THE ORIGIN OF THE MAMMALIAN FAUNAS OF NORTH AND SOUTH AMERICA.

By

WILLIAM BERRYMAN SCOTT

(Princeton).

(*Eingelangt am 20. Juli 1927.*)

All naturalists are familiar with the conception that the present distribution of animals over the land surface of the earth is the outcome of a long series of antecedent changes — changes in geography, in climate, and in the evolutionary development of the animals themselves. However paradoxical and anomalous the present distribution may seem to be, it can always be explained, provided we have the necessary historical information, and the progress of discovery in the various continents is continually bringing this information to light. Not that there are not many unexplained phenomena of distribution. Probably there always will be such unexplained residua. But in all such instances the inexplicable nature of the case is due to our lack of information. The relations between North and South America have been very complex, as have also the relations between each of these continents and the various land masses of the eastern hemisphere.

We have first to consider what are the facts of existing distribution of mammals in the American continents. These relations are in general terms broad and simple, though there are exceptional facts which still await explanation.

All of South and Central America, including the tropical lowlands of Mexico *(Tierras Calientes)* and the West Indian Islands, belong to a single zoological region, the Neo-Tropical (WALLACE and SCLATER). North America, on the other hand, is divided between two regions. The northern portion, including all of Canada and Alaska, is a part of the vast northern land mass which forms the Palaearctic region of the zoological geographers. Secondly, the Sonoran region covers the United States and the Mexican Plateau. The Boreal or Palaearctic portion of North America belongs to the great realm of Arctogaea, which includes all of the continents of the eastern hemisphere save Australia. Throughout this immense area, with all of its great local differences, there is an unmistakable unity in the character of its animal life, which is in remarkable contrast to the life of South America and Australia.

The curious patchwork which the zoological regions make, when mapped on the various continents, would be entirely inexplicable on the basis

of present geography and present climatic conditions; but this geography has been repeatedly modified in the past ages of the earth's history. There can be nothing clearer, and nothing is more definitely established, than the oft repeated land connection between North America and Asia by way of the shallow waters of what are now Bering Sea and Bering Strait. Probably also the 1000 fathom line, which extends from Greenland, by way of Iceland and the Faroes, to Scotland and Scandinavia, marks out another connection between Europe and North America. The evidence for this hypothetical land bridge is not so complete and convincing as that for the bridge between Alaska and northeastern Siberia; but it seems, nevertheless, distinctly indicated by the distribution of early Tertiary mammals in the northern hemisphere, as combined with the known facts of geology of that date. Similarly, the connections between North and South America have been several times established and interrupted.

The fauna of the West Indian Islands, on the other hand, forms a very difficult problem by itself, which is not involved in the general discussion of the relations between the two major western continents.

The northern portion of North America thus contains a fauna which differs in relatively small degree from that of the northern portion of the Old World. The Sonoran region is more or less peculiar, but does not contain very many mammals confined to itself; and some zoological geographers doubt the advisability of giving the Sonoran the rank of a region, preferring to regard it as a subdivision of the great Palaearctic. In short, nearly all of North America is more or less closely and distinctly related, zoologically speaking, to Europe and Asia. It contains very few of the southern or Neotropical mammals. Indeed, there is only one genus, the tree porcupine *(Erethizon)* which is of undoubted Neotropical origin.

On the other hand, South America contains a great many northern types, which include all of the carnivorous animals, all of the hoofed animals, and all of the rodents except the great porcupine group, the Hystricomorpha. Mingled with these, however, are many highly characteristic and peculiar mammals which have no relations in the north. All of the Edentata, the ant bears, the armadillos, the sloths, the New World monkeys, and the host of porcupine-like rodents; these make South America the most peculiar of all regions, after Australia. This mingling of northern and indigenous mammalian types seems a very anomalous condition, and yet is very fully explained by the facts of geology and palaeontology.

It should be noted, however, that both North and South America suffered great loss through the vast Pleistocene extinction, which fairly decimated their mammals, removing all of the larger, more bizarre, and fiercer types. As one works backward from the present to the Pleistocene, he observes an immense increase in the numbers and manifold variety of mammals, both in North and South America. Many of the groups, even the orders which throve in the Pleistocene and the Tertiary, are now altogether extinct; and others, like the elephants, have been restricted to areas which are but a fraction of their former range. In the Pleistocene, representatives of the

Proboscidea occurred in all of the continents, perhaps even in Australia, from which mastodon teeth have been reported, though not very convincingly. Now they are restricted entirely to the tropical and sub-tropical regions of Africa and southern Asia.

In dealing with the origin of American faunas, therefore, it is best to take the Pleistocene as the standard of comparison, Pleistocene mammals being so much more varied and numerous than those of the present.

In the upper half of the Cretaceous period, there can be little doubt that the Americas were connected by land, as is shown by the complete distinction of the marine faunas of the Atlantic and the Pacific. Hardly a single species is common to these two provinces. The land barrier which effected this separation was a shifting one, as is shown by the extension of the Atlantic fauna westward and the Pacific fauna eastward; so that they in places overlap, but nowhere do they mingle. Little is known as yet concerning the nature of the South American dinosaurs and therefore it cannot be stated whether they were derived from North America, or from some other continent; but certainly the existence of dinosaurs in the Mesozoic rocks of all the continents shows that during that era all of the great land masses were directly or indirectly in communication with one another; not necessarily all at the same time, but in such a manner that a group originating probably in Europe or Asia was enabled to spread to all of the continents, and this could not have been done save by land communications.

In early Tertiary times the land bridge between North and South America was submerged. This is conclusively shown, in the first place, by the geology of the Isthmus of Panama, where there is a marine limestone carrying Miocene fossils high up in the Culebra Hills which form the continental divide. Many years ago JORDAN and EVERMAN arrived at the same conclusion from a study of the existing marine fishes of the two coasts of the Isthmus, the Bay of Panama and the Caribbean Sea. They came to the conclusion that the separation between the Atlantic and the Pacific must have occurred during the Miocene, and that before that time there had been an open sea over the site of the Isthmus. This conclusion was reached at a time when the geology of the Isthmian region was still unknown, and was entirely a deduction from the observed facts according to the principles of evolution. The conclusion is thus in perfect harmony with that reached by the geologist, and also with that which results from a comparison of the Tertiary mammals of North and South America. It is also sufficiently proved by other evidence, especially by the complete and total difference between the mammals of the northern and southern continent.

Throughout the Tertiary period there is a great likeness between the mammals of North America and the Old World, a likeness which is sometimes much greater than at other times, indicating periods of time when Alaska and Siberia were connected and those in which Bering Strait and Bering Sea separated these land areas.

The Paleocene mammals of North America, like those of the Cernaysian formation in France, are of Mesozoic and archaic type, and they include few, if any, ancestors of modern groups.

The beginnings of the modern mammalian fauna are to be found in the lowest Eocene of North America and Europe, when there was an identity in the genera and families of mammals such as was never found again in subsequent periods. It is perfectly evident that this Lower Eocene fauna, as a whole, is immigrant from some other region, as yet unknown. With very great probability that region was Asia, whether southern or central remains to be determined.

Throughout all of this complicated history, the migrations of mammals from one continent to another played a very important role. It should, however, be clearly understood that the word „migration" in this connection denotes a phenomenon entirely different from the seasonal migrations of birds. It would be better to speak of the d i f f u s i o n of mammals, rather than the m i g r a t i o n, because the process was a slow and gradual and unintentional one on the part of the mammals. As the members of any species increased, they merely spread farther and farther from their place of origin until stopped by some impassable barrier. There was nothing of the back and forth movements which characterize bird migrations.

This Lower Eocene fauna contains, in recognizable form, the ancestors of most existing orders of terrestrial mammals; Artiodactyla, Perissodactyla, Carnivora, Insectivora, Rodentia, and Primates are all represented in it. Other groups, like the elephants, did not reach the northern lands until a much later date; and of course the terrestrial formations of the high plains of the western United States give no information concerning marine mammals, such as seals and whales.

If we take as a point of comparison the Miocene mammalian faunas of North and South America, we find them most radically distinct. In North America, for instance, there are found a great variety of hoofed animals, including many lines of horses, the tapirs, the rhinoceroses, the peccaries, the camels and llamas, and the peculiar American family of the oreodonts, which flourished in great abundance from the Upper Eocene to the Pliocene, where it reached its highest point in variety and differentiation. No member of this group has ever been found in any other continent; though there is every reason to expect that it will eventually turn up in Mongolia, where so many other extraordinary American groups are represented. The more primitive types of deer and antelopes and the early mastodons are also found here. Among the Carnivora are to be found a surprising variety of dogs and cats (both the true cat and the sabre-tooth subdivisions), many of the weasel and the badger tribe, and the raccoons. Of rodents, the North American Miocene contained the ancestors of modern forms of rats and mice, squirrels, beavers, marmots, etc., but not a single porcupine-like form. So far as is known, this fauna contained no monkeys, and very few marsupials, if any. Both before and after that time, opossums have been found in North America, but only in restricted numbers and of small variety. As compared with the Old World

Miocene, America had curious lacks. America had not then, and never has had, any representatives of the hyaenas, or of the viverrines, with the possible exception of certain Eocene forms which may be referable to the latter family; but if so, the line speedily became extinct on this side of the ocean. It never had any hippopotamuses or giraffes, the latter a family which played such a very important role in the upper Miocene and lower Pliocene of all the Mediterranean world, from the south of France to the Philippine Islands.

The South American fauna of the Miocene, which is admirably preserved in the volcanic ash beds and tuffs of the Santa Cruz formation, is so completely unlike that of North America as to make certain that there could have been no land connection between the two continents at that time. This fauna is a very rich and varied one; but it differs from that of Arctogaea in having none of the familiar groups. It contains no Artiodactyls, no Perissodactyls, no Proboscidea. It contains no true Carnivora, and its rodents all belong to the porcupine subdivision of that order, having no rats or mice, no squirrels, no marmots, no beavers, no hares or rabbits, all of which were in the Miocene of North America.

But the Santa Cruz fauna cannot be described in negative terms, because it is extremely rich and varied. To a very large extent, its mammals belong to groups which are altogether extinct and have left no descendants in the present day. The hoofed animals, for instance, belong to peculiar South American orders which have never been found outside of that continent. The Toxodontia, the Typotheria, the Homalodotheria, the Astrapotheria, and the Litopterna, are all well defined orders of unmistakable Ungulata; but, with the possible exception of the Litopterna, these orders are all utterly different from those of Arctogaea. No one has ever suggested the reference of any Arctogaean fossil to any of these South American orders. The Litopterna, it is true, are regarded by some eminent authorities as referable to the Perissodactyla; but if this reference is accepted, it must be admitted that these South American forms constitute an altogether exceptional and aberrant group of the Perissodactyla. Personally, I do not believe that the Litopterna are directly connected with the perissodactyls.

The Santa Cruz fauna does not lack for beasts of prey, although it contains no true Carnivora. The place of these was taken by the carnivorous Marsupials, which closely resemble the Thylacinus of Tasmania. There were several other groups of Marsupials, which formed one of the most conspicuous elements in the Santa Cruz fauna. One of these has been variously interpreted as representing the Australian phalangers, though this is denied by other authorities. The third Marsupial group was the enormously represented series of small mammals, of which the only existing representative is the little *Caenolestes* of Peru. Finally, there were numerous opossums, in contrast to the scarcity, or perhaps complete absence, of these animals in the North.

Another very conspicuous element in the Santa Cruz fauna is that of the Edentates, especially the extinct sub-orders of the ground sloths, the Gravigrada, and the Glyptodonts, or giant armadillos. These are extremely

abundant and of incredible variety. Armadillos are likewise very frequent in the beds; but the other two modern sub-orders, the ant eaters and the true sloths, have not yet been assuredly found. There can be little doubt that these orders were already in existence and living in South America; but they probably did not extend to the almost treeless plains of Patagonia, where alone the Santa Cruz fauna is adequately represented.

Another very abundant and very characteristic element in the Santa Cruz assemblage is that of the rodents, which, as already mentioned, consisted exclusively of Hystricomorpha, the porcupine-like forms which ranged in size from tiny rat-like and mouse-like creatures up to the largest of the tree porcupines, and the still larger water hog, or Capybara, though this family has not yet been found in Patagonia.

Among these animals there was in Santa Cruz times, as there is to-day, an African element, especially represented by the spiny rats, which of course are not true rats at all. There are two other African elements in the Santa Cruz fauna. One is the little genus of Insectivora, *Necrolestes*, an Insectivore which is close to the Cape golden moles, Chrysochloridae of to-day. This is all the more notable because modern South America has not a single Insectivore within its boundaries; and in the whole Neotropical region, it is only the Greater Antilles, Cuba, Hayti, and Porto Rico, that have representative members of this group.

A difficult problem in distribution is offered by the South American monkeys. It is almost certain that they could not have been derived from North America, which, so far as the fossil records go, has contained no undoubted member of the Primates later than the Middle Eocene. If the South American monkeys, which are a very distinctive and separate group of the Primates, were not derived from North America, they must have come from Africa; and this suggestion finds confirmation in the existence of monkeys with South American affinities found in the Eocene of the Fayum in Egypt. This is but one of many reasons for assuming the existence of a land bridge in tropical latitudes between Africa and South America, an assumption which will be discussed later.

It will be noted that the Santa Cruz fauna contains not a single one of those animals of northern type, or anything which can be regarded as ancestral to those mammals which now occur in South America and which were referred to at the outset as being unmistakably of northern origin, as all of the existing carnivores and hoofed animals, and rodents, other than the Hystricomorpha. Those mammals could not have reached the southern continent because of the sea which covered the Isthmian region. We have definite reason to say that the emergence of the Isthmus and of Central America, and in consequence the formation of a land connection between North and South America, took place after the middle Miocene. Immediately mammals from each continent began to invade the other. The first indication of the southern invasion is the discovery by SINCLAIR of ground sloth remains in the Upper Miocene of eastern Oregon. And similarly, the first definitely known northern creature to be found in South America is a raccoon-like carnivore found in

the Lower Pliocene, or possibly the uppermost Miocene, of Catamarca, an Andean province of Argentina. From this beginning, wave after wave of immigration flowed in both directions; and in both instances, many mammals migrated to the new continent which were not able to maintain themselves there, but after a longer or shorter stay, disappeared altogether. In the case of North America, nearly all of the southern immigrants perished in the great Pleistocene extinction. The wonderful accumulations of Pleistocene mammal bones which have been preserved in the tar pits of southern California and in the Sheridan formation of the Great Plains region, give eloquent testimony to the great extent of the invasion of North America by Neotropical forms. Many varieties of ground sloths and Glyptodonts, the armadillos, the hystricomorph rodents, including the great water hog or Capybara, reached the northern land; but, as stated at the outset, only the Canadian porcupine, *Erethizon*, remains of all this immigrating group.

In South America the permanent results were very different. It is not necessary to enumerate again the northern types of mammals which now occur in the southern continent, and of which the ancestors are so plainly to be discerned in the Miocene and Pliocene faunas of North America; but it should be noted that many mammals became extinct in the southern continent, after a longer or shorter stay there. Some of these, like the mastodons, horses, sabre-tooth cats, and short-faced bears, became extinct everywhere in the western hemisphere. Others, such as the antelope found in the Brazilian caverns, are still found in the northern continent.

At every connection between Alaska and Siberia which was established during the Tertiary Period, migrant mammals poured into North America from Asia, beginning with the oldest Eocene fauna, that of the Wasatch Epoch, and continuing at intervals until the Pleistocene. The Boreal or Palaearctic portion of North America thus contains a fauna which is essentially that of the Old World; and many of the species are so nearly like those of Asia and Europe that naturalists dispute whether or not they should be referred to those Old World species, or whether they should be regarded as distinct. The northern deer, which did not extend into the Sonoran region except along the mountains, such as the various species of caribou, the wapiti (miscalled elk), and the moose, are all of them late arrivals, and in the comparatively brief period of their residence in North America, they have undergone very little change. The same is true of the American bison, and the mountain antelope (erroneously called goat) of the northwest is closely allied to the chamois of Europe. The northern wolves, foxes, and bears, are all very much the same as those of the other portions of the Palaearctic region. Almost the only large mammal which is peculiar to the Boreal zone is the muskox; and that has been made exclusively American by its extinction in the eastern hemisphere in Pleistocene times, when it extended into Siberia and even westward to Great Britain.

The Sonoran region contains the mammals which are peculiarly and characteristically North American. Some of these have had a long period of development in their present homes, so much so that they might fairly be

called indigenous. The several species of southern deer, the prong-horned antelope, etc. are illustrations of this kind. They are derived from migrants which came into North America from the eastern hemisphere in the Miocene.

In the period of time which elapsed after the oldest Eocene, North America was the site of the development of many families of which it no longer has any representatives. The history of the horses, for instance, is for nearly all of the Tertiary period confined to North America. The same thing is true of the camel family, all stages of which are to be found in the Tertiary deposits of the western United States. To a great extent the history of the rhinoceroses and tapirs is American. But for some unknown reason these various creatures, which migrated to South America on the one hand and to the Old World on the other, became extinct in their original home; and thus North America has not a single perissodactyl, while during the Tertiary period it was the principal area of perissodactyl evolution.

The peccaries, also, are of North American origin; but are now almost exclusively South American, extending only into Texas as their extreme range. They continued to be abundant in the northern continent throughout the Pleistocene, but disappeared in the post-glacial climatic changes.

The explanation of the North American fauna is thus, in its main outline, sufficiently clear. It is made up of two different elements; first, those mammals which have been descended from ancestors that were American back to the Lower Eocene; and secondly, those which have been derived by successive waves of immigration from the eastern hemisphere. The South American immigration, as we have seen, produced practically no permanent result, only a single mammal remaining of that invasion.

In the case of the South American fauna, the problem is far more complicated, and cannot yet be said to have found any definite solution, other than certain obvious facts. It is plain enough that the mammals which were listed as of norhtern origin drifted down from the north in successive waves of migration or diffusion, contributing a very large and important immigrant element to the South American fauna, as well as many which disappeared in the great Pleistocene extinction. So much is simple enough.

When we come to consider the origin of the indigenous South American types, as we may call them, we are confronted with great difficulties. I am convinced that in the Eocene and even the early Miocene, South America was connected with Australia, and that the large marsupial element in the Santa Cruz and earlier faunas was of Australian origin. This conclusion is confirmed by a number of extraordinary facts, which find their only explanation in such a land connection. For example, the horned tortoise, *Miolania*, a most remarkable and peculiar fossil, has been found in Australia and in South America, and nowhere else. The marine invertebrate fossils of the Patagonian formation are so like those of corresponding formations in Australia and New Zealand as to demand a continuous coastline or chain of islands and shoals between those now widely separated regions. This connection was probably indirect, and difficult of passage for land creatures, or there would have been a more complete identity of faunas than appears to

have been the case. On the other hand, it must be remembered that we have practically nothing of Australian Tertiary mammals; and what they will reveal, if and when they are discovered, remains to be learned. It would be useless to speculate on the results.

A much more difficult question is that which concerns the origin of the indigenous element of South American mammals. Whence came that great horde of hoofed animals peculiar to the southern continent, and which extends back in time so far as the Tertiary is recorded in Patagonia and adjacent territories? Could these animals have had a common origin in Cretaceous, or earliest Tertiary, times with the familiar types of Arctogaea? If so, is this to be explained by the Cretaceous connection with North America, which, we have seen, there is every reason assume? Especially difficult to explain is the fact that these South American forms were exclusively such in their distribution; that no representative of them has ever been found outside of the limits of South America, including in that term Central America, because they have been discovered as far north as Nicaragua. This must be regarded as an unsolved problem.

Again, we know as yet nothing concerning the origin of the Edentata, which played such a conspicuous role in South American history. The Pampean deposits of Argentina have yielded a vast assemblage of wonderfully preserved Pleistocene fossils, in which the extinct monsters of the Gravigrada and the Glyptodontia, as well as of the peculiar Toxodonta, Typotheria, and Litopterna; but all of these disappeared in the great Pleistocene extinction, for South America suffered even more severely from the loss of its most characteristic types than did North America.

Another difficult problem which still remains open is the significance of the African element in the South American fauna. This is to be noted in the community of the Hystricomorph rodents, some of which, like the spiny rats, are confined to Africa and South America; in the Insectivores of the golden mole type; in the monkeys and marmosets, which it seems impossible could ever have been derived from North America, and which were already present in the Santa Cruz beds at a time when there can have been no communication with the northern continent. Everything points to the derivation of these creatures from Africa; but with a long history in South America, during which they were able to develop the peculiarities of the Platyrrhina, they became sharply demarcated from the monkeys of the Old World. Granting a land connection, this is a reasonable explanation of the South American Primates; but, as in the case of Australia, we must wonder why the community of life is so limited and restricted.

Whichever hypothesis we adopt, to account for the elements common to the African and South American faunas and floras, we are confronted with difficulties which are, as yet, unexplained; but, on the whole, the most probable explanation would seem to be a land-bridge between the two continents and in tropical latitudes. Soundings across the Atlantic Ocean in this region indicate that the bed of the sea is there much broken by faults and is in sharp contrast to the flatness which usually characterizes the floor

of the deep sea. Professor ENGLER has strongly advocated the existence of this land-connection in the early Tertiary period, as needed to account for the great similarity between the tropical floras of Africa and South America, with their many common or representative genera. The late Professor EIGENMANN, who devoted many years to the study of South American fresh-water fishes, was decidedly of the opinion that they could be accounted for only by assuming a connection with Africa not earlier than the Cretaceous period.

A very interesting confirmation of these conclusions is given by the researches of Professor MAYNARD METCALF, of the Johns Hopkins University, upon the Amphibia and their parasites. In a letter, from which he has kindly permitted me to quote, he writes: „I have been inclined to place an Antarctic connection between South America, New Zealand, and Australia, in the early Miocene, and to regard its interruption as occurring in the late Miocene."

„I have wondered if there were not two land connections between Africa and South America, one from Northern Africa to the Guianas, and another from South Africa to Patagonia. The presence of *Heleophryne* (two species) in South Africa, an undoubted Leptodactylid, seems to show clearly the southern connection at a time later than the evolution of the Leptodactylid family."

„The Hylidae and Leptodactylidae seem to have evolved from primitive toads in South America during the Cretaceous or the early Tertiary, the Hylas to the north and the Leptodactylids to the south of the trans-South American sea, which did not disappear until the Pliocene, or possibly the latest Miocene."

The solution of these questions must await the discovery of the successive Tertiary land-faunas of Australia and Equatorial Africa. At present, we can give but a tentative answer to the questions.