DISTRIBUTION AND ORIGIN OF SOME EASTERN OCEANIC INSECTS[1]

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THE foundations of our knowledge of biogeographical distribution are rooted in taxonomy, but any comprehensive studies must also impinge upon geology, paleontology, genetics and evolution. To interpret correctly the Pacific faunas and floras, the geological, paleontological and biological histories of other insular areas and continents must be taken into account. Thus, in a study of the origin and distribution of Pacific insects, it is necessary to consider all groups of organisms found in the endemic insular faunas.

Much confusion exists in literature and in the minds of students concerning Oceania and its inhabitants. Many authors feel that the Pacific is shrouded in mystery, and they begin their studies biased and under false impressions.

I. GEOLOGICAL FOUNDATIONS

Though much of the geological research in the Pacific basin is in a reconnaissance stage, the major structural and physiographic features have been outlined, and for some of the islands detailed studies have been completed. In general, it may be said that in so far as they are related to biological problems, the fundamental geological factors, topography, climate, soil, the indigenous floras and faunas and proven human immigrations are fairly well known. It may be assumed that most geologists know

[1] Excerpts from an address delivered to The Pacific Science Survey Group of the Hawaiian Academy of Science, University of Hawaii, Honolulu, March 21, 1940. Unless otherwise stated, the opinions expressed in this paper are principally those based upon the study of insects. My sincere thanks are due to several workers who have offered constructive criticism and especially to Dr. H. E. Gregory for his aid in editing the original manuscript.

more about geology than do most biologists, and therefore much of the controversy between biologists and geologists in regard to the extent, distribution and age of lands and seas could be avoided if the biologists would be more careful in their assumptions and give more credit to the work of geologists.

As the result of geological study, it is known that the Pacific basin is underlain by heavier rocks than are the continents bordering it; that in the continents lighter rocks rest on heavier under layers; and that continental shelves extend for various distances under shallow coastal waters and then terminate abruptly at the edge of the deep water which is remarkably uniform at 12,000 to 14,000 feet deep in the true Pacific basin; that the volcanoes now above sea level have arisen from great depths and have brought with them heavy basalts and no light rock, and that in no islands in the eastern Pacific basin have true continental rocks been found. So far as it is known to geologists, the only pre-existing extensive land masses in the tropical Pacific since the rise of modern floras and faunas are those west and north of Australia and on the New Guinea-New Caledonia-New Zealand axis, possibly extending eastward to near the Tongan trough in the neighborhood of Fiji. There is no geological evidence to indicate the existence of any large land masses east of Tonga.

However, in spite of the geological evidence, some biologists accept the dictum of Meyrick,[2] who writes, "A rise of 12,000 feet in the sea-bottom of the South Pacific is required to show these results, but I entertain no doubt that such an elevation must have existed since the Eocene period, because it is absolutely the only explanation possible" to account for the distribution of a genus of moths represented by species in Australia and southeastern Polynesia. Meyrick nonchalantly raised over 2,000,000 square miles of land to account for the distribution of a few moths and sank it into oblivion, leaving no trace of

[2] *Trans. Ent. Soc. London*, 24: 271, 1926.

the major diastrophic action necessary to raise and lower such a block of sea-bottom.

So many continents and land bridges have been built in and across the Pacific by biologists that, were they all plotted on a map, there would be little space left for water. Whenever a particularly puzzling problem arises, the simplest thing seems to be to build a continent or bridge, rather than to admit defeat at the hands of nature, or to consider the data at hand inadequate for solving the problem. Most of the land bridges suggested to account for the distribution of certain plants and animals in the Pacific create more problems than they solve. If the central[3] and eastern Pacific ever included large land areas and land bridges, there should be some indication of the consequent peculiar development of the faunas and floras, but there is no such evidence.

As I see the problem, the eastern oceanic insect faunas could not have become what they are with any great land areas or bridges in the central Pacific; their very character precludes those possibilities. The known groups are the results of overseas sifting; there are too many groups lacking for any other means of dispersal to have been involved. If biologists want to find out the ages of their insular floras and faunas, let the geologists tell them the probable ages of the lands upon which they exist; then, and then only, can they begin to compute the ages of locally developed groups with some degree of accuracy.

Geologists argue among themselves as to how atolls were formed, but apparently few of them advance the thesis that they may be formed by several different methods; some may be caused by subsidence, some by elevation, others by glacial control, others by marine planation. Geologists, like biologists, often fail to take into consideration the inherent variability of nature and

[3] For our purposes, it is convenient to consider those islands east of the International Date Line to Easter Island as being in the central Pacific, but they belong to *eastern Oceania,* because Oceania is a term applied to the *islands* of "Polynesia, Micronesia, Melanesia, Australasia and Malaysia" (Century Dictionary).

search for one theory of explanation of natural phenomena. It is probable that much light could be thrown upon the atoll problem by a comprehensive study of the underlying framework of the atolls of the Tuamotu archipelago; some of those islands are large enough to enclose the entire islands of Tahiti and Moorea with room to spare. Present knowledge of the great atolls of eastern Polynesia rests largely on conclusions reached by geologists who have never seen them.

Though the evidence for former extensive land masses in the Pacific basin is lacking, it is probable that high islands other than those represented on maps existed in past ages. There are numbers of volcanic cones below sea level, some of which come close to the surface.[4] There might well have been some high islands between Hawaii and the south and western Pacific. Such islands, when above water, may have been used by plants and animals as stepping stones. There have been shifts of sea level of at least 1,000 feet in Hawaii; such shifts in the south Pacific would change the appearance of the map. Some fast constructions seem necessary to account for such steepsided, lofty masses as isolated Wake Island, which arise abruptly from great depths, and when it is recalled that the Mexican volcano, Jorollo, burst through a level plain and rose 1,600 feet in a single night, it is easy to think of similar occurrences and great changes in the central Pacific. Such phenomena are not, however, inconsistent with the belief in a relatively stable sea bottom. At least for eastern Oceania the distribution of insects could have been accomplished with little change in the present proportions of land and sea.

II. Dispersal

It might be said that the reliable knowledge of the distribution of oceanic insects consists of the facts that they

[4] For example, submarine mountains rise as much as 13,500 feet about 140 miles S.S.W. of Honolulu; Raita Bank has a shoal area about 25 miles long, and in some places it has only about 50 feet of water over it; there is a submarine range of high mountains about 200 miles southwest of Necker Island.

occur on various islands and have been derived from certain related faunas of other islands or continental areas. It is not known how the ancestors of each group of insects reached their present habitats. However, to me the crux of the problem is not so much how the various groups have been spread, but from what areas they have been derived and to what areas they have been distributed. Insects do inhabit all habitable insular groups no matter how great the isolation, and, therefore, they possess some advantages that better fit them for selection by agents of overseas distribution than do some other animals. It seems appropriate to speak of a Polynesian flora or a Polynesian fauna, not with the understanding that this fauna or flora has originated in Polynesia and is thus characteristic of it alone, but rather that the inhabitants of the area are the descendants of those which the selective agents of distribution have dispersed. This statement does not preclude the possibility of later local developments within the area, however. Many of the insect genera inhabiting the central Pacific are flightless, and because they inhabit islands separated by hundreds of miles of open sea, their distribution is obviously independent of their ability to walk. These insects have crossed, and undoubtedly still are crossing, large bodies of sea, not because they have wanderlust, but because of forces beyond their control—forces undoubtedly adverse to their general well-being. It is in the methods of transport that so many students disagree and so many hypothetical data are advanced. In my opinion, the ways and means of dispersal is a field unsuited for dogmatic statements. It is highly improbable that dispersal can be assigned to any one factor; it is the result of a combination of factors acting over long periods of time, and different groups of organisms may be dispersed by diverse methods. Chance and time accomplish much, or, as Herodotus put it in 400 B.C., "If one is sufficiently lavish with time, everything possible happens."

The three principal means of transport generally advanced are: marine drift, wind and aid from other organisms.

Marine drift. Thousands of bottles thrown overboard from vessels sailing the Pacific have given a pretty good idea of the set of normal contemporary currents. Logs from northwest America are washed up on Hawaiian shores, and fish-net floats from Japanese waters are brought to these islands by the currents. Bottles thrown into the sea off the Central American coast or south of Hawaii drift to the Philippines or to islands between the Solomons and Borneo, and some of these bottles make a speedy journey. These are the normal currents of to-day. In general, however, the endemic insect faunas of the south Pacific lack American elements, and, therefore, these normal currents can not be looked upon as the agents responsible for their distribution. Probably the distance and time factors involved eliminate the possibility of the introduction of an American element into the south Pacific by normal drift; but what about abnormal currents that flow opposite to the normal currents? Currents set up by cyclonic disturbances and anti-trade winds are quite different from normal drift.

There are numerous records of live animals being transported for considerable distances by sea drift. Large rafts of debris have been seen floating out to sea from the rivers of Borneo, Fiji and other islands. I have seen large trees with branches riding high out of the water floating out to sea after a Tahitian storm. A Solomon island crocodile came ashore in Fiji and killed several natives before it was destroyed. I found a live ant on a floating leaf in the Korokoro sea several miles from land. Wheeler[5] described a new species of ant from a colony that was carried from Brazil to San Sebastian Island in a floating log. A fur seal came ashore on the tropical island of Mangaia in the Cook group. Dr. C. H. Edmondson recently gave me a well-developed, living larva of a longhorn beetle, which he took from a dead

[5] *Psyche*, 23: 180, 1916.

mangrove tree found afloat in Hawaiian waters. A living boa constrictor floated about 200 miles to St. Vincent Island on a tree. This list, which could be greatly enlarged, is indicative of possibilities.[6]

I believe it probable that part of the insect faunas of the central Pacific islands may have been derived from ancestors that drifted with marine currents. The larger part of the faunas of high oceanic islands[7] are made up of weevils, especially cossonine weevils, which are quite resistant to wetting. I do not believe, however, that this method of transport accounts for the dispersal of the bulk of the genera. It seems improbable that certain land snails, for example, could be so transported. The great difficulty in the dispersal of animals from one locality to another on floating vegetation appears to be not so much dependent upon their being cast adrift and being transported, but rather in their landing in another locality and becoming established in a foreign and perhaps hostile environment. Sea beaches upon which flotsam is cast are not usually favorable environments for the establishment of most terrestrial organisms.

Winds. Normal winds are usually not strong enough to transport even small insects for significant distances across open bodies of sea. The trade winds of the south Pacific blow from the east, away from the American continent. Hurricanes, however, have often swept from the west, crashed through insular forests, stripping trees of their leaves and twigs, churned across the sea, and passed over the islands eastwardly of their origins. It is these abnormal winds which I believe have accounted for the distribution of the bulk of the insects of the south central Pacific.

There are numerous records of the transport of insects and other animals by wind. Hundreds of moths were taken at sea almost 1,000 miles from their homes in the

[6] Additional notes in summary form may be found in Hesse, Alee and Schmidt, ''Ecological Animal Geography,'' 1937.

[7] Oceanic islands are either coralline or volcanic; continental islands contain metamorphic or light rocks.

Cape Verde islands. Large numbers of dragon flies were driven by strong winds 700 miles from Sumatra and Java to Cocos-Keeling island. De la Torre[8] has shown that certain Cuban land snails have been carried to Florida by hurricanes; he goes so far as to say that he can plot out colonies in the exact paths of known hurricanes.[9] Mosquitoes and other insects are regularly carried almost 100 miles by wind from Cuba to Rebecca Shoal light. In 1830 Kotzebue recorded swarms of butterflies and land birds about his ship during a heavy wind while he was between the Ellice and Gilbert islands. Land birds are frequently blown far by storms and appear in unexpected places. A Chinese cuckoo was recently blown to Wake island by a westerly storm of several days' duration. A pair of North American kingfishers, after probably being blown out to sea, arrived by flight in Hawaii and were observed fishing for some time before they disappeared. In Hawaii, winds blow wingless mealybugs about from one pineapple field to another.

The extensive studies recently made by P. A. Glick[10] of the distribution of arthropods in the air provide much pertinent information. Glick's work covered a period of five years with over 1,000 hours of airplane trap flights made. Glick concludes that "some of the most dangerous insect enemies of cultivated plants and the carriers of dreaded diseases of man and animals spread to distant places with the aid of air currents." Not only were thousands of insects taken at various altitudes up to 14,000 feet, but spiders and mites, wingless creatures, were not uncommonly captured. One spider was taken at 15,000 feet. Some opponents of dispersal by wind say that certain insects are weak fliers and are therefore not capable of traveling great distances on the wind. These weak fliers are just the insects which Glick found to be

[8] See note by Thone, *Science,* 86: 2232, suppl. p. 8, 1937.

[9] W. J. Clench discusses hurricane distribution of land snails in the Bahamas in *Bull. Mus. Comp. Zool.,* Harvard, 80 (14): 489, 1938.

[10] *U. S. D. A. Tech. Bull.* 673, 1939.

the most abundant in the air and which were carried to the greatest heights. Heavy-bodied, strong-flying insects were not taken high in the air. Not only were winged adult insects collected, but larvae, nymphs and wingless adult insects were captured as high as 14,000 feet. Glick says these wingless forms are all at the complete mercy of the upper air currents. F. C. Fraser,[11] speaking of the widespread damselfly, *Ischnura aurora* Brauer, which is found from western India to southeastern Polynesia, says, "In Coorg I have often watched this species taking flight after emerging, and have followed it with my eyes as it rose almost perpendicularly in the air, until finally lost to sight at a great height. Such a frail, tiny insect floats like a piece of gossamer, and is borne by the upper air currents to immense distances. In fact its very weakness becomes a source of strength, enabling it to spread over, and populate a vast area." Glick found that convection currents were responsible for carrying large numbers of insects high in the air, and that, during periods of strong winds, more specimens were captured than during calm periods. It appears that convection currents may carry insects into the air, even as high as the anti-trade-wind zone. Upon attaining such high elevations considerable distances could be traversed. Winds with high velocities are not uncommon over the Pacific. It may be noted that the endemic Hawaiian spider fauna is made up only of those groups that can be wind-borne; all other groups are wanting.

Dispersal aided by other organisms. Aid in the dispersal of plants and animals by other organisms, principally birds and mammals, has received much attention, and many factual data have been accumulated.[12] There is no reason to doubt such dispersal in continental areas, but there appears to be considerable reluctance to recog-

[11] *Insects of Samoa,* 7 (1): 23, 1927.

[12] Extensive discussions bearing on this subject may be found in many works, including H. N. Ridley's "The Dispersal of Plants throughout the World," 1930; H. B. Guppy's "Plants, Seeds and Currents in the West Indies and Azores," 1917, and Darwin's "Origin of Species," chapter 12.

nize the possibility that dispersal aids in overseas populating of islands. However, such objections are untenable in the face of abundant data.

Pseudoscorpions regularly attach themselves to insects and are carried far and wide in this manner. I took a live bark beetle from deep among the feathers of an owl in the highlands of Fiji. The owl is a wide-ranging creature. Perkins records finding a living land snail attached to a Hawaiian bird. A mallard duck shot in the Sahara had snail eggs on its feet. Fresh-water snail eggs have been found on strong-flying water beetles, and many small animals are transported from one body of water to another by insects. Some sea birds nest in mountain forests among native vegetation and might be expected to serve as agents of dispersal. Shearwaters and tropic birds nest as high as 4,000 feet or more in the forests of some islands. In the interior rain forests of Samoa, I have observed white-tailed tropic birds alighting time after time on the branches of large trees covered with epiphytes and have seen them nesting in the crotches of the trees and in *Asplenium nidus* ferns. As graceful as these birds are in the air, they are most clumsy when on trees. When they alight, they beat the surrounding foliage with their wings and claw it with their feet. These habits appear to fit them admirably for having insects, land snails and seeds lodge on their bodies and thence be carried to new localities by the wide-ranging birds. Some sea birds burrow in soil or nest on the ground, and it appears to me quite possible that insects, seeds and even land snails may become attached to them. There is a well-known Boreal element in the endemic Hawaiian flora and, to a lesser degree, in the Hawaiian fauna. I wonder what the golden plover or migratory ducks bring with them on their annual visits from the north, and what they bring back with them after their sojourns in the islands to the south. According to E. H. Bryan, Jr. (personal communication) more than 40 species of birds that are either strays or migrants from

North America are seen commonly or rarely in Hawaii. Of these, five in the plover and sandpiper families and two or three ducks are regular migrants. Plovers have been known to fly about 3,000 miles in ten days. It appears to me that the rôle played by birds in the dispersal of the terrestrial floras and faunas of eastern Oceania may be greater than is recognized at present.

One of the most conspicuous features of the insect faunas of the eastern oceanic islands is the entire absence of some large groups, families and orders common to all continents. They have been eliminated by the selective agents of overseas dispersal. Scarab beetles comprise one of the most dominant groups of all the continents, yet there is not a single native species on the central Pacific islands. Most of them are subterranean in their larval stages, and most are strong fliers. The family is greatly developed in western Oceania. To my knowledge, the only native beetles that have true subterranean larvae that occur on the islands of Oceania east of Samoa belong to the flightless genus *Rhyncogonus*—but the eggs of these weevils are deposited on leaves. The absence of endemic Chrysomelidae, or leaf beetles, from Oceania east of Samoa is difficult to explain; they are extensively developed in the western Pacific. With few exceptions, the entire endemic beetle fauna of southeastern Polynesia is composed of small, predominantly flightless species that breed in dead twigs, dead leaves or in or under dead bark, and these forms are more extensively developed than any of the other groups of terrestrial animals in that region.

We will do well to keep in mind Darwin's remark, "How ignorant we are with respect to the many curious means of occasional transport."

III. Distribution

The distribution of oceanic insects is not so simple and orderly as it may first appear. It is complex. There are many anomalies, many internal and local developments, many puzzling problems. However, careful study of enough groups will result in obtaining an average distribution that does show a definite pattern.

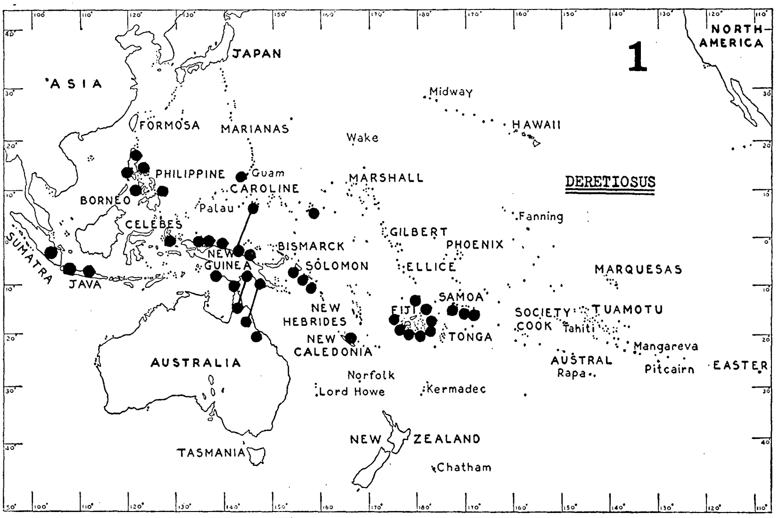
In the belief that the desired information can be more satisfactorily conveyed to the reader by diagram than by an expanded discussion in this section, I present here a few charts from a series I have prepared to show some typical distributions of oceanic insects.

IV. Origins of Insular Species

Although much has been written about insular speciation, little is known concerning the actual mechanisms at work or the speed of evolution among insular faunas. I have read remarks to the effect that no factors not found on continental areas exist on islands to account for any more rapid speciation. I believe that such statements need close scrutiny. One must see islands and actually work among their floras and faunas to appreciate the special conditions surrounding their populations. But even given the opportunities, some biologists are misled and arrive at false conclusions. It appears difficult for students unfamiliar with oceanic islands to understand the diversity of ecological situations that may exist in a small area.[14] Different sides of a ridge may present very different environmental conditions. Within a distance of two to five miles one may pass from a low-lying, hot, dry region, in which xerophytic vegetation thrives, to a cool rain forest rising several thousands of feet into the wet, windswept cloud zone. Such diversity in habitat must exert a great influence on the development of the biota and may have been a major contributing factor to the extensive speciation found in the tropics. Geneticists have not yet studied indigenous oceanic populations in detail in the field.

One of the characteristics of the insect faunas of the

[14] For those interested in additional information, reference can be made to the First Progress Report of the Territorial Planning Board, published in Honolulu in 1939. Plates 8, 16–23, 50–56 are maps that give data on rainfall, soils, climate, etc.



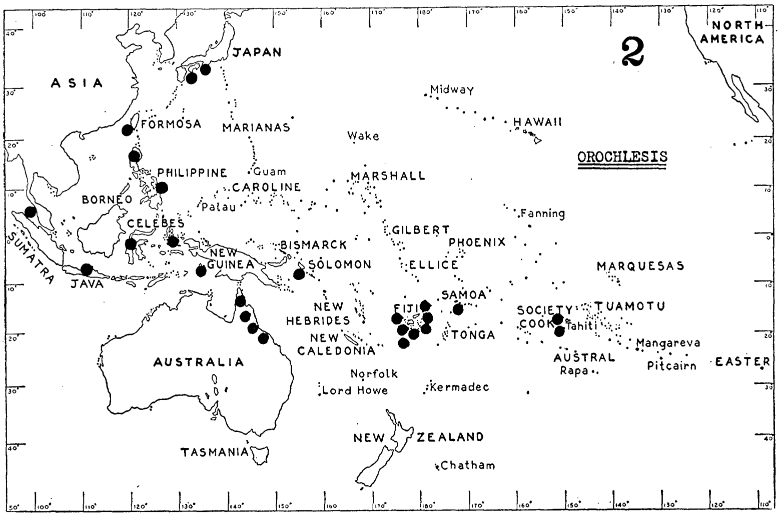


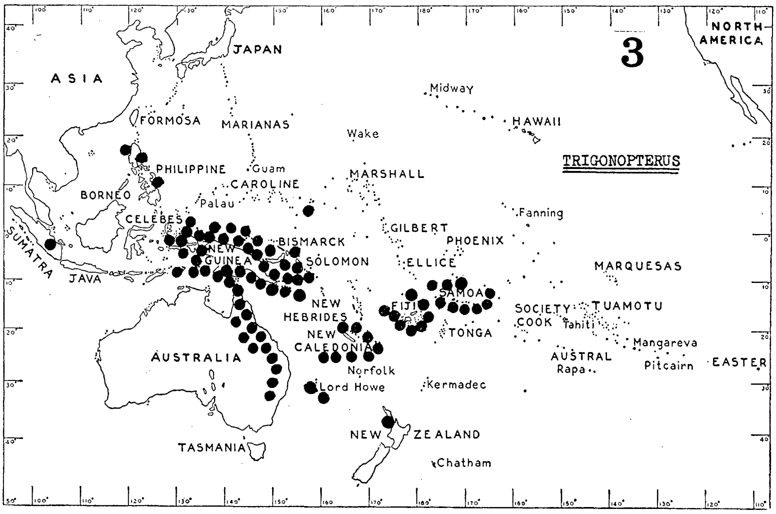
FIG. 1. Known distribution of the species of *Deretiosus* (Coleoptera, Curculionidae). Each dot indicates a species; those dots connected by lines indicate that the same species is found in two localities separated by sea. In this and the other charts, the dots show only the approximate position of the species or refer to the island group in which they occur, because the small size of the map does not permit the exact localization of each species. This chart is typical of the distribution of many Indo-Pacific insect genera, charts of whose distribution could be superimposed upon this chart with but minor

normal[15] high islands of eastern Oceania is that they harbor comparatively few genera that have a disproportionately great number of species within many of those genera. For example, the weevil subfamily Cossoninae averages about 2.5 species per genus in America north of Mexico, but in Hawaii there are more than 8 species per genus. Casey gave the average of North American species of Cerambycidae at 3.0 to the genus; there are more than 10 to the genus in Hawaii. One genus represents the coleopterous family Aglycyderidae (Proterhinidae) in Hawaii, but that genus contains 175 described species. *Hyposmocoma,* a genus of small moths, contains about 220 described species in Hawaii. There are more than 170 described species of the hymenopterous genus *Sierola* in Hawaii. There are more species of *Drosophila* in Hawaii than in all North America. Hawaii has an area of only about 1/1200 the size of North America but, according to Dr. C. Montague Cooke, Jr., it is probable that there are about as many land snails in Hawaii as there are in North America. I should emphasize the fact that such explosive speciation is not confined to insects and land snails, but also call attention to the similar development of genera, species and subspecies among Hawaiian drepanid birds, the birds of the Galapagos, and among plants. Among the islands of the Indo- and Austro-Malayan subregions there is said to be about 250 kinds of *Rattus* as against 3 for North America. On the other hand, there are genera which have not developed species complexes in the islands. *Parandra,* for example, is considered one of the most primitive genera of the Cerambycidae (longhorn bettles) and is world-wide in distribution. It has only one endemic species in Hawaii and only one in Fiji. I see no reason for considering that

[15] By normal I mean the high forested islands in contrast to atolls, newly emerged volcanic cones and low, barren or semi-barren remnants of islands.

differences in extent of distribution. The species of *Deretiousus* are fully winged and capable of active flight; the larvae live in dead wood.

FIG. 2. Known distribution of the species of *Orochlesis* (Coleoptera, Curculionidae). All the known species are active fliers; their larvae are found in dead wood.



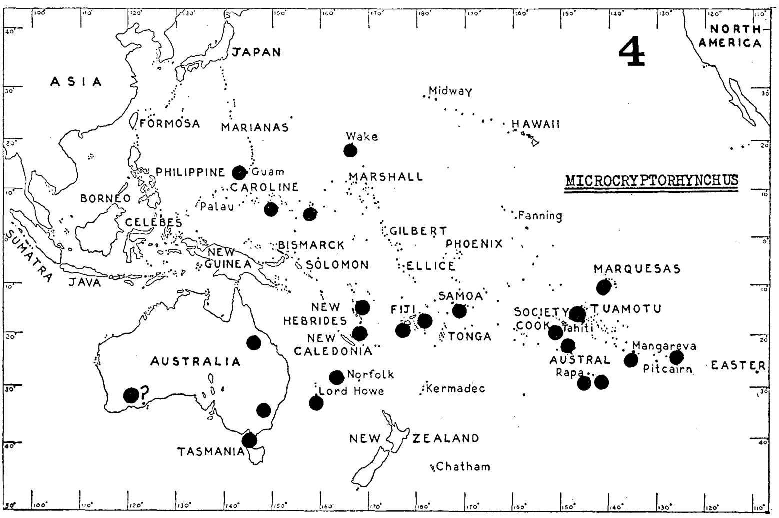


FIG. 3. Known distribution of the species of *Trigonopterus* (Coleoptera, Curculionidae). All the species are fightless; I believe that the larvae are dead wood feeders.

FIG. 4. Known distribution of more than 150 species (some undescribed) of *Microcryptorhynchus* (Coleoptera, Curculionidae). Most of these tiny beetles are less than 2 mm long and all of them are fightless; their larvae live in dead twigs, limbs and fern fronds. Each dot on the chart indicates the presence of the genus in a given locality, but does not indicate the number of species present in each region. For example, there are 43 described

the ancestors of the Hawaiian *Parandra* arrived in Hawaii at any later date than did the ancestors of the *Plagithmysus* group; yet the *Plagithmysus* group has split up into six groups called genera and no less than 95 species. I do not know why *Parandra* should not have followed the course of *Plagithmysus*—but there is probably a good reason, hidden at the moment, which some geneticist might interpret in the future. The rate of evolution is certainly subject to considerable variation among and within different groups of insects.

In the ages past great floras and faunas were developed, and they flourished and waned. When new groups, such as the Sequoias, dinosaurs and marsupials appeared, they developed and spread vigorously, but they have all dwindled or disappeared. The marsupials found a safe haven in insular Australia and have persisted there and developed up to the present time. Pacific insular faunas have essentially a similar story. When certain vertebrates originated, they had little opposition and became widespread and diverse in form. When competition arose, their ranges were cut down until they were restricted to certain areas or became extinct. In the central Pacific islands, the insects have followed a similar course. When a given species arrived that was destined to split up, it found quantities of unused food, few or no competitors, a variety of unoccupied ecological niches, and it expanded rapidly and divergently until a typical large species complex was formed. If a parasite arrived later, its path could be similar, because the same situation of food and competition existed, and the parasite could take the same explosive course that was taken by its host. These complexes prevail in the lower as well as the

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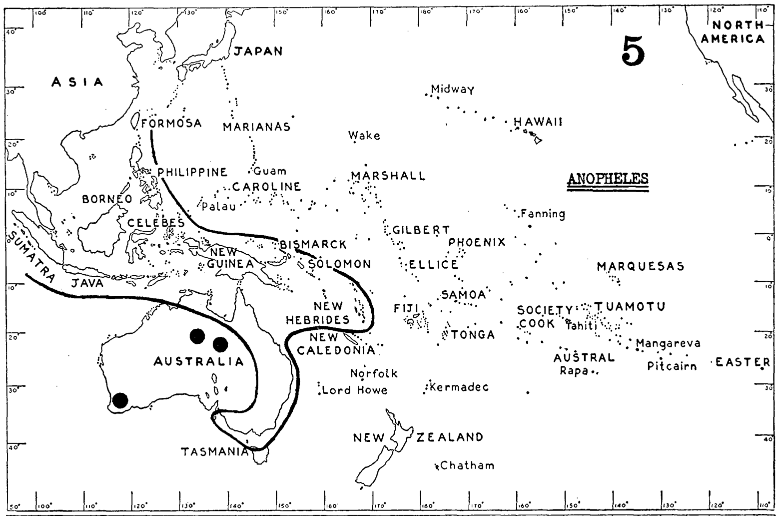
species in Rapa. Knowledge of the distribution of this genus has expanded greatly in the last few years. If, for example, Bishop Museum's Mangarevan Expedition of 1934 had been sent out ten years earlier to Rapa alone, a very different interpretation of facts might have been made by an unwary worker, for it could have been shown that there were 43 species on Rapa, three in Australia and none elsewhere. Some writers have based broad conclusions on such incomplete data.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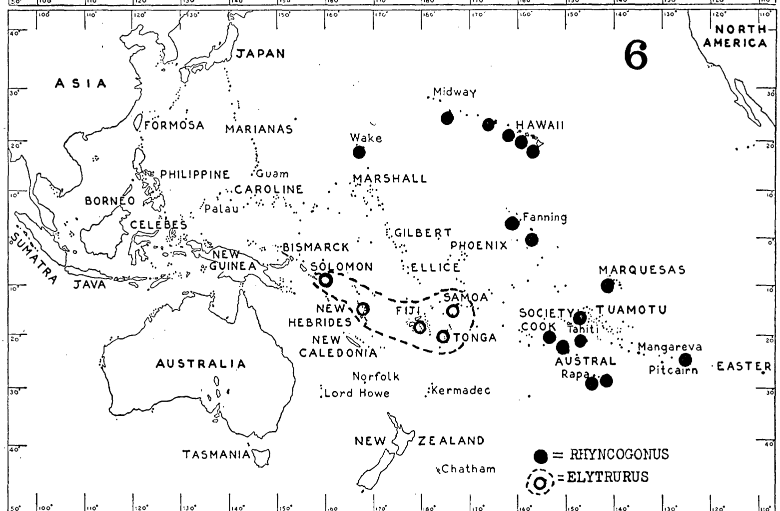
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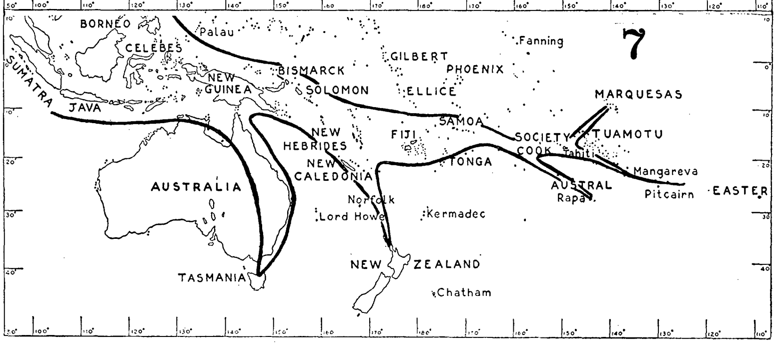
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higher orders, from *Leptogryllus* in the Orthoptera to *Sierola* in the Hymenoptera, from *Megalagrion* in the Odonata to *Drosophila* in the Diptera. Many of the large species complexes of Hawaii can well be the descendants of a single fertilized female immigrant. Research has led me to believe that new lands opened for colonization are conducive to speciation. To-day competition is coming in; ranges are being more and more limited; certain species, genera and families are being driven out of some areas, reduced in numbers or are becoming extinct. Many endemic Hawaiian moths taken by Mr. O. H. Swezey 25 to 30 years ago are now rarities and are heavily parasitized by introduced parasites. Almost the entire endemic beetle fauna of the Hawaiian lowlands has been exterminated throughout the range of the voracious introduced ant *Pheidole megacephala.*

Rate of Speciation. Those who assign great ages to the central Pacific islands cite numerous examples of apparently slow evolution. Some groups of insects have gone through the Tertiary or longer with little change. Wheeler[16] has shown that ants were about as fully developed in the Oligocene (as shown by Baltic amber fossils) as they are to-day. They had their casts, their hosts, their parasites, and even mites were carried on them in the same places as to-day. Many modern genera of ants now foraging fields and forests had their representatives

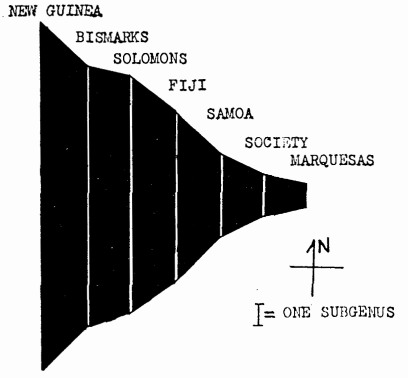
[16] "Social Life Among the Insects," p. 6, 1923.

FIG. 5. Known distribution of *Anopheles* mosquitoes and malaria in the Pacific. Some discrepancies may exist in the continental Australian part of this chart because of my lack of detailed information from that region. It is interesting to note that *Anopheles* occurs in islands only a few miles away from New Caledonia, but that they are not known in New Caledonia.

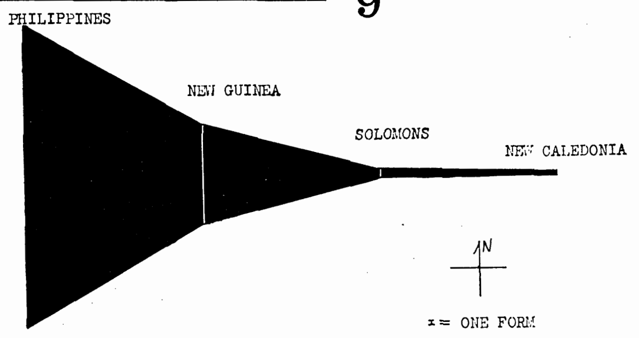
FIG. 6. Examples of peculiar localized or internal developments, showing the distributions of the species of the genera *Rhyncogonus* and *Elytrurus.* Both genera belong to the same group of genera (Curculionidae, Celeuthetini), which is widely spread in the Indo-Pacific regions. The circles and dots do not indicate individual species, but only the presence of the genus. *Rhyncogonus* contains 96 species, *Elytrurus,* 36.

FIG. 7. A rough diagram indicating the average normal derivations of the endemic insects of the South Pacific.

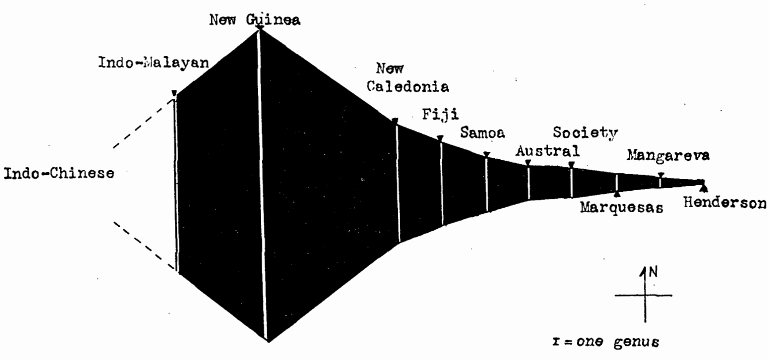
SUBGENERIC DISTRIBUTION OF MOSQUITOES **8**



SPECIFIC DISTRIBUTION OF MUTILLIDAE **9**



GENERIC DISTRIBUTION OF CRYPTORHYNCHINAE **10**



caught in Oligocene pitch. However, there seems no reason for believing that an area with a rich contemporary cockroach fauna existed since the Carboniferous just because cockroaches were dominant among the Carboniferous insect faunas. Certainly we can not assign a flora or fauna to an age older than that indicated by the fossil record. Conifers were present in the early Paleozoic, but flowering plants had their great development in the Cretaceous. Miocene times saw the increase of grasses and culmination of the mammals. It is said that higher birds came in the Eocene, but perching birds are not well represented until the Pleistocene. Perhaps the best fossil histories of animals concern the vertebrates. We are told that the horse began in the Eocene as a small four-toed creature about the size of a small dog, and passed through a number of family and generic changes, and ended in the group of large, single-toed species of *Equus* in Pleistocene and modern times. Although the ancestors of the horse are believed to have originated in America, they did not reach Europe until the Pliocene and found their way to Africa in the Pleistocene. The earliest known ancestors of elephants come into the fossil

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FIG. 8. Diagram showing the distribution of the subgenera of mosquitoes from New Guinea to the Marquesas.

FIG. 9. Diagrams showing the specific and subspecific distribution of the Mutillidae (velvet wasps). This is a continental group of heavy-bodied, parasitic wasps whose females are wingless. None have been found on oceanic islands.[13]

FIG. 10. Diagram showing the distribution of the genera of Pacific Cryptorhynchinae (Coleoptera, Curculionidae). This chart is based upon the distributions of several hundred species contained in more than 100 genera. Probably no other subfamily of insects in the Indo-Pacific is so diversified and extensively developed as this one. How like a great funnel fitted with graded filters this chart is. If one turns the figure on its side so that the point is downward, it may be more effective, and one can visualize the barriers between the islands acting as finer and finer sieves or filters that progressively exclude more and more genera as one progresses from west to east. My data on the developments of the genera west of New Guinea are not so complete as I should like to have them. However, the information at hand indicates that the greatest diversification of genera centers around New Guinea and that in the Malay Peninsula and India the number of genera is smaller.

[13] C. E. Mickel, *Trans. Royal Ent. Soc. London,* 83: 177–312, 1935.

picture at a somewhat later date than the horse. Such data based on careful observation and comparison are lacking in fossil histories of insects. The fossil record of the cockroach is probably the most complete among insects, and it is none too good. Unfortunately, the Mesozoic is mostly *terra incognita* to paleoentomology.

Confronted with such data presented by paleontologists and the conclusions of geologists that the eastern oceanic islands date no farther back than late or middle Tertiary, I am inclined to believe that a considerable amount of the insect speciation within these islands may be called comparatively rapid. I do not believe that the insect faunas of eastern Oceania contain any elements that demand any great age for the developments that have taken place.

It is well to keep in mind that rapid multiplication—especially in the tropics—may be conducive to rapid speciation among insects. The number of offspring arising in a year from a single pair of insects is often surprisingly great. Rapid reproduction of large numbers of short-lived individuals provides more opportunity for mutation. It would be expected that, in general, specific evolution in insects would take a more rapid course than in mammals. Some insects may have 40 or more generations a year. Most of them are short-lived; they live for a year or a season or less. New blood from a new generation is, more often than not, available to each succeeding generation. There is a great mixing of genotypes, and crossing between one pair is unlikely to occur more than once. Most mammals live several to many years and the same blood flows longer. There appear to be no indigenous elements in the eastern oceanic insect faunas that demand as great or greater age for their developments as for such creatures as the horse and elephant, or, for that matter, man, who, it is believed, developed from Miocene primates derived from the Eocene lemuroides of North America.

In the groups I have studied, the continental species are usually more distinct from their allies than are many of those found among insular species complexes. Muir[17] found the same condition among insular Homoptera, and wrote, "While working on material from the Hawaiian Islands one finds that in many instances 'species' have not the same value as among continental faunas, and one hesitates to give many forms that status, . . ." Maulik[18] expressed the same opinion when studying insular leaf beetles and said, "in insular faunas species tend to become more plastic than in continental faunas." Systematists can usually distinguish species quite readily, but there are natural species complexes existing that defy attempts at facile classification. These complexes are natural, and we may expect them to exist. They are particularly common among oceanic insects and terrestrial mollusca.

Many naturalists cling to the theory of extreme slowness in evolution. Some organisms undoubtedly change slowly, and many have passed through eons of time with little visible mutation. Scorpions have come down from Silurian seas, when trilobites were their contemporaries, unchanged except for minor details that fit them for life on land. Modern genetics and paleontology have shown that such slow change is not universal; it is exceptional. Mutations, even great mutations, occur alike in wild populations and in laboratory or field cultures, though, because they are mostly recessives, they are not often seen in nature. Thus Dobzhansky[19] cites Romashov as finding a population of *Drosphila,* containing a large number of flies homozygous for an aborted wing character, breeding on fruit in a deep ditch. When disturbed, the normal flies flew away and left the flightless flies isolated in the ditch. *Drosophila* studies have shown that mutations may be brought out as homozygous forms in the laboratory by controlled isolation and inbreeding.

[17] *Proc. Haw. Ent. Soc.,* 3 (3): 171, 1916.

[18] *Insects of Samoa,* 4 (3): 191, 1929.

[19] *Biological Reviews,* 14: 355, 1939.

In islands built by successive lava flows and pyroclastic ejecta the formulation of species through isolation may be facilitated by the production of "kipukas"—areas of laterized volcanic soil surrounded and isolated by, but not covered by later lava flows. In these micro-ranges the indigenous flora and fauna remain undisturbed while those in the surrounding areas are destroyed by fresh lava and ash, which can sustain a climax association of plants and animals only after long periods of weathering. Some Hawaiian "kipukas" contain an endemic flora—the survivors of former wider-ranging species now elsewhere extinct.

It seems probable that it is not so much the ages of the islands alone that accounts for the endemic developments of their floras and faunas, but their distinctiveness records prolonged isolation[20] to a greater degree and age to a lesser degree. A rule may be formulated thus: The greater the age and isolation of a high eastern oceanic island the greater will be the percentage of endemism and peculiar types of life. The more anomalies in the isolated fauna, the greater is the age. Age alone, without isolation, is not conducive to distinctiveness. The size of a normal high oceanic island is not as important as its age in the development of plants and animals.

Most of the Hawaiian Islands are older and all are more isolated than Tahiti, and the Hawaiian flora and fauna are much more distinctive than are those of Tahiti. Hawaii is younger that Fiji, but Hawaii is more isolated and has more peculiar developments.

No one method seems essential in the formation of oceanic species complexes. The problem is extraordinarily complex. The combination of factors involved in the evolution of land snails with their sedentary habits may not be the same as those influencing flying insects. Romanes[21] considered that heredity, variation and isola-

20 Isolation from other high oceanic islands as well as continents or continental islands, and not only greater spacial isolation but more constant, more prolonged isolation.

21 "Darwin and after Darwin," 1897.

tion formed a tripod on which evolution is based. For more stability of this foundation I would add another leg—that of extinction. These four factors are inseparably linked together, but perhaps the most important to insular speciation is isolation. Isolation should receive much stress in discussions of insular speciation—not only spacial isolation, but also ecological, physiological and morphological.

It might be expected that a genus of flightless insects is more suited to speciation than winged forms. However, the absence of wings does not appear to be more conducive to speciation on oceanic islands than is the presence of wings. *Hyposmocoma,* with about 220 Hawaiian species, is winged: *Proterhinus* in Hawaii, with 175 species, is wingless. Both winged and wingless genera in various orders present great species complexes.

The genitalia of most insects are complex mechanisms. In many groups it is physically impossible for the male of one species to cross with the female of another. It has been said that the key of the male fits only the lock of the female of his own species; although that statement may not be universally true, it holds good in many groups. The genitalia of Microlepidoptera are so individually distinct that, without seeing the entire insect, Mr. August Busck, an international authority on the group, can identify one out of several thousands of species if given the genitalia alone. If differences in genitalia inhibit crossing, then mutations of genital structures should be conducive to speciation. It might even be said that if genitalia are subject to common mutation, this method of isolation might account for insular species complexes, such as those found in *Hyposmocoma, Microcryptorhynchus,* and *Proterhinus.*[22] Experiments[23] show that female

[22] We have too little basic knowledge in this field to go far with our discussions. Professor Dobzhansky, after reading this section, wrote me that "The problem of mutations in genitalia or in other isolating mechanisms interests me greatly. I confess, I am rather lost in the woods in this respect. An 'isolating' mutation, if it is even neutral in all other respects, will be, at least at the start, selected against, since its carrier has less chance to

mammals can be immunized against the sperm of their own species so that the spermatozoa are rendered inactive and quite incapable of fertilization, or, if fertilization does take place, abortion or absorption of the embryo may result. If some mutation occurred that changed the physiological set-up in the genital tract, a cryptic factor of isolation would be at work. Gulick[24] has pointed out that if this phenomenon occurred congenitally in the genital tract, it might set up a sterility between human types. The shape and action of the spermatozoa of two allied forms might be so distinct that penetration of the ova of any but one form would not occur.

In a recently published paper, Stebbins[25] points out that polyploidy influences not only the morphology but also the physiology and fertility of the plant species. To me, one of the most remarkable discoveries of modern genetical studies is that by means of polyploidy a sterile hybrid can be made to produce a fertile constant species; that not only can some different species be crossed by using polyploid individuals, but that generic crosses can be made by multiplying the number of chromosomes in one to approach the number in another. Stebbins says that ''Polyploidy, . . . tends to break down genetic barriers and to permit exchanges of genes between genetic systems that in the diploid condition are completely isolated from each other.'' ''The evidence from the Plant Kingdom, as a whole . . . suggests that polyploidy has been most important in developing large complexes and widespread genera; but that in respect to the major lines of evolution, it has been more important in preserving

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produce offspring by crossing to a majority of the species individuals than a 'normal' individual has. Why and how can we visualize the establishment of a mutant which is immune to the sperm of most of its neighbors? One may invoke the help of isolation, but even so the problem is an extraordinarily difficult one, and I see no entirely satisfactory solution.''

23 M. F. Guyer and P. E. Claus, *Physiological Zoology,* 6 (3): 253–288, 1933.

24 A. Gulick, ''John Thomas Gulick, Evolutionist and Missionary,'' 1932.

25 Am. Nat., 74 (750): 54–66, 1940.

relics of old genera and families than in producing new ones.'' Stebbins calls attention to the fact that polyploids are the ones most apt to expand into new areas and take over new ecological niches. He cites the redwood as a polyploid relic. If there is as much truth as theory in this polyploid research, it may be shown some day that much responsibility for the formation of large insular species complexes among plants can be attributed to polyploidy. Polyploidy does not apply to insects, however.

Controlled crosses that produce organisms which essentially are new species are made by geneticists. In fact, the forms produced are so distinctive that they would probably be described as rare new species if they were collected in the field. If such combinations can be made in the laboratory, doubtless nature herself may now and then produce new forms with like rapidity. I can not conceive of a slow, gradual change bringing forth the flightless Hawaiian Diptera or Neuroptera from their close allies. These aberrant species more probably have had their origins in abrupt mutations of their ancestral stocks. The flightless brown lacewings of Hawaii have arisen, I believe, independently from four different fully winged ancestral species on four different islands and probably at four different times. I have shown[26] that among the cryptorhynchine weevils of Rapa there has been a splitting-up of groups of species which, if continued, along with extermination of intermediates, would form various species groups which would be called genera, ultimately to be placed in different tribes. Rapa is an insular laboratory; what has happened and is happening there is obvious. There has been enacted on that small, isolated island a story similar to that played innumerable times on other islands and continents. There appears to be every reason to believe that comparative sudden mutations of forms have occurred in Rapa, and not a slow, gradual change from one type to another. However, I do not wish to imply that I believe all insular

[26] *Bishop Mus. Bull.*, 151, pp. 1–75, 1938.

species are the results of large, abrupt mutations rather than series of smaller mutations. Probably there is truth in both theories.

The opinions here expressed regarding rapid speciation are not in agreement with those of some leading students of Mollusca. The fossil record shows that many molluscs are apparently slow in evolving; some species have gone through ages of geological time with little change. Dr. C. Montague Cooke, Jr., has shown me specimens of some Hawaiian genera that have apparently lain fossil for thousands of years, and which do not appear different from present forms. In general, however, it appears to me that most of the Pacific island groups are by no means slow in developing molluscan species complexes. Most oceanic land snails are sedentary animals, and isolation of individuals is easily attained. Different forms are found in areas separated by only a few yards. I am told that isolation of colonies on different trees or in different rock piles is so complete that the individuals of the different colonies take on distinctive facies. The very fact that many endemic land snails set up local colonies at every opportunity is to me indicative of rapid change and speciation. Speciation among oceanic land snails is a field open to genetic investigation and rich with ripe fruits for the student.

V. Summary and Conclusions

The high islands of the central Pacific harbor peculiar endemic insect faunas of predominantly small forms normally belonging to few genera containing large numbers of closely allied species, having absolute or almost absolute uni-insular endemicity. With the exception of some uncertain elements in Hawaii, these endemic faunas have been derived from western Pacific ancestors. There is nothing in these insect faunas to indicate any great age for their developments and nothing that would demand extensive land area or land bridges in the Pacific. In the south Pacific, the diversity and richness of the fauna of any high island is inversely proportional to the distance between that island and the Papuan region.

An important problem confronting students of Pacific floras and faunas is the elimination of erroneous data: the broad conclusions based on incomplete collections, meager information or small groups of organisms. There has been too much assumption and too little actual knowledge. In order to assign a given island to its correct position in our scheme, it is essential to take the sum of the floras and faunas and derive the average from them, and to recognize that chance, working over eons of time, is of paramount importance. Abnormal, rather than normal, conditions account for the origins and dispersals of eastern oceanic insular life.