



The Biological Investigation
of Malpelo Island, Colombia

JEFFREY B. GRAHAM
EDITOR

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ABSTRACT

Graham, Jeffrey B., editor. The Biological Investigation of Malpelo Island, Colombia. *Smithsonian Contributions to Zoology*, number 176, 98 pages, 35 figures, 1975.—The results of joint Smithsonian Institution and U. S. Navy terrestrial and marine investigations of Malpelo Island, Republic of Colombia are reported in 15 papers in this volume. A new species of lizard (*Phyllodactylus*), a new starfish (*Tamaria*), two new species of shrimp (*Alpheus* and *Synalpheus*), and a new species of fish (*Chriolepis*) are described. The terrestrial ecology of Malpelo and the behavior and natural history of the lizards *Anolis agassizi* and *Diploglossus millepunctatus* are described and discussed. Genic variability in *A. agassizi* has been investigated and karyotypes of *A. agassizi* and *D. millepunctatus* are reported. The ecology of the island's benthic marine communities is detailed and papers listing and discussing zoogeographically interesting features of the island's crustacean, starfish, and fish species are included. The geology of Malpelo is briefly described and an improved map of the island is presented. The importance of Malpelo Island in the understanding of biogeographic problems in the eastern tropical Pacific Ocean is reviewed.

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The Biological Investigation of Malpelo Island, Colombia

Introduction

Jeffrey B. Graham

On 28 February 1972 a group of 17 scientists representing the Smithsonian Tropical Research Institute, the Republics of Panama and Colombia, and several U.S. universities embarked on a six day expedition to investigate the marine and terrestrial biota of Malpelo Island, Colombia, a small isolated Pacific island 270 miles to the west of Colombia and south of Panama. The expedition, a joint project of the U.S Navy and the Smithsonian Tropical Research Institute, was undertaken to gain a more comprehensive understanding of ecological processes and the natural history of plants and animals on Malpelo. The scientific party consisted mostly of biologists who made collections, carried out field observations, and conducted experiments on the island and in the waters around it. (The Malpelo scientific party consisted of C. Birkeland, J. B. Graham, D. L. Meyer, A. S. Rand, A. Rodaniche, W. L. Smith, J. P. Stames, and H. Wolda, all of the Smithsonian Tropical Research Institute (STRI); O. Arroyo, Colombian Institute of Natural Resources (INDERENA); J. Barreto S., Universidad George Tadeo Lozana, Colombia; G. C. Gorman, University of California Los Angeles (UCLA); J. A. Hoffman, Smithsonian Astrophysical Laboratory; A. R. Kiester, Museum of Comparative Zoology; D. B. Macurda, University of Michigan; W. M. Rand, Massachusetts Institute of Technology (MIT); T. L. Chorba,

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U.S.S. *York County*; J. A. Stead, U.S. Navy Hydrographic Center. R. J. Kinney, USN, served as expedition physician. The geology of Malpelo was studied and a more accurate map of the island was made by an exploration team.

The scientists were transported from Panama to Malpelo by the U.S.S. *York County* (LST 1175) commanded by LCDR Lauren Seeber. At Malpelo, the scientists were supported by *York County* crewmen who did everything from prepare box lunches to operate small boats and assist in the collection and sort of specimens. While on station the *York County* conducted sea trials and made numerous depth soundings and positional sightings of the island. This work, while helping to establish that the peaks on Malpelo are some 125 meters higher than previous maps indicated, will also improve the hydrographic charts of this area.

The Smithsonian-U.S. Navy Expedition to Malpelo marked the fourth time that Smithsonian scientists and their colleagues have been able to use a U.S. Navy vessel for research purposes. In March 1970 biological investigations of the Secas Islands in the Gulf of Chiriqui, Panama, were conducted by scientists aboard the U.S.S. *Traverse County*. Later in the same year the U.S.S. *Walworth County* supported marine studies at Coiba Island, Panama. In 1971 the U.S.S. *Terre Bonne Parish* carried a research team to Bocas del Toro, Panama, for three days of field work. In the summer of 1973, while the volume on Malpelo was

being compiled, the fifth and most ambitious expedition was undertaken when the U.S.S. *Spartanburg County* took 25 scientists to Cocos Island, Costa Rica, 550 miles southwest of Panama.

These expeditions have been fruitful. The largest and best developed coral reef formations to be found thus far in the eastern tropical Pacific were discovered and subsequently studied by Peter Glynn and colleagues during the Gulf of Chiriqui trip (Glynn, Stewart, and McCosker, 1972). Previous to these investigations it was thought that no well-developed coral reefs occurred in the eastern tropical Pacific. The coral-eating starfish *Acanthaster planci* was found in great abundance and several species of Indo-Pacific corals were also discovered by Glynn and his co-workers during the same expedition. Our understanding of the faunal composition and zoogeography of eastern tropical Pacific fishes has benefited significantly from Navy-supported research in this region (Rosenblatt, McCosker and Rubinoff, 1972).

The use of Navy ships is a valuable addition to the research capacity of the Smithsonian Tropical Research Institute. Navy vessels allow many scientists to participate in the expeditions and it is possible to visit localities beyond the range of small research vessels. Needless to say, costs and the logistical support problems are also vastly reduced.

ACKNOWLEDGMENTS.—It is a pleasure to acknowledge Admiral C. H. Griffiths, Commander of the United States Navy, Fifteenth Naval District, Fort Amador, Canal Zone, and his staff who made arrangements for the Malpelo Expedition. We also thank Captain Lauren Seeber and the officers and men of the U.S.S. *York County* for supporting our investigations. We express our appreciation to the Foreign Ministry of the Republic of Colombia for permitting us to visit Malpelo Island and to the U.S. Army Southern Command, 352nd Aviation Detachment, for providing an aerial reconnaissance of the island. I would like to thank my colleagues: L. G. Abele of Florida State University, D. Dexter of San Diego State University, J. McCosker of the California Academy of Sciences, and A. S. Rand, I. Rubinoff, and R. R. Warner, all of the Smithsonian Tropical Research Institute, for their advice and assistance in the preparation of this volume; I acknowledge the technical assistance of I. Downs, A. Kourany, and V. Vergel of the Smithsonian Tropical Research Institute.

Island Biology and Its Biogeographical Significance

The biological investigation of islands has made a valuable contribution to the studies of evolution, biogeography, and ecology. Islands, by virtue of their differences in size, shape, climatic conditions, and distances from continents, present a stepped progression of natural experimental areas (MacArthur, 1972). Darwin's ideas on the natural variability and selection of species developed in part through his observations at the Galapagos Islands. Some biologists investigate islands to test different aspects of modern evolutionary theory. Islands, however, are intrinsically interesting because each is unique, and they afford biologists the chance to study the effects of isolation on the resident species. Island populations may have greatly expanded or otherwise modified niches and may have decreased levels of genetic variability or, if isolated for a long period, endemic species may be formed (MacArthur and Wilson, 1967).

Malpelo Island ($3^{\circ}51'07''N$, $81^{\circ}35'40''W$) is one of several oceanic islands in the eastern tropical Pacific. It is the only island on the Malpelo Ridge (Figure 1) a solitary volcanic submarine ridge that extends in a northeast-southwest direction with a length of 150 miles and a width of 50 miles (Chase, 1968). An oceanic island, Malpelo occurs outside the continental shelf and it is separated from the mainland of Central America by depths greater than 1800 fathoms. Malpelo has never been connected, even by shallow water, with any other islands or the mainland.

Malpelo's distance from the mainland and the depths of water between the island and the mainland are significant barriers to the colonization of both terrestrial and shallow-water marine organisms. Colonization therefore must occur through sea surface currents which would transport rafting terrestrial organisms and the planktonic larvae and subadults of marine forms to the island. Malpelo is closer to the mainland than Cocos and the Galapagos islands (Figure 2) and it is reasonable to assume it serves as a stepping stone for marine forms enroute, via oceanic currents, to these islands.

Consideration of the complex pattern of surface circulation in the eastern tropical Pacific Ocean

(Wyrтки, 1965) provides insight as to how surface currents may serve for transport from the mainland to Malpelo and beyond to Cocos and the Galapagos islands. Only general features of surface circulation in the area of these islands for the months of January and July are presented (Figure 2) and the reader is referred to Wyrтки's paper for details on monthly current vectors, velocities, and the persistence of flow for the different areas in the eastern tropical Pacific.

In the months from January to March the trade-winds cause a strong current flow (0.5 knots) out of the Gulf of Panama towards Malpelo and the Galapagos islands (Figure 2). A small anticyclonic

gyre that borders the mainland and encompasses Cocos and Malpelo islands is also formed at this time. If winds blow strongly for long periods the condition known as "El Niño" occurs. This results in the transport of a larger than normal amount of warm surface water, which displaces the Peru current to the southwest away from South America and the Galapagos Islands. During El Niño the Galapagos Islands may be completely bathed in warm tropical waters.

The Equatorial Countercurrent (Figure 2) does not penetrate very far into the eastern tropical Pacific from January to April, but from May to December this current is strong and reaches the

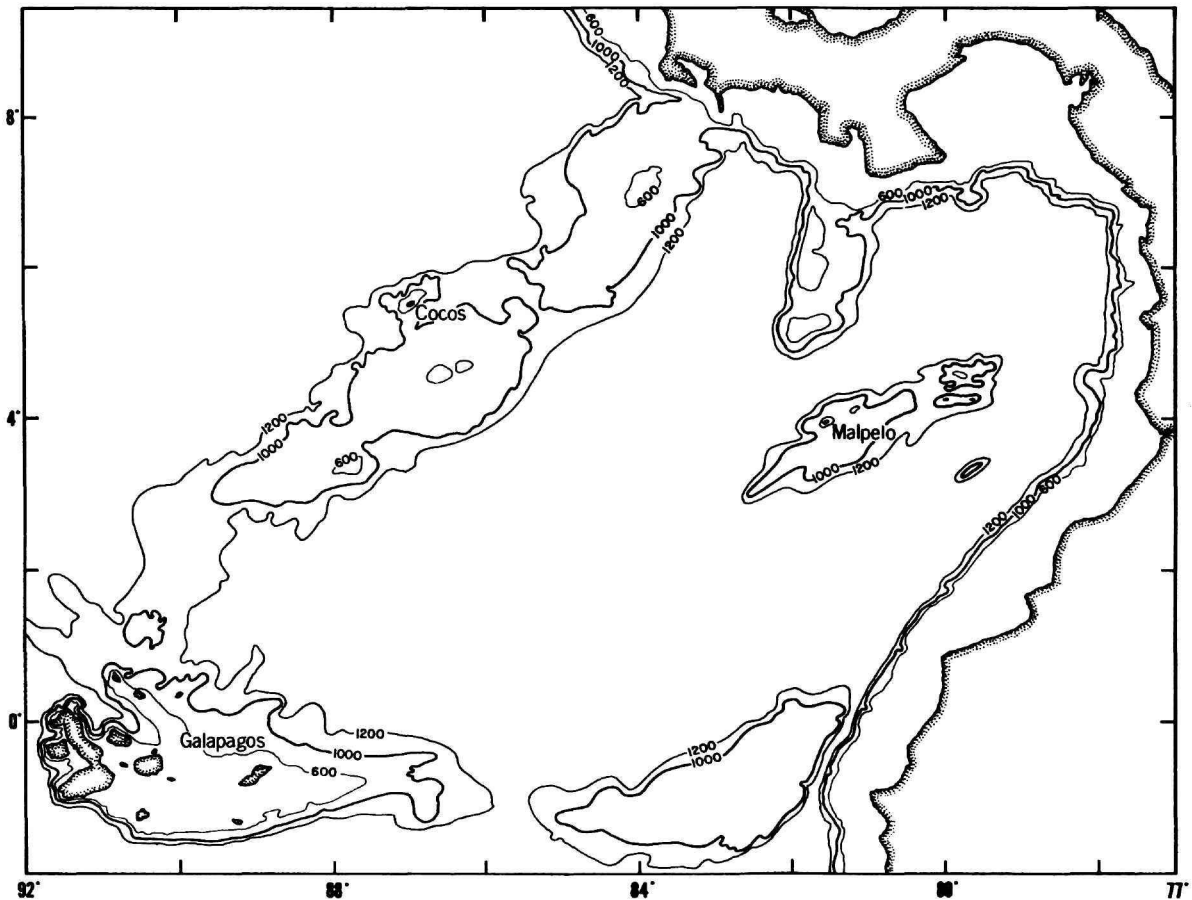


FIGURE 1.—Submarine topography of the central eastern tropical Pacific Ocean in the vicinity of Malpelo, Cocos, and the Galapagos islands. The lines are 600, 1000, and 1200 fathoms. Data are from Chase (1968).

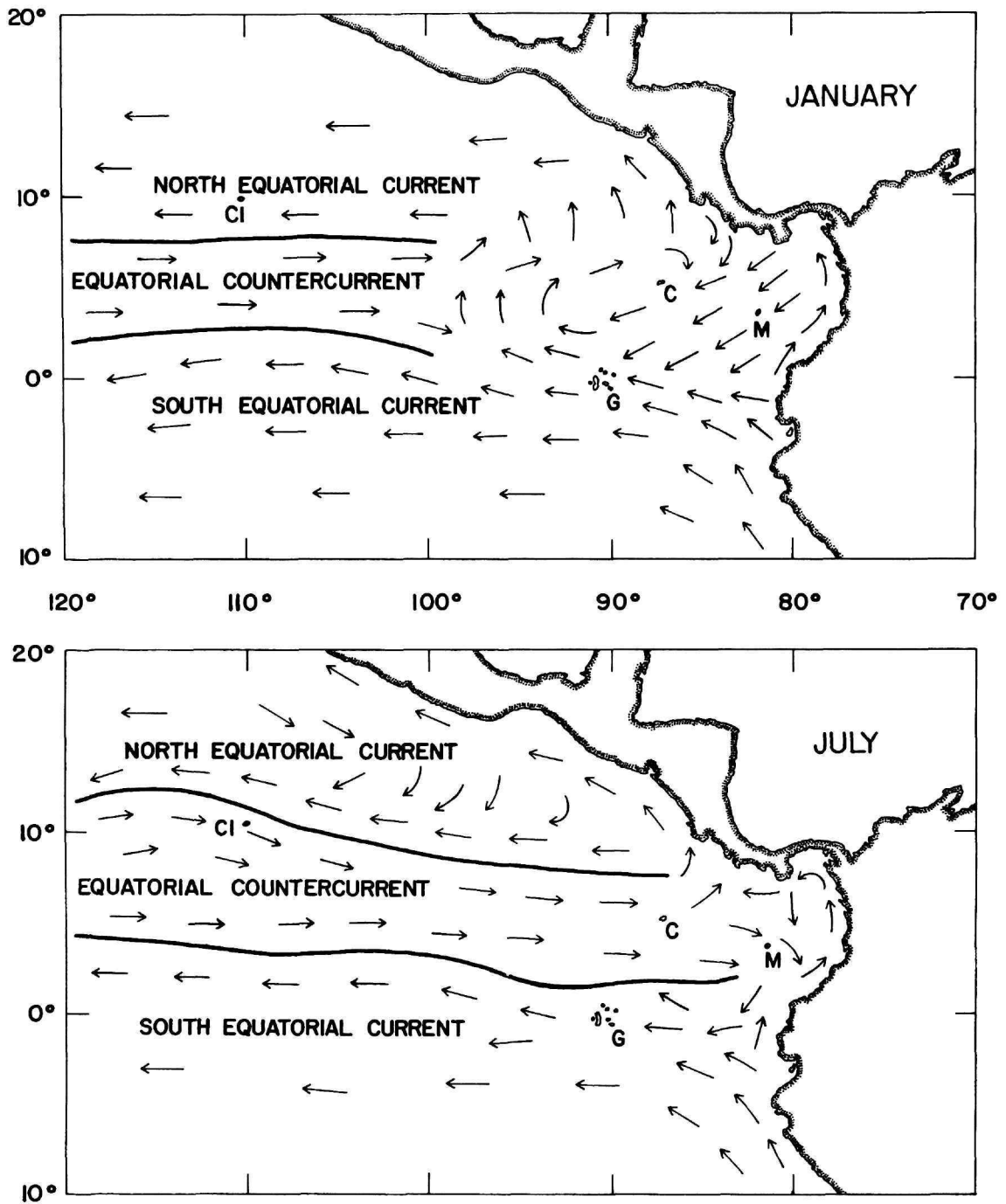


FIGURE 2.—Surface currents around the major oceanic island in the eastern tropical Pacific Ocean. The islands indicated are Clipperton (CI), Cocos (C), Galapagos (G), and Malpelo (M). Data are from Wyrtki (1965).

coast of Central America where it divides. The major part of the Equatorial Countercurrent flows northwest along Central America, while the remainder flows south and then turns west as part of the South Equatorial Current. From May to December Clipperton, Cocos, and Malpelo islands lie in the swath of the Equatorial Countercurrent, and the Galapagos Islands occasionally receive water from the southern part of this current from August to October. The combination of strong southern surface flow in the months from January to May and the circulation pattern of the Equatorial Countercurrent probably account for the dispersal of mainland marine organisms to these islands.

Another phenomenon that is of special interest to marine zoogeographers is the presence and dispersal patterns of Indo-Pacific organisms (corals, mollusks, crustaceans, and fishes) at the eastern tropical Pacific islands and on the Central American mainland (Costa Rica and western Panama). This has been recently reviewed for fishes by Rosenblatt, McCosker, and Rubinoff (1972). Larvae of these animals are apparently transported across 1000 miles of open sea by the Equatorial Countercurrent, which, as was shown above, extends to the mainland of Central America and sweeps across some oceanic islands for long periods of the year. It is not presently known how many species have successfully completed this transit or whether they more frequently colonize oceanic islands or the mainland.

Summary of the Malpelo Expedition

The amount of information that was accumulated in the four full days of field work on Malpelo is gratifying. Part of the expedition's success lay in what was learned about the island by its earlier explorers. Gorman and Chorba have traced the history of Malpelo's exploration, which goes back to 1542. Early visitors to Malpelo had the impression that the flow of energy to the terrestrial ecosystem had to be sustained by the sea and that this was done mainly by birds. While acknowledging that the success of the land crab (*Gecarcinus*) and the large lizard (*Diploglossus*) definitely depends on the activity of birds, Wolda has found that the terrestrial community is much too large and complex for this to be the only pathway. He concludes

that lichens and mosses constitute the important lower trophic levels for the land community.

Malpelo's endemic lizards were well studied on this expedition. A new species of gecko (*Phyllodactylus transversalis*) was discovered and this is described by Huey. This species, while similar in many ways to Peruvian species has its closest affinity to Mexican *Phyllodactylus*. The depth of biological knowledge about mainland and island *Anolis*, together with their extensive research experience with anoles enabled Rand, Gorman, and Rand to ask specific questions about the ecology and behavior of Malpelo's *A. agassizi*. The Malpelo anole is larger than most other anoles isolated on islands and it reproduces seasonally. Its social behavior is strikingly different from that of other *Anolis*; it is not territorial, there is little aggression, and its displays are few and simple. *Anolis agassizi* is an active, curious lizard that is readily attracted to things that appear in its habitat: scientists, their equipment, and their fruit and candy as well. Their curiosity and the remarkable tolerance of individuals for each other, these authors believe, enables *A. agassizi* to take advantage of resources such as water and food that have variable distributions in time and space on Malpelo. Kiester describes *Diploglossus millepunctatus* as curious and opportunistic and draws basically the same conclusions about the ecological significance of this behavior as were made for *A. agassizi*. Interestingly, Kiester postulates that *D. millepunctatus*, because of its dependence on birds, may have its reproductive seasonality synchronized with that of the nesting seabirds. This awaits further study. Webster measured a low degree of genic variability in *A. agassizi*. From what is presently known this seems to be a characteristic of old, solitary anole populations. Stamm and Gorman found that the karyotypes of *A. agassizi* and *D. millepunctatus* are similar to the more primitive groups in these two genera. Taken together these observations might suggest that Malpelo's *Anolis* and *Diploglossus* have been in residence for a very long time. But as Webster and Stamm and Gorman point out, our present knowledge is too limited to say this with certainty.

Kiester and Hoffman surveyed the island and, with special climbing equipment, scaled its summits. Sightings from the peaks and from the bridge of the *York County* enabled them to determine

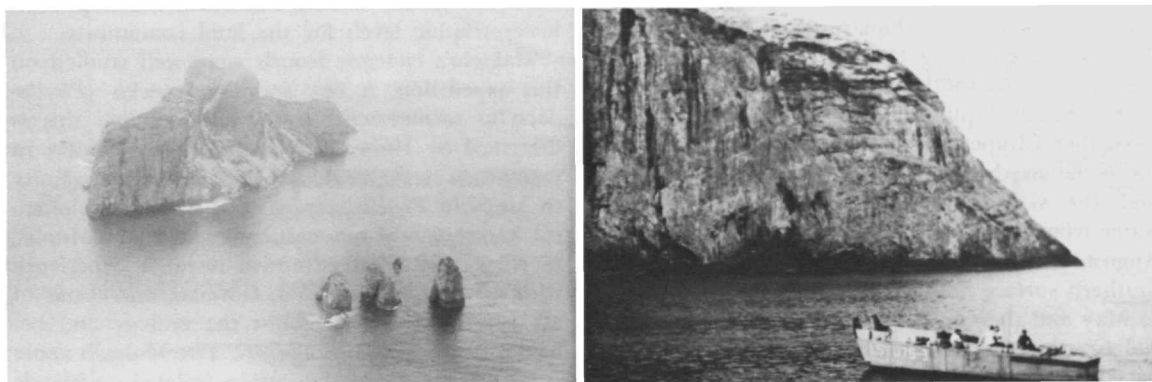


FIGURE 3.—Left: Aerial view (4000') of Malpelo Island. The northern end of the island is in the foreground. Right: A York County landing craft approaching the west side of Malpelo Island.

that the highest elevations of Malpelo are almost 125 meters higher than early maps indicated. Stead conducted a geological survey of Malpelo. His description of the island's weathering, together with a compilation of the York County's depth soundings around Malpelo enables us to appreciate the original size of this rock. Once 8 to 10 times its present size, Malpelo has been steadily worn by the persistent pounding of the sea. When we brought our small boats close to shore and tried to land on the island we keenly sensed the intensity of the struggle between Malpelo and the sea (Figure 3).

Rough water and the island's steep slope made getting from the boat to shore and returning a major undertaking for the terrestrial party. Exploration ended prematurely for one scientist in this group who severely injured his arm while trying to get from the island into the boat. In spite of these obstacles none in the terrestrial group elected to spend their nights on Malpelo and, at days end, all were glad to return to the haven of the York County. The warship took on a curious appearance at this time of day. Its main deck was littered with biological specimens and collecting equipment and was crowded with seamen who were rapidly transformed into eager assistants, audiences, or both. The crewmen relished this and took great pleasure in hearing about the discoveries and adventures of the day. Accounts were passed rapidly to the sailors on watch and expedition progress reports were included in the ship's daily bulletin. News of

the discovery of the new *Phyllodactylus* species at Malpelo may have traveled faster than any other species discovery in history as it was flashed the same day to the ship's home port at Little Creek, Virginia. Sorting, preservation, and labeling continued past dark while at the same time, in other parts of the ship, other men worked, and scuba tanks, thermos bottles, and lunch containers were refilled for use the next day. When work was finished for the day, showers, warm food, a recounting of the day's adventures, a soft bed, and last, but by no means least, the evening movie fully restored us for the next day.

Investigation of Malpelo's marine habitat was also rewarding. The water was so rough, however, that the small boats we had brought for the diving teams were unsafe and diving operations had to be staged from one of the York County's boats. We initially tried to use the ship's landing crafts but these had so much freeboard that they were not practical. After struggling through a day's diving from the landing craft, I related this difficulty to Captain Seeber, who immediately offered us the use of his launch. Thus it came to be that the elegantly furnished Captain's Gig became our diving boat. No doubt the launch has seen better days both before and since we loaded it with divers, their gear, and specimens. But it proved an invaluable asset at Malpelo. There were many sharks around the island; they were seen at the surface and on every dive. No particularly dangerous encounters occurred with sharks during our dives,

but their omnipresence was sobering and at times their proximity was slightly unnerving.

Birkeland and colleagues completed their ambitious project of studying and characterizing the subtidal benthic communities at Malpelo. The smooth vertical subtidal walls are dominated by large, sparsely distributed barnacles. Recruitment success for transforming barnacle larvae is low but once they are established, adults may live for a long time. On the gently sloping southeastern edge of Malpelo, Birkeland's group found extensive coral development. Although they do not constitute a true coral reef, these corals are luxuriant and depth zonation is marked for different species. The occurrence of corals to as deep as 30 meters, about the deepest known in the eastern tropical Pacific, is attributable to the clear water around Malpelo. A list of all the marine invertebrates known from Malpelo is appended to the Birkeland et al. paper. Abele records 43 species of decapod crustacea (18 species of macrurans) at Malpelo and describes two new species of snapping shrimp. Abele lists the distribution of each species and, by drawing upon his other recently completed studies, he makes an interesting observation about the species diversity of decapod crustaceans at Malpelo, Cocos Island, and several other eastern tropical Pacific localities. The diversity of starfish at Malpelo is low and Downey lists only six species in her paper. Three species occur throughout the eastern tropical Pacific and a new species of *Tamaria* and a new subspecies of *Narcissia* are described for Malpelo. Until Downey's work, one Malpelo starfish (*Leiaster*) was previously known to occur only at the Hawaiian Islands.

Our knowledge of the Malpelo fish fauna is still incomplete but McCosker and Rosenblatt report that 70 species of fish are now known for the island. In the specimens collected in the Smithsonian-Navy Expedition, McCosker and Rosenblatt found several new species, as well as a new genus of fish; all awaiting description except the new species of goby (*Chriolepis*) described by Findley. The Abele, and McCosker and Rosenblatt papers demonstrate several interesting features that the decapod crustaceans and fishes of Malpelo have in common. The majority of species in both groups are Central American mainland forms; there are also Indo-Pacific species and some endemics. Both groups contain species that were previously

thought to be endemic at Cocos or the Galapagos islands or were known only from these two localities. These findings strongly suggest that Malpelo is a stepping-stone for marine mainland species enroute to more distant islands and, as the surface current patterns indicate, for Indo-Pacific species as well. Some of the terrestrial invertebrates listed by Wolda appear to be most closely related to Indo-Pacific groups, which prompts the conclusion that these were rafted from the old world to Malpelo via the Equatorial Countercurrent. The exchange of species between Malpelo, Cocos, and the Galapagos Islands is implied by their similar fish and decapod faunas and by the marked faunal similarity observed by Birkeland et al. between Malpelo and the Galapago Islands. Further work with these faunas will clarify these relationships.

Although much was learned at Malpelo the short time for study has left questions and the biota of the island would doubtlessly be better understood if more sampling, observation, and experimentation could be conducted. It was agreed that additional visits should be made, ideally at different times of the year so that the possible influence of seasons could be assessed. That there is much to learn is evident when it is pointed out that we still do not know how much rain annually falls on Malpelo. Murphy (1945) suggested that the island never receives rain, but Malpelo does lie within the range of the convergence of the trade winds (Intertropical Convergence Zone, Wyrтки, 1965), which suggests a seasonal rainfall. The island does have weathered, phosphatized rock (McConnell, 1943), and seepage marks, dry stream beds, and pools of water were found by the Smithsonian-Navy expedition. All of these suggest that rain is not uncommon but expeditions to the island have practically all been during the months of the dry season (December to March) and we can only speculate about amounts of rain in the rest of the year.

This volume, by reviewing and compiling Malpelo's literature and by reporting results to date of the most thorough investigation of the island sets the stage for future exploration. It describes Malpelo but it cannot convey the impressive scenario of that island. When viewed objectively it is an isolated, inhospitable island, which by these

virtues has remained a natural laboratory for the study of evolution.

When seen first hand, however, Malpelo is a large grotesque rock that rises rudely, ominously out of a monotonous sea. As we contemplated this rock we reminded ourselves, and took pleasure in the fact, that it was a sight that few people have ever seen.

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Terrestrial Biology of Malpelo Island: A Historical Review

George C. Gorman
and Terence L. Chorba

ABSTRACT

Records of the exploration of Malpelo Island date back to 1542. Early biological investigations mainly concerned the terrestrial fauna, particularly the island's lizards. The complete list of Malpelo's avifauna is presented. The etymology of Malpelo is discussed.

That the biology of Malpelo would be poorly known should surprise few people. The island couples geographic isolation with hazardous accessibility. It also lacks spectacularly unique denizens such as Komodo dragons or giant tortoises. Thus interest in Malpelo is primarily restricted to the dedicated naturalist who can appreciate that the very isolation makes it a laboratory of evolution, and who realizes that a species need not be the largest or the strangest to be of genuine biological interest. The joint Smithsonian-U.S. Navy Expedition to Malpelo was not the first to visit this unique corner of the world; others have stopped on the island, perhaps while enroute to the Galapagos, or while collecting marine life off the coast of South America. Our expedition probably was the first to be dedicated to the Malpelo ecosystem per se, to attempt to collect and identify as many of the living forms as was feasible, to examine the behavior and ecology of at least some of the species,

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and to attempt to understand the flow of energy in the system. The expedition will have been successful if, for no other reason, others are inspired to visit this unique massive rock to pursue further some of the interesting problems raised in these pages.

The first record of a landing on Malpelo that we know of took place in the late 18th century. The Spanish Commodore, Alejandro Malaspina (in Malaspina and Bustamente, 1885:551) quoting one of his officers wrote:

One of the shipmasters in the local trade, favoured by fine weather and a smooth sea, once landed on a shelf of rock on the north face of the island, and after climbing thirty steps down hewn out by hand, came upon a large pool of rain-water, which was not overclean and had some bird feathers in it; but . . . he used the opportunity to fill some casks. This . . . is all that can be said about Malpelo.

At the time there was more that could have been said, but Malaspina either was not familiar with any previous mention of the island by the chroniclers, or did not consider what they said to be of sufficient importance.

Pedro de Cieza de León (1881:92) wrote that the Spanish colonial administrator in Peru, Cristóbal Vaca de Castro, en route from Panama to Buenaventura in 1542 "came to a rocky islet which the sailors call Mal Pelo."

Literally, Malpelo means "bad hair." The origin of this name is unknown but the island appears on a parchment map of the world of 1550 (Desceliers, 1550) that is in the British Museum. The name on the map is "ye mallabry." The term "malabrigo" was frequently used by cartographers to designate islands and bays. Literally, "malabrigo" means

shelterless. Such a name would be well deserved. Another possibility, however, is that the word "Malpelo" has roots in the Latin *malveolus* (literally "inhospitable" or "spiteful"), which in the vernacular could have degenerated to "malbolo" and at some point been interpreted as "malpelo."

At the time that Vaca de Castro sailed past Malpelo, though perhaps unknown to the Crown, the island was a territory of Spain by virtue of the Papal Bull issued in 1493 by Pope Alexander VI, and the Treaty of Tordesillas (1494) under which Spain and Portugal divided the non-Christian world in half. Subsequently, Malpelo passed automatically to Peru and later to Colombia without dispute. Inaccessible, uninhabitable, lacking arable land and suitable anchorage, it is not the kind of real estate for which one battles furiously.

One of the first scientists to discuss life on Malpelo was C. H. Townsend (1895), who visited the island in March 1891 on board the U.S. Fish Commission Steamer *Albatross*. During the brief visit, Townsend collected a Swallow-tailed Gull (*Creagrus furcatus*) and noted that seabirds of several species swarmed about the inaccessible summit.

Townsend also collected the first reptiles with the locality data "Malpelo Island." These lizards were described as *Anolis agassizi* (Iguanidae) by Stejneger (1900:163), who reported:

Mr. Charles H. Townsend, who collected these specimens in Malpelo, informs me that they were running over the rocks near the water. The island was too steep to afford a landing, but the lizards were shot off or whisked off the face of the cliffs, thus falling into the water, whence they were secured by the collector.

Two years prior to the publication of Townsend's report, Faxon (1893) described the common land crab of Malpelo as *Gecarcinus malpilensis* (Gecarcinidae) from a single male specimen collected by the same expedition in which Townsend collected the lizards. No notes other than a description were provided.

In November and December of 1927, Captain A. G. Hancock made a trip to the Galapagos. J. R. Slevin of the California Academy of Sciences was along, and when the boat passed near Malpelo, Slevin and a colleague were able to effect a landing from a small skiff on the northeast corner of the island. They collected 27 *Anolis* (a medium-sized lizard) and 10 specimens of a large anguid lizard

which Slevin (1928) named *Celestus hancocki*. He claimed that this lizard was most closely related to *Celestus millepunctatus* O'Shaughnessy known from a single specimen of unknown provenance, but that it differed from *C. millepunctatus* in several features of scutellation and limb development.

Slevin did not explore the island. All his specimens of *Celestus* were taken within a few feet of the water's edge on a rocky ledge. When wounded, he claimed that they would take to the water. Stomach contents consisted of feathers and remains of crabs.

The George Vanderbilt South Pacific Expedition of 1937 stopped at Malpelo in February. Some field notes by the Vanderbilt's collector Ronald Smith were published by Fowler (1938).

Smith was confused in his taxonomy, since he believed that there were five species of lizards roaming about. But from his descriptions it is obvious that there were only the two known forms. Sexual dimorphism, and perhaps distinctive size classes led to his erroneous conclusion. Since we can easily determine when Smith was referring to *Anolis*, and when to *Celestus*, we might mention a few of his ecological observations. He claimed that the *Anolis* was found throughout the island, all the way to the summits, but that the *Celestus* was limited to the height of 150 meters. He also reported a habitat difference. The anoles were seen mostly amongst loose rocks and exposed surfaces, whereas the *Celestus* were found primarily in small cave-like formations. The lizards were described as fearless and quite bold.

The Vanderbilt expedition collected four specimens of *Anolis* and seven *Celestus*, and this served as impetus for Dunn (1939) to reconsider the lizard fauna of the island. He made two major decisions at the generic level, one that has stood the test of time, the other that has not. Dunn pointed out that the genus *Celestus* could not be maintained as distinct from *Diploglossus*. He assigned the large anguid to *Diploglossus*, the generic name that it still bears. More interestingly, he demonstrated that the previously described *C. millepunctatus* was not distinct from Slevin's *C. hancocki*. Thus the specimen described by O'Shaughnessy in the mid-nineteenth century was almost certainly obtained from Malpelo, although no records of an expedition to the island have been

found. The second decision was to raise the anole to a distinct genus (*Mariguana*). This decision has not been accepted (Etheridge, 1960).

Bond and deSchauensee (1938) presented an annotated checklist of the birds of Malpelo based upon the observations and collections of the Vanderbilt expedition and incorporating data from Townsend (1895). It is reprinted below in its entirety.

ANNOTATED LIST OF THE BIRDS
OF MALPELO ISLAND

1. *Sula dactylatra granti* Rothschild. (Sulidae, Pelicaniformes) Masked Booby. Two adult males were collected February 8, and an immature female February 9.
2. *Fregata* sp. (Fregatidae, Pelicaniformes). None collected but Smith notes: "Man o'War Birds 50; small colony on one of the outlying rocks on the southwest of the island."
3. *Falco peregrinus anatum* Bonaparte. (Falconidae, Falconiformes) Duck Hawk. Not collected but two birds observed twice by Smith on Malpelo Island.
4. *Actitis macularia* (Linnaeus). (Scolopacidae, Charadriiformes) Spotted Sandpiper. Not collected but "ten seen in company with tattlers."
5. *Heteroscelus incanus* (Gmelin). (Scolopacidae, Charadriiformes) Wandering Tattler. One male and two females, in winter plumage, were collected February 8 and 9. About twenty-five individuals were seen.
6. *Creagrus furcatus* (Neboux). (Laridae, Charadriiformes) Swallow-tailed Gull. An adult male and female as well as a nestling were collected February 8 and 9. Smith records a colony of thirty birds on the island.
7. *Anous stolidus ridgwayi* Anthony. (Laridae, Charadriiformes) Noddy. An adult female, the only specimen seen, was secured February 9. It was not in breeding condition.
8. *Anous minutus diamesus* (Heller and Snodgrass). (Laridae, Charadriiformes) Black Noddy. An adult male collected February 9, was the only specimen seen. The bird was not in breeding condition.
9. *Hirundo rustica erthrogaster* Boddaert. (Hirundinidae, Passeriformes) Barn Swallow. An immature female was secured February 8. Four birds were seen flying out of a cave.
10. *Progne* sp. Martin. (Hirundinidae, Passeriformes). Recorded by Townsend but none secured. Smith did not see any martins.

During March 1941, the schooner *Askoy* approached Malpelo and Dr. Robert Cushman Murphy and another member of his party made a landing. His popular article (Murphy, 1945) provides the best summary of the natural history of the island. He estimated the booby population at about 25,000; added an additional species to the

bird list of Malpelo (Red Billed Tropic Bird, *Phaëthon aethereus*); examined the stomach contents of a gull and found that it was eating marine crabs; and, most important, noted the presence of a diversity of invertebrates including spiders, pseudoscorpions, beetles, flies, ants, and other insects. Samples of Malpelo rocks were obtained by Murphy and a study of phosphatization at Malpelo was published by McConnell (1943).

The land crabs (*Gecarcinus*) impressed Murphy (1945:16) who described them as

ghoulish in appearance . . . , fat and bloated looking creatures with shells of a ghostly white. They may be quite harmless toward human beings, yet they seem to eye a visitor with an intent that grows uncomfortable. If you sit long enough the crabs will move up closer and closer, as if with whetted appetites, and I have a feeling that they would make life miserable for anyone who had to sleep ashore.

Garth (1948) provided important information on this crab. He did not agree with Faxon (1893) that it was an endemic species, but considered it *G. planatus* Stimpson, a species widespread from Baja California to Acapulco, that has successfully colonized the Revillagigedo Islands and Clipper-ton, but that is notably absent from the Galapagos.

There have been additional landings on Malpelo, some documented by specimens. For example, the San Diego Society of Natural History has lizards collected in December 1931 and January 1933, by Cyrus Perkins. There is, however, little additional published information about the ecology and natural history of the island or its inhabitants. What inspired the present expedition? Why travel hundreds of miles to visit a barren rock? The very harshness of the environment raises interesting questions. In addition to sea birds, and a few nonmarine birds that are very strong flyers but presumably not residents, only three common terrestrial residents, *Anolis* and *Diploglossus* (lizards) and *Gecarcinus* (a crab) had been described and identified. What species of plants (if any) and invertebrates would be found? What are their biogeographic affinities? How does such a community maintain itself?

Our working assumption was that this was a terrestrial ecosystem dependent upon primary production on the sea and not on the land itself. Presumably the birds which fed upon marine life provided food resources for small terrestrial inver-

tebrates (parasites, carrion eaters, egg predators, etc.) which in turn provided sustenance for the lizards.

Several of us were specifically interested in the *Anolis* lizards. The genus is comprised largely of tropical arboreal species. They tend to be highly territorial, defending fixed perch sites with elaborate displays. Here was an environment devoid of the typical plant cover that we associate with *Anolis*. Did they have any special physiological adaptations that permitted life on warm, exposed rocks? Was there any modification of the social structure of populations in the absence of typical perch sites that are associated with their territoriality?

These are the kinds of questions that were on our minds when we first discerned the form of Malpelo Island, gray itself against the gray of the early dawn on the sea on 29 February 1972. Answers are what we sought when we braved the steep swells and jumped off the landing craft to begin serious exploration of the island and its life.

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Reconnaissance and Mapping of Malpelo Island

A. Ross Kiester
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ABSTRACT

Daily observations of the exploration party are reported. Early maps of Malpelo show it to have one peak with a maximum elevation of about 300 m. The exploration party surveyed and mapped the island and found that the island has twin peaks, which are both approximately the same height and about 150 m higher than previous maps indicate. An improved map of Malpelo is given. It is believed that the Smithsonian exploration team is the first to reach the island's summit.

Introduction

An overflight of Malpelo Island, arranged through the courtesy of the U. S. Army, in preparation for the U. S. Navy-Smithsonian Expedition to Malpelo showed serious defects in the official map based on a 1954 aerial survey. The published U. S. Navy Hydrographic Office map (No. 1685, North Pacific Ocean, Isla del Coco, Malpelo Island inset) showed a single major peak of 260 meters (845 feet) on the island. Observers in the overflight reported two distinct peaks of nearly the same height, read as roughly 390 meters (1200 feet) on the plane's altimeter. Initial observations from the ship on arrival at Malpelo did not reveal which of the peaks was higher. They were so close in height that whichever peak was closest to the ship appeared the highest. A previous expedition had re-

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ported reaching the summit of the rock, but had not indicated which of the two summits they considered this to be. Indeed very little general description of the topography of the island existed in the literature, and no mention was made of the existence of the two peaks. Because of this confusion, a general survey of the topography of the island was one of the expedition's scientific objectives.

In pursuit of this objective, two members of the terrestrial party of the expedition extensively explored the entire island, while other members of the party carried on intensive studies at one site. In this report we give a general description of the island as obtained by the survey party, and discuss the mapping of the island.

Mapping Technique

As the party traversed the island, measurements were made of the horizontal and vertical angles between the various summits and landmarks. All measurements were made with a marine sextant and a Brunton compass. Further surveying was done from the ship. Sextant measurement of the angles between the various features of the island can give the height of these if the distance to the island is known. This method, however, limited the survey to the various peaks and ridges visible in profile from the ship. An accurate knowledge of the location of each feature on the island was necessary for the reduction of sextant sights. While the ship was circling the island, azimuth bearings were taken with a pelorus at regular intervals on all of the main features, including the north and

south tips of the island. An attempt to use gun-ranging radar to fix the distance from the island was frustrated by an uncertainty in determining the radar reflection point on the island. Lacking this distance measurement, the position of the ship was fixed by the intersection of the azimuth bearings to the tips of the island and to the "South Peak," which position was shown on the old map. Further surveying had to accept the island outline and scale of the published Hydrographic Office map. But these are less likely to be in error than the photographically determined contour lines. The intersections of the azimuth bearings to each of the features from the various ship positions located each feature on the map. Heights were determined from vertical sextant measurements of the angles between the features and the waterline, and horizontal angle measurements of the width of the island. An azimuth bearing to the South Peak combined with the horizontal angle fixed the ship's position during this phase of the surveying. The linear heights of the features were then obtained by solving a simple proportional equation and correcting for the height of the observer above the waterline of the ship.

Itinerary of the Exploration Party

A preliminary idea of the topography of the island was gained the first morning by making a complete circuit of the island close into shore. This survey also provided an opportunity to pick out possible landing sites. The island is quite steep along the sides and has a rather flat-topped appearance. It has three distinct peaks (Figure 4). At the north end of the island is the smallest of the three which was termed "North Peak." This summit is sharply set off by nearly vertical walls all of the way around it. The top, however, appears to be relatively flat. This peak is separated from the next by an east-west fault. This next peak south is cylindrical and butte-like, and is much higher than the first. It appears to have equally as steep sides and is also flat on top. This peak was referred to as "Plug." To the south of it, separated by a huge east-west fault which split the entire island is a more rounded peak which appeared to be of the same height as Plug. This summit was called "South Peak." From it the island slopes down to the south until it reaches the rather sheer cliffs at

the southern end. Beside the peaks the most conspicuous feature of the island is a large arm extending out on the west side of the island and forming a small bay (Figure 4). The bay is narrow and the cliffs surrounding it are very sheer, giving a fjord-like appearance. Several sea caves and arches were also seen on the circuit. Besides the main island itself, there are several other rocks and sea stacks in the vicinity. The two largest groups of these rocks are clustered to the north and to the south of the island.

A total of three days were spent exploring the main island and one day was spent exploring the largest of the offshore rocks.

After the circuit of the island, a landing site was chosen on the south side of the end of the spur which forms the fjord-like bay on the west side of the island. This site became the base for most of the exploration and the location of most of the intensive studies of the terrestrial biology of the island. This landing and study site was designated Landing Site 1 (Figure 4). After landing the entire party and its equipment, the exploration team started climbing up the spur. The vista up the

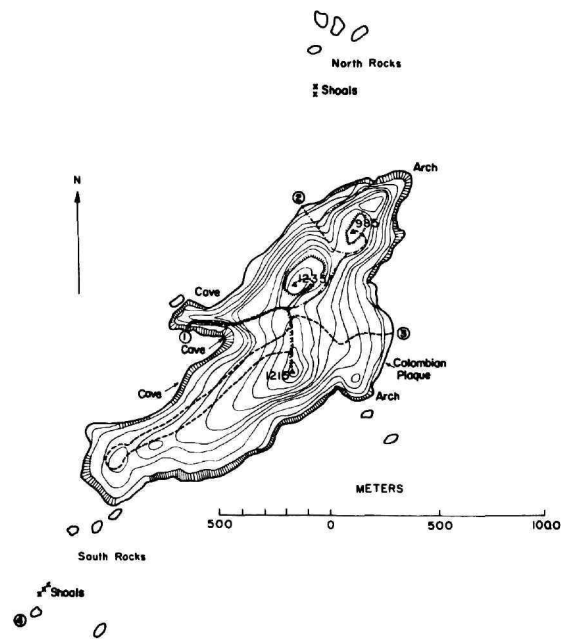


FIGURE 4.—Reference map of Malpelo showing the various landing sites (1-4) mentioned in the text, the routes taken by the exploration party, and significant landmarks.

spur toward the saddle between Plug and South Peak was a rocky slope completely devoid of vegetation. Climbing up the spur the party found several caves of various sizes, including one which went through the spur from one side to the other. The only vegetation that could be found was algae which was growing inside of the caves and crevices where some moisture was present. After some scrambling, the saddle was reached. Here a cairn with a bottle containing the names of several Colombians from two mapping and survey expeditions was found. In the saddle the lava was shot through with holes of varying diameter, making movement slow. From here the party ascended to the summit of South Peak. Once on the summit the party had a view down the entire south end of the island. This view corresponded exactly to the photograph taken from the summit by the Vanderbilt Expedition of 1937 (Bond and deSchauensee, 1938, plate 10a). Thus it was concluded that the Vanderbilt Expedition had in fact climbed South Peak.

As sighted from South Peak, the Plug had an elevation of 1° to 1.5° horizontal, showing it to be the true summit of the Malpelo rock massif. As surveyed from the ship, Plug was determined to be approximately 6 meters higher than the South Peak. The root mean square errors for the measurements of the two peaks from various ship positions are about equal to the difference in height of the two peaks. The 1° to 1.5° elevation of the northern peak as sighted from the southern corresponds to a height difference of 6–9 meters, which agrees with the difference as determined by sextant sights from the ship.

From South Peak the party returned to the saddle and climbed up to the base of Plug. From this point the climbing became more difficult. After some searching, a chimney on the east side of Plug was found that afforded a relatively easy, but nonetheless technical (class 5), climb up to the top. No bottles or cairns were found on this summit plateau. None of the previous parties climbing on the island had mentioned the necessity of technical rock climbing for the routes they used. Thus, the Smithsonian party seems to have been the first to reach the summit plateau of Plug.

As with the southern summit, Plug was devoid of vegetation. However, both species of lizards (*Anolis* and *Diploglossus*) were common up to the

top of the two peaks, as were the land crabs (*Gecarcinus malpilensis*). Blue-faced Boobies (*Sula dactylatra*) were also omnipresent. At the top of both peaks a strong breeze was blowing continuously in contrast to the still conditions lower down on the leeward side of the island. From Plug the party climbed back down to the saddle and thence down to the landing site.

On the second day the party landed on the northwest edge of the island (Landing Site 2, Figure 4). While two members of the party worked near the shore, two others climbed towards North Peak. Initially the peak was attempted by climbing around the west side to its north face, which had several large chimneys. Also in the area is a spectacular spire isolated from the main peak. The route was frustrated because the chimneys were seen to contain formidable chock-stones. On the less steep slope to the northwest of the North Peak were some of the few patches of grass to be found on the island. The largest of these patches was not more than several square meters in area. Retracing their steps the party then climbed to below the saddle between Plug and North Peak. Here there was a gully which led up to the saddle. In the gully several large pools of water were observed. One of these was perhaps one-half meter deep and was the largest body of standing water seen on the island. The pools contained some aquatic insects which unfortunately could not be collected. Continuing up the gully into the fault proved difficult and roped climbing was necessary to scale a 25-meter lava wall. From the saddle it was a relatively easy scramble up to North Peak. Again both species of lizards and numbers of boobies were present all the way up to the summit, and the wind was blowing steadily in contrast to the leeward side. From here the party climbed down along the east side of Plug and over the saddle south of Plug and down to Landing Site 1.

On the last day of exploration of the main island, a party of two landed on the east side of the island (Landing Site 3, Figure 4). This landing site was used by a Colombian expedition which had placed a bronze plaque to mark the site. The party made its way up to the saddle south of Plug and then up to South Peak. From there they climbed down to the southern end of the island. The area southwest of South Peak is relatively the flattest part of the island. The slope leading

from South Peak down to the end of the island was a scree slope with small rocks cemented by solidified lava. Lava bombs were strewn about liberally, and all over the lava had solidified into cubist architectural forms. The south end of the island was extremely dry. Few lizards were seen on the central dome of the south ridge, but both species as well as the land crab were abundant on the extreme south end. There was a small patch of grass on the southernmost cliff. From the south end the party hiked back up over South Peak and then back down to Landing Site 1.

On the fourth day, the party visited the largest of the offshore rocks (Landing Site 4, Figure 4). This rock is in the South Rocks group and like the other rocks it is quite steep. A landing was difficult and roped climbing began from the tiny shelves near the water. Near the top of the rock (45m = 130 ft) the slope decreased appreciably. Rather surprisingly, a large patch of grass was found here. This was the largest and lushest stand of vegetation found anywhere. *Anolis* were common in the grass as well as on much of the top of the rock. *Diploglossus* were also found, but not in large

numbers. No land crabs appeared to be on the rock. Several small bushes and a fern were growing at the top of the rock. The bushes frequently showed large trunk masses with only small green shoots. This was suggestive of large seasonal variations in rainfall.

A Red-footed Booby (*Sula sula*) was sighted perched in the middle of the bushes. This species habitually perches in trees in contrast to the Blue-faced Booby, and has not previously been reported from Malpelo Island. Positive identification was made when one of the members of the party was able to climb down to within a few meters of the bird before it flew, and secure several good photographs showing the characteristic red feet of this species.

As with the landing, departure from the rock was somewhat difficult due, in part, to the nearby shoals.

Conclusion

The survey undertaken by the exploratory party resulted in the map shown in Figure 5. As mentioned above, the outline of the island and the scale are taken from the old Hydrographic Office map, but the topography and contour lines are the result of the new survey. It should be borne in mind that the map may not be entirely accurate due to the rugged nature of the terrain, and to the limited time and equipment of the survey party.

Future visitors to Malpelo should be able to make substantial improvements in the map, particularly with regard to geological details. Any extensive on-site surveying, however, could not be accomplished without a good deal of technical climbing. We hope that this map will be of some help to any future visitors.

Finally we remark that the rather dry description given here in no way does justice to the sustained surrealism of this unique and unusual island.

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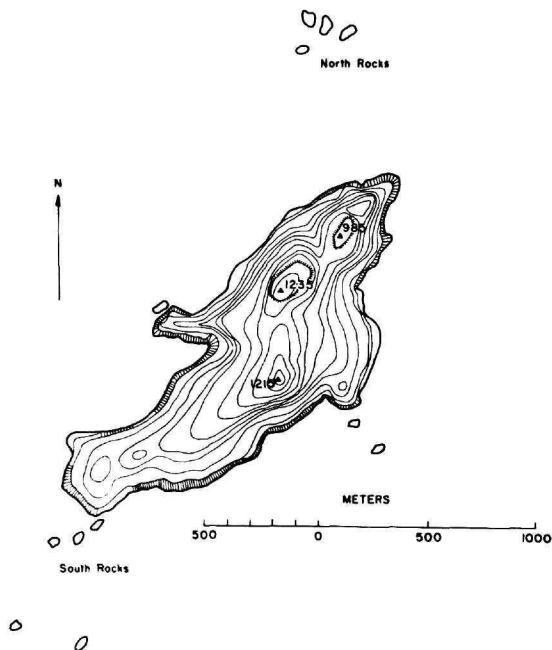


FIGURE 5.—A revised map of Malpelo showing summit altitudes and land contours based on the surveying of the STRI exploration party in March 1972.

Field Observations on the Geology of Malpelo Island

Jeffrey A. Stead

ABSTRACT

Malpelo Island had a volcanic origin. Depth soundings around the island indicate that it was once 8 to 10 times larger than its present size. Marine weathering has eroded the island and has formed steep cliffs and sea caves along its sides. Several types of igneous rocks and minerals occur on the island. The distribution of major joints and faults is shown.

Published accounts of the geology of Malpelo Island include McConnell's (1943) analysis of three rocks from the island and the field observations of Murphy (1945, also in McConnell, 1943). The amygdaloid specimen assayed by McConnell (1943) showed a small amount of phosphatization (replacement of natural minerals by phosphate compounds derived from guano) while this process was very advanced in another rock (phosphate rock). The specimen of augite andesite was only slightly altered by phosphates. Murphy reported that guano was not very concentrated on the island and McConnell (1943) concluded that phosphatization occurs mainly in porous areas of the island (along faults and fractures) where guano could be carried and concentrated by rains.

Malpelo is volcanic in origin, the present island is the remnant of a much larger structure. Most of the island's perimeter consists of nearly vertical rock faces which extend from 60 to 230 meters above sea level (Figure 6).

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Several types of igneous rocks are present on Malpelo. Field identifications are as follows: dacite, trachyte, tuff, basalt, and andesite. Up to an altitude of 210 to 240 meters, the island appears to be mostly trachyte, with lesser amounts of dacite and tuff. This lower zone is intruded by at least two sets of dikes made up of basic rocks. The top of the island is covered by an andesite cap.

Field identification of minerals is as follows: Specimens of dacite collected near the landing site contained amygdules of quartz and apatite. One amygdule contained fine, hairlike, zeolite crystals coated with hematite. Small amounts of chrysocolla were found in a joint at an altitude of about 240 meters. Guano occurs in limited amounts on all parts of the island.

Fresh water seepage was observed in several places. Red streaks of iron oxide are deposited on the rock faces where seepage has occurred. Some of these streaks represent principal areas of runoff following rainstorms rather than permanent seepage areas.

Steep cliffs around the perimeter are probably maintained by the combined effects of wave action, which loosens and removes rock in low areas (Steers, 1953), rain, and alternate heating and cooling, which loosen the soft lavas (mostly trachytes) above the normal splash zone until they fall off along joints. The lava cap is a very resistant rock, and probably does not fall until the rock underneath it has been weathered away.

Sea caves (Figure 6) are formed by the scouring action of waves on brecciated rocks around faults (Guilcher, 1958). There are many small faults on Malpelo, most of which intersect the waterline at large (60°-90°) angles. The largest cave was estimated to be 9 meters wide and 13 meters high

(above sea level) and to have a 10-fathom water depth at its mouth. Some of the caves have a white formation on their ceilings which resembles flowstone. This is probably composed of insoluble substances from guano, washed down along the faults and redeposited on the ceilings of the caves.

Small amounts of soil, consisting of variable mixtures of clay and animal feces, are found in sheltered areas of the island. Soil is found nowhere in large amounts, but increases in abundance with increasing altitude, and rarely occurs below 90 meters. The absence of soil in the lower levels can be attributed to steep slopes, rain, and to wave action which, during severe storms, can splash water to considerable heights (Johnson, 1919).

Two major sets of joints and faults were measured in the fjord area (Figure 7). Their average measurements were as follows: strike 210°T , dip 79°NW ; strike 110°T , dip 82°SW . The eastern wall of the fjord is the scarp of a major fault, represented by a cliff over 60 meters high and half a kilometer long. This fault, which is the most promi-

nent feature of the fjord, strikes 205°T and dips 78°NW . The largest sea cave on the island is at the apex of the fjord (Figure 7).

The U.S.S. *York County* made continuous depth soundings around Malpedo Island. These soundings, plus those from a 1952 U.S. Navy sketch survey, are shown in Figure 7.

Bottom depth falls off greatly to 50–60 fathoms on all sides of the island, but the bottom gradient increases rapidly at 60–70 fathoms (Figure 7). The area out to the 60-fathom curve may represent a wave-cut plateau formed during the Pleistocene (Shepard, 1963). If this is assumed, the 60-fathom curve would indicate the minimum size of the original volcano. A line has been drawn (Figure 7) to indicate a depression in the sea floor. This may be a fault. Its trend, 218°T , is close enough to the $210^{\circ}\pm\text{T}$ average of one of the major joint sets on the island to strongly indicate a structural relationship. The dashed line trends 136°T , and also may indicate a fault, or it may mark the division between two previously existing cones.



FIGURE 6.—The southwestern tip of Malpedo Island showing the lava cap, the steep cliffs, and narrow caves that occur at the waterline all around the island.

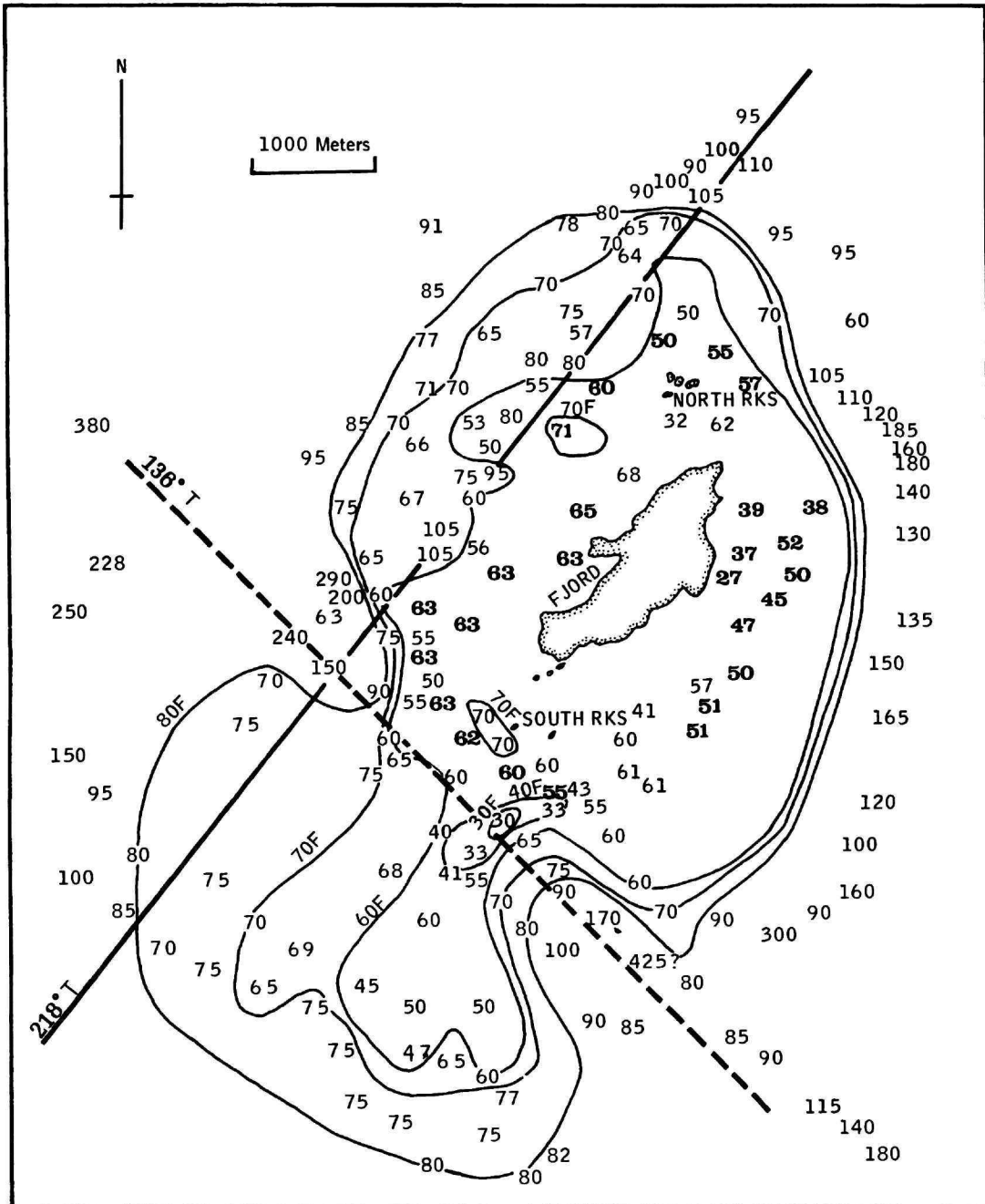


FIGURE 7.—Map of Malpelo Island showing depth soundings from a U.S. Navy 1952 sketch survey (boldface numbers), those from the U.S.S. York County (lightface numbers) and depth profiles around the island. The location of two submarine faults (218°T and 136°T) are indicated.

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The Ecosystem on Malpelo Island

Henk Wolda

ABSTRACT

A rather high percentage of predators was found among the terrestrial invertebrates of Malpelo Island. Except for the birds and one of the lizards, almost all of the animals depend on a purely terrestrial economy based on numerous algae, lichens, and mosses.

Studies on the biota of isolated islands and groups of islands have produced exciting results, influencing and even initiating the theory of evolution. Almost all existing islands have now been surveyed, at least to some extent, but until 1972 Malpelo remained a notable exception. Except for the vertebrates no collections had been made, presumably because it is remote and almost inaccessible. The location of the island, however, suggests that it may contain species that are highly interesting biogeographically, especially because introductions of species by man are very unlikely. Although some landings have been made (Fowler, 1938; Bond and deSchauensee, 1938), very few people have ever set foot on the island.

A number of seabirds, a land crab, and two species of lizards are known from Malpelo, but statements in the literature about plants and invertebrates are not very encouraging. It is reported that there is very little (Bond and deSchauensee, 1938) or no (Slevin, 1928) plant life that could support a community of animals. In fact, Slevin (1928) reports that he could not find "any life whatever" except for the species mentioned above. Such a situation seems a priori very unlikely. Even very forbidding habitats, including bare rocks in

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the Pacific (Clapp, 1972) are known to contain a variety of species and all kinds of animals are able to reach islands more remote than Malpelo (Carlquist, 1965). Moreover, one would expect at least one of the lizards (*Anolis agassizi*) to feed predominantly on insects. Indeed, Dunn (1939) found "two or three species of insects" in stomachs of *Anolis*. Bond and deSchauensee (1938) report an abundance of "small black gnats or flies" and a chirping, as if by crickets. The most encouraging statement is that of Murphy (1945), who, in the stomachs of *Anolis*, found "remains of small crabs, spiders, pseudoscorpions, beetles, flies and fly larvae, ants and other insects." The problem to be

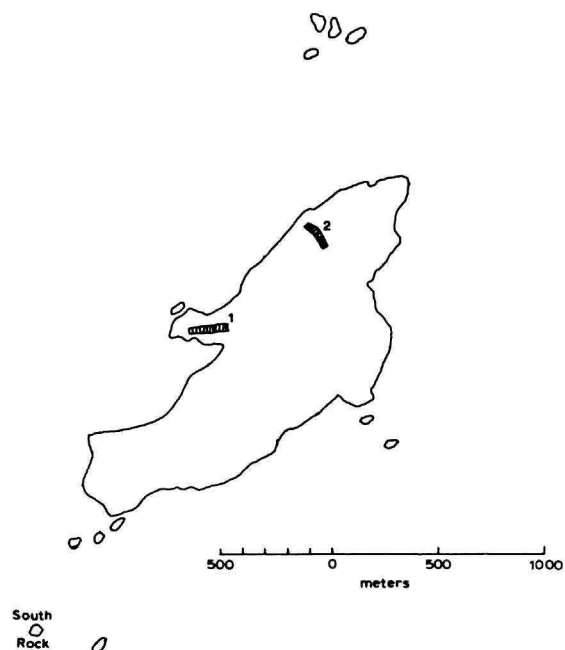


FIGURE 8.—Map of Malpelo Island with collecting sites.

investigated is what animals occur on the island and how do they make a living. The near-absence of plant life reported in the literature suggested that the economy of Malpelo is entirely based on the birds bringing in food from the ocean, their droppings, and dead bodies.

In the first week of March 1972, I was able to test this idea. My collections and observations were made in localities indicated on Figure 8 and I examined some material collected from the South Rock.

The general impression one obtains from the main island is that it is bare rock (Figure 9), with no higher plants except for very few small patches of a yet unidentified grass. On the South Rock this grass was fairly abundant and here also a shrub occurred, possibly a legume, and a fern, *Pityro-*



FIGURE 9.—General view of site 1.

gramma dealbata (Presl) Tryon. On the main island, however, lower forms of plant life were abundant. On vertical rock faces moist with fresh water and under ledges, algae, mosses, and lichens could be found everywhere (Figures 10, 11). A few pieces of rock were collected and eight species of lichens were identified from them: *Caloplaca* sp., *Candelbria* sp., ?*Aspicilia* sp., ?*Diploschistes* sp., *Lecidea* sp., *Graphidaceae* sp., ?*Basidea* sp. and *Pyxine* cf. *glebosa* Tuck. Considering the smallness of the sample, the number of species present may be much larger than this.

This vegetation is the basis for quite a complex community of animals. In crevices and, especially, under rocks, a multitude of animals was discovered. My collection probably does not cover all the species present, but the fact that mine was about as good as the anoles (see below) suggests that I may not have done too badly. I did not make extractions from soil under the rocks and any microarthropods living there would have been missed. The abundance and diversity of the invertebrates obtained (Table 1) is rather impressive. At least 17 species of insects were found, belonging to 8 orders. The "black flies" mentioned by Bond and deSchauensee (1938) represent a new genus of Chloropidae and the crickets they heard belong to the genus *Hygronemobius*, related to *H. liura* described from British Guyana (Gurney, pers. comm.). These two species were among the most abundant insects, together with a little black ant (*Pheidole* sp.) and staphylinid beetles. The two species of snails were fairly common in clusters under rocks at locality 1. There was an extraordinary variety of spiders, some eleven species of Araneida, none of which were webbuilders. Worms and isopods were abundant under rocks at locality 2, far above the intertidal zone.

It is much too early to start speculating about the origin of the species found, but there are indications that some of them may have come from the Indo-Pacific. After a preliminary investigation of the centipeds, Crabill (pers. comm.) suggests that the closest relatives of some of these may not be South American species. Representatives of the opilionid family Assamididae seem to be mostly living in the Indo-Malayan region (Brues, Melander, and Carpenter, 1954). The land crab and all three species of lizards (including the new gecko

described by Huey, pp. 44–46 herein) are all found on Malpelo only, but how many of the other species are endemic is not yet known.

To depict the structure of the ecosystem on Malpelo, i.e., to construct a foodweb, roles had to be assigned to each of the species concerned. The classification of these species as a herbivore, a predator, or a scavenger is based on what is known about relatives living elsewhere and on some observations. The classification of the staphylinids as herbivores, for instance, was made because they were very abundant and found mostly among mosses. The beetle, *Enochrus*, is classified as a predator, although the adults may be omnivorous. The results are included in Table 1 and the tentative foodweb is illustrated in Figure 12. The landcrab *Gecarcinus malpilensis*, was very common and was frequently observed nibbling on stones, presumably feeding on lichens and algae. Remains of insects were often found in their feces. Many of these may have been scavenged or obtained while eating the feces of lizards, but the crabs can also act as predators. On one occasion I saw two crabs that were holding a male *Anolis*, which was still very much alive, although one of its hindlegs was already eaten. A third crab was eating the tail. These crabs also feed on dead birds. They are opportunistic omnivores, but probably mostly scavengers.

I had the opportunity to examine the gut contents of 38 individuals of *Anolis agassizi* from the

main island, plus five from the South Rock. These were kindly given to me by A. S. Rand. Virtually all the items listed in Table 1 were observed, including some juvenile crabs. The only obvious exception were the earthworms, presumably because they are living in soil under rocks and thus inaccessible. It is certainly not because they are distasteful. When I removed the rocks, several anoles came in immediately and feasted on the worms. The anoles from the South Rock also had a variety of arthropods in their guts, but differed from those from the main island in that they had their rectums filled with grass seed.

Both individuals of the gecko, *Phyllodactylus*, had eaten crickets, a few ants (probably *Strumigenys*) and a lepidopteran larva, possibly *Ereunetis*. The number of species per individual was much smaller than that observed in *Anolis*. Ants (*Pheidole* sp.) and staphylinid beetles, both of which made up the bulk of the diet of anoles, were absent in the geckos. These differences could be accidental, but are probably real, *Anolis* being diurnal and *Phyllodactylus* nocturnal.

Nematodes, probably several species, were found in 60 percent of the anoles, averaging three per individual (range 1 to 14). The geckos had 11 and 12 nematodes, respectively.

The large lizard, *Diploglossus millepunctatus*, has a quite different way of life. The feces that I examined did not contain any arthropods at all. They were observed feeding on fish regurgitated



FIGURE 10.—Moist rock face and land crabs at site 1.



FIGURE 11.—Moist wall of empty creek bed at site 2.

by boobies (*Sula dactylata granti*), on fish leftovers after the boobies had fed their young, and on fresh bird droppings. Slevin (1928) and Dunn (1939) found crab remains in *Diploglossus*' stomachs and Garth (1948) suggested that this lizard feeds on both crabs and bird eggs. The latter may be true, but I have no evidence to support this idea.

The foodweb (Figure 12) shows two interesting features. The first relates to the rather large variety of predators, some 24 species, including two lizards. In contrast I found only nine species of herbivores and eight scavengers. This suggests that among the

species living on Malpelo, an unusually high percentage are predators, many of which may be generalists rather than specialists. Two of the herbivores, the snails, seem to be eaten exclusively by the lizards, not by any of the invertebrate predators. These predators are all eaten by *Anolis*, but the bulk of their food consists of herbivores. More exhaustive collections, made at different times of the year, are needed to determine whether indeed the predators make up such a large proportion of the fauna. If this is so, it might have some bearing on theoretical considerations which state that the

TABLE 1.—List of invertebrates found on Malpelo Island with estimate of their food habit (H = Herbivore; P = Predator; S = Scavenger; Par. = Parasite; O = Omnivore)

Oligochaeta		1 (?) sp.	S
Nematoda		spp.	Par.
Gastropoda		2 spp.	H
Diplopoda		sp.	H
Geophilomorpha	Chilenophilidae	Ribautis sp.	P
Scolopendromorpha	Cryptopidae	Scolopocryptops sp.	P
"	"	Cryptops sp.	P
Decapoda	Gecarcinidae	Gecarcinus malpilensis	O
Isopoda		sp.	S
Chelonethida		sp.	P
Araneida	Oecobiidae	sp.	P
"	Selenopidae	Selenops sp.	P
"	Agelenidae	spp.	P
"	Lycosidae	spp.	P
"	Salticidae	about 3 spp.	P
"	Segestriidae	?Ariadna sp.	P
"	Pholcidae	sp.	P
Opilionida	Assamidae	Paramitraceras sp.	P
Schizomida		sp.	P
Acarina		sp.	Par.
Thysanura		sp.	H
Collembola	Entomobryidae	Lepidocyrtus capreli	S
"	"	Lepidocyrtus sp.	S
Orthoptera	Gryllidae	Hygronemobius sp.	H
Hemiptera	Enicocephalidae	Systelloderes sp.	P
Coleoptera	Hydrophilidae	Enochrus sp.	P
"	Staphylinidae	sp.	H
"	Scydmaenidae	?Euconnus sp.	P
Diptera	Ephydriidae	Nostima sp.	S
"	"	Scatella sp.	S
"	Sciaridae	Bradysia sp.	S
"	Chloropidae	sp.	H
Lepidoptera	?Pyralidae	sp.	H
"	Tineidae	Ereunetis sp.	S
Hymenoptera	Formicidae	Odontomachus sp.	P
"	"	Pheidole sp.	H
"	"	Strumigenys sp.	P

number of predator species can never exceed the number of prey species (cf. Levins, 1968), except in some special circumstances (Stewart and Levins, 1973). If the phenomenon is real, it could be that some of the necessarily simplified assumptions on which such theories are based are violated. It could be that predation by the lizards on the invertebrates, prey and predators alike, is so intense, at least during some times of the year, that competition between the invertebrate predators is greatly reduced, thus enabling more of them to coexist. In that case, the problem boils down to what limits the numbers of lizards. We found no evidence of predation by birds on the lizards, nor do the

anoles seem to limit their density through behavioral means, as they are nonterritorial (see Rand, Gorman, and Rand, pp. 27-38 herein). Their gut contents did not suggest that they were experiencing food shortage, but in other seasons this could be different.

The other interesting feature of the foodweb is that my original idea, that the entire economy of the island was based on the sea, may be wrong. Only the birds and *Diploglossus* depend completely, and the landcrab partly, on income from the ocean. All the other species seem to depend on a purely terrestrial economy. I would predict that if the birds, which provide the link between the

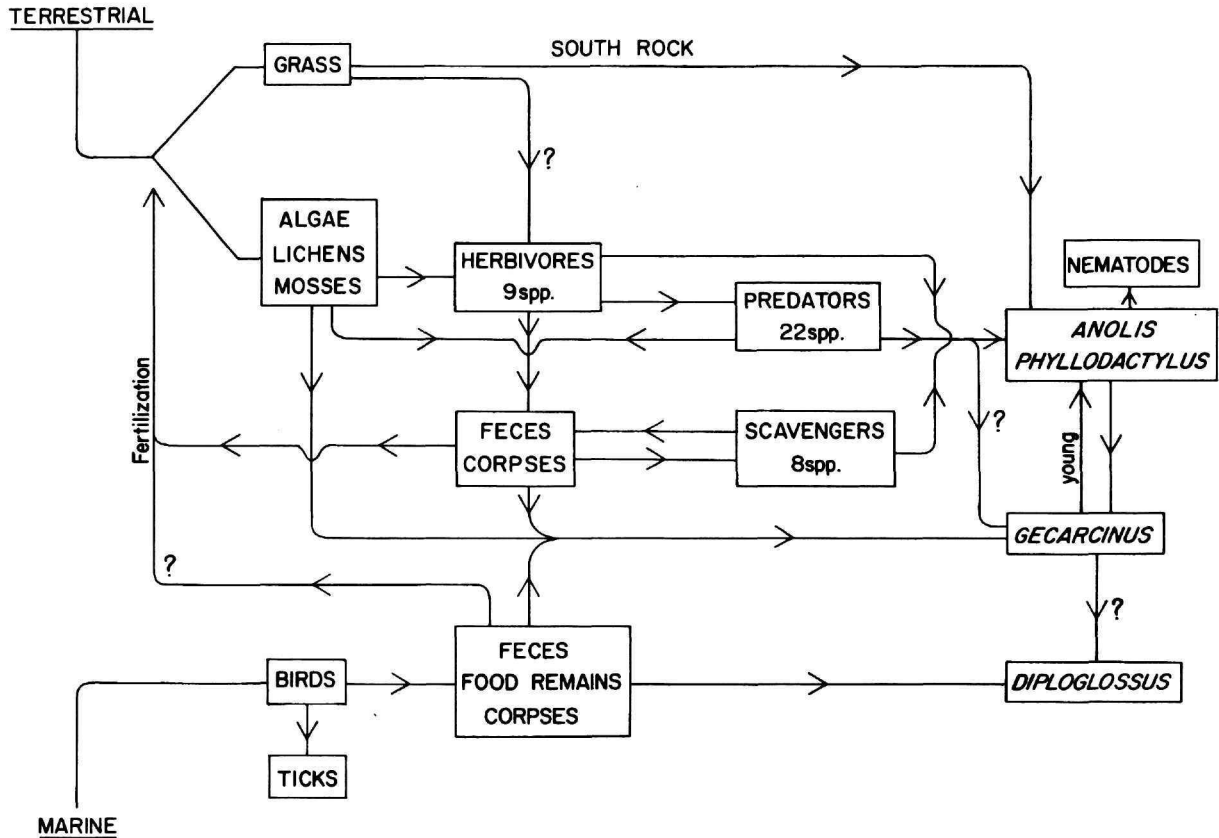


FIGURE 12.—Tentative structure of the foodweb on the island of Malpelo. The four question marks refer to uncertainties in utilization of grass by the herbivores, crabs eating living insects, *Diploglossus* taking living crabs, and the importance of bird droppings in providing nutrients for the plants. For simplicity, some relationships are omitted. These include lizards and crabs providing food for the scavengers and ticks being eaten by *Anolis*.

ocean and the land, disappeared, *Diploglossus* would soon be extinct and the land crab would reach lower densities, but that this would have little, if any, effect on the rest of the fauna. The only condition under which this would not be true is when the weathering rock would not provide enough nutrients for the plants to grow, so that fertilization (e.g., phosphates) by the birds is of vital importance.

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Natural History, Behavior, and Ecology of *Anolis agassizi*

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and William M. Rand

ABSTRACT

Anolis agassizi is found throughout Malpelo Island, and in places is extremely abundant. In one study area we estimated one lizard per two square meters. Social behavior contrasts markedly with other anoles in the apparent lack of territoriality, infrequent aggressive encounters, and reduced display repertoire. There is a strong tendency for social facilitation—the species is aptly described as “curious.” Home ranges are large, and lizards tend to move long distances during the course of the day. Resources such as food, water, and perch sites may be shared by many individuals. There appear to be no special adaptations to temperature extremes nor to desiccation. Reproduction is apparently highly seasonal, as evidenced by the complete absence of small juveniles in museum collections made in December and January, and in our collections of February and March. In our sample about half the females were carrying eggs. The species is larger than most solitary anoles (adult males often > 100 mm) and markedly sexually dimorphic for size (males larger). Adult males fall into two discrete reproductive categories that have morphological correlates. Some have black heads and permanently erect nuchal crests—these have active testes. Others lack the nuchal crest and have spotted heads like the females—these have completely regressed testes.

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Introduction

Almost all islands in the Caribbean have been colonized by one or more stocks of *Anolis* lizards. Patterns of distribution, ecological relationships, and behavior have been extensively studied in these West Indian anoles by Ruibal (1961), Rand (1964), Gorman (1968), Schoener (1969), Schoener and Schoener (1971), Lazell (1972), Williams (1972) and many others. The Pacific waters adjacent to the tropical American landmass are relatively impoverished in islands, and only two are inhabited by *Anolis*. One is Cocos Island, and the second is Malpelo. Malpelo is more isolated than any of the West Indies, which have been naturally colonized by anoles, although strictly in terms of distance it is within the limits known for colonizations by Caribbean *Anolis* (Williams, 1969; Rand, 1969). Malpelo is also more devoid of vegetation than any West Indian island. Caribbean anoles are mostly arboreal, in the strictest sense, the exceptions usually perch on other sorts of vegetation (bushes, grass, cactus, etc.). There are a few anoles associated with rocks, such as *A. rimarum* on boulders in Hispaniola and *A. bartschi* on cliffs around cave entrances in Cuba; but none is from an environment so devoid of higher plants as is Malpelo Island.

Previous to the expedition reported here, our knowledge of *Anolis agassizi* was limited, but the very nature of the habitat suggested that this species might be rather different in behavior and ecology from better known anoles of the Antilles. The species was first described by Stejneger (1900: 161–163) with a detailed account of external mor-

phology. The paper included a superb watercolor plate of an adult male. Stejneger also provided the few field observations available: "Mr. Charles H. Townsend, who collected these specimens in Malpelo, informs me that they were running over the rocks near the water. The island was too steep to afford a landing, but the lizards were shot off or whisked off the face of the cliffs, thus falling into the water, whence they were secured by the collector." Slevin, in 1927, landed briefly on Malpelo and collected a series of *A. agassizi*, but he did not explore the island.

Ronald Smith of the George Vanderbilt South Pacific Expedition of 1937 did explore the island and found anoles all the way to the summit. He described them as fearless and quite bold (Fowler, 1938). Dunn (1939) utilized the Vanderbilt Expedition specimens to reconsider the status of the lizards of Malpelo. Because of peculiarities, particularly a small throat fan, he erected a new, monotypic genus for *agassizi*. This he called *Marijuana*. He reported that the *agassizi* stomachs contained small insects of two or three species. He remarked that the unusual color pattern (see below) was similar to that of the other totally unrelated lizard species on the island, *Diploglossus millepunctatus*.

Etheridge (1960) considered the relationships of all available species of anoline lizards including *agassizi*. He showed that this species fit squarely into the *latifrons* species group of *Anolis*, and he therefore did not recognize the validity of *Marijuana*. The *latifrons* series is an osteologically primitive group of anoles otherwise restricted to the southernmost of the Lesser Antilles and the tropical American mainland from Costa Rica southward. *Anolis agassizi* is virtually indistinguishable from the Lesser Antillean members of the *latifrons* series on osteological characters alone, but genetic similarity evidence (Webster, p. 50 herein) implies that it is not particularly close to either the island or continental species examined.

Compared with West Indian anoles, the Malpelo species was known to be unusual but not unique in several aspects of its biology. *Anolis agassizi* is larger than most anole species that occur on islands without congeners (Schoener, 1969:389), but it is somewhat smaller than *Anolis ferreus* of Marie Galante. *Anolis agassizi* has a very reduced dewlap in both sexes, but not more reduced than

A. hendersoni of Hispaniola or *A. bartschi* of Cuba. The color pattern of *A. agassizi* is unusual, consisting of minute light spots on a very dark ground color, but many species of *Anolis* on small islands have unique color patterns.

We were able to verify these attributes and to discover additional peculiarities particularly in the social behavior of *A. agassizi* during our visits from 29 February to 3 March 1972.

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Distribution and Numbers

Anolis agassizi were found everywhere on Malpelo from sea level to the highest peaks, and also on the only one of the small rocks south of the island that was explored. They were rare on the south plateau and uncommon on the black rocks in the lowest 3 meters.

Anoles seemed less common on the large smooth rock faces than on the more irregular rocky areas which provided more hiding places and probably more food and water. They certainly did not avoid either the vertical cliffs or the more nearly horizontal edges. The concept of structural niche as defined by perch dimensions (Rand, 1964) fails completely in an environment such as Malpelo.

Home Range Size and Population Density

Our home range data are based on marked individuals. On the first afternoon we marked all of the anoles that we could catch in an area of perhaps 20 m long by 10 m high (Figure 13). We visited this area on three succeeding days and recorded the numbers of anoles seen, as well as their activities.

We marked 29 anoles. Of these, we saw 21 again during the next three days. Of the six large adult males marked, five were resighted. The marked lizards did not seem to prefer specific perches; rather they moved back and forth across the rocks,

some moving 5 to 10 meters during a morning. One lizard was seen about 150 meters away from where it had been marked; however, another marked lizard was seen at virtually the same spot on three successive days.

Anoles gathered from distances as great as 10 to 15 meters at concentrated resources, such as the oranges and jellied candy ("Chuckles") that we offered, and at water seeps. Home ranges are large and, even for adult males, are widely overlapping and seem little defended. The long distance moved by one anole and the fact that several marked animals were not resighted suggests that there is a floating population like those postulated for other anoles (e.g., Philibosian, 1972).

During our observations, and when lizards congregated at sliced oranges we had set out (p. 31), we made periodic counts of the numbers present and the proportion of these that were marked. Eleven counts showed 8 to 25 anoles present (an



FIGURE 13.—Part of the study area on Malpelo where *Anolis agassizi* were marked and observed and the orange and "Chuckles" experiments conducted.

average of 16 anoles) of which 0 to 31 percent (average of 16 percent) were marked. If we were seeing about the same proportion of unmarked as of marked anoles, and assuming that of the 29 marked anoles, 20 remained in the area, then the total number of anoles in our area would have been about 120. With this small sample and these many assumptions, we hesitate to calculate confidence intervals. We estimate, however, that anoles were concentrating at the oranges from an area of perhaps 500 to 1000 square meters. This would indicate a population density of about one anole per 5 to 10 square meters. Although not all areas of the island are equally habitable by *Anolis*, there must be at least 100,000 *Anolis agassizi* on the island.

Measurements were taken from 45 animals, which were preserved and deposited in the Museum of Comparative Zoology. This series contained four juveniles whose sex could not be determined, 14 adult females (snout-vent length, SV \bar{x} 77.1 [71–84] SD 4.6) and 27 males. Fourteen of the males had enlarged testes, dark heads, and well-developed nuchal crests (SV \bar{x} 97.6 [89–114] SD 7.3). The remaining 13 had small testes, female-like coloration, and small, if any, nuchal crests (SV \bar{x} 84.2 [71–99] SD 7.9). (The latter males are discussed on p. 32).

Weights of these animals just before preservation were found to be highly correlated with snout-vent length in each sex ($r = 0.96$ for males, $r = 0.85$ for females). The lower correlation for females is due primarily to their smaller size range. The linear regression equations for weight (W) on snout-vent length (SV) are: males, $W = -40 + 0.62 SV$; females, $W = -18 + 0.35 SV$. Only a small number (13.4 percent) of the lizards captured had unbroken tails, and an additional 6.8 percent were broken in capture. The sexes do not differ in the percentage of tails broken (p. 32). In the 18 lizards with unbroken tails, the tail was slightly more than twice SV (mean = 2.19; SD = 0.12). The regression of tail length (T) on SV is $T = 22 + 1.9 SV$, with an r of 0.92.

Schoener (1969) has shown that *Anolis* species which live on islands without congeners tend to fall into a restricted size range. The largest third of the males usually have a snout-vent length between 55 and 90 mm, and the females between 40 and 60 mm (for any given species, the female is

always significantly smaller). *Anolis agassizi* is an exception. The largest third of the males averages 105.4 mm SV, the maximum is 114 mm. The comparable female average is 85.2 mm SV with a recorded maximum at 87 mm. Thus *A. agassizi* is about the size of the Lesser Antillean giants *A. richardi* and *A. bimaculatus*, both of which are sympatric with smaller species.

Two hypotheses come to mind to explain the larger than predicted sizes of *A. agassizi*: (1) There was a congener on the island that is now extinct. This is unknowable, but unlikely. The very remoteness of the island makes the probability of a second colonization extremely low; and insertion of a new colonist onto a small, already occupied island is the exception rather than the rule for West Indian *Anolis*, where competitive exclusion seems to prevail (Williams, 1969; Gorman and Boos, 1972). (2) The average prey size is larger on Malpelo than in the Antilles. This is simply not the case (see below).

Any number of additional hypotheses to explain the body-size anomaly could be conjured up (e.g., selection to resist predation; intense sexual selection), but we have only our ignorance of the historical factors that have acted during the evolution of this species with which to discuss such hypotheses. Thus we resign ourselves to the observation that *A. agassizi* is large.

Food and Feeding

FIELD OBSERVATIONS AND ANALYSIS OF STOMACH CONTENTS.—The stomachs of 43 anoles were examined and the contents identified by H. Wolda, who collected invertebrates on Malpelo (see Wolda's paper herein). Most of the species of invertebrates that he found on Malpelo, except earthworms, were represented in the *Anolis*' guts. Major groups taken by the anoles include: snails, juvenile land crabs, isopods, millipedes, centipedes, spiders, pseudoscorpions, ticks, and insects. The insects included beetles, flies, true bugs, caterpillars, ants, crickets, and Thysanurians. Many of these animals are cryptic. They were found under rocks and in crevices. Anoles certainly do enter crevices and holes in the rocks where they probably catch some prey.

The most common items in the stomachs were ants. These occurred in all guts and in larger num-

bers than any other prey. The next most common items were beetles, both larvae and adults, which occurred in 72 percent of all guts. Together, beetles and ants made up the majority of the food eaten and probably more than half of the biomass.

The food items were small, nothing longer than 20 mm, few over 10 mm. The majority of the items and probably of the volume was in the 5 mm class.

This range of prey corresponds with our subjective impressions of what was available. We saw almost no invertebrates longer than 20 mm except earthworms, which were perhaps too well concealed to be captured, and the large land crabs, which were too big to be taken.

As previously pointed out, *A. agassizi* is larger than might be predicted on the basis of Schoener's (1969) study of single species anole communities. The feeding data, however, do not support the hypothesis that *A. agassizi* is larger because it feeds on unusually large prey. No precise comparisons can be made, but the food of *A. agassizi* is certainly smaller than that of the smaller mainland species *A. polylepis* (Andrews, 1971), and on the same order as that of the smaller *A. roquet*, which is alone on the island of Martinique (Schoener and Gorman, 1968).

Anoles made repeated efforts to catch a hookless trout fly which we presented to them. They jumped into the air for it when the artificial fly was dangled overhead. One suspects that they may gather at a bird carcass to feed on the invertebrates which also gather there. In this situation, they may leap into the air to catch circling flies.

A small series of anoles was taken from one of the south rocks, where grass and bushes grew much more abundantly than on Malpelo itself. All of these anoles had their lower intestines packed with grass seeds which appeared to be undigested.

About 60 percent of the guts contained a few (1 to 4) small, presumably parasitic, nematodes.

FEEDING EXPERIMENTS.—As pointed out above, the anoles seemed particularly bold and curious, and often came to us and even jumped on us. Casual observation implied that they were particularly attracted to the color orange. Thus, they seemed especially interested in a Kodak film package and in an orange screw-cap on a container of suntan lotion. This led us to perform two very simple field experiments.

The Orange Experiment: On several occasions in and near the study area, we set a half of an orange on a rock. Anoles from the surrounding areas gathered at the orange to lick repeatedly at the cut surface, and to bite, pull off, chew, and swallow, bits of the pulp (Figure 14). They also licked the peel, but did not persist in this. The anoles were initially attracted by the bright color of the orange, and persisted because of its taste.

We saw lizards come to the orange from as far as 15 meters across the rock face. Five or ten individuals would feed at the orange itself at one time, while another 10 to 20 remained within a 2 meter radius of it. There was almost no aggression shown at the orange though a male occasionally spread his small throat fan or bobbed.

The anoles seemed attracted to the area of the orange by the activities of the anoles already there, as well as by the orange itself. On one occasion we saw a succession of anoles drinking (1 to 4 at a time) from a small wet spot on the rocks. Again we had the impression that these lizards were attracted by the activities of other individuals.

Anoles did not stay at the orange for more than a few minutes though the same lizard might have returned several times in the course of an hour or two.

The "Chuckles" Experiment: To test the possibility that the anoles actually showed a color preference in making initial feeding choices, we used the jellied candy called "Chuckles." A package of



FIGURE 14.—*Anolis agassizi* gathered about an orange half.



FIGURE 15.—*Anolis agassizi* making a choice between two equal sized pieces of "Chuckles."

this candy contains five colors (flavors): red, green, black, orange, and yellow. Comparisons of different colored candy were made by setting out pairs of equal sized bits of candy close together in areas where we had not conditioned the lizards to oranges. We noted which bit of candy was selected by the first lizard to approach (Figure 15).

The results (Table 2) show that yellow and orange are equivalent and that they both are chosen more frequently than the other colors ($p < 0.01$). Of the remainder, red and green are about equal, and both preferable to black, though the difference is not significant ($p > 0.05$). We hasten to add that this appears to be a color preference and not a taste preference, for once the less optimal candy was licked by the lizard, it was immediately eaten.

We cannot separate hue from brightness in these color choices, but all candies presented were conspicuous.

TABLE 2.—Candy color preferences of *Anolis agassizi* (numerator is the number of times "Color selected" was chosen before "Other color in test pair"; denominator is the total number of trials)

Color selected	Other color in test pair			
	Yellow	Red	Green	Black
Orange	3/7	3/3	6/6	6/8
Yellow	—	5/6	4/6	6/6
Red	—	—	2/6	5/6
Green	—	—	—	4/6

The preference for orange and yellow seems most peculiar because there are certainly no fruits of this color on the island. The only objects that we could find in this color range were the large land crabs, and the anoles showed not the least interest in these. One possible explanation is that the anoles are attracted to and feed on the yolks of broken seabird eggs. Many boobies nest on Malpelo and broken eggs may be a frequent occurrence at certain times of year.

Predation

The most conspicuous potential anole predators on the island are the large lizards, *Diploglossus*, the land crabs and the birds. The seabirds could certainly eat anoles, but Neal Smith (pers. comm.) says this is unlikely. The peregrine falcon (*Falco peregrinus*) has been recorded on the island (Bond and deSchauensee, 1938), but it is normally a bird predator. The land crabs were everywhere. We saw a small group tearing apart and eating a still living anole (see p. 23). How it was caught is unknown for the crabs are relatively slow moving animals.

The *Diploglossus* appear to depend largely on the exuvia of boobies and on land crabs for food, and they gather where an adult booby is feeding its young. They do occasionally eat anoles, however, for a specimen in the American Museum of Natural History collections had one in its stomach (C. Meyers, pers. comm.). The *Diploglossus* could not be induced to eat oranges, but one big male repeatedly approached an orange that had attracted a large group of anoles, and the *Anolis* hurriedly fled at each approach. Though this *Diploglossus* was much swifter than the land crabs, the anoles were even faster and easily evaded him by keeping about a meter ahead of him on the rocks.

There is strong circumstantial evidence that predation is important. Approximately 85 percent of the anoles that we examined had their tails broken and regenerated. Given the low level of aggressiveness that we observed and the fact that females showed as high a percentage of breakage as males, the implication is that the breakage was not caused by interaction with conspecifics, but rather by predation attempts. Pianka (1970) has argued for a correlation between frequency of

tail breakage and intensity of predation in lizards of the western United States.

If, as it seems likely, crabs and *Diploglossus* are the important predators of anoles, it is likely that they catch more small than large ones. The color patterns of *Anolis* are highly cryptic on the rocks, suggesting selection by a visually hunting predator.

Adult males with their permanently erect nuchal crests and black heads are very striking and are more conspicuous than females and juveniles. Adult males of many Antillean *Anolis* also are more conspicuous than females, presumably because sexual and social selection favors conspicuousness in males and the larger size of the males reduces their predation and consequently the selection against being conspicuous.

Temperature

An open question in our minds, before seeing the anoles of Malpelo in the field, concerned temperature adaptations. This species lives on bare rock near the equator. Would *A. agassizi* prefer high body temperatures? Would it be able to resist high environmental temperatures?

Our short-term, relatively simple studies indicate conclusively that with respect to temperature *A. agassizi* is a rather typical anoline lizard. Forty body-temperature measurements of active animals were taken in the field with a Schultheis thermometer. The mean temperature, representing pooled samples of several mornings and early afternoons was 30.6°C (24–38°C) with a standard deviation of 1.8. We believe that this approximates the preferred body temperature as, quite obviously, the lizards could easily have had higher body temperatures by sunning themselves briefly on exposed rocks. Conversely, by spending more time in crevices, lower body temperatures could have been maintained. The *A. agassizi* temperatures were very similar to the Lesser Antillean species *A. richardi* and *A. aeneus* (Schoener and Gorman, 1968), and comparable to, but slightly lower than, *A. homolechis* on Cuba (Ruibal, 1961), a filtered sun animal.

Anolis agassizi does not show a temperature adaptation to particularly high or low temperatures. This is what one might expect from the structure of the island, which receives a great deal of insolation but also provides a great many hiding

places to escape the sun. The most extensive slopes and cliffs orient north and south so that large parts of the island are in total shade for either the morning or the afternoon. This is probably the most peculiar aspect of this anole's thermal ecology. The *A. agassizi* were active during most of the day in the shade and were seen basking only briefly when the sun first reached them. Since we worked on the west side, there were large areas where we saw anoles active in the early morning and which they abandoned fairly shortly after the sun reached them (see p. 35).

The situation is quite unlike that which is usual for a tree lizard who seldom needs to move more than a few inches to get into the shade. An *A. agassizi* must move several meters if it is to exploit many of the rocks and cliffs. In the absence of flying predators it does not need to worry about keeping close to shelter.

Anoles that live in areas of high insolation tend to have either enlarged scales or black peritoneal pigment. *Anolis agassizi* has the latter. The walls of the body cavity are pigmented, most heavily on the posterior half. There is some pigment on the heart and on the last 1 or 2 cm of the intestine. In some examined *A. agassizi* the entire dorsal surface of the lower intestine is pigmented.

To determine adaptations to high temperatures, a simple heating experiment was performed on animals brought to Panama from Malpelo. These experiments were conducted immediately upon our return, and the lizards could not have acclimated to the new climatic regime. Individuals representing all size classes were tested. In these experiments we suspended a bright lamp above a cage that measured approximately 30 × 30 × 45 cm. The cages were constructed of wood with two glass sides. Two parallel series of experiments were run: in one, the lamp was placed at a height of 30 cm above the cage top; in the second, at 42 cm. Each individual was dropped into the cage, the light turned on, and the response observed for 3 minutes.

It has been observed that when an anole is dropped into a novel situation its typical first response is to "freeze." As it warms up under these experimental conditions, it starts moving about with the onset of discomfort; finally it opens its mouth and begins panting (Ruibal, 1961).

All lizards moved within 50 seconds with the

light source at 30 cm, and in less than two minutes with the light source at 42 cm. The temperature of onset of panting was not correlated with body size, and only slightly with the distance between heat source and cage. With the heat source at 30 cm, ten lizards began panting at a mean body temperature (MBT) of 34.8°C; with the heat source at 42 cm, seven lizards began panting at MBT of 33.7°C.

We scored trials only when the lizard moved, then panted, the reason being that occasional animals opened the mouth soon after being dropped into the cage. In all cases where mouth opening preceded movement, the time of the trial was very short and the body temperature was well below that of all other trials. To confirm that movement was a response to the heat, a transparent heat filter was inserted between the light and the cage. In eight of 10 cases the lizard did not move at all for more than 2.5 minutes (trial was discontinued at 3 minutes).

This temperature at which panting begins (pooled mean, 34.2°C) is considerably lower than published data for several Puerto Rican species of *Anolis* (Heatwole et al., 1969), and is between data for two Cuban species (Ruibal, 1961), *A. allogus* of deep shade (30.3°C) and *A. homolechis* of filtered sun (36.2°C).

Quite clearly, *A. agassizi* is not specifically adapted to high body temperatures. Because of the north-south orientation of Malpelo and the great contrast between sun and shade on each part of the island with the passage of each day, some of the social organization discussed below may be related to the lack of temperature adaptation. An animal cannot afford to defend a restricted territory if it is unliveable for half of every day.

Water and Drinking

Many anoles that occur in very arid microhabitats (*A. poncensis* in Puerto Rico, *A. auratus* in Panama) tend to have enlarged dorsal scales. *Anolis agassizi* does not. This reinforces our impression that Malpelo is not as dry as the lack of vegetation suggests. Lying within the doldrums and being of some height, Malpelo probably receives frequent rain during most of the year. Water probably does not stand very long on the exposed bare surfaces of cliffs and rocks. But fresh water was found spottily over most of the island during our

visit, even though it did not rain. The volcanic rock of which the island is made is porous and there are many small seeps, springs, and rock pools. We saw anoles drinking together at a small seep and it may be that much of their water comes from such limited and shared sources.

Initial tests done by Paul Licht of the University of California at Berkeley on captive *A. agassizi* suggest that they lose water under drying conditions much as typical Antillean anoles do, and have no special adaptations either to prevent desiccation or to tolerate water loss. Several specimens collected on Malpelo immediately excreted fluid urine, implying no special need for water conservation.

Reproduction, Sex Ratio, and Size Class Distribution

Our collection on Malpelo leads to the conclusion that the lizards must be highly seasonal (or at least periodic) in their reproduction, or that we were guilty of very biased sampling, or both (they are not mutually exclusive). The smallest lizard collected was 41 mm (SV). This is well above the hatching size of 25 to 30 mm (p. 35). Thus, we failed to find evidence of any really young lizards. It is often the case that *Anolis* are more secretive as young juveniles and special efforts are needed to collect them, but we had enough people spending enough time in prime lizard habitat to make us believe that hatchlings were truly scarce, if not totally absent.

One of us (GCG) examined the two large museum series of *A. agassizi*: the Slevin specimens in the California Academy of Sciences, collected in December 1927; and the Cyrus Perkins specimens in the San Diego Society of Natural History, collected in December 1931 and January 1933. Slevin (1928) wrote of his trip to Malpelo, whereas no information is available on the two journeys made by Perkins. Both these series then were made at approximately the same time of year (December-January) and ours was made in the first days of March. The smallest lizards in these collections were 64 mm (San Diego) and 56 mm (California Academy). Thus nothing is known about the time of hatching or hatchling ecology in nature.

Studies on the reproductive cycles of tropical *Anolis* (Licht and Gorman, 1970; Sexton et al.,

1971) indicated that within a population some females were likely to be reproductive (with an oviducal egg or an enlarging follicle) throughout the year, the percentage seemingly affected by rainfall. Thus in wet months 100 percent of the females might be scored reproductive, but in extensive dry seasons, reproductivity could approach zero.

The reproductive condition of the females on Malpelo also hints at seasonality. In our collection, five females had oviducal eggs, the smallest female being 72 mm SV; two additional females had enlarging follicles, these were both large specimens (86 and 87 mm). Without adequate samples we cannot determine the size at sexual maturity. Since our smallest reproductive was 72 mm, let us consider this our cut-off point. There were six females larger than 71 mm which were completely nonreproductive. Thus, in early March, about 50 percent of the collected female *A. agassizi* (6 of 13) were nonreproductive. In the museum samples (December-January) six of eight females (75 percent) larger than 71 mm were nonreproductive. To determine whether there is true seasonality or whether there is merely a low level of reproductive activity parceled out throughout the year would take further collections of *A. agassizi*.

The males presented the most aberrant and unexpected findings. They could be divided into three groups. There were large males with the obviously developed secondary sexual characters, e.g., black head and erect nuchal crest. These lizards ranged from about 90 to 114 mm SV and in weight from 13 to 34 grams. There were also smaller males (71 to 85 mm SV and 7 to 13 g) that were sexually mature, but lacked the impressive secondary sexual characters of their larger neighbors. In other words, they looked like females. This is not particularly surprising, for in other studies of *Anolis*' reproductive cycles (Licht and Gorman, 1970) it has been noted that males are physiologically sexually mature long before they are fully grown and, in fact, before they could be categorized as socially mature, i.e., assuming the social role of an adult male.

But there was a remaining class of animals that puzzled us in the field. Six male specimens (75, 85, 86, 90, 94, and 100 SV) lacked male secondary sexual characters. Of interest is that three of these were 90 to 100 mm long and were as large as some

black-headed males, yet all six had completely regressed gonads, to the extent that we at first labeled them "intersexes." Microscopic examination led to the conclusion that these were fully regressed males. Nothing like this has been seen in studies of Caribbean *Anolis*. Although most tropical anole species show a moderate seasonal cycle for gonad size, the testes are never completely regressed; they are always obviously testes, and in most species they produce sperm throughout the year. Thus there is a testes weight cycle in Malpelo *Anolis*. Furthermore, the population rarely shows a large variation for testes condition, i.e., the males are generally in phase with one another. In contrast, on Malpelo, we found some males that appeared fully reproductive and others that appeared fully regressed.

The museum collections also had specimens with fully regressed gonads. In the San Diego collection there were putative males of 69, 78, 79, 82, and 83 mm SV that were fully regressed, yet males as small as 74 that were reproductive. There is no way to determine whether this is a seasonal phenomenon or whether it is a population phenomenon. The general lack of aggression that we observed (p. 36) might be related to the large number of nonreproductives in the population.

Male *Anolis* are often more conspicuous than females and more likely to hold their ground against an approaching collector. Thus they have greater likelihood of ending up in museum jars. Our collection consisted of 27 males and 14 females, a sex ratio of almost 2:1. A pool of our sample with the museum collections (and restricting ourselves to animals 72 mm and greater) shows a sex ratio of 62:27, favoring males. We find it hard to believe that this is simply sampling artifact, but serious demographic study would have to be undertaken to resolve the problem.

Reproduction in Captivity

Four females returned to Panama laid eggs, one at a time. Time intervals ($n = 18$) between successive eggs varied from 4 to 27 days ($\bar{x} = 13.6$). Eggs were kept under ambient climatic conditions in Panama (which must be close to those on Malpelo) and 13 hatched with an incubation time of 48 to 69 days ($\bar{x} = 57.8$). The hatchlings mea-

sured 25 to 30 mm SV ($\bar{x} = 27.7$) and weighed 0.42 to 0.81 g ($\bar{x} = 0.62$).

Social Interactions

The anoles literally swarmed in our study area. The most impressive observation was the relative lack of aggressive encounters. There appears to be a very strong tendency towards social facilitation, i.e., when an anole took the initiative to approach an object, others in the area were likely to follow suit. They also appear to have a strong tendency to examine any unusual object, making it very difficult to perform unbiased observation without a blind. Thus the anoles frequently made active approaches to the observers, on several occasions even climbing on the camera and tripod set up to film their behavior. We could do little to avoid them—backing off is not recommended on Malpelo's steep cliffs.

We interpret the social facilitation as an adaptation to patchy but superabundant food sources. Thus it is likely that the carcass of a bird may often serve as a focus for feeding of many anoles in a given area. In the West Indies, a well-established method for attracting large numbers of anoles is to break open a termite nest. Under such conditions, large numbers will often gather and feed actively with little aggressive interaction. The entire social organization of *A. agassizi* seems to be based upon this type of situation.

Home ranges were large and activity was not restricted to a few preferred perches. The following anecdotal observations support the conclusion that home ranges overlap widely with residents showing little aggression. Up to 8 anoles simultaneously would lick an orange, with up to 15 within a meter of it. One morning, approximately a half dozen lizards that had been active on a smooth rock ledge moved laterally about 10 meters to a cliff face. This occurred about a half hour after the sun reached the ledge. Presumably, they were abandoning a foraging area that had become too hot. Many then gathered to try to catch a dangling trout fly without showing any aggressive interaction. On one occasion, a group of about a dozen anoles assembled at our portable radio and climbed all over it, though it provided neither food nor water. After some moments, all drifted away. This

is an example of the social facilitation referred to above.

H. Wolda reported that as he turned over rocks looking for invertebrates, he was followed by a group of anoles that fed on the food that he exposed. The *A. agassizi* in a walk-in cage in Panama gather around anyone who enters, as if expecting food.

Occasionally we saw aggressive interactions between individuals, including chasing and some display. The instances involved crested vs. crested males, crested vs. noncrested males, and noncrested vs. noncrested individuals of unknown sex. But we emphasize that we saw remarkably little display in comparison to our experiences with West Indian anoles. The only display that we saw was a very simple multiple bob. This varied somewhat in amplitude and it was given sometimes with and sometimes without the dewlap being spread. The display was usually seen in seemingly aggressive situations, but was also occasionally given in a somewhat less vigorous form when a lizard moved and stopped.

The captive anoles in Panama have shown little in the way of additional kinds of display. We have seen males jaw fencing, jaw locking and biting one another. More elaborate displays have not been seen, nor any other simple displays. Males in captivity that are courting approach the female with the simple multiple bob, followed by pauses. This is similar to courtship displays of other *Anolis* species. *Anolis agassizi* has a display repertoire that is more reduced than is typical for the genus and appears more like a sceloporine lizard. This is probably a secondary simplification.

In a large outdoor cage in Panama, adult males show evidence of having developed a rather complex dominance hierarchy.

On Malpelo, the anoles exhibited direct competition for food. Frequently, when an anole had worried off a bit of orange pulp or picked up a piece of "Chuckle" too big to swallow, immediately it would run off with it. Sometimes it was pursued by several other lizards, including much smaller individuals that would try to seize the food from its mouth. In these cases there was very little aggression shown.

No anoles attempted to monopolize the resource by chasing or displaying at others. This was true even of the first individual to arrive at a resource.

There was not an initial territoriality that subsequently broke down under repeated attacks as has been described for gulls by Drury and Smith (1968).

At the orange, when a new lizard arrived with a rush, one already there might run off. In general, large anoles supplanted smaller ones, but no organized dominance hierarchy was evident.

Introducing anoles tethered to a long stick at various spots both close to and far from other anoles produced a little interaction and in one case an attack and bite. It also produced a little display. The residents did not seem to be afraid of the intruder, nor of the way it was presented but in most cases they were just not very interested.

The social behavior in *Anolis agassizi* differs from that described for any other species of anole. This is most readily interpretable in terms of the atypical structural niche, *viz.*, in place of discrete defensible perch sites (tree trunks, fence posts, etc.) there are large areas of cliff face that are exposed to complete shade or complete sun for many consecutive hours each day. In addition, food resources are presumed to be much patchier than in a typical tropical environment.

The basic difference in social organization of this species lies in the reduced overt aggressive interactions among individuals, and the high degree of social facilitation such that directional movements of one individual are likely to prompt similar investigatory movements in several other individuals. In anthropomorphic terms, this species is extremely curious.

Both males and females seem to have overlapping home ranges. They do not defend territories or individual areas. There is a high degree of tolerance for the close approach of conspecifics at a common resource, be it food, water, or perch site. There are occasional overt aggressive interactions when "individual distance" appears to be violated, but aggression is seemingly not associated with violation of specific space (territory). Widely overlapping home ranges without aggression have been observed in females of *A. valencienni* in Jamaica (R. Trivers, Harvard University, pers. comm., and *A. biporcatus* in Panama, A. S. Rand and pers. obs.). But in both these species the males are much less tolerant of members of the same sex.

Anolis agassizi not only has a reduced frequency of display interactions but also seems to have a re-

duced display repertoire. This is in strong contrast to the anoline species in the West Indies (Gorman, 1968) and to *A. townsendi* of Cocos Island (Carpenter, 1965). Our tentative explanation is: first, that, with reduced aggression and territorial defense, there are fewer bits of information to be communicated; and second, that the striking, permanently displayed color pattern and erect nuchal crest of adult, reproductively active males assume much of the communication function otherwise transmitted by complex movements of head, dewlap, and tail (display action patterns). The only West Indian anole known to have reduced display is *Anolis ferreus* of Marie Galante which is like *A. agassizi* in being unexpectedly large and in having a very striking permanently erect crest (in this case on the tail) in adult males.

We would suggest that the reduced aggression is a direct adaptation to living under conditions where resources are scattered so that a large home range is necessary to include them. Furthermore, the resources are often so abundant that there is enough for all and consequently little advantage gained by attempting to monopolize them. The reduced amount of display permits efficient utilization of common resources. The social facilitation ("curiosity") aids in the discovery of these resources.

The social organization that we have described for *A. agassizi* is very different from that described in studies of *A. sagrei* (Evans, 1938), *A. carolinensis* (Greenberg and Noble, 1944), *A. lineatopus* (Rand, 1967), and *A. nebulosus* (Jenssen, 1970). From these studies we have come to expect anoles to show a more or less similar pattern. In these species the adult male maintains a small home range centering on one or more preferred perches. The home range is defended against other adult males as a territory and the resident gives frequent assertion displays. An adult female maintains a still smaller home range which she may defend against other females and against similarly sized subadult males. The territory of an adult male typically overlaps those of one or more adult females. All of the species showing this general pattern of social behavior have similarities in their ecologies. Evidence is accumulating from recent studies of species with different ecologies (e.g., *A. aeneus*, Stamps, 1973; *A. valencienni*, Trivers, pers. comm.; *A. biporcatus*, A. S. Rand, pers. obs.) that

there is more variability between species of *Anolis* in social organization than had been realized. We have attempted to show in this paper that the rather unusual social organization of *A. agassizi* is an adaptation to its unusual environment. We predict that *A. agassizi* will remain an extreme in the continuum of social organization among anoles, but that intermediates between it and the more common types exist and, further, that the continuum will be expanded in several quite different directions as species adapted to unusual ecologies are described.

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Notes on the Natural History of *Diploglossus millepunctatus* (Sauria: Anguidae)

A. Ross Kiester

ABSTRACT

The natural history of the large anguid lizard *Diploglossus millepunctatus* from Malpelo Island is described. This species is characterized by its abundance, flexible thermal regime, euryphagy, and curiosity.

Introduction

The large anguid lizard *Diploglossus millepunctatus* is one of the most conspicuous elements of the fauna of Malpelo Island. Because the island is seldom visited little has been reported of its natural history. Here we begin to fill in some of the gaps in our knowledge of this species.

Diploglossus millepunctatus was first described by O'Shaughnessy (1874) who listed the type-locality as "the north-west coast of America." Slevin (1928) described *Celestus hancocki* from Malpelo Island, noting that it was similar to the unique type of O'Shaughnessy. Dunn (1939), who had additional material, synonymized Slevin's name on the basis of similarities of his series with the type of *millepunctatus* and the fact that there was some indirect historical evidence that the original specimen could indeed have been collected on Malpelo. Dunn also placed the species in the genus *Diploglossus* arguing that *Celestus* was not recognizable. While Dunn's generic allocation of the species *millepunctatus* has prevailed, the issue

of the validity of the genus *Celestus* requires further attention (Myers, 1973).

Diploglossus millepunctatus is among the largest of the anguids, ranging up to 250 mm snout-vent length with a tail length of 162 mm and a weight of 268 grams. It is rather heavy-bodied with short limbs. Older males possess the enlarged wide heads that are characteristic of some other anguid genera such as *Gerrhonotus* (Stebbins, 1954). The body has a very shiny metallic appearance and like that of other anguids is encased in a solid armor of osteoderms. The tail tends to be rather blunt in adults but is more typically tapered in the young. The color pattern is dark black or brown-black with small yellow or yellow-white flecks in great profusion, as the specific name suggests (Figure 16).



FIGURE 16.—*Diploglossus millepunctatus* aggregated about a young Blue-faced Booby (*Sula dactylatra*) which has just been fed.

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Habitat

Diploglossus millepunctatus is found virtually everywhere on the island from next to the water's edge to the top of the summit (376.4 m). Lizards usually did not occur far from the crevices into which they retreated. Otherwise, they scramble over the bare rocks and cracks, sometimes moving with agility in an almost serpentine fashion, but also occasionally falling.

Although these lizards live next to the ocean and are capable of swimming, we were unable to get any individuals to enter the water voluntarily as Slevin (1928) reported they would do.

Population Size and Structure

These animals are extremely common. No quantitative measurements of population density were attempted, but rough counts indicated that a density of 1 per 10 square meters was perhaps a reasonable estimate. The population seems to consist mostly of adults. Of the literally hundreds of animals that were observed only three young were observed. Except for these individuals, the entire population fell into a size range of approximately 180–260 mm snout-vent length. The juveniles were approximately 75 mm snout-vent length and no animals of an intermediate size were seen. This striking size distribution might possibly be due to the fact that younger animals tended to remain hidden in crevices. However, the fact that some young were seen while no intermediate sized animals were found seems to indicate that the observations reflect a real phenomenon, namely that reproduction is seasonal or erratic and that our sample was taken prior to a period of reproductive activity.

Activity and Thermal Relations

Although no nights were spent on the island, it seems likely that *D. millepunctatus* spends nights inside crevices. Upon arriving on the island at 0800 or earlier we observed few lizards out in the open but saw many in crevices. Later, the lizards moved out to bask in the midmorning sun. By midday most had retreated back into the crevices. During the afternoon most remained in or adjacent to crevices and only an occasional individual roamed in the open.

Overall mean body temperature (cloacal temperature \pm se) of 12 *D. millepunctatus* during activity was $27.5 \pm 0.64^\circ\text{C}$ (range 24.8 to 32°C). However, body temperatures shifted upward between morning and afternoon. The mean body temperature of six lizards active between 0838 and 0910 was $25.8 \pm 0.3^\circ\text{C}$, whereas the mean body temperature of six lizards active between 1324 and 1342 was $29.3 \pm 0.7^\circ\text{C}$. There was no overlap in body temperature between these two samples, and the difference between the samples is significant ($p = 0.01$, Kolmogorov-Smirnov test, Siegel, 1956: 127).

Among anguids only *Ophisaurus attenuatus* is reported to have a higher body temperature (Fitch, 1956:444). However, as with *Anolis agassizi* (p. 33), *D. millepunctatus* appears in general to have no special physiological adaptations to the extreme thermal environment in which it lives. The ready availability of the cooler crevices seems to afford *D. millepunctatus* a means of cooling itself when the temperatures on the exposed parts of the island are extreme. On the other hand, much of the island remains in the shade until the very late morning, by virtue of the steep rock walls, and this species can also be active at lower temperatures. Thus it appears to be flexible with regard to the temperatures at which it is active.

Drinking and Water Relations

Diploglossus millepunctatus drinks readily in captivity. On Malpelo standing fresh water was observed in a few locations and water seepages were seen in many of the crevices, although most of the island was dry. It is impossible to know from our observations what the seasonal pattern of water availability is, or whether there is water available

in the deeper crevices. Rock surfaces on Malpelo ranged from very porous to extremely smooth and hard. In either case it seems that water would not stand on the surface of the island for any appreciable time after a rain storm, either percolating down into the rock, running off rapidly, or evaporating. Although it did not rain during our visit, captive animals displayed an extremely rapid response to water. When kept in a large pen with no available water, the animals would respond to the first drops of water sprayed into the cage by running immediately to the nearest puddle that was forming. This response seemed to be about as fast a movement as the animals were capable of. They responded by coming out of crevices or down off the tops of large bricks that were in the cage. This rapid response appears to be a specific behavioral adaptation to a transiently available water supply.

Food and Feeding Behavior

Although this species will eat the usual kind of prey items that are to be expected for a lizard of this size, such as insects and invertebrates, the bulk of the food taken by adults is quite out of the ordinary for a lizard. There are small insects on Malpelo, and in captivity *D. millepunctatus* will readily take crickets and mealworms. Actual feeding on insects on the island was not observed, however, probably because the insects occur only inside the crevices. Out in the open the lizards were observed to feed on a variety of bizarre foods. Both Slevin (1928) and Dunn (1939) reported finding



FIGURE 17.—*Diploglossus millepunctatus* feeding on a fish regurgitated by the booby.

crabs in the stomachs of the animals they examined, and Slevin also reported finding feathers. We observed this species feeding on carrion consisting of both dead crabs (*Gecarcinus malpilensis*) and a Blue-faced Booby (*Sula dactylatra*). In the case of the booby, the lizards may have also been feeding on the insects attracted to the carcass.

Most of the feeding observed was connected with the activities of living boobies. On two occasions animals partially consumed fresh booby feces. The most spectacular feeding behavior occurs when an adult booby is feeding its young regurgitated fish. When an adult bird returns and alights near its young, the young bird begins to squawk loudly. This noise attracts the attention of any nearby *D. millepunctatus* which immediately run to the vicinity of the two birds. If any of the fish is dropped, the waiting lizards immediately snatch the food and drag it away. We observed this complete sequence of behavior on two occasions, and saw lizards attracted to calling boobies on several others. In one case, more than seven adult lizards that had aggregated about two birds successfully carried off and consumed an entire fish (Figures 16, 17). During such activity the birds appear oblivious to the lizards. In captivity these lizards would readily eat canned tuna or fish-flavored cat food.

It appears that the boobies provide a substantial amount of food for the lizards, at least during the nesting season. Obviously this source of food is not available year round. The lizard's large stumpy tail may possibly serve as a storage organ, and several of the individuals which we examined had large fat bodies in the abdominal region. Presumably the young feed more on the insects that are available in the crevices and that may not be as seasonal as the supply of fish.

Social Behavior

In general this species does not appear to have a complex social behavior system. Individuals frequently ignore each other, although short chases were occasionally observed. The only activity that could be interpreted as a display is a particular "head-up" posture in which a lizard sits with its head held back so that it points almost directly upwards. Although two lizards within eyesight of each other could be observed to do this, no obvious reaction was observed. Further observations will

be needed to confirm that this is indeed a display.

Social facilitation for feeding appears to be well developed in this species. A running individual seems to attract the attention of others who frequently give chase. This reaction appears to be in contrast to the response elicited by a slowly moving individual. When food or a source of food is present, it is not clear how much of the attraction is due to the food itself and how much to the other lizards; however, aggregation can be extremely rapid. As mentioned above, seven or eight animals aggregated about two boobies, and the aggregation took place in a radius of over 5 meters in about 2 minutes. Rapid aggregation in itself is evidence for social facilitation (Kiestler and Slatkin, 1974), but this point needs to be investigated experimentally.

One pair was observed copulating. They were found in a crevice in the shade. The male held the head of the female in his jaws, biting from the side. His body was positioned laterally and intromission took place from the side. The pair was found in copulation in the midmorning and remained in the same position for two and one-half hours. The position is similar to that described for *Gerrhonotus multicarinatus* (Fitch, 1935:18).

Reproduction

A series of 18 specimens collected on a single day during the visit (early March) showed marked reproductive activity. Females had many well-developed embryos, and males had large testes. Females brought to Panama and maintained in captivity gave birth to live young two months later. Other females in this same group and some females taken to Cambridge, Massachusetts, which initially appeared gravid showed no embryos on examination after their death some weeks later. Thus it may be possible that resorption of embryos can occur.

We may conjecture that *D. millepunctatus* will have its reproductive cycle tied to that of the booby. From our collections we know that the lizards were in reproductive condition (and often fat) near the end of the fledging period of the boobies. If the amount of food available to the adult lizards is markedly increased by the appearance of nestling boobies which need to be fed, then breeding by the lizards might be expected to follow this period.

Conclusions

This species appears to be very opportunistic, ready to take advantage of a transiently available resource on split second notice. Associated with this opportunism is a high level of curiosity and a tendency to respond to anything novel or disturbing in the environment. We found that individuals of *D. millepunctatus* would approach human beings or their artifacts with little regard for possible danger. This curiosity seems linked to the unpredictable and meager food supply on Malpelo Island where any disturbance may likely mean food rather than danger for the lizards, since there are no natural predators (with the possible exception of migrating raptors; Bond and deSchauensee, 1938). Thus the benefits of curiosity are great while the disadvantages normally associated with this behavior are reduced or absent. In this way *D. millepunctatus* is typical of predators on remote islands (Carlquist, 1965).

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A New Gecko from Malpelo Island (Sauria: Gekkonidae: *Phyllodactylus*)

Raymond B. Huey

ABSTRACT

Phyllodactylus transversalis, a new gecko from Malpelo Island, Colombia, is characterized by absence of tubercles on arms, legs, rear of head, and tail; absence of ear denticulation; absence of abdominal plaque; slight enlargement of dorsal tubercles, which form only two distinct paravertebral rows; terminal lamellae of digits distinctly widened and truncate; 13 to 15 fourth toe lamellae; ground color medium gray-brown with dark chocolate bands. Source of this species is uncertain.

Introduction

The gekkonid genus *Phyllodactylus* is widely distributed in the western hemisphere. Recent reviews by Dixon (1962, 1964a, 1964b) and Dixon and Huey (1970) have revised all New World members of the genus except species from the Galapagos Islands. Some 45 species are currently recognized.

The collection of lizards from the Smithsonian-U. S. Navy Expedition to Malpelo Island, Colombia, included two specimens of *Phyllodactylus*, a genus not collected by the few previous expeditions to the island. Morphological characteristics indicate distinctness of these specimens, which I here describe following the methodology of Dixon (1964a).

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Phyllodactylus transversalis (new species)

FIGURE 18

HOLOTYPE.—Adult female, Museum of Comparative Zoology (MCZ 130042), collected by A. Stanley Rand from under a rock near the first collecting area on Malpelo Island, Colombia, February 1972.

PARATYPE.—Immature specimen (MCZ 130043) collected from under a rock on Malpelo Island by Hendrik Wolda, February 1972.

DIAGNOSIS.—Differs from the Central American *tuberculosis* group, the Mexican *delcampi* group, and most South American groups by having small and scattered dorsal tubercles forming only two paravertebral rows; differs from *unctus* group in possessing dorsal tubercles; differs from *gerrhopygus* group by absence of abdominal plaque; from the species *microphyllus* by having expanded terminal lamellae and a small nostril; and from *inaequalis* in having dark chocolate dorsal bars, more fourth toe lamellae (13 to 15 vs. 10 to 12), smaller head scales (third labial snout scales 32 vs. 20 to 24; scales between eye and nostril 14 to 15 vs. 11 to 12).

DESCRIPTION OF HOLOTYPE.—Rostral twice as wide as high, its dorsal edge almost straight with a dorsal vertical groove one-half depth of rostral; 2 internasals, somewhat rounded, their median edges in broad contact, bordered posteriorly by 7 small granules and a postnasal on each side; nostril

surrounded by rostral, labial, internasal, and 2 postnasals; first supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals, slight depression in frontal region; 15 scales on line between nostril and eye; scales in posterior loreal region slightly larger than scales in mid-orbital region; 32 scales across snout at level of third labial; 22 interorbital scales; eye large, its diameter contained in snout length about 1.5 times; eyelid with 2 inner rows of granules, a median row of larger scales, and 1 row of large scales on the edge, the last 8 to 9 are pointed; ear large, its diameter contained in the eye diameter 2.7 times; scales on anterior edge of ear opening



FIGURE 18.—Holotype of *Phyllodactylus transversalis*, adult female, MCZ 130042, dorsal view.

flattened, overlapping, those on posterior edge smaller and granular; rear of head granular without intermixed tubercles; 5 supralabials and 4 infralabials to a point below center of eye; mental bell-shaped with posterior median edge sharply angular, as wide as long, bordered posteriorly by 2 postmentals; postmentals slightly longer than wide, their median edges in broad contact, followed by transverse row of 5 flattened scales.

Dorsum with scattered, small, conical tubercles; only 2 paravertebral rows evident, extending onto neck; paravertebral rows separated by 3 to 5 irregular rows of small granules; 40 paravertebral tubercles between axilla and groin, separated by 0 to 2 granules; remaining dorsal tubercles not in distinct rows; dorsal granules irregular; postanal tubercles 3 on each side, not distinct; enlarged abdominal plaque absent; venter with 27 scales across belly, from throat to vent 69.

Dorsal surface of upper arm with rounded, slightly elevated scales; forearm with slightly smaller scales of similar shape; dorsal surface of thigh and tibia with granular scales; claw long, visible from above and below; terminal toepad greatly enlarged, longer than wide, truncate; fourth toe lamellae 13 to 14; tail partially regenerated, original tail stub with a few wide median scales on ventral surface, devoid of tubercles on dorsal surface, but with scattered, flattened tubercles at base.

Measurements (in mm): Snout-vent length 57, axilla-groin length 26, length of leg 25, length of arm 17, length of tail 22 + 18, length of head 15.5, depth of head 5.7, width of head 11.2, length of snout 6.4, diameter of eye 4.3, diameter of ear 1.6, distance from eye to ear 5.7.

Color in Alcohol: Dorsum medium gray-brown ground color with white speckles; 8 distinct broad chocolate brown transverse bars from base of head to base of tail, somewhat broken along midline; width of bars slightly larger than ground interspaces; lateral area of trunk as dorsal ground; arms and legs with dark chocolate ground suffused with light scales and small light spots, without definite pattern; top of head with suffusion of dark brown and small light blotches, no definite pattern; dark chocolate brown stripe from nostril to eye, blending with head color posterior to eye, bordered below by a pale whitish line from first infralabial through ear; belly pale yellow.

VARIATION (based on paratype).—Similar to holotype except in the following characters: 14 scales between nostril and eye; 24 interorbital scales; 6 supralabial and 5 infralabial scales to a point below center of eye; mental nearly triangular; no contact between postmentals, followed posteriorly by transverse row of 6 flattened scales; venter with 30 scales across belly, from throat to vent 67; 39 tubercles in paravertebral row between axilla and groin; fourth toe lamellae 15–14; tail regenerated 3 + 19; snout-vent length 36 mm.

NATURAL HISTORY.—Both geckos were collected during the day under rocks. Because of the topography of Malpelo, these geckos are necessarily scansorial. Dixon and Huey (1970:66) have shown that scansorial *Phyllodactylus* have expanded toe-pads, a characteristic of *P. transversalis*.

Two large diurnal lizards are also present on Malpelo (*Diploglossus millepunctatus* and *Anolis agassizi*) and eat crustaceans as well as booby regurgitations and feces. Ants and crickets were found in the stomachs of *P. transversalis* (A. S. Rand, pers. comm.).

Accompanying papers in this volume describe Malpelo Island (Kiester and Hoffman, pp. 13–16) and the biology of the diurnal lizards (*D. millepunctatus*, Kiester; *A. agassizi*, Rand, Gorman, and Rand).

ZOOGEOGRAPHIC RELATIONSHIPS.—The dorsal cross-banding and the two rows of dorsal tubercles of *P. transversalis* are distinctive. These unique char-

acters suggest long isolation from source areas and hinder analysis of affinities.

Phyllodactylus transversalis shares many external morphological characters with the *inaequalis* group of Peru (Dixon and Huey, 1970:69). After examining the type and paratype, however, J. R. Dixon (pers. comm.) suggested that *P. transversalis* may be closer to certain Mexican species (*P. paucituberculatus*, *P. unctus*, and *P. delcampi*). There are no obvious affinities with *Phyllodactylus* from the Galapagos. The source of this gecko is thus equivocal.

ETYMOLOGY.—The specific name refers to the distinctive dorsal cross-bands (Figure 18).

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Electrophoretic Estimates of Genic Variation in, and the Relationships of, *Anolis agassizi*

T. Preston Webster

ABSTRACT

From data on proteins representing 30 genes, an average individual of *Anolis agassizi* is estimated to be heterozygous at 2.1 percent of its loci. This low value is similar to that found in other solitary anoles and in some anole populations of relatively recent origin, but it contrasts sharply with results from some Greater Antillian species. Very little genetic similarity was found in the comparison of *A. agassizi* to five congeners.

Introduction

An insular lizard population may have relatively little genic variation as a result of random processes and natural selection acting during its establishment. The small size of the propagule, perhaps only a single impregnated female, should limit variation. This holds whether the alleles carried by the founder or founders are a random or a selected sample of those in the parental population. Subsequently, random allelic loss (genetic drift) during the initial or secondary periods of small population size and selection would further reduce variation. A low level of heterozygosity could endure, but in a persistent population many new polymorphisms might accumulate.

A considerable loss of genic variation may have occurred during the arrival and life of *Anolis agassizi* Stejneger on Malpelo Island. Malpelo may have received anoline immigrants only once and, as the source population is extinct, there certainly

have been no recent immigrants bearing new alleles. On such a small island, secondary reductions in population size are possible. The founders probably encountered more extreme conditions on Malpelo than those to which they were adapted, even if the source population, like those anoles that have been successful colonists in the Caribbean (Williams, 1969), occurred in open, edge situations. *Anolis agassizi*, however, is a long established population that has perhaps experienced pressures and had time to reacquire heterozygosity.

In this study, genic variation in *A. agassizi* was estimated by electrophoretic examination of enzymatic and non-enzymatic proteins. Since there is no prediction to which this result can be compared, it is considered in the context of similar estimates from other anole populations. Secondarily, many of the same proteins were used to estimate the genetic difference between *A. agassizi* and five congeners.

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Materials and Methods

Plasma and hemolysate were obtained from 32 *A. agassizi* collected at the first landing site on the west side of Malpelo. Six individuals were used for chromosome studies and preserved, and the remaining 26 were homogenized in distilled water (1:2, W:V). Homogenates were centrifuged and stored at -80°C .

Electrostarch was used for horizontal starch gel electrophoresis. Each protein was examined in as many electrophoretic environments as convenient and feasible. In several cases this multiplicity of observation increased the number of mobility differences detected. Many of the buffer systems and protein assays were those previously used in studies of *Anolis* (Webster, Selander, and Yang, 1972; Webster and Burns, 1973). Additional techniques are those commonly used in studies of vertebrate proteins (Brewer, 1970; Shaw and Prasad, 1970; Selander et al., 1971).

Twenty-eight enzymatic and nonenzymatic proteins were examined: leucine aminopeptidase, two peptidases, fumarase, creatine kinase, phosphohexose isomerase, eight dehydrogenases (lactate, two malate, two isocitrate, alcohol, α -glycerophosphate, and 6-phosphogluconate), indophenol oxidase, two aspartate aminotransferases, two phosphoglucomutases, an esterase, three "general proteins" (A,B,C), hemoglobin, transferrin, and three plasma proteins. Like other anoles (Webster, Selander, and Yang, 1972), *A. agassizi* appears to have four or five genes encoding the polypeptides that are subunits of hemoglobin, but it is treated here as if it were under two-gene control. Lactate dehydrogenase is encoded by two genes. Since each of the remaining proteins appears to be encoded by a single gene, the products of 30 genes have been examined.

Many of the proteins studied in *A. agassizi* were compared with their apparent homologues in these congeners: *A. garmani* (Jamaica: Mandeville), *A. luciae* (St. Lucia: Vigie Beach), *A. squamulatus* (Venezuela: Parque Nacional Rancho Grande "Henry Pihier"), *A. marmoratus* (Guadeloupe: 3.6 km SW Capesterre), and *A. singularis* (Haiti: Savane Zombi). To obtain an estimate of differentiation between members of the same species group, *A. luciae* was compared to *A. extremus* (St. Lucia: Vigie Beach, a recently introduced popula-

tion). Single individuals or pooled extracts were used in these comparisons, but the variation in each population has been studied and considered.

Genic Variation

In *A. agassizi* variation was detected at 4 of the 30 loci. One of 26 individuals was heterozygous for Protein B, 2 of 26 were heterozygous for one of the malate dehydrogenases, and 2 of 26 were heterozygous for one of the peptidases. Transferrin was represented by 3 variants, with 14 of 32 individuals heterozygous. The remaining 26 genes appear to be monomorphic. Thus the average individual of this population is estimated to be heterozygous at 2.1 percent of its loci ($H = 0.021$).

This result can be evaluated within the context of a broad range of estimates of H from anole populations (Table 3). Since a large proportion of protein polymorphism is expected (Lewontin and Hubby, 1966) and known (Boyer, 1972) to be undetectable by electrophoresis, such values are surely underestimates of the actual extent of genic variation. Their comparison requires both that the electrophoretically determined H be considered as having some value as an index to actual genic variation among structural loci or within the genome as a whole and that some standard error or arbitrary criterion for difference be assigned.

From a joint consideration of morphological variation and electrophoretically determined H , Soulé et al. (1973) concluded that H has considerable power as an index to genic variation, even when only 20 to 25 loci are examined. Two other studies support this relationship. Kluge and Kerfoot (1973) examined several sets of vertebrate populations, finding that within each the average variability of a morphological character is correlated with the extent to which there has been divergence in its mean. Webster, Selander, and Yang, (1972) provided the complementary relationship, although their measure of morphological divergence was relatively crude. They found that among *Anolis* species, those with higher values of H were differentiated into more geographic races. The genetic base for both morphological variation and divergence probably involves many more genes than the handful examined in the direct estimation of H . But whether these relationships are simply evidence for the strength of H as an index

to heterozygosity at structural loci or if they extend it to other components of the genome is a matter for further study.

The estimates of H for anoles are based on similar sets of genes that received similar technical

treatment. I suggest that an H of 0.02 should be considered indicative of less genic variation than occurs in a population with an H of 0.08 or more. The reader is encouraged to provide his own criterion.

TABLE 3.—*Electrophoretic estimates of genic variation (H) in populations of Anolis lizards*

<i>Species</i>	<i>Populations</i>	<i>Loci</i>	<i>H</i>	<i>Source</i>
CONTINENTAL SPECIES				
<i>A. carolinensis</i> Southeastern U.S.	3	29	0.036–0.057	Webster, Selander, and Yang, 1972:529
GREATER ANTILLEAN SPECIES				
<i>A. stratulus</i> Puerto Rico	1	22	0.024	Soulé, et al., 1973, fig. 1
<i>A. poncensis</i> Puerto Rico	1	22	0.035	"
<i>A. evermanni</i> Puerto Rico	1	22	0.070	"
<i>A. gundlachi</i> Puerto Rico	1	22	0.082	"
<i>A. krugi</i> Puerto Rico	1	22	0.104	"
<i>A. pulchellus</i> Puerto Rico	1	22	0.129	"
<i>A. porcatus</i> Havana, Cuba	1	24	0.079	Webster, in prep.
<i>A. distichus dominicensis</i> Bon Repos, Haiti	1	21	0.090	"
SOLITARY SPECIES				
<i>A. extremus</i> Barbados	1	22	0.036	Soulé, et al., 1973, fig. 1
<i>A. roquet</i> Martinique	1	21	0.041	"
<i>A. luciae</i> St. Lucia	1	27	0.012	Webster, in prep.
<i>A. marmoratus</i> Guadeloupe	3	21–23	0.014–0.033	"
<i>A. agassizi</i> Malpelo	1	31	0.021	Webster, herein
RELATIVELY RECENT POPULATIONS				
<i>A. carolinensis</i> South Bimini	1	29	0.064	Webster, Selander, and Yang, 1972:529
<i>A. angusticeps</i> South Bimini	1	25	0.000	"
<i>A. distichus</i> South Bimini	1	27	0.043	"
<i>A. sagrei</i> South Bimini	1	26	0.009	"
<i>A. sagrei</i> Swan Island	1	28	0.052	Lister and Webster, in prep.

Unfortunately, H has not been estimated for any of the South or Central American anoles. Whether *A. carolinensis*, a secondarily continental species, has more genic variation than *A. agassizi* is questionable (Table 3).

Many of the Greater Antillean species represent stocks long established on islands so large and biologically diverse that they probably have a continental influence on genic variation. Estimates of H have a broad range, but many of the values are higher than those obtained from anoles in any other evolutionary or ecological context. Source island populations of two good colonists in the Caribbean, *A. porcatus* and *A. distichus*, appear to be more variable than *A. agassizi*.

Like *A. agassizi*, many of the species of the Lesser Antilles have been long established and occur in the absence of congeners. Their islands, however, tend to be larger than Malpelo and provide a more typical anole environment. Estimates of H from four species are nonetheless similar to that from *A. agassizi*.

The South Bimini and Swan Island populations represent colonizations that are relatively recent (Williams, 1969). It is in such populations that any loss of heterozygosity during and soon after founding should be most visible. The populations of *A. sagrei* and *A. angusticeps* on South Bimini have little or no detectable genic variation, although the *A. angusticeps* have some esterase variation that was refractory to interpretation and was omitted from the reported H of 0.00. Elsewhere in the Bahamas and the West Indies, however, these species have more variation (Webster, in prep.; Lister and Webster, in prep.; see Table 3, *A. sagrei*, Swan Island). These results and those for insular populations of *Peromyscus* (Selander et al., 1971) and cave populations of *Astyanax* (Avisé and Selander, 1972) suggest that a major loss of heterozygosity may frequently occur during the colonization of islands; however, the South Bimini populations of *A. distichus* and *A. carolinensis* seem to have been less affected.

Since several Greater Antillean species appear to have as little genic variation as *A. agassizi*, there is no compelling reason for concluding that it lost much during and subsequent to its colonization of Malpelo. If it did, it is likely that both random and selective processes played a role, but their relative importance cannot be determined. It is

interesting to note that no variation was observed for three esterases (only one of which was included in the estimate of H). These enzymes usually show complex patterns of variation in anole populations, including some with little genic variation. That the estimates of H for *A. agassizi* and several other solitary anoles are fairly uniform suggests that the net influence on genic variation may be quite similar in these older populations. If this consistency is confirmed by further studies of solitary species, it will be appropriate to consider selective explanations.

Genetic Differentiation

On the basis of a protein phenotype including the products of 24 genes, *A. agassizi* is quite distinct from all five of the species with which it was compared (Table 4). Two of the species are also members of the *latifrons* series of the alpha section (Etheridge, 1960): *A. luciae* (St. Lucia, Lesser Antilles), like *A. agassizi*, has retained caudal autotomy, but *A. squamulatus* (Mainland, Venezuela) has lost it. Since the *latifrons* series is defined by character states that are ancestral for the alpha section (Etheridge, 1960), it is not surprising that the species within it should have diverged to such an extent. Even two members of the apparently monophyletic *roquet* species group (Gorman and Atkins, 1969), *A. luciae* and *A. extremus* (native to Barbados, Lesser Antilles), differ completely at 17 of the 29 genes examined. *Anolis singularis* is as distinct from *A. agassizi* as are members of the *latifrons* series; and the fourth alpha section species, *A. marmoratus*, has no shared electrophoretic mobilities. The beta section *A. garmani* is no more distinct than some of the alpha section species.

These findings shed no new light on the affinities of *A. agassizi*. Except for very closely related populations, electrophoretically determined genetic difference is always an underestimate of genetic distance. When the species compared are as distantly related as these, it even becomes unreliable as an index to genetic distance. Thus the small differences in similarity that were observed in this study should be considered meaningless. As concluded previously (Webster, Selander, and Yang, 1972), when only 20 to 30 proteins are examined, electrophoresis has little value in anoline taxonomy beyond the species group.

TABLE 4.—Similarity (j_{rs} ; Nei, 1972) of electrophoretic mobilities of proteins in comparisons between *Anolis agassizi* and five congeners

Protein	<i>A. garmani</i>	<i>A. marmoratus</i>	<i>A. singularis</i>	<i>A. squamulatus</i>	<i>A. luciae</i>
aspartate aminotransferase-1	0.00	0.00	0.00	1.00	0.00
phosphohexose isomerase	0.00	0.00	1.00	0.00	1.00
leucine aminopeptidase	0.00	0.00	1.00	1.00	1.00
isocitrate dehydrogenase-2	1.00	0.00	0.00	0.00	0.00
lactate dehydrogenase-1	0.00	0.00	0.00	1.00	0.00
lactate dehydrogenase-2	0.00	0.00	0.00	1.00	0.00
malate dehydrogenase-1	1.00	0.00	1.00	0.00	0.00
malate dehydrogenase-2	0.00	0.00	0.00	0.00	1.00
α -glycerophosphate dehydrogenase	0.00	0.00	0.00	0.50	1.00
Sum of Similarities	2.00	0.00	3.00	4.50	4.00
(Σj_{rs})					

Values for the following are 0.00: 6-phosphogluconate dehydrogenase, aspartate aminotransferase-2, peptidase, isocitrate dehydrogenase-1, two phosphoglucomutases, fumarase, indophenol oxidase, alcohol dehydrogenase, albumin, proteins A, B, and C.

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Notes on the Chromosomes of
Anolis agassizi (Sauria: Iguanidae)
and *Diploglossus millepunctatus*
(Sauria: Anguinae)

Brad Stamm and George C. Gorman

ABSTRACT

The karyotypes of *Anolis agassizi* and *Diploglossus millepunctatus* are very similar. When compared to other species in their respective groups, the karyotypes of the two Malpelo lizards are considered primitive.

During the past ten years description of reptilian karyotypes has moved from relative novelty to virtually routine. Chromosome preparations of Malpelo lizards were made directly from testes following methods described by Gorman, Atkins, and Holzinger (1967).

Both *Anolis agassizi* and *Diploglossus millepunctatus* have karyotypes consisting of six pairs of metacentric macrochromosomes and 12 pairs of microchromosomes, $2n=36$ (Figure 19a,b).

Among anguid lizards previously studied, this karyotype was found in *Diploglossus costatus* (the only other *Diploglossus* studied to date) but not in the genera *Gerrhonotus*, *Anguis*, and *Ophisaurus* (Bury, Gorman, and Lynch, 1969). McDowell and Bogert (1954) considered the diploglossines the most primitive of the anguids.

Similarly, representatives of the most primitive group of *Anolis*, the Lesser Antillean *roquet* group (alpha group, *latifrons* series; Etheridge, 1960),

have this same karyotype. Although many species groups of *Anolis* show highly derived chromosomal morphology, a large section of the genus has been conservative and retained the ancestral karyotype (for review, see Gorman, 1973).

Anolis agassizi is also a member of the *latifrons* group. This species group has representatives on the South American mainland as well as the Lesser Antilles (the term *roquet* group follows Underwood, 1959). The Malpelo anole and the *roquet* group all possess fracture planes in the caudal vertebrae, hence caudal autotomy is commonplace. This character appears to have been secondarily lost among living mainland forms. Thus the presumed ancestors of *A. agassizi* and the Lesser Antillean *latifrons* anoles are extinct, and the living South American anoles are more derived (Etheridge, 1960).

Chromosomes tend to support this contention. Many members of the *roquet* group have a karyotype virtually indistinguishable from *A. agassizi*. Only a single mainland *latifrons* member has been previously studied, *A. jacare*, and it has a derived karyotype of $2n = 32$, with a reduction in chromosome number (Williams et al., 1970). For comparison we add data on two other mainland *latifrons* species, *A. frenatus* from Panama, and *A. squamulatus* from Rancho Grande, Venezuela. Webster, Hall, and Williams, (1972) argued convincingly that within *Anolis*, 12 metacentric macrochromosomes and 24 distinctly smaller microchromosomes is the primitive condition. *Anolis squamulatus* (not illustrated) has the typical primitive complement. *Anolis frenatus* has $2n = 36$, which is the typical

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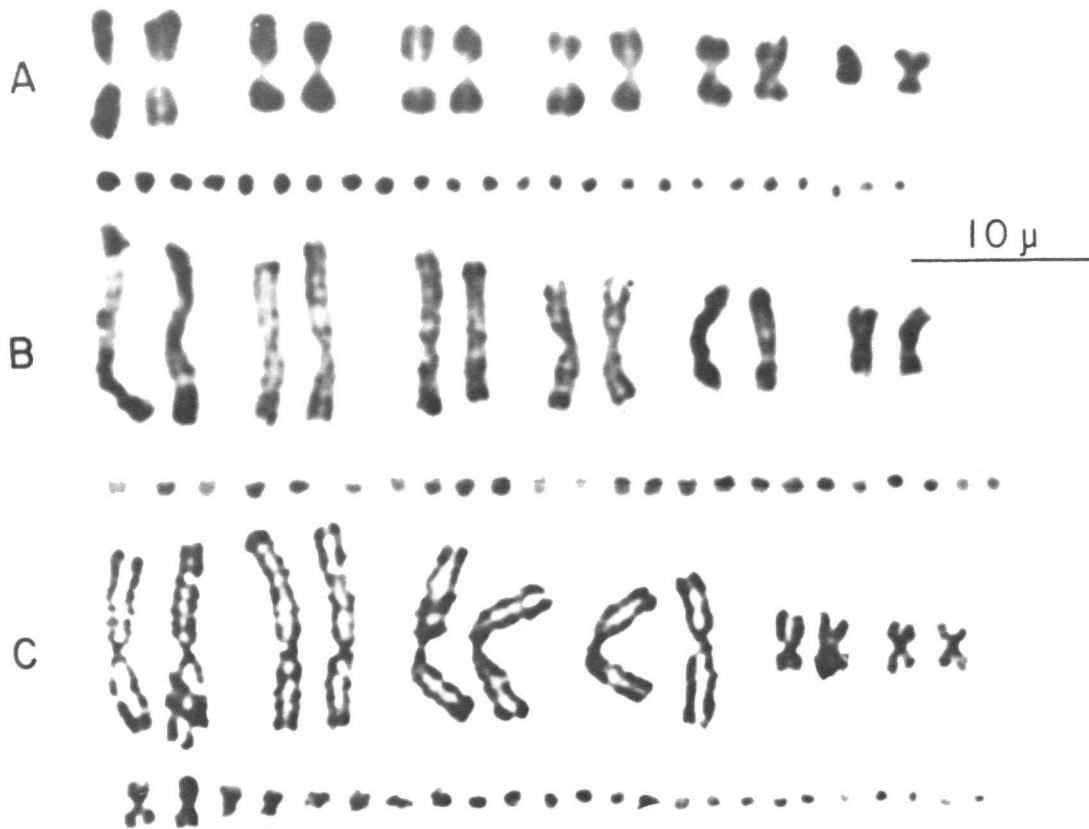


FIGURE 19.—Lizard karyotypes: *A*, *Anolis agassizi* ♂, $2n = 36$, 12 ca. metacentric macrochromosomes and 24 microchromosomes (pair 6 appears heteromorphic in this preparation, but we lack sufficient numbers of metaphase plates, and have no data on females to confirm this); *B*, *Diploglossus millepunctatus* ♂, $2n = 36$, 12 ca. metacentric macrochromosomes and 24 microchromosomes; *C*, *Anolis frenatus* ♂, $2n = 36$, size break between pairs 4 and 5, macrochromosomes do not break sharply from microchromosomes; pair 7 is intermediate in size.

saurian diploid number; but there is an enlarged metacentric pair of "microchromosomes," and a break in size between pairs four and five implying a derived karyotype (Figure 19c).

The similarity between *A. agassizi* and the *roquet* group of Lesser Antillean *Anolis* in both osteology and karyotype substantiates the belief that both retain primitive character states. We do not argue for common origin between these two groups. The similarity in karyotype between the *Diploglossus* and *Anolis* of Malpelo is fortuitous. This chromosomal formula is common to representatives of numerous lizard families, often

among the most primitive representatives, as determined osteologically (Gorman, 1973).

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Subtidal Communities of Malpelo Island

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ABSTRACT

The subtidal communities of Malpelo are described in terms of the pattern of spatial coverage of sessile organisms. The Malpelo subtidal is characterized by a prevalence of large barnacles (*Balanus peninsularis*) on steeply sloping rock walls and a highly structured community of hermatypic corals on gradually sloping substrata, both communities extending to a depth of about 30 meters. The rock wall communities of Malpelo have significantly more free space available for recruitment (38.6%) than do comparable communities in continental regions (7.3%). Size distribution suggests that recruitment is a greater risk, but conditions for adults are better on Malpelo than in continental regions. Observations suggesting the importance of fish grazing are discussed. An expanded depth range at Malpelo provides clearer zonation of the coral community than along the Panamanian coast. Although coral growth is rich in terms of surface coverage and size of colonies, a true reef is not formed.

Introduction

The subtidal communities at Malpelo had never been observed before our brief visit, and thus our objective was to describe these communities in quantitative terms that would be useful for comparisons to other areas and for any return visits to the island.

We have utilized the relative surface area coverage of macroinvertebrate species as the quantitative expression of community composition. Since

the Malpelo subtidal consists almost entirely of vertical rock walls, surface area data were easily acquired from underwater photographic transects, using color and black-and-white film. Relative surface area coverage was then estimated by tabulation of randomly located points on the projected transparencies and by planimetry (Tables 5,6,8). Photographs used for the quantitative survey are on file with C. Birkeland. We found that such a method was most efficient for acquiring basic information from a large, unfamiliar, area within a limited time. Photographic transects have the following additional advantages for primary survey of an unexplored underwater area: First, size distribution of the predominant sessile organisms can sometimes be used to deduce aspects of the age or recent history of a community, such as the frequency or heterogeneity of disruptive factors. Second, the extent of available unoccupied space in a habitat is often an important limiting factor for sessile organisms. Finally, the habitat or nursery of certain motile animals is often defined by specific sessile organisms and, therefore, the sessile organisms may provide the best definition of the community as a whole (e.g., coral reef, oyster bed, kelp bed, sea grass bed, etc.).

Dives were made at each of eight stations (Figure 20). At all stations except Station 6, the basaltic rock wall sloped steeply, sometimes vertically, to a depth of about 37 meters on Malpelo itself or about 49 meters on the offshore pinnacles (Stations 4 and 5). Sometimes a talus slope of large boulders provided a more gentle slope in deeper water (below about 20 m; Stations 3, 7, and 8). Station 6 was the only area found with a gradual slope and it was the only location of a rich community of hermatypic corals.

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TABLE 5.—Percent coverage of primary substrata on rock walls of Malpelo Island, 1 to 3 March 1972

	Depth range (meters)				
	0-3	3-6	6-27	27-37	37-50
No. of points (sample size x 50)	450	1350	2800	500	350
"OPEN SPACE"					
bare rock or sediment	1.1	1.6	4.6	5.2	5.4
*crustose coralline algae	17.8	30.1	34.0	24.6	20.3
"OCCUPIED SPACE"					
* <i>Balanus peninsularis</i> (live)	5.3	14.0	5.8	1.8	1.1
* <i>Balanus peninsularis</i> (dead, test)	16.8	23.6	8.7	6.6	2.8
<i>Balanus peninsularis</i> (total)	22.1	37.6	14.5	8.4	3.9
* <i>Lobophora variegata</i>	11.6	3.8	1.0		
*"algal scuz"	4.9	6.0	5.2	18.8	12.0
"red algal crust"	-	0.7	1.2	2.2	1.4
branching coralline algae (mostly <i>Amphiroa</i> spp.)	5.1	0.1	0.8	-	-
* <i>Polyfibrospongia</i> sp.	30.7	6.7	1.1		
*orange flat sponge	-	0.1	1.6	6.0	13.1
yellow flat sponge	-	0.1	0.5	0.2	0.6
red flat sponge	0.4	0.1	1.6	-	0.6
*white flat sponge	-	-	0.3	6.2	11.1
white lumpy sponge	-	-	0.5	-	0.6
blue sponge	-	0.1	-	-	-
greenish gray sponge	-	-	-	0.2	-
gray-brown sponge	-	-	-	-	0.3
hydroid	-	-	-	-	1.7
bryozoan	-	-	-	-	7.7
<i>Lichenopora</i> sp.	-	0.1	+	-	-
<i>Pacificorgia</i> spp.	2.9	4.0	10.0	2.6	0.0
<i>Lophogorgia alba</i>	-	-	0.6	-	-
gorgonacean	-	-	-	-	6.6
<i>Errinopora pourtalesii</i>	-	-	0.3	7.6	2.3
<i>Tubastraea aurea</i>	-	0.3	2.4	0.6	1.1
<i>Tubastraea aurea</i> (dead)	-	0.1	0.5	0.2	-
<i>Pocillopora robusta</i>	-	0.4	0.9	-	-
<i>Porites</i> spp.	-	-	9.0	-	-
<i>Astrangia</i> sp.	-	-	-	1.4	-
<i>Pavona varians</i>	-	-	0.5	-	-
<i>Ostrea irridescens</i>	-	-	3.0	6.4	8.0
<i>Ostrea irridescens</i> (dead)	-	0.1	-	-	-
<i>Ostrea fisheri</i>	-	-	-	0.8	-
<i>Didemnum candidum</i>	3.3	7.2	1.7	5.4	2.6
<i>Didemnum</i> sp.	-	0.4	3.3	1.4	+
<i>Polyandrocarpa tinctoria</i>	-	-	-	0.8	-

* Predominant categories. An organism that occupies over 10 percent of the primary substrata is arbitrarily defined as predominant.

+ indicates that the organism was present in photographs of the area, but it did not appear as data in surface-coverage counts from contact of random points.

TABLE 6.—Proportion of space open for invasion, as opposed to space occupied by macroscopic sessile organisms other than crustose coralline algae, comparing Malpelo Island and the continental coast of the eastern tropical Pacific (coverage estimated by number of rectangular coordinate points—taken from a random number table—falling on the image of each category; 50 points tallied from each quadrat photograph; several points in the continental photographs fell into shadow so were not determined)

Region	No. of quadrats	Open space	Occupied space	Total no. of points	Mean percent of open space
Oceanic (Malpelo)	56	1081	1719	2800	38.6
Continental (Taboguilla Is., Panama and Playas del Coco, Costa Rica)	59	213	2705	2918	7.3

$\chi^2 = 800, 1 \text{ d.f.}$

Reject H_0 : conclude significantly more "open space" exists in subtidal communities of Malpelo than in comparable communities of mainland.

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crabs; and Janet Haig, also with the Allan Hancock Foundation, identified the porcellanid and diogenid crabs. L. G. Abele of Florida State University completed the list of crabs and provided a complete list for the decapods. Joseph Rosewater of the National Museum of Natural History, Smithsonian Institution, confirmed and corrected the lists of mollusks. Alan J. Kohn of the University of Washington verified the species of *Conus* and Dora P. Henry, also from the University of Washington, identified the barnacles. Peter W. Glynn of the Smithsonian Tropical Research Institute confirmed and corrected our identification of scleractinian corals. J. W. Wells of Cornell Uni-

TABLE 7.—Colony-polyp-number distributions in populations of *Tubastraea aurea* at Malpelo compared with colony polyp number distributions in two areas near the continental coast (counts were made from quadrat photographs)

Region	A Total no. colonies examined	B No. solitary polyps	C No. colonies with 10 or more polyps	Mean no. polyps per colony ($\pm SE$)*
Oceanic (Malpelo)	372	88	102	11.6 \pm 0.8
Continental (Taboguilla Is., Panama and Playas del Coco, Costa Rica)	408	135	92	10.0 \pm 0.8

* Solitary polyps not included in analysis ($N=A-B$).

$\chi^2 = 6.78, 2 \text{ d.f.}$ (categories compared were B, C, and A-B-C).

Reject H_0 : conclude significantly fewer solitary polyps in proportion to number of larger colonies (> 10 polyps) in a single sample of Malpelo populations when compared with a 3 year sample of several mainland populations.

TABLE 8.—Zonation of the coral community of Malpelo Station 6: percent coverage by each species, bare rock, or dead coral substrata (data acquired by planimeter measurements on tracings of projected photographs)

	Depth range (meters)					
	9.2 & 10.7	12.3	13.8 & 15.4	16.9	18.4	26.1 & 27.6
No. of planimeter samples	8	10	13	4	4	2
PERCENT OF SURFACE						
Live hermatypic corals	57.2	69.3	74.8	89.2	58.6	42.7
Dead coral substrata	24.5	27.6	22.7	10.8	29.8	18.0
Rock or sediment substrata	18.3	3.1	2.5	—	11.6	38.4
PERCENT OF LIVE CORAL SURFACE						
<i>Pocillopora robusta</i>	94.3	80.5	14.4	2.4	—	—
<i>Porites</i> spp.	5.7	19.5	77.3	43.2	80.5	47.4
<i>Pavona clivosa</i>	—	—	8.3	54.4	19.5	—
<i>Agariciella planulata</i>	—	—	—	—	—	52.6

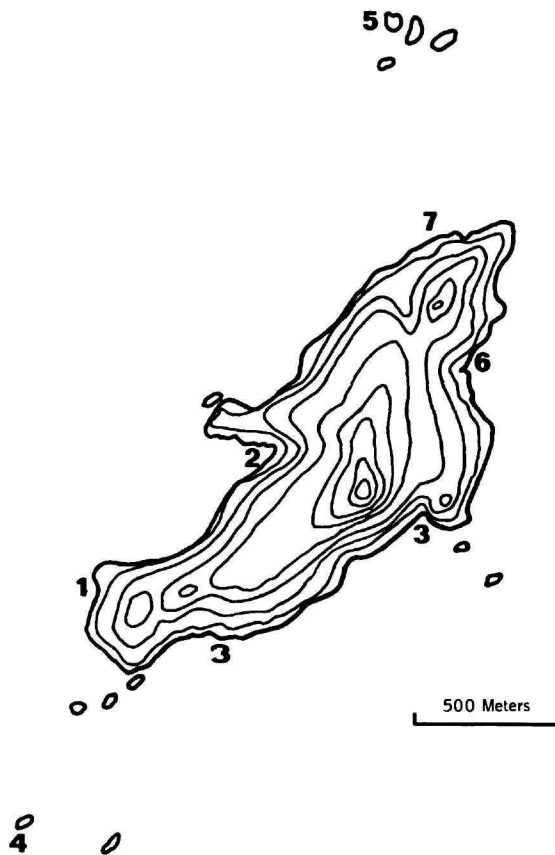


FIGURE 20.—Subtidal collection stations at Malpelo Island.

versity identified the hydrocoral and George Hechtel of the State University of New York at Stony Brook identified the sponge.

Rock Wall Communities

The steep rock walls (Figure 21) were predominantly occupied by the large barnacle *Balanus peninsularis* (Table 5). Sixty to 80 percent of the *Balanus* space was occupied by empty tests (Figure 22) which remained on the walls after the death of the barnacles because their predators were snails (probably *Thais planospira* and possibly *Purpura pansa*) rather than sea stars. These tests provide a major source of shelter or habitat for many polychaetes, mollusks, crustaceans, and fishes (*Entomacrodus chiostrictus*) and a substratum for hydroids, sponges, and tunicates. The prevalence of barnacles is reflected in the white sand sediment which encircles the island at the base of the rock wall. This sand is composed almost entirely of fragments of *Balanus* tests.

A clear zonation was observed on the vertical walls (Table 5). To a depth of 3 meters, the large black sponge *Polyfibrospongia* sp. occupied over 30 percent of the space. The brown alga *Lobophora variegata* was also prevalent above 3 meters. Both *Polyfibrospongia* and *Lobophora* decreased rapidly in abundance between 3 and 6 meters where *Balanus* tests occupied nearly 37 percent of the space. From 6 to 27 meters the substratum was



FIGURE 21.—Vertical rock wall community; Station 3, 15 m depth. Prevalent animals are *Pacificorgia media* (left), *Porites* sp. (right), and *Balanus peninsularis*.

very clear of "scuz" (filamentous algae, hydroids, etc.) and was covered mostly with crustose coralline algae and scattered patches of anthozoans, i.e., hermatypic corals (mostly *Porites* spp.) an ahermatypic (*Tubastraea aurea*), and gorgonaceans (*Pacifigorgia* spp.). Below 27 meters, filamentous algae, small flat encrusting sponges, oysters (*Ostrea irridescens*), and the violet branching hydrocorals (*Errinopora pourtalesii*) became prevalent. Although occupying only 7.6 percent of the substratum, the vivid violet hydrocorals appeared as a "field of *Errinopora*" below 27 meters. Certain motile animals were also found only at depths of 27 meters or below: the basket star, *Astrodictyum*

panamense, and the sea stars, *Tamaria* sp. and *Narcissia gracilis*.

The most striking aspect of the occupation of the subtidal substrata at Malpelo was the amount of "open" or "free" space. Table 6 compares the amount of open space in 59 permanent quadrat photographs from small Pacific islands less than 14 km from the mainland in Costa Rica and Panama with the amount in 56 survey photographs from Malpelo. Bare rock or space occupied by crustose coralline algae is available as attachment space for other sessile or sedentary organisms. Between the depths of 6 and 27 meters near the mainland, an average of 7.3 percent of the space is



FIGURE 22.—A typical example of the rock wall community; Station 7, 10 m depth (1 = *Balanus peninsularis*, 2 = *Porites* sp., 3 = *Tubastraea aurea*, 4 = *Pacifigorgia media*).

available as open space in rock wall communities. In comparable rock wall communities at Malpelo, 38.6 percent of the space is available.

Many of the prevalent sessile organisms were common to continental and oceanic rock wall communities. The oceanic Malpelo populations for both *Tubastraea aurea* and *Lophogorgia alba* appeared to be characterized by size distributions in which larger individual colonies were more prevalent and less recruitment was observed in comparison with the continental populations. The number of polyps in each *Tubastraea aurea* colony in Malpelo photographs were counted and the polyp-number distribution (presumed to be a form of age distribution) was compared with polyp-number distribution in Panama mainland quadrats (Table 7). The distributions differ significantly by chi square when the proportions of recruitment for solitary polyps, colonies of 2 to 9 polyps, and colonies of 10 or more polyps are compared. The mainland data are from several areas through all seasons over a 3-year period while the Malpelo data are from a single survey. The significant difference in age distribution could be the result of a particularly poor year, or time of year, in which the Malpelo survey was made, rather than to differences between oceanic and continental populations. If the solitary polyps are excluded from the analysis, the polyp-number distributions do not differ significantly by *t*-test. Nevertheless, we predict that more data from further surveys would confirm a general trend towards proportionately less recruitment and longer adult life in oceanic populations.

A similar trend is evident for closely related species living on the island and mainland, respectively. For instance, *Balanus trigonus* (adults ca. 0.8 cm basal diameter) is the prevalent species in continental areas examined while *Balanus peninsularis* (adults ca. 6 cm basal diameter) is the prevalent species at Malpelo. The same generalization could be drawn comparing colonial tunicates of the genus *Didemnum*.

In summary, the oceanic rock wall communities at Malpelo had over five times as much open space as the continental rock wall communities. Since space is a limiting resource for sessile benthic organisms on solid substrata, the abundant availability of open space at Malpelo implies that recruitment is a more difficult problem for these populations. Once established, however, an individual

lives under less crowded conditions. In other words, an individual may be subjected to greater risk initially, but may attain greater fecundity if it survives until adulthood.

The reason for reduced recruitment success is unknown but two possible causes can be hypothesized: isolation from other populations and heavy grazing by fishes. Isolation may reduce recruitment of shallow benthic organisms because most, perhaps 85 percent of the species (Thorson, 1961:456), have pelagic larval stages for which the mean duration is about 2 weeks. Only about 30 percent have planktonic stages longer than 5 weeks (Thorson, 1961:459). Malpelo is small, isolated, and surrounded by deep water. It seems likely that a large portion of the larvae may be carried away before settlement can occur. The water moving past Malpelo comes predominately from the northeast where the nearest shallow water is around the Azuero Peninsula, 367 km away. The fauna of Cobb Seamount, 430 km west of Washington State in the northern Pacific, has large populations of brooding species usually found only in the intertidal or shallow subtidal (Birkeland, 1971). Once a population of a brooding species is established on an isolated pinnacle, it may have a generally better chance of maintaining a population than species with planktonic larvae. The emplacement of settling plates at Malpelo would provide particularly interesting quantitative data for comparison with data from plates set nearer the mainland.

The sessile ciliate protozoan *Folliculina* was found on some of the Malpelo algae and it may have arrived by rafting on drifting algae. However, Scheltema (1973) has recently presented data showing that dispersal of this organism can also occur by attachment to the shells of veliger larvae. *Folliculina* is often found on the larger species of veligers which are "long-distance larvae from shoal-water bottom-dwelling organisms of the shelf" (Scheltema 1973:123).

The effects of grazing fish in producing open space is implied by some general observations concerning algae and is based on the assumption that grazers of algae also remove recently settled benthic animals. Algae and juvenile sessile organisms were very sparse on Malpelo (Tables 5, 6), yet the exceptionally clear water should provide favorable growth conditions for algae. As an example, one small sprig of *Sargassum* was found at 46 m. The

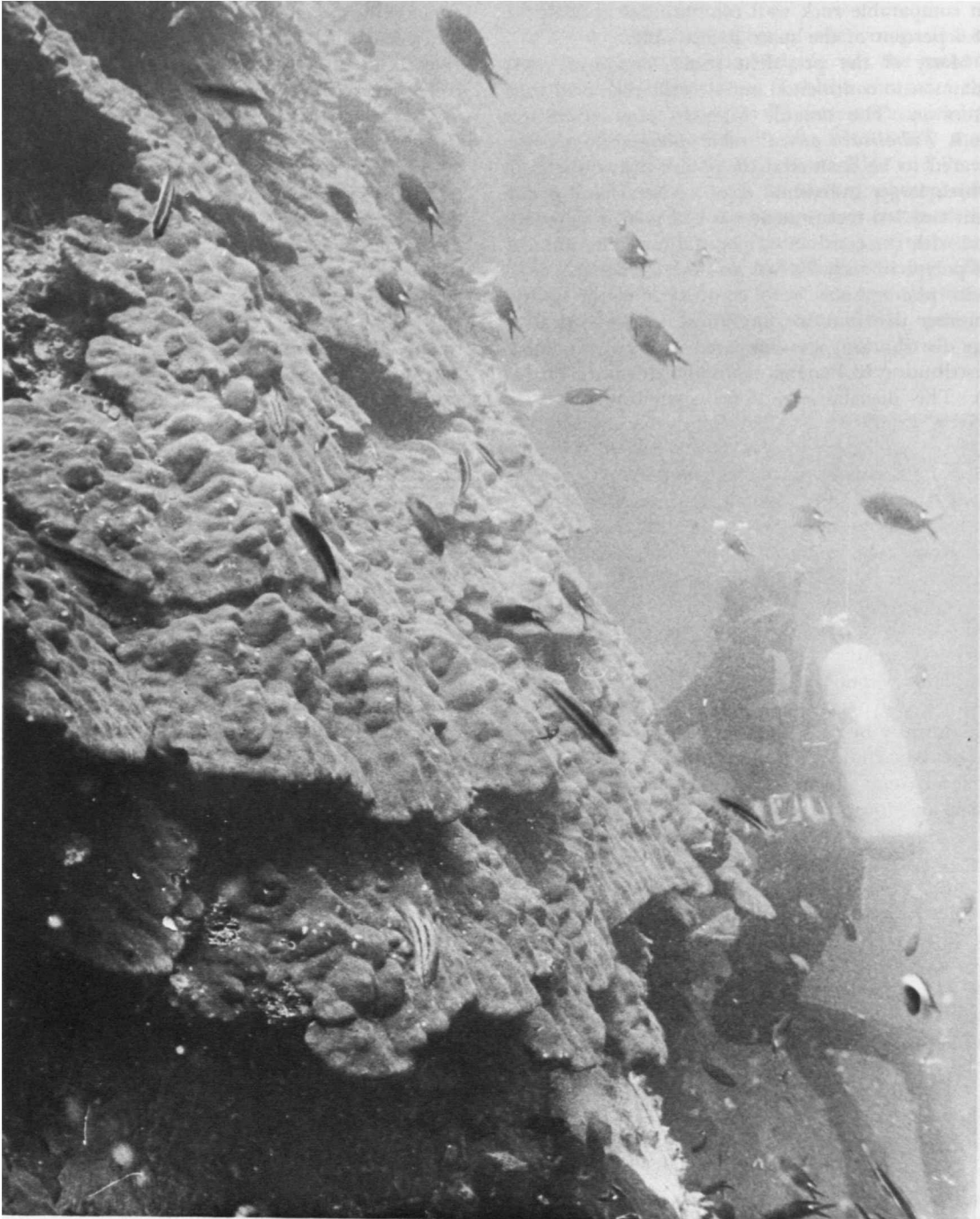


FIGURE 23.—“Shingle” formation of *Porites* sp. on the rock wall community.

substrata in shallower water presumably had enough available light and other conditions for growth of *Sargassum*. The large schools of acanthuroids may have kept the algae (and settling larvae) under heavy grazing pressure. This hypothesis could be simply tested by the emplacement of fish exclusion cages for 4 to 12 weeks.

A species list from the collections and observations made during the survey is given in the Appendix. The most prevalent of all animals, *Balanus peninsularis* (Table 5), is known from the Galapagos but not from the mainland. Since its test provides a major source of shelter or habitat for motile animals and a substratum for sessile organisms, the prevalence of *B. peninsularis* may be

the major factor contributing to the strong faunal similarities between Malpelo and the Galapagos Islands. Many familiar tropical eastern Pacific mainland species were conspicuous by their absence: *Muricea* and antipatharians (the usually present arborescent coelenterates), and the sea stars *Pharia* and *Phataria*. Scarid fishes, hermit crabs, and gastropods were remarkably scarce.

Coral Communities

On the steeply sloping rock walls typical of the Malpelo subtidal, hermatypic corals occur only as a veneer interspersed with other growth (Figure 22) or in some cases as shingled, overhanging

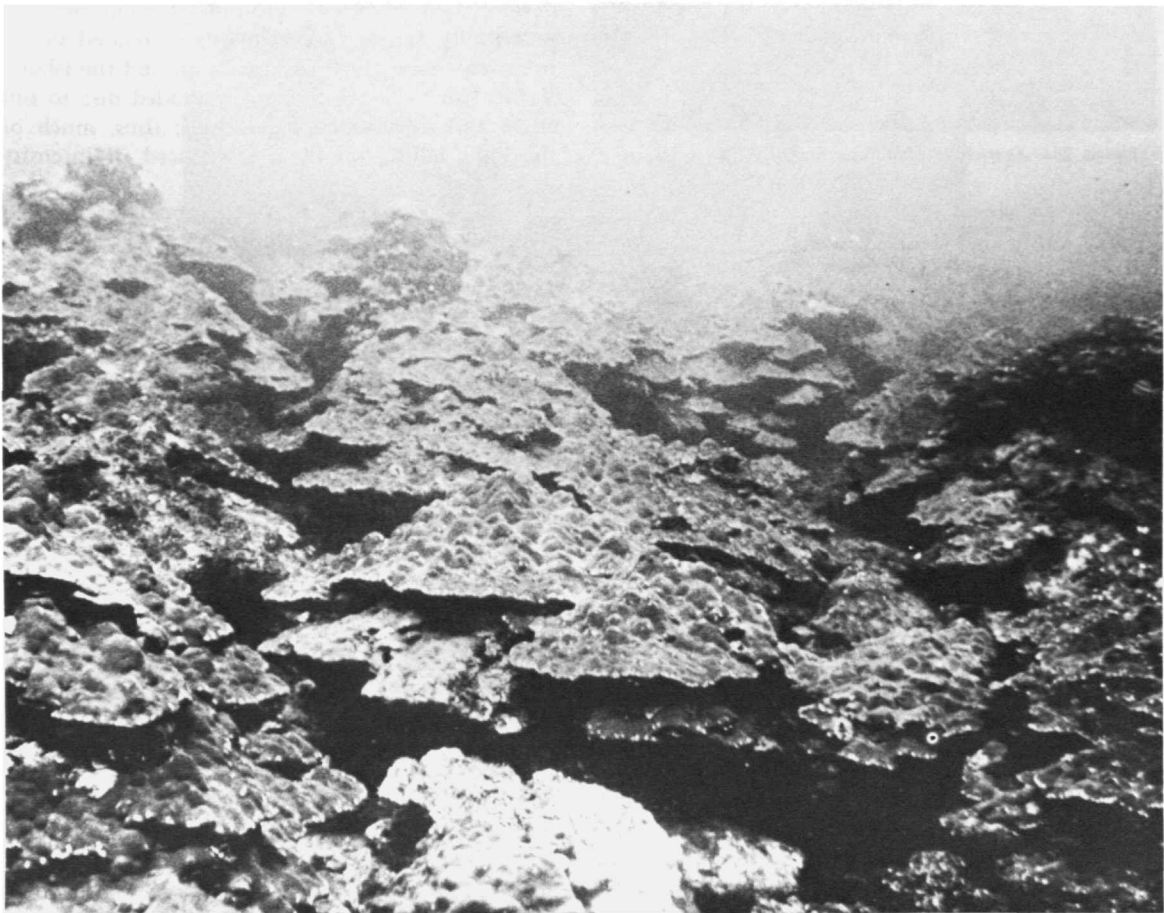


FIGURE 24.—*Porites* heads in the coral community; Station 6, 18 m depth.



FIGURE 25.—*Agariciella planulata*; Station 6, 30 m depth.

masses (Figure 23). Table 5 shows that the grand average surface area coverage by hermatypic corals on steep rock walls is only about 10 percent. In contrast, a more gradual slope at Station 6 supports an extensive coral community (Figure 24) extending to 30 m depth. Table 8 shows that hermatypic corals dominate the surface area coverage of this slope. At 15 meters depth, a continuous growth of *Porites* sp. measured 6.7 meters across by 2 meters high. At 28 meters, a continuous growth of *Agariciella planulata* covered an area of 3 by 1.8 meters. Figure 25 illustrates that coral coverage at about 30 meters is extensive and not merely confined to isolated colonies.

The rich development of hermatypic corals at Station 6 suggests that conditions for coral growth are highly favorable at Malpelo. The lack of coral development elsewhere around Malpelo may be principally due to two factors, both related to the prevalence of vertical rock walls around the island. Vertical surfaces are frequently shaded due to sun angle and substratal irregularities; thus, much of the light falling on them is reduced in intensity

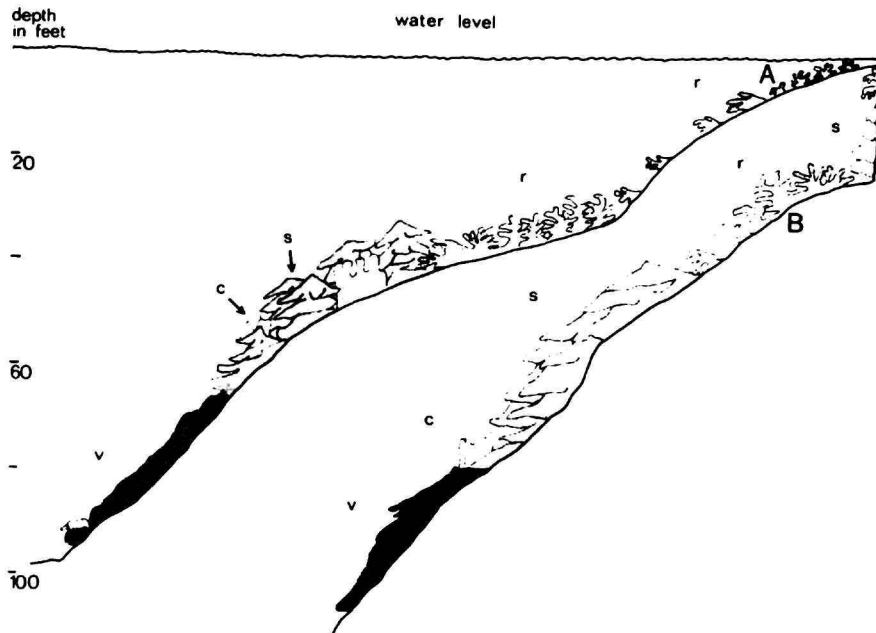


FIGURE 26.—Profile diagram of the coral community at Station 6. As the diver faces shore, transect A is to the left and transect B is to the right with a sand and cobble channel separating them (r = *Pocillopora robusta*, s = *Porites* spp., c = *Pavona clivosa*, and v = *Agariciella planulata*).

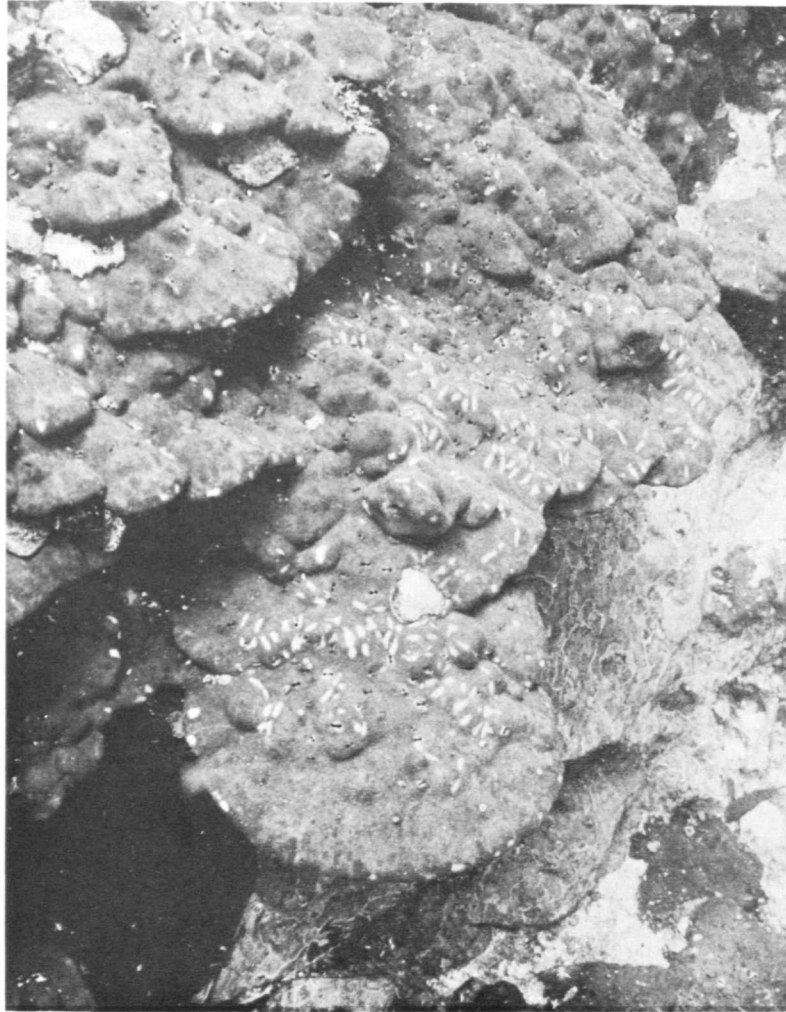


FIGURE 27.—Nicks from fish grazing on *Porites* sp.

and quality by scattering or by passing obliquely through the water mass. By contrast, intensity on horizontal surfaces at a similar depth would be greater. Calcification in corals is enhanced by the photosynthesis of their symbiotic zooxanthellae (Goreau, 1959) and it is likely that the small amount of coral noted along vertical walls at Malpelo is partly due to lower light intensities.

The second factor possibly contributing to the lack of extensive coral development at Malpelo is simply the lack of horizontal support on which

corals can build a reef. Figure 23 shows that corals growing on the vertical faces tend to extend out into the water mass to form a more horizontal surface which would better intercept light. This process can proceed only so far until erosion by burrowing animals causes collapse. Furthermore, subtidal talus piles and the eroding aspect of the cliffs above suggest that rockfalls are a frequent occurrence at Malpelo. Some talus appeared to be of recent origin, judging from the low numbers of large encrusting organisms. These rockfalls prob-

ably constitute a major disruptive phenomenon which prevents dense coral buildup.

Even at Station 6 the prolific coral growth was not developed above 10 meters depth, and it was not clear that the living corals were growing on a pre-existing coral framework. We thus hesitate to refer to Station 6 as a coral reef. It is possible that the development of a true reef is prevented at Malpelo by other factors, one of which may be temperature. Surface temperatures were usually about 26.5°C, but an abrupt thermocline was formed at various depths. Temperatures below the thermocline were as low as 19.5°C and it has been suggested that this is cool enough to limit coral growth (Glynn and Stewart, 1973).

To the casual observer, the pattern of coral zonation is more clearly expressed at Malpelo than in continental eastern Pacific coral communities because the greater depth range at Malpelo allows the lower zones to spread out over a larger area (Figure 26). For instance, *Pocillopora* spp., *Pavona gigantea*, and *Pavona varians* are all intermixed between 6 and 7 meters at Uva Island, near the coast of Panama (cf. Figure 8 in Glynn, Stewart, and McCosker, 1972) while *Pocillopora robusta*, *Pavona clivosa*, and *Agariciella planulata* are separated by depth at Malpelo (Figure 26).

As on coral reefs in continental regions of the tropical eastern Pacific (Glynn, Stewart, and McCosker, 1972), signs of the effects of grazing by fishes are prevalent. The edges of the ridged extensions of the large *Pavona clivosa* colonies were lined with nicks scraped by browsing fishes. Figure 11 in Glynn, Stewart, and McCosker (1972) is a typical illustration of this phenomenon. Occasionally, concentrations of nicks also occurred on sheets of *Porites* (Figure 27). Only three individuals of the scarid fish, *Scarus rubroviolaceus*, were seen at Station 6 and none were observed at other stations. The tetraodontid, *Arothron meleagris*, and balistids were common at all stations and probably these fishes, rather than scarids, were responsible for most of the damage to corals (Figure 27).

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Appendix

A List of Marine Invertebrates Identified from Malpelo Island

PROTOZOA

Folliculina sp.

PORIFERA

Polyfibrospongia sp.

COELENTERATA

Hydrozoa

Errinopora pourtalesii (Dall)

Anthozoa

Pacificorgia media (Verrill)

Pacificorgia sp.

Lophogorgia alba (Duchassaing and Michelotti)

Pocillopora robusta Verrill

Pavona clivosa, Verrill

Pavona varians Verrill

Agariciella planulata (Dana)

Porites spp.

Astrangia sp.

Tubastraea aurea (Quoy and Gaimard)

MOLLUSCA

Gastropoda

Diodora saturnalis (Carpenter)

Seila assimolata (C. B. Adams)

Epitonium billeanum (DuShane and Bratcher)

Hipponix grayanus Menke

Hipponix panamensis C. B. Adams

Crepidula aculeata (Gmelin)

Capulus sp.

Erato (?*columbella* Menke)

Cypraea albuginosa Gray

Cypraea isabellamexicana Stearns

Cypraea teres pellucens Melvill

Simnia aequalis (Sowerby)

Cymatium pileare (Linnaeus)

Colubraria ochsneri Hertlein & Allison

Muricanthus princeps (Broderip)

Coralliophila sp.

Coralliophila (?*neritoides* [Lamarck])

Quoyula madreporarum (Sowerby)

Thais planospira (Lamarck)

Acanthina brevidentata (Wood)

Purpura pansa Gould

Morula lugubris (C. B. Adams)

Anachis (?*coronata* [Sowerby])

Mitrella sp. 1

Mitrella sp. 2

Fasciolaria princeps Sowerby

Conus diadema Sowerby

Conus dalli Stearns

Tylodina fungina Gabb

Chromodoris sedna (Marcus)

Bivalvia

Arca mutabilis (Sowerby)

Barbatia reeveana (Orbigny)

Septifer zeteki Hertlein and Strong

Lithophaga aristata (Dillwyn)

Lithophaga plumula (Hanley)

Isognomon recognitus (Mabille)

Ostrea fisheri Dall

Ostrea (?*iridescens* Hanley)

ARTHROPODA

Cirripedia

Balanus peninsularis Pilsbry

Tetraclita stalactifer (Lamarck)

Heteralepas quadrata (Aurivillius)

Lepas anserifer Linnaeus

Decapoda

PALAEMONIDAE

Brachycarpus biunguiculatus (Lucas, 1849), circumtropical

Harpiropsis depressus (Stimpson, 1860), Indo-Pacific-western America

Pseudocoutierea elegans Holthuis, 1951, western America

Veleronia laevifrons Holthuis, 1951, western America

Periclimenaeus hancocki Holthuis, 1951, western America

GNATHOPHYLLIDAE

Gnathophylloides mineri Schmitt, 1933, circumtropical (?)

ALPHEIDAE

Alpheus lottini Guérin, 1830, Indo-Pacific-western America

A. malleator Dana, 1852, western America, eastern & western Atlantic

A. grahami Abele, new species, endemic to Malpelo (see paper by Abele in this volume)

Synalpheus charon (Heller, 1861), Indo-Pacific-western America

S. nobilii Coutière, 1909, western America

S. digueti Coutière, 1909, western America

S. biunguiculatus (Stimpson, 1860), Hawaii, Clipperton, Malpelo

S. bannerorum Abele, new species, endemic to Malpelo (see paper by Abele in this volume)

Pomagnathus corallinus Chace, 1937, western America

HIPPOLYTIDAE

Lysmata galapagensis Schmitt, 1924, Galapagos Island, Malpelo

L. trisetacea (Heller, 1861), Indo-Pacific-offshore islands

Palinuridae

Panulirus penicillatus (Oliver, 1791), Indo-Pacific-offshore islands

PORCELLANIDAE

Petrolisthes haigae Chace, 1962, western America

P. glasselli Haig, 1957, western America

Pachycheles biocellatus (Lockington, 1878), western America

Clastocheilus diffractus (Haig, 1957), western America

PAGURIDAE

Pagurus sp., western America

DIOGENIDAE

Aniculus elegans Stimpson, 1858, western America

Trizopagurus magnificus (Bouvier, 1898), western America

DYNOMENIDAE

Dynomene ursula Stimpson, 1859, western America

PORTUNIDAE

Euphyllax dovii Stimpson, 1860, western America

XANTHIDAE

Quadrella nitida Smith, 1869, western America

Trapezia digitalis Latreille, 1825, Indo-Pacific-western America

T. ferruginea Latreille, 1825, Indo-Pacific-western America

Menippe obtusa Stimpson, 1859, western America

Domecia hispida Eydoux and Souleyet, 1842, Indo-Pacific-western America

Medaeus spinulifer Rathbun, 1898, western America

Pilumnus pygmaeus Boone, 1927, western America

Globopilumnus xantusii (Stimpson, 1859), western America

Ozius perlatus Stimpson, 1859, western America

Carpilodes cinctimanus (White, 1847), Indo-Pacific-western America

GRAPSIDAE

Grapsus grapsus (Linnaeus, 1758), western America, eastern and western Atlantic

GECARCINIDAE

Gecarcinus mapeiensis Faxon, 1893, endemic to Malpelo

MAJIDAE

Teleophrys cristulipes Stimpson, 1959, western America

Mithrax pygmaeus Bell, 1835, western America

Microphrys platysoma (Stimpson, 1859), western America

Lissa tuberosa Rathbun, 1898, western America

ECHINODERMATA

ASTEROIDEA

Leiaster callipeplus Fisher

Narcissia gracilis malpeloensis, new subspecies

Tamaria stria Downey, new species, endemic to Malpelo (see paper by Downey in this volume)

Mithrodia bradleyi Verrill

Nidorellia armata (Gray)

Asterope carinifera Müller and Troschel

OPHIUROIDEA

Astrodictyum panamense (Verrill)

Ophiocoma aethiops Lütken

Ophiocoma alexandri Lyman

Ophiactis savignyi (Müller and Troschel)

Ophiothela mirabilis Verrill

ECHINOIDEA

Diadema mexicanum A. Agassiz

Eucidaris thouarsii (L. Agassiz and Desor)

Triploneustes depressus A. Agassiz

Echinometra sp.

CHORDATA

ASCIDIACEA

Polyandrocarpa (*Eusynstyela*) sp. aff. *tincta* (Van Name)

Didemnum (*Didemnum*) sp. aff. *candidum* Savigny

Didemnum (*Didemnum*) sp. aff. *moseleyi* (Herdman)

The Macruran Decapod Crustacea of Malpelo Island

Lawrence G. Abele

ABSTRACT

Eighteen species of *Macrura* are reported from Malpelo Island. Two new species of Alpheidae, *Alpheus grahami* and *Synalpheus bannerorum*, are described and *S. nobilii* and *S. digueti* are re-described. Notes are given on *Periclimenaeus hancocki*, and *Gnathophylloides mineri* is recorded from the eastern Pacific.

Ecologically about half of the 43 decapods known from Malpelo are commensals with other invertebrates, mostly *Pocillopora* coral. Two species are semiterrestrial or terrestrial and the remaining species occur in a variety of subtidal habitats.

Zoogeographically decapod fauna of Malpelo (43 spp.) is most closely related to that of the western American mainland with 62 percent or 27 species occurring there. Nine species (20%) occur in the Indo-Pacific region and seven of these reach the western American mainland. There are three endemic species, two circumtropical species, and two species known only from offshore islands.

The very limited data available at present suggest a species-area effect on the shallow water decapods associated with oceanic islands.

Introduction

The first report of a decapod crustacean from Malpelo Island was that of Faxon (1893) who described a land crab, *Gecarcinus malpilensis*, based on material collected by the *Albatross*. This species was considered to be a synonym of *G. planatus* by Rathbun (1918), but Turkey (1970) recognized

G. malpilensis as a species endemic to Malpelo. In 1948, Garth reported on the *Askoy* collections, which included three species taken at Malpelo: an intertidal crab, *Grapsus grapsus*, the land crab, *Gecarcinus malpilensis*, and a pelagic portunid, *Euphylax dovii*, which was abundant in the waters around the island. No additional material of decapod crustaceans appears to have been collected at Malpelo until the Smithsonian Tropical Research Institute and U. S. Navy expedition visited the island in 1972.

Several members of the expedition independently made collections of decapods and sent them to various individuals for study. I was unaware that both Janet Haig and John S. Garth were studying material from Malpelo when I began studying the present collections. My study was then restricted to the macrurans, the subject of the present report. A complete list of the decapods reported from Malpelo is included in the Birkeland et al. appendix (pp. 66-68, herein), and, therefore, it is unnecessary to repeat here.

The macrurans collected at Malpelo Island form a small but interesting collection of 18 species. Two species were previously undescribed, three species are recorded for the first time since the original description, the genus *Gnathophylloides* is recorded from the eastern Pacific for the first time and many of the remaining species were previously known from only a few records.

Collections of macrurans came primarily from two localities on Malpelo Island referred to in the descriptions as: "Malpelo coll. no. 3," which was made on the southeastern section of the island among coral in 10 m depth on 2 March 1972, and "Malpelo coll. no. 4," which was made on the west side of the island in 15 m depth on 3 March 1972.

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"Malpelo coll." refers to general collecting around the island from 29 February to 3 March 1972. The abbreviation *cl* refers to carapace length excluding the rostrum, *tl* to total length excluding the rostrum unless otherwise specified and USNM to the National Museum of Natural History, Smithsonian Institution, Washington, D.C. All of the material will eventually be deposited in that institution.

ACKNOWLEDGMENTS.—I thank Jeffrey B. Graham for entrusting me with the study of this interesting collection. Charles Birkeland supplied me with a collection of shrimps and the color slide of *Panulirus penicillatus*. The following three individuals contributed so much to this study that completion would not have been possible without their aid: Dora M. Banner and Albert H. Banner of the University of Hawaii, examined alpheid material and loaned material of *Alpheus crockeri*. Fenner A. Chace, Jr., of the Smithsonian Institution, has once again given his time and energy to the completion of a study. He loaned material of *Periclimenaeus pearsei* and compared material of *Pseudocoutierea*, *Veleronia*, and *Gnathophylloides* with type and other material in the Smithsonian Institution collections.

PALAEEMONIDAE

Brachycarpus biunguiculatus (Lucas, 1849)

Palaemon biunguiculatus Lucas, 1849:45, pl. 4: fig. 4.
Brachycarpus biunguiculatus (Lucas).—Holthuis, 1952:3, pl. 1.—Chace, 1962:606; 1966:625; 1972:18.

MATERIAL.—3 males, 6 non-ovigerous females, 5 ovigerous females, 1 juvenile, Malpelo coll. no. 3; 2 males, 2 non-ovigerous females, Malpelo coll. no. 4.

MEASUREMENTS.—Males *tl* (including rostrum) 36.1–40.7 mm; non-ovigerous females *tl* 22.7–28.7 mm; ovigerous females *tl* 31.5–41.3 mm.

DISTRIBUTION.—This species is circumtropical in distribution occurring on most oceanic islands.

REMARKS.—All of the Malpelo material agrees with the description and illustrations of *B. biunguiculatus*, which has an extensive synonymy discussed by Holthuis (1952). A second recognized species of *Brachycarpus*, *B. holthuisi*, has been described from deeper waters (30–60 m) off Brazil by Fausto Filho (1966). The present species occurs

in shallow waters in a wide variety of habitats: on coral reefs, in tide pools, on grass flats, and among subtidal rocks (Chace, 1972).

Periclimenaeus hancocki Holthuis, 1951

FIGURE 28B–D

Periclimenaeus hancocki Holthuis, 1951:97, pl. 29a–k.

MATERIAL.—1 male, 1 ovigerous female, Malpelo coll.

MEASUREMENTS.—Male *cl* 6.0 mm, ovigerous female *cl* 8.4 mm.

DISTRIBUTION.—The unique holotype was collected from Pinas Bay on the Pacific coast of Panama. It is now reported from Malpelo Island.

REMARKS.—The male specimen agrees with the description of the unique male holotype given by Holthuis (1951). The lamella of the scaphocerite, however, does not extend as far beyond the lateral tooth as figured by Holthuis. The female specimen differs in several respects. The rostrum is relatively shorter than that of the male and it is armed with four rather than five dorsal teeth. Holthuis had only the male holotype of *P. hancocki* available when he noted certain differences between this

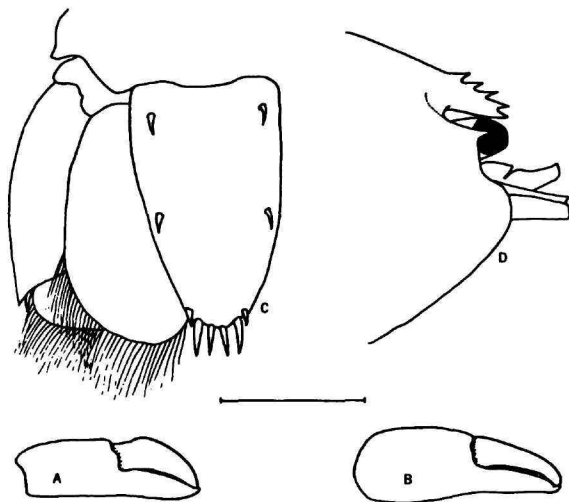


FIGURE 28.—*Periclimenaeus pearsei* Schmitt: A, chela of first pereiopod; *Periclimenaeus hancocki* Holthuis: B, chela of first pereiopod; C, telson and left uropod of female; D, anterior portion of carapace of ovigerous female. [Scale = 1 mm for A, B; 2 mm for C, D.]

species and the closely related species, *P. pearsei* Schmitt, 1932 from the western Atlantic and these are listed in his key (1951:78). The present female, and to a lesser extent the male, bridge these differences with one important exception: the form of the dactylus of the chela of the first pereopods. In *P. pearsei* (Figure 28A), of which two males and two females (USNM 65113, 65114) were available for comparison, the dactylus is high and convex while in *P. hancocki* (Figure 28B) it is low and not nearly as wide. This distinct and so far constant difference seems to warrant continued specific recognition of these two closely related species.

The eggs of both species are small (about 0.45×0.3 mm) and numerous.

Harpiliopsis depressus (Stimpson, 1860)

Harpilius depressus Stimpson, 1860:38.

Periclimenes pusillus Rathbun, 1906:921, fig. 71, pl. 24: fig. 7.—Bruce, 1970:306, fig. 1.

Harpiliopsis depressus (Stimpson).—Holthuis, 1951:70, pl. 21, pl. 22a-f.

MATERIAL.—1 male, Malpelo coll. no. 3.

MEASUREMENTS.—Male *cl* 2.5 mm.

DISTRIBUTION.—Red Sea and Seychelles Islands, islands of the central Pacific and the west coast of America from the Gulf of California to Colombia.

REMARKS.—Bruce (1970) examined the status of *Periclimenes pusillus* Rathbun from Hawaii and concluded that it represents a juvenile of *Harpiliopsis depressus*. Two color forms of this species occur on *Pocillopora* coral heads in Panama and Australia. Their status is being investigated by A. J. Bruce.

The translucent form of this species is one of the most abundant *Pocillopora* commensals in Panama (Abele, 1972).

Pseudocoutierea elegans Holthuis, 1951

Pseudocoutierea elegans Holthuis, 1951:182, pl. 55a-r [pls. 55 and 57 reversed, legends are not].—Chace, 1972:45.

MATERIAL.—3 males, 6 non-ovigerous females, 7 ovigerous females, Malpelo coll.

MEASUREMENTS.—Males *tl* 7.1–7.3 mm, non-ovigerous females *tl* 8.1–8.4 mm, ovigerous females *tl* 7.4–8.6 mm.

DISTRIBUTION.—California, Santa Catalina Island, Mexico, Baja California off Idefonosos Island,

Guerrero south of White Friars. Ecuador, Galapagos Islands, Bindloe Island. It is now reported from Malpelo Island.

REMARKS.—The present material differs in several respects from the description of *P. elegans* given by Holthuis (1951). All of the Malpelo specimens are smaller (*tl* 7.1–8.6 mm) than those listed by Holthuis (*tl* 9–16 mm). The lamella of the scaphocerite is less produced in the Malpelo specimens than those figured by Holthuis. In the original description he notes that larger specimens tend to have the dactylus of the larger second pereopod robust with a large proximal tooth. Even the smallest of the Malpelo specimens have this characteristic. The rostrum of the Malpelo material seems to be shorter than Holthuis' material. The Malpelo males lack a spine on the posterior margin of the third pleuron, which is present in Holthuis' figure (see Chace, 1972:45). Dr. Fenner A. Chace, Jr., compared Malpelo material with paratypes of *P. elegans* and noted that the Malpelo specimens seem to have the cornea set less obliquely on the eyestalk and the general body form more depressed.

Given, however, the relatively few specimens available from such widely scattered localities and the variation known in other pontoniids, it seems best to refer the present material to *P. elegans* until more material is available.

Veleronia laevifrons Holthuis, 1951

Veleronia laevifrons Holthuis, 1951:199, pl. 63f-m.

MATERIAL.—3 males, 3 non-ovigerous females, 4 ovigerous females, Malpelo coll.

MEASUREMENTS.—Males *tl* 4.2–4.9 mm, non-ovigerous females *tl* 6.4 mm, ovigerous females *tl* 5.4–6.6 mm.

DISTRIBUTION.—Ecuador, off Cape San Francisco and Santa Elena Bay, Galapagos Islands (Hood Island). The species is now reported from Malpelo Island.

REMARKS.—Dr. Fenner A. Chace, Jr., compared the present material with paratypes of *V. laevifrons* from Hood Island and concluded they were conspecific.

Schmitt (in Holthuis, 1951:200) gives color notes on specimens of this species that were found on a gorgonian.

GNATHOPHYLLIDAE

Gnathophylloides mineri Schmitt, 1933

Gnathophylloides mineri Schmitt, 1933:7, fig. 3; 1935:167, fig. 31.—Lewis, 1956:288, figs. 1, 2.—Chace, 1972:52.—Bruce, 1973:27.

MATERIAL.—1 ovigerous female.

MEASUREMENTS.—Ovigerous female *cl* 1.9 mm, *tl* 5.5 mm.

DISTRIBUTION.—Southeastern Florida, Yucatan, and Caribbean Sea (Chace, 1972). The species is now reported from the eastern Pacific at Malpelo Island.

REMARKS.—Dr. Fenner A. Chace, Jr., compared the Malpelo specimen with Atlantic material of *G. mineri* and was unable to find any obvious differences such as those noted by Bruce (1973) in his comparison of *G. mineri* with *G. robustus*.

In the Atlantic the species occurs under stones or in coral, but it is usually found on the spines of sea urchins (*Tripneustes* and *Lytechinus*). A species of *Tripneustes*, *T. depressus*, is known to occur at Malpelo Island (Birkeland et al., Appendix, this volume).

ALPHEIDAE

Alpheus lottini Guérin-Meneville, 1830

Alpheus lottini Guérin-Meneville, 1830, pl. 3.—Holthuis, 1958:22.

Alpheus ventrosus H. Milne Edwards, 1937:352.—Banner, 1958:164, fig. 4.

Alpheus laevis Randall, 1839:141.

Crangon ventrosa (H. Milne Edwards).—Banner, 1953:84, fig. 28.

Crangon latipes Banner, 1953:82, fig. 27.

MATERIAL.—2 ovigerous females, 1 juvenile, Malpelo coll. no. 3.

MEASUREMENTS.—Ovigerous females *cl* 5.2, 8.2 mm, juvenile *cl* 2.9 mm.

DISTRIBUTION.—Red Sea and South Africa, across the Central Pacific to western America where it occurs from Baja California to at least Panama. It is now reported from Malpelo.

REMARKS.—This species is a characteristic member of the *Pocillopora* coral community where it usually occurs in male-female pairs. Patton (1973) has dealt with aspects of the biology of this colorful species.

Alpheus malleator Dana, 1852

Alpheus malleator Dana, 1852:557; 1855, pl. 31: fig. 9a-h.—Crosnier and Forest, 1966:240, fig. 10.

MATERIAL.—11 males, 2 non-ovigerous females, 2 ovigerous females, 7 juveniles.

MEASUREMENTS.—Males *cl* 7.8–11.9 mm, non-ovigerous females *cl* 5.2–5.4 mm, ovigerous females *cl* 7.8–11.4 mm.

DISTRIBUTION.—Western Atlantic: southern Florida to Sao Paulo, Brazil. Eastern Atlantic: Senegal to the Congo. Eastern Pacific: Gulf of California to Ecuador, the Galapagos Islands, and now Malpelo Island.

REMARKS.—None.

Alpheus grahami new species

FIGURE 29A-C, E-J

MATERIAL.—2 ovigerous females (smaller specimen is holotype), 2 juveniles, Malpelo coll. no. 3.

MEASUREMENTS.—Ovigerous female holotype *cl* 11.1 mm, paratypes, ovigerous female *cl* 12.3 mm, juveniles *cl* 3.7, 4.2 mm.

TYPE-LOCALITY.—Southeastern side of Malpelo Island, Colombia in 10 m depth among coral.

DISTRIBUTION.—Known only from the type-locality.

DESCRIPTION.—The rostrum is short and triangular with an acute apex; it extends to about the middle of the basal antennular segment. The orbital teeth are triangular, subacute, and extend almost to the apex of the rostrum.

The first three abdominal pleura are rounded; the fourth and fifth are bluntly angled and the sixth is subacute. The sixth segment is slightly longer than the fifth and is about 0.7 of the length of the telson. The telson has the length about 1.8 times the width. The distal lateral angles are armed with a pair of spines, the inner one being longer and stronger. Two pairs of dorsal spines are present; the anterior pair is placed slightly less than half the distance from the anterior margin and the posterior pair is located about three-fourths the distance from the anterior margin. The uropods extend well beyond the distal margin of the telson. The lateral uropod is armed with a strong movable spine at the distal lateral angle that is adjacent to a smaller immovable spine.

The stylocerite extends distinctly beyond the distal margin of the basal antennular segment. The visible portion of the basal segment is about three-fourths the length of the second segment. The third segment is about three-fourths the length of the second segment.

The basicerite is unarmed dorsally, the angle being blunt. The lateral spine is short and acute, extending to about half the length of the stylocerite. The scaphocerite is widest proximally and

does not extend beyond the antennular peduncle.

The third maxilliped extends beyond the carpo-cerite by the distal third of the ultimate segment. The distal portion of the ultimate segment is armed with strong setae but no spines.

The first pereiopods are strong and unequal. The ischium of the major cheliped is armed with about four spinules on the inferior margin and a single spine on a lobe on the distal superior margin. There are about 10 movable spinules on the

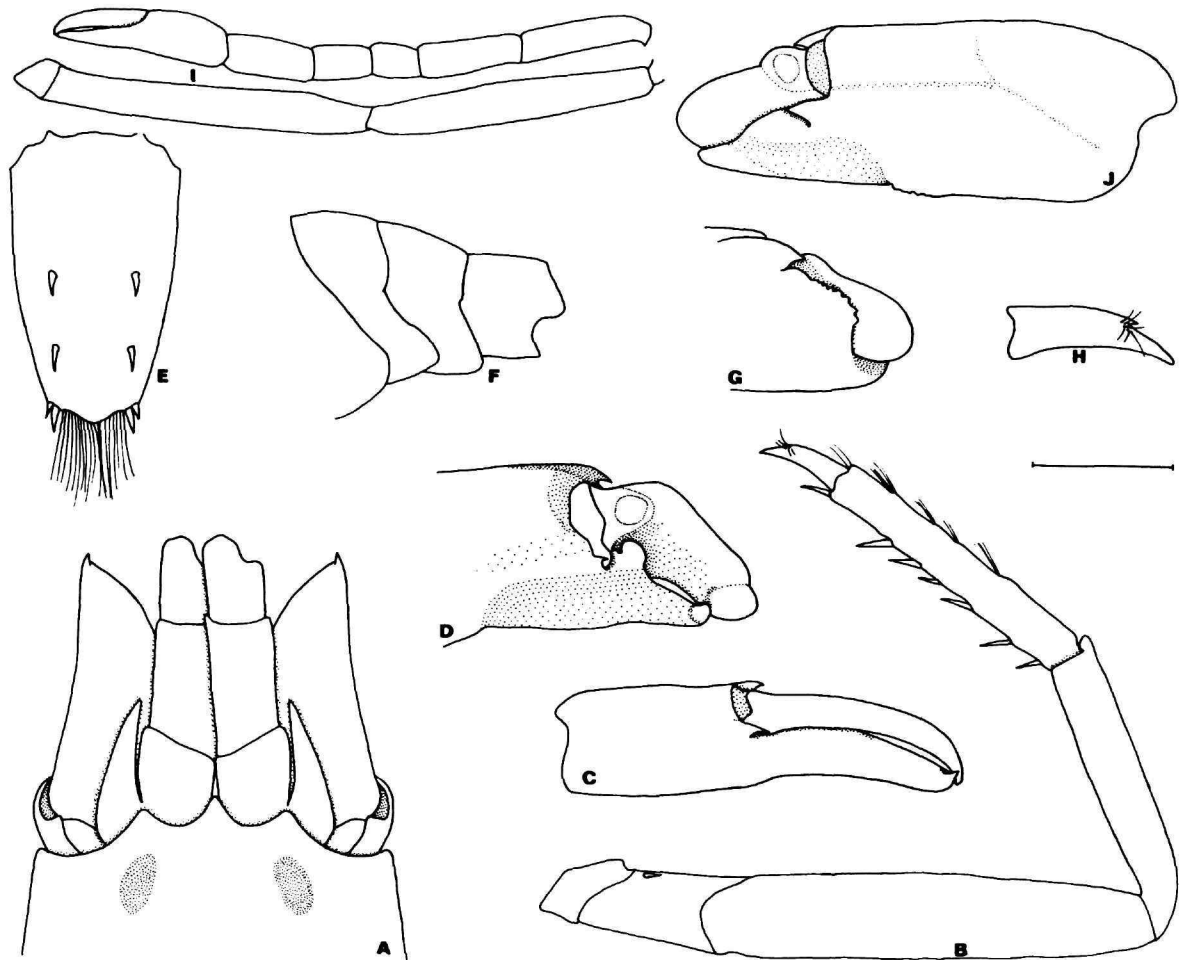


FIGURE 29.—*Alpheus grahami*, new species: A, anterior portion of carapace; B, third pereiopod; C, small chela of first pereiopod; E, telson; F, third through fifth abdominal pleura; G, anterior portion of major chela of first pereiopod; H, dactylus of third pereiopod; I, second pereiopod; J, major chela of first pereiopod. *Alpheus crockeri* (Armstrong): D, anterior portion of major chela of first pereiopod. [Scale = 2 mm for A, B, D, E, I; 4 mm for C, F-H, J.]

inferior margin of the merus; the distal margin is unarmed. The major chela is about three times as long as high. There are no superior notches but a sulcus is present on the medial surface below the superior margin. It extends from the base of the movable finger to about the middle of the chela where it bifurcates; the upper portion extends only a short distance but the lower portion extends downward almost to the proximal margin of the chela. The lower margin of the chela is compressed proximal to the base of the immovable finger resulting in the formation of a weak inferior notch adjacent to two weak tubercles. The distal margin of the chela is armed with a pair of large, acute teeth, one on either side of the movable finger. Below the lateral (outside) tooth, the margin of the chela leading to the immovable finger is high and crenulate. The movable finger is high, slightly compressed, and blunt, although in the single chela available the apex may be damaged. The ischium of the minor chela is armed with about six spinules on the inferior margin and a spinule on a lobe on the distal superior margin. The merus is armed with about 11 spinules on the inferior margin; the distal margin is unarmed. The chela is about 1.7 times as long as high. The movable finger is almost 0.6 the length of the chela and is somewhat flattened dorsally. The distal margin of the palm is armed with two strong teeth, one on either side of the movable finger. The tips of both fingers are acute; the hand is not balaeniceps in form. The second pereiopods are subequal and extend beyond the carapocerite by the distal three segments of the carpus. The ischium is slightly longer than the merus and both are shorter than the carpus. The carpus is subdivided into five segments; the first is the longest being slightly longer than the second and the fifth, which are subequal in length. The third and fourth segments are subequal in length and are slightly less than half the length of the first. The movable finger is slightly more than half the length of the chela. The fingers are unarmed. The third through the fifth pereiopods are similar in form. Three of the four available specimens have a small movable spinule at the base of the ischium of pereiopods three and four. This spinule is relatively large on the two small specimens (*cl* 3.7, 4.2 mm), but it is small and difficult to see on one of the larger females (*cl* 12.3 mm) and it is absent on the other female (*cl* 11.1 mm).

The third pereiopod has the ischium less than half the length of the merus. The merus is slightly less than five times as long as wide; it is about 1.5 times the length of the carpus, about 1.3 times the length of the propodus and about 5 times the length of the dactylus. The propodus is armed with about nine movable spines on the inferior margin. The dactylus has a minute accessory tooth, surrounded by setae, on the superior margin. The eggs are small and numerous.

REMARKS.—This species seems to be most closely related to *Alpheus crockeri* (Armstrong, 1941) (= *Crangon tuthilli* Banner, 1953) known from the Central Pacific Ocean, Thailand (Banner, 1953; Banner and Banner, 1966) and the eastern Atlantic (Crosnier and Forest, 1966). Three specimens, through the courtesy of D. M. and A. H. Banner, of *A. crockeri* were available for comparison: 1 male *cl* 8.0 mm, 2 non-ovigerous females *cl* 5.0, 6.9 mm from Oahu, Hawaii. The two species are very similar, and were it not for the extreme differences in the form of the major chela, other differences would have been attributed to variation. In *A. crockeri* (Figure 29b), the movable finger is greatly compressed, with the superior margin being defined by a knife-like ridge; it is twisted in a horizontal plane and the apex is bulbous. The immovable finger has a large, high proximal tooth present and is twisted in a horizontal plane. In *A. grahami* (Figure 29c, f), the movable finger is robust and only slightly compressed; it is not twisted and the width is the same throughout. The immovable finger lacks a proximal tooth and is not twisted.

Other differences between the two species are slight but are constant in the material examined. In *A. crockeri* the stylocerite is narrow and extends almost to the distal margin of the basal antennular segment, while in *A. grahami* the stylocerite is more robust and extends distinctly beyond the basal segment. The antennular peduncle of *A. crockeri* is slender with the second segment having the length about twice the width, while in *A. grahami* the length is distinctly less than twice the width. The scaphocerite of *A. crockeri* is slender and extends to or beyond the distal margin of the antennular peduncle, while in *A. grahami* it is shorter than the antennular peduncle. The pereiopods of *A. crockeri* are slender with the length of the merus being about six times the width while in

A. grahami the length is about five times the width. From illustrations in the literature (Banner and Banner, 1966; Crosnier and Forest, 1966) it would appear that the rostrum of *A. crockeri* is longer and more acute than that of *A. grahami*, but the specimens of *A. crockeri* from Oahu, Hawaii have a rostrum similar to that of *A. grahami*.

ETYMOLOGY.—The species is named for Jeffrey B. Graham, who collected the specimens and entrusted them to me for study.

Synalpheus biunguiculatus (Stimpson, 1860)

Alpheus biunguiculatus Stimpson, 1860:31.

Synalpheus biunguiculatus (Stimpson).—Banner, 1953:32, fig. 9.

MATERIAL.—1 ovigerous female, 2 specimens, Malpelo coll. no. 3; 1 specimen, Malpelo coll. no. 4; 1 specimen, Malpelo coll.

MEASUREMENTS.—Ovigerous female *cl* 4.2 mm; other specimens *cl* 2.7–5.7 mm.

DISTRIBUTION.—Hawaiian Islands (Banner, 1953), Clipperton Island (Chace, 1962), and now Malpelo Island.

REMARKS.—The Malpelo material all lack the major chela making the identification somewhat uncertain. They agree in most respects with the description and illustrations of Banner (1953). The carpocerite in the Malpelo material is somewhat longer than the spine of the scaphocerite, but the species is variable in this and other characters (Chace, 1962).

Synalpheus nobilii Coutière, 1909

FIGURE 30

Synalpheus nobilii Coutière, 1909:40, fig. 22.—Schmitt, 1924:162, fig. 39.—Sivertsen, 1934:22.—Schmitt, 1939:12, 24.—Chace, 1962:613.

MATERIAL.—23 specimens (6 ovigerous), Malpelo coll. no. 3; 4 specimens, Malpelo coll. no. 4; 10 specimens, Malpelo coll.

MEASUREMENTS.—Ovigerous females *cl* 4.1–4.9 mm, other specimens *cl* 1.8–6.2 mm.

DISTRIBUTION.—St. Helena, Ecuador (Coutière, 1909), Galapagos Islands (Schmitt, 1924), Clipperton Island (Chace, 1962) and now Malpelo Island.

Specimens were also examined from Punta Paitilla, Panama.

DESCRIPTION.—The rostrum is narrow and acute, not extending to the distal margin of the basal antennular segment. It is on a higher level and extends beyond the orbital teeth, which are small acute extensions on the orbital hoods.

The third abdominal pleuron is obtusely rounded, the fourth and fifth are bluntly angled and the sixth is acute. The fifth segment is slightly shorter than the sixth, which is slightly more than half the length of the telson. The telson is slightly longer than its anterior width. It narrows distally and has a distinct constriction proximally. The telson is armed with two pairs of spines at the distal lateral angles; the lateral spine is about one-third the length of the medial. There are two pairs of dorsal spines present; the first pair is located slightly anterior of the middle and the second is located about four-fifths of the distance from the anterior margin. The uropods extend well beyond the distal margin of the telson. The lateral branch is armed with a strong movable spine situated between two immovable spines at the level of the diaeresis.

The stylocerite is long and slender extending to about the middle of the second antennular segment. The visible portion of the basal segment is slightly longer than the second segment, which is distinctly longer than the third segment.

The basicerite is armed with strong dorsal and lateral spines; the dorsal spine is about half the length of the lateral. The lateral tooth of the scaphocerite extends beyond both the antennular peduncle and the carpocerite.

The third maxilliped has the apex armed with nine strong, dark-colored spines arranged in a circle. The ultimate segment extends slightly beyond the scaphocerite.

The first pereiopods are strong and unequal. The superior distal margin of the merus is armed with a tooth. The major chela has the length slightly less than three times the height. The distal margin of the palm is unarmed. A tubercle is present on the medial margin of the palm just below the distal margin. The immovable finger is armed with two teeth proximally. The movable finger is slightly less than one-third the length of the chela. The superior distal margin of the merus of the smaller chela is armed with a tooth. The smaller

chela has the length slightly more than three times the height. The distal margin of the palm is unarmed. The fingers are unarmed; the movable one is about one-third the length of the chela. The second pereiopods are equal and extend beyond the scaphocerite by the distal segment of the carpus. The ischium is about three-fourths the length of the merus, which is slightly shorter than the carpus. The carpus is subdivided into five segments; the first is slightly less than five times the length of the second, third, and fourth, which are subequal, and about twice the length of the fifth. The movable finger is about half the length of the chela. The third through the fifth pereiopods are similar. The merus of the third is about three

times as long as wide and is unarmed. It is about twice the length of the carpus and about 1.3 times the length of the propodus. The propodus is armed with six movable spines, the sixth being paired, on the inferior surface. The carpus has a distal extension on the superior margin and a pair of spines on the distal inferior margin. The dactylus is bifid with a small ventral protuberance; the ventral tooth is wider than the dorsal and slightly shorter. The eggs are small and numerous.

REMARKS.—Specimens of this species have been collected from the rocky intertidal zone in the Bay of Panama. The material from Malpelo Island came from among coral and coral rubble in about 10 m depth.

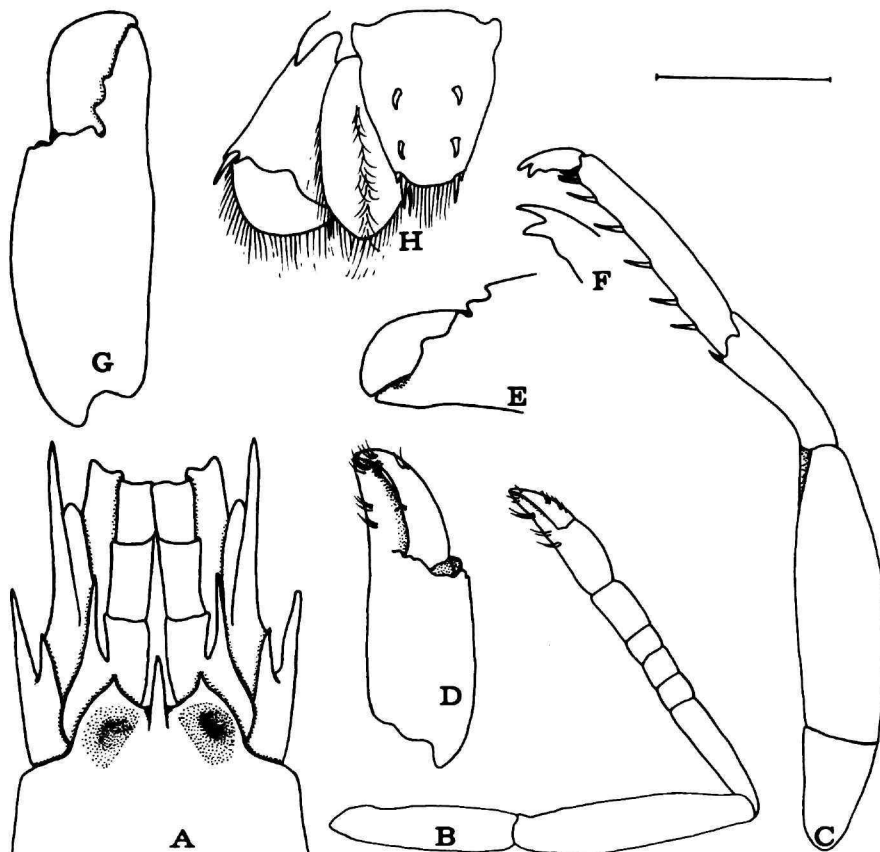


FIGURE 30.—*Synalpheus nobilii* Coutière: A, anterior portion of carapace; B, second pereiopod; C, third pereiopod; D, small chela of first pereiopod; E, anterior portion of major chela of first pereiopod; F, distal portion of dactylus of third pereiopod; G, major chela of first pereiopod; H, telson and left uropod. [Scale = 4 mm for E, G; 2 mm for A-D, H; 1 mm for F.]

Synalpheus digueti Coutière, 1909

FIGURE 31

Synalpheus digueti Coutière, 1909:48, fig. 28.—Chace, 1937: 123.

MATERIAL.—4 ovigerous females, 36 specimens, Malpelo coll. no. 3; 3 specimens, Malpelo coll. no. 4; 16 ovigerous females, 40 specimens, Malpelo coll.

MEASUREMENTS.—Ovigerous females *cl* 5.2–8.4 mm, other specimens *cl* 3.0–7.6 mm.

DISTRIBUTION.—Baja California (Coutière, 1909; Chace, 1937). The species is now reported from Malpelo Island. Material from Taboguilla Island

and the Pearl Islands, Panama, was also examined during the present study.

DESCRIPTION.—The rostrum is narrow, subacute, and short; extending to about one-fourth of the length of the basal antennular segment. The orbital teeth arise from the anterior margin of the carapace; they are triangular, subacute, almost twice as broad as the rostrum, and are subequal in length to it.

The third through the fifth abdominal pleura are bluntly angled; the sixth is acute. The fifth segment is almost equal in length to the sixth which is slightly more than half the length of the telson. The telson is longer than wide with two pairs of spines on the distal lateral angles; the

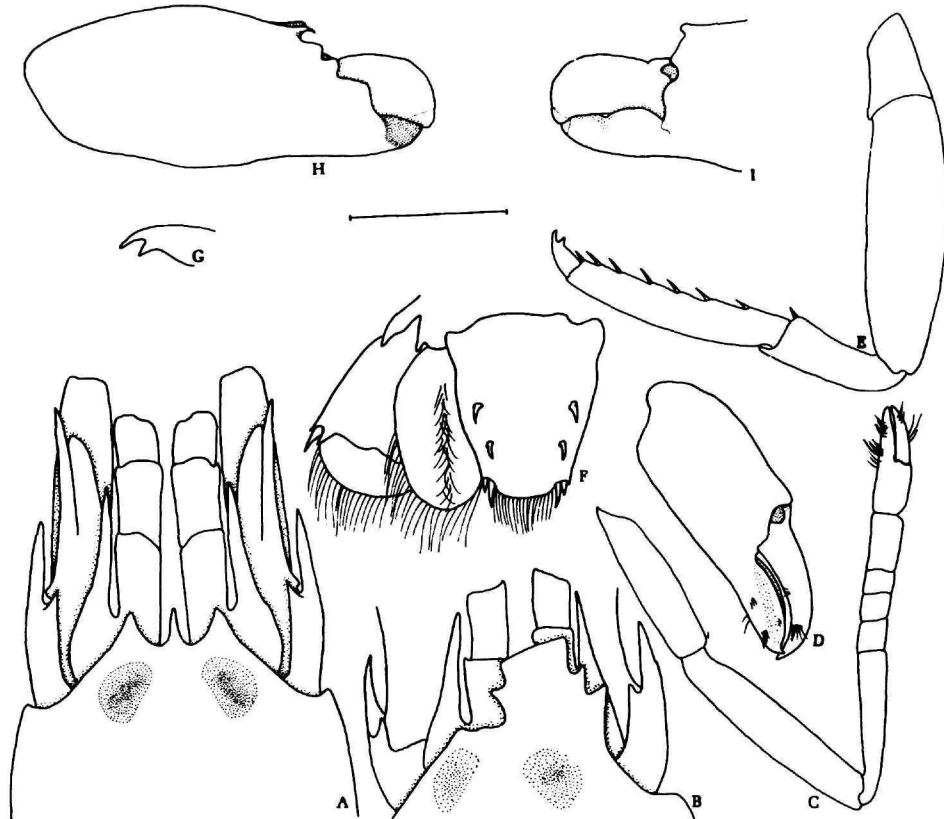


FIGURE 31.—*Synalpheus digueti* Coutière: A, anterior portion of carapace; B, anterior portion of carapace of aberrant specimen; C, second pereiopod; D, minor chela of first pereiopod; E, third pereiopod; F, telson and left uropod; G, anterior portion of dactylus of third pereiopod; H, major chela of first pereiopod; I, anterior portion of major chela of first pereiopod. [Scale = 2 mm for A–F; 1 mm for G; 4 mm for H, I.]

lateral spine is slightly more than half the length of the medial. The distal margin of the telson is convex and extends to about two-thirds the length of the medial spine. There are two pairs of dorsal spines; the first pair is located at about the middle of the telson and the posterior pair is located slightly more than two-thirds of the distance from the anterior margin. The uropods extend beyond the distal margin of the telson. The lateral branch is armed with a strong movable spine situated between two immovable spines at the level of the diaeresis.

The stylocerite is long and acute, extending slightly beyond the middle of the second antennular segment. The first antennular segment is about 1.4 times the length of the second and about twice the length of the third.

The basicerite is armed with dorsal and lateral spines; the dorsal spine extends to about one-fifth of the length of the lateral. The lateral tooth of the scaphocerite is long and acute and extends beyond the antennular peduncle. The carpopocerite is long and broad, extending well beyond the lateral tooth of the scaphocerite.

The first pereiopods are robust and unequal. The merus of the major cheliped is unarmed. The chela is about 2.6 times as long as high. The distal margin of the palm is armed with a downwardly directed spine. There are two tubercles on the lateral margin of the palm at the insertion of the movable finger. The distal portion of the immovable finger is compressed. The movable finger is slightly more than one-fourth the length of the chela. The merus of the smaller cheliped is unarmed, as is the chela. The length of the chela is about 2.5 times the height. The movable finger is about half the length of the chela. The second pereiopods are subequal. The ischium is unarmed and is about three-fourths the length of the merus. The merus is unarmed and is about four-fifths the length of the carpus. The carpus is subdivided into five segments; the first is over five times the length of the second, third, and fourth which are subequal and which are half the length of the fifth. The movable finger is slightly more than half the length of the chela. The third through the fifth pereiopods are similar. The ischium and merus are unarmed. The ischium is slightly less than one-third the length of the merus. The carpus has an

extension on the distal superior margin and a pair of spines on the distal inferior margin. The carpus is about half the length of the merus. The propodus is about four-fifths the length of the merus and is armed with seven movable spinules on the inferior margin; the last spinule is paired. The dactylus is bifid; the superior tooth is slightly longer than the inferior tooth and they are subequal in width at the base.

The eggs are small and numerous.

In fresh material the body is translucent, the appendages are blue, and the tips of the fingers of the first pereiopods are red.

REMARKS.—The rostrum was somewhat variable in form often being wider than figured here. One specimen (Figure 31B) has a highly aberrant rostrum but was normal in other features. Three of the 99 specimens examined lack a tooth on the distal margin of the major chela. In other features the species was not variable.

In the Gulf of Panama *Synalpheus digueti* occurs as male-female pairs (the female is usually ovigerous) in *Pocillopora* coral heads.

Synalpheus charon (Heller, 1861)

Alpheus charon Heller, 1861:27.

Synalpheus helleri de Man, 1911:246, pl. 8: fig. 37.

Synalpheus charon (Heller).—Banner, 1953:37, fig. 11.—

Banner and Banner, 1964:88.

Synalpheus charon obscurus Banner, 1956:329, fig. 5.

Synalpheus charon charon (Heller).—Banner, 1956:331.

MATERIAL.—3 ovigerous females, 11 specimens, Malpelo coll. no. 3.

MEASUREMENTS.—Ovigerous females *cl* 4.6–5.3 mm, other specimens *cl* 2.6–4.9 mm.

DISTRIBUTION.—Red Sea across the Pacific to Baja California (Banner and Banner, 1966; Chace, 1937). During the present study, material was also examined from the Pearl Islands and Taboguilla Island in the Gulf of Panama.

REMARKS.—This species is a characteristic member of the *Pocillopora* coral community, occurring deep inside the coral at the base of the branches (Banner and Banner, 1964). It is common in this habitat in the Gulf of Panama where it usually occurs in male-ovigerous female pairs. The body and appendages of fresh material is an even red color.

Synalpheus bannerorum, new species

FIGURE 32

MATERIAL.—5 ovigerous females (holotype *tl* 11.1 mm, *cl* 4.4 mm), 23 specimens, Malpelo coll. no. 3 (paratypes); 2 specimens, Malpelo coll. no. 4.

MEASUREMENTS.—Ovigerous females *cl* 4.0–4.7 mm, *tl* 9.9–11.1 mm, other specimens *cl* 3.3–5.0 mm, *tl* 8.5–11.4 mm.

TYPE-LOCALITY.—Southeastern side of Malpelo Island, Colombia, in 10 meters depth among coral.

DISTRIBUTION.—Known only from the type-locality.

DESCRIPTION.—The rostrum is narrow and acute; it does not extend to the distal margin of the basal antennular segment. It is on a higher level than the orbital teeth, which are small, acute, directed slightly medially, and do not extend to the apex of the rostrum.

The first five abdominal pleura are rounded; the sixth is subacute. The fifth segment is subequal in length to the sixth, which is three-fourths the length of the telson. The anterior width of the telson is greater than the length; it narrows distinctly in the posterior half. The posterior margin is less than one-half the width of the anterior margin. The distal lateral angles of the posterior margin are acute and armed with a pair of spines; the lateral pair being shorter and more robust than the medial. Both extend well beyond the lateral angles of the telson. The dorsal surface of the telson is armed with a pair of strong spines; the first pair is located about two-thirds of the distance from the posterior margin and the second pair is located about one-third of the distance from the posterior margin. Both pairs are set in well from the lateral margins. The lateral angle of the outer uropod is armed with a long movable spine set

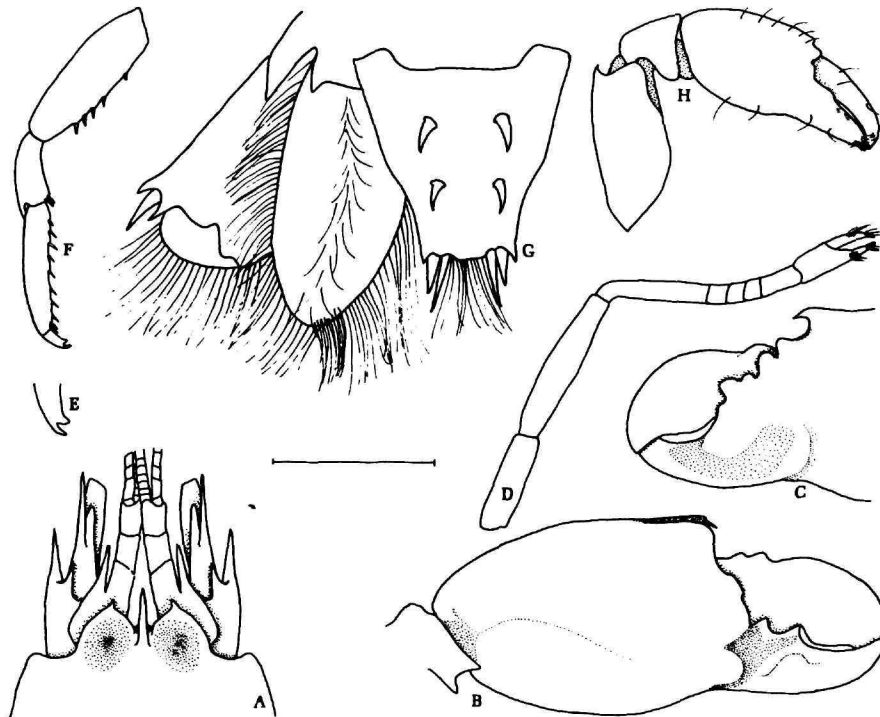


FIGURE 32.—*Synalpheus bannerorum*, new species: A, anterior portion of carapace; B, major chela of first pereiopod; C, anterior portion of major chela; D, second pereiopod; E, anterior portion of dactylus of third pereiopod; F, third pereiopod; G, telson and left uropod; H, minor first pereiopod. [Scale = 2 mm for A–D, F, H; 1 mm for E, G.]

between a pair of smaller acute immovable spines at the level of the diaeresis. The medial uropod is longer than the lateral, which is subequal in length to the telson.

The stylocerite is acute and extends to about the middle of the second antennular segment. The basal antennular segment is longer than the second and third, which are subequal in length.

The basicerite is armed with strong, acute dorsal and lateral spines; the dorsal spine extending to slightly over one-third of the length of the lateral. The scaphocerite is reduced in size but the lateral spine is strong, extending beyond both the antennular peduncle and the carpoцерite. The carpoцерite extends slightly beyond the antennular peduncle.

The third maxilliped has the tip of the apex armed with six dark-colored spines. It extends beyond the carpoцерite by the distal third of the ultimate segment.

The first pereopods are unequal and robust. The merus of the major cheliped is armed with a tooth on the distal superior margin. The carpus is armed with two acute extensions. The major chela is about 2.3 times as long as high. The distal margin of the palm is armed with a small downwardly directed spine. There is a large tubercle at the base of the immovable finger which is followed by a deep depression and then another tubercle. The other side of the finger is also depressed giving a pinched appearance to the base of the finger. The immovable finger is armed with two strong, acute teeth in the proximal portion. The movable finger is more than one-third the length of the chela and has two distinct tubercles on the proximal dorsal surface. There is a series of about five unequal tubercles on the medial surface of the palm between the acute distal spine and the base of the immovable finger. The merus of the minor cheliped is armed with an acute spine on the superior distal margin. The carpus is cup-shaped. The chela is unarmed; the movable finger is slightly less than half the length of the chela. The second pereopods are subequal. The fingers are unarmed and the movable finger is slightly more than half the length of the chela. The carpus is subdivided into five segments; the first is about six times the length of the second, which is subequal in length to the third and fourth, which are about half the length of the fifth. The ischium is about half the

length of the carpus and about three-fifths the length of the merus. The third through the fifth pereopods are similar and robust. The ischium is unarmed. The merus of the third is armed with four to six movable spines. The length is slightly more than three times the width. The carpus is armed with two distal spines. The propodus is armed with about nine movable spinules on the inferior margin. The dactylus has the superior tooth longer and slightly more than half the width of the inferior. The merus of the fourth pereopod is armed with three or four movable spines. The merus of the fifth pereopod is unarmed. The eggs are small and numerous.

REMARKS.—This species differs from all known eastern Pacific species in the form of the meri of the third and fourth pereopods and in the form of the major chela. It is the only western American species in which the meri of the third and fourth pereopods are armed and the constriction of the immovable finger of the major chela appears also to be unique. There is one east American species of *Synalpheus* (*S. dominicensis* Armstrong, 1949) from the Dominican Republic, which has the meri of pereopods three and four armed. *Synalpheus bannerorum* can be distinguished from *S. dominicensis* by the form of the anterior portion of the carapace, by the armature of the telson, by the form of the major chela and by the form of the dactyli of pereopods three through five. In *S. dominicensis* the medial margins of the orbits meet the rostrum at a sharp angle while they blend into the carapace before they meet the rostrum in *S. bannerorum*. The dorsal spines of the telson are both located in the posterior half of the segment in *S. dominicensis*, while in *S. bannerorum* only the posterior pair is located in the posterior half. The major chela of *S. dominicensis* is not compressed at the base of the immovable finger as it is in *S. bannerorum*. The dactylus of the third pereopod in *S. dominicensis* has the lower tooth less divergent than that of *S. bannerorum*. *Synalpheus bannerorum* is also related to Indo-Pacific members of the genus, but the form of the chela appears to distinguish it from all other species of the genus.

ETYMOLOGY.—This species is named for Dora M. Banner and Albert H. Banner who have contributed so much to the knowledge of the Alpheidae and who have shown interest in the present study.

***Pomagnathus corallinus* Chace, 1937**

Pomagnathus corallinus Chace, 1937:124, fig. 5.—Schmitt, 1939:12.—Chace, 1962:612.

MATERIAL.—3 ovigerous females, Malpelo coll. no. 3.

MEASUREMENTS.—Ovigerous females *cl* 4.6, 4.7, 5.4 mm.

DISTRIBUTION.—Arena Bank, Baja California (Chace, 1937), Clipperton Island (Schmitt, 1939; Chace, 1962). Specimens from Taboguilla Island in the Gulf of Panama were also examined during the present study.

REMARKS.—The present material agrees with the description and illustrations of Chace (1937). The species commonly occurs on *Pocillopora* coral in the Gulf of Panama.

HIPPOLYTIDAE***Lysmata galapagensis* Schmitt, 1924**

Lysmata galapagensis Schmitt, 1924:165, fig. 41.—Sivertsen, 1934:22.—Hult, 1939:6.—Schmitt, 1939:12.—Chace, 1962:616.

MATERIAL.—2 males, Malpelo coll. no. 3.

MEASUREMENTS.—Males *cl* 2.6, 3.5 mm.

DISTRIBUTION.—This species was previously known from two records off Santa Cruz Island in the Galapagos Islands, and is now reported from Malpelo Island.

REMARKS.—Both specimens agree in all respects with the description and illustration of Schmitt (1924). The rostral formula of both specimens was one postorbital, five preorbital and one sub-apical ventral teeth. The occurrence of this species with *L. trisetacea* offers additional support (Schmitt, 1939; Chace, 1962) for the specific distinctness of these two species.

***Lysmata trisetacea* (Heller, 1861)**

Hippolyte trisetacea Heller, 1861:29.

Hippolysmata paucidens Rathbun, 1906:913, pl. 24: fig. 4.

Lysmata paucidens (Rathbun).—Schmitt, 1939:12.

Lysmata trisetacea (Heller).—Holthuis, 1947:19, 65.—Chace, 1962:614.

MATERIAL.—6 males, 1 immature male, 5 non-ovigerous females, 9 ovigerous females, Malpelo coll. no. 3.

MEASUREMENTS.—Immature male *cl* 1.8 mm, males *cl* 2.9–3.8 mm, non-ovigerous females *cl* 2.9–6.0 mm, ovigerous females *cl* 4.0–5.1 mm.

DISTRIBUTION.—The species has previously been reported from the Red Sea, western Indian Ocean, the Malay Archipelago, Micronesia, New Zealand, Hawaiian Islands, Clipperton Island (Holthuis, 1958; Chace, 1962), and now Malpelo Island. Neither this species nor *L. galapagensis* appear to occur on the western American mainland. *Lysmata californica* (Stimpson, 1866) occurs in California and is common in the Gulf of Panama while *L. porteri* (Rathbun, 1907) occurs in Chile. The record of Sivertsen (1934) for *L. intermedia* (Kingsley, 1878), a western Atlantic species, is based on a single specimen from the Galapagos Islands, which appears to be within the range of variation of *L. californica* (see Sivertsen, 1934, pl. 2: figs. 9–15; and Limbaugh, Pederson, and Chace, 1961, fig. 7).

REMARKS.—Chace (1962) discussed variation in this species and noted three differences between material from Clipperton Island and material from the Hawaiian Islands. In some Hawaiian specimens the posterior ventral rostral tooth is behind or opposite the anterior dorsal tooth while in most of the Clipperton specimens both ventral teeth, when present, are well in advance of the anterior dorsal tooth. In larger adults from Hawaii the fused part of the upper antennular flagellum is not much shorter than the free portion of the shorter branch while in large Clipperton specimens the fused portion is distinctly less than half the length of the free portion. The average number of carpal segments in Hawaiian material (23) tended to be higher than that of Clipperton material (21).

These three characters were examined in the Malpelo material with the following results. The rostral formula was (number of specimens in parentheses): 2+2/2 (16), 2+3/2 (1), 2+2/3 (1), 2+2/1 (1), 1+2/2 (1), 1+2/1 (1). All specimens with two ventral teeth had them both placed well in advance of the anterior dorsal tooth; those with one ventral tooth had it placed well in advance of the anterior dorsal tooth. The Malpelo material agreed also with the Clipperton material regarding the relative lengths of the fused and free portions of the upper antennular flagellum. The number of carpal segments in Malpelo material varied

from 21–26 distributed as follows (number of specimens in parentheses): 24 (5), 22 (3), 21 (2), 23 (2), 25 (1), 26 (1). The average was slightly more than 24 agreeing more with the Hawaiian material than with the Clipperton material. These differences warrant further consideration when comparing material from throughout the range of *L. trisetacea* as suggested by Chace (1962) and Holthuis (1947).

PALINURIDAE

Panulirus penicillatus (Olivier, 1791)

Astacus penicillatus Olivier, 1791:343.

Panulirus penicillatus (Olivier).—Holthuis, 1946:125.—Holthuis and Loesch, 1967:217, pl. 8.

MATERIAL.—None, the species was identified from color slides.

MEASUREMENTS.—*Cl* 91–137 mm (Holthuis and Loesch, 1967).

DISTRIBUTION.—This species occurs in the Indo-West Pacific region: Red Sea, Southeast Africa to Korea, Formosa, and Polynesia. In the eastern Pacific it occurs at Revillagigedo Islands, Clipperton Island, Cocos Island, Galapagos Island (Holthuis and Loesch, 1967), and now is reported from Malpelo Island. It has not been found on the western American mainland.

REMARKS.—Although no material of this species was collected, comparison of color slides taken by Dr. Charles Birkeland with the color plate of this species given by Holthuis and Loesch (1967) permitted identification.

Ecology

The short time available to members of the expedition did not permit detailed collecting notes on so many different groups of organisms (see Appendix in Birkeland et al., this volume). However, some observations are possible based on published information and my own experiences in Panama (Abele, 1972).

Perhaps the most interesting observation is the large percentage of decapods from Malpelo Island which are commensals. Almost half of the 43 species occur in close association with some other invertebrates. Most occur with *Pocillopora* coral,

including the following: *Harpiliopsis depressus*, *Alpheus lottini*, *Synalpheus charon*, *S. digueti*, *Pomagnathus corallinus*, *Petrolisthes haigae*, *P. glasselli*, *Pachycheles biocellatus*, *Pagurus* sp., *Trapezia digitalis*, *T. ferruginea*, *Domecia hispida*, *Medaeus spinulifer*, *Carpilodes cinctimanus*, *Teloeophrys cristulipes*, and *Mithrax pygmaeus*. Both *Veleronia laevifrons* and *Pseudocoutierea elegans* are associated with gorgonians. *Gnathophylloides mineri* occurs on the spines of sea urchins and *Periclimenaeus hancocki* probably occurs with sponges.

Two species, *Grapsus grapsus* and *Gecarcinus malpilensis*, occur intertidally and supratidally, respectively.

The remaining species occur in a variety of subtidal habitats, mostly with rocks and coral rubble.

Distribution

The decapod fauna of Malpelo Island has affinities with both the western American mainland and Indo-Pacific decapod faunas (p. 67). Twenty-seven species, 63 percent of the Malpelo fauna, occur on the western American mainland. Nine species, 21 percent of the fauna, occur in the Indo-Pacific region and seven of these reach the western American mainland. The other two, *Lysmata trisetacea* and *Panulirus penicillatus* occur from the Indo-Pacific only to the offshore islands of the eastern Pacific. Three species, *Gecarcinus malpilensis*, *Alpheus grahami*, new species, and *Synalpheus bannerorum*, new species, appear to be endemic to Malpelo Island. Two species, *Brachycarpus biunguiculatus* and probably *Gnathophylloides mineri* are circumtropical in distribution. *Lysmata galapagensis* is only known from the Galapagos Islands and Malpelo Island, while *Synalpheus biunguiculatus* is known from Hawaii, Clipperton Island, and Malpelo Island.

The decapod fauna of Malpelo Island then has its greatest affinities (63%) with that of the western American mainland, next is the Indo-Pacific region (21%), then endemic (7%), circumtropical (4%), and island species (4%).

Comparison with Other Islands

A detailed comparison, at the species level, of the decapod faunas of the offshore islands of the

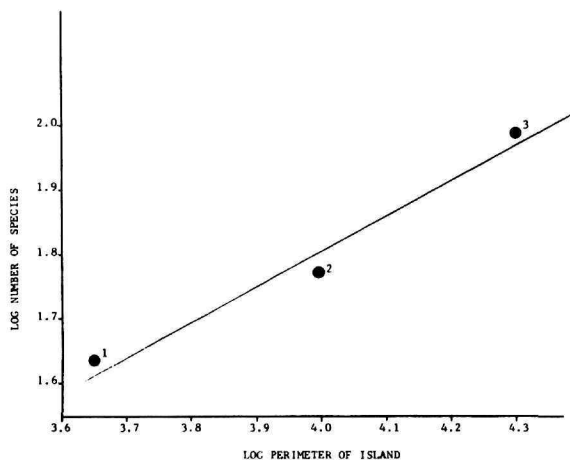


FIGURE 33.—The relationship between island perimeter and the number of decapod crustacean species present at (1), Malpelo, (2) Clipperton, and (3) Cocos islands. Refer to text for discussion.

eastern Pacific will have to await more data on other islands.

Some comparisons can be made, however, between numbers of species of decapods associated with oceanic islands (Figure 33). There are 25 species of decapods known from Saint Helena (Chace, 1966; 1968), an isolated island in the south Atlantic. Twenty percent, five species, are endemic. There are 58 species of decapods known from Clipperton Island (Chace, 1962; Garth, 1965) in the eastern Pacific. None of these species is endemic. I have found about 100 species known from Cocos Island in the eastern Pacific of which at least six (6%) are endemic. Malpelo Island has a decapod fauna of 43 species with three (7%) of them being endemic.

Within a given region there generally exists an orderly relation between numbers of species and the size of the area sampled. This relationship has been worked out for a number of terrestrial organisms occurring on islands (MacArthur and Wilson, 1967). In comparing shallow water organisms associated with islands, it seems more appropriate to use island perimeter rather than island area. A comparison between island perimeter and numbers of decapod species of three eastern Pacific islands (Saint Helena, having a different faunal source, is not included), Malpelo, Clipperton, and Cocos, is shown in Figure 33. The relationship is strik-

ing, although the slope ($z=0.56$) is higher than that reported for other area-species curves ($z = 0.20-0.35$; MacArthur and Wilson, 1967). The present curve may not be representative being based on only three islands and is presented here primarily to stimulate interest in examining this relationship in other marine organisms.

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Asteroidea from Malpelo Island with a Description of a New Species of the Genus *Tamaria*

Maureen E. Downey

ABSTRACT

One new species, *Tamaria stria*, and a new subspecies, *Narcissia gracilis malpeloensis*, are described from shallow waters of Malpelo Island. A collection totaling six species of starfish is described, with notes on distribution.

Introduction

In the course of the faunal survey of the shallow waters (0–50 m) of Malpelo conducted by C. Birkeland and his colleagues, only six species of starfish were collected; however, all are species with interesting or unusual distribution patterns, and included in the collection are a new species of the genus *Tamaria* and a new subspecies of *Narcissia gracilis*. The abbreviation R refers to the major radius from center of disc to tip of arm; and r refers to the minor radius, from center of disc to interradial margin.

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OREASTERIDAE

Nidorellia armata (Gray)

- Pentaceros* (*Nidorellia*) *armata* Gray, 1840:277; 1866:7, pl. 14: fig. 1–3.
Oreaster armatus (Gray).—Mueller and Troschel, 1842:52.—Lutken, 1864:148.—Bell, 1884:79.—von Martens, 1865:433.
Goniodiscus armatus (Gray).—Lutken, 1859:75.
Goniodiscus conifer Mobius, 1859:10, pl. 3: fig. 5–6.
Nidorellia armata (Gray).—Verrill, 1867:280.—Perrier, 1876: 67.—Viguier, 1878:193.—Leipoldt, 1895:634.—H. L. Clark, 1910:332, pl. 4: fig. 2.—Doderlein, 1916:418; 1936:316, pl. 21: fig. 1–6a.—Boone, 1926:3, pl. 1; 1933:73, fig. 2.—Ziesenhenné, 1937:216.—H. L. Clark, 1940:333.—Steinbeck and Ricketts, 1941:381, pl. 10: fig. 1, pl. 11: fig. 2.—Ely, 1945:15.—Caso, 1943:9, 66, pl. 22: fig. 1–2, pl. 23: figs. 1–2; 1953:221; 1961:63, figs. 22–23.—H. L. Clark, 1958:95.—Caso, 1962:63, figs. 22–24.
Nirodella armata (Gray).—Stanek, 1955:48.

Nidorellia armata is represented in this collection by one specimen, quite large and heavy (R 10 cm, r 6.5 cm, dry weight 177 grams). The marginals, particularly the distal ones, are tremendously swollen and most bear 1 or 2 stout spines or low tubercles. The much smaller principal plates of the abactinal surface usually bear 1 or 2 low tubercles. The papular areas of the abactinal surface are covered with pedicellariae of the split granule type. This is a common shallow water species of the eastern tropical Pacific, known from lower California to Peru and the Hawaiian Islands.

OPHIDIASTERIDAE

Leiaster callipeplus Fisher

- Leiaster callipeplus* Fisher, 1906:1083, pl. 30: figs. 1, 1a, pl. 31: fig. 3.

Leiaster callipeplus is a Hawaiian species, reported by Fisher from Maui, Lanai, Kauai, and Bird Islands, in 58–124 meters. One fine specimen, collected at Malpelo in 49 meters at the base of a rock wall (Station 5, Birkeland et al., Appendix, this volume) measures R 20 cm, r 2.9 cm. *Leiaster callipeplus* has also been collected near the central American mainland in the Gulf of Chiriqui, Panama (Birkeland, pers. comm.).

***Narcissia gracilis malpeloensis*, new subspecies**

Narcissia gracilis malpeloensis is represented in this collection by six specimens. The species, described by A. H. Clark (1916:58) has previously been collected from Baja California to the Galapagos Islands. The average size of these specimens is R 12 cm, r 2.5 cm. The Malpelo specimens represent a new subspecies of *N. gracilis*, differing from the type-specimen and Clark's description in the following respects:

Narcissia gracilis gracilis: Pedicellariae abundant on all surfaces, of 2 slender valves with expanded toothed tips, lying in alveoli; granules hemispherical; subambulacral spines in 3 rows; madreporite round; papulae single; and proximal marginals longer than broad.

Narcissia gracilis malpeloensis: Few or no pedicellariae—when present, of 2 stout curved untoothed valves of uniform thickness, not in alveoli; granules flat-topped, polygonal; subambulacral spines in one row, plus other spines not in rows; madreporite triangular; papulae usually double; and proximal marginals broader than long.

Although the above differences are minor, and abundant pedicellariae versus few or no pedicellariae might be accounted for by the difference in size (holotype: R 54 mm, r 8.5 mm) between these specimens and the type (starfishes frequently have many pedicellariae when young and few or none when fully grown), the very dissimilar character of the pedicellariae, plus the other variations listed above seem, in view of Malpelo's isolated position, to warrant separation at the subspecific level.

***Tamaria stria*, new species**

FIGURE 34

DESCRIPTION.—R 44 mm, r 8 mm. Disc small, arms five, long, blunt, cylindrical. Carinal, adra-

dial, superomarginal, and inferomarginal plates diamond-shaped, slightly overlapping distal corner of preceding plate, connected transversely to adjacent row of plates by small, irregular, secondary plates. Six rows of papular areas, 6–10 pores per area. Three rows of rounded actinal intermediate plates, becoming two distally. Entire body, up to adambulacral armature, covered with close uniform coating of granules, those in papular areas slightly smaller than those on plates. Adambulacral furrow spines two, one small, acicular, the other heavy, flared at tip, broad in plane of furrow. Subambulacral spines single, heavy, thick, longer than broad. No pedicellariae noted. Madreporite small, round, covered with fine radiating gyri. Anus subcentral, inconspicuous. Ocular plates large, rounded, raised, mostly bare, with few granules. Color in life is reddish orange; dried, bright orange with blue papular areas.

MATERIAL EXAMINED.—Holotype, USNM E11838, Station 4, Malpelo Island, 49 m, on rubble near base of vertical rock wall. Paratypes, USNM E11839, 4 specimens, Stations 4 and 5, Malpelo Island, 36–49 m.

ETYMOLOGY.—The species name is the latinized acronym for the Smithsonian Tropical Research Institute.

DISCUSSION.—Only one other species of *Tamaria*, *T. obstipa* Ziesenhenné, has been described from the eastern tropical Pacific, *Tamaria obstipa* is known from the type-locality, Cocos Island, Costa Rica, and from James Island, Galapagos Islands. The present species agrees closely with *T. obstipa*, but differs in having secondary connecting plates not only intermarginally but between all abactinal plate rows; in having a carinal series, lacking in *T. obstipa*; in the nature of the adambulacral armature; and in the lack of pedicellariae. The number of pores per papular area is smaller in *T. stria* (6–10) but is within the range of *T. obstipa* (6–24).

MITHRODIIDAE

***Mithrodia bradleyi* Verrill**

Mithrodia bradleyi Verrill, 1867:288.—Perrier, 1878:77.—Sladen, 1889:539.—Fisher, 1906:1094, pl. 36: figs. 1, 2, pl. 37: figs. 1–3; 1925:68; 1928:491.—H. L. Clark, 1910:327, pl. 6: fig. 1.—A. H. Clark, 1946:9.—Steinbeck and Ricketts, 1941:380, pl. 23: fig. 3.—Ely, 1945:27, pl. 8A, B.—Caso, 1944:

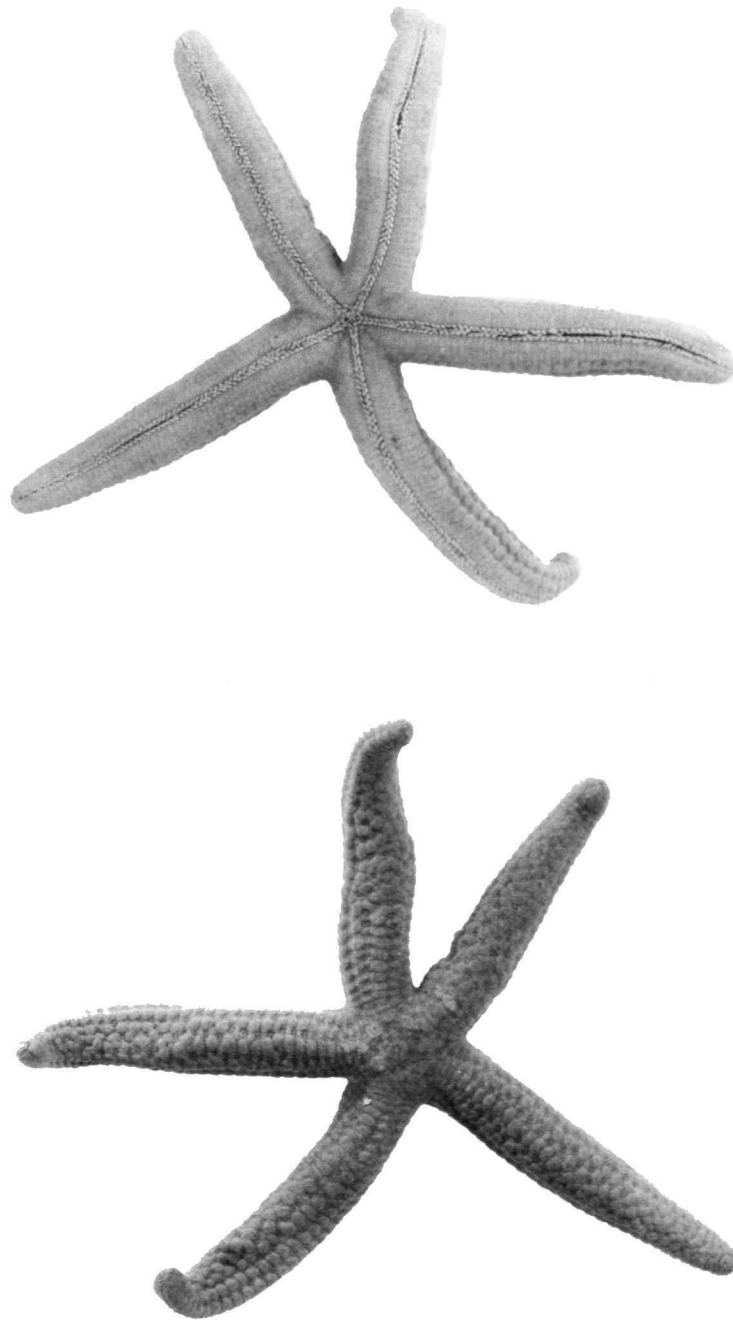


FIGURE 34.—*Talaria stria*, new species, holotype, USNM E11838.

253; 1953:214; 1961:92, figs. 34-36; 1962:92, figs. 34-36; 1963:300.—Engel, John, and Cherbonnier, 1949:1.
Mithrodia clavigera Perrier, 1875:360.—Ives, 1889:171.

Three specimens of *Mithrodia bradleyi* were collected at Malpelo at depths from 12 to 14 meters; the known distribution for this species is from Baja California to the Galapagos Islands. The Malpelo specimens have many more pedicellariae than specimens from Baja California in the collections of the National Museum of Natural History, Smithsonian Institution, but correspond well with material from the Colombian coast.

PORANIIDAE

Asteropsis carinifera (Lamarck)

Asterias carinifera Lamarck, 1816:556.
Asterope carinifera (Lamarck).—Mueller and Troschel, 1840:104.—H. L. Clark, 1920:33, pl. v: fig. 2.
Asteropsis carinifera (Lamarck): Mueller and Troschel, 1840:322; 1842:63.—A. M. Clark, 1967:37.—McKnight, 1968:713.
Gymnasterias inermis Gray, 1840:278.
Gymnasterias spinosa Gray, 1840:278.
Gymnasterias carinifera (Lamarck).—deLoriol, 1885:67, pl. 20: figs. 7-10.—Leipoldt, 1895:649, pl. 32: fig. 13.

One specimen of *Asteropsis carinifera* was collected at Malpelo on a vertical rock wall at 36 meters. It is distributed throughout the Indo-Pacific and the tropical eastern Pacific. This species is apparently attacked by the shrimp *Hymenocera* (Birkeland, pers. comm.), well known as a predator on *Acanthaster planci*, the crown-of-thorns starfish.

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Fishes Collected at Malpelo Island

John E. McCosker
and Richard H. Rosenblatt

ABSTRACT

Seventy species of shore fishes are reported from Malpelo Island, the majority of them previously unrecorded from that locality. Four species are undescribed and may be endemic to Malpelo. No new taxa are described. On the basis of these collections, it appears that the fauna is primarily eastern Pacific mainland in composition, although five species are shared only with the Galapagos and Cocos islands.

The fish collections made by the expedition contain the first shore fishes taken by rotenone ichthyocides and diving at Malpelo. Previous collections of Malpelo fishes were limited to those caught by hook and line (Fowler, 1938, 1944) or dipnetted beneath surface night lights (Clemens, 1957; Clemens and Nowell, 1963). Important material representing several new species and many new locality records was obtained by the STRI expedition. The collections, however, were limited in scope and are not sufficiently representative of the probable total ichthyofauna to allow any definitive statements concerning the faunal composition.

Malpelo occupies an important zoogeographic location in that it arises from deep water beyond the continental shelf, and could provide a "stepping-stone" to the Galapagos Archipelago for shore fishes. The known fauna is mainly eastern Pacific mainland in origin. However, there are certain similarities to both the Galapagos and Cocos islands. This is evidenced by the presence

of *Mycteroperca olfax*, *Apogon atradorsatus*, *Eupomacentrus arcifrons*, and *E. beebei*, species otherwise known only from those localities. Other specimens collected included fishes previously thought to be Galapagos endemics, e.g., *Labrisomus dendriticus* and possibly a deep water species of *Lythrypnus*. The presence of certain reef-associated Indo-Pacific species, e.g., *Gymnothorax flavimarginatus*, *Zanclus canescens*, and *Acanthurus glaucopareius*, is relatable to hydrographic and ecological conditions found on other eastern tropical Pacific offshore islands (Rosenblatt, McCosker, and Rubinoff, 1972). Included in the Malpelo collections were undescribed, and apparently endemic, species of *Chriolepis*, *Acanthemblemaria* and *Axoclinus*, and an undescribed genus and species of tripterygiid.

The following annotated list of fishes from Malpelo Island is based primarily on those collected by J. B. Graham and party at two localities, and underwater photographs and sight records made by C. Birkeland (pers. comm.). Fishes from the first locality (SIO 72-96) were collected along a sloping basalt and sparsely covered *Pocillopora* bottom between the surface and 6 meters along the western edge of the island. The second collection (SIO 72-97) is a composite of small east and west shore stations, from the surface to depths of 20 meters. Fishes and photographs are deposited in the Marine Vertebrates Collection of the Scripps Institution of Oceanography (SIO), University of California at San Diego. Verified records from hook and line and night-light stations are also included. The basis of identification is indicated by the following abbreviations: * specimens collected and deposited at SIO, ^S sight record by STRI diving party, ^P photographed underwater by C. Birkeland, ¹ recorded by Fowler (1938), ² recorded by

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Fowler (1944),³ recorded by Clemens (1957),
⁴ recorded by Clemens and Nowell (1963).

CARCHARHINIDAE

Carcharhinus galapagensis (Snodgrass and Heller)¹
C. falciformis (Müller and Henle)² as *C. malpeloensis*
C. leucas (Müller and Henle)³
Triaenodon obesus Rüppell⁵

SPHYRNIDAE

Sphyrna sp. ⁵

MURAENIDAE

Gymnothorax flavimarginatus (Rüppell).^P Abundant in the
 West Indo-Pacific and Hawaii, and several eastern Pacific
 offshore and nearshore localities (Rosenblatt, et al., 1972).
G. castaneus Jordan and Gilbert ^P
G. dowii (Günther) ^P
Muraena lentiginosa Jenyns ^P

HOLOCENTRIDAE

Myripristis leiognathus Valenciennes * ³
Holocentrus suborbitalis (Gill) ⁵

KUHLIIDAE

Kuhlia taeniura (Cuvier) ^{5,1,2}

APOGONIDAE

Apogon atradorsatus Heller and Snodgrass.* Previously
 known only from the Galapagos and Cocos islands.

SERRANIDAE

Epinephelus dermatolepis Boulenger *
E. labriiformis (Jenyns) *
Paranthias furcifer (Valenciennes) *¹
Mycteroperca olfax (Jenyns).¹ Previously known from the
 Galapagos, Malpelo, and Cocos islands. Phillip C. Heemstra
 had kindly reexamined Fowler's specimens (ANSP 89121)
 and found their gill rakers and dorsal spine profile to
 agree with Galapagos specimens of *M. olfax*.

MULLIDAE

Pseudupeneus grandisquamis (Gill).⁴ Based on surface dip-
 netted prejuvenile specimens.
Mulloidichthys dentatus (Gill) ⁵

CARANGIDAE

Selar crumenophthalmus (Bloch) ¹
Caranx caballus Günther ⁵
C. vinctus Jordan and Gilbert ⁵

C. melampygyus Cuvier and Valenciennes ^P
Elagatis bipinnulatis (Quoy and Gaimard) ²

LUTJANIDAE

Lutjanus jordani (Gilbert) ^{1,P}
Lutjanus viridis (Valenciennes) ^{1,2,P}

POMACENTRIDAE

Chromis atrilobata (Gill) ^{4,*}
Eupomacentrus arcifrons (Heller and Snodgrass).^{1,*} Known
 only from Malpelo, the Galapagos, and Cocos islands.
E. beebei (Nichols).^{*} Previously known only from the Gala-
 pagos and Cocos islands.
Microspathodon dorsalis (Gill) ^{*}

LABRIDAE

Thalassoma lucasanum (Gill) ^{*}
Bodianus diplotaenia (Gill) ^{1,*}

SCARIDAE

Scarus rubroviolaceus Bleeker ⁵

KYPHOSIDAE

Sectator ocyurus (Jordan and Gilbert) ⁵
Kyphosus sp. ⁵

CHAETODONTIDAE

Holacanthus passer Valenciennes ^{1,*}
Heniochus nigrirostris (Gill) ^P
Pomacanthus zonipectus (Gill) ⁵

CIRRHITIDAE

Cirrhitichthys oxycephalus (Bleeker) *
Cirrhitus rivulatus Valenciennes ^{1,2,*}

SCORPAENIDAE

Scorpaenodes xyris (Jordan and Gilbert) *
Scorpaena plumieri Bloch *

AULOSTOMATIDAE

Aulostomus chinensis L.⁵

FISTULARIIDAE

Fistularia petimba Lacépède ⁵

GOBIIDAE

Lythrypnus sp. A *
Lythrypnus sp. B *
Chriolepis lepidotus Findley (see paper by Findley in this
 volume)

GOBIESOCIDAE

- Tomicodon* cf. *petersi* (Garman)*
Arcos decoris Briggs*
Labrisomus cf. *dendriticus* (Reid). * Previously known only from the Galapagos Islands.
Parastathmonotus culebrai (Seale)*

TRIPTERYGIIDAE

- Axoclinus* new species*
 Genus and species.* An undescribed species, closely related to *Enneapterygius corallicola* Kendall and Radcliffe from the Galapagos Islands, and an undescribed species from Panama and Costa Rica.

CHAENOPSIDAE

- Acanthemblemaria* new species*

BLENNIIDAE

- Ophioblennius steindachneri* Jordan and Evermann 34,*
Entomacrodus chiostictus (Jordan and Gilbert)*
Hypsoblennius brevipinnis (Günther)*
Plagiotremus azaleus (Jordan and Bollman)*

ANTENNARIIDAE

- Antennarius sanguineus* Gill*

ACANTHURIDAE

- Acanthurus glaucopareius* Cuvier*
A. xanthopterus Valenciennes^S
Prionurus laticlavus (Valenciennes)^S
Zanclus canescens (Linnaeus)^S

CANTHIGASTERIDAE

- Canthigaster punctatissima* (Günther)*

TETRAODONTIDAE

- Arothron meleagris* (Bloch and Schneider)*

BALISTIDAE

- Sufflamen verres* (Gilbert and Starks)¹
Melichthys niger (Bloch).^{1,P} As *M. buiva* in Fowler, 1938.
Canthidermis maculatus (Bloch). As *C. sp.* in Clemens, 1957.
Cantherhines dumerilii (Hollard)^S
Alutera scripta (Osbeck)^S

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A New Species of Goby from Malpelo Island (Teleostei: Gobiidae: *Chriolepis*)

Lloyd Talbott Findley

ABSTRACT

Two specimens representing a new species of the gobiid fish genus *Chriolepis* were collected during the 1972 Smithsonian Institution-U.S. Navy Expedition to Malpelo Island. The new species is herein described, and its taxonomic relationships are briefly discussed.

Introduction

METHODS.—Measurements were made with dial calipers to the nearest 0.1 mm, and are expressed as percent of standard length (SL) in Table 9. Counts and measurements requiring explanation are as follows: Head length is distance from anterior margin of upper lip to upper attachment of opercular membrane. Head depth is depth of head at the vertical, posterior margin of preoperculum. Head width is the maximum width between cheeks. Depth at anal fin origin is shortest distance between base of anal spine and dorsal fin base. Post-orbital distance is the distance from posterior rim of eye to upper attachment of opercular membrane. Transverse scale rows is the number of scale rows, counted upward and forward, between the last anal ray and dorsal fin base. The last dorsal and anal rays, branched to their bases, were counted as one.

The holotype and paratype (the only known specimens) are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D. C.

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Chriolepis lepidotus, new species

FIGURE 35

HOLOTYPE.—USNM 211456, adult male, 30.0 mm SL, Malpelo Island, Colombia, east side of island, depth ca. 10 m, above the coral zone, cobble bottom with some calcareous sand and boulders, very sparse algal growth; collected by J. B. Graham using rotenone ichthyocide and SCUBA, 2–3 March 1972.

PARATYPE.—USNM 211457, adult male, 29.1 mm SL; collected with holotype.

DESCRIPTION.—(See Table 9 for meristic and morphometric data). A robust species. Head plump, with wide cheeks, more or less rounded; depth at preoperculum 0.71 (holotype) and 0.68 (paratype) of head width. Mouth oblique, forming an angle about 40°–45° with body axis, the posterior angle reaching a point approximately under rear margin of pupil. Interorbital narrow, about one-third or

less of eye length. Pectoral base broad. Gill slit narrow; opercular membrane attachments at upper and lower edges of pectoral base in advance of insertion of fin rays.

Gill rakers short on first arch, those on second and following arches shorter; 3+8=11 on outer face of first arch; 9 on lower limb of second arch. Pseudobranchiae in four small tufts.

Head without pores or barbels. Sensory papillae on head relatively large; in rows below eye, on cheek, at edge of preoperculum, on operculum, on snout, and on dorsal and ventral surfaces of head

TABLE 9.—Counts and measurements of the holotype and paratype of *Chriolepis lepidotus*

Characters	Holotype (USNM 211456)	Paratype (USNM 211457)
Sex	♂	♂
Standard Length (mm)	30.0	29.1
COUNTS		
Dorsal fin rays	VII-1,10	VII-1,10
Anal fin rays	1,9	1,9
Pectoral fin rays (left/right)	20/20	20/20
Pelvic fin rays	1,5	1,5
Segmented caudal fin rays	17	17
Branched caudal fin rays	15	14
Procurrent caudal fin rays (upper/lower)	5/5	6/5
Gill rakers (outer face of first arch)	11	11
Longitudinal scale rows	ca. 34	ca. 35
Transverse scale rows	13½	13½
PROPORTIONS (% of SL)		
Head length	33.3	32.2
Head depth	15.5	15.6
Head width	21.8	23.5
Base of second dorsal fin	28.5	27.2
Depth at anal fin origin	16.8	17.5
Pectoral fin length	27.3	24.7
Pelvic fin length	20.5	21.0
Caudal fin length	24.7	23.5
Caudal peduncle length	16.0	13.6
Caudal peduncle depth	13.7	13.8
Eye length	6.7	6.2
Snout length	7.6	6.9
Mouth length	13.4	12.5
Width between mandible tips	10.2	10.1
Interorbital width	2.4	1.9
Width between posterior nostrils	4.1	5.1
Length between anterior & posterior nostrils	2.9	2.3
Postorbital distance	19.6	19.1

including mandibular area, and similar to other species in the genus (Figure 35). A low, shallowly V-shaped, transverse, fleshy crest on head behind eyes. A low, short, fleshy "keel" extending medially between nostrils. Nostrils tubular; anterior tube narrow, its length about equal to pupil diameter; posterior tube wider, its length about one-half that of anterior tube. Tongue tip truncate.

Teeth in rows in both jaws, relatively large, sharp, mostly caniniform, slightly to distinctly recurved, mostly depressible and with faint yellowish apical tips; outer row teeth in upper jaw enlarged; outer and inner row teeth in lower jaw enlarged. Lower jaw with (1) abbreviate outer row of large, slender, recurved, well-separated teeth confined to anterior portion of jaw; (2) behind outer row anteriorly is a patch of many small (about ¼ to ½ length of outer row teeth) closely set, less recurved teeth in irregular rows, becoming fewer in number, more widely spaced, and confined to one row posteriorly at side of jaw; (3) inner row of large, slender, recurved, well-separated teeth anteriorly, becoming more widely spaced and stouter posteriorly, until 2 to 3 much enlarged and recurved "fanglike" teeth at side of jaw, followed by a few, much smaller, closely set teeth. Upper jaw with (1) outer row of large, slender, recurved, well-separated teeth anteriorly and at side of jaw (not absent posteriorly as in outer row of lower jaw); (2) behind outer row anteriorly is a patch of many small, closely set, less recurved teeth in irregular rows, becoming fewer in number posteriorly; (3) inner row of many small, closely set teeth, becoming more widely spaced posteriorly. No teeth on vomer or palatines.

First dorsal fin with seven flexible spines; bases of first five spines equally spaced; the last two spines widely separated from the first five, their bases widely spaced. Third and fourth spines slightly the longest, but no spine notably longer than any other, and none filamentous.

Second dorsal fin separated from first dorsal fin by distance slightly more than eye length. First element of both second dorsal and anal fins a flexible spine; remaining elements are subequal, segmented, branched rays, with the last branched to their bases.

Pectoral fins when adressed reach past tips of pelvic fins to level of end of spinous dorsal; all pectoral rays branched.

Origin of pelvic fins in advance of pectoral base. Pelvic fins short, not reaching anus; separated and diverging, not united by a membrane into an adhesive disc as in most gobiids; interspinal membrane absent, but pelvic bases slightly connected by a very low, inconspicuous frenum. Pelvic spine flexible; segmented pelvic rays well developed and branched, most with three main branches, the innermost ray branching less than others, but not reduced or splinted to the fourth. Fourth ray slightly the longest, then the third, then the fifth (which is almost equal to the third). Caudal fin short, rounded.

Urogenital papilla of male long, slender, attenuate; with a few scattered melanophores.

SQUAMATION.—Four enlarged strongly ctenoid basicaudal scales (some lost from both specimens); the outer two (at upper and lower angles of caudal fin base) slightly narrower and longer than the inner two. Body extensively scaled. Scales along midline extending forward from hypural to near axil, beneath origin of spinous dorsal fin (Figure 35), in about 34–35 more or less irregular longitudinal rows; difficult to enumerate (some scales lost from both specimens, but scale pockets usually discernible). Fewer scales in anterior rows; in a wedge-shaped pattern as approaching axil. Transverse scales difficult to enumerate, about $13\frac{1}{2}$ in an irregular row (first scale at base of last anal ray very narrow in comparison to scales above it, counted as $\frac{1}{2}$ scale).

Posterior scales large, with prominent ctenii; be-

coming progressively smaller, thinner, more embedded, and with fewer and shorter ctenii, until cycloid anteriorly. Ctenii becoming progressively restricted to central portion of posterior edge of each scale proceeding anteriorly, until completely lost at about twelfth scale along midline in advance of hypural. Anteriormost scales cycloid, minute, embedded, and difficult to see.

A naked area beginning near base of sixth dorsal spine, equivalent to one scale width from base of sixth spine to below base of fifth spine, to two scale widths below fourth spine, becoming wider and sloping downward and forward to near upper margin of pectoral base. A lower naked area from under pectoral base sloping downward and backward to near midline of venter, continuing as a narrow strip around anus to about base of fourth anal ray. Head, nape, chest, and venter scaleless.

COLORATION IN ETHYL ALCOHOL.—Background color of head and body brownish yellow. Head with a number of prominent black spots, especially laterally and ventrally. An elongate spot at mid-posterior edge of eye (diffuse in paratype); one behind eye at dorsal edge of cheek near end of low transverse dorsal crest; one at dorsal margin of preopercular-opercular junction; one at midanterior edge of operculum which begins a row of about 9 or 10 widely spaced spots lying in preopercular-opercular groove, following curvature of groove downward and forward and onto the immediately adjacent branchiostegal membrane, then continuing forward ventrally below lower jaw to

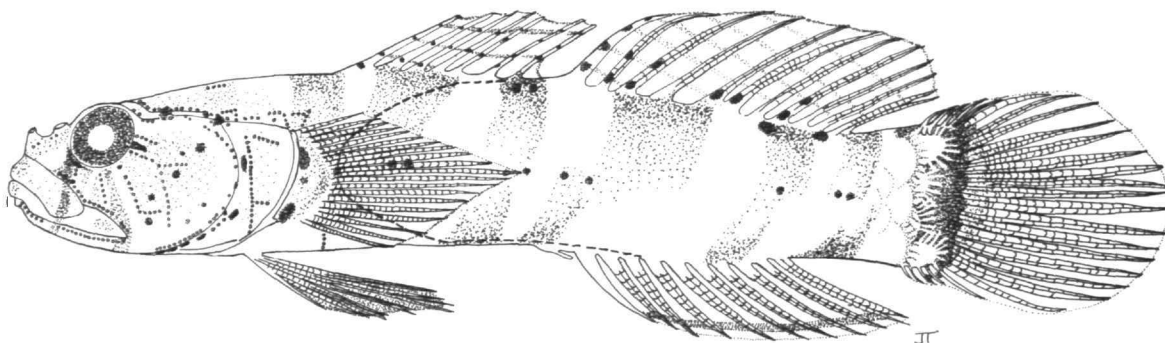


FIGURE 35.—*Chriolepis lepidotus*, holotype, USNM 211456, male, 30.0 mm SL, Malpelo Island, Colombia. Most scales not shown; the dashed line indicates anterior limit of squamation. The row of specialized basicaudal scales is a composite from paratype and right side of holotype. Sensory papillae on head shown as small circles and are a composite from both specimens.

near symphysis. This row is partially duplicated by a shorter row of about 5 spots beginning at lower posterior edge of preoperculum, running forward below lower jaw to near symphysis, the spots lying close to and opposite the spots of row described above. About 5–8 widely spaced spots scattered over cheek (more prominent on paratype). A spot (on paratype) at posterior end of interorbital, followed by profuse minute melanophores on the low transverse dorsal crest. A spot at posterior dorsal corner of operculum. A prominent spot on upper and lower angles of outer pectoral fin base; a more distal irregular spot at bases of fifth to eighth pectoral fin rays (slightly larger on paratype). A small spot on inner pectoral fin base near upper margin.

A black bar below anteroventral edge of eye, passing obliquely downward across suborbital and jaws, terminating in anteriormost ventral spot of the series described above. A fainter dark bar extends from midventral edge of eye downward across suborbital region, and curves around end of lower jaw. Snout, nostrils, upper jaw, and anterior portion of lower jaw densely peppered with minute melanophores.

Two wide, transverse, light brown bars across dorsal surface of head, the posterior is across the nape and bisected at either side by pectoral fin. Five wide, vertical, light brown bands on body, most noticeable dorsally as dark saddles, becoming more diffuse ventrally, and terminating near midventral line. Brownish yellow interspaces between bands with a few scattered melanophores. Each band with one or two adjacent, prominent, black spots at midline. Anteriormost body band crosses dorsum between first and fifth dorsal spines, and passes downward behind pectoral fin; second band between sixth spine and end of spinous dorsal fin; third band between second and fifth dorsal rays; fourth band between seventh and ninth rays; fifth band behind end of second dorsal fin on anterior portion of caudal peduncle. Dorsal segments of bands 3 and 4 appearing as darker blocks offset posteriorly from their ventral counterparts below midline, with dorsal block of band 3 most noticeable and lying over the interspace between third and fourth ventral blocks. An irregular dark blotch behind fifth band at dorsal edge of caudal peduncle, adjacent to first procurent ray. A narrow vertical bar of darker pigment underlying basicaudal row of specialized ctenoid scales.

Dorsal fins with about four or five oblique rows of dark lines, noticeable as prominent black spots on spines and rays (membranes torn in both specimens). A dark horizontal bar on anal fin membrane, running the length of fin near its edge. A few faint diffuse spots on caudal rays suggest three or four vertical lines. Pectoral fins slightly dusky on interradial membranes. Pelvic fins dark.

Chest and venter whitish, with numerous minute melanophores, appearing "peppered" on microscopic inspection. Inside of gill chamber with a dark horizontal stripe ventrally, in advance of lower pectoral base; a few melanophores dorsally in area surrounding pseudobranchial tufts.

RELATIONSHIP.—The general head shape, relatively high number of fin rays, and general color pattern suggest a relationship with a species complex of *Chriolepis*, most of whose members in the eastern tropical Pacific are undescribed. Among the described species, *C. lepidotus* is perhaps closest to *C. minutillus* Gilbert, 1891, and *C. tagus* Ginsburg, 1953 (judging by original description only). Complete discussion of relationships within the genus *Chriolepis* and allied genera of seven-spined gobiids with separate pelvic fins is deferred pending completion of a revision in progress by the author of all known species in the eastern tropical Pacific.

COMPARISONS.—*Chriolepis lepidotus* differs from other described congeners in the eastern tropical Pacific in the extent of its squamation; its scales extend forward to beneath the origin of the spinous dorsal fin. Among the other described species, *C. minutillus* Gilbert, 1891 (Gulf of California), most closely approximates this condition; its scales extend forward to beneath or slightly in advance of midspinous dorsal. From the description of *C. tagus* Ginsburg, 1953 (Galapagos Islands), and in *C. zebra* Ginsburg, 1938 (Gulf of California), scales only extend forward to beneath the end of the spinous dorsal, or slightly posterior to this position in the latter species.

The new species also differs from other described eastern tropical Pacific congeners in having the highest number of pectoral fin rays (20 vs. 19 in *C. tagus*; 17 or 18 in *C. zebra*; 15 or 16 in *C. minutillus*.) The prominent black spots on the head further serve to distinguish *C. lepidotus* from the other species described from these waters.

Chriolepis lepidotus further differs from *C. min-*

utillus in having a larger mouth (posterior angle extends to below posterior margin of pupil vs. to below midpupil in *C. minutillus*), shorter pelvic fins (when adpressed, not reaching anus vs. reaching or almost reaching anus in *C. minutillus*), and more gill rakers on the outer face of the first arch (11 vs. 8 or 9 in *C. minutillus*).

The new species further differs from *C. zebra* in having a rounded rather than a depressed head, a larger mouth (posterior angle extends only to below midpupil in *C. zebra*), and more second dorsal fin rays (11 vs. 10 in *C. zebra*).

Chriolepis lepidotus differs from the description of *C. tagus* in having fewer second dorsal fin rays (12 in *C. tagus*), and fewer anal fin rays (10 vs. 11 in *C. tagus*).

DISTRIBUTION.—*Chriolepis lepidotus* is presently known only from Malpelo Island, Colombia.

ETYMOLOGY.—From the Greek *lepidotos* (scaly), referring to its squamation, the most extensively known in the genus.

REMARKS.—The genus *Chriolepis* was erected by Gilbert (1891:557–558) for the species *C. minutillus*, which he described as being totally scaleless on the basis of a single specimen trawled by the *Albatross* in the Gulf of California. His description was in error, since the holotype retains a single basicaudal scale, as mentioned by Ginsburg (1938:111; 1953:21), and confirmed by examination of the type by D. F. Hoese and R. J. Lavenberg (pers. comm.). Recently collected material of *C. minutillus* under study by the author shows that, indeed, squamation is extensive in this species, less so than in *C. lepidotus*, but more so than in *C. zebra*, for example.

Species of *Chriolepis* are sublittoral in habitat and secretive, hiding under rocks and in crevices. Until recently, few specimens were known, but with the introduction of SCUBA and rotenone ichthyocide collecting techniques by diving ichthyologists, specimens have begun to accumulate. These will allow for a comprehensive systematic, zoogeographic, and evolutionary treatment of the genus and its allies (briefly treated by Böhlke and Robins, 1968:129–131) in the eastern tropical Pacific. There remain about five undescribed species of *Chriolepis* in these waters.

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