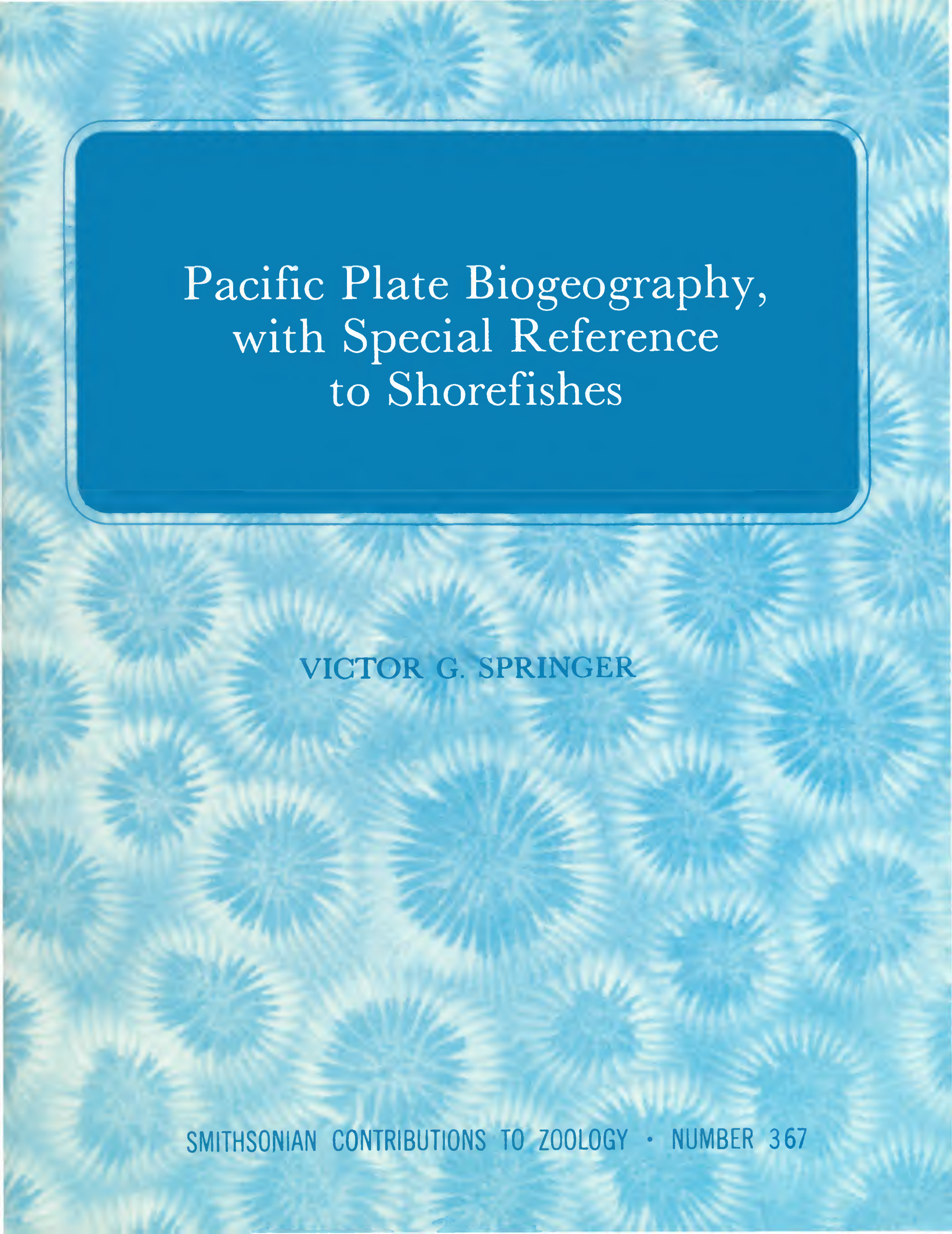

Pacific Plate Biogeography, with Special Reference to Shorefishes

VICTOR G. SPRINGER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 367

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Pacific Plate Biogeography, with Special Reference to Shorefishes

Victor G. Springer

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ABSTRACT

Springer, Victor G. Pacific Plate Biogeography, with Special Reference to Shorefishes. *Smithsonian Contributions to Zoology*, number 367, 182 pages, 65 figures, 5 tables, 1982.—It is the thesis of this study that the Pacific lithospheric plate (Pacific Plate) forms a major subunit of the Indo-Pacific biogeographic region. This thesis is defended on two primary grounds: the sharp decrease in numbers of taxa as one proceeds eastward across the western margin of the Pacific Plate, and the presence of a high degree of endemism on the Plate. The complex geotectonic history of the Plate and adjacent plate margins is discussed and the vicariance scenarios that produced the three main types of endemism (widely distributed Plate endemism, endemism restricted to a limited region on the Plate, and endemism restricted to single islands or island groups) are hypothesized.

Anecdotal discussions of the distributions of 179 shorefish family groups are presented, as well as discussions of the distributions of selected terrestrial and marine taxa of other organisms. Particular attention is given to presumed erroneous or exceptional distributions of fishes on the Pacific Plate, including, but not limited to, north-south disjunct distributions, Hawaiian Islands' exceptional distributions, and distributions involving the Caroline Islands, which serve as stepping stones for dispersal onto the Pacific Plate.

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Contents

CORRECTIONS FOR PACIFIC PLATE BIOGEOGRAPHY

Page 10, Fig. 5. *Acanthurus achilles* has been reported from the southern tip of Baja California based on a sight record (D. A. Thomson, et al., 1979, *Reef Fishes of the Sea of Cortez*)

Page 15, col. 1, line 14. replace *tachycephalus* with *dasycephalus*

Page 25. Replace Branchiostegidae with Latilidae

Page 27. Under Caracanthidae. Mizuno and Tominaga were in error; caracanthids are not present at the Galapagos (M. and T, in litt. to W.N. Eschmeyer, pers. comm.)

Page 28, col. 1, penultimate line. Replace carapodid with carapid

Page 60. Replace Monocentridae with Monocentrididae

Page 63. Under Nomeidae, 7th and 8th lines from bottom delete the three words "eastern Atlantic and"

Page 88, Figure 39 caption. Delete sentence, "While this study was in press..." *Sarda* is not known from Fiji.

Page 91. Under Scorpididae. Delete *Parapsettus* [belongs in Ephippididae]

Page 100. Under Torpediniformes and Figure 44. I missed a report of the occurrence of electric rays on the Nazca Ridge, Nazca Plate.

Page 149, right column, 4th line, replace corroroborate with corroborate.

Page 165. Under Chubb, replace 1974 with 1934.

Pacific Plate Biogeography, with Special Reference to Shorefishes

Victor G. Springer

Introduction

The Pacific Plate (Figures 1, 2) is the largest of all the earth's lithospheric plates and occupies most of the area that has been referred to as the Pacific Basin (Figures 3, 4). Although the Pacific Basin has been the subject of numerous biogeographic studies, there are only two studies (Springer, 1981a; Rotondo et al., 1981) that have alluded to the Pacific Plate as a separate biogeographic unit. I will not recount the Pacific Basin literature here, but refer the reader to two studies that together summarize the subject admirably. Van Balgooy (1971) gave a comprehensive and scholarly rendering of the general literature on Pacific Basin biogeography in his analysis of Pacific plant distributions. The main deficiencies of van Balgooy's treatise are the absence of reference to the importance of plate tectonics (a subject probably too new for him to have incorporated) and the use of a solely phenetic approach to relationships. Zoogeographers seem to be unaware of van Balgooy's work, which merits wider attention than it has received. Kay (1980), who did not cite van Balgooy, published an excellent essay on the development of ideas concerning Pacific Basin biogeography and included a brief discussion of the importance of plate tectonic effects for the distribution of Pacific Basin organisms.

My study is concerned primarily with the distributions of the shorefishes of the Indo-Pacific as these distributions relate to the Pacific Plate. I propose to demonstrate that the Pacific Plate defines a biogeographic region of major significance, and I will hypothesize the biological and geological factors that produced the region. I believe that study of the Pacific Plate provides new insights into the patterns of organismal distributions in the Indo-Pacific, both aquatic and terrestrial. From this it follows that many of the constraints to dispersal ordinarily invoked to explain only the distributions of endemic terrestrial and freshwater organisms are equally important in explaining the distributions of endemic, shallow-dwelling marine organisms.

The day I began to write this introduction, I received a new issue of *American Scientist* that included an article on chance dispersal by Carlquist (1981). In that article (p. 415) was the following statement, "Those who investigate organisms capable of long-distance dispersal have not adopted the methods of vicariance biogeography." If this is true, my study is an exception; many shorefishes appear to be so capable. The land masses of the Pacific Plate are islands (Figure 2), many of which are highly isolated, and I will

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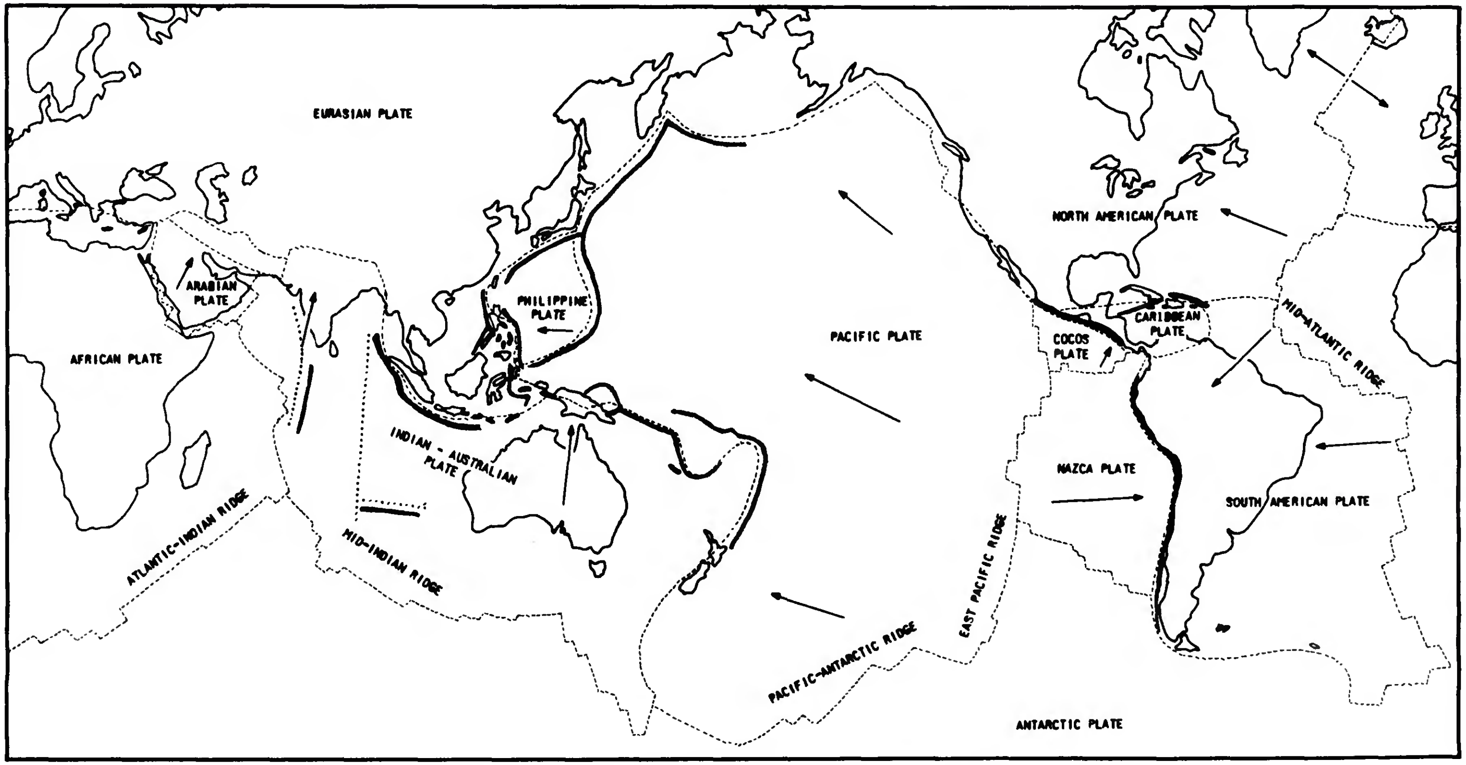

Figure 1.—Some important geotectonic features of the world (dashed lines denote margins of major lithospheric plates, based on a map in Toksöz, 1975:90–91; arrows indicate direction of plate movements and subduction along deep-sea trenches; heavy dark lines denote deep-sea trenches, based on Figure 3, with the exception of two old trenches shown in Indian Ocean; dotted lines indicate prominent inactive ridges in Indian Ocean).

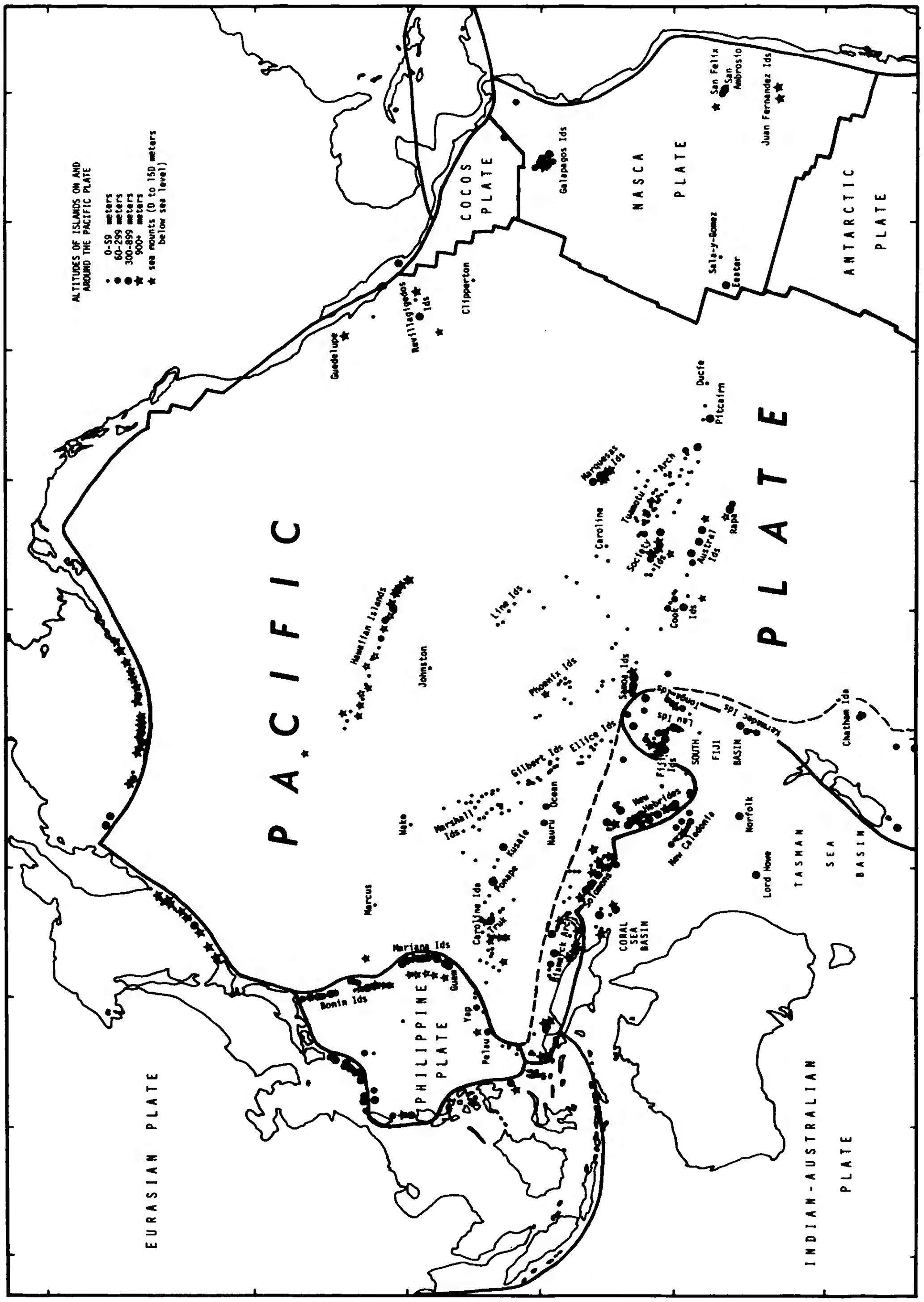

FIGURE 2.—Islands and shallow sea mounts on and around the Pacific Plate (heavy lines indicate plate margins; dashed line indicates portion of Andesite Line (Appendix I) that does not correspond to western margin of Pacific Plate; Kusaie = Kosrae).

rely heavily on vicariant events to develop hypotheses to explain endemism among these islands.

Carlquist apparently thought he was pointing out a weakness in the methodology of vicariance biogeography (Nelson and Platnick, 1981; henceforth, I refer to the subject as vicariography), but he failed to realize that dispersal is not the material of that discipline. The materials of vicariography are the geological and physical factors that contributed to the geographical isolation of biotic populations and permitted those populations to speciate. The dispersal that expands the range of a species becomes of interest to a vicariographer when the dispersal is interrupted. The interruption is the vicariant event, and the cause of that interruption needs to be explained. It is a premise of vicariography that a vicariant event affects a spectrum of organisms that are not necessarily related phyletically and do not necessarily have the same general ecological requirements. If an island exhibits high endemism in both its land snails and shorefishes, for instance, it is more informative and economical to search first for a general explanation of the isolation of the island's biota than it is to search for the possible factors that might have pertained to a single species or ecological grouping of species. Birds might have populated an island with land snails, but they certainly did not populate it with shorefishes. It is possible, of course, that the endemism of the land snails and shorefishes might have entirely different explanations, and if they do, the vicariographer is more likely to determine this than is the dispersalist, because the methodology of vicariography allows for the falsification of its hypotheses, and even defines the evidence for dispersal (sympatry of sister taxa). I know of no methodology of dispersalism that might lead to falsification of its hypotheses or alternate (vicariance) interpretations.

Knowledge of sister-group relationships and

FIGURE 3.—Topography of the Pacific Basin (from B.C. Heezen and M. Tharp, *World Ocean Floor* [chart], United States Navy, Office of Naval Research, 1977).

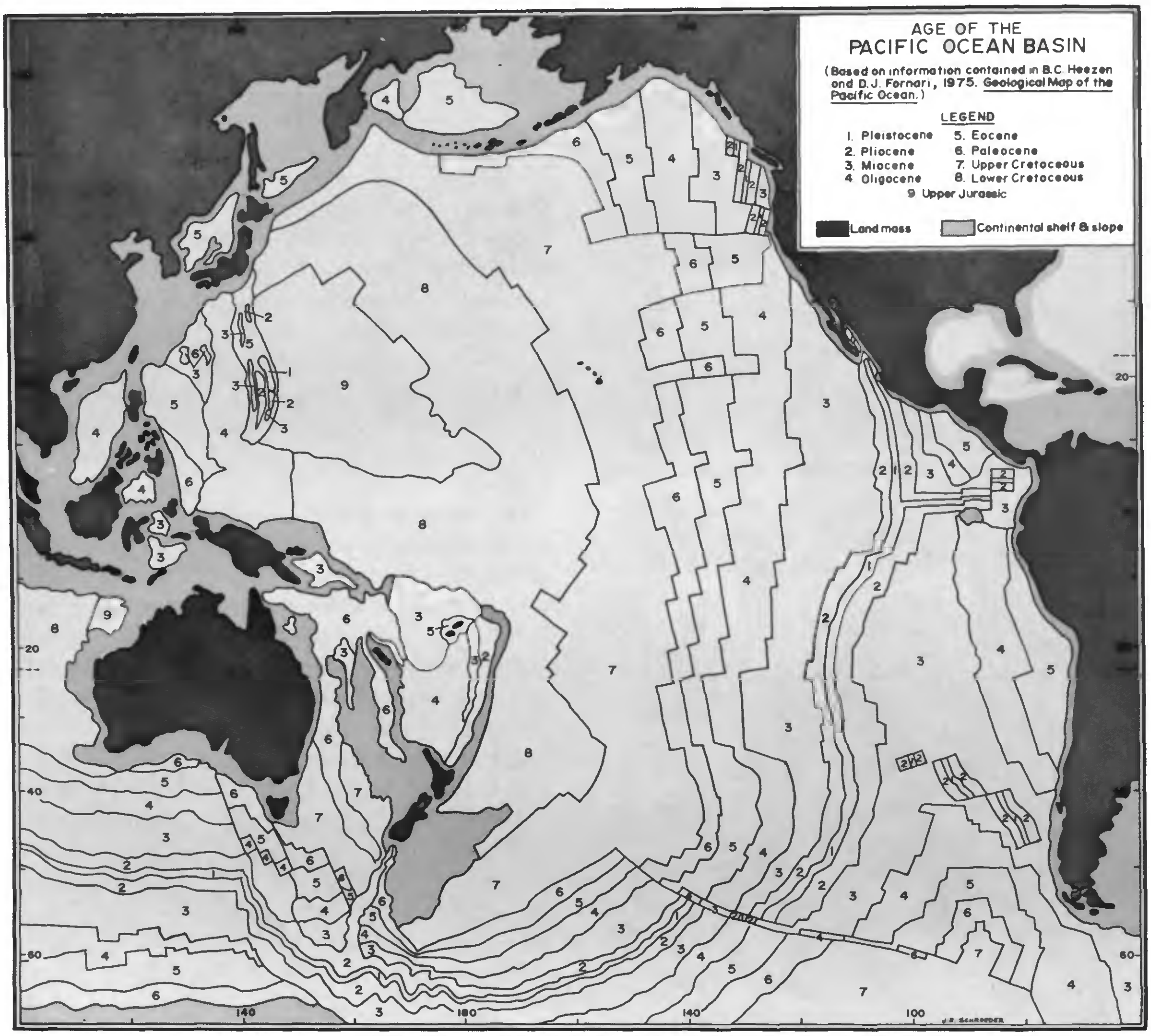

FIGURE 4.—Age of the Pacific Ocean Basin.

distributions are of the utmost importance for vicariographic studies. If one knows the cladistically determined closest relatives (sister groups) of endemic taxa, and the distributions of those relatives, one can narrow the geographic and temporal search for the pertinent vicariant events. Unfortunately, few cladistic studies of Indo-Pacific organisms are available, and for species of Indo-Pacific fishes, none (however, see Vari, 1978, for an Indo-West Pacific fish family). In constructing my hypotheses I have had to rely on the inferences and intuitive assessments of relationships as given by authors, and on some verbal assessments made at my request. That these statements of relationships tend to support my findings based solely on areas of endemism is not surprising to me, but I recognize the deficiences of my study and look forward to its correction, elaboration, falsification, or corroboration—by others.

Acknowledgments

Numerous individuals have provided information or other assistance that has been incorporated into my study; others listened patiently to my discussions and constructively challenged my ideas or offered suggestions for improvement of certain sections of the manuscript. To all of them I here extend my sincere appreciation: Gerald R. Allen, K. Amaoka, William D. Anderson, Jr., Albert H. Banner, Hans Bath, Marie Louise Bauchot, Ross T. Bell, Adam Ben-Tuvia, Marinus Boeseman, James E. Böhlke (deceased). Kurt Bruwelheide, Warren E. Burgess, Bruce A. Carlson, John H. Caruso, E.H. Chave, Barry Chernoff, Daniel M. Cohen, Bruce B. Collette, Leonard J.V. Compagno, Roger F. Cressey, William P. Davis, Charles E. Dawson, Guido Dingerkus, Terry Erwin, William F. Eschmeyer, Isabel P. Farfante, Norma Feinberg, Ross M. Feltes, William L. Fink, Thomas H. Fraser, Warren C. Freihofer, John A.F. Garrick, Ray W. George, Robert H. Gibbs, Jr., J. Gill, Janet R. Gomon, Martin F. Gomon, Patricia H. Hansen, Phillip C. Heemstra, John B. Heiser, Dannie A. Hensley, Robert W. Hiatt, Douglas F. Hoese, Walter Ivantsoff, E. Dale Jackson (deceased), Susan Jewett, G. David Johnson, Robert K. Johnson, Harry T. Kami, Robert Kanazawa, E. Allison Kay, Leslie K. Knapp, Alan J. Kohn, Karl F. Koopman, Louis S. Kornicker, Ernest A. Lachner, Harry S. Ladd, Raymond S. Manning, John D. McEachran, R.J. Mackay, John E. McKosker, William G. Melson, Henry W. Menard, Robert Rush Miller, Robert F. Myers, Izumi Nakamura, Gareth Nelson, Dan Nicholson, James N. Norris, N.V. Parin, David L. Pawson, Theodore W. Pietsch, Winston Ponder, Stuart G. Poss, Christopher Powell, John E. Randall, Harald A. Rehder, Clyde F. Roper, Donn E. Rosen, Richard H. Rosenblatt, Joseph Rosewater, W.C. Ruark, Barry C. Russell; Joseph L. Russo, Seymour O. Schlanger, James B. Shaklee, Takeshi Shimuzu, Eli Silver, William F. Smith-Vaniz, August E. Spreitzer, Michael J. Sweeney, Leighton R. Taylor, W. Ralph Taylor, Thomas B. Thorson, Enrico Tortonese, Ethelwyn Trewavas, James C. Tyler, Richard P. Vari, Gilbert L. Voss, Richard C. Wass, George E. Watson, Alwyne C. Wheeler, Peter J. Whitehead, Austin B. Williams, Jeffrey T. Williams, Richard Winterbottom, George R. Zug.

The base map used for most of the distributions was prepared by August E. Spreitzer. Jack R. Schroeder masterfully rendered Figure 3, and Penelope K. Hollingsworth, Figures 61 and 63.

Complete drafts of the manuscript were generously reviewed and constructively criticized by Gareth Nelson, John E. Randall, and Richard H. Rosenblatt. Especial appreciation goes to my editor, Barbara T. Spann, who found innumerable ways to improve the manuscript and bring it to a publishable state.

Acknowledgment is accorded Elsevier Publishing Company for permission to reproduce the information in Figure 62.

Grants for fieldwork from the Max and Victoria Dreyfus Foundation, the Lewis and Rosa Strauss Memorial Fund, and the Smithsonian Scholarly Studies Program enabled me to obtain important distributional data on fishes.

Above all, the contribution of John E. Randall stands out. His incomparable knowledge of Indo-Pacific fishes, his publications, and his collections, together with his unstinted imparting of information, permeate my study. To him I dedicate this study. Thank you, Jack, even though you continually encouraged me to shelve it and return to revising genera. You may well have been correct.

Methods

DISTRIBUTION MAPS.—The distribution maps include delineations of the major lithospheric plates and the distributions are based on information taken from the pre-1982 literature (including several studies in press), specimens I examined in museum collections (particularly the National Museum of Natural History (USNM), Australian Museum, California Academy of Sciences, Academy of Natural Sciences of Philadelphia, and Bishop Museum), and information supplied by colleagues based on their unpublished studies or examination of collections under their care. In most instances restricted (exact) localities were plotted, but it will be recognized that the diameter of the symbols used to indicate localities cover a radius of 50–100 km on the maps. In some instances I have had to indicate generalized distributions, but I prefer, and strongly recommend to others, plots of specific localities in compiling distribution maps. Usually, no attempt was made to verify identifications or locality records taken from the literature unless there was reason to doubt their validity (for instance, a conspicuous separation of a locality record for a taxon from all other records for the taxon, especially if the record was on the Pacific Plate). After investigation, many of the questionable locality records proved to be erroneous or suspicious on additional grounds. A number of these emanated from specimens that were procured for the now defunct Museum Godeffroy of Hamburg and were reported on by A. Günther and R. Kner in the late 19th Century. If I did not accept a locality record I give my reasons in the discussion under the pertinent family account. Although I attempted to make the distribution maps exhaustive, I recognize that I probably missed numerous records. I personally plotted and compiled the information for most of the maps, but the data for a few were furnished by colleagues, and a few others were compiled by assistants under my close supervision.

TERMINOLOGY.—Because my usage of certain terms varies somewhat from traditional usage, these terms are defined below.

Shorefishes: In general, warm-temperate to tropical fishes dwelling at depths to about 100 m close to shore. Shallow-dwelling fishes that are typically restricted to the offshore oceanic (epipelagic) realm (for instance, Molidae) are excluded, as are some typically deep-dwelling forms (for instance Myctophidae) that often occur at shallow depths near shore.

Indo-Pacific (*not* synonymous with Indo-West Pacific): The Indian Ocean, including contiguous seas, and the Pacific Ocean as far east as Easter Island, but excluding the area occupied by the coast and offshore islands (Guadalupe, Revillagigedos, Clipperton, Galapagos, San Felix, San Ambrosio, Juan Fernandez, etc.) of the Western Hemisphere.

Eastern Pacific: The eastern portion of the Pacific Ocean not included in the Indo-Pacific.

Western Pacific: The Pacific ocean west of the western margin of the Pacific Plate (mostly composed of inland seas: South China Sea, Arafura Sea, Coral Sea, etc.); depending on the context used, may also include the area along the western margin of the Pacific Plate (see "Pacific Plate Distributions").

Indo-West Pacific: Indian Ocean plus "western Pacific," *not* synonymous with Indo-Pacific. The area of the Indo-Pacific that is always excluded from the Indo-West Pacific is the nonmarginal portion of the Pacific Plate.

PACIFIC PLATE DISTRIBUTIONS.—Except as noted, I consider any taxon that occurs on the nonmarginal portions of the Pacific Plate to have a Pacific Plate distribution. If such a taxon is limited to the Pacific Plate or to the Pacific Plate and localities on other plate margins adjacent to the Pacific Plate margin, it is considered to be endemic to the Pacific Plate. On the other hand, Indo-West Pacific taxa that reach their eastern distributional limits at localities on the western margin of the Pacific Plate are not considered to have Pacific Plate distributions. The Pacific Plate is subducting the Indian-Australian Plate, and some portions of the latter plate are situated well east of the Pacific Plate margin; for instance, the continental shelf of New Zealand, including the Chatham Islands. Taxa occurring on the New Zealand continental shelf do not have a Pacific Plate component in their distribution unless they occur otherwise, and nonmarginally, on the Pacific Plate.

Easter Island is located on the Nasca Plate close to that plate's western margin, which is being formed at the crest of the East Pacific Ridge (as is also the eastern margin of the Pacific Plate). Because most Easter Island genera occur otherwise only in the Indo-Pacific, and are on the Pacific Plate, I recognize Easter Island taxa as part of the Pacific Plate assemblage, with one exception: eastern Pacific taxa (for instance, the fish family Girellidae) that reach their western distributional limits at Easter Island, are not considered to be Pacific Plate taxa. Some Pacific Plate taxa that have their western distributional limits along the western margin of the Philippine Plate, usually the northern portion of that margin, are considered to be Pacific Plate restricted. The reasons for this consideration are explained in the discussions of Types 1 and 2 endemism.

FAMILY-GROUP NAMES.—With the exception of Carapidae, I follow Steyskal (1980) for the spelling of family-group names of fishes. Steyskal informs me that his use of Carapodidae for this family was based on an erroneous treatment of the stem.

CLASSIFICATION.—I follow Compagno (1973a) for the classification and composition of the elasmobranchs (sharks and rays). Most of the other shorefish family groupings are those usually recognized in the ichthyological literature, and where I differ, I cite references, colleagues, or other reasons for my usage.

ABBREVIATIONS.—The following abbreviations are employed: FL = fork length; m.y. = million years; SL = standard length; TL = total length; NMNH = National Museum of Natural History, Smithsonian Institution; USNM = United States National Museum collections, Division of Fishes, NMNH.

ORGANIZATION OF THE STUDY.—The study is presented as follows: (1) consideration of shorefish distribution patterns within each family and of the distributions of other organisms; (2) a general descriptive synthesis of shorefish distributions on and off the Pacific Plate, with discussion of hypotheses for explaining those distributions; and (3) discussions of patterns of endemism on the Pacific Plate and the formation of hypotheses to explain those patterns.

Distributions of Indo-Pacific Organisms

Shorefishes

In the discussions that follow, families known to occur within the warm shallow waters of the Indo-Pacific region are presented. Their arrangement is alphabetical to facilitate locating them, and follows the listing in Table A (Appendix 2). The information given focuses on how the family distributions, and those of the taxa within the families, relate to the Pacific Plate. Attention is given to presumed erroneous Pacific Plate distributions that surfaced in the course of my investigations. These presumed erroneous distributions are tests of the validity of my proposition that the Pacific Plate is a biogeographic unit. The weight of evidence for this proposition was so heavy that I was able to presume distributions might be erroneous only because they represented exceptional occurrences of a taxon that was otherwise distributed only on or off the Plate. Subsequent examination of the records on other grounds tends to confirm the suspicion of error.

By treating the Pacific Plate as the "hole in a doughnut," one can define the Plate just as surely by what is absent as by what is present. For this reason I have presented distribution maps of numerous taxa (orders, families, genera, species) that reach the margins of the Plate but do not extend beyond. In some instances, ichthyologists have stated that the absence of a taxon from Oceania is a result of lack of collecting. I believe that the discussions and distribution maps will overwhelmingly demonstrate that such assumptions are often unwarranted.

One locality, the Hawaiian Islands, frequently represents an area where valid exceptional occurrences of taxa appear nonmarginally on the Pacific Plate. I term each such occurrence an "Hawaiian exception." Discussion of the Hawaiian Islands will be found in the section on endemism. Another exceptional area for the occurrence of taxa on the Pacific Plate is in the Eastern Caroline Islands chain, which I treat as the "Caroline Islands conduit." The conduit is discussed in the section on boundary effect.

ACANTHOCLINIDAE

This family is restricted to the Indo-Pacific, where it comprises three genera and about five species of small (largest species about 300 mm SL), rock or reef inhabiting forms. *Acanthoclinus*, with two species, occurs only in New Zealand, and possibly Australia (Glover, 1979:151). *Acanthoplesiops* contains two species and ranges from southern India eastwards to the Marshall Islands. *Acanthoplesiops* is poorly known, and only one species, the diminutive *A. hiatti*, occurs nonmarginally on the Pacific Plate, where it is recorded only from the Marshall Islands. *Belonepterygion* is monotypic (*B. fasciolatum*) and ranges from southern Japan and Taiwan (USNM collections) through the Philippines (USNM) to southern Queensland, Lord Howe Island, and New Caledonia (*Calliblennius rubescens* Aoyagi, 1954, new genus and species, from the Ryukyus, is a junior synonym of *B. fasciolatum*). See "Addendum."

ACANTHURIDAE

The surgeonfishes comprise six genera (Randall, 1955a and pers. comm.) and about 70 species of small- to moderate-sized (to about 700 mm TL), free-swimming, reef-inhabiting fishes with planktonic larvae.

Acanthurus contains about 35 species (Randall, 1956, 1960, and in litt.; Shen and Lim, 1973, described three additional species, not recognized here, based on what appear to be juvenile specimens of described species) and is the only acanthurid genus that is found in all warm seas.

Twenty-eight species of *Acanthurus* occur in the Indo-Pacific, of which three range into the eastern Pacific as well. Of the 28 Indo-Pacific species, eight are restricted to the Indo-West Pacific, and 20 occur nonmarginally on the Pacific Plate. One species, *A. dussumieri*, otherwise widely distributed in the Indo-West Pacific, has been reported on

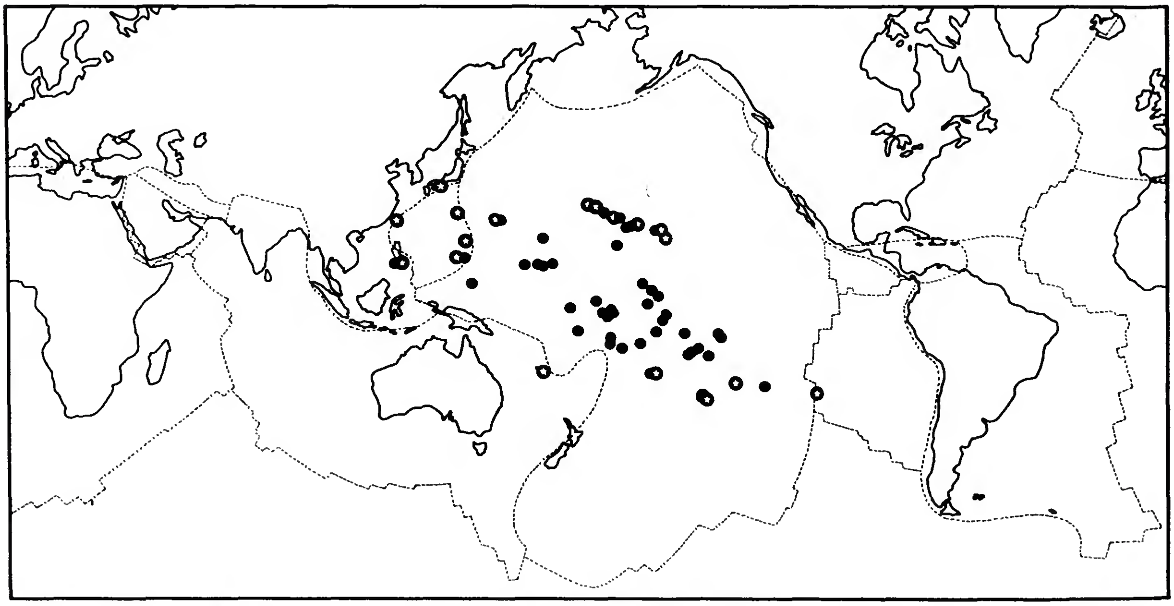

FIGURE 5.—Distribution of two widely distributed, Pacific Plate species of surgeonfishes, *Acanthurus achilles* (solid circles) and *A. leucopareius* (stars).

the Plate only from the Hawaiian Islands, but J.E. Randall informs me he sighted a specimen in the Line Islands in 1968. The species can probably be considered as an Hawaiian exception with occasional waifs appearing elsewhere on the Pacific Plate. Two species, *A. achilles* and *A. leucopareius* (Figure 5), should possibly be considered as widely distributed Pacific Plate endemics that have undergone a relatively recent westward dispersal which has enabled them to reach the western margin of the Philippine Plate (see section on geology of Pacific and Philippine plates). *Acanthurus achilles* is known nonmarginally off the Pacific Plate only from Cebu, Philippines (Rau and Rau, 1980), where it and *A. leucopareius* appear uncommonly in the fish market (N. Rau, in litt.). The distribution of *A. leucopareius* is also noteworthy because of its disjunct, antiequatorial nature (Randall's 1976 report of *A. leucopareius* from Lord Howe Island was in error; Marcus Island—on the Pacific Plate—was the intended locality; Randall, in litt.).

Acanthurus nigroris also appears to be a widely distributed Pacific Plate endemic, although Randall (in litt.) suggests that it may occur west of the Plate as a straggler (see Whitley, 1958, for a record from the Great Barrier Reef). There is one other Pacific Plate endemic species of *Acanthurus*, *A. chronixis*, known only from Kapingamarangi, Eastern Caroline Islands (Randall, 1960, and pers. comm.; misidentified from New Guinea by Burgess and Axelrod, 1975, fig. 418 = *A. pyroferus*). The intrageneric relationships of the Plate endemic species of *Acanthurus* are unknown.

Ctenochaetus comprises six species (Randall, 1955c, 1960) and ranges throughout the Indo-Pacific, one species also reaching the eastern Pacific. At least five of the species occur on the Pacific Plate nonmarginally, and one, *C. hawaiiensis*, is a widely distributed Pacific Plate endemic, known from the Mariana, Marcus, Marshall, Hawaiian, Line, Austral, Society, Samoa, Tuamotu, and Pitcairn Group islands.

Naso (including *Axinurus* and *Callicanthus*) contains about 16 species (Smith, 1966a; Randall and Struhsaker, 1981; J.E. Randall, in litt.), of which at least nine extend onto the Pacific Plate nonmarginally (eight ranging from the east coast of Africa, and one restricted to Japan and the Hawaiian Islands). The other seven species are restricted to various parts of the Indo-West Pacific, and some are of questionable validity.

Prionurus (including *Xesurus*) has six species, of which two are limited to the eastern Pacific, one to the eastern Atlantic, and three to the western Pacific (Smith, 1966a). *Prionurus* is the only acanthurid genus that is absent from the nonmarginal portions of the Pacific Plate.

Paracanthurus is monotypic (Randall, 1955b) and ranges throughout the Indo-Pacific, from the east coast of Africa to at least the Line Islands (Chave and Eckert, 1974), but it is absent from the Hawaiian Islands.

Zebrasoma contains seven species. Randall (1955b) recognized six species, but now (in litt.) recognizes a seventh, *Z. desjardinii*, for the Indian Ocean populations of the species he treated as *Z. veliferum* from the Indo-Pacific. Two other species (*Z. gemmatum*, *Z. xanthurum*) are restricted to the Indian Ocean, and one species (*Z. scopas*) ranges from the western Indian Ocean to the Society Islands. *Zebrasoma rostratus* is a Pacific Plate endemic known positively only from the Tuamotu, Marquesas, Line, and Rapa islands. *Zebrasoma flavescens* should possibly be considered a Plate endemic; it has been reported from Taiwan and the Ryukyu Islands, along the western margin of the Philippine Plate, where it appears to be uncommon, east to the Bonin, Mariana, Marshall, Wake, Marcus, Hawaiian, and Johnston islands.

In summary, there are five genera and 64 Indo-Pacific species of acanthurids, of which 39 species occur on the Pacific Plate nonmarginally, and possibly seven of these 39 are Plate endemics.

ALBULIDAE

The bonefishes comprise two genera (Forey, 1973): *Pterothrissus* (sometimes placed in its own family, Pterothrissidae) with two, moderately deepwater species (one known from off Japan, the other from off west Africa), and *Albula*, with perhaps as many as six species, several of which have been confused with one of the two currently recognized species, *A. vulpes* (Shaklee and Tamaru, 1981, and Shaklee, pers. comm.).

Albula is distributed circumglobally (as are, perhaps, two of its species), and occurs close to shore, where it is avidly sought by sportfishermen; larvae are taken pelagically.

AMBASSIDAE

The ambassids are a family of small fishes in need of revision. There are 40 nominal species (R.P. Vari, pers. comm.), but perhaps only 20 valid species, which usually occur in estuarine and mangrove areas. The ambassids have been reported to range from the east coast of Africa to the Philippines, southern Japan, Guam, and Samoa, on the margin of the Pacific Plate, and are known to occur on the Pacific Plate nonmarginally only at Ponape (*Ambassis*; USNM collections). The presence of ambassids at Ponape is evidence favoring the operation of the Caroline Islands conduit.

AMMODYTIDAE

The sand lances are a small family of small fishes that are antitropically distributed: widely distributed in the warm-temperate marine waters of the northern hemisphere, but known only in the Indo-Pacific in the southern hemisphere, where they occur in southern Africa, southern Australia (as far north as southern Queensland), and Pitcairn Island (where they were collected along shore; J.E. Randall, in litt.). Aside from Pitcairn, they are known on the Pacific Plate nonmarginally only from the Hawaiian Islands, where a few specimens of *Bleekeria gilli* have been obtained from tuna spewings (Gosline and Brock, 1960); hence, the species is probably pelagic offshore. *Bleekeria gilli* also is reported from the Galapagos (Seale, 1940) and Baja Calfornia (Duncker and Mohr, 1939). Fowler (1928) believed the unknown type locality of *B. gilli* was probably the Bonin Islands. The appropriateness of including the Ammodytidae among the warm-water shorefish families is questionable.

ANGUILLIDAE

The freshwater eels consist of a single genus, *Anguilla*, with 16 species (Ege, 1939) that spawn in deepwater well out to sea, and have long-lived planktonic larvae. The young ascend rivers and attain maturity in freshwaters. The largest species attains a length of about 2 m. The anguillids are widely distributed in the tropical and temperate waters of the Indo-Pacific and north Atlantic, but are absent from the eastern Pacific, most of the west coast of Africa, and almost all of the Atlantic coast of South America (for a world distribution map see Schmidt, 1925; for distribution maps of the Indo-Pacific species see Ege, 1939).

Fourteen of the *Anguilla* species are limited to the Indo-Pacific, and of these, only three (none endemic) occur on the Pacific Plate nonmarginally. Although *Anguilla* is widely distributed on the Pacific Plate, the genus is notably absent from the Hawaiian Islands.

ANOMALOPIDAE

The flashlight fishes comprise four monotypic genera of small (to about 300 mm TL), reef-inhabiting fishes. Two genera are restricted to the Indo-Pacific, one to the eastern Pacific, and one to the Caribbean. Records of flashlight fishes are relatively few because, until recently, the habits of the species, which reside in deep crevices in the daytime and enter shallow waters only on moonless nights, make them generally unavailable to collectors. On the Pacific Plate, nonmarginally, they are known only from Kwajalein (Marshall Islands; *Photoblepharon*; J.E. McCosker, pers. comm.), Rarotonga (Cook Islands; *Anomalops*; Seale, 1906), and the Tuamotus (*Anomalops*; Günther, 1876). Both *Anomalops* and *Photoblepharon* occur in the Banda Islands, Moluccas, and I have seen and participated in collections of both genera on the same night on the same reef at Mactan Island, Philippine Islands. *Anomalops* has not been reported from the Indian Ocean, but *Photoblepharon* ranges westward to the Red Sea (which has an endemic subspecies of *Photoblepharon*) and Comoro Islands.

ANTENNARIIDAE

The frogfishes comprise 12 genera and 40 species of small- to moderate-sized fishes (to about 360 mm SL) that are (with one exception) benthic, shallow to moderately deep dwelling, and occur primarily on rocky and coral reefs. A few species may occasionally enter brackish water. Ten genera are restricted to the Indo-Pacific and about 30 species occur in that region, but only nine species occur on the Pacific Plate nonmarginally, and of these, only *Antennarius duescus*, known from two specimens from the Hawaiian Islands, is apparently endemic to the Plate. (T. Pietsch, in litt., and pers. comm.)

One antennariid, *Histrio histrio*, occurs only in floating *Sargassum*, and has the potential for widespread distribution. *Histrio histrio* is often cited as cosmopolitan in warm seas, but its distribution appears to be restricted to the Atlantic and Indo-West Pacific. There are four reports of *H. histrio* from the Pacific Plate and one from the eastern Pacific (Galapagos). I consider all five suspect. Fowler (1928, 1931) reported *H. histrio* from Raiatea and Huahine, both Society Islands, on the Pacific Plate, based on listings of *Antennarius marmoratus* and *A. multiocellatus* in Shmeltz (1877, 1879; references examined for me by W.F. Smith-Vaniz). Shmeltz's papers are catalogs of the Museum Godeffroy collections, and the catalogs contain no descriptive material or illustrations. Fishes in the Godeffroy collections were obtained by commercial collectors and boat captains, and localities assigned many Godeffroy specimens have proved to be well outside the established ranges for the species and not confirmed by prior or subsequent collecting. The location of the Godeffroy specimens supposedly representing *Histrio* is not known. Fowler gave no reasons for recognizing the Godeffroy specimens as *H. histrio*, and Randall (1973), who spent many months collecting in the Society Islands, did not report *Histrio* from those islands. T. Pietsch, who has revised the antennariids, saw no material of *Histrio* from the Societies. Without reconfirmation, I consider the presence of *Histrio* in the Society Islands to be unsubstantiated.

It is noteworthy also that R.C. Wass, who has spent several years in the Samoan Islands and concentrated on obtaining records and specimens of all Samoan fishes, has not obtained *Histrio* in Samoa. *Histrio* is known at Guam (on the eastern margin of the Philippine Plate) from only two specimens taken about ten years apart (R.S. Myers, in litt.) in spite of many years of intensive collecting at that island. There are no records of *Histrio* from Palau.

Eydoux and Souleyet (1842) described *Chironectes barbatulus*, a synonym of *H. histrio*, and stated that they were unable to give the locality of origin for their specimen. Le Danois (1964), without explanation, listed the type locality of *Chironectes barbatulus* as Hawaii. Dr. M.L. Bauchot (in litt.) reconfirmed the lack of associated locality data with the holotype of *C. barbatulus*. Schultz (1957) reported *H. histrio* from the Hawaiian islands based on specimens labelled as having been taken by the Wilkes Expedition of 1838–1842 at Maui. There are no subsequent reports of *Histrio* from the Hawaiian Islands in spite of many years of intensive collecting in those islands, even though *Sargassum* is present. If *Histrio* occurs in the Hawaiian Islands it probably does so as a straggler brought in by ocean currents (Kuroshio Extension) from Japan.

Schultz (1957) also reported *Histrio* from the Galapagos based on specimens first cataloged at USNM in 1877, and listed as having been collected by a Captain Heerendeen (or Herrendea, inscription unclear) of Woods Hole, Massachusetts. There are no other records of *Histrio* for the eastern Pacific. In accord with R.H. Rosenblatt (pers. comm.), I do not believe that the species occurs in the Galapagos or elsewhere in the eastern Pacific.

It is of interest that *Sargassum* is reported from many of the high islands (including at least Hawaii, Tahiti, Ponape) on the Pacific Plate, but with the exception of Laysan Atoll (Hawaiian Islands) is noticeably absent from low islands (Doty, 1954; Tsuda, 1976).

APLOACTINIDAE

The velvetfishes comprise about 15 genera and about 25 species that appear to live on rocky or coral rubble bottoms, bottoms with coralline algae, or among vegetation (Poss and Eschmeyer, 1978, 1979, 1980; Eschmeyer and Allen, 1978; Eschmeyer and Dor, 1978) at depths from near shore to 510 m, and are found only in the Indo-West Pacific; none occurs on the Pacific Plate.

APOGONIDAE

The cardinalfishes comprise about 20 genera and over 200 species of small (to about 553 mm SL for *Epigonus*, a pelagic genus, but most reef forms are well under 200 mm), predominantly coral-reef fishes, with some deep-dwelling or pelagic species and some estuarine and freshwater species. A revision of the most speciose genus, *Apogon*, is greatly needed. As far as known, the species are all mouth brooders, and larvae are restricted to shelf waters (T.H. Fraser, pers. comm.). The family is distributed circumglobally, with most species occurring on the reefs of the Indo-Pacific. Many of the species are wide ranging; for instance, *Apogon kallopterus*, a known mouthbrooder, ranges from the east coast of Africa to the Hawaiian, Marquesas, and Tuamotu islands (Fraser, pers. comm.). Even more spectacular, *Apogon evermanni*, a moderately deep-dwelling reef form (available to SCUBA-equipped divers), is known from the Hawaiian Islands (Hawaii, Oahu), the Marquesas (Nuku Hiva, Fatu Hiva), Kwajalein (Marshalls), Florida Island (Solomons), Ambon (Moluccas), Maldives, Chagos, Cocos-Keeling, and Mauritius (all Indian Ocean), and Cozumel, Curaçao, and Bahamas (all western Atlantic; Randall and Böhlke, 1981). T.E. Fraser informs me that there is a rapid dropoff in the number of apogonid species as one crosses the western margin of the Pacific Plate from the west. He notes that there are endemic apogonids in various Pacific Plate island groups (Hawaiian, Marquesas, Easter), but that he knows of no widely distributed Pacific Plate endemics. There are probably no more than 50 species of Apogonidae on the Plate.

The apogonids demonstrate that mouth brooding is obviously not a factor limiting distributions, although the absence of the mouth-brooding families Ariidae and Opistognathidae from the Pacific Plate might be ascribed to such a habit.

ARACANIDAE

The aracanid trunkfishes comprise eight genera and about 12 species of small (to about 30 mm TL), often moderately deep-dwelling, benthically associated fishes. The family has a primarily antitropical distribution, is restricted to the Indo-West Pacific, except for its exceptional occurrence in the Hawaiian Islands, and is questionably included here as a shorefish group. *Aracanostracion* is known only from southernmost Africa; *Aracana*, *Anoplocapros*, *Caprichthys*, and *Capropygia* are limited to the cooler coasts of Australia; *Polyplacapros* is known from a seamount east of New South Wales (132 m deep) and along the Norfolk Ridge (ca. 167°33′E, 28°–33°S; 79–161 m); *Strophiurichthys* occurs in Queensland (at depths to about 64 m) and has been reported erroneously from the Solomon Islands (Randall, in press b); and *Kentrocapros* (presently monotypic) is known from Japan (Sagami Bay south to Kyushu), Korea (Pusan), Taiwan (20–30 m depth), the Hawaiian islands (from at least 104 m depth), and presumably, from off eastern Australia (Fujii and Uyeno, 1979).

The distribution of the Aracanidae, which is often considered as a subfamily of the Ostraciidae, contrasts strongly with the distribution of the Ostraciidae (sensu stricto), which occur circumglobally in primarily warm, shallow seas.

ARIIDAE

The marine catfishes comprise about 140 species of moderate size that are distributed circumglobally, except that none occurs on the Pacific Plate other than marginally. The eastern limits of the family in the Indo-Pacific are almost, if not entirely, identical with those of the croakers, Sciaenidae (Figure 38). As far as known, all the species have large eggs and are mouthbrooders (see discussion under Apogonidae), and most spend some portion of their life history in estuaries. Several species are restricted to freshwater, and it is probable that the family is derived from a freshwater ancestor (W.R. Taylor, pers. comm.).

There are three, notably erroneous, distribution records for ariids in the Indo-Pacific. *Arius tachycephalus* was described by Günther (1864) from Hawaii. This species is a common one limited to the eastern Pacific. Kner and Steindachner (1866) described *Arius graeffi* from Samoa, based on a Museum Godeffroy specimen, and Schmeltz (1879, reference examined for me by W.F. Smith-Vaniz) listed *Arius thalassinus* from the Tonga Islands, also based on a Museum Godeffroy specimen. No other records of ariids are known for Samoa and Tonga, and there is none for the nearby, and larger, Fiji Islands.

ATHERINIDAE

The silversides are a large, circumglobal family of small, free-swimming, close-shore fishes. Most of the species are marine, but some are strictly freshwater (Celebes, North America) inhabitants. There are four marine genera with about 18 species in the Indo-Pacific. All the genera, but only six of the species, occur nonmarginally on the Pacific Plate, and one of the species is endemic to the Hawaiian Islands. (W. Ivantsoff, pers. comm.).

AULOSTOMIDAE

The trumpetfishes comprise a single genus, *Aulostomus*, and three species (Wheeler, 1955): one limited to the western Atlantic, one to the eastern Atlantic, and one to the Indo-Pacific (including the Pacific Plate nonmarginally) and eastern Pacific. In the latter area it is known only from offshore islands (Rosenblatt et al., 1972). The species of *Aulostomus* are slender, less than 1 m TL, free swimming, and reef inhabiting.

BALISTIDAE

(not including Monacanthidae)

The triggerfishes comprise 12 genera (Matsuura, 1980; 1981) and about 30 moderately large (to about 750 mm TL), free-swimming species with pelagic young. All the genera, except *Xenobalistes*, and most of the species occur in the Indo-Pacific; however, *Balistes*, otherwise restricted to the Atlantic and eastern Pacific, occurs in the Indo-Pacific only in the Hawaiian Islands and only as a rare straggler (the common eastern Pacific species *Balistes polylepis*, which has usually been misidentified as *B. fuscus* in Hawaiian references; J.E. Randall, pers. comm.; I have not included *Balistes* in Appendix 2, Table C). All but one of the native Indo-Pacific genera, *Abalistes*, monotypic, occur on the Pacific Plate, but not all the Indo-Pacific species in these genera occur on the Plate.

Odonus and *Balistapus* are monotypic, widely distributed in, and restricted to, the Indo-Pacific. *Xenobalistes*, also monotypic, is known from a single specimen from the stomach of a marlin caught off the Mariana Islands.

Canthidermis contains five species (Fedoryako, 1981), one (*C. maculatus*) present on the Pacific Plate and distributed in all oceans but the eastern Pacific; one (*C. villosus*) known only from the Gulf of Aden, one (*C. rotundatus*) limited to the Indo-Pacific), one (*C. willughbeii*) restricted to the eastern Pacific, and one (*C. sufflamen*) restricted to the western Atlantic.

Pseudobalistes contains three species, two (*P. fuscus*, *P. flavimarginatus*) occurring on the Plate as well as widely distributed in, and restricted to, the Indo-Pacific, and one (*P. naufragium*) restricted to the eastern Pacific.

Melichthys contains three species (the first two being present on the Plate): one is circumtropically distributed, one is limited to the Indo-Pacific and eastern Pacific, and one is limited to the Indian Ocean (Randall and Klausewitz, 1973).

Abalistes stellatus is a common, widely distributed triggerfish that occurs in a wide variety of marine habitats, including coral reefs and over sandy and muddy bottoms. It ranges from the Red Sea and southeastern South Africa eastwards to Japan (Honshu), New Guinea, New Ireland, and Fiji, but is absent from the Pacific Plate nonmarginally.

Xanthichthys comprises five species (Randall, Matsuura, and Zama, 1978). One species (*X. ringens*) is restricted to the western Atlantic, and four are found in the Indo-Pacific, but one of the four (*X. lineopunctatus*) has not been taken on the Pacific Plate nonmarginally. Another (*X. mento*) is distributed from the eastern Pacific only as far west as the Ryukyu and Izu islands along the western margin of the Philippine Plate. The distribution of these last two species emphasizes the biogeographic boundary between the continental and oceanic plates.

Balistoides contains two species, both present on the Plate and widely distributed in and restricted to the Indo-Pacific.

Sufflamen comprises four species, three present on the Plate and restricted to, and widely distributed in, the Indo-Pacific, and one restricted to the eastern Pacific.

Rhineacanthus is restricted to the Indo-Pacific and comprises about six species (one undescribed, J.E. Randall, in litt.), of which at least three occur on the Pacific Plate nonmarginally.

BATRACHOIDIDAE

The toadfishes comprise 19 genera and 64 species of small to moderate size, few, if any, attaining a standard length of 400 mm (B.B. Collette, pers. comm.). The species are all primarily benthic in habit and most, if not all, occur at shallow depths during some period of their life history. Gilbert (1968) quotes a responsible report of an unidentified species of *Porichthys* that was seen in numbers at the surface of waters at least 1000 fathoms (1829 m) deep 30 miles (50 km) off the Pacific coast of Panama. Gilbert may have been referring to the same incident as mentioned in Walters and Robins (1961) of *Porichthys* being rafted on logs 25 miles (40 km) from land in the Gulf of Panama. Adult *Porichthys* may also occur at very shallow depths. Variously, the species of

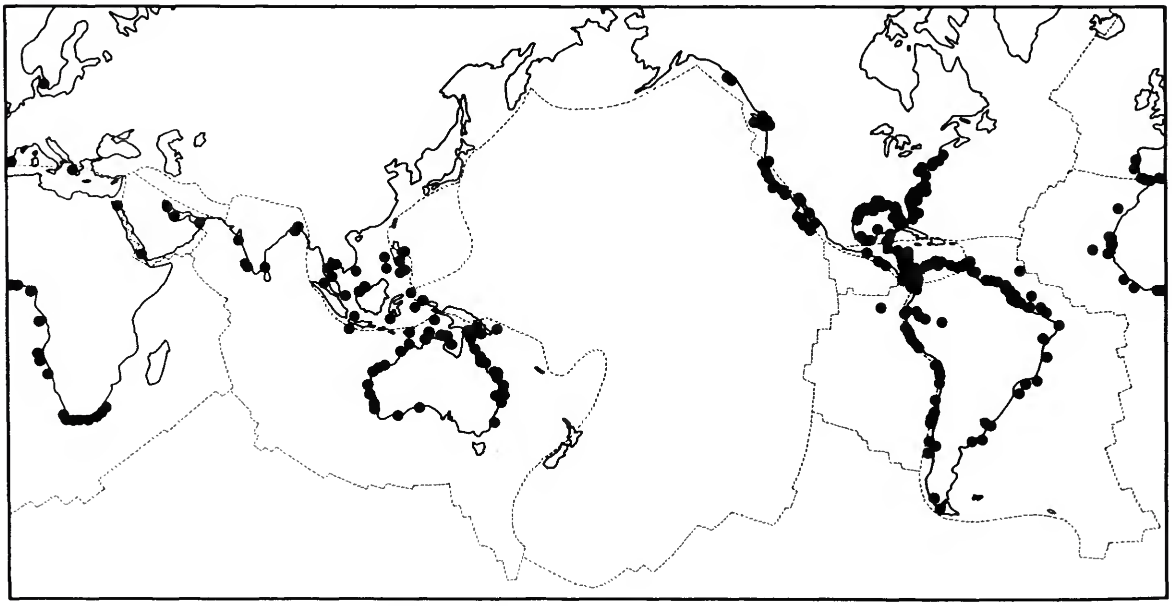

FIGURE 6.—Distribution of the toadfish family Batrachoididae.

batrachoidids occur in, or are restricted to, a variety of habitats: freshwater rivers, estuaries, coral reefs, rocky or shelly marine bottoms, muddy sand, and in the intertidal, where they may even be stranded out of water for several hours without harm. Eggs are deposited in, and attached to, almost any type compartment: jars, shells, holes, cans, crevices. Nests are guarded and the young, upon hatching, are demersal.

Mead (1970) believed that the toadfishes are distributed worldwide. Toadfishes are widely distributed latitudinally and longitudinally, but are notably absent from the Pacific Plate (Figure 6). The largest numbers of genera and species of toadfishes are found in the western Atlantic (seven genera, 25 species, plus three more species in Atlantic freshwater drainage systems). Only three genera and about nine species occur in the Indo-West Pacific, excluding the highly restricted five endemic genera from southernmost Africa (Collette and Russo, 1981; Hutchins, 1976). The apparent absence of toadfishes from most of the Indian Ocean coast of Africa, and from the coasts of Madagascar and mainland China is surprising.

BELONIDAE

The needlefishes comprise nine genera and 30 species of epipelagic fishes found in freshwaters, estuaries, and marine habitats, both inshore and offshore. Needlefishes have a maximum body length ranging from 42 mm (two South American freshwater species) to 950 mm for one worldwide marine species, *Tylosurus acus*, which consists of five well-differentiated subspecies (one western Atlantic, one Mediterranean, one eastern Atlantic, one eastern Pacific, and one Indo-Pacific; the Indo-Pacific subspecies extends eastwards to the offshore eastern Pacific islands of Cocos and Revillagigedós; Collette and Parin, 1970). Needlefish eggs bear entangling filaments and are demersal unless attached to floating objects (summarized in Breder and Rosen, 1966).

Cressey and Collette (1971) give distribution maps for many of the needlefish species. Collette (pers. comm.) has many more Indo-Pacific records for *Tylosurus acus* than are indicated on Cressey and Collette's figure 177, which might otherwise appear to indicate an example of an Hawaiian exception distribution.

Strongylura, the most speciose genus of needlefishes, comprises 13 species, of which two are strictly freshwater, one estuarine, and ten marine, many of which ascend freshwaters. Five species of *Strongylura* (four marine, one estuarine) occur in (and are limited to) the Indo-Pacific, but only one, a marine species (*Strongylura incisa*), extends nonmarginally onto the Pacific Plate (Cressey and Collette, 1971). *Strongylura incisa*, together with the four worldwide species (*Ablennes hians*, *Platybelone argalus*, *Tylosurus acus*, *T. crocodilus*), make a total of five species of needlefishes present on the Pacific Plate.

Aside from the two worldwide species of *Tylosurus*, there are three other species of *Tylosurus*: *T. choram*, known only from the Red Sea and northwestern Indian Ocean, *T. gavialoides* from northern Australia, and *T. punctulatus*, from the Malayan and Philippine area. The five species of *Tylosurus*, the five marine and estuarine species of *Strongylura*, and the monotypic *Ablennes* and *Platybelone* comprise the 12 species of needlefishes found in the Indo-West Pacific.

BLENNIIDAE

The blennies are a circumglobal family that comprises five tribes, 54 genera, and about 300 species of small (maximum adult sizes ranging from about 15 to 532 mm SL, but few exceed 150 mm), predominently near-shore, benthic fishes. Most of the species are restricted to warm marine waters, but a few species occur in temperate marine or warm freshwaters. As far as known, all the species are nest builders, and although prejuveniles of several species may occur planktonically a short distance offshore, the unmetamorphosed young are generally taken with the adults. Individuals of a few species have been taken around floating sargassum or other objects, and one Indo-West Pacific species (*Omobranchus punctatus*), of an otherwise Indo-Pacific restricted genus, occurs in the Caribbean, possibly as a result of an introduction (Springer and Gomon, 1975).

TABLE 1.—Distribution of numbers of genera and species in the tribes of the fish family Blenniidae in the Indo-Pacific[a]

Tribe	Number of genera	Genera in Indo-Pacific[b]	Genera on Pacific Plate[c]	Genera endemic to Pacific Plate[c]
Blenniini	16	3	1	0
Salariini	26	24	14	1
Omobranchini	6	6	4	0
Phenablenniini	1	1	0	0
Nemophini	5	5	5	0
Totals	54	39	24	1

Tribe	Number of species	Species in Indo-Pacific[b]	Species on Pacific Plate[c]	Species endemic to Pacific Plate[c]
Blenniini	70[a]	13[a]	1	0
Salariini	150[a]	141[a]	45[a]	25[a]
Omobranchini	31	31	5	0
Phenablenniini	1	1	0	0
Nemophini	41	40	11	2
Totals	293	226[b]	62	27[d]

[a] Estimated.

[b] Includes Easter Island.

[c] Other than only marginally present, but includes Easter Island.

[d] Twenty-one known: seven only at Hawaiian Islands, four only at Marquesas, two only at Easter Island, one only in Tuamotus, and seven more widely distributed.

All of the tribes, 72 percent of the genera, and 77 percent of the species occur in the Indo-Pacific (Table 1), and all but one of the tribes, Blenniini, have their centers of taxonomic abundance in that area. The Blenniini, in contrast, has its largest representation in the Western Hemisphere and Mediterranean, where the other tribes are poorly represented or absent. The Salariini is represented in the Western Hemisphere and eastern Atlantic by only three genera: *Entomacrodus*, which is circumtropical; *Ophioblennius*, which is restricted to the Western Hemisphere and eastern Atlantic; and *Scarticthys*, which is restricted to the eastern Pacific. The Nemophini is represented outside the Indo-Pacific by only one of the 11 species of *Plagiotremus*, *P. azaleus*, which is endemic to the eastern Pacific. The Omobranchini and Phenablenniini occur only in the Indo-Pacific (except for the presumably introduced species of *Omobranchus* in the Caribbean).

Blenniini: This is the least specialized tribe of blenniids, and probably is not monophyletic, as there is no specialization that unites its components. The presence of an unidentified species of *Parablennius* in the Hawaiian Islands (reported here for the first time based on specimens from Oahu I examined at the Hawaii Institute of Marine Biology many years ago) constitutes an example of an Hawaiian exception, pertaining, in this case, to a tribe, genus, and perhaps species that are otherwise absent from the Pacific Plate. A revision of *Parablennius* (which includes *Pictiblennius*; H. Bath, in litt.) will be necessary before it will be possible to identify the Hawaiian species.

Springer (1967b) and Strasburg (1956) discussed the erroneous reports from the Hawaiian Islands of the eastern Pacific species *Hypsoblennius sordidus* and *H. brevipinnis*.

Salariini: *Alloblennius* contains four species and is restricted to the western Indian Ocean and Red Sea (Springer and Spreitzer, 1978; H. Bath, ms.).

Alticus is in need of revision, but ranges over much of the Indo-Pacific. An endemic species occurs in the Marquesas Islands on the Pacific Plate (Smith-Vaniz and Springer, 1971).

Andamia is in need of revision. It ranges from the eastern Indian Ocean to the western margin of the Pacific Plate in the New Guinea region (Smith-Vaniz and Springer, 1971; Springer, unpublished data).

Antennablennius, which has been revised by H. Bath (ms.), contains seven species and is restricted to the Red Sea and Indian Ocean (Smith-Vaniz and Springer, 1971).

Atrosalarias is monotypic, but with two allopatric subspecies: one restricted to the Indian Ocean and Red Sea, the other ranging from Western Australia to well out on the Pacific Plate (Springer and Smith-Vaniz, 1968; Smith-Vaniz and Springer, 1971).

Cirripectes, which ranges throughout the Indo-Pacific, is being revised by J.T. Williams, who informs me that two (of the approximately 25) species are widely distributed Pacific Plate endemics: *Cirripectes jenningsi* from the Gilbert, Tokelau, Phoenix, Line and Tuamotu islands; *Cirripectes variolosus*, with representation in every major nonmarginal island group on the Plate (except the Pitcairn Group and Hawaiian Islands) and from Guam, the Palaus, and the Tonga Islands, all adjacent to the margin.

Cirrisalarias is monotypic and ranges from the Comoro Islands, Indian Ocean, to Samoa, on the margin of the Pacific Plate (Springer and Spreitzer, 1978:1). See *Medusablennius* below.

Crossosalarias is monotypic and is known from the Ryukyu Islands south to the Moluccas and eastward to New Guinea and southeast to the Tonga Islands; hence, it is absent from the Pacific Plate nonmarginally (Smith-Vaniz and Springer, 1971; USNM).

Dodekablennos is monotypic and known only from Mauritius (Springer and Spreitzer, 1978).

Ecsenius comprises about 30 species (including undescribed forms) of predominently benthic coral-reef inhabitants (Springer, 1971, 1972a; McKinney and Springer, 1976). Each of two species (*E. opsifrontalis*, *E. oculus*) consists of several recognizably distinct, allopatric color-pattern populations (McKinney and Springer, 1976). *Ecsenius* species are known from depths of less than one to about 45 m. Only three species occur other than marginally on the Pacific Plate, and two of these, *E. midas* and *E. bicolor*, have the greatest overall ranges of any of the species of *Ecsenius*. *Ecsenius midas* (east coast of Africa to the Marquesas) is one of the few species of *Ecsenius* that rises above the bottom and becomes free swimming; *E. bicolor* (Maldives to Marshall and Samoan islands), however, is closely tied to the substrate. The third Plate species, *E. opsifrontalis* (not free swimming) consists of several color-pattern populations. The population of *E. opsifrontalis* on the Pacific Plate consists of a color-pattern type that is restricted to the Plate and its margins (Springer and Bruwelheide, unpublished data). The other color-pattern populations of *E. opsifrontalis* are restricted to Pacific areas west of the Plate or on the Plate margin.

Entomacrodus comprises 22 species (several species consist of unnamed, but recognizably distinct populations; Springer, 1967a, 1972a, and unpublished data) that live in the shallows adjacent to shore and in the intertidal. Of the 17 Indo-Pacific species, 13 occur nonmarginally on the Pacific Plate, and I consider nine of these to be endemic to the Plate (including margins and Philippine Plate; Figures 7, 8). Two of the endemics, *E. cymatobiotus* and *E. sealei*, are widely distributed. Springer (1972a) noted that a specimen of *E. sealei*, the only one known from New Guinea, had a different color pattern from all other available specimens of the species, and questioned if the color pattern was normal. A second specimen, exhibiting the same peculiarities of color pattern, from Indonesia (Ternate, Halmahera; USNM collections) was recently obtained. *Entomacrodus sealei*, thus consists of two allopatric color-pattern types that are separated along the western margin of the Pacific Plate. *Entomacrodus caudofasciatus*, which I do not include among the Plate endemics, embraces five color-pattern types (Figure 7), of which one is widely distributed along the southern island chains on the Pacific Plate, and a second, which I reported (1967a) from two widely separated groups of localities, might also prove to

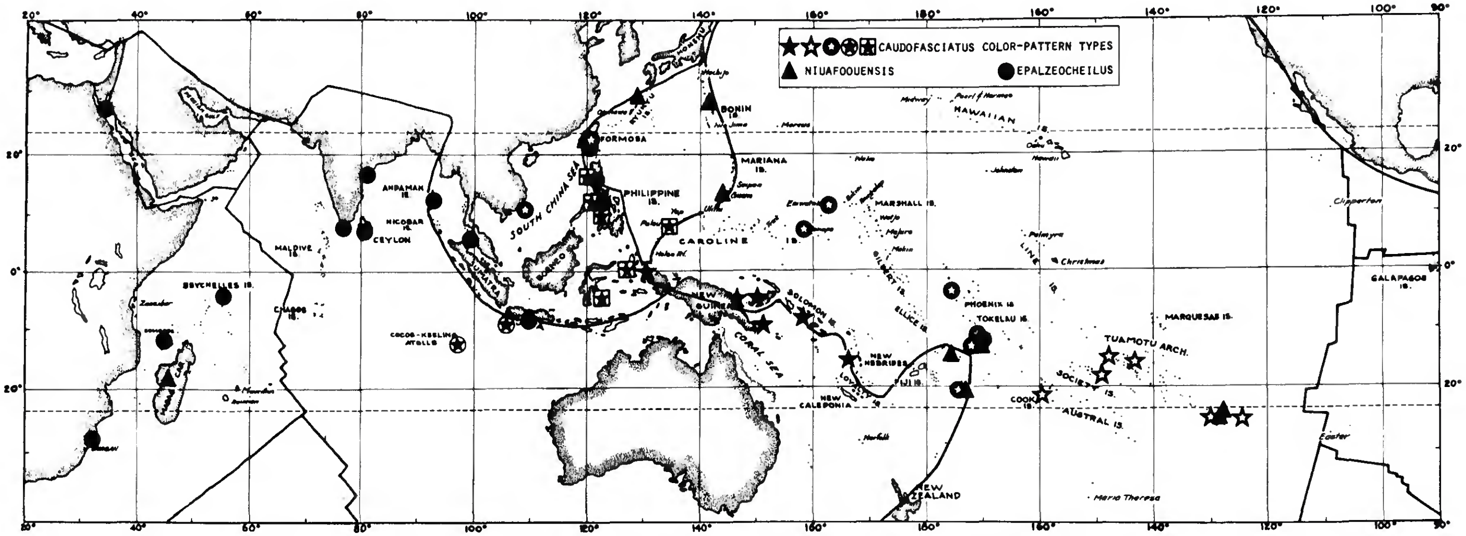

FIGURE 7.—Distributions of certain species of the blenniid fish genus *Entomacrodus*.

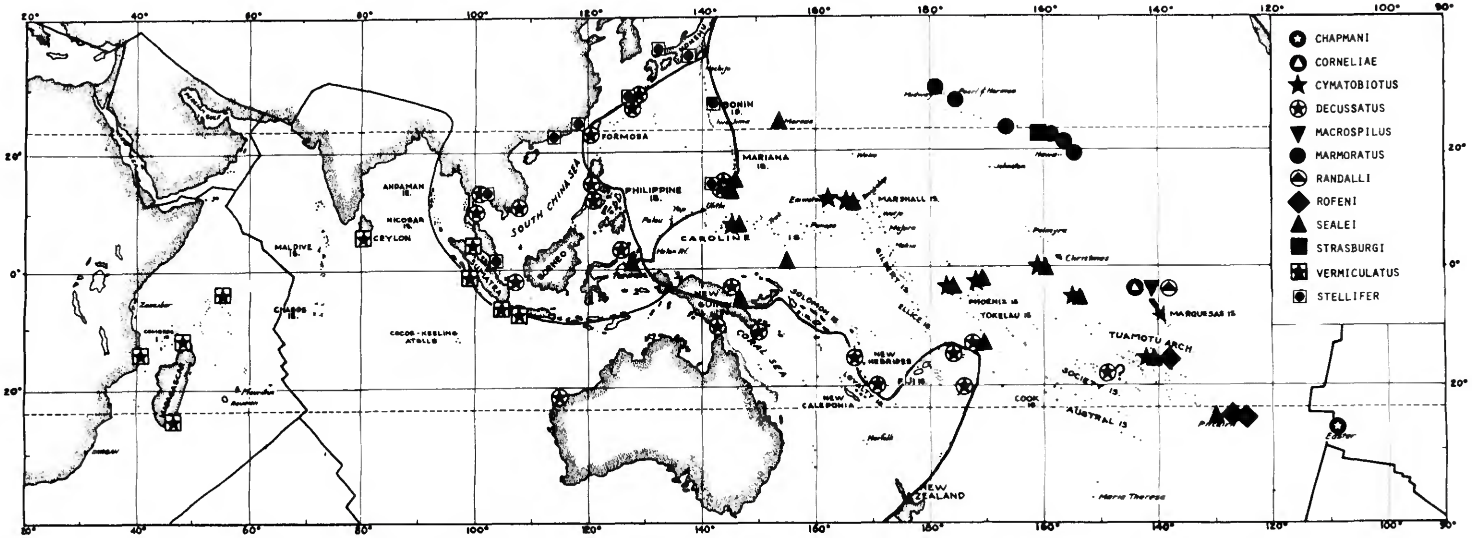

FIGURE 8.—Distributions of certain species of the blenniid fish genus *Entomacrodus*; specimens of *E. sealei* from Ternate and New Guinea have a different color pattern from that of specimens from other localities.

be Plate restricted if a reappraisal shows my lumping of the color patterns from the separated localities to be in error.

Springer (1967a) considered three species of *Entomacrodus* to form a closely related group, which is restricted to the Pacific Plate: *E. cymatobiotus* (widely distributed, but absent from the Hawaiian Islands and Easter Island), *E. strasburgi* (known only from Oahu), and *E. chapmani* (known only from Easter Island). The group was not defined on the basis of a shared specialization and the sister species group was not proposed. The three species are quite similar and I intuitively believe they form a monophyletic group.

Exallias is monotypic and ranges throughout most of the Indo-Pacific (Smith-Vaniz and Springer, 1971).

Glyptoparus is monotypic (Smith-Vaniz and Springer, 1971) and ranges from the western Indian Ocean to the western margin of the Pacific Plate, and is known from the Pacific Plate nonmarginally only at Ponape (USNM collections), Eastern Caroline Islands, where I consider its presence as evidence favoring operation of the Caroline Islands conduit.

Hirculops is monotypic and known only from the Indian Ocean (Smith-Vaniz and Springer, 1971).

Istiblennius is in need of revision; it is distributed widely in the Indo-Pacific (Smith-Vaniz and Springer, 1971).

Litobranchus is monotypic and known only from the Philippines and New Guinea, along the western margin of the Pacific Plate, and possibly from Gebe Island (between Halmahera and New Guinea; Smith-Vaniz and Springer, 1971).

Medusablennius, which is the smallest blenniid, is monotypic and known only from Raroia, Tuamotus, on the Pacific Plate (Figure 60). I consider the monotypic *Cirrsalarias*, which is restricted to the Indo-West Pacific, to be the sister genus of *Medusablennius* (Springer, 1976; Springer and Spreitzer, 1978).

Mimoblennius contains four allopatric species and ranges from the Red Sea and western Indian Ocean to the Bonin Islands on the eastern margin of the Philippine Plate (for a distribution map see Springer and Spreitzer, 1978, fig. 6; a record for the Philippine Islands can now be added; USNM). Only one species reaches the Plate margin.

Nannosalarias is monotypic and ranges from Christmas Island, eastern Indian Ocean, eastwards to New Guinea and the Tonga Islands, adjacent to the margin of the Pacific Plate (Smith-Vaniz and Springer, 1971), and is known nonmarginally on the Plate only from Ponape (USNM), which I consider evidence for operation of the Caroline Islands conduit.

Pereulixia is monotypic and known only from the southeastern coast of Africa (Smith-Vaniz and Springer, 1971).

Praealticus is in need of revision; it ranges from the eastern Indian Ocean to well out on the Pacific Plate.

Rhabdoblennius is in need of revision: it ranges from the Philippines to well out on the Pacific Plate (Smith-Vaniz and Springer, 1971).

Salarias is in need of revision; it ranges from the western Indian Ocean to well out on the Pacific Plate.

Stanulus contains two species. One species is restricted to the Great Barrier Reef and Lord Howe Island; the other ranges from the western Indian Ocean to well out on the Pacific Plate (Springer, 1968; Smith-Vaniz and Springer, 1971).

Omobranchini: *Omobranchus* comprises 20 species of close-shore inhabitants, rarely occurring at depths greater than 0.5 m (Springer and Gomon, 1975; Springer, 1981b). Larvae and adults are generally taken together, but there is at least one record of a larva having been dipnetted at the surface offshore (Springer and Gomon, 1975). Several species are restricted to estuaries or mangrove habitats; others occur on rocky shores in undiluted sea water. One otherwise marine and estuarine species has been taken in a freshwater lake in the Philippines. I collected two species (not together) at the mouths of freshwater streams in Ambon Bay, Indonesia, and both have been taken also in strictly marine waters at other localities. One of the two species, *O. rotundiceps*, is the only species of *Omobranchus* that occurs other

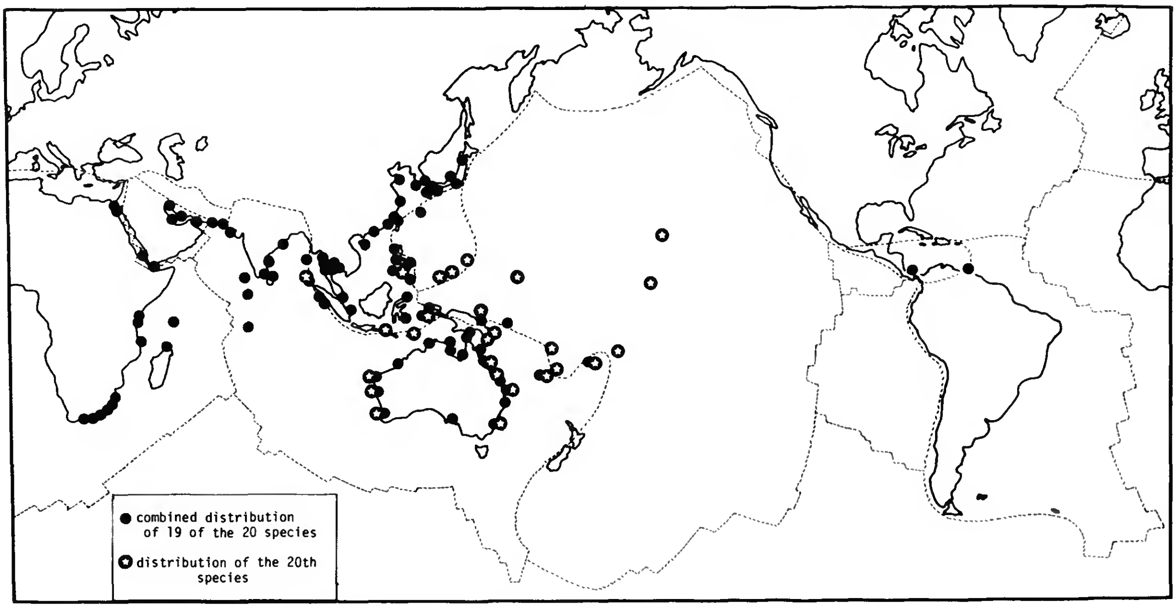

FIGURE 9.—Distribution of the blenniid fish genus *Omobranchus*; no more than five species are known from a single locality.

than marginally on the Pacific Plate; Ponape, Oahu, and Palmyra (Figure 9). Springer and Gomon (1975) proposed that *Omobranchus* evolved in continental waters and that time has been insufficient for more species of the genus to colonize Pacific oceanic islands. They believed that there must be more than one satisfactory niche available for *Omobranchus* in Oceania. One species, *O. punctatus*, which ranges from the Red Sea and east coast of Africa to the Solomon Islands and Fiji, along the margin of the Pacific Plate, is also known from Trinidad and the Caribbean entrance to the Panama Canal (Springer and Gomon, 1975, fig. 7). These Caribbean occurrences were ascribed by Springer and Gomon to an accidental introduction. *Omobranchus punctatus* is the only close-shore (adjacent to shoreline) fish species with an Indo-West Pacific and Caribbean distribution (see Apogonidae: *Apogon evermanni*).

Enchelyurus, comprises five species (Springer, 1972b) inhabiting shallow, rocky, fully marine areas (Figure 10). Two species, *E. brunneolus* and *E. ater*, occur on the Pacific Plate nonmarginally. *Enchelyurus brunneolus* is endemic to the Hawaiian Islands; *E. ater* ranges from Lord Howe Island east to the Tuamotus and Rapa; *E. kraussi* ranges from the Red Sea and Comores east to the Marianas and New Guinea, on the margin of the Pacific Plate; *E. petersi* is known only from the northern Red Sea; and *E. flavipes* is known only from the Indo-Malayan area. *Enchelyurus kraussi*, *E. ater*, and *E. brunneolus* form a closely related species group that can be defined by synapomorphies (most restricted gill openings in *Enchelyurus*; males with pattern of stripes or vermiculations on head, as opposed to uniformly colored). A cladistic classification of the three species has not been possible, but based on their distributions it seems probable that one of the vicariant events (at least two are required to give rise to three species) occurred along the western margin of the Pacific Plate and the other may have occurred on the Plate.

Parenchelyurus contains two species, one ranging from the western Indian Ocean to the Marshall Islands, on the Pacific Plate; the other known only from the Philippines, New Guinea, and northern Australia (Springer, 1972b; Springer and Gomon, 1975).

Laiphognathus is monotypic, a coral-reef species,

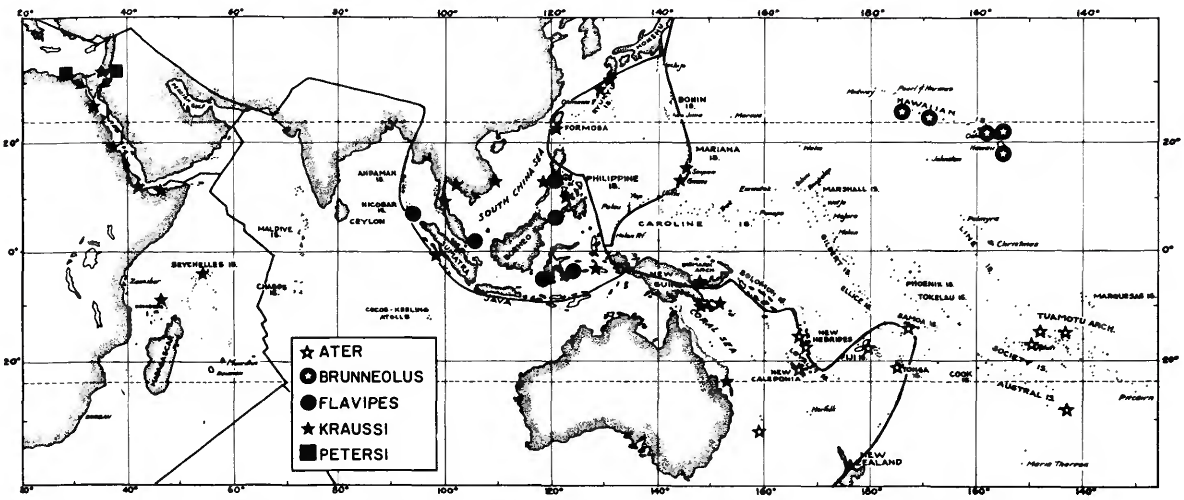

FIGURE 10.—Distributions of the five species of the blenniid fish genus *Enchelyurus*.

and ranges from the east coast of Africa to the Bismarck Archipelago and Solomon Islands on the margin of the Pacific Plate (Springer, 1972b, 1981b).

Omox, a mangrove inhabitant, contains two species (Springer, 1981b) and ranges from the South China Sea to Palau, and the Bismarck Archipelago, and is known nonmarginally on the Pacific Plate only from Ponape (*O. biporos*), which provides evidence favoring operation of the Caroline Islands conduit.

Haptogenys is monotypic (Springer, 1972b), an estuarine inhabitant, and is known only from Calicut, India, and Thailand (Springer and Gomon, 1975).

Phenablenniini: This tribe is monotypic (*Phenablennius hyeligeri*) and restricted to freshwater and estuaries in Borneo, Sumatra, and Cambodia (Springer and Smith-Vaniz, 1972; Smith-Vaniz, 1975).

Nemophini: This tribe was monographed by Smith-Vaniz (1976), who provided distribution maps for all included taxa. Most of the information I report on the Nemophini is derived from his study.

Aspidontus comprises two free-swimming, coral-reef species, and both range from the east coast of Africa to at least the Society Islands.

Meiacanthus comprises 16 species, all but one of which occur in coral-reef areas; the exception is *M. anema*, which inhabits freshwater streams and estuaries. The species are often free swimming, just above the substrate, but most reside in worm tubes. Only one species, *M. atrodorsalis*, is known unequivocally to occur on the Pacific Plate nonmarginally (Figure 11), a situation comparable to that described above for *Omobranchus* (Figure 9). Smith-Vaniz questioned the Tahitian locality accorded a specimen of *M. procne*, which is otherwise known only from the northern Tonga Islands, collected in 1931 by Zane Grey, a novelist and game fisherman (see also *Chaetodon plebeius*, family Chaetodontidae, for another questionable Zane Grey locality).

I have seen three species of *Meiacanthus* (*M. atrodorsalis*, *M. grammistes*, and *M. vittatus*) swimming together on the same coral reef in the vicinity of Port Moresby, Papua-New Guinea. *Meiacanthus atrodorsalis* was the least common of the three species. I would expect that *M. grammistes*, which ranges over much of the western Pacific (Okinawa south to Australia, and Marianas), would be a successful colonizer of the Pacific Plate if it were able to disperse to the Plate.

Petroscirtes comprises 10 species, most of which are benthic and occur around vegetation; however, *P. fallax*, which mimics *Meiacanthus lineatus*, swims freely in the water column. *Petroscirtes lupus* uses dead mollusk shells as nests. Its larvae, based

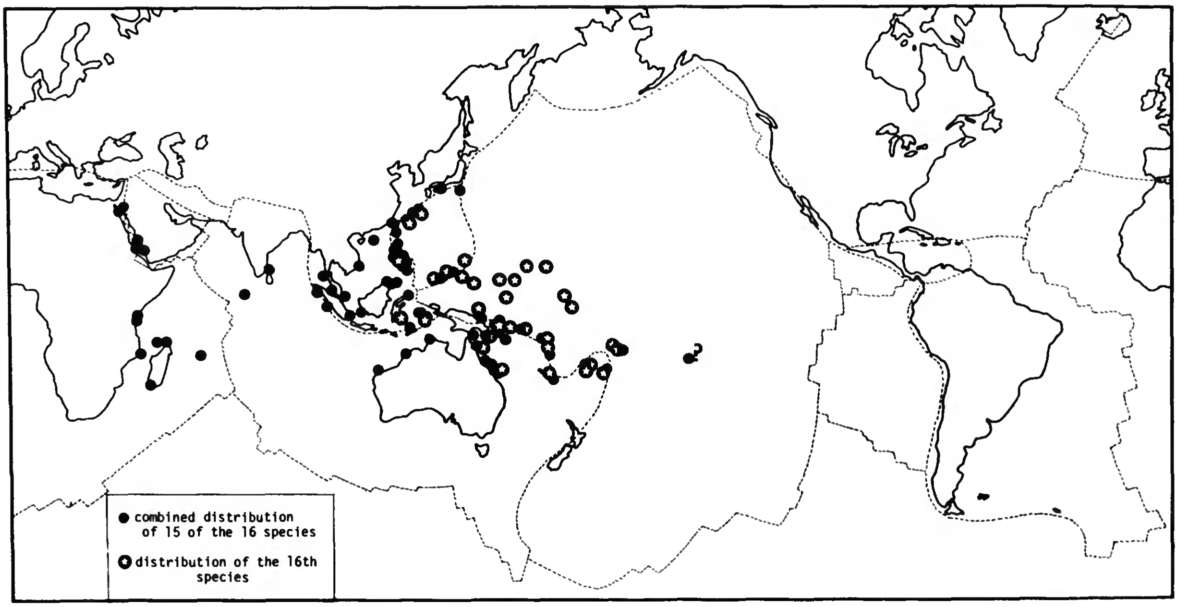

FIGURE 11.—Distribution of the blenniid fish genus *Meiacanthus*; no more than four species are known from a single locality.

on aquarium observations, congregate at the surface on hatching, and after one week begin to feed on the bottom. Young *Petroscirtes* often occur near floating *Sargassum*. Only two species, *P. mitratus* and *P. xestus*, occur other than marginally on the Pacific Plate. Both are wide ranging, extending from the east coast of Africa to the Marshall or Line and Society islands, but neither is present in Hawaii. Three other species of *Petroscirtes* have the eastern limits of their distributions at the western margin of the Pacific Plate, but only one of these, *P. breviceps*, ranges as far west as the east coast of Africa.

Plagiotremus comprises 11 species of free-swimming fishes that use abandoned worm tubes in reefs as shelter. Five species occur on the Pacific Plate, of which two, *P. ewaensis* and *P. goslinei*, are known only from the Hawaiian Islands, and two others, *P. rhinorhynchos* and *P. tapeinosoma*, range from the east coast of Africa through much of Oceania, but are absent from the Hawaiian Islands (each of the two Hawaiian species appears to have a different one of the wide-ranging species as its sister species). The fifth, *P. laudandus*, occurs from the Philippines east to the Gilbert Islands, with one of its two subspecies restricted to Fiji. One species, *P. azaleus*, occurs only in the eastern Pacific. The other five species are variously restricted to the Indo-West Pacific and do not reach the western margin of the Pacific Plate.

Xiphasia comprises two species of tube-dwelling (in soft bottoms), eel-like blennies. *Xiphasia setifer* ranges from the east coast of Africa to the western margin of the Pacific Plate; *X. matsubarai* also ranges from the east coast of Africa to the western margin of the Pacific Plate, but one collection, from 11°40′S, 175°10′E, is just north of the Pacific Plate margin. While I consider *X. matsubarai* to occur nonmarginally on the Pacific Plate, the species is essentially absent from the Plate, and the exceptional collection may represent a waif (see Smith-Vaniz, 1976, fig. 38).

Summary: While reasonably complete information on Indo-Pacific blenniid distributions is far from available, what is known is probably indicative, and can be summarized as follows.

Although it is unknown how many species of Blenniini reach the western margin of the Pacific

Plate, only one species occurs on the Plate nonmarginally.

Of the 19 genera of Salariini that reach the western margin of the Pacific Plate from the west, only 13 extend onto the Plate nonmarginally. Of the 12 species of *Ecsenius* that reach the western margin of the Pacific Plate from the west, only three extend onto the Plate nonmarginally, and one of the three is represented by allopatric color-pattern populations that are restricted to one side or the other of the Plate margin. Of the six species of *Entomacrodus* that similarly reach the western margin of the Plate, only four extend nonmarginally onto the Plate.

Of the six genera and seven or eight species of Omobranchini that reach the western margin of the Pacific Plate from the west, only four genera and four species extend onto the Plate nonmarginally.

Of the five genera and 19 species of Nemophini that reach the western margin of the Pacific Plate from the west, all the genera but only nine species occur on the Plate nonmarginally, and one of the nine (*Xiphasia matsubarai*) has been reported only once from the Plate, and not very far from the margin.

It can be surmised from these data that the western margin of the Pacific Plate delineates a sharp break in the distribution of blenniid fishes. The margin, as a feature of biogeographical importance, is further emphasized by the presence of widely distributed blenniids endemic to the Plate.

BOTHIDAE

The lefteye flounders are a large group (Nelson, 1974, estimates that there are 36 genera and about 212 species) of shallow- to deep-dwelling, benthic, and small- to moderate-sized fishes with planktonic larvae. The family occurs circumglobally in tropical and temperate seas, and consists of two or three subfamilies, only one of which, Bothinae, the most speciose, occurs on the Pacific Plate. It is represented there by three genera with probably five species. The Indo-Pacific species are not well known, but one species, *Bothus mancus*, is reported from localities ranging from the east coast of Africa eastward into the eastern Pacific, and another, *Bothus pantherinus*, ranges from the Red Sea to the Society Islands. Several deep-dwelling genera (*Chascanopsetta*, *Parabothus*, *Pelecanichthys*, *Taeniopsetta*) not included in Table C (Appendix 2) are present nonmarginally on the Pacific Plate only in the Hawaiian Islands.

BRACHAELURIDAE

This family is discussed under the Orectolobidae.

BRANCHIOSTEGIDAE

(not including Malacanthidae)

The tilefishes comprise three genera and 23 species (two questionable) of moderately large (230–867 mm SL), moderately deep-dwelling (20–600 m), commercially important, epibenthic or benthic fishes with pelagic larvae (Dooley, 1978; 1981; Berry, 1978).

Dooley (1978:14), who revised the family, described its distribution as "worldwide in tropical, warm and cold temperate waters along the edges of continental shelves and the upper slopes of continental margins; occasionally found around continental or oceanic islands." I have plotted the distribution of the Branchiostegidae (Figure 12) based on information in the studies of Dooley and Berry and a record for Fiji (Carlson, ms.), and find that these fishes are well represented in the New World tropics, but they are absent from most of the Old World tropics. Indeed, they appear to be distributed antiequatorially in the Indo-West Pacific. Except for a Red Sea–South African species, none of the Indo-West Pacific species occur both north and south of the equator. The family is absent from the nonmarginal portions of the Pacific Plate.

BREGMACEROTIDAE

The codlets consist of a single genus (*Bregmaceros*) and about five species (Belyanina, 1974) of small fishes. The codlets are distributed circum-

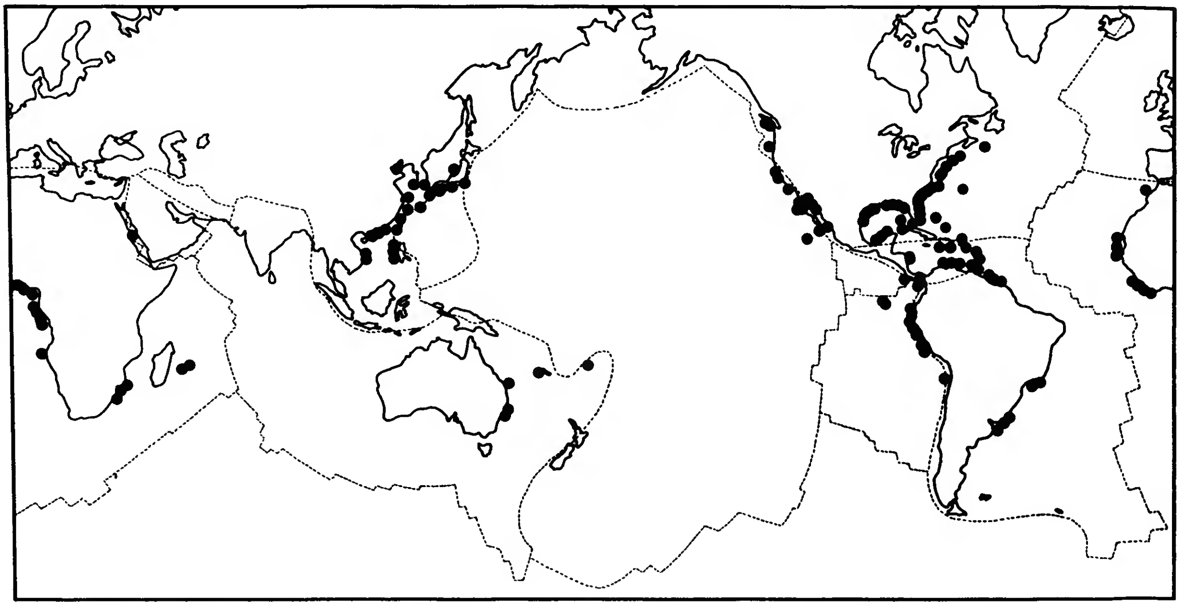

FIGURE 12.—Distribution of the tilefishes, Branchiostegidae.

globally (see D'Ancona and Cavinato, 1965, and Belyanina, 1974, for distribution maps), and occur at depths from the surface to perhaps 1000 m or more. The adults of some species are known only from shallow coastal waters. Most specimens in collections are larvae and juveniles taken in plankton nets. Although I have collected specimens in a shell dredge close to shore in Indonesia, depth unknown, but probably less than 50 m, I only tentatively characterize the codlets as shorefishes.

BYTHITIDAE

The bythitids are a speciose group of small, viviparous fishes distributed circumglobally. Cohen and Nielsen (1978) have reviewed the genera and provided general information on distributions; the species are poorly known taxonomically. They occur at depths of less than a meter down into the bathypelagic; at least one species occurs in freshwater. Four genera (probably ten species) are reported from nonmarginal areas of the Pacific Plate.

CAESIONIDAE

The caesios comprise four genera (Johnson, 1980) and perhaps 25 species of small (to about 400 mm TL), free-swimming fishes that occur only in the Indo-Pacific. *Gymnocaesio* and *Dipterygonotus*, each with two species, are restricted to the Indo-West Pacific, variously occurring from the Gulf of Aden east to Melanesia, north to (southern?) China, and south to the East Indies. As many as ten species of *Caesio* and *Pterocaesio* may be present nonmarginally on the Pacific Plate. These genera are widely distributed in the Indo-Pacific and in need of revision; some of the species are restricted to the Indo-West Pacific; but it is doubtful that any of the others are Pacific Plate endemics.

CALLIONYMIDAE

The dragonets comprise several genera and about 130 species (Fricke, 1981c) of small (maximum about 300 mm TL), benthic fishes occurring almost circumglobally in shallow to moderately deep temperate and tropical marine waters. Most species live on sandy or muddy bottoms, but two species enter and live in freshwater (Fricke, 1981c).

Diplogrammus comprises five allopatric species (Fricke, 1981a): one restricted to the Red Sea, one to the Arabian Sea, one to the western Indian Ocean, one to Japan, and one distributed from the Ryukyu Islands south to Queensland and east to the Marshall, Fiji, and Samoan islands.

Pogonymus comprises four species, each known from a single area (W.P. Davis, pers. comm.): Hawaiian Islands, Japan, India, Nigeria. The Hawaiian species apparently constitutes an example of an Hawaiian exception (for a genus) on the Pacific Plate.

Synchiropus was revised by Fricke (1981b). The genus contains 26 species and is found in all warm-temperate and tropical seas, from shallow to moderately great depths. The Mediterranean–eastern Atlantic, western Atlantic, and eastern Pacific regions each harbor one endemic species. The remaining 23 species are variously distributed in the Indo-Pacific, with six species restricted to the Indian Ocean. Five species occur nonmarginally on the Pacific Plate, of which one (*S. rubrovinctus*) is an Hawaiian endemic, two are widely distributed endemics (*S. laddi*: Palau Islands, Bikini, Rongelap, Enewetak, and Raroia, and an additional locality, Cuyo Islands, Philippines, noted by Fricke, in litt.; *S. morrisoni*: Ulithi, Bikini, Tutuila), one (*S. altivelis*) is an example of an Hawaiian exception (otherwise ranging from Indonesia and the Philippines north to Japan), and one (*S. splendidus*) occurs widely in the western Pacific, but nonmarginally on the Pacific Plate only in the Eastern Caroline Islands (thus providing evidence favoring operation of the Caroline Islands conduit). Fricke did not treat the relationships of *Synchiropus* cladistically, but his stated relationships of the two widely distributed endemics are of interest as both were related to species that do not occur on the Pacific Plate nonmarginally. He related *S. morrisoni* to *S. ocellatus*, which is restricted to the Indo-West Pacific as far west as Vietnam and as far east as Palau to Tonga, which are on plate margins adjacent to that of the Pacific Plate, and to *S. stellatus*, which is an Indian Ocean endemic. He related *S. laddi* to *S. postulus* and *S. minutulus*, both of which are Indian Ocean endemics.

The *kaianus* species group of *Callionymus* was revised by Fricke (1981c). This group comprises 13 deep-dwelling species (most taken at over 100 m) that are confined to the Indo-West Pacific (east coast of Africa east to Japan, Philippines, New Ireland, and New Caledonia). Probably no more than three other species of *Callionymus* occur on the Pacific Plate.

CARACANTHIDAE

The caracanthids comprise a single genus, *Caracanthus*, with four small (to about 50 mm TL) species of coral-dwelling fishes. The family is widely distributed in the Indo-Pacific, and ranges from the east coast of Africa eastwards to the Galapagos Islands (Mizuno and Tomiaga, 1980, fig. 3) in the eastern Pacific. One species is restricted to the western Indian Ocean, one to the Hawaiian and Johnston islands, one widely distributed in the western and central Pacific Ocean (but not at Hawaiian and Johnston islands), and one species ranges from the east coast of Africa to the Society and Galapagos islands (W.N. Eschmeyer, pers. comm.).

CARANGIDAE

The jacks comprise about 140 species (W.F. Smith-Vaniz, pers. comm.) of small to large fishes (maximum about 1.75 m TL) with planktonic larvae. The species are free-swimming and some pelagic species are circumglobally distributed (Briggs, 1960). Many species limited to the Indo-Pacific appear to be widely distributed; however, some genera and species are notably absent from the Pacific Plate. In all, 29 species in 14 genera are present nonmarginally on the Plate.

Berry and Cohen (1974, fig. 1) gave the distribution of the 13 species of *Trachurus* (reduced to 12 species by Stephenson and Robertson, 1977, and to 11 species with several allopatric subspecies—for a total of 14 taxa—by Shaboneeve, 1980, who provides a more detailed distribution map). *Trachurus* occurs along coasts bordering all oceans, but is noticeably absent from the Pacific Plate. While the Atlantic species are continuously distributed from about 30°N-30°S, the Indo-West Pacific species are essentially antitropical in distribution.

The Indo-Pacific genus *Scomberoides* contains four species. All are widely distributed in the Indo-West Pacific, but only one (*S. laysan*) extends nonmarginally onto the Pacific Plate (to Hawaii, Marquesas, and Tuamotus; Smith-Vaniz and Staiger, 1973).

Megalaspis (monotypic) is widely distributed and very common in the Indo-West Pacific. It has been reported (Jordan et al., 1927) only once from the Pacific Plate, from a single specimen that was seen at the Bishop Museum in Honolulu, and presumed to have been taken in Hawaiian waters. It seems doubtful that this specimen actually came from the Hawaiian Islands, which have been credited with numerous dubious or erroneous records of fishes (as well as valid exceptional occurrences for the Pacific Plate).

CARAPIDAE

The pearlfishes comprise six genera and about 30 species (Cohen and Nielsen, 1978) of small (to about 309 mm TL) coastal fishes. Most, if not all, have planktonic larvae, and most are internal associates of echinoderms and mollusks. The family is almost circumglobally distributed, being absent only from the islands (Ducie, Easter) nearest the eastern margin of the Pacific Plate. Most of the species live in shallow water, but the free-living *Snyderia canina* has been taken in a dredge haul made at a depth of over 2000 feet (610 m) off the Hawaiian Islands. About six shallow-dwelling species of pearlfishes have been taken nonmarginally on the Pacific Plate. The total number of Indo-Pacific carapodid species probably does not exceed 10.

CARCHARHINIDAE

The requiem sharks are a circumglobal family comprising 11-12 genera and about 45 species of small to very large fishes (maximum adult size ranging from about 0.6-5.5 m). The species are free swimming, shallow dwelling, carnivorous, live bearing, marine (a few species enter fresh or brackish water), and may be restricted essentially to littoral areas or the open ocean.

Carcharhinus has been revised by Garrick (in press), who later (in prep.) included five additional species. *Carcharhinus* is the most speciose genus in the family, with 30 species, ranging in adult size from 0.95-3.62 m TL. Twenty-six of the species occur in the Indo-Pacific, but only nine (34.6%) of these occur on the Pacific Plate nonmarginally, and none of these is endemic to the Plate. Of the nine species on the Plate, four large species (2.6-3.0 m) are worldwide in distribution and common in all areas (two of these species are oceanic and the only ones so restricted in the genus); two species, *C. plumbeus* and *C. altimus* (2.4 and 2.8 m), are distributed circumglobally, but are known nonmarginally on the Pacific Plate only from the Hawaiian Islands (examples of Hawaiian exceptions), and three species (1.8-2.5 m) are widely distributed in the Indo-Pacific. *Carcharhinus melanopterus*, the smallest of the three widely distributed Indo-Pacific species, ranges from the Red Sea and east coast of Africa to the Tuamotus and Marquesas, and has been reported recently from the Mediterranean, possibly as a migrant through the Suez Canal. *Carcharhinus albimarginatus*, the largest of the three widely distributed Indo-Pacific species, ranges into the eastern Pacific as well.

Of the 17 Indo-West Pacific species of *Carcharhinus* that do not occur on the Pacific Plate, four (*C. brevipinna*, *C. brachyurus*, *C. leucas*, *C. obscurus*) are among the largest species of *Carcharhinus* (2.78, 2.92, 3.24, 3.62 m) and are circumglobally distributed except for their noticeable absence from the Pacific Plate. The other 10 Indo-West Pacific species of *Carcharhinus* are distributed as follows: four (0.95-1.66 m) widely distributed but restricted to the Indo-West Pacific; one (2.23 m) in the eastern Atlantic and Indo-West Pacific; three (1.0–1.5 m) only in the western Pacific; one (1.72 m) only in the western Indian Ocean; and one (1.34 m) in the western Atlantic, eastern Pacific, and western Pacific.

From the information presented above, it is apparent that size alone is insufficient to account for the presence or absence of *Carcharhinus* species on the Pacific Plate (although all four of the worldwide species are large). The large proportion of the species that reach the margin of, but do not extend out on, the Plate, agrees with my findings on other elasmobranch groups, which, in general, tend to be absent from the Pacific Plate.

To avoid the possible criticism that there are probably inadequate data available for large sharks on the Pacific Plate, it is noted that Strasburg (1958) reported on longline collections that covered much of the central Pacific during a four-year period and produced over 6000 specimens of sharks, but only 12 species, of which only three were *Carcharhinus*.

Triaenodon contains two species. *Triaenodon obtusus* is known only from the holotype from India (Taniuchi, 1975). *Triaenodon obesus*, which attains a length of 2.13 m, is found only near coral reefs, often resting in caves, yet it ranges from the Red Sea and east coast of Africa eastward to Panama (Randall, 1977). Randall (1977) tagged 124 *T. obesus* at Johnston Island and recovered seven after 16 days to two years; none had moved more than 2.9 km from their tagging site (tagging information in the abstract to Randall's paper expands on tagging data reported in the body of the paper). One may wonder, as did Randall, how such a sluggish, reef-associated shark was able to cross the Pacific. A possible answer to this question is discussed in the section on the geological history of the Pacific and Philippine plates.

Scoliodon, *Loxodon*, and *Rhizoprionodon* comprise small, shallow-dwelling sharks with maximum total lengths of about 350–1000 mm. The species are of commercial importance in Asia. The genera were revised by Springer (1964). *Scoliodon* is monotypic and its distribution is coastal, from about Bombay, India, east and south to Java and north to Tinghai, Chekiang Province, China, and Japan (and perhaps to the Bonin Islands; see Zama and Fujita, 1977, as *S. wahlbeemi*). It is also recorded from Sarawak, but not the Philippines. *Loxodon* is also monotypic, but with a wider Indo-West Pacific distribution (Figure 13) than *Scoliodon*. *Loxodon* is the only one of the three genera that occurs on islands (Seychelles, Mascarene Plateau, including, perhaps, Mauritius) remote from continents. Springer (1964) reported extreme and discontinuous variation in numbers of precaudal vertebrae in different populations of *Loxodon*, indicating that a species complex might be involved. The Seychelles and Mascarene Plateau are continental fragments (Scrutton, 1976), and it is possible that the populations of *Loxodon* were left behind to diverge (vertebrally) when the continent, or continents (India, Africa), that were associated with the fragments disappeared or moved away.

Rhizoprionodon, with seven species (three Indo-West Pacific, of which one also occurs in the eastern Atlantic; one eastern Pacific; and three western Atlantic) is more widespread (Figure 13) than *Loxodon*, occurring more or less circumtropically, but absent from the Pacific Plate.

It is not hard to visualize the distributions of *Loxodon* and *Scoliodon* as representative of levels of increasing restriction in distribution from what were previously widespread distributions similar to that found for *Rhizoprionodon*; especially as all three genera occur together over much of their Indo-West Pacific distribution. Bearing on this are the distributions of the two subgenera of *Rhizoprionodon*. The type subgenus has the same overall distribution as the genus, whereas the other subgenus, *Protozygaena*, has a disjunct distribution, occurring from India to Queensland in the western Pacific, and from Panama to southern Brazil in the western Atlantic. If the distribution of the subgenus *Protozygaena* is segregated, the order of increasing distributional restriction is as follows: *Rhizoprionodon*, *Protozygaena*, *Loxodon*, *Scoliodon*.

Galeocerdo (tiger shark), monotypic, is a large

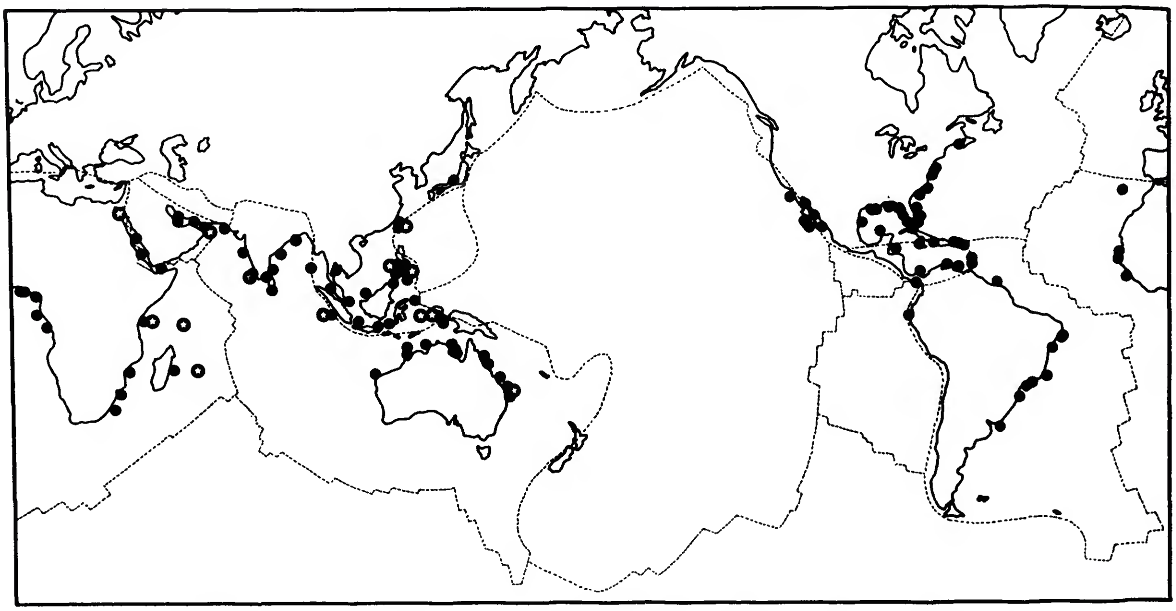

FIGURE 13.—Distributions of the carcharhinid shark genera *Rhizoprionodon* (solid circles) and *Loxodon* (stars).

species that appears to be circumglobally distributed along warm, shallow, marine coasts, including the Pacific Plate. The species purportedly attains about 9 m TL, but there are few, if any, authenticated records of specimens over 5.5 m TL.

Dirrhizodon (often referred to as *Hemipristis*), monotypic, attains about 2.5 m TL, and is restricted to the Indo-West Pacific, from the Red Sea and western Indian Ocean to the Gulf of Thailand.

CENTRISCIDAE

(excluding Macrorhamphosidae)

The shrimpfishes consist of two genera (*Aeoliscus*, *Centriscus*) and four species of small (to about 150 mm TL), shallow-dwelling, suprabenthic fishes presently found only in the Indo-Pacific (Macfarlane, 1923:243, reported a fossil species of centriscid as common in the Oligocene rocks from Alsace to Baku, central Europe). They occur in a variety of habitats, from coral-reefs to muddy bottoms near mangroves. The family ranges from the Red Sea and eastern Indian Ocean to along much of the western margin of the Pacific Plate (however, unknown from Samoa). I know of only three records from the Pacific Plate nonmarginally: one for Honolulu (Fowler, 1928), one in the USNM collections supposedly collected by Alexander Agassiz in 1899 from Makemo, Tuamotus, and one at the Bishop Museum from Ponape. I consider the first two of these records as questionable, as does J.E. Randall (in litt.). On the other hand, the Ponape record (*Aeoliscus*) is undoubtedly valid, and R.A. Croft, Fisheries Officer in Ponape and a marine fish collector, informs me that he has obtained shrimpfish in Ponape. The presence of shrimpfish in the Eastern Caroline Islands chain, which extends westward to the Yap and Palau islands (where centriscids are common; California Academy of Sciences collections) on the margin of the Philippine Plate, is evidence for operation of the Caroline Islands conduit, which is allowing dispersal onto the Pacific Plate from the continental areas to the west.

CENTROPOMIDAE

The snooks, according to Greenwood (1976), comprise three extant genera (*Centropomus*, *Psammoperca*, *Lates*) and about 18 species of moderately large (to about 1.5 m), free-swimming fishes. Seven of the species are in African freshwaters. The marine species frequently enter brackish water, and some species that live primarily in freshwater spawn in estuaries (Lake, 1971). There are three Indo-West Pacific marine species with an overall range from the Persian Gulf to Taiwan, the Philippines, and northern Australia. The remaining species are in the New World tropics (Greenwood, 1976, fig. 36, presents a world distribution map for the family). A western Atlantic species of the western hemisphere genus *Centropomus* has been reported (Fraser-Brunner, 1931) at least once from West Africa (Nigeria). The individual was probably a waif. The fossil record for the family ranges from the Eocene of Monte Bolca, northern Italy, to the Holocene, and includes also the Paris Basin, Austria, Portugal, and Croatia to Egypt, the Sahara, and eastern Africa (Greenwood, 1976).

In the Caribbean, snooks are seen occasionally in coral-reef areas adjacent to mangroves (Randall, 1968).

CEPOLIDAE

(including Owstoniidae)

The bandfishes comprise four or five genera and about 10–15 species of small (to perhaps 700 mm TL), benthic or suprabenthic fishes that usually occur in moderately deep water (up to 400 m), but are often taken at much shallower depths (almost on shore after storms in the Mediterranean-Atlantic area). The species occur on rocky or muddy bottom. Little is known about their reproductive biology.

The bandfishes occur from the eastern Atlantic eastward to the western margins of the Philippine and Pacific plates (Figure 14). There is a single western Atlantic record (Kanazawa, 1952) of a cepolid (*Cepola*), which is based on a specimen taken from the stomach of a grouper (Serranidae) caught at Bermuda. The specific identification of the specimen was not possible because of its poor

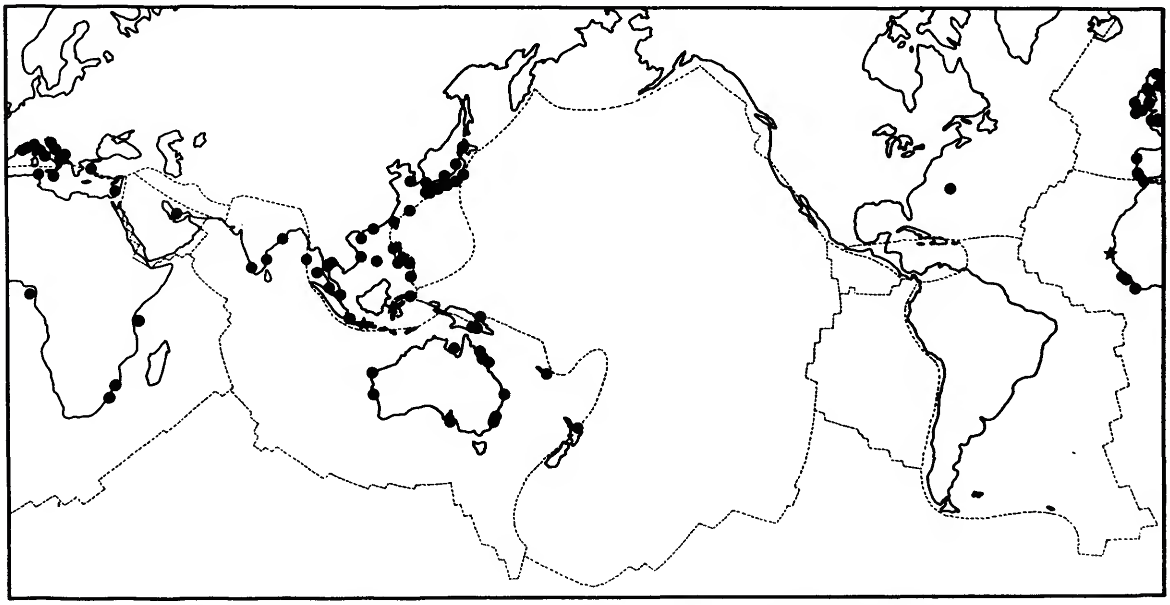

FIGURE 14.—Distribution of the fishes of the family Cepolidae (stars indicate unspecified localities in general area).

condition. Bandfishes are either adventitiously present in the western Atlantic, or deep-dwelling in that region in areas inaccessible to normal fishing gear.

CHAETODONTIDAE

The butterflyfishes comprise ten genera and 116 species (total derived from the following: Allen, 1980; Allen and Kuiter, 1978; Burgess, 1979; Lubbock and Edwards, 1980; Myers, 1981). The species are small (to about 300 mm TL), suprabenthic, predominantly coral-reef dwelling, and conspicuously colored, with planktonic larvae. The family is circumglobally distributed, and only one genus and 17 species (in three genera) do not occur in the Indo-Pacific. *Johnrandallia* (= *Pseudochaetodon*) is limited to the eastern Pacific. Only one of the Indo-Pacific species, *Forcipiger flavissimus*, ranges out of that region (to the eastern Pacific).

Five of the nine Indo-Pacific chaetodontid genera (*Chelmon*, *Chelmonops*, *Coriadon*, *Parachaetodon*, *Amphichaetodon*, including nine species) are widely distributed in the Indo-West Pacific but are absent from the Pacific Plate, except marginally. *Amphichaetodon* is also represented by an endemic species in the San Felix Islands, off Chile.

Of the 99 Indo-Pacific chaetodontid species, 38 occur nonmarginally on the Pacific Plate. Of the 38, ten occur only on the Plate and 28 also occur in the Indo-West Pacific. Five of the ten endemics are known from single islands or island groups: three at the Hawaiian Islands (including Johnston Island), one in the Marquesas, and one at Pitcairn. The other Plate endemics are more widely distributed: *Hemitaurichtys thompsoni* (Hawaiian, Johnston, and Tokelau islands, Burgess, 1979; Samoa, R.C. Wass, ms.; Guam and Rangiroa, J.E. Randall, in litt.); *Chaetodon trichrous* (Society, Tuamotu, Marquesas and possibly Gilbert islands; Allen, 1980:232, cited a questionable record from Palmyra, Line Islands); *C. quadrimaculatus* (Hawaiian, Line, and Tuamotu islands, Burgess, 1979; southern Japan, Society, Pitcairn, Phoenix, Marshall, Wake, and Marquesas islands, Allen, 1980; Samoa, Guam, and Saipan, C. Birkeland, in litt.); *C. smithi* (= *C. hemichrysus*; Pitcairn, Rapa); and *C. tinkeri* (Hawaiian Islands and Enewetak, Marshall Islands, J.E. Randall, in litt.; also mentioned in Myers, 1981).

There are also two species restricted to the margins adjacent to the Pacific Plate: *Chaetodon flavocoronatus* from Guam (Myers, 1981) and *C. litus* from Easter Island (both of which I have included as Pacific Plate species for the purposes of Table C, Appendix 2).

Of the 59 Indo-West Pacific species of chaetodontids that do not occur on the Pacific Plate nonmarginally, or are restricted only to the margins, 34 have their eastern distributional limits well west of the Plate's western margin and 25 reach to, or close to, that margin. Therefore, there are a total of 55 species of chaetodontids that reach the western margin of the Pacific Plate from the west, but, as noted above, only 28 (50.9%) of these continue onto the Plate. The western margin of the Plate thus delineates an effective barrier to the eastward dispersal of chaetodontids.

One of the species, *Chaetodon plebeius*, that is included among the 25 that reach only to the western margin of the Pacific Plate was reported by Burgess (1979) as occurring from the western Indian Ocean to Fiji, and disjunctly, Tahiti, which is the only nonmarginal Pacific Plate record for the species. The Tahitian record is based on a specimen collected in April 1931 by Zane Grey, a sport fisherman and writer, who, during May 1931, also collected *C. plebeius* in Fiji, where the species has been taken by other collectors as well. Randall (1973) and Allen (1980) did not report *C. plebeius* from Tahiti, and R.C. Wass (ms.) does not list it for Samoa. I believe the Zane Grey record of *C. plebeius* to be an error in labelling. Smith-Vaniz (1976, fig. 48) also questioned a Zane Grey Tahitian record for *Meiacanthus procne* (Blenniidae).

There is only one example of an Hawaiian exception among the Chaetodontidae. *Heniochus diphreutes* occurs from the western Indian Ocean to Japan and Australia, and then appears in Hawaii (Allen and Kuiter, 1978, figs. 1 and 2).

Its occurrence in Hawaii is possibly the result of dispersal from Japan via the Kuroshio extension.

CHANIDAE

The milkfish, *Chanos chanos*, is the sole member of the family. It attains a length of more than a meter, spawns in the sea, and the fry may enter freshwater, where they remain for several years until they are about 600 mm or more in length; thereafter, they return to the sea (Herre and Mendoza, 1929). The milkfish is widely distributed in the tropical Indo-Pacific. It ranges from the east coast of Africa eastward to the eastern Pacific.

CHEILODACTYLIDAE

The morwongs are a family of moderate-sized fishes (to about 400 mm FL) with pelagic eggs (Tong and Vooren, 1972). The family is in need of revision, but probably contains fewer than 20 species.

The general distribution of the morwongs can be described as antiequatorial. They are distributed in the southern hemisphere on the warm-temperate, rocky coasts of the continents and continental islands, ranging as far north as southern Queensland (Grant, 1978), in Australia. In the northern hemisphere they range from Japan and Korea south to about Hong Kong. On the Pacific Plate there are only two species: *Cheilodactylus vittatus*, with a north-south disjunct distribution (Hawaiian Islands, Lord Howe Island, New Caledonia), and an undescribed species known only from Rapa and Easter Island (Randall, In press b, c).

CHIROCENTRIDAE

The wolf herrings consist of a single genus, *Chirocentrus*, and two species of free-swimming, voracious, near-shore fishes with pelagic eggs. The wolf herrings are often reported (on hearsay) to reach a length of 12 ft (3.6 m). I have been unable to locate the initial report listing this size, which I have traced only as far back as Bleeker (1869–1875). The next largest size that I have been able to locate for wolf herrings is 4.5 ft (1.4 m, Grant, 1978). Reports over 1 m are uncommon.

The wolf herrings are absent from the Pacific Plate, but are widely distributed in the Indo-West Pacific, from the eastern Indian Ocean to Fiji, adjacent to the western margin of the Pacific Plate.

CIRRHITIDAE

The hawkfishes comprise 9 or 10 genera and about 35 species (Randall, 1963, and pers. comm.; Lavenberg and Yañez, 1972; Lubbock, 1978) of small- to moderate-sized (maximum, 550 mm SL), benthic, reef-dwelling fishes. One species is limited to the Caribbean and St. Helena, in the eastern Atlantic; one species is endemic to Ascension, in the eastern Atlantic; one species is endemic to the west African coast; and one is endemic in the eastern Pacific. The remaining 31 species are restricted to the Indo-Pacific, except that two species (*Oxycirrhitus typus*, *Cirrhitichthys oxycephalus*) range from the western Indian Ocean, and one species (*Cirrhitichthys serratus*) ranges from Guam (but see Myers and Shepard, 1981:343–344) and the Ryukyu Islands, into the eastern Pacific. Of the 31 Indo-Pacific species, 14 do not occur on the Pacific Plate nonmarginally and 17 do. Nine of the 17 are widely distributed in the Indo-Pacific, seven occur only at Pacific Plate localities (two also occur at Philippine Plate localities, but all seven are considered here as Pacific Plate endemics), and one species, *Cirrhitichthys serratus*, has a remarkable distribution: Guam (Kami et al., 1968; but see Myers and Shepard, 1981:343–344), Maug (northern Marianas, J.E. Randall, in litt.), Samoa (R.C. Wass, ms.), questionably, Oahu (Randall, 1963, and in litt.), and Gorgona Island (Colombia, eastern Pacific; Randall, 1963). *Cirrhitichthys serratus* is the only sedentary reef species I know that appears to be limited to the Pacific Plate and the eastern Pacific. Randall (in litt.) suspects that it may be synonymous with the widely distributed western Pacific species *C. falco*, which occurs as far east as the western margin of the Philippine and Pacific Plates, between the Marianas and Fiji.

Four of the endemic Pacific Plate species are widely distributed on the Plate (Figure 60), and include one monotypic, endemic Plate genus, *Isocirrhitus* (*I. sexfasciatus*, Marshall and Tuamotu islands), and possibly a second, undescribed (for *Cirrhitus wilhelmi*; J.E. Randall, pers. comm.; Cressey and Randall, 1978, assigned *C. wilhelmi* to *Amblycirrhitus* without comment). The proportion of cirrhitids restricted to the Pacific Plate is, perhaps, the highest among all the Indo-Pacific fish families.

Relationships among the cirrhitid species have not been treated cladistically. If, however, Randall's (1963) comments to the effect that certain species are more closely related can be extrapolated to indicate sister-species groups, then the closest relative of the Pacific Plate endemic, *Paracirrhites xanthus* (Tuamotu, Society, and Marquesas islands, Caroline Atoll; Randall, 1963, and in litt.) is the allopatric western Pacific species *P. amblycephalus* (Sangi Islands). *Paracirrhites nisus* (Tuamotu, Oeno, and Phoenix islands; Randall, 1963, and in litt.) and *P. bicolor* (Caroline Atoll and Tuamotus; Randall, 1963, and in litt.), both Plate endemics, were considered to be closely related, and are sympatric in at least part of their ranges. It is not possible to decide the sister species of this pair from Randall's study. The two species of *Cirrhitops* are allopatric: *C. fasciatus* from the Indo-West Pacific (Japan, Madagascar, Mauritius) and the Hawaiian Islands (Hawaiian exception) and *C. hubbardi* from the Bonin, Phoenix, Gilbert, and Tuamotu islands. As implied above, Randall (1963) considered *Cirrhitichthys serratus* to be "very closely related" to *C. falco*. The western margin of the Pacific Plate separates the distributions of the two species. Randall noted that the Plate endemic *Paracirrhites typee* (Marquesas and Guam; Kami, 1971) was "morphologically similar" to *P. forsteri* and *P. hemistictus*, both widely distributed Indo-Pacific species, and Randall (1973) stated that *P. typee* and *P. forsteri* are probably synonymous. The last two named species then, are very close, if not identical.

Lavenberg and Yañez (1972) stated that *Cirrhitus wilhelmi* (Easter Island, Rapa, Ilots du Bass, Pitcairn Island group; Randall, pers. comm.) and *C. splendens* (Lord Howe Island) form a "group" within *Cirrhitus*. If true, the endemicity of the "possibly new genus" on the Pacific Plate (Figure 60) would be eliminated; however, Randall (in litt.) does not consider these two species to be congeneric.

The evidence, although weak, seems to indicate that the Pacific Plate endemic cirrhitids tend to have allopatric Indo-West Pacific sister species (or slightly differentiated populations); however, a new revision seems desirable.

CITHARIDAE

The Citharidae (= Eucitharidae) is a small family consisting of five monotypic genera (Hubbs, 1945) of small, bottom-dwelling flatfishes (probably not attaining 300 mm TL) that ordinarily occur at depths of 100–200 m. The family is distributed from the Mediterranean south to about 16°S latitude on the west African coast, and from the Red Sea south to southeast Africa and eastward to Japan, the Philippines, and Arafura Sea. One species, *Brachypleura novazeelandiae*, was described from New Zealand, but Chabanud (1954) believes that locality to be erroneous, and cites the distribution of this species as Maldives to the Arafura Sea.

CLINIDAE

The blennioid fishes of the family Clinidae (as defined by George and Springer, 1980, who excluded the Tripterygiidae, Labrisomidae, and Chaenopsidae, which have often been treated as clinids) comprises about 20 genera and 70 species, most of which are restricted to Australia and Africa. The species are small (few, if any, reaching 300 mm SL) and benthic, although some species inhabit kelp forests off California. The western hemisphere and Mediterranean species are all

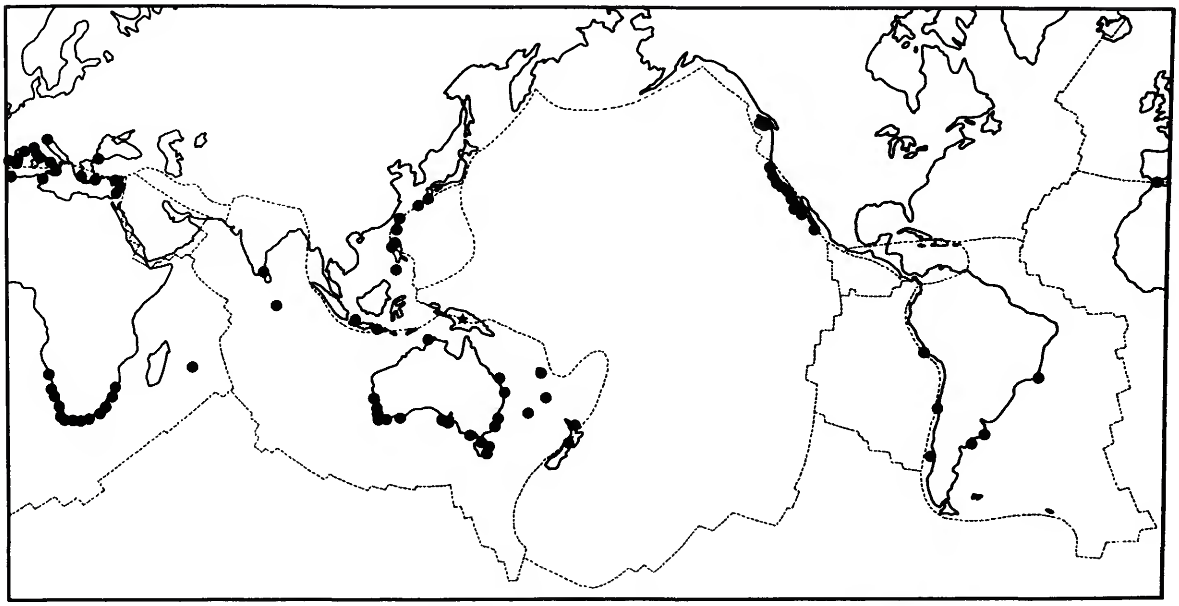

FIGURE 15.—Distribution of the fishes of the family Clinidae sensu George and Springer, 1980 (star indicates unspecified New Guinea locality).

oviparous, hence unspecialized, relative to the Indo-Pacific species, which are all viviparous. All but four or five (tropical) species are limited to warm-temperate waters. The family appears to have an antiequatorial distribution (Figure 15), except for the Indo-Malayan region, and is absent from the Pacific Plate.

CLUPEIDAE

The herring family comprises about 64 genera and 196 species (P.J. Whitehead, in litt.) of small (usually under 500 mm SL), free-swimming fishes with planktonic young. The herrings are usually marine coastal fishes, but several species are restricted to freshwater, particularly in the western hemisphere.

The herrings are distributed circumglobally in tropical and temperate waters. Because of a lack of recent comprehensive revisions within the family, it is not possible to detail distributions, but it appears that no more than about six of the 104 Indo-Pacific species occur on the Pacific Plate nonmarginally (Whitehead, in litt.). The western Plate margin, therefore, represents a strong barrier to the eastward dispersal of the clupeids.

Randall (1973) mentions several records of clupeids from the Society Islands that Whitehead (in Randall, 1973) considers questionable because the species are not otherwise reported from Oceania. For instance, Randall considered the record of *Sardinella gibbosa* from the Society Islands (derived from Günther's 1909 report of *Clupea gibbosa*) plausible because the species was also reported (by Günther) from Fiji, Tonga, and Samoa. On only this basis I would question the plausibility of *S. gibbosa*'s occurring in the Society Islands, because Fiji, Tonga, and Samoa are on or close to the margin of the Pacific Plate, and many otherwise continental plate species have their eastern limits in these islands. However, Randall did not mention Günther's inclusion of Ponape (Eastern Caroline Islands) in the range of *S. gibbosa*, and with this added locality I am more inclined to accept the Society Islands record of *S. gibbosa*. On the other hand, there have been so many suspect records of species occurring on the Pacific Plate based only on Museum Godeffroy specimens, as were Günther's, that I remain skeptical of the Society Islands record of *S. gibbosa*. If the Society Islands record is in error, the presence of the species in Ponape may possibly indicate operation of the Caroline Islands conduit.

Sardinella is represented by about 17 species (Chan, 1965; Whitehead, 1967) in the Indo-Pacific, of which only two or three appear to be present nonmarginally on the Pacific Plate. Only one species appears to be endemic to the Plate, *S. marquesensis* from the Marquesas. *Sardinella marquesensis* has been introduced artificially into the Hawaiian Islands, where it has become established (Berry and Whitehead, 1968; Randall and Kanayama, 1972). There are no species of *Sardinella* native to the Hawaiian Islands.

The clupeid subfamily Dorosomatinae, gizzard shads, comprises about 17 species (Nelson and Rothman, 1973) of large clupeids (to about 520 mm SL). They occur in habitats ranging from freshwater lakes and rivers to fully marine bays. The western hemisphere species are almost entirely restricted to freshwater. The absence of gizzard shads from the Pacific Plate (Figure 16) is possibly the result of lack of habitat, and this absence is duplicated by most of the Indo-Pacific genera and species of clupeids. Based on the successful introduction of *Sardinella marquesensis* in Hawaii, it would appear that more clupeids could exist on the Pacific Plate if they could invade the area.

Whitehead (1963) revised the subfamily Dussumieriinae (which he recognized as a family), in which he recognized six genera and ten species. Five genera and eight species were recorded from the Indo-Pacific, but only *Spratelloides delicatulus* was reported to occur nonmarginally on the Pacific Plate, and then only at Hawaii. Whitehead's distribution reports are misleading as he made no mention of the numerous and undoubtedly valid reports of dussumieriins from Plate localities, including, at least, the Marshall, Caroline, Gilbert, Phoenix, and Tuamotu islands (Herre, 1939; Schultz and Welander, 1953; Randall, 1955d; Schultz, 1943; Harry, 1953). Most of these reports refer only to *Spratelloides*, but *Dussumieria* has been

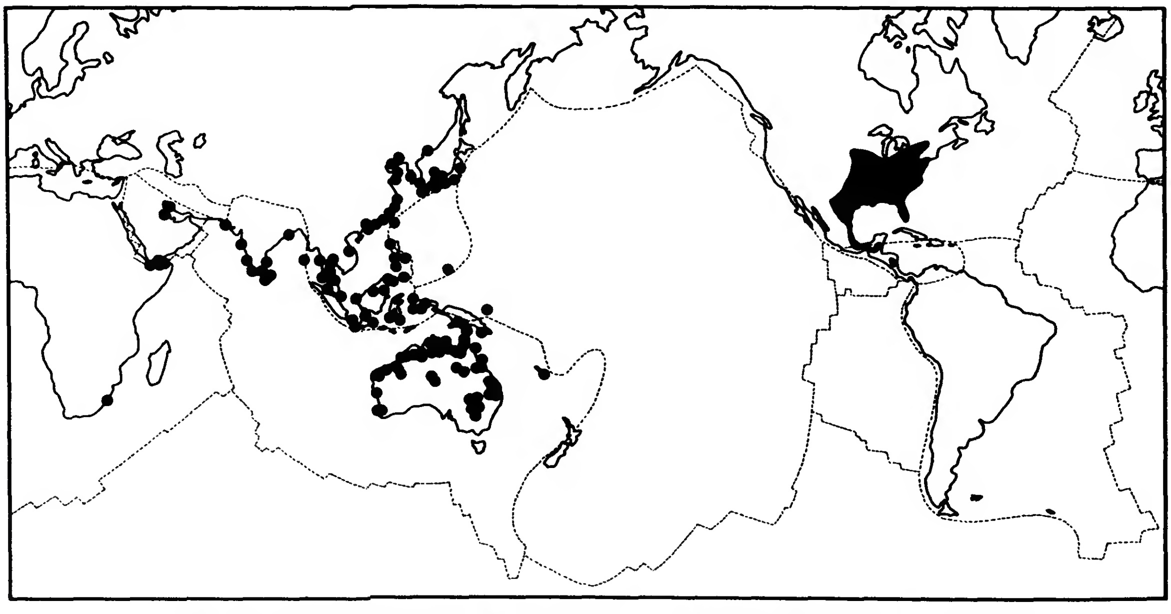

FIGURE 16.—Distribution of the fishes of the clupeid subfamily Dorosomatinae, gizzard shads (dark areas in North and Central America indicate generalized freshwater distribution).

reported from the Marshalls and Hawaii, and G. Nelson (in litt.) informs me that *Etrumeus* (*E. micropus*) occurs in the Hawaiian Islands (Hawaiian exception; the same species also occurs in Japan). Whitehead (in litt.), however, doubts that *Dussumieria* occurs in the Hawaiian Islands. Whitehead (1973) essentially duplicated the distribution data of his earlier paper; however, most of the dussumierins do appear to be restricted to continental plate coastal areas.

CONGRIDAE

The conger eels are probably distributed circumglobally and consist of at least 21 genera and 80 species (R. Kanazawa, pers. comm.) of moderate to very large (to at least 2.7 m TL) fishes. They occur in waters from a few centimeters to several hundred meters depth, but most known species are shallow dwelling. Breeding probably takes place at great depths; the larvae are planktonic.

There are few shallow-dwelling species of congrids on the Pacific Plate. *Conger cinereus* ranges throughout the Indo-Pacific (the Hawaiian population has been recognized as an endemic subspecies), and there is one other species of *Conger* on the Plate, an Hawaiian endemic.

The monotypic *Poeciloconger* is known only from Mauritius (J.E. Böhlke, pers. comm.), Madagascar, Celebes, and Tahiti (Klausewitz, 1971). The Tahitian record is based on a Museum Godeffroy specimen (Günther, 1910), and for this reason alone might be suspect, but the rarity of this eel leaves open the question of the Tahitian record.

The garden eels (subfamily Heterocongrinae) are represented on the Pacific Plate by three species, of which two are endemics: *Heteroconger lentiginosus* from the Marquesas and Societies (Böhlke and Randall, 1981), and *Gorgasia hawaiiensis* from the Hawaiian Islands (Randall and Chess, 1980). The other Plate species, *Heteroconger hassi*, ranges from the Maldives east to the Marshalls (Böhlke and Randall, 1981).

There are two species of *Ariosoma* reported from the Pacific Plate: *A. obud* from the Marshall Islands (Schultz, 1953a; also known from the Philippines), and *A. bowersi*, which is probably endemic to the Hawaiian Islands, where it is common. Günther (1910) reported on a specimen (as *Congromuraena bowersii*) procured by the Godeffroy Museum from south of the Gilbert Islands. The specimen is in the British Museum collections and its identification should be verified.

CONGROGADIDAE

The congrogadids comprise about ten genera and 20 species (Winterbottom, 1980) of small (maximum size about 300 mm SL), elongate fishes restricted to the reefs and rocky bottoms of the Indo-West Pacific (Figure 17). Castle (1980) has shown that a report of *Congrogadus* from the Hawaiian Islands was based on a congrid eel.

CORACINIDAE

The coracinids consist of a single genus, *Coracinus*, with two species. They are of moderate size (to over 500 mm TL and 7 kg), free swimming, and limited to the southern and southeastern coasts of Africa and Madagascar (Smith, 1953). They are here questionably considered to be warm-water fishes.

CORYPHAENIDAE

The dolphins consist of one genus and two species (*Coryphaena hippurus*, *C. equisetis*), approximately 1500 and 570 mm maximum TL, that are circumglobally distributed in warm waters (Gibbs and Collette, 1959; Collette, Gibbs, and Clipper, 1969). The species are primarily pelagic, but the young are often taken inshore. *Coryphaena equisetis* has been reported on the Pacific Plate only from the Hawaiian Islands, but J.E. Randall (in litt.) has obtained specimens from numerous island groups on the Plate.

CREEDIIDAE

The Creediidae was reviewed by Nelson (1978, 1979), who recognized seven genera and 12 species. The identifications of several specimens he examined were left in doubt; hence, the species distributions and/or numbers of species as extracted here will undoubtedly change. The family consists of very small fishes (maximum SL ranging from 29–72 mm) that live on and in sandy and gravelly bottoms, and are restricted to the Indo-Pacific.

Apocreedia (monotypic) is restricted to southeast Africa; *Creedia* and *Shizochirus* (both monotypic) are restricted to Australia; and *Tewara* (monotypic) is restricted to New Zealand.

According to Nelson (1978), *Chalixodytes* contains two species, one (*C. chameleontoculis*) restricted to the Indian Ocean—Mauritius, Aldabra, Denis Island (Seychelles), southeast coast of Africa, and Cocos-Keeling Island—and the other (*C. tauensis*), a widely distributed Pacific Plate endemic—Tau and Tutuila islands (Samoa), Bikini, Rongerik, Rongelap, and Enewetak (Marshalls), Pitcairn, Saipan, and Palau (the last two localities on the Philippine-Pacific Plate margin). Nelson's specimens of *C. chameleontoculis* from Cocos-Keeling, which is intermediate in location between the areas where the other populations of the two species of *Chalixodytes* occur, are intermediate in dorsal- and anal-fin ray counts (which Nelson considered important for distinguishing the two species) between *C. chameleontoculis* and *C. tauensis*. It seems possible, therefore, that the two species may only represent geographic populations of a single species. However, the extensive geographic gap between the two groups of populations, from which no specimens of *Chalixodytes* are known, may be indicative of a barrier that is effectively isolating the populations and allowing them to diverge. Interestingly, Allen and Steene (1979), who did not refer to Nelson's paper, reported *C. tauensis* from Christmas Island (Indian Ocean), which is relatively close to Cocos-Keeling. At my suggestion, Allen re-examined his Christmas Island specimens and informed me (in litt.) that they also were intermediate in dorsal and anal-fin ray counts between the two species of *Chalixodytes*.

Crystallodytes (monotypic: *C. cookei*) is reported from the Hawaiian Islands (an endemic subspecies) and Enderbury (Phoenix) and Tau (Samoan) islands (with a common endemic subspecies). Randall (1973) reported *Crystallodytes* sp. from Tahiti, and there are specimens in the

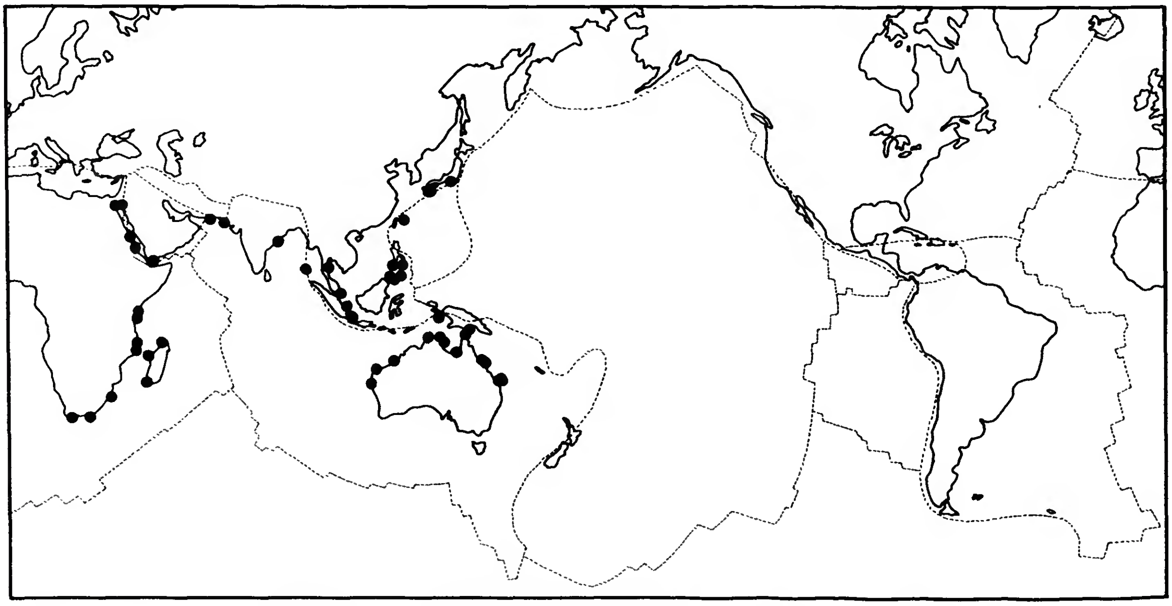

FIGURE 17.—Distribution of the fish family Congrogadidae (compiled by R. Winterbottom).

USNM collections from McKean (Phoenix Islands), Vostok, Jarvis, and Malden (all Line Islands). Randall (in litt.) informs me that he collected *Crystallodytes* at Easter Island; the identity of his species has not been established. *Crystallodytes* appears to be a widely distributed Pacific Plate endemic genus (Figure 60). Its closest sister group is undecided. The distribution of the two subspecies of *Crystallodytes cookei* parallels the distribution of the two subspecies of *Hyporhamphus acutus* (Hemirhamphidae, q.v.).

Limnichthys contains five species: two are restricted to New Zealand and the Chatham Islands; one is widely distributed in, and limited to, the Indian Ocean; one (*L. donaldsoni*) is widely distributed on the Pacific Plate (but not in the Gilbert Islands) and perhaps also occurs at Taiwan; and one (*L. fasciatus*) is widely distributed in the western Pacific with a lone occurrence in the Gilbert Islands, on the Pacific Plate.

CYNOGLOSSIDAE

The tongue soles comprise three genera and perhaps over 100 species of small- to moderate-sized (up to about 500 mm TL), benthic fishes that are found on sandy and muddy bottoms at depths ranging from a few centimeters (particularly some juveniles) to almost 2000 m. Some species enter freshwater, others are common in brackish or marine waters. Eggs and larvae are pelagic.

Cynoglossus (49 species, restricted to the Indo-West Pacific and upper west coast of Africa) and *Paraplagusia* (three species, restricted to the Indo-West Pacific) were revised recently (Menon, 1977, 1980). *Symphurus* is distributed circumglobally in tropical and warm-temperate waters, but, other than marginally, is known on the Pacific Plate only from the Hawaiian Islands (Hawaiian exception; Figure 18), where two endemic species occur at depths of about 100 m or more.

The inability of cynoglossids to colonize the littoral portions of many islands of the Pacific Plate may be a consequence of improper ecological conditions. On the other hand, the true soles (Soleidae), which appear to occupy habitats similar to those of the tongue soles, and may even be collected together with them, are found at various islands on the Pacific Plate. I have obtained

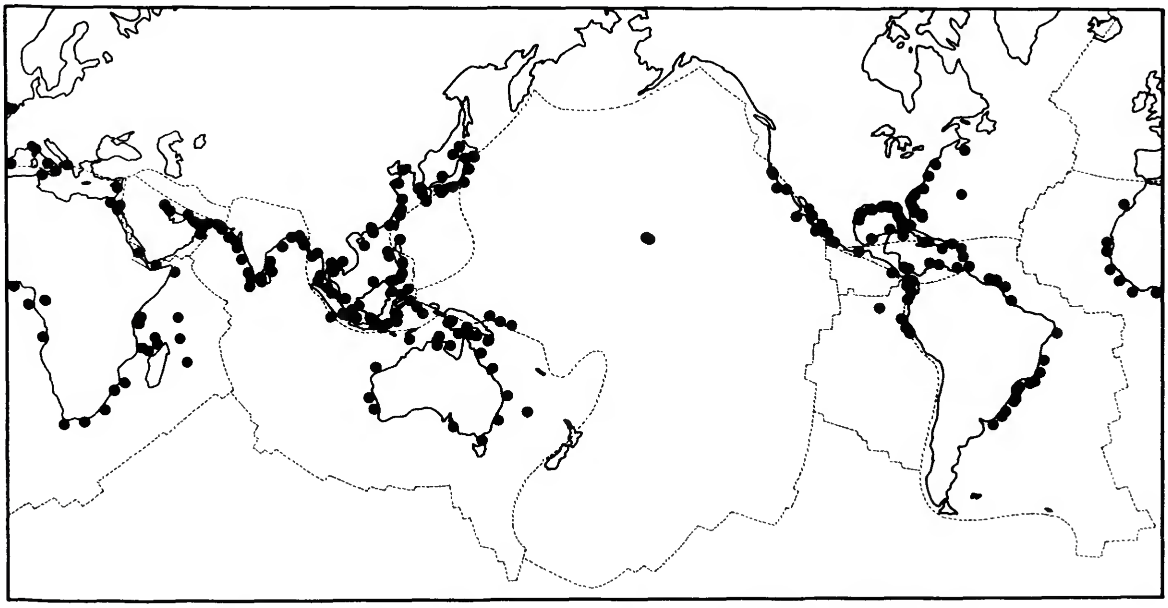

FIGURE 18.—Distribution of the fishes of the family Cynoglossidae (tongue soles).

tongue soles in habitats on the coast of Florida that were seemingly very similar to habitats on the coast of Ponape, where I obtained none. I, therefore, doubt that ecological conditions are responsible for the general absence of cynoglossids from the Pacific Plate.

DACTYLOPTERIDAE

The flying gurnards comprise two to four genera and five species of moderate-sized, benthic fishes (to about 500 mm SL) with planktonic larvae and young. The family is distributed almost circumglobally. One species is restricted to the Mediterranean, Atlantic, and eastern Pacific, and four are found in the Indo-Pacific. Only one of the Indo-Pacific species, *Dactyloptena orientalis*, occurs on the Pacific Plate, and in that area has been reported nonmarginally only from the Hawaiian, Society, and Tuamotu islands (Pacific Plate distributions similar to this one often characterize endemic species; reexamination of specimens from these localities might be of interest). Two of the remaining three species of flying gunards are widely distributed in the Indo-West Pacific, and have their eastern distributional limits along the western margin of the Philippine Plate. The third species (undescribed; W.N. Eschmeyer, pers. comm.) is known only from the Philippine Islands.

DASYATIDIDAE

The stingrays comprise four or five genera and a large number of viviparous, benthic species, some of which attain great size (breadth about 2 m, weight about 135 kg). There are few records of stingrays from the Pacific Plate, possibly because collectors avoid the group, most of the species of which are extremely venomous. Probably five species in four genera occur nonmarginally on the Plate. John E. Randall (pers. comm.) recently obtained a large specimen of an unidentified species of *Urogymnus* from Enewetak. This constitutes the only record of *Urogymnus* from the Pacific Plate.

DIODONTIDAE

The porcupinefishes comprise two or three genera and about 15 moderate-sized species of fishes with planktonic eggs and young. Only one genus, *Diodon*, has been revised in recent times (Leis, 1978; see also Kotthaus, 1979, for an additional, probably invalid, species). *Diodon* comprises five species, four of which occur nonmarginally on the Pacific Plate (Leis, 1978, figs. 8 and 14 are world distribution maps) as well as in the Indo-West Pacific. The fifth species is restricted to southern Australia.

Chilomycterus, which has a circumglobal distribution, has been reported nonmarginally from the Pacific Plate only from the Hawaiian Islands (*C. affinis*; Hawaiian exception). *Chilomycterus affinis* is also reported from Japan and the eastern Pacific, and Randall and Cea Egaña (in press) report it from Easter Island.

DREPANIDAE

The Drepanidae (sometimes considered a subfamily of the Ephippididae) consists of one genus and one or two species of moderate-sized (to about 400 mm TL), free-swimming fishes that range from the tropical west African coast eastward to Japan, New Guinea, and Samoa on the western margin of the Pacific Plate. The absence of drepanids from the nonmarginal portions of the Pacific Plate is perhaps unexpected.

ECHENEIDIDAE

There are four genera and eight species of remoras. These vary in maximum size from about 300–1000 mm TL. The species are usually found attached by their sucking disks to free-swimming vertebrates, but some are also free swimming. All but one species (*Echeneis naucratoides*), which is restricted to the Atlantic, are reported to be worldwide in distribution (Lachner, 1978), but I have been informed by E.A. Lachner (pers. comm.) that *Remora australis* has not been recorded from anywhere in the Indo-Pacific (except southeasternmost South Africa) and that *Echeneis naucrates* is either rare or absent in the eastern Pacific. Probably six species of Echeneididae are present nonmarginally on the Pacific Plate.

ELEOTRIDIDAE

The sleepers are a speciose family of small- to moderate-sized (maximum about 500 mm TL) fishes occurring circumglobally in habitats ranging from freshwater to coral reefs. The Indo-Pacific genera are in need of revision. Many marine Indo-Pacific genera treated as eleotridids in the literature belong in the family Gobiidae. According to Larson and Hoese (1980), there are only four genera of eleotridids confined to coral reefs in the Indo-Pacific (*Allomicrodesmus*, *Xenisthmus*, *Calumia*, and one undescribed); the other Indo-Pacific genera inhabit fresh and brackish water.

Allomicrodesmus was described from a single specimen from the Marshall Islands and placed in the Microdesmidae by Schultz (1966a). D.F. Hoese (in litt.) believes *Allomicrodesmus* is a highly aberrant eleotridid, and states that he has a specimen from the northern Great Barrier Reef. I know of no other records for this genus.

Calumia contains two reef-dwelling species (Larson and Hoese, 1980): *C. godeffroyi*, which ranges from the east coast of Africa to Tahiti, and *C. profunda*, known from the Philippines, Moluccas (Ceram), western Admiralty, New Britain, Solomon, and New Hebrides islands (Larson and Hoese, 1980; E.A. Lachner, unpublished data); hence, absent from the Pacific Plate nonmarginally.

The widely distributed Indo-West Pacific genus *Butis*, which occurs in rivers and estuaries, and mangroves, is known from the Pacific Plate nonmarginally only at Ponape (USNM collections), which provides evidence for operation of the Caroline Islands conduit. See also "Addendum."

ELOPIDAE

(including Megalopidae)

The tarpons and ladyfishes comprise three genera of free-swimming fishes with planktonic young that enter and develop in shallow coastal areas and estuaries. The adults may ascend rivers. *Elops* is, perhaps, circumglobally distributed, but has not been reported from the easternmost islands on the Pacific Plate. *Elops* contains three to eight species (a revision is needed) of moderate size (to about 1 m SL). Two of these occur nonmarginally on the Pacific Plate. *Tarpon* is monotypic, very large (to about 2.4 m TL and 160 kg), and restricted to the warm waters of the Atlantic, both sides. *Tarpon* reaches the Pacific terminus of the Panama Canal from the Atlantic, but apparently has not established a breeding population in the eastern Pacific. *Megalops* is monotypic, of moderate size (to about 550 mm TL), and ranges from the east coast of Africa to the Society Islands. Interestingly, *Megalops* has not been reported from the Eastern Caroline, Marshall, Gilbert, Ellice, Line, Tuamotu, or Hawaiian islands. Possibly, *Megalops* occurs only as a straggler on the Pacific Plate, although Randall (in litt.) does not believe it to be a straggler in the Society Islands. More records from Plate localities, including the occurrence of young, would be desirable.

EMMELICHTHYIDAE

The emmelichthyids comprise three genera and ten species of small (to about 500 mm SL), moderately deep-dwelling fishes (Heemstra and Randall, 1977), which, as adults, are suprabenthic at depths of 100–400 m. The only records for the Pacific Plate are either marginal or for the Hawaiian Islands, where three species occur (Figure 19), Hawaiian exceptions. Of the three Hawaiian species, one also occurs at Japan, Australia, and the Philippines (Randall, in press b), one also at Easter Island and Guam (Myers and Shepard, 1981), and which may be limited to the Pacific Plate and its margins, and the third is either an Hawaiian endemic or also occurs at Okinawa (Heemstra and Randall, 1977). Because of the difficulty of collecting emmelichthyids, their occurrences as Hawaiian exceptions may be a collecting artifact. The family seems to be restricted somewhat to subtropical and temperate areas in the Indo-West Pacific, which may explain its general absence from the Pacific Plate islands. Nonmarginal Pacific Plate records are worth reporting.

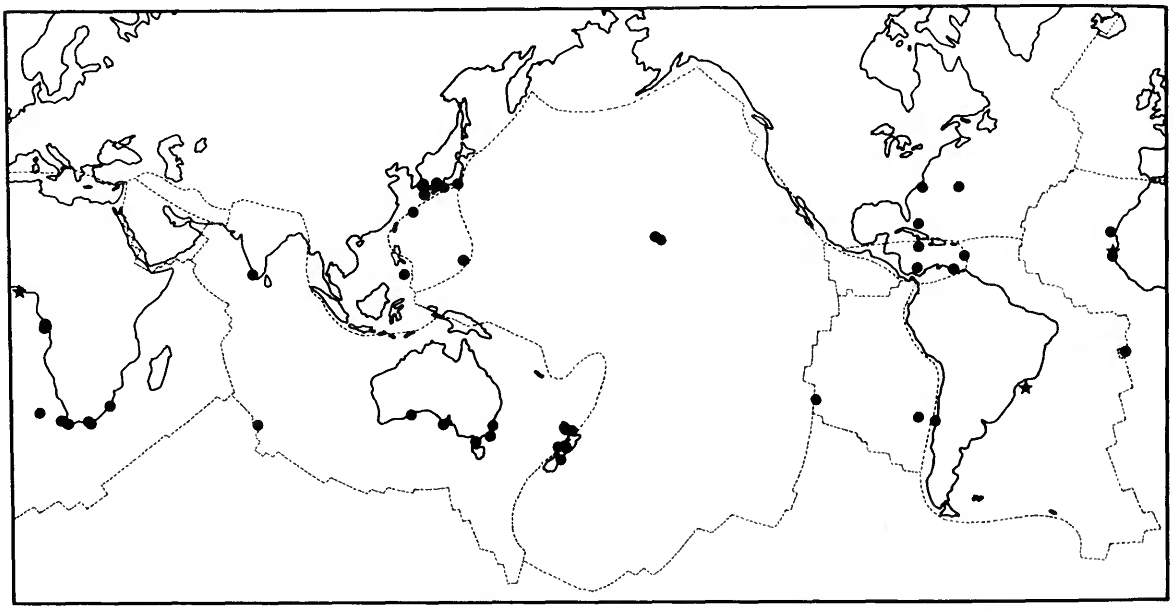

FIGURE 19.—Distribution of the fishes of the family Emmelichthyidae (stars indicate unspecified localities in certain areas of the southeast Brazilian (Zavala-Camin, 1981) and west African coasts.

ENGRAULIDIDAE

The anchovies are a circumglobally distributed group of small, free-swimming fishes (largest species attaining about 350 mm TL) that inhabit coastal areas. Many species appear to live primarily in fresh or low salinity waters. There are 15 genera and 128 species of anchovies, and eight genera and 62 species occur in the Indo-Pacific (P.J. Whitehead, in litt.), but only two genera (*Stolephorus*, *Encrasicholina*) and four species occur nonmarginally on the Pacific Plate (G. Nelson, in litt.).

ENOPLOSIDAE

There is but one species of enoplosid, *Enoplosus armatus*, a small fish attaining about 250 mm TL, and primarily restricted to the cooler waters of southern Australia, but occasionally reaching southern Queensland and entering freshwater (Lake, 1971). Nelson (1974) included Celebes in the range of *Enoplosus*, based undoubtedly on Norman's (1966) erroneous synonymy of *Pterapogon kauderni* Koumans (1933) with *Enoplosus armatus*. *Pterapogon kauderni* bears a striking, but superficial, similarity (see Koumans, 1933, pl. 1: fig. 1) to the way one might expect the young of *E. armatus* to appear, but Koumans was correct in considering *Pterapogon* to be an apogonid (see also Fraser, 1972).

EPHIPPIDIDAE

(including Platacidae)

The spadefishes are perhaps a circumglobal family, but they are unreported from the easternmost islands on the Pacific Plate. The family includes six genera and about ten species of moderate-sized (to about 9 kg), free-swimming fishes. Four genera and about seven species occur in (and are restricted to) the Indo-Pacific, but only one genus, *Platax*, and only one or two of its approximately five species, occur nonmarginally on the Pacific Plate.

EXOCOETIDAE

(not including Hemiramphidae)

There are about eight genera and perhaps as many as 100 species-group taxa of flyingfishes, of which the Indo-Pacific forms are most poorly known systematically. The family is circumglobally distributed and the species are epipelagic and, in general, widely distributed. The young are often taken inshore. Possibly five genera and 15 species occur nonmarginally on the Pacific Plate.

FISTULARIIDAE

The cornetfishes consist of a single, circumglobally distributed genus, *Fistularia*, and four species. The species are free swimming and attain a maximum length of 1–2 m. Fritzsche (1976) revised *Fistularia* and presented a distribution map for the species. One species is restricted to the tropical eastern Pacific and one to the tropical Atlantic (both sides). One species occurs from the east African coast to the tropical coasts of the eastern Pacific. The fourth species, *F. petimba*, is almost circumglobal and has an Hawaiian exception distribution: both sides of the tropical Atlantic; Indo-West Pacific from Madagascar to Japan, Philippines, and Australia; and Hawaiian Islands (only nonmarginal Pacific Plate occurrence). Although *Fistularia* is not present in the Mediterranean, it is reported from the Miocene of that region (Arambourg, 1925).

FORMIONIDAE (= APOLECTIDAE)

There is but a single, monotypic genus in the Formionidae, *Apolectus* (= *Formio* = *Parastromateus*), a free-swimming fish probably not attaining more than 300 mm TL, but occasionally stated to reach 600 mm TL. Witzell (1978, fig. 8) reported on the distribution of *Apolectus*, which extends from eastern Africa eastward to Japan, Philippines, and eastern Australia. Additionally, Zama and Fujita (1977) give citations to the occurrence of *Apolectus* in the Bonin, or Ogasawara, Islands, adjacent to the margin of the Pacific Plate, and Dor (1970), reported it from the Red Sea. Reports of the occurrence of *Apolectus* in Hawaii all appear to emanate from Matsubara (1955:565). Matsubara's listing is probably in error (see also Menidae). I know of no other nonmarginal Pacific Plate record for *Apolectus*.

GERREIDAE

The mojarras are a family of small, free-swimming, epibenthic fishes (maximum size about 400 mm TL) that are poorly known taxonomically. There are about six genera and perhaps 40 species. The species are primarily marine but often enter brackish or freshwater, and are found on the warm coasts of all oceans; however, they are reported nonmarginally from the Pacific Plate only from the Eastern Caroline, Gilbert, Ellice, and Marshall islands (Fowler, 1928, 1931, 1934). These records probably involve only species of *Gerres*. Randall (1973) discounts Jordan and Seale's (1906) report of *Gerres argyreus* (as *Xystaema argyreum*) from Tahiti.

GINGLYMOSTOMATIDAE

This family is discussed under the Orectolobidae.

GIRELLIDAE

The girellids are a small family containing one or two genera and about 15 species of moderate-sized fishes (to about 625 mm TL and 8 kg) that are absent from the Pacific Plate. These fishes are questionably included here as a warm-water group. The family is antiequatorially distributed, and occurs on the coasts of Japan, China, southern Australia (as far north as southern Queensland), Lord Howe and Norfolk islands, New Zealand, Easter Island, California to, and including, the Gulf of California, Galapagos, Chile and its offshore islands, Peru, and the Cape Verde and Canary islands in the eastern Atlantic (D.F. Hoese, in litt.). Lee and Chang (1981) reported

Girella punctata from Batan Island, which lies midway between Taiwan and Luzon, and is politically part of the Philippines. I have not included the Girellidae as part of the Philippine fauna for the purposes of Tables A and B (Appendix 2).

GLAUCOSOMATIDAE

This family contains a single genus, *Glaucosoma*, and four species (Arai and Fujii, 1981) of free-swimming fishes that attain a maximum total length of about 450 mm. The species have been reported only from the coasts of Japan, China, Philippines, and Australia. In Queensland, it is known only from the offshore southern portions of the coast; therefore, the overall distribution of *Glaucosoma* appears to be antiequatorial.

GOBIESOCIDAE

The clingfishes comprise about 40 genera and 110 species of small (largest species is about 300 mm TL, but most are under 75 mm), benthic, nest-building fishes with planktonic larvae. The species occur in a variety of habitats, including freshwater rivers and coral reefs. Several species live commensally with crinoids. Clingfishes occur in all oceans, as well as the Mediterranean and Black Sea, and are generally widely distributed along continental coastlines. Most of the genera, but only about one-third of the species, occur in the Indo-Pacific. Only four species are known from the nonmarginal areas on the Pacific Plate, and on the Plate each is known from a single locality. One of these species, *Trachelochismus pinnulatus* (otherwise restricted to New Zealand), questionably occurs at the Chatham Islands, which, although nonmarginal on the Pacific Plate, are on the continental shelf of New Zealand. Hence, *T. pinnulatus* is excluded from further consideration here.[1] *Pherallodus indicus* is reported from several Indonesian localities and from Raroia, Tuamotus (Briggs, 1955). *Liobranchia stria* is reported only from Saipan, Marianas, and Bikini, Marshalls (Briggs, 1955; Schultz, 1966b). *Liobranchia*, is possibly a Pacific Plate endemic genus (Figure 60). Randall (in press b) obtained *Lepadichthys frenatus* from the Pitcairn Island group; this species is otherwise known only from widely scattered localities in the western Pacific. Briggs (1955:215, map) inadvertently indicated the presence of *Lepadichthys* [*minor*] in the Ellice Islands, on the Pacific Plate; Samoa was intended, as indicated in his materials list.

Most species of tropical Indo-Pacific clingfishes are tiny, and more will probably be found to occur on the Pacific Plate.

GOBIIDAE

The gobies are probably the largest family of fishes, perhaps containing as many as 2000 species (Hoese and Allen, 1977). Most of the species are small, and among these are the smallest vertebrates (some species of *Eviota* mature at less than 10 mm SL; E.A. Lachner, pers. comm.). Among the largest gobies is the Japanese genus *Synechogobius*, which attains a total length of 500 mm (Takita, 1975). Gobies are essentially benthic or suprabenthic in habit. Some species are restricted to freshwater, some are estuarine, but most are reef or near-reef inhabitants. Hoese and Allen (1977) estimate that 400–600 species of gobiids occur on the coral reefs of the Indo-Pacific.

The taxonomic limits of gobiid genera are poorly known and very few of the Indo-Pacific genera have been revised in recent years. The list of Pacific Plate genera (estimated 150 species; Table C, Appendix 2) was compiled from the literature, USNM collections, and in consultation with D.F. Hoese (see also "Addendum"). Among the genera, *Lentipes* (adults of which inhabit freshwater in Hawaii), with one species (Maciolek,

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[1] Hutton (1896) described *Crepidogaster simus* (a synonym of *T. pinnulatus*) from "Lyttleton Harbor [New Zealand] and Chatham Islands." Information in the description appears to refer to a single specimen. If only one specimen was involved, it could not have come from both localities. *Trachelochismus pinnulatus* has been collected at New Zealand localities many times, but has not been reported to have been collected at the Chatham Islands subsequent to the initial report.

1978), and *Vitraria* (coral-reef inhabitant), with one species, appear to be Pacific Plate endemic genera (Figure 60). The presence of *Lentipes* in the Ryukyus is based on a species described by Sakai and Nakamura (1979); its generic allocation should be verified.

Kelloggella was revised by Hoese (1975) and a new record added by Kuramochi (1980). Hoese (in litt.) informed me of an additional species (undescribed) and of changes (pers. comm.) in the reported distributions of two described species. The distribution of the five *Kelloggella* species is given in Figure 20. Except for endemic genera, *Kelloggella* is unique among fishes in having more Pacific Plate species than Indo-West Pacific species.

Among the reasonably well-known Indo-Pacific goby genera that are excluded from the Pacific Plate is *Gobiopsis* (sensu stricto), with ten species (Lachner and McKinney, 1978, 1979), which are often collected on coral reefs. *Gobiopsis* sensu stricto is distributed from southeastern Africa to the western margin of the Pacific Plate. One of three species of *Gobiopsis*, not included in *Gobiopsis* sensu stricto, reaches from the Indo-West Pacific to the Gilbert Islands (Lachner and McKinney, 1979). *Signigobius*, monotypic, also a reef inhabitant (Hoese and Allen, 1977), is distributed from the Philippine and Palau islands to the Great Barrier Reef and Solomon Islands, and is, thus, limited in the east by the margin of the Pacific Plate. *Oxuderces*, monotypic, a muddy bottom inhabitant, ranges from India to the Gulf of Carpentaria, Australia (Springer, 1978, and Australian Museum collections).

Feia was discussed by Lachner and McKinney (1979). They recognized one species in the genus, but noted that their Indo-West Pacific specimens (Mozambique, Seychelles, Banda, and Great Barrier Reef) were separable from their Rapa Island (Pacific Plate) specimens, based on meristics and pigmentation, indicating that two taxa are possibly involved.

Eviota comprises about 60 species of diminutive coral-reef gobies, all restricted to the Indo-Pacific (S. Jewett, pers. comm.). Lachner and

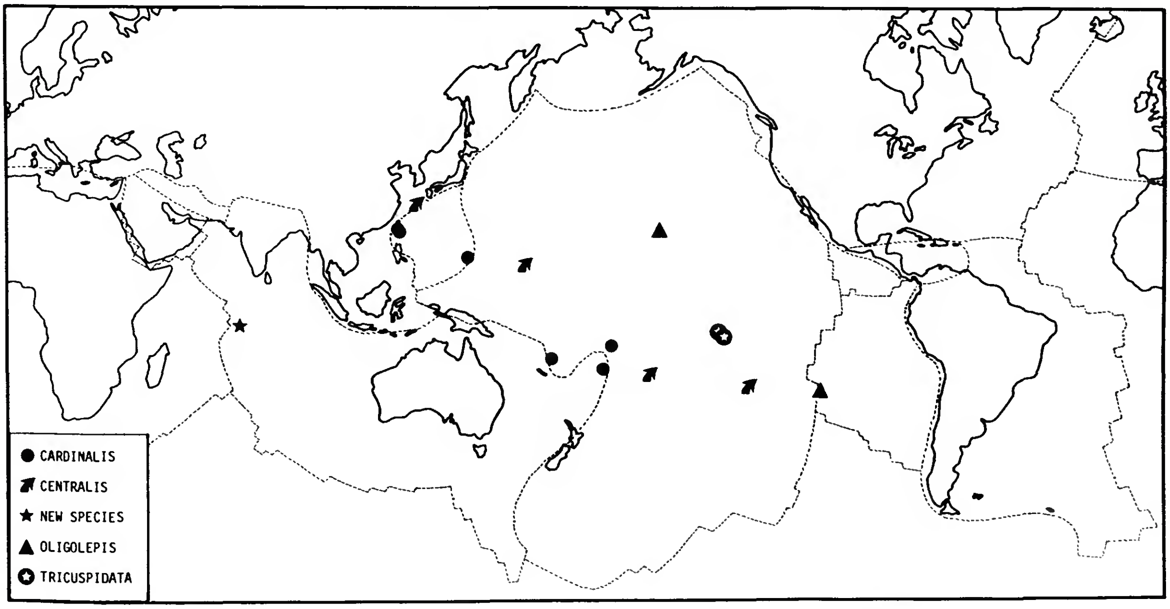

FIGURE 20.—Distributions of the species of the gobiid fish genus *Kelloggella* ("new species" per D.F. Hoese, in litt.).

Karnella (1980) revised 31 of the species, and Karnella and Lachner (1981) revised three others. Of the 34 species revised, 23 reach the western margin of the Pacific Plate from the west, but only 11 of the 23 (48%) extend nonmarginally onto the Plate. One of the 11, *E. lachdeberei*, is known on the Pacific Plate only from Ponape (USNM collections) and Truk, Eastern Caroline Islands, providing evidence favoring operation of the Caroline Islands conduit. Two species are Pacific Plate endemics: *E. epiphanes*, from Hawaiian, Johnston, and Christmas (Line) islands; *E. disrupta*, from the Tonga, Samoan, Society, and Tuamotu islands.

Nemateleotris contains three species of coral-reef gobies (Randall and Allen, 1973): *N. decora*, which ranges from the western Indian Ocean to the western margin of the Pacific Plate; *N. helfrichi*, which is a widely distributed Pacific Plate endemic; and *N. magnifica*, which completely overlaps the range of the other two species (Figure 21). The three species are sympatric in the Palau and Samoan islands, both along the margin of the Pacific Plate. It is not possible to decide from Randall and Allen's study whether *N. decora* and *N. helfrichi* are sister species, but these two species were keyed out together and show greater morphological similarity to each other than either does to *N. magnifica*. The evidence is slight, but there is a good chance, in the present case, that an Indo-West Pacific species is the sister species of a Pacific Plate endemic, and that the two species have undergone slight dispersal since their divergence, which would account for their sympatry along the Pacific Plate margin.

Periophthalmus, a mangrove inhabiting genus in need of revision, occurs on the tropical west African coast as far south as Angola. It reappears on the east African coast and ranges westward to the western margin of the Pacific Plate, and is known nonmarginally on the Plate only from Ponape, Eastern Caroline Islands, which provides evidence for the operation of the Caroline Island conduit. Disjunct west African distributions of otherwise Indo-Pacific fishes is a repeated distribution pattern (for some additional examples see Lethrinidae).

Discordipinna is monotypic, diminutive (to 20

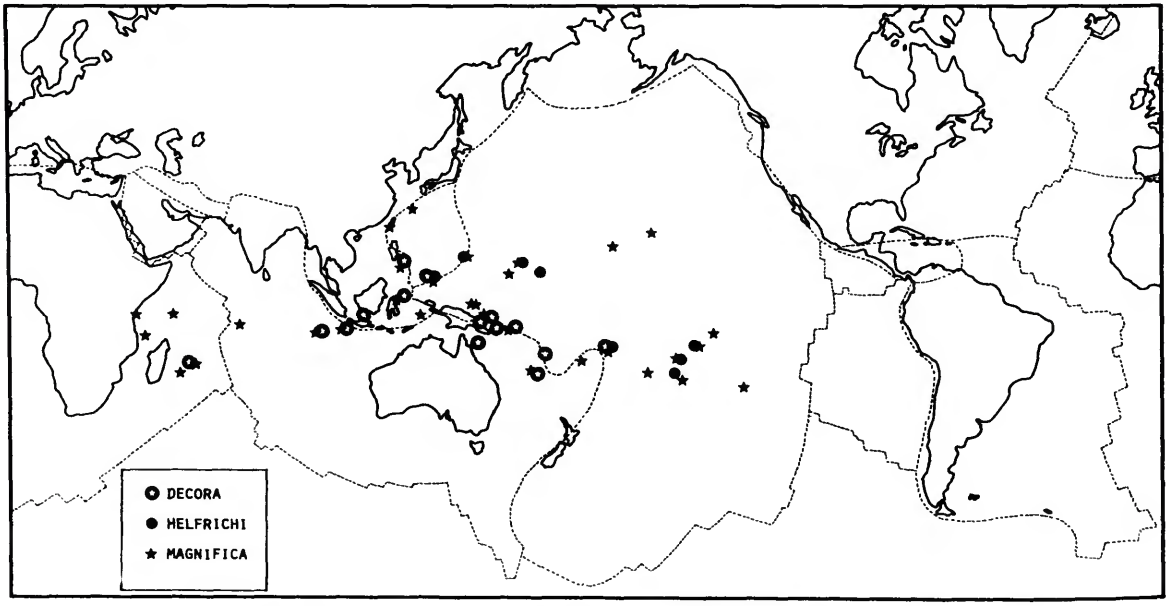

FIGURE 21.—Distributions of the three species of the gobiid fish genus *Nemateleotris*.

mm SL), and a reef inhabitant. It ranges from the Red Sea to the Hawaiian and Marquesas islands (Randall, 1981a).

GOBIOIDIDAE

(including Taenioididae)

The gobioidids are small, elongate fishes (maximum size about 470 mm SL) living benthically on muddy bottoms, typically in brackish bays, although the same species may be taken offshore in marine waters and well up freshwater rivers. There are several genera, but probably fewer than 20 species, and these occur, variously, along the warm coastal areas of the eastern Pacific, eastern and western Atlantic, and Indo-West Pacific from Africa to Guam and New Guinea. Prior to my 1980 collecting trip to Ponape, Eastern Caroline Islands, gobioidids were unknown on the Pacific Plate nonmarginally. I obtained two genera (Table C, Appendix 2) in a single collection at Ponape, in a coarse muddy area adjacent to a river mouth and mangrove shore. The Caroline Islands chain apparently serves as a conduit permitting gobioidids to disperse to the Pacific Plate. I doubt that they occur further east than Kosrae (Kusaie) at the end of the chain. See also "Addendum."

GONORYNCHIDAE

The Gonorynchidae consists of a single genus, *Gonorynchus*, and perhaps as many as six species (the genus has not been revised). The gonorynchids attain a maximum size of about 600 mm TL and are suprabenthic on sandy bottoms. The family occurs nonmarginally on the Pacific Plate only at the Hawaiian islands (Hawaiian exception); it is otherwise antitropically distributed. Gonorynchids have been reported most often from the Indo-West Pacific: Japan and Korea south to the Pescadores Islands, southern Australia (as far north as southern Queensland), New Zealand, Réunion, and southeastern Africa, but they also occur at St. Helena in the eastern Atlantic (Penrith, 1976), and Mead (1970) and McCosker (1971) quote R.H. Rosenblatt as stating that the Scripps Institution of Oceanography marine vertebrate collection has a specimen from the Juan Fernandez and San Felix Ridge, off Chile. Some authors believe that there is only one species of gonorynchid, but the north-south disjunct distribution of the family suggests the possibility that two species or more are involved.

GRAMMATIDAE

The monophyly of the Grammatidae is open to serious question. For instance, Nelson (1974) included the following in the Grammatidae: *Pseudochromichthys*, which is a synonym of the plesiopid genus *Plesiops* (Aoyagi, 1943; Schultz, 1943); *Fraudella*, which is a plesiopid (G.D. Johnson, pers. comm.; incidentally, the Plesiopidae also appears to be polyphyletic); and *Pseudocrenilabrus*, which is a cichlid (Trewavas, 1973). Even without these three genera there is little evidence to unite the remaining five genera, and perhaps 20 species that could be considered in the family (as most recently defined by Böhlke, 1960). The western Atlantic genera (*Gramma*, *Lipogramma*) are coral-reef forms of shallow to moderate depths. *Stigmatonotus* is known only from coastal Western Australia. *Grammatonotus* is known from deep water off Hawaii (Hawaiian exception; only nonmarginal Pacific Plate occurrence of Grammatidae), the western Indian Ocean (based on the type species of *Parabarossia* Kotthaus, 1976, which Kotthaus assigned to the Plesiopidae), Japan, Philippines, New Caledonia (G.D. Johnson, pers. comm.), and the Kei Islands, Indonesia. The nominal species of *Callanthias* all appear to belong in the Grammatidae, as considered here. They have been reported, variously, from southern Africa, southern Australia, New Zealand, Japan, the Mediterranean-eastern Atlantic, and the Nasca Ridge (G.D. Johnson, pers. comm.) and San Felix and Juan Fernandez islands in the eastern Pacific, and are, thus, bitemperately distributed.

GYMNURIDAE

The butterfly rays probably consist of a single genus, *Gymnura*, and fewer than ten, viviparous, species. The largest species attain over 2 m breadth. The family is circumglobally distributed, except that it is apparently absent from the Pacific Plate other than marginally, a distribution pattern duplicated by most elasmobranch groups.

Fowler (1928, 1941) placed *Raia pastinaca* variety *altavela* Forster (not Linnaeus), from Tana (New Hebrides), marginally off the Pacific Plate, into the synonymy of *Gymnura poecilura* (Shaw), an Indo-West Pacific species. Fowler did not give his reasons for the synonymy, which I believe was in error, and also mistakenly placed Tana in the Society Islands, which are well out on the Pacific Plate. Forster's (1844) description was based on an observed specimen that, apparently, was not retained. Forster included in his description a statement that there was a single row of small spines on the middle of the dorsum of his specimen. Gymnurids lack such a feature. Forster's specimen was probably a dasyatid. In the Indo-West Pacific, gymnurids range from the Red Sea and east coast of Africa eastward to Japan, and south to the Philippines and eastern Australia. There are no records of gymnurids from New Guinea or any other islands along the southwestern margin of the Pacific Plate. Based on present information, I do not believe that gymnurids occur in the New Hebrides or on the Pacific Plate. Bigelow and Schroeder (1953:398) probably followed Fowler (1928, 1941, 1944) in including Polynesia in the range of gymnurids.

HAEMULIDAE

There are 17 genera (Johnson, 1980) and about 100 species of grunts. The species are of small to moderate size (to about 610 mm TL), free swimming, suprabenthic, and usually associated with coral reefs or rocks. Although the family is circumglobally distributed, no genus is that widely distributed. *Pomadasys*, the most widely distributed genus of grunts, is found in the eastern Pacific, western Atlantic, Mediterranean, eastern Atlantic, and throughout the tropical Indo-West Pacific up to the western margin of the Pacific Plate (absent from the Pacific Plate nonmarginally). Eleven of the haemulid genera are restricted to the western hemisphere; two occur only in the eastern Atlantic, one (*Diagramma*) only in the Indo-West Pacific (absent from the Pacific Plate), one (*Parapristipoma*) only in the eastern Atlantic and Indo-West Pacific (absent from the Pacific Plate), and one (*Plectorhynchus*) in the Mediterranean, eastern Atlantic, and throughout much of the Indo-Pacific (but absent from the Hawaiian Islands), where it is represented nonmarginally on the Pacific Plate by five species at most. The family has, hence, only token representation on the Pacific Plate.

HARPADONTIDAE

The Bombay ducks comprise a single genus, *Harpadon*, and four species of small- to moderate-sized fishes (to about 710 mm TL) of commercial importance. These fishes are found in close-shore waters, estuaries, and relatively deep continental shelf waters (R.K. Johnson, pers. comm.) of the Indo-West Pacific, but are absent nonmarginally from the Pacific Plate. Sulak (1977) placed *Saurida* (which in my study is included in the Synodontidae) and *Harpadon* in a subfamily, Harpadontinae, of the Synodontidae. The constitution of these family-group taxa in my study reflects only common usage.

Harpadon has a spotty distribution. It appears to be present along the northeast and northwest coasts of India, but absent from around southern India and Ceylon, and ranges eastward through the Bay of Bengal to Sumatra, Java, Borneo, New Guinea, northern Australia, Philippines (Rau and Rau, 1980), and northward to the Yellow Sea as far as Korea. A number of authors list Zanzibar in the range of *Harpadon*, the earliest of which that I can locate is Bleeker (1866–1872). These reports appear to be second hand and, I believe, erroneous. Playfair and Günther (1866) did not report *Harpadon* from Zanzibar, nor did they in their subsequent papers on additions to the Zanzibar fish fauna. *Harpadon* is frequently dried for commercial purposes. In view of the extensive dhow movements around the Indian Ocean it could be expected that dried *Harpadon* would find its way to Zanzibar markets (and other ports of call) and be mistakenly believed to have originated in that area.

HEMIRAMPHIDAE

The halfbeaks are a family of small- to moderate-sized, nearshore, epipelagic fishes present in all tropical and warm-temperate seas. Some species enter brackish and freshwater. The family consists of 12 genera and 75 species (B.B. Collette, pers. comm.). Most species are oviparous, but some are viviparous. Eggs of marine forms bear numerous filaments and are often found attached to floating objects. N.V. Parin, B.B. Collette, and Yu. N. Shcherbachev (1980) revised the Indo-Pacific halfbeaks and presented distribution maps for the species (see also Collette, 1976, for a distribution map of *Rhynchorhamphus*, four species, which ranges from the Gulf of Aden to New Guinea, on the margin of the Pacific Plate).

In the Indo-Pacific there are seven marine genera with 40 species, three freshwater genera with eight species, and one genus (*Zenarchopterus*) with about 15 species, some of which are restricted to freshwater. Only four of the marine genera, represented by about eight species, and one euryhaline species of *Zenarchopterus* (*Z. dispar*) occur on the Pacific Plate nonmarginally. Two of the eight marine species (*Hyporhamphus acutus*, *Hemiramphus depauperatus*) are widely distributed Pacific Plate endemics.

Hyporhamphus acutus consists of two subspecies: one at Johnston and Hawaiian islands, the other widely distributed on the Pacific Plate, but absent from Johnston and Hawaiian islands (Figure 22; Collette, 1974). The taxa Collette (pers. comm.) considers to be most closely related to *H. acutus* are essentially absent from the Pacific Plate, allopatric, and consist of a group of three species restricted to southern Australia, Lord Howe, Norfolk, New Zealand, and the Chatham Islands. Specimens of *Hyporhamphus a. acutus* reported by Collette (1974) for the Tonga Islands, which are marginally off the Pacific Plate, may not have come from Tonga as the Tongan locality is en-

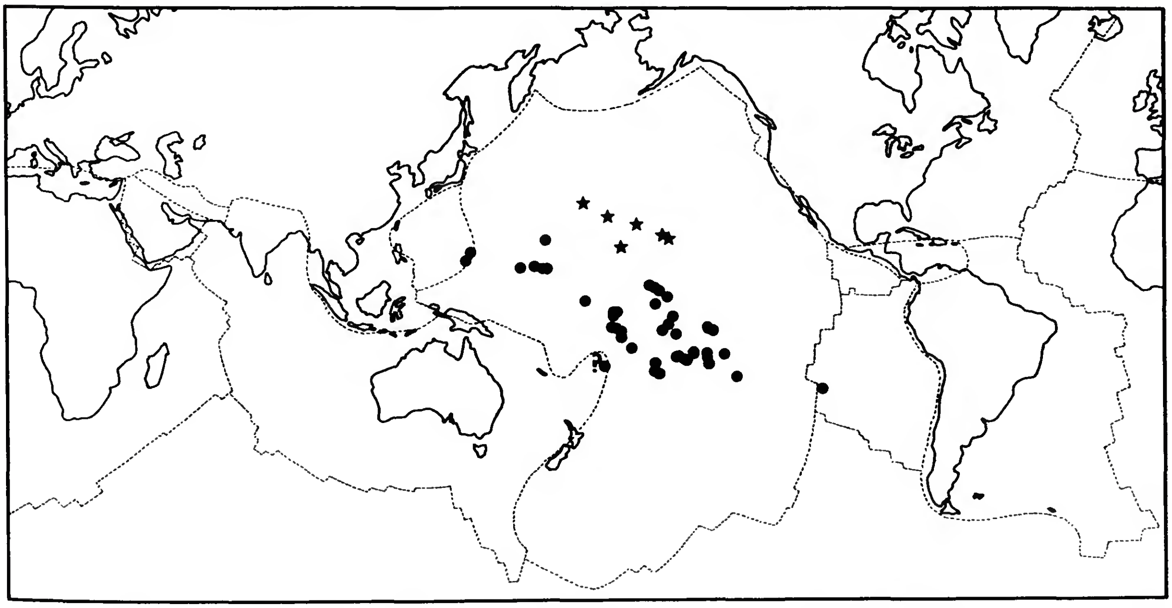

FIGURE 22.—Distributions of the two subspecies of the hemiramphid fish, *Hyporhamphus acutus*.

tered in the USNM catalog as questionable; however, the occurrence of *H. a. acutus* at Tonga would not be unexpected.

Hemiramphus depauperatus is known only from the Hawaiian, Line, Society, and Marquesas islands (Parin et al., 1980, fig. 34). Its closest relative is allopatric, either *H. saltator*, of the eastern Pacific, or *H. lutkei* (B.B. Collette, pers. comm.), which is widely distributed in the Indian and western Pacific oceans as far east on the Pacific Plate as the Gilbert, Marcus, and Kapingamarangi islands.

Oxyporhamphus is a circumglobal, oceanic, epipelagic genus that contains two species. *Oxyporhamphus micropterus* consists of two subspecies, one in the Atlantic (both sides and centrally) and one in the Indo-Pacific and eastern Pacific. *Oxyporhampus convexus* also contains two subspecies: *O. c. bruuni*, which occurs only in the Red Sea and northwest Indian Ocean, and *O. c. convexus*, which ranges (allopatrically) from the east coast of Africa to the western margin of the Pacific Plate. Parin et al. (1980, fig. 47) included a single nonmarginal Pacific Plate record for *O. c. convexus*, from the Eastern Caroline Islands. I questioned Parin about this exceptional record, and after reexamination he wrote that the specimens were misidentified and belonged in *O. micropterus*.

I collected *Zenarchopterus dispar* in the rivers of Ponape, eastern Caroline Islands, above the level of tidal influence, as well as in the mangrove areas along seashore. These specimens represent the only nonmarginal Pacific Plate records of *Zenarchopterus* and offer evidence favoring operation of the Caroline Islands conduit.

HEMISCYLLIIDAE

This family is discussed under the Orectolobidae.

HETERODONTIDAE

The horn, or Port Jackson, sharks comprise a single extant genus (*Heterodontus*) with eight species variously restricted to the Indo-West Pacific and Eastern Pacific (Figure 23). These sharks are relatively small (less than 1.5 m TL), sluggish,

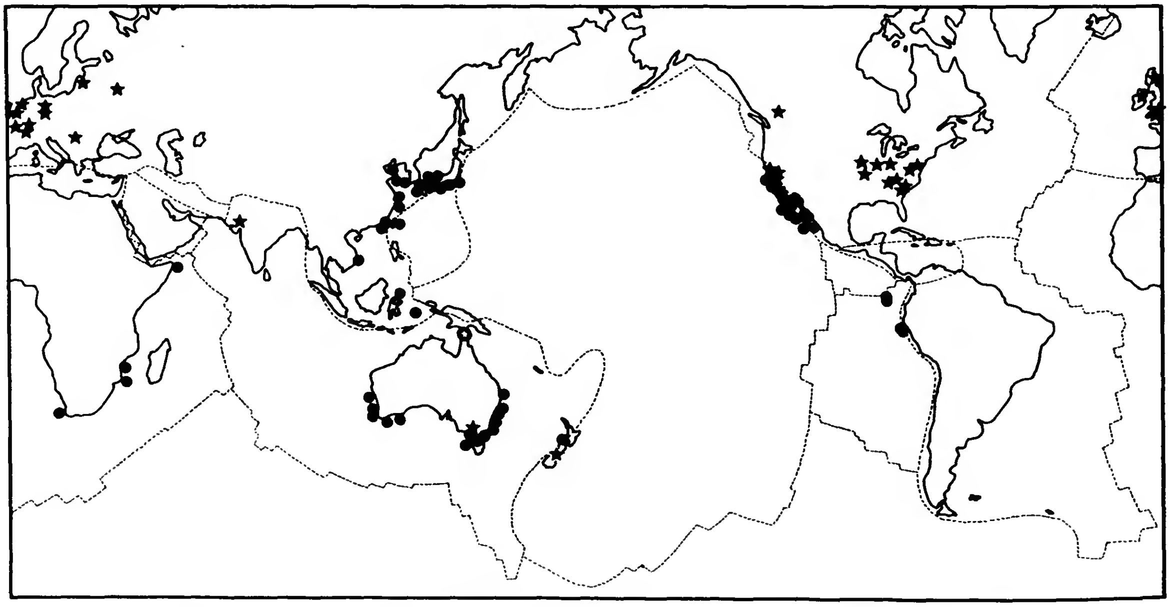

FIGURE 23.—Distribution of the shark family Heterodontidae (horn sharks) (closed circles indicate recent records; solid stars indicate fossil records; open star represents record based on an egg case).

oviparous, and benthic in shallow marine waters (to a maximum depth of about 170 m). The combined geographic distribution of the extant species is primarily antiequatorial.

Heterodontids (including *Heterodontus*) first appear in the Jurassic of Europe (Casier, 1954), and the fossil record, so far as I have been able to extract it (Figure 23), indicates the presence of heterodontids in eastern North America and western Europe (Atlantic) from the Mesozoic to the Eocene or Oligocene. Romer (1945, 1966) lists heterodontids as occurring during the Miocene in South America, but I have been unable to locate the origin of Romer's report or the specific locality.

J.A.F. Garrick (in litt.) states that there is only one firm (nonfossil) record of *Heterodontus* from New Zealand, from a gill net in shallow water near Makara, Wellington, in 1954. He considers the occurrence to have been the result of straggling. The same situation probably explains Bleeker's (1856, 1860) unrepeated records of *Heterodontus zebra* from Amboina and Celebes, if these records are valid; however, Fourmanoir and Nhu-Nhung (1965) reported *H. zebra* to be common during the summer at Nha-Trang, Viet Nam. The egg cases of some heterodontids have tendrils that may become entangled in marine plants, which in turn may spread about during storms. Heterodontid egg cases have been reported from areas where no free-living heterodontids are known. For instance, Whitley (1940) reported an egg case from Moa Island, north Queensland (Figure 23), whereas the sharks themselves have not been taken farther north than southern Queensland on the Australian coast. Hatching time has been reported variously to take from five to nine months, and an egg case would have considerable time to be dispersed before hatching. The narrow distributions of the living heterodontids, however, lead me to believe that the species have not dispersed widely in recent times.

HOLOCENTRIDAE

The squirrelfishes are a circumglobally distributed family comprising about 50–75 species. The species are small (reported to attain an SL of over 600 mm, but specimens 300–400 mm are not common), suprabenthic, live primarily around coral reefs and rocks, and have planktonic larvae. A revision (which I have not seen) of *Ostichthys* and description of a new genus is in press (Randall, Shimuzu, and Yamakawa, in press).

Among the squirrelfishes, the species of *Myripristis* have received the most attention systematically (Greenfield, 1965, 1968, 1974; Randall and Guézé, 1981). Even so, there is much useful work to be done on the classification, relationships, and distribution of the species. There are about 19 species of *Myripristis* in the Indo-Pacific. Most of these species are widely distributed, and include one species that ranges into the eastern Pacific. Four species appear to be restricted to areas west of the Pacific and Philippine plates, and four appear to be restricted to the Pacific Plate (Figure 24), of which, three are widely distributed Pacific and Philippine plate endemics (Table 2). Twenty-five other species are present nonmarginally on the Pacific Plate. Greenfield (1968, 1974) discussed relationships of the species in noncladistic terms. He related the widely distributed Pacific Plate endemics most closely to other widely distributed Pacific Plate endemics or to widely distributed Indo-Pacific species.

ISONIDAE

The isonids are a small, poorly known family comprising two genera and probably fewer than ten species of small (to about 50 mm SL) fishes that are often taken in the heavy surf zone (but I have collected them in protected areas in Taiwan). They have been collected along the coasts of southern and southeastern Africa, West Pakistan, northwestern India, southern Japan to southern Taiwan, the Admiralties, southern New South Wales (a doubtful record also from Freemantle, Western Australia), Samoa, Hawaii, Pitcairn, Rapa, and both sides of the southern end of South America (W. Ivantsoff, B. Chernoff, and J.E. Randall, pers. comm.; R.C. Wass, ms.).

ISTIOPHORIDAE

The billfishes, including the sailfishes and marlins, are large, primarily open ocean forms with

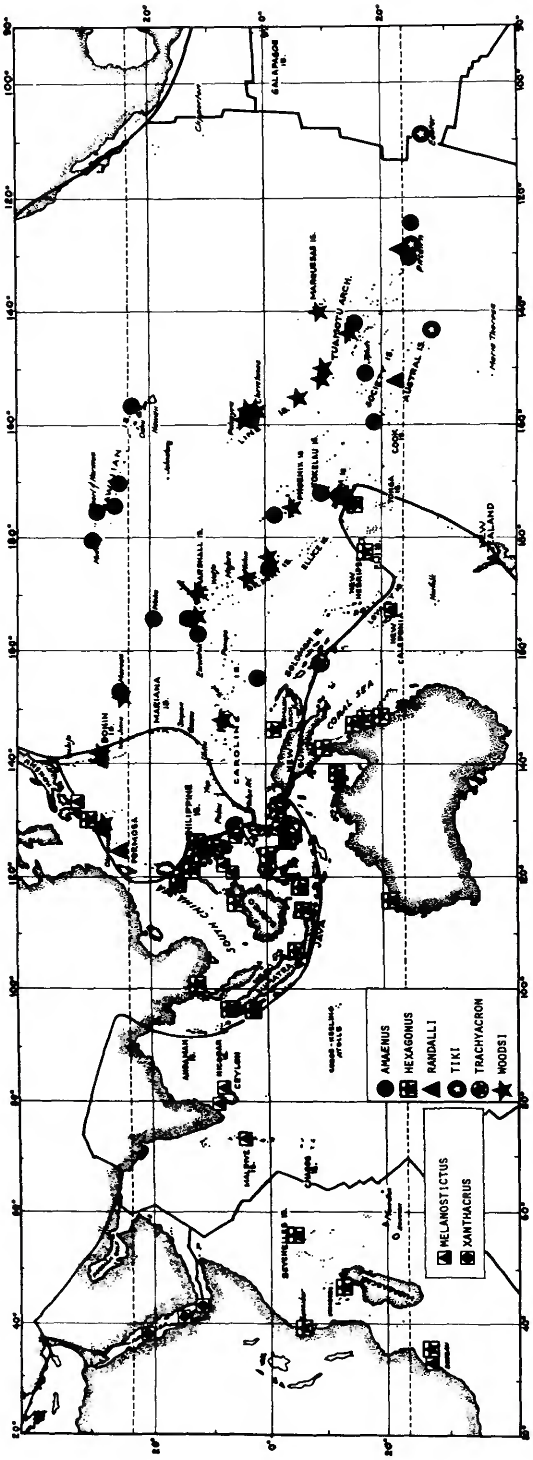

FIGURE 24.—Distributions of certain species of the holocentrid fish genus *Myripristis*.

planktonic larvae and widespread distributions. They are included here because they are caught occasionally close to shore. Such records for two istiophorid species have been reported for the Pacific Plate.

KRAEMERIIDAE

The kraemeriids, a poorly known group taxonomically, are small (not exceeding 40 mm SL), benthic fishes consisting of three genera (*Kraemeria*, *Gobiotrichonotus*, *Parkraemeria*) and about nine species. They occur in sandy areas close to shore, and although primarily marine, also occur in freshwater. They are distributed from the east coast of Africa (Winterbottom, 1976) eastward to Japan, Australia, New Guinea (USNM collections), Hawaiian Islands, and Tahiti.

KUHLIIDAE

The kuhliids comprise a single genus (*Kuhlia*), and about six species of small fishes (to about 560 mm TL). Most authors include *Nannoperca*, *Nannatherina*, and *Edelia* in the Kuhliidae, but these three Australian freshwater genera belong in the Percichthyidae (G.D. Johnson, pers. comm.). The kuhliids are free swimming and suprabenthic in habit. Both young and adults may enter freshwater. The kuhliids range throughout the warm portions of the entire Indian and Pacific oceans. A revision of the family is needed.

KURTIDAE

The kurtids contain a single genus, *Kurtus*, and two species of small fishes (maximum size about 600 mm TL). The kurtids are primarily fresh and brackish water inhabitants that range hundreds of kilometers upstream (Lake, 1971). Males carry the eggs attached to a special process on top of the head. The kurtids, which are absent from the Pacific Plate nonmarginally, are distributed from

Ceylon and the east coast of India eastward through Indonesia, as far as Borneo and New Guinea. In Australia they range from northern Queensland northward around Australia to northern Western Australia. They are often listed as occurring in "China," but I find no verifiable reference for China, and doubt that they occur even as far north as southern China. Kurtids are not reported from South Viet Nam or the Philippines. A fishery for kurtids exists in the Bay of Bengal (Kuthalingam, 1967).

KYPHOSIDAE

The chubs comprise three genera and fewer than ten species of moderate-sized (to over 600 mm TL), free-swimming fishes. *Hermosilla* (monotypic) is restricted to the eastern Pacific, and *Kyphosus*, with several species, is circumglobally distributed on warm coasts. Randall (1961) and Rosenblatt et al. (1972) reported on the peculiar distribution of the monotypic *Sectator*, which is known only from the Hawaiian and Society islands in the central Pacific, and from Cabo San Lucas, Baja California, south to Isla La Plata, Ecuador, in the eastern Pacific.

LABRACOGLOSSIDAE

The labracoglossids are a poorly known family consisting of two genera and perhaps fewer than five species. The species probably do not much exceed 250 mm TL, are free swimming, and are primarily antiequatorially distributed. They are common in Japan (Honshu; also Bonin Islands on margin of Pacific Plate), and occur as far south as the Philippines. They are absent from the Indo-Malayan area but reappear to the south in New South Wales and New Zealand, and Norfolk, Lord Howe, Rapa (Randall and Sinoto, 1978), and Easter islands. Bruce A. Carlson (ms.) questionably assigned this family to a specimen he obtained in Fiji. As labracoglossids might be expected to occur in Fiji, I have listed the family as present in Fiji in Table A (Appendix 2); corroboration of the family in Fiji is desirable.

With the exception of *Bathystethus* at Rapa, which island is marginally tropical, and one other questionable record, labracoglossids are unknown from the Pacific Plate nonmarginally. Lindberg and Krasnyukova (1971) stated that labracoglossids were "indicated for the Vostok Islands [sic] in the South Pacific" [translation]. Vostok Island is one of the Line Islands, which are tropical. I have been unable to locate the source of the Vostok record, which does not appear to have originated with Lindberg and Krasnyukova. The possibility comes to mind that the "Vostok Islands" are those islands that exist off Vladivostok, Russia, which is possibly in the range of labracoglossids.

LABRIDAE

The wrasses comprise over 50 genera and perhaps as many as 500 species of small-to-large, free-swimming, epibenthic, or benthic fishes. The family is distributed circumglobally in tropical and warm-temperate marine coastal waters. There are no freshwater species and only a few species occur under estuarine conditions. The wrasses form a conspicuous element of the coral-reef fish fauna. The following discussion treats only those genera for which the Indo-Pacific species are reasonably well known.

Anampses is restricted to the Indo-Pacific and consists of 12 species (Randall, 1972a, 1974). Only six species occur on the Pacific Plate nonmarginally, and two of these are endemic to the Hawaiian Islands, including Johnston Island; the other four species occur also in the Indo-West Pacific. Six species are limited to various parts of the Indo-West Pacific.

Bodianus, a circumglobal genus, consists of 29 species (Gomon, 1979; Lobel, 1981b), of which 22 occur in and are limited to the Indo-Pacific (includes one species known only from a specimen obtained in the Tokyo fish market, and seven species restricted to the Indian Ocean). Of the Indo-Pacific species, only seven occur nonmarginally on the Pacific Plate, and of the seven, two species, two of the three subspecies of a third species, and one of the two subspecies of a fourth species are endemic to the Plate. The endemics are distributed as follows: one species (*B. sanguineus*) is endemic to the Hawaiian Islands and one (*B. prognathus*) is known only from Fanning Island, Line Islands; one subspecies (*B. bilunulatus albotaeniatus*) is endemic to the Hawaiian and Johnston islands, and a conspecific subspecies (*B. bilunulatus busellatus*) is limited to the Marquesas, Henderson, and Ducie islands (the third conspecific subspecies, *B. b. bilunulatus*, is distributed from the east coast of Africa to Japan, Philippines, Moluccas, New Guinea, and New Caledonia, hence, limited to continental plates); one subspecies (*B. loxozonus trotteri*) is distributed in the Line, Marquesas, Tuamotu, and Austral islands (the other conspecific subspecies, *B. l. loxozonus*, ranges from Vietnam to Japan, Taiwan, and the Philippines, is absent from these areas eastward to the Marshall Islands, where it occurs, and southward to New Caledonia and the Tonga Islands, where it also occurs, and is, surprisingly, also present in the Tuamotus together with the conspecific *B. l. loxozonus*). The distribution of one species, *B. vulpinus*, appears to be antiequatorial, and is an Hawaiian exception as well: Ryukyu and Hawaiian islands in the north, southeast and southwest Australia, New Zealand, Lord Howe, and Easter Island in the south.

Lobel (1981b) appears to have related the Pacific Plate restricted *B. prognathus* most closely to *B. diana*, which ranges from the east coast of Africa eastward to the Palau and Solomon islands along the margin of the Pacific Plate. If Lobel's assessment of relationships is true, the Plate margin separates the distributions of the two species, albeit there is an apparent distributional gap between the Plate margin and the most western occurrence of *B. prognathodes*.

Choerodon, with 25 species, is limited to the Indo-West Pacific, from the Red Sea and eastern Africa to the western margins of the Philippine and Pacific plates (Gomon, 1979).

Diproctacanthus is monotypic and is limited to the Indo-West Pacific, from Java east to the Palau and Admiralty islands, on the western margin of the Pacific Plate (Randall and Springer, 1973, and museum collections).

Epibulus contains two species, one of which is widely distributed in, and restricted to, the Indo-Pacific, and the other (undescribed) is known only from the Philippine and Palau islands (J.E. Randall, in litt.).

Labrichthys is monotypic and is distributed from eastern Africa to Samoa and the Marshall Islands, on the Pacific Plate (Randall and Springer, 1973). Randall and Springer considered a report (Fowler, 1931) of *Labrichthys* from Tahiti to be questionable.

Labroides consists of five small species of cleaner fishes and is limited to the Indo-Pacific from the east coast of Africa to the Pitcairn Island group (Randall, 1958; Randall and Springer, 1975). The distributions of two species, *L. dimidiatus* (well known as the model in a mimetic association with the blenniid fish *Aspidontus taeniatus*) and *L. bicolor*, cover, in general, the entire range of the genus (both species, however, are absent from the Hawaiian Islands). The three remaining species of *Labroides* are more localized and allopatric with regard to each other (Figure 25), but may occur sympatrically with either or both of the two widely distributed species. *Labroides rubrolabiatus* is a widely distributed endemic on the Pacific Plate, but is absent from Plate localities where its presumed closest relative, *L. pectoralis* (Randall and Springer, 1975) occurs. *Labroides phthirophagus* is an Hawaiian endemic and appears to be the sister species of *L. pectoralis* and *L. rubrolabiatus*.

Labropsis was revised by Randall (in press a), who recognized six species. *Labropsis* is restricted to the reefs of the Indo-Pacific. Two species (*L. manabei*, *L. australis*) are restricted to the western Pacific, one (*L. xanthonota*) ranges from the east coast of Africa eastward to the Marshall Islands, one (*L. alleni*) ranges from the Moluccas eastward to the Marshall Islands, and two are endemic to the Pacific Plate: *L. polynesica* from Rarotonga (Cook Islands), Tahiti, Moorea, and Tetiaroa (Society Islands), Rangiroa, Takaroa, and Tikahau (Tuamotus), and Temoe (Gambier Group of Tuamotus), and *L. micronesica* from Enewetak and Kwajalein (Marshalls), Guam (Marianas), and Palau and Ifaluk (Carolines). Randall stated that

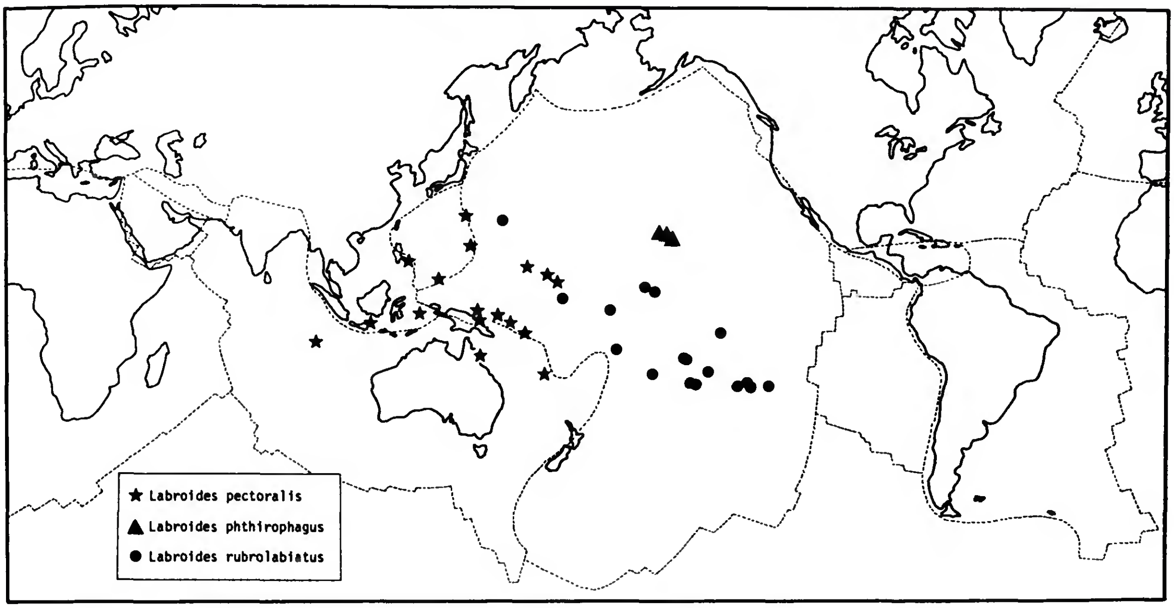

FIGURE 25.—Distributions of three of the five species of the labrid fish genus *Labroides*; the other two species of *Labroides* are widely distributed in the Indo-Pacific.

the closest relative of *L. polynesica* is the widely distributed, but allopatric *L. xanthonota*, and the closest relative of *L. micronesica* is the allopatric, western Pacific *L. australis*, which has been taken along the marginal Plate islands from the Solomons to Fiji, Samoa, and Tonga. Thus, for one of the Plate endemics, the Plate margin is the boundary separating it from its proposed closest relative.

Leptojulis comprises three species and is restricted to the Indo-West Pacific. One species is known only from the Philippines, one only from Thailand (Indian Ocean coast) and Ceylon, and one from the Gulf of Oman eastward to the Solomon Islands, along the margin of the Pacific Plate (Randall and Ferraris, 1981).

Macropharyngodon, with ten species, is limited to the Indo-Pacific, from the Red Sea to the Pitcairn Island group (Randall, 1978b; Shepard and Meyer, 1978). Most of the species are restricted in distribution, with three known only from the western Indian Ocean, one only from eastern Australia, one only from southern Japan, and one from eastern Australia and New Caledonia. There are three species on the Pacific Plate: one is endemic to the Hawaiian Islands; one ranges from the Philippine Islands and New South Wales to the Pitcairn Island group; and the third ranges from the Philippines and Okinawa east to the Marshall Islands.

Paracheilinus, with seven species (Randall and Lubbock, 1981b), is limited to the Indo-West Pacific, from the Red Sea and western Indian Ocean to the Philipines, New Guinea, and Solomon Islands, on the western margin of the Pacific Plate.

Polylepion is a moderately deep-dwelling genus with two species. The genus is known only from the Ryukyus, Hawaiian Islands (Hawaiian exception), and the tropical eastern Pacific (Gomon, 1979).

Pseudojuloides, an Indo-Pacific genus, was revised by Randall and Randall (1981), who recognized eight species: three restricted to the western Indian Ocean (two to Mauritius, one to Zanzibar and Aldabra), two restricted to the western

Pacific (one in Japan, Australia, and New Zealand, one in the Philippines), one widely distributed in the Indo-Pacific (from the east coast of Africa to the Society Islands), and two endemic to the Pacific Plate: one, *P. pyrius*, to the Marquesas, the other, *P. atavai*, to several island groups in southeast Oceania and Guam (J.E. Randall, in litt.; hence, can be considered to be a widely distributed Plate endemic).

Stethojulis was synopsized by Randall and Kay (1974), who recognized nine species. Shepard and Randall (1976) tentatively treated two of the nine species as subspecies of a single species. Three of the species are widely distributed in the Indo-Pacific including the Pacific Plate (one of which reaches the eastern Pacific as well); one is endemic to the Hawaiian Islands; one is known from southern Japan south to Okinawa and the Bonin Islands; one is known only from the Indian Ocean; and the species with two subspecies is reported from Japan, on the one hand, and the Indo-Malayan region on the other.

Suezichthys comprises about eight species (B.C. Russell, pers. comm.) and is widely distributed in, and limited to, the Indo-West Pacific, except for the occurrence of one species in the Hawaiian Islands (Hawaiian exception).

Thalassoma, which is distributed circumglobally, has been revised by Heiser (1981), who recognized 21 species (including one undescribed): two restricted to the western Atlantic, two restricted to the eastern Atlantic (including one endemic to Ascension and St. Helena), three restricted to the western Indian Ocean and/or Red Sea, three restricted to the eastern Pacific, one restricted to the western Pacific (southern Japan), one restricted to the Indo-West Pacific, one ranging from the western Pacific to the Socorro Islands in the eastern Pacific, five widely distributed in the Indo-Pacific, and three endemic to the Pacific Plate (two to the Hawaiian Islands, and one, undescribed, to Pitcairn and Ducie). There are, therefore, nine species of *Thalassoma* present on the nonmarginal portions of the Pacific Plate.

Xiphocheilus is a monotypic genus restricted to the Indo-Malayan region and Palau Islands (Gomon, 1979).

Of the 17 labrid genera discussed above, 12 occur on the Pacific Plate nonmarginally; none of the 12 is endemic. The 17 genera are represented by about 125 Indo-Pacific species, but only 45 (36%) of these occur nonmarginally on the Pacific Plate, and 14 (31%) of the 45 are endemics. Of the 45 Plate species, 11 are found on the Plate only in the Hawaiian Islands (and for a few, Johnston Island also). The relatively few species of labrids found on the Pacific Plate and the relatively high number of these that are endemics, emphasize the distinction of the Plate as a biogeographical unit within the Indo-Pacific region.

LACTARIIDAE

This family consists of a single genus and species (*Lactarius lactarius*) of moderate-sized (to about 500 mm TL), free-swimming coastal fish distributed from the Persian Gulf eastward to Taiwan and the Admiralty Islands, and south to northern Australia and Fiji (Carlson, ms.). It has not been reported from the Pacific Plate nonmarginally.

LAMNIDAE

The mackerel sharks, including the great white shark and makos, are large, widely distributed, viviparous species that are usually taken offshore. The makos are commonly taken by fisherman at Pacific Plate localities. The great white shark, *Carcharodon carcharias*, is recorded from all oceans, but on the Pacific Plate has been taken only in the Hawaiian Islands, where it is uncommon, and from six miles (10 km) off Bikini, Marshall Islands, based on a single specimen (Schultz, 1953b). Strasburg (1958) did not record *Carcharodon* during longline collections that covered much of the central Pacific (see his fig. 1) during a four-year period that produced over 6000 specimens of sharks (*Carcharodon* is known to be taken on longlines—I obtained a specimen during longline fishing off the New Jersey coast). *Carcharodon* appears to be primarily antiequatorially distributed in the Pacific.

LEIOGNATHIDAE

The Leiognathidae were reviewed by James (1978). He recognized four genera and 17–20 species, the largest of which attains 242 mm TL. The species are epibenthic, schooling fishes of commercial importance. They are primarily marine but often occur in brackish or mangrove areas, and occasionally enter freshwater. Leiognathids have not been reported to occur outside the Indo-Pacific except for an immigrant species of Red Sea origin in the eastern Mediterranean (Ben-Tuvia, 1966). Leiognathids are widely distributed and common in the Indo-West Pacific from the Red Sea and east coast of Africa to Japan, the Mariana, Palau, and Bonin islands, New Guinea, Fiji, and Samoa. I collected *Gazza minuta* and an unidentified species of *Leiognathus* at Ponape, Eastern Caroline Islands; otherwise, there have been only two reports of leiognathids from the Pacific Plate nonmarginally, both based on specimens collected over 100 years ago. In these reports, four species (in three genera) were recorded from Tahiti. Randall (1973) discussed these reports, noted that he had not collected leiognathids in all Polynesia, and questioned the validity of the Tahitian records, especially as three genera and three species emmanated from one collection (Kner, 1865). Fowler (1928) listed two species of leiognathids from Ebon Atoll (Marshall Islands), which is near Kosrae (easternmost of the Eastern Caroline Islands), where leiognathids might be expected to occur. In spite of considerable, relatively recent collecting in the Marshall Islands, however, there are no other records of leiognathids from those islands. I believe that leiognathids on the nonmarginal portions of the Pacific Plate are restricted to the Eastern Caroline Islands chain, which has acted as a conduit permitting leiognathids to disperse onto the Pacific Plate.

LEPTOBRAMIDAE

This family consists of a single genus, *Leptobrama*, and two species of small (to about 430 mm TL), free-swimming fishes that occur on the coasts of Western Australia, Queensland, Northern Territory, and the Gulf of Papua (P. Heemstra, in litt.). In Australia, they occur mainly along beaches and in river mouths in brackish water (Lake, 1971), but have been taken 50 km above the mouth of the Aird River, which empties into the Gulf of Papua.

LETHRINIDAE

The Lethrinidae comprises five genera (Johnson, 1980) and about 30 species of commercially important, moderate-sized (to about 1 m TL), free-swimming, suprabenthic fishes. *Monotaxis* (monotypic) and *Gnathodentex* (monotypic) are limited to, and widely distributed in, the Indo-Pacific. *Gymnocranius* (at least two species) is limited to the Indo-West Pacific from the Red Sea and eastern Africa to Japan, New Guinea, Solomons, Samoa (Wass, ms.), and Australia (south to southern Queensland); and *Wattsia* (monotypic) is limited to the Indo-West Pacific, from the Red Sea east to at least the South China Sea. *Lethrinus* has 26 species (Sato, 1978) of which 25 occur in the Indo-Pacific and one is limited to the tropical eastern Atlantic from Cape Verde south to Gabon (several other primarily Indo-Pacific fish families have disjunct representation along the tropical west African coast, for example: Mugiloididae, Platycephalidae, Psettodidae, Monodactylidae). Of the 25 Indo-Pacific species, only five occur nonmarginally on the Pacific Plate (four of these range as far west as the western Indian Ocean and Red Sea, and one only as far west as the East Indies. Of the 20 species restricted to the Indo-West Pacific continental areas, at least 10 reach the western margin of the Pacific Plate.

In summary, three of the four genera of lethrinids, but only seven of the 29 Indo-Pacific species, occur nonmarginally on the Pacific Plate; no species is endemic to the Plate.

LOBOTIDAE

The tripletails consist of two genera, each with two species. *Datnoides* is a genus of small fishes (to about 350 mm TL) that inhabits freshwater and may enter brackish water. The genus ranges from northeast India (Ganges) to Borneo and New Guinea.

Lobotes attains a moderately large size (to about 1 m and 14 kg) and is often, erroneously, reported to be worldwide (circumtropical) in distribution. The genus is present in the eastern Pacific (an endemic species), on both sides of the tropical Atlantic, although infrequently reported from the west African coast, and in the Mediterranean. In the Indo-West Pacific, it is recorded from the east coast of Africa east to New Guinea and New Britain, north to Japan and Korea, and south to Fiji (Carlson, ms.) and southern Queensland. *Lobotes* has been reported from only three localities nonmarginally on the Pacific Plate: Ponape, where R.A. Croft, local fisheries officer, informed me that he had seen (collected and discarded) only one individual in his six years of residence on that island; the Hawaiian Islands, where it is rare (J.E. Randall, pers. comm.) and was first taken in 1957 (Gosline and Brock, 1960); and Tahiti, where it has been reported only once (Gosline and Brock, 1960). There are, however, no specimens or subsequent reports of *Lobotes* from Tahiti, and its presence there remains to be verified. Of interest here is that R.C. Wass (ms.) does not record *Lobotes* despite several years residence and collecting fishes in Samoa, which is much closer to well documented areas of occurrence of *Lobotes* than is Tahiti. Young *Lobotes* often occur around floating seaweed, and it is possible that Hawaiian specimens emanate from Japan via ocean currents. I do not believe, however, that there is a breeding population of *Lobotes* present on the Pacific Plate nonmarginally.

LOPHIIDAE

The goosefishes are primarily a benthic, deep-water, shelf group. They are included here only for the sake of completeness as a few species occur at shallow depths in northern, temperate waters of the western hemisphere. There are four genera and 25 species of goosefishes (Caruso, 1981), of which only two species (of *Lophiodes*, which comprises 13 species) are known from the Pacific Plate nonmarginally, and both are endemic to the Hawaiian Islands (Hawaiian exceptions) and known only from depths of 274–576 m. *Lophiodes* is otherwise restricted to the eastern and western Atlantic and eastern and Indo-West Pacific.

LUTJANIDAE

The snappers are a circumglobally distributed family comprising 17 genera (G.D. Johnson, 1980) and about 75 species of small to moderately large, free-swimming, suprabenthic fishes, many of commercial importance. All but three lutjanid genera occur in the Indo-Pacific, and of the 14 that do, seven are monotypic. Four of the monotypic genera (*Pinjalo*, *Symphorichthys*, and *Symphorus*, which are shallow dwelling, and *Lipocheilus*, which occurs at depths of 94 m or more) do not occur on the Pacific Plate nonmarginally. *Macolor* and *Aprion*, both monotypic and shallow dwelling, are widely distributed in the Indo-Pacific, as is the deep-dwelling, monotypic *Randallichthys*, which is known only from the Hawaiian Islands, New Caledonia, and Okinawa at depths of 152–293 m (Anderson et al., 1977). *Parapristipomoides*, monotypic, is a deep-dwelling (160–430 m) Pacific Plate endemic known only from Rapa and Easter islands. Kami (1973) described *Parapristipomoides* as a subgenus of *Pristipomoides*, but G.D. Johnson (1980) recognizes both as genera. Of the seven polytypic Indo-Pacific genera (all in need of revision), *Lutjanus* (the only circumglobally distributed genus of lutjanids) and *Aprion* (both shallow dwelling), and *Aphareus* and *Pristipomoides* (both deep dwelling) are widely distributed in the Indo-Pacific, and *Etelis* (deep dwelling), *Apsilus*, and *Paracaesio* (both shallow dwelling) are restricted to the Indo-West Pacific.

Several species of *Lutjanus* have been introduced into the Hawaiian Islands, where the genus did not occur naturally (Randall and Kanayama, 1972). Although some of the introduced species appeared to survive for several years, only two species, *L. kasmira* (introduced in 1955, 1956, and 1958) and *L. fulvus* (introduced in 1956 and 1958), established breeding populations, and *L. kasmira* has become so abundant that fisherman "believe" it is replacing more desirable native species, particularly goatfishes (Tabata, 1981; J.E. Randall, in litt.). The two introduced species of snappers are common and widely distributed in the Indo-Pacific, and it was presumed when they were introduced that they would compete only with labrids, holocentrids, synodontids, cirrhitids, scorpaenids, and deep-water lutjanids, which have similar feeding habits to those of the snappers. All these families and *Lutjanus* (and the successfully introduced serranid, *Cephalopholis guttatus*, a senior synonym of *C. argus*) occur together commonly at many Pacific Plate localities, and I presume that the success of the introduced snappers (and *Cephalopholis*) is due to the lack of native predators. The mugilid *Chelon engeli*, introduced into Hawaii in 1955, also appears to be competing with native *Mugil cephalus* (Randall and Kanayama, 1972), although *M. cephalus* is still one of the most abundant Hawaiian fishes (Hawaii Division of Fish and Game, 1979).

It may be argued that a complex ecosystem, as must exist in the Hawaiian Islands, may take many years before reaching equilibrium when a relatively few species are added to the system. In other words, the replacement (extinction) of a native (or introduced) species will not become apparent for many more years than the 20+ years that have passed since the successful introductions were made. On the other hand, several species of *Lutjanus* and *Epinephelus* (Serranidae) that were introduced in quantity into the Hawaiian Islands simultaneously with the successful species did not succeed in colonization (Randall and Kanayama, 1972). Many reasons for the failures can be postulated, but the important point for the present is that there is no evidence that a native species has been replaced.

MALACANTHIDAE

(not including Branchiostegidae)

The sand tilefishes consist of two genera, *Malacanthus*, with three species (Dooley, 1978), and *Hoplolatilus*, with eight (Randall, 1981b). Maximum adult size is about 100–700 mm SL, depending on the species. The species build burrows in rubbly or sandy bottom. *Malacanthus* is often seen swimming well up in the water column, but *Hoplolatilus* appears to remain close to its burrows. Larvae or prejuveniles are planktonic.

Hoplolatilus is restricted to the Indo-Pacific, and the distributions of its species are poorly known because the species are difficult to collect. Only three species of *Hoplolatilus* occur nonmarginally on the Pacific Plate (Dooley, 1978, Randall, 1981b), and all three occur also in the western Pacific or farther west.

Malacanthus has a wider distribution (Dooley, 1978, fig. 37) than *Hoplolatilus*. It is almost circumtropically distributed, but is known from only one locality in the eastern Atlantic, Ascension. The two Indo-Pacific species of *Malacanthus* range from the east coast of Africa well out onto the Pacific Plate, and one of these, *M. brevirostris*, reaches the eastern Pacific.

MENIDAE

This family consists of a single genus and species (*Mene maculata*) of small (to about 200 mm TL) coastal fish that may enter estuaries. It is distributed from the east coast of Africa eastward to Japan, New Britain, northern Queensland, and Fiji (Carlson, ms.). It is absent from the Pacific Plate nonmarginally. Reports (all apparently emanating from Matsubara, 1955; see also Formionidae) of *Mene*'s occurring in the Hawaiian Islands are probably erroneous. There are no specimens from these islands, nor has it been seen there by J.E. Randall or W.A. Gosline (pers. comms.).

MICRODESMIDAE

The wormfishes comprise five genera and about 35 species (some undescribed) of small (to about 250 mm SL) fishes that are found in all warm seas. The species are indwellers in shallow sandy, muddy, or coral rubble bottoms, and occasionally in estuaries. The postlarvae are planktonic. The two genera that occur in the Indo-Pacific are restricted to that region. *Gunnellichthys* is distributed from eastern Africa to the Society

Islands and *Paragunnellichthys*, from the Red Sea to the Eastern Caroline Islands; none of the species are Pacific Plate endemics (C.E. Dawson, 1974, and pers. comm.).

MOBULIDAE

The manta rays comprise two to four genera of large to extremely large fishes. The taxonomy of the family is poorly known, probably as result of the large size of the species and concomitant lack of specimens for study. Only *Manta* and *Mobula* are generally accepted as valid genera in the family; the number of species in each is questionable. *Manta* is circumglobal in distribution; *Mobula* is, perhaps, circumglobal, but has been reported only from the Hawaiian Islands nonmarginally on the Pacific Plate, and the Hawaiian record is considered questionable (Gosline and Brock, 1960).

MONACANTHIDAE

There are 28 genera and about 75 species of filefishes (Hutchins, 1977; J.C. Tyler, pers. comm.). The species are of small to moderate size (to about 1 m TL), free swimming, or associated with vegetation or soft and hard corals; some species have pelagic young, often associated with floating *Sargassum.* All the genera, and 54 of the species (Hutchins, 1977), occur in Australia, the only relatively limited area where all the genera occur. Only nine genera are present on the Pacific Plate nonmarginally.

Randall (1964) revised *Amanses* and *Cantherhines*. *Amanses* is monotypic and ranges from the Red Sea to the Tuamotus. Randall recognized 11 species in *Cantherhines*, but Hutchins (1977) synonymized one of these (*C. melanoides* with *C. pardalis*) and referred another (*C. longipinnis*) to *Cantheschenia* (with two species; genus known only from Lord Howe Island and Great Barrier Reef). Hutchins and Randall (in press) have described an additional species of *Cantherhines*. Of the ten species of *Cantherhines*, two (*C. macroceros*, *C. pullus*) are restricted to the western Atlantic, two (*C. verecundus*, *C. sandwichiensis*) are endemic to the Hawaiian Islands, one (*C. rapanui*) is endemic to Easter Island, one (*C. longicaudus*) is restricted to southeast Oceania (Tahiti and Rarotonga), two (*C. multilineatus*, *C. fronticinctus*) are restricted to the Indo-West Pacific (Randall, 1964; Kyushin et al., 1977; reaching the western margin of the Pacific Plate), one (*C. pardalis*) ranges throughout most of the Indo-Pacific, but is absent from the Hawaiian Islands, and one (*C. dumerili*) ranges throughout the Indo-Pacific (including the Hawaiian Islands) to the Revillagigedo Islands in the eastern Pacific. The distribution patterns of the various species of *Cantherhines* seem to reflect most of the main patterns exhibited by Indo-Pacific fish taxa, with the notable lack of Indian Ocean and widely distributed Pacific Plate endemics.

Oxymonacanthus and *Paraluteres* are both monotypic and range from the east coast of Africa to at least the Marshall Islands; however, the Red Sea population of *Oxymonacanthus* has been recognized as a separate species (Marshall, 1952).

Pseudomonacanthus contains five species (Fraser-Brunner, 1940; Randall, 1975a). Four of the species are known only from the region comprising northern Australia, East Indies, Philippines, and Singapore. The fifth species, *P. garretti*, is known only from the Hawaiian Islands and would constitute an Hawaiian exception (for the genus), but I am informed (J.B. Hutchins in J.E. Randall, in litt.) that *P. garretti* is a species of *Thamnaconus*.

MONOCENTRIDAE

There are two genera (*Monocentris*, *Cleidopus*) and three species of pinecone fishes. The species are small (to about 230 mm TL), usually deep dwelling, free swimming, and predominantly restricted to the Indo-West Pacific. The family is distributed from the east coast of Africa to Japan, the Philippines, and Australia; there are no records from the Pacific Plate. *Monocentris* has been reported from the Juan Fernandez Islands, off the coast of Chile, based on a single dried specimen (Fowler, 1955; Schultz, 1956), but R.H. Rosenblatt (pers. comm.) believes that the species, which is otherwise known only from San Felix Island (Scripps Institution collections), probably came from San Felix, which is also off the coast of Chile.

MONODACTYLIDAE

The monodactylids comprise one genus (*Monodactylus*) and two or three species of small fishes (to about 200 mm SL). *Schuettea*, a South Australian genus, was excluded from the family by Tominaga (1968). The species are free swimming and enter freshwater. The family is distributed from the tropical east coast of Africa to the Eastern Caroline Islands, Fiji, and Samoa (Wass, ms.); there is, in addition, a disjunct representation of *Monodactylus* on the tropical west coast of Africa (however, absent from the coast of Angola), a distribution pattern similar to that of several other primarily Indo-Pacific fish families (see also Lethrinidae). *Monodactylus* has been reported only from Ponape and Suvarow, Eastern Caroline Islands, on the Pacific Plate nonmarginally (Herre, 1939; Fowler, 1928), and the presence of *Monodactylus* at these two islands is evidence for the operation of the Caroline Islands conduit. The essential absence of *Monodactylus* from the Plate may be a consequence of its requirement for brackish water for the proper development of its eggs and larvae (Ogasawara et al., 1978; Akatsu et al., 1977). The high island of Ponape has river runoff but Suvarow is an atoll and should lack freshwater runoff. Sterba's (1962, fig. 1022) distribution map for the family fails to include areas (Fiji, Samoa, Ponape) to the east of Australia and New Guinea as part of the range of *Monodactylus*.

MORIDAE

The morids are a circumglobally distributed group of primarily deep-dwelling, cool-water fishes that are poorly known taxonomically. There are perhaps 15 genera and 75 species (D.M. Cohen, pers. comm.). A few species have been collected at depths of under 100 m in the Indo-Pacific, but only one shallow-dwelling species has been collected on the Pacific Plate nonmarginally, and only at Rapa (*Lotella* sp., J.E. Randall, in litt.). *Lotella* is antiequatorially distributed: South Australia, Lord Howe Island, New Zealand, Rapa, Juan Fernandez Islands, and Japan south to 13°40′N (D.E. Cohen, pers. comm.).

MORINGUIDAE

The moringuid eels are indwellers of sandy bottom, but become free swimming when sexually mature. They have planktonic larvae and attain a total length of up to 1200 mm. The family contains two genera, *Moringua*, with fewer than ten species and in need of revision, and *Neoconger*, with three species. *Moringua* is distributed throughout the Indo-Pacific from the east coast of Africa to Easter Island, and is also present in the western Atlantic. *Neoconger* is represented by a different species in each of the following areas: western Atlantic, eastern Pacific, and Australia (only the larval stage is known of the Australian species; Smith and Castle, 1972).

MUGILIDAE

The mullets are a circumglobal family of epipelagic shorefishes of commercial importance. A few species appear to be confined to freshwater, but many marine species may enter fresh and brackish water. Spawning occurs offshore. Maximum size attained is about 1 m TL (Smith, 1953:323). The mullets are poorly known taxonomically. Possibly ten species in seven genera occur nonmarginally on the Pacific Plate. For a discussion of the successful introduction of *Chelon engeli* into the Hawaiian Islands see Lutjanidae.

MUGILOIDIDAE

The mugiloidids are a benthic group of small fishes (less than 500 mm TL) and are poorly known taxonomically. Several species are undescribed, and some described species are possibly representative of different sexes of the same species, although some species are hermaphroditic (Marshall, 1950). There are about three genera (not including the New Zealand freshwater genus *Cheimarrichthys*, which has been referred to the Mugiloididae on occasion). The most speciose genus, *Parapercis*, contains perhaps 50 species, and is distributed from the Red Sea and east coast of Africa to New Zealand and the Pitcairn Island Group (J.E. Randall, in litt.), and also is present off the southwest and southeast coasts of South America, and along the central west coast of Africa.

In examining the literature on Indo-Pacific *Parapercis* species (see Gomon, 1981, for compilation), I find that only seven of the 36 currently recognized species occur nonmarginally on the Pacific Plate. Five of these seven are widely distributed in the Indo-Pacific, one (*P. multifasciata*) is known only from Japan and Hawaii (Hawaiian exception), and one (*P. hexophthalma*) is widely distributed in the Indo-West Pacific with a single report (Fowler, 1928) from the Pacific Plate, Tahiti. The Tahitian record is based on a specimen obtained by Andrew Garrett and deposited at the Museum of Comparative Zoology, Harvard. I consider the Tahitian record to be highly suspect, especially in view of the numerous suspect localities assigned to many specimens obtained by Garrett for the Museum Godeffroy.

MULLIDAE

The goatfishes are a circumglobal group of small (to about 520 mm TL), commercially important fishes with planktonic larvae. The family consists of six genera and, perhaps, as many as 50 species. *Mullus* occurs only in the Atlantic and Mediterranean; *Pseudupeneus* occurs only in the eastern Pacific and Atlantic; *Upeneichthys* occurs only in Australia and New Zealand; *Paraupeneus* occurs only in the Indo-Pacific; and *Upeneus* and *Mulloides* (replaces *Mulloidichthys*, P.C. Heemstra, pers. comm.) occur only in the Indo-Pacific and western Atlantic. The last three genera are present nonmarginally on the Pacific Plate. Although Thomas (1969) reviewed all the Indo-Pacific genera, except *Upeneichthys*, a modern revision is still needed.

Mulloides mimicus is a Pacific Plate endemic currently known only from the Marquesas and Line Islands (Randall and Guézé, 1981). Its presumed closest relative, *M. vanicolensis*, is widely distributed in the Indo-Pacific, including the Line and Marquesas islands.

Randall (1981a) reported the first records (obtained in 1976 and 1977) of *Upeneus vittatus* from the Hawaiian Islands. He believes that the occurrence of this species in Hawaii is the result of an introduction in 1955 from the Marquesas Islands; however, the possibility that the species is a straggler from Japan, where the species is common, should be considered.

MURAENESOCIDAE

The muraenesocids comprise eight genera and 18 species of eels (Castle and Williamson, 1975) with pelagic larvae. The largest muraenesocids attain lengths as great as 2.1 m, and are of commercial importance, at least in Japan. The group is primarily marine, but some species may enter brackish water. The muraenesocids are distributed cirrcumglobally in the warm shelf and shore waters of the continental plates, but are absent from the Pacific Plate nonmarginally (Castle and Williamson, 1975, provide distribution maps for the seven species included in *Muraenesox*, *Congeresox*, and *Cynoponticus*).

MURAENIDAE

The moray eels include about ten genera and over 100 species of short to very long (to 3.8 m TL) fishes with planktonic larvae. The family is distributed circumglobally (nine genera nonmarginally on the Pacific Plate), but outside the western Atlantic is very poorly known taxonomically. The presence of *Muraena* on the Pacific Plate is based on the widely distributed *Muraena pardalis*, which possibly merits a different (new) genus (J.E. Randall, in litt.).

MYLIOBATIDIDAE

The eagle rays comprise four genera and fewer than 20 species of viviparous, free-swimming fishes. They are poorly known systematically probably because of their large size (maximum disc width about 2.5 m) and concomitant lack of specimens in collections. Two of the four genera, and most of the species, are unreported from the Pacific Plate nonmarginally, a common circumstance for many elasmobranchs.

Aetobatus is circumglobally distributed.

Aetomylaeus is distributed from the Red Sea to Japan, the Philippines, and Australia, but is absent from the Pacific Plate.

Myliobatis, with about 11 species, is the most speciose genus in the family. It is almost circumglobally distributed, but does not occur on the nonmarginal portions of the Pacific Plate.

Pteromylaeus is reported from the eastern Atlantic and Indian oceans, and the Pacific Ocean from the east coast of Australia north to the Admiralty Islands and east to the Gilbert Islands, on the Pacific Plate.

NEMIPTERIDAE

The Nemipteridae comprises three genera (*Nemipterus*, *Pentapodus*, *Scolopsis*; Johnson, 1980) of small (maximum TL, 764 mm; most species under 400 mm), free-swimming, reef-inhabiting fishes that are confined to the Indo-Pacific. The three genera are in need of revision, but probably include fewer than 50 species. Rao and Rao's (1981) putative revision of *Scolopsis* is vastly incomplete.

Nemipterus ranges over most of the tropical Indo-West Pacific, but is absent other than marginally from the Pacific Plate, except for a specimen purportedly obtained by the *Albatross* at Erben Guyot at a depth of about 350 m. Erben Guyot is about 1100 km west of Los Angeles, California. Barry C. Russell (pers. comm.), who is revising *Nemipterus*, considers the Erben Guyot record suspect. *Pentapodus* and *Scolopsis* are distributed similarly to *Nemipterus*, but there are a few reports of *Pentapodus caninus* from the Gilbert and Marshall islands (see Fowler, 1928, for citations), *P. microdon* from the Gilbert Islands (Weber and de Beaufort, 1936), and *Scolopsis* from the Eastern Caroline Islands (Ponape; Herre, 1939; I have also collected *Scolopsis* from Ponape), Marshall Islands (Fowler, 1928; Hiatt and Strasburg, 1960), and Gilbert Islands (Fowler, 1928). *Scolopsis* has also been reported from the Hawaiian Islands (Cuvier and Valenciennes, 1830), but the lack of subsequent records (J.E. Randall, in litt.) for Hawaii raises doubts as to its presence there. (*Gnathodentex aureolineatus*, Lethrinidae, has often been reported from Pacific Plate localities as *Pentapodus aureolineatus*.)

NEOSTETHIDAE

The neostethids comprise six to eight genera and about 15 species of tiny (to about 25 mm SL), oviparous, free-swimming fishes that are restricted primarily to the fresh and brackish waters of the Philippines, Borneo, Malay Peninsula, and northwest Sumatra. They occasionally occur in fully marine waters, probably adventitiously, and for that reason only are included here. The family is sometimes considered to be a subfamily within the Phallostethidae, which includes primarily freshwater species that are occasionally taken in estuarine waters.

NOMEIDAE

The nomeids comprise three genera (*Cubiceps*, *Nomeus*, *Psenes*) and about 14 species of oceanic fishes, which are occasionally taken close to shore. The species are of small to large size (largest, over 1 m TL), have planktonic larvae (Ahlstrom et al., 1976), and many of the species are widely distributed. Probably five species are present nonmarginally on the Pacific Plate.

Nomeus, the man-of-war fish, is monotypic, occurs in all warm oceans except the eastern Atlantic and Mediterranean, and its young stages are often associated with the pelagic coelenterate *Physalia* (Haedrich, 1967). The distribution of *Nomeus* (and *Physalia*, the world distribution of which I have been unable to ascertain) in the central Pacific is worthy of further study. *Physalia* occurs irregularly at Guam, but *Nomeus* has not been taken there (R.F. Myers, pers. comm.), or at Fiji and Samoa. *Nomeus* on the central and eastern Pacific Plate is known only from three areas: the Hawaiian Islands, where it (and *Physalia*; Woodcock, 1956) is common; a specimen from 06°N, 162°W (near northern Line Islands; reported by Fowler, 1928); and some specimens from off the Marquesas, 10°S, 130°W and more easterly (Scripps Institution of Oceanography collections). If the distribution of *Nomeus* on the nonmarginal Pacific Plate is reasonably well reflected by the information given here, the distribution is similar to that of some endemic Pacific Plate species of fishes: *Hemiramphus depauperatus* (Hemiramphidae) and *Ostracion whitleyi* (Ostraciidae) and, perhaps, *Eviota epiphanes* (Gobiidae) and *Scorpaena coniorta* (Scorpaenidae), which two species are, however, unreported from the Marquesas. It is possible that the presence of *Nomeus* on the Pacific Plate is adventitious and the result of two different ocean current regimes: the Kuroshio extension flowing from Japan (where *Nomeus* occurs) toward the Hawaiian Islands and the westward flowing North and South Equatorial currents from the warm latitudes of the west coast of the Western Hemisphere (where *Nomeus* also occurs).

Butler (1979) gives detailed distribution maps for the seven species of *Cubiceps*.

NOTOGRAPTIDAE

The notograptids consist of single genus, *Notograptus*, and two or three species (Tyler and Smith, 1970; Whitley, 1964:54) of small (to about 130 mm TL), mangrove or reef inhabiting eel-like fishes that are restricted to the Northern Territory and Queensland coasts of Australia and the Fly River area of southern Papau-New Guinea.

ODONTASPIDIDAE

The sand-tiger sharks consist of two genera, each with one or two species (L.V.J. Compagno, pers. comm.). The family is in need of revision. These sharks are viviparous, of medium to large size (reported to attain 6 m TL, but probably rarely, if ever, exceeding 3.5 m). *Eugomphodus* is frequently present in shallow depths along shore, as well as at moderate depths offshore, but *Odontaspis* seems to frequent deep water. *Eugomphodus* is widely distributed on the tropical and warm-temperate coasts of the Western Hemisphere, eastern Atlantic, western Indian Ocean, Australia, and eastern Pacific, but has not been reported from the Pacific Plate. *Odontaspis* is known from the Mediterranean, eastern Atlantic, eastern Pacific, Indian Ocean, Japan, southern Australia, New Zealand, and the Hawaiian Islands, where two specimens were taken from gill nets set at depths of 185–310 m (Clarke, 1972). According to Tinker (1978), *O. kamoharai* occurs in the Hawaiian Islands, but L.V.J. Compagno informs me that this species belongs in *Pseudocarcharias* (Pseudocarchariidae, an epipelagic group not included in my study). One may question whether the occurrence of *Odontaspis* in the Hawaiian Islands is a case of an Hawaiian exception, representative of stragglers (from Japan), or an indication that *Odontaspis* is distributed more widely on the Pacific Plate, but is less available because it is relatively deep dwelling. With regard to the last mentioned possibility, it is noteworthy that Strasburg (1958) failed to record *Odontaspis* among the 6000+ sharks taken during several years of longline operations over much of the central Pacific.

OGCOCEPHALIDAE

The batfishes comprise nine genera and about 60 species (Bradbury, 1967) of small (to about 300 mm TL), benthic fishes. The family occurs in the warmer latitudes of all three major oceans, but is absent from the Pacific Plate nonmarginally, except for the occurrence of five species in the deep waters of the Hawaiian Islands (three of the Hawaiian species also occur in Japan). Batfishes occur in both deep and shallow depths in the tropical western Atlantic and in some portions of the eastern Pacific, but are rarely reported from less than 100 m depth in the Indo-Pacific.

OPHICHTHIDAE

The snake eels comprise about 50 genera and 200 species of small to moderately long (less than

200 mm to over 2 m TL) fishes that are predominantly shallow-water, benthic indwellers (but there are two monotypic midwater genera, one undescribed) with pelagic larvae (McCosker, 1977, and pers. comm.).

The family is circumglobally distributed, with the largest number of genera (25) occurring in the Indo-Pacific. Seventeen of the genera are reported from the Pacific Plate, and at least two of these (*Cirricaecula, Schismorhynchus*) are restricted to the Plate or its margins (Figures 26 and 60). An additional genus, *Evips*, is known only from Palau, on the eastern margin of the Philippine Plate (Figure 60) and conceivably may occur otherwise only on the Pacific Plate. *Cirricaecula* and *Evips* are known from only a few specimens, but the monotypic *Schismorhynchus* is a widely distributed Plate endemic. McCosker (1977) considered *Schultzidia*, with two species, to be the closest related genus to *Schismorhynchus*. *Schultzidia johnstonensis* is known from the Palau, Johnston, Hawaiian, Samoa (Wass, ms.), and Christmas (Pacific) islands, and *Schulzidia retropinnis* is known from Kapingamarangi, Palau, and the Philippines (McCosker, in litt.). *Schismorhynchus labialis* is sympatric with both species of *Schultzidia* in Palau and with *Schultzidia johnstonensis* at Johnston and the Samoan islands. Dispersal has, thus, obscured the vicariant event that initiated the divergence of *Schultzidia* and *Schizmorhynchus* from their common ancestor.

McCosker (1979) reported on the ophichthids of the Hawaiian Islands and found five species to be endemic; however, four were rare, deepwater species or belonged to genera in need of revision. McCosker noted that there are recognizably distinct populations of several other ophichthid species in the Hawaiian Islands, but declined to accord names to these populations.

Castle (1972) discussed the distribution of the monotypic, deep-dwelling, pelagic ophichthid genus *Benthenchelys*, and provided a distribution map for its three allopatric subspecies. One subspecies ranges from the northeast Indian Ocean to New Caledonia, one from the Sulu Sea to Palau (margin of the Pacific Plate), and one is restricted to the area of the Phoenix Islands (Pacific Plate). Although ophichthids appear to have

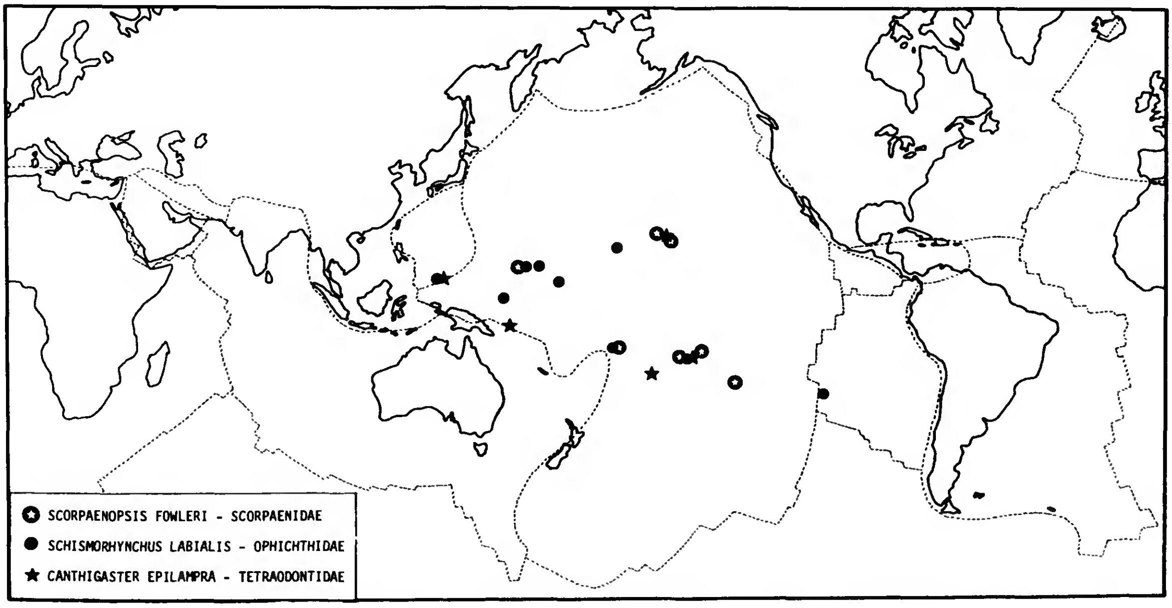

FIGURE 26.—Distributions of three widely distributed Pacific Plate endemic fishes, including a monotypic genus, *Schismorhynchus* (for the other Pacific Plate endemic genera see Figure 60).

long pelagic stages (10–12 months; Castle, 1965), the formation of narrowly restricted endemic populations is not precluded, and the western margin of the Pacific Plate holds promise as defining the vicariant event that permitted divergence of conspecific populations on either side of the margin. The fact that pelagic ophichthid larvae do not necessarily disperse great distances is further demonstrated by the benthic genus *Neenchelys*. Castle (1981) plotted the distributions of the larvae and adults of the two species of *Neenchelys*, which genus is restricted to the Indo-West Pacific. The larvae of both species of *Neenchelys* reach the western margin of the Pacific Plate, but do not occur on the Plate. Most of the larvae were collected by the *Dana* expeditions, which also made collections in Polynesia on the nonmarginal portions of the Pacific Plate (Greve, 1934, pl. 1).

OPHIDIIDAE

(including Brotulidae)

The cuskeels are a speciose group of small to large fishes that are circumglobally distributed, and occur at depths of less than 1 m to the greatest depths where a fish has been caught. Only two shallow-dwelling species have been reported nonmarginally on the Pacific Plate: *Brotula multibarbata*, which is widely distributed in the Indo-Pacific, and *B. townsendi*, which is reported only from the Marshall, Hawaiian, and Johnston islands, and may be endemic to the Pacific Plate (and is undoubtedly more widely distributed than is indicated, as there are many unidentified collections of *Brotula* from Plate localities). *Ophidion*, another genus of shallow-dwelling cuskeels, occurs at Easter Island, and represents an eastern Pacific component in the Easter Island fish fauna.

OPISTOGNATHIDAE

The jawfishes comprise three or four genera and about 60 species of small (25–600 mm SL) fishes (W.F. Smith-Vaniz, pers. comm.). The species are all marine, with a few occasionally occurring in estuaries. They are all burrow dwellers and, as far as known, mouth brooders. They occur at depths as shallow as a few centimeters to as great as 375–384 m. Aquarium-reared larvae of one species were free swimming for 18 days and then entered burrows (Colin, 1972). Dispersal by currents is, therefore, feasible. Jawfishes are found only in the waters of the Western Hemisphere and the Indo-West Pacific; they are absent from the Pacific Plate except marginally (Figure 27).

OPLEGNATHIDAE

This family, which is included here only for the sake of completeness, consists of one genus (*Oplegnathus*) and about six species of moderate-sized (to about 1 m TL), free-swimming fishes with planktonic larvae. The family is antitropically distributed, and occurs only in the Pacific Ocean: Vladivostok south to southern Japan, Hawaiian Islands (Hawaiian exception), southeastern coast of Africa, southern coast of Australia, Galapagos Islands, Peru, and Chile.

Oplegnathus (*O. fasciatus*, a Japanese species) has been reported in the literature only once from the Hawaiian Islands (Steindachner, 1893), and this report has been considered of questionable validity (Gosline and Brock, 1969; Tinker, 1978). There are valid recent records of *Oplegnathus* from the Hawaiian Islands, however. One record, based on a photograph of a specimen taken at the island of Hawaii in 1978 (specimen discarded), was shown me by a resident. A recent mimeographed project report (Hawaii Division of Fish and Game, 1979) records captures of *Oplegnathus punctatus* (also a Japanese species) from Midway and Kure, northernmost Hawaiian Islands. The presence of *Oplegnathus* in the Hawaiian Islands is probably the result of dispersal from Japan via the Kuroshio extension. It would be interesting to determine if breeding populations of *Oplegnathus* have become established in the Hawaiian Islands.

ORECTOLOBIDAE

The order Orectolobiformes comprises seven families and 12 genera of sharks (Compagno,

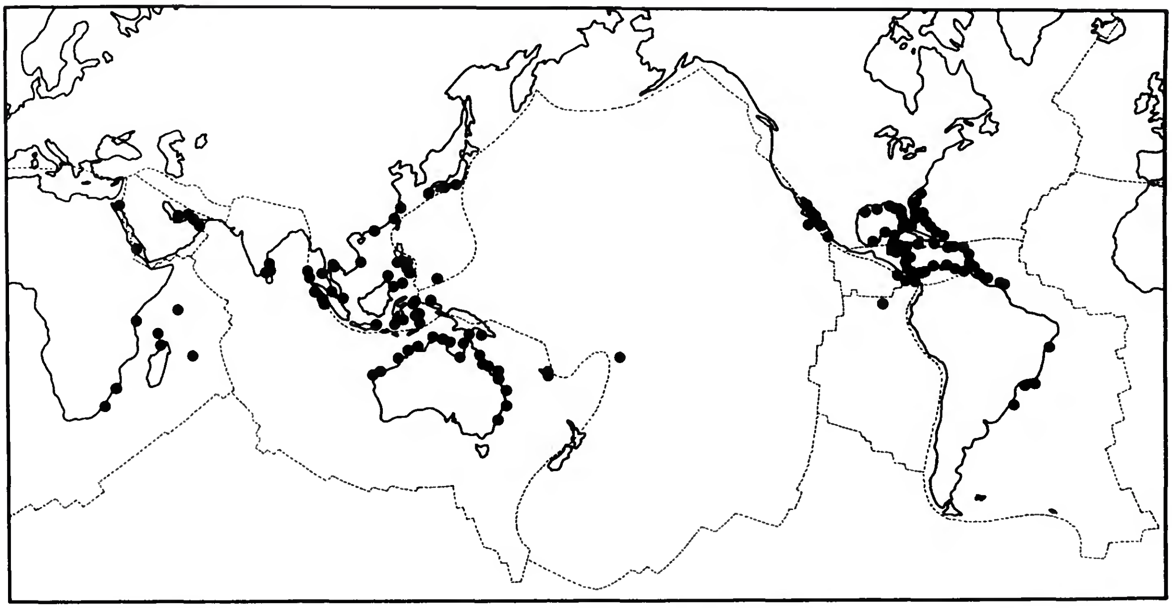

FIGURE 27.—Distribution of the jawfishes, family Opistognathidae (compiled by W.F. Smith-Vaniz); while this study was in press I collected *Opistognathus* in the Fiji Islands.

1973a, and pers. comm.), all of generally sluggish behavior, and most, benthic in habit. The number of species included is not large (probably less than 30), but has not been established for most of the families. The Rhiniodontidae, or whale sharks, comprises a single monotypic genus, *Rhiniodon*, which is an egg layer, the largest of all fishes (to 18 m TL or more), pelagic in habit, and circumglobally distributed. The other six families in the order have usually been combined in the literature and treated as one family, Orectolobidae. I recognize all six families, but treat them together here for the sake of convenience.

The Orectolobidae (sensu stricto: *Eucrossorhinus*, *Orectolobus*) are viviparous and restricted to the western Pacific; they do not occur nonmarginally on the Pacific Plate. Bigelow and Schroeder (1948) list the eastern Pacific within the range of *Orectolobus*, but neither I nor L.J.V. Compagno (pers. comm.) know of an eastern Pacific record for the genus.

The Parascylliidae (*Parascyllium*, *Cirrhoscyllium*) are moderately deep-dwelling, outer shelf or slope forms known only from the western Pacific.

The Ginglymostomatidae, which are shallow dwelling, include *Ginglymostoma*, a viviparous genus (with two or three species), which is distributed on the warm coasts of the Atlantic, eastern Pacific, and western Indian oceans, and *Nebrius* (two species, but only one on Pacific Plate nonmarginally), which is oviparous and widely distributed in the Indo-Pacific, at least as far east as Samoa and the Marshall Islands. *Nebrius ferrugineus* has frequently been assigned to *Ginglymostoma*, accounting for the supposed occurrence of that genus in Oceania (L.J.V. Compagno, pers. comm.).

The Stegostomatidae (*Stegostoma*) are oviparous, shallow dwelling, and widely distributed in the Indo-West Pacific, but absent from the Pacific Plate nonmarginally.

The Hemiscylliidae (*Hemiscyllium*, *Chiloscyllium*) are shallow-dwelling, oviparous sharks that are restricted to the Indo-West Pacific, from the eastern Indian Ocean to the Philippines, Japan, New Guinea and northern Australia.

The Brachaeluridae (*Brachaelurus*, *Heteroscyllium*) are viviparous, shallow dwelling, and restricted to Australia.

Thus, all of the 12 genera of the Orectolobiformes occur in (and nine are restricted to) the Indo-Pacific area, but only two genera (and two species) occur nonmarginally on the Pacific Plate, and one of these genera (*Rhiniodon*, monotypic, pelagic) is circumglobally distributed. The pattern exhibited by the Orectolobiformes is the same shown by many elamosbranch groups, which tend to be restricted to continental plates.

OSTRACIIDAE

(not including Aracanidae)

The ostraciid trunkfishes comprise up to six genera and, perhaps, as many as 25 species of small (maximum size about 460 mm TL), shallow-dwelling, benthically associated fishes. The family is distributed circumglobally in warm waters. The Indo-Pacific species are particularly in need of revision, but one species, *Ostracion whitleyi*, appears to be a widely distributed Pacific Plate endemic: Marquesas, Tuamotus, Society, Hawaiian, and Johnston islands (Randall, 1972b). Randall (1975c) considered *Ostracion tracys*, which is known only from Mauritius, to be the closest relative of *O. whitleyi.* If the distributions and relationships are as Randall has reported, the distributions are relict, and extinction must have occurred over the great distance separating the nearest populations of the two species.

PATAECIDAE

The prowfishes comprise three genera and about six species of small (to 230 mm TL), rare fishes restricted to the more southern coasts of Australia, but reaching as far north as southern Queensland. They are questionably included here as warm-water inhabitants.

PEGASIDAE

There are four genera and five species of sea moths (T. Pietsch, in litt.). The species are small (to about 100 mm TL), benthic inhabitants of shallow to moderately deep water (to about 150 m), but juveniles of 10 mm have been taken at the surface in the Hawaiian Islands (USNM collections). The family is restricted to the Indo-Pacific (Figure 28), but is represented on the Pacific Plate only marginally and by an endemic, moderately deep-dwelling (to about 150 m as adults) Hawaiian species, *Eurypegasus papilio* (Hawaiian exception). There is only one other species of *Eurypegasus*, *E. draconis*, which ranges from the east African coast to southern Japan and Australia; hence, the distributions of these two sister species are separated by the margin of the Pacific Plate.

A specimen of pegasid in the marine vertbrate collection at Scripps Institution of Oceanography was taken from the stomach of a tuna reportedly caught in the vicinity of Tahiti. I have not entered this record on the distribution map of the family, nor two others, one in the Scripps collection, supposedly from California, that was obtained by a diver, and one in the Charleston (South Carolina) Museum, purportedly taken off Charleston and provided by a commercial seafood dealer. These last two specimens are identifiable as Indo-West Pacific species (T. Pietsch, in litt.).

PEMPHERIDIDAE

The sweepers comprise three genera and probably fewer than 25 species of small (to about 200 mm TL), free-swimming fishes that usually occur about rocks and reefs, and most often in caves. The genera are greatly in need of revision. *Liopempheris* is known only from Australia; *Parapriacanthus* is broadly distributed from the Red Sea and east coast of Africa eastward to at least the Marshall and Phoenix islands; *Pempheris* is distributed similarly to *Parapriacanthus*, but is also disjunctly present along the warmer coasts of the western Atlantic. There are no sweepers in the eastern Pacific, eastern Atlantic, or Mediterranean.

PENTACEROTIDAE

The boarfishes were revised by J.L.B. Smith (1964), who recognized five genera and 12 species.

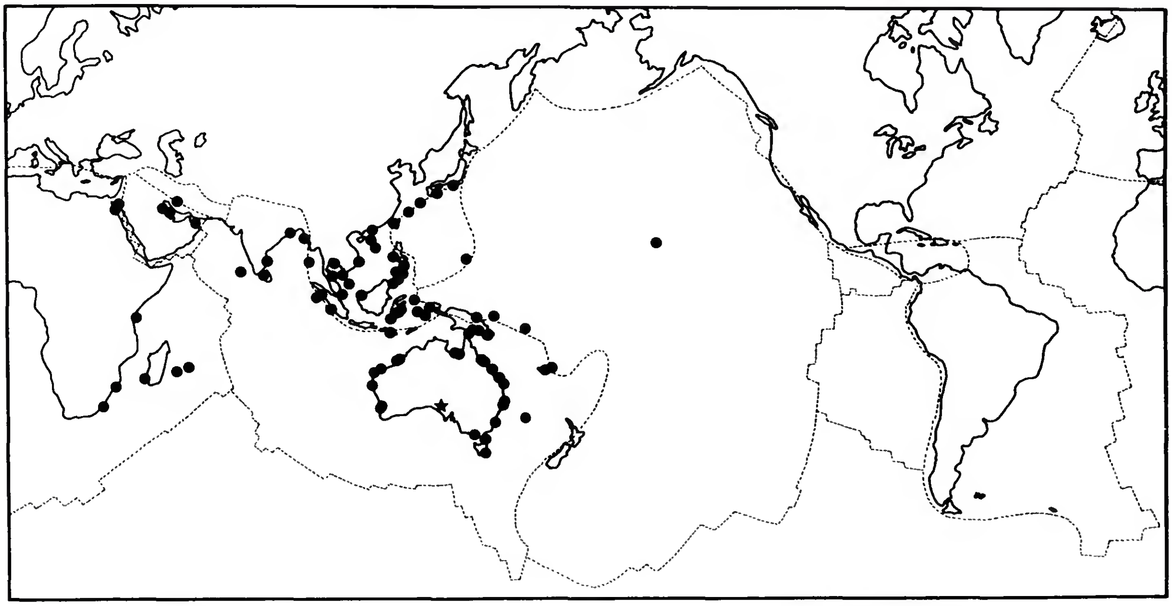

FIGURE 28.—Distribution of the fishes of the family Pegasidae (star indicates unspecified locality on the coast of South Australia).

The boarfishes tend to be deep-dwelling inhabitants of temperate coastal waters, but are taken occasionally in tropical areas and at depths accessible to SCUBA divers. The young (and rarely the adults) of some species have been taken at the surface. Most species are known from specimens under 500 mm TL, but one species attains 900 mm. The family is included here for the sake of completeness and because the reported distribution of one genus (*Histiopterus*) provided a test of my observations on Pacific Plate biogeography.

Three of the genera of boarfishes (*Zanclistius*, *Paristiopterus*, *Pentaceropsis*), including five species, are found only in the waters of southern Australia.

Pentaceros includes four deep-dwelling species. (1) *P. decacanthus*, known only from two juveniles collected over 100 years ago, one without locality data, the other supposedly from the southeast Atlantic at 10°25′S, 30°W (a Museum Godeffroy specimen; Günther, 1873). The western Atlantic has been well and continuously sampled ichthyologically. It is, therefore, surprising that no other pentacerotid specimens have been taken in the western Atlantic for over 100 years. For this reason, and because many Museum Godeffroy specimens seem to be accompanied by questionable locality data, I am doubtful that the locality accorded Günther's specimen is correct. (2) *P. capensis* from southern and southeastern Africa. (3) *P. japonicus* from Japan, southern Australia, and the following localities, which have been reported since Smith's revision: Bonin (Ogasawara) Islands (Zama et al., 1977) and Taiwan (Burgess and Axelrod, 1974). (4) *P. richardsoni*, Tristan da Cunha, southernmost Africa, Japan, New Zealand, Leeward Hawaiian Islands and seamounts (Randall, 1981a), Alaska to California, and southernmost South America (hence, antiequatorially distributed). Penrith (1967) believes that *P. richardsoni* is distributed throughout the world in warm-temperate waters and that the known distribution only reflects fishing intensity.

The distribution of *Histiopterus*, with three species was mapped by J.L.B. Smith (1964, fig. 1), and is reproduced here as Figure 29A, but with the addition of three recent locality records: off the southwest coast of India (Kotthaus, 1975), Lord Howe Island (Allen et al., 1976), and the

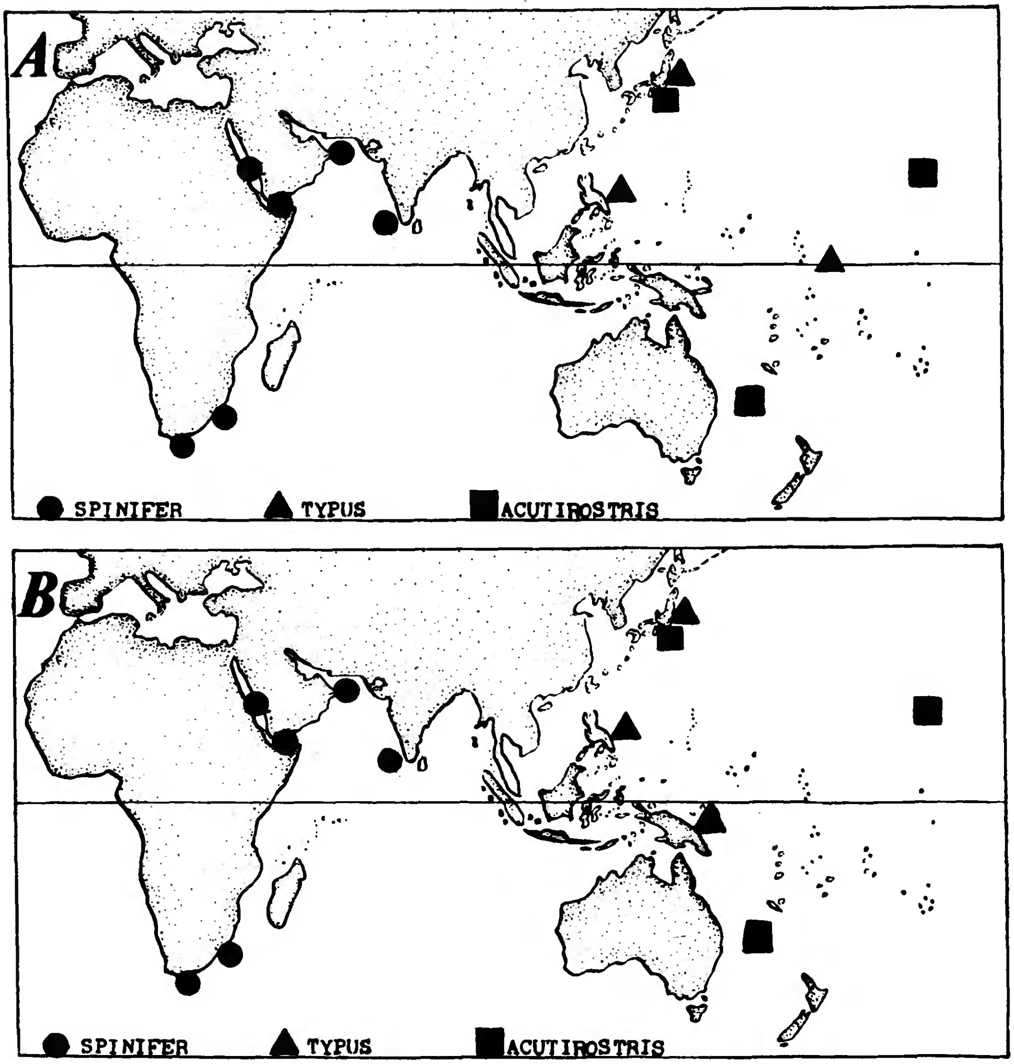

FIGURE 29.—Distributions of the species of the pentacerotid fish genus *Histiopterus*: A, uncorrected, after J.L.B. Smith (1964, fig. 1) with additional records entered for southwest India, Lord Howe Island, and the Red Sea; B, corrected (see page 69).

Red Sea (Klausewitz, 1980). My examination of Smith's distribution map of *Histiopterus*, even before the addition of the recent records, aroused my suspicions that one of Smith's records might be in error: "Duke of York Is. (9°S × 172°W)." Except for the Duke of York record, the map appeared to me to be a normal Hawaiian exception type distribution. Smith mentioned that the Duke of York specimen had been examined for him at the British Museum by G. Palmer, and as there is a Duke of York Island at about the coordinates Smith gave (in the Tokelau Islands), I was inclined to drop my suspicions and ascribe the lack of reports of *Histiopterus* from Oceania to collecting deficiencies. Smith, however, mentioned that the Duke of York specimen had been reported originally by Günther (1877), and although Smith did not cite the reference more fully, I decided to find it and determine if Günther might have been in error. Günther, however, had not made an error, but Smith had! The specimen did come from the Duke of York Island—not the one in the Tokelaus, but the one between New Britain and New Ireland, on the western margin of the Pacific Plate (see corrected distribution map, Figure 29B), which is consistent with an Hawaiian exception distribution pattern. The three recently reported records of *Histiopterus* are congruent with this pattern. This is a small but didactic example of the usefulness of a Pacific Plate biogeographic hypothesis. Had I not been aware of the Hawaiian exception type of distribution, I would have had no reason to question Smith's distribution map. Similar incidents involving other fish groups occurred often during the course of my study.

In summary, the Pentacerotidae are primarily antiequatorially distributed, but are absent in the Mediterranean and Atlantic, except for occurrences at Tristan da Cunha and around the southern tips of Africa and South America (recorded from Cape Horn), and Günther's (1873) questionable record of a juvenile from off Brazil. The pentacerotids are also unreported in the eastern Pacific south of California (except for Cape Horn) or from the Pacific Plate, except marginally and at the Hawaiian Islands.

PHOLIDICHTHYIDAE

The western Pacific family Pholidichthyidae includes a single genus and species, *Pholidichthys leucotaenia,* which is a small (to 337 mm TL) inhabitant of shallow rocky and coral-reef areas, even when young (at least as small as 15 mm). Springer and Freihofer (1976, fig. 1) give a distribution map for the species, which was known to them only from the Solomon Islands, southeast New Guinea, Ambon, northeast Borneo, and Palawan (Philippine Islands). To these localities may be added Negros Oriental, Philippine Islands, based on a collection I made in 1978, and New Caledonia (Burgess and Axelrod, 1975:1429). Burgess and Axelrod did not report *Pholidichthys* from New Caledonia, but in their photograph of an aggregation of *Plotosus anguillaris*, they call attention to two nonplotosids in the aggregation. These nonplotosids are juvenile *Pholidichthys* (brought to my attention by J.R. Gomon).

PLATYCEPHALIDAE

The flatheads comprise about 12 genera and about 60 species of small to large (0.23–1.20 m maximum TL), mostly shallow-dwelling, benthic fishes that occur on sandy, muddy, and rubbly bottoms in habitats as diverse as coral reefs and estuaries. The family is limited to the Indo-Pacific, from the Red Sea and east coast of Africa eastward to the Pitcairn Island group, except for a disjunct, endemic species, *Grammoplites gruveli*, on the tropical west coast of Africa (for some other Indo-Pacific taxa with disjunct west African representation see Lethrinidae). *Grammoplites* is otherwise restricted to the Indian Ocean and a recent immigration into the eastern Mediterranean via the Suez Canal.

Only three genera and five species of flatheads occur nonmarginally on the Pacific Plate, and none of these taxa is endemic to the Plate. Numerous species are widely distributed in the Indo-West Pacific and find their easternmost limits along the eastern margin of the Philippine Plate or western margin of the Pacific Plate; other species are restricted to the Indian Ocean. No flatheads have been reported from the Hawaiian Islands (the Bembridae is here recognized as a separate, deep-dwelling family). (Most of the information on this family was supplied by L.W. Knapp.)

PLESIOPIDAE

The Plesiopidae consists of small fishes (under 300 mm TL) that inhabit rocky and coral-reef areas of the tropical and warm-temperate Indo-Pacific. The family includes six genera and about 20 species. I do not believe the family is a monophyletic group.

Fraudella (monotypic), *Paraplesiops* (about five species), and *Trachinops* (four species; Allen, 1977) are restricted to Australia, and all but *Fraudella* are warm-temperate water inhabitants.

Assessor (three species), a mouth brooder, is known only from the Great Barrier Reef, the Ryukyus, northern Philippines, and a visual report from New Caledonia (Allen and Kuiter, 1976; Randall, in press b); its distribution is antiequatorial.

Plesiops (about six species; last revised by Inger, 1955) ranges from the Red Sea and east coast of Africa to the Marshall, Gilbert, and Phoenix islands. Only one or two species occur on the Pacific Plate nonmarginally, and these are not endemics.

McCosker (1978) gave the distribution of *Calloplesiops* (monotypic) as "Tuamotus, Palau, Philippines, Indonesia, Maldives, Grande Comore, Seychelles, Zanzibar, Mozambique, Pemba, several Red Sea localities, Ryukyus Islands, and Southern Japan." To these may be added Guam (Kami, 1975), One Tree Island (Great Barrier Reef, in Australian Museum collections), and Hermit Islands (Bismarck Archipelago), Fiji, and Ponape (all USNM collections). The only nonmarginal Pacific Plate records for *Calloplesiops* are Ponape and Tuamotus, an unusual distribution for an area that has been so well collected in recent years. Without the Tuamotus record, I would expect that *Calloplesiops* was an Indo-West Pacific taxon that dispersed onto the Pacific Plate via the Caroline Islands conduit. I, therefore, question the Tuamotus record, which is supposedly based on the relatively modern collections made at Raroia by the George Vanderbilt Foundation's 1952 expedition. The field data sheet (GVF Reg. #67) for the collection that pertains to the *Calloplesiops* specimen (California Academy of Sciences 40448) mentions that 21 species and 39 specimens were taken in the collection. The list of species accompanying the field data sheet refers to only 18 species and 36 specimens and does not include mention of a plesiopid. While it is possible that the additional three specimens listed on the field data sheet include *Calloplesiops*, I will remain skeptical until all specimens in Reg. #67 are accounted for and shown to provide for inclusion of the *Calloplesiops* specimen, or *Calloplesiops'* presence in the Tuamotus, or some neighboring island group (such as Societies, Line Islands, or Marquesas), is corroborated.

PLEURONECTIDAE

The flounders are a moderately large family of taxonomically poorly known, small to large, benthic fishes that are primarily inhabitants of deep or temperate waters. Only two genera are reported nonmarginally from the Pacific Plate. *Samariscus* is a common, widely distributed Indo-Pacific genus of small fishes, and *Poecillopsetta* is a deep-dwelling genus of small fishes found in the western Atlantic and Indo-Pacific, but known nonmarginally on the Pacific Plate only at the Hawaiian Islands.

PLOTOSIDAE

The plotosid catfishes comprise about ten genera and 30 species of small to moderately large (to 1.3 m TL) fishes that are restricted to the Indo-Pacific, probably to the Indo-West Pacific (Figure 30). More than half the species are essentially confined to freshwater, although some of these enter brackish water. The other species are found in brackish and marine waters, some occurring normally on coral reefs. Unlike many catfishes, the plotosids are not mouth brooders. As far as known, they lay demersal eggs in nests (freshwater) or rock crevices (marine). Young marine plotosids are not planktonic, but occur in dense spherical aggregations in shallow water, sometimes almost at the shoreline. Adults are usually suprabenthic, but may occur at shallow depths around pilings. Few, if any, of the marine forms occur at depths greater than about 20 m.

The Plotosidae have not been revised, but J.R. Gomon and W.R. Taylor are studying the marine genera and G. Nelson and N. Feinberg, the freshwater genera. All four of these investigators consider the three nonmarginal Pacific Plate records

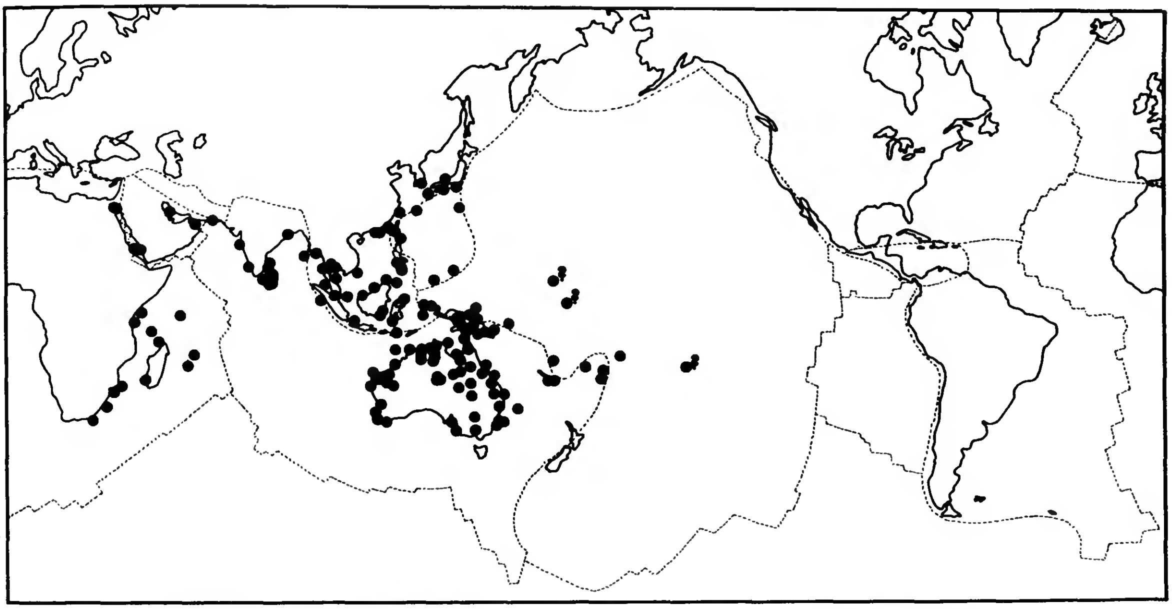

FIGURE 30.—Distribution of the fishes of the family Plotosidae (compiled by N. Feinberg, J. Gomon, G. Nelson, and W.R. Taylor; see discussion under "Plotosidae" for questionable locality records).

of plotosids (*Plotosus lineatus*, Figure 30) as suspect: Kingsmill Group (Gilbert Islands), Society Islands, and Jaluit (Marshall Islands). The first two localities are based on old Museum Godeffroy specimens, which have been the source of many puzzling distribution records (Randall, 1955b, 1973, did not record plotosids from the Gilbert or Society Islands). The Jaluit record is based on a relatively recently collected specimen in the Paris Museum (the collector and details of the collection are unknown to the current curator, M.L. Bauchot, in litt.). Because *Plotosus lineatus* usually occurs in large numbers, is easy to collect, and there have been no other reports from the heavily collected Marshall, Society, and Gilbert islands, I believe the Pacific Plate locality records are either in error or the result of straggling. Furthermore, I did not see or collect plotosids at Ponape (where I would expect them to occur if anywhere on the Pacific Plate), and the local fishery officer, R.A. Croft, at Ponape had no knowledge of their occurrence at that island, despite his six years residence there and active reef-fish collecting.

POLYNEMIDAE

The threadfins comprise seven genera (Myers, 1936) and about 35 species of small to moderately large (to 2 m TL), commercially important, suprabenthic fishes that are almost circumglobally distributed on warm, marine shores. Some species enter freshwater.

Pentanemus (monotypic) is restricted to the tropical west African coast, with a single, questionable record from Cuba (R.M. Feltes, who is revising the family, pers. comm.). *Galeoides* is represented by a common species on the west African coast. A second species of *Galeoides* was described by Steindachner (1869) from a single specimen from "China," and subsequent specimens have not been reported. There is also no indication that the holotype has been re-examined since its description, and I suspect that the generic allocation or locality of the specimen is erroneous. Of the remaining five genera, *Filimanus* (monotypic), *Eleutheronema* (two species), *Polynemus* (seven species), and *Polistonemus* (monotypic) occur only in the Indo-West Pacific, variably from India or the Malay Archipelago east to the western margins of the Philippine and/or Pacific plates. *Polydactylus*, the largest genus of polynemids, with about 20 species, occurs in all oceans, and in the Indo-Pacific ranges from eastern Africa to the Pitcairn Island group. The species of *Polydactylus* are in need of revision, but of the 10-15 Indo-Pacific species, probably no more than two or three occur nonmarginally on the Pacific Plate.

It is clear from this information that the western margin of the Pacific Plate delineates a strong barrier to the eastward dispersal of polynemids.

POMACANTHIDAE

There are seven to nine genera and about 78 species of marine angelfishes (Allen, 1980; W.E. Burgess, pers. comm.). The species are moderately small (maximum size varying from 75 to 600 mm TL) and free swimming, but are obligatory reef inhabitants. The family is distributed circumglobally in warm, shallow seas.

Holacanthus, with eight species (one undescribed, W.E. Burgess, pers. comm.) occurs only in the eastern Pacific and western Atlantic.

Pomacanthus (Allen, 1980, includes *Arusetta* and *Euxiphipops* in *Pomacanthus*; I treat them separately) has nine species, of which two are restricted to the Atlantic and one to the eastern Pacific. All the remaining six species occur in the Indo-West Pacific, but only *Pomacanthus imperator* ranges nonmarginally onto the Pacific Plate.

Centropyge has about 30 species (including at least two undescribed, W.E. Burgess, pers. comm.). Two species are restricted to the western Atlantic, one to Ascension in the eastern Atlantic, and all the others to the Indo-Pacific. Of the 25 described Indo-Pacific species, 15 occur nonmarginally on the Pacific Plate, and of the 15, six are endemic to the Plate. Of the six endemics, three are widely distributed *C. loriculus, C. multicolor*, and *C. nigriocellus*, Figure 31), one is limited to a restricted region (*C. hotumatua*), and two (*C. fisheri, C. potteri*) occur only in the Hawaiian Islands. One of the endemics, *C. loriculus*, is represented by a slightly differentiated population in the Marquesas (Randall, 1980a). Another species, *C. shepardi* (Figure 31), appears to be endemic to the eastern margin of the Philippine Plate, and another, *C. interruptus* (Figure 31), which was believed to be endemic to southern Japan, was recently collected at Réunion (Randall, in press b), in the Indian Ocean, and at Kure, northernmost of the Hawaiian Islands (Ralston, 1981), possibly carried there by the Kuroshio extension. It is doubtful that breeding populations of *C. interruptus* are present at Kure. The large gap in the distribution of *C. interruptus* is probably a collecting artifact, but seems unusual in view of the large amount of collecting in the area of the gap in recent years (see also *Pomachromis richardsoni*, Pomacentridae).

The remaining six genera of pomacanthids occur only in the Indo-Pacific. *Arusetta*, monotypic, does not occur on the Pacific Plate nonmarginally.

Euxiphipops, with three species, is restricted to the Indo-West Pacific, except that one species, *E. xanthometopon*, is present on the Pacific Plate nonmarginally at Ponape (personal observation) and Kosrae (Eldredge et al., 1979), which I consider evidence for operation of the Caroline Islands conduit.

Chaetodontoplus, with nine to 11 species, is probably absent from the Pacific Plate, but there is a report of *C. mesoleucus* that requires mention. Fraser-Brunner (1933) and Fowler (1934) considered Borodin's (1930) *Holacanthus bicolor* variety *oahuensis* to be a synonym of *Chaetodontoplus mesoleucus* (Bloch), and Fowler considered the Hawaiian locality accorded Borodin's specimen to be in error (see also discussion of Sparidae for another suspicious Borodin locality). Fraser-Brunner did not discuss Borodin's locality but gave the distribution of *C. mesoleucus* as "East Indies," indicating that he did not consider the Hawaiian Islands to be within the range of the species.

Apolemichthys contains seven species (Carlson

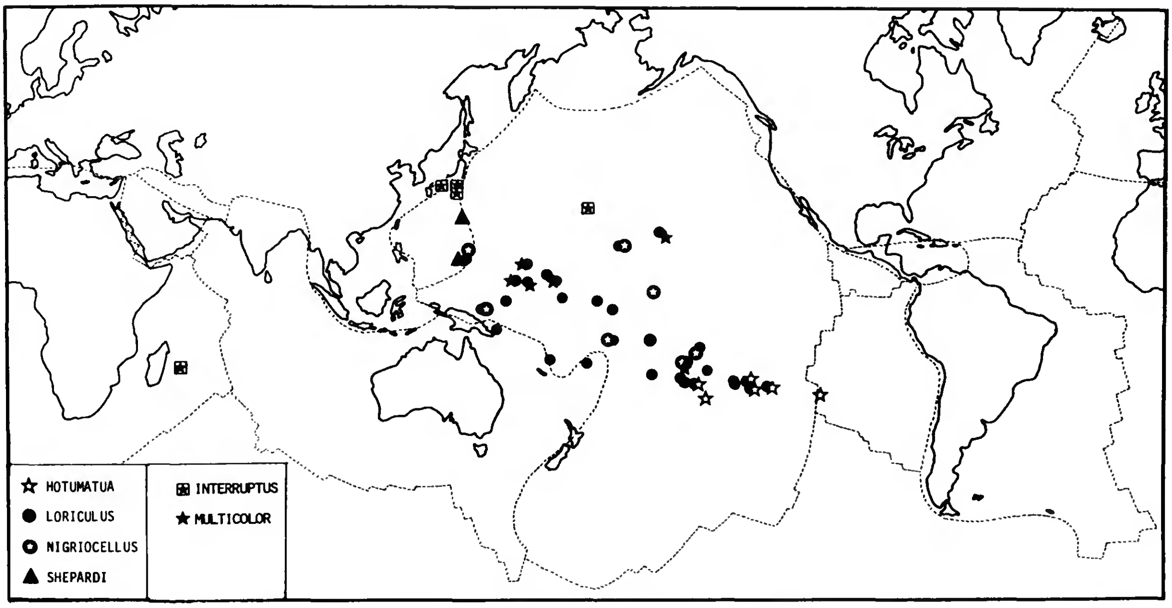

FIGURE 31.—Distributions of certain species of the pomacanthid fish genus *Centropyge*.

and Taylor, 1981), of which three occur on the Pacific Plate nonmarginally: *A. arcuatus*, endemic to the Hawaiian Islands, *A. xanthopunctatus*, widely distributed Plate endemic recorded from Fanning (Line Islands) and Kapingamarangi (Eastern Caroline Islands), and *A. griffisi*, recorded from Fanning and Christmas (Line Islands), Canton (Phoenix Islands), and the Gilbert Islands. Three species of *Apolemichthys* are variously restricted to the Red Sea and western and central Indian Ocean, and one species (*A. trimaculatus*) ranges from the east coast of Africa to at least New Guinea (Steene, 1978; Allen, 1980). I question Allen's (1980, table 4) unsubstantiated listing of *A. trimaculatus* from the Marshall and Gilbert Islands.

Pygoplites, monotypic, is widely distributed in the Indo-Pacific.

Genicanthus, with nine species, is represented on the Pacific Plate by four species, of which two are endemic, one to the Hawaiian Islands, the other to Pitcairn and the Austral Islands (Randall, 1975b), and two have their eastern distributional limits along the western margin of the Pacific Plate (Allen, 1980).

In summary, the Indo-Pacific pomacanthids consist of eight genera and 60–63 species, of which six genera and 25 species (11 endemic) occur nonmarginally on the Pacific Plate. Sister species of the Plate endemics are not known, but it is inevitable that one or all the sister species of the Plate endemic species of *Apolemichthys* are Indo-West Pacific species that do not occur on the Pacific Plate. This fact in addition to the large number of endemic Plate species of *Pomacanthids* indicates that the western margin of the Pacific Plate delineates an important boundary for the distribution and speciation of the Pomacanthidae.

POMACENTRIDAE

The damselfishes consist of 27 genera and about 300 species of small (maximum size about 350 mm TL) fishes. The family is circumglobally distributed and primarily restricted to warm marine waters and reef habitats, but a few species occur on temperate coasts or in freshwater in the tropics. Few genera have been revised in recent years, but much information, particularly on the

Indo-Pacific forms, can be found in Allen (1975) and several of his subsequent studies.

Only five genera (*Azurina, Hypsypops, Nexilosus, Nexilarius, Microspathodon*) that occur in the Atlantic and/or eastern Pacific, do not occur in the Indo-Pacific. Three genera (*Chromis, Abudefduf, Stegastes*) are circumglobally distributed. The remaining 19 genera are confined to the Indo-Pacific, and of these, 11 genera with about 45 species reach the western margin of the Pacific Plate, but do not occur nonmarginally on the Plate: *Acanthochromis* (monotypic), *Amblypomacentrus* (monotypic), *Cheiloprion* (monotypic), *Dischistodus* (6 species), *Hemiglyphidodon* (monotypic), *Neopomacentrus* (about 15 species; Allen and Randall, 1980), *Paraglyphidodon* (6 species), *Parma* (9 species), *Premnas* (monotypic), *Pristotis* (3 species), and *Teixeirichthys* (monotypic).

The following discussion treats the 11 genera with nonmarginal Pacific Plate representation.

Abudefduf contains 13 species, one of which is represented by two subspecies (D.A. Hensley, pers. comm.). The Atlantic has only one species (endemic subspecies; the other subspecies occurs throughout the Indo-Pacific) and the eastern Pacific has only one species, an endemic. The remaining 11 species (and the subspecies—of a 12th species—mentioned above) are confined to the Indo-Pacific, but only six of these taxa occur nonmarginally on the Pacific Plate. One of these six, *A. notatus*, has been reported on the Plate only from the Phoenix and Marquesas islands (Fowler, 1928; Borodin, 1932, as *Glyphidodon*), but Hensley believes that Borodin's Marquesas report is based on a misidentification or erroneous locality assignment (see Pomacanthidae and Sparidae for other questionable Borodin reports). One of the six Pacific Plate taxa of *Abudefduf* is endemic to the Hawaiian Islands; the other five range from the Indian Ocean eastward to well out on the Plate. Hensley and Allen (1977, fig. 4) mapped the distribution of two *Abudefduf* species restricted to the Indo-West Pacific that they considered to be a sister pair.

Amblygliphidodon contains seven species (Allen, 1975; Allen and Randall, 1980), three that extend nonmarginally onto the Pacific Plate (none endemic), and four that do not.

Amphiprion, the clownfish genus, contains 27 species (Allen, 1972, 1973, 1975; Burgess, 1981), all obligatorily associated with sea anemones. Only five species occur nonmarginally on the Pacific Plate. One of the five, *A. clarkii*, is known nonmarginally on the Plate only at Truk (Figure 32), Eastern Caroline Islands, and a second species, *A. tricinctus*, is known only from the Marshall Islands, an unusual area for endemism in fishes. A third species, *A. chrysopterus*, is a widely distributed Pacific Plate endemic (Figure 32). Allen (1972) considered *A. chrysopterus* and *A. tricinctus* to be most closely related to *A. clarkii.* If Allen's assessment of the relationships of these three species is correct it would appear that a vicariant event occurred along the western margin of the Pacific Plate that divided a widely distributed ancestral population of *Amphiprion* into two populations: one, which evolved into *A. clarkii*, on the west side of the margin, and the other, which evolved into the population ancestral to *A. chrysopterus* and *A. tricinctus*, on the east side of the margin. The location of the vicariant event that resulted in the formation of *A. tricinctus* and *A. chrysopterus* is not hypothesized here. Subsequent breakdown of the barrier separating the Pacific Plate populations from those to the west has allowed dispersal and sympatry to develop between *A. clarkii* and *A. chrysopterus-tricinctus.* I believe that the Caroline Islands conduit provides the means for this dispersal. Allen included seven other species in his "Clarkii Complex," all of which are restricted to areas well west of the Pacific Plate margin. *Amphiprion melanopus* and *A. peraderaion*, which are not members of the Clarkii Complex, are widely distributed both on and off the Pacific Plate, but do not occur in the Indian Ocean.

Chromis is the most speciose genus of damselfishes. *Chromis* contains about 65 species (including several undescribed species). About 15 species are confined variously to the eastern Pacific and Atlantic-Mediterranean. Of approximately 50 Indo-Pacific species, about half (24) occur non-

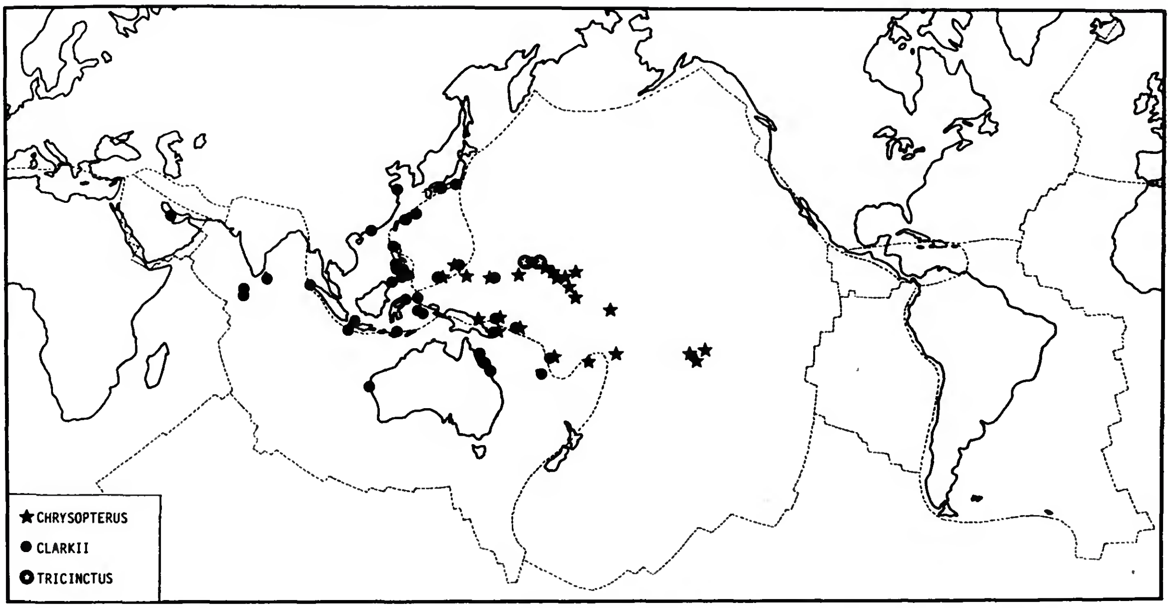

FIGURE 32.—Distributions of three species of the pomacentrid fish genus *Amphiprion* that Allen (1972) considered as forming a closely related group.

marginally on the Pacific Plate (the Easter Island species, an endemic, is included in this group). Eleven or 12 of the Plate species are endemics, variously restricted to the Hawaiian, Marquesas, Pitcairn, and Easter islands. One of these species ranges from Rapa and the Gambier Islands Group to Pitcairn, and another, *C. opercularis*, is listed in Allen (1975, table 2) as occurring at the Tuamotus, Marquesas, Tahiti, and Pitcairn islands. Allen does not discuss this species in his text, although he mentions that there are 36 species of *Chromis* in the South Seas, and he discusses 36. Allen and Steene (1979) reported that *C. opercularis* was a widely distributed Indian Ocean species (hence my reference to "eleven or 12" endemic species of *Chromis* on the Pacific Plate). The other 12 Plate species are more widely distributed on the Plate, and one of these, *C. acares*, is possibly a widely distributed Plate endemic. *Chromis acares* is reported (Randall and Swerdloff, 1973; Allen, 1975) to occur at the following islands, which are either on the Pacific Plate or marginally off the Plate: Cook, Austral, Egum Atoll, Samoan, Line, Marshall, Mariana, New Hebrides, Johnston, Oahu, Gilbert, and Society. Allen's (1975) tables 1 and 2 also list New Guinea and Pitcairn Group within the range of *C. acares*. Randall and Swerdloff (1973) mentioned that Allen had informed them that he had observed *C. acares* at Osprey Reef off northern Queensland, a nonmarginal, continental plate locality; Allen (1975) did not mention Osprey Reef within the range of *C. acares*. Even if Allen's observation is valid, the presence of *C. acares* at Osprey Reef may only indicate a relatively recent westward range expansion of what appears to be a common, widely distributed Pacific Plate endemic. Possible supporting evidence favoring recency of westward range expansions might be Davies and Kinsey's (1977) finding that Great Barrier Reef coral reefs probably date from only 9000 years ago. Randall and Swerdloff considered *C. acares* to be most closely related to *C. lineata*, which ranges from Christmas Island (Indian Ocean) to Palau, New Britain, and the Solomons, and is, thus, only marginally present on the Pacific Plate, and to *C. vanderbilti*, which ranges from the Great Barrier Reef eastward to the Pitcairn Group, and is, thus, sympatric with *C. acares* over much of its range.

Chrysiptera (= *Glyphidodontops*) contains about 25 species, of which only six occur nonmarginally on the Pacific Plate. At least two of the six Plate species are endemic: *C. galbus*, from the Cook, Austral, Tuamotu, Rapa, and Pitcairn islands (Allen and Randall, 1974; Allen, 1975), and *C. rapanui*, endemic to Easter Island (just east of the Plate margin). These two species were considered (Allen and Randall, 1974) to form a closely related group with *C. notialis*, which is known from New South Wales, Lord Howe Island, and New Caledonia, all off the Pacific Plate, but reaching close to its margin, and in line with the southern island chains in which *C. galbus* and *C. notialis* occur. The eastern and western margins of the Pacific Plate, thus, are boundaries along which probable vicariant events occurred that separated more widely distributed ancestral species into populations and allowed them to diverge. The vicariance mechanism resulting in Easter Island endemism is discussed on pages 136–139.

Dascyllus comprises nine species, of which seven occur nonmarginally on the Pacific Plate (H.A. Randall and Allen, 1977). Of the seven, three are Plate endemics: *D. albisella* (Hawaiian Islands), *D. strasburgi* (Marquesas Islands), *D. flavicaudus* (Society, Pitcairn, Tuamotu, and Rapa islands). Randall and Allen reported that *D. albisella* and *D. strasburgi* are most closely related to *D. trimaculatus*, which ranges from the Red Sea and east coast of Africa to Pitcairn, but is allopatric to the other two species. The origin of *D. albisella*, which Randall and Allen considered to be more differentiated from *D. trimaculatus* than is *D. strasburgi*, probably antedates the origin of *D. strasburgi*, and may be the result of island integration (Rotondo et al., 1981; see also discussion about Hawaiian Islands, page 132). The origin of Marquesas Islands endemics is discussed in the section dealing with endemism in those islands. *Dascyllus flavicaudus* was reported to be most closely related to the allopatric *D. reticulatus*, which ranges from the eastern Indian Ocean to just west of the Society Islands, which are the western distribution limits of *D. flavicaudus*. The vicariant event, and possibly dispersal events, that resulted in the distributions of these last two species, if they are sister species, is difficult to propose. *Dascyllus melanurus*, which is widely distributed in the western Pacific, is known on the Pacific Plate nonmarginally only from Ponape (my collections) and Kosrae (Eldredge et al., 1979), Eastern Caroline Islands, although it probably occurs in other, more western, islands of the chain, which have been little collected. I believe the presence of *D. melanurus* in the Eastern Caroline Islands chain to be evidence for the operation of the Caroline Islands conduit.

Lepidozygus is monotypic and ranges over much of the Indo-Pacific.

Plectroglyphidodon contains eight described and at least two undescribed species (Allen, 1975). Apparently, only the eight described species occur nonmarginally on the Pacific Plate. Two species, *P. flaviventris*, from the Tuamotus, and *P. sindonis*, from the Hawaiian Islands, are localized endemics. *Plectroglyphidodon imparipennis*, which should probably be considered a widely distributed Plate endemic, is listed by Allen (1975) as occurring at the Palau, Marshall, Line, Fiji, Tahiti, Tuamotu, Marquesas, Rapa, Pitcairn, Line, Hawaiian, and New Hebrides islands, which are either on, or marginally off, the Plate, and New Caledonia and the Loyalty Islands, which are just west of the marginal Plate areas (R.C. Wass, ms., reports *P. imparipennis* from Samoa). Allen (1975) listed *P. phoenixensis* as present in the Marshall, Gilbert, Fiji, Samoan, Society, Tuamotu, Marquesas, Phoenix, Wake, and Marcus islands, which are either on, or marginally off, the Plate, and from Kenn Reef in the Coral Sea, which is somewhat west of the Plate margin. The last locality may indicate a recent westward dispersal of *P. phoenixensis*, which I have included as a type I plate endemic in Table 2. Allen also mentioned Mauritius as a possible locality for *P. phoenixensis*, but the Mauritius specimens are at least a "color variant" of the typical form. The relationships of

P. imparipennis and *P. phoenixensis* have not been proposed.

Pomacentrus comprises 60 species (Allen and Woods, 1980), but only four species, all widely distributed, occur nonmarginally on the Pacific Plate; however, one of these four, *P. melanopterus*, is known nonmarginally on the Pacific Plate from a single specimen collected at Rongelap in the Marshall Islands (Woods and Schultz, 1960); reconfirmation of the presence of *P. melanopterus* on the Pacific Plate is desirable. At least 18 species of *Pomacentrus* have their eastern distribution limits along the western margin of the Pacific Plate. It is remarkable that so speciose a coral-reef genus as *Pomacentrus* is so poorly represented on the Pacific Plate.

Pomachromis contains four species. Three of these are restricted to the Pacific Plate and its margin: *P. guamensis* (Guam), *P. exilis* (Truk and Enewetak), *P. fuscidorsalis* (Society, Tuamotu, Pitcairn Group islands). The fourth species, *P. richardsoni*, ranges from Mauritius (only Indian Ocean record; see also *Centropyge interruptus*, Pomacanthidae) eastward to the Ryukyus and Samoa, on the Plate margin. Although there are several possible cladograms that can be constructed for these species, it is clear that one of the vicariant events resulting in the present distributions occurred along the margin of the Pacific Plate.

Emery and Allen (1980) estimate that there are about 35 species of *Stegastes* (= *Eupomacentrus*), and Allen and Randall (1980) and Allen and Woods (1980) estimate that there are about 30 species, of which eight occur in the Indo-Pacific. Of these, five occur nonmarginally on the Pacific Plate, and two of the five are Plate endemics. *Stegastes aureus* is a widely distributed endemic: Tuamotus, Marquesas, Line, Gilbert, Phoenix, and Samoan islands. *Stegastes emeryi* is endemic to southeast Oceania: Tuamotus and Pitcairn Island Group. The relationships of *S. aureus* were not proposed, but Allen and Randall (1974) related *S. emeryi* most closely to *S. jenkinsi* (a junior synonym of *S. fasciolatus*), which is widely distributed in the Indo-Pacific and sympatric with *S. emeryi* in the Pitcairn Island Group (Allen, 1975).

In summary, there are 22 genera and about 225 species of pomacentrids in the Indo-Pacific. Eleven genera (50%) and about 72 species (32%) occur nonmarginally on the Pacific Plate, and of the 72, about 28 (39%) are endemic to the Plate. Overall, the Plate endemics account for more than 12% of the Indo-Pacific pomacentrids.

POMATOMIDAE

This family consists of a single, monotypic genus, *Pomatomus saltatrix*, the bluefish or tailor (the deepwater genus *Scombrops* is sometimes included in the Pomatomidae, but is not considered here). The bluefish is a commercially and recreationally important species. It is a strong swimmer and ferocious predator, attaining a moderately large size (to perhaps 1.5 m TL, although rarely exceeding 1 m). The bluefish has been reported to occur in vast shoals extending over several hundred square kilometers (Lund and Maltezos, 1970). In the western Atlantic, bluefish spawn between 55 and 148 km offshore. The eggs and larvae concentrate at the surface along the edge of the continental shelf, but the juveniles apparently descend to deepwater before moving inshore (Norcross et al., 1974; for additional information on spawning, and distribution of juveniles, see Kendall and Walford, 1979). Both young and adults may occur in close shore waters as well as estuaries. Adults are known to make extensive longitudinal migrations.

The distribution of the bluefish (Figure 33) is not approximated by any other fish I know. The species is discussed here primarily because it is often reported as occurring in the warm waters of all seas. My findings do not support such claims. Some distributional reports of bluefish appear to be erroneous, while others are probably so, although the possibility of strays cannot be discounted. There are numerous reports of bluefish occurring at Valparaiso, Chile, but all of these emanate from Gay (1848), who reported on a specimen in the collections of the Paris Museum. Attempts by myself and C.E. Dawson, on my

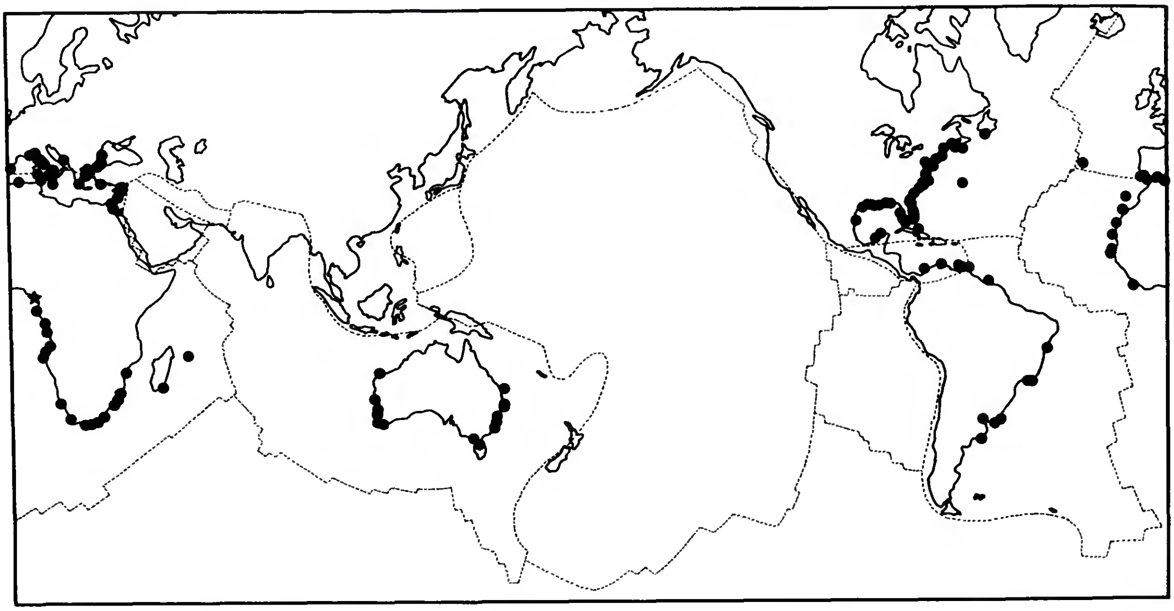

FIGURE 33.—Distribution of the monotypic fish family Pomatomidae (*Pomatomus saltatrix*) (star denotes unspecified locality in Gulf of Guinea).

behalf, to verify the presence of bluefish in Chile have failed, and I do not accept the Chilean record (see also Kendall and Walford, 1979), although one must wonder at the absence of bluefish in the eastern Pacific.

Bleeker's (1844) record of bluefish (as *Temnodon*, a junior synonym) from Djakarta (as Batavia), Java, is also doubtful. The record was reported in Bleeker's first ichthyological publication (of several hundred) at a time "when still an amateur, without sufficient education or literature, and without any experience in this discipline [ichthyology]" (M. Boeseman, in litt.). The material on which Bleeker based his identification is not known to exist, and I know of no other specimens of bluefish from the Indo-Malayan area. Furthermore, Bleeker never again mentioned the bluefish in any of his numerous compilations of Indonesian fishes. Records of bluefish for the Malay Peninsula (for example, La Monte, 1952) and New Zealand (for example, Liem and Scott, 1966) are also doubtful. Colleagues (J.A.F. Garrick and J. Moreland, in litt.) in New Zealand have not encountered bluefish although on alert for the species for many years, and J.S. Scott (1959) a Malaysian fisheries biologist, did not list bluefish in his *Sea Fishes of Malaya.*

Given their general robustness, strong swimming ability, and pelagic eggs and young, it seems surprising that bluefish are not more widely distributed than they are. On the other hand, it is probably worth examining whether the Atlantic and Indo-Pacific populations are truly conspecific.

PRIACANTHIDAE

The bigeyes consist of three genera (*Priacanthus, Pristigenys, Cookeolus*) and probably fewer than 20 species of small (probably rarely, if ever, attaining 600 mm TL), suprabenthic fishes. They inhabit reef and shelf areas and have planktonic larvae. Some species are reported to have very broad distributions, and one, *Priacanthus cruentatus*, is circumtropically distributed.

All three genera of priacanthids are reported from the Indo-West Pacific, but only *Priacanthus* and *Cookeolus* are reported nonmarginally from the Pacific Plate.

PRISTIDAE

There are two genera (*Pristis, Anoxypristis*) and five or six species of sawfishes. Some of the species rank among the largest fishes and are reputed to attain lengths up to 35 ft (10.7 m), but it is doubtful that many, if any, exceed 8 m. The species are viviparous and usually benthic in habit in shallow water (to depths of about 10 m), but often are seen swimming when attacking prey. Although sawfishes usually occur in marine waters, they may ascend great distances up rivers and are even found in freshwater lakes (Thorson, 1978).

In view of the wide distribution of sawfishes (Figure 34), including such isolated islands as Bermuda, Bigelow and Schroeder (1953) stated, "It is probable that the failure of scientific literature to report their presence for any of the island groups of the western tropical Pacific chiefly reflects the imperfection of the published record." In contrast, I believe that the available distribution records for sawfishes gives a reasonably good indication of the group's overall distribution, which is limited to continental plate areas and is repeated by many other elasmobranch groups.

Günther's (1870) record of *Pristis* from the Cape of Good Hope is included in Figure 34; however, Penrith (1978) reported that *Pristis* is absent from the African coast between Mocamedes, Angola, and Natal, southeast Africa.

PSETTODIDAE

The Psettodidae contains a single genus, *Psettodes*, and three species (Stauch and Cadenat, 1965) of moderate-sized (to about 640 mm TL, 9 kg) shallow-dwelling, benthic flatfishes. The family has a disjunct distribution, two species occurring on the tropical west African coast and one in the Indo-West Pacific from tropical east Africa eastward to southern Japan, Queensland, and New Guinea (see Lethrinidae for other families with similar disjunct distributions; also Gobiidae for *Periophthalmus*). The Psettodidae do not occur on the Pacific Plate nonmarginally.

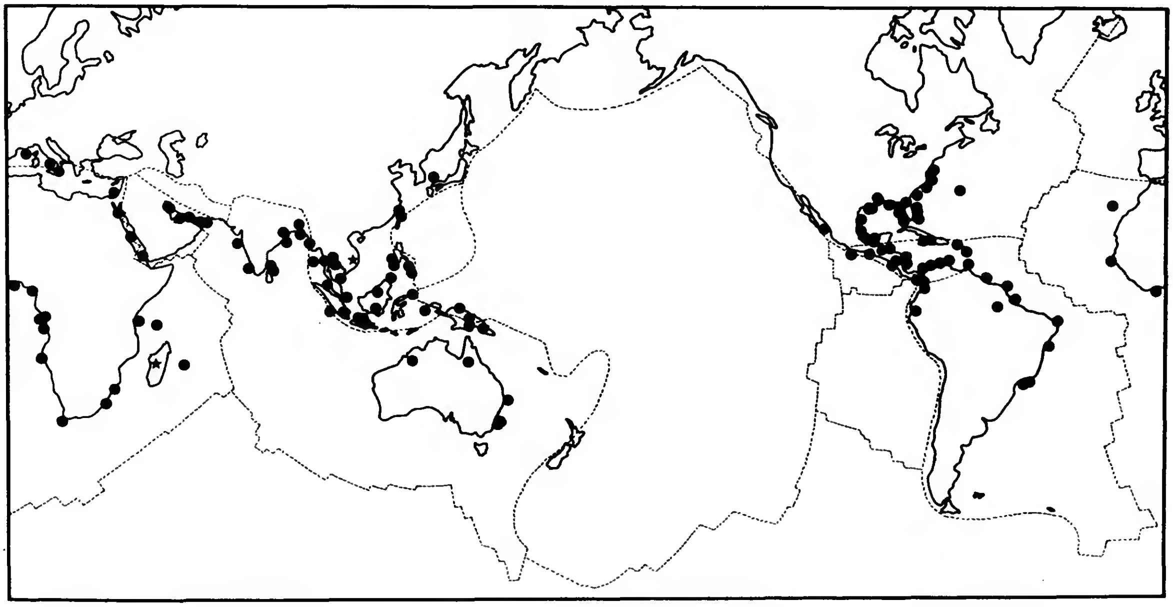

FIGURE 34.—Distribution of the sawfishes, family Pristidae (stars represent unspecified locality records for Madagascar and Vietnam).

Pseudochromidae

This Indo-Pacific family includes the formerly recognized Pseudoplesiopidae and Anisochromidae (Springer et al., 1977). The Pseudochromidae contains about five or six genera and 100 species (including undescribed species) of small (to about 200 mm TL), colorful, reef-associated fishes. Lubbock (1975) described the spawning behavior of *Pseudochromis* in aquaria, but was unsuccessful in rearing the larvae. The genera, except *Anisochromis*, which contains only two species and is restricted to the western Indian Ocean, and *Labracinus*, which contains four species (Schultz, 1967) and is restricted to the western Pacific (except for the Indian Ocean coast of Australia) from Japan south to Australia, are in need of revision. The most speciose genus, *Pseudochromis*, contains more than half the species in the family, but only the Indian Ocean species are well known. All but one or two of the Indian Ocean and Red Sea species of *Pseudochromis*, and all the Indian Ocean and Red Sea species of *Chlidichthys*, appear to be endemic to various parts of those areas (Lubbock, 1975, 1976, 1977, 1980). Most of the other species of pseudochromids also appear to be highly localized, and on this basis Pacific Plate endemics in the family can reasonably be expected. Pseudochromids have not been reported east of the Marshall and Gilbert islands, except for the Pitcairn Island Group (Randall, in litt.).

Pseudotrichonotidae

This family contains a single monotypic genus, *Pseudotrichonotus*, of small fishes (to 88 mm SL) known only from sandy bottom in southern Japan (Masuda et al., 1975).

Rachycentridae

The family Rachycentridae (cobias) consists of a single genus and species, *Rachycentron canadum*, of moderately large size (to about 2 m TL and 50 kg). It is an excellent food and game fish, but does not occur in sufficient concentrations to support a commercial fishery. Little is known of the biology of *Rachycentron*. The adults are usually caught pelagically offshore over the continental shelf. Eggs are planktonic offshore (Joseph et al., 1964), and juveniles may occur as far as 111 km from shore (Dawson, 1971), or almost at the shoreline (Springer and Woodburn, 1960). *Rachycentron* appears to be attracted to boats and offshore oil-drilling rigs.

Rachycentron is often reported to occur in "all warm seas." Its distribution does not warrant such claims, which in part, have been fostered by reports of its occurrence in the Juan Fernandez Islands (De Buen, 1957) or Chile (for example, Mann, 1954). *Rachycentron*, however, has not been reported elsewhere in the eastern Pacific, or other than marginally on the Pacific Plate (Figure 35). There are no specimens that bear eastern Pacific locality data, and my attempts and those of C.E. Dawson, on my behalf, to confirm the existence of *Rachycentron* in Chile have failed. I believe that all reports of Chilean *Rachycentron* stem from Delfin (1899), who reported *Elacate chilensis* [nomen nudum], based on an identification by Philippi (in Delfin), from the Juan Fernandez Islands. Delfin, however, believed the species to be the same as the species called "dorado" at Iquiqui. *Elacate* is a junior synonym of *Rachycentron*, whereas dorado (or dorado de alta mar) is the Ecuadorian, Peruvian, and Chilean common name for the unrelated *Coryphaena hippurus*, the dolphin, which is common in the eastern Pacific. Delfin should actually be credited with disposing of Chilean records of *Rachycentron*, but his actions obviously have been misinterpreted. It seems remarkable to me, nevertheless, that *Rachycentron* does not occur in the eastern Pacific, or, for that matter, other than marginally on the Pacific Plate.

Adam Ben-Tuvia (in litt.) recently obtained a specimen of *Rachycentron* from Haifa, Mediterranean coast of Israel. This is the only record of *Rachycentron* for the Mediterranean and undoubtedly represents a recent introduction from the Red Sea through the Suez Canal.

Suborder Rajoidei

The Rajoidei comprises four families (Anacanthobatidae, Arhynchobatidae, Pseudorajidae,

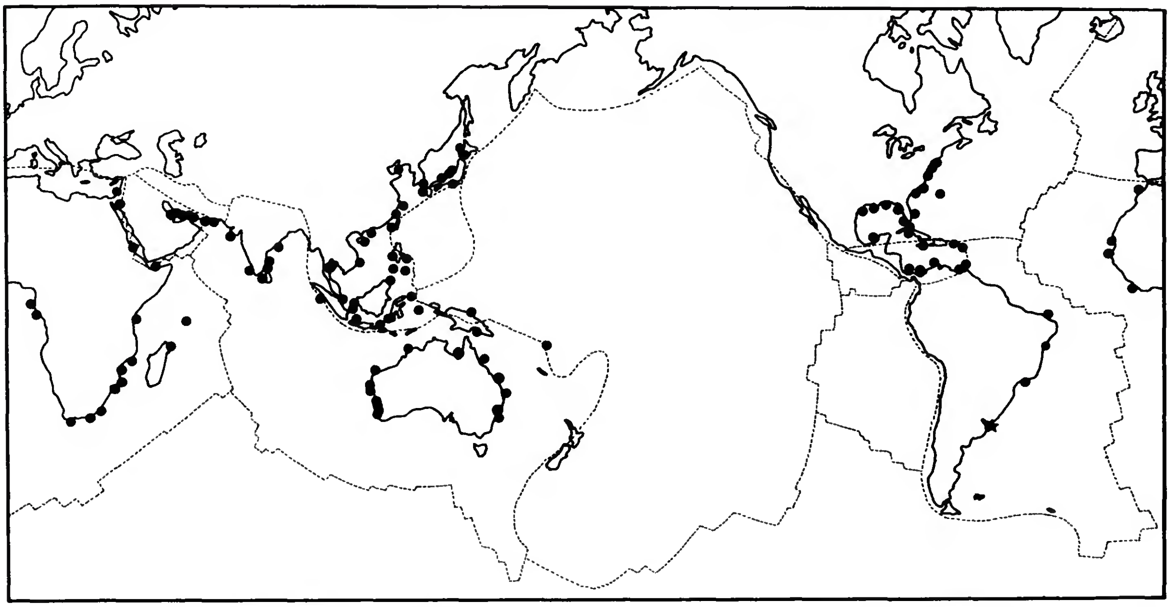

FIGURE 35.—Distribution of the monotypic fish family Rachycentridae (*Rachycentron canadum*) (star represents unspecified locality for Argentina; Markle et al., 1980, reported a larval specimen from off Nova Scotia that has not been plotted here).

Rajidae; Compagno, 1973a), 11 genera, and about 200 species, of rays, of which about half are in the genus *Raja* (J. McEachran, pers. comm.). The species are oviparous and benthic in habit, of moderate to large size (to about 2 m TL), and occur at depths from less than 1 m to over 2900 m. The four families are treated together here for the sake of convenience.

The distribution map (Figure 36) for the Rajoidei does not include records from the Antartic Plate or for northern regions not shown on the map. Most of the records of rajoids from the Pacific Plate are from locations on the New Zealand Plateau or Chatham Rise, which are part of the continental shelf of New Zealand. Eastern Pacific records of rajoids on the Pacific Plate are also associated with juxtaposed continental areas. While it is possible that the deeper, cooler waters overlying nonmarginal portions of the Pacific Plate may harbor rajoids, and, thus, de-emphasize the Plate boundaries as limits to rajoid distribution, it is noteworthy that deep bottom collections in the vicinity of the Hawaiian Islands, which have provided many exceptional distribution records of otherwise continentally restricted taxa, have failed to produce a single record of a rajoid (P. Struhsaker, in litt.). A partial search of several thousand Pacific deep-sea bottom photographs have also failed to give evidence of rajoids on the Pacific Plate (David Pawson, pers. comm.).

The order Rajiformes comprises the suborders Rajoidei and Rhinobatoidei. The distribution of the entire order parallels the distribution of many other elasmobranch taxa, which appear to be absent from the Pacific Plate, except marginally.

Suborder RHINOBATOIDEI

The Rhinobatoidei comprises four families (Platyrhinidae, Rhinidae, Rhinobatidae, Rhynchobatidae; Compagno, 1973a), and about 50 species (most in the genus *Rhinobatos*) of moderately large to large fishes (up to about 3 m TL) that are benthic and viviparous in habit, and occur at depths ranging from less than 1 m to about 100 m. The species are primarily marine but some enter freshwater. The four families are treated together here for the sake of convenience.

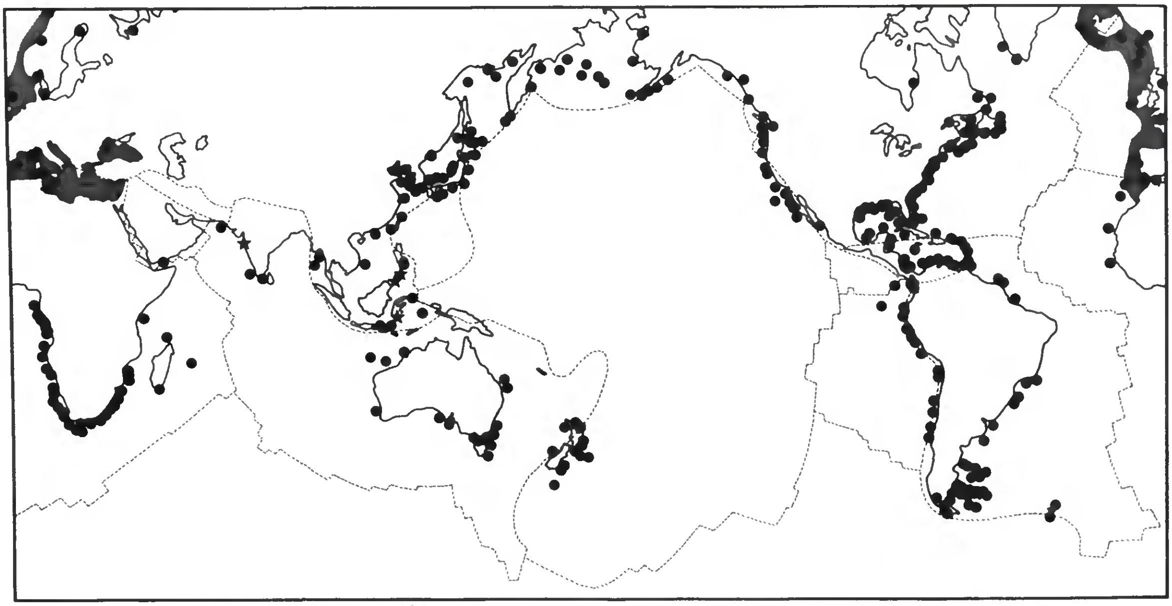

FIGURE 36.—Distribution of the elasmobranch fishes of the suborder Rajoidei, excluding localities on the Antarctic Plate and in the northernmost portions of the Northern Hemisphere; the Rajoidei and Rhinobatoidei (Figure 37) compose the Order Rajiformes (stars denote records based on egg cases; gray areas denote generalized range).

The rhinobatoids are absent from the Pacific Plate, except marginally (Figure 37; records for Samoa and Saipan are based on photographs: J.E. Randall, in litt., Myers and Shepard, 1981).

The order Rajiformes comprises the suborders Rajoidei and Rhinobatoidei. The distribution of the entire order parallels the distributions of many elamsobranch groups, which appear to be absent from the Pacific Plate, except marginally.

RHINOPRENIDAE

This family contains a single genus and species, *Rhinoprenes pentanemus*, of small fish (to about 160 mm TL) that is known only from the Gulf of Papua, New Guinea, and Western Australia (G.R. Allen, pers. comm.). It is apparently restricted to muddy bottoms and areas influenced by river runoff.

RHINOPTERIDAE

The cownose rays comprise a single genus, *Rhinoptera*, and less than ten species of large (disc width to about 2.2 m), free-swimming, viviparous fishes. The family is present in all tropical and warm-temperate seas, but is absent from the Pacific Plate. In the Indo-Pacific it occurs as far east as Australia and Okinawa, but has not been reported from New Guinea or other marginal Pacific Plate localities. The distribution of cownose rays conforms to a pattern exhibited by numerous other elasmobranch groups, which are absent from the Pacific Plate, except, perhaps, marginally.

SCARIDAE

The parrotfishes are a circumtropically distributed group consisting of about ten genera and 70 species. Although numerous species have been revised recently (e.g., Randall and Choat, 1980), none of the genera have been completely and critically revised recently. The parrotfishes are among the more conspicuous inhabitants of coral reefs. They are free swimming and range in size from about 0.3 to 1.3 m TL. Thirty-one species

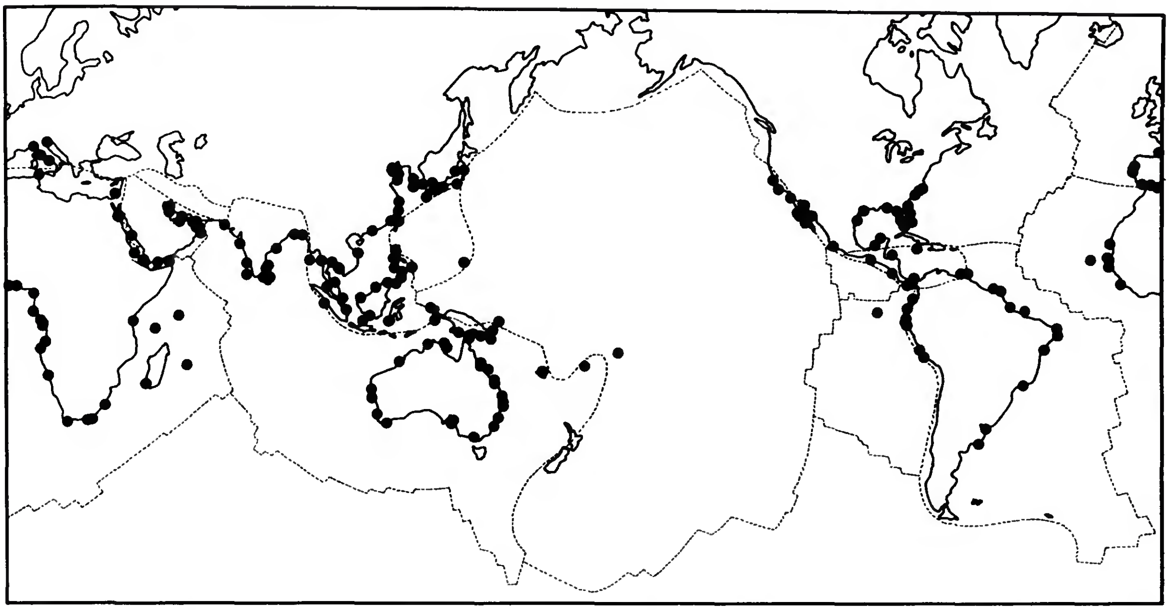

FIGURE 37.—Distribution of the elasmobranch fishes of the suborder Rhinobatoidei; the Rhinobatoidei and Rajoidei (Figure 36) compose the order Rajiformes.

in six genera are present nonmarginally on the Pacific Plate (J.E. Randall, in litt.).

SCATOPHAGIDAE

The scats consist of two genera and three species of small (to about 400 mm TL), shallow-dwelling fishes that occur primarily in brackish water, but are not uncommon in freshwater or the sea. Until now, they have been reported to occur only in the Indo-West Pacific, from the east coast of Africa eastward to Japan, Palau, Yap, New Guinea, Fiji (Carlson, ms.), and New Caledonia. I collected *Scatophagus argus* in Ponape, Eastern Caroline Islands, where it is common in freshwater streams and river mouths. The presence of scats in Ponape is evidence for the operation of the Caroline Islands conduit, which probably enabled the scats to penetrate the Pacific Plate.

Sterba (1962, fig. 1024; reproduced in Nelson, 1974, map 39) gives a distribution map for the Scatophagidae, but omits the western Indian Ocean portion of the distribution, of which Sterba was aware (see his page 656), and Palau and Yap (specimens at California Academy of Sciences), and Ponape.

SCHINDLERIIDAE

This family contains a single genus, *Schindleria*, and two species of very small (to about 25 mm TL) pelagic fishes. Apparently, the species are common (Gosline and Brock, 1960, considered them to be possibly among the commonest fishes in the Hawaiian Islands), but because of their small size and transparent bodies, have been reported only from widely scattered localities (Madagascar and intermediate localities east to Hawaii and Tahiti; Sardou, 1974). Specimens are usually taken under lights at night with fine-mesh dip nets, but I obtained a specimen (see "Addendum") in a rotenone collection on a coral reef at depths of about 9.5–12.5 m in Fiji.

SCIAENIDAE

The Sciaenidae (croakers and drums) comprises about 40 genera and 150–175 species of small to large (weights up to 66 kg have been reported for the western Atlantic species, *Pogonias cromis*; Jordan and Evermann, 1905), shallow-dwelling, suprabenthic fishes. Many of the species are of commercial or sport-fishery importance. The species are oviparous and the larvae, at least of the marine forms, are planktonic. Most of the species are coastal marine or estaurine, but a few New World species are restricted to freshwater (a pattern duplicated by the subfamily Dorosomatinae of the Clupeidae) or have become adapted exclusively to coral reefs. Surprisingly, there do not appear to be any coral-reef adapted species of sciaenids in the Indo-Pacific (see also discussion of Sparidae for a similar pattern of reef exclusion). The world distribution of sciaenids is given in Figure 38. The absence of sciaenids from the nonmarginal areas of the Pacific Plate and from the islands of the Indian Ocean is noteworthy, in view of their presence on the islands of the Caribbean. Another aspect of sciaenid distribution is unusual: less than half the species occur in the Indo-Pacific (Trewavas, 1977; L. Chao, pers. comm.). Most families common to the Indo-Pacific and the New World have more species in the former area than in the latter (the Batrachoididae are similarly exceptional).

SCOMBRIDAE

The Scombridae, or mackerels and tunas, comprises 15 genera and 48 species (Collette, 1979) of small to very large (to over 450 kg), strong-swimming, epiplelagic marine fishes of great commercial and recreational importance. A few species enter estuaries and ascend rivers, and all of the species appear to have pelagic young. In the following discussion, an asterisk marks genera I consider to be high-seas forms.

* *Acanthocybium* is monotypic and found primarily in the high seas around the world in tropical and subtropical waters (Collette 1979); however, John E. Randall (in litt.) informs me that he has seen *Acanthocybium* near coral reefs.

* *Allothunnus* is monotypic and found around the world in the southern oceans south of 35°S (Collette and Chao, 1975, fig. 69), with one highly

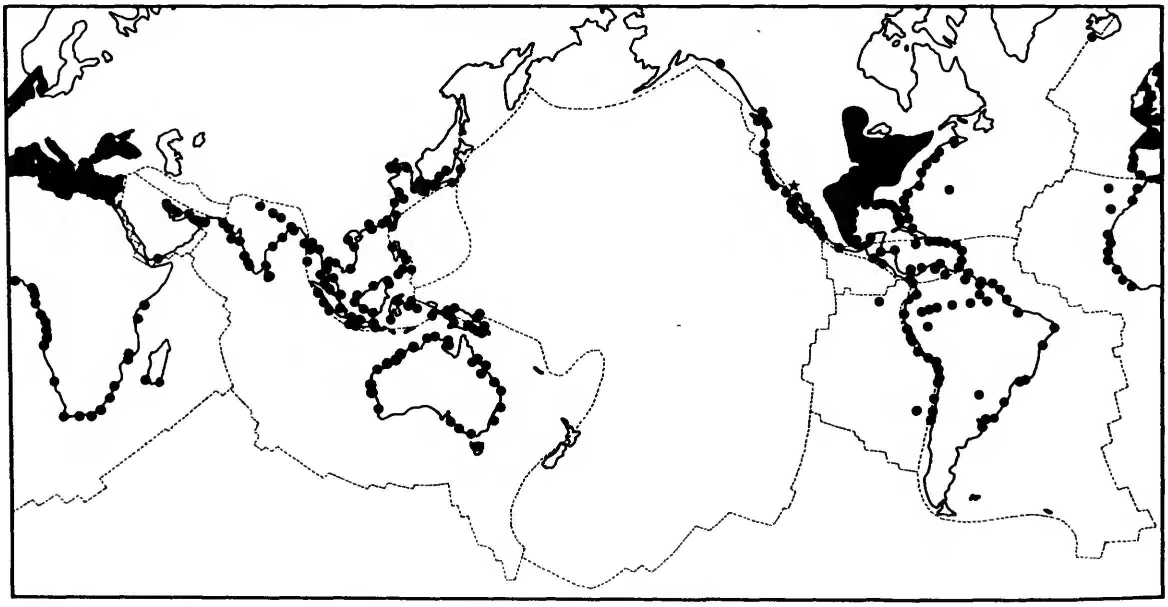

FIGURE 38.—Distribution of the fishes of the family Sciaenidae (solid dark areas represent generalized distributions; star represents Salton Sea introduction).

unusual record from the southern coast of California (Collette, 1979).

There are two species of **Auxis*, both of which are oceanic and at least one of which, *A. thazard*, is circumglobally distributed in warm waters (Collette, 1979; and various authors).

Cybiosarda is monotypic and is distributed along the northern three-quarters of the coast of Australia and the Gulf of Papua (Collette, 1979).

There are three, essentially allopatric, species of *Euthynnus: E. alletteratus*, in the Atlantic; *E. affinis*, found throughout the Indo-Pacific, with a single, valid record from the eastern Pacific; and *E. lineatus*, from the eastern Pacific, with two valid records from the Hawaiian Islands (Collette, 1979).

The monotypic genus *Gasterochisma*, which probably should be placed in a separate family, occurs only in the temperate waters of the southern hemisphere (Collette, 1979).

Grammatorcynus is monotypic and restricted to, and widely distributed in, the Indo-Pacific (including the Pacific Plate nonmarginally), especially near coral reefs (Collette, 1979).

Gymnosarda is monotypic and widely distributed throughout the tropical Indo-Pacific, including the Pacific Plate nonmarginally (Collette and Chao, 1975, fig. 69).

**Katsuwonus* is monotypic and cosmopolitan in tropical and subtropical seas (Collette, 1979).

Orcynopsis is monotypic and restricted to the eastern Atlantic and Mediterranean (Collette and Chao, 1975, fig. 69).

Rastrelliger comprises three species (Matsui, 1967) and is restricted to the Indo-Pacific, except for a recent immigration from the Red Sea through the Suez Canal (Collette, 1979). Prior to my 1980 collecting trip to Ponape, Eastern Caroline Islands, where I obtained specimens of *R. kanagurta, Rastrelliger* was not known to occur on the Pacific Plate nonmarginally. Through a fortuitous error, a distribution map of *R. kanagurta* (Fischer and Whitehead, 1974) indicated the presence of the species in the Eastern Caroline Islands and other nonmarginal localities on the Pacific Plate at a time when *R. kanagurta* was neither known nor suspected to occur at these localities (B.B. Collette, pers. comm.). *Rastrelliger kanagurta* appears to have used the island stepping stones of the Caroline Islands conduit to penetrate the Pacific Plate, but the other two species of *Rastrelliger*, which reach the western margins of the Philippine and Pacific plates, are still unknown from the nonmarginal portions of the Pacific Plate. See also "Addendum."

Sarda (bonitos) comprises four allopatric species (Collette and Chao, 1975) that are usually found in bays and close to shore, although reported to spawn up to 80 miles (153 km) offshore (Walford, 1937). Their eggs are pelagic, but little is known about their larvae and juveniles, which have been taken pelagically both offshore and nearshore (Klawe, 1961). The species undergo migrations and during some periods are absent from certain areas where they are otherwise known to occur (Demir, 1962; Pinkas, 1961). *Sarda* is restricted almost entirely to continental plates (Figure 39), with the Hawaiian islands a noteworthy exception (see also *Scomber* above). The Hawaiian species, *S. oreintalis*, is the same as that which occurs in Japan, Philippines, Indian Ocean, and the tropical eastern Pacific. The other Indo-West Pacific species, *S. australis*, is restricted to New Caledonia and the southeast coast of Australia. It is interesting that the distribution of *S. orientalis* in the eastern Pacific separates the distribution of the other eastern Pacific species of *Sarda, S. chilensis*, into two discontinuous areas, north and south of, and allopatric to, the distribution of *S. orientalis* (Collette and Chao, 1975, fig. 70).

Scomber comprises three species: *S. scombrus*, from the north Atlantic; *S. australasicus*, in the western Pacific from Japan south to southern Australia, and east to the Hawaiian Islands (Hawaiian exception), and Socorro Island off Mexico; *S. japonicus*, antiequatorially distributed worldwide (Collette, 1979). While it is possible that *S. japonicus* occurs nonmarginally on the Pacific Plate, only *S. australasicus* is definitely so reported (Matsui, 1967). *Scomber japonicus* has been reported often from the Hawaiian Islands, but these reports predate Matsui's revision and may be misidentifications. The distribution of *Scomber* is similar to that of *Sarda* (Figure 39).

There are 18 species of *Scomberomorus* (Collette and Russo, 1979; 1980). The genus is distributed throughout the warm shore waters of all oceans, but is noticeably absent from the Pacific and Philippine plates nonmarginally (Figure 40). Ten of the 18 species occur in the Indo-West Pacific. Nine of the Indo-West Pacific species are relatively restricted in their distributions (see Collette and Russo, 1979, figs. 9-11 for distribution maps of all species of *Scomberomorus*), but the distribution of the tenth, *S. commerson*, extending from the Red Sea and east coast of Africa eastward to Fiji, almost covers the entire range of the other nine. *Scomberomorus commerson* the largest *Scomberomorus* species (to 2.2 m fork length) has also recently invaded the eastern Mediterranean via the Suez Canal. In contrast, *S. multiradiatus*, which is the smallest species of *Scomberomorus* (to about 300 mm FL), has the most restricted distribution of the species: Gulf of Papua. I find it surprising that *Scomberomorus* does not occur at the nonmarginal islands of the Pacific Plate, in view of the commoness of *Scomberomorus* in coral-reef habitats elsewhere, including the Caribbean.

There are seven species of tuna, **Thunnus: T. atlanticus* of the western Atlantic; *T. tonggol* of the Indo-West Pacific (absent from the Pacific Plate nonmarginally); *T. albacares*, pantropical; *T. thynnus* (with different subspecies in the Atlantic and Pacific), *T. obesus*, and *T. alalunga*, all worldwide in tropical and temperate waters; and *T. maccoyi* worldwide in southern temperate waters.

In summary, all but one (*Orcynopsis*) of the 15 genera of scombrids occur in the Indo-Pacific; two of the Indo-Pacific genera (*Scomberomorus, Cybiosarda*) are absent from the Pacific Plate, and three genera (*Rastrelliger, Sarda, Scomber*) have been reported on the Plate nonmarginally only from the Eastern Caroline or Hawaiian islands. Of the other nine genera of scombrids, the monotypic *Grammatorcynus* is restricted to, and widely distributed in, the Indo-Pacific, and the other eight genera are circumglobal in distribution, although some species are restricted to the cooler waters of the southern hemisphere. Of the 28 tropical species of scombrids in the Indo-Pacific, only 11-13

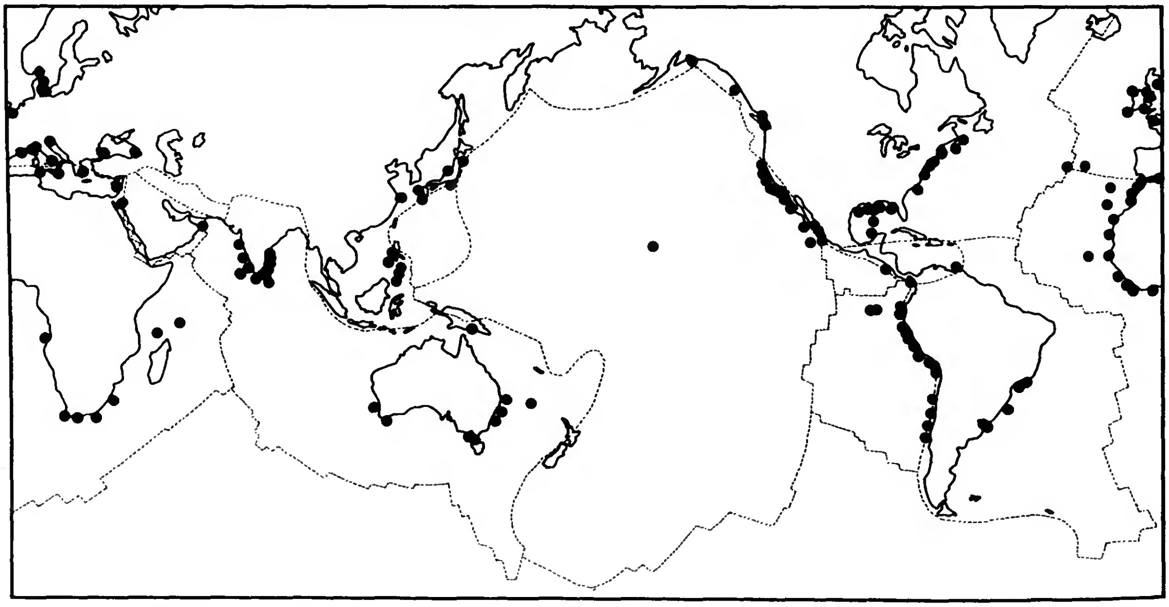

FIGURE 39.—Distribution of the fishes of the scombrid genus *Sarda*. While this study was in press, A.D. Lewis informed me that he had obtained *Sarda* in the Fiji Islands.

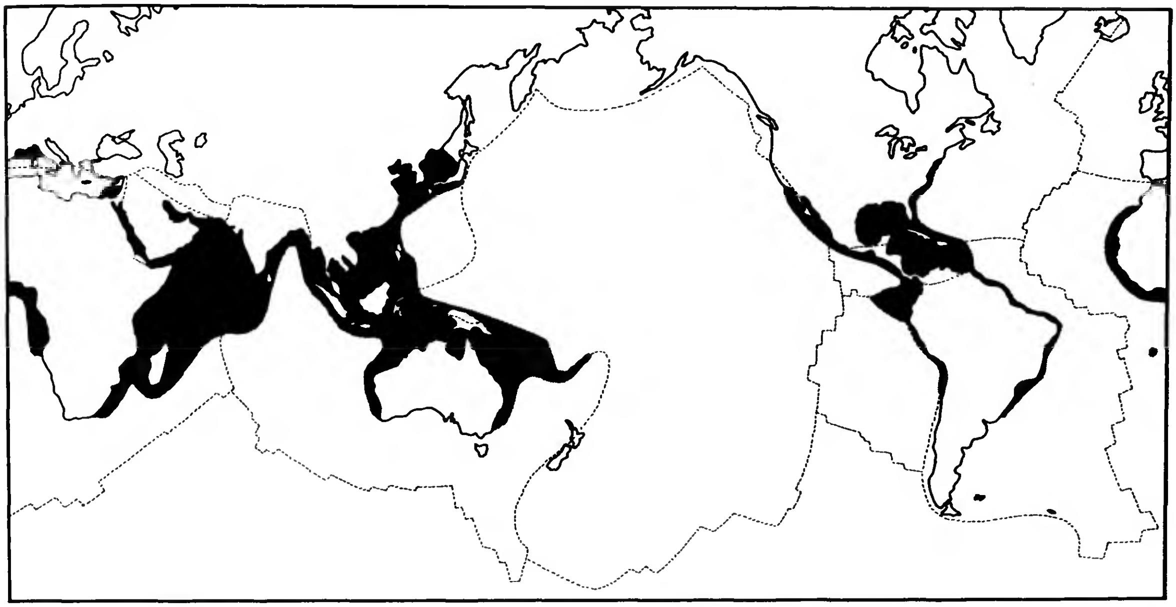

FIGURE 40.—Generalized distribution of the scombrid fish genus *Scomberomorus* (compiled from Collette and Russo, 1979, and Kong, 1978; dark area in eastern Mediterranean Sea represents recent dispersal of widely distributed Indo-West Pacific *S. commerson* through the Suez Canal).

(including high seas species) occur nonmarginally on the Pacific Plate. The six genera I consider to be shorefishes (Appendix 2, Table C) are represented on the Pacific Plate by only seven species.

Collette and Russo (1979, fig. 68) have presented a phylogenetic tree for the scombrid genera. If *Gasterochisma*, which they consider to be the most primitive genus, and which is questionably included in the Scombridae, is excluded, the most primitive genera tend to be restricted to continental plates and the most specialized genera tend to be circumglobally distributed.

SCORPAENIDAE

(including Synanceidae)

There are about 60 genera and 400 species of scorpionfishes (W.N. Eschmeyer, pers. comm.). The species vary in maximum size from about 40 mm to over 1 m TL (most tropical species are under 400 mm) and are found at depths from under 1 m to several thousand meters (most tropical species occur at depths under 50 m). The family is circumglobally distributed in tropical and temperate waters. Most of the cool-water species are viviparous, and all the shallow-dwelling tropical species are oviparous; however, little is known of their reproductive biology. The species are predominantly sedentary (most tropical species) or free-swimming suprabenthic (most cool-water species), and occur in a wide variety of marine habitats, with a few tropical species entering freshwater streams. Much revisionary work remains to be done in the family.

Minous, sole genus of the subfamily Minoinae, contains ten species (Eschymeyer, Hallacher, and Rama-Rao, 1979; Amaoka and Kanayama, 1981), which are found on soft bottoms in depths of 10–240 m. The genus ranges from the Red Sea and east African coast to Japan and Australia, but is absent from the Pacific Plate nonmarginally. Distribution maps for nine of the species of *Minous* are given in Eschmeyer, Hallacher, and Rama-Rao (1979, fig. 1).

Choridactylus (two species) and *Inimicus* (eight species) form the subfamily Choridactylinae.

These genera are found on silty or open-sand bottoms from near shore to 90 m depth, but most of the species occur at less than 40 m. The two genera are widely distributed in the Indo-West Pacific (Eschmeyer, Rama-Rao, and Hallacher, 1979, fig. 8), but are absent from the Pacific Plate nonmarginally. According to Eschmeyer, Rama-Rao, and Hallacher (1979), these fishes "seemingly could, but [do] not cross the Andesite Line."

The subfamily Synanceiinae (stonefishes) consists of six genera: *Erosa*, *Dampierosa*, *Pseudosynanceia*, *Leptosynanceia*, and *Trachicephalus*, all monotypic, and *Synanceia*, with four or five species (Eschmeyer and Rama-Rao, 1973). These genera are restricted to the Indo-Pacific and occur in shallow water in habitats varying from coral reefs to muddy bottoms in estuaries. Only one of the species, *Synanceia verrucosa*, occurs on the Pacific Plate nonmarginally, and it ranges from the Red Sea and east coast of Africa to the Tuamotus. Günther (1860) reported a common Indo-West Pacific species of stonefish (*S. horrida*) from several Pacific localities and from St. Helena in the Atlantic. Eschmeyer (1971:503) believed the St. Helena locality was probably in error, and this was reaffirmed by Eschmeyer and Rama-Rao (1973:3). Briggs (1974:93) unfortunately (but understandably) overlooked Eschmeyer's references and accepted the presence of *Synanceia* at St. Helena.

The subfamily Tetraroginae was tentatively recognized by Poss and Eschmeyer (1975), in which they included *Amblyapistus*, *Hypodytes*, *Liocranium*, *Ocasia*, *Paracentropogon*, *Ptarmus*, *Snyderina*, *Tetraroge*, and "several other genera of uncertain status." The Tetraroginae are confined to the Indo-West Pacific (absent from the Pacific Plate) and occur in shallow water out to depths of about 300 m. Only *Ocosia*, with five species, has been revised in recent years, although information on some of the genera and species can be found in J.L.B. Smith (1958).

The subfamily Pteroinae can be inferred from Eschmeyer and Rama-Rao's (1977) study of *Ebosia* to include *Ebosia*, *Pterois*, *Dendrochirus* (including *Brachirus*), *Parapterois*, and *Brachypterois*, which are found only in the Indo-Pacific. Only *Ebosia*, with two species, has been revised recently, and only *Pterois* and Dendrochirus, widely distributed in the Indo-Pacific, are present on the Pacific Plate nonmarginally. The single species, each, of *Pterois* and *Dendrochirus* that occur in the Hawaiian Islands, are endemics (Eschmeyer and Randall, 1975).

The subfamily Pteroidichthyinae includes *Rhinopias*, *Pogonoscorpius*, *Hipposcorpaena*, and *Pteropelor* (Eschmeyer, Hirosaki, and Abe, 1973), which are restricted to the Indo-Pacific. *Rhinopias*, with four species, is the only one of these genera that is reasonably well known and that occurs on the Pacific Plate (Hawaiian Islands and Condor Reef, Eastern Caroline Islands). The other genera are rare and probably monotypic. All the genera are moderately deep dwelling, although species of *Rhinopias* occur at depths available to SCUBA divers.

The genera that follow are discussed without reference to subfamily.

Six deep-dwelling genera, two represented by Hawaiian endemics, are reported from the Hawaiian Islands (Eschmeyer and Randall, 1975), but are otherwise unknown on the Pacific Plate: *Ectreposebasetes* (circumglobal), *Neomerinthe* (Hawaiian endemic), *Phenacoscorpius* (also western Atlantic, western Pacific), *Plectrogenium* (monotypic, Japan and Hawaiian Islands), *Pontinus* (circumglobal with Hawaiian endemic species), *Setarches* (monotypic, Atlantic and Indo-Pacific). The circumglobal genus *Helicolenus*, also deep dwelling, has been reported (Abe and Eschmeyer, 1972) on the Pacific Plate nonmarginally only from the Emperor Seamount chain, which is continuous with the Hawaiian Island chain.

Taenianotus is monotypic and widely distributed in the Indo-Pacific. William N. Eschmeyer informs me that *Taenianotus* has been photographed in the eastern Pacific (Galapagos Islands), but that no specimens from that area are available.

Scorpaena and *Scorpaenodes* are speciose genera that are circumglobally distributed; *Scorpaenopsis* is also speciose, but restricted to the Indo-Pacific.

Most of the species of these three genera are shallow-dwelling reef inhabitants. Many of the species are island endemics, and at least two may be widely distributed Pacific Plate endemics: *Scorpaena coniorta*, reported only from the Hawaiian, Johnston, Wake, and Line islands (Eschmeyer and Randall, 1975), but present also at Marcus and Makatea islands (J.E. Randall, in litt.), and *Scorpaenopsis fowleri*, known only from the Tuamotu, Society, Marshall, and Hawaiian islands (Figure 26; Eschmeyer and Randall, 1975). The closest relative (sister species) of *Scorpaena coniorta* has not been proposed, but Eschmeyer and Randall (1975) and Eschmeyer (pers. comm.) state that *S. coniorta* belongs to a group (*Sebastapistes*) containing three other species: *S. albobrunnea* (widely distributed in the Indo-Pacific), *S. tinkhami* (Asian, poorly known), and an unnamed species from French Oceania (Pacific Plate locality). Thus, there is a one-in-three possibility that the sister species is restricted to the Indo-West Pacific. The sister species of *Scorpaenopsis fowleri* has not been proposed.

From the sample of scorpaenids discussed above, it is obvious that there are many more genera and species present in the Indo-West Pacific than are present on the Pacific Plate nonmarginally. Many of the genera that are missing on the Plate are shallow reef-dwelling forms that might be expected to occur on the Plate. On the other hand, there are a few widely distributed Plate endemics (as well as some species restricted to single island groups), and this number will probably be increased when the species of unrevised genera are better known.

SCORPIDIDAE

The composition of the Scorpididae appears to be unsettled, but includes at least the following nominal genera: *Scorpis*, *Atypichthys*, *Medialuna*, *Microcanthus*, *Parascorpis*, *Parapsettus*, *Neatypus*, and *Neoscorpius*. It does not appear that there are more than about ten species in the family; only one of the genera, the monotypic *Microcanthus* (*M. strigatus*), occurs nonmarginally on the Pacific Plate, and it occurs only in the Hawaiian Islands (Hawaiian exception).

Microcanthus is a small, free-swimming, suprabenthic species, probably not attaining 200 mm TL, that is found close to shore, even in tide pools as juveniles, in rocky and coral-reef areas. The species is antiequatorially distributed: Hawaiian Islands; Japan south to Hong Kong and Taiwan; southern Queensland; New South Wales; southwestern Western Australia; Lord Howe Island; and New Caledonia (see also *Aulacocephalus* under Serranidae). Reports by various authors that *M. strigatus* occurs in the Philippines appear to stem from Weber and de Beaufort's (1936) statement that the species "probably" occurs in the northern Philippines. That may be, but there is no firm record from the Philippines. The presence of *M. strigatus* in the Hawaiian Islands is possibly the result of dispersal from Japan via the Kuroshio extension.

The other genera mentioned above are variously found along the southern half of the coast of Australia, Lord Howe Island, south coast of Africa, North Island of New Zealand, and temperate eastern Pacific. The distribution of the family is, therefore, antiequatorial.

SCYLIORHINIDAE

The catsharks comprise 17 genera and 86 species of small- to moderate-sized (to about 1.5 m), predominantly bottom or near-bottom dwelling fishes (S. Springer, 1979). The catsharks contain viviparous and oviparous species, and shallow and deep-dwelling species. A few species are found in Indo-West Pacific reef-type habitats, but the distribution of the family is best characterized as antiequatorial in nature. As is true of most elasmobranchs, the catsharks, with one exception, are restricted to continental plates. The only occurrence of a catshark on the Pacific Plate nonmarginally is that of *Parapristiurus spongiceps*, which was collected in the Hawaiian Islands at a depth between 572 and 1462 m. The same species has also been reported from the Banda Sea (Weber, 1913).

SERRANIDAE

(including Grammistidae and Pseudogrammidae)

The sea basses are a circumglobally distributed family containing more than 50 genera and possibly more than 400 species. Much revisionary work is needed in the family, and the Indo-Pacific forms are the poorest known. All the genera, and most of the species, that occur on the Pacific Plate appear to range widely in the Indo-Pacific. (See Lutjanidae for discussion of introduction of *Cephalopholis* into the Hawaiian Islands, where the genus is not native.)

Serranids, for the most part, are shallow-dwelling and benthic or suprabenthic in habit. They occur primarily around rocky areas and coral reefs. They vary in adult size from under 100 mm to about 2.5 m TL. Nineteen genera and about 82 species are present nonmarginally on the Pacific Plate (J.E. Randall, pers. comm.).

Diploprion, a coral-reef genus with two species (Randall et al., 1971), is restricted to the Indo-West Pacific. One species, *O. drachi*, is endemic to the Red Sea, the other, *D. bifasciatum*, ranges from India to Ceylon eastward to the Solomon Islands and New Hebrides (both on the margin of the Pacific Plate), southward to New Caledonia (Fourmanoir and Laboute, 1976) and the Great Barrier Reef, and northward to southern Japan.

Belonoperca, monotypic (*B. chabanaudi*), is a coral-reef inhabitant that ranges from the east coast of Africa eastward to Samoa and the Gilbert Islands, on the Pacific Plate. Randall et al. (1980, fig. 2) give a spot distribution map for Belonoperca, to which can be added Ponape and Ant Atoll, Eastern Caroline Islands (my collections, USNM).

Cromileptes, monotypic (*C. altivelis*), is also a coral-reef inhabitant, and ranges from the Nicobar Islands, eastern Indian Ocean, eastward to southern Japan, Guam, Admiralty Islands, and New Caledonia. It is known nonmarginally on the Pacific Plate only from the Hawaiian Islands, where only a single specimen has been obtained (Randall, 1981a) and another observed, both recently. Randall believes that the occurence of *Cromileptes* in the Hawaiian Islands is the result of aquarium releases but wafting from Japan via the Kuroshio Extension is another possibility. I have not included *Cromileptes* in Appendix 2, Table C.

Aulacocephalus, monotypic (*A. temmincki*), is an Indo-Pacific genus inhabiting shallow, rocky areas. It has an essentially antiequatorial distribution in the Indo-Pacific. On the Pacific Plate, it is known only from Rapa, where it was taken in relatively deep water (70 fathoms = 107 m; Randall, 1978a). It is also known from middle Japan and Cheju Island, Korea, south to Taiwan and Thailand, from southern Africa, Mauritius, Kermadec Islands, New Zealand, and the Andaman Islands (Randall, in press b).

The subgenus *Mirolabrichthys* of *Anthias* was revised by Randall and Lubbock (1981a). Katayama and Masuda (1980) and Randall and McCosker (in press) described two species not treated by Randall and Lubbock. *Mirolabrichthys* comprises 13 species of small, planktivorous, reef inhabitants restricted to the Indo-Pacific (the distributions of eight of the species are given on Figure 41). Eight species occur on the Pacific Plate nonmarginally, of which four are endemic to the Plate: *A (M.) regalis*, endemic and common in the Marquesas; *A. (M.) bartlettorum*, from the Marshall, Phoenix, and Line Islands (Randall and McCosker, in press, give records for the last two island groups); *A. (M.) aurulentus*, from the Line Islands; and *A. (M.) pascalus*, widely distributed on the Plate and reaching the western margin of the Philippine Plate (Figure 41). The distribution of the other species is as follows: two species (*A. (M.) evansi*, *A. (M.) ignitus*) restricted to the Indian Ocean, three (*A. (M.) pavirostris*, *A. (M.) flavoguttatus*, *A. (M.) tuka*) limited to the western Pacific, two (*A. (M.) smithvanizi*, *A. (M.) bicolor*) widely distributed in the Indo-Pacific, at least as far west as Cocos-Keeling, one (*A. (M.) dispar*) widely distributed on the Pacific Plate and in the western Pacific, and one (*A. (M.) lori*) limited to the western Pacific and Pacific Plate.

Prior to Randall and Lubbock's revision, *A. (M.) tuka* and *A. (M.) pascalus* were considered to

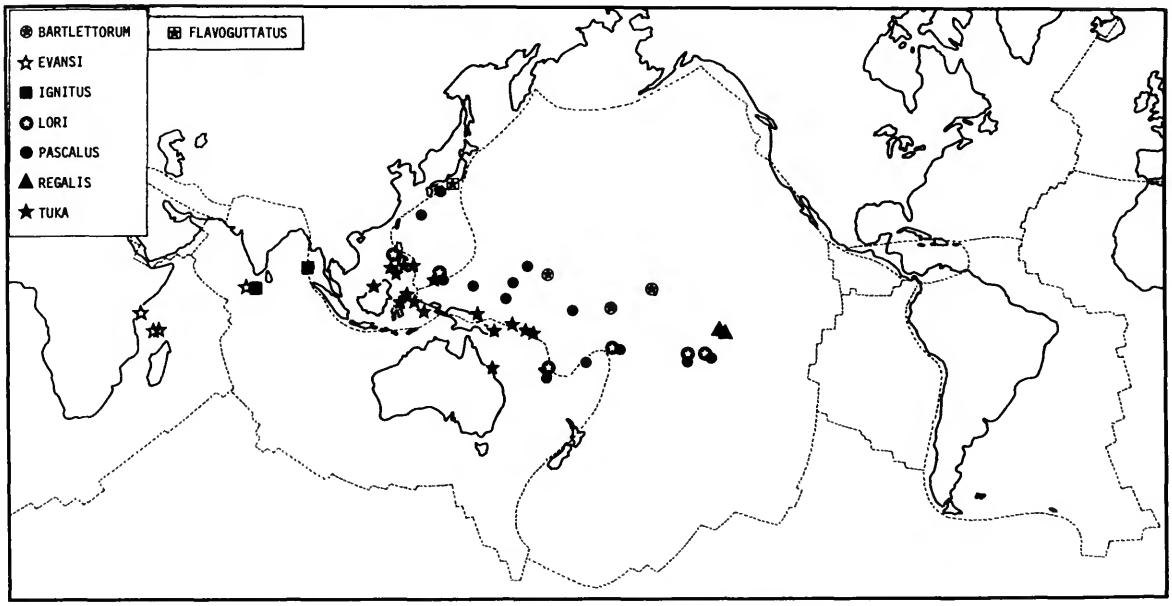

FIGURE 41.—Distributions of eight of the 13 species forming the subgenus *Mirolabrichthys* of the serranid fish genus *Anthias*.

be conspecific subspecies, and even Randall and Lubbock included them in the same key couplet, indicating the possibility that they are sister species. These two species are sympatric in the Palau Islands, on the eastern margin of the Philippine Plate (see also discussion of *Nemateleotris*, Gobiidae), but their distributions, otherwise, are allopatric and defined by the joint margin of the Philippine and Pacific plates (Figure 41). If *A. (M.) tuka* and *A. (M.) pascalus* prove to be sister species, the vicariant event that divided the range of their common ancestor would appear to have occurred along the joint margin of the plates. Sympatry of the two species in the Palaus indicates that subsequent dispersal has occurred, with the Caroline Islands conduit permitting the Pacific Plate species to disperse westward.

Odontanthias comprises nine species and occurs only in the Indo-Pacific (Mauge, 1980). One species is confined to the western Indian Ocean, five to the western Pacific (from Celebes to Guam), and three to the Pacific Plate (two in the Hawaiian Islands; one in the Cook and Society islands); hence, none of the species ranges across the margin of the Pacific Plate.

Plectranthias was revised by Randall (1980b); an additional species was described from Japan by Katayama and Masuda (1980) and another from the Coral Sea by Fourmanoir and Rivaton (1980). The genus contains 32 small species, most of which occur at depths of over 100 m; however, several species are shallow dwelling. One species is limited to the tropical western Atlantic, but all the others are restricted to the Indo-Pacific. Seven species, including two that are deep dwelling, occur nonmarginally on the Pacific Plate, and three of these are each endemic to single islands: *P. helenae* (Oahu, deep-dwelling), *P. taylori* (Canton, deep dwelling), *P. cirritoides* (Rapa, shallow dwelling). Interestingly, two shallow-dwelling species, *P. nanus* and *P. fourmanoiri*, are widely distributed on the Pacific Plate, but are otherwise known only from Christmas and/or Cocos-Keeling islands, both eastern Indian Ocean. If the two species are actually absent from the area between the Indian Ocean and Pacific Plate, extinction of populations from the intermediate area is indicated.

John E. Randall informs me (in litt.) that *Epinephelus socialis* is a widely distributed Pacific Plate endemic. The Bishop Museum has specimens from the Society Islands, Tuamotus, Pitcairn Group, and Rapa. The USNM collections have specimens additionally from the Tokelau, Samoan, Phoenix, Line, and Marshall islands.

SIGANIDAE

The Siganidae contains a single genus (*Siganus*) and 26 species of small (to about 425 mm TL), free-swimming, shallow-dwelling fishes. A revision of the family, which I have not seen, by D.J. Woodland is nearing completion. The species are abundant in reef areas, particularly on the grassy flats around reefs. Pelagic young are often taken close to shore under a light at night. The family is widely distributed in the Indo-Pacific, from the Red Sea and east coast of Africa to the Pitcairn Island group. Two species have become well established in the eastern Mediterranean, having invaded that area via the Suez Canal (Ben-Tuvia, 1966). The fact that an endemic siganid species occurs in the Fiji Islands (Gawel and Woodland, 1974) suggests the possibility that other siganids may be endemic to Pacific Plate island groups.

SILLAGINIDAE

The Sillaginidae comprises three genera and about 25 species of small (to about 500 mm TL) suprabenthic, shallow-dwelling fishes that occur in marine and estaurine areas, and occasionally enter freshwater. They usually occur over sandy bottom. The family is restricted to the Indo-West Pacific (Figure 42), except for a recent introduction into the eastern Mediterranean via the Suez Canal (Mouneimne, 1977). A revision of the family by R.J. McKay is nearly completed.

SOLEIDAE

(including Achiridae)

The soles are poorly known taxonomically. Norman (1966) reported that there are 31 genera, and Nelson (1974) 117 species, of soles. About half the genera and species are restricted to the Indo-Pacific, although the family is almost circumglobally distributed in shallow tropical and warm-temperate marine waters. Some species occur well up rivers, and some in deep coastal waters, but all appear to be inhabitants of sandy and muddy bottoms. Most of the species are under 300 mm TL, but some soles in European waters may attain over 500 mm TL. The larvae are planktonic.

Soles are poorly represented on the Pacific Plate, where only two genera, *Soleichthys* and *Aseraggodes*, are known. Both are in need of revision. Pietschmann's (1938) report of *Achirus thepassi* from Honolulu appears to be a misidentification of a damaged specimen of *Aseraggodes kobensis* (see also Clark and George, 1979:106).

Of the Indo-West Pacific genera, only *Pardachirus* has been revised recently. Clark and George (1979) recognized four species, with the overall range for the genus extending eastward from the Red Sea and east coast of Africa to southern Japan and Palau, Solomon, New Hebrides, Tonga, and Samoan islands, along the margin of the Pacific Plate (see their fig. 1 for a distribution map). One species inhabits estaurine areas, others occur in sandy areas about reefs.

SOLENOSTOMIDAE

The Solenostomidae consists of a single genus, *Solenostomus*, and perhaps as many as five species of small (to about 160 mm TL), benthic, marine fishes restricted to the Indo-Pacific. The family is widely distributed (but rarely collected) in the Indo-West Pacific, from the Red Sea and east coast of Africa eastward to Japan, Guam, New Guinea, Australia, and Fiji (Carlson, ms.). The only nonmarginal Pacific Plate records for *Solenostomus* are for a single specimen (25.7 mm SL) taken off Bikini Atoll in an open plankton net lowered from the surface to 175 fathoms (320 m) and hauled open to the surface (Schultz, 1953c), and a photograph of an adult taken by a Kwajalein resident (J.E. Randall, in litt.). It seems possible that *Solenostomus* is wafted planktonically onto the Pacific Plate, but that breeding popu-

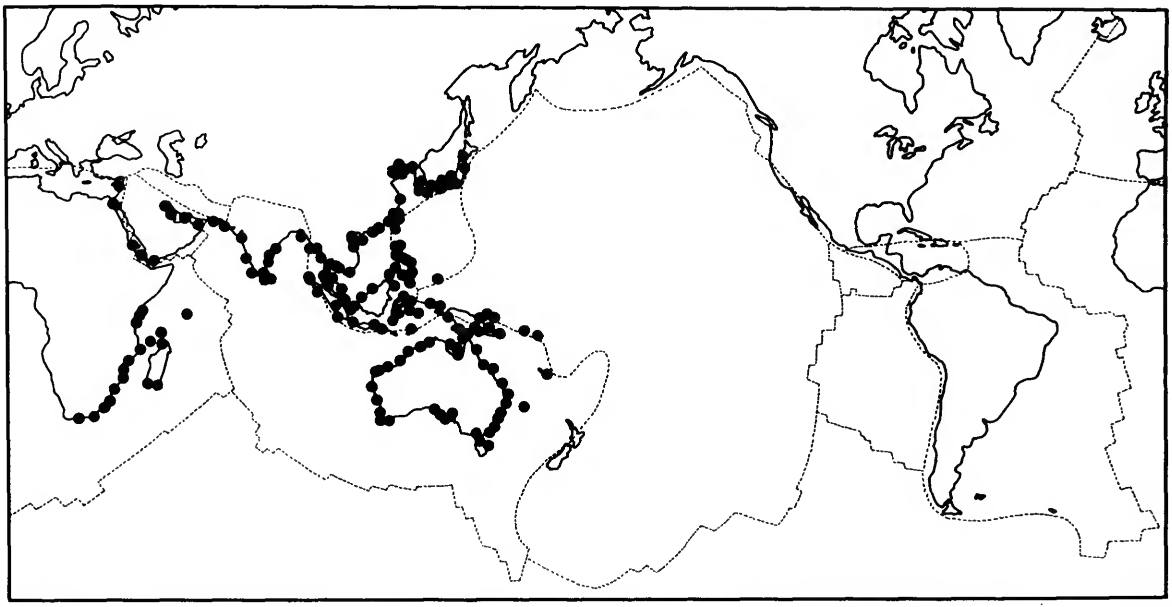

FIGURE 42.—Distribution of the fishes of the family Sillaginidae (compiled mostly from information provided by R.J. McKay, with additions from the literature).

lations do not exist in that area. I have, nevertheless, recognized the family as represented on the Pacific Plate (Appendix 2: Tables A, B, C).

SPARIDAE

The porgies are a large family containing over 25 genera and 100 species of small to moderately large, suprabenthic fishes, many of which are of commercial importance. The species are typically marine, but some frequently enter estuaries. They occur over all types of bottom in habitats as diverse as mangrove swamps and coral reefs. The family is distributed worldwide in tropical and temperate shelf waters, but with one exception (see below) has not been reported from the nonmarginal portions of the Philippine and Pacific Plates (*Monotaxis*, which is a lethrinid, has often been reported as a sparid from Pacific Plate localities). Sparids are common about the coral reefs of the Caribbean, just as some sciaenids are, but neither of these two families occurs on the coral reefs of the Indo-Pacific.

Munro (1949) reported the distribution of the genus *Mylio*, which comprises seven species and is limited to the Indo-West Pacific, except for one record of *M. berda* from Raiatea, based on a report by Borodin (1932). The distribution of *M. berda*, which was mapped by Munro (1949, fig. 3), almost covers the combined distributions of the other species of *Mylio*. The Raiatea record is prominent for its wide geographic separation from all other records of *Mylio*, which are from continental plate areas. It would be most noteworthy if *Mylio* occurred on the Pacific Plate nonmarginally, but I suspect that Borodin either misidentified or associated incorrect locality data with his specimen (see Pomacanthidae and Pomacentridae for other questionable Borodin reports). Munro (1949, fig. 5) also figured the distribution of *Rhabdosargus sarba*, which closely parallels the distribution of *Mylio* (less Raiatea), and which embraces the distribution of the other species of *Rhabdosargus*, which are confined to the western Indian Ocean (Smith, 1979).

SPHYRAENIDAE

The barracudas consist of single genus, *Sphyraena*, and about 20 species (de Sylva, 1974) of small to moderately large (to about 2 m TL), free-swimming fishes. The genus is almost circumglobally distributed in tropical and warm-temperate marine waters. There are about 11 species in the Indo-Pacific, but their distributions within the area are inadequately known (de Sylva, 1974). At least two species occur nonmarginally on the Pacific Plate, and one of these, *S. barracuda*, essentially duplicates the entire range of the genus, except that it is absent from the eastern Pacific (de Sylva, 1963), where other species of *Sphyraena* occur.

SPHYRNIDAE

The hammerhead sharks consist of a single genus, *Sphyrna*, and nine viviparous species (Gilbert, 1967) of moderately large to very large fishes (maximum TL varying from about 1.0 to more than 6.0 m). The family is circumglobally distributed, as are two of the three largest species: *Sphyrna zygaena* has a bitemperate distribution, essentially surrounding the distribution of *S. lewini*, which is circumtropical (both species occur in Hawaiian waters). The third large species, *S. mokarran*, which apparently occurs along all warm continental coasts, is absent from the Pacific Plate nonmarginally. All the other, small, species, except *S. blochii*, are variously restricted to the coastal waters of the Atlantic and eastern Pacific. *Sphyrna blochii* is limited in distribution to the northern coasts of the Indian Ocean, including the Red Sea and Persian Gulf, and to the coasts of Indonesia and Malaya, eastward to the Philippines. The supposed occurrence of *S. blochii* in Australia has been discredited by Scott (1973).

SQUATINIDAE

The angel sharks comprise a single genus, *Squatina*, and about ten species of small to moderately large (to about 2 m TL), benthic, viviparous fishes. The species live in shallow to moderately deep coastal waters, and the genus is, for the most part, antiequatorially distributed on all continental plates (continuously distributed from the Mediterranean to Angola in the eastern Atlantic). Reports of *Squatina* from tropical latitudes usually indicate depths of capture in excess of 100 m (Poll, 1951; Bullis and Thompson, 1965; Cervigon, 1966). Angel sharks, like most elasmobranchs, are absent from the nonmarginal portions of the Pacific Plate. Their easternmost occurrences in the Indo-West Pacific are in Japan and Australia (New South Wales).

Kossmann and Räuber (1877) reported on a Mediterranean species of angel shark, *Squatina squatina*, that reputedly was taken in the Red Sea. Kossmann's collections were obtained from both the northern (including the Gulf of Suez) and southern portions of the Red Sea and were mixed. Possibly the *Squatina* specimen came from the Gulf of Suez and represents an incursion from the Mediterranean. There are no other reports of angel sharks from the Red Sea (or northern portions of the Indian Ocean) and I question the validity of Kossmann and Räuber's report.

STEGOSTOMATIDAE

This family is discussed under the Orectolobidae.

STROMATEIDAE

The pomfrets comprise three genera (*Pampus, Peprilus, Stromateus*) and about 15 species, of small (to about 500 mm TL), commercially important fishes that are widely distributed, but restricted to tropical and warm-temperate continental plate coastlines, where they may enter brackish water. Haedrich (1967) gives a generalized distribution map for each of the genera, which are mostly allopatric, and notably absent from the coasts of eastern Africa, the Red Sea, Australia, and New Guinea. *Pampus* has been reported from Hawaii by Fowler (1938), who questioned (as did Haedrich, 1967) the correctness of the locality assigned his specimens. *Pampus*, which is restricted to, and is the only genus of the family in, the Indo-West Pacific, does not occur on the Pacific Plate. *Pampus* was reported from the Adriatic by Soljan (1963; as *Stromateus griseus*), but this record is also untenable.

SYNGNATHIDAE

The pipefishes and seahorses comprise about 56 genera and 240 species (C.E. Dawson, pers. comm.) of small (to about 610 mm TL) fishes. The species are usually shallow dwelling and benthic in marine waters, but may occur at moderate depths, in freshwater, and pelagically (usually associated with seaweed). Young are carried by the males until parturition, after which the young may become pelagic. Much revisionary work remains to be done among the syngnathid genera, but a number of the Indo-Pacific genera have been revised recently and these are discussed.

Apterygocampus is monotypic and known only from Ceram, Moluccas (Dawson and Allen, 1978).

Bhanotia contains two species that are restricted to the Indo-West Pacific, from the eastern Indian Ocean eastward to the New Hebrides, on the margin of the Pacific Plate (Dawson, 1978b, fig. 4).

Campichthys contains four species and occurs only in the Indo-West Pacific, from the east coast of Africa and Australia (Dawson, 1977c, fig. 19).

Choeroichthys contains five species and occurs only in the Indo-Pacific (Dawson, 1976, 1978a). Two species are widely distributed in the Indo-Pacific, one is limited to the western Indian Ocean, one to the Moluccas, and one to Australia.

Corythoichthys contains ten species and occurs only in the Indo-Pacific (Dawson, 1977b, figs. 6 and 11). Although eight species range onto the margin of the Pacific Plate, only four continue nonmarginally on to the Plate.

Doryrhamphus was revised by Dawson (1981), who recognized five species (including eight taxa; one species with three subspecies, another with two subspecies). The genus is restricted to the Indo-Pacific except for *D. e. excisus*, which ranges from the east coast of Africa to the Gulf of California and Galapagos Islands in the Eastern Pacific. Four taxa reach the western margin of the Pacific Plate, but of these only *D. e. excisus* occurs nonmarginally on the Plate. Dawson provides distribution maps for all the taxa.

Enchelyocampus is monotypic and is known only from Australia and Palau, on the margin of the Pacific Plate (Dawson and Allen, 1978).

Festucalex contains five species and occurs only in the Indo-Pacific (Dawson, 1977c, fig. 10). Only one of the species occurs on the Pacific Plate nonmarginally, and only at the Hawaiian Islands (Hawaiian exception).

Halicampus contains two species (Dawson and Randall, 1975) and is restricted to the Indo-West Pacific (Red Sea to Solomon Islands; C.E. Dawson, pers. comm.).

Hippichthys contains three species and is restricted to the Indo-Pacific (Dawson, 1978c, fig. 3). Two of the species range from the western Indian Ocean to the margin of the Pacific Plate; the third ranges from the western Indian Ocean to the Eastern Caroline and Gilbert islands, well out on the Plate.

Ichthyocampus is monotypic and known only from the Indo-West Pacific, from the west coast of India to Borneo and Java (Dawson, 1977c, fig. 4).

Lissocampus contains five species and is known only from Australia, New Zealand, Chatham Islands (nonmarginal Pacific Plate locality, but on the continental shelf of New Zealand, hence, not considered a Plate locality for my purposes), and the Red Sea (Dawson, 1977a).

Mannarichthys is monotypic and is known only from the Indo-West Pacific, from the east coast of Africa to the Great Barrier Reef (Dawson, 1977c, fig. 4).

Nannocampus contains two species, one known only from the southeast coast of Africa, the other from Australia and Indonesia (Dawson, 1979b).

Notiocampus is monotypic and known only from Australia (Dawson 1979b).

Oostethus is monotypic and consists of four allopatric subspecies (Dawson, 1979a). The genus occurs along all warm coastlines (including islands on the Pacific Plate), except those of the eastern Pacific, with one exception: the western Atlantic subspecies is present on the Pacific coast of Panama, and Dawson believes it to have reached that area via the Panama Canal. Another subspecies is restricted to the Western Indian

Ocean, the third to the eastern Indian Ocean and central and western Pacific Ocean, and the fourth to the west coast of Africa.

Penetopteryx contains two species (Dawson and Allen, 1978). One species ranges from Mauritius to the Line Islands; the other is known only from the Bahamas.

Phoxocampus contains three species and is found only in the Indo-Pacific (Dawson, 1977c, fig. 4). Only one of the species occurs on the Pacific Plate nonmarginally.

Siokunichthys contains six species and is restricted to the Indo-West Pacific, from the Red Sea to Fiji, on the margin of the Pacific Plate (C.E. Dawson, pers. comm.).

Stipecampus is monotypic and known only from southern Australia (Dawson, 1977c, fig. 10).

Urocampus contains two species and is known only from the Indo-West Pacific: Japan south to Ryukyu Islands, Australia, and New Guinea (Dawson, 1980).

Yozia contains three species and is distributed from the Red Sea and east coast of Africa to Japan and Australia (Dawson et al., 1979).

In summary, of the 22 genera and 54 species of Indo-Pacific pipefishes discussed, only eight genera and 12 species (22.2%) are present on the Pacific Plate nonmarginally. No Pacific Plate endemics are among these taxa. Five other genera (Appendix 2, Table C) and perhaps 13 more species of pipefishes also occur on the Pacific Plate, but I expect that the species in these genera that are restricted to the Indo-West Pacific will exhibit the same or greater ratio to the genera and species occurring on the Pacific Plate as noted so far.

SYNODONTIDAE

(not including Harpodontidae)

The lizardfishes comprise three genera and about 45 species of small- to moderate-sized (maximum about 635 mm TL), benthic fishes with pelagic larvae. The species occur on rocky, sandy, or muddy bottoms, often about coral reefs, and occasionally in estuaries. Most are shallow dwelling, but some species are taken at depths exceeding 500 m. The family is circumglobally distributed, as is one of the three genera, *Synodus*.

Trachinocephalus is monotypic. It is present in the eastern and western Atlantic and throughout the Indo-West Pacific. It is absent from the eastern Pacific and has been obtained on the Pacific Plate nonmarginally only in the Hawaiian and Society islands (Anderson et al., 1966, fig. 15). *Trachinocephalus* was reported to occur on the Pacific Plate at the Society Islands (Vaillant, 1887; Fowler, 1938) and the Cook Islands (Seale, 1906). Fowler (1928) reidentified Seale's Cook Islands specimens as a *Synodus* species (Anderson et al. noted Seale's misidentification, but erroneously entered the Cook Islands record on their fig. 15). Randall (1973) cast doubt on Vaillant's Society Islands record, which Randall believed was probably based on a species of *Synodus*. Fowler's (1938) Society Islands specimens are postlarvae; their identification has been verified by Randall (1973) and W. Saul (Academy of Natural Sciences of Philadelphia, pers. comm.). It would be of interest to ascertain the presence of adult *Trachinocephalus* on the Pacific Plate other than at the Hawaiian Islands.

Saurida has a distribution similar to that of *Trachinocephalus*, except that *Saurida* is more commonly distributed on the Pacific Plate. Shindo and Yamada (1972) reported that there are nine species of *Saurida* in the Indo-Pacific, but recent study of the genus indicates that there is at least one undescribed species in the area and that a revision is needed (R. Waples, in litt.). Sulak (1977) includes *Saurida* with the Harpadontidae (q.v.).

There are about 30 species of *Synodus*, of which 21 occur in the Indo-Pacific.(R.F. Cressey, 1981, and pers. comm.). Only eight of the Indo-Pacific species occur on the Pacific Plate nonmarginally, and one of these is a Plate endemic. Two species, *S. usitatus* and *S. ulae*, are known only from Japan and the Hawaiian Islands. *Synodus capricornis* is known only from Easter and Pitcairn islands.

TERAPONTIDAE

There are 15 genera and about 40 species of terapontids (Vari, 1978; Vari and Hutchins, 1978, and Vari, pers. comm.). The species are of small to moderate size (65–800 mm maximum SL). More than two-thirds of the species are restricted to freshwater; the remaining species, although primarily marine, often enter fresh and brackish water, but breed in the sea. Vari believes that the terapontids originated in freshwater, with a series of marine representatives having been derived from the freshwater forms, followed by a secondary reinvasion of the freshwaters of Australia and New Guinea. The species are all shallow dwelling and suprabenthic, although I have seen the young of a marine form bury themselves in sand close to shore. Little has been reported on the life history of terapontids, but Munro (1945) reported that the postlarvae of one species are planktonic in shallow water. The family is restricted to the Indo-West Pacific (Figure 43), except for a recent introduction into the eastern Mediterranean (Lourie and Ben-Tuvia, 1970).

TETRAODONTIDAE

The pufferfishes are a circumglobal family comprising about 14 genera and 110 species (J.C. Tyler, pers. comm.) of small to moderate size (maximum TL ranging from about 50 to 760 mm). The species are mostly suprabenthic, shallow-dwelling, tropical and warm-temperate marine forms, but some species are pelagic in the open sea; others enter or occur only in freshwater (tropically), and some occur only at moderate depths (to about 500 m). The Indo-Pacific species of only one tropical genus have been revised in recent years. Probably 20 species in four tetraodontid genera occur nonmarginally on the Pacific Plate.

Canthigaster contains 24, primarily reef-inhabiting, species (Allen and Randall, 1977; Lubbock and Allen, 1979). One species is restricted to the Atlantic, occurring in both the eastern and western portions, and one species is restricted to the tropical eastern Pacific. Among the 22 Indo-Pacific species (one of which reaches the eastern Pacific), four occur only in the Red Sea and/or Indian Ocean. The remaining 18 species are variously distributed in the Indo-Pacific, with 13 ranging onto the Pacific Plate nonmarginally. Of the 13, eight are widely distributed in the Indo-Pacific, two are known only from the Hawaiian

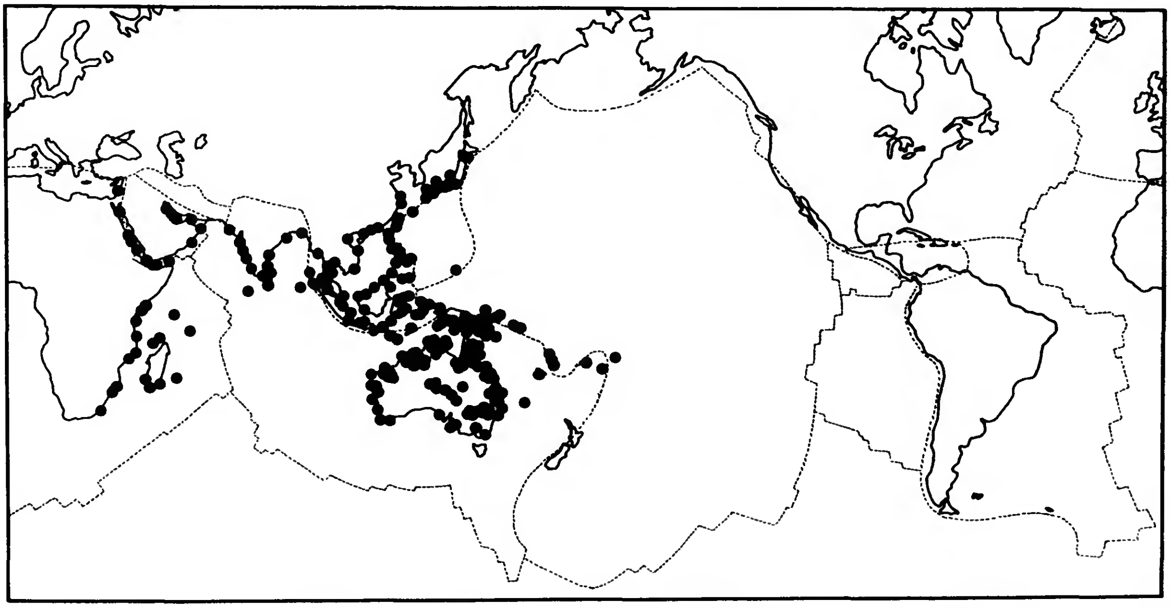

FIGURE 43.—Distribution of the fishes of the family Terapontidae.

Islands, one only from Rapa, one only from the Marquesas, and one, *C. epilampra*, appears to be a widely distributed Pacific Plate endemic (Hawaiian, Society, Rarotonga, Palau, and Solomon islands; Figure 26). Allen and Randall related *C. epilampra* most closely to the Marquesas and Rapa endemics, and these three species were related to an Indian Ocean species and a widely distributed Indo-Pacific species. If these relationships are cladistically supportable, the vicariant event that initiated formation of the three Plate endemic species of the *C. epilampra* group has been obscured by dispersal of the widely distributed species or by extinction of *Canthigaster* populations between the Indian Ocean and the Pacific Plate.

Order TORPEDINIFORMES

The electric rays, or torpedos, comprise four families, ten genera (Compagno, 1973a), and about 35 species of small to large (about 200–2000 mm TL), benthic, viviparous fishes that occur at depths of from less than 1 m to about 1100 m. The families are combined here for the sake of convenience (while it was easy to identify reports of torpedos in the literature, it was often not possible to determine what family was involved). The only records of torpedos (Figure 44) from the Pacific Plate, other than marginally, are for the Chatham Islands, which are on the continental shelf of New Zealand (hence not considered Pacific Plate for the purposes of the present study) and the deep sea off the Hawaiian Islands (Tinker, 1978).

TOXOTIDAE

The archerfishes consist of a single genus, *Toxotes*, and six small (to 400 mm SL) species (Allen, 1978). The species occur in freshwater and brackish mangrove habitats, and are restricted to the Indo-West Pacific, ranging from the east coast of India to the western margin of the Pacific Plate: Palau (Koror; Herre, 1939), Admiralty, Solomon, and New Hebrides islands. Whitley (1927) reported *Toxotes* from Fiji, based on a listing in a Shmeltz catalogue (number 5, 1874, reference not available to me) of the Museum Godeffroy; however, neither B.A. Carlson (pers. comm.), who collected fishes while resident in Fiji, P.A. Ryan (1980 and pers. comm.), nor I collected *Toxotes* in Fiji. All of us believe it does not occur there.

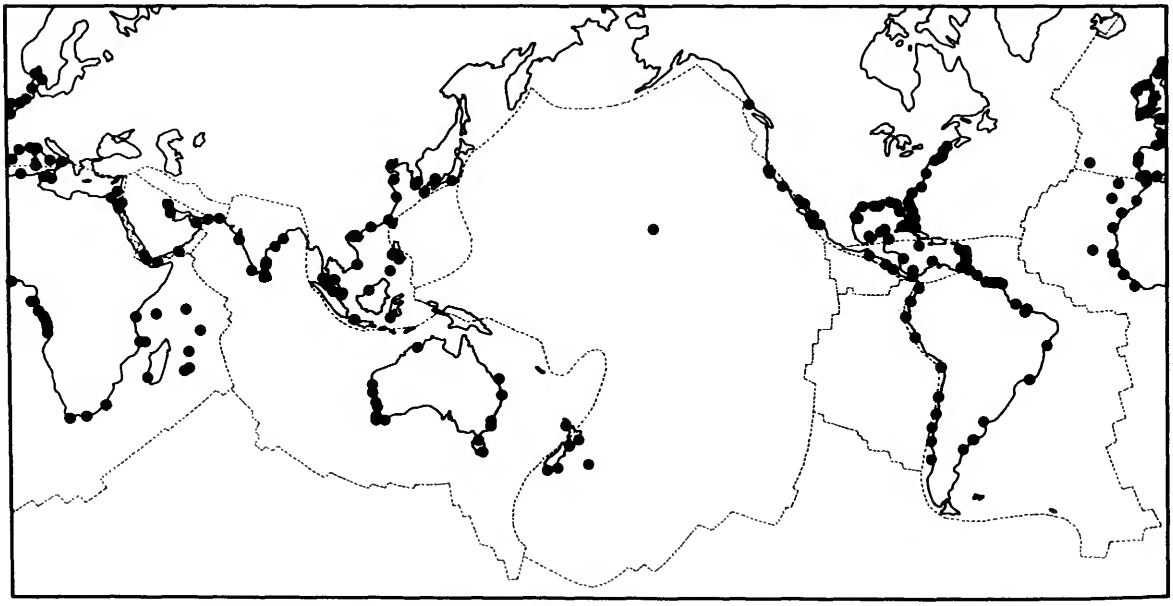

FIGURE 44.—Distribution of the elasmobranch fishes of the order Torpediniformes.

In the Pacific, the archerfishes range north only to the Philippines and south to northern Queensland and New Hebrides. One species, *T. jaculator*, extends over the entire coastal range of the genus. It is surprising, perhaps, that the archerfishes have not invaded the Pacific Plate nonmarginally, particularly the Eastern Caroline Islands, where the proper habitat appears to be present.

Sterba (1962, fig. 1015) gave a generalized distribution map for the Toxotidae (reproduced in Nelson, 1974, map 38) and included the northern Indian Ocean coast from southern India to the southern Red Sea within the range of the family. I know of no records of toxotids west of the southern tip of India (see also Allen, 1978, map 1, for a reasonably complete distribution map).

TRIACANTHIDAE

The triacanthids consist of four genera and seven small (to 272 mm SL) species of benthic fishes (Tyler, 1968, 1970) that are restricted to the Indo-West Pacific, ranging from the Persian Gulf eastward to New Guinea, northward to Japan, and southward to New South Wales (Tyler, 1968, fig 3, gives a generalized distribution map for the family). Fossil genera and species of triacanthids are known from the Upper Eocene of Italy, Oligocene of Switzerland, and Miocene of Celebes, indicating a much broader distribution in the past. Tyler believes that the triacanthids evolved from the deep-dwelling Triacanthodidae, which are found in the western Atlantic, Indo-West Pacific, and Hawaiian Islands on the Pacific Plate; hence, are also restricted to continental plates except for the Hawaiian occurrence of an endemic species of *Hollardia*, which genus is otherwise known only from the western Atlantic. If the ancestor of the Triacanthidae and Triacanthodidae was a deep-dwelling form, one can only wonder why shallow-water representatives did not also evolve in the Pacific Plate area.

TRIAKIDAE

The Triakidae comprise ten genera (Compagno, 1973b) and about 37 species (L.V.J. Compagno, pers. comm.; P. Heemstra, in litt.) of viviparous, deep or shallow-dwelling, small (to about 1.5 m TL) sharks. The family is distributed primarily in the vicinity of continental coasts, and is absent from the Pacific Plate nonmarginally, as are many other elasmobranch groups. Triakids are mostly deep-dwelling or antiequatorially distributed in the Indo-West Pacific, but mainly shallow-dwelling, tropical or subtropical along the continental coasts in other areas where they occur.

TRICHIURIDAE

The limits of the cutlassfish family (for instance, whether it should be included with the Gempylidae or divided into more than one family) are uncertain. In Tucker's (1956) revision of the Trichiuridae, two apparently closely related monotypic genera, *Trichiurus* and *Lepturacanthus*, were recognized as composing the subfamily Trichiurinae, and only this taxon, which is almost circumglobally distributed, but is absent from the Pacific Plate nonmarginally, is considered here. In the literature, *Trichiurus* and *Lepturacanthus*, which have similar habits and are sympatric over part of their ranges, are often not clearly distinguished by authors. It is possible, therefore, that some of the localities marked for *Trichiurus lepturus* (Figure 45), especially those in the area from India to Australia, may represent *Lepturacanthus savala*. The addition of the distribution of *L. savala* to Figure 45 would not change the general limits of the distribution as given for *T. lepturus*. Mainly, the addition would be noticeable only by the presence of more spots along the coasts of Australia (from Northern Territory to New South Wales), India, and the South China Sea. The records of *Trichiurus* from Palau and Fiji (Figure 45) are based on reports by Abe (1939) and Carlson (ms.).

Trichiurus lepturus is a ribbonshaped, free-swimming, predatory species that has planktonic larvae and attains a maximum size of about 1.5 m TL. It occurs along the continental shelf to depths of up to about 100 m; it also enters shallow estuaries.

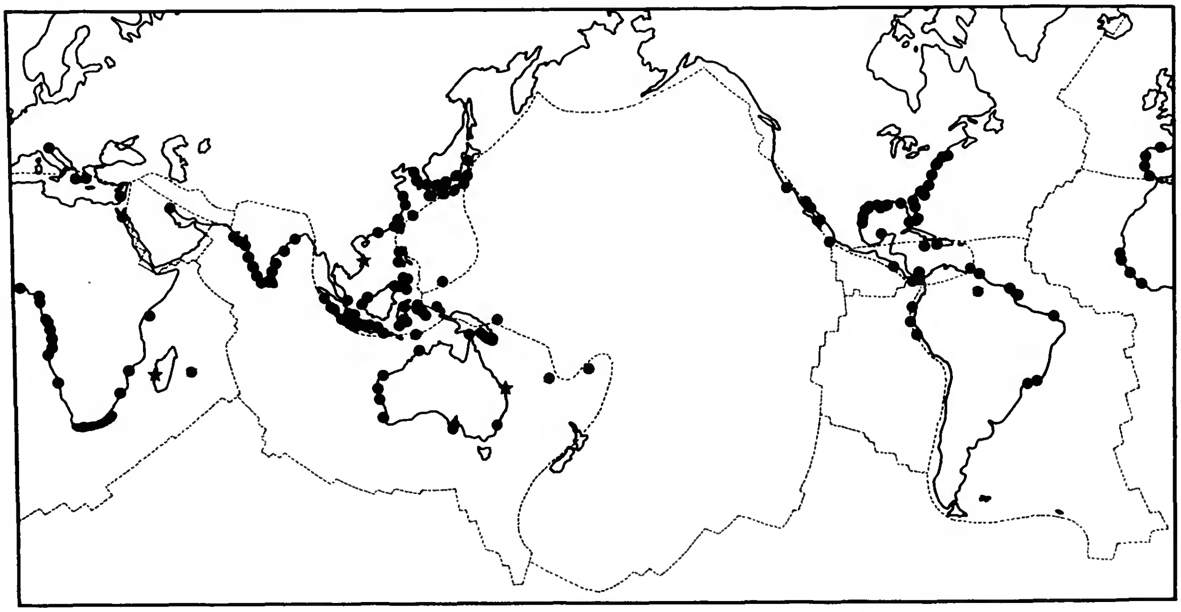

FIGURE 45.—Distribution of the trichiurid fish *Trichiurus lepturus* (stars indicate unspecified localities in general areas; shaded area is generalized distribution).

TRICHONOTIDAE

The Trichonotidae is a poorly known family of small (to about 250 mm TL), sand-dwelling fishes that occur in marine and estaurine areas. The family consists of two genera, *Trichonotus*, with at least three species (at least one undescribed), and *Lesseurina*, monotypic, which questionably belongs in the family.

Trichonotus is distributed from the Red Sea and east coast of Africa to Japan, Philippines, Queensland, Guam, Palau, New Hebrides, and Fiji (Carlson, ms.), and is known from a single locality, Enewetak, on the nonmarginal portions of the Pacific Plate (J.E. Randall, in litt.). Its distribution on the Plate is probably more extensive than presently indicated. Munro (1958) reported *Trichonotus* from Port Moresby, Papua-New Guinea, and Jaquinot Bay, New Britain. Although *Trichonotus* should be expected to occur at these localities, the specimens, which were larvae (Munro, 1967), and upon which Munro's reports are based, leaves doubt as to their correct identification.

Lesseurina is known only from southern Australia.

TRIGLIDAE

The triglids are poorly known taxonomically. There is a question as to whether the family should include the Peristediidae, a usually deep-dwelling, benthic group of moderately small fishes found in continental coastal waters round the world, but only at the Hawaiian Islands on the Pacific Plate nonmarginally. The nonperistediid triglids are small to moderately large (up to 1 m TL), benthic forms, usually shallow dwelling in marine and brackish water, and exhibit much the same general distribution as the peristediids, with the following differences: they apparently occur farther north in the Atlantic and are absent from the Pacific Plate nonmarginally, except for a report of a single specimen of the shallow-dwelling *Cheilodonichthys kumu* (as *Trigla kumu*; Pietschmann, 1930), from Hawaii. *Cheilodonichthys kumu* is otherwise widely distributed in the Indo-West Pacific. The absence of other reports of nonperistediid triglids from the Hawaiian Islands leads me to question the validity of Pietschmann's report.

TRIODONTIDAE

The Triodontidae consists of a single genus and species of small fish (to about 480 mm SL), *Triodon macropterus*, which is questionably included here as a shallow-dwelling form. According to Tyler (1967), the only depth records available for the species are 150 m and 200-300 m. *Triodon* ranges from the east coast of Africa eastward to Guam, Volcano, Fiji, and Samoan islands (Tyler, 1967; Kami et al., 1968; Carlson, ms.; Wass, ms.); the last four localities are on the western margin of the Pacific Plate. Although *Triodon* is generally considered to be a rare species, and few specimens are available in museum collections, Fourmanoir and Laboute (1976) reported that they obtained 20 specimens from the stomachs of tunas caught in the vicinity of New Caledonia and the New Hebrides.

TRIPTERYGIIDAE

The triplefins are a very poorly known family taxonomically, with as many as one-third of its estimated 20 genera and 150 species as yet undescribed. The family is circumglobally distributed in tropical and warm-temperate waters, and the species are predominantly benthic inhabitants of rocky and coral-reef areas. The species are all small, ranging in maximum size from about 15 to 200 mm SL (the largest species is in the New Zealand genus *Notoclinus*), although most species attain less than 75 mm. A revision of the southeastern Atlantic and Indo-Pacific genus *Helcogramma* by P.H. Hansen is nearing completion; there appears to be one widely distributed Pacific Plate endemic species among its approximately 12 included species. Probably nine other tripterygiid species are present nonmarginally on the Pacific Plate.

TRYPAUCHENIDAE

The trypauchenids comprise about four genera and fewer than ten species of small (to about 220 mm TL), burrowing fishes that are found in muddy bottoms in salt and brackish waters from near shore to depths of about 100 m. The family is limited to the Indo-West Pacific, from the east coast of Africa (Smith, 1959) to New Guinea (Munro, 1958, as *Ctenotrypauchen* under Taenioidae), on the margin of the Pacific Plate. In the western Pacific they occur as far south as Queensland and as far north as Japan.

URANOSCOPIDAE

The stargazers comprise about ten genera and 30 species of small- to moderate-sized fishes (up to about 750 mm TL). As juveniles and adults the species are benthic in habit, burrowing into sand and mud. They occur at depths varying from less than a meter down to about 550 m. Most species are marine, but some occur in brackish estuaries. Haast (1873) reported specimens obtained in freshwater as much as 40 miles (67 km) upstream from river mouths, and others buried in sand well above low-tide mark along the New Zealand coast. Little is known about their life history, but the species are reported to have planktonic larvae (Pearson, 1941; Fierstine and Werner, 1963).

The uranoscopids are restricted almost entirely to continental plate coastlines, and occur only marginally on the Pacific Plate (Figure 46). Bloch and Schneider (1801) reported a uranoscopid from Tahiti based on information in an unpublished manuscript by Forster. The same species, which occurs in New Zealand, was also reported by Bloch and Schneider from New Zealand. I consider the Tahitian record to be improbable and erroneous as did McCulloch (1929).

UROLOPHIDAE

The urolophids comprise two genera and 21 species (Chirichigno and McEachran, 1979) of

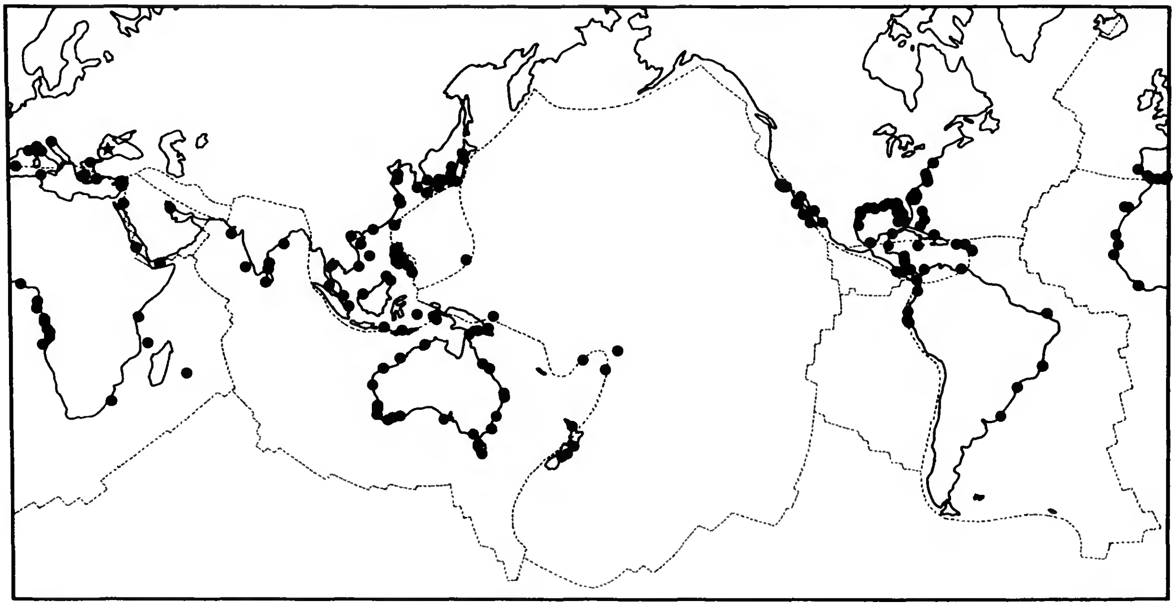

FIGURE 46.—Distribution of the fishes of the family Uranoscopidae (star represents unspecified locality in Black Sea).

benthic, viviparous rays of moderate to very large size (to about 2.7 m TL and 119 kg). These rays are found in the eastern Pacific (five species), western Atlantic (one species), and Indo-Pacific (15 species) on muddy or sandy bottoms, often in shallow waters, but are unknown in the eastern Atlantic. *Urotrygon daviesi* is the only urolophid known from the Pacific Plate nonmarginally. It is recorded from depths of 144–1800 feet (44–549 m) and reported only from South Africa (Wallace, 1967), the Bay of Bengal (Nair and Soundararajan, 1973), and Hawaii (Tinker, 1978). As is true of most elasmobranch groups, the urolophids are essentially absent from the Pacific Plate.

XENOCONGRIDAE

The xenocongrid eels consist of seven genera and 15 species (Böhlke and Smith, 1968), but there are large unstudied collections available that probably include several undescribed species (J.E. Böhlke, pers. comm.). These eels are all small (largest species, 436 mm TL, but most species not attaining 200 mm), and occur only in the sea, from near shore to depths of at least 355 m. As adults they are burrowers, but may come to the surface (to spawn?). Their larvae are planktonic.

The family is probably circumglobally distributed. The deep-dwelling forms tend to be widely distributed with wide gaps separating collections; for example, *Chlopsis dentatus* (from about 126–355 m) is known from the western Indian Ocean and Caribbean, and *Robinsia catherinae* (52–243 m) from off Kenya and the Atlantic coast of Panama. One shallow-dwelling species, *Kaupichthys hyoproroides*, occurs widely in the Caribbean and Indo-Pacific, but is absent from the eastern Pacific and eastern Atlantic. While some of the Indo-Pacific species are known only from the Indian Ocean, others are widely distributed. The monotypic genus *Powellichthys* is known from a single specimen (ripe female) taken at the surface over a depth of 500 fathoms (914 m; Smith, 1966b) off Cook Island (= Tarawa, Gilbert Islands) and could be a deep-dwelling endemic on the Pacific Plate; however, I believe that the available information of xenocongrid species and their distributions is much too meager to be accepted as definitive. Perhaps five species of xenocongrid eels are present nonmarginally on the Pacific Plate.

ZANCLIDAE

The Zanclidae consist of a single genus and species, *Zanclus cornutus*, the Moorish idol. *Zanclus* is a free-swimming, coral-reef species that attains a maximum size of 250 mm TL. It is distributed throughout the tropical portions of the Indo-Pacific, from the east coast of Africa to at least the Tuamotus, and is also present in the eastern Pacific.

Other Organisms

The discussions of the taxa that follow are treated in the same manner as those for fishes. I made no attempt to be inclusive, as I did for the shore fishes. The nonfish taxa were selected to demonstrate that distribution patterns commonly exhibited by the fishes are also exhibited by a wide variety of other organisms. There is no meaning to be inferred from my arrangement of the phyla, or the taxa within a phylum.

Phylum MOLLUSCA

Class GASTROPODA

Abbott (1960) revised the Indo-Pacific species of the conch genus *Strombus* (Strombidae), which is distributed circumglobally in the shallow portions of warm seas; its larvae are planktonic. *Strombus* comprises 51 extant species and 60 species-group taxa (including subspecies; I have made no attempt to determine if additional new taxa of *Strombus* have been described since Abbott's revision). Forty-nine species-group taxa of *Strombus* occur in the Indo-Pacific, and of these, 12 have the eastern limits of their distributions along the western margin of the Pacific Plate (see Figure 47 for the distribution of one of these, *S. labiatus*), 13 range from the Indo-West Pacific well out onto the Plate, and five are endemic to the Plate, including its margins. *Strombus helli* and *S. vomer hawaiiensis* occur only in the Hawaiian Is-

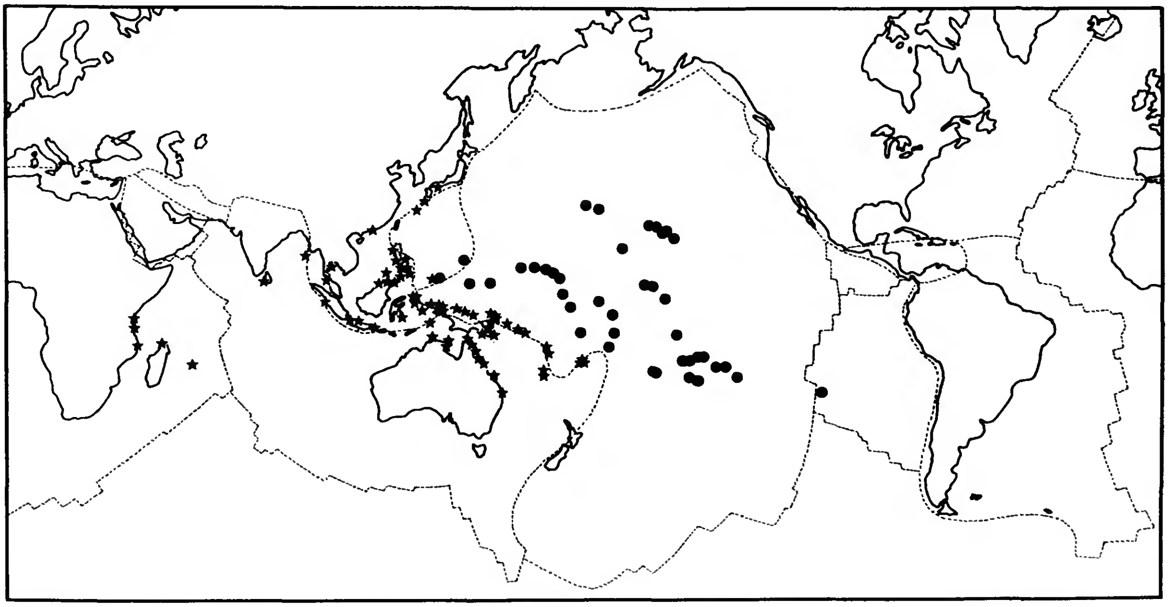

FIGURE 47.—Distributions of two species of the marine mollusk genus *Strombus* (Gastropoda), compiled from the literature and museum collections (stars = *S. labiatus*; closed circles = *S. maculatus*).

lands (the other two subspecies of *S. vomer* occur as follows: *S. v. vomer*, Ryukyus and New Caledonia; *S. v. iredalei*, western and northern Australia; hence, the subspecies of *S. vomer* do not cross the margin of the Pacific Plate). *Strombus variabilis athenius* occurs in the Marshalls, Eastern Carolines, northwestern New Guinea, Samoa, Fiji, and New Caledonia. The nominal, and only other, subspecies of *S. variabilis* ranges from Sumatra to Palau, Bougainville, and northern Australia; hence, one subspecies of *S. variabilis* ranges from the western Pacific to the western margin of the Pacific Plate, and the other subspecies ranges from the western margin of the Pacific Plate out onto the Plate.

Strombus maculatus is a widely distributed Pacific Plate endemic (Figure 47). Abbott stated that *S. maculatus*, *S. microurceus*, and *S. mutabilis* form a natural group within the subgenus *Canarium*. These three species have quite different distributions. *Strombus microurceus* ranges through much of the western Pacific, but occurs nonmarginally on the Pacific Plate only in the Eastern Caroline Islands, where it is sympatric with *S. maculatus* (Abbott, 1960, plate [= figure] 47). The presence of *S. microurceus* in the Eastern Carolines is evidence favoring operation of the Caroline Islands conduit. *Strombus mutabilis* ranges from the Red Sea and east coast of Africa to the Tuamotus, and thus overlaps most of the range of the other two species (it is absent from the Hawaiian Islands; Abbott, 1960, plate 50). If *S. microurceus* is the sister species of *S. maculatus*, and there is a good chance that it is, the Pacific Plate boundary is probably the area where the vicariant event occurred that divided the ancestral population that gave rise to these two species. Subsequent dispersal would then have resulted in the partial sympatry of these two species in the Eastern Caroline Islands. The distributions of the three species of the subgenus *Canarium* closely parallel the distributions of the three species of the gobiid fish genus *Nemateleotris* (Figure 21).

The members of the family Littorinidae are found in most coastal regions of the world, and occupy habitats from relatively shallow waters below the intertidal zone to high above the sea, where they are wet only occasionally by ocean spray (Rosewater, 1970). Certain species are able to survive for long periods without immersion in seawater. Most of the species release pelagic egg capsules and only a few deposit egg masses on the substrate or are ovoviviparous. In the Indo-Pacific, only one species, *Littorina scabra* (subspecies *scabra*), is ovoviviparous. It has by far the broadest distribution of all the species in the genus in the Indo-Pacific (from the east coast of Africa to the Gambier Group of islands), between 28°N-S latitudes (Rosewater, 1970, plate [= figure] 354), but is notably absent from the Marquesas (Rosewater recognizes three subspecies in *S. scabra: S. s. scabra*, Indo-Pacific; *S. s. aberrans*, eastern Pacific; *S. s. angulifera*, eastern and western Atlantic).

The subfamily Tectariinae (Littorinidae) contains a single genus, *Tectarius*, and three subgenera (Rosewater, 1972). The subgenus *Tectarius* contains five extant species and one fossil species (from Java). Of the extant species, two are restricted to the Pacific west of the Pacific Plate margin, two have their eastern limits along the western margin of the Pacific Plate, and one, *T. grandinatus*, is a widely distributed Pacific Plate endemic, ranging from the Tonga Islands to the Gambier Group islands in the Tuamotus. The closest relative of *T. grandinatus* is, then, a continental form, which Rosewater believes is *T. rugosus*, confined to the Philippines and Celebes, thus, not quite reaching to the western margin of the Pacific Plate.

Emerson and Cernohorsky (1973) revised the genus *Drupa* (Thaisidae) in the Indo-Pacific. Among the species, one, *Drupa elegans*, is a widely distributed Pacific Plate endemic known from the following islands: Wake, Enewetak, Bikini, Flint, Caroline (Line Islands), Niue, Akamaru, Manihiki, Marutea, Vahitahi, Nengonengo, Anau, Napuka, Taenga, Fakahina, Gambier, Pitcairn. The sister species was not indicated.

Cernohorsky (1976) revised *Mitra* (Mitridae). Among the species, *Mitra testacea* is a widely distributed Pacific Plate endemic, known from the following islands: Kingsmill Group of the Gilberts, Palmerston, Rarotonga, Tahiti, Anaa, Garumaoa, Raroia, Aukena, Pitcairn. The sister species was not indicated.

Rehder (1980) reported on the mollusks of Easter Island and provided overall distributions of each species. The following gastropod species are widely distributed Pacific Plate endemics (families not indicated): *Cerithium rubus* (Line, Tokelau, Cook, Samoan, Palmerston, and Easter islands); *Dendropoma platypus* (Marshall, Hawaiian, and Easter islands); *Planaxis fasciatus* (Niuafoou and Samoan islands east to Easter Island); *Balcis aciculata* (Hawaiian, Cook, Tuamotu, and Easter islands); *Natica ochrostigmata* (Hawaiian, Cook, Samoan, and Easter islands); *Trimusculus odhneri* (Micronesia, Polynesia, Niuafoou).

Many marine gastropods have Indo-West Pacific distributions with their eastern distribution limits along the western margin of the Pacific Plate. One need only to leaf through the issues of *Indo-Pacific Mollusca* to find them.

Distribution patterns exhibited by marine gastropods are also duplicated by terrestrial gastropods. The family Endodontidae comprises about 475 species of minute land snails (Solem, 1976; Solem's delimitation of the family is not accepted universally: see Sirgel, 1980). The endodontids are restricted to the islands on the Pacific Plate and its margins (Figure 48). Solem (1981) states that the Charopidae are the closest related family to the Endontidae, and the charopids most intermediate [closely related to?] between the Charopidae and Endodontidae occur in southwestern Australia; hence, somewhat west of the margin of the Pacific Plate. The charopids are distributed in North and South America, St. Helena, portions of southeast Africa, Australia, New Zealand, and the Indo-Malayan area as far north as the Philippines (Solem, 1981, fig. 5.5), all localities where endodontids do not occur. The charopids also occur in several Pacific Plate island groups where endodontids are also known: Cook, Ellice, Samoa (marginal), Tonga (marginal), Palau (marginal). Solem (1976) reported that the Caroline, Mar-

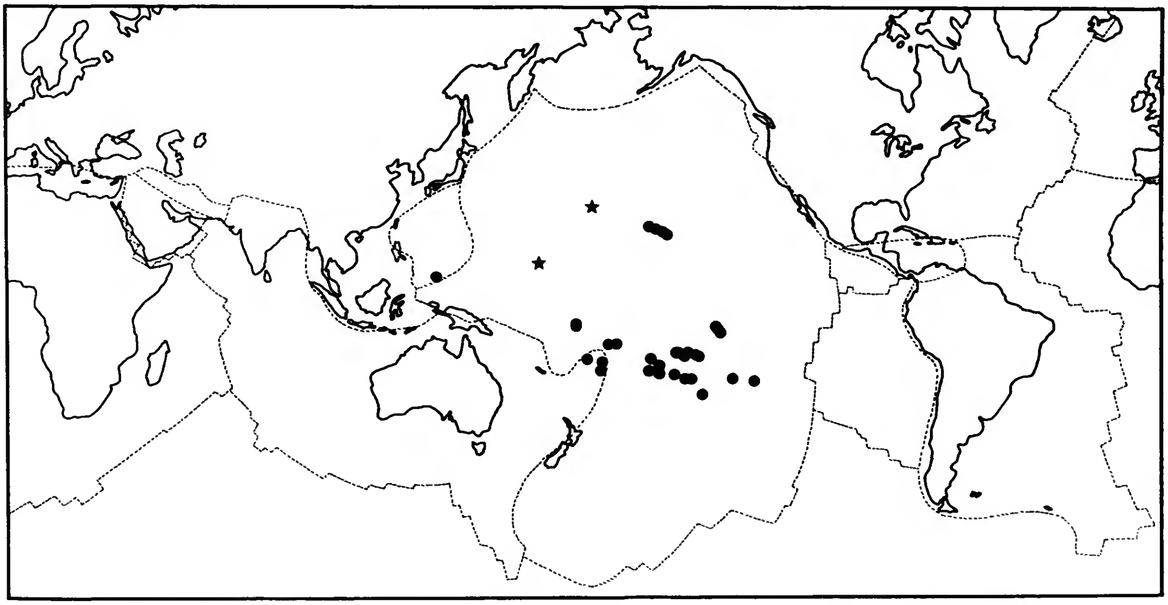

FIGURE 48.—Distribution of the land snail family Endodontidae (Mollusca: Gastropoda), compiled from Solem, 1976 (stars indicate localities where only fossils are known; the genera represented by fossils are extant on other islands).

iana, and main Fiji islands have charopids, but no endodontids, and (as is also true for the endodontids) occur only as fossils at the Marshall Islands. If the southwestern Australian charopids are the sister group of the endodontids, the partial sympatry that presently exists with these two families would indicate that dispersal occurred subsequent to the evolutionary divergence of the two families (Springer 1981a).

Class Pelecypoda

Rosewater (1961) revised the Pinnidae of the Indo-Pacific. The distribution of one species, *Pinna bicolor*, is of interest here. *Pinna bicolor* ranges from the Red Sea and east coast of Africa eastwards to Japan, The Philippines, New Guinea, and New Caledonia (all on or west of the western margin of the Pacific Plate). *Pinna bicolor* also is present on the Pacific Plate nonmarginally, but only in the Hawaiian Islands. Rosewater (1961:195) stated that "the sporadic appearance of *P. bicolor* in Hawaii is probably the result of chance introduction." Rosewater was unaware, understandably, that an Hawaiian exception type of distribution is a common occurrence among marine organisms, and there is no need to rely on chance introductions to account for such distributions. It is possible that the presence of *P. bicolor* in the Hawaiian Islands is the result of dispersal via the Kuroshio extension, which may also account for numerous fish species common to Japan and only the Hawaiian Islands on the Pacific Plate.

Rehder (1980) listed three widely distributed Pacific Plate endemic species of pelecypods (families not indicated here): *Malleus maculosus* (Micronesia, Tuamotus, and Easter islands); *Lasaea hawaiensis* (Hawaiian, Gambier Group, Easter, and Rapa islands); *Semele australis* (Cook Island north to Hawaiian Islands and east to Easter Island, with a single valve each from Bikini, Marshall Islands, and Lifu, Loyalty Islands).

Class Cephalopoda

There are about 100 species in the cuttlefish genus *Sepia* (Sepiidae), most of which are highly restricted in distribution and occur in the Indo-West Pacific (Voss, 1977). The species are small, the largest attaining a maximum total length of about 600 mm (G.L. Voss, pers. comm.). The species are primarily benthic, but occur in a wide variety of habitats ranging from the open sea surface down to depths of, perhaps, 1000 m (Adam and Rees, 1966; Roeleveld, 1972), along shore, intertidally, and on coral reefs. At least one species occurs in shallow estuaries. The species lay encapsulated eggs, which they attach to almost anything on the substrate, including seaweeds and phanerogams. The oldest known fossils of *Sepia* are from the Eocene of continental areas.

Only one species of *Sepia* has been obtained other than marginally from a Pacific Plate locality: Arno Atoll, Marshall Islands (Figure 49; Arno specimens in collection of Division of Mollusks, NMNH). The identification of this species is uncertain. *Sepia* is obviously a continental plate genus and its exceptional occurrence on the Pacific Plate only at Arno Atoll is unexpected. *Sepia* is often obtained in rotenone collections of fishes and its absence from Ponape, Eastern Caroline Islands, and Bikini, Marshall Islands, both of which have been intensively collected with rotenone emphasizes the unusual nature of its presence at Arno. I have no explanation for its occurrence at Arno and encourage others to be alert for its possible occurrence elsewhere on the Pacific Plate.

The living Nautilidae were revised by Saunders (1981), who recognizes a single genus and four species. The distribution of *Nautilus*, based on live specimens, includes the region from the Andaman Islands east to Japan, south to the Philippines, through Palau, to southern Australia, and east to Fiji; hence, absent all but marginally from the Pacific Plate (Saunders, 1981, fig. 1). *Nautilus* is moderately deep dwelling, and Saunders allows that its distribution may be more extensive than presently indicated. Additionally, fresh, drifted shells have been obtained from Majuro, Marshall Islands, and Kosrae, Eastern Caroline Islands, localites upcurrent from potential sources of drift shells (drift shells have been taken as far west as the coast of Africa; I am unaware of drift shells

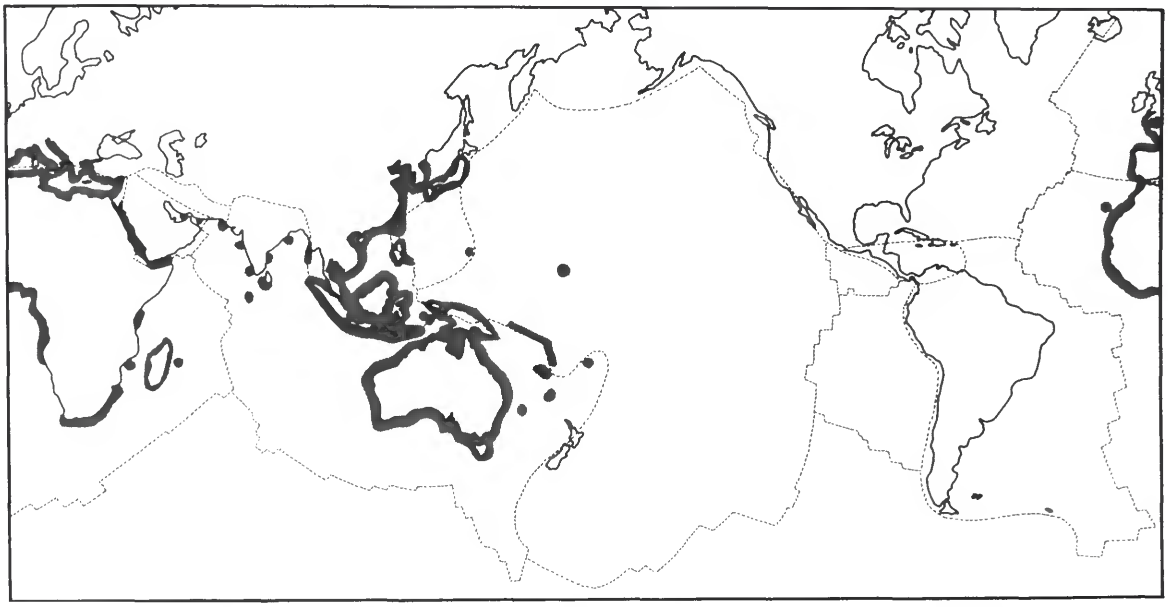

FIGURE 49.—Generalized distribution of the cuttlefish genus *Sepia* (Mollusca: Cephalopoda), compiled from Adam and Rees, 1966, Lubet, 1973, and G.L. Voss, in litt.

having been taken at other Pacific Plate localities, with the exception of the Samoan Islands, cited by Toriyama et al., 1965, supposedly based on literature, which Saunders, apparently did not accept). The presence of *Nautilus* in the Eastern Carolines, if verified, would be evidence favoring operation of the Caroline Islands conduit. Majuro is close to, and down current from the Carolines, so that *Nautilus* drifts from the Carolines might be expected.

Phylum ARTHROPODA

Class CRUSTACEA

The crab genus *Latreillia* (Latreillidae) has been revised by A.B. Williams (in press). *Latreillia* contains six small (maximum carapace length about 20 mm), benthic species that occur at depths of 35–474 m. The genus is broadly distributed, but noticeably absent from the eastern Pacific (Figure 50). One species. *L. metansea*, is a widely distributed Pacific Plate endemic, and the only one of the four Indo-Pacific species to occur on the Plate. Its nearest relative, based on a shared specialization (synapomorphy: presence of a dorsal spine on the constricted anterior portion of the carapace) is *L. valida* (Williams, pers. comm.), which is restricted to the Indo-West Pacific, ranging from the southeast coast of Africa to Japan, the Philippines, and eastern Indonesia (two of the other three Indo-West Pacific species of *Latreillia* have similar eastern distributional limits). A vicariant event occurring along the western margin of the Philippine and/or Pacific plates could have divided a widely distributed population ancestral to these two species, permitting speciation of the two populations, and resulting in the distribution patterns presently manifested.

Banner and Banner (1975, 1981) reported on the pistol shrimp *Alpheus lobidens* (Alpheidae). This is a small (to 50 mm long), burrowing species consisting of two subspecies: *A. lobidens lobidens*, which ranges from the Mediterranean and Red Sea to southern Japan, Yap, New South Wales, and Lord Howe Island, and *A. l. polynescia*, which ranges widely on the Pacific Plate and its western margin (Figure 51). Banner and Banner (1975)

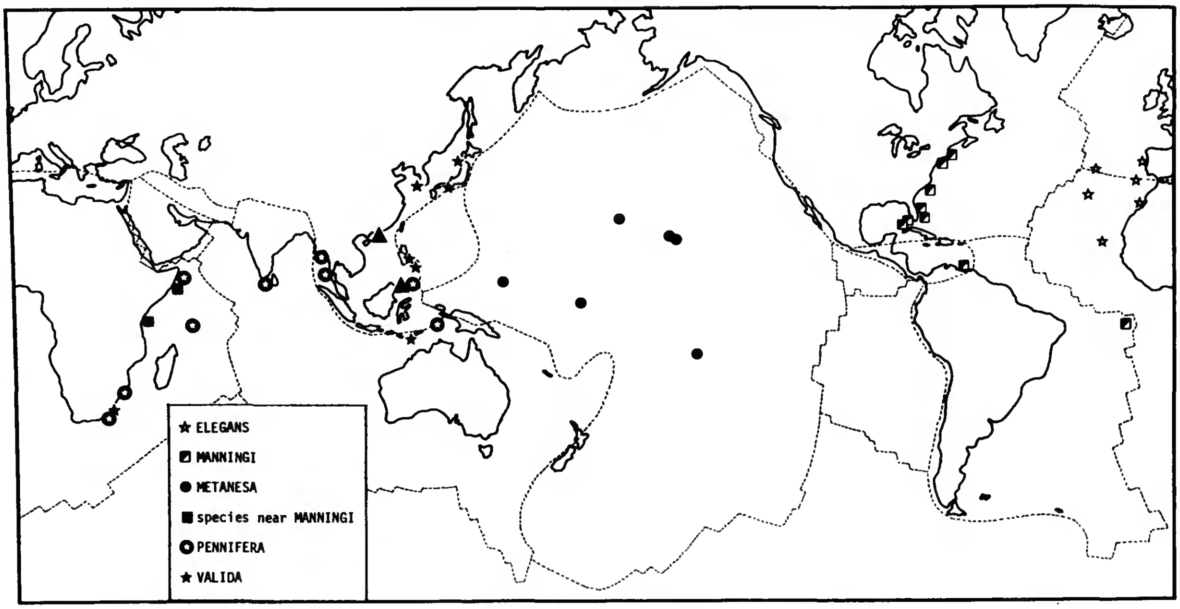

FIGURE 50.—Distributions of the species of the crab genus *Latreillia* (Arthropoda: Crustacea), after Williams (in press).

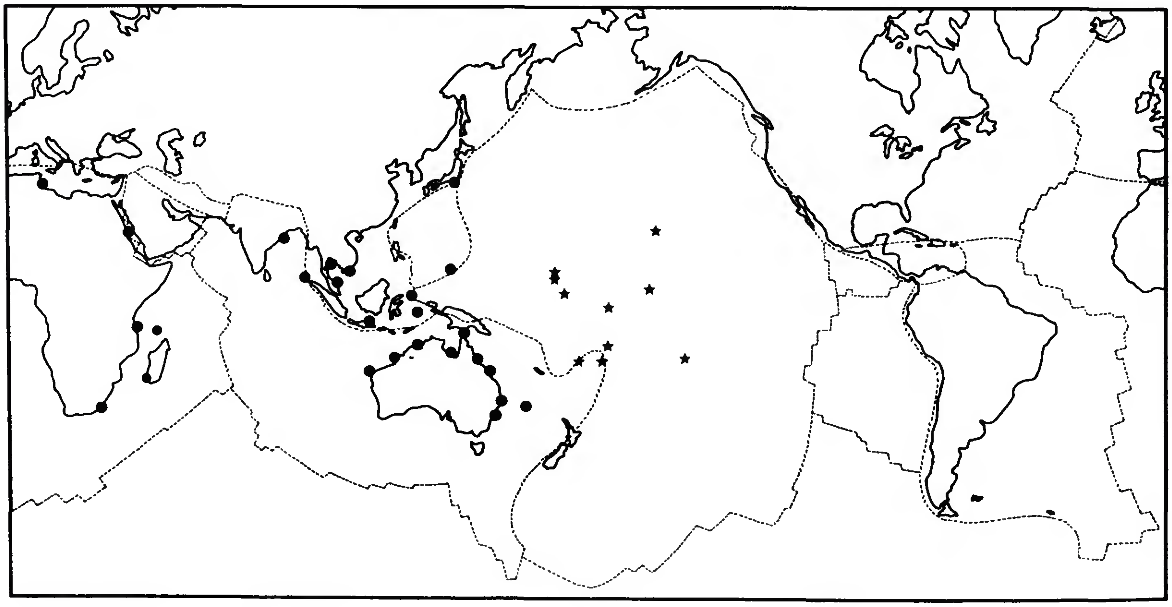

FIGURE 51.—Distributions of the two subspecies of the alpheid shrimp *Alpheus lobidens* (Arthropoda: Crustacea), after Banner and Banner, 1975, 1981 (closed circles = *A. l. lobidens*; stars = *A. l. polynesica*).

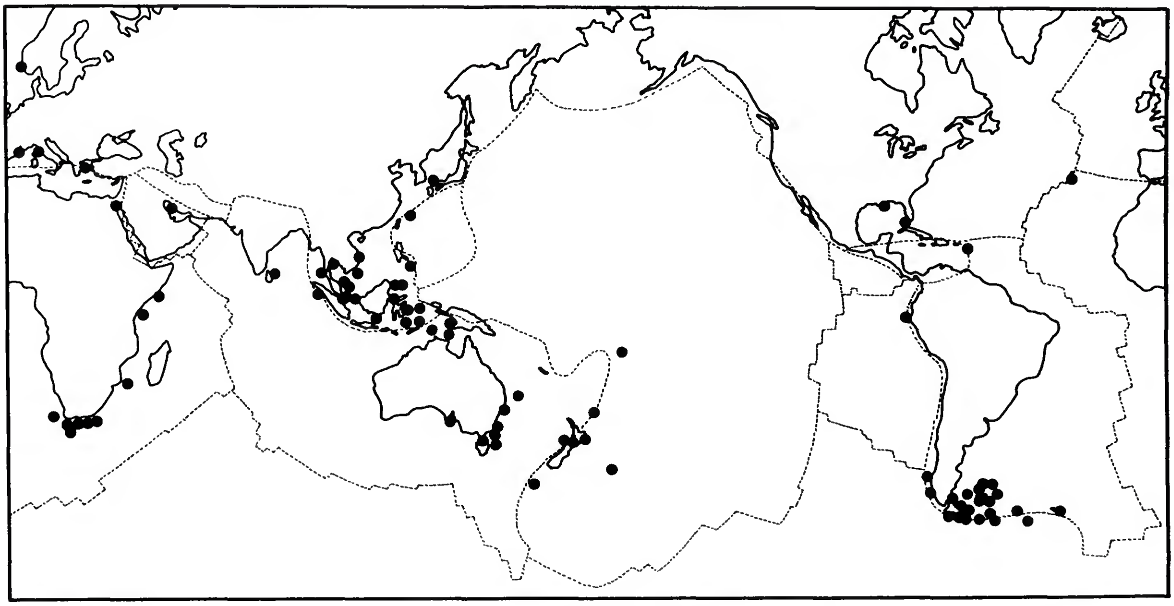

FIGURE 52.—Distribution of the approximately 75 benthic species of the ostracode family Cypridinidae (Arthropoda: Crustacea), based on data provided by L.S. Kornicker; records for Antarctic Plate are incomplete.

were unable to identify their Philippine specimens, which were too small to exhibit the differentiating character for the subspecies, but the nominal subspecies would most probably be expected in the Philippines. While there is an area between the distributions of the two subspecies from which no specimens of *A. lobidens* are available, the separation between the two subspecies appears to be delineated by the western margin of the Pacific Plate and the result of a scenario similar to that proposed above for *Latreillia*.

Recent ostracods in the suborder Myodocopina, especially the benthic species, generally tend to have localized distributions, and are generally absent from the Pacific Plate nonmarginally. There are about 20 genera and 100 species in the family Cypridinidae. Fourteen of these genera, including about 75 species, are primarily benthic inhabitants. The remaining genera and species in the family are planktonic. Of the 75 benthic species, 40 occur in the Indo-Pacific, but only one of these (*Hadacypridina bruuni*) is known to occur other than marginally on the Pacific Plate (on the Chatham Rise, which is part of the continental shelf of New Zealand, hence excluded from the Pacific Plate for my purposes; Figure 52). Of the planktonic genera, three (*Codonocera, Melavargula, Monopia*), with a total of 13 species, are restricted to the Indo-West Pacific. Of the other three planktonic genera (*Cypridina, Gigantocypris, Macrocypridina*), nine of the ten included species have Indian and/or Pacific ocean distributions, but only five species occur on the Plate nonmarginally. In addition to the Cypridinidae, there are four other families of myodocopid ostracodes, all primarily benthic. They comprise about 33 genera and more than 200 species, of which only two species are known to occur other than marginally on the Pacific Plate. For example, the family Cylindroleberididae comprises three subfamilies, of which one contains both deep- and shallow-dwelling species and is absent from the Pacific Plate. The other two subfamilies (comprising about 60 species) are essentially restricted to

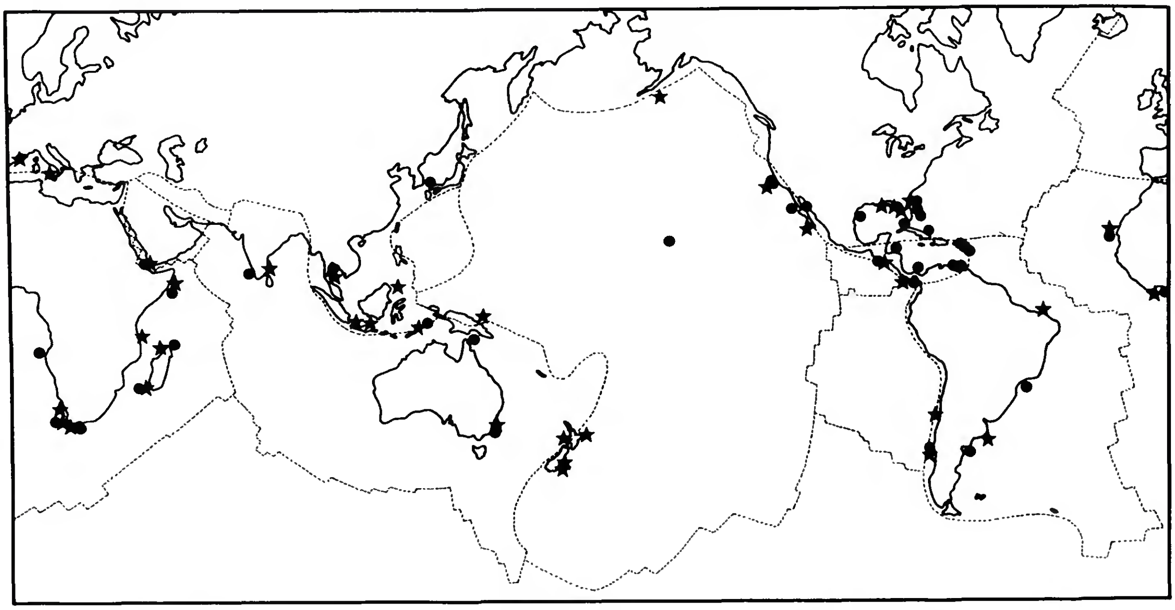

FIGURE 53.—Distributions of two of the three subfamilies of the ostracode family Cylindroleberididae, based on data provided by L.S. Kornicker (closed circles = Asteropteroninae; stars = Cyclasteropinae).

depths under 100 m. One of these last two subfamilies is absent from the Plate nonmarginally and the other is present on the Plate nonmarginally, but only at the Hawaiian Islands (Hawaiian exception; Figure 53). While the evidence tends to support a continental plate type distribution for the Myodocopina, L.S. Kornicker, who provided all my information on the Myodocopina, believes that a cautionary note is necessary: there have been few studies of myodocopid ostracodes in Pacific Plate areas. In contrast to Kornicker, I believe that the present data provide a good indication of the overall distribution of the known benthic species. There is evidence that the other ostracode suborder, Podocopina, may also contain taxa that duplicate distribution patterns found in the Myodocopina; for instance, the Tertiary to Recent distribution of the marine genus *Caudites*, whose distribution was mapped by McKensie (1967, fig. 5). *Caudites* is distributed throughout much of the world's warm seas, but is absent from the nonmarginal portions of the Pacific Plate in the Indo-Pacific.

There are about 300 species of mantis shrimps, Stomatopoda, which as far as known, have planktonic larvae (R.B. Manning, pers. comm.). The genus *Harpiosquilla* comprises some of the largest species of mantis shrimps (up to 335 mm TL). *Harpiosquilla*, with seven species, is a benthic indweller of soft bottom in the tropical marine and brackish waters of the Indo-West Pacific (Figure 54) from depths of less than 2 m to 206 m (Manning, 1969). Manning (1969) wrote that the absence of *Harpiosquilla* from Oceania reflects a lack of suitable habitats. I doubt this explanation, as shallow, soft bottoms in brackish areas exist at localities both on and off the Pacific Plate (New Guinea, New Caledonia, Fiji, Palau, Eastern Caroline Islands, Society Islands, etc.) where *Harpiosquilla* is not known. While the absence of *Harpiosquilla* from these localities may be due in part to collecting deficiencies, I do not believe either collecting deficiencies or lack of suitable habitat provide a satisfactory explanation for the absence of *Harpiosquilla* from the Pacific Plate. There is a remarkable similarity between the distribution of

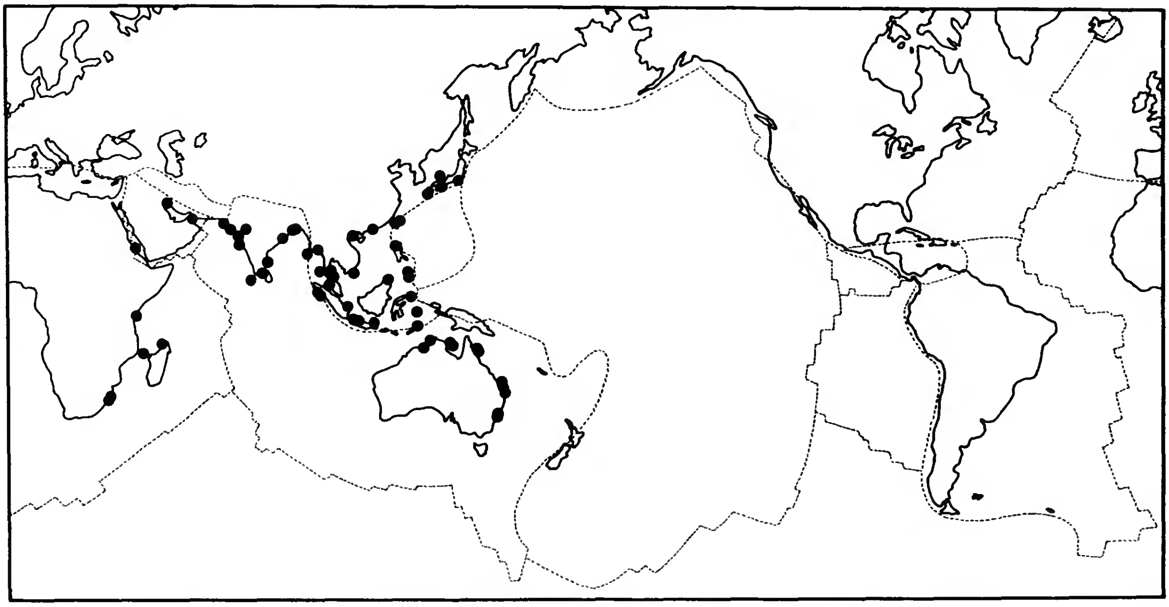

FIGURE 54.—Distribution of the mantis shrimp genus *Harpiosquilla* (Arthropoda: Crustacea), based on Manning, 1969.

Harpiosquilla and the distributions of the fishes of the family Congrogadidae (reef inhabiting; Figure 17), the Indo-West Pacific distributions of the toadfish family Batrachoididae (reef and estuary inhabiting; Figure 6), and the shark genera *Loxodon* and *Rhizoprionodon* (both free swimming; Figure 13). The similar distribution of these different taxonomic groups (some with habits and habitat preferences similar to, and others with habits and habitat preferences dissimilar to, those of *Harpiosquilla*) indicates to me that these distributions are part of a common pattern involving groups of continental origin that have been unable to disperse onto the Pacific Plate.

Class INSECTA

There are about 300 species of rhysodine beetles (Carabidae; Rhysodini), all of which live in dead wood, both as larvae and adults, and are distributed throughout much of the tropical and warm-temperate portions of the world (Figure 55). The species are gregarious, and up to 50 individuals have been found in a single log. Although most species are winged, there are no published flight records, and it is believed that if they fly at all, it is only as a means to reach decayed areas in the upper branches of trees; dispersal by human transport of wood, or by rafting logs seems feasible (Bell, 1979). Only three species of rhysodines occur other than marginally on the Pacific Plate, all in the Eastern Caroline Islands. Two of the three species are endemic to the Plate and the third has been reported otherwise only from Palau, based on a possibly mislabelled, old specimen. Three other species of rhysodines are restricted to Palau, Yap, and Ulithi, islands along the eastern margin of the Philippine Plate. There are no other species reported from these islands. Of the six species included in the present discussion, three are found on more than one island (up to four islands), and it is believed that each of the three originally occupied only one island, with human associated introductions accounting for the spread to other islands (R.T. Bell, in litt. and pers. comm.). The Pacific Plate distribution of the Rysodini appears to be an example of the operation of the Caroline Islands

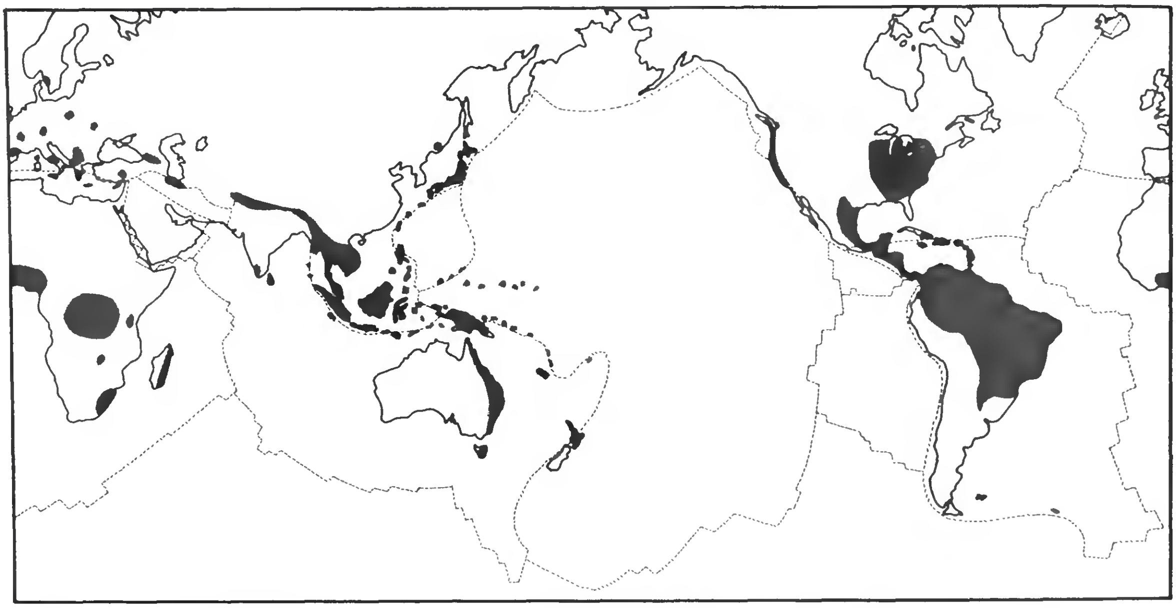

FIGURE 55.—Generalized distribution of the carabid beetles of the tribe Rhysodini (Arthropoda: Insecta), based on information provided by R.T. Bell.

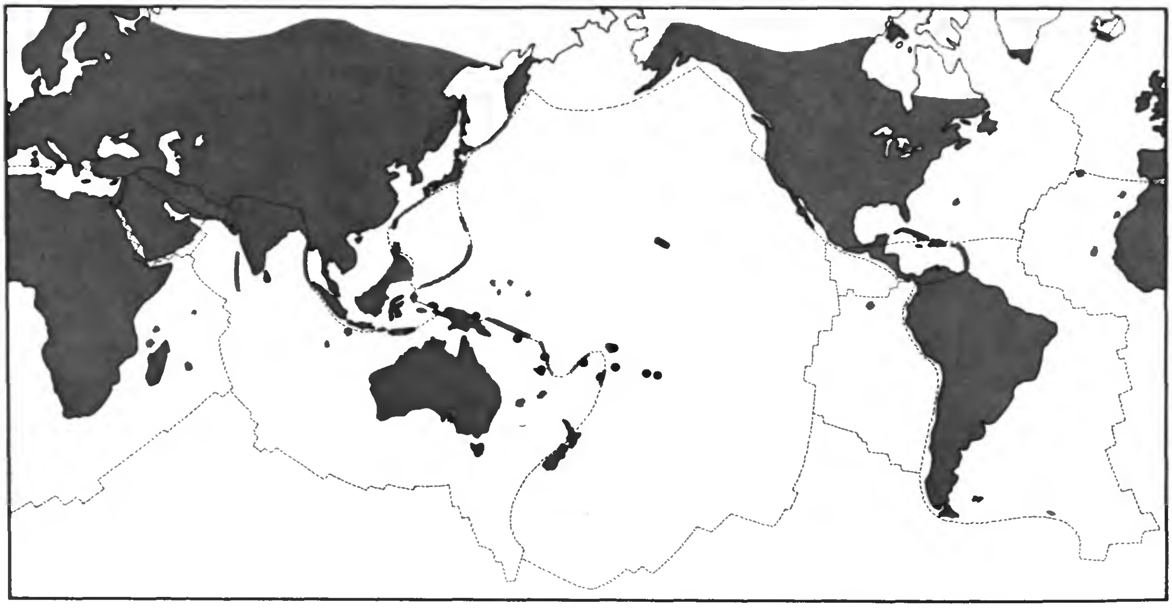

FIGURE 56.—Generalized distribution of the bats (Chordata: Vertebrata), based on information provided by K.F. Koopman (closed circles represent distribution of *Pteropus tonganus*, mostly after Wodzicki and Felten, 1981).

conduit, which has similarly affected the distributions of numerous other terrestrial, and marine, organisms.

Phylum CHORDATA

Class MAMMALIA

With the possible exception of rodents, bats (order Chiroptera) are the most widely distributed group of mammals (Figure 56). Most bat species are highly localized and, unlike rodents, have not been subject to widespread introductions by humans (Koopman, 1970). There are 169 genera and about 847 species of recent bats (Koopman and Knox Jones, 1970). Only three genera (*Emballonura, Pteropus, Lasiurus*) and seven species occur other than marginally on the Pacific Plate. *Lasiurus cinereus* is the only bat on the Hawaiian Islands, and the only bat species on the Pacific Plate (nonmarginally) that has its closest relationships in the Western Hemisphere. *Lasiurus cinereus* is widely distributed in the Western Hemisphere, where *Lasiurus* (with six species) is otherwise restricted. *Emballonura* and *Pteropus* are restricted to the Indo-Pacific area, and five of the six nonmarginal Plate species in these genera occur on various of the Eastern Caroline Islands. Of the five species, four are endemic to the Eastern Caroline Islands; the fifth also occurs to the east of the Pacific Plate margin. The presence of bats in the Eastern Caroline Islands is evidence favoring support of the Caroline Islands conduit. The seventh Plate bat species, *Pteropus tonganus*, comprises two subspecies, which occur only on islands on and near the Plate margin (Figure 56). While the bat distribution map is not as "clean" as the other distribution maps given in my study, I believe that it basically conforms to a continentally restricted pattern, with indications of recent dispersals and speciations in Pacific Plate areas adjacent to the western margin of the Plate. (Much of the information presented in this discussion was provided by K.F. Koopman, in litt. and pers. comm.)

PLANTS

Data on plant distributions were more difficult for me to obtain and interpret than similar data on animals. Although distributions parallel to those described for animals exist, in some cases commonly, I have selected only a few to illustrate the parallelisms, and most of these are from the pages of the volumes of *Pacific Plant Areas*.

Van Steenis and van Balgooy (1966) mapped the distribution of *Korthalsella platycaula* (Loranthaceae), which is a widely distributed Pacific Plate endemic that ranges from Samoa east to Henderson Island, and north to the Hawaiian Islands. The species is parasitic on woody dicotyledonous trees and shrubs, mostly on high islands. The closest relative was not indicated. Van Balgooy (1975) mapped the distribution of *Hedyotis romanzoffiensis* (Rubiaceae), also a widely distributed Pacific Plate endemic, which is a low shrub restricted to coral islands. The closest relative was not indicated.

Van Balgooy (1975) mapped the distribution of *Gunnera* (Haloragaceae), which contains 30–50 species of perennial, herbaceous plants up to 6 m in height that, in the tropics, occur only in montane areas. *Gunnera* is widely distributed in continental plate areas, but on the Pacific Plate nonmarginally, it occurs only in the Hawaiian Islands (Hawaiian exception distribution).

The eastern portion of the distribution of *Rhizophora apiculata* (Rhizophoraceae) was mapped by van Steenis (1963). This mangrove attains a height up to 30 m, occurs in muddy marine areas, and has buoyant seeds. The eastern limits of the distribution of *R. apiculata* is generally defined by the western margin of the Pacific Plate between the Marianas and Santa Cruz islands, and the species is absent from the Pacific Plate nonmarginally except for its occurrence in the Eastern Caroline Islands, evidence favoring the operation of the Caroline Islands conduit.

The order Coniferales includes about 50 extant genera and about 600 extant species of typically woody and evergreen plants, such as pines, spruces, hemlocks, firs, cypresses, junipers, sequoias, podocarps, araucarias, and larches. The species vary from only 8 cm to 90 m in height at maturity. They occur in habitats ranging from sea-level swamps to dry, rocky, mountain sides at 3400 m altitude. Species are found in the tropics as well as at the timberline within the Arctic circle, where temperatures drop to −45° C. In the warmer parts of their range, conifers usually prefer higher altitudes (Wiggins, 1974).

The conifers first appear in the fossil record during the Carboniferous of the Paleozoic, but the earliest known contemporary genera are from the middle Jurassic, with few contemporary genera known earlier than the Cretaceous (Miller, 1978).

Conifers are frequently reported to occur natively throughout the world, but it is obvious from their distribution (Figure 57) that they are absent from the nonmarginal portions of the Pacific Plate. Conifers have been introduced into various Plate islands, particularly the Hawaiian Islands, mostly as ornamentals. Pines do not adapt well in the Hawaiian Islands, but araucarias do (F.R. Fosberg, pers. comm.).

Van Balgooy (1971:143), who discussed the relationship of dispersibility to plant distribution was hard put to explain the absence of conifers (and other plants of low dispersibility) from Pacific islands east of the Andesite Line (essentially the same as the western margin of the Pacific Plate; Figure 2). He noted the presence of conifers on islands along and west of the Andesite Line that were no more isolated from each other than they were from islands lacking conifers to the east of the Line. In referring to these nonconifer-inhabited islands, van Balgooy (1971:146) stated, "The floristic character of [these islands] pleads for rather difficult accessibility. Yet under the present day configuration of land and sea the facts found are also difficult to explain. They can best be explained by archipelagic conditions." I am unable to determine from van Balgooy's study what he was implying by archipelagic conditions (perhaps he was ascribing unique ecological conditions to archipelagos), but his understandable

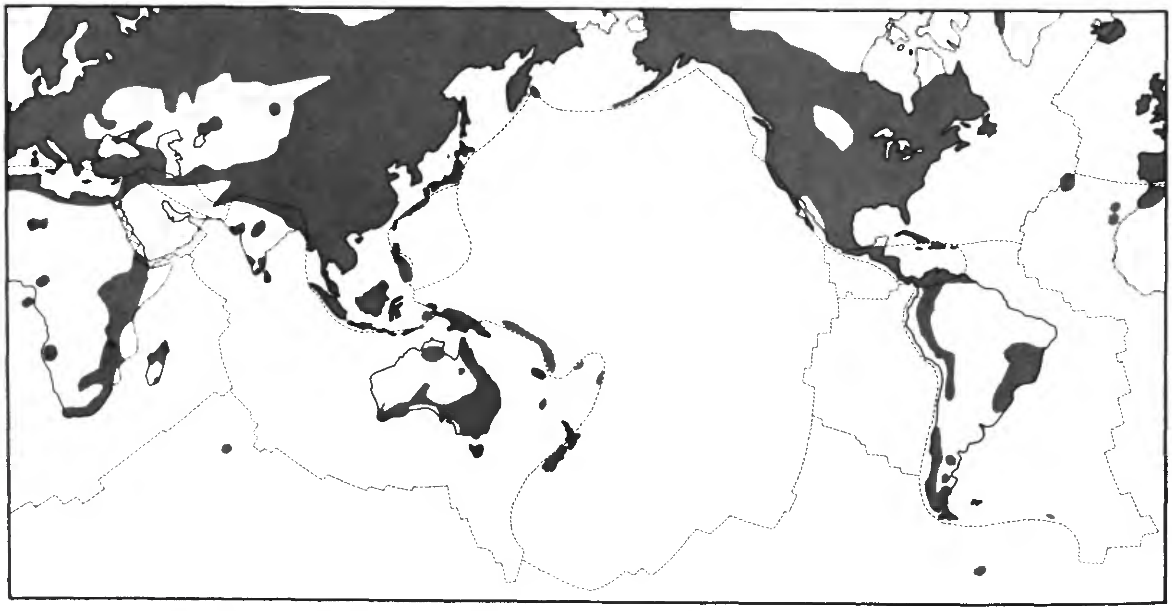

FIGURE 57.—Combined generalized distribution of fossil and recent plants of the order Coniferales, based on Florin, 1963; there are some northern distributional records for areas not shown on map.

loss at explanation pervades this portion of his study. I find the similarities exhibited by the distributions of the terrestrial conifers and the marine rajoid rays (Figure 36), in so far as they can be compared, given the general habitat requirements of the two groups, to be striking. These two groups are of continental plate origin and are bound to continental plates simply because they have low dispersal abilities. Their distributions are the result of fragmentations and movements of the continental lithosphere to which they are attached; ecological factors affect only relatively minor areas within the overall ranges of their distributions.

Discussion

Numbers of Shorefish Families

The warm, shallow-water fish fauna of the Indo-Pacific is summarized in Appendix 2, Tables A and B, and has been discussed under the family accounts. There are about 179 fish families (three orders of elasmobranchs are treated as families for convenience) with warm, shallow-water representation in the Indo-Pacific (henceforth, these families will be termed shorefish families). Of these shorefish families, only 121 (68%) have nonmarginal representation on the Pacific Plate, and 15 (12%) of the 121 have nonmarginal representation only in the Hawaiian islands, 6 (5%) only in the Eastern Caroline Islands, and 3 (2%) only in the Marshall Islands. Ten of the 15 families that occur on the Plate only in the Hawaiian Islands, occur there only in deep water, effectively reducing the number of families with shorefish representation on the Plate to 111 (or 62% of the total number of shorefish families). All of the Pacific Plate shorefish families are widely distributed in the Indo-West Pacific, if not even more widely. In contrast, several of the Indo-West Pacific shorefish families have highly restricted distributions; for instance, Coracinidae, only in the western Indian Ocean; Pataecidae and Brachaeluridae, only in Australia; Leptobramidae, Notograptidae, Rhinoprenidae, only in Australia and New Guinea; Pseudotrichonotidae, only in southern Japan. A few shorefish families, aside from those limited on the Pacific Plate to its margins or to the Eastern Caroline, Marshall, and Hawaiian islands, appear to be highly restricted in their distribution on the Pacific Plate: Moridae, Hawaiian and Rapa islands; Labracoglossidae, Rapa and Easter islands; Cheilodactylidae, Hawaiian, Rapa, and Easter islands; Isonidae, Samoa, Hawaiian and Pitcairn islands. It is significant, perhaps, that most of the shorefish families that have limited distribution on the Pacific Plate (including those occurring only at the Hawaiian or Eastern Caroline islands) are confined to high islands. On the other hand, high island groups (Society, Cook, Marquesas, for instance) do not necessarily have exceptional shorefish family representation.

The greatest number of shorefish families present in any general area in the Indo-Pacific is about 163 (Appendix 2, Tables A, B; Figure 58), or about 90 percent of all such families included here; this occurs along the Queensland coast. The diversity of shorefish families in Queensland is partly explained by the presence in northernmost Queensland of some families (for instance, Notograptidae, Kurtidae, Rhinoprenidae, Menidae, Lactariidae, etc.) that are otherwise restricted to areas of the western Pacific north of Queensland, and the presence in southernmost Queensland of some families (for instance, Scorpididae, Gonorynchidae, Enoplossidae, Glaucosomatidae, etc.) that are otherwise restricted to areas of Australia south of Queensland (some of these last-named families are antiequatorially distributed). Any Indo-West Pacific area, except for a few marginally located islands, has more shorefish families than the number (121) of such families that occur on the entire Pacific Plate nonmarginally.

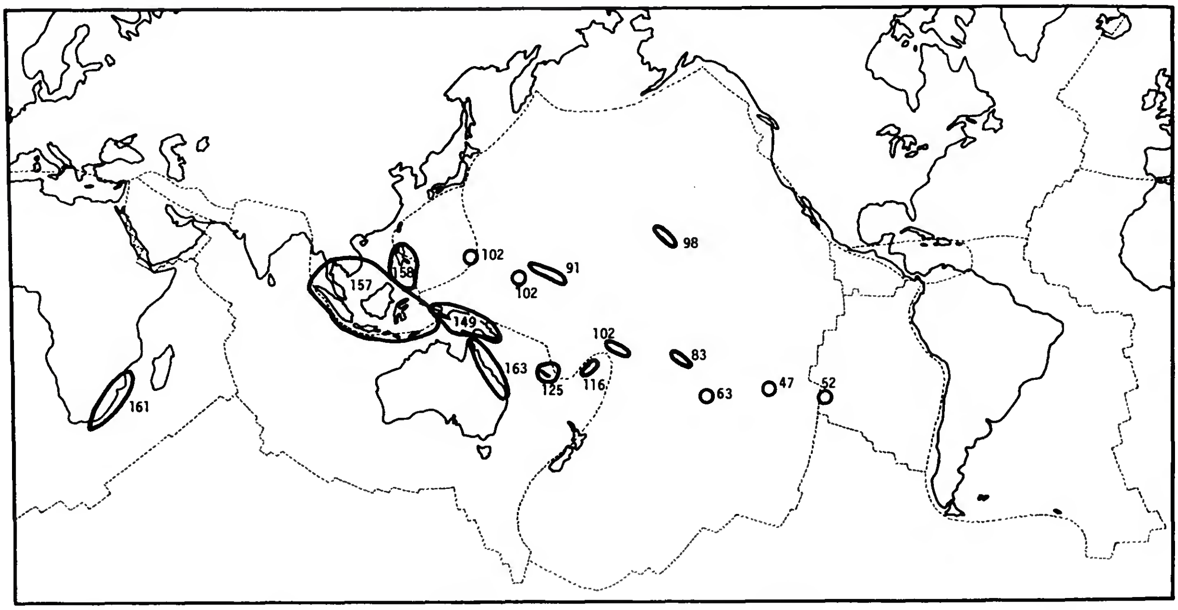

FIGURE 58.—Numbers of shorefish families known and expected to occur in various areas in the Indo-Pacific, based on information in Appendix 2, Table B.

Closely similar to Queensland in numbers of shorefish families present are the southeast coast of Africa, with about 161 families, the Philippine Islands, with about 158, and the Indo-Malayan region, with about 157. Although Queensland and southeast Africa have almost identical numbers of families, they do not share all families. Fourteen of the Queensland families do not occur (or are not expected to occur) in southeast Africa, and 13 of the southeast African families do not occur (or are not expected to occur) in Queensland.

Some portion of the central Indo-West Pacific region is almost invariably considered by zoogeographers to be the center of greatest taxonomic diversity, with a progressive decrease in numbers of taxa occurring in Indo-Pacific areas outside the region. Talbot (1970), Goldman and Talbot (1976), and Sale (1980), all of whom discussed numbers of fish species, believed that the decrease emanated in all directions. Cohen (1973), however, based on a study of selected fish groups, found no decrease in numbers between the eastern and western Indian Ocean. My findings, based on numbers of shorefish families, tend to agree with those of Cohen's. Areas such as Queensland and southeast Africa are considerably removed from each other, yet have about the same numbers of shorefish families, and have slightly more than the Philippine or Indo-Malayan regions, and only two or three fewer families than the combined Indo-Malayan and Philippine regions. While it is presently not feasible to determine if the distribution of numbers of families is paralleled by numbers of genera and species, I would not be surprised to find that it is for genera, but is not for species.

The problem is complicated by the subjective choice of how large an area one selects to constitute the central Indo-West Pacific region. Abbott (1960, pl. 19; reproduced here as Figure 59) presented a distribution map for the numbers of Indo-Pacific species of the gastropod genus *Strombus*. Abbott's delimited areas are somewhat comparable to mine. His findings, however, contrast with mine—particularly for the southeast African coast and Queensland, which have many fewer species of *Strombus* than do the Indo-Malayan,

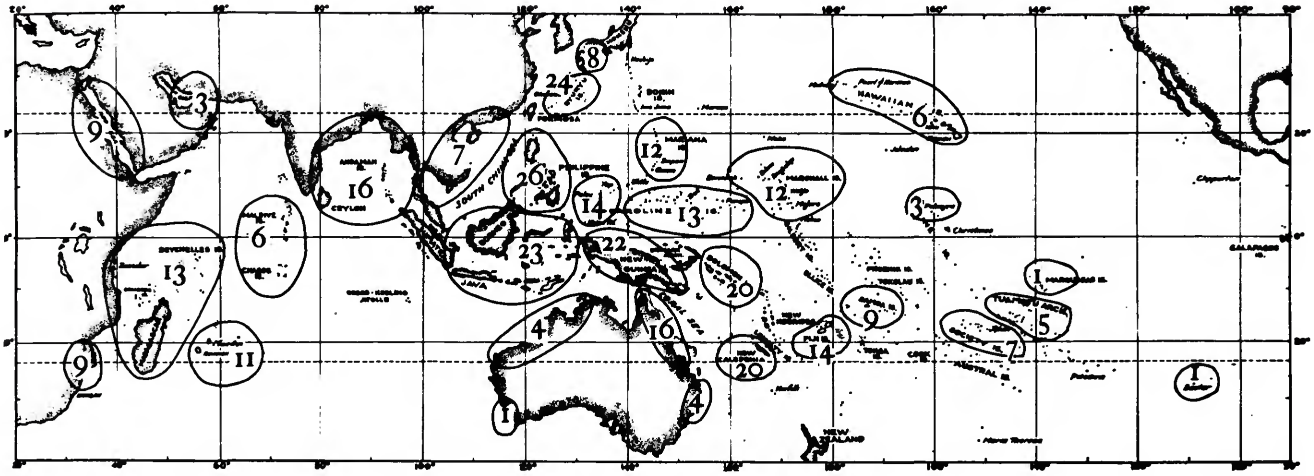

FIGURE 59.—Numbers of taxa of the gastropod genus *Strombus* at various Indo-Pacific localities; total number of taxa in area, 60 (after Abbott, 1960, pl. 19).

Philippine, or New Guinea regions—and, thus, support generally held opinions about relative diversity of taxa in a central Indo-West Pacific area. Most attempts to explain species diversity in the Indo-West Pacific have been couched in ecological terms (warm temperatures, climatic stability), but I must agree with Sale (1980) who stated that the high diversity of the central Indo-West Pacific may have historical causes that are outside the scope of ecological investigation. Taxonomic diversity is to a large degree dependent on the number of vicariant events that have occurred in an area, and there have probably been more such events in Indonesia (as politically defined today) than in any other equivalent surface area in the Indo-Pacific.

Numbers of Shorefish Genera and Species

The 111 families with shorefish representation on the Pacific Plate nonmarginally include about 461 genera and an estimated 1312 species (Appendix 2, Table C). The list of genera was compiled from the literature, museum collections, and in consultation with numerous colleagues, and is probably reasonably complete. The number of species was similarly compiled, but includes numerous estimates that might affect the total by 10 percent. If the estimates are reasonably approximate, the five most speciose families (Gobiidae, Labridae, Serranidae, Pomacentridae, Blenniidae) together contain about 29 percent (136) of all shorefish genera and about 36 percent (466) of all shorefish species on the Plate nonmarginally. If the genera and species of the next six most speciose families (Apogonidae, Chaetodontidae, Ophichthidae, Acanthuridae, Muraenidae, Scorpaenidae—the last two families tied for tenth place) are added, these figures are increased to about 42 percent (194) of the genera and about 54 percent (705) of the species. Thus, 10 percent of the Plate families (111 with shorefish representation) account for over half of the species present. Similar figures for these families were reported by Myers and Shepard (1981) for Guam alone, on the margin of the Pacific Plate. These same families form an important part of the shorefish faunas in all parts of the world, but nowhere else, including the Indo-West Pacific, are they so dominating a component.

Using information developed from the analysis of the Pacific Plate shorefish fauna, I attempted to ascertain the total number of shorefish species for the entire Indo-Pacific. I did this in two ways: one, by assigning known or estimated numbers of species to each family and, two, by estimating the total number based on the proportion of the total number of Indo-Pacific species represented on the Plate in certain reasonably well-known and speciose groups of fishes (for instance, Labridae, Pomacentridae, Pomacanthidae, Syngnathidae). The first method resulted in an estimate of 3966. Using the second method, percentage representations in the Plate groups range from about 20 to 50 percent, and average about 33 percent, giving a total of 3936 (±10 percent) shorefish species for the Indo-Pacific. This latter figure is probably low because it does not allow for the numerous families that have no Pacific Plate representation. It overcompensates, however, for monotypic families with 100 percent representation. The two methods, nevertheless, are in remarkable agreement, and an estimated total of about 4000 shorefish species for the Indo-Pacific is probably close to reality. Such a total is about 30 percent greater than the only other recent estimate of which I am aware, "—probably more than 3000 (Briggs, 1974:13)," which may have been based on the numbers included in the outdated 11 volumes of *The Fishes of the Indo-Australian Archipelago.* Cohen (1973) offered a guess that there may be 3000–4000 species of tropical shorefishes in the Indian Ocean, where there is considerable endemism (the Red Sea alone may have as much as 15 percent endemic fishes; see Briggs, 1974, for discussion). If Cohen's estimates are correct, my estimated total of 4000 for the entire Indo-Pacific is much too low.

Boundary Effect between Pacific Plate and Indo-West Pacific

While there is reason to question whether there is a decrease in taxonomic diversity as one moves west from the Indo-Malayan region, there is unquestionably a decrease in diversity as one moves east (Figures 58, 59). The nature of this decrease, whether abrupt or gradual, is of interest here.

Ekman (1953:18) was uncertain where to draw the boundary between the marine faunas of the Indo-Malayan region and the oceanic islands of the Pacific, and remarked that it was not known whether there was "any definite border or transitional zone or whether the transition is gradual and uniform." Hedley (1899), however, had already discussed the presence of a sharp break in both the terrestrial and marine molluscan faunas to the east of the continental islands ranging from New Guinea to Fiji. The phenomenon of a sharp break was reviewed by Thorne (1963) for the terrestrial biota and emphasized for plants by van Balgooy (1971), but recent general discussions of Indo-Pacific biogeography (Briggs, 1974; Kay, 1980), and the fish literature in general, do not mention a sharp break. My findings on shorefish families support both a sharp break in numbers of families and a gradual decrease in numbers of families as one proceeds across the western margins of the Philippine and Pacific plates. The decrease, whether sharp or gradual, depends on the path one follows from the continental areas and on the groups of fishes one selects.

If one proceeds southeast from New Guinea along the continuous island chains to Fiji and then east along the island chains to Easter Island, the decrease in number of shorefish families is gradual (Figure 58). If one proceeds due east from the Philippine Islands or New Guinea, the decrease is abrupt: an immediate 32–36 percent of the families drop out as one reaches or leaves the western margin of the Pacific Plate. On a group basis, the elasmobranchs are conspicuous for an abrupt decrease in numbers as one enters the Pacific Plate at any point along its eastern margin. The entire order Rajiformes (Figures 36 and 37) and the entire families Pristidae (Figure 34), Gymnuridae, Rhinopteridae, Squantinidae, Triakidae, Stegastomatidae, Orectolobidae, Brachaeluridae, Hemiscylliidae, and Parascylliidae (all but the Parascylliidae with shorefish components), and certain genera of Carcharhinidae (at least *Loxodon*, *Scoliodon*, *Rhizoprionodon* (Figure 13), and *Dirrhizodon*) are all absent from the Pacific Plate. Other elasmobranch groups are known nonmarginally on the Plate only from a single species each, and only from deep water at the Hawaiian Islands: Urolophidae, Scyliorhinidae, Odontaspididae, Torpediniformes (Figure 44). A perusal of the distribution maps I present for many teleost groups emphasises the sharpness of the break in the distributions of shorefishes along the Pacific Plate margin, regardless of the direction taken from the continental areas, indicating, that absences from the Plate may be selective, rather than only random.

The sharp decrease in taxa as one proceeds eastward across the Pacific Plate's western margin has not been explained. Two hypotheses have bearing on any proposed explanations.

Reality Hypothesis: Those taxa that are absent from the Pacific Plate have never been present on the Plate.

Extinction Hypothesis: Those taxa that are absent from the Pacific Plate were once present on the Plate, but have become extinct there.

Although I believe that the Reality Hypothesis is the more parsimonious and pertains to a large majority of the taxa that are absent from the Pacific Plate, there is merit in both hypotheses and both will be discussed.

REALITY HYPOTHESIS.—The only direct evidence that would confirm this hypothesis would be the presence of a Plate endemic sister taxon for each of the Indo-West Pacific taxa that are missing from the Plate. In the case of fish families, there are no Plate endemic shorefish families. With regard to fish genera, there are about ten endemic to the Plate (Figures 26 and 60). Sister-group relationships for these genera have not been proposed formally, but for one of them, the minute *Medusablennius* (Blenniidae), known only from the Tuamotus, the sister genus is probably *Mimoblennius* or *Cirrisalarias* (based on synapomorphies involving nostril size and distribution of nasal cirri), both of which are widely distributed, and restricted to the Indo-West Pacific. There are numerous endemic Plate species (Table 2 lists some of the more important ones for this discussion, the widely distributed Plate endemics). Unfortunately, the sister-group relationships of these taxa also have not been proposed formally. Some species distributions, however, are strongly suggestive of relationships, and for some species the specialists' intuitive statements of relationship are probably correct; a few of these distributions and relationships are discussed here.

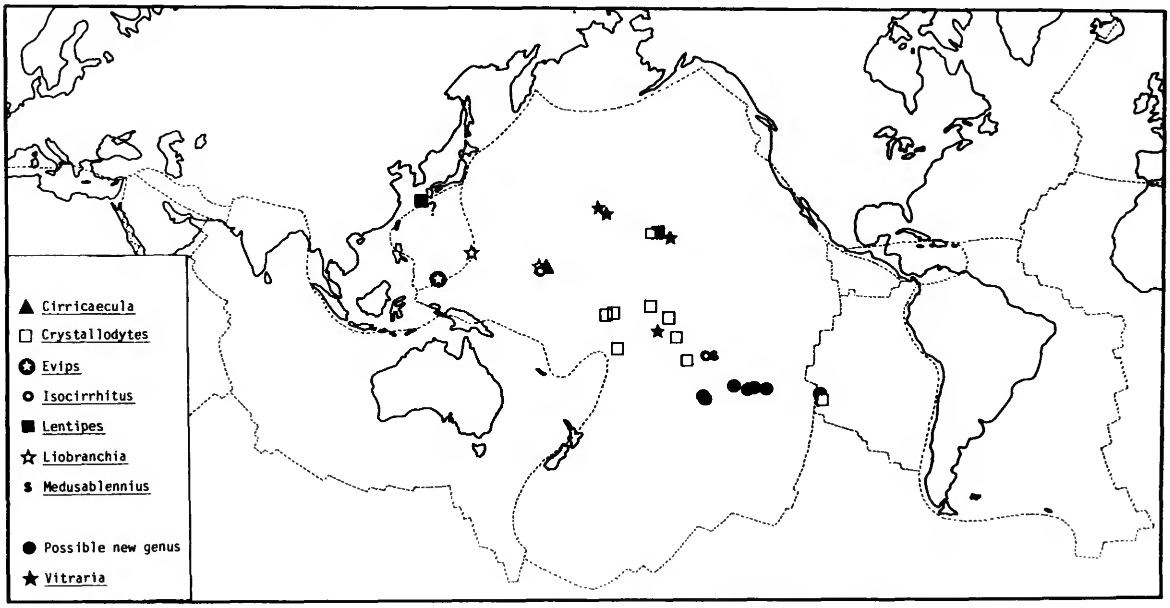

FIGURE 60.—Distributions of nine of the ten shorefish genera endemic to the Pacific Plate and its margins; for tenth genus see Figure 26; all endemic genera are monotypic, with possible exception of *Lentipes* (see "Gobiidae," page 44).

TABLE 2.—List of probable Type 1 (widely distributed) Pacific Plate endemic fishes

Family/Species/Subspecies	Distribution map
Acanthuridae	
Acanthurus achilles	Figure 5
A. leucopareius	Figure 5
A. nigroris	
Ctenochaetus hawaiiensis	
Zebrasoma flavescens	
Blenniidae	
Cirripectes jenningsi	
C. variolosus	
Entomacrodus cymatobiotus	Figure 8
E. sealei	Figure 8
Callionymidae	
Synchiropus laddi	
S. morrisoni	
Chaetodontidae	
Chaetodon quadrimaculatus	
C. trichrous	
Hemitaurichthys thompsoni	
Cirrhitidae	
*Cirrhitichthys serratus**	
Cirrhitops hubbardi	
Isocirrhitus sexfasciatus	Figure 60
Paracirrhites nisus	
Creediidae	
Chalixodytes tauensis	
Crystallodytes cookei	Figure 60
Gobiidae	
Kelloggella centralis	Figure 20
K. oligolepis	Figure 20
Nemateleotris helfrichi	Figure 21
Hemiramphidae	
Hemiramphus depauperatus	
Hyporhamphus acutus	Figure 22
Holocentridae	
Myripristis amaenus	Figure 24
M. randalli	Figure 24
M. woodsi	Figure 24
Labridae	
Bodianus loxozonus trotteri	
Labroides rubrolabiatus	Figure 25
Pseudojuloides atavai	
Ophichthidae	
Schismorhynchus labialis	Figure 26
Ostraciidae	
Ostracion whitleyi	
Pomacanthidae	
Apolemichthys griffisi	
A. xanthopunctatus	
Centropyge loriculus	Figure 31
C. multicolor	Figure 31
C. nigriocellus	Figure 31
Pomacentridae	
Amphiprion chrysopterus	Figure 32
Plectroglyphidodon imparipennis	
P. phoenixensis	
Stegastes aureus	
Scorpaenidae	
Scorpaena coniorta	
Scorpaenopsis fowleri	Figure 26
Serranidae	
Anthias bartlettorum	Figure 41
A. pascalus	Figure 41
Epinephelus socialis	
Tetraodontidae	
Canthigaster epilampra	Figure 26

* Also recorded off Pacific coast of Colombia in the eastern Pacific.

Bruce B. Collette (in Springer, 1981a) believes that the closest relatives of the widely distributed Plate endemic, *Hyporhamphus acutus* (Hemiramphidae), is a group of species limited to the Australian–New Zealand Region. There are only two species of *Chalixodytes* (Creediidae), one a widely distributed Plate endemic, the other endemic to the Indian Ocean. Randall (in press a) believes that the closest relative of the Plate endemic labrid, *Labropsis polynesica* (ranging from the Cook to Gambier islands), is *L. australis*, which is known only from the Great Barrier Reef and islands along the western margin of the Pacific Plate, from the Solomons to Fiji, Samoa, and Tonga. Perhaps not so clear-cut, but still suggestive, are the three species of *Nemateleotris* (Gobiidae): one, a widely-distributed Plate endemic; one, widely distributed in, and restricted to, the Indo-West Pacific; and one encompassing the range of the other two species (Figure 21).

Several invertebrates provide evidence comparable to that provided by fishes. Rosewater (1972) believed that the closest relative of the widely distributed Pacific Plate endemic gastropod, *Tectarius grandinatus*, is *T. rugosus*, known only from the Philippine Islands and Celebes. Solem (1981; see also Springer, 1981a) seems to indicate that the closest relatives of the widely distributed Pacific Plate endemic land snail family Endodontidae are those members of the Charopidae confined to southwestern Australia. Banner and Banner (1975) recognize two subspecies of the pistol shrimp, *Alpheus lobidens*, one a widely distributed Plate endemic, the other widely distributed in the Indo-West Pacific, with a single, disjunct occurrence in the Mediterranean (Figure 51). Austin B. Williams (pers. comm.) believes that the closest relative of the widely distributed Plate endemic crab, *Latreillia metansia*, is *L. valida*, which ranges from the east coast of Africa to Japan and Philippines (Figure 50).

If one accepts these presumed sister taxa relationships, then the reality hypothesis has been corroborated. Certainly, more rigorous corroboration is needed.

It is desirable to explain why many taxa that are widely distributed in the Indo-West Pacific (and, variously, throughout the world) have not become established on the Pacific Plate. An obvious first premise would be that a physical barrier to dispersal is present along the western margin of the Pacific Plate.[2] Depending on when this barrier first appeared, it might also have served to isolate taxa on the Pacific Plate and permitted them to speciate.

The western margin of the Pacific Plate is outlined by a series of deep-sea trenches (Figure 1), which probably represent a barrier that prevents some shallow-benthic marine fishes and other organisms from dispersing onto or off the Plate, but great depths alone are not barriers to the dispersal of forms with pelagic life-history stages, which many Plate-absent and Plate-endemic shorefishes possess. Nor, obviously, are great depths a barrier to the dispersal of terrestrial organisms.

In contrast to the overwhelming majority of the fish families that are well represented on the Pacific Plate, a large proportion of the Plate-absent families, including several that are widely distributed in the Indo-West Pacific, have components with a strong estuarine or freshwater parameter in their ecology: Ariidae, Batrachoididae, Centropomidae, Chirocentridae, Kurtidae, Plotosidae, Pristidae, Sciaenidae, Sillaginidae, Sparidae, Terapontidae, Toxotidae, Trichiuridae. One might assume therefrom that the paucity of estuarine and freshwater habitats on the Pacific Plate provides an ecological basis for the inability of some taxa of these families to become established on the Plate. On the other hand, five families (Ambassidae, Gobioididae, Leiognathidae, Monodactylidae, Scatophagidae) with strong estuarine and freshwater parameters in their ecology do occur, variously, in the three widely separated high islands (Truk, Ponape, and Kosrae-Kusaie) of the Eastern Caroline chain where rivers and estuaries exist (none of the species in these families is represented by endemics in the Carolines). One might wonder, therefore, why more such families are not present at these islands.

Springer (1981a), in calling attention to the existence of widely distributed Pacific Plate endemics, noted that plate margins are characterized by frequent and varied tectonic activity, and that physical evidence for a barrier on the western margin of the Pacific Plate may have been subducted and lost forever. If so, one might expect that recent dispersal would be obscuring the effect of the former barrier, and there is reason to believe that it is.

The east-west Caroline Islands chain is being carried westward on the Pacific Plate as it moves toward the Philippine Plate margin (Figure 1), and islands on the eastern margin of the Philippine Plate are moving eastward through the mechanism of back-arc spreading (Karig, 1971, 1974). If no islands of the relatively young Caroline Islands chain[3] on the Pacific Plate have been

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[2] The well-known East Pacific Barrier (Ekman, 1953; Briggs, 1961), a long expanse of ocean separating the islands of the Pacific Plate from the coasts of the eastern Pacific, is, with very few exceptions (only about 40 Indo-Pacific shorefish species occur in the eastern Pacific; Rosenblatt et al., 1972), effective in isolating the Plate biota from that of the eastern Pacific, but will not be considered further. The obvious relationships of the shallow marine forms of the western and central Plate areas are predominantly with the biota of the Indo-West Pacific, and it is the possibility of barriers along the western margin of the Plate that concern me.

[3] Recent unpublished radiometrically determined ages for Kosrae, Ponape, and Truk, in order, are 4, 8, and 12–14 million years (B. Keating, Department of Geology and Geophysics, University of Hawaii at Manoa, pers. comm.; also mentioned in Kerr, 1981). My extrapolation from the spac-

lost through subduction (Pacific Plate under Philippine Plate), the expanse of open water separating the Caroline Islands on the Pacific Plate from the eastern margin of the Philippine Plate must have been greater than it is today (see section on geological history of Pacific and Philippine Plates). If such an expanse existed, it could have served as a barrier to dispersal. Today, however, the westernmost islands of the Caroline chain on the Pacific Plate are proximate to the islands on the eastern margin of the Philippine Plate and seem to be serving as a conduit (which I define as an essentially unidirectional corridor; see McKenna, 1972) that permits both terrestrial and marine organisms to island hop (disperse) onto the Pacific Plate. Some possible examples of dispersals using the Caroline Islands conduit are: Ambassidae, Centriscidae, Gobioididae, Leiognathidae, Monodactylidae, Scatophagidae, *Periophthalmus* (Gobiidae), *Butis* (Eleotrididae), *Omox*, *Glyptoparus*, *Nannosalarias* (all Blenniidae), *Synchiropus splendidus* (Callionymidae), *Zenarchopterus* (Hemiramphidae), *Calloplesiops* (Plesiopidae), *Dascyllus melanurus* (Pomacentridae), *Euxiphipops navarchus* (Pomacanthidae), *Rastrelliger kanagurta* (Scombridae), *Belonoperca* (Serranidae), all of which are widely distributed in the Indo-West Pacific and present on the Pacific Plate nonmarginally only in the Eastern Caroline Islands. Examples from other organisms include certain beetles (Figure 55), certain bats (Figure 56), and a mangrove, *Rhizophora apiculata* (van Steenis, 1963:253). The conduit must be relatively recent because its influence seems not to have greatly diluted the integrity of the Pacific Plate biota. One can expect that it is merely a matter of time before other fishes (and other organisms) currently missing from the Pacific Plate are able to disperse onto the Plate. Of interest here is a recent report (Allen, 1974) of the occurrence of a marine crocodile, *Crocodylus porosus*, at Ponape. *Crocodylus porosus* is distributed from India eastward only as far as Palau, Bismarck Archipelago, Solomon Islands, New Hebrides, and Fiji, all along the margin of the Pacific Plate. A 2.8 m long specimen was trapped at Ponape in 1971, where it was believed to have been resident for at least six months, based on the disappearance of pigs tethered at the shoreline. While no other crocodiles are known to have occurred at Ponape (information obtained during my visit in 1980), the potential exists for crocodiles to colonize Ponape (providing they avoid pigs and people).

The western margin of the Pacific Plate need not be the site of a physical barrier to dispersal in order that it sharply delimit the distribution of Indo-West Pacific organisms. It might simply be that these organisms lack the ability to actively disperse. It is significant, therefore, to note that fishes, such as *Scomberomorus* (Figure 40), that have planktonic young and fairly large free-swimming adults, have distributions similar to those of fishes, such as the Batrachoididae (Figure 6), that are relatively small and benthic and have large, demersal eggs and no pelagic life-history stages (at least in the Indo-West Pacific). Both groups are widely distributed along continental coasts and absent from the Pacific Plate. If there were no widely distributed endemic Pacific Plate fish species, I could accept that a physical barrier to dispersal along the western margin of the Pacific Plate is not needed to restrain the dispersal onto the Plate of species presently restricted to the Indo-West Pacific. I can only conclude, under the circumstances, that a barrier (or barriers) must exist, or have existed.

EXTINCTION HYPOTHESIS.—There are no fish fossils reported from the islands on the Pacific Plate, hence, no evidence that any of the families, genera, or species of fishes currently limited to the Indo-West Pacific were once present on the Plate. Fossils of other organisms are present on the Pacific Plate, and are best documented for the Mollusca, although I found it difficult and unfeasible to assess all the possibly relevant data.

The most informative areas on the nonmarginal portions of the Pacific Plate that are reported to have marine molluscan fossils are: Enewetak and Bikini, Marshall Islands; Funafuti, Ellice Islands; and the Hawaiian Islands. All the

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ing of the dated islands would indicate that edifices of the chain nearest the subduction zone could be about 16–20 million years in age.

fossils from these islands are from the Cenozoic. Information on older fossils is too sketchy to appraise (for instance, see Kauffman, 1976).

Ladd (1966, 1972, 1977) reported on the abundant chiton and gastropod molluscan fossils at Bikini, Enewetak, and Funafuti (at least one additional report in this series is in preparation). These fossils range in age from about Eocene to Recent, and include 48 families, of which only four (Melongenidae, Turritellidae, Potamididae, Iravadiidae, all gastropods) are not known to be extant on the Pacific Plate, but are extant in the Indo-West Pacific. Three of the four families that appear to be absent are inhabitants of estuarine or mangrove habitats, and the fourth, Turritellidae, is a sand-dwelling group that has been found in harbors, and, thus, may have an estuarine component in its ecology. Estuarine and mangrove habitats are not common on the Plate, and are predominantly restricted to high islands. The appearance of the four families in the Eocene to Pliocene strata of the Marshall Islands, which are atolls today, indicates that these islands were formerly high islands with brackish and mangrove environments. It is quite possible that some, or all, of the four missing families will be found extant at high islands, such as Ponape, which has extensive estuarine and mangrove habitats, but whose molluscan fauna has not been well studied or collected (H.A. Rehder, pers. comm.).

Ladd reported on numerous fossils of genera in families extant at both Pacific Plate and Indo-West Pacific localities. It was not feasible for me to determine which of these genera were extant and, if so, where; however, the range of one of the genera, *Cynisca* (Turbidinidae), was discussed by Ladd (1966). *Cynisca* is known only from Miocene fossils at Bikini and several extant species from the seas off South Africa. If the known distribution is truly indicative of the present distribution of this micromolluscan genus (maximum dimension of Ladd's specimens, 4.5 mm), extinction of *Cynisca* would appear to have occurred in all the extensive area between South Africa and Oceania.

The manner in which extinctions have generally affected marine molluscan distributions on the Pacific Plate is possibly exemplified by what has occurred in the Hawaiian Islands. Kohn (1980, based mostly on Kosuge, 1969) discussed the presence of fossil marine mollusks in the Hawaiian Islands. He noted that of 163 species known as fossils there, only three endemic pelecypod species in two genera (*Ostrea*, *Septifer*; based on Kosuge, 1969) and one endemic gastropod (a species of *Conus*) are universally extinct. All three genera, however, are represented by extant species in the Hawaiian Islands. Eight other species that are extinct in the Hawaiian Islands are extant and common at other islands on the Pacific Plate. The remaining 152 species of fossils are also represented in the extant fauna of the Hawaiian Islands.

A perusal of all the issues of the journals *Indo-Pacific Mollusca* and *Monographs of Marine Mollusca* evinced no examples of families, genera, or species that were extant on the Pacific Plate, but are now absent. Indeed, none of the larger-sized mollusks (macromullusca) that are presently confined to the Indo-West Pacific are known as fossils on the Pacific Plate, leading one to the conclusion that the supposed absence of some extant Indo-West Pacific taxa known otherwise only as fossils on the Plate is a consequence of their having been overlooked. The largest dimension of any of the Plate fossils reported by Ladd (1962, 1972, 1977) is about 50 mm, but for many is less than 5 mm. That Ladd reported on so many diminutive taxa is the result of his detailed examination of core samples from a deep-drilling program. In the same three studies, Ladd did record fossil mollusks of larger sizes, but only from andesitic localities (Fiji, Marianas, etc.) along the western margin of the Pacific Plate. Similarly, the journals mentioned above also include numerous listings of large-sized molluscan fossils, but only from continental areas and the Hawaiian Islands.

Comparing mollusks with fishes, it might be argued that mollusks are more susceptible to extinction than fishes, because mollusks are predominantly sedentary and less able to actively avoid conditions adverse to their existence than are fishes. The larvae of mollusks, however, are predominantly planktonic and could recolonize areas on the Plate that offered proper habitats[4] if they were ever able to colonize the Plate. Similarly, large, strong, free-swimming fishes (such as *Scomberomorus*, *Rachycentron*, and certain species of *Carcharhinus*) should be able to colonize the Plate, but do not in spite of the fact that proper habitats seem to be present, and some of these fishes have planktonic larvae. Furthermore, if a taxon were widely distributed on the Plate, extinction would have to cover an extraordinarily broad area and innumerable islands, factors that would seem to buffer whatever unfavorable effects were causing extinctions on one part of the Plate. Cases in point are the eight species of marine mollusks that are represented only by fossils in the Hawaiian Islands, but are extant at other islands on the Pacific Plate. To these cases may be added some terrestrial examples.

The land snail family Endodontidae (Gastropoda), which is endemic to the Pacific Plate and its margins, has been extensively studied (Solem, 1976, 1977). The endodontids are minute forms and are known as fossils only from Midway (Hawaiian Islands) and Bikini (Marshall Islands). The fossil species at Bikini belong to the genera *Cookeconcha* (a lower Miocene species) and *Minidonta* (a Pliocene-Pleistocene species). *Cookeconcha* is extant only on the principal Hawaiian Islands. *Minidonta* is extant on the Samoan, Cook, Austral, and Gambier islands, and Henderson Island. The fossil species at Midway belong to *Cookeconcha* and *Protoendodonta* (a Pleistocene species in each). *Protoendodonta* is known only from Midway.

The evidence favoring the selective extinction of Pacific Plate taxa as an explanation for the restriction of the range of extant members of the same taxa to the Indo-West Pacific or continental plate areas seems much weaker and less promising than that favoring the Reality Hypothesis. There are numerous opportunities for corroborating or falsifying the Reality Hypothesis, but these will require the difficult, although not impossible, work of establishing the sister species of the widely distributed Pacific Plate endemics. Nevertheless, it is instructive to examine the causes (particularly the geotectonic causes) and results of the limited types of extinctions that may occur on the Pacific Plate.

Based on the examples of extinctions discussed above, one might expect to find geographically patchy distributions of organisms relatively commonly among the islands on the Pacific Plate. Kay (1976, 1980) noted that patchy distributions of mollusks are common among the islands of the central Pacific, and ascribed such distributions to patchy ecology, at the same time excluding collecting artifacts and chance dispersal as contributing factors. Although some patchy distributions may be ascribable directly to patchy ecology, I believe the major causes are extinctions resulting from physical processes, which, of course, directly affect ecology. The presence of proper habitat, as shown above (footnote 4), is insufficient of itself to assure the presence of a species adapted for that habitat. Physical processes that affect extinc-

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[4] Evidence that proper habitats are available on the Pacific Plate for species that do not occur there naturally is to be found in the cases of successful introductions. The commercially important gastropod, *Trochus niloticus* (Trochidae) is widely distributed in the Indo-West Pacific, from the Andaman Islands in the west through Indonesia to the Philippines, Yap, Palau, New Guinea, New Caledonia, northern Australia, and the Admiralty, Solomon, New Hebrides, and Fiji islands (McGowan, 1958). *Trochus niloticus* was unknown from Pacific Plate localities, but was introduced by the Japanese into the Eastern Caroline and Marshall islands (includes high islands and atolls) in the late 1920s and 1930s (McGowan, 1958), and now forms an important food resource in islands where it was introduced. *Trochus niloticus* is a shallow-dwelling species that prefers the ocean sides of reefs as its habitat. Although *T. niloticus* has spread, apparently by larval dispersal (McGowan, 1958), to other locations on the immediate islands or atolls where it was introduced, it apparently has not spread to other islands or atolls. Heslinga (1981) ascribes the limited distribution of *T. niloticus* to the short duration of its planktonic stage. Yet, its natural, widespread occurrence in the Indo-West Pacific, including many islands, might tend to discount this factor.

The cichlid fish, *Sarotherodon mossambicus* (tilapia) is a freshwater and estuarine species native to Africa. In 1958, tilapia were introduced into the lagoon at Fanning Atoll, Line Islands (Lobel, 1981a). Tilapia are presently living and reproducing in the lagoon, which is fully marine. Of similar nature to the *Trochus* and tilapia introductions are the introductions of *Lutjanus* (Lutjanidae, snappers), *Cephalopholis* (Serranidae, groupers), and *Sardinella marquesensis* (Clupeidae, sardines) into the Hawaiian Islands from the Society and Marquesas islands (see discussions under family accounts).

tions include volcanism, tectonics, weathering, and glacioeustatic changes in sea level. These processes may act alone or in concert to cause extinctions or modify ecology. To understand how these processes operate on the Pacific Plate, the following generalized scenario is presented.

Islands on the Plate arise by volcanism. At the completion of formation, an island is usually a high island. High islands are more complex ecologically than low islands or atolls and can support many more species than low islands or atolls. After formation, island height is lowered by weathering, which destroys habitats. The Pacific Plate is moving in a northwesterly direction and carries islands with it, moving them into different climatic regimes, which will cause extinctions if the island species do not evolve adaptations to compensate for these climatic changes. The Pacific Ocean increases in depth from east to west and, thus, Plate movement carries islands into deeper water. While coral reef growth in tropical latitudes can offset some of the effects of deepening waters, an island is ultimately drowned and eliminated as it approaches subduction zones along the Plate margins—its terrestrial and shallow-dwelling biota extinguished. Glacioeustatic changes (see footnote 5), aesthenospheric bumps (Menard, 1973), and crustal loading (McKnutt and Menard, 1978) can also temporarily increase effective island height, or lower it, but, again, these changes come to naught. If an island is of the solitary type that forms near a fault zone or on the rise formed by a seafloor spreading zone, its biota can survive only if the island integrates (Rotondo et al., 1981) with a younger, higher island, or if another island, by chance, appears nearby (see section on Easter Island). In contrast, an island that forms as a result of the periodic activity of a melting anomaly (hot spot), which by its intermittent activity gives rise to the relatively closely spaced islands of an island chain, such as the Hawaiian Islands, elements of the island's biota can survive by dispersing back to a recently formed (high), nearby island (in such an instance, the age of an island's biota is not necessarily equal to that of the island, but to that of the island chain). On the Pacific Plate today, there is only one hot spot that is presently forming islands, and that is the Hawaiian hot spot (there may be a second in the Eastern Caroline Islands, but this has not been clearly established, nor has it been effective for four million years). Other than the Hawaiian Islands, no islands have been forming on the Plate for about a million years (Pitcairn, which is about 0.9 m.y. old, appears to be one of the youngest). If these circumstances persist, all the islands on the Pacific Plate, except the newly formed ones at the Hawaiian hot spot, will gradually become low islands, then atolls, drowned, and then be subducted, causing partial and then total extinction of their biotas. Inasmuch as all islands are not synchronously or equally affected by the physical processes described, patchy extinctions result, which are reflected by patchy distributions.

Endemism

ENDEMICITY OF SHOREFISH FAMILIES AND GENERA.—Although several shorefish families are endemic to the Indo-West Pacific, none is endemic to the Pacific Plate. The only possibility of family level endemism among fishes on the Plate is that of an undescribed family, genus, and species of large shark collected in 1976 at a depth of 150 m off the Hawaiian Islands (Tinker, 1978). The 3.5 m long specimen was entangled in a sea anchor. It seems probable that this shark species is more widely distributed in the sea than present information indicates.

Among the shorefishes, I have found only ten genera (2.2 percent of the number of genera present nonmarginally on the Pacific Plate; appendix 2, Table C) that appear to be endemic to the Plate (Figures 26 and 60). Among the endemics I have included one genus that ranges, questionably, to the northwestern margin of the Philippine Plate (see *Lentipes* in Gobiidae), and another, *Evips*, which is known only from the holotype of its type-species, collected at Palau on the eastern margin of the Philippine Plate. All of the endemic genera, with the possible exception of *Lentipes* and a possible new genus of cirrhitid (see *Cirrhitus wilhelmi* in Cirrhitidae) are monotypic.

The endemic genera belong in the following families: Blenniidae (*Medusablennius*), Cirrhitidae (*Isocirrhitus* and possible new genus), Creediidae (*Crystallodytes*), Gobiesocidae (*Liobranchia*), Gobiidae (*Lentipes*, *Vitraria*), and Ophichthidae (*Cirricaecula*, *Evips*, *Schismorhynchus*). In addition to the ten genera, there is one endemic, monotypic subgenus, *Acanthotaurichthys* (proposed somewhat cryptically by Burgess, 1979:218; Chaetodontidae, genus *Hemitaurichthys*), known only from Pitcairn Island.

It is possible that some of the genera now considered as endemics will be shown to be more widely distributed in the Indo-Pacific. For example, during much of the time my study was in progress I believed that the gobiid genus *Kelloggella* was a Plate endemic, but a species (undescribed, D.F. Hoese, in litt.) was obtained recently in the Indian Ocean (Figure 20; see discussion in Gobiidae). I doubt, however, that many, if any additional Plate endemic shorefish genera will be recognized.

Although only indirectly relevant to my study, it appears that there may be numerous endemic deep-slope fish genera on the Pacific Plate, for example: *Parapristipomoides* (Lutjanidae), *Neomerinthe* (Scorpaenidae), *Stethopristes* (Zeidae; see Heemstra, 1980, for a world distribution map of the species of this moderately deep-dwelling family), *Pelecanichthys* (Bothidae), and, possibly, the shark mentioned above.

ENDEMICITY OF SHOREFISH SPECIES.—The lack of endemic shorefish families and paucity of endemic shorefish genera on the Pacific Plate are not duplicated at the species level. The commoness of endemic shorefish species on the Plate, particularly the widely distributed endemics, convinced me of the importance of the Pacific Plate as a biogeographic region. I have arbitrarily divided the endemic species into three types: (1) widely distributed endemics occurring in numerous island groups or in widely separated island groups; (2) endemics limited to a few islands or island groups within a limited area on the Plate; and (3) single island or island group endemics. Types 2 and 3 endemics have been recognized often in the literature, but it is only recently (Collette, 1974; Springer, 1981a) that attention has been called to Type 1 endemics.

A list of the 48 Type 1 endemics that I have been able to determine is given in Table 2, and each is discussed or mentioned in the appropriate family account. There are undoubtedly many more Type 1 endemics, and colleagues actively revising Indo-Pacific fish groups continually apprise me of them. Examples of Type 1 endemics among invertebrates have been mapped in Figures 47, 48, 50, 51, and several others are mentioned in the discussion under "Other Organisms."

Most Type 2 endemics are confined to the southern islands of the Plate in the area between the Cook and Society islands in the west, and Pitcairn and Easter in the east. A high proportion of these islands are high islands (Figure 2). Examples of Type 2 endemics are *Heteroconger lentiginosus* (Congridae; Marquesas and Society Islands); *Chaetodon hemichrysus* (Chaetodontidae; Rapa and Pitcairn); *Cirrhitus wilhelmi* (Cirrhitidae; Rapa to Easter; see "possible new genus" on Figure 60); *Entomacrodus rofeni* (Blenniidae; Tuamotu, Henderson, and Ducie islands; Figure 8); a color-pattern type of *E. caudofasciatus* (Rarotonga to Ducie; Figure 7); *Centropyge hotumatua* (Pomacanthidae; Rapa to Easter; Figure 31); four species of Pomacentridae: *Stegastes emeryi* (Tuamotu and Pitcairn islands), *Chrysiptera galbus* (Cook to Pitcairn islands), *Pomachromis fuscidorsalis* (Society Islands to Pitcairn), and *P. exilis* (Eastern Caroline and Marshall islands); *Synodus capricornis* (Synodontidae; Pitcairn and Easter); *Cantherhines longicaudus* (Monacanthidae; Rarotonga and Tahiti); *Eviota epiphanes* (Gobiidae; Hawaiian, Johnston, and Line islands); *E. disrupta* (Tonga, Samoa, Society, and Tuamotu islands); *Mulloides mimicus* (Mullidae; Line and Marquesas islands); *Bodianus bilunulatus busellatus* (Labridae; Ducie, Henderson, and Marquesas islands; M.F. Gomon, 1979); *B. b. albotaeniatus* (Hawaiian and Johnston islands; perhaps, more appropriately considered as a Type 3 endemic); *B. loxozonus trotteri* (Line, Marquesas, Tuamotu, and Austral islands); *Labropsis polynesica* (Labridae; Rarotonga to Gambier Islands); *L. micronesica* (Guam, Palau, Ifaluk, Enewetak, and Kwajalein); *Pseudojuloides atavai* (Labridae; southeast Oceania); *Thalassoma* undescribed species (Heiser, 1981; Labridae; Ducie and Pitcairn); *Zebrasoma rostratus* (Acanthuridae; Tuamotu, Marquesas, Line, and Rapa islands). Cressey and Randall (1978) list three additional species that are confined to the islands from Rapa or Pitcairn to Easter: *Pseudolabrus fuentesi* (Labridae), *Gymnothorax nasuta* (Muraenidae), *Goniistius* (= *Cheilodactylus*) species (Cheilodactylidae).

The most common type of endemism on the Plate consists of Type 3 endemics, and most of these endemics occur at high islands. For instance, 29 percent of the 442 species of Hawaiian shorefishes, about 10 percent of the approximately 350 species of Marquesas Islands shorefishes, and about 27 percent of the 99 species of Easter Island shorefishes are Type 3 endemics (Randall, 1976, 1978a). The number of endemics present in these three island groups totals about 190, or about 14 percent of the estimated total number of shorefish species on the Plate. Although Easter Island is not on the Pacific Plate, it is close to the Plate's eastern margin, and I consider its fish fauna, which is most closely related to that of the rest of the Indo-Pacific (Randall, 1976), to be part of the Plate fauna. Rehder (1980) similarly related the molluscan fauna of Easter Island most closely to that of the Indo-Pacific. No recent compilation of Marquesas Islands fishes has been published. Randall's (1978a) assessment of endemism at these islands was based on his extensive knowledge of Indo-Pacific fishes, including his collecting expeditions to the Marquesas. Based on my investigations of blenniid fishes at the Marquesas, I can concur completely with Randall.

Examples of low-island Type 3 endemics are few, and most are known from one or a very few collections; probably they will be found to occur more widely. Some apparent low-island Type 3 endemics are: *Medusablennius chani* (Blenniidae; Raroia, Tuamotus; Figure 60), *Amphiprion tricinctus* (Pomacentridae; Marshall Islands; Figure 32), *Plectroglyphidodon flaviventris* (Pomacentridae; Tuamotus), *Acanthurus chronixis* (Acanthuridae; Kapingamarangi), *Cirricaecula johnsoni* (Ophichthidae; Enewetak, Figure 60); *Bodianus prognathus* (Labridae; Fanning, Line Islands).

The total number of the three types of endemics (species only; subspecies excluded) mentioned or alluded to in the previous discussion is equal to about 20 percent of the estimated nonmarginal Pacific Plate shorefish fauna. I predict that total endemism of shorefishes on the Plate will reach 22 to 25 percent. The information offered here is in direct contrast to generally held opinions that "the homogeneity of the Indo-Pacific [fish] fauna is at once apparent from the fact that great numbers of shore species exist from one end of it to the other" (Myers, 1940:203; Cohen, 1973:453). Great numbers, perhaps, but considering the great numbers of families, genera, and species that reach, but do not transgress the western margin of the Pacific Plate, and the large percentage of species that are restricted to the Plate, homogeneity is hardly descriptive at the species level. I would agree wholeheartedly, however, with recognition of the Indo-Pacific as a biogeographic unit, with the Pacific Plate distinguished as a major subunit.

The importance of knowing the sister-group relationships of the endemic species on the Pacific Plate, and the distributions of the sister groups, was mentioned in the discussion of the Reality Hypothesis, and the few Type 1 Pacific Plate endemics for which sister species could be surmised reasonably, were mentioned. If more information on sister-species relationships was generally available it would serve to direct our search for the mechanisms (vicariant events) that divided ancestral populations into separate subpopulations and allowed these subpopulations to diverge. For Indo-Pacific fishes, there is scant information on sister-group relationships. This deficit exists because cladistic analyses have begun to appear only recently in the literature, and because meaningful cladistic analyses of sister-group taxa are often exceedingly difficult to produce. Sister-species distributions and relationships for Types 2 and 3 endemic Plate species are also lacking, but information bearing on the origin of these types of endemics is known or can be hypothesized. In the sections that follow, I first treat the three main areas (Hawaiian, Easter, and Marquesas islands) of Type 3 endemism on the Pacific Plate, and follow these with a discussion of possible mechanisms in the formation of Types 1 and 2 endemics.

HAWAIIAN ISLANDS AND NORTH-SOUTH DISJUNCT DISTRIBUTIONS ON THE PACIFIC PLATE.—More is known about the geology and biology of the Hawaiian Islands than any other island area in the Indo-Pacific. A current geological view of the Hawaiian Islands is contained in Jackson et al. (1980), and some interrelated aspects of the geotectonics and biology of the Islands were discussed by Schlanger and Gillett (1976) and Rotondo et al. (1981). The latter paper will be treated in more detail in this section.

Knowledge of the geology and terrestrial biota, primarily the insects, of the Hawaiian Islands through 1948 was eloquently presented by Zimmerman (1948), and his treatise still merits attention. Like all previous and subsequent students of the Hawaiian biota, Zimmerman noted the high degree of endemism in the islands, which he attributed to their great geographical isolation. He gave a long and classical discussion of dispersal, which he emphasized as the primary mechanism by which the Hawaiian Islands obtained its biota. Interestingly, he accounted for adaptive radiations within the islands primarily by the mechanism of vicariant events. Zimmerman concluded that the geographical affinities of the greatest proportion of the terrestrial endemic biota was with the biota of the Polynesian region, which includes only islands on the Pacific Plate (see his fig. 26).

Van Balgooy (1971) published a comprehensive summary of plant biogeography in the Pacific. He stated (p. 116) that the "floristic alliance [of the Hawaiian Islands] is most pronounced with SE. Polynesia," but rephrased this statement (p. 128),

> Hawaii is another island group without any strong relations with other groups. The relatively high Kroeber coefficient [a measure of biotic similarity] with Clipperton I. is easily explained by the fact that nearly all the widespread Clipperton genera are also found on Hawaii. The same is true for Easter I. Leaving these out of consideration, Hawaii shows distinct but weak relations with some SE. Polynesian island groups: Marquesas, Society Is., S. Tuamotus and Rapa but not with the approximately equidistant E. Carolines and Marianas or Revilla Gigedo and Galapagos Is.

Van Balgooy concluded (p. 146), "The (archipelagic) connections of Hawaii towards Malesia appear not to have been direct through Micronesia, but by way of SE. Polynesia." The important point that van Balgooy makes is basically the same as Zimmerman made, that the closest biotic similarity of the Hawaiian Islands is with the islands of Oceania, particularly southeast Oceania. Whether this similarity is strong or weak is secondary. Van Balgooy refrained from trying to explain the distribution patterns he found, but noted significantly that the usual methods of dispersal did not seem to account for them (p. 143):

> In the present state of our knowledge I cannot find a clear correlation between distribution and dispersal. The impression is that the island plants "got there" despite lack of efficient dispersal ability rather than on account of superior dispersal capacity.

Kay (1967) indicated that the Hawaiian Mollusca showed a closer relationship with the wide-ranging Indo-West Pacific Mollusca than with Pacific Basin restricted Mollusca. Kay (in litt.) now informs me that a small proportion of the Hawaiian mollusks have their closest relationships (not cladistically determined) with mollusks on the Pacific Plate. In a fine essay on Pacific Basin biogeography, Kay (1980) presented a generalized explanation for the distribution patterns in that area. She drew upon recent geotectonic literature and the classical island biogeographic and ecological literature in proposing that a former, widely distributed, Mesozoic, or early Cenozoic, biota became isolated in the Pacific Basin, was variously extinguished because of changes in island morphology, positions, and climatically induced sea-level changes,[5] and is today repre-

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[5] Comment on interpreting the effects of paleoclimates on sea level is offered here because these effects have generally been invoked uncritically by biogeographers. For instance, Briggs (1974:427) stated that glacioeustatic sea-level changes would have affected the north Atlantic and north Pacific about equally. Perhaps, but geotectonic activity may have

sented by relict elements in isolated islands or island groups. Two of the studies Kay cited (Springer, 1981a; Rotondo, Springer, Scott, and Schlanger, 1981, cited by Kay as Rotondo and Scott, 1979) were unpublished at the time, and this fact is noted here to stress the original concepts independently arrived at by her and me, and to be further developed in this section.

Rehder (1980) reported that 10 percent of the well-studied mollusk species (99) that occur at Easter Island, which is on the Nasca Plate but close to the East Pacific Rise, are known otherwise only from the Hawaiian Islands. He reported that another 9 percent of the Easter Island species, consisting only of endemics, had their closest relationships (not cladistically determined) with Hawaiian species. Rehder's finding of a molluscan relationship between the Hawaiian Islands and Easter Island contrasts with van Balgooy's for plants. Van Balgooy's findings, however, were based on the generic taxonomic level, and a cladistic analysis of the species might provide a different conclusion. In any event, Rehder's findings provide added support for an Hawaiian–southeast Oceania relationship. Further support is found in the distribution of the marine water-striders (Insecta). *Halobates hawaiiensis* is known only from the Hawaiian Islands and the southeast Polynesian islands: Marquesas, Society, and Tuamotus (Cheng, 1973). *Halobates hawaiiensis* is not among the five species of *Halobates* that have invaded the open ocean (Cheng, 1973; Cheng and Shulenberger, 1980), and it is the only species of *Halobates*, other than some of the five oceanic species, that occurs in these four island groups.

The Hawaiian Islands–southeast Oceania type distributions are, perhaps, part of a general pattern of north-south disjunct distributions that has most often involved organisms restricted to continental seas. This pattern has been referred to variously as: bipolar, biboreal, bitemperate, antitropical, or antiequatorial, depending on how distant the disjunct populations are from the equator (see Ekman's, 1953, discussion of bipolarity). To explain the north-south disjunctions, some authors, such as Rehder (1980), have assumed that the low-latitude portions of the distributions of formerly widely distributed forms were eliminated. Rehder explained these eliminations by hypothesizing a combination of competitive exclusion (a difficult, if not impossible, hypothesis to corroborate and which has often been invoked) and drowning of centrally located islands. Island drowning, or changes in island morphology as proposed by Kay (1980), would have been enough. The fact that high islands on the Pacific Plate are today essentially restricted to southern Oceania and the Hawaiian Islands (excluding islands adjacent to the North American coast; Figure 2) and thus correlate with north-south disjunct distributions on the Plate corroborates the Kay-Rehder proposal (see section under "Extinction Hypothesis" for a geotectonic explanation of the distribution of high and low islands).

Other authors (most recently, Randall, in press b, for fishes) have proposed that higher latitude forms were able to cross the tropics during times when temperatures were cooler and the extent of the tropics considerably decreased. Briggs (1974) and others have commented, however, that the climatic history of the Indo-Pacific has been stable. Recent information bearing on the paleosea-surface temperatures is worth noting. A plot (CLIMAP Project Members, 1976, fig. 1) of sea-surface isotherms for the most recent glacial period, 18,000 years ago, for example, shows little shift toward the equator for the 20° C isotherms when compared with the 20° isotherms of today

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resulted in a different net effect in each area, or even in different parts of each area. Frakes (1979) summarized available information on the effects of past climates on sea level. He noted that it is possible presently only to recognize relative changes in sea level through time (p. 208): "It would be desireable to estimate the extent to which the sea has risen or fallen against a fixed bench mark but this is not possible because the landmasses themselves may have moved vertically in unison . . . vertical tectonic activity continuously affects the configuration of the sea floor itself. Glacioeustatic changes in sea level are recognized in the geologic record but *tectonic movements of one sort or another would appear to be responsible for most major changes in relative sea level*" (italics mine).

(Sverdrup et al., 1942, charts II and III), but there may have been greater temperature shifts in earlier Cenozoic times.[6] Frakes (1979) provided some general estimates of the equatorial surface temperatures during the Tertiary: 16–17° C in the Pacific at some time during the mid-Miocene (p. 214); 13° C in the eastern Pacific and 22° in the western Pacific at some time during the Oligocene (p. 194: fig. 7-3); 21° C in the eastern Pacific and 29° C in the western Pacific at some time during the Eocene (p. 193: fig. 7-2); 17–19° C for the global ocean during late Paleocene–early Eocene (p. 214). If the coolest of these temperatures existed in the equatorial regions of the Indo-Pacific, it would seem that the coral reefs would have been eliminated. It is known, however, that coral reefs have been continuously present at Enewetak, Marshall Islands, since at least early Miocene, and possibly since Eocene (Schlanger, 1963; Ladd, 1966). Reefs were present during early Eocene at Enewetak, but the Oligocene is represented by a hiatus. Even though Frakes stressed that all paleotemperature data should be used with caution because of problems in determination, and also noted that it may not be proper to assume that temperature requirements of organisms of the distant past can be inferred from the requirements of similar organisms today, I am skeptical, given the evidence, that north-south disjunct distributions on the Pacific Plate resulted from a depression of sea-surface temperature in the low latitudes on the Plate. For a recent, strong opinion to the contrary, but with no more direct data from the tropics than presented here, see Fleming (1979).

Another scheme that has been used often to explain north-south distributional disjunctions of marine forms is that of equatorial or isothermic submergence: cool-dwelling forms descend to deeper, cooler waters in equatorial regions and ascend to shallower waters once having traversed those regions. This mechanism may provide an explanation for the distribution of some eurybathic, strictly biboreal or bitemperate taxa (C.L. Hubbs, 1952), but it is doubtful that littorally restricted taxa, such as the blenniid fish *Entomacrodus niuafoouensis* (Figure 7) or the surgeonfish *Acanthurus leucopareius* (Figure 5), of the warmer antiequatorial regions on the Pacific Plate, are capable of isothermic submergence either as adults or larvae.

Rotondo et al. (1981) presented geological evidence to show that the Hawaiian Islands have incorporated volcanic edifices that originated to the southeast of the Hawaiian Islands. Using the geological data, they hypothesized a vicariant mechanism, island integration, to explain the origin of some of the endemism in the Hawaiian Islands. They offered island integration primarily as an alternative to founder principle (Mayr, 1942), a dispersalistic mechanism that is invoked most often to explain island endemism (for a dispersalistic view of endemism among Hawaiian fishes see Gosline, 1957, 1971). Island integration also may explain some north-south disjunct distributions on the Pacific Plate, particularly distributions involving the Hawaiian Islands and islands in southeast Oceania. Rotondo et al. outlined island integration as follows.

> Islands of the Hawaiian–Emperor chain have been forming intermittently during the past 70+ million years over a relatively fixed and isolated melting anomaly in the aesthenosphere below the rigid Pacific lithospheric plate. As the Pacific plate moved in a northwesterly direction over this anomaly, the islands and seamounts so formed were carried with the plate. Gradually, the islands subsided, eroded, formed atolls while in warmer waters, were then inundated, and those that reached the continental margin were subducted. Concurrent with the formation of some of the Hawaiian–Emperor chain islands, other island groups formed well to the SE on the Pacific plate close the East Pacific Rise. These latter islands shared a biota that was not present at/on the emergent Hawaiian Islands of the time. As the Pacific plate moved, many of these islands became deeply submerged, but a few may have remained emergent as volcanic islands or atolls, thus becoming relatively isolated. As a result of this isolation, components of their biota began to diverge (speciate). Ultimately, these emergent islands integrated

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[6] It seems unnecessary to push the origins of present-day distributions back beyond the Tertiary, as most modern family-level taxa of fishes appear to have originated no earlier than Lower Tertiary (Andrews et al., 1967). Most modern genera and species probably date little, if any, earlier than Miocene, where there is a preponderance of first appearances of modern, widely distributed taxa.

with emergent Hawaiian Islands, thus combining non-Hawaiian biotas with the Hawaiian. Continued isolation of the Hawaiian Islands reinforced the developing endemism, which we recognize today.

If this scheme is correct, and it is geologically reasonable, the relationships of the endemics so produced should exhibit their closest affinities with different elements of the biota on the Pacific Plate, particularly southeast Oceania. Undifferentiated elements of the integrated biota might also be shared only with southeast Oceania. Cladistic analyses of the Hawaiian biota are essentially nonexistent, but one can note, with much interest, the congruence of Zimmerman's and van Balgooy's generalized conclusions, and Rehder's distributional data, with an island integration hypothesis.

With regard to the littoral marine fishes, there are several patterns of relationships: (1) species that support direct relationships between Hawaiian Islands' endemics and non-Hawaiian Pacific Plate endemics; (2) apparently undifferentiated species that the Hawaiian Islands share only with islands to the south and east on the Pacific Plate, or near the Plate's southeastern margin; and (3) species groups whose individual species distributions have good potential for supporting Hawaiian Islands–southeast Oceania relationships, pending cladistic studies of the groups. Examples follow. A few taxa of shorefishes are known only from the Hawaiian Islands and relatively nearby Johnston Island. For the purposes of my study I consider these species to be Hawaiian endemics. Gosline (1955) considered Johnston Island to be an outlier of the Hawaiian fish fauna.

The littoral epipelagic halfbeak *Hyporhamphus acutus* (Figure 22) and the benthic, sand-dwelling creediid *Crystallodytes cookei* (Figure 60) each comprises two subspecies, and each is represented by an endemic subspecies in the Hawaiian and Johnston islands and an endemic subspecies that is widely distributed among, and limited to, the other islands of the Pacific Plate.

Springer (1967a) considered the Hawaiian endemic blenniid *Entomacrodus strasburgi* to be most closely related to *E. chapmani*, endemic to Easter Island (on the Nasca Plate near the East Pacific Rise), and *E. cymatobiotus*, widely distributed, but restricted to the islands of the Pacific Plate, excluding the Hawaiian and Easter islands (Figure 8). The halfbeak *Hemiramphus depauperatus* is known only from the Hawaiian, Line, and Marquesas islands (Parin et al., 1980). The trunkfish *Ostracion whitleyi* is known only from the Hawaiian, Johnston, Marquesas, Tuamotu, and Society islands (Randall, 1972b). The gobiid *Eviota epiphanes* is known only from the Hawaiian, Johnston, and Line islands (Lachner and Karnella, 1980). The gobiid *Kelloggella oligolepis* is known only from the Hawaiian and Easter islands (Figure 20).

Gomon (1979) recognized three subspecies for the labrid *Bodianus bilunulatus*: one endemic to the Hawaiian and Johnston islands, one restricted to the Marquesas, Henderson, and Ducie islands in southeast Oceania, and one ranging from the east coast of Africa to Japan, Philippines, Moluccas, New Guinea, and New Caledonia (hence, restricted to the Indo-West Pacific). If a cladistic analysis of these three subspecies should indicate that the Hawaiian-Johnston subspecies is the sister group of the subspecies in southeast Oceania, or the sister subspecies to a sister subspecies group formed by the subspecies in southeast oceania and the Indo-West Pacific, the relationships would be congruent with the island integration hypothesis. A sister-subspecies relationship between the Hawaiian subspecies and the Indo-West Pacific subspecies would not be congruent with the island integration hypothesis.

Under the family account of the Blenniidae, I have asserted the monophyly of three of the five species of *Enchelyurus*: *E. brunneolus*, endemic to the Hawaiian Islands, *E. ater*, ranging from Lord Howe Island east to the Tuamotus, and *E. kraussi*, ranging from the Red Sea and western Indian Ocean east to the Marianas, New Guinea, and Great Barrier Reef (Figure 10). I am unable to decide on the sister-species relationships within this group. If a future analysis supports a sister-species relationship between *E. brunneolus* and *E. ater*, or between *E. ater* and *E. kraussi*, the relationships would be congruent with the island integration hypothesis. A sister-species relationship involving *E. kraussi* and *E. brunneolus* would be incompatible with the island integration hypothesis.

Although the island integration hypothesis is straightforward, cladistic relationships that indicate congruence with the hypothesis could be misleading, because the same relationships may also be congruent with an extinction (or other) hypothesis, particularly where the area cladogram includes two antiequatorial (disjunct) areas on the Pacific Plate. To illustrate the problems, the following discussion[7] is presented and diagrammed (Figure 61).

The island integration hypothesis (Figure 61: Hypothesis I) presupposes that at Time Period 1 there was a uniform biota widely distributed on the Pacific Plate (Figure 61: P), or more widely, including southeast Oceania (Figure 61: S), but absent from the Hawaiian Islands (Figure 61: H). At Time Period 2, two possible vicariant events occurred, one of which is island integration (Figure 61: Hypothesis Ia) and one of which is not (Figure 61: Hypothesis Ib); in the latter case, southeast Oceania is isolated from the remainder of the Pacific Plate. In Time Period 3, according to Hypothesis Ia, a vicariant event isolated southeast Oceania from the remainder of the Pacific Plate, and according to Hypothesis Ib, island integration occurred. The area cladograms given at each time stage reflect the possible cladistic relationships of the endemic taxa formed as a result of the vicariant events.

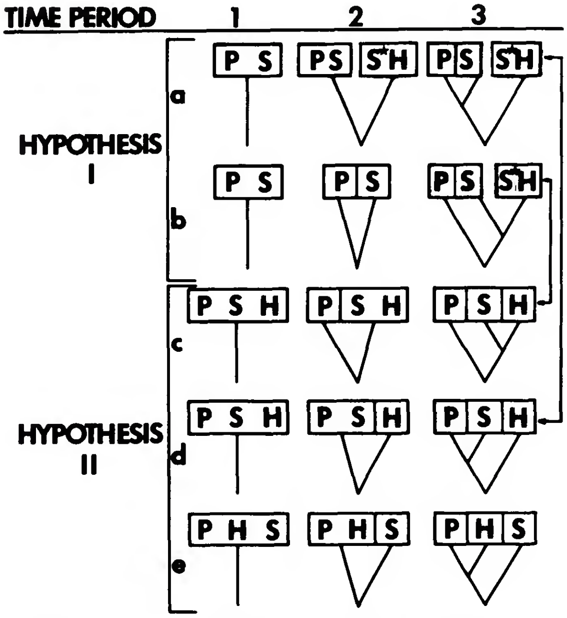

FIGURE 61.—Area cladograms for two hypotheses involving relationships of some Hawaiian Islands endemics (brackets on the left denote two hypotheses and embrace cladogram possibilities; pointed brackets on right indicate homocladograms; P = Pacific Plate islands less Hawaiian Islands and islands of southeast Oceania; S = islands of southeast Oceania; S* = islands of southeast Oceania that have integrated with Hawaiian Islands; H = Hawaiian Islands; see discussion under "Hawaiian Islands and North-South Disjunct Distributions on the Pacific Plate").

It is possible to arrive at two three-taxa cladograms that are identical with those resulting from island integration, but that are the result of a different set of vicariant events (Figure 61: IIc and IId). To arrive at these "homocladograms" it is necessary to hypothesize that there was a uniform biota that was widely distributed on the Pacific Plate (or more widely), including the Hawaiian Islands. A third area cladogram (Figure 61: IIe) can be developed from this same initial hypothesis that would result in a three taxa statement that is not compatible with the island integration hypothesis. In summary, there are five possible three-area cladograms that can be developed from the two initial hypotheses, and from these one can arrive at three three-taxa cladograms, of which only two are congruent with the island integration hypothesis. On what basis can one determine which of the cladograms of each homocladogram pair is to be preferred (i.e., Ia or IId; Ib or IIc), or in other words, how can one decide whether the antecedents of (some) Hawaiian Islands' endemics were part of an undifferentiated biota that included the Hawaiian Islands and other Pacific Plate islands, or only

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[7] I am indebted to R.P. Vari for the details of this analysis. A general discussion of the use of area cladograms in biogeography is provided by Platnick and Nelson (1978) and Nelson and Platnick (1981).

other Pacific Plate islands (a continental area could be added to, or replace Pacific Plate islands at time period one)? Unfortunately, there is no unequivocal answer to this question.

There is one other aspect of the distribution of Hawaiian Islands' fishes that may also have bearing on north-south disjunct distributions: the "Hawaiian exception." I have used this term frequently in the family accounts to denote Indo-Pacific taxa that occur nonmarginally on the Pacific Plate only at the Hawaiian Islands. These taxa usually occur also in Japan and/or the Ruykyu Islands, and many are antitropically distributed in the Indo-West Pacific; some are restricted to north of the tropics and some are moderately deep dwelling. In the following examples an asterisk denotes species discussed by Randall (in press b), but not in the family discussions herein: *Microcanthus strigatus* (Scorpididae), *Gonorynchus* (Gonorynchidae), *Sarda orientalis* (Scombridae), *Kentacapros aculeatus* (Aracanidae), *Cirrhitops fasciatus* (Cirrhitidae), *Oplegnathus fasciatus* and *O. punctatus* (Oplegnathidae), *Histiopterus acutirostris* (Pentacerotidae), *Malthopsis jordani*, *M. mitrigera*, and *Dibranchus stellulatus* (Ogcocephalidae), *Myripristis chryseres** and *Ostichthys archiepiscopus** (Holocentridae), *Seuzichthys* species (Labridae). These species probably dispersed from the Japanese area to the Hawaiian Islands via eddies from the Kuroshio extension, or in the case of the some of the deeper dwelling forms, possibly by dispersal northward from Japan along continental coasts to the Emperor Seamounts and down the Emperor Seamounts to the Hawaiian Islands. Ralston (1981) noted that the common southern Japanese angelfish, *Centropyge interruptus*, is otherwise known only from Kure, northern and westernmost of the Hawaiian Islands. He made reference to unpublished studies of E.S. Hobson and L.R. Taylor that indicated that the fish fauna of the northern Hawaiian Islands showed closer relationships to the Japanese fauna than to that of the southern Hawaiian Islands. In a case like *Pseudocaranx dentex* (Carangidae), which in the Indo-Pacific portion of its distribution is known only from Japan, Hawaiian Islands, southern Africa, Australia, New Zealand, Rapa, Pitcairn, and Easter (thus antiequatorially distributed; W.F. Smith-Vaniz, pers. comm.), antiequatoriality on the Pacific Plate may only be a secondary reflection of antiequatoriality that developed initially in continental areas (see also family account of Isonidae for another example).

With the exception of the young Eastern Caroline Island chain and Nauru and Ocean islands, high islands on the Pacific Plate, as noted earlier, are distributed antiequatorially (Figure 2). For ecological reasons other than temperature, then, one might expect antiequatorial distributions of organisms on the Plate. The distribution of the extant members of the land snail family Endodontidae (Figure 48) duplicates closely the distribution of high islands on the Plate. The presence of fossil endodontids of Miocene to Pleistocene age at Bikini and Midway atolls, where there are no extant endodontids, is evidence that these two islands were high during the times of endodontid extancy (Solem, 1977). Schlanger (1963) presented data in support of a statement written me (Schlanger, in litt.) that "entire atoll groups in the Pacific were high limestone island groups in Miocene and perhaps Eocene time as well as in Pleistocene time." The land snail data are congruent, therefore, with an hypothesis of extinction as an explanation for north-south disjunct distributions on the Plate.[8]

Before concluding discussion of north-south disjunct distributions I wish to call attention to the special case of antiequatorially distributed high-seas organisms.

Cheng (1973) and Cheng and Shulenberger (1980) detailed the distribution of the five high-seas species of the surface-dwelling insect genus *Halobates* (comprising 42 species). One of the five species, *H. sericeus*, which is confined to the Pa-

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[8] One can wonder at the biogeographical significance of the fact that the two fossil endodontid genera that occurred at the geographically somewhat intermediate Bikini Atoll were not contemporaneous, and that each of the genera is extant in a different island group: the lower Miocene *Cookeconcha* is extant only in the Hawaiian Islands; the Pliocene-Pleistocene *Minidonta* is extant only in southern Oceania.

cific, is antiequatorially distributed (Cheng and Shulenberger, 1980, fig. 2c). In the Northern Hemisphere, *H. sericeus* ranges along a broad swath from Taiwan and Japan to Mexico, and in the Southern Hemisphere, it ranges along a broad swath from Australia to off Chile. Cheng and Shulenburger noted that the distributions of *H. sericeus* and three of the other high-seas species of *Halobates* conform with the dominant oceanic surface current patterns, and in the case of *H. sericeus*, with two subtropical anticyclonic gyres. Numerous species of midwater zooplankton (Reid et al., 1978) and fishes (R.H. Gibbs, Jr., pers. comm.) have similar distribution patterns to that of *H. sericeus* (and the other three oceanic species of *Halobates*). Restriction of the zooplankton and fishes to these anticyclonic gyres is believed to be dependent on the physicochemical characteristics of the water. Whether the distribution of *H. sericeus* is similarly limited is not known. No mechanisms have been proposed to explain the distribution of *H. sericeus*, but those that have been proposed to explain the distributions of the other organisms are different from those so far discussed by me for the shorefishes (and implied by me for *Halobates hawaiiensis*; see early part of discussion in this section). Brinton (1962) suggested that a 2.5° C ocean-wide cooling (at 200 m depth) would permit southern gyre euphausids to transgress the equatorial regions in the eastern Pacific (only) and become established in the northern gyre. Subsequent warming would isolate certain organisms in the two gyres, resulting in antiequatorial distributions. Reid et al. (1978) believed that the southern gyre mixes with the equatorial current system in the eastern Pacific (only) and permits southern gyre organisms to enter the northern gyre. Because these organisms are adapted to the physiocochemical parameters of the gyres, it can be inferred that they cannot maintain populations in the convergence areas. I do not believe that either of these two mechanisms can be used to explain shorefish distributions.

EASTER ISLAND.—The first general acknowledgment that high endemism might be characteristic of Easter Island is that of Briggs (1974). No explanation for the endemism has been proposed, although the extreme geographic isolation of the island is usually mentioned as an implied explanation. In the following discussion I will propose a geotectonic hypothesis for Easter Island endemism.

The geology and tectonics of Easter Island and nearby Sala-y-Gomez were most recently discussed by Clark and Dymond (1977) and Bonatti et al. (1977). Much of the following discussion is based on geological information contained in these two studies. Most of the edifice ages I cite were published prior to 1977, and were compiled and assessed by Jarrard and Clague (1977).

Easter and Sala-y-Gomez rest on the Nasca Plate, which is forming at the East Pacific Rise and moving eastward to a subduction zone along the west coast of South America (Figure 1). Easter and Sala-y-Gomez are the westernmost edifices of an east-west oriented chain of edifices (Easter volcanic chain) that terminates 2400 km east with San Felix and San Ambrosio islands off the coast of Chile. There are no islands between these two pairs of islands, but there is a fairly dense band of seamounts between them (many of these seamounts appear on Figure 5, but more complete representation can be found in Mammerickx et al., 1975, fig. 1—a bathymetric chart of the east-central Pacific). Easter lies about 250 km east of the East Pacific Rise in an area where the spreading half-rate of the ocean floor is the fastest known (about 10 cm/yr; Herron, 1972). The ocean bottom on which Easter rests is in the region between magnetic anomalies 2 and 3, and would be about 3 m.y. old (Heirtzler et al., 1968, fig. 3). Easter Island cannot, therefore, be very old, and the age of its rocks confirm this. Subaerial volcanism at Easter occurred during three periods: 2.5, 0.9, and 0.4 m.y. ago. The spreading rate taken together with the earliest date for subaerial Easter Island volcanism suggest that Easter Island was formed at or adjacent to the East Pacific Rise (0.1 m/yr × 2.5 m.y. = 250 km, the distance between Easter Island and the crest of the East Pacific Rise today).[9]

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[9] Jackson et al. (1972) summarized available data on time

Sala-y-Gomez rests on ocean bottom in the region of magnetic anomaly 5, which has been dated at about 9 m.y. Only a few rocks from Sala-y-Gomez have been dated, and these provide ages of 1.3 and 1.9 m.y. While the latter age is considered a minimum for the island, and is based on a dredged sample, the former is based on subaerial samples and believed to indicate an average age for subaerial volcanism at Sala-y-Gomez. The spreading half-rate at anomaly 5 is only 5 cm/yr; thus, Sala-y-Gomez was probably formed close to its present location.

There are no dated rocks for San Ambrosio and San Felix, but volcanic activity at San Ambrosio last occurred in 1922, and sheer cliffs at San Felix are believed to indicate that it is at most only a few million years old. These two islands are, thus, near or at their location of origin. Only three of the over 50 seamounts between Sala-y-Gomez and San Felix have been dated: 8.0 m.y. (located presently about 1400 km east of the crest of the East Pacific Rise on ocean bottom with an age of 20 m.y.); 1.7 m.y. (1500 km east of the Rise, also on ocean bottom about 20 m.y); and 30 m.y. (about 2600 km east of the Rise on ocean bottom about 30 m.y.; therefore, this last seamount quite possibly originated near the crest of the East Pacific Rise).

It is apparent from these data that edifices in the Easter volcanic chain were not propagated from a single fixed mantle plume (hot spot), as were the Hawaiian Islands (however, see Rotondo et al., 1981, for exceptions). Two or more mantle plumes have been active, and edifices have been propagated intermittently for at least 30 m.y. Some, if not many, of the edifices (including some at each end of the chain) were islands that originated near the crest of the East Pacific Rise.

For the purposes of this discussion of Easter Island endemism, I hypothesize that islands have been appearing on the Nasca Plate near the East Pacfic Rise at the latitude of Easter Island for several million years. As erosion and subsidence drowned these islands, elements of their biota were able to disperse to a nearby, newly formed island.

The edifice chain including Ducie Atoll rests on the Pacific Plate and appears to commence about 300 km east of Ducie (or about 1200 km west of the East Pacific Rise), where a pair of seamounts is emplaced (Mammerickx et al., 1975, fig. 1) in the vicinity of magnetic anomaly 6 (20 m.y.). Between these seamounts and the East Pacific Rise the seafloor appears to be devoid of volcanic edifices (Figure 3), indicating that a volcanically quiet period has existed in this region of the Pacific Plate for about 20 m.y. There is a paucity of data for this region, however, and a remote possibility exists that other seamounts are present (Epp, 1978).

Ducie and Henderson atolls, the next edifices west of the paired seamounts, and the paired seamounts, have not been dated. Ducie and Henderson are emplaced on ocean floor about 20–27 m.y. in age, and must be much older than Pitcairn Island, the nearest aged edifice, which is little, if any, older than 0.95 m.y. (Duncan et al., 1974) and rests on ocean bottom about 30 m.y. in age. Few Pacific atolls have been dated but those that have are usually more than 10 m.y. old, and often more than 37 m.y. old (Jarrard and Clague, 1977). Mururoa Atoll, in the northern Tuamotus, appears to be an exception, and has been aged at 7 m.y. Schlanger and Gillett (1976) have shown that it takes about 15 m.y. for a high island in the Hawaiian chain to become an atoll, and this time period is probably reasonable for such conversions in other island chains. High islands are, expectedly, relatively young, with ages for those dated ranging generally from less than 1 m.y. to about 12 m.y. Exceptionally, Tubai, a high island in the Austral chain, has been dated at about 10.9±1 to 24.9±10 m.y., but there is some question about the data, and Mangaia, a high island in the Cook Islands, has been well dated at about 18 m.y. Mangaia has been greatly uplifted, and

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required to form Hawaiian volcanic shields: "The available evidence strongly suggests that the tholeiitic phase of volcanism on individual shields in the Hawaiian-Emperor chain may have a total lifetime of only 0.5 to 1.5 m.y., and the oldest K-Ar ages on subaerial tholeiitic flows . . . will be only slightly younger than the date of birth of these volcanoes." I have assumed that the rate of Easter volcanism is probably commensurate with that of the Hawaiian volcanoes; the age-distance data are reasonably congruent with this assumption.

the normal erosional processes and subsidence that would have converted it into an atoll or seamount have been offset (although it probably existed as an atoll in the past).

The aged edifice nearest to Pitcairn is in the high Gambier Islands group (4.7-7.1 m.y.) of the southern Tuamotu Archipelago. This archipelago, which otherwise consists almost entirely of atolls formed on a rise, arches northwest from Pitcairn Island and is continuous with the Line island chain (together called the Tuamotu-Line Rise by Morgan, 1972), apparently following an earlier pole of rotation (direction of movement) of the Pacific Plate. Morgan (1972) believed that the Tuamotu-Line Rise and the Sala-y-Gomez-Nasca Rise originated contemporaneously from the same hot spot on the crest of a spreading rise (East Pacific Rise). Morgan's hypothesized origin of the Tuamotu-Line and Sala-y-Gomez-Nasca rises has not survived (Bonatti et al., 1977; Clark and Dymond, 1977), but the contemporaneity and juxtaposed origins of the Tuamotu and Nasca portions of the rises on opposite sides of the East Pacific Rise at about the latitude of Easter Island still seems probable (H.W. Menard, pers. comm., April 1981), indicating that littoral conditions existed on the rise contemporaneously with littoral conditions in the Tuamotus, and ocean bottom ages in the two areas cover about the same time span.

Based on the previous discussion, I propose the following scenario to account for Easter Island endemism (a similar, but generalized scenario for Pacific island plants was proposed by Axelrod, 1972).

Until about 20 m.y. ago, there was a common biota inhabiting the islands of southeast Oceania on both sides of the East Pacific Rise at about the latitude of Easter Island. The uniformity of this biota was maintained in the face of diverging oceanic lithospheric plates (seafloor spreading) and the subsidence and drowning of islands on each side of the East Pacific Rise by the periodic formation of new islands within biotic dispersal distance on each side of the Rise. Island formation on the Nasca Plate in the vicinity of Easter Island has been continous, but about 20 m.y. ago, island formation on the Pacific Plate adjacent to the same vicinity ceased. Westward movement of the Pacific Plate gradually increased the distance between Pacific Plate islands and islands of the Easter volcanic chain until interchange between these two groups of islands was no longer possible. The resulting isolation of the more western islands of the Easter volcanic chain allowed many species in these islands to diverge, accounting for the high degree of endemism that we recognize today.

Within the Easter volcanic chain, the islands that appeared in the more central parts of the chain permitted dispersal of biotic elements to islands in the eastern portion of the chain. Subsequent drowning of these more central islands resulted in isolation of the easternmost islands, permitting elements of their biota to diverge (see following discussion). Because the present islands at the eastern end of the chain are young, they must have derived their endemic elements from now drowned islands. There are numerous seamounts in the vicinity of San Felix and San Ambosio (Mammerickx et al., 1975, fig. 1) that possibly served as biotic suppliers to these young islands. One particularly shallow seamount (hence, possibly drowned relatively recently) is shown in Figure 2).

The fishes and mollusks of Easter Island were discussed by Randall (1976) and Rehder (1980). These two groups of organisms exhibit 27 and 42 percent endemism, respectively. Although there are no cladistic studies of these organisms available, the general relationships of both groups are clearly with the fishes and mollusks of the central and western Pacific (see discussion of the Hawaiian biota in the previous section).

The mollusks and fishes of Ducie Atoll were reported by Rehder and Randall (1975). These two groups are represented overwhelmingly by species that also occur farther west. A few of the species are restricted to southeast oceania, and some of these range to Easter Island.

Nothing is known about the fishes of Sala-y-Gomez, and only three mollusk species have been reported from there, all common at Easter Island (Rehder, 1980). On the basis of nearness and small size of the island (maximum length 700 m, maximum width 400 m), one can expect that the biota of Sala-y-Gomez will be closely allied to, and a subsample of, that of Easter Island.

The closest islands to the east of Sala-y-Gomez are San Felix and San Ambrosio, which are 2400 km distant. I know of no faunal reports devoted to the mollusks or fishes of these two islands, although various revisions include mention of selected San Felix fishes. The most comprehensive collection of San Felix fishes (includes some types) resides at Scripps Institution of Oceanography. R.H. Rosenblatt provided me with a listing of the 31 species (not all identified to species) in the San Felix collection. As best I can determine, well over half of these species appear to be either endemic to San Felix or to San Felix and the Juan Fernandez Islands,[10] situated to the south of San Felix (Figure 2). About six of the species also occur on the mainland coast of the Western Hemisphere, and a few others range widely in the southern Pacific. The overall relationships of the fishes seem to lie more closely with western Pacific genera and species than with eastern Pacific genera and species. Greenfield and Woods (1980: 633–634) noted the same general geographical direction of the relationships for San Felix–Juan Fernandez fishes, based on the few available published references to these fishes and their own study of *Chromis meridiana* (Pomacentridae). Quite possibly, the strong, cold, northward flowing Peru Current along the west coast of South America prevents the eastward dispersal of San Felix–Juan Fernandez fishes to the South American coast.

The labrid fish genus *Pseudolabrus* is known from the coasts of Japan and China in the Northern Hemisphere, and from southeast Australia east to San Felix and Juan Fernandez islands in the Southern Hemisphere (B.R. Russell, pers. comm.). The single *Pseudolabrus* species at San Felix and Juan Fernandez islands is endemic (Russell and Randall, 1980), as is one of the two *Pseudolabrus* species at Easter Island (the other Easter Island species occurs otherwise only in southeast Oceania, including Pitcairn Island). Russell (pers. comm.) beieves that a Rapa Island endemic species of *Pseudolabrus* is the sister species of the Easter Island endemic. The distribution and supposed relationships of the *Pseudolabrus* species, thus, seem to support the scenario developed above to account for Easter Island endemism, and endemism at San Felix (and, perhaps, Juan Fernandez) Island.

In closing this discussion of Easter Island endemism, I wish to reiterate the fact that nine percent of the Easter Island mollusks and several species of the island's fishes are found otherwise only in the Hawaiian Islands. I explained this distribution pattern by invoking island integration (Rotondo et al., 1981; see discussion of Hawaiian Islands). Island integation and the scenario proposed here to account for the high degree of endemism at Easter Island are compatible.Taken together, they serve to demonstrate the complexity of geotectonic events in the Pacific Basin and how these events can complicate and contribute to the resolution of biotic distributions involving a few remote and well separated islands.

MARQUESAS ISLANDS.—The Marquesas Islands are a short (about 350 km long), relatively young, high-island chain increasing gradually in age from about 1.3 m.y. for Fatu Hiva at its southeastern end (Duncan and MacDougall, 1974) to about 5.1–8.7 m.y. for Eiao at its northwestern end (Brousse and Bellon, 1974; because of problems with argon enrichment, these authors preferred an average date of 6.3 m.y., but other authors citing their work—e.g., Jarrard and Clague, 1977, Epp, 1978—do not). The progression rate of the chain is about 10 cm/yr, so a presumed hot-spot origin of the chain would probably be not more than 300 km southeast of Fatu Hiva (Brousse et al., 1978, fig. 6), and perhaps as little as 12 km southeast (Duncan and MacDougall, 1974). Although there is no question about the youth of the Marquesas, the alignment of the chain, relative to alignments of the Hawaiian-Emperor chains, would indicate that the Marquesas were initiated more than 68 m.y. ago (Epp, 1978). For this reason, Epp conjectures that

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[10] In the Juan Fernandez Islands, Mas-a-tierra has been dated at 2.0–3.9 m.y. and 6±3 m.y., and Mas-afuera at 0.87–1.3 m.y., with two, apparently radiogenic Ar enriched, dates of 13 and 19.6 m.y. (Ferrara et al., 1969).

the Marquesas may be a recent group that took its alignment from a propagating fracture system that formed more than 68 m.y. ago, rather than from a hot spot. The Marquesas alignment, as would be expected in such a case, is perpendicular to the Marquesas Fracture Zone and the southeastern end of the islands almost abuts the Zone (Mammerickx et al 1975, fig. 1[11]), which tends to support Duncan and MacDougall's (1974) placing the origin of the chain only 12 km southeast. Such an origin would make Brousse and Bellon's 5.1–8.7 m.y. age for Eiao about 1.6–5.2 m.y. older than expected (350 km length ÷ 10 cm/yr propagation rate = 3.5 m.y., probable age for Eiao).

The Marquesas are separated from their nearest island neighbors, in the Tuamotus, by about 500 km. There are no seamounts that could have been littoral or subaerial and served as dispersal stepping stones between the Marquesas and any other islands. Even if the Marquesas were 300 km southeast of their present position at some time between 5.1 and 8.7 m.y. ago, and the Tuamotus are rotated (by eye) back up to 300 km along the Tuamotu alignment, the Marquesas do not appear to approach the Tuamotus more closely than they do today. The geographical isolation of the Marquesas, thus, appears to have remained the same during their entire existence.

Concerning the marine biota, the only list of Marquesas fishes is that of Plessis and Maugé (1978), which is uncritical, incomplete for the period covered, and contains numerous errors. Randall (1978a), based on his own collecting, estimated that 10 percent of the Marquesas fishes are endemics, and my own studies of the blenniid genera *Entomacrodus* and *Alticus* (Springer, 1967a; Smith-Vaniz and Springer, 1971) also indicate a high degree of endemism. There are no compilations of Marquesas mollusks, but Rehder (1968) estimated that 20 percent of the Marquesas mollusks are endemics. Next to the Hawaiian Islands and Easter Island, the Marquesas, thus, appear to exhibit the highest endemism for fishes and mollusks of any island or island group in Oceania. This high endemism is unexpected in view of the fact that the Marquesas are less isolated geographically than several other Pacific Plate islands that exhibit little or no endemism, for instance, Wake Island, Johnston Island (which, however, shares some endemics with the Hawaiian Islands, but has none of its own), Rapa and Marotiri (together), Malden and Starbuck, and Howland and Baker; Rapa and Marotiri, among these, are the only high islands.

There are other unexpected conditions existing in the Marquesas. In spite of the fact that the islands are situated between 07°S and 12°S latitude, well within the tropics, no marine groups are particularly well represented there. Coral reefs, which surround the other tropical islands of the Indo-Pacific, are reduced and present only in protected bays in the Marquesas (Chevalier, 1978). The lack of reefs undoubtedly limits the variety of the reef-associated biota. Brousse et al. (1978) discussed possible causes for this poor reef development, including those proposed by earlier authors. They were able to discount the importance of all proposed explanations, which included the following: rapid subsidence; absence of a shallow, pre-existing platform (necessary for colonization); cold water temperatures (surface waters range from 25.2° to 29.4°C, depending on time of year); hydrodynamic forces (heavy wave action); terrigenous deposition; and geographic isolation. They concluded that the reasons for poor reef development were unknown and proposed that the solution to the problem probably concerned physiochemical properties of the local seawater, for which they lacked information.

The general relationships of Marquesas fishes can be assigned to the Indo-Pacific, to which region many of the Marquesas genera and species are restricted. Formal cladistic relationships of the Marquesas endemics have not been proposed, but these relationships are clearly with other species on the Pacific Plate. For instance, according to Randall (1978a), "the fiery red angelfish *Centropyge loriculus* [a widely distributed Pacific Plate endemic] has lost its dark bars [which character-

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[11] This figure indicates that the fracture zone is separated into eastern and western segments with a broad discontinuity between the segments. The Marquesas abut the region of discontinuity.

ize the species at other Pacific Plate localities]," and Springer (1967a) considered *Entomacrodus macrospilus*, a Marquesas endemic, to be most closely related to *E. thalassinus*, which is widely distributed in the Indo-Pacific, but absent from the Marquesas (these two species share two specializations, synapomorphies, in *Entomacrodus*: absence of lip crenulae, smallest maximum size).Two other Marquesas endemic species of *Entomacrodus* (*E. randalli, E. corneliae*) appear to be most closely related to other Indo-Pacific species on the Pacific Plate that are absent from the Marquesas. Without pursuing this line of evidence further, I would propose that the ancestors of the Marquesas endemics were widely distributed and included in their range both the Marquesas and other Pacific Plate islands. A vicariant event occurred that isolated the Marquesas from the other islands on the Pacific Plate and allowed divergence of (at least) the Marquesas populations.

It is difficult to decide the nature of the vicariant event that gave rise to Marquesas endemism. Unlike the Hawaiian Islands and Easter Island, where geological information allows plausible vicariance scenarios, the Marquesas do not appear to have been isolated by a geological event, at least not in the same way as were those two other island groups. While there are probably several ways that could be proposed to isolate the Marquesas, I will present only two here, one geological, the other oceanographical; the first is, perhaps, less likely.

The existence of a former intra-Pacific Plate spreading ridge (Tamaki et al., 1979) and an inactive intra-Plate fracture system (Farrar and Dixon, 1981) have been proposed (the fracture system presumably split the Pacific Plate into eastern and western halves that underwent differential offsets). The ages of these two features are too old, more than 60 m.y., and their positions too removed to have affected the Marquesas Islands. If, however, younger, similar features should be found to have existed between the Marquesas and the Tuamotus, either type feature could have resulted in an increase in distance between the two island groups and effected their isolation.

For an oceanographical scenario, I propose the following: past local ocean currents (or eddies) that permitted biotic dispersal from the Tuamotu region to the Marquesas were gradually modified (deflected) and eliminated as the Marquesas increased in linear extent. It might be possible to test such a proposal by preparing a scaled model of the Pacific in the Tuamotu-Line islands region without the Marquesas, applying a fan-diven wind to simulate present-day wind circulation in the region, and then gradually adding the Marquesas Island lineation to see what effect it would have on the water movement. Surface currents around the Marquesas (Sverdrup et al., 1942, chart 7) indicate that present-day transport is generally from the Marquesas to the Tuamotus, thus isolating the former against "infection" from the latter, but, seemingly not the latter from the former. The coarse, general rendition of surface currents on charts can be misleading. For instance, localized, but persistent, eddies (Royce, 1978) can provide countercurrent transport, as can repeated, seasonal changes in current patterns. It would be desirable, therefore, to have detailed information on water transport in the Marquesas region.

The alternative to a vicariant event as an explanation for Marquesas endemism is founder principle (Mayr, 1942; critically reviewed by MacArthur amd Wilson, 1967, who combined it with founder effect). In a founder principle scenario, numerous different species would have independently dispersed to the Marquesas, each as a small propagule. Selection on descendants of each of these propagules would have had to operate rapidly in order that subsequent dispersal from the parent population of each species would not dilute the gene pool of the founding propagule's descendants. Additionally, the newly evolved taxa would have to competitively exclude subsequent dispersals from the parental population, otherwise both members of each pair of sister taxa would occur together, at least occasionally. There is no evidence that the sister species of any Marquesas Island endemic occurs in the Marquesas. For that reason and because of the repeated complex, multiple conditions necessary

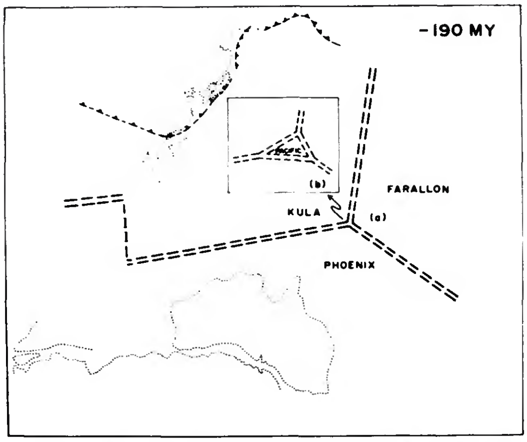

Fig. 3. (a) Plate, ridge, transform fault, and subduction zone locations in the Western Pacific at —190 m.y. (b) Pacific plate origin at about —185 m.y. Features shown in this figure and Figs. 4—7, except for Asia and Antarctica, are schematically located on a Mercator projection in their paleopositions as determined from paleomagnetic data. Because of the complex and less certain paleomagnetic determination for Asia and because Asia and Antarctica have apparently been subject to relatively little movement for most of the period of our reconstruction (—190 m.y. to present) when compared to the other plates involved, we have assumed they have remained fixed in their present positions.

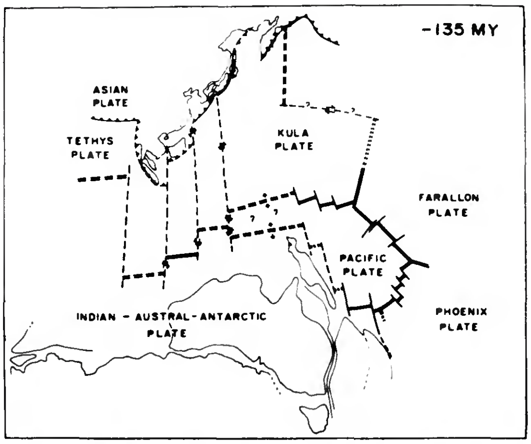

Fig. 4. Plate, ridge, transform fault and subduction zone locations at —135 m.y.

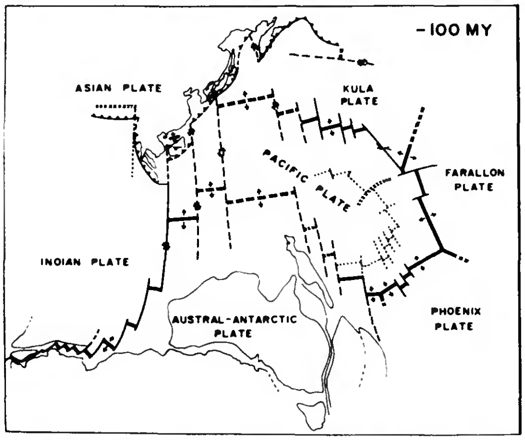

Fig. 5. Plate, ridge, transform fault and subduction zone locations at —100 m.y. The —135 m.y. magnetic lineation and fracture zone pattern of the Pacific plate is shown by short dashed lines.

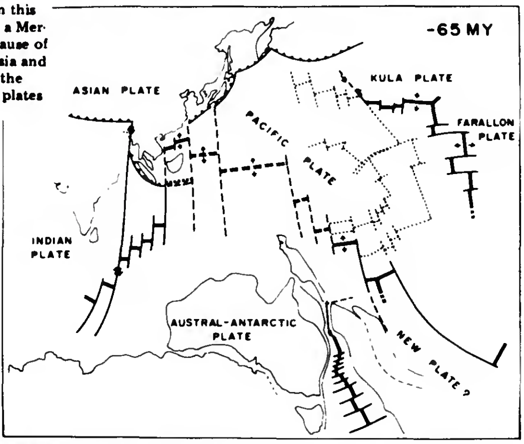

Fig. 6. Plate, ridge, transform fault and subduction zone locations at —65 m.y. The —135 m.y. and —100 m.y. magnetic lineation and fracture zone pattern of the Pacific plate is shown by short dashed lines.

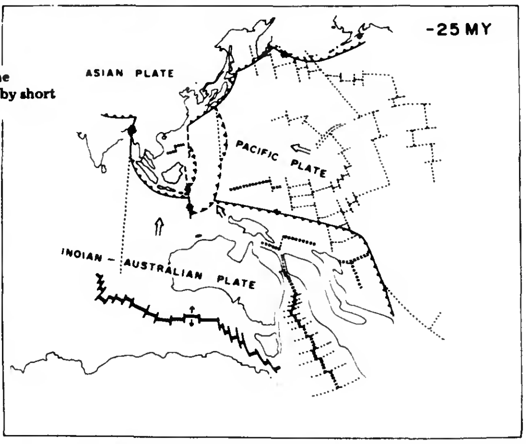

Fig. 7. Plate, ridge, transform fault, and subduction zone locations at —25 m.y. The —135 m.y., —100 m.y., and —65 m.y. magnetic lineation and fracture zone pattern of the Pacific plate and other inactive features are shown by short dashed lines.

FIGURE 62.—Hypothesized orgin and development of the Pacific Plate (from Hilde et al., 1977, figs. 3-7). Apices of triangles indicate direction of subduction; double lines indicate spreading ridges, associated arrows indicate direction of spreading; straight lines indicate transform faults, associated arrows indicate relative movement on either side of fault; open arrows denote direction of plate movements.

to establish and evolve each of the numerous Marquesas endemics under a founder principle scenario, I believe a vicariant explanation for the high degree of Marquesas endemism is preferable to one based on founder principle.

GEOLOGICAL HISTORY OF THE PACIFIC AND PHILIPPINE PLATES AND ADJACENT MARGINS AS RELATED TO FORMATION OF TYPES 1 AND 2 ENDEMICS.—The origin and general development of the Pacific Plate, particularly as pertains to the tectonically complex western portions, has been summarized by Hilde et al. (1977), and their account distilled by Uyeda (1977). A schematic presentation of their ideas is contained in Figure 62, which reproduces figs. 3–7 in Hilde et al. (1977; the same figures, except for the first, are also reproduced in Uyeda, 1977). These authors hypothesized that the formation of the Pacific Plate commenced about 190 m.y. ago, prior to the breakup of Gondwanaland. The oldest extant ocean bottom representing the Plate, however, is from the Upper Jurassic (Figure 4), and dates from about 160–140 m.y. ago. Older, non-extant portions of the Pacific Plate are believed to have been subducted below the continental areas that border the Plate's western margin. The propelling force that produces the northwestward movement of the Plate (Figure 1) from its active area of formation (East Pacific Rise) is not known.

Movement of the Plate, volcanism, transform faults, and subduction are major contributors to the topography of the Plate and areas along its western margin (Figure 3). Some island chains on the Pacific Plate appear to be ascribable to melting anomalies (hot spots, mantle plumes) in the aesthenosphere below the Plate. The hot spots are relatively fixed in position, and as the Plate moves, intermittent, basaltic volcanism occurs above the hot spots and gives rise to island chains (the magma forming the Plate at the East Pacific Rise is also basaltic). A change in the direction of movement (from NW to WNW) of the Plate (which occurred about 43 m.y. ago), is associated with subduction along the margin of the Asian Plate of a spreading rise that presumably existed as a western offset extending from the southern spreading rise of the Pacific Plate (Figure 62: fig. 5 shows this offset rise due east of Borneo) and is most recognizable by a bend in the Hawaiian-Emperor volcanic chain. Similar bends, although less obvious than the Hawaiian-Emperor bend, presumably appear in island chains that were being actively constructed more than 43 m.y. ago and continued forming after that time (this model has been modified by Farrar and Dixon, 1981, who proposed that the Pacific Plate was formerly split into eastern and western portions, and that rotation affected only the western portion and volcanic edifices, such as the Emperor chain, on that portion). Volcanic edifices have also appeared irregularly as the result of magmatic release along intraplate transform fault or fracture zones and at the East Pacific Rise. There was also an unexplained episode of massive Cretaceous volcanism over an extensive area of the Pacific Plate that produced numerous edifices, most of which are now drowned (for instance, the Mid-Pacific Mountains); some of the atolls of the Marshall and Line islands probably orginated during this episode (Schlanger and Premoli-Silva, 1981).

As the Pacific Plate moves, it gradually subsides into deeper water and subducts adjacent plates at deep trenches along its western margin. As the subducting Plate approaches the mantle under adjacent plate margins, it remelts and induces melting in the supra-adjacent mantle, which gives rise to andesitic volcanism on the margins of the obducting plates (Arculus, 1981). The western margin of the Pacific Plate, hence, delineates the Andesite Line of biogeographers and geologists (for an historical discussion of the Andesite Line see Appendix 1). Andesitic volcanism is the source of island arcs on the eastern margins of obducting plates. For unclear reasons, an island arc tends to divide along its longitudinal (volcanic) axis. The portion closest to the margin of the plate moves opposite to the direction of subduction, leaving a sunken, inactive (fossil, back arc) ridge behind the volcanically active frontal arc. Between the back arc and frontal arc is a widening sea basin. Hence, part of an island arc that formed adjacent to a continental plate margin may, with time, become increasingly distant from any land mass on the plate.

The account of the Philippine Plate (also known as the Philippine Sea Plate) that follows is distilled mostly from information contained in Hilde et al. (1977), Shih (1980), and Scott et al. (1981).

Late in the Paleozoic, before the formation of the West Philippine Basin (Figure 63), subduction presumably occurred along the eastern side of the Asian Plate giving rise to the Ryukyu Arc. Except for some Paleocene to early Oligocene igneous activity in the Ryukyu Arc, no volcanism occurred along that portion of the Asian Plate boundary until late Miocene, when spreading began in the Okinawa Trough behind (west of) the Arc (the Arc and Trough are not labelled on Figure 63). In the Mesozoic (Upper Cretaceous, Hilde et al., 1977; see their figs. 5 and 6 on my Figure 62) subduction presumably continued and consumed the proto-Pacific Plate along the Asian continental margin. Early in the history of the Pacific Plate it is believed that there were a series of transform faults extending north-south just west of the Pacific and Kula plates (Figure 62: fig. 4). These transform faults intersected the spreading rise that was continuous (with offsets) with the spreading rise forming the southwestern margin of the Pacific Plate. The two easternmost of these transform faults bordered a region of ocean bottom that was to become the West Philippine Basin of the Philippine Plate (Figure 63). Subduction along the margin of the Asian Plate of the spreading rise intersected by the transform faults occurred about 43 m.y. ago (noted above) and is associated with the change in direction of movement of the Pacific Plate and spreading behind the Oki Daito Ridge (Figure 63). This change in movement appears to have converted the easternmost of the two transform faults into a subduction zone (Pacific Plate subducting) that resulted in the formation of a rise (Palau-Kyushu Ridge, Figure 63), which entrapped the ocean bottom to the west (West Philippine Basin). The westernmost of the two transform faults was similarly converted into a subduction zone (West Philippine Basin subducting) along the Philippine Islands lineament. Sea-floor spreading about the Central Basin Ridge (Figure 63) to the west of the Palau-Kyushu Ridge, occurred prior to entrapment of the West Philippine Basin and continued for a short while after entrapment. The West Philippine Basin is believed to have moved north about 15°-20° and rotated clockwise about 50°-70° during the past 35-40 m.y. (Shih, 1980).

The West Philippine Basin and the basins and islands arcs to the east form the Philippine Plate (Figure 63; often called the Philippine Sea Plate). The formation of the eastern basins have a considerably different history from that of the West Philippine Basin. After formation of the Palau-Kyushu Ridge in middle Oligocene, volcanism continued on the active Ridge until early Miocene, terminating about 29 m.y. ago, when the Ridge sundered along its volcanic axis. The western segment of the sundered ridge became the inactive Palau-Kyushu Ridge, and the eastern segment (fore-arc) became the precursor of the West Mariana Ridge. Back-arc-basin spreading commenced between the two portions of the sundered ridge driving the fore-arc eastward and opening the Parece Vela Basin. The Shikoku Basin opened simultaneously, and it and the Parece Vela Basin are considered to be sections of a single, large marginal basin (Karig, 1975). There is no evidence of volcanism in the area for the period 29-20 m.y. ago. About 20 m.y. ago, island-arc volcanism began again, immediately behind the fore-arc, and formed the West Mariana island arc (ridge).

Formation of the Parece Vela Basin continued until sometime between 18 and 14 m.y. ago. About 11 to 9 m.y. ago, arc volcanism on the West Mariana Ridge subsided, and roughly 5 m.y. ago sundering of the Ridge formed the Mariana Trough and eastwardly displaced the new West Mariana fore-arc region, which eventually became the present Mariana Island Ridge. Subsidence of the Parece Vela Basin and the West Mariana Ridge occurred at the same time as the Mariana Trough was spreading, and continues to spread. In the Pliocene, volcanism began along the Mariana Ridge and has continued to

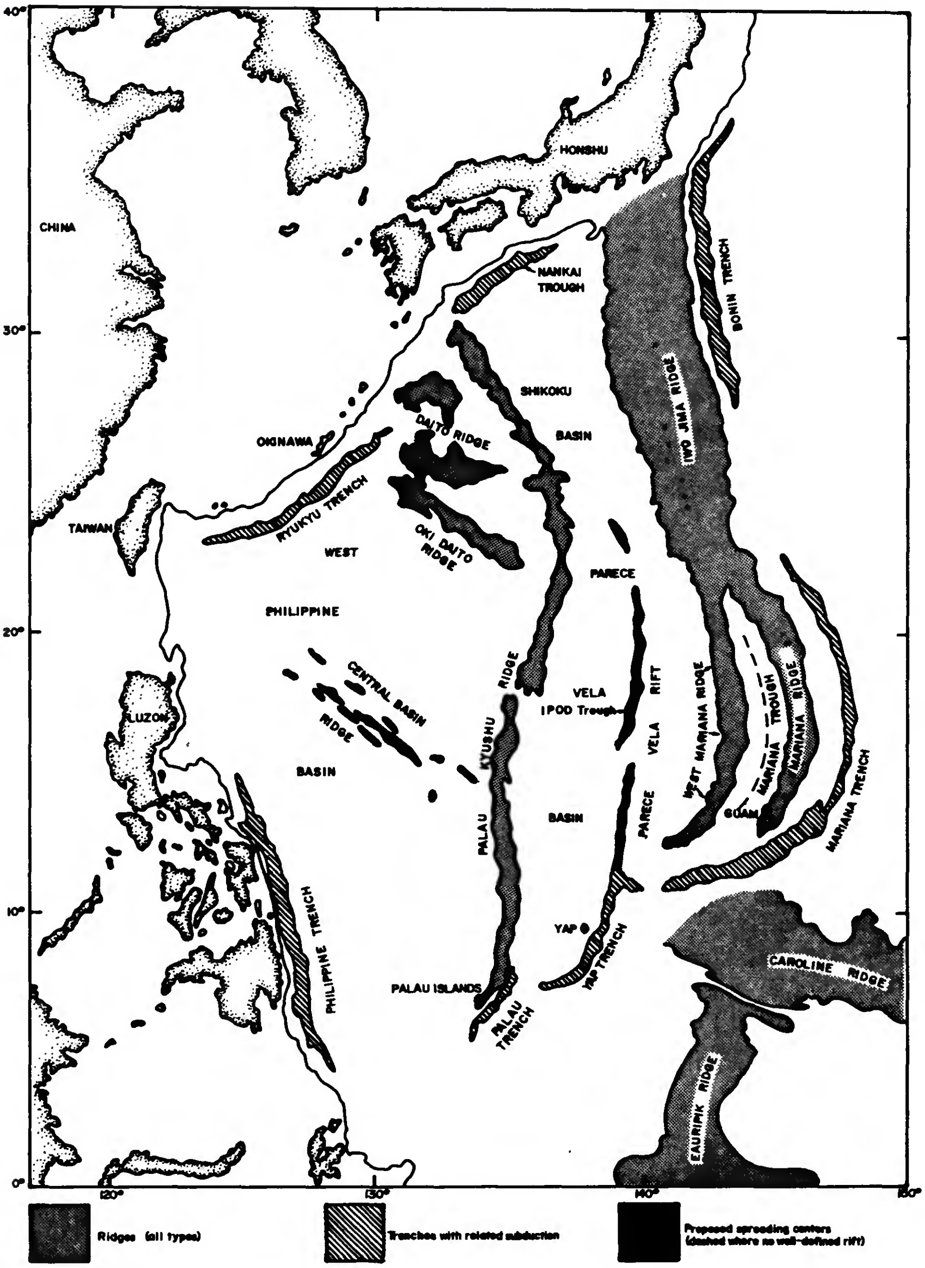

FIGURE 63.—Topographic features in the Philippine Plate area (redrawn from Scott et al., 1981, fig. 1).

the present. The Iwo Jima Ridge is a northern extension of the West Mariana and Mariana ridges, and it takes its origin from the combined Iwo Jima-Palau-Kyushu ridge of 25 to 18 m.y. ago (Karig, 1975). The Iwo Jima Ridge is presently in an early stage of sundering.

It can be surmised from the geologic history of the Marianas that these islands had their origin on the Palau-Kyushu Ridge about 40 m.y. ago and over 1000 km west of their present-day location. Sea-floor spreading that occurred after formation of the Palau-Kyushu Ridge, clockwise rotation, and considerable northward movement of the West Philippine Basin, probably indicate that the Marianas originated south and even further west, probably close to the Indonesian-Philippine arc systems (Karig, 1975). Species of continental origin would, consequently, have had a shorter distance to disperse to colonize the Marianas. If other (now subducted) islands existed on the Pacific Plate adjacent to the proto-Marianas, these in turn could have been colonized and led to the colonization of other Pacific Plate island groups. Later distancing, and associated rotation, of the Marianas created an islandless void between the Marianas and the continental coasts to the west. The void could have isolated the Pacific Plate in this region, at least, and contributed to subsequent divergence of the Plate biota (or the formation of Type 1 endemics). Myers and Shepard (1981) additionally attribute present-day isolation of the Marianas Islands from the continental coast to the prevailing westward flow of ocean currents in the region, making the islands net exporters of fish larvae, perhaps accounting for the western distributional limits in this region of taxa otherwise restricted to the Pacific Plate.

It is because of the integral association and development of the Philippine and Pacific plates that I treat distributions of Pacific Plate species having their western limits along the western margin of the Philippine Plate as Pacific Plate distributions.[12] In general, I believe such distributions to have been attained by westward dispersal from the western Pacific Plate margin. It appears that the species involved are uncommon on the western margin of the Philippine Plate, and one may question whether breeding populations exist (some examples: *Acanthurus achillies*, *A. leucopareius*, Figure 5). The Marianas also serve as the eastern distributional limits, in this region, of some otherwise continental plate limited taxa (for example, Terapontidae and Uranoscopidae, Figures 43 and 46).

The geotectonic history of the islands along the Pacific Plate margin extending from New Guinea to the Tonga Islands is highly complex, and much remains to be explained. These islands have been termed the Melanesian Borderlands by Coleman and Packham (1976), who attempted a regional geological synthesis. The discussion here is mainly limited to that portion of the margin extending from the New Hebrides to the Tonga islands. Most of the Type 2 endemics (see discussion of species endemism) I report from the Pacific Plate are limited to the islands ranging east from the Tonga Islands to Easter Island. If one presumes that the Type 2 endemics in the Polynesian area of today have sister taxa whose distributions extend westward from the Pacific Plate margin toward the Australian region, then one must also presume that the common ancestor of the two sister taxa had a distribution that included, at least, contiguous portions of the ranges of both sister taxa. A logical search for the vicariant event that divided the ancestral population would, then, be expected to have occurred in the general region of Australia (New Hebrides to Tonga islands). The same vicariant event could enforce the endemism of the widely distributed Pacific Plate endemics (Type 1).

With the possible exception of its north coastal portion, which may be an accreted arc segment, New Guinea has always been part of the Indian-Australian Plate, but the remaining islands of the Melanesian Borderlands formed variously during the past 80-odd m.y., probably as island arcs. The New Hebrides, Fiji, and Tonga islands are emplaced on a ridge that originated during the Eocene (at about the time Australia separated from Antarctica, about 50 m.y. ago) on the Australian side of a west-dipping subduction zone that marked the boundary between the Indian-Australian and Pacific plates. The present arrangement of the islands on the ridge is believed to be the result of fracturing of the ridge effected by complex tectonic processes. In some areas

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[12] Moberly, 1972:43, indicated the possibility that the northern part of the Philippine Plate was probably the old western part of the Pacific Plate.

subduction zones shifted westward reversing arc polarity, as occurred in the New Hebrides lineament.

The oldest rocks of Fiji are upper Eocene, of Tonga, pre-upper Eocene, of Lau, Miocene, and of the New Hebrides, Oligocene. Gill and Gorton's (1973, fig. 5) proposed reconstruction of the original ridge supporting these islands consisted of a northwest to southeast trending segment (the New Hebrides Ridge, on which the New Hebrides and Fiji islands were positioned) bent rather sharply at its eastermost limit and continuing as a southerly extending segment (the Lau-Tonga Ridge, on which the Lau and Tonga islands were positioned). The Lau-Tonga Ridge was probably continuous with the Kermadec Ridge (but today there is a discontinuity between the ridges), which supports the Kermadec Islands and continues to New Zealand.

The Lau-Tonga Ridge sundered along its volcanic (longitudinal) axis about 5.5 m.y. ago into the present-day Lau-Coleville Ridge to the west and Tongan Ridge to the east (these two ridges can be seen on Figure 3 extending north from New Zealand). The Lau-Coleville Ridge (a remnant arc) is currently inactive, but the volcanically active Tonga Ridge continues its eastward movement, carrying the Tonga Islands away from Fiji and over the edge of the Pacific Plate. During early separating, the Lau-Coleville Ridge moved westward, and the northern end of the Ridge together with Fiji underwent a counterclockwise rotation. The separation of Fiji and the New Hebrides is believed to have occurred earlier (Middle Miocene or Tertiary, 9–12 m.y. ago) than the Fiji-Tonga separation. Fiji today is much further from the New Hebrides than it was 9–10 m.y. ago.[13] It also appears that the eastward moving Tonga Islands and the westward moving Samoan Islands, which are on the Pacific Plate near the subduction zone, are much closer today than they were in the Miocene (if the Samoan islands were in existence then; the Samoan Islands have not been dated, but Hawkins and Natland, 1975, proposed an age of only 1 to 2 m.y., or less).

The Cenozoic history given here seems to be of little consequence for an explanation of today's biotic isolation of the Pacific Plate in the Polynesian area. While there is possibly pertinent information available that I have overlooked that might afford such an explanation, I must leave that for the future. Although I am reluctant to extend the search for an explanation to the pre-Cenozoic, it is possible that Cretaceous to Paleocene events are responsible for some Pacific Plate endemism. My reluctance stems from the fact that endemism of fishes (but not necessarily other groups) on the Pacific Plate is almost entirely restricted to the species level; whereas, the fossil record (limited to continental areas for fishes), in general, gives little evidence for the existence of extant generic taxa earlier than Eocene (Romer, 1966; I question whether many of the Eocene genera are correctly identified with the extant; my limited experience with fossil fishes would indicate that few extant genera are present prior to the Miocene). The following discussion presents a possible scenario for pre-Cenozoic vicariance events that could lead to Pacific Plate endemism.

Schlanger and Premoli-Silva (1981) and Schlanger et al. (1981) have reasonably defended the existence of a Cretaceous episode 110 to 70 m.y. ago of widespread volcanism on the Pacific Plate. The volcanism resulted in a regional uplifting of the Plate reminiscent of Menard's (1964) Darwin Rise. Subsidence has now drowned most, if not all, the islands that were formed, and increased the depth of the seamounts. Before subsidence the numerous volcanic edifices could have served as stepping stones (Schlanger et al., 1981, fig. 5) reaching from Australia across the Pacific Plate, and onto the now mostly subducted Farallon Plate (the Farallon and Pacific Plates shared a common spreading ridge, Figure 62, and, thus, the age progression of the ocean bottom

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[13] The movements that separated Fiji from the New Hebrides to the east and the Tonga Islands to the west may have been the vicariant events that permitted the development of endemic fish species in the area. Smith-Vaniz (1976) recognized the following endemic blenniids: *Meiacanthus bundoon*, *M. atrodorsalis ovalauensis*, *Plagiotremus laudandus flavus* (all from Fiji), and *Meiacanthus procne* (from Tonga).

on the two plates would form mirror images; the Farallon Plate split into the Cocos and Nasca plates during the Pliocene, Figures 1, 2, and 4). Schlanger and Premoli-Silva's (1981) evidence for the action of stepping stones is based on the presence of a benthonic, reef-associated fauna of large pseudorbitoid foramnifera known only from the Upper Cretaceous of Central America, the Line Islands, the Nauru Basin, and New Guinea. Later subsidence of edifices on the western portion of the Pacific Plate could have isolated the shallow-water and terrestrial biotas of the edifices to the east and allowed them to diverge. More recent island building on the Pacific Plate would have provided havens for the biota of subductng edifices; however, this would not allow for the extinction of the pseudorbitoid foramniferan fauna in the area, which may have entailed widespread, deep subsidence of the entire occupied area.

It is possible that the opening of the Tasman and Coral sea basins (Figure 2; sea-floor ages for these basins are indicated on Figure 4) were as important as subsidence for isolating the Pacific Plate biota. The Tasman Sea Basin began opening in the Upper Cretaceous, about 80 m.y. ago (Hayes and Ringis, 1973) and the Coral Sea Basin began opening in the Paleocene about 62 m.y. ago (Weissel and Watts, 1979). Both basins ceased opening in the Paleocene, about 56 m.y. ago (Weissel and Watts, 1979). The opening of these basins drove the margin of the Indian-Australian Plate perhaps as much as 1500 km east of the coast of Australia (personal inference based on current positions). If no islands that could have served as stepping stones were present in these basins during spreading, increased distance of Australia from islands on the western Pacific Plate margin could have served as a barrier to dispersal between the Indian-Australian and Pacific plates in this region. Islands along the New Hebrides to Tonga lineament would have been further distanced from Australia by opening of the South Fiji Basin (Figure 2) in Oligocene, about 29–35 m.y. ago (Watts and Weissel, 1977). Despite their remoteness from Australia, these islands have a decided continental component in their biota (Appendix 2: Table B, column A), which is explainable by dispersal from New Guinea along the closely spaced islands to Tonga, and even Samoa. Raven and Axelrod (1972), who were concerned with terrestrial biogeography, developed a partially similar scenario, postulating that Fiji was formerly much closer to Australia, but derived its continental biota, in part, by this continguity and, in part, by overwater dispersal from both Malaysia and Polynesia.

Schlanger et al. (1981) noted similarities in the geology of the Nauru Basin (area labelled 8 just west of New Guinea on Figure 4), on the western part of the Pacific Plate (Figure 1), and the Caribbean Plate, which has been considered a detached relic of the Darwin Rise (Mattson, 1969), hence, possibly a former part of the Farallon Plate (Figure 62). It is interesting to speculate that the seemingly anomalous distribution of iguanine lizards (Fiji, Tonga, Galapagos, Caribbean, and South America; none of the genera are trans-Pacific; G. Zug, pers. comm.) may be explained by Cretaceous stepping stones, but whether the stepping stones have anything to do with Pacific Plate endemic fish species, is another matter. At the risk of undermining my own reservations, it will be recalled that I mentioned in the discussion of the shark family Carcharhinidae, the difficulty of explaining how *Triaenodon obesus*, a sluggish, shallow-dwelling, obligate coral-reef inhabitant, which is widely distributed in the Indo-Pacific and otherwise known only in the eastern Pacific, came to be so distributed. Cretaceous stepping stones?

Epilogue

In my study I have attempted to mesh the relatively little that is known about the distributions and relationships of the shorefish fauna of the Pacific Plate with the relatively little that is known about the geotectonics of the Plate. The information available in both subject areas is greatly imperfect, but it is difficult for me not to draw certain conclusions. (1) A large proportion of the Indo-Pacific shorefish fauna is divided into two geologically associated types: continental lithospheric plate and oceanic lithospheric plate. The distinction is not as striking as the distinction between black and white, but there is only a narrow gray line that separates great expanses of the shades on either side. (2) If a Pacific Plate endemic taxon is widely distributed, there are often hints that its closest relative is to be found restricted, or nearly restricted, to a continental plate area, often including the joint continental and oceanic plate margins. If formal cladistic studies (now lacking) corroroborate these relationships, and I predict that they will, a causal relationship between present distributions and past geotectonic events along the joint continental and oceanic plate margins will be unavoidable.

Addendum

While this study was in press I had the opportunity to collect fishes in the Fiji Islands. I obtained the first records for Fiji of four shorefish families (specimens to be deposited at USNM): Acanthoclinidae (*Acanthoclinus hiatti*), Gobioididae (*Taenioides* sp.), Opistognathidae (*Opistognathus* sp.), and Schindleriidae (*Schindleria praematura*). The first two families were not indicated as expected to occur in Fiji (or New Caledonia), but the Opistognathidae and Schindleriidae were listed as expected (present or expected in New Caledonia) in Appendix 2, Table A. These new records increase by two the number of families present or expected in Fiji (Appendix 2, Table B; Figure 58). I now expect that the Acanthoclinidae and Gobioididae will also be found to occur in New Caledonia, thus increasing by two the number of families expected at that locality.

A.D. Lewis, Principal Fisheries Officer in Fiji, informed me that he had records, but no specimens, of *Rastrelliger* (Scombridae) from the Marshall Islands. J.E. Randall (pers. comm.), who has spent much time collecting in the Marshall Islands and is preparing a checklist of Marshall Islands fishes, has expressed doubt that *Rastrelliger* occurs in the Marshalls. Verification by specimens is desirable.

I am informed by J.I. Ford (in litt., June 1982) that he recently obtained the following genera of eleotridids and gobiids in the freshwaters of Ponape, Eastern Caroline Islands (specimens to be deposited at the Bishop Museum): *Ophiocara*, *Bunaka*, *Oxyeleotris* (all Eleotrididae), *Stigmatogobius* (= *Pseudogobius*?), *Pandaka*, *Sicyopus* (all Gobiidae). These genera represent first records for the nonmarginal area of the Pacific Plate, and give futher evidence for operation of the Caroline Islands conduit.

Appendix 1

The Andesite Line

Gutenberg and Richter (1939) stated that Suess (1888) was among the first to notice that there was a line of demarcation separating structures of two different types in the western Pacific, but it was Born (1932) who coined the term *Andesite-Linie*, which he illustrated on a map of the western Pacific (reproduced here as Figure 64). Born's intent was to stress the sharp difference in the composition of the rocks of the islands of the Pacific Basin from the rocks of the land masses to

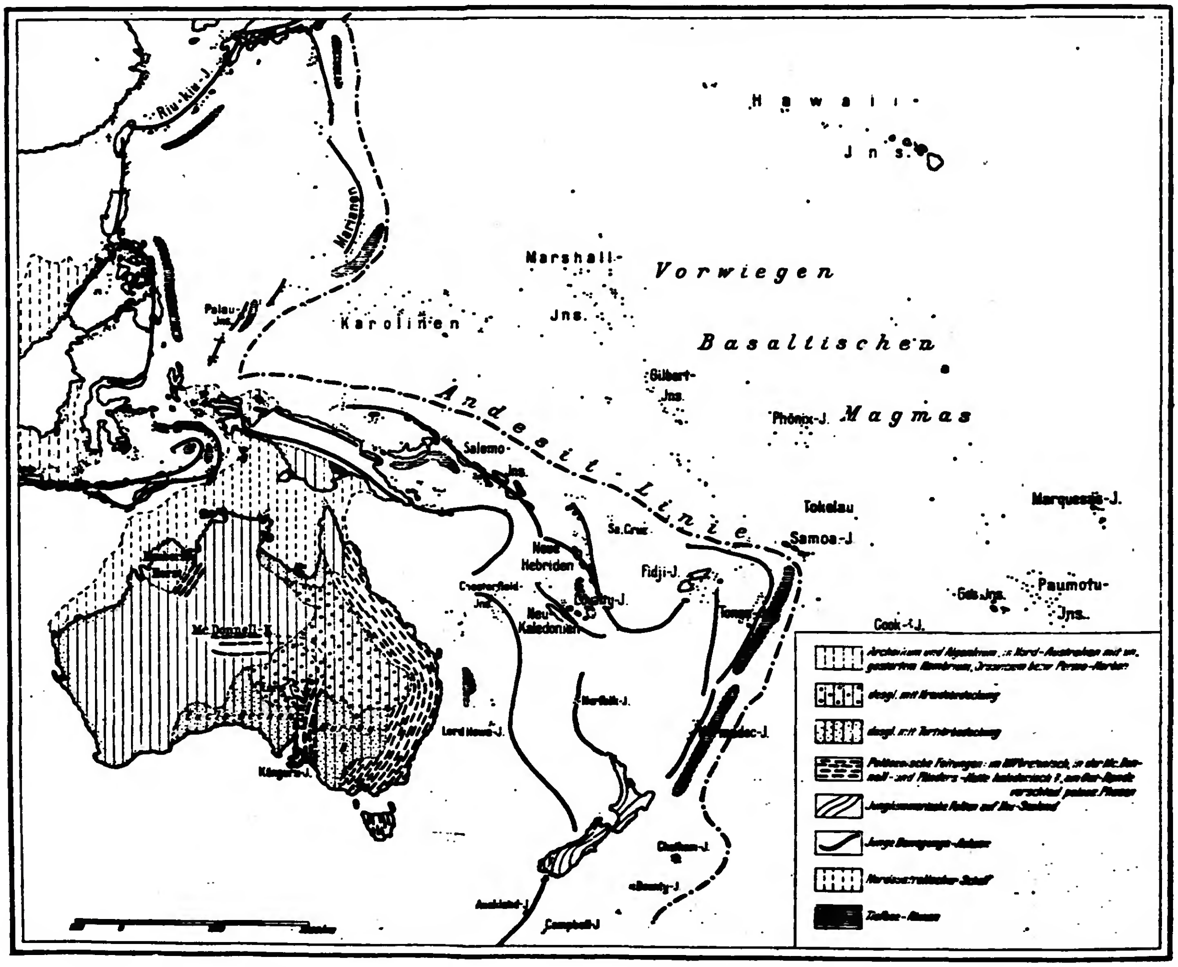

FIGURE 64.—The Andesite Line (from Born, 1932, fig. 306).

the west of the Basin. Born's term was incorporated into the geological literature, where it is still used, although Born's name is rarely associated with the term. Phytogeographers frequently mention the Andesite Line in passing, but seemingly have not found the feature meaningful. In contrast, the zoogeographical literature, and particularly the ichthyological, often invokes the Andesite Line as an important faunistic boundary, describing the easternmost limits of the distribution of Indo-Pacific species.

Chubb (1934), in a literature compilation of the limits of the "andesite zone" of the Pacific, did not refer to Born (1932). Chubb's Pacific Basin (1934, fig. 1), margined by andesite, represented, in effect, an extension of the Andesite Line around the northern Pacific and down the coast of the Western Hemisphere. Chubb's andesite zone in the western Pacific deviated from Born's by improperly including many of the Eastern Caroline Islands. Chubb, however, correctly included the Indian Ocean side of the Indonesian island arc in the zone.

Gutenberg and Richter (1941) stressed the strong association of Pacific Basin seismicity with the Andesite Line. The distribution of earthquake epicenters caused them to favor Born's delineation of the Andesite Line over Chubb's definition of the limits of the andesite zone, where the two conflicted.

MacDonald (1949) incorporated the Andesite Line (without mentioning the term), with a modification in the eastern Pacific, to define a hypothetical boundary of the Pacific Basin (Figure 65 reproduces MacDonald's figure 11). It is interesting, but not surprising, to note how closely MacDonald's Pacific Basin compares with present concepts of the Pacific Plate (Figure 1).

After MacDonald, the importance of andesite and the integrally associated patterns of seismicity were rapidly incorporated into the developing plate tectonic paradigm. The Andesite Line is

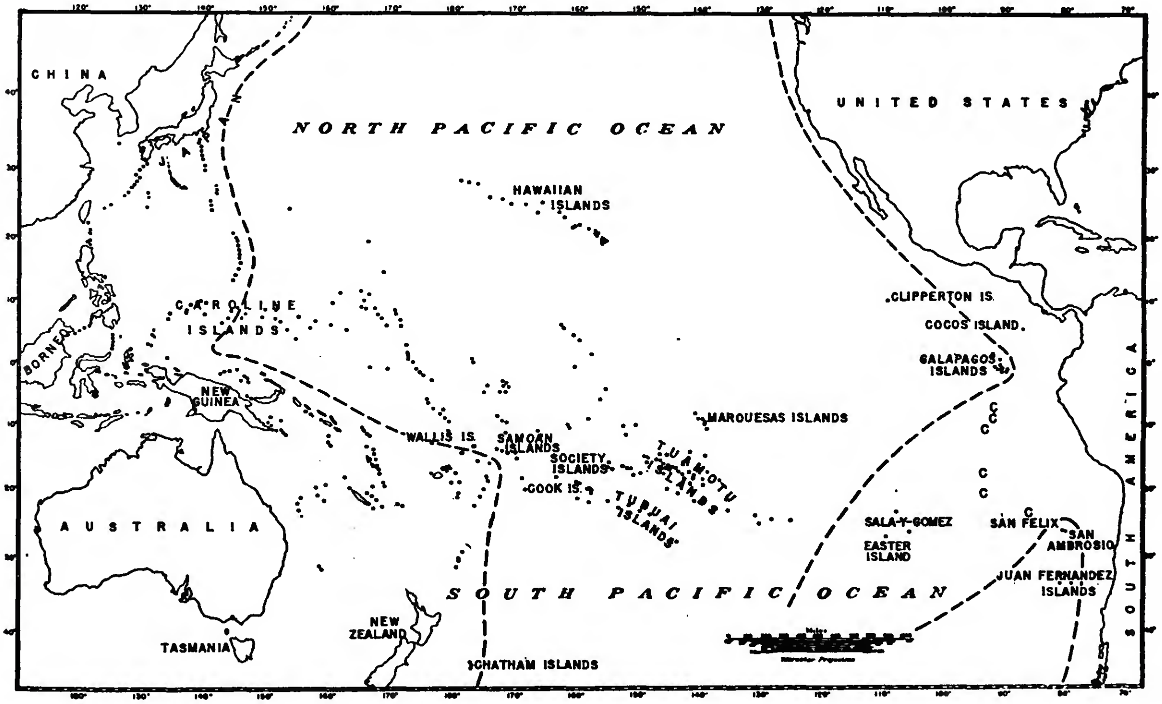

FIGURE 65.—The Andesite Line (from MacDonald, 1949, fig. 11).

still referred to frequently in the geological literature as a descriptive convenience. The current geological significance of the Line has been described by Holmes (1978:664).

> The boundary between the basalts of the oceanic crust and islands, and the andesite-dacite-rhyolite volcanic rocks of the circum Pacific belt, is called the andesite line, and it turns out to be essentially the boundary between the continental crust with sial and the oceanic crust without sial, and to follow the ocean trenches. The only exceptions to this generalization are due to the occurrence of a few isolated shreds and patches of sial left stranded in the Pacific floor, eg Macquarie Island and possibly Easter Island. The andesite line around the Pacific and its continuation around the Indonesian Arc is . . . "one of the fundamental geological boundaries" of the earth. It has turned out to be the line where oceanic lithosphere is subducting along Benioff zones.

The term "stranded" is open to question. Easter Island andesitic basalts are typical of those that may occur in other oceanic rocks of hot spot origin and are unlike the andesite of continental margins, hence they are not the result of stranding (Bandy, 1937; Bonatti et al., 1977).

For geological purposes, and probably biological also, the western margin of the Pacific Basin can be described best by the andesitic line of greatest seismicity, with a secondary margin along the boundary between the Philippine and Pacific plates. Born's Line must also be shifted to the east of the subduction zone in the region of the Solomon to New Hebrides islands, where arc polarity has been reversed.

The Andesite Line has also been referred to infrequently as the Sial Line or Marshall Line, but I have been unable to determine the origins of these designations, which are apparently more recent. I have not seen them used without indication that they are synonyms of the older term.

Appendix 2

Tables

Table A.—Distribution of the Indo-Pacific families (and one order and two suborders) of warm-water, marine shorefishes (A = absent from Pacific Plate except possibly marginally; B = present on Pacific Plate nonmarginally only in Hawaiian Islands; C = present on the Pacific Plate nonmarginally only in the Eastern Caroline Islands; D = present on the Pacific Plate nonmarginally other than only in the Hawaiian or Eastern Caroline Islands; AE = Africa, southeast coast; IM = Indo-Malayan region; PI = Philippine Islands; NG = New Guinea and Bismarck Archipelago; QD = Queensland; GU = Guam; PO = Ponape; MI = Marshall Islands; HI = Hawaiian Islands; NC = New Caledonia and New Hebrides; FI = Fiji Islands; SA = Samoan Islands; SI = Society Islands; RI = Rapa Island; DI = Ducie Island; EI = Easter Island; + = applicable distribution pattern; X = present; 0 = expected; – = absent; * = questionably characterized as shorefishes; ** = questionably characterized as warm-water inhabitants)

Family, Suborder, Order	A	B	C	D	AE	IM	PI	NG	QD	GU	PO	MI	HI	NC	FI	SA	SI	RI	DI	EI
Acanthoclinidae				+	X	X	X	0	X	–	0	X	–	–	–	–	–	–	–	–
Acanthuridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Albulidae				+	X	X	X	X	X	0	0	–	X	X	0	X	X	X	–	–
Ambassidae			+		X	X	X	X	X	–	X	–	–	X	X	X	–	–	–	–
Ammodytidae**				+	X	–	–	X	X	–	–	–	X	–	–	–	–	–	–	–
Anguillidae				+	X	X	X	X	X	X	X	–	–	X	X	X	X	X	–	–
Anomalopidae				+	0	X	X	X	–	X	0	X	–	X	X	X	–	–	–	–
Antennariidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	X
Aploactinidae	+				X	X	X	X	X	–	–	–	–	0	X	–	–	–	–	–
Apogonidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aracanidae*		+[a]			X	–	–	–	X	–	–	–	X	–	–	–	–	–	–	–
Ariidae	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Atherinidae				+	X	X	X	X	X	X	X	X	X	X	X	X	0	X	–	–
Aulostomidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Balistidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Batrachoididae	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Belonidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Blenniidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Bothidae				+	X	X	X	X	X	0	X	X	X	X	X	X	X	X	X	X
Brachaeluridae	+				–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–
Branchiostegidae	+				X	X	X	0	X	X	–	–	–	X	0	–	–	–	–	–
Bregmacerotidae*				+	X	X	X	X	X	X	0	X	X	0	X	0	–	–	–	–
Bythitidae				+	X	X	X	X	X	X	X	X	X	X	0	X	–	–	X	–
Caesionidae				+	X	X	X	X	X	X	X	X	–	X	X	X	X	X	–	–
Callionymidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Caracanthidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Carangidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Carapidae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	–	–	–
Carcharhinidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Centriscidae			+		X	X	X	X	X	–	X	–	–	X	–	–	–	–	–	–
Centropomidae	+[b]				–	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Cepolidae	+				X	X	X	X	X	–	–	–	–	X	–	–	–	–	–	–
Chaetodontidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chanidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Cheilodactylidae				+	X	–	–	–	X	–	–	–	X	X	–	–	–	X	–	X
Chirocentridae	+[b]				X	X	X	X	X	–	–	–	–	X	X	–	–	–	–	–

TABLE A.—Continued

Family, Suborder, Order	A	B	C	D	AE	IM	PI	NG	QD	GU	PO	MI	HI	NC	FI	SA	SI	RI	DI	EI
Cirrhitidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Citharidae*	+				X	0	X	0	–	–	–	–	–	–	–	–	–	–	–	–
Clinidae	+				X	X	X	–	X	–	–	–	–	X	–	–	–	–	–	–
Clupeidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Congridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	X
Congrogadidae	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Coracinidae* *	+				X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coryphaenidae				+	X	X	X	X	X	X	0	X	X	X	X	X	0	X	0	0
Creediidae				+	X	X	0	0	X	0	0	X	X	0	0	X	X	0	X	X
Cynoglossidae		+[a]			X	X	X	X	X	–	–	–	X	–	–	–	–	–	–	–
Dactylopteridae				+	X	X	X	X	X	X	0	–	X	X	X	X	X	X	–	–
Dasyatididae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	–	–	–
Diodontidae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	X	X	X
Drepanidae	+[b]				X	X	X	X	X	–	–	–	–	0	0	X	–	–	–	–
Echeneididae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	X	0	X
Eleotrididae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–	X
Elopidae				+	X	X	X	X	X	X	0	0	X	X	X	X	X	–	–	–
Emmelichthyidae*		+[a]			X	–	X	–	–	X	0	–	X	–	–	–	–	–	–	X
Engraulididae				+	X	X	X	X	X	X	0	0	X	X	X	X	X	–	–	X
Enoplosidae* *	+				–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–
Ephippididae				+	X	X	X	X	X	X	X	X	–	X	X	X	X	–	–	–
Exocoetidae*				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0	X
Fistulariidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Formionidae	+[c]				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Gerreidae				+	X	X	X	X	X	X	X	X	–	X	X	X	–	–	–	–
Ginglymostomatidae				+	X	X	X	X	X	X	0	X	–	X	X	X	X	–	–	–
Girellidae* *	+				–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	X
Glaucosomatidae	+				–	–	X	–	X	–	–	–	–	–	–	–	–	–	–	–
Gobiesocidae				+	X	X	X	X	X	X	0	X	–	X	X	X	–	–	–	–
Gobiidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gobioididae			+		X	X	X	X	X	X	X	–	–	–	–	–	–	–	–	–
Gonorynchidae* *		+			X	–	–	–	X	–	–	–	X	–	–	–	–	–	–	–
Grammatidae		+[d]			X	X	X	–	–	–	–	–	X	X	–	–	–	–	–	–
Gymnuridae	+				X	X	X	–	X	–	–	–	–	–	–	–	–	–	–	–
Haemulidae				+	X	X	X	X	X	X	X	X	–	X	X	X	X	X	–	–
Harpadontidae	+				–	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Hemiramphidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0	X
Hemiscylliidae	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Heterodontidae	+				X	X	–	–	X	–	–	–	–	–	–	–	–	–	–	–
Holocentridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Isonidae				+	X	–	–	–	–	–	–	–	X	0	–	X	–	–	–	–
Istiophoridae*				+	X	X	X	X	X	X	0	0	X	X	0	X	X	X	0	X
Kraemeriidae				+	X	0	X	X	X	X	0	X	X	0	0	X	X	–	–	–
Kuhliidae				+	X	X	X	X	X	X	X	X	X	0	X	X	X	X	X	X
Kurtidae	+				–	X	–	X	X	–	–	–	–	–	–	–	–	–	–	–
Kyphosidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Labracoglossidae* *				+	–	–	X	–	–	–	–	–	–	0	X	–	–	X	–	X
Labridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lactariidae	+				–	X	X	X	X	–	–	–	–	0	X	–	–	–	–	–
Lamnidae*				+	X	X	X	0	X	0	0	X	X	X	X	X	X	X	0	X
Leiognathidae			+		X	X	X	X	X	X	X	–	–	X	X	–	X	–	–	–
Leptobramidae	+				–	–	–	X	X	–	–	–	–	–	–	–	–	–	–	–
Lethrinidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–

TABLE A.—Continued

Family, Suborder, Order	A	B	C	D	AE	IM	PI	NG	QD	GU	PO	MI	HI	NC	FI	SA	SI	RI	DI	EI
Lobotidae				+[e]	X	X	X	X	X	–	X	–	X	0	X	–	–	–	–	–
Lophiidae*		+[a]			X	X	X	–	X	–	–	–	X	–	–	–	–	–	–	–
Lutjanidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Malacanthidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Menidae	+[c]				X	X	X	X	X	–	–	–	–	0	X	–	–	–	–	–
Microdesmidae				+	X	X	X	X	X	X	X	X	X	0	X	X	X	–	–	–
Mobulidae				+	X	X	X	X	X	0	0	X	X	X	0	0	X	X	–	–
Monacanthidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Monocentrididae	+				X	X	X	–	X	–	–	–	–	–	–	–	–	–	–	–
Monodactylidae			+		X	X	X	X	X	X	X	–	–	X	X	X	–	–	–	–
Moridae* **				+[f]	X	X	X	X	0	–	–	–	X	0	X	–	–	X	–	–
Moringuidae				+	X	X	X	X	X	X	X	X	X	0	X	X	X	X	X	X
Mugilidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	–
Mugiloididae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Mullidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Muraenesocidae	+				X	X	X	X	X	–	–	–	–	0	X	–	–	–	–	–
Muraenidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Myliobatididae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	–	–	–
Nemipteridae				+	X	X	X	X	X	X	X	X	–	X	X	X	–	–	–	–
Neostethidae	+				–	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–
Nomeidae*				+	X	X	X	0	X	X	0	X	X	0	0	0	–	–	–	–
Notograptidae	+				–	–	–	X	X	–	–	–	–	–	–	–	–	–	–	–
Odontaspididae		+[a]			X	0	–	–	X	–	–	–	X	–	–	–	–	–	–	–
Ogcocephalidae*		+[a]			X	X	X	X	X	–	–	–	X	–	–	–	–	–	–	–
Ophichthidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ophidiidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	X
Opistognathidae	+				X	X	X	X	X	–	–	–	–	X	0	X	–	–	–	–
Oplegnathidae**		+			X	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–
Orectolobidae	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Ostraciidae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	X	0	X
Pataecidae**	+				–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–
Pegasidae		+[g]			X	X	X	X	X	X	–	–	X	X	–	–	–	–	–	–
Pempherididae				+	X	X	X	X	X	X	X	X	–	X	X	X	X	X	X	–
Pentacerotidae* **		+			X	–	X	X	–	–	–	–	X	–	–	–	–	–	–	–
Pholidichthyidae	+				–	X	X	X	–	–	–	–	–	X	–	–	–	–	–	–
Platycephalidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	–	–	–
Plesiopiodae				+	X	X	X	X	X	X	X	X	–	X	X	X	–	–	–	–
Pleuronectidae				+	X	X	X	X	X	0	0	X	X	0	X	X	X	–	–	–
Plotosidae	+[e]				X	X	X	X	X	–	–	–	–	X	X	X	–	–	–	–
Polynemidae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	X	–	–
Pomacanthidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pomacentridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pomatomidae	+				X	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–
Priacanthidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pristidae	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Psettodidae*	+				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Pseudochromidae				+	X	X	X	X	X	X	X	X	–	X	X	X	–	–	–	–
Pseudotrichonotidae	+				–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rachycentridae	+[b]				X	X	X	X	X	–	–	–	–	–	–	–	–	–	–	–
Rajoidei (suborder)	+				X	X	X	–	X	–	–	–	–	–	–	–	–	–	–	–
Rhinobatoidei (suborder)	+				X	X	X	X	X	0	–	–	–	X	X	X	–	–	–	–
Rhinoprenidae	+				–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–
Rhinopteridae	+				X	X	X	–	X	–	–	–	–	–	–	–	–	–	–	–

TABLE A.—Continued

Family, Suborder, Order	A	B	C	D	AE	IM	PI	NG	QD	GU	PO	MI	HI	NC	FI	SA	SI	RI	DI	EI
Scaridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Scatophagidae			+		X	X	X	X	X	-	X	-	-	X	X	-	-	-	-	-
Schindleriidae				+	X	0	0	X	0	0	0	X	X	0	0	X	X	-	-	-
Sciaenidae	+[b]				X	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-
Scombridae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Scorpaenidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Scorpididae		+			X	-	-	-	X	-	-	-	X	X	-	-	-	-	-	-
Scyliorhinidae		+[a]			X	X	X	-	0	-	-	-	X	-	-	-	-	-	-	-
Serranidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Siganidae				+	X	X	X	X	X	X	X	X	-	X	X	X	X	X	-	-
Sillaginidae	+				X	X	X	X	X	-	-	-	-	X	-	-	-	-	-	-
Soleidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	-	-	X
Solenostomidae				+[h]	X	X	X	X	X	X	0	X	-	0	X	-	-	-	-	-
Sparidae	+				X	X	X	X	X	-	-	-	-	X	-	-	-	-	-	-
Sphyraenidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-	-
Sphyrnidae				+	X	X	X	X	X	X	0	X	X	X	X	X	X	X	-	-
Squatinidae	+				X	-	0	X	-	-	-	-	-	-	-	-	-	-	-	-
Stegostomatidae	+				X	X	X	0	X	-	-	-	-	0	X	X	-	-	-	-
Stromateidae	+				X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Syngnathidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-	X
Synodontidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Terapontidae	+				X	X	X	X	X	-	-	-	-	X	X	X	-	-	-	-
Tetraodontidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0
Torpediniformes (order)		+[a]			X	X	X	-	X	-	-	-	X	-	-	-	-	-	-	-
Toxotidae	+				-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-
Triacanthidae	+				-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-
Triakidae	+				X	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-
Trichiuridae[b, i]	+				X	X	X	X	X	-	-	-	-	X	X	-	-	-	-	-
Trichonotidae[j]				+	X	X	X	X	X	X	0	X	-	X	X	-	-	-	-	-
Triglidae	+				X	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-
Triodontidae*	+				X	X	X	0	-	X	-	-	-	X	X	X	-	-	-	-
Tripterygiidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-
Trypauchenidae	+				X	X	X	X	X	-	-	-	-	-	X	-	-	-	-	-
Uranoscopidae	+				X	X	X	X	X	X	-	-	-	-	X	X	-	-	-	-
Urolophidae		+[a]			X	X	-	X	X	-	-	-	X	-	-	-	-	-	-	-
Xenocongridae				+	X	X	X	X	X	X	X	X	X	0	X	X	X	-	-	-
Zanclidae				+	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-
Totals	58	15	6	100	*Grand Total*		179													

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[a] Known nonmarginally on Pacific Plate only from deep water in Hawaiian Islands.

[b] Nonmarginal Pacific Plate distribution is indicated for some species on generalized distribution maps in Fischer and Whitehead, 1974; I have been unable to verify such distributions, and in many instances these nonmarginal representations are known to be erroneous (for example, *Scomberomorus commerson*, fide B.B. Collette, pers. comm.).

[c] Indicated for Hawaiian Islands by Matsubara (1955), probably erroneously.

[d] Family composition undecided; Pacific Plate species is deep dwelling in Hawaiian Islands.

[e] Apparently occurs nonmarginally on Pacific Plate only as a straggler.

[f] A shorefish species of *Lotella* occurs at Rapa; otherwise, family is known on Pacific Plate only from deep water.

[g] Known nonmarginally on Pacific Plate only from Hawaiian Islands and from stomach of tuna caught off Tahiti.

[h] Known nonmarginally on Pacific Plate only from a single, juvenile specimen taken in a plankton tow off Bikini Atoll (Schultz, 1953c) and from a photograph of an adult taken by a resident at Kwajalein (both localities in Marshall Islands).

[i] Here considered to include only *Trichiurus* and *Lepturacanthus*.

[j] Known nonmarginally on Pacific Plate only from Enewetak, Marshall Islands.

TABLE B.—Summary of data on numbers of families of shorefishes in Table A (for a geographic plot see Figure 58)

Locality		A	B	C	D	Known	+ Expected	= Total
Africa, SE coast	(AE)	42	14	6	99	160	1	161
Indo-Malayan Region	(IM)	47	8	6	96	153	4	157
Philippine Islands	(PI)	46	9	6	97	155	3	158
New Guinea-Bismarck Archipelago	(NG)	42	4	6	97	141	8	149
Queensland	(QD)	50	10	6	97	160	3	163
Guam	(GU)	2	2	5	93	94	8	102
Ponape	(PO)	0	1	6	95	73	29	102
Marshall Islands	(MI)	0	0	0	91	88	3	91
Hawaiian Islands	(HI)	0	15	0	83	98	0	98
New Caledonia-New Hebrides	(NC)	19	3	5	98	104	21	125
Fiji Islands	(FI)	15	0	4	97	106	10	116
Samoan Islands	(SA)	8	0	2	92	99	3	102
Society Islands	(SI)	0	0	0	83	82	1	83
Rapa Island	(RI)	0	0	0	63	62	1	63
Ducie Island	(DI)	0	0	0	47	40	7	47[a]
Easter Island	(EI)	1[b]	1	0	52	50	2	52

[a] Not included here as present or expected at Ducie are 20 families obtained by John E. Randall (in litt.) from Ducie's nearest neighboring islands (nearest about 600 km west): Henderson, Pitcairn, and Oeno. It is possible that some of these families reach east to Ducie. Of note here is that Randall spent only 2.5 days collecting at Ducie, an atoll, but a month at Pitcairn, a high island. The families are Ammodytidae, Antennariidae, Caesionidae, Callionymidae, Caracanthidae, Carapidae, Congridae, Dactylopteridae, Gobiesocidae, Isonidae, Mugiloididae, Ophidiidae, Platycephalidae, Pleuronectidae, Polynemidae, Pseudochromidae, Siganidae, Soleidae, Sphyraenidae, Xenocongridae.

[b] Eastern Pacific representation; not present on Pacific Plate nonmarginally.

TABLE C.—List of Indo-Pacific families and genera of warm-water shorefishes that occur other than marginally on the Pacific Plate. A few of the families and genera are questionably warm-water and/or shorefishes. Some families and genera not included in this list have been indicated as occurring on the Pacific Plate nonmarginally in Fischer and Whitehead, 1974 (see footnote b to Table A). Numerous genera have been omitted on the strength of unpublished synonymies from several sources. Numbers following family names indicate known or estimated total numbers of warm-water shorefish species that occur nonmarginally on Pacific Plate. Numbers following generic names indicate known total numbers of warm-water shorefish species that occur nonmarginally on Pacific Plate allowing for numerous unpublished records and undescribed species.

ACANTHOCLINIDAE		1
Acanthoplesiops	1	
ACANTHURIDAE		39
Acanthurus	20	
Ctenochaetus	5	
Naso	9	
Paracanthurus	1	
Zebrasoma	4	
ALBULIDAE		2
Albula	2	
AMBASSIDAE		1
Ambassis	1	
AMMODYTIDAE		1
Bleekeria	1	
ANGUILLIDAE		3
Anguilla	3	
ANOMALOPIDAE		2
Anomalops	1	
Photoblepharon	1	
ANTENNARIIDAE		10
Abantennarius		
Antennarius		
Phrynelox		

Table C.—Continued

Apogonidae		50
Apogon		
Apogonichthys		
Archamia		
Cheilodipterus		
Foa		
Fowleria		
Gymnapogon		
Neamia		
Pseudamia		
Pseudamiops		
Rhabdamia		
Siphamia		
Sphaeramia		
New genus[a]		
Atherinidae		6
Atherinomorus (includes *Pranesus*)		
Atherion		
Hypoatherina		
Stenatherina		
Aulostomidae		1
Aulostomus	1	
Balistidae		19
Balistapus	1	
Balistoides	2	
Canthidermis	2	
Melichthys	2	
Odonus	1	
Pseudobalistes	2	
Rhineacanthus	3	
Sufflamen	3	
Xanthichthys	3	
Belonidae		4
Ablennes	1	
Platybelone	1	
Strongylura	1	
Tylosurus	2	
Blenniidae		62
Alticus		
Aspidontus	2	
Atrosalarias	1	
Cirripectes		
Ecsenius	3	
Enchelyurus	2	
Entomacrodus	13	
Exallias	1	
Glyptoparus	1	
Istiblennius		
Medusablennius	1	
Meiacanthus	1	
Nannosalarias	1	
Omobranchus	1	
Omox	1	
Parenchelyurus	1	
Petroscirtes	2	
Parablennius	1	
Plagiotremus	5	
Praealticus		
Rhabdoblennius		
Salarias		
Stanulus	1	
Xiphasia	1	
Bothidae		5
Arnoglossus		
Bothus		
Engyprosopon		
Bregmacerotidae		3
Bregmaceros		
Bythitidae		10
Brosmophyciops		
Dinematichthys		
Microbrotula		
Oligopus		
Caesionidae		10
Caesio		
Pterocaesio		
Callionymidae		10
Callionymus		
Diplogrammus	1	
Pogonymus	1	
Synchiropus	5	
Caracanthidae		3
Caracanthus	3	
Carangidae		29
Alectis	1	
Atule	1	
Carangoides	4	
Caranx	5	
Decapterus	4	
Elagatis	1	
Gnathanodon	1	
Naucrates	1	
Pseudocaranx	1	
Scomberoides	1	
Selar	1	
Seriola	4	
Trachinotus	2	
Uraspis	2	
Carapidae		6
Carapus		
Encheliophis		
Onuxodon		
Snyderidia		
Carcharhinidae		12
Carcharhinus	9	
Galeocerdo	1	
Negaprion	1	
Triaenodon	1	
Centriscidae		1
Aeoliscus	1	
Chaetodontidae		40
Chaetodon	30	
Forcipiger	2	
Hemitaurichthys	3	
Heniochus	5	
Chanidae		1
Chanos	1	
Cheilodactylidae		2
Cheilodactylus	2	
Cirrhitidae		17
Amblycirrhitus	1	
Cirrhitichthys		
Cirrhitops	2	
Cirrhitus	1	
Isocirrhitus	1	
Neocirrhites	1	
Oxycirrhites	1	
Paracirrhites	6	
New genus[b]	1	
Clupeidae		6
Dussumieria	1	
Etrumeus	1	
Herklotsichthys	1	
Sardinella	2	
Spratelloides	1	
Congridae		8
Ariosoma	2	
Conger	2	
Gorgasia	1	
Heteroconger	2	
Poeciloconger	1	
Coryphaenidae		2
Coryphaena	2	
Creediidae		4
Chalixodytes	1	
Crystallodytes	1	
Limnichthys	2	
Dactylopteridae		1
Dactyloptena	1	
Dasyatididae		5
Dasyatis		
Himantura		
Taeniura		
Urogymnus		
Diodontidae		5
Chilomycterus	1	
Diodon	4	

TABLE C.—Continued

ECHENEIDIDAE		6
Echeneis		
Phtheirichthys		
Remora		
ELEOTRIDIDAE		15
Allomicrodesmus	1	
Bostrycthus		
Butis	1	
Calumia	1	
Eleotris		
Hypseleotris		
Xenisthmus		
ELOPIDAE		3
Elops	2	
Megalops	1	
ENGRAULIDIDAE		4
Encrasicholina	1	
Stolephorus	3	
EPHIPPIDIDAE		2
Platax	2	
EXOCOETIDAE		15
Cypselurus		
?Exocoetus		
Fodiator		
?Parexocoetus		
Prognichthys		
FISTULARIIDAE		2
Fistularia	2	
GERREIDAE		3
Gerres		
GINGLYMOSTOMATIDAE		1
Nebrius	1	
GOBIESOCIDAE		3
Lepadichthys	1	
Liobranchia	1	
Pherallodus	1	
GOBIIDAE		150
Acentrogobius		
Amblyeleotris		
Amblygobius		
Asterropteryx	2	
Awaous		
Bathygobius		
Cabillus		
Callogobius		
Cryptocentroides	1	
Cryptocentrus		
Ctenogobiops		
Discordipinna	1	
Drombus		
Eilatia		
Eviota		
Exyrias		
Feia	1	
Fusigobius		
Gladygobius		
Glossogobius		
Gnatholepis		
Gobiodon		
Gobiopsis		
Istigobius		
Kelloggella	4	
Lentipes	1	
Macrodontogobius		
Mugilogobius		
Nemateleotris	2	
Oplopomops		
Oplopomus		
Opua		
Oxyurichthys		
Paragobiodon	1	
Parioglossus	2	
Periophthalmus		
Pleurosicya		
Priolepis		
Psilogobius		
Ptereleotris	2	
Redigobius		
Sicydium		
Sicyopterus		
Stenogobius		
Stiphodon		
Stonogobiops		
Trimma		
Valenciennea		
Vanderhorstia		
Vitraria	1	
Waitea		
Yongeichthys		
Undescribed genus[c]		
GOBIOIDIDAE		2
Brachyamblyopus	1	
Taenioides	1	
GONORYNCHIDAE		1
Gonorynchus	1	
HAEMULIDAE		5
Plectorhynchus		
HEMIRAMPHIDAE		9
Euleptoramphus	1	
Hemiramphus		
Hyporhamphus		
Oxyporamphus	1	
Zenarchopterus	1	
HOLOCENTRIDAE		29
Adioryx	13	
Flammeo	4	
Myripristis	12	
New genus[b]	1	
Ostichthys	2	
Plectrypops	1	
ISONIDAE		2
Iso	2	
ISTIOPHORIDAE		2
Istiophorus	1	
Makaira	1	
KRAMERIIDAE		2
Kraemeria		
KUHLIIDAE		3
Kuhlia		
KYPHOSIDAE		4
Kyphosus		
Sectator	1	
LABRACOGLOSSIDAE		1
Bathystethus	1	
LABRIDAE		100
Anampses	6	
Bodianus	7	
Cheilinus	9	
Cheilio	1	
Cirrhilabrus		
Coris	8	
Cymolutes		
Epibulus	1	
Gomphosus	1	
Halichoeres	12	
Hemigymnus	2	
Hologymnosus	2	
Labrichthys	1	
Labroides	5	
Labropsis	4	
Macropharyngodon	3	
Novaculichthys	2	
Polylepion	1	
Pseudocheilinus	5	
Pseudocoris	2	
Pseudodax	1	
Pseudojuloides	3	
Pseudolabrus	3	
Pteragogus	1	
Stethojulis	4	
Suezichthys	1	
Thalassoma	9	
Wetmorella	1	
Xyrichtys		
LAMNIDAE		3
Carcharodon	1	
Isurus	2	
LEIOGNATHIDAE		2
Gazza	1	

TABLE C.—Continued

Leiognathus	1	
LETHRINIDAE		7
Gnathodentex	1	
Lethrinus	5	
Monotaxis	1	
LOBOTIDAE		1
Lobotes	1	
LUTJANIDAE		15
Aprion	1	
Lutjanus		
Macolor	1	
MALACANTHIDAE		5
Hoplolatilus	3	
Malacanthus	2	
MICRODESMIDAE		4
Gunnellichthys	3	
Paragunnellichthys	1	
MOBULIDAE		2
Manta		
Mobula		
MONACANTHIDAE		17
Aluterus	2	
Amanses	1	
Brachaluteres		
Cantherhines	6	
Oxymonacanthus	1	
Paraluteres	1	
Pervagor	2	
Thamnaconus	1	
MONODACTYLIDAE		1
Monodactylus	1	
MORIDAE		1
Lotella	1	
MORINGUIDAE		3
Moringua		
MUGILIDAE		10
Chelon		
Crenimugil		
Liza		
Mugil		
Neomyxus		
Plicomugil		
Valamugil		
MUGILOIDIDAE		7
Parapercis	7	
MULLIDAE		20
Mulloides	4	
Parupeneus		
Upeneus		
MURAENIDAE		35
Anarchias		
Echidna		
Enchelycore		
Enchelynassa		
Gymnomuraena		
Gymnothorax		
?*Muraena*		
Rhinomuraena	1	
Uropterygius		
MYLIOBATIDIDAE		2
Aetobatis	1	
Pteromylaeus	1	
NEMIPTERIDAE		5
Pentapodus		
Scolopsis		
NOMEIDAE		5
Cubiceps		
Nomeus	1	
Psenes		
OPHICHTHIDAE		40
Achirophichthys	1	
Apterichtus		
Brachysomophis		
Callechelys		
Cirrhimuraena		
Cirricaecula	1	
Ichthyapus		
Lamnostoma		
Leiuranus	1	
Muraenichthys		
Myrichthys		
Myrophis		
Ophichthus		
Phaenomonas	1	
Phyllophichthus	1	
Schismorhynchus	1	
Schultzidia	1	
OPHIDIIDAE		2
Brotula	2	
OPLEGNATHIDAE		2
Oplegnathus	2	
OSTRACIIDAE		6
Lactoria	3	
Ostracion	3	
PEGASIDAE		1
Eurypegasus	1	
PEMPHERIDIDAE		3
Parapriacanthus	1	
Pempheris		
PENTACEROTIDAE		1
Histiopterus	1	
PLATYCEPHALIDAE		5
Onigocia		
Thysanophrys		
Wakiyus		
PLESIOPIDAE		3
Calloplesiops	1	
Plesiops	2	
PLEURONECTIDAE		2
Samariscus		
POLYNEMIDAE		3
Polydactylus		
POMACANTHIDAE		25
Apolemichthys	3	
Centropyge	15	
Euxiphipops	1	
Genicanthus	4	
Pomacanthus	1	
Pygoplites	1	
POMACENTRIDAE		72
Abudefduf	6	
Amblyglyphidodon	3	
Amphiprion	5	
Chromis	24	
Chrysiptera	6	
Dascyllus	7	
Lepidozygus	1	
Plectroglyphidodon	8	
Pomacentrus	4	
Pomachromis	3	
Stegastes	5	
PRIACANTHIDAE		3
Cookeolus	1	
Priacanthus		
PSEUDOCHROMIDAE		5
Pseudochromis		
Pseudoplesiops		
SCARIDAE		31
Bolbometopon	1	
Calotomus (includes *Scaridea*)	2	
Cetoscarus	1	
Hipposcarus	1	
Leptoscarus	1	
Scarus	25	
SCATOPHAGIDAE		1
Scatophagus	1	
SCHINDLERIIDAE		2
Schindleria	2	
SCOMBRIDAE		7
Euthynnus	2	
Grammatorcynus	1	
Gymnosarda	1	
Rastrelliger	1	
Sarda	1	
Scomber	1	
SCORPAENIDAE		35
Dendrochirus		

TABLE C.—Continued

Iracundus	1	
Pterois	3	
Rhinopias	1	
Scorpaena (includes *Sebastapistes*)		
Scorpaenodes		
Scorpaenopsis		
Synanceia	1	
Taenianotus	1	
SCORPIDIDAE		1
Microcanthus	1	
SERRANIDAE		82
Anthias (includes *Mirolabrichthys* and *Pseudanthias*)	16	
Anyperodon	1	
Aulacocephalus	1	
Belonoperca	1	
Cephalopholis	8	
Epinephelus	19	
Gracila	1	
Grammistes	1	
Grammistops	1	
Holanthias	3	
Liopropoma	9	
Luzonichthys	2	
Odontanthias	3	
Plectranthias	5	
Plectropomus	4	
Pogonoperca	1	
Pseudogramma (includes *Aporops*)	4	
Suttonia	1	
Variola	1	
SIGANIDAE		5
Siganus (includes *Lo*)		
SOLEIDAE		4
Aseraggodes		
Soleichthys		
SOLENOSTOMIDAE		1
Solenostomus	1	
SPHYRAENIDAE		5
Sphyraena		
SPHYRNIDAE		2
Sphyrna	2	
SYNGNATHIDAE		25
Choeroichthys	2	
Corythoichthys	4	
Cosmocampus		
Doryrhamphus	1	
Dunkerocampus	2	
Festucalex	1	
Hippichthys	1	
Hippocampus		
Micrognathus		
Oostethus	1	
Penetopteryx	1	
Phoxocampus	1	
Syngnathoides	1	
SYNODONTIDAE		12
Saurida		
Synodus	8	
Trachinocephalus	1	
TETRAODONTIDAE		20
Arothron		
Canthigaster	13	
Lagocephalus		
Sphoeroides		
TRICHONOTIDAE	1	
Trichonotus	1	
TRIPTERYGIIDAE		10
Enneapterygius		
Helcogramma		
Norfolkia		
XENOCONGRIDAE		5
Chilorhinus		
Kaupichthys		
Powellichthys		
ZANCLIDAE		1
Zanclus	1	

[a] E.A. Lachner, pers. comm.

[b] J.E. Randall, pers. comm. and in litt.

[c] D.F. Hoese, pers. comm.

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Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

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A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

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