New Guinea and Insect Distribution

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ABSTRACT

New Guinea has played a strategic role in the spread of insects in various directions. It has functioned as an area of evolution of higher categories, and of dissemination, as well as a zone of mixture of two distinct zoogeographical regions. In a sense it has functioned as a buffer zone, isolated at different times to varying degrees. New Guinea has a distinctive insect fauna which apparently evolved in long isolation from ancient southeast Asian ancestors. During this period—perhaps over much of the Tertiary it consisted of a land mass (often called the Melanesian continent) more isolated than the present New Guinea, and centered farther to the northeast. The area may have been quite large, but probably never extended as far east as Fiji or New Caledonia, as claimed by some workers. Quite early the mass may have divided into a Solomons and a New Guinea part, each of which much later further divided. Possibly part of New Britain (except the Gazelle Peninsula), Manus Island, and the Cyclops Mountains of northcentral New Guinea are the only remaining parts of the original New Guinea portion. Southern New Ireland was apparently part of the Solomons Division. In the Pliocene much of the present high portion of New Guinea rose from sea bottom, and in the Pleistocene further elevation connected New Guinea with Australia for a sufficient period to permit exchange of the two faunae. However, the result was to give northeastern Australia more of a New Guinea fauna, and New Guinea rather limited Australian elements. These latter are largely limited to Eucalyptus *and* Melaleuca *forests in parts of southern New Guinea.*

New Guinea has exercised considerable influence on the insect fauna of the oceanic Pacific Islands, and there is evidence of this in widely separated island groups. There is a distinct depauperization in representation of higher categories with greater distance from New Guinea, with age of island groups and other factors also having their effect. In some cases, as in western Micronesia, there is also much influence from eastern Indonesia and the Philippines. There appear to be relationships between New Guinea and New Zealand, through New Caledonia, which do not involve Australia.

To date, the New Guinea fauna is insufficiently known to draw definite conclusions on many detailed aspects of this subject.

From glancing at a map of the general southwest Pacific-southeast Asia area one might tend to assume, on the basis of geographical appearance, that there would be a general gradation of zoogeographical relationship, from one island group to the next, in passing from southeast Asia, through Indonesia, to New Guinea, Australia, and the islands of the southern Pacific. For in many parts of the world reasonable deductions can often be made that adjacent areas may be similar in fauna, and that the fauna of a mountain area may be similar to that at a lower altitude some distance away, while progressing farther from the equator, likewise that isolated mountain masses of similar latitude may possess elements in common—often archaic remnants of former widespread types since confined to the higher areas by climatic change, or invasion of the sea, or gradual migration under changing circumstances, resulting in extinction in the lower intervening areas. However, as the fauna of New Guinea and nearby islands becomes better known, a number of striking and puzzling facts confront us. Unfortunately, the knowledge of the insect fauna of this area is still at such an early stage that firm conclusions cannot be drawn. As a matter of fact, some strongly contradictory views are held by different workers. Of course, it is quite true that different relationships and distribution patterns are manifested by different groups of insects with different evolutionary histories, or different habits and different methods of dispersal. And the geological history of the area is apparently such that development or spread in different periods of time could have profoundly affected the nature of contemporary distribution. On the other hand, the collections which have been studied for the area have been of such uneven geographical representation, and so incomplete, that different conclusions have necessarily resulted from the work of taxonomists studying particular collections.

That different groups present different patterns is conspicuously emphasized by different geographic relationships between insects in general on one hand and higher vertebrates on theother. For the mammal fauna of New Guinea is to a considerable degree Australian, whereas though early workers assumed that the same relationship applied to insects, more and more studies are showing this not to be so in general. The native mammals of New Guinea are entirely marsupials, monotremes, rodents and bats. Thus they are all animals which could have migrated over a land connection from Australia or whose ancestors might have come by "island hopping" from the west. In western Indonesia, southeast Asia and in the Philippines there are nine orders of mammals—insectivores, pangolinsifly, ng lemurs, primates, carnivores, lagomorphs, proboscideans, artiodactyls and perissodactyls none of which are represented in New Guinea. Only a few species of these groups are found in the Celebes area, and marsupials extend westward to Celebes. When Wallace (1869) crossed over from western Indonesia to Celebes he noticed the very great contrast in many forms of life between the two areas. The line he drew dividing the archipelago was later called "Wallace's Line". Though later study of some groups has shown that the contrast was not quite as great as assumed by Wallace, nevertheless the line does have considerable significance and forms the boundary line of the generic ranges of many insects. Furthermore the number of genera represented just west of the line is very much greater than just east of the line. Thus it represents a barrier of long standing both to eastward and westward migration. The Philippines, however, though possessing much in common with Borneo, nevertheless likewise have considerable in common with "Wallacea" and the New Guinea area. The suggestion has been made (Gressitt, 1956a) of a diversion or forking of the line to go between Borneo and most of the Philippines, following Dickerson *et al.* (1928) and others. Furthermore, there are a number of genera or tribes common to the Philippines and New Guinea area which are absent from, or hardly represented in Celebes.

These circumstances suggest that New Guinea has had some connection with the Philippines through the Moluccas, at least in part independant from Celebes, but at quite ancient periods. As shown by Karny (1929), Toxopeus (1950), and others, the insect fauna of New Guinea is basically of ancient Asian origin, with only recent invasion from Australia. (See Lam. 1934, for similar view regarding the flora). Any direct Asian connections must have preceded the Tertiary or much of it and antedated the spread of higher mammals. The connection could have been later than the development and spread of marsupials, as these became extinct west of the old Wallace Line from competition with higher mammals. As the Philippines and New Guinea on one hand and the Philippines and Borneo on the other hand, have relatively more in common with each other than have Borneo and Celebes, it seems likely that the early connections of New Guinea were with Asia through the Moluccas, Philippines and Borneo. Celebes has evidently been isolated for a very long period, and has a number of endemic genera, besides absence of many genera found in the nearby areas. Although somewhat of a mixing zone, it must have once been smaller and more isolated from neighboring areas, particularly from Borneo. The sea separating Celebes from Borneo, though not very wide, is very deep, giving added evidence of long isolation. The geological history of the eastern Indonesian area has apparently been very complicated, with much rising and falling, so that at different periods there have been various temporary partial land bridges or stepping stones, permitting partial faunal mixture. Australia has apparently had little direct influence, except for Timor.

I have already cited evidence (1956a) for the relationship of the New Guinea fauna with that of the Philippines, on the basis of the distribution of several conspicuous groups of beetles. Toxopeus (1950) has stressed the general Malayan relationships of the New Guinea butterflies, stating that Australia has had only a minor influence except in southeastern New Guinea.

In attempting to explain the origin of faunae of oceanic islands, we conclude that most of the immigration has been by means of transport in air currents. One might then ask if such transport is not constantly occurring from rich continental areas to nearby continental islands, or from one large continental island to another, particularly since most of these we are considering are relatively much closer to each other than are many of the oceanic islands to their supposed faunal source areas. In view of the distinct identity of the faunae of some of these continental islands, presumably the answer may be that such immigrants to rich continental areas rarely have the chance to establish because of the rigorous competition, predation or parasitism, they encounter in a rich harmonic fauna, whereas on an oceanic island with highly disharmonic fauna they are likely to find themselves in an empty ecological niche, or at least encountering few competitors, predators or parasites. To be sure such introductions to continental islands must take place, and possibly actual continuous land connections were not as complete as supposed. On the other hand, the distinctness of the Celebes fauna, in the light of its proximity to Borneo, seems to argue that aerial migration has played a minor role in contributing to the faunae of these old continental islands.

Even with continental islands, of course, we must distinguish categories on the basis of length of isolation, for New Guinea presents a quite different situation from that of Borneo. Though continental, the New Guinea fauna has been inherited from ancient, and later temporary, connections, and is not a fully harmonic or true continental fauna, in spite of being so rich. In that sense also, to be sure, the rich Australian fauna, and more so that of New Zealand, is not fully harmonic, for some major categories of insects are lacking, as well as many important groups of higher vertebrates. Speaking of the Papuan Subregion (Moluccas to the Solomons and Cape York Peninsula), the area possesses a very large number of endemic genera, as with a well isolated group of old oceanic islands, or a continent. Borneo, on the other hand, with its tremendous number of genera, has very many of them in common with Sumatra and southeast Asia. The Papuan Subregion is thus a very distinct subregion, whereas the Philippine Subregion is less distinctive, and the Malayan Subregion tends to merge with the Philippine and Indo-Chinese subregions.

In speaking of the age and long isolation of the New Guinea fauna, we must bear in mind that much of New Guinea is extremely young geologically. It is said that the high ranges extending east and west along the axis of the island are partly among the youngest in the world, and that these were elevated from shallow sea bottom only in the Miocene and Pliocene periods, even to the end of the latter. Then with the Pleistocene ice age sea level recessions, the new southern part of New Guinea came in contact with northeastern Australia across the shallow Torres Straits, and the faunal exchange took place. Apparently parts of eastern New Guinea and part of the north coast area such as the Cyclops Mountains near Hollandia are of very much greater age (Cheesman, 1951). Some of these mountains have been stated to have been continuously above water since pre-Cambrian times.

The ancient true New Guinea fauna must have developed on the so-called "Melanesian continent", formerly situated just to the north of the present New Guinea. Probably Manus Island and the Cyclops Mountains, and the Solomon Islands, are remnants of this ancient continent. We shall return to that subject in a moment.

There is much evidence, geological and biological, for the youth of much of New Guinea. The coral limestone found at many of the high altitude areas can be rather accurately dated. Erosion patterns, changes in river routes, rivers passing through later raised mountain ranges, and many other phenomena are demonstrative. In the Wisselmeren area of western Netherlands New Guinea, just west of the Snow Mountains, recent changes are quite obvious. Of this group of four lakes, one (Kamo Valley) has become a great stretch of marsh and swamp, the latter supporting some spreading forests. Another (Paniai) is being invaded by marshes, as rivers drain in from the Snow Mountains, and with the recent change in outlet draining to the south coast instead of to the north coast as it formerly did. The earlier outlet has left a deep canyon cut from the former edge of the lake, which latter is now nearly 50 meters in altitude above the present lake surface. Earthquakes are frequent here. One the year before my visit partly changed the course of a stream entering the lake. Toxopeus (1950) describes other evidence of geologic youth in the area where he worked in the Snow Mountains.

On the south side of the Snow Mountains is a cliff over 3,000 meters high, the highest in the world, said to have resulted from the snapping of rock masses in relieving crustal stress, with a differential movement on the two sides of the fault. Much of the old rock structures are exceedingly tilted and folded. These crustal movements took place in Pliocene times, say two or three million years ago (Hodge-Smith). This can be compared with the last major crustal deformations in Australia which are said to have died out in the Carboniferous, about 250 million years ago. About 40 years ago there was a subsidence of two meters along the coast at Aitape, northern New Guinea. Along much of the north coast there are strongly meandering rivers, extensive swamps, and often very low narrow beaches, indicating stress.

Many of the high mountain ranges in eastern New Guinea such as the Bismarcks and related ranges and the Owen Stanley Range, are of great geological age, even consisting of pre-Cambrian schists and gneisses, but have been raised and lowered at different periods. Much of the time they have formed islands, as have other New Guinea ranges up into the Pliocene. This archipelagoan nature of New Guinea through much of the later Tertiary contributed to the development of local endemism, which has been perpetuated in the mountain ranges since the islands were united. With the various earlier periods of subsidence of these islands, limestone beds were laid down, which now may be found high in the mountains. In the west they completely cover the old metamorphic rocks. There are many intrusions of granite and diorites. Vulcanism and lava outpouring continued through the Tertiary, on down to the present time. During the periods of Pleistocene glaciation there were glaciers extending down to altitudes of less than 3,000 meters.

Most of the fossils found are marine deposits, often coralline or forminiferal limestones, or sandstones or mudstones containing marine shells. Some of the Pleistocene rocks contain fossil emu and cassowary bones, or those of the extinct *Nototherium*, a large rhinoceros-like marsupial.

As pointed out by Toxopeus (1950) New Guinea does not possess a true alpine fauna. This is in spite of New Guinea having one of the world's highest mountain ranges, with conditions favorable for life, and plants growing up to nearly 5,000 meters in altitude. This strongly suggests that the connections of New Guinea with other areas existed at low altitudes preventing high altitude forms from reaching the island. There are no coniferous forests in the very high mountains, the conifers being mainly auracarians, podocarps, and cupressines, occurring at medium or even fairly low altitudes. The insect fauna of the high altitudes represents a recent development, of lowland forms adapting themselves to a cooler climate. At the highest altitudes butterflies are rare or absent, and those reaching high altitudes belong to the same genera as those occurring much lower down. Though Darlington (1952) has described considerable neoendemism on the generic level in carabid beetles for the Mt. Wilhelm area, in some other groups there is not a great deal of local generic endemism. Many of the strictly Papuan genera may be widespread within New Guinea.

At 3600 meters altitude on Mt. Wilhelm I collected local species of the dominant Papuan longicorn genus *Tmesisternus*. This genus is represented by many species at sea level. In Toxopeus' collection there are likewise endemics from the Snow Mountains in this genus. Other cerambycids are also represented by different species within the same genus from sea level to fairly high altitudes. Among the hispine beetles, the highest collections made, at just under 2,000 meters, both in western and eastern New Guinea, represented a genus, *Brontispa*, found predominently at sea level. Although *Troides* (*Ornithoptera*) butterflies are characteristic of the lowlands, I found the chrysalis of one species at close to 2,000 meters altitude (Gressitt 1956b).

In a rough comparison of material I collected at similar altitudes in the mountains of eastern and western New Guinea, 1,000 kilometers apart, definite differences in faunal make-up were noticed. For instance, broad-nosed weevils were dominant in the highlands of the northeast, and cryptorhynchine weevils were dominant in the Wisselmeren area. Also, more types familiar in southeast Asia were noticed in the latter area, both of insects and plants. In general, more species of cerambycids were taken at lower altitudes, and more chrysomelids at higher altitudes, but this may have been partly a matter of favourable environments and unequal sampling. In the more densely populated mountains, there is more cleared land, favoring shrubs and herbs, and thus likewise favoring the leaf beetles.

In the lowlands, a single species may extend very great distances, as all the way from Waigeo Island at the far northwestern end of New Guinea, along the north coast far into eastern Papua (Gressitt, 1955). On the other hand in the mountains there is great development of local species endemism.

The extent of representation of true Australian groups in New Guinea obviously varies considerably, as suggested in connection with the Australian nature of the mammal fauna. Certainly for many groups of insects (Lieftinck, Karny, Toxopeus) the New Guinea fauna is Australian only to a minor degree. In the Cerambycidae and Chrysomelidae the percentage of genera in common between New Guinea and Australia south of the Cape York Peninsula is very low. A few of the Australian genera are widespread in New Guinea, but others are limited to the southeastern portion, as are, to a large extent, the *Eucalyptus* and *Melaleuca* savanna forests. The evidence in the beetles I have studied strongly suggests that much of the faunal representation on the Cape York Peninsula is of Papuan origin, particularly that found in the rain forests. This suggests that previous to the Pleistocene connection there may not have been much of a locally developed rain forest flora and fauna in that area, or that the invading Papuan biota was better adapted to the climate of the area. Also that the Australian insect forms invading New Guinea encountered the competition of a fairly rich and balanced fauna, which was not the case with the mammals. The typical Australian forms are largely limited to the *Eucalyptus* savanna, just as they are in New Guinea. In the hispines, the genus *Eurispa*, the only large Australian genus in the subfamily, barely extends into southeastern New Guinea, with two known forms, besides a few on the Cape York Peninsula. In the rain forests of Cape York Peninsula the hispine are represented entirely by typical New Guinea genera, which in some cases extend all the way to Indonesia. Toxopeus (1950) points to a secondary invasion of Papuan types to the Cape York Peninsula through the Aru-Merauke ridge, from the direction of the southern Moluccas. According to some geologists New Guinea was also connected with Australia in the Paleozoic. If so, the connection must have had very little permanent effect on the fauna as a result of later submersions or ecological incompatibility of the Australian fauna with the New Guinea environment.

The old Melanesian continent, on which evolved many of the typical Papuan genera, apparently divided into two major islands at some period of the Tertiary before the Pliocene. The west division then developed the particular New Guinea elements, partly before breaking up into the various islands which developed more local endemism, now perpetuated in various of the mountain ranges of New Guinea. The eastern division of the Melanesian continent gave rise to the Solomon Island fauna. New Guinea is said to have consisted of two major islands, the east and west portions, during part of the Pliocene, but were connected both earlier and later. The Solomon Islands, at least in part, appear to have been individually isolated from each other for a considerable period, perhaps at least since well back into the Pliocene. Evidence for this includes the fairly deep water between many of the major islands, and the considerable development of endemism for single islands, or parts of the chain. Probably some of the islands of the Solomons have been separated from each other longer than have parts of the Bismarck Archipelago from the New Guinea mainland.

New Ireland holds an interesting position in the relationship of the supposed two major divisions of the old Melanesian continent. For in spite of its proximity to New Britain and others of the Bismarcks, it has a number of elements in common with the Solomons. Southern New Ireland has ancient metamorphic rocks well in evidence, whereas most of New Britain consists of raised marine limestone or recent volcanic deposits, at least on top of the older rocks. The New Ireland population of the birdwing *Troides priamus d'urvillianus* is blue like those of the Solomons, instead of green like the New Britain population. In my collecting in southern New Ireland a few weeks ago I took a new hispine beetle related to a form described as an endemic genus from Malaita (latter also occurring on Guadalcanal). Another species on Manus Island may be a connecting link between this genus and one restricted to New Guinea and Waigeo, though showing its next closest affinity in Madagascar. Another form just taken in New Ireland seems to represent a new genus without known close affinity in the Solomons or New Guinea, but having a general similarity to some Philippine forms. Still another seems to have its closest affinity in New Britain. But with many of the common insects taken in southern New Ireland, there appeared to be more affinity with species of Bougainville than with those of New Britain.

It can be noticed that the Solomon Islands are principally arranged in two parallel rows, which appear to unite at each end, in Bougainville and San Cristobal, respectively. It has been stated that southern New Ireland represents a continuation of the southern chain of the Solomons, and that the several small islands paralleling New Ireland on the northeast represent the continuation of the north chain of the Solomons. Not enough collecting has been done to present much evidence on this point, or to adequately characterize the relationships of New Ireland, New Hanover, the St. Matthias group, Manus, and New Britain. At any rate, New Britain has much in common with the New Guinea mainland, although plenty of local species endemism. Possibly Manus is a little less closely similar in its fauna to New Guinea, than New Britain is to New Guinea.

The submarine land connections in the Solomons (Lever, 1937) show that Bougainville connects with the Shortlands, Choiseul, Ysabel, Nggela, Russell Islands, and Guadalcanal, shallower than the 1200 meter line, whereas the New Georgia group, Malaita and San Cristobal are each isolated by water from 1200 to 2000 meters in depth. Further, Rennell and Bellona are separated from the rest of the Solomons by water more than 4,000 meters deep. In my recent collecting on Bougainville and Guadalcanal, I noted many common types on the two islands that superficially appeared to be very similar or identical, as might be suggested by these ocean depths. However, in the hispines, of six kinds taken on Bougainville and 11 on Guadalcanal, only two on each represent close relationships, and one of these is a widespread coconut pest. Some of the others represent new genera, for the time being endemic to one or the other of the two islands. Some were found on one island in ecologic niches which seemed to be vacant on the other, and vice versa. Mr. E. S. Brown (personal communication) tells me that in his recent collecting, he noted that Malaita appears to have a very rich fauna, with some types he did not note on Guadalcanal, and that the fauna of San Cristobal appears still more distinct, though not as rich. Within the New Georgia group there is some distinct local speciation (Mayr, 1932; Lever, 1953), with several of the various islands having endemic species. In spite of close proximity, some of the water separating these islands is a few hundred fathoms deep. Much of the rocks on the main Solomons are igneous, and many of them may date from the Cretaceous Period. Limestone terraces indicate that there has been elevation in recent times. Rennell Island, which stands apart from the double chain, is a raised atoll. It has a rather distinct, though poorer, fauna.

When the faunae of the Solomons, Bismarcks and New Guinea are better known, it will be very interesting to compare the nature of speciation on these now isolated islands, with that on the mountain ranges of the New Guinea mainland, since the latter are said to have been, to a great extent, isolated islands in the late Tertiary.

The fauna of the New Hebrides is still less adequately known, but the apparent much greater poverty, and lack of many groups found in the Solomons has lead some (Mayr, 1941; Gressitt, 1956a) to call these islands oceanic. Others, however, have classified not only the New Hebrides, but also Fiji and New Caledonia, or even Samoa, as continental islands.

New Caledonia appears to represent a relic of a possibly important phase in the history of the New Guinea fauna. Karny (1929), Malaise (1950), and others, have pointed out South American relationships in the New Guinea insect fauna. There is much evidence of faunal relationships between New Guinea and New Caledonia, and again between New Caledonia and New Zealand (Gressitt, 1956a). Many of these relationships do not involve Australia, and it seems to be a rather safe assumption that the New Guinea—South American relationships may stem from connections through the Solomons, New Caledonia, New Zealand, and Antarctica, completely independent of Australia, in addition to other connections which may have existed between Australia and South America. New Caledonia has very ancient rocks, with much serpentine. Its fauna and flora possess a very high percentage of both specific and generic endemism.

Lord Howe Island, off the east coast of Australia, is also significant from the standpoint of zoogeography in this area. It possesses a number of endemic forms without relatives in Australia, or with no relatives in Australia south of the Cape York Peninsula. This suggests that its fauna may have been derived from islands to the north. Some of the Lord Howe forms represent the southernmost extent for particular genera. The island lacks many dominant types of insects found in New Zealand and Australia. The flora, as well as the insect fauna, indicates a more tropical derivation, for there are four endemic species of palms on the island.

The Papuan Subregion has exercised a great influence on the insect fauna of Polynesia (Mayr, 1941; Gressitt, 1956). Briefly, the bulk of the Polynesian fauna may be said to have