









ON THE ANIMALS WHICH ARE MOST NEARLY INTERMEDIATE BETWEEN BIRDS AND REPTILES.\*

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THOSE who hold the doctrine of Evolution (and I am one of them) conceive that there are grounds for believing that the world, with all that is in it and on it, did not come into existence in the condition in which we now see it, nor in anything approaching that condition. On the contrary, they hold that the present conformation and composition of the earth's crust, the distribution of land and water, and the infinitely diversified forms of animals and plants which constitute the present population of the globe, are merely the final terms in an immense series of changes which have been brought about, in the course of immeasurable time, by the operation of causes more or less similar to those which are at work at the present day.

Perhaps this doctrine of Evolution is not maintained consciously and in its logical integrity by a very great number of persons.† But many hold particular applications of it without committing themselves to the whole; and many, on the other hand, favour the general doctrine without giving an absolute assent to its particular applications. Thus, one who adopts the nebular hypothesis in Astronomy, or is a Uniformitarian in Geology, or a Darwinian in Biology, is, so far, an adherent of the doctrine of Evolution. And, as I can testify from personal experience, it is possible to have a complete faith in the general doctrine of Evolution and yet to hesitate in accepting the Nebular, or the Uniformitarian, or the Darwinian hypotheses in all their integrity and fulness. For many of the objections

\* A Lecture delivered before the Royal Institution of Great Britain on February 7, 1868.

† The only complete and systematic statement of the doctrine with which I am acquainted is that contained in Mr. Herbert Spencer's "System of Philosophy;" a work which should be carefully studied by all who desire to know whither scientific thought is tending. The volumes at present published are entitled, "First Principles," and "Principles of Biology."

which are brought against these various hypotheses affect them only, and even if they be valid, leave the general doctrine of Evolution untouched.

On the other hand, it must be admitted that some arguments which are adduced against particular forms of the doctrine of Evolution, would very seriously affect the whole doctrine if they were proof against refutation. For example, there is an objection which I see constantly and confidently urged against Mr. Darwin's views, but which really strikes at the heart of the whole doctrine of Evolution, so far as it is applied to the organic world. It is admitted on all sides that existing animals and plants are marked out by natural intervals into sundry very distinct groups:—Insects are widely different from Fish—Fish from Reptiles—Reptiles from Mammals—and so on. And out of this fact arises the very pertinent objection, How is it, if all animals have proceeded by gradual modification from a common stock, that these great gaps exist? We, who believe in Evolution, reply, that these gaps were once non-existent; that the connecting forms existed in previous epochs of the world's history, but that they have died out.

Naturally enough then, we are asked to produce these extinct forms of life. Among the innumerable fossils of all ages which exist, we are asked to point to those which constitute such connecting forms. Our reply to this request is, in most cases, an admission that such forms are not forthcoming, and we account for this failure of the needful evidence by the known imperfection of the geological record. We say that the series of formations with which we are acquainted is but a small fraction of those which have existed, and that between those which we know there are great breaks and gaps. I believe that these excuses have very great force; but I cannot smother the uncomfortable feeling that they are excuses. If a landed proprietor is asked to produce the title-deeds of his estate, and is obliged to reply that some of them were destroyed in a fire a century ago, that some were carried off by a dishonest attorney, and that the rest are in a safe somewhere, but that he really cannot lay his hands upon them; he cannot, I think, feel pleasantly secure, though all his allegations may be correct, and his ownership indisputable. But a doctrine is a scientific estate, too often the Philosopher's only estate, and the holder must always be able to produce his title-deeds, in the way of direct evidence, or take the penalty of that peculiar discomfort to which I have referred. You will not be surprised, therefore, if I take this opportunity of pointing out that the objection to the doctrine of Evolution, drawn from the supposed absence of intermediate forms in the fossil state, certainly does not hold good in all cases. In short, if I cannot produce the complete title-deeds of the doctrine of

animal Evolution, I am able to show a considerable piece of parchment evidently belonging to them.

To superficial observation no two groups of beings can appear to be more entirely dissimilar than Reptiles and Birds. Placed side by side, a Humming-bird and a Tortoise, an Ostrich and a Crocodile, offer the strongest contrast, and a Stork seems to have little but animality in common with the Snake it swallows. Careful investigation has shown, indeed, that these obvious differences are of a much more superficial character than might have been suspected, and that Reptiles and Birds do really agree much more closely than Birds with Mammals, or Reptiles with Amphibians. But still, "though not as wide as a church-door or as deep as a well," the gap between the two groups, in the present world, is considerable enough.

Without attempting to plunge into the depths of anatomy, and confining myself to that osseous system to which those who desire to compare extinct with living animals are almost entirely restricted, I may mention the following as the most important differences between all the Birds and Reptiles which at present exist.

1. The pinion of a Bird, which answers to the hand of a man or to the forepaw of a Reptile, contains neither more nor fewer than three fingers. These answer to the thumb and the two succeeding fingers in man, and have their metacarpals connected together by firm bony union, or, in other words, are ankylosed. Claws are developed upon the ends of at most two of the three fingers (that answering to the thumb and the next), and are sometimes entirely absent (Plate XXVII. fig. 2). No Reptile with well-developed forelimbs has so few as three fingers; nor are the metacarpal bones of these ever united together; nor do they (Plate XXVII. fig. 1) present fewer than three claws at their terminations (with the exception of the marine *chelonia*).

2. The breast-bone of a Bird becomes converted into a membrane-bone, and ossification commences in it from at least two centres. The breast-bone of no Reptile becomes converted into membrane-bone, nor does it ever ossify from several distinct centres.

3. A considerable number of caudal and lumbar, or dorsal, vertebræ unite together with the proper sacral vertebræ of a Bird to form its "sacrum." In Reptiles the same region of the spine is constituted by the one or two sacral vertebræ.

4. In Birds the haunch-bone (ilium) extends far in front of, as well as behind, the acetabulum; the ischia and pubes are directed backwards, almost parallel with it and with one another; and the ischia do not unite in the ventral middle line of the body (Plate XXVII. fig. 4). In Reptiles, on the contrary, the

haunch-bone is not greatly produced in front of the acetabulum ; and the axes of the ischia and pubes diverge and lie more or less at right angles to that of the ilium. The ischia always unite in the middle ventral line of the body (Plate XXVII. fig. 3).

5. In all Birds the axis of the thigh-bone lies nearly parallel with the median plane of the body (as in ordinary *Mammalia*) in the natural position of the leg. In Reptiles it stands out at a more or less open angle with the median plane.

6. In Birds one half of the tarsus is inseparably united with the tibia, the other half with the metatarsal bone of the foot. (Plate XXVII. fig. 6). This is not the case in Reptiles (Plate XXVII. fig. 5).

7. Birds never have more than four toes, the fifth being always absent. The metatarsal of the hallux, or great toe, is always short and incomplete above.\* The other metatarsals are ankylosed together, and unite with one half of the tarsus, so as to form a single bone, which is called the *tarsometatarsus* (Plate XXVII. fig. 6). Reptiles with completely developed hind-limbs have at fewest four toes, the metatarsals of which are all complete and distinct from one another (Plate XXVII. fig. 5).

Although all existing Birds differ thus definitely from existing Reptiles, one comparatively small section comes nearer Reptiles than the others. These are the *Ratitæ*, or Struthious birds, comprising the Ostrich, Rhea, Emeu, Cassowary, *Apteryx*, and the but recently extinct (if they be really extinct) birds of New Zealand, the *Dinornithidæ*, which attained gigantic dimensions. All these birds are remarkable for the small size of their wings, the absence of a crest or keel upon the breastbone, and of a complete furcula ; in many cases, for the late union of the bones of the pinion, the foot, and the skull. In this last character, in the form of the sternum, of the shoulder-girdle, and in some peculiarities of the skull, these birds are more reptilian than the rest ; but the total amount of approximation to the reptilian type is but small, and the gap between Reptiles and Birds is but very slightly narrowed by their existence.

How far can this gap be filled up by a reference to the records of the life of past ages? This question resolves itself into two:—

1. Are any fossil Birds more reptilian than any of those now living?

2. Are any fossil Reptiles more bird-like than living reptiles? And I shall endeavour to show that both these questions must be answered in the affirmative.

\* It is almost always free—the Frigate bird presenting the only example of its ankylosis with the rest with which I am acquainted.



It is very instructive to note by how mere a chance it is we happen to know that a fossil bird, more reptilian in some respects than any now living, once existed. Bones of birds have been obtained from rocks of very various dates in the Tertiary series without revealing any forms but such as would range themselves among existing families. A few years ago the great Mesozoic formations had yielded only the few fragmentary ornitholites which have been discovered in the Cambridge greensand, and which are insufficient for the complete determination of the affinities of the bird to which they belonged. However, the very fine calcareous mud of the ancient oolitic seabottom which has now hardened into the famous lithographic slate of Solenhofen, and has preserved innumerable delicate organisms of the existence of which we should otherwise have been, in all probability, totally ignorant, in 1861 revealed the impression of a feather to the famous palæontologist, Herman von Meyer. Von Meyer named the unknown bird to which this feather belonged *Archæopteryx lithographica*, and in the same year, the independent discovery by Dr. Häberlein of the precious skeleton of the *Archæopteryx* itself, which now adorns the British Museum,\* demonstrated the chief characters of the very early bird thus named. But it must be remembered that this feather and this imperfect skeleton are the sole remains of birds which have yet been obtained in all that great series of formations known as Wealden and Oolite, which partly lie above and partly correspond with, the Solenhofen slates. Some palæontologists may be forced by a sense of consistency to declare that the class of birds was created in the sole person of *Archæopteryx* during the deposition of the Solenhofen slates; that they disappeared during the Wealden, to be re-created in the Greensand; and that they vanished once more during the Cretaceous epoch and were regenerated in the Tertiaries; but I incline to the hypothesis that many birds beside *Archæopteryx* existed throughout all this period of time, and that we know nothing about them, simply because we do not happen to have hit upon those deposits in which their remains are preserved.

Now, what is this *Archæopteryx* like? Unfortunately, the skull is lost, but the leg and foot, the pelvis, the shoulder-girdle, and the feathers, so far as their structure can be made out, are completely those of existing ordinary birds. On the other hand, the tail is very long, and more like that of a reptile than that of a bird in this respect. Two digits of the manus have curved claws, much stronger than those of any existing bird; and, to all appearance, the metacarpal bones are quite free and

\* The fossil has been described by Professor Owen in the "Philosophical Transactions" for 1863.

disunited. Thus it is a matter of fact that, in certain particulars, the oldest known bird does exhibit a closer approximation to reptilian structure than any modern bird.

Are any fossil reptiles more bird-like than those which now exist? As in the case of birds, the Tertiary formations yield no trace of reptiles which depart from the type of the existing groups. But, otherwise than is true of birds, the newest of the Mesozoic formations, the Chalk, makes us acquainted with reptiles, which, at first sight, seem to approach birds in a very marked manner. These are those flying reptiles, the Pterodactyles, which resemble the great majority of birds in the presence of air-cavities in their bones, in the wonderfully bird-like aspect of their coracoid and scapula, and in their broad sternum with its median crest. Furthermore, in some of the Pterodactyles, the premaxillæ and the symphyseal part of the mandibles were prolonged into beaks, which appear to have been sheathed in horn, while the rest of each jaw was armed with teeth. But horn-sheathed beaks are found in living chelonian reptiles as well as in birds; the structure of the scapulocoracoid arch and of the sternum, and the pneumaticity of the bones, vary greatly among birds themselves; and these characters of the Pterodactyles may be merely adaptive modifications. On the other hand, the manus has four free digits, the three inner of which are strongly clawed, while the fourth is enormously prolonged, in total contrast to the abortion of the corresponding digit in birds. The pelvis is as wholly unlike that of birds as are the hind-limb and foot.

Thus it appears that Pterodactyles, among Reptiles, approach birds much as Bats, among Mammals, may be said to do so. They are a sort of reptilian Bats\* rather than links between Reptiles and Birds, and it is precisely in those organs, the manus and the pes, which, in birds, are the most characteristically ornithic, that they depart most widely from the ornithic type. Clearly, then, the passage from Reptiles to Birds is not from the flying Reptile to the flying Bird. Let us try another line. I have already observed that, in the existing world, the nearest approximation to Reptiles is presented by certain land Birds, the Ostriches and their allies, all of which are devoid of the power of flight by reason of the small relative size of their fore limbs and of the character of their feathers. Can we find any extinct Reptiles which approached these flightless birds, not merely in the weakness of their fore limbs, but in other and more important characters? I imagine that we can, if we cast our eyes in what, at first sight, seems to be a most unlikely direction.

\* It will be understood that I do not suggest any direct affinity between Pterodactyles and Bats.



The *Dinosauria*, a group of extinct reptiles, containing the genera *Iguanodon*, *Hadrosaurus*, *Megalosaurus*, *Poikilopleuron*, *Scelidosaurus*, *Plateosaurus*, &c., which occur throughout the whole series of the Mesozoic rocks, and are, for the most part, of gigantic size, appear to me to furnish the required conditions. In none of these animals is the skull,\* or the cervical region of the vertebral column, completely known, while the sternum and the manus have not yet been obtained in any of the genera. In none has any trace of a clavicle been observed. With regard to the characters which have been positively determined, it has been ascertained, that: 1. From four to six vertebræ enter into the composition of the sacrum, and become connected with the ilia in a manner which is partly ornithic, partly reptilian. 2. The ilia are prolonged forwards in front of the acetabulum as well as behind it, and the resemblance to the bird's ilium thus produced is greatly increased by the widely arched form of the acetabular margin of the bone, and the extensive perforation of the floor of the acetabulum (Plate XXVIII. fig. 3, *Il.*). 3. The other two components of the *os innominatum* have not been observed actually in place; indeed, only one of them is known at all, but that one is exceedingly remarkable from its strongly ornithic character (Plate XXVIII. fig. 3, *Is.*). It is the bone which has been called "clavicle" in *Megalosaurus* and *Iguanodon* by Cuvier and his successors, though the sagacious Buckland had hinted its real nature.† But these bones are not in the least like the clavicles of any animal which possesses a clavicle, while they are extremely similar to the ischia of such a bird as an ostrich (Plate XXVIII. fig. 1. *Is.*); and in the only instance in which they have been found in tolerably undisturbed relation with other parts of the skeleton, namely, in the Maidstone *Iguanodon*, they lie, one upon each side of the body, close to the ilia. I hold it to be certain that these bones belong to the pelvis, and not to the shoulder-girdle, and I think it most probable that they are ischia; but I do not deny that they may be pubes. 4. The head of the femur is set-on at right angles to the shaft of the bone, so that the axis of the thigh-bone must have been parallel with the middle vertical plane of the body, as in birds. 5. The posterior surface of the external condyle of the femur presents a strong crest, which passes between the heads of the fibula and the tibia as in birds. There is only a rudiment of this structure in other reptiles. 6.

\* The cranium of *Scelidosaurus* is most completely preserved, but lacks the extremity of the snout.

† The so-called "coracoid" of *Megalosaurus* is the ilium. I am indebted to Professor Phillips, and to the splendid collection of Megalosaurian remains which he has formed at Oxford, for most important evidence touching this reptile.



The tibia has a great anterior or "procnemial" crest, convex on the inner, and concave on the outer, side. Nothing comparable to this exists in other reptiles, but a correspondingly developed crest exists in the great majority of birds, especially such as have great walking or swimming powers. 7. The lower extremity of the fibula is much smaller than the other; it is, proportionally, a more slender bone than in other reptiles. In birds the distal end of the fibula thins away to a point, and it is a still more slender bone. 8. *Scelidosaurus* has four complete toes, but there is a rudiment of a fifth metatarsal. The third or middle toe is the largest, and the metatarsal of the hallux is much smaller at its proximal than at its distal end. *Iguanodon* has three large toes, of which the middle is the longest. The slender proximal end of a first metatarsal has been found adherent to the inner face of the second, so that if the hallux was completely developed it was probably very small. No rudiment of the outer toe has been observed (Plate XXVIII. fig. 7). It is clear, from the manner in which the three principal metatarsals articulate together, that they were very intimately and firmly united, and that a sufficient base for the support of the body was afforded by the spreading out of the phalangeal regions of the toes.

From the great difference in size between the fore and hind limbs, Mantell, and more recently Leidy, have concluded that the *Dinosauria* (at least, *Iguanodon* and *Hadrosaurus*) may have supported themselves, for a longer or shorter period, upon their hind legs. But the discovery made in the Weald, by Mr. Beckles, of pairs of large three-toed footprints, of such a size and at such a distance apart that it is difficult to believe they can have been made by anything but an *Iguanodon*, lead to the supposition that this vast reptile, and perhaps others of its family, must have walked, temporarily or permanently, upon its hind legs. However this may be, there can be no doubt that the hind quarters of the *Dinosauria* wonderfully approached those of birds in their general structure, and therefore that these extinct Reptiles were more closely allied to birds than any which now live.

But a single specimen, obtained from those Solenhofen slates, to the accident of whose existence and usefulness in the arts palæontology is so much indebted, affords a still nearer approximation to the "missing link" between reptiles and birds. This is the singular reptile which has been described and named *Compsognathus longipes* by the late Andreas Wagner, and some of the more recondite ornithic affinities of which have been since pointed out by Gegenbaur (Plate XXVIII. fig. 2). Notwithstanding its small size (it was not much more than two feet in length), this reptile must, I think, be placed among, or



these tracks reveal is, that, at the commencement of the Mesozoic epoch, bipedal animals existed which had the feet of birds, and walked in the same erect or semi-erect fashion. These bipeds were either birds or reptiles, or more probably both; and it can hardly be doubted that a lithographic slate of Triassic age would yield birds so much more reptilian than *Archæopteryx*, and reptiles so much more ornithic than *Compsognathus*, as to obliterate completely the gap which they still leave between reptiles and birds.

But if, on tracing the forms of animal life back in time, we meet, as a matter of fact, with reptiles which depart from the general type to become bird-like, until it is by no means difficult to imagine a creature completely intermediate between *Dromæus* and *Compsognathus*, surely there is nothing very wild or illegitimate in the hypothesis that the *phylum*, or genealogical tree, of the class *Aves* has its root in the Dinosaurian reptiles; that these, passing through a series of such modifications as are exhibited in one of their phases by *Compsognathus*, have given rise to the *Ratitæ*; while the *Carinatæ* are still further modifications and differentiations of these last, attaining their highest specialisation in the existing world in the Penguins, the Cormorants, the Birds of Prey, the Parrots, and the Song-birds.

However, as many completely differentiated birds in all probability existed even in the Triassic epoch, and as we possess hardly any knowledge of the terrestrial reptiles of that period, it may be regarded as certain that we have no knowledge of the animals which linked Reptiles and Birds together historically and genetically; and that the *Dinosauria*, with *Compsognathus*, *Archæopteryx*, and the Struthious Birds, only help us to form a reasonable conception of what these intermediate forms may have been.

In conclusion, I think I have shown cause for the assertion that the facts of Palæontology, so far as Birds and Reptiles are concerned, are not opposed to the doctrine of Evolution, but, on the contrary, are quite such as that doctrine would lead us to expect; for they enable us to form a conception of the manner in which Birds may have been evolved from Reptiles, and thereby justify us in maintaining the superiority of the hypothesis, that Birds have been so originated, to all hypotheses which are devoid of an equivalent basis of fact.



## EXPLANATION OF THE PLATES.

## PLATE XXVII.

- FIGS. 1, 3, 5. The *manus*, or fore-paw; the *pelvis*; and the *pes*, or hind-foot of a crocodile.
- „ 2, 4, 6. The corresponding parts of a swan.
- „ I. II. III. IV. V. The digits, commencing with the thumb or great toe:—*cp.* the carpus; *mc.* the metacarpus; *ph.* phalanges; *Il.* the ilium; *Is.* the ischium; *Pb.* the pubis; *Am.* the acetabulum; *Ts.* the tarsus; *Mt.* the metatarsus.
- FIG. 7. Front view of the foot of *Iguanodon*. The metatarsal bones are not quite naturally articulated together. Reduced from the figure given by Professor Owen in the Palæontographical Society's publications.

## PLATE XXVIII.

- FIG. 1. The left *os innominatum* of a young ostrich.
- „ 2. *Compsognathus longipes*, reduced from the figure given by the late Professor A. Wagner in the *Abhandlungen der k. Baierischen Akademie*. *Scp.* scapula; *H.* humerus; *R.U.* radius and ulna.
- „ 3. Those parts of the skeleton of *Iguanodon* which are certainly known:—*Mn.*, the mandible, is very possibly too large; all the other bones are drawn in their true proportions, as shown by the Maidstone specimen.