral zone" (Stephenson and others, 1931, p. 85, pl. 17; Manton, 1935, p. 306, pl. 15), the general features and location of the *A. palifera* zone in relation to reef and lagoon is more nearly analogous to that of

the lagoon fringe at Saipan. The zones of larger and smaller coral heads of Odum and Odum (1955, p. 295-297, figs. 2-3, 5) together are very like the "anchorage coral zone" at Yonge reef and basically equivalent to the lagoon fringe at Saipan—a feature of interisland reefs.

4. The *staghorn Acropora zone* (biotope III) is the dominating concentric feature next inshore from the lagoon fringe of the northern barrier reef segment (pls. 123, 126C, E). This expression of the outer lagoon shelf is missing elsewhere. The current-stripes or sediment paths that radiate across this zone impress on it a superficial radial pattern of erosional origin. Although no area exactly like this can be cited for comparison, parts of it are comparable with the "Madrepore fields" of the Great Barrier Reef reports or the *Acropora* thickets of various authors.

5. An *offshore zone of accreting limesands with seaweed* (parts of facies 4 and 5) comes next inshore from the belt of staghorn *Acropora*, along the inner edge of the outer lagoon shelf. Ecologically this zone is like other local areas of relatively stable limesand bottom with seaweed in which marine angiosperms predominate. Its location, however, is distinctive, and the dense plant growth here also serves the important function of entrapping sediments as they move lagoonward from the reef, thereby building up the outer lagoon shelf and at the same time retarding obliteration of the lagoon proper. Functionally comparable areas are described by Molinier and Picard (1952) and ecological comparison is made under zone 8.

6. The *lagoon proper* (biotopes IV and V) is an area of water mainly deeper than 2 fathoms, with a distinctive association of discrete reef patches rather abundantly interspersed on a limesand bottom. Only this part of Tanapag lagoon has features that would be considered distinctively lagoonal out of context. Indeed the features of this part of the lagoon and the reefs around it are such that the interpretation might be advanced that the reef along its outer edge is the only true barrier reef at Saipan. This is a fair alternative to the empirical interpretation here followed, which classes as barrier reef all of the peripheral reef behind and through or around which normal boat traffic is practicable under natural conditions. In terms as broad as those here used, it seems that most Pacific reef lagoons no deeper than this one are generally similar to it. Although published descriptions are not conducive to detailed comparison, the shallow reef lagoons familiar to me are similar, and those described to me orally by associates appear to be similar.

7. A discontinuous *nearshore zone of reef clusters* or shore reefs (facies 25, 26, 27) borders the inner edge

of the lagoon proper northeast of the port area and has a counterpart in the algal reef patches off Muchot point (facies 28). In fact one of the striking unexplained features of the reef complex is the way the reef clusters between Dogas and Flores points line up with the reef patches off Muchot point, and the peripheral reefs both north and south.

Possibly the reef clusters mentioned, together with the peripheral reefs beyond represent a former fringing reef complex that was interrupted at the middle by a broad pass and margined offshore by a shallow bench. If this be the case, the barrier reef north from the present harbor entrance is of different and primarily younger origin than the rest of the reef complex and, as mentioned above, could well be considered the only true barrier reef at Saipan. However, this is entirely in the realm of fancy, with no evidence except broad morphological alinement to support it. It also involves the inherent difficulty of explaining how it happens, if true, that the reef clusters are not a continuous linear rim (Cloud, 1952, p. 2135). If this explanation should be adopted, it also calls for some special explanation of the later upgrowth of the present barrier reef. Groups of "shore reefs" that have been described by various authors are analagous to this zone, but the so-called coral knolls of Emery, Tracy, and Ladd (1954, p. 147) and of Wells (1954, p. 401) are much taller features that rise from relatively great depths.

8. A *nearshore zone of limesands with seaweed* (much of biotope I) is the last of the eight principal concentric zones of the Saipan reef complex. It resembles zone 5, an offshore zone of sands with seaweed, except that the bottom sediments are seemingly richer in organic matter, large areas are partly exposed at spring low tides, and algae are generally more abundant than marine angiosperms. Here also are the only areas of the large grasslike *Enhalus*, comparable to the "muddy zone" and the "*Enhalus acoroides* zone" of Abe (1937, p. 228, 249-251), and the "sandy flat" zone of Hiro, as found at Iwayama Bay, Palau Islands. Similar areas, characterized by generically different angiosperms but much the same algae have a circumtropical distribution.

Last inshore, of course, is the beach itself, which is not considered as a part of the reef complex and requires no further discussion. The interested reader, however, will find that Hiro (1936) has provided considerable detail on the ecologic and biotic features of both limestone and volcanic shores at Palau.

EVOLUTION

The geologic record shows that Saipan has been fringed since sometime in the Pleistocene at least, and probably throughout the Pleistocene, by a reef complex

having characteristics similar to those existing today. That the present reef complex is but the latest step in a long evolution is, thus, not seriously to be questioned. The steps in the process, however, are complex, are in part self-cancelling, and can be considered with satisfaction only in broad terms.

Reefs and reef complex sediments of the Mariana limestone grew and accumulated during much of Pleistocene time, to the accompaniment of various rises and falls of sea level that necessarily resulted from melting and accumulation of Pleistocene ice sheets and local tectonic movements. The oldest clearly definable set of reef surfaces around Saipan that follows a pattern strongly resembling that of the present reef system, however, is that of the Tanapag limestone. This reaches up to about 100 feet above sea level, a fact which suggests a possible beginning during the last major interglacial stage. It ends with a reef surface 12 to 15 feet or so above sea level that, according to earlier listed carbon-14 results, may have been flourishing about 20,000 years ago. At that time, according to other carbon-14 dates, the continental glaciers had not yet begun or were only beginning their final retreat, and the sea should have been lower than it is now instead of higher. Thus either the 12- to 15-foot bench and reef surface was not eustatic (Chapter A suggests that it probably was eustatic), or revision of some carbon-14 dating is called for.

Taken at face value the data presented here and elsewhere (chap. A, p. 87, 106-107; Cloud, 1954) imply positive eustatic stands of the sea at 12 to 15 feet perhaps 20,000 years ago and at 5 to 6 feet about 3,000 ($\pm 1,500$) years ago. During these and other higher and lower stands of sea level, elevated groove and spur systems were cut and notches were formed that range from 40 feet above the present surface of the sea down to probably at least an equivalent depth. Remnants of a flourishing reef surface that probably lived at the time of the 6-foot eustatic stand are known from a number of localities beyond Saipan (for example, the east coast of Pagan and southwest Guam).

Lowering of sea level by about 6 feet in the last 3,000 years or so, and subsequent recovery by several inches in the last 100 years accounts for most of the superficial features to be observed on the reefs of Saipan, as at other localities (Cloud, 1954). The 6-foot sea level drop was accompanied by erosion of the present fringing reef benches into older limestone, reef rock, and even volcanic sediments. It also set the pattern for the latest phase in the evolution of the radial groove and spur systems that scallop the reef front today. The end of falling sea level, and the beginning of its rise about 100 years ago led to a partial recovery of organic growth; and, although many benches around Saipan

had not been fully reduced to the new sea level when recovery began, the development of at least a thin organic overgrowth is now widespread.

The reef alignments of the inner lagoon (zone 7 of foregoing section) could have evolved separately, or behind and concurrently with an offshore barrier reef. Separate evolution would have necessitated earlier fringing reef development, with later offshore upgrowth of a barrier reef from the edge of a former bank that may have been upthrown to its approximate present position by faulting or brought in to the zone of vigorous reef growth by change of sea level. This involves difficulties mentioned, as well as a reversal of the usual local fault pattern, but it would account for the striking reef trends observed. Concurrent evolution is favored here, instead of the hypothesis just outlined, mainly because it does not involve special explanations for which there is no independent evidence and because the reef clusters of facies 25 follow the characteristically diffuse pattern of protected waters.

An uneasy approximate equilibrium now prevails—with an apparent long range trend toward shoaling and narrowing of the lagoon, and perhaps slow seaward growth of the reef front locally. Fringing reef fronts seem to be growing slowly seaward, but storms probably keep them trimmed back to some degree and add slowly to the reef talus below. The barrier reef front is a zone of mainly weak organic growth, which nevertheless is in no imminent threat of destruction and is probably repaired in one place about as rapidly as it is eroded somewhere else. Sediments that result from both organic growth and organic and physical erosion are added to the floor of the lagoon, but are also moved seaward by bottom currents. They are probably not building up the lagoon proper very much faster than sea level is rising, except in the deeper nearshore area which is bordered seaward by a 5-fathom sill to the level of which sediments may be expected to accumulate in the next several thousand years.

Through encroachment of beach and peripheral reef, through sedimentation, and through spread of sediment entrapping reef patches the bulk of the present lagoonal area may yet be wrested from the sea. Long before this might happen under existing conditions, however, changing climate or local tectonism will almost surely have altered existing base levels and controls, setting new rates and timetables for all events.

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D, dead shell. *Italic symbol indicates sight record only: identification by Cloud!*

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APPENDIX—Tabulation of animals and plants

[Occurrence symbols: A, abundant; C, common; R, rare; X, no record of abundance;]

	Gross habitat	Shoreline		Barrier reef lagoon and contiguous fringing reef moats																												
				Lagoon proper																												
	Biotope	Sand beach	Rocky shore	I Limesand with seaweed							II Gravel	III Limesand with <i>Acropora</i>			IV Interspersed reef patches and limesand																	
				2		4		5				6	7	8	10		11			12			13									
Facies	8b	6a	6a	13x	D3	Gx	A1a	3	B1b	B3	C4	B2	B7	E4	C2	B8	4	B4	A5a	A7	A8	D6	D7	A5	D5	D8	D9	2	A11	5		
Collecting station																																
ANTHOZOA—Continued																																
Hexacorallia—Continued																																
Scleractinia—Continued																																
Fungiida—Continued																																
Poritidae:																																
	<i>Porites lichen</i> (Dana).....																															
85	<i>lutea</i> Edwards & Haim.....																															
86	sp.....																															
87	<i>Goniopora fruticosa</i> Saville-Kent.....																															
88	Favilida:																															
Favilidae:																																
	<i>Echinopora lamellosa</i> (Esper).....																															
89	<i>Favia pallida</i> (Dana).....																															
90	<i>speciosa</i> (Dana).....																															
91	<i>stelligera</i> (Dana).....																															
92	sp.....																															
93	<i>Favites abdita</i> (Ellis & Solander).....																															
94	<i>halicora</i> (Ehrenberg).....																															
95	<i>Goniastrea pectinata</i> (Ehrenberg).....																															
96	<i>retiformis</i> (Lamarck).....																															
97	sp.....																															
98	<i>Leptastrea bottae</i> (Edwards & Haim).....																															
99	<i>purpurea</i> (Dana).....																															
100	<i>transversa</i> Klunzinger.....																															
101	<i>Leptoria phrygia</i> (Ellis & Solander).....																															
102	<i>Platygyra rustica</i> Dana.....																															
103	<i>sinensis</i> (Edwards & Haim).....																															
104	sp.....																															
105	Oculinidae:																															
	<i>Acrhetia horrescens</i> (Dana).....																															
106	<i>Galaxea fascicularis</i> (Linné).....																															
107	sp.....																															
108	Mussidae:																															
	<i>Lobophyllia corymbosa</i> (Forskål).....																															
109	Pectinidae:																															
	<i>Echinophyllia aspera</i> (Ellis & Solander).....																															
110	Caryophyllida:																															
	Caryophylliidae:																															
	<i>Euphyllia glabrescens</i> (Chamisso & Eysenhardt).....																															
111	Zoanthidea:																															
	<i>Zoanthus</i> sp.....																															
112	<i>Palythoa</i> sp. (common but mainly unrecorded).....																															
113	Actinaria:																															
	<i>Metarhodactis boninensis</i> Carlgren (Identified by Carlgren).....																															
114	Alcyonaria:																															
	<i>Helopora coerulea</i> (Pallas).....																															
115	<i>Tubipora musica</i> (Linné).....																															
116	<i>Sinularia</i> sp. (common but not collected).....																															
117																																
HYDROZOA																																
Milleporina: (Identified by John W. Wells).																																
	<i>Millepora tenera</i> Boschma.....																															
118																																
PLATYHELMINTHES																																
(Identified by Libbie H. Hyman)																																
119	<i>Euplana gigas</i> (Schmarda)?.....																															
120	<i>Labocestidae</i> gen. & sp.?.....																															
121	<i>Ommatoplana</i> , n. sp.....																															
122	<i>Pseudoceros</i> , n. sp.....																															

See footnotes at end of table.

D, dead shell. *Italic symbol indicates sight record only; identification by Cloud*

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APPENDIX—*Tabulation of animals and plants*

[Occurrence symbols: A, abundant; C, common; R, rare; X, no record of abundance;

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Facies				2	4	5	6	7	8	10		11			12			13														
Collecting station		8b	6a	6a	13x	D3	Gx	A1a	3	B1b	B3	C4	B2	B7	E4	C2	B8	4	B4	A5a	A7	A8	D6	D7	A5	D5	D8	D9	2	A11	5	
BRACHIOPODA																																
123	<i>Thecidellina</i> aff. <i>T. mazilla</i> Hedley.....																															
BRYOZOA																																
124	Schizoporellid gen. & sp. ? (Identified by R. S. Bassler).																															
SIPUNCULOIDEA																																
(Identified by W. K. Fisher)																																
125	<i>Aspidosiphon pachdermatum</i> Wesenberg — Lund.																															
126	<i>steenstrupii</i> Diesing.....																															
127	<i>truncatum</i> Keferstein.....																															
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APPENDIX—*Tabulation of animals and plants*

[Occurrence symbols: A, abundant; C, common; R, rare; X, no record of abundance;]

Gross habitat		Shoreline		Barrier reef lagoon and contiguous fringing reef moats																												
				Lagoon proper																												
Biotope	Facies	Sand beach	Rocky shore	I Limesand with seaweed							II Gravel	III Limesand with <i>Acropora</i>			IV Interspersed reef patches and limesand																	
				2		4		5				6	7	8	10	11			12			13										
Collecting station		8b	6a	6a	13x	D3	Gx	A1a	3	B1b	B3	C4	B2	B7	E4	C2	B8	4	B4	A5a	A7	A8	D6	D7	A5	D5	D8	D9	2	A11	5	
ARTHROPODA—Continued																																
Crustacea—Continued																																
Decapoda—Continued																																
Brachyura—Continued																																
Xanthidae—Continued																																
391																																
392																																
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413																																
414																																
415																																
Anomura:																																
Coenobitidae:																																
416																																
417																																
418																																
419																																
420																																
421																																
Macrura:																																
Axillidae:																																
422																																
423																																
424																																

See

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				8b	6a	13x	13x	D3	Gx	A1a		3	B1b	B3	C4	B2	B7	E4	C2	B8	4	B4	A5a	A7	A8	D6	D7	A5	D5
Facies		Collecting station																											
ECHINODERMATA—Continued																													
Asteroidae:																													
478	<i>Culcita novae-guiniae</i> Müller & Troschel.....																												
479	<i>Disasterina spinulibera</i> H. L. Clarke.....																												
480	<i>Fromia milleporella</i> (Lamarck).....																												
481	<i>Linckia guildingii</i> Gray.....																												
482	<i>laevigata</i> (Linné).....																												
483	<i>mutifora</i> (Lamarck).....																												
484	<i>Othilia luzonica</i> Gray.....																												
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485	<i>Ophiarthrum elegans</i> Peters.....																												
486	<i>Ophiocoma erinaceus</i> Müller & Troschel.....																												
487	<i>scolopendrina</i> (Lamarck).....																												
488	<i>Ophiocometella clippertoni</i> A. H. Clark.....																												
489	<i>Ophiopsis cincta</i> Müller & Troschel.....																												
490	<i>Ophiomastix mixta</i> Lütken.....																												
491	<i>notabilis</i> H. L. Clark.....																												
492	<i>Ophioneis porrecta</i> Lyman.....																												
493	<i>Ophiopozella spinosa</i> (Ljungman).....																												
494	<i>Ophiothrix longipeda</i> (Lamarck).....																												
495	<i>plana</i> Lyman.....																												
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496	<i>Holothuria atra</i> Jaeger.....																												
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(Identified by L. P. Schultz and associates)																													
Apodes:																													
Muraenidae: (marine eels)																													
498	<i>Anarchias allardicei</i> (Jordan & Starks).....																												
499	<i>Gymnothorax margaritophorus</i> Bleeker.....																												
500	<i>Oropterygius concolor</i> Rüppell.....																												
501																													
Berycoidei:																													
Holocentridae: (soldier fishes)																													
502	<i>Holocentrus</i> sp.....																												
Thoracostei:																													
Syngnathidae: (pipe fishes)																													
503	Genus and species?.....																												
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Apogonidae: (cardinal fishes)																													
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507	Lutjanidae: (snappers)																												
508	Genus and species?.....																												
Chaetodontidae: (butterfly fishes)																													
509	<i>Chaetodon auriga</i> Forskal.....																												
510	<i>Chaetodon</i> sp.....																												
Acanthuridae: (surgeon fishes)																													
511	<i>Acanthurus nigricans</i> (Linné).....																												
Cataphracti:																													
Scorpaenidae: (scorpion fishes)																													
512	<i>Pterois volitans</i> (Linné).....																												
513	<i>Scorpaena</i> sp.....																												
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514	<i>Synanceya verrucosa</i> Block.....																												
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515	<i>Caracanthus unipinnus</i> (Gray).....																												

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								2		4		5		6	7	8	10	11			12			13									
Facies				8b	6a	6a	13x	D3	Gx	Ala	3	B1b	B3	C4	B2	B7	E4	C2	B8	4	B4	A5a	A7	A8	D6	D7	A5	D5	D8	D9	2	A11	5
Collecting station																																	
FISHES—Continued																																	
Chromides:																																	
Pomacentridae: (demoiselle fishes)																																	
516	<i>Abudefduf biocellatus</i> (Quoy and Gaimard)																						X										
517	<i>Amphiprion</i> sp.																																
518	<i>Chromis caeruleus</i> (Cuvier)																																
519	<i>Dascyllus aruanus</i> (Linne)																																
520	<i>Pomacentrus</i> sp.																																
Pharyngognathi:																																	
Scaridae: (parrot fishes)																																	
521	"Scarus" (At all localities near reefs; none collected).																																
Gobioidae:																																	
Gobiidae: (gobies, part)																																	
522	<i>Gobiodon</i> sp.																																
523	Genera and species?																						X			X							
Eliotridae: (gobies, part)																																	
524	<i>Eviota</i> sp.																							X									
525	Genera and species?																								X								
Jugulares:																																	
Blennidae: (blennies)																																	
526	<i>Entomacrodus thalassinus</i> (Jordan and Seale)																																
527	<i>Alticus saliens</i> (Lacapède)																																
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528	<i>Carapus mourlani</i> Petit																		R						R						R		
Xenopterygii:																																	
Gobiesocidae: (sucker fishes)																																	
529	Genus and species?																																
Plectognathi:																																	
530	Tetraodontidae: (puffers)																																
531	<i>Arothron</i> sp.																																

¹ No collections from biotope XV, which has limesand bottom.² See chapter H for complete list of Foraminifera, based on dead tests in sediment samples.³ From de Laubenfels collection, probably biotope I, facies 3.⁴ The species listed are grouped in several subgenera by some authors.⁵ There are unidentified genera and species in most lagoonal sediments, but no live specimens were taken.⁶ Most subtidal localities contained specimens that were not collected or identified by genera and species.⁷ From facies 42, northwest coast; not on check list.

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PLATES 123-139

PLATE 123

[Photographs by U. S. Navy Squadron VU-7 (B), June 1949]

- A. View east across Tanapag lagoon and along peripheral reef complex, showing transition (arrow) from barrier reef in foreground to fringing reef at left background. At right edge are algal reef patches off Muchot point. Mañagaha islet, a sand cay, relates this view with plates 123B and 124B.
- B. View south across Tanapag lagoon and along southern arm of barrier reef. Transition from barrier to fringing reef here occurs just under tip of plane wing in right distance. Parallel zonation of reef complex is well shown in this and preceding view. Shoreward from the sea the conspicuous zones are: 1, reef front; 2, peripheral reef flat; 3, lagoon fringe of barrier reef (or *Acropora palifera* zone); 4, staghorn *Acropora* zone; 5, offshore zone of accreting limesands with seaweed; 6, lagoon proper; 7, nearshore zone of reef clusters; and 8, nearshore zone of limesands with seaweed.



GENERAL VIEWS OF WESTERN REEF COMPLEX



REEF PATCHES, REEF CLUSTERS, AND TRANSITION OF WESTERN BARRIER REEF TO FRINGING REEF

PLATE 124

[Photographs by U. S. Navy Squadron VU-7 (B), June 1949]

- A. View south toward Dogas point (D) across transition zone from barrier reef to fringing reef. Irregular dark area right from center (a) is a dense thicket of staghorn *Acropora* that connects lagoon fringe of barrier reef to reef clusters (p) that extend almost to beach. Fish traps (t) are in broad moat behind transition area. Rare weak grooves of upper reef front (1) contrast with those of plate 125A, where land behind narrow reef causes strong return current flow. Numerous narrow grooves in lower tier in left half of reef front, presumably an older generation kept open by weak return current flow. Zone Nos. 1-3 explained in plate 123B.
- B. View southeast across widest part of Tanapag lagoon to port area. Generally dark reef patches or mounds that rise toward surface from surrounding limesand bottom accumulate a light cap of detritus and pavement algae where they break the surface as in the larger patches at left (p) and around Mañagaba islet. Inner reef flat (3) here is a consolidated version of lagoon fringe of barrier reef, in process of annexing adjacent reef patches by lagoonward growth. Ripple marks are conspicuous in limesands of right foreground. Quaquaversally dipping beach rock is prominent at b, and its dark strips contrast with the beach and foreshore sands all around the islet. Zone Nos. 1-3 explained in plate 123B.

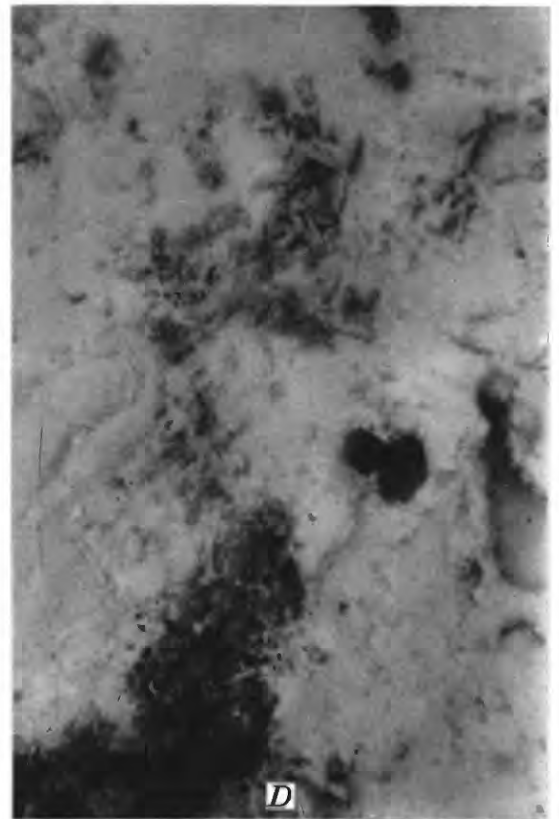
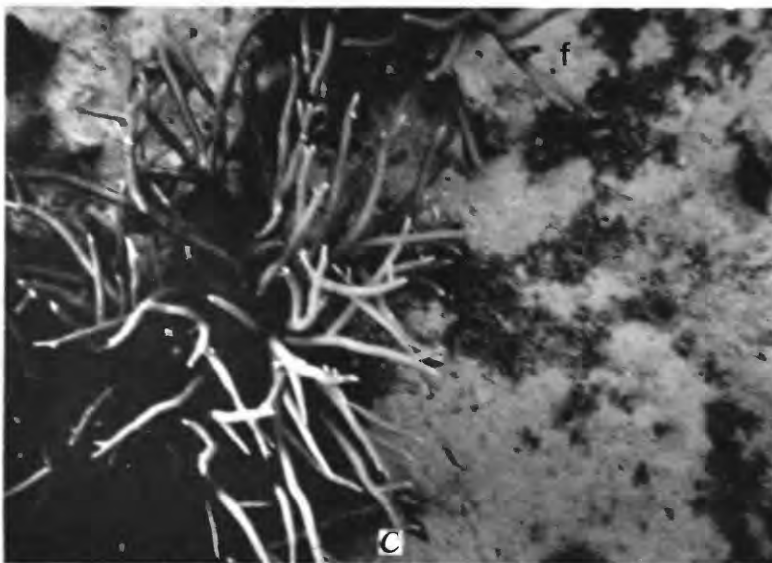
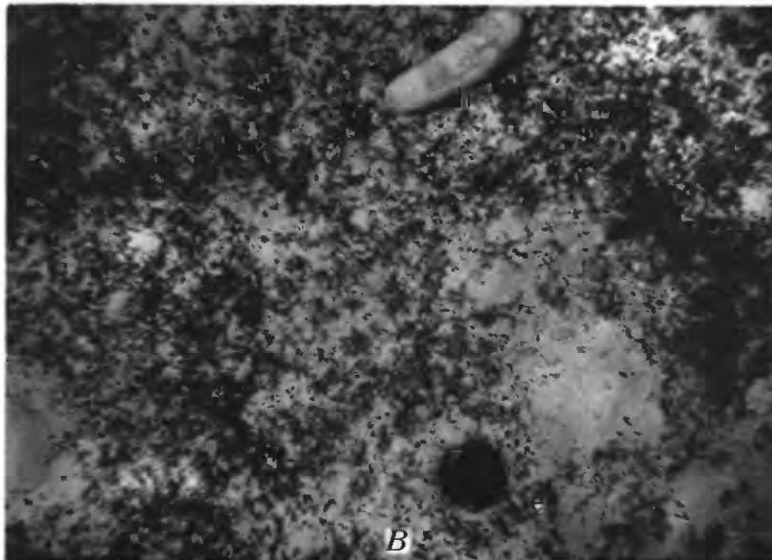
PLATE 125

[Photographs A-D by U. S. Navy Squadron VU-7 (B), June 1949]

- A. Fringing reef at north end of western reef complex (facies 33). Groove and spur system at reef front here believed due to maintenance of grooves in area of generally marked organic overgrowth by return current flow induced by nearness of shore. Reef and beach rock makes dark streaks at right and left ends of beach. The thriving reef flat is crisscrossed by vehicle tracks.
- B. Barrier reef and shoal lagoon near traverse E. Current-striped gravels and coarse sands of biotope II are conspicuous to right of partly filled channel. Dark mottling along shore and at left is seaweed growing on limesand. The mainly algal reef is advancing over limesand (right) and rocky (left) off-reef bottom at depths of 2 to 4 fathoms.
- C. South end of barrier reef complex off Susupe point. Sporadic irregular reef front grooves and spurs of facies 45 can be seen here. Vehicle tracks crisscross sands and gravels of facies 24 between reef flat and dark seaweed meadows (mainly of *Zostera*). Seaweed is very sparse on the light-colored inshore sands.
- D. Fringing reef at south end of western reef complex. Algal mat of biotope VII occupies shoreward half of moat. Grooves and spurs are better developed along reef front here than at other places along west coast south of figure A.
- E. Apparent intertidal solution of fragments of limestone aggregate in portland cement matrix (lower half of photograph). Jetty on ocean-facing shore of Key West, Fla., at Casa Marina hotel. Jetty constructed 1919-1920, photograph November 1954.
- F. Undercut side (right) of erosional groove on sea level bench at east end of Tarague Beach, north Guam. Tide is near high, water 3 to 3½ feet deep, water surface at upper left.



WESTERN FRINGING REEF ENDS, SOUTHERN BARRIER REEF COMPLEX, AND EXAMPLES OF SHOAL MARINE EROSION



CLOSE VIEWS OF LIMESAND BOTTOM AND STAGHORN *ACROPORA* ZONE

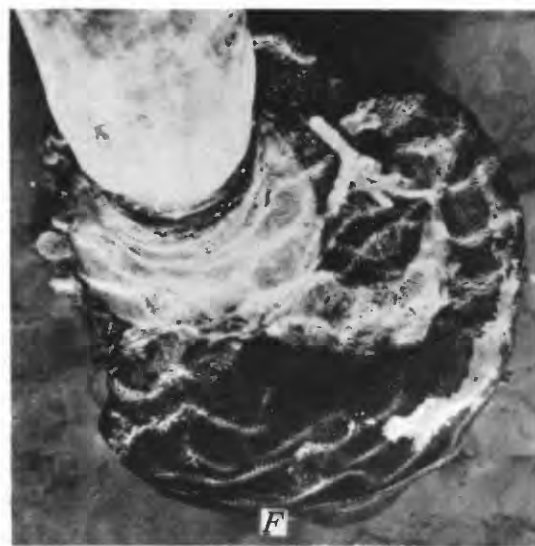
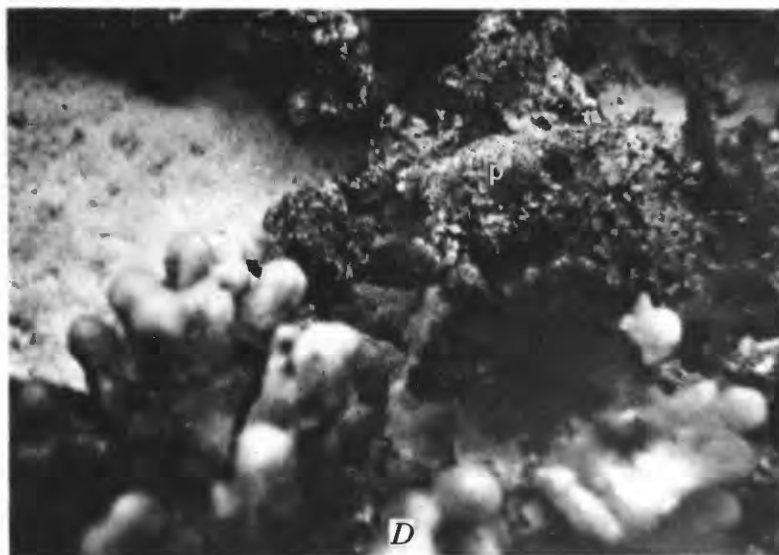
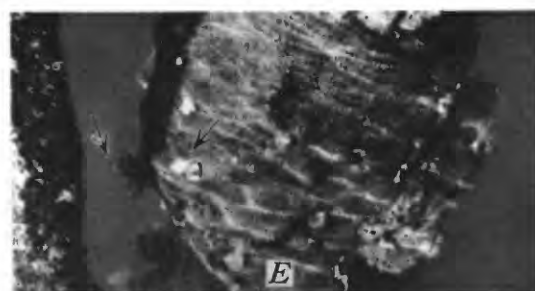
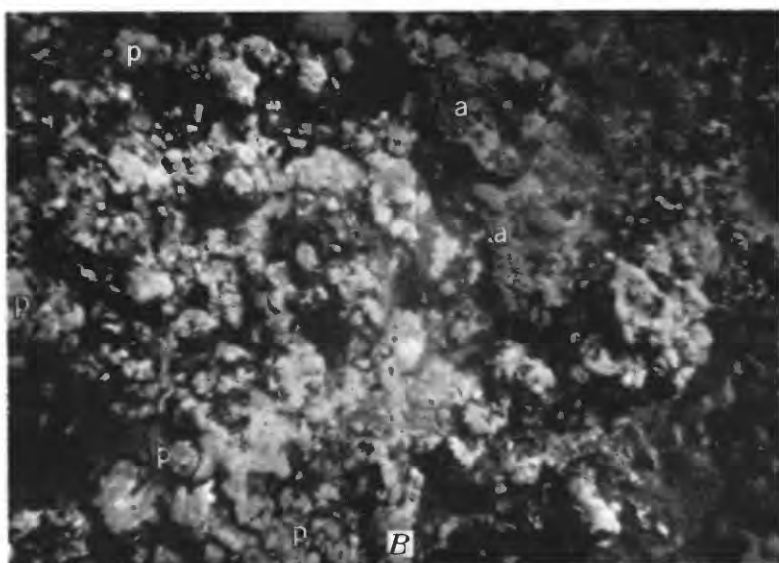
PLATE 126

- A. Richly organic limesands of facies 4 at shore end of traverse *B*. Broad flats exposed at spring low tide. Mounds of numerous burrowing organisms are conspicuous, and scattered *Enhalus* reaches almost to shore.
- B. Holothurian (*Holothuria atra*, h) and echinoid (*Tripneustes gratilla*, e) on limesand bottom with moderate seaweed growth (facies 5), between traverses *B* and *C*. The holothurian is about 10 inches long.
- C. Living staghorn *Acropora* and limesand of facies 8 near *location 4*. *Dascyllus aruanus*¹ at f.
- D. Limesands and dead *Acropora* of facies 7 thinly veneering cavernous bottom of coral-algal rock near *location 4*. Holes like those at right center are favorite hiding places for fish, octopus, and eels.
- E. Living staghorn *Acropora* of facies 8 near *location 4*. The fish at f is *Chaetodon auriga* Forskal,¹ a bit below and to the left is *D. aruanus*¹ again.

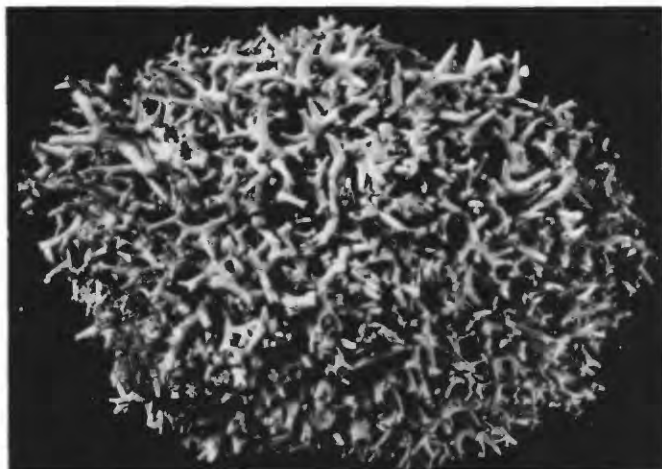
¹ Identified by J. C. Randall. Authors of species not named for those listed in the appendix.

PLATE 127

- A. Collection of corals from coral-algal clumps of facies 8 at *location 4*, including *Acropora palifera*, *Pocillopora damicornis caespitosa*, *Porites lutea*, and *Goniastrea retiformis*. The starfish *Culcita novae-guinae* in left foreground is the usual host of the transparent pearl-fish *Carapus mourlani* in this area.
- B. Surface of mainly dead coral-algal rock at about 4 fathoms, at station *D9*, facies 12. Living material includes white patches of encrusting coralline algae; small lumps of the brown, sand-imbedding zoanthid *Palythoa* (p); botryoidal-looking alcyonid clusters (a); and dark film of soft algae on dead rock.
- C. Living coral in a few feet of water, facies 17, *location 8*. *Acropora humilis* nearly fills the picture.
- D. Lagoon fringe of barrier reef at station *C7a*, facies 31. A black comatulid crinoid (*Comanthus* sp.) about 6 inches across clings by its basal cirri to a shallow depression just right of center and below the p. Living *Acropora palifera* fills the foreground around the crinoid and mainly dead and porous coral-algal rock with occasional *Palythoa* (p) extends below it to coarse limesands at a depth of 9 feet.
- E. Meandriform coral infested with plumose serpulid annelids cf. *Spirobranchus* (arrows) on piling at Garden Key, Dry Tortugas, Florida. The colorful spiral plumes of the circumtropical tubicolous borer *Spirobranchus giganteus* are common in the living coral at Saipan.
- F. Meandriform coral growth on sunlit side of piling at Fort Jefferson wharf, Garden Key, Dry Tortugas, Florida. Photograph made November 1954 of piling believed driven in 1890. Coral extends 14 inches out from piling, whose underwater diameter is 15 inches. Similar pattern of inhibited growth on the wharf side was observed on piling on all sides of this structure.



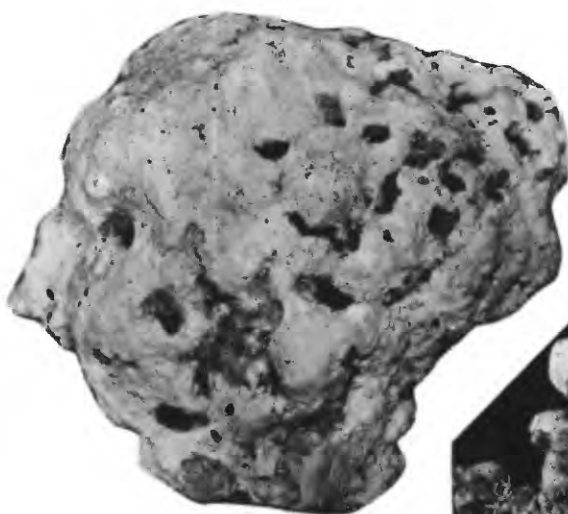
REEF BUILDERS



A



B



C



D



E

SOME REEF-BUILDING AND SEDIMENT-FORMING ALGAE

PLATE 128

[All 0.8 natural size]

- A. Crustose coralline alga of the branching type (*Lithophyllum moluccense*) from shallow, sandy, seaweed covered bottom at station *B1b*, facies 4. USGS Paleobot. loc. D260, algae a575.
- B. Crustose coralline alga of the branching type (*Lithophyllum moluccense*) from algal reef patch at station *D6*, facies 28. USGS Paleobot. loc. D264, algae a576.
- C. Pavement-type crustose coralline alga (*Porolithon oncodes*) from fringing reef on south coast, *location 14*, facies 38. Photograph by J. H. Johnson. USGS Paleobot. loc. D498, algae a577.
- D. Articulate coralline alga (*Cheilosporum*) of type that flourishes in rimmed pools, and on benches and terraced ramps of east coast. Southeast Saipan, specific locality unrecorded. Photograph by J. H. Johnson. USGS Paleobot. loc. D279, algae a37.
- E. *Halimeda opuntia*, showing sediment entangled holdfast and adventitious pieces of *H. tuna*. Station *B2*, facies 4 USGS Paleobot. loc. D497, algae a574.

PLATE 129

A-B. Reef-imbedding gastropod *Magilus antiquus* (natural size) from *location 4*, facies 8. USNM mollusk coll. 595414.

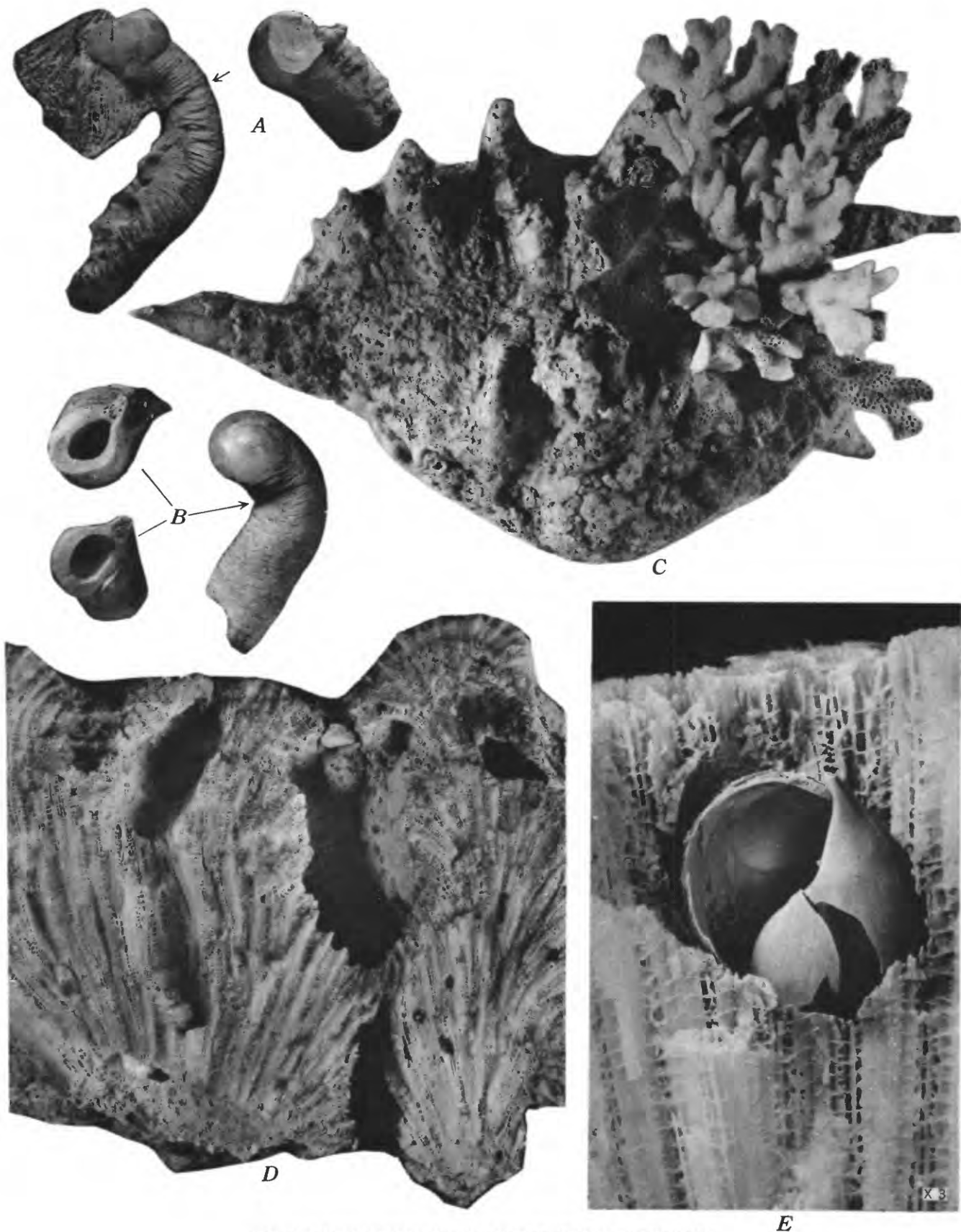
(A) Lateral view of mature specimen with coiled apical portion partly surrounded by host coral at left; transverse view of solid proximal end of shell at right. Arrow points to line along which surface of right view was broken.

(B) Apical view of another specimen at right; cross sections of transversely broken specimen at left. Arrow indicates point of fracture. In contrast to the nearly solid preceding shell this one is hollow for nearly 4 cm behind aperture to primary coiled portion.

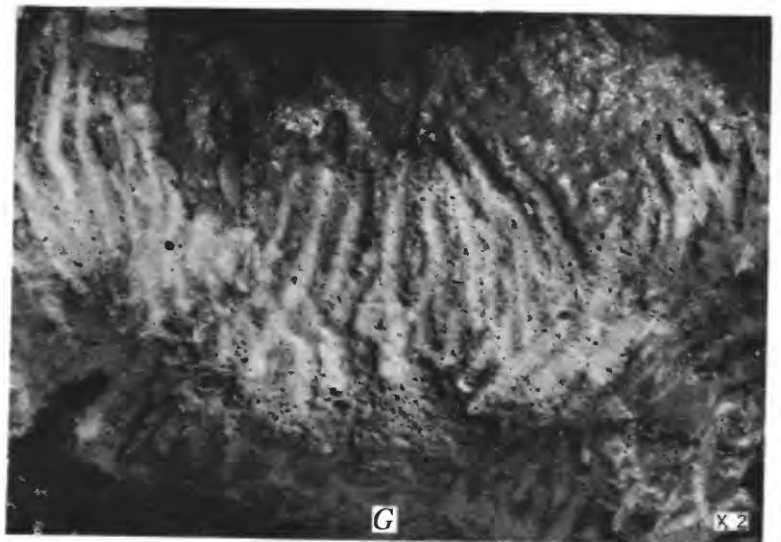
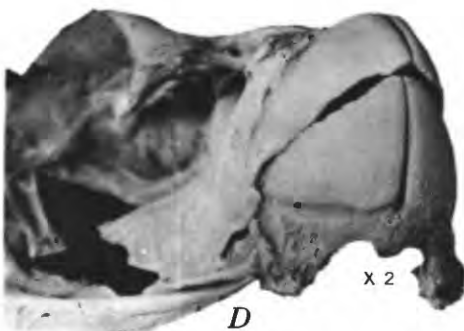
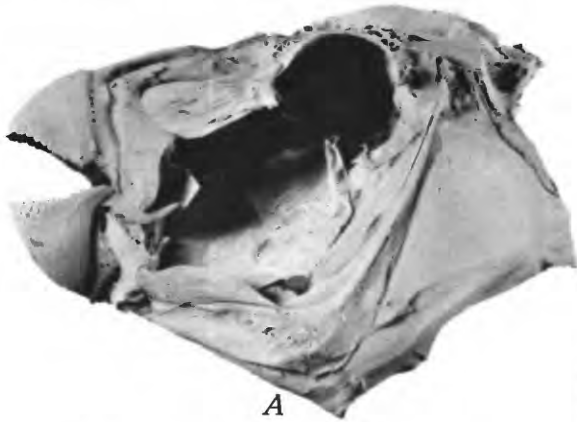
C. This "spider shell" (*Lambis lambis*), alive when taken at *station FX*, carries on its back a several-inch-high cluster of equally healthy *Pocillopora* (both natural size). The good condition of the delicately branching *Pocillopora*, and the worn state of the gastropod's marginal "fingers" indicate that the latter are effective protection against overturning. USNM mollusk coll. 609932.

D. *Goniastrea retiformis* from *location 4* (facies 8), showing small-bore polychaete burrows, irregular hollows such as xanthid crabs nestle in, and (at left) fingerlike burrow of the gastropod *Magilopsis lamarcki* (natural size). USNM mollusk coll. 609931.

E. *Magilopsis lamarcki* in living position just beneath surface of another part of same *Goniastrea retiformis* as D (magnified 3 times). This shell was dead when taken and was broken on removal. It sits in a pit that barely fits its shell and not at the end of a burrow as in D. USNM mollusk coll. 609931.



SOME DISTINCTIVE REEF-ASSOCIATED GASTROPODS



WORK OF SEDIMENT-PRODUCING FISH

PLATE 130

A, B, F. Skull ($\times 1$), beak ($\times 2$), and elements of pharyngeal dentition ($\times 1$) of a parrot fish (*Scarus* sp.) from Onotoa Atoll, Gilbert Islands. USNM fish coll. 164322.

C-D. Skull ($\times 1$) and beak ($\times 2$) of the puffer fish *Arothron hispidus* (Lacapede)¹ from Onotoa Atoll, Gilbert Islands. USNM fish coll. 164320.

E-G. Beak-markings ($\times 1$, $\times 2$) of parrot fish on living surface of hydrocoralline *Millepora* sp. from seaward reef front at Carysfort Light, east coast of Florida.

¹ Identified by J. C. Randall.

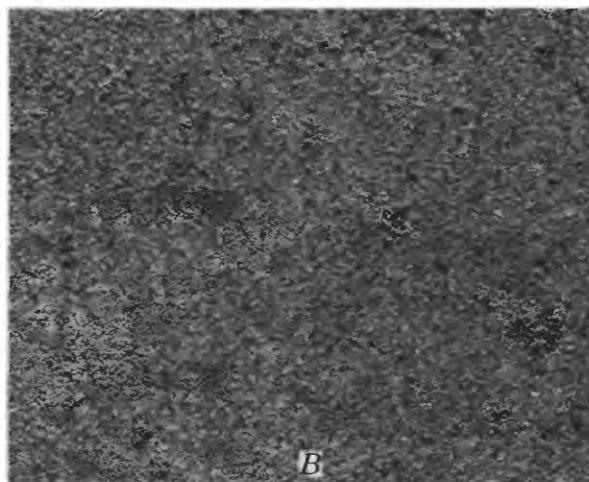
PLATE 131

- A-B. Limesand ($\times 10$, $\times 1$) from gut of parrot fish (*Scarus* sp.) taken at Onotoa Atoll, Gilbert Islands. The 1.5-mm-long papillose spindles, the spicules of the alcyonarian, *Sinularia*, are common in the lagoonal limesands of Onotoa and Saipan. USNM fish coll. 164322.
- C, F, H. Skull ($\times 1$), beaklike dentition ($\times 2$), and sample of gut contents ($\times 1$) of the trigger fish *Balistapus undulatus* (Mungo Park)¹ from Onotoa Atoll, Gilbert Islands. USNM fish coll. 164321.
- D. Ctenoid dentition ($\times 3$) of the algal browsing *Acanthurus achilles* Shaw,¹ a surge-channel-dwelling surgeon fish from Onotoa Atoll, Gilbert Islands. USNM fish coll. 164319.
- E. Molariform and "fang" dentition of the snapper fish *Monotaxis* cf. *M. grandoculis* (Forskål)¹ from Onotoa Atoll, Gilbert Islands. An omnivorous eater of sediments, it may use its "fangs" to break into small echinoids and crustaceans. USNM fish coll. 164323.
- G. Debris ($\times 1$) from gut of puffer fish *Arothron nigropunctatus* (Bloch)¹ taken at Onotoa Atoll, Gilbert Islands. Most particles are the freshly bitten-off growing tips of a delicately branching species of *Acropora* (largest measured piece from this fish 15 by 5 mm). USNM fish coll. 164320.

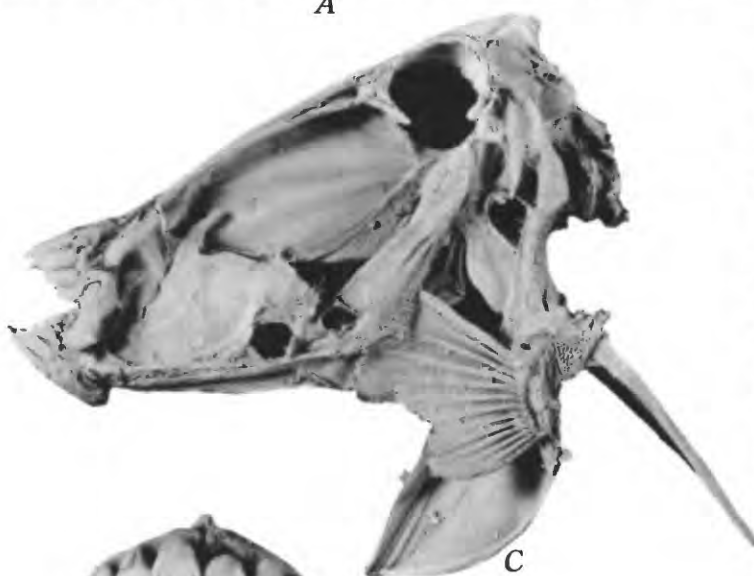
¹ Identified by J. C. Randall.



A



B



C



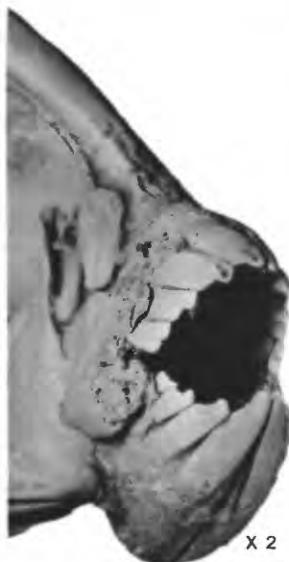
G



D



E

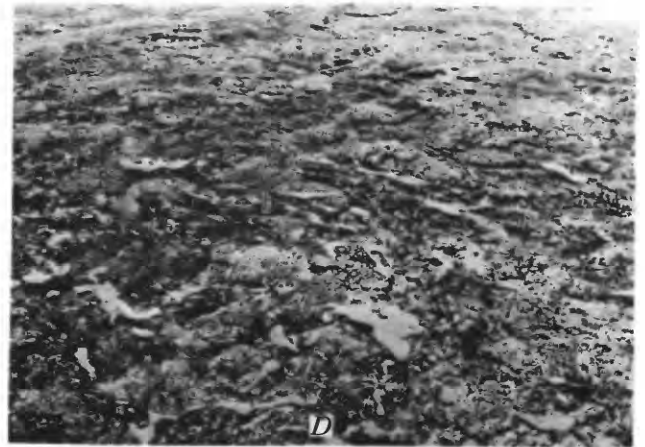


F



H

WORK OF SEDIMENT-PRODUCING FISH



FRINGING REEFS WITH SHALLOW MOATS, AND REEF FRONTS WITH MANY GROOVES AND SPURS

PLATE 132

[Photographs A and B by U. S. Navy Squadron VU-7 (B), June 1949]

- A. Fringing reef with shallow moat (facies 38) and grooved reef front (facies 47) northwest from Obyan point (0). Narrow terraced ramp around point (facies 43).
- B. Fringing reef with shallow moat to right of Maigo Fahang islet (facies 38) in Fañunchuluyan bay. Erosional bench in dacitic pyroclastic rocks around and left of islet, with thick and vigorous organic veneer to left (facies 40).
- C-D. Unusually vigorous coral and branching coralline algal growth at fringing reef edge near *location 14* (facies 38). Coral mainly *Pocillopora elegans*, but *Acropora humilis* shows above h in figure D. The crustose coralline alga *Lithophyllum* cf. *L. kotschyannum* is prominent at X in both figures. Photographs by J. H. Johnson, 1949.
- E. Cross-reef groove on fringing bench just inshore from reef edge at Tarague beach, Guam, showing a pair of the foam-flecked surgeon fish *Acanthurus guttatus* Bloch ¹ which habitually frequents the turbulent water of the reef edge and surge channels.

¹ Identified by J. C. Randall.

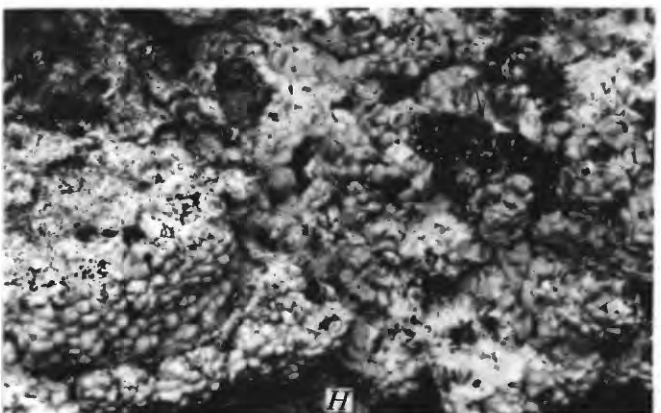
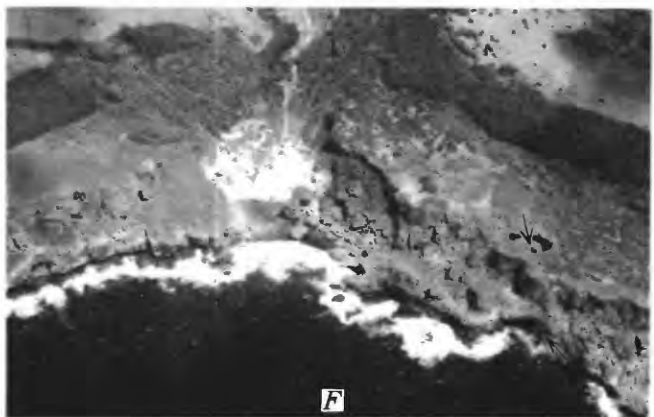
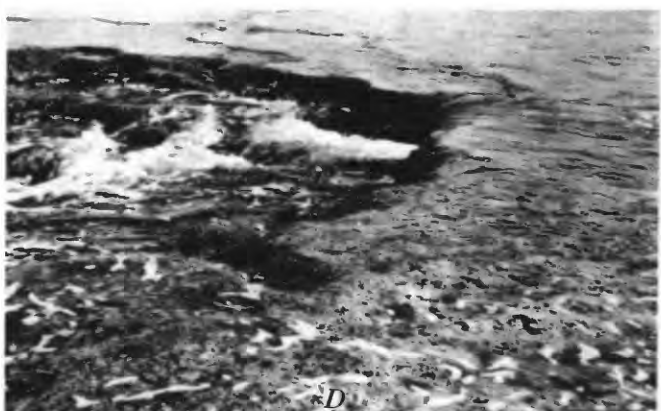
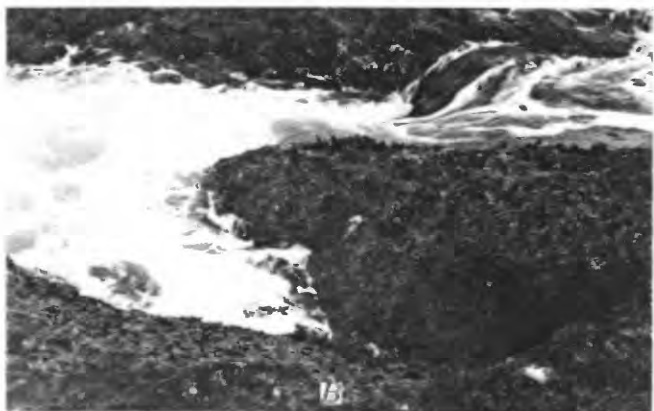
PLATE 133

[Photographs A and B by U. S. Navy Squadron VU-7 (B), June 1949]

- A. Narrow algal-covered fringing reef bench (facies 39) with irregular reef front spurs (facies 47) just east of Obyan point. Pattern here strongly suggests spurs to be primarily constructed by algal outgrowth and coalescence of lines of algal bosses.
- B. Broad algal-covered fringing reef bench around Trinchera, on north shore of Laulau bay. This bench is described in text as *location 13a* (facies 39). Large boulders are prominent at right side of bench. Reef front grooves irregular and broadly spaced; not like most of facies 47, with which they are grouped mainly for convenience.
- C. Algal-veneered fringing reef bench at Halaihai beach (*location 11*, facies 39) at midlength of east coast, grading to broader than usual terraced ramp around point to left. Photograph suggests heavy algal veneering of groove and spur system (facies 47).



EROSIONAL FRINGING BENCHES WITH THIN ORGANIC VENEER, AND REEF FRONTS WITH MANY GROOVES AND SPURS



SURGE CHANNELS AND SURFACES OF FRINGING BENCHES

PLATE 134

- A-B. Algal veneered surface along outer edge of reef flat at Halaihai beach (*location 11*, facies 39).
- C. Low algal terraces of outer reef flat at North Laulau beach (*location 12*, facies 39).
- D-E. Algal veneered surface of surge channels and broad spurs along outer edge of reef flat at North Laulau beach (*location 12*, facies 39).
- F-G. Braided surge channels, terraced ramp and pedestals, and sea cave (arrows) at I Hasngot beach (next southwest of *location 10*).
- H. *Porites lutea* encasing small *Tridacna gigas* (arrow) in pool on fringing reef bench in volcanic rocks just north of Hagman bay and plate 135A (facies 40). Umbo down, the gaping *Tridacna* exposes its thick crenulate mantle edges, purple from the zooxanthellae which it "farms" in the fleshy parts. Low tide level is indicated by the flat white algal veneer on the dead *Porites* surface at the left.

PLATE 135

- A. Hagman bay (*location 13*), showing principal reef area in volcanic rocks. Well-developed small-scale erosional surge channels at X are shown in detail in photograph B. These lead into larger and more widely spaced grooves and spurs of uncertain origin along the reef front. Photograph by U. S. Navy Squadron VU-7 (B), June 1949.
- B. Detailed view north along bench edge at point X of photograph A, showing small-scale erosional surge channels and spurs in andesitic conglomerate. These shallow channels are 2 to 3 feet across and are separated by spurs several times as wide. They seem to grade seaward into a much coarser pattern in which individual grooves and spurs are several hundred feet long.
- C. Surface of bench in volcanic deposits north of Hagman bay and photograph A, showing boulders of andesitic conglomerate and cementation of fallen limestone blocks to volcanic surface.



FRINGING BENCH IN VOLCANIC CONGLOMERATE AND GROOVE AND SPUR SYSTEM ON VOLCANIC SUBSTRATUM



NARROW FRINGING BENCH OF LIMESTONE VENEERED WITH ALGAE AND VERMETID GASTROPODS,
AND REEF FRONT WITH TIERED GROOVE AND SPUR SYSTEM

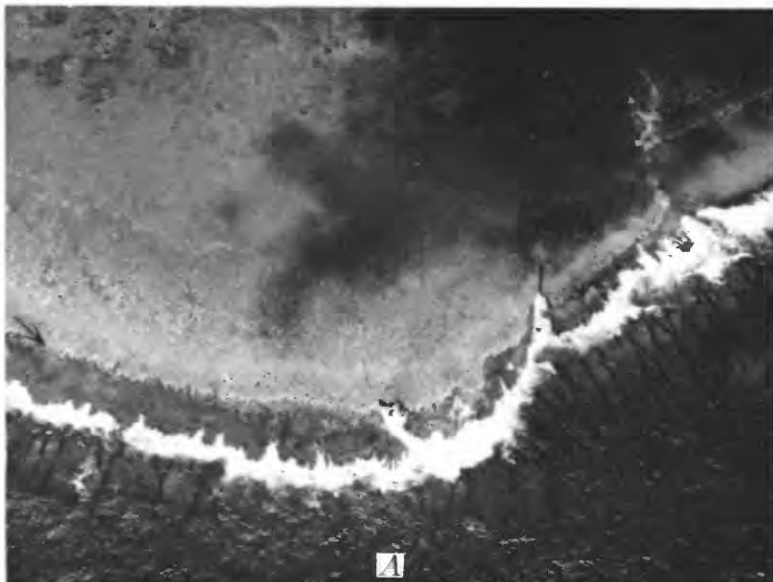
PLATE 136

[Photographs by U. S. Navy Squadron VU-7 (B), June 1949]

- A. Northeast coast of Saipan. A concentric line of no grooving (arrow) separates offshore groove and spur system (facies 46) into two tiers in middle of this stretch of reef, and a similar tiering is suggested at the right by a change in amplitude of grooves and spurs above a line at same level. This is interpreted to mean relation of tiers to separate bench levels, the deeper being the older. Algal overgrowth and extension of upper spur fronts point to eventual merging. Emerged tiers of grooves are also seen ashore. X marks site of photograph plate 137A.
- B. Closer aerial view just right of photograph A, at north tip of Saipan. Emerged grooves of 12-to-15-foot shore bench indent older Pleistocene limestones and are erosional. Present reef front seems to be supporting extensive algal growth on spurs, which is to some extent growing over grooves. However, constant movement of sediment seaward through grooves keeps them open. Break in reef at right is due to marine cliff-sapping, whereby undercutting in poorly consolidated deposits (possibly dacitic pyroclastics) causes slumping of rocks above and disruption of reef line.

PLATE 137

- A. Close aerial view of northeast tip of Saipan at site of X on plate 136A. Reef front grooves at right are long narrow chutes (facies 46). Erosional reef bench is veneered by algae and vermetid gastropods (facies 41). Saw-toothed edge of the 12- to 15-foot shore bench (arrow) is ragged edge of a partly eroded presumably late Pleistocene fringing reef surface. Photograph by U. S. Navy Squadron VU-7 (B), June 1949.
- B. View southeast along narrow reef bench shown in plate 136A, showing stubby surge channels and flat erosional surface with thin cover of algae and vermetid gastropods (see pl. 139E).
- C-E. Views of unusual fringing reef surface of facies 42 (northwest coast), showing pits, pinnacles, blowhole, growth rims around pinnacles and solution pitting of rough coastal cliffs.
- F. Rimmed pools of terraced ramp (facies 43) just north of photographs C-E. Partial submergence and algal patching of an area like the deeply pitted bench above these pools could result in a reef surface like that of C-E. Elevated sea cave above 40-foot notch in distance.



NARROW ALGAL-VENEERED AND PITTED FRINGING SURFACES AND TERRACED RAMP



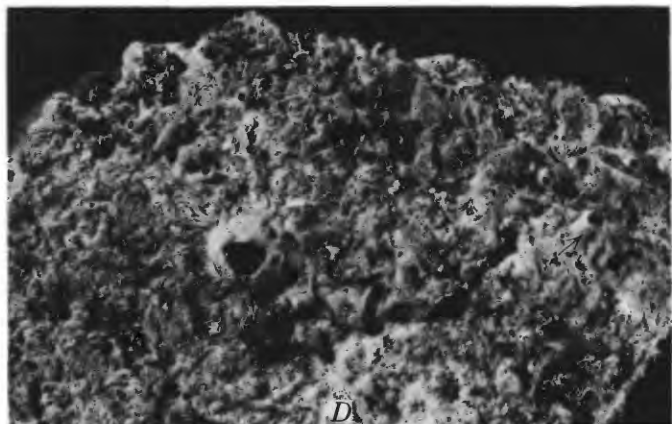
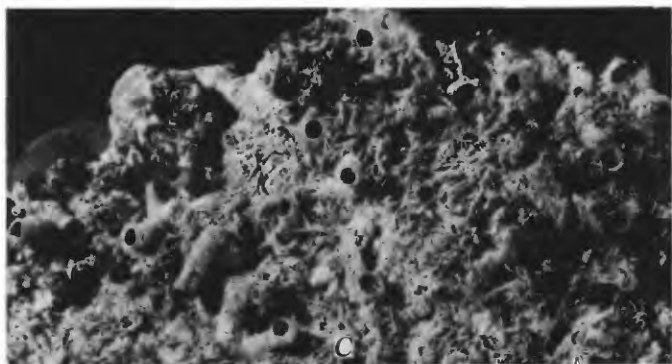
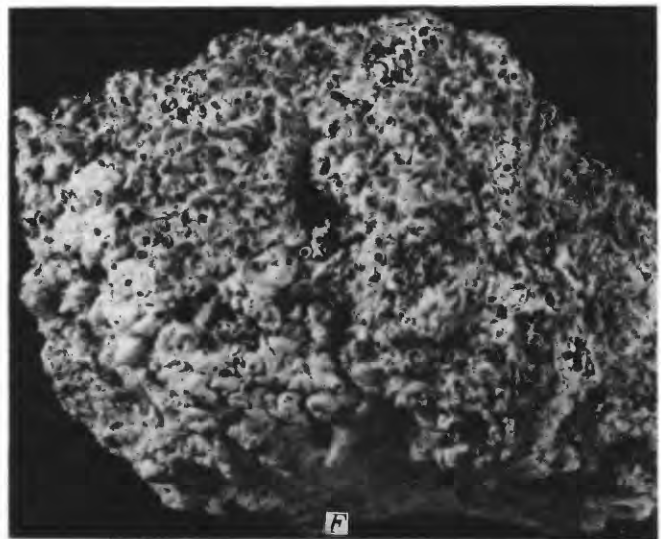
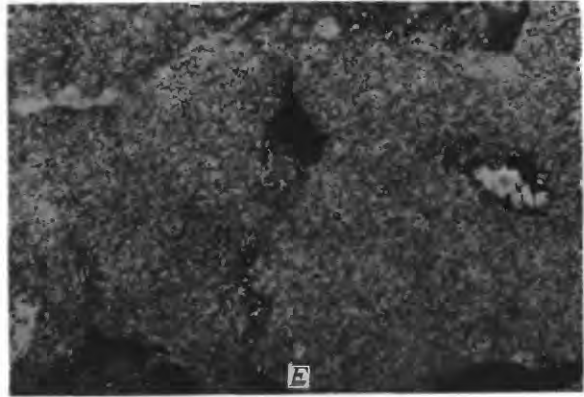
TERRACED RAMPS AND PEDESTALS, BLUNT SURGE CHANNELS, AND IRREGULARLY PITTED LOW ROCKY SHORE WITH SPRAY POOLS

PLATE 138

- A. Cove reef at Nanasu beach, showing terraced pedestals in front of reef, slump blocks annealed to reef flat, and blunt surge channels.
- B. Cove reef, terraced pedestal, and terraced ramp at Talofoto beach (see also pl. 139*A-B*).
- C-D. Blunt surge channel at edge of terraced ramp just north of Talofoto beach. Although surface of bench here is only inundated at highest tide, the constant splash keeps it wet and algal growth seems nearly in balance with destruction. Views *C* and *D* are of same surge channel as seen at retreating and advancing wave fronts.
- E. Terraced ramp (X) and solution-pitted low bench with spray pools (S) just above. East coast south of Talofoto beach.

PLATE 139

- A. Cove reef at Talofoto beach. Erosion levels with algal rims. Habitat of *Colobocentrotus* and *Heterocentrotus* at reef edge.
- B. Rimmed pools at south edge of cove reef at Talofoto beach (facies 43). Basins maintain rims at even level by combined effect of calcareous algal growth, vermetid gastropod growth, and entrapment of chalklike ultra-fine-grained (physicochemically precipitated?) calcium carbonate.
- C-D. Vermetid gastropods (*Petalochorus?* sp.) and finely tufted articulate coralline algae (probably *Jania* sp.) form rim of shallow basin on narrow fringing reef bench at northeast corner of island. Site is near left side of plates 136A and 137A. USNM mollusk coll. 609934. (C) Upper left edge of D, $\times 1.7$. (D) Piece of basin rim at $\times 0.8$ natural size to show felted mat of intertwining vermetid tubes, articulate coralline algae, chalklike calcium carbonate, and occasional balanid barnacles (arrows).
- E. Surface covering of vermetid gastropods on bench at northeast shore of Saipan (pls. 136B, 137B).
- F-G. Vermetid gastropods (*Petalochorus?* sp.) and minor algal tufts binding chalklike calcium carbonate, from rim of basin at site of figure B. USNM mollusk coll. 609933. (F) View of living upper surface, $\times 0.8$ natural size. (G) Intertwined dark vermetids and chalklike calcium carbonate; view of broken under surface of same piece as F, $\times 1.7$.



REEF-VENEERING GASTROPODS, TERRACED BASINS, AND COVE REEF

Geology of Saipan Mariana Islands

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Thomas B. Nolan, *Director*

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