6

DISTRIBUTION OF FAUNAL SPECIES IN OCEANIA

By R. J. A. W. Lever.

(Read 18th October, 1945)

1.—Types of Islands.

In order to understand the distribution of species in the islands of the Pacific it is first necessary to appreciate the different types of islands occurring in Oceania. These are of two main types, oceanic islands which have never formed part of a continent, being separated by great depths from other islands, and continental islands which were once connected to a larger land mass and are now separated by a lesser depth of water from adjoining land. Examples are:—

1. Oceanic—
   (a) Coral or "low" type—Gilbert and Ellice, Tuamotu, Sikaiana.
   (b) Volcanic or high—Samoa, Tahiti, Marquesas and Hawaii.
   (c) Crystalline elevated coral, intermediate—Rennell in Solomons, Niue in Cooks and Makatea in Tuamotus.
2. Continental—
   Sedimentary, metamorphic and volcanic—Fiji, Solomons, New Hebrides and New Caledonia. All "high" types.

In a previous paper it was explained that the Pacific fauna showed a diminution in genera and species as one went from west to east. Thus crocodiles, the *Anopheles* mosquito and Mutillid or velvet wasps occur in the Solomons and all but crocodiles in New Hebrides; but all three are absent from Fiji, while Fiji itself has hawks, swallows, frogs, ground beetles (Carabids) and fresh water sponges which are absent from Samoa. This paucity in species is continued as one goes further and further eastwards, leaf-beetles being absent in the smaller islands of Polynesia.

2.—Former Land Connections.

Briefly one can summarise past land connections by saying that species could once cross what is now the Torres Strait from Northern Queensland to New Guinea—hence the presence of spiny ant-eaters in both countries—and there was once a connection between New Guinea and the Bismarck Archipelago and the Solomons.

(1953) Trans. Proc. Fiji Soc. 3:

Fiji is generally regarded as having formed the extreme eastern limit of the Melanesian plateau and it is a fact that its fauna is more akin to that of the New Hebrides and New Caledonia, which are far further from Fiji, than Samoa and Tonga which are much nearer. Both of these latter groups are oceanic islands, all their fauna having reached them by flying, drifting, or floating, i.e., other than by land connection. Modern workers are generally agreed not to invoke extensive land bridges once so popular. Examples of more isolated oceanic islands are Rapa (south of the Societies) and Rapanui or Easter Island where species-formation is both common and more rapid than in many of the larger and less isolated islands.

3.—Endemism and Species-Formation.

One of the most interesting phenomena encountered when dealing with Pacific faunal groups is the varying degree of endemism present, i.e., the numbers of species strictly confined to the islands concerned. Probably in no group is this percentage higher than in Hawaii where no less than 80 per cent of the insects are endemic and a glance at the map shows how isolation alone could account for much of this, Honolulu on Oahu being 2,000 miles from western California. Later an attempt will be made to account for varying degrees of endemism and species-formation (speciation) in the Pacific but remoteness from land masses is one main factor which is accentuated by a great depth of sea. Oceanic islands have high endemism and an absence of many faunal elements.

4.—Species-Formation in Some Selected Islands.

(i) Galapagos.

In the space available one can only choose a few groups of islands; and the Galapagos must be included despite a paper dealing with them read in 1940. These small equatorial, volcanic islands were visited by Darwin on H.M.S. *Beagle* in 1835, and greatly impressed him by the variation between the islands in the species of birds, reptiles, molluscs and plants. Of the twenty-six land birds no fewer than thirteen are finches; and they, and the mocking thrushes, have a very high percentage of endemism. Although the marine iguana is found throughout the islands yet the closely related land species occurs only in the central islands of the group, and Darwin suggested it had been too recently evolved to have spread north and south. The giant tortoises are so distinct that even laymen can distinguish each separate species and assign it to its respective islands. Of the shells 47/90 were endemic and similar proportions were found in plants. These islands are all similar in soil, climate, vegetation and altitude, have never been united and here evolution could be said to be visibly in action.

(ii) Hawaii.

Hawaii—a mere 4,000 miles to the north-west—is the only group of Pacific islands about which full details of the fauna have yet been published. These islands are, of course, oceanic and volcanic with active volcanoes. The flora reaches the astonishing percentage of 85 per cent endemism in the higher plants—a unique record. Fiji is fortunate that it, so far, has escaped the large destruction of forests and heavy introduction of harmful insects, chiefly ants, which have decimated or even destroyed much of the indigenous Hawaiian insects. The work on these insects was done chiefly by R. C. L. Perkins in the 'nineties who showed that although these islands have relatively few genera they are very rich in species in these genera. He also drew attention to the tendency of oceanic insects to have a limited range, a limited local distribution and a specialisation of habits, coupled with a general loss of wings. Among both shells and insects some species seem to have reached the furthest point of development and so have become stable or non-variable through sheer inability to give rise to more forms or races.

The origin of the oceanic insect fauna can be set down to the arrival of a few, or even single, ancient immigrants which, having once landed, gave rise to breeds which in course of time varied enough to form distinct species. Three examples of the richness of species are *Proterhinus* (beetle) 136 species, *Nysius* (bug) with 50 and *Odynerus* (wasp) 100 species.

(iii) Marquesas.

Much more could be said of Hawaii but it is necessary to refer to the Marquesas, some 2,000 miles to the south-east. From a general viewpoint the Marquesas can be compared with the Galapagos as both are summits of large volcanoes and both are separated by great ocean distances, the former being 800 miles from the nearest land (the Society Islands) and 3,000 miles from the nearest continent (North America).

A study of the fauna shows it to have originated from the south-west and there is a close similarity between the Marquesas and the Society Islands but next to none with Hawaii; the fauna can be regarded as an impoverished replica of that in Samoa and Tonga. The weevil *Rhyncogonus* has no fewer than twenty-three species, eight occurring on one of the largest islands, five on another and only one on the largest island. This genus is also found in Hawaii with thirty-three species, Society two and both Wake and Rapa one each.

Endemism is very high among the molluscs, no less than eighty out of the ninety known species being confied to these islands. Geologists seem to regard the separation of the Marquesas as having occurred in mid-Tertiary time, say the Miocene.

(iv) Samoa.

Samoa, 2,000 miles due west, is the final example of an oceanic island. Professor Buxton, who collected here in 1924-25, estimated that out of 1,600 known species of insects 49 per cent were endemic; but realised that some of these will later be found in Tonga and Fiji and so cease to be peculiar to Samoa, thereby lowering the figure of 49. There is much less speciation, i.e., less formation of separate species, than in either Hawaii or the Marquesas; and this is accounted for largely through the isolation of Samoa being so much less intense. Besides the absence of many families there is an over-representation of many of the families which do occur compared with continental islands. As was mentioned earlier, Fiji is the extreme range of swallows, hawks, frogs, ground beetles and fresh water sponges, none of which are present in Samoa; the summit of Savaii being over 6,000 feet in height.

(v) Fiji.

The examples selected from this archipelago are the birds known as thick-heads (*Pachycephala pectoralis*) and a genus of weevils. The original stock of these birds (now forming two subspecies) with a yellow throat and no breast-band is confined to the main islands of Viti Levu and Vanua Levu, exclusive of Natewa Peninsula. Later, immigrants from the west arrived with a white throat and a breast-band (this is the type found in the New Hebrides) now forming three sub-species confined to Kadavu and Beqa, Gau and southern Lau, but in course of time they hybridised with the original yellow-throated birds without a breast-band. As the yellow colour proved dominant to the white and the presence of the band to its absence, hybrid subspecies arose with these characters (yellow throat and breast-band), and are now found in Moturiki, Ovalau, Koro, Vatuvara, Tavenui, Rabi and across to Natewa Bay, where they have kept distinct from the sub-species present elsewhere in Vanua Levu, which has no breast-band. This, it is submitted, is a very good example of a bird whose speciation has taken place comparatively recently and about which something definite can be found. It took 300 skins from eighteen islands to get these data.

Elytrurus is a fairly common leaf-eating weevil found throughout the western Pacific where thirty-six species have so far been described between the eastern Solomons in the wst and Tonga in the east. It is interesting to note how it just failed to make the most easterly of the main Solomon islands—San Cristobal—only one species each reaching the islands of Vanikoro and of Santa Ana to the south-east. The New Hebrides has nine, Samoa two and Tonga but one species while the centre of origin and dispersal—Fiji—has no less than twenty-two species, one of which—*E. griseus*—occurs in all the small islands even when each

of these have, in addition, their own particular species. Thus Ovalau has *cervinus*, Moala has *moalaensis* and Kadavu *smaragdus*, but *griseus* in each case is present as well.

Here we have then a rigid species—*griseus*—occurring in each island with, in addition, more plastic species arising by isolation in different islands. Certain obvious questions stand out: thus what would result in crossing the variety *griseus taveuni* (which is not specific enough to be called species *taveuni*) with a closely related species near it? What made this sudden blossoming into these various species and is it completely over? Is it not likely that the large island of Vanua Levu has more species than Taveuni and Ovalau?

(vi) New Caledonia.

New Caledonia has an area of 6,250 miles (just exceeding that of Viti Levu combined with Vanua Levu), is about 250 miles long and has two peaks over 5,400 feet. As already mentioned, it formed with Fiji, the New Hebrides and the Solomons part of the Melanesian plateau which was once joined to Australia. Since its isolation it has produced many interesting forms of life including the heron-like *kagu* whose nearest living relatives are now confined to South America and Madagascar suggestive of a former connection with the long-submerged Gondwanaland. Of interest also are the large land snails of the genus *Placostylus* of which New Caledonia has no less than forty-five species compared with sixteen for the Solomons, only five for the New Hebrides, fourteen from Fiji, one from Lord Howe Island and two from the extreme north of the North Island of New Zealand. As might have been expected it is absent from Tonga and of course from Samoa. The high total of forty-five can be attributed to the long isolation of New Caledonia coupled by its peculiar topography caused by the steep mountains very close to the sea giving rise to many rapid rivers dividing the coast into a series of natural areas demarcated from each other.

(vii) Solomons.

The Solomons, the last group to be dealt with, possess an obviously continental fauna and a marked absence of certain species in particular islands. Thus the hornbill and cockatoo are absent from San Cristobal, an example of thinning out within an island group itself; but it is necessary to confine attention to a portion of the Solomon archipelago, namely New Georgia and its associated islands. On the islands of Rendova and Tetipari there are distinct species of birds (white eyes or *Zosterops*) and the same holds good for the fly-catcher *Monarcha* on the islands of Vellalavella, Ganoga and Kolombangara where they all differ from the species on the main islands of New Georgia and Gatukai. This seems unaccountable at first sight as the distances involved are so small; but a study of the chart reveals the clue in the

exceptional depths of sea between the small islands themselves and New Georgia. If we compare a section of forty miles or so in this area, with a similar area in Lomaiviti in Fiji we soon see both the greater height and especially greater depths, found in the former from which we can conclude that the isolation in these Solomon islands has been more intense than in comparable islands in Fiji where this species-formation is absent.

Finally among the weevils there is a similar marked endemism; one of the best known to the writer, *Exophthalmida* from Vellalavella has split into a sub-species on both Kolombangara and Ganonga plus Gizo; the males varying more than the females. It is of further interest that this genus was never taken after several years collecting on the larger islands, though it is almost certain to occur on New Georgia. Here then is evidence of species in the making; and further collection in those beautiful islands will pay good dividends to anyone prepared to collect thoroughly and intelligently in practically any class of the animal kingdom. It is unfortunate that very scanty details are given on Vellalavella and Ganonga on the latest available Admiralty charts, no soundings having been recorded for these still inadequately surveyed islands.

EXHIBIT.

In many cases evolutionary problems have been worked out with dull and obscure-looking insects but in the case of the bird-winged butterflies they are both brilliantly coloured and large.

Two species occur in the Solomons—*Ornithoptera priamus urvillianus*—extending from New Britain to Guadalcanal and the other—*Ornithoptera victoriae*—being confined to the Solomons Archipelago. Of more direct concern is this latter which has given rise to no less than six sub-species, which in the course of time, say half a million years, can be expected to form as many true species. As the specimens and map shows these are:—

1. Variety *regis* on Bougainville and the Shortlands.
2. Variety *resplandens* on Choiseul.
3. Variety *rubiana* on New Georgia and adjacent islands.
4. Variety *isabellae* on Isabel.
5. Variety *reginae* on Malaita.
6. Variety *victoriae* on Guadalcanal, Gela or Florida and San Cristobal, the extreme known range.

Here is a good example of incipient speciation in one archipelago.

CONCLUSION.

The following general conclusion from the areas examined are noted. First it is an axiom that the diversity and richness of a fauna of any high island in the Pacific is directly proportional to the nearness of that island to New Guinea or another large island mass. Also, the greater the age and isolation of such island

the greater will be the percentage of endemism in it. Thus although Hawaii is geologically younger than Fiji, yet its isolation both in space and time, is much greater and so its endemism is much higher.

It is difficult to reconcile the value of species on continents *vis à vis* those in islands, as in the latter the fauna tends to be more plastic and so more variable. Further, the lower percentage of parasitic and predatorial insects on islands makes the struggle for existence there less severe than on continents and so many species are able to survive which would perish on larger land masses.

If one allows half a million years for the formation of well-marked species one can soon build up a fairly rich variety of species and there is less need for postulating the handy but unproven land bridges of Victorian biologists.

This paper has introduced problems and drawn attention to the great need for more and more accurate collecting in Pacific islands before conclusions are drawn. It has been necessary to deal only very briefly with many of the groups of islands but it will be due to the huge area involved—the Pacific Ocean being sixty-four million square miles in area and having over 2,500 main islands, the main groups each having its own problems.

In the words of a Hawaiian entomologist—Mr. Zimmerman—who has collected for many years throughout the eastern Pacific, including Fiji: " Oceania is largely a *terra incognita* to entomologists and collecting is patchy, incomplete, inconclusive and insignificant."

DISCUSSION.

Mr. Harvey dealt wth the influence of man in transporting insects, which the speaker said was more a question of the accidental arrival of new species than of actual species formation. Examples were cited by the lecturer of mosquito larvae being carried in Dalo plants from Samoa to New Georgia and of the larvae, called by the Fijians *Kutu ni Tanna*, because of its appearance among New Hebridean labourers from Tanna Island. The speaker asked for any known record of crocodiles having drifted to Fiji, referring to a recent Australian paper.

Mr. Derrick suggested that the local mynahs might be dividing up into two species but this was stated by the lecturer not to be correct as there are already two good species in Fiji, the house and the field mynah. A point about the depth of water between various islands in New Georgia in relation to species formation was dealt with. Mr. Derrick suggested that the difference between the vegetation in the Natewa peninsula and the rest of Vanua Levu might account for there being two species of thickheads on the island and with this the speaker agreed.

Mr. Maude gave an instance of a recent arrival which he had seen, viz., that mosquitoes were absent from Christmas Island in 1937 but present in abundance in 1944. An expected change in the flora and climate of Henderson Island was likely because of the introduction of goats. He gave an instance of crocodiles being stranded at Butaritari in the Gilberts about 1925.