Modern Progress in Vertebrate Palæontology.*

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IN a paper read to the Zoological Society in 1880, Huxley remarked that the astronomer who had determined three places of a new planet could calculate its place at any epoch, however remote; and if the law of evolution was to be depended upon, the zoologist who knew a certain length of the course of that evolution in any given case, might with equal justice reason backwards to the earlier but unknown stages. He accordingly surveyed the backboneed or vertebrate animals, both living and extinct, so far as they had then been discovered, and he defined the successive stages through which they must have passed before they ended in the higher warm-blooded quadrupeds and birds which dominate the world of life to-day. He pointed out how, in the existing world, most of the earlier stages are represented only by animals with very special adaptations to their several modes of life, which give little idea of the variety displayed by animals of the same stage in former geological periods. He concluded that a multitude of extinct groups of each stage had still to be revealed, most of those groups being short-lived adaptations to the several spheres of life which were open to them at the time, and only a small proportion on the direct line of ancestry of the existing vertebrate animals. The actual links in the chain of life from the lowest to the highest rank must, therefore, have been comparatively few.

Even in Huxley's time there were already indications of several more extinct groups than those he dealt with in his researches, but the fossils by which they were known were too fragmentary to be satisfactorily interpreted. During more recent years, those early discoveries have been supplemented by numerous collections from various parts of the world; while the methods of preparing and studying even the most unpromising fossils have in all respects greatly improved. Much progress has, therefore, been made in understanding the relationships of the extinct forms of life, and in using them for discussing the problems of organic evolution. The vertebrates, especially, have proved remarkably interesting.

The earliest forerunners of the vertebrate animals (the Hypichthyes of Huxley) have not yet been found among fossils, probably because they had no hard parts capable of being preserved in ordinary circumstances in rock. They are still known only by their highly modified living representative, *Amphioxus*. Huxley's second stage, however, that of the Myzichthyes, represented by the lampreys and hag-fishes at the present day, has now been identified among fossils exactly where it might have been expected. It flourished especially in the latter part of the Silurian period, but ranged from the Ordovician to the Devonian. It included free-swimmers like the Anaspida, which have been

found well preserved in the Upper Silurian (Downtonian) rocks of southern Norway and southern Scotland. They had an external skeleton enough to show that, while they agreed with the lampreys in the single narial opening and in the pouched gills, they had less degenerate jaws and possessed incipient paired pectoral fins. They also resembled the larva of the existing lamprey in having the end of the body turned downwards into the tail fin. They were accompanied by other Myzichthyes, like the Cephalaspicians, which were bottom-dwellers and had both an external skeleton and an internal head-skeleton so well ossified that in specimens discovered in Spitsbergen, Prof. Erik A. Stensiö, of Stockholm, has been able to recognise many of their lamprey-like characters. The surviving lampreys and hag-fishes, therefore, give no idea of the variety and adaptations of the Myzichthyes in their prime, when they dominated the world of life.

The next stage, that of the Chondrichthyes, represented by the existing sharks, skates, and chimaeroids, has also lately been recognised as dominant in its proper place in the geological record. Thanks especially to the researches of Stensiö, it now seems clear that during the latest part of the Silurian period and the Devonian period, when these fishes were in the forefront of progress, they developed true bone both externally and internally. They included the free-swimming Acanthodians, which are very shark-like, but have long been puzzling because, although their skeleton does not consist of typical bone, it is of more complex structure than the hard tissue of any modern shark or skate. The Chondrichthyes also included the heavily-armoured grovelling fishes like *Coccosteus* and *Dinichthys*, which are now generally known as *Arthrodira*. Quite lately, Prof. F. Broili has described a skate-shaped fish, *Gemuendina*, from the Lower Devonian of Germany, which seems to combine the characters of an Arthrodiran with those of a skate. Also, not long ago, Prof. P. Pruvost found, in the Lower Carboniferous of Belgium, part of a peculiar shark, *Cratoselache*, which retains the remnants of the bones of an Arthrodiran in the roof of its skull.

Huxley's next stage in the evolution of the vertebrates, that of the Herpetichthyes, or fishes which gave rise to the lung-breathers as well as to the typical modern fishes, proves to be represented among fossils not precisely as he supposed it to be. The Dipnoi, which he thought were the ancestral lung-breathers, seem now to be merely an offshoot which ended in the existing *Lepidosiren*, *Protopterus*, and *Ceratodus*. The real links between the Herpetichthyes and the earliest lung-breathers or Amphibia are the osteolepid fishes, which begin just where they might be expected, in the Middle Devonian rocks.

The Amphibian stage occupied the foremost place in the world of life of the Carboniferous period, and

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Prof. D. M. S. Watson has shown that some of its representatives during this period, the early stegocephalians, are remarkable links between the osteolepid fishes and the later amphibians.

The next or Hypotherian stage, which flourished in the Permian and Triassic periods, included the ancestors of the mammals besides those of the reptiles and birds. Huxley did not recognise the former, but since 1880 the discoveries of Seeley, Watson, Haughton, and especially Broom, in South Africa, have revealed skeletons of cynodonts which can scarcely be distinguished from those of primitive mammals. In general appearance the skull always resembles that of a carnivorous mammal, and the teeth are arranged as if they were incisors, canines, premolars, and molars. The teeth also differ from those of ordinary reptiles in having scarcely any replacing teeth. Still more remarkable is the lower jaw, which consists almost entirely of the pair of dentary bones, as in a mammal, the other bones being reduced to a little cluster behind where they articulate in the reptilian way with the quadrate bone of the skull. In some of the little cynodonts which are no larger than rats (*Ictidosauria*), the quadrate bone is so small that it forms only part of the articulation for the lower jaw, the rest being formed by the squamosal bone, which extends to the whole of it in mammals. Through the cotylosaurian reptiles there are indications of every gradation between these cynodonts and the earlier amphibians, so that satisfactory links between the lowest and the highest land vertebrates will probably soon be forthcoming.

It is especially interesting to note that the nearest approach of the hypotherian stage to the next higher or prototherian stage is made by species of comparatively small size; for when undoubted Prototheria first appear later in the Jurassic rocks, scarcely any of them are larger than rats. When the first known representatives of the next higher mammalian stages of Metatheria and Eutheria follow them in the Upper Cretaceous rocks, the species are of equally small size. So far as palæontologists have experience at present, all links between the greater groups of vertebrate animals are to be found among the smallest, not the largest species.

Owing to the fragmentary nature of the fossils, little can be said about the Prototheria, which are represented in the existing world only by the monotremes of the Australian region. During the Jurassic and Cretaceous periods, they were overshadowed by the reptiles which flourished everywhere, and they seem always to have occupied a subordinate position. Very little is known also of the earliest Metatheria and Eutheria, which are represented at the present day by the marsupials and the higher (placental) mammals respectively. They appear together in the Upper Cretaceous formations of western North America, and skulls of small Eutherians have lately been found by an American expedition in corresponding rocks in Mongolia. It is clear, however, that by the beginning of the succeeding Tertiary period, which has well been named 'The Age of Mammals', the

chief groups of Eutherians were already diverging into the several lines which have eventually become more clearly separated and even again subdivided. In certain paragraphs of his classic paper of 1880, Huxley distinctly recognised these facts and briefly stated them. It is, therefore, curious that he used parallel lines instead of diverging lines to represent the hypothetical pedigrees in his "Table of the Arrangement of the Mammalia", which has accordingly been criticised with some justification.

Huxley's interest in the subject was first roused by the numerous discoveries of ancestral mammals which were being made in the 'seventies in the Tertiary land deposits of western America, and especially by his visit to Prof. O. C. Marsh in 1876, when he examined the great collection of fossils in the Museum of Yale University at New Haven. At this time, Prof. Marsh had just arranged a series of specimens to show the genealogy of the horses, beginning with little four-toed swamp animals which had low intelligence and crushing teeth, and ending in the largest one-toed, plain-roaming animals, which had a much superior brain and grinding teeth. Subsequent more elaborate collecting and research in the same rocks by Prof. H. F. Osborn and his colleagues, of New York, have shown that the gradual evolution of the horses can sometimes be followed even in the most minute characters. At the same time, they have proved that the tracing of genealogies among the fossil mammals is not so easy as was at first supposed, even when the specimens are numerous and display well-preserved important features. It now appears that in each group there is no single line of advance, but there are several lines all changing in the same direction, only with slight differences and often at different rates. These are generally assemblages adapted for somewhat different modes of life. Such parallel developments have been observed in America among the fossil rhinoceroses, camels, cats, and other groups; and they are especially evident in the extinct hoofed animals known as the Titanotheres, which have lately been described by Prof. H. F. Osborn in the most exhaustive treatise ever devoted to a group of fossil vertebrates. There can, indeed, no longer be any doubt that each great group starts its career in geological time with certain innate potentialities which we do not understand, but which compel all its members, however varied may be their respective adaptations and modes of life, to follow the same course to the end.

In the Old World, we have had fewer opportunities of following the evolution of the Eutherian mammals, because the fossil record has so far proved much more incomplete. Among achievements during this century, however, must be specially mentioned the discovery by the late Dr. Charles W. Andrews of the pedigree of the elephants. Even in this case, we now realise that some remarkable changes occurred independently in more than one line. Among the later elephants, at any rate, there must have been several parallel series evolving in the same direction.

The Old World, nevertheless, has its compensations, for here we are able to study the most fascinat-

ing problem of all among mammals, the ancestry of man himself. There can now be no doubt that the man-like apes have always been restricted to the Old World, and that the ancestors of man must be sought among their ancestors. Hitherto, we have not made much progress, but the few discoveries that have rewarded our efforts during the present century are decidedly encouraging. In Huxley's time, the only fossil man known which exhibited more resemblances to the ape than any existing man, was that of the race first met with in 1856 in a cave in the Neanderthal, near Düsseldorf, Germany. His skull resembled that of the apes in its great bony brow-ridges; and his lower jaw lacked the usual prominence at the bottom of the bony chin. Among subsequent discoveries, the fragment of skull of *Pithecanthropus* from Java has still more prominent brow-ridges; and a human lower jaw from Heidelberg has a still more ape-like bony chin. On the other hand, the equally ancient skull of *Eoanthropus* from Piltdown, Sussex, has a good forehead without brow-ridges, and it approaches apes chiefly in its remarkable lower jaw and teeth. Now we welcome the recent discoveries of skulls and teeth of another fossil man, *Sinanthropus*, which have been made in a cave not far from Peking, in China. These fossils date back to a geological period at least as remote as those of *Pithecanthropus*, *Eoanthropus*, and the Heidelberg man, and it is not impossible that they are more ancient. They are, therefore, of extreme interest, and Dr. Davidson Black's preliminary descriptions and beautiful photographs of them show that they are specially important as displaying in combination several characters which in previous specimens have been separate and distinctive. In top view, for example, the skull of *Sinanthropus* looks astonishingly like that of *Pithecanthropus*, with the same bony brow-ridges; but the frontal region and parietal bosses are more tumid, and the bone is much thicker. The brain-case is as thick as that of *Eoanthropus*, and the bone has the remarkably fine spongy texture which has previously been observed only in the Piltdown fossil. The skull of *Sinanthropus* is also low and squat, with the same broad base and peculiarly-shaped occiput as in *Eoanthropus*. It also has the modern-looking deep sockets for the articulation of the lower jaw. The lower jaw and teeth of *Sinanthropus*, however, are more like those of Heidelberg man. This combination is indeed curious, and each new discovery makes it more clear that modern man is the sole and successful survivor of many and very varied former approaches to the unique position which he now holds.

In conclusion, the question arises as to whether such modern advances as have been described here, in the study of fossil vertebrate animals, are definitely leading to a better understanding of the general principles of our science. We may reply that the progress already achieved has, indeed, been helpful in this respect, and that it is now much easier to predict lineages and the course of discovery than it was in 1880, when Huxley ventured on his pioneer essay. We have made distinct progress in

correlating changes in the world of life with alterations in surrounding conditions, and we can often trace gradual improvement in adaptation to controlling circumstances.

It seems possible to recognise now even that the few fundamental advances in the evolution of the vertebrates have all coincided with widely spread "revolutions of the globe", to adopt Cuvier's old expression, which we may now use in a new sense. The passage of the Myzichthyes into the Chondrichthyes seems to have occurred when fishes first ventured from the shallows into the open ocean. The Herpetichthyes probably began in adaptation to the conditions of the fresh-water lakes, in the deposits of which we first find them. During the Devonian period, when this adaptation was complete, the rocks show that there was widely-spread desiccation in many parts of the world. Conditions were, therefore, favourable for the origin of the amphibia, which seem to have appeared at about this time. In the Permo-Triassic period there were again most extensive deserts, and the speculation has been hazarded that the reptiles, which had then become established, were stimulated to activity and evolution by the need for long journeys in search of food. Some of the earliest reptiles, or Hypotheria, passed into the Prototherian mammals when genial conditions were advancing. The Metatherian and Eutherian mammals first began to spread and take the place of the vanished dominant reptiles at the end of the Cretaceous period, when there were world disturbances in mountain building and a cooling of the climate in large areas of the northern hemisphere. Finally, man emerged from the ape grade probably in the northern hemisphere during the hard circumstances at the beginning of the Great Ice Age in the Pleistocene period.

Direct competition between the representatives of one stage and the next seems rarely to have happened. The giant land reptiles, for example, which dominated the world during the Jurassic and Cretaceous periods, can scarcely have been exterminated by the competition of the mammals, which were all very small and scarcely came in contact with them. The mammals spread and flourished only when the lands had become practically vacant; and long after the reptiles had disappeared, even so late as the Lower Eocene period, there were still no land animals of any kind larger than a pig. Similarly, the great sea reptiles which lived until the end of the Cretaceous period, were not exterminated by the whales which eventually took their place. We now know that the whales originated only after the ichthyosaurs, plesiosaurs, and mosasaurs had vanished, and that even the comparatively small ancestors of the whales never entered into competition with these forerunners in their sphere in the oceans.

It is, indeed, probable that the procession of life which we observe has depended as much on the influence of surrounding conditions as on the inherent characters and tendencies of the various groups of organisms themselves. For a further understanding of the subject, therefore, geologists and biologists must still continue to co-operate.