geologist—would for a moment admit the hypothesis that the present state of underground heat is due to a heating of the surface at so late a period as 20,000 years ago. If that is not admitted we are driven to a greater heat at some time more than 20,000 years ago. A greater heating all over the surface than 100° Fahrenheit would kill nearly all existing plants and animals, I may safely say. Are modern geologists prepared to say that all life was killed off the earth 50,000, 100,000, or 200,000 years ago? For the uniformity theory, the further back the time of high surface-temperature is put the better; but the further back the time of heating, the hotter it must have been. The best for those who draw most largely on time is that which puts it furthest back; and that is the theory that the heating was enough to melt the whole. But even if it was enough to melt the whole, we must still admit some limit, such as fifty million years, one hundred million years, or two or three hundred million years ago. Beyond that we cannot go." [1]

It will be observed that the "limit" is once again of the vaguest, ranging from 50,000,000 years to 300,000,000. And the reply is, once more, that, for anything that can be proved to the contrary, one or two hundred million years might serve the purpose, even of a thoroughgoing Huttonian uniformitarian, very well.

[1] *Loc. cit.* p. 24.

But if, on the other hand, the 100,000,000 or 200,000,000 years appear to be insufficient for geological purposes, we must closely criticise the method by which the limit is reached. The argument is simple enough. *Assuming* the earth to be nothing but a cooling mass, the quantity of heat lost per year, *supposing* the rate of cooling to have been uniform, multiplied by any given number of years, will be given the minimum temperature that number of years ago.

But is the earth nothing but a cooling mass, "like a hot-water jar such as is used in carriages," or "a globe of sandstone," and has its cooling been uniform? An affirmative answer to both these questions seems to be necessary to the validity of the calculations on which Sir W. Thomson lays so much stress.

Nevertheless it surely may be urged that such affirmative answers are purely hypothetical, and that other suppositions have an equal right to consideration.

For example, is it not possible that, at the prodigious temperature which would seem to exist at 100 miles below the surface, all the metallic bases may behave as mercury does at a red heat, when it refuses to combine with oxygen; while, nearer the surface, and therefore at a lower temperature, they may enter into combination (as mercury does with oxygen a few degrees below its boiling-point), and so give rise to a heat totally

distinct from that which they possess as cooling bodies? And has it not also been proved by recent researches that the quality of the atmosphere may immensely affect its permeability to heat; and, consequently, profoundly modify the rate of cooling the globe as a whole?

I do not think it can be denied that such conditions may exist, and may so greatly affect the supply, and the loss, of terrestrial heat as to destroy the value of any calculations which leave them out of sight.

My functions as your advocate are at an end. I speak with more than the sincerity of a mere advocate when I express the belief that the case against us has entirely broken down. The cry for reform which has been raised without, is superfluous, inasmuch as we have long been reforming from within, with all needful speed. And the critical examination of the grounds upon which the very grave charge of opposition to the principles of Natural Philosophy has been brought against us, rather shows that we have exercised a wise discrimination in declining, for the present, to meddle with our foundations.

XI

PALÆONTOLOGY AND THE DOCTRINE OF EVOLUTION

[1870]

It is now eight years since, in the absence of the late Mr. Leonard Horner, who then presided over us, it fell to my lot, as one of the Secretaries of this Society, to draw up the customary Annual Address. I availed myself of the opportunity to endeavour to "take stock" of that portion of the science of biology which is commonly called "palæontology," as it then existed; and, discussing one after another the doctrines held by palæontologists, I put before you the results of my attempts to sift the well-established from the hypothetical or the doubtful. Permit me briefly to recall to your minds what those results were:—

1. The living population of all parts of the earth's surface which have yet been examined

has undergone a succession of changes which, upon the whole, have been of a slow and gradual character.

2. When the fossil remains which are the evidences of these successive changes, as they have occurred in any two more or less distant parts of the surface of the earth, are compared, they exhibit a certain broad and general parallelism. In other words, certain forms of life in one locality occur in the same general order of succession as, or are *homotaxial* with, similar forms in the other locality.

3. Homotaxis is not to be held identical with synchronism without independent evidence. It is possible that similar, or even identical, faunæ and floræ in two different localities may be of extremely different ages, if the term "age" is used in its proper chronological sense. I stated that "geographical provinces, or zones, may have been as distinctly marked in the Palæozoic epoch as at present; and those seemingly sudden appearances of new genera and species which we ascribe to new creation, may be simple results of migration."

4. The opinion that the oldest known fossils are the earliest forms of life has no solid foundation.

5. If we confine ourselves to positively ascertained facts, the total amount of change in the forms of animal and vegetable life, since the

existence of such forms is recorded, is small. When compared with the lapse of time since the first appearance of these forms, the amount of change is wonderfully small. Moreover, in each great group of the animal and vegetable kingdoms, there are certain forms which I termed PERSISTENT TYPES, which have remained, with but very little apparent change, from their first appearance to the present time.

6. In answer to the question "What, then, does an impartial survey of the positively ascertained truths of palæontology testify in relation to the common doctrines of progressive modification, which suppose that modification to have taken place by a necessary progress from more to less embryonic forms, from more to less generalised types, within the limits of the period represented by the fossiliferous rocks?" I reply, "It negatives these doctrines; for it either show us no evidence of such modification, or demonstrates such modification as has occurred to have been very slight; and, as to the nature of that modification, it yields no evidence whatsoever that the earlier members of any long-continued group were more generalised in structure than the later ones."

I think that I cannot employ my last opportunity of addressing you, officially, more properly—I may say more dutifully—than in revising these old judgments with such help as further know-

ledge and reflection, and an extreme desire to get at the truth, may afford me.

1. With respect to the first proposition, I may remark that whatever may be the case among the physical geologists, catastrophic palæontologists are practically extinct. It is now no part of recognised geological doctrine that the species of one formation all died out and were replaced by a brand-new set in the next formation. On the contrary, it is generally, if not universally, agreed that the succession of life has been the result of a slow and gradual replacement of species by species; and that all appearances of abruptness of change are due to breaks in the series of deposits, or other changes in physical conditions. The continuity of living forms has been unbroken from the earliest times to the present day.

2, 3. The use of the word "homotaxis" instead of "synchronism" has not, so far as I know, found much favour in the eyes of geologists. I hope, therefore, that it is a love for scientific caution, and not mere personal affection for a bantling of my own, which leads me still to think that the change of phrase is of importance, and that the sooner it is made, the sooner shall we get rid of a number of pitfalls which beset the reasoner upon the facts and theories of geology.

One of the latest pieces of foreign intelligence which has reached us is the information that the Austrian geologists have, at last, succumbed to

the weighty evidence which M. Barrande has accumulated, and have admitted the doctrine of colonies. But the admission of the doctrine of colonies implies the further admission that even identity of organic remains is no proof of the synchronism of the deposits which contain them.

4. The discussions touching the *Eozoon*, which commenced in 1864, have abundantly justified the fourth proposition. In 1862, the oldest record of life was in the Cambrian rocks; but if the *Eozoon* be, as Principal Dawson and Dr. Carpenter have shown so much reason for believing, the remains of a living being, the discovery of its true nature carried life back to a period which, as Sir William Logan has observed, is as remote from that during which the Cambrian rocks were deposited, as the Cambrian epoch itself is from the tertiaries. In other words, the ascertained duration of life upon the globe was nearly doubled at a stroke.

5. The significance of persistent types, and of the small amount of change which has taken place even in those forms which can be shown to have been modified, becomes greater and greater in my eyes, the longer I occupy myself with the biology of the past.

Consider how long a time has elapsed since the Miocene epoch. Yet, at that time there is reason to believe that every important group in every order of the *Mammalia* was represented. Even the

comparatively scanty Eocene fauna yields examples of the orders *Cheiroptera*, *Insectivora*, *Rodentia*, and *Perissodactyla*; of *Artiodactyla* under both the Ruminant and the Porcine modifications; of *Carnivora*, *Cetacea*, and *Marsupialia*.

Or, if we go back to the older half of the Mesozoic epoch, how truly surprising it is to find every order of the *Reptilia*, except the *Ophidia*, represented; while some groups, such as the *Ornithoscelida* and the *Pterosauria*, more specialised than any which now exist, abounded.

There is one division of the *Amphibia* which offers especially important evidence upon this point, inasmuch as it bridges over the gap between the Mesozoic and the Palæozoic formations (often supposed to be of such prodigious magnitude), extending, as it does, from the bottom of the Carboniferous series to the top of the Trias, if not into the Lias. I refer to the Labyrinthodonts. As the Address of 1862 was passing through the press, I was able to mention, in a note, the discovery of a large Labyrinthodont, with well-ossified vertebræ, in the Edinburgh coal-field. Since that time eight or ten distinct genera of Labyrinthodonts have been discovered in the Carboniferous rocks of England, Scotland, and Ireland, not to mention the American forms described by Principal Dawson and Professor Cope. So that, at the present time, the Labyrinthodont Fauna of the Carboniferous rocks is more

extensive and diversified than that of the Trias, while its chief types, so far as osteology enables us to judge, are quite as highly organised. Thus it is certain that a comparatively highly organised vertebrate type, such as that of the Labyrinthodonts, is capable of persisting, with no considerable change, through the period represented by the vast deposits which constitute the Carboniferous, the Permian, and the Triassic formations.

The very remarkable results which have been brought to light by the sounding and dredging operations, which have been carried on with such remarkable success by the expeditions sent out by our own, the American, and the Swedish Governments, under the supervision of able naturalists, have a bearing in the same direction. These investigations have demonstrated the existence, at great depths in the ocean, of living animals in some cases identical with, in others very similar to, those which are found fossilised in the white chalk. The *Globigerinæ*, Cyatholiths, Coccospheres, Discoliths in the one are absolutely identical with those in the other ; there are identical, or closely analogous, species of Sponges, Echinoderms, and Brachiopods. Off the coast of Portugal, there now lives a species of *Beryx*, which, doubtless, leaves its bones and scales here and there in the Atlantic ooze, as its predecessor left its spoils in the mud of the sea of the Cretaceous epoch.

Many years ago[1] I ventured to speak of the Atlantic mud as "modern chalk," and I know of no fact inconsistent with the view which Professor Wyville Thomson has advocated, that the modern chalk is not only the lineal descendant of the ancient chalk, but that it remains, so to speak, in the possession of the ancestral estate; and that from the Cretaceous period (if not much earlier) to the present day, the deep sea has covered a large part of what is now the area of the Atlantic. But if *Globigerina*, and *Terebratula caput-serpentis* and *Beryx*, not to mention other forms of animals and of plants, thus bridge over the interval between the present and the Mesozoic periods, is it possible that the majority of other living things underwent a "sea-change into something new and strange" all at once?

6. Thus far I have endeavoured to expand and to enforce by fresh arguments, but not to modify in any important respect, the ideas submitted to you on a former occasion. But when I come to the propositions touching progressive modification, it appears to me, with the help of the new light which has broken from various quarters, that there is much ground for softening the somewhat Brutus-like severity with which, in 1862, I dealt with a doctrine, for the truth of which I should have been glad enough to be able to find a good

[1] See an article in the *Saturday Review*, for 1858, on "Chalk, Ancient and Modern."

foundation. So far, indeed, as the *Invertebrata* and the lower *Vertebrata* are concerned, the facts and the conclusions which are to be drawn from them appear to me to remain what they were. For anything that, as yet, appears to the contrary, the earliest known Marsupials may have been as highly organised as their living congeners; the Permian lizards show no signs of inferiority to those of the present day; the Labyrinthodonts cannot be placed below the living Salamander and Triton; the Devonian Ganoids are closely related to *Polypterus* and to *Lepidosiren*.

But when we turn to the higher *Vertebrata*, the results of recent investigations, however we may sift and criticise them, seem to me to leave a clear balance in favour of the doctrine of the evolution of living forms one from another. Nevertheless, in discussing this question, it is very necessary to discriminate carefully between the different kinds of evidence from fossil remains which are brought forward in favour of evolution.

Every fossil which takes an intermediate place between forms of life already known, may be said, so far as it is intermediate, to be evidence in favour of evolution, inasmuch as it shows a possible road by which evolution may have taken place. But the mere discovery of such a form does not, in itself, prove that evolution took place by and through it, nor does it constitute more than pre-

sumptive evidence in favour of evolution in general. Suppose A, B, C to be three forms, while B is intermediate in structure between A and C. Then the doctrine of evolution offers four possible alternatives. A may have become C by way of B; or C may have become A by way of B; or A and C may be independent modifications of B; or A, B, and C may be independent modifications of some unknown D. Take the case of the Pigs, the *Anoplotheridæ*, and the Ruminants. The *Anoplotheridæ* are intermediate between the first and the last; but this does not tell us whether the Ruminants have come from the Pigs, or the Pigs from Ruminants, or both from *Anoplotheridæ*, or whether Pigs, Ruminants, and *Anoplotheridæ* alike may not have diverged from some common stock.

But if it can be shown that A, B, and C exhibit successive stages in the degree of modification, or specialisation, of the same type; and if, further, it can be proved that they occur in successively newer deposits, A being in the oldest and C in the newest, then the intermediate character of B has quite another importance, and I should accept it, without hesitation, as a link in the genealogy of C. I should consider the burden of proof to be thrown upon any one who denied C to have been derived from A by way of B, or in some closely analogous fashion; for it is always probable that one may not hit upon the exact line of filiation,

and, in dealing with fossils, may mistake uncles and nephews for fathers and sons.

I think it necessary to distinguish between the former and the latter classes of intermediate forms, as *intercalary types* and *linear types*. When I apply the former term, I merely mean to say that as a matter of fact, the form B, so named, is intermediate between the others, in the sense in which the *Anoplotherium* is intermediate between the Pigs and the Ruminants—without either affirming, or denying, any direct genetic relation between the three forms involved. When I apply the latter term, on the other hand, I mean to express the opinion that the forms A, B, and C constitute a line of descent, and that B is thus part of the lineage of C.

From the time when Cuvier's wonderful researches upon the extinct Mammals of the Paris gypsum first made intercalary types known, and caused them to be recognised as such, the number of such forms has steadily increased among the higher *Mammalia*. Not only do we now know numerous intercalary forms of *Ungulata*, but M. Gaudry's great monograph upon the fossils of Pikermi (which strikes me as one of the most perfect pieces of palæontological work I have seen for a long time) shows us, among the *Primates*, *Mesopithecus* as an intercalary form between the *Semnopitheci* and the *Macaci;* and among the *Carnivora*, *Hyænictis* and *Ictitherium* as intercalary,

or, perhaps, linear types between the *Viverridæ* and the *Hyænidæ*.

Hardly any order of the higher *Mammalia* stands so apparently separate and isolated from the rest as that of the *Cetacea*; though a careful consideration of the structure of the pinnipede *Carnivora*, or Seals, shows, in them, many an approximation towards the still more completely marine mammals. The extinct *Zeuglodon*, however, presents us with an intercalary form between the type of the Seals and that of the Whales. The skull of this great Eocene sea-monster, in fact, shows by the narrow and prolonged inter-orbital region; the extensive union of the parietal bones in a sagittal suture; the well-developed nasal bones; the distinct and large incisors implanted in premaxillary bones, which take a full share in bounding the fore part of the gape; the two-ranged molar teeth with triangular and serrated crowns, not exceeding five on each side in each jaw; and the existence of a deciduous dentition—its close relation with the Seals. While, on the other hand, the produced rostral form of the snout, the long symphysis, and the low coronary process of the mandible are approximations to the cetacean form of those parts.

The scapula resembles that of the cetacean *Hyperoodon*, but the supra-spinous fossa is larger and more seal-like; as is the humerus, which differs from that of the *Cetacea* in presenting true

articular surfaces for the free jointing of the bones of the fore-arm. In the apparently complete absence of hinder limbs, and in the characters of the vertebral column, the *Zeuglodon* lies on the cetacean side of the boundary line; so that upon the whole, the Zeuglodonts, transitional as they are, are conveniently retained in the cetacean order. And the publication, in 1864, of M. Van Beneden's memoir on the Miocene and Pliocene *Squalodon*, furnished much better means than anatomists previously possessed of fitting in another link of the chain which connects the existing *Cetacea* with *Zeuglodon*. The teeth are much more numerous, although the molars exhibit the zeuglodont double fang; the nasal bones are very short, and the upper surface of the rostrum presents the groove, filled up during life by the prolongation of the ethmoidal cartilage, which is so characteristic of the majority of the *Cetacea*.

It appears to me that, just as among the existing *Carnivora*, the walruses and the eared seals are intercalary forms between the fissipede Carnivora and the ordinary seals, so the Zeuglodonts are intercalary between the *Carnivora*, as a whole, and the *Cetacea*. Whether the Zeuglodonts are also linear types in their relation to these two groups cannot be ascertained, until we have more definite knowledge than we possess at present, respecting the relations in time of the *Carnivora* and *Cetacea*.

Thus far we have been concerned with the intercalary types which occupy the intervals between Families or Orders of the same class; but the investigations which have been carried on by Professor Gegenbaur, Professor Cope, and myself into the structure and relations of the extinct reptilian forms of the *Ornithoscelida* (or *Dinosauria* and *Compsognatha*) have brought to light the existence of intercalary forms between what have hitherto been always regarded as very distinct classes of the vertebrate sub-kingdom, namely *Reptilia* and *Aves*. Whatever inferences may, or may not, be drawn from the fact, it is now an established truth that, in many of these *Ornithoscelida*, the hind limbs and the pelvis are much more similar to those of Birds than they are to those of Reptiles, and that these Bird-reptiles, or Reptile-birds, were more or less completely bipedal.

When I addressed you in 1862, I should have been bold indeed had I suggested that palæontology would before long show us the possibility of a direct transition from the type of the lizard to that of the ostrich. At the present moment, we have, in the *Ornithoscelida*, the intercalary type, which proves that transition to be something more than a possibility; but it is very doubtful whether any of the genera of *Ornithoscelida* with which we are at present acquainted are the actual linear types by which the transition from the

lizard to the bird was effected. These, very probably, are still hidden from us in the older formations.

Let us now endeavour to find some cases of true linear types, or forms which are intermediate between others because they stand in a direct genetic relation to them. It is no easy matter to find clear and unmistakable evidence of filiation among fossil animals; for, in order that such evidence should be quite satisfactory, it is necessary that we should be acquainted with all the most important features of the organisation of the animals which are supposed to be thus related, and not merely with the fragments upon which the genera and species of the palæontologist are so often based. M. Gaudry has arranged the species of *Hyænidæ*, *Proboscidea*, *Rhinocerotidæ*, and *Equidæ* in their order of filiation from their earliest appearance in the Miocene epoch to the present time, and Professor Rütimeyer has drawn up similar schemes for the Oxen and other *Ungulata*—with what, I am disposed to think, is a fair and probable approximation to the order of nature. But, as no one is better aware than these two learned, acute, and philosophical biologists, all such arrangements must be regarded as provisional, except in those cases in which, by a fortunate accident, large series of remains are obtainable from a thick and widespread series of deposits. It is easy to accumulate probabilities—hard to make out some

particular case in such a way that it will stand rigorous criticism.

After much search, however, I think that such a case is to be made out in favour of the pedigree of the Horses.

The genus *Equus* is represented as far back as the latter part of the Miocene epoch; but in deposits belonging to the middle of that epoch its place is taken by two other genera, *Hipparion* and *Anchitherium*;[1] and, in the lowest Miocene and upper Eocene, only the last genus occurs. A species of *Anchitherium* was referred by Cuvier to the *Palæotheria* under the name of *P. aurelianense*. The grinding-teeth are in fact very similar in shape and in pattern, and in the absence of any thick layer of cement, to those of some species of *Palæotherium*, especially Cuvier's *Palæotherium minus*, which has been formed into a separate genus, *Plagiolophus*, by Pomel. But in the fact that there are only six full-sized grinders in the lower jaw, the first premolar being very small; that the anterior grinders are as large as, or rather larger than, the posterior ones; that the

[1] Hermann von Meyer gave the name of *Anchitherium* to *A. Ezquerræ*; and in his paper on the subject he takes great pains to distinguish the latter as the type of a new genus, from Cuvier's *Palæotherium d'Orléans*. But it is precisely the *Palæotherium d'Orléans* which is the type of Christol's genus *Hipparitherium*; and thus, though *Hipparitherium* is of later date than *Anchitherium*, it seemed to me to have a sort of equitable right to recognition when this Address was written. On the whole, however, it seems most convenient to adopt *Anchitherium*.

second premolar has an anterior prolongation; and that the posterior molar of the lower jaw has, as Cuvier pointed out, a posterior lobe of much smaller size and different form, the dentition of *Anchitherium* departs from the type of the *Palæotherium*, and approaches that of the Horse.

Again, the skeleton of *Anchitherium* is extremely equine. M. Christol goes so far as to say that the description of the bones of the horse, or the ass, current in veterinary works, would fit those of *Anchitherium*. And, in a general way, this may be true enough; but there are some most important differences, which, indeed, are justly indicated by the same careful observer. Thus the ulna is complete throughout, and its shaft is not a mere rudiment, fused into one bone with the radius. There are three toes, one large in the middle and one small on each side. The femur is quite like that of a horse, and has the characteristic fossa above the external condyle. In the British Museum there is a most instructive specimen of the leg-bones, showing that the fibula was represented by the external malleolus and by a flat tongue of bone, which extends up from it on the outer side of the tibia, and is closely ankylosed with the latter bone.[1] The hind toes

[1] I am indebted to M. Gervais for a specimen which indicates that the fibula was complete, at any rate, in some cases; and for a very interesting ramus of a mandible, which shows that, as in the *Palæotheria*, the hindermost milk-molar of the lower

are three, like those of the fore leg; and the middle metatarsal bone is much less compressed from side to side than that of the horse.

In the *Hipparion*, the teeth nearly resemble those of the Horses, though the crowns of the grinders are not so long; like those of the Horses, they are abundantly coated with cement. The shaft of the ulna is reduced to a mere style, ankylosed throughout nearly its whole length with the radius, and appearing to be little more than a ridge on the surface of the latter bone until it is carefully examined. The front toes are still three, but the outer ones are more slender than in *Anchitherium*, and their hoofs smaller in proportion to that of the middle toe; they are, in fact, reduced to mere dew-claws, and do not touch the ground. In the leg, the distal end of the fibula is so completely united with the tibia that it appears to be a mere process of the latter bone, as in the Horses.

In *Equus*, finally, the crowns of the grinding-teeth become longer, and their patterns are slightly modified; the middle of the shaft of the ulna usually vanishes, and its proximal and distal ends ankylose with the radius. The phalanges of the two outer toes in each foot disappear, their metacarpal and metatarsal bones being left as the "splints."

jaw was devoid of the posterior lobe which exists in the hindermost true molar.

The *Hipparion* has large depressions on the face in front of the orbits, like those for the "larmiers" of many ruminants; but traces of these are to be seen in some of the fossil horses from the Sewalik Hills; and, as Leidy's recent researches show, they are preserved in *Anchitherium*.

When we consider these facts, and the further circumstance that the Hipparions, the remains of which have been collected in immense numbers, were subject, as M. Gaudry and others have pointed out, to a great range of variation, it appears to me impossible to resist the conclusion that the types of the *Anchitherium*, of the *Hipparion*, and of the ancient Horses constitute the lineage of the modern Horses, the *Hipparion* being the intermediate stage between the other two, and answering to B in my former illustration.

The process by which the *Anchitherium* has been converted into *Equus* is one of specialisation, or of more and more complete deviation from what might be called the average form of an ungulate mammal. In the Horses, the reduction of some parts of the limbs, together with the special modification of those which are left, is carried to a greater extent than in any other hoofed mammals. The reduction is less and the specialisation is less in the *Hipparion*, and still less in the *Anchitherium*; but yet, as compared with other mam-

mals, the reduction and specialisation of parts in the *Anchitherium* remain great.

Is it not probable then, that, just as in the Miocene epoch, we find an ancestral equine form less modified than *Equus*, so, if we go back to the Eocene epoch, we shall find some quadruped related to the *Anchitherium*, as *Hipparion* is related to *Equus*, and consequently departing less from the average form?

I think that this desideratum is very nearly, if not quite, supplied by *Plagiolophus*, remains of which occur abundantly in some parts of the Upper and Middle Eocene formations. The patterns of the grinding-teeth of *Plagiolophus* are similar to those of *Anchitherium*, and their crowns are as thinly covered with cement; but the grinders diminish in size forwards, and the last lower molar has a large hind lobe, convex outwards and concave inwards, as in *Palæotherium*. The ulna is complete and much larger than in any of the *Equidæ*, while it is more slender than in most of the true *Palæotheria*; it is fixedly united, but not ankylosed, with the radius. There are three toes in the fore limb, the outer ones being slender, but less attenuated than in the *Equidæ*. The femur is more like that of the *Palæotheria* than that of the horse, and has only a small depression above its outer condyle in the place of the great fossa which is so obvious in the *Equidæ*. The fibula is distinct, but very slender, and its distal end is

ankylosed with the tibia. There are three toes on the hind foot having similar proportions to those on the fore foot. The principal metacarpal and metatarsal bones are flatter than they are in any of the *Equidæ;* and the metacarpal bones are longer than the metatarsals, as in the *Palæotheria.*

In its general form, *Plagiolophus* resembles a very small and slender horse,[1] and is totally unlike the reluctant, pig-like creature depicted in Cuvier's restoration of his *Palæotherium minus* in the "Ossemens Fossiles."

It would be hazardous to say that *Plagiolophus* is the exact radical form of the Equine quadrupeds; but I do not think there can be any reasonable doubt that the latter animals have resulted from the modification of some quadruped similar to *Plagiolophus.*

We have thus arrived at the Middle Eocene formation, and yet have traced back the Horses only to a three-toed stock; but these three-toed forms, no less than the Equine quadrupeds themselves, present rudiments of the two other toes which appertain to what I have termed the "average" quadruped. If the expectation raised by the splints of the Horses that, in some ancestor of the Horses, these splints would be found to be complete digits, has been verified, we are fur-

[1] Such, at least, is the conclusion suggested by the proportions of the skeleton figured by Cuvier and De Blainville; but perhaps something between a Horse and an Agouti would be nearest the mark.

nished with very strong reasons for looking for a no less complete verification of the expectation that the three-toed *Plagiolophus*-like "avus" of the horse must have had a five-toed "atavus" at some earlier period.

No such five-toed "atavus," however, has yet made its appearance among the few middle and older Eocene *Mammalia* which are known.

Another series of closely affiliated forms, though the evidence they afford is perhaps less complete than that of the Equine series, is presented to us by the *Dichobune* of the Eocene epoch, the *Cainotherium* of the Miocene, and the *Tragulidæ*, or so-called "Musk-deer," of the present day.

The *Tragulidæ* have no incisors in the upper jaw, and only six grinding-teeth on each side of each jaw; while the canine is moved up to the outer incisor, and there is a diastema in the lower jaw. There are four complete toes on the hind foot, but the middle metatarsals usually become, sooner or later, ankylosed into a cannon bone. The navicular and the cuboid unite, and the distal end of the fibula is ankylosed with the tibia.

In *Cainotherium* and *Dichobune* the upper incisors are fully developed. There are seven grinders; the teeth form a continuous series without a diastema. The metatarsals, the navicular and cuboid, and the distal end of the fibula, remain free. In the *Cainotherium*, also, the second

metacarpal is developed, but is much shorter than the third, while the fifth is absent or rudimentary. In this respect it resembles *Anoplotherium secundarium*. This circumstance, and the peculiar pattern of the upper molars in *Cainotherium*, lead me to hesitate in considering it as the actual ancestor of the modern *Tragulidæ*. If *Dichobune* has a fore-toed fore foot (though I am inclined to suspect that it resembles *Cainotherium*), it will be a better representative of the oldest forms of the Traguline series; but *Dichobune* occurs in the Middle Eocene, and is, in fact, the oldest known artiodactyle mammal. Where, then, must we look for its five-toed ancestor?

If we follow down other lines of recent and tertiary *Ungulata*, the same question presents itself. The Pigs are traceable back through the Miocene epoch to the Upper Eocene, where they appear in the two well-marked forms of *Hyopopotamus* and *Chœropotamus*; but *Hyopotamus* appears to have had only two toes.

Again, all the great groups of the Ruminants, the *Bovidæ*, *Antilopidæ*, *Camelopardalidæ*, and *Cervidæ*, are represented in the Miocene epoch, and so are the Camels. The Upper Eocene *Anoplotherium*, which is intercalary between the Pigs and the *Tragulidæ*, has only two, or, at most, three toes. Among the scanty mammals of the Lower Eocene formation we have the perissodactyle *Ungulata* represented by *Coryphodon*,

Hyracotherium, and *Pliolophus*. Suppose for a moment, for the sake of following out the argument, that *Pliolophus* represents the primary stock of the Perissodactyles, and *Dichobune* that of the Artiodactyles (though I am far from saying that such is the case), then we find, in the earliest fauna of the Eocene epoch to which our investigations carry us, the two divisions of the *Ungulata* completely differentiated, and no trace of any common stock of both, or of five-toed predecessors to either. With the case of the Horses before us, justifying a belief in the production of new animal forms by modification of old ones, I see no escape from the necessity of seeking for these ancestors of the *Ungulata* beyond the limits of the Tertiary formations.

I could as soon admit special creation, at once, as suppose that the Perissodactyles and Artiodactyles had no five-toed ancestors. And when we consider how large a portion of the Tertiary period elapsed before *Anchitherium* was converted into *Equus*, it is difficult to escape the conclusion that a large proportion of time anterior to the Tertiary period must have been expended in converting the common stock of the *Ungulata* into Perissodactyles and Artiodactyles.

The same moral is inculcated by the study of every other order of Tertiary monodelphous *Mammalia*. Each of these orders is represented in the Miocene epoch: the Eocene formation, as

I have already said, contains *Cheiroptera, Insectivora, Rodentia, Ungulata, Carnivora,* and *Cetacea.* But the *Cheiroptera* are extreme modifications of the *Insectivora,* just as the *Cetacea* are extreme modifications of the Carnivorous type; and therefore it is to my mind incredible that monodelphous *Insectivora* and *Carnivora* should not have been abundantly developed, along with *Ungulata,* in the Mesozoic epoch. But if this be the case, how much further back must we go to find the common stock of the monodelphous *Mammalia?* As to the *Didelphia,* if we may trust the evidence which seems to be afforded by their very scanty remains, a Hypsiprymnoid form existed at the epoch of the Trias, contemporaneously with a Carnivorous form. At the epoch of the Trias, therefore, the *Marsupialia* must have already existed long enough to have become differentiated into carnivorous and herbivorous forms. But the *Monotremata* are lower forms than the *Didelphia* which last are intercalary between the *Ornithodelphia* and the *Monodelphia.* To what point of the Palæozoic epoch, then, must we, upon any rational estimate, relegate the origin of the *Monotremata?*

The investigation of the occurrence of the classes and of the orders of the *Sauropsida* in time points in exactly the same direction. If, as there is great reason to believe, true Birds existed in the Triassic epoch, the ornithoscelidous forms by

which Reptiles passed into Birds must have preceded them. In fact there is, even at present, considerable ground for suspecting the existence of *Dinosauria* in the Permian formations; but, in that case, lizards must be of still earlier date. And if the very small differences which are observable between the *Crocodilia* of the older Mesozoic formations and those of the present day furnish any sort of approximation towards an estimate of the average rate of change among the *Sauropsida*, it is almost appalling to reflect how far back in Palæozoic times we must go, before we can hope to arrive at that common stock from which the *Crocodilia*, *Lacertilia*, *Ornithoscelida*, and *Plesiosauria*, which had attained so great a development in the Triassic epoch, must have been derived.

The *Amphibia* and *Pisces* tell the same story. There is not a single class of vertebrated animals which, when it first appears, is represented by analogues of the lowest known members of the same class. Therefore, if there is any truth in the doctrine of evolution, every class must be vastly older than the first record of its appearance upon the surface of the globe. But if considerations of this kind compel us to place the origin of vertebrated animals at a period sufficiently distant from the Upper Silurian, in which the first Elasmobranchs and Ganoids occur, to allow of the evolution of such fishes as these from a Vertebrate

as simple as the *Amphioxus*, I can only repeat that it is appalling to speculate upon the extent to which that origin must have preceded the epoch of the first recorded appearance of vertebrate life.

Such is the further commentary which I have to offer upon the statement of the chief results of palæontology which I formerly ventured to lay before you.

But the growth of knowledge in the interval makes me conscious of an omission of considerable moment in that statement, inasmuch as it contains no reference to the bearings of palæontology upon the theory of the distribution of life; nor takes note of the remarkable manner in which the facts of distribution, in present and past times, accord with the doctrine of evolution, especially in regard to land animals.

That connection between palæontology and geology and the present distribution of terrestrial animals, which so strikingly impressed Mr. Darwin, thirty years ago, as to lead him to speak of a "law of succession of types," and of the wonderful relationship on the same continent between the dead and the living, has recently received much elucidation from the researches of Gaudry, of Rütimeyer, of Leidy, and of Alphonse Milne-Edwards, taken in connection with the earlier labours of our lamented colleague Falconer; and

it has been instructively discussed in the thoughtful and ingenious work of Mr. Andrew Murray "On the Geographical Distribution of Mammals."[1]

I propose to lay before you, as briefly as I can, the ideas to which a long consideration of the subject has given rise in my mind.

If the doctrine of evolution is sound, one of its immediate consequences clearly is, that the present distribution of life upon the globe is the product of two factors, the one being the distribution which obtained in the immediately preceding epoch, and the other the character and the extent of the changes which have taken place in physical geography between the one epoch and the other; or, to put the matter in another way, the Fauna and Flora of any given area, in any given epoch, can consist only of such forms of life as are directly descended from those which constituted the Fauna and Flora of the same area in the immediately preceding epoch, unless the physical geography (under which I include climatal conditions) of the area has been so altered as to give rise to immigration of living forms from some other area.

The evolutionist, therefore, is bound to grapple

[1] The paper "On the Form and Distribution of the Land-tracts during the Secondary and Tertiary Periods respectively; and on the Effect upon Animal Life which great Changes in Geographical Configuration have probably produced," by Mr. Searles V. Wood, jun., which was published in the *Philosophical Magazine*, in 1862, was unknown to me when this Address was written. It is well worthy of the most careful study

with the following problem whenever it is clearly put before him:—Here are the Faunæ of the same area during successive epochs. Show good cause for believing either that these Faunæ have been derived from one another by gradual modification, or that the Faunæ have reached the area in question by migration from some area in which they have undergone their development.

I propose to attempt to deal with this problem, so far as it is exemplified by the distribution of the terrestrial *Vertebrata*, and I shall endeavour to show you that it is capable of solution in a sense entirely favourable to the doctrine of evolution.

I have elsewhere[1] stated at length the reasons which lead me to recognise four primary distributional provinces for the terrestrial *Vertebrata* in the present world, namely,—first, the *Novozelanian*, or New-Zealand province; secondly, the *Australian* province, including Australia, Tasmania, and the Negrito Islands; thirdly, *Austro-Columbia*, or South America *plus* North America as far as Mexico; and fourthly, the rest of the world, or *Arctogæa*, in which province America north of Mexico constitutes one su
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Now the truth which

[1] "On the Classification an
morphæ;" *Proceedings of the Z*