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

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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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Review of the Fauna of the Marquesas Islands and Discussion of its Origin

By

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 freshwater 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 con-

tinuously 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.

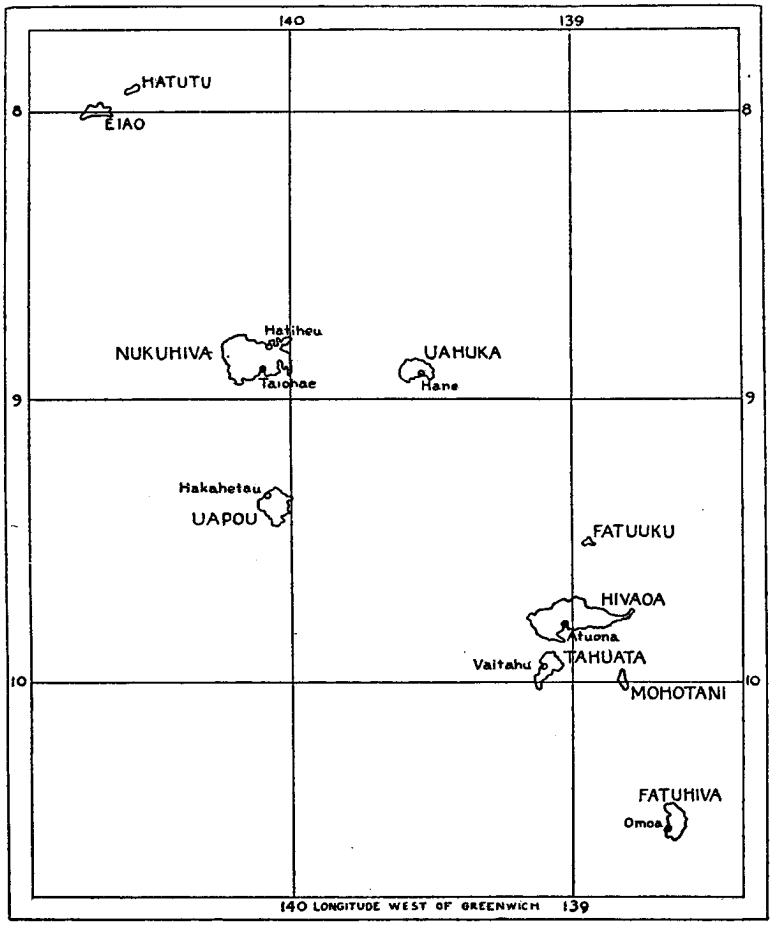

FIGURE 2.—Map of the Marquesas Islands.

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.)

Tabular Review of Marquesan Non-marine Fauna and its Probable Affinities

	Endemic spp.	Non-endemic spp.	Indo-Malayan	Australian	American	Hawaiian	"Mid-Pacific"
PROTOZOA		x					
PLATYHELMINTHES	?	?					
NEMATHELMINTHES	?	x					
TROCHELMINTHES		?					
ANNULATA							
Oligochaeta		x					
MYRIOPODA							
Chilopoda							
Scolopendridae		x	x				
Oryidae		x					
Mecistocephalidae		x	x				
Symphyla							
Scutigerellidae		x					
Diplopoda							
Polydesmidae		x					
Trigoniulidae		x					
Cambalidae		x					
CRUSTACEA							
Ostracoda	?	?					
Copepoda	?	?					
Amphipoda							
Talitridae	x	x	x				?
Isopoda							
Oniscidae	x	x					?
Decapoda							
Atyidae		x	x				
Palaemonidae		x	x				
INSECTA							
Thysanura							
Lepismatidae	?	x		x			
Collembola							
Poduridae	x	x	x				
Entomobryidae	x	x				x	
Sminthuridae	x						
Orthoptera							
Blattidae	x	x	x	x			
Phasmidae		x					
Acrididae	x						
Tetrigidae	x						?
Tettigoniidae	x	x	x	?			?
Gryllidae		x					

TABULAR REVIEW OF MARQUESAN NON-MARINE FAUNA AND ITS PROBABLE AFFINITIES—Continued.

	Endemic spp.	Non-endemic spp.	Indo-Malayan	Australian	American	Hawaiian	"Mid-Pacific"
Dermaptera							
Labiidae		x	x				
Labiduridae		x	x				
Isoptera							
Kalotermitidae	x	x			?		?
Rhinotermitidae	?		x				
Embioptera							
Oligotomidae		x					
Psocoptera	?	?					
Anoplura							
Mallophaga							
Menoponidae	?	x					
Philopteridae		x					
Trichodectidae		x					
Siphunculata							
Pediculidae		x					
Haematopinidae		x					
Odonata	x	x					
Thysanoptera	x	x					
Hemiptera — Heteroptera							
Pentatomidae	x	x					
Coreidae	x	x					
Lygaeidae	x	x	?				
Aradidae	x						
Veliidae	x	x					
Reduviidae	x						
Nabidae	x	x					
Anthocoridae	?	?					
Miridae	?	?					
Hemiptera — Homoptera							
Cicadellidae	x	x	x		x	x	?
Cixiidae	x	?				?	
Delphacidae	x	?				?	
Psyllidae	x	x				?	
Aphididae	?	x					
Aleyrodidae		?					
Coccidae	?	x					
Neuroptera							
Chrysopidae		x					
Hemerobiidae	x						
Lepidoptera							
Eucosmidae	x	x					

TABULAR REVIEW OF MARQUESAN NON-MARINE FAUNA AND ITS PROBABLE AFFINITIES—Continued.

	Endemic spp.	Non-endemic spp.	Indo-Malayan	Australian	American	Hawaiian	"Mid-Pacific"
Gelechiidae		x					
Cosmopterygidae	x	x					?
Heliodinidae	x						
Glyphipterygidae	x						
Gracilariidae	x	x					
Lyonetiidae	x	x	x				
Tineidae		x					
Tortricidae	x			?			?
Phycitidae	x	x					
Pyraustidae	x	x				x	?
Nymphalidae	x	x					
Sphingidae	x	x					
Geometridae	x	x					
Arctiidae	x		?	?			
Noctuidae	x	x					
Coleoptera							
Carabidae	?	x					
Dytiscidae	?	?					
Staphylinidae	x	x	?				
Histeridae		x					
Trogositidae		x					
Nitidulidae	?	x					
Cucujidae	?	x					
Cryptophagidae	?	?					
Mycetophagidae		x					
Colydiidae	?	x					
Endomychidae		x					
Coccinellidae		x					
Dermestidae		x					
Hydrophilidae		x					
Cantharidae	x						
Cleridae		x					
Anobiidae	x						
Bostrychidae		x					
Lyctidae		x					
Cisidae	x						
Buprestidae	x	x	x				
Elateridae	x	x					?
Tenebrionidae		x					
Oedemeridae		x					
Bruchidae		x					
Xylophilidae	x						
Cerambycidae		x					

TABULAR REVIEW OF MARQUESAN NON-MARINE FAUNA AND ITS PROBABLE AFFINITIES—Continued.

	Endemic spp.	Non-endemic spp.	Indo-Malayan	Australian	American	Hawaiian	"Mid-Pacific"
Brenthidae		x					
Anthribidae	x	x	x				
Curculionidae	x	x	x				?
Platypodidae		x					
Scolytidae	x	x	x				
Aglycideridae (Proterhinidae)	x						?
Scarabaeidae		x					
Hymenoptera							
"Parasitica" (inadequately known)	x	x					
Formicoidea	?	x	x	?		?	
Vespoidea							
Bethylidae	x					x	
Eumenidae		x					
Vespidae		x					
Apoidea							
Andrenidae	?	?					
Apidae		x					
Diptera							
Nematocera							
Tipulidae	x	x	?				?
Psychodidae		?					
Culicidae		x					
Chironomidae	x	x					
Ceratopogonidae	x	x					
Simuliidae	x						?
Brachycera							
Stratiomyidae		x					
Dolichopodidae	x	x					
Aschisa							
Pipunculidae	?	?					
Syrphidae		x					
Schizophora — Acalypterae							
Ortalidae	x	x					
Trypetidae	x	x	?	?			
Sapromyzidae	x	x					
Agromyzidae	x						
Drosophilidae	x	x					
Ephydridae	x	x					
Chloropidae	x	x					
Asteiidae	x						
Schizophora — Calypterae							
Muscidae (incl. Anthomyidae)	x	x					

TABULAR REVIEW OF MARQUESAN NON-MARINE FAUNA AND ITS PROBABLE AFFINITIES—Continued.

	Endemic spp.	Non-endemic spp.	Indo-Malayan	Australian	American	Hawaiian	"Mid-Pacific"
Sarcophagidae		x					
Oestridae		?					
Pupipara							
Hippoboscidae		x					
Siphonaptera							
Pulicidae		x					
ARACHNIDA							
Scorpionida		x					
Pseudoscorpionida	x						
Araneida							
Dysderidae	x					x	
Sicariidae		x					
Oonopidae		x					
Drassidae	x			?			
Clubionidae		x	x				
Sparassidae		x					
Thomisidae	x						
Pholcidae		x					
Salticidae	x	x	x			x	?
Theridiidae	x	x					
Argiopidae	x	x	x				?
Pisauridae	x						
Dictynidae	x			?			
Uloboridae		x					
Acarina							
Macrochelidae	x						
Laelaptidae	x	x					
Celaenopsidae	x						
Sejidae		x					
Antennophoridae	x						
Trachyuropodidae	x						
Uropodidae	x	x					
Bdellidae		x					
Erythraeidae	x						
Anoetidae	x						
Proctophyllodidae		x					
Eriophyidae		x					
Tyroglyphidae	x						
Oribatidae	x	x	x		x	x	
Phthiracaridae	x						
Ixodidae		x					

TABULAR REVIEW OF MARQUESAN NON-MARINE FAUNA AND ITS PROBABLE AFFINITIES—Continued.

	Endemic spp.	Non-endemic spp.	Indo-Malayan	Australian	American	Hawaiian	"Mid-Pacific"
MOLLUSCA							
Gastropoda							
Zonitidae	x						?
Endodontidae	x						?
Stenogyridae		x					
Pupillidae	x	x					?
Partulidae	x						x
Tornatellinidae	x	x					x
Succinidae	x						?
Helicinidae	x						?
Limacidae		x					
Assimineidae		x					
Hydrocenidae		x					
Neritidae		x					
Melaniidae		x					
PISCES							
Muraenidae		x	?				
Mugilidae		x	?				
Eleotridae		x	?				
Gobiidae	x	x	?				
REPTILIA							
Lacertilia							
Scinidae		x	x				
Geckonidae		x	x				
AVES							
Ardeidae		x					
Rallidae		x					
Columbidae		x					?
Psittacidae	x	x	x				
Micropodidae	x		?	?			
Alcedinidae	x		x				
Sylviidae	x		?	?			
Muscicapidae	x		?				
Sturnidae		x					
MAMMALIA		x					

Protozoa

The Protozoa of the Marquesas are almost unknown and little work has been done on those of other central Pacific islands. Calkins (33) writes: "The common Protozoa of our ponds and pools are exactly the same in genera and species as those found in similar places in Europe, Asia, Siberia, South America and Australia." It therefore appears that these organisms are of relatively little importance in the study of geographical distribution.

Porifera

Fresh-water sponges appear to have their eastern limit in the central Pacific in Fiji, where *Spongilla gilsoni* was described by Topsent (233).

Coelenterata

No records of fresh-water Coelenterates in remote Pacific islands have been published, though zoologists in Honolulu have told me that *Hydra* occurs there.

Platyhelminthes

The only flatworms collected in the Marquesas were a few land Planarians, probably of one species which is not uncommon in wet vegetation. In other central Pacific islands the only known Platyhelminthes appear to be a few widespread species, one or two undetermined Planarians in Hawaiian streams, and two tapeworms in Hawaiian Drepanid birds. Further collecting may add some endemic parasites to the meager list. New Caledonia has a large number of endemic land Planarians (Schröder, 204).

Nemertinea

A few land Nemerteans are known in Samoa (Hett, 120, Buxton, 31) but none farther east in the central Pacific.

Nemathelminthes

A few small nematodes, not yet determined, were collected in wet humus in Marquesan forests. *Rhabditis coarctata* Leuckart was found on caterpillars, and three well-known human parasites—*Enterobius vermicularis* (L.), *Ascaris lumbricoides* L. and *Filaria bancrofti* Cobbold—probably occur. Many species have been described from soil in other Pacific islands, especially in Hawaii, but their geographical relations are little known. Of Acanthocephala only the Hawaiian *Apororhynchus hemignathi* Shipley appears to be known in the non-marine fauna of central Pacific islands.

Trochelminthes

A few unidentified Rotifers were collected in the Marquesas. Probably all those recorded from other islands are widely distributed species (Murray, 177). Records of Gastrothricha appear to be entirely lacking.

Molluscoidea

The only fresh-water Polyzoans recorded from the central Pacific are the endemic *Hyalina vaihiriae* Hastings and the widespread *Plumatella emarginata* Allman from Tahiti (Hastings, 111).

Annulata

A few species of earthworms, not yet identified, were collected in the Marquesas. No leeches were found.

The Oligochaeta is one of the large groups surprisingly absent from the endemic faunas of all remote islands. (See especially Stephenson, 224.) Among leeches, however, *Philaemon minutus* Blanchard appears to be endemic in Samoa (Buxton, 31) and two undetermined species are reported in Hawaiian streams (Bryan, 29).

Arthropoda

Many orders of Insecta, and the Araneida and Acarina in the Arachnida, are well represented in the endemic Marquesan fauna. In the meager Crustacean fauna only a few endemic species occur; no endemic Myriopods have been thus far collected; Onychophora are probably absent in the central Pacific east of Fiji.

Crustacea

Entomostraca

No fresh-water Branchiopoda or Cladocera were found in the Marquesas, and only one Ostracod—*Cypretta nukuhivana* Furtos (98)—and a few undetermined Copepods. Few fresh-water Entomostraca are known in other Pacific islands and they are of little biogeographical interest. Four species of Cladocera recorded by Ueno (234) from Mauna Kea, Hawaii, at altitudes up to 13,000 feet, are all of very wide distribution.

Amphipoda

The non-marine Amphipods of the central Pacific are restricted to a few terrestrial Talitridae. In the Marquesas three species are known: the widely distributed *Orchestia floresiana* Weber and *Talitrus sylvaticus* Haswell, and the presumably endemic *Orchestia marquesana* Stephenson (224).

Isopoda

A semi-aquatic, widely distributed Ligiid—*Ligia vitiensis* Dana—and 12 terrestrial Oniscidae are known in the Marquesas (Jackson, 125). Five of these wood lice are wide-ranging species. *Philoscia fasciata* Jackson, also found in Tahiti, is abundant at all altitudes. An interesting group of six species of Armadillinae, of which *Echinodillo montanum* Jackson and *Tridentodillo squamosus* Jackson belong to endemic genera, is apparently restricted to the cloud zone. The non-marine Isopods of the Society Islands, though little known, appear to be similar to those of the Marquesas. The apparent absence of fresh-water species and the presence of a small endemic element in the Armadillinae are features common to most central Pacific archipelagoes.

Decapoda

Three small Atyid shrimps—*Caridina weberi* de Man, *Atya serrata* Spence Bate, and *Ortmannia alluaudi* Bouvier—and three large prawns of the family Palaemonidae—*Palaemon lar* Fabricius, *P. dispar* von Martens and *P. latimanus* von Martens—are common in Marquesan streams (Adamson, 2). All of these species range widely from the Marquesas across the Pacific islands, many of them reaching as far as Madagascar and other islands in the western part of the Indian Ocean. This very interesting distribution may have been acquired secondarily by the Palaemonids, many of which are known to enter brackish water from the sea, but the Atyidae are of ancient fresh-water habit and the occurrence of several species on widely separated islands remains without explanation. (See Edmondson, 77, and Buxton, 31.) A recent discovery of great interest is that of an endemic Atyid, *Caridina rapaensis* Edmondson (78), on Rapa.

MYRIOPODA

Seven species of Chilopoda, five of Diplopoda, and one of Symphila (*Hanseniella orientalis* Hansen) have been found in the Marquesas (Adamson, 1, and Silvestri, 215). It is very surprising that none of these is endemic, because the collections made, though probably far from complete, appear to be fairly representative. A few endemic species occur in most other high island groups. The affinities of the Marquesan centipedes and millipedes are with those of regions to the southwest.

INSECTA

Of the 23 orders of insects commonly distinguished, the following eight are known to be represented by many endemic species in the Marquesas: Collembola, Orthoptera, Thysanoptera, Hemiptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera. A few endemic species are already known in the

Thysanura, Isoptera, Odonata, and Neuroptera and a considerable number probably occur in the Psocoptera, which have not yet been studied. Widespread but probably native species are known in the Dermaptera, Embioptera, and Anoplura; only introduced species, presumably by human agency, are known in the Aphaniptera. The following six orders are not known to occur in the Marquesas and most of them are probably entirely absent: Protura, Plecoptera, Ephemeroptera, Mecoptera, Trichoptera, and Strepsiptera.

Thysanura

Only four species of Thysanura, all in the Lepismatidae, are known from the Marquesas, but further collections, particularly with apparatus of the Berlese funnel type, will probably reveal other families. *Isolepisma mumfordi* Silvertri is known only from the Marquesas, and *Acrotelsella producta* Escherich, which occurs also in northern Australia, is represented by two presumably endemic varieties. Silvestri (214) regards both these species as "typical of the Australian region" and *Ctenolepisma reducta* Folsom and *Nicoletia meinerti* Silvestri as obvious introductions by man.

The Thysanura of other islands in French Polynesia are almost unknown. In Hawaii nine species in three families have been found; four endemic, two indigenous but occurring elsewhere, and three introduced. In Samoa Carpenter (37) has recorded four species of the Lepismatidae: two endemic, one introduced, and one undetermined as to species.

There is obviously little to be learned from the above about geographical relations, but the meager Thysanuran fauna of the Marquesas, so far as it is known, points toward the southwest as its probable source.

Protura

No member of the Protura is known from the Marquesas; as in most parts of the world, a search for them has never been made. I have seen one species in Hawaii, collected by R. H. Van Zwaluwenburg near Honolulu.

Collembola

Springtails are abundant at all altitudes in the Marquesas. They were collected in the course of general field work without using special methods. Nevertheless interesting results are given in Carpenter's (38) report on the 14 species found. These are included in ten genera, of which *Meganurida, Echinanura,* and *Sericanura* are "new and remarkable generic types" of the family Poduridae; each is represented by a single species taken at high altitudes. Two other species of Podurids were found, in the genus *Neanura,* one of them new. The Entomobryidae are represented by eight species, of

which two are new. In the Sminthuridae a single species, *Dicyrtoma insularis* Carpenter, was taken at the very summit of Mount Ooumi on Nukuhiva.

Of the 14 species, seven are thus new and undoubtedly represent an endemic element. Three species of Entomobrinae are as yet known only from the Marquesas and Hawaii, which may indicate a Hawaiian affinity. One species occurs also in Java, and three are widespread in both hemispheres.

The Collembolan faunas of Hawaii (Folsom, 92) and the Marquesas are of considerable interest, though as yet little known. In both groups endemic genera and species occur. In other islands in the central Pacific almost no work on this order has been done. In Samoa, for example, only four species are known (Carpenter, 37), one endemic and one world-wide species of Poduridae and two Entomobryids of wide distribution in Indo-Malaya. Little is known of the geographical relations of the central Pacific Collembola.

Dermaptera

Six species of earwigs are recorded from the Marquesas by Hebard (114): one, *Euborellia annulipes* (Lucas), in the Labiduridae and five in the Labiidae. None of them is endemic. *Labia dubronyi* Hebard is known only from the Marquesas and Hawaii; *Sphingolabis hawaiiensis* Bormans and *Chelisoches morio* (F.) extend across the Pacific as far as Indo-Malaya, and *Labia pilicornis* (Motschulsky) as far as Ceylon; *Euborellia annulipes* (Lucas) and *Labia curvicauda* (Motschulsky) are circumtropical. Other species doubtless occur, and some of them may be endemic, but the habitats of earwigs were sufficiently explored to make the above list representative of the fauna.

In the Society Islands six widespread species of earwigs are known (Hebard, 115), and in Samoa one of the 12 known species (Borelli, 21) is endemic. Three of the 12 species found in Hawaii (Hebard, 112-114) are peculiar to the group, but may yet be found on other islands. There is a rich endemic fauna of earwigs in New Caledonia, but in the central Pacific it appears that a truly endemic fauna has scarcely been developed, though a thorough search may reveal many endemic species in the Society Islands and perhaps elsewhere.

Orthoptera

Of the seven families of Orthoptera, four—the Blattidae, Acrididae, Tetrigidae, and Tettigoniidae—contain endemic Marquesan species. The Phasmidae are represented by a single species, *Graffea crouanii* (Le Guillou), the coconut stick insect, which is widely distributed through the Pacific and is the only member of the family in eastern Polynesia. Of the Gryllidae, only five widespread species are known in the Marquesas. The Mantidae and Grylloblattidae are probably entirely absent from the Marquesas and, except

for some introduced Mantids, from all central Pacific islands. The Marquesan Orthoptera are discussed by Hebard (114).

Blattidae. The cockroaches are among the most important families in the Marquesan endemic fauna. Seventeen species are already known: six endemic, one (*Kuchinga remota* Hebard) found only in the Marquesas and Society Islands, three of wide distribution but not beyond the Indo-Malayan and Australian regions, and seven cosmopolitan species. Of the 11 genera represented, three are endemic: *Maretina* with two species, *Aneurina* with three, and *Microblatta* with one. *Maretina* and *Aneurina* have apparently been derived from the same ancestors as *Mareta,* an Ectobiine genus of the Old World tropics, especially in Australia. *Microblatta uapou* Hebard is related to the Mexican *Ceratinoptera tropaia* Hebard, but all other Marquesan cockroaches are of Indo-Malayan and Australian affinity.

A surprising feature of the Hawaiian fauna is the absence of any endemic cockroach. In the Society Islands (Hebard, 115) only five species are recorded: *Kuchinga remota* Hebard, which occurs also in the Marquesas, and four species of wider distribution. In Samoa (Chopard, 45) about 20 species are known; most of the native species are in Pseudomopinae, to which subfamily the Marquesan *Microblatta* belongs.

Acrididae (Tetrigidae excluded). The three Marquesan short-horned grasshoppers constitute an endemic group of considerable interest. *Ootua antennata* Uvarov, belonging to an endemic genus named after the highest peak on the eastern central range of Hivaoa, has been found only on Hivaoa in small groups at intermediate and high altitudes. *Valanga marquesana* Uvarov is probably less common and has been found only on Nukuhiva, at low and intermediate altitudes. *Patanga pinchoti* Caudell occurs in great numbers on the remote island of Eiao. Flights of more than a few yards were not observed, but it is nevertheless remarkable that so abundant a grasshopper should be confined to a single island.

No native Acridids are known in Hawaii or in the islands of French Polynesia outside the Marquesas. It is likely, however, that several species will be found in the Society Islands and perhaps elsewhere. The Acridid fauna of Samoa is surprisingly meager, with only four known species, of which only *Valanga stercoraria* Holdhaus, of Australian affinity, is endemic.

Tetrigidae. Only one species of Tetrigid, the endemic *Hydrotetrix marquesana* Hebard, has been found in the Marquesas. The genus is semi-aquatic, inhabiting the banks of streams and swimming strongly under water. It is confined to the Marquesas and the Society Islands, where *H. aspera* Uvarov and *H. cheesmanae* Uvarov occur. Grouse locusts are unknown in Hawaii; in Samoa there are four known species.

Tettigoniidae. Hebard's Marquesan report includes eight species of long-horned grasshoppers, of which five are endemic and three of wide distribution in the Pacific as far as Indo-Malaya. One of the endemic species, the Listrosceline *Phisis marquesana* Hebard, is closely allied to a Samoan species, which in turn has affinities in Papua and Malaya. The others are remarkable Conocephalines: the distinctive *Conocephalus tridens* Hebard, and three species in the endemic and related genera *Fatuhivella* and *Nukuhivella*. *Fatuhivella colorata* Hebard was collected twice on Fatuhiva; since 36 specimens were taken, it seems probable that it is restricted to that island. *F. marmorata* was taken only once on Fatuhiva. *Nukuhivella agraecioides* Hebard is a very aberrant grasshopper, collected only at high altitudes on Nukuhiva.

The Hawaiian fauna is rich in Tettigoniidae (Hebard, 112), but almost all of them are in the endemic Copiphorine genus *Banza*. Very little is known of the species in other parts of the mid-Pacific. Samoa has relatively few species, of which about four are endemic.

Gryllidae. Small tree crickets are common in the Marquesan forests, but Hebard's report includes only five species of which all are widely distributed, except *Metioche tahitensis* (Saussure) of the Marquesas and Society Islands. In the Society Islands *Tahitina mumfordi* Hebard belongs to an endemic genus allied to *Cophonemobius* in Samoa. In Hawaii and Samoa there are very rich Gryllid faunas, including several endemic genera in each archipelago.

The origin of the Marquesan Orthoptera, apart from species of doubtful affinity, is clearly from the southwest. Except for the paucity of Marquesan Gryllidae the order is developed in much the same way, though to a less extent, as in Samoa. A general similarity between the Marquesas and Society Islands will probably be found on further collecting; the two archipelagoes are already known to have important features in common, especially the presence in them alone of the genus *Hydrotetrix*. The contrast between the Marquesan and Hawaiian Orthoptera is almost complete. As Hebard (114) points out, in the Orthoptera "not one endemic Hawaiian species belongs even to the same subfamily as an endemic Marquesan species."

Plecoptera

No stone flies have been reported from the central Pacific islands. Their absence in Hawaii seems certain, in Samoa probable, in the Society Islands quite uncertain because little collecting has been done. In the Marquesas it is safe to conclude that only rare or highly restricted species could have escaped discovery. Probably the order has not reached the islands of the central Pacific.

Isoptera

In the Marquesas special attention was paid to the collecting of termites, with interesting results as recorded by Light (143-145). The order is well represented throughout the archipelago, though one of the commonest species, *Kalotermes dolei* Light, was not found above 2,000 feet. Otherwise the distribution of the species seems to be little affected by altitude or by the ocean barrier between the islands. The termites of other parts of the central Pacific are listed by Light and Zimmerman (147), whose nomenclature is followed here.

Eight species have been collected in the Marquesas: *Coptotermes pacificus* Light, which is unknown elsewhere; *Kalotermes* (*Rugitermes*) *athertoni* Light, also in Tahiti, Society Islands; *Kalotermes* (*Cryptotermes*) *piceatus* Snyder, also in Hawaii; *Kalotermes* (*Neotermes*) *connexus* Snyder of the Marquesas, Hawaii, and Society Islands; *Kalotermes* (*Cryptotermes*) *dolei* Light and *hermsi* Kirby of the Marquesas, Society, Austral, and a few other mid-Pacific islands; *Kalotermes* (*Kalotermes*) *immigrans* Snyder of the Marquesas, Hawaii, Pacific equatorial islands, Galapagos, and Ecuador; and *Kalotermes* (*Glyptotermes*) *xantholabrum* Hill, known in the Marquesas, Society Islands, Samoa, and New Britain.

In the termite fauna of the central Pacific 16 species are known including the eight listed above and the following: *Kalotermes* (subgenus uncertain) *rapae* Light and Zimmerman, known only from Rapa; five species of Kalotermitidae (including *K. xantholabrum* listed above), *Prorhinotermes inopinatus* Silvestri (Rhinotermitidae), and *Microcerotermes peraffinis* Silvestri (Termitidae) in Samoa; and *Coptotermes formosanus* Shiraki, a highly destructive immigrant from the Orient, in Hawaii.

It is noteworthy that almost all of these termites belong to the primitive family Kalotermitidae, and that there are only three members of the Rhinotermitidae (in *Coptotermes* and *Prorhinotermes*), and only one (the Samoan *Microcerotermes*) in the Termitidae, which is the highest family of termites and dominant in and largely restricted to the tropics. It should also be noted that the Kalotermitidae, living entirely in wood which is usually hard and dry, are more likely to be distributed by human commerce than termites of other families.

Six species of termites, which have been recorded only from the central Pacific east of Samoa, may belong to a characteristically mid-Pacific fauna. *Kalotermes immigrans* has recently been recorded from the Galapagos and Ecuador by Light (146), and *K. athertoni* is believed to be related to an undescribed species from Ecuador (147). This apparent Neotropical affinity may, however, be due to the frequent communication between central Pacific islands and South America in the days of the early whalers.

Psocoptera

Many Psocids were collected in the Marquesas, and my impression was that there was a fair degree of diversity in them. No report on them has yet been published. Banks has recently recorded 16 species, of which eight are described as new, from Hawaii; and Karny (133) 11 species, of which seven are new, from Samoa. Among the Samoan species is a Zorapteron, *Zorotypus buxtoni* Karny; no member of this suborder was found in the Marquesas.

Embioptera

A single species of Embiid, *Oligotoma vosseleri* (Krauss), is widely distributed throughout the Marquesas Islands. It occurs also in the Society Islands and Easter Island, which is the type locality. A single species, *Oligotoma insularis,* is doubtfully native in Hawaii. No other Embiids are known in the central Pacific and the order appears to be absent from New Zealand (Friederichs, 96).

Anoplura

Little attention was paid to the lice of the Marquesas (Ferris, 88-89), because the birds, the only group of possible hosts well represented in the islands, had already been adequately collected by the Whitney South Sea Expedition and because the French authorities had forbidden the killing of native birds by foreign visitors. No ectoparasites were found on several specimens of the green fruit-eating pigeon (*Ptilopus dupetithouarsi*), and of the kingfisher (*Halcyon godeffroyi*). On the Marquesan swiftlet (*Collocalia ocista*) a single species of louse (*Dennyus distinctus* Ferris), known also from a Javan *Collocalia,* was taken. A few species of Mallophagan lice were found on Marquesan sea birds and, though some of them were new, they do not concern us here. Nor do the two human lice, *Pediculus humanus* and *Phthirius pubis,* introduced to the Marquesas probably since the arrival of white voyagers; the common lice which are everywhere present on domestic fowls; the rat louse *Polyplax spinulosa*; and the world-wide pig louse *Haematopinus suis.* Some interest has been attached to the presence in Samoa of *Haematopinus suis* var. *adventicus* Neum., described from wild swine (*Sus vittatus*) in southeast Asia, but Ferris (*in litt.*) states that it is not a distinct variety but a strict synonym of *H. suis. Hoplopleura oenomydis* Ferris was found on Marquesan rats, but it occurs on many hosts as far from the Marquesas as East Africa and the Philippines (88), and Ferris believes that *H. pacificus* Ewing, described from *Rattus hawaiiensis,* is a synonym of *H. oenomydis.*

Thysanoptera

Small collections have so far shown the presence in the Marquesas of less than ten species of Thysanoptera, of which four in the genera *Isoneuro-*

thrips, Bolothrips, and *Cryptothrips* are not known elsewhere. Though 44 species in 23 genera are recorded from Hawaii by Moulton (167), the thrips fauna of other Pacific islands is so little known that it is scarcely worth attempting an analysis of its affinities. The order stands in greater need of study than any other large group of insects in the Pacific.

Odonata

A few dragon flies of wide range have been collected in the Marquesas, but only three species as yet unknown elsewhere: *Coenagrion interruptum, Pseudagrion demorsum,* and *Hemicordulia mumfordi,* all described by Needham (178-179). It seems certain that many endemic species remain to be found, especially because the endemic dragon flies appear to be uncommon and localized in the Marquesas. There is an extensive dragon fly fauna in Hawaii. According to Bryan (28) 30 of the 35 species are endemic, but all belong to genera occurring elsewhere. Little is known of the dragon flies in other central Pacific islands, though 39 species are known in Samoa. I have seen no analysis of these faunas in connection with their affinities, and have not attempted one myself.

Hemiptera-Heteroptera

There appears to be a striking difference between the affinities of the Hemiptera-Heteroptera and those of the Hemiptera-Homoptera; therefore the two suborders are discussed separately.

The aquatic series Cryptocerata is entirely unknown in the Marquesas and very few species, if any, are likely to be found. In Hawaii there are only the foreign Notonectid *Bueno palpipes* Fabr. and the peculiar but doubtfully endemic Corixid *Artocorisa blackburni* White; in the Society Islands only the endemic Notonectid *Anisops tahitiensis* Lundblad; and in Samoa only two endemic Notonectids and a widespread Gelastocorid. It thus appears that the fauna of these islands is as poor in strictly aquatic Hemiptera as it is in other groups of fresh-water animals.

The Gymnocerata are at present known to be represented in the Marquesas by a considerable endemic element in the Lygaeidae and Nabidae, and by a small endemic element of one or two species in the Pentatomidae, Scutelleridae, Aradidae, Reduviidae, Miridae, Hydrometridae, and Veliidae. A few families still await study, among which the Anthocoridae are probably important. In the large families Coreidae, Pyrrhocoridae, and Tingitidae no endemic species have been found. Most of the records of Marquesan Heteroptera are in papers by Van Duzee (236-237).

Lygaeidae. The Lygaeid genus *Germalus* is one of the most important in the Marquesas. Seven species are already known, all endemic except *G. uni-*

color Montadon which has been found also in Java. The Marquesan species are distributed rather evenly throughout the archipelago, one of them on as many as six islands and others on three islands. In individuals the genus is very abundant, but on the higher islands it is almost confined to the cloud zone. Being represented in Samoa and other Pacific islands, the genus is almost certain to be found in the mountains of the Society Islands. Its further distribution extends to Ceylon, Madagascar, and Mauritius.

Three other endemic Lygaeids are known in the Marquesas: *Neocymus insularis* Van Duzee in an endemic genus, and *Ptochiomera caeca* Van Duzee and *P. castanea* Van Duzee.

The Hawaiian fauna is rich in Lygaeids, mostly in the world-wide genus *Nysius,* in which there are 27 Hawaiian species. In Samoa only eight of 18 known species are endemic. Scarcely anything has been written about this family in the Society Islands.

Nabidae. The Nabidae are represented in the Marquesas by a group of four endemic species of *Nabis,* as well as the widespread *N. capsiformis* Germ. In Samoa a single endemic Nabid is known. In Hawaii there is a great development of species in the world-wide *Reduviolus* and *Nabis.*

This meager Heteropteran fauna is somewhat similar, as regards the development of the several families, to that of Hawaii and Samoa. The most important families in all three groups are the Lygaeidae, Miridae, Nabidae, and Reduviidae (on the assumption that more Mirids and Reduviids will be found in the Marquesas) and perhaps also the Anthocoridae, though the Marquesan specimens have not been determined and none is yet known from Samoa. The Pentatomidae are poorly represented in all three archipelagoes, and the Coreidae, Pyrrhocoridae, and Tingitidae by only a few species, all in Samoa. The aquatic families are almost unrepresented in all three groups. China (43) has made a careful analysis of the Samoan Heteropteran fauna and finds it to be "an impoverished replica" of that of Fiji, "most closely related to that of the Australo-Oriental subregion, and has obviously been derived from it," though other elements are not entirely excluded. China inclines to favor "a former land connection which existed during late Mesozoic times between Papua and New Zealand" as the probable means of dispersal to Fiji and Samoa, though it may have taken place "later by the agency of winds and currents, over a long period of time." I see no reason to doubt that the Marquesan fauna is a still further impoverished relic of the same fauna that reached Fiji and Samoa. The origin of the Hawaiian Heteroptera is obscure.

Hemiptera-Homoptera

This is one of the most interesting groups of insects as regards their geographical distribution in the central Pacific. In the Marquesas and also

in Hawaii there are important endemic elements in the Cicadellidae, Delphacidae, Cixiidae, and Psyllidae only. There are almost no native species in the central Pacific in the great families Aphididae, Aleyrodidae, and Coccidae. A single endemic aphid, *Aphis mumfordi* Takahashi (229), is known from the Marquesas, and one endemic scale insect, *Lepidosaphes marginata* Ferris (90), which is common on the leaves of two endemic Araliaceous trees of the mountain forest. The Aleyrodidae from the Marquesas have not yet been identified, but I believe that all the white flies I saw belong to a single species, present also on Tahiti and affecting especially the widespread shrub *Morinda citrifolia.* The Cicadidae, Cercopidae, and Membracidae appear to be totally absent from the Marquesas and from Hawaii except for introduced Membracids. The Cicadidae are not known in the central Pacific east of Samoa. A species of the Cercopidae ranges as far east as Henderson Island. I do not know the eastern limit of the Membracidae; I found none in the Society Islands and have seen no reference to them in the literature on Samoa.

Cicadellidae. The Cicadellid leafhoppers constitute one of the largest and most interesting families in the endemic Marquesan fauna. Thirty species are already recorded by Osborn (180), and of these only two, of wide distribution to the west and southwest, are known outside the Marquesas. Twelve genera, of which seven are peculiar to these islands, are represented. The others are the world-wide *Bythoscopus, Cicadula, Nesosteles,* and *Empoasca,* and the genus *Dryadomorpha* which is confined to the southern Pacific. Of the endemic genera, *Nesophyla* has eight species, *Cicaduloida* two, and *Scophoidulina, Calotettix, Nesoniella,* and *Marquesia* one species each. In the non-endemic genera, *Cicadula* has four endemic Marquesan species, *Bythoscopus* and *Empoasca* three, *Nesosteles* two, *Dryadomorpha* one.

The Cicadellids are restricted almost entirely to high altitudes of the Marquesas. Four of the 28 endemic species were found only above 3,000 feet, 23 of them only above 2,000 feet. Only three endemic species were ever found below 1,000 feet, and two of these were from the comparatively low islands of Eiao and Hatutu. Allowing for differences in size, topography, and flora of the islands, there seems to be a fairly even allocation of species of Cicadellids to the several islands, except that relatively few were found on Fatuhiva and many on Uapou. There is little indication of island endemism in these islands, each of many species being found on three or four islands. The distribution of the 16 species recorded from only one island each may be extended on further collecting.

Osborn finds that the affinities of the Marquesan Cicadellidae as a whole are Malayan, from a region including the Malay Peninsula and East Indian Islands, with Fiji and Samoa as intermediate stations for at least some of the ancestral forms. But he writes of possible "affinities with the faunas of

the Oriental or Malayan regions on the one hand and South America or Hawaii on the other."

Cixiidae. Members of the genus *Oliarus* were found in considerable numbers in the Marquesan rain forests at altitudes over 2,000 feet. These, along with the Delphacidae, were being studied by the late Frederick Muir just before his death. Muir reported, in letters, that a considerable amount of species formation had occurred on each of the higher islands, and that no species had been collected on more than one island. In both the Cixiids and the Delphacids he found a close and striking affinity with Hawaii rather than with the islands to the southwest.

Delphacidae. Muir reported that the Delphacid leafhoppers were represented by many insular species, and that they showed the same Hawaiian affinity as the Cixiidae. In the field it was apparent that there was a Delphacid fauna rich in genera and species, restricted largely to high altitudes in the Marquesas; results of considerable interest are to be expected when the collections, now at the British Museum, have been carefully studied.

Psyllidae. Psyllid leafhoppers were found as a small but characteristic element in the mountain fauna above 2,000 feet. So far only part of the collection has been studied by Klyver (135), who describes *Anomoterga tahuata* in an endemic genus found only on Tahuata, and *Trioza alipellucida* and *T. alifumosa,* in a world-wide genus which includes many endemic Hawaiian species.

There are at least 15 species of Psyllids in Hawaii, all of them endemic and the descendants of a few ancestral forms, which Crawford (64) regards as transoceanic immigrants. In Samoa, Crawford (65) records five genera with only nine species of which four are described as new. The genus *Trioza* occurs in the Hawaiian, Marquesas, and Samoan islands. It is at present impossible to decide whether the Marquesan Psyllids are more closely related to those of Hawaii or of Samoa.

The Marquesan Homoptera resemble those of Hawaii in the considerable development of only four of the many large families (Cicadellidae, Cixiidae, Delphacidae, and Psyllidae) and in parallelisms in the development of some genera in the two archipelagoes. Resemblances to the Marquesan fauna may be found in the Tahitian Homoptera when they are better known, but so far no affinity as strong as that with the Hawaiian fauna has been found between the Marquesan leafhoppers and those of the Society or Samoan islands. Instead there is the important difference that the Cercopidae as well as the Issidae and Derbidae (specimens collected by me on Tahiti are tentatively referred to these two families) appear to be absent from the Marquesas but are probably present in other parts of French Polynesia. The

Cercopidae have been carefully studied by China (44). His genus *Lallemandia* includes many species from the Malayan region eastward as far as the Tuamotus. In Samoa there are about eight species, as well as two apparently endemic species of *Aufidus*. Farther east *Lallemandia* is the only genus, with three species: *L. fenestrata* of wide distribution in the Pacific and *L. cheesmani* (Lallemand) and *L. mumfordi* China, collected only in the mountains of Tahiti. In *L. fenestrata,* China finds well-defined characters to separate 11 insular subspecies, each on a single island: five on Tahiti, and one each on Moorea, Borabora, Henderson (Elizabeth), Samoa, and Tonga. China writes that in spite of the complete insular endemism in the subspecies of *Lallemandia,* "there is little doubt that the fauna originated from the Austro-Oriental subregion."

Ephemeroptera

The strictly aquatic order of May flies has not been reported, and may well be entirely absent, from any of the central Pacific islands east of Samoa, where only three specimens of *Chloeon samoense* Tillyard and Lestage (232) have yet been found.

Trichoptera

The caddis flies are almost as poorly represented in the central Pacific as the May flies. It seems certain that none will be found in Hawaii or perhaps in the Marquesas, though if rare they might easily have been overlooked there. Dr. J. S. Philipps, who spent a short time in Tahiti, told me that he found a single, undetermined species of caddis fly. Mosely (166) records one undetermined specimen from Samoa, and remarks that the order must be extremely rare in these islands.

Lepidoptera

Having devoted little time to collecting butterflies and moths in the Marquesas I shall merely summarize very briefly the results recorded by Meyrick, Collenette, Prout, and Poulton and Riley.

First, attention must be drawn to the extreme paucity of butterflies in the central Pacific islands. In Hawaii *Vanessa tammeamea* Esch. is the only native butterfly known. In the Marquesas the only species that I saw personally were the abundant and widespread *Danaida plexippus* L. and *Hypolimnas bolina* L., though two species collected in small numbers have recently been described from the Marquesas: *Atella marquesana* Riley and *Libythea collenettei* Riley. Only 20 species, including immigrants, are given in Swezey's (227) list of Samoan butterflies. It is astonishing that a group so large and ubiquitous as the butterflies, some of which are able to fly across thousands of miles of ocean, should have gained so little footing in these islands.

Many families of moths, however, are well represented throughout the Pacific. In the Marquesas the following families include endemic species: Phycitidae, Pyraustidae, Tortricidae, Eucosmidae, Cosmopterygidae, Heliodinidae, Glyphipterygidae, Gracilariidae and Lyonetidae (Meyrick, 163-165), Arctiidae, Noctuidae and Sphingidae (Collenette, 56-57), and Geometridae (Prout, 190-192).

In the distribution of several genera of moths, especially the Tortricid genus *Dichelopa* and the Cosmopterygid *Asymphorodes,* Meyrick finds proof of the existence of a former continent, "Palaeonesia", in the central Pacific. According to Poulton and Riley (189) the affinity between *Atella marquesana* and *A. geberti* Guérin of the Society Islands supports Meyrick's hypothesis.

Coleoptera

The following families of beetles are known to be well represented in the endemic Marquesan fauna: Staphylinidae, Elateridae, Cisidae, Curculionidae, and Scolytidae. In the following there is a small endemic element: Lathridiidae, Cantharidae, Anobiidae, Bostrychidae, Buprestidae, Anthribidae, and Aglycideridae (including Proterhinidae). In the following families the collections have not been sufficiently studied and reported upon for full discussion now: Dytiscidae, Trichopterygidae, Trogositidae, Nitidulidae, Cucujidae, Cryptophagidae, Mycetophagidae, Colydiidae, Endomychidae, Hydrophilidae, and Brenthidae; a few of these are likely to include some endemic species. The following great families of beetles, of world-wide distribution, are apparently unrepresented in the endemic Marquesan fauna: Cicindelidae, Silphidae, Histeridae, Coccinellidae, Dermestidae, Cleridae, Lyctidae, Tenebrionidae, Bruchidae, Chrysomelidae, Cerambycidae (??), Lucanidae and Scarabaeidae (*s. lat.*). Most of these families, notably the Coccinellidae, Dermestidae, Tenebrionidae (?), Bruchidae, Chrysomelidae, and Scarabaeidae, are unrepresented in the Hawaiian endemic fauna also.

Carabidae. Not a single Carabid was collected by the Pacific Entomological Survey in the Marquesas, though a few have been recorded in the literature of the nineteenth century. The family is one of the largest and most ancient among the beetles, and though it attains its highest development in northern temperate climates, it is abundantly represented in almost all parts of the world. The Hawaiian fauna is exceptionally rich in endemic genera and species of Carabidae; in Samoa the family is relatively poorly developed. In the Marquesas a great deal of time was devoted to collecting in habitats in which I had found Carabids abundantly in Hawaii, and if any are present in the Marquesan forests, they must be rare or of very restricted distribution. It is possible, however, that the introduced destructive ant, *Pheidole megacephala,* has reduced the numbers of native Carabids more than most other

insects, since their larvae are soft-bodied and of less cryptic habit than those of many insects. The absence of Carabids from the collections is one of the most surprising results of field work in the Marquesas.

Staphylinidae. Small Staphylinids are common among dead leaves and in similar habitats in the Marquesan rain forests, and Cameron (34) lists 20 species, 12 of which are endemic and one of which represents the endemic genus *Nanolobus*. One species, *Trogophloeus mumfordi* Cameron, is known only in the Marquesas and Society Islands, three have a wider distribution in the Pacific islands, and three range even farther. The family is well represented on other Pacific islands. Most of the Hawaiian species belong to endemic genera in the Aleocharinae, a subfamily which includes endemic species in the Marquesas and Samoa.

Elateridae. The click beetles are of considerable interest in most of the Pacific islands. In the Marquesas there are, in addition to a few widespread species, 13 endemic species of the genus *Pacificola,* recently described by Van Zwaluwenburg (242). Almost all of these were found only at high altitudes, and all but *P. obscura,* from Uahuka and Uapou, were collected each on a single island. Most of the species are so rare that knowledge of their distribution in the Marquesas is far from complete, but there appears to be a high degree of island endemism. *Pacificola* is apparently a central Pacific genus, with 13 species in the Marquesas, one (described from Tahiti as *Oophorus instabilis* Fairm., but probably a *Pacificola*) from the Society Islands, one (*P. compta* Van Zwal.) from Samoa and one (*P. vitiensis* Van Zwal.) from Fiji.

Buprestidae. Three Buprestids are known in the Marquesas: *Argilus indignus* Fairm., which is widely distributed in the Pacific, and the presumably endemic *Cyphogastra bedoci* Théry and *Pleiona tayauti* Guérin. The two endemic species are of considerable size and great brilliance, and they are almost identical in superficial appearance. *Pleiona tayauti* was described from an unknown locality in 1909 and not rediscovered until 1933, when Le Bronnec collected no less than 35 specimens at an altitude of 450 feet on Hivaoa. *Cyphogastra bedoci* is abundant on Uapou and Fatuhiva and sufficiently well known to receive the Marquesan name *he* (also used for the stick insect *Graffea crouanii*) on Uapou. Marquesans assert that it occurs also on Tahuata. If it is present on other islands it must have habits different from those on Uapou, where it could not fail to attract attention. Blair (19) distinguishes three insular varieties of *C. bedoci,* one each from Uapou, Fatuhiva, and an unknown locality in the Marquesas. According to Blair (17), *Cyphogastra taitina* Kerr and *C. similis* Kerr of Tahiti are very close to *C. bedoci.* There are a few endemic Buprestids in Samoa, including a *Cyphogastra,* and none, I believe, in Hawaii.

Cisidae. Six species of minute Cisid beetles have been collected in the Marquesas (Blair, 19), all in the world-wide genus *Cis* and all presumably endemic except *C. collenettei* Blair, which was found also on Tahiti and Moorea. The genus attains a surprising development in Hawaii, with 34 species described in the "Fauna Hawaiiensis". In Samoa three endemic species of *Cis* are known as well as an endemic genus, *Scolyticus*.

Cerambycidae. The longicorn beetles form one of the largest and most interesting families in the Hawaiian fauna; in Samoa, Aurivillius (9) lists 16 genera and 35 species, of which 23 are endemic with many confined to single islands. It was therefore surprising to find that none of the nine species collected in the Marquesas (Blair, 20) is endemic. Five are very widely distributed, and three are confined to islands of the Pacific. The fauna of the Society Islands, with ten known species, is very similar to that of the Marquesas. Blair states that half the introduced species of the two archipelagoes are of Central American origin. Future collectors will probably find many endemic Cerambycids in the Society Islands and perhaps in the Marquesas.

Anthribidae. Six Marquesan species of Anthribidae are listed by Jordan (132), two in the endemic *Aethessa,* two known also on other Pacific islands, and two ranging as far as the Indian Ocean. All are of "an Indo-Pacific type". Perkins (182) states that he found no native Anthribids in Hawaii. In Samoa there is a considerable endemic element (Jordan, 130) and in the family as a whole the affinities are especially with those of the Philippines.

Aglycideridae. The two genera of Aglycideridae, *Aglycideres* and *Proterhinus,* constituted separate families until recently united by Perkins (183). Their distribution is of great interest. *Aglycideres* is represented in the Canary Islands by *A. setifer* Wollaston, the type species, and in New Zealand by two rare species, *A. wollastoni* Sharp and *A. badius* Brown. *Proterhinus* was for a long time known only in Hawaii, where about 176 species, many of them strictly limited to single islands and to single food-plants, had been evolved. Within the last few years Perkins has described *P. samoanus* from Samoa, *P. phoenix* from the Phoenix Islands, and *P. mumfordi* and *P. adamsoni* from the Marquesas. Oddly enough the second of the Marquesan species was collected on a shrub of wide distribution, on the small dry island of Hatutu. Zimmerman (252) states that about ten species of Aglycideridae, some of them probably in new genera, were found by the Mangarevan Expedition in the Austral and Society Islands and in Rapa. The genus is characteristically mid-Pacific.

Curculionidae. The weevils are by far the largest family of animals in most, if not all, island faunas. In the Marquesas they are represented by the allied Otiorrhynchine genera *Rhyncogonus* and *Microgonus,* many small

beetles in the Cryptorrhynchinae and related subfamilies, many Cossoninae, and a few introduced species of little interest here. Systematic reports on the smaller weevils are still in course of publication by Bishop Museum.

The genus *Rhyncogonus* (Van Dyke, 238) is one of the most important and characteristic in the fauna of the central Pacific islands. The beetles are among the largest on these islands, and as the adults feed mostly on the leaves of trees and shrubs, their distribution is better known than that of most genera of insects in the Pacific. Some 70 species have been described: from the Hawaiian islands (33 species), Wake Island (1), Marquesas (23), Society Islands (2), and Rapa (1), and about 30 more were recently collected in Rapa and other islands in southeastern Polynesia (Zimmerman, 252). The genus has not been found in Samoa. In Hawaii almost all the species are rare, but in the Marquesas many of them are extremely abundant, above altitudes of 1,500-2,000 feet on the higher islands, and in most parts of Eiao. Only a few specimens are yet recorded from the Society Islands. Van Dyke divides the genus into species-groups, each confined to a single archipelago. The Marquesan species, both individually and as a whole, stand well apart from the Hawaiian, and those of one archipelago seemingly have not been derived directly from those of the other.

Each species of *Rhyncogonus* of both the Marquesas and Hawaii is restricted to a single island. In the Marquesas the species are divided fairly evenly among the islands, except that only one, *R. walkeri* Perkins, has been found on Nukuhiva, against eight on Hivaoa and five on Fatuhiva. This is not explicable in terms of the time spent in collecting, or, so far as can be seen, by difference in size, topography, and flora of the islands. It is also noteworthy that on Nukuhiva few *Rhyncogonus* were seen below 3,000 feet, whereas in parts of Hivaoa they are abundant from about 1,500 feet upwards.

Until recently the Hawaiian islands might have been considered the original center for *Rhyncogonus* or at least its present headquarters. Now it appears that the number of species in the Marquesas, despite the smaller size of the islands, may be greater than in Hawaii, for future collecting will probably add more species to the Marquesan than to the Hawaiian fauna. Moreover, as Van Dyke states, there is a greater divergence in specific characters in the Marquesas than elsewhere, and in the Marquesas the genus *Microgonus* has apparently been derived from *Rhyncogonus*. It is represented by a single species, *M. oodemaformis* Van Dyke, and as yet by only one specimen, which was found at 4,000 feet on Nukuhiva. Van Dyke believes that further collecting will show that *Rhyncogonus* was derived from ancestors in "western Polynesia", but that "it is also barely possible that the ancestral home of the genus was Antarctica." Judging by the amount of specialization in the Marquesas, he estimates the time of the original settlement by *Rhyncogonus* or its ancestors as early Pliocene or Miocene.

The Hawaiian weevils are very numerous and there are many endemic genera, especially in the Cossoninae. Some of these genera, like *Rhyncogonus* and *Proterhinus,* may be found in the Marquesas and Society Islands. In Samoa Marshall (159) lists 86 species of Curculionidae of which 78 (80 percent) are endemic, and 55 genera of which ten are endemic. The Samoan weevils seem to have been derived from Malaya by way of New Guinea, with little or no direct influence from Australia. *Rhyncogonus* has not been found in Samoa, but there are four endemic species in other Otiorrhynchine genera, and one, *Trigonops spongicollis* Fairm., described from Tahiti. It is interesting to note that the Samoan fauna, though much more diverse than that of the islands farther east, contains as yet only two peculiar species of the Calandrinae, a subfamily apparently unrepresented in the endemic fauna of the Marquesas and of Hawaii. *Diocalandra taitensis* (Guér.) is a common pest of the coconut palm on many Pacific islands (Herms, 118-119).

Strepsiptera

No search was made in the Marquesas for the aberrant, parasitic order Strepsiptera. Of their principal hosts, the higher Hymenoptera are very poorly represented but in the Homoptera there is a rich endemic fauna. Perkins (182), in the "Fauna Hawaiiensis", has described *Elenchus melanias* from many genera and species of Hawaiian Delphacids.

Neuroptera

Only three species of the order Neuroptera are known in the Marquesas (Esben-Peterson, 85) : *Chrysopa basalis* Walker (previously reported also as *C. flaveola* Schneider and *C. delmasi* Navas) in the Chrysopidae, *Megalomus* sp. and *Nesomicromus marquesanus* Kimmins in the Hemerobiidae. The green lace wing *C. basalis* is one of the commonest of Marquesan insects, from sea level into the cloud zone. It has a wide distribution outside the Marquesas. The other two species, which may be endemic, were first collected by the St. George Expedition, and *N. marquesanus* was taken by LeBronnec at high altitudes on Hivaoa and Uapou.

In Hawaii there is a great development of endemic species in the Chrysopid genus *Amalochrysa* and the Hemerobiid *Nesomicromus.* Two species of the Myrmelionidae are listed in the "Fauna Hawaiiensis". In Samoa, Esben-Petersen (84) records a single Myrmelionid and a few Hemerobiidae and Chrysopidae, but among these "the two genera *Amalochrysa* and *Eucarobius,* and probably also *Buxtonia,* seem to be representative of a peculiar endemic fauna of the Hawaiian-Polynesian Islands." It is noteworthy that none of the aquatic families of Neuroptera is known in these central Pacific islands.

Mecoptera

I have found no record of the small order Mecoptera in Samoa and the central Pacific islands east of it.

Hymenoptera

The suborder Symphyta of the Hymenoptera has not been found in the Marquesas or other parts of French Polynesia, and its absence from Hawaii seems well established. I have seen no reference to this suborder in Samoa.

In the Aculeates there are many endemic Marquesan species of the so-called "Parasitica"; scarcely any are known in the higher superfamilies Formicoidea, Sphecoidea, Vespoidea, and Apoidea. Thus far few of the families of the "Parasitica" have been studied by specialists. Fullaway (97) describes 11 species of the Bethylid genus *Sierola,* and states that five of the species are "very near to" or "resemble" Hawaiian species. Fouts (93) describes five new species of Platygasteridae. The Hawaiian Hymenoptera have been well studied, but there is scarcely anything in literature concerning the smaller Hymenoptera of other central Pacific islands.

Formicoidea. The ant faunas in the central Pacific are relatively meager in number of species, and most of these are of very wide distribution. In the Marquesas (Wheeler, 246-247) 31 species are known, of which only *Ponera mumfordi* Wheeler is peculiar to the Marquesas, though a few endemic subspecies and varieties occur. Wheeler states that all are "small or very small ants, the fecundated females of which might have been transported to the islands by violent winds or as stowaways in native canoes, on logs, or on other flotsam and jetsam." In Hawaii, Wheeler (248) lists 35 species, subspecies, and varieties, most of which are relatively recent immigrants of Old World origin or affinity. Five species (six according to Wheeler, since he overlooks the occurrence of *Ponera perkinsi* Forel in the Marquesas) are peculiar to Hawaii, all in the primitive subfamily Ponerinae, and all "diminutive, blind or myopic, subterranean ants." Wheeler makes the interesting suggestion that they may owe their survival as relics from an original early Tertiary fauna, in an unfavorable volcanic environment, to their subterranean habit. In Samoa Santschi (198) lists 45 species: 11 endemic, 26 found in other parts of the Pacific, Australia, and Indo-Malaya and eight tropicopolitan. A Neotropical element seems to be entirely absent in the indigenous ants of central Pacific islands. Even the recent immigrants are almost all from the Old World.

Sphecoidea. The Sphecoid wasps of the Marquesas (Williams, 250) include only seven species: the widely distributed *Sceliphron caementarium* (Drury) in the Sphegidae; *Tachysphex fanuiensis* Cheesman, a Larrid known also from the Society Islands; and five species of the Trypoxylonid genus

Pison, all of which range far southwest from the Marquesas. The Society Islands have the same seven species and in addition *Oxybelus utoroae* Cheesman, known only from these islands. Williams shows how easily all these wasps may be transported by ships. Though 29 or 30 Sphecoid wasps are endemic to Hawaii, only the Mimesidae and Crabronidae are well represented there. In Samoa only four endemic Sphecoids are known, two in the Larridae and two in the Trypoxylonidae, and these may yet be found on other islands.

Vespoidea. A few introduced species of *Polistes* in the Vespidae and some wide-ranging species of *Odynerus* in the Eumenidae comprise the known Vespoid fauna of the central Pacific islands, with the exception of the endemic species of *Odynerus* in Hawaii and of the Pompilid *Anoplius spirohirtus* Perkins and Cheesman in Samoa. The Hawaiian species of *Odynerus* number over a hundred, but they may all be descendants of a single ancestral immigrant.

Apoidea. The honey bee (*Apis mellifica* L.) and a few non-endemic Megachilidae are found on almost all central Pacific islands. Apart from these, the only representation of the Apoidea in Marquesan collections is the head and thorax of an Andrenid, probably in the genus *Halictus,* which is merely enough to suggest that the bees may be represented in the endemic Marquesan fauna. In Hawaii the North American *Xylocopa blackburni* is well established, and endemic bees are limited to the primitive genus *Prosopis* with a large number of species. *Prosopis* is not known from other parts of central Polynesia. In Samoa most of the native bees are Halictines, of which six species may be endemic.

Diptera

Nematocera

Among the many families of Nematocerous flies the following are known to contain endemic species in the Marquesas: Tipulidae, Mycetophilidae, Chironomidae, Ceratopogonidae, and Simuliidae. A few specimens of the Psychodidae have not been determined. Only introduced Culicidae are known. The most important remaining family, the Cecidomyidae, is not represented in Marquesan collections.

Tipulidae. A few Marquesan species of *Gonomyia* are described by Alexander (5). The genus is abundantly represented throughout the central Pacific.

Culicidae. The widespread *Culex fatigans* Wied. and *Aedes* (*Stegomyia*) *scutellaris* Walker are recent immigrants to the Marquesas and, like the only three mosquitoes known in Hawaii, probably came in barrels of drinking

water on whalers or other ships. The eastern limit of endemic mosquitoes in the central Pacific is Tahiti in the Society Islands, where one of six known species, *Culex atriceps* Edwards, is presumably endemic. It is unlike any species of *Culex* known in the Australasian or Oriental regions. In Samoa, Edwards (80) lists seven species of which *Culex samoensis* (Theobald) is peculiar to these islands. He writes that the mosquitoes of Samoa are clearly derived from the west. (See also Buxton, 32.) In the Marquesas the only disease known to be transmitted by mosquitoes is elephantiasis. Either *Culex fatigans* or *Aedes scutellaris,* or both, may be the carriers, since they are proven vectors in other places.

Chironomidae. These midges are an important element in the faunas of all central Pacific islands, but so little known that their geographical relations cannot be determined at present. In the Marquesas (Edwards, 82) 10 or 11 species were collected, mostly by sweeping, some of which in the genus *Spaniotoma* are probably endemic. Three species, collected at light on Eiao, are marine. It is worth noting here that the only species of insect known to spend all or almost all of its life history below the surface of the sea is the midge *Pontomyia natans* Edwards, which was first found in coral lagoons of Samoa. The same or a closely related species has recently been found in Japan (Buxton, 32).

Ceratopogonidae. Though about 1,500 specimens of the Ceratopogonidae were collected in the Marquesas, the family as a whole is little known. Macfie (150) records 12 Marquesan species, of which seven are described as new. The affinities of central Pacific Ceratopogonids are at present uncertain, since even those of Hawaii are as yet very imperfectly known. A blood-sucking species, *Styloconops albiventris* (De Meijere), is common on a few sandy beaches in the Marquesas. I was never attacked by it more than a few yards away from the seashore. Marquesans regard it as a recent immigrant, which they name *nono purutia* ("Prussian" *nono*), because its introduction is supposed to be connected with the appearance of German warships at Taiohae during the World War.

Simuliidae. The distribution and habits of the Simuliid flies of Polynesia are of exceptional interest (Edwards, 79, 81-83). They form a distinct group of species, three in the Society Islands and three or four in the Marquesas. None has been found in Hawaii or Samoa, in spite of much collecting along the streams. A single species is known in Fiji.

In the Marquesas *S. mumfordi* Edwards is known only by a few adults from Hivaoa, *S. adamsoni* by two from Hivaoa and one from Fatuhiva; some larvae from Uapou probably represent a distinct, undescribed species. *S. buissoni* Roubaud has beeen found on all the islands except Mohotani, Fatuuku, and Hatutu. The typical variety occurs on Nukuhiva, Uahuka, and Eiao, and

the variety *gallinum* Edwards on Uapou, Hivaoa, Tahuata, and Fatuhiva. *S. buissoni* is the notorious *nono* fly, mentioned by Herman Melville and many others as a veritable plague. In Taipivai (Melville's "Typee" Valley) on Nukuhiva, even Marquesans occasionally burn smoke smudges, and they as well as foreign visitors frequently develop sores as a result of the bites. Biting *nono* flies belong to the typical variety and are now known only on Nukuhiva in large numbers at almost all altitudes, and on Eiao where their distribution is restricted by the small number of streams during dry spells. They do not bite on Uahuka, though the typical variety occurs there; Edwards finds that the proboscis of specimens from Uahuka appears to be slightly shorter than in those from Nukuhiva and Eiao. The variety *gallinum* has not been observed in large numbers or biting human beings, though it is known to bite chickens on Hivaoa. On Uapou, where *gallinum* occurs and where the typical variety has not been collected, the *nono* flies were pests until about 50 years ago. There is good authority for this from reliable Marquesans and other informants, and James Alexander (6) writes that a Hawaiian missionary and his companions "then went to Uapou, and first resided at Hakahetau on that island, but the sand-flies were so numerous and intolerable that they removed to a neighbouring valley, Aneau." It is difficult if not impossible to account for the present restriction of biting Simuliids to two islands, and for their apparent extinction or change of habit on Uapou.

Along the Papenoo River in Tahiti I was irritated by the presence of swarms of *Simulium tahitiense* Edwards, along with *S. oviceps* Edw. and *S. cheesmanae* Edw., but I was never, to my knowledge, bitten by a Simuliid fly in Tahiti. On the Tairapu peninsula of Tahiti, however, Cheesman (40) found Simuliid bites as irritating as those of the Marquesan *nono*.

Brachycera

Only one family, the Dolichopodidae, of Brachycerous flies is known in the endemic fauna of the Marquesas, Society and Hawaiian islands. In Samoa Ricardo (195) lists a few endemic Stratiomyids and Asilids and a single Tabanid, *Tabanus samoensis* Ferguson; I have found nothing in the literature on Samoa on families other than these three and the Dolichopodidae. Therefore it appears that few if any of the following great families have gone farther east than Samoa, except as recent immigrants: Stratiomyidae, Leptidae, Tabanidae, Asilidae, Therevidae, and Bombilidae. Some of these may not have reached Samoa. The Dolichopodidae, however, have developed abundantly on central Pacific islands. In Hawaii (Bryan, 28), there are 48 known species, about 30 of them in the genus Campsicnemus. Little is yet known about the Dolichopodids in other Pacific islands, but several endemic species have been collected in the Marquesas and Society Islands, and about ten species have been recorded from Samoa. Lamb (141) states that no con-

clusions on the distributional relations of the Samoan Dolichopodids can yet be made.

Aschiza

The most important family of the Aschiza, the Syrphidae, is the only one recorded in the Marquesas, where it is represented by two widespread species, *Volucella obesa* F. and *Ischiodona scutellaris* F. All the Syrphids of Hawaii are likewise of wide distribution and of the 11 species in Samoa eight occur also in Fiji and five as far as the Asiatic mainland. I believe that I collected at least one Pipunculid fly in the Marquesas, but it has not been determined. In Hawaii there are many endemic species of *Pipunculus,* and at least one in Samoa. Other families of the Aschiza are little known or absent in the central Pacific islands.

Schizophora : Acalypterae

In contrast to most other groups of families, the superfamily Acalypterae (Malloch, 151-154, 157-158) has a large proportion of families in the Marquesan endemic fauna, including the following: Ortalidae (Otitidae), Trypetidae, Sapromyzidae, Agromyzidae, Drosophilidae, Ephydridae, Oscinidae (Chloropidae), and Asteiidae, and doubtless others as yet insufficiently known.

Ortalidae (Otitidae). Ten species of Ortalids are known from the Marquesas, six endemic, one widespread, and two others confined to Pacific islands. There are two endemic species in *Euxesta,* of which *E. hyalinipennis* Malloch unites the Oriental and American species groups of this genus. The other endemic species belong to endemic genera: *Perissoneura,* in a group of closely allied genera, represented in both Old and New Worlds, with *P. diversipennis* Malloch from Fatuuku and Hatutu and *Heterodoxa,* with a heterogeneous assemblage of four species, each collected only once or twice in the Marquesas.

Trypetidae. *Dacus perfusus* (Aubertin) belongs to the endemic subgenus *Marquesadacus,* which is related to the subgenus *Chaetodacus* of the Oriental and Australian regions. *Trypanea simplex* Malloch is an endemic species of a world-wide genus. *Paroxyna sororcula* Wied. is widely distributed in both the Old World and the New.

Sapromyzidae. Nineteen species of Sapromyzid flies have been described from the Marquesas by Malloch, 15 in the genus *Prochaetops* which is represented also in Fiji, and three in *Chilocryptus,* an endemic genus possibly derived from ancestors similar to those of *Prochaetops.* In *Prochaetops* two subgenera peculiar to the Marquesas are described by Malloch. *Homoneura hawaiiensis* Van der Wulp is known from the Marquesas, Hawaii, Samoa, and the Society Islands.

Agromyzidae. *Melanagromyza marquesana* Malloch is a leaf-miner reared from *Sclerotheca* sp. of the mountain forest on Hivaoa and the only Marquesan representative of the Agromyzidae. It is allied to a Fijian species.

Drosophilidae. The family Drosophilidae is one of the most important in the Marquesas, as in Hawaii. Eight of the known Marquesan species are endemic, four in endemic genera which are as yet monotypic and four in the widespread genus *Scaptomyza.* Of the endemic genera, *Dicladochaeta* is compared by Malloch to the tropical American *Cladochaeta,* but a true affinity between them may be lacking; *Bunostoma* and *Marquisea* are related, respectively, to the world-wide *Scaptomyza* and *Drosophila,* and *Rosenwaldia* to the genus *Stegana.* Though there are many endemic species of *Drosophila* in Hawaii and some in Samoa, the three Marquesan species so far known occur in other parts of the central Pacific or range still farther. *Mycodrosophila halterata* Malloch is known only in the Marquesas and Society Islands; the genus is almost cosmopolitan.

Ephydridae. This is a family in which the larvae are mostly aquatic, and which might have been expected to be absent from the Marquesas. However, 12 species are known in these islands, two of them widely distributed and ten endemic. Three of the latter belong to the widespread genus *Scatella*; one to *Hecamede,* of the Old World, ranging from the Palaearctic region to New Zealand; and four to genera peculiar to the Marquesas—*Notiocanace, Neoscatella, Apulvillus,* and *Neohydrella.*

Chloropidae. A heterogenous group of six species in five genera is known in the Chloropidae of the Marquesas. Three of these are endemic, one occurs also in the Society Islands, and two are widely distributed.

Asteiidae. Five species of *Asteia* are endemic to the Marquesas.

Schizophora : Calypterae

The Calyptrate flies (Malloch, 155-156) are represented in the endemic Marquesan fauna only by the family Muscidae (as defined by Malloch) with many species, and the Calliphoridae with two. The Sarcophagidae are represented only by *Sarcophaga taitensis* Schiner, a species of wide distribution. Some undetermined larval parasites taken in sheep may belong to *Oestrus ovis,* though no adult Oestridae were collected; it is probable that no endemic species occur.

Muscidae. About ten species of Muscid flies are known in the Marquesas, seven unrecorded elsewhere, five found in other Pacific islands or farther west or even cosmopolitan. In the subfamily Lispinae—in which only four genera are now known, and of which the larvae are most aquatic—there

is a single known Marquesan species, *Coenolispa erratica* Malloch, in a monotypic genus represented only in the Marquesas. Most of the Marquesan Muscids are in the subfamily Phaoniinae, which is world-wide but most abundantly represented in the Orient. *Ophyra chalcogaster* Wied. occurs from the China Sea to the Marquesas, but *O. trochanterata* Malloch is endemic. Four species of *Limnophora* are also presumably endemic. In *Atherigona*—a genus confined to the Old World, except for the widespread *A. excisa*—*A. ustipennis* Malloch is known only from the Marquesas and Society Islands; *A. excisa* was collected once on Hivaoa. In the Muscinae, only the house fly (*Musca domestica* L.) and *Musca* (*Byomya*) *sorbens* Wied. were found in the Marquesas.

The Marquesan Calypterae are remarkably similar to those of Hawaii, the Society Islands, and Samoa in the presence and development of the several families and subfamilies. In all four archipelagoes there is a large endemic element only in the subfamily Phaoninae and, according to some systems of classification, its allies. Endemic Anthomyinae (as defined by Malloch) are absent or nearly so from all these islands and also from Fiji. The Tachinidae are almost certainly unrepresented in the native Hawaiian fauna, and none has been recorded in the Marquesas and Society Islands.

Pupipara

The Pupipara are represented in the Marquesan collections by a widespread Hippoboscid found abundantly on the magnificent frigate bird (*Fregata minor*). Other members of the Pupipara, if present, are likely to be species of as great or greater range. Some of the Hippoboscids in Hawaii may be endemic, but they have not yet been adequately studied. In Samoa five species of the Hippoboscidae are recorded (Ferris, 87). On Samoan bats there are two species of the Streblidae, unknown elsewhere (Falcoz, 86).

Siphonaptera

The cosmopolitan *Pulex irritans* L., *Ctenocephalides felis* Bouché, and *Xenopsylla cheopis* Rotsch. were the only fleas collected in the Marquesas (Stewart, 225). *Pulex irritans* was surprisingly rare. *Ctenocephalides felis* frequently bites man, as well as infesting dogs and cats everywhere. Strangely enough, the true dog flea, *C. canis,* has not been found on the central Pacific islands.

The distribution of fleas might be expected to elucidate the problems concerning the so-called native species of *Rattus* on Pacific islands. The Marquesan rats yielded interesting parasitic mites and lice but no fleas, and Buxton (31) believes that in Samoa *Mus* (*Rattus*) *exulans* has no fleas peculiar to it. In Hawaii, however, *Xenopsylla hawaiiensis* Jordan (131) was recently

described from *Rattus hawaiiensis*; it is a near relative of *X. vexabilis* Jordan of Australia (and New Guinea?) and of *X. vesiotes* Jord. and Rotsch. of Christmas Island in the Indian Ocean.

ARACHNIDA

Only three orders of Arachnida, the Chelonethida, Araneida and Acarina, are represented in the endemic faunas of the central Pacific. Two widely distributed scorpions, *Isometrus europaeus* (Linnaeus) and *Hormurus australiae* (Fabricius), extend to Tahiti, but only the former to the Marquesas and Hawaii where it is a recent immigrant. The Pedipalpi and Phalangida extend, probably as immigrants, only as far east as Samoa. The Solpugida and Ricinulei are unknown in central Pacific islands. Of the little known Microthelyphonida, the only record I have found is that of a species of *Koenenia* in Hawaii (Van Zwaluwenburg, 241).

Chelonethida

Three undescribed pseudoscorpions were collected in the Marquesas, belonging to the Garypid genus *Geogarypus,* the Chernitid *Lamprochernes* and the Atemnid *Oratemnus* (Chamberlin, MS). A few endemic species have been found on many central Pacific islands, but their geographical relations are little known.

Araneida

The spiders have been rather extensively collected, and carefully studied by Berland (13, 16), and are among the most interesting and best known Marquesan animals. They are abundant throughout the islands, especially in the mountains, and are represented by all the most important groups except the Mygaloidea, Angelenidae, and Lycosidae. Forty-eight species are now known, of which 25 are endemic, 14 are found in other Pacific islands or farther west, and 9 are cosmopolitan. The endemic element is strongest in the Argiopidae, Salticidae, and Theridiidae, but a few endemic species are divided between the Dysderidae, Drassidae, Thomisidae, Pisauridae, and Dictynidae. Four Argiopid genera, *Hivaoa, Uapou, Uahuka,* and *Nukuhiva,* named after the islands where they were collected, are presumably endemic; the first three belong to a group almost entirely confined to temperate regions. A Hawaiian affinity is shown in the development of the Salticid genus *Sandalodes.* Otherwise the affinities of Marquesan spiders are clearly with islands to the southwest and in turn with Malaya. Berland's general conclusions on the origin of the spiders of Pacific islands from Malaya, by former land connections, have already been discussed (p. 18).

Acarina

The collections of free-living mites in the Marquesas are probably representative enough to give some idea of the extent of diversity among them. No special methods, such as the use of a Berlese funnel, were employed in collecting the free-living species and few vertebrate hosts were searched for parasites. The Acarine fauna as a whole is therefore very inadequately known. Most of the collections have been reported upon by Jacot (127), Vitzthum (244) and Ferris (88).

There is a considerable endemic element, both in genera and species, in the Marquesan mites, especially in the Parasitidae (*s. lat.*) and Oribatidae and to a small extent in the Erythraeidae, Phthiracaridae, and Tyroglyphidae. Many insular subspecies and varieties are described by Jacot, though these may have developed rapidly and do not necessarily indicate a prolonged separation between the islands. Jacot writes that "The relations of the fauna are with New Zealand (*Acronothrus nukuhivae*), South America (*Paraschelobates*), but chiefly with East Indies and Hawaii." Vitzhum's conclusions are similar to those of Jacot.

Several species of Tyroglyphine mites described from Hawaii by Jacot are represented by subspecies endemic in the Marquesas. This indicates affinity between these islands, but its significance cannot be estimated in view of the very meager data on the mites of the Society Islands and neighboring groups to the southwest.

Of the few parasites found on vertebrates in the Marquesas the most interesting is the minute *Listrophoroides expansus* Ferris, described from Marquesan rats, and possibly belonging to a separate genus, unknown elsewhere. Other rat-mites found were *Laelaps hawaiiensis* Ewing, also on Hawaiian and Samoan rats, and *L. echidninus* Berlese, which occurs as far off as the East Indies.

No fresh-water mites were found in the Marquesas. Some minute species may occur but the true water mites or Hydracarina are probably absent from the central Pacific.

Mollusca

A fairly representative collection of Marquesan land and fresh-water mollusks is being studied by Dr. C. Montague Cooke, Jr., and brief summaries of the results have already been published (Cooke, 60; Adamson, 2).

About 90 species of land snails have been collected in the Marquesas, representing probably between 50 and 75 percent of the total number present. About 80 percent of these 90 species are endemic and divided between seven families: Zonitidae (about 28 species), Endodontidae (about 12), Pupillidae (6), Partulidae (about 18), Tornatellinidae (about 11), Succinidae (2) and

Helicinidae (about 8). A few immigrants represent the families Stenogyridae, Vaginulidae, Assimineidae, and Hydrocenidae. No Pelecypoda occur in the streams of the central Pacific islands. The fresh-water Gastropods of the Marquesas include only four species: one each in *Neritina* and *Navicella,* and two in *Melania.*

The affinities of Marquesan land snails are with those of islands to the southwest. Island endemism is pronounced. No endemic genera are known, but the species of *Partula* constitute a subgenus peculiar to the Marquesas and highly specialized characters have been evolved in several genera. The general conclusions of Cooke, Pilsbry, and other malacologists on Pacific land snail faunas have already been considered (p. 16). The distribution of land snails within the Marquesan archipelago is of great interest, and has been discussed in a previous publication (Adamson, 2).

Chordata

The non-marine vertebrate fauna of the central Pacific islands is fairly well known. Only the birds are well represented, the other classes being almost entirely absent from the endemic faunas of all the islands east of Fiji.

Pisces

A small collection of fishes made in the Marquesan streams is probably sufficiently representative for discussion, though doubtless incomplete. It has been worked up by Fowler (95) and contains only eight species. Two of these, the Syngnathid *Coelonotus platyrhynchus* (Duméril) and the Ophichthyid *Caecula polyphthalmus* (Bleeker), were found only at the mouths of streams. The others are *Muraena mauritiana* (Bennett), *Mugil macrolepis* A. Smith, *Eleotris fusca* (Schneider) and three Gobies: *Sicyopterus marquesensis* Fowler, *Stiphodon elegans* (Steindachner), *Bryanina inana* Fowler. The Gobiidae is the most important family in the fresh waters of central Pacific islands. The Marquesan *Sicyopterus* belongs to a species unknown elsewhere and the genus *Bryanina,* described by Fowler (95), is known only in the Marquesas and Society Islands. The non-endemic species are all of wide distribution in other parts of the Pacific or even farther west.

In Tahiti 13 fresh-water fishes are listed by Johannes Schmidt (200): three eels of the genus *Anguilla,* two species of Syngnathidae, one each in the Kuhlidae and Eleotridae and six in the Gobiidae. All of them are known to occur in other Pacific islands, and the range of some of them extends as far as the Indian Ocean.

So far as I know, all these fishes are recent descendants of marine forms or, like the eels, spend part of their time in the ocean, and I believe that this is true alike of the fresh-water fishes of the Marquesas, Hawaiian, Society, and

Samoan islands. Buxton (31) states that all the Samoan species are clearly recent immigrants from the sea, and even in New Caledonia only *Galaxias neocaledonicus* Weber and De Beaufort belongs to a group of fishes long established in fresh water. It appears justifiable, then, to assume that all fishes in the streams of central Pacific islands attained their present distribution before any of them became exclusively fresh-water species.

The distribution of the eels of the family Anguillidae is of great interest. They occur on the western side of the Pacific and extend as far as eastern Polynesia. Three species of *Anguilla* are known in Tahiti and, though the genus does not seem to have been recorded from the Marquesas, it probably occurs there. These eels are not present in the rivers entering the Pacific from the Americas, and their absence from Hawaii also is regarded by Germain as an important argument for separating Hawaii from the rest of the central Pacific islands, uniting it instead with America.

AMPHIBIA

No amphibians are known to occur naturally in any central Pacific island east of Fiji. A few frogs and toads have been introduced to the Hawaiian islands, where they flourish. I have learned of no attempt to introduce any of the Amphibia to the Marquesas Islands.

REPTILIA

The only reptiles known from the Marquesas are eight species of lizards (Schmidt and Necker, 202), most of which are abundant at low and intermediate altitudes throughout the archipelago. In the Geckonidae there are five species: *Lepidodactylus lugubris* (Duméril and Bibron), *Hemidactylus garnotii* (D. and B.), *Peropus mutilatus* (Wiegmann), *Gehyra oceanica* (Lesson) and *Hemiphyllodactylus leucostictus* (Stejneger); and three in the Scincidae: *Leiolopisma noctua* (Lesson), *Emoia cyanura* (Lesson) and *Ablepharus boutonii* (Wiegmann). Seven of these lizards are widely distributed throughout most of the Pacific islands or still farther west. The eighth species, *Hemiphyllodactylus leucostictus,* has been found as yet only in the Marquesas and Hawaii.

The reptilean faunas of the Hawaiian, Society, and Samoan islands are almost the same specifically as those of the Marquesas. In Hawaii Stejneger (222) lists four geckoes and three skinks; in Tahiti Cheesman (40) records five geckoes and two skinks; and in Samoa Buxton (31) lists 10 or 11 lizards divided equally between those two families and all of wide distribution. In Samoa and Tonga there is a land snake, the boa *Engyrus bibroni,* but none is known farther east, except a burrowing *Typhlops* accidently introduced at Honolulu, and doubtfully established on Oahu. Sea snakes are represented by four species in Samoa, and they extend sporadically much farther eastward. *Crocodilus maximus* occurs in the Solomons and probably in many islands to

the east. The extreme eastern limit of crocodiles in the Pacific is not established. The late Mr. Gerrit Wilder of Honolulu told me in 1932 that the skeleton of a crocodile had recently been found during the excavation of phosphate deposits on Makatea, on the southwestern margin of the Tuamotus. So far as I know this record has not been published.

It appears, then, that the reptilean fauna of the central Pacific islands is limited to about 12 small lizards, all of wide distribution, except *Hemiphyllodactylus leucostictus* of Hawaii and the Marquesas and one snake, *Engyrus bibroni,* on Samoa and Tonga. There is little point in speculating on the significance of the distribution of the *Hemiphyllodactylus* and *Engyrus*. As for the other lizards, it is enough to state that many of them were probably carried both deliberately and accidentally by early Polynesian navigators and that this dispersal has doubtless been continued by modern commerce.

AVES

The birds of the Marquesas and most other parts of the central Pacific have been adequately collected and systematically studied. Few, if any, species remain to be discovered in the Marquesas. It is possible that some may have been exterminated recently by introduced cats and pigs, since several species once known to occur on many islands are now much restricted in distribution.

Here I shall review briefly the avian fauna, on which systematic reports have appeared in the publications of the Whitney South Sea Expedition (Murphy, 174; Murphy and Mathews, 175). Exclusive of marine, introduced, migratory, and other wide-ranging species, 15 species are known in the Marquesas. Thirteen are endemic, in the Columbidae, Psittacidae, Micropodidae, Alcedinidae, Sylviidae, and Muscicapidae; two in the Rallidae and Ardeidae are presumably indigenous to the Marquesas though widespread in Polynesia. In the Columbidae, Sylviidae and Muscicapidae most of the species have developed insular subspecies.

Ardeidae. The sacred herron, *Demigretta* (*Herodias*) *sacra,* is common round the coasts of the Marquesas and many other Pacific islands.

Rallidae. A single species of rail, *Porzanoidea tabuensis* (Gmelin), is known in the Marquesas. It has a wide distribution in Polynesia which it has presumably attained without human aid. In the Marquesas it probably occurs on all the larger islands, at high altitudes only, and is so shy and perhaps so uncommon that I never saw one. It is likely that pigs and cats have reduced its numbers.

Columbidae. The large saddle-billed pigeon, *Serresius galeatus* Bonaparte, belongs to an aberrant genus and is now rather rare and restricted to Nukuhiva, probably on the western side only. It may once have occurred on other islands, but I learned nothing to suggest that it did.

The green fruit-eating pigeons of the genus *Ptilopus* (*Ptilinopus*) are characteristic of the south Pacific islands, and are represented in the Marquesas by two species. *P. dupetithouarsi* (Neboux) is common on all the islands except Hatutu, Eiao, and Fatuuku; the typical variety occurs on the southeastern islands, the variety *viridior* Murphy on the central islands. The red-crowned *P. tristrami* Salvadori is uncommon and has been reported only from Hivaoa, though Marquesans assert that it occurs on Tahuata and Fatuhiva also.

An endemic ground-dove, *Gallicolumba rubescens* (Vieillot), occurs on Fatuuku and on the uninhabited island of Hatutu, where I have seen coveys of several birds. Since these are the only islands free from both introduced cats and pigs, it seems likely that they are the last refuges of a species once present throughout the archipelago.

Psittacidae. *Coriphilus ultramarinus,* a small lory, is abundant at low and intermediate levels on Uapou and unknown elsewhere. There are several small native parrots in the Tuamotus. Some of them are kept as pets by the Polynesians, and it is therefore possible, though unlikely, that the Marquesan species was brought from the Tuamotus and subsequently became extinct in the latter islands.

Micropodidae. An endemic swiftlet, *Collocalia ocista* Ober., is common on all the larger, higher islands.

Alcedinidae. *Halcyon godeffroyi* is common on Hivaoa, Tahuata, and Fatuhiva, and probably absent elsewhere. *Todirampus tutus* is less common, and I do not know the extent of its distribution in the Marquesas.

Sylviidae. A single species of reed warbler, in the genus *Conopoderas,* is common on all the islands except Fatuuku. Murphy and Mathews (175) give it the name *Conopoderas caffra* (Sparrman), a species which occurs also in the Society Islands, but they distinguish no less than eight subspecies in the Marquesas. Each of these is restricted to a single island, with the exception of the subspecies *mendanae* of Hivaoa and Tahuata. Fisher and Wetmore (91), however, separate the Marquesan warblers as the endemic species *C. mendanae* (Tristram).

Muscicapidae. Endemic flycatchers of the genus *Pomarea* are common on all the islands except Fatuuku and Hatutu. In *P. mendozae* (Hartlaub) four subspecies are distinguished by Murphy and Mathews, one on Hivaoa and Tahuata, and one each on Mohotani, Uapou, and Nukuhiva. *P. iphis* Murphy and Mathews is represented by a subspecies on Uahuka and one on Eiao. On Fatuhiva are two species, *P. whitneyi* and *P. nigra* M. and M., which are unknown elsewhere.

Frequent but transient visitors to the Marquesas are the Pacific golden plover (*Pluvialis dominicus* var. *fulvus*), the wandering tattler (*Heteroscelus incanus*) the bristle-thighed curlew (*Numenius tahitensis*), and the long-tailed cuckoo (*Urodynamis tahitensis*). None of these birds affords much evidence on the distributional problems discussed here. On their influence as possible agents of dispersal of other animals and plants, we need note here only the frequent visits of a few species from one island group to another throughout the central Pacific.

The jungle fowl (*Gallus gallus* L.) was introduced by the early navigators to the Marquesas and other parts of the Pacific. In his elaborate study of these birds, Ball (10) shows that they had changed little from the wild Indian ancestors when brought into the Pacific, that slight natural modifications have taken place since then, and that present heterozygy is probably the result of introductions within historic times. In the Marquesas fowls run wild in great numbers on all the islands except Fatuuku and Hatutu, and have doubtless had some destructive influence on the native fauna.

The introduced birds include ducks, of which there are now a few; geese, peacocks, and turkeys which were no longer present at the time of my visit; pigeons, abundant in many islands, mostly wild; the aggressive and nefarious Indian mynah, *Acridotheres tristis* (L.), recently brought to Hivaoa, increasing there but fortunately absent from other islands; and a small Tahitian passerine (Tahitian *vini*) recently brought to Uapou and common there. A hawk and an owl, whose specific names I did not learn, were brought to Hivaoa within the last twenty or thirty years, but apparently were not established.

The avian fauna of the Society, Tuamotu, and other groups in the south-central Pacific is remarkably uniform and similar to that of the Marquesas. The same genera, *Ptilopus, Pomarea,* and *Conopoderas,* are dominant in numbers of endemic species; the rails, parrots, swiftlets, and kingfishers are similarly represented by a few odd species. The Tahitian and Marquesan warblers are so close that Murphy and Mathews (175) regard them as co-specific. The Samoan fauna also is somewhat similar (Buxton, 31), though with 14 endemic species it is slightly richer than the faunas farther east. *Ptilopus, Todirampus,* and *Halcyon* are common to Samoa and to most of the other islands, but *Conopoderas* and *Pomarea* are absent from Samoa, and also *Hirundo tahitica* which occurs in the Society Islands, Bismarcks, Solomons, New Hebrides, and Fiji. In Samoa there are four genera, *Zosterops, Lalage, Pinarolestes,* and *Didunculus,* not found farther east. Of these *Didunculus,* the remarkable monotypic genus of tooth-billed pigeons, is at present placed in a separate family, the Didunculidae, peculiar to Samoa.

The rich and remarkable avian fauna of Hawaii remains almost completely dissociated from that of other Pacific islands. Only two families, the Rallidae

and Muscicapidae, and not a single genus in the endemic fauna of Hawaii are represented also in the endemic faunas of the Marquesas and, I believe, of other islands of the south-central Pacific. This is astonishing, especially to an advocate of dispersal across the ocean, but also to one who favors past land connections. Dissimilar though the Hawaiian and Marquesan faunas and floras are, there are also many resemblances and it is difficult to explain why the land birds of the two groups should differ so strikingly.

A study of the distribution of birds within the Marquesas shows (a) that two genera, *Serresius* on Nukuhiva and *Coriphilus* on Uapou, a few species, and many subspecies are restricted to single islands, showing the effectiveness of an ocean barrier a few miles wide, and a lapse of time sufficient for considerable differentiation; (b) a rather even distribution in total number of species and number of insular species and subspecies throughout the archipelago, at least one subspecies being peculiar to each island except Fatuuku; (c) a separation of the three groups of islands, northeast, central, and southeast, as shown by species and subspecies of *Ptilopus*; (d) the affinity of the faunas of Hivaoa and Tahuata, as shown by the two subspecies of *Conopoderas* and *Pomarea* common to them.

MAMMALIA

It seems certain that except for bats man was the first terrestrial mammal to reach the central Pacific islands. To the early Polynesian voyagers must be attributed the introduction on these islands of the so-called "native" rats and of domestic pigs, and to white voyagers and commerce the presence of all other mammals, with the doubtful exception of dogs and mice on some of the islands.

No bats are reported from the Marquesas and if any were present they would be well known to the natives. A single species, *Lasiurus semotus,* occurs naturally in Hawaii, and three in Samoa, two of the fruit-eating *Pteropus* and the small insectivorous *Emballonura semicaudata.* It is difficult to avoid the conclusion that all of these bats reached the islands by flight.

The "native" rats of the Pacific islands are of considerable interest, but unfortunately they have not been adequately studied for the purpose of a geographical discussion. Those collected by myself and others in the Marquesas have not yet been determined. The Marquesans told us of two or three recognizable types of native rats (*kioe enata*), but it is impossible to say how much significance should be attached to such views. In Hawaii a distinct species, *Rattus hawaiiensis,* has been described by Stone (226), though he admits doubt as to its status. In Samoa and many other parts of the Pacific the "native" rats are commonly referred to *Rattus exulans.* Little can be concluded as yet from a study of ecto-parasites, such as *Laelaps hawaiiensis* on *Rattus*

hawaiiensis in Hawaii and on *Rattus* sp. (or spp.?) from the Marquesas, and *Xenopsylla hawaiiensis* Jordan only from *Rattus hawaiiensis.*

The mammals brought to the Pacific islands by man are of interest to the biologist principally as destroyers of the flora and in turn of the fauna, and even of everything on the islands save bare rock.

ENDEMISM AND AGE OF THE MARQUESAN FAUNA

Endemism in the Marquesas

Precise figures for endemism in Pacific island faunas, based on present collections and published reports, with all consequent and other uncertainties, are obviously of doubtful significance. It is valuable, however, to discuss endemism in general terms. It is apparent from the above review of the fauna that specific endemism in the Marquesas is high, the majority of the species in the most characteristic and well-developed groups of animals being peculiar to the Marquesas and presumably having been evolved there. Among the land snails, for example, all the species are supposed to be endemic, with the exception only of those believed to have been introduced by human agencies.

Specific endemism in Hawaii, in both fauna and flora, is significantly higher than in the Marquesas and other islands. Bryan (28) gives 81 percent endemism among the 4,620 species of insects in Hawaii and Buxton (32) gives 49 percent for the 1,603 known in Samoa. It is impossible at present to make a precise comparison between the degree of specific endemism in the Marquesas, Society, Austral, and Samoan islands; probably the differences between them are relatively small, perhaps not much more than 10 percent, though this is little more than a guess. Brown (25) states that specific endemism in the Marquesan flora is similar to that in the plants of the Society Islands. In Tonga there is a very meager endemic fauna, for reasons yet incompletely known. Relatively few endemic plants have been found in Rarotonga (Wilder, 249) and the fauna and flora of all the Cook Islands may be perhaps of low endemicity. In the faunas of atolls and raised coral islands there are of course few endemic species.

Many genera of animals are known only from the Marquesas, though at present only in the Isopods, insects, spiders, and mites. Of the three Isopod genera with endemic species in the Marquesas, *Echinodillo* and *Tridentodillo* are as yet unknown elsewhere, though it would not be surprising to find them in the Society Islands. Of the 16 genera of spiders with endemic Marquesan species, four are peculiar; the Pisaurid *Nukuhiva,* and the small Argiopids *Uapou, Hivaoa,* and *Uahuka.* In the mites there is only one known peculiar genus, *Nesiotizetes,* and one subgenus *Paraschelobates* (genus *Scheloribates*), both in the Oribatidae.

To indicate the degree of generic endemicity in the Marquesan insects, the following families are selected as important and sufficiently well known for consideration; the first figure following each is the number of presumably endemic genera now known, and the figure in parenthesis is the total number of genera with presumably endemic species: Collembola: Poduridae 3 (4); Orthoptera: Blattidae 3 (4), Acrididae 1 (3), Tetrigidae 0 (1), Tettigoniidae 2 (3); Hemiptera-Heteroptera: Lygaeidae 1 (3); Hemiptera-Homoptera: Cicadellidae 7 (12), Psyllidae 1(2); Coleoptera: Staphylinidae 1 (8), Buprestidae 0 (1), Cisidae 0 (1), Elateridae 0 (1), Anthribidae 1 (1), Curculionidae, subfamily Otiorrhynchinae 1 (2), Scolytidae 0 (5); Diptera: Tipulidae 0 (1), Simuliidae 0 (1), Asteiidae 0 (1), Chloropidae 0 (3), Drosophilidae 4 or 5 (6), Ephydridae 4 (8), Muscidae 1 (4).

Only one known genus of plant, the primitive Lobelioid *Cyrtandroidea,* is peculiar to the Marquesas.

No Marquesan genus is known to have evolved into a large number of species on one island only. It is perhaps unlikely that there are any genera comparable to many Hawaiian genera, such as those of the Achatinellidae, a family restricted to the small island of Oahu.

What has been written on the comparative degrees of specific endemism in the central Pacific applies in large measure to genera also. The Hawaiian islands are outstanding in the number of large and isolated generic types, and even of endemic families of land snails and birds. Rapa has an astonishing number of endemic genera. Differences between the degrees of generic endemism on most other central Pacific islands are probably slight.

Island endemism in the Marquesas is considerable but variable. All or nearly all species of the large genera *Rhyncogonus* and *Pacificola* in the Coleoptera and of the Cixiidae and Delphacidae in the Hemiptera-Homoptera appear to be restricted to a single island. These are outstanding examples, to which many others could be added. But in many important orders and families of animals it is already evident that island endemism in the Marquesas is low or entirely lacking. This is true especially of the spiders, Cicadellid leafhoppers, Lygaeids of the genus *Germalus,* and many if not most families of flies. In the mites, island endemism is shown mostly among subspecies and forms. Among the land snails, in which endemism is generally high throughout the Pacific, some species are apparently limited to single islands in the Marquesas, while others range over many islands. Of the two known species of *Vitrina,* for example, one inhabits four islands, the other only one; both species are so abundant that their distribution is presumably well known.

These variations in degree of island endemicity from one family to another, and even within one genus, are surprising and difficult to explain. Differences in the conception of specific limits by individual specialists account for some but by no means all of them.

Age of the Marquesan Fauna

There are no ancient fossil deposits on central Pacific islands. Estimation of age by the relative antiquity of existing animals and by the extent of differentiation in genera and species is difficult because of uncertainties regarding the affinities of many animals and the rate of evolution. Species formation on Pacific islands may be more rapid than is generally supposed, so that assumptions of relative antiquity, on the evidence of numerous insular species, must be made with caution.

It appears, however, from the above discussion of endemism that the Marquesan group, and the individual islands within it, have had a long history. Van Dyke (238) writes that the original settlement of *Rhyncogonus* in the Marquesas occurred "at a very early period, early Pliocene if not Miocene." Berland (14) believes that the isolation of insular spider faunas of the central Pacific dates from the middle of the Tertiary and perhaps much earlier. Both these authors write with authority on groups in which numerous endemic species and even genera occur in the Marquesas; their opinions may be accepted as a basis for discussion. In the literature on other central Pacific faunas there are few estimates of the age of the islands. Most authors place the origin of the islands, by the subsidence of large land masses or by the upheaval of oceanic volcanoes, after the beginning of the Tertiary.

All families of land snails native to central Pacific islands, especially the Partulidae and the related Hawaiian Achatinellidae and Amastridae, are believed to be ancient, while all relatively modern families, now dominant on the continents, are represented only by species introduced by man. In the termites of Samoa and all central Pacific islands east of Samoa only the relatively primitive Kalotermitidae are well represented. There are a few species of Rhinotermitidae; and of the highly evolved Termitidae, which are dominant in most parts of the tropics, there is a single species in Samoa and none farther east. Some other groups most characteristic of the mid-Pacific, such as *Rhyncogonus* and *Proterhinus,* are probably ancient types. So far as I know, an attempt to analyze mid-Pacific faunas with reference to their relative antiquity has been made only by the malacologists. A fuller analysis is not possible with the present knowledge of faunas of the Pacific and of its western margin, but when made it will probably afford evidence of much significance.

FAUNAL AFFINITIES

Relations to other Pacific islands

There are many features common to the faunas and floras of all central Pacific islands, in spite of individual peculiarities especially in Hawaii. Some general considerations must therefore precede comparisons between individual islands.

The following groups of animals appear to be unrepresented in the endemic non-marine faunas of all islands in the central Pacific east of Fiji: Porifera; Coelenterata; Oligochaeta; Onychophora; all or almost all fresh-water Crustacea, though this is little more than a guess as regards the Entomostraca; Plecoptera; Phasmidae and Mantidae; Embioptera (?); Nepidae, Naucoridae, Belastomatidae, and Corixidae (?); Membracidae; except for a very few known species, the Aphididae, Coccidae, and Aleyrodidae; almost all families of butterflies; Cicindellidae, Dermestidae, Silphidae, and Scarabaeidae; all but three, the Hemerobiidae, Chrysopidae, and Myrmelionidae, of the families of Neuroptera; Mecoptera; the suborder Symphyta in the Hymenoptera, and many large families of the Aculeates, especially in the higher superfamilies; almost all of the Diptera-Brachycera, and most of the Calyptrate Diptera, in which only the subfamily Phaoniinae or related Muscid flies are well represented; most of the Pupipara; Microthelyphonida, Pedipalpi, Ricinulei, Solpugida, and Phalangida; Mygaloid spiders; Pelecypoda and other fresh-water Mollusca, and all the more modern families of Gastropoda; fresh-water fishes, except recent immigrants from the sea; Amphibia; Reptilia; all mammals except a few bats.

Endemic members of the following groups appear to have their eastern limit in Samoa; some of them are very meagerly represented there; some of them will probably be recorded after further work in the Society Islands and perhaps in neighboring islands: Pyrrhocoridae, Tingitidae, Gelastocoridae; Cicadidae; Ephemeroptera; Dytiscidae (?), Coccinellidae, Tenebrionidae, Chrysomelidae; Stratiomyidae, Tabanidae, Asilidae, Syrphidae; a few families and genera of birds.

The following appear to be represented in the endemic fauna of the Society Islands but not farther east; further work will probably add many others to this list: Polyzoa; Notonectidae; Cercopidae (except for a subspecies on Henderson Island), Issidae (?), Derbidae (?) and probably other Fulgoroidea; Trichoptera; Culicidae.

The most important features common to central Pacific faunas are in the many large genera and even families which are characteristic of and largely confined to these islands. They are discussed on pages 73-74.

SOCIETY, AUSTRAL, AND COOK ISLANDS

So little information on the fauna of these islands is available that only a few points of affinity and dissimilarity with the Marquesas can be presented here.

The Tetrigid genus *Hydrotetrix* is known only from the Marquesas and Society Islands. The Simuliidae, unknown in Hawaii and Samoa, are represented in the Marquesas and Society Islands by allied species forming a group peculiar to these islands. Meyrick's (163) "Palaeonesian" fauna of moths,

though in some respects associated with the Hawaiian fauna, belongs essentially to the Marquesas, Society, Austral, and neighboring islands, and is sharply dissociated from the Samoan and Fijian faunas. The bird fauna of French Polynesia is very uniform, as regards the families and genera and even some species represented.

The impoverishment of the fauna that occurs between Samoa and the Society Islands—a distance of about 1,000 miles, with the Cook Islands intervening, though not directly—is probably much greater than between the Society Islands and the Marquesas, a distance of over 800 miles, interrupted only by the low Tuamotus.

Many groups of animals, however, occur in the Society Islands and not in the Marquesas, and other dissimilarities already mentioned show that, though the histories of these islands as a whole must have been intimately connected, they have diverged in many important respects. Many of these features, however, may be due merely to the greater isolation of the Marquesas.

SAMOA

The affinities and dissimilarities between the Marquesas and Samoa are mostly features that apply to other Pacific islands, and do not call for a separate discussion.

HAWAII

The following groups of animals, which are known in the endemic fauna of the Society Islands and other parts of the central Pacific, are almost certainly absent from the Hawaiian endemic fauna and probably from that of the Marquesas also: Polyzoa; Notonectidae, Cercopidae, and all the Fulgoroidea except the Cixiidae and Delphacidae; Trichoptera; Culicidae. Further work will probably show that many other groups of animals extend east as far as the Society Islands, but not to the Marquesas and Hawaii. An important group of common negative characters is thus evident.

Positive affinities between the Marquesas and Hawaii, not shared with other islands, are few but well defined and significant. In the Hemiptera-Homoptera as a whole there is a much closer affinity between the Marquesas and Hawaii than with other islands. This was emphasized by Muir (*in litt.*) with regard to the Cixiidae and Delphacidae. In the Cicadellidae, though the general affinities of the Marquesas are with islands to the southwest and in turn with Indo-Malaya, there are many resemblances between the Marquesan and Hawaiian faunas. There are resemblances in species of Psyllidae also, though the family is as yet little known in the Marquesas. The genus *Sandalodes,* in the Salticid spiders, has developed extensively in the Marquesas and Hawaii alone in the Pacific. The Dysderid genus *Ariadna* has one endemic species

in Hawaii and one in the Marquesas, but none in other parts of the central Pacific. According to Meyrick the Hawaiian and Marquesan moths of the Pyraustid genus *Scoparia* have a common origin.

A few species of animals are known only from the Marquesas and Hawaii, notably the lizard *Hemiphyllodactylus leucostictus,* some Oribatid mites, some ecto-parasites of rats, the ant *Ponera perkinsi,* three species of Collembola, the earwig *Labia dubronyi,* and a few Acalyptrate flies.

There is a close similarity in the relations between insects and their food plants in the two archipelagoes (p. 26), though further work in other islands may show that similar relations exist there.

The dissimilarities between the Marquesan and Hawaiian faunas are of much greater significance than the affinities, and, due largely to the highly peculiar and isolated nature of the Hawaiian fauna, they apply to the Pacific islands as a whole and not especially to the Marquesas. The Blattidae are exceptionally well represented in the endemic Marquesan fauna and in the Acrididae there is a small but interesting endemic element; both families are represented in Hawaii only by species of wide distribution. Other groups of animals with endemic species in the Marquesas and not in Hawaii are the Tetrigidae, Isoptera, Buprestidae, Simuliidae, some families of birds.

The affinities between the Marquesas and Hawaii appear to be more important in the flora than in the fauna.

Because of the geographical relations, Hawaiian affinities might be expected to be greater in the Marquesas than in the islands farther south. This appears to be true, though opinions may differ as to the significance of these affinities. But while it is evident that the Hawaiian and Marquesan faunas as a whole are profoundly different, certain parts of their history have been intimately connected.

"Mid-Pacific" Faunal Element

It is only recently that attempts have been made to recognize and evaluate faunal and floral elements peculiar to the central Pacific islands and sufficiently distinct to be named. The most important contribution is that of Skottsberg, who has designated an "Old Pacific" flora, derived perhaps from Tertiary Antarctica. Setchell (208) agrees with much of Skottsberg's hypothesis. The discussion by these authors is as yet limited for the most part to individual genera. Still less has been done by zoologists, other than malacologists (p. 16). Meyrick (163-165) has recognized a group of moths restricted to the south central Pacific, on which he bases his assumption of the former continent of "Palaeonesia". He does not attempt to trace its origin. Unfortunately the fossil fauna of Antarctica is unknown, whereas the fossil flora, though few plants have been discovered, shows that there was a rich vegeta-

tion in Tertiary Antarctica. Van Dyke (238) mentions the possibility that the weevil genus *Rhyncogonus* may have originated there.

The following important groups of animals, represented in the Marquesas and in other islands, are restricted to the central Pacific, east of Fiji, or are represented only meagerly in other regions: the Elaterid genus *Pacificola;* the weevils of the genus *Rhyncogonus*; the aberrant genus *Proterhinus*; the "Palaeonesian" moths of Meyrick; and the molluscan families Partulidae and Tornatellinidae. The Hawaiian families Achatinellidae and Amastridae, being related to the Partulidae, may belong to the same mid-Pacific fauna. Smaller groups are the six species of termites of mid-Pacific islands; the Tetrigid genus *Hydrotetrix* and the species group of Simuliid flies, found only in the Marquesas and Society Islands.

In addition, many genera endemic to single archipelagoes may belong to the same faunal element. At the present stage of this inquiry it would be unwise to form a conclusion regarding them—indeed, affinities of many genera are uncertain and may be with animals well represented beyond the central Pacific. It must be admitted also, that the groups of animals named "mid-Pacific" may not represent a distinct faunal element, because some of them may be merely ancient immigrants from Indo-Malaya, though as yet without known relatives there.

The name "Old Pacific", proposed by Skottsberg for plants, may be applicable to the fauna tentatively named "mid-Pacific" here.

Indo-Malayan Affinities

As shown in the table on pages 28-33 the affinities of most Marquesan animals are ultimately Indo-Malayan. The most important exceptions are in the animals of uncertain affinity, especially those which may constitute a "mid-Pacific" fauna, and in some of these, at least, relatives in Indo-Malaya may yet be found. Other exceptions, for example some of the Australian affinities, may be only apparent, and due to derivation of both Australian and mid-Pacific elements from a common Indo-Malayan source.

Australian and New Zealand Affinities

Few Australian affinities have been recognized in the Marquesan fauna, and some of these are probably indirect. The data available at present are inadequate for an evaluation of true Australian elements in the Marquesas. It appears likely that, while they are by no means insignificant, they do not suggest a prolonged communication, by past land masses or otherwise, between these regions.

New Zealand affinities in the Marquesan fauna, direct or indirect, appear to be almost lacking.

American Affinities

It is especially interesting to determine American affinities in the fauna of the Marquesas, because they are the most eastern of important mid-Pacific islands, and also the closest both geographically and biologically to Hawaii, in which large American elements are recognized by some zoologists and botanists.

It may be stated at once that scarcely any American influence can be recognized in the Marquesan fauna. Among the known exceptions are: the termite *Kalotermes* (*K.*) *immigrans,* known only in the mid-Pacific and in the Neotropical region, but possibly introduced by whalers or otherwise across the Pacific; several Cicadellids of Neotropical affinity; the large proportion of American species of Cerambycidae in the Marquesas, probably a result of human commerce; a few native Diptera of uncertain but possibly American affinity; some mites apparently of Neotropical affinity.

CONCLUSIONS

From the evidence that has been presented, the following conclusions on the affinities and age of the Marquesan fauna appear to be indisputable. The native fauna, in common with those of the Society, Austral, Samoan, and neighboring groups, was derived largely from Indo-Malaya, with only a small and probably mostly indirect influence from Australia, and scarcely any from America and New Zealand. In addition, a faunal element of unknown affinity developed throughout the mid-Pacific as far north as Hawaii. There are a few direct affinities between the faunas and more between the floras of the Marquesas and Hawaii, not shared with other Pacific islands. The degree of endemism and relative antiquity of the fauna suggest that the Marquesas have been an isolated archipelago since early Tertiary times, if not earlier.

In deciding the manner in which the islands acquired their native faunas and floras, however, it is necessary to choose between past land connections and transoceanic dispersal. There are many forceful arguments both for and against each view. Land connections provide a ready explanation for the existence of a diversified fauna and for the homogeneity characteristic of many parts of the faunas throughout mid-Pacific islands. Though the opinions of geologists are divided, geological evidence is strongly against land connections, which afford no explanation for the absence of many large groups of animals from the central Pacific. These absences strongly suggest that transoceanic dispersal alone has occurred, and all groups of animals present are probably capable, at least to some significant extent, of such dispersal. But the difficulties presented by ocean barriers of many hundreds of miles are obviously great, and the distribution of some of the most characteristic members of the endemic faunas of the central Pacific, particularly those which are

homogeneous, is strongly against hazardous and chance agencies, such as winds, birds, and ocean drift, as the only means of communication between the faunas. It appears, then, that to adopt either of these views may be to "assume the impossible and believe the incredible." Therefore I shall conclude with an attempt to outline the history of the Marquesan fauna, firstly on the assumption of land connections of considerable extent, and secondly on the assumption that all the islands within the Pacific depression are of oceanic origin.

Origin of the Marquesan Fauna on the Assumption of Past Land Connections

By late Mesozoic or early Tertiary times, an extensive fauna is supposed to have developed in lands of considerable extent in the area now forming the western and central portions of the Pacific Ocean. Most of this fauna came eastward by land connections stretching more or less continuously from the mid-Pacific to Indo-Malaya, probably near present New Guinea and probably without direct and independent connection to Australia. If there were land connections across the eastern Pacific to any part of America, they may have affected Hawaii, but not directly any other central Pacific islands. In addition to faunal elements derived from the west, there was an important element, tentatively designated here as "mid-Pacific", of unknown origin. Among its most characteristic members in existing faunas are the Partulidae in the land snails, the Otiorrhynchine genus *Rhyncogonus,* and the aberrant Rhyncophorus genus *Proterhinus.* These are probably ancient types, and the "mid-Pacific" fauna as a whole, like Skottsberg's "Old Pacific" floral element, may have preceded other elements in origin and dispersal. There is some evidence that the "Old Pacific" flora was related to that of Tertiary Antarctica, and there may therefore have been direct land connections between mid-Pacific lands and the Antarctic continent. It is possible, however, that "mid-Pacific" faunal elements were derived from Indo-Malaya, though as yet without known affinities there.

The central Pacific faunas probably lacked many features of truly continental faunas. The supposed land connections to Asia may not have been continuous, so that animals to which an ocean barrier was entirely impassible were excluded. It is difficult, however, to suggest the extent of the interruptions in land connections, both in time and place. But if there were large land areas in the central Pacific they probably persisted after all connections to Asia had been completely severed, so that the later development of a "Eu-Pacific" fauna was largely independent of other regions.

After subsidence along the western margin of the present Pacific depression, the mid-Pacific lands are supposed to have been reduced by further subsidence to the summits of a few volcanoes appearing above the sea and,

according to Darwin's theory, the coral atolls built upon those which were completely submerged. Isolation of Hawaii preceded that of other islands. The Marquesas and most other central Pacific islands were isolated probably in early Tertiary times. The distribution of several genera of moths suggests that there were land connections between the Marquesas, Society, Austral, and Cook Islands, forming the "Palaeonesian" land mass of Meyrick, after the subsidence of land between this area and that of Samoa and other parts of the western Pacific.

Some elements in the Hawaiian flora and a few in the fauna, notably among the Homoptera, appear to have reached the Marquesas and not islands farther southwest. These may indicate independent land connections between the Marquesas and Hawaii, but their influence on the Marquesan fauna as a whole was slight.

During disturbances resulting in supposed vertical movements of considerably more than 10,000 feet, it is probable that subsidence was far from continuous and uniform throughout the mid-Pacific, and that the relations between the land areas were subject to many complicated changes before stability was attained. Moreover, since volcanic activity was general, considerable portions of the faunas of all the existing "high" islands may have been destroyed. After their isolation the Marquesas may have received a few immigrants by overseas dispersal but the development of the fauna was mostly independent of outside influence until the advent of man. On the assumption of extensive subsidence in the mid-Pacific, the Marquesas Islands were probably first isolated as a single large land mass. In the Hawaiian and Society Islands there is evidence, both biological and geological, of greater antiquity toward the northeastern end of the chains of islands, but no similar relation is apparent in the Marquesas, where all the islands appear to have been isolated for about the same length of time. There may have been a subdivision into three land masses, now represented by the northwestern, central, and southeastern groups of islands, but such an assumption is scarcely necessary. There may, however, have been independent connection between Hivaoa and Tahuata, since the channel between them is relatively shallow. The affinities between the faunas of these two islands may indicate a relatively prolonged connection between them or it may be merely an expression of their close proximity. Eiao and Hatutu probably had a considerable fauna and flora, now greatly reduced by supposed subsidence and consequent change to a relatively dry climate. Mohotani and Fatuuku, having a very meager fauna composed mostly of widespread species, may have originated independently by elevation at a relatively recent date, or their faunas may have been largely destroyed by vulcanism.

After the islands attained their present form and relations, there appears to have been little interisland dispersal of some genera, with the consequent development of many insular species. Among many other genera, however,

island endemism is of such low degree that the ocean barrier appears to have been of little effect. The explanation of this anomaly is not apparent.

With the advent of Polynesians a few thousand years ago a large number of plants were introduced. Some of these, such as *Hibiscus tiliaceus* and *Gleichenia linearis,* are now dominant over large areas. The additions to the fauna, such as fowls, rats, a few lizards, earthworms, small terrestrial Arthropods, were probably relatively unimportant. Since the arrival of white voyagers, however, destruction of the native fauna has proceeded rapidly throughout the islands. At low and intermediate levels and on all parts of Eiao and Mohotani, much of the fauna has become extinct. It is impossible to estimate how much destruction has occurred in the high mountains, to which the greater parts of the native fauna and flora are now restricted.

Origin of the Marquesan Fauna on the Assumption of Transoceanic Dispersal

By agencies possibly more potent than at present, there was a considerable dispersal of animals eastward from the western margin of the Pacific depression to the islands which are supposed to have arisen within it, by volcanic upheaval, about early Tertiary times. The number of immigrants diminished with increasing distance from the continental margins, but a considerable number reached the Marquesas by way of the intervening Society, Cook, and Samoan islands.

Subsidence along the western margin of the Pacific depression, with consequent reduction of the faunas of that region, and possibly combined with climatic changes, resulted in a great reduction in dispersal toward the east, so that the later development of mid-Pacific faunas was to a considerable extent independent. Some of the early immigrants or their descendants, notably the Partulidae, *Rhyncogonus,* and *Proterhinus,* may thus have developed extensively on the islands and not elsewhere. It is necessary to assume that after a considerable amount of immigration, agencies of dispersal became less effective, not only from Asiatic lands but also throughout the Pacific, because large numbers of insular species were evolved on most of the high islands. Indeed, for many animals, including winged insects, most interisland dispersal for distances even of a few miles appears to have ceased long ago. In many animals, however, the loss of wings or other changes in structure and habit may explain the development of insular species from immigrants originally transported for long distances overseas.

The Marquesas received most of their fauna from the southwest, presumably by winds especially, though birds and ocean drift may have played a small part. A few immigrants came from Hawaii, but failed to establish themselves on islands southwest of the Marquesas. The great distance between the

Marquesas and American coasts apparently presented an impassable barrier until the advent of man.

A solution of these problems will be brought considerably nearer by the results of the Mangarevan Expedition of Bernice P. Bishop Museum to southeastern Polynesia in 1934. Further researches most needed are: extended study of the faunas of the Society, Austral, and Cook Islands especially, but also of the Marquesas and Samoa, in the central Pacific; and, for the determination of affinities, throughout Melanesia and Indo-Malaya, and on the fossil fauna of Antarctica. Perhaps agreement will not be reached by biogeographers until the geologists agree regarding the history of the Pacific Ocean, and until a fuller understanding of problems of dispersal, establishment, and evolution is made possible.

SUMMARY

An attempt has been made to discover how the Marquesas Islands acquired their fauna, after presenting as much available biological, geographical, and geological evidence as space permits.

The Marquesas Islands are farther from continents than any others except Mangareva. The ten islands are clearly remnants of the summits of volcanoes, which on geological evidence alone may date only from the Pliocene, though of relatively great age among mid-Pacific islands. The marine fauna is little known and apparently relatively meager because of adverse ecological conditions. Among endemic land animals only the Amphipoda, Isopoda, Insecta, Pseudoscorpionida, Araneida, Acarina, Gastropoda, and Aves appear to be well represented, and among endemic fresh-water animals only some insects.

The history of the Marquesan fauna apparently began not later than the early Tertiary. Specific endemism is of high degree; island endemism within the Marquesas is pronounced but only in certain families. Ancient types predominate in land snails and probably other groups, but an analysis of the entire fauna, as regards relative antiquity, awaits further data.

The zoogeographical scheme of Wallace and others, in which Oceania is a subregion of the Australian region, should be abandoned, but no alternative comprehensive scheme has been proposed. Affinities of Marquesan animals are predominantly with those in the Society, Austral, Cook, Samoan and neighboring islands. There are a few significant features common to the Marquesas and Hawaii alone. Ultimate affinities of the Marquesan fauna are largely Indo-Malayan, a few Australian, almost none Neotropical or New Zealand. An important group of animals—notably the Partulidae, and their relatives, the Hawaiian Achatinellidae and Amastridae, the Rhynchophorous *Proterhinus* and *Rhyncogonus,* the Elaterid *Pacificola,* the "Palaeonesian" moths of Meyrick—are characteristic of the central Pacific and may constitute an element distinct from others of known affinity. The term "mid-Pacific" is

provisionally adopted for this element, but further study may show that Skottsberg's name "Old Pacific", for a floral element of supposed Tertiary Antarctic origin, is applicable.

The assumption that extensive central Pacific lands existed until submerged in the Tertiary, and the assumption of oceanic origin for all islands within the Pacific depression are discussed and almost incontrovertible arguments for and against each view are presented. The paper concludes with an outline of the probable history of the Marquesan fauna, first by assuming land connections and second by assuming transoceanic dispersal alone.

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