2. NEW FACTS bearing on the INQUIRY concerning FORMS intermediate between BIRDS and REPTILES. By HENRY WOODWARD, Esq., F.R.S., F.G.S., British Museum. (Read November 5, 1873.)

THERE is perhaps no single point along the whole line of defences raised by the opponents of the theory of Evolution which has been more warmly contested than the question of the significance attaching to the relationship of birds to reptiles. Professor Huxley truly remarks that "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" *.

"In perfect strictness," writes the same authority †, "no doubt, it is true that birds are no more modified reptiles than reptiles are modified birds, the reptilian and ornithic types being both, in reality, somewhat different superstructures raised upon one and the same ground-plan; but it is also true that some reptiles deviate so very much less from that ground-plan than any bird does, that they might be taken to represent that which is common to both classes without any serious error."

"A lizard is not very far from being the centre of the circle, the periphery of which is occupied by *Chelonia*, *Ichthyosauria*, *Plesiosauria*, *Pterosauria*, and *Aves*" ‡.

If we consider for a moment what are the peculiarities presented by each of these divisions of the SAUROPSIDA (under which great class Prof. Huxley has proposed to unite these several orders), we shall begin to perceive that the peculiar and distinctive characters which we have hitherto assumed to be expressive of the class *Aves* are not more remarkable than many which distinguish the divisions of the *Reptilia* from one another.

On what grounds, then, are their wide differentiation insisted upon by the separatists, and their combination advocated by evolutionists? In the case of those who insist on their separation, it is urged that we have no connecting links demonstrable between these widely different forms of to-day; whilst on the other hand it has already been shown by Prof. Huxley and others that there are abundant points of anatomical structure shared even by existing *Aves* and *Reptilia*, and that many of the desiderated forms, exhibiting intermediate points of structure, have already been noticed among the recent discoveries which have rewarded the labours of the geologist and palæontologist, not only in Europe, but also in America.

Admitting generally that all existing birds differ definitely from living reptiles, "one comparatively small section, nevertheless, cer-

* Huxley's Lecture, Royal Institution, February 7th, 1868.

† Proc. Zool. Soc. Lond. 1867, p. 415.

‡ *Ibid.*

tainly does come nearer reptiles than the others. These are the *Ratite*, or Struthious birds, comprising the Ostrich, *Rhea*, Emu, Cassowary, *Apteryx*, and the but recently extinct birds of New Zealand, the *Dinornithes*, 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 breast-bone, and of a complete furcula, and, 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"*.

All the living, or recently extinct, wingless birds, however, deserve to be specially mentioned, not only on account of the more generalized type of structure which they offer, but because they present, in their distribution, one of the most interesting geographical problems to the consideration of naturalists and palæontologists.

Africa has its Ostrich†; Madagascar had its *Aepyornis*; Java and the adjacent islands of the Indian archipelago the Cassowary; Australia its Emu and extinct *Dromornis*‡; New Zealand its *Dinornis*; South America its *Rhea*; the London Clay its *Dasornis londiniensis*§. Thus, then, we have this most ancient type of wingless running birds presenting not merely the greatest range in time, but also the widest geographical distribution over the globe of any order of its class. None of these forms, however, depart in the main from the avian type, and we must seek still further for modifications of even greater import than the wingless birds present.

Is there any thing in the *Pterosauria* which affords a missing link?

If we examine that remarkable group the "flying lizards," or *Pterodactyles*, extending in time from the Lias to the Chalk, we find they exhibit many adaptive modifications of the avian type, such as the great air-cavities in the bones, and the prolongation of the præmaxillæ into beaks (which were probably sheathed in horn), although the rest of the jaw was armed with teeth. But the *manus*, with its four free digits (three armed with claws, and the fourth enormously prolonged to support the wing-membrane), the non-avian characters of the pelvis and hind limbs, all depart *most widely* from the ornithic type.

But among the various additions made to our knowledge of extinct forms, some at least may certainly be claimed as affording links

* See Huxley's Lecture, *Geol. Mag.* 1868, vol. v. p. 360.

† Formerly the geographical range of the Ostrich extended into Arabia, Persia, and part of India, within the Historic period; but it has been exterminated by the agency of man.

‡ *Dromornis australis*, Owen, *Trans. Zool. Soc.* 1873, vol. viii. part vi., and *Geol. Mag.* 1869, vol. vi. p. 383.

§ See *Trans. Zool. Soc.* 1872, vol. vii. p. 123, pl. 16. This specimen was detected and its avian characters pointed out by Mr. Davies, of the British Museum.

by which to unite more closely the SAUROPSIDA to one another as a class. Foremost of these in importance must be mentioned:—

I. The discovery of that remarkable Mesozoic type of bird, the *Archæopteryx macrura* (Owen), with its peculiar reptilian-like tail, composed of twenty free and apparently unanchylosed cylindrical vertebræ, each supporting a pair of quill-feathers, the last fifteen vertebræ having no transverse processes, and tapering gradually to the extremity.

Two of the digits of the wing (or manus) have curved claws, much stronger than those of any existing bird; and the metacarpal bones appear to be quite free and disunited.

In these particulars the *Archæopteryx* certainly does exhibit a closer approximation to reptilian structure than any modern bird*.

II. The next remarkable fossil bird to be enumerated is the *Ichthyornis dispar* (Marsh), discovered by Prof. O. C. Marsh, in 1872, in the Upper Cretaceous beds of Kansas, U.S. It possessed in both jaws well-developed teeth, which were quite numerous, and implanted in distinct sockets. The teeth were small, compressed, and pointed, and all similar in character. Those in the lower jaw number about twenty in each ramus, and are all more or less inclined backward. The series extends over the entire upper margin of the dentary bone, the front tooth being very near the extremity. The maxillary teeth appear to have been equally numerous and essentially the same as those in the mandible. The jaws were, apparently, not encased in a horny sheath. The bones of the wings and legs all conform to the true ornithic type. The vertebræ were all biconcave, the concavities at each end of the centra being distinct and nearly alike. The tail does not appear to have been preserved. The bird was about the size of a pigeon. The bones do not appear to have been pneumatic, although most of them are hollow. The species, Prof. Marsh considers, was carnivorous and probably aquatic.

A second form discovered has been named *Apatornis celer* (Marsh).

Prof. Marsh thinks it probable that *Archæopteryx* possessed teeth and biconcave vertebræ. In confirmation of the former suggestion, it may be mentioned that part of a small detached jaw with teeth was detected by Mr. John Evans, F.R.S., Sec. Geol. Soc., upon the slab containing the skeleton, and possibly may have belonged to it, although referred by Prof. Owen to the "præmaxillary bone of a fish"†.

In an article published by Mr. Evans in the 'Natural History Review' for 1865, vol. v. p. 415, he carefully and critically discusses this question; and he furthermore cites the opinion of the late illustrious Hermann von Meyer, that the teeth observable in the jaw were unlike any heretofore known from the lithographic stone, although they somewhat resembled those of *Acrosaurus*. On

* See Prof. Owen on *Archæopteryx*, Phil. Trans. 1863.

† Phil. Trans. 1863, p. 33. See also article by H. Woodward in 'Intellectual Observer,' Dec. 1862, vol. ii. p. 313, and plate; and by S. J. Mackie, 'Geologist,' 1863, vol. vi. p. 1.

the whole, however, Von Meÿer concludes that there can be little doubt the jaw really belonged to *Archæopteryx*; and he expressed his conviction that this singular feathered fossil cannot be looked upon as a bird with persistent embryonic characters, but rather as a distinct type, and perfect of its kind.

In this article Mr. Evans also gives the result of his researches in reference to a certain nodular mass having a distinctly bilobed outline which he had observed upon the slab containing the *Archæopteryx*. Mr. Evans, having prepared casts of the brain-cavity of a great number of living birds, was enabled to institute a long series of careful comparisons, and to demonstrate most satisfactorily the correctness of his determination, that the mass in question represented a cast of the anterior portion of the brain-cavity of *Archæopteryx*.

III. Prof. Owen has added to his ornithological researches another Eocene bird from the London Clay of Sheppey *, to which his attention had been drawn by Mr. W. Davies, of the British Museum, who also worked it out with his own hands.

This bird, which he has named *Odontopteryx toliapica*, is rendered remarkable by the very prominent denticulation of the alveolar margins of the jaws, to which its generic appellation refers.

The denticulations are intrinsic parts of the bone bearing them, and are of two sizes, numerous smaller denticles occupying the spaces between the larger ones, which are about half an inch apart.

When perfect the skull was probably 5 to 6 inches in length; but the anterior extremity is wanting.

Prof. Owen concludes the *Odontopteryx* to have belonged to or near the *Anatide*, and that it was web-footed and a fish-eating bird, for which its serrated jaws would admirably adapt it.

As we have not the other parts of the bird, but the skull alone, it would be presumptuous to surmise as to the presence or absence of other modifications besides the pseudo-teeth with which the jaws are armed †.

From the extreme rarity of all terrestrial animal remains preserved in a fossil state, it may justly be concluded that many more such archaic birds, having reptilian modifications, actually existed in the Mesozoic epoch, although they may possibly never be discovered by geologists.

Passing from birds to *Dinosauria*, we are able to enumerate several forms of reptilia which appear to offer points of structure tending towards the so-called "wingless birds," or those birds which are devoid of the power of flight by reason of the relatively small size of their fore limbs and the feathers which they support.

* See Quart. Journ. Geol. Soc. for November 1873, and abstract in Geol. Mag. August 1873, p. 376.

† Many living birds, and notably the *Merganser serrator*, have a denticulated mandibular border which, although connected only with the horny covering, and not with the bones of the mandibles (as in *Odontopteryx*), yet is sufficient to prove that the presence of feathers can no longer be looked upon as necessarily implying that the beak with which they were preened must have been edentulous. (John Evans, *op. cit.* p. 421.)

I. The first of these is a small and very singular reptile from the Oolite of Solenhofen, which, notwithstanding its minute size, Prof. Huxley thinks must be placed with the Dinosaurs (the *Compsognathus longipes* of Andreas Wagner), not much more than 2 feet in length, having a small head, with toothed jaws, supported on a long and slender neck. The iliac bones are prolonged in front of and behind the acetabulum; the pubes were long and slender. The bones of the fore limb are very small, and probably furnished with two clawed digits. The hind limb is very large, and disposed as in birds, the femur being shorter than the tibia. The proximal division of the tarsus is ankylosed with the tibia as in birds. The distal ends of the tarsal bones in the foot are not united with the three long and slender metatarsals, corresponding with the second, third, and fourth toes. There is only a rudimentary metatarsal to the fifth toe.

It is impossible to look at the structure of this strange reptile and to doubt that it hopped or walked in an erect or semierect position, after the manner of a bird, to which its long neck, slight head, and small anterior limbs must have given it an extraordinary resemblance*.

II. Much of the recently acquired knowledge of the huge *Dinosauria* of our own Secondary rocks has resulted from the earnest labours of Professor Phillips, bestowed upon the remarkable series of remains in the Oxford Museum.

We now know certainly that the *Megalosaurus*, that huge carnivorous lizard, perhaps 30 feet long, which ranged from the Lias to the Wealden, had strong but not massive hind limbs, and short reduced fore limbs, five ankylosed sacral vertebrae (Owen), the ilium, ischium, and pubis slender and bird-like, as in the Ostrich, the scapula and coracoid resembling those of the *Apteryx*. From all these considerations Professor Phillips agrees with Profs. Owen and Huxley in viewing the *Megalosaurus*, "not as a ground-crawler, like the alligator, but moving with free steps, chiefly, if not solely, on the hind limbs, and claiming a curious analogy, if not some degree of affinity, with the Ostrich" †.

What we have cited as regards the carnivorous *Megalosaurus* is true also of the vegetable-eating lizards of the Mesozoic rocks (*Iguanodon*, *Scelidosaurus*, &c.).

The sacrum is composed of from four to six vertebrae. The pelvic bones are bird-like in form and disposition; there is a strong crest which passes between the head of the fibula and the tibia, as in birds. The tibia has a great anterior or "procnemial" crest, not seen in other reptiles, but existing in most birds, especially the running and swimming birds. The toes are reduced in number; *Scelidosaurus* has four toes and a rudiment of a fifth; *Iguanodon* has three, with a rudimentary indication of a fourth.

There is evidence in "the manner in which the three principal metatarsals articulate together, that they were very intimately and

* Prof. Huxley's Lecture, *loc. cit.*

† 'Geology of Oxford and the Valley of the Thames,' by John Phillips, M.A., F.R.S., F.G.S., &c., 1871, p. 196.

firmly united, and that a sufficient base for the support of the body was thus afforded by the spreading out of the phalangeal regions of the toes." (Huxley, *loc. cit.*)

Mantell long since, and more recently Leidy, have concluded, from the great difference in the size between the fore and hind limbs, that *Iguanodon* and *Hadrosaurus*, as well as other *Dinosauria*, may have supported themselves for a time at least upon their hind legs. But Mr. Beckle's discovery of pairs of large three-toed foot-prints, of such a size and at such a distance apart that it is difficult to believe they have been made by any thing but *Iguanodon*, leads to the supposition that this vast reptile, and perhaps others of its family, must have walked temporarily or permanently upon its hind legs (Huxley, *loc. cit.* p. 364).

Many years since, Mr. Allan Cunningham (H. M. Botanical Collector for Kew), who accompanied the Expedition to survey the Intertropical and Western Coasts of Australia, from 1818 to 1822, under Captain Philip King, R.N., F.R.S., secured a specimen of a remarkable Frilled Lizard, which had *perched* itself upon the stem of a small decayed tree, at Careening Bay, Port Nelson*. This has been named *Chlamydosaurus Kingii*, by Dr. Gray. The stuffed specimen is preserved in the British-Museum collection in a semi-erect position, its fore feet (which are *very much smaller* than the hind feet) scarcely touching the ground at the extremities of the claws. I had the advantage (in company with my esteemed colleague, Dr. Günther, the Assistant Keeper of the zoological collections of the British Museum) to hear the remarks of an Australian resident on this lizard, which is common about the gardens in the environs of Sydney. This observer reports that the lizard in question not merely sits up occasionally, but habitually runs *upon the ground* on its *hind legs*, its fore paws not touching the earth. This statement interested me immensely; and on repeating it to Prof. Huxley, I learnt that that acute observer, Mr. Gerard Krefft, of the Sydney Museum, had noted the same peculiarity. With this upright carriage, special modifications of the sacrum and pelvic bones are necessary; and, no doubt, when a specimen is dissected, this very interesting point will be corroborated by the form and articulation of the bones. As geologists, we cannot but be interested in this peculiarly modified existing type of lizard, occurring, as it does, on the continent of Australia (which has yielded such a remarkable assemblage of Tertiary and existing Marsupialia to be critically examined and chronicled by our great anatomist, Professor Owen)—a land also remarkable for the possession of many living Mollusca of Mesozoic types on its coasts.

It is noteworthy in connexion with these observations on bipedal reptilia (existing and extinct), to find that the Solenhofen Limestone, which has yielded both the long- and short-tailed *Pterosauria*, the long-tailed Reptilian-like bird†, and the long-necked short-armed Avian lizard‡ supplies a bipedal track upon one of its slabs, which

* See King's 'Survey of Australia,' 8vo, 1827, vol. ii., Appendix, p. 424.

† *Archaeopteryx*.

‡ *Compsognathus*.

Track of Saurian from the Solenhofen Limestone (*Ichnites lithographicus*, Oppel), one fourth natural size.

reminded me at once of what *Chlamydosaurus* or *Compsognathus* might produce under favourable conditions. The slab presents a median track formed by the tail drawn along on the ground; the two hind feet with outspread toes leave their mark, whilst the fore paws just touch the ground, leaving a dot-like impression on either side of the median line (see figure). Dr. Oppel has named this track *Ichnites lithographicus**.

In calling attention to the slab, Dr. Oppel remarks that the footsteps are ranged in two parallel lines with a middle continuous impression alternately stronger and fainter. The footsteps go in pairs. It resembles no other form of track already noticed or described from this or any other formation.

Dr. Oppel thinks *Archæopteryx* might have formed such a track, although he is unable to explain the alternate deepening of the middle track.

Remembering that the tail of *Archæopteryx* is bordered all the way by feathers, it will at once be seen that it could not leave behind a clear and simple furrow, but a broad smudge composed of many lines, like that left by a flat colour-brush drawn along upon paper.

The tail of a lizard progressing by hops and supporting itself upon its hind limbs and tail, would, however, produce just such impressions, the deepening of the furrow made by the tail being caused by the depression of the tail in making each onward hop.

Viewed by the additional light which our present knowledge of the structure of the Mesozoic Dinosauria and of the existing *Chlamydosaurus*

* Paläontologische Mittheilungen aus dem Museum des Königl. Bayer. Staates von Dr. Albert Oppel. Stuttgart, 1862, tab. 39, p. 121.

affords, we need no longer be doubtful as to the origin of the many bipedal tracks which occur in the Trias and upwards.

Some are very probably the "spoor" of Struthious birds which may have existed fully as far back as the beginning of the Secondary Period; but most are, no doubt, due to the bipedal habit of our Secondary reptiles, a peculiarity still maintained by the Australian *Chlamydosaurus*.

DISCUSSION.

Mr. SEELEY thought that the footprints on the slab cited in the paper had been produced by some saurian, such as a Pterodactyle, the fore limbs of which were wider apart than its hind limbs, rather than by *Compsognathus*. If the foot-track had been due to a saurian walking on its hind legs only, he thought that the principal impressions must of necessity have been nearer together. He disputed the correctness of the term "adaptive modification" as applied to the air-cavities in bones. He was inclined to regard the Pterodactyle as more closely allied to birds than did the author of the paper. The condition of the carpus, as well as the tarsus, in these reptiles showed their ornithic affinities. He cited jerboas, kangaroos, and other forms, in which the hind legs were mainly used for progression, but in which the sacrum and other bones were not modified, as instances calculated to inspire caution in connecting the mode of progression with structure.

Mr. HULKE could not regard the tracks as those of a Pterodactyle, as the inner marks were much less distinct than the outer, and would therefore hardly be due to the hinder limbs, on which the weight would mainly fall.

Mr. BLANFORD agreed with Mr. Seeley that the mere fact of the *Chlamydosaurus* walking on its hind legs did not suffice to prove any affinity with Dinosaurians.

Mr. WOODWARD, in reply, stated that the two points on which he had mainly founded the paper were:—1st, the occurrence of footprints in the Solenhofen limestone, characteristic of a bipedal progression of some saurian, which had, moreover, used its tail from time to time to give it a forward impetus; and 2ndly, the method of walking of *Chlamydosaurus*. With regard to animals thus progressing, he was not prepared to accept the view that there was no corresponding modification in structure.