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XXXVII.—*An Epitome of the Evidence that Pterodactyles are not Reptiles, but a new Subclass of Vertebrate Animals allied to Birds* (Saurornia). By HARRY SEELEY, Esq.*

BARON CUVIER assumed that Pterodactyles were Reptiles, and as reptiles they have since been described. It was by no rigorous determination such as modern science would give that the great master assigned to the tribe of Saurians this extinct group of animals. Other authors have referred them to mammals, to reptiles, and to birds; but Cuvier, regarding the latter hypothesis as scarcely worth notice, devoted much of his demonstration to proving that they were not mammals, and much of it to assuming that therefore their structure was reptilian. Of course there is some truth in this, as there is sure to be in every conviction of Cuvier's; and facts were then more favourable to such a view than they are in the eyes of modern discovery. But the evidence on which Cuvier relied was furnished chiefly by two individuals, neither of which showed the details of structure seen in Cambridge specimens; hence it will not be surprising if the facts which suggested the reptilian hypothesis prove, on examination, to point to another conclusion.

Quoting from the new edition of the '*Ossements Fossiles*' (that of 1824), in Cuvier's own words, we shall endeavour to illustrate the results at which he arrives.

First, then, he says—"Ayant encore porté mon attention sur le petit os cylindrique marqué *g* [*i. e.* os quadratum] qui va du crâne à l'articulation des mâchoires, je me crus muni de tout ce qui étoit nécessaire pour classer ostéologiquement notre animal parmi les reptiles." The exact relations of the quadrate bone are not seen in either Cuvier's or Von Meyer's figures of *Ptero-*

* The substance of this paper was communicated to the Cambridge Philosophical Society, as part of a monograph of Pterodactyles, read March 7 and May 2 & 16, 1864.

dactylus longirostris; but in the figures of *P. crassirostris*, *P. longicollum*, and *P. Kochi* it appears to be a free bone articulated to the squamosal and petrosal region of the skull and with the lower jaw. This is the case neither with Chelonians nor Crocodiles, and is only in a certain sense found in lizards and serpents; while, on the contrary, it is characteristic of the whole class of birds. The form of the bone is certainly not more Lacertian than Avian, while its direct attachment to the bone of the brain-case finds no parallel among lizards, but is exactly paralleled in all birds.

Cuvier then goes on to say, "Ce n'étoit pas non plus un oiseau, quoiqu'il eût été rapporté aux oiseaux palmipèdes par un grand naturaliste." Which position he supports as follows:—

(1) "Un oiseau auroit des côtes plus larges, et munies chacune d'une apophyse récurrente*; son métatarse n'auroit formé qu'un seul os, et n'auroit pas été composé d'autant d'os qu'il a de doigts."

These, though they may not be characters which are those of birds, are certainly not eminently reptilian. The elongated form of the tarsals in birds is peculiar, but quite functional, as may be seen among the penguins, where, when the so-called tarso-metatarsal bone is no longer erect, it becomes much shorter, and is nearly separated into three distinct bones. And it would be premature to assert that this tarsus has no analogue in the Cretaceous *Pterodactyles*.

(2) "Son aile n'auroit eu que trois divisions après l'avant-bras, et non pas cinq comme celle-ci."

This is a difference of detail only. The creatures have wings, and they are formed on the same general plan as those of birds. Most birds have two phalanges in the long finger, though some have three. One *Pterodactyle* is described as having only two phalanges in the wing-finger, while most of them appear to have four phalanges, and others but three. But in birds the longest finger appears to be the middle one, whereas in *Pterodactyles* it is the outermost one. This adds nothing to its supposed reptilian characters.

(3) "Son bassin auroit eu une toute autre étendue, et sa queue osseuse une toute autre forme; elle seroit élargie, et non pas grêle et conique."

I am not aware of any evidence tending to show that the pelvis of *Pterodactyles* was materially different from that of some birds. And the discovery of a long-tailed bird like the

* This is shown in other specimens figured since, and in the specimen from Stonesfield, in the Oxford Museum.

Archæopteryx shows that the tail is like that of old birds, even if it presents some analogy in form to that of certain reptiles.

(4) "Il n'y auroit pas eu de dents au bec; les dents des *harles* ne tiennent qu'à l'enveloppe cornée, et non à la charpente osseuse."

This is not a reptilian character. Among reptiles some tribes have teeth, others want them; and among mammals some animals are without teeth, though they are so characteristic of the class. And therefore it seems an anomaly that birds should all be toothless. And so, without citing the supposed teeth of *Archæopteryx*, it may be affirmed that it would be no more remarkable for some birds to have teeth than it is for some mammals and reptiles to be without them.

(5) "Les vertèbres du cou auroient été plus nombreuses. Aucun oiseau n'en a moins de neuf; les palmipèdes, en particulier, en ont depuis douze jusqu'à vingt-trois, et l'on n'en voit ici que six ou tout au plus sept."

This, again, is a variation of detail such as, had it occurred among ordinary birds, would not have occasioned remark. When the variation of the neck-vertebræ ranges from twenty-three to nine, the further reduction of the number to seven becomes insignificant, and is certainly far from going to show that the animal was a reptile.

(6) "Au contraire, les vertèbres du dos l'auroient été beaucoup moins. Il semble qu'il y en ait plus de vingt, et les oiseaux en ont de sept à dix, ou tout au plus onze."

This modification is so obviously the result of small development of the pelvic bones, and hence of the small number of vertebræ in the sacrum, that it cannot be held to bear against the avian relations of Pterodactyles any more than it supports their reference to the class of reptiles.

These are Cuvier's arguments; and in them is found nothing against the ornithic affinities of the tribe, except the tarsus, and absolutely nothing to support the hypothesis that Pterodactyles are reptiles.

Further on (tome v. part 2. p. 363), speaking of the teeth, it is said—"Elles sont toutes simples, coniques, et à peu près semblables entre elles comme dans les crocodiles, les monitors, et d'autres lézards." Now the teeth of Pterodactyles are (in the skull) all, or nearly all, in the premaxillary bones, in which it is so characteristic for the teeth of animals to be merely conical and simple. Therefore it would have been difficult to imagine the teeth to have been anything but what they are, whatever the affinities of the Pterodactyle might be.

At p. 367 it is remarked—"La longueur du cou est proportionnée à celle de la tête. On y voit cinq vertèbres grandes et

prismatiques comme celles des oiseaux à long cou, et une plus petite se montre à chaque extrémité." This adds nothing to the evidence for its assumed reptilian character.

"Ce qui est le plus fait pour étonner, c'est que cette longue tête et ce long cou soient portés sur un si petit corps; les oiseaux seuls offrent de semblable proportions, et sans doute c'est, avec la longueur du grand doigt, ce qui avoit déterminé quelques naturalistes à rapporter notre animal à cette classe." Nor can this be taken as evidence that the animal was a reptile. And in many other minor matters Cuvier is careful to show how their modifications resemble those of birds; and when this is not so, birds are the only animals from which he finds them varying. And the few suggestions which are thrown out respecting affinities to lizards are upon points which are also common to birds. Thus what Cuvier did was to distinguish these animals from birds, and incidentally to show that their organization was only a modification of that of the avian class. And the legitimate inference from this would have been that their systematic place was that of a new group of birds, and not that they were reptiles.

None of the long list of writers reviewed or cited by the learned author of the 'Fauna der Vorwelt' appear to have adduced anything of importance in favour of the presumed reptilian relations of *Pterodactyles*. And what Professor Owen has incidentally stated in his descriptions would go far towards demonstrating them to be bird-allies, while he, no more than preceding or succeeding writers, has pointed out any characters which would justify the position that has been assigned to them in the reptilian class. In a case like this it may be remembered to Prof. Owen's honour that he described certain fragments of bones of *Pterodactyle* as those of birds, and never allowed that the determination was erroneous, as many maintained.

Seeing, then, that *Pterodactyles* have hitherto been placed with reptiles, on Cuvier's dictum, and on the trivial data which I have quoted that their nature might be apparent, I believe it will be readily conceded that the proofs that *Pterodactyles* are reptiles have yet to be found.

In determining and arranging the osteological remains which adorn the collections of the Woodwardian Museum, I was struck with the almost invariably ornithic characters of the bones of *Pterodactyles*, and was led to the conclusion that, as the principle of organization was avian, and the bones were nearly all avian in their modifications, the animal must have been avian. And comparative diagrams of the corresponding parts of *Pterodactyles* and birds were exhibited to prove it when, in 1864, I read a paper on the *Pterodactyle* as evidence of a new subclass

of birds, at the meeting of the British Association in Bath. And now Prof. Owen, in his 'Comparative Anatomy,' elevates the Pterodactyles to the rank of the highest group of reptiles—thus placing them between the recognized Reptilia and Aves, as I had done.

Under these circumstances I venture to submit an epitome of the evidence which led to the conclusion that Pterodactyles are a subclass of bird-allies, and have nothing whatever to unite them with the Reptilia—a result which has been chiefly worked out from Cambridge specimens, which have been almost invariably determined by comparing the articular surfaces of the bones. And thus the osteology of the group has been made out independently of comparison with the bones of other animals.

In a former paper attention was drawn to the equality in size between the fore and hind limbs of Pterodactyles; and anyone who examines the figures of the species *longirostris*, *brevirostris*, *crassirostris*, *scolopaciceps*, *longicollum*, *Meyeri*, *micronyx*, &c., will observe that the clawed phalanges of the hand are spread out like those of the foot, while the wing-finger is bent back in front, often against the metacarpal bones. The small bones of the hand are often not dissimilar to those of the foot. From these facts, and from a consideration of the joints, I find that the Pterodactyle was quadruped, and, when not flying, carried its wings folded up in front of the fore limbs. For if it were true, as the restorations and figures of Pterodactyles flying would lead us to believe, that the large wing-metacarpal was only used to support the wing, and the small metacarpals only used to support the claws by which the creature is imagined to have suspended itself like a bat, it would be impossible to believe that the force of flying so exactly corresponded to the force of suspension as to cause the large and the small metacarpals invariably to attain the same length. A correspondence of this kind in structure, as it seems to me, can only indicate a correspondence in function; and as the animal did not fly by means of its claws, the only other inference is that it walked by means of its metacarpal bones. There are plenty of instances of inequality in thickness of metacarpal and metatarsal bones where the major part of the work of running or jumping is thrown on some special bone, but there are probably no instances of inequality in length where the function is exactly the same; and hence it may be shown that it would be contrary to all considerations, both theoretical and empirical, to suppose the growth would be the same though the functions were so different as those supposed. But in birds, where the functions of the different metacarpals are not very dissimilar, one metacarpal is exceedingly short; very much less, then, could they all be expected

to correspond in length in an animal where one was used for flying and the others for clinging. But they do correspond ; and therefore I conclude that they were not used in dissimilar, but in the same function. And hence, as the only way in which they could have been equally used was in walking, it follows that the *Pterodactyle* was quadruped. This, as we shall see, is a consideration of theoretical value, as bearing on their position in the animal kingdom, and will help to show their affinity to birds in a direction which removes them far from reptiles.

It is well known that many bones of most birds are filled with air, and that, as a principle, the more the motion of the animal, the greater is the number of bones filled with air. This air is received from the air sacs, which receive it from the lungs and return it through the lungs again. Thus there is in birds a sort of supplemental lung-system, which circulates air through the body. Nothing of this sort is observed in reptiles, even the lungs with them being generally in a very rudimentary condition, while in birds the respiratory system is more perfect and complex than in any of the other Vertebrata, and, as a result, the temperature of the blood is hotter.

Now in *Pterodactyles* the bone-walls are all very thin, the bones being hollow and showing pneumatic apertures, which are large, precisely as in birds of great flight. The fact that the bones are supplied with air necessitates an elaborate system of air-sacs to furnish the supply ; and the existence of these air-sacs speaks incontestably to bronchial tubes opening on the surface of the lungs to supply them, and to the existence of lungs essentially like those of birds. But the circulation of this air through the body was seen in birds to have relation to rapid motion through the air, which necessarily would produce more rapid respiration. But rapid respiration only means more rapid oxidation of the blood, and conversion of the purple cruorine into scarlet cruorine—that is, the conversion of venous blood into arterial blood. And if venous blood is rapidly converted into arterial blood, there must be rapid circulation. Now rapid circulation cannot take place without a heart with two auricles and two ventricles ; therefore I conclude that *Pterodactyles* had the heart like that of birds and mammals : and hence it follows that they must have had hot blood. But it has been seen that the *Pterodactyles* were quadrupedal ; and hence it may fairly be concluded that they could not have moved so much through the air as birds, and therefore the stimulus to active respiration could not have been so great ; and yet they possess to perfection the elaborate respiratory system of the most active birds ; and so it follows that their circulatory and respiratory organs were not less developed than in birds, but rather more developed.

This alone is ample evidence, were there no other, that our animals were near allies of the birds; but it will be seen that the correspondence is not limited to the general principle of organization, but extends to many of its details.

I have been able to examine fragments of several skulls from the Cambridge Greensand, one of which is of great size, and shows the interior of the front part of the skull, exhibiting the form, size, and characters of the front part of the brain. The brains of birds and reptiles are both so characteristic that there can be no doubt about the conclusion to be drawn from this evidence. In Pterodactyles the large hemispheres are extremely high, and terminate in front in well-rounded convexities, between which there is a little depression. This is most characteristically avian, and would be quite sufficient to show that the Pterodactyles ought not to be expected to have any resemblance to reptiles. I have also been able to examine three skulls of which the occipital and parietal regions are well preserved, and can confidently assert that the brain is not less developed than in birds; indeed it is only by some minor modifications of the basal region that any one could distinguish the skulls from those of ordinary birds. There is nothing in the brain to show that the Pterodactyles were not more highly organized than birds.

Although Pterodactyles were quadrupeds, they were flying quadrupeds; and it has been generally assumed that they flew by means of membranous wings, like the mammalian bats. But their wings have little in common with the mammalian wing, not being formed by prolongations of all the fingers; and *no reptile known, from recent or fossil specimens, has wings*. Therefore there only remains the birds with which the Pterodactyle wing can be compared; and with them, as will be seen, the correspondence of plan is perfect. In ordinary birds it is singularly close, but in the *Archæopteryx* it is closer. Each of these groups of animals has a well-developed humerus, and ulna and radius not very dissimilar, as was to be expected. In both, the carpals are short, small bones; in both, the metacarpals are long, slender bones: there are three in ordinary birds (one short), four in the *Archæopteryx*, and four in most known Pterodactyles. In ordinary birds, one of the fingers which these support sometimes terminates in a claw; in *Archæopteryx* two of the fingers appear to terminate in claws, while in Pterodactyles three of the fingers have claws. In birds two of the metacarpals, more or less ankylosed together (and therefore functionally one), with their phalanges, terminate the wing; but in Pterodactyles there is one large metacarpal which supports a number of long phalanges, varying to as many as four, while in birds the number is usually limited to two. Thus, however dissimilar they

may look at a glance, the wings of birds and *Pterodactyles* do not differ in kind, but only in degree. The plan is the same, but the modifications of it are different. And these divergences seem chiefly to have reference to the fact that *Pterodactyles* were quadrupeds; whence it comes that while in birds the whole limb is modified for flight, the whole limb in *Pterodactyles*, excepting one finger, is also modified for standing. And thus it happens that in birds the bones of the arm and forearm are enormously long, while in *Pterodactyles* they are comparatively short, and that, while in *Pterodactyles* the phalanges of one finger are enormously elongated to form a wing, in birds, where they have no such function, they are short.

Therefore I affirm that the fore limb of *Pterodactyles* has nothing reptilian in its mode of construction, but is essentially avian in type; and even if it should be found that the wing-finger supported a membranous wing, which there are no sufficient reasons for assuming as certain, that would rather show an approximation towards mammals than the faintest affinity with the Reptilia.

Then the form of body and proportions of its parts are worth remark in *Pterodactyles*; for they find no parallel among the Reptilia, but are very bird-like. The large, long head, tapering in front, is essentially the head of the bird in form, and probably, but for the teeth, would have been always so regarded. Although Plesiosaurs and turtles both have long necks, the proportions of the neck in *Pterodactyles* are decidedly those of a bird. The length of the limbs finds its parallel in no group of reptiles, but is characteristic of birds; and the proportions and form of the breast-bone are only to be matched among birds. Neither the length of the tail in some tribes nor its shortness in others is opposed to our knowledge of the structure in birds. Therefore it is not astonishing to find that Blumenbach considered the *Pterodactyles* to be birds, that Sömmering named the genus *Ornithocephalus*, or that Prof. Hermann placed it between the birds and mammals.

I will now briefly give some of the results of a consideration of the several bones. And here, no more than in the organization, do I find any characteristics of reptiles, or anything to make me doubt that the *Pterodactyles* were, even in the details of structure, formed essentially on the ornithic plan.

If the reader will refer to any figure of the skull of a *Pterodactyle*, and compare with it any similarly formed skull of a bird (say that of the heron), it will be found that the form and size of the region for the brain is the same in both, and that all the cavities of the skull, orbits, nares, and the apertures between them, correspond exactly in the two. The eye is usually more

developed in the Pterodactyle than in birds, is similarly defended with sclerotic plates, and, as a result of larger size no less than of the greater intensity of life in the animal, it is surrounded with bone. The lachrymal, similar to that of a bird, grows down from above, and meets a process of the jugal, of which there is a trace in some birds, which grows up from below. Then the eye extends down to the quadrato-jugal, which accordingly is much thickened, and appears to extend up the inner side of the quadrate bone (from which it sometimes cannot be separated) to meet the outward process of the alisphenoid and squamosal bones. This slight and evidently functional difference is almost the only important deviation from the bird-type seen in the Pterodactyle skull. As I have already remarked, the quadrate bone, both in form and in its relations to the skull, is quite the same as that of a bird; and the articulation with the lower jaw is exactly matched by the complex articulation of some birds. The relations and proportions of the premaxillary, maxillary, and nasal bones are those of birds; and, as far as can be judged from figures, the other bones of the skull are not less avian. As regards Cambridge specimens, I can confidently say that, if seen separately, and their history were unknown, no anatomist would ever dream of their being anything but a new tribe of birds.

The vertebral column of true birds is very peculiar, and, with some few exceptions, is readily distinguished from that of all other animals by the concavo-convex articular surfaces. No Pterodactyle is at present known to show this character, though both kinds of articulation exist in the class. The *Dimorphodon* has vertebræ which are *convex* in front, while the Pterodactyloid animals from the Cretaceous beds have the vertebræ *concave* in front; hence, seeing that the development is entirely functional, it would not be surprising to find Pterodactyles with vertebræ like birds; for the bird's vertebra might be easily modified into the concave or the convex type. But it would seem to be by no means necessary that a bird should have this concavo-convex articulation to the vertebræ; for, as Prof. Owen has stated, "in the third to the eighth dorsal vertebræ of *Aptenodytes*, the fore part is simply convex, while the hind part is concave." Thus the Pterodactyle may be regarded as a case in which all the vertebræ have a like simplicity of articulation; for in all their other features, from the atlas and axis downwards, they present characters which have been recognized by Cuvier, Owen, and other observers as only comparable to those of birds. In the pectoral apparatus every bone might have been that of a true bird, nor can any characters be given sufficient to distinguish them well.

Prof. Owen remarks that "the scapular arch is remarkably

similar to that of a bird of flight." And, again, the same able authority remarks, "In the main, the Pterosaurian breast-bone, like the scapular arch, is formed on the ornithic type; but the postcoracoid lateral emarginations are distinctive Pterosaurian characters." And, going into details, Prof. Owen observes, "Only in birds are distinct synovial articulations provided for the coracoids, which, in the main, are situated and shaped as in the Pterodactyle." After so clear an exposition, I cannot draw the conclusion that, because the Pterodactyle has the characters of a bird, therefore it must be a reptile.

The compact pelvic bones are distinctive. The femur, tibia, fibula, and humerus are in the main avian. Nor will any of the remaining bones be found to show reptilian characters. From facts such as these it seems to me no hard task to determine whether the Pterodactyle has the organization of a reptile or of a bird. I find it in every essential principle to be formed on the avian plan. Yet it differs more from existing birds than they do among themselves, and therefore cannot be included as an order of Aves; for the points of structure in which it differs from birds are those in which all existing birds agree. I therefore regard it as forming a group of equal value with Aves, each as a subclass, forming together a great class of birds. Its distinctive characters are—in having teeth, in the simple convex or concave articulation of the vertebræ, in the separate condition of the tarsal and metatarsal bones, in having three bones in the forearm instead of two, in a peculiar carpal bone, in the sacrum formed of few vertebræ, and in the modification of the wing by the enormous development of the phalanges of one finger. The subclass so characterized forms a parallel group with the true birds. Whether it may not in some points of organization rise above birds, is a question on which I offer no opinion, further than to state that in none of the typical mammalian characters does it approach the mammals. Reptiles, as may naturally be expected, resemble the Pterodactyles, because the gap between reptiles and birds is smaller, and the osteological correspondences between them are many. Hence those parts in which the Pterodactyle falls short of the specialized characteristics of true birds may rightly be regarded as those in which it is more Saurian. Such are the quadruped motion, the lizard-like hand, the simple articulation of the vertebræ, the smaller sacrum and less-developed pelvic bones, the divided condition of the tarsals and metatarsals, the succession of the teeth, and the often long tail. But, while making it more Saurian, they do not necessarily imply that the animal was more reptilian in the sense of being of lower organization, but only that it diverged less from the Saurian type on which the osteology of the bird seems founded. Therefore the

Pterodactyle's place in nature appears to be side by side with the birds, between the reptiles and mammals, thus:—

Mammalia

Saurornia

Aves

Reptilia.

XXXVIII.—*On the Developmental History of the Nematode Worms.* By RUDOLPH LEUCKART*.

THE investigations and discoveries of the last few years have in many respects modified our notions on the particulars of parasitic life, and enriched our knowledge with a great number of important details. Of many parasites, even of man, we have now the entire life-history clearly before us. But there still remain many gaps in our observations; and these are nowhere so great and so serious as in the group of the Nematoda, or Roundworms.

Our present knowledge of the life-history of these parasites (with the exception of the *Gordiacei*, which are parasitic only in the lower animals) is pretty nearly limited to what has been ascertained by Virchow, Zenker, and myself with regard to the *Trichinæ*. At any rate the *Trichinæ* are the only (true) Nematoda whose natural history is known in all phases, and through all migrations.

In the same way as the other known Entozoa, the *Trichinæ* live under different conditions and in different animals in their young and adult states. In order to arrive at sexual maturity, they must pass from the muscle of one bearer into the intestine of another; from rats and mice they migrate into cats and pigs, and from the latter find their way again into their former hosts. That man and other mammals occasionally come within the developmental cycle of the *Trichinæ* is to be regarded, in a helminthological point of view, as merely accidental, notwithstanding its fatal significance. The intercalation of these organisms represents to a certain extent a collateral course, which is just as unimportant for the circulation of the *Trichinæ* as the occurrence of *Cysticerci* in the muscles of rats or dogs in the life-history of the Tapeworms of man, which primarily requires only the interchange with the pig or the ox.

* Translated by W. S. Dallas, F.L.S. &c., from a copy of the paper in the 'Archiv für Heilkunde,' Band ii. pp. 195–235, communicated by the author.

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