

RESULTS OF THE  
PURITAN-AMERICAN MUSEUM OF  
NATURAL HISTORY EXPEDITION  
TO WESTERN MEXICO

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GULF OF CALIFORNIA

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## INTRODUCTION

THE PURITAN-AMERICAN MUSEUM Expedition was among the first to the Gulf of California to have as one of its purposes the collection and study of stony corals and the description of structures formed by these corals. Although the Gulf of California had been the scene of operations of several previous expeditions, resulting in studies of the coral faunas, none had had the opportunity of studying the living reefs or of collecting corals except casually. It was therefore one of the major objectives of the group (hereafter referred to as the Puritan Expedition) to allocate as much time as possible to underwater observation and collection. Because of the severe time limitations placed upon such a broad-scale operation, the areas visited were only those that were known to have extensive coral growths, or presumed to be suitable for coral growth as indicated by charts and such scant data on the physical environment as were available. The results were so vastly satisfactory that the expenditure of time was repaid many fold. It is interesting to compare this statement with one made by Steinbeck (Steinbeck and Ricketts, 1941, p. 79): "On several occasions we wished for diving equipment, but never more than here at Pulmo, for the under-cut shoreward side of the reef concealed hazy wonders which we could not get at. It is not satisfying to hold one's breath and to look with unglazed eyes through the dim waters."

Time was the severest limiting factor of the latter half of the Puritan Expedition. A budget of approximately 40 days in which to cover the entire Gulf region allowed only a superficial examination of most regions. Weather, although satisfactory for most of the trip, reduced the time scheduled for certain stops, for example, El Pulmo to three days, for on two of the days it was impossible to take a small boat into the region. As a result of the winds encountered, the sediments were often stirred up, handicapping underwater observations and making underwater photography impossible. The observations recorded are of a reconnaissance nature, somewhat more complete than those of previous expeditions in terms of area covered, and

vastly superior in the techniques that were used. Detailed surveys of various portions of the Gulf will result in a clearer understanding of the distribution of corals and in the ecology of the marginal reefs.

Among the many reasons for engaging in a study of the stony corals of the Gulf of California is the geographic position. The northern boundary between the subtropical Panamic faunal province and the north Pacific temperate region lies approximately at the latitude of the southern tip of Baja California. Collections made during the Puritan Expedition indicate that some elements of the Panamic fauna may extend northward into the shallow bays on the western side of the peninsula, particularly Magdalena Bay, but the essential boundary is to the south. The Gulf region represents a northward extension of the subtropical fauna into higher latitudes than would normally be expected, although some elements of the northern fauna have affinities with the temperate faunas of the West Coast. Not only are the relationships of the Gulf of California fauna with the neighboring regions of interest, but the larger-scale relationships may have some significance in the history of these areas. The apparent isolation of this fauna from the main body of the Indo-Pacific because of the east Pacific barrier (Ekman, 1953) has been discussed in some detail by many workers. In recent years there has been more of a tendency to recognize closer relationships between Indo-Pacific shallow-water corals and those of the eastern Pacific. The taxonomy of the shallow-water forms developed in this study goes further in this direction than that of earlier workers. This is a direct result of the larger suites of material collected and the amount of comparative material utilized in the identification of the Gulf of California corals.

The historical relationships of the Panamic fauna with the West Indian tropical fauna are of considerable interest because of the demonstrated presence of marine connections between these two areas. Close similarities in species between the tropical western Atlantic and Panamic regions known to exist in

many groups of marine animals are apparently lacking among the shallow-water corals and Mollusca. The fossil record of the Gulf region has been well studied and, although restricted in time span, seems to provide somewhat conflicting results. Without doubt the area will require more careful investigation.

Another consideration is the history of climatic changes within recent geological time, as documented by its effect upon the fossil coral faunas of the Gulf of California. Situated on the northern boundary of the subtropical faunal province, the Gulf of California is an excellent area in which to study the marginal development of reefs. Here, in the frontier of ideal environments for reef development, a succession of reef and reef-like communities indicates the types of developments which may be associated with both local marginal conditions and broad-scale climatic gradations of a nature detrimental to corals. Certainly the old saw that a coral reef is indicative of tropical conditions is erroneous. Many students of coral reefs (e.g., Crossland, 1927; Yonge, 1940) state that coral reefs are generally absent from the western borders of continental masses or, conversely, the

eastern margins of seas. This is in general correct. In the degree that coral reefs exist in the Gulf of California, some new light may be shed on this problem.

Although much work remains to be done before the distribution and ecological aspects of many of the Gulf of California corals and their associations can be clarified, Durham correctly states (1947, p. 5) that, except for deeper water corals, the fauna of the Gulf of California is rather well known. Almost untouched are the coral faunas of the Gulf of Panama, for, with the exception of the Allan Hancock Expeditions which obtained material largely by dredging, little has been done in this area since the initial studies by Verrill. As this area encompasses the true tropical region of the eastern Pacific, it is there that one might expect to find the greatest diversity of species, better developed reefs, and perhaps the clues to the final portions of the history of the Pliocene West Indian corals of the Imperial Valley of California. Likewise, the faunas of the Galapagos Islands together with those of other offshore islands will bear investigation, particularly because of their independence from possible thermal effects of upwelling cold waters.

#### PREVIOUS STUDIES OF GULF OF CALIFORNIA CORALS

Apparently the first notice of corals from the Gulf of California was that given by Grewingk (1848) who recorded a specimen of *Porites* from the Salt Flats of Carmen Island. However, it was not until various collections obtained by Yale University were described by A. E. Verrill (1864, 1866, 1868-1870, 1869) that an appreciable knowledge of the eastern Pacific coral faunas was obtained. It is a matter of record that many of the species listed by Verrill as from "La Paz, Lower California," were so labeled because they lacked other data than the information given on the shipping tickets. Several of the original labels have been located, and in certain instances a locality of Bay of La Paz was given by the original collector. However, the uncertainty of the labeling has resulted in confusion, now largely alleviated except for one specimen, *Montipora fragosa*, which is known only from Verrill's original specimen. Many of Verrill's distinctions were finely made, a factor,

coupled with brief descriptions and a general lack of illustrations, that clouded the interpretation and usage of his names.

Vaughan (1907, 1917) made incidental remarks concerning the coral faunas of the Gulf of California, and in the latter paper discussed the zoogeographic relationships of the fauna. The 1914 "Albatross" Expedition to the Gulf of California resulted in a collection of corals dredged from various depths which remained largely unknown until Durham (1947) described the collection in conjunction with other materials. The various New York Zoological Society cruises to the eastern Pacific ("Noma," "Arcturus," "Antares," Templeton Crocker, and "Zaca") from 1923 to 1938 resulted in collections, the present location of which is unknown to me. Incidental specimens were mentioned by Durham (1947), and a small suite of their materials in the collections of the American Museum of Natural History are recorded here.

Steinbeck and Ricketts (1941) made the first modern contribution to the Gulf of California scleractinology, summarizing known data and describing the reef suite at El Pulmo. During 1940 a joint cruise of the Geological Society of America and the Scripps Institution of Oceanography to the Gulf of California added considerably to our knowledge of the distribution of fossil corals from the Gulf of California, particularly the northern region of the Gulf. Durham (1947) utilized the specimens taken during this cruise and other existing collections to place the nomenclature of eastern Pacific corals on a firm foundation when he reviewed and figured Verrill's specimens, many for the first time. In this work Durham also made preliminary observations on distribution and ecology of the Gulf of California corals. In 1950, Durham (1950a) published the geological results of the "E. W. Scripps" cruise, reviewing the occurrences of fossil corals.

Durham and Barnard (1952) reported on the series of eastern Pacific collections made by the Allan Hancock Foundation cruises dating from 1931. The taxonomic enrichment of the coral fauna as a result of this publication is somewhat offset by overly fine specific distinctions. It is, however, the basis for the greatest portion of our knowledge of the eastern Pacific coral fauna distribution. Occurrences of fossil corals are given in many faunal lists, among which are Jordan (1936) and Hertlein (1957).

All the collections that were made before the Puritan Expedition obtained coral specimens from chance collections, no specific at-

tempt being made to assemble suites of specimens (Durham and Barnard, 1952, pp. 3, 4). Seldom were over a dozen specimens of a species available for study. The majority of the records are based on dredged materials or beach wash, resulting in a nearly complete lack of specimens from the shallower depths as well as an absence of data on habitat, distribution, and population density. It was in these areas that the Puritan Expedition concentrated. Large suites of specimens were assembled in every instance, allowing for shipboard observations and later laboratory studies. Approximately half again as many specimens of the shallow-water forms as are presently in the collections were examined on board and then discarded (because of space limitations). More than 200 specimens of shallow-water species were returned to the Museum for study, allowing relatively extensive suites of material to be used in comparisons.

Large-scale collections are a necessity for the study of reef corals, for individual variation may be of considerable importance, and intensive study of a few specimens may lead to conclusions incorrect in terms of population variation. Reef corals are known to be extremely plastic in growth form and in certain other characters. Collections obtained from shoal waters or specimens found in beach drift may reflect local conditions, such as exposure and wave impact, causing alterations in appearance which may be interpreted as morphologically significant when specimens from somewhat deeper waters are not available for comparison.

#### ACKNOWLEDGMENTS

Emerson (1958) outlined the program and itinerary of the Puritan-American Museum Expedition and gave a listing of personnel, to all of whom I am indebted for their cooperation and patience. I am very grateful to the sponsor of the expedition, Mr. Harry J. Bauer, for making this study possible.

It is a pleasure to record here the efforts of Messrs. Donald Travis and Collins Christie of the crew of the "Puritan" who unstintingly gave of their time, free from shipboard duties, to assist in skindiving activities. Because of

their industry, abilities, and keenness the scope of these activities was very greatly enlarged and the completeness of the collections was enhanced. Mr. Frederick Schmidt, Engineer of the "Puritan," and my colleague Dr. Richard Van Gelder at various times also participated in the under-water work.

Mr. Luis Collins, Hotel Mission de la Paz, La Paz, owner of land at El Pulmo, spent considerable time in showing us his collection of aerial photographs of that region, thereby

increasing the accuracy of the maps. Sr. Jesus Castro Fiol, a resident and former pearl diver at El Pulmo, gave us much information on the history of the region and offered many suggestions on the position and depths of reefs.

For permission to study specimens at the various institutions, or for permission to borrow types, I should like to thank Dr. Willard Hartman, Peabody Museum of Natural History, Yale University; Dr. N. T. Mattox, Allan Hancock Foundation, University of Southern California; Dr. Leo G. Hertlein, California Academy of Sciences; Dr. John W.

Wells, Cornell University; and Dr. Harald Rehder, United States National Museum. Mr. Conrad Limbaugh, Scripps Institution of Oceanography, forwarded a small suite of West Coast corals for comparisons. Mr. E. P. Chace, San Diego Natural History Museum, lent specimens of *Pocillopora* from Guadalupe Island.

Finally, I should like to thank Dr. John W. Wells for his many helpful suggestions regarding the systematics developed here and for conversations relevant to the conclusions drawn as a result of the study.

# CORAL REEFS AND THEIR ECOLOGY

## DEFINITIONS

THE CORAL REEFS of the Gulf of California and the western coast of Mexico have attracted some attention because of the generalization that coral reefs are absent or poorly developed on the western shores of continents. The absence of well-developed hermatypic coral faunas in the eastern Pacific has variously been attributed to detrimental factors such as the usual low, prevailing water temperatures encountered there and such purely local conditions as the absence of suitable substrate. Thermal control on reef development is well known, active reef growth being confined largely to areas with a mean annual thermal range of 25° to 29° C., although component corals of the reefs may exist well outside these general limits. As mean temperatures drop below the preferred range, some corals, and particularly many other organisms important in the interlocking biologic and structural framework of the reef complex, decrease in abundance, until, at about 18° C., the coral reef may cease to exist as an entity, although a few of the hardy hermatypic corals may be present.

Within the Gulf of California is a profusion of ecological situations. The presence or absence of reefs within this region must therefore be due to general factors rather than local considerations. Temperature, which is known to be a primary aspect in the distribution of the hermatypic corals, is one of the most easily measured ecologic factors and is also the one most frequently called upon to account for regional ecologic control of faunal distribution. Within the Gulf of California surface temperatures range from about 15° C. to a high of about 28° C. through the course of the year. This range is such that many species of hermatypic corals could live in the southern half of the Gulf although partially in reproductive isolation. The Gulf of California must then be considered as a marginal region thermally for the development of coral reefs and one in which the temperature gradient extends from satisfactory to unsatisfactory values. But, as is developed in the discussion below, an equally important consideration is the degree of iso-

lation and restricted character of the fauna in combination with local facets of the ecology.

Great stress is often placed on the presence or absence of coral reefs in the interpretation of past climates. In many of these citations little thought has been given to the actual biologic character of the reef, and no weight has been given to the degree of coral development or diversity. To this end, the term "reef" is somewhat at fault, for in its unqualified connotations it is usually taken to indicate optimal climatic conditions and evokes visions of tropical atoll reefs of the highest quality. From a biologic standpoint a coral reef is essentially a marine faunal community dominated by corals. This simple statement makes no pretense of indicating degree of development, variety of contributing species, or density of population. Therefore a biologically defined "reef" might be composed of a single species of hermatypic coral living on the fringe of ecologic conditions for successful existence, or a limited assemblage of corals living in such density as to affect the environment in a magnitude proportional to the best-developed Indo-Pacific reefs. Reefs such as these need not be developed in tropical waters, or even in shallow waters, and may be formed by the group of corals commonly known as "deep sea," but more properly termed ahermatypic. Associations of this type are well known from the north Atlantic Ocean (Dons, 1944) and from the margins of the continental shelf of the European coast (Le Danois, 1921, 1948). These banks, or reefs as they are locally known, are extensive areally and are often composed of one or two species, particularly *Lophelia*, *Dendrophyllia*, and *Madrepora*, all of which are found in waters with a temperature range of 5° to 15° C. Associated with the coral banks is a well-defined fauna of invertebrates and vertebrates, many of which are exclusively associated with the coral banks in the same fashion as the tropical reef floras and faunas. The nature and significance of these deep-cold coral assemblages have recently been the subject of a review by Teichert (1958).

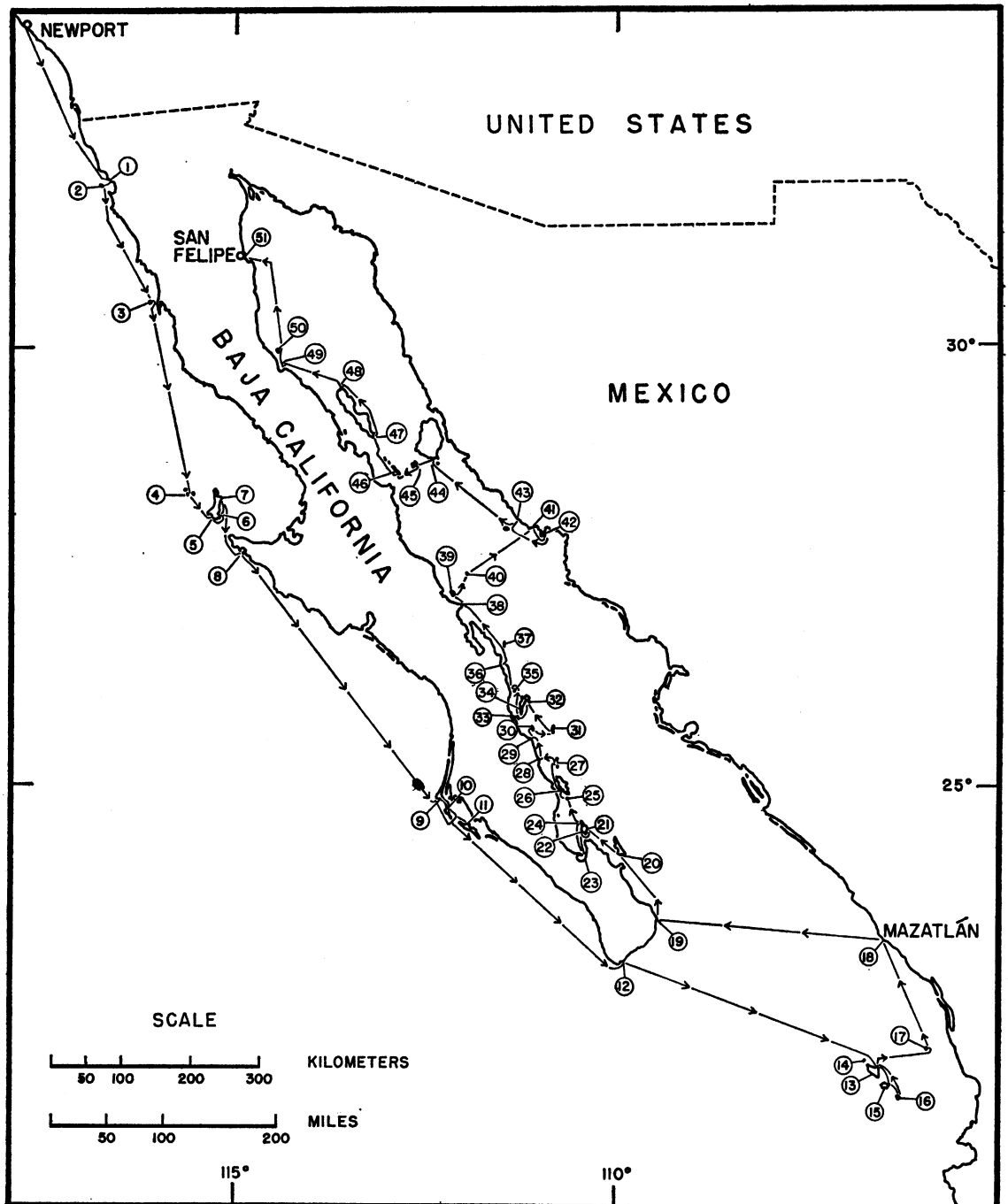


FIG. 1. Route of the Puritan-American Museum of Natural History Expedition. The localities visited are indicated by numbered circles and are as follows:

- |                           |                              |
|---------------------------|------------------------------|
| 1. Todos Santos Bay       | 5. South Bay, Cedros Island  |
| 2. Todos Santos Islands   | 6. Village, Cedros Island    |
| 3. San Martín Island      | 7. Lighthouse, Cedros Island |
| 4. West San Benito Island | 8. Bahía San Bartolomé       |

From a sedimentological point of view, marginal reefs are unimportant and often may not be so recognized in a fossil occurrence. The mass of lime rock (the reef wall) that characterizes reef suites so clearly may be absent through the lack of binding elements in the reef flora and fauna. In the case of many of the fossil reefs of the Gulf of California, coral heads in some abundance are found *in situ*, not bound together or to a firm substrate but rather surrounded and supported in their position by the accumulation of bioclastic sands, often of molluscan origin (see pl. 30, fig. 6). Except for the happy circumstance that these reefs were developed in sheltered regions, there would be no record of the existence of the reef other than an abundance of coral fragments. Storm waves, or even normal wave attrition, would have reduced these reefs, lacking cohesion, to fragments of its constituents.

In the discussions that follow, the biological usage of the term "coral reef" is utilized to denote a community dominated by corals in which there is a degree of interdependence between members of the constituent flora and fauna. To this is added the provision that the community must have an appreciable areal

dimension and definable continuity.

Studies of the coral reefs of the Gulf of California have greater significance than solely the adding to the knowledge of the conditions existent in this eastern Pacific region. Their role as marginal types both in an ecological and faunal sense (in reference to their isolation from the main body of the Indo-Pacific) makes a study of the community of value in the interpretation of the way in which reef communities falter on the outer edges of the area of successful dominance, and permits a fuller understanding of the values that can be placed on structures of this type (if they are recognized) in the fossil record.

Because the Gulf of California is a blind arm of the Pacific Ocean and opens into that body of water at approximately the boundary between the subtropical Panamic region and the temperate region of the western coast of Baja California, and because the ecological gradients that exist within the Gulf are more or less evenly distributed, it is a satisfactory area in which to consider marginal reef developments.

The first reference to coral reefs within the Gulf of California that I have found is that given by Steinbeck and Ricketts (1941, pp.

- 
- |  |  |
|--|--|
| 9. Santa María Bay   | 31. Santa Catalina Island  |
| 10. Puerto Magdalena, Magdalena Island                         | 32. Salinas Bay, Carmen Island   |
| 11. Puerto Cortes, Santa Margarita Island                      | 33. Puerto Escondido and Danzante Island                               |
| 12. San Lucas Bay  | 34. Marquer Bay, Carmen Island   |
| 13. Puerto Balleto, María Madre Island                         | 35. Coronados Island   |
| 14. San Juanito Island   | 36. Pulpito Point  |
| 15. María Magdalena Island                                     | 37. Ildefonso Island   |
| 16. María Cleofas Island                                       | 38. Santa Inez Island  |
| 17. Isabel Island  | 39. San Marcos Island  |
| 18. Mazatlán   | 40. Tortuga Island   |
| 19. Los Frailes Bay  | 41. San Carlos Bay   |
| 20. Cerralvo Island  | 42. Guaymas  |
| 21. Espíritu Santo Island (southeast side)                     | 43. San Pedro Bay and San Pedro Nolasco Island                         |
| 22. San Gabriel Bay, Espíritu Santo Island<br>(Ballena Island) | 44. Tiburón Island   |
| 23. La Paz   | 45. San Esteban Island   |
| 24. Isla Partida   | 46. South San Lorenzo Island   |
| 25. San Francisco Island                                       | 47. Angel de la Guarda Island (southeastern tip)<br>and Partida Island |
| 26. Amortajada Bay, San José Island                            | 48. Puerto Refugio, Angel de la Guarda Island                          |
| 27. San Diego Island   | 49. Gonzaga Bay (= San Luis Gonzales Bay)                              |
| 28. San Carlos Bay, Santa Cruz Island                          | 50. San Luis Island  |
| 29. Aqua Verde Bay   | 51. San Felipe   |
| 30. Monserrate Island  |  |

77, 334, pl. 21, fig. 3) who collected at El Pulmo Bay. They considered the reefs there as a true fringing reef composed largely of a single species of *Pocillopora*. Their observations, however, were confined to the surface and the intertidal region (although regretfully, see p. 334). At the time of their visit they were able to work along the upper surface of the reef because of favorable tide conditions, and their observations of this portion of the reef are quite detailed. Steinbeck and Ricketts (1941, p. 266) also called attention to the presence of large coral heads in San Gabriel Bay, although no further details were given.

As a result of the 1940 cruise of the "E. W. Scripps" to the Gulf of California, Durham (1947, 1950a) was able to report in some de-

tail many of the fossil reefs of the Gulf. The program of the expedition was such that only the northern regions of the Gulf were visited. Durham (1947, p. 11) cited the Pulmo reef, quoting Steinbeck and Ricketts, and called attention to coral aggregates, both fossil and living, at other localities. Durham also summarized available information on the distribution of corals within the Gulf of California and drew some preliminary conclusions regarding the climatic significance of late Tertiary faunal groupings and distribution.

Anderson (1950) and Durham (1950a) report the observations of Durham (1947) but give more details concerning the stratigraphic position and geologic setting of the fossil reefs.

## DESCRIPTION OF REEF SUITES

### EL PULMO REEF TRACT

El Pulmo reefs are located in El Pulmo Bay, Baja California, at approximately latitude 23° 26' N., longitude 109° 25' W., between two prominent rocky capes, Cabo Pulmo on the north and Los Frailes on the south. The reefs project off shore in a northeasterly direction from the southern portions of the bay and form an integral part of the Arena Shelf. Small craft may find anchorage on the shore side of the innermost reef, but larger vessels usually anchor approximately 3 miles to the south, at Los Frailes. A small ranch house has stood at El Pulmo for some time, but there is no other settlement. A dirt road connects this region with the small village of Los Frailes to the south and other settlements to the north. Recently Mr. Luis Collins of La Paz has established an airstrip for small aircraft at El Pulmo and has begun other construction.

Although a quiet area at the present time, El Pulmo was once the site of a thriving pearl fishery (*Pinctada mazatlanica*). Through the graciousness of Sr. Jesus Castro Fiol, a resident of El Pulmo and for 35 years a pearl diver there, the following historical information was obtained. The El Pulmo reefs were known for the excellence both of pearl and of shell and supposedly had the highest

percentage of pearl per ton of shell of all the Gulf of California pearl fisheries. Most of the diving for pearl was undertaken on the deeper portions of the northern reefs and from the outermost reef (fig. 2). The reefs of the southern portion of the bay were reported to be largely unproductive, although within the range of most of the pearl-diving operations (5 to 14 fathoms). Sr. Fiol stated that during the height of the pearl-fishing industry, as many as 200 canoes and 400 divers were operating in the El Pulmo region. According to Sr. Fiol, the pearl fisheries began to die out in about 1937 because of the non-maturing of the pearl oysters.

Apparently the only citation in the literature of El Pulmo and the reefs is that by Steinbeck and Ricketts (1941, pp. 77, 78, 334; pl. 21, fig. 3). Durham (1947, p. 11) quoted Steinbeck and Ricketts but did not visit the area.

The Sailing Directions for the Gulf of California (United States Hydrographic Office, 1951, p. 69) make the following statement: "El Pulmo is a coral reef that projects in a northeasterly direction from the shore southward of El Pulmo Ranchhouse and ends in a depth of 10 feet about  $\frac{1}{2}$  mile eastward of Cape Pulmo. Between the reef and the cape is a small harbor, good for boats and other

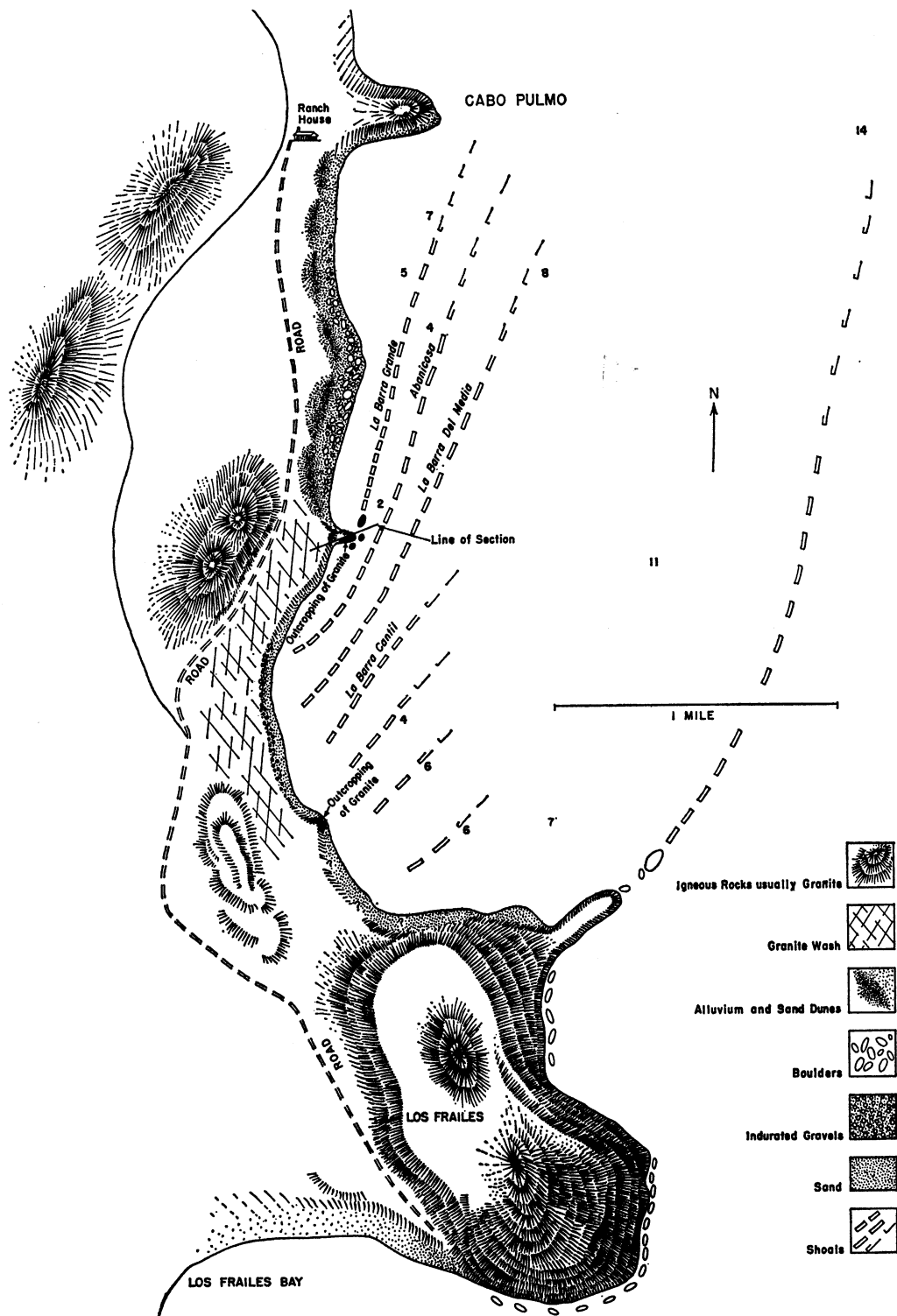


FIG. 2. Sketch map of El Pulmo reef area based on United States Hydrographic Chart 1664, modified on aerial photographs by Sr. Luis Collins. Position of "reefs" in southern portion of bay is approximate.

small craft in which there are depths of  $2\frac{1}{2}$  to 3 fathoms. The channel leading to this harbor lies between the cape and the end of the reef."

Behind the usually narrow beach of Pulmo Bay is a sea cliff varying in height from 20 to 40 feet. The beach, which is almost exclusively sand, seems to be composed of bioclastic material mixed with larger amounts of material from the sea cliff. The cliff is best developed in the southernmost portion of the bay (fig. 2) where it extends almost continuously to Los Frailes, but it is not a continuous outcropping of Pleistocene sediments. At the northern end of the embayment it is replaced by a series of dune ridges developed across the mouth of a shallow arroyo. The northern termination of the cliff is an outcropping of granite.

Above the sea cliff, the land surface slopes gently upward in a broad alluvial plain to a range of mountains with elevations up to 2000 feet, several miles to the west. Near the coast are a few monadnock-like peaks, composed of a pink granite, only one of which was examined because of time limitations. This one, roughly elliptical in basal outline, rose steeply from the alluvial fan to an elevation of 80 to 100 feet. Cabo Pulmo is itself a bluff of "red rock" trending in an east-west axis, nearly at right angles to the hill described above, and has an approximate elevation of 75 feet. Approximately one-quarter of a mile to the west of the cape is a second peak reported to be (United States Hydrographic Office, 1951) 830 feet high. The alluvial material forming the plain is composed mainly of slightly weathered granitic material, presumably derived from the peak described and the mountains to the west. As observed in outcroppings on the sea cliff, the depth of the granite wash is approximately 10 to 15 feet.

Outcrops of Pleistocene sediments in the sea cliff are not common because of slumping of the overlying wash, but two sections were exposed, both associated with outcroppings of the pink granite. The granite in both cases was exposed from below tide line to about 6 feet above mean tide level. In all cases it was observed to have great relief on the exposed surface. Overlying the granite and filling the unconformity is a fossiliferous Pleistocene section (fig. 3). At the southernmost outcrop

slumping of the section had proceeded to a point at which a measured section could not be obtained. Immediately above the granite is a coarse boulder conglomerate composed of well-rounded boulders of igneous rocks of diverse types cemented by a calcareous shell breccia containing a few identifiable fossils.

#### FOSSILS FROM BASAL CONGLOMERATE

##### Corals

*Porites* sp.

*Pocillopora* cf. *P. elegans* Dana

Mollusca (identified by W. K. Emerson)

*Ostrea chiliensis* Philippi

*Spondylus* aff. *S. princeps* Broderip

The thickness of the basal material is completely dependent upon the relief of the eroded surface of the underlying granite but averages about 4 feet. The upper surface of the boulder conglomerate in turn appears to be an erosional one, or a surface dipping to the southeast. Unfortunately the scale of the outcrop is such that no conclusive evidence could be obtained on this important point. Above the boulder conglomerate, and rather sharply separated from it, is a pebble conglomerate containing a few boulders the composition of which is approximately the same as that for the underlying materials. An exposed section above the finer conglomerate shows about 10 feet of finely bedded sediments in unequal thicknesses, becoming more fine towards the top of the section. The uppermost portion of the section contains cross-bedded sands which are unfossiliferous. Sands below this level are marine and contain both fragmentary shell material and identifiable fossils but no corals. The section is rather abruptly terminated and capped by a 10- to 15-foot thickness of apparently unbedded granitic wash.

#### FOSSILS FROM UPPER PORTION OF PLEISTOCENE SECTION

Mollusca (identified by W. K. Emerson)

*Glycymeris maculata* (Broderip)

*Chione californiensis* (Broderip)

*Cardium biangulatum* Broderip and Sowerby

*Lucina* sp.

*Oliva* sp.

The El Pulmo reef does not consist of a single reef, contrary to the statement of Steinbeck and Ricketts (1941), but is rather a series of rock ridges extending outward in a

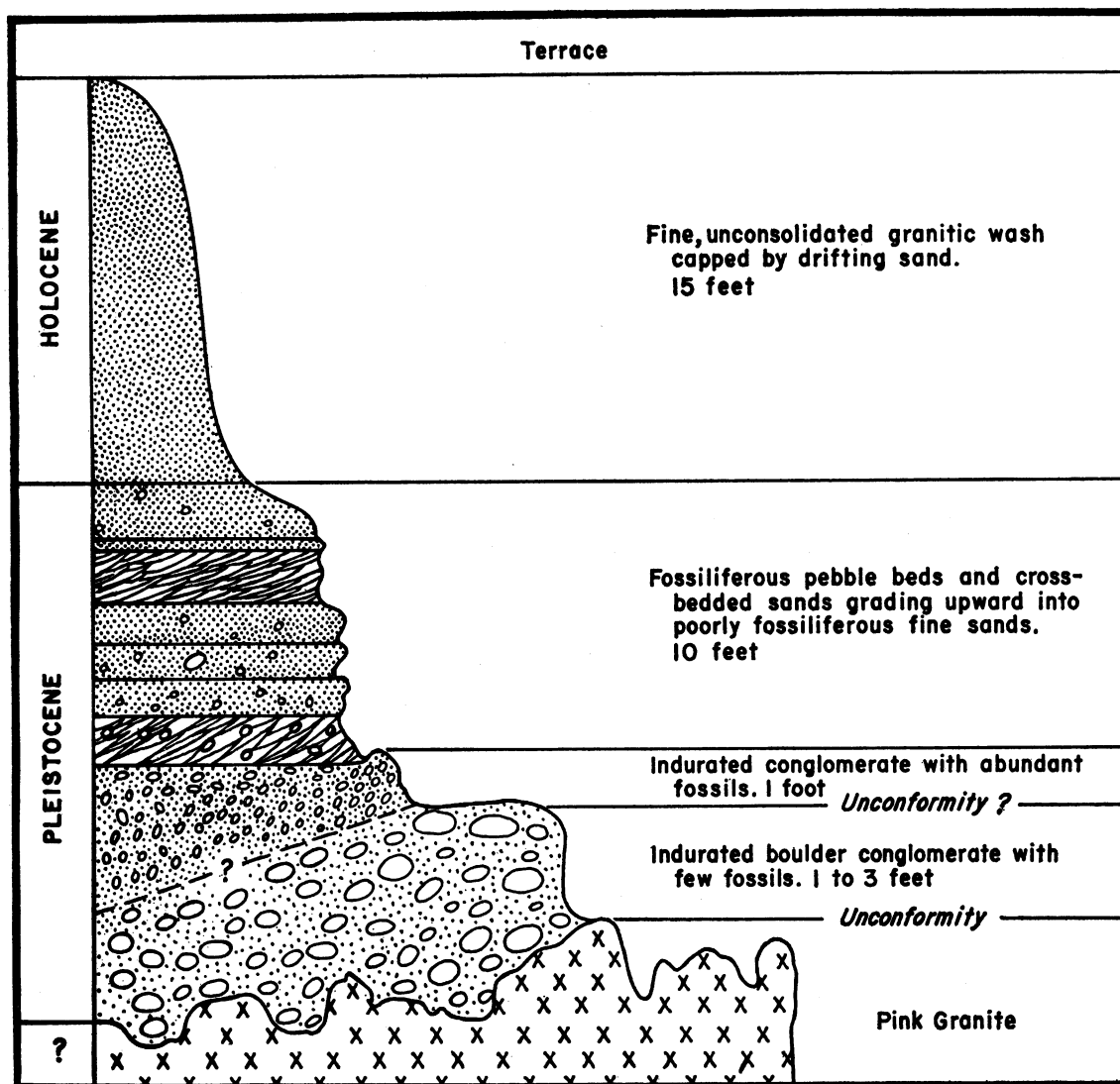


FIG. 3. Section of the Pleistocene exposure, El Pulmo Bay, Baja California. Position of the section is indicated on figure 2. The section is photographically shown on plate 30, figures 1, 2.

northeasterly direction from the shore. The northernmost of these commences at the base of the section just described. The ridges are not straight but arc slightly to the east, so that their trace is concave to the north. Near shore the northernmost ridge is exposed at low tides, but lies in deeper waters to the northeast, to depths of 6 fathoms. The southernmost ridges are deeper near shore, never becoming exposed.

Sr. Jesus Castro Fiol supplied the local names for the reefs that are used in this dis-

cussion. The northernmost is La Barra Grande, with succeeding southerly reefs named Abanicos, La Barra del Media, and La Barra del Cantil. Our reconnaissance indicated the presence of at least three reefs to the south of the last-named of these, indicated on the map (fig. 2) as reefs 5, 6, and 7. Finally, there is an offshore reef indicated to us by Sr. Fiol which extends from the northeastern tip of Los Frailes outward to a point approximately one mile offshore, and then approximately north to a point about east of

Cabo Pulmo, where it is lost. Off Cabo Pulmo this last-named reef has a depth of 14 fathoms.

A single reef, as well as the whole assemblage of rock reefs, indicates a general dip of a supposed contiguous surface, now broken into a series of parallel linear ridges, to the southeast (fig. 2). As mentioned above, the southern reefs are much deeper, and all reefs deepen towards the east. Unfortunately attempts at sampling outcrops by skindiving were often unsatisfactory because of the destruction of the rock by boring organisms. However, we were successful in recovering a piece of conglomerate from the area between La Barra Grande and Abanicos. This specimen is in all respects similar to the basal conglomerate exposed above the granite. Near the shore, La Barra Grande is composed of granite, and it may be presumed that this and other of the ridges are in part granitic.

Although El Pulmo reefs are not coral reefs in a constructional sense, they are coral communities. Under more favorable conditions, the coral growth of the reefs might have been more impressive, but owing to stormy weather during and preceding the visit, the waters were turbid, the reefs of deeper water were poorly lit, and the shallower ones were inaccessible because of breakers. Algae of non-calcareous types abound on the reefs and are the dominant element of the biota on the upper or flat surfaces of the reef ridges. Occasional growths of *Pavona clivosa* and *P. gigantea* are present, as are *Pocillopora elegans* and other species. Encrusting *Porites* is also common on the reef. Sea fans (*Gorgonia* sp.) are common on the upper surfaces, in water 30 feet in depth. The coral fauna was most abundant on the margins of the ridges, with large-lobed and bladed coralla of *Pavona* up to 3 feet in diameter being the dominant coral, while small, hemispherical coralla of densely branched *Pocillopora damicornis* and *P. elegans* were extremely abundant. Sea whips were more abundant on the margins than elsewhere. The lesser degree of faunal development on the upper surface of the ridges can be attributed to the accumulation of sediment at that point, for during the period of our observations many of the organisms were coated with a fine deposit of sediment. The area between ridges is inhabited

by much the same type of fauna as that above, although the most common coral is *Porites*, domed coralla being the most common.

In shallower water, all species became less abundant, and only *Pocillopora* and *Porites* seemed able to withstand the surf action on the shoaler portions (cf. Steinbeck and Ricketts, 1941, p. 77). To the south, reefs 5, 6, and 7 had a very reduced fauna consisting largely of heads of *Pocillopora*, but nowhere was the abundance so great as on La Barra Grande or Abanicos. Between La Barra Grande and Abanicos, and to the north of La Barra Grande, there was a thin accumulation of bioclastic sand above the rock floor. In places the accumulation may be several feet thick. In water 20 feet in depth and less there was evidence that the sand is in periodic movement. Conspicuously absent from these areas was any evidence of an accumulation of coralla. It must be presumed that these are rapidly destroyed either by wave action or by the action of boring organisms. Possibly in deeper waters there may be such accumulations, but we did not observe them.

From the observations briefly outlined above, the youthfulness of the El Pulmo reefs is demonstrated. The foundation rock reefs have their origin in the Pleistocene, when they were tilted into their present attitude through uplift and warping. As a test of this hypothesis, a sample of shells of *Glycymeris maculata* (Broderip) collected from immediately above the upper conglomerate was submitted to the Geochemical Laboratories of Lamont Geological Observatory for carbon-14 analysis. Dr. Wallace Broecker (written communication) states that this sample (L438-A) has an apparent age of 25,000+700 years,<sup>1</sup> or is in excess of 25,000 years. The upper sequence of beds then belongs to the Wisconsin stage of glaciation, a fact that, among others, may account for the absence

<sup>1</sup> Since completion of the manuscript, the published account of this date (Olson and Broecker, 1959, p. 16) has appeared. The usual corrections have been made to the original determination, so that the age of the specimens is now given as 25,400±1000 years and is stated to be a minimum age. The implication of this dating is that the entire sequence of deposition at El Pulmo may be pre-Wisconsin.

of corals in the entire upper section. Unfortunately samples of fossils obtained from the lower conglomerate were unsatisfactory for carbon-14 analysis.

On the basis of field observations and the correlative age determination supplied by the Lamont Geochemical Laboratory, the basal conglomerate which forms the backbone of the reefs may be considered as pre-Wisconsin or early Wisconsin in age. The rather scant fossil evidence indicates (if equivalent facies be assumed throughout the section) that the conglomeratic portions may have been deposited in warmer waters. *Porites* sp. was found only in this portion of the section, while the upper section was rather more restricted faunally. During Wisconsin time, possibly prior to the deposition of the upper sequence or following it, uplift and tilting placed the sequence in its present attitude. Erosion of the seaward portion of the sequence has resulted in the formation of the series of ridges upon which coral growth is now proceeding. Determination of the time of tilting and, for that matter, direct evidence for tilting will depend on critical examination of the possible unconformity indicated in the section (fig. 3). It seems quite certain, however, that the Arena Shelf and the El Pulmo reef suite are structural rather than purely erosional features.

The presence of late interglacial or early Wisconsin sediments on an uplifted terrace requires uplift to equate the present position of the section with the negative eustatic change which occurred during the glacial stages. Beal (1948) has suggested that considerable range of submergence and emergence must be postulated for the peninsula to account for the position and presence of sediments of late Tertiary age on presently elevated regions. Certainly the degree and comparative recency of this activity are more than sufficient to account for the sequence observed at Pulmo.

The upper section of granitic wash can best be attributed to an interrupted formation of an alluvial fan developed relatively recently and subsequently partially eroded. Accumulation of alluvial materials from the mountains to the west of El Pulmo is now going on slightly to the north of this area.

It is clear that the El Pulmo reef is not a

coral reef in the customary physiographic sense. The coral community is locally concentrated on the rock ledges and is dominant only in certain areas there. No appreciable material of bulk is being contributed to the accumulating sediments from the coral community.

Thermal data for the region are scattered and often of questionable value. Puritan Expedition records give a temperature of 22° C. for April 17, both on the surface and at a depth of 20 feet. Sverdrup (1940, fig. 2) indicates a value of 17° C. for the period of February–March, 1939, although this temperature is for a station some distance offshore. Data from the hydrographic office charts of surface temperatures (United States Hydrographic Office, 1948; Roden, 1958) show a range in temperature for El Pulmo of 18° to 26° C., with a high in the months of July, August, and September, and a low during January and December. Therefore, for at least a portion of the year, the temperature range at El Pulmo Bay is suitable for the development of coral reefs, but for a period of several months the temperature drops to a level too low for the survival of many of the less tolerant species. It is this level that is the controlling thermal regime for the region.

Of far greater significance than the thermal limitations, or for that matter any of the other common ecological restrictions on the El Pulmo coral fauna, is the fact that all the most common Panamic species of reef builders are present there. The table of distribution of species given by Durham and Barnard (1952, table 1) shows that the following hermatypic corals are absent: *Agaricia* sp., known only from a single fragment worn and dredged; *Montipora fragosa*, a poorly documented record based on a single specimen collected nearly 100 years ago and never collected since; *Pavona* spp. (not *P. clivosa*, *P. gigantea*), known mostly from single specimens of less common species; *Psammocora* spp., probably overlooked in collecting but occurring much farther north in the Gulf of California; *Solenastrea ecuadoriana*, known from a single specimen; and *Tubastrea aurea*, usually found in a different environment (see p. 427). It is apparent, then, that all the common reef builders are present. The situation at El Pulmo must meet at least minimum

requirements for these forms, and the absence of a well-defined reef or a more diversified reef coral fauna can be attributable only to the restricted nature of the eastern Pacific fauna, which is due to the isolation of this fauna from the major Indo-Pacific region.

#### REEFS AT SAN GABRIEL BAY, ESPÍRITU SANTO ISLAND

San Gabriel Bay, latitude 24° 26' N., longitude 110° 21' W., is situated on the south-eastern portion of Espíritu Santo Island. It is a large horseshoe-shaped embayment over a mile in width (fig. 4). Although largely filled with sand, there is a channel on the eastern side of the bay which permits entrance of small craft, but larger vessels must anchor well outside the bay. Because of its position on the protected side of the island, the embayment is not subjected to severe wave action and is protected even more by high rocky headlands. A fringe of sand beach fronts much of the bay, and the northern end is backed by a stand of mangroves.

Although there is no permanent village on the island there is a history of commercial enterprise for San Gabriel Bay. During the years of maximum pearl fishing in the Gulf of California, the *Compania Criadora de Concha y Perla de la Baja California*, of La Paz, began the culturing of pearl oysters in a lagoon on the eastern shore of the bay. This operation, which commenced in 1908 and terminated about 1920, was apparently a successful venture in its early years (Townsend, 1916, p. 434). Shortly after destruction of the buildings by fire, the sea wall separating the culturing lagoon from the open bay was penetrated, and limited circulation was restored. The culturing pen is now inhabited by a thriving flora and fauna in which pearl oysters are a conspicuous element. Although many specimens were taken by members of the expedition, no pearls were found. Little remains of the structure of the pearl-culturing operation except for some of the masonry work associated with the handling of settling pans (see Townsend, 1916).

There has been little mention of this bay in the literature, despite evidence to the effect that it has been visited several times by scientific parties. Steinbeck and Ricketts (1941, p. 266) noticed "a fine big patch of green

coral almost emerged from the water. It was green and brown coral in great heads." These heads comprise the coral community described here. Fraser (1943, fig. 85) illustrated an extensive growth of *Porites californica* in the shallow waters of the bay.

San Gabriel Bay is situated at the foot of a broad wash extending inland to the east and slightly north. On each side of the wash and forming the headlands on each side of the entrance to the bay are volcanic lava flows and agglomerate. On the northern margin of the bay is a stand of mangroves fronted by a mud flat which is exposed at low tide. The floor of the bay is nearly flat, sloping with very gentle gradient to the mouth of the bay, and towards the channel. The sands of the bay are white and largely bioclastic. On the western margins of the bay, where hundreds of feet from shore the water depths are less than 3 feet at low tide, the sand cover is thick and inhabited by a well-developed infauna, locally characterized by *Pinna* shells. The sand is frequently found to be rather firmly bound together, largely through the action of the tufted green algae which form "grassy" areas. The eastern margin of the bay is not so sandy and slopes more rapidly to the tortuous channel leading into the bay. The northern or back-bay region is shallow and much muddier than the lateral regions and is faunally characterized by a denser growth of *Pinna*.

In a region roughly bounded by the contours of 6- and 15-foot depths and lying in the central portion of the bay is an extensive growth of *Pocillopora elegans*. The growth is not in the form of a continuous reef but rather consists of a series of extensive heads of coral up to 40 feet in diameter, aligned to form a "barrier" approximately 300 feet long and several hundred feet in depth. Each "head" of coral is actually a single colony or several closely packed colonies in which the branches are closely packed and up to 5 feet in length. The heads of coral range in height from 4 to 8 feet and from a few feet in diameter to the greatest masses which are over 40 feet in width. In their arrangement these coral heads are much like that of the hedges of a formal garden. The area between coral heads is largely sand and forms level, narrow, tortuous "paths" circling some heads,

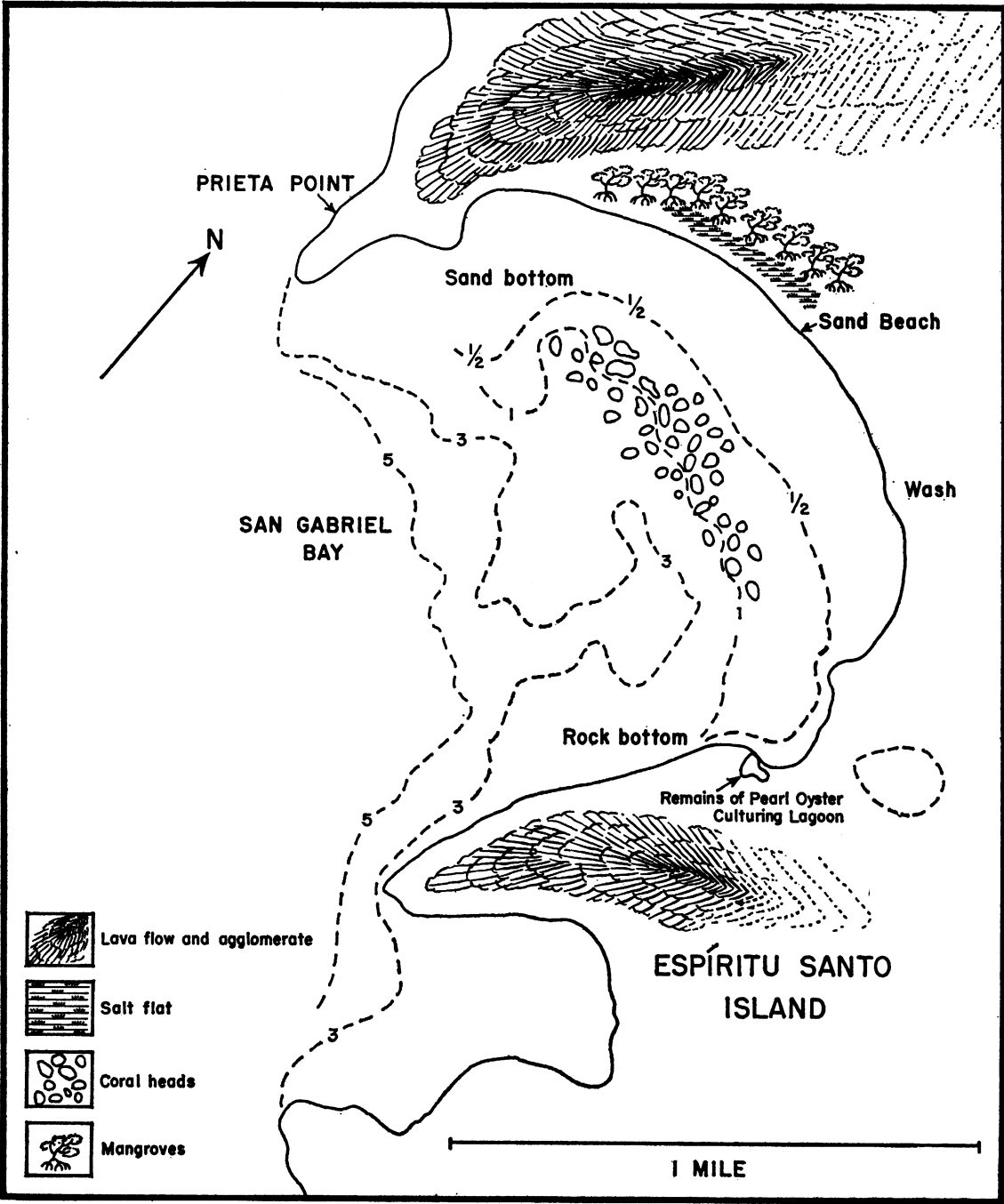


FIG. 4. Reef area, San Gabriel Bay, Espiritu Santo Island.

or blocked passages where lateral growth has caused two heads to join. The tops of the heads are flat or concave, quite evidently the result of cessation of upward growth once low-tide level has been reached.

Competition for space is intense. The upper surfaces of the heads are largely dead and inhabited by lush growths of filamentous green algae and invertebrates, among which are crustaceans, Mollusca, and other corals. *Porites californica* is found in this situation rarely and is the only occurrence of *Porites* in the reef area. On the lateral faces of the large heads, the struggle for space between algae and coral is great, in some places the algae being dominant to the detriment of the coral. A surprising feature is the apparent absence of epifauna from the sand surrounding the heads. Aside from numerous fish which swim about, in, and under the coral heads, the intervening areas are very sparsely populated. Locally lush growths of filamentous green algae may be present.

The bay has three general faunal regions: the coral community, or reef, the most conspicuous; marginal and shoreward of the reef, largely in shallower water than the reef, a region dominated by molluscan infauna and the clam *Pinna*; and on the eastern shore, which is rocky, a concentration of heads of *Porites californica* exposed at low tide (Fraser, 1943, fig. 85).

Aside from the actual living coral heads, there is little evidence that the corals are contributing greatly to the accumulation of sediment. Although dead branches may occasionally be observed, they are a minor constituent of the bottom. How greatly the decay of the interior of the heads is affecting sedimentation in the region cannot be assessed.

There can be little doubt that the reef in San Gabriel Bay plays an important role in the distribution of biotopes, for it is a barrier in position and, despite the protected regime of the entire bay, affects circulation of waters on the shoreward margins. Within itself it provides a habitat without equivalent in the region. Coral structures such as the one described here are also found in the fossil record of the Gulf of California, although formed by a different species. To a certain extent, the same combination of factors is reproduced in

northern regions of the Gulf, where the coral is represented by the large, laminated, algal fronds forming barrier structures.

San Gabriel Bay is within the same thermal zone as El Pulmo Bay, but higher temperatures prevail in the Bay during the summer months, causing a greater range of thermal extremes. One measurement of temperature of 24° C. on an ebbing tide is significantly higher than temperatures for the surrounding region. Despite the local effects, temperatures are on the minimal portion of the range required by the hermatypic species.

Palmer (1928), in discussing the reefs of Oaxaca, notes the presence of *Pocillopora* reefs in two localities. In one instance, heads 4 feet or more in diameter form a patch 20 yards wide, and at Escondido Bay, Puerto Angelito, an inlet 500 feet wide is reportedly filled with coral of one species. Because these reefs have not been collected under water, their monospecific nature must be questioned. Surface examination of the reefs at El Pulmo would almost undoubtedly lead to the conclusion that *Pocillopora* was the principal coral, although *Pavona* and *Porites* are equally abundant at greater depths. An occurrence of *Pocillopora* in a somewhat different fashion was noted at Ballena Island, a sharply tilted fault block on the western coast of Espíritu Santo Island. There, in a small cove on the western side, a concentration of smaller heads of *Pocillopora* (the only coral observed) was found in the northeastern corner. None of the heads attained a size greater than 3 feet in diameter, and the distribution was not equivalent to that of the heads of San Gabriel Bay.

Monotypic reef faunas are not unknown; for example, Crossland (1927, p. 553) states that in the Marquesas the only reef observed was composed of *Porites*. In the West Indian region stands of the great palm coral *Acropora palmata* are often monospecific, possibly because of the shading effect of the dense overgrowth. I have observed patches of *Porites porites* var. *furcata* several hundred feet in diameter in which this was the only species of coral. Similar occurrences of *Acropora cervicornis* and its Indo-Pacific equivalent, *A. formosa*, are known, as are similar instances in many other species.

Studies by Edmondson (1929) on the

growth rates of Hawaiian corals showed that under the conditions prevailing in Hawaii, yearly branch length increments for *Pocillopora* were 14 mm., while Mayor (1927), working with *Pocillopora* from Samoa, found rates as high as 23 mm. per year. Under the conditions present in San Gabriel Bay, the lateral development of a colony may exceed these records because of the great competition for external surface and light and lack of lateral interference of growth between individual heads. Temperature data are not sufficient for the effect of a possible lower than optimal value which would result in lowered metabolic activity and reduced growth rates to be appreciated.

#### SAN TELMO REEF SUITE

To the north of San Carlos Bay, Baja California, and just south of San Telmo Point (latitude 25° 18' N., longitude 110° 57' W.), is an unnamed bay, first visited by the "E. W. Scripps" expedition, in which there is a series of exposures of a Pleistocene reef. Because the bay affords anchorage to moderate-sized vessels, it was used by both the "E. W. Scripps" and the "Puritan" while attempts were made to collect at localities several miles to the north. There are apparently no villages in the area, although scattered ranches are located about water holes. The region is linked to the interior by a trail leading to the towns of Tijuana, Rosario, and Batequitos.

To the north of San Telmo Point are the lower Miocene beds containing remains of the desmostyloid *Cornwallius*. It was presumably in conjunction with the investigation of that area that Anderson and Durham (Anderson, 1950, p. 15) first found the locality. Anderson (*op. cit.*) described the occurrence of coral reef zones, algal limestones, and fossiliferous gravels exposed in the sea cliffs of this bay. Apparently two sequences are represented as a lower fossiliferous series truncated by a terrace and succeeded by other fossiliferous gravels. These, according to Anderson, contain a fauna similar to that of the Pleistocene deposits of Coronados Island. Durham (1950a) regarded the lower sequence as lower Pleistocene solely on the presence of two fossiliferous sequences.

In the course of the "Puritan" investiga-

tions, the bay was selected as an anchorage, while a party (Squires and Van Gelder) went ashore to collect (unsuccessfully) at the Miocene *Cornwallius* locality. Emerson collected and photographed the sections described by Durham and Anderson. The return from the Miocene exposures to the north was made by foot along a circuitous route through the foothills several miles inland. The return to the coast along roughly an easterly course made a traverse across a complete section of Pleistocene exposures contemporaneous with those of the sea cliff, demonstrating some interesting facies changes. Because of the limitations in time, the lower section was restudied by myself during the early morning, and the map (fig. 5) was drawn. The chart, based on a visual inspection of the region, must be considered only as a first approximation.

Exposures of fossiliferous deposits were found on the southern margin of the bay. At the southeastern point of the bay red conglomerates and sandstone are exposed (fig. 6A) which have an apparent dip to the east of about 8 degrees. This sequence of sediments has been tentatively assigned to the Salada group. Several hundred feet to the west of this exposure, 6 feet of conglomerate are overlain unconformably by 5 feet of white sand containing numerous boulders. This section (fig. 6B) is capped by 1 to 2 feet of a dense, lithified, calcareous material interpreted as a surficial concentration or caliche, which may be the algal limestone of Anderson (1950, p. 15). Sections to the west show only the Pleistocene materials, all sections differing slightly and their components apparently lenticular and discontinuous. Fossils are scattered throughout the section, but, in the main, the boulder beds are less fossiliferous than the sands.

At the westernmost extremity of the southern shore of the bay, local oyster aggregations may be found at the basal portion of the section. Slightly above the oyster patches is the reef facies. Often the basal 6 to 8 feet of the section may be composed largely of pinnacled masses of *Porites* (pl. 31, fig. 1). The density of coral growth is less at the base than at the top, which is rather abruptly truncated by a capping of 10 to 15 feet of gravel. In the bluff of the arroyo (fig. 6D) another exposure of the reef facies shows 15 feet of admixed

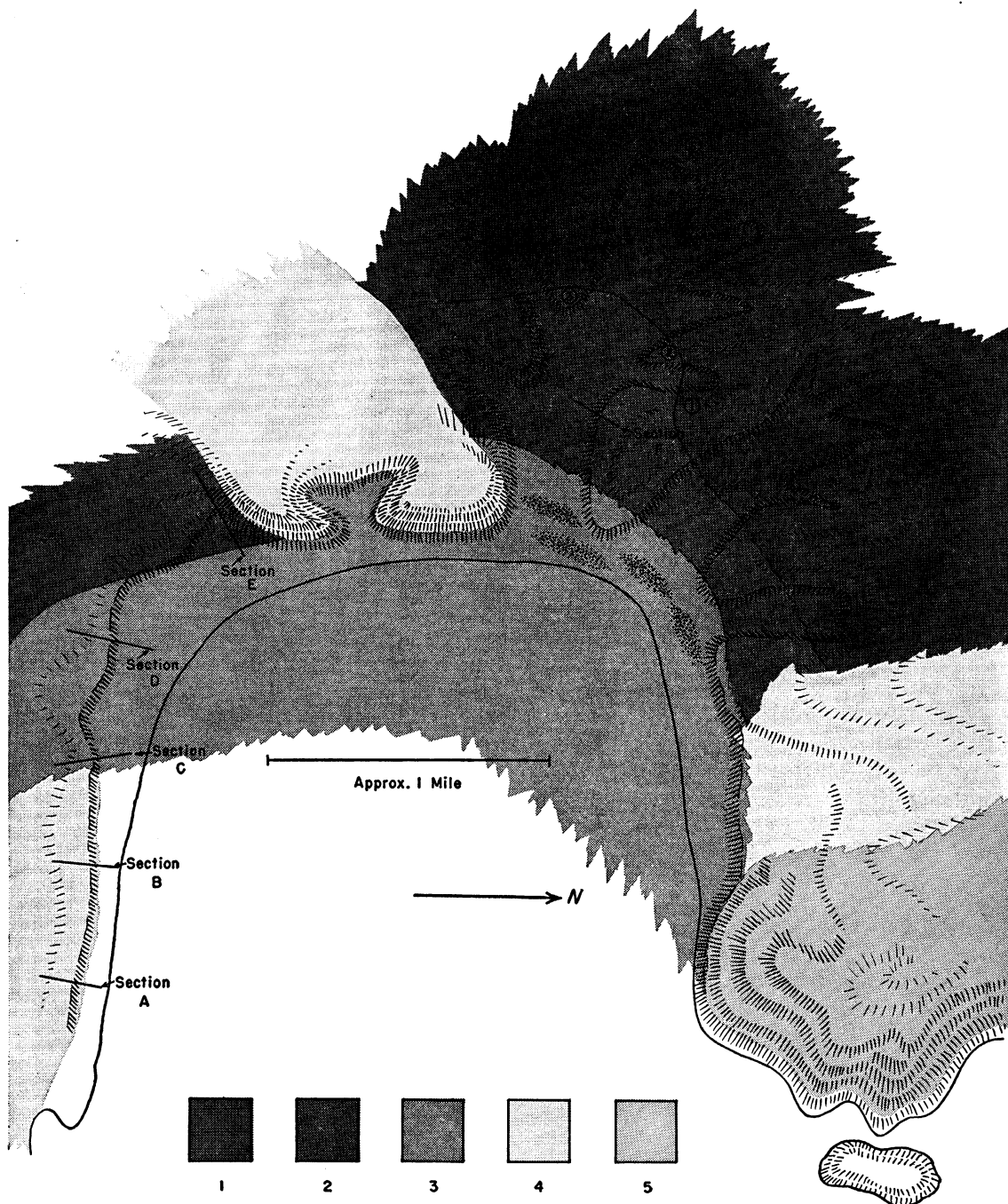


FIG. 5. Sketch map of the Pleistocene reef suite south of San Telmo Point, Baja California. Tinted areas correspond to various facies: 1, back-reef, mangrove-mud-flat facies; 2, reef facies; 3, fore-reef facies; 4, outcroppings of Salada group, probably representing island areas; 5, granite outcroppings representing island areas. See also plate 30, figures 5, 6. See text figure 6 for sections at points indicated. Numbers in circles refer to sections described in the text.

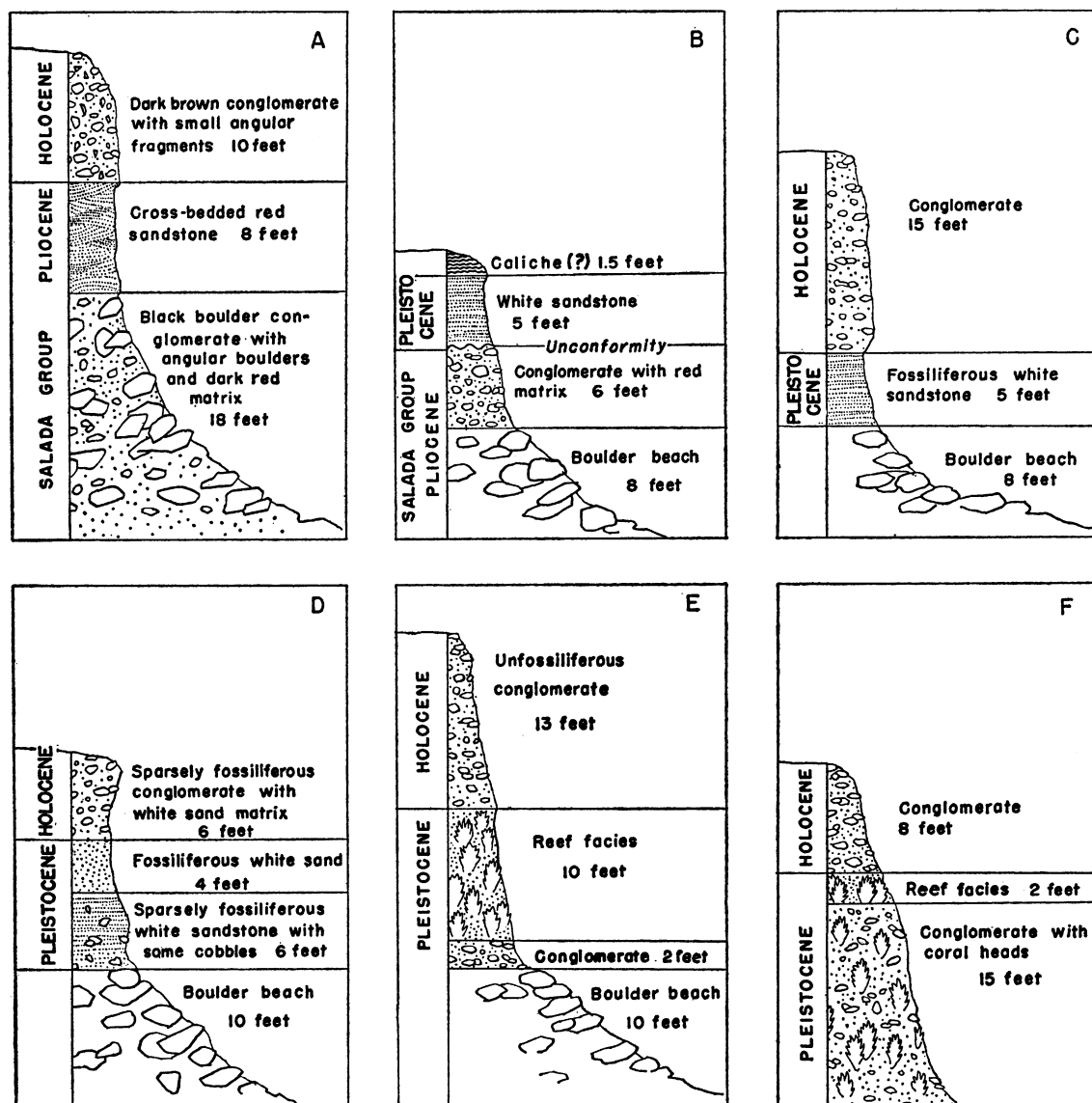


FIG. 6. Sections of Pleistocene exposures in bay south of San Telmo Point, Baja California. See text figure 5 for position of sections. Photographs of some of these sections are shown on plate 31, figures 1-6.

boulder and coral heads, the latter largely in place. This is succeeded by 2 feet of coral beds, which are in turn overlain by 8 feet of gravel.

FOSSILS COLLECTED FROM PLEISTOCENE EX-  
POSURES AT SAN CARLOS BAY-  
SAN TELMO POINT AREA

Gastropoda (identified by W. K. Emerson)  
*Acmaea* sp. indet.

*Astraea unguis* (Wood)  
*Bulla punctulata* A. Adams  
*Calliostoma eximium* (Reeve)  
*Cerithium maculosum* Kiener  
*Clava gemmata* (Hinds)  
*Conus brunneus* Wood  
*Conus nux* Broderip  
*Conus perplexus* Sowerby  
*Conus princeps* Linnaeus  
*Conus purpurascens* Broderip  
*Conus* cf. *C. regularis* Sowerby

*Crucibulum imbricatum* (Sowerby)  
*Crucibulum spinosum* (Sowerby)  
*Cypraea annettae* Dall  
*Cypraea arabicula* Lamarck  
*Fissurella* sp.  
*Hanetia pallida* (Broderip and Sowerby)  
*Hipponix* sp.  
*Knefastia olivaceus* (Sowerby)  
*Modulus cerodes* A. Adams  
*Oliva* cf. *O. polpasta* Duclos  
*Olivella dama* (Wood)  
*"Phyllonotus"* aff. *P. erythrostomus* (Swainson)  
*Polinices bifasciatus* (Gray)  
*Polinices uber* Valenciennes  
*Pusula solandri* (Gray)  
*Strombina maculosa* (Sowerby)  
*Strombus galeatus* Swainson  
*Strombus granulatus acutus* Durham  
*Tegula mariana* (Dall)  
*Turbo fluctuosus* Wood  
*Vasum caestus* (Broderip)

Pelecypoda (identified by W. K. Emerson)

*Antigona multicostata* (Sowerby)  
*Apolymetis cognata* Pilsbry and Vanatta  
*Arca multicostata* Sowerby  
*Arca reeveana* d'Orbigny  
*Arca solida* (Sowerby)  
*Cardita crassicostrata* (Sowerby)  
*Cardita megastropya* (Gray)  
*Cardium biangulatum* (Broderip and Sowerby)  
*Cardium consors* (Sowerby)  
*Chama pellucida* Broderip  
*Chione tumens* Verrill  
*Chione undatella* (Sowerby)  
*Codakia distinguenda* (Tryon)  
*Codakia mexicana* Dall  
*Divaricella lucasana* Dall and Ochsner  
*Dosinia ponderosa* (Gray)  
*Glans affinis* (Sowerby)  
*Glycymeris multicostata* (Sowerby)  
*Lima tetrica* Gould  
*Macrocallista squalida* (Sowerby)  
*Modiolus capax* (Conrad)  
*Nucula declevis* Hinds  
*Ostrea fischeri* Dall  
*Ostrea palmula* Carpenter  
*Ostrea* cf. *O. cummingiana* Dunker  
*Pecten circularis* (Sowerby)  
*Pecten subnodosus* (Sowerby)  
*Pecten vogdesi* Arnold  
*Pinctada mazatlanica* (Hanley)  
*Pseudochama exogyra* (Conrad)  
*Spondylus calcifer* Carpenter  
*Tellina cumingii* Hanley

Corals

*Pocillopora elegans* Dana

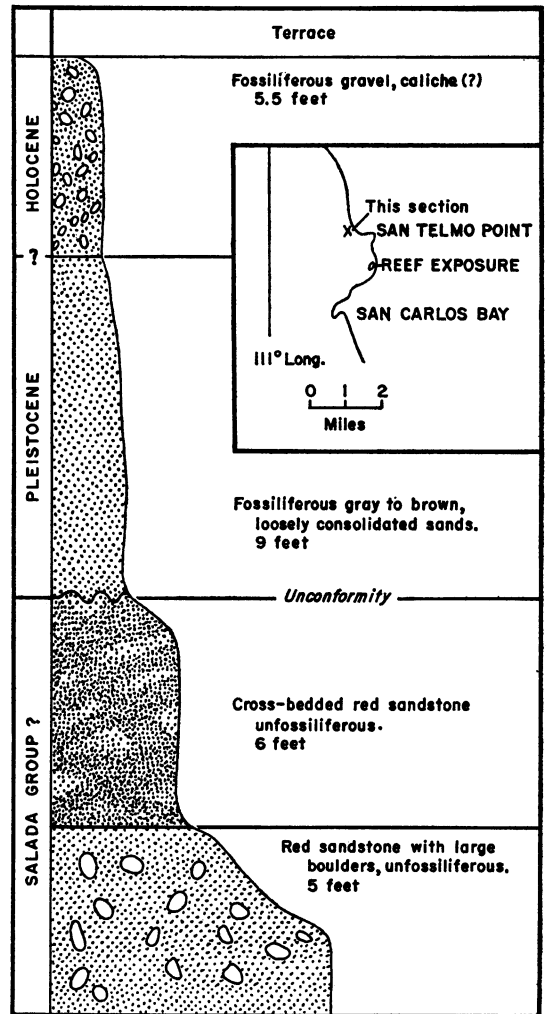


FIG. 7. Exposure of Pleistocene sediments north of San Telmo Point, Baja California. Compare with plate 30, figure 3.

*Porites californica* Verrill  
*Porites sverdrupi* Durham  
*Porites* sp.

Other facies are present. For example, in the northern arroyo about 6 feet of fine argillaceous sand were exposed. Although slumping made measurement of the section difficult, it was possible to see that in addition to the sand, many fine pebbles and rhizomorphs were present. In some instances specimens of the mangrove oyster, *Ostrea palmula*, are attached to the rhizomorphs. Directly to the west the mangrove facies is farther inland from the reef facies and is separated from it

by a reddish muddy sand containing a fauna dominated by *Tagelus*, representing a mud flat, back-reef environment. Westward, or inland of this facies, were red sands containing a few mangrove oysters, worn shell fragments, and bits of coral debris. Outcroppings of the Salada (?) group on the southeastern point and in the western and northern portions of the bay represent islands in the Pleistocene embayment.

The reef suite exposed in the lower terrace and sea cliff of this bay are clearly indicative of a reef environment similar to that existing at San Gabriel Bay at the present time. The chief differences are in the reef-forming coral. *Pocillopora*, the reef former at San Gabriel Bay, is present at San Telmo but only as scattered fragments in the fore-reef facies.

Sequentially, the area was first pioneered by molluscan elements and scattered corals. In very shallow water, the *Porites* reef became established. It maintained itself throughout the continued flooding of the region, although there is reason to believe that periodically the reef was overwhelmed by sediment, probably materials carried down during flood stages from the mountains to the west. In the deeper waters before the reef, *Pocillopora* and *Porites* flourished along with a well-developed molluscan fauna. The effect of periodic influx of sediments was not so strongly felt in this facies. Probably at a time coincident with maximal sea level, the reef facies was overwhelmed by a deluge of coarse material from the west. Careful collecting on the fore-reef facies might indicate the same sort of environmental change.

The peculiar growth form of *Porites* observed in this reef was found in the fossil populations at several other occurrences, notably Coronados Island, where growths of the same general type are present (fig. 8), but the coral population is of lesser density. From three localities living examples of this growth form were collected, all of which shed some light on the ecology of this particular growth form. In the inner harbor of Puerto Escondido (fig. 9) along the western shore, in 3 feet of water, approximately 6 feet laterally from the mangroves, was a thin but persistent line of this growth form. It fronted the mangroves for a distance of about 100 feet. Nowhere else in the bay was this growth form found, although

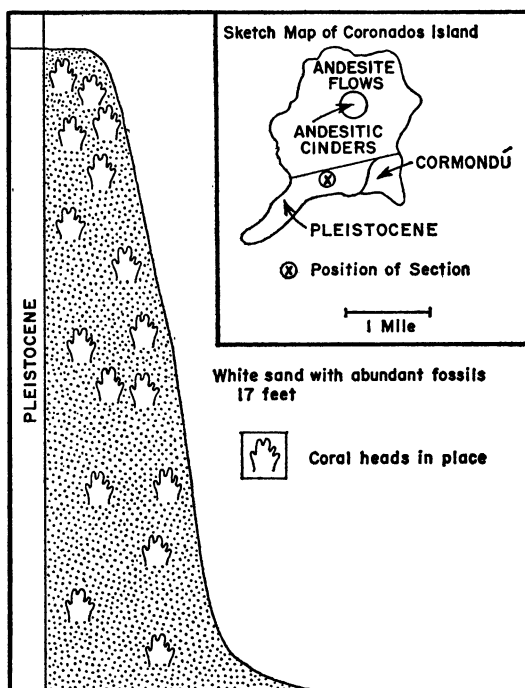


FIG. 8. Section of Pleistocene coral bearing sediments at Coronados Island. Sketch map after Anderson (1950).

*Porites* is rather widely distributed. Similarly, at Aqua Verde Bay on the southern shore, surrounding a rock pinnacle at depths varying from 4 to 10 feet, were scattered growths of *Porites californica* in this phenotype. Competition between the coral and laminar algae was apparent. However, the bottom there was rocky. Similar to the fossil occurrence is a reef development on the eastern shore of Salinas Bay (fig. 10). Some distance offshore (approximately 100 feet), and separated from the extensive salt flats to the east by a boulder rampart largely composed of *Porites* coralla, is a dead or dying reef composed of this phenotype of *Porites*. The water is shallow and quite muddy. Travis and Collins, who investigated the region, reported high salinities, detected both by taste and by buoyancy of the swimmer. The coralla collected were largely dead except for the tips of the pinnacles. My colleagues reported that the reef arose from the bottom rather sharply, was about 5 feet in breadth, and was covered by a lush growth of filamentous algae.

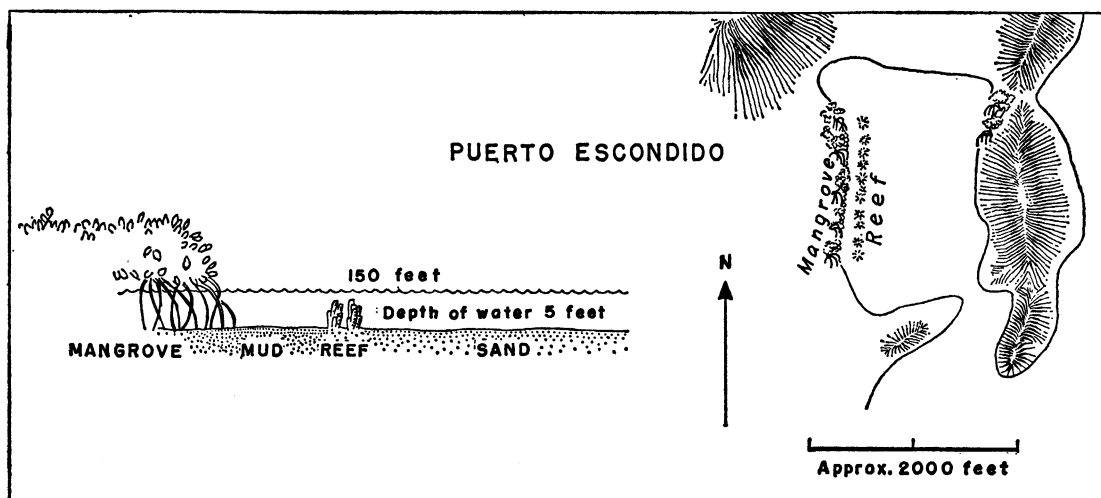


FIG. 9. Representation of coral growth and distribution in bay at Puerto Escondido, Baja California.

#### OTHER REEF OCCURRENCES

All the brief statements that follow are taken from discussions to be found in Durham (1947, 1950a) and Anderson (1950). Some of these reef areas were visited, but no detailed observations were made, as they seemed superfluous. Large living colonies of *Porites* sp. were noted by Durham (1947, pp. 11, 22) at Marquer Bay, Carmen Island, and it was suggested that they might be reefs. A

morning spent in searching the bay by surface observation failed to reveal any extensive coral growths, although scattered heads of *Pavona* and *Porites* were collected.

Fossil reefs comparable to those described from San Telmo Point region are not uncommon. The best known are those described by Durham (1947, p. 22) from the upper Pliocene of Marquer Bay and Puerto Balandra, Carmen Island. Similar occurrences are

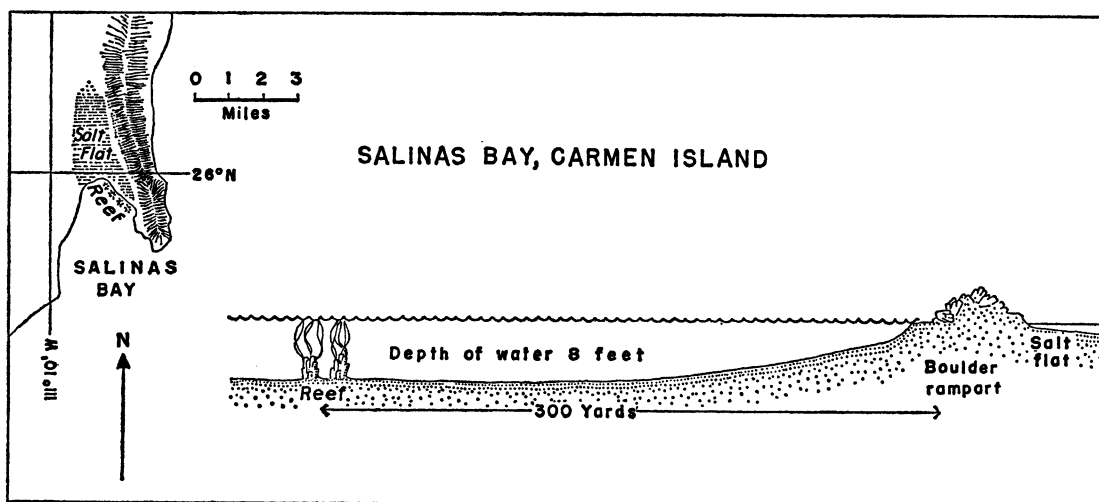


FIG. 10. Representation of coral growth and distribution in eastern Salinas Bay, Carmen Island.

noted from the Pleistocene of Coronados Island and Carmen Island. Occurrences of *Porites* sp. in some numbers, but not necessarily forming reefs, are also reported from San Marcos and Tiburón Islands.

At Marquer Bay, the reef is about 10 feet thick and can be traced for several hundred yards laterally. Its depth is approximately half of its width. The cross-sectional form of the reef is lenticular, the base being relatively

flat. The base of the reef is developed on a marly sand with occasional large boulders. The corals are relatively densely packed and almost without exception are *in situ*. The largest coralla of *Porites californica* are those found in the Pleistocene of Coronados Island, where Durham (1947) reports heads 2 feet in diameter and up to 4 feet in height. Smaller coralla were observed in the section shown in figure 8.

### ECOLOGY OF REEF SUITES

In classical terms the living and fossil reefs discussed here are of the barrier type although most feebly developed. With the exception of the El Pulmo reef suite, they are rather closely related in terms of ecology and physiography although differing in faunal components. All the reefs have in common their extreme youth. None of the regions of the Gulf of California in which reefs have been found can be considered as stable tectonically, a fact attested to by the piecemeal preservation of the stratigraphic section. Recent reefs certainly seem to have been in existence only a relatively short time, with the Pulmo sequence being perhaps the youngest.

As is noted above, the coral fauna of the El Pulmo reef suite is that of the Panamic faunal region, with only minor exceptions, and in this respect it differs from the other reef communities which are essentially monospecific. It is a flourishing community but has as yet not developed into a constructional phase. Eventually the reef may take on some configuration other than that imposed by the trends of the rock ridges upon which it is currently situated. In brief, El Pulmo reefs are approximately what might be expected of a northern reef type, one nearly at the extreme limit of development for the hermatypic corals. It is a community in which size and density are reduced both individually and collectively. Ecologic extremes have not reached the point at which individual species may be discriminated against, but yet have limited coral growth only to those areas most favorable for development. It is pertinent here to consider the aspects of El Pulmo that make it a favorable site. Among those factors that should be considered are: shallow-water rock ridges providing a suitable substrate

and attachment of the coralla for development; protection from extremes of wave activity, but yet receiving sufficient water agitation to fulfill the necessary requirements; absence of quantities of fine sediments from the water; and its position on the northern portion of the embayment. The density of coral population is usually greater on the northern side of embayments. Perhaps the most striking example of this was found in the small embayment on the western side of Ballena Island. There, a dense growth of *Pocillopora elegans* on the northeastern side of the bay thins progressively on the eastern side, until only scattered heads were found in the southeastern portion, and no coral was found in the southern sector. Dead coralla were noted in the northwestern and southeastern sectors only. The effects on temperature and sedimentation of the strong northern winds which are encountered in the Gulf are not known. Certainly cold northern waters are moved southward during such a storm, but surficial mixing would not permit extremes necessary for coral kill to accumulate. Sediment accumulation in southern portions of bays was noted, but was not invariable.

The presence of more or less continuous rock surfaces is the most conspicuous difference between El Pulmo and other areas. Coral growths of a very local nature, but of the same variety of species and nearly the same density of population, were found at Los Frailes Bay, Ballena Island, and Cerralvo Island. In every instance these were developed on isolated rocks or patches of rock surrounded by sand. The presence of a coral population that has both vertical and horizontal linear dimensions of some magnitude is much more apt to be considered as a reef

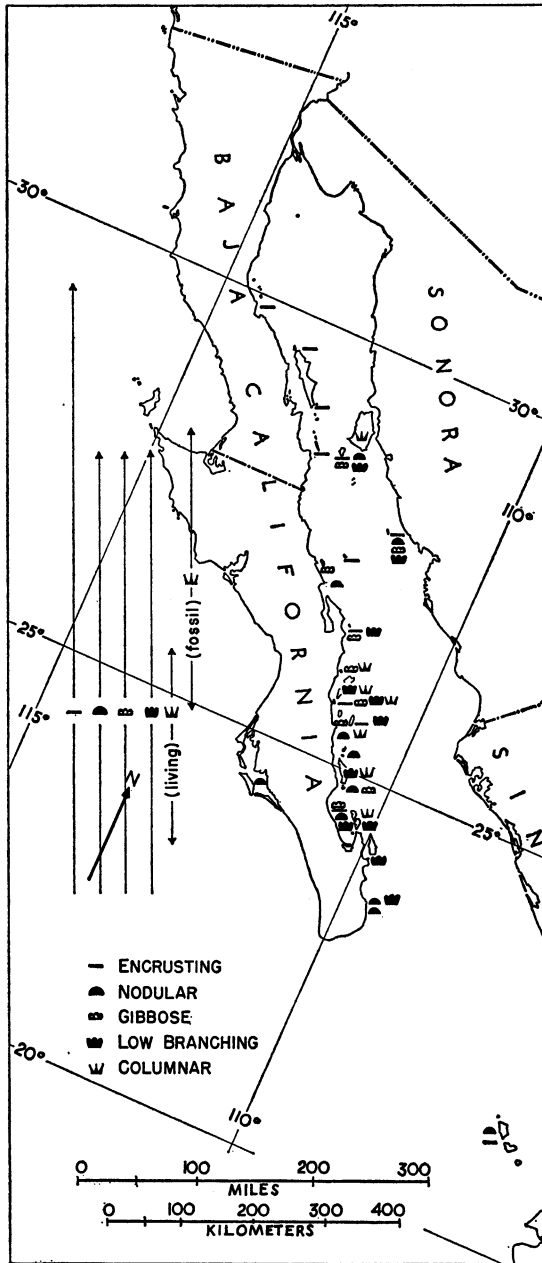


FIG. 11. Distribution of the phenotypes of *Porites californica* Verrill. Fossil distribution is shown only for the reef phenotype (symbols on land areas).

than isolated coral patches. This is true not only of the Gulf of California, but of other coral areas as well. An analogy may be made with the so-called "coral heads" of the Bahama Islands, which in reality are localized

growths often of 15 to 20 species of coral forming clearly defined units which rise above the bottom for a height of several feet. These heads are often separated from one another by many hundreds of yards, or even miles, of bare sand. These "microreefs" are not reefs in the usual sense, although, if placed in proximity, a reef structure could be defined.

The occurrences of *Porites californica* in reef suites as well as the development of *Pocillopora* at San Gabriel Bay are all of the same general type, although the biologic entity involved is different. In every case the associations of this type are barrier in nature and are found slightly off shore in protected embayments. The barrier is crescentic in outline, with the concave side towards the sea, and roughly parallels the beach line. The distance from the shore varies according to the local physiography, but the depth at which the reef develops seems to be equally as important as the rate of positive eustatic change in determining the eventual thickness of the reef suite.

In all instances of *Porites* reefs, a particular phenotype (pl. 33, fig. 3) is present, one that has a rather remarkable distribution (fig. 11). The obvious occurrence of a growth form such as this in sheltered bays to the exclusion of other more or less protected environments is significant, but the reasons for its limitation to the central portion of the range of the species are at the present time unaccounted for and should prove an interesting subject for further investigation.

An interesting series of parallels may be made between the occurrence of *Pocillopora*, *Porites*, and the laminar brown algae (kelp) in similar positions of comparable environments. Barrier associations of *Pocillopora* of various degrees of development are recorded in my notes as occurring at San Gabriel Bay and western Ballena Island. Associations of the branching phenotype of *Porites californica* of scattered occurrence or reef density are recorded from San José Island, Agua Verde Bay, Salinas Bay, Carmen Island, Puerto Escondido, Coronados Island, and San Marcos Island. The occurrences at each extreme of this distribution are of scattered heads, the total density being less than that of the barriers. Growths of kelp of the barrier pattern are recorded as occurring at Salinas

Bay, Carmen Island, Coronados Island, Tortuga Island, South San Lorenzo, southern Angel de la Guarda Island, and Pulpito Point. The association of kelp and *Porites californica* at Salinas Bay and Coronados Island was intimate, the kelp apparently succeeding the coral in the former instance.

The distribution of similar ecotypes seems to be a response to decreasing temperature as a principal factor. Certainly the great correspondence in position and similarity in effect on the leeward environment should not be overlooked. Behind coral barriers, despite the fact that in several instances the coral heads did not reach the surface of the water, there was an increase in the finer sediments. In several instances, notably San Gabriel Bay and the fossil reef at San Telmo, faunal suite differences correlated with the change in the substrate. The situation found in these bay barrier reefs is apparently an example of ecological replacement along a physical gradient, presumed to be thermal. It is the situation one would expect under the circumstances of a marginal reef.

Reef suites described by Palmer (1928) from the western coast of Mexico are exclusively *Pocillopora* in composition. It is presumed from the descriptions given by Palmer that the occurrences of reefs are in much smaller bays, and that because of either a longer history or more favorable growing conditions the embayments have been more or less completely filled by the coral. None of

these reefs has been so completely studied that their monospecific nature can be positively stated. *Pocillopora* are the common shallow-water constituent of these associations, *Pavona* and other corals occurring in somewhat greater water depths.

The sequence of reef development in the region of the Gulf of California can be taken as an example of gradational depletion of reef-forming elements (corals) until monospecific reefs are formed. It should be noted here that, although the San Gabriel reef is formed essentially by one genus of coral (*Pocillopora*), *Porites* are present in the area and are intimately associated with the reef. At the northern extremity of coral growth, the niche is occupied by kelp to a greater degree. The effectiveness of the latter as a barrier can be attested to by the difficulty with which it is penetrated by either boat or diver and the damping effect that it has upon waves. Unfortunately, the effectiveness of the kelp "reef" as a trap for sediment in the Gulf of California cannot be completely demonstrated, for, with the exception of the South San Lorenzo and Salinas Bay occurrences, the steep bottom profiles of the areas were not conducive to sediment collection. However, Ginsburg and Lowenstam (1958) cite examples in the West Indies of plants acting as sediment traps and quote D. G. Moore (Ginsburg and Lowenstam, 1958, p. 314, footnote) as reporting the kelp's acting as a sediment trap in southern California.

TABLE 1  
DIMINUTION OF THE HERMATYPIC CORAL FAUNA OF THE GULF OF CALIFORNIA  
COMPARED WITH LATITUDE AND TEMPERATURE

Area	Genera	North Latitude	Temperature Range <sup>a</sup> (Centigrade)
El Pulmo	<i>Pavona</i> <i>Pocillopora</i> <i>Porites</i>	23° 26'	18°-27°
San Gabriel Bay	<i>Pocillopora</i> <i>Porites</i>	24° 25'	17°-26°
Puerto Escondido	<i>Porites</i>	25° 49'	16°-25°
Salinas Bay	<i>Porites</i>	26° 00'	16°-25°
South San Lorenzo	Kelp Kelp	28° 35'	14°-23°

<sup>a</sup> Temperature data must be considered as only approximations and may be significantly different from the values given in the local areas considered.

TABLE 2  
 DIMINUTION OF THE CORAL FAUNA OF THE GREAT  
 BARRIER REEF COMPARED WITH LATITUDE  
 AND TEMPERATURE  
 (Data from Wells, 1955.)

Number of Genera and Subgenera	South Latitude	Minimum Temperature (Centigrade)
60-59	9° -17°	25°-21°
59-53	17° -20½°	21°-20°
53-35	20½°-23½°	20°-18°
35-25	23½°-24½°	18°-17°
25-12	24½°-27½°	17°-16°
12- 2	27½°-34°	16°-13°

The numerical depletion of genera along thermal gradients is a known phenomenon and perhaps best exemplified by the situation presented on the Great Barrier Reef. Wells (1955, p. 4) notes that the attenuation of the coral fauna there is one of subtraction, with no known additions to the fauna as it decreases in numbers from north to south. A summary table from Wells (1955) is repro-

duced here for comparison with data from the Gulf of California (tables 1, 2). It is interesting that, of the six hermatypic corals recorded from the southernmost latitudes (*Plesiastrea*, *Turbinaria*, *Pocillopora*, *Montipora*, *Pavona*, and *Cyphastrea*), two are also found in the Gulf of California (excluding the questionable occurrence of *Montipora*). *Porites*, the longest-ranging eastern Pacific form, is not known below latitude 24° S. Wells (1955, p. 4) notes that there is a sharp break in the fauna at a minimum temperature of about 20° C., below which the number of genera decreases rapidly. This same isotherm is selected as the boundary between the Panamic faunal province and the temperate California province. Unfortunately data on the thermal regime of the Gulf are so poorly known that no direct comparisons can be made.

Although the Gulf of Panama faunas are imperfectly known, the diversity there cannot be much greater than that now recorded. To schedule the complete diminution of the fauna one must consider the depletion resulting from the degree of isolation from the Indo-Pacific region.

## FAUNAL RELATIONSHIPS AND DISTRIBUTION

### PLIOCENE CORALS OF THE GULF OF CALIFORNIA

AT THE HEADWATERS of the Gulf of California, in the Imperial Valley of California, is an upper Tertiary reef coral fauna which is of great importance in the interpretation of the eastern Pacific coral history. There is no new evidence presented here, and the implications of this fauna can only be reviewed. Vaughan (1917) discussed the faunas of the Carrizo Creek exposures and their significance. Six genera of corals are recorded from the formation: *Eusmilia*, *Dichocoenia*, *Diploria*, *Solenastrea*, *Siderastrea*, and *Porites*. Of these, only the last three are known from the Pacific region today. *Porites* is not significant, for it is circumtropical in distribution, while *Siderastrea* is confined to the Red Sea (Wells, 1954), and only *Solenastrea* has been recorded from the eastern Pacific, that record being a beach-worn specimen reported by Durham and Barnard (1952).

Durham (1950a, p. 30) has summarized various viewpoints on the age of the Imperial formation and concludes that the San Marcos formation of the Gulf of California is the closest correlative of the Imperial formation, which must then be considered as lower Pliocene. Vokes (*in* Wilson, 1955, p. 32) concludes that the Boleo formation of the Santa Rosalia area, Baja California, is a correlative of the Imperial formation. Anderson (1950, p. 12, footnote) states that the relationship between the San Marcos and the Boleo formations is very close. Others (see Durham, 1950a) have assigned a Miocene age to the Imperial formation. The final decision will probably rest on the interpretation of the vertebrate-bearing sediments overlying the marine sequence.

In the Pliocene of María Madre Island, Tres Marías Group, was found a coral identified as *Solenastrea* cf. *S. fairbanksi* Vaughan by Durham (1950a, p. 30). There seems little doubt, following personal examination of the specimen, that it is identical with *S. fairbanksi* var. *minor* from the Imperial formation. This occurrence on María Madre Island has been dated as middle Pliocene (Durham, 1950a, p. 30). Although Durham questions the value of the specimen, because it was collected as a loose block, Jordan and Hertlein

(1926, p. 210) report: "large blocks of reef coral are irregularly distributed in the formation." Hanna (1926, p. 69) states: "During a portion of Pliocene time large coral reefs existed around this old land mass [the granitic core of María Madre Island] and large blocks of the fossiliferous material, firmly cemented, have fallen down from the exposures and have rolled indiscriminately far out into the forest."

"North of the town a large wash comes into the sea from the westward [Arroyo Hondo] and in the bed we found pieces of Pliocene float conglomerate and large blocks of coral several feet square."

It is unfortunate that no collections containing coral have been made from these exposures since that time, for the variety of genera involved will contribute greatly to our understanding of the fate of the Imperial fauna.

Felix (1905) records fossil corals from Cartagena, Colombia, including *Orbicella* [= *Montastrea*] *theresiana*; *Isastrea turbinata* [= *Solenastrea bournoni* Milne-Edwards and Haime, Vaughan (1919, p. 190)], and *Stephanocoenia* [= *Solenastrea*] cf. *fairbanksi*. Unfortunately the last species is neither figured nor described, so that it cannot be properly evaluated. The presence of elements of the Imperial fauna on the Atlantic side of the Panamanian Isthmus would be of great interest and should be verified.

If the dating of the Imperial formation is lower Pliocene (absolute age is not so important for the following discussion as is relative age), and the correlations with the San Marcos and Boleo formations of the Gulf of California are accepted, several surprising facts appear. No lower Pliocene corals except in the Imperial formation are known in the southern region, although apparently similar facies are represented elsewhere. Upper Pliocene (Marquer formation) corals are abundant in the southern Gulf of California, particularly in the Carmen Island and Coronados Island region. The fauna consists solely of *Porites californica*, which was previously unknown in the Gulf region. This

species later becomes associated with an Indo-Pacific fauna during the Pleistocene and is believed to represent a preliminary invasion by a Pacific fauna. A comparison of *Porites californica* and *Porites carrizensis* is difficult, but they are apparently not the same. It is also interesting that the reef phenotype of *Porites californica* is the first to appear. The only coral known from the middle Pliocene of western Mexico is the specimen from the Tres Mariñas.

It seems that the Imperial formation coral fauna was short-lived in the Gulf of California. It is suggestive, but far from conclusive, that as the Imperial formation grades upward into non-marine sediments, so do correlative sedimentary sections farther to the south. Following Comondú time (upper Miocene), deformation on the eastern border of lower California was followed by "... invasion of the sea east of lower California extending into southeastern California where the Imperial formation (lower Pliocene) accumulated" (Anderson, 1950, p. 48). The basal portion of the Imperial formation contains the largest fauna and all the corals, while the upper portion is a transition to the non-marine, overlying, Palm Springs formation. Tarbet and Holman (1944) report *Ostrea vespertina* and other marine fossils from the Palm Springs equivalents in the San Felipe hills. (Beal, 1948, considered the San Felipe section to be non-marine and unfossiliferous.)

The San Marcos and Boleo formations apparently are equivalent in age to the Imperial, or at least the lower portion thereof is. Wilson (1955, p. 31) states that the conglomerates and tuffs that form the bulk of the Boleo formation in the Santa Rosalia region are believed to grade into marine beds north-eastward towards the Gulf and become more fine-grained and better sorted in that direction. The Boleo formation is separated from the overlying Gloria by an unconformity. Anderson (1950) shows that the fossiliferous beds at San Marcos Island are above the gypsum and concludes that the saline sea

from which they were evaporated was opened following their deposition to more general circulation. As indicated by Durham (1950a) the San Marcos is separated from the overlying Carmen formation by an unconformity in most areas of its occurrence.

Durham (1950a, pp. 17, 20) concludes that most of the fauna of the San Marcos formation is characteristic of it and of the Imperial formation, particularly the basal portion. There are several extinct species in the San Marcos fauna that are not found in the overlying Carmen formation. He also indicates that the Carmen formation fauna may be correlated with that of the San Diego formation, while the fauna of the San Marcos formation shows no close relationship to the fauna of the San Diego formation or any younger coastal California fauna. Aside from the stratigraphic implications of these statements, there is a suggestion of differences in origin of the San Marcos faunas and those of succeeding formations.

It may be postulated therefore that the Imperial fauna, including the faunas of the correlative San Marcos and Boleo formations, was largely eliminated from the Gulf region by shoaling waters and possibly complete regression before renewed transgression in middle Pliocene time. The fauna then was of Indo-Pacific nature or highly modified from the lower Pliocene West-Indian-derived fauna. It is possible that the decrease of temperature was a factor in prohibiting the reimmigration, although other local factors may well have been significant. Until the coral faunas living in the Gulf of Panama are more completely known, it is impossible to postulate the ultimate fate of the Imperial fauna. Many elements of this fauna may be represented there, now suggested by the problematic finds of a beach-worn *Solenastrea* and a badly worn fragment of *Agaricia* (?) (Durham and Barnard, 1952). No corals of West Indian affinities are known from the Gulf of California.

#### PLEISTOCENE CORALS OF THE GULF OF CALIFORNIA

Pleistocene sediments bear a much more complete fauna than the Pliocene rocks. *Porites*, *Astrangia*, *Pocillopora*, *Pavona*, and

*Psammocora* are all represented, although not in the diversity of species present in the Recent fauna. As would be expected, the

deeper-water corals are not represented and probably will not be found in any surface exposures. Apparently none of the Pleistocene species is extinct; several of the species known only from the fossil record are here considered as identical with living species. One *Pocillopora*, a form described as *P. palmata* Palmer, 1928, is much restricted in its distribution compared with its Pleistocene range.

Durham (1947, 1950b) stimulated some interest in the problems of distribution of reef corals during the Pleistocene. He (Durham, 1950b) considered the distribution of coral genera through the entire Tertiary in relation to postulated isothermal movements, but the study has no direct bearing on the history of the Gulf of California. In the earlier study Durham concluded (1947, p. 11):

"Within the Pleistocene *Psammocora* (*Stephanaria*) *stellata* and *Pocillopora robusta* extended their range north to the Carmen-Coronado islands area, thus indicating a warmer climate than at present. There are indications that the climate may have warmed at two distinct intervals; one probably corresponds to the time *Porites californica* extended its range around Cape San Lucas to Magdalena Bay."

Because the distributions of many of the key species utilized by Durham in his study were not completely documented, the analysis is in need of revision. Figure 13 shows the distribution of many species of shallow-water forms known from the Recent and the Pleistocene fauna. It may be seen here that, with the exception of *Psammocora* and *Pavona*, most of the shallow-water genera have a more northerly range at the present time than during the Pleistocene. As a result of the "Puritan" collections, *Pavona* and *Psammocora* were both found to have a much greater range than previously known. In particular *Psammocora* may be easily overlooked because of its occurrence in narrow crevices and encrusted on rock surfaces. More northern occurrences of *Pavona* would not be surprising. On the other hand, *Porites*, *Astrangia*, and *Pocillopora* had more restricted distributions during the Pleistocene. In the case of the first two genera, the lack of known outcrops north of Tiburón Island may cause a distortion of the distribution pattern. Hertlein and Emerson (1956), reporting on Pleis-

tocene invertebrates from Puerto Penasco, list 64 species of invertebrates, but no corals are included. I am reluctant to base any interpretations of past climate on such patterns of distribution. A consideration of the distribution of the reef-forming phenotype of *Porites californica* leads to the same conclusion reached by Durham (1947; see fig. 11 of the present paper), that the reef facies was farther north during portions of the Pleistocene. Unfortunately I have not seen the northernmost specimens of Pleistocene *Porites californica* and cannot be entirely certain of their position in the gradation of growth forms, and the extension of range of this phenotype may therefore not be so extensive.

In contrast, interglacial marine climates were definitely warmer outside the Gulf in the coastal waters of the Pacific. The best evidence for this is not the extension of the *Porites californica* range to Magdalena Bay (where it is presently known to be living) during the Pleistocene, but rather a remarkable occurrence of *Pocillopora* on Guadalupe Island. Chace (1958, p. 321) reported collecting from Pleistocene exposures on Guadalupe Island and remarked that the molluscan fauna was apparently a warm-water one. Through the courtesy of Dr. Chace, I have been able to examine a coral from Guadalupe Island and find it a species of *Pocillopora* apparently closely related to *P. palmata* Palmer, and specimens of *P. robusta* Verrill, recorded as having prominent septa by Durham and Barnard (1952). The occurrence of *Pocillopora* at that latitude indicates a northern shift of approximately 8 degrees of latitude from the most northerly occurrence of *Pocillopora* outside the Gulf of California at the present time. The distribution of the species of *Pocillopora* is shown in figure 15. Palmer (1928) notes that *P. palmata* is rare in the Recent fauna (as represented by beach wash) but is abundant in the Pleistocene. None of the specimens collected from the Pleistocene or the Recent fauna of the Gulf of California is of the type having prominent septa. The apparent anomaly presented in these situations is that a latitudinal shift of approximately 8 degrees occurred outside the Gulf of California, while within it an apparent change of magnitude of less than 3 degrees is known.

Hubbs (1948) and Garth (1955), discussing

fish and brachyuran crabs, respectively, argue that the fauna of the northern portion of the Gulf of California is more closely allied to the southern Californian and northern Baja Californian fauna than to the Panamic fauna. They postulate immigration, during one or more glacial stages, of this colder-water fauna through the now tropical region into the Gulf of California, and that it is now isolated by the warm waters to the south. Unfortunately eustatic changes of sea level occurring in the Pleistocene (cf. Garth, 1955, p. 24) were positive during the warm period, during which isotherms presumably shifted to the north, and negative during glacial stages when isotherms shifted south. Flooding of the Magdalena Plain such as that postulated by Garth would have occurred only during an interglacial stage, although Beal (1948, p. 119) suggested a submergence of 1600 feet during the Pleistocene. Unfortunately much of the basis for this submergence is the presence of supposed, but unverified, Pleistocene shell deposits at these elevations. Until the true nature of these deposits (marine deposits versus kitchen middens) can be determined, physical evidence for the uplift and submergence is lacking. This point could be easily verified through carbon-isotope dating. The strong possibilities of tectonic uplift (and submergence) are not ruled out at this time.

Hertlein and Emerson (1956) considered the alternatives of a mid-peninsula connection between the Gulf and the Pacific or of surface cooling of a magnitude possible to permit migration of cool-water faunas around Cape San Lucas. Although evidence for such a migration is present in the molluscan, arthropod, and fish faunas, the knowledge of the corals at the northern end of the Gulf in its present state does not indicate such a migration.

The apparent anomaly presented in the interglacial latitudinal shift of approximately 8 degrees outside the Gulf, while the magnitude of northern movement of faunas in the Gulf was approximately one-quarter of that, can probably be resolved through considerations of physiography. Until the question of degree of emergence and submergence of peninsular Baja California is fully settled, it is probable that any external connections of the Gulf were at least as far south as the Mag-

dalena Plain. The upper end of the Gulf then formed a cul de sac, which would have warmed only through slow admixture of waters and solar heating. Local conditions produced by flooding in the northern region may have made the upper portion of the Gulf an unsatisfactory habitat for most corals.

#### DISTRIBUTION OF RECENT CORALS

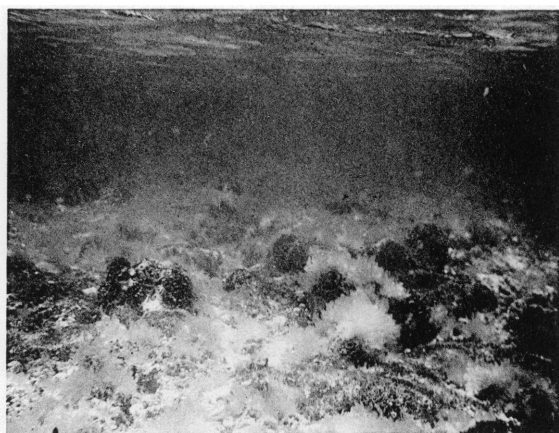
There is no clear-cut distinction between the shallow-water coral faunas of the northern Gulf and those of the southern, but rather a steady diminution of the faunas in a northern direction (fig. 12). This conclusion is in more or less agreement with the statements of Ricketts (*in* Steinbeck and Ricketts, 1941, p. 306) who concluded that the "color" of the Gulf littoral fauna as a whole was tropical and constituted a northward continuation of the Panamic faunal region. However, Ricketts (*in* Steinbeck and Ricketts, 1941, p. 307) goes on to state that the faunal differences between the northern and southern regions are well marked in most groups. He divides the Gulf into two regions on the basis of a line drawn between Guaymas and Santa Rosalia, indicating that its true position may be somewhat to the south.

Durham (1947) hints at a faunal division between the northern and southern Gulf at about the position of Carmen Island, but to a large extent he was hampered by incomplete distribution records. *Tubastrea* is presently known to extend much farther to the north than was known then, as are *Pocillopora* and *Pavona*. Three critical areas are seen in figure 12: San Francisco Island, Carmen Island, and San Marcos Island. It would be premature to postulate thermal restrictions (or any other restrictions, for that matter) for this distribution, for many of these ranges will be extended northward with further collecting.

Distribution of the deeper-water corals is not plotted, for their ranges are very poorly known and subject to variation according to the intensity of dredging operations and, to a great extent, the effect of the sedimentation on the delta of the Colorado River. In the deepest portions of the Gulf, distribution patterns will probably be affected to a greater extent by topography, as there are several relatively isolated basins.



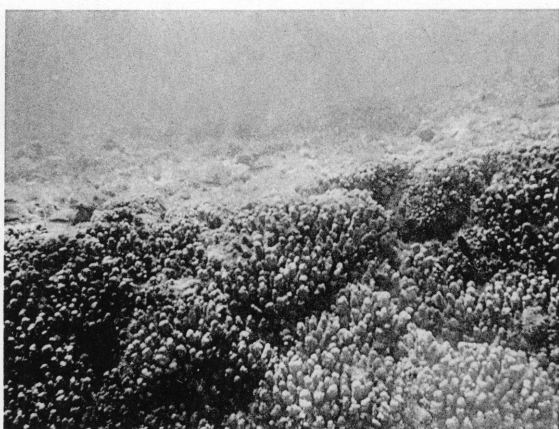
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1. Frontal portion of the San Gabriel Bay reef, with dense *Pocillopora elegans* growth. 2. Lateral portion of the San Gabriel Bay reef facies, with small heads of *Pocillopora* nearly overwhelmed by green filamentous algae. 3. Algal growth in the fore-reef facies. 4. View across the top of a *Pocillopora* coral head, San Gabriel Bay, showing the depressed central region with algae and *Porites*. 5. Central portion of bay south of San Telmo Point. Arroyo to the right of the headland is shown on the map (text fig. 5). 6. View of outcropping Pleistocene sediments on the south shore of bay south of San Telmo Point



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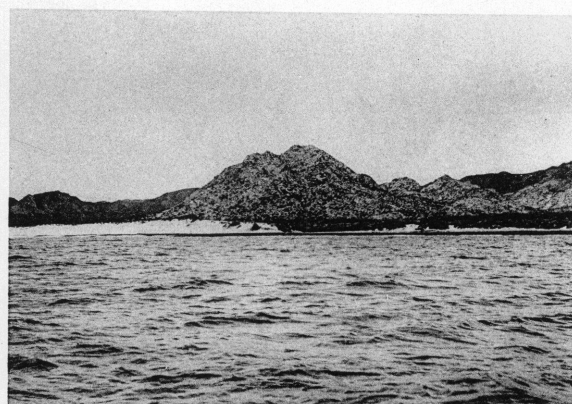
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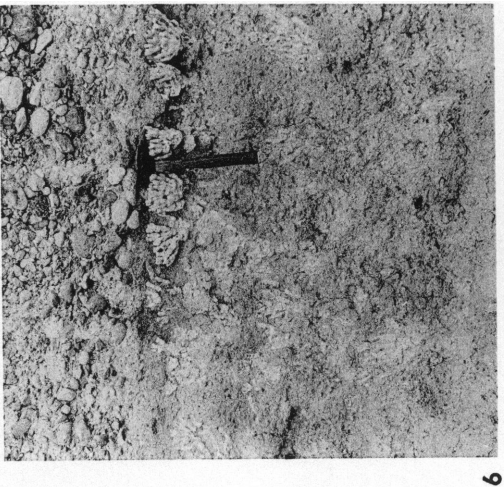
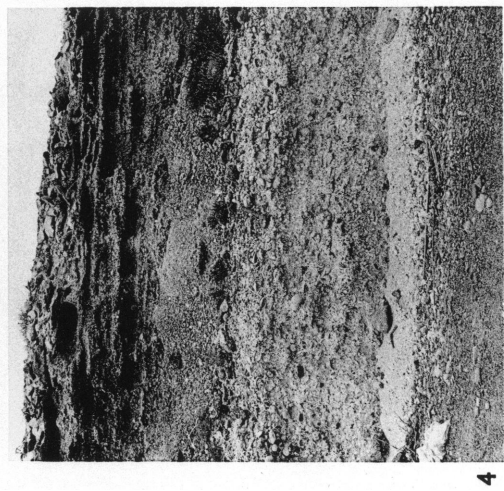
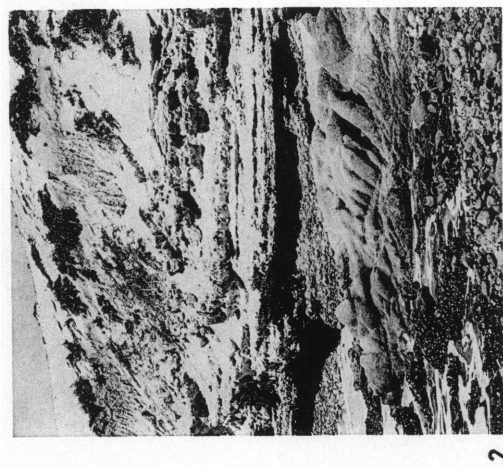
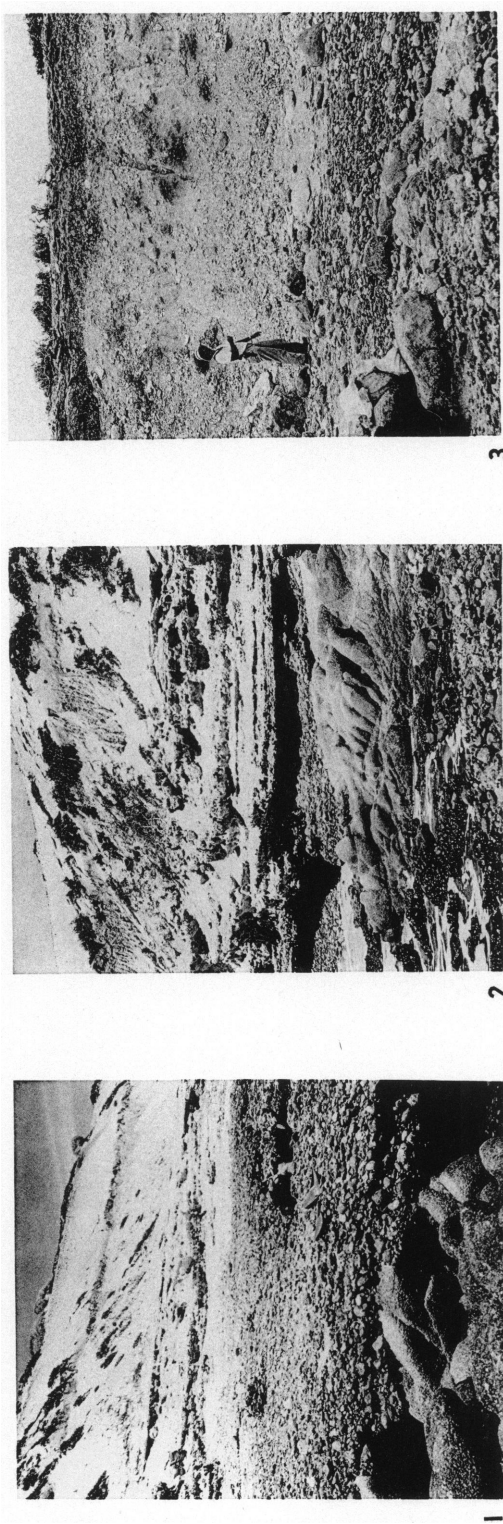


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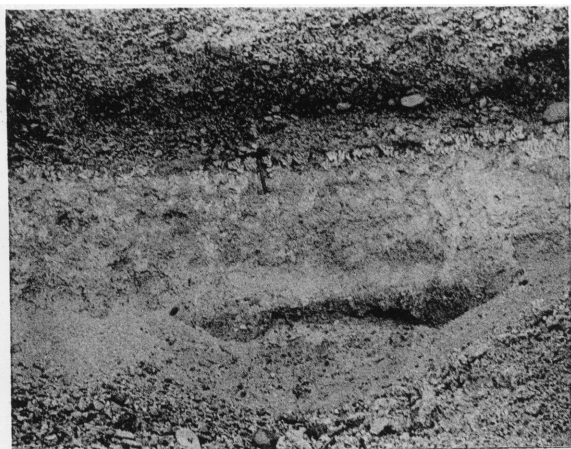


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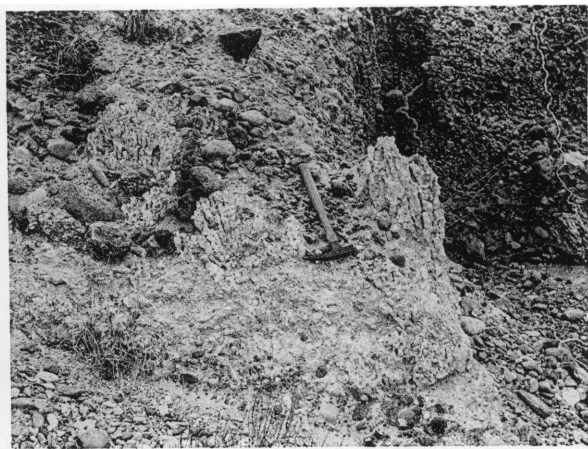
1. Panorama of the southern portion of El Pulmo Bay. The conglomeratic mass projecting into the bay is the shore portion of La Barre Grande (see text fig. 2). 2. Southerly view of the beach at El Pulmo. The gravel in the middle ground is derived from the erosion of La Barre Grande. 3. View north from the position of the outcropping shown in 1. 4. View of La Barre Grande, El Pulmo Bay, with the waves breaking across the reef. 5. Westerly view of the granite peak in the central portion of El Pulmo



1. The Pleistocene section at El Pulmo, with the contact between granite and conglomerate shown. 2. Southerly view of the exposure shown in 1. 3. Pleistocene section north of San Telmo Point (see text fig. 7). 4. Pleistocene section in bay south of San Telmo Point. The fore-reef facies underlies sparsely fossiliferous Holocene sediments. 5. Occurrence of *Pocillopora* and molluscan shells in the fore-reef facies in Pleistocene exposures south of San Telmo Point. Photograph by W. K. Emerson. 6. Reef formed by *Porites californica* in Pleistocene section south of San Telmo Point. Photograph by W. K. Emerson



1



2



3



4

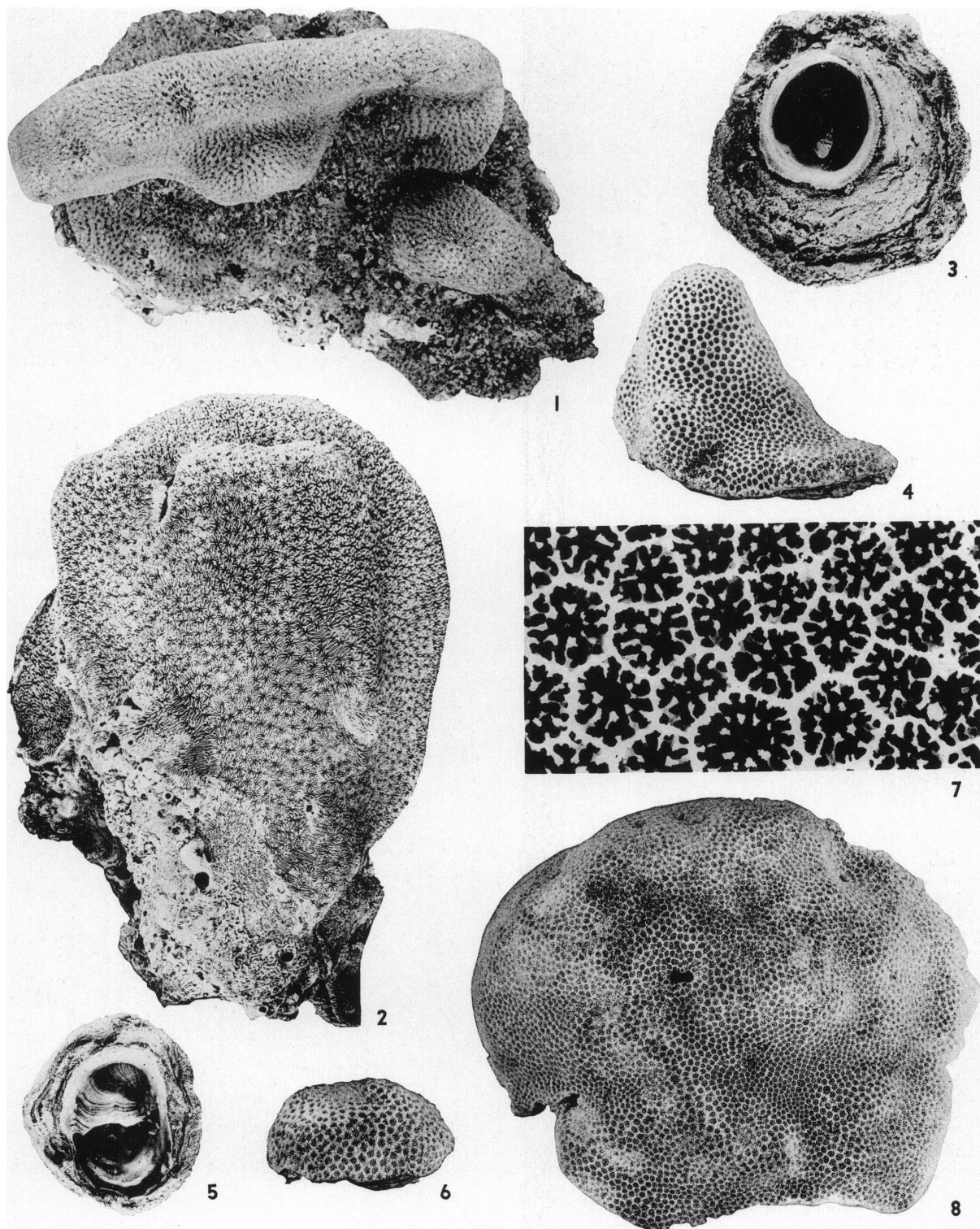


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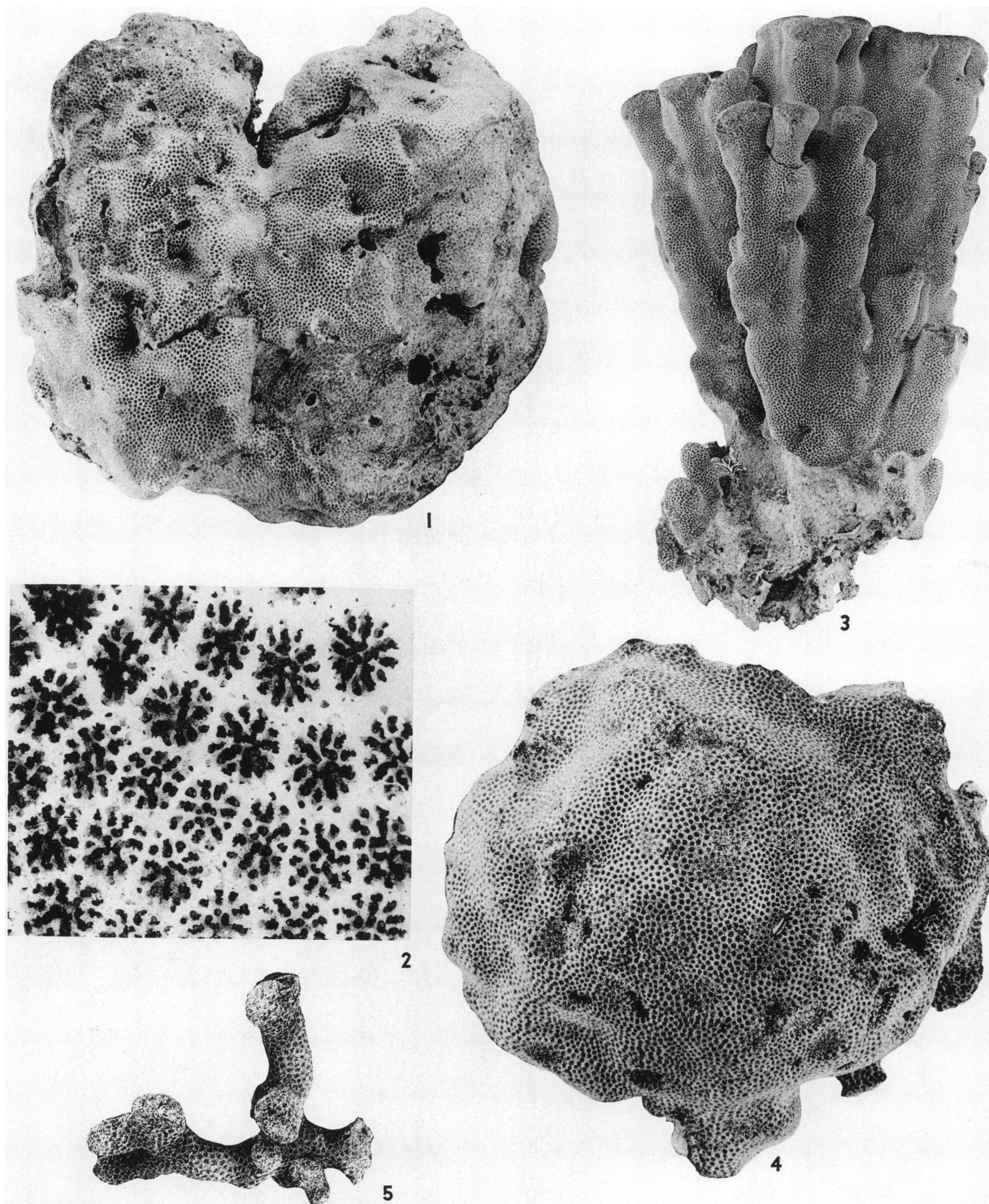


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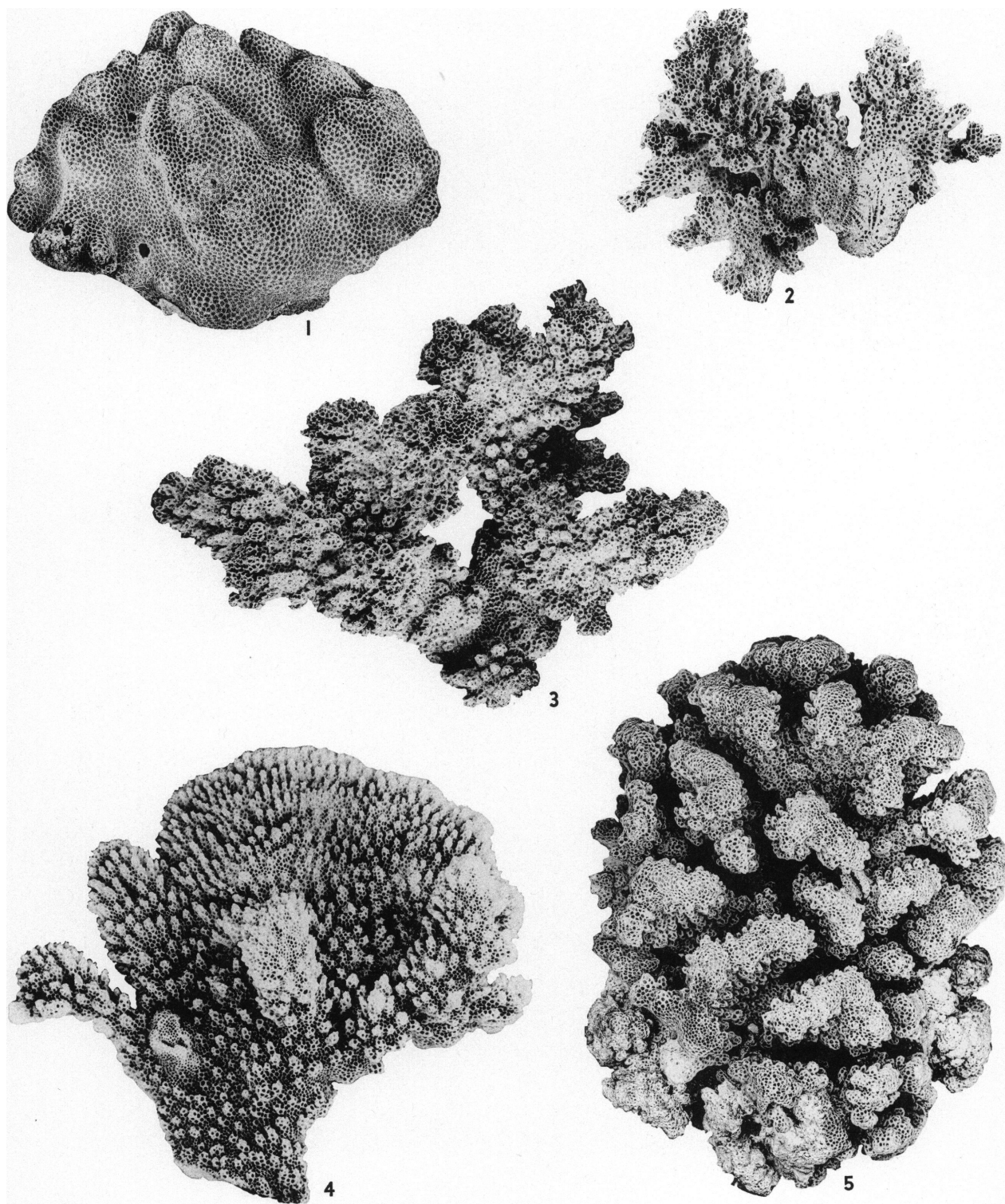
Pleistocene sections exposed in bay south of San Telmo Point. 1. Reef facies composed exclusively of *in situ* *Porites californica*. 2. Slumped portion of reef facies. 3. Pleistocene sediments overlapping darker Salada (?) group conglomerates. 4. Salada (?) group conglomerates overlain by sparsely fossiliferous Holocene deposits. 5. General view of Pleistocene and Holocene exposures. 6. Occurrence of *Ostrea* in the fore-reef facies. All photographs by W. K. Emerson



1. *Pavona clivosa* Verrill, A.M.N.H. No. 3349, El Pulmo Bay, corallum seen from above,  $\times 0.66$ . 2. *Pavona gigantea* Verrill, A.M.N.H. No. 3350, El Pulmo Bay, side view of corallum,  $\times 0.75$ . 3-6. *Porites californica* Verrill. 3, 4. A.M.N.H. No. 3351, Agua Verde Bay, basal and side views of corallum on the snail *Hipponyx*,  $\times 1.1$ . 5, 6. A.M.N.H. No. 3352, Isla Partida, basal and side views of corallum on the snail *Crepidula aculeata* Gmelin,  $\times 1.1$ . 7, 8. *Porites baueri*, new species, A.M.N.H. No. 3348, holotype, María Madre Island, Tres Mariás Islands. 7. Calices,  $\times 11.0$ . 8. Corallum viewed from above,  $\times 0.8$ . Photographs by G. R. Adlington



1, 2. *Porites excavata* Verrill, Peabody Museum Yale College No. 1677, cotype. 1. Corallum, approximately  $\times 0.5$ . 2. Calices,  $\times 12.0$ . 3, 4. *Porites californica* Verrill. 3. A.M.N.H. No. 3353, Agua Verde Bay, side view of reef-facies corallum,  $\times 0.4$ . 4. A.M.N.H. No. 3354, El Pulmo Bay, nodular corallum seen from above,  $\times 0.8$ . 5. *Porites sverdrupi* Durham, A.M.N.H. No. 3355, Isla Partida, 5-7 fathoms, corallum,  $\times 0.8$ . Photographs by G. R. Adlington



1. *Porites californica* Verrill, A.M.N.H. No. 3356, San Carlos Bay, corallum,  $\times 0.7$ . 2. *Pocillopora damicornis* (Linnaeus), A.M.N.H. No. 3357, Los Frailes Bay, corallum,  $\times 0.7$ . 3. *Pocillopora verrucosa* (Ellis and Solander), A.M.N.H. No. 3358, El Pulmo Bay,  $\times 0.7$ . 4. *Pocillopora meandrina* Dana, A.M.N.H. No. 3359, San Gabriel Bay, Espiritu Santo Island,  $\times 0.7$ . 5. *Pocillopora elegans* Dana, A.M.N.H. No. 3360, El Pulmo Bay, corallum seen from above,  $\times 0.6$ . Photographs by G. R. Adlington



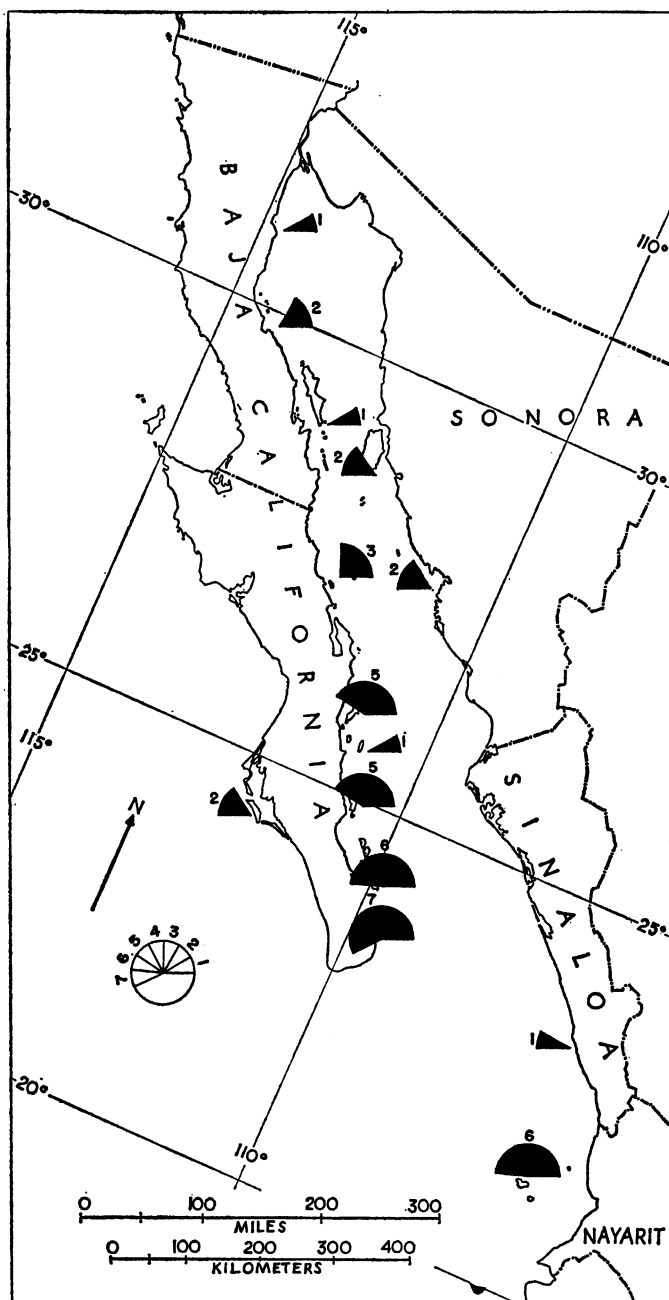


FIG. 12. Numerical distribution of 13 shallow-water species representing the genera *Pocillopora*, *Pavona*, *Psammocora*, *Porites*, *Astrangia*, and *Tubastrea*. The size of the pie-shaped segment is proportional to the number of species (also given numerically) present at various localities.

The relationships of the Gulf of California coral fauna to that of the Panamic faunal province as well as the northern Pacific and other areas have been reconsidered as a result of the systematic studies reported on here. In this respect it is interesting to note that Durham and Barnard (1952) considered 94 species of corals from the eastern Pacific, 34 of which occurred in the Gulf of California. In table 3, the total number of species is re-

duced to 77, 26 of which are found in the Gulf of California. In many respects this is confirmation of Durham's statement (1947, p. 5), "Except for deep water corals it is believed that the Gulf of California fauna is now rather well known." It is almost certain that this number of species will be further reduced, as our knowledge of the faunas to the south of the Gulf of California is increased, particularly in the case of the shallow-water species.

TABLE 3  
DISTRIBUTION OF GULF OF CALIFORNIA SPECIES

	Western Pacific	Hawaiian Islands	Clarion, Socorro Islands	Clipperton Island	Gulf of California	Tres Marias Islands	Western Coast of Mexico	Galapagos Islands	Gulf of Panama	Western Coast of Baja California	California Coast
<i>Psammocora brighami</i>	—	x	—	—	x	—	—	—	—	—	—
<i>Psammocora stellata</i>	x	x	—	—	x	x	—	x	x	—	—
<i>Pocillopora damicornis</i>	x	x	—	—	x	—	x	x	x	—	—
<i>Pocillopora elegans</i>	x	x	x	—	x	x	x	x	—	x	—
<i>Pocillopora verrucosa</i>	x	x	?	x	x	x	—	—	—	—	—
<i>Pocillopora meandrina</i>	x	x	—	x	x	x	—	—	—	—	—
<i>Montipora fragosa</i>	—	—	—	—	x	—	—	—	—	—	—
<i>Pavona clivosa</i>	—	—	—	—	x	—	—	x	x	x	—
<i>Pavona gigantea</i>	—	—	—	x	x	—	x	—	x	—	—
<i>Cycloseris elegans</i>	—	—	x	—	x	x	—	—	—	—	—
<i>Cycloseris mexicana</i>	—	—	—	—	x	x	x	x	x	x	—
<i>Astrangia haimeii</i>	—	—	—	—	x	—	x	—	x	x	x
<i>Astrangia costata</i>	—	—	—	—	x	—	—	—	x	—	—
<i>Astrangia californica</i>	—	—	—	—	x	—	—	—	—	—	—
<i>Astrangia conferta</i>	—	—	—	—	x	—	x	—	—	—	—
<i>Phyllangia dispersa</i>	—	—	—	—	x	—	—	—	x	—	—
<i>Porites baueri</i>	—	—	—	—	—	x	—	—	—	—	—
<i>Porites californica</i>	—	—	—	—	x	x	—	—	x	x	—
<i>Coenocyathus bowersi</i>	—	—	—	—	x	—	—	—	—	—	x
<i>Bathocyathus consagensis</i>	—	—	—	—	x	—	—	—	—	—	—
<i>Ceratotrochus franciscana</i>	—	—	—	—	x	—	—	—	—	—	—
<i>Heterocyathus aequicostatus</i>	x	—	—	—	x	—	—	—	—	—	—
<i>Paracyathus tiburonensis</i>	—	—	—	—	x	—	—	—	—	—	—
<i>Balanophyllia tiburonensis</i>	—	—	—	—	x	—	—	—	x	x	—
<i>Dendrophyllia cortezi</i>	—	—	—	—	x	—	—	—	—	—	x
<i>Endopachys vaughani</i>	—	—	—	—	x	—	—	x	—	—	—
<i>Tubastrea aurea</i>	x	x	—	—	x	x	—	—	x	x	—

TABLE 4

COMPARATIVE DISTRIBUTION OF EASTERN PACIFIC SPECIES OF REEF- AND NON-REEF-BUILDING CORALS EXPRESSED IN NUMBERS OF SPECIES AND PERCENTAGE COMPOSITION OF THE TOTAL FAUNA

	Reef Corals (22 species)	Non-Reef Corals (55 species)
Northern Pacific	—	16 (29.1)
Northern Pacific and Gulf	—	1 (1.8)
Gulf of California	1 (4.5)	4 (7.3)
Gulf and Panamic	5 (22.7)	7 (12.7)
Panamic	3 (13.6)	18 (32.7)
North Pacific, Gulf, and Panamic	—	2 (3.6)
Panamic and Indo-Pacific	4 (18.2)	—
Gulf and Indo-Pacific	1 (4.5)	1 (1.8)
Gulf, Panamic, and Indo-Pacific	6 (27.3)	1 (1.8)
Panamic and West Indian	2 (9.1)	2 (3.6)
North Pacific and West Indian	—	—
Gulf and West Indian	—	—
Cosmopolitan	—	3 (5.5)

Table 4 cross-indexes the relationships of the eastern Pacific species, which have been divided into two groups, the reef-forming corals (hermatypic) and ahermatypics. This has the effect of eliminating from the shallow-water group the astrangiid corals, which do not have the thermal limitations of the hermatypic genera. It is clearly apparent that the Gulf of California, Panamic, and Indo-Pacific faunas are closely related, and it is impossible to consider the Gulf of California a separate province on the basis of corals alone. The sole "endemic" species in the Gulf of California is the problematical *Montipora fragosa*, known from a single, poorly documented specimen. The number of "endemic" species of Panamic corals will be reduced as study of these faunas increases.

Among the other corals the degree of endemism in the north Pacific, Gulf, and Panamic regions is more pronounced but may in many instances represent inadequate sampling of the fauna. Despite this tendency there is an apparent relationship between the deeper-water corals of the Panamic region and those of the Gulf region, which is sufficiently great to make unnecessary any distinctions between the two regions.

The coral faunas of the Gulf of California may then be said to represent a modified Panamic fauna, in which the number of spe-

cies is reduced and the specific composition somewhat altered, particularly in the case of the deeper-water corals. With further collecting along the western coast of Central America there will undoubtedly be modifications of our knowledge of the faunas that will strengthen this concept. The division between the north Pacific fauna and the Panamic fauna is, however, sharp. The boundary between them lies near the southern tip of Baja California. Durham (1947) suggested that Cape San Lucas be considered as the line of demarcation, calling attention to the fact that during the Pleistocene *Porites californica* had extended around the Cape to Magdalena Bay. It is known now, as a result of the Puritan Expedition, that *Porites californica* is present today in Magdalena Bay. It would seem quite probable that other bays to the north might contain elements of the Panamic subtropical fauna, making the establishment of a sharp division between these faunas undesirable. A generalized statement that the boundary between subtropical and north temperate faunas lies somewhere along the southern peninsula of Baja California is more correct.

The relationships between the eastern tropical Pacific and the main mass of the tropical Indo-Pacific region are of great interest. Distribution records for the shallow-water corals

show that the offshore islands, including the Galapagos, Clipperton, Socorro, and Clarion Islands, have a fauna, in so far as is known, that is the same as or contains more Indo-Pacific elements than the Panamic fauna. This should be compared with the statements of Ekman (1953, p. 45). The effect of the Eastern Pacific Barrier (Ekman, 1953, p. 72) has apparently been negligible in so far as the corals are concerned. Distributional data based on Verrill's work would have showed a high degree of isolation, but more recent work, particularly that of Durham and Barnard (1952) and studies of the fauna of Clipperton Island (Hertlein and Emerson, 1957) have shown that, for the corals at least, the relationships with the Indo-Pacific are quite close. Wells (1954) records six genera of Indo-Pacific corals from the Panama region, all among the most widely distributed. As a result of the study of the corals collected during the Puritan Expedition, it has been found that not only are there genera in common, but there is a strong relationship between species. In so far as our knowledge of systematics permits, there are apparently many species of the more hardy scleractinian corals that have a distribution covering the entire longitudinal expanse of the Pacific Ocean. The distributional mechanism for the corals is known to be a relatively long larval life, one that would permit long voyages of transplantation, but, unfortunately, many of the physiological details of this mechanism are unknown to us at the present time.

What then of the supposed close relationship between tropical western Atlantic and tropical eastern Pacific faunas? Among the reef corals, the only similarities are in the common presence of the genus *Porites* in the two areas and two poor records of *Solenastrea* and *Agaricia*. *Porites* are of little significance, because the genus is circumtropical in distribution. Table 4 shows the relationships of the faunas of the Gulf of California with those of other areas. Wells (1954) notes that the only reef coral remaining in the Indo-Pacific region that is characteristic of the Tethyan fauna and the tropical Atlantic is *Siderastrea*, now confined to the Red Sea and the Atlantic.

If the eastern Pacific reef-coral genera are to be derived from the Tethyan fauna by migration from the West Indian region, then this migration must have occurred during the early Miocene, for it is during the Miocene that the greatest change in the West Indian faunas occurred. Although all the genera of Indo-Pacific corals present on the western shores of Central America are represented in the lower Tertiary fossil faunas of the West Indies, evidence for or against such a migration is completely lacking. The fossil record of the tropical region, such as it is, is highly inconclusive and indicative only of Pliocene migrations. Until such areas as the western shore of Mexico, and Central America, have been more completely explored and collected, little can be said concerning this portion of the history.

The absence of further information on the Pliocene of the Tres Marias Islands is a great hindrance, for the record of *Solenastrea* from that area is very suggestive but not conclusive. This area should become the focal point for new investigations. If the records of *Agaricia* and *Solenastrea* reported from the Panamic region by Durham and Barnard (1952) stand up to further collecting, and these genera, and probably others, are found living in the tropical eastern Pacific, then the history of the Imperial formation coral fauna will be completed. These genera are apparently so restricted in their ecology that they have not penetrated the northern marginal regions.

As indicated in table 4, the relationships of the Gulf of California corals are strongest with the Panamic fauna and that of the Indo-Pacific. In comparison with the deeper-water corals, the absence of strong ties with the West Indian region is striking. Several species of corals from deeper waters have been described as identical (Durham, 1947; Durham and Barnard, 1952), and, with further collecting and better comparisons with species from the West Indies and the Gulf of Mexico, it is probable that even closer affinities will be shown. To some extent this is a reflection of the generally wide distribution of deeper-water coral species.

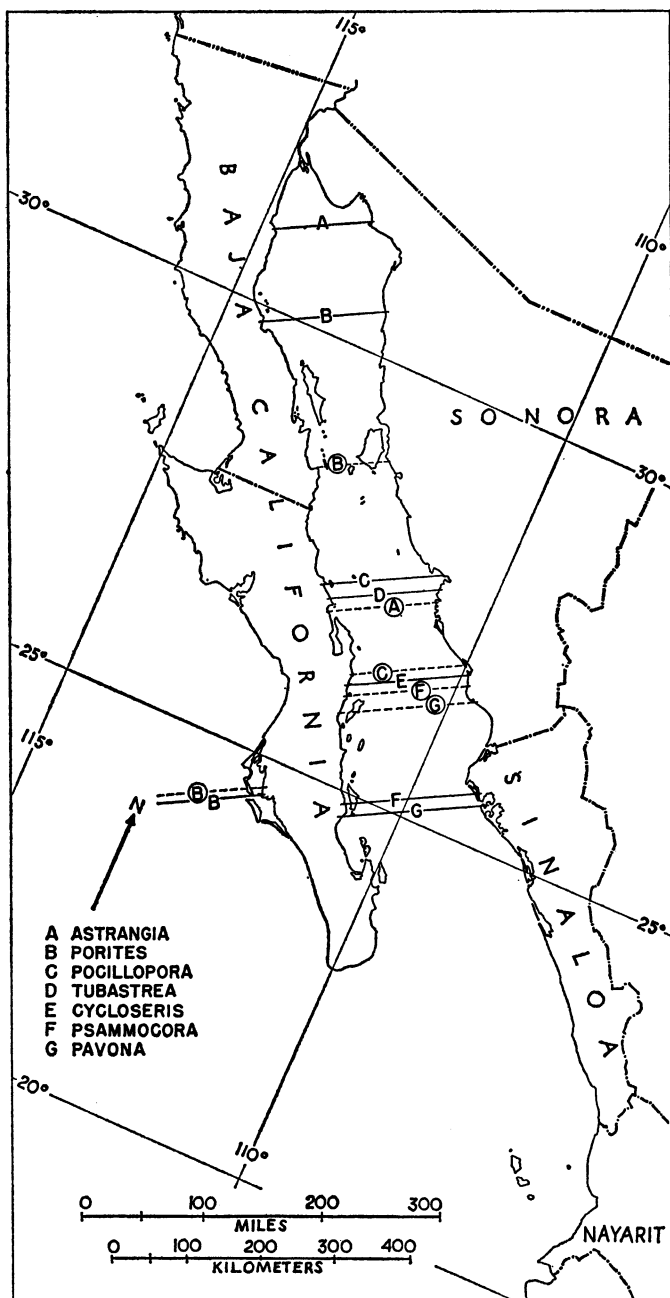


FIG. 13. Comparative ranges for shallow-water genera in the Pleistocene and present-day Gulf of California region. Letters refer to northernmost occurrences of these genera in the Gulf today, while the circled letters are the northernmost occurrences in Pleistocene exposures.

## SYSTEMATIC DESCRIPTIONS

THE CLASSIFICATION of the Scleractinia followed here is that of Wells (1956). Synonymies have been restricted as much as possible, only the latest complete one found acceptable being cited in most instances. Most species have been adequately described and figured in other accessible papers, and only those descriptions necessary for clarification are given here.

Occurrences are listed in as complete a fashion as possible. The initial references are to the "Puritan" collections and are followed by station numbers (in parentheses) that correspond to the numbers given in Emerson (1958, pp. 16-25) in the general account of the expedition. Other localities for the species are followed by a citation, the complete reference for which may be found in the bibliography. Species not collected by the Puritan Expedition, but which are known from the Gulf of California, are included for completeness.

### CLASS ANTHOZOA EHRENBERG, 1834

### SUBCLASS ZOANTHARIA DE BLAINVILLE, 1830

### ORDER SCLERACTINIA BOURNE, 1900

### SUBORDER ASTROCOENINA VAUGHAN AND WELLS, 1943

### FAMILY THAMNASTERIIDAE VAUGHAN AND WELLS, 1943

### GENUS PSAMMOCORA DANA, 1846

### SUBGENUS STEPHANARIA VERRILL, 1867

### *Psammocora* (*Stephanaria*) *brighami* Vaughan, 1907

*Psammocora* (*Stephanaria*) *brighami* Vaughan, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 29, pl. 2, figs. 7a, 7b. Synonymy.

This species was not taken by the Puritan Expedition and apparently is not common.

OCCURRENCE: San Lorenzo Channel, Gulf of California (Durham and Barnard, 1952). Oahu, Hawaii (Vaughan, 1907).

### *Psammocora* (*Stephanaria*) *stellata* (Verrill), 1866

*Psammocora* (*Stephanaria*) *stellata* (Verrill), DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 29, pl. 2, fig. 8. Synonymy.

Three suites of this species were collected. Those taken alive at San Francisco Island indicate the probability that this species may be overlooked by the casual collector, as the specimens were found closely encrusting in crevices and joint planes of rocks at depths of from 6 to 10 feet. The color of the living coral ranges from light to dark brown and does not contrast with the usual background. Specimens from the Tres Mariás Islands were taken dead and slightly worn.

OCCURRENCE: Cleofas Island, Tres Mariás (61); María Madre Island, Tres Mariás (72), San Francisco Island, Gulf of California (111). Pearl Islands, Panama; La Paz, Gulf of California (Verrill, 1866). Panama; Molokai and Oahu, Hawaiian Islands (Vaughan, 1907). Honolulu, Hawaiian Islands; Kandavu, Fiji (Quelch, 1886). Cocos Island, Costa Rica; Galapagos Islands; Bahía Honda, Panama; La Libertad, Ecuador (Durham and Barnard, 1952). Pleistocene: Coronados Island (Durham, 1947).

### FAMILY POCILLOPORIDAE GRAY, 1842

### GENUS POCILLOPORA LAMARCK, 1818

Vaughan (1907, pp. 84-86) reviewed the Pacific species of this genus with emphasis on those found in the Hawaiian Islands. Although the systematics developed as a result of his study are not currently used, the scheme he utilized is the basis for more recent thoughts on the discrimination of species in the genus *Pocillopora*. According to the system developed by Vaughan and modified by Wells (1957; MSS notes) and others, the species of *Pocillopora* may be grouped broadly as follows: (1) those species with septa and columella that are conspicuous, such as *P. eydouxi* Milne-Edwards and Haime; and (2) those in which the septa and columella are inconspicuous, such as *P. elegans* Dana. Within each of these groups there is a morphological gradient from speci-

mens with finely divided coralla to those with bladed or meandrine branches. Vaughan (1907, p. 100) noted, "*P. damicornis*, *danae*, *verrucosa*, *meandrina* and *elegans* form a series so indistinctly broken that one is led to suspect that they are really continuous." The validity of growth form as a taxonomic character is always subject to scrutiny, as this is one aspect of colonial coralla that has often been convincingly shown to be affected by ecologic factors, particularly position (Vaughan, 1918; Jones, 1907, 1910). The task of reevaluation of the species of this genus is beyond the scope of this study and requires not only the review of large collections but careful field study for the degree of phenotypism present in such characters to be determined.

Important in the definition of species of *Pocillopora* are the height and character of the verrucae, the appearance of the terminal ends of the branches, and, to some extent, the size and arrangement of the calices.

*Pocillopora* is possibly second in importance only to *Porites* in the Gulf of California. For that reason the factors of distribution, ecology, and faunal relationships have been given considerable attention, and closely compared with those of other species described from the Pacific area. The close resemblance of the large suite of specimens from the Gulf of California (nearly 200 specimens collected) to Indo-Pacific species is striking. An examination of specimens from many areas in the Pacific in the collections of the American Museum of Natural History, the United States National Museum, the Peabody Museum, and at Cornell University has strengthened this impression and forms the basis for the following discussion. The relationships below may distress the proponents of closer specific determination and also certain schools of zoogeographic thought. The eventual recognition of subspecies is quite probable, but must await the time when understanding of speciation in this group has found a more satisfactory basis.

Verrill described the following species of *Pocillopora* from the Gulf of California and adjacent areas: *P. capitata* (1864) from Acapulco, Mexico, and later the Socorro Islands, Pearl Islands, and La Paz, Gulf of California; *P. lacera* (1869) from the Pearl Islands,

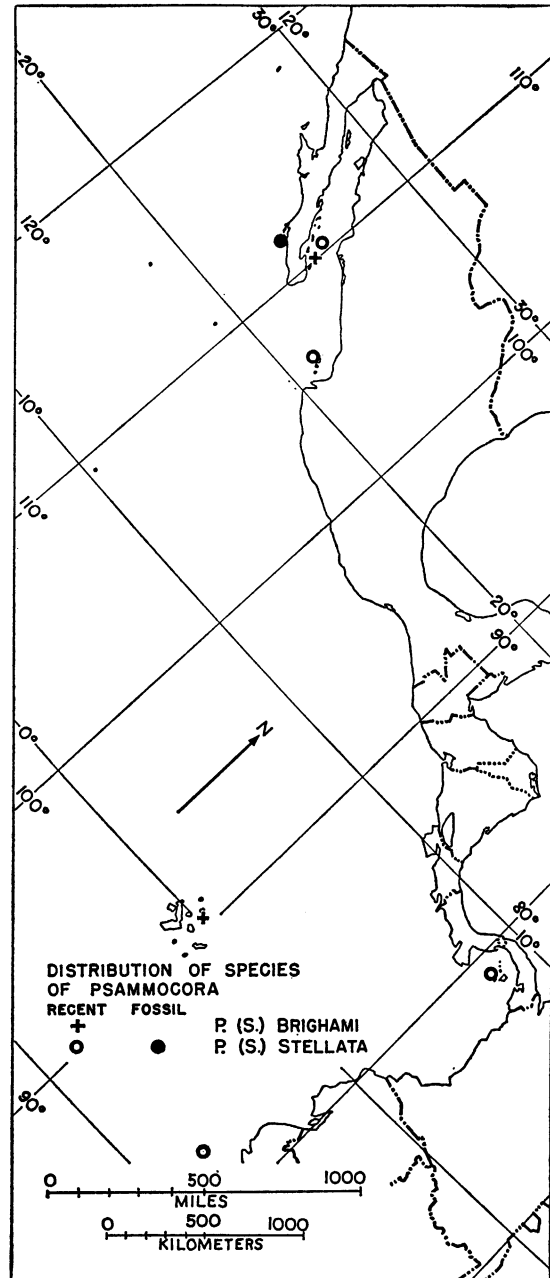


FIG. 14. Pleistocene and Recent distribution of species of *Psammocora* in the eastern Pacific.

Panama, and Acajutla; *P. capitata* var. *robusta* (1868-1870), La Paz, Gulf of California; *P. capitata* var. *pumila* (1870), La Paz, Gulf of California. Later, Vaughan (1906) cited *P. lacera* Verrill from Tobaquilla Island, Bay of Panama. Palmer (1928) described *P.*

*palmata* from Oaxaca, Mexico. Steinbeck and Ricketts recorded *P. capitata* Verrill from the Pulmo reef tract (1941, pp. 76, 334, pl. 21, fig. 3).

Durham (1947) reviewed Verrill's specimens, selected lectotypes, and figured many species for the first time. He retained the names *P. capitata*, *P. porosa*, and *P. robusta*, considering *P. pumila* and *P. palmata* as synonyms of *P. robusta*. *Pocillopora robusta* was the only species he recorded from new material from the Gulf of California. Durham and Barnard (1952) followed this general scheme, again with *P. robusta* as the only species of *Pocillopora* represented from the Gulf of California in the new collections. Significantly, however, *P. damicornis* var. *cespitosa* Dana was recorded there for the first time from the Galapagos and Secas Islands. Durham (in Hertlein and Emerson, 1957) recorded *Pocillopora meandrina nobilis* Verrill, *P. verrucosa* Ellis and Solander, and *Pocillopora* sp. [sic] from Clipperton Island.

***Pocillopora damicornis* (Linnaeus), 1758**

Plate 34, figure 2

*Pocillopora lacera* VERRILL, 1869, Proc. Essex Inst., vol. 6, p. 100; 1870, Trans. Connecticut Acad. Arts and Sci., vol. 1, p. 523. VAUGHAN, 1906, Bull. Mus. Comp. Zool. Harvard, vol. 50, p. 61. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 20, pl. 1, fig. 4.

*Pocillopora damicornis* (Linnaeus), WELLS, 1954, Prof. Paper U. S. Geol. Surv., no. 260-I, p. 412, pl. 99, fig. 2. Synonymy.

Not *Pocillopora damicornis* var. *cespitosa* Dana, Durham and Barnard, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 20, pl. 1, figs. 3a, 3b, 3c.

Three specimens in the "Puritan" collections can be referred to this species in addition to many field records of its occurrence. All have in common the strongly lacerate branching characteristic of this species, most verrucae being sufficiently elongated to be termed branches. Calice diameter is variable, with a range of 0.4 to 1.0 mm. observed in the various specimens illustrated by Vaughan (1907, pl. 10, figs. 1, 2) as *P. cespitosa* typical and by Vaughan (1918, pl. 21, figs. 2, 3) as *P. damicornis* var. *cespitosa*.

Two of these specimens represent a deep-water facies, relative to the distribution of *Pocillopora*, from about 20 feet in depth. One specimen taken from San Gabriel Bay is a near-shore specimen and not collected in conjunction with the reef facies there.

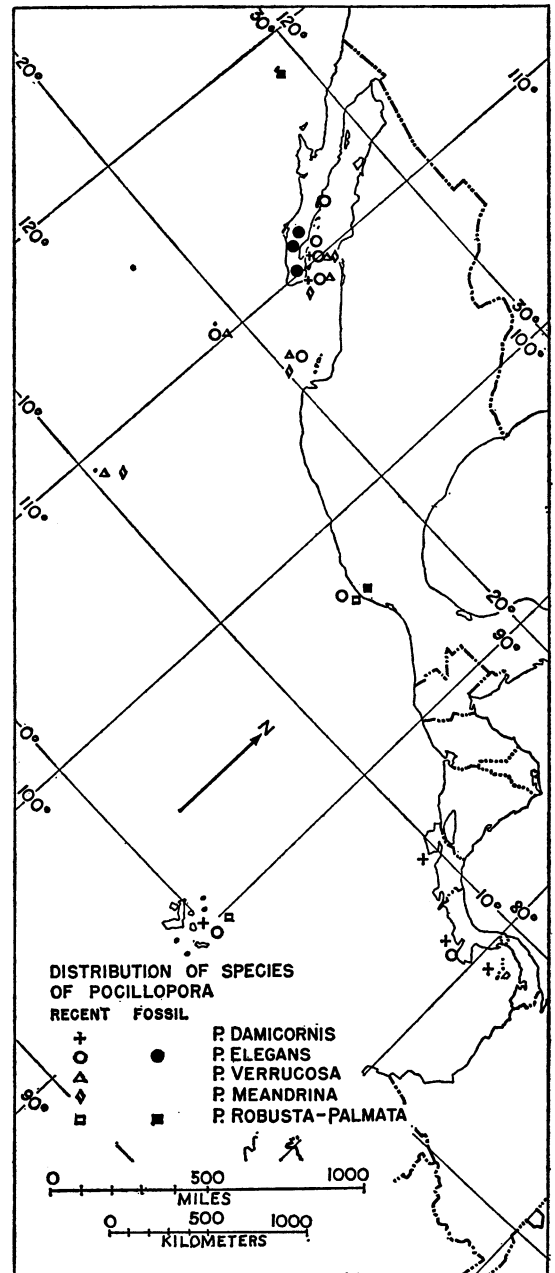


FIG. 15. Pleistocene and Recent distribution of species of *Pocillopora* in the eastern Pacific.

Included in the synonymy is *P. lacera* Verrill as figured by Durham and Barnard, as it is clearly apparent that the specimen is one of the variations of *P. damicornis*. The figured specimen referred to *P. damicornis* var. *cespitosa* (Durham and Barnard, 1952, p. 20, pl. 1, figs. 3a, 3b, 3c) is not included.

**OCCURRENCE:** Los Frailes, Baja California (85); El Pulmo Bay, Baja California (87); Cerralvo Island, Gulf of California (90); off Bonanza Point, Espíritu Santo Island, Gulf of California (94); San Gabriel Bay, Espíritu Santo Island, Gulf of California (98); Ballena Island, Gulf of California (102). Port Guatulco, Mexico; Afuera Island, Panama; Port Parker, Costa Rica; Uvita Bay, Costa Rica; Jasper Island, Gulf of Nicoya, Costa Rica ("Zaca" Expedition collection). Galapagos Islands; Tabago Island, Panama (Durham and Barnard, 1952). Eastern Indian Ocean eastward to the Hawaiian Islands (Wells, 1954).

***Pocillopora elegans* Dana, 1846**

Plate 34, figure 5

*Pocillopora elegans* Dana, WELLS, 1954, Prof. Paper U. S. Geol. Surv., no. 260-I, p. 412, pl. 95, fig. 2. Synonymy.

*Pocillopora capitata* VERRILL, 1864, Bull. Mus. Comp. Zool. Harvard, vol. 1, p. 60; 1869, Proc. Essex Inst., vol. 6, p. 99; 1870, Trans. Connecticut Acad. Arts and Sci., vol. 1, pp. 520, 521. DURHAM, 1947, Mem. Geol. Soc. America, vol. 20, p. 16, pl. 7, fig. 3, pl. 8, fig. 4.

*Pocillopora capitata* var. *robusta* VERRILL, 1870, Trans. Connecticut Acad. Arts and Sci., vol. 1, p. 522. PALMER, 1928, Proc. Amer. Phil. Soc., vol. 67, p. 31.

*Pocillopora robusta* Verrill, DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 17. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, p. 26, pl. 1, figs. 5, 5a.

*Pocillopora capitata* var. *pumila* VERRILL, 1870, Trans. Connecticut Acad. Arts and Sci., vol. 1, p. 522.

*Pocillopora damicornis* var. *cespitosa* Dana, DURHAM AND BARNARD, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 20, pl. 1, figs. 3a, 3b, 3c.

Not *Pocillopora palmata* Palmer, 1928, Proc. Amer. Phil. Soc., vol. 67, p. 31, pl. 2, figs. 2, 3; pl. 3, fig. 1. Durham, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 17.

In order to clarify the situation in regard to the identity of specimens assigned to this species, large numbers of specimens were examined, including the types of Verrill's species at the Peabody Museum, Yale University. Specimens from the Gulf of California were found to be nearly identical to *P. elegans* in almost every respect. From a typological viewpoint, the specimens differ from the types of *P. elegans* Dana (Peabody Museum) only in the somewhat larger calices of the eastern Pacific specimens together with a tendency for the verrucae of the type of *P. elegans* to be narrower, more obliquely inclined, and somewhat more numerous. These differences between type specimens are not believed to be significant, except perhaps as subspecific criteria. Variation in these characteristics is rather great even in collections from a single locality. A statistical approach to these questions is necessary for the validity of the conclusions drawn here to be determined.

The type specimen of *P. capitata* (Durham, 1947, pl. 8, fig. 4) is quite obviously a member of the species group characterized by obsolete septa and columella, although it has somewhat more lacerate branches than typical *P. elegans*. *Pocillopora robusta* as described by Verrill (1870) and figured by Durham (1947, pl. 7, fig. 1, pl. 8, figs. 3, 6) is characterized by the presence of six, often 12, septa. However, Durham noted that these septa are rudimentary, being composed of a number of nearly horizontal fine spines. The calices figured by Durham which display the septa quite clearly are not typical of the entire specimen. Variation in this character is well displayed in the specimens illustrated by Durham (1947): the lectotype (pl. 8, fig. 6) shows little trace of septa, while a paratype (pl. 8, fig. 3) has more distinct septa and columella.

Durham and Barnard (1952) distinguished four variations of *P. robusta*. All are similar to *P. elegans* in growth form, although the first described has verrucae tending towards the type found in *P. verrucosa*, while the first three variations are described as having prominent septa and columella. Those specimens have not been seen, but it is my intention to separate those forms in which the septa are poorly developed and place them in

*P. elegans*. Examination of those specimens in which septa and columella are well developed may show them to be identical with the common Indo-Pacific species that parallels *P. elegans* in growth form, *P. eydouxi* Milne-Edwards and Haime.

Durham (1947) and Durham and Barnard (1952) synonymized *P. palmata* Palmar with *P. robusta* Verrill, considering the species as an extreme variant of the common Panamic form. Under the interpretation given here, the synonymy is not permissible on two grounds. As illustrated by Palmer (1928, pl. 2, figs. 2, 3, pl. 3, fig. 1) the species apparently has well-developed septa and columella, making comparisons with *P. eydouxi* Milne-Edwards and Haime or *P. woodjonesi* Vaughan necessary. Secondly, if the septa and columella are not developed to the extent to warrant inclusion in that species group, then a more apt comparison can be made with *P. grandis* Gardiner and its associated species.

*Pocillopora elegans* is a common coral in the commerce of Sonora, Mexico, many specimens being utilized in decorative handicrafts exhibited in the shops at Mazatlan and Guaymas. Attempts to localize the source of the coral were usually fruitless, although it is quite apparent from conversations with manufacturers that the coral is taken from areas along the coast south of the latitude of Baja California.

Verrill (1870) and Durham (1947) regarded *P. pumila* as a variety of *P. robusta* (= *P. elegans*), usually a development of broken fragments in the course of their regrowth, or a stunted variety growing in shallow water.

**OCCURRENCE:** San Juanito Island, Tres Mariás Islands (36); off Cleofas Island, Tres Mariás Islands (61, 62); Los Frailes Bay, Baja California (85, 86); El Pulmo Bay, Baja California (87); Ceralvo Island, Gulf of California (90); San Lorenzo Channel, Gulf of California (93); San Gabriel Bay, Espíritu Santo Island, Gulf of California (98); off Ballena Island, Gulf of California (102); Isla Partida, Gulf of California (108); San Francisco Island, Gulf of California (110). Albemarle Island, Galapagos (the American Museum of Natural History collection). Widespread in the Indo-Pacific (Wells, 1954). Pleistocene: El Pulmo, Baja Cali-

fornia; southern Ceralvo Island, Gulf of California; San Telmo, Baja California, Recent: Gulf of California south to Oaxaca, Mexico; Carmen Island (Durham, 1947). Pleistocene: Carmen Island, Gulf of California; Monserrate Island, Gulf of California, San Telmo Point, Baja California (Durham, 1950a).

Records for *P. robusta*: La Paz south to Panama (Verrill, 1868-1870); San Marcos Island, Gulf of California south to Ecuador, Socorro and Galapagos Islands (Durham and Barnard, 1952).

***Pocillopora verrucosa* (Ellis and Solander), 1876**  
Plate 34, figure 3

*Pocillopora verrucosa* (Ellis and Solander), WELLS, 1954, Prof. Paper U. S. Geol. Surv., no. 260-I, p. 413, pl. 98, figs. 5, 6. Synonymy.

*Pocillopora porosa* Verrill, DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 16, pl. 8, fig. 5, pl. 10, fig. 8. Synonymy.

This species is very close to *P. elegans* in general form, except that the summits of the branches usually bear verrucae, but there is a gradation between the two types.

*Pocillopora porosa* Verrill is known only from the type specimens reported from La Paz and an unfigured specimen cited by Durham and Barnard (1952) from the Socorro Islands. The type specimen, which I have seen, seems to belong here.

**OCCURRENCE:** María Madre Island, Tres Mariás Islands (25); San Juanito Island, Tres Mariás Islands (36); Isabel Island (75); Los Frailes Bay, Baja California (86, 87); El Pulmo Bay, Baja California (87); Ceralvo Island, Gulf of California (90); San Lorenzo Channel, Gulf of California (93); San Gabriel Bay, Espíritu Santo Island, Gulf of California (98); Isla Partida, Gulf of California (108). La Paz, Baja California (Verrill, 1869). ?Socorro Islands (Durham and Barnard, 1952). Clipperton Island (Durham, *in* Hertlein and Emerson, 1957). Eastern Indian Ocean eastward to Hawaiian Islands (Wells, 1954).

***Pocillopora meandrina* Dana, 1846**  
Plate 34, figure 4

*Pocillopora meandrina* Dana, VAUGHAN, 1907, Bull. U. S. Natl. Mus., no. 59, p. 97, pl. 14, figs. 3, 4, pl. 22, figs. 1, 1a, 2, 2a, pl. 23. Synonymy.

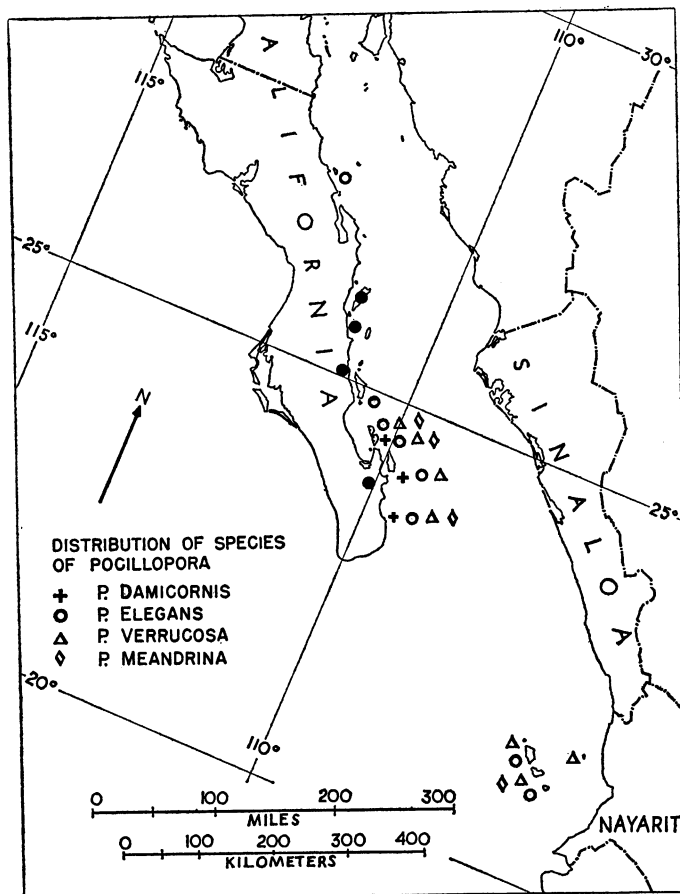


FIG. 16. Pleistocene and Recent distribution of species of *Pocillopora* in the Gulf of California.

VAUGHAN, 1918, Papers Dept. Marine Biol., Carnegie Inst. Washington, vol. 9, p. 78.

As indicated by Vaughan (1918) this species is very closely related to *P. elegans* and *P. verrucosa* and is possibly one of a series of variants. As presently used, the species includes those forms in which the terminal portions of the branches are meandrine, or bladed. I was able to examine one of Dana's specimens of this species at the Peabody Museum (P.M.Y.C. No. 640) and found the same general relationship between specimens from the Gulf of California and the type of *P. nobilis* (= *P. meandrina*) as was found between specimens from the Gulf assigned to *P. elegans* and the type of that species. The verrucae are, in general, slimmer, somewhat more numerous, and are not so steeply inclined in the type of *P. nobilis*. Again it must be cautioned that the variation of those char-

acters mentioned observed in many specimens does not admit separation even on a subspecific level.

OCCURRENCE: María Magdalena Island, Tres Marias Islands (47); Los Frailes Bay, Baja California (85); El Pulmo Bay, Baja California (87); San Gabriel Bay, Espíritu Santo Island, Gulf of California (98); Isla Partida, Gulf of California (108). Indo-Pacific (Vaughan, 1918). Clipperton Island (Durham, in Hertlein and Emerson, 1957). Pulau-Pulau Banda northeastward to Hawaiian and Bonin Islands (Wells, 1954).

#### FAMILY ACROPORIDAE VERRILL, 1902

GENUS *MONTIPORA* QUOY AND GAIMARD, IN DE BLAINVILLE, 1830

#### *Montipora fragosa* Verrill, 1870

*Montipora fragosa* Verrill, DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 18, pl. 6, figs. 3-5. Synonymy.

The only known specimen of this species is the type and represents the only record of this genus in the eastern Pacific. Diligent searching in the southern reaches of the Gulf of California failed to detect additional material. As is the case with many of the species listed by Verrill from La Paz, the occurrence in the Gulf of California must be questioned, for the record is based on the collections of Captain Pedersen, who did not always append locality data with his specimens. Pedersen's shipment of corals to Verrill was made from La Paz, a fact that has generally been cited as the reason for giving this locality to the species in question. However, certain other specimens collected from the Gulf of California by Pedersen bear the label "Gulf of La Paz." Until additional specimens of the species are collected, the record of their occurrence of the species in the Gulf of California must remain in question.

OCCURRENCE: ?La Paz, Baja California (Verrill, 1868-1870).

SUBORDER FUNGIINA VERRILL, 1865

FAMILY AGARICIDAE GRAY, 1847

GENUS PAVONA LAMARCK, 1801

*Pavona clivosa* Verrill, 1869

Plate 32, figure 1

*Pavonia clivosa* VERRILL, 1869, Proc. Boston Soc. Nat. Hist., vol. 12, p. 395.

*Pavona (Pavona) clivosa* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 37, pl. 2, fig. 12. Synonymy.

*Pavona (Pseudocolumnastrea) galapagensis* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 44, pl. 3, figs. 16a, 16b.

The species has not previously been recorded from the Gulf of California and is known to have a much more limited distribution than *P. gigantea*, which follows. Large heads, several feet in diameter, of this species were collected from El Pulmo Bay, where it is an important constituent of the fauna. The most common form of the corallum is one in which upward growth is concentrated into oblong, flange-like projections, which in some instances may be arranged at nearly right angles to form a reticulated structure of some coarseness. The flanges often reach a thick-

ness of an inch or more. The color of the polyps is usually a light brown to buff, but basally may be altered to greens or blues. One

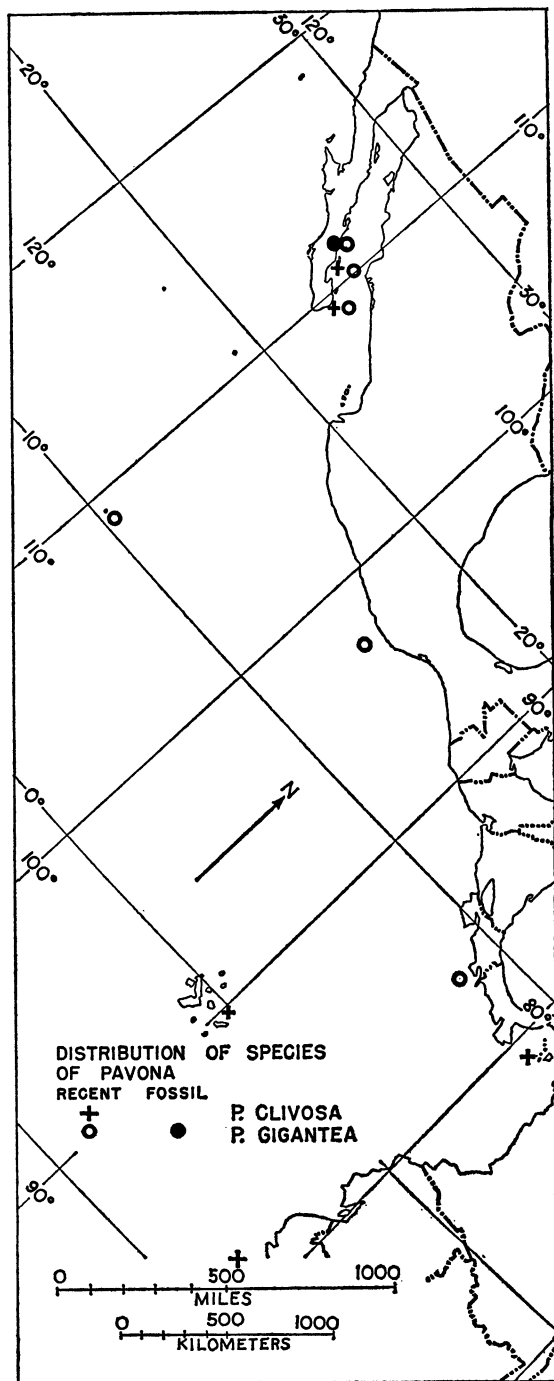


FIG. 17. Pleistocene and Recent distribution of species of *Pavona* in the eastern Pacific.

or two specimens totally blue, or blue-gray, were taken.

The walls of *P. clivosa* are quite variable in their character. The most common type of wall, where present, is thick, but not conspicuously formed of trabeculae. However, on the upper surfaces of coralla, trabecular walls are encountered and are similar in their structure to those of *P. maldivensis* Gardiner. Vaughan (1918, pl. 56, figs. 3, 3a, 3b, 3c) illustrates a specimen referred to this species which possesses typical *P. clavus* walls in one area, and trabecular walls similar to those of *P. maldivensis* in another. Van der Horst (1922) placed *P. maldivensis* of Vaughan in *P. clavus* (Dana), but Wells (1954) considered that *P. maldivensis* (Gardiner) may be related to the subgenus *Pseudocolumnastrea*, characterized by the possession of separate walls and plocoid coralla. The presence of a variety of wall types in a single specimen, both in the case of the specimen illustrated by Vaughan and several from the Gulf of California, renders the usefulness of the subgenus doubtful.

In the specimens from the Gulf of California, the development of synapticular walls unthickened by stereome is often, but not invariably, accompanied by an increase in the lateral ornamentation of septa. No other characters may be correlated directly with the presence of synapticular walls, although specimens that most prominently show the condition are more commonly nodular and lacking in the development of the large, flat, oblong prominences.

*Pavona clivosa* Verrill is closely related to *P. clavus* (Dana) [= *P. duerdeni* Vaughan, 1907] from the Hawaiian Islands and the Indo-Pacific region. The principal differences between the two species are in the relative sizes of the calices and the septal number. *Pavonia clavus* has calices of an average diameter of 1.5 mm. and usually has about two cycles of septa. *Pavona clivosa*, on the other hand, has calices over 2 mm. in diameter, and usually has an appreciable number of third-cycle septa present. There is a tendency for intergradation between the two in the suites of specimens examined, but not to a sufficient degree to permit synonymy.

Durham and Barnard (1952) described *Pavona* (*Pseudocolumnastrea*) *galapagensis*

for four specimens of *Pavona* possessing synapticated walls. In all other characters these specimens are identical with *P. clivosa*, in particular those portions of Gulf of California specimens having synapticate walls.

OCCURRENCE: El Pulmo Bay, Baja California (87); Cerralvo Island, Gulf of California (90); San Francisco Island, Gulf of California (111). Pearl Islands, Panama (Verrill, 1869). La Plata Island, Ecuador; La Libertad, Ecuador; Galapagos Islands (Durham and Barnard, 1952).

***Pavona gigantea* Verrill, 1869**

Plate 32, figure 2

*Pavonia gigantea* VERRILL, 1869, Proc. Boston Soc. Nat. Hist., vol. 12, p. 394.

*Pavona* (*Pavona*) *gigantea* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 43, pl. 3, fig. 14. Synonymy.

The specimens collected by the Puritan Expedition, as well as those figured by Durham (1947, pl. 3, figs. 2, 7) and Durham and Barnard (1952, pl. 3, fig. 14), are nearly identical with a specimen in the Peabody Museum (P.M.Y.C. No. 3855) which bears the original label (presumably Verrill's) "peculiar variety of this [*P. gigantea*] or *P. clivosa*." In this "variety" the calices are much closer together than in the type specimens in the Verrill suite (see Durham, 1947, pl. 3, fig. 1). As all the specimens that have calices closely adpressed are from the Gulf of California, with the exception of the specimen figured by Durham and Barnard from Panama, there is a possibility that the condition may represent a morphological response to differing environments. The supposition must be tested with many more specimens than are available at the present time for its validity to be proved. *Pavona gigantea* and *P. clivosa* are well differentiated, as the former has larger calices, more prominent exsert septa, and generally thicker walls than the latter, and is characterized by a distinct synapticular wall.

*Pavona gigantea* is most common at El Pulmo, where it is an important constituent of the reef community at depths of over 15 feet. Large coralla several feet in diameter were common, the upper portions being always in the form of nodular clumps. The color of the polyps is darker than that of *P.*

*clivosa*, ranging from the dark browns to blue-browns.

Durham and Barnard (1952) referred various fragmentary specimens of agariciid corals to the species *Pavona* cf. *P. explanatula* (Lamarck) and *P.* cf. *P. varians* Verrill. Better specimens are wanted before the presence of a greater variety of *Pavona* from the eastern Pacific can be certain, but their presence is suggestive.

**OCCURRENCE:** El Pulmo Bay, Baja California (87); Cerralvo Island, Gulf of California (90); San Francisco Island, Gulf of California (111); Marquer Bay, Carmen Island, Gulf of California (141). Port Parker, Costa Rica ("Zaca" Expedition collection). Puerto Escondido, Baja California; east side of Carmen Island, Gulf of California; Escondido Bay, Oaxaca (Durham, 1947). Clipper-ton Island, Taboga Island, Panama (Durham and Barnard, 1952). Pleistocene: Salt Flats, Carmen Island, Gulf of California (Durham, 1947).

**FAMILY FUNGIIDAE DANA, 1848**

**GENUS CYCLOSERIS MILNE-EDWARDS  
AND HAIME, 1849**

***Cycloseris elegans* (Verrill), 1870**

*Cycloseris elegans* (Verrill), DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 24, pl. 9, figs. 1-3, 5, 6, 11, 12. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 52, pl. 4, figs. 20a, 20b.

The species does not have a wide distribution. None of the specimens taken by the Puritan Expedition was alive, and it is difficult to determine which of the specimens recorded from the Gulf of California in the literature were taken alive. The bathymetric range of the species seems to be from about 6 to 40 fathoms, based on the scant data available.

**OCCURRENCE:** María Magdalena Island, Tres Marías Islands (52, 58); María Madre Island, Tres Marías Islands (72, 73); Espíritu Santo Island, Gulf of California (96); San Diego Island, Gulf of California (120). La Paz (Verrill, 1868-1870). Clarion Island, Panama; San Lorenzo Channel, Gulf of California (Durham and Barnard, 1952).

***Cycloseris mexicana* Durham, 1947**

*Cycloseris mexicana* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 24, pl. 9, figs. 4, 7-10.

DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 52, pl. 4, fig. 21.

This species is much more widely distributed than the preceding and has been taken

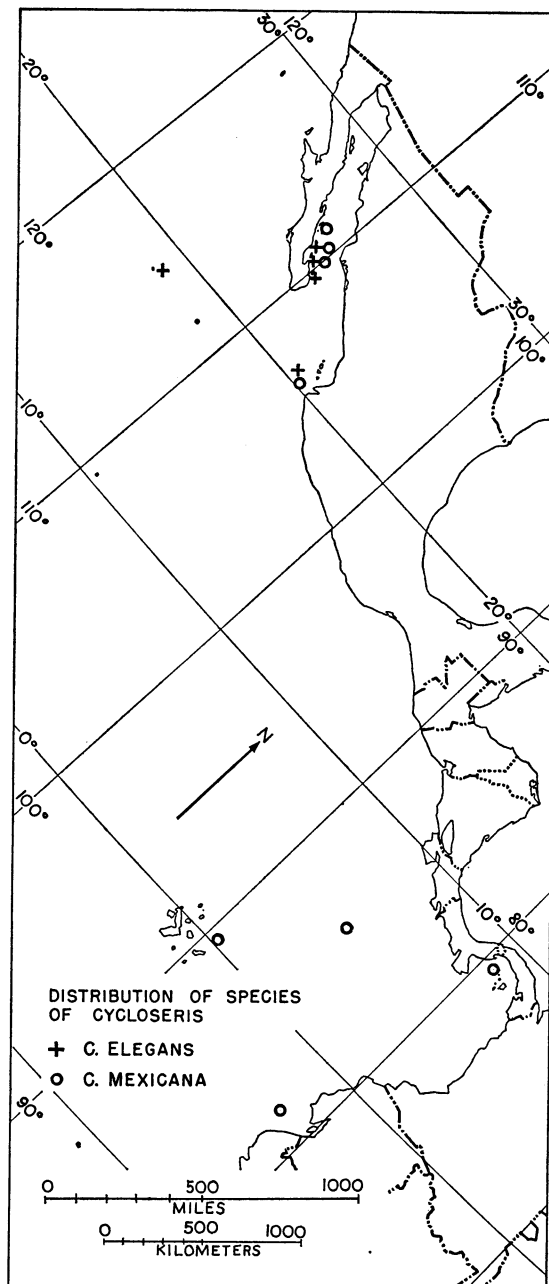


FIG. 18. Present distribution of *Cycloseris* in the eastern Pacific.

alive at most localities. The color of the polyp is generally dark brown. When the species is present, many specimens are taken, usually the greater percentage of the material being fragmentary. In general, the species seems to have the same bathymetric range as the preceding, 6 to 40 fathoms, but is most common in the shallower portions of this range.

**OCCURRENCE:** María Magdalena Island, Tres Marias Islands (58); María Madre Islands, Tres Marias Islands (59, 72, 73); Espíritu Santo Island, Gulf of California (96); Isla Partida, Gulf of California (106, 107); San Diego Island, Gulf of California (120); Salinas Bay, Carmen Island, Gulf of California (132); Coronados Island, Gulf of California (144). Aqua Verde Bay, Baja California; Carmen Island, San Diego Island, Gulf of California; San Evaristo Bay, Mexico (Durham, 1947). La Libertad, Ecuador, north to Port Culebra, Panama; Cocos Island, Costa Rica; Galapagos Islands; Puerto Escondido, Baja California; San Lorenzo Channel, Gulf of California (Durham and Barnard, 1952).

**SUBORDER FAVIINA VAUGHAN AND WELLS, 1943**

**FAMILY RHIZANGIIDAE D'ORBIGNY, 1851**

**GENUS ASTRANGIA MILNE-EDWARDS AND HAIME, 1848**

At the present time more than 20 specific names are in use for the genus *Astrangia* as it occurs along the eastern Pacific shores. Durham (1947, p. 25) stated: "This genus appears to be represented by many species in this area. Unfortunately, most of the species are not represented by abundant material, although for some species there are 15 to 20 specimens from a single locality. All such material from a locality has been constant in its characters, and this constancy has formed the basis for the establishment of the present species. Extensive collecting and study of such material may show that some of the species here described are ecologic variants and the species should be reduced perhaps by a third, but lacking such material it is felt that they are best separated." Six species of *Astrangia* were then described as new, in addition to five previously described by Verrill. Durham and Barnard (1952) named eight additional new species.

Although the "Puritan" collections were not very productive of rhizangiid corals, specimens were recovered from 21 stations (all dredge material), and in most instances numerous individuals were present. Most productive bottoms were those composed of a rubble of shell material and calcareous algae. Attempts to resolve these specimens into the 10 species described from the Gulf of California met with little success. There can be little doubt that the characterization of species in the past has been drawn too finely. Variation within a single corallum is often such that more than one described species is present, if existing definitions are followed. I have found that characters such as depth of calice, height of corallum, shape of corallum, length of paliform lobes, and external nature of the corallum are influenced greatly by the attitude and surroundings of the coralla. Specimens that have been grown over by calcareous algae usually are greatly elongated, the calicular pit is deep, and the costae, where exposed, are minute. Corallites that grow free upon a shell tend to be more closely spaced, shorter, and with a shallower calicular pit. Similarly, there should be no basis for a separation on number of septa or on calicular diameters, as these characters are apparently influenced by the immediate environment. After a critical examination of the "Puritan" collections and many of the types of previously described species of *Astrangia*, it appears to me that there are perhaps five species of this genus found along the eastern Pacific shores. Only one of these is common in the Gulf of California and represented in the "Puritan" collections.

***Astrangia (Astrangia) haime* Verrill, 1866**

*Astrangia haime* VERRILL, 1866, Proc. Boston Soc. Nat. Hist., vol. 10, p. 330; 1870, Trans. Connecticut Acad. Arts and Sci., vol. 1, p. 526, pl. 9, figs. 6, 6a. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 71, pl. 6, fig. 30.

*Astrangia (Astrangia) caboensis* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 26, pl. 4, figs. 1, 2.

*Astrangia (Astrangia) conceptionensis* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 26, pl. 4, fig. 5. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the Univer-

sity of Southern California, vol. 16, no. 1, p. 62, pl. 5, fig. 26.

*Astrangia (Astrangia) concinna* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 62, pl. 5, figs. 25a, 25b. Synonymy.

*Astrangia (Astrangia) coronadoensis* Durham, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 63, pl. 7, fig. 35. Synonymy.

*Astrangia (Astrangia) cortezi* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 68, p. 5, figs. 28a, 28b.

*Astrangia (Astrangia) hancocki* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 72, pl. 6, fig. 31.

*Astrangia (Astrangia) lajollaensis* Durham, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 74, pl. 7, fig. 34. Synonymy.

?*Astrangia oaxacensis* PALMER, 1928, Proc. Amer. Phil. Soc., vol. 58, p. 29, pl. 3, fig. 2. DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 29.

*Astrangia (Astrangia) pedersenii* Verrill, DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 29, pl. 4, fig. 6. Synonymy.

*Astrangia (Astrangia) pulchella* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 75, pl. 7, figs. 36a, 36b. Synonymy.

*Astrangia (Astrangia) sanfelipensis* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 76, pl. 7, figs. 37a, 37b, 37c.

*Astrangia (Astrangia) santelmoensis* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 30, pl. 5, figs. 1, 2.

Corallum usually encrusting but may become arborescent in larger colonies. Encrusting forms vary from radiating groups of corallites (usually found on clean surfaces) to diffuse masses (usually embedded in a mass of Bryozoa or coralline algae). Individual corallites vary in shape from ceratoid to cylindrical, young individuals tending towards the trochoid while larger or longer ones are more cylindrical. Walls of the corallites are usually thin and, where naked, costate. Costae correspond to the septa and are generally al-

ternate in width, and are covered by scattered granulations.

Septa usually in three complete cycles, with portions of the fourth cycle present. Some large corallites may have four complete cycles, with portions of the fifth cycle present. Septa slightly exsert, those of the first and septa adjacent to them more so. From a rounded top, the septa slope evenly inward towards a narrow papillose columella. Rate of descent of septa proportional to the depth of the corallite. Dentations on the proximal margins of the septa increase in size towards the columella and merge with the papilli of the columella. The last two to five dentations of the septa may become sufficiently distinct to be classed as paliform lobes. More cylindrical corallites have a greater calicular depth and often have the most proximal dentations drawn out to long, rod-like, paliform lobes. Lateral edges of septa with scattered granulations grading to dense spinose granulations. Width of septa variable, usually thinner than septal interspaces. Various combinations of septal granulation and septal widths produce different degrees of calice "openness."

Height of corallites and depth of calice are dependent on circumstances of growth. Diameters of corallites range from 2.5 to 5.5 mm.

My interpretation of the *Astrangia* "problem" is obviously different from that stated by Durham and Barnard (1952, p. 4): "The large number of the species of the genus *Astrangia* recognized, raises some doubt as to the validity of the specific criteria used in determining them. For this reason they should be restudied when more material is available. However, it is to be noted that all of the specimens from any single locality appear to be moderately restricted in the individual variation present, thus tending to confirm the limited specific variation recognized. In explanation of the large number of species it may be suggested that possibly conditions in the eastern Pacific are highly favorable to this genus, and that the planulae may have a very short motile stage, with the consequent development of numerous local endemic species." In view of the generally recognized plasticity of corals in response to environmental influences, I am more inclined to an interpretation of local phenotypism. Observa-

tions on the materials collected by the Puritan Expedition indicate that greater variability is present among the *Astrangia* than previously recognized in this area.

According to the present definition of *Astrangia haimeii*, the species is primarily characterized by a papillose columella and by septa with dentate margins which blend with the columella. This contrasts with a second group of species which includes the following: *Astrangia equatorialis* Durham and Barnard, *A. gardnerensis* Durham and Barnard, *A. howardi* Durham and Barnard, *A. browni* Palmer, *A. costata* Verrill, and *A. californica* Durham and Barnard. These species possess a columella that is papillose on the surface but is of a more spongy texture and does not merge with the dentations of the septa. *Astrangia browni* Palmer, based on illustrations given by Palmer (1928, pl. 1, fig. 1), and *A. gardnerensis* Durham and Barnard definitely show a tendency towards the *A. haimeii* type of columella.

*Astrangia hondaensis* Durham and Barnard seems to stand alone, although it may ultimately prove to be a member of the *A. haimeii* group. It seems to be sharply differentiated from other species by having unusually tall pali which are formed as curled laths and appear to be flat topped. I have examined only the type; additional specimens demonstrate the variability of the species.

*Astrangia tangolaensis* Durham may be a worn specimen of the *Astrangia californica* type, but, as characterized by Durham (1947, p. 30), it is unique in the absence of defined dentations and the lack of paliform lobes. The columella is of the *A. californica* group, having pronounced papilli.

*Astrangia dentata* Verrill, as represented by the cotypes, is unusual, the first- and second-cycle septa being conspicuously non-dentate until they reach the bottom of the calice. The only similar species is *A. pedersenii* Verrill in which the first- and second-cycle septa are more minutely dentate than those of the higher cycles.

NOTES ON DISTRIBUTION: *Astrangia haimeii* as here defined is found from Panama northward to the southern California coast. It seems to be much less common in the southern portions of the Gulf of California, where it is known only from La Paz and the Cape

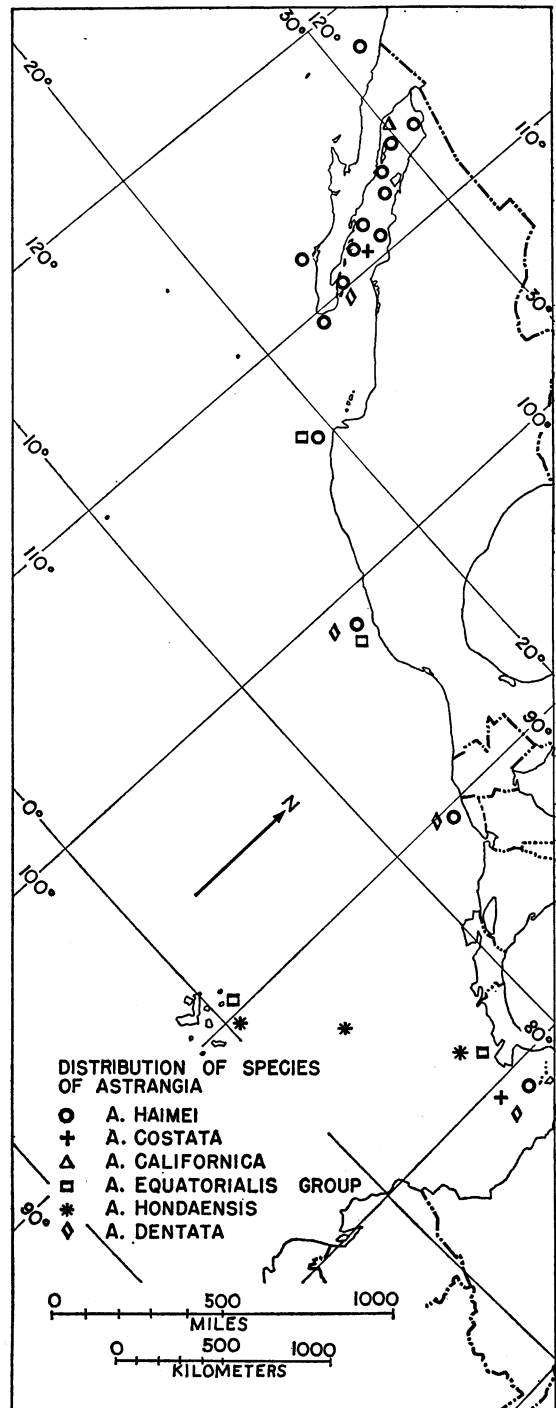


FIG. 19. Distribution of species of *Astrangia* in the eastern Pacific.

region (*A. caboensis*, *A. conceptionensis*).

The group of species including *A. equa-*

*torialis* (see above) is mainly distributed about the Galapagos Islands and the Bay of Panama. However, Durham has recognized *A. costata* from Carmen Island, and Durham and Barnard described *A. californica* from Gonzaga Bay, Baja California. Aside from these, the only astrangiid found in the Gulf of California is *A. haimeii*.

**OCCURRENCE:** Santa Margarita Island (24); Espíritu Santo Island, Gulf of California (96); San José Island, Gulf of California (117); Salinas Bay, Carmen Island, Gulf of California (131, 132); Puerto Escondido, Baja California (139); Coronados Island, Gulf of California (144); San Marcos Island, Gulf of California (151); south end, Tiburón Island, Gulf of California (159, 160, 161, 162); San Esteban Island, Gulf of California (164); south end, Angel de la Guarda Island, Gulf of California (167, 168); north end, Angel de la Guarda Island, Gulf of California (172, 173). Punta Cholla, Sonora, Mexico (Emerson collection). Cerralvo Channel, Gulf of California at 46 fathoms ("Zaca" Expedition collection). San José del Cabo, Baja California; Concepcion Bay, Puerto Escondido, Baja California; San Marcos Island, Coronados Island, Gulf of California (Durham, 1947). Panama; Pearl Islands; Acajutla, Realejo, La Union, San Salvador; Zorritos, Peru; Acapulco, Sonora, Mexico; Guaymas, Sonora, Mexico; La Paz, Baja California (Verrill, 1868-1870). Tenacatita Bay, Cape Corrientes, Mexico; Concepcion Bay, San Felipe Bay, Baja California; Angel de la Guarda, Consag Rock, Gulf of California; Cabeza Ballena, Baja California; Santa Margarita Island, Magdalena Bay, Baja California; off California coast (Durham and Barnard, 1952). Pleistocene: Magdalena Island, Baja California; Coronados Island, Santa Inez Island, San Telmo Point (Durham, 1947).

***Astrangia (Astrangia) costata* Verrill, 1866**

*Astrangia (Astrangia) costata* Verrill, DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 27, pl. 5, figs. 5, 7. Synonymy.

This species was not taken by the Puritan Expedition. It is discussed with the preceding species.

**OCCURRENCE:** Panama (Verrill, 1868-1870); Carmen Island, Gulf of California (Durham, 1947).

***Astrangia (Astrangia) californica* Durham and Barnard, 1952**

*Astrangia (Astrangia) californica* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 61, pl. 5, figs. 24a, 24b.

This species was not among the "Puritan" collections.

**OCCURRENCE:** Willard Point, Gonzaga Bay, Baja California (Durham and Barnard, 1952).

***Astrangia (Coenangia) conferta* Verrill, 1870**

*Astrangia (Coenangia) conferta* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 77, pl. 8, fig. 38. Synonymy.

This species was not taken alive by the Puritan Expedition, although a single specimen was collected from Pleistocene deposits.

**OCCURRENCE:** Gulf of California; Guaymas, Sonora (Verrill, 1870). Acapulco, Tehuantepec, Mexico (Durham, 1947). Santa Maria Bay, Baja California (Durham and Barnard, 1952). Pleistocene: Magdalena Island, Baja California.

**GENUS PHYLLANGIA** MILNE-EDWARDS AND HAIME, 1846

**?*Phyllangia dispersa* Verrill, 1864**

*Phyllangia dispersa* Verrill, DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 31, pl. 7, figs. 4, 5. Synonymy.

Two specimens, one of which is worn, the other abnormal, are referred to this genus, albeit irresolutely. The worn specimen (station 133) represents single calices partially grown over by algae and bryozoans. There is sufficient coral exposed to indicate that the generic assignment is correct. Another specimen (station 117) is exceedingly large for this species, having a calicular diameter of approximately 15 mm.

**OCCURRENCE:** San José Island, Gulf of California (117); Salinas Bay, Carmen Island, Gulf of California (133). Panama; Pearl Islands; Gulf of Nocoya (Verrill, 1868-1870).

**FAMILY PORITIDAE GRAY, 1842**

**GENUS PORITES LINK, 1807**

The species of this genus have long presented systematists with a considerable prob-

lem. Few other corals are capable of the plasticity and morphological variation that this genus attains. The variations among *Porites* from the Gulf of California are not exceptions, but were, fortunately, early recognized to be of gradational aspect on a regional basis. Ricketts (*in* Steinbeck and Ricketts, 1941) acknowledged this in speaking of *Porites porosa* [sic]: "In the south and on the Lower California shores of the Gulf, it occurred in dome shaped heads up to 8" in diameter, or in variously shaped masses and clusters. But at Puerto Refugio and on the southern end of Tiburón Island, the thin encrustations on tide pools was scarcely recognizable as the same species."

Verrill (1868-1870) recognized five species of *Porites* from the west coast of Mexico and the Gulf of California. Ricketts (*in* Steinbeck and Ricketts, 1941, p. 334) quotes Wells as suggesting the synonymy of *P. porosa* Verrill and *P. californica* Verrill, an action later carried out by Durham (1947) following an examination of the type specimens. Durham (1947) named a new species, *P. sverdrupi*, for the finely branching forms of *Porites* from the Gulf of California which, as he surmised, are more widely distributed than indicated by previous records. It is quite probable that the specimen referred to *Porites* cf. *nodulosa* Verrill [sic] by Ricketts (*in* Steinbeck and Ricketts, 1941) and suggested by Wells (*op. cit.*, quotation) as being a new species, belongs to *P. sverdrupi* Durham.

As mentioned above, the growth forms of the species of *Porites* from the Gulf of California are quite striking, particularly in the gradation from nodular or branching forms to flat encrusting types as one proceeds northward in the Gulf. Although the species is widely distributed, and in the northern portions of the Gulf the most common and often the only coral seen (the astrangiid corals being easily overlooked), collecting it is more difficult in the northern regions because of its tendency to form flat encrustations, which, although extensive, may be only a few millimeters thick. Because of these variations, the least difficult task is to sort the specimens without regard for their septal and calicular characters into the varieties of growth forms. In following the more difficult but the only obvious path, I found that all the "species,"

with the exception of *P. sverdrupi*, may be shown to grade into the more encrusting type of growth form of the northerly direction.

A few notes of a general biological nature may be properly injected here. On making the first extensive collections of corals on the Puritan Expedition from El Pulmo Bay, we found that the usual brilliant green hues of *Porites* were often interrupted by irregular splotches of a lighter shade, most frequently yellow. For some time the cause of this irregular coloration remained unknown, until parrot fish were observed to be feeding on nodular heads of *Porites*. Collecting then showed that the yellow areas were coincidental with those portions damaged by the feeding of the fish. Further, the intensity of the color was found to depend on the amount of tissue (and skeletal) material removed, or on the degree of regeneration that had occurred to the damaged area. The color change can best be attributed to the removal of tissue containing the densest population of zooxanthellae. The areas thus damaged are apparently not killed, but regrow. The groove cut by the teeth of the fish, although deep, does not penetrate the polyp layer.

In the middle regions of the Gulf, several small specimens of nodular coralla of *P. californica* were found growing on the free valve of the small *Hipponyx*. Growth of the coral often extended only a short distance laterally to the shell and therefore formed a covering to the snail, but, in at least two instances, the coral growth had extended laterally several inches in all directions so that the snail was completely submerged by the coral. In every instance, the coral was attached to the shell of the snail and not to the substrate, and removal of the specimen resulted in the separation of the "valves" of *Hipponyx*. In all cases the *Hipponyx* were alive, and attachment by the coral was made to the dorsal "valve." Yonge (1953), in a discussion of the common West Coast member of the genus, *Hipponyx antiquatus*, reports that the most common occurrence of the species is in crevices and crannies in the rock where it is protected from the full force of the surf. Further, *Hipponyx* is a sessile snail and primarily a detritus feeder, browsing with the proboscis. It is difficult to understand how much material can be brought into the cavity

beneath an essentially encrusting coral extending laterally beyond the shell, unless the motion of the snail lifts the coral sufficiently far off the substrate to permit circulatory movements of the water.

A single specimen of *P. californica* was taken adhering to the shell of *Crepidula aculeata* Gmelin. Again, *Crepidula* is among the more sessile snails, but the growth of coral would in no way inhibit movement by the snail. The cause for this rather common selection of habitat site can be best attributed to the absence of clean, algal-free rock in the regions in question. Presumably coral larvae found the shells a more suitable settling ground than surrounding substrate.

***Porites baueri* Squires, new species**

Plate 27, figures 7, 8

**HOLOTYPE:** A.M.N.H. No. 3348, Department of Fishes and Aquatic Biology; off lighthouse, south of Puerto Balleto, María Madre Island.

**DESCRIPTION:** Corallum encrusting, forming masses several inches thick over the substrate. Surface nearly flat, with slight irregularities. Calices 1.0 to 2.0 mm. in diameter, the average being about 1.5 mm., varying greatly in size but not in relation to position in corallum. Calices polygonal, not excavated, the pali being at about the same level as the trabeculae of the wall. The wall is straight, thin, dense, and nearly smooth on the upper margin. Inner synapticular ring absent. Septa are reduced to nearly horizontal spines in the upper portions of the calice, but become more continuous at depth. The trident structure of the septa is not clearly apparent, but the apparent arrangement is plan F of Bernard's (1905) scheme.

The species is most nearly related to *Porites excavata* Verrill, both specimens of which are before me (P.M.Y.C. No. 1677; pl. 33, figs. 1, 2). They differ from the new species in that the calices are excavated and the walls are more porous. *Porites excavata* is apparently related to *P. paschalensis* Vaughan from Easter Island. Vaughan (1906) discusses the relationships of *P. paschalensis* in some detail. *Porites compressa*, described by Vaughan (1907) from the Hawaiian Islands, is quite similar in most characters to *P. baueri* except for the depth of the calices of the former.

Vaughan (1907) and Wells (1954), discussing *P. compressa* and *P. lichen* Dana, respectively, both indicate great variation in depth of calices, construction of wall, and presence of an inner synapticular ring in these species. *Porites baueri* may represent a northern variant of *P. excavata*, a species that is very poorly known.

Verrill (1868, p. 504), in regard to *P. excavata*, remarks on the presence of a large number of calices having septa in excess of the usual 12. This is also the case in *P. baueri*, at least one calice per square centimeter being both larger in diameter and having three or more cycles of septa.

**OCCURRENCE:** María Madre Island, Tres Marias Islands (25); María Magdalena Island, Tres Marias Islands (47).

***Porites californica* Verrill, 1870**

Plate 32, figures 3–6; plate 33, figures 3–5

*Porites californica* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 46, pl. 3, figs. 17a, 17b. Synonymy.

*Porites porosa* VERRILL, 1870, Trans. Connecticut Acad. Arts and Sci., vol. 1, p. 504.

*Porites nodulosa* Verrill, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 46, pl. 3, fig. 18. Synonymy.

*Porites sverdrupi* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 23, pl. 12, fig. 4, pl. 13, fig. 2.

Durham (1947, p. 21) has already discussed the synonymy of *P. californica* and *P. porosa*. The conclusion of common identity for the remaining species is based on examination of more than 200 specimens of *Porites* from the Gulf of California. Several attempts were made to differentiate species on a consistent pattern. Most nearly successful were separations based on the character of the wall and septa, with two major groups being differentiated: those corals having denticulate septa and generally thick walls, and those with septa sparsely denticulate and with thin walls. This difference was found to be quite variable, both conditions frequently being found on a single corallum, as noted by Durham (1947, p. 21). Other characters, such as size and depth of calices, were found to vary from one corallum to another in no consistent fashion and, even more startling, according

to the position of the calice on the corallum. The character of the wall varies from lightly denticulate to highly denticulate according to the depth of calice and the position of the calice on the corallum. The paler ring in the great majority of instances is incomplete, the usual paler number being five. The differences between *P. californica* and *P. nodulosa* cited by Durham (1947, p. 23) seem to be a matter of degree and not of specific significance.

*Porites sverdrupi* and *P. nodulosa* intergrade in the form of the corallum to a rather remarkable extent. The character of the spinosity of the septa of the former noted by Durham (1947, p. 23) seems to be correlated with the more finely branched nature of the corallum, as is the shallowness of the calices. As interpreted on the basis of the "Puritan" collections, *P. sverdrupi* is a deeper-water phase of the common *P. californica*. This is borne out by the records for occurrence, as *P. sverdrupi* has not been reported from depths of less than 5 fathoms, while *P. nodulosa* from depths of 4 fathoms is very close to *P. sverdrupi* in the form of the corallum. All characters of septal arrangement and trabeculae seem to be identical in the two types.

Specimens of the *P. sverdrupi* type were taken alive in only a few instances. The polyps are colorless and difficult to observe. The form has an apparent depth range of 5 to 50 fathoms, although the specimens from the deeper portion of the range may well have been transported.

Of note is the occurrence of *P. californica* alive in the Magdalena Bay region where it had previously been known only from the Pleistocene (Durham, 1947; Jordan, 1936, as *P. panamaensis*). The ecological situation in Magdalena Bay is such that once larvae had successfully been introduced, the species could well survive in the shallow, sun-warmed waters of that bay. All specimens collected there were hemispherical in form, with no tendency to branch. Most were collected from very shallow water.

As discussed above, there is a gradation in growth form of the shallow-water *Porites* from the southern portion of the Gulf of California to the northern areas. Southern specimens were nodular or slightly branched, while the northern specimens were more generally encrusting. If local variations in this

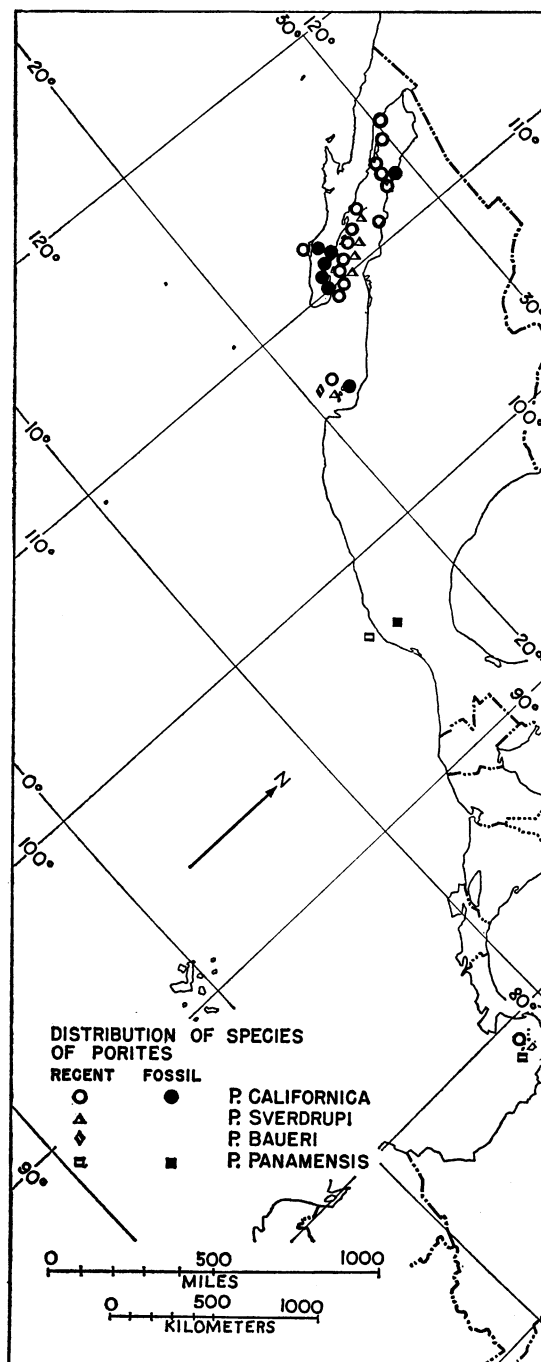


FIG. 20. Pleistocene and Recent distribution of *Porites* in the eastern Pacific.

trend caused by substrate conditions are allowed for, the gradation is quite even (fig. 10). In the center of the range occurs a group of

highly branched, pinnacled, or turreted growth forms associated with the reef facies. It is interesting to compare the distribution of this phenotype as it occurs today with the Pleistocene and Pliocene occurrences of the same form (fig. 10).

**OCCURRENCE:** *Porites californica* (shallow-water phase): Santa Margarita Island, Magdalena Bay, Baja California (24); San Juanito Island, Tres Mariás Islands (36); María Magdalena Island, Tres Mariás Islands (44); Los Frailes Bay, Baja California (85, 86); El Pulmo Bay, Baja California (87); Cerralvo Island, Gulf of California (90); Espiritu Santo Island, Gulf of California (94, 98); Isla Partida, Gulf of California (100, 108); San Francisco Island, Gulf of California (110, 111); San José Island, Gulf of California (112); San Diego Island, Gulf of California (118); Aqua Verde Bay, Baja California (123); Monserrate Island, Gulf of California (126); Santa Catalina Island (130); Salinas Bay, Carmen Island, Gulf of California (134); Puerto Escondido, Baja California (136); Marquer Bay, Carmen Island, Gulf of California (141); Coronados Island, Gulf of California (165); Pulpito Point, Baja California (147); Santa Inez Island, Gulf of California (148); Lobos Rock, San Marcos Island, Gulf of California (152); San Carlos Bay, Sonora (155); Tiburón Island, Gulf of California (158); San Esteban Island, Gulf of California (164); Gonzaga Bay, Baja California (175).

*Porites californica* (deeper-water phase = *P. sverdrupi*): María Magdalena Island, Tres Mariás Islands (70); María Madre Island, Tres Mariás Islands (72); Isla Partida, Gulf of California (106, 107); Salinas Bay, Carmen Island, Gulf of California (134); Puerto Escondido, Baja California (139). Salinas Bay, Carmen Island, Gulf of California; Aqua Verde Bay, Baja California; Lobos Rock, San Marcos Island, Gulf of California (Durham, 1947). Puerto Escondido, Baja California (Durham and Barnard, 1952). La Paz, Baja California (Verrill, 1868–1870). Angel de la Guarda and southward (Durham, 1947). Gulf of California; Secas Islands, Panama (Durham and Barnard, 1952). Gulf of California (Hertlein, 1957). Pliocene: Marquer Bay, Carmen Island; Puerto Balandra, Carmen Island, Gulf

of California; Coronados Island, Gulf of California (Durham, 1950a). Pleistocene: West side of Magdalena Island; east side of María Madre Island; north side of María Cleofas Island; San José Island, Gulf of California; San Diego Island, Gulf of California; San Telmo point region, Baja California. Salinas Bay; Marquer Bay, Carmen Island; Coronados Island, Gulf of California; Santa Inez Bay, Baja California; Tiburón Island, Gulf of California; San Telmo Point region, Baja California (Durham, 1950a).

**SUBORDER CARYOPHYLLIINA VAUGHAN AND WELLS, 1943**

**FAMILY CARYOPHYLLIIDAE GRAY, 1847**

**GENUS COENOCYATHUS MILNE-EDWARDS AND HAIME, 1848**

***Coenocyathus bowersi* Vaughan, 1906**

*Coenocyathus bowersi* Vaughan, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 83, pl. 10, figs. 45a, 45d. Synonymy.

Two specimens of this species were taken in one haul during the Puritan Expedition. The largest specimen, consisting of one cluster of seven corallites with two single associated corallites, was taken alive. Its color when wet, but not expanded, was a delicate shade of coral, lighter about the margins of the calice. Although the specimen was kept alive for one day, it was not observed in an expanded condition. The largest cluster of corallites was firmly attached to the ligamental platform of *Navicula pacifica*, while the two single corallites were attached to the right valve. The clam was also alive.

**OCCURRENCE:** San Diego Island, Gulf of California (120). Monterey Bay, San Diego, San Pedro, Channel Islands, La Jolla Canyon, California (Durham, 1947). Puerto Escondido and Isla Partida, Gulf of California; widely distributed along the California coast (Durham and Barnard, 1952).

**GENUS BATHYCYATHUS MILNE-EDWARDS AND HAIME, 1848**

***Bathycyathus consagensis* Durham and Barnard, 1952**

*Bathycyathus consagensis* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California,

vol. 16, no. 1, p. 79, pl. 8, figs. 40a-40e, pl. 9, fig. 40f.

Two suites of specimens are placed in this species, although both are badly worn and the characters of the upper calices cannot be determined. The relationship between this species and *B. chiliensis* Milne-Edwards and Haime, 1848, is of interest, but the illustration given by them provides little information.

**OCCURRENCE:** Southeastern end of Angel de la Guarda Island, Gulf of California (167, 168). Off Consag Rock, Gulf of California; off Willard Island, Gonzaga Bay, Baja California; Magdalena Bay, Baja California (Durham and Barnard, 1952).

GENUS **CERATOTROCHUS** MILNE-EDWARDS AND HAIME, 1848

**Ceratotrochus (Ceratotrochus) franciscana**  
Durham and Barnard, 1952

*Ceratotrochus (Ceratotrochus) franciscana* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 82, pl. 9, figs. 44a, 44b.

A single specimen is referred with some question to this species. It is obviously a young caryophyllid and apparently belongs to this genus. There is little discrepancy between its characters and those of the genus except for the presence of a great deal of endothecal material.

**OCCURRENCE:** San Diego Island, Gulf of California (121). San Francisco Island, Gulf of California (Durham and Barnard, 1952).

GENUS **HETEROCYATHUS** MILNE-EDWARDS AND HAIME, 1848

**Heterocyathus aequicostatus** Milne-Edwards and Haime, 1848

*Heterocyathus aequicostatus* Milne-Edwards and

Haime, DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 87, pl. 11, figs. 49a-49d.

This species is not represented in the collection made by the Puritan Expedition.

**OCCURRENCE:** Puerto Refugio, Angel de la Guarda Island, Gulf of California; Banderas Bay, Mexico (Durham and Barnard, 1952). Western Pacific and Indian oceans.

GENUS **PARACYATHUS** MILNE-EDWARDS AND HAIME, 1848

**Paracyathus tiburonensis** Durham, 1947

*Paracyathus tiburonensis* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 35, pl. 3, figs. 5, 6.

Several specimens of this species were taken alive.

**OCCURRENCE:** San Diego Island, Gulf of California (119, 120); Salinas Bay, Carmen Island, Gulf of California (133); northern end of Angel de la Guarda Island, Gulf of California (173).

SUBORDER **DENDROPHYLLINA** VAUGHAN AND WELLS, 1943

FAMILY **DENDROPHYLLIIDAE** GRAY, 1847

GENUS **BALANOPHYLLIA** WOOD, 1884

**Balanophyllia tiburonensis** Durham, 1947

*Balanophyllia tiburonensis* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 41, pl. 10, figs. 5, 7. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 101, pl. 15, figs. 64a, 64b.

One dead specimen of this species was taken from the Gulf of California by the Puritan Expedition.

Species of *Balanophyllia* have often proved to be difficult to distinguish, and many phenotypes have been described as species. There

TABLE 5  
COMPARISON OF EASTERN PACIFIC SPECIES OF *Balanophyllia*

	Northern <i>B. elegans</i>	Southern <i>B. elegans</i>	<i>B. cedroensis</i>	<i>B. tiburonensis</i>
Shape of corallum	Subcylindrical	Subcylindrical	Turbinate	Turbinate
Septal granulation	None	Coarse, dense	Coarse, sparse	Fine, numerous
Serrated septa (cycle)	All but 1, 2	All but 1, 2	All slightly	All but 1, 2
Slope of proximal face of septa	Sloping	Sloping	Vertical	Vertical

TABLE 6

LOCALITIES FROM WHICH FOSSIL CORALS WERE COLLECTED DURING THE PURITAN-AMERICAN  
MUSEUM OF NATURAL HISTORY EXPEDITION

Locality Number	Age	Locality Description
F-5	Pleistocene	West side of Magdalena Island, just south of Puerto Magdalena. Fossils from base of sea cliff of a 20-foot terrace. (See Jordan, 1936.) Emerson coll. <i>Porites californica</i> , <i>Astrangia</i> ( <i>Coenangia</i> ) <i>conferta</i> , <i>Astrangia</i> ( <i>Astrangia</i> ) <i>haimeii</i>
F-6	Pleistocene	West side of Magdalena Island, $\frac{1}{2}$ mile north of Puerto Magdalena. Emerson coll. <i>Porites californica</i> , <i>Astrangia</i> ( <i>Astrangia</i> ) <i>haimeii</i>
F-11	Pleistocene?	East side of María Madre Island, Tres Mariás. Fossils in coarse sand-pebble conglomerate exposed in path from camp to salt works at elevation of about 150 feet. Emerson coll. <i>Porites californica</i>
F-15	Pleistocene	North side of María Cleofas Island, Tres Mariás. Fossils in bluff about center of cove in a sand-pebble conglomerate near top of exposure. Near top of bluff are <i>Porites</i> heads in a boulder conglomerate. Emerson coll. <i>Porites californica</i>
F-22	Pleistocene	Point midway on western shore of El Pulmo Bay, Baja California, above granite outcropping. Basal portion of sequence dated as $25,400 \pm 1000$ years. Squires coll. <i>Porites</i> sp., <i>Pocillopora elegans</i>
F-23	Pleistocene	South side of Cerralvo Island, Gulf of California. Fossils from coarse yellowish sand and pebbles, locally conglomeratic with boulders and <i>Porites</i> heads, 5 to 12 feet above high tide. Emerson coll. <i>Porites</i> sp. <i>Pocillopora elegans</i>
F-24	Fossil?	Amortajada Bay, San José Island, Gulf of California. <i>Porites</i> on oyster shells possibly representing a kitchen midden. Emerson coll. <i>Porites californica</i>
F-25	Pleistocene	South side of San Diego Island, Gulf of California. Terrace deposit exposed in cliff behind beach at elevation of 20 feet. <i>Porites</i> heads on boulders in conglomeratic lens. Emerson coll. <i>Porites californica</i>
F-26	Pleistocene	North of San Carlos Bay and south of San Telmo Point in small cove. Terrace face and sea cliff exposure with a maximum elevation of about 26 feet. University of California locality A3596. (See Durham, 1950a.) Emerson and Squires coll. <i>Pocillopora elegans</i> , <i>Porites</i> cf. <i>P. sverdrupi</i> , <i>Porites californica</i> , <i>Porites</i> sp.
F-28	Pleistocene	Approximately $3\frac{1}{2}$ miles north of Point San Telmo, Baja California. Sandy conglomerates grading upward into muddy sands. Squires coll. University of California locality A3595. (See Durham, 1950a.) <i>Pocillopora elegans</i> , <i>Porites</i> sp.
F-30	Pliocene	Marquer Bay, Carmen Island, Gulf of California. Coral bed on top of fine siltstone at about 50 feet elevation. Squires coll. University of California locality loc. A3519. (See Durham, 1950a.) <i>Porites californica</i> .

seems to be an interesting sequence of the three common species of this genus along the western coast of North America. *Balanophyllia elegans* Verrill ranges from British Columbia southward to the northern portion of Baja California, and, as noted by Durham (1947, p. 41), individuals from the northern end of the range are characterized by smooth septa both laterally and proximally, while

specimens from the southern portions of the range are characterized by more highly ornamented septa. *Balanophyllia cedrosensis* Durham is, unfortunately, known from only a few specimens from the western coast of Baja California.

*Balanophyllia tiburonensis* ranges from the Gulf of California southward to Ecuador. Several of the more important morphologic

TABLE 7

DISTRIBUTION OF SPECIES COLLECTED IN THE DREDGING OPERATIONS OF THE PURITAN-AMERICAN MUSEUM OF NATURAL HISTORY EXPEDITION

Station Number <sup>a</sup>	Depth in Fathoms	Type of Bottom <sup>b</sup>	Species Collected
María Magdalena Island, Tres Marias			
58	7-8	S	<i>Cycloseris elegans</i> , <i>C. mexicana</i>
Cleofas Island, Tres Marias			
61	5	R	<i>Psammocora</i> ( <i>Stephanaria</i> ) <i>stellata</i> , <i>Pocillopora elegans</i> var. <i>pumila</i>
62	9-10	R	<i>Pocillopora elegans</i> var. <i>pumila</i>
María Magdalena Island Tres Marias			
70	20-24	S	<i>Porites californica</i> var. <i>sverdrupi</i>
María Madre Island, Tres Marias			
72	14-15	S	<i>Cycloseris elegans</i> , <i>C. mexicana</i> , <i>Porites californica</i> var. <i>sverdrupi</i> , <i>Psammocora</i> ( <i>Stephanaria</i> ) <i>stellata</i>
73	6-10	SC	<i>Cycloseris mexicana</i> , <i>C. elegans</i>
Espíritu Santo Island			
96	10-24	CS, CA	<i>Cycloseris mexicana</i> , <i>C. elegans</i> , <i>Astrangia haimeii</i>
Isla Partida			
106	6	S	<i>Cycloseris mexicana</i> , <i>Porites californica</i> var. <i>sverdrupi</i>
107	5-6	S	<i>Cycloseris mexicana</i> , <i>Porites californica</i> var. <i>sverdrupi</i>
San José Island			
114	22-25	CS	<i>Cycloseris mexicana</i>
115	13.5-17.5	CS	<i>Cycloseris mexicana</i> , <i>Astrangia haimeii</i>
116	36.5-40	S?	<i>Endopachys vauhani</i>
117	35-41.5	S?	<i>Cycloseris mexicana</i> , <i>Balanophyllia tiburonensis</i> , <i>Astrangia</i> sp., <i>Phyllangia dispersa</i> ?
San Diego Island			
119	—	S, CA	<i>Porites sverdrupi</i> , <i>Astrangia haimeii</i> , <i>Paracyathus tiburonensis</i>
120	25-40	CS	<i>Endopachys vauhani</i> , <i>Cycloseris mexicana</i> , <i>Coenocyathus bowersi</i> , <i>Astrangia</i> sp., <i>Paracyathus tiburonensis</i>
121	40-50	S?	<i>Ceratotrochus</i> ( <i>Ceratotrochus</i> ) <i>franciscana</i> ?
Carmen Island			
131	41-45	S?	<i>Endopachys vauhani</i> , <i>Astrangia haimeii</i> , <i>Astrangia</i> ? sp.
132	14-30	S, CA	<i>Cycloseris mexicana</i> , <i>Astrangia haimeii</i>
133	20	S?	<i>Phyllangia dispersa</i> , <i>Paracyathus tiburonensis</i>
134	—	CS	<i>Porites californica</i> var. <i>sverdrupi</i>
Puerto Escondido, Baja California			
139	40-46	S	<i>Porites californica</i> var. <i>sverdrupi</i> , <i>Astrangia haimeii</i>

TABLE 7—(Continued)

Station Number	Depth in Fathoms	Type of Bottom	Species Collected
Coronados Island			
144	13–16.5	CS	<i>Cycloseris mexicana</i> , <i>Astrangia haimeii</i>
145	40–45	CS	<i>Endopachys vaughani</i>
San Marcos Island			
151	—	CS	<i>Astrangia haimeii</i>
Tiburón Island			
159	10	CS	<i>Astrangia haimeii</i>
160	20–22	CS	<i>Astrangia haimeii</i>
161	30–32	CS	<i>Astrangia haimeii</i>
162	40	BS	<i>Astrangia haimeii</i> , <i>Astrangia</i> sp.
Southern Angel			
de la Guarda Island			
167	15–17	S?	<i>Bathycyathus consagensis</i> , <i>Astrangia haimeii</i>
168	16–17	S?	<i>Bathycyathus consagensis</i> , <i>Astrangia haimeii</i>
Puerto Refugio,			
Angel de la Guarda Island			
172	16–18	M, S	<i>Astrangia haimeii</i>
173	17–19	CS	<i>Astrangia haimeii</i> , <i>Paracyathus tiburonensis</i>

\* The location of these stations can be found in Emerson (1958); or see the paragraphs on Occurrence in the present paper for the respective species.

<sup>b</sup> B, boulders and cobbles; BS, bryozoan sand; C, coral; CA, calcareous algae; CS, coarse sand; M, mud; R, rock; S, sand; SR, shell rubble.

characters distinguishing these species are given in table 5.

**OCCURRENCE:** San José Island, Gulf of California (117). South of Tiburón Island, Gulf of California (Durham, 1947). La Plata Island, Ecuador, Bahía Honda, Panama (Durham and Barnard, 1952).

**GENUS DENDROPHYLLIA** DE BLAINVILLE, 1830

**Dendrophyllia cortezi** Durham and Barnard, 1952

*Dendrophyllia cortezi* DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 102, pl. 16, figs. 66a, 66b.

A single specimen of this species was taken with other balanophyllid corals in a rock-bottom dredging. The polyps were a dark purple-brown but were so badly damaged that no other details could be obtained.

Three species of *Dendrophyllia* are known from the west coast of Central and North America: *D. californica* has a range, aside from the species reported here, from the central portions of western Baja California northward to southern California; *D. oldroydi* Faustino, from the southern California coasts; and *D. cortezi* Durham and Barnard

is known only from the northern Gulf of California. The columella of the specimen collected on the Puritan Expedition differs from that figured by Durham (1947) or by Durham and Barnard (1952), as it is composed of curled laths which are very symmetrically arranged and closely spaced.

**OCCURRENCE:** Tiburón Island, Gulf of California (163). Isla Partida, Gulf of California; Angel de la Guarda Island, Gulf of California (Durham and Barnard, 1952).

**GENUS ENDOPACHYS** LONSDALE, 1845

**Endopachys vaughani** Durham, 1947

*Endopachys vaughani* DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 39, pl. 11, figs. 6–8, 10, 11. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 103, pl. 16, figs. 67a, 67b.

None of the specimens taken by the Puritan Expedition was alive.

I have considered the characterization of this species with regard to *Endopachys oahense* Vaughan from the Hawaiian Islands and the common *E. grayi* Milne-Edwards and Haime from the western Pacific. It is un-

fortunate that Vaughan's species was based on a single specimen, for it is well known that the species of this genus are quite variable. Durham (1947, p. 40) differentiated *E. vaughani* from *E. oahense* on the basis of the well-developed lateral wings and lenticular transverse outline of the former, the latter species apparently lacking the aliform extensions and being somewhat more rounded in outline. There are, in the "Puritan" collections, specimens that lack any lateral extension and are remarkably like the specimen figured by Vaughan. These characters, which are subject to wide variation, are of little significance. In particular, the development of the aliform extensions may be a reflection of substrate and current relationships, as it is apparently a stabilizing mechanism. There seems to be a consistency of one character: the prominence and exert condition of the septa of the first two cycles. In this respect, the species differs from *E. grayi* Milne-Edwards and Haime. There is some indication that the same condition may prevail in *E. oahense*, but such a determination must rest upon the observation of other specimens.

**OCCURRENCE:** San José Island, Gulf of California (116); San Diego Island, Gulf of California (120); Salinas Bay, Carmen Island, Gulf of California (131); Coronados Island, Gulf of California (145). Mouth of Gulf of California (Durham, 1947). West of Isla Partida, Gulf of California; Albermarle Island, Hood Island, Galapagos Islands; Gorda Point; Cabeza Ballena Point, Baja California (Durham and Barnard, 1952).

GENUS *TUBASTREA* LESSON, 1834

*Tubastrea aurea* (Quoy and Gaimard), 1833

*Tubastrea tenuilamellosa* (Milne-Edwards and Haime), DURHAM, 1947, Mem. Geol. Soc. Amer., vol. 20, p. 38, pl. 11, figs. 1, 2, 4, 9, pl. 12, figs. 6, 7. DURHAM AND BARNARD, 1952, in Allan Hancock Foundation publications of the University of Southern California, vol. 16, no. 1, p. 105, pl. 12, fig. 50d.

*Dendrophyllia aurea* (Quoy and Gaimard), VAN DER HORST, 1926, Trans. Linnean Soc. London, ser. 2, vol. 19, pt. 1, p. 46, pl. 2, figs. 1-4, 8, 9. Synonymy.

Verrill (1868-1870, 1869) recognized *Dendrophyllia tenuilamellosa* and *Astropsammia pedersenii* from La Paz, Gulf of California, based on the collections made by Captain J.

Pedersen. As is noted above, this collection probably was taken from several localities and La Paz represents the address from which the collection was shipped. Durham (1947) correctly recognized that *A. pedersenii* was based on beach-worn specimens of *Tubastrea tenuilamellosa*. He differentiated *T. tenuilamellosa* from *T. aurea* on the basis of several characters of the calice and the costae. I have had the advantage of being able to examine a rather large number of specimens from the Gulf of California and a suite of specimens of *Dendrophyllia manni* Verrill (= *Tubastrea aurea*) from Hawaii. In both suites, the characters used by Durham have been found to be quite variable. Width of columella, width of septa, and smoothness of septa vary widely within a single corallum, largely in direct relationship with the diameter of the calice. The nature of the costal granulations and the width of the costae are similarly found to be variable within a single individual and are apparently functions of the degree of etching that has occurred in conjunction with the cleaning of the corallum, or possibly to ecological factors affecting thickness of the wall.

This species has been widely collected from the Gulf of Panama, the Pearl Islands, and the Galapagos, but no specimens other than those mentioned by Verrill had been taken in the Gulf of California prior to the Puritan Expedition. Although the species was collected by us from only four localities, I am convinced that it is much more widely distributed. Because of its known preference for shade, it is usually found in areas otherwise not productive of corals. Where found, however, it occurs in great abundance. At Lobos Rock, south of San Marcos Island, for example, a rock face approximately 8 feet high and 12 feet long was completely covered by well-developed coralla. All were a bright orange-red, with long yellow tentacles and a bright yellow stomadeum.

As suggested by Durham and Barnard (1952) *Tubastrea surcularis* (Verrill) may be an exceptionally large individual of this species. Verrill (1869, p. 393) gives the calicular diameters as 0.6 to 0.8 inches (15 to 20 mm.) and the height of the projecting corallites as 1.0 to 1.4 inches (25 to 35 mm.). The largest corallites of the specimens collected by the Puritan Expedition are 14 mm. in diameter

and protrude 15 mm. above the coenenchyme.

OCCURRENCE: Isla Partida, Gulf of California (108); San Marcial Rock, Baja California (124); Danzante Island, Gulf of California (142); Lobos Rock, San Marcos Island, Gulf of California (152). Jasper Island, Gulf of Nicoya, Costa Rica; La Plata Island, Ecuador ("Zaca" Expedition collec-

tion). La Paz, Baja California (Verrill, 1868-1870, 1869). Panama (Milne-Edwards and Haime, 1848). Pearl Islands (Verrill, 1868-1870, 1869). Acapulco, Galapagos, Santa Isabella Island (Durham, 1947). Galapagos, Costa Rica (Durham and Barnard, 1952). Hawaiian Islands west to Murray Island (van der Horst, 1926).

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