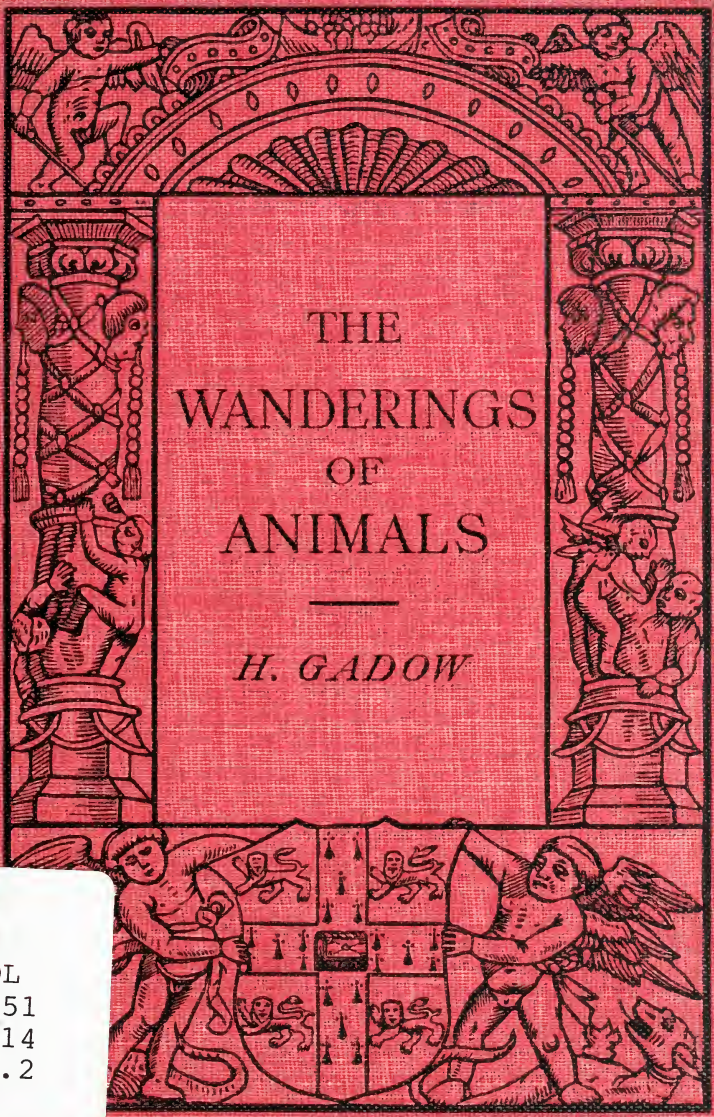
THE WANDERINGS OF ANIMALS

H. GADOW



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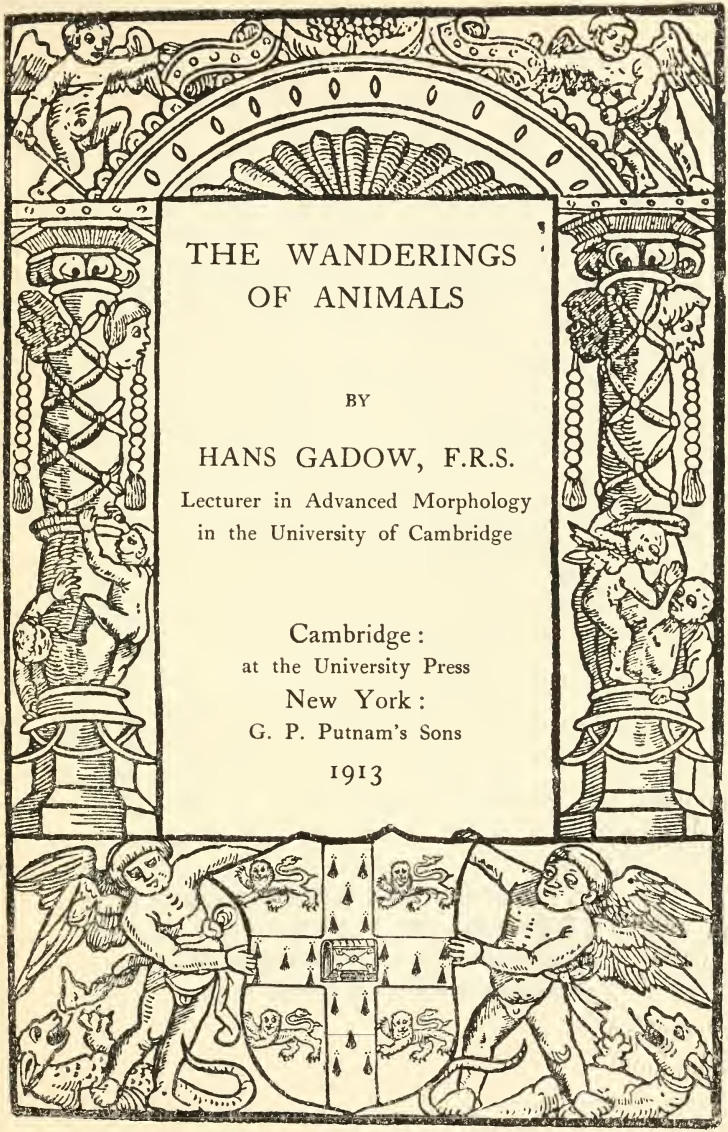

THE WANDERINGS OF ANIMALS

BY

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PREFACE

THESE outlines of the distribution of animals deal with a rather young branch of science. An attempt has therefore been made to sketch its rapid growth from small beginnings until it has become boundless, because the interpretation of at first seemingly simple facts in the domain of the zoologist, had soon to enlist the help of well-nigh all the other branches of Natural Science. The subject of geographical distribution is the dispersal of life, the greatest mystery of all, in space and time. The key to the present lies in the past.

The historical and introductory chapter is followed by a few sketches of the home, as most intensified kinds of which have been selected tropical forests, deserts and high mountains with their various effects of climate and the interdependence of animal and plant life. Next come some short chapters on the modes, means and rates of spreading; and as one of its main causes is the natural increase in numbers, a few tentative remarks on numbers of species and individuals, on rich and scanty faunas and kindred questions have been added. Last, not least, given the creatures, their home requirements and their need to wander, the majority of them could not have attained their present distribution, and the various countries could not have got their present mixed faunas, unless the map of the world had undergone

many and vast changes. Some of these have therefore been indicated in a tentative way. Like other previous hypothetical maps they will be objected to by the timid, on principle ; critics with more expert knowledge will amend them. Meanwhile, may the reader not forget that he has embarked in a frail craft upon a romantic voyage across unknown seas in search of undiscovered lands.

Herewith ends the general part, the principles of distribution. The special part deals with the distribution of a considerable number of various groups of animals, mostly terrestrial vertebrates, selected for their fitness as test cases. Some seem to tell their story well ; others, owing to remote age, insufficient data, and want of fossils, have got their record into a tangle. In a few sample cases, for instance the marsupials, an attempt has been made to unravel such a tangle, and to spin a coherent yarn. Since this cannot be done without recourse to many technical terms and names, it makes rather stiff reading. Such technicalities are the bane of the general reader be he never so interested in the subject, but where homely words and names are wanting, he has to put up with them. Further, he should know the geological time-table as well as his geography.

H. G.

February, 1913.

CONTENTS

GEOLOGICAL TIME TABLE

	System or Period	Series or Epoch	Notable Localities	First known occurrence
CENOZOIC ERA	Recent ..	——	——	——
	Pleistocene ..	Glacial Gravels and Boulder Clay.	——	Man.
TERTIARY ERA	Pliocene ..	Red Crag	Norfolk, Greece, N.W. India	Horse, Dog, Stag, Camel.
	Miocene ..	Molasses and Brown Coals	S.W. Germany, U.S.A., Patagonia	Cats, Bears, Monkeys, Deer, Cattle, Boar.
	Oligocene ..		W. Europe, Egypt, U.S.A. ..	Rhinos, Tapirs, 3-toed Horses. Pike, Land Tortoise.
	Eocene ..	London Clay and Sands	W. Europe, Egypt, U.S.A. ..	Snakes, Lemurs, Bats, Swine.
MESOZOIC	Cretaceous	Upper: Chalk .. .. / Upper Greensand ..	Cretaceous deposits of Europe N. and S. America	Crocodiles, Mud Turtles. Marsupials.
		Lower: Gault .. .. / Lower Greensand .. / Wealden	Britain, U.S.A. .. .. / Belgium	—— / Newts (Urodela).
	Jurassic ..	Oolites .. .. / Lias	Europe, U.S.A.	Frogs (Anura), Birds. Early Crocodiles.
	Triassic ..	Rhaetic .. .. / Keuper	S. Africa .. .. .. / Würtemberg, Connecticut, Britain	Mammals, Marine Turtles. ——
		Muschelkalk .. / Bunter	Germany .. .. .. / S. Africa, Brazil	—— / ——
PALAEO-ZOIC	Permian ..	Magnesian Limestone and Red Sandstones	S. Africa, Ural Mts., Bohemia, India, Colorado	Reptiles.
	Carboniferous ..	Coal Measures .. / Mountain Limestone	Europe, N. America .. / Northern Europe	Amphibians. ——
	Devonian ..	Old Red Sandstone ..	Scotland, Canada	——
	Silurian ..	.. ..	.. ..	Fishes, Insects, Scorpions, Marine Arthropods.
	Ordovician ..	.. ..	.. ..	Brachiopods and Trilobites.
	Cambrian ..	.. ..	.. ..	
	Metamorphosed crystalline schists and slates.			

INTRODUCTION

Everybody knows that if he [illegible]

ERRATA

p. 44 4th line bottom

Instead of highest mountain *read* height of mountain

p. 90 lines 7, 8

Read the occurrence of closely allied species in New Zealand and in Australia

p. 118 line 15

Read Peratherium

buffalo, none of which occur south of Mexico. He may well ponder over these facts, especially as in the Northern Hemisphere wild cattle, sheep, antelopes and deer live in close proximity to each other. It is common knowledge that before the Glacial epoch, geologically not so very long ago, there lived in England, elephants, rhinoceros, hippopotamus, hyaenas, crocodiles and pelicans, all of which have since withdrawn further south. To understand this does not

	System or Period		Series or Epoch	wn occurrence
CENOZOIC OR TERTIARY ERA	Recent	..	——	——
	Pleistocene	..	Glacial Gravels an Boulder Clay.	Man.
	Pliocene	..	Red Crag ..	, Stag, Camel.
	Miocene	..	Molasses and Bro Coals	s, Monkeys, Deer, oar.
	Oligocene	..		pirs, 3-toed Horses. nd Tortoise.
	Eocene	..	London Clay and Sa	murs, Bats, Swine.
MESOZOIC	Cretaceous	Upper	Chalk ..	, Mud Turtles.
			Upper Greensand	s.
		Lower	Gault ..	——
			Lower Greensand	
			Wealden ..	rodela).
	Jurassic	..	Oolites ..	aura), Birds.
			Lias ..	ocodiles.
	Triassic	..	Rhaetic ..	s, Marine Turtles.
			Keuper ..	——
			Muschelkalk	——
			Bunter ..	——
PALAEO-ZOIC	Permian	..	Magnesian Lin and Red San	s.
	Carboniferous	..	Coal Measures	bians.
			Mountain Lin	——
	Devonian	..	Old Red Sand	——
	Silurian	..	.. .	, Insects, Scorpions, ine Arthropods.
	Ordovician	..	.. .	iopods and Trilobites.
	Cambrian	..	.. .	
	Metamorphosed crystalline schi			

INTRODUCTION

EVERYBODY knows that if he wants to shoot a lion, he must go to Africa, and to India for a tiger. The sportsman bent upon making a collection of antlers, will find some kind of deer or other from Spain through the whole length and width of Europe and Asia, he may cross Behring Strait and again he will meet stags from Alaska through the whole length of the Americas down to Patagonia. Well may he conclude that deer are cosmopolitan and yet he would be mistaken, since with the exception of the Fallow deer in Algeria there is not a single kind in the whole of Africa. There on the other hand lives an abundance of hollow-horned game, antelopes and buffalo, none of which occur south of Mexico. He may well ponder over these facts, especially as in the Northern Hemisphere wild cattle, sheep, antelopes and deer live in close proximity to each other. It is common knowledge that before the Glacial epoch, geologically not so very long ago, there lived in England, elephants, rhinoceros, hippopotamus, hyaenas, crocodiles and pelicans, all of which have since withdrawn further south. To understand this does not

require a great stretch of imagination. It is another thing to be told that such an essentially Asiatic beast as the camel had its origin in North America, where now there are none, whilst, to balance the account, the American bison is a rather recent immigrant from the Old World, where he lingers now in the Caucasus only. We may well feel bewildered by such exchanges, and are forced to give up the cherished notion that the original home of a creature is that country where it is now most abundant. If this were always the case, zoological geography would be an easy matter. To trace the animals back to their original home, to follow their wanderings, successes and failures, the changes which they have undergone by adaptation to new and altered environment, and to account for the composition of faunas of the various countries and seas, is the fascinating study of animal distribution.

This study has itself passed through various stages. The legend of Noah's flood contains a considerable amount of shrewd sense. It is the first treatise on geographical distribution. Given the animals—and in spite of all the advances of modern science we have to abide by the same premises—the limited fauna of that part of the world started afresh on Mount Ararat, the only remaining land, or, as we put it now in scientific terms, the only continental remnant which was not affected by a world-wide

transgression of the sea. Thence the creatures dispersed, multiplying, migrating and accommodating themselves, each according to its kind, in a country which possessed the greatest variety of physical features, where snow-clad mountains arise from a semi-tropical lowland. That at least some of these wanderings wrought change in the emigrants is clearly expressed by the statement that Noah's children, presumably all Semites, became the founders of the white and black races of mankind. The environmental conditions in Africa made Ham's descendants melanistic. It was a crude way of accounting for things, and yet, if we honestly condense all our up-to-date knowledge into one sentence, the result would not be very much superior. At best our treatise is a Romance of Land and Water.

CHAPTER I

HISTORY OF GEOGRAPHICAL DISTRIBUTION

THE first general ideas about geographical distribution may be found in some of the numerous speculations contained in Buffon's *Histoire naturelle*, the brilliant style of which greatly enhanced the interest taken in natural history. The first special treatise on the subject was, however, written in 1777

by E. A. W. Zimmermann of Brunswick, whose large volume *Specimen Zoologiae Geographicae Quadrupedum* deals in a statistical way with the mammals. In the following year appeared the *Philosophia Entomologica* by J. C. Fabricius of Kiel, who was the first to divide the world into eight regions. In 1803 G. R. Treviranus of Göttingen devoted a long chapter of his great *Biologie* to a philosophical and coherent treatment of the distribution of the whole animal kingdom. Remarkable progress was made by F. Tiedemann of Heidelberg, whose *Anatomie und Naturgeschichte der Voegel*, 1810, deals with some of the most subtle and fundamental causes of distribution, for instance the influence of environment, distribution and migration upon the structure of birds. None of the many subsequent writers seem to have known of the ingenious way in which Tiedemann marshalled his statistics in order to arrive at general conclusions. The entomologist Latreille of Paris proposed the view that temperature was the main factor in distribution. This was combated in 1822 by Desmoulins of Bordeaux, who in a most suggestive paper introduced the idea of 'analogous centres of creation,' meaning that similar groups of creatures may have arisen independently in different parts of the world. The first book dealing with the 'geography and classification' of the whole animal kingdom, was written by W. Swainson in 1835, but

it suffered from the mysticism of the author's 'quinary system.' Ch. Lyell's *Principles of Geology* should have marked a new epoch, since in his *Elements* he treats of the past history of the globe and the distribution of animals in time, and in his *Principles* of their distribution in space in connexion with the actual changes undergone by the surface of the world. But as he restricted himself to the comparatively minor modern changes, and believed in the permanency of the great oceans, he did after all advance our problems but little. Meanwhile E. Forbes of Edinburgh devoted himself to the marine fauna, especially the Mollusca. He established nine 'homozoic zones,' subdivided into 25 'provinces' based chiefly on the isotherms or belts of equal temperature. J. D. Dana of New Haven taking mainly the Crustacea as a basis, and as leading factors the mean temperatures of the coldest and of the warmest months, arrived at five latitudinal zones, with many provinces. In 1853 L. K. Schmarda of Vienna published his two volumes comprising the distribution of the whole animal kingdom. After devoting many chapters to the possible physical causes and modes of dispersal from original centres of creation, he divided the land into 25 'realms,' some of which were well selected, but they were obviously too numerous for general purposes. This drawback was overcome in 1857 by P. L. Sclater with the now

classical six 'regions,' which he named Palaearctic, Ethiopian, Indian, Australian, Nearctic and Neotropical. Those of the Old World were brigaded as Palaeogaea and the two Americas as Neogaea, a fundamental mistake. Broadly speaking these six regions are equivalent to the great masses of land; they are convenient terms for geographical facts, especially since palaearctic expresses the unity of Europe with the bulk of non-tropical Asia. Unfortunately these regions are not of equal value. Therefore, instead of keeping up the popular distinction between the Old and the New World, Huxley in 1868 gave reasons (cf. Gallinaceous birds) for dividing the world transversely, into an Arctogaea or North World in a wider sense, comprising N. America, Asia, with Europe and Africa; and Notogaea or South World, which he divided into New Zealand, Australasia and Austro-Columbia, the latter an unfortunate substitute for Neotropical. Although applicable to various groups of animals, the combination of S. America with Australia in opposition to the rest of the world was gradually found to be too sweeping a measure. The satisfactory solution was provided by W. T. Blanford, who in 1890 recognised three main divisions, namely Australian, South American and the rest, for which the already existing terms *Notogaea*, *Neogea* and *Arctogaea* have come into general use.

Meanwhile in 1859 Darwin's *Origin of Species* had given a great impetus to the study of geographical distribution and caused a parting of the ways in its treatment, especially in the mapping of the world into regions or other divisions. Whilst some writers were, and are, satisfied to express by their realms, regions, or zones the recent, actually existing, statistic similarities and differences of the faunas of the various countries, other workers, more appreciative of evolution, tried to apply genetic principles to the selection of their divisions, which they rightly considered as original centres of creation and subsequent dispersal.

Haeckel, the foremost apostle of 'Darwinism' in Germany, has given us in his *Generelle Morphologie*, 1866, the terms *Oecology*, the relation of organisms to their environment, and *Chorology*, their distribution in space. The 14th chapter of his *History of Creation*, 1868, is devoted to the distribution of organisms, with the emphatic assertion that 'not until Darwin can chorology be spoken of as a separate science, since he supplied the acting causes for the elucidation of the hitherto accumulated mass of facts.'

One of the earliest writers to grasp the new situation was Pucheran[1] in France. He pleaded that

[1] Pucheran had already, in 1865, insisted upon the essential unity of the faunas of Europe, Asia and Africa, and on the necessity of

the Sahara, formerly a marine basin, was peopled by immigrants from the neighbouring countries, and these became new animals by adapting themselves to the new environment; the agreement in coloration between the desert and its fauna is 'une harmonie post-établié.' They did not survive because they happened to be of desert-colour, but assumed that colour because they found themselves in a desert. He also discussed, besides similar questions, the Isthmus of Panama with regard to its having once been a strait. A strong proof of the new influence upon this French scientist is the following sentence: 'As the various parts of the world successively were formed and became habitable their respective contemporaneous faunas spread by radiation, each from its centre, and became modified according to the local physical conditions.'

In 1866 appeared Andrew Murray's *Geographical Distribution of Mammals*, an important work, illustrated with 101 coloured maps, the first of its kind[1]. Like Forbes he did not shrink from assuming

separating S. America as well as Australia from the rest of the world. Of far reaching influence was also the excellent Zoo-geographical sketch *Ueber die Herkunft unserer Thierwelt* by the Swiss Palaeontologist L. Rütimeyer, published at Basel in 1867.

[1] The earliest maps dealing with our subject seem to be those in H. Berghaus' *Physikalischer Atlas: Thiergeographie*, Gotha, 1852. In the third edition, 1887, this has been enlarged into an *Atlas der Tierverbreitung*, by W. Marshall.

enormous changes in the configuration of the continents and oceans because the theory of descent, with its necessary postulate of great migrations, required them.

In the same year Moritz Wagner showed that migration implies not only new environmental conditions but also secures separation from the original stock and thus eliminates or lessens the reactionary dangers of panmixia or promiscuous interbreeding. This idea had been discovered before and it has been rediscovered several times after Wagner. Through the heated discussions of the more ardent selectionists, Wagner's theory came to grow into an alternative instead of a great help to the theory of selectional evolution. Separation is now rightly considered a most important factor in the making of new species. C. Semper could well say in his suggestive work *Existenz-Bedingungen der Thiere*, also published in the fertile year 1868, that 'our whole Zoogeography is indeed nothing but a big heap of bricks, piled up without sense,' and he was one of the first to elucidate the distribution of a group—Holothuria or Sea Cucumbers—by tracing the relationship of its genera and species, whilst distinguishing between their centres of origin and their subsequent migrations, and not losing sight of former geological conditions.

In 1872 Alexander Agassiz of Harvard followed with a morphological systematic revision of the Sea

Urchins, which led him to establish four realms of the oceans, justified also by climatic and other physical conditions.

In an anniversary address to the Geological Society, 1870, Huxley pleaded for various former land connexions and considerable marine changes.

Whilst English, American, German and French scientists were thus hard at work at reconstructing the history of the world—it having become thoroughly understood that the key to the present distribution of any group of animals or plants lies in the past—the year 1876 marks a new period with the appearance of A. R. Wallace's great work. These volumes, supplemented by the fascinating *Island Life*, have indeed popularised the study of geographical distribution, and there is now an ever widening circle of enthusiasts far beyond the professional brotherhood. His works have become the classics of our science and they will remain so, but they have also had some influence not altogether advantageous.

He accepted Sclater's six regions with slight modifications and divided each into four subregions, but did not follow Huxley's courageous changes and logical subordinations. Holding the view of the permanence of the oceans and therefore comparatively small changes of land, he accounts for the colonisation of outlying islands (especially his 'oceanic islands') by further elaborating the views of Lyell

and Darwin. The subsequent literature is full of devices for the mechanical dispersal of animals, as marine currents, floating logs and icebergs, storms and waterspouts.

Wallace's method of arriving at the degree of relationship of the faunas of the various regions is eminently statistical. Long lists of genera determine by their numbers the affinity and hence the source of colonisation. This statistical method has found many followers, who, relying more upon quantity than quality, have obscured the problem.

An extensive literature has since grown up, almost bewildering in its range, diversity of aims, and style of procedure. So prominent, as to almost constitute a characteristic period, has become the search by specialists for either the justification or the amending of the Sclater-Wallace regions. As class after class of animals was brought up to reveal the secret of the true regions, some authors saw in their different results nothing but the faultiness of the regions established by their predecessors; others looked upon eventual agreements as their final corroboration, especially when such diverse groups as, e.g. mammals and scorpions, could, with some ingenuity, be made to harmonise. But the undeniable result of all these efforts was the growing knowledge that almost every class, nay many an order or even family, seemed to follow principles of its own. The

resulting regions tallied neither in extent nor in numbers, although most of them gravitated more and more towards three centres, namely Australia, South America and the rest of the world.

Let us take up the account with the establishment of the Noto- Neo- and Arctogaea in the year 1890, when Trouessart of Paris, by adding an arctic and an antarctic region to those of Wallace, increased them to eight, but he also suggested that these might be recombined into three 'zones,' namely an Arctic (=Heilprin's and Newton's Holarctic), an Antarctic (South America and Australia) and an Old-World tropical zone. The latter idea was taken up in 1892 by Allen of New York who, after a study of the Mammalia, joined the Old Oriental and Ethiopian regions into one Indo-African. Meanwhile A. Heilprin of Philadelphia in 1887 accepted the Neotropical, Australian, Oriental and Ethiopian regions, but at the suggestion of A. Newton combined the Nearctic and Palaearctic as Holarctic; further, he carved out two new regions, one Mediterranean, the other Sonoran; for the Nearctic, now reduced to Canada and Alaska, together with the Palaearctic Blanford suggested the name Aquilonian, whilst for the Sonoran he revived Cope's term Medi-Columbian. We have only to add that some Zoo-geographers treat as principal regions what others consider as subregions, that some speak of eight realms and others of only three regions, and

still another of as many as nine 'Gaeans' as chief units, and others prefer six zones, to indicate that chaos reigns instead of order.

Although with this wild search for the true regions the value of the fossil animals became fully recognised as the only absolute evidence of distribution in the past, it was frequently ignored that the various groups of animals have appeared in successive geological epochs and also at many places remote from each other. The key to the distribution of any group lies in the geographical configuration of that epoch in which it made its first appearance! If, for argument's sake, some group of land animals had come into existence in Africa, when this was still continuous with Madagascar, the present descendants of these animals may well be found in both countries, but this could not be the case with another group which was evolved after Madagascar had become an island. This is so obvious as to sound like a platitude.

If all the various groups of creatures had come into existence at the same epoch and at the same place, then it would be possible, given sufficient data as to present and past distribution, to construct a map showing the generalised results applicable to the whole animal kingdom. But the premises are wrong. Whatever regions or primary centres we may seek to establish as applicable to all classes, we are necessarily mixing up several principles, namely time

and space, occasionally the past of North and South with the present East and West.

In short, there are no generally applicable zoological regions, not even for each class taken separately, unless the life of this class is confined to a comparatively short geological period. Most of the greater groups have far too long a history and have evolved many successive divisions. Let us take the mammals. Marsupials or pouched mammals still live in Australia and in both Americas because they existed already in Mesozoic times. But hoofed beasts, Ungulata, existed at one time or other all over the world, except in Australia, because they, as a group, are post-Cretaceous. Deer and bears, as examples of still more recent northerners in origin, are found on every continent except Australia and Africa. Each of these groups teaches a valuable historical lesson, but when these and others are combined into a few mammalian realms or regions they mean nothing but statistical majorities. If there is one at all, Australia is such a realm backed against the rest of the world, but as certainly it does not represent an original mammalian creative centre. So far as mammals are concerned, New Zealand has none indigenous; it is a Mesozoic derelict, and is a 'region' with a negative character. Australia became a separate complex after it had received, not evolved, the stock of its most characteristic fauna which has since flourished so as to produce

many peculiar forms. Madagascar, also considered as a region by some authorities, became an island about mid-Tertiary times. Therefore, concerning mammals, the world would not have been affected in the least if neither Madagascar nor Australia had ever existed. How different is the case of Africa. This ancient and radiating centre has had an enormous effect upon the fauna of well-nigh the rest of the world.

There may be regions of birds, others of fishes and others of beasts, but the search for generally applicable regions is a mare's nest.

What, then, is the object of the study of Geographical Distribution? It is nothing less than the history of life in space and time. The attempt to account for the present range of any group of animals (the special scope of Zoo-geography) involves the aid of every branch of science. Our subject began in a mild statistical way, restricting itself to the present faunas and floras, and to the present configuration of land and water. Next came Oceanography concerned with the depths of the seas, their currents and temperatures; then inquiries into climatic changes, culminating in irreconcilable astronomical hypotheses as to glacial epochs, the causes of which are still a mystery; theories about changes of the level of the seas, from the point of view of the geologist, the physicist and the astronomer. Then

came to the front the importance of the geological record, hand in hand with the fossil data and the search for the natural affinities, the pedigrees of the organisms. The biologists not only set the problems; they alone can check the solutions offered by physicists and geologists, and rightly so, because they concern living matter, and life has been continuous ever since the unfathomable dawn. The mere fact that subtropical plants occur in the Miocene of Spitzbergen, led to an hypothetical shifting of the axis of the world rather than to the assumption, by way of explanation, that the plants themselves might have changed their nature. As the men of the Dordogne in the south of France hunted the reindeer, we want explanations why it was so cold. And since there are plenty of bones of hippopotamus in the Cambridge gravel, washed into it out of Pliocene crag, we require an answer as to why East Anglia enjoyed a mean annual temperature perhaps 20 degrees higher than now.

One of the most valuable aids, often the only means for reconstructing the face of the earth in by-gone periods, is afforded by fossils, but only the morphologist can pronounce as to their trustworthiness as witnesses, because of the danger of mistaking analogous for homologous forms. This difficulty applies equally to living groups and is of the utmost importance.

The affinity question can be settled only by

the morphologist, whose special business is the study of the anatomical structure and the weighing of these characters as to their classifying or taxonomic value. To see through the resemblances, to see what is due to blood-relationship or descent and what is due to adaptation to similar mode of life is the whole art of the builder of classifying systems, but many of these pedigree problems are still unsolved.

The study of geographical distribution is now proceeding in two main directions. I. Chorological. According to the method employed this is *either* zoological geography, proceeding by essays on the faunas of selected countries, and thence, so to speak, letting the research radiate in ever widening circles. An example of this method is Scharff's *European Animals*. *Or* geographical zoology, which takes selected groups of animals and traces their changes of range in time and space, e.g. Ortmann's *Geographical Distribution of Freshwater Decapods*. Both methods are of great interest, and each has its advantages in working at the reconstruction of the geography of former epochs. In short they are both essentially chorological, a term which, although strictly meaning distribution in space, must be understood to include the factor of time. II. Oecological, the study of animals with regard to their environment. Instead of searching for pedigrees, or of showing how and when the animals got to the various countries, it

investigates the prevailing local physical conditions and how these have influenced the faunas. The cultivation of this field promises fair to throw much light upon Nature's way of making species, and it is all the more enchanting because here the animals, whether recent or extinct, are brought before us as living fellow creatures. The main purpose of an organism is to live. If 'purpose' be objected to, let us say it is its business, that with which it is busy.

But the broadest of land connexions is of no avail to the dwellers of forests if it is a desert, or even a prairie. What is attractive to some is repellant to others. It is the environment, the condition of the home, the *oikos*, which decides the tenants, hence the importance of oecology.

CHAPTER II

FEATURES OF ENVIRONMENT

Tropical Forests.

NECESSARY conditions for the production of a typical tropical forest are moisture and heat. The mean temperature is that of the tropics, say 80° F. rarely sinking below 70° or exceeding 90°. The moisture must be due to rain with an annual minimum of at least 60 inches, a fair average being

80 inches for a 'rain-forest,' the more the better. This rain must be distributed rather evenly, that is, seasons of drought must not be too prolonged. The dry period, if there is one at all, must not amount to more than three months, lest there be a standstill of the vegetation, causing deciduous leaves and other great changes in the general aspect.

An annual rainfall of 80 inches is, in itself, not terrific. For comparison it may be stated that we call a climate with half this amount decidedly wet. The North-West of Scotland and the wettest parts of Ireland enjoy about 60 inches, but in the tropics the rain makes itself more impressive by frequent thunderstorms and by falling within a few hours of the day. A fall of half an inch if spread over the twenty-four hours, makes with us a very wet day. A fall of an inch during a few hours' storm is of common occurrence in the tropics, and the mere mechanical effect of such a mass of falling water upon animals and plants is considerable. The electric discharges which accompany these torrential storms produce a great amount of nitric acid which is washed out of the air into the humus, and this process contributes much to the wonderful exuberance of the vegetation in every tropical rainy district.

There are three large regions in the world, which fulfil these conditions.

First: Tropical America, with the huge basin of

the Amazon as its centre. It extends through Central America into Mexico, mainly on the Atlantic side, the backbone of the country causing a very striking division.

Second: Equatorial West and Central Africa, mainly the Congo basin.

Third: Indo-China with the Malay and Papuan Islands.

Smaller centres within various other parts of the world, for instance on the Zambesi, the east coast of Madagascar, the Seychelle Islands, the south-west coasts of S. India and Ceylon, the north coast of Queensland and parts of Papuasia; several West Indian islands.

What is the general impression of a rain-forest? It does not begin gradually. On its outskirts it forms an impenetrable wall of luxuriant herbage, shrubs and creepers. It can be entered only by slashing a path through the tangle, which closes up again within a few weeks, except where traffic or game has produced a meandering track, without a chance of our deviating either to right or left. Once inside, we are in a gloomy, stuffy forest of tall straight trees which branch out high above us, then interlacing and forming a dense canopy of green, through which passes but little sunlight. This absence of direct light prevents the growth of underwood, and there are no green luxuriant plants, no flowers

and no grass. The ground is dark, covered with many inches of rotting leaves and twigs, all turning into a steaming mould. From our standpoint below the canopy, the leaves, branches and even bright-coloured birds, look black, and this is still more the case where, by contrast, these objects are seen through a rift against the glaring sky. Many of the tree-stems are entwined by the twisted rope-like stems of lianas, long strands looking like rusty and frayed out wire-cables, ugly in shape, without branch or leaf, until they reach the crowns of the trees, where they intermingle with the other verdure and creep across the tree-tops, perhaps for hundreds of feet. Many a liana has strangled its support, which has rotted away, and the creeper, now anchored in the ground, ascends straight through mid-air and there vanishes. Many of them are vines; where these are not indigenous one or other of the numerous Bignonias or plants of some other family undergo the same modification.

Wherever there is a break, where a tree has crashed down, the other trees are covered with masses of climbing arums. Philodendrons send down their wire-like air-roots until these are anchored in the ground; the blooms, large scrolls of white, yellow, or red, are visible from afar; the supporting stem is covered with a network of the climbers, which acting as receptacles for the collection of mould, become hotbeds for Selaginellas, ferns, lichens and a host of

gorgeous orchids, bromelias and other epiphytes, the seeds or spores of which have started many feet above the ground, so that these plants never know the ground proper. They were born aloft, have grown aloft generation after generation until they have forgotten what it was like to grow up from the bottom, and thus they have become epiphytes or even parasites. Many of these, though never the primary supporting trees themselves, have ingenious methods for conducting, collecting and storing the rainwater; either all their leaves form a nest-like whorl, as is the fashion of some Bromelias and Tillandsias; or, may be, one leaf is turned into a scroll.

A striking feature of such a tropical forest is that it is composed of an astonishing number of different genera and species of trees, forming the greatest possible mixture, while continuous groves of one kind are rarely met with. Whilst the temperate region has extensive oak, beech and pine forests, no such uniformity exists in the tropical belt unless we ascend into the mountains. There is a cause for this variety. The exuberance of life is so great, and therefore the struggle for individual existence is so severe that there is little chance for two trees of the same kind to succeed in growing up side by side. It is almost by a lucky accident that one grows up at all where hundreds of other plants want to do the same.

Such a forest brings home to us what the struggle for life really means and what it can do. Here it is the struggle for sunlight and for rainwater and to get them at first hand. One of the results is the height of the trees, to which, so to speak, they have forced each other, tall, often slender, branchless stems, with an interlaced canopy above. A plant that cannot grow tall by itself, climbs on to its neighbour's shoulders. Even a cactus in a forest can climb like ivy, and many of them have learned the trick so successfully that they have been transformed into epiphytes, either remaining still upright, or in the guise of big, many-tailed pendent bunches.

Such is the forest. Let us now consider the inhabitants. The observation of animal life is most disappointing to the novice. He may roam about in this gloomy forest for hours and hear little and certainly see less. Where are the two hundred different kinds of mammals, birds, reptiles, and amphibians which we know to exist in a Mexican tropical forest? Most of them inhabit the top storey, the roof-garden which is formed by the tree-tops. If by a lucky chance we obtain a bird's-eye view from a precipice or from a river, we behold a different world. A dense green carpet overstrewn with mauve, pink, yellow or white flowers, visited by butterflies which are preyed upon by lizards and tree-frogs, these being in turn sought after by tree-snakes. Of bird life also

there is plenty, often gorgeous and beautiful in colour. Vividly coloured are also many of the other creatures, frogs, snakes, lizards and butterflies. Colour has to be laid on vividly, quiet coloration being out of place. The blooms have begun the race. Red, yellow or white, self-colours, are very effective against the green. If a creature intends to be seen, for beauty's sake, it has to use bright colours, since it is only by contrast that it can attract attention. Again those which do not want to be seen must dress as loudly, and in tints as saturated, as are the prevailing tones of the environment.

Most of the tree-frogs are green, unless they are delicate studies in brown with irregular markings to suit the moss- and lichen-coloured branches upon which they rest. Some have 'flash colours,' orange, yellow or red on parts which are quite concealed when the creature sits still. It trusts to not being discovered; but touch him and there is a flash of yellow in the air, which vanishes in a moment, the frog also vanishing. He has dazzled his pursuer by this sudden and unexpected display of colour, has then caught hold of a leaf with some of his adhesive finger disks, vaulted on to it and there sits demurely indistinguishable from the foliage.

Many tree-snakes are green and so are many parrots, motmots and other typical tropical forest birds. Other parrots, pigeons, toucans are loudly

coloured, but these very colours mingle with the bright surroundings to a marvellous extent. Tropical light can be so fierce and resplendent, that a whole flock of bright parrots in a tree will simply vanish. In a museum we find it hopeless to understand how such conspicuous objects can ever manage to elude discovery.

If we now descend in our survey below the tree-roof there are of course many creatures which live habitually upon the branches or stems of the trees. These have sombre tints, brown, speckled or barred. Lastly, those which live on the ground-floor, or in the basement, are mostly dark. It would be of no avail to wear a beautiful dress in a badly lighted place.

Another point concerning the coloration of dwellers in forests is the pattern. Except when this is more or less uniform, the ground-colour is broken up by white or yellowish spots, arranged in several longitudinal rows. Many snakes and lizards are thus marked; the young of many mammals pass through a stage of this kind, notably those of deer, pigs, the American tapir and those of the cat-tribe. There are no striped lights in a forest; what sunlight there is, appears in the shape of little round disks, tiny sun images, and these are—let us put it boldly—stamped upon the skin. If we follow the same kind of dark-skinned, white-spotted lizard out of the forest into the savannah, into the grassland, its

corresponding race or species has no spots, but longitudinal stripes; and the species of the same genus which live in the desert have a pale ground-colour with dark spots.

Most of the inhabitants of tropical forests lead an arboreal life. There is no need for hurry, but they must be able to climb well.

The majority of the Anura have acquired arboreal characters. The hind limbs are long and slender, to jump distances, and for catching hold of a leaf or twig the fingers and toes are provided with adhesive disks. Such arboreal Anura are found in all suitable forests, and the significant fact is that these climbers by no means all belong to the family of Hylidae, but nearly every one of the various families of the Anura has produced at least some typically arboreal genera in spite of the considerable internal, structural differences which distinguish, for instance, toads from frogs. The majority belong to the family *Hylidae*, but where, as in Africa and Madagascar, there are no Hylas, the 'tree-frogs' are modified *Ranidae*, since these happen to be the material available for counterfeiting them. In this respect the forests have succeeded so well that it is for instance impossible to distinguish certain green tree-frogs of the African genus *Rappia* from a *Hyla*, unless we cut them open. If they lived side by side, which they do not, this close resemblance would be extolled as an example

of mimicry. In reality it is a case of convergence, brought about by identical environmental conditions. One might almost say that tropical moist forests must have tree-frogs, and that these are made out of whatever suitable material happens to be available.

The same remark applies to tree-snakes, and it is immaterial whether the available stock be boas or pythons, harmless colubrines, cobras, vipers or even pit-vipers. In India all these groups have contributed. Typical tree-snakes invariably have a very long, slender body with an excessively long whip-like tail. Thus they can glide through the foliage from tree to tree, their long body and tail always finding some support.

Boas and pythons have short and strong prehensile tails, and the numerous chameleons of Africa and Madagascar have grasping hands and feet as well. This principle of prehensile organs is carried to an extreme in various mammals, of which it is sufficient to mention monkeys and lemurs, the pangolins and sloths among edentates, palm-martins among carnivores, arboreal porcupines among rodents, and opossums among marsupials. All have either specially modified climbing hands and feet, or tails, or both.

But the especial home of prehensile-tailed mammals is in the tropical forests of America. There alone live the prehensile-tailed monkeys. Nearly all its marsupials are arboreal opossums. Even two

ant-eating edentates, *Myrmecophaga tetradactylus*, and *Cyclothurus didactylus*, as well as the climbing porcupines, *Synetheres; Cercoleptes caudivolvulus*, the kinkajou, with its indiarubber-like tail-tip, is a representative of the carnivores.

Another feature, peculiar to intensely arboreal animals, is the principle of the parachute, some distension of the skin to break the fall. Some kinds of the otherwise widely distributed frog genus *Rhacophorus*, in the Malay Islands, have the webs between their fingers and toes enlarged to an almost absurd extent, so that these 'flying frogs' can glide through the air in a slanting direction.

The little 'flying dragons,' Agamid lizards of India and Malaya, possess a folding parachute, with stays furnished by the much lengthened posterior ribs. In Borneo lives a tree-snake which by spreading its ribs and thus flattening and broadening the body, is said to glide from tree to tree.

The parachute is carried to extreme perfection in the now cosmopolitan bats; less extensive parachutes restricted to folds of the skin between the sides of the body and the limbs, we find in other mammals, mostly in the Malayan and Australian forests. For instance *Galeopithecus*, the flying insectivore; flying phalangers among marsupials, the flying rodent *Anomalurus* in West Africa; and of course flying squirrels which have attained a wide holarctic range.

It is a very interesting fact, over which one may ponder deeply, that where parachuting is such a fashionable contrivance as it is in the Indo-Australian countries, prehensile tails are almost absent. The reverse is the case in the tropical American forests in which there does not occur a single instance of a parachute.

Intensely arboreal life leads to many other, sometimes most unexpected, habits, structural modifications, and sometimes to limited distribution. The scroll-like receptacles of leaves, before mentioned, hold water and some frogs use them as nurseries, or they glue the leaves together, fill the space with a foamy lather and deposit their eggs therein, the development of which is so accelerated that the babies are hatched as tiny frogs, having dispensed with the tadpole stage. Or the male glues the few but large eggs on to the female's back, a trick common in Africa and on the Seychelles. In some Brazilian tree-frogs a slight fold of skin is raised along the sides of the back, to prevent the eggs from slipping off. In some other kinds these folds enlarge during the hatching season into a kind of hood, e.g. in *Hyla goeldi*. In a few tropical Americans this hood has become a permanent organ, a pouch on the back. *Nototrema* is the generic name of these marsupial frogs! It has been suggested, upon weighty reasons, that even the marsupial mammals owe their survival

to the retention of the pouch in correlation with the arboreal life which the immediate ancestors of all the recent marsupials are known to have led. Arborealism may have been forced upon the primitive, indigenous fauna as a means of escaping competition against the coming higher placental mammals.

Tropical forests teach two impressive lessons: the awe-inspiring competition into which plants and animals alike are forced in their struggle for life, and the fact that the fight is so fierce, because the physical conditions—plenty of warmth, water and food—are so favourable to all. Every living thing is modelled by adaptation to the prevailing surroundings, coupled with the cumulative inheritance of the characters acquired.

Deserts.

A characteristic essential feature of deserts is the scarcity of rain. An annual amount of rainfall of less than eight inches inclines a country towards desert conditions. Much depends upon the distribution of the rain, whether the few inches come down in the shape of half a dozen or more days of good rain, at various times of the year in little doses, or whether there is a drought of twelve months, or even longer, and the whole scanty allowance pours down in one dose, most of which is thus squandered since there is no time for it to soak in. There are in fact various

degrees of deserts, unmitigated deserts, periodical deserts shading into rather arid stretches, semi-deserts, and lastly steppes, pampas or prairies which are subject to prolonged drought, periodical or uncertain. As a rule bad deserts are surrounded by a belt of half-deserts, and these pass into fair pasture land. The French word prairie, the Russian steppe and the South American pampa practically mean the same, namely grassy plain.

We mostly associate with the idea of a desert a boundless extent of sand without any vegetation, but this is not necessarily the case. There are huge deserts, which are stony, or rocky tablelands, or full of chains of mountains, and again there are sandy deserts with even tree-like growth on them, and certainly with grass, which however may be so scanty that one appreciates it only if he lies down upon the ground and then observes the grey-green shimmer.

There are, broadly speaking, five such arid complexes in the world.

1. The largest extends from the coast of North-West Africa through the Sahara and thence with many interruptions through Arabia and Persia into North-West India; the neighbourhood of Lakes Caspi and Aral, Turkestan, great portions of Tibet and of Mongolia, there as the so-called Gobi or Shamo, i.e. sea of sand.

2. The greater portion of Middle and Western Australia.

3. South-West Africa, from the coast of Damaraland inwards, including the so-called Kalahari, which however seems to be more like a steppe.

4. Parts of the South-West of the United States, e.g. Salt-Lake desert, Californian desert, Colorado and Mojave desert of Arizona. This complex stretches far into Northern Mexico.

5. Parts of Patagonia and Argentina, and a narrow strip along the west coast of Chile.

As examples of the smallest average annual amount of rainfall the following places may be mentioned: Copiapo in Chile, less than $\frac{1}{2}$ inch; Mojave (Arizona), Suez and Amu Daria (Turkestan) $2\frac{1}{2}$ inches. For comparison, Cambridge with 23 inches.

It is a common error that such deserts are the beds of former seas. This is true of some, but by far the greater part are not of marine origin; moreover an old sea-bed need not be barren. The factors which cause deserts have nothing to do with the sea. Most of those areas of land which have no river-drainage into the sea are in time converted into deserts. Witness the Salt Lake of Utah, the Caspi, Aral and the Dead Sea; they all are centres of sandy deserts, because their rivers cannot carry away the sand out of the country. Sand is, by the way, nothing but the comminuted débris of rocks, of mountains.

The disintegration of the rocks goes on quickest when they are subject to great and frequent variation of temperature. The sun heats and expands, the cold of the nights contracts ; cracks are caused, water gets into them, freezes and bursts them, etc. Every river carries some sand. The sand of the seashore is nothing but the ground down mountains of the far inland, carried to the sea by the rivers. A look at the map of Central Asia, Central Australia, or the Sahara shows many river courses which run inland and never reach the sea ; they either end in a land-locked lake, or they lose themselves in the sand, all of which they themselves have helped to carry down. They are burying themselves. The more sand, the more dust, and enormous dustclouds sweep over the country forming shifting dunes, or they deposit other so-called aeolic formations, for instance the loess of China, a kind of loam, very fertile if irrigated. But the greater the masses of sand, the less becomes the rainfall and the making of deserts becomes intensified. Sometimes existing outlets are barred by a slow steady upheaval of neighbouring tracts of country, which are then doomed to become deserts. The lakes of deserts are almost invariably alkaline, salty or bitter because the rivers wash the salt, saltpetre and other soluble mineral matter out of the mountains, thus rendering the lakes increasingly unfit for life.

The making of deserts is still going on in various parts of the world. It is quite likely that many of the Central Asian desert regions were more habitable even within historic times, and that, when their conditions changed for the worse great migrations of the people were the result. (See Sven Hedin's and Aurel Stein's descriptions of the sand-buried cities of Tibet.) The same applies to the extensive ruins in Arizona, New Mexico and North Mexico, affording incontestable evidence of former thriving populations.

Now, what applies to people, applies also to other animals. The change of a country from bushland or a fertile prairie into a semi-desert may sweep off all the original inhabitants if that change is quick; but if it is slow and gradual, many plants and creatures will have a chance of adapting themselves to the new conditions.

Such conditions are: (1) scarcity of water, especially rain. (2) Abundance of sand and dust. (3) Great variations of temperature, not only with the seasons, but often daily. For instance in the Mojave desert it may be insufferably hot in the daytime, under a broiling clear sky with shade temperature far above 100° F.; shortly before sunrise, owing to the unchecked radiation the water freezes in an open pan. Before sunset you do not know where to hide from the heat: amidst an ocean of glaring sand, with sandspouts swirling over the

plateau, hotter rocks, and nowhere a shade-giving tree. Before sunrise the traveller shivers in his blankets near the much needed camp fire.

Paradoxical as it may seem, there is often a heavy dew. This is not so much falling dew, moisture condensed out of the atmosphere by the cold ; it is rather the direct evaporation from the subsoil and this vapour is condensed near the ground before it gets well into the dry desert air. In many sandy deserts there is plenty of subsoil water, but the difficulty is to get at it in drinkable quantities.

Animals and plants must have water. In the desert they must be economical with it, not to perspire but to have provisions for holding it, or to catch even the smallest quantities. The roots of trees and shrubs often go down to astonishing depths ; frequently there is much more of such plants below than above the ground. Many plants are furnished with woolly hairs ; others have very narrow, slender leaves, standing together like bunches of wire ; this arrangement enhances the radiation, and the resulting coolness causes deposition of the dew upon them and this is what these plants want. Striking examples are the Tillandsias, related to the Bromelias, but instead of making a scroll, or rain-catching nest of their leaves as they do in tropical forests, these plants in arid regions grow upon the most exposed branches of the trees and are transformed into small

grey branches of wiry tufts. There are no broad-leaved plants: most of the leaves are lance-shaped, spiky, thorny, e.g. Yuccas; or the leaves are large, thick, full of juice, but covered with an air- and water-tight epidermis, again spiky like the African aloes and the American agaves; or the plants have dispensed with leaves altogether, having turned them into thousands of hooks and spikes, and the whole, often large, stem has a green rind. The chlorophyll is spread over the stem instead of in the leaves; for instance the cactus-tribe of America, and exactly the same transformation occurs in the Euphorbias of Africa where there are no cacti. A large globular cactus stores water sufficient to last it for years, or the plants adopt the principle of the bulb. These produce a short-lived glorious bloom in the short wet season, and during the greater part of the year, or occasionally for several years on end, the bulb sleeps unnoticed underground.

A very peculiar feature, not easily explained, is that in arid districts the perennial vegetation always grows in patches, with bare spaces between. This patchiness is carried even further. Some sprawling shrub gives, so to speak, shelter to other plants and thus a little colony is formed, but it remains an isolated patch and they never join. Sagebush, artemisias, hard wiry tussocks of grass, cactus, broom-shaped leafless euphorbias, here and there a big tree-like Yucca, are characteristic of desert vegetation.

The general impression is the same in Africa, America and Australia, often to a surprising extent, so that it is difficult to believe that the respective plants have all been evolved out of different and often not closely related families.

Rain or the seasons produce a marvellous change in the look of many a semi-desert. Within a few days after a drought of perhaps 13 months the same impressively desolate stretch of North Mexico is transformed into a green prairie with countless blooming bulbs, and there is plenty of animal life. In Turkestan spring comes with a rush. The snow melts rapidly under the warm south wind, a carpet of tulips delights the eye for a few glorious weeks, and in the month of May all this vegetation becomes scorched and shrivelled and vanishes under the hot blasts, the dust and sands of the desert; and during the long, severe winter it is swept by icy storms and covered with snow.

Life in the desert is fearfully severe. There is very little competition, a desert fauna is always scanty, and there is plenty of room. But the struggle to make a living and the fight against the elements are so severe, that comparatively few creatures have succeeded in adapting themselves to such a life.

Let us now consider some of their peculiarities. The northern half of the Old World is divided by a belt of enormous extent, from the Canaries to

Mongolia, which is unfavourable to amphibia, especially newts, a broad barrier which cannot be passed, and there are none of them, except in China and Burmah, south of this belt. Since these creatures practically are restricted to the north of this belt, in the Old World, we conclude that they had their origin in the northern regions.

In Australian deserts some of the few kinds of Cystignathid toads burrow into the clay of the drying-up water pans; the clay becomes hard-baked, and there they sleep until the next rains, whenever these may fall. Their whole body-cavity, many subcutaneous spaces and the bladder are full of water; the body is swollen into a shapeless mass, ugly, without any pretty coloration. When the rain releases them, they at once spawn, the tadpoles develop with great rapidity, soon to aestivate as tiny frogs. The adult gorge themselves with caterpillars and beetles which are then also swarming, and thus they fatten themselves preparatory for the next torpid season, which may be protracted for several years owing to the uncertainty of the rains. The Australian desert members of the genera *Chiroleptes* and *Heleioporus* are always ready to spawn; to miss the opportunity would be disastrous to the race in a country where the meteorological conditions are so uncertain.

Reptiles of the desert, to avoid the cold of the

night, bury themselves in the sand by various contrivances. Some have a depressed, somewhat flattened body, and the scales on the sides form rows of ledges, so that a shuffling motion heaps the sand upon the body. The scales are sharply keeled and so arranged in slanting rows that the sand rolls by itself into the required position. This also serves admirably for concealment, and the head, sticking out, is armed or rather dissembled by spikes, which then look like seeds, fallen thorns or broken bits of pebbles strewn over the ground. This is a striking likeness between the so-called horned toads, *Phrynosoma* of North America and Mexico, which are Iguanids, and the *Moloch* of West Australia and kinds of *Phrynocephalus* of Turkestan, which belong to the family of Agamids.

Almost all deserticolous lizards are great burrowers. Some, which inhabit loose sand, for instance many skinks, are quite smooth, slippery, without any spikes, and the limbs show a great tendency to being reduced to tiny stumps or to disappear altogether. These creatures literally swim wriggling through the sand. In America, Africa and Asia the numerous kinds of the families of skinks and of tejus show stages from fully developed limbs to none, wherever there is a desert. Illustrations of convergent evolution.

The nostrils of such dwellers in dry sand can be

closed by neat valves. Some have strong ridges over the eye-brow region, formed by modified scales to make the sand fall off properly when the creatures emerge. The ear-opening is protected by a fringe of scales, or it is very small, even quite abolished.

Most wonderful is the protection of the eyes. In many desert lizards the lower eyelid has a transparent disk in its middle, so that when this lid is drawn up, the eye is closed and yet the lizard can see. Several species of the Lizard genus *Eremias* in India and Africa and the Indian *Cabrita* possess such a transparent window. In another Lacertid genus, *Ophiops*, this arrangement is carried to the extreme. The transparent lower lid is permanently drawn up and fused with the rim of the much reduced upper lid. Exactly the same modification has been hit upon by *Ablepharus*, a genus of skinks widely distributed in the Old World, and by *Xantusia* in the Californian and Mexican deserts.

To enable certain lizards to run over the sand, they have lateral fringes on the fingers and toes ; for instance the North American Iguanid *Uma*, in Turkestan and Persia the Agamid *Phrynocephalus*; and what is more surprising, the same occurs in some desert geckos, e.g. *Ptenopus* and *Stenodactylus* of Africa, and *Teratoscincus* in Turkestan. Reference has been made to the growth of the vegetation in patches. Connected with this is the astonishing quickness of many

dwellers in deserts. Lizards are fond of disporting themselves in the open, to feed, to play and to bask. Their only shelter, if they are not diggers, is afforded by the tussocks and shrubs, to reach which they have to run fast. Desert snakes, excepting those which dig, and have rough oblique rows of scales like *Eryx* or *Echis*, are remarkable for the great number of ventral shields and these correspond with the number of vertebrae. To be overtaken in the open, with places of refuge far and wide between, is detrimental; the most alert and quickest is most likely to escape, or to win if he is the aggressive foe.

The characteristic feature of desert mammals is their swiftness, and their large ears if they are nocturnal. Toes short and compact, close together, limbs elongated and slender. Witness the gazelles, springboks and other antelopes. Or there is the tendency to elongate the hind limbs, while the fore limbs remain short or even are shortened. This principle leads to the more typical dwellers in plains and semi-deserts, as illustrated by the jumping kangaroos of Australia; the same modifications, different in detail, but with precisely the same effect occur in the jumping hares, *Pedetes* (a rodent) and in the *Macroscelides* or elephant shrew (Insectivore) of Africa, the little Jerboas *Dipus*, in South-East Russia and Asia; and North America has produced similar jumping mice of the genus *Zapus*. All have a rather

long, balancing tail, often with a tassel of long hair.

Water being scarce in deserts the inhabitants eke out the deficiency by the dew, or they are forced to wander far and wide in search of scanty pools. Various ruminants have developed an astonishing power of enduring long intervals between drinks. In Mexico and Arizona, for instance, and around the Indian desert the cattle can sometimes return to the drinking places only every other, or even every third day, because the scanty pasture obliges them to roam so far afield. We all know of the unique water-storing arrangement of the camel's stomach which enables these animals to subsist for well-nigh a week upon the thorniest and driest of food without a drink. But the most universal feature of nearly all desert animals is their coloration, be they birds, beasts or creeping things. They all are of the colour of the desert, shades of yellow, light brown, reddish, sandy; often very pretty in delicate detail, with wonderful, small patterns. Black, white, blue and green are absent. Many of these animals are monochrome; stripes are absent. If the ground-lizards are not monochrome, uniform in colour, the runners among them have a pale ground-colour with dark spots. The harmony between deserts and their inhabitants is striking. Every animal has those colours and that pattern stamped upon its dress which make up the

average sum-total of the characteristic colours, lights and shades of its usual environment. The main advantage of this harmony is protection. This does not mean only concealment and protection from enemies, from other creatures; to an equally great extent it means protection from elemental influences, as temperature and sun rays, also from the colours reflected by the environment. The prevailing colours of the desert being shades of brown, reddish and yellow, only a dress of the same tints can possibly be in physical equilibrium with the desert; and there is no vivid white, black, blue or green, because those colours are physically impossible in the desert.

High Mountains and Vertical Distribution.

A universal feature of mountains is the decrease of temperature with increasing height, the result being a so-called arctic climate if the mountain is high enough, with preponderance of snow and subsequent suspension, or suppression of life.

Since, as a general proposition, temperature decreases also from the equator to the poles there is a fixed correlation in the temperature of a mountain station between its latitude and its height. This law of latitudinal equivalent in altitude has been formulated by A. von Humboldt, the father of the study of vertical or altitudinal distribution.

Broadly speaking the annual mean temperature decreases towards the poles at an average of 1° F. for each degree of latitude. With increasing height the temperature falls nearly a thousand times as rapidly, namely 0·5° centigrade for every 100 metres; this is equal to 1° F. for every 365 feet, an easy number to remember. On mountains the rate is somewhat greater, 1° F. = 300 feet. Given the temperature and height of a lower station and the height of the mountain its temperature at the summit can easily be calculated[1]. In our latitude a mean annual temperature of 32° F. or 0° centigrade is reached at a height of about 5000 feet, but under the equator this 'snowline' lies at about 15,000 feet, and near the arctic circle it approaches the level of the sea.

Atmospheric pressure also decreases, roughly by 1 inch with every 1000 feet of elevation, so that at a level of 10,000 feet we experience only two-thirds of the normal pressure at sea-level; which implies of

[1] The formula for centigrades and metres is $Ut = Lt - \frac{d}{200}$.

For degrees of Fahrenheit and feet the formula is $Ut = Lt - \frac{d}{300}$.

Ut = Mean temperature of the upper station.

Lt = Mean temperature of the nearest known lower station.

d = difference in height of the two stations.

Example: Highest mountain 5000 ft.

Temp. at nearest sea-level 50° F.

Temp. on top $= 50 - \frac{5000}{300} = 50 - 17 = 33°$ F.

course that the same volume of air contains only two-thirds the amount of oxygen. Animals rapidly taken up to high levels find it difficult to adjust themselves to these conditions. The thinness of the air, combined with the cold, causes absence of vapour ; radiation, loss of warmth of the ground heated by the sun's rays, is unchecked. On the other hand moisture in the air diminishes the loss of heat by radiation and directly increases the temperature of the atmosphere, because the warmth given off by the heated ground is largely absorbed by the aqueous vapour. Consequently on a brilliant day, on a high snow field it may be scorching hot in the sun, whilst the temperature of the air, as measured in your own shade, shows several degrees of frost.

In the temperate and cold regions the differences due to latitude and altitude are greatest in the winter and least in the summer. Under the tropics the differences due to altitude are greatest within the 24 hours of day and night. It follows that places of the same mean annual temperature may have widely different summer temperatures ; and conversely that places receiving the same amount of summer heat may have widely different annual means. The significance of these facts becomes apparent in the study of the distribution of animals and plants. The distribution of the various species is governed in the main by the temperature of the warm season,

whilst the mean annual temperature is of little consequence. In many cases the lowest extremes of temperature are also important. If you want to cultivate Indian corn at a certain place its mean annual temperature may be dismissed; the success depends upon the number of days sufficiently warm to ripen the corn, and we are not concerned about the cold of the winter. The latter may, however, be of great importance to the growth of perennials, shrubs and trees.

Temperature and humidity seem to be most important factors in distribution.

High mountains have a more or less permanent belt of clouds; what determines its height above the neighbouring plain is not known. This belt is naturally the zone of greatest moisture; although it rains more below, the permanence of such a belt ensures greater effects of the moisture. A mountain standing on the southern edge of a plateau has a higher temperature at a given altitude on its north slope than on its south side, because the sun-warmed surface of the plateau is nearer to the mountain top than is the lower, although hotter, southern plain. This explains why, e.g., in the Himalayas the snow and timber-line on the north side are about 3000 feet higher than they are on the south side.

The side of a mountain exposed to the prevailing sea wind is moist, whilst the lee side may be arid.

Thus the western coasts of India, exposed to the monsoon, have a much greater rainfall than the inland districts on the other side of the coast range. In Mexico the Pacific side is much drier than the very wet Atlantic side, this difference being responsible for remarkably different faunas and floras.

The possible number of floral and faunal zones on a mountain is greatest in the tropics, since its base may be in the hot tropical lowlands and its top above the permanent snow-line. A mountain of the same height, but situated in the arctic region, may be entirely within the snow-line. The width of the zones (not of course their vertical thickness), and the abruptness of the change from one to another are proportional to the steepness of the slope.

Every 'complete' mountain arising high within the tropics shows the following five belts or zones.

1. Tropical belt. Climate hot, according to circumstances either moist or dry, or both according to seasons. Vegetation evergreen, but deciduous when there is a pronounced dry season. The upper limit of this zone may be put near 3000 feet above the level of the sea.

2. Warm temperate belt. The difference between summer and winter begins to get marked, and there may be cool nights. Vegetation chiefly evergreen, and if the leaves are deciduous this is due to a prolonged dry season.

3. Cool temperate belt, frequently coinciding with the normal cloud-belt. Those trees which are deciduous lose their leaves during the winter season, which is well marked. The upper limit of this belt coincides with the 'upper tree line.'

4. Cold belt. Characterised by grassy slopes with abundance of flowering annuals. Higher up the grass gives way to mosses and lichens.

5. Arctic belt, the lower limit of which is near the permanent snow-line, which within the tropics is somewhere near 15,000 feet elevation.

Now, since an isolated mountain is like a cone, it is of the greatest significance that its successive vertical zones, if projected in Mercator's fashion, are practically repeated in a grander scale by the zones on a map of the northern half of the world. We may compare the mountain cone with the northern hemisphere of a globe. The agreement is somewhat distorted by the configuration of the continents, by the high elevation of Central Asia and by the introduction of deserts. There are in the northern hemisphere:

1. A tropical belt, either moist, with tropical forests, as in Central and South America, parts of Africa, Indo-Malaya and Papuasia; or dry, 'torrid,' like the Sahara and Arabia.

2. A warm temperate belt, sub-tropical.

3. A cool temperate belt, with much woodland

and arable land; abundance of mostly deciduous trees and shrubs.

4. A cold belt across Canada, Scandinavia, Northern Russia and Siberia, which belt includes the northern tree-line, to the south of which are huge timber forests, composed chiefly of conifers. Enforced hibernation during the severe winter.

5. The arctic, circumpolar region, with prevalence of ice and snow; the permanent vegetation represented mainly by mosses on the Siberian 'tundras,' by lichens on the North American 'barren lands.'

Because of this agreement the study of certain climatic effects upon the 'Biota,' i.e. flora and fauna, can be made on a complete mountain within a small compass. We can also investigate the effect of the change of habitat.

Let us take the simplest case, a mountain with its whole base in tropical lowland. Its whole Biota may then be assumed (excepting the few instances of conveyance by wind, etc.) to have ascended from the plains, and if the top species are different from those at the bottom, they probably have been modified by the conditions prevailing on the mountain.

The case is more complicated if the mountain has two bases, one in the tropical lowland, the other a high temperate plateau, which probably has an endemic Biota of its own, differing from that of the

likewise extensive lowlands. The Biota of such a mountain will be a compound from two perhaps very different sources.

Or the mountain itself may have an original Biota of its own, especially if the mountain is due to a process of folding or other rising of the crust of the globe, instead of being a piled-up volcano, which would of course begin as an absolutely barren terrain.

Lastly, the most complicated conditions prevail if the mountain forms part of a long range extending into distant countries. In this case it is an important consideration, whether such a range runs from north to south like the chief systems in America, or from west to east as they do in the Old World.

Whilst west to east, latitudinal or zonal ranges often act as powerful barriers, shutting off a southern from a northern Biota, a north to south, longitudinal or meridional range more often acts as a conductor in the exchange of southern members to the north and for northern migrants into the south. This is especially the case, when, according to the law of latitudinal equivalent in altitude, such a range begins low in the north and increases in height towards the south. An excellent illustration is the great central plateau of Mexico which begins at the northern frontier with a few thousand feet elevation and steadily rises to 7500 feet near Mexico City and there forming the northern base of some of the giant

mountains, whilst the other side slopes rapidly down into the hot lands.

The component species of the faunas and floras of such mountain zones can be collected and studied as to their affinities and variations. Some creatures seem to be quite indifferent to climate, and therefore have a long vertical and horizontal range. The puma, for instance, ranges from Canada to Patagonia; it makes raids into the hot lands and ascends to the upper tree-line. The nine-banded armadillo is equally at home in the moist hot lands and in the clammy pine forests of 9000 feet elevation in Mexico. A certain kind of small lizard, *Sceloporus microlepidotus*, of the same country occurs in the lowlands and ascends to the very tree-line where it is obliged to hibernate through perhaps half the year, whilst below it aestivates during the torrid season. Other species, although scattered widely over the country, have a very short vertical range, so strictly limited that these animals and plants indicate the elevation above sea-level as safely as a barometer. Ultimately most animals are dependent upon the vegetation, the state of which depends greatly upon climate and soil. The jaguar lives on herbivorous game. Rattlesnakes subsist mainly upon rodents, and mice ascend as far as there are roots and seeds for them to eat. Where the winter time is severe many animals have either to migrate into lower, warmer climes, or they are forced

to hibernate; even during the cold nights of their summer the cold-blooded kinds become lethargic. In conformity herewith we find that specimens of the same kind, which in the warmer zones live an all-the-year-round life, have learned to hibernate in the upper levels. High up there under the very tropics, but at 10,000 feet elevation, the summer is so short that stationary creatures like lizards and snakes lead only a kind of one-quarter life. This implies that, for instance, a four-year-old snake has really lived, that means to say eaten, grown and loved, only for twelve months. The result is that many a high-mountain fauna contains not a few small-sized species in comparison with their more favourably placed relations lower down. Another result seems to be that many cold-blooded vertebrates have given up the laying of eggs which might not be hatched on the clammy ground, and have become viviparous, undoubtedly a safer mode of looking after the welfare of their kind.

The present writer has made a special study of altitudinal distribution in Mexico. It remains to be seen whether the following conclusions apply to other countries, and therefore are widely applicable general laws.

1. Hot land species ascending into cooler zones are liable to lose their specific characters and to assume others; that means to say they change into new species.

2. Temperate species are more powerfully influenced by ascent into the cold zone, than by descent into the hot lands.

3. The change into a colder environment is a more powerful factor than change into a warmer climate.

The Mexican Biota is composed of (1) endemics, (2) nearctics, immigrants from the north, (3) neotropical immigrants from the south. Of these the nearctics are more long-ranged than the tropicals, i.e. they are more hardy, in the sense of being resistant, dominant, able to accommodate themselves to new environment without becoming changed. The short-ranged among the nearctics are mostly those which have become modified for cold life.

Since the majority of the genera and species of tropical or southern origin are short-ranged, this means either that they are softer, more pliable, recessive; or that they are more influenced by ascent. Species B at the bottom has changed into B^1 in the middle region, and into B^2 towards the top; hence three short-ranged species. A hot land or bottom species can obviously change only into cooler climes, but an originally temperate species may ascend or descend.

If the three rules enumerated above hold good, it seems paradoxical that denizens of the hot lands transported into a cold place stand this change much

better than specimens taken from a high mountain down into the tropics. We ourselves experience the same effects. No doubt more diseases are rife in the tropics, especially bacterial and parasitic. But this does not go to the root of the problem. A tropical creature, or plant, transported into a cold region, may live, but it will not breed, or ripen its seeds. A cold country species introduced into the tropics is much more likely to die from the shock, but if it lives it will breed. Many tropical plants can be cultivated in temperate countries where they have to adapt their economy to shorter summers, whilst northern plants, subjected to tropical conditions, are mostly failures since they exhaust themselves through want of rest. Annuals seem naturally to have better chances than perennials. But nature's way of altitudinal spreading is slow and steady, not by sudden transports.

Cold can be counteracted in many ways by animals, as by more food, motion, shelter, a warmer coat, etc. But transference from the changeable temperate to the hot zone with its much more equable climate always implies an excess of warmth over that which the species was accustomed to.

If the third rule allows of general application it would be of far-reaching importance; it would allow the further conclusion that a world-wide lowering of temperature has been a most powerful factor in the

production of new forms of life. Let us apply this principle to geological changes.

Elevation of a whole country, or of a range of mountains, or a cold epoch following upon a warm one, would be very productive of new forms. The same effect would be produced by the spreading of a glacial epoch from the pole. The tropical creatures, coming under the cooling influence, would change readily, and the old species within the polar circle would be changed into arctic forms, as the glacial wave passed over them. But those which, for some reason or other, were driven south, would remain unchanged because they counteract the new climatic influence by their migration. Such a glacial epoch would thus bring about a great faunistic intermingling, but it also would actually produce new forms, namely arctics, and those transformed southerners which did not, or could not, withdraw.

What would happen with the turn of the tide, when a spell of warm climate spreads again towards the pole, as has taken place during the so-called interglacial epochs? No changes whatever, except that the arctics will die out or remain occasionally as derelicts, while all the rest, both northerners and southerners alike, will surely reclaim the old ground so far as it suits them. There will be comparatively little making of new species, provided our principle is right, that increase of temperature has a minor effect.

It would be absurd to conclude that cold is a more favourable factor to life than warmth. It is quite a different question whether a change from hot to cold may not have a profoundly stirring influence upon organisms. The Permian period was one of widely spread coolness, which has played havoc at least with the marine fauna, by reducing its numbers of individuals and species, but it also ushered in, or prepared, a new and remarkable terrestrial vertebrate fauna. Our last northern glacial epoch may have killed out much of the warm Pliocene life, but it has given us the present arctic fauna, which is very considerable, and remarkable for being very up-to-date, singularly free from old-fashioned types. The place for these are the tropics, because there the climate has changed least in the equatorial belt, which seems to have been hot since the Triassic period.

A statement which has been repeated so often as to amount almost to a creed, is that the typical animals and plants of snow mountains in the temperate and even in the tropical regions have their nearest relations in the arctic regions; that they are derelicts, shut off by the recession of the glacial epoch, instead of being modifications, suited to a more rigorous climate, of the lower or basal faunas of the country in which these mountains are situated. This is a much overrated statement. These faunas and floras

have an arctic 'facies' or look, mostly cases of convergent evolution, and the term arctic, if used for such high-alpine organisms, must not be confounded with boreal or polar. In fact true instances of boreal derelicts on far southern mountains are very rare. The idea was based upon the supposed similarity between Scandinavia and the Alps, the favourite example being the arctic hare. This *Lepus variabilis* turns white in winter; its present distribution is circumpolar, from Scandinavia through Siberia to Alaska and Greenland and Newfoundland, but also in Scotland, Ireland, in the Pyrenees, Alps, the Caucasus and in Japan. But none of the other typical arctic animals are found in the Alps, neither reindeer, polar fox, glutton or wolverene, lemming, or snowy owl. Nor do any of the creatures, typical of high mountains in temperate countries, like steinbok, rocky mountain goat, bighorn and argali, marmot, chinchilla, extend their range into the polar regions. We agree with those authorities who explain the occurrence of the comparatively few closely related species of animals and plants in Scandinavia and the Alps as due to independent immigration from some common Central Asiatic centre.

It is always difficult to prove a case of convergent development. It can so easily be ruled out of court in the present instance, because we know that during the height of the glacial epoch the northern ice-sheet

extended southward to a line drawn from London to Moscow, and the strip of country intervening between this line and the Alps and Pyrenees was certainly cold enough to support reindeer in the south of France and lemmings even in Portugal, so that there may easily have occurred a shifting of Scandinavians to the Alps, and the reverse current of spreading with the recession of the ice-sheet. Such spreading and contracting with consequent isolation has no doubt taken place in many parts of the world. We must resort to it for the present discontinuous distribution of many similar, even identical, species on that large system of mountains from the Pyrenees, the Alps, the Caucasus, right into and beyond Central Asia.

But this same principle emphatically cannot be applied to the many alpine districts which exist within the tropics and are isolated from each other. Here we have to remember that most of the great ranges of the world are of comparatively recent date, chiefly mid-Tertiary ; and as during these epochs the world seems to have enjoyed a decidedly warm climate, it follows that the respective faunas and floras must have assumed their 'arctic facies' after the origin of these mountains and independently of each other.

Summary of the Influence of Environment.

Having reviewed the main features of the faunas characteristic of forests, deserts and high mountains, each of which may be taken as intensified samples of environment, we may draw some conclusions.

Since it is obvious that typical desert specialists cannot live in forests, and as high mountains also possess inhabitants of their own, it follows that these various faunas can have attained their present, often widely scattered, discontinuous range only under one of the two following conditions. Either the respective faunas had a multiple origin, and are instances of convergent evolution where similar environmental conditions prevailed ; these cases are of enormous biological importance. Or, if the respective creatures are truly blood-related, above all if they belong to the same genera or species, they must have spread from a common centre. This would imply continuous forests for some, uninterrupted deserts for others, extending perhaps all over the world, not necessarily at the same time, but forest succeeding desert, and arid highlands taking the place of lowland swamps. The mere emergence of a land-bridge would help no monkey across, unless or until it was covered with suitable vegetation.

If the specialised features of the dwellers in forests and deserts had arisen from preformed latent variations,

to be picked out by natural selection, and further developed by cumulation, it would follow that each ancestral group possessed a whole arsenal of every kind of variation, ready to be selected when occasion required it. Descendants of the same frog, which found themselves in a forest, drew upon its incipient finger-disk variations, be these ever so tiny; others, in inundated country, improved upon the webbed propensities, and yet others encouraged those variations which assured a chance of digging feet. This is of course, to a certain extent, our idea of a 'generalised ancestor,' some kind of anurous Amphibian, for all the toads, frogs and tree-frogs.

This view implies that by this time the arsenal of variations has been exhausted, there being in forests only forest creatures, in deserts only desert specialists, all of which have of course lost the other non-fitting characters by the process of weeding out. Consequently any further change in the environment would kill the present faunas. What was easy for an indifferent organism, must have become increasingly difficult for the specialist, and an all-round specialisation in every direction is impossible. This is covered to a great extent by Cope's law of the over-specialised, and by D. Rosa's 'progressive reduction of variability.' We cannot here enter into a discussion of these important topics. Suffice it to say that variability is not the same as the incessant cropping up of slight,

spontaneous variations in every direction ; it is the plasticity of the individuals, their being able to be moulded by circumstances. That this plasticity should react so quickly and to the point, if not impaired or lost by specialisation, is itself the outcome of the long training which protoplasm has undergone since its creation. This very quickness seems to have initiated our mistaking the variations called forth for something latent or preformed.

In nature's workshop the successful competitor is not he who has ready an arsenal of tools for every conceivable emergency, but he who can make a tool on the spur of the moment. The ordeal of the practical test is Darwin's and Wallace's elaborated conception of natural selection.

CHAPTER III

SPREADING

Since there are now countless species and genera with a very wide, continuous or scattered distribution they must have attained this range by spreading from centres where the respective kinds made their first appearance. The fundamental impulses to all spreading, wandering, migrating are hunger and love

and the fact that two creatures require more space than one.

If cattle require three acres of grazing land per head to keep themselves during the year, a herd of one hundred must have 300 acres, and if this herd increases to 1000 head it must have 3000 acres of grass land, to find which, however, they may have to roam over much more than five square miles. Thus they spread. From a broad point of view spreading proceeds peripherally, in epicycles, each pair representing a centre of its own, and since the middle of the area is already occupied, new land is available only outside. This spreading may be a very slow process, but it tends to increase by geometrical progression, and there is practically unlimited time. If a couple of earthworms are sufficient to occupy one square yard per year with their offspring, their descendants long before 30,000 years (a not improbable estimate of the time since the end of our glaciation) would have choked the whole world[1].

[1] This time-honoured kind of calculation implies a great fallacy. It is, to a certain extent, applicable to animals with practically unlimited power of locomotion, for instance to a herd of cattle entering a new, unoccupied country. In the case of earthworms the actual resulting numbers would soon be infinitely less than the calculated result, because of the choked, inner parts of the area, the inhabitants of which could not possibly pass over those living near the periphery, where alone new land and food is available. In a few years the centrifugal velocity of spreading, necessary to cope with these

Supposing a family moved, gipsy fashion, only on one day every week, and not more than three miles, then it would cover about 156 miles in one year. For example, the Mongols, crossing Behring's Strait might have arrived at this rate at the Straits of Magellan in about 50 years.

Let us follow the herd of grazing cattle. They roam about mainly in search of food; they follow the grass. Where its growth is seasonal, the beasts make seasonal 'migrations,' like the American bison, which moved twice annually between Canada and Mexico. What we usually understand by periodic migrations cannot have sprung into existence suddenly; it is more like the cumulative effect of the doings of countless generations. The faculty of shifting the abode was of course always there, the necessity of moving further on was also present, and those members of a species which went in the wrong direction came to grief, whilst the others flourished and could return with their progeny. At first they did not cover great distances, but just enough to find

conditions, would surpass all reasonable limits. The phenomenon is comparable with the progress of a 'fairy-ring' except in so far as the inside will contain a population of just comfortable density. If we apply these considerations, the ring of worms will be found to have made astonishingly little progress in a thousand years, and, except at the periphery, the whole area will contain at best only a comfortably dense population, instead of countless millions.

unoccupied ground. The annual repetition became an established habit, at last an ineradicable instinct.

The prime impulse is want of food. The new growing grass on the prairie attracts every year those creatures which live upon pasture. The tropical belt of the world is so crowded that there is the keenest competition, whilst in the temperate and cold regions occurs a long winter unfit for the support of many kinds, whereupon in the summer these same regions are covered with new vegetation, with its concomitant abundance of insects and other invertebrates. The tables are decked again, and these opportunities are not wasted.

Hard and fast differences between periodical migrations, sporadic changes of the abode, and other fluctuations do not exist, they are a question of degree. The grey plover of America breeds within the arctic circle and winters in tropical countries; many other birds shift their abode only a few hundred miles. To complicate matters further, it is not necessary that the migration be undertaken periodically, more than once, by the same individual. The common eel ascends the rivers as an 'elver,' in its youth; years after, it returns to the sea, there to breed and die, whilst many other fishes come and go, year after year. Many birds are still immature in their second year, and yet they migrate like their adult relations. It seems permissible to take this fact as an indication

that the breeding as such is not a prime reason for their wanderings.

The phenomenon of migration, in its most striking cases, is now very complicated. Many a bird goes to the very arctic regions for the shortest of summers, and it spends most of the year within the tropics or it may even overshoot the equator and winter in a south temperate country. On the other hand the members of many species do not all go so far north, but stop and breed in the intermediate regions. We must not take the extremes when trying to unravel the development of the problem.

It has been argued with some show of reason that the real home of a bird is that country in which it was born, where the species breeds, but this is not in every case a valid conclusion. Although it applies to most creatures, there are so many exceptions that we must leave sentiment aside. When it comes to a question of domicile, the ten weeks' sojourn of the swift in England are to be set against the nine months or more which these birds spend in Africa. The breeding time is the busiest period of a bird's life. Then the numbers of each species are suddenly multiplied and so is the stress of providing food, and the particular kind of food which is best for the young may not be available in every country.

Speaking broadly, any migratory bird breeds in the coldest climate which it visits on its migration; this

means that it requires a pronounced spring or early summer season. The idea that the arctic circle was the original home of the many kinds of birds which breed there, whence they are now annually driven away by stress, has been coupled with the glacial epoch, that panacea of so many difficulties. One had only to assume that the progressive glaciation drove the ancestors away from their circumpolar home, towards the equator, and that when times improved again, the birds returned to their old home. This plausible view implies several monstrous assumptions. The birds are supposed to have inherited such a loving reminiscence of their old home that they returned to it after a banishment of thousands of generations. The enforced sojourn, and of course the breeding of all these generations, was not sufficient to naturalise them, to supplant the love of their prehistoric home!

That the last glacial epoch has driven the limit of many kinds of animals and plants further south, is as certain as that many have recovered the lost ground after the recession of the cold spell, but this must have been by very slow and steady process of spreading. It probably does account for the present annual visitations of arctic lands, but as a phenomenon which has been evolved *de novo*, which would have come to pass even if no birds had existed in preglacial times.

The question how birds manage to find their way thousands of miles across land and water, has been

extolled as a mystery of mysteries. That they can cross many hundreds of miles of sea without stopping is a fact; it means an amount of endurance which we do not expect in small birds. The whole question reduces itself to a sense of direction, a faculty which is possessed by nearly all animals, e.g. the proverbial cat which escapes out of the bag and finds its way home. There is no mystery, except that we, the most intellectual of mankind, should so well-nigh have lost this sense, and even this regrettable fact is simply an instance of the loss of a faculty through long continued disuse.

In comparison with the periodic, annual migrations of so many birds, those of other creatures are scarce and insignificant, excepting fishes.

The most regular and least limited migrations among mammals seem to be those of the eared seals. The walrus goes northwards in the summer. The cetacean *Delphinapterus leucas* regularly ascends the Amoor to a distance of 400 miles, when the ice breaks. Certain bats are supposed to migrate. Various kinds of game have been recorded to make periodic wanderings over the South African veldt. Such instances are obviously a mere matter of commissariat.

The so-called migrations of the lemming are instructive. They are quite sporadic, stampedes. When owing to combination of some favourable

circumstances these rodents suddenly increase, enormous numbers radiate from the highlands of Norway into the lowlands. At any given spot they seem to keep to the same direction, but taken as a whole, they disperse to anywhere. The overcrowded condition of their homes impels them to leave, and this impulse they follow blindly, even, it is alleged, into the sea. But they do not attempt to settle in a new district. A year or two after such an irruption not a lemming is to be found, and where, during the stampede they came across suitable districts, they found these already occupied by resident lemmings.

The same applies to the countless numbers of sand-grouse, *Syrrhaptes paradoxus*, which in the spring of 1888 came from somewhere in Central Asia and spread over the whole of Europe, like a wave reaching from Norway to England and Spain. Many did breed in suitable places in the same year, few in 1889 when they were exterminated.

Such and similar irruptions have no doubt taken place often during the world's history, and yet such sporadic stampedes into a foreign country hardly ever lead to regular settlements, especially if such a country already possesses a kindred fauna of its own. Almost every year some North American birds are reported on the west coast of Europe; but although such stragglers must have come over to Europe for thousands of years, the respective species

have not established themselves here. Many fishes make periodical migrations for breeding purposes and in enormous numbers. The herring and the cod and their kindred collect on certain breeding grounds. The tunny, which has a world-wide distribution, passes through the Straits of Gibraltar into the Mediterranean Sea in the month of May there to breed, and in the month of July it returns to the ocean.

Many, known as *anadromous*, ascending, fishes, feed and mature in the sea, but ascend the rivers as the impulse of reproduction grows strong, e.g. the salmon, sturgeon, the shads and the mayfish of the Rhine.

Few fishes are *katadromous*, i.e. their usual habitat is in rivers and lakes, whence they descend into the deep sea for breeding purposes. The common eel is the classical example.

CHAPTER IV

NUMBERS AND DENSITY OF SPECIES

Everybody knows that some kinds of animals are common and others are rare. Why this should be so is easy to understand when the rare species has a very limited distribution, but there are also birds and

beasts and others which have an almost world-wide range and yet are much more scarce than their nearest allies. For instance, ravens compared with crows. Some kinds exist in literally countless millions, others perhaps only in thousands. About these numbers of individuals we know nothing; the only species of which a rough census has been made is man. But for some conspicuous animals we can at least calculate a rough upper limit. It is unlikely that there exist, or have ever existed, more than one million lions in the whole of Africa, because we can construct their annual food-bill, etc. and thus narrow the probabilities. The existing stock of orang utans in Borneo has been guessed at 50,000.

Countless species have died out whilst others have come on, a process which is still at work, but from a broad point of view (omitting local fluctuations) the general impression of a fauna is that the relative and actual numbers of the individuals hold their own, that there is neither an undue increase nor a marked decrease. How this balance of nature works is in well-nigh every case an absolute mystery. This is due to our ignorance of the economics, the complex correlations, of every animal and plant. We do not know them of ourselves. Every kind of animal, living under favourable conditions (and nearly all live only where they find such), would in the natural course of events increase its numbers

by leaps and bounds and the whole habitable world would soon be choked. We do not know the factors which keep down the numbers of such powerful and sagacious birds as macaws. The osprey is one of the most cosmopolitan birds of prey; it is stronger than most other fish-eating birds, and there are surely enough fish in the rivers and lakes for more ospreys, yet they are nowhere common.

We know that over-crowding, over-population of a district, engenders diseases, or rather let us say that these diseases are always present somewhere, comparatively harmless if kept going by a chance victim, but that they spread in a crowd. If a species has become so numerous that there is practically contact between its members throughout its range, the whole may be carried off. Only those which happen to live in some isolated district, cut off by chance, will be saved and, like the animals disembarking from the Ark, start afresh. The degree of the density of population necessary to produce this 'contact' we do not know. Countries with locusts and Bombycidae or spinning moths are also inhabited by ichneumon wasps. They balance each other, but when there occurs one of the great irruptions into the North German pine forests by the moth *Gastropacha pini*, the caterpillars of which then devastate whole forests, in the second or third year the ichneumons have also become so abundant that every caterpillar is attacked

by them and dies. The plague has wrought its own remedy.

Now let us consider man. With the present rate of British increase (an annual gain of 14 per 1000) the population doubles itself in about 50 years. If we apply this rate, which is not at all excessive, to the present 1600 million people of the whole world, there would be, 1000 years hence, a total population of 1660 million millions; and the whole land surface of the globe would not afford sufficient standing room for this number of people.

If we apply the same rate backwards, we find that five people, starting 400 *Anno Domini*, would have been sufficient to produce the present world's population. So far as actual conditions are concerned this is pure nonsense, but let us consider that:

1. A population cannot hold its own unless every potential couple is some day supplanted by another.

2. A population cannot increase, unless, on the average, there are more than two children, not only born, but brought up to propagate the race.

3. It is absolutely certain that the origin of man, as such, dates back into the Pliocene, a time of which 300,000 years would be a conservative estimate, and for argument's sake representing 10,000 generations of mankind.

4. If we assume that the human race started as the traditional Adam and Eve pair, within the

Pliocene, the rate of increase necessary to account for the present total population would be so small as to render the calculation quite preposterous. The necessary gain would be 1000 : 1002 per generation ; 2 per 1000 people every 30 years, instead of 14 per 1000 annually as is now the case in England. This implies that of all the thousands of children born to 500 couples during 30 years only two survived to add to the race. This being an unthinkable state of affairs, it follows that the rate of propagation has been always as large as it is now all over the world, but over and over again whole tribes have been well-nigh wiped out, by each other, by epidemics or by accidents. Just like the Red Indians of North America, who, instead of well filling that large continent, have reasonably been computed never to have amounted to more than a few hundred thousand souls.

What constitutes a rich or a poor fauna? The number of species and the number of the greater groups, or variety of types, to which the species belong. For instance, the mammalian fauna of Australia cannot be called rich, since it consists mainly of the variations of one type only, that of marsupials.

The tropical belt of the world is teeming with a great variety of terrestrial life, while the number of species decreases to almost nought towards the poles. The arctic and antarctic regions are so poor

in permanently resident species, and devoid of Amphibia, reptiles and freshwater fishes, that they may be left out of a census of the world's 'terrestrial inhabitants' if we want to compare the various land complexes as to the richness of their faunas. To illustrate shortly the principle involved, we must further restrict ourselves to the number of species. The bulk of generally habitable land may be reduced to the conveniently round number of 40 million square miles.

The vertebrate fauna, omitting strictly marine fishes, may be stated in the following conservative numbers of species: freshwater fishes, 6000; Amphibia, 1000; reptiles, 3500; mammals, 2500; birds, 12,000. Total, 25,000 species.

This gives on an average one species to every 1600 square miles, and this may be called the *areal density* of the world's vertebrates.

The areal density is expressed by the quotient of the number of species of a country into the area in square miles. The quotient, therefore, expresses the specific areal density in an inverse ratio. The richer the country, or the greater its number of species, the smaller is the index figure. Examples :

	In thousands of square miles.	Numb. of species.	Areal density.	Group of animals.
Total habitable land	40,000	25,000	1600	All vertebrates
,, ,, ,,	,,	4500	8888	Amphibia & reptiles
,, ,, ,,	,,	12,000	3333	Birds
,, ,, ,,	,,	2500	16,000	Mammals
,, ,, ,,	,,	6000	6666	Freshwater fish
British India	1678	1630	1000	Birds
,, ,,	,,	666	2520	Amphibia & reptiles

Rich and poor are arbitrary conceptions. Moreover a country may be rich in birds and poor in some other class. We may, however, fairly assume that, class for class, an index below the world's average means a decidedly poor fauna, and an index double that of the world means a rich fauna. The reptilian fauna of India is as notoriously rich as that of North America is poor, and that of Europe is still poorer. The bird faunas of South America and India are twice or even three times as rich as those of Europe. Such calculations yield valuable results, sometimes so startling that the underlying causes have to be inquired into, which then occasionally reveal unexpected correlations.

CHAPTER V

FORMER CONFIGURATIONS OF LAND AND WATER

In the majority of cases the present distribution of animals cannot be accounted for without the assumption of enormous changes in the configuration of land and water. It is no explanation to say that most groups had a 'universal or sub-universal range' and that their now discontinuous occurrence is simply the result of their members having died out in the intervening countries owing to unsuitable environmental changes. Of course that has often happened, but the sub-universalists avoid the question how the world-wide range had been attained. Further, to account for the undeniable affinity between the South American and African faunas, some writers, instead of admitting a direct land-connexion, rather resort to a roundabout journey from America by Behring's Strait through Asia to West Africa, assuming further that all along this route the respective animals have since died out. If this is supported by fossils, well and good. Cases of such a roundabout spreading are known. We dismiss the many, well-ascertained instances of occasional dispersal (by the proverbial floating log, currents, storms and water-spouts) as insignificant, and quite inapplicable to most creatures.

Land tortoises (genus *Testudo*), have reached the Galapagos by land, not astride a log, just as certain as lemurs in Madagascar and elephant remains in the Andes are evidence of former land-connexions. Oceanic islands have at best a scanty terrestrial fauna, but it is a mistake to refer this entirely to accidental spreading. It would first have to be shown whether these islands arose out of the ocean, or whether they are remnants of sunken continents. If Africa subsided two miles there would remain a few isolated volcanic peaks, like Cameroon and Kenia, with all the appearance of oceanic islands, but with a derelict indigenous fauna. It depends upon the age of such islands, whether they could have only reptiles, or also mammals, and even then absence of, say, mammals on the Galapagos proves but little since so much depends upon the physical conditions of the land (cf. p. 59).

Of course enormous subsidences and elevations of extensive areas are required, although many authorities shrink from their application. The permanence of the great ocean basins had become a dogma since it was found that a universal elevation of the land to the extent of 100 fathoms would produce but little changes, and when it was shown that even the 1000 fathom-line followed the great masses of land rather closely, and still leaving the great basins, by general consent this quite arbitrary unit of about one mile

was allowed as the utmost speculative limit of subsidence. Two or three miles, the average depth of the oceans, seems enormous, and yet it is as nothing in comparison with the size of the earth. On a clay model globe ten feet in diameter the highest mountains would be smaller than the unavoidable grains in the glazed surface of our model. There are but few countries which have not been submerged at some time or other, and most of the great chains of mountains, Andes, Rockies, Pyrenees, Alps, Himalayas, are only of Tertiary date.

Many attempts have been made to construct maps purporting to show the configuration of land and water at various epochs. Although the results by no means tally with each other, owing to the lamentable deficiencies of geological and fossil data, the hypothetical results are sure to be corrective and supplementary; the problems will be solved, since they are not imaginary. The bolder the outlines are drawn, the better, whilst the insertion of detail and the clinging to present coasts give such maps a fallacious look of certainty. Further, when we draw a broad belt of land across an ocean, this belt need never have existed in its entirety at any one time. The features of dispersal intended to be explained by it, would be accomplished just as well by an unknown number of islands which have joined here, whilst others have subsided elsewhere; like a pontoon-bridge which may

be opened anywhere. Lastly, just as it is impossible to make a political world-map of, say, the 19th century, it is futile to chart a geological epoch. We might as well attempt to fit in one picture a series of superimposed dissolving views.

The evidence for reconstructions is direct and circumstantial. Marine fossils indicate sea, terrestrial fossils land at the respective time. In North America occurred a void gap of land-vertebrates during the Jurassic epoch, but towards its close came in a rich fauna of Dinosaurs, tortoises and mammals of sorts known to have existed long before in Europe. Between Alaska and Canada came in the most specialised Ichthyosaurs and Plesiosaurs, closely related to those of the European seas, showing that there must have existed seaway from Europe to the north of Greenland, whilst Canada-Greenland-Europe formed a barrier to marines but a bridge to terrestrials. Then, during the upper Cretaceous North America was severed into an eastern and a western half, so that the gulf-fauna could mix with another from the polar sea.

There is obvious affinity between the faunas of South America and Africa, besides groups which probably have got there from a common North American-European centre. Some of the circumstantial evidence for a direct South American-African connexion is as follows :

Close affinity between fossil corals of the Antilles and North-West Africa suggests a coast, at least a shallow Atlantic sea. There is no affinity between the marine shells of Argentina and those of the Antilles; this suggests land between Brazil and Africa as an effective barrier, which in turn would account for affinities of the terrestrial faunas. Most authorities agree as to the existence of such a 'bridge' during Mesozoic times, the only question is whether it lasted long enough into the Tertiary to be available for certain groups which have not yet been traced back further than the Oligocene. Evidence is, however, rapidly accumulating that not only families but even many genera are much older than have been supposed.

Instead of maps the schemes of diagrams introduced on pages 84, 85 may serve to indicate in the most condensed style the hypothetical configurations in successive geological epochs.

Straight lines mean continuity of land; dotted lines show transient connexion; parallel lines indicate separation by sea. The position of the present continents, etc. is expressed by their initials. Want of space forbids any attempt to justify these broad suggestions, but the chapter dealing with the present and past range of selected groups of animals will supply a considerable number of test cases.

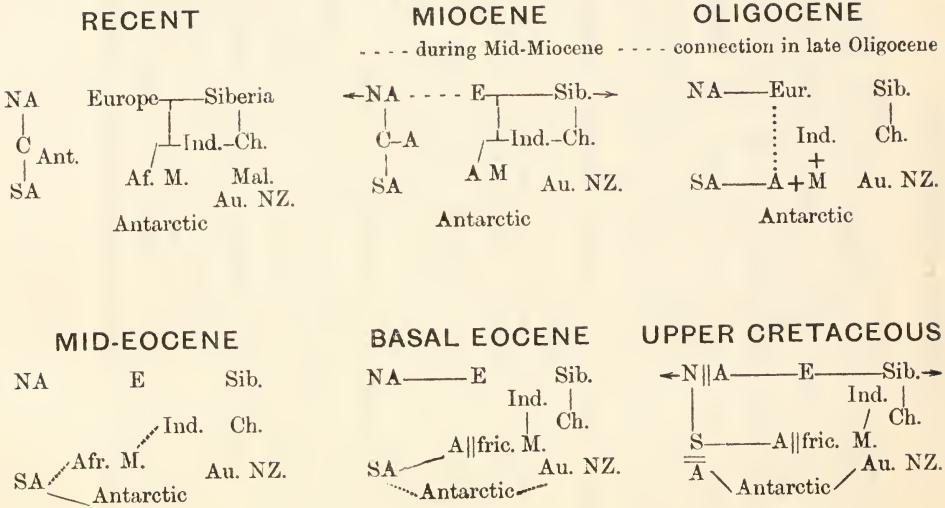
In its broadest outlines the history of the lands and seas since the Carboniferous period may be read

as follows. There were two huge masses of land, a high Southland extending from South America across Ethiopia and India to Australia, and a low Northland comprising Canada, Greenland, Scandinavia and Siberia. These two lands were separated by a broad Mediterranean sea, an east and west extension of the Pacific basin. Nothing is known about the antarctic regions. Two new features are indicated in Carbo-Permian times; joining of the north- and southland somewhere between South-East Europe and Africa, perhaps by emergence of South-West Asia; isolation of North America with Greenland from the Europe-Siberian mass during the whole of the Permian. With the Trias this connexion is restored, but towards the close of this epoch Siberia becomes isolated, the European sea communicating with the Pacific to the north of India; another lower Triassic land connexion of Western, Atlantic, Europe, with North-West Africa is also lost. With the later Jurassic a complete rearrangement has taken place. There are three separate masses of land: a northern Atlantic land, namely North America with North Europe; a Siberian-East Asia-Australian mass, and a so-called Gondwanaland proper, namely South America with Africa-Madagascar and India. The old Southland has been severed in two. Great changes have been effected during the Cretaceous, at least they become now for the first time discernible: connexion of Western

North America with a Western South America, continued across the Antarctic to Australia which is still joined to Eastern Asia and Siberia, the latter continuous with North America but separated from Europe. Consequently an enormous ring of land encircles Gondwanaland which, it must be noted, is quite separated. During the Upper Cretaceous, Siberia joins Europe and Canada, but North America is divided into an east and west. Severance of Chile-Patagonia from the rest of now consolidated South America. Severance of Australia from Asia. Consequently there is now a greater antarctic complex, from Chile to Australia, whilst the rest of the world forms a huge ring with a gap through North America. During the earlier half of the Tertiary epoch the North American, European and Siberian lands separate and rejoin variously, continuous perhaps across the polar sea, sometimes transversely. Antarctica separates from America and from Australia. Gondwanaland breaks up. India becomes for a while an island. Ethiopia becomes isolated owing to the Mediterranean joining the Indian Ocean, and on the other side joining the South Atlantic, thereby severing Ethiopia from South America, which however still remains connected with North-West Africa. Next the African continent is consolidated; the North and South Atlantic Oceans become confluent and South America is isolated. During the Miocene

only Australia, New Zealand and Madagascar are isolated entities of importance. All the rest of the world is at some time or other in roundabout, or direct, continuity, chiefly owing to the juncture of Africa by Arabia with India and the long-since consolidated Asia; the two Americas are joined, for a time also the Antilles. Since the Pliocene they remained islands. North America finally separates by the North Atlantic from Europe, but is variously connected with Siberia across Behring's Straits.

The most changeable of all regions was Europe, not because it is geologically the best known, but it is the newest continent. During Cretaceous and far into Tertiary times Northern and Western Europe formed an extension of the Canada-Greenland mass, quite separate from Asia; Central and South Europe consisted mainly of a variable number of much-changing island complexes. With the Miocene separation from Greenland took place and joining of the growing Europe to Siberia and South-West Asia, and the central and southern islands became absorbed into the continent in the Pliocene. During Pleistocene times Europe seems to have attained its greatest dimensions, and with the receding ice the Rhine and Elbe flowed across the present North Sea.


RECENT
NA
C
Ant.
SA
Europe
Siberia
Ind.–Ch.
Af. M.
Mal.
Au. NZ.
Antarctic
MIOCENE
- - - - during Mid-Miocene - - - - connection in late Oligocene
NA - - - - E
Sib.
C–A
Ind.–Ch.
SA
A M
Au. NZ.
Antarctic
OLIGOCENE
NA
Eur.
Sib.
Ind.
+
Ch.
SA
A+M
Au. NZ.
Antarctic
MID-EOCENE
NA
E
Sib.
Ind.
Ch.
Afr. M.
SA
Au. NZ.
Antarctic
BASAL EOCENE
NA
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UPPER CRETACEOUS
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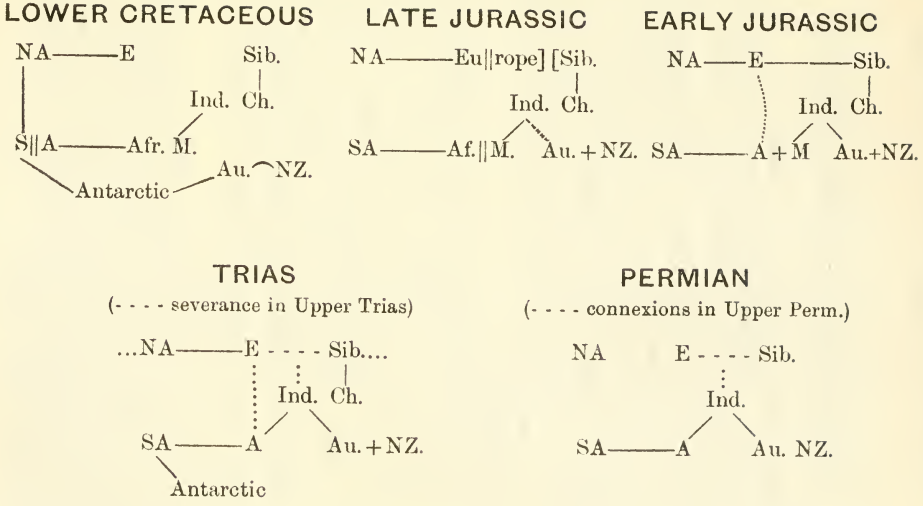
Antarctic


LOWER CRETACEOUS
NA——E
Sib.
Ind. Ch.
S||A——Afr. M.
Au. NZ.
Antarctic
LATE JURASSIC
NA——Eu||rope] [Sib.
Ind. Ch.
SA——Af.||M. Au.+NZ.
EARLY JURASSIC
NA——E——Sib.
Ind. Ch.
SA——A+M Au.+NZ.
TRIAS
(- - - - severance in Upper Trias)
...NA——E - - - - Sib....
Ind. Ch.
SA——A Au.+NZ.
Antarctic
PERMIAN
(- - - - connexions in Upper Perm.)
NA E - - - - Sib.
Ind.
SA——A Au. NZ.

Probable Age of Certain Islands.

Great Britain became an island after the last glacial epoch. Ireland separated a little earlier; its latest connexion was with Scotland, whence it was re-stocked after the glaciation, with the possible exception of those few plants and animals which had not been affected by the ice in the most southern part.

Iceland, Faröer and Greenland date from the Pliocene. Iceland's fauna was destroyed by Pliocene lavas. Its separation from Greenland preceded that from the Shetlands.

Corsica and Sardinia were connected with Northern Italy well into the Pliocene; Sicily also with Africa. The latter was repeatedly in contact with Europe during the Tertiary period, especially across the Aegean Sea. Crete for instance is but of Pliocene date. Communication of the Mediterranean with the Atlantic has been interrupted more than once, not always at the present Straits of Gibraltar, which are of rather recent date.

Newfoundland was last connected with Labrador, whence it was re-stocked after the glaciation. The Greater Antilles became severed from Central America and from each other within the Pliocene, when they underwent considerable submergence. The Galapagos date from the same epoch.

During the Jurassic, Cretaceous and early Tertiary Madagascar, together with India, formed a long island, or complex of islands (practically the much debated 'Lemuria' of Sclater and Haeckel). Madagascar was separated from Africa since the Lias, with a rather problematic restoration of an Oligocene bridge. The connexion with India lasted well into the Oligocene.

Sumatra, Java and Borneo were Asiatic continental until the Pleistocene; Celebes and the Philippines until the Pliocene; whilst New Guinea and Tasmania were Australian. New Zealand, as a whole, seems to be the earliest island-complex of importance. Its final separation, however, need not date back further than into mid-Cretaceous times.

CHAPTER VI

DISTRIBUTION OF SELECTED GROUPS

Earthworms.

The terrestrial earthworms have the reputation of great zoo-geographical importance, and in the hands of an expert, unbiassed in the interpretation of the actual facts, they may some day yield valuable results which are in harmony with those indicated

by other groups of animals. Unfortunately there are no fossil data. The following points are in favour of the importance of earthworms: they are in their welfare and possibility of spreading dependent upon the existence of vegetable mould; they cannot stand sea-water, and their mode of dispersal depends entirely upon their own powers of locomotion, which are considerable; accidental, occasional lifts of the worms, or of their cocoons, are practically excluded, except by human agency since prehistoric times. There are for instance in the Sandwich Islands more than a dozen kinds of earthworms, of genera, which are not restricted to these islands. On the contrary, some of them have a very wide distribution. Consequently these worms must have come from elsewhere, and speaking geologically, not so very long ago.

A very different case is presented by various Antarctic islands, e.g. Kerguelen and Marion to the south-east of the Cape. Their characteristic worms belong to the presumably ancient Acanthodrile group, and are, according to Beddard and Michaelson, quite indigenous, since they are all different as species and found nowhere else. The further contention that these islands are not truly oceanic but the remnants of a former much larger mass of land may also be valid, but it does not follow that this land was part of a former northern extension of the Antarctic continent. Like the fish-genus *Galaxias* (cf. p. 95)

these worms would prove rather too much, because other allied species and genera of Acanthodriles live in Cape Colony.

The present distribution of this important family reaches from South America, over Africa and Madagascar, to New Caledonia and New Zealand, with this restriction that in Patagonia, the Falklands, New Georgia, Kerguelen and Marion Islands, they form almost the only worm-fauna, whilst they are in the minority in the more temperate and tropical parts of the southern continents. Their distribution is therefore compatible with that of the ancient Gondwanaland, and this would not have prevented them from availing themselves also of the Patagonian-Antarctic-Australian bridges.

The other main groups of earthworms strongly indicate a South American + African + Madagascar complex and an Oriental-Australian community, whilst the *Lumbricidae* (supposed to be the youngest family) are with few exceptions the only earthworms of Eurasia proper whence, however, they have spread over most of the world. The Pleistocene glaciation seems to have played sad havoc with the worms of North America since Canada and the Northern States possess no indigenous species, all the earthworms being identical with European species. But those in the Southern States show a marked influence from Central America.

Peripatus.

Peripatus is the sole surviving genus of the Protracheata. The group, ancestral to spiders and insects, must be of enormous age, but this genus need not date further back than into the Cretaceous to allow us to account for the scattered distribution of its species as follows: the occurrence of the same species in Australia, including Tasmania, suggests this region as the original centre, whence other species spread into New Britain and Indo-Malaya. Then extension across Antarctica by Patagonia to Chile, whence into the rest of South America (Guiana) as this became consolidated in Tertiary times. For getting to the West Indies and into Mexico they would have had to wait until the Miocene, but long before that time they could arrive in Africa, there surviving as a Congolese and a Cape species; but they never reached Madagascar.

Insects.

The genus *Carabus*, flightless beetles, lives to the north of about the 30th parallel in both hemispheres and reappears in Chile: by no means a solitary instance of such a discontinuity in America, e.g. bears.

Molluscs.

Of bivalves only the *Unionidae* and *Cycladidae* are freshwater families, both with world-wide range. Of the marine *Mytilidae, Dreyssena polymorpha* is the only freshwater species. Its home is the Volga basin, whence it became accidentally introduced into Western Europe in the 18th century. It is now in the interesting stage of spreading through all rivers and even into land-locked lakes. Those which ascend the Danube basin are meeting others from the Rhine which they have reached by Baltic shipping.

The true mother-of-pearl, genus *Meleagrina*, ranges from the coast of Persia to Celebes and Melanesia, reappearing on both coasts of Mexico and Central America.

Freshwater Crabs and Crayfishes.

The freshwater Decapods have been studied exhaustively by Ortmann, who in a classical paper has based upon their distribution the most suggestive reconstructions of Cretaceous and Tertiary geography.

Crayfishes are older than crabs, and they can inhabit cold regions, whilst the crabs are essentially tropical. The crabs comprise (1) the *Potamoninae* in Africa and Madagascar, India and China, Malay and Papuasian islands; with their northern limit South Japan, Asia Minor, Greece and South Italy;

(2) the *Deckeniae* in East Africa and one species on the Seychelles; (3) the *Potamocarcinae* in tropical America, including Antilles. Thus they occupy the whole intertropical belt and this divides the crayfishes into the northern *Potamobiidae* and the southern *Parastacidae*. Only in a few countries do crabs and crayfishes slightly overlap, e.g. South Mexico and Papua. Crabs are destructive to the crayfishes, so that the latter cannot enter countries already tenanted by the former. Crayfishes are assumed to have originated during the Cretaceous in Southern Asia, where they no longer exist.

Their southern descendants, the *Parastacidae*, survive in New Zealand, Fiji, Melanesia, New Guinea, Australia and Tasmania, whence they crossed by Antarctica into the southern temperate part of South America. There is also one solitary form, *Astacoides madagascariensis*, in Madagascar.

The northern descendants of the ancient crayfishes are the *Potamobiidae*, comprising only three genera. *Astacus* (e.g. the common crayfish, renamed *Potamobius* by purists) in Europe and *Western* Siberia, and in the North-West United States. The discontinuous range is mitigated by a few species in the Amur, Korea and North Japan, where they form the sub-genus *Cambaroides*. Lastly *Cambarus*, to which *Astacus* is directly ancestral, in the eastern half of North America, Mexico and Cuba.

Scorpions.

This group is a good illustration of the effect of great antiquity. Scorpions already existed in the Silurian, and even some existing species date back to the Coal-measures ! They have had every chance of spreading widely. A species of *Tityus* is preserved in Miocene amber of the Baltic ; this genus is now restricted to southern South America. The group is cosmopolitan, limited only by cold, yet it is absent from New Zealand. They show scarcely any generic affinity between the Old World and the New, nor between South America and Australia. They have had sufficient time to develop along lines aloof from each other in these great land complexes.

Fishes.

Eels are cosmopolitan ; those which live in rivers must descend into deep seas to breed. For some reason the Black Sea is a closed sea to eels, consequently there are none in that large part of Middle and Eastern Europe which drains into this sea. Nor are there any in the Volga basin, although this contains a sturgeon.

Pikes (*Esocidae*), a small well-defined family of freshwater fishes, with only two genera. *Esox* occurs first in European Oligocene. *E. lucius*, the common pike, inhabits Europe, excluding Spain, Siberia and a

broad belt across temperate and cold North America, with several other species in the north-east. The other genus is *Umbra*, with one species in Hungary, the other in North-East America.

Cichlidae, a numerous family of freshwater fishes, with many kinds in tropical America and the whole of Africa, with Madagascar, and only three species in South India and Ceylon.

Characinidae, an ancient freshwater family, with many species in tropical America, excluding Antilles, and tropical Africa including the whole Nile, but excluding Madagascar for which they were too late in their progress from America through Africa.

Cyprinidae: carp, minnow, tench, bream, barbel, etc.; the majority of the freshwater fishes of the northern hemisphere. The distribution of the family is most important, namely over the whole of Arctogaea; absent from South America, Madagascar, Australia, New Guinea and New Zealand. According to Boulenger the Cyprinids originated from the Characinids as a northern offshoot in North American Eocene, whence they spread into Eurasia at least during the Upper Eocene; with the Miocene they reached India and then Africa, checking thereby the eastward spreading of their older cousins, the Characinids. This assumed spreading from North America by Asia to India and Africa is an example which is applicable also to other orders and classes of animals.

Galaxiidae, a small freshwater family of trout- and pike-like appearance. *Galaxias*, the main genus, has become famous as one of the earliest and chief supports of the former connexion of Australia with South America. The same species, *G. attenuatus*, inhabits the streams of New Zealand, Tasmania, South Australia, the Falklands, South Patagonia and Chile; others occur at the southern end of America, in Southern Australia, New Zealand and neighbouring islands, and one at the Cape. One species (Chatham islands), is said to be marine. The existence of a species at the Cape would prove rather too much for connexion *viâ* Arctica, but, although it is not impossible that these fishes are the remains of a family which inhabited the southern shores of the Great Gondwanaland, it is scarcely credible that a species like *G. attenuatus* should have survived since at least the Eocene.

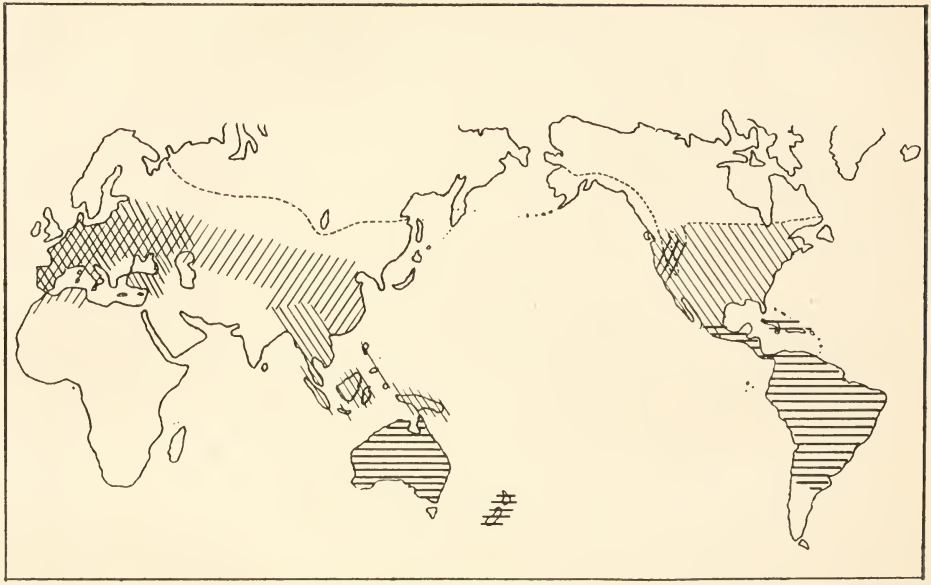
Amphibians.

Amphibians cannot endure saltwater, nor can they spread across deserts. Most abundant in the tropics, they decrease rapidly towards the arctic circle, their northern limit following roughly the 58th parallel in Eurasia and the 50th in America.

The tailed amphibians, Urodela, are essentially holarctic, with three main centres, European, Eastern

Asiatic and North American with closest affinity between the two last. North America contains the greatest number of diverse forms, including members of every sub-family, Plethodonts being the most numerous. Asia is richest in *Amblystomatinae*; Europe is characterised by tritons and salamanders. Significant is the occurrence of *Cryptobranchus*, the 'Giant Salamander,' in Japan, Manchuria, Eastern U.S.A. and fossil in European Miocene, and with close relations in the Oligocene. One kind of *Amblystoma* lives in China, all the other species of this genus in North America, e.g. *A. tigrinum*, which in certain Mexican lakes breeds as the famous axolotl. The Plethodont genus *Spelerpes* has many species in America, from Canada to South America, including Antilles, and one solitary species in the Riviera and in Corsica! The nearest relation of the blind *Proteus* in caves of Istria is the *Necturus* of the American lakes. In the Old World the southern progress of newts has been barred by the great belt of deserts and the Mediterranean, there being none in Africa and India, but many in China, whence at least one has extended into Siam and Burmah. The oldest Urodela occur in the Belgian Wealden, related to the American mud-eel, *Amphiuma*.

The tailless amphibians, Anura, are quite cosmopolitan. Their oldest remains are scanty, from the Upper Jurassic of Wyoming and Spain. With the



Map 1

Examples of now very discontinuous distribution. The dotted line indicates the limit of permanently frozen subsoil.

Cystignathidae or Frog-Toads. //// Discoglossidae, *e.g.* Firebellied and Midwife Toads

\\\\ Pelobatidae or Spadefoot Toads.

early Miocene most of the chief families seem to have been already developed. Unfortunately our knowledge of their pedigrees is still very deficient. It is for instance at least doubtful whether the 'Firmisternia' (Ranidae + Engystomatidae + Dyscophidae) form a natural division. Only the more significant cases of distribution can be mentioned. The most archaic but also most specialised are the *Aglossa*, namely *Pipa*, the 'Surinam toad,' mainly Brazilian, *Xenopus* in Africa, and *Hymenochirus*, intermediate in structure, in the Congo district.

The *Discoglossidae* also are ancient, with a very scattered range, namely the 'fire-bellies,' *Bombinator*, from France to Manchuria, the 'midwife toad,' *Alytes*, *Discoglossus* in West Europe, and *Ascaphus* in North-West United States. The equally ancient *Pelobatidae* or 'spade-foots' and allies range from North America, Europe and India into Papuasia.

Bufonidae, typical 'toads,' are cosmopolitan, excepting Madagascar, New Guinea, Tasmania and New Zealand. The genus *Bufo* has the same wide range, but is also absent from Australia. The centre of the *Hylidae* or 'tree-frogs' is South America, whence they have spread, since the Miocene, to the Antilles and Central America, and in ever decreasing numbers into North America, and only two or three closely allied species occur in Eurasia, from Japan to the Himalayas and to western Europe, excluding Britain.

No *Hylidae* exist in Africa and Madagascar nor India and the Malay Islands, but there are plenty in Australia. The same principle, suggestive of a former antarctic connexion, is followed by the *Cystignathidae*, which are plentiful in South and Central America (a few in the U.S.A.) and Australia, and the solitary *Liopelma* in New Zealand.

The opposite principle of dispersal applies to the *Ranidae* or typical frogs. The greatest number of their many genera with near 300 species occurs in Africa and the Indo-Malayan countries. All the numerous species of the whole of North America and Eurasia belong to the genus *Rana*, except the closely allied arborealised *Rhacophorus* which ranges from Japan through India and Malaya ('flying frog') to Madagascar. *Rana* itself, with about 150 species, has nearly the same range as the family, and, what is most significant, a few species have reached north-west South America, but not the Antilles; it occurs also in Madagascar, New Guinea, Northern Australia and the Solomon Islands. Thus the frogs, toads and tree-frogs still proclaim the fundamental divisions of the Old South and North World.

Crocodiles.

Crocodiles in a wide sense are known from the Lower Jurassic epoch and they developed an abundance of marine and freshwater groups all over the

world, of which the present 20 species are the scanty remainder. Long-snouted gavials occur in the Upper Cretaceous of New Jersey and Europe, in the Miocene of Europe, now restricted mainly to the Ganges and Malay Islands. Crocodiles have lived in Europe since the Upper Chalk, and many kinds flourished there, and in North America during Tertiary times; now in Africa, India to North Australia, and in tropical America, including the West Indies. Alligators and caimans, formerly also in England, are now almost entirely American, but one species lives in the Yang-tse-kiang as a reminder of the probable Eurasian origin of the whole group.

Tortoises.

The marine turtles are found in all the warm to temperate seas. Most of the groups of the land and freshwater tortoises were evolved before the Tertiary period, and attained a perhaps world-wide range, so that the present distribution of the 200 species represents only the remainder of a sub-class which has had its day.

Pleurodira, or water-tortoises, which tuck away their long neck sideways, were plentiful in Mesozoic times in Europe, India and North America; now restricted to Africa and Madagascar, South America and Australia. On the latter continent they are the

only tortoises, family *Chelydidae*, which flourish also in South America, e.g. *Matamata*. The other family, *Pelomedusidae*, is Afro-American; of these *Podocnemis*, now in Madagascar and Brazil, occurs in early Tertiary of Egypt and Angola. The *Cryptodira*, tortoises which draw in the neck straight, are most developed in North America. The genus *Testudo*, the most typical land tortoises, ranges over the world, excepting the Australian quarter, and is limited northwards only by the cooler climate. Its earliest occurrence is in the mid-Eocene of Wyoming, since the Oligocene in Europe, still later in India, where in Pliocene times it attained truly gigantic size (*T. atlas*). Somewhat smaller kinds lived in Miocene Europe and North America, now restricted to some of the islands near Madagascar, and to the Galapagos, i.e. 'Turtle-islands.' Of course this implies former land connexions. And so does *Miolania*, the most aberrant of all tortoises, known from the Pleistocene of Queensland, Lord Howe's Island and Argentina. *Trionychidae*, river or 'mud-turtles,' with a much-reduced, leather-covered shell, since the Cretaceous in North America, in early and mid-Tertiary of Europe, now in North America, Southern Asia and the African continent.

Lizards.

Geckos, probably the oldest family, are found in all warm countries and islands, even in New Zealand and the Sandwich Islands, being particularly fit for accidental transport. Equally cosmopolitan are the also very ancient Skinks.

The following families are restricted to the Old World: (1) *Chameleons* in Africa and Madagascar, and a few in Syria and Arabia, South India and Ceylon; (2 and 3) *Agamas* and *Varans* or 'Monitors,' in the whole of Africa, Asia Minor to China and to Tasmania; absent from New Zealand and Madagascar; (4) *Lacertidae* or lizards proper, in Africa, Europe, Asia; absent from Madagascar and Australasia.

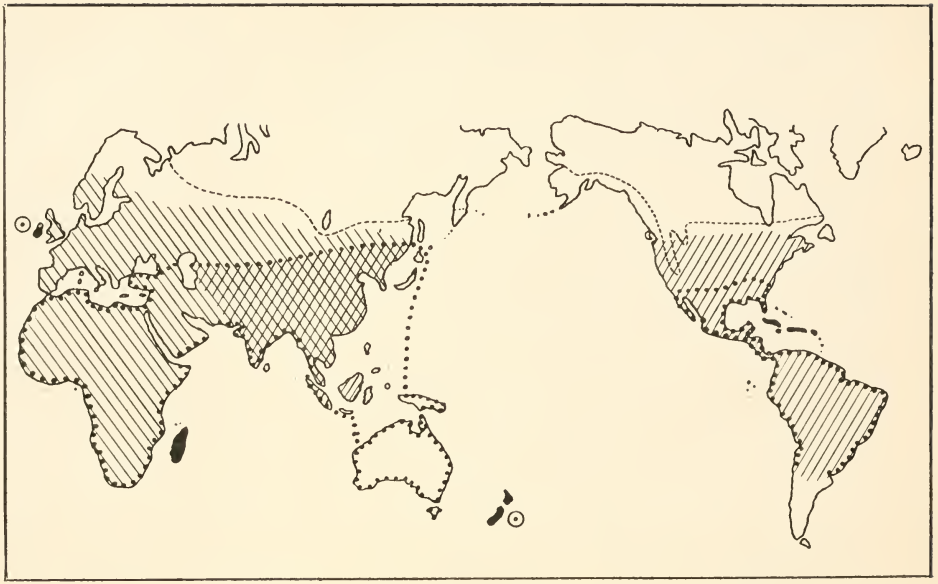
The following occur in both the Old and the New World: (1) Amphisbaenas, burrowing, worm-shaped; in the warmer parts of America, including Antilles; the whole of continental Africa and Mediterranean countries, like Spain, Sardinia, Corsica, Cyprus and Asia Minor, a strong indication of Tertiary Afro-American connexion. (2) Slow-worms or *Anguidae*; centre of dispersal probably middle America, the home of the limbed genera, now extending to Vancouver and to Costa Rica and the Antilles. The only kinds in the Old World are limbless: the slow-worm, *Anguis fragilis*, is European; of the glass-snakes, *Ophisaurus*,

one occurs from Marocco to the Caspian, another from Himalayas to China, the third in the United States. (3) *Iguanidae* or iguanas, basiliscs and 'horned toads.' Essentially American, with the remarkable occurrence of two genera in Madagascar and one in the Fiji and Friendly Islands. Madagascar presents no difficulty, since iguanas are known from French and English Eocene, and their total absence from Africa and India may be accounted for by the inroad of the fierce carnivorous Varans, which, too late for Madagascar, exterminated the chiefly herbivorous iguanas. The Fijian *Brachylophus* remains a puzzle, but on the Galapagos, nearly 600 miles from America, live two kinds of antediluvian-looking Iguanids, one of which, *Amblyrhynchus*, is semi-marine, feeding upon algae.

Strictly American are the families of Teijus and Ameivas.

Snakes.

The earliest remains date from the Lower Eocene of Egypt, amongst them gigantic forms allied to boas or pythons which are still found in all tropical countries. The majority of the snakes belong to the cosmopolitan *Colubridae*, which seem to have given rise in divergent directions to the poisonous *Elapinae* and to the equally poisonous *Viperidae* ; the latter are naturally divided into vipers and pit-vipers. The



Map 2

Distribution of Poisonous Snakes.

····· Elapine; Cobras and Allies.

//// Crotaline; Pit-vipers, Rattlesnakes.

\\\\ Viperine; Vipers.

■ No poisonous Snakes. ⊙ No Snakes.

poison snakes are of considerable geographical importance.

Australia has only Elapines, but in abundance. America has Crotalines and Elaps. Africa has hooded Elapines and abundance of vipers. Europe has now only vipers, in former epochs also Elapines and Crotalines. The Indian countries alone are cursed with members of all three groups.

Elapinae, culminating in the hooded cobras, genus *Naja*, which ranges all through continental Africa and the whole of temperate and warm Asia. Other genera in India and thence in Australasia down to Tasmania. America has received, or developed, only the genus *Elaps* with many species from the States to Patagonia; none in the Antilles.

Crotalinae or *Pit-vipers* in the southern half of Asia, from Asia Minor to Borneo and Japan and throughout North and South America. Both the chief genera *Lachesis* and *Ancistrodon* exist in the Old and New World. A further modification of pit-vipers are the rattlesnakes proper, with present headquarters in the South-Western States and Mexico, whilst only one species, *Crotalus terrificus*, has entered South America, now ranging from Arizona to Argentina.

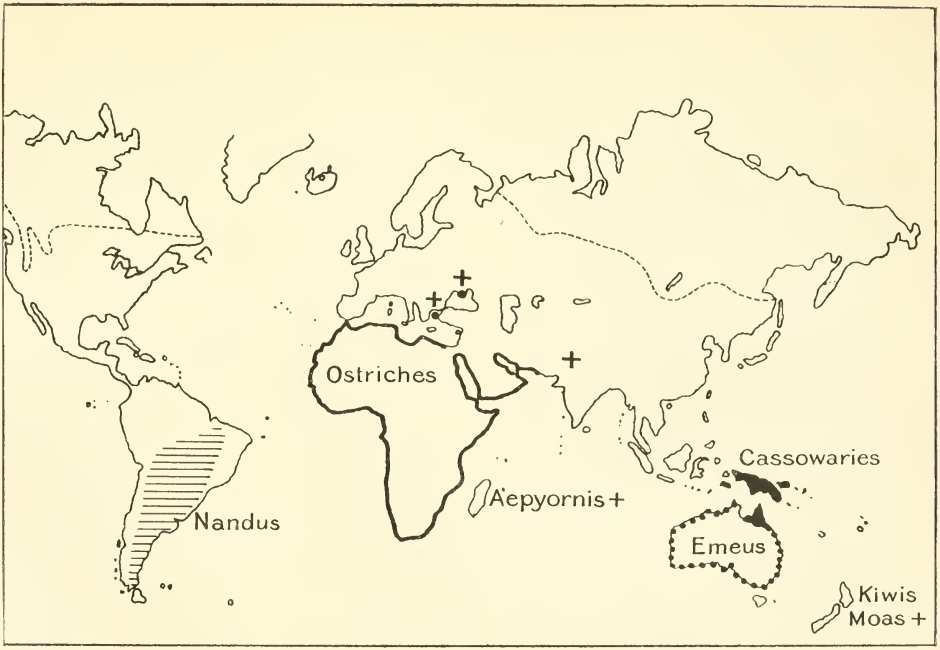
Viperinae, vipers without a sensory pit between nose and eye, all over Eurasia and Africa, respecting Wallace's line like the hooded cobras. The efficiency

of this line (between Borneo and Celebes, Java and Lombok), and their absence from North America, point them out as the most recently evolved group of poisonous snakes. The original centre of them all seems to have been Eastern Asia, and the dispersal had taken place with the Miocene.

Birds.

"Ratitae" are not a natural group; they are related to each other only in so far as that they are the flightless descendants of that stock of terrestrial birds which has given rise to the Tinamoos, Cranes and Fowls. Since the early Tertiary, Ratitae have arisen at different times and in various countries, independently of each other. Many are now extinct. *Rhea* lives in South America. *Struthio*, the ostrich, now in Africa and Arabia; known from Pliocene of Samos, North-West India and Northern Asia. Cassowaries chiefly in Papuasia, emus in Australia. *Aepyornis* in Madagascar, where extinguished possibly by man; the '*Ruk*' of the fable. New Zealand and Stewart Island have the kiwis (*Apteryx*), and there was an abundance of moas (*Dinornis*), some of them gigantic, extinguished by the Maoris.

Penguins are essentially antarctic, also on the south coasts of New Zealand, Australia, the Cape and South America, on the west coast of which they



Distribution of Ratite Birds. + Ostriches, Pliocene.

Map 3

extend northwards with the cold Humboldt current, which may account for their existence on the Galapagos, right under the equator. Fossil penguins are known from the Oligocene of New Zealand and Miocene of Patagonia.

Divers and *Grebes.* Divers (*Colymbus*) and Grebes (*Podicipes*) seem to be connected by the Oligocene French genus *Colymboides.* The four kinds of recent divers are restricted to the northern hemisphere. Grebes are cosmopolitan, with one interesting flightless kind on Lake Titicaca in Bolivia.

Petrels and *Albatrosses* are cosmopolitan groups; albatrosses are, however, more common in the southern hemisphere.

Gannets and *Cormorants* are cosmopolitan, *Pelicans* are restricted to the warmer zones. The largest cormorant happens to be a flightless species of the Galapagos Islands. Fossil *Steganopodes* (i.e. rudder-feet, so called because all these birds have all the four toes webbed together) are known from the Oligocene onwards.

Herons are cosmopolitan. The tall *Balaeniceps,* whale-headed heron or shoebill of the Upper Nile, and the small *Cancroma* or boatbill in tropical America, are remarkable illustrations of isotely or so-called parallel development or convergence.

Storks proper are essentially an Old World family, namely Indo-African, whence some species migrate

to breed in the northern temperate zone. They are entirely absent from North America, but South America possesses one kind of *Ciconia*, besides the Jabiru-stork which has its other relations in Africa, India and Australia. Both marabous and adjutants are Indo-African.

Flamingoes began to evolve out of stork-like birds in the Lower Miocene, e.g. *Palaelodus* of France. Now they inhabit lagoons and inland lakes of Africa, Madagascar, India and tropical America, including the West Indian Islands. The common African species has summer colonies in Andalusia and near the mouth of the Rhone.

Ducks, *Swans* and *Geese* are quite cosmopolitan groups. Spur-winged geese or tree-ducks range from tropical America, through Africa and Madagascar to India, but are absent from the Australian countries.

The ancient *Palamedeae*, crested screamers or chájàs, are restricted to South America.

Limicolae. Many of the plovers, sandpipers and so forth, being shore-birds are great migrants and rather closely allied to each other; they are more or less cosmopolitan and do not yield any important geographical results.

Thick-knees or stone-curlews (*Oedicnemus*) are absent from North America, Central Asia and New Zealand. The 'Painted Snipes' (*Rhynchaea*) range from Africa and Madagascar to Formosa and

Australia and to South America. The Jaçanas (*Parra*, etc.) have a similar tropical range, excepting Australia. The 'Seed-snipes" (*Thinocorys*) are restricted to Western South America, from Ecuador to the Falklands. The only other family with a somewhat restricted range are the Coursers, Pratincoles and Crab-plovers which inhabit the shores of the whole Indian ocean, whence they extend far into the Old World continents.

Gulls and *Terns* are cosmopolitan families.

Auks and *Guillemots* are decidedly northern, the southern limits of these strictly marine shore-birds being Massachusetts, Brittany, the Baltic, the north coast of Siberia, North Japan to Lower California. The famous 'Great Auk,' the only really flightless member, had been exterminated in Iceland in 1844; it was formerly common on the coasts of Denmark and Ireland, and on the opposite shores of North America.

Sand-grouse. The genus *Pterocles* dates from the early Tertiary of France ; ranging now from Spain and Cape Colony to Madagascar. *Syrrhaptes paradoxus*, Pallas' Sand-grouse, is at home in Central Asia, whence it has made irruptions in enormous numbers into Europe ; cf. p. 68.

Pigeons are apparently an Old World group, dating with certainty from the Lower Miocene; they are now quite cosmopolitan. Especially rich in the production of genera have been tropical islands, above

all Malaya, Papuasia and Polynesia, perhaps, as Darwin pointed out, owing to the absence of monkeys and other noxious, egg-stealing mammals. Flightless, large-sized pigeons were the recently extinguished Dodo of Mauritius and Bourbon, and the Solitaire (*Pezophaps*) of Rodriguez.

Gruiformes or *Cranes* and *Rails* are an important order on account of the distribution of the genera, some of which are at least of Oligocene date. Taken as a whole, this order indicates common origin and descent from an equatorial belt of land when South America, Africa and India were still more or less connected; after this time the development of entirely Old World families becomes marked.

Rails are cosmopolitan, but interesting because of the tendency of reduction of their wing power. Beginning for instance with birds like the Weka Rails (*Ocydromus*) of New Zealand, they are liable to become flightless, with a much-reduced keel of the breastbone. This has happened, especially on small islands, e.g. Chatham Island with *Diaphorapteryx*, Rodriguez with *Erythromachus*, Mauritius with *Aphanapteryx*, all of which have died out recently. Although they are structurally so much alike, that we might unhesitatingly put them into one genus, if they did occur together, they have each received a second generic name; rightly though, because they must have developed independently of each other

into what they are. It was a great mistake to use these recent rails, simply because they were flightless, as a support of the former existence of the great southern continent. On Tristan da Cunha, in the middle of the South Atlantic, lives the tiny flightless *Gallinula nesiotis*.

Cranes are an Old World group, most numerous in Africa, less numerous in Eurasia; only one kind of crane lives in Western North America and one in Australasia. Cranes are absent from New Zealand, the Malay Islands, Madagascar, Central and South America. This is very remarkable considering that these birds are some of the best-flying migrants.

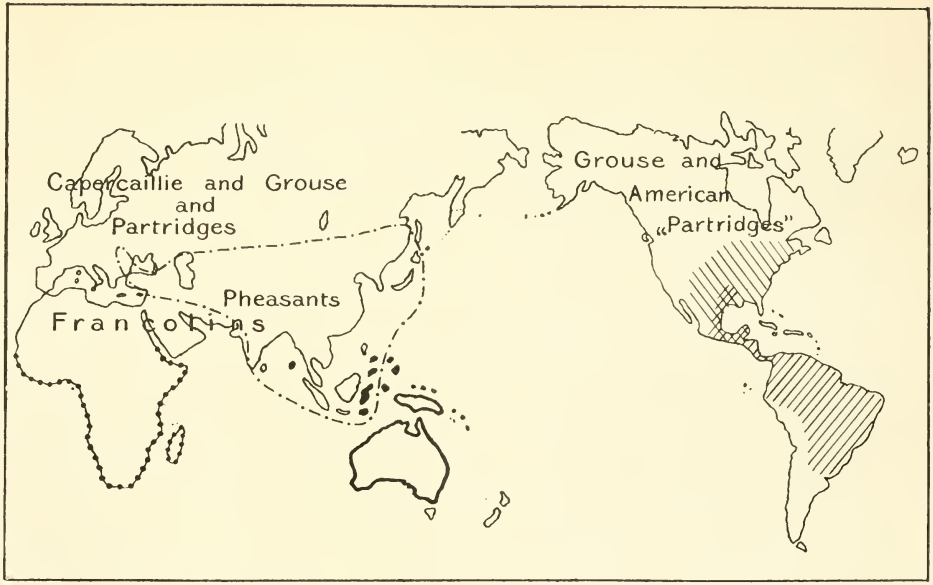
Other genera, combining specialised with ancient characters, have very isolated ranges, an indication of the great age of the whole group. For instance, the Cariama and Chuña in South America; also *Psophia*, the Trumpeter, to which is undoubtedly related the Miocene Patagonian *Phororhacus* with its gigantic, monstrous skull. *Rhinochetus*, the Kagu, is restricted to New Caledonia. *Eurypyga*, the Sunbittern, in tropical America, together with *Heliornis*, the Finfoot, which is scarcely generically distinct from *Podica* in Africa and further India.

Bustards are really rails adapted to life on grassy plains. They form an absolutely Old World family, inhabiting Europe, Asia, Africa and Australia, but

neither New Zealand, nor the naturally unsuitable Malay Islands, nor Madagascar.

Birds of Prey. The American vultures or *Cathartae* form a separate sub-order; absolutely restricted to both Americas. The Old World scavengers, *Vulturidae*, are chiefly African, whence they extend in a peculiar manner. They occur regularly in Mediterranean countries, thence far into India but stopping short of China, Borneo, Sumatra, Ceylon and Madagascar. The osprey, *Pandion*, is cosmopolitan, with the curious exceptions of Ireland, Iceland and New Zealand. *Accipitres*, the diurnal birds of prey, without the *Cathartae*, are known from French Oligocene, e.g. the 'secretary-bird' which is now restricted to Africa. They are an essentially Old World order, which however has sent many eagles, hawks and falcons to America.

Gallinaceous Birds. It was upon the present distribution of the fowl tribe that Huxley to a great extent founded his division of the globe into a north and south world. I. Peristeropodous or pigeon-footed fowls, i.e. with all the toes on the same level, are (1) the Megapodes or Talegallas or brush turkeys in Australasia, from Tasmania to the Philippines; (2) the American forest fowls, curassows and guans, or Cracidae from Paraguay to Texas, excluding Antilles. II. Alectoropodous or cock-footed, with the hind-toe rooted above the front-toes. To these *Gallidae* belong



Map 4

Distribution of Gallinaceous Birds.

— Megapodes or Mound-builders. //// Turkeys. ····· Guinea fowls.

//// Curassows and Guans. -·-·- Pheasants.

the following somewhat arbitrary sub-families, each with a still well-marked radiating centre. Guinea-fowls restricted to Africa and Madagascar. Pheasants, 'fowls' and peacocks essentially southern Asiatic. Turkeys are peculiar to North and Central America. The *Tetraoninae* are essentially holarctic: most numerous in North America, e.g. prairie fowls, others in tropical America; grouse are circumpolar; capercaillie Eurasian, also partridges; francolins are Indo-African; quails have the widest distribution, over most of the Old World, including Madagascar, and even New Zealand had one, quite recently extinguished, species.

Cuckoos are a cosmopolitan family, even New Zealand possessing several kinds. Our common cuckoo ranges over most of the Old World. The present distribution of the various sub-families yields no tangible results, since most of them have allied genera in Asia, Africa and South America, and there is no convincing ground for assuming that their original centre was Eastern Asia. The Turacoes or helmet-cuckoos are an entirely Ethiopian family.

Parrots seem to have originated in the Australian region, which alone contains members of all the sub-families and the more ancient forms, whilst other continents possess only members of the family *Psittaciae*. South America has the structurally most advanced genera. India and Africa are poor in

parrots. Brush-tongued parrots, *Trichoglossidae*, are strictly Australasian (east of Wallace's line to Tahiti), chiefly 'lories,' with the ancient 'keas,' *Nestor*, in New Zealand and Norfolk Island. *Psittacidae*, comprising all the others, have a smooth tongue. *Stringops*, the kakapo or owl parrot, with weak flying power and much reduced keel of the breast-bone, in New Zealand. Cockatoos are abundant in Australia and Papuasia.

Coraciiformes. Rollers, bee-eaters, kingfishers, hoopoes and hornbills represent closely related families of undoubtedly Old World origin. The numerous family of kingfishers is cosmopolitan, most abundant in Papuasia, but only a few species of the otherwise widely-distributed genus *Ceryle* are the sole representatives in America. Hoopoes and hornbills are Afro-Indian, but absent from Madagascar; on the other hand hornbills extend far beyond Wallace's line, through New Guinea into the Solomon Islands. The screech- or *barn-owl* inhabits almost every country in the world, Scandinavia, America north of 45°, and New Zealand being the principal exceptions. *Humming-birds* are a highly specialised and probably recent family of neotropical origin; they exend to Tierra del Fuego, to the far outlying island Juan Fernandez, to the Galapagos and of course the Antilles; towards the north they become scarce, but one kind is a summer visitor of Mount

Elias in Alaska, and the tiny *Trochilus colubris* breeds in Canada and Labrador.

Trogons are tropical; America, Africa, excluding Madagascar, Indian and Malayan. Most of the Old World genera retain a colour-pattern which is juvenile in the American species, which comprise also the most gorgeous kinds. They point to a direct Afro-American connexion, and this is quite compatible with the occurrence of Trogons in French Oligocene.

Woodpeckers also seem to have originated in South America; now the family is cosmopolitan with the exception of Madagascar, Australian countries and Polynesia.

Passeriformes. More than half the number of recent birds belong to this order. The lesson of their distribution cannot be appreciated without reference to their systematic affinities.

I. *Clamatores*, with imperfectly developed singing apparatus; the few muscles are attached either to the middle, or to the dorsal, or to the ventral edge of each bronchus. Structurally the lowest Passeres are the broadbills or *Eurylaemidae*, restricted to the Indies and Malaya. Allied are the ant-thrushes or pittas from New Britain to Madagascar and West Africa; *Xenicus* and a few others in New Zealand. Lastly, tyrants, manakins, bellbirds, ant-birds, in all about 1000 kinds in South America, whence many of

the tyrants have spread into North America, chiefly as migrants.

II. *Oscines* or singing birds ; with the muscles attached to the dorsal and to the ventral edge on either side of the syrinx. The lowest of these birds are the *Suboscines*, of which the only representatives are the lyre-bird, *Menura*, and two small kinds of scrub-bird, *Atrichornis*, in Australia. The rest, half of the species of the whole class, are the *Oscines* or singing birds proper, which having probably originated in the northern half of the Old World have since attained world-wide distribution.

Mammals.

The earliest remains of mammals have been found in the Triassic of Carolina, *Dromatherium* and *Microconodon*, and of South Africa, *Tritylodon* and *Theriodesmus* ; others have been described from Patagonian Eocene. This is practically all we know of possible *Prototheria* or representatives of the earliest stage of mammals, of which the monotremes are supposed to be the sole and much-modified survivals. Of the next stage, the *Metatheria*, the marsupials are the modernised survivals, or side branch, whilst from the main Metatherian stem has been evolved the last or Eutherian stage, comprising the placental mammals. As to the place of origin

of earliest mammals it does not matter much where they are found, because, being of at least Triassic age, the whole world may have been overrun by them during the enormous stretch of the Jurassic period. In any case there was time for them to have reached Australia, immaterial whether still quite Prototherian or already recognisable as Monotremes.

The recent Monotremes are the duck-bill, *Ornithorhynchus*, and a few species of spiny ant-eaters, *Echidna*, in Tasmania and Australia, and *Proechidna* in New Guinea.

Marsupials.

The pouched mammals, comprising about 170 recent species, have a very discontinuous distribution. Their headquarters are now Australia with Tasmania and the Papuan Islands; two phalangers have reached Celebes, and two dozen species, mostly opossums, survive in America.

It is customary to divide the marsupials into I. *Polyprotodonta*, with three or four pairs of lower incisors, e.g. *Didelphidae* or opossums, mostly in Central and South America; but one, *Didelphys virginiana*, the common opossum, ranges from Argentina far into the United States. *Chironectes*, the little water opossum, lives in tropical America. *Dasyuridae* comprise the 'native devils' and the wolf-like *Thylacinus* or Tasmanian 'tiger.' Allied is the

'ant-eater' *Myrmecobius* of West Australia and the small 'marsupial mole,' *Notoryctes typhlops*, a blind digger in the barren centre. II. *Diprotodonta*, with only one pair of lower incisors, usually enlarged, e.g. the numerous kangaroos, *Macropodidae*, one genus of which, *Dendrolagus*, contains the tree-kangaroos. The phalangers are a very diversified family; all are climbers; some, e.g. *Petaurus*, look exactly like flying squirrels, others like mice. The tiny *Tarsipes* lives in Western, the koala or 'native bear,' *Phascolarctos*, in East Australia. Two phalangers are restricted to Celebes. *Phascolomys*, the wombat, has assumed rodent-like characters. Lastly, two small species of *Caenolestes* in Ecuador and Colombia are also diprotodont and possibly more nearly related to the Australian phalangers than to the strictly American opossums.

A time-honoured explanation of the present distribution of marsupials is that they had an almost world-wide range when Australia was still accessible from the north. When, after the separation, the Placental mammals had been evolved in Arctogaea, the marsupials could no longer hold their own, except those which were safely shut up in the Australian region, and except the few opossums in America which saved themselves by early adopting an arboreal life. In principle this story is right, but wrong in detail. It is also awkward for this hypothesis that

hitherto not one single marsupial fossil is known from India, nor from any other part of Asia.

Many pre-Tertiary mammalian remains are known from Europe, North and South America, mostly nothing but teeth and under-jaws. Presumably all the Jurassic and Lower Cretaceous mammals were Metatheria, leaving aside the Monotremes, q.v., but it is often impossible to decide whether the Upper Cretaceous and even some of the Eocene creatures were still in the Metatherian stage, whether they were already Placentals or whether they were typical marsupials. We begin to discern three great groups.

1. Archaic Metatheria with Diprotodont tendency. The so-called *Multituberculata* or *Allotheria*, e.g. *Microlestes* from Upper Trias of Europe; *Plagiaulax* from Upper Jurassic of Europe and North America; *Meniscoessus* from Upper Cretaceous of North America; *Polymastodon* and *Neoplagiaulax* from North America and European Palaeocene. Others, supposed to be related to the *Allotheria*, have been described from Patagonian Cretaceous and Eocene deposits. But these *Allotheria* (i.e. 'different beasts') have not much to do with the true marsupials, certainly not with the *Diprotodonta*, although they are diprotodont, a feature which has been evolved at various times and by various orders. However, the *Allotheria*, of which many remnants are known, mostly from Wyoming and Patagonia,

undoubtedly indicate land connexion of North and South America during at least part of the Cretaceous epoch, and a longer intercourse between North America and Europe.

2. Archaic Metatheria of Jurassic date, some of which are supposed to be ancestral to the Insectivora, e.g. *Triconodon, Amphitherium, Dryolestes* of England and North America.

3. Archaic or ancestral marsupials.

(*a*) *Polyprotodonta*, with a complete set of four pairs of lower incisors, e.g. *Pediomys* and *Didelphops* of North American Upper Cretaceous. *Borhyaena* from South America, Eocene to Miocene, supposed to be nearly allied to the Australian *Thylacinus*. *Paratherium* from Lower Eocene into Oligocene in North America where it died out, but continued in Europe from Upper Eocene into Lower Miocene, indistinguishable from the recent *Didelphys*, which is also known from South American Pleistocene, whence one species, the common opossum, *D. virginiana*, now extends far into the United States.

(*b*) *Diprotodonta*. Many species of *Epanorthus* and *Abderites* in Patagonian Tertiary, considered as allies of the recent Colombian *Caenolestes*. Their diprotodont feature may be a case of parallelism with the Australians, but it is significant that the recently discovered *Wynardia bassiana*, described by Spencer

from Tasmanian early Tertiary, is said to be intermediate between Australian Poly- and Diprotodonts.

To sum up. Metatheria existed during the Jurassic period both in England and in North America. They disappear in Europe, but reappear in North America with the Upper Cretaceous as undoubted direct forerunners of marsupials, and they extended their range during the same epoch into South America. Opossums appeared in America in the Eocene, whence they spread into Europe, but neither they, nor others, flourished in the northern continents, probably because the Eocene also marks the appearance of the Placentalia, with which the inferiorly organised marsupials could not compete. But that marsupial stock which had got into South America was safe there, because that continent we know to have been separated from the north from Eocene to Miocene times. There they produced a considerable number of forms, until these also vanished before the inroad of carnivorous Placentals, excepting the opossums. Further, to the South American marsupials the way was open to the antarctic lands, which in turn were connected with Australia, long after the latter, with Papuasia, had been severed from Asia. The marsupials, after their long wanderings over three-quarters of the globe, had found in the Australian region a wide expanse of country in which they have developed groups analogous to

many of the Placentals, for instance the rodent-like wombat, phalangers resembling flying squirrels, *Notoryctes* like a blind mole, the ant-eater *Myrmecobius*, fleet pasturing herds of kangaroos and a fierce wolf-like *Thylacinus*.

It is of the greatest significance that all the recent marsupials have feet modified for arboreal life (either with an opposable hallux, or with the second and third toes joined together) or at least show unmistakeable traces that their immediate ancestors have passed through such an arboreal modification, even the large kangaroos and the clumsy monster, *Diprotodon* of Central Australian Pleistocene. They all had been fitted for life in the trees, and when in Australia this necessity was removed, some of them again took to living on the ground.

Edentates.

Three dozen species, most of them in tropical America, a few in Africa, India and Malaya, are the survivors of an ancient assembly of terrestrial mammals, which are reasonably supposed to be an early offshoot of the Placentals.

Scaly ant-eaters or pangolins, *Manidae*, date from mid-Oligocene of France ; now mostly prehensile and arboreal, in tropical Africa and India to Celebes ; absent from Madagascar.

The Cape ant-eater, *Orycteropus*, with other species in West and East Africa; fossil from Miocene France, Pliocene Samos and Persia and Pleistocene Madagascar.

All the other Edentates are American, appearing suddenly in a great variety of forms in the Upper Miocene of South America; extending to North America with the Pliocene.

Ground-sloths, *Megatherium*, etc. are now extinct. Neomylodon (=*Grypotherium domesticum*), with dried skin and hair, has been found recently in a Patagonian cave.

Armadillos with an abundance of Tertiary genera, are now much reduced in numbers. The nine-banded armadillo has the widest range, from Argentina to Texas.

Ant-eaters, *Myrmecophaga*, and sloths, *Bradypus*, are confined to tropical America.

If the Edentates of the Old and New World are related to each other, they may be the remainder of an old Afro-Indian fauna of Eocene date. They could have spread by Asia Minor into Europe; or some of the common stock may have found their way to Brazil where they developed into the '*Xenarthra*' typical of South America, whence by the end of the Miocene they could extend into North America, although no longer into the Antilles. If, however, the Taeniodonts and Ganodonts of the Lowest and

Low Eocene of North America should prove to be 'primitive Edentates,' and if *Metachiromys* of North American Eocene were an armadillo, as has been asserted and denied, then we might look for the original home of the order in North America, whence they spread into the south, leaving a blank in the north. The north and south connexion became available in the Miocene, in time enough for the outburst of the order in South America, but far too late for Africa and Europe.

Rodents.

This vast order comprises almost 1000 recent species and is, as an order, quite cosmopolitan; some of the families are already recognisable in the Eocene.

Hares, with the chief genus *Lepus*, date from American Oligocene; earliest occurrence in Eurasia not until the Pliocene. Now on every continent; absent from Australia and all ancient islands. The *variable hare*, which turns white in winter, ranges from Greenland and Canada through Siberia and Scandinavia, with the outlying centres of Ireland, Scotland, Pyrenees, Alps, Caucasus and Japan.

Squirrels, etc. are cosmopolitan excepting Australasia, Madagascar and Antilles. Flying squirrels have developed in India, northern Europe and Siberia, and thence in the pine forests of North America.

A peculiar flying form is *Anomalurus*, the palm-marten of West Africa. Other outlying forms are the jumping hares, *Pedetes*, of the South African veldt.

Beavers of temperate and cool Eurasia came late into North America.

Rats and mice are absolutely cosmopolitan. Even Australia has several peculiar genera: the aquatic *Hydromys*, the Queensland rat *Xeromys* and several 'jumpers.' Many genera in Eurasia and North America, whence steadily decreasing through Central into South America. Remarkable are the *Dipodidae*, known from American Eocene onwards: *Zapus* in Canada and China; alactagas and jerboas from Eastern Asia to North Africa, the former extending into interglacial Europe as typical steppe-creatures. The *brown rat* is Asiatic, crossed the Volga in 1727, arrived in Germany in 1770, shipped a few years later to North America and has since overrun the whole world.

Porcupines in the wider sense, or Hystrichomorpha, are important: Afro-Indian and tropical American; whilst many fossils are known from European Eocene and Oligocene, none occur in North America. Chinchillas, agutis, guinea-pigs, etc. live in Central and South America. *Porcupines*: *Hystrix* mid-Miocene in Europe, now Afro-Indian; prehensile-tailed tree-porcupines, e.g. *Synetheres*, from Bolivia to Mexico;

only one genus, *Erethizon*, has reached North America, now up to Alaska and Labrador. Lastly, the *Octodont* family: *Aulacodus* in North Africa and Abyssinia; *Capromys* in the Bahamas and others in South America, where they existed in the Miocene. There can be no doubt that the Hystricho-morphs are of Old World origin. Long before the mid-Miocene, divers members must have passed from Africa directly into tropical America, which by the Upper Miocene had already become a new centre of dispersal. It is certain that this continent did not receive its supply from the north.

Insectivores.

The order, with 200 recent species, is cosmopolitan with the exception of the South American continent and Australasia. There are some in Cuba and Hayti, many in Madagascar, but none on other outlying or oceanic islands. Occurring already in the Eocene of North America and Europe, they died out in the former continent which has received its present supply of 'star-nosed' and 'web-footed' moles and shrews from Eurasia in late Tertiary times.

Centetidae and allies. Beginning in Lower Oligocene of North America with forms allied to *Solenodon* of Cuba and Hayti, a most primitive, generalised Placental. These are related to the Ethiopian

Potamogale and *Geogale* of Madagascar, which in turn are allied to the Tenrecs, e.g. *Centetes* of Madagascar, where this family flourishes in many genera and species. *Centetes* and *Solenodon*, with striking mutual resemblances, have been a sore puzzle to the zoo-geographer.

Golden moles (*Chrysochloris*) inhabit South Africa, but undoubtedly related to them is *Necrolestes* of the mid-Miocene in Patagonia. Considering that the above-mentioned families are not known from Europe, these Insectivores with V-shaped molars indicate an early Tertiary Afro-American land connexion.

Hedgehogs in the wider sense disappeared from America in the Oligocene; descendants are the Indian *Gymnura* and *Erinaceus*, the hedgehogs proper, now in Eurasia and North America.

Moles and shrews are now arctogaean, but with very few in Africa, and the American immigrants mentioned above have not reached tropical America.

Tree-shrews, *Tupaia*, are Oriental; the elephant shrew, *Macroscelides*, and other jumping shrews are African.

Bats.

Bats have a world-wide distribution, limited only by the polar climates. Some of the present genera are first known from the Eocene of Europe, and yet, and in spite of their power of flight, bats did

not reach America until the Pleistocene. Moreover some of the chief families, and still more the smaller groups, are restricted in their range, which means that even these well-flying creatures consider not only oceans, but narrow seas as obstacles.

The *Pteropodidae* or flying foxes, strict vegetarians, inhabit all the warmer countries of the Old World, from Africa to India, Australia and Tahiti, but not New Zealand.

The *Rhinolophidae* or leaf-nosed bats, e.g. our horse-shoe bats, are also restricted to the Old World.

The *Phyllostomidae* or vampires are tropical American, including Antilles. Of them only *Desmodus* and *Diphylla* are true blood-suckers, but not the genus *Vampyrus*! North America proper possesses only members of the quite cosmopolitan family *Vespertilionidae.*

Carnivores.

This large order of almost 300 recent kinds is cosmopolitan, excepting New Zealand, many small oceanic islands and Australia but for the solitary Dingo.

The Carnivores are undoubtedly of northern, holarctic, origin, but their centre of evolution was soon shifted to Eurasia. During the Pliocene none persisted in North America but dogs, coons and skunks. Bears and true cats have entered that

continent later. India possesses representatives of all the recent families; Africa proper has all but bears; South America is relatively the poorest continent.

Creodonta or archaic mammals with a carnivorous dentition have existed, in great numbers, since the Eocene in North America, whence they spread into Europe, and later into Africa. Most of these beasts died out with the Eocene, or rather they were modernised into the typical Carnivora, in various parts of the world. Some however kept on to almost recent times as highly specialised Creodonts, e.g. the sabre-toothed tigers: *Nimravus* in North American Oligocene; *Machaerodus* from Miocene to Pleistocene in Europe and Asia, whence in the Pleistocene it appeared as *Smilodon* in America which this terrible beast conquered to the far south. Meanwhile, with the mid-Miocene, somewhere in Eurasia were evolved modern cats of the genus *Felis*. With the Pliocene these found their way into North America and later into the south; being such late arrivals, they were debarred from the Antilles. Cats are now cosmopolitan excepting the Antilles, Madagascar and the countries to the east of Java and Borneo.

Civet-cats or viverras are an exclusively Old World family, dating from Eocene Europe. Their great age explains the existence of the Fossa (*Cryptoprocta*), and some others peculiar to Madagascar.

Hyaenas, since Miocene in England and Asia, now in the whole of continental Africa and the south-west quarter of Asia. Both the striped and the spotted kind, the latter now only in South Africa, lived in interglacial England.

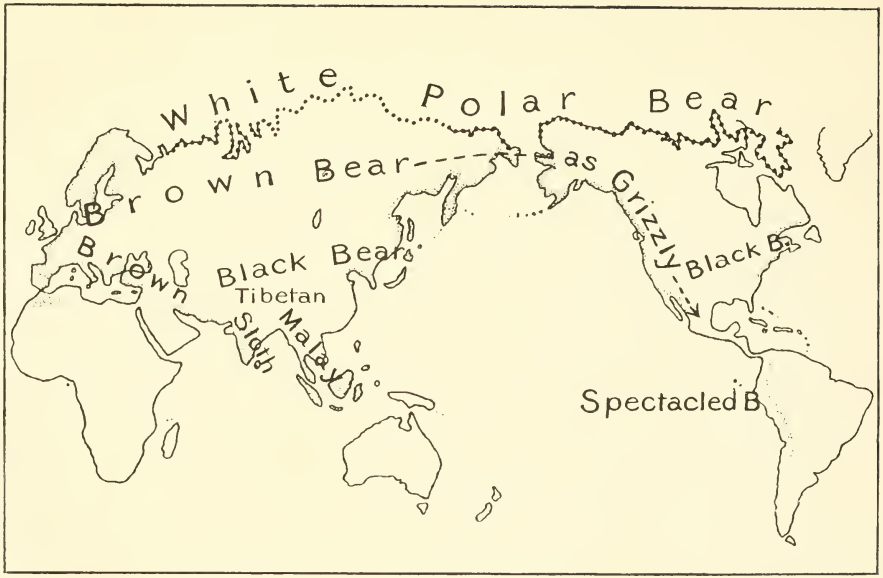
The dog-tribe date from late Eocene in North America and Europe, now cosmopolitan even in the Falkland Islands, but absent from Antilles, Madagascar and to East of Wallace's line. Australia is overrun by the Dingo, a dog of unknown origin.

The genus *Canis* was not ready until the Pliocene. *Weasels* and *otters* have the same wide range.

Bears appear as various genera in Eurasian Miocene. The genus *Ursus* appeared with the Pliocene, and with the Pleistocene entered North America, ranging into Mexico and reappearing on the Andes. Although inhabiting all Asia and until recent days all Europe, bears never seem to have found their way into Africa proper, excepting the Atlas range.

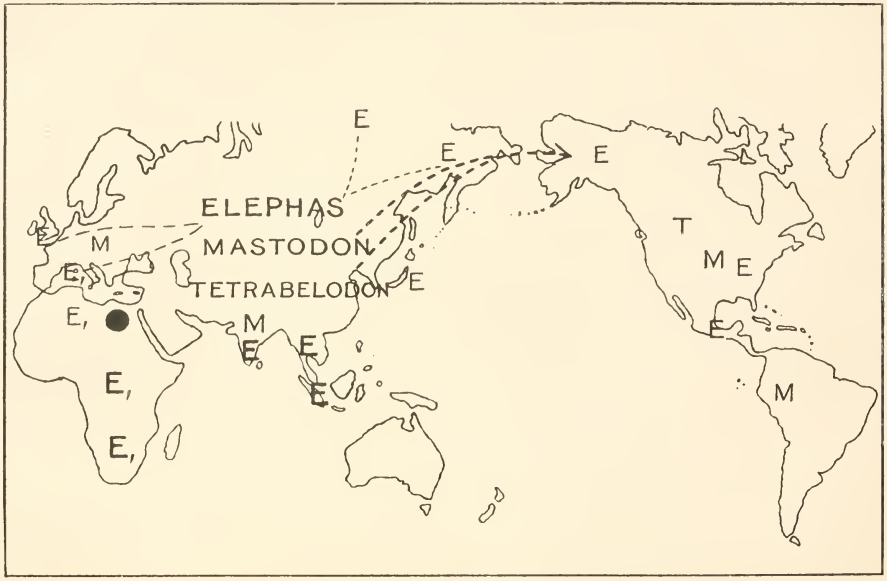
Elephants.

The earliest archaic elephantine beasts have been discovered in Egyptian Upper Eocene: *Moeritherium* and *Palaeomastodon*, the latter with a pair of upper tusks pointing downwards, and a pair of lower, spoon-shaped incisors. With the Miocene appears *Tetrabelodon*, with upper and lower tusks, curved upwards,



Distribution of Bears.

Map 5



Map 6.

Distribution of Elephants.

T = Tetrabelodon, Miocene. M = Mastodon, Pliocene. E = Elephas, Pleistocene.
E = Elephas, Recent range. ● = Archaic ancestors, Eo-Oligocene.

in Europe, India and North America. They change into 'Mastodonts' proper, characterised by reduction and loss of the lower tusks and more complicated molars. Such mastodonts flourished during the Pliocene and overran not only Eurasia but also America to the Andes. *M. americanus* survived far into Pleistocene. Meanwhile in some of the Asiatic stock the molars not only had changed the 'lumpy teeth' into such with transverse, numerous, lamellae but into practically evergrowing teeth by delay of root-formation. Such 'elephants' proper are the *E. indicus* now of India and Sumatra, a close ally of the *E. meridionalis* and of *E. primigenius*, the 'hairy mammoth' of Pleistocene Europe and Siberia. It entered America late. Somewhat earlier arrivals in North America meeting there the mastodon, were *E. columbi* and *E. imperator*, the largest of all, extending their range into Southern Mexico. But this sojourn in the New World was short lived. Meanwhile somewhere in Asia a side departure was marked by lozenge-shaped, instead of parallel molar lamellae, e.g. *E. antiquus* of the Lower Pleistocene of Europe and North Africa, which now culminates in the African elephant, separated as *Loxodon* on account of its tooth pattern.

Thus it has come about that these powerful beasts after having overrun the world so far as it was accessible to them, have within quite recent times

become restricted to the southern countries of the Old World, India and Africa, whence they originally started.

Swine and Hippopotamus.

Small swine were plentiful in Upper Eocene Europe, later in North America, where they have left only the Peccaries, which now range from Texas to Argentina. In Eurasia pigs have produced a number of surviving genera. *Sus*, dating from Upper Miocene, has the widest range, from Ireland (exterminated) and Morocco to New Guinea and Japan. The *Babirusa*, with its four up-curled tusks, is peculiar to Celebes. Warthogs and riverhogs are now African, south of the Sahara, with one riverhog also in Madagascar. This is paralleled by the former existence of a small hippopotamus in the same island, allied to the pigmy hippo in Liberia, whilst *the* hippo, formerly in India and Europe, lives now in Africa, south of the Sahara.

Camelidae.

The few surviving members of the *Tylopoda*, i.e. pad-footed ruminants, tell a remarkable history of dispersal. From the Upper Eocene of North America they can be traced through an unbroken series of still generalised forms into the Pliocene, when they split into early camels, e.g. *Procamelus*, and early

llamas, *Pliauchenia*. Both groups spread far beyond North America. During the Pliocene, *Auchenia* appeared in South America, where this genus is still represented by lamas and huanacos on the Andine tablelands. *Pliauchenia* had found its way to India, where it died out. Early camels likewise must have reached Asia, because in India appears the first true *Camelus*, which in Pleistocene times spread into North Africa, and also into North America, where it met several other aboriginal camel-like forms. Then they all died out there, so that now this once flourishing family of enormous and continuous range, is rent in two, its members existing in a wild state only on the Andes and the Central Asian highlands.

Chevrotains.

The Chevrotains comprise a few small-sized animals which still resemble primitive or ancestral deer-like ruminants, since they are intermediate in structure between pigs, camels and deer. Their earliest ancestors have been traced to the Upper Eocene of Europe and North America. The only still existing genera are first *Hyomoschus*, the water-chevrotain of West Africa, also in the Pliocene of Asia and in the Miocene of Europe, although those fossils are usually mentioned as *Dorcatherium*. Secondly, several species of *Tragulus*, often called Moose-deer, in Indo-Malay countries.

Deer.

Modern deer, ruminants with yearly-shed antlers, are of exclusively Eurasian origin, and the first brockets were developed in mid-Miocene times. They are absent from Australasia, Madagascar, Africa south of Barbary and the Antilles.

Stags (*Cervus*) existed, since the Pliocene in Europe and Asia, whence the wapiti spread into America with the Pleistocene. Somewhat earlier immigrants produced there the slightly different American deer, *Cariacus*, which now extends from the States to Patagonia.

Reindeer, elk or moose are circumpolar. The roebuck, *Capreolus*, is Eurasian.

The peculiar prongbuck, *Antilocapra*, of the south-west States and tableland of Mexico has no deciduous antlers but sheds the horny sheaths of the bony cores. In this respect it is intermediate between deer, the giraffe (now African, with related genera in Pliocene Greece and India) and the following tribe:

Cattle and Antelopes.

Hollow-horned ruminants with a permanent horny sheath to the bony core of the horns, appear first in Eurasian Miocene. Omitting the arctic musk-ox, the whole tribe of oxen, sheep, goats and antelopes live in the Old World, with few exceptions: the Rocky

Mountain goat, which is really a modified chamois, the big-horn sheep, and the bison, all of which are Pleistocene immigrants to North America. Antelopes are abundant in continental Africa, few in Central Asia, whence the steppe-loving saiga-antelope visited interglacial Europe.

The 'Mountain Antelopes' have now a very discontinuous distribution. *Rupicapra*, the chamois, ranges from the Cantabrian mountains through the Pyrenees and Alps to the Caucasus; with somewhat distant relations in India and Central Asia; and with *Haploceras*, the 'Rocky Mountain goat.' Sheep and goats are natives of Asia and of Mediterranean countries and islands; one goat lives in Abyssinia and two big-horn sheep, allied to the Argali, etc. of Asia occur in Western North America. The bovine beasts, or cattle proper, are also very limited in numbers of species. The yak is confined to the high mountain ranges of Central Asia. The scanty survivors of the two bisons linger, the one in North America, the other in the Caucasus and in Poland. The bantengs are Oriental from Northern India to Java. Of the buffaloes, one inhabits India, another is confined to the Philippine Islands, and two others live in Africa. Celebes has the peculiar rather ancient anoa. The ancestor of our domestic cattle is lost in obscurity, although probably allied to the aurochs (*Bos primigenius*) of medieval Central Europe.

Rhinoceros.

The whole drama of the evolution of the true rhinos has been played in Eurasia.

In the Oligocene of Europe and America appear hornless Aceratheres and pair-horned Diceratheres, e.g. also *Arsinoetherium* of Egypt. None of the right-and-left horned beasts have left descendants; nor did the hornless forms in America, but in Asia some introduced the principle of median horns and such single and tandem-horned rhinos alone have survived in the Old World, whilst those which reached America in mid-Miocene times died out.

Two-horned Old World species are: *R. sumatrensis*; *R. etruscus*, in Pliocene and early Pleistocene Europe; its much larger and very hairy successor *R. megalorhinus* of mid-Pleistocene Europe; *R. tichorhinus-antiquitatis*, of the steppes and tundras of interglacial Europe and Siberia, closely related to the black or long-lipped and the white orsquare lipped rhinos of Africa. *R. indicus* has one horn.

Tapirs.

The cradle of the future tapirs stood somewhere in Northern Asia; the earliest recognisable genus *Systemodon* of the American Lower Eocene being a blind offshoot. With the Lower Oligocene appears *Protapirus* in Europe; it found its way into North

America where it changed into *Tapiravus* and continued well into the Miocene when it died out. But in Eurasia *Protapirus* changed into *Paratapirus* which in turn produced the Pliocene *Tapirus* proper. Formerly also in Europe its only descendant in the Old World is now the Indo-Malay species, none having made their way into Africa. Others however got, in Pleistocene times, into North America, soon to die out there, except those two or three kinds which are now in tropical America, including South-East Mexico.

Thus has come about the striking case of discontinuous distribution of a small and very natural family at two opposite parts of the equator.

Horses.

The story of the horse tribe is based upon such an abundant material that pedigrees with dozens of generic names have been constructed, and its very intricate story has been so often condensed and popularised that the horse has become the show-animal of evolution. Yet, although the evolution of the tribe as such is well understood, often in minute detail, that of the genus *Equus*, the horses, asses and zebras proper, is not known. The main reason is that since early Tertiary times there existed in America, Asia and Europe a bewildering mass of odd-toed

creatures which drifted towards that goal of perfection which has been reached only by the horse. Number of toes, length of limbs and neck, shape of the skull, pattern of teeth, general size, all were in a flux towards certain improvements, but these many characters did not all keep step in the same creatures. The Hyracotheres of Eocene America and Europe (scarcely larger than a cat, with four front and three hind toes, e.g. the so-called *Eohippos*) are still so very generalised that they lead to horses, rhinos and tapirs, as well as to other distinct groups. We therefore disregard them and begin with the *Mesohippos* of American mid-Oligocene; size of a sheep, three-toed, with somewhat elongated limbs. Later relations, during the Upper Oligocene, are perhaps *Miohippos*, and *Anchitherium* which soon made its appearance in Europe, flourishing there during the whole of the Miocene, when its line became extinct. In any case *Anchitherium* was an offshoot. Meanwhile in American Miocene steady progress is represented by a line of successive forms (*Desmat-Para-Hypo-Merychippus*), and all promised well, when, about the end of the Miocene, this stock came to an end in America. Whether members of this same stock had spread into Asia, or whether there had taken place a similar parallel evolution out of the ancient common stock, we do not know. Suffice it to state that with the Upper Miocene we have to start

again with *Protohippos* which suddenly appears in America, together with the Eurasian *Hipparion.* The latter persisted in Europe into the Upper Pliocene (Britain to Africa, Persia, Russia, China and India); with the early Pliocene it also crossed into America, where its various kinds are distinguished as *Neohipparion,* and some of these which got right into South America are called *Hippidion.* All these Hipparions had admittedly too specialised a tooth-pattern to serve as the ancestors of *Equus*; their feet were still tridactyle, but the side-toes were slender and only just touched the ground. Here is a gap, usually slurred over. Creatures intermediate between these three-toed animals and the genus *Equus* (in which the side-toes are reduced to splints on either side of the middle or cannon-bone) are unknown.

The genus *Equus* appears as *E. sivalensis* in Pliocene Asia; other species, e.g. *E. stenonis,* in Europe, supposed ally of zebras. *E. caballus, the horse,* appears with the Pleistocene in Europe, North Asia and North-West America from Alaska to California; and a whole crowd of other horses, amongst them the large pony-sized *E. scotti,* overran the whole of America, all to die out there with the Pleistocene epoch. But in Asia and in Mediterranean countries appear the asses, tarpan and djiggetai and this dweller of steppes extended in interglacial times

to Germany and Switzerland. Przewalsky's horse in Central Asia is the only really wild horse still in existence.

Dugongs and Seals.

The earliest *Sirenians* are known from the Eocene of Jamaica and Egypt, others from Oligocene and Miocene of France and Italy, and from Pliocene North-West America and Japan. They are a strong support of the existence of a transatlantic bridge, along the northern coast of which they lived in early Tertiary times, and of an Atlantic-Mediterranean-Indian sea. The present distribution of the few recent kinds still bears this out. *Manatis* inhabit the coasts of the Antilles, Central and South America, and Africa from the Senegal to Natal, ascending also the big rivers on either side. *Dugongs* live along the coasts of the Indian Ocean, from Mozambique to the northern coasts of Australia. *Rhytina, Steller's sea-cow*, was North Pacific, exterminated in 1768.

Seals, to mention another order of marine mammals. The walrus is polar ; during the glacial epoch it extended down to the coast of France. *Eared seals* are Northern Pacific, from Japan to Mexico, and with a wide equatorial interval on both coasts of South America, Southern Australia, New Zealand and Antarctica. The *earless seals* have a still wider range; around the antarctic continent and southern islands,

e.g. Kerguelen (sea-elephants, etc.) and in the Northern Atlantic, Baltic and the whole polar basin. Of special interest is the occurrence of the two monk seals, *Monachus tropicalis* in the Mexican gulf and *M. albiventer* from the Canaries into the Eastern Mediterranean. Further, a land-locked seal in the Caspian and another in Lake Baikal, the former identical with our common *Phoca vitulina*, and the other with the northern ringed seal, *P. foetida*.

Lemurs and Monkeys.

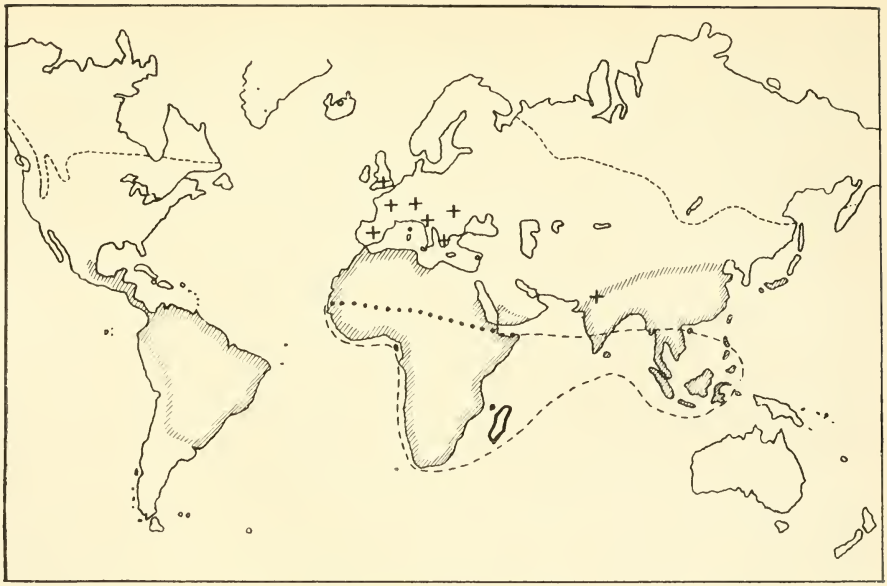
Remains of archaic lemur-like creatures have been found in Patagonian Paleocene, in somewhat later Eocene of North America and in Europe where they extend into the Oligocene. Then they vanish and there is a break between them and the recent lemurs of tropical Africa and Madagascar, with another centre in Malacca and the three great Malay islands; and with the ancient queer little *Tarsius spectrum* in Sumatra, Borneo, Celebes and the Philippines.

There is also a complete gap between lemurs and monkeys; and further a still unbridged gulf between the marmosets and prehensile-tailed monkeys, all of which are tropical American, and the Old World monkeys which inhabit now the whole of Africa (excluding Madagascar), South Arabia, India to South Japan and

the Malay Islands. Such monkeys are known from Miocene Europe, even an ape-like *Dryopithecus*. The famous *Pithecanthropus erectus* of Java is but of Pleistocene date and would do well enough for ancestral man, if we did not feel sure that the genus Homo must date back at least into the Pliocene epoch. But that is another story.

Summary of Mammalian Dispersal.

Australia as the earliest great mass of land permanently severed from the rest is in almost undisturbed possession of the lowest mammals. It is the sole refuge of the monotremes, and the marsupials have narrowly escaped a similar fate. They take us to the next independent continent, South America. This had three chances, or epochs, of being stocked with mammals. Within the Cretaceous period it seems to have received its marsupial stock from the north, the progenitors of all modern marsupials. A second influx, during the early Tertiary brought edentates and rodents as its first Placentals from Africa, and those queer Ungulates the Toxodonts and Pyrotheria, unless we prefer to look upon these Eocene extinct orders as truly aboriginal to South America, when this was still continuous with the ancient Brazil-Afro-Indian Gondwanaland. The third and last inroad came once more from the north, when



Map 7

Distribution of Primates.

Monkeys. + Fossil Apes. – – – Lemurs.

with the close of the Miocene permanent connexion with North America was reestablished. This brought the modern odd-toed and pair-toed Ungulates, with dogs, cats and bears in their wake, and lastly man.

There remains the huge North World. Eurasia and North America have always formed a wide circumpolar ring, which repeatedly broke and joined again. Whatever group of terrestrial creatures was developed in the eastern, Asiatic, half, was sure to turn up in the western, and *vice versa*.

Lastly, the mysterious African continent. It began originally as the centre of the ancient equatorial South World; it has lost these connexions and has become joined to the northland, after many vicissitudes. It is therefore most difficult to apportion its fauna rightly; moreover for fossils it is almost a blank, except Egypt. It must have had some share in the evolution of mammals, like edentates, rodents, Insectivores, hyrax, elephants, sirenians and lemurs, all groups with an ancient stamp. But what share it had, against Eurasia, in the development of say Ungulates, Carnivores, monkeys, we do not know. Not much is likely to have originated in Europe; the elephants, rhinos, hippos, lions and hyaenas were migrants rather from than to Africa, rarely across some Mediterranean bridge, usually by Asia Minor.

The more dominant forms of our present fauna have originated, to use an expression of Darwin's,

'in the larger areas and more efficient workshops of the north,' and the balance is in favour of Asia as the cradle of modern mammals.

Is it an idle dream to think of the future? A survey of the past reveals the vanishing of whole faunas from extensive countries, which were then repeopled by other forms from elsewhere. What has happened before, may happen in times to come. Countless groups, once flourishing, are no more; many others have had their day and are now on the decline, whilst others are flourishing now, are even on the increase and seem to have a future before them. Such favoured assemblies are the toads and frogs, lizards and snakes, Passerine birds and rodents, mostly the small-sized members of their tribes; the days of giants are past. All this has happened in the natural course of events, without the influence of man, who only within most recent times has become the most potent and destructive factor to the ancient faunas of the world.

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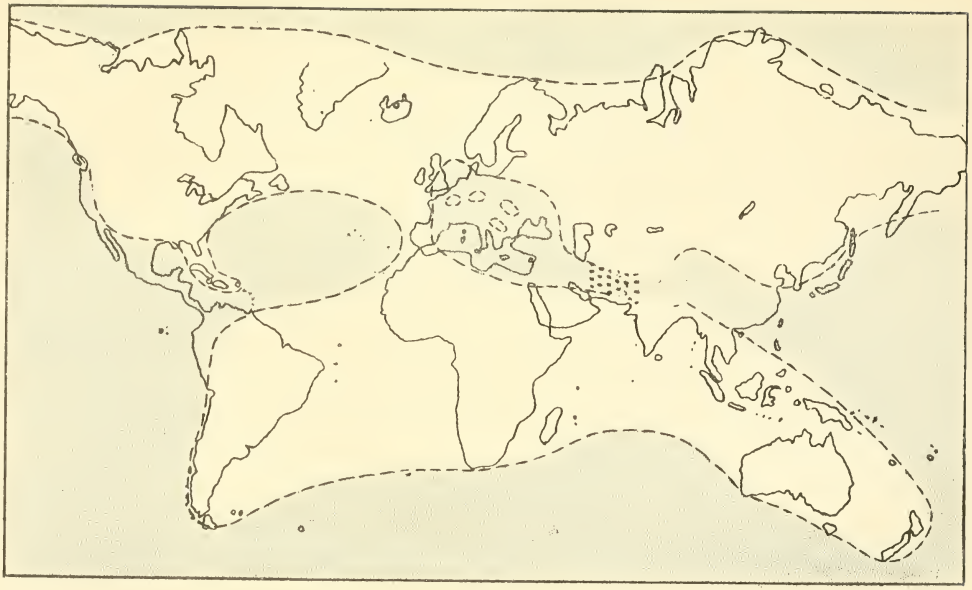
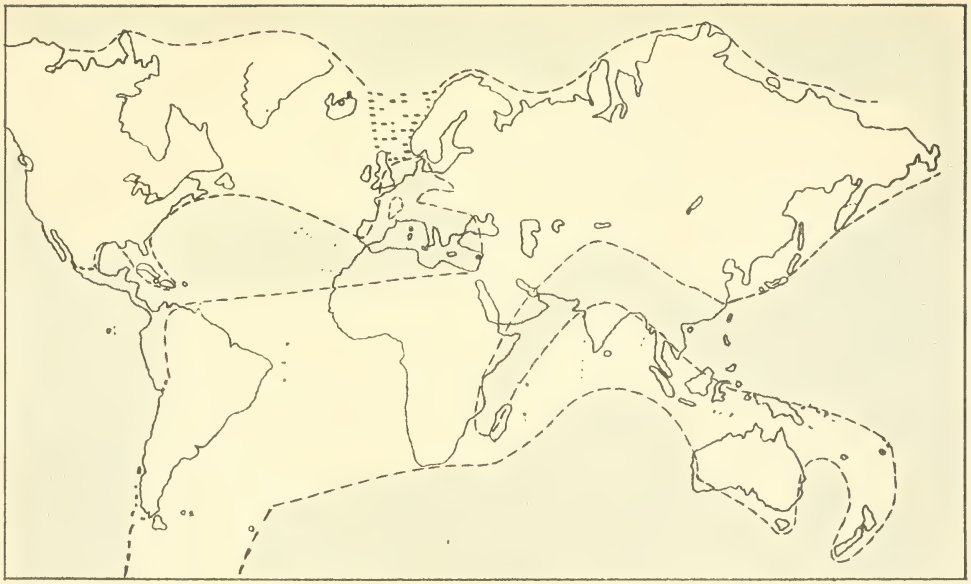


Lower Trias.

Temporary Land.

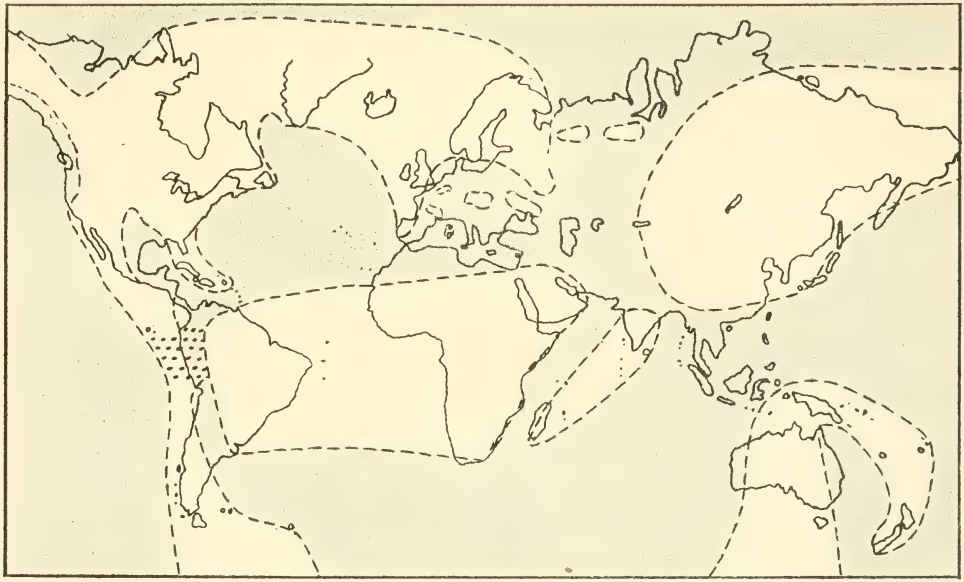
Map 8



Lower Jurassic.

Land during Mid-Jurassic.

Map 10



Lower Cretaceous.

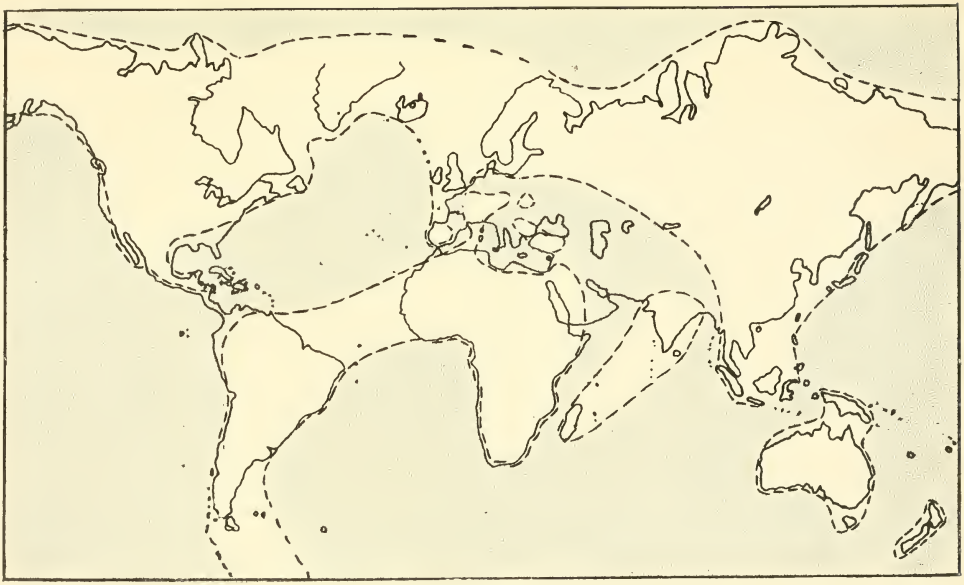
Land?

Map 11

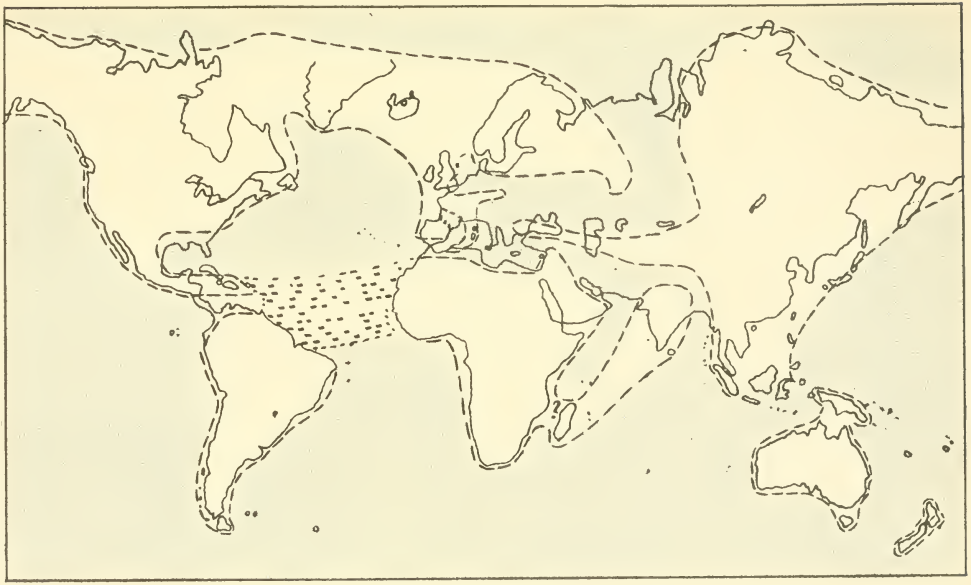
Upper Cretaceous.

Land?

Map 12



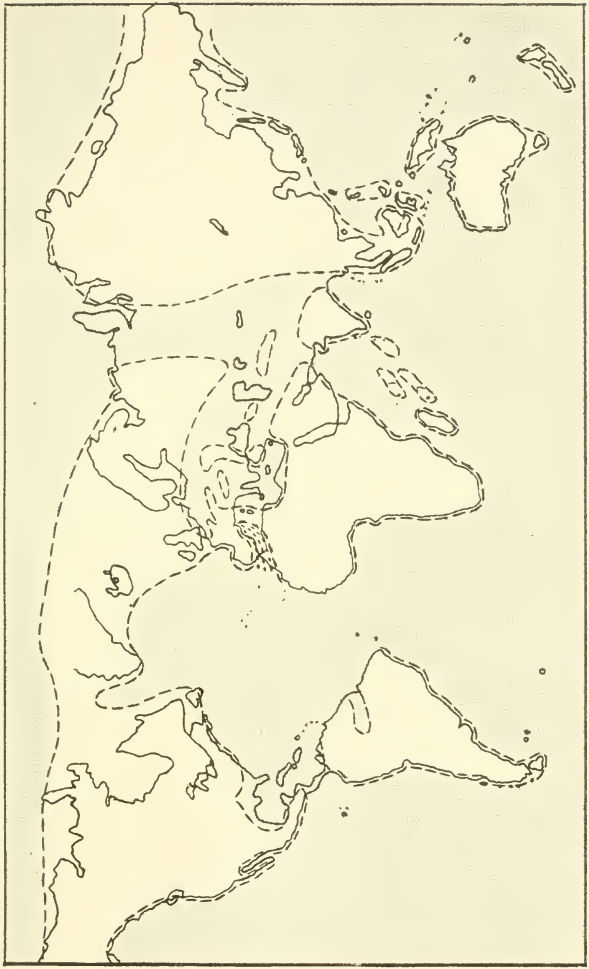
Upper Eocene.



Early Oligocene.

Temporary Land.

Map 14



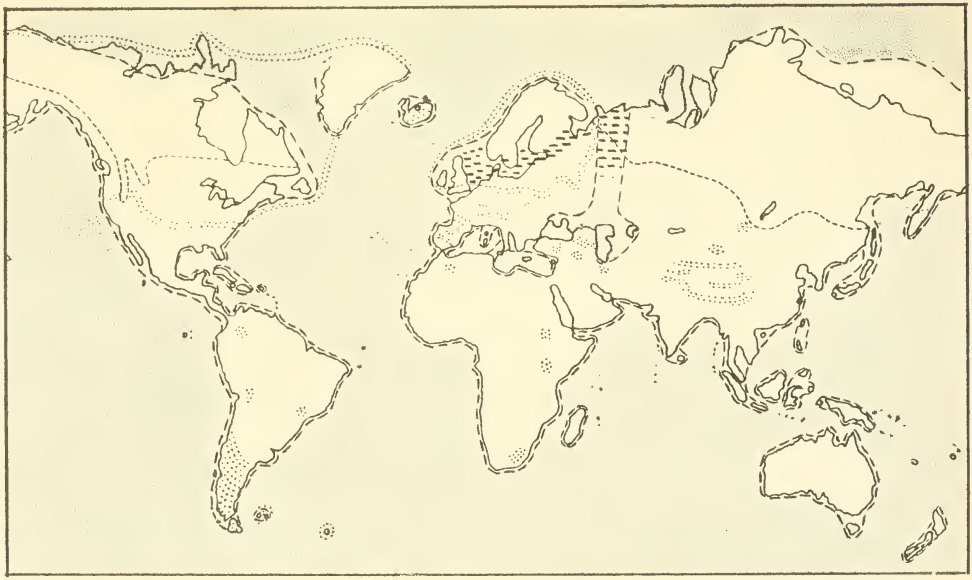
Late Oligocene.

Map 16

Late Miocene.

Land during Mid-Miocene.

Temporary Land after Mid-Miocene.



Map 17

Early Pleistocene.

Extent of Maximum Glaciation. ····· Present limit of frozen subsoil.

Postglacial Sea and Lakes.

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