

THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS.

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A few generations ago the curious differences between various parts of the world as regards the creatures to be found therein were accepted as part of the general order of things, as pre-ordained and therefore inexplicable.

There were hippopotamus in Africa and tigers in India because they had been created there, and there was no more to be said about it.

The great upheaval of this view produced by Lyell's "Principles of Geology" and Darwin's "Origin of Species" resulted in a totally different point of view. Animals of a certain kind live in a certain place because their *ancestors* lived there; but there is more than this to be said. Their ancestors were not *exactly* like themselves, and study of fossil remains of creatures of other days shows that the present-day distribution of a type does not correspond with the distribution of its bygone relatives. To take a simple example: at the present day the hippopotamus does not live in Madagascar, but there are found abundantly remains of a small kind of Hippo which shows that it did live there once though not quite in the same form as the massive animal so well known on the African continent. Now as it is unlikely that the ancient form of hippo swam across the wide gap separating Madagascar from the mainland we must postulate a former closer connection between the two, and we shall see later that there is geographical evidence for this. This is the kind of problem that makes the study of the distribution of animals (and of course of plants also) so very interesting.

The only intelligible explanation of the differences in distribution of animals and plants over the surface of the earth is one of constant changes in the distribution of land, water, and ice, and therefore of climates. These changes have been associated with constant evolution of forms of life, at least of those which had in them sufficient adaptability to meet changes. Some, not easily adapting themselves to changed conditions have completely died out and have left no descendants, for instance the gigantic reptiles known as Deinosauris: others, once very prevalent in numbers are now represented by scattered descendants in different parts of the world, such as the Giraffe, Okapi, and Prong-horn buck of N. America which, though at the present day placed in two different families, are closely united by fossil forms.

Again, long ages ago some ancient forms became isolated from other creatures because the area they inhabited was cut off from adjacent areas by subsidence beneath the water of an intervening portion. If this area for long ages was exposed to uniform conditions its inhabitants may have remained more or less unaltered; but if the conditions were variable the animals subjected to them may have struck out along a line of their own unhampered by competition from the outer, larger, world. In one case we should find animals of lowly, unspecialized type; in the other, very peculiar and highly specialised forms. It must be remembered that the changes in the face of the earth, and therefore of climate must have caused great migrations of the beasts of days long past, which sought to avoid excessive heat or cold, flooding or drought, growth or disappearance of forest, etc., etc., produced by the gradual but long continued changes in elevation of the surface of the land. It is most important thoroughly to assimilate the modern view of constant change for ages past in the features of the earth, and to bear in mind that only adaptable organisms could survive through these changes unless they found somewhere where they could seek refuge from change, as in the deepest parts of the ocean. Forms of life known as Crinoids or "Sea-lilies" are now to be found in the abysses of the ocean whose ancestors, in untold myriads, are largely responsible for forming great beds of limestone by the deposition of their calcareous framework at the bottom of shallow seas: changed conditions proved inimical to them and their descendants can only live in the deeper waters. Through adaptation to meet changing conditions the descendants of a group existing at any one time may be very different indeed from their ancestors. The simple example of the "Woolly Rhinoceros," which at one time inhabited the land that is now England, illustrates this. This animal lived in times of ice and cold and had a dense woolly coat. As the glacial epoch passed away the climate became warmer and the thickly-clad animal had to face a different kind of world. Certain individuals proved adaptable and they and their descendants lost their thick coats and so were better able to live in the greater heat. Rhinoceros at the present day is entirely a tropical genus. It is also important to remember that, speaking very broadly, one at least of the large land areas of the present day, Eurasia, has always been there, or at least that there have always (of course, by "always" is meant during the time of evolution of mammals) been some areas of land more or less connected with each other at different periods in the position now occupied by Europe and Asia. This great centre seems in very many cases to have been the cradle from which families dispersed in all directions, even the remote ancestors of man and his near relations, apes and monkeys..

If the surface of the globe be considered from the point of view of the naturalist, it will be found that geographical regions do not at all exactly coincide with zoological regions.

In spite of the vast distance between Great Britain and Japan there is a great deal in common between the animal life of these two groups of islands: if the traveller knows his British birds he will at once recognise similarity in the type of Tits, Wagtails, Wrens, Sparrows, Thrushes, etc., some even identical with the British species. Insects, too, may be found of the same general types as those he knows.

Yet, in the Malay Archipelago there are two islands about as large as Corsica, separated by a strait only fifteen miles wide at its narrowest part, whose birds and animals differ far more than do those of England and Japan, although there are a certain number of forms common to both. (See map II.)

These are selected cases; but even in large areas the zoological and geographical areas do not coincide.

Thus, the term Europe does not define accurately the range of any genus of mammals or birds; they range into Asia or Africa as well: but there are a few species limited to part of Europe, though a species of wide distribution through Europe is not necessarily confined to that continent. Many animals are found in Asia and Africa, *e.g.*, the leopard. In Africa very few groups of animals range over the whole of it without going into Europe, Asia Minor, or Arabia.

Australia does agree better with both points of view, but as we shall see, zoological and geographical definitions of Australia are not the same.

Naturalists have differed somewhat as to the best way in which to mark out the zoological regions of the world: that adopted here was planned by A. R. Wallace, the co-discoverer with Darwin of the basic principle of evolution through Natural Selection, and is described in his most fascinating works "The Geographical distribution of animals" and "Island Life."

Europe with most of Asia and Africa north of the tropic are linked together to form the Palaearctic region.

The continent of Asia south of the Himalayas, with the north-west half of the Malay Archipelago may be given, roughly, as the extent of another region of equal zoological importance with the

MAP I.



WALLACE'S ZOOLOGICAL REGIONS.

1. Laccadive Isles, 2. Makive Isles, 3. Chagos Isles.
4. Seychelles, 5. Aldabra Isles, 6. Comoro Isles, 7. Mauritius & Bourbon.
8. Rodriguez.

Palaeartic, though very much smaller in area. This is known as the Oriental region. The other half of the Malay Archipelago, with Australia, New Guinea, New Zealand and innumerable islets forms the Australian region. Africa, south of the tropic, forms the Ethiopian region: this also embraces the southern half of Arabia, but no other part of Asia.

As regards the New World the zoological divisions correspond more nearly with the geographical, save that "Central" and S. America are classed together, making one region, the Neotropical.

North America forms the Nearctic region, the name indicating sufficiently well the resemblance to the Palaeartic or old world northern region.

Let us now take these five regions, of more or less equal zoological value, and see what are their characteristics. In order to do this a few technical terms must be used in connection with the classification of things in general. The system of classification now used was devised by the great Swedish naturalist of the eighteenth century, Linnaeus, and many of his names are used at the present day. The smallest unit is the species, which is the name for a number of individuals which, closely resembling one another will breed with each other and produce fertile offspring. Species of course may be composed of many or few individuals, and are then known as "common" or "rare" species. Since no two individuals of a species are *exactly* alike in all their details we must admit another grading into varieties. Generally speaking, varieties of a species will breed together, but if very well marked two distinct varieties may be sufficiently different not to breed together, at any rate to any great extent, although each may breed with an intermediate form: these may then be termed sub-species. Sometimes varieties differing very widely from each other at the extremes of the range of a species may only be known as forms of one species by the transitional forms from regions in between the extremes. The extreme forms are known as Geographical races.

Examples of species are Lions and Leopards: the lovely Snow-Leopard of Thibet and the Himalayas and China is a geographical race: the Black Leopard is a variety; it is not confined to any particular locality, though it occurs more commonly in Asia than in Africa. The Black and Snow-Leopards would probably not breed together, yet they can be shown to be of the same species by connecting links.

Now lions and leopards have certain characteristics in common, for instance, the retractile claws. This unites them into a larger group known as a genus, the genus *Felis*.

This genus has certain characters in common with another genus, that known as *Cynaelurus*, or the Cheetah. Their dental formula for instance is the same but *Cynaelurus* differs from *Felis* in not having retractile claws. These two genera are contained in the family *Felidae*. Another family, *Canidae*, or dogs is distinguished by well marked characters: their teeth are decidedly different from those of the cats for instance.. But in both families they are of a type framed for flesh eating, so these families with others, are united in a higher group or order, *Carnivora*. But these animals have certain characters in common with members of others orders such as Rodents (Rabbits, Rats, etc.) or Primates (Man and Monkeys): they all have hair and suckle their young. These orders are therefore united into a higher group, the class *Mammalia*.. But Mammals share with Reptiles, Frogs, and Birds the structure known as backbone or vertebral column, and are therefore united with them into one of the main divisions of the animal kingdom, the Phylum *Vertebrata*, of equal rank with other Phyla such as *Mollusca* (snails, mussels, slugs, etc.) or *Arthropoda* (spiders, crabs, insects, centipedes, etc.)

When one has mastered the elementary principles of classification it is easier to understand the arguments used in discussing the curiosities of geographical distribution. It must be remembered that this system is of the same character as a genealogical tree: all members of one group are descended from some member of bygone days belonging to the group next above: that is, while lions and leopards can boast a common ancestor of so close a degree that they can almost be called first cousins, we must search very much further back for the common ancestor of lions and wolves, and even more remotely for an ancestor who would be shared by these animals as well as by buck, rats, and whales, not to mention mankind.

The earliest known mammal appears to have been an extremely insignificant beast, and would probably be despised by an up to date guinea pig!

Armed with this small vocabulary of technical terms let us commence with the animals of the Palaeartic, or old world northern region. As regards mammals there are some very well marked characteristics. The entire group of goats and sheep, with the exception of the Rocky Mountain goat of N. America and one wild sheep in the Nilgiris of S. India, is confined to this region. The well-known Barbary sheep of N. Africa, with the long flowing hair on its throat and chest, exemplifies well that that part of Africa is, zoologically Europe and not Africa.

The true moles, family *Talpidae*, are confined to the Palaeartic and Nearctic regions, and there are two genera peculiar to the former.

Typical hedgehogs are characteristic of this region, though they are also found in S. Africa and the northern part of the Oriental region.

True Badgers of genus *Meles* are only found here, and there are several peculiar genera of deer.

Among birds many genera are only Palaearctic; Robins, the Long-tailed Tit, Bullfinches, Pheasants (except for one species in Formosa which lies in the Oriental region). There are genera of reptiles confined to this region such as *Lacerta*, to which belongs our common English lizard and the green lizard of South Europe. Among amphibia the newt-like Salamander is confined to the Palaearctic region.

Insects characteristic of this region are the curious butterflies of genus *Parnassius* found on mountains: the European species thinly scaled dull yellowish white spotted with black and red or yellow are, some of them, familiar to visitors to Switzerland in the summer: a few species are known also on the Rocky Mountains. A very important genus of ground beetles, *Carabus*, familiar to gardeners, is also characteristic of the Palaearctic region.

We now pass to consider the Ethiopian region, composed of the African continent south of the tropic, that part of Arabia south of the tropic, and Madagascar with its associated isles.

This region is characterised very clearly by deficiencies as well as by the presence of certain predominant groups. For instance the Ethiopian region differs from all the others save the Australian in having no bears and no deer, both of which occur in that northern part of Africa belonging to the Palaearctic region. Nor has it any wild oxen which abound in Asia and even occur in Europe—or did, until the European bison of the Caucasus was destroyed by the Bolsheviks as having been reserved for royal hunters. Wild sheep also are absent from this region. As if to compensate for this the Ethiopian region is characterised by the great development of other families of hollow-horned ruminants commonly grouped together under the popular "Antelopes." While these are wholly absent at the present from the Palaearctic region, they are sparsely represented in the Oriental region by the Nygliare and Blackbuck, and in the Palaearctic region by a single rather curious animal connecting antelopes with giraffes and deer, namely the Prong-horn buck. Other well-known characteristics of the Ethiopian region are the Hippopotamus, and Giraffe with its cousin the Okapi. This region shares with the Palaearctic the family *Equidae* to which the Zebras and Wild-Asses belong, and with the Oriental region Elephants, Rhinos, Lions, Leopards, Civets, Hyaenas, etc.

The higher monkeys known as Anthropoid apes are especially characteristic of the Ethiopian and Oriental regions: Gorillas and

Chimpanzees are found only in the former. Baboons are found nowhere else. The very peculiar lemurs—the lowest members of the order Primates—which represent a stage in the past history of man and the monkeys are found in this region in so great a proportion of their total numbers that they are extremely characteristic of it: a few occur in the Oriental region. The families of Elephant-Shrews and Golden Moles are only found in the Ethiopian region. The very lowly order of *Edentata* is represented by forms such as the Aard-vark peculiar to this region, while others, such as the *Manis*, often erroneously called Armadillos, are shared with the Oriental region. Among birds, Guinea-fowls, Plaintain-eaters, and Colies or “ Mouse birds ” are found nowhere else. Hornbills and Sunbirds are shared with the Oriental region: the Ostrich family is shared with the Oriental and Neotropical regions. The Secretary bird and Whale-headed Stork form genera found nowhere else.

Among reptiles may be mentioned Puff Adders and Chamaeleons as confined to the Ethiopian region: while it shares with the Oriental region such families as Pythons and Cobras.

Among insects one family of butterflies is particularly characteristic, namely the *Acraeinae*, which is familiar to everyone by at least one or two common species of black and scarlet, or brown, or yellow, conspicuous butterflies of forests and woodlands.

Among two winged flies the genus *Glossina* or Tse-tse flies is at the present day confined to this region, and the fact that one species extends into Arabia shows well the difference between geographical and zoological regions: another fact, that *Glossina* is found in Colorado shows well the difference between present and past distribution of a species.

The molluscs of the Ethiopian region also show peculiarities—the huge *Achatina*, largest of all known land shells, are confined to it.

We now come to consider the Oriental region, geographically small but zoologically of high importance. Roughly, it comprises the mainland of Asia south of the Himalayas and a rather ill-defined line eastwards to the coast of China, and the Malay Archipelago as far as the Philippines, Borneo and Java. There is not, as there was shown to be in the Ethiopian region, a great development of one group of animals characteristic of the Oriental region, but there are many peculiar forms. Thus the strange insectivorous creature known as *Galeopithecus*, which volplanes from tree to tree by virtue of parachutes of skin stretched between its limbs, is found nowhere else. A whole family of large, furry tailed Tree-Shrews is only found in this region. Among the *Felidae* while Lions and Leopard are shared with the Ethiopian region, the Tiger is peculiar.

The anthropoid apes are represented by the Gibbons, and the Orang Utang, confined to Borneo.

An extremely interesting large animal, illustrative of the peculiarities of distribution, is the Tapir of Malay, whose nearest living relative is found in South America!

Of birds, there are many splendid Pheasants confined to this region, and the jungle fowl from which are derived our fowls also is not found elsewhere: the same is the case with the Tailor birds. Abundant Hornbills and Barbets are shared with the Ethiopian region. Reptiles are extremely abundant but the species are not especially characteristic. The insects of the Oriental region are of extreme beauty; the Swallow-tail butterflies reaching a size and grandeur unsurpassed elsewhere.

Contiguous with the Oriental region, indeed separated from it only by a very remarkable boundary line to be discussed later, is the Australian region which has more peculiarities than any other. Its great feature is the almost total absence of the forms of animals which abound elsewhere, their place being taken in a remarkable manner by the order of Marsupials, characterised by the pouch in which the young animal, born in a very incomplete state of development, is nourished until it is able to get about. The different types of smaller animals in the regions previously mentioned are matched by marsupials; some are analogous to wolves, others take the place of Genets, Weasels, etc.: some are rabbit-like, some insectivorous, but there are none to represent the larger herbivores: there is a marsupial mole, even! It is perhaps too much to expect marsupial bats! Well-known examples of Marsupials are Kangaroos and their smaller relations Wallabies, Bandicoots, and the Opossums (or Phalangers, for the name Opossum more properly belongs to the American animal).

Especially to be noted in the Australian region are the lowliest of all Mammals, the Duck-billed Platypus and spiny Anteater or Echidna, which have reptilian affinities and lay eggs like reptiles and birds. The birds of the Australian region are by no means so remarkable as the mammals, although there are remarkable absentees: for instance, such widely distributed families as Vultures, Woodpeckers, Barbets, Pheasants and Bulbuls are quite unrepresented.

Parrots are extremely abundant and great Goatsuckers ("More-porks") and Kingfishers (Laughing Jackass) are noticeable features of bird life.

Lyre-birds, and the remarkable Mound-building Megapodes which leave their eggs to hatch in a heap of vegetable refuse, are only found in the Australian region. The Ostrich family is represented by,

Emus and Cassowaries. The wonderful Birds-of-Paradise are found nowhere else in the world but in a part of this region, namely New Guinea and its neighbouring islands. As regards Reptiles, this region possesses an example which equals in interest to the Duck-billed-platypus, as it is of extreme antiquity and the only living representative of a group that flourished in the age of reptiles before mammals appeared, this is the lizard-like Tuatera of New Zealand.

We now come to America, divided into Nearctic and Neotropical regions. The Nearctic region is so close to the Palaearctic, and passage across the narrow straits from one to the other would be made so easy by slight alterations of level of the submerged land that it is not surprising that there are no very marked differences between the respective faunas.

The Nearctic region has no Hedgehogs, Wild Pigs, or Dormice and only one species of wild Goat (the Rocky Mountain Goat) opposed to score of Sheep and Goats in the Palaearctic region. But Cats, Wolves, Foxes, Bears, Squirrels, Beavers, Marmots, Reindeer, Elk, all show very close relations between these two regions. Even the bison, now thought of as so characteristic of America, has its counterpart in the European bison of the Caucasus, though I believe they have now all been destroyed by the Bolshevists.

The Racoons, however, are peculiar to this part of the world, and the Skunks are quite different from their nearest Asiatic relations.

The Prong-horn buck is a very interesting animal peculiar to this region and forms a special family which is in some ways a link between deer and antelope. The American Opossum is of great interest as it is of the ancient family of Marsupials which are so prominent a feature in the Australian fauna.

Among birds there is the same general likeness to the Palaearctic fauna, but at the same time there are real differences, for instance, true Starlings and Fly-catchers are absent. But certain well-marked families are only found in the Nearctic region, for instance Turkeys and Blue-Jays. The reptiles are more characteristic; one need only mention Rattlesnakes and Iguanas which are found nowhere else.

Lastly, there is the Neotropical region, comprising, roughly, Central and South America where we find a very remarkable assemblage of peculiar forms. Thus, the monkeys with prehensile tails, Marmosets, blood-sucking Bats, Sloths, Armadillos, and Ant-eaters are found nowhere else. The pig family is represented by the Peccaries, the Camel family by llamas: among rodents the Chinchillas, Capybara and Agoutis are peculiar to the Neotropical region.

The Tapir of South America has its only near relative in the Malay Archipelago. There are some interesting links with the

Ethiopian region among the mammals of the very lowly group Edentata—the lowest group but one of mammals. The Edentates reach their maximum number in the Sloths, Armadillos, and Ant-eaters of South America, but there are representatives in Africa in the scaly Manis (often erroneously called Armadillos, just as the big monitor lizard is erroneously called iguana) and the curious ant-eating “ Aard vark ” (*Orycteropus*). Another link with the Ethiopian region is provided by Snakes, a certain family of which is almost entirely confined to South America, but one species occurs in Africa: it is at present only known by two specimens, one from Katanga in the Brussels Museum and one, found by the writer in Portuguese East Africa, in the British Museum.

The birds of the Neotropical region are as characteristic as the mammals. Humming-birds, for instance, Tanagers, Toucans, Macaws, Curassows and many others whose names are less familiar. It is interesting to note that the ostrich family is represented by the Rhea. As with mammals, there are striking absentees. Thus there are no Tits, true Flycatchers, Shrikes, Sunbirds, Starlings, Bee-eaters, or Rollers. Among insects may be mentioned the very characteristic butterflies *Heliconinae* and *Ithomiinae*.

Study of the vegetation of these five main regions shows similar phenomena: for instance the *Eucalyptus* of Australia; but there is no occasion here, as we are dealing with animals, to go into the flora. Suffice it to say that any naturalist dropped from the skies into a region of whose place on the map he was ignorant would soon be able to decide by the life around him what part of the globe he had entered.

This important principle leads us to a most fascinating theme, the decision as to the origin of any island or group of islands by the study of the forms of life found upon it.

The history of this subject is important and goes back to Charles Darwin's epoch-making voyage round the world in the “ Beagle ” in 1831-36. At that time it was, of course, known that a group of islands might show great differences in the animals inhabiting the separate islands of the group, which also might be even more different from their relations on the nearest mainland.

It was supposed, however, that they were thus different “ because they were so created,” which “ explanation ” sufficiently stifled all further enquiry. On his visit to South America Charles Darwin noted that he was particularly struck by the character of the fossils which he found there. As we have seen, one of the characteristics of the Neotropical fauna is that here is the metropolis of the lowly mammals known as *Edentata*, and Darwin was much impressed by finding abundant fossils of extinct beasts of giant size belonging to the same

order. He was thus led to conclude that there was *some relation by descent between animals succeeding each other in the same area.* This conclusion, of the most fundamental importance, was thus directly opposed to the theory of special creation.. For why should a series of animals following each other in time bear obvious resemblances to each other if each type was specially created?

On the other hand, as Darwin wrote in his journal, "this wonderful relationship in the same continent between the dead and living will, I do not doubt, hereafter throw more light on the appearance of organic beings on our earth and their disappearance from it, than any other class of facts."

The other fact of supreme importance which impressed Darwin was the relation between the animals and plants of several islands of the Galapagos archipelago on the equator in the South Pacific Ocean, and also the relation between the archipelago as a whole and the mainland of South America, six hundred miles to the east (Map I.). Darwin wrote in his journal, "one is astonished at the amount of 'creative force' displayed on these small barren and rocky islands and still more so at its diverse and yet analogous action on points so near each other."

A little more detail about the forms of life on these islands will help the understanding of the argument.. On the archipelago there are probably no mammals indigenous, save possibly one species of mouse. Of twenty-six species of land birds twenty-five are peculiar to the islands and thirteen of these are "a most singular group of finches," showing great differences on individual islands but forming such a nicely graded series in such matters as the size of the beak that, as Darwin wrote, "one might really fancy that from an original paucity of birds in this archipelago one species had been taken and modified for different ends." Even more striking than the birds of this small group of islands are the reptiles. A genus of large lizards is represented by two species found nowhere else in the world, one of them being terrestrial, the other aquatic; their nearest allies are the Iguanas which are confined to South America, a significant fact. (This is, perhaps, a suitable place in which to make a strong protest against the widespread and erroneous habit of calling the big Monitor, or Varanus, lizard by the same name as the very distinct South American species.. This habit of transferring names from one continent to another is almost as confusing to the uninitiated as the wonderful grouping of animals, as in a menagerie, in that famous book, "The Swiss Family Robinson."!).

The Galapagos lizards are herbivorous, the aquatic species being remarkable for that reason as it is the only known existing lizard which lives on sea-weed.

Perhaps the best known inhabitants of the Galapagos isles are the Giant Tortoises, some of which may be seen in Zoological gardens; they are found in nearly all the islands of the archipelago.

A most important point is that amphibia (frogs, toads, etc.), are not found on these islands, which peculiarity at once stamps them, with others sharing the same feature, as forming a zoological class of islands: more will be said on this point.

Taking the Galapagos fauna as a whole it is found that its natural affinities are with South America.. Now if the fauna was produced by a special act of creation, why should it especially resemble that of South America any more than that of Africa or elsewhere?

But if a theory of descent is considered, what more natural than that the animals of Galapagos should have been derived from some ancestors which in the far, far past found their way to the islands, and then, being isolated from the competition by large numbers of other similar organisms which is so fierce in large densely populated areas, developed along their own lines into the peculiar genera and species now found nowhere else in the world.

In the fossils of the South American mainland and the fauna of the Galapagos archipelago we have two facts which did more than any others to set Darwin at work on his hypothesis of evolution; the doctrine of the origin of species by means of natural selection modifying the material offered by forms each bound by heredity to a certain degree of resemblance to their parents and each as certainly bound by the fundamental facts of variation to differ from them.

Let us now turn aside for a moment from the study of life to the study of islands in their purely geographical aspect: we shall see that there are two types.. It must be remembered, as I said before, that the details of the surface of the earth have changed immensely in level and that what is now dry land may have been under water; but the reverse is also the case.

So study of the present coast line of an island must be associated with investigation of the past history of that island, by an examination of the submerged land in its vicinity.

There are seen to be two main types. Firstly those which are separated from the adjacent continental areas by such shallow water that a comparatively slight elevation of the submerged part would connect up the whole. Such islands are spoken of as *continental*: that is, at some time or another they have formed part of a continent.

The most obvious example is Great Britain.

The second type of island was clearly expounded by Darwin who showed that with very few exceptions all the remoter islands of the

great oceans were of volcanic or coralline formation and that none of them contained indigenous mammals or amphibia. Such islands are termed Oceanic; they are usually surrounded by seas of considerable depth and occupy isolated positions; such are the Galapagos islands already discussed. It is quite obvious that oceanic islands, having been for all time isolated, cannot be expected to support, by any theory of descent, any four-footed animals except under very exceptional circumstances; for how would their ancestors have got there? But if the fauna of any island were specially created as such there seems no reason why four-footed animals should not have been created there as easily as on mainland.

The same applies to the amphibia. Consequently, the fact that oceanic islands are without indigenous mammals or amphibia is a very powerful argument for evolution. The difficulty that amphibia have to face is not that of transport of the *adults*, but of the eggs. In reptiles it is probable that the eggs, protected by shells, have been transported great distances on floating timber, torn up from a river bank by a flood and washed out to sea. But the soft shell-less eggs of amphibia which require fresh water for their development cannot be thus transported.

Birds can be carried by gales—so can insects; molluses, and eggs of insects, can be transported on trees like those of reptiles. Even adult reptiles are known to have been carried enormous distances across seas in this way.

It is sometimes difficult to realise that the creatures on an oceanic island must be descendants of some individual that has been brought there by chance from time to time since long ages ago, but if the prevailing winds and currents are studied it will be found that the characteristics of the fauna of an oceanic island are such that their ancestors *could* have been brought there by winds and currents. In the case of the Galapagos islands there are very strong currents runnings thither from the American coast; had they been from the opposite direction the island fauna would have been very different, possibly Australian in character.

Let us take another example of an oceanic island, St. Helena, which occupies a very isolated position in the middle of the South Atlantic ocean, eleven hundred miles from Africa and eighteen hundred miles from South America (Map I.). It is wholly volcanic, and descends extremely steeply into the ocean: within about a mile and a half from the coast there is an abrupt ledge beyond which no bottom is reached with a sounding line of 250 fathoms. Between St. Helena and Africa is a profound gulf reaching a depth of 2,860 fathoms, and an equally deep area extends to the west and south-west.

It is clear that this island can never have been connected with any mainland.

What do we find as regards indigenous fauna? There are no indigenous mammals, reptiles, freshwater fishes, or true land birds, nor any fresh-water beetles or snails.

The chief peculiarity lies in the insects, of which the beetles have been especially studied. Two hundred and three species are known but of these seventy-four are common and widespread and have certainly been introduced by human agencies.

One hundred and twenty-nine are truly aboriginal and all of them but one are found nowhere else in the world. Their affinities are widely spread, for their nearest living relations are found in Europe, Madeira, or South Africa. Now if the insect life of past days is traced back by fossils it is found that in the Miocene age of the Tertiary epoch there were living in what is now Switzerland beetles of types which at the present moment are found in Europe, tropical, and South Africa, and South America. It is therefore possible that the insect fauna of St. Helena has an origin as remote as the Miocene age; that the ancestors may have reached the island from Europe, Africa, or America.

The characteristic vegetation of St. Helena has been almost entirely destroyed by human agencies, but the remnant that is still to be found in the less accessible parts of the island is as peculiar as the fauna. There are now about fifty truly indigenous-flowering plants, of which forty are absolutely peculiar to the island, and their affinities are mainly African. It has been reported that seeds which must have floated round the Cape from Madagascar or Mauritius have been thrown on the shores of St. Helena and have sometimes germinated. On the other hand there is a distinctly American relationship, especially among the species which bear evidence of greatest antiquity.

In conclusion, Wallace's words may be quoted: "We have here an island of small size and great antiquity, very distant from every other land, and probably at no time very much less distant from surrounding continents, which became stocked by chance immigrants from other countries at some remote epoch and which has preserved many of their more or less modified descendants to the present time."

Now let us turn to Continental islands, commencing with Great Britain. The fauna of our native land is in the great majority of cases identical with that of Europe showing that the separation from the continent must have been very recent so that there has not been sufficient time for British species to become, through isolation and cumulative selection of small variations, very different from their

cousins on the continent. Yet there *are* some differences and it may surprise some readers to hear that in the Red Grouse we have a bird peculiar to Britain, though it is doubtful whether the differences which distinguish it from its nearest relative, the Willow-grouse of Norway, are sufficient to entitle it to rank as a good species. More interesting still, from its extremely limited distribution, is a species of Wren only found in St. Kilda's isle.

As regards fish, Wallace gives a list of "no less than fourteen well-marked species of fresh-water fishes altogether peculiar to the British Isles"; all belonging to the salmon family and some of them only to be found in one or two small lakes in Wales!

As regards insects, we had at one time a definite British butterfly, a form of the "Large Copper" of the continent.

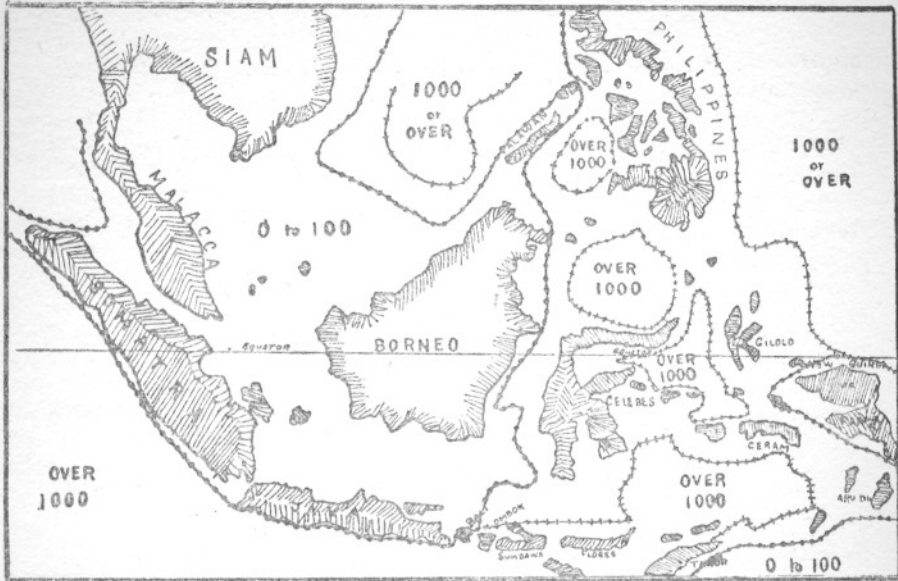
On the whole, however, the fauna of Great Britain is strictly continental and indicates very recent union with the continent.

Let us now go to the east and examine a similar state of affairs in the largest island of the Oriental region, namely Borneo. This island has about one hundred and seventy-five species of mammals, of which one-third are peculiar to it: for instance the extraordinary "Proboscis monkey." But, taken as a whole there is an almost perfect identity in *general* character with the fauna of Sumatra and the Malay peninsula to the west. So that it seems as if Borneo as an island may be no older than Great Britain, as it is separated from the mainland nowhere by a depth greater than 100 fathoms. But the matter is not so simple as it seems at first sight, and a little study of the conditions on Java will help to elucidate matters. (Map II)..

Java has ninety species of mammals, fewer than Borneo, and apparently less peculiar. But there are remarkable absentees from Java such as Elephants, Bears, and the Malayan Tapir, all found on Borneo. Of birds there are at least twenty-five genera typically Malayan, which are absent from Java. There are other curious facts: thus there are several cases in which a species occurs on Borneo, Sumatra, and the Malay peninsula, but is replaced on Java by an allied species. But there are also special relations between Java and the Asiatic continent. Thus, a Rhinoceros and a species of Hare are natives also of Indo-Chinese countries, *but not of typical Malaya*. There are five genera of birds inhabiting Java, Indo-China, and Himalaya but not Malacca, Sumatra, or Borneo. The very distinct Javanese peacock only inhabits Java *and* the Indo-Chinese countries.

How can these—and other facts which are too numerous to be given here—be explained?

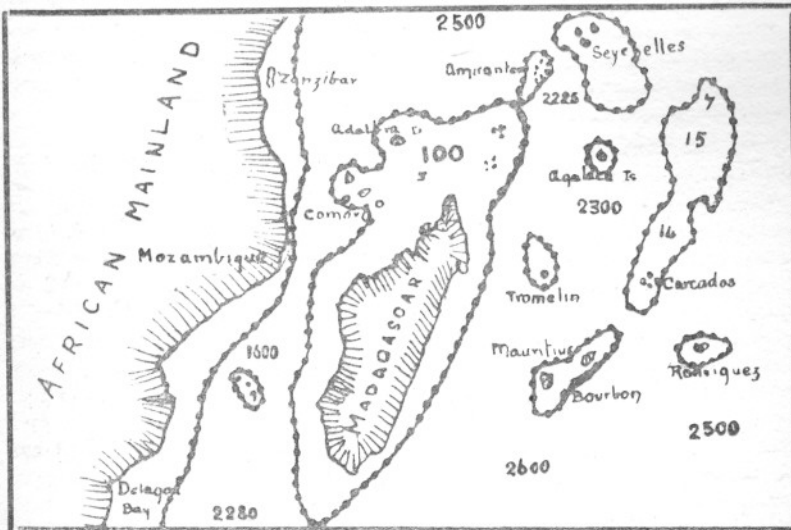
MAP II.



Adapted from two Illustrations of WALLACE's in "The Malay Archipelago"

--- Separates 100 from between 100 and 1000. Depths in fathoms.
 -o-o-o- Separates 1000 from over 1000.

MAP III.



THE MADAGASCAR GROUP, (after Wallace)

-o-o-o- Boundary between depths under and over 1000 fathoms.
 Figures show depths in fathoms.

Java and Sumatra are mainly volcanic, but not entirely, for in Sumatra are extensive tertiary rocks of Eocene age overlain by beds of coal through which the volcanoes have burst. In the southern part of Java there are rocks of Miocene age: that is to say they are of later date than the tertiaries of Sumatra which were above water, while the Javanese rocks were still being deposited under water.

In the Miocene age Java was probably three thousand feet lower than at the present time and entirely submerged, while Sumatra and Borneo were fragmentarily represented by a few small islands. Elevation at a later date raised these so that the whole became united with the continent. When the northern hemisphere was cooled by the glacial epoch a few Himalayan species of birds and animals may have found their way into suitable parts of the whole area. Java then became separated by subsidence, so that the visitors were imprisoned, while those in the remaining parts could again migrate northwards and follow the cooler climate as the glaciers receded: the equatorial forests being unsuited to creatures from the cooler climes of the Himalayan area, but more suited to the typical Malayan fauna. At a later date, the subsidence continuing, Borneo and Sumatra would have been separated from each other and from the continent, so that on each island specialisation would continue, but they would contain few of the continental species still left on Java.

In such a way does the study of animal life and its distribution help us to understand past changes in geography.

When dealing with the Malay region it is extremely interesting to note that in the chain of islands running eastwards from Java we gradually approach the north coast of Australia. The next isle to Java is Bali, then comes Lombok, and beyond Lombok some half dozen more, ending with Timor, the Aru islands, and New Guinea. (Map II.).

Now one end of the chain, Java, is typically Oriental in its fauna, the other, New Guinea, as typically Australian, and it was one of Wallace's masterpieces of natural history to discover that between the small islands of Bali and Lombok, a most definite line of demarcation runs, which has been aptly termed Wallace's line. The fauna on islands to the west of this line is mainly derived from the Oriental region, to the east, from the Australian region. In Wallace's great work "The Geographical distribution of animals," a very full account of this wonderfully interesting difference is given, but as I have not a copy with me at the moment a quotation may be made from the same author's "Island Life."

"In the Malay Archipelago there are two islands named Bali and Lombok, each about as large as Corsica, and separated by a

strait only fifteen miles wide at its narrowest part. Yet these islands differ far more from each other in their birds and quadrupeds than do England and Japan. The birds of one are extremely *unlike* those of the other, the difference being such as to strike even the most ordinary observer. Bali has red and green Woodpeckers, Barbets, Weaver-birds and Black and White Magpie-robins, none of which are found in Lombok, where, however, we find screaming Cokatoos and Friar-birds and the strange mound-building Megapodes which are all equally unknown in Bali."

There can hardly be a better example of the fascination of the study of the distribution of animals and the unexpected results to which it leads, so different from what might have been expected from a study of the map.

A study of purely geographical features would leave anyone hopelessly confused who tried to draw a line between Asia and Australia: zoology says clearly that the line lies between Bali and Lombok.

Let us now turn to another of the great Malay islands, Celebes, whose peculiar shape makes it readily found on a map: it lies between Borneo and the New Guinea group of islands; that is, it has on its west the Oriental fauna, on its east the Australian fauna.

The Asiatic isles are bounded to the east by a submarine bank, mostly less than fifty fathoms below the surface, stretching out from the Malay Peninsula as far as Java, Sumatra, Borneo, and the Philippines. Eastwards another bank unites New Guinea and the Papuan isles with Australia.

The zoology of Celebes is peculiar and it cannot be said to belong definitely to either Oriental or Australian regions. There are on this island only forty-four terrestrial mammals, so that there is a great contrast with Borneo. Twenty-three of these mammals are peculiar to Celebes; of those species not peculiar the greater number are found in the Malayan region and the Asiatic continent, but there are several peculiar mice and two marsupials (Phalangiers, or Australian Opossums), which must have come from the Australian region.

Indications of isolation and extreme insular antiquity are the facts that the fauna on the whole is poor in species and that while the arboreal rodents are better represented than most other orders there is a large proportion of peculiar species. The fact that there are peculiar species of monkeys and squirrels which here reach the farthest extension of these groups in the eastern tropics, and the two marsupials which here represent the farthest extension westwards of this group, illustrates well the double origin of life on Celebes. Moreover, Celebes possesses three large animals not closely allied to any species found

elsewhere in Asia! One is a tail-less, black, baboon-like ape; another, the Anoa, which is in some degree transitional between antelopes and buffalos, and the third is a most monstrous form of pig called the Babirusa whose great upturned tusks find their nearest analogy in the African 'Wart-hog.

There seems thus to be a certain indication of affinity with the Ethiopian region, the headquarters of the antelopes and the only part of the world where Baboons and Wart-hogs are found; but this does not necessarily imply land connection. These three animals are of probably ancient types which have been preserved in Celebes by long isolation but in Africa gave way to the more specialized descendants of the present day. It is therefore clear that Celebes must have been separated from the great northern continent at a much earlier date than Borneo, Sumatra or Java, when the more primitive animals held sway. But why did so few obtain access to the land which now forms the island of Celebes? Possibly the connection was so poor, so incomplete, or lasted for comparatively short a time that only a few animals found their way across narrow straits.

This supposition is supported by study of the birds. As with animals there are peculiar types indicating long isolation but also there are lacking so many of the important Oriental families that it is impossible to suppose that Celebes can ever have had broad connection with the main mass of Asia, but that at long ages past a few forms found their way across a narrow strait or by a chain of islets.

Celebes can thus not be claimed as a Continental island as strictly as Borneo or Great Britain, in so far as possible connection with Asia is concerned. But the same arguments hold good against extensive land connections with Australia, for of all the hosts of marsupial animals in Australia only two small arboreal forms occur in Celebes which might easily have been carried across on trees uprooted by floods or earthquake disasters. The Australian members of the Ostrich family (Emu, Cassowary) never reached Celebes.

Among insects, the butterflies of Celebes have some well-marked peculiarities. Many of them, belonging to different families, show a peculiar arched shape of the front margin of the fore-wings at once distinguishing them from their near relatives elsewhere and implying prolonged isolation of the island.

The facts quoted above, together with others which need not be given in detail here, thus suggests that Celebes is a fragment of the great eastern continent of bygone ages—perhaps of Miocene date—which has preserved little altered some remnants of its ancient animal life. As Wallace says: "there is no other example on the globe of an island so closely surrounded by other islands on every side yet preserving such a marked individuality in its forms of life."

We now turn to the study of the history of Africa in the view of light thrown up on it by zoology, in particular that of Madagascar and the neighbouring islands. It will be remembered that Africa lies in two zoological regions; north of the tropic it is Palaearctic and has relations with Europe; south of the tropic it forms the Ethiopian region whose characteristics have been already broadly outlined. (Map I.).

Soundings of the Indian Ocean around Madagascar and its neighbours show that Madagascar and the Comoro Isles lie on a bank only one thousand fathoms below the surface so that an elevation of that amount would immensely narrow the Mozambique channel to about a quarter of its present width (Map III.). In passing it may be said that an elevation (or depression) of part of the earth's surface for six thousand feet is perfectly possible, as shown by geology in many parts of the world—the Alps, for instance, and the Andes of South America, where strata are found which must have been laid down beneath water.

North of Madagascar, the Seychelles and some other islands lie on another very extensive bank marked by the thousand fathoms line. To the east there is another bank marked out by the same line almost as large as Madagascar itself, and south of that, and due east of Madagascar lies another bank enclosed by the thousand fathom line and containing the islands of Bourbon and Mauritius. These two however are separated from Madagascar, as is Madagascar from the mainland, by a channel of over one thousand fathoms depth which due east of Madagascar exceeds two thousand fathoms.

To the north-east of all these and across the Indian ocean are the Chagos and Maldive archipelagos: coral islands that possibly mark the position of other bygone islands now sunk beneath the sea which, with those already mentioned would form a series of stepping-stones between Africa and India. (See Map I.).

Before considering the fauna of Madagascar in particular let us consider some families of the animal kingdom which the Ethiopian region shares, or does not share, with other regions of the globe.

The Camel family is well-known in geographical Africa at the present day, but does not occur, broadly speaking, in the Ethiopian region. (As a matter of fact there are no *wild* Camels anywhere in Africa: the present day African Camel is always domesticated and its origin is "wrap in mystery"). But they are represented in Asia, and in South America by the Llamas).

Bears, similarly, occur in the Palaearctic region, also in the Oriental, Nearctic, and Neotropical regions, but are absent from the Ethiopian. The Ostrich family is represented in the Ethiopian, Neotropical, and Australian regions but not at the present day, in the

Oriental or Palaerctic regions, though fossil members of the family are found in India, Russia, and Greece. As regards Camels, fossils show that they were a very important group in bygone days, and especially abounded in America. Asia has for all time been so close to America that it is not surprising that the Camels should range into the Palaearctic region which, it must be remembered includes *north* Africa. But, apparently, at the hey-day of camel life their transit further south into Africa was denied by the existence of a broad sea covering what is now the Sahara.

The Bear family, similarly, appears to have ranged widely over the old and new world but at a time when the Sahara sea prevented access to the Ethiopian region. Otherwise was it with the Ostrich family which ranged all over the world at a time when free access from north to south Africa was possible, and it occurred in all the great regions

The somewhat curious distribution of the Antelope family shows that whereas the ancestors must have entered Africa at a time when there was free communication with Asia (for there are several antelopes in Asia and one in North America) their extraordinary development in the Ethiopian region shows that before the family reached its zenith the Sahara was submerged and the southern forms were left to develop along their own lines, secure from competition by their near relatives the sheep and goats and more remote cousins the deer, which never reached Ethiopia although found in Palaearctic Africa.

Presumably a similar chronological history accounts for the absence of bear from Ethiopia.

Such are some of the very interesting broad questions of distribution as they affect the Ethiopian region, and they help us to understand the peculiarities of the fauna of Madagascar; the process of isolation from the mainland of Africa seem to have effects analogous to the separation of the Ethiopian region from the great northern mass of land. Madagascar possesses no less than sixty-four species of mammals, which is certain proof that at one time it was part of a continent. Yet with what continent was it united?

The characteristics of Africa are the Monkeys, Great Cats, Wild Asses and Zebras, Elephants, Rhinoceroses, Buffaloes, Giraffes, and Antelopes. But no one of these, *nor anything like them*, is found in Madagascar. Yet the Bears, Deer, and other animals equally characteristic of Asia are also absent!

Investigation of the wealth of animals peculiar to Madagascar shows that the predominant mammals are the Lemurs, lowly organised and primitive members of the order of Primates to which belong man, the Apes, and Monkeys. Although a few Lemurs are found in West

and East Africa, India, Ceylon and the Malay Archipelago, their headquarters are without doubt in Madagascar where they are more abundant than anywhere else in the world, and more numerous than the members of any other order of mammals.

One of the most interesting little Lemurs is the *Tarsius* of Malay, held by anatomists to represent one of the direct links in the evolution of the human race, owing to the fact that hers for the first time is the anatomy of the visual centres in the brain of a type different from that of lower animals and the same as in the higher monkeys and man.

But Madagascar is not only remarkable for its Lemurs. The order of Insectivora (represented in England by Moles and Shrews) has no less than five genera of a peculiar family which exists nowhere else in the world but in Cuba and Hayti!

The few carnivora are represented by an extremely peculiar and isolated form, the *Fossa*, having no allies in any part of the world, and by eight Civets whose nearest allies are African.

African affinities are more clearly shown by the presence of a River-hog and a recently extinct small Hippopotamus, both of which might be accounted for a chance transit across the Mozambique channel at a date when it was much narrower than it is now.

As regards birds, it may be briefly said that they exhibit the same peculiarities of presence and absence as the mammalia; that is to say, numbers of the families which seem most characteristic of the African continent are absent, such as Plantain-eaters, Glossy-Starlings, Barbets, hornbills, while out of the total of 150 land birds known to exist on Madagascar, 127 are peculiar to the island.

As regards reptiles, one of the most important families of snakes, the *Colubridæ* is represented in Madagascar by two genera found elsewhere, not in Africa or Asia, but in America, and by another genus found also in China and America. There are also two species of lizards of the family *Iguanidæ* which is otherwise exclusively American, and a genus of gecko found also in America and Australia.

What conclusions can be drawn from these strange facts? The main feature of the fauna of Madagascar is great abundance of a lowly form of mammalian life (Lemurs) coupled with absence of most of the typical higher forms of the African mainland.

Now, study of the life of bye-gone days by means of fossils shows that animals of the Lemur type occurred widely all over the world at a time before the higher types of mammals had been so abundantly developed but while the lowlier Civets and Insectivora were flourishing. In the lower Miocene period of the Tertiary epoch the peculiar family of Insectivora (*Centetidæ*) already alluded to as only found at the

present day in Madagascar and the West Indies, occurred in France. Thus their present distribution is not contrary to the argument that at that time Madagascar could have obtained its stock from Europe through Africa: if the stock had come, for instance, from America, there would not have been Civets which are not found there, nor are they found in fossil forms.

The conclusion is that the animals now isolated in Madagascar are remnants of groups which formerly were much more widely distributed, and in their comparatively lowly state of organisation are only able to hold their own because, since the hey-day of their ancestors the formerly very narrow channel between Madagascar and Africa which their ancestors were able to cross has been so widened by subsidence that the higher types such as Antelopes, big Cats, etc., never found their way across.

Imagine what havoc a Leopard would have made among the Lemurs! Probably at the time when the early forms of Lemurs and Civets were able to find their way across to Madagascar the land that is now Sahara was submerged so that the higher animals were cut off from the Ethiopian region. By the time that the Sahara emerged from the water Madagascar was too far isolated for the big Cats, Elephants, Rhinoceroses, Giraffes, Antelopes, Monkeys, etc., to get to it, although two large, freely swimming animals managed to get to it, viz., a form of Hippopotamus and a River-hog.

Birds show exactly the same thing.

Madagascar is famous for the fossil remains of gigantic birds of the Ostrich family not found elsewhere (*Aepyornis*): they are parallel with the Lemurs, but have not managed to survive to the present day.

The birds which are absent from Madagascar are analogous to those mammals which were prevented from entering it. The Plantain-eaters, for example, are known to have lived in Europe together with the large mammals characteristic of the Ethiopian region.

A certain number of birds in Madagascar are of *Oriental* rather than *Ethiopian* affinities. This can be explained by the fact that, like many other African and Indian genera, in bye-gone days they inhabited Europe too, for instance the wild Jungle-fowl, the ancestor of domestic poultry, which is found as fossils in France.

Another possibility is that the ancestors of these Indian-like birds found their way across the stepping-stones formed by the Maldiva and Chagos archipelagoes and possibly other archipelagoes of the past which are now indicated only by sunken reefs, and then to the Comoro and Seychelle islands and so to Madagascar. (Map III.).

There is not space to enter at length into the peculiarities of the fauna of the islands round Madagascar. The most famous example is that extraordinary caricature of a bird, the Dodo, a very degraded form of pigeon which from long freedom from the attacks of enemies on an isolated island had lost the power of flight and was ultimately exterminated by man so completely and thoroughly that there is not even a stuffed specimen in a museum!! It lived only on Mauritius, and an allied but less specialized form was found on the adjacent isle of Bourbon, and was known as the Solitaire.

Mauritius and Bourbon are both lofty volcanic islands and were probably never connected with Madagascar, but their existing birds show that their ancestors came from Madagascar. The dodo's ancestors probably date back to the Miocene times, that is, the time when Lemurs abounded in Africa and Madagascar was more nearly within reach. It is interesting to note that Bourbon has a snake of the Boa family found nowhere else in the world: its nearest living allies are in Australia!

The Comoro Islands contain a Lemur and a Civet closely allied to those of Madagascar so that these island were formerly more closely connected with Madagascar than they are now.

The Seychelles are more interesting. They stand on a granite bank which is probably a continuation of the main backbone of Madagascar, and are linked with it by an intervening chain of banks and islets; but at the present date they are separated by channels of one thousand fathoms or more. The entire absence of indigenous land mammals show that the Seychelles can never have been actually united with Madagascar. The birds have many peculiarities. Thirteen out of fifteen indigenous species occur nowhere else in the world: their relations are primarily with Madagascar but there are affinities with Indian species. The reptiles of the Seychelles are numerous and three of the seven species of lizards are confined to those islands. The presence of four species of Amphibia (two frogs and two of the peculiar snake-like forms known as *Coeciliadae*), shows that the Seychelles cannot be considered as true oceanic islands.

The general conclusion that can be drawn from a study of the fauna of Madagascar and the adjacent islands is as follows: these remarks are practically a quotation from Wallace's "Island Life."

Madagascar is a continental island of immense antiquity; the Comoros and Aldabra are fragments detached from it. The Seychelles are fragments of another very ancient island which *may* never have been continental; Mauritius, Bourbon, and Rodriguez are undoubtedly three oceanic islands, while in the extensive banks and coral reefs of Cargados, Saya de Malha, the Chagos and Maldive isle we have indications of the submergence of many large islands which may have

aided the transmission of organisms from India. But between and around all these islands are depths of 2,500 fathoms, or more, which render it very improbable that there has ever been a continuous land surface within the periods during which mammals were evolved. This conclusion, founded on study of the form of the sea bottom, is supported by zoological data.

If there had been continuous land connection with India as is supposed by some there should have been on Madagascar some forms of animals which could have entered from India. The Indian forms in Madagascar and adjacent islands are just those that could have passed as by steppingstone from island to island, and their relationships show that many of them came across in late Tertiary (i.e., comparatively recent) times, though others indicate a more ancient connection.

But the mammals which require continuous land connection are absent. The fact that Lemurs, mainly found in Madagascar, occur also in Asia in the Oriental region, is explicable by the fact that the animals of the present day are survivors of a very ancient family widely dispersed from Europe where it existed in very early (Eocene) Tertiary times.

Exactly the same argument applies against the supposed need for a former direct land connection with South America (perhaps via the south polar continent) and Australia. Those animals of Madagascar showing affinity with America, the curious insect-eating *Centetidae* of Madagascar and Cuba are of primitive type and may well be isolated survivors of a family more widely diffused in previous times, and similarly, the lizards which show affinity with Australia.

The further back in geological history that animals and plants are traced the wider appears to have been their distribution: in the Palaeozoic times the majority of the groups of animals and plants appear to have had a world-wide range.

Wide areas of marine deposits of early Tertiary (Eocene) age show that at that time Africa was cut off from Eurasia by an arm of the sea. But before that Africa, with Madagascar closely connected, had received the early types of mammals, and the ancestors of the Ostriches and their gigantic *Aepyornis* relatives now only known from fossils in Madagascar, and the reptiles and insects of American affinities.

At that time fossils show that all the types of large mammals now found in Africa but absent from Madagascar inhabited Eurasia and many of them (in the middle tertiary period) also North America.

But before the later, continental period in the history of Africa, when the larger animals could have passed across the Sahara,

Madagascar had become separated from the mainland and was able to develop in a particular direction its Lemurs and Ostrich-like birds. From it the adjacent small islands received such animals as could cross over, and in its turn, it received from India, through them, a small proportion of Indian creatures.

I now propose to spend a little time in consideration of interesting facts of geographical distribution brought out by the study of butterflies and more particularly the phenomena known as mimicry. In this matter we have no fossils to guide us, for fossil butterflies do not show the colours on which mimicry depends.

By mimicry is meant, not likeness to twigs, rocks, leaves, thorns, etc., which is more accurately known as cryptic resemblance, but the resemblance of one insect to another of a group quite distinct from it in anatomical features, though the degree of relationship may be of all kinds, from the close affinity between species of the same genus to the immense difference between, say, an insect and a spider.

In order to have a mimic there must be a model; this term is applied to the insect which enjoys a relative degree of immunity from attacks of insectivorous animals or birds owing to unpleasant qualities advertised by simple and easily recognised colours and patterns. The mimic has been altered from its former appearance by the action of natural selection upon chance variations which provided a first degree of likeness to some model; this likeness being intensified by selection during successive generations. It is not intended here to enter into a discussion of mimicry as such; it is used here to exemplify some of the facts of distribution. By a curious coincidence, as I was preparing this article, I received a recent publication of the Entomological Society (Parts III., IV., of the Transaction for 1923) in which is a paper on mimicry in the butterflies of Fiji by Professor Poulton, F.R.S., of Oxford.

He produces evidence in support of Wallace's theory of the crossing of birds from India to Madagascar by means of island stepping stones. A family of butterflies possessing all the necessary characters of models is the *Euplœinae*, very common and widespread in the east, and much mimicked by other butterflies, including species of *Hypolimnas* nearly related to the well-known *H. misippus* common all over Africa and elsewhere.

A very common and widespread species in the east is *Hypolimnas bolina*, which has extended its range from India to Madagascar in the present century. The Indian race of *bolina* was first seen in Madagascar in 1903 and has very rapidly increased its range and numbers throughout the island.

But on the Chagos Islands in the Indian Ocean, far to the north-east of Mauritius and Bourbon is a peculiar race found nowhere

else in the world. Professor Poulton says: " This race must have reached these islands long ago, for the female form is different from any other in the known range of *bolina*, being an evident mimic of *Euplœa euphon* now only known in Mauritius but mimicked by the female of *Papilio phorbanta* in Bourbon and therefore formerly a resident in that island. A glance at the map of the Indian Ocean at once suggests that this Oriental *Euplœa*, and *E. mitra* of the Seychelles, reached their present localities by way of the Laccadive, Maldiva, and Chagos groups and the islands between them; thence westward and south-westward by many other scattered islands. The route of the invading *euphon* clearly passed through the Chagos group, and it is not an extravagant exercise of the imagination to see in the race *bolina euphonoides* the persistent effect of its residence in these islands."

Thus does a type of butterfly which serves as a model leave its footprints in the country through which it passes!

The most widely known mimic in Africa (because the first described example in our continent) is the swallow-tail, *Papilio dardanus*, about which Professor Poulton has written an account especially for this journal.

But as I have said so much about Madagascar in this article, I cannot refrain from pointing out the great interest of this butterfly in connection with Madagascar. The host of forms of female on the continent, all differing from the male and from each other, are quite unrepresented in the race of this butterfly (or perhaps the allied species) named *meriones* which is only found on Madagascar. In *meriones* the female only differs from the male very slightly, and is held to represent the ancient type from which the females of the continent developed along different lines after Madagascar was widely separated from the mainland.

Now let us turn to other examples of the effects produced by a distasteful butterfly which penetrates into some distant country and alters by its presence the appearance of some of the indigenous fauna.

There is, in East and South Africa, a handsome butterfly belonging to the well-known sub-family *Danainæ* but quite different in appearance from the vast majority of its nearest African relatives. This species is a handsome one with a pattern of numerous bright blue spots and streaks upon a black background. Its name is *Melinda (Tirumala) petiverana*, and it is entirely different in pattern from *Danaïa chrysippus* or any of the numerous species of *Amauris* which belong to the same family. There are one or two other species of *Melinda* somewhat similar in pattern but brown or cream instead of blue. Now the blue and black of *petiverana* is shown, by a study of geographical

distribution, to be very characteristic of the Oriental *Danaina*, there being numbers of species in that region nearly resembling *petiverana*.

The distribution of *petiverana* in East and South Africa, and the fact that in those parts it is the only one of its type, is highly suggestive of the conclusion that it is a descendant of some species of this type of colouration that entered Africa from the Oriental region.

The result has been most interesting, and is somewhat similar to the effect upon a human invader! The intruder tends to take on some of the characteristics of the aborigines. But the parallel is not quite fair, for in the case of mankind the assimilation of the invader is due to intermarriage whereas in the case of this butterfly the resulting phenomena are due to mimicry.

In East Africa *petiverana* has held its own and has proved itself to be a model sufficiently powerful to alter the appearance of a common butterfly of the Swallow-tail family, *Papilio leonidas*, so that the *Papilio* has a strong resemblance to the *Danaine*.

But as this *Danaine* intruder penetrated westwards into the heart of Africa it came into contact with a powerful "ring" or combination whose total influence must be immeasurably more powerful: I refer to the typically Ethiopian genus *Amauris*, *Danaine* butterflies also, but rather distantly related to *petiverana*. These *Amauris*, black and white, abundant, conspicuous, and distasteful, have exercised so strong an influence upon the intruder that as it came within their territory it became altered itself, and in West Africa we find, not the blue and black *petiverana* but a much darker, black and white, species known as *morgeni* resembling the dominant *Amauris* pattern of that neighbourhood. These phenomena illustrate remarkably well the complexity of mimicry; in this case the resemblance is of the class known as Mullerian, or Synaposematic; the likeness being between two groups of distasteful butterflies for their common benefit. This is not true mimicry; that term is best reserved for Pseudaposematic resemblance, that is, the resemblance of an edible species to one more distasteful, whereby one lives on the evil reputation of another. Apropos the genus *Tirumala* Professor Poulton, in his paper on the butterflies of Fiji already mentioned, shows that a species of *Tirumala* which found its way into those islands from Asia there met so strong a combination of another section of the Danaid butterflies, namely the *Euplœine* already mentioned, that the *Tirumala* has been distinctly altered to resemble the *Euplœa* pattern in those islands where the Euplocine influence is most powerful. These facts have only been made out by laborious study of great numbers of specimens most carefully labelled by the captor with exact geographical data: it may be said here, and cannot be too strongly emphasised that any collection of specimens is useless (or worse than useless because possibly leading to error) unless furnished

with the most exact data of time and place. Professor Poulton found a large number of specimens in the National collection at the British Museum quite useless for the purpose of exact study because they were only labelled Fiji and gave no information as to the individual island from which each specimen came.

Another remarkable instance of changes wrought in the indigenous fauna by the intrusion of a dominant species from elsewhere is seen in North America.

Here the invasion appears to have been from Asia by way of the Behring Straits. The very abundant butterfly—perhaps the commonest butterfly in the world—*Danais chrysippus* has already been alluded to: it is orange brown with the black tips of the forewings containing a conspicuous white patch. In Asia there are numbers of Danaines with that general type of colour and pattern, but with the "veins" of the wings heavily marked in black. This colour scheme has its headquarters in Asia, and the Danaines possessing it serve as models for mimics belonging to other groups. An abundant species of Danaine is *archippus*. This, or some ancestor resembling it, has apparently in the far past found its way into Canada and America and become slightly modified to form the species known as *plexippus*. This intruder, exactly as *petiverana* in East Africa, has modified one of the indigenous butterflies of the *Limenitis* (to which the English "White Admiral" belongs) to be a wonderfully close mimic of itself in two forms. These phenomena show conclusively that mimicry cannot be attributed to similar effects produced on different butterflies by meteorological or other local conditions. Were this so the invading species, being presumably an example of the effects produced by the conditions from which it came (Asia for example) should adopt the living of the inhabitants of the new country. Yet the reverse is the case, and the invader appears to have imposed the effect of Asiatic conditions upon species subjected to American conditions!

Lastly, let us take that most interesting and wonderful Ethiopian butterfly *Pseudacraea eurytus*, belonging to the Nymphaline sub-family, and to that section of it which includes our English "White Admiral." This is perhaps one of the most remarkable species of animal living on account of the variety of forms in which it exists, which until quite recently were all thought to be different species. The first known form was described by the great Linnaeus in 1878 from the West Coast, but the total number of distinct forms is not yet known, for new ones are constantly being discovered. The energetic secretary of this society has within the last few months obtained a new form from near Marsabit, by which the known range of *eurytus* has been enlarged to the north.

This butterfly is found in forested country from West Coast to Mombasa and from the northern border of Kenya through Tanganyika Territory, Nyasaland and Natal to Pondoland. There are wide gaps in its distribution, however: for instance, between the Uganda-Kenya border and Rabai near Mombasa I am not aware of the existence of any forms.

While the headquarters are undoubtedly in West Africa where it exists in great variety, there are several forms in Uganda, some of which are not found in West Africa. Some of the forms are confined to the male sex, others to the female, others again occur in both sexes, but, in Uganda at any rate, all these can interbreed one with another.

Until Dr. van Someren's valuable recent discovery only two forms were known in Kenya, from near Mombasa, male differing from female but both distinct from forms occurring anywhere else. In Tanganyika Territory occur a male and female, also different from each other and from anything else: similarly in Nyasaland. In Natal, however, male and female are less different from each other and one form of female resembles the male: these again are not found elsewhere. The single specimen that is known from Pondoland is again different. Taking the number of forms in Uganda as six, we must allow at least twice as many for the West Coast, so that there are at least thirty quite distinct forms of this one species of butterfly.

Imagine thirty animals each of which was really a lion; yet differing from each other as much as the lion, leopard, puma, jaguar, and other big cats which must be imagined!

There is only one explanation of these facts, this is mimicry. Every form of the one species of *Pseudacraea* is a mimic of some species of butterfly of an extremely different family, the *Acrainæ*, which have already been mentioned as so characteristic of Ethiopia. The models are species of the genus *Planema* and we find that in localities where the model is sexually di-morphic—as for instance in Kenya at Rabai—the mimic copies it sex for sex; where male and female *Planema* are alike as in two species serving as models in Uganda, the forms of *eurytus* that resemble this species are also monomorphic.

It is interesting here to note that *Pseudacraea eurytus* does not occur in Madagascar: evidently it has developed along its own lines since the wide separation of the island from mainland. But the genus *Pseudacraea* does occur on Madagascar, only the few species are non-mimetic. Now the occurrence of *Pseudacraea eurytus*, a forest loving species, over such a wide area is evidence that in former times the type of forest it requires was probably much more continuous than at the present day. We know even within our own experience the havoc wrought by native methods of cultivation and fires, and it

seems quite probable that in the presence of this butterfly at Marsabit for instance we have an indication of much more extensive forest connection with the west coast than exists at the present day. The peculiar forms of Nyasaland occur on the isolated Mount Mlanje, which may be regarded as a continental island of forest isolated by a sea of more open country.

In fact, the present discontinuity of distribution in Africa of *Pseudacraea eurytus* shows the same phenomena, from which the same conclusions can be drawn, as the world distribution at the present time of such a group as camels and ostriches.

Finally, it may be said that this article has been written to stimulate enquiry into, and collection of data bearing on, the subject of distribution of living things over the surface of the globe. Such studies cannot be pursued without collection of large numbers of specimens, but such specimens are worse than useless unless accompanied by minutely accurate data of time and place. The ideal museum has been described as "an interesting collection of labels illustrated by specimens." But at the back of every display there should be a store of great numbers of specimens from the whole area inhabited by each for the purposes of scientific study. One or two specimens of any species tell us very little about the wider facts of its life and environment.