REVIEW OF THE FAUNA OF THE MARQUESAS ISLANDS AND DISCUSSION OF ITS ORIGIN

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Publications have been issued by the Museum as follows:

1. Marquesan Insects—I, Bulletin 98, 1932.
2. Check list of Tipulidae of Oceania, by Charles P. Alexander, Occasional Papers, vol. 9, no. 21, 1932.
3. Check list of the Elateridae of Oceania, by R. H. Van Zwaluwenburg, Occasional Papers, vol. 9, no. 23, 1932.
4. Fresh-water fishes from the Marquesas and Society Islands, by Henry W. Fowler, Occasional Papers, vol. 9, no. 35, 1932.
5. The lizards of the Marquesas Islands, by Karl P. Schmidt and Walter L. Necker, Occasional Papers, vol. 10, no. 2, 1933.
6. Society Islands Insects, Bulletin 113, 1935.
7. Marquesan Insects—II, Bulletin 114, 1935.
8. Marquesan Insects—III, Bulletin 142, 1939.
9. Marquesan Insects: Environment, Bulletin 139, 1936.

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A. M. Adamson

FOREWORD

In 1929 and 1930 it was my good fortune to spend fifteen months in the Marquesas Islands collecting insects and other invertebrates on seven of the ten islands in the group. This was a very interesting experience because the islands, which are of extraordinary beauty and romantic charm, were at that time an almost virgin field for most kinds of scientific exploration.

The literature on the faunas and floras of the central Pacific islands is very extensive and many biologists and geologists have written on the problem of their origin. Scarcely any writer, however, has attempted to solve the problem, even for a single archipelago, by a comprehensive and detailed examination of all the evidence—biological, geographical and geological. Most of the theories proposed are based on a study of individual groups of animals and plants, and often without reference to conflicting evidence from other sources. The most comprehensive early works were those of Guppy (109)[1] on Pacific floras and of Perkins (182) on the Hawaiian fauna. Most of our knowledge of the biology of central Pacific islands, other than Hawaii, has been acquired within the last twenty years. With this information at his disposal Buxton (31, 32) has considered carefully and in detail most of the evidence bearing on the origin of the fauna of Samoa. His papers have done more to extend our understanding of the biogeography of the central Pacific than any other publication since Perkins' classic "Introduction" to the "Fauna Hawaiiensis", written in 1913 (182).

The main contribution attempted here is a review of the land and fresh-water fauna of the Marquesas Islands. A discussion of the origin of the fauna has been included, in spite of the complexity of the problem, and an attempt has been made to consider all the available evidence in as much detail as space has allowed. Many of the opinions expressed here are offered tentatively. Indeed, it must be admitted that a decision has not been reached on what is perhaps the most important question of all: whether the islands could have acquired their fauna and flora by transoceanic dispersal alone or whether it is necessary to assume the existence of former land connections across the central Pacific.

[1] Numbers in parentheses refer to Bibliography, p. 80.

authors divert the line eastward to include Samoa in the marginal area; however general opinion leaves Samoa well to the east of the line.

Within the Pacific depression are archipelagoes and isolated islands of three well-defined types:

(1) High, volcanic islands, composed largely of basalts, without metamorphic or ancient sedimentary rocks, and mostly but not all surrounded by fringing and barrier reefs. Excluding Tonga, the important groups are Samoa, the Cook, Austral, Society, Marquesas, and Hawaiian islands, and the very small groups and isolated islands of Rapa (sometimes included in the Austral Islands), Mangareva, Easter Island, Sala y Gomez, Pitcairn Island, and Guam. On almost all of these islands the land faunas and floras are rich in endemic species.

(2) Coral atolls, only a few feet high, with meager faunas and floras composed almost entirely of species of wide distribution. These are the Tuamotu Islands, the scattered equatorial atolls, and the many archipelagoes of Micronesia, such as the Phoenix, Gilbert, and Marshall Islands. Many atolls occur in the groups of high islands. For some of these, for example in the long chain of leeward Hawaiian islands, it is difficult to decide whether they are typical atolls or the worn-down remnants of high islands.

(3) Elevated coral islands, composed entirely of coral rocks, and almost all with faunas and floras similar to those of atolls. Such islands are mostly isolated. Examples are Mitiaro and Monowai in the Cook Islands, and Makatea on the western margin of the Tuamotus.

The eastern half of the Pacific is continuous deep sea. Almost all the islands are in the western half, and in many respects, both geographical and biological, the Pacific is, as H. E. Gregory (106) expresses it, an "Asiatic Ocean". All the archipelagoes within the Pacific depression are separated by very deep sea, and their isolation is of enormous degree.

The Hawaiian islands are biogeographically the most isolated in the world, being about 2,000 miles from the nearest continental area to the east, nearly 3,000 from the margin of the Pacific depression to the west, and 2,000 miles from the nearest high islands, the Marquesas. Easter Island holds the second place in degree of isolation in the Pacific, and then the Marquesas, which are almost exactly in the center of the Pacific, some 3,000 miles from the nearest American coast, 2,700 miles from the western margin of the Pacific depression and 800 miles from the nearest high islands, those of the Society group. For other central Pacific islands the distances to the western edge of the Pacific depression are: Mangareva 2,700 miles, Society Islands 1,600, Austral Islands 1,500, Cook Islands 1,000, Samoa 500.

On the history of the Pacific Ocean the opinions of geologists and biologists are sharply divided and conflicting. According to one view, presented authoritatively and concisely by H. E. Gregory (105), the only major changes in its form, since early geological times, have been along its margins. The islands within the Pacific depression are of oceanic origin, probably not before the beginning of Tertiary times, and since then there has been little change in their size and relations. The islands therefore acquired their faunas and floras by comparatively recent overseas dispersal. According to the opposing view, set forth in considerable detail by J. W. Gregory (107), there were extensive land masses in the area now occupied by the Pacific depression, which were submerged in the late Secondary or early Tertiary. The present insular faunas and floras were thus derived from large, and probably ancient, continental lands.

Extent of Biological Exploration on Central Pacific Islands

MARQUESAS ISLANDS

Before 1929 the most important field work on the Marquesan fauna was done by Jardin (128), who gives little information on the endemic fauna; Garrett (101), who made a fairly extensive collection of land snails; the Whitney South Sea Expedition (172, 173), which made a very extensive, probably nearly complete, collection of birds; and the St. George Expedition (66), which spent about four weeks on Hivaoa, Tahuata, Fatuhiva, and Nukuhiva, devoting attention especially to Lepidoptera and other insects, general marine zoology, and geology. Most of the Marquesan results of the Whitney Expedition have been published by Murphy (174) and Murphy and Mathews (175). Results of the St. George Expedition on marine zoology are recorded by Crossland (67), and on entomology by Cheesman (39, 41), Collenette (56, 57), and others. In 1929 the Pinchot South Sea Expedition spent a few weeks collecting mostly land snails, birds, and marine fishes on five of the islands, as recorded by Pinchot (188), Fisher and Wetmore (91), and Fowler (94). In addition to these publications very little information on the endemic Marquesan fauna had been published before 1929.

From 1929 to 1932 members of the Pacific Entomological Survey collected extensively on all of the islands, dividing attention more or less evenly among all classes of animals, with the exception of microscopic forms, the birds and their parasites, and to some extent the meager fresh-water fauna. The publication of the results is still in progress by Bishop Museum in Honolulu. The non-marine fauna of the islands is therefore sufficiently well known for the recognition of its major features. Except for microscopic animals, most of the families present are represented in the collections, though a fair number have yet to be found. In the terrestrial Arthropods and mollusks probably between 50 and 75 percent of the species have been collected.

Little has been written on the marine fauna, except on the corals by Agassiz (4) and Crossland (67), the sea birds, and on general ecology by Crossland (67).

The flora of the islands is almost as well known as the fauna. Until recently the principal work was that of Drake del Castillo (75). The standard is now the "Flora of southeastern Polynesia" by F. B. H. and E. D. W. Brown

(23, 25, 27), which deals with the vascular plants only, largely those of the Marquesas. The Cryptogams of these islands are little known.

Only Chubb (50, 52, 53) of the St. George Expedition has studied the geology of the Marquesas, though Lacroix (137-140) and Williams (251) have written on collections received from the islands. Meteorological records are limited to a few made in 1900-01 by the anthropologist Von den Steinen and published by Hellmann (117), and those begun by the Pacific Entomological Survey in 1929 and published by Leighly (142).

The history, general geography, and anthropology of the Marquesas are described in considerable detail especially by Handy (110), Linton (148, 149), and Rollin (197).

SOCIETY, AUSTRAL, AND COOK ISLANDS AND RAPA

Despite the great interest, both popular and scientific, in the island of Tahiti, published information on the endemic fauna and flora of the Society Islands is extremely meager. This is due to the difficulty of field work in the rugged, pathless, and densely forested mountains to which most endemic animals and plants are now confined. Most of the animals and plants thus far recorded from the Society Islands have been collected at altitudes of less than 2,000 feet. A small part of the endemic land fauna of the Society and Austral Islands and Rapa has been described in the publications of the St. George Expedition and from collections I made on Tahiti and Moorea (Bishop Mus. Bull. 113). The land snails of the Society Islands were collected extensively by Garrett (100); Crampton (62, 63) has made exhaustive studies on the Partulidae. Little is known of the endemic fauna of the Cook Islands. The published reports are entirely inadequate for an analysis of the fauna of these three island groups.

Many of the general features of the flora of the Society Islands can be recognized. (See especially Setchell, 208-210, and Copeland, 61.) The coral reefs and lagoons have been extensively studied by Setchell (208, 211, 212) and Crossland (68, 69). The geology of the interior of the Society Islands is little known (251). Parts of the Austral Islands (51, 221) and of the Cook Islands (160, 161) have been explored geologically.

A considerable advance in the knowledge of the fauna and flora of all these islands will be made when the results of recent field work for the Bishop Museum are published. M. L. Grant is preparing a report on the flowering plants collected by him in the Society Islands in 1930-31. In 1934 the Mangarevan Expedition under C. Montague Cooke, Jr., with H. St. John and F. R. Fosberg as botanists, and E. C. Zimmerman and D. Anderson as zoologists, made very valuable collections in the Society, Austral, Tuamotu and Mangareva Islands, as well as on Rapa, Pitcairn and Henderson Islands.

Reports on many of the Curculionidae have already been published by Zimmerman (252-254).

SAMOA

The natural history of Samoa has been fairly well described, though in much less detail than that of Hawaii. Buxton (31, 32) has written extremely valuable accounts of the islands and their fauna from the point of view of geographical distribution. The series "Insects of Samoa and other Samoan terrestrial Arthropoda", based largely on the collections of Buxton and Hopkins, probably includes considerably more than half the species of Arthropods existing in these islands, and it is possible to recognize the major features of the Samoan fauna as a whole. The flora has been extensively studied, especially by Setchell (207) and Christophersen (49). The geology of the islands is fairly well known (71, 231), and a fully equipped meteorological station has been maintained for many years at Apia.

HAWAIIAN ISLANDS

The natural history of Hawaii is perhaps better known than that of any other region except parts of Europe and North America. In the non-marine fauna little attention has been devoted to microscopic animals, but relatively few species of other animals have yet to be recorded, and all general features of the fauna are well known. The collections made up to twenty or thirty years ago are described in the "Fauna Hawaiiensis", and more recent work has been published chiefly by the Bishop Museum and the Hawaiian Entomological Society. But a comprehensive and modern review and analysis of the fauna as a whole has not been written. Such a work would be an extremely important advance in the study of insular faunas.

Means of Dispersal for Pacific Insular Faunas and Floras

The presence or absence of species of organisms in any area depends on a complicated series of factors, involving dispersal, establishment, and persistence, or their opposites. Setchell (208, 213) has emphasized the necessity of considering all of these factors and the partial neglect of the problems of establishment and persistence by biogeographers. A discussion of the extremely complex problems of establishment and persistence would be out of place here, but it is desirable to consider in detail the means of dispersal. For insular faunas and floras there are two possible means: by former land connections, such as past continents, land bridges, chains of islands, extensions from present continental margins, and so on; and by transoceanic movement—that is, for non-marine organisms, by flight, wind, ocean currents and drifts, on birds, especially migrants, and by man.

LAND CONNECTIONS

It is generally agreed that the western Pacific islands, as far east as Fiji and perhaps farther, were formerly united to the continents adjacent to them (p. 4). Beyond Fiji, within the Pacific depression, the possibility of former land connections is a highly controversial question. The evidence in favor of such connections is almost entirely biological, though this evidence is accepted by some authorities, notably the late J. W. Gregory (107), as not inconsistent with purely geological considerations. J. W. Gregory (107) summarizes much of the biological evidence in favor of the former large land masses in the central Pacific, especially as afforded by the past and present distribution of vertebrates in the continents now bordering the Pacific. A discussion of most of Gregory's views being beyond the scope of the present paper, it must suffice here to quote his agreement with those biologists who demand "extensive Pacific lands on which developed a Eu-Pacific fauna and flora," and his statements that "lands survived across the Central Pacific apparently until the Lower Kainozoic . . . " and that "Darwin's theory of coral islands . . . implies the sinking of a belt across the Southern Pacific during the Upper Kainozoic." These opinions are highly controversial, and direct evidence, especially geological, is conspicuously lacking.

In his "Types of Pacific islands", H. E. Gregory (105) gives an emphatic statement of geological opinion against land connections that might have provided a means of dispersal for central Pacific faunas and floras. He finds no conclusive geological evidence of vertical movements of greater range than 1,200 feet. His view that the Pacific depression is an area of remarkable stability is supported by the work of Marshall (160) in the Cook Islands, Williams (251) in the Society Islands and Chubb (54) in Easter Island. Williams (251) states that "the islands of the South Central Pacific as a whole seem to indicate a vast region of comparative stability." The question of subsidence in the Marquesas is discussed on page 23.

Among the principal modern students of Pacific faunas and floras the following are in favor of past land connections, of greater or less extent, within the Pacific depression: the zoologists Berland, Cooke, Crampton, Germain, Meyrick, and Pilsbry, and the botanists Brown, Campbell, Guillaumin and Skottsberg(?). The following more or less strongly assert that all or some of these central Pacific islands have apparently always been oceanic: the zoologists Buxton, Crawford, Hedley, Holdhaus, Muir, Perkins, and P. J. Schmidt, and the botanists Guppy, Setchell, and Merrill.

The arguments in favor of past mid-Pacific land connections are based largely on a disbelief in the possibilities of transoceanic migration, and on the partial homogeneity and similar features in central Pacific faunas and floras. The clearest evidence is afforded by the land snails, which are represented on the islands only by a few ancient families, some of which are found throughout the central Pacific and are more or less restricted to it. This is difficult to explain except by the assumption of extensive land connections which were submerged after these families had attained a wide distribution in the area now occupied by the Pacific Ocean and before the more modern and dominant families of snails were evolved on the continents now bordering the Pacific.

It is obvious that land connections afford a ready explanation of the occurrence of considerable native faunas and floras on the Pacific islands. The chief difficulty is that they provide too liberal a source of population, their assumption being inconsistent with the very large gaps in the faunas and floras of all central Pacific islands. The gravity of this difficulty is generally recognized, but the extent to which it is insurmountable is of course a matter of opinion. Scott (206), while writing in general agreement with the view of Mumford and Adamson (171) that these gaps are evidence against past land connections, points out that many large groups of animals are absent also from the fauna of some islands not of volcanic or purely oceanic origin. The Plecoptera, Mecoptera, and Hymenoptera Symphyta are unknown in the Seychelles, "an ancient granite archipelago believed to be the remains of a much larger land," and these groups of insects appear to be very poorly represented in Ceylon. Moreover, some of the animals absent from the Marquesas and other islands are meagerly represented in many parts of the tropics. The argument, however, as Scott admits, does not go far toward removing this objection to the assumption of past continental connections.

An interesting possibility is that volcanic activity, not long extinct on central Pacific islands, may on one or more occasions have destroyed all the fauna and flora except for a few chance survivors. The possibility was first suggested to me by Dr. Sydney Harland of the Cotton Research Station in Trinidad, B. W. I., and it is interesting to find it advanced by Wheeler (248) to explain the restriction of endemic Hawaiian ants to a few species of subterranean habit, enabling them to survive the heat which may have killed all other ants. The recent volcanic eruption of Krakatoa apparently almost sterilized the island, and it is not difficult to conceive of partial sterilization in the history of many Pacific archipelagoes. It may be objected that this hypothesis, like that of transoceanic dispersal alone, is inconsistent with the homogeneity in many groups of animals and plants throughout the islands. For example, if the Fulgoroid leafhopper fauna of Hawaii and the Marquesas is restricted to the Cixiidae and Delphacidae because other families in this large superfamily were destroyed by vulcanism, it is difficult to explain why the same two families alone survived on each archipelago. It is possible, of course, that all the Fulgoroidea were destroyed on one of them, which was subsequently repopulated by the survivors on the other. Such an argument, however, to some extent increases the difficulty which it attempts to solve.

TRANSOCEANIC DISPERSAL

Flight. Many birds, some locusts, butterflies, moths, dragonflies, and other insects can probably fly across hundreds and even thousands of miles of ocean. The distances covered by bats are little known, but it is significant that bats are the only mammals that may be assumed to have reached Hawaii and Samoa without human aid. For the majority of winged insects long flights are probably dependent upon sustained strong winds.

Winds. It is obvious that high winds, especially hurricanes such as those which occur in most parts of the central Pacific, can carry many animals and plants, in the adult or other phases, for considerable distances. This applies especially to winged animals, young spiders, and seeds adapted for wind-dispersal, but also to many small organisms and to those which may be attached or cling to dead leaves and other wind-borne objects. While an adult land snail like *Partula* could not be carried far by the wind, it is possible that even relatively heavy gastropod eggs could be borne for long distances on a dead leaf. The question of wind dispersal has been so much discussed in literature that only certain aspects of the problem need be considered in detail here. (See Gregory, 105, for an important recent discussion.) While some authors attribute the dispersal of many animals and plants to the winds, others reject winds almost entirely as an important factor in the origin of insular faunas and floras. Jacot (127), for example, can almost as easily conceive of wolves and tigers being blown out of the forests as mites out of moss! If any animals can be dispersed as passengers on wind-borne vegetation, it might be expected that minute mites with powerful claws would be more susceptible to such dispersal than almost any other wingless animals except those that are still smaller.

Of great interest here are the recently discovered anti-trade winds, blowing steadily and strongly at altitudes of 4 to 20 kilometers eastward across the Pacific. According to Andrew Thomson (230), observations at Apia, Samoa, show a maximum velocity of 10.5 m/sec. at an altitude of 11.5 km. The high anti-trades, combined with violent local disturbances to lift objects to high altitudes, appear to provide a more potent and constant agency of dispersal across the Pacific than any previously recognized. It is significant that, unlike the trades at lower levels, they blow from the west, whence most organisms on the islands appear to have been derived. Moreover, as H. E. Gregory (105) has well emphasized, the cyclonic storms of the central Pacific more frequently blow toward the east and north than toward the west and south.

There may have been significant changes in the power of the wind as an agent of dispersal after subsidence along the western margin of the Pacific depression, and also in the central Pacific if extensive subsidence occurred there. But if the Pacific was always nearly as wide as it is now, it cannot be assumed with any assurance that there were great changes in the power of the wind over its center.

Ocean currents. It is obvious that ocean currents may transport even large animals and growing plants as passengers on floating logs and other flotsam, but it is nearly as obvious that this means of dispersal must be almost ineffectual over distances such as those which separate the islands of the central Pacific. After a voyage of a few hundred miles almost all parts of drifting vegetation are permeated by sea water, adhering soil is removed, and drifting logs may even be stripped of their bark. It may therefore appear unnecessary to point out that the movement of the surface waters over most of the central Pacific is a slow drift in a general westerly direction, while a narrow equatorial counter-current flows eastward. Changes in direction of these movements follow changes in the direction of the wind, but are probably never of sufficient duration to transport any flotsam for very long distances, for example from the Society Islands to the Marquesas.

The drift of surface waters must have been profoundly altered if changes occurred in the area of mid-Pacific land. It is useless to speculate as to their courses. But whenever there was a great expanse of ocean in the central Pacific, the main drift across it must have been in a general westward direction, because its direction, like that of the winds, is partly determined by the rotation of the earth.

Migratory birds. Few modern biogeographers consider that migratory birds have acted as important agents of dispersal for the animals and plants that present the most important problems in the biogeography of the Pacific. Among the animals most readily dispersed by birds are the Protozoa, Trochelminthes, Polyzoa, and the entomostracan Crustacea, all of which are at present little known on Pacific islands and, perhaps because of dispersal by birds, are probably represented chiefly by widespread species. Moreover, the majority of endemic species in the invertebrate faunas of central Pacific islands belong to the Myriopods, terrestrial Amphipods and Isopods, insects, spiders, and terrestrial Gastropods, all of which are less likely to be distributed by birds than many other animals. Guppy's (109) views on the importance of migratory birds in the dispersal of plants to Pacific islands have been largely rejected. The possibility of a greater influence by an avian fauna now extinct can scarcely be made the basis of valuable speculation.

Man. Though the influence of man in the central Pacific, both prehistoric and recorded, appears to have begun only a few thousand years ago (106), it has wrought great changes in the fauna and flora of the islands. Some account of what has happened in the Marquesas is given on pages 26-27, and only one general problem is considered here.

In attempting an analysis of the fauna and flora of any area, the first problem is to divide them into species introduced intentionally or otherwise by man, and species not so introduced. Generally this is easier than might be supposed because there are many sources of reliable evidence: historical and similar data, inference from distribution of the species in other parts of the world, association of phytophagous animals with native or introduced plants and, conversely, the extent of the fauna attached to particular plants, and so on. Moreover, for many important genera, such as the weevil genus *Rhyncogonus* in which there are many species restricted largely to single islands, it is obvious that distribution has been little influenced, unless negatively, by man. There remain, however, many species, both animal and plant, for which it is almost impossible to decide whether or not they originally came to the islands in human boats. It is also difficult to estimate how much differentiation in species, subspecies, and forms has occurred since the arrival of man. Finally, it is obvious that allowance must be made for the extinction of species as a result of changes wrought by man, and the extent of this extinction is of course difficult to determine even in general terms.

Perhaps the best known and one of the most forceful arguments for overseas dispersal is that most groups of animals, to which an ocean barrier is effective, are absent from remote islands, and conversely, that a large proportion of the native animals are better adapted than most for crossing the ocean. In the endemic faunas of central Pacific islands there are no vertebrates except birds, a few bats, and, in Samoa only, a few doubtfully native species of lizards and snakes. Among invertebrates the following are totally lacking in the endemic faunas: fresh-water Pelecypod mollusks; all Malacostracan Crustacea, except the Atyid shrimps (which are of ancient fresh-water habit); almost all orders and many superfamilies and families of strictly aquatic insects; earthworms; most Polyzoa and Coelenterata; and all sponges. The absence of so large a portion of the animal kingdom is difficult to explain except by an impassable ocean barrier.

Many native animals present on central Pacific islands are known to be readily dispersed for great distances by flight, wind, or birds: Protozoa, Trochelminthes, the few Polyzoa known, many if not all of the smaller Crustacea, some winged insects such as dragonflies, many Lepidoptera, most spiders, birds, and bats, and parasites associated with these animals.

There remain for consideration the following groups known to have a significant representation in the native faunas: Myriopods, Atyid shrimps, terrestrial Amphipods and Isopods, most insects, pseudoscorpions, some spiders, mites, and land snails. The origin of the Atyidae is an unsolved problem, but at least an attempt can be made to explain that of the other animals by overseas dispersal. Insects, partially aquatic, are the only abundant endemic members of the fresh-water fauna. A very large proportion of the animals present are small or minute, the absence of very large species being a striking feature of all groups in the native faunas. The animals which appear to be too large to be carried far by the wind are the Myriopods, terrestrial Crustacea, many insects such as Orthoptera, the large weevils of the genus *Rhyncogonus* and other beetles, and the land snails. But in many of these the eggs and juvenile phases are sufficiently small to be borne on a dead leaf, and the eggs of a considerable number of them are laid on leaves or among dead vegetation. Though transportation for long distances on drifting logs is at least difficult to assume, it is not entirely inconceivable that many wood-boring insects, such as termites of the family Kalotermitidae, Buprestids, Cerambycids, Lucanids and some weevils, can be so dispersed.

It therefore appears that there are scarcely any native animals on central Pacific islands which are incapable, at least to some significant degree, of overseas dispersal. This is obviously an important conclusion, whatever its implications may be.

One of the strongest objections to transoceanic dispersal for Pacific island faunas is that if it ever played an important part it has long ceased to do so. For example, apparently no relatively modern family of land snails reached the central Pacific until brought by man. More significant still is the pronounced island endemism in many archipelagoes, in which an entire family like the Achatinellidae of Oahu, and many genera and species of almost all kinds of animals and plants, are restricted to single islands. An ocean barrier a few miles wide is apparently effective even for many birds and winged insects. It is difficult to answer this objection except by the doubtful assumption of important changes in the power of the wind and other agents of dispersal.

Biogeographic Theories about Pacific Islands

The problems of biogeography in the central Pacific having been partially outlined and discussed, it remains here to summarize the hypotheses that have been advanced by biologists to explain the present distribution of the faunas and floras. No modern and comprehensive zoogeographical or phytogeographical scheme for the Pacific islands as a whole, based on a consideration of all the important evidence, has yet, so far as I know, been proposed. An attempt to do so should be made soon, for much of the necessary evidence from such central Pacific islands as Samoa, the Society, Austral, and Marquesas Islands has been made available within the last ten years, and a comprehensive treatment of the problems would provide a much-needed basis for future research.

Zoological Theories

According to the views proposed in the second half of the nineteenth century, and repeated in most textbooks of zoogeography, the central and southwestern Pacific islands are regarded as appendages of the Australian region. In the "Atlas of Zoogeography", Bartholomew, Clarke, and Grimshaw (11) divide this region into four subregions, of which the "Polynesian subregion" includes all Pacific islands within an area bounded by lines passing through and including Hawaii, the Marquesas, and Pitcairn Island on the east, the Austral Islands and New Caledonia on the south, the New Hebrides, Santa Cruz, Carolines, Palau, Yap, Guam, and Marianas Islands on the west, and the Marianas, Wake, and Hawaiian islands on the north. This scheme was based largely on a study of vertebrates, especially birds, and with few data from the central Pacific. Moreover, as recently discussed by Buxton (31), the faunal relations at the junction of Oriental and Australian regions in the Malay Archipelago are much more difficult to determine than might be supposed from a discussion like that of Wallace (245). It is therefore apparent that the zoogeographical scheme proposed by Wallace and his followers for the central Pacific is based on inadequate evidence and should be abandoned.

Since no comprehensive system has been proposed to replace that of Wallace and his successors, all that can be presented here is a summary of the opinions advanced by a few specialists on individual groups of animals. Among the first to challenge the old system was Hedley (116), who found it impossible to regard New Zealand and the central Pacific islands as appendages of Australia. In proposing "A zoogeographical scheme for the mid-Pacific", he devotes most attention to land snails, especially *Placostylus*. Migration is supposed to have occurred by former land connections between New Guinea, the Solomons, New Hebrides, Fiji, New Caledonia and New Zealand, and by overseas drift from a region near Fiji to Samoa and other remote central Pacific islands.

It might be expected that modern students of Pacific land snails, which have received more attention than other invertebrates, would elucidate their affinities and origin. Though they advance the strongest evidence for former land connections in the mid-Pacific, Pilsbry, Cooke, and Crampton have written little on the ultimate affinities of the land snails, because the affinities are obscure and the more urgent problem now is to collect material for subsequent analysis. Cooke (58), however, writes briefly on successive waves of migration, of which the first was that of the Partulidae, Achatinellidae, Amastridae and related families, so long ago that no snails related to them have been recognized in the faunas of existing continents. Later movements were those of the Zonitidae, Endodontidae, Succinidae, Pupillidae, and Tornatellinidae, which are represented in continental faunas, but Cooke does not state definitely where the affinities of the central Pacific members of these families lie. Pilsbry (186), however, asserts that no American influence is recognizable in the mid-Pacific land snail faunas.

Germain (102-104), writing principally on land snails, separates Hawaii and Easter Island from the rest of the central Pacific to unite them with the American continents in Cretaceous or early Tertiary times. Some elements of the Hawaiian fauna, however, came from parts of Polynesia south of Hawaii. The faunas of mid-Pacific islands other than Hawaii and Easter Island, according to Germain, are also of great antiquity, without American affinity, and came across land connections that stretched from the Mangareva and Marquesas Islands westward to the Carolines and Philippines. Fiji is made the eastern limit of the Melanesian fauna; New Caledonia and New Zealand are said to have received land snails from the north by way of the New Hebrides, New Guinea, and the Solomons, and from the south from Antarctica.

Perkins (182) regards the fauna of Hawaii as composed of the descendants of "waifs and strays" of overseas dispersal, and of such obscure and scattered affinity that he advances no conclusion as to whence came the fauna as a whole. In regarding the Hawaiian islands as oceanic in origin, Perkins is followed by some other Hawaiian entomologists, notably the late F. W. Muir (169, 170) who held the same view regarding Samoa. Buxton (31, 32), considering the entire Samoan fauna, also believes in the oceanic origin of the islands and states that the fauna, though largely Indo-Malayan, contains Australian elements of which the extent and importance are difficult to determine.

Holdhaus (124), writing on insects, retains much of the old scheme of Wallace and others. He places Hawaii in a separate region and divides the Australian region into four subregions: (1) extra-tropical Australia and Tasmania; (2) New Zealand and adjacent islands; (3) Melanesian subregion, with tropical Australia and the islands westward as far as and including Fiji, Tonga, and Samoa; (4) Polynesian subregion, with the Micronesian archipelagoes and central Pacific islands east of Samoa as far as Easter Island and Sala y Gomez. He regards Samoa and islands to the west as once part of a continent, and islands east of Samoa as oceanic. It is important to note that Holdhaus had at his disposal very little information on central Pacific islands; he refers only to a few papers in the series "Insects of Samoa" and to none of those on the Marquesas and Society Islands published since 1932.

Meyrick (163-165) makes an important contribution by recognizing in some genera of moths a faunal element characteristic of mid-Pacific islands east of Samoa. The argument is based especially on the occurrence on many islands of endemic species of the Cosmopterygid *Asymphorodes* in the Microlepidoptera, the Tortricid *Dichelopa,* and the Pyraustid *Scoparia* and *Mestolobes* and the Phycitid *Ernophthora* (*Aspithra*) in the Pyraloid moths. According to Meyrick's interpretation of this evidence, a former continent, "Palaeonesia", extended from Rapa on the south to the Marquesas on the north, and from Pitcairn on the east to the Society and Cook Islands on the west. It was associated in geological time with Hawaii, where there are species of *Scoparia* allied to those of the Marquesas, and was dissociated from Samoa and Fiji. He recognizes that such a change in the past area of land involves vertical movements of no less than 12,000 feet. It is interesting to note that Meyrick explains the occurrence of a few species of *Dichelopa* in Australia by a single form transported originally by a chance storm from "Palaeonesia".

Chopard (45) divides the Orthopteran faunas of Pacific islands into three groups: (1) Hawaiian, of obscure affinities; (2) New Caledonian and New Hebridean, of affinities with northern Australia and New Guinea; (3) Polynesian and Micronesian, including the Fijis and islands north and east of them, of affinities largely Malayan. Chopard inclines to favor past land connections in order to explain the occurrence of large apterous grasshoppers of the genus *Rhaphidophora* from India as far as Samoa.

Berland (14) has, I believe, made the most important attempt yet published to solve the problems of geographical distribution of any single group of animals in the central Pacific. He recognizes the following "provinces" for the spiders of Pacific islands: (1) "australo-canaque", including Australia, New Caledonia, New Zealand, and islands adjacent to them; (2) "papouasienne", closely allied to the preceding with New Guinea, the Solomons, New Hebrides, and neighboring archipelagoes; (3) "polynésienne", with Fiji, Tonga, Samoa, and other islands as far as Easter Island, the Marquesas, and Hawaii, of affinities mentioned below; (4) "micronésienne", with the many, little known Micronesian archipelagoes; (5) "néotropicale", with the Galapagos and Juan Fernandez Islands off the west coast of South America; (6) "antarctique", with the Campbell, Auckland, Kerguelen and other sub-antarctic islands, as well as Tierra del Fuego. Berland shows clearly, I believe, that the spider faunas of the islands in his "province polynésienne" are sufficiently alike to have been derived from common sources, namely from Indo-Malaya. He summarizes his conclusions thus:

> Tout semble bien indiquer que le peuplement du Pacifique s'est fait par des migrations provenant de la région indo-malaise, migrations qui auraient probablement été multiples et suivant plusieurs courants distincts. L'un de ces courants aurait peuplé en même temps la partie est de l'Australie ainsi que ce que j'appelle la province australo-canaque; un courant de migration bien distinct, mais de même origine, aurait peuplé la Polynésie, dont les archipels actuels ne constituent probablement que le morcellement d'un continent plus étendu, avec un rameau se détachant vers les Hawaï; un autre courant va vers la Micronésie. Il n'y a aucune relation visible entre l'Amérique et le Pacifique; mais par contre les Galapagos aussi bien que les Fernandez ont reçu leur faune d'Amérique du sud, et l'on trouve des traces évidentes de liaison entre cette dernière et l'Australie, par les terres australes.
>
> Par ailleurs les îles du Pacifique présentent presque toujours un endémisme très prononcé, qui témoigne d'un isolement fort ancien, et il faut fixer leur séparation à une époque assez reculée, au moins vers le milieu du Tertiaire, et peut-être bien avant.
>
> J'ajouterai que l'étude de plusieurs groupes zoologiques, ainsi qu'on peut le voir dans cet ouvrage, arrivent, indépendamment les unes des autres, à des conclusions si proches des miennes, que celles-ci me paraissent en recevoir une solide confirmation.

In discussing the distribution of fishes, P. J. Schmidt (203) asserts that "the Pacific was formed in very ancient geological times and has undergone no important changes. It existed in the Triassic, Jurassic and Cretaceous epochs as a basin of nearly the same dimensions as now, and had a fauna of the same character."

C. E. and M. D. Burt (30) trace the migration of reptiles of the Pacific islands along lines from the neighborhood of Papua which pass northeast to Micronesia and southeast to the New Hebrides, New Caledonia, Fiji, Samoa, and as far as the Marquesas. The fauna of all these islands was apparently derived from the East Indian archipelagoes, and its relations to Australian and New Zealand reptiles are only indirect and due to derivation from the common source in the East Indies.

BOTANICAL THEORIES

A grave deficiency in biogeographical theory is the lack of correlation between zoological and botanical schemes. Therefore it is not surprising that little attempt has been made to explain by a single scheme the distribution of animals and plants of mid-Pacific islands. On the question of past land connections the botanists are divided in the same manner as the zoologists and even more divided regarding floral affinities. The generally accepted modern view on affinities seems to be that of Skottsberg, Setchell, Campbell, Copeland, and a few others, who assert that the floras of the central Pacific have been derived from the southwest, with little or no influence from the Americas. Campbell (35, 36) finds a larger Australian element in Hawaii than most botanists admit. The importance of a possible element from Tertiary Antarctica is emphasized by Skottsberg (216, 218-219) and approved by Setchell (213). This argument is based largely on a few genera, notably *Astelia* and *Gunnera,* which have a tricentric, circumpolar distribution.

Guillaumin (108) and Brown (24) derive the Hawaiian flora almost exclusively from America, as Rock (196) does the Hawaiian Lobeliads. Brown (25-27) would extend the American influence across all central Pacific islands. His views, which have already been discussed in some detail (3), are in direct opposition to those of most botanists. The importance of the American element in Hawaii has diminished in modern opinion. Keck (134), reexamining examples of supposed affinities of this kind, rejects almost all of them. Regarding the Hawaiian Silverswords he writes: "By thus divorcing *Argyroxiphium* from the American genera to which it has been thought related, the most persistently proposed connection between the ancient element in the Hawaiian flora and the New World has been shattered."

Most botanists are apparently opposed to the hypothesis of former land connections in the central Pacific. Merrill (162), writing on the Gymnosperms which are represented by a single species in Samoa and Tonga and are absent farther east, states: " . . . Samoa, Tahiti, Hawaii and the Marquesas are oceanic islands . . . " Hillebrand (122) regarded the Hawaiian flora as oceanic. Setchell (208) finds land connections more difficult to accept than transoceanic dispersal and in a recent paper (213) he proposes open seas, uninterrupted by land bridges, in the Tertiary Pacific, to explain the distribution of marine flowering plants. Skottsberg (220) cannot dispense altogether with land connections but suggests changes in land areas mostly around the margins of the Pacific, leaving "an open sea in the sense of Setchell." Campbell (35, 36) requires land connections between Hawaii and Indo-Malaya and Australia, and Brown (26) suggests that the atolls of the Tuamotus were once high mountains.

SUMMARY OF BIOGEOGRAPHICAL THEORIES

The above review of literature on the affinities and origin of central Pacific faunas and floras may be summarized as follows:

Authors are almost equally divided between those who require past land connections and those who reject them. A decision between the opposing views can scarcely be made on the basis of published opinion.

The old view that almost all Oceania forms a Polynesian subregion of the Australian region has been rejected by most competent authorities and should be abandoned altogether. It is generally agreed that the central Pacific islands constitute a subregion, or area of similar or rather smaller content, but few authors have even attempted to define its limits. Hawaii is included by some, excluded by others; some biologists regard Hawaii as a separate region, and a few unite it with parts of America. Some divide the Polynesian from the Melanesian faunas at a line east of Samoa, others so far to the west as to include Fiji.

According to almost all authors who have written on the subject, the affinities of central Pacific faunas and floras, excluding those of Hawaii which are obscure, are predominantly Indo-Malayan. Australian affinities are considerably important, though clearly less so than the Indo-Malayan; in some instances they are probably not direct, but due, at least in part, to derivation from a common source in Indo-Malaya. New Zealand affinities are of small significance, and possibly only indirect. American affinities are few, and perhaps altogether lacking in most large classes of animals and plants. According to Skottsberg, there is an "Old Pacific" floral element, derived from Tertiary Antarctica, in the central Pacific. No comprehensive attempt has been made to determine whether a similar element is present in mid-Pacific faunas.

THE MARQUESAS AS AN ENVIRONMENT FOR A FAUNA

In a previous paper (3) I have attempted to describe the Marquesas Islands as an environment for a fauna. Here I briefly summarize parts of that paper, especially those topics bearing most closely on the origin of the fauna.

Geography

The Marquesas Islands lie near the center of the Pacific Ocean, between latitudes 7°50′ and 10°35′ S and longitudes 138°25′ and 140°50′ W (fig. 1). They are among the most isolated of all islands. The nearest land is that of the Tuamotuan atolls, 300 miles to the south; the nearest high islands, those of the Society group, are 800 miles to the southwest; the nearest continent is 3,000 miles to the east. The Marquesas are separated from other land by depths of probably not less than 2,000 fathoms.

The following table is based on all available data but most of the figures are only approximate.

Dimensions of the Marquesas Islands

	Area (sq. mis.)	Length max. (mis.)	Breadth approx. max.	Greatest altitude (ft.)	Area above 2,000 ft. (sq. mis.)
Fatuhiva	30.0	9.0	4.5	3670	5
Mohotani	6.0	5.0	1.5	1700	—
Tahuata	20.0	9.0	5.0	3280	2
Hivaoa	125.0	25.0	8.0	4130	25
Fatuuku	0.5	1.5	0.5	1180	—
Uapou	40.0	9.0	8.0	4040	3
Uahuka	30.0	9.0	5.0	2805	1
Nukuhiva	130.0	16.0	12.0	4000	30
Eiao	20.0	8.0	4.0	2000	—
Hatutu	7.0	5.0	2.0	1380	—

The total area of the Marquesas Islands is about 400 square miles. They are thus smaller and lower than Hawaii, Samoa, and the Society Islands, but much larger and higher than the Austral, Cook, Mangareva Islands, and Rapa.

The Marquesas form an irregular chain about 50 miles wide and 230 miles long, divided into three groups by intervening distances of about 60 miles: Fatuhiva, Mohotani, Tahuata, Hivaoa and Fatuuku in the southeast, Uapou, Uahuka and Nukuhiva in the center, and Eiao and Hatutu in the northwest (fig. 2). Interisland channels are from 3 to 25 miles wide and most of them are probably over 1,000 fathoms deep. Only two of the larger islands, Hivaoa and Tahuata, which are only 3 miles apart, are known to be separated by depths of less than 1,000 fathoms.

All the islands are more or less clearly the summits of large extinct volcanoes. In most of them a central ridge probably represents the rim of a large crater. In central Nukuhiva and in parts of Hivaoa there are small plains between 2,000 and 3,000 feet high. In the larger islands the floor of the principal valleys is flat for a few miles inland from the sea, but elsewhere the topography is extremely rugged. All the islands are almost continuously bounded by high cliffs and are unprotected by coral reefs, the almost complete absence of which is one of the most striking features of the Marquesas.

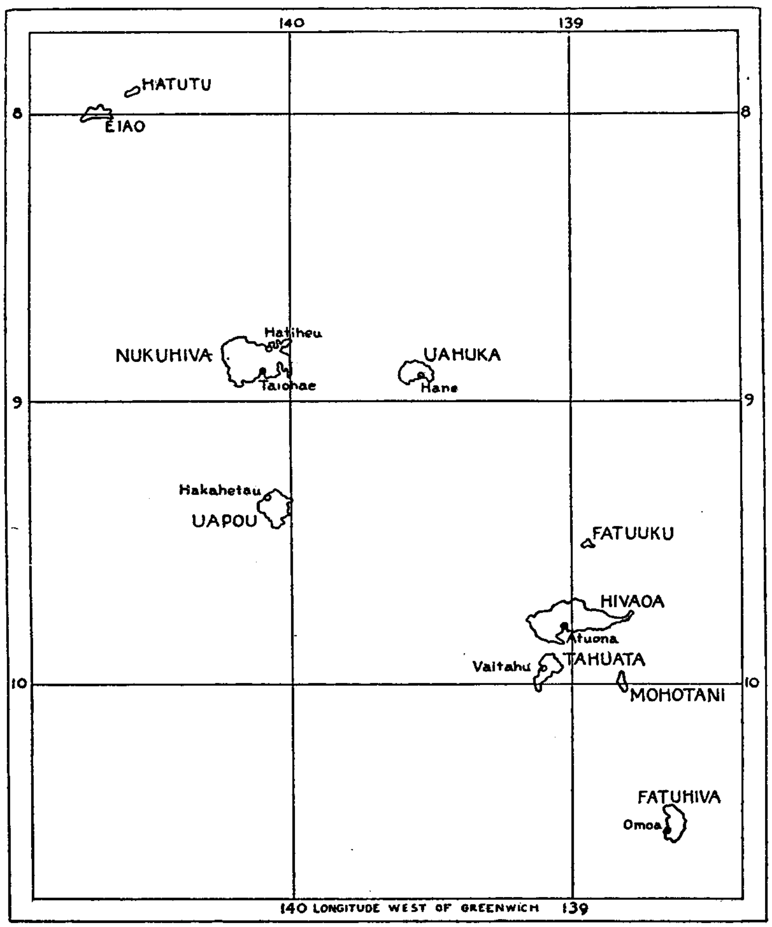

FIGURE 2.—Map of the Marquesas Islands.

There are abundant streams on all of the six highest islands, but lakes and swamps are unknown and scarcely any pools of stagnant water exist in the interior. Habitats for fresh-water animals are thus very restricted in variety, as they are on most central Pacific islands.

GEOLOGICAL HISTORY

According to Chubb (52, 53), the only geologist who has worked in the Marquesas, the islands appear to have arisen by outpouring of lava from fissures on the ocean floor. After periods characterized by explosions, mostly of ash, and then by extrusion of dykes and sills, extensive faulting produced the coastal cliffs and the amphitheatres now representing volcanic craters. After a long period of wave erosion, elevation of 2,000 to 3,000 feet is said to have occurred, followed by subsidence of at least 600 feet, as shown by the embayment of the coastline. Though Chubb is satisfied with the evidence for the above hypotheses, some of the data may be open to other interpretations (Williams, 251, and Adamson, 3) and the geological questions most important to a biologist cannot yet be answered with assurance.

Estimating the age of central Pacific islands is difficult because of the absence of ancient fossils. Judged by their present physiography, the Marquesas appear to be younger than Hawaii, of about the same age as the leeward Society Islands and the oldest islands in Samoa. They are probably older than Tahiti. Schuchert (205) believes that the Hawaiian islands arose in early Cretaceous times. According to Marshall (160) Rarotonga in the Cook Islands is probably of early Tertiary origin. Williams (251) believes that the Society Islands arose not later than the Pliocene. Daly (71) found lavas of Pliocene or greater age in Tutuila, the oldest island of Samoa.

Therefore it may be concluded tentatively on the meager geological evidence, that the Marquesas became habitable for a land fauna and flora during the Pliocene or probably later. Vulcanism sufficiently violent to render such small islands uninhabitable may have continued through the Pleistocene. Judged by the amount of erosion, the six larger islands of the Marquesan group may be regarded as of similar habitable age. Mohotani may be younger than the others (Chubb, 52). I know of no geological data on the relative ages of the remaining islands: Eiao, Hatutu, and Fatuuku.

Climate

A few records of rainfall in the Marquesas have been published by Hellman (117) and a general account of the climate, based on observations made by members of the Pacific Entomological Survey, by Leighly (142).

The mean annual temperature at Atuona (south coast of Hivaoa) in 1930 was 25.8°C., the mean maximum 31.9°, the mean minimum 22.4°, the "mean annual range" 2.1°. Mean monthly temperatures at 2,000 feet on Nukuhiva were 5° to 6° lower than at sea level.

The annual rainfall at sea level varies between 40 and 120 inches, there being great fluctuations from year to year. Precipitation in the mountains of the six largest islands is very high, but the islands of Eiao, Hatutu, Mohotani, and Fatuuku are too low to cause much precipitation from the normal trade winds.

The trade winds blow almost continuously in the Marquesas, usually from east to southeast during April to October and from east to northeast for the rest of the year. High winds are rare and so far as I know hurricanes have not been recorded. The following summary on the Marquesan climate is taken from Adamson (3, p. 21).

The greater part of the endemic fauna, being now restricted to high altitudes, has a physical environment which is remarkably constant in all respects, with very moist conditions, and a climate that is temperate rather than tropical. At low and intermediate levels on the higher islands, and everywhere on the lower islands, the climate is tropical, but without extremely high temperatures. Periods of several years of abundant rain appear to alternate with periods of prolonged drought; on the leeward sides of the higher islands, and in all parts of the lower islands, the drought may amount to desiccation and cause the withering of most of the herbaceous vegetation. Fatuhiva appears to be rainier, relatively to its altitude, than the other islands. All elements other than precipitation vary within narrow limits. Seasonal variations in most climatic elements are irregular and of small degree. Diversity of habitat, in comparison with conditions on many other central Pacific islands, is great with respect to rainfall and small with respect to temperature.

Flora

General Features

The Thallophyta of the Marquesas are little known. The vascular plants have been extensively but far from exhaustively collected. F. B. H. Brown and E. D. W. Brown in the "Flora of southeastern Polynesia" (23, 25, 27) record 72 species of pteridophytes, 98 of monocotyledons, and 287 of dicotyledons. Of these about 20 percent are endemic, 20 percent indigenous but occurring elsewhere, 20 percent aboriginal introductions, and 40 percent have probably arrived since the discovery of the islands by Mendaña in 1595.

Characteristic and noteworthy features of the floras of the central Pacific islands are the almost complete absence of native gymnosperms, which have their eastern limit, with only one species, in Samoa and Tonga (162); the relative abundance of ferns, with a correspondingly small representation of herbaceous flowering plants; the dominance of such families as the Myrtaceae, Rubiaceae, Euphorbiaceae, Compositae, Piperaceae, and Urticaceae, which are represented mostly by trees and shrubs. Thus, though the floras of these remote islands are rich in species, the habitats and food afforded for animals are limited and specialized.

For a student of the fauna, the vegetation of the larger islands in the Marquesas may be divided into three zones:

(1) Rain forest of the cloud zone, 1,500-2,500 feet and upward to the summits of the mountains, forming an almost continuous and very dense covering. Very tall trees and pure stands are not found, and the undergrowth is composed largely of ferns. The branches of the trees are heavily overgrown by epiphytic mosses and pteridophytes. On some exposed ridges and slopes the forest is reduced to stunted trees less than 2 feet high or to an association of pteridophytes, *Freycinetia,* and stunted shrubs. Almost all

species of plants are endemic or at least indigenous, and many are entirely restricted to the cloud zone.

(2) Intermediate zone of moderately heavy rainfall, from 1,000-1,500 to 2,000-2,500 feet, covered by mesophytic forest, and in many parts by secondary growth of staghorn fern (*Gleichenia linearis*) and grasses. Both native and introduced plants are well represented. Herbaceous flowering plants, especially grasses, are more abundant than in the cloud zone and the pteridophytes less so. Indigenous animals are abundant, though fewer than in rain forest.

(3) Low levels from the sea to 1,000-1,500 feet, and regions of low rainfall up to 2,000-2,500 feet, characterized by a dominance of introduced species and absence of most endemic species. Forests with some tall trees and a thick undergrowth occupy many valleys and even exposed slopes, but over large areas there is only open forest of drought-resisting trees or a scrubby growth of xerophytic shrubs. Much of the lowland slopes is covered by grasses or by *Gleichenia,* and considerable areas have been completely denuded by introduced grazing animals. The fauna supported by the lowland flora is meager and includes few endemic invertebrates.

On the uninhabited islands the altitude is not sufficiently great for the development of well-defined zones of vegetation, the entire flora being similar to that of the lowland zone of the higher, inhabited islands.

Hivaoa and Nukuhiva, the largest islands, probably have the richest floras, but those of Fatuhiva and Uapou are nearly as varied. Many characteristic members of the rain-forest flora are absent or present in very small numbers on Uahuka. The uninhabited islands lack most of the plants of the mountain flora, the vegetation being largely xerophytic, and almost all of the trees and shrubs are species of wide distribution. Eiao, however, has a much richer flora (and fauna) than Mohotani. On Hatutu only one species of tree (*Pisonia*) was found, but a few *Sapindus, Thespesia,* and *Hibiscus* trees, as well as *Pisonia,* grow on Fatuuku.

According to the above general observations the islands may thus be placed in the following order with respect to the number of species in their floras: Hivaoa and Nukuhiva, Fatuhiva, Uapou and Tahuata, Uahuka, Eiao and Mohotani, Hatutu and Fatuuku.

FOOD-PLANTS OF MARQUESAN INSECTS

The interrelations of animals and plants afford interesting data on geographical distribution. One of Perkins' (182) criteria for deciding whether an insect was native or foreign in Hawaii was its association with indigenous or introduced plants, and Swezey (228) has written on "The insect fauna of trees and plants as an index of their endemicity and relative antiquity in the Hawaiian islands."

In the Marquesas, two trees support a much larger insect fauna than any others: *Metrosideros collina,* a polymorphic species widely distributed in the Pacific, and *Weinmannia marquesana,* endemic but allied to the Tahitian *W. parviflora.* Other food-plants of greatest importance are *Crossostylis* *biflora,* also in Tahiti and Samoa; *Vaccinium cereum,* also in the Society and Cook Islands and possibly in the Austral Islands and Tonga; and endemic Marquesan species of *Cyrtandra, Ilex,* and *Sclerotheca.* It is interesting to note that *Metrosideros collina* is one of the first two species in Swezey's (228) list of Hawaiian plants supporting the largest insect fauna. (The other, *Acacia koa,* does not occur in the Marquesas.) In some other features of interrelations between insects and plants the Hawaiian and Marquesas Islands are remarkably similar (3, p. 41). This may indicate an important affinity, but unfortunately little is known about this subject on other Pacific islands.

Influence of Man on the Fauna and Flora

The Marquesans are Polynesians who reached the islands in canoes probably less than 2,000 years ago (106, 110). It seems certain that the Polynesian race as a whole came from Asia, and if there was ever communication between the Marquesas and America in prehistoric times, it had little or no influence on these islands. Wherever they went, the Polynesians introduced a large number of food-plants; according to Brown (25, 27) nearly 100 species of vascular plants were introduced to the Marquesas by intent or accident. Some of these plants are now dominant over large areas in the islands, notably *Hibiscus tiliaceus* which is the most abundant forest tree up to about 2,500 feet in many parts of the islands, and the staghorn fern (*Gleichenia linearis*) which has replaced all other vegetation over many large areas up to 2,500 feet and which is an important element in the vegetation even to the summits of the mountains. A considerable amount of forest was destroyed by clearing for cultivation, but probably not at high altitudes.

To the early Polynesians must be attributed the introduction of pigs, fowls, rats, and probably other animals such as lizards, some centipedes, and many other stowaways. The influence of these on the native fauna, however, was probably small.

The Spanish admiral Mendaña "discovered" the southeastern Marquesas Islands in 1595, coming from Peru and remaining for fifteen days. The visit of his ships had probably little permanent effect on the islands, though some human diseases may have been introduced. The next visit was that of Cook in 1774, again to the southeastern islands only. Other islands were discovered in 1791 by Ingraham, and subsequent visits followed at short intervals. The first missionaries came in 1797. Permanent occupation of the islands by the French began in 1842.

For nearly 150 years, then, the Marquesas have been influenced by western civilization, with results probably more disastrous than anywhere else in the Pacific islands. The Marquesans, once numbering between 50,000 and 100,000 people of magnificent physique, have been reduced to a mere 2,000. Goats, sheep, cattle, pigs, horses (and asses on Uapou) have reduced the dry, leeward slopes of most of the larger islands to semi-desert. The destruction of the forests and ultimate denudation of Eiao by sheep, cattle, pigs, horses, and asses, and of Mohotani by sheep, are imminent. Cats, escaped from domestication, are abundant almost everywhere. The Marquesas have not been afflicted by lantana, but guava and many other noxious plants are now widespread. The worst of these is probably *Paspalum conjugatum,* a grass which can kill forest trees, and which is invading the mountains where other foreign influences are as yet not very destructive. The nefarious mynah bird (*Acridotheres tristis*) has been introduced only on Hivaoa. The flora of almost all regions below about 2,000 feet is therefore composed largely of foreign plants, and the habitats for native animals have thus been profoundly altered.

Apart from the devastation on Eiao and Mohotani, the most destructive of all foreign enemies of the native fauna is probably the ant *Pheidole megacephala* F., which is abundant everywhere up to 2,000-3,000 feet, and in smaller numbers to the summits of the highest mountains. In Hawaii this ant has exterminated most of the native insects up to about 2,000 feet, which is near its upper limit (182). There are no comparative data to indicate how much change it has made in the Marquesan fauna, but it seems certain that a considerable impoverishment of many groups of insects has already occurred and is continuing.

SYSTEMATIC REVIEW OF THE MARQUESAN FAUNA

In the following systematic review of the fauna of the Marquesas Islands I have devoted special attention to those groups in which I was most interested in the field and to those which are most interesting biogeographically. As a review of the non-marine invertebrates, exclusive of insects, has already been published (2), I give here only the briefest summaries on these animals.

An attempt to list all the known species has been made only in certain groups, but the table on pages 28-33, which shows the families and higher groups present in the Marquesas, has been made as complete as possible.

The marine fauna is not included in the review, because little has been published about it and because it throws relatively little light on the biogeographical problems considered here. It is clear, however, in reports from other islands, especially Hawaii, that the marine animals of the central Pacific islands have come from the southwest, with little influence from America. The most striking feature of the fauna of the Marquesan coasts is the absence of large coral reefs, and the poverty of the marine fauna in general. This is due in part to the small area under shallow water round the precipitous coasts, and to other adverse ecological conditions, some of which are obscure. (See Crossland, 67; Chubb, 52; and Adamson, 3.)