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THE TRANSFORMATIONS OF THE ANIMAL WORLD

BY

CHARLES DEPÉRET

CORRESPONDANT DE L'INSTITUT, DOYEN DE LA FACULTÉ DES SCIENCES DE LYON, ETC.

BEING THE AUTHORIZED TRANSLATION OF "LES TRANSFORMATIONS DU MONDE ANIMAL"

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CONTENTS

BOOK II

THE TRANSFORMIST HYPOTHESIS

CHAPTER IV

CHAPTER V

CHAPTER VI

CHAPTER VII

CHAPTER VIII

BOOK III

EVOLUTIONARY IDEAS IN PALÆONTOLOGY

PART II

THE LAWS OF PALÆONTOLOGY

CHAPTER XIII

BOOK IV

THE VARIATION OF SPECIES IN SPACE AND TIME

CHAPTER XIV

CHAPTER XV

CHAPTER XVI

CHAPTER XVII

CHAPTER XVIII

BOOK V

THE CAUSES OF THE EXTINCTION OF SPECIES

CHAPTER XIX

CHAPTER XX

CHAPTER XXI

BOOK VII

THE ACTION OF MIGRATIONS

CHAPTER XXVI

CHAPTER XXVII

BOOK VIII

CHAPTER XXVIII

EDITOR'S PREFACE

THE publication of Darwin's *Origin of Species* worked one of those revolutions in popular thought which occur only at very rare intervals. Up to 1859 both the naturalist—to use a word more common then than now—and the generally well-informed man were usually content to accept the fact that different species of animals and plants existed, without troubling themselves as to how these different species came to be. After that date, and so soon as Darwin's ideas triumphed, as they speedily did, over all opposition, the doctrine of evolution was accepted by every one, and, on its elaboration by Herbert Spencer, came to be recognized as one of the most widely spread of all the laws of nature. Yet the very completeness of the revolution blinded us to many of the points of this doctrine. There were evolutionists before Darwin, and some of these—Lamarck, for instance —had gone even further than he in their researches into the modification of animal forms by their environment, and into the process of geologic changes. Moreover, a great many features in Darwin's picture of the animated world were left by him either entirely blank, or so slightly sketched that they required filling in before even their outlines could be grasped by any one whose attention had not till then been given to their subject. Does the study of fossils, for instance, offer us any example of a regular chain of animal forms showing the gradual transformation of one type into another? Or, is natural selection the only means that Nature employs to produce variations? To such questions the teaching of Darwin, as he left it, hardly suggested an answer.

To give a summary of the views on these and other connected points that have achieved the most success has been the task of M. Depéret, and is one for which he is admirably fitted. In addition to his high academical position, which has given him much insight into the way in which these subjects are regarded by untrained as well as by trained minds, he has himself been an ardent worker in the field of zoological evolution, and his publications on *Les Animaux de Roussillon*, *Le Bassin de Marseille*, and *Les Terrains de la Bresse* are all valuable contributions to the material evidence on which the theory is based. Moreover, he has not gone astray, as have so many German and some

English biologists, after the brilliant paradox of Weismann, which asserts that acquired characters are not and never can be inherited, and as will be seen later (p. 266 *infra*), he classes this with the hypothesis of Nägeli, that every individual is endowed with an innate tendency towards perfection, as theories on which no agreement between naturalists seems even probable. His method, too, as shown in the book of which the following pages are a translation, seems to be not only the best possible, but the only one which can convey to the general reader a fair idea of the problems set before him in a reasonably limited space. In the First Part of the book, he gives a summary of the work of the principal authors of the evolutionist theory, including therein Darwin's precursors as well as his successors, and in the Second Part he deals with the different processes of the variation and the extinction of species, together with the effect of migrations, and the interesting problem of the first appearance of life on our globe. That the work is well abreast of modern research is, I think, evident from the space he devotes to the "saltation" theory of de Vries and Nilsson, and from his remarks on the light likely to be thrown on the earliest forms of life by the exploration of the Polar regions now in progress.

It only remains to be said that the two tables of the Ages of the Earth and the Classification of the Animal Kingdom respectively, have been so bound as to admit of their being left open during the reading of the book, and that my own very few notes may be distinguished from the author's by the signature "Ed."

F. LEGGE.

ROYAL INSTITUTION OF GREAT BRITAIN,
November, 1908.

PART I

THE HISTORICAL DEVELOPMENT OF IDEAS

THE TRANSFORMATIONS OF THE ANIMAL WORLD

BOOK I

THE FIRST PERIODS OF PALÆONTOLOGY

CHAPTER I

EARLY HYPOTHESES

Plastic force—Theories of the Flood—The inventory of fossil remains.

The hypotheses designed to explain the manifold and astounding transformations of the animal kingdom during the various ages of the earth are of a relatively recent date, and could only assume a really scientific form with the aid of the very modern progress of that science dealing with the study of early beings which has received the name of *Palæontology*.

The Greeks and Romans were acquainted, as we see in *Herodotus*, *Strabo*, and *Ovid*, with the presence of shells left by the sea in the interior of continents, but were unable to draw from it any conclusion other than that of the displacement of the foreshore. As to the origin of these shells and petrified fish, they were restricted, like Aristotle, to the notion of a sort of spontaneous hatching of organic beings born in the mud without the aid of parents.

The *Middle Ages* retained the ideas of Aristotle, and almost unanimously adopted the theories of the spontaneous generation of *fossils* or *petrifactions* under varying formulas, such as plastic force, petrifying force, action of the stars, freaks of nature, mineral concretions, carved stones, seminal vapours, and many other analogous theories. These ideas continued to reign almost without opposition till the end of the sixteenth century, notwithstanding the efforts of a few master minds—such as *Leonardo da Vinci*, *Fracastoro*, and *Bernard Palissy*—to attribute petrified shells and the teeth of fishes, or *glossopetræ*, to animals who had lived in the sea at the very place where they were actually observed.

The seventeenth century saw little by little the antiquated theories of plastic force and of carved stones disappear, and the animal or vegetable origin of fossil remains was definitely established. Unfortunately the progress of palæontology was to be retarded for a long space of time by the rise and the success of the *diluvian theories*, which attributed the dispersion of fossils to the universal deluge, and endeavoured to adapt all these facts to the Mosaic records. Such, for instance, was the case with the famous "man, eye-witness to the Deluge," described at Œningen by Jacques Scheuchzer, whose skeleton, now in the museum at Haarlem, is that of a gigantic salamander.

Yet there were, among these partizans of the Flood, a few men of worth, whose principal merit, outside their too frequent extra-scientific speculations, was that they deeply studied fossils and spread the better knowledge of them by exact representations.

This task of the description and illustration of fossil animals, chiefly the marine shells, was especially the work of the scholars of that eighteenth century which was the age of *systematic zoology*. From all quarters they set themselves to gather and collect fossils, to study and describe them by the aid of plates often of great beauty of execution, to which modern palæontologists are still compelled to have recourse. We may quote the names of *Walch*, *Knorr*, and *Klein*, in Germany; of *Born*, in Austria; of *Bourguet* and *Gessner*, in Switzerland; of *Burtin*, in Belgium; of *Faujas-Saint-Fonds*, in Holland; of *Brander* and *Solander*, in England; of *Soldani*, *Poli*, and *Volta*, in Italy; of *Guettard* and of *Bruguières*, in France.

But the naturalists of that epoch lacked one fundamental notion, without which the problems relating to the origin and transformations of living forms could not even be enunciated: this was an exact notion of the species and groups that have *died out* or *disappeared*. These learned observers had doubtless noticed striking differences between the fossil shells of our countries and the living shells of the neighbouring seas; but they could not free themselves from the idea that these fossil species would some day be discovered in a living state in distant seas or in the unexplored depths of our oceans. In vain the mathematical philosopher, *Robert Hooke*, suspected, as early as 1705, the presence of *extinct species* quartered in certain places, and even following one another in a certain chronological order. These ideas, somewhat inexact moreover, could not fructify in a medium still too deficient in the most essential data of stratigraphic geology.

It was only in the second half of the eighteenth century that methods of determining the age of sedimentary soils by means of fossils were able to triumph in geology, under the influence of the remarkable generalizations of *Buffon* in the *Epoques de la Nature,* and still more of the local monographs of *Fuchs* in Thuringia, of *Werner* in Saxony, of *Giraud-Soulavie* in Auvergne, and especially of *William Smith* on the secondary formations of the London basin.

At the dawn of the nineteenth century, the importance of fossils was at last everywhere appreciated at its right value, and their infinitely varied forms became the objects of study to numerous scholars, whose descriptions assumed a new character of exactness, thanks to the definitive adoption of the binominal (i.e. generic name and specific name) Linnæan nomenclature. The hour had at last arrived for the production of the genius-inspired work of Georges Cuvier.

CHAPTER II

GEORGES CUVIER AND LES RÉVOLUTIONS DU GLOBE

Creation of comparative anatomy and palæontology—The gradual perfecting of fossil faunas — The revolutions of the globe — The changes of faunas by migration.

The universal admiration excited in the scientific world by the series of memoirs which G. Cuvier began to publish in 1798, and which were collected in 1812 under the title of *Recherches sur les Ossements Fossiles*, has not diminished in our own days, notwithstanding that more than a century has elapsed. Every naturalist wishing to familiarize himself with the organization of the higher animal world, living or fossil, must, even at the present day, begin his studies by reading this masterly work, in which are set forth, with luminous clearness and precision, the fundamental notions of the two sister sciences—*Comparative Anatomy* and the *Palæontology* of the Vertebrates.

The palæontological researches of Cuvier were at first directed to the bones buried in the gypsum quarries of the hill of Montmartre, and resulted in the reconstitution of a world of extinct animals, of which the *Palæotherium*, the *Anoplotherium*, the *Xiphodon*, the *Dichobunus*, the *Chæropotamus*, and the *Adapis* are the principal representatives. Here we were no longer dealing with marine animals which a lucky cast of the lead might some day bring up from the depths of the seas—as had already happened in the case of the *Pentacrinum* and the *Trigonia*—but with genera and even families of terrestrial mammals entirely different from the existing mammals. The zoological exploration of our continents was complete enough for Cuvier to be able to affirm the unlikelihood of any further discoveries of great living mammals. This presumption has been otherwise verified, with a few rare exceptions, of which the most striking have been the discoveries of the rhinoceros of Java, the white-backed tapir of Sumatra, and—quite recently—the Okapi of the great African equatorial forest.

Not only do the sedimentary layers of the earth's surface contain genera and species of extinct animals, but these vanished populations have been several times renewed. This important conclusion was suggested to Cuvier by the study of the innumerable materials sent by scholars in all countries to the illustrious specialist, as well as by numerous visits to the lands and geological collections of Germany, Belgium, Switzerland, and Italy. After the very remarkable epoch of the gypsum of Montmartre, nearly all the genera of which have vanished, came the epoch of the deposit of alluvial soils, in which predominate the mastodon, the hippopotamus, and the elephant, accompanied by the horse, by various ruminants, and the great carnivora of like stature with the lion, the tiger, and the hyena. But it is a remarkable fact that although most of these genera have continued to exist in our present world, their species, at least, are entirely distinct from the living forms. It is only in the most recent alluvions that we at length find species of animals quite similar to our own.

If, on the other hand, we descend lower into earth's strata, we no longer find mammals, but only oviparous quadrupeds. The chalk contains numerous tortoises, crocodiles, and, at the Mont Saint Pierre in Maestricht, a gigantic marine lizard, the *Mososaurus*. In the ferruginous sands below the Chalk we observe in England, besides the crocodiles and the tortoises, some large reptiles, some carnivorous like the *Megalosaurus*, others herbivorous like Mantell's *Iguanodon*. Still lower down, the compact limestone of the crests of the Jura contains, near Soleure, a considerable number of species of fresh-water tortoises, or *Emydes*. In the Jurassic schist and limestone is found a world of reptiles, of various forms and sometimes of gigantic size—the *Ichthyosauri*, the *Plesiosauri*, gavial-like *Crocodiles*, the remarkable *Megalosaurus*, and the flying lizards or *Pterodactyls*. Still further back, reptiles are again found in the conchiferous limestone of the Muschelkalk of Germany and Lorraine. Finally, it is in the cuprous and bituminous schists of Thuringia that we observe the first trace of oviparous quadrupeds, in the form of reptiles similar to our great *Monitors*, accompanied by fish of an unknown genus.

Thus Cuvier not only showed the presence in the sedimentary strata of a series of terrestrial faunas, superposed and distinct, but he was the first to have, and that very clearly, the notion of the gradual organic improvement in these faunas, from the earliest to the most modern. This is a fundamental idea, the merit of which we are too often apt to forget is due to Cuvier, in view of the excessively severe and often unjust judgments which the partizans of transformism have passed and still pass on "Cuverian ideas" in matters of philosophical palæontology.

But what was, according to Cuvier, the mechanism of these renewals of fauna which he so happily brought to light? The illustrious naturalist sets forth his ideas with his customary clearness in the admirable *Discours sur les Révolutions du Globe,* which forms the introduction to his great work on fossil bones. In his opinion the extinctions of faunas have been at once complete and sudden, and were provoked by violent geological events or revolutions of the globe, largely, but not absolutely, general in character. In favour of this hypothesis, Cuvier adduces numerous facts of a geological order, which, taken separately, and having regard to the documents known at that epoch, are rigorously exact. It is only their relations to each other which have become disputable or even inexact.

The existence of these revolutions of the globe is attested by precise observations, some of which have but a moderate value, such as the preservation in the ice fields of Siberia of the corpses of great quadrupeds, frozen with their skins, their hair, and their flesh intact; or, again, the position of fragments of rocks and stones which have slipped down between the solid strata of the earth's crust.

But, to make up for this, other series of facts reveal in the author most remarkable powers of observation and geological sagacity—we allude to the vertical direction of the sedimentary strata in mountain chains. In the plains these strata are horizontal and almost all filled with innumerable marine products, especially shells, which have passed their existence in the spots in which they are found, these fossil shells denoting important changes both in extent and in position in the basin of the seas. In mountains of the second class the conchological deposits are as rich as those of the plains, but the strata are no longer horizontal; they lie obliquely or even vertically, and their succession is easy to observe in the cuttings of the valleys. Still higher up, towards the summits of the great primitive crests, the remains of animals become more rare, and even vanish altogether; yet the stratification shows that these deposits have also taken place under water, that they have been overturned, upheaved, and again thrown down at a very remote period, and that their summits were already above the water level when their conchological deposits were formed.*

What geologist, however, if imbued with the importance of active causes in geology, would refuse at the present day to consider these upheavals and folds in sedimentary strata as phenomena relatively sudden, as violent crises which have interrupted at various epochs the quiet continuity of the history of the earth?

On the other hand Cuvier saw—less happily, no

* Can we not see in this account a very clear glimpse of the successive phenomena of the wrinkling of the earth's crust and even of the method of determining the age of mountain chains which were shortly afterwards to be exactly set forth in the remarkable researches of Elie de Beaumont in 1829?

doubt—proofs of violent upheavals in the alternations often noticed by him of salt and fresh water deposits, these last, in general, alone containing the bones of terrestrial animals. This repeated alternation implies a displacement of the seas in several directions. "The changes in the height of the waters," he writes, "are not due solely to a withdrawal more or less gradual, and more or less general; successive irruptions and withdrawals [we should nowadays say incursions and retreats of the sea] have taken place, the definite result of which has been, however, a universal lowering of levels." Here, again, the most scrupulous geologist might subscribe to these conclusions, and would have to use almost the same language, while modernizing the expressions.

Finally, from the palæontological point of view, the sudden extinction of faunas was upheld by Cuvier, with the support of proofs unimpeachable in the light of the facts then known. No common genus, no transitional form, connects the mammals of the Paris gypsum with those of the deposits containing mastodons, elephants, and hippopotami which succeeded them after several invasions of the sea; no identical species connects this last fauna to the species in the most recent alluvions or to animals in the present world. The renewal of the faunas might therefore well appear complete, and the eminently positivist mind of G. Cuvier refused to go beyond this rigorous fact to adopt, without material proofs, the transformist speculations of de Maillet or the still very nebulous hypotheses of Lamarck.

As to the process by which this renewal was effected, it has often been made a reproach to Cuvier that he admitted, in its turn, another hypothesis quite as incapable of scientific demonstration as the last, to wit, that of *successive creations*. This, again, is an absolutely unjustifiable criticism. Nowhere in the work of Cuvier is the word " creation " to be met with, and we have only to read attentively the *Discours sur les Révolutions du Globe* to see that in the mind of the illustrious scholar it was simply a question of the *invasions* of new animal forms suddenly arriving from distant and unknown countries. Here the idea is fundamental enough to warrant its quotation : " Moreover, when I maintain," says Cuvier, " that the beds of rock contain the bones of several genera and the friable strata those of several species which no longer exist, *I do not assume that a new creation was necessary to produce the existing species.* I simply say that they did not exist in the same places, and must have come there from elsewhere. Suppose, for instance, that a great irruption of the sea were to cover the continent of New Holland with a mass of sand ; it would bury in it the corpses of kangaroos, phascolomes, dasyures, perameles, flying phalangers, echidnæ, and ornithorhynci, and would entirely destroy the species of all these genera, since none of them exist in other countries.

" Let this same cataclysm turn into dry land the numerous small straits which separate New Holland from the continent of Asia, and it will open up a passage to rhinoceroses, buffaloes, horses, camels, tigers, and all the other Asiatic animals, which will thus people a land where they were until then unknown.

"Now let a naturalist, after studying this animated nature, set to work to search the soil on which it lives, and he will discover in it remains of entirely different beings.

"What, under this supposition, New Holland would be, Europe, Siberia, and a great part of America are in fact; and perhaps it will be found one day, when other countries, including New Holland itself, are examined, that they have all undergone similar revolutions, I might almost say *exchanges of production.* For, let us carry the supposition further: subsequent to this transport of Asiatic animals into New Holland, let us admit a second cataclysm, which should destroy Asia, their primitive country, and we should be as much at a loss to discover whence they came as we can be to find the origin of our own animals" (*Discours Préliminaire*, 1812, p. 81).

The reader will no doubt kindly excuse the length of this extract, which is of considerable interest. It gives evidence that to Cuvier must be ascribed the honour of having stated with admirable clearness and exactness the highly important and fruitful hypothesis of the *renewal of faunas by migration.*

Thus the ideas of Cuvier on the transformations of the terrestrial faunas in geological times may be summed up in the following points: (1) successive faunas are entirely or almost entirely different from one another; (2) their extinction results from sudden revolutions, that is to say, subsidences of the earth's crust, followed by invasions by the sea of continents once dry; (3) other revolutions resulting in the upheaval of mountain chains have again cast back the waters and allowed, on the foundation of the dried bottom of the sea, the constitution of continental soils favourable to the expansion of new terrestrial faunas; (4) these new faunas are not created on the spot, but come from distant regions, their migration from which has become possible owing to temporary bridges between continents.

Without doubt geologists and palæontologists could not accept the whole of these propositions without important reservations. It would seem difficult for us at the present day, to admit for instance the rapid destruction of terrestrial animals by an incursion of the sea. The advances of the sea appear to us rather as phenomena so relatively slow and localized that it must always have been possible for the inhabitants of districts threatened by the sea to escape and to carry on in safer quarters the peaceful continuity of their evolution.

No doubt also the influence which the upheavals of mountain chains may have had on the retreats and incursions of the sea may be questioned, and is much disputed even nowadays. But none can deny the paramount importance of migrations in the changes of faunas, the repeated exchanges between the populations of terrestrial animals passing from one continent to another, the intermittent connections established or destroyed by the phenomena of the retreat or incursion of the sea, of the splitting up, the subsidence, and the wrinkling of the earth's crust—phenomena to which it seems to some at least, difficult to refuse that character of sudden occurrences, or true revolutions of the globe—which so greatly impressed the mind of the illustrious creator of palæontology.

CHAPTER III

THE THEORY OF SUCCESSIVE CREATIONS

Alcide d'Orbigny, d'Archiac, and Agassiz—The catalogue of fossil beings—The extinction and the sudden appearance of species.

THE researches of Cuvier had been almost exclusively directed to vertebrate animals; but while his fine work was proceeding, other palæontologists—such as Lamarck, Bruguières, A. Brongniart, d'Orbigny, Deshayes, and Marcel de Serres, in France; Von Schlotheim, Leopold de Buch, Zieten, Reinecke, and Goldfuss, in Germany; Parkinson, Brander, Mantill, and Sowerby, in England; Eichwald, in Russia; Nillson, in Sweden; Brocchi, Cortesi, and Fortis, in Italy—to quote only the earliest names—were actively drawing up an inventory of marine fossils, such as molluscs, echinoderms, polyps, bryozoa [sea mosses], and foraminifera, from that time indisputably recognized as extinct species characteristic of the geological horizons in which they are found. In the first half of the nineteenth century we witness the brilliant expansion of stratigraphic palæontology, which was soon to take a synthetic form in the *Index Palæontologelicus* of Bronn (1848), in which the species are catalogued in geological order, and in the *Prodrome de Paléontologie Stratigraphique* of Alcide d'Orbigny (1850). This last work contains an orderly enumeration of eighteen thousand species of fossil invertebrates, arranged in the chronological order of their appearance during the twenty-seven successive stages which, according to the author, constitute the sedimentary crust of the earth. From the whole of this immense work there breathed into the minds of nearly all the palæontologists of that epoch—and among them may be cited the illustrious names of Agassiz and d'Archiac—the most striking confirmation of the theories of Cuvier on the fixity of species and the almost complete renewal of successive faunas. Alcide d'Orbigny again proclaimed himself, in 1849, in his *Cours élémentaire de Paléontologie Stratigraphique*, the convinced champion of Cuvier's ideas by pushing them far beyond the limits acknowledged by the master. The theories of d'Orbigny may be summed up as follows : From the first to the latest epoch of the animated world we see appear at all points of it, at one and the same time, a great multitude of different species belonging to all branches of the animal kingdom, of which there are no signs in the preceding periods.

" The first creation shows itself in the Silurian stage. After its annihilation through some geological cause or other, a second creation took place a considerable time after in the Devonian stage, and, twenty-seven times in succession, *distinct creations* have come to repeople the whole earth with its plants and animals after each of the geological disturbances which destroyed everything in living nature. Such is the fact, certain but incomprehensible, which we confine ourselves to stating, without endeavouring to solve the superhuman mystery which envelops it" (*Cours élémentaire*, t. II., p. 251).

Thus two points are, in d'Orbigny's mind, absolutely certain: on the one hand, the creation of complete faunas at one swoop—an opinion never formulated by Cuvier; on the other hand, the sudden disappearance of each of these faunas. As regards the first of these great facts, the learned palæontologist does not, as we have seen above, attempt the slightest scientific explanation. As to the disappearance of faunas, he, on the other hand, discusses the probable causes, and puts aside as wholly insufficient the biological or climatological changes at various epochs in the existence of the earth. There only remains, as an explanation of the annihilation of all the beings which have twenty-seven times succeeded one another on the globe, the effects of geological disturbances, or powerful dislocations of the earth's crust bringing about a great displacement of the seas, which must have reacted at once on both terrestrial and marine animals. This, as will be seen, is an almost integral reproduction of the *Révolutions du Globe* of Cuvier with a still wider generalization.

My readers will no doubt ask themselves what powerful motives, drawn from observed facts, can have brought about so clear and so deep a conviction in the mind of an eminent naturalist like Alcide d'Orbigny, who was also a sagacious and strict observer of the relations and differences between fossil species, and an indefatigable traveller who had studied on the spot the conditions of the fossil deposits of most countries in Europe, and even of the far-off regions of South America. D'Orbigny has been very careful to thus set forth his reasons himself.

Each of the stages which follow one another in the geological series possesses its own particular fauna, distinct from that of the stages which precede or follow it ; and these different faunas are in no way linked by forms passing from one to the other, nor by gradual replacement of one by the other, but always by sudden extinction. The fauna of one stage stop at the late strata of that stage, and at the first strata of the following stage animals quite different from the first appear and constitute a new fauna. The number of fossil species which pass from one stage to another is exceedingly restricted, and in Jurassic and Cretaceous soils—the more special object of d'Orbigny's studies—this proportion does not reach one per cent. These rare species, common to two or three stages, must have passed over the borders, either very accidentally when in the living state, or more often in the condition of dead shells. Shells provided with air chambers, and therefore light—such as those of the cephalopods—were better able than others to float after the death of the animal, and to mix with the littoral fauna of the following stage.

These various propositions, notwithstanding the strict and almost mathematical form given to them by d'Orbigny, are yet far from offering so absolute a character of certainty as he wished. The reason is that they depend to a great extent on the wholly personal and therefore somewhat arbitrary appreciation which every naturalist makes of the limit of a species and its degree of variation. When d'Orbigny speaks of species which, in an exceptional state, pass through several geological stages, we are rarely dealing with forms entirely identical at these various levels. An attentive observer will nearly always be able to perceive between these successive forms of the same type appreciable variations either in the size or the shape of the shell, or in the details of its markings—slight, but constant, variations, no doubt, which are sufficient to enable a practised eye to recognize with every assurance the precise level from which this variety comes, or as we now say, following Waagen, this stratigraphic *mutation*.

When, on the other hand, d'Orbigny separates under two distinct names two forms of the same genus belonging to two successive geological stages, it must not be thought that it is always a question of considerable differences which force upon the mind the idea of a distinct origin. In certain zoological groups, of which the analytical study has been carried especially far—in the shells of Ammonites, for example—ribs more or less fine or more or less numerous, more or less sinuous or more or less bent inwards, spiral coils more or less close, suffice to enable palæontologists, even d'Orbigny himself, to separate two species, because this distinction often has a great interest for the characteristics of two stratigraphic zones. From this point of view certain genera of molluscs—for example, the *Perisphinctæ* or the *Hoplites* among the Ammonites, the *Trigoniæ* among the Lamellibranchs, and most kinds of sea-urchins—have been literally *pulverized* by describers of species. It would be an exaggeration to claim that differences such as these are fundamental and exclude all links of relationship between these forms. It may even be said that this want of exactness, this absence of a criterion for the limits of the species, this multitude of regional or stratigraphic variations raised by some to the dignity of species, but regarded by others as simple varieties of one specific type, constitute at the present day the strongest argument in favour of the transformist hypothesis in palæontology.

But, after making these reservations against the too absolute ideas of d'Orbigny, the observations of this scholar remain none the less exact in their broad lines, and the sudden replacing of marine faunas when passing from one stage to another, or even from one zone to another zone, must be considered almost a general rule. If the explanation of this great fact by means of *successive creations* cannot satisfy us from a scientific point of view, we shall have, later on, to seek for it a rational interpretation in the phenomena of the *migration of faunas* or of *migration of environments*, similar to those which Cuvier had already made so evident with regard to terrestrial animals.

BOOK II

THE TRANSFORMIST HYPOTHESIS

CHAPTER IV

THE FORERUNNERS AND FOUNDERS OF TRANSFORMISM

The Forerunners: Buffon, Goethe, and Oken—*The Founders of Transformism:* Lamarck, Etienne Geoffroy-Saint-Hilaire, and Charles Darwin.

§ 1. *The Forerunners:* BUFFON, GOETHE, AND OKEN. —Two hypotheses only can be imagined which explain the manifold changes of living forms which we notice from the appearance of life on our globe down to the fauna of the present day. These are, the hypothesis of independent creations for each species, and that of the connection of animal forms with each other by descent or gradual transformations. It is therefore not astonishing to see the transformist hypothesis appear at an early epoch in the mind of man, if not in the form of a veritable scientific theory, at least in that of a more or less vague philosophical conception. It has thus been possible, by giving a certain elasticity to the texts, to discover the forerunners of Darwin among the Greek and Latin philosophers—*Anaximander*, *Empedocles*, and *Lucretius ;* but the idea of evolution is there so hidden in the midst of a shapeless mass of beliefs in spontaneous generation, in the creative powers of terrestrial mud, and in the birth of monstrous and chimerical beings, that it would be better to abstain from drawing from oblivion these works of pure imagination.

We ought to be nearly as severe with the naturalist philosophers of the Renaissance and of the eighteenth century—*Bacon*, *Pascal*, *Charles Bonnet*, *Maillet*, *Maupertuis*, and *Kant*, with whom the transformist idea vaguely disentangles itself from the conceptions relating to the spontaneous apparition of germs or of animal species.

Oken, *Goethe*, and *Buffon* bring to the study of the transformation of living beings their solid qualities of observers of nature, and lead the question into a more precise and fruitful path. *Goethe*, following *Oken*, dwells on the repetition and on the metamorphosis of organs. Among vegetables the leaf transforms itself into the coverings and organs of the flower; in the higher animals the spine becomes modified, and enlarges so as to form the cranium. The primitive forms of animals and of plants thus become, little by little, more complicated by the repetition and differentiation of like parts. *Buffon* already held very exact notions on the succession of beings at the various *Epoques de la Nature*, the title of one of his most important works.

The early seas nourished numerous forms of molluscs, crustaceans, and fishes of a type now vanished. These animal forms have been again and again renewed, some becoming more perfect, others degenerating; these last, being less perfect and less active, have yielded to the first-named, and have either disappeared, or will do so in time. We here for the first time find a fairly clear conception of the *struggle for life* to which the works of Charles Darwin were a little later to claim in such a masterly manner the attention of the world of scholars.

§ 2. *The Founders of Transformism:* LAMARCK, ETIENNE GEOFFROY-SAINT-HILAIRE, AND DARWIN.—Everything has long since been said on the works of the illustrious founders of transformism—Lamarck, Geoffroy-Saint-Hilaire, and Darwin. Many scholars * have set forth and discussed at length their conceptions, which, moreover, differ much from each other, on the mechanism and the processes of evolution of living beings. Among these are the influence of the *wants* and *habits* on the development, or, on the contrary, as Lamarck said, on the atrophy of the organs; the direct action of the surrounding media, as noted by Geoffroy-Saint-Hilaire; and the *struggle for life*, and, as a consequence, *natural selection* complicated by sexual selection, as set forth by Darwin. At the present day, biologists are still arguing as to the comparative value and importance of these different causes which modify living beings, and it certainly seems to result from these discussions that if some of them appear to exercise a partial influence on the phenomena of morphological evolution, none of them yet suffices to give a satisfactory and

* Two very interesting works may be consulted on this subject: *Le Transformisme* (1888) and *La Philosophie Zoologique avant Darwin* (1884); both by M. Edmond Perrier.

definitive solution of this complex and enthralling problem.

It does not come within the scope of this work to study in detail the physiological aspect of the transformist hypothesis, and we shall only incidentally touch upon the discussion of those biological arguments which constitute the fundamental, and often the exclusive part of the works of Lamarck, Geoffroy-Saint-Hilaire, and Darwin. On the contrary, we shall examine carefully that which may be called the historical side of the labours of these scholars, that is to say, the *synthetical essays* sketched out by these illustrious zoologists for the purpose of constructing, from the documents supplied by living and fossil animals, the early pedigrees of the beings which have peopled the earth. These important questions, which should be the definite conclusion, and, so to speak, the proof of the transformist hypothesis, have too often been left in the background by the commentators of Lamarck and Darwin. Perhaps many readers of this work will experience some surprise when noting, with precise documents before them, if not an absolute void, at least an extreme weakness in the attempts made on these lines by the illustrious founders of Transformism.

CHAPTER V

LAMARCK AND LAMARCKISM

Zoological philosophy—Spontaneous generation of germs—Plan of pre-existing progression—Influence of wants and habits—First attempt at a genealogy of beings.

No one could refuse to Lamarck the glory of having been the first to gather together in a really scientific and doctrinal form the scattered hypotheses then current, concerning the *variability of species* and the transition from one animated form to another through gradual modifications. But after rendering to the learned classifier of the *Animaux sans vertèbres* the just tribute of admiration due to him, it is easy to explain to oneself at once the trifling success of works such as the *Philosophie Zoologique* and the slight influence they exerted on the minds of contemporary naturalists. A cumbrous and diffuse style sometimes barely intelligible, incessant and useless repetitions, a dogmatic exposition too rarely illustrated by concrete examples briefly quoted and often ill-chosen, and endless digressions into the domain of physics, render the reading of Lamarck's philosophical works at once arduous and of little profit to the naturalist. The contrast is striking with the concise and exact documentation of the works of Georges Cuvier, the contemporary and colleague of Lamarck in another chair of the Paris Museum, who was, besides, the determined champion of the fixity of species. There is therefore nothing surprising in the fact that Cuvier never even deigned to discuss seriously the ideas of Lamarck, while he waged with his other colleague, Etienne Geoffroy-Saint-Hilaire, a resounding polemic which excited the whole of scientific Europe.

We can sum up in a few simple and fundamental propositions the broad lines of the Lamarckian philosophy :—

1. Nature herself creates by means of direct or spontaneous generation, the first traces of life in *gelatinous* masses for animals and in *mucilaginous* ones in the case of vegetables, into which masses penetrate subtle fluids, particularly abundant in warm and moist places. These fluids, by enlarging the interstices of the gelatinous mass, transform it into cellular tissue, and render it fit for the phenomena of life.

2. Living beings have formed, since their first appearance on this globe, several co-ordinate series which have developed from the simple to the most complex forms, and realize the various phases of a *pre-existing plan* made by the supreme Author of all things.

3. The development of this plan of progression is hindered by external circumstances, which give to animals certain wants and, later, certain habits. These necessitate the more frequent use of this or that organ, which develops and enlarges it, while disuse diminishes and finally causes it to disappear.

4. It follows that external circumstances influence the form and organization of animals.

These modifications are transmitted by generation and retained by heredity so long as new wants do not intervene.

Such is the theoretical and by far the most seductive side of the philosophical work of Lamarck. Let us now see how the learned naturalist of the Museum succeeded in applying these principles to the history of the development of the animated world.

Although Lamarck was acquainted with and has described many species of fossil invertebrates, he ventured seldom and seemingly against his will into the field of philosophical Palæontology. It was still a question for him whether, in view of the means taken by nature to assure the preservation of species, entire races could have been annihilated or lost. The extinction of species only seems to him admissible so far as regards the great terrestrial animals, and to be then only due to the active intervention of man. Nor did it seem to him impossible that we might some day, in some unexplored part of our planet, discover *species termed extinct,* and even the Palæotherium, the Anoplotherium, the Megatherium, and the Mastodon of Cuvier.

If the ideas of Lamarck are thus very belated compared with those of Cuvier as regards the succession of faunas through the geological ages, on the other hand he protests with much justice against the idea of *universal catastrophes* having annihilated the majority of species over the whole surface of the globe. Nature only shows us local catastrophes, such as volcanic eruptions, earthquakes, etc., whose actions, however energetic, are always limited, and do not stop the general march, slow and progressive as it is, of natural phenomena. It is thus permissible to consider Lamarck as a forerunner of the school of *existing causes* in geology.

Lamarck, as we have already said, did not make any use of or draw any argument from fossil animals in support of his theoretical conceptions on the evolution of beings ; but he had the merit of being, without doubt, the first of all naturalists of his time to attempt the construction, in the final chapter of his *La Philosophie Zoologique*, of a *genealogical table* of animal forms, from the most primitive types to the Mammals, man being excluded.

This genealogical tree of Lamarck is *diphyletic*, that is to say, composed of two branches which very early diverge. Life appeared in the bosom of the waters (which is nearly in conformity with the existing hypotheses), or at least in very moist places.

The initial gelatinous matter commenced by creating a first branch, which starts with the infusoria and by way of the polyps passes into the *Radiaries* or *Radiated* animals.

The second branch took their rise in the bodies of other animals, especially in the form of *intestinal worms* and of *parasites ;* then some of the aquatic worms, such as the *Gordians*, became *accustomed to exposure to the air*, and gave us the gnats, Ephemerides and other *insects*. Amongst these, some, by solitary or concealed habits of life, produced the *Arachnidæ*. These last again took to the water and brought about, by the intermediary of the Scolopendra, the Iuli, and the Cloports, the formation of the great group of *Crustacea*.*

The other worms, retaining aquatic habits, gave the *Annelides*, the *Cirripedes*, and finally the *Molluscs*.

As to the first vertebrates, notwithstanding the considerable *hiatus* between them and other animals, Lamarck does not hesitate to connect them with the molluscs, first under the form of the Fishes, which afterwards served to form the Batrachians and the Reptiles. It is seemingly from these last, that by two distinct branches, the higher vertebrates are derived: the first branch leads from the *Chelonians* to the *Birds*, and perhaps through the Penguins and Wingless Birds to the *Monotreme mammals* (Ornithorhyncus); the second branch of the Reptiles leads through the *Saurians* and *Crocodiles* to the Amphibious Mammals. These last are the source whence *all other mammals have derived their origin*. The Amphibious Mammals have, for this purpose, become divided into three branches: one, remaining marine, the *Cetacea*; the second, of littoral and herbivorous habits, has developed into the *Ungulates*; while the third with carnivorous feeding became the *Unguiculates*. As

* For the benefit of those unacquainted with zoological divisions, it may be said that the commonest example of the Arachnidæ is the *spider*, while the animals that the author calls Iuli and Cloports are the myriapods or animals which have no separate abdomen, properly so-called, but bear a pair of legs under each segment of the body, like the common centipede. So the commonest example of the Crustacea or shellfish is the crab. It will of course be plain from what follows that this order of development is not accepted by later naturalists.—ED.

for *Man,* he occupies a special place and *his origin is different.*

I have thought it right to quote in some detail this first genealogical essay of Lamarck, an essay in which every reader, however little familiar with the operations of nature, will already have perceived that nearly all the links accepted by the author are inexact, superficial, and contradicted by all embryological and palæontological data. How can Lamarck, well acquainted as he was with invertebrate animals, on simple considerations of *habitat* have connected insects with intestinal worms, caused the Crustacea to be derived from the Arachnids, and the latter from the Insects, contrary to the geological order of appearance of all these groups? How can he have conceived for the Vertebrates such monstrous pedigrees as those which allow him to derive the Fishes from the Molluscs, and the Birds from the Tortoises, and to take certain marine Mammals, which are of relatively recent date, for the founders of all terrestrial Mammals? Such conceptions are really disconcerting on the part of such an eminent observer as Lamarck, and can hardly be explained otherwise than by an immoderate desire to construct in great haste, even at the cost of error, a grandiose synthesis of the whole animal kingdom. Too many examples of such hasty and generally false syntheses will reveal themselves to us as we pursue the history of palæontological doctrines down to the present time.

CHAPTER VI

ETIENNE GEOFFROY-SAINT-HILAIRE

Direct action of the environment—Hypothesis of sudden variations—Phenomena of arrested development.

LIKE his colleague at the Jardin des Plantes, Etienne Geoffroy-Saint-Hilaire was a convinced transformist. As regards the mechanism of evolution it may be said that his ideas only differ from those of Lamarck by a few tones. Like Lamarck, he admits the unity of a pre-established plan, the realization of which takes place partly under the influence of wants and habits, but still more under the *direct action of the surroundings,* among which Geoffroy considers as the most important: the cooling of the earth, and still more the gradual diminution of the quantity of oxygen contained in the air. Thence comes the preponderating influence which this scholar is led to attribute to modifications of the act of respiration.

But Geoffroy-Saint-Hilaire remained, even more than Lamarck, a stranger to palæontology, and to the real genealogical history of living beings, a fact which prevents us from dwelling much on his works. On the other hand it is interesting to point out in his work two ideas personal to himself, and both destined to be developed later in the history of the transformist doctrines. There are, first, the *hypothesis of sudden variations,* substituted for that of the *slow transformations* admitted by Lamarck and Darwin. On this hypothesis, the rapid changes of the surrounding medium act by preference on the embryo, and determine a somewhat sudden production of new forms, just as monsters are experimentally produced by placing embryos in abnormal conditions of development. These new species, once formed, will be preserved by the laws of heredity. This hypothesis, the paternity of which incontestably belongs to Geoffroy-Saint-Hilaire, has reappeared on several occasions in science under the name of *saltation*, and has received in these latter days a new form and actuality from the curious botanical observations of M. Hugo de Vries. We shall have to discuss it later on from the palæontological point of view.

More important still from its theoretical and practical consequences is the idea of which Geoffroy-Saint-Hilaire had a glimpse from the comparison of the adult state of inferior animals with the embryonic stages of animals in higher stages of organization. The inferior animals thus appear as if they had been struck by an arrest of development in the realization of their initial plan. It is doubtless allowable to see in these ideas of Geoffroy-Saint-Hilaire the germ of the theories of parallelism between *individual embryological development and the palæontological evolution of the same animal form*, a fruitful theory if not carried too far, and of which we shall have to show some happy applications to the history of several groups of fossil animals.

CHAPTER VII

CHARLES DARWIN AND DARWINISM

The *Origin of Species*—Darwinian Selection—The gaps in Palæontology—The *Descent of Man*.

THE transformist ideas of Lamarck and of Geoffroy-Saint-Hilaire found but a very feeble echo among contemporary naturalists. They succumbed for the moment—in France especially—to the preponderating and somewhat masterful influence of Georges Cuvier and his school. It is with great difficulty that we find, during the period of forty years that elapsed between Lamarck and Darwin, a few scattered naturalists giving vent, more or less vaguely, to transformist opinions. Such were Herbert, Rafinesque, Naudin, and Hooker, in botany; Grant, Haldemann, Schaffhausen, Isidore, Geoffroy-Saint-Hilaire, and Wallace, in zoology; and d'Omalius d'Halloy and Keyserling, among geologists. When Charles Darwin's work on the *Origin of Species* appeared in 1859, this event, which marks a memorable date in the history of natural sciences, might be regarded as a veritable revelation.

Darwin's work is too well known to need being set forth here at any length. It is enough to remember that the master idea of the learned English zoologist was to apply to *natural evolution* the processes of artificial selection effected by English breeders for the production of numerous varieties —subsequently becoming fixed by heredity—among the races of domestic animals, such as pigeons, cattle, pigs, horses, dogs, etc. In nature a *natural selection* would occur, much more slowly, no doubt, among animals in a wild state, and under the exclusive influence of the *struggle for life* would bring about the extinction of the forms less fitted to maintain this struggle, and, at the same time, the survival of such new variations as were more adapted to the surrounding conditions. By the side of this principal factor in evolution other causes—such as the influence of habits, or the more direct one of the environment—act only a subordinate part not easy to define.

Darwinism may with good reason be taxed with being in this respect too exclusive, and with rather misunderstanding the importance of the transforming influences brought to light by the French scholars Lamarck and Geoffroy-Saint-Hilaire, whose works we have just analyzed. The *Struggle for Life* of Darwin, very attractive as an explanation of the extinction of species, and even of the disappearance of intermediate varieties, takes no account of the production of new variations—so little, indeed, that Darwin is compelled to relegate this point to simple chance, that is to say, to the unknown.

On the other hand Darwin's work is much more exact, and especially much better supported by proofs, than those of his predecessors. Endowed with a marvellously observant mind, which extensive travel had early sharpened and developed, ready to grasp and set forth clearly the complicated relations of biology and of the manners of plants and animals, and powerfully assisted by an almost universal erudition, the illustrious English naturalist was able to use in defence of the transformist theory a force of demonstration which was lacking to his predecessors, and could not fail to obtain in a short space of time the adhesion of the majority of biologists.

But it is important to notice that Darwin was very little of a palæontologist. The only fossil animals he had personally studied, and that with a very real talent—the *Cirripedes* Anatifa, Balana, and Coronula—form a group degraded in their adult state by fixation or parasitism, and but little fitted on that account to make any interesting contribution to the history of evolution. Darwin also approached only with extreme diffidence the palæontological, but most important side of the transformist hypothesis; yet his vast erudition enabled him to appreciate at its just value the weight of the objections raised against this theory by men of such authority as E. Forbes, Woodward, Murchison, Sedgwick, Pictet, Agassiz, Barrande, d'Archiac, and many other determined partizans of the fixity of species, and of the integral renewal of the fossil faunas. Compelled to answer these objections of fact, Darwin could only combat them by theoretical arguments, often of mediocre value, but always ingenious.

If we so rarely observe, he replies, in the layers of the earth's crust, the innumerable intermediate forms required by the transformist theory, it is because these forms have only been able to be reproduced in very restricted regions, and have had also to disappear rapidly through the competition of varieties better endowed with the means of supporting the struggle and more capable of spreading by migrations over vast surfaces of the globe. On the other hand, the continuity, necessary in the transformist hypothesis, of animal forms slowly modified from one stage to the other, is found to be interrupted by the inevitable *lacunæ* which the order of sedimentary deposits implies and the importance of which it is still difficult to appreciate.

Lastly, and above all other arguments, Darwin pleads the evident penury of palæontological proofs. Of the whole surface of the globe, Europe and part of North America alone could be assumed, in Darwin's time, to have been sufficiently examined to have yielded a good part of the archives buried under the soil. What may we not expect from the future exploration of the immense territories of Central Asia, Africa, Australia, and South America ?

All this reasoning, correct as it is to a certain extent, cannot, however, take the place of the necessary checking of the transformist theory by facts, that is to say, by the exact and real reconstitution of the series of forms through which, during the long series of geological ages, each of the existing types of living beings must have passed. Darwin never dared to undertake this work of the reconstruction of pedigrees, with one exception, which is that relating to the *descent of man.*

This burning question of the origin of man was too often made an objection to Darwin, either by naturalists or, oftener, by philosophers and the followers of method, for the author of the *Origin of Species* to leave the objection without a decisive answer. And it is, perhaps, in this response that that contrast most clearly stands out which characterizes on so many points the work of Darwin. On the one hand we have his admirable ingenuity in his comparative studies of the anatomical, intellectual, and psychical characters of man and of animals; on the other, the really deceptive weakness of the positive arguments and the precise facts relative to the *real* reconstitution of the human branch. Let us, together with the author under discussion, cast a rapid glance on the principal stages of this history.

The numerous facts of the material and moral resemblance between man and animals, studied at length in the *Descent of Man*, show in the clearest manner, says the author, that man descends from an *inferior type.* In spite of the remarkable development of his brain and the richness of his mental faculties, man cannot claim that he forms by himself a special *kingdom*, or, as Owen maintained, a sub-class of the Mammals, or even an *order* of this class, or order of Bimana, as Blumenbach and Cuvier proposed. Linnæus was right in bringing man with the Quadrumana into the single order of Primates. Huxley divided the Primates into three sub-orders: *Man*, the *Apes*, and the *Lemurs*. But this sub-order is still too high in rank for man, who, from a genealogical point of view, should at the most represent a family or, even better, a simple sub-family of the Primates.

The *Apes*, or *Simiadæ*, comprise two groups, the apes of the old world (*Catarrhine* group), and those of the new world (*Platyrhine* group, distinct from the first one by the large and flattened nose, and by an extra premolar to each jaw). By his dentition, reduced to thirty-two teeth, and by the conformation of his nostrils, man belongs to the first group; it cannot be denied that he is a descendant of the Simian stock of the old world.

In this group itself, the Anthropomorphous * Apes—the Gorilla, Chimpanzee, Orang-outang, and Gibbon—form a natural sub-group, which man resembles by certain traits, such as the absence of callosities and tail, and by his general appearance. We may conclude from this that Man owes his origin to some early member of the sub-group of the Anthropomorphs. This ancestor probably lived on the African continent, the native place of the Gorilla and the Chimpanzee, and his divergence from the Catarrhine stocks goes very far back, perhaps to an epoch as far off as the Eocene period. The absence of intermediate forms cannot surprise us, in view of the very first principles of the theory of natural selection, and, on the other hand, of the backward or almost negative state of geological researches in those tropical regions where man could have been born.

All this we easily see is only hypotheses and probabilities, some of which at least seem inexact in the actual state of our knowledge. For example, the African origin of man and the throwing back to the Eocene period of the first progenitor of the

* The corresponding phrase used by English zoologists is of course "Anthropoid" Apes.—Ed.

human branch. We shall see that the search for the lower steps of the genealogy of man will show themselves still more nebulous.

Below the Apes Darwin goes to the group of Pseudo-apes or Lemurs. For what reason? Simply because these animals are lower in the scale than the true Apes, because they are geologically earlier, and finally because they form a diversified group leading by an insensible incline to the lowest placental mammals, who are also the smallest and the least intelligent.

Considerations similar to the preceding bring Darwin down to the *Marsupia*, then to the *Monotremata*, and through these latter to the *Reptiles*, without our being able to discover in all this exposition any attempt, however rudimentary, to state precisely the fossil genera through which this lengthy genealogy must have passed.

Coming still lower down in the scale of beings, Darwin recognizes that the five great classes of vertebrates—Mammals, Birds, Reptiles, Amphibians, and Fishes—descend from one prototype, seeing that all animals comprised in these classes possess, especially during the embryonic state, a large number of common characteristics. All vertebrates must descend from some pisciform stock, which has passed through stages similar to that of the *Lepidosiren*, of the *Ganoïd Fishes*, and lower still of the *Amphioxus*. From this last, the lowest in the scale of all existing vertebrates, and entirely deprived of a cerebral bulb, he passes, following the researches of Goodsir, to the larvæ of the *Ascidians*—furnished with the rudiment of a spinal cord—that is to say, to the *Marine Worms*.

It is into these really rudimentary sketches, borrowed, moreover, from the researches of Huxley, Kowalevsky, and Goodsir, that Darwin's sole attempt to reconstruct the genealogy of one branch of living beings resolves itself. Am I too severe in concluding that, palæontologically at least, the question of the *Origin of Species* remains unsolved ?

CHAPTER VIII

ERNST HEINRICH HAECKEL: THE EMBRYOGENIC METHOD

The *History of Creation*—Parallelism of Ontogeny and Phylogeny—Stages of the embryonic development—Study and criticism of the phylogenical essays of Haeckel—Human genealogy—The crisis of transformism.

THE transformist ideas so brilliantly set forth by Charles Darwin were still to remain a long time without echo among the French naturalists, enamoured, almost without exception, of Cuverian ideas. As a compensation Darwin found immediately in England, and still more in Germany, a very favourable scientific public, and even a certain number of passionate adepts. One of the most enthusiastic among these fervent propagators of the Darwinian doctrine was Professor Ernst Haeckel, of the University of Iena. In his renowned works, *Generelle Morphologie*, and *Naturliche Schöpfungsgeschichte*,* Haeckel analyses all the consequences of the transformist hypothesis, and, like Darwin, studies them exclusively as a zoologist to whom the domain of palæontology is closed, or at least very unfamiliar.

Haeckel's method is essentially an embryogenical or ontogenical one, to use this scholar's neologism.

* This last has been translated into English and revised by Professor Ray Lankester as the *History of Creation* (2 vols., Kegan Paul and Co., 1899).

It reposes on the important law of which Geoffroy-Saint-Hilaire, Serres, and Müller had already obtained glimpses, and which was appealed to over and over again by Darwin—which law may be formulated in the following terms : *the embryogenical development of an actual living being is a brief abstract of the phases through which has passed the palæontological development of the group to which the species under examination belongs.* In other words, adopting the language of Haeckel, "*The ontogeny is a repetition, a brief and rapid recapitulation of the phylogeny* conformably to the laws of heredity and adaptation."

This law of the parallelism of phylogeny and of ontogeny, very important from the philosophical point of view, and capable of casting a general light on the researches into the evolution of animals, requires, nevertheless, to be handled with extreme prudence. It could in no case allow us to dispense with the control furnished by *real evolution*, that is to say, by the knowledge of the palæontological documentary evidence. Its too strict and exclusive application could not fail to lead Haeckel into grave errors.

Bolder than Darwin, the learned German zoologist did not hesitate to set about reconstituting by the embryogenic method, the general pedigree of organized beings, animal and vegetable, commencing with the appearance of life on the globe down to the present day. At the head of his system stands a primary and inevitable hypothesis, that of the apparition of the first germ of life by means of spontaneous generation.

This spontaneous production of very simple organisms, formed solely of a homogenous protoplasm, without either nucleus or cellular envelope, such as the existing *Monera*, must have taken place at the inception of evolution on the globe, and as soon as the conditions of life were realized on its surface ; but it must also have continued in later periods, and may still occur before our eyes, although up to now it has not been possible to obtain a strict demonstration of it.

At the base of his genealogical system Haeckel, then, introduces the Monera, associated with a few other low types of a slightly higher organization, such as the Amœbas, the flagellated Infusoria, the Diatoms, the myxomycetous fungi, and the Rhizopods. In the mind of the author all these beings are frankly neither animals nor vegetables, and deserve to form a kingdom apart, under the name of *Protista*.

But it is to the Monera that is more particularly given in Haeckel's system the leading part as starting point in the genealogical tree of living beings. This tree may have been either monophyletic or polyphyletic, according to whether we recognize the primordial existence of monera of a single type or of monera of the three types—animal, vegetable, and neuter. These last are taken as the starting point of the kingdom of Protista. Haeckel leans, however, visibly towards the monophyletic system.

Confining ourselves here to the evolution of the animal kingdom, we see that Haeckel establishes by the method of comparative ontogeny the simple or monophyletic origin of seven principal types of this kingdom. All animals pass, in the course of their embryogenic development, through the following stages :—

1. Cells without nucleus (impregnated egg), corresponding to the type Moneron.

2. Cell with nucleus, represented by the type Amœba.

3. Simple polycellular state or *Morula*, fixed at the present day under the form Synamœba.

4. Cellular flattened mass, or *Planula*.

5. Cellular mass with cavity, or type *Gastrula*. This stage is met with in the ontogeny of all types, from the Sponges, Medusæ, Corals, Worms, Tunicata, and Radiata up to the Molluscs and even to the lower vertebrates. It must have existed at the Laurentian epoch in the shape of an hypothetical animal group, the *Gastreades*.

From this common starting point the evolution of the six higher zoological groups follows a divergent course. The Gastreades first form two branches. In the first the animals attach themselves to the sea-floor and become the root-form of the *Zoophytes*, which are subdivided into Sponges, Polyps, and Medusæ. The second branch retains free power of locomotion and passes into the primitive type of the *Worms*. It is from the four sections of this last group that are derived the two highest animal types—on the one hand the *Echinoderms* and the *Arthropods*, and on the other the *Molluscs* and the *Vertebrates*.

It does not form part of the plan of this work to follow out in all their details the ideas of Haeckel on the special evolution of each of these great types of organization. But on the other hand we must examine with care on what palæontological bases the phylogenic deductions of the learned zoologist of Jena rest.

The group of Protozoa should comprise the most simple as well as the most ancient types of the animal kingdom. Haeckel *supposes* the existence at the Laurentian epoch of types related to the phases *Moneron*, *Morula*, *Planula*, and *Gastrula;* but these are simply visions of the mind. We shall see in the chapter of this book devoted to the beginnings of life on the globe that the only fact of geological observation on which the hypothesis of Haeckel rests—that is to say, the famous *Eozoon canadense* of the Laurentian gneiss of Canada, considered by Dawson and Carpenter as a giant Foraminifer—must be reduced to the condition of a simple mineralogical structure.

The phylogeny of the *Sponges* and of the *Acalephs* or Medusæ is founded, in Haeckel's book, on no documents of a geological order. It is otherwise with the *Polyps* or corals. The *Tetracorals*, or Corals with four radiating walls, represent, according to the author, the ancestral trunk whence started, like two diverging branches, the two legions of the *Hexacorals* and the *Octocorals*, characterized by six and by eight radiating walls. Palæontologically, the Tetracorals did, in fact, precede the other two groups, and are particularly abundant in primeval soils.

The branch or *phylum* of the *Worms* naturally offers us no palæontological support by reason of the soft nature of these animals. Yet it is from the various types of this branch that are derived, according to Haeckel, all the groups of the higher animals.

The *Molluscs* would seem, at first sight, bound to supply us with exact phylogenic documents by reason of the abundance of their *calcareous shells* in all geological strata. But, on the one hand, the shell is a morphological organ of little importance, and on the other, the four great orders of molluscs : the *Brachiopods*, the *Acephala*, the *Gastropods*, the *Cephalopods*, are already entirely differentiated in all their characters from the very lowest strata of the primary era. The evolution of the group is therefore still earlier and the distant ages in which it must have occurred have left us no traces of fossil forms to guide us as to the origin and differentiation of these beings. It may be said, however, that the Brachiopods, which occupy the lowest rank among these orders, swarm in primary times, while the Lamellibranchs and Gastropods must have developed as two diverging branches of types very near, at least, to the present Brachiopods. As to the very much higher group of Cephalopods, comprising Octopods, cuttle fishes, Sepias, and the modern Calamaries, whose apogee goes back to secondary times, they would be derived, according to Haeckel, from the lower branches of the order of Gastropods ; but, on the author's own showing, the transitional forms are palæontologically totally lacking.

The history of the Echinoderms is somewhat better known, thanks to their abundance in most geological strata and to their remarkable individual evolution. The most primitive group is that of the Sea star-fish or *Asterida*, whose rays are not yet fixed at the number of five. Haeckel considers these animals as an assemblage of articulated worms developed by a radiated sprouting round a central worm; but it is now known that this idea rests on palæontological observations recognized as erroneous. Asterida should be derived from Crinoïdea or Sea lilies, through the fixation of an asterid by means of a more or less lengthened stem; some Crinoïdea, such as the Comatula, pass through a second stage, in which they end by breaking away from their stem.

In the other two types of Echinoderms, the *Urchins* and *Holothuriæ*, there are no longer any free arms; these are fixed in a disc, globular in the first named, prolonged in the second. This phylogeny of Haeckel fairly agrees with the palæontological history of the group; yet, in the present state of our knowledge, Crinoïdea are quite as old as Asterida, and are known to occur ever since the Cambrian age. The Echinida and the Holothuriæ are more recent and hardly reveal themselves before the second half of Primary times.

The Arthropods or articulated animals comprise both aquatic types or *Crustacea* and terrestrial types including the *Insects*, *Myriapods*, and *Spiders*. All the first pass through a larval stage, known as *Nauplius*, characterized by rudimentary segmentation and derived, according to Haeckel, from a branch of the articulated worms. But this descent is quite hypothetical, since the most ancient fossil-bearing strata of the globe already contain true marine crustacea belonging to two groups, the Trilobites and the Gigantostraca.

The Arthropods with aerial respiration, descend also, according to the author, either from another branch of the articulated worms, or from a very early bifurcation of the aquatic Arthropod branch. Gegenbaur has endeavoured to show the analogy of the external branchio-tracheas of the larva of the Ephemeridæ and the Libellules with the dorsal branchiæ of certain crustacea and Annelids, the formation of internal tracheas being of recent acquisition. Be this as it may, the high geological antiquity of the Scorpionidæ, which date from the Silurian period, would singularly thrust back the epoch of this hypothetical bifurcation.

Finally, Haeckel reaches the Vertebrates which are, of all geological groups, those which contribute the most exact documents to the evidence of descent. Here again, individual embryology plays a paramount part in the demonstration by showing us in all vertebrates the essentially similar evolutionary stages starting from the ovum and preserving a similitude the more continuous the nearer that these groups are to one another in the natural classification.

The origin of the Vertebrates is made clearer, as Darwin had before pointed out, by the discoveries of Kowalevsky on the unexpected resemblance of the embryology of the *Ascidians* and of the *Amphioxus*, or very low skull-less Vertebrate. The presence of a spinal cord and of a rudimentary marrow in the embryos of the Ascidia enables us to catch a glimpse in the large group of Worms of an hypothetical ancestor common to the Tunicates and to the Vertebrates.

From the *Acranian Vertebrates* may have issued, on the one hand, the class of *Cyclostoms* or lampreys having a circular mouth serving as sucker; on the other that of fish possessing two jaws and two pairs of limbs. The group of *Selachians*, comprising the two types of Dog fish and Skates with cartilaginous frame, may be the most primitive of all and have produced, by bifurcation, on the one hand, the *Ganoïd and Bony Fishes;* on the other, the *Amphibians*, by passing through the *Dipneusta* with duplicate respiration at once branchial and pulmonary. From the group of Fishes may also descend the curious and important group of the swimming Halisaurians, comprising the genera Icthyosaurus and Plesiosaurus, which peopled the seas in the Triassic, Jurassic, and Cretacean epochs.

The Amphibians possessing, in the adult, aerian respiration and pentadactyl limbs gave birth to the higher Vertebrates, characterized by having their embryos enveloped in an amnion or membrane. This evolution must have been produced by two diverging branches, the one terminating in the Reptiles and Birds, the other in the Mammals.

The whole of this genealogy of the Vertebrates by Haeckel is far from indisputable from a palæontological point of view. The Selachians, very common, it is true, in Primary times, are not the earliest Fishes known and are preceded in the lower Silurian by the *armoured Ganoïds* or Placoderms. On the other hand no palæontologist would subscribe without diffidence to the direct linking of the

Ichthyosaurs with the group of Fishes, under the rather superficial pretext of polydactylism. Finally, the existence of a double occipital condyle in the Amphibians and Mammals, as opposed to the single condyle of the Reptiles, appears now to have lost much of the importance formerly attributed to it as a proof of the direct amphibian origin of the Mammals.

But let us return with Haeckel to this last group, the most interesting of all, since it contains the beings highest in organization and, in particular, Man. Our author considers the Mammals as having issued from a group of animals of the Triassic epoch which must have possessed many of the characteristics of the actual *Monotremata*, including the Echidna and the Ornithorhyncus of New Holland. These essential characteristics must have been: the presence of a cloaca, at once the vestibule of the digestive and genito-urinary passages, the welding of the two clavicles into a forked bone and the existence of a well developed coracoid, all equally very early characteristics. But these primitive hypothetical Monotremata must have possessed toothed jaws instead of the horny beak of the only two existing descendants in Australia of this group.

The *Marsupials* or Pouched Mammals would constitute a link between the Monotremes and the higher Mammals or Placentals. This group of Marsupials, still richly represented in Australia and in America, is however in course of vanishing and must have been at its apogee towards the middle of Secondary times. In any case, it is certain that all the known remains of mammals of the Secondary epoch belong either to the Monotremata or to the Marsupials.

These various hypotheses of Haeckel on the relations of these two large groups of mammals are far from being certain palæontologically; it is in no way demonstrated that any of the Triassic Mammals possessed a monotrematic organization and the oldest authentic mammal known, the *Dromatherium sylvestre* of the Trias of Carolina, seems on the contrary to approach more nearly to the Marsupials. It is therefore far below the Trias that we must look for the quite hypothetical monotrematic ancestors of this last group.

As to the higher Placental Mammals, that is, mammals with a complete intra-uterine development, Haeckel assumes them to be derived through one or two branches detached from the stem of the Marsupials at the commencement of Tertiary times. But the Jena professor is himself obliged to acknowledge that palæontological proofs are lacking for the solution of this difficult question. He therefore examines separately the evolution of the two great groups of Placentals.

1. The *Ungulates* with diffused placentas, which are retained—an important ancestral group of animals with manifold branches, from which in later times were detached, through a special adaptation to the environment, the *Cetacea* and the *Edentata*. Haeckel recognizes perfectly the fundamental division of the primitive Ungulates into those with an odd number of toes or *Imparidigitatæ* and Ungulates with an even number or *Paridigitatæ;* but it may be said generally, all attempts to construct

a pedigree of the families or genera are totally erroneous.

2. The *Unguiculates*, with zoned or distoïd placentas, which are not retained. Haeckel assigns to the *Lemurs* or *Prosimians*, the part of the common ancestral type from which have issued all the other orders, such as the Rodents, Cheiroptera, Insectivores, and Apes, with the exception, perhaps, of the Carnivora and the Proboscidians, which would proceed subsequently, the first from the Insectivores, the latter from the Rodents. The Lemurs would themselves descend from the Sarigues, or Marsupials with prehensile fingers. All these genealogical views are extremely superficial and it may even be said, quite inexact, at least as regards most of them.

Haeckel finally arrives, in a chapter which has remained famous, at an examination of the order of Apes, and more particularly of the series of the ancestors of Man, considered as the highest term of this order. The characteristic of this essay in human phylogeny consists in the small number of zoological stages which elapse from the primitive Moneron down to man.

The twenty-two stages of human evolution are as follows:

1. An original *Moneron* stage, that is, of protoplasm without nucleus or cellular membrane.

2. An *Amœba* stage, or single cell with nucleus, clothed with a membrane; this stage corresponds to the egg.

3. A stage of compound Amœba or *Synamœba*, represented to-day by the mass of cells resulting

from the segmentation of the human egg or the form *Morula*.

4. A *Planead* stage, similar to the ciliated larvæ of the Invertebrates and of the *Amphioxus*.

5. A *Gastreada* stage, in which the embryo is hollowed out from a cavity like the *gastrula* of the lower invertebrates.

6. A stage similar to that of the existing *Turbellarian worms*, that is to say, long in shape and without a general cavity of the body.

7. A *Scolecide* stage, differing from the preceding by the presence of a sanguine liquid and of a splanchnic cavity.

8. A *Sack-worm* stage, approaching the existing Tunicates and presenting, like the larvæ of the Ascidia, a rudiment of spinal marrow and of backbone.

9. An *Acranian Vertebrate* stage, of which the existing *Amphioxus* can give us a near idea.

10. A *Monorhinian* stage analogous to the lamprey type, with a rudimentary cranium without jaws.

11. A *Selachian* stage, very like the lower dog fishes of the present time ; the division of the nostrils and the apparition of a frame of jaws and of two pairs of limbs differentiate it from the preceding stage.

12. A *Dipneustal* stage, the first type of pulmonary respiration marking the first step towards the Amphibians. The present *Lepidosiren* gives us an approximate idea of this.

13. A *Sozobranch* stage, with lungs and persistent gills, as in the existing Axolotl; this type is

important from the first appearance here of the division of the extremities into five digits.

14. A *Sozurian* stage, amphibious and losing the gills in the adult state, but retaining the tail like our Salamanders and Tritons.

15. A *Protamniotic* stage, characterized by the disappearance of the gills and the development of an amniotic membrane. This type, entirely hypothetical, is justified by the numerous characteristics common to the Reptiles, Birds, and Mammals.

16. A *Promammalian* stage, an unknown type, no doubt akin to the present Ornithorhyncus and the Echidna, but having toothed jaws.

17. A *Marsupial* stage, superior to the preceding by the division of the cloaca, the formation of breasts and the reduction of the clavicles. The present Sarigues may give an idea of this.

18. A *Prosimian* stage, similar to the short-pawed Lemurians, like the Makis ; they are distinguished from the preceding by the development of a placenta and by the loss of the marsupial pouch, as well as the marsupial bones to support it.

19. A *Monocercal* stage, similar to the long-tailed Apes of the Old Continent, such as the Semnopitheci ; these forms issued from the Prosimians by the transformation of the teeth and the change of the claws into nails.

20. An *Anthropoïd* stage, issued from the preceding by the loss of the tail, of a portion of the hair and by the development of the skull. None of the existing great Anthropoïds exactly represents this vanished type.

21. A Man-Ape stage, hardly differentiated from

Man except by the absence of speech ; it proceeds from the Anthropoïds by becoming habituated to the vertical position and the differentiation of the feet and the hands.

22. This stage leads direct to the *Human* stage.

If these twenty-two stages of the human genealogy of Haeckel are submitted to palæontological checks it must at once be noted that the first nine stages are utterly unknown to us in the fossil state. The tenth, or Monorhine stage, is perhaps represented by some small isolated dental organs, the *Conodontes* of the lower Silurian in Russia, but at the same epoch we already know some veritable Placodermal ganoïd fish in the limestone of Canyon city (Colorado).

No palæontological fact authorizes us to consider the eleventh or Selachian stage as having given birth to the Dipneuston stage, this latter being already clearly characterized as early as the lower Devonian by the genera *Coccosteus* and *Dipterus*.

The fourteenth, or Triton stage, is observed, it is true, in the small Labyrinthodons of the Coal and of the Permian periods, but it is already accompanied by reptilian types of a high organization.

When Haeckel arrives at the fifteenth stage, he finds himself face to face with the difficult problem of the first origin of the Mammal type. He solves it by imagining at one bound two hypothetical types without analogies in the present or in the fossil world, the Protamniotic and the Promammalian. These types are destined to fill the enormous void which separates the lower mammals or Monotremata from the Salamandriform Amphibians to which our author would link them by relying almost entirely on a single characteristic, that of a double occipital condyle opposed to the single occipital condyle of the Reptiles and Birds. The recent tendencies of palæontologists who rather lean towards the Anomodont Reptile group as the origin of the Mammals are totally contrary to this purely theoretical view which at the present day no longer seems to have a single champion.

On arriving at the Mammals, Haeckel finds himself, in appearance at least, on more solid ground, that is to say, in possession of more extensive geological evidence. Few palæontologists, no doubt, will refuse to admit that the primitive Mammals must have passed through the Monotrematic and Marsupial stages before reaching the Placental. This idea is in accord with the fact that all the known Mammals of Secondary times seem really to belong to these two first groups, but it must be acknowledged that notwithstanding all that may have been written on the *submarsupial* characters of the Carnivorous Creodonts of the lower Tertiary, the intermediate types between Marsupials and Placentals, or, if preferred, the primitive types of the Placentals, are still quite unknown to us.

At the base of the placental ancestors of man, Haeckel places the Prosimian or Lemur stage. This idea does not lack probability, for we are, in fact, acquainted with the lower Primates from the earliest Tertiary of America and Europe. But how far did these ancient Primates resemble the Lemurs ? This is a point which is far from being settled. We are still less agreed with regard to the passage, favoured by Haeckel, from the Prosimian to the Catarrhinian stage, that is, to the lower Apes of the Old Continent. For the moment, we must acknowledge, while keeping within the limits of the documents known, that the exact origin of the order of Apes wholly escapes us. All the hypotheses which have been made, outside that of Haeckel, especially those of Filhol and of Gaudry, on the connection between the Apes and the Suidæ are quite as superficial and still more inexact. Finally, the point of bifurcation of the Anthropoïd group has still to be discovered beyond the Miocene. The hypothesis of the linking of Man with the Anthropoïds has found in the discovery of the *Pithecanthropus* of Java alone a more positive and more recognizable proof.

I have dwelt rather at length on the *Schöpfungs geschichte* of Ernst Haeckel for the reason that the publication of that book in 1867 marks a double date in the historical development of the evolutionary idea. It characterizes, on the one hand, the general triumph and, so to speak, a kind of resounding apotheosis of the transformist doctrine ; but, at the same time, it fixes the commencement and, up to a certain point, the wherefore of an attack of prudence with regard to the exaggerations of that doctrine. I have shown in the preceding pages the almost general weakness of the palæontological arguments adduced by Haeckel in all the chapters of his work and the definite downfall of the greater part of his most fundamental hypotheses. Many excellent naturalists, in France especially, could not help being shocked, like Milne-

Edwards, Gervais, de Lacaze-Duthiers, and so many others, by these rather too imaginative tendencies of the evolutionist school, and remained attached to the more patient but surer method of the strict examination of facts. Moreover, the bursts of social philosophy which mark nearly every page of Haeckel's work, by accentuating the combative turn of this book strongly tended to repel from evolution those naturalists who seek, without prejudice, in the study of nature, reasons of the positive order before adhering to even the most seductive hypotheses.

BOOK III

EVOLUTIONARY IDEAS IN PALÆONTOLOGY

From the date of the appearance of the works of Haeckel — that is to say, from about the year 1870—the publication of zoological studies founded on transformist theory became so abundant that it would be difficult for us to follow, even at a distance, the progress and development of the evolutionist doctrine in the various fields of embryology, comparative anatomy, morphology, and the classification of the living animal kingdom. Before this overflowing invasion of facts and theories, we shall be compelled to abandon almost entirely the zoological side of the question and to restrict ourselves to the study of fossil animals and to the examination, in the light of the descent hypothesis, of the most important works to which these beings have given rise. We shall leave on one side works of detail and only consider works of generalization in which we can more easily follow the dawn of leading ideas and the exposition of principles in the matter of philosophical palæontology.

CHAPTER IX

MELCHIOR NEUMAYR—"DIE STAMME DES THIERREICHS"

(THE BRANCHES OF THE ANIMAL KINGDOM)

The connection between Zoology and Palæontology—Variation of existing types—Series of forms—Mutations—Transitional types—The gaps in Palæontology.

THE year 1889 saw appear a work of the very highest rank, due to one of the most brilliant minds in modern palæontology, viz: *Melchior Neumayr*, whose name will remain closely associated with that of the illustrious geologist *Edward Suess* in the universal brilliancy of the Austrian geological school of the end of the nineteenth century.

The work of Neumayr is, strictly speaking, a treatise on palæontology, but a philosophical treatise, and the first in which the history of fossil beings was presented with the help of a method which endeavours to follow in time the evolution of every group under examination. The premature decease of the learned Viennese unfortunately stopped the work at its first volume, which is devoted to the lowest form of animals up to the Brachiopods. But the lengthy and masterly *Introduction* with which the book commences is a luminous exposition of the philosophical principles which had guided the author in his fine researches on transformist palæontology.

Neumayr establishes, in the first place, the inseparable connection of palæontology with zoology. The study of fossil animals is only the more delicate in that the solid parts alone—bones, teeth, and shells—have been preserved in the act of fossilization; entirely soft animals have generally left no traces of their presence. In addition, the erosion of the littoral deposits has too often caused to vanish the collection of beings which dwelt on the shores of the early seas, faunas necessarily more rich and varied than the faunas of deep waters. Consequently the inventory of fossil animals is far from complete compared with that of living animals; in one of the geological periods with which he was best acquainted—that is, the great Jurassic period—Neumayr estimates the probable number of species at 750,000, of which we as yet know hardly 10,000—a proportion of two per cent. The palæontologist must therefore expect numerous gaps when he endeavours to reconstitute the series of vanished forms. We here again meet with, we see, the pleading of Darwin as to the insufficiency of palæontological documents on this point, but this time with more exact facts.

Neumayr also devotes a good portion of his introduction to the study of transformism considered in existing nature. The most important question, the one which overshadows all others in the matter of evolution, is that of the *variability of species*, the constant starting-point of all transformist theories since Lamarck. Among living forms this variability is far from general, which explains the belief of many naturalists of high standing in the fixity of specific forms. But there exists in the present world a certain number of groups which, on the contrary, show a tendency to variation without end. Such are, for example, among continental molluscs, the *Melanopses* of the Mediterranean basin; their forms are connected with one another by so many transitions that the distinction of species lacks any exact basis. Some scholars have divided these shells into three genera and a number of species, while others unite all these forms into one or two species at the most.

Such, again, are the *Helices* of the *Iberus* group, widely spread in Sicily. Their variations are considerable, and the extreme types represented by a tall and globular form and by a very squat and carinated [keel-shaped] form are very dissimilar. Each variety is special to a locality limited in extent; but in two neighbouring districts there can be observed transitional forms quartered in the intermediate zone. Thus, taken as a whole, this Sicilian group forms a continuous series. If, from one cause or another, certain intermediate zones were to be depopulated, the series would become divided into very distinct groups, the connection of which with each other would become impossible to demonstrate.

The *Achatinellæ* of the Sandwich Islands have recently made known to us a phenomenon of *dissociation* of this kind. The group is special to the Sandwich Archipelago, where more than two hundred species have been observed. The large Island of Hawaii raises but six species, while the Island of Oahu, which is one sixth of the size, contains a very great number. Each of these species is strictly confined to one of the wooded ravines which exist everywhere in this island. Nearly every ravine contains its species, and the closer the ravines are to each other, the closer is the resemblance between their respective species. Between the species of each island there exist hardly distinguishable transitional forms which are wanting in the case of species belonging to different islands. Now, quite recent circumstances have determined the complete extinction of a great number of the species of Oahu, so that the former continuity of these forms is to-day broken. At the present moment the Achatinellæ of the Island of Oahu are no longer represented save by a small number of species, very distinct from each other, without transitional forms, just as if they were species belonging to different islands. Thus, by chance we have been able to see the actual operation of a natural process of *dissociation of species* by the extinction of intermediate varieties. This allows us to understand that types now clearly distinct and separated may be only the *survivors* of a formerly continuous series.

But what are the causes that can have led to the variation of this primitive series? According to Neumayr, this variability is closely connected with the habitat, that is, the changes produced in the conditions of existence of the animal. He finds, as did Darwin, very remarkable examples in the changes of fauna which take place in islands isolated in the bosom of great oceans. These islands, generally of volcanic origin or of reef formation, and in consequence somewhat recent, can only have been peopled by means of migration. If we except actual species daily brought over by currents, winds, or in the claws of birds, there remains in each of these islands a special fauna, composed of distinct species, which yet preserves incontestable analogies with that of the neighbouring continents whence these forms have been brought at a more or less early epoch. It is thus that we can explain to ourselves the analogies of the fauna of the Azores with that of Southern Europe, the fauna of the Galapagos Islands with that of America, the fauna of the Sandwich Islands with that of Australia, the fauna of St. Helena with that of tropical Africa, etc. These faunas, degenerated by a long stay in restricted and not very favourable surroundings, are, in general, bound to succumb before the more vigorous animals and plants of the existing fauna imported by man or by natural phenomena.

It is also by modifying at his will the external or internal conditions of animals that man has succeeded in creating among the domestic races those strange varieties which have been studied in so masterly a manner by Darwin.

These facts of modification and separation of specific types by isolation or, on the contrary, by migration, will necessarily exercise the greater influence as the observation of them extends over a longer period. It is therefore natural to expect to see these causes of variation play a predominant part, if instead of contenting ourselves with observing the effects at this present time, we go far back into geological times.

Notwithstanding the importance of the gaps which often separate the forms of fossil animals from one another and constitute at times an insuperable obstacle to the perception of the relations of continuity which must have linked these forms together, there can, fortunately, be chosen, as we have seen above for living forms, a few special groups which lend themselves better than others to the reconstruction of *continuous series*, or series of forms (*Formenreihe*), according to Neumayr's expression. To obtain this result we must deal with a very large number of individual subjects gathered from a series of strata in regular succession without gaps and in analogous conditions of deposit. The first palæontologists to adopt this course were, on the one hand, Hilgendorf, in his memorable work on the variations of the *Planorbis multiformis* of the fresh-water beds of Steinheim; on the other, Waagen, in his researches on the series of the Ammonites of the group *Ammonites subradiatus*. The number of *series of forms* which it has till now been possible to reconstitute is more limited than one might think on *a priori* grounds. However, for Primary times, certain groups of Brachiopods, of Polyps, and of Crinoids show us series of gradual variations. In Secondary times there may be quoted among the best examples the shells of Ammonites, a few kinds of Lamellibranchs, Pholadomyæ, Inoceramiæ, Halobiæ, Brachiopods, and also a few kinds of Urchins. But it is the Tertiary epoch which best lends itself to this kind of research, thanks to the abundance of fossils and to their excellent state of preservation. A long time before Darwin's book, Moritz Hörnes had shown perfectly, and without any theoretical preconception, the gradual variations of the shells of the group *Cancellaria cancellata*, from the Miocene type of the Vienna Basin down to the living form in the Mediterranean. But the most striking genealogical series of all is furnished to us by the researches of Neumayr and Paul on the Paludina of the *Levantine* fresh water strata in the Danube Basin. The Paludines or *Vivipara* are fresh-water molluscs which dwell in large numbers in our lakes and rivers; their shells have the form of somewhat lengthened spirals with convex whorls devoid of all ornament. In the Pliocene lacustrine strata there are found, at the bottom of the series, Paludines with smooth whorls similar to the existing types; when found in rather younger strata, the whorls of the spiral of the Paludines become flattened, then hollow out with a flattened median line, with a tendency to a carina [keel] becoming more and more marked at the top of each coil; then a second carina appears at the base of the spiral whorl; finally each of these carinas becomes denticulated and bristles with increasingly distinct tubercules in the higher strata of the formation. It is a strange and almost unexplained fact that similar tendencies to the formation of keels and tubercules manifest themselves in the same Levantine stage, among other fresh-water molluscs belonging to very different families—the *Melanopses*, the *Neritinæ*, and the *Unios*, for example. But whatever may be the cause, we can establish among these various kinds of molluscs continuous genealogical series the evidence of which forces itself upon any observer. It is very curious to note that almost similar variations appear among the existing Paludines which are found in the province of the Yunnan : the *Paludina Margeriana* of Lake Tali-Fu presents smooth and keel-shaped forms quite comparable to the group Paludina Neumayri-Hornesi of the Danubian Pliocene.

An important distinction should, however, be made between the variations which are produced together in any one epoch—whether it be the existing epoch or the early periods—and the variations which a similar type undergoes in a series of successive epochs, connected, in this latter case, with active causes spread over a length of time. Waagen has suggested reserving the name of *varieties* for the first, while the variations of chronological order would receive the name of *mutations*. Each mutation may be accompanied by a train of varieties, but these last have a lesser value than the first, and the extreme forms which result from them are less different from each other than those proceeding from chronological variations. This can be ascertained by comparing the varieties of Paludines found in any one stratum of the Levantine stage with the extreme mutations which represent the general evolution of the group. This is also shown to us in researches on the line of suture of the Ammonites of the genus Phylloceras.

The mutations have further this special characteristic, that they are always produced in the same direction, without oscillations or retrograde steps. There is no example of any single series of forms which has reproduced at the termination of its evolution, its original type ; if we sometimes find one of the characteristics of this type in the series called regressive, the new types are always distinguished from the primitive types by special features easy to recognize.

The extreme rarity of really continuous series has led some naturalists to suppose that, in many cases at least, the transition from one form to another or from one series of mutations to another series must have occurred by *sudden leaps*. Perhaps also we ought to think that the development of the series has been characterized by short periods of rapid changes separated by longer periods of relative steadiness. But the slow and gradual variation of species remains none the less established by a complete series of certain proofs.

If, now, we desire to carry further the problem of the great transformations which took place in geological times, we shall no longer find proofs as immediate as those we have pointed out in the narrow field of the formation of species, thanks to the *series of natural forms* and to the experiments on domestic races. Palæontology nowhere shows us a series of transitional types between distant groups, as would be, for instance, a series going from the Protista to the Mammals; we shall here have to content ourselves with conclusions from analogies and with proofs by probabilities, which otherwise will not be wanting in the very different groups of fossil animals.

A first comprehensive glance at the succession of fossil faunas shows a continuity very favourable to the descent hypothesis. If, leaving the present world, we plunge into more and more ancient strata, we shall see the differences from living forms more and more accentuated. On the other hand, the faunas of two stages resemble each other the more the nearer the two epochs are to one another. In the most ancient formations the animal population is almost special; the principal part is taken by classes and orders now vanished, such as the Tetracorals, the Graptolites, the Cystidea, the Blastoïds, the Trilobites, the Eurypteridæ, etc. On the other hand, there are not found with them any signs of the very important groups of the existing world — the Amphibians, Reptiles, Birds, and Mammals; a few rare genera of this epoch have descended to us, but not a single species. As we go higher in the series of strata, these foreign elements diminish and disappear, replaced by genera and species more and more near to ours. It seems impossible to explain, apart from the descent hypothesis, this progressive regularity of the development of beings in the direction of our existing world. Yet, if we attempt to establish a direct genetic connection between these organisms of the ancient world and the totality of our existing one, we only come to probabilities. Thus from the most distant times, such as the Cambrian epoch, we already note the presence of all the great fundamental types of the Animal Kingdom, with the exception of the Vertebrates. Classes, orders, and even some genera common to living nature are there represented by types already highly specialized, which bar us from further research in that direction.

Thus compelled to abandon the study of evolution taken as a whole, we shall have to be content with the evidence supplied by certain particular groups; for example, the Mammalia, the Ammonites, and the Echinida, which give us either relatively short *series of continuous forms*, or more extended series, only a few of the links of which are connected by gradual transitions, but of which the whole is modified in the same direction. These *intermittent series* show us the road by which the animals of early times have accomplished their evolution towards the types of existing nature.

As an example in support of his theoretical ideas, Neumayr takes the classic series of the ancestral line of the Horse. This animal, from the point of view of the reduction in the number of digits, which comes down to one (the third)—accompanied by two bony splints which are the rudiments of the fourth and fifth digits—represents the extreme term of a series of which the primitive types must have had five digits, as in all the other higher Vertebrates. In the Tertiary we have long been acquainted with a certain number of animals which enable us to follow step by step the successive stages of this reduction in the number of digits. There is the *Palæotherium,* with its three toes nearly equal and resting on the ground; the *Anchitherium,* with its highly developed median toe and its two reduced lateral toes no longer resting on the ground; and by a still more marked reduction of the lateral toes, the *Hipparion* brings us down to the existing Horse. These modifications of the foot are correlated to other modifications of the hinder limb, of the dentition, and of the form of the skull. More recently the American palæontologist, Marsh, has made known to us in the Western territories of the United States another series of ancestors of the horse, which can be carried back further than the European series right up to the primitive and pentadactylar types. Strange to say, the precursors of the Horse in America differed from those of the old world, and the singular conclusion has been drawn from this that two series of fossil animals, entirely different at their outset, have tended more and more to assimilation until they unite in a common descendant. This *convergence* of two distinct branches is, truth to say, highly improbable. It is safer to suppose that, when dealing with such similar *series of intermittent forms,* it becomes impossible to settle which, in the series of eventual ancestral forms, is the real starting-point of the branch. Let us assume, for instance, that the evolution of the Equine series in the same direction still continues; it would, in the course of a few million years, finally end in animals which had lost all traces of the lateral toes, still present in a rudimentary state in our existing Horse. The palæontologists of the epoch would then be able to recognize the existence of an ancestor which possessed somewhat the same characteristics as our Horse, but would not be able to determine whether it was the Horse, the Ass, the Zebra, or the Quagga, that should be regarded as the true precursor of this new type.*

* The genealogy of the horse is explained more satisfactorily by intermittent and irregular migrations of the American types into the Old World.

Outside the consideration of *series of forms*, great importance must be accorded to certain extinct types which take their place between two zoological groups now entirely distinct, and establish a link between them. There is no more decisive example than that of the *Archæopteryx*, the bird of the lithographic limestone of Solenhofen; its beak furnished with teeth planted in gums, its tail formed of elongated vertebræ, its wings bearing at their extremities distinct fingers with claws, the presence of ventral ribs, and the arrangement of the bones in the phalanges, all constitute an aggregate of reptilian characteristics which permit us, without any hesitation, to consider the class of Birds as derived from the stock of Reptiles. We are acquainted, at the present moment, with a certain number of these links between orders and even classes now quite distinct; for example, between the Amphibians and the Reptiles, and between the Cystidea, on the one hand, and the Blastoïds, the Crinoïds, and the Echinida, on the other. These transitional types point out to us the road taken in the development of life; but we must not forget that their number is exceedingly restricted, and that the *majority of the fundamental types of the animal kingdom come before us without any links between them from a palæontological point of view.*

Should this absence of transitional forms be taken as a decisive objection to the Darwinian theory? Neumayr does not think so, and strives to give in various cases plausible explanations of these lacunæ. Thus we have not discovered the primitive type of the great group of Vertebrates; but this type must have been inferior to the simplest of the Fishes, such, for instance, as the existing Amphioxus. An animal so deprived of all bony parts naturally could not be preserved in geological strata. As regards the transition between the Fishes and the Amphibians, we ought to expect types with but slightly ossified skeletons; we can hardly find much more than their teeth, the importance of which is too slight to give the sought-for link. Finally, just like Darwin, Neumayr pleads the insufficiency of our palæontological discoveries, and trusts that a happy chance may some day bring to light types which will enable these great gaps to be filled up.

There remains, it is true, the embryological method, of which Haeckel has given the exact formula as follows: "The individual development is a shortened repetition of the ancestral development." This interesting law meets with a few happy applications in palæontology, especially in the group of Ammonites and in that of the Vertebrates; but it requires to be handled with the most extreme prudence.

However this may be, it is certain that in the earliest fossiliferous strata all the fundamental types of the animal kingdom existed, with the exception of the Vertebrates. It is, moreover, probable that there have existed still earlier faunas, of which all the species have disappeared through the metamorphism of the corresponding strata. As regards these really primitive faunas the night is complete, and there is every indication that the veil will never be lifted.

As may be apprehended from this substantial summary of the ideas of Neumayr, this eminent naturalist resolutely follows the Darwinian school, and accepts the transformist theory as the most probable, and even as the only one permitting a rational explanation of all the facts observed in palæontology, when coupled with those in living nature. We owe to him the buttressing of the descent hypothesis by palæontological facts and proofs which were either wanting, or only appeared in a very superficial form, in the researches of the founders of transformism. Especially we must grant him the merit of having largely contributed to bring to light, and of having illustrated by valuable examples, the *series of forms* showing the variation of specific types through the course of ages. These series are still, at the present day, the most solid argument in favour of the hypothesis of descent. But we have also been able to repeatedly admire the prudent reserve, the critical mind, and even the rational scepticism of Neumayr, whenever there is a question of going back to the causes and of stating clearly the laws of palæontological evolution. No doubt it seemed possible to him thenceforth to regard the whole animated world as the result of the gradual transformation of extremely simple primitive organisms. These successive forms are due, probably, to the accumulation of individual variations, according to purely mechanical laws. But of these laws we are only acquainted with a meagre portion. We are still ignorant, notwithstanding the hypotheses of Lamarck, Darwin, and many other transformists, of the real causes of individual variations; we are unable to explain either the origin or the reciprocal relations of the great groups of fossil animals; and the problem of the beginning of life will, no doubt, always remain outside the limit of our field of study.

CHAPTER X

THE EVOLUTION OF THE VERTEBRATES: EDWARD COPE

Neo-Lamarckism—The variation of genera and families—Errors of the embryological method—Progressive and regressive evolution—The law of increase in size—The general lines of the evolution of the Vertebrates.

THE studies of Neumayr were essentially directed to the invertebrate animals. Notwithstanding his vast erudition, which often enabled him to explain his theoretical ideas by examples drawn from the great group of the Vertebrates, the learned Viennese only ventured into that field with greatest circumspection. But the theory of descent had early found, with regard to the higher animals, an ardent, or we might even say an impassioned, champion in the eminent American anatomist and palæontologist, *Edward Cope*. Gifted with an eminently philosophical mind, apt to seize and to bring to light the most delicate anatomical relations of fossil and living beings, Cope appears to us as a bold spirit, who never draws back before a new or unexpected hypothesis. In point of audacity, sometimes a little too rash, in theoretical conceptions, the American scholar comes near to the school of Haeckel, with whom he shares the manifest tendency to frequently wander off into the domain of psychology, morals, or metaphysics. But Cope shows himself greatly superior to the German transformist by the precision of the evidence he adduces in support of his hypothesis, thanks to his thorough knowledge of the comparative anatomy of the lower Vertebrates, and especially to the equipment which he had just acquired by his admirable discoveries into the then almost unexplored lands of Western America. We will endeavour to glean from the immense and very original work of Cope, the principles of the transformist philosophy scattered through his innumerable memoirs, of which the most interesting from this point of view bear the following titles:—*The Origin of Genera,* 1868; *The Method of Creation of Organic Forms,* 1871; *A Review of the Modern Doctrine of Evolution,* 1880; *The Progressive and Regressive Evolution of the Vertebrates,* 1884; *The Origin of the Fittest,* 1897; and *The Primitive Factors of Organic Evolution,* 1896.

Cope was, very early, a convinced transformist. As early as 1868, at the age of twenty-eight, he wrote an interesting paper on the origin and the variations of genera. By his tendency to attribute a preponderating part in the changes in the structure of beings to the influence of a conscious or unconscious will, and consequently to habit, he draws near to the French School of Lamarck, and deserves to be called the head of *Neo-Lamarckism.* While admitting the views of Darwin, *i.e.* that the struggle for life and for reproduction is a cause capable of explaining the *survival of the fittest* and the extinction of the species less well adapted for the maintenance of the equilibrium with regard to the environment, Cope refuses, and not without reason, to admit Darwinian selection as the *true cause* of the production of new forms: *the survival of the fittest is not the origin of the fittest.*

The variation of beings occurs in the species, but also in the genus and even in the family. Cope quotes numerous examples of this, both from living beings and from fossil animals. Among the first he dwells on the characteristics of gradual transition between certain families of Batrachians by the progressive addition of a new characteristic, which superadds itself, during the development of the embryo, to the characteristics of the preceding family. Thus, the lowest family of Batrachians, the *Bufoniformes* [toads], possess a movable scapulary girdle (or embryonic *sternum*) and no teeth; the next family, the *Arciferi*, have the same scapulary girdle as the toads, but have, in addition, teeth; lastly, the family of *Raniformes*, or frogs, have both a fixed scapulary girdle (complete *sternum*) and teeth. It is evident that a slight improvement of the scapulary girdle would transform an Arcifer into a Raniform; the appearance of teeth in a Bufoniform would make it an Arcifer. The changes of species, genera, or families, therefore, appear not only as additions, but, sometimes also as subtractions of characteristics in the embryogenic history of the modified generation.

The palæontological history of the Camelidæ offers us another striking example of the same facts. The action of geological times has operated on this group, first by the progressive consolidation of the bones of the foot into a single, or *cannon* bone, and, secondly, by the reduction of the incisors and premolars. Now the fœtal state of the existing Camel shows us a cannon bone divided as in the *Pœbrotherium* and, on the other hand, incisors as in the *Protolabis*; very young camels at the present possess also the additional premolar of a *Pliauchenia*, rarely found in the adult camel.

This brings us back, with very little alteration, to the law of Haeckel regarding the parallelism of the embryological and of the palæontological development of beings. But Cope protests vigorously against too exclusive an application of this law, and appeals, with good reason, to the compulsory checking of palæontological evidence.

The reason for this distrust of the indications furnished by embryonic development is to be found in an original philosophical conception, on which the American scholar dwells without ceasing, and which is, so to speak, his guiding idea in the study of the phenomena of evolution. This is that evolution has been *progressive* or *regressive*, as the case requires; in other words, the modifications of structure have been produced, sometimes by the addition, and sometimes by the subtraction of organs or parts of organs. When we find ourselves confronted with rudimentary organs, such as fingers, limbs, fins, or teeth, it is often difficult to decide whether we have to do with persistent primitive conditions which permit these types to be considered as the ancestral forms of existing beings, or if, on the contrary, these reductions of organs are the result of degeneration, and consequently have a relatively modern origin. The beings presenting these characteristics may be, in a word, either primitive ancestors or degenerate descendants. But what is to be understood by degeneration ? It must be defined as a loss of parts without a corresponding development of other parts. From this point of view all animals are degenerate on some point or other ; mammals, for example, as regards the weak development of the pineal gland and of the coracoïd bone. It may be affirmed that there is degeneration only when the sum of the subtractions is greater than that of the additions.

Embryology often furnishes us with interesting data on the correct interpretation of rudimentary and of vanished organs, and thus indicates to us the phylogenic connections between various beings. Without embryological studies we should probably never have suspected that the Tunicates were derived from primitive forms analogous to the Vertebrates. But embryology has its limits, for *the transitory characteristics presented by the embryo are but a partial reminiscence of the structural types through which its ancestors have passed during the geological ages.* In addition, the characteristics of the embryos are often but special adaptations to the necessities of their embryonic life ; as, for example, the allantoid and the placenta of the Vertebrates. In a goodly number of cases the phylogeny can only be established and confirmed by the discovery of the geological ancestors themselves. It is the observation of real phylogenetic series which demonstrates the existence or non-existence of such and such an intermediate type ; it allows us to decide whether the rudimentary structures represent organs in course of formation, or, on the contrary, result from a degeneration of organs formerly well developed.

Cope admits the difference between adaptive and non-adaptive structures so brilliantly set forth by Kowalevsky. Then, generalizing still further this conception, he succeeds in formulating, under the name of *doctrine of non-specialization*, a law which is, in his eyes, one of the most important as regards evolution, and, as it were, the touchstone of the method. This interesting point demands an explanation. Palæontology shows that the succession of beings has not followed one single direct line ; there exists a large number of diverging lines, many of which are extinct. Life has been, with reason, compared to a tree with many and ramified branches, of which many do not reach the top. Even for those branches which we can trace from their inferior lineaments up to our own day, there are many which in their existing state have become incapable of giving birth to higher forms. The branches which have thus arrived at a certain *specialization of structure* can no longer vary in a direction very different from the one they have already taken. These specialized types have had much less chance of survival, and have perished or are destined to perish through changes in their surroundings. The evolution of the Vertebrates furnishes Cope with very demonstrative examples of the ineptitude of specialized forms. Thus, the different classes of the Vertebrates must certainly descend from the Fishes, but it would not be possible to trace downward any actual type of our too specialized bony fishes. To discover the origin of the Batrachians, we must come down to more generalized and earlier forms, such as the *Dipneusta*. In the same way we could not derive the Mammals from any type of existing reptiles, and must go back to the Permian to discover their origin in the Theromorphs. From the point of view of prophetic resemblances, these animals are inferior to the modern Reptiles, and recall some of the early stages of the Reptiles, as well as of the Mammals. In the group of Mammals, the Apes could not have descended from the Carnivora nor from the Ungulates and reciprocally, and we can only trace their slender affinities back to the Bunodont types of the lower Eocene. Finally, the various groups of Ungulates must all be attached to the hardly specialized group of Amblypods, with their poorly developed brain and their plantigrade foot with its five toes. It is easy to understand that the generality and the plasticity of all these forms is the reason of the existence of their ancestral relations.

It is this inferiority, arising from a too-advanced specialization, which enables us to understand the extinction of forms, the most powerful of any from their size and from their perfected natural weapons. Accustomed to live in *luxurious indolence*, these immense beasts could neither bear the diminution of their food nor the other changes of the environment. It is a well-established fact that none of the large types of terrestrial animals has been able to maintain for long its supremacy in the course of the geological ages. *All the groups of the Carnivora, of the Ungulates and of the Quadrumana known in detail, commence with types small in size* *and of puny strength*—a fruitful law of which the exact formula seems indeed to be due to Cope, and which serves as a real clue to the researches of modern palæontology.

After having thus attempted to unravel or to render precise some of the great laws of the evolution of beings, Cope applies his theoretical ideas to the phylogeny of the Vertebrates. The great palæontological discoveries in America enable the lines of precise descent of several small groups to be determined, and even give us a glimpse of the phylogenetic relations of some of the orders or classes of this great division of the animal kingdom. In accordance with his theoretical ideas, Cope strives to show that the evolution of the Vertebrates has been not only progressive, but more often than it was supposed, regressive; this last feature being more frequent in the lower than in the higher groups.

Leaving on one side the two lower groups of the *Leptocardia* (*Amphioxus*) and of the *Marsipobranchia* (Lampreys), which are not, with any certainty, represented in a fossil state, the American scholar studies the origin and the relations of the Fishes, Batrachians, Reptiles, Birds, and Mammals.

The Mammals are linked to the Theromorphic Reptiles through the intermediary of the *Monotremata*. The birds, or some of them at least, seem to be derived from the *Dinosaurian* Reptiles. The latter, in their primitive form of *Theromorphs*, descend from the rachitomous Batrachians. The *Batrachians* issue from a sub-class of the Fishes, the *Dipnoes*, but the true primitive form is unknown to us. The true Fishes, or *Hypomata*, have descended from an order of dogfish, the *Ichthyotomi*, which possess also the characteristics of the *Dipneusta*, that is to say, a duplicate aerian and aquatic respiration. The origin of the Dog-fish remains, like that of the Fishes proper, entirely unknown. Perhaps we may admit, as does Dohrn, that the Marsipobranchia have acquired their actual characteristics by regression. As to the origin of the Vertebrates, it is as yet totally unknown, Kowalevsky deeming them descended from the Ascidians, and Semper from the Annelids.

I cannot here follow the illustrious palæontologist through the special study of the evolution of each of the great orders of Vertebrates; but I cannot resist the desire to make known, or at least to summarize, one of the most curious and most philosophical of his works, the one relating to the *general line of evolution of the Vertebrates*. Cope analyses and examines the changes which have taken place in the course of development of these animals, in their circulatory, their nervous, and their osteological structure.

Starting as a simple tube in the Leptocardia, the heart divides itself into two cavities in the Marsipobranchia and the Fishes, into three in the Reptiles and the Batrachians, and into four in the Birds and Mammals. The arcs of the aorta amount to numerous pairs in the Leptocardia, are reduced to seven in the Marsipobranchia, to five in the Fishes, to four or three in the Batrachians (at which point their branchial function generally stops), to two and one in the Reptiles, to a single one on the right side, in the Birds, and to one on the left side in the

Mammals. Taken as a whole, this is an *ascending process;* it corresponds to an adaptation from aquatic to aerial life and to the change from a type of cold-blooded animal to a warm-blooded type.

The brain and the nervous system also show an evident general progression. As to the successive relations of the skeleton in the various groups of Vertebrates, special attention must be given to the ossification of the base of the cranium, to the suspensory apparatus of the mandibles, to the scapulary and pelvian arcs, and finally to the limbs.

The persistence of the primitive cartilage in any point of the skeleton is, embryologically, *a mark of inferiority.* It is the predominant condition among the lowest Vertebrates. In the Leptocardia the cranium is membranous; in the Marsipobranchia and in many Elasmobranchia (Dog-fish), it is cartilaginous; in the other Fishes and in the Batrachians, the axis of the base of the cranium is still cartilaginous, and we have to get as far as the Reptiles before we see appear the sphenoïd and the bony presphenoïd characteristic of the Birds and Mammals. The spinal column follows more or less exactly the history of the base of the cranium in this *progressive* development.

There is progression likewise in the structure of the suspensory apparatus of the mandible. Here the gradual reduction from four to zero of the number of bones in the mandibular visceral arc has the effect of shortening the arm of the lever, and increasing its functional power. In the Fishes we note a hyomandibular bone, a symplectic, a lower square, and an articular bone. Among the Batrachians, the Reptiles, and the Birds, there only remain the square and the articular bone which, in their turn, disappear in the Mammals.

As regards the scapulary girdle we note that, in the lower types with fins, the lateral portions of this belt join underneath the body, without the intervention of a median element or sternum which shows itself in the air-breathing types. The large number of the segments of the pectoral arc constitutes, from the mechanical point of view, an inferiority which places this type of structure in the lowest rank. On the other hand, the presence, in the Reptiles, of a *sternum* accompanied by a clavicle, a procoracoïd, and a coracoïd, assigns to these animals the highest place for mechanical force. The absence of the coracoïd in the Tailed Batrachians, and the loss of this and of the procoracoïd in the Mammal constitutes an element of weakness. The line of evolution is, here, no longer progressive.

The absence of the basin or pelvis or its rudimentary state places the Fishes at the extreme base of the line of evolution. The development of the ilion in front of the coxa in some Batrachians and in the Mammals may be compared with its backward direction in the Reptiles and its extension in both directions in the Birds. These conditions are derived by descent from a strictly intermediate situation in the Batrachians and the Reptiles of the Permian epoch. The extension forward of the pelvis must be regarded as mechanically superior to its extension backwards; for the first of these types of structure shortens the vertebral column, and draws the fore closer to the hind limb; it follows from this that the Mammals become fit to hold themselves erect on the ground, while Reptiles crawl on their bellies.

Finally, as regards the lower arc of the pelvis, the Mammals have another advantage in the strong bony median symphysis uniting the ischion and the pubis. This characteristic, general in all the Vertebrates of the Permian age, has been lost by modern Reptiles and Birds, and re-acquired by the Mammals. The line of evolution, except for these last, is, therefore, retrograde in both directions as regards the pelvis.

We shall here close these examinations of the work of Cope, which will suffice to bring to light the really marvellous ingenuity of his theoretical views, together with his profound knowledge of the comparative anatomy of the existing Vertebrates, joined to a very personal palæontological science applied to all groups, from the Fishes up to the Mammals. These brilliant and solid qualities give to the work of the American scholar a special place and an incontestable superiority over all attempts hitherto made to grasp the difficult problem of the palæontological evolution of the Vertebrates.

CHAPTER XI

ALBERT GAUDRY. LES ENCHAÎNEMENTS DU MONDE ANIMAL

The concatenations of the animal kingdom and Philosophical Palæontology—The progress of the animated world—The stages of evolution—The methods of functional adaptations—Artificial concatenations

At about the time that Edward Cope, still a very young man, was beginning the publication of his admirable researches on palæontology and the evolution of vertebrates, a French palæontologist, Albert Gaudry, was pursuing the same studies. At that time, that is, about the middle of the nineteenth century, the whole school of French naturalists, with but few exceptions, was imbued with the Cuverian theories on the fixity of species, and more or less openly repudiated the descent hypothesis. The merit of Gaudry was to be one of the first, in our country at least,* to adopt the transformist theory, and to endeavour to apply it to the study of fossil mammals. In his first work, on the fauna of the *Miocene Vertebrates of Attica* (1867), Gaudry endeavoured to show that the genera of the Mammals were not so clearly separated as was at that time supposed, and that certain new types of the fauna

* France is, of course, here meant.—Ed.

of Pikermi constituted true intermediate types between genera or even families now distinct.

A little later, in a work on the *Animaux fossiles du Mont Luberon* (1875), he endeavoured to show that the fossil species of the end of the Miocene period had undergone variations considerable enough to justify the separation of several distinct races characterized by the slightness, or, on the other hand, by the clumsiness of the form of the paws among the Hipparions ; or by the closeness together or the distance apart of the horns in the Antelopes of the genus Tragoceros.

All these works, as well as some others, were only, so to speak, the prelude to a great synthetical work in three volumes, which appeared from 1878 to 1890, and bore the suggestive title, *Les Enchaînements du Monde Animal.* Finally, from this endeavour to apply the transformist method to the beings of Primary, Secondary and Tertiary times, Gaudry contrives to disentangle the principles involved in the evolution of fossil animals in the form of an *Essai de Paléontologie Philosophique* published in 1896.

These books of Gaudry had an undoubted influence on the transformist outlook of the younger generation of French naturalists. This was due in great measure to the simplicity of the exposition, to the seduction of their style, to the studied geniality of the thoughts expressed, to the visible effort to be understood by all, and, finally, to the wealth and beauty of the illustrations. But, taken in its entirety, and compared with the almost contemporary scientific and philosophical work of

Edward Cope, the work of Gaudry remains far behind that of the American palæontologist in the scope of the views, the breadth of the ideas, the extent of the knowledge, and the originality of the principles of transformist philosophy, which the two scholars studied on parallel lines. Truth to say, there cannot be discovered either in the *Enchaînements* or in the *Paléontologie Philosophique* any really new theory on the subject of evolution. The *Unity of the plan of Creation*, the *Constant progress of the animated world* since the appearance of the first beings down to existing nature and man, " who in himself sums up all its marvels," such is the general theme which pervades the whole work of Gaudry. But do we not know that the principle of the *progressive development* of the organic world was already, as we have seen above, in germ in the works of Georges Cuvier, and had been set forth in all its details by Darwin, by Haeckel, by Huxley, and by so many other masters of the transformist school? Gaudry, however, tried to rejuvenate the idea by seeking manifold proofs of it among fossil beings, either in their general *multiplication* on the surface of the globe, or in their *differentiation* and their *growth*, or, again, in the special progress of their *activity*, their *sensibility*, and their *intelligence*. Let us examine, with Gaudry, a few examples of this assumed progress of beings.

The peopling of the globe by the successive faunas which have taken possession of it was facilitated, according to Gaudry, " through the first arrivals being better protected or less attacked than their descendants." It is thus that the Polyps of

Primary times were protected by thick walls and calcareous tablets, whence their name of Tabulated; that some among them, such as the Calceola, closed their orifices by a lid; that many Brachiopods were *articulated* with their two valves strongly geared into each other; that several genera of Cephalopods possessed a shell with a narrow, and, as it were, almost contorted opening; that certain fishes had even cuirasses of bony plates protecting the head, back, belly, and also the arms; that other fishes, called Ganoïds, were covered with thick bony scales, ornamented with a brilliant enamel, and forming an impenetrable envelope; and, finally, that the air-breathing Vertebrates, the Amphibians, and the Reptiles, had a ventral plastron likewise formed of bony scales.

On the other hand, these early beings had fewer enemies:

"The creatures of primary times found their salvation in the shell or cuirass which covered them, while those of the end of the Tertiary era and of our own epoch mostly sought protection in flight."

All these considerations have a certain poetical seduction about them, but are, for the most part, extremely disputable. There existed, in fact, in the earliest seas animals with but little protection, the Brachiopods with horned shells, for example, which in no way prevented certain of them, the Lingulæ, from surviving in our existing seas. In the Cambrian and Silurian epochs we are acquainted with *tubular* Polyps without walls or calcareous tablets, Medusæ entirely gelatinous, almost soft

Starfish, bivalve Molluscs with thin and gaping shells, Pteropods with very fragile shells, Gastropods, like the *Bellerophon* and the Pleurotomary, whose shell carries a slit the whole length of the spire, and Cephalopods like the Nautilus, with widely opened chamber, marine Worms which dig, as at the present day, holes in the sand, and those great Crustaceans, the Merostomes, with a rather thin and chitinous carapace. The Carboniferous era offers us the Arachnides and the Insects. The cartilaginous and naked fishes, akin to our Dog-fish, abound in all Primary deposits, and have only been preserved to us, thanks to their teeth and the spines of their fins. There are reasons for thinking that entirely soft, low-class Vertebrates, analogous to our Lampreys, existed in the Cambrian Sea. Lastly, a few puny Amphibians of the Permo-carboniferous epoch were as little protected as are our Batrachians. In reality, naked, or but slightly protected, animals are not rare in early geological deposits, and if they are not still more common, it is for the very simple reason that their preservation is difficult, and that most of them have disappeared without leaving any traces. We might even go further, and by a converse reasoning to that of Gaudry, show that the best fortified animals, the Cystidea, the tesselated Crinoïds, and the armoured Fishes have had a less powerful vitality than that of the other groups, and have died out more rapidly, giving place to groups of animals apparently less well protected against the attacks of their enemies.

Other forms of progress recognized by Gaudry are no more in conformity with the evidence of facts; for example, the progress in the organ of vision. Why should the primary Trilobites, with their large compound eyes, furnished with thousands of little facets, have been inferior to other beings in the matter of perfection of sight? Why should the gigantic Phasmidæ of the Coal period have had sight less sharp than our present insects? For what reason should the Ichthyosaurs with their enormous eyes have less easily pierced the obscurity of the waters than our present Cetacea, with eyes proportionately so much smaller? Why should the Jurassic *Archæopteryx* have had a less piercing eye than the astonishingly perfect eyes of our Birds? The erroneous argument proceeds from the comparison of qualities which are not comparable: each of the groups of the animal kingdom possessed in geological times, as in our days, sensory organs perfectly adapted to the environment for which their use was required: the *Agnostus* of the Cambrian Seas was blind because it dwelt in deep seas where light did not penetrate, as in the same way a large number of types of the deep-sea fauna of the present day are blind. The Ichthyosaurus and the Pterodactyl had large and very perfect eyes, because that organ was indispensable to them, as to our existing Raptores, in seizing their prey. Progress, in all this, is not absolute, but proportionate to the needs; in other words, an organ is perfect when it fulfils its object perfectly.

Notwithstanding these necessary restrictions to the ideas of Gaudry on the details of the progress of beings—ideas steeped in an exaggerated, and at times a somewhat artless sentimentalism—it cannot be denied that, taken in its entirety, the palæontological evolution represents a gradual improvement from the Primary epoch down to our own day. We shall, however, have to return to this point, and to show that recent discoveries, by pushing further and further back in time the first appearance of the highest groups in the animal series, tend to diminish little by little the evidence of this principle, and to cut out one by one the proofs of it until now deemed the most demonstrative.

Another philosophical idea which crops up at intervals in the works of Gaudry relates to the *stages of evolution* of fossil animals and to the use that can be made of these stages to determine the ages of the strata containing their remains. This point of view is only, after all, a sort of direct corollary of the idea of the continuous progress of beings.

"If palæontology enables us to assist at a regular evolution of the animated world, it is evident that the stage of development of fossils must correspond to their geological age; we then understand why such and such fossils are met with at such and such levels. The geologists who bring to us the bones of Vertebrates that we may declare the age of the soil in which they were discovered, are aware that our first care is not to inquire whether they are any of the numerous known species, but that we seek to determine to what stage of evolution they belong, because the stages of evolution which mark the changes in organization, at the same time mark the principal divisions of geological times. Here are two different deposits; I note that the animals in the one indicate a less advanced stage of evolution than in the other ; I conclude therefrom that the first is of an earlier epoch."

To make this method clear, Gaudry sets forth a series of examples from which I make a selection ; the Echinoderms were, in the first place, fixed to the submarine soil by a stem and, later on, became detached ; in this same group, the calcareous case which encloses them was first formed of pieces without any order in the Cystidea of the Silurian, then of pieces arranged in numerous lines in the Devonian and carboniferous Sea-urchins, and finally in rows reduced to the number of twenty in the Secondary as in the existing sea-urchins. These stages of the direction and of the reduction of the parts of the "Test" [integument] of the Echinoderms enable us to recognize each of these epochs.

The Cephalopods enclosed in a shell, like the Nautilus or the Orthoceras, characterize Primary times ; in Secondary times there is found a mixture of enveloping shells like those of the Ammonites, and of internal or non-enveloping shells as in the Belemnites. Lastly, the naked Cephalopods, such as the Polyps and Cuttle fish, reign almost exclusively in Tertiary times. The degree of complication in the sutural line, which separates the successive chambers of these Cephalopods, offers valuable proof of the stages of evolution. In Primary times the Nautilidæ preponderate, with simple or slightly sinuous lines of suture or *partitions.* Later on came the Ammonites with partitions at first simply denticulated, then with slashes of increasing variety. Finally, towards the end of their reign, several Ammonites, *as if weary of their* *luxuriant expansion*, no longer had strength to coil themselves and thus formed less complicated partitions. The first stage belongs to the Primary epoch, the second is Jurassic, and the third Cretaceous.

The evolution of the Bony Fishes offers us, according to Gaudry, remarkable stages. At the outset there are strata where no remains of the Fishes are found. This is the commencement of the Primary. A little later, in the Devonian epoch, fishes are observed devoid of spinal column or at least in whom this column is soft and formed of embryonic tissue. A little further still, at the end of the Primary, the fishes have a vertebral column incompletely ossified, the arcs of the vertebræ being bony, while the centres are not yet so. At the commencement of the Secondary, the centre of the vertebræ is partly ossified; in the middle of the Secondary, the geological strata contain, together with species with the substance of the vertebræ not ossified, others having it partly so and others again having it completely so. Finally, when strata are found where the ossification of the vertebræ is completed, we may guess that we are at the end of Secondary times, or at a more recent epoch.

This continuous progress in the ossification of the internal skeleton of the Fishes is, according to Gaudry, correlative to a converse development, that is to say, to a progressive reduction of the external one. In the first Fishes, in the middle of Primary times, the body is covered with very hard, large bony plates, which have earned for these animals the name of *Placoderms*. When we see fishes appear with scales thick, bony, and covered with shining enamel, and called, for this reason, *ganoïds*, we say that we are at the end of Primary or at the commencement of Secondary times. The assemblage in the same stratum of hard, bony-scaled ganoïds, ganoïds with less bony scales, and finally, fishes with soft scales, characterizes the middle of Secondary times. Lastly, if there only remain fishes with soft scales like our existing fishes, we have the right to conclude that this stratum is at the end of the Secondary or of a more modern age.

The stages of evolution of the Reptiles afford us analogous indications. In the Primary epoch the ossification of their skeleton is very incomplete ; the great bones of the limbs have not their extremities well defined, and a thick cartilage represents the heads of these bones ; in the same way, the centre of the vertebræ is formed of distinct segments surrounding a part of the dorsal cord which has remained in the state of embryonic tissue ; they are the *unfinished* quadrupeds. A little later, types of reptiles somewhat akin to the preceding, but larger, have an entirely ossified skeleton ; we are then in the Trias.

But it is doubtless in the Mammals that these stages of development have been most precisely studied. . . . The *Marsupial* stage, that is, the one in which the developments of the embryo is partly extra-uterine, is common to the majority of the Mammals of the Secondary era in Europe and America. At the commencement of the Tertiary epochs, the placental stage—with complete intra-uterine development—begins to appear ; but it is mixed up with the true Marsupials and with other types which have preserved some characters of this last group. When, in a deposit, we no longer meet, in Europe, any but placental Mammals, we are at a more recent period than the Oligocene.

The study of the teeth offers us, among the Mammals, some interesting characters of evolution. Thus the pre-molars of several families of Pachyderms were at first triangular before becoming quadrangular by the addition of a fourth point to the three preceding. This modification is noticed in the Tapir, Rhinoceros, Palæotherium, the Equidæ, etc. The triangular or quadrangular stage of the upper pre-molars will thus indicate to us an early or, on the contrary, a more recent age.

These examples will no doubt suffice to make thoroughly plain the method set forth by Gaudry and applied by him in a more or less happy manner to the study of a certain number of groups of fossil animals. This method will perhaps appear seductive at first sight ; I will even add that it is susceptible of rendering service to palæontologists, by translating, in a few brief and clear formulas, *evolutionary tendencies* suitable to this or that well defined natural group. But it requires to be handled with extreme prudence under penalty of inducing error. Evolution does not present itself, in fact, with the same orientation in all the groups ; it is, following the idea so happily expressed by Cope, sometimes progressive and sometimes regressive, without anything to enable us to foresee this change of direction. To keep to the Mammals only, examples abound with contradictory tendencies. The back molars become more and more complicated in the primitive Marsupials, in the Proboscidians, in the Suidæ, in several families of Carnivora ; they become simplified in most of the Eocene Ungulates, in the toothed Cetacea, or Cetodonts. The premolars increase in complication with the Tapirida, the Lophiodontidæ, the Palæotheridæ, the Equidæ ; they become reduced and simplified with the Cervidæ, the Bovidæ, and generally with the Ruminants. Very simple in structure with one or at most three denticules in the majority of the Mammals of the Secondary or the commencement of the Tertiary, the teeth acquire, at the same epoch, in the Multituberculata, the highest degree of complication ever realized. Similar contradictions abound in the history of palæontology. They lead us scientifically to observe a wise reserve towards the deductions, brilliant but too often deceptive, which can be drawn from the *state of evolution* of an organ or even of a group of organs in fossil animals.

Together with the general exposition of his principles of transformist philosophy, Gaudry took pains, either in his special monographs or in his work on the *Enchaînements du Monde Animal*, to accumulate manifold proofs of the gradual transition from one genus to another, from one family to another family, and even from one large group to another large group, often at a great distance. According to him, naturalists were first struck by the *differences* existing between beings and had rather too much neglected the *resemblances*, whence the necessity for modern palæontologists to turn their minds to the *approximations*. These resemblances Gaudry sees everywhere, and sometimes, by dwelling on very superficial characteristics, he manages to recognize strange relationships which are disconcerting to a naturalist. I shall confine myself to quoting one of the most extraordinary of these comparisons. The Conulary of the Silurian epoch, with its conical shell similar to that of our existing Pteropods, is regarded by Gaudry on account of certain concave walls at the extremity of the shell and notwithstanding the absence of any syphon, as representing possibly the original form of the Cephalopods. The curious molluscs of the family of Chamacea, known by the name of Rudista on account of their thick and rugged epidermis, are considered by him as likely to have ancestral relations with the rugged operculous Polyps, such as the Calceola of the Devonian.

Noticing Cephalopods with uncoiled shells, both among the Nautilids of Primary times and among the Ammonites of the Secondary, Gaudry does not hesitate to frame the supposition, notwithstanding the most fundamental differences of structure, that "several forms of Nautilids have directly given birth to the form of Ammonitidæ which correspond to them." In the same way the superficial resemblance of the phragmocone or partitioned part of the shell of the Belemnites with the partitioned shell of the Orthoceras of Primary times, inspires Gaudry with the idea that these animals, different as they are in organization, might be derived one from the other. Finally, as to those curious Placoderm fishes of the Silurian and the Devonian, so remarkable by their cuirass of bony plates and yet deprived of all apparent traces of ossified vertebral column, Gaudry sees nothing extraordinary in linking them with the Crustacea as their probable ancestors and thus making them the bridge, so often dreamed of, between the world of the Invertebrates and that of the Vertebrates.

These conceptions are so strange and correspond to such fundamental errors that we might almost imagine them to be simple paradoxes, in no way dangerous to readers with even a little instruction. But unfortunately it is not the same with many of the other essays in phylogeny by the same scholar which deal with less restricted groups and especially with the Tertiary Mammals. The special competence of Gaudry in these matters, and the more plausible appearances of natural links among the forms examined, have diffused through the world of naturalists and even in the schools of the State a certain number of incorrect *affiliations*, the appearance of which seem to me due to a vice of *general method* to which attention should be drawn.

The method in question almost always adopted by Gaudry, in continuation of the remarkable memoirs of Waldemar Kowalevsky, rests on the consideration of *functional adaptations*. It consists in studying, in a series of genera which follow each other more or less exactly in chronological order, the functional modifications of a *single organ or of a single group of organs*. The nature of these organs is moreover variable according to the groups under study. Thus the reduction of the lateral digits in the Imparidigitates and the Paridigitates, the complication of the pre-molars in the Tapiridæ, that of the tuberculous teeth in the Ursidæ, the development of the nasal bones and of the frontal and nasal horns in the Rhinoceroses, and that of the antlers in the Cervidæ, have all been taken in their turn as *guiding lines* in the establishing of the *concatenations* to which has been accorded the value of *natural series,* the various terms of which are related by way of descent.

This method certainly presents the greatest dangers. It leads, in fact, to the confusion of the *real evolution* of a natural group of fossil animals with what is, in effect, only the *functional evolution of an organ* in a series of genera belonging to different natural branches and having no direct relationship. Two examples of these series which have become classical and we consider as *artificial* and inexact, namely, that of the Equidæ and that of the Ursidæ, will make this demonstration clear.

The ancestry of the Equidæ has been studied, at the same time by Huxley and Kowalevsky in Europe, and by Marsh and Cope in America. We will, here, only examine the European series ; this series, starting from the *Palæotherium* and from the *Paloplotherium*, comes down to the horse by the intermediary of the *Anchitherium* and of the *Hipparion.* These genera form, in fact, a very remarkable series—nearly always cited as a classical example of evolution—from the point of view of the gradual atrophy of the second and fourth toes and of the definitive predominance of the third toe in the *solipedal* hoof of the Horse. Yet, Mdme. Pavlow, and Schlosser and Weithofer as well, have proved that neither the *Palæotherium* nor the *Hipparion*—I readily add nor the *Anchitherium*—

should be comprised in the direct ancestry of the Horse. They are distinct and parallel branches, which became extinct without leaving descendants, and whose hypothetical relations may some day be discovered only by going back to very much earlier periods. Moreover, geological observation positively establishes that there exists no gradual transition between these genera. The last *Palæotherium* had long disappeared, *without transforming itself*, before the first *Anchitherium* appeared, and this last had in turn vanished, *without modification*, before it was suddenly replaced by the invasion of the *Hipparion*. The *supposed* pedigree of the Equidæ is a deceitful delusion, which simply gives us the *general process* by which the tridactyl hoof of an Ungulate can transform itself, in various groups, into a monodactyl hoof, in view of an adaptation for speed ; but it in no way enlightens us on the palæontological origin of the Horse.

The pedigree of the Bears has been the object, on the part of Gaudry and of Boule, of a study founded on the progressive development of the tuberculous teeth and the correlative reduction of the pre-molars in various types of Tertiary Carnivora. This pedigree begins with the *Amphicyon* to end in the Bears through the intermediate stages of the *Hemicyon* of the middle Miocene, of the *Hyænarctos* of the higher Miocene and Pliocene, and lastly of the existing *Œluropus*. This series, well enough arranged from the special point of view of the surface increase of the tubercules, is certainly inexact so far as real ancestry is concerned. It suffices, in order to prove this beyond doubt, to state that there existed, as early as the middle Miocene period, small carnivora which already present, in their dental and osteological structure, nearly all the characteristics of the true Bear excepting its size. M. Schlosser has rightly given the name of *Ursavus* to these miniature bears, which exist both in the middle and upper Miocene. These facts permit us to foresee the discovery of still smaller Ursavuses in the lower Miocene and perhaps in the Oligocene. Consequently Gaudry and Boule have only studied various degrees of the adaptation of tuberculous teeth to a carnivorous diet in several groups of Carnivora ; they certainly have not elucidated the real origin of the Bear group.

It now becomes easy, thanks to these examples, which could be multiplied, to estimate precisely, from the point of view of the general principles of evolution, the kind of errors created by the method Gaudry has employed to establish his *Enchaînements* :—

1. *The establishment of artificial affiliations*, which would derive one genus of animals from another with which it has no real genealogical link. A formal criterion of these inexact affiliations is the *total absence of transitional forms* between the genera wrongly grouped together. It is nowise sufficient to plead, as has often been done since Darwin, the insufficiency of the palæontological evidence. The transitional forms between these genera not only do not exist, *but cannot possibly have existed*, since the facts observed point out to us that we are dealing with distinct and parallel branches, each of

which has had an independent evolution and an independent history.

2. *Too short duration attributed to the evolution of groups.*—The haste, which would transform a *Palæotherium* into a Horse during the term which has elapsed since the Oligocene, and an Amphicyon into a Bear since the middle Miocene, does not correspond to the reality of facts. We are already able to show that the *natural phyletic branches* of the Mammals are extremely extended and run parallel to each other without touching, up to nearly the beginning of the Tertiary period, and probably further back still.

It seemed to me necessary to develop somewhat this discussion of the philosophical principles and the general methods employed by Gaudry in his essays on the *Enchaînements du Monde Animal* as they have had a very great reputation in France. Among these principles, the exactness of some is undisputed, such as the ideas, old as they are, of *the continuous progress of beings and of the parallelism between individual development and palæontological evolution*, with as their consequence the point of view, now and then interesting, of a geological chronometry founded on the stages of evolution. But we have seen that somewhat grave errors have resulted from a too rigorous and somewhat hasty application of these principles, which require to be handled with extreme reserve and with due consideration of the forward or backward state which certain branches may present relatively to the others in their degree of evolution. We must pronounce a still severer judgment on the superficial and paradoxical comparisons between groups which have nothing in common, and even on a great number of the *concatenations* pointed out by Gaudry with regard to the Tertiary Mammals. Nearly all these pretended pedigrees, built up on the deceptive appearances of the modification of a single organ by functional adaptations, are artificial, inexact, and unable to bear examination in the light of knowledge already acquired on the *real evolution* of these groups. Notwithstanding these too numerous errors, it must be acknowledged that Gaudry's works on philosophical palæontology have spread over the history of the evolution of animals a certain poetical charm which renders the reading of these works easy and attractive, and has largely contributed to the diffusion of the transformist doctrine in France.

CHAPTER XII

KARL VON ZITTEL. THE UNCERTAINTIES AND DECEPTIONS OF PALÆONTOLOGICAL EVOLUTION

The *Handbuch der Palæontologie**—A warning against the exaggerations of Transformism—Phylogeny and Ontogeny—Dangers of the phylogenic method—An appeal to prudence.

PALÆONTOLOGY in the course of the nineteenth century made marvellous progress. The unceasing flow of discoveries of fossil animals on all sides and in all countries had begun to render difficult even to specialists, the task of keeping pace with these new facts disseminated in numerous papers in very various languages. Not only did the field of palæontology thus become considerably enlarged, but new roads were opened since the study of fossils was no longer a simple dependency of geology, or a practical method for settling the age of the globe's strata. By the light of the hypothesis of evolution, palæontology conquered its independence, and now advanced, on an equality with biology, to the discovery of the history of the development of beings and of the general laws which preside over these incessant transformations.

Admirably fitted by important special researches on nearly all the groups of fossil animals—radiolaria,

* München, 1876. The English version, the first volume of which was published in 1900, offers some advantages.—ED.

sponges, crinoïds, branchiopods, lamellibranchs, gastropods, cephalopods, cirripedes, fishes, and reptiles—Zittel formed, as early as 1876, the bold project of accomplishing a complete and detailed revision of the knowledge acquired of fossil animals and plants. But this considerable work, published from 1876 to 1893 under the modest title of *Handbuch der Palæontologie*, was not to be, in the author's mind, a simple work of compilation; there was question of a severe critical revision, founded both on a wide knowledge of the innumerable papers published on the extinct types of the animal kingdom, and on a personal study of their families and genera. An overwhelming task for one man, but more possible to Zittel than to any other, thanks to an incomparable power of work, to a wide erudition, and still more to a personal study of the rich palæontological documents collected and classified by the eminent professor of Munich University.

The work was truly and at all points masterly. Not only all the fossil genera described up to that time by the palæontologists of all countries were made the object of a new delimitation and a new diagnosis, but each great group was studied in the relations of its anatomical and zoological organization with the representative forms in our present world, in such a way as to give to each fossil type the rational place which it should occupy in a general classification of the series of beings. Finally, the lofty tendency to scientific philosophy which characterizes the work of Zittel is shown by a substantial summary placed at the end of the study of each group, a summary in which the learned palæontologist strives to retrace the *history* of the group, its origin in time, its evolution in the series of ages, and its most probable genetic relations with its ancestral forms and its kindred branches. And here most strikingly appear the masterly qualities which, to my mind, give to the work of the Munich professor a character of precision, one might say of scientific honesty, which is really admirable. On the one hand there is the boldness necessary to attack in front and fearlessly the always delicate and sometimes insoluble problems raised by palæontological evolution; on the other, the critical mind and the wise reserve which guard us against hasty or risky solutions, and are not ashamed to acknowledge our ignorance, temporary as it is, of the most fundamental data of this evolution.

The mind of Zittel was at root in sympathy—this is clearly shown in all his work—with the transformist ideas. He did not refuse to recognize the great idea of unity in the plan of creation, nor to set forth the facts which militate in favour of the genetic relations of classes, orders, families, and genera, when these relations appeared to him to stand out clearly from their succession in time and their morphological characters. To compare new forms with those already described, to study their genetic relations, their descent, and their ulterior evolution is, in his opinion, the supreme and final goal of palæontology.

But this theoretical starting-point once admitted, we must honour Zittel for having been one of the first to utter with unquestionable competence a warning cry against the sorry exaggerations, not of the theory, but of the theorists of transformism. It was at Zurich, after the appearance of the last volume of his *Handbuch*, that Zittel set forth before the International Congress of Zoology, with entrancing clearness and eloquence, the uncertainties and deceptions of palæontological evolution. *Phylogeny, Ontogeny, and System*, such is the suggestive title of this memorable lecture, which made such a noise in the palæontological world that it seems indispensable to give at least a sketch of it.

The theory of descent rests to some slight degree on palæontological facts. The most solid argument consists, as Neumayr had already said, in the *series of similar species* which can be followed from individual to individual through geological formations, and show at least *the probability* of a phylogenetic descent. Nevertheless, these series do not generally form a continuous chain of which the links are joined to one another, mutation to mutation, and species to species ; there are often intermittent series, the ends of which are all modified in a given direction, and establish the stages of an evolution crowned by recent or existing forms. One can describe similar series more or less close to each other in the Camelidæ, the Suidæ, and the Ruminants among Mammals, in the Crocodilians among Reptiles, and in the Amiadæ and the Physostomes among Fishes.

The terminal types of these series are in general distinguished from their ancestors by a more marked differentiation, which makes them more specialized, and, so to speak, more finished beings. The theory of descent is alone capable of giving a rational explanation of these series of forms.

In the same way the resemblance of the faunas of the same geological age and the geographical distribution of extinct and living animals bring very strong arguments in favour of this theory. But, after all, we cannot forget that there exists an immense number of creatures without intermediate links, and that the relations of the great divisions of the animal or vegetable kingdom are much less strict than the theory demands. Even the Archæopteryx, the sensational discovery of which established a relationship between two such distinct classes as Birds and Reptiles, but very imperfectly bridges over this gap, and does not indicate to us the point of bifurcation of these two classes. Intermediate links are wanting between Amphibians and Reptiles. Mammals, likewise, are very isolated, and the wide gap which separates them from the other Vertebrates cannot be contested by any zoologist. We do not even know with certainty a single type of mammal so nearly approaching to the lower Vertebrates as is the present Ornithorhyncus. The keenest partisans of the descent theory must acknowledge that the fossil links between the classes and orders of the two kingdoms exist in infinitesimally small numbers.

There exists, it is true, within the great groups, *series of forms* which not only show the plasticity of beings, but also inform us of the processes by which these series have transformed themselves in the course of time. But, even on these lines, it is easier to accumulate probabilities than certainties. The genealogical trees we are able to draw up by relying upon morphology and on chronological series are subjective to the feeling of each observer.

Another group of facts seems to allow us to establish by a different road the genealogical relations of fossil animals. I refer to the *ontogenic method*, that is, the study of embryonic characteristics, or, more exactly, the characteristics of youth, which, transitory among recent types, persist in the adult state among the earliest forms of the same natural groups. This method, first observed by Agassiz, one of the most fervent adversaries of the descent theory, has throughout been in high favour amongst the philosophers of transformism, and has received from Haeckel a precise formula under the name of *fundamental biogenetic law*. "The history of individual development, or *ontogeny*," he says, "is but a short recapitulation of the long palæontological history or *phylogeny*." Our existing embryology should then be, if this law be exact, equal to the reconstruction, in at least an approximate manner, of the fossil precursors of each group, and if these precursors were susceptible of preservation, they should be discovered in the terrestrial strata.

If we appeal to palæontology, it must be recognized that this hypothesis is by no means verified. There do exist here and there a few fossil genera, which have retained all their lives certain youthful characteristics apparent in their living descendants; but when it comes to reconstructing whole series chronologically continuous, grave contradictions are met with, and it is only in the groups of the Mammals and perhaps of the Reptiles that it becomes possible to present a few examples sufficiently demonstrative. Thus the Eocene, Oligocene, and also in part the Miocene Mammals may be looked upon up to a certain point as early forms of the existing types. There can be determined, in most orders of mammals, a certain number of primitive characteristics which correspond to various adolescent stages in the existing representatives of these groups. On the other hand, these early mammals are deprived of some of the most remarkable peculiarities of the present types, such as the horns and their bony antlers, the welding together of certain bones, and the reduction in the number of the teeth and some portions of the skeleton. It is thus possible, by studying carefully a series of the kindred genera of different geological ages, to see appear, one after another, in the series of time, the characteristics of differentiation and of progressive specialization of the modern types.

But this is only a very fragile and very uncertain basis for the reconstruction of the faunas and floras of the past. Experience has taught us to what uncertainties and to what errors the study of palæontological facts by the method of embryology might lead us. Let us imagine a zoologist who would wish to attempt the reconstruction of the series of ancestors of the Crinoïds by means of the ontogeny of the *Antedon*. The lowest types of his pedigree would have to possess a stalk with a cup without handles, formed of five basal and five oral pieces close together; then would come genera in which the cup would be complicated by the addition of five small radial pieces between the basal and the oral; then should be found forms furnished with five arms, at first short and simple, and later longer and more ramified, and so on. All palæontologists know how far the geological history of the group is from this theoretical scheme.

What zoologist could have foreseen from the development of our existing Sea-urchins that the *irregular* type with bilateral symmetry, was derived from the *regular* with radiating symmetry, and that this latter proceeded from fossil-ancestors of the Palæoechinida type, with manifold rows of meridian plates? In the ontogeny of the Cœlenteria, nothing recalls with certainty the anterior existence of the *cyathophyllidæ* and of the *cystiphyllidæ*. No embryological observation could have allowed us to foresee the existence of the early Graptolites nor of the Stromatopores. No stage of development of the existing Branchiopods recalls the numerous forms, with spiral branchial supports, of the branchiopods of Primary and Secondary times.

It would be easy to multiply these examples. They will suffice to show what a dim light ontogenic researches on existing beings cast on those of the earlier geological periods. From the practical point of view, we may say that the stages of embryonic development have not been preserved, and that it cannot be expected that they will be discovered in the terrestrial strata. It might not, perhaps, be so if we were dealing with post-embryonic stages; but, as regards the Invertebrates at least, the attention of naturalists has been but little drawn to that quarter.

Notwithstanding these difficulties, it is possible, however, to cite, among fossil animals, a few cases of the preservation of embryonic stages. The Palæozoïc Belenuridæ resemble the young larva of the existing Limulus. The pentacrinoïd larva of the *Antedon* is more akin to certain fossil Crinoïds than is the adult animal. Several fossil Sea-urchins retain the permanently linear ambulacra and pentangular peristome which are the transitory and adolescent characteristics of their existing descendants. Even in groups entirely extinct, some series of ontogenic characteristics may be sometimes successfully retraced; the fine researches of Hyatt, Wurtemberger, and Branco have shown that the Ammonites and Ceratites pass through a Goniatite stage, and that the internal whorls of some genera of Ammonite reproduce, in a transitory state, the form, the ornamentation, and the lines of suture possessed, in the adult state, by certain other genera of a former geological epoch.

The series of forms of which the consecutive links accord with the adolescent stages of more recent types do not offer us only an image of the progress of development of a given group. The reconstruction of such genealogical trees form the most important desideratum in palæontology. But we are yet very far from the goal. Nothing shows more how arbitrary these genealogies are than the unsatisfactory state of our knowledge as to the evolution of the great Ammonite group.

Finally, von Zittel terminates with an admirable appeal to prudence :—

"The theory of descent," he says, "has introduced new ideas into descriptive natural history, and has assigned to it a more noble aim. But we must not forget *that it is at present only a theory,* which requires to be proved. I have endeavoured to show what interesting proofs have been brought to its support by palæontological researches, but I ought not to conceal the great gaps in our demonstrations. Science aspires above all to truth. The more we are convinced of the fragile nature of the bases of our theoretical knowledge, the more should we aim at solidifying them by facts and by further observations."

Wise advice, which might well be thought over and followed by those palæontologists with adventurous minds, eager to construct, with feverish haste, genealogical trees without end, of which the rotten trunks, according to the picturesque expression of Rütimeyer, beaten down as soon as they are set up, encumber the soil of the forest, and render access more difficult to the progress of the future.

PART II

THE LAWS OF PALÆONTOLOGY

CHAPTER XIII

A GLANCE AT THE PROGRESS AND PRESENT STATE OF PHILOSOPHICAL PALÆONTOLOGY

THE appearance of the *Handbuch der Palæontologie* of von Zittel at the dawn of the twentieth century marks a memorable date in the history of the progress of this science. It is truly one of those glorious stages where one rests for a moment to cast a look back on the path traversed before setting out with renewed ardour on the forward march to new progress.

In the preceding historical sketch we have witnessed, in the course of the past century, the birth of the science of vanished beings and its development. We have seen burst forth, one after the other, general ideas and philosophical hypotheses, some of them destined to a brilliant evolution, others to oblivion. With Georges Cuvier, the real founder of the science of palæontology, we have witnessed the triumph of the beliefs since abandoned in *the fixity of species* and *in the integral renewal of faunas* by the revolutions of the globe; but we have, at the same time, seen appear, with thrilling clearness, in the writings of the illustrious naturalist, the fruitful ideas of the *gradual progress of beings* and of *the changes of faunas by migration.* The hypothesis, not very tenable from a philosophical point of view, of *successive creations* has been maintained with real talent by the disciples of the Cuverian school, by d'Orbigny, Agassiz, d'Archiac, and Barrande, all exaggerating, and even going beyond the idea of the master. On a track directly opposed to this, Lamarck and Geoffroy-Saint-Hilaire constructed on purely biological bases the *doctrine of descent*, the transformations of beings resulting, according to Lamarck, from an *adaptation to physiological needs*, and according to Geoffroy, from the *direct influence of the surrounding media* ; while the last-named at the same time sowed in the science the germ of the *hypothesis of sudden variation* and the *theory of the parallelism between individual embryonic development and palæontological evolution.* After a partial eclipse, we have seen the transformist hypothesis receive a new and definitive impulse from the ingenious researches of the illustrious Darwin on the processes of transformation of living beings by *artificial selection* and *natural selection*, the latter having for cause the eternal *struggle for life* and for *reproduction. Darwinism,* though greatly inferior to *Lamarckism* as regards the importance and the real efficacy of the causes of evolution, definitely triumphed over all the resistance of the last partisans of the fixity of species, thanks to the co-operation of passionate champions of the transformist hypothesis — R. Wallace, T. H. Huxley, and Edward Haeckel. This last, by a *method purely embryological*, endeavoured to demonstrate the *monophyletic evolution* of the two kingdoms, and from *the parallelism of Ontogeny and of*

Phylogeny evolved *the fundamental biogenetic law.* But there are still wanting to all these theoretical formulas of the transformist hypothesis the support and control of *real evolution;* that is to say, of the *palæontological history of beings.* Superficially sketched by Darwin on data of pure descriptive zoology, then by Haeckel pushing even to error the exaggerations of the embryological method, *palæontological evolution* at last became, in the last thirty years of the nineteenth century, an embodied doctrine, scientifically established, thanks to the researches of a pleiad of specialists, such as Cope, Kowalevsky, Rütimeyer, Gaudry, Waagen, Neumayr, von Zittel, and many other more modern palæontologists. Waagen, Neumayr, and von Zittel showed the importance of *series of forms* or *mutations* patiently followed from strata to strata through the soils of the earth's crust. Cope, more of a theorist, revived a sort of neo-Lamarckism by attributing the majority of facts in evolution to conscious and unconscious physiological actions. His principal theoretical formulas are those of *an evolution at once progressive and regressive* and the *law of non-specialization*, that is to say, *the arrest in development of over-specialized forms.* Gaudry develops, with evident exaggeration, the *law of the continuous progress of early beings*, both in their general structure and in the detail of their organs, and strives to establish the *stages of evolution* of each group at various moments of its geological life;—a brilliant but no doubt delusive method, which has too often led this palæontologist into error in the attempts embodied in his *Enchaîne-*

ments du Monde Animal. Finally, von Zittel synthesized with admirable exactness the important general facts which, from the end of the nineteenth century onward, could be disentangled from the enormous and growing mass of palæontological materials, and slowly led our science toward the discovery of its principles and of its laws.

At the present moment it would be rash to affirm that we know satisfactorily the *general law* which has presided over the unceasing transformation of beings from the apparition of life down to our existing world. Neither the mechanism of physiological adaptations, nor that of the direct action of the surroundings, nor, still less, that of the struggle for life, are adequate to furnish a rational and complete explanation of the magnificent picture of palæontological evolution. There still exist in this evolution, without even mentioning the first origin of life, many mysterious points and important facts, explanations of which escape us.

But if we can make up our minds to abandon in future this general and theoretical side of evolution, it will be possible, as a compensation, to settle exactly a certain number of *laws of detail,* or, more exactly, *of frequent repetitions of the same facts,* which, if they have not the absolute value of the great physical or mathematical laws, present none the less a philosophical interest of the highest order, and throw thenceforth a strong light on the natural process of the transformation of early beings.

I propose to set forth and discuss, in the following chapters, those of these *palæontological laws* which seem best established.

BOOK IV

THE VARIATION OF SPECIES IN SPACE AND TIME

The tendency of species towards variation has been, since the very origin of the transformist hypothesis, the starting-point and the strongest foundation of this doctrine. But it is necessary, at the outset, to make a distinction of great importance between *variation in space,* that is the variation of a species at a given moment—whether of the present epoch or of past times—and *variation in time,* that is, the changes in species in the series of successive strata of the earth's crust.

CHAPTER XIV

VARIATION IN SPACE AT THE PRESENT EPOCH

Examples of variation in living species—Variation among Land Molluscs: Groups of forms, of varieties, local races, and modes of variation.

The variability of existing species, already well studied by Lamarck, has especially been brought to light by the memorable observations of Darwin on the races of domestic animals, as well as on wild species. These are classical data to which I shall not further refer. I have, likewise, in a previous chapter, recalled the remarkable facts of specific variation instanced by Neumayr in several genera of land shells, the *Melanopsis* and the *Iberus* of the Mediterranean regions, and the *Achatinella* of the Sandwich Islands. Without multiplying these examples *ad infinitum*, I shall simply take a few facts chosen from among animals of our European fauna : the hares in the temperate zones of the north and centre of France are always distinguished from the hares in the south of Provence, and more generally of all the Mediterranean countries, by their greater size, longer and more abundant fur, long and hairy ears, and darker colour, in which black, grey, and white predominate over the reddish tints. These differences are still more accentuated if from Provence we pass over into Africa. Algerian hares hardly exceed one-half the size of the great European hares, and are remarkable by their generally light red coat. Finally, in the Saharian region hares are very small in size and of a dun colour. Some excellent observers have not hesitated to see among these hares representatives of several species. The northern type retains the Linnæan name of *Lepus timidus*, while that of the south takes that of *Lepus Mediterraneus*. And, lastly, the dun-coloured hares of the desert regions receive the new name of *Lepus isabellinus*. Analogous specific distinctions have been made, and for similar reasons, between the foxes and the weasels of the north and south of Europe ; they imply, as will be seen, a good deal of personal opinion. Other naturalists, quite as conscientious, do not admit these variations to the rank of species, and simply count them as *races* or *local varieties*.

But it is to the study of the shells of Molluscs that the talent for analysis of descriptive naturalists has, above all, been directed. The illustrious founder of binominal nomenclature, Charles Linnæus, created species on a very wide basis, which was, no doubt, even too wide in many cases. The Linnæan species has often and rightly had to be subdivided, after a more minute and precise study of its morphological characters. But, carrying to the extreme this necessary distinction in the *forms* realized by nature, a certain school of conchologists, represented in France by Bourguigniat and Locard, have pushed the separation of species, as it were, to the point of pulverization. Thus in the single genus of our fresh-water mussels or *Unios*, Locard has described, for the fauna alone of the rivers and lakes of France, two hundred and twenty different species which the author distinguishes by characteristics drawn from the general outline of the shell, from its length or its obliquity, and the more or less eccentric position of the tip, etc. It must be said, however, in defence of this patient and able observer, that these manifold species have been grouped into twenty-six sections, each having as its principal type a species easy to recognize, and admitted by the majority of naturalists. Under these conditions, it is permissible for every one to admit or pass over *forms* and *sub-species*, and to keep to the principal sections recognized by the author. But this precaution has not always been observed by the partisans of the same school, and the multiplication of specific names has become in certain hands so overdone that there are no longer species, but only individuals.

If, returning to our example of the Unios of France, we examine more closely one of the groups of the species described by Locard, such as the *Unio rhomboideus* of Linnæus, we shall note that of the nine species of this group, three are found indiscriminately throughout all the rivers in France, and should be considered as real ubiquitous *varieties* of the typical species, *Unio rhomboideus*, itself enjoying a very extended geographical dispersion. The other six, on the contrary, are strictly localized from a geographical standpoint: the *U. moulinsianus* in the Cher and in the Creuse; the *U. bigorriensis* in the Western Pyrenees; the *U. astierianus* in the Lake of Meyranne in Provence; the *U. circulus* and *sphœricus* in the rivers of Saône-and-Loire; and the *U. Pacomei* in the Rhone and the Saône, near Lyons. The like remarks could be made regarding the majority of other genera of Molluscs of the fauna of France. We thus arrive at an interesting distinction between the variation produced on a given spot, and in all places round it of a given type, and that which is only observed in geographically distinct regions often entirely isolated as regards intercommunication. If we give to the different sub-species of a Linnæan type the general name of *forms*, we may designate the forms produced on the spot by the name of *varieties*, and reserve for variations of a geographical order the name of *local* or *regional races*. While the causes of the creation of *varieties* is hidden from us, it may be said that we shall be completely correct in attributing to climatic and surrounding causes, which, together, are designated by the name of *habitat*, a preponderant part in the determination of the *local races*.

An ingenious French conchologist, M. G. Coutagne, seems to me to have brought us in the study of the variation of land Molluscs some very interesting and exact data. The shells of these animals, particularly those of the innumerable family of the *Helicidæ* commonly called snails, lend themselves marvellously to a precise study of this variation, owing to their easy preservation, their abundance in any given place, and lastly, and especially, to their slight aptitude for even limited displacements. Their areas of dispersion, or in other words their domains, are small in extent, and the important study of the limits and forms of these domains can be easily effected. The method followed by Coutagne consists in collecting and examining *the greatest possible number* of shells belonging to what he calls a *colony*, that is to say, a gathering of individuals of the same type dwelling in the same limited locality, and so little different from each other that the crossing of these individuals among themselves may be considered possible and may give fertile results. If we find, for instance, on the same rock *Helix alpina* and *Helix lapicida*, we may say that these Helices constitute two colonies; for it will never enter the mind of a malacologist that there can be fertile crossing between these two groups. It is possible thus to appreciate at first sight the variation undergone by the closely related individuals of the same colony.

But then the different colonies of the same species from more or less distant stations must be compared.

Coutagne was in this manner enabled to establish that different colonies had often each a sort of *special physiognomy* manifesting itself by characteristics difficult to clearly define, such as colour of the epidermis, thickness of the test, relative size of the shell, etc. In addition, it is often observed that these same characteristics are again met with in other species from the same locality, so that their production may reasonably be attributed to the influence of the environment. We arrive, it will be seen, by a stricter and more exact method, at the distinction pointed out above between variations produced on the spot or *varieties*, and variations at a distance or *local races*.

Coutagne has contrived to systematize with precision the various *modes* by which these variations in land shells are effected. He observes first of all that certain species, the *Helix lapicida*, for instance, have *almost no polymorphism*. Doubtless certain individuals are a little flatter, others, on the contrary, have a higher spiral: the carina is more or less sharp, the umbilic more or less open. But all these variations alter so slightly the physiognomy of the shell, or, if preferred, the characters of the species, that the least expert conchologists will never hesitate, after they have once seen this species, to recognize it among all these slightly differing varieties.

Other species, on the other hand, are more polymorphous. It might almost be laid down as a rule that the variability of a Linnæan species may be in some sort measured by the number of *forms* or so-called species into which it has been dismembered by modern authors. Let us take for an example a species of moderate polymorphism, the *Bulimus detritus*, a pretty shell very common in the south-east of France. The variations of this species may rest—

1. On the size of the shell : modes *major*, *medius*, *minor*.

2. On its more or less inflated form : modes *inflatus*, *normalis*, *elongatus*.

3. On its white, striped, or semi-transparent colour : modes *albidus*, *radiatus*, *corneus*.

4. On the coiling of the spiral : modes *regularis*, *irregularis*.

5. On the smooth or rough aspect of the epidermis: modes *lævigatus*, *excoriatus*.

These thirteen *modes*, to which a few others might be added, are not met with in all the stations of this species ; each colony may be characterized, on the contrary, by the absence, the presence, or the frequency of one or other particular mode. In one, for instance, all the individuals may be long, mode *elongatus ;* in another all very small, mode *minor*. Often there are combinations, two to two, or three to three, of these different modes. In the *Bulimus detritus* most of these modes are met with here and there in different places, without any very precise geographical distribution. However, the mode *corneus* is almost special to Auvergne (*Bulimus corneus*), and the association of the modes *minor*, *elongatus*, and *irregularis* characterizes a form quartered on the east slope of Mont Lepine in Savoy, which has received from Bourguigniat the name of *Bulimus sabaudinus*. These two forms, therefore, enter into the category of *local races*.

This *scattered polymorphism* is still more accentuated in other species. In the *Helix striata*, to be found nearly throughout France, save on the high mountains, there can easily be distinguished twenty *modes* of variation which, grouped together, may give a total of 1458 combinations. The attribution of a specific name to each of these *shades* would be, therefore, irrational, and would only impede the exposé of general facts which the consideration of *modes* allows us to set forth. Thus, in flinty regions the shells are thin, mode *tenuis*; in the limestone regions they are thick, mode *solidus*. In the Paris Basin, the northern part of the domain of the species, the shells are large and the test is thin; in the warm and dry regions of the south, as in Provence, the shells are small with a thick test, and the inner membrane of the peristome becomes larger and of a pink colour; lastly the epidermis is adorned with dark-coloured bands, sometimes almost touching each other. These two modes might receive the names of *Septentrionalis* and *Meridionalis*. When the influence of the environment has the effect of reducing the period of development, whether this is occasioned by heat or cold, the spiral has half a turn or a whole turn or several turns less than usual; and at the same time, some of the characters of the adult, the structure of the peristome, or the deviation of the spiral, appear prematurely,—mode *prematurus*, in opposition to a mode *productus* observed more rarely in subjects endowed with greater vitality or placed in exceptionally favourable conditions, which exceed in some measure the ordinary term of their growth. In these different cases the influence of the nature of the environment on this variation becomes perfectly evident, thanks to this method, which leads us directly to the *trinominal nomenclature*,* that is to say, to the necessity of using three names—the name of the genus, name of the species, and the name of the mode of variation—to designate a shell. Take as an example *Helix striata præmatura*.

In view of the very great polymorphism of certain species of land shells, does a criterion exist which allows us to fix the point where variation stops and where the next species begins? In a word, is it possible to give a precise definition of a species? This is an old question, often discussed, and never definitely solved. A purely morphological definition is subject to error for the reason that polymorphism sometimes leads, between the subjects of two good neighbouring species, to an inversion, or, at least, to an equalization, of one or several of the normal and distinctive characteristics. Thus a big-bellied mode of the *Helix acuta* may resemble, to the point of being confused with it, a *Helix ventricosa*. To guard against such errors, it is necessary to look at the average characteristics of each colony, rather than the individual ones of this or that subject. But the naturalist has yet at his disposal

* I am entirely of the opinion of Coutagne on this point, and think that the adoption of a trinominal nomenclature is the sole means of stemming the rising flood of so-called new species, described without check and at the chance caprice of anyone, which threatens to transform descriptive natural history into a veritable Tower of Babel, where no one in future will be able to understand his neighbour.

other methods, viz: a *physiological* method, which studies the special reaction of each species with regard to the circumstances of its environment; a *geographical* method, if the domains of the two species are entirely distinct or overlap each other; finally, and above all, a *mixiological* method, when the two species form common colonies. The boundaries are then established by a sort of *genetic barrier*, due either to the impossibility of cross-breeding or to an instinctive repulsion of the two species from each other, or, again, to the infertility of the cross. Observation shows us, in this case, the complete absence of intermediate forms in common colonies. This is the case with the *Helix acuta* and *ventricosa*. In other species, it is true, for example in the *Helix hortensis* and *nemoralis*, so like each other in many points, in a few sparse localities there may be observed a certain number of intermediate examples which are probably hybrids; but even the very small number of these crosses is an indication of a veritable genealogical barrier between the two species. By the analytical application of these two criterions it seemed possible to Coutagne to distinguish between the colonies of the different species and the different species of the same locality; in a word, to separate neighbouring species. This was only possible, however, by ignoring those innumerable pseudo-species which modern authors have described from simple and insignificant morphological variations, often peculiar to individuals, which bring into the system of land shells an almost inextricable confusion.

The facts that Coutagne so well observed in this philosophical research into the variation of land Molluscs might be repeated for all the other groups of existing animals. It is perfectly exact that, notwithstanding the polymorphism of certain types, the limits of the *great species* always remain easy to define.

We recalled previously the regional races of the common hare, *Lepus timidus*, from the temperate zones of the centre of Europe to the Sahara. These various races are, indisputably, only climatic variations of a single species ; these variations, in fact, only affect the external characteristics of size and fur, and leave intact the deeper and more intimate characteristics, such as dentition. But, towards the northern limits of its domain, the *Lepus timidus* comes into contact with another hare of a more northern habitat, the *Lepus variabilis*, which, outwardly, is not very different from it, having only rather shorter ears and grey and black fur like that of the common hare, which becomes entirely white in winter, thus adapting itself to the colour of the snowy countries it inhabits. If, however, one compares the dentition, we observe that the first upper molar in these two hares has a different shape. In the *Lepus timidus* it is rounded on the inside, while in the *Lepus variabilis* it shows a deep furrow between two ridges of enamel. In addition, the arch of the palate in the northern species is larger, and does not become narrower behind, as is the case with the common hare. These characteristics of a deeper order than that of the fur will always enable the two species to be distinguished. Even in the countries of the north of

Europe, in Scotland, in Sweden, and in Russia, where their areas of dispersion meet and overlap reciprocally, we never meet with a cross or transitional form, which proves the existence of a mixiological barrier between the two species.

The fauna of our European Mammals and Birds would offer us examples without end of this absence of transitional forms between two or several neighbouring species living together in the same localities. Every one knows that the flocks of hooded crows which invade our country in winter time include, beside the black, which is the most numerous, other crows ornamented with a sort of light grey mantle on their wings. This is the mantled crow, a species whose real domain is further east. These two species form the same flocks, take part in the same hibernal migrations, but do not mingle genetically. No transitional forms can be observed between the black and the mantled crow. In our countries, also, two sparrows, the domestic and the tree sparrow, live side by side, without ever mingling or hybridizing; so do two tits, the large and the small; two wrens, the *Regulus cristatus* and the *ignicapillus*, etc., etc. If at times a certain difficulty is experienced in distinguishing between the species of certain genera, the peewits, the gulls, and the sea-swallows, for example, a careful examination of certain characteristics, the relative length of the wing feathers, the colour of the eyes, the disposition of the scales on the feet, etc., will enable a practised ornithologist to avoid any errors in determining these species.

To sum up, observation shows us that, in actual nature, certain species vary very little, while others are subject to a more or less wide polymorphism, which is sometimes even excessive. It is this maximum of variation observed *in a very small number of groups* which has always been the chief argument used by the champions of the transformist hypothesis in demonstrating the variability of species. We have seen Neumayr apply this consideration successfully to a few types of land Molluscs, the *Melanopsis*, the *Iberus*, and the *Achatinella*. Closely analyzed, *nearly all living species* can be sub-divided into a certain number of *forms*, or, if you will, of *sub-species*. Certain nomenclators have unfortunately thought of separating these under distinct names, which no longer permit the natural links with the parent species to be recognized. Of these forms, arranged according to certain definite *modes* of variation, some are produced *on the spot*, that is to say, almost everywhere and in the same localities as the typical species; and these are the *varieties*. The rest are confined to certain regions, and offer still more interest than the first, because we must see in them the result of the special action of the general surroundings; these are the *local* or *regional races*. But it is important not to lose sight of the fact that these *groups of forms*—which constitute, perhaps, the most real and the most striking of all natural classifications—are linked to a *typical species*, more largely conceived and bounded, and acting, so to speak, the part of a centre of radiation to all these forms. Do these *great species*, termed, not always correctly, *Linnæan species*, pass one into the other by gradation, as has so often been maintained? In living nature, observation enables us to answer that this is in no way the case. *Existing species*, setting aside certain rare cases of hybridization, *are not connected with one another by imperceptible transitions.* This is an important fact which did not fail to impress Darwin, and one which that eminent observer endeavoured to explain by hypotheses on the extinction of intermediate forms. However ingenious these hypotheses may be, they should not cause us to forget the great observed fact, which is general among existing animals.

CHAPTER XV

VARIATION IN SPACE IN GEOLOGICAL TIMES

Examples of variation: The *Nassa* of Piedmont, the Ammonites of Crussol—Regional races at the Cambrian, Liassic, and Pliocene epochs—Conclusions.

If from existing nature we go back to geological times, with the object of studying in them the *variation* of *fossil species in space*, that is to say, in each of the epochs of the life of the globe, we shall have to make, but less easily, observations quite analogous to those above. Nature has not varied its processes, however early the period in view. Two examples, borrowed, one from Tertiary, the other from Secondary times, will enable us to fix our ideas with regard to this.

In the Tertiary basin of Piedmont a clever palæontologist, Bellardi, has described and drawn with care the Miocene and Pliocene Gastropods of the valley of the Po and of the Ligurian Apennines. The genus *Nassa* in this basin is particularly rich in varied forms, and Bellardi has made known no less than three hundred and sixteen species or varieties, of which more than three-quarters are considered new, and receive, for the most part, a specific name. But we are here really dealing with a numerous series of superposed stages with distinct faunas. Let us confine our analysis to two of these faunas, the one from the serpentine green sandstone of the Turin hills, or Helvetian stage, and the other from the blue clay of the Tortonais or Tortonian stage; the first comprises 120 and the second 122 species or varieties. But it is easy to see by examining the plates, and thanks to the care which the author has taken to draw his species side by side in sections or groups of natural affinities, that there is here no question of real species, independent from the point of view of genetic relations, but of simple forms which pass by ordered transitions from one to the other when they belong to the same group, but are separated by a serious gap from the forms of the neighbouring group. A naturalist less scrupulous than Bellardi in the art of distinction might easily, and no doubt with advantage, reduce the number of the species of *Nassa* to some twenty for the Helvetian, and some thirty at most for the Tortonian, with numerous *varieties.* No doubt we are indebted to Bellardi for having made known to us, by excellent drawings, all these numerous varieties of *Nassa* found in Piedmont; we are thus able to arrive at a more precise idea of the limits of variation of each species. But the work would have been more interesting and more philosophical if the author had reduced the species to the number strictly necessary, or, to express it better, to the *real number*, by grouping round each *great species* a certain number of varieties that he might have designated by the third name of a trinominal nomenclature.

As to the Jurassic period, an eminent geologist of Lyons, F. Fontannes, has described with minute care the numerous Ammonites gathered in the limestone quarries of the Crussol mountain, which rises on the right bank of the Rhone opposite Valence. Among the most abundant genera of Ammonites in this limestone, the genus *Neumayria* of the Oppeliides group certainly takes the chief place. These are shells much convoluted, the last spiral, almost entirely covering the inner ones, ornamented on the flank with contorted ribs, and bearing on the external border a row of tubercules, in general smooth and rounded. The elegant ornamentation of these Ammonites is most varied according to the subject: the umbilic is more or less open, the ribs more or less firm and numerous, and of a more or less sinuous form; the tubercules of the external border are sometimes close together, sometimes wide apart, now round, now lengthened in the direction of the spiral. Sometimes they disappear on the fully grown whorls; at other times they develop and take the form of bristling spikes. From these modes of variation, and from some others which it is superfluous to point out, Fontannes has thought proper, in one natural group alone of this genus, that of *Neumayria flexuosa*, to separate and describe a dozen different species. The individuals of this group are so plentiful sometimes as to touch one another in certain blocks of these limestone rocks. We find there young and adult specimens of all sizes massed together pell-mell. Every palæontologist who has gathered, as I have done myself, Neumayria in the quarries of Crussol, is unable to free himself from the idea that all these individuals must have bred among themselves, and, consequently, belong to one species endowed with an intense polymorphism. There are there only simple forms, or, to be more precise, *varieties*, since these Ammonites dwelt together in the same locality in the Jurassic sea, and, moreover, passed from one to the other by gradual transitions.

Should we, then, accuse Fontannes of having failed to notice these evident links of relationship ? Assuredly not. This scrupulous palæontologist kept solely in view the making known to us and exactly defining by his drawings the limits of variation of a a very polymorphous type. Has he perchance gone too far in this direction, and multiplied uselessly imaginary species founded on subtle differences in the ornamentation of the shells ? The transitions between the Neumayrias of Crussol are, in fact, so gradual that it is often difficult to affix a precise name to the specimens collected, and every palæontologist might, according to his personal whim, either multiply further the divisions made by Fontannes, or, on the contrary, reduce them in a large proportion.

The criticisms just formulated are not specially aimed either at Bellardi or at Fontannes, but really at the *method* generally employed in palæontology for the delimitation of species. The subject cannot be exhausted in a few words. Two extreme cases may present themselves. Either the palæontologist who attempts the description has at his disposal only a small number of specimens of the same group, gathered from one or several deposits. In this case he need hardly trouble himself about transitions between the forms under consideration. He has before him only subjects with very clear and distinct characteristics, and will describe them as so many different species, thus leaving it to chance to declare which form shall be distinguished by a specific name out of all the other possible forms of the same species. Or, on the contrary, he is dealing with a very rich deposit, which allows him to gather together some hundreds of subjects grouping themselves round an average type. The most usual process is to arrange all these shells in a continuous series, guided by some characteristic, such as length of the spiral and number of ribs or of rows of tubercules, if dealing, for example, with Gastropods. These characteristics will either become less, or, on the contrary, more marked from one end to the other of the series. The most logical process, the one most in conformity with the truth of Nature, would be to draw, side by side, the principal graduated steps in this series, leaving to the whole body a specific name, and taking as varieties the most important modes of variation. This process has the material inconvenience of necessitating very copious and costly illustrations. Palæontologists have acquired the habit, a sorry one in my idea, of making up in this continuous series a certain number of arbitrary sections, each corresponding to the variation of one or of several characteristics, and of giving a name belonging to a species to each section. It will be seen how much this purely morphological notion of the species in palæontology differs from the definition at the same time morphological, genetic, and geographical, which we have admitted for the living species.

The facts above mentioned all apply to variations of a fossil type in the same deposit or in neighbouring beds, that is to say, what we have termed *varieties*. But would it be possible to detect in early times variations of a geographical order, reproducing the *local races* so frequent among living species? The attention of palæontologists does not appear, till now, to have been much drawn to this point. A learned French geologist, J. Bergeron, who has discovered and made known the earliest fossil fauna in our country, that of the Cambrian soil of the Montagne Noire, has noticed that the Trilobites of this southern district belonged to species almost identical with those of the Bohemian Cambrian, but showing certain constant differences in the details of the ornamentation of the chitinous test. In the same way the *Conocorypha coronata* of Languedoc and Spain differs from the typical species of Bohemia by the presence of a spike instead of a tubercule on the occipital ring and by a coarser granulation of the whole surface of the head. The *Paradoxides rugulosus* is, in its turn, not quite identical with that of Bohemia, for it exhibits no tubercule on the occipital ring. With a reserve which should find many imitators, Bergeron did not deem it needful to separate these *southern forms* under a new specific name, the least inconvenience of which would have been the concealment of the natural affinities of the species of Trilobites of these two distant regions.

In Secondary times, there may be quoted, as a good example of regional variation, the two forms of the *Gryphœa arcuata,* a very characteristic species of the lower Lias or Sinemurian stage. In the Paris Basin, and as far as North Burgundy, this oyster presents itself in its classical aspect, with, that is to say, a narrow and deep shape, a large valve with a very big and very incurved top on the opercular valve, with a very pronounced furrow on one of the sides. As soon as we advance to the south, towards the Macon and Lyons districts, the beds of *gryphœæ,* then contain only rarely this northern form and we find predominating a race with a wider and shallower shell, with the top of the great valve thinner and less curved, and a fainter lateral furrow. This form, sometimes designated by the name of *Gryphœa striata,* constitutes a real southern or Rhodanian race of the same species.

In the Tertiary age the facts of the regional localization of certain forms have been better brought to light, amongst others, by Sacco for the Tertiary Molluscs of the valley of the Po, and by Fontannes for the Pliocene Molluscs of the valley of the Rhone and of Roussillon. This last scholar, of whom I have pointed out above the ultra-sectionist tendencies as regards the Ammonites of Crussol, has since become wiser by experience and much more cautious in the creation of new species. Out of three hundred and fifteen species, of which is composed the fauna of the Molluscs of the Pliocene gulf of the Valley of the Rhone, eighty are described as simple *varieties* of the species known in the Italian deposits, and Fontannes brings out the regional character of these varieties by such names as *rho-*

danicus, comitatensis, bollenensis, ruscinensis, pyrenaicus, perpinianus, etc., which indicate their geographical origin. "The only constant difference in the sub-Apennine species is the size, generally smaller in the basin of the Rhone, a difference which is only noticeable towards the end of the gulf to the north of Avignon. . . . Most of these varieties correspond to regional varieties, and would be considered as real species by sectionists à outrance." The localization of these races in the basin of the Rhone is easily explained, moreover, by the obstacle which the existence of a long Corsican and Sardinian peninsula united to Provence must have raised against the communication of Molluscs of the Rhodanian gulf with those of the Ligurian shore or of Tuscany.

These interesting facts concerning the localization of regional races at the various geological epochs would appear with still more frequency if palæontologists had not acquired the deplorable habit of designating these races by distinct specific names, which have had the consequence of breaking the natural links uniting the different forms of the same group.

Taking altogether the facts set forth above, it follows that the variability of species was the same in early times as in the present epoch. This variability shows itself by a polymorphism at times almost null, and at others intense among certain species. The result is the creation of *groups of forms,* among which we ought to make a distinction between *varieties* produced everywhere and without apparent reason round some specific central type, and *local* or *regional races* due to the circumstances of the environment, and which sometimes are perceptibly removed from the original type. These *forms,* too often considered by the naturalists describing them as *distinct species,* are nearly always linked together by imperceptible transitions. But it is important to remark that these *groups of forms,* assembled round a central type, like the different stars round a nebula, have a veritable objective reality, and almost always remain sharply separated from the neighbouring groups, if we neglect a few extremely rare cases of hybridization. These are the groups which answer, or should answer, to the *true definition of the species* characterized at once morphologically, genetically, and geographically. It is in this sense that we are able to affirm *that the great species do not pass gradually from one to the other,* either in existing nature or at any of the early epochs in the life of the globe.

This conclusion, which could easily have been foreseen a priori, is, moreover, in no way contrary to the descent hypothesis. If this hypothesis is correct, we must admit that the transformation of species must have corresponded to phenomena of the same order as those to which we owe our *local* races—that is to say, to a prolonged isolation in very different conditions of environment. It is already remarkable to see how these *local races* in living nature at times depart from the original type.

It would be irrational to suppose that this departure could, in one epoch, go as far as a complete separation of two great species ; and observation shows us, in fact, that groups of forms usually remain distinct. To obtain so considerable a transformation, it is evident that there must be a prolonged intervention of modifying causes. It is with this *action of time* that we will now deal.

CHAPTER XVI

VARIATION IN TIME

Two ways of studying evolution in time—Approximate method —Method of actual evolution—The series of forms or phyletic ramifications—Polyphyletic genera—Discontinuous series—Varying rate of evolution of branches.

PALÆONTOLOGICAL evolution, that is, the transformation of animal forms through the series of ages of the earth, of all evidence constitutes the most direct and the most demonstrative proof of the transformist hypothesis. Rather neglected by the creators of the descent theory, chiefly on account of the scarcity of documents, it has become, on the contrary, in the last thirty years of the nineteenth century, the principal object of the efforts of modern palæontologists.

The study of the changes of fossil animals has been approached in several ways. The most logical, and, at the same time, the most exact, is the patient and close reconstitution of the gradual series of forms through which a given branch of the animal kingdom has passed when rising from one geological stage to another, and even, if possible, from one stratum to another of the same stage. With this method we connect the names of Waagen, Neumayr, von Zittel, Hyatt, Mojsisovics, Osborn, Schlosser, Stehlin, etc.

It may be termed the *method of real evolution*, because it leaves as restricted a place as possible for the establishment of hypothetic affiliations ; it is likewise the one we have constrained ourselves to follow personally in all our researches.

But before setting forth the very interesting and positive results obtained by this rigorous method, it is necessary to say a few words and make short work of another and more hypothetical method, by means of which the history of evolution becomes a sort of *representative* image of the changes in beings, instead of corresponding to the real picture of past events. This approximative method has been partly employed in the works of Huxley, Kowalevsky, Marie Pavlow, and in the highest degree in those of Gaudry and his school. It consists, when one is given a genus of existing or recent animals of which we wish to study the genealogy, in seeking in the series of earlier geological periods for some other genera presenting a certain degree of analogy with the first in the structure of an organ or of a small number of organs, and in composing by the help of these genera an apparently natural series by the aid of mere modifications of the organs thus under consideration. In the case of the Mammals, for example, we should take as criterion either the structure of the molars, or of the canines, or the progressive reduction of the lateral toes, or, again, the gradual development of the nasal bones, or of horns or antlers, leaving on one side, or nearly so, the rest of the organism. In the Ammonites, notice would be taken exclusively of the greater or less complication in the lines of suture, ignoring the general form of the shell, its style of ornamentation, the arrangement of the mouth, etc. We do not trouble overmuch, moreover, about the chronological order of the appearance of the fossil forms which one puts in series. Thus to establish the pedigree of the Ursidæ, Gaudry and Boule introduce between the Hyænarctos of the upper Miocene and the first Ursi of the Pliocene an actual genus, the *Œluropos* of China, because this animal realizes, from the point of view of the progressive development of the tuberculous teeth, an intermediate state between the two genera it is sought to connect. These are absolute anachronisms, and, to my mind, utterly inadmissible.

This method assuredly presents the greatest dangers, because it leads one to confound with the *real evolution* of a group what is, in fact, simply the *functional evolution* of an organ in a series of genera belonging to different natural branches having no kind of ancestral kinship between them. It could not fail to lead to the manufacture of artificial and incorrect concatenations, as I have already had occasion to point out regarding the families of the Horses and the Bears. It may not be useless to give a few more examples. The evolution of the family of the Rhinoceroses has been studied by Gaudry from the gradual development of the nasal bones since the *Palæotheria* of Eocene times down to the two-horned rhinoceros of the present day. The series commences with the *Palæotherium medium*, whose slender and short nasal bones suggest the existence of a fleshy trunk;

then comes the *Palæotherium crassus,* in which the larger nasal bones no longer leave room for a trunk; afterwards comes the rhinoceros without horns, or *Acerotherium*; first the *Acerotherium incisivum* of Eppelsheim, with nasal bones almost as small as in the *Palæotherium crassum,* and then the *Acerotherium tetradactylum* of Sansan. Horns begin to appear with the rhinoceros of the sandy district of Orleans, which is furnished with a very small nasal horn. In the *Rhinoceros Schleiermacheri* of the upper Miocene the bones of the nose are slightly larger than in the Orleans species; they become still thicker in the *Rhinoceros pachygnathus* of Pikermi, already furnished with a nasal horn and a second frontal one; in the *Rhinoceros etruscus* of the Pliocene the nasal bones are supported from beneath by a partly ossified partition; finally, in the *Rhinoceros tichorhinus* of the Quaternary they have become as massive as possible, and are supported throughout their length by a bony partition. Without even referring to several anachronisms, no palæontologist would hesitate to affirm that this pedigree is incorrect in almost all its parts. There exists no transitional form between the *Palæotherium* and the group of rhinoceroses, for the simple reason that the latter arrived suddenly in Europe towards the commencement of the Oligocene period, by a migration probably from America. On the other hand the *Acerotheria* are not the ancestors of the horned rhinoceros; the appearance of this last in Europe, at the commencement of the Miocene, is likewise the result of a sudden migration of Africano-Asiatic origin. Lastly, even in the true rhinoceros, the above-mentioned series *links together* species, such as the *Rhinoceros Schleiermacheri* and the *Rhinoceros pachygnathus*, which have nothing in common and correspond to the parallel evolution of two distinct branches. It may, therefore, be said that Gaudry has studied, not the evolution of the rhinoceros group, but simply the gradual thickening of the bones intended to support the horns in a series of genera in no way related. Almost similar functional series might be described in all the other groups of horned vertebrates.

The functional organization of a paw destined for burrowing in the earth gives rise to almost identical structures, whatever the group to which the burrowing animal may belong. The ungual phalange becomes very large, and is provided with a groove to receive the insertion of the horny claw. But this burrowing arrangement is awkward for progression, so that special dispositions of the articulations of the joints with the metacarpus allow the animal to raise the digits and to walk on the palm of the hand. This structure may be observed more or less developed in several genera of existing animals, the Tatus, Pangolins, etc., forming part of the order—a not very natural one, by the by—of the *Edentata*. Misled by his constant habit of comparing functional adaptations, Gaudry could not fail to see a transition between the Edentata and the Ungulata, in that curious family of Tertiary Mammals, the *Schizotherium*, the *Macrotherium*, and the *Chalicotherium*, in which the front paw presents in the highest degree the burrowing structure above described. But, in reality, there exists no kind of relationship between these strange Chalicotheridæ and the existing or early Edentata. A deep study of the structure of the cranium, of the vertebræ, of the bones of the arm and forearm, and of the tibia, clearly shows that we are dealing with a true Ungulate, exceptionally adapted for burrowing functions.

Taking up the difficult problem of the origin of the Apes, Gaudry solves it by relying solely on the conical form of the denticles which bristle on the crown of the molars in several of the existing Apes, the Macaques, for instance. He believes that these Apes are closely related to certain Tertiary Ungulata, the *Acotherulum*, the *Hyracotherium*, and especially the *Cebochœrus* of the Vaucluse lignites, whose molars, furnished with four rounded denticles, have a singular resemblance to those of the Apes. "Gervais had the happy idea of dubbing this animal "with the name Cebochærus (ape-pig), which well "expresses its relations with the Pachyderms as "well as with the Apes." But while some fossil Pachyderms show a tendency towards the dentition of the Apes, there is an ape, the *Oreopithecus* of the Italian Miocene, which appears to have retained in its molars some vestige of the Pachyderm form. There is hardly need to say that there is nothing serious in these hypotheses; on the one hand, the Cebochærus, from all its characteristics, dental and cranial, is, undoubtedly, a true Suides in no way connected with the Primates. On the other hand, is it not known that the rounded denticles of the molars indicate a simple adaptation to an omnivorous diet, and are found, to a more or less perfect degree, in the most diverse representatives of nearly all orders of Mammals ?

These examples, which it would be easy to multiply as regards other groups of fossil animals, will suffice to explain why modern palæontologists have abandoned these *approximative methods*, which lead, almost fatally, to a *fantastical evolution*. Perhaps these crude theories may not have been useless in the past, when there was a struggle to bring about the acceptance of evolutionary ideas ; but they are now unfavourable to progress by fostering illusions as to the real state of advancement of our science. The time has come when *palæontological evolution* should be the history of what has really taken place, and not a poetic image of what might have occurred in early times.

Let us now return to a more scientific method, of which the essential theme is the exact and minute reconstitution of the *real branches* which represent the *direct* genealogy of our animal forms. The inception and merit of this must be accorded to the remarkable researches of the Austrian palæontologists on the *Formenreihe*, literally the *series of forms*—a term which I prefer to render by the more expressive name of *phyletic branches*. The process of reconstruction of these series, simple as it is in theory at any rate, consists in following step by step in a succession of regularly superposed and continuous geological strata, the chronological variations of the same type or of types sufficiently linked together by their natural affinities for their genealogical relations to force themselves upon any impartial observer. For these series to be demonstrative, it is plain that there must be no *lacunæ* in them, or that such *lacunæ* should be so infrequent as not to interrupt the general view of the continuity of the variation. Each of the closely linked terms of any series has received from Waagen the name of *mutation*, a term which it would be most advantageous to use more frequently than we do in palæontological nomenclature by designating as *ascending mutations* the forms which follow each other while rising to our present period, and *descending mutations* those met with when sinking into ever earlier strata. It thus becomes possible to recognize the intensity of the chronological variation, that is to say, the *action of time* on the characteristics and structure of one zoological type. And I purposely employ in this first sketch the rather vague term of *type* instead of the terms *species* or *genus*, because we shall have to discuss later on how these two degrees in the zoological hierarchy may be introduced between the different terms of the same phyletic and well-arranged series.

The first *series of forms* well studied and solidly established were first discovered in the world of Invertebrates. Waagen made us acquainted with the series of mutations of a group of Jurassic Ammonites, that of the *Ammonites subradiatus*. Neumayr, extending this fertile idea, illustrated it with the magnificent example furnished by the series of *rapid evolutionary* forms of the Pliocene Paludines of the Danube basin. I must refer the reader to the summary indications already given regarding the researches of Neumayr on this fine phyletic series.

THE POLYPHYLETIC GENERA.—But this learned palæontologist has taken us still further into the natural processes of realization of these phyletic series. He has shown us, in fact, in his brilliant study on the Ammonites of the genus *Phylloceras*, that each great genus, however homogeneous it may appear, does not evolve in one single line, but really comprises a series of parallel branches of simultaneous evolution of unequal duration. We are here confronted by a truly general law of the highest importance, which seems to justify a rapid analysis of the evolution of the genus *Phylloceras* so well studied by Neumayr.

The *Phyllocerata* are closely coiled shells, the last whorl of which completely envelops the inner ones. It has a smooth surface, or one very slightly ornamented with fine stripes, excrescences, or transverse furrows. This genus, which is very homogeneous, if we consider its numerous species as a whole, is especially characterized by the leaf-like termination of the prominent parts of its sutures, whence the generic name given to it by Ed. Suess. The family of which this genus forms part is known as early as the Trias; but the *Phyllocerata* properly so-called only commence at the infra-Liassic epoch, and continue as far as the Upper Chalk. Neumayr recognized among the Jurassic and Cretacean forms five parallel phyletic series which he describes as follows :—

1. The *Phylloceras heterophyllum* series, with either a smooth shell or one ornamented with fine

transverse stripes. This branch goes from the lower Lias to the Turonian.

2. The *Phylloceras Partschi* series, with the last whorl ornamented with large folds with transverse stripes. This branch extends from the Lias to the Barremian.

3. The *Phylloceras tatricum* series, with a shell ornamented with transverse excrescences at intervals, but not striped. This extends from the lower Jurassic to the Barremian.

4. The *Phylloceras capitanei* series, ornamented with from four to nine constrictions, directed obliquely forward. Extends from the middle Lias to the end of the Jurassic.

5. The *Phylloceras ultramontanum* series, ornamented with constrictions first directed forward, then bent back at right angles and towards the rear. Has besides coarse stripes on the outer half. Extends from the lower Jurassic to the Valanginian.

These five series follow one another clearly, with a richness of form varying with the epoch and the series ; but they possess a somewhat different vitality. The fourth does not go beyond the Jurassic ; the fifth reaches the Valanginian ; the second and third persist up to the end of the Neocomian ; and finally, the first alone survives the Jurassic and the lower Cretacean period and ends in the Chalk.

Most of the genera called *bushy*, that is to say rich in species, exhibit an evolution by parallel branches similar to that of the *Phyllocerata*, and merit, like the latter, the name of *polyphyletic genera*. Very numerous examples may be quoted in the great group of Ammonites, the *Lytocerata*, the *Arietitæ*, the *Perisphinctæ*, and the *Hoplites*, to mention only the most typical. The polyphyletic genera are also very common in the other groups of Invertebrates: the Spirifers, the Rynchonellæ, the Terebratulæ, among Brachiopods; the Oysters, the *Pectines*, the Trigoniæ, the Pholadomyæ, the Hippuritæ, among the Lamellibranchs; the Pleurotomaries, the *Trochi*, the Paludines, the Turritella, the Nerineæ, the Cerithia, the Nassæ, the Pleurotomas, the Murices, the Coni, among the Gastropods; and the *Orthocerata*, the Nautiluses, among the tetrabranchial Cephalopods, are examples very familiar to all palæontologists. I shall show further on, that polyphyletism is also very evident in a certain number of the genera of Tertiary Mammals. It can already be foreseen that all, or nearly all, the genera of fossil animals when they have been studied with precision in their mutations, will become more or less *polyphyletic*. Monophyletism is hardly noticed except in genera poor in species, apparently endowed with a vitality of very little energy, and showing a weak tendency to variation in time. Perhaps even this monophyletism is only seeming and provisional, and is limited to certain periods and to certain regions for the same type, and is, no doubt, subject to intermittences in the expansive force of the branch.

Discontinuous Series.—The essential criterion of a phyletic series is continuity. There exist, however, a pretty good number of indisputably natural branches in which this continuity is interrupted by gaps, that is to say, by the absence now and then of some of the mutations necessary to complete the series. A very clear example of these *discontinuous series* is offered by the evolution of the Gryphæa, a genus akin to our oysters, but distinguished by a deep left valve with a top more or less incurved, and a flat and opercular right valve. The earliest species is the *Gryphœa arcuata*, which forms immense beds in the lower Lias, and presents in a high degree the characteristics of the genus, viz.: a narrow and deep shape of the large valve, the top of which is very thick, and sharply bent over on to the small valve. As early as the higher part of the Lias a first mutation is met with which has received the name of *Gryphœa obliqua*. The shell here is less deep, wider, and the top smaller and less incurved. If we go to the middle Lias, another form is found: the *Gryphœa cymbium*, a little larger in size, and the shell wider, much deeper, with a top thin and slightly bent back. Then the series momentarily disappears in the higher Lias, the Bajocian and the Bathonian, to reappear in the Callovo-Oxfordian marls under a form slightly modified, larger and more spread out in width, which has rightly received the name of *Gryphœa dilatata*. The branch ceases to show itself in the last stages of the Jurassic, and in the whole of the lower Cretacean, and when it reappears in the higher Chalk with the *Gryphœa proboscidea* and *vesicularis*, the characteristics are strongly modified: the general form of the shell is much greater in width and almost circular, the top is blunt and but little bent over as if merged into the rest of the shell. Its general appearance so slightly resembles that of the Gryphæas of the Lias as to make one question whether it is really a prolongation of the same branch.

Another fine example of discontinuous series is offered to us by the bivalve Molluscs of the family of the *Megalodontidæ*, which have thick shells, triangular in form, with flattened and slightly spiral tops, and furnished with strong teeth in the hinge. The earliest representatives grouped under the generic name of *Megalodon* appear in the middle Devonian of the Eifel under the form of the *M. cucullatus*, with a relatively small and sub-rounded shell.

We must then go up to the top of the Trias of the Eastern Alps to again meet with, in the limestone of the Dachstein and the Hauptdolomit, the *Neomegaladontidæ*, now become gigantic and modified in some of the details of their hinge. The branch then prolongs itself in a more or less continuous manner through the Rhætian and the Lias, and after another gap we may see it terminate in the *Pachymegalodon* of the upper Jurassic with a very thick shell.

In the group of Ammonites a learned specialist, Gustave Sayn, has shown that the *Pulchellia* of the Barremian stage, with its elegantly ornamented shell, should be genetically attached to the smooth and discoid Ammonites of the Valanginian, which he designates by the name of *Garnieria ;* these in turn are connected with the *Oxynoticeras* of the upper Jurassic of Russia, and the latter might perhaps be, notwithstanding the enormous geological *lacuna* which separates them, the direct descendants of the typical *Oxynoticerata* of the lower Jurassic.

Without multiplying further these examples of discontinuous or intermittent series, it will be seen what special difficulties these gaps cause in the certain reconstitution of phyletic branches. It may, however, be hoped that these difficulties will disappear, one by one, as more complete geological researches enable us to discover the intermediate links which for the moment are unknown.

VARIABLE RATE OF THE EVOLUTION OF BRANCHES.—Nothing seems to have been more variable than the rapidity of the comparative evolution of the different phyletic branches. In a certain number of them the chronological modifications are insignificant or almost null during nearly the whole duration of the geological periods. An often quoted example is that of the genus *Lingula*, belonging to the group of inarticulated Brachiopods characterized by a thin, chitinous shell, with equal valves, subrectangular in form, with a somewhat prolongated top, and fixed to submarine bodies by a long, flexible pedicule. The *Lingulæ* figure among the earliest organisms known in the Primary seas. Without taking into account the *Lingulella* of the Cambrian, which would appear to constitute a small independent branch, the true *Lingulæ* first appear in the Silurian, where they comprise, according to Bigsby, about a hundred species. They are already diminished in numbers in the Devonian and the Carboniferous strata, and still more so in Secondary and Tertiary times. But the branch none the less persists down to the tropical seas of the present day, where they are fished up from a slight depth. If we compare one of the earliest species of Lingulæ, for instance, the *Lingula Lewisi* of the Silurian of Gothland, with the living *Lingula anatina*, we shall hardly note any other modification than the greater size of the existing shell, its rather narrower form, and its rather more triangular top. It may thus be said that the evolution of the phyletic branch of the Lingulæ has been almost null since the beginning of Primary times. No doubt this remarkable slowness of evolution bears relation to the constancy of the conditions of the marine environment in which these animals have lived.

Numerous examples of slow evolution as remarkable as that of the Lingulæ are known in the history of palæontology. The genera *Lagena* and *Rotalia*, of the order of Foraminifera, extend from the Silurian to our own day. The regular Urchins of the *Cidaris* type are known from as early as the Permian, and still exist in our tropical seas. The Brachiopods of the genus *Crania* have lived, like the Lingulæ, from the lower Silurian to the present time. In the Lamellibranch Molluscs, the living genus *Solenomya* commenced in the Carboniferous strata ; the present *Nuculæ* and *Ledas* are found in the series of strata from the Silurian onward ; in the Jurassic some *Pinnæ* are known, very slightly different from living forms ; the *Trigoniæ* constitute a numerous series of parallel branches in the Jurassic and the Cretacean, and have persisted, though much reduced in importance, down to our existing tropical seas ; the interesting family of the Pectinidæ comprises *Chlamydes* from the Triassic period, and *Amussia* from the Lias; the marine mussels or *Mytili* have changed little since the Trias. The Gastropods also show a few branches with very tenacious forms; the pateloïd shells of the genus *Acmæa* have existed with hardly any modification since the Cambrian; the rare *Pleurotomaria* of the present day is connected with a series of very abundant forms in the Jurassic; the Fissurellæ, the *Pseudomelaniæ* have been known since the Carboniferous; the *Capulus* is present in the whole series of fossiliferous strata; the existing *Actæonina* commences with the Carboniferous; the terrestrial Pulmonates of the *Pupa* group have been discovered as early as the Coal. The bivalve carapaces of the Phyllopod Crustacea of the type *Estheria* abound in the brackish deposits of all epochs, from the Devonian to the Quaternary; that of the Ostracods of the living genera, *Bairdia*, *Cytherella*, and *Cypridina*, go back as far as the Ordovician. The Balana of the genus *Creusia* have fixed themselves to rocks ever since the lower Devonian. The present Limuli have for precursor a small species discovered in the lower Trias of the Vosges. The *Eoscorpius* of the Carboniferous strata of Illinois and the *Protolycosa* of the Coal of Silesia differ but little from our present scorpions and our existing spider *Lycosa*.

As a set off, other phyletic branches have had a more rapid evolution. I have already referred to the curious example of the Levantine *Viviparas* which, during the Pliocene epoch alone, passed from their first smooth form to carinated and tuberculous forms, such as the *Vivipara Sturi* and *Hornesi*, sufficiently different in aspect to the true *Vivipara* for some malacologists to separate them from these last under the generic name of *Tulotoma*.

In the course of the geological ages a few groups can be named, the different parallel branches of which have appeared and rapidly disappeared. The enormous Brachiopod *Stringocephalus* is only known from the upper Silurian to the middle Devonian, and the strange *Uncites* is even limited to one single zone of this last rock. The bivalves of the *Cardiola* group also only lived during the Silurian and the Devonian. Most of the branches of the great family of the *Rudistæ* or Chamidæ have a very limited duration: the *Dicerata* are stationed in the higher Jurassic, the Requienias in the Urgonian, the Hippuritæ in the Chalk beginning with the upper Turonian. Among the Pteropods, the curious family of *Tentaculites* has only lived from the Silurian to the Devonian. Among the Gastropods, the *Lychni* are quartered in the Danian. Many branches of Nautilids appear and vanish in the Silurian epoch alone. Among the Ammonians the isolated group of the *Clymenias* completes its evolution in the upper Devonian. Finally, most of the families of Trilobites have a very brief evolution: the Conocoryphids in the Cambrian, the Olenids and the Agnostids in the Cambrian and the Ordovician, and the Asaphids and the Trinucleidæ in the Silurian only.

In a pretty general way it may be said that *the rapidity of evolution of a group is in inverse ratio to its longevity.* The phyletic branches which extend through the whole or a great part of the geological periods most often undergo but slight modifications; as, for instance, the Lingulas or the *Capuli*. On the contrary, the short-lived families, like the Trilobites of the Cambrian, the Rudistæ of the Cretacean, and the Arietitæ of the Lias, reveal a more energetic vitality, which betrays itself by rapid changes in passing from one stage to another, or even from one stratum to another. Thus stratigraphers advantageously use these rapidly evolving branches as a chronometric scale, that is, as fossils characteristic of different zones of the same stratum.

It is, however, possible that the feeble longevity of certain branches is much more apparent than real, and is due to provisional gaps in our observations. If, in fact, the dates of the extinction of each group are almost always known with certainty, it is not the same with the dates of their first appearance. Later discoveries are, no doubt, preparing for us the surprise of seeing that the origin of these branches which are supposed to be very short, is carried further and further back into the depths of the sedimentary strata of the earth's crust. The study of the evolution of the Vertebrates will, later on, furnish us with many proofs of this.

CHAPTER XVII

PHYLETIC BRANCHES AMONG THE VERTEBRATES

Branches of rapid and of slow evolution among the Fishes, Amphibians, and Reptiles—Phyletic branches among the Mammals—Marsupials and Multituberculata—Anthracotherids—Proboscidians—Conclusions.

In studying the laws which govern the evolution of phyletic series we have, until now, taken all our examples from the Invertebrates, for the historical reason that these animals have furnished Waagen, Neumayr, and other palæontologists with their materials for study and the first really demonstrative facts.

The evolution of the Vertebrates remained for a long time a stranger to these methods; or, at any rate, the specialists engaged upon them preferred to take other lines. Instead of setting themselves to follow step by step—going back stratum by stratum through the series of sedimentary deposits—the slow and gradual mutation of a given branch, these palæontologists thought themselves very early in possession of documents sufficient to enable them to retrace the genealogical links, not only of genera and of families, but often of the orders and even of the classes of the animal kingdom. These syntheses possess a brilliant side well calculated to captivate superficial minds or those little versed in the science of palæontology, but it must be owned that they have nearly always ended in erroneous conclusions. I have already had occasion, in a former chapter, to criticize this method, and to show by examples drawn from the attempts at affiliation made with the Equidæ, the Ursidæ, the Rhinoceroses, the Apes, etc., that the precipitate linking of one genus to another by trusting to analogies in the structure of an isolated organ or of a small number of organs, has resulted in the setting up of *artificial pedigrees*, showing a descent one from the other of genera which have never had any *real genealogical connection*.

Another error of this hasty method is the attribution of much too short duration to the evolution of each branch. It has been often repeated that the evolution of a group was the more rapid the higher the place occupied by it in the scale of beings. The Tertiary Mammals have always been appealed to in support of this rule. Do not the remarkable transformations of the placental Mammals seem, outwardly at least, to have been wholly accomplished during the relatively short space of time represented by the Tertiary strata? Formulated thus, this proposition is much too exclusive.

Assuredly some branches have always existed among the Vertebrates, such as those of the Placodermal fishes like the Labyrinthodonts and of the Theromorphs, the rapidity of whose evolution may be compared to that of the Trilobites and the Rudistæ. But it is now extremely probable that the majority of the families of the Ungulata, of the Creodonts, and of the Primates, have an evolution not confined to the Eocene epoch, and must in some as yet unknown country cast deep roots into Secondary times. In any case, a jump such as those described, which would transform in the period elapsed since the Oligocene a Palæotherium into a Horse, and in that since the middle Miocene an Amphicyon into a Bear, does not correspond to the real facts.

As we have seen above, in the case of the Invertebrates, the phyletic branches are, in a general way, extremely long, and continue parallel without meeting during a long geological period. With these reservations, I will endeavour to show that all the laws of evolution of the phyletic series, established by the help of the lower animals, are met with among the Vertebrates without any exception whatever.

It is only, we may say, in the last few years that palæontologists have set themselves in a connected fashion to precisely reconstruct the phyletic branches among the Vertebrates, and more especially among the Mammals. Yet it has been long known that a few types of the lower Vertebrates manifest great geological longevity. The Squalaceous [shark-like] type seems to have varied little since its first appearance at the end of the Silurian. Thus the grey Sharks of the genus *Notidanus* have left certain remains in the Lias, and had perhaps precursors in the Coal.

The Sharks of the *Cestracion* type, which inhabit the warm regions of the Pacific, have, as ancestors, the *Acrodus* of the Secondary and the *Orodus* of the Carboniferous era, and the branch probably goes back as far as the Silurian. The Lamias or *Lamnidæ,* with long triangular teeth, have appeared since the Carboniferous epoch. The genus *Squatina* or Sea-Angel has representatives very near to the present type, in the lithographic limestone of Bavaria, and, perhaps, in the Permian of Thuringia. The group of existing *Chimæras,* with the mandible completely welded to the cranium, dates at least from the Jurassic, and even, according to Newberry, from the Devonian. The sensational discovery of the Dipneuston named *Barramundi,* in the rivers of Queensland, which was recognized to be identical in kind with the *Ceratodus* of the Trias, is still in the minds of all naturalists. The Polyptera of the Nile is, no doubt, the little modified descendant of the rhomb-scaled Ganoïds, such as the *Osteolepis* of the Devonian red sandstone. The two branches of the existing American Ganoïds, *Lepidosteus* and *Amia,* go back at least to the lower Eocene. The type of our pike or Esocidæ already exists with few modifications in the upper Cretacea of New Jersey; the genus herring or *Clupra* in the Neocomian of the Voirons. The salmon has for precursors the Osmeroïdæ of the English Chalk; the genus *Beryx* goes back to the higher Cretacean. The anurous Amphibians of the Toad group are now known even in the upper Jurassic. The swimming marine Reptiles of the Ichthyosaurus and Plesiosaurus types have evolved into numerous branches in the Secondary seas from the Trias till the end of the Cretacean, and we may expect to some day discover their precursors in Primary strata. The highly specialized group of the Chelonians is already represented, from the upper Trias onwards by the two much-differentiated types of the Shield Turtles or Dermochelydæ, ancestors of the existing *Sphargis*, and of the pleuroderic Elodites, which continues in the genus *Podocnemis* in the fresh waters of South America. The *Sphenodon* of New Zealand is to-day the sole representative of an ancient branch of reptiles, the *Rynchocephalians* very common in the shallow seas of the upper Jurassic of our own country, and may be traced with slight modifications as far as the Permian red sandstone of Saxony. The Lacertians of the Varans family are already represented in the lower Cretacean of the isle of Lesina by a hardly distinct form of the existing *Hydrosaurus*. We see clearly by these examples that the longevity of certain phyletic branches of the Fishes, Amphibians, and Reptiles in no way yield the palm to that of the majority of the branches of the Invertebrates.

A demonstration as complete as this is awkward to furnish in the actual state of the science, in the case of the higher Vertebrates, and especially of the Mammals. However, we know already that the first origin of the mammalian trunk goes back extremely far, and is very certainly earlier than the upper Trias, the earliest stage in which there has been noted the existence of true Mammals coming within the normal type of structure of this class. That Triassic Mammal, the *Dromatherium sylvestre* of North Carolina, as far as can be judged from the one half-mandible known till now, assimilates closely enough to the type of the *Marsupiales polyprodontes* (with more than four incisors in each jaw) for Osborn not to hesitate to consider it as the ancestral form of our small carnivorous Marsupials, such as the existing Didelphs or Sarigues. We here see, then, a first branch of lower Mammals which extends, with few interruptions and geographical displacements, from our present period back to the Trias, and probably very much further.

The order of the *Multituberculata* supplies us with a second branch of quite as great geological longevity. We have from the Rhætian of Wurtemburg and England the isolated molars of a quite small Mammal, the *Microlestes*, which, notwithstanding the paucity of proofs, really seems to be the most ancient known representative of the family of *Plagiaulacidæ*. The genus *Plagiaulax*, the type of the family, is also only known by some small mandibles furnished with a large conical incisor analogous to that of the Rodents, with four compressed molars, sharp at the top, and ornamented with oblique lines on the sides, and, lastly, with two little cup-like posterior molars surrounded by five small tubercules. The *Plagiaulax* has been found in the strata of Purbeck, that is to say, in the last layers of the Jurassic, and, notwithstanding the great geological lacuna which separates it from the *Microlestes*, no palæontologist disputes the close affiliation of these two genera. After another no less important lacuna, which comprises nearly the entire Cretacean, we find in the terminal strata of the American Cretacean (Laramie stage) a new representative of this family, the *Ctenacodon*, and, a little later, in the lower Eocene of Cernay near Rheims, another form so closely allied to the

Plagiaulax that Lemoine has bestowed on it the name of *Neoplagiaulax*, which implies a direct ancestral relationship. The small Plagiaulacides of Rheims only differs, in fact, from the Jurassic genus by the reduction in number of the pre-molars, which from four come down to one, this single pre-molar becoming enormous while retaining the sharp edge and the elegant oblique striæ characteristic of the branch.

Finally, after a new disappearance for the whole of Tertiary times, we have to seek the probable descendants of the *Plagiaulax* in the Diprotodont Marsupials (with two lower incisors only) of the Australian Continent, such as the gigantic *Thylacoleo* of the Quaternary of Queensland, or, perhaps, the small kangaroo-rats or *Hypsiprymnus*, of which the long conical incisor and the large pre-molar recall in a striking manner the dentition of the *Neoplagiaulax* of Rheims. The phyletic branch of the Plagiaulacidæ thus presents all the features of slowness and discontinuity of evolution which we have noted in the most classic series of forms of the group of the Invertebrates.

We now arrive at the higher or Placental Mammals, which have always been used as an argument, seemingly decisive, in favour of a rapid evolution of these different branches. It is certain that in the present state of science—leaving aside for the moment the question, still vexed, of the Cretacean Mammals of Patagonia—the placental Mammals appear, both in Europe and in the United States, only in the very lowest strata of the Tertiary. The faunas of Puerco and of Torrejon in America, and that of Cernay-les-Rheims in France, are the first faunas where, side by side with Multituberculata and polyprodont Marsupials, we note the presence of undoubted placental Mammals. But it should be remarked that already, from the ancient epochs of the lower Eocene, the Placentals are differentiated into distinct groups, in which it is easy to recognize the representatives of several orders, some extinct, like the *Condylarthra*, the *Amblypods*, the *Tillodonts*, and the carnivorous *Creodonts;* the others, the Insectivora and the Primates, continuing with light modifications to our own time. Perhaps, as has frequently been said, the differential characters of the orders are not, in these early faunas, as sharply separated as in our time; or perhaps a few types of Cernay or of Puerco present some *mixed* or *inclusive* characters which, at times, render it difficult to attribute this or that genus to the Creodonts or the Condylarthra, or to these last or the Primates respectively. In any case, this *effacement* of the limits between the orders, which so much struck Dr. Lemoine in his excellent studies on the Mammals of Cernay, seems to me to have been singularly exaggerated by some pseudo-philosophical palæontologists, who strive to see links everywhere, and thus run the risk of confusing everything. It cannot be denied that the first fauna of Placental Mammals known already shows very evident differentiations in several directions, an important fact which necessarily implies the earlier existence of placental faunas still less differentiated, which we may expect later on to discover far back in Secondary times.

Thus limited by the small progress in palæontological exploration to the study of the Tertiary mammals alone, we may yet point out even now some phyletic branches, the *real evolution* of which continues over a notable part of Tertiary times. To our knowledge, one of the longest branches it is possible to reconstruct with certainty at the present time is that of the family of *Anthracotherides.* The theoretical importance of this demonstration induces me to enter here into a few details.

The Anthracotherids belong to the Sullian Paradigits, that is to say, to the Ungulates with an even number of digits bordering on the Swine, with whom they have many points of structure in common. They are distinguished from the Suidæ by the profile of their skulls, which are lower behind, less raised in the occipital region, and by the less bunodontal type of structure of their molars—that is to say, these teeth are formed of denticles more or less compressed into half-crescents, instead of being almost regular cones; this last type, which is that of the Swine, seems adapted to a more completely omnivorous diet. This family of the Anthracotherids, which predominates in a maximum degree in the Oligocene epoch, is easily separated into a fairly large number of phyletic branches, of which the three principal are: (1) the *Anthracotherium* branch, characterized by a moderately long skull, and by molars having five short and conical tubercules (type Brachybunodont); (2) the *Brachyodus* branch, with a not very long skull, and molars having five short tubercules, half-crescent shaped (type Brachyselenodont); (3)

the *Ancodus* branch, with very lengthy muzzle and cranium, and molars with very long denticles in half-crescents (type hypsoselenodont). The third branch, that of the *Ancodus*, is very short, and limited, as far as we know, to the later part of the Oligocene epoch. The other two branches, on the contrary, are both very long, and, while remaining distinct, persist from their simultaneous appearance in the middle Eocene or Lutetian stage. One of them, the *Anthracotherium*, continues down to the end of the Oligocene or Aquitanian stage; the other, the *Brachyodus*, as far as the lower Miocene or Burdigalian stage. I have personally, and with care, studied the phyletic series of the Brachyodus of the middle Eocene down to the lower Miocene, the lengthy space of seven great geological stages, and have established the very gradual series of mutations in the Table on page 177.

The variation of the series of the Brachyodus consists: (1) in a gradual increase in size from an animal no larger than a Chevrotain to one as large as our Rhinoceros; (2) in the progressive reduction of the pre-molars which are long and a continuous series in the early forms, but become shorter and reduced in proportion in recent types, while, at the same time, the first, and sometimes the second, are separated by intervals from the other pre-molars, as well as from the canine; (3) by the rapid increase in size of the upper canine, which becomes a kind of dagger with crenellated edges in the *Brachyodus borbonicus*, and a long triangular tusk in the *Brachyodus onoidens*. But, notwithstanding these differences, of great importance if we consider the ex-

Lower Miocene	Burdigalian Stages	*Brachyodus onoidens*	Large animal equal in size to an ordinary Rhinoceros: enamel of the molars finely wrinkled, large triangular canines.
Oligocene	Aquitanian Stage	Mutation still unknown in the fauna of Saint Gérand-le-Puy.	
	Upper Stampian Stage	*Brachyodus borbonicus*	Size of large boar, aquatic and carnivorous animal: long canines compressed, with crenellated edges.
	Lower Stampian Stage	*Brachyodus porcinus*	Size of small pig, characters much the same as the above.
	Sannoisian Stage	*Brachyodus porcinus*	Identical with the last as to molars.
	Sannoisian Stage	*Brachyodus Cluai*	Species the size of the B. porcinus, but with slightly more bunodont molars; probably represents a small lateral shoot from the branch.
Eocene	Ludian Stage	*Brachyodus Crispus*	Notably inferior in size to the B. porcinus and Cluai species; only a few molars belonging to it are known.
	Bartonian Stage	*Catodus robiacensis*	This form differs somewhat notably from the last by its smaller dimensions, its flatter molars, and its pre-molars longer and in continuous line; to be placed with difficulty in the same genus.
	Lutetian Stage	*Catodus Rutimeyri*	Characters identical with those of the Bartonian species, but of still smaller dimensions. Size not larger than that of a small Chevrotain.

treme terms of the series, there remains none the less between all these animals a family likeness, which, thanks to the paucity of transitions, gives one the idea of a direct affiliation. Lastly, I will remark that this branch of the *Brachyodus* only presents one fairly restricted discontinuity between the upper Stampian and the lower Miocene. We are commencing, moreover, to recognize a small-sized mutation of the *Brachyodus onoidens* from Chitenay, which already diminishes the wholly provisional gap which separates the Stampian type from the large species of the sands of the Orleanais.

It would be easy to construct a series, analogous to the preceding, among the *Anthracotheria*, a branch in which the highest term only is lacking, for the reason that this group became extinct at the end of the Oligocene. On the other hand, while the Brachyodus have shown us an almost monophyletic branch, with the exception of the small lateral twig of the *Brachyodus Cluai*, the Anthracotherium series is polyphyletic, and ought itself to be broken up into three parallel sub-branches, of which two are constituted of small forms, and one leads up by a gradual increase in size to the *Anthracotherium magnum* of the higher Oligocene, with dimensions comparable to those of the great Miocene *Brachyodus*.

Instead of describing in detail the mutations of the *Anthracotherium*, it seems preferable to change to another group, and to examine the very instructive pedigree of the Proboscidians, of which one well-known branch alone, that of the Elephants, has continued down to our own times. The Proboscidians are represented in Europe, during the second half of Tertiary times, by three chief and parallel branches of gigantic creatures, the Elephants, the Mastodons, and the *Dinotheria*. Of these three groups, the first was introduced very late into Europe, coming from the Indian regions at the end of the Pliocene; the other two arrived earlier, but no less suddenly, at the commencement of the Miocene. They had, moreover, a very different fate. The *Dinotheria* became extinct in its gigantic forms at the end of the Miocene, while the Mastodons survived them through the whole of the Pliocene, and one of their sub-branches even prolonged itself in North America by a final species which appears to have existed at the time of Quaternary man. The table of the evolution of the Proboscidians in Europe, in Africa, and in North America may be represented in five branches, as on the following page.*

This table shows clearly the manner in which we must understand the evolution of a group by *parallel branches* not in contact and having no *transitional form* from one branch to another. It shows also, as mentioned above, the different destiny of each of these branches. Finally, it enables us to appreciate the variable rate of their evolution. Thus the branch Dinotherium changed very little since its apparition in our countries at the beginning of the Miocene until its extinction at the end of that period. Everything

* I have left on one side the curious *Stegodon* of India, often considered as forming a bridge between the Mastodons and the Elephants, because the stratigraphical level of their species is still very uncertain.

		Mastodons		Elephants	
	Dinotherium	Molars with conical mounds	Molars with transverse ridges	Molars with parallel lamellæ	Molars with lozenge-shaped lamellæ
Present Epoch . .	—	—	—	*E. Indicus*	*E. Africanus*
Quaternary Epoch .	—	—	*M. Americanus*	*E. Antiquus*	*E. priscus*
Upper Pliocene Epoch	—	*M. arvernensis*	*M. Borsoni*	—	—
Lower do. do.	—	*M. arvernensis*	*M. Borsoni*	—	—
Upper Miocene do.	*D. gigantissimum* *D. giganteum*	*M. longirostris*	*M. Turicensis*	—	—
Middle do. do.	*D. lævius*	*M. angustidens*	*M. Turicensis*	—	—
Lower do. do.	*D. Cuvieri*	*M. angustidens* *Mut. pygmæus*	*M. Turicensis*	—	—
Oligocene Epoch . .	—	*Palæomastodon Beadnelli*	—	—	—

resolves itself, it would seem, into a gradual and very perceptible increase of size from the relatively small form of the beginning, the *D. cuvieri* of the sands of the Orleanais up to the enormous animal of the Pontic strata of Roumania, named by Stefanesen *D. gigantissimum*, and without doubt the most formidable terrestrial mammal who lived in geological times. On the contrary, the second branch, that of the Mastodons with molars bristling with conic mounds, offers some somewhat important modifications of structure. Indeed, the *Mastodon angustidens* of the lower and middle Miocene is an animal relatively small and of low stature, and his short limbs in no way recall the huge pillars of the modern Elephant. His jaws are furnished with four nearly straight tusks, two long ones in the upper jaw and two rather shorter in the mandible, which wear away by friction against the upper. In the *Mastodon longirostris* of the upper Miocene the general dimensions are much greater and the stature higher. The upper tusks remain very long, but the lower ones are much diminished in proportion, and hardly attain 0·50m. beyond the mandible. In the *Mastodon arvernensis* of the Pliocene the height, the molars, and the long upper tusks are almost identical with those of the *Mastodon longirostris*, from which it would be difficult to distinguish it if the lower tusks had not entirely disappeared together with the bony sockets in which they were fixed, so that the symphysis of the mandible is short and bent over downwards, instead of being plainly projected forward, as was the case with the Miocene Mastodons. In this case the functional modification goes as far as an almost perfect resemblance with the mandible of the Elephants, to which the *Mastodon arvernensis* is yet a stranger so far as ancestral affiliation is concerned.

The branches of the Proboscidians, which we have just been studying in Europe, have always had a remarkable geological longevity. But this longevity has recently been singularly extended by the discoveries made a few years ago in the Oligocene and Eocene soils of the Libyan desert. In the portion of that desert which adjoins the pleasant and cultivated valley of the Fayûm, the researches of the English geologists, Lyons, Beadnell, and Andrews, have made us acquainted with the ancestors of our Proboscidians, the origin of which had till then remained an insoluble problem to palæontologists. In a mass of Oligocene, and, probably, Stampian strata, Andrews has described under the name of *Palæomastodon,* an Ungulate which is proved by evidence to be the ancestor of our Mastodons with conical teeth-mounds. It is inferior in size to the smallest forms of the *Mastodon angustidens* (the *pygmæus* mutation of the Burdigalian stage), and the skull is long, as in this last species; the upper tusks are much shorter and slightly cast downwards; the symphysis of the mandible is long, but less in proportion than in the *Mastodon angustidens*, and it carries two tusks likewise rather small. Finally, the molars, to the number of six all in their places at the same time, thus come near to the normal type of the Ungulates, instead of showing the progressive reduction of the pre-molars which characterizes the dentition of the Miocene Mastodon. Having regard to all these different points, the *Palæomastodon* is a type of primitive characteristics at all points, such, in a word, as we should have imagined the hypothetical ancestor of the branch of Mastodons to have been. Perhaps, even, the branch may be followed down as far as the Eocene in which there has been discovered another Ungulate, the *Mæritherium*, whose cranial characteristics are rather in conformity with a generalized proboscidian type, but with six incisors in the upper and four in the lower jaw, the second pair of which tends to develop in the form of small tusks with a sub-vertical direction, instead of being projected forward as in the *Palæomastodon*. But, for want of transitional types, there still exists some uncertainty as to the precise genetic relations of these two genera.

In any case, we are now able to follow, save for a slight discontinuity in the higher Oligocene, one of the branches of the Proboscidians from the *Mastodon arvernensis* of the Pliocene down to the *Palæomastodon Beadnelli* of the Middle Oligocene. In all this long geological journey, which comprises much more than half of Tertiary times, the characteristics of the branch become only slowly modified even as regards the details of the structure of the molars, the number and direction of the tusks, etc. We are very far from those rapid and radical transformations, from those manifold transitions from genus to genus and from family to family, which have been so greatly overdone in phylogenetic works on the Tertiary Mammals.

CHAPTER XVIII

ON SPECIES AND GENUS IN ZOOLOGY AND PALÆONTOLOGY

THE considerations just set forth on the series or phyletic branches among fossil animals have already taught us some of the laws governing the evolution of these branches; and these laws are the same for both Vertebrates and Invertebrates. We have seen that this evolution is effected at a variable rate of speed, but always by means of a numerous series of branches, which develop on parallel lines and by gradual mutations through the different geological stages, without contact or transition from one branch to another, except in those cases of bifurcation which we can very rarely grasp with certainty. We have seen, also, that certain groups, families, or genera are shown to be *monophyletic*, and develop their mutations through one series alone; other genera, on the contrary—and these are the most numerous—are polyphyletic, that is, formed of a manifold sheaf of sub-branches, which develop on parallel lines by following the same laws as the principal branches. Finally, the course of these branches is sometimes very long, and may even cover almost the whole extent of geological times, but is sometimes shorter and limited to a few stages. But I have also said that the progress of palæontological discovery tends to lengthen more and more towards the root most of these shortened branches, whose apparently slight longevity can be most often explained by simple gaps in our knowledge.

Given the constitution of the phyletic branches by a series of mutations passing from one to another by imperceptible transitions, except in the case of series provisionally discontinuous, it is natural to inquire what, in such series, becomes of the limits of the species and of the genus, and whether the palæontological signification of these two principal terms in nomenclature is in conformity with that generally accepted in zoology.

Let us first examine the question from the theoretical point of view. Consider A, A^1, A^2, A^3 . . .; B, B^1, B^2 . . .; C, C^1 . . .; as a certain number of animal forms taken from the fauna of the present day; we group these forms in categories which we call *species* when their important characteristics are the same and they only differ from each other by constant but slight details. When we studied above variation in living nature, we said that species, considered in a broad sense and without assigning a specific name to all individual or local varieties, are perfectly independent of each other, and are not connected by transitional forms, save in a few exceptional cases of hybridism. All naturalists are aware that, in general, species arrange themselves naturally into sheaves or groups of species more or less numerous—A, A^1, A^2, A^3, etc., separated from another neighbouring sheaf, B, B^1, B^2 . . ., by characteristics more important than those which distinguish the forms of the same group. Some give to these groupings of species the name of *sub-genus*, while others individualize them more completely by according them the hierarchical value of a true *genus*. But, this question of words apart, we may affirm that these small limited genera constitute the most solid and the most natural grouping in all zoological nomenclature. It goes without saying that the *sub-genera*, or *sections*, as they are sometimes termed, may be united, if desired, into *genera* more important and wider in extent. But, in all cases—and this is the essential point—these various groupings, *species*, *sub-genera*, *great genera*, preserve towards each other a complete independence, and their limits, except in very rare cases, can be settled satisfactorily.

It would be the same if, in lieu of considering the living fauna, we directed our analysis towards one or other of the faunas which lived in early times, provided we deal with animals rigorously contemporaneous, that is to say, belonging to the same strictly limited geological horizon. There we should again meet with morphological variation, either individual or regional, under the well-known form of *varieties* or *local races;* but we should, in general, have no difficulties in demarcating the large species, the sub-genera, and, above all, the great natural genera.

But the problem presents itself in very different conditions if, instead of considering the elements of contemporaneous faunas, we attempt to apply the same rules of nomenclature to the representatives of several superposed geological faunas. We here find ourselves confronted by phyletic branches composed of forms or *mutations* following each other step by step through time, and only separated from one another by shades, the slighter as we dissect with more minuteness the stages, the positions, or even the strata of each find-spot. On the other hand, if the differences are slight between a mutation and the one immediately following it, these differences, generally tending in the same direction, add themselves together, and end in uniting in one continuous chain of beings related to each other by direct descent, of animal forms which no zoologist accustomed to the study of actual types would hesitate to consider as species, or even as distinct genera. But how then can a natural division be effected in these continuous series, analogous to the species and to the genera of zoological nomenclature? It must be owned that this task is almost impossible when dealing with a branch whose several series of mutations are complete and without lacunæ. In this case the demarcation of the species and of the genus, phyletically considered, becomes purely artificial and subordinate, it may be said, to the personal feeling of the observer.

To make this clear by an example, let us go back to the table given above of the pedigree of the Proboscidians, and in particular consider the branch of the Mastodons with molars formed of conical mounds, a branch of which the *Mastodon arvernensis* is the last representative. Between this last form, which characterizes the Pliocene as a whole, and the

Mastodon longirostris of Eppelsheim, it is very easy to put a limit of species. The Pliocene animal has a chin shortened and deprived of lower tusks, while the Miocene type has two small tusks set in a rather protruded mandible. The mounds of the molars have in the first an alternation marked from one half of the crown to the other half ; in the second they are disposed in an almost perfect transverse line. But this facility of demarcation between the two species is certainly due to the momentary lacuna in the intermediate mutations. We do not yet know of a Mastodon whose lower tusks are exceedingly small, and we may expect to discover this form at the lowest point of the Pliocene formations. But we already know in the last strata of the upper Miocene — in the environs of Lyons in particular—a Mastodon which comes within the *longirostris* type by the size of its lower tusks, but whose molars possess the alternate arrangement which characterizes the *arvernensis* type, to such a degree that some isolated molars of this last mutation of the Miocene cannot be distinguished from those of the Pliocene animal. The *longirostris* and *arvernensis* Mastodons will probably be one day seen to be united by a series of continuous mutations, and all demarcation between the species will then become impossible.

This continuous connection exists at present between the different Miocene forms of the same branch, from the *Mastodon longirostris* of the upper Miocene to the *pigmy* form of the *Mastodon angustidens* which begins in the lower Miocene. In fact, the progressive increase in size is most regular in this series, from the earliest to the latest form; while the structure of the molars also presents a complication equally progressive. In the *angustidens* species and its mutations, the molars which precede the last are composed of three transverse ranges of mounds, whence the term *trilophodont* structure, which has sometimes been raised to the rank of a sub-genus, under the name of *Trilophodon.* In the *longirostris* species these molars have four ranges of mounds, whence the sub-generic name of Tetralophodon. But, in studying the Mastodons of this branch, which we meet with in the highest strata of the middle Miocene—at Villefranche d'Astarac in the Gers, for example—we note that the heel of the last molar is doubled, so that we may reckon, if we will, one mound the more; and, owing to this intermediate mutation, the distinction between the genus *trilophodon* and the genus *Tetralophodon* becomes quite illusory. On the other hand, in the small forms of the lower Miocene, the last range of mounds diminishes in importance with the last molar, and may be considered in certain specimens as a simple heel to the tooth; a Mastodon in which the last molar thus only carries three ranges of mounds approaches visibly the normal type of structure of the genus *Palæomastodon* of the middle Oligocene of the Fayûm. Yet in the present state of our knowledge this genus can still be easily separated from the true Mastodons by its puny size, by its much simpler last molar, and, above all, by the presence of five molars in simultaneous function in each jaw. But this facility of diagnosis of the two genera is simply due to some of the intermediate mutations being still unknown to us; and when we shall have discovered the representatives of this same branch in the middle and upper Oligocene, it will doubtless be no longer possible to determine where the *Palæomastodon* ends and the real Mastodon begins.

These inextricable difficulties in the division of the phyletic branches into genera and species susceptible of an exact diagnosis are due, in my opinion, to the fact that palæontologists persist in designating by the same name things entirely different from each other. On the one hand, the species and the genus at a specified epoch; on the other, the species and the genus in time. To help the reader to understand and appreciate the importance of this distinction, I will draw up the following brief table:—

Let there be A, A^1, $A,^2$ three species of an existing genus; B, B^1, two species of a second genus; and one species of a third genus, all alike existing. According to the laws we have recognized regarding variation in living nature, these genera and these species are easy to characterize, since there is generally no transition between them. Let us establish elsewhere the phyletic branches of each of these species by utilizing the representative forms of each branch throughout a series of geological periods. We shall thus have a sort of rectangular construction in which the horizontal lines will represent the fauna of the same epoch and the vertical lines the successive forms of the same branch throughout time.

Phyletic Branches	A	A^{1}	A^{2}	B	B^{1}	C	...	Existing	Fauna
	A^{a}	A^{1a}	A^{2a}	B^{a}	B^{1a}	C^{a}	...	Pliocene	,
	A^{b}	A^{1b}	A^{2b}	B^{b}	B^{1b}	C^{b}	...	Miocene	,,
	A^{c}	A^{1c}	A^{2c}	B^{c}	B^{1c}	C^{c}	...	Oligocene	,,
	A^{d}	A^{1d}	A^{2d}	B^{d}	B^{1d}	C^{d}	...	Eocene	,,
	A^{e}	A^{1e}	A^{2e}	B^{e}	B^{1e}	C^{e}	...	Cretacean	,,

It will be seen, by this very simple table, that the species and genera of existing nature—or, what comes to the same thing, those of each of the faunas which succeeded each other in the life of the earth—comprise a horizontal line drawn through a series of branches evolving on parallel lines, and most often without any known point of contact. From this there results a relatively very large facility in establishing the natural divisions.

When it is a question, on the contrary, of phyletic branches, we have to deal with vertical lines composed of a series of forms closely related by means of direct descent, and connected from stratum to stratum by imperceptible transitions. We cannot, therefore, wonder at the difficulties, nay, more, at the impossibility which palæontologists encounter in establishing divisions of which the demarcations have become artificial and fleeting, and are contrary to the very essence of the constitution of these branches. There is, in my opinion, no way out of this difficulty but to adopt resolutely a nomenclature different from the zoological nomenclature. This was well understood by Waagen and Neumayr when they proposed to substitute for the term species that of ascending or descending *mutation*. Being no longer embarrassed by comparisons with the value of the actual species, there is nothing to prevent a distinguishing name from being given to each well-established mutation, and these names from being multiplied as often as may be necessary to designate the successive stages of the evolution of the same branch. As to the phyletic branches themselves, which in no way correspond to the conception of *genus* in existing nature, it would be very simple to apply to them the name of *branch*, or, optionally, of *phylum*, which has already been employed by the German palæontologists, and which would more easily receive international acceptance. I am convinced that palæontological researches would gain much in clearness and in precision by the use of this simple reform of nomenclature.

BOOK V

THE CAUSES OF THE EXTINCTION OF SPECIES

CHAPTER XIX

THE LAW OF INCREASE IN SIZE IN PHYLETIC BRANCHES

Generality of the law—Special difficulties among the Invertebrates—Examples of the law of growth among the lower Vertebrates—The law considered as a criterion of the evolution of branches among the Mammals—Examples from the Proboscidians and Lophiodonts—Is there sometimes a diminution in size ?—The dwarf Elephants of the Mediterranean Islands.

SEVERAL times in the course of the chapter devoted to the study of the phyletic branches, I have had occasion to notice, in passing, the gradual increase in size of the mutations of the same branch, rising from the earliest to the latest forms. This law, which we will call simply *The law of increase of size in phyletic branches*, is one of the most curious and, from its generality, most important, which has been brought to light by the researches of modern palæontologists. It is observed almost without distinction in all classes of the animal kingdom, but presents more numerous and clearer applications in the group of the Vertebrates than in that of the Invertebrates. Conditions peculiar to the Invertebrates only complicate, as a matter of fact, the evidence as to the law of progressive growth in size. The phyletic branches are here more numerous, closer together, and it seems that since the remarkable attempts of Waagen, Neumayr, Wurtemberger, Mojsisovics, and Hyatt, palæontologists have not made the necessary efforts to reconstruct with precision the branches and parallel sub-branches which represent evolution of a rather entangled kind. In general there has been too hasty a wish to establish the genealogical relations of the great genera and families, instead of following step by step the series of gradual mutations of a given specific type. Certain great genera, like the genus *Hoplites* among the Ammonites, the genus *Cerithium* among the Gastropods, the genus *Pecten* or *Trigonia* among the Lamellibranchs, each contain, perhaps, more than twenty independent phyletic branches, which would have to be solidly reconstructed before we could argue on the phylogeny of the genus. Moreover, among the Invertebrates the phyletic branches with very slow or almost negative evolution seem more frequent than with the Vertebrates. Numerous genera of Foraminifera and of Radiolaria are found with forms and dimensions identical from Primary times up to the present epoch. I have already cited facts of the same order among the *Cidarides*, the *Lingulæ*, the *Craniæ*, the *Nuculæ*, the *Mytili*, the *Acmæa*, the *Capuli*, the *Estheriæ*, the *Cypridinæ*, etc.

Finally, and this is a last condition which must not be overlooked, it is often difficult to decide if any fossil specimen discovered has attained the maximum growth of the species it represents, or if it was still capable of growth in the course of its individual evolution. This is very frequently the case with the shells of the Nautilids or of the Ammonites, which construct successive dwelling-places in the course of their growth, and whose characteristics of senility, obliteration of ornamentation, and irregular coils are not always easy to recognize.

Notwithstanding these difficulties, the law of progression in size is yet verified in a certain number of phyla among the Invertebrates. In the order of Foraminifera, we may cite the phyletic branch of the Orbitolinæ, which develops itself from the Barremian to the Cenomanian. In the Barremian and the lower Aptian are found small Orbitolinæ a few millimetres in diameter, to which has been given the name of *Orbitolina conoidea.* At the terminal extremity of the branch in the Cenomanian, the Orbitolinæ are represented by the *Orbitolina concava*, having a very flattened form, and capable of attaining nearly three centimetres in diameter—a gigantic dimension for a Foraminifer. Between these extreme forms there are observed in the upper Aptian and in the Gault, particularly in the mountains of La Clape and the Corbières, a whole series of intermediate mutations of size, increasing as they get higher up, which render quite illusive and artificial any specific separation between the *Orbitolina discoidea* and the *concava.* The Foraminifera of the Orbitoïdæ family, and, in particular, the Lepidocyclinæ of the Oligocene, offer us a similar progression. The forms of the larger sizes of this branch are found in the terminal strata of the Aquitanian, for instance, in the Vicentine region. In the great class of the Echinida, the genus *Clypeaster* commences by forms of mediocre size in the Eocene of Upper Italy and Egypt, and attains in the Miocene the considerable dimensions of the *Clypeaster altus*, *crassicostatus* and *Ægyptiacus* of Malta, the Vienna Basin, and the environs of Gizeh. Similarly, the small *Megalodon* of the Devonian announce and precede the enormous Triassic shells of this genus. The shells of the tribe of Diceratinæ which, with the genera *Diceras* and *Heterodiceras*, peopled the coral reefs of the higher Jurassic, attain in the Tithonic reef of the Echaillon the astounding dimensions of certain samples of the *Diceras Luci*, which form part of the collections of the University of Grenoble. We may even draw an argument from these enormous Dicerata to affirm that this branch cannot have had any direct descendants in the Cretacean. The Ammonites, notwithstanding the unfavourable conditions pointed out above, show us, in the terminal mutations of some branches, species of very great size; for instance, the *Pinacoceras* of the Trias, the *Arietites* of the Lias, the *Stephanoceras* of the Portlandian, the *Ancyloceras* of the Aptian, the *Scaphites* of the Senonian, the *Pachydiscus* of the terminal strata of the Upper Chalk; and it is with this last genus, composed of forms of large size and senile characteristics, that the evolutionary activity of the great group of the Ammonites appears definitely to exhaust itself. Finally, I shall further point out in the great class of the Crustacea the interesting little branch of the Limulidæ, which takes birth in the Trias with quite small forms, such as the *Limulus priscus* of the Muschelkalk of Bayreuth, continues in the higher Jurassic with types of average size, like the *Limulus Walchi* of the lithographic stone of Solenhofen, then with the *Limulus Decheni* of the Oligocene, and attains the apogee of its dimensions in the *L. polyphæmus*, still existing in the Gulf of Mexico.

The lower Vertebrates supply us in their turn with numerous examples of the law of progression in size of each branch. The Sharks of the genus *Carcharodon* include, in the lower Eocene, species of medium size, like the *Carcharodon appendiculator* of the Tunisian plateau, continue to increase in size in the middle Eocene and the Oligocene, and attain in the Miocene and the Pliocene the astounding dimensions of the *Carcharodon megalodon*, certain triangular teeth of which twelve centimetres in length indicate a Shark of a total length of twenty metres. There is known in the Primary formations, from the higher Silurian to the Permian, a group of Elasmobranchial Fishes, the *Acanthodæ*, characterized by their firmly shagreened skin and their fins strengthened by a large spiky ray. The representative forms of this group in the red Devonian sandstone, such as the *Acanthodes Mitchelli*, are quite small fishes, with a body not exceeding seven centimetres in length. When we reach the Carboniferous, the *Acanthodes Wardi* grows to twenty-seven centimetres, and certain unequal spines of fishes of this group, known by the name of *Gyracanthus*, indicate in the Coal and in the Permian species of still larger dimensions.

The group of Dipneusta offers us in the order of the Sirenoïds facts of the same nature. The earliest genus, the *Dipterus* of the Devonian epoch, carries on each of the branches of its jaws one large tooth, the surface of which is ornamented with ten enamelled crests with crenellated edges. These large dental plates are hardly more than a centimetre across in the *Dipterus Valenciennesi* of the old red sandstone of Scotland. The dental plates, almost identical, which we find in the Coal of England, which have received the name of *Ctenodus*, measure as much as six centimetres; the first correspond to a fish of fifty centimetres at most, the second to an animal exceeding a total length of 1.50 m.

The Palæozoic Amphibians designated by the general name of Stegocephala, by reason of the bony dermic plates which form a perfect cephalic shield, lived from the Carboniferous to the end of the Trias. The group as a whole presents a most regular progression in size, commencing with the small forms of the lower Carboniferous up to the gigantic types of the upper Trias of Suabia. But we are here dealing with a very abundant group, evidently composed of a great number of parallel branches. If we confine ourselves to the single suborder of the Labyrinthodons, of which the conical teeth are ornamented with deep and meandriform furrows, we may note in the Coal of England the genera *Loxomma* and *Anthracosaurus*, of which the skull already attains from thirty to thirty-five centimetres in length, which we may say in passing allows us to predict the future discovery of smaller ancestors in the Devonian and in the Silurian. But these animals, already of a respectable size, are greatly surpassed by the Triassic Labyrinthodons, the *Capitosaurus*, the *Metopias*, and, above all, by the gigantic *Mastodonsaurus*, whose skull measured nearly a metre in length.

But it is above all in the mammals that the law of increase in size presents itself most clearly, to the degree of being utilizable by modern palæontologists as a veritable criterion for the reconstruction of phyletic branches. We must here limit ourselves to a few examples among those most remarkable. I have pointed out above the progressive evolution of size in the branch of the *Brachyodus* from the *Catodus Rutimeyeri* (the size of a small hare), up to the gigantic *Brachyodus onoidens,* which attains that of a large Rhinoceros. By referring to the table which indicates the evolution of the branches of the Proboscidians we may also note a very regular progression in size in several branches : that of the *Dinotheria,* from the small *Dinotherium Cuvieri* of the Orleanais up to the *Dinotherium gigantissimum* of Roumania, the giant form of the whole group. In the same way the branch of the Mastodons with molars composed of rounded mounds begins in the Oligocene of Egypt with the *Palæomastodon Beadnelli*, of which the size, relatively small for a Proboscidian, does not exceed that of a tiny Rhinoceros ; then comes the Burdigalian, the *pygmæus*, a mutation of the *Mastodon angustidens ;* next the normal type of this species in the middle Miocene of Sansan ; after that the larger forms with more complicated molars, of Villefranche d'Astarac ; finally the great *Mastodon longirostris* of the upper Miocene, and the not less mighty *Mastodon arvernensis* of the Pliocene.

Finally, I will set forth, with a few details, a last and interesting example of this same evolution, that of the *Lophiodontidæ*, which will enable us to see precisely, and to better understand, the general mechanism which regulates the evolution of nearly all the groups of fossil animals. The Lophiodontidæ are Ungulates with an uneven number of digits very abundant in Europe at the Eocene epoch ; they form a small natural family composed of two principal phyla, that of the *Chasmotherium* and that of the *Lophiodon*, this latter comprising in itself three parallel sub-branches with independent evolution. The table on the opposite page indicates the series of the mutations of the diverse branches through the Ypresian, Lutetian, and Bartonian stages.

The *Chasmotheria* differ from the *Lophiodons*, especially on account of their pre-molars being more complicated, and furnished with two internal mounds like the rear molars. Though contemporaneous with the *Lophiodons*, they have reached a more advanced stage of evolution as regards uniformity of structure in their dentition, that is to say, the tendency to *homœodonty*. The branch of the *Chasmotheria*, now well known as to the series of its mutations, starts suddenly at the end of the Ypresian stage with the small *Chasmotherium Stehlini* of Cuis, and continues with gradual increase

	Chasmotherium Branch	Lophiodon Branch		
Bartonian Stage	*C. Cartieri*	*L. Lautricense*	*L. Thomasi*	*L. Leptorhyncum*
Upper Lutetian Stage	*C. Cartieri*	*L. Rhinocerodes* *L. Tapiroides* *L. Isselense*	*L. Parisiense*	*L. Occitanicum*
Lower "	*C. Minimum*	"	*L. Medium*	*L. Subpyrenaicum*
Ypresian Stage	*C. Stehlini*	*L. Remense*	*L. Remense*	

of size up to the *Chasmotherium Cartieri* of the Upper Bartonian of Robiac, with which it becomes definitely extinct. The rapidity of the increase in size of this branch is slight, the last mutation being hardly twice as large as the first.

The three branches of the *Lophiodons* are later than that of the *Chasmotherium* as regards the uniformity of structure in the pre-molars and molars; the two mutations of their branches, *Lophiodon lautricense* and *Lophiodon Thomasi*, hardly beginning this at the very moment when they become extinct. The three branches obey, however, the law of increase in size, but with very unequal rates of speed. The first grows with an extreme rapidity; starting with the small *Lophiodon remense*, of which the size is about that of a Tapir, it rapidly reaches huge forms like the *Lophiodon* of Issel, and winds up with a giant mutation, the *Lophiodon* of Lautrec, which exceeds the dimensions of the largest existing Rhinoceros. The second branch evolves much less quickly; starting, no doubt, from a point common to the preceding branch, it reaches, in the *Lophiodon Thomasi*, the size of an animal hardly half as big as the *Lophiodon lautricense.* Finally, the third branch is composed of quite small forms, for the reason that its evolution of growth is very slow; it starts, so far as we know, by a mutation, the *Lophiodon subpyrvenaicum*, smaller than the initial mutation of the two other branches, and terminates with the *Lophiodon leptorhynchum*, which is hardly larger than the *Lophiodon remense.*

Thus the four phyletic branches known at the present time of the Lophiodontidæ all conform to the law of increase in size, but with very unequal intensity. We might even imagine a fifth branch, in which the increase should be still slighter, or even almost nil.

And this is not simply an exceptional fact. I might quote a great number of families of Tertiary mammals, the Palæotheridæ, the Anthracotheridæ, the Rhinocerotidæ, the Amphicyonidæ, the Viverridæ, the Mustelidæ, the Felidæ, etc., etc., in which the law of increase in size applies under almost similar conditions to those of the Lophiodontidæ, that is to say, that certain branches, endowed with very great evolutionary power, rapidly reach gigantism, while others adopt a moderate pace, and others, again, remain almost without increase in size. It is for this reason that we observe almost constantly in the same natural family and at the same epoch, large types of great size, medium, and small or dwarf forms. Existing nature offers us numerous examples in the Felines, the Stags, the Antelopes, and, to generalize, in all groups of the animal kingdom.

There might be made, it is true, a somewhat specious objection in principle to this interpretation. Why should this differentiation in size, which is observed in nearly all families of living or fossil animals, be reached solely by the process stated above, that is, of the growth at unequal speed of several parallel branches, instead of being produced by degeneration, that is, by the decrease of size of certain branches? Is it possible to establish, in the present state of palæontology, the existence of phyletic branches whose successive mutations show a gradual decrease in the size of the body? It seems little probable to me, although, at various times, endeavours have been made to invoke facts of this nature. One of the most classical is that of the dwarf Elephants discovered in several islands in the Mediterranean, the *Elephas melitensis* of Malta, the *Elephas mnaidrensis* of Sicily, and other similar forms in Cyprus, Sardinia, Greece, and Gibraltar. These dwarf elephants, some of which are no larger than a pony, are of a recent geological age, going no further back than the beginning of the Quaternary. They are connected with the branch of the gigantic *Elephas antiquus*, which Pohlig, and with him nearly all palæontologists, have considered to be insular forms. But recently Miss Bate has given, as regards the *dwarfism* of the Elephants of the Mediterranean islands, an explanation which, to my mind, is more satisfactory. Why suppose, in the first place, that a large island like Sicily was incapable of producing for Elephants, as races degenerated through a long isolation, food enough to maintain their vitality and size? This reasoning might appear alluring as regards very small islands; it cannot be so in the case of such spacious ones as Sicily. It seems more rational, on the contrary, to consider the *Elephas melitensis* and the other rather larger mutations, as the primitive forms of the branch of the *Elephas antiquus* isolated in these islands by geological upheavals, and having found in this dissociation of their geographical area a special cause of preservation. A similar reasoning might serve to interpret the small Hippotamus of Madagascar, the *Tapirus Bairdi* of Central America, etc., without having to bring into play a law of *decrease in growth* which no exact observation appears to justify.

CHAPTER XX

THE LAW OF SPECIALIZATION OF PHYLETIC BRANCHES

Progressive specialization of Branches—Specialization of organs with different functions—The runner's foot of the Ungulates—The swimming limbs of the Sirenians—The natatory paddle of the Ichthyosaurs—Production of offensive or defensive weapons—Non-functional specializations: line of suture and uncoiling of the Ammonites—The Rudistæ—The Senility of Branches.

At the same time that the mutations of a same branch increase in size during their evolution, they are influenced by another law, which is that of a more or less marked specialization in one direction. This phenomenon did not escape the sagacity of Cope, who formulated it in a rather different form and so to speak, inversely: i.e. as the *law of non-specialization.* Organic types which are not specialized are alone, according to him, capable of an ulterior evolution. Since the time of Cope, the progressive specialization of phyletic branches has been the object of very many researches among all groups of fossil animals; but here again, as in the question of increase in size, the most convincing proofs will be derived from the vertebrate animals.

Generally speaking, the specialization does not apply to the organism as a whole, but only to one organ or a group of organs more or less connected from the functional point of view. Specialization, indeed, most frequently seems to have no other aim than the gradual improvement of some determinate function, such as natation, flight, leaping, running, etc. In this last order of ideas, all naturalists are acquainted with the fine researches of Kowalevsky and of Cope on the progressive transformation of the *plantigrade* and five-fingered or five-toed, paw of the primitive Ungulates into a *semi-plantigrade* one, then into a *digitigrade*, and finally into the *unguligrade*, with one or two toes, of many modern Ungulates. This transformation is effected by (1) a gradual upward movement of the metapods, whose position gets nearer and nearer to the vertical; (2) a lengthening of these metapods, accompanied by a correlative elongation of the whole limb; (3) an enlargement of certain metapods and digits at the expense of their neighbours, which become reduced and finally disappear; (4) lateral displacement and a more solid setting of the bones of the carpus and of the tarsus, arranged primitively in parallel ranks; (5, and last) a welding together of several parts at first separate from the carpus, the tarsus, and the metapod. Kowalevsky, Cope, and Osborn have attempted some ingenious mechanical explanations of these phenomena of adaptation for running, that is to say, for a specialization produced on parallel lines in the course of ages and at a more or less rapid pace in the most varied branches of the Imparidigitæ or the Paradigitæ.

The Sirenians offer us on their side a marvellous example of a better and better specialized adaptation of their organs to their aquatic environment. All palæontological data relative to this group, which habitually dwells on the seashores and in the mouths of great rivers (Siren and Lamantin [Manati]), favour the hypothesis of Owen and Flower, who consider these beings as early terrestrial Ungulates, which have become aquatic and whose bodily form, skin, dental system, skull, and especially limbs, have undergone modifications in harmony with their new environment. The most primitive and no doubt the earliest genus, the *Prorastomus* of the Jamaica Eocene, is distinguished from all other Sirenians by the almost normal dentition of an Ungulate, with incisors and canines in function in both jaws, by molars with transverse ridges, by small maxillaries not directed downwards, as in the *Halitherium* of the Oligocene, whose incisors become at once rudimentary and useless, and in which the canine transform themselves into a pair of strong tusks. A still more important functional modification happens to the limbs: the anterior limb, an essential organ for propulsion through the water, retains its normal structure, except that the metacarpal bones and the phalanges lengthen so as to support a powerful paddle. On the other hand, the posterior limb, useless to a lengthened and pisciform body, is gradually atrophied. In the *Halitherium* of the Oligocene and Miocene a small basin hollowed out of a small cotyloïd cavity exists and is furnished with a thin femur in the shape of a rod: in the *Metaxytherium* of the Pliocene, this basin persists and still shows a certain width at the level of the ilium, but there is no longer any cotyloïd cavity or femur; in the Siren or *Halicore* of the present day the pelvis has almost disappeared and is replaced by a pair of slender rod-shaped bones united by a symphysis and corresponding to the ischion alone. As is the case with the Ungulates, the specialization of the Sirenians has taken place on parallel lines in the different phyletic branches representing the evolution of that order.

The two foregoing examples show us a functional specialization obtained by a *process of reduction* of certain organs. At other times, on the contrary, there is an abnormal multiplication of certain elements. Such a case is presented by the special structure of the natatory paddle in the Icthyosauridæ. Here, the humerus is a short and flattened bone; then come numerous rows of polygonal plates almost identical, in which it is somewhat difficult to distinguish the radius and the cubitus; and then two rows of carpal bones, a row of metacarpals, and numerous phalanges formed of bones gradually lessening towards the extremity of the limb. The most remarkable specialization about this natatory paw, covered with one common skin, consists in the indeterminate number of the digits, which may reach eight or nine in certain species. This is a unique peculiarity which greatly struck Haeckel and Gegenbaur and led them to detach the Ichthyosaurs from the other Reptiles and derive them from the Selachians. Baur sees in this, on the contrary, as in the fins of the Cetacea, a simple secondary adaptation to aquatic life and considers the Ichthyosaurs as very specialized descendants of the terrestrial Reptiles, more or less related to the primitive types of the order of the Rhynchocephalians. The marine Mammals of the family of the Whales show a specialization of their anterior limb, which does not lack similarity to that of the Ichthyosaurs, notwithstanding that the number of digits remain at the normal figure of five.

The transformation of the anterior limb of the Vertebrates into an organ of flight would show us in the same way a specialization by *atrophy* of the hand in the Birds, and, on the contrary, by an exaggerated development and *multiplication* of the phalanges of the fifth finger, in the Flying Reptiles or Pterosaurians of Secondary times.

Another mode of specialization common to a great number of phyletic branches consists in the production of offensive or defensive weapons carried to the most remarkable perfection. Into this order of ideas there enters the differentiation, among Carnivora, of the canine teeth into sharp daggers with edges sometimes sharp and sometimes saw-like. The most different groups, the Stegocephala, the Theromorphs, the Dinosaurs, and the Mammals, all offer examples of this differentiation of the canine. We can point as extreme degrees of specialization to the formidable tooth, shaped like a curved sword blade, of the Jurassic *Megalosaurus* and to the terrible canine tooth possessed by the great felines of the extinct branch *Machairodus*,* towards the end of the Tertiary and up to Quaternary times. Other still more specialized dental forms are the tusks which attain in the Proboscidian group their maximum power. In the *Mastodon arvernensis*,

* The sabre-toothed tiger.—Ed.

the almost straight upper tusk measured about three metres, and in the great species of fossil elephants, the Southern Elephant, the *Elephas antiquus*, and the Mammoth, the tusks curved either in spiral or in lyre-shaped form, reached no less gigantic proportions. We have really a right to ask ourselves of what use could such cumbersome weapons be to these animals.

The bony or dermic productions designated by the names of horns or of antlers, likewise show very curious peculiarities in a great number of branches. There is even known an Ammonite, *Schlœnbachia inflata* of the Upper Gault, whose adult shell bears on its median *carina* a veritable curved or even spiral horn, recalling the form of a ram's horn. Among Vertebrates there exist horned animals in nearly all groups. A gigantic land Turtle, the *Miolania* of the Queensland quaternary deposits, has on its cranium nine bony pegs more or less protuberant, two of which, directed towards the side, are real horns and were covered with epidermic plates during the animal's life. Among the carnivorous Dinosaurs or Theropods, the Ceratosaurus of the higher Jurassic of California bore on the median line of the nose a high, lengthy, and narrow bony crest which is a true nasal horn.

The eminent American palæontologist, Marsh, has made known to us, under the name of *Ceratopsidæ*, a whole family of large herbivorous Dinosaurs, of which the strangely horned cranium bears, in the *Triceratops*, a small bifid nasal horn, and two enormous bony frontal horns above the orbit, in addition to a series of small parietal horns of dermic origin, which ornament, like a semi-circular crown, the sides and posterior part of the head.

The class of Birds presents us with little more than the cephalic protuberance of the helmeted Casoar; on the other hand, the Mammals testify, on this point, to a most varied specialization. Every one is acquainted with the nasal and frontal horns of the Rhinoceros family, the frontal bony pegs of the Antelopes and the Bovidæ, and, lastly, the bony and elegantly ramified prolongations which constitute the antlers of our Cervidæ. In this last family, the complication of the antlers has been pushed to the extreme in certain Pliocene species; for example, the *Cervus dicranius* of the Val d'Arno, whose cranium, exhibited in the Florence Museum, is a real branching bush. In geological times we find, besides those groups actually in existence, other types of horned animals. The *Titanotheria*, gigantic Imparidigitæ almost the size of Elephants, bore at the limit of the frontal and nasal bones two strong and divergent bony horns. In the family of the Cervidæ, the male *Protoceras* of the Oligocene of Montana, had three pairs of bony cranial protuberances, one on the anterior border of the maxillary and two unequal ones on the frontal bones. The *Sivatherium* of the Miocene of India, a relation of the Giraffes, presented at the exterior angles of the frontal bones two powerful ramified bony branches, and another pair at the anterior part of the forehead. Finally, the very specialized American Branch, the *Dinocerata* of the order Amblypods, may be reckoned among the most colossal and strange of terrestrial Mammals, owing to their enormous dagger-shaped upper canines, and to their three pairs of horns ranged on the upper part of the cranium and increasing in size from front to back.

From the standpoint of the Darwinian hypothesis it would be logical to attribute to the struggle for life the survival of all these forms, either very well adapted to their functions, or very well armed for attack and defence; and one might even be brought to see in the struggle for life the fundamental cause of the progress of the specialization of the organs in a given direction. It would, therefore, seem a priori that the phyletic branches most capable of preservation must be those whose mutations most rapidly reached a great stature, an adaptation perfect for their wants, and a powerful offensive or defensive armament. We shall see, a little later, when studying the causes of extinction in species, that the problem is far from being so simple, and that a too advanced degree of specialization, however useful it may seem to be to the animal possessing it, is, on the other hand, generally a cause of decline and of death.

This is because the general law which drives phyletic Branches to advance towards an ever-increasing specialization of a few, at least, of their structural features, does not always appear to be clearly connected with the simple satisfaction of functional needs, and with a better adaptation to the environment. Consider, for instance, the characteristics of evolution in the innumerable branches of the Ammonites. One of the most habitual phenomena of this evolution consists in a gradual and increasing complication of the figure of the *line of suture*, that is to say, of the intersection of the separating partitions of the inhabited parts with the external wall of the shell. These successive partitions are secreted by the "mantle" of the animal, the border of which, more or less cut out and jagged, reproduces its form in the sutural line of the shell. The more or less complicated jagged edge of the mantle constitutes, it must be owned, a zoological character of feeble importance, in which it is difficult to see any progress for the branch or any improved adaptation to its physiological needs. And yet, the progressive complication of the lobes and saddles of the sutural line presents itself, as a rule, in all the phyla of the Ammonites, to such a degree that the characteristics drawn from the shape of the partitions have been chosen by palæontologists as the most essential basis of the establishment of genera and of families. The complication of the partitions seems to me a normal phase, advanced or, if you like, highly specialized, of the evolution of each branch of the Ammonoids.

Almost as much might be said, but with less generality, perhaps, for the *uncoiling* of the shell of the Ammonites, a phenomenon which occurs at various epochs, and in various degrees, in absolutely distinct branches. I shall only quote, in the Triassic epoch, the genera *Rhabdoceras* and *Cochloceras;* in the Rhætian epoch, the *Choristocerata;* in the Jurassic epoch, the *Sphærocerata*, *Patocerata*, and *Baculinæ*. But it is, above all, in the Cretacean epoch, that is, towards the end of the reign of the Ammonoids, that the phenomena of the uncoiling of the whorls reach their maximum of frequency with the *Leptocerata*, the *Hamulinæ*, the *Criocerata*, the *Ancylocerata*, the *Macroscaphitæ*, the *Heterocerata* of the Neocomian, and the *Scaphitæ*, *Turrilitæ*, *Bostrychocerata* and *Baculitæ* of the upper Chalk. A few palæontologists, Steinmann in particular, have indeed attempted to give a mechanical explanation of the uncoiling of the Ammonites by maintaining that the shells that are much coiled occupy the smallest possible space without having their freedom of motion impeded. But this explanation seems very nebulous, and it would be better to consider this uncoiling as a phenomenon of specialization carried to the extreme or to look upon it, with von Mojsisovics, Pompecky, and Hyatt, as a *senile phase* in the evolution of the branches.

The Lamellibranch Molluscs of the family of the Chamacæ will give us, in the Secondary epoch, an example of specialization not less remarkable and quite as incapable of a mechanical or physiological explanation. The Chamæ are unequal-valved shells, with lamellated epidermis, with their tops slightly crooked, which have existed without any great changes from the Chalk down to our seas of to-day. But, from the upper Jurassic epoch—and without its being possible for a moment to recognize in them any ancestral forms—we see appear a branch of these Chamacæ, the *Diceratinæ*, composed of shells large in size, thick, with spiral tops like rams' horns, and with a large cardinal tooth in the form of a gutter. These *Dicerata* people the coral reefs till the end of the Jurassic times. From the lower Cretacean, the branches of the Chamacæ multiply with the *Valletia*, the *Requienia*, the *Monopleura*, and the *Caprina* of the Neocomian and the Urgonian, and become specialized in manifold directions. In the upper Cretacean the differentiation of the group is still more marked in those strange Rudistæ in which the shell attains its maximum inequality of valve:—the lower valve lengthening, in the Hippuritæ, into a long conical horn fixed at the point, while the upper one is reduced to a mere operculum; at the same time, the cardinal teeth and the myophorous plates lengthen into long columns, which penetrate into the deep cavities of the lower valve. With these shells we are as far as possible from the normal type of the Lamellibranchs, and it is not to be wondered at that skilful naturalists have been so misled as to the real affinities of the Rudistæ as to connect them with the Brachyopods or the Polyps. Here again we are permitted to say that the high specialization of the Radiolitæ and Hippuritæ is a mark of very advanced evolution, or of the senility of these branches.

Without any necessity to multiply these examples, it is plain that phyletic branches are subject to a general law which drives them more or less rapidly, and often without any apparent mechanical or functional cause, towards a more and more marked stage of specialization. We shall see that this specialization, far from being a cause of the prosperity and the long duration of a branch, is, on the contrary, a mark of senility which heralds in and precedes, only by a short space of time, their extinction.

CHAPTER XXI

THE PHENOMENA OF REGRESSION AND OF CONVERGENCE

Regression by parasitism and fixation—Rudimentary organs—Progressive and regressive Evolution—Functional and non-functional regression—Regressive characteristics of the Ammonoids—Phenomena of total or partial convergence—Conclusions.

ALL naturalists know that under the influence of conditions, among which the *parasitic life* and *fixation* are the chief, certain animals belonging to the most varied groups are subject, in the course of their individual life, to those phenomena of arrested development, or even of degradation and degeneration, which we call by the general name of *phenomena of regression.* The disappearance of the digestive organs, the loss or complete transformation of the apparatus of locomotion, are the most habitual marks of this regression which may affect other organs, or even almost the whole of the organism. The Cirripedes, such as the Balanæ and the Anatifæ, are a classical example of these facts ; after having passed through a larval state of the Nauplius type identical with that of the other lower Crustacea, then through a stage similar to the one realized by the adult *Cypris,* the animal remains stationary, greatly alters its form, and surrounds itself with a true calcareous shell of many pieces, which for a long time caused this order of the lower Crustacea to be ranked among the Molluscs. The fixation of the free larva of certain Lamellibranchs, such as the oysters and the *Pectines*, likewise brings about regressive modifications of structure, although less important. Jackson has shown that the young forms of these Molluscs were provided with byssus and with two adductor muscles, while the adult forms lose by regression the byssus and the anterior muscle, the disappearance of which is accompanied by other notable changes in the general form of the body.

These very various modes of adaptation to different environments have led in the living animals of the present day to innumerable cases of reduction which betray themselves by the presence of *rudimentary organs*, whose signification can only be established by referring to the genealogical history of the group. Such are the bony stylets hidden under the skin and representing the rudiments of the lateral toes which were unconfined in the ancestors of the Horse; such again, the traces of dental germs which we discover in the beaks of young Parrots and are an atrophied remnant of the teeth persisting into the adult age in the Birds of Secondary times; such is the pelvis reduced and deprived of limbs, of the Sirenians and Cetacea, or the pineal eye of the *Hatteria*, hidden under an opaque dermic plate and recalling the functional Median eye of several palæozoic Reptiles. Darwin and many other naturalists have, with reason, insisted on these well-known facts as one of the most remarkable proofs of the transformist hypothesis.

Cope has endeavoured to show, with the support of many documents, that the palæontological evolution of the Vertebrates was at one time progressive and at another regressive. This means that the necessity for adaptation to needs has led sometimes to the augmentation of the constituent parts of an apparatus, at others to a diminution in the number of those parts. Thus, the hand of the Bird, with its three metacarpal bones and its three fingers with the elements stuck together or atrophied, is a *reduction* relatively to the normal pentadactyl hand of a Reptile or a Primate. On the other hand, the natatory paddle, with its multiple elements, of an ichthyosaurus, intimates a *progressive* adaptation. Naturally, the reduction only affects certain organs or certain apparatus; thus the Mammals are in a state of regression compared with the Reptiles, by reason of the atrophy of the pineal gland and of the coracoïd bone. There is only, according to Cope, a complete regression (degeneration) when the sum of the subtractions is greater than the sum of the additions.*

The phenomena of regression have thus acted in the evolution of fossil animals a rather notable part, which modern palæontologists have striven to set forth with sometimes, perhaps, a little exaggeration. For, as among living animals, the regressive characteristics of fossil beings may relate either to

* The analysis given above of the work of Cope is referred to for further details on these ingenious and philosophical ideas of the learned American naturalist.

a single organ, or correlatively to a group of organs or apparatus.

A certain number of facts of regression are easily explained by the necessities of functional adaptation. I shall confine myself to recalling the well-known examples of the reduction of the lateral digits in the Equidæ and the Ruminants, with the object of increasing the speed; and that of the pelvis of the Sirenians, the Cetacea, and the Pythonomorphs, with the object of concentrating the effort of natation on the anterior limb and the tail. The Marine Turtles offer, as regards this, a rather special complication. The Chelonidæ of pelagic habitat have lessened by regression the weight of the bony case which encloses them, by the aid of empty spaces or *fontanelles* placed on the sides of the carapace and in the centre of the breastplate; but the Athecæ, or Spargidæ, under the influence of a return to land life, have retained the reduced shield of the Chelones by replacing it by a secondary shield composed of polygonal dermic plates superposed, without being welded together, on the rudiment of the primary one.

In many other cases regression occurs without apparent object, and as a normal consequence of the evolution of a group. In the Cephalopod class in particular, a whole series of facts have been interpreted as *regressive characteristics*. The example most often quoted is that of the Ammonites of the upper Chalk (*Tissotia*), which were at first connected with the Ceratitæ on account of their very simple line of suture, composed of whole saddles and slightly denticulated lobes. According to Douvillé, there is in this no question of direct descent from the Triassic Ceratitæ, but a regression which has brought back to the adult state the Ceratite phase of certain early Ammonoids. Even the genus *Neolobites* of the Cenomanian stage constitutes a final term of this regression, in which the saddles and the lobes remain whole and go back to the Goniatite phase. In the same way, the effacing of the ornamentation observed in the last whorl in most of the genera of the Ammonites, or else the uncoiling of the spiral, so frequent in various families of Cretacean Ammonites, have often been considered as regressive characteristics. Modern palæontologists are more inclined to see in this, as does Hyatt, an indication of a senile or *gerontic* phase which reproduces, nearly at least, the infantile or *nepionic* phases by which the evolution of each branch begins. We shall return to these facts when we study the causes of the extinction of species.

The natural tendency presented by certain groups of fossil animals to modify in the same direction and by a kind of parallel course, the characteristics of the individual or of the group taken collectively, enables us to understand how in certain cases, *appearances* of connection, of resemblance or even of more or less complete confusion, between species belonging to genera whose starting points have been totally distinct, may be produced. These curious facts, carefully studied by modern palæontologists, have received the name of *phenomena of convergence.*

Theoretically an absolutely perfect convergence going so far as the confusion of generic characters is, in my opinion, altogether improbable, unless we are dealing with extremely simple organisms, such as *bacilli* or *micrococci*. Nature does not possess, in fact, the means of varying otherwise than in its dimensions a plan of structure reduced to a sphere or a simple rod, and we all know that bacteriologists have found themselves compelled to appeal to reactions of the environment to differentiate micro-organisms of which the monotonous morphology did not lend itself to any specific description. It is, therefore, strictly possible that fossil animals with a very simple structure, like certain Radiolaria (Monospheridæ) or Foraminifera (Globigerinæ), may have lent themselves to such convergences, which are difficult otherwise to demonstrate.

We shall also easily recognize that certain organs preserved in the fossil state, like the most simple forms of the shells of the Molluscs, the scales or dermic plates of the Fishes or the Reptiles, even sometimes the isolated teeth of certain Mammals, may succeed among distinct groups in converging in a manner complete enough to deceive the observer. But, when it is a question of complex organisms, or even of partial structures presenting a certain degree of complication, the convergences produced seem always to be of a somewhat superficial nature, limited to one or to a small number of points, which cannot resist a rigorous comparison of the organization as a whole.

This *superficial* appearance of convergence appears very clearly, especially when we deal with the higher groups of fossil animals. One of the examples most often quoted is the convergence of the Secondary Marine Reptiles of the order of the Ichthyosaurs with the Tertiary and existing Dolphins. The general form of the body, the long snout furnished with conical teeth, the very short neck, the transformation of the fore limb into a natatory paddle, cause between the Ichthyosaurs and the Dolphins great analogies in appearance and in biological character, striking enough to have fostered the hypothesis of an ancestral parentage; but they cannot stand against an examination of the structure as a whole. Similarly neither the convergence of some characteristics between the Flying Reptiles or Pterosaurians and the Birds, nor the presence of a horny bill in the genus *Pteranodon*, the birdlike head placed at right angles on a long and strong neck, and the pneumatic nature of the bones can prevent, notwithstanding the authority of Seeley, our recognizing the essentially Reptilian characters of the Pterodactyls.

A mode of convergence rather more embarrassing —at least as far as outward appearance goes—is furnished by that tendency to excessive elongation of the body with a more or less complete disappearance of the limbs, which leads to the type called anguilliform or serpentiform, according to whether it refers to aquatic or terrestrial Vertebrates. Several very different families of the lower Vertebrates exhibit this type of structure. The *Dolichosoma* of the Carboniferous epoch among the Stegocephalic Amphibians, the Eel and many other genera among Fishes, the Ceciliæ among existing Batrachians, the Amphisbænas among the Lacertians, the order of the Cretacean Pythonomorphs, and finally the whole group of Serpents. But there is hardly need to add that even a superficial examination of the cranial and skeletal characteristics suffices to show the slight importance of these analogies, and to enable each of these serpentine animals to be ascribed to the zoological rank to which it really belongs.

It would be easy to multiply these examples of superficial convergences by showing the resemblance, as regards the hind limb and the tail, between the *Iguanodon* and the Kangaroos, that of several Reptiles of the South African Trias (*Lycosaurus* and *Dicynodon*) to the Carnivorous Mammals and the Walruses, etc. But it will be easily seen that this is simply a question of the phenomena of adaptation to identical functions.

We cannot, however, be satisfied with a similar explanation for the comprehension of some cases of remarkable convergence furnished to us by organs limited and relatively of small importance to the structure as a whole. I refer to the dermic plates and the teeth. It is known that a large number of living or fossil Amphibians and Reptiles, belonging to very different groups, have the head or the body protected by bony dermic plates of very varying forms and sizes. Similar cutaneous plates are found in a few Mammals, such as the Tatus of South America. When these dermic plates are met with in an isolated state in terrestial strata, it is not always easy to determine the genus, or often even the group of animals of which they formed part. One might hesitate to attribute an isolated plate of the kind to a crocodile rather than to a Stegocephalus, or another to a Marine Turtle rather than to a gigantic Edentatus. An example taken from recent controversies will show us the possibility of an almost complete convergence. Certain small-sized polygonal dermic plates found by Filhol in the phosphorites of the Department of the Lot, were ascribed by this scholar to portions of the carapaces of Tatus, and the opinion of Filhol was founded not only on the identical aspect of the details of ornamentation, but further, on a histological study of these organs. Now these plates are found *in situ* on the cranium of a Reptile of the Upper Eocene described long ago by Gervais under the name of *Placosaurus*, and our contemporary, Leenhardt, has recently described a second cranium of this animal armed with its cephalic shield. There is here an identity of structure really surprising and, it must be owned, rather inexplicable.

The teeth of fossil mammals, generally so specialized and so characteristic of each group, present, however, a certain number of cases of almost complete resemblance in structure among animals belonging to very different families and even orders. Such is the case, for example, with the long, thick, and smooth canines of the Ungulates of the genus *Lophiodon*, which resemble, most deceptively, the canines of the Ursidæ; such is, again, the case of the canines, flattened like sword blades and crenellated, of the powerful Felines of the genus *Machairodus*. We have recently observed in a species of Ungulate of the genus *Brachyodus* of the Oligocene, canines so similar to those of a small *Machairodus* that we should not have hesitated to ascribe them to a Carnivore of this genus, had these crenellated canines not been found *in situ* in the skull of a *Brachyodus*.

Convergences no less curious are also observed in the structure of the molars. All palæontologists know the astonishing resemblance of the molars of the Tapirs, both living and fossil, to those of the great Miocene Proboscidian, the *Dinotherium*. This resemblance is so great that it managed to deceive G. Cuvier, and led this illustrious anatomist to consider some isolated *Dinotherium* teeth to have belonged to a gigantic Tapir. This type of molar, in which the denticles are welded into two transverse ridges perpendicular to the crown (type called Tapiroïd or *Lophiodont*), is found with a few slight modifications in the Imparidigits of the family of Lophiodontidæ, parallel with that of the Tapirs; among the Amblypods in the *Coryphodon* and the *Pyrotherium* of Patagonia; and among the Rodents of the Hare family, etc. In the same way, the type of molar termed *bunodont*, in which the crown bristles with conical mounds generally arranged in transverse pairs, is a primitive type met with in a great number of families of mammals, such as the Mastodon among the Proboscidians, the Suidæ among the Ungulates, and the family of Rats or Muridæ among the Rodents. Nothing is more curious than to place the tiny first molar of a rat side by side with the enormous molar of an omnivorous Mastodon, such as the *Mastodon angustidens*. It would be almost possible to ascribe these two teeth to one and the same genus, were we not prevented by the enormous difference in size which separates them.

These frequent convergences of the dermic plates or of the teeth of Vertebrates appear to me to be easily enough explained by the fact that Nature cannot indefinitely vary her processes for incrusting the skin of an animal with osseous tissues, or for grouping the points, primitively distinct, which adorn the surface of the crown of a molar. Let these primitive denticles remain conical and apart, and we have the bunodont type. Let them be welded to each other two by two, closing in from front to back, and we are at the lophiodont type; finally, let these same denticles arrange themselves in V-shaped curves, and we arrive at the semi-crescent or selenodont type which characterizes the molars of the Ruminants and of several other groups of mammals.

It is for a like reason—i.e. the poverty of natural processes of structure or of ornamentation in very simple organs—that the numerous facts of convergence observed in invertebrate animals, and especially in the shells of molluscs, are justified. Very curious examples can be instanced: among the Foraminifera, in which the fundamental division into orders is founded on the nature, perforated or non-perforated, of the calcareous test, the Cretacean and Tertiary *Alveolines* recall in an astonishing manner the Carboniferous *Fusulines*, either by their exterior form of a lengthened spindle, or by the close coiling of the spiral whorls. Similarly, certain simple Polyps of the Apores group, such as the *Turbinolia*, would be distinguished with difficulty by their exterior form from certain *Eupsammias* with porous partitions. In the Gastropod molluscs the spiral coil, or, on the other hand, the uncoiling of the shell is produced by parallel processes in groups very dissimilar as regards their internal organs. Thus the form of shell in a simple surbased cone, with the hardly projecting head of which the Limpets which fix themselves on the rocks of our coasts offer the best-known type, manifests itself again in the Prosobranchs in the families of the Fissurellids (*Emarginula, Parmophorus*), of the Neriditæ (*Navicella*), of the Tecturidæ (*Patella, Helcion*), of the Capulidæ (*Capulus, Calyptrœa*), of the terrestrial Pulmonates (*Ancylus*), or Thalassophilæ (*Siphonaria*) *;* and, lastly, among the Opisthobranchs (*Umbrella*). It is true that a naturalist with a little experience will not hesitate to recognize by this or that morphological detail to which of these numerous *patelloïd* groups should be ascribed any shell submitted to him for examination.

But it is especially in the fossil Cephalopods that the ingenuity of palæontologists has been most successful in discovering facts of convergence. For a long time there have been known, and I have had occasion to dwell on this point, the parallel cases of the uncoiling of the shell among the Nautilidæ and the Ammonites. In these two groups there can be established a series of forms going from a straight shell to a closely coiled one like that of the Nautilus, by the intermediary of forms more and more incurved or with loose coiling. But, here at least, it will always be possible to distinguish the straight Nautilus *Orthoceras*, with partitions added end to end, from the equally straight Ammonite or *Baculites*, owing to the line of suture being rectilinear in the first-named, and strongly sinuous and scalloped in the second. The convergence is, therefore, very superficial, and due solely to the impossibility of arranging in any other form than that of a conical rod, a rectilinear series of chambers in the form of a truncated cone and gradually increasing in size. But, in the Ammonites, the convergence is sometimes carried much further, and affects either the general form of the shell or the disposition of the sides or of the tubercules, or even the type of the sutural line. Among the most remarkable cases, I shall quote the great similarity of external form (discoïd, flat, or sharp edged shell), of the Triassic *Pinacocerata*, of the *Oxynoticerata* of the Lias, of certain *Oppeliæ* of the upper Jurassic, and of the *Cœlopocerata* of the Cretacean, etc. I might also quote the recurrence of the forms of the Liassic *Arietitæ* (narrow whorls, square and strong transverse ribs, and the ventral region marked with a double furrow) in the *Peroniceras tricarinatum*.

Here, again, the study of the sutural line remains the criterion of the demonstration of a convergence which bears only on external characteristics. But, when in cases, doubtless very rare, like that which our contemporary Kilian has just described with regard to certain Cretacean Ammonites of the Antarctic regions, the convergence rests at one and the same time on the general form and on the characters of the partitions, the explanation of the phenomenon of convergence becomes an almost insurmountable difficulty.

To sum up, the phenomena of convergence noticed in nearly all the groups of fossil animals seem to me to have been singularly exaggerated. In the majority of cases the similarities of this nature are very superficial, are easily explained by the facts of adaptation to common functions, and only affect a small number of organs, the limbs, the dermic plates, the teeth, or the shell, according to the group. Almost always it is easy for the naturalist to unmask these deceptive analogies by appealing to the organization as a whole. It is only in a very small number of cases, in the order of the Ammonites, in particular, that Nature, powerless to vary indefinitely the processes of ornamentation on a shell coiled on itself, has reproduced repeatedly in the series of ages, analogous or almost identical forms, susceptible of momentarily misleading the observer in his researches as to the natural relations of the numerous genera of this great order.

CHAPTER XXII

THE EXTINCTION OF SPECIES AND GROUPS

Sudden disappearance of groups—Groups extinct and evolved—Causes of extinction—Weakness of the Darwinian hypothesis—Extinction by gigantism—Laws of Dollo on the irreversibility and the limitation of evolution—Progressive reduction of variability—Phases of youth, maturity, and senility of branches—Primitive and senile stages in Mammals—Recapitulation.

We have seen that the evolution of the branches among Fossil animals is regulated by two general laws: that of the *increase in size* of the body and that of progressive specialization. These data will enable us to approach with profit the interesting problem, which has been often discussed, of the causes of the extinction of species and of groups in the course of the geological ages. Nothing is indeed more striking, in following the palæontological history of the globe, than to see the species, the genera, the families, and even the groups of higher order, appear, pass through an evolution with varying wealth of forms, and then decrease and vanish, nearly always with some abruptness. It will be sufficient to recall certain great classical facts. In Primary times, the Graptolites, the Cystoidea, the Blastoïds, the Tetracorals, the Palechinida, the Clymeniæ, the Trilobites, the Eurypheridæ, and the Placodermal Fishes appeared and vanished, some like the Graptolites and the Placoderms in the short space of two geological periods, or even like the Clymeniæ in a single stage of the Devonian epoch. In the course of Secondary times we also see the appearance and the disappearance of the Belemnites, the Diceratidæ, the Rudistæ, the Ichthyosaurs, the Plesiosaurians, and the Pterosaurians, and we witness the reign and extinction of several other groups which appeared at the end of Primary times —the Spiriferidæ, the Ammonites, the Stegocephalic Amphibians, the Dinosaurs, the Theromorphs, the *Archæopteryx*, etc. The Tertiary era saw the commencement and the end of the true Nummulites and the extinction at least of several groups of mammals, the Multituberculata, the Condylarthra, the Creodonts, the Amblypods, the Toxodonts, the Typotherians, the Tillodonts, and among the Ungulates, the families of the Hyracotheridæ, the Palæotheridæ, the Lophiodontidæ, the Macrauchenidæ, the Titanotheridæ, the Chalicotheridæ, the Anthracotheridæ, the Oreodontidæ, the Anoplotheridæ, the Protoceratidæ, the Sivatheridæ, etc. We should have to multiply these cases of extinction *ad infinitum* if we wished to enter into the details of the families and genera which have entirely vanished.

However, as Abel has observed, it is expedient to make reservations with regard to certain groups which are only apparently extinct, but are, in reality, simply transformed by evolution, at least so far as some of their branches are concerned. Thus it appears difficult not to seek the origin of the regular Urchins of the family of the Cidaridæ in the ancestral forms very near akin at least to the *Archæocidaridæ* of the end of the Primary, though the multiplicity of their rows of interambulacrary plates have led to classing these latter zoologically in a sub-class of the Palechinida, which is in appearance quite separate from the Euechinida. Thus we are beginning, thanks to the researches of Hyatt and other palæontologists, to recognize, in the varied types of the Palæozoic Goniatites, the origin of several branches of true Ammonites, till then classed in a sub-order of Prosiphonata quite distinct from the Retrosiphonated Goniatites. Finally, to quote a last example among the Vertebrates, the Crocodilians were separated by Huxley into two sub-orders, the *Mesosuchians* of the Jurassic and the lower Cretacean, characterized by bi-concave or *amphicœlian* Vertebræ and the *Eusuchians* of the upper Chalk and of the Tertiary, whose vertebræ are convex behind or *procœlian*. But Lydekker has shown that it would be more rational to separate the true Crocodilians into two great parallel branches easy to characterize and to trace starting from the Lias, and called the *Brevirostres* and the *Longirostres*, each of them comprising Mesosuchian forms in the Jurassic and the lower Cretacean, and Eusuchian forms from the upper Cretacean onward. The separation proposed by Huxley was, therefore, artificial, and rested on a stage of ossification of the vertebral column less advanced in the Jurassic Crocodiles than in their Cretacean, Tertiary, or existing descendants.

Notwithstanding these restrictions, it is quite certain that the geological ages witnessed the extinction of a very great number of phyletic branches — I might almost say of the majority, for, among these innumerable branches, relatively very few have possessed the vital force sufficient to continue them down to our own times. But if the mere fact of these extinctions is easily proved, on the other hand, the precise cause of it has long remained obscure, and even at the present day is far from being fully apparent. It is not that there has been any lack of hypotheses since the old conception of Cuvier as to the destruction of fossil species by revolutions of the globe and the ingenious explanation of Darwin founded on the struggle for life. The direct strife with other species not seeming applicable to the great mammals and the gigantic Dinosaurians, the illustrious reviver of transformism was thrown back as regards these giant beings on the difficulty of procuring a sufficient supply of food—an explanation of almost infantine weakness, seeing that it refers to herbivorous animals who dwelt in almost boundless continents, such as the vast Jurassic plains of Central and Western America must have been.* Darwin also rightly recognized the point of the objections raised against the hypothesis of the struggle for life from the well-known fact of the almost simultaneous extinction of all the branches of certain great groups spread over vast geographical districts, such as the

* The Dinosaurs were not all herbivorous. But apart from this, the extinction of the American Bison in our own days may show how enormous is the range of pasture that wild animals of this order require.—Ed.

Trilobites at the end of the Primary, and the Ammonites at the end of the Cretacean. Of course, he essayed to answer this by showing that these extinctions were not so sudden as people tried to make out, and that the vanishing of groups was stretched out over several geological periods. But still it had to be explained why none of these genera or species, with their vast extension, had been able to produce anywhere a descendant capable of surviving, when it is a principle in the Darwinian theory that every organism can and must transform itself, provided the necessary time be accorded to it. The struggle for life is decidedly insufficient to explain the reason of the extinction of species.

Eminent minds, like those of Quenstedt and Neumayr, struck by these difficulties, had recourse to the very improbable hypothesis of *epidemics* to explain the phenomena of degeneration, such as the uncoiling of the shells of the Ammonites, closely preceding the extinction of branches. Other naturalists with a more mystical mind have invoked *predestination* in the duration of the existence of species, genera, or families. It is curious that this supernatural hypothesis should have, in our own times, found a champion of the weight of Kobelt.

If it is difficult at the present day to go back to the true causes of the extinction of branches, we are at least beginning to grasp the mechanism or, if it be preferred, the conditions in which the phenomenon is usually produced. Two of these essential conditions are most often united in the two laws of increase in size of the body and specialization of the organism. We are, in fact, permitted by palæontological observation to note, in a very general way, that the giant forms which have at the same time been highly specialized are never met with at the inception, but only at the end of branches. I have had occasion to quote above numerous examples, and shall confine myself to recalling the gigantic *Mastodonsaurus* in whom the group of Stegocephala becomes extinguished: the *Brontosaurus*, the *Diplodocus*, the *Titanosaurus*, which terminate the branches of the Sauropod Dinosaurs; the *Titanotherium*, the *Ancylotherium*, the *Dinoceras*, the *Dinotherium*, and the *Mastodons*, whose colossal dimensions announce the end of so many phyla of the Ungulates. Even in the matter of the genera, the *Lophiodon lautricense*, the *Anthracotherium magnum*, the *Rhinoceros antiquitatis* are the giant and the last representatives of their branches. It would be easy, according to this law, to predict the approaching natural extinction of the Elephant, of the Hippopotamus, of the Whale, and of some other huge species of our present time, even without the intervention of man to hasten their disappearance. Lastly, this phenomenon is equally noticeable among the Invertebrates. We know that the giant forms among the Ammonites, the *Pinacoceras*, the *Arietites*, and the *Pachydiscus* are found only at the end of their branches; the *Megaladons*, the *Dicerata*, the *Caprinæ* reckon their hugest species in the most recent levels of their geological duration. It would be easy to recall many other similar cases.

The curious remark was long since made that it is at the very moment when the species of a group have reached the maximum of power, either by the dimensions of the body or by the perfection of offensive or defensive weapons which would seem to afford protection against all enemies, that these species are on the eve of vanishing. All evolution progressive in appearance, and all new adaptations, are an extra danger for the survival of the type.

Many palæontologists have endeavoured, in the course of the last few years, to examine still more searchingly into the mechanism of the extinction of species. As early as 1893, Dollo formulated, in the concise form customary with him, the laws of palæontological evolution :—*development proceeds by bounds, is irreversible, and limited.* The first of these propositions deals with the problem of the formation of species, and will be the subject of discussion later on. The two other laws, that of *irreversibility* and of *limitation* of development, furnish precise statements of interest in the question before us. By irreversible evolution is meant that a branch, once started on the lines of a given specialization, can, in no case, travel backwards on the track traversed. Thus, the Horse, having lost the lateral digits of its Tertiary ancestors—or, at least, transformed those metapods into two osseous stylets buried in the flesh—will never be able to develop anew those rudimentary digits, which must, on the contrary, tend more and more to disappear. The Sirenians, descended, according to all indications, from terrestrial Ungulates adapted by degrees to aquatic life, whose hind limb has been progressively reduced to an interior bony rod which is the simple rudiment of the iliac bone, have now become incapable, under any conditions, of again forming a complete hind limb, and of reassuming quadrupedal functions. Should the circumstances of their surroundings become modified in a manner unfavourable to their natatory existence, the Manatee and the Siren would suddenly become extinct, but without leaving survivors adapted to different functions. In the same way the Ammonites, such as the *Pinacocerata*, in which the line of suture has acquired an elegant degree of complication exceeding, doubtless, that of all the other branches of the Cephalopods, died out at the end of the Triassic period, without perpetuating themselves in the branches with simpler partitions of the commencement of Jurassic times.

By the side of the law of Irreversibility, it is right to make an interesting place for an idea, already ancient, but which has acquired a new lustre from the recent writings of Rosa. I refer to the law of the *progressive reduction in variability*. Haeckel had already shown that groups on the road to extinction produced no new varieties, and taking, with Wallace, the standpoint of Darwinian selection, it must be admitted that the chances of survival of a type are in direct ratio to the number of favourable varieties it produces. Rosa proves that every series of forms specialized in one direction is doomed to extinction, for the reason that these forms are no longer competent to vary sufficiently. It is perfectly true that the number and extent of the variations diminish as fast as the specialization increases. Palæontology can furnish numerous proofs of this. The great group of

Trilobites which became extinct at the end of Primary times no longer comprises after the Carboniferous epoch more than one branch, that of the *Phillipsiæ*, which continues as far as the Permian with nothing but insignificant mutations or variations. The Brachiopods of the family of the Spiriferidæ, so brilliantly represented in Primary times at the end of their existence in the Lias, are no longer represented except by two small genera, *Spiriferina* and *Suessia*, with forms very little varied. The tetrabranchial Cephalopods, whose forms, varied to infinity, were the ornament of the Silurian seas, already lose the major part of their branches in the Devonian, and after the end of the Trias only figure in the shape of nautiloïd shells of so uniform a type that palæontologists have some difficulty in distinguishing species among them. In the Vertebrates the phenomenon is likewise very frequent. The evolution of the branch of the *Dinotheria*, for instance, passes, in Europe, through the whole of the Miocene times without any other variation than a regular progression in size, so that, without this characteristic, all specific distinction would be impossible. Many similar remarks might be made regarding other groups extinct or in course of extinction; for example, in the Palæotheridæ, the Tapiridæ, the Oreodontidæ, the Anoplotheridæ, the Mastodons, the Taxodons, the Hyracoïds, the Hyænodontidæ, etc. It must, however, be acknowledged that the law of Rosa constitutes in one way a vicious circle, for it would be quite as easy to assume that if branches which have arrived at the termination of their geological duration vary very little, it is for the very reason that they are in course of extinction.

Thus we note that the duration of existence of phyletic branches is not *indefinite*, as demanded by the logic of Darwin's hypothesis and maintained by Weismann quite recently. This *limitation* takes place under the influence of the action of several natural laws, such as the exaggerated size of the body, the over-accentuated hypertrophy or specialization of certain organs, the irreversibility of evolution, and, finally, in a certain measure perhaps, the progressive reduction in variability. It must also be remembered that each phyletic branch goes through a kind of geological course, in which may be discerned a phase of *youth*, of *maturity*, and, finally, one of *senility* or degeneration preparing the extinction of the type. We can henceforward, at least as regards certain groups, commence to define and recognize the characteristics of each of these phases. Hyatt has shown that, in the great group of the Nautilidæ, each of the branches starts with an infantile stage, in which the successive dwelling-chambers constitute a straight shell or *Orthoceraconus ;* then we have an adolescent stage, in which the shell is more or less incurved, forming a *Cyrtoceraconus* or *Gyroceraconus ;* then an adult stage, in which the coiling of the chambers gives a spiral shell or *Nautiloconus ;* and, finally, a senile stage, manifested by the uncoiling or asymmetrical coiling, which we have seen above in the case of the Ammonoids. It is only important not to forget that these stages occur at varying epochs in each branch, in such a way that we find straight shells or Orthoceraconi belonging to different phyla from the Cambrian down to the Trias.

Concerning the shells of the Ammonoids, the evolution of the coil passes also through the stages of youth, maturity, and senility, which we meet with alike in nearly all the innumerable branches of this group. Hyatt has given the name of *Bactriticoni* to the straight shells such as the *Bactrites*, that of *Mimoceraconi* to the loosely coiled shells of the type *Mimoceras*, that of *Ammoniticoni* to the normal adult stage characterized by a closely spiral coiling; finally, the name of *Torticoni* to all senile cases of asymmetric coiling.

It has been known for a long time that the evolution of the line of suture allows us in the same way to establish among the Ammonoids, stages with increasing complication which are found, at different epochs, in all the branches.

Among the Vertebrates analogous observations have been made in different groups; for instance, in the Ganoïd Fishes. The primary types of this order present youthful characteristics which manifest themselves by an ossification, either nil or very little advanced, of the vertebral column, which remains soft and in the state of embryonic tissue. A little later, at the Liassic epoch, this ossification invades, little by little, the vertebræ, and towards the middle Jurassic the family of the *Leptolepidæ* has acquired an ossified vertebral column similar to that of our existing bony Fishes. The Amphibians present, on their side, at the Carboniferous and Permian periods, stages of ossification quite comparable to those of the Ganoïds.

It is equally possible to point out in the Tertiary Mammals, especially in the cranial characteristics, *primitive stages* which may be set against other stages of more advanced specialization, or *senile stages*. These primitive or *archaic* characteristics, which are found on parallel lines in groups quite independent of each other, are, among others, as follows: (1) the bones of the cranium are distinct or joined only by sutures; (2) the longitudinal profile of the head is depressed and rectilinear, rising only a little or not at all towards the occiput; (3) the snout is long, and the well-developed nasal bones are articulated to the pre-maxillaries; (4) the orbit is opened out backwards, and communicates with the temporal fossa; the frontal and parietal regions are smooth, without projecting crests, antlers, or horns; (6) the glenoïd cavity of the articulation of the mandible is of small depth, and allows of movements in every direction; (7) the two branches of the mandibles are joined by ligaments, instead of being welded together. The senile stages naturally answer to opposite characteristics, such as the welding together of the skull bones; the raising of the profile of the head towards the rear; the shortening of the nasal bones; the closing of the orbit; the presence on the cranium of protuberant ridges, branches, horns, or antlers; the limiting of the movements of the mandible; and the welding together of the branches of the mandible. It should not be forgotten that, as with the Nautilidæ, these stages of development do not manifest themselves in all branches at the same period of their geological course, the rapidity of the evolution being essentially variable according to the group. Thus the *Hyrax* or present Daman possesses an entirely primitive skull, comparable, in degree of evolution, to those of several small Ungulates of the Eocene period. It will be seen what grave errors one would be led to commit did one attempt to use these stages of evolution, as Gaudry proposed, as the sole criterion for determining the absolute age of fossil animals.

Thus the general evolution of the animal kingdom presents itself to us as being constituted by a sheaf of innumerable phyletic branches parallel in their evolution, and without ever having intermingled during a more or less long series of geological periods. Each of these branches arrives, with more or less speed, at mutations of great size and of very specialized characteristics, which vanish without leaving descendants. When a branch disappears by extinction, it is, so to speak, *replaced* by another branch having an evolution until then slower, which in its turn passes through those phases of maturity and old age which conduct it to its end. The species and genera of the present time represent those which have not yet arrived at the senile phases ; but it can be foretold that some among them, the Elephants, the Whales, the Ostriches, etc., are approaching this final phase of their existence. The mechanism of the extinction of species commences, therefore, to show itself with a certain clearness. We should now ask ourselves how much knowledge we have of the opposite side of the problem of life, I mean of the origin of species and groups of a higher order.

BOOK VI

THE MECHANISM OF THE PRODUCTION OF NEW FORMS

CHAPTER XXIII

THE LAWS OF CONTINUOUS PROGRESS AND THE APPEARANCE OF GROUPS

Law of the late appearance of the higher types—Discoveries making against this law—The epochs of the first appearances of groups found to be more and more remote.

THE notion of a continuous progress in the general evolution of the animal kingdom from the earliest fossil faunas down to Nature at the present day has struck the mind of observers ever since the very dawn of palæontology. Cuvier had already stated perfectly clearly the principal stages of this progress, as I had occasion to demonstrate above, when analysing the work of this great naturalist. A little later, the masters of transformism, Darwin, Wallace, Haeckel, etc., developed at length this idea, which, in their hands, became one of the principal arguments in favour of the hypothesis of evolution. More recently still, different palæontologists have insisted afresh on the gradual perfection of fossil animals, and in France Gaudry has devoted his entire *Essai de Palæontologie*

Philosophique to the demonstration of this progress, both in the general organization of beings and in the details of each function. It might almost be said that this notion had become commonplace through being constantly reproduced in so many works.

We cannot, in fact, fail to recognize that, on the whole, the most perfect groups, that is to say, those highest in the zoological hierarchy, have appeared at relatively recent epochs. We do not, as yet, know of any Vertebrates in the Cambrian or in the pre-Cambrian. Primary times are characterized by the reign of several inferior groups, the Tetracorals the tessellated Crinoïds, the Cystoidea, the Blastoïds, and especially the Brachiopods. Among Vertebrates, the cold-blooded and lower types alone are represented in these periods by the Fishes, Amphibians, and Reptiles. Up till then no bird or mammal appears to have arrived on the palæozoic continents. In Secondary times the Invertebrates have hardly any further progress left to achieve; but in the world of Vertebrates the marine and terrestrial Reptiles occupy easily the first rank. The Birds are rare, and among Mammals those orders with lower organizations, marsupial or monotreme, alone appear to be represented. Finally, in the Tertiary era, the orders of Mammals belonging to the highest or the most differentiated types, like the Proboscidians, Equidæ, Ruminants with antlers or with horns, and Apes only appear in Neogenic times, and Man, who represents, in point of cerebral development at least, the highest point of the organized world, seems, as far as our knowledge goes, to have entered as the last actor upon the changing stage of the world.

Still we are compelled to acknowledge that the seeming regularity of this picture has been rather seriously affected by the latest palæontological discoveries. The Molluscs were considered but a few years ago as having first appeared in the Tremadoc stage at the borders of the Cambrian and the Silurian. Walcott has described a tiny Lamellibranch, *Modioloides*, in the lower Cambrian, and he has just pointed out some patelloïd shells of the genus *Chuaria* in the pre-Cambrian of the Rocky Mountains. The Cephalopods, who are the highest organized Molluscs, were for a long time only known from the Ordovician stage onward. There have now been found in the Cambrian of Esthonia and Nova Scotia straight-shelled Nautilidæ of the genus *Volborthella*. The true Ammonitidæ, with slashed and speckled partitions, were long considered as special to the Secondary times: but palæontologists in India, in the Ural, in Sicily, and in the Pyrenees have revealed to us their presence in the lower Permian, and the existence, at this level, of manifold branches, giving us a glimpse of a still earlier ancestry. The appearance of natatory Crustacea of the order of Trilobites, after having been pushed back from the Ordovician to the middle Cambrian, and then to the lower Cambrian, has been also noticed in the pre-Cambrian of North America. It is the same with another order of great marine Crustacea, the Gigantostraca, or Eurypterids, of which the stratigraphic extension seemed limited from the upper Silurian to the end of Primary times ; recent discoveries in the cañons of Montana push back this lower limit to the pre-Cambrian.

The palæontological history of the Vertebrates will yield us still more striking examples of this successive pushing back of the date when several groups first appeared on the earth. When Murchison discovered in the last strata of the upper Silurian of England, the fin-spines and teeth of Selachians, mingled with the dermic shields of Placoderms, it was for a long time thought that we were dealing with the earliest Fishes of all. But here again North America has disclosed to us the existence, as early as the Ordovician stage, of numerous remains of Ganoïd Fishes which open out horizons of still earlier ichthyological faunas in the Cambrian or the pre-Cambrian. We know now, thanks to a lucky discovery by Lohest, that the Amphibians already existed at the epoch of the formation of the schists of the Fammene, that is, in the upper Devonian. The true Reptiles were long supposed to have appeared only at the commencement of Secondary times. Several orders, of marine or terrestrial habitat, of this class, have been discovered later in palæozoic find-spots. Among the most ancient types the group of the Rhynchocephalians should be noted, with a lacertiform body, bi-concave vertebræ, and a breastplate of highly developed ventral ribs, of whom only one existing representative, the genus *Hatteria*, dwells on the coasts of the New Zealand Archipelago. Credner has shown us that a species very nearly akin to the existing type, the *Palæohatteria*, already lived in the lagoons of Saxony at the middle of the Permian epoch. Still more recently Thevenin has described in the upper Coal formation of Commentry a genus *Sauravus*, which seems properly to belong to the same group, and whose very perfect ossification of the skeleton implies the existence of numerous precursors at still earlier epochs. In the course of late years, Amalitzky has discovered in the Permian of the banks of the river Dwina terrestrial Reptiles far advanced in evolution, and belonging to the three great groups of the Pareiasaurians, the Dicynodonts, and the Dinosaurs. We can distinguish a time approaching when the kingdom of Reptiles will stretch over a large part of Primary times. Every now and then some sensational discovery brings us unexpected revelations on the antiquity of groups. Thus Vidal suddenly discovered in the lithographic limestone of the upper Jurassic of Catalonia, a *Palæobatrachus*, a real anuric Batrachian, of which the existence as a group appeared to go back hardly to the beginning of the Oligocene. Similarly, the highly specialized type of the Turtles had for a long time no known representative further back than the upper Jurassic of Soleure, where Rütimeyer made known a great number of species, with marine habitat, appertaining to the two sub-orders of the Pleurodera and the Cryptodera. The differentiation of these two groups as early as the end of the Jurassic, of itself showed us the great antiquity of the Chelonian type; in fact, Quenstedt was not long in discovering in the sandstone of the upper Trias of Suabia a Pleuroderous Turtle, the *Proganochelys*, whose existing descendants dwell in the fresh waters of the Southern Hemisphere. As we know, on the other hand, that marine Turtles of the group of Turtles with dermic breastplates, or Athecæ, already lived in the Triassic and infra-Liassic seas, we may predict the future discovery of Chelonians of the Permian epoch and probably even much earlier.

The warm-blooded Vertebrates are likewise much older than we suppose at the present time. The discovery of the *Archæopteryx* of the upper Jurassic of Bavaria with its separate fingers armed with claws, its beak furnished with conical teeth, and its long lizard's tail, if it has demonstrated beyond dispute the reptilian connections of the class of Birds, in no way enlightens us as to the precise period when the divergence of these two organic types occurred. The *Archæopteryx* is already, in its structure taken as a whole, a true Bird furnished, without any doubt, with a very long ancestral genealogy, which for the present escapes our observation.

Mammals, if we take the class as a whole, appear for the first time in the higher Trias and in the Rhætian. The *Dromatherium sylvestre* of the Trias of Carolina, so far as may be judged from one single semi-mandible, seems to be connected with the group of insectivorous Marsupials, but has less complicated molars with a single point. As to the *Microlestes antiquus* of the Rhætian of Wurtemburg and England, it seems logical to connect it with the Plagiaulacidæ, that is to say, with the *Multituberculata* having a marsupial or perhaps a monotrematic organization. What is certain is, that as early as the end of the Trias two groups of the lower Mammals were already sharply differentiated. Different palæontologists, Owen, Seeley, Osborn, etc., have attempted, with great skill, to show the affinities which the class of Mammals presents, from the osteological point of view, with the Theriodont Reptiles of the South African Trias. Without ignoring the curious resemblance of the molars of the *Tritylodon* with those of the Multituberculate Mammals, and the resemblance of the bones of the limbs of the *Theriodesmus* with those of the Lemurians and Carnivora, one could no way dream of deriving the Triassic Mammals directly from any of the known forms of these African Reptiles, who are animals of relatively great dimensions. The law of increase in size demands, in fact, for small animals like the *Dromatherium* or the *Microlestes*, ancestors still more tiny, which should be sought for in Primary strata. We are logically brought to foresee the presence of true mammals at perhaps very remote epochs of Palæozoic times.

If we enter into the details of the Mammalian groups, we shall have to register similar pushings back in the case of many branches. It was the rule a few years ago to affirm that the Placental Mammals only commenced in the Tertiary epoch. This was in truth a very improbable proposition, since in the very lowest Eocene both of Europe and North America, Placentals belonging to several already well-differentiated orders, Insectivores, Creodonts, Condylarthra, Amblypods, Tillodonts, and even Lemurians, have been discovered. The presence of Primates in the so-called primitive fauna of Cernay and of Puerco is particularly instructive, and constitutes a highly valuable argument against the theory of the continued progress of beings. It is in vain that Dr. Lemoine, in his fine researches on this lower Eocene fauna of the environs of Rheims, has attempted to prove that it was impossible to include the Mammals of Cernay in the orders of existing Placentals ; the differentiation of the great groups, though less perfect than in more recent faunas, is none the less obvious to a palæontologist, and forcibly leads us to the conviction that these Placentals of the very lowest Eocene possessed a long line of ancestors dating from Secondary times. But here we are verging upon the unknown, and every possible hypothesis has been proposed for finding a *centre of dispersion* for the Placentals, sometimes in the Arctic Continent, and sometimes in some Pacific Continent supposed to have disappeared by subsidence. If the recent data brought by F. Ameghino to the study of the faunas of the Cretacean Mammals of Patagonia are confirmed from a stratigraphic point of view, it would perhaps be expedient to seek in the Continent of South America for the real primitive ancestors of our Tertiary Primates and Ungulates.

Even for the most specialized groups, such as the Proboscidians, the recent discovery in the Oligocene of the Libyan desert, of the *Palæomastodons,* the ancestral forms of our Miocene and Pliocene Mastodons show us at what remote period in the geological past we shall one day discover the points of differentiation of each branch.

To sum up, it will be seen that the epochs of appearance of each great group of fossil animals—even of those highest in the zoological scale—go further and further back into time as palæontological discoveries accumulate. We have long known that in the Cambrian epoch most of the great groups of the Invertebrates were already sharply distinct, and that, consequently, we must almost give up the hope of one day discovering the primitive types of the Foraminifera, the Sponges, the Corals, the Cystoidea, the Crinoïds, the Brachiopods, the Lamellibranchs, the Gastropods, the Cephalopods, the Trilobites, the Merostomes, and even, no doubt, the air-breathing Articulates. It is probable that in a few years we shall have to say the same of the great classes of the Vertebrates, since already we are certain that the Fishes go back at least to the Ordovician, the Amphibians to the Devonian, the Reptiles to the Carboniferous, and the Mammals to the Trias. If there has really been, as is probable, a gradual improvement in the organic world, and if the animal types are the more recent as their organization is higher, we shall certainly be called upon to push back for several geological periods all the dates which mark provisionally the inception of all our branches.

CHAPTER XXIV

INDIVIDUAL AND PALÆONTOLOGICAL EVOLUTION: ONTOGENY AND PHYLOGENY

The great biogenetic law of Haeckel—Embryological acceleration or tachygenesis—Embryonic types persisting in the fossil state—Study of individual development in the Ammonoids and the Lamellibranchs—The milk teeth of Mammals.

THE law of progress manifests itself quite as plainly in the development of the individual as in that of a group. *Omne vivum ex ovo* has become a commonplace axiom, affirming that the most complicated individuals proceed from an egg, that is, from a monocellular being similar to the lowest types of the animal scale. The species born from the egg subsequently passes through a series of phases of development, more complex and more numerous as the group is higher in the scale. Very early came the idea of comparing the phases of the individual development with those traversed by the group itself in the course of its palæontological evolution, and of establishing a parallel between these two developments: the first very rapid, the second much slower. The concordance of Ontogeny and Phylogeny has become, in the hands of Geoffroy-Saint-Hilaire, of Serres, of Müller, and, above all, of Haeckel, the *great biogenetic law*, transformed into an instrument of research, and into an obligatory criterion of all studies on the origin and the pedigree of living and fossil beings.

It is indisputable, if we only consider the most general features, that the history of the development of an individual is a kind of rapid recapitulation of the slow phases of the evolution of the species and of the branch. This recapitulation is, moreover, very often shortened and simplified, especially in the most differentiated groups, by the fact that the embryo passes through certain stages very rapidly, or even suppresses them altogether. This phenomenon has received the name of embryogenic acceleration or *Tachygenesis*. The embryology of living animals has furnished numerous proofs in support of these laws. Without dwelling on the point, I will confine myself to recalling the case of the Cirrhipedes, so different from the Crustacea in the adult stage that they were taken for Molluscs, and with larvæ which develop themselves after the Nauplius type, like that of the Crustacean Ostracods, Phyllopods, and Copepods. I will also remind the reader that the embryos of all classes of the Vertebrates resemble each other in the first stages of their development to such a degree that it is difficult to distinguish one from the other, and that they only acquire little by little the characteristic traits of each group.

Has Palæontology completely confirmed the conclusions thus drawn from the embryology of existing beings ? We may approach this important question by two different methods.

The first method, which is the oldest and the one most generally employed, consists in finding in geological strata forms which in the adult state reproduce one of the transitory phases through which the development of an existing animal passes. We give to these fossil forms the name of *Persistent Embryonic types*. Palæontology is able to furnish us with a fairly large number of examples of this. Thus the Fishes of the Primary epoch, such as the scaly Ganoïds, have a soft vertebral column in a state of embryonic tissue or *notochord*, as in the embryos of existing Ganoïds or Teleosteans. The ossification of the vertebral column takes place progressively from the Silurian to the middle Jurassic, thus spreading over a very long geological period the stages of the individual development of our present Fishes. In the same way the palæozoic Amphibians pass, as regards the ossification of the vertebral column, through a series of progressive phases : first the *lepospondylian* stage, in which the bony tissue forms a simple sheath round the centrum which remains soft and embryonic (*Branchiosaurus*) ; then the *temnospondylian*, in which several points of ossification develop themselves in the vertebral arcs and apophyses, and give bony segments which remain apart from, and do not adhere to, the centrum (*Archegosaurus*) ; and, finally, the *Stereospondylian* stage, in which the vertebra is completely ossified, as in the Triassic Labyrinthodons. These different phases are reproduced in the development of our present Reptiles and Amphibians. In recent and modern Ruminants the bones of the metacarpus and of the metatarsus, separate in the embryo and the young animal, become welded later in the adult into a cannon-bone caused by the fusion of two metapods. We know among the early Ruminants genera such as the *Pœbrotherium* among the Camelidæ, and the *Gelocus* among the Tragulidæ, in which the metacarpal and metatarsal bones remain distinct in the adult stage.

We may also quote a few persistent embryonic types among the Invertebrates. Certain palæozoic Belinuridæ, the *Prestwichia,* strangely resemble the young larvæ of the existing Limulus. The *Pentacrina* larva of our *Antedon,* is very comparable to many fossil Crinoïds. The early Urchins with linear ambulacra retain in the adult state the transitory stage through which pass the more recent Urchins with petaloïd ambulacra. Lastly, among Brachiopods, Baecker has shown that each stage of growth of the brachial supports in the modern Terebratulidæ corresponds to some genus of fossil Terebratula.

But it must be very clearly stated that these examples of representation in fossil adult species of the embryonic, or more correctly, of the youthful characteristics of existing animals, cannot be generalized, and that they remain up till now in the state of exceptional facts.

A second mode of investigation, more direct and more sure, consists in studying the individual evolution of the fossils themselves, from their early, if not their embryonic, state to that of their adult form. Unfortunately it is confronted in practice, in most cases at least, by almost insurmountable material difficulties, proceeding from the dearth of young forms whose preservation during the act of fossilization is more uncertain.

Certain groups, however, and particularly the Gastropod and Cephalopod Molluscs, retain interesting traces of their youthful stages, at least as far as regards the characteristics of the shell, thanks to the construction by the animal, in the course of its individual growth, of spiral whorls, or successive dwelling-chambers, the modifications of which it is fairly easy to study. It is open to us, for this purpose, either to examine the individuals of various sizes, and, consequently, of various ages, in one species, or—which is a still more effective process—to break open the shell, in order to study its internal windings, to take it to pieces, so to speak, room by room, from the embryonic whorls down to the adult and even the senile ones. On these lines the shells of the Ammonites, in the hands of Sandberger, Keyserling, Hyatt, Branco, Karpinsky, Mojsisovics, etc., have given exceedingly interesting results, both from the point of view of the general evolution of the group, and from the genetic relations of genera and families.

Attention has been specially directed to the development and progressive complication of the *partitions,* that is to say, the suture line which marks the separation of the different chambers. In the most primitive Ammonoids the first partition formed immediately after the initial ovoïd chamber is straight or hardly marked with a slight sinus, and thus reminds one of the adult partitions of the Nautilidæ; it is the saddleless type of Branco. This very simple type of partition only persists, in the adult state, in a very small number of genera of the Devonian epoch (*Cyrtoclymenia, Mimoceras*); in the other *saddleless* genera of the Primary epoch it is limited to the first partition. In a second type, the *broad-saddled* type of Branco, the first suture is characterized by a large convex sinus forward, or *ventral saddle.* This type is only observed in the Ammonoids of the Primary epoch, and in a few families of the Triassic. In all other Ammonites, Triassic, Jurassic, and Cretacean, the first suture denotes the third or *narrow-saddled* type, characterized by a long and narrow central saddle. There is then in the form of the first suture of the Ammonians a progression from the saddleless type to the narrow-saddled, with embryogenic accelerations (*tachygenesis*), that is to say, suppression first of the saddleless stage, and then of the broad-saddled one, as we rise in the series of ages.

If, starting from the first saddleless, broad-saddled, or narrow-saddled type, all of which are very simple, we study the successive sutures of the same species of Ammonite, these partitions are observed to become gradually more complicated; the median or ventral saddle first becomes hollowed out in the middle with a sinus or *ventral lobe,* at the bottom of which there frequently appears a projection or secondary ventral saddle. At the same time one sees produced, on the sides of the suture line, saddles and lateral and more and more complex lobes and accessories. Beginning at the third suture, in all Ammonoids there occurs the *Goniatite* stage, characterized by several simply undulated lobes or bands, without secondary denticulations. All forms of the saddleless or broad-saddled animals in which the sutures in *the adult* remain at this slight degree of complication, constitute the group of Goniatites, which are peculiar to Primary times. This great family presents very varied types, of which each one marks an arrest in one of the phases of development through which pass the Ammonites properly so called. In these, the suture line does not remain in this simple state; it is complicated by the multiplication of the bands and lobes, and by the subdivision of these parts. In the *Ceratitæ* of the Trias the first degree of complication appears, in which the bands or convex parts remain intact, while the lobes or concave parts are slashed with fine dentelations. Lastly, in most Ammonites, the bands and lobes are not only dentelated, but subdivided *ad infinitum*, giving the type of spangled partition, reminding one of the manifold crimpings of a parsley leaf.

One of the most interesting results of these studies has been the established fact that the Ammonites with, in the adult stage, the most complicated compartments successively present first the *Goniatite* stage, and then sometimes the *Ceratite* before reaching the Ammonite stage, which is acquired at a diameter of three to four millimetres at most. Hyatt and Branco have shown, however, that the Ceratite stage is generally passed over, and that the suture of the Goniatite type passes direct to the Ammonite stage.

Modern palæontologists make use with great advantage of the characteristics of the suture line in the embryonic and ephebic whorls of the Ammonites, to discover the ancestral relations of genera apparently far apart from each other, as shown by the characteristics of the adult whorls. Among the most remarkable attempts in this line we must quote the researches of Karpinsky on the phylogeny of the *Prolecaniditæ* family, a work in which the Russian scholar has followed with the greatest care and through several branches the ontogenic development and the order of apparition of the genera, from the *Ibergicerata* and the *Prolecanitæ* of the Devonian down to the *Lecanitæ* and *Noritæ* of the Triassic epoch. In the same way Hyatt, utilizing at once the development of the compartments, the coiling of the shell, and the details of its exterior ornamentation, has essayed to trace the evolution of the genera of the great family of the *Arietitæ*. Joined, perhaps, to the Triassic *Gymnitæ*, the radical form of the group is the genus *Psiloceras*, of the Hettangian stage, from which would be derived two branches of Arietites. The first or *plaited branch* has for ancestral form a plaited variety of *Psiloceras planorbis*, which passes by way of the contraction of the plaits and their transformation into prominent ribs, to the successive species of the genus *Schlotheimia*. This same branch gives by bifurcation another series characterized by the apparition on the median line of a large keel between two longitudinal furrows. This series gives successively the *Caloceras*, and then the *Vermiceras* of the lower Lias. The second, or *smooth branch*, is derived from a smooth variety of the same *Psiloceras planorbis* with a more complicated suture. The embryonic whorls of all forms of this branch will, therefore, be smooth ; then ribs and a strong keel appear in the *Arnioceras* ; this keel finally becomes accentuated, and in the enormous *Coroniceras* of the Sinemurian, is bounded by two furrows. A subdivision of this branch, in which the whorls become gradually less spiral and the shell flattens, brings us, through the intermediary of the *Agassiceras*, to the discoïd and sharp-edged shells of the *Oxynoticeras*. Again, it is by studying the individual evolution of the suture line that G. Sayn has proved the unforeseen ancestral connections of these smooth and sharp-edged shells of the *Oxynoticerata* of the Jurassic with the very elegantly ornamented shells which constitute the interesting little family of the Barremian *Pulchelliidæ*. It may be hoped that at no very distant future specialists may arrive, by the aid of this method of individual ontogeny, at tracing with exactness the innumerable phyletic branches of the great group of the Ammonoids.

For the study of the evolution of the Lamellibranchs, Felix Bernard has employed a method somewhat different from the one I have just indicated as regards the Ammonites. He has examined with attention the embryonic shells (nascent)* found in extraordinary abundance in certain Tertiary deposits, such as the Miocene sands of Saint Paul de Dax, and has been able to follow the modifications of the hinge, and the position of the ligament and of the adductor muscles common to certain genera

* *Naissain.* Name applied to young oysters still in their beds.—Ed.

in the course of their individual evolution. Jackson, who, on his side, has followed up the different stages of development of a great number of forms, has shown that the primitive shell commences as a thin cuticle in the shape of an uneven saddle, like the primitive shell of the Gastropods; then a deposit of lime occurs at the two extremities of this membrane, forming a bivalvular shell, or primitive *prodissoconch*. In all the genera in which it has been observed, oysters, cockles, scallops, etc., the prodissoconch is equivalvular, with a straight hinge, void of teeth, with a rounded and not very prominent top. In all cases the animal is provided with two adductor muscles, and only becomes monomyous * by subsequent modifications, which likewise influence the direction of the hooks, the position of the ligament, the fixation of the shell, its ornamentation, etc. The prodissoconch often remains visible and sharply distinct from the rest of the shell up to a certain age. The development of the teeth of the hinge is particularly interesting to follow in certain families. In oysters, without teeth at the adult stage, Munier-Chalmas was able to observe on embryonic shells teeth ranged in series, as in the existing Nuculas and Arcas. This type of hinge, with crenellated teeth, or *Taxodont* type, appears to be, in fact, according to Jackson, the most primitive form of the hinges of the Lamellibranchs; the Nuculas, the Arcas, the living *Pectunculus* would thus be, in a way, the *persistent embryonic types* of this order of Molluscs. On the other hand, in the Pectinidæ, also without cardinal

* Single-muscled.—Ed.

teeth in the adult stage, there exist, at first, two pairs of oblique, symmetrical teeth, which recall the teeth of the Spondyls and of the Plicatules, and point to ancestral affinities with the types of the *Isodont* group. Thus the study of the embryonic stages has already permitted, and no doubt will still further permit, the real phylogenic relations between the different families of the Lamellibranchs to be established.

As regards Vertebrates, the study of individual development is more restricted in its application, for the reason that embryonic or even young subjects are not generally preserved in the fossil state, and that the progress of ossification naturally causes the disappearance in the adult stage of those phases through which the embryo and the young individual have passed. There can be quoted, as an exceptional example, the milk teeth of the Mammals, which are frequently enough preserved in a fossil state, and furnish very interesting indications, but of which the interpretation is somewhat difficult. Many opinions have, in fact, been formulated on the signification of milk teeth in relation to the definitive dentition. Some have seen in them a sort of reminiscence of ancestral dental structure. According to Rütimeyer, the milk teeth of the Ungulates not infrequently preserve characteristics belonging to forms geologically and genetically earlier, which are no longer present in the definitive dentition. We ought thus to have a means of securing a retrospective view of the genealogy of each group. Other palæontologists have seen, on the contrary, in the structure of the milk teeth a "prophetic echo" of future dentition in the descendants of the same group. Impartial observation discloses that neither of these hypotheses is completely justified. The milk molars of the Ungulates and of the majority of other orders are distinguished from the second set by their longer form, their lower crown, their thinner enamel, and their more complicated structural details. According to Stehlin, the milk molars of the Imparidigitæ are, on certain points, more conservative, on others more progressive than the permanent molars. On the one hand, they preserve the low-crowned or *brachyodont* type of the early types of this group in opposition to the high or *hypseledont* type of its more modern representatives, and, from this fact, we may be allowed to see in them a kind of ancestral reminiscence. On the other hand, however, the complication of the folds of the enamel, the development of ridges, of hooks, of supernumerary tubercules, etc., are more connected with a progressive evolution, which is sometimes shown in the definitive dentition of the descendants, and must then, perhaps, be regarded as a prophetic echo. Yet in many cases, according to Stehlin, these complications of structure may more simply be attributed to the slight density of the enamel.

CHAPTER XXV

THE ORIGIN OF SPECIES AND GENERA

Our ignorance of first causes—Two hypotheses: slow and abrupt variation—Slowness of the direct or normal evolution—Divergence through geographical isolation—Abrupt variation or saltation of de Vries—Its application to fossil animals—Conclusions.

We now approach one of the most important problems set before us, that of the origin of species and genera during the course of the palæontological history of the earth. I shall not here go in detail into the oft-renewed discussion on the *first causes* of the variations which have happened to beings, living and fossil; that is to say, on the formation of new species. Are we, with Lamarck, Herbert Spencer, Roux, Cope, Osborn, Hyatt, and the whole of the modern neo-Lamarckian school, to seek the cause of these changes in an active mechanical strain of organisms, or in the effort of beings towards an adaptation as perfect as possible to the conditions of their environment? Or shall we look for it with Isidore Geoffroy-Saint-Hilaire, Semper, Clessin, Locard, Dall, Schmankewitz, etc., in a direct and passive action of the floating environment on the organs of animals, and, in the end, on their general structure? Ought we, with Darwin, Wallace, Huxley, Haeckel, and all the Darwinian school, to regard the efficient cause of the changes in beings in the struggle for life leading to a natural selection with survival of the fittest? Is it expedient to listen to more mysterious and obscure causes, such as the theory of Weismann on the *continuity of the germ-plasm*, transmitted by parents with special qualities which selection afterwards develops, or to the hypothesis of Naegeli on a natural and permanent tendency in each individual towards a more perfect state, a tendency which added to Darwinian selection determines the evolution of morphological characters? Carried into this field, the question of the origin of species is raised to a problem of sublime biological philosophy, the discussion of which is still open, and an agreement upon which among naturalists is not on the eve of conclusion.

What we may affirm is that the too exclusive Darwinian theory of the struggle for life has been subjected for the last quarter of a century to a bombardment of serious objections, which have made it lose much ground. Brown and A. Braun have pointed out the uselessness of many organs which, on the hypothesis of selection, could neither have been produced nor modified. H. Spencer has shown that very slight variations could neither be of use to the individual nor afterwards be adopted by selection. Finally, Dollo and Rosa have proved in recent years that the variation of groups is not indefinite, as required by Darwin's theory, but, on the contrary, limited by a duration of time varying according to the groups.

It appears that the majority of modern naturalists adhere from choice to the Lamarckian theories founded at once on the action of external conditions and on the mechanical reaction of the organism (use or non-use of the organs, different strains and pressures, etc.) with regard to the environment which surrounds them. But many palæontologists, rightly struck by the inexplicable facts of the abrupt extinction of whole groups, like the Trilobites, the Ammonites, the Dinosaurs, etc., and by the constant progress of phyletic branches towards an intensive and often exaggerated specialization, wish to add to these causes—rather external than anything else —of variation, another *unknown force* of a more internal order, which limits the variation of the groups, as if every one of them at its inception possessed a given amount of sap, the exhaustion of which sooner or later takes place and brings about the fatal extinction of the branch.

Leaving on one side these burning but difficultly solved problems, we will take our stand on the narrower sphere of palæontological facts, and attempt to fix the visible mechanism of the apparition of fossil forms, or, if you prefer it, the processes worked by Nature in the formation of species and genera, and in the development of new branches. Two opinions have been long since put forth on the mode of the birth of new species. Some see in it the result of *slow and gradual modifications* accumulated by lapse of time. Others, on the contrary, believe in the *abrupt* and spontaneous apparition of variations, distinct enough at the outset to constitute real species; this is the hypothesis of abrupt variation or *saltation*.

It does not seem impossible to me to assign, perhaps, a part to both these processes ; but we must first establish a fundamental distinction—which seems to me to have been hitherto too much neglected—between the *direct* and, so to speak, normal *evolution* of a branch already formed, and the *lateral variation* which alone can lead to the birth of new branches and to the divergence of groups.

By referring to the notions acquired above on *phyletic branches*, we know, through the important researches of Waagen, Neumayr, Branco, Mojsisovics, Hyatt, etc., that it is possible to constitute, by the aid of fossil animals, many *series of forms* whose different terms or *mutations*, taken step by step, stage by stage, and even zone by zone, are linked to one another by almost imperceptible transitions. The number of these series, established first in a few families of the Molluscs, has to-day become very considerable, and they have been found with identical characteristics in all the groups of the Invertebrates and of the Vertebrates. If we confine ourselves to the comparison of immediate mutations, the differences which separate them are very slight, and appear too insignificant to deserve to be distinguished as species. But if we pass over a certain number of these intermediate forms, and especially if we happen to compare the extreme types of the same branch, we notice differences important enough to justify the separation, not only of species, but sometimes even of perfectly legitimate genera. Every palæontologist who has carefully studied any group whatever of fossil animals has found himself face to face with these series of forms or *phyletic branches* which split up by transverse segments into species and genera. I have above shown remarkable examples of this among the Proboscidians and the Anthracotheridæ.

It is true—and this remark is important—that the species and the genera thus formed by the direct and normal evolution of a branch always remain very closely related to each other, and do not present differences considerable enough for them to be ranked as distinct natural families. It must also be observed that this evolution seems to take place in, so to speak, a spontaneous manner, independent of the action of modifying causes derived from the external environment. *The process of slow variation thus forces itself upon every observer as the general rule of the direct evolution of phyletic branches.*

Let us now follow up the lot of these natural series, on the one hand, to their end, and, on the other, towards their beginning. I have already said, with regard to the causes of the extinction of species, that the duration of these branches is more or less long, but that always, after having obeyed the laws of increase in size and of progressive specialization, they abruptly ended in extinction without issue. We must, of course, make exception of those branches which are evolving before our eyes, and which comprise all the animals of the existing fauna. At their lower part, phyletic branches may also be followed for a longer or shorter time, but they nearly always end in an abrupt way ; or, rather, they *appear* to do so, for the observer is confronted by a *hiatus*, explainable by a *migration* of distant origin of the group under discussion. In order to follow up the evolution of the branch, it would, perhaps, be necessary to transport ourselves into distant geographical centres, or often to unexplored ones. I shall return later on in detail to these phenomena of *migrations*, which have played a most important part in the changes of the faunas of geological times. It is probable that when the exploration of the globe is more advanced, it will be possible for palæontologists to join end to end these *segments* broken by the phenomena of migration, and to re-establish the continuity of the successive mutations of the innumerable parallel branches which represent the collective animal world. *Slow transformation* will doubtless then present itself as the most normal and the most generalized process of palæontological evolution.

But, if the mechanism we have just studied offers an explanation of the regular development of the species and genera of the same natural branch, it does not seem, on the other hand, sufficient to provoke the divergences necessary to bring about the bifurcation of the various branches of the same family, and those still more important differences which must lead to the differentiation of the orders, the classes, and the higher divisions of the animal kingdom. It is here probably that those more rapid mechanisms come into play, which we will now endeavour to analyse.

A first and still rather slow process of divergence is offered to us by *geographical isolation*, combined with *changes of the environment*. The study of the variation of species in existing Nature has already shown us the important part played by geographical limitation in the creation of *varieties* or *local races*, particularly numerous among the Molluscs of terrestrial or fluvio-lacustrine habitat. We have seen, with Neumayr, the remarkable examples of limitation furnished by the Achatinellæ of the Sandwich Islands, the *Iberi* of Sicily, and the *Melanopses* of the Mediterranean basin. In these three groups the divergence of the extreme forms is so marked that no naturalist hesitates, notwithstanding the existence of intermediate forms, to recognize in them perfectly distinct species. A few malacologists have even proposed to recognize in the *Melanopses* the formation of three genera, closely related, it is true. Isolation in islands constitutes for terrestrial animals, whether Vertebrates or Invertebrates without means of aerian locomotion, one of the most favourable conditions for the divergence of local forms. One of the most remarkable cases of this is assuredly that of the giant land Turtles, which constitute two groups of species, nearly every one of which is peculiar to one of the islands of the Archipelagos of the Mascareignes and of the Galapagos. Doubtless each of these groups represents the differentiation of the same original type gradually modified by insular isolation.

The modifying influence of isolation is also very easy to observe among our fresh-water animals, whether of rivers or of lakes. The species of Unios, Anodonts, and Limnæas are often strictly confined to the same hydrographical basin. All naturalists are acquainted with the great morphological and physiological changes, such as the loss of pulmonary respiration, undergone by certain forms of deep-water Limnæas dwelling in the vast depths of Lake Leman. Isolation is here accompanied, as in almost all similar cases, by concomitant modifications in the conditions of the environment. The example, often quoted since the researches of Neumayr and Paul, of the ornamented Paludines of the great Levantine lakes is particularly instructive on this point. These great sheets of fresh water, which covered the basin of the Danube, the Balkan peninsula, and a part of the present Ægean Sea, during the Pliocene epoch, must doubtless, owing to the intensifying phenomena of evaporation, have presented a very complete saturation with salts of lime, which has aided the thickening of the shell in the form of keels and tubercules which become more marked as we rise higher in the series of strata. This chemical or other similar explanation is all the more probable that the phenomenon not only affects the Paludines, but nearly all the other genera of Molluscs in these Levantine formations. The divergence which separates the ornamented from the smooth Paludines of our existing fresh waters is marked enough not only to justify the creation of a great number of species, but even of those real genera, which have received the names of *Tulotoma*, *Tylopoma*, and *Boscovicia*. In this case, the influence of isolation is associated with changes in the nature of the waters, and leads to the formation of manifold small branches with longer or shorter parallel evolution.

The strangely varied fauna of the Molluscs of

Lake Tanganyika offer us a striking example of the extent of these divergences derived from geographical isolation. Several of the genera of freshwater shells peculiar to this lake remind one by their external form of certain genera of marine Molluscs, such as *Trochus*, *Turbo*, *Littorina*, etc., to such a degree that it has sometimes been maintained that we are really dealing with a *residual marine fauna* enclosed by a continental depression, and adapted by degrees to waters becoming gradually less salt. It seems more probable that the genera of the Tanganyika should be considered as very divergent Melanidæ, that is to say, as types of fresh or slightly brackish waters, separated for several geological periods from their congeners, and having acquired through isolation very specialized characteristics giving them the value of genera and perhaps even of distinct families.

In the case of animals of marine habitat the conditions of isolation are more difficult to realize than in the case of terrestrial and freshwater animals, so that the divergences which separate regional forms are, as a rule, much less marked. This constantly observed fact is a very solid argument in favour of the influence of geographical isolation on the formation of species and genera by means of lateral divergence.

But this influence of isolation, important as it may be in the creation of new phyletic branches, is certainly not exclusive of other causes of variations still more speedy in their effects. I refer to the phenomenon of abrupt variation, or *saltation*, to which the attention of naturalists has so forcibly been drawn by the researches of Nilsson and of Hugo de Vries. Indeed, the hypothesis of variation of species by sudden skips is of very ancient date. Already very clearly perceived by Isidore Geoffroy-Saint-Hilaire, it was adopted and championed by Haldemann, Cope, Dollo, and many other palæontologists. These last especially saw in it a convenient way of explaining on other lines than by the rather worn-out and eternal argument of the insufficiency of palæontological documents, the sudden apparitions of groups and the absence of transitional forms, which are such frequent and, if one might say so, such general phenomena in the history of the development of fossil animals. But, it has to be acknowledged, that saltation has always remained in the realm of palæontology a simple theoretical hypothesis without any sanction of real and demonstrative fact. It is no longer permissible now to address this criticism to the curious researches made on the sudden variation of some of our present vegetables.

The starting-point of the experiments of de Vries has been the cultivation of *abnormal or monstrous varieties* of certain wild plants. The *Cardère* * gave him, in particular, a variety with a spiral stem, whose embryo is distinguishable from the normal type by three cotyledons instead of two. This twisted variety, which appears accidentally and in a sudden manner, is kept up by heredity. But the leading discoveries of the Amsterdam professor have been effected on the Œnotheras, garden

* *Dipsacus: Anglicé,* teazle.

plants with large yellow flowers of American importation. In a fallow field near Hilversum, invaded by *Œnothera Lamarckiana*, he noticed among this species many monstrous varieties, some with twisted stems, others with branches stuck together, others, again, with concave leaves or petals in varying numbers. Among these abnormal forms, two especially were remarkable from the absence of individuals intermediate either between each other or between these varieties and the parent type. They were two true species, till then unknown, and, without any possible doubt, were detached from *Œnothera Lamarckiana* within less than twenty-five years. These new species have retained their characteristics with constancy in all the cultures made by this scholar on thousands of plants. The origin of these new Œnotheras can only be explained by the fact of an *abrupt apparition* of abnormal individual plants having, perhaps, undergone during their seed life, as occurs in the Cardère, an accidental modification which is betrayed by an equally abrupt variation in the adult plant. These variations are indefinitely kept up by heredity, so that there is no excuse for refusing them the title of species.

Nilsson has obtained similar results by observing, in the laboratory of Svalöf, in Sweden, the abrupt variations arising in the ears of divers kinds of cereals. A few of these variations advantageous to agriculture constitute veritable new species, the characteristics of which are kept constant by heredity under all conditions of environment.

As to the ultimate cause of these abrupt variations,* which deserve to be called by the name of *explosions*, it is difficult to arrive at it with exactness. Some have thought them due to lesions in the embryo or in the young individual (Blaringhem); others to the stings of insects (A. Gautier); others, again, to the acts of parasitical fungi. But we must admit that the search after these first causes remains, as in all scientific matters, wrapt as yet in deep obscurity.

Do palæontological observations allow us to recognize in the transformations of fossil animals any process of explosion similar to those so clearly brought to light by modern botanists? As already said above, we cannot treat as satisfactory in so grave a question any simply *theoretical* answer which would discover in abrupt variation a more or less plausible explanation of the difficulties which confront in palæontology the exact demonstration of the transformist hypothesis. It would be, indeed, too convenient to say that if we do not meet in terrestrial strata with any intermediate form between the Gastropods and the Lamellibranchs, or between the Reptiles and the Mammals, it is because the first Lamellibranch or the first Mammal appeared by a process of divergence so rapid that there remain no traces of the intermediate links necessitated by the hypothesis of a slow and con-

* De Vries proposes to call these phenomena of abrupt change by the name of *mutations*. This is a very regrettable expression, and cannot be accepted, since Waagen, long before de Vries, gave this very name to the diametrically opposite phenomenon of the slow and gradual variation of fossil species, which he studied step by step and from strata to strata throughout the sedimentary deposits. It is preferable to give to the phenomenon observed by de Vries the name, which is moreover much more expressive, of *explosions*.

tinuous evolution. It must, moreover, be remarked that the explosions of de Vries or Nilsson, interesting as they may be from a biological point of view, go no further than to determine the creation of kindred species so near to each other that no naturalist would dream of grouping them in different genera. Supposing, therefore, that palæontological evolution has proceeded by skips as modest as those of the Œnotheras or the cereals, we should none the less be compelled, in order to prove the Reptilian origin of the Mammals, to exhume from the Permian or Triassic strata a long series of intermediate genera and species which at the present moment are totally wanting.

Confining ourselves strictly to ascertained facts, it cannot be said that palæontology at the present day allows us to specify one single well-demonstrated fact of *saltation,* or one single series of abrupt changes warranting us in thus explaining the divergence of two genera, of two families, and still less of two orders of fossil animals. There exists, however, a certain group of facts not infrequently observed, which bring to the hypothesis of abrupt variation at least a certain degree of probability in a few cases. I refer to the intermittent tendency shown by branches of producing, at certain moments of their regular evolution, numerous variations round about the parent type, which variations some palæontologists term varieties, while the majority describe them as distinct species. These periods of crisis, or, if you will, of aberration, in the morphology of certain types generally alternate with relatively calm periods of a slighter variation, during which the branch pursues with deliberation and regularity the normal course of its development. It is thus that the Ammonites of the genera *Neumayria* manifest at the Kimmeridgian epoch in the limestones of Crussol a veritable explosion of manifold forms contrasting with the dearth of variations of the same branch during the Oxfordian and the Sequanian. We may also quote in the same group of Ammonites the brilliant blossoming, at the Barremian epoch, of the Pulchelliidæ, of which there are only found, for the first time, a few meagre representatives in the Hauterivian and Valanginian stages which precede it. I may also mention, in the same order of ideas, the fine expansion at the Miocene epoch, of the Urchins of the Clypeaster genera and of the Molluscs of the family of the Pectinidæ, both of them groups which are very poor in species, and, moreover, of small dimensions, in the first half of Tertiary times. The Vertebrates also present analogous facts : the abrupt expansion of the Ichthyosaurs in the Lias, of the Pythonomorphs in the White Chalk, of the Sauropod Dinosaurs in the upper Jurassic, the multiplicity of the branches of the *Lophiodons* in the middle Eocene, of the *Palæotheria* in the upper Eocene, of the Antelopes in the upper Miocene, of the Cervidæ in the recent Pliocene, etc., indicate, in these different groups *moments* of very intense vitality which agree well enough with the hypothesis of a more or less sudden divergence of their numerous branches.

Thus the evolution of fossil beings appears to present two distinct *mechanisms* : the one continuous and, so to speak, normal, in which phyletic branches once formed develop slowly, by gradual mutations following certain laws which fatally lead them to senility and extinction; the other intermittent, in which new branches are evolved by divergence from branches which are older and have already more or less experienced evolution. This divergence seems, moreover, to be affected by at least two processes: one of them *geographical isolation* of certain and of relatively slow action, but able to lead to considerable divergences, which assume, according to the lapse of time, the value of local races, species, and genera; the other less clearly perceptible, but with a greater rapidity of action, of which the *explosions* or sudden creations of species studied by de Vries in existing plants may doubtless give us an idea.

We are able to conceive by the aid of both these processes the differentiation of species, of genera, and, perhaps, even of families, by recalling to mind the almost unlimited duration of geological times. But we have to confess that at the present day we are utterly unable to see and even to explain otherwise than by simple theoretical views the fundamental divergences which separate the orders, classes, and great ramifications of the animal kingdom.

BOOK VII

THE INFLUENCE OF MIGRATIONS

CHAPTER XXVI

THE MIGRATIONS OF MARINE ANIMALS

The relation of the migration of beings to Palæogeography—The migrations of marine animals—The influence of ocean currents—The displacement of foreshores and the migration of the environment—The part played by incursions of the sea.

WHEN palæontologists attempt to trace, through earlier and earlier geological periods, the series of animal forms which represent the natural evolution of a branch, they are nearly always stopped, after a more or less long geological course, by an absolutely impassable *hiatus*. Just as we have seen branches at their highest point end by abrupt extinction, so it seems that the majority of them appear abruptly and complete as if they had been created altogether in the region under observation. This *apparent arrest* at the outset of the evolution of each branch is explained by the sudden arrival of the group under notice in the region of the globe under study. It is expedient to state precisely this general law of the changes of faunas through migrations, and to show its great importance.

The importance of the migrations of terrestrial animals correlative to great changes in the *palæogeography* of continents was fully recognized a century ago by G. Cuvier. The illustrious founder of palæontology was struck with good reason by the absence or rarity of forms of transition between superposed fossil faunas. Exaggerating, no doubt for want of documentary evidence, the consequences of this observed fact, Cuvier concluded that an integral renewal of faunas had taken place, not by successive *creations*, as he has often been wrongly reported to have said, but by distant migrations of animals foreign to the region. Later, numerous palæontologists, Darwin, Wallace, Lydekker, Zittel, Schlosser, Gaudry, Dollo, Osborn, Matthew, Ameghino, and Depéret with regard to the terrestrial Vertebrates, Pictet, Desor, Fischer, Tournouër, Wood, Murray, Dolfus, Fontannes, Van den Broeck, etc., in the case of the Invertebrates, have directed their researches to these phenomena and have made their bearing apparent. Though the observations in this respect still present numerous gaps and include a good many rather hypothetical data, the results obtained up till now none the less offer the greatest interest and deserve all our attention.

In a very general way, it may be affirmed that the evolution of a group has hardly ever been effected on one and the same spot on this globe. Nearly always the successive representatives of a branch endowed with any considerable longevity have emigrated several times in the course of their history, becoming extinct in one region, to carry on in another and more or less distant one a new phase of their morphological destiny. The evolution of a group, therefore, presents itself, whenever we are able to reconstitute it with precision, in the form of a broken line; the different segments are derived from sometimes very distant geographical centres, and can often only be brought together by the progress of geological exploration in regions still imperfectly examined. It may be said that the majority of attempts at *phylogeny* or *concatenations* sketched out by palæontologists fail especially because their authors have nearly always sought, on the spot and in the very soil of the country in which they are, the different links of evolution of the same group. To reconstruct a real palæontological history of a branch of fossil animals, one must expect to have to change countries several times over.

The migrations of marine or terrestrial animals are necessarily closely dependent on geographical changes, such as the subsidences which open up new communications between two seas hitherto distant, or, on the contrary, retreats of the sea which permit connections between continents originally separate. Thus, to mention an example taken from fairly recent geological events, it was the subsidences at the end of the Pliocene which created the Ægean and the Sea of Marmora, and opened the Bosphorus and thereby enabled the existing Mediterranean fauna to take possession of the Black Sea region, up till then occupied by landlocked seas with a very special brackish water fauna of their own.

Thus also, the closing of the Isthmus of Panama at the Pliocene epoch established the very recent connection between the two Americas, which allowed at that epoch alone exchanges in both directions of terrestrial animals, the Mastodons and Horses emigrating to the South, whilst by an inverse migration the Edentata were introduced into North America.

The exact history of these modifications in the forms of seas and continents in each geological epoch is, therefore, a necessary element of and a solid basis for the comprehension of the migrations of fossil beings. Since this path has been opened up by the brilliant attempt of Neumayr at a geography of Jurassic times, palæographical studies have taken an increasingly important place in the researches of geologists. We possess, at the present time, a series of geographical sketches by various authors, Lapparent, Frech, Osborn, Matthew, etc., which attempt to retrace the relative positions of lands and seas from the latest to the earliest geological epochs. These sketches differ somewhat according to the interpretation of geological facts, and principally from the degree of importance attributed by the authors to the phenomena of erosion and the denudation of early Marine formations. One map, for example, supposes, as does Neumayr, the central plateau of France to have been entirely covered by the Jurassic seas, while another represents this same plateau as an island of greater or smaller dimensions. The agreement of the various authors is generally more completely established the nearer we get to our own times. Thus the maps of the different Tertiary stages offer, at this moment, a basis of argument much more precise than those of Secondary times, and a great deal more so than those of Primary ones.

But if palæogeography can enlighten us upon the phenomena of migration, on the other hand the well-proved facts of the displacement of marine and a fortiori of terrestrial animals bring to the reconstitution of ancient geography decisive arguments and uncontrovertible proofs. Thus it is that the presence in England of the *Mastodon arvernensis*, of the *Elephas meridionalis*, and of the Mammoth—to mention Proboscidians only—implies the existence of an isthmus connecting England and France during the whole of a geological phase extending from the Pliocene to the end of Quaternary times. We have even been able to note the very recent separation of Corsica from the Continent of Provence by the discovery in that island of a Stag (*Cervus Cazioti*) belonging to an extinct group peculiar to the extreme end of the Pliocene epoch.

The study of the phenomena of migration offers more complex conditions as regards marine animals than in the case of continental faunas. Naturally, when seas of large expanse are in question, the migration of beings is not impeded by any material obstacle, and the geographical distribution of faunas is affected chiefly by the conditions of *temperature* and *depth* of the waters of the sea. Accordingly the distribution of certain genera is often very extended in our existing seas, and it seems to have been more so in the Secondary, and still more so in the Primary ones. This specially applies to animals which inhabit the mid-ocean, whether on the surface or in the depths of its waters. A great number of Ammonites possess an almost universal geographical distribution, certain species being found with identical or almost identical characteristics from Central Europe to as far away as South America, Natal, and Japan. Notwithstanding these unfavourable conditions, it has been possible to observe, even among the Cephalopods, certain interesting facts of migrations: the genus *Virgatites,* so characteristic of the deposits of the upper Jurassic of Russia (the Arctic province) spread in a short period through Germany to the Boulonnais and to Specton Cliff on the English North Sea Coast. To explain this migration it seems difficult to discard the hypothesis of a cold current starting from the region of the White Sea and propagating itself along a northern continent formed by Lapland, Finland, and the Scandinavian peninsula. But an explanation so simple does not appear sufficient to account for other migrations in mass of certain groups of Ammonoids which we find on several occasions invading European seas in Primary and Secondary times. These intermittent invasions, which bring into the regions of Central Europe certain genera of Cephalopods till then unknown which have no origin in earlier formations, seem especially connected with the epochs of great incursions of the sea during which it must have overflowed its earlier shores, and have spread far over the solid continents, bringing with it colonists from the ocean depths, or, at all events, from more distant marine provinces. I will quote, for example, the sudden introduction of the group of Clymenias with the incursion of the upper Devonian time, that of the *Psilocerata* with the incursion of the infra-Liassic, the invasion of the *Amaltheæ* and of the *Cœlocerata* with the deepening of the middle Liassic seas, the arrival of the Oppeliidæ and of the Haploceratidæ with the incursion of the Bajocian era, that of the *Cardiocerata* with the great Callovo-Oxfordian incursion, the sudden expansion of the *Hoplites* and of the *Holcostephani* with the incursion of the upper Tithonian era, the apparition of the *Desmoscerata* and the *Mortonicerata* with the Valanginian, of the *Holcodisci* with the Hauterivian, of the *Silesitæ*, and the *Costidisci* in the Barremian, of the *Douvelleicerata* in the Aptian, of the *Scaphitæ*, and the *Stoliczkaiæ* in the Cenomanian, and lastly, that of the Pseudoceratitidæ with the Turonian. The phenomena of incursion, alternating with the epochs of the retreat of foreshores or regressions, seem thus to have been one of the most important causes of the repeated renewal, or of the intermittent *remodelling* of the faunas of animals of the high seas.

The same causes of migration have naturally reacted, with even greater intensity, on littoral faunas, coast-animals being still more sensitive than the high-sea types to the various changes which affect the marine environment. Migrations determined by a modification of the temperature of the waters of the sea seem above all to depend on the direction of the currents, some warm and superficial, others cold and deep. P. Fischer and after him Locard have shown that the existing littoral Molluscs in the arctic regions of the North Atlantic have propagated themselves towards the

South as far as the Equatorial region by following the deep and cold double current which follows the coast lines of Europe and of North America. From these cold waters, becoming deeper and deeper as they proceed towards the South, there has resulted a curious adaptation of these types, of littoral habitat in their birth place, to a more and more pronounced deep-sea life as they approach the Equator. It is, possibly, to the simple introduction of a deep and cold current rather than to a general refrigeration of our seas that should be attributed also the introduction into the Mediterranean basin, towards the end of the Pliocene era, of certain species of Arctic sea shells, such as *Trichotropis borealis*, *Astarte borealis*, and *Trophon antiquum*, which characterize the *Sicilian* deposits round Palermo and a few other points in the Mediterranean.

The changes in the depth of waters, produced by the positive or negative, though slight, oscillations of the shore-lines, determine on their side the emigration of whole faunas, the more so that to the changes of a bathymetrical kind are added parallel modifications in the nature of the sediments. This is the phenomenon to which Van den Broeck has given the picturesque name of *Migration of the Environment*. Let a region of sandy beaches be deepened by a flooding of the foreshore, and slimy deposits will be seen to superpose themselves on the sandy bottoms of the preceding period; and this change will suffice to determine both the retreat, or even the local extinction of the early inhabitants, and the introduction of other species or genera which affect slimy soils. If, on the contrary, the shore has undergone a retreat of the sea which has facilitated at that point the establishment of a world of lagoons or estuaries, we see brackish deposits with a special fauna of Cyrenas, Potamidæ, and Melanias superpose themselves on the thoroughly marine sands of the earlier period. These are constant facts in the history of all seas on this earth ; and it might even be said that the geological history of each region of the globe is nothing but a long alternation of those oscillations of the bottom of the sea which, at the present time, manifest themselves in repeated superpositions of the strata termed *heteropic*, that is to say, of diverse nature and *facies*, at once lithological and faunic. I will make these facts more precise by a few examples.

The history of the Pliocene period in the basin of the Rhone, in Italy, in Spain, and, more generally, in the whole Mediterranean basin, comprises the following series of episodes. To begin with, a period of great submarine subsidences, accompanied by phenomena of the deep scooping out of all the continental valleys. After this, the sea penetrates, by progressive incursions, into these deep and narrow valleys : we first observe, at the bottom of the Pliocene deposits, layers of the fauna of brackish waters (Strata of Congeries) indicating a first stage of lagoons ; then the incursion becomes quicker, and at a depth of several hundred metres under water there is formed a blue slime, characterized by certain species of smooth Pectinidæ, Dentals, Pleurotomas, etc. ; this is the *Plaisantian* stage. After this, the sea tends to retreat by degrees towards its proper limits: on the blue slime are superposed fine sandy deposits with a much more littoral fauna, characterized by an abundance of the great bivalves, Naticas, Conoids, Balanas, etc.; these are the deposits of the Astian stage. Towards the end of this stage, the retreat of the sea becomes evident by an abundance of oyster beds with which estuary shells, such as the Potamidæ, begin to be associated; then the freshening of the waters becomes more marked, and we find a second lagoon phase with a fauna of Congeries and Melanopses greatly similar to that of the phase at the beginning of the Pliocene. Finally, all traces of brine disappear, and we see superposed on the Astian layers a marl containing fresh water Molluscs, and at length river sand and pebbles containing no other fossils than the bones and teeth of Mastodons and other terrestrial animals.

These phenomena taken as a whole, from the irruption of the sea into the pre-Pliocene valleys to the filling up of these valleys with the river pebbles, constitute what may be termed a *cycle of sedimentation*. We should meet with a very analogous cycle if we wrote the history of the Miocene period in the same Mediterranean basin. The Eocene history of the Paris basin is likewise composed of a repeated series of similar, but less complete, cycles, with alternations of incursion periods with frankly marine faunas and of retreats of the sea with brackish faunas, and with the formation of lagoons in which was accumulated gypsum, a product of the evaporation of sea water.

It now becomes easy to understand why, given the generality of these oscillations of the foreshore, accompanied by the formation of superposed heteropic deposits, palæontologists are so rarely able to follow in one spot the regular evolution of marine faunas of littoral habitat through the successive stages of the same country. In the upper Tertiary lands of Belgium, Van den Broeck has shown that the malacological fauna of the black upper Miocene sands of Antwerp has no roots in the subjacent Oligocene clay, the more so that there is a gap in the upper Oligocene at this point. These ancestors and these affinities of the Black Crag fauna must be sought for farther East in the early Miocene deposits of North Germany, whence the sea reached, by overflooding in the second half of the Miocene period, the till then reclaimed Belgian plains. This Belgian Miocene fauna, progressing with slight modifications continuously from East to West, causes the blossoming, in the Suffolk of England, of a Pliocene fauna, less southern in character, which forms its natural descendant. Finally, cold currents from North America have caused the gradual refrigeration of the Anglo-Belgian basin and finally introduced into these regions northern forms, an indication of a new flooding of the deposits from West to East, in an inverse direction to the former one. The influence of currents is here combined with the displacements of foreshores to bring about the migration of fauna, and of their essential modifications throughout Neogene times.

Fontannes has made analogous observations on the Neogenous faunas of the basin of the Rhone.

Two incursions of the sea characterize the Tertiary geological history of this region: one corresponds to the lower and middle Miocene (Burdigalian and Helvetian stages), the other to the early Pliocene (Plaisantian and Astian stages); between these two marine phases there occurs an important phase of retreat of the sea during the upper Miocene or Ponticate stage. It results from this fact that there exists no relation of direct descent between the Miocene and Pliocene forms of the same kind of Molluscs in this valley. The *Pecten restitutensis* of the lower Miocene, for example, though near akin to the *Pecten latissimus* of the Pliocene, always preserves its distinctive characteristics, and no transitional form can be detected between the two species. But if we go to the basin of the Danube, we note in the middle Miocene round Vienna, the co-existence of the two forms: the first in the lime, the second in the sand deposits. It is probably in this eastern basin and under the influence of the varied conditions of the environment that the differentiation of the two species must have taken place, one of which, the *P. restitutensis*, became extinct without leaving descendants, while the other, *P. latissimus*, spread by migration over the whole of the Pliocene Mediterranean.

This way of looking on the succession in time of kindred forms could be supported by many other examples. I shall also quote, with Fontannes, the faunas of land Molluscs, Limnæas, Planorbes, Hydrobias, and Valvata, so common in fresh water strata, which mark the two phases of retreat at the end of the Miocene and Pliocene in the Rhodanian Gulf.

The species of these two faunas are only separated by shades, at times almost imperceptible, but remaining constant to a practised eye. Must it necessarily be deduced from this relationship that they are gradual mutations of the same type? From the absence of transitional forms, Fontannes does not think so, but finds it quite reasonable to suppose that the regular series of these mutations must have occurred farther north, in a region unpenetrated by the Pliocene sea and where the two Continental phases, Miocene and Pliocene, fuse into one great epoch. I have succeeded in showing, with Delafond, that these conditions are absolutely realized in the small basin of the Bresse, which seems to have had to play the part of a *restocking centre* for the water courses and Pliocene lakes of the southern part of the basin of the Rhone.

Without there being any need to dwell at greater length on these facts, we see what a paramount part the phenomena of migration play in those changes of faunas, sometimes so complete and apparently so inexplicable, which we notice in the various superposed stages of the marine formations. Among the principal conditions which have influenced or determined these migrations, we have been able to perceive: the direction of sea currents, the perpetual oscillations of foreshores, and, lastly, great marine incursions which carry with them the inhabitants of distant seas, snatched, so to speak, from their country of origin, to be transplanted, like settlers, in points of the globe where their ancestors did not exist.

CHAPTER XXVII

THE MIGRATION OF TERRESTRIAL VERTEBRATES

Importance of these migrations—Migrations in Primary times—Palæogeographical sketch of the Primary and Secondary Articulates—Migrations of Secondary times—Evolution of the Continents—Migrations of Tertiary Mammals.

EVEN more than the marine animals, the terrestrial, and especially the Vertebrates, whether Amphibians, Reptiles, or Mammals, furnish exact documents interesting for the study of geological migrations. This is mainly due to their limited means of locomotion, which are closely connected with the continuity of the continental base on which they live. It may even be asserted that the migrations of terrestrial Vertebrates, when founded on sure evidence, constitutes the firmest foundation and the clearest demonstration of the palæogeographical sketches founded generally on the distribution of marine deposits.

By reason of the importance of these facts, I think it well to enter into a few details on the subject, which as yet has been somewhat slightly treated by palæontologists, and we will proceed to study, one after the other, the migrations of the Primary, Secondary, and Tertiary epochs.

I. MIGRATIONS OF PRIMARY TIMES.—Towards the end of Primary times, the geographical distribution of certain genera of Stegocephalous Amphibians, who inhabited the marshy lagoons of the Coal and the Permian epoch, clearly points out to us the easy communications established, on the one hand, between Europe and North America, and, on the other, between South Africa, India, and Australia.

In the group of small salamander-like forms called *Microsaurians*, the *Lepterpeton* and *Keraterpeton* genera are met with at once in the coal seams of the Ohio, in those of Ireland, and in the gas coal of the lower Permian of Nyram in Bohemia. The genus *Hylonomus* of the Nova Scotian Coal recurs in a hardly different form in the lower Permian of Bohemia. A lacertiform type of larger size, the *Dendrerpeton*, has been found, as its name indicates, in the hollow tree trunks of the coal forests of Nova Scotia and in the gas coal of Bohemia. A certain number of other European genera possess, in North America, representative forms so near to them that it is impossible to doubt the easy geographical connections existing at that epoch between the two worlds.

In the same way, in the Southern Hemisphere, from the sandstone of Karroo in South Africa, from the strata of Gondwana, in the Indian Archipelago, and, lastly, from the Triassic strata of Australia, have been dug up several genera of Amphibians, the *Micropholis*, the *Bothriceps*, and the *Brachyops*, in part common to these three regions, between which geographical connections doubtless established easy communications for terrestrial and fresh-water animals.

Thanks to these early phenomena of migration, of which it is, however, difficult for us at the present day to settle the exact direction, we are able to mark out very clearly, towards the border line of Primary and Secondary times, the existence of two Continental masses spreading from east to west, that is to say, in the converse direction to that of the present great Continents: (1) a *Boreal Mass* comprising the North of America, Greenland, the Northern regions of the Atlantic, the British Isles, Scandinavia, Russia as far as the Ural, and then, on the other side of an arm of the Sea of Ural, an Asiatic land which was Ed. Suess's *Continent of Angara*; and (2) an *Austral Mass*, extending from Australia to the Indian peninsula and to South Africa, which, doubtless, was prolonged across the Atlantic to South America. This was the *Great Continent of Gondwana*.

Between these two great masses there existed a vast arm of the sea, going from Central America to Indo-China across the Atlantic and the Mediterranean, in an almost equatorial direction; this was the *Great Central Mediterranean* of Neumayr, the *Thethys* of Ed. Suess, the *Mesogea* of modern palæogeographers.

This Mesogea was not, however, always an insuperable obstacle to the migrations of terrestrial animals. At certain epochs, which correspond to the most energetic phases of the wrinkling of the earth's crust, bridges have been, so to speak, momentarily thrown across between the Austral and Boreal Masses. It is thus that, towards the end of Primary times, especially at the Permian epoch, connections established between Africa and Western Europe, perhaps through the region of Spain and the Pyrenees, opened the passage from one Continent to the other for certain of the most remarkable terrestrial Reptiles. Among these types, belonging to the great order of the *Theromorphs,* I shall mention the *Dicynodons,* huge lacertiform reptiles with rounded cranium, one pair only of long sloping canines, and cranian profile resembling somewhat that of a walrus. These strange *Dicynodons* abound in the sandstone deposits of the upper Permian and of the Trias of South Africa (near Karroo), which is probably their original home. Thence they appear to have emigrated, on the one hand, into Hindustan, on the other into Scotland, where they were discovered, much to our surprise, in the Triassic sandstone of Elgin.

More recently a Russian scholar, Amalitzky, has discovered them in the upper Permian of the banks of the Dwina, a tributary of the White Sea, that is to say, near the eastern extremity of the great Continent of the Northern Hemisphere.

A second group of Theromorphs, not less remarkable, the *Pareiasauridæ,* accompanied the *Dicynodons* in their migration. The Pareiasauri were reptiles with a short, flat head, having jaws with a continuous row of many cutting teeth, a short tail, and a skin covered with large thick scales. Their centre of origin seems also to have been Southern Africa, where they abound in the Permian and Triassic formation of Karroo. As in the case of the *Dicynodons*, Amalitzky has found them in the upper Permian of the Dwina, and in such quantities that the Russian palæontologist has been able to reconstitute the complete skeletons of about a dozen individuals. Their unexpected presence in the Northern Continent can only be explained by an African migration, favoured by a temporary communication across the Mesogea, at the time of the great persistent retreat of the sea, which followed upon the Hercynian wrinklings of the terrestrial crust.

II. Migrations of Secondary Times.—Geographical conditions, very similar to those just described, persisted, with a few modifications, during the greater part of the Secondary era. The obstacle raised by the presence of the great area of the Mesogean Sea was still at certain moments surmountable. It would otherwise be impossible to explain the presence in the continents, Austral and Boreal, of certain types of terrestrial Amphibians and Reptiles. Thus there have been found in the strata of Tiki and of Maleri in the East Indies a few remains of the great *Labyrinthodons* (*Capitosaurus* and *Mastodonsaurus*) which characterize, by their frequency, the Triassic strata of Central Europe. The genus *Hyperodapedon*, of the order of Rynchocephalous Reptiles, is found both in the Trias of Elgin in Scotland, and in the strata of Maleri in Hindustan. But still more important data are supplied to us by the giant terrestrial Reptiles of the order of *Dinosaurians*. In this group, with various forms, must be quoted the *Megalosaurus*, a formidable carnivore with a crenellated scimitar-shaped canine tusk, which existed in Europe during the whole Jurassic and Cretacean periods. It must have emigrated to the South at the middle Cretacean period, for it is found with insignificant modifications in the Chalk of Madagascar, of India, and of Patagonia.

It is the same with another herbivorous and plantigrade Dinosaur, the *Titanosaurus*, which dwelt in the British Isles at the lower Cretacean epoch, and which survived in Languedoc and Provence down to the Rognac strata, that is to say, to the extreme end of Cretacean times. The Titanosaurus has been discovered in the upper Chalk of India, Madagascar, and Patagonia, and these discoveries appear clearly to indicate that this gigantic Dinosaur followed the Megalosaurus in its migration to Southern lands. These various facts are, therefore, an assured indication of two migrations having occurred from the North to the South, one at the commencement of the Trias, and the other towards the middle Cretacean.

If we continue to follow the evolution of the continents during the Secondary era, we shall especially have to show the gradual parcelling-out of the two great continental masses of North and South. I have already stated that the Boreal Continent comprised two distinct expanses at the end of the Primary Era : an Asiatic expanse, the Angara Continent, and a European - American expanse separated from the first by an arm of the sea in the Sub-Ural region. The complete absence of palæontological documents relating to the Land of

Angara precludes the study of possible migrations between these two northern masses.

But so far as the Western mass is concerned, we know that subsidences occurring in the North Atlantic early brought about a separation, for at least a time, between the lands risen from the sea in Northern Europe and those in Northern America, comprising therein Canada and a good part of the United States. Yet this separation did not exist at the Permian epoch, as is testified by several types of Amphibians and even of terrestrial Reptiles, such as the *Naosaurus*, common to the two regions.

It would seem that communications may still have continued to exist, though with greater difficulties, up to the end of the Trias, as is indicated by the presence in Connecticut of Crocodiles of the *Beloder* genus, and of the Dinosaurians, *Palæosaurus* and *Thecodontosaurus*. But from the Lias onwards a great number of families and even of orders of terrestrial Reptiles become peculiar either to Europe or to America. Among the long-beaked crocodilians, the *Teleosauridæ* and the *Metriorynchidæ* are exclusively European families. Among the Dinosaurians of exclusively terrestrial habitat, the *Scelidosauridæ*, great herbivorous animals with spatuliform teeth, dwelt on the European Continent from the Lias to the lower Cretacean. It is the same with the gigantic *Iguanodons*, with their tripod gait, recalling the existing kangaroos. On the other hand, the great horned flesh-eating saurians or *Ceratosauridæ* are confined to the upper Jurassic of the United States.

More frequently still we may note between the two regions the presence of *representative,* but not identical genera, showing that similar groups followed their evolution on parallel lines, but independently of each other. Thus in the primitive Crocodilians of the Trias, the *Belodon* of Wurtemburg is represented by the *Episcoposaurus* of New Mexico. The curious *Aetosaurus* of Stuttgart, with its slender snout and back adorned with rows of oblique plates, is represented by the *Typothorax* of the United States. In the group of carnivorous Dinosaurs, the *Zanclodontidæ* of the European Trias offer a parallel development to that cf the American *Anchisauridæ.* The genus *Cœlurus,* a type of the family of the light and agile Cæluridæ, is represented in Europe by the *Aristosuchus* of the Isle of Wight. Among the clumsy Sauropods, the gigantic *Atlantosaurus* of the Colorado upper Jurassic is fairly near to the Oxford *Cetiosaurus,* and the American *Morosaurus* is represented by the *Ornithopsis* of the English Wealdian. Finally, the great horned Dinosaurs of the group of *Ceratopsidæ,* which imitate so singularly the carriage of the Rhinoceros and are so brilliantly represented in the higher Cretacean of the Rocky Mountains by the *Ceratops* and the *Triceratops,* count among their members, in Europe, closely similar forms in the *Struthiosaurus,* and the *Danubiosaurus* of the horizon of Gosan, in the Neue Welt, near Vienna.

Notwithstanding this geographical individualization, already marked in the Trias and still more so in the Jurassic and Cretacean, a certain number of palæontological facts favour partial migrations between the two countries. The first proof is supplied by the presence of some common genera. The terrible *Megalosaurus*, which inhabited Europe from the Bathonian to the Cretacean, is found again in the upper Jurassic of Colorado, and the same type continues, with hardly any change, as the modified *Lælaps* of the upper Chalk of New Jersey and of Montana; and the migration of this European genus into America does not appear doubtful. In the family of Cæluridæ, with longer and slender paws, the genus *Tanystrophæus* is found identical in the Muschelkalk of Bayreuth and in the Trias of New Mexico. Finally, among the ponderous *Stegosauridæ*, with their powerful dermic armour, the genus *Stegosaurus* is the same, according to Marsh, as the *Omosaurus* of the Kimmeridgian of England.

A second order of proofs, rather less direct, results from the passage from one country to another, not of genera, but of highly specialized families or groups of terrestrial animals. Such is the case with the voracious Turtle-Alligators, or *Chelydridæ*, and the *Pleuroderous* Turtles who passed from Europe into America in the upper Cretacean period, and are still in existence, the first in the rivers of North America, the latter in the fresh waters of the Southern Hemisphere. The entire order of Dinosaurian Sauropods made its appearance in Europe as early as the Bathonian, and may well have passed into America only in the upper Jurassic. Lastly, there is no doubt that the entire group of flying Reptiles or Pterosaurians, appearing early in the Rhætian of Suabia, emigrated to America and are found in the upper Jurassic of Colorado.

It really seems to result from the facts collected above that migrations must have taken place from Europe to America at three different periods of Secondary times: first in the Trias, next in the upper Jurassic, and lastly in the middle Cretacean age. In any case, no other explanation can be imagined for the interchanges of faunas, such as the passage from Europe to America of the Megalosauridæ, the Sauropods, the Pterosaurians, the Pleuroderous Turtles, and for the probably converse migration of the Cæluridæ, the Stegosaurians, and the Ceratopsidæ.

Like the Boreal Continent, the great Continent of the Austral Hemisphere, or *Continent of Gondwana*, extending from Australia to South America, commenced to break up during the Secondary era. At an early date, starting from the Liassic epoch, a zone of marine subsidence, in a north to south direction, separated this great tract into two distinct fragments: on the east, the *Australian-Indo-Madagascar Continent*, comprising Australia, the Indian Peninsula, the site of the present Indian Ocean, and Madagascar; on the west, beyond the slightly enlarged Mozambique, the *Africano-Brazilian Continent*, composed of the greater part of Africa and South America joined across the South Atlantic.

This Secondary palæogeography, founded on the distribution of marine deposits, is confirmed and made clear by the migrations of terrestrial animals. At the Triassic epoch, the Continent of Gondwana probably still existed in its entirety. Amphibians of several groups possess in fact representative forms similar enough, in Australia and India, on the one hand, to those in South Africa on the other. For instance, in the group of Temnospondylians with as yet incompletely ossified vertebræ, the *Bothriceps* of the Australian Trias recalls the *Gondwanasaurus* of the East Indies and the *Micropholis* of South Africa. The special group of Labyrinthodons with the ivory of the teeth deeply folded, is represented by the *Mastodonsaurus* and the *Capitosaurus* of Bengal, and by the *Rhytidostens* of the Trias of Orange. Finally, the genus *Massospondylus*, common to the Trias of the Cape and of the East Indies, confirms the unobstructed dispersion of the Dinosaurian Theropods over the whole extent of the Gondwana Continent.

These communications cease from the time of the Lias throughout nearly the whole of the Jurassic and Cretacean, except, perhaps, for the short period of the Turonian or lower Senonian, during which the Dinosaurian Sauropods were able to emigrate from India as far as Patagonia, by passing through the great island of Madagascar. With this exception, the two parts of the Gondwana Continent proceed in evolution independently of each other, and even tend to subdivide themselves. Australia seems to have separated itself rather early from the Indian Continent; but the connection between India and Madagascar is clearly indicated down to the Senonian epoch, by the close affinity of the *Dryptosaurus* and *Titanosaurus*, two genera of Dinosaurs common to both regions. Alone, the great marine incursion of the upper White Chalk period seems to have brought about the temporary isolation of the Seychelles and the Indian peninsula.

We lack the exact palæontological data for fixing the date of the separation of Africa from South America, but, judging from the distribution of marine deposits, it may very well be that the connection of these two countries lasted down to the time of the great Senonian incursion.

III. Migrations in Tertiary Times.—The study of migrations in the Tertiary epoch becomes even more interesting and more capable of precision than those of Secondary times, thanks to the remarkable development of the class of Mammals.

The first appearance of the Mammals, so far as our present knowledge goes, is indeed fixed at a fairly remote date in the Secondary era. From the higher Trias and the commencement of the Rhætian, there suddenly appeared two distinct types of this class: on the one hand the Insectivorous *Marsupials*, akin to the present Didelphidæ of the two Americas, appear for the first time in the upper Trias of North Carolina; on the other part the *Allotherians*, or *Multituberculata*, as they are called from the manifold series of tubercules which bristle on the crowns of their molars, make their appearance, in the diminutive forms of the family of Plagiaulacidæ, in the Rhætian of Stuttgart and of the South of England. This family perhaps still exists at the present day as the Kangaroo-rats of Australia. Were we to rely exclusively on known facts, we should presume that the first centre of dispersion of the Marsupials was North America, and that the centre of the Multituberculata was the European Continent, which was also joined to the first by intermittent connections across the North Atlantic or the Arctic lands. But this rational hypothesis has had to contend up till now with the complete absence of any possible ancestor of the Mammals in the ante-Triassic strata of the Great Boreal Continent.

The speculations of modern palæontologists are to-day rather directed to South Africa, where, at the end of the Permian and during the Trias, a whole group of terrestrial Reptiles, the *Theromorphs*, developed, some of which present curious affinities in certain details of their organism, with the lower Mammals. Thus the *Tritylodon*, with its upper molars furnished with three rows of rounded tubercules, so much recalls the dental characteristics of the Multituberculata that for a long time it was considered a true Mammal, notwithstanding the decidedly reptilian features of its skull. Similarly, the bones of the limbs of the *Theriodesmus*, which are perhaps those of the *Tritylodon*, recall, according to Seely, the structure of those of the Lemurians and Carnivora. Other Theromorphs from the Karroo likewise present rather curious mammalian affinities : the *Dicynodon* in the structure of the pelvis, and the *Cynodraco* in the form of the humerus, furnished with an inner arterial bridge like that of the Felidæ. But, notwithstanding these interesting affinities, which are, perhaps, only adaptations to identical functions, we cannot say that any one of the known Theromorphs can have directly given birth to the first Mammals, and we are forced to take refuge in the vague hypothesis of common ancestors yet unknown, from which these two groups must have issued.

If we adopt this entirely provisional hypothesis, we should have to suppose at the same time a South African migration, which, at the end of the Trias, would have brought the Multituberculate Mammals across the Mesogean arm of the sea into Europe. As regards the Marsupials, hypotheses are still more misty; the most ancient representatives of the group, the *Dromatherium* and the *Microconodon*, appear suddenly in the Trias of North Carolina without any known ancestor. From the United States, thus considered as the probable centre of dispersion of the group, the flesh-eating Marsupials must have emigrated; on the one hand, to Europe, where we discover them in the lower Jurassic of Stonesfield and in the last layers of the Jurassic of the Isle of Purbeck, and still higher in the form of the Didelphids in the upper Eocene and in the Oligocene of France and Germany; on the other hand, towards South America, the present home of the Sarigues, where Ameghino has discovered for us the *Proteodidelphys* of the lower Cretacean of Patagonia. It is, no doubt, from the South American Continent that the Marsupials have been able, at a recent epoch (the upper Tertiary or Quaternary) to emigrate to Australia and Tasmania, the present geographical centre of these non-placental Mammals. It appears probable, conformably with the hypothesis of Osborn, of Matthew, and Ameghino, that this American migration towards Australia can only have been effected by the intermediary of a bridge-forming Continent, the *Antarctic*, now in great part subsided under the southern seas.

We come to the higher or Placental Mammals, whose origin and centre of dispersion are still at this moment an utterly insoluble enigma. All the hypotheses possible have been examined by palæontologists. Central Asia, Africa, the Arctic regions (Matthew), Patagonia (Ameghino), even the submerged Pacific Continent! (Haug), have been successively pointed out as the starting-point of their migrations. It is curious to remark that all these hypotheses, save that of Ameghino, refer to regions palæontological documents from which are utterly wanting, and this is no doubt why they have been preferred by the authors of these hypotheses.

Leaving on one side these vain and unproved speculations, we will take the problem in hand by the light of the known facts alone. One great fact to be put in evidence is that we are cognizant of no transition, of no intermediate between the lower Mammals without placentas and the higher Mammals with complete intra-uterine development. A possible common origin of these two great groups is, therefore, entirely hypothetical. We must confine ourselves, following the method we have already applied to the Marsupials, to the endeavour to ascertain on what point of the globe, and at what geological date, we see the earliest types of the Placentals make their first appearance.

These types show themselves almost simultaneously in three distinct regions: i.e. the United States, France, and Patagonia. In North America, the strata of the horizon of Puerco and the slightly higher ones of Torrejon in New Mexico have furnished a rich fauna of placental Mammals, already differentiated into perfectly distinct orders, viz. Ungulates (*Condylarthra*, *Amblypods*, *Tillodonts*), primitive Carnivora (*Creodonts*) and Primates (*Pachylemurians*). These faunic elements, excepting the Amblypods and the Tillodonts, are discovered in the unique European deposit of the lowest Eocene (Thanetian stage), that is to say, in the strata of Châlons-sur-Vesle and of Cernay, near Rheims. Finally Ameghino has brought to our notice in Patagonia the very rich fauna of the horizon represented by the *Notostylops*. Of this fauna a few genera of Condylarthra and Primates show such affinities with the earliest types of the northern hemisphere that we are induced to attribute to them an age doubtless differing little from that of the deposits in New Mexico and in the neighbourhood of Rheims.

It is inadmissible that Mammals so near akin to each other can have appeared independently in three distinct centres, and we can only explain these palæontological affinities by migrations. But of these three regions, the United States, Europe, and Patagonia, which are we to consider the true centre of dispersion of the Placentals ? In other words, which is the country containing the earliest deposit of the remains of these animals ? Until lately no doubt as to this seemed possible. Osborn showed that the stratum of Cernay-les-Rheims was the exact equivalent of the American level of Torrejon, and that there existed in Europe no

Tertiary fauna as early as that of the horizon of Puerco. North America, it appeared, therefore should be looked upon as the true cradle of the Placentals, who early emigrated to Europe across the territories of the North Atlantic which had risen from the sea.

Quite recently, however, Florentino Ameghino has attempted to raise the whole problem anew by maintaining that the *Notostylops* strata in Patagonia are of the upper Cretacean age, and that, consequently, it was from South America that the migrations of the Placentals issued. According to the Argentine savant, these animals must first have reached the African continent then joined to America (the *Archellenis* of Ihering), then Europe across the Mesogean, and, lastly, North America. The circle of migration would thus have been nearly complete. This seductive hypothesis is unfortunately based on the consideration of the Cretacean age as that of the Patagonian fauna, which is contested by many geologists, this fauna being referred by them to, at least, the lowest point of the Eocene formations.

Whatever may be the solution reserved in the future to this important problem, we must, at all events, admit the fact of extensive migrations, which at the commencement of the lower Eocene dispersed over the globe from the United States to Europe, and as far as the lowest point of South America, representatives of several already perfectly differentiated orders of placental Mammals.

To follow from the lower Eocene the complex series of migrations and interchanges of fauna between the various continents of the Earth, it is necessary first to take a bird's-eye view of the general features of the geography of Tertiary times. These *shields*, to use the picturesque expression of Ed. Suess, are distributed as follows. Three in the Northern Hemisphere, to wit, the *Canadian shield*, which includes a good part of the United States; the *Scandinavian shield*, including, besides Finland, the Russian tableland, the north part of the British Isles, and extending, at certain points, as far as the Ardennes and the expanse of the Rhine; and, finally, the *Sino-Siberian shield*, or Angaran continent. In the Southern Hemisphere, the Brazilian continent, the continent of Africa, Madagascar and the neighbouring islands, the Indian peninsula, and Australia constitute so many solid nuclei which have, in a great measure, withstood the invasion of the Tertiary seas and acted in the same manner as the shields of the Northern Hemisphere. To this enumeration must be added a great Antarctic polar continent, the Antarctic.

The history of Tertiary times may be summed up as a series of connections followed by phases of separation of these early nuclei under the influence of the phenomena of the wrinkling or of the subsidence of the earth's crust, and of the marine incursions and retreats which were their consequences. It is, therefore, quite natural that terrestrial animals should have availed themselves of these temporary bridges between continents, to spread afar, by means of reciprocal changes, genera and families till then restricted to a single region only.

We are still a long way from being able to write a detailed history of all these exchanges of faunas. As regards some of the continents, particularly the two Asiatic nuclei of the North and South, the documents for this history are either utterly lacking, as in the case of the Siberian one, or else restricted to the most recent fauna, as happens with China and the Hindu expanse. *The history of the development of the Tertiary fauna on the Asiatic continent constitutes, at the present moment, the most fundamental gap in our knowledge.* It is patent to us that a certain number of groups of Mammals, which suddenly appeared on the continent of Europe in the first half of Tertiary times, such as the *Palæotheridæ*, the *Anoplotheridæ*, the *Canidæ*, the *Mustelidæ*, the *Suidæ*, the *Tragulidæ*, the *Cervulidæ*, etc. are Asiatic immigrants ; but it is, for the moment, totally impossible to prove it.

It is, fortunately, otherwise as regards the migrations occurring between a few other regions. Among the best known of these migrations may be pointed out the exchange of faunas happening on several occasions between Europe and North America.

The first North American migration brings to Cernay, in Europe, at the beginning of the Pliocene, several families of Creodonts (*Proviverridæ*, *Arctocyonidæ*, *Mesonychidæ*), as well as the Condylarthra, neighbours of the famous *Phenacodus*, to whom was too hastily attributed the part of ancestor of all the other Ungulates.

A second migration, still more clearly defined, that of the *Sparnacian* epoch, passes over into England and France some other Creodonts, such as *Palæomitis* and *Pachyæna* the Amblypods of the genus *Coryphodon*, and perhaps even some Tillodonts.

The American migrations are a little less distinct in the Londinian and Lutetian epochs. It seems, however, plausible to seek in them the origin of several Primates, such as the *Protoadaptis* and the *Necrolemur*, neighbours respectively of the American *Notharctidæ* and of the *Anaptomorphidæ*, of the Rodents of the group of the *Pseudosciuridæ* and the true *Sciuridæ*, of the Ungulates of the family of the *Lophiodontidæ*, and perhaps also of the group of the Suillian Paridigits. The sudden introduction into Europe of the *Chalicotheridæ*, strange Ungulates adapted to burrowing habits, seems likewise to indicate an American migration at the Bartonian epoch.

The communications between Europe and America, already difficult at the end of the middle Eocene, appear to cease entirely at the *Ludian* epoch. The introduction into Europe of the Didelphidæ at the end of the upper Eocene, may be explained, in fact, quite as well by a South American migration.

As a set-off to this, the commencement of the Oligocene marks the re-opening of the connection between the two continents, clearly indicated by the sudden arrival in the deposits of the upper Sannoisian of the first Rhinoceros (*Ronzotherium*), and of the Achænodontidæ (*Entelodon*). These communications are maintained in the Stampian epoch and determine the importation from America into Europe of the first Tapirs, of the Amynodontidæ (*Cadurcotherium*) and of the Rodent *Lagomorphs*.

The last periods of the Oligocene (Aquitanian) correspond to a rupture of the connection between the two countries. But the connection is renewed at the commencement of the Miocene by the emigration into Europe of the *Anchitherium* at the Burdigalian epoch, of the *Titanotheridæ* (*Leptodon*) and of the *Hipparion* in the upper Miocene. However, it is not impossible that these last genera may have come from America by way of China and the Asiatic continent, that is, through the region of Behring Straits. A proof of this is seen in the abundance of *Hipparion* and other Tridactyl Equidæ in the Miocene deposits of the North of China and the foot of the Himalayas. Should this last supposition be correct, it must be admitted that the separation of North America and Europe was definitive from the middle Miocene till the end of Tertiary times.

We have just recorded the existence of at least seven Tertiary migrations, all in the same direction, that is, from the United States towards Europe. But as a compensation other families of Mammals took at the same epoch the contrary direction, from Europe to America. Indeed, the American White-River epoch, which corresponds to the Oligocene in Europe, shows us the arrival in America of the *Anthracotheridæ* (*Ancodus*), of the *Tragulidæ*, of the *Castoridæ* (*Steneofiber*), of the *Cricetidæ*, of the Canidæ (*Galecynus*), of the *Mustelidæ* (*Palæogalus*), and of the great Felines of the type *Machairodus* (*Dinictis*). A second emigration of European forms is manifest in the Miocene of John Day and of Deep River, where we see appear in America the Cervulidæ

(*Blastomeryx*, akin to the *Dicrocerus*), and the Mastodons with tapir-like teeth. Finally, a last invasion shows itself at the Pliocene epoch in the strata of Loup-Fork, in which are discovered the *Mustelæ*, the Otters and the *Pseudoluri*. Given the small probability of direct connection between Europe and America in Neogene times, this rather favours the idea that the two last migrations may have arrived in North America by way of the Asiatic countries and the Behring Straits.

However this may be, the great retreat of the sea which characterizes the first half of the Quaternary brought about the emergence of a great Arctic continent which favoured the dispersion over the whole region of the North of Asia, Europe, and America, of a fauna which comprises the Elk, the Reindeer, the Musk-ox, the Mammoth, the Marmot, the Field-mice, the Lemmings, the Shrew-mice, the Bears, and the great Quaternary Felines.

I shall be more concise as regards the other continents of the earth. The fragments of the great Austral continent : South America, Africa, Madagascar, the Indian Peninsula, and Australia, must likewise have been connected at certain periods of the Tertiary era. I have already pointed out above the migration towards Australia at a recent epoch, difficult to define, of the group of Flesh-eating Marsupials coming probably from South America by way of the Antarctic continent. The communications between South America and Africa seem likewise established by the migration of the Hyracoidæ, the Hystricomorphous Rodents and, perhaps, the Edentata with normal Vertebræ, Orycteropes and Pangolins. Notwithstanding the scarcity of early palæontological proofs on African territory, all these groups can hardly have reached Europe in the Second half of the Tertiary times, except by way of Africa, where their descendants exist at the present day. According to Ameghino, the migrations from Patagonia to Africa have been more numerous and more important still. It is by means of this route that this palæontologist sees the peopling of the whole Boreal hemisphere by Primates, Condylarthra, Imparidigitæ, Amblypods, Proboscidians, Suillians, Tillodonts, Creodonts, Rodents, etc. I can only make passing mention of these bold views of the Argentine scholar, which are in opposition to all classical ideas and tend to represent Patagonia as the true and only centre of origin of all the placental and non-placental Mammals.

The great island of Madagascar, separated from Africa since the commencement of the Secondary, but remaining, on the other hand, connected with the Hindu continent till the end of the Cretacean, again contracted, during the Tertiary, fugitive connections with South America, as is shown by its Edentata of the genus *Bradytherium*, Insect-eaters of the Centetidæ family, on the one hand, and with India (evidenced by its eaters, Roussettes*, dispersion of Lemurians, etc.) on the other, and finally with Africa across the Mozambique Canal. Communication with this last must have taken place, according to Lemoine, first at the Oligocene epoch (Orycteropes, Lemurians, Viver-

* Fruit-eating chiroptera like the squirrel.—ED.

ridæ), then at a very recent epoch, with the introduction of the existing African genera, Hippopotamuses and Potomacheræ.

Finally, I have to point out the important migrations of terrestrial Mammals across the Mesogea, whether in the old world or in America. The exchange of faunas between the two Americas, almost permanently separated by the extension of the Mesogea across the Gulf of Mexico and the Isthmus of Panama, are only really verified from the Pliocene epoch. It is, however, probable that the great retreat of the sea at the absolute commencement of Tertiary times, permitted the diffusion, in the two American Continents, of a few groups of ancient Mammals: i.e. the flesh-eating Marsupials, Condylarthra, Creodonts, Imparidigitæ, and Primates. But after this exchange of primitive Mammals, terrestrial communications were completely interrupted, and the development of the mammalian fauna proceeds independently in the two Americas. We have to get to the end of the Tertiary to observe that the closing of the Isthmus of Panama at the Pliocene and at the beginning of the Quaternary epoch allowed the emigration towards the south of the Mastodons, Tapirs, Equidæ, Cervidæ, Dogs, Skunks, Ursidæ, Cats, *Machairodus*, etc., etc.; while, in the contrary direction a current of Patagonian types flowed towards the United States, comprising the great gravigrade Edentata: *Megalonyx*, *Morotherium*, and *Mylodon*, the Glyptodons, Tatus (*Chlamydotherium*), and Hystricomorphous Rodents (*Hydrochœrus* and *Amblyrhiza*).

The route from Africa towards Europe was opened, perhaps for the first time, at the beginning of or half-way through the Oligocene (Orycteropes and Pangolins of the Phosphorites of Quercy), and then, for certain, at the beginning of the Miocene (Burdigalian), either by way of Spain or Sicily, or through the Ægean Sea. By one or other of these routes there arrived in Europe the Mastodons and the *Dinotherium*, escorted by the first Apes, by the branched Ruminants, and the true horned Rhinoceros. In return, Europe sent to North Africa, about the middle of the Oligocene period, the Suidæ (*Genyohyus*), the Anthracotheridæ (*Brachyodus*), and the Creodonts (*Hyœnodon*, *Pterodon*), discovered by Andrews in the rich deposits of the Fayum, on the confines of the Libyan desert.

Other exchanges of fauna between Europe and India may be pointed out from the upper Oligocene to the Pliocene epoch, thanks to the rich deposits described by Cautley and Falconer in the sub-Himalayan formation of the Siwaliks Hills. Europe appears to have sent into Asia the *Anthracotherium*, the great *Brachyodus*, the Suidæ, the *Amphicyon*, etc., and it received in return, without possible doubt, the Hipparion, Horses, Giraffes, Gazelles, Oxen, Goats, Sheep, Hyænas, Anthropoid Apes, and the first fossil precursor of Man.

BOOK VIII

CHAPTER XXVIII

THE APPEARANCE OF LIFE ON THE GLOBE

The geological problem of the beginnings of life—The Silurian world—The primordial fauna of Barrande—The Cambrian world—The pre-Cambrian fossils of Brittany and of the Rocky Mountains—The crystallophyllian earths and the metamorphism of the old sediments.

One last and most burning question presents itself to us at the end of this sketch of the transformations of the animal world on the surface of the terrestrial globe. It is that of the very origins, or, more exactly, of the first beginnings of life on the earth.

There can be no question here of considering the problem from its biological side. How did the mysterious flame which we call life come, at a given moment in the geological evolution of our planet, to animate inert organic matter and transform these compounds of a little carbon, water, and nitrogen into a living cell, or even into the first granule of irritable and mobile protoplasm ? Here is, no doubt, a fundamental question, but one entirely beyond the scope of a geologist and palæontologist. It may even be fearlessly added that this redoubtable problem has till now defied the efforts of every biologist, notwithstanding some bold attempts at the artificial production of cells analogous, at least morphologically, to those which constitute living beings.*

The geological problem of the beginnings of life is more modest and at the same time more positive. In order to handle it profitably, it will be necessary to draw up, like a scrupulous and exact historian, an inventory of the documentary proofs we possess at the present day regarding the most ancient traces of living beings, patiently exhumed one by one from the lowest strata of the sedimentary crust of the globe.

If we look back as far as the middle of the past century, we shall observe that, at that epoch, the strata containing the remains of the earliest fossil beings known to us corresponded to that part of the Primary era which geologists have called since the days of Murchison the Silurian period, from the Silurian tribe who, at the Anglo-Roman epoch, inhabited the present county of Shropshire. These Silurian strata of the north-west of England are very rich in remains of marine organisms, and, as far back as 1840, the illustrious geologist, Murchison, published, under the title of *Siluria*, a work which is still classic, wherein were catalogued and described about 950 species of fossil animals belonging to nearly all the fundamental divisions of the animal kingdom.

The Silurian fauna comprises, in fact, among the Invertebrates, silicious *Sponges*; numerous *Polyps*

* See especially the experiments of M. Stephane Leduc reproduced in M. Gustave Le Bon's *Evolution of Forces*, Vol. XCI of this Series, pp. 359–360 and Pls. 41-42.—Ed.

already brought together into real coral reefs; some special *Hydroïds*, Stromatopores, and Graptolites; some *Echinoderms*, even then represented by five types of this great group, Crinoids, Cystoidea, Blastoids, Asteroïds, and Echinida; some *Bryozoaria*, and innumerable Brachiopods, followed by Molluscs of every group, Lamellibranchs, Gastropods and tetrabranchial Cephalopods or Nautilidæ. These last attain at this period their maximum of expansion. Even certain types of entirely soft animals, such as the Medusæ and marine worms, have left traces of their presence, the first in the form of natural casts of their general cavity, the latter by their perforations in the sand, their calcareous tubes, or the chitinous joints of their jaws.

The ramification of the articulated animals or Arthropods is brilliantly represented both by inferior types, such as *Cirrhipedes*, *Ostracods*, and by the higher groups of *Trilobites* and *Gigantostraca*. These Trilobites, to which I shall several times have to return, are curious natatory marine Crustacea, of which the carapace, composed of a head, a thorax with mobile segments, and a tail or *pygidium* with rigid segments, is divided into three lobes by two longitudinal lines. Their limbs, rarely preserved, are slender, formed of two articulated branches, and pretty uniform in the different regions of the body. They are absolutely peculiar to the Primary era, and their apogee coincides exactly with the Silurian epoch, in which they count about 75 genera and more than 900 species. The Trilobites represent a group apart, very distinct from all other orders of existing Crustacea, with the exception of the order of *Merostomata*, of which one genus, the *Limulus*, still exists in our own seas. The group of Merostomata is also of very early date; forms of great size, joined under the name of Gigantostraca, lived side by side with the Trilobites in the Silurian seas. I shall have to return to this group also when dealing with the first beginnings of life.

But the Silurian marine fauna is not confined to the Invertebrates only. Already the lower Vertebrates, the Fishes at least, had appeared, and figure simultaneously under three distinct and sharply differentiated types. The Selachians or cartilaginous Fishes carnivorous like our Sharks, Ganoids with enamelled scales recalling the existing Polyptera of the Nile, and lastly the *Placoderms* or *armoured Fishes*, so remarkable from their elegant carapace of great bony plates protecting the head and the fore part of the body. The higher Vertebrates—Amphibians, Reptiles, Birds, and Mammals—are still unknown at this epoch.

But this picture of Silurian life would be incomplete without mention of the highly important fact of the first appearance of air-breathing beings. In the present state of our knowledge the Arachnidæ of the Scorpion group alone remain to indicate to us the settlement on the Silurian continents of terrestrial animals with trachean respiration, seemingly issued from marine ancestors.

Thus the Silurian world presents itself to us as a very complex, very rich, and very progressive world, since we find in it beings so complicated and so perfect as the Cephalopods, Crustacea, and Fishes. These animals undeniably had ancestors, but we had to go to Bohemia to discover them. Prague is a large and fine city, gracefully situated on the two banks of the Moldau, in a schistous region, having a rather ungrateful and sterile soil, not wanting in analogy with certain portions of the central tableland of France, the Limousin, for example.

Natural sciences are held in honour in this town, and it is not without a feeling of rather jealous admiration that one beholds a magnificent building, the National Museum, erected by the Czech nation to Bohemia's glory. This superb palace contains all the national collections of archæology, of Prehistory, of living natural history, and also geological and palæontological collections.

The visit to the museum of Prague is for the naturalist, and particularly for the French geologist, a pilgrimage to a real sanctuary. This museum, in fact, vibrates with the memory of one of our most learned countrymen, Joachim Barrande. Barrande lived for many long years in Bohemia, and he profited by this sojourn and the liberality of a Royal patron to devote himself to a profound study of the Silurian Basin of Bohemia. Prague is, in fact, situated in the centre of a cuvette, or large basin, for the most part composed of Silurian strata. Barrande studied patiently, and layer by layer, the strata of this basin, and collected the innumerable fossils contained in each of them. The results of his admirable discoveries are recorded in a magnificent series of volumes entitled *The Silurian System of*

Central Bohemia, which form an entire library and a monument which still serves as a basis for all researches on the animals of Primary times.

The memory of Barrande has remained alive in Bohemia, and it is with legitimate satisfaction that a French geologist, when passing through the country round Prague, perceives, on the bank of the Moldau, the name of Barrande graven on the rock over the Konieprus quarries which yielded to him an important part of their riches.

The collections of Barrande remain in the Prague Museum, where they are placed on the second floor of the National Museum in an immense hall called the *Barrandeum*. In a corner of this hall, at the base of a monument, a sort of altar on which stands the bust of Barrande, are placed the hammers used in his researches, and a collection of the works written by him. It is, as I said above, a veritable place of pilgrimage.

Barrande deserves, in all respects, this honour and this worship. Not only did he describe and make known the Silurian fauna of Bohemia, which is doubtless the richest fauna of that epoch known, but he had the merit and the glory of demonstrating that this Silurian fauna was preceded by an earlier world, to which, in the enthusiasm of his discovery, he applied the name of *Primordial fauna*.

The strata contemporary with this primordial fauna exists indeed in England, where Sedgwick, in 1835, gave them the name of *Cambrian*, from the old Roman name for Wales. But these layers of sandstone and schist lower than the Silurian, had not then yielded any organic remains, and were called by English geologists "a barren grey-wack." As against this, Barrande discovered in the Cambrian strata of Bohemia a world of marine animals quite different from the Silurian world.

If we cast a glance on the geological structure of the Prague basin, we shall notice that the primary strata are disposed in concentric hollows, starting from the crystalline schists which form their edges, and designated by Barrande by the letter A. The other more recent layers are modestly marked B to H. The C layer is the home of the Primordial fauna contained in the greenish brown schists which crop up on both sides of the hollow in the two celebrated villages of Skrej and Ginetz.

The primordial fauna of Bohemia is, above all, rich in Trilobites divided into seven different genera, the most characteristic of which are the *Paradoxides* and the *Agnostus*. The first named has a large parabolic head, prolonged at the base and on the sides by two long points, a thorax with many segments and a very small pygidium ; the second has a cylindrical head and pygidium, joined by a tiny thorax with two segments. The Agnostus and a few other genera of the Primordial fauna are blind, which leads to the belief that these Trilobites lived in a relatively deep sea. There is, therefore, no reason for wonder at the relative dearth in this fauna of organisms other than Trilobites ; in fact, they are restricted to a few Brachiopods, a Pteropede Mollusc of pelagic habit, and to some remains of Echinoderms of the group Cystoidea.

After the sensational discovery of Barrande, the primordial fauna has been found in nearly every direction, in Sweden, England, Spain, and America ; in France, it for a long time escaped the search of geologists, till Bergeron had the good fortune to discover it in 1888 on the Southern slopes of the Montagne Noire. But already, at that date, the fauna of the Paradoxides had been despoiled of its halo as being the most primitive of all. Dr. Hicks had, in fact, discovered in the very lowest Cambrian strata in Wales, near the small town of St. Davids, the rudiments of a new fauna having certainly great affinities with that of Bohemia, but distinguished from it by its genera of Brachiopods, and situated, without any possible doubt, still lower than the layers characterized by the genus Paradoxides. The fauna of the lower Cambrian was not long after discovered in various regions, and was characterized by a special genus of Trilobites, the *Olenellus*, distinguished from *Paradoxides* by its shorter cephalic points and its fewer segments in the thorax. Through these discoveries, the fauna of Bohemia ceased to be the primordial and fell back to its former state of characteristic middle Cambrian fauna.

In the present state of our knowledge the total number of fossil animals collected from the whole thickness of the Cambrian soil all over the globe forms a very remarkable whole, the most essential characters of which we must analyse. There are first simple traces, the footprints of animals in the sand or the marine slime. Palæontologists are puzzled by these imprints and know not to what zoological group they should be ascribed. They must often confine themselves to giving them provisional names, trusting that some lucky chance may some day allow a more precise determination. Some of these footprints, such as the *Oldhamia*, radiate round one central point; others, the *Arenicolitæ*, are small striated lines ranged in two files and attributed to the passage of marine worms or Annelidæ; and others again are formed of two parallel furrows, and are doubtless the tracks of Crustacea.

By the side of these *problematic organisms*, we find well marked zoological forms, such as the spicula of Silicious *Sponges*, very primitive *Corals*; chitinous *Alcyonaries* of the extinct group of *Graptolites*; *Echinoderms* belonging to the three types of *Crinoïds*, *Cystoidea*, and *Asterias*; numerous Brachiopods, of which one family, that of the Lingulæ with horned shell, has passed from the lower Cambrian through the entire series of geological formation down to our own seas, without undergoing hardly the slightest morphological modification. Molluscs, though relatively few in number, are, however, represented by a few species of Lamellibranchs of the *Arca* family, and especially by several genera of pelagic habitat, of the group of Pteropods. Cephalopods themselves, the highest type of the Mollusc class, have been recently discovered in the Cambrian of Esthonia and of Canada in the form of straight shelled Nautilidæ, akin to the Orthocerata (genus *Volborthella*).

Finally the class of Marine Arthropods is richly represented either by a few *Ostracods* enclosed between their two calcareous valves, or by some of the *Malacostraca*, lesser neighbours of the existing

Nebalias, and especially by the then flourishing group of *Trilobites*. Of about 150 known genera of this group, one third or 50 genera with 250 species, have been discovered in the Cambrian system. The Trilobite fauna of the Cambrian is entirely distinct from that of the Silurian, but a very small number of genera, such as *Agnostus* and *Conocoryphus*, pass into the Silurian fauna. Contrary to what we noticed in the Silurian epoch, no trace of Vertebrates has yet been seen in Cambrian strata ; and it seems logical to consider the absence of the Fishes in the seas of that epoch as simply a temporary gap in our discoveries.

The Cambrian world, therefore, shows itself, the Vertebrates apart, to be largely constituted of the same general elements as the Silurian world. All the great groups of Invertebrates are there represented, and by the most highly organized types, such as the *Cephalopods* in the branch of Molluscs, and the Crustacea in the branch of Articulates. May we not suppose without any great improbability that these animals, so complex and so advanced in evolution—to use the transformist language,—have been preceded by more simple ancestors, belonging to the lower groups of the same branch ? The material answer to this question has only been supplied within a very few years.

We have not, in fact, yet terminated our journey into the depths, in search of the first traces of life in the thickness of the sedimentary crust of the Earth. Beneath the Cambrian soil there exists in different countries, in France, in England, in Finland, and in North America, enormous masses of sedimentary strata, such as schists and conglomerate or calcareous sandstone, for a long time assumed to be azoïc. These are still designated by the general name of pre-Cambrian or Huronian, on account of their great development on the shores of the great Canadian lake (Huron). In France, the schistous strata known by the names of *Schists of Rennes*, *Phyllads of Saint Lô*, or of *Douarnenez*, are very clearly the representatives of these pre-Cambrian strata in the old Armorican expanse.

The absence or extreme rarity of organic remains in this soil is easily explained by the fact that these very early sediments have frequently experienced, in the course of geological times and under the influence of causes of internal origin which I shall have to analyse later on, structural modifications designated by the general term of *metamorphism*. These schists, instead of being earthy and amorphous, are satiny or shiny through the development of membranes of mica or sericite. The limestones have become Marmorean or Saccharoid, and at times even the crystallinity of these sediments has attained a more accentuated degree, comparable to those generally observed in soils termed *primitive* or *crystallophyllian*. This partial or total metamorphism has had for a first effect that of destroying the fragile traces of the beings of varied form who doubtless peopled the waters of the pre-Cambrian seas, and this it may safely be affirmed is the most general case.

At certain privileged points, however, and owing to circumstances difficult to define, metamorphism has very fortunately spared a portion of the sediments of that epoch, of which the texture then remains absolutely the same as those of the most normal primary sediments. Thus it was not long before, in various directions, more or less defined traces of life commenced to be distinguished. First footprints or perforations of *problematic* animals were discovered in the sandstone of the Scottish Highlands, and found again by Lebesconte in the schists round Rennes. In the same district of Brittany, another French scholar, Cayeux, while examining some narrow cuttings effected in certain pre-Cambrian carboniferous schists, thought he recognized in these preparations some elegant lattice-work spherules, identical with the Silicious shells of certain of our present Radiolaries. He, moreover, described traces therein, rather less defined, it is true, of the shells of Foraminifera and of the spiculæ of Sponges. Although the authenticity of these organisms has given rise to certain controversies, it was impossible not to be struck, at least, by the fact that the simplicity of organization of these pre-Cambrian animals belonging to the very lowest groups of Invertebrates, answered well enough to the a priori idea which we must conceive of a really primitive fauna. The pre-Cambrian fauna of Brittany certainly possessed the most probable characteristics of an animal world still very near to its own origins. Once again, however, this simple way of regarding the matter had to be abandoned.

The methodical exploration by the American geologists of the ancient soils of Canada and of the Rocky Mountains reserved for us, indeed, quite unexpected discoveries. In Canada and in Newfoundland, we find first, according to the researches of Matthew, the same tracts of the sand-haunting worms or other problematical animals which are already known to us from Scotland and Armorica, and there were, further, traces, somewhat confused indeed, of a Mollusc shell. But the interest of all these observed facts almost vanishes before the astounding revelations supplied by the celebrated regions of the cañons in Western America.

Few regions of the globe have a more thrilling interest for a naturalist than the great bare and sterile tablelands which, in the states of Montana, Utah, Wyoming, and Colorado, constitute the successive steppes of the Rocky Mountains to the westward of the vast fertile prairies of the Missouri and the Mississippi. In these tablelands, in strata which have remained almost horizontal since the most distant times in the life of the globe, the rivers are scooped out by gigantic ravines caused by erosion or *canyons,* sometimes more than a kilometre deep, whose steep sides arranged in steps with many-coloured tints, offer to the eyes of the geologist the nearly complete series of sedimentary formations, from the primitive foundation up to the end of Secondary times.

The pre-Cambrian sediments formed by a mighty accumulation of 3500 metres of sandstone, schists, and limestone play an important part in the structure of the ancient base of the Rocky Mountain tablelands. These layers, resting on the early gneiss, seem to have escaped almost entirely metamorphic action. It is, therefore, not very surprising that they should have at last yielded some remains of organisms to the investigations of the Geological Survey of the United States. In the great cañon of the Rio Colorado, the finest and most magnificent of these great gashes in the Earth's crust, Charles Walcott made known to us five years ago the presence of colonies of Hydroids related to the Stromatopores, who are Molluscs possessing a conical shell (genus *Chuaria*) resembling the limpets which cling to the rocks on our own shores, the presence, perhaps, of pelagic Pteropods, and, lastly, of a well characterized Trilobite ring, seemingly akin to the Cambrian forms.

Farther north, in Montana, the pre-Cambrian series is locally designated by the name of the *Belt series*, and comprises 3600 metres of schists, quartzites, and limestone. At two different points, at the entry to the Deep Creek Cañon and in that of Sawmills, traces of organisms have likewise been discovered, such as the tracks of Annelids belonging to four different species and numerous other tracks due to Molluscs or Crustacea. But these layers contain, in addition, *in immense quantities*, the remains of one or several genera of large sized Crustacea, deformed, flattened and generally in fragments, of which the most characteristic form has received the name of *Beltina Danai*, in memory of the illustrious geologist Dana. It is no longer possible to doubt the existence, in the pre-Cambrian seas, of Molluscs, Trilobites, and Gigantostraca, analogous to those which swarm in the Cambrian and Silurian strata.

What conclusions should be drawn from these truly stupefying discoveries? One alone offers itself, and that with irresistible conviction. *The pre-Cambrian world was already a very old one*, and its discovery does not bring us much nearer to the beginning of life on the earth than did the memorable discoveries of Murchison, Barrande, and Dr. Hicks, in the more and more distant zones of the Silurian and Cambrian strata of the Old World. We are condemned to descend much lower still through the enormous thicknesses of the oldest sediments.

But here we find ourselves arrested by an almost insurmountable difficulty. Wherever it is possible to observe the base of the pre-Cambrian strata, they are seen to rest on a soil of which the mode of formation for a long time remained enigmatical, and which was prematurely described by the name *primitive soil*, on the hypothesis that it resulted from the consolidation of a thin but solid crust upon the surface of the terrestrial globe, itself in a state of igneous fusion. This soil is essentially composed of mica, schist, and gneiss, amongst which are sometimes intercalated bands of crystalline limestone, or *amphibolites*, rich in lime and magnesia. All these rocks offer a dual character, being composed, on the one hand, of perfectly crystalline silicated minerals, which from a chemical and mineralogical point of view assimilate them to the eruptive rocks of the granite family; but, on the other, the elements of these rocks have a clearly foliated structure quite similar to that of the most normal sedimentary rocks. By reason of this double modality, a Belgian geologist, d'Homalius d'Halloy, proposed nearly a century ago the designation of *Crystallophyllian soil*, which is very apt, and has been favourably received by the learned world. The term *Archean soil* is also very frequently used.

Very few geologists at the present day refuse to admit that these schistous and crystalline strata with surfaces sparkling with spangles of mica and sericite, must have been originally true amorphous sediments deposited in the state of slime, sand, and limestone at the bottom of the primitive oceans. The presence of perfectly preserved calcareous bands, of beds of sandstones, and of conglomerates recalling to mind the early sand and pebbles of the seashore, and the frequent parallelism of these strata with that of the pre-Cambrian and Cambrian soil which covers them, are strenuous arguments in favour of this point of view, which has been championed in France by Michel Lévy. What kind of mechanism is it that has produced this profound metamorphic modification of ancient sediments thus changed into the state of crystalline rocks almost similar to eruptive rocks? It is necessary, in order to arrive at anything like a clear idea of this, to cast a glance on the series of phenomena which have accompanied the deposit of marine sediments during the long series of geological ages. These sediments, of almost wholly continental origin, accumulate in enormous thicknesses in certain depths of the oceans, which are a kind of shallow basin of very large diameter, to which Dana has applied the name of *geo-synclinals*. The bottom of these vast depressions must present two necessary conditions: (1) it must not be too far off the shores of a continent, the source and starting-point of the material carried down by the rivers; (2) it must possess a base so little rigid as to allow the gradual subsidence of the terrestrial crust at that point, partly, probably, under the actual weight of the sediments accumulated at the bottom of the geo-synclinal.

The consequences of this subsidence, often uninterruptedly continued for several successive geological periods, are not difficult to appreciate. When subsiding, the lower part of this series of layers, sometimes piled on each other to a thickness of several kilometres, gets nearer to the terrestrial crust, and is subjected to higher and higher temperatures. One must even suppose that if the movement of subsidence is sufficiently prolonged, these sedimentary layers come into more or less direct contact with a part of the internal magma, imprisoned, in a state of fusion and at temperatures of from 1.500° to 2.000° C, below the solid crust, which constitutes, over a thickness of only a few kilometres, a thin pellicule on the surface of the terrestrial globe. Drawn into such a medium, the sediments are subjected to the action of vapours of high temperature, alcaline, fluoric, boric, etc., all endowed with the most intense chemical activity. These vapours impregnate the sediments through the thousand fissures which penetrate them, and combine with the silicious, argillaceous, or calcareous matter of which they are constituted, so as to transform it into various silicates, such as feldspar, mica, amphibolites, and pyroxenes, which are precisely the crystallized mineral components of the granitic rocks. A part of the sediments must even have been entirely *digested* and incorporated into the internal magma, thus losing every trace of the original foliated structure. *The entire basis of the series of sedimentary strata deposited in the earliest seas is probably destroyed by this process, and definitively withdrawn from our observation.*

What is there astonishing, then—supposing this theory of a general metamorphism to be correct—in the fact of all traces of organisms having entirely disappeared from those Archean strata which living beings had to abandon at the time of the deposit of these strata in the early oceans? In fact, the crystallophyllian series, which, at some points of the globe attains a thickness of more than 20 kilometres of superposed strata, seems entirely devoid of fossils, and it appears very improbable that any will ever be found therein.

Yet, nearly half a century ago, a glimpse of hope on this question appeared. The Canadian geologists, when studying the Archean layers on the shores of the St. Lawrence, remarked on the surface of a bed of serpentine limestone, intercalated in the early gneiss, some protruding nodes jutting out in semi-relief and of varying dimensions extending to the size of a child's head. Examined microscopically in sections, these nodes showed themselves formed of thin concentric and alternate bands of calcite and serpentine, the first being traversed, besides, by a system of perpendicular and ramified tiny canals. Eminent palæontologists, such as Dawson and Carpenter, thought they could see in these kidney-shaped lumps the characteristic structure of certain Foraminifera, like the Nummulites, and that they had come across the most ancient organic remains of which traces were left on the earth, whence the name of *Eozoon*, or Dawn of the Animal World. Observed soon afterwards in the Archean gneiss of Ireland, Bohemia, Bavaria, and the Pyrenees, the *Eozoon* became the object of passionate controversy, some electing for the organic nature of this strange giant among Foraminifera, and others refusing to see anything in it but a simple mineral concretion. This last interpretation forced itself on all minds after the discovery by Johnston-Lavis in the lava of Vesuvius and on the flank of the Somma, of volcanic concretions absolutely similar to the *Eozoon*, and the result, as in Canada, of a close mineralogical admixture of calcareous and serpentine elements. The Dawn of Life thus once again withdrew itself from the deceptive investigations of geologists.

Is it to be concluded from these facts that we must for ever abandon the solution, or at least the attempt to solve the entrancing problem of the commencement of life on our globe? This, unfortunately, it must be acknowledged, is the most probable prospect. The only hope remaining to us is that we may find, in some unexplored region where the Archean soil crops up, some portion of these layers which have, through local circumstances, escaped the destructive action of metamorphic agents. This is not absolutely impossible, since the pre-Cambrian soil is nearly everywhere metamorphosed, and has only yielded fossil-bearing layers in very limited points of its outcrop.

The least improbable chances of success seem as if they ought to be met with in the exploration of the polar regions. Our present knowledge of the history of the formation of continents and mountain ranges authorizes us to think that it is in the Arctic and Antarctic regions that the earth's crust first became cooler, contracted, and wrinkled. It is there that the first continental ridges must have emerged at an early date from the surface of the first seas. These desolate regions have exhibited from the most remote periods of the life of the globe a character of stability and rigidity of the most remarkable kind, as contrasted with the mobility and lesser resistance of the earth's crust in the temperate and equatorial regions. It is, therefore, in the vicinity of the Poles that the earliest sediments may perhaps have escaped metamorphism by reason of their rapid incorporation into continents and the absence of a heavy superposition of later deposits.

There is, no doubt, room for hope in this direction of important revelations as to the ancestors of the Cambrian and pre-Cambrian animals, especially if some heat-wave passing over the terrestrial atmosphere, or some inter-glacial phase like those which must several times have occurred during Quaternary times, were to temporarily free the polar continents from their coat of ice, and thus uplift for us a corner of the veil which still covers the all-absorbing problem of the apparition of life on the globe.

INDEX OF SUBJECTS

INDEX OF NAMES

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I.—TABLE OF THE AGES OF THE EARTH

Eras		Periods			Stages
TERTIARY ERA	Neogene Strata	Pleistocene or Quaternary			Upper
					Lower
		Pliocene	Upper		Sicilian
			Middle		Astian
			Lower		Plaisancian
					Pontian
		Miocene	Upper		Sarmatian
			Middle		Tortonian
			Lower		Helvetian
	Eogene Strata	Oligocene	Upper		Burdigalian
			Middle		Aquitanian
			Lower		Stampian
					Sannoisian
					Ludian
		Eocene	Upper		Bartonian
			Middle		Lutetian
			Lower		Londinian
					Sparnacian
					Thanetian
					Montian
SECONDARY ERA	Cretacean Strata	Upper Cretacean	Danian		
			Senonian	Upper	Campanian
				Lower	Santonian
			Turonian	Upper	Angoumian
				Lower	Ligerian
			Cenomanian		
		Lower Cretacean	Albian or Gault	Upper	Vraconian
				Lower	Albian *proper*
			Aptian	Upper	Gargasian
				Lower	Bedulian
			Barremian		
			Hauterivian		
			Valanginian		
			Berriasian		
	Jurassic Strata	Higher Jurassic	Portlandian or Tithonic		Purbeckian
					Portlandian *proper*
					Bononian
			Kimmeridgian		Virgulian
					Pterocerian
			Sequanian		Astartian
					Rauracian
			Oxfordian		Argovian
					Oxfordian *proper*
			Callovian		
		Lower Jurassic	Bathonian		
			Bajocian		
		Lias	Toarcian		
			Charmouthian		
			Sinemurian		
		Infra-Lias	Hettangian		
			Rhœtian		
	Triassic Strata	Trias	Upper		Keuper (iridescent marl)
			Middle		Muschelkalk
			Lower		Streaked Sandstone
PRIMARY ERA	Palæozoic Strata	Permian	Upper		Thuringian
			Middle		Saxonian
			Lower		Autunian
		Carboniferous	Upper		Stephanian
			Middle		Westphalian
			Lower		Dinantian
		Devonian	Upper		Fammenian
					Frasnian
			Middle		Givetian
					Eifelian
			Lower		Coblentzian
					Gedinnian
		Silurian	Upper		Gothlandian
			Lower		Ordovician
		Cambrian	Upper		Potsdamian
			Middle		Acadian
			Lower		Georgian
		Pre-Cambrian or Huronian			

CRYSTALLOPHYLLIAN STRATA (Gneiss and Mica schists)

II.—TABLE OF CLASSIFICATION OF THE ANIMAL KINGDOM

Classes	Orders	Sub-Orders	Principal Types
PLACENTAL MAMMALS	Primates	Bimanes	Man
		Anthropoids	*Pithecanthropus*, Orang, Chimpanzee, Gibbons
		Catarrhinian Apes	Macaques, Semnopithecus, etc.
		Platyrrhinian Apes	Howlers, Wistitis
	Carnivora	Carnivora	Dogs, *Amphicyon*, Bears, Weasels, Otters, Civets, Cats, *Machairodus*
		Creodonts (Primitive Carnivora)	*Arctocyon*, *Hyænodon*, *Pterodon*
		Pinnipeds	Seals, Walruses
	Chiroptera	Frugivora	Roussettes
		Insectivora	*Vespertilio*, *Rhinolophus*
	Insectivora	Insectivora	*Adapisorex*, Moles, *Centeta*, Shrew Mice, Hedgehogs
	Rodents	Protrogomorphs	*Pseudosciurus*, Dormice
		Sciuromorphs	Squirrels, Beavers
		Myomorphs	Rats, Field Mice
		Hystricomorph	Porcupines, *Cavia*
		Lagomorphs	*Lagomys*, Hares
	Tillodonts	. . .	*Esthonyx*
	Ungulates	Hyracoidæ	Daman
		Typotherians	*Typotherium*
		Toxodonts	*Astrapotherium*, *Toxodon*
		Proboscidians	*Elephas*, *Mastodon*, *Palæomastodon*, *Dinotherium*
		Amblypods	*Coryphodon*, *Dinoceras*
		Paridigits	*Anthracotherium*, *Brachyodus*, *Ancodus*, Swine, Hippopotamuses, Camels, *Anoplotherium*, *Xiphodon*, Tragulæ, *Cervulus*, Deer, Antelopes, Cattle
		Imparidigits	*Hyracotherium*, *Palæotherium*, Horses, *Hipparion*, *Anchitherium*, Tapirs, *Lophiodon*, Rhinoceros, *Acerotheria*, *Amynodon*, *Titanotherium*, *Chalicotherium*
		Condylarthra	*Phenacodus*
	Sirenians	. . .	Lamantins [Manatees], Dugongs
	Cetacea	. . .	Whale, Balænoptera, Sperm Whale
	Edentata	Nomarthra	Orycterope, Pangolin
		Xenarthra	Anteater, Sloth, Gravigrades, *Glyptodon*, Tatus
NON-PLACENTAL MAMMALS	Marsupials	Polyprodonts	*Didelphys*, *Amphilestes*, *Dromatherium*
		Diprotodonts	Kangaroos, *Thylacoleo*, Kangaroo Rats
	Multituberculata or Allothorian	. . .	*Plagiaulax*, *Microlestes*, *Polymastodon*
	Monotremata	. . .	Echidna, Ornithorynchus
BIRDS	Carinata	Without teeth	Nearly all the existing Birds
		With teeth	*Ichthyornis*
	Ratita	Without teeth	Ostrich, Casoar, *Epyornis*, *Apteryx*
		With teeth	*Hesperornis*
	Saurura	With teeth	Archæopteryx
REPTILES	Pterosaurians	. . .	*Pterodactylus*
	Dinosaurians	Ornithopods	*Stegosaurus*, *Ceratops*, *Iguanodon*, *Hadrysaurus*
		Theropods	*Zanclodon*, *Anchisaurus*, *Megalosaurus*, *Ceratosaurus*
		Sauropods	*Cetiosaurus*, *Atlantosaurus*, *Brontosaurus*, *Ornithopsis*
	Crocodilians	Eusuchians	*Longirostres*: *Teleosaurus*, Gavials. *Brevirostres*: Crocodiles, Alligators
		Pseudosuchians	*Ætosaurus*
		Parasuchians	*Belodon*
	Ophidians	Parasuchians	Pythons, Adders, Vipers, *Typhlops*
	Lacertians	Pythonomorphs	*Mosasaurus*
		Lacertilians	*Dolichosaurus*, *Placosaurus*, Monitors, Lizards, Skink
	Rynchocephalians	Lacertilians	*Sphenodon* or *Hatteria*, *Sauranodon*, *Proterosaurus*, *Palæohatteria*
	Theromorphs	Theriodonts	*Naosaurus*, *Lycosaurus*, *Cynodraco*
		Pareiasaurians	*Pareiasaurus*
		Placodonts	*Placodus*
		Anomodonts	*Dicynodon*
	Chelonians	Pleurodères	*Proganochelys*
		Cryptoderes	*Dermochelys*, *Chelona*, *Idiochelys*, Chelydra, Emydea, *Testudo*
		Trionychians	Trionyx
	Sauropterygians	. . .	*Nothosaurus*, *Plesiosaurus*
	Icthyosaurians	. . .	Icthyosaurus
AMPHIBIA	Cecilians	. . .	Cecilia
	Urodeles	. . .	Salamanders, *Andrias*
	Anura	. . .	Frogs, Toads
	Stegocephala	Stereospondylians or Labyrinthodonts	*Anthracosaurus*, *Mastodonsaurus*, *Capitosaurus*
		Temnospondylians	*Archegosaurus*, *Eryops*, *Dendrerpeton*
		Lepospondylians	*Branchiosaurus*, Microsaurians
FISHES	Teleosteans (Bony Fishes)	. . .	Siluri, Pike, Salmon, Herring, Perch, Cod, Sole
	Scaly ganoids	. . .	Sturgeon, Polyptera, *Acanthodes*, *Lepidosteus*, *Osteolepis*, *Leptolepis*, *Pycnodus*
	Placodermal ganoids	. . .	*Pteraspis*, *Cephalaspis*, *Bothriolepis*
	Dipneusta	. . .	*Coccosteus*, *Dipterus*, *Ceratodus*
	Plagiostomata	Squalidæ	Sharks, Dog-fish
		Batidæ	Skates
	Marsipobranchia	. . .	Lampreys
	Leptocardia (Acranians)	. . .	*Amphioxus*

Classes	Orders	Sub-Orders	Principal Fossil Types
		ARTHROPODS	
INSECTS	Insecta		
ARACHNOIDÆ	Arachnoidæ		*Eophrynus*
	Scorpionidæ		*Palæophonus*
MYRIAPODS			Julæ
CRUSTACEA	Malacostraca	Decapods: Brachyoura	Crabs
		Decapods: Macroura	Shrimps
		Isopods	Woodlice
		Phyllocaridæ	*Nebalia*, *Ceratiocaris*
	Merostomata	Xiphosura	Limulus, *Belinurus*
		Gigantostraca	*Eurypterus*, *Pterygotus*, *Bettina*
		Trilobites	*Agnostus*, *Paradoxidæ*, *Conocorypha*, *Phacops*
	Entomostraca	Phyllopods	*Apus*, *Estheria*
		Ostracods	*Cypris*, *Leperditia*
		Cirrhipedes	Balana, Anatifa, Coronula
		MOLLUSCS	
MOLLUSCS (properly called)	Cephalopods	Dibranchials: Octopods	Argonauta
		Dibranchials: Decapods	Octopus, Cuttle Fish, Belemnite, Spirula
		Ammoneans: Prosiphonata	Ammonites
		Ammoneans: Retrosiphonata	Goniatites, Clymenia
		Tetrabranchials	Nautilus, *Orthoceras*, *Cyrtoceras*
	Gastropods	Scaphopods	*Chiton*
		Prosobranchs	Limpet, Cerithium, Whelk, *Natica*
		Heteropods	Carinary
		Opisthobranchs	*Aplysia*, *Actænella*
		Pulmonates	Helix, Limnæa, Planorbis
	Pteropods		*Hyalæa*, *Conularia*
	Lamellibranchs	Siphonata	*Venus*, *Cyrena*, Chama, *Requienia*, *Diceras*, Rudistæ
		Asiphonata: Homomyaries	Arca, Trigonia
		Asiphonata: Heteromyaries	Avicula, Mussels
		Asiphonata: Monomyaries	Oyster, *Pecten*
MOLLUSCOIDS	Brachiopods	Articulates	Terebratula, Rynchonella, *Stringocephalus*, Spirifer, Orthis
		Inarticulates	Lingula
	Bryozoaries		*Cellepora*
		WORMS	
ANNELIDS			Serpula
PROBLEMATIC TYPES			*Nereites*, *Arenicolites*, *Oldhamia*
		ECHINODERMS	
HOLOTHURIDÆ			Holothuria
ECHINIDA	Irregular	Atelostomata	*Spatangus*
		Gnathostomata	*Clypeaster*
	Regular		*Cidaris*
	Palechinida		*Archæocidaris*
ASTERIDS	Palechinida		Star-fish, Ophiura
CRINOÏDS	Eucrinoids		*Eucrina*, *Pentacrina*, Comatula
	Cystidea		*Echinosphærita*
	Blastoids		*Pentremitæ*
		CÆLÆNTARIES	
HYDROMEDUSÆ	Discophora		Medusæ
		Hydrocorallina	Stromatopores
	Hydroids	Graptolites	*Monograptus*, *Didymograptus*
ANTHROZOARIA	Zoantharies (Polyps)	Hexacorals	*Favosita*, *Astræa*
		Tetracorals	*Zaphrentis*
	Alcyonnaria	—	Gorgona, *Isis*
SPONGIARIA	Sponges: Calcareous, Silician, Horned	—	—
		PROTOZOARIES	
RADIOLARIA	—	—	Monospheridæ
FORAMINIFERA	Perforata	—	*Globigerina*, *Fusulina*, *Nummulites*
	Imperforata	—	*Alveolina*, *Miliola*

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