Some Distribution Patterns of Pacific Island Faunae

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THIS paper concerns problems in the zoogeography of Pacific islands, based primarily on two families of insects, and notes comparisons with patterns in some other groups of animals. Some of the views here expressed are based on uncompleted research and are thus tentative.

The insects of Pacific islands are too insufficiently known for one to draw comprehensive conclusions on the basis of distribution, so only preliminary deductions can be made. The insect faunae of the various island groups are quite unequally known. For instance, those of Hawaii, Samoa, Marquesas, and New Caledonia are moderately to fairly well known, whereas those of Tonga, New Hebrides, and others have hardly been investigated. Extensive collections from Micronesia are now being studied at the Bishop Museum. Large collections from Fiji and Southeastern Polynesia, also at the Bishop Museum, have only been studied in small part. Furthermore, the rich source areas of the Solomons, New Guinea, and the Philippines, or regions to the westward, are imperfectly known. Among the studies of insect distribution made so far, widely conflicting views have been expressed.

Mayr (1941*a, b*) has given an excellent discussion of the distribution in Polynesia of birds, the best known group of animals, and has modified the outlines of the Polynesian Subregion. Mayr's outline differs from that accepted by most entomologists, and my early impression was that insect distribution would dictate conclusions other than those reached by Mayr. However, on analyzing distribution in the groups under study, my tentative outlines are not greatly different from Mayr's, as far as Polynesia is concerned. Further studies of insect distribution in the area will determine how correct Mayr may be in assuming that tropical land birds are as adequate indicators of insular zoogeography as are other groups of terrestrial animals.

In this discussion the following assumptions or facts are taken as basic to an understanding of the distribution of terrestrial organisms on Pacific islands, but space will not be taken for elaboration of each point. (See Mayr, 1941*b;* Usinger, 1941; Zimmerman, 1942, 1948; Baker, 1951; Gressitt, 1954.)

1. All outlying Pacific islands (except Galapagos, Juan Fernandez, New Zealand, and islands near New Zealand) belong to the Oriental Region and not to the Australian Region, although there is conspicuous New Zealand influence in New Caledonia, and New World and Holarctic influence in Hawaii.

The entire area (Fig. 1) may be termed the Polynesian Subregion, though more accurately it is a tapering fringe of the Papuan Subregion with overlapping influence from the Philippine Subregion and other areas. Within Polynesia, Hawaii and New Caledonia may each be assigned to a division of its own, and the rest to the division Polynesia proper, consisting of the subdivisions Micronesia (Bonin, Mariana, Caroline, Marshall, and Gilbert Islands), Eastern Melanesia (Santa Cruz, New Hebrides, and Fiji), Central Polynesia (Tonga, Samoa, Ellice, Phoenix Islands, etc.), and Southeastern Polynesia (Marquesas, Society, Tuamotu, Mangareva, Austral, Cook Islands; Rapa, and Easter Island). These subdivisions are not strict zoogeographical areas, but are used more for convenience, and express, in part, degrees of impoverishment and, in part, different source areas. For instance, the boundaries between Gilbert and Ellice, Gilbert and Phoenix, and Phoenix and Fanning, are of minor significance, whereas between Fiji and Samoa, and Samoa and Society, greater contrasts exist.

2. There is a general tapering of quantitative representation (for islands of similar size) from west to east, particularly in relation to distance from continental areas.

3. There is also a qualitative tapering from west to east, rendering more isolated islands highly disharmonic in their faunae (fewer major categories represented). This is true even for larger or older islands with greater numbers of species than there are on intervening smaller or younger islands.

4. The extent of speciation on an island is directly related to the island's age, size, isolation, and diversity of environment. The degree of disharmony (scarcity of higher categories) and number of empty ecological niches are also of prime importance, as are climatic fluctuation, elevation and subsidence, eruptive cycles, and erosion cycles.

5. Atolls and other low coral islands have a small fauna—similar in widely separated groups of islands—which is limited by the lack of ecological diversity, the limited halophytic strand flora, the presence of brackish ground-water, the scarcity of soil, and exposure to salt-spray. High islands, on the other hand, can support much more harmonic faunae.

6. There is a general similarity in faunal composition on widely separated groups of islands. This is because they share to a greater or lesser extent a common source (Papuan-Philippine, with other lesser influences), and also because of the similarly selective means of transportation to the islands.

7. Certain types of animals are more likely to be dispersed across the sea than others are, and also more likely to establish themselves on oceanic islands (those islands not recently connected with continents and whose faunae could have arrived by dispersal over sea). In general, small insects and mollusks are dominant animals on most oceanic islands. Animals characteristically absent or scarce on oceanic islands are mammals (other than bats and rats), amphibians, land snakes, fresh-water insects, fresh-water fish, etc. Rats on all outer islands have probably been transported by man.

8. Animals are transported to oceanic islands by air currents (particularly in storms, or in currents circulating in directions opposite to vortices and to the general east-west trade winds, or in upper air currents), by floating logs or trees, or are carried on the feathers or feet of birds, or by man. (See Darlington, 1938; Zimmerman, 1942, 1948; Gressitt, 1954, for several of the preceding points.)

9. Evolution may be rapid on isolated islands characterized by empty ecological niches, an absence of predators and competitors, and a lack of gene-intermixture from parent populations; but long periods of time are necessary for an accumulation of colonists to pass successfully the obstacles of the "sweepstakes" route (Simpson, 1953) and reach such islands. Chances of survival are related to an inverse power of the distance, size of island (1/500 of the Pacific is land), and difficult physiological (as well as other) obstacles. Species that have evolved on old isolated islands appear to be subject to ready extermination under changing ecological conditions. This tendency has been explained on the basis of a depletion of their genic variability; however, this idea does not conform to the current thought of some geneticists. Some of these factors are not fully clarified. Oceanic insects are for the most part small and sedentary, and are generally represented by small populations with restricted distribution. They often appear to represent relicts, but the genetic explanation of relicts is still unsatisfactory. Yamashina (1953) attempted to show that populations on smaller islands produced new

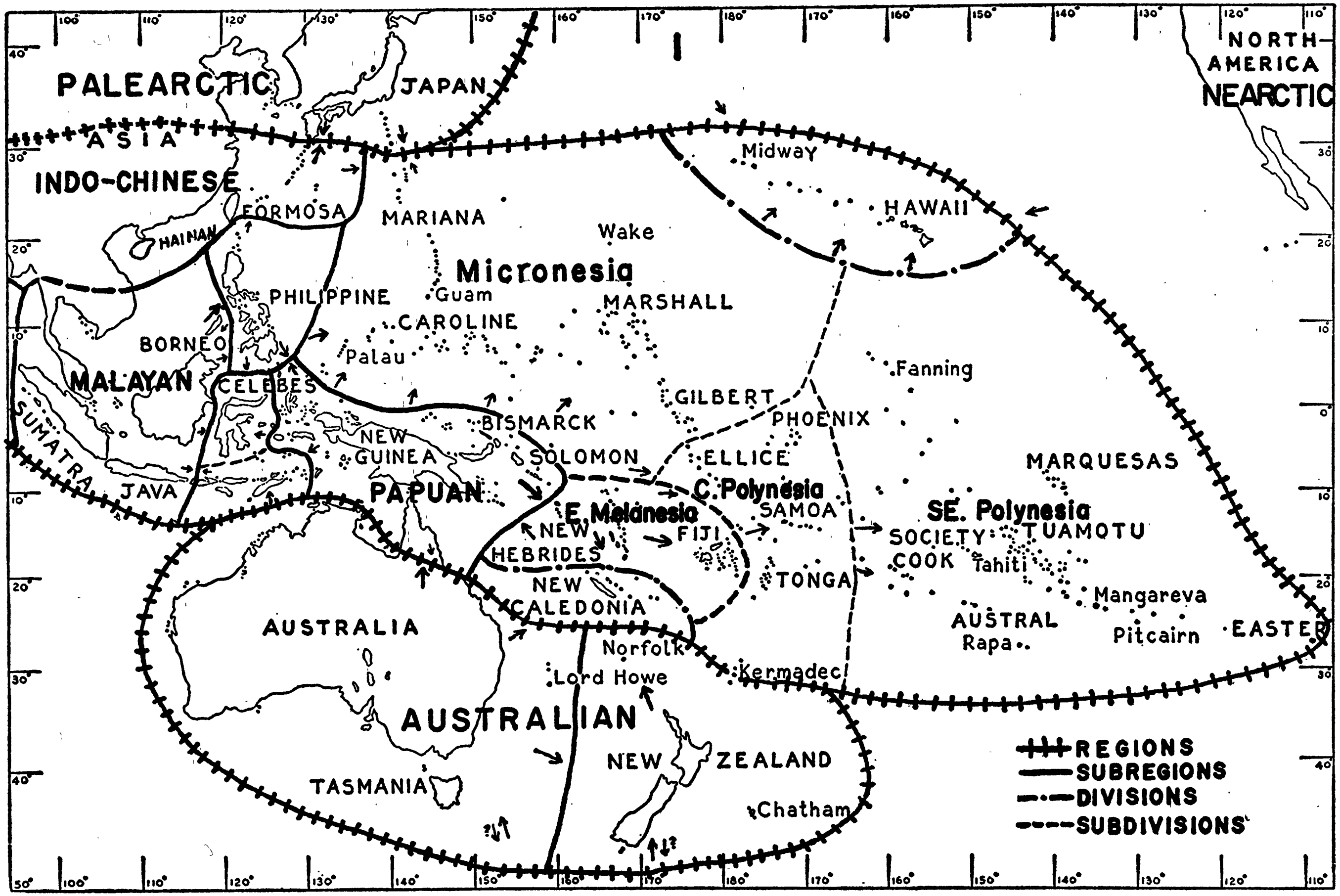

FIG. 1. An attempt at a faunal subdivision of the Pacific area. Portions of the Palearctic and Nearctic, and all of the Australian Region are included, but the greater part of the map is concerned with subdivisions of the eastern part of the Oriental Region. The Indo-Chinese, Malayan, Philippine, and Papuan Subregions of the Oriental are indicated. The Celebes area (old Wallacea) is a heterogeneous transition area of less than subregion rank, and the subdivisions indicated are rather arbitrary. Weber's Line, separating this area from the Moluccas, is in part of less value than the border of a subregion. The remaining areas combined may be called the Polynesian Subregion, but constitute a fringing area of gradually diminishing representation. The fauna of this Subregion is admixed with those of the other subregions and regions shown on the map, especially with that of the Papuan, and, in its western part with those of both the Philippine and Papuan Subregions. Micronesia, Central Polynesia, Southeastern Polynesia, and Eastern Melanesia together comprise the division which can be called Polynesia proper (of equal value with Hawaii and New Caledonia), with the first three of much lesser value than Eastern Melanesia. Arrows indicate probable directions of faunal interchange in later periods of geologic time. Size of arrows suggests relative importance of influence.

genera more rapidly than those on larger islands.

10. The general conformation of the Pacific Basin is of a relatively permanent nature, and probably few relatively major changes of land and ocean bottom have taken place. There have been some changes of sea-level (elevation or subsidence), development and erosion of volcanoes, and growth of coral. The mid-Pacific continents and numerous landbridges of some earlier zoologists have already been dispensed with by Mayr (1941*a*), Usinger (1941), Zimmerman (1942, 1948), and others. However, there have apparently been more high islands in the central Pacific in the past than there are at present (see below).

11. Not all islands with continental rocks are necessarily continental in fauna. To a zoologist, continental islands are those that have been connected to a continental area in relatively recent times, say, since the Mesozoic, and have since remained above water. Thus they do not require over-sea dispersal to explain their fauna.

Oceanic or Continental?

Mayr (1941*a, b*), in discussing the distribution of birds, claims that Fiji, New Hebrides, and New Caledonia are oceanic islands, in addition to Polynesia and Micronesia. Entomologists have rather consistently called them continental, and some have even called Tonga, Samoa, Palau, and Yap, continental (Esaki, 1950, and others). The faunae of Fiji, New Hebrides, and New Caledonia are much richer than those of the other island groups; they include many insects of large size, more groups appear to be represented in them, and they have developed many endemic genera. However, a comparison of subfamilial and tribal representation in the Cerambycidae (longicorn beetles) and Chrysomelidae (leaf beetles) indicates that Fiji has only one more subfamily of Cerambycidae than does Micronesia or Samoa, and only one less subfamily in the Chrysomelidae than does Samoa. New Guinea has at least twice as many subfamilies of Chrysomelidae as Fiji (which has six), and in addition there are two subfamilies known from the Philippines which may also occur in New Guinea. Fiji has more tribes of Cerambycidae than Samoa has, but fewer than Micronesia; Fiji has a few more tribes of Chrysomelidae than either Micronesia or Samoa. New Guinea has about three times as many tribes of Cerambycidae as Fiji, and about six times as many genera. Furthermore, the Fiji fauna for these groups is better known than is that of New Guinea. More of Fiji's genera of Cerambycidae are apparently endemic than is the case for either Micronesia or Samoa. This, however, is not true for the Chrysomelidae. It is undeniable that these islands are within the Sial, or Andesite, Line, but so are the Bonin and Mariana Islands, which are obviously oceanic in fauna.

New Caledonia has a high proportion of endemic genera, but a total of less than one-half as many tribes of Cerambycidae and less than one-quarter as many genera as New Guinea, even though its fauna is probably better known than that of New Guinea. An additional factor in the case of New Caledonia is that its rocks are largely serpentine, soil from which supports a most primitive and peculiar flora. This flora undoubtedly restricts the types of insects that could establish there. These cerambycid beetles of New Caledonia have clear relationships with those of New Zealand as well as those of New Guinea, but rather little with those of Australia, despite this continent's proximity. New Caledonia is less clearly oceanic, and less clearly Polynesian, than are the New Hebrides, Fiji, and the rest of Polynesia. The Loyalty Islands apparently fall into the same category as New Caledonia. The insects of New Hebrides are little known. New Hebrides appears to be oceanic with a poor fauna as compared with that of the Solomons, and it has far fewer endemic genera than has either New Caledonia or Fiji. The Santa Cruz Islands are entomologically more related to New Hebrides than to the Solomons (R. A. Lever, personal communication).

Frogs (Fig. 2) are present in Palau and Fiji, but they are of types whose larvae do not require abundant water. Their presence should not be taken as proof of the continental origin of these islands (Myers, 1953*a*). The Palau species, *Platymantis pelewensis,* lays its eggs on grassy ground, and the larva metamorphoses in three weeks, living entirely on the yolk. There are no gills, and respiration is aided by a great expansion of the abdominal skin (Atoda, 1950). The two or more Fiji species belong to *Platymantis* and *Cornufer* and appear to be endemic (Brown and Myers, 1949). Inger (1954) unites *Platymantis* with *Cornufer*. Several kinds of snakes also occur in Palau and Fiji, but raft dispersal should not be ruled out.

Fiji, New Hebrides, and New Caledonia, as well as Palau, do not possess mammals other than bats and rodents, and in this respect also are oceanic. Palau, in spite of having a more harmonic fauna than the other parts of Micronesia, has conspicuous gaps including insect groups well represented in the Philippine-Papuan area. If any of these island groups had continental connections in the Tertiary and were not since submerged, insects of many more higher categories should be represented. Many unexploited ecological niches can be observed. The normal low population densities and the cryptic nature of the fauna of oceanic islands are characteristics also evident on these islands.

Contrary to the situation on many oceanic islands, some quite large insects do occur here, particularly in Fiji. Among these are very large stick insects and one of the largest beetles in the world. The latter is a prionid like the largest beetles in Micronesia and Samoa. These develop in dead wood and, like many weevils, are heavily sclerotized, and tenacious of life. Moderately large stick insects are fairly well represented on many oceanic islands, such as the Marianas, Carolines, Marshalls, and Samoa. They could have traveled on floating trees, or in palm-frond baskets holding food provisions in early sailing canoes. Stick insects also have well-protected eggs.

Distribution Patterns

Certain patterns are evident from a preliminary analysis of the distribution of certain families of insects among Pacific island groups. A few groups are found on almost every island with endemic species on the high islands. Many of the genera, including some endemic to Polynesia, are of wide distribution. Other groups are of sporadic occurrence, or are found on the island groups less distant from the Papuan Subregion. Some insects associated with strand vegetation are widespread on coral islands and the shores of high islands.

Drawing outlines of the distribution limits of certain groups (Fig. 2), one finds that the weevils are the most widespread group, being found on nearly all islands. They have speciated extensively and are often flightless. Weevils are perhaps the toughest of insects, and thus most likely to survive over-sea dispersal. Most of them feed in dead wood, twigs, seeds, or leaves, any of which could be carried through the air, or float, to islands. Zimmerman has studied the speciation of certain weevil genera on Rapa (1938) and other islands in Southeastern Polynesia (see also Van Dyke, 1937). When the Pacific weevils have been more thoroughly studied, a better picture of Polynesian zoogeography should develop. The ciid and anobiid beetles are also widely distributed. The beetle family Proterhinidae, formerly thought to be endemic to part of eastern Polynesia (Buxton, 1935), has been united with the Aglycideridae. The latter, though absent on the major continents, occurs in New Zealand and some Atlantic islands. A species was recently taken on Kusaie Island, extending the family's range to Micronesia.

Some small moths (Microlepidoptera) are also represented even on outlying is-

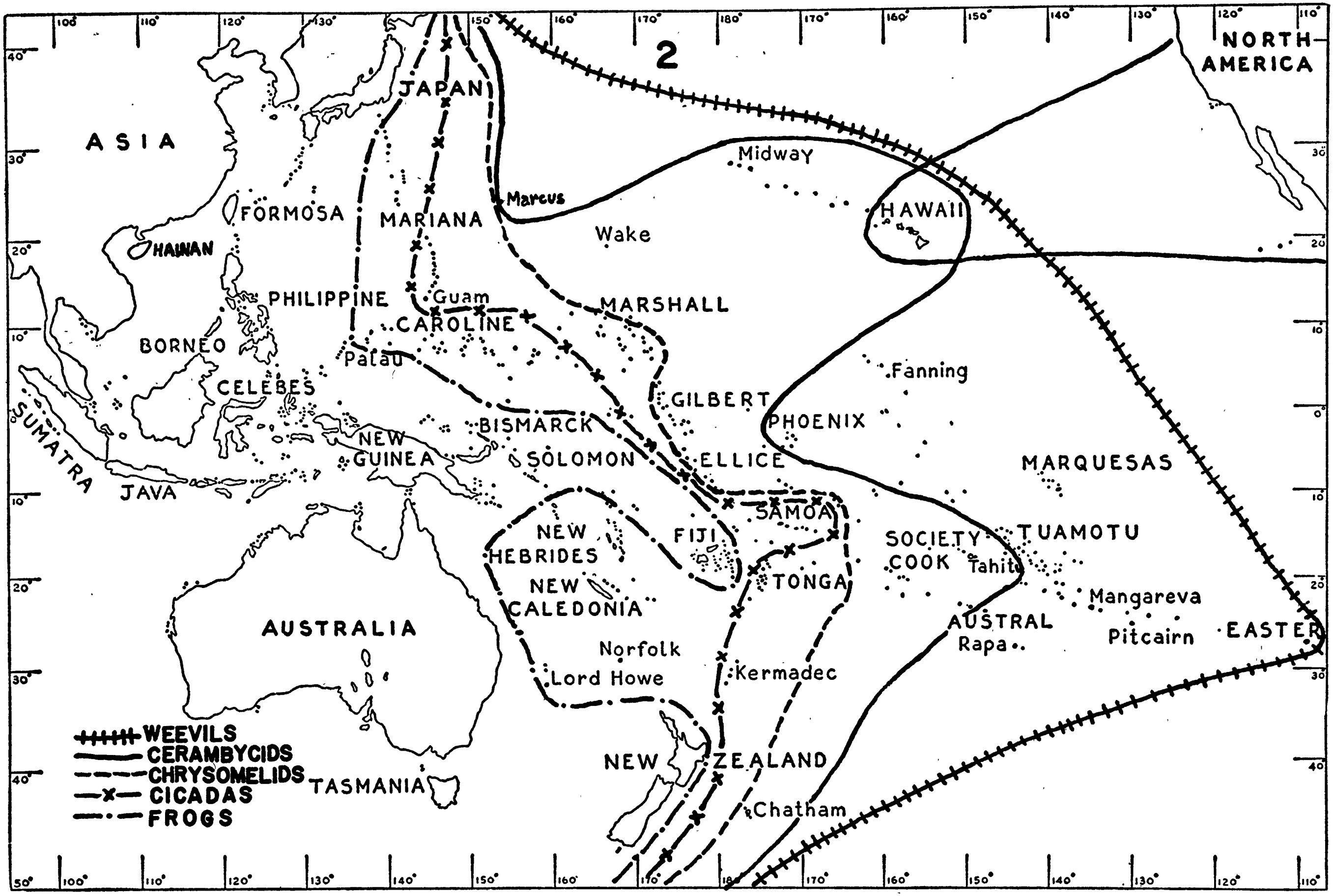

Fig. 2. The limits of distribution in Polynesia of five groups of animals representing different abilities for oversea dispersal. The two lines for cerambycids indicate that parent sources were both Oriental and American.

lands. Unfortunately, land-bridges were invoked to explain their distribution (Meyrick, 1926), whereas such bridges would have brought many other groups which have never occurred on the islands. Furthermore, many of these small moths develop as miners in leaves, as borers in twigs or seeds, or as denizens of bark or debris, all of which could be carried through the air.

Land snails are well represented in Polynesia. Contrary to the situation in insects, three (or four) of the fifteen (sixteen) families (*sensu lato*) of Polynesian land mollusks appear to be endemic. According to Kondo (personal communication) the Tornatellidae (Achatinellidae) are well developed in Hawaii, the Austral-Rapa-Mangareva area, and Juan Fernandez, and also occur in the Bonin, Mariana, Caroline, Society, and Kermadec Islands. A few species are more widely distributed, and one even occurs on Mauritius. The Partulidae occur on most oceanic high islands except Hawaii, Truk, Juan Fernandez, and the Bonin Islands. The existence of Partulidae also in the New Hebrides, Solomon, Bismarck, and Admiralty Islands suggests an Indo-Malayan origin, but there may be a remote South American and Asiatic relationship through Antarctica. The Amastridae are endemic to Hawaii, having evolved from the widespread Cochlicopidae through one or two chance migrants (waifs). The Zonitidae, non-endemic and widespread, are largely derived from southeast Asia, but with a part derived from the Holarctic (supposedly transported by birds), while a third section is endemic to Polynesia. The supposedly endemic families are all primitive and low in the scale of Pulmonata, according to Kondo. They may be relicts whose continental ancestors have disappeared through their failure to meet competition with higher forms, as suggested below for certain beetles.

The Cerambycidae represent a slightly less extensive distribution pattern, with endemic species apparently absent on many outlying groups or low islands, such as the leeward Hawaiian Islands, Marcus, Johnston, the Phoenix and Line Islands, Christmas Island, the Marquesas, Tuamotu, Mangareva, Austral, and Cook Islands, Rapa, and Easter Island. The family is represented on some of these islands or island-groups, but only by widespread Polynesian species, which may in part have spread from Samoa and Tonga, or perhaps for the most part were spread from these sources via Tahiti by the migrations of the Polynesians. A few species are of wide Oriental distribution, and a few, particularly in the Marquesas, have been recently introduced from the New World. On further study, the representatives of the Polynesian genera which occur on a few of these outlying island groups may prove to be endemic forms.

In Hawaii the Cerambycidae are represented by about a hundred endemic forms (apparently descended from only three original colonists) as well as by widespread forms introduced by man. Of the three ancestral native strains, two are primitive nocturnal forms feeding in dead trunks; each of these is still represented by a single endemic species typical of the ancestral genus. One is Oriental, the other nearly cosmopolitan. The third line is more advanced (of diurnal habit), and has speciated into about a hundred kinds, which have been assigned to six closely knit genera. Many of these attack living plants, exhibit extreme host-specificity, and are limited in distribution. Some of the known species are already extinct, and some lowland species probably never were collected. This situation is somewhat similar to that in the native Hawaiian birds, which boast the endemic family Drepanidae; these birds, however, are probably of American origin, whereas most groups of Hawaiian animals are of Oriental (and a few of Australian) derivation.

In Micronesia (Gressitt, 1956) 88 percent of the 100 indigenous cerambycids are endemic. They belong to 34 genera, only five of which are endemic. Two of the endemic genera, one in the Bonins and one in Palau, are flightless. Two other endemic groups show a tendency towards reduction of wings. One minute species among these has developed the faculty of jumping. The relationship of 16 percent of this group is Oriental, 12 percent Oriental-Papuan, 14 percent Philippine-Papuan, and 58 percent Papuan-Oceanic (including some Malagasy relationships discussed below). The Bonins possess some southern Japanese or Ryukyuan forms of Oriental genera, but these islands are clearly Polynesian (Micronesian). The Mariana and Palau Islands possess a higher proportion of Philippine elements than does the rest of Micronesia, although Palau is also strong in its Papuan relationship. Palau is the richest group in Micronesia.

Twenty-three of the 35 Samoan species of Cerambycidae are endemic, and the rest are held in common with Tonga or Fiji. Their relationships are 30 percent Central Polynesian, 15 percent Micronesian, 10 percent Fijian, and 45 percent Papuan-Oceanic. Eight of the nine non-endemic genera, including some thought earlier to be endemic, occur also in Micronesia. Three genera appear to be endemic. In Fiji 105 of the 112 species are endemic, and 18 of the 42 genera are endemic, with relationships dominantly Papuan, or Papuan-Oceanic. Tonga and the Society Islands possess only a few known endemics.

The longicorns from Micronesia, Central Polynesia, and Fiji, discussed above, belong largely to groups of nocturnal habit which bore in dead twigs, branches, or trunks. This suggests that they might have reached the islands in storm-blown twigs or floating logs, or might as adults have been carried in air currents. Being nocturnal, they would be more likely to be on the wing in bad weather. Some large tribes or genera of conspicuous diurnal cerambycids, well represented in the Philippine-Papuan area, are completely absent in all of Polynesia. Since many of these bore in living trees as larvae and are active and sun-loving as adults, they are unlikely to be on the wing in bad weather, or successfully to immigrate on log rafts. In general, the situation in this family seems to be similar to that in birds, as outlined by Mayr (1941*a, b*), although there appear to be no endemics on some outlying groups. The New Caledonian picture, however, is rather different, in that there appear to be almost no close ties with Australia, but rather a high generic endemism with both New Zealand and Papuan relationships. The New Caledonia-New Zealand relationships are largely in a tribe (Enicodini) limited to the two island-groups, but of principally Papuan rather than Australian affinity (Fig. 5). Many families of insects appear to have distribution patterns in Polynesia which are similar to that of the Cerambycidae.

The closely related beetle family Chrysomelidae (Gressitt, 1955), however, has a more restricted pattern. Although on the continents this family has more species than does the Cerambycidae, it is less well represented on oceanic islands. This relatively poorer representation is possibly due to the fact that these leaf-beetles are less sclerotized, shorter-lived, and diurnal, and require more food in the adult stage; furthermore, many have larvae which live in more exposed situations (on leaves, or on roots) and are thus in danger from salt-spray or brackish ground water. Of the 30 species thought to be indigenous to Micronesia, 26 are endemic; two (in the Bonins) may be of southern Palearctic or Indo-Chinese origin, and the rest are Philippine-Papuan or Papuan-Oceanic. Six live in the crowns of large monocots, both as larvae and as adults; three are case-bearers as larvae, and at least one is a leaf-miner. Those with root-feeding larvae are found only on high islands and only in Western Micronesia. Only one occurs in the Marshalls; this is the coconut hispid, occurring also on Kusaie and Ponape.

Chrysomelidae are absent from the native Hawaiian fauna, and also from the Marquesas and Society Islands and all of eastern Polynesia. In Samoa, 13 of the 17 species are endemic, and two genera appear to be endemic. The relationships are Papuan-Fijian, having less in common with Micronesia than in the case of the Cerambycidae. The fauna of Fiji includes 45 endemic species out of 60, and these exhibit Papuan-Asiatic affinity. There is only one endemic genus in Fiji. Many of the Fijian and New Caledonian species belong to the subfamily Eumolpinae, which is moderately represented in Samoa and Micronesia.

An example of a still more restricted distribution in Polynesia is the Cicadidae (Fig. 2), with about seven species each in the Carolines and Fiji, three species in Samoa, and two in the Bonins. This roughly parallels the distribution of the best-represented thoroughly aquatic order of insects, the Trichoptera, which has one species in the southern Mariana Islands; one to three on each high group of the Carolines (three in Yap), one in Samoa, and perhaps ten in Fiji. Cicada nymphs are root-feeders, a habit that limits their dispersal and survival ability.

Of the most restricted occurrence, perhaps, are the frogs (Fig. 2) in Palau and Fiji, the four land snakes in Palau and eight in Fiji, the single mayfly in Yap and the one in Samoa. Scarab beetles, with their soil-inhabiting grubs, are found only in Palau and a few other islands, though some introduced species are quite successful on high islands. The hardier freshwater insects such as beetles and true bugs are widespread, particularly the beetles, which have a few representatives in Hawaii, the Marquesas, and the Society Islands. The marine waterstriders are widespread, but have local endemic species.

Other groups poorly represented by endemics are the Embioptera (delicate barkdwellers), Anoplura and Siphonaptera (associated with mammals), Strepsiptera (complicated host relationships), butterflies (sensitive larvae, fragile wings), and other fragile insects. Groups totally absent include the Plecoptera, Megaloptera (aquatic), Mecoptera (delicate), and Hymenoptera-Symphyta (exposed leaf-feeders); but these are also in part predominantly temperate.

Among several insect families represented in Polynesia, direct relationships with the Malagasy Subregion have been noted. Several of these involve closely related species in Micronesia and central Polynesia and in the Seychelles, Mascarene Islands (particularly Mauritius), or even Madagascar (Figs. 3, 4, 7, 8). In some of these cases [including *Glaucytes* (Gressitt, 1953), *Longipalpus, Prosoplus, Brontispa,* and other beetle genera the taxonomy of which is not yet published] the genera are not known from continental Asia, or even from New Guinea. The latter, or most of them, may represent survival of primitive forms on oceanic islands or elsewhere with restricted competition from advanced forms. Alternatively, some may represent inter-island waif dispersal of forms that could not establish themselves on continental Asia. Since the fauna of India is fairly well known, these patterns are puzzling, though a few of the genera involved are represented in Ceylon. Wider studies must be made, and New Guinea better investigated, before conclusions are drawn. On the other hand, some Micronesian relationships with India which seem to skip the Philippine and Papuan Subregions are also appearing.

Recent Geological History

Thus far, no clear evidence has been found in Micronesia of remnants of a fauna of former islands in the central Pacific which might have served as "stepping-stones" for the Hawaiian fauna of Oriental-Papuan derivation. It has become evident that in spite of the improbability of a former mid-Pacific continent, there has been considerable sinking in the central Pacific for some time (Mayr, 1953*a*). Two more recent discoveries throw further light on the problem. Both suggest that the ocean floor has sunk at least 1500 meters in the area of the Marshall Islands and to the east, south of Hawaii. Surface-living Creta-

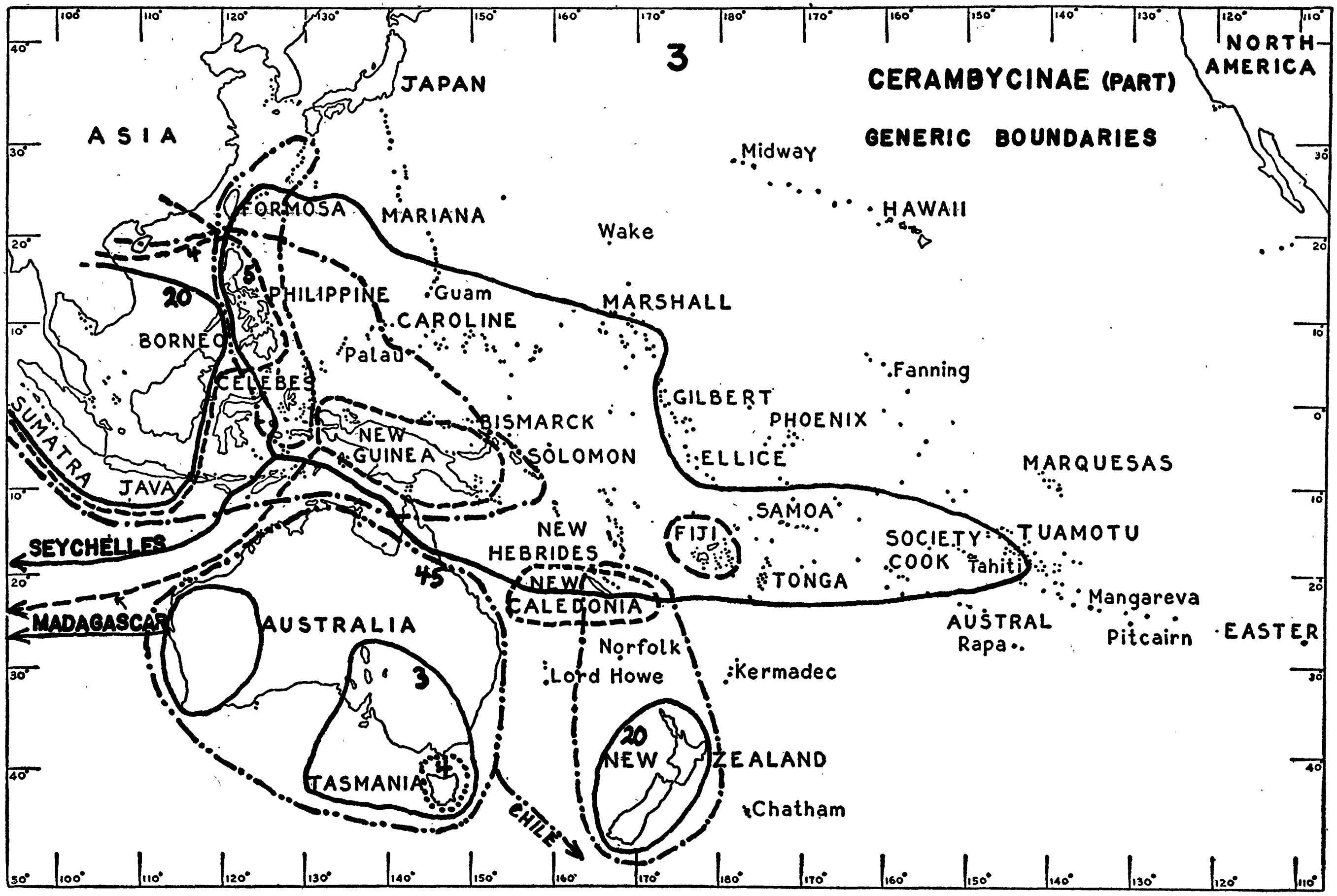

FIG. 3. Generic boundaries in some of the more primitive tribes of the subfamily Cerambycinae, family Cerambycidae. Each line represents the range of a single genus, except where figures are given. Asian genera not reaching Wallace's Line are omitted. Further data presented in Figure 4.

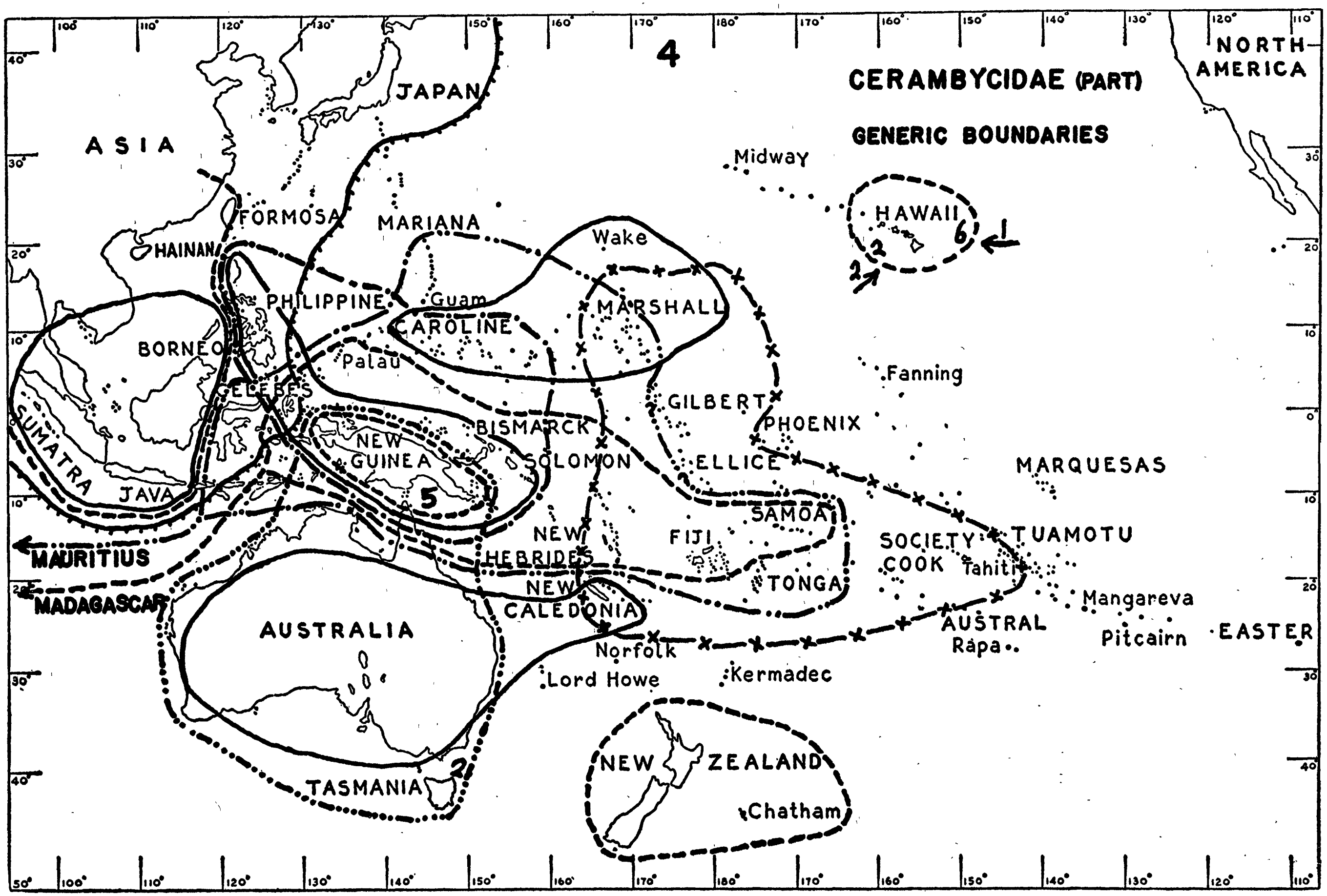

FIG. 4. Generic boundaries in Cerambycidae. The ranges of twelve genera in outer Polynesia, including all eight genera native to Hawaii. Each line represents the range of a single genus, except where figures are given. Arrows for Hawaii indicate source of origin, with numbers by arrows indicating number of genera of original immigrants.

ceous Foraminifera have been found on guyots (flat-topped sea mounts) below this depth (Hamilton, 1953). The borings in the Marshalls, at Bikini, and particularly the 1952 drillings at Eniwetok Atoll (Ladd *et al.,* 1953) have for the first time proved the existence of a volcanic foundation of an atoll, as hypothesized by Darwin. The evidence indicates that the latter atoll developed around a sinking volcano which was once above water. Although erosion may have first reduced the volcano to sea level, as is demonstrated in various stages in the leeward Hawaiian Islands, much gradual subsidence has also taken place. The two drillings first reached basalt underlying the coral, at about 1300–1400 meters below sea level, which is nearly 100 times the depth to which coral grows. Apparently the island started to subside in the Eocene; this might make it too old to have served as a direct stepping-stone, though its fauna might have been passed on to other high islands which later disappeared. At any rate, the present atolls could hardly support many remnants of a high-island fauna.

The insects of the Marshall Islands are largely forms of wide distribution although, interestingly, a few apparently endemic species of Polynesian or Oceanic (Malagasy to Polynesia) genera have been found. The nearby high islands, Kusaie and Ponape, do not appear to have many old relicts, and their fauna is younger than that of Hawaii, with few endemic genera. The eastern Carolines have many faunal elements in common with Samoa and Fiji, and these are probably forms capable of over-sea transport from Papua. When comparing the assemblage of these phytophagous beetles in the eastern Carolines with that of Hawaii, it is seen that the eastern Carolines have endemic species in more genera of Cerambycidae than Hawaii does, even though the total number of endemic species is far smaller. The eastern Carolines have endemic species in four genera of Chrysomelidae, but the family is absent from Hawaii. This correlates with geological evidence for the younger nature of the eastern Carolines, and also with their lesser degree of isolation. If Hawaii had many large "stepping-stones" in the mid-Pacific at the proper times, it might have a more harmonic fauna. However, the Hawaiian Islands may be older than indicated by Zimmerman (1948). There are many Hawaiian-Marquesan relationships (Adamson, 1939).

Sources of Polynesian Fauna

For sources of the Polynesian insect fauna the general Papuan-Philippine area is clearly indicated. Despite the facts that the insects of this rich fauna are too inadequately known, and that the relations of this area to Australia and the Malayan Subregion are insufficiently known, there nevertheless appear certain rather striking indications of strong differences and relationships. Examples will be given from the groups that I have studied, which present a picture somewhat different from the evidence from bird distribution (Mayr, 1944, 1953*b*), but which agree in part with proposals made by some botanists and entomologists (Dickerson, Merrill, *et al.,* 1928; Karny, 1929; Lam, 1934; Scrivenor, *et al.,* 1943; Lieftinck, 1949, 1953).

Primarily on the basis of geographical boundaries of genera in the two families of beetles discussed above, the following tentative points seem indicated. New Guinea has a rich fauna which has had wide influence in Polynesia, and is also felt as far northwest as the Philippines, as far west as Celebes, as far south as northern Queensland, and less directly, to (or possibly from) New Zealand, through New Caledonia. The influence of South America—through Antarctica and New Zealand stepping-stones—may have extended as far as New Guinea, or farther. The northern boundary of the Australian region is just north of Australia, except that the Cape York Peninsula of northern Queensland is excluded and is considered with New Guinea as part of the Papuan

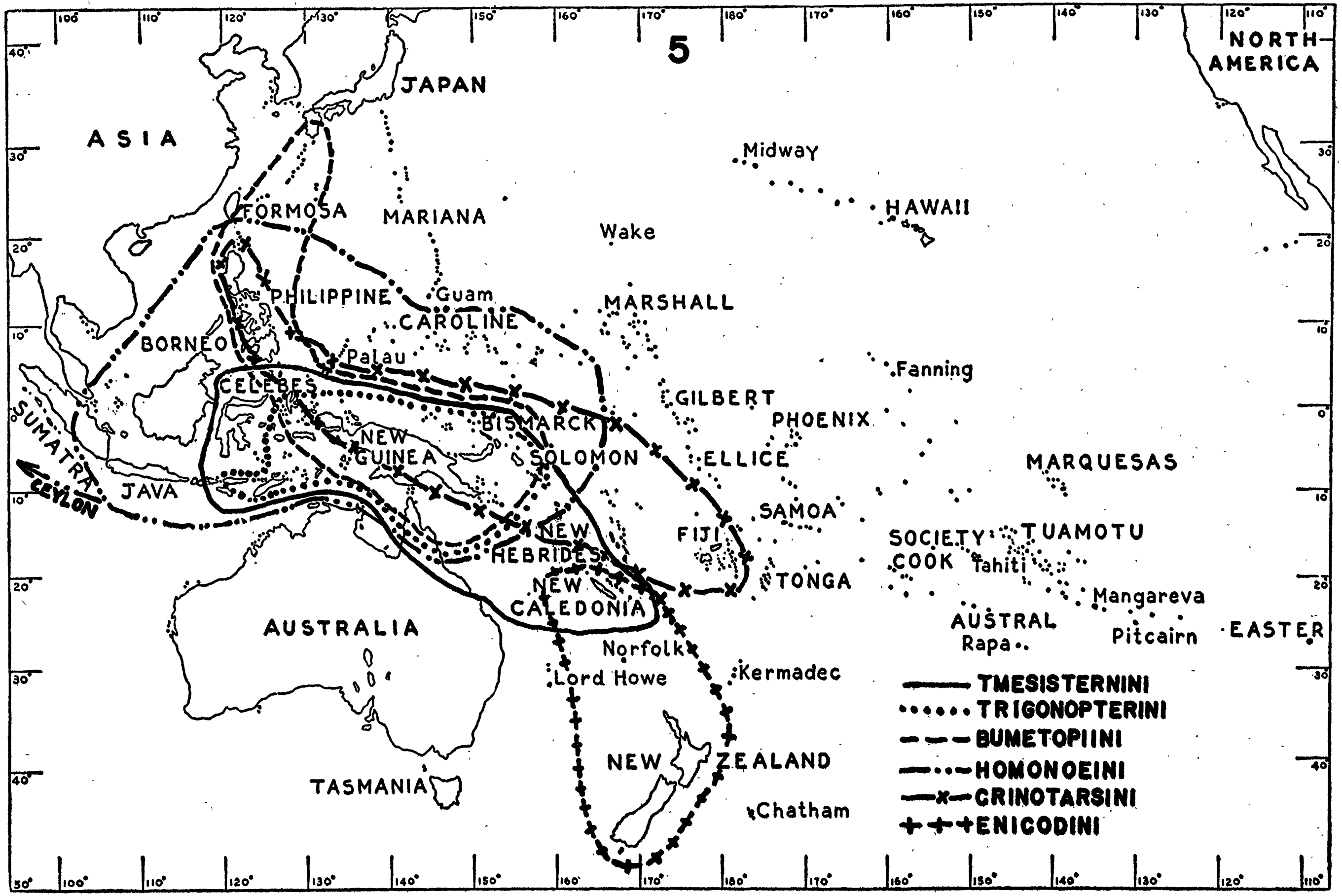

Fig. 5. Outlines of the distribution of the six tribes of the very distinct Tmesisternini tribal complex (Cerambycidae: Lamiinae), which has several hundred species. Only a very few of these occur west of Celebes or north of the Philippines, and the group has no clear outside affinities except in New Zealand.

Subregion of the Oriental Region. The Australian Region includes New Zealand as an extremely strong subregion which has had long isolation and some ancient (or over-sea) interchange with Papua and also with Antarctica and Chile, although Simpson (1940) has questioned such interchange. New Guinea is in part extremely old, with rocks in the north said never to have been submerged since pre-Cambrian time (Cheesman, 1951), although other views have been expressed (Lam, 1934; Mayr, 1953*b*). It may have had early Mesozoic connections with Asia, which gave it an Oriental fauna essentially different from that of Australia, at a period when New Guinea and Australia were well isolated. Miocene-Pliocene tectonic movements raised New Guinea until it was connected with the Cape York Peninsula, allowing an interchange. Australian elements among these beetles, as among the marsupials, went as far as Celebes, but are principally limited to New Guinea, particularly to the less humid southern part. New Guinea elements went as far as the Cape York Peninsula and there were halted by climatic barriers or other barriers perpetuated by climatic barriers.

Thus, at the time when New Guinea was temporarily united with Australia (as has probably happened more than once subsequently, during the Pleistocene sea-level fluctuations), New Guinea had already been long separated from Asia by a wider gap than at present (possibly between Weber's and Wallace's Lines). This prevented most Asian mammals from penetrating the intervening younger area —often called Wallacea (Celebes, Lesser Sunda Islands)—and the Papuan Subregion. At the same time, marsupials were prevented from reaching Asia. The New Guinea mammals include only bats, rodents, marsupials, and a monotreme (Tate, 1951), a fact that points to Australian relationship. The birds also show more Australian than Asian relationship (Mayr, 1953*b*), contrary to the situation in various groups of beetles.

During part of the mid-Tertiary, New Guinea and the Philippines may have had closer stepping-stones, permitting more interchange, at a time when the Philippines were more isolated from Borneo. This resulted in New Guinea and the Philippines having many elements in common which are not found west of the Philippines. On the other hand, some of the elements in the Philippines and New Guinea that are not found west of Celebes and the Philippines may represent primitive forms which have been pushed eastward from southeastern Asia and become extinct from inability to meet competition west of the line. This would be similar to the case of some Amphibia, as has been determined by Inger (1954). Insect distribution suggests that the presence of fresh-water fish in Mindanao might be attributed to human agency, or at least some factor other than a recent Borneo-Sulu-Mindanao land-bridge as suggested by Myers (1953*b*). According to Myers (1953*a*), Luzon has never been connected with Sundaland, and New Guinea and Australia never connected with Asia, at least since the Paleozoic.

Examples of distribution patterns of genera of the more primitive tribes of the subfamily Cerambycinae (Phoracanthini, Cerambycini, and others) are shown in Figures 3 and 4, with the addition in Figure 4 of a few samples of other patterns in other groups of Cerambycidae in eastern Polynesia. The former groups are extensively developed in the Australian Region and have relationships with the Neotropical fauna. Strong demarcation of ranges along the eastern border of the Malayan Subregion and along the northern border of the Australian Region are quite evident. The relative poverty of Celebes and the Lesser Sunda Islands is demonstrated, as is the possession of common elements by the Philippines, Moluccas, and New Guinea, or these in addition to parts of Polynesia. Four genera are common to areas east of the modified Wallace's Line and to the Seychelles, Mascarenes, or Madagascar, and another is common to Australia and Madagascar,

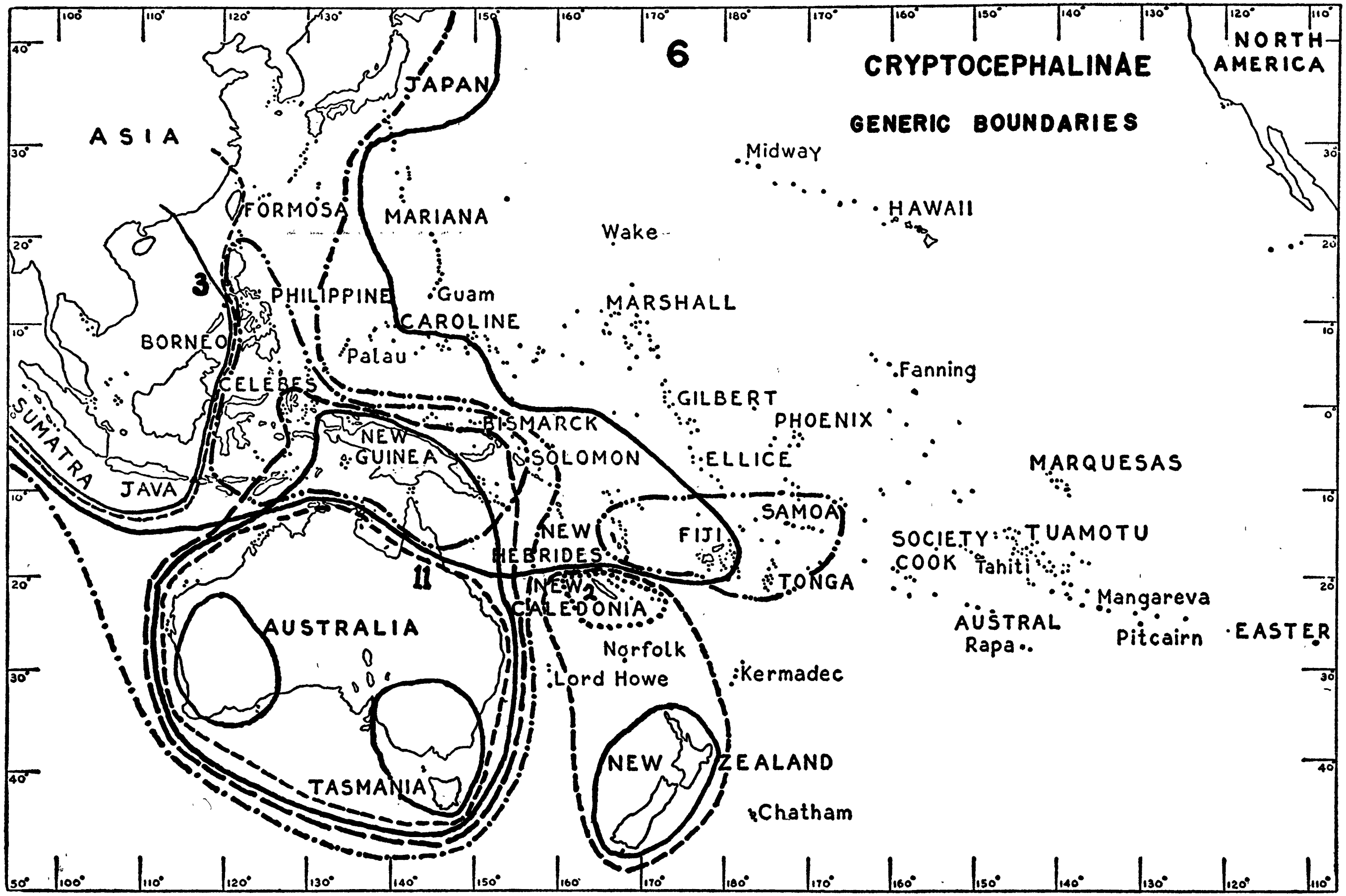

Fig. 6. Generic boundaries of the subfamily Cryptocephalinae, Family Chrysomelidae. Each line represents the range of a single genus, except for three genera limited on the east by the modified Wallace's Line. Two genera are limited to New Caledonia, and eleven to Australia proper (exclusive of North Queensland) besides two with more limited distribution in Australia. Asian genera not reaching Wallace's Line are not shown.

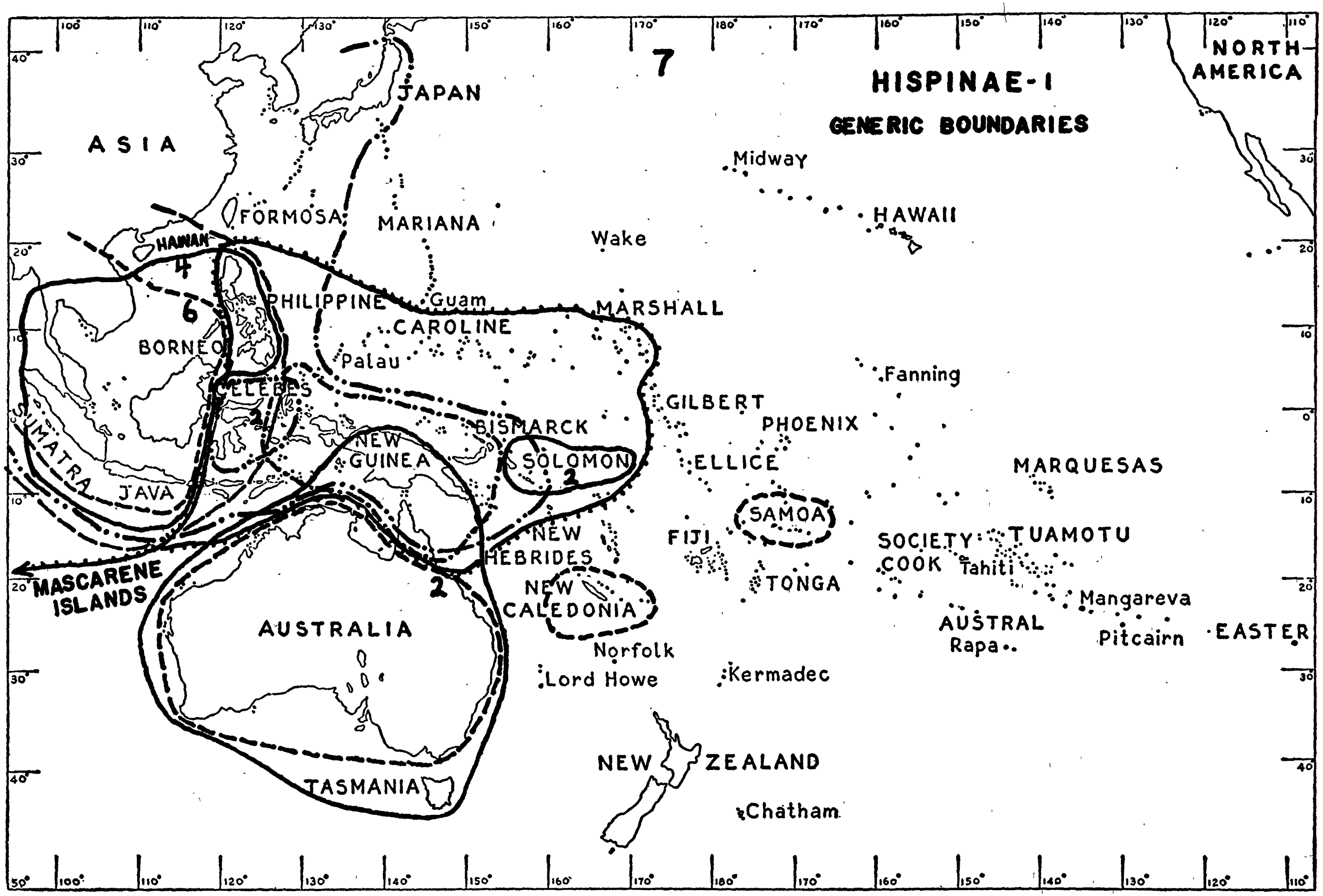

FIG. 7. Generic boundaries for a part of the subfamily Hispinae, Chrysomelidae. Further data for subfamily in Figure 8. Each line represents the range of a single genus, except that six genera are not found east of the Sunda Islands or Palawan, four are common to the Sunda Islands and the Philippines, two are restricted to Celebes and the Moluccas, two to the Solomons, and two to Australia exclusive of Cape York Peninsula, besides one common to Australia and New Guinea.

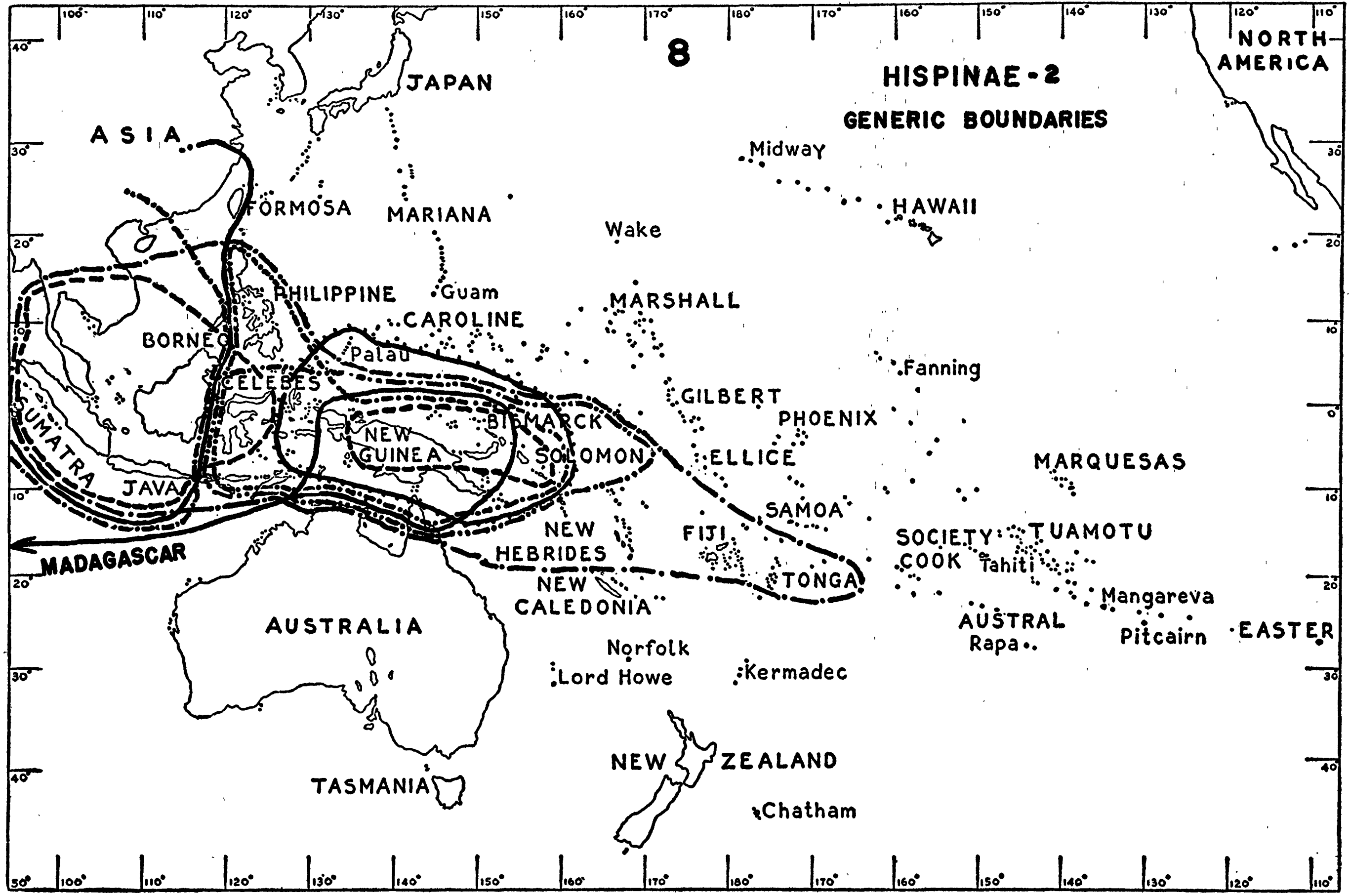

FIG. 8. Generic boundaries in the rest of the subfamily Hispinae, Chrysomelidae (see also Fig. 7). Each line represents the range of a single genus. Asian genera not reaching Wallace's Line are omitted.

Australia possesses 56 genera, and New Guinea 12, but only two are common to both. The situation in these groups approaches that in the gryllacridids, in which Karny (1929) stated that, with the exception of one group, the relationships between Australia and South America were closer than those between Australia and New Guinea.

The groups of cerambycids detailed above show one genus in common between Australia and New Caledonia, and none between New Guinea and New Caledonia. However, in the Tmesisternini complex (Fig. 5), a closely knit group of several tribes of the cerambycid subfamily Lamiinae, relationships between New Guinea and New Caledonia, and (again) between New Caledonia and New Zealand, are clearly shown. Karny also noted that his groups of gryllacridids showed New Caledonia to be more closely related to New Guinea than to Australia. The tribes of cerambycids shown in Figure 5 include a total of a few hundred species and are comprised of peculiar, conspicuous beetles of medium to large size. Furthermore, the very small number of species of Homonoeini known from the Malayan Subregion (and one in Ceylon), and the two or three species of Bumetopiini known from north of the Philippine Subregion, are not likely to be greatly increased by further collecting, whereas more are continually being found in New Guinea. Therefore, statistically these groups may bear even more weight when our faunal knowledge is improved. It is possible that this complex is very old, though most workers have considered it specialized. Its absence on continental Asia suggests, again, that it might be a primitive group now extinct there, although if the age of part of New Guinea suggested by Cheesman (1951) is correct, the group might have evolved locally.

The generic ranges in the leaf beetle subfamily Cryptocephalinae (Fig. 6) also appear to emphasize the boundary north of Australia (excepting Cape York Peninsula) and the modified Wallace's Line. However, New Caledonia appears to be more closely related with New Zealand. The genus common to Australia and mainland Asia (*Cryptocephalus*) is practically cosmopolitan, although absent in New Zealand and Polynesia. The genus common to Fiji and mainland Asia (*Coenobius*) is widely distributed in the Old World but is absent from the Australian Region. Another genus, recorded from Australia and Fiji, is not shown and requires further study. Australia possesses nearly one-half of the world genera in this subfamily.

In the leaf beetle subfamily Hispinae (Figs. 7 and 8) the contrasts are somewhat similar, except that the Philippines appear to have four genera in common with Borneo which are not found in Celebes or New Guinea, and only two found in the Philippines and New Guinea which are not in Borneo. Nine genera occurring in Borneo are absent in the Philippines, but one of these also occurs in Celebes. Eight genera of this specialized subfamily are found in Celebes, nearly three times as many as occur in the Australian Region. The subfamily is absent from New Zealand, and only four genera extend into Polynesia. Two genera found east of the modified Wallace's Line occur also in the Mascarenes or Madagascar. The New Caledonian and Samoan genera are relatives of the one extending to the Mascarenes (*Brontispa*).

The chrysomelid subfamily Cassidinae similarly is absent in New Zealand, is poorly represented in Australia exclusive of Cape York Peninsula, and has most of its Philippine genera common to the Greater Sunda Islands (Gressitt, 1952). The subfamily is also absent in Tasmania and in Polynesia except for New Caledonia, if one excludes a species (living on the sweet-potato) that has been introduced into Samoa and two others introduced into western Micronesia (Gressitt, 1955). Among other subfamilies of Chrysomelidae, Australia possesses a considerable proportion of the genera of Sagrinae, but a rather small proportion, or none, of most of the remainder.

The broad-nosed weevil tribe Pachyrrhynchini presents some interesting evidence in regard to the relationships of the Philippine fauna with that of the Greater Sunda Islands and New Guinea. This conspicuous group of weevils is centered in the Philippines (Fig. 9), with 160 species on Luzon, 110 in the central Philippines, and 41 on Mindanao. There are practically no species west of the Philippines proper, but a moderate number in the Papuan Subregion, and interestingly, only one known from Celebes. This again suggests Philippine-Papuan relationships, or at least some exchange. The evidence in this group, among other animals, together with botanical evidence, was used by Dickerson, Merrill, and others (1928) in following Huxley (1868) in modifying Wallace's Line to go west of the Philippines, between the Sulu Islands and Borneo, and between Mindoro on the east and the Calamian Islands (Busuanga) and Palawan on the west, and then between Luzon and Taiwan. Possibly in the long run the biota of the Philippines will prove

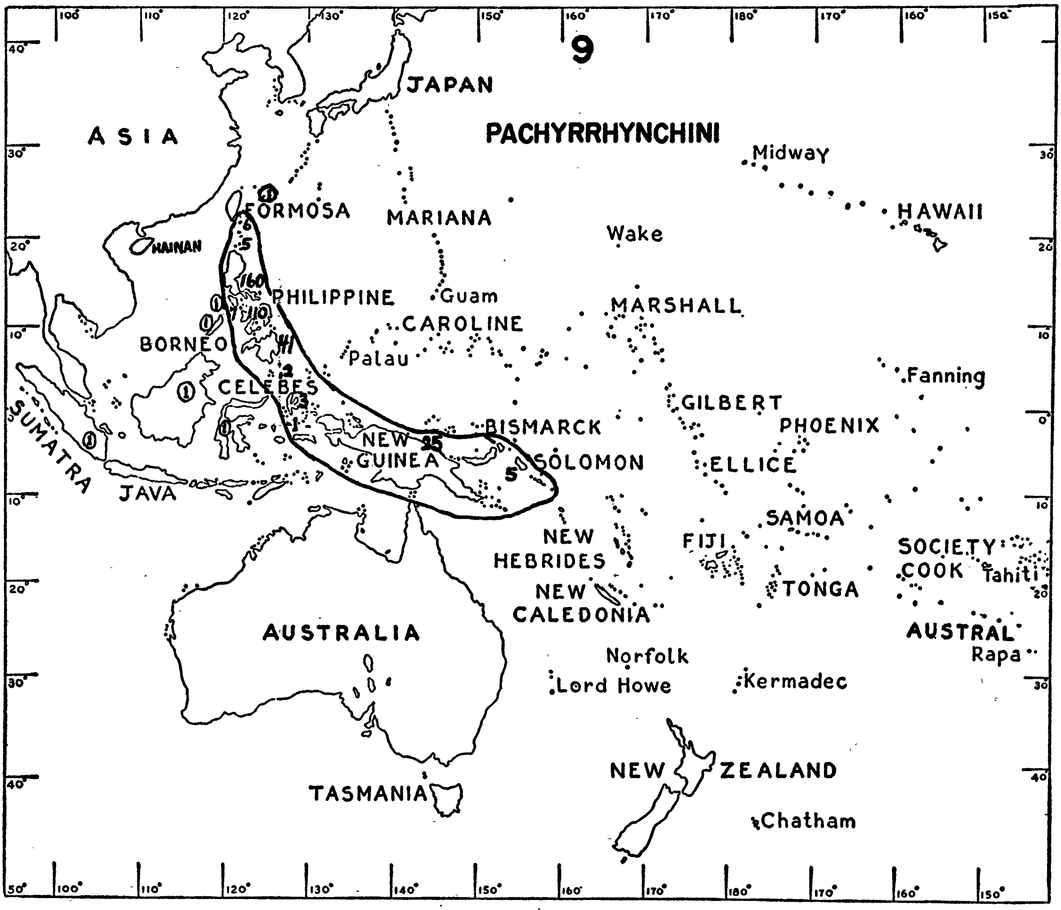

FIG. 9. Distribution of the weevil tribe Pachyrrhynchini. This conspicuous group has one species in the southern Ryukyu Islands, two on Samasana, six on Botel-Tobago, five in the Batanes, 160 on Luzon, seven on Mindoro, and only one each on Busuanga, Palawan, Borneo, Sumatra, and Celebes. Southward from Luzon there are several each on the islands of the central Philippines, 41 on Mindanao, one or two each in Talaud and Sanghir, three in the Moluccas, about 25 in New Guinea, and five in the Solomons.

to be more closely related to that of Borneo than to that of the Papuan Subregion, and Wallace's Line maintained between Celebes and the Philippines, as indicated for many groups. However, many of the groups I have studied lend weight to the above modification. Possibly a forking of Wallace's Line to branch both south and west of the Philippines proper, as shown in the subregion boundaries (Fig. 1), may be the solution. The Pachyrrhynchini extend northward, with five species in the Batanes, six on Botel-Tobago (Kotosho, Lan-yu) just east of the southern tip of Taiwan, two on Samasana Island (Kashoto, Lu-tao) just to the north of Botel-Tobago, and one in the southern Ryukyu Islands. Kano (1931*b*, 1935*b*) further modified Wallace's Line to go northward between Botel-Tobago and Samasana on the east, and Taiwan on the west, thus putting these two islands in the Philippine Subregion, and separating them from Taiwan and the Ryukyu Islands. I concur with this move, at least in the matter of putting these islands in the Philippine Subregion. Of 100 species of beetles on Botel-Tobago, only 11 occur also in Taiwan and seven in the Ryukyus, whereas 46 also occur in the Philippines (Kano, 1931*a*, 1935*b*; Gressitt, 1951*b*).

Taiwan has a fauna differing greatly from that of the Philippines. Of 465 species of cerambycids on Taiwan, only 2 percent are also found in the Philippines, and most of these may be traced through the Indo-Chinese and Malayan subregions, whereas 25 percent of the total are common to Taiwan and the mainland of Asia (Gressitt, 1951*b*). Hardly any genera are restricted to Taiwan and the Philippines together, most of their common genera being of widespread Oriental distribution.

The Ryukyu Islands also belong to the Indo-Chinese Subregion, and the chain formed a peninsula from South China, through Taiwan, during the Oligocene, late Pliocene, and early Pleistocene. At an earlier time, the chain had been connected with Japan, and there is a strong Palearctic element which the ancient mountain range transmitted to the mountains of Taiwan, where it is more extensively preserved. The Ryukyus have been more deeply submerged than at present, and there has been considerable depauperization of the fauna (Inger, 1947; Gressitt, 1951*a*, and in press).

Hainan Island is likewise part of the Indo-Chinese Subregion. It has a higher percentage of species in common with the mainland than does Taiwan and lacks the Palearctic elements found in the higher and more northern mountains of Taiwan. Less than 2 percent of the Hainan cerambycids occur also in the Philippines, and again these can be traced through the peninsula of Southeast Asia and the Sunda Islands (Gressitt, 1940). The southern border of the Indo-Chinese Subregion is a somewhat arbitrary boundary marking the gradual change to the almost uniformly tropical humid climate of the Malay Peninsula and the Greater Sunda Islands, i.e., the Malayan Subregion.

The insects of the Pacific require much more collecting and further taxonomic investigations and evolutionary studies. Only then will the insects provide an adequate basis for far-reaching conclusions about the zoogeography of these island chains, and particularly of New Guinea and the neighboring islands. Distribution patterns in different groups of animals often appear to be widely dissimilar because the dispersal, survival, and evolution of each is affected by different factors. Thus, final conclusions cannot be drawn on the basis of some limited, closely related groups as has been done in this paper. Particularly among insects, there is a need for further insight into their phylogeny, in terms of the historical geology, geography, ecology, and climatic history of the region.

Summary

1. Oceanic Pacific islands belong to the Oriental Region and, although assigned to a Polynesian Subregion, actually have a composite fauna which represents a grad-

ual attenuation of the fauna of the Papuan Subregion, and to a lesser extent of those of the Philippine Subregion, "Wallacea," and the Malayan and other subregions. Australian, American, and Holarctic influences are each relatively minor.

2. Faunal representation on Pacific islands demonstrates an attenuation, qualitatively and quantitatively, the more isolated islands having less harmonic faunae. Some groups of animals are more successful than others in colonizing islands distant from continents and continental islands.

3. Most insects on isolated oceanic islands are small and sedentary, often living in somewhat protected environments. The ancestors of most of them could plausibly have been carried to the islands by natural over-sea dispersal—by winds or floating trees, or by birds.

4. Among the groups widely represented on these oceanic islands are weevils, other small beetles living in dead plant materials, other small insects, and certain groups of land snails. Animals generally absent on islands distant from continents are mammals, land snakes, amphibians, water insects, fragile-winged insects, and most types of large insects, most butterflies, and many soil insects.

5. Studies to date in two of the principal families of phytophagous beetles indicate that those forms (mostly nocturnal as adults), living in dead twigs, dead logs, and seeds, and those mining in leaves, are more widely distributed than those boring in living plants, those feeding on roots in the larval stage, and those with unprotected exposed larvae on leaves or in soil.

6. These studies also suggest, as indicated by Mayr for birds, that Fiji, New Hebrides, and New Caledonia are oceanic islands, as they lack so many higher categories represented in the Solomon Islands and New Guinea; and also that there have been no very large bodies of land in the central Pacific. The present fauna of these oceanic islands does not require land-bridges or former continents to explain its origin.

7. Land snails on oceanic Pacific islands appear to include at least three endemic families, contrary to the situation in other land animals. Some of the relationships appear to be Indo-Malayan, some perhaps Neotropical, and some Holarctic. Their ancestors were probably introduced by birds or by wind-blown or floating debris.

8. In several groups of beetles, and in some snails, there are distinct relationships between the Micro-Polynesian fauna and that of islands in the western Indian Ocean, such as the Mascarenes and Seychelles, or even Madagascar. In most of these the groups concerned are absent from continental Asia and even from the Malayan Subregion, although some do occur in New Guinea. This suggests a survival of primitive forms which have become extinct in continental areas where more advanced forms exist.

9. The beetles studied suggest that the New Guinea fauna is more closely related to that of the Philippines than to that of the Sunda Islands, and that the differences between the faunae justify the modifying (or bifurcation) of Wallace's Line to go northward between the main Philippines on the east and Palawan and Borneo on the west, and further between Botel-Tobago and Samasana on the east and Taiwan on the west.

10. Further studies on insects, particularly of the New Guinea area, are needed fully to clarify faunal relationships in this region, because the Asiatic connections of New Guinea are so ancient as to antedate the evolution of most higher mammals and some birds. The influence of later connection with Australia is thus more strongly emphasized in higher vertebrates than in most insects.

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descriptions are much better than he has been given credit for. Many thanks. D. S. Jordan." Undoubtedly that was not always the opinion of Jordan and unfortunately many other taxonomists in the fields of botany, ichthyology, and malacology have not enjoyed the same experience.

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Editor,
SYSTEMATIC ZOOLOGY:

Re Dr. Hyman's "How Many Species?" (*Syst. Zool., 4,* 142–143).

We are fully cognizant that inaccuracies exist in the preliminary chart of "The Relative Number of Living and Fossil Species of Animals," particularly with regard to the groups of animals on which there are divergent opinions on the number of living and fossil species.

We wish to repeat: "It is hoped that even in its incomplete form the compilation may prove to be of sufficient interest to fellow systematists to induce them to offer their critical comments and to contribute what basic data they may have on hand toward the improvement of the diagram."

We thank Dr. Hyman for the valuable information on nematodes.

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(*Concluded from p. 32*)

Faunal Distribution

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