THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS: GENERAL CONCLUSIONS.[1]

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HAVING now closed our survey of the animal life of the whole earth, — a survey which has necessarily been encumbered with a multiplicity of detail, — we proceed to summarize the general conclusions at which we have arrived, with regard to the past history and mutual relations of the great regions into which we have divided the land surface of the globe.

All the palæontological no less than the geological and physical evidence, at present available, points to the great land masses of the northern hemisphere as being of immense antiquity and as the area in which the higher forms of life were developed. In going back through the long series of the Tertiary formations in Europe, Asia, and North America, we find a continuous succession of vertebrate forms, including all the highest types now existing or that have existed on the earth. These extinct animals comprise ancestors or forerunners of all the chief forms now living in the northern hemisphere; and as we go back farther and farther into the past, we meet with ancestral forms of those types also, which are now either confined to or specially characteristic of the land masses of the southern hemisphere. Not only do we find that elephants and rhinoceroses and hippopotami were once far more abundant in Europe than they are now in the tropics, but we also find that the apes of West Africa and Malaya, the lemurs of Madagascar, the Edentata of Africa and South America, and the marsupials of America and Australia were all represented in Europe (and probably also in North America) during the earlier part of the Tertiary epoch. These facts, taken in their entirety, lead us to conclude that during the whole of the Tertiary and perhaps during much of the Secondary periods, the great land masses of the earth were, as now, situated in the northern hemisphere; and that here alone were developed the successive types of vertebrata, from the lowest to the highest. In the southern hemisphere there appear to have been three considerable and very ancient land masses, varying in extent from time to time, but always keeping distinct from each other, and represented, more or less completely, by Australia, South Africa, and South America of our time. Into these

[1] Chapter xvi. of The Geographical Distribution of Animals. New York: Harper and Brothers.

flowed successive waves of life, as they each in turn became temporarily united with some part of the northern land. Australia appears to have had but one such union, perhaps during the middle or latter part of the Secondary epoch, when it received the ancestors of its Monotremata and marsupials, which it has since developed into a great variety of forms. The South African and South American lands, on the other hand, appear each to have had several successive unions and separations, allowing first of the influx of low forms only (Edentata, Insectivora, and lemurs), subsequently of rodents and small Carnivora, and latest of all of the higher types of Primates, Carnivora, and Ungulata.

During the whole of the Tertiary period, at least, the northern hemisphere appears to have been divided, as now, into an eastern and a western continent, always approximating and sometimes united towards the north, and then admitting of much interchange of their respective faunas, but on the whole keeping distinct, and each developing its own special family and generic types, of equally high grade, and generally belonging to the same orders. During the Eocene and Miocene periods, the distinction of the Palæarctic and Nearctic regions was better marked than it is now, as is shown by the floras no less than by the faunas of those epochs. Dr. Newberry, in his Report on the Cretaceous and Tertiary Floras of the Yellowstone and Missouri Rivers, states, that although the Miocene flora of Central North America corresponds generally with that of the European Miocene, yet many of the tropical, and especially the Australian types, such as *Nakea* and *Dryandra*, are absent. Owing to the recent discovery of a rich Cretaceous flora in North America, probably of the same age as that of Aix-la-Chapelle in Europe, we are able to continue the comparison, and it appears that at this early period the difference was still more marked. The predominant feature of the European Cretaceous flora seems to have been the abundance of Proteaceæ, of which seven genera now living in Australia or the Cape of Good Hope have been recognized, besides others which are extinct. There are also several species of *Pandanus*, or screw-pine, now confined to the tropics of the eastern hemisphere, and along with these oaks, pines, and other more temperate forms. The North American Cretaceous flora, although far richer than that of Europe, contains no Proteaceæ or *Pandani*, but immense numbers of forest trees of living and extinct genera. Among the former we have oaks, beeches,

willows, planes, alders, dogwood, and cypress, together with such American forms as magnolias, sassafras, and liriodendrons. There are also a few not now found in America, as *Araucaria* and *Cinnamomum*, the latter still living in Japan. This remarkable flora has been found over a wide extent of country, New Jersey, Alabama, Kansas, and near the sources of the Missouri in the latitude of Quebec, so that we can hardly impute its peculiarly temperate character to the great elevation of so large an area. The intervening Eocene flora approximates closely in North America to that of the Miocene period, while in Europe it seems to have been fully as tropical in character as that of the preceding Cretaceous period, fruits of *Nipa*, *Pandanus*, *Anona*, *Acacia*, and many Proteaceæ occurring in the London clay at the mouth of the Thames.

These facts appear, at first sight, to be inconsistent, unless we suppose the climates of Europe and North America to have been widely different in those early times; but they may perhaps be harmonized on the supposition of a more uniform and a somewhat milder climate then prevailing over the whole northern hemisphere, the contrast in the vegetation of these countries being due to a radical difference of type, and therefore not indicative of climate. The early European flora seems to have been a portion of that which now exists only in the tropical and subtropical lands of the eastern hemisphere, and as much of this flora still survives in Australia, Tasmania, Japan, and the Cape of Good Hope, it does not necessarily imply more than a warm and equable temperate climate. The early North American flora, on the other hand, seems to have been essentially the same in type as that which now exists there, and which in the Miocene period was well represented in Europe; and it is such as now flourishes best in the warmer parts of the United States. But whatever conclusion we may arrive at on the question of climate, there can be no doubt as to the distinctness of the floras of the ancient Nearctic and Palæarctic regions; and the view derived from the study of their existing and extinct faunas — that these two regions have, in past times, been more clearly separated than they are now — receives strong support from the unexpected evidence now obtained as to the character and mutations of their vegetable forms, during so vast an epoch as is comprised in the whole duration of the Tertiary period.

The general phenomena of the distribution of living animals, combined with the evidence of extinct forms, lead us to conclude

that the Palæarctic region of early Tertiary times was, for the most part, situated beyond the tropics, although it probably had a greater southward extension than at the present time. It cer tainly included much of North Africa, and perhaps reached far into what is now the Sahara, while a southward extension of its central mass may have included the Abyssinian highlands, where some truly Palæarctic forms are still found. This is rendered probable by the fossils of Perim Island a little farther east, which show that the characteristic Miocene fauna of South Europe and North India prevailed so far within the tropics. There existed, however, at the extreme eastern and western limits of the region, two extensive equatorial land areas, our Indo-Malayan and West African sub-regions, both of which must have been united for more or less considerable periods with the northern continent. They would then have received from it such of the higher vertebrates as were best adapted for the peculiar climatal and organic conditions which everywhere prevail near the equator; and these would be preserved, under variously modified forms, when they had ceased to exist in the less favorable and constantly deteriorating climate of the north. At later epochs, both these equatorial lands became united to some part of the great South African continent (then including Madagascar), and we thus have explained many of the similarities presented by the faunas of these distant and generally very different countries.

During the Miocene period, when a subtropical climate prevailed over much of Europe and Central Asia, there would be no such marked contrast as now prevails between temperate and tropical zones; and at this time much of our Oriental region, perhaps, formed a hardly separable portion of the great Palæarctic land. But when, from unknown causes, the climate of Europe became less genial, and when the elevation of the Himalayan chain and the Mongolian plateau caused an abrupt difference of climate on the northern and southern sides of that great mountain barrier, a tropical and a temperate region were necessarily formed; and many of the animals which once roamed over the greater part of the older and more extensive region now became restricted to its southern or northern divisions, respectively. Then came the great change we have already described (vol. i. p. 288), opening the newly formed plains of Central Africa to the incursions of the higher forms of Europe, and following on this, a still further deterioration of climate, resulting in that marked contrast between temperate and tropical faunas, which is

now one of the most prominent features in the distribution of animal as well as of vegetable forms.

It is not necessary to go into any further details here, as we have already, in our discussion of the origin of the fauna of the several regions, pointed out what changes most probably occurred in each case. These details are, however, to a great extent speculative, and they must remain so till we obtain as much knowledge of the extinct faunas and past geological history of the southern lands as we have those of Europe and North America. But the broad conclusions at which we have now arrived seem to rest on a sufficiently extensive basis of facts, and they lead us to a clearer conception of the mutual relations and comparative importance of the several regions than could be obtained at an earlier stage of our inquiries.

If our views of the origin of the several regions are correct, it is clear that no mere binary division into north and south, or into east and west can be altogether satisfactory, since at the dawn of the Tertiary period we still find our six regions, or what may be termed the rudiments of them, already established. The north and south division truly represents the fact that the great northern continents are the seat and birthplace of all the higher forms of life, while the southern continents have derived the greater part, if not the whole of their vertebrate fauna from the north; but it implies the erroneous conclusion that the chief southern lands, Australia and South America, are more closely related to each other than to the northern continent. The fact, however, is that the fauna of each has been derived, independently, and perhaps at very different times, from the north, with which they therefore have a true genetic relation, while any intercommunion between themselves has been comparatively recent and superficial, and has in no way modified the great features of animal life in each. The east and west division represents — according to our views — a more fundamental diversity, since we find the northern continent itself so divided in the earliest Eocene and even in Cretaceous times, while we have the strongest proof that South America was peopled from the Nearctic, and Australia and Africa from the Palæarctic region; hence, the eastern and western hemispheres are the two great branches of the tree of life of our globe. But this division, taken by itself, would obscure the facts, firstly, of the close relation and parallelism of the Nearctic and Palæarctic regions, not only now, but as far back as we can clearly trace them in the past; and

secondly, of the existing radical diversity of the Australian region from the rest of the eastern hemisphere.

Owing to the much greater extent of the old Palæarctic region (including our Oriental) and the greater diversity of Mammalia it appears to have produced, we can have little doubt that here was the earliest seat of the development of the vertebrate type, and probably of the higher forms of insects and land-mollusks. Whether the Nearctic region ever formed one mass with it, or only received successive immigrations from it by northern land connections both in an easterly and westerly direction, we cannot decide; but the latter seems the most probable supposition. In any case, we must concede the first rank to the Palæarctic and Oriental regions, as representing the most important part of what seems always to have been the great continent of the earth, and the source from which all the other regions were supplied with the higher forms of life. These once formed a single great region which has been since divided into a temperate and a tropical portion, now sufficiently distinct, while the Nearctic region has, by deterioration of climate, suffered a considerable diminution of productive area, and has in consequence lost a number of its more remarkable forms. The two temperate regions have thus come to resemble each other, more than they once did, while the Oriental retains more of the zoölogical aspect of the great northern regions of Miocene times. The Ethiopian form having been once an insular region, where lower types of vertebrates alone prevailed, has been so overrun with higher types from the old Palæarctic and Oriental lands that it now rivals, or even surpasses, the Oriental region in its representation of the ancient fauna of the great northern continent. Both of our tropical regions of the eastern hemisphere possess faunas which are to some extent composite, being made up in different proportions of the productions of the northern and southern continents, — the former prevailing largely in the Oriental, while the latter constitutes an important feature in the Ethiopian fauna. The Neotropical region has probably undergone great fluctuations in early times; but it was, undoubtedly, for long periods completely isolated, and there developed the Edentate type of mammals and the Formicaroid type of passerine birds into a variety of forms, comparable with the diversified marsupials of Australia, and typical Passeres of the eastern hemisphere. It has, however, received successive infusions of higher types from the north, which now mingle in various degrees with

its lower forms. At an early period it must have received a low form of Primates, which has been developed into the two peculiar families of American monkeys; while its llamas, tapirs, deer, and peccaries came in at a later date, and its opossums and extinct horses probably among the latest. The Australian region alone, after having been united with the great northern continent at a very early date (probably during the Secondary period), has ever since remained more or less completely isolated, and thus exhibits the development of a primeval type of mammal, almost wholly uninfluenced by any incursions of a later and higher type. In this respect it is unique among all the great regions of the earth.

We see, then, that each of our six regions has had a history of its own, the main outlines of which we have been able to trace with tolerable certainty. Each of them is now characterized — as it seems to have been in all past time of which we have any tolerably full record — by well-marked zoölogical features, while all are connected and related in the complex modes we have endeavored to unravel. To combine any two or more of these regions, on account of existing similarities which are for the most part of recent origin, would obscure some of the most important and interesting features of their past history and present condition. And it seems no less impracticable to combine the whole into groups of higher rank, since it has been shown that there are two opposing modes of doing this, and that each of them represents but one aspect of a problem which can only be solved by giving equal attention to all its aspects.

For reasons which have been already stated and which are sufficiently obvious, we have relied almost exclusively on the distribution of living and extinct Mammalia in arriving at these conclusions. But we believe they will apply equally to elucidate the phenomena presented by the distribution of all terrestrial organisms, when combined with a careful consideration of the various means of dispersal of the different groups and the comparative longevity of their species and genera. Even insects, which are perhaps of all animals the farthest removed from Mammalia in this respect, agree in the great outlines of their distribution, with the vertebrate orders. The regions are admittedly the same, or nearly the same for both, and the discrepancies that occur are of a nature which can be explained by two undoubted facts, the greater antiquity, and the greater facilities for dispersal of insects.

But this principle, if sound, must be carried farther and be applied to plants also. There are not wanting indications that this may be successfully done; and it seems not improbable that the reason why botanists have hitherto failed to determine, with any unanimity, which are the most natural phytological regions, and to work out any connected theory of the migrations of plants is, because they have not been furnished with the clue to the past changes of the great land masses, which could only be arrived at by such an examination of the past and present distribution of the higher animals as has been here attempted. The difficulties in the way of the study of the distribution of plants, from this point of view, will be undoubtedly very great, owing to the unusual facilities for distribution many of them possess and the absence of any group which might take the place of the Mammalia among animals and serve as a guide and standard for the rest. We cannot expect the regions to be so well defined in the case of plants as in that of animals, and there are sure to be many anomalies and discrepancies, which will require long study to unravel. The six great regions here adopted are, however, as a whole, very well characterized by their vegetable forms. The floras of tropical America, of Australia, of South Africa, and of Indo-Malaya stand out with as much individuality as do the faunas, while the plants of the Palæarctic and Nearctic regions exhibit resemblances and diversities of a character not unlike those found among the animals.

This is not a mere question of applying to the vegetable kingdom a series of arbitrary divisions of the earth, which have been found useful to zoölogists, for it really involves a fundamental problem in the theory of evolution. The question we have to answer is, firstly, whether the distribution of plants is like that of animals, mainly and primarily dependent on the past revolutions of the earth's surface, or whether other and altogether distinct causes have had a preponderating influence in determining the range and limits of vegetable forms; and secondly, whether those revolutions have been in their general outlines correctly interpreted by means of a study of the distribution and affinities of the higher animals. The first question is one for botanists alone to answer, but on the second point, the author ventures to hope for an affirmative reply, from such of his readers as will weigh carefully the facts and arguments he has adduced.

The hypothetical view as to the more recent of the great

geographical changes of the earth's surface here set forth, is not the result of any preconceived theory, but has grown out of a careful study of the facts accumulated, and has led to a considerable modification of the author's previous views. It may be described as an application of the general theory of evolution, to solve the problem of the distribution of animals; but it also furnishes some independent support to that theory, both by showing what a great variety of curious facts are explained by its means, and by answering some of the objections which have been founded on supposed difficulties in the distribution of animals in space and time.

It also illustrates and supports the geological doctrine of the general permanence of our great continents and oceans, by showing how many facts in the distribution of animals can only be explained and understood on such a supposition, and it exhibits in a striking manner the enormous influence of the Glacial epoch, in determining the existing zoölogical features of the various continents. And lastly, it furnishes a more consistent and intelligible idea than has yet been reached by any other mode of investigation of all the more important changes of the earth's surface that have probably occurred during the entire Tertiary period, and of the influence of these changes in bringing about the general features, as well as many of the more interesting details and puzzling anomalies of the geographical distribution of animals.

RECENT LITERATURE.

MEMOIRS OF THE GEOLOGICAL SURVEY OF KENTUCKY.[1] — The first fruits of the reëstablished Geological Survey of Kentucky appear in a large and admirably illustrated volume of memoirs. Professor Shaler publishes papers on the antiquity of the caverns and on the fossil brachiopods of the Ohio Valley, and, in conjunction with Mr. Carr contributes the first of a series of papers on the prehistoric remains of Kentucky; while Mr. Allen furnishes an elaborate memoir on the American bisons, living and extinct. The first of Professor Shaler's papers has already appeared in the memoirs of the Boston Natural History Society, and Mr. Allen's monograph is published simultaneously by the Museum of Comparative Zoölogy. The latter paper forms the bulk of the volume (246 pp.) and is illustrated by twelve plates, half of them double, and by a map of North America. It is one of the most com-

[1] *Memoirs of the Geological Survey of Kentucky.* N. S. SHALER, Director. Vol. I. Cambridge, 1876. 4to, pp. 360, 27 plates, 1 map.