

# PROBLEMS IN THE ZOOGEOGRAPHY OF PACIFIC AND ANTARCTIC INSECTS<sup>1</sup>

By J. Linsley Gressitt

BERNICE P. BISHOP MUSEUM, HONOLULU, HAWAII

with appendices by

T. C. Maa, I. M. Mackerras, S. Nakata, L. W. Quate

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## ABSTRACT

Insects have been the most successful animals in colonizing isolated islands. Only lands snails approach insects in the degree to which they have occupied islands and speciated there. Abundant evidence shows that many islands have arisen directly from the ocean bottom and were never connected with continents. It is also clear that some ancient islands have existed which are now represented only by atolls or submarine mountains. Such relict islands must have been important in the evolution of the present fauna of isolated island groups and some probably formed stepping stones to existing islands.

Correlation of results of trapping at sea and in the air with types of insects native on oceanic islands strongly indicates dispersal across open ocean from source areas primarily by air currents. The study of the distribution and speciation of insects on Pacific islands may be an important key to the knowledge of the history of islands, of the nature of dispersal, and of the evolution of species in the insular environment.

## INTRODUCTION

In recent years interest has been growing in the question of the origin and history of Pacific island terrestrial fauna. With the technical advances in the Pacific area and concomitant improvement in communication and transport, more entomologists have been finding their way to the area and more representative collections are coming into the hands of systematic entomologists. It is still early to attempt a general summary of the subject, for so little of a comprehensive nature has been published. However, it seems desirable to present an outline of the problems and to discuss some of them in the light of the apparent situation in certain insect groups. Emphasis will be placed on the oceanic islands and apparent source areas of their fauna.

The terrestrial fauna of the oceanic islands is characterized by poverty and disharmony (lack of many groups). Vertebrate animals are poorly represented. Insects make up the bulk of the terrestrial fauna, to a greater degree than on continents, and land snails are second in importance. Mammals are almost entirely absent and are represented under natural conditions only by bats, rats and mice, with the rats and mice chiefly distributed by man. Birds consist largely of wide-ranging sea birds, with very few land birds on small isolated islands except where age and isolation of a group of islands has permitted radiative evolution. Reptiles are represented mainly by skinks and geckos. Amphibians are lacking on most oceanic islands, as are true fresh water fish.

Because of the dominance of insects within the oceanic faunal picture, and because they are almost entirely limited to terrestrial environments, it seems important to survey the patterns of insect distribution on islands. The subject is of interest not merely because we eventually want to know what insects live on which islands and whence they came, but there are many other interesting ramifications of the subject and economic implications. It is apparent that there is a direct relationship between the faunal and geological histories of the various islands. Also involved are the histories of climate, especially air and sea currents, and evolution of insular flora.

In general, the knowledge of insect zoogeography is much less complete (Gressitt, 1958a) than that of vertebrate animals (Darlington, 1957). This is a reflection of the greater knowledge and the far fewer species of vertebrates. The incompleteness of our

knowledge of the insect fauna of various islands is demonstrated by the following estimates of the percentage of the total fauna now known: 5 % for New Guinea, 30 % for New Caledonia, 10 % for Fiji, 30 % for Samoa and 50 % for Hawaii (Gressitt, 1958b).

As studies of zoogeography have progressed, they have become involved in various fields of study. Zoogeography concerns the geographical manifestation of the evolution of animals and not only involves the distribution and evolution of animals but also relates to that of plants and the physical environment. Historical geography (geologic and climatic changes), ecology (ecological opportunity and pressure) and vagility (facility of dispersal) have been important determiners of the distribution of animals. Zoogeographical work cannot be on a solid basis unless it takes full account of ecology, phylogeny, geography, geology and climate—both in space and time. One must approach the question of why a particular species or group of animals does or does not occur in a given area or particular habitat. The phenomena of dispersal, establishment, competition and survival cannot be expressed in terms of static laws, but must be appraised at different time levels in terms of evolution of species and evolution of the environment.

It is common knowledge that most animals are limited to a particular part of the world, and do not occur elsewhere under natural conditions. It is also known that large vertebrate animals, and many others, are not to be found on most islands away from continents. Although vertebrate animals are poorly represented on the more isolated islands, insects are established on all but the youngest or smallest of islets and may be represented by many species on even quite isolated islands. Thus it is evident that insects have been able to colonize many islands inaccessible to certain other animals. Some groups of land snails have also been successful in colonization, and in the radiation of species on certain island groups.

Mounting geological evidence indicates that many isles of the Pacific have never had continental connections, and were elevated from the ocean bottom. Thus animals requiring land connection for dispersal were excluded from reaching such islands. Other geological and paleontological evidence indicates that ancient islands existed which are represented now by atolls or submarine mountains. These former islands could have served as developing ground for old elements (both insects and land snails) which have changed and proliferated into many species or genera in insular isolation over long periods of time. In some cases this has proceeded to the point of obscuring the origin and relationships of the existing elements. It also has apparently contributed to the present existence of more numerous closely related species, and parallelisms among related species-groups, than would be expected to have evolved on certain small and not very ancient islands.

Isolated islands with an old history, or those not too far from other pre-existing isolated islands, have a more spectacular, and sometimes richer fauna, as a rule. Also, more isolated islands (even old ones) have fewer ancestral lines and are thus more disharmonic than island groups nearer the continents or "stepping stones."

It appears that most immigration to the oceanic islands must have been by over-water dispersal, most of it from the Southwest Pacific area in storm winds contrary to directions of prevailing winds. There is fairly good correlation between the types of insects trapped at sea and the primarily small insects which have populated more isolated islands.

*History:* The foundations of zoogeography were laid down a century ago by A. R. Wallace (1860, 1876) and Sclater, and later more lucidly by Wallace (1880), with more

reference to islands in particular. With minor changes, Wallace's six zoogeographical regions still stand today. Only in the Pacific were many of the assumptions incorrect, as far as insects are concerned. This was partly because information was then so incomplete for this part of the world, and partly because higher vertebrates (so much better known than insects) were used as primary criteria. The higher vertebrates, however, are nearly lacking on oceanic islands, and on the continental islands of the Southwest Pacific they present a different distributional picture than most insects and plants. Wallace included most of the oceanic islands in the Australian Region. Actually, their fauna is in general much more closely related to those of Southeast Asia and neighboring islands, all of which should be included in the Oriental Region (Mayr, 1941a; Gressitt, 1956a, 1958a). Insects are much more widely distributed than mammals, and can cross many more barriers. What may be barriers to mammals may be "filter bridges" or "sweepstake routes" (Simpson, 1953) to many groups of insects. Insects are among the most widely distributed classes of animals. The distribution of established insect populations corresponds somewhat with that of non-marine plants and sometimes apparently follows plants in new establishments.

Some past workers, studying fragmentary collections, came to conclusions which we find it necessary to refute. The tendency was to assume past existence of many land-bridges to account for apparently closely related forms in widely separated localities. But these hypothetical bridges usually failed to account for other great differences in the respective faunas. Others attributed indications of poverty purely to lack of field work. A "mid-Pacific continent" was suggested (Pilsbry, 1900) to account for the evolution of Pacific land snails.

A great step forward in the progress of knowledge of insular fauna resulted from publication of the "Fauna Hawaiiensis" (Sharp, Perkins, *et al.*, 1899-1910), largely based on careful field work by R. C. L. Perkins.

Buxton (1930, 1935) made some important contributions to the study of the distribution of insects in mid-Pacific, particularly Samoa. Adamson (1939) made a valuable analysis of the fauna of the Marquesas Islands. Esaki (1950) discussed both Micronesia and the entire Pacific island area. Zimmerman (1948a) presented a very clear picture of the remarkable insect fauna of Hawaii, including its probable history and (1942a) discussed the insects of southeastern Polynesia, besides doing much taxonomic work on insects in both areas (1936a-d, 1938a, b, 1940a, 1948b-e, 1957, 1958a, b). Usinger (1941a, b, 1942, 1953, 1958, 1960), Gressitt (1954, 1955, 1956a-c, 1957a-c, 1958a-c, 1959a, b, 1960a-d), Beier (1957), Bohart (1957), Fennah (1950, 1956, 1958), Kaszab (1955), Linnavuori (1960), Matsuda and Usinger (1957), Quate (1959a, b, 1960), Tokunaga (1959a, b), Wygodzinsky and Usinger (1960) and others have recently completed studies on the general subject or on certain areas, as Micronesia, Fiji, or New Guinea. Gressitt and Weber (1960) discussed the Antarctic-Subantarctic problem.

*Unsolved questions:* Even if all the insect species of the Pacific islands were known—as they certainly are not—there still would be many unsolved problems for the zoogeographer. To begin with, the incomplete state of our knowledge of insect phylogeny and relationships, makes it difficult to establish close affinities of the various elements of the fauna. Extensive recent and past extinction and evolution renders the correlation of faunal units particularly difficult. Finally, since the subject is interrelated with geological his-



tory, climate, plant distribution and ecology, zoogeography cannot be considered without reference to these subjects, which themselves are still incomplete.

Many questions remain to be answered before Pacific zoogeography will be clearly understood. Some of these questions relate to methods of dispersal, ages of faunas, origins, affinities, establishment, speciation, speed of evolution, and geological history, particularly of the ocean bottom, southern continents, and "fossil magnetism" (Irving, 1957-1960). Perhaps some of the most pressing problems are these:

1. Sources and histories of the faunas of isolated oceanic islands.
2. Nature and history of dispersal.
3. Nature of "southern continent" relationships, and geological history of these areas.
4. Relationships of the Oriental and Australian regions.

Among geographical areas needing further field work before they are sufficiently known faunistically for adequate studies of insect zoogeography are the Society Islands, Cook Islands, Tonga, certain Caroline Islands (Yap, Truk and Kusaie), Gilbert and Ellice Islands, New Hebrides, New Guinea and the Solomons, eastern Indonesia, certain subantarctic islands, and various parts of Antarctica.

Among groups of terrestrial arthropods which have been largely overlooked are the mites and spiders, centipedes and millipedes, tardigrades, springtails, grasshoppers and other orthopteroids, smaller moths, beetles and flies, parasitic wasps, and others. Among recently studied groups still needing more attention, and undoubtedly of considerable zoogeographical significance, are terrestrial amphipods (Talitridae), Fulgoroidea, Cicadellidae, weevils, and many other groups of phytophagous insects. The need to fill gaps in our knowledge of insects (and other animals and plants) is urgent, because the native species are often readily destroyed in the activities of man—the most destructive of all forces to the native fauna and flora of islands. Already many animals have become extinct and forever lost to science. This problem was recognized many years ago by Blackburn (1894) regarding the Australian fauna.

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## ENVIRONMENT

The Pacific area is a major feature of the earth's surface, and impinges directly upon all the zoogeographical regions except the Ethiopian (fig. 2). The area is difficult to define, since the Pacific Ocean more or less borders on all the continents except Europe and Africa, and is continuous with the Indian and Antarctic (Southern) Oceans and with the Atlantic through the Arctic Sea and Antarctic Ocean.

Although the Pacific Ocean extensively borders on five of the six zoogeographical regions, the influence of the respective regions on the fauna of the Pacific islands is markedly unequal. To be sure, the continental islands (those at some time connected with the adjacent continent) have essentially the same fauna as the respective neighboring continental area, but influences of the surrounding continents on the oceanic Pacific island fauna is far from equal. The Oriental Region influence dominates the fauna of the mid-Pacific as well as western Pacific isles. The influence of the Nearctic (North America) and the Neotropical (Central and South America) is quite minor west of the Galapagos and Juan Fernandez Islands. In Hawaii, which is nearest to North America, American elements are not dominant (except in the birds), and in the Marquesas and Society Islands American influence is still less. Further to the west, New World elements are obscure or lacking. Intrusion from the Palearctic Region (temperate Asia and Europe) is quite weak; it is evident in the Bonin and Mariana Islands and less distinct in Hawaii. Australian influence on the oceanic fauna is weak beyond New Zealand, New Caledonia, New Guinea and adjacent islands and even in some of those islands, Australian influence is very weak in some groups of insects.

The mid-Pacific is strewn with numerous small islands arranged in various patterns, often in long fairly straight lines, or in double lines (Gressitt, 1954). Most of these strings of islands represent lines of volcanic activity of various periods. Some are still active for a considerable length, as in the Northern Mariana Islands and in the New Hebrides,

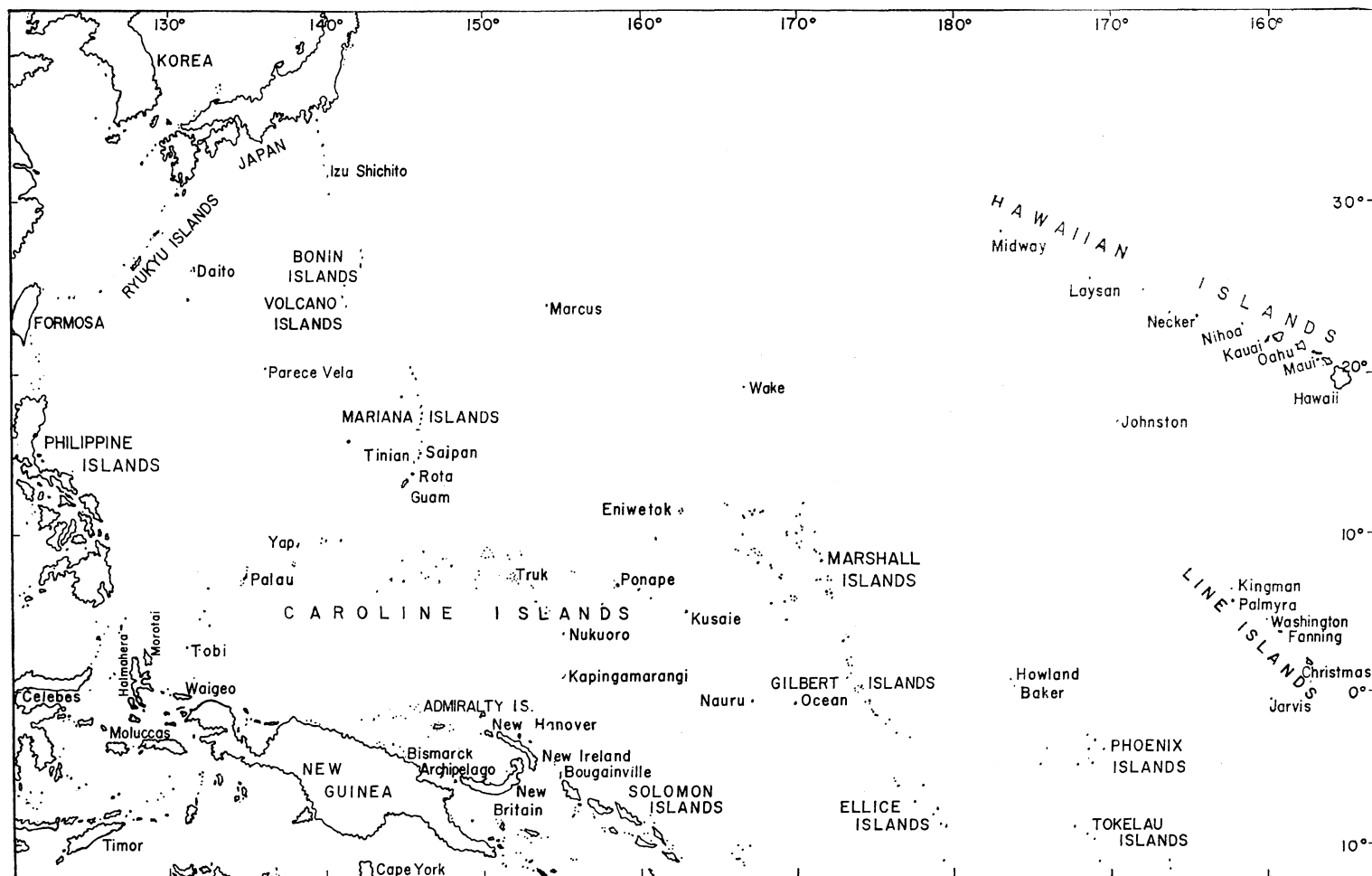


Fig. 1. Map of Western Pacific.

and others are active at one end of a chain, as in Hawaii and Samoa. Others are entirely extinct, as in the Carolines and Society Islands, and many others have eroded and sunk to the point where they are represented merely by atolls of coral growth at sea level. Some islands consist of slightly to greatly raised coral islands. Closer to the continents there are islands with much older metamorphic rocks of various sorts. Fiji is the group in this category extending farthest out in the Pacific, with others to westward.

All of these various islands support insects and other life, except those newly emerged from the sea through volcanic action or elevation. In general there is a distinct correlation of variety of insects on an island with its age, but other important related factors are its isolation from other islands and its distance from the nearest continent, as well as its size and height, climate and flora. All of these factors contribute to the ecological opportunity for the inhabitants, in terms of potential food, niches and suitable environment. The more diverse the ecological opportunity, the more extensive will be the insect fauna, given sufficient time for populating the island through dispersal, establishment and speciation.

Atolls and other low coral islands form an exception to the above generalization, for their lowness greatly limits both the terrestrial plant and animal life which they can support. Only a small number of plants can survive the salt spray, saline soil, salt contamination around shores or from storms, and salt water beneath the thin lens of fresh water which rises and falls in the island with the tides. This in turn limits the number of species of insects which can become established and survive. In general the atoll species are widespread and different atolls have very similar faunas.

The high islands, therefore, in contrast to the low coral islands, can develop rich and varied faunas through evolution, subject to limitations on immigration and establishment. On more isolated islands the evolution has been more spectacular.

## DISPERSAL

Various evidence, including the disharmonic nature of the fauna, the isolation and the geological histories of islands, indicates that oceanic islands must have been populated by some sort of oversea dispersal. Four methods of oversea dispersal have been cited: 1) in air currents; 2) on floating trees, logs or natural rafts; 3) on the feet or feathers of birds; and 4) by man. This subject has been much discussed (Darlington, 1938, 1957; Zimmerman, 1942a, 1948a; Gressitt, 1956a, 1958a), but not sufficiently documented to reasonably estimate what percentages have been carried by the first three methods.

Documentation of the dispersal of insects by air currents is being accumulated. Hardy and Milne (1937) reported trapping insects from ships in the North Sea. Glick (1937, 1957) reported on extensive series of trappings of air-borne insects from small airplanes. More recently trappings have been carried on from ships crossing the Pacific (Gressitt and Nakata, 1958; Yoshimoto and Gressitt, 1959, 1960), and from ships and planes in the Antarctic area (Gressitt, Leech and O'Brien, 1960, and unpublished data), and results of trapping at sea on the world cruise of the Danish research vessel "Galathea" are being processed. Also, trapping has recently been carried on for Bishop Museum on the Scripps Institute of Oceanography's "Monsoon Expedition" across the Pacific and Indian oceans, and a trap has been developed and used in a Super-Constellation plane operating between United States and Antarctica.

Although the trapping of air-borne insects over the Pacific, Antarctic and nearby seas has not produced very extensive data to date, the results are nevertheless of great interest. 1075 insects have been trapped in screening over 25 cubic kilometers of air in these areas. The significant fact is that the types of insects being trapped correlate extremely well with the prevailing representation of insects on the more isolated islands. These essentially are small insects, particularly those of low specific gravity and less compact bodies. They include representatives of Psocoptera, Homoptera, Diptera and Hymenoptera, with lesser numbers of spiders, Collembola, Heteroptera, Microlepidoptera, Coleoptera, and a few other groups. Although much more data is needed, results to date support the view that air dispersal is the most important method of travel to oceanic islands by the native insects.

An important short-coming of the trapping program is that in most cases it is impossible to tell whether the insects were alive or dead when trapped. It is, of course, safe to assume that most of those taken great distances from land and at high altitudes were dead. The chances of an insect being carried great distances and still being in condition to reproduce are slight. However, they are not inconsistent with the conclusions cited below in which over a period of a few million years only about 250 successful and perpetuated establishments were necessary to account for the present insect fauna of Hawaii.

The trapping results may be briefly tabulated as follows:

Order	Total trapped	Max. Dist. from land in Kilometers <sup>2</sup>	Gen. area
Araneida	35	600	Pac.-Ant.
Acarina	4	200	W. Pac.
Collembola	3	100-1000	Antarctic
Blattaria	2	500	"
Orthoptera	6	200	W. Pac.
Psocoptera	16	900	Pac.-Ant.
Isoptera	5	1000	W. Pac.
Homoptera	166	1200	Pac.-Ant.
Heteroptera	53	700	"
Thysanoptera	27	500	"
Ephemeroptera	1	200	W. Pac.
Neuroptera	10	400	Pac.-Ant.
Lepidoptera	22	3000	"
Coleoptera	74	900	"
Diptera	376	1100	"
Hymenoptera	172	700	"

Some large insects, as dragon-flies and sphinx moths, may have reached isolated islands by a combination of passive transport in storm winds and active flying in the vicinity of land, as is often observed with stray birds landing on ships or on isolated islands. A butterfly found in good condition on the deck of an ice-breaker at 71° South Latitude just off the coast of Antarctica would fall into this category.

2. By land is meant nearest probable source, considering fauna of intervening islands and direction of wind.

Directions of prevailing air currents often prove to be unfavorable for direct transport from a continent to an island. This is not in itself an argument against the air dispersal theory, although it indicates one of the obstacles to successful dispersal. Counter-currents, higher jet-streams moving in a favorable direction, and particularly erratic conditions during storms have all to be taken into account. Tropical cyclones (Dunn, 1951) are frequent occurrences and involve currents and counter-currents of air in all possible directions and over a wide range of altitude. Direct evidence of hurricane dispersal has been presented by Herring (1959). Müller (1871) and C. B. Williams (1957) have dealt with this subject, including presumed voluntary flights over ocean. Yasumatsu and Nakao (1957) demonstrated dispersal of young scale insects in air currents. A scale insect recently established in New Zealand is suspected of having been brought from Australia by air currents.

In regard to other means of over-water dispersal, it is hard to document travel on floating trees, logs or natural rafts. On occasion logs washed ashore on isolated islands have been shown to contain living termites (Emerson, 1955). Termites are actually poorly represented on oceanic islands and presumably they are not very resistant to sea water. This is probably also true of most insects. Wheeler (1916) reported ants floating from continent to islands in a log. Some large insects, as heavy-bodied beetles inhabiting dead logs, could have come by this method and been protected within the cavities in the log.

The transport of small invertebrates on the feet or feathers of birds is not to be ruled out. They may be attached by normal secretions, oils, excrements or mud. Zimmerman (1948a) described the landing and take-off of sea birds in forest in which they thrashed about in the vegetation and could have picked up or dropped eggs, seeds or other organisms. More documentation of this type, and thorough examination of migrants and strays, could provide interesting and pertinent data.

It is generally a simple matter to determine what insects have been transported to islands by man. These are generally common, cosmopolitan species associated with man, including "domestic" insects (ectoparasites, cockroaches, house flies, etc.) and those associated with domestic animals, crops, stored foods, drugs and leather goods.

## ESTABLISHMENT

Foremost among the obstacles to successful establishment of an animal on a Pacific island is the slight chance of finding land. Only 3 % of the total area is land and away from continental islands a mere 1/500 of the Pacific is above water. Other obstacles include damage in strong winds; desiccation, particularly in clear weather (an important consideration for insects with a large body surface relative to size); deleterious effects of salt from the ocean or wind-blown spray; injury on landing; and unavailability of suitable food and breeding sites.

If an insect can survive the journey to an island and manages to reproduce, it may become established in an empty niche, enter into competition with relatives, or compete with unrelated ecologic equivalents. Usinger (Usinger and LaRivers, 1953) found that two species of *Nysius* occurred in the Marshall Islands, but never on the same island. He concluded that *N. picipes* was the original, precinctive (endemic) form. On islands where military operations had occurred, such as Majuro and Kwajalein, *picipes* was completely replaced by *pulchellus*. Evidently the two are completely equivalent ecologically and the

latter replaces the former when they come into competition. Referable here is Gause's Law, which states that two species cannot occupy the same niche at the same time. Other examples of replacement of one species by another are given by Wilson (1958-1959) in Melanesian ants; it is seen in *Pheidole* and Argentine ants; and Lieftinck (1953) discussed the replacement of Odonata on various islands.

The question of availability of appropriate food depends again on the age, isolation and climate of the island, not to mention other factors. From this standpoint not much of an insect fauna can become established until the development of the flora has progressed to some degree. It seems generally agreed that plants establish themselves more rapidly on islands than insects and most insects cannot establish themselves unless vegetation is already present.

It seems fair to assume that most successful establishments have resulted from a single gravid female landing on an island, with some of its eggs hatching, even if the parent did not survive the ordeal itself. For more isolated old island groups like Hawaii, with only a small number of evolutionary lines, it is safely inferred that only about one successful establishment every 20,000 years is necessary to account for the present fauna (Zimmerman, 1948a).

Leston (1957) noted a striking similarity of numbers of establishments of phyletic lines of families of Heteroptera in the Azores, Hawaii, Guam and Samoa. Miridae came first and Lygaeidae second in the case of each geographical unit. Leston noted that this correlated with usual light-trapping results and that it indicated (with qualifications) a propensity for flight in general and thus related to propensity for successful colonization. (Miridae and Lygaeidae are also well represented in air trappings at sea.) Coreidae, abundant on continents, are poorly represented on oceanic islands, and Emesinae are represented on islands far above the ratio for other Reduviidae and other Heteroptera on continents. Leston stated that the "relative number of species of each taxon reaching an oceanic island reflects a property of the taxon rather than past or present geographical factors." He characterized vagility in terms of "spread potential," and presented the formula:

$$SPt = \frac{100 \cdot \sum (Sit + Spt) \cdot Nk}{\sum (Sik + Spk) \cdot Nt}$$

where  $s$  = number of species

$n$  = number of islands or archipelagoes

$t$  = taxon under investigation

$k$  = standard taxon

$i$  = immigrant species

$p$  = prototype species

## EVOLUTION

The evolution of species or genera on islands is a fascinating subject, yet one rather inadequately understood. From the faunal nature of various islands, it is evident that the results of evolution differ greatly in different island groups. Many factors are involved, and their relative importance is not clear. It is obvious that age and isolation of an island are extremely important, for it is only on the older and more isolated islands that extraordinary local evolution has taken place. This goes hand in hand with disharmony, for

with fewer families represented, there is less competition and more empty ecological niches, permitting more scope for evolution.

The speed of evolution is a disputed matter difficult to document. There is no doubt that under different circumstances, the rate varies (Rensch, 1938; J. Huxley, 1938, 1942; Mayr, 1942; Zimmerman, 1948a; Keast, 1959). Certainly the pressures of competitors, of populations within the species, and various selective factors in the environment affect the nature and rate of evolution in a given group. Likewise, the genetic make-up of a population, including its variability and size, closely affect the situation. Rensch (1938) demonstrated chains of related populations diverging in isolation, as on a series of islands.

When the nature of evolution is better understood and the ages and histories of islands more fully elucidated, various aspects of the problem on islands will become clearer. At the same time, the circumstances relating to evolution on islands are such that the island environment should be an ideal one for pursuing evolutionary studies—a subject which has received inadequate attention. Probably the speed of evolution is not so very much more rapid on small islands than elsewhere and much less rapid than suggested for Hawaii by Zimmerman and others. More geological evidence is coming to light to suggest the evolution of the old Hawaiian fauna on former islands now beneath the sea.

Some atolls appear to have precinctive species, whereas some evidence suggests that atolls are young as far as present land biota is concerned. Such endemism might be the result of local evolution or inheritance from a former island.

*Speciation*: Insular speciation is a conspicuous aspect of island life. A critical question is the manner in which populations broke up into sections that were prevented from interbreeding. Perhaps this genetic isolation would have to be maintained for periods on the order of 100,000 years to produce separate species. If a complex on an island group evolved from a single ancestor, progeny would presumably have had to disperse to various islands within the island group and to have remained isolated for long periods. On the other hand, if there were repeated successful immigrations they would have had to have been separated by long enough periods to develop genetic isolation between colonizations. The former alternative seems more likely. Another suggestion has been made that speciation occurs in some way not yet visualized by population geneticists, but this seems unlikely. Zimmerman pointed out how lava flows isolate populations, but for many groups of insects it is difficult to visualize how such isolation could be complete and of long enough duration to produce species.

In more isolated island groups, speciation has often been more prolific than in less isolated islands. This can be correlated with marked disharmony in the fauna and reduced competition for food and niche. For instance, the cerambycid subfamily Lamiinae is lacking in the native fauna of Hawaii, permitting the single ancestral strain of Cerambycinae (Clytini)—the only native element in the family except for two primitive Prioninae which have not speciated—to have proliferated very extensively, into over 100 species variously classified in from three to eight genera. Perhaps the absence of Chrysomelidae (*s. lat.*) from Hawaii helped permit the extensive speciation in certain groups of Homoptera, Heteroptera, Microlepidoptera, Curculionoidea, and other phytophagous groups.

Zimmerman (1948a-e, 1957, 1958a, b) has presented extensive evidence of the striking speciation in certain groups of insects represented in the restricted native fauna of Hawaii. In several different groups, mostly in Homoptera, Heteroptera, Lepidoptera, Coleoptera,



Diptera and Hymenoptera, elements in just a few families have speciated extensively, often with 100 or so species in a single compact group, each group apparently from a single ancestral introduction. In many cases other subfamilies or families with similar niche and habits are unrepresented in the fauna, unless by species recently introduced by commerce. Hardy (1960) has indicated speciation in certain families of Diptera. The family Drosophilidae, so important in the field of genetics, has speciated phenomenally in Hawaii (Zimmerman, 1959; Hardy, in press).

Usinger (1941b, 1942) made a detailed study of speciation of the genus *Nysius* and its allies (Heteroptera) in Hawaii. Usinger demonstrated that the Hawaiian Orsillini show all stages in speciation and insular evolution. In the lowlands endemic species of the worldwide genus *Nysius* occur in introduced weeds and on some of the native plants that still remain. In the native forests the endemic genera *Nesies* and *Oceanides* have radiated and now have species or species groups attached to various genera of plants in the native forest. Two species, *Nesies hiloensis* and *N. nitidus*, occur together on *Pipturus* on each of the islands (except Kauai) with slightly different populations (subspecies) on each island. Further studies of this sort for other groups of insects on islands are badly needed.

The Marquesas are apparently younger than the Hawaiian Islands, but are less effectively isolated. There is no conspicuous evidence of speciation in Marquesas Cerambycidae, which suggests those islands received their immigrant cerambycids later than Hawaii. Chrysomelidae are absent. Cixiids (*Oliarus*) are present and have speciated in the Marquesas and in Hawaii to an extent unparalleled elsewhere (Fennah, 1958). Absence of the derbids and issids, which compete with cixiids in continental areas, may make this speciation possible in leaving many niches unoccupied. Other Polynesian species of *Oliarus* in the Cook, Austral and Society Islands are in different species groups than the Marquesas species and do not show the spectacular speciation of the group in the Marquesas and Hawaii.

The delphacine genus *Nesosydne* (Alohini) is found in Hawaii, southeastern Polynesia and the Juan Fernandez Islands. It has speciated in each island group in an analogous manner, suggesting that it is a very old resident of the area. Other groups which have produced fewer species presumably reached the islands at later dates than those which have proliferated extensively. Some of these genera found only in these island groups may have evolved on older islands now represented by groups of atolls, such as the Tuamotu Islands (Fennah, 1958).

The problem of assessing the degree of differentiation of populations on separate islands of an archipelago is a difficult one. Whereas the populations may be effectively isolated, the degree of differentiation in the various populations may be minor. Opinions differ as to whether such elements of incipient speciation should be characterized as species or subspecies. This may be considered as of minor significance in comparison with the question of whether the populations represent spread from one island to the next, concomitant dispersal of members of the same or similar populations from a common source, or some other origin. Fennah (1956) in discussing Micronesian fulgoroids indicated that the taxonomic status of the various units was clear enough on morphological grounds, but that different degrees of speciation were presumably related to immigration by different species groups, or other categories, at different periods of time. Of course many factors may be involved, including islands of various types, ages and ecological environment within an archipelago, and the distance from source areas.

A species restricted to two islands may presumably have evolved on one island and recently spread to the other. Two very different species on the same or different islands may represent separate colonizations. On the other hand, an extensive complex of many species of an endemic genus or complex of genera on an isolated island group, and without close relatives elsewhere, may represent evolution from a single ancestral immigrant.

On islands less distant from source areas, a single species (or a species complex) may not represent the progeny from a single ancestral immigrant. Immigrants of the same species, but of different genetic make-up or of different strains might arrive periodically and tend to reduce the chances of the insular population becoming a new species. Or the immigrants may be so few as to have little effect on the diverging population and later colonists may eventually be incapable of further breeding into the offspring species.

Although there are many analogies between the faunas of Samoa and the Caroline Islands, not just in groups represented, but in actual closely related forms, suggesting common source-areas, there are considerable differences in extent of speciation. In general it is more extensive in the Carolines, and this may be correlated with the latter's much greater geographical diversity, with the islands divided into groups and long linear chains and some units widely separated. In general, more genera are represented in the Carolines, and some of these genera include numbers of species strewn along the island chain. The cerambycid genus *Sciadella* and relatives (Lamiinae: Acanthocinini) are broken up in the Carolines into many units, perhaps all the way from genera to subspecies, some of them quite distinct and tending to lose their power of flight, whereas in Samoa there seem to be only a few plastic species starting to differentiate. This, again, might suggest greater youth of Samoa, or more recent immigration to Samoa. There are parallels of this situation in many other groups. Fiji has a fauna as rich as the Carolines, or richer in many of these insect groups, with speciation more extensive on single islands, perhaps reflecting greater age and ecological diversity, besides greater size of individual islands. The genus *Ceresium* (Cerambycinae) is found on nearly all Pacific islands. On the more isolated island groups it is represented by a very widespread species, perhaps spread by the Polynesians. It would be difficult to judge the place of origin of this species, though it might be New Guinea. In Samoa the genus has speciated slightly, and in Fiji and Micronesia extensively. New Guinea seems to be the center of distribution of the genus, and has the greatest development of species.

Isolation and age of islands are not the sole requirements for insect speciation. Ecological diversity is important, and this is related to general favorable nature of the environment, including climate, soils, topography, water and other factors, and naturally vegetation which again depends on the same basic requirements. The Subantarctic islands have produced some remarkable results of evolution in isolation, but the less favorable environment has severely restricted degree of speciation.

#### NATURE OF ISLAND POPULATIONS

Population studies of native Pacific insects are meager. There is great need for research on this matter. Some good starts have been made by Taylor (1937), Usinger (1942), Dorsey (1947), Lange (1952), Wilson (1958, 1959), Brown (1959), Gressitt (1959c), and Holdgate (1960a, b). Many more studies have been made of insects introduced by man

(Williams, 1931; Tothill, Taylor and Paine, 1930; Taylor, 1935; Gressitt, 1953; Tanada and Beardsley, 1958; and others).

One pertinent question is the size of populations of native insects. Rapid rate of evolution is often attributed to small populations. It seems almost certain that many populations on certain islands are extremely small. Many species in the Hawaiian islands, in particular, have been collected only once, in spite of various collectors searching for particular species in the appropriate environments. That many species in Hawaii have extremely limited ranges, as well as small populations, is much quoted (Zimmerman, 1948a). The reasons for this are obscure, but must relate in part to a rather delicate balance of existence, in terms of limited extent of adequately favorable environment. On small islands environments which appear similar may actually differ in minor ways, such as varying exposure to prevailing winds, and difference in rainfall, soil and topography. These and other factors must be taken into consideration besides the specific food requirements of the species.

Pertinent here is the Sewall Wright principle of genetic drift and random fixation in small populations, permitting rapid speciation. This seems to be applicable to populations on adjacent islands, or those otherwise isolated. The proliferation of land snails on isolated islands has been spectacular. Local isolation has been extensively cited, but the situation probably has been over-rated and over-simplified (Cooke and Kondo, 1960).

*Ecology*: An understanding of the ecological relationships of the various species on a given island should contribute to knowledge of distribution. To understand dispersal, establishment and survival in the island environment, it is necessary to know the precise niche, food, enemies and competitors. Those insects which require particular hosts, such as plants, insects, or other animals, for food, naturally would have more difficulty in establishment than species with less specific requirements. As the flora and fauna of an island increases, the chance of establishment of certain new types of insects likewise increases. The more diverse an island is, the greater is the ecological opportunity, or availability of more environments for establishment of various types of insects.

Too little is known of the ecology of islands. With progressive extinction now in process on many islands, the time is drawing to a close in which the desired work can be done. Studies including food chains or cycles or general discussion of hosts and interrelationships, such as those by Buxton and Hopkins (1927), Bohart and Gressitt (1951), Usinger and LaRivers (1953), Swezey (1954), Gressitt (1954), Laird (1951), Wilson (1958, 1959), van den Assem (1958), and Brown (1959), would be desirable.

## FAUNAL ORIGINS AND AFFINITIES

Generally speaking, the insect fauna of the entire Pacific oceanic area, and of the islands of the Southwest Pacific, belongs to the Oriental Region (fig. 2). This area includes the islands from Lord Howe Island, Norfolk Island, Kermadec Islands, Rapa and Easter, northward to Hawaii, westward to the Bonins and Palau and again eastward and southward to include the New Hebrides, Santa Cruz Islands and New Caledonia. The last-named presents special circumstances involving relationships with New Guinea, Australia and New Zealand. These are discussed below. To the westward of this great oceanic area, the other islands, "subcontinental" and continental, from the Solomon Islands west-

ward to Southeast Asia, and as far north as the Ryukyu Islands, and including southeastern Asia, also belong to the Oriental Region. The remaining area, essentially Australia, Tasmania, New Zealand and the Chatham Islands, comprises the Australian Region, but overlaps with the Oriental Region, as noted below. However, New Zealand's fauna is very different from that of Australia. The subantarctic islands south of New Zealand and Australia do not fall well into the above system, and must be classed with other subantarctic islands and with the Antarctic continent, around which they are scattered. These represent the extremes of tolerance of life, grading southward. They possess a fauna of an oceanic type and in each case are related to the nearer continental areas to some extent.

Overlapping between the Oriental and Australian regions occurs, roughly speaking, in southern New Guinea and northern Australia. The areas of Australian influence in New Guinea are largely represented by the savanna regions. Those of Papuan influence in Australia are represented by the tropical or semi-rain forests of the northern part of the Northern Territory and east of the Great Dividing Range in Queensland and, for some groups, northeastern New South Wales. This suggests Pleistocene connections between the two areas, after each had developed its characteristic fauna over great periods of isolation (more particularly isolation of Australia) during the Tertiary.

The origins and affinities of the oceanic fauna largely concern the continental and sub-continental areas of the Oriental Region, to the west; but in the eastern portions, such as Hawaii and the southeastern extremities of Polynesia, there are varying degrees of American influence, with some Holarctic influence in Hawaii. However, the Oriental influence still dominates. In these eastern islands "Antarctic" or New Zealand relationships are less distinct with insects than with plants. There are some other scattered relationships, such as Japanese influence in the Bonin Islands, Australian influence in Timor (perhaps retroactive, as with Australia and New Guinea), various relations in New Caledonia, and Malagasy or at least western Indian Ocean island relationships in Micronesia and elsewhere (Gressitt 1956a). Some of these problems are further discussed below.

Mackerras (pers. comm.) feels that the Oriental Region was originally weak and was populated by an earlier Ethiopian intrusion and a later Palearctic influx and that the former has had more influence in the southern Pacific.

*Distribution patterns:* With the general dominant Oriental influence upon the oceanic fauna, there are certain patterns of distribution, varying somewhat among different groups of insects, but to some extent similar. The most evident feature is the successive diminution in representation with progression eastwards from Asia, producing a successively more disharmonic fauna from west to east. (Exceptions to this generalization largely involve atolls and other low coral islands which do not offer sufficient ecological diversity, young islands which have had insufficient time to develop a diverse fauna or greatly disturbed islands which have lost faunal elements). Additionally certain island groups which have had a longer history show results of active local evolution. They may thus have (like Hawaii) a fauna rich in numbers of species, but nevertheless still strongly disharmonic and with original faunal elements often obscured.

By plotting on a map the extreme limits of distribution of selected groups of insects (fig. 3), one may demonstrate the progressive reduction in representation in the insular fauna. This gives evidence of the weakening faunal influence with distance from the continental source areas, and at the same time suggests differing abilities of over-sea dispersal

among different types of insects. Analogies of pattern with some other groups of animals may be made, but in general the land snails show greater degree of development in isolation within the oceanic area (Kondo *in* Gressitt, 1956a; Solem, 1958, 1959; Cooke and Kondo, 1960). The limits of the Tabanidae (Mackerras and Rageau, 1958) are slightly more restricted than the Chrysomelidae. Distribution patterns in two families of beetles are discussed in greater detail in the last section of this paper in an attempt to correlate the patterns with the factors relating to source areas, dispersal and establishment. Some results obtained by other entomologists will be cited. These, in the main, tend to corroborate my views expressed earlier or modified slightly in this paper. Some of the authors of these papers have adhered to Wallace's assignment of the islands eastward of Borneo (east of Wallace's Line) to the Australian region, whereas actual study of their conclusions on affinities of the material they studied indicates that their material contradicted this old thesis.

Certain groups seem to be characteristically oceanic, like some of the land snail groups alluded to above. Perhaps the most conspicuous example among the insects is the beetle family Proterhinidae (Aglycideridae), which is known only from eastern Polynesia (including Hawaii), from Kusaie Island (easternmost of the Carolines), from New Zealand, and from certain Atlantic islands like the Canaries. Perhaps rather than a group which evolved in isolation, this may represent a primitive group which has not been able to meet competition with more highly evolved forms on continental and subcontinental areas and has disappeared there. Other less far-flung patterns include beetle genera, such as *Brontispa*, with species on western Indian Ocean islands, eastern Indonesia, Philippines, New Guinea, Solomons, southern Micronesia, eastward to Samoa and southward to Lord Howe Island and Norfolk Island, but with little or no representation in Australia and none on the continent of Asia. Apparently a number of other genera have analogous patterns, some of them more restricted, but with representation in the Seychelles or Mascarene Islands, as well as Micronesia, Samoa, or intervening islands, or with the closest relatives indicating this pattern (Kaszab, 1955; Gressitt, 1956a). Likewise, survival under insular conditions of less rigorous competition seems to be indicated.

The numerous gaps in our knowledge make delineation of patterns of relationship difficult at this time. Probably when these gaps are filled, a number of genera now considered restricted to certain oceanic islands will be found to occur also in New Guinea or the Solomons. Patterns shown below (figs. 36-40) for the subfamily Hispinae demonstrate that most of the genera on oceanic islands are common to New Guinea and the Solomons, although on New Caledonia there are endemic genera. This appears to contradict the idea of oceanic nature for the New Caledonia fauna, but as indicated below its fauna is quite disharmonic, even though old.

Various aspects of the oceanic insect fauna and its patterns have been treated by Usinger (1941), Zimmerman (1942a, 1948a), Esaki (1950), Gressitt (1954, 1956a), and others. Wider coverage of animals has been given by Hedley (1899), Mayr (1941a, b; 1942, 1953a), Hesse, Allee and Schmidt (1951), and Darlington (1957). Ladd (1960) gives strong evidence for spread of shallow water marine animals from the mid-Pacific to the Indonesian area, but the evidence is largely irrelevant to insect distribution, except for the old island stepping stones. These simplify the insect distribution picture by providing sites for the breaking up of populations and production on different islands, of species which may now occur on the same islands.

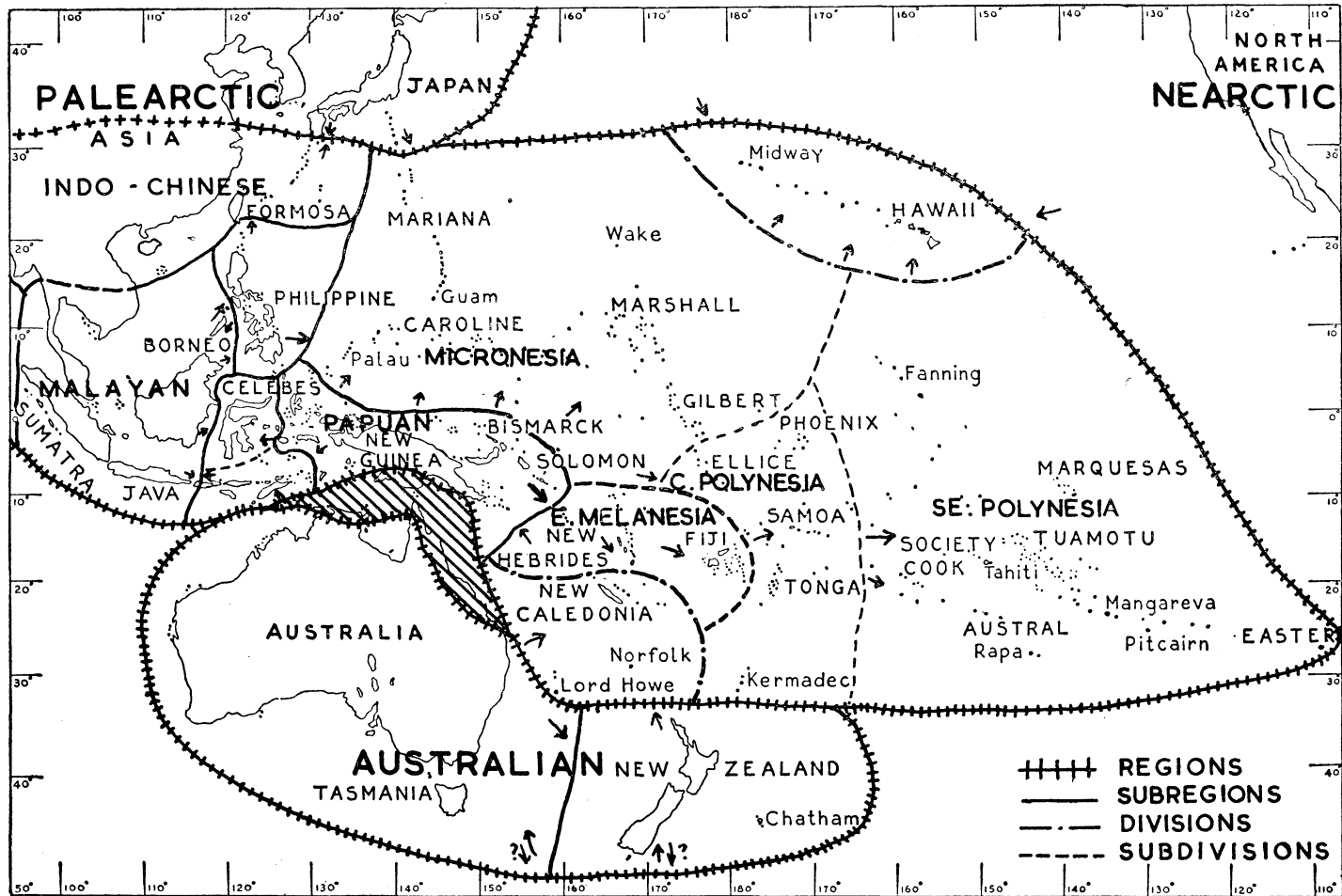


Fig. 2. Map of zoogeographical areas of the Pacific: lines of crosses represent regions, solid lines subregions and dashed lines subdivisions of different value, the weaker dashed lines indicating less distinct divisions. Arrows suggest directions of dispersal.

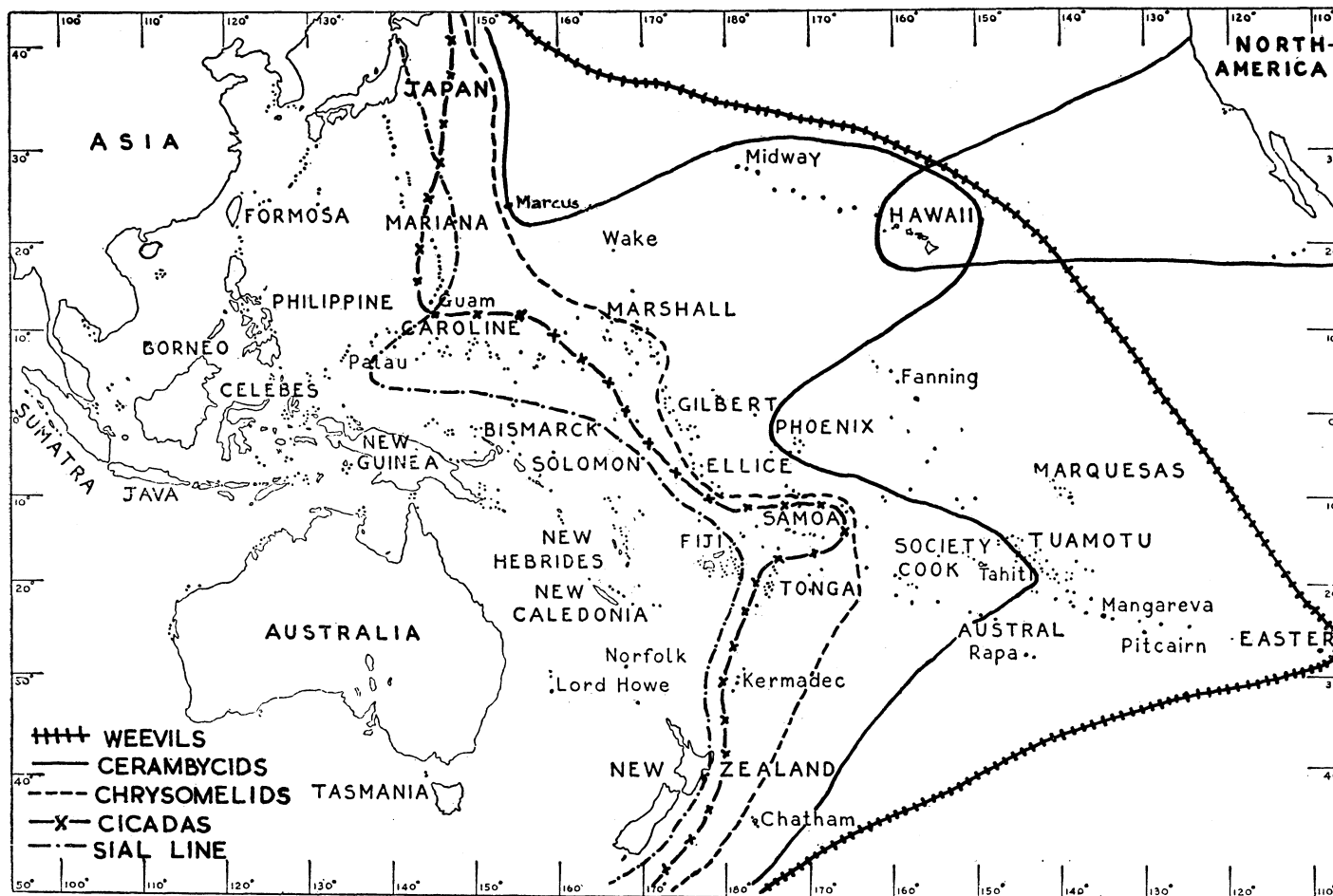


Fig. 3. The limits of distribution in Polynesia of four groups of insects representing different abilities for overseas dispersal. The two lines for cerambycids indicate that parent sources were both Oriental and American. The sial line is the division separating the andesite volcanoes on the west from the basalt volcanoes on the east.

*Geological indications:* The general outline and conformity of the Pacific Ocean is of great age, but there are indications of considerable change in details. Change in the mid-Pacific has apparently involved gradual sinking of the ocean bottom of about 1500 meters (or isostatic sinking of the islands), which has reduced high volcanic islands to coral atolls (Cloud, 1958) and reduced shallow seas or reefs to submarine plateaus (guyots, volcanic mounds, or flat-topped sea mounts; Hess, 1946; Menard, 1959; Ladd, 1960). This is suggested by discovery of fossils of shallow-water animals (Cretaceous Foraminifera) on guyots below 1500 meters (Hamilton, 1953, 1956). Drilling to basalt cores of atolls in the northern Marshall Islands (Eniwetok and Bikini) at depths of about 1500 meters has revealed that the cores were surrounded by coral and other fossils which could have lived only at less than 1/100 that depth (Ladd *et al.*, 1953; Emery, Tracey and Ladd, 1954; Ladd, 1960). It is not difficult to visualize gradual sinking of the high islands on which insects and other terrestrial fauna have evolved. As the islands sank and become atolls, most of the high island fauna would have perished. Only by transferring to younger, existing high islands could they have survived. This process must have involved both loss of faunal elements and also transfer of an old fauna to a younger island. Transformations of this nature appear to help explain the development over great periods of time of endemic elements (as in Hawaii and southeastern Polynesia) which may be older than the islands they occupy. Gradual geological changes have undoubtedly been most effective in fostering evolutionary change rather than the sudden changes such as volcanic eruptions and other cataclysms.

Various lines of geological evidence are now developing, partly as a result of extensive international research in Antarctica, which will throw light on the history of climate, biota, land connections, "stepping stones," continental drift, polar changes and other phenomena disputed in the past. The theory of rock magnetism ("fossil magnetism") as an indication of past wandering of the poles (Irving, 1956, 1957, 1960) sheds new light on the problem of southern continental relationships. A recent Darwin-Wallace symposium publication (University of Tasmania) treats continental drift. Britton (1957) cites evidence for explaining insect distribution on the basis of continental drift. Undoubtedly within a few years the geophysical evidence accumulating will permit solution of these and other problems which have plagued biogeographers in the past.

## THE ISLAND GROUPS

### HAWAII

The Hawaiian Archipelago exhibits the most conspicuous case of insular isolation. Isolation, combined with considerable age, has fostered the evolution of a most remarkable endemic fauna. This fauna represents an extreme case of disharmony, undoubtedly the most extreme for a fauna of such size. A fauna of over 5,000 species of insects has apparently evolved from only about 250 progenitors (Zimmerman, 1948a). The ancestors were successful immigrants from elsewhere, some of which evolved into many species, in some cases apparently into more than one genus, while others failed to differentiate. The disharmony is further shown by the fact that the 250 lines of evolution represents only 103 families and 575 genera of about 900 world families of insects. Some of those lacking are large families on continental areas with as many as 50,000 species. The insect fauna



of Hawaii is now fairly well known (Sharp, Perkins *et al.*; Zimmerman, 1948a-e, 1957, 1958a-b; Hardy, 1960), so future studies are unlikely to give any significant changes.

Undoubtedly the remarkable Hawaiian fauna did not completely evolve on the present major islands. Most of the western islands of the chain are eroded and/or sunken down to a few remnants. Most of them are atolls, and those in the central part include fragments only of former high islands, in the form of rocks, pinnacles, and much-eroded remnants. Probably the original immigrant ancestors of many of the groups of Hawaiian insects started their local evolution on older islands which are now worn down to atolls, and representatives of the various lines passed down the island chain during the course of its evolution, with island-building from basaltic outpourings at the eastern end and progressive erosion at the west.

Zimmerman suggested that this remarkable fauna evolved from these few ancestors in just a few million years. However, geological evidence now suggests that this fauna evolved on now extinct islands over a very long period. Ladd (1960) indicated a probable geological history that would allow ample time for this evolution, involving former islands to the west of the Hawaiian Chain.

Adamziewski (1951) remarked on species of Alucitidae found on many Pacific islands, but lacking in Hawaii and New Zealand, where they might have had more chance of introduction by man. He stated that the primitive types are widely distributed, that the more specialized are less widely spread and that those of most limited distribution are most specialized. He stated also that the temperate genera are more variable in character, more limited in distribution, and more numerous in species.

#### SOUTHEASTERN POLYNESIA

In general, the fauna of southeastern Polynesia is a poor one, both in the sense of great disharmony and in general poverty of species. On some more isolated islands, such as Rapa (Meyrick, 1926; Zimmerman, 1938a, 1942a), with a very disharmonic fauna, some of the groups have speciated extensively and in a conspicuous manner, reminiscent of that in Hawaii. But in many of the island groups the fauna is less spectacular, often with more erratic endemism. The islands may be said to have a very restricted fauna, limited by the obstacles of the "sweepstakes route" (Simpson, 1953) of dispersal over great distances of ocean, partly over islands which are younger and have been developing their fauna over shorter periods of time. There have probably been some older "stepping-stones" for some of this fauna, in the form of ancient high islands which have eroded and/or sunken away to be marked only by the present Tuamotu Archipelago, which includes some large atolls (see Fennah, 1958). Some aspects of the origin of the fauna of these scattered island groups may be difficult to resolve because of the many gaps, great distances and great time periods involved. Much extinction has taken place particularly in the Mangareva Islands and on Easter Island, through destruction of the native vegetation before adequate collections were made. Thus some of the evidence is completely lost. The weevil genus *Rhyncogonus* has speciated extensively in eastern Polynesia (Van Dyke, 1937). It occurs also in Hawaii.

Fennah (1958) considered that the fauna of southeastern Polynesia comprises three elements: 1) recent immigrants, perhaps introduced by man, 2) restricted fauna derived from Philippines-Queensland arc of islands, and representing a very attenuated Fiji fauna,

and 3) an older fauna, restricted to the central and eastern Pacific, of possible Tertiary Antarctic origin.

*Easter Island*: Unfortunately Easter's fauna has largely been lost, but it could never have been very rich. With such isolation, and with limited size of the island, the number of successful immigrants would be small. Skottsberg, *et al.* (1921-1956) has discussed the flora and fauna in detail, but the information on insects is meagre. There is little evidence of old elements in the fauna, so that zoologically the island may be relatively young. Many of the insects now on the island have been carried there by man.

The Juan Fernandez Islands, though not part of southeastern Polynesia, and not far off the coast of Chile, nevertheless have some very interesting relationships to Polynesia. They possess (Skottsberg *et al.*, 1921-1956; Kuschel, 1960) a rather rich oceanic fauna with some conspicuous elements present in southeastern Polynesia and apparently absent from South America, including a family of land snails and various insects (Fennah, 1958).

The Galapagos Islands, with a remarkable oceanic fauna (Darwin, 1839; Lack, 1947) indicating great age which permitted extraordinary evolution, appear to have little in common with Polynesia, and to have derived their fauna from South America.

*Mangareva Islands*: These very distant islands, with Henderson and Pitcairn to their east, have a very poor fauna, without any conspicuous speciation. In general, there are a few endemic species of genera widely distributed in Polynesia. (Zimmerman, 1936a-c, 1938b; Fennah, 1958). Probably there are rather few endemic genera. However, as mentioned above, there has definitely been much extinction before adequate collections were made.

*Marquesas Islands*: These islands are the most isolated in distances from the continents, but biologically they are less isolated than the Hawaiian Islands, because they are closer to other islands which must have served as stepping stones for the influx of faunal elements. The Marquesas fauna is by no means so peculiar, disharmonic and specialized as the fauna of Hawaii, or the Galapagos, for instance. Many more families, subfamilies and genera are represented by native species than in Hawaii. This also helps to give the impression of a younger fauna, with less spectacular speciation. Nevertheless, the fauna is not young, and its pronounced disharmony together with varied degrees of evolution of endemic elements indicates over-sea dispersal to the islands over a long period (see Adamson, 1939). Fennah (1958) considered it remarkable that no derbid has managed to establish in the Marquesas, considering the extent to which the group is represented on other island groups in southeastern Polynesia. Derbid nymphs feed on fungal hyphae in rotting vegetation. Issids, also, are lacking in the Marquesas, though found in the Society, Austral and Mangareva Islands, as well as Henderson and Pitcairn. There are two endemic genera of Hydrometridae in the Marquesas of the five genera in the world. The insects of Marquesas are discussed in Mumford, Adamson, *et al.*, 1932-1939.

*Tuamotu Islands*: This extensive group of large atolls does not possess a rich fauna. This is to be expected on atolls so distant from continental areas. However, the islands do possess a number of precinctive species, including representatives of various groups lacking from the Marquesas (Fennah, 1958). As noted above, the former high islands of this group may have played an important role in the evolution of the fauna of southeastern Polynesia. In the Emesinae (Reduviidae) there prove to be some remarkable endemic forms (Usinger, pers. comm.).

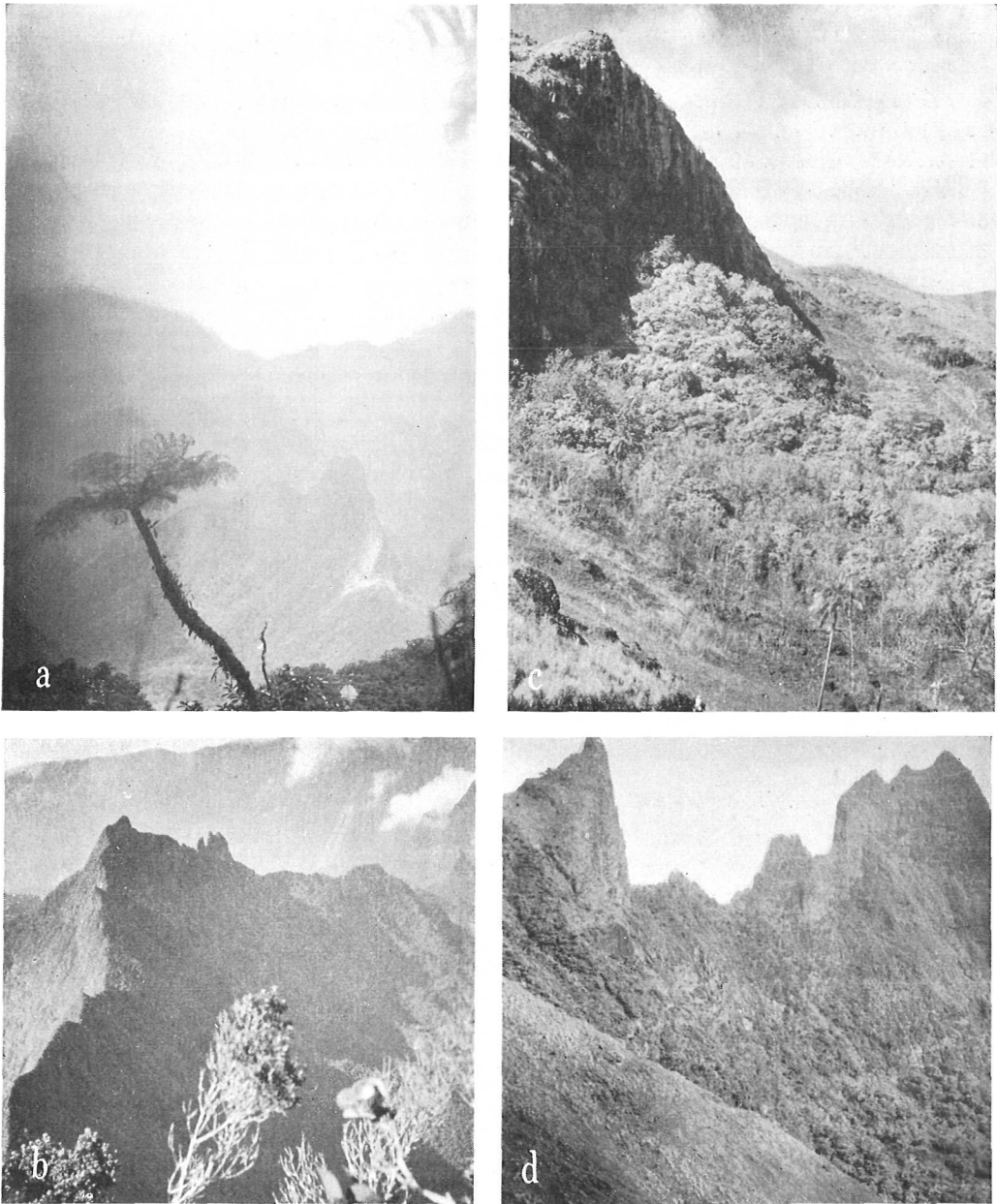


Fig. 4. Mountains on oceanic islands in Southeastern Polynesia. There are many similarities between the biota of the sharp ridges and peaks of the oceanic islands and that of high peaks of New Guinea. Some of the differences involve smaller number of genera and the presence of primitive relics on oceanic islands. Some of the primitive forms now on oceanic islands have been lost in continental areas, but may still be found on isolated ranges in New Guinea or offshore islands or on certain of the Solomon Islands: a, Papenoo Valley and southwest ridge of Mount Orofena, Tahiti. *Cyathea* in the foreground. Collecting is most difficult in such situations because of lack of trails, dense vegetation and steep slopes. Ferns and mosses are abundant (Bishop Museum photo by Fosberg); b, west from Orofena to Punaruu Valley, Tahiti (Bishop Museum photo by St. John); c, Rau-riki Forest, base of Mount Duff, Rikitea, Mangareva (Bishop Museum photo by Emory); d, Mangaao Peaks and Mount Tautauta, Rapa. Rapa is rather rich in endemics. Isolated peaks and islets provide conditions for isolation of populations and fostering local speciation. Many of the genera have speciated considerably (Bishop Museum photo by St. John).

*Society Islands*: These islands also have a meagre fauna, but have many more higher categories than do the Marquesas, Mangareva and Tuamotu Islands. There is also a fair degree of speciation in certain groups, such as weevils (Zimmerman, 1936a, d, 1938a, b), delphacids and issids (Fennah, 1958) and other groups (Buxton, 1935; Bishop Mus. Bull. 113, 1935; Iyengar, 1960). The well-eroded high islands, in some respects similar to Kauai Island of the Hawaiian chain, and Kusaie Island of the eastern Carolines, offer considerable ecological diversity. Because of the great isolation and necessity of over-sea dispersal, many of the ecological niches have not been occupied. Chrysomelidae are absent from the native fauna, and Cerambycidae have had a limited development, as in the Marquesas.

The Austral and Cook Islands each have a fauna analogous to that of the Society Islands, but are poorer and likewise insufficiently known. Rapa Island, the southernmost of eastern Polynesia, is more isolated and exhibits interesting speciation (Zimmerman, 1938; Fennah, 1958).

#### CENTRAL AND WESTERN POLYNESIA (E. MELANESIA)

*Samoa*: The fauna of Samoa gives the impression of being fairly young with few endemic genera. The islands present several analogies with those of Hawaii, in that there is a string of islands, with the most eroded and steepest at one end, and the largest, youngest and most gently sloping at the other end, still showing active vulcanism. However, Samoa lacks the long continuation at the end of the chain with old islands remaining as rocks and pinnacles or completely eroded or sunken to mere atolls, which could have supported the evolving fauna over a much greater period of time. Samoa has only a very few off-lying atolls (the Tokelau Is.), which may or may not have been involved in its faunal history. Also, Samoa is not as isolated as Hawaii. At any rate, Samoa's fauna is very different from that of Hawaii, for it is much more harmonic and has many families or orders lacking in the native Hawaiian fauna. Correspondingly, Samoan insects have not speciated to the remarkable degrees that groups represented in Hawaii have.

In many respects, the Samoan fauna resembles that of Micronesia, and particularly the Caroline Islands, both in constitution and relationships, with many genera in common, although Linnavuori (1960) stresses differences. This similarity strongly suggests the dominance of over-water dispersal from the same general source areas (Indonesia-New Guinea-Solomons), except for greater Philippine influence in the western Carolines (particularly Palau), and more relationship with Fiji in Samoa. It is to be expected that many elements in Fiji are lacking in Samoa, for the latter is younger, smaller and more distant from the common source areas. Many early workers, and some today, have classed Fiji as continental and Samoa as oceanic (some even as both continental), but the faunas are really quite analogous, and differ largely in degree. They both strongly contrast with the New Guinea-Solomons fauna, having much greater disharmony.

The Samoan fauna, likewise, has much in common with that of the New Hebrides in degree of disharmony and in many genera in common. This strengthens the view that Samoa, Micronesia, and New Hebrides all obtained much of their fauna through over-sea dispersal over a shorter period of time, and in part over greater distances, than did Fiji.

Buxton (1930, 1935) discusses the environment and fauna, as well as speciation (1938) in Samoa.

*Tonga Islands* (Friendly Islands): Tonga appears to have a younger fauna than Samoa, and a much poorer one. The active vulcanism and the lower altitudes of the islands suggest that they are younger or that there has been much subsidence as well as overrunning of islands by destructive vulcanism. Actually, the insect fauna is not well known, so it cannot be adequately analysed. As might be expected, it has much in common with both Fiji and Samoa. Some of the species are coconut pests or other pests which have undoubtedly been carried from one island to another by canoe travel before modern times. Invasions of one island from another by Polynesians are well known. Tongans dominated the eastern Fiji Islands for long periods.

There are apparently very few endemic genera in Tonga. Much of the fauna must have come by over-sea dispersal from the west and no doubt some directly from Fiji and Samoa. I am not aware of any clear evidence of influence from New Caledonia.

*Fiji Islands*: Fiji has a rather rich fauna indicating speciation over a considerable period. The fauna is much richer than Samoa or the New Hebrides, and in some groups perhaps as rich as New Caledonia. It has the largest island of Polynesia (zoogeographic sense) excluding New Caledonia. The islands have a varied geology, with numerous "continental rocks", as well as volcanics, and islets of raised coral reefs in the east. However, they seem to satisfy the requirements for oceanic islands. Most of the insect inhabitants could have come by over-sea dispersal. This may have happened extensively during a period when the New Hebrides were more elevated, and possessed a much richer fauna which was later exterminated, or partly exterminated by submersion (followed by more recent elevation).

The general aspect of the Fiji fauna includes conspicuous lack of many genera, tribes, or subfamilies present in New Guinea and the Solomons. Of course their absence might be explained by extermination through subsidence and volcanic disturbance, and perhaps more recent evolution of some of the forms in the Solomons, but it seems more likely that the fauna is disharmonic through having spread across sea, which prevented many groups from reaching the islands. The general abundance of species and their apparent plastic nature suggest active speciation among groups which succeeded in over-water dispersal. Some large insects are present, and these might have come on floating trees. Kaszab (1955) stated that on the basis of the Tenebrionidae the fauna is continental, but I believe the Cerambycidae and Chrysomelidae indicate it is oceanic.

*New Hebrides*: The New Hebrides present a puzzle on account of the poverty of their fauna as compared with the very rich Solomons just to the northwest and with the fairly rich Fiji Islands to the east and New Caledonia to the south. One would expect the fauna to be much richer from the close proximity of the islands to a rich subcontinental fauna like that of the Solomons. To find them poorer than Fiji and New Caledonia which are farther from the source areas is still more surprising. The great contrast in numbers of species and in groups represented strongly suggests that the line separating continental (subcontinental) and oceanic faunas is to be drawn between the Solomons and New Hebrides. The Santa Cruz and Banks Islands presumably belong to the latter. Many genera and tribes, and even subfamilies, appear to have their eastern limits in the Solomons. This line is also the eastern limit of mammals other than bats, rats and mice, and of various other groups. It is possible that the Solomons have ten times as many species and a few times as many genera as the New Hebrides,

One significant aspect of the geology of the New Hebrides is that although there are extensive "continental rocks" present, including various metamorphics, most of the peaks in the island chain, other than recent or active volcanoes, are capped with deposits of marine limestone. This indicates that the islands were submerged for considerable periods in the not too distant past, after having been islands, or part of the "Melanesian Continent". This is not true of much of the Solomons which mainly have been above water for long periods.

The extent of uni-insular endemism in the New Hebrides is not well known. Many species are only known from single records, but they might occur on other islands of the group. There does not seem to be much evidence of local speciation in any particular patterns. However, a majority of species in the New Hebrides are apparently restricted to the island group. There do not seem to be many genera restricted to these islands. Many are in common with the Solomons, Fiji or New Caledonia. The general aspect of the New Hebrides fauna seems to suggest that it is a young one largely brought by over-water dispersal in recent times. Kimmins (1958) indicated that in the Odonata and Neuroptera Asiatic relationships only slightly exceed the Australian. Cheesman (1957) claimed that the insect relationships showed that the southern New Hebrides were connected to New Caledonia until late Miocene and early Pliocene, but Solem (1958, 1959) contradicted this on the evidence from land snails. Only one of 58 species of land shells in New Hebrides also occurs in New Caledonia. In some insects the picture more nearly reflects that of snails, but the snail fauna seems to suggest greater age than does the insect fauna.

*New Caledonia*: New Caledonia holds a position by itself and cannot be strictly classified as oceanic or subcontinental. It has characteristics of the former in lacking mammals other than bats and rats, and in having a quite disharmonic fauna among the insects with many groups unrepresented. At the same time, it has a fairly rich fauna with many endemic genera and indications of considerable age. Thus the fauna has a very different aspect than that of the New Hebrides with apparently many more species and genera, quite a few of them endemic. Among evidences for great age of New Caledonia are its geology with extensive deposits of metamorphics, its representatives of the "southern flora", including several species of *Araucaria* and *Nothofagus*, and the presence of various relics spread between New Guinea and New Zealand, or all the way to southern South America. It is said to have formed part of the former "Inner Melanesian Arc" stretching from New Guinea and/or Queensland to New Zealand. This arc may not have been continuous land, at least not for a very long time, but more extensive land must have served as "stepping stones". In New Caledonia there are six genera of Hispinae with endemic species. Five of these genera are themselves precinctive and all belong to a single tribe. This suggests that the island separated early from the chain and the fauna had an opportunity to evolve and proliferate during a long period. According to Solem (1958), New Caledonia and the New Hebrides had separate connections with New Guinea and the former connection is older.

Monrós (1958) erected a new subregion to include the southwestern Pacific isles plus southern South America on the basis of some relationships in the Chrysomelinae.

*Loyalty Islands*: Paralleling New Caledonia on the northeast, these islands essentially belong with New Caledonia, although they have many forms peculiar to themselves. These include old relics of types not found in the New Hebrides or Fiji. The islands should be

considered as an isolated part of the old Melanesian Arc which preserved some elements that did not persist in New Caledonia.

*Lord Howe Island*: This isolated small island (32° South Latitude) is of great zoogeographical significance. It provides the southernmost records for several groups of insects, as well as strong indications of tropical elements in its flora (such as four endemic species of palms). It possessed a large, heavy-bodied stick insect *Dryococelus* (*Carabidion*), which was precinctive, but closely related to *Eurycantha* of New Guinea and nearby islands. This was exterminated by introduced rats in recent years. In the Chrysomelidae (subfamily Hispinae) the southernmost species of the genus *Brontispa* is on Lord Howe (see below). This is a distinct species without any known close relatives. Paramonov (1959, 1960) stressed the tropical nature of the island, but in birds and flies he noted dominance of Australian relationships. Paramonov stressed the incompleteness of collections and our inadequate knowledge of the insect fauna. One conspicuous element in the fauna is the homopterous family Peloriidiidae, found also in eastern Australia, Tasmania, New Zealand and Chile (Evans, 1959).

Lord Howe is a small island, greatly eroded and fractured. It is a remnant of a much larger volcanic island, apparently of considerable age. Its flora, as compared with that of Australia, lacks *Eucalyptus* and *Acacia*. The island has an oceanic aspect since it lacks native mammals, amphibians, and so many other groups. There are almost no New Zealand elements. Nevertheless it seems to have some paleoendemism, such as in the Peloriidiidae.

*Norfolk Island*: Norfolk is a small well-isolated volcanic island about halfway between New Caledonia and New Zealand. It is nearly three times as far from Australia as Lord Howe Island.

Norfolk is famous for the "Norfolk Island Pine" (*Araucaria excelsa*), native only to this small island. The genus *Araucaria* is also in New Guinea, northeastern Australia, New Caledonia and southern South America. Fossils are known from New Zealand, southeastern Australia and Tasmania. Thus it has a rather broad "southern distribution", and is used as evidence for the importance of Antarctic flora to the vegetation of the southern areas around the Pacific.

The insects of Norfolk do not seem to present such striking evidence as does *Araucaria*. Unfortunately, they have not been adequately collected, and probably much extinction has taken place, so the true native fauna will probably never be known properly. The fauna seems to be more typical of younger isolated oceanic islands than that of Lord Howe. However, there are some interesting insects restricted to Norfolk. One is a species of *Brontispa* (Chrysomelidae), the second most southerly species (Gressitt, 1960a). It is not closely related to the Lord Howe species, but rather to one peculiar to New Caledonia (Gressitt, 1960b). Another is a genus of tineid moths known only from Norfolk (Bradley, 1956). Hawkins (1942) made a survey of the insect fauna which indicated that the majority of identified Lepidoptera, and of some other groups, are possessed in common with Australia.

*Kermadec Islands*: Little is known of the insects of the Kermadec Islands. These islands are apparently oceanic. They are small, and the fauna is rather poor. No conspicuous endemics have come to my attention, although a number of species have been de-

scribed from the island, mostly Lepidoptera and Coleoptera. Some of them represent New Zealand genera, and others Australian, oceanic, or widespread genera.

#### MICRONESIA

Micronesia is very large and includes islands of all types and of various ages. Its fauna is entirely oceanic, and demonstrates increasing disharmony from west to east, with some exceptions. Going northward from Guam and southward from the Bonin Islands there is an impoverishment, in the Volcano and Northern Mariana Islands, related to greater distance from continental islands as well as to smaller size and younger nature of the islands.

In his analysis of the pseudoscorpions of Micronesia, Beier (1957) considered that the fauna is essentially indistinct from a tropical continental fauna. Of seven endemic genera, three were considered Oriental and four "Australian (Melanesian)." He considered the latter to be older elements of the fauna and those of Oriental origin to be more recent immigrants without any tendency to splitting. One species appeared to have Neotropical relationship.

Goodnight and Goodnight (1958) stated that four of the five genera of opilione spiders were otherwise found in New Guinea, Indonesia and the Philippines, with the relationships mostly with New Guinea and the Philippines.

In discussing Micronesian Fulgoroidea, Fennah (1956) noted a general symmetry of fauna whereby islands of equal size had equivalent fauna. He discussed the discontinuity between the Marianas and the Bonins, and concluded that the bulk of the fauna entered through Palau, with little evidence of Papuan elements in the eastern Carolines. Fennah raised the question of why some groups should be repeatedly successful at establishment and others not. The answer may relate to abundance, vagility and simplicity of nutrition requirements. In the Cicadellidae (Linnavuori, 1960) relationships are primarily Oriental, but there is also marked relationship to Japan, Taiwan and the Philippines.

One genus of the Enicocephalidae (Usinger and Wygodzinsky, 1960), is pantropic and occurs in Fiji, New Guinea, the Philippines, and westward, and the other occurs in Hawaii, Micronesia, New Guinea and the Philippines. The species are all single island endemics. In the Reduviidae (Wygodzinsky and Usinger, 1960) 21 of the 30 species are endemic. The great majority of these are Emesinae, which is disproportionate to the ratio of subfamilies in continental areas. The relationships are mostly with Samoa, Fiji, New Caledonia, New Guinea and the Philippines. In the Aradidae (Matsuda and Usinger, 1958) 37 of the 40 kinds are endemic with predominantly Samoan, Philippine and Papuan relationships.

There are the largest numbers of mosquitoes on Palau (Bohart, 1957), but Ponape has the highest rate of endemism, followed by Palau, Kusaie, Truk, Southern Marianas, Bonins and Northern Marianas, respectively. Oriental influence is strong and Australian weak. As with many insect groups, there are no strictly atoll endemics. The subgenus of Psychodidae described as new by Quate (1959) has proved to be a synonym of a widespread genus with an Indo-Pacific section extending to Micronesia and Polynesia (Quate, pers. comm.). Members of *Trichomyia* might have rafted to the islands as they breed in decaying wood; the lack of *Pericoma* in Micronesia is a conspicuous gap (Quate, 1959). Hardy





(1957) remarked on the presence in Palau of a family (Coelopidae) previously known only from arctic and subantarctic areas. Tokunaga and Murachi (1959) found the relationship of the Ceratopogonidae predominantly Oriental.

Barnard (1960) showed that only Truk and Ponape appeared to have endemic species (2 each) of terrestrial amphipods, whereas two widely distributed species each are found in Palau, Yap, the Caroline atolls and Kusaie. A single widespread species each is found in the Marshalls and Gilberts. Relationships of the Tenebrionidae (Kulzer, 1957) are primarily with the Philippines, Asia, New Guinea, Fiji and eastern Polynesia. For the Platypodidae and Scolytidae, Wood (1960) stressed unexpected numbers of species of some groups, and apparent total lack of others. General relationships were indicated with the Philippines, New Guinea and neighboring areas, including Polynesia.

*Bonin Islands:* The Bonins are the northernmost islands of Micronesia (and of Polynesia in the zoogeographical sense). They are often excluded from both, but nevertheless are oceanic and do not belong with the Palearctic Region. There are definite Japanese relationships, and also some with the Ryukyu Islands. However, many of the genera present have their northernmost limits here. The fauna is not very rich. The islands to the north, the Izu Shichito, are much younger, some being active volcanoes, so the invasion by some of the Japanese elements may be very recent.

*Volcano Islands:* These islands are much younger than the Bonins and are entirely volcanic. The fauna appears to be young and fragmentary. There are very few known endemic elements. Rather few insects have been collected, and the vegetation of Iwo Jima was largely destroyed during World War II. Kita and Minami Iwo Jima have hardly been investigated. They rise steeply from the sea, and are well vegetated. They were not overrun during the war, so may retain some interesting faunal elements.

*Mariana Islands:* This archipelago, extending north and south like the preceding groups, consists of two separate groups, Northern and Southern. The former consists of younger islands, some of them active volcanoes, with very poor fauna, with few known endemics. The relationships appear to be mostly with the Southern Mariana Islands. The latter are older, mostly larger, and consist to a considerable degree of raised marine limestone. They have a varied fauna with many endemics. Guam, the largest island of Micronesia, has many elements not known from the rest of Micronesia, but some of these are introduced. Guam's fauna is better known than those of the other islands, but it is poorer than that of Palau. Philippine influence is fairly strong, but relationships extend in various directions, even to Hawaii and Samoa. The Guam weevils (Zimmerman, 1942b) show relationships involving Polynesia and the arc from the Solomons to the Philippines, although ties with the Philippines are weaker than might be expected.

*Caroline Islands:* This extensive east-west chain consists of five groups of high islands (Palau, Yap, Truk, Ponape, Kusaie – the last two essentially single islands) and many atolls strewn among them. Palau, the southwestern-most major unit of Micronesia, and possibly the oldest, has the richest fauna, with many groups represented which are not found to the north or east within Micronesia. However, the fauna is most disharmonic as compared with the Philippines, Indonesia or New Guinea, to all of which it is related faunally. Yap is much poorer, but has a few elements not otherwise known from Micronesia. Truk has a less harmonic fauna, but possesses some unexpected elements of vari-



Fig. 6. Guam: a, Point Oca, scrub and weeds at top of limestone cliffs, 1951; b, north-central limestone plateau, mixed forest, with breadfruit, *Pandanus* and papaya, 1945; c, north-central plateau, natural forest with *Pandanus* and *Cycas*, 1945.



Fig. 7. Babelthuap: a, coconut palms damaged by *Oryctes*, one bearing large nest of *Nasutitermes brevisrostris*, Ulimang, 1951; b, *Pandanus* mangrove swamp, lower Ngaremeskang River near Ngaremedu Bay; c, upper tidal area in Ngaremeskang River, with *Pseudopinanga* palms; d, *Freycinetia* hanging from jungle trees on upper Ngaremeskang River, 1952. (Palau).



Fig. 8. Ponape rainforest, slope of Mount Nahnalaud, at about 450 m, with seedlings of *Exorrhiza ponapensis*, fallen fronds at left (Glassman, 1949).

ous relationships, including some with New Guinea. The islands of Truk may be too close together to foster separate speciation. Ponape is probably richer than Truk, but lacks some of the latter's elements. Ponape appears to be younger and to enhance speciation, whereas Truk seems to be sinking and to be losing some of its faunal relics by destruction and disturbance of its forests. Kusaie may be the youngest, and appears to have an attenuated Ponape fauna, but again has elements not found to the west, including some in common with the Marshall Islands. Going eastward in the Carolines there is varying reduction of Philippine influence and increasing Papuan or "oceanic" influence. The Carolines (and also Micronesia in general) seem to have much in common with Samoa and Fiji, particularly Samoa. This is partly by analogy of faunal composition, but also by evident relationships. Some genera are common to the Carolines, Fiji and Samoa, and others apparently only to the Carolines and Samoa. Perhaps common source areas and vagility are involved in some cases, rather than direct exchange between the two areas. On the other hand, some of these genera may prove to occur still in New Guinea or the Solomons. Actually, the neighboring areas are so little known in many groups that precise relationships are not clear.

*Marshall Islands:* This large assemblage of atolls in general has a poor and uniform fauna, but the southern atolls are wetter and richer. Atolls affected by the war, and administrative-commercial centers, tend to have more introduced species, which in some cases have replaced native species (Usinger, 1958, 1961). There are some species which appear



Fig. 9. Ponape, 1953: a, cloud forest ridge between two highest peaks (Nahnalaud and Ngihneni) at about 800 m, *Exorrhiza* palms at left; b, swampy slope just below summit of Mount Nahnalaud, with *Exorrhiza* palms, *Pandanus* (right) and *Thoracostachyum* (center); c, wind-blown ridge between Nahnalaud and Ngihneni, with *Cyathea* tree fern.

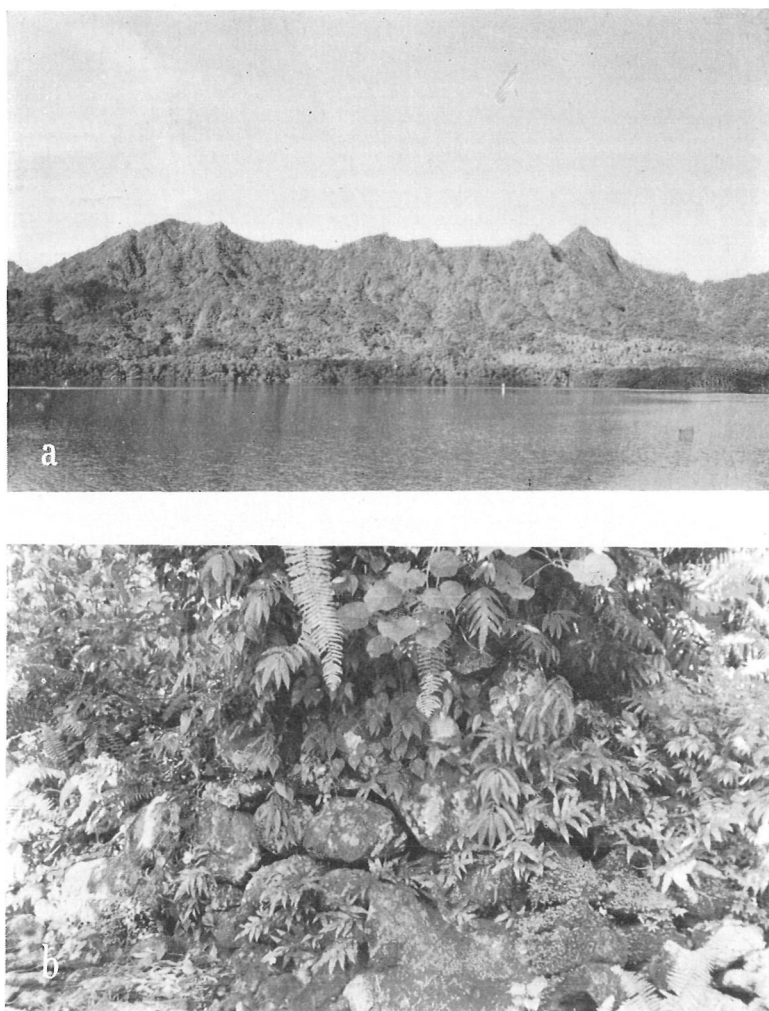


Fig. 10. a, central portion of Kusaie from Lele Island, Mount Fuinkol in center, Fuinwukat at right, 1953; b, ancient ruins, Lele Island, Kusaie, *Nephrolepis* above, *Piper* in upper center, *Procris pedunculata* (slender leaves) at right center and *Phymatodes scolopendria* at lower left, 1953.

to be restricted to the Marshalls or certain Marshall atolls. Whether these evolved on the atolls, are carry-overs from the pre-existent high islands, or shifted from Kusaie, is not certain. A good picture of the fauna of Arno Atoll, one of the wetter Marshalls, was given by Usinger and La Rivers (1953), where the insect fauna was estimated at 500 species.

*Gilbert Islands*: The Gilberts also consist entirely of atolls. They are fewer in number and smaller in average circumference, but some are larger in land area with much wider islets. This suggests that the pre-existent high islands were smaller, and have been submerged for a longer time. If so, they would have had a lesser role in evolving fauna,



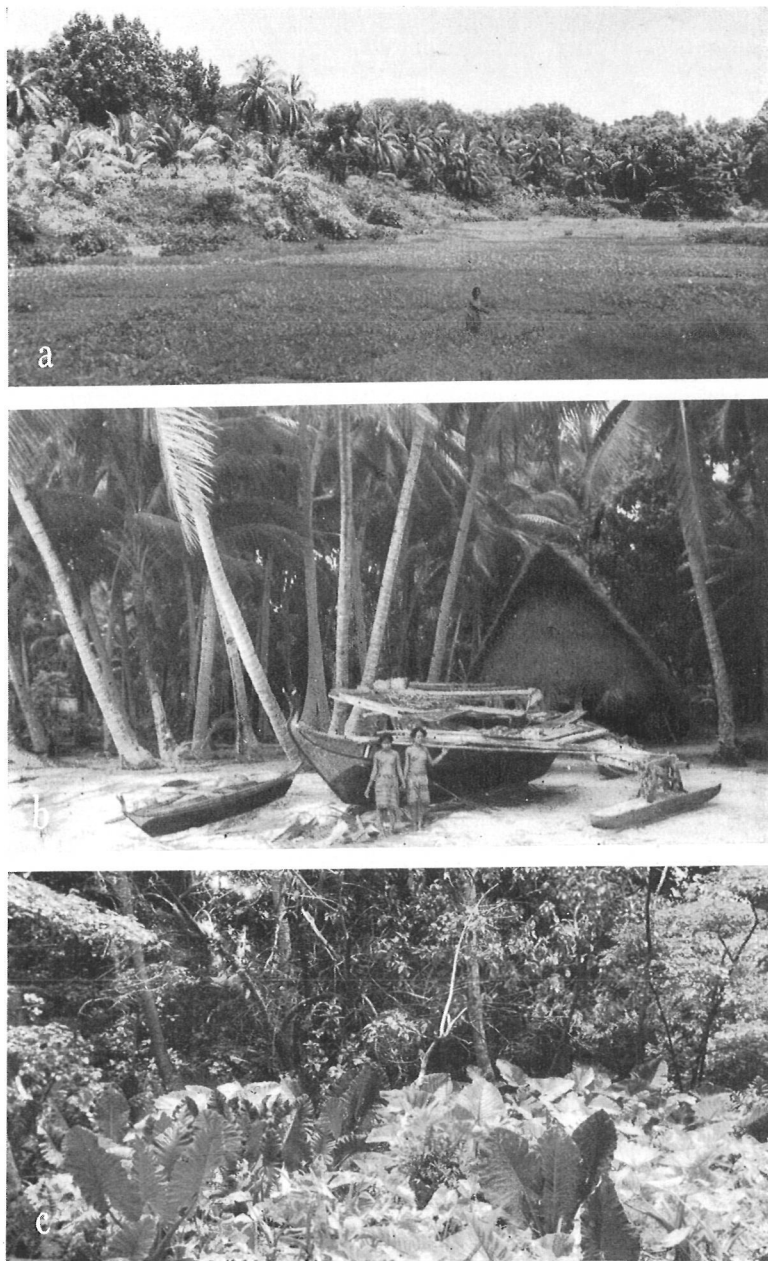


Fig. 11. Western Caroline low islands: a, center of Tobi Island, taro swamp in old lagoon of raised atoll; b, beach on lagoon side of Ifaluk Islet, Ifaluk Atoll c, taro swamp in center of Merir Island (Krauss, 1952).



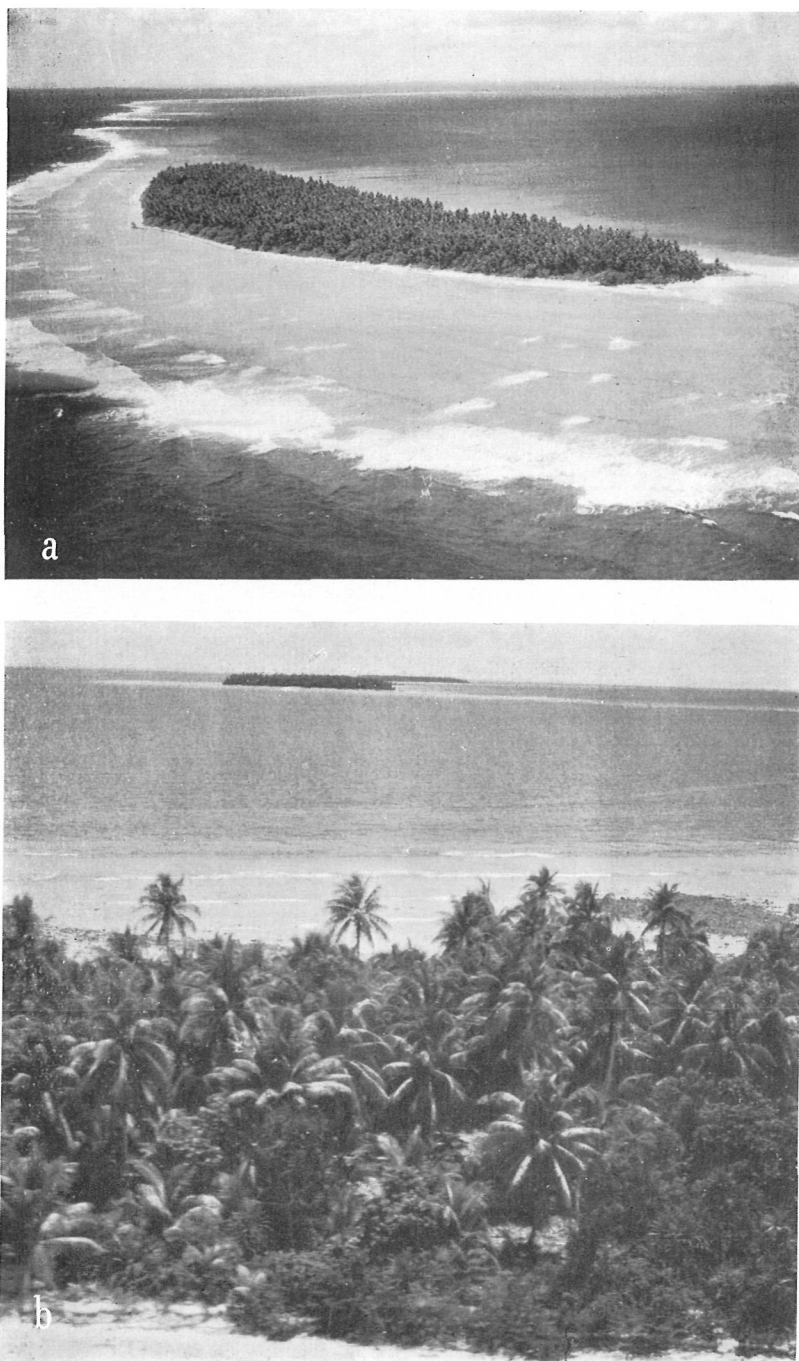


Fig. 12. Ulithi Atoll, air views: a, an islet showing seaward side at left and in foreground and lagoon side at right, with two very small islets on reef in distance; b, view across an islet from lagoon side, showing another islet beyond indentation on seaward side of reef (U. S. Navy).



Fig. 13. Eauripik Atoll: air view from east-southeast, showing Siteng Islet at bottom of picture, Eauripik Islet above it and Oao Islet at far upper left; surf suggests wind is from northeast (U. S. Navy).

and in exchange between the Carolines and Fiji or Samoa. The fauna appears to be poorer than that of the Marshalls, mainly because the atolls are drier, particularly in the south. This reduces chance of recent faunal exchange.

The Ellice Islands are not classified in Micronesia, but are close to, and similar to, the Gilberts. They have a similarly poor fauna and offer little opportunity for fauna exchange between central Polynesia and Micronesia.

*Isolated small low islands:* Within Micronesia, as well as along its northern fringe and to eastward in the mid-Pacific, are a number of small atolls, single low coral islands, or slightly raised atolls. These, including Marcus, Wake, Ocean, Nauru, the Line Islands, and Phoenix Islands, have a poor atoll fauna with many aspects of faunal composition in com-

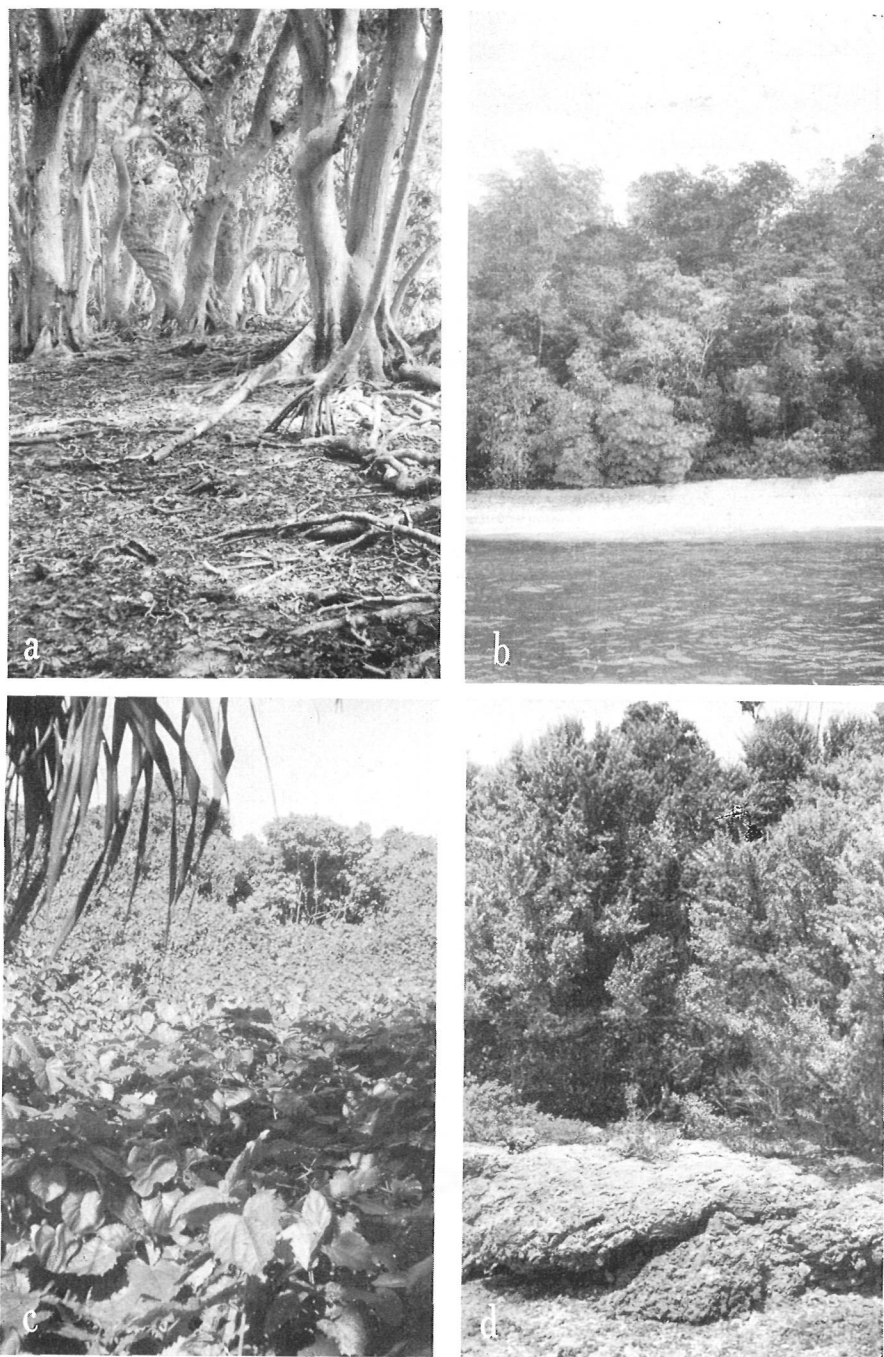


Fig. 14. Northern Marshalls: a, *Pisonia* forest, Enewetak Islet, Kwajalein Atoll; b, *Pisonia* forest, Enewetak Islet, Kwajalein, leeward lagoon side; c, opening in mixed forest occupied by a blanket of *Wedelia biflora*, Lae Islet, Lae Atoll; d, *Pemphis* forest on slightly emerged reef limestone, Enellap Islet, Ujelang Atoll (Fosberg, 1952).



Fig. 15. a, forest edge, Bokerok Islet, Ujae Atoll, with *Pisonia*, *Scaevola* and *Pemphis*, drift log in foreground; b, windbeaten *Scaevola* scrub, Bekrak Islet, Utirik Atoll (Fosberg, 1952).

mon. Even a number of actual species are in common because the fauna consists largely of widespread species. Some or all of these islands at one time may have had one or more endemic species of their own. However, as a result of activities of man, many of these have become extinct. Some endemic species taken on Wake Atoll in 1924 have not

been found since. A few species described from Marcus may actually occur elsewhere, and may even have been introduced by man. The fauna of an atoll suffers greatly from changes imposed by man. The mid-Pacific atolls are mostly very dry and support few plants. Certain plants only appear when more than the normal rain falls in one season. This may be true of some insects. The atolls at the west end of the Hawaiian chain fall in the same general category. The fauna of Midway, Wake and Canton, in particular, has fluctuated considerably with activities of man, including frequent temporary establishment of introduced plants and insects.

The changing insect fauna of Canton Atoll, a dry and much disturbed mid-Pacific atoll, was discussed by Van Zwaluwenburg (1943). This is to be contrasted with the situation on Arno Atoll (Usinger and La Rivers, 1953). A good discussion of Washington Island is given by Wentworth (1931). It possesses a fresh-water lake and bogs. Fosberg (1953) discussed vegetation of central Pacific atolls. According to some theories, terrestrial life on atolls is of rather short history. However, this is disputed, and the atolls themselves are ancient and were probably mostly high islands at one time (Cloud, 1958; Ladd, 1960).

#### WALLACE'S LINE AND NEARBY ISLANDS

Wallace's Line is not as distinct a boundary for insects as it is for higher vertebrates, particularly mammals. The narrow water barriers have not prevented many insects from crossing. Many years ago Pascoe (1864) indicated a general uniformity of beetle fauna on both sides of the line, from the Sunda Islands to New Guinea, as contrasted with great differences between New Guinea and Australia. However, there is a considerable reduction in number of genera to the east of the line, with some additional genera appearing farther to the east, in New Guinea. Many Southeast Asian genera appear not to extend beyond Borneo and others not beyond the Philippines. In the Cerambycidae many genera cross the line and a fair number do in the Chrysomelidae. Wallace's Line has not been crossed by the tabanid genus *Haematopota*, but *Chrysops* and *Tabanus* have crossed it rather freely (Mackerras, 1958; Philip, 1959).

Celebes has many endemic elements and lacks some in common between the Philippines and New Guinea as well as many genera found in Borneo. The Philippines are related both to Borneo and New Guinea, but Palawan's fauna is closer to that of Borneo than it is to the rest of the Philippines. Taiwan's fauna is closely related to that of South China and Hainan Island's to that of Indo-China. Both have very little in common with the Philippines. However, Botel-Tobago Island (Kotosho, Lan-yu) has a clearly Philippine fauna even though it is just east of Taiwan, and some Philippine elements not in Taiwan occur in the southern Ryukyu Islands (Kano, 1931a, b, 1935-1936; Gressitt, 1956a, 1957c). The weevil tribe Pachyrrhynchini and the lamiine complex of Tmesisternini and related tribes have a predominantly Philippine and Papuan distribution, extending to Botel-Tobago and the Ryukyus to the north and to Queensland to the south and some of the tribes extend further to New Caledonia and New Zealand. The insect fauna of the Moluccas is very close to that of New Guinea and both belong to the Papuan Subregion. Aru and Kei Islands also are Papuan. The Lesser Sunda Islands have a mixed fauna with Sunda elements extending eastward and intermingling with Wallacean, Papuan and Australian elements. Timor shows considerable exchange with Australia. Philip (1959)

discussed the validity of Wallace's Line in regard to the Tabanidae. Mayr (1944) reduced the value of Wallace's Line as far as bird distribution is concerned and indicated various lines of gradating fauna, including one bordering on the Sahul Shelf with many Papuan or Australian forms limited to its east. Scrivenor *et al.* (1943) also criticized Wallace's Line and presented various divergent views.

#### PAPUAN SUBREGION

New Guinea, the Bismarcks, Solomons, Moluccas and nearby islands comprise the Papuan Subregion of the Oriental Region. This area overlaps with the Australian Region in northern Australia and parts of southern New Guinea. New Guinea apparently had most of its early relationships with Asia through fluctuating bridges or series of stepping stones. During much of the Tertiary it apparently was greatly isolated from Australia, and each of the two land masses developed its own characteristic fauna. The older parts of New Guinea are in the north, including parts of the Bismarck Archipelago and the Cyclops Mountains (Cheesman, 1951), whereas much of central and southern New Guinea is quite young geologically (Hodge-Smith, 1943; Toxopeus, 1948; Gressitt, 1958c). Probably the old New Guinea (or western half of the "Melanesian Continent") consisted of an archipelago, permitting development of many localized species or genera. The eastern half of the land-mass, which separated quite early, remains largely as the Solomons. These have in part been separate islands for considerable periods from their faunal distinctness and intervening sea depths (Mayr, 1932; Lever, 1937).

New Guinea presents a number of puzzling problems. To begin with, the insect distribution picture is different from that of the vertebrate animals. The mammals of New Guinea belong to the same four orders as occur in Australia, and there is much affinity in the bird and reptile faunas of New Guinea and Australia. However, the insect fauna is primarily Oriental. This discrepancy is provisionally attributed to the long insular history of New Guinea, antedating the age of mammals and preventing influx of terrestrial higher animals from Southeast Asia, whereas insects could cross the water barriers. There was ample opportunity for exchange between New Guinea and Australia across Pleistocene connections. The Australian mammals, in particular, found little competition in New Guinea, but invading insects encountered a reasonably complete fauna in both cases. Also, environmental differences helped to keep the faunas distinct.

New Guinea, the second largest island in the world, presents a rich environment, as yet inadequately studied. It is entirely tropical, although its high mountains (up to over 5,000 meters altitude) are temperate in climate. Glaciation occurred in the past, and the remnant of a glacier persists in the Snow Mountains. An alpine fauna, however, appears to be lacking. This suggests lowland tropical derivation of the fauna. The nearest mountain of any comparable height is Mt. Kina Balu in North Borneo and the next on Taiwan and well into Asia near the borders of Tibet. Much of New Guinea's vegetation is rain forest of one type or another. Only limited parts of the island are grassland ("kuna") or, in certain of the southern parts, *Eucalyptus* and *Melaleuca* savanna woodland. The extensive mid-altitude *Nothofagus* forests suggest relationship to South America through New Caledonia and New Zealand or through southeastern Australia and Tasmania. The ties with South America are not obvious in some groups of insects, but there are more clear relationships with New Caledonia and New Zealand, than with Tasmania.



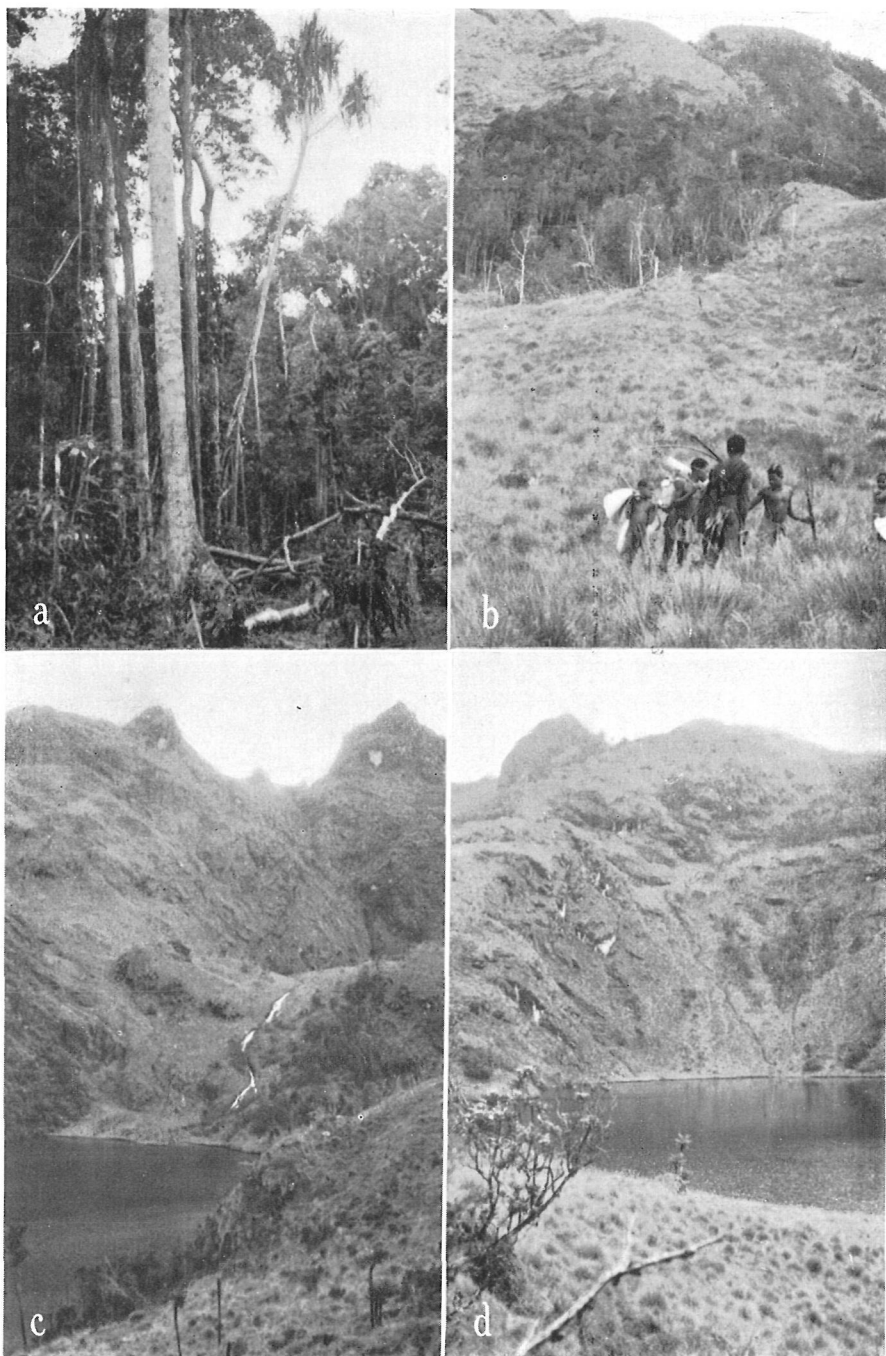


Fig. 16. a, Brown River lowland rainforest, near Port Moresby, Papua; b-d, Mt. Wilhelm, Northeast New Guinea; b, just below Lake Aunde, 3,550 m; c, Lake Aunde, 3,600 m, looking northwest; d, Lake Aunde, looking east. 1955.

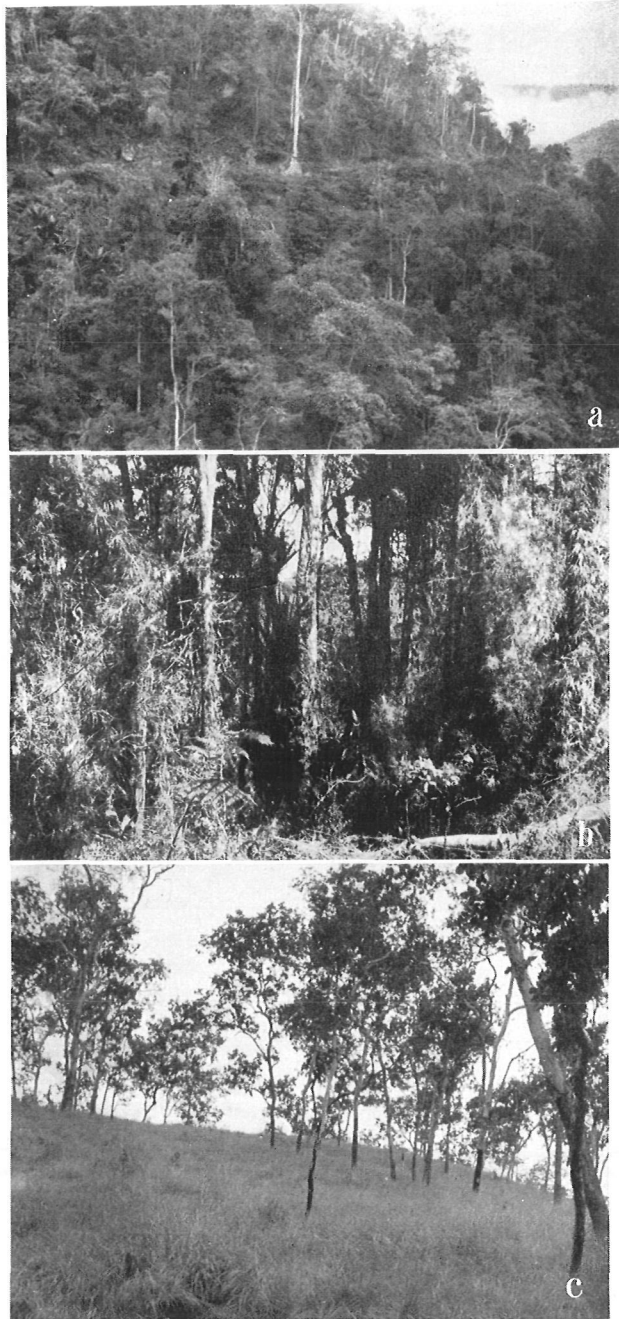


Fig. 17. a, forested hillside, 1000 m, at Tapini, Central District, Papua, 17 May 1961; b, disturbed highland rainforest (1800 m), Eastern Highlands, NE New Guinea, with climbing bamboo; c, *Eucalyptus* savanna woodland, near sea level, near Port Moresby, Papua



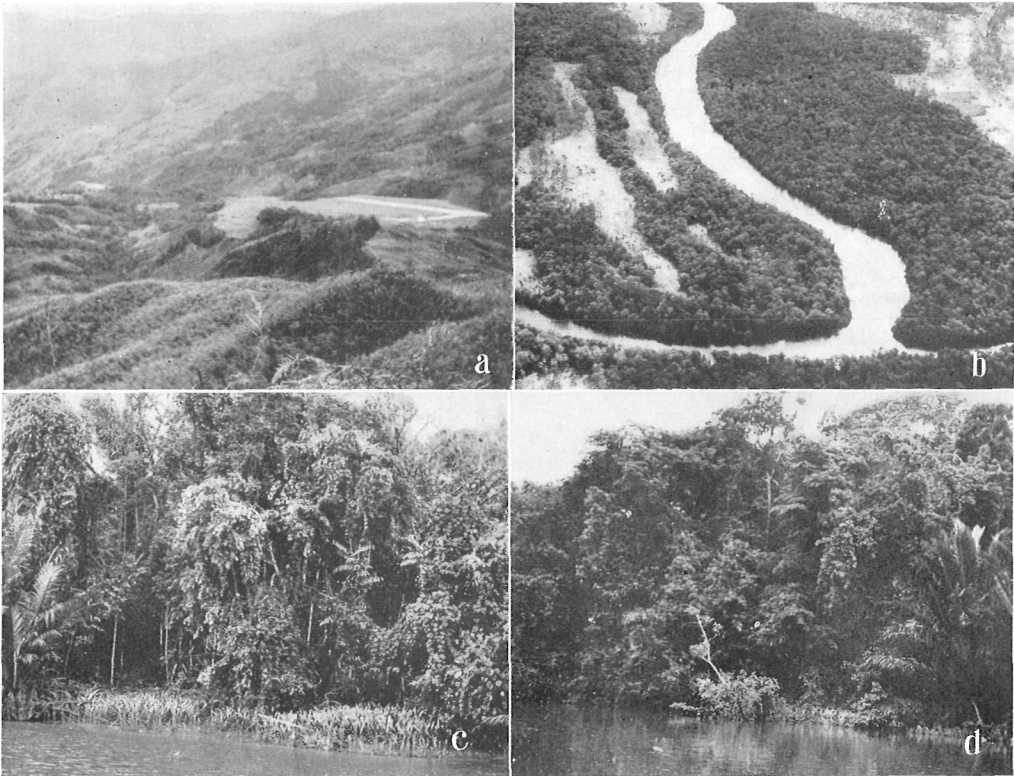


Fig. 18. a, Swart Valley, Neihelands New Guinea, Kadubaka airstrip, 1400 m, in right center, Nov. 1958; b, mangrove and savanna near Cape Rodney, E. Papua, Nov. 1960; c, Lowland rain forest, bank of Oriomo River Western Papua, Oct. 1960; d, bank of Oriomo River, Western Papua, with d'Albertis creeper, Sept. 1960 (J. J. H. Szent-Ivany).

Many groups of insects demonstrate the affinity of the Papuan fauna with Asia and Indonesia as contrasted with Australia (except for greater or lesser overlap in Queensland and southern New Guinea). Marshall (1956) indicated predominant Philippine and Asian relationships of the celeutethine weevils. Drake (1960) indicated similar relationships for Tingidae. Tokunaga (1959) believed the Ceratopogonidae are largely Oriental or endemic. Lieftinck (1942, 1949a, b) demonstrated Oriental affinities for the Odonata, Karny (1929) for Orthoptera, Usinger and Matsuda (1959) for Aradidae (*Artabanus-Rossius* group of genera only in New Guinea and the Oriental Region) and other studies show similar relationships. Diakonoff (1955) indicated dominance of precinctive elements and relationships with both Indonesia and Australia in the Microlepidoptera. Toxopeus (1948) has discussed the relationships of New Guinea butterflies and noted the lack of a distinct alpine fauna in New Guinea. Mackerras and Rageau (1958) showed that the Tabanidae of New Guinea have more tribes than do those in Australia and nearly three times as many as in any of the islands east of New Guinea. Darlington (1952) attributed Oriental affinities to many of his new genera of New Guinea Carabidae. Malaise (1950) attempted to prove a trans-Pacific connection between New Guinea and South America. Willemse (1959)

showed that the genus *Salomona* (fig. 34) is dominantly Papuan and has species in the Philippines (5), Botel-Tobago (1), and the Sunda Islands (6), none known from Celebes, one questionable species from Australia and scattered species in the Bismarcks, Solomons, New Hebrides, New Caledonia, Fiji, Samoa and Western Micronesia. Analogous distribution in chrysomelid genera is discussed below.

There appears to be much in common between the relationships of the New Guinea insects and the New Guinea plants as indicated by Lam (1934).

There are a number of distinct faunal affinities between the Philippines and New Guinea as discussed above.

New Guinea has undoubtedly played an important role in the development of the fauna of surrounding areas, particularly of that to the east. As additional insect groups are worked out, more relationships will probably come to light and more elements may be found in common between New Guinea and islands to the east and north.

An interesting aspect of the Papuan-Australian overlap is that the rain forests in Queensland and the *Eucalyptus* and *Melaleuca* savannas in Papua are rather poor in insects. The former might suggest that the insects are not as tolerant of cooler conditions as the plants, and this agrees with the fact that many tropical plants in New Guinea extend higher in the mountains than insects which feed upon them (Gressitt, 1959a). In spite of this, New Guinea may have made more of an impact on the fauna of Queensland than the reverse during the Pleistocene interchange.

The insect fauna of the Bismarck Archipelago is related to that of New Guinea, but with local speciation. Manus Island has certain distinct relationships with Biak and Wai-giou Islands, and some of these extend to New Ireland. On the other hand, New Ireland has much in common with the Solomon Islands, and may have been partly derived from the eastern and partly from the western halves of "Melanesian Continent". Southern New Ireland may represent a continuation of the southern chain, of the two chains of the Solomons (which meet in Bougainville and San Cristobal). There is much in common between New Ireland and New Britain, as against common differences from Manus Island; and New Britain and New Guinea have much in common. New Britain appears to be largely covered with marine limestone or recent volcanic deposits, yet it is extremely rich in species.

The Solomon Islands possess an extensive and little-known insect fauna. It has much in common with that of New Guinea and New Britain, but nevertheless it is fairly distinct. It is a less harmonic fauna, though clearly subcontinental. In many groups there appears to be extensive speciation even within an island, as well as between different islands. In some genera common to New Guinea and the Solomons, there appear to be more species in the latter, although further studies may prove the situation otherwise. There is much in common between the islands of the northern chain, from Bougainville to Malaita, whereas islands in the southern chain (New Georgia and nearby islands) between Bougainville and Guadalcanal tend to be more distinct in fauna, with more local speciation. The fauna of Guadalcanal is closer to that of Malaita, as proximity and shallower intervening channel would cause one to predict.

#### AUSTRALIA

This ancient continent has the most specialized and peculiar fauna of all the continents.

Although each has its peculiar elements, the majority of them have close relatives elsewhere, as between North and South America, North America and Eurasia, Africa and the Orient. But Australia's elements are mostly restricted to this continent or partly shared with New Zealand or New Guinea. The country is largely arid and many forms are found only on the fringes where there is more rainfall. Long isolation has permitted evolution and preservation of primitive forms, some of which existed on other continents but have become extinct there, perhaps through competition with more advanced forms which have not reached Australia.

In the tropical northeastern part of Australia (Queensland east of the Great Dividing Range), where rain forest occurs, there is a strong inter-mixing of Papuan elements. In Tasmania and southeastern Australia, there are temperate sclerophyll forests, or temperate rain forests, which harbor a number of the elements possessed in common with other southern continents. These two areas of external faunal relations meet in the mountains along the border between Queensland and New South Wales.

Another area of faunal mixture is in central north coastal Australia, in the northern part of Northern Territory, as well as the northern part of Western Australia. These areas have a long dry season and do not support true rain forests, although there is some swampy jungle with palms, *Flagellaria*, and ecologically related plants, as well as mangrove. Some of these small patches of jungle support certain typical Papuan elements found in Australia only here and in northeastern Queensland, but in the Northern Territory they represent only a very small segment of the fauna.

Four major chronological components of the Australian fauna are cited by Evans (1957, 1959):

- 1) Forms of Pre-Tertiary Indian origin.
- 2) Southern elements with relatives in other southern continents.
- 3) Endemic forms which evolved during the Tertiary isolation of Australia.
- 4) Elements which entered Australia during late Tertiary Indo-Malayan invasion.

To document his view that category 2) proves that Australia was joined to other southern continents as late as towards the end of the Mesozoic, Evans cited genera in eight orders with common southern continent distribution, in all cases including at least southern South America and Tasmania, and in many cases also New Zealand and / or southern Africa and southeastern Australia. The following groups are cited:— Ephemeroptera: *Atalonia*, *Atalophlebia*; Odonata: Petaliinae; Plecoptera: Eustheniidae and Notonemourinae; Megaloptera: *Archichauliodes*; Trichoptera: *Hudsonema*; Diptera: Blepharoceridae: *Edward-sina*; Simuliidae: *Cnephia*, *Austrosimulium*; Neuroptera: Stenosmylinae, Calosmylinae; Mecoptera: Nannochoristidae. These groups are all aquatic or live in very damp environments, as do the Peloridiidae (see Evans, 1941, Woodward, 1956a), and would not be very prone to air dispersal between continents. Evans gives reasons against the possibility of these groups having had a world-wide distribution with later extermination in all areas but their present southern occurrence. Mackerras (pers. comm.) considers the "Antarctic" elements in Australia the oldest, except a few archaic relics. The "Antarctic" elements were followed by an invasion of old Ethiopian-Oriental forms and later by the modern "Malayan" groups which perhaps came in no later than the Pleistocene.

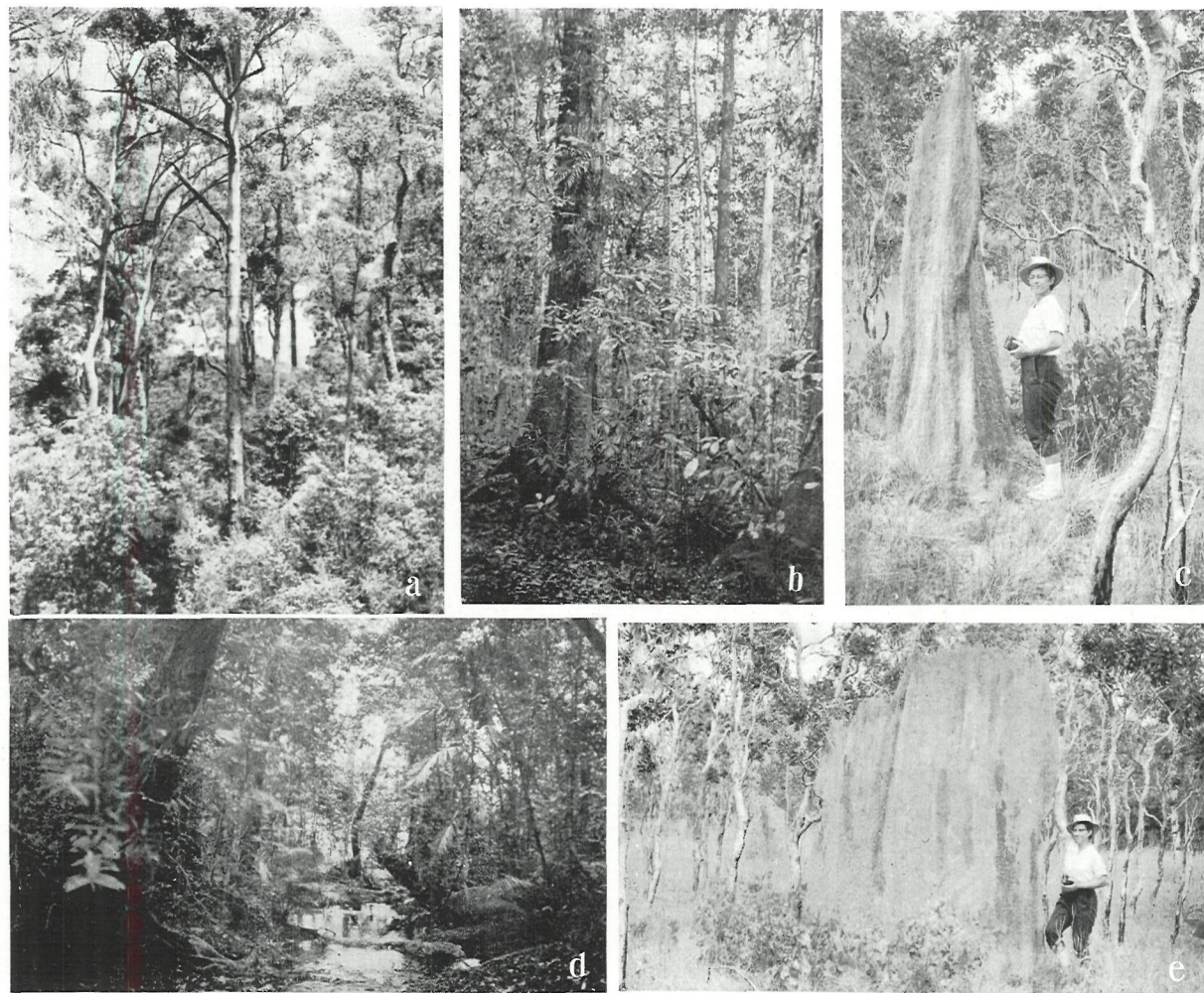


Fig. 19. a, Karri Eucalyptus forest, East Brook, 150m, Pemberton, south-western Australia, 4 Jan. 1961; b, disturbed rainforest, Malanda, 1400m, Atherton Tableland, near Cairns, N. Queensland, 12 May 1961; c, "magnetic" termite nest (end view) in *Melaleuca* — *Banksia* savanna woodland between Silver Plains and Rocky River, 300 m, NE of Coen, Cape York Peninsula, Margaret Gressitt, 28 April 1961; d, rain forest near top of Tulley Falls, 1300 m, south of Evelyn Tableland, N. Queensland, 11 May 1961; e, Same termite nest as in c, side view.

Keast (1959b) cited different theories of the history of Australia's geology. He estimated the insect fauna at well over 50,000 species. Paramonov (1959a) stressed the links of Australian flies with those of other continents, and also extensive speciation of some archaic or isolated groups, such as Mydidae, Apioceridae, *Comptosia* (Bombyliidae), and *Rutilia* (Tachinidae), the last showing active speciation in relation to precise niches. Paramonov also emphasizes both Malayan and Papuan invasion, slight New Zealand relationships, and elements common to the other southern continents ("paleoantarcts"). He speaks for a geological connection with South America via Antarctica. Paramonov proposes the faunal division of the continent into "Australia Deserta" (Eyrean) and "Australia Sylvatica", the latter divided into "Australia westralica, bororientalis" (Torresian) and "merorientalis" (Bassian). The terms in parentheses are the old, well known divisions. The southwestern division is not sufficiently distinct from the Bassian in many groups (Mackerras, 1950).

Key (1959) demonstrated that the evolutionary radiation of grasshoppers in Australia is the result of interplay between the constitution of the grasshopper groups which have reached Australia and the peculiarities of the Australian environment. He stressed the role of ecology, and indicated lack of close relationships with other southern continents. Calaby and Gay (1959) stressed survival of the most primitive termites in Australia, apparent great difference between the termite faunas of Australia and New Guinea, and the role of ecological factors.

Mackerras (1954, 1960) showed that the Australian Tabanidae lack several important, widely distributed tribes (4 of 10), but also have several in common with other southern continents only. Most of these are primitive southern groups (Mackerras, 1956) and there was lateral spread both north and south of a large band of sea. In Australia speciation has depended on barriers dividing populations of tabanids during past periods such as the ice ages (Mackerras, in press). Heslop-Harrison (1949) stated that in the Miocene Australia had a great influx from Antarctica of insects of South American relationships.

Australia seems to have had rather minor influence on the fauna of Pacific islands, aside from New Guinea, the Solomon Islands, New Caledonia, Lord Howe Island and New Zealand. Even many dominant Australian elements are lacking from these adjacent islands, which in many insect groups have surprisingly little in common with Australia. Iyengar (1960) stressed some of these points for South Pacific mosquitoes.

I earlier (1956a) indicated northern Queensland as part of the Papuan Subregion. Hedley (1894) had suggested this earlier as have others. However, this only applies to rain forest areas of Queensland, and Australian elements extend into southern New Guinea in *Eucalyptus* or *Melaleuca* savanna woodland. A more realistic indication is given in fig. 2, with the two areas indicated as an overlap zone.

For land snails, Solem (1958, 1959) indicated that all those in the southern continents had a northern origin, and that primitive relics have been preserved in the southern refuges. For these no Antarctic connections are required, as for mammals (Simpson, 1939, 1953) and vertebrates in general (Darlington, 1957).

Wittmann (1934) treated faunal relationships of southern continents, but many of the groups cited were poorly known then. Munroe (1958) discussed the distribution of the Scopariinae (pyralid moths), which occur widely, and the genus *Eudisia* which has speciated in Australia, New Zealand and Hawaii, as well as to a lesser degree in the Marquesas,



Tahiti, Rapa and islands south of New Zealand. It is striking that Australia appears to be extremely deficient (or even lacking) in native Aphididae (Carver, 1959). This is also true of New Zealand, and most of the tropical and southern Pacific islands. Kuschel (1960), in discussing the relationships of the fauna of southern Chile, pointed to relationships with the other southern continents and stressed the role of Antarctica as a center of distribution.

#### NEW ZEALAND

The New Zealand fauna is one of the most intriguing in the world. Although it has obviously been isolated for a very long period, it shows some extremely interesting, and sometimes close, relationships to the fauna of South America on the one hand and New Caledonia on the other. At the same time, it is part of the Australian Region and some elements are shared with Australia, but very many Australian elements are lacking. It thus has a distinctive fauna, and possesses many archaic and primitive types. Conspicuous examples are the flightless birds, with the recently extinct giant moas, and the existing kiwi and others. The insect fauna is no less interesting and includes many unexpected elements. The fauna is rich, although it is not harmonic. Many important subfamilies or tribes are lacking from the fauna, including quite a number found in Australia. The lack of mammals and some other characteristics of the fauna put it almost in the class with oceanic islands, but this is not the correct picture. Apparently it has been separated from other major areas long enough that mammals and other more lately evolved groups did not have access to it. At the same time this no doubt permitted the continued existence of primitive elements which might otherwise have become extinct through competition.

New Zealand might be termed "subcontinental", recognizing it as the remnant of a formerly more extensive land mass, which has experienced such long term isolation that it lacks many advanced groups found on most continents, and even many of the groups characteristic of Australia. One of the conspicuous elements of southern distribution in the flora is the southern beech genus *Nothofagus*, which also occurs in New Guinea, south-eastern Australia, Tasmania, New Caledonia and temperate South America. There are other elements which parallel this distribution (see *Araucaria* under New Caledonia). The lack of *Eucalyptus*, so dominant in Australia, is striking.

One of the primitive "southern" elements in New Zealand is the family Peloridiidae (Homoptera), which is restricted to wet moss in rain forests. The family is found in eastern Australia, Tasmania, Lord Howe Island, New Zealand and Chile. The Aradidae (Heteroptera), according to Usinger and Matsuda (1959), have a number of primitive elements surviving in New Zealand, including one subfamily restricted to New Zealand, another to New Zealand and Australia, and a third known only from New Zealand, Australia and temperate South America (in *Nothofagus* forest). These authors also noted a parallelism in evolution of forms in Fiji and Samoa, as against some in New Zealand. Woodward (1956b) showed that the New Zealand Enicocephalidae consist largely of primitive groups with relationships in Patagonia, Crozet Island and other southern areas.

The chironomid flies of New Zealand (Freeman, 1959) present similarities and contrasts to the respective fauna of southern South America. New Zealand possesses Podoninae but appears to lack Clunioninae. These are the two subfamilies represented in Ant-

arctica itself, and also well represented in South America. There are apparently no genera in common with South America, although two are similar to others in Patagonia. Four genera are endemic and one is common to New Zealand and New Guinea. The tabanid flies (Mackerras, 1957) are represented by only three of ten tribes and the whole family was derived from extensive Antarctic radiation. Some groups became extinct in New Zealand during the Pleistocene.

The carabid beetles of New Zealand are said (Britton, 1949) to show strong evidence of southern continental connections (Paleantarctic continent) from their similarity to those in southern South America. On the other hand Ball (1956) attempted to prove an opposite view, to the effect that the Broscini could have been distributed around the North Pacific, and passed across the Bering Arc, thus not requiring an Antarctic connection. In the Cerambycidae (see below) the New Zealand fauna has strong affinity with that of New Guinea through New Caledonia, and American relationships are not so evident.

Evans (1957) considered that the southern continents may have been in contact as late as the Cretaceous, unless southern distribution is to be explained as relics of former world-wide distribution followed by extinction in the northern continents. Evans (1959) listed several groups of insects, mainly aquatic, found in New Zealand and the southern continents which strongly argue for southern land connections before the end of the Mesozoic. Brehm (1936) stressed southern continent relationships of aquatic fauna. Paramonov (1955) considered that the New Zealand Cyrtidae are more closely related to those of South America than of Australia.

*The Chatham Islands*: These islands, nearly as far distant from New Zealand as is Norfolk Island, have a remarkably rich insect fauna, particularly considering the latitude, which is nearly 45° S. Latitude. Many groups of insects are represented, including Trichoptera and Plecoptera, which are rarely found on oceanic islands. The fauna almost suggests that the islands are a remnant of a much larger land-mass, perhaps once connected with New Zealand, and have been able to maintain elements of the original fauna. On the other hand, it would not have been impossible for these elements to have come by over-water dispersal over a very long period.

#### SUBANTARCTIC ISLANDS

The subantarctic islands are mostly between 48° and 55° South Latitude, although some islands farther north are arbitrarily classified in this category because of close faunal analogy through strong isolation and exposure to strong cold winds from Antarctic areas.

In considering the zoogeographical relationships of subantarctic islands, several complicating factors must be considered, some of which do not enter into the picture, or are of lesser significance, in tropical areas. Foremost among these is the question of survival under adverse climatological circumstances. Another is the historical question relating to geographical and climatological differences in the past. The fauna of a subantarctic island cannot represent a clear cross-section or common denominator of zoogeographical relationships between surrounding continental areas because the present climate is much more rigorous than those of the continental areas (other than Antarctica). Also, its limited land area restricts ecological opportunity, as do the climatological and other limitations, which likewise affect the plant and other host inhabitants. Thus the potentialities for livelihood in the terrestrial fauna are severely limited. The position of birds, of course, is somewhat

different, as they (and marine mammals) gain their food from the sea.

It may not be safe to assume that the subantarctic islands are remnants of a former larger land-mass or parts of southern continents. Some of the islands are volcanic, and may not have been involved in possible inter-continental connections. Their inhabitants must have come from neighboring continental areas, presumably by aerial dispersal in the main. The fact that many of the present inhabitants are flightless does not necessarily contradict this theory. It has been postulated that material reduction in wing size can take place in a few tens of thousands of years and that the rate of wing reduction is more rapid on islands that are smaller and subject to adverse weather conditions. These same islands, because of adverse factors, can only support a small number of groups and a limited number of species. These factors probably foster more rapid evolution, as does the small size of the populations of many of the species.

In comparing the insect fauna of subantarctic islands with those of isolated tropical islands a few interesting contrasts are to be noted. Conspicuous is the scarcity of Heteroptera and particularly Homoptera from subantarctic islands. These are abundant on tropical islands and often constitute a considerable fraction of the fauna (up to 10 %), whereas on subantarctic islands they comprise less than 1 %. Hymenoptera also seem to make up only about 1 % of the fauna of subantarctic islands, but on the tropical islands they constitute 5-10 %. Ants are notably absent in the subantarctic. Orthopteroid insects, Psocoptera, Ephemeroptera, Plecoptera and Trichoptera are also completely absent or poorly represented.

The following summaries are largely after Gressitt and Weber (1960). General comments were given by Hudson (1909) on the insects of the New Zealand subantarctic islands and by Broun (1909) on the Coleoptera and by Lamb (1909) on the Diptera. Jeannel (1938) discussed a group in the Auckland Islands, Falkland Islands, Tierra del Fuego, Chile, New Zealand, Tasmania and eastern Australia. Holdgate (1960b) made a faunal analysis of Tristan da Cunha and Gough Islands.

*Bounty Islands*: This group and the next two are on the border line of the Subantarctic Zone, southeast of New Zealand, between 48° and 49° South Latitude. The Bounty Islands have probably been insufficiently investigated. Only about eight species of terrestrial arthropods have been recorded, including two spiders, a wingless grasshopper, two beetles and three flies, including a semi-apterous psychodid. Undoubtedly mites and spring-tails are present.

*Antipodes Islands*: This slightly more southerly group has at least 20 species known, including a tick, five moths, 13 flies and a flea. Other groups are sure to be present.

*Snares Islands*: Closer to New Zealand, these islands are quite small and the known fauna includes 18 species: four spiders, an orthopteran, a moth, seven beetles and five flies.

*Auckland Islands*: At 50° S. Latitude, the Aucklands may be the richest subantarctic group. They are only on the border of the zone, and are almost directly south of New Zealand. The terrestrial arthropod fauna numbers about 151 recorded species, exclusive of mites, and includes representatives of at least nine orders of true insects, besides Chilopoda, Araneida, Opiliones and ticks. There are many Collembola (Salmon, 1949). Diptera are represented by 54 species (Harrison, 1956) and Coleoptera by 64 species (Brookes, 1951). There are a number of conspicuous wingless or short-winged species of normally-winged groups. The wingless species often tend to be more active than the winged species and





Fig. 20. a, nylon nets ( $23 \times 75$  cm diam.) for air-borne insects on "Magga Dan",  $48^{\circ}$  S. Lat., en route Macquarie I., 3 Dec. 1960; b, top of plateau, north-central Macquarie I., 300 m, with feldmark and tarns, 6 Dec. 1960; c, Macquarie I., from NE corner of plateau to Wireless Hill; d, *Pleurophyllum* and *Azorella* on NE part of plateau, 250 m, Macquarie, 10 Dec. 1961; e, E. slope Macquarie, near Gadget's Gully, *Poa* (tussock grass) and *Stilbocarpa* (Macquarie cabbage); f, Green Gorge, E. Coast near middle of Macquarie, with king penguins and elephant seals.

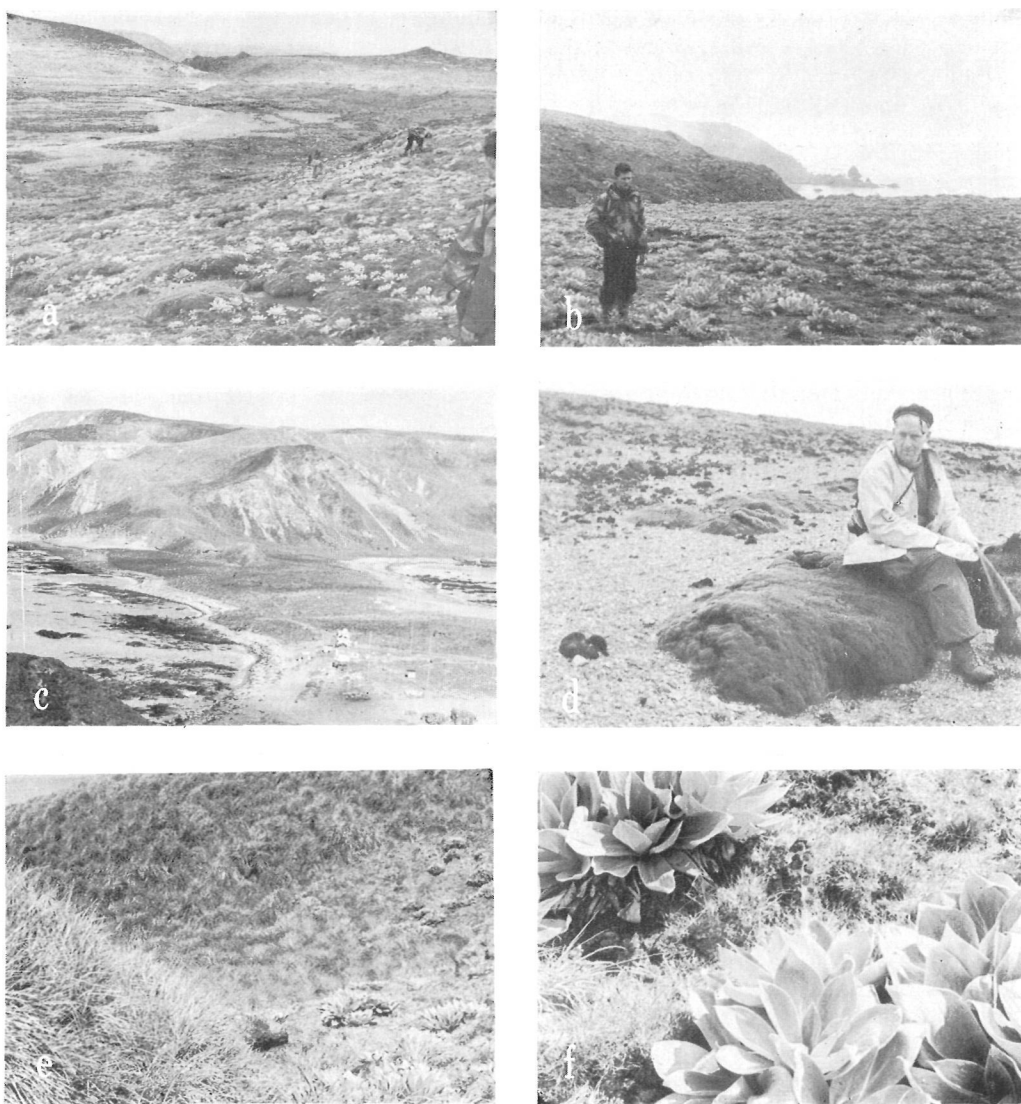


Fig. 21. a, west-central plateau Macquarie I., with *Pleurophyllum* and *Azorella*; b, plateau, Macquarie, with *Pleurophyllum*, moss; c, plateau and isthmus from Wireless Hill; d, Feldmark: *Azorella* in rows: J. Calaby (C. S. I. R. O.), Dec. 1960; e, *Poa* and *Pleurophyllum*, Wireless Hill; f, *Pleurophyllum* and grass, same locality as e. (Macquarie I.).

the latter are rarely observed in flight. These islands have forests of trees which provide a fair amount of protected environments. Kimmins (1951) treated the Nemouridae which are found here and in New Zealand, Tasmania, Australia, southern South America and South Africa.

*Campbell Island*: This more southerly island (52° S. Lat.) has a less favorable climate,

but nevertheless has some woody plants and a fairly rich fauna of 107 recorded species, including most of the orders found in the Aucklands. It is particularly rich in springtails (Salmon, 1949), moths (Salmon and Bradley, 1956) and flies. Harrison (1956) recorded 39 species of flies and Brookes (1951) listed 26 species of beetles. Some of the flightless moths have the habit of leaping and tend to fall down in the grass when disturbed.

*Macquarie Island*: The southernmost (54° 30' S. Lat.) major subantarctic island, Macquarie has no woody plants and only a few dominant herbs besides grasses, ferns, mosses and other lower plants. Thus the ecological diversity is limited. About 41 species of ten major groups have been recorded, but more species and orders were added during my recent visit to the island. Enderlein (1930b) listed 11 species and Tillyard *et al.* (1920) listed 12. Macquarie is farther south than Kerguelen, Heard and South Georgia (the other major southern subantarctic islands) and its fauna appears poorer. This is particularly surprising, since the Antarctic Convergence reaches or exceeds the other three, but does not quite reach Macquarie and gives the latter a milder climate. Also, Macquarie is the only one of the four without glaciers and is said to have more species of higher plants than the others. To explain the relative poverty of Macquarie it must be assumed that its geological history has been less favourable for the preservation or establishment of terrestrial fauna. Macquarie is evidently the remnant of a much larger land-mass of volcanic origin, which has undergone extensive erosion, including glaciation. Perhaps an earlier fauna might have been completely or largely exterminated by late volcanic and/or glacial action. The fact that Macquarie has a lower percentage of species with reduced wings also suggests that the fauna is younger than those of Kerguelen, Heard and South Georgia. Perhaps some of the species present are rather recent arrivals through transport in air currents. Some, however, were no doubt brought by man.

The fauna of Macquarie includes about 10 species of mites, a tick, a few spiders, about 10 Collembola, one Homoptera, one Psocoptera, one Lepidoptera (Gelechiidae), four Coleoptera (Staphylinidae), seven Diptera (Psychodidae, Tipulidae, brachypterous Dolichopodidae, Coelopidae, Milichiidae, wingless Ephydriidae), two Hymenoptera (Scelionidae, Diapriidae), and ectoparasites, which include biting lice on birds, a sucking louse on sea elephant and some fleas. This wingless scelionid wasp (Brues in Tillyard, 1920) appears to breed in an herb, *Azorella*, which has the growth form of a moss. So also do some of the flies and staphylinids. Collembola and mites are abundant among tussock grass, *Poa*, near the beaches and around wallows of the elephant seals. A kelp fly and wingless ephydrid are found on or under kelp washed up on the beaches. Staphylinids, flies and Collembola occur in the wilted leaves of *Pleurophyllum* (figs. 20, 21), one of the three largest plants on Macquarie. The aphid was found on this plant. *Psychoda spatulata* flies were found around the Macquarie cabbage (*Stilbocarpa*; fig. 20) and on or under drying elephant seal carcasses. The common moth and the crane fly (both winged) are exceedingly numerous and are found flying (in rare good weather) or resting on various plants from the coastal strips to high areas of the plateau.

*Kerguelen Island*: This island has perhaps the most spectacular insect fauna among the subantarctic islands. It is larger and higher than Macquarie, and has some glaciers. Jeannel (1940) treated aspects of the insect fauna in detail, covering Coleoptera (17 species) and other groups. Seguy (1940) listed 13 species of Diptera. Paulian (1952) treated the whole fauna. Besides a number of very interesting wingless or short-winged flies, moths

and beetles, there is an interesting enicocephalid bug and other conspicuous elements. Kerguelen has about 73 recorded species of terrestrial arthropods.

*Heard Island*: This high, extensively glaciated island (53° S. Lat.) is farther south than Kerguelen, but not very far from it. Heard seems to have a slightly attenuated Kerguelen fauna. It has local species of several of the genera described from Kerguelen (Brown, in press). It would appear as if Heard had derived many of its faunal elements from Kerguelen. Probably both were once much larger or united, permitting a common origin of the fauna. There are about 27 previously recorded species on Heard, besides more in press.

*Marion Island*: The fauna of this small island (47° S. Lat.) is not well known, but about 17 species have been recorded with Coleoptera ranging highest with four species. A few lice have been recorded from the not far distant Prince Edward Island, but perhaps no free-living insects.

*Crozet Islands*: These small islands (46° S. Lat.) are about midway between Marion and Kerguelen. The insect fauna may be fairly well known and numbers about 44 recorded species, exclusive of lice and fleas. Highest ranking groups are mites (9 species), spiders (6 species), Coleoptera (11 species) and Diptera (7 species; Seguy, 1940). A species of Thysanoptera is recorded from Crozet, whereas there may be no other records of this order from subantarctic islands. Thrips have been taken much farther south in trapping at sea. Brinck (1945) pointed out that all the genera of beetles on Crozet were also found on South Atlantic islands.

*St. Paul Island*: This island (39° S. Lat.) is well northeast of Kerguelen, and is actually outside the subantarctic zone, but its fauna is quite analogous to those of the other islands included. There are 34 species recorded, but probably more occur. Seguy recorded eight species of flies in 1940. A small collection was made for Bishop Museum late in 1960 by the "Monsoon Expedition" of Scripps Institute of Oceanography.

*Amsterdam Island*: This small island (37° S. Lat.) is not far from St. Paul. It has not been well collected, and a number of groups have not been recorded. However, at least 14 species are known from the island, including seven species of Lepidoptera and five species of Diptera. Of the seven Lepidoptera Viette (1959) stated that three are probably not endemic. One has very small wings and another reduced wings.

*Tristan da Cunha*: This South Atlantic group (36–37° S. Lat.) is also outside the subantarctic zone, but has an analogous fauna. Over 100 species of terrestrial arthropods have been recorded with about 70 % endemic. The composition is not very different from that of Kerguelen, except that there are more Hemiptera. Gough Island, south of Tristan da Cunha, has a poorer, but analogous fauna, including some of the same species or related ones. The fauna has recently been analyzed by Holdgate (1960b).

*Falkland Islands*: These islands (52° S. Lat.), of the same latitude as Campbell Island, have a few more insects recorded than Campbell, but fewer than Auckland Islands. Their proximity to South America suggests that they should be richer than they appear to be. There has been much extinction from introduced animals such as goats. The fauna includes most of the orders which have been recorded from subantarctic islands.

*Tierra del Fuego*: This and nearby small islands represent the southern-most continental area other than Antarctica. The area falls within the range of latitude of the more



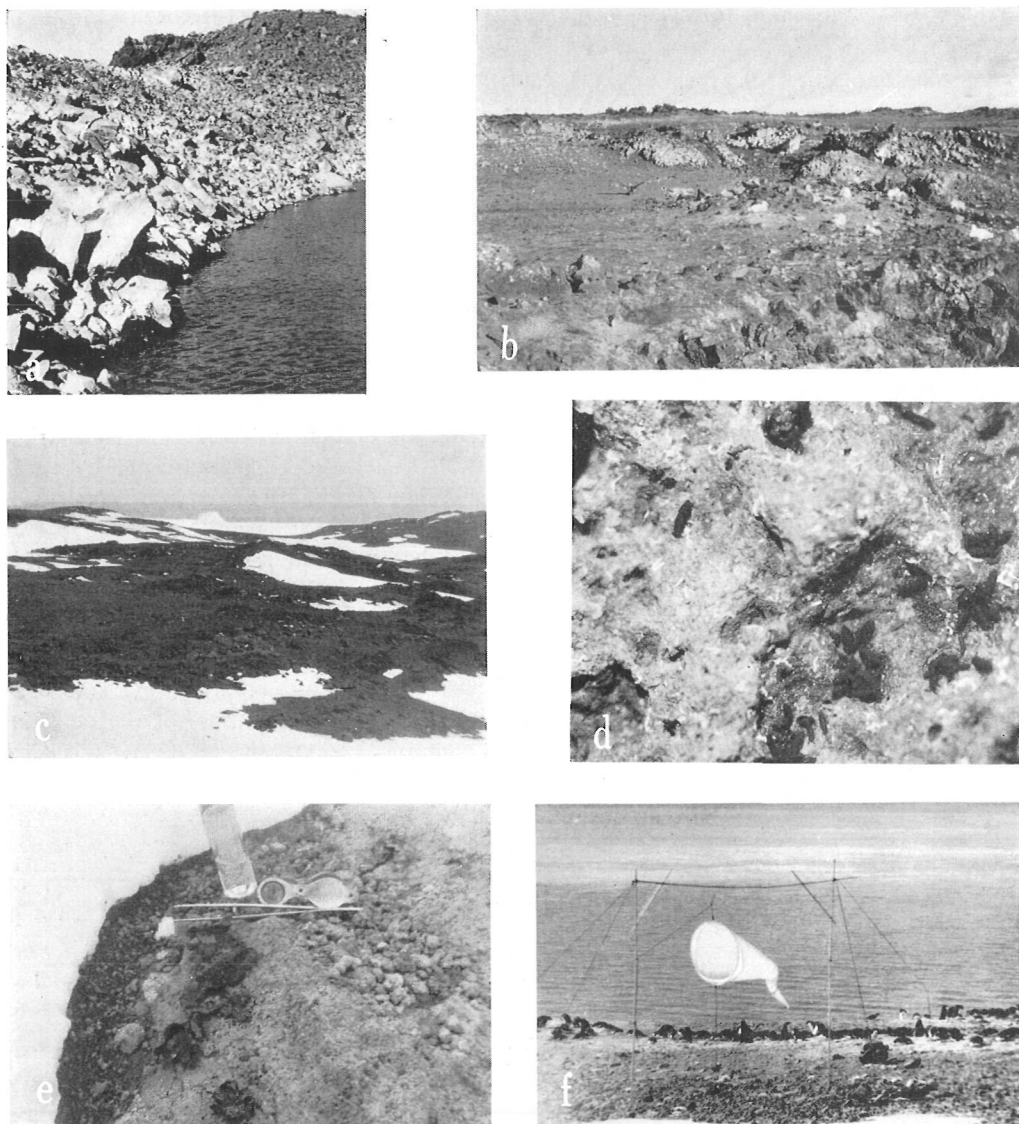


Fig. 22. a, habitat of *Podonomus steineni*, southernmost winged insect, sea level crater, Penguin I., S. Shetlands, Jan. 1960 (R. E. Leech); b, Penguin I., grass, moss and lichens, giant petrel rookery (R. E. Leech); c, Behind Cape Royds, locality for mites and springtails, Ross I.; d, close-up of springtails and exuviae, *Gomphiocephalus hodgsoni* (R. E. Leech); e, edge of snow bank, volcanic rock (kenyite) with lichens bearing springtails, Cape Royds; f, air net at Adelie penguin rookery at Cape Crozier, Ross I., Jan. 1960. (Antarctica).

southern major subantarctic islands (South Georgia, Heard and Macquarie), and just south of the Falklands and Campbell. The fact that the fauna of southern Tierra del Fuego is very limited and analogous to that of the isolated subantarctic islands strongly suggests



Fig. 23. a, four 1-meter nets for air-borne insects on U. S. S. Arneb, Beaufort I. and Ross I., Ross Sea, 10 Dec. 1959; b, grass, moss and lichens, insect environment, Penguin I., S. Shetland Is., Jan. 1960 (R. E. Leech); c, flying Otter plane insect trap in Victoria Valley, Victoria Land, Piedmont glacier in foreground; d, nets for air-borne insects, Observation Hill, McMurdo U. S. A. R. P. installation, Ross I., Jan. 1960; e, Otter plane trap, Taylor Dry Valley, Victoria Land, Jan. 1960; f, "Bali H'ai" and mouth of Hood Glacier, southernmost collecting sites for animals (mites and springtails), and edge of Ross Ice Shelf, 83° 55' S. Lat., Dec. 1959 (H. Tynedale-Biscoe, copyright New Zealand Alpine Club).

the climatological and environmental factors have a strong bearing on limitation of the fauna of the isolated islands. Thus if environments were more hospitable, more types of insects would have been brought by air currents and established on the isolated islands, as in the tropical regions. A collection was made on Tierra del Fuego for the Bishop Museum by Borys Malkin early in 1961.

*South Georgia*: This major subantarctic island (53–54° S. Lat.) is the same latitude as Tierra del Fuego, and is just south of the Falklands in latitude. However, it lies well within the Antarctic Convergence, which here extends more northward. Thus it has a more rigorous climate and is largely covered with glaciers. Its fauna appears to be more limited than that of Kerguelen or Macquarie although it has more beetles (Brinck, 1945) than Macquarie appears to.

*South Sandwich Islands*: These are the southernmost subantarctic islands (56–59° S. Lat.), if 60° is taken as the boundary between subantarctic and Antarctic. Bouvet Island (55° S. Lat.) is also south of the major subantarctic islands. However, it appears that no insects are recorded from these islands. They are small volcanic islands largely covered with glaciers and free-living terrestrial arthropods must be extremely limited in occurrence.

The South Shetland and South Orkney islands are south of 61° S. Lat. and are considered with Antarctica. The former extend south of the tip of the Palmer Peninsula, and are almost adjacent to it.

#### ANTARCTICA

The insect fauna of Antarctica consists of slightly under 50 recorded species of terrestrial arthropods (Gressitt and Weber, 1960). A few additions have recently been made (Gressitt, 1960c, 1961). About one-half of the 50 are Mallophaga on birds or Anoplura on seals, and the other half ticks, mites (mostly free-living) springtails and two chironomid flies (one wingless and the other fully winged). Enderlein (1909, etc.) made many early reports on Antarctic and subantarctic insects.

The free-living insects and mites occur on exposed rock surfaces, generally associated with lichens, algae or mosses, and usually hide in the plants or under loose rocks except when temperatures are high enough for activity (Gressitt and Leech, 1961). Springtails and mites occur from the fringes of the continent southward to some of the southernmost exposed rocks almost to 84° S. Latitude (Tyndale-Biscoe, 1960) where winter temperatures are probably as low as –65°C. for long periods. The springtails and mites have also been found at altitudes over 1800 meters at 77° S. Latitude (Gressitt *et al.*, in press). Even in summer in many areas where insects occur, general air temperatures almost never rise above freezing, but activity of the insects is possible as result of rise in temperature of the microhabitat through absorption of solar energy. As the sun does not rise during winter, and is low in spring and autumn, it is probably only in summer that activity is possible among the free-living insects. Much information remains to be gleaned on the habits of insects under such rigorous environmental conditions (Pryor, in press). Not only are temperatures very low, but winds are extremely strong, and bare ground is too dry to support life when far from melting ice.

The inhabited areas are free of permanent ice largely because of topography, with strong winds preventing the accumulation of snow. Most of the insect environments are in expos-

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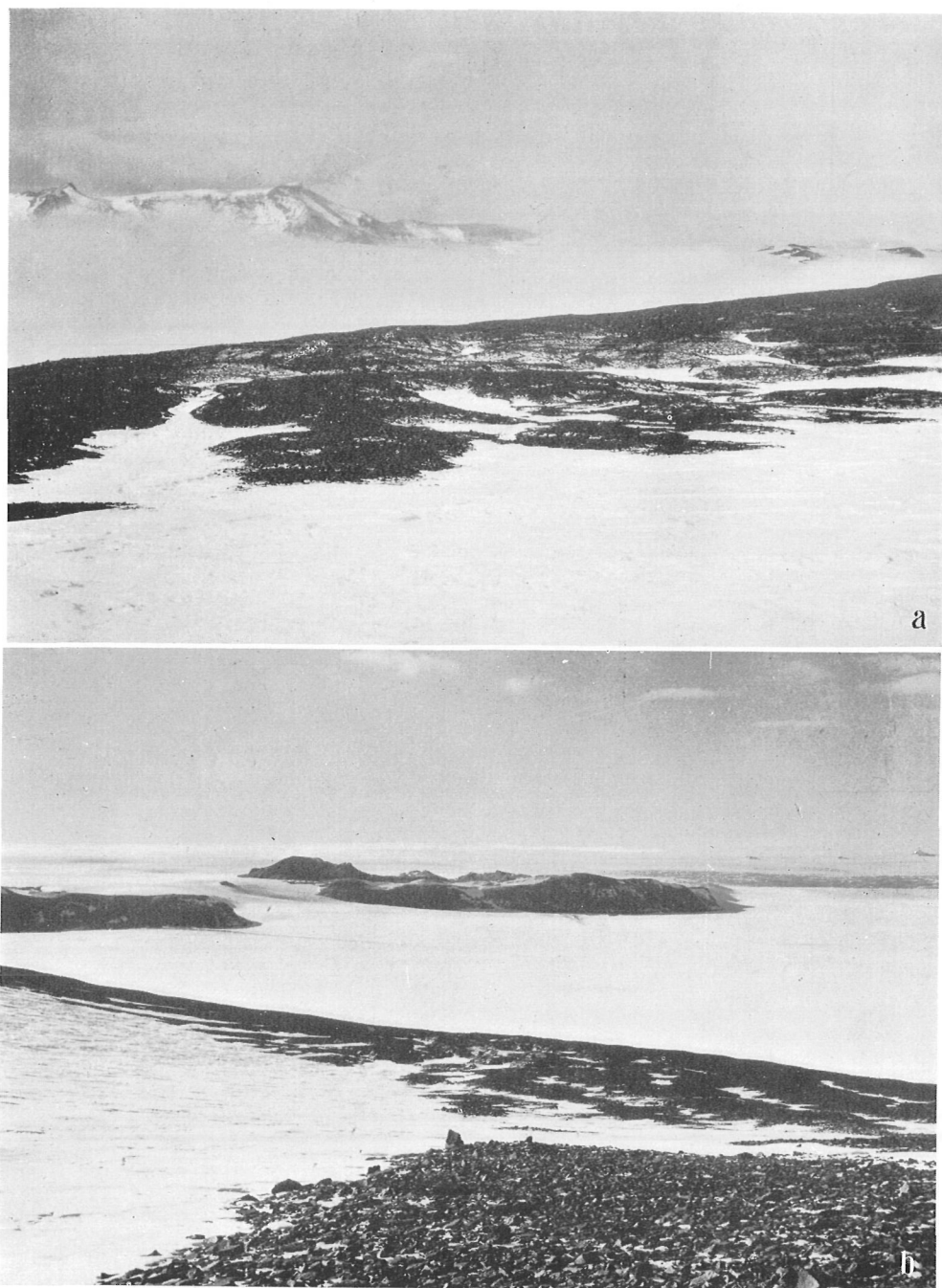


Fig. 25. a, high collecting sites, Upper Mackay Glacier, Victoria Land, Antarctica, plateau foreground, site of white *Collembola* collection, Dec. 1960 (Wise); b, Upper Mackay Glacier, white *Collembola* taken in central area, mites at right, looking west, northern tip of Willett Range at left, Dec. 1960 (K. A. J. Wise)

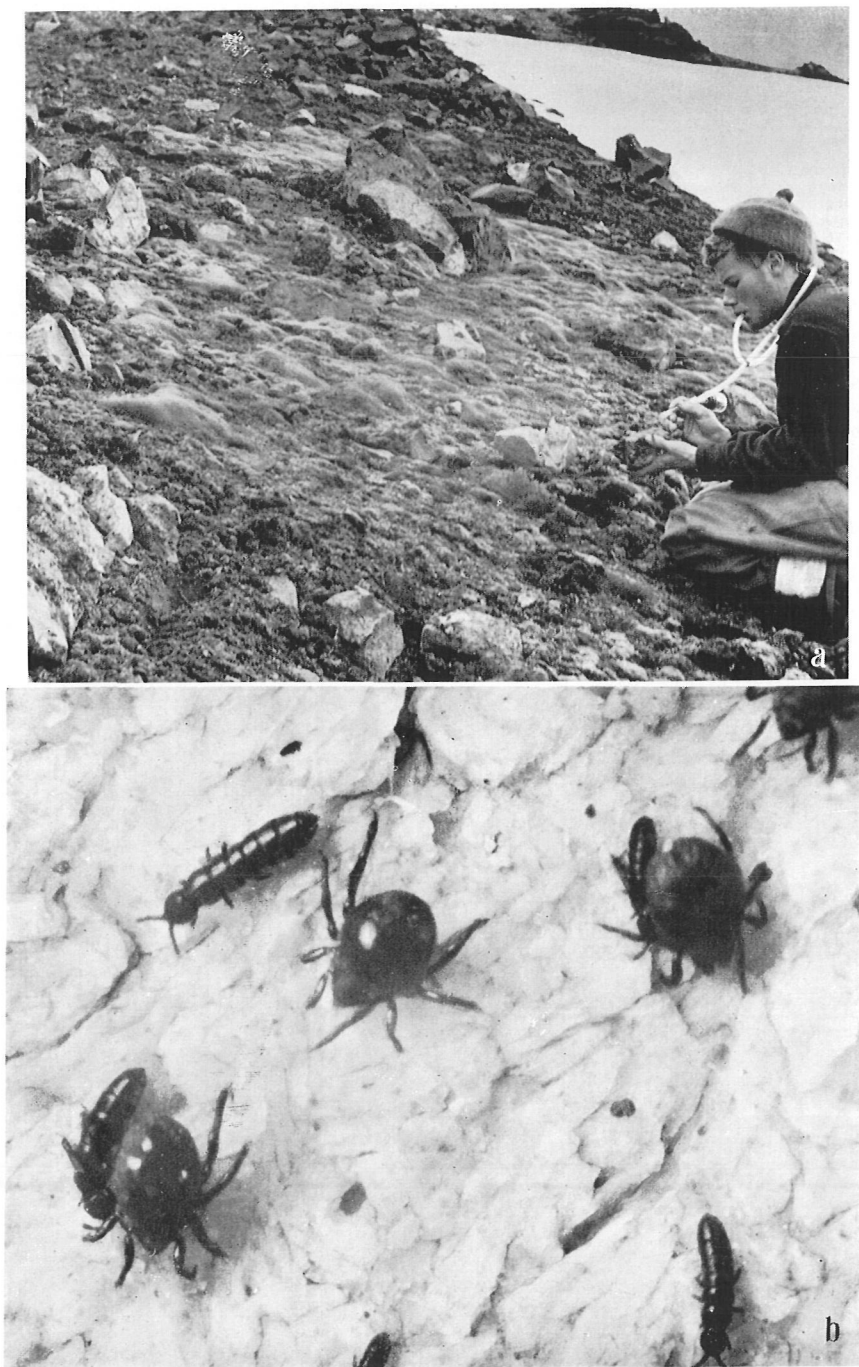


Fig. 26. a, environment of mites and Collembola, Deception I., S. Shetland Is., Antarctic, T. S. Leech at right, Jan. 1961 (R. E. Leech); b, mites and Collembola on old whale bone, eggs above center, Admiralty Bay, King George I., S. Shetland Is., Antarctica, 16 Mar. 1961 (R. E. Leech).

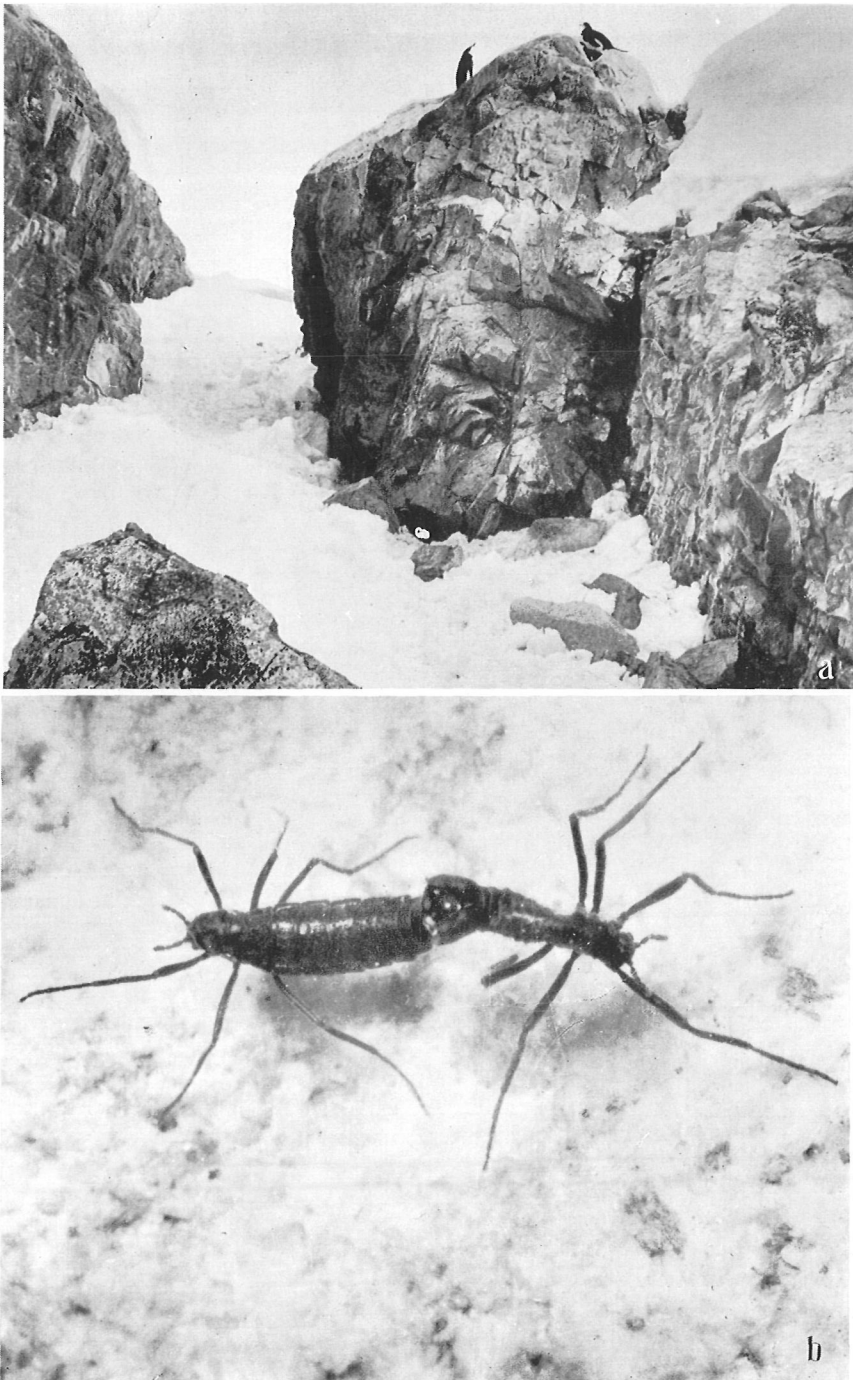


Fig. 27. a, environment of mites, Collembola and wingless chironomid fly (right side of photo), Base Gonzales Videla, Danco Coast, Palmer Peninsula, Antarctica, 64° 49' S. Lat., 62° 51' W. Lat., 6 Jan. 1961 (R. E. Leech); b, mating apterous chironomid, *Belgica antarctica*, same location as above, 20 Feb. 1961 (R. E. Leech)

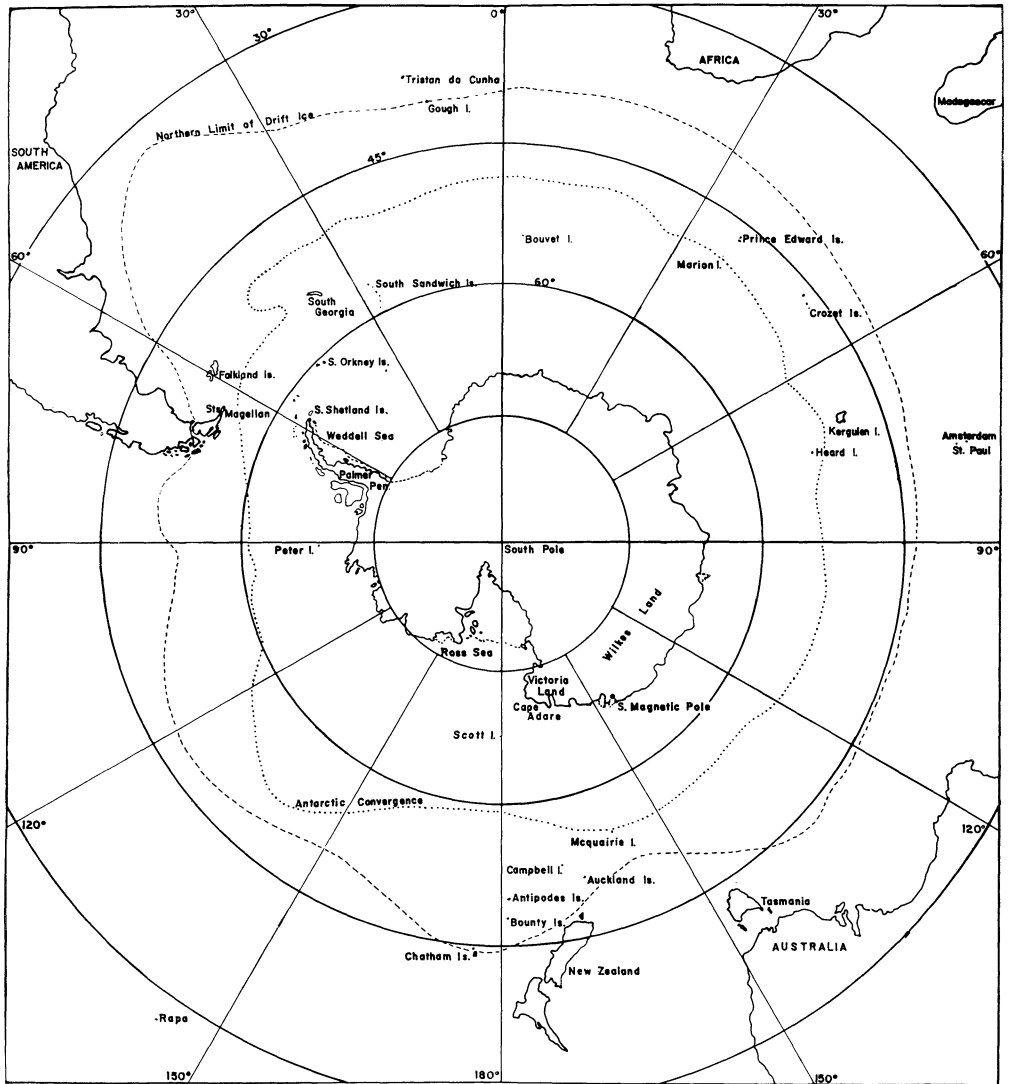


Fig. 28. Map of Antarctica, showing Antarctic Convergence, northern limit of icebergs and Subantarctic islands.

ed places, such as on ridges, peaks, nunataks, capes, promontories and steep slopes. Northward facing slopes, where maximum solar radiation is experienced, are likely to be more favorable for life.

The ticks and the two flies have been found only in the northernmost part of Antarctica, on the Palmer Peninsula and the South Shetland Islands. The ticks have been found associated with penguins, albatrosses or cormorants. The flies breed in snowmelt or coastal water. None of the ticks or flies are peculiar to Antarctica. Rübsamen (1906) and Torres

(1953) discussed the wingless fly *Belgica antarctica* and its habitat. It is also found in southern South America. Torres (1956) recorded the chironomid *Podonomus steineri*, southernmost winged insect, from the South Shetland Islands just off the Palmer Peninsula. It was originally described from South Georgia.

Several of the springtails and free-living mites are known only from the continent, but others occur also on subantarctic islands, or are still more widespread. Dalenius and Wilson (1958) treated the oribatid mites and discussed their ecology. They show that some of the Antarctic species are found on various fringes of the continent, and are found also on various subantarctic islands. Further locality records have been made for several of the species during the past few Antarctic summers.

An unanswered question is whether the present free-living arthropod fauna of Antarctica represents relics from an ancient temperate fauna or whether it represents recent overseas dispersal from surrounding continents or subantarctic islands since the period when the continent was more extensively glaciated than at present. The answer may involve both sources, but a majority probably represent post-Pleistocene immigration. Perhaps the continent could not have been so completely glaciated as to eliminate all possible niches to support insects. There is evidence from trapping that insect dispersal by winds within the continent occurs frequently (Gressitt, Leech and O'Brien, 1960). Some recently deglaciated areas have proved to be inhabited by insects, as has moraine on ice being pushed by the end of a glacier and the northward-moving edge of the Ross Ice Shelf. This suggests frequent air dispersal within the continent and colonization or re-colonization of favorable environments. Colonization from outside the continent is undoubtedly a rare event because of the inhospitable environment. Most insects which might be blown to Antarctica would be unable to establish themselves because of lack of appropriate food and environment, besides the severe climatological limitations.

Some of the faunal relationships between southern continents presumably having involved Antarctica in the past are discussed above under Australia, New Zealand or other areas.

#### THE FAMILY CERAMBYCIDAE

This large family of beetles is one of the best represented on oceanic islands. It is probably found on all high islands and occurs on many atolls. A few species have very wide distribution, but most are limited to a single island or island group. This suggests that members of the group are not readily distributed by man and that the present distribution in the result of natural phenomena. Except for a few large types (Prioninae and some others) it is felt that most members of this family have been transported to the islands by air currents. Some were probably carried as free adults and others as larvae, pupae or adults in dead branches or twigs which formed the larval niche. Although members of many genera or tribes (Callichromini, Gleneini, etc.) of the family found in the continental areas of the southwest Pacific (including the Philippines, Indonesia, New Guinea and the Solomon Islands) are borers in living trees in the larval state, almost none of these have been found on oceanic islands. Living branches are much less likely to be broken off by wind than dead branches, and larvae requiring growing wood would not survive as easily as those feeding in dead wood. Additionally, those boring in living trees

are mostly diurnal as adults, whereas those living in dead wood are mostly nocturnal. It is felt that nocturnal insects are more likely to be on the wing in inclement weather, and that therefore strictly diurnal insects, hiding when the sun is not shining, are less likely to be caught up in storm winds and carried great distances.

In Hawaii and the Society Islands there is some American influence, but otherwise the relationships of the oceanic islands are dominantly with Southeast Asia, New Guinea or intervening islands. In Hawaii (fig. 30) a single American immigrant (Clytini) has given rise to a complex which has been classified in six or more genera. These include about 100 species, representing a remarkable case of extensive proliferation from a single ancestor over a great period of time. This must have occurred partly on islands which no longer exist because of the time necessary to evolve so many species from one ancestor. It is probable that the number of genera in this complex will have to be reduced from six to perhaps three. The other two native genera in Hawaii are each represented by a single species and each belongs to a separate tribe of the primitive subfamily Prioninae. These might have come in floating logs from eastern Asia or the southwest Pacific.

In Micronesia and other parts of Polynesia there is no such spectacular evolution as in Hawaii. There are several widespread genera, such as *Ceresium*, *Dihammus*, *Ropica*, and *Sybra*, which are well represented in New Guinea, Indonesia, the Philippines and southeast Asia. *Ceresium*, in particular, is represented on most oceanic islands by one or two widespread species (perhaps largely spread by man) and a number of local species restricted to an island or island group. This genus has many species in New Guinea and might have originated there. In addition to the above, there are a few genera well represented on the oceanic islands which do not occur on continental areas or at most on subcontinental areas, such as New Guinea. Among these are *Prosoplus*, *Oopsis* and *Sciadella*. *Longipalpus* occurs on many oceanic islands, throughout the Papuan Subregion (including rain forests of eastern Queensland), and in the Ryukyu Islands, the Philippines and in Mauritius and the Seychelles (fig. 29). This and other genera (some mentioned below under Chrysomelidae) may be primitive types which have survived in insular isolation and disappeared from continental areas. Scott (1933) gave an interesting picture of the Seychelles fauna, which may be compared with a Pacific insular fauna.

In addition to the above and other fairly widespread genera, there are Asian genera which have reached only a few oceanic islands and may be represented by a single species in an island group, as in the Bonin Islands, Palau, or others. There are also Papuan genera which have only reached certain islands. Further, there are local endemic genera in many of the island groups and a few are flightless. Most of them appear to have their closest relationships in New Guinea or nearby areas. There is a considerable development of endemic genera in New Caledonia, indicating great age of the fauna. Most of the relationships, where traceable, are with forms in New Guinea and the Solomons on one hand and with New Zealand on the other. Very few clear relationships exist with Australia. Some of the relationships go through the New Hebrides, but few to Fiji except for widespread Pacific elements. Some of the New Caledonia genera belong to the Tmesisternini complex of tribes which include a few hundred species and are centered in New Guinea (fig. 31). This conspicuous and distinct group of fairly large beetles is represented by only a few species west of the modified Wallace's Line and yet is hardly represented in Australia outside the northeastern rain forests. This speaks for considerable age and local evo-

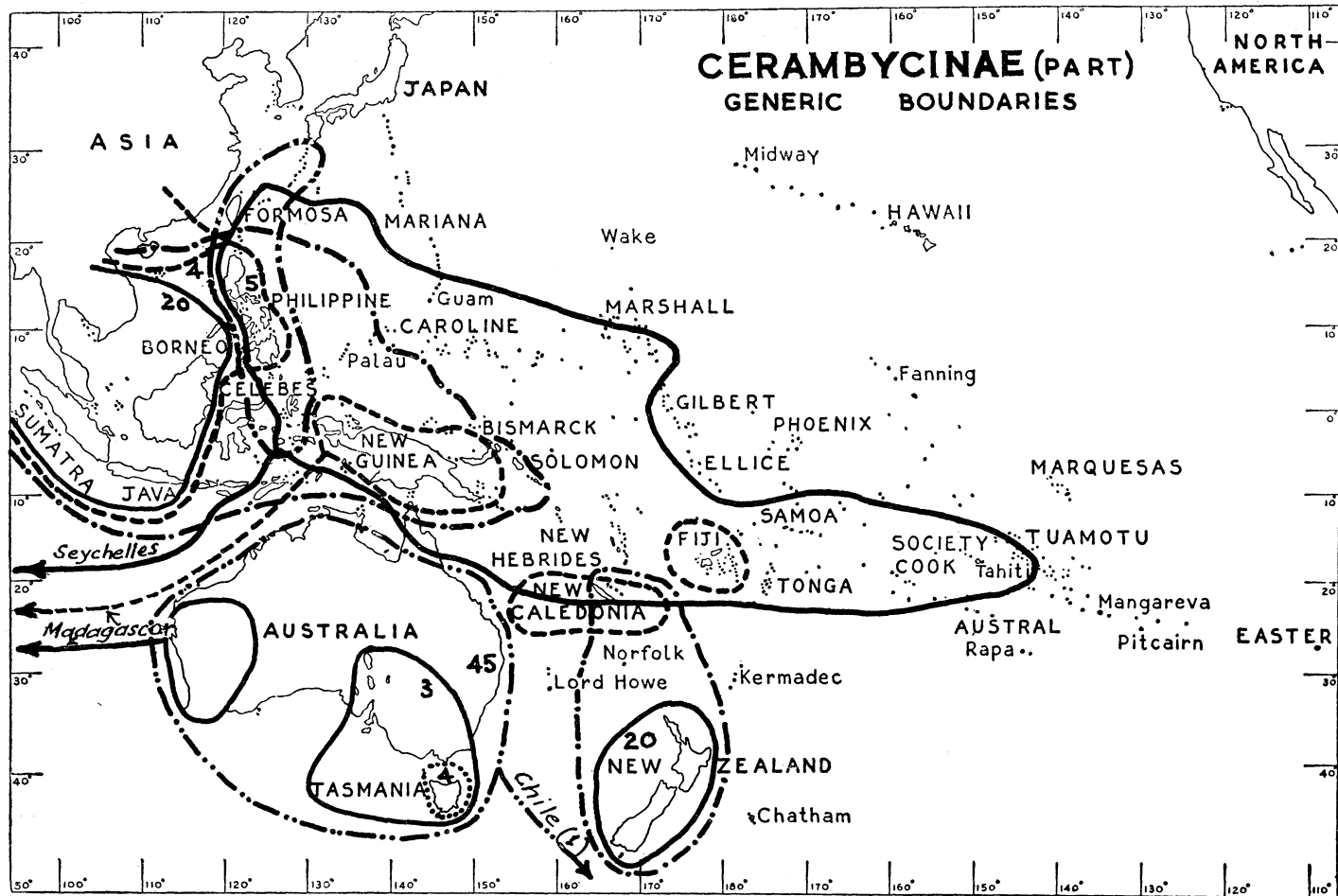


Fig. 29. Generic boundaries in some of the more primitive tribes of the subfamily Cerambycinae, family Cerambycidae. Each line represents the range of a single genus, except where figures are given. Asian genera not reaching Wallace's Line are omitted. Further data presented in Figure 30.

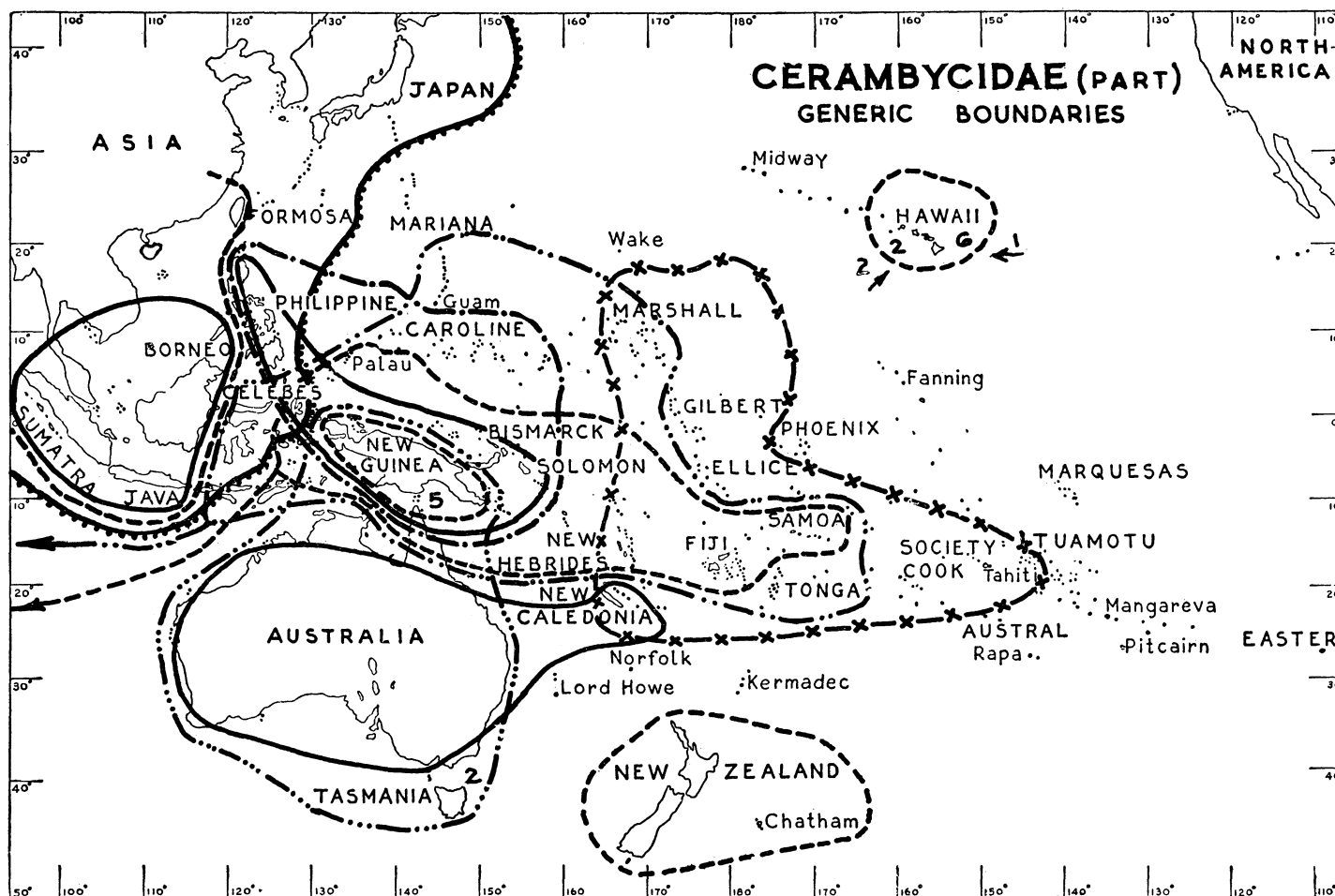


Fig. 30. Generic boundaries in Cerambycidae. The ranges of twelve genera in outer Polynesia, including all eight genera native to Hawaii. Each line represents the range of a single genus, except where figures are given. Arrows for Hawaii indicate source of origin, with numbers by arrows indicating number of genera of original immigrants.



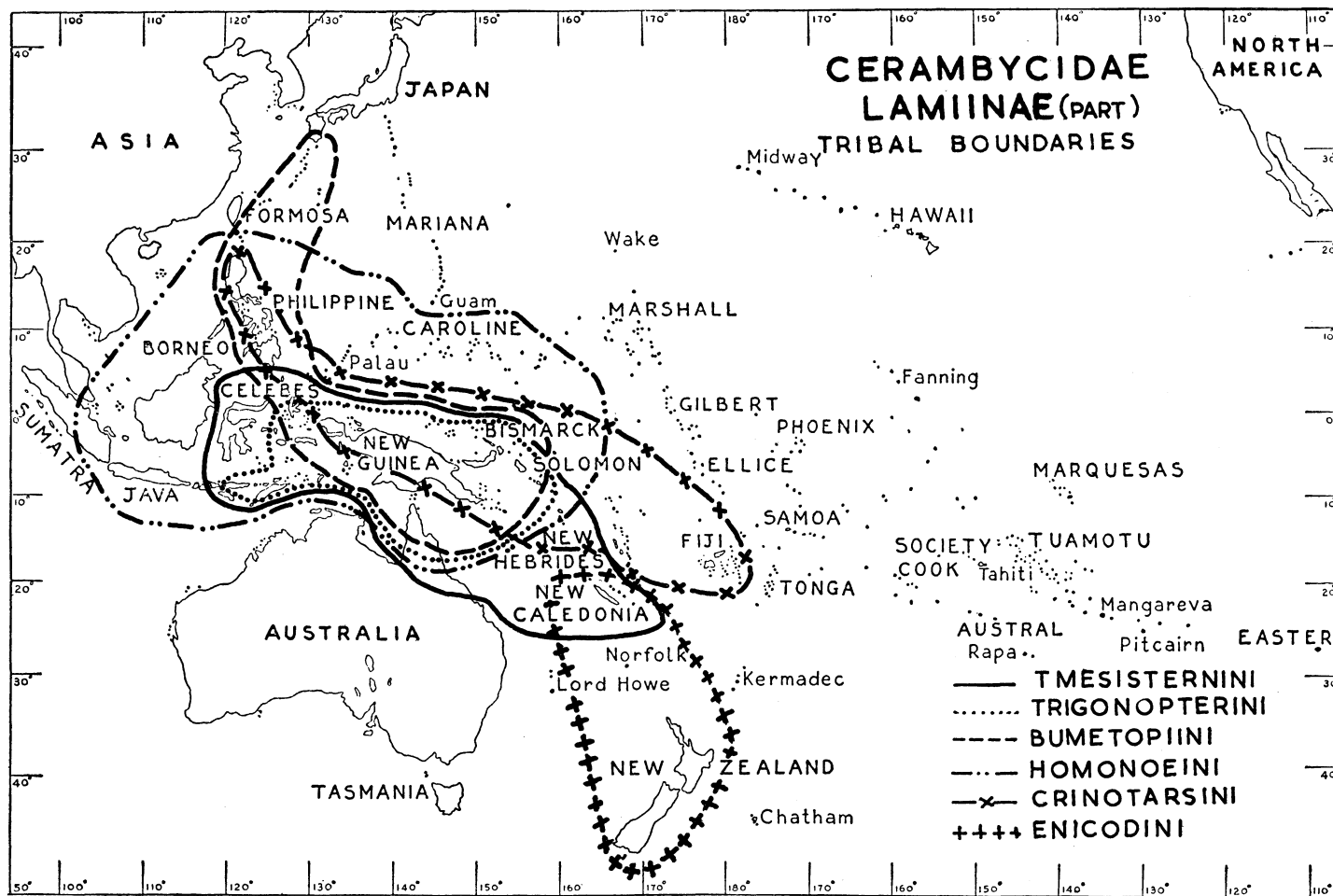


Fig. 31. Outlines of distribution of six tribes of the very distinct Tmesisternini tribal complex (Cerambycidae: Lamiinae), which has several hundred species. Only a very few of these occur west of Celebes or north of the Philippines, and the group has no clear outside affinities except in New Zealand.

lution with some degree of isolation of the Papuan beetle fauna.

The cerambycid fauna of New Guinea is very different from that of Australia. This is partly shown in figures 29 and 30 and in Table 1. There are rather few genera in common except those common to New Guinea and the rain forest areas of eastern Queensland. There is very different relative representation of the different subfamilies. Australia is the only region where the subfamily Cerambycinae exceeds the Lamiinae in number of species. In New Guinea and most other parts of the world, the Lamiinae has several times as many species as the Cerambycinae. In the primitive subfamilies, including the Cerambycinae, at most one-third of the New Guinea fauna is of possible Australian derivation (Gressitt, 1959a). In the Lamiinae the Australian influence is much lower. There are a few ties between New Guinea or Australia and Madagascar on the one hand, and in other cases with South America on the other. There is little relationship between New Zealand and Australia in this family. The relationships between New Guinea and Australia involve different groups from those between New Guinea and New Zealand. There are many genera in common between the Papuan and the Malayan subregions, but also many restricted to one or the other. There appear to be fewer genera in the Papuan subregion, but this may be related to incomplete knowledge.

Table 1. Relative representation of subfamilies of Cerambycidae in Pacific area (figures represent percentage of species; mostly estimates).

	SE Asia	Australia	New Guinea	Oceanic
Prioninae	4	5.5	3.5	3
Aseminae	0.3	0	0	0
Disteniinae	0.7	0	0.2	0
Lepturinae	1	0	0.3	0
Cerambycinae	24	51	20	30
Lamiinae	70	43.5	76	67
Estimate of fauna (number of species)	4000	2000	3000	700

The table shows that there are two subfamilies represented in New Guinea which are absent from Australia, and that the proportionate representation of Cerambycinae and Lamiinae are most strongly contrasted between New Guinea and Australia, of the areas compared. The Lepturinae are represented by a few species in New Zealand.

The Australian cerambycid fauna shows some relationship to that of South America with a few primitive tribes in common (Linsley, 1961). Some of these are associated with *Nothofagus* and some with *Araucaria*. There are also a few indications of relationship between New Zealand and South America and one case also involving *Nothofagus* at least in South America.

#### THE FAMILY CHRYSOMELIDAE

The Chrysomelidae represents a group with a much more limited oceanic distribution than that of the Cerambycidae. It is likewise a major family with over 30,000 known species. On the continents the Chrysomelidae has more species than the Cerambycidae (it is relatively less known than the latter), but on oceanic islands the reverse is conspicuous.

ly the case. The Chrysomelidae are absent from the native fauna in many of the more isolated groups of islands, including the Hawaiian Islands, the Marquesas, the Society Islands (with some question), Mangareva, Tuamotu, Easter, Rapa and others, and probably the Cook Islands. The family is absent from the subantarctic islands (possibly excluding the Falklands and Tierra del Fuego). Chrysomelidae are poorly represented in Samoa, Tonga, Micronesia and the New Hebrides. They are not very well developed in New Caledonia where the fauna is quite disharmonic. In New Zealand they are very disharmonically represented, with some subfamilies lacking and others very weak. In Fiji they are highly disharmonic, but with a considerable development in the Eumolpinae (as in New Zealand).

On the continental tropical Pacific islands the family is extremely well represented in numbers of species, but some subfamilies are absent or weakly represented. This is partly related to dominance of such subfamilies in temperate regions, but in the case of islands like New Guinea and the Solomons it certainly must in part relate to isolation from Asia and/or Australia, which in certain periods must have been greater than at present, as on the old "Melanesian Continent."

Within the Chrysomelidae the spread to oceanic islands is unequal, with some subfamilies absent or rarely present, and others more conspicuous (see table 2). The primi-

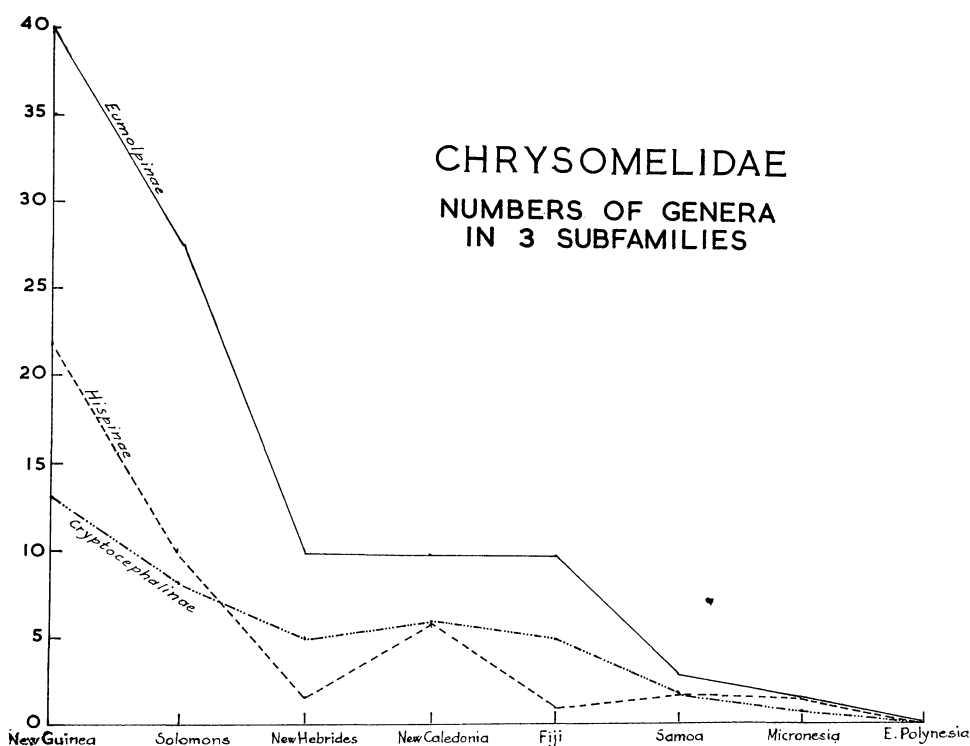


Fig. 32. Graph of respective numbers of genera of Cryptocephalinae, Eumolpinae and Hispinae in the South Pacific.

tive subfamilies (Sagrinae to Megalopinae) are hardly represented, as are the more highly specialized (Hispinæ and Cassidinae). The Eumolpinae is best represented, but the equally large subfamilies Galerucinae and Alticinae have fewer species. The Chrysomelinae, dominant in both north temperate regions and in Australia, is almost lacking from oceanic islands. The same may be said for the fairly large subfamilies Criocerinae and Clytrinae, although Cryptocephalinae does have some representation in Micronesia, New Hebrides, Fiji and Samoa (but not in proportion to its abundance in Australia). Cryptocephalinae are also rather weak in New Guinea, the Solomons and New Zealand, though very well represented in Australia.

The reasons for the disproportionate representation of certain chrysomelids on oceanic islands and the lack of the family on many island groups is probably related to poor vagility. The chrysomelids do not live as long as the cerambycids, feed only on live plant tissues and require live plant food in the adult as well as the larval stage. This greatly limits the vagility in terms of survival during dispersal. Likewise the establishment of chrysomelids on oceanic islands is limited by the food requirements—not merely of living plant tissues, but specific ones as most groups are limited in their host range and some feed only on one family or one genus of plants.

Additional reasons for the poor spread of chrysomelids to islands involve their larval habits. Some, like the Chrysomelinae, Galerucinae, and Cassidinae, have the larvae exposed while feeding on leaves. They are not well adapted to free transport on leaves in wind and are apt to drop from the leaves when disturbed. Others, including at least some of the Eumolpinae and Alticinae, are root-feeders and therefore the larvae are unlikely to become air-borne and if they did, they would be susceptible to desiccation. Perhaps the reason Eumolpinae are so well represented on some islands, is their great abundance on

Table 2. Relative representation of subfamilies of Chrysomelidae in Pacific area (figures represent percentage of species; mostly estimates).

	SE Asia	Australia	New Guinea	Oceanic
Sagrinae	1	1.5	0.2	0
Donaciinae	1.2	0.2	0.1	0
Orsodacninae	0.1	0	?	0
Zeugophorinae	0.8	0	?	0
Synetinae	0.1	0	0	0
Megalopodinae	1.8	?	0.2	0
Criocerinae	7	1.1	1	0.5
Clytrinae	4	0.1	0.5	0.5
Cryptocephalinae	11	28.5	3	10
Chlamisinae	3	?	1	0
Lamprosomatinae	1	?	0.2	0
Eumolpinae	18	14	36	40
Chrysomelinae	7	33	1.8	0.5
Galerucinae	13	9.7	19	19.5
Alticinae	15.5	4.5	24	23
Hispinæ	8.5	0.9	8	5
Cassidinae	7	1.5	5	1
Estimates of fauna (number of species)	5000	4000	4000	400

New Guinea and neighboring areas. They might have been transported as adults, perhaps when hiding in dead twigs or old leaf-mines in windy weather. Others on oceanic islands include leaf-miners of the Alticinae and Hispinae and could obviously have been carried in their mines as mature larvae, pupae or adults. The representation of certain Galerucinae on some islands may relate, again, to their great numbers on the nearby continental areas. The Cryptocephalinae are case-bearers as larvae and are more protected and adapted to free air transport, although the compact nature of the larval cases would reduce their chances of being so distributed.

The relationships of the oceanic chrysomelids are clearly with the neighboring Oriental areas, from the Philippines to the Solomons. There is almost no Australian influence except for possibly a little in New Caledonia. (The two Australian species recorded from Fiji are somewhat questionable). The differences between the New Zealand and Australian representation of chrysomelids is very great. There is little evidence of relationship. Part of the New Zealand affinities are clearly with New Guinea through New Caledonia. There are some South American relationships and more may come to light. Reference to table 2 will show great differences between New Guinea and Australia of the various subfamilies. The Cryptocephalinae and Chrysomelinae are dominant in Australia but weak in New Guinea. Relative numbers of genera in the subfamilies Cryptocephalinae, Eumolpinae and Hispinae are shown for several areas in figure 32.

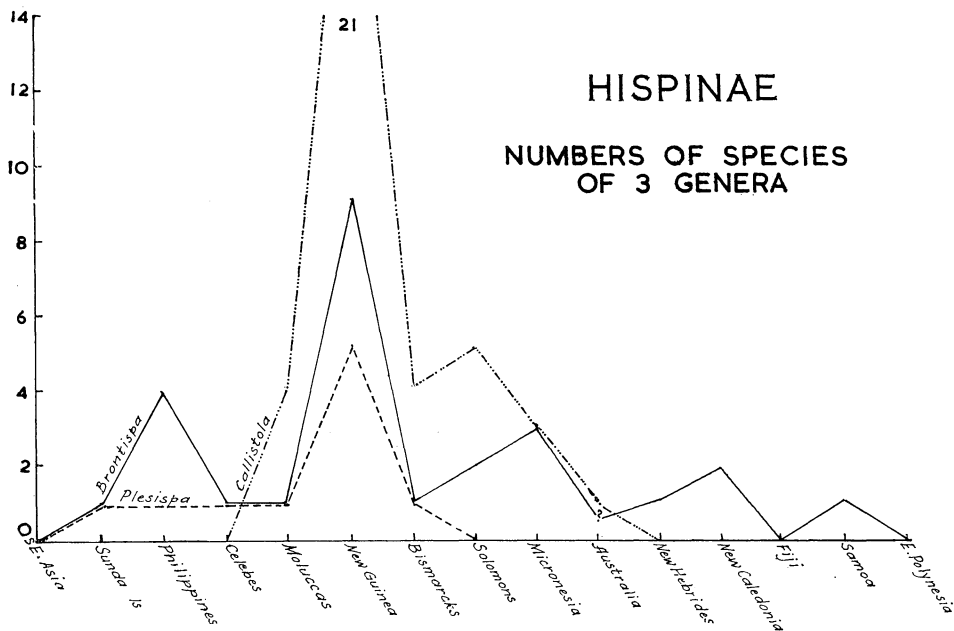


Fig. 33. Graph of numbers of species of *Brontispa*, *Plesispa* and *Callistola* (Hispinae) in Southwest Pacific.

The subfamily Cryptocephalinae (fig. 35) shows the fairly distinct nature of the New Guinea and Australia chrysomelid faunas. Most of the Papuan genera are common to Asia and most of the Australian genera are precinctive. These data are preliminary and fur-

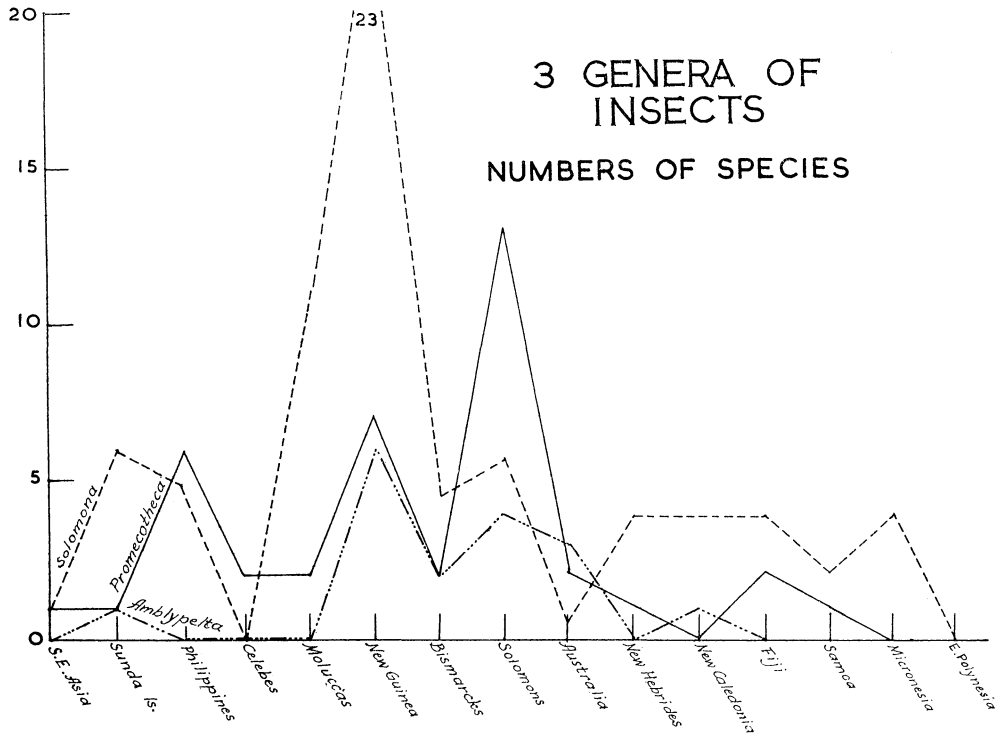


Fig. 34. Graph of numbers of species of *Promecothea* (Hispinæ), *Salomona* (Tettigonioidæ) and *Amblypelta* (Coreidæ) in the Southwest Pacific, showing Oriental relationships and poverty in Australia.

ther study may indicate some modifications of the distribution patterns.

The subfamily Hispinæ (figs. 36–40) indicates a fairly distinctive Papuan element in New Guinea mixed with genera also found in the Malayan subregion or Wallacea. There is little in common between New Guinea and Australia except a few Papuan genera in the rain forest of northern Australia. As shown on the maps, the genera *Brontispa*, *Plesispa*, *Callistola* and *Promecothea* are distributed throughout the Papuan subregion and some spread into neighboring areas. *Plesispa* and *Promecothea* are found in limited areas of northern Australia. *Palmispa* is limited to New Guinea. *Freycinetispa*, *Aulostyrax* and *Calamispa* are limited to the Solomons. *Oxycephala* is limited to the Bismarck Archipelago. *Ceratispa* and *Enischnispa* occur in New Guinea and the Bismarcks, but the former also reaches northern Queensland. *Hispodonta* and *Micrispa* range from New Guinea westward to Indonesia and the latter extends to the Bismarcks. *Dactylispa*, *Di cladispa* and *Hispellinus* occur more or less throughout the continental and sub-continental parts of the Oriental Region; the first two go east as far as the Solomons or Santa Cruz Islands and the first and last south to Australia. The true Australian fauna is poor and consists of only three genera, two of them with one or two species each. *Eurisp*a is moderately developed and extends into southern New Guinea.

In summary, the New Guinea fauna of Hispinæ is fairly rich and distinctive and

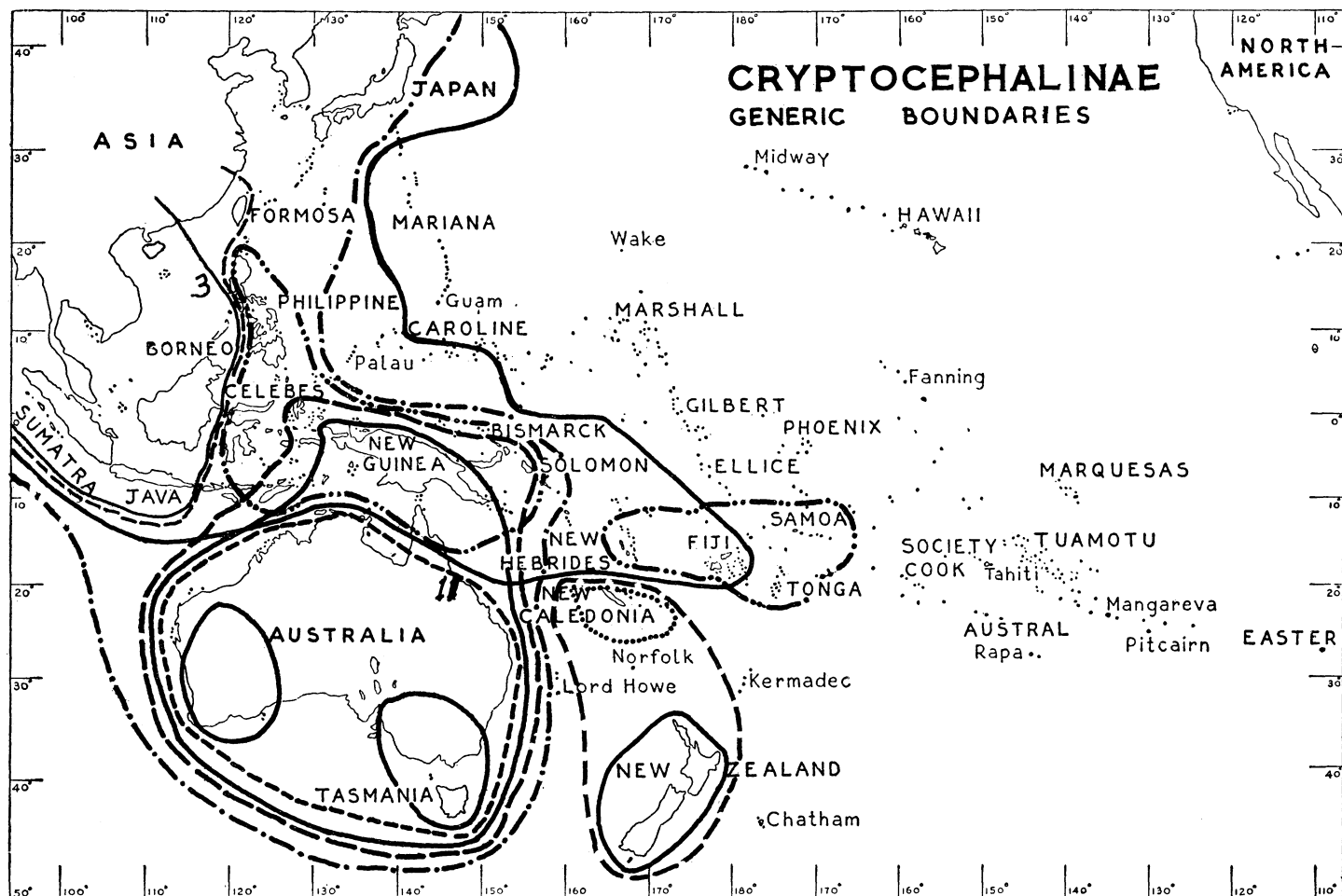


Fig. 35. Generic boundaries of the subfamily Cryptocephalinae, Family Chrysomelidae. Each line represents the range of a single genus, except for three genera limited on the east by the modified Wallace's Line. Two genera are limited to New Caledonia, and eleven to Australia proper (exclusive of North Queensland) besides two with more limited distribution in Australia. Asian genera not reaching Wallace's Line are not shown.



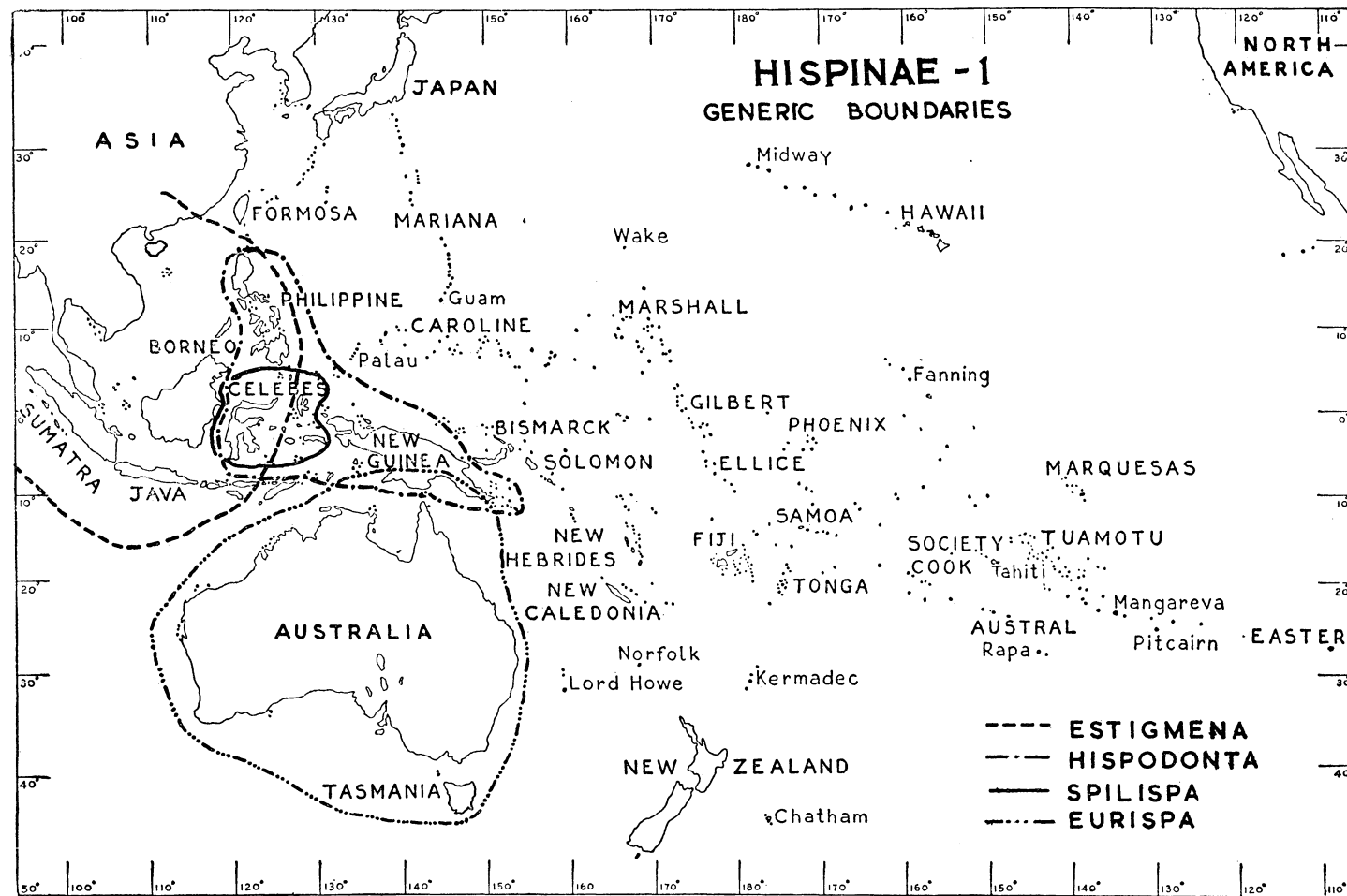


Fig. 36. Map of distribution of Papuan-Polynesian genera of Hispinae-1.

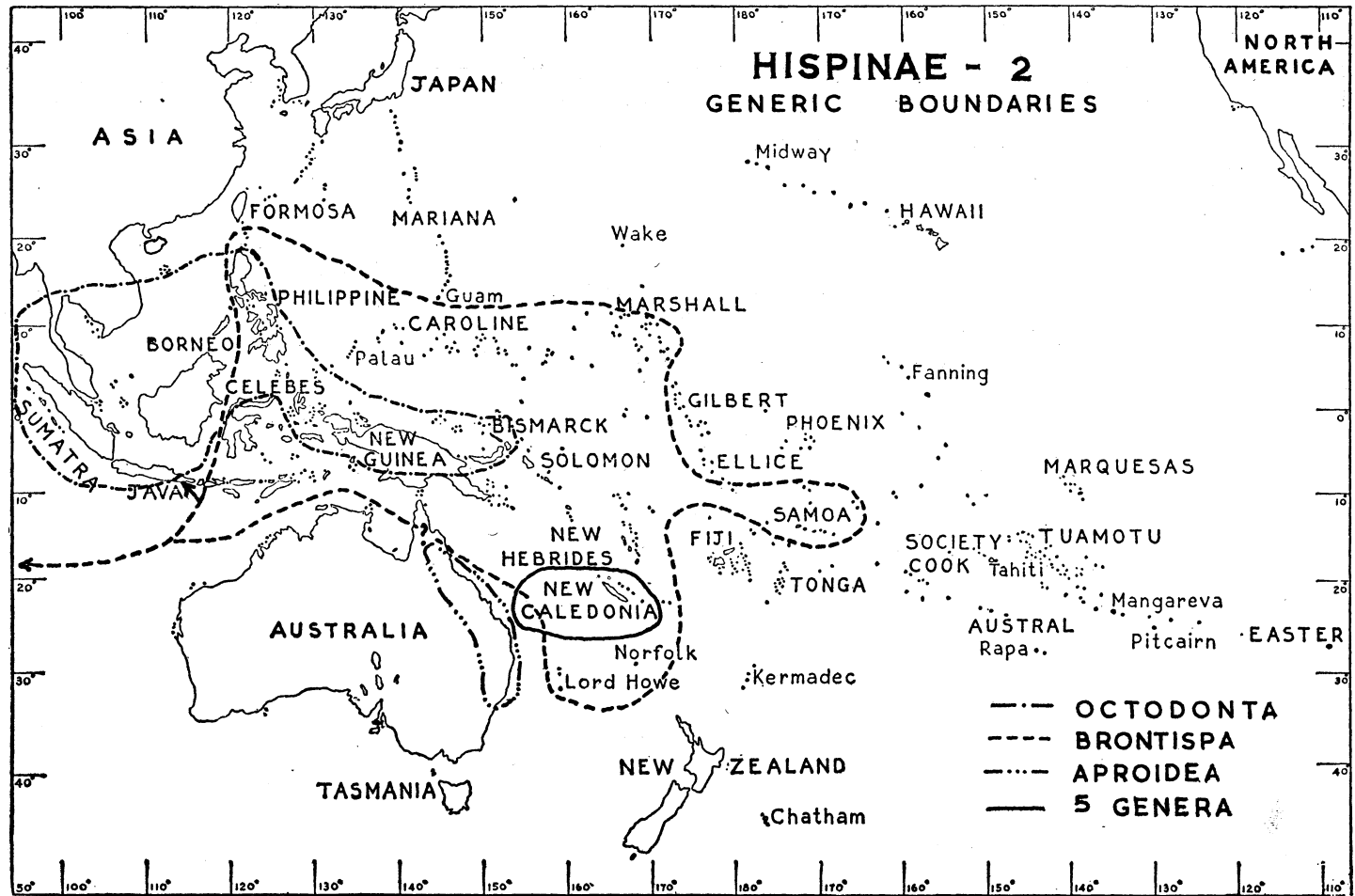


Fig. 37. Map of distribution of Papuan-Polynesian genera of Hispinae-2. The 5 genera limited to New Caledonia are *Caledonispia*, *Stephanispia*, *Teretrispa*, *Torquispia* and *Isopedhispa*.

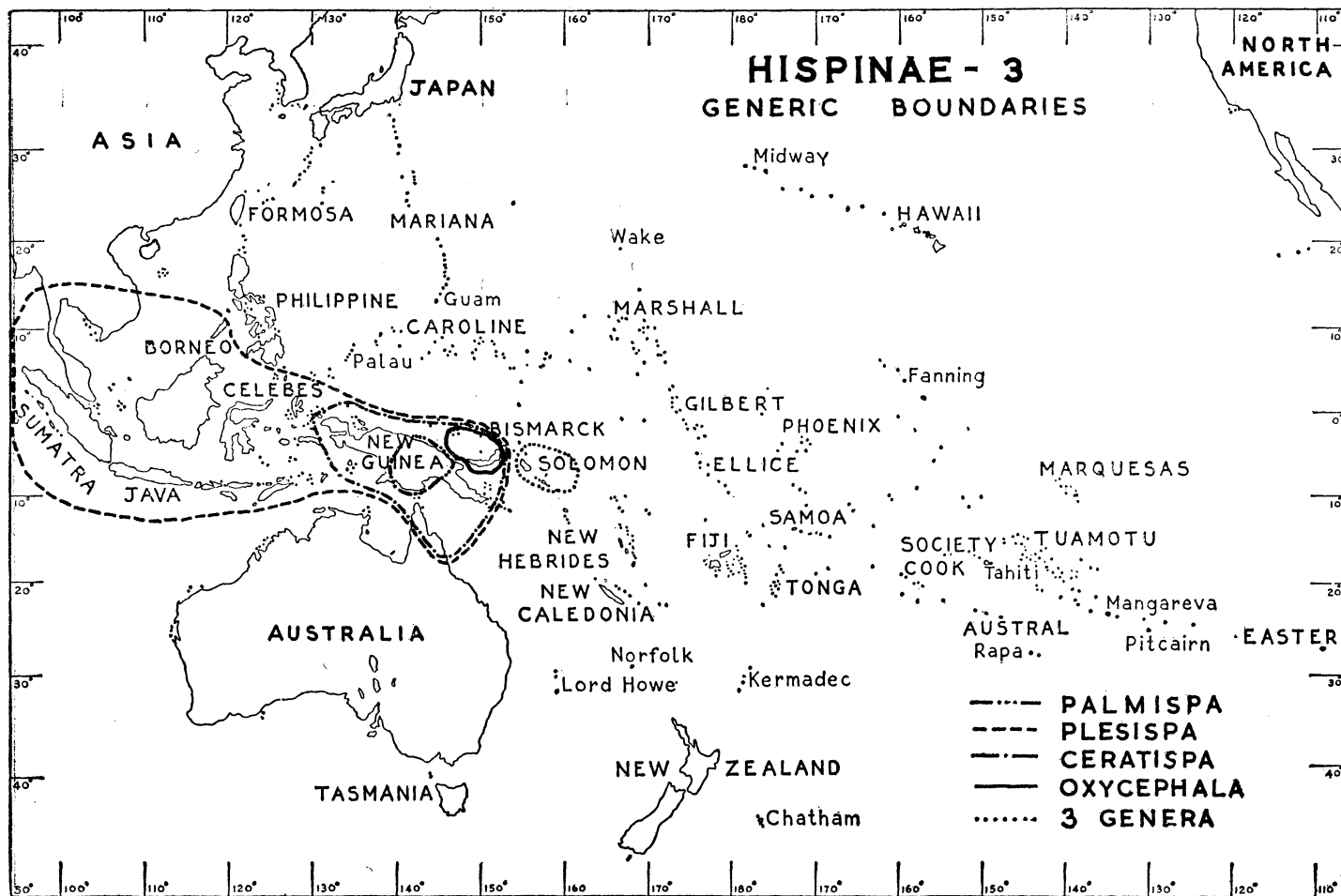


Fig. 38. Map of distribution of Papuan-Polynesian genera of Hispinae-3. The 3 genera limited to the Solomons are *Freycinetispa*, *Calamispa* and *Aulostyrax*.

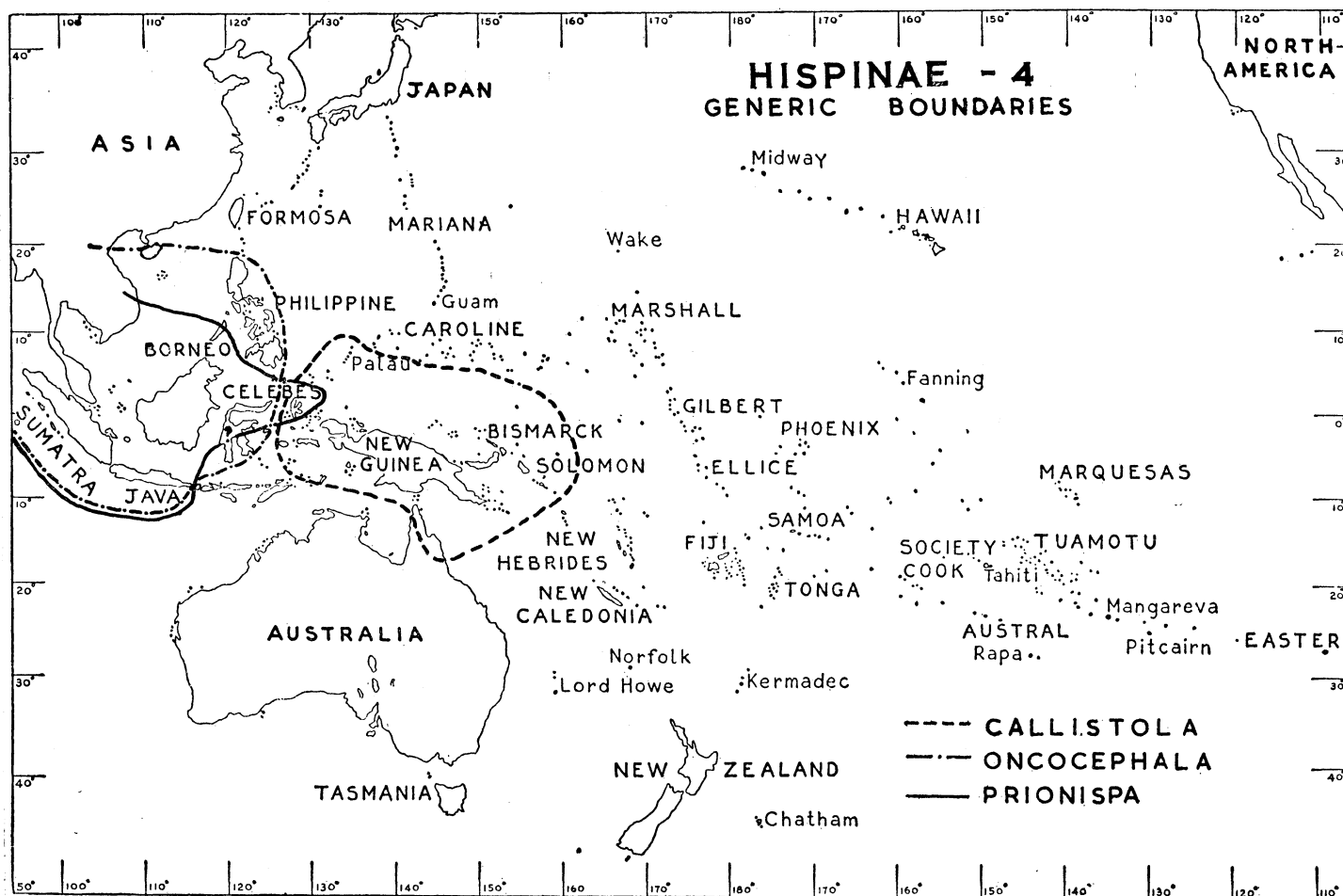


Fig. 39. Map of distribution of Papuan-Polynesian genera of Hispinae-4.

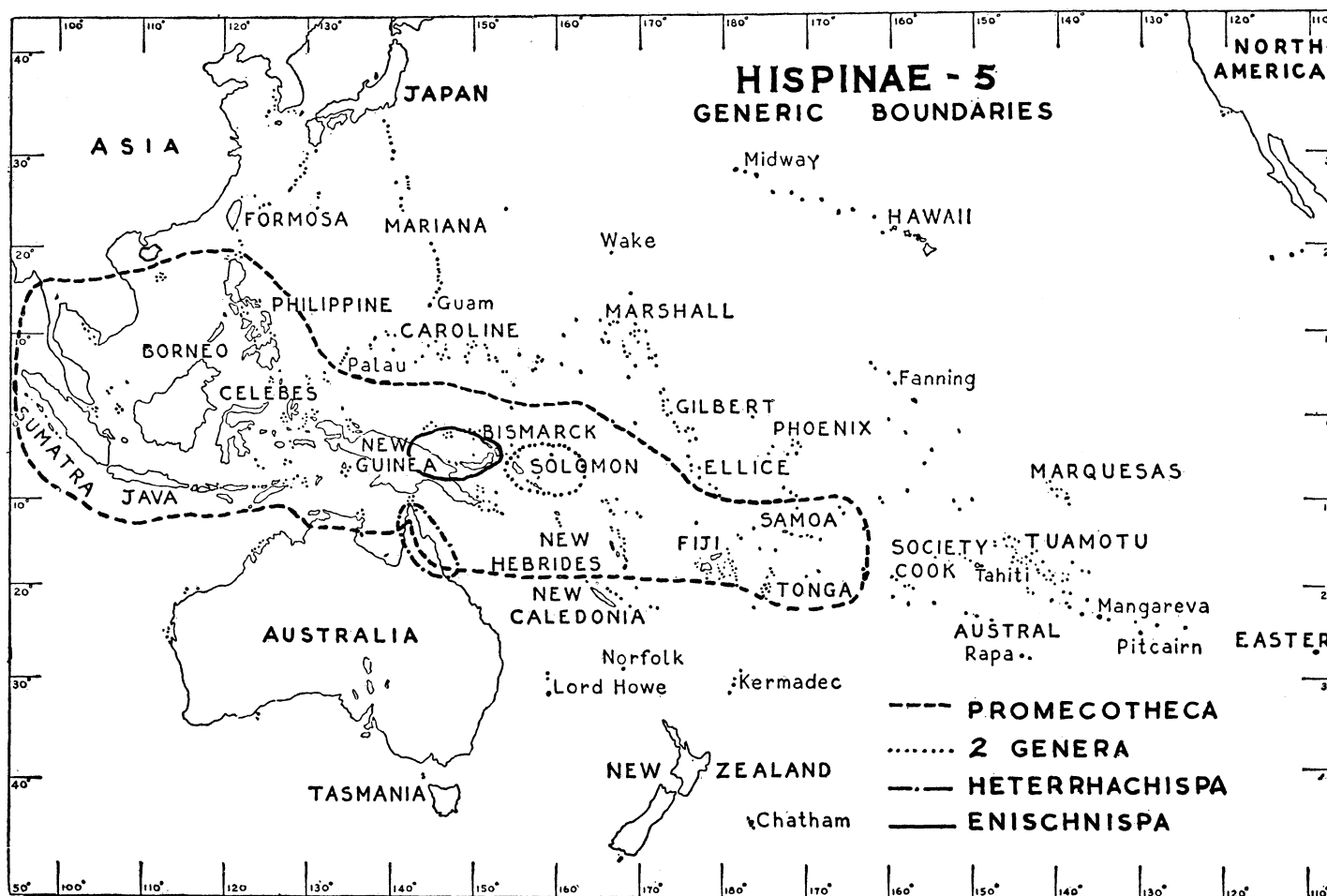


Fig. 40. Map of distribution of Papuan-Polynesian genera of Hispinae-5. The 2 genera limited to the Solomons are *Cyperispa* and *Pharangispa*.

the Australia fauna very poor. New Guinea has fewer tribes and genera than the Malay-an subregion, but has a large number of species.

The Hispinae are rather specific in their host preference and often appear to be quite localized in distribution. They feed almost entirely on monocotyledons. Related genera have similar host plants, but sometimes a genus of beetles will feed on several families of plants. Single species of beetles are often restricted to a single host species or genus.

Table 3. Hosts and niches of New Guinea Hispinae.

	Musaceae	Araceae	Zingiberaceae	Nyssa	Metroxylon	Palmae rattans Cocos	Rhopaloblaste	Areca	other palms	Pandan- aceae Pandanus	Freyinetia	Cyperaceae	Gram- ineae canes	grasses	Dicotyledons
Callispini															
Hispodonta					1										
Eurispini															
Eurispa												3		3	
Cryptonychini															
*Palmispa						2									
Octodonta						2			2						
Brontispa							2	2		2				3	3
Plesispa							2	2		2		3		3	3
*Ceratispa					1	1		1							
*Oxycephala						1	1								
Callistola		(3)								3	3				
Coelaenomenoderini															
*Enischnispa					4										
Promecothecini															
*Freycinetispa											4				
Promecotheca			(4)	4	4	4		4	4	4	4		(4)	(4)	
Gonophorini															
*Aspidispa					4				4						
Gonophora	4		4									4			
Hispini															
Hispellinus														4	
Dactylispa															4
Dicladispa														4	
Platypria															4

Note: Numbers refer to larval niche: 1) between base of the petiole and main stem; 2) among new unfolding leaflets; 3) at bases of leaves; 4) leaf-miners. Asterisk indicates genus is endemic to the Papuan Subregion. Parentheses indicate hosts of Solomon Island species.

These data are summarized in table 3.

The Hispinae in Micronesia, Fiji, Samoa and New Hebrides all belong to genera found in New Guinea. However, the New Caledonia species belong to six genera, five of them limited to the island. The other, *Brontispa*, is found throughout the Papuan subregion, Philippines, parts of Indonesia, islands in the western Indian Ocean, Micronesia, Samoa, Norfolk Island and Lord Howe Island (Gressitt, 1957, 1960a, b). The endemic New Caledonia genera are related to some in New Guinea. The subfamily is absent from New Zealand and the Papuan—New Caledonia tribes are not found in South America. Thus there is no indication of a southern continent relationship in this group as far as is now known.

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