## ANIMALS AND THEIR NATIVE COUNTRIES.

In the December number of this Review, Mr. P. L. Sclater called attention to the subject of the geographical distribution of animals in its bearing on the theory of evolution, and gave numerous special cases in which the actual distribution of particular species and groups is very difficult to explain on that theory without making assumptions which, in his opinion, the evidence at our disposal does not warrant. Difficulties of this nature are so numerous, and many of them seem to him so weighty, that, in order to explain them, he is led to question, what is almost an axiom with evolutionists, that identity of structure is, without exception, an indication of descent from a common parent. Similar doubts, though not stated in exactly the same terms, have been felt by Professor Mivart; and it therefore becomes a matter of interest to examine a little more closely into the alleged difficulties, in order to see whether they are not really explicable on the principle of descent with modification, only calling to our aid such general assumptions as are fully warranted by what we actually know of the migrations and extinctions of living things, and of the past changes in the physical condition of the earth and its inhabitants.

As Mr. Sclater's article gives an excellent summary of the nature and meaning of zoological distribution, and of the main general conclusions arrived at by naturalists, our purpose will be best attained by proceeding at once to consider his special cases of difficulty; and in doing so we shall have occasion to discuss, as fully as may be required, the general principles and particular illustrations needed to elucidate them.

We have first the case of the Little Blue Magpie of Spain, which has a very close ally in the extreme parts of Eastern Asia and Japan, while there is nothing closely allied to these in all the intervening regions or in any other part of the world. This is said to be an infringement of the canon as to the continuity of specific areas, and as such to require explanation. Before proceeding further, it will be well to inquire into the value of this canon of continuity,

<sup>1</sup> Genesis of Species, chap. iii.

to varieties which have also become dominant species and genera, which, under the somewhat changed physical conditions that in time have come about, beat it in the battle of life, and force it to retire step by step from the vast area it had overrun. First one species and then another will dwindle away and become finally extinct, and by so doing will necessarily leave gaps in its area of distribution. This process going steadily on, the time will at last come when two or three species only will remain, most likely in widely separated parts of its former area; their position being determined either by the competition being there somewhat less severe, or by some speciality of conditions which are exceptionally favourable to the dying-out group. Then one and then another of these species will die out, and the once extensive genus will only be represented by a single species inhabiting a very restricted locality. This will become rarer and rarer, the necessary preliminary to that final extinction which we know to be the fate, sooner or later, of every group of living things.

Most working naturalists (and none better than Mr. Sclater) are acquainted with genera whose distribution will illustrate all the successive phases of this hypothetical history; while palæontology furnishes us with some actual examples of the progress of a group from its rise to its decay, though, owing to the extreme imperfection of the geological record (and its total absence for important epochs in many parts of the globe), we can never trace the complete history of such a group. A little consideration will show us, however, why it is that continuity of generic and specific areas appears to be the rule, discontinuity the exception. There can be no doubt that the development of an extensive genus is a slow process, while its decay and final extinction need not be slow, and may conceivably be extremely rapid. Geological and geographical changes may be long in preparation, but finally very abrupt. Land may sink a thousand feet without producing any very important effect except diminution of area, but the next hundred feet of depression may cut it off from a continent, and may alter the direction of ocean currents, thus producing a greater organic and physical change than had been brought about by the previous subsidence occupying ten times as long. Again, such a change as that which admitted the highly organised Miocene mammalia of Europe into Tropical and South Africa must have led at once to the extermination of many of the indigenous species, and have restricted the area of many more. It is also important to remember that the dominant or growing species and genera, which are those having continuous areas, will be necessarily more prominent, more numerous in species and individuals, and therefore far better known; while those in process of extinction, and for that very reason having discontinuous areas, will be less numerous, far less common, and in fact often very rare, and therefore much less known. In many cases, too, it will happen that the discontinuity

is not great as regards distance, and it will then not be noticed, or will be imputed to want of knowledge, although it may be quite as real as when half a continent lies between the two species.

It appears, therefore, that the discontinuity of many genera and higher groups, so far from being difficult of explanation, is really one of the inevitable results of the process of extinction which is always going on. The peculiarity of the particular case we are considering is that it is somewhat extreme in the fact of two species only being left, occupying limited areas situated at the opposite extremities of the immense Palæarctic region. But this is not very extraordinary, because there are in Western Europe and Japan a number of pairs of closely allied species whose extinction in the intervening areas would lead to an exactly similar phenomenon to that we are considering. Such are the European and Japanese jays, bullfinches, goldcrest warblers, and wrens, all of which are closely allied to each other, while they are separated by a wide area in Central Asia often occupied by species which differ considerably from both. Should either of these groups die out, we might expect that the species inhabiting the comparatively desert and inhospitable regions of Central Asia would succumb first, while those living in the milder and more equable climates of Western Europe and Japan would probably linger on, the last of their race. It is very interesting to note that in most cases of such widely separated but closely allied species or groups there is a decided similarity in the general physical conditions of the countries they inhabit. The ally of the Spanish blue magpie is found in North-eastern Asia from Shanghai to Pekin and the Amoor, as well as in Japan; and these countries reproduce the hot summers and the cold winters, the rugged mountains and the sheltered valleys of Spain, while both areas are subject to the influence of the vicinity of the ocean in an almost equal degree.

Before going further we must guard against a misconception as to the progressive rise and decay of species, genera, and higher groups. It is not maintained that this will always take place uninterruptedly or continuously. On the contrary, it is certain that the decay of a group may run its course for a time, and then, owing to changed conditions, may be checked, and even be changed into a new growth and development. Hence arise those isolated groups, which yet, by their abundance in species and the considerable area they occupy, show that they are in a flourishing condition—of which the tanagers in South America, the broadbills (Eurylamidae) of Asia, and the colies of Africa, may serve as examples. When an extensive group is in process of extinction, it may become broken up into many isolated portions, sometimes in juxtaposition to each other, sometimes separated in remote parts of the globe. Changes of conditions, whether physical or organic, may favour first one, then

another, of these portions, or the same portion may be subject to alternate phases of progression and decay several times repeated. How can we wonder that the final result of such complex processes, whose general nature we can understand, but whose details it is impossible for us to trace, should often lead to anomalies in geographical distribution? And when we consider that these processes have been often intensified and further complicated by geographical mutations, and by those forced migrations induced by the climatal changes which culminated in the glacial epoch, the wonder rather is that we can account for so much, than that there should be matters of detail which we cannot explain.

It is clear, then, that the case of the Little Blue Magpie of Spain and its close ally in Eastern Asia is simply an example of a dyingout group, of which two species only remain isolated in countries favourable to their existence; and further, that the supposition of their common ancestors having once occupied the intervening region, so far from being unwarranted, is supported by the analogy of several other groups of birds in the same area.

Mr. Sclater's next two cases may be sufficiently explained by the application of the general considerations and examples already adduced. We have two allied species of Oxyrhamphus isolated in South-East Brazil and Central America-countries, it may be remarked, about equally removed from the equator and enjoying very similar climates; while in the cuckoos of the genus Neomorpha we have a similar phenomenon in nearly the same two areas, with the addition of three species in the intervening districts which are not closely allied to the two others.

We have here really only the same class of facts as occur plentifully in the Palæarctic region, in which the species of the eastern and western extremes are often alike, while those that intervene are more diverse. We can, without much difficulty, refer this latter peculiarity to diversity or similarity of climate and physical conditions, while in the Neotropical region it is more probable that a diversity of organic conditions may have been the agent at work. There is some reason to believe that the great plateau of Guiana long formed an island, and that this isolation led to the development of several peculiar forms, which have in some cases spread into Upper Amazonia. A range of plateaux and hills, on the other hand, connects Brazil with the Andes, and has thus kept up a greater zoological continuity with Central America than the intervening area of Guiana has been able to do.

Mr. Sclater's third problem, that of Pitta angolensis, is very interesting, and will afford us an opportunity of discussing some of the most curious phenomena of distribution, and of bringing forward some considerations which I believe will go far towards the removal of most of the difficulties they present. The case is that of an extensive and very beautiful group of birds, ranging from the Himalayas to Eastern Australia, but having one species isolated in Western Africa. Mr. Sclater has himself mentioned a few parallel cases, but there are others equally interesting, a consideration of which may aid us in our attempted explanation. We have first the gorilla and chimpanzee, corresponding to the orange of Borneo and Sumatra; and among the quadrumana the genus Cercocebus allied to the Eastern macaques is wholly West African, while Colobus, closely allied to the Asiatic Semnopithecus, is found in Abyssinia as well as in West Africa. Among birds we have Alethe, a genus of babblers, and Pholidornis, one of the Dicaida, allied to Asiatic forms; while the genus of crested hornbills, Berenicornis, has one species in Sumatra and the only other in West Africa. The fruit-thrushes of the genus Criniger, so abundant in Asia and Malaya, are also found in West and in South Africa, while the beautiful eastern parroquets of the genus Palæornis inhabit West Africa and Abyssinia. Among reptiles and amphibia we have three families which follow the same rule. Lizards of the family Acontiadæ are confined to the Moluccas, Ceylon, and West and South Africa; toads of the family Engystomidæ have nearly the same range, but are more widely spread in Asia; while snakes of the family Homalopsidæ are abundant in tropical Asia and America, and are even found in Europe, while in Africa they are confined to the western districts.

These numerous cases of the occurrence of what are otherwise Eastern groups in West Africa, undoubtedly suggest some correspondence of physical conditions which renders this portion of the continent alone suitable to them. The further question, how they got there at all, is elucidated by what we know of the past history of Africa and Europe. It is now generally admitted that, before the Miocene period, Africa was cut off from the great continent of the northern hemisphere by a wide arm of the sea. It was then in fact an island, or perhaps a group of large islands, and probably contained only some of the lower forms of mammalian life, among which the lemurs and the insectivora were conspicuous. When, during the Miocene period, it became united to Europe and Asia, it was at once overrun by a number of the large mammalia of that continent, such as elephants, rhinoceroses, lions, giraffes, antelopes, hippopotami, apes, and many other forms whose remains are found in abundance in the Miocene deposits of France, Germany, Hungary, Italy, and Greece. South Europe must have then possessed a sub-tropical, if not a tropical, climate, the gradual deterioration of which led to the extinction of most of these animals, while in Africa they have survived and greatly multiplied. Among the European fossils of this period we find some of especial interest. Such are, the genus Hyomoschus, mentioned by Mr. Sclater as one of the Indian group of chevrotains still living isolated in West Africa; a monkey closely allied to Colobus and

Semnopithecus, and perhaps an ancestral form of these two groups now separated in Asia and West Africa; and among birds the snake-eating secretary bird; Necronis, supposed to be allied to the peculiarly African plantain-eaters; and a parrot allied to the well-known grey parrots of Africa. Here, then, we have traced the origin of the resemblances between certain animal forms of tropical Asia and West Africa to their having been derived from a common source in the great northern continent, and we are justified in supposing that the Pitta angolensis is also a descendant of one of these Miocene forms. A species of Pitta even now inhabits Japan, so that we may well suppose the genus to have originated in Europe or Western Asia in the warm Miocene period. It was probably once more abundant in Africa, but, along with the Hyomoschus and the crested hornbill, is now in process of extinction in the one continent, while its allies continue to flourish in the other.

Leaving for the present the next three cases of difficulty adduced by Mr. Sclater, we will pass on to the subject of allied forms occurring in the tropics of both hemispheres. Besides the barbets, which occur in the tropics of Asia, Africa, and America in almost equal abundance, we have the trogons, abundant in Asia and America, but with a single peculiar genus of two species in Africa, and the tapirs confined to the Malay islands and tropical America, while equally remarkable are two genera of snakes, Dryiophis and Dipsadoboa, confined to West Africa and tropical America. Towards an explanation of these curious anomalies we have the very interesting fact, that tapirs closely resembling those now living abounded in Europe during the Miocene period, and continued to live in the Pliocene period, both in France and England, as well as in North America. This suggests that a tropical climate is not essential to these animals, and that their present restricted range is due to other than climatal causes. We may also be sure that if they could live so far north as our island in the Pliocene period, they might have ranged considerably further north during the earlier and warmer Miocene. The only difficulty is, how did these Miocene tapirs reach America? and if we can find any reasonable answer to this question we may consider that it will equally apply to all the other cases which have been mentioned.

The close relation between many of the extinct mammalia of North America and Europe at successive periods, while in other cases entire groups have always been restricted to one continent only, renders it certain that there existed at several distinct epochs some land connection sufficient to enable terrestrial animals to pass between them. The sea at Behring Strait is so shallow that we may safely conclude that the continents of Asia and America have here been recently connected, while the shallow Okhotsk, Japan, and Yellow seas indicate a large extension of the lowlands of Eastern Asia; but the very deep Atlantic comes up to beyond 55° N. latitude on the east side of

Kamschatka, so that this part of the connecting land would probably always have had a temperate rather than a tropical climate. On the European side we find between the west of Ireland and Newfoundland a maximum depth of about 12,000 feet, but with large areas between 5,000 and 10,000 feet deep; and although this implies an immense subsidence, it is not very improbable that all the area from this line northward to Greenland and Iceland was dry land during some part of the Miocene period. In support of this view it may be noted that the Alps, the Pyrenees, the Rocky Mountains, and even the Himalayas, were all in early Miocene times many thousand feet lower than they are now. This is proved by the fact of Eocene and Miocene marine deposits of great thickness, which must have been formed in rather deep water, being found elevated from ten to sixteen thousand feet above the sea-level. As an example we may mention the Dent du Midi in Switzerland, where marine shells of early Miocene or late Eocene type are found at an elevation of 10,940 feet; and, as this mountain must have suffered enormous denudation, these figures can only represent a portion of the rise of the land, most of which has occurred during the Miocene period. To balance this rise over extensive areas on both sides of the Alantic, there must have been corresponding areas of subsidence, and we may fairly locate these where the indications of palæontology and geography concur in rendering them probable. We have already seen that the migrations of mammalia between Europe and America have been such as to render some land route necessary,2 while the broken-up character of the coasts of Ireland and Newfoundland, Labrador, Greenland, and Iceland, with the extensive bank of the Azores, all point to a certain amount of recent sinking of land on the outskirts of this area of great depression.

which afforded the passage of the tropicopolitan forms from one continent to the other?—it may therefore be answered: It existed in the north temperate zone during some part of the Miocene period, at the time probably when a rich temperate flora covered what are now the icy wastes of Greenland and Spitzbergen. In the North Atlantic a continuous land may have united Europe and America at about the latitude of London, without implying a greater amount of subsidence than would balance the elevation which we know has occurred over extensive areas in Europe and America. We also know that two of the most characteristic tropicopolitan forms—the tapirs and the trogons—existed in Europe in Miocene times; and every geologist will admit that there must have been many others, especially among birds and reptiles, whose remains we have not yet discovered, and never may discover. The transmission of similar forms to tropical Africa and Asia has

<sup>&</sup>lt;sup>2</sup> For particulars of these migrations see the writer's Geographical Distribution of Animals, vol. i. pp. 140, 153.

already been explained in reference to Pitta angolensis; and thus, it appears to me, the problem of tropicopolitan forms is completely solved, without making any assumptions but such as are warranted by admitted geological and palæontological facts. It has been necessary to treat the question broadly, and to omit many details which require fuller elucidation. I can only now call attention to the obvious fact that the geological age of the remains of any animal type in a given area cannot be held to denote the period of its earliest appearance in that area by migration or otherwise, because, till it became somewhat abundant, there would be little chance of its remains being preserved or discovered. This will apply to the case of the tapirs which are supposed to have migrated to North America in the Miocene period, but whose fossil remains are not found in any deposits earlier than the Pliocene.

We will now return to Mr. Sclater's fourth problem, that of the occurrence of the curious insectivorous mammal, Solenodon, in the Antilles, while its nearest allies are to be found in Madagascar. By the help of the conclusions we have already arrived at, much of the marvel and difficulty of this curious case of geographical distribution vanishes. It is simply an extreme instance of a family of animals which has been long dying out, but which maintains a lingering existence in two remote island groups where it is comparatively free from the competition of higher types, and where the general physical conditions are favourable. The fact that the family Centetidæ consists of six very distinct genera (five in Madagascar and one in the Antilles) is a sufficient indication that it was once an extensive group. In the Lower Miocene of Auvergne, the fossil remains of a small animal has been found, which is provisionally classed in this very family; and both in Europe and America a considerable number of the remains of Insectivora of peculiar genera have been discovered, indicating that this order of mammals is a very ancient one, which probably long ago arrived at its maximum of development, and has been diminishing in proportion as the larger and more perfectly organised forms have been increasing. It is interesting to note that the two localities where the Centetidæ still linger have many remarkable similarities and correspondences. Both are insular groups of the first rank; both are separated from their adjacent continents by very deep sea; both are situated just within the line of the tropic; both are subject to hurricanes; both are very mountainous; in both all the higher mammalia are very deficient; and the differences of their forms of life from those of the adjacent lands are such as to indicate that they have both remained insulated for a considerable period geologically. There can be little doubt that these resemblances have something to do with the continued existence in both of isolated members of a once widespread group of mammals, of a comparatively low type of organisation, and unable to

bear the competition to which they have been exposed in continental areas. The same principles will, of course, explain the presence in Madagascar of a mouse allied to an American group, of three American genera of colubrine snakes, and of lizards belonging to the peculiar American family Iguanidæ, as well as of the beautiful green diurnal moths of the genus Urania, and several beetles of decidedly South American affinities. In some other cases we have, as it were, a relic of the former wide extension of now restricted groups. Thus, one genus of snakes, Ahætulla, is found in Africa and South America as well as in Madagascar; while a genus of geckoes, Phyllodactylus, inhabits also America and Australia, and there are many similar

cases among insects.

After what has been now advanced, the distribution of the lemurs (which forms Mr. Sclater's fifth case) will offer little difficulty. Every indication points to this being a group of great antiquity, and to its having been once very widely spread. Its still existing remnants are scattered from Sierra Leone to Celebes, and from Natal to Eastern Bengal and South China; and they are so varied that they require to be classed in three distinct families and thirteen genera. Still more important is the proof of their extreme antiquity afforded by the recent discovery, in the Eccene deposits of the South of France, of a skull of an unmistakable lemur, allied to one of the still living forms of West Africa known as the 'Potto'; while several other fossils of the same age are also believed to belong to the lemurine group. In North America, too, abundant remains have been found in the Lower Eocene deposits, which are believed to be intermediate between lemurs and the South American marmosets. This clear evidence both as to the antiquity and the wide range of the lemurs renders it quite unnecessary to postulate any special changes of sea and land to account for their actual distribution. Inhabiting Europe in Eccene times, they were probably spread over the whole northern continent, and would as easily migrate southward into their present habitats as the hedgehogs, the civets, the chevrotains, or the porcupines, which have all a somewhat similar, but far more extensive distribution. Like the Centetidæ, the lemurs find Madagascar best suited to them, more no doubt from the absence of competitive forms than from any peculiar physical condi-On the great continents they are usually scarce, and are protected by their nocturnal habits and by frequenting dense forests. They thus continue to survive in the midst of creatures of a higher type and more recent origin than themselves, and, together with the opossums of America and some of the smaller marsupials of Australia, seem to have handed down to us a sample of the forms of life which flourished in the earliest tertiary or even in mesozoic times.

The last case of anomalous distribution—that of the giant landtortoises of the Mascarene and Galapagos islands-offers perhaps less real difficulty than any of the preceding, on account of the existing wide range and the extreme antiquity of the genus Testudo to which they all belong. This genus occurs in the Miocene deposits of Europe and India, and in the Eocene of North America; and living species are abundant in Africa and Asia, and are also found in South Europe and North America. It has evidently, therefore, been a dominant group during a large portion of the tertiary epoch, and it still maintains a vigorous existence. There does not seem to be any evidence that these giant species of the two hemispheres are more closely allied to each other than the smaller forms of remote regions; for though the Galapagos tortoises and the extinct species of the Mascarene islands both belong to a flat-headed type, they may have differed in important external characters. Their gigantic size is evidently due to their seclusion for countless generations in islands where they were entirely free from the attacks of enemies, and where they could procure abundance of food; both natural and sexual selection giving the advantage to the larger and stronger individuals. The only difficulty is how they reached the Galapagos. But as we may go back to the middle of the tertiary epoch for this event, it is not an improbable supposition that the coast of South America then extended considerably westward, while the islands themselves may have been more extensive, thus reducing the dividing strait to a width across which either the adult animals or their eggs might be floated by currents or surface-drifts. Their entrance to the Mascarene islands from Africa might have been effected in a similar This is the solution suggested by Dr. Günther himself,<sup>3</sup> and it is one which perfectly harmonises all the known facts.

The only other difficulty suggested by Mr. Sclater rather applies to the theory of natural selection itself than to geographical distribution. He asks how we are to account for closely allied forms so frequently inhabiting the same area, while in so many other cases allied species are strictly limited to distinct areas, to the diverging physical and organic conditions of which they are supposed to be adapted. We think that Mr. Sclater has himself furnished a clue to one mode of solution, in his statement that the willowwarbler and the chiff-chaff, though so alike externally, are yet quite distinct in mode of life and habits. It is evident, that a variation in the habits of a portion of the individuals of a species would lead to their mutual association and at the same time to their separation from the parent form, and would thus obviate that tendency to the intercrossing of the different varieties which would undoubtedly occur if the variation were one of colour or form only. Is it not probable, therefore, that where two or more closely allied species inhabit the same area, they have arisen at first by means of useful variations of instincts or habits; while those which inhabit adjacent but separate areas may have arisen by favourable variations of colour, form, or constitution only? In support of this view it may be noted that the coal and marsh titmice, which are very closely allied, differ considerably in habits; while the great and blue titmice, which are very different in external characters, agree closely in habits, and are often seen together.

Returning to the general question of zoological distribution and its anomalies, it has been shown, I trust, that the only mode of explaining the existing distribution of living things is by a constant reference to those comparatively slight but often important changes of sea and land, which the most recent researches show to be alone probable; and, what is still more important, by recognising the undoubted fact that every group of animals whose distribution is discontinuous is now more or less in a fragmentary condition, and has, in all probability, once had a much more extensive range, to which its present distribution may offer no clue whatever. Who would ever have imagined, for example, that the horse tribe, now confined to Africa and Asia, formerly ranged over the entire American continent, north and south, in great abundance and variety; or that the camel tribe, now confined to Central Asia and the Andean region of South America, formerly abounded in North America, whence in fact our existing camels were almost certainly derived? How easy it is to imagine that analogous causes to those which have so recently exterminated the horses of America and Europe might have acted in a somewhat different direction, and have led to the survival of horses in South America and Africa, and their extermination elsewhere. Had this been the case, how strong would have been the argument for a former union of these two continents; yet we now know that these widely separated species would be merely the relics of a once dominant group which had occupied and become extinct in all the northern continents.

Discoveries of extinct forms remote from the countries they now inhabit, are continually furnishing us with new proofs that the great northern continents of the two hemispheres were really the birthplace of almost if not quite all the chief forms of animal life upon the globe; while change of climate, culminating in the glacial epoch, seems to have been the motive power which has driven many of these forms into the tropical lands where they now alone exist.

If we give full weight to these various considerations, and at the same time bear constantly in mind the extreme imperfection of our knowledge of extinct land animals, we shall, I believe, have no difficulty in explaining most of the apparent anomalies in zoological distribution, and in imagining a possible and even probable solution for those extreme cases of difficulty which the facts at our command do not yet permit us to explain in detail.

Let us now briefly summarise the general principles on which the solution of problems in zoological distribution depends.

During the evolution of existing forms of animal life, we may picture to ourselves the production of successive types, each in turn increasing in variety of species and genera, spreading over more or less extensive regions of the earth's surface, and then, after arriving at a maximum of development, passing through various stages of decay, dwindling to a single genus or a single species, and finally becoming extinct. While the forms of life are thus, each in turn, moving on from birth to maturity and from maturity to decay and death, the earth's surface will be undergoing important physical changes, which will sometimes unite and sometimes separate contiguous continents or islands, leading now to the intermingling, now to the isolation, of the progressing or diminishing groups of animals. Again, we know that climates have often changed over a considerable portion of the earth, so that what was at one time an almost tropical region has become at another time temperate, and then even arctic; and these changes have, it is believed, been many times repeated, leading each time to important changes, migrations, and extinctions of animal and vegetable life.

It is by the combined effect of these three distinct sets of causes, acting and reacting on each other in various complex ways, that have been produced those curious examples of erratic distribution of species and genera which have been so long a puzzle to the naturalist, but which have now, it is believed, been shown to be the natural and inevitable results of the process of animal development, combined with constant changes in the geography and in the climate of the earth.

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