M. Deshayes was unable to ascertain if the nucleolar whorls were arranged in the form of a little sinistral embryonic shell, as they are in all true Pyramidellids; and, unfortunately, neither is Mr. M'Andrew's shell in a condition to prove the fact, the apex of the spire being broken off. I am of opinion, however, that *Scalenostoma* belongs to Styliferidæ, and probably should include *Chemnitzia Rangii* of Folin, Méléagrinicoles, pl. 6. f. 1.

X.—*Remarks on* Prof. Owen's *Monograph on* Dimorphodon. By Harry G. Seeley, F.G.S., Assistant to Prof. Sedgwick in the Woodwardian Museum of the University of Cambridge.

In this work several views are urged in osteology which seem to me inconsistent with facts; principles in philosophy are advanced which, if true principles, must place the science of physiology upon a different foundation from that which it has now; and a position is taken by Prof. Owen towards previous writers and with his readers which, if not new, demands explanation before the scientific truths of the memoir will be fairly stated.

I would guard myself here from the suspicion that I may be writing merely to correct mistakes or point out oversights. No writer can afford to do that. And errors of that kind are only defects, often unaccountable, in contributions to knowledge which are made in strivings to attain to truth. But all through this monograph there runs a bias which warps its osteology and philosophy, and leads to conclusions which seem to me to be erroneous, unscientific, and unjust. The passages which will be extracted from the monograph will make this clear, while the remarks appended will contribute the best elucidation of the truth that I can give.

First, of Osteology.—This is descriptive of specimens of *Dimorphodon* from the Lias, and interpretative of the osteology of the whole class of these animals by the evidence from the specimens described. Prof. Owen begins with the skull. Herein, so far as the general osteology went, he was preceded by Von Meyer and other comparative anatomists of Germany, whose labours have cleared the chief difficulties from the subject. Upon the skull Von Meyer is quoted and argued against, but, I think, both misunderstood and misrepresented; so that it has seemed to me desirable to reproduce as well as I was able in English the following account which Von Meyer

gives of the skull in Ornithosaurians from the Lithographic slate*.

"The skull of the Pterodactyles, which Oken placed between Chameleon and Crocodile, after all can only be compared to the skulls of birds and of lizards. The preponderating resemblance to the bird's head cannot be disputed; but, on the other hand, it has opposed to it a surprising dissimilarity in certain parts, which incline to the type of the Sauria. Several species are characterized by an exceedingly depressed snout, which occurs more frequently in birds. In other respects, also, the general shape of the head is more like birds than it is like reptiles, which show a cranium more or less flattened. The bats, which deserve notice as flying Vertebrata, are entirely mammalian animals, and totally different, especially in their heads. In Pterodactyles, as in birds, the bones of the skull blend together so imperceptibly that their sutures at best are only indistinctly seen, and are sometimes obliterated; while even in full-grown reptiles they are all to be made out with great distinctness. There is the more difficulty in ascertaining the structure of the Pterodactyle skull, since generally only the lateral aspect is exposed, and hence we get scarcely any information about its upper and under surfaces. Among the skulls which are exposed from the side, information is at times afforded by those in which the parts have suffered some displacement; but the separations so produced are to be accepted with great caution, for they do not always coincide with the real boundaries of the bones.

"The temporal bone in *Pterodactylus* contributes essentially to the formation of the arch of the skull or brain-case, which is considered to be one of the chief characteristics of a bird's skull, and finds no counterpart in the skulls of Lacertians. The snout also shows the most marked similarity to that of birds, since it comprises only one bone (regarded as the intermaxillary), which constitutes in *Pterodactylus* the anterior margin of the anterior nares: exceptions to this seem to be *Pterodactylus longicollum* and *P. scolopaciceps*. As in birds, the intermaxillary is prolonged backward as far as the region of the orbits, to the principal frontal bone, in the form of a bone-ridge (Knochenleiste). A similar intermaxillary ridge is also found in *Monitor*, but of less extent. The simple bone which constituted the beak in *Pterodactylus*, however, was not of a spongy nature, favourable for the reception of air, as in birds; and the reason probably was that the bone had not to

* From 'Zur Fauna der Vorwelt. Reptilien aus dem lithographischen Schiefer, &c.,' von Hermann von Meyer, (Frankfurt am Main, 1859. Folio) pp. 15, 16.

carry a horny beak. For this reason, also, it was not required that the intermaxillary ridge should become elastic or form a sort of hinge before it met the chief frontal bone, by which means, as is well known, the beak of birds becomes movable. It consists of dense solid bone, which at the utmost can only be distinguished from the other bones of the head (which are exceedingly thin, as in birds) by its presenting a finely striated surface, which, however, is also sometimes to be seen in other Pterodactyle-bones. Here, therefore, we see the beak of birds adapted to an animal with an immovable snout armed with teeth.

"How little the horny beak or the horny covering of the jaw is connected with the blending by anchylosis of the skull-bones, and with the formation of a bird-like intermaxillary, is demonstrated by the fact that in turtles the bones are seen to be separate; the toothless *Rhynchosaurus* also proves it, as does the *Dicynodon*, whose jaws show teeth and horn-covering at the same time, which one could hardly even deny to birds, if the two little teeth which subserve the rubbing through of the egg-shell were to be regarded as true teeth. Mayer of Bonn has proved those on the upper beak of the mature chick in the egg to be tegumentary structures*. The like structure is found in the crocodile, and to some extent in turtles also.

"The highest point in the profile of the skull is formed by the principal frontal bone. This accords with the arrangement in birds as much as does the fact that the principal frontal bone is double, bounds the whole of the upper and hind part of the orbit, and covers the greater part of the cerebrum, which consisted of two hemispheres, in which Oken recognized a resemblance to higher animals.

"The posterior vault of the skull is bird-like. The double parietal bone succeeds behind the principal frontal bone, and is constituted as in birds. Geoffroy, regarding the mastoid as the parietal, described this bone in birds as the interparietal.

"The supraoccipital seems to be single as in birds, and tolerably well expanded; it generally forms that part of the skull which lies furthest back. The side bone of the occiput [exoccipital] lies lower down, and was probably directed somewhat forward, as in birds. No information could be obtained about the lower bone of the occiput [basioccipital], owing to the lateral position in which the Pterodactyle skull is generally found. From the form, however, of the back part of the skull, it may be concluded that the foramen magnum must have been situate inferiorly, as in birds; and we may therefore assume that the head and neck were moved in the same way as in birds, and not as in mammals and reptiles.

* Froriep's Neue Notizen, No. 5. Bd. xx. Oct. 1841.

"The temporal bone lies on the outside of the parietal and principal frontal bones, and chiefly forms the temporal fossa. Anteriorly it does not appear to enter into the formation of the margin of the orbital cavities, as it does in birds, but is rather displaced here, as in the Sauria, by the postfrontal bone. This bone approximates to that of the chameleon; its hindmost branch (which cannot very well be regarded as a backward extension of the jugal) forms the exterior boundary of the temporal fossa, by uniting with a process, probably of the mastoid, since it can hardly be supposed to come from the exoccipital. I would here remark that the exterior closing of the cavity or ring for the passage of the temporal muscles also occurs in birds.

"The malar and superior maxillary do not follow the type of birds. The malar consists of a single bone, which forms the greater part of the anterior and inferior boundary of the orbit of the eye (which is surrounded with bones), and in this respect resembles most of all certain lizards, such as the dragons and Iguana. In birds the cavity for the eye is not generally closed below with bones; but whenever it is so closed, it is not by the malar bone.

"The process of the malar bone which ascends in front of the orbit connects itself, while closing the margin of the eye-cavity, with a bone descending from above. It is the more difficult to determine this bone, since immediately in front or at some distance from it is seen a similar bone, which points downward and attenuates towards the end. Of these two bones the hinder one represents a similar bone in the bird's skull; only there, owing to the peculiar construction of the malar bone, it hangs down free, and has been termed by Bojanus correctly the lachrymal, and by others the supraorbital. In that case the foremost of the two bones is the prefrontal bone, which in birds is clearly developed at the back corner of the nostril. In certain living lizards (*Monitor*, *Iguana*, *Stellio*) the prefrontal bone also contributes towards the formation of the margin of the nares; and in Lacertians in general the lachrymal bone connects itself with the malar bone to form the front part of the border of the orbital cavity. In addition to this, there is to be found (in *Monitor*, for instance) a supraorbital bone, which also characterizes certain birds.

"The great orbital cavities (bordered all round with bones) in the back part of the skull were at least partially separated by a bony partition, and contained, as in some lizards and birds, a bony ring for strengthening the sclerotic membrane. In some Pterodactyles this sclerotic ring seems to be absent; at least I have not yet been able to find it in *Rhamphorhynchus*.

When this ring is found, it either consists of a single smooth piece (*Pterodactylus scolopaciceps*, *P. crassirostris*) or is made up of small plates, which lie over each other, and which may be either smooth (*Pterodactylus Kochi*) or granulated (*P. Meyeri*).

"The nostril was double, and often distinguished by its large size. The two holes, however, were not separated internally by a partition of a partly bony consistence, as Oken supposed. In *Pterodactylus Kochi*, and still more distinctly in *P. longicollum*, it can be seen that the part which was thought to be the bony remnant of this septum is really the exterior bone, in which the anterior corner of the nostril is seen to be cut out. This bone, like most of the skull-bones of the Pterodactyles, is very thin. But as the intermaxillary ridge, which overlies it and extends to the principal frontal bone, is considerably thicker, as is also the lower margin of the jaw, which in that part is generally provided with teeth, it could not but happen, owing to the pressure to which these petrifactions have been subjected, that the thin exterior bone received a more depressed position in comparison with its borders. It thus acquired the appearance of a thin bony partition in the inside of the skull.

"Between the nostril and the orbit lies a third opening, which again reminds one of the bird's skull, which also possesses a boneless space between the prefrontal and lachrymal bones; this middle opening is seen to be completely surrounded with bones in the *Rhamphorhynchi*, where it is smaller and lies lower down, and also in some short-tailed Pterodactyles, as in *Pterodactylus crassirostris*, for instance, and perhaps also in *P. brevirostris* and *P. Meyeri*. In others, however, this opening is only partially separated by bones from the nostril, and varies in size according to the distance of the prefrontal from the lachrymal. These two bones are sometimes so near together, that the middle hole seems scarcely developed, or may even not be noticed at all, as, for instance, in *P. Kochi*; and *P. longicollum* and *P. rhamphastinus* may justify the conviction that there are Pterodactyles which really have no middle hole. Where the middle hole is completely bordered by bones, the separation between it and the orbital cavity is made by the malar and lachrymal bones; and the separation between it and the nostril is made, if not wholly, as in birds, at least for the most part, by the prefrontal bone, and probably only to a very small extent by the maxillary.

"One of the most important bones is the quadrate, to which the lower jaw articulates. This bone is not quadratic, as in birds, but cylindrical and shaft-like, which circumstance was

regarded by Cuvier and Oken as an infallible sign that the Pterodactyle was a saurian reptile, and not a mammal. In this, as in some other parts, the animal shows the greatest similarity to the chameleon, in which, however, the back of the skull is not arch-like, as in birds, but sharper in its backward prolongation, and therefore quite different from *Pterodactylus*. It is characteristic of *Pterodactylus* that the articulation of the lower jaw lies more or less in front of the posterior angle of the orbit. In birds this region lies further backward; and in lizards it is coincident with the posterior termination of the temporal fossa.

"At the same time the lower jaw of the Pterodactyle, except in being armed with teeth, closely resembles that of birds. The very firm union of its rami, their flat ledge-like form, their straight antero-posterior direction, and slight vertical curve, the facing of its articular surface (which lies rather backward), and the surprising shortness of the process which is behind it greatly remind us of the lower jaw in birds, and, among reptiles, of the chameleon and the turtle. Sometimes traces of sutures are visible, by which the composition of the lower jaw may be apparently made out. Externally, between the teeth and the articular cavity, is a small marginal ledge, separated by a suture, and on the lower margin of a similar ledge is seen the angular bone. On the space between these two ledges no other suture can be distinguished. It is not conceivable that the dentary bone, which forms the chief part of the lower jaw, extended as far back as the region of the articulation: it is rather to be presumed that the piece which lies between the two ledges belonged to the coronoid bone, although its anterior and posterior boundaries cannot be defined. In the crocodile the superior margin between the teeth and the articular cavity is formed by the coronoid bone, which in this region shares with the angular bone in chiefly forming the outer surface. In lizards the upper margin is bounded by the coronoid [Mondbein], which is not seen externally in crocodiles, but in the chameleon it forms a surprisingly strongly developed coronoid process which does not occur in Pterodactyles. In birds, however, as in Pterodactyles, one seems to see traces of a small upper marginal ledge, which would belong to the coronoid. The angular bone also shows itself externally in birds and lizards, as well as in Pterodactyles, only as a small marginal ledge; but at the same time, in birds and lizards, at the spot where both ledges terminate anteriorly, a clear separation between the coronoid and dentary bones may be seen. Hence it results that the lower jaw of the Pterodactyles, at any rate, is, even in its composition, only to be compared to

those of birds and lizards; but the foramen is missing from it which perforates the hinder half of the lower jaw in birds and in crocodiles. With all this resemblance, it is amazing to see the jaws armed with teeth, which are planted in separate alveoli, like those of crocodiles, and which have the successional tooth at the side of the old one, as in lizards. The mechanism of the hyoid bone is more bird- and reptile-like."

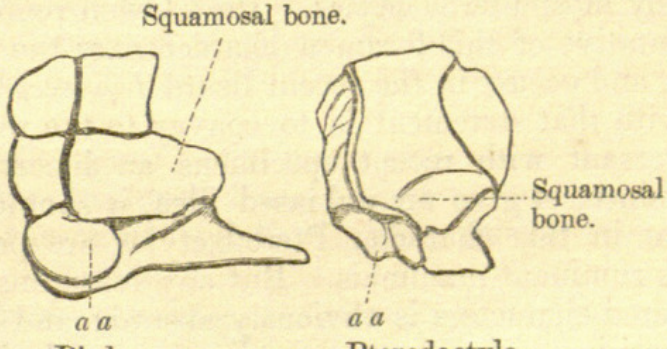
So far as the evidence goes, Von Meyer is clear about the avian character of the premaxillary bone. This Professor Owen ignores: but in the description of his plate 17 the premaxillary is made very small, after the manner of crocodiles; and the maxillary bone accordingly holds most of the teeth. This was the view held by Prof. Owen in his 'Odontography.' In the Palæontographical Society's volume for 1851 was figured the premaxillary bone of *Pterodactylus compressirostris* (Owen), which extended back to the nasal cavity, and demonstrated that the teeth were in the premaxillary bone. Accordingly Prof. Owen made a restoration of the skull, in which the premaxillary and maxillary bones have avian proportions. But in *Dimorphodon* it is said of the premaxillary, "*The pair*, by confluence or connation, constitute the fore part of the upper jaw" (p. 58). And in the description of plate 17 it is said, "Beyond the fourth alveolus the maxillary (20) appears, underlapping the part of the premaxillary (22″) which defines the lower and anterior part of the narial vacuity; the maxillary is continued straight backward," &c. (p. 43). This is substantially repeated at p. 58, where the length of the lateral alveolar rays of the premaxillary bone is given at about $1\frac{1}{2}$ inch. Accordingly I turn to the figures: plate 17 is lettered to agree with the description; but plate 18 (the new specimen on which the monograph is chiefly founded) is lettered so as not to agree with the description, since the whole of the teeth are put into the premaxillary bone, which is represented after the type of Cretaceous and German Ornithosaurians, only of greater extent, and separated from the small maxillary bone by a well-marked suture. But at p. 64 it is said, "In no Pterosaurian has any obvious and unmistakable suture been seen indicative of the respective shares taken by maxillary (21) and premaxillary (22) in the formation of the dentigerous part of the upper jaw," &c. If so, it is not evident why Prof. Owen asserted, but a few pages before, that there was a suture, and described the extent and character of the alveolar rays of the premaxillary bone. If we are to believe this last statement, then it is evident that both views given in the plates are incorrect, and that every passage in

the text which describes the limit of the premaxillary bones is equally erroneous. Yet, notwithstanding this statement, Prof. Owen continues, in the next sentence: "Both bones combine to support the array of teeth; they have coalesced, at least at their external or faci-alveolar plates, as likewise have the right and left premaxillary portions forming the fore end of the upper jaw. The suture between this premaxillo-maxillary bone and the suborbital portion of the zygomatic arch remains. Accordingly there is a choice of analogies in the interpretation of the observed facts: a portion of the compound bone may be assigned to the premaxillary, according to the analogy of the crocodile and lizard; or the whole may be called premaxillary, according to the analogy of the Ichthyosaur." If the latter part of this paragraph is true, it convicts the former part of stating things about the bones which are obviously erroneous. But it is not clear why Professor Owen names an avian affinity Ichthyosaurian. It looks as though there was a foregone conclusion that the animal must be a reptile; and if not allied to living types, then it must be allied to a fossil reptile. But Prof. Owen is unable to determine the affinities of *Ichthyosaurus*; for in the 'Comparative Anatomy of the Vertebrates' it is both classified with the Monopnoa and written of as an extinct order of Dipnoal reptiles. In the 'Annals' for May 1866, I drew attention to the fact that, the teeth being in the premaxillary bone (as I inferred from Cretaceous and Solenhofen specimens, in accord with Von Meyer), they were simple and conical in most animals, and that the argument for their reptilian affinity on which Cuvier relied was worthless. Even if they had been in the *maxillary bone*, such an argument could have no value, since such teeth occur in Cetaceans. If Prof. Owen was battling against this fact, I think he has failed; nor has any evidence been adduced to overthrow Von Meyer's determination. The accusation against Von Meyer that he arbitrarily assumed the avian affinity of the bone is unjust, since the translation has shown he had found other avian affinities in the skull; while, even if the other affinities had been conspicuously Ichthyosaurian (which they are not), it would have been unphilosophical to affiliate the animal to *Ichthyosaurus*, which is not a known standard of organization.

On the lower jaw it is observed, "The dentigerous mandible, like the maxilla, speaks for the reptilian affinity of Pterosauria." This is contrary to fact. There is nothing in the dentition which might not be expected in a group of animals allied to Birds, while some of its more important features are characteristic of both mammals and reptiles. If the osteo-

logical affinities of birds are stronger with reptiles than with mammals, the teeth also might be expected, in a bird-ally, to have some reptilian characters. But to assert, without evidence or argument, that the dentition of these animals is reptilian, seems to dogmatize on a matter against which there is actual evidence and theoretical improbability. It can only be by suppression of facts that the teeth are named reptilian. No one has asserted that they are avian; but the absence of teeth from the jaws of *Echidna*, *Myrmecobius*, and *Balæna** among Mammals, and from the jaws of Chelonians* among Reptiles, is quite consistent with their having allies in which teeth are developed; and similarly the absence of teeth from the jaws of birds cannot militate against bird-allies having teeth, if such animals existed. If, therefore, it shall be evident that Pterodactyles have strong affinity with birds, it would be unphilosophical and untrue to speak of the dentigerous mandible as necessarily reptilian.

Prof. Owen makes a difficulty about determining Von Meyer's temporal bone. *Schläfenbein* is commonly used by German osteologists to indicate the bone in the skull which gives attachment to the lower jaw. In the higher Vertebrata Prof. Owen names this bone squamosal; in some of the lower Vertebrata the bone which has that function is named by Prof. Owen the mastoid. Hence the difficulty is not with Von Meyer, but follows from Prof. Owen's theory of the skull. Von Meyer is singularly clear about the relations of his temporal bone: entering into the brain-cavity as in birds, and forming much of the temporal fossa, it is exterior to the parietal and frontal bones, and does not enter into the orbit. These are the relations of the squamosal bone in the common cock; and I have accordingly (as the *Ornithocheirus* from the Cambridge Greensand entirely agrees in these points with Von Meyer's description) made a preparation of the skull of a chicken, which is here figured side by side with a Greensand



Bird. Pterodactyle.

* As is well known, teeth have been demonstrated in an early stage of life in *Balæna* and *Trionyx*.

Ornithosaurian cranium. It appears to me to demonstrate that there can be no doubt about Von Meyer's "*Schläfenbein*" being the squamosal, and that it is altogether avian.

Yet, notwithstanding this clear and incontrovertible evidence, Prof. Owen concludes that the result of his "analysis of a main ground of Von Meyer's assertion as to the incontestable similarity between the Pterosaurian and Avian types of cranial structure" has not a little tended to shake his confidence in the grounds on which Von Meyer pronounced definite judgment in the matter. If Prof. Owen was conversant with the facts, as I have here figured them, this is a gross misrepresentation of Von Meyer; and if he was not cognizant of the true structure of the bird's skull, the remarks upon Von Meyer which I have quoted should not have been written. German Ornithosaurians differ from birds in having a postfrontal bone of Lacertian form; but the fact that that bone may articulate with the squamosal does not alter the avian characters of the squamosal bone, which does not enter, in any reptile, into the formation of the cranial cavity.

Prof. Owen states that the quadrate bone (tympanic, Owen) is immovably articulated to the squamosal (mastoid, Owen), opisthotic (paroccipital, Owen), and quadrato-jugal (squamosal, Owen). These relations are not evident either from the description or figures of *Dimorphodon*. And, so far as the Ornithosaurians from the Cambridge Greensand are concerned, the statement is erroneous; for the quadrate bone had a free and bird-like articulation with the skull, and a bird-like union with the quadrato-jugal, with which bone in some species it is anchylosed. No specimens afford such facilities for examination as those from the Upper Greensand; and it is not improbable that identical characters occur in other Ornithosaurians, though in a group so large much variation may be anticipated.

In most birds there is in the skull a middle hole between the nasal and orbital holes; and in this character they are matched by most Pterodactyles. Prof. Owen reminds us that a representative of this foramen characterizes the extinct Teleosauria, and occurs in the recent lizard *Lyriocephalus*. But to stop with that statement is to convey to the reader who is not conversant with recent specimens an incorrect idea of affinity, since, to give an unbiased idea, it should have been added that in this character Pterodactyles are paralleled by numerous ruminant mammals. But any reasoning on affinity from isolated characters is obviously absurd; and this character, as reptilian, avian, or mammalian, can only have weight in the sum of those characters which define the animal's plan of structure.

The malar bone is discussed in a similar spirit, it being said that therein the Pterodactyles resemble Crocodiles. On all occasions resemblances to the crocodile are seen. Thus the squamosal bone (mastoid of Owen) is affirmed to resemble that of the crocodile; the postfrontal bone is likened to that of a crocodile; the middle hole of the skull is compared to lizards' and crocodiles'; the premaxillary in proportion is compared to lizards' and crocodiles'; the quadrate bone is compared to lizards' and crocodiles'; the mandible in some of its characters is compared to a fish's, in others to a crocodile's. All this has a tendency to make readers believe, if they have no other source of information, that the Pterodactyle skull is crocodilian, which it is not.

This crocodilian bias or taint running through Prof. Owen's memoir deprives his comparisons of all value; for it prevents him from stating the whole truth; and to state that the malar bone is crocodilian is so to state a truth as to make it convey an erroneous idea. The malar bone of the Ornithosauria may be said with equal truth to be chelonian, and, so far as its essential relations to the orbit, maxillary, and frontal bone go, might be compared to that of the Mammalia. The postfrontal, in those German Pterodactyles in which its characters are unmistakable, such as *P. scolopaciceps*, is certainly not crocodilian, but lacertian. In the Ornithosaurians from the Cambridge Greensand there is no evidence whether it existed; and if it was developed, it could only have been applied to the exterior of a bird-like cranium. And for the other alleged crocodilian characters, I can state that no one of them has even slight evidence to support it: the premaxillary there is no reason for thinking other than avian; and the quadrate bone is avian.

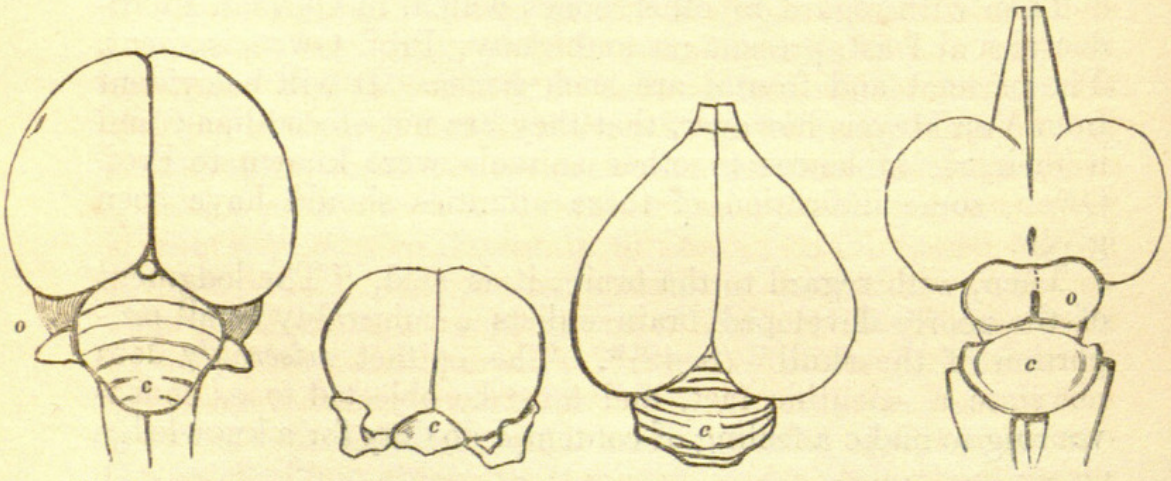
Then with regard to other bones which, in German Pterodactyles at least, present no ambiguity, Prof. Owen is silent. The parietal and frontal are such bones. It will be evident from Von Meyer, however, that they are not crocodilian; and if their resemblances to other animals were known to Prof. Owen, some indication of these affinities should have been given.

Then, with regard to the brain, it is said, "The lodgment of the poorly developed brain enlists a miserably small proportion of the skull" (p. 49)*. The epithet *miserably* does not state a scientific fact, and must be objected to as endeavouring to make a feeling of contempt do duty for a knowledge

* Prof. Owen (Anat. Vertebrates, vol. ii. p. 121) says, in the huge *Dinornis* the brain does not exceed 2½ inches in length, and 2 inches in width.

of structure. Immediately afterwards, however, it is justly remarked that the skull is enormously large in *Dimorphodon*, even for an Ornithosaurian. It is also remarked that "the parietals swell out slightly at the temporal foss, indicative of the size and saurian position of the mesencephalon"—that is, of the optic lobes. It is due to a correct appreciation of this fact to mention that in the Report of the Syndics of the Cambridge University Museums to the Senate for 1868–1869, Prof. Sedgwick stated that I had been able to prove, by casts [natural moulds] from the brain-cavity, that Pterodactyles possessed a cerebral organization as high as that of birds. A copy of that report was sent to Prof. Owen; and thereupon Prof. Owen wrote to me asking for a cast of the brain-cavity. No casts have been taken; and the specimen was placed in my hands on the condition that no casts were to be distributed till the specimen was figured and described by me. I accordingly mentioned to Prof. Owen the main facts proved by the specimen about its avian characters. Therefore, long before his monograph was published, Prof. Owen was aware that a specimen existed, and was about to be figured, which would show that the size and position of the mesencephalon was not saurian, but avian. Nor was Prof. Owen unaware of the value of this character; for in the 'Comparative Anatomy of the Vertebrates' it is said of the bird's brain, "It differs from the brain of every other class in the lateral and inferior position of the optic lobes."

I know nothing of the brain of *Dimorphodon*; but the second figure represents the outline of the cerebrum and cerebellum in an Ornithosaurian from the Cambridge Greensand. Another specimen* shows the lateral and inferior position of the optic lobes.



Strix otus. Pterodactyle. Ornithorhynchus. Crocodile.

o, optic lobes; *c*, cerebellum.

* Figured in my work on the Ornithosauria.

In the Pterodactyle here figured, the region of the cerebellum is only partly preserved, and, as is also proved by the fragments of the squamosal bones at the sides, was longer. On comparing it with the other figures, I do not think there can be any doubt that, so far as it differs from the bird's brain, it approaches mammals rather than reptiles. Now, since the Pterodactyle has an essentially avian brain, I hold that the legitimate inference in any case of divided affinity with regard to the skull-bones is that the true affinity is avian. Therefore I infer that the existence of middle holes in the Perodactyle skull is avian, and neither reptilian nor mammalian—and that those other points of structure which are common to reptiles are proved by these brains to be consistent with an avian plan of organization, and that in this case they were indispensable for its manifestation. If this result is legitimate (and I can see no bar against it, unless it were wholly contradicted by the remainder of the organism), the fact becomes one of the highest possible importance in the investigation of the fossil animals usually named reptiles, because it enables us to use the Ornithosaurian structures as data for comparison and reasoning, in a way that gives a new classificational value to the structures which approximate to them.

I next turn to the vertebral column. Here, too, Prof. Owen presses for a predominant crocodilian affinity. It is observed, "Counting the axis with the small coalesced atlas as one, I give seven cervical vertebræ to the *Dimorphodon macronyx*"—that is, eight cervical vertebræ; and it is added, "Cuvier concluded that there were not fewer than seven, as in Crocodilia and Mammalia, or more than eight, as in Chelonia." If those vertebræ in which the rib is partly supported by the neural arch and partly by the centrum are counted separately and named pectoral, then the crocodile has eight cervical vertebræ and Chelonians nine. Further on, Prof. Owen says that *Rhamphorhynchus Gemmingi* has six cervicals (counting the atlas and axis as one (though why this is done is not evident), and he suspects a seventh—concluding, "Thus it is plain that the Pterosauria exemplify the crocodilian affinity in the cervical region of the vertebral column." On this matter Prof. Owen has adduced no evidence except what I have quoted. Hence it is clear that even the number of vertebræ is not certainly in accord with crocodiles, and may be mammalian; while no Pterodactyle has ever shown the cervical ribs of a crocodile, any more than any crocodile has ever shown the neural arch or pneumatic foramina of a Pterodactyle; so that, so far from the case being as Prof. Owen represents it, no Pterodactyle has shown any evidence of crocodilian affinity in this part of its body.

Buckland's inference that the dorsal vertebræ are crocodilian is quoted with approval, and supported, though with the caution that the procœlian cup and ball is also Lacertian and limited among crocodiles to the newer type. In the Cretaceous Ornithosauria, on which I can speak with most confidence, the dorsal vertebræ no more show crocodilian characters than do the cervical vertebræ. Speaking very vaguely, it might be suggested that the typical mammalian modification of the earlier vertebræ is to have the ball in front, and the typical reptilian condition to have the cup in front, while in birds the cup and ball are combined in one anterior articular surface; but the exceptions are so considerable that the idea is merely suggestive of affinities. In young pigeons the cartilaginous epiphyses come away from the dorsal centrum, and leave flat or slightly concave articular ends—a condition characteristic of some dorsal vertebræ of Cretaceous birds. The procœlous articulation can only be a mark of crocodilian affinity in a crocodile.

On the sacrum it is remarked, "With all the evidence that the Pterosauria, like the Dinosauria and Dicynodontia, exceeded the sacral formulæ prevailing in existing Crocodilia and Lacertia, we should gain no firm ground therefrom for predicating avian affinity or for building thereon a derivative hypothesis of the class of Birds. Many existing Chelonian reptiles have a sacrum composed of more than two vertebræ." The Pterodactyle sacrum has nothing in common with that of any true (*i. e.* living) reptile. There is no evidence on record that I am aware of sufficient to prove that either Dinosaurs or Dicynodonts are reptiles. Nor have I ever seen three vertebræ anchylosed into a sacrum in any Chelonian; and even if such a specimen could be found, mere number of bones would not settle the question. On the other hand, the sacrum of an Ornithosaurian is very unlike that of a true bird.

On the tail it is said, "As we cannot, with Sömmerring, insist on the shortness of the tail in some Pterosauria as proof that they were birds, so neither can we conclude, from the length of the tail in other Pterosauria, that they were reptiles." But in this part of the skeleton Ornithosaurians differ in more important characters than the number of the vertebræ. The highly organized Cambridge family Ornithocheiridæ have caudal vertebræ in which the neural arch is persistent down the tail, as in reptiles and birds; while some at least of the German specimens have the mammalian modification in which the tail terminates with vertebræ from which the neural arches have disappeared, as in *Dimorphodon*.

From these considerations it seems to me that, without deviating from fact, Prof. Owen might have given to his account

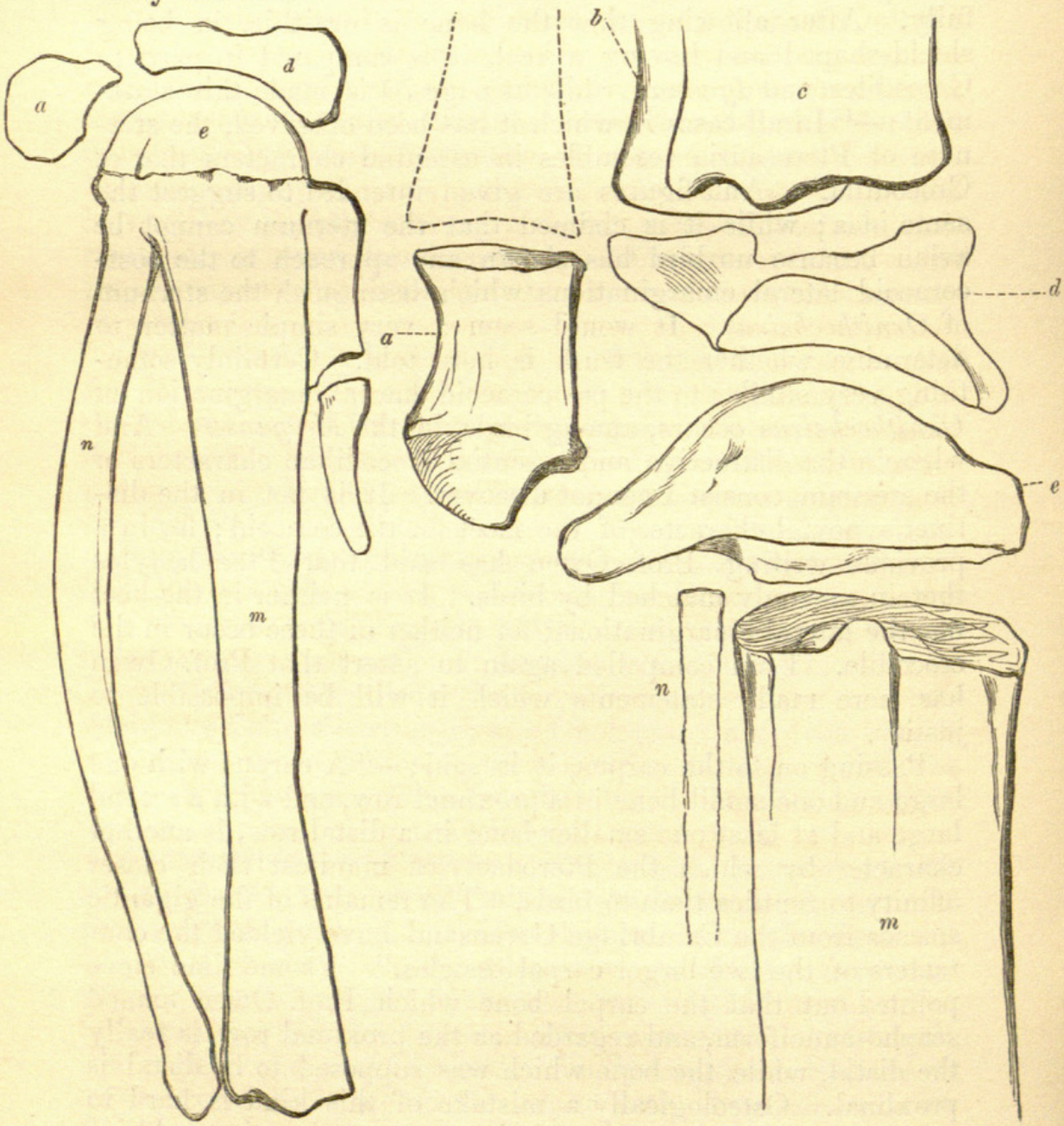
of the vertebral column less of a crocodilian bias. If its procœlous character is reptilian, its pneumatic character is avian. In its details it has distinctive characters of its own.

Prof. Owen says of the scapular arch, it retains in Pterosauria its crocodilian simplicity. I may state that in *Dimorphodon* it has long been recognized as entirely avian, the scapula being much more bird-like than in *Ornithocheirus*. But upon the sternum of Ornithosaurians Prof. Owen remarks fully. After allowing that the bone is ornithic, in being shield-shaped and having a keel, it is compared in parts to Crocodiles and *Iguana*; while at page 70 is made this statement:—"In all cases in which it has been observed, the sternum of Pterosauria resembles in essential characters that of Crocodilia." And figures are given intended to suggest the same idea; while it is claimed that the sternum cannot be avian because no bird has shown any approach to the postcoracoid lateral emarginations which distinguish the sternum of *Ornithocheirus*. It would seem a very simple matter to determine whether the truth is here told. Certainly something very similar to the postcoracoid lateral emargination of *Ornithocheirus* occurs, among birds, in the *Merganser*. And wherein the distinctive and essential crocodilian characters of the sternum consist I cannot discover. It is not in the distinct synovial character of the facet for the coracoid; for in a previous writing Prof. Owen has said that Pterodactyles therein are only matched by birds. It is neither in the keel nor the lateral emarginations; for neither of these occur in the crocodile. I am compelled again to assert that Prof. Owen has here made statements which it will be impossible to justify.

Passing on to the carpus, it is said:—"A carpus with one large and one small bone in a proximal row, and with a second large and at least one smaller bone in a distal row, is another character by which the Pterodactyles manifest their closer affinity to reptiles than to birds. The remains of the gigantic species from the Cambridge Greensand have yielded the characters of the two larger carpal ossicles." I some time since pointed out that the carpal bone which Prof. Owen named scapho-cuneiform, and regarded as the proximal row, is really the distal, while the bone which was supposed to be distal is proximal. Osteologically a mistake of this kind is hard to avoid; but it is of considerable importance, since it would involve regarding the back of the hand as the front, and the "little finger" as the index finger. To the talon of the distal carpal was attached the lateral carpal or pisiform bone, which, as in *Chrysochloris*, supported the third bone of the forearm. The distal carpal shows the articular surface for the meta-

carpal of the wing-finger. Now, seeing that the pisiform bone is always on the side of the hand towards the little finger, it follows that the wing-metacarpal is on the side towards the index finger, and is the index finger, as in birds.

I here give for comparison diagrams of the carpus and metacarpus of the Ostrich and of the Pterodactyle *Ornithocheirus*; and I can only draw the conclusion that the carpus is essentially ornithic.



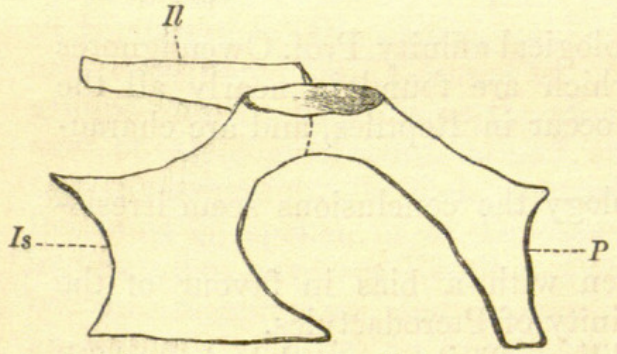
Carpus and Metacarpus of Ostrich. Carpus and adjacent bones of Ornithocheirus.

a, lateral carpal; *b*, ulna; *c*, radius; *d*, proximal carpal; *e*, distal carpal; *m*, index metacarpal; *n*, third metacarpal.

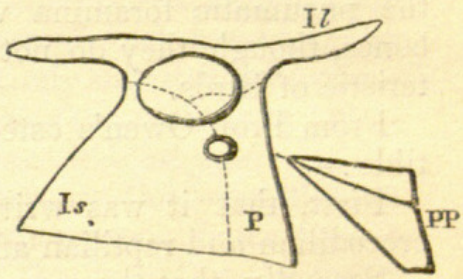
Among important bones there remains the pelvis. Prof. Owen figures the pelvis in the two different specimens, and in

the explanation adopts the reptilian views on the subject held by Von Meyer.

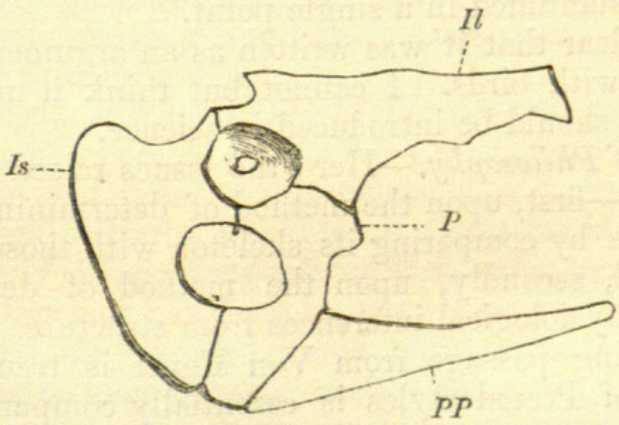
In the 'Fauna der Vorwelt' the case is stated thus. After remarking upon the reptilian character of the ischium, it is observed:—"This is still more applicable to the os pubis, which we have compared to the marsupial bones in certain mammals. In birds the os pubis is quite distinct, and indeed occupies a different position. It is a similar stiliform bone directed backward, and it takes part in the formation of the acetabulum. Wagner believes that in Pterodactyles the three pelvic bones take part in forming the pelvic acetabular cavities. The os pubis appears to me to be excluded therefrom, and to have degenerated to an appendage to the ischium. The exclusion of the os pubis from the acetabulum is observed, among saurians, in the crocodile." Two years ago a study of the original specimen of *Dimorphodon* convinced me that the bones which Von Meyer thought pubic, and compared to the marsupial bones, really were representatives of the marsupial bones; and as I was able to demonstrate the fact by the aid of Cambridge specimens, a paper was communicated to the Cambridge Philosophical Society "On the Mammalian Affinities of Pterodactyles." The fact was quoted by Mr. Clifford in a Royal-Institution lecture. Here is shown the arrange-



Iguana, seen from below.



Dimorphodon.



Echidna.

Il. Ilium; *Is.* Ischium; *P.* Pubis; *PP.* Prepubic.

ment in the original specimen, which is repeated in the new specimen described by Prof. Owen. It may be compared with the similar bones in *Echidna* and *Iguana*.

If the anterior free triangular bone is identified as the pubic, then the pelvis has most in common with the crocodile; but if the bone is the prepubic* or marsupial bone, then the pelvis is not reptilian but mammalian, and any superstructure of affinities built upon its presumed reptilian characters is obviously worthless.

The foramen below the acetabulum is a representative of the obturator foramen of the marsupials, which occurs between the ischium and pubis. In the Cambridge genera the os innominatum closely resembles that of *Dimorphodon*, and through the foramen passes the vertical suture which divides the pubis from the ischium, while a transverse suture divides the ilium from both the other bones. Therefore the bone which Prof. Owen has named the ischium is clearly both ischium and pubis, while the free triangular bone is as clearly no part of the pubis, but a prepubic bone, only comparable to the marsupial bones of mammals. This disposes of the crocodilian theory of the pelvis. I have seen the prepubic bone also in both the Pterodactylidæ and Rhamphorhynchidæ; and, like the other pelvic bones, it differs in form in the different families.

Finally, as a mark of osteological affinity Prof. Owen ignores the pneumatic foramina which are found in nearly all the bones, though they do not occur in Reptiles, and are characteristic of Birds.

From Prof. Owen's osteology the conclusions seem irresistible:—

First, that it was written with a bias in favour of the crocodilian and reptilian affinity of Pterodactyles.

Secondly, that the crocodilian affinity was a delusion which cannot be substantiated in a single point.

It is also clear that it was written as an argument against their affinity with birds. I cannot but think it undesirable that such bias should be introduced in science.

Secondly, of Philosophy.—Here the issues raised are of the gravest kind:—first, upon the method of determining an animal's affinities by comparing its skeleton with those of other animals; and, secondly, upon the method of determining affinities by physiological inferences from structure.

The following passage from Von Meyer is translated:—"The skull of Pterodactyles is essentially comparable only

* By an oversight this word has been printed "epipubic" in my book of Pterodactyles.

with that of Birds and Saurians. The preponderating resemblance with the bird's skull cannot be contested. Against this, however, is a remarkable dissimilarity in certain parts, which, on the other hand, approximates it to the type of Saurians." Prof. Owen's comment upon this is as follows:—"The term Sauria is here used in the sense of Brongniart and Cuvier; and it is open to the unbiased investigator, and, indeed, becomes plainly his business, to determine not merely whether avian or saurian characters predominate in the Pterosaurian skull, but to define the degree of affinity or correspondence of cranial structure therein traceable to such structures in Enaliosauria, Dinosauria, Dicynodontia, Crocodilia, Lacertia, each of which may be a group organically of coordinate value with Aves." This passage seems to me to strike at the very existence of comparative anatomy. The object with comparison is, I suppose here, to elucidate affinity,—that is, to be able to infer from the hard parts of the skeleton what were the soft and vital organs which determine the systematic place of the animal. This comparison can be made with birds, and with the living orders of reptiles, because the skeleton in them is the exponent of definite and known kinds of organization in the lungs, and heart, and brain, and reproductive organs. If it were not, comparison could give little or no clue to affinity. But in Enaliosauria, Dinosauria, and Dicynodontia not one of these organs is known; and I cannot but consider the packing of these groups into the Reptilia, in the absence of such knowledge or even of osteological coordination*, entirely subversive of scientific investigation. If such comparisons are made, the affinities must be spoken of as Dinosaurian or Ichthyosaurian for instance, but never as Reptilian; otherwise the word Reptile becomes meaningless, and we substitute personal fancies about an animal's affinities for knowledge; this would be the result of accepting Prof. Owen's views. Prof. Owen, however, has abstained from making any other comparisons of this kind, except those already noticed.

"The length and flexibility of the neck is correlated with the covering necessitated by the high temperature of the bird. The cold-blooded flying reptiles have a comparatively short and rigid neck," &c. (p. 67). Such a doctrine is misleading, since in many Plesiosaurs the neck is even longer than in birds, and often not less flexible; yet there is no ground for affirming that they were covered with feathers or had hot blood; while in mammals the neck is usually at least as short as in Pterosaurs. The argument about the covering is con-

* This I have attempted in a MS. catalogue of the Woodwardian Museum.

tinued in these passages:—"The plumous covering of the long-tailed bird of the period [*Archæopteryx*] proves its hæmatothermal character, as the want of it shows the long-tailed Pterosaur to have been cold-blooded" (p. 73). "The constant correlative structure with hot-bloodedness is a non-conducting covering to the body. We may with certainty infer that *Archæopteryx* was hot-blooded because it had feathers, not because it could fly" (p. 73). Living crocodiles, chelonians, lizards, and serpents are more or less perfectly covered with bony scutes or horny scales, or, as in the case of some chelonians, with both; neither of these conditions, nor, indeed, any covering is known in Ornithosaurs; therefore Prof. Owen has no reason for inferring from the covering of the body that the Pterodactyles were reptiles or that they were cold-blooded. Yet even scales might not be conclusive of reptilian character, for something analogous to a scaly covering is seen on the legs of birds; but to infer that the animals were cold-blooded because there is no evidence of their having had feathers, is plainly an absurdity. Not to mention other cases, our own species and whales are instances of warm-blooded animals in which the skeleton could show no trace of any non-conducting covering to the body, even if it existed; it therefore seems to me that in these matters Prof. Owen's philosophy has no basis in fact.

At p. 73 Prof. Owen argues against flight having any relation to high temperature; and he adds, p. 80, "By the pneumaticity of the bones of the Pterodactyle, it might be inferred from a single bone, or portion of bone, to have been an animal of flight. For, although certain volant vertebrates, *e.g.* the Bat and the Swift, may not have air-bones, no vertebrate, save of a volant kind, has air admitted into the limb-bones." In his remarks in support of the proposition that temperature does not depend on exertion, Prof. Owen quotes the beetle *Melolontha*, in which the temperature is only raised one degree above the temperature of the atmosphere by the work done in flight. Sharks are cited as animals not less active than Porpoises, and yet cold-blooded; and it is concluded, "With the cooling of the air in the summer-night the temperature of the *Melolontha* concurrently falls. So likewise would that of the flying reptile, whatever amount of oxidation and evolution of waste products in the form of carbonic acid might have attended their flight."

In these passages it appears to me that errors are made of two kinds:—first, in considering functions without regard to their correlative structures; secondly, in not reasoning from structures back to the functions of which they are the evi-

dence. On the first head, the energy of the individual is clearly not distinguished from the organization; for, in other words, the argument is, because a beetle flies and does not become hot-blooded by flight, so also the Pterodactyle which flew could not have been hot-blooded. The beetle is not comparable with a Pterodactyle, having a different plan of organization; and for the same reason the shark cannot be compared with the Cetacean. In both cases the energy of the individual may be greatest in the beetle and the shark, but the energy of their respective plans of organization is totally different. Flight alone would be no evidence of temperature; but the amount of oxidation and evolution of waste products is evidence, when it does not depend upon the individual muscular power, but upon the plan of structure characteristic of the race, because this arterialization cannot be stopped while life lasts, even by absolute muscular quiescence. The amount of heat manifested in arterialization is now being determined by Dr. Gamgee. But seeing that the combustion of one pound of carbon in oxygen is found to heat 8080 pounds of water one degree Centigrade, it is probable that some considerable heat is due to this cause. And the considerations urged by Prof. Owen against an animal's temperature being dependent upon exertion, seem to me not in accord with physics, and to support the views against which they are adduced; for I think Prof. Owen has not distinguished between an animal's kinetic energy and its potential energy, without which physiology as a philosophy can, I submit, have no existence. Thus the grade of organization is potential energy gained for the individual by inheritance, since it is thus placed in a position of mechanical advantage with regard to gravity as definite as is the advantage of a head of water. It is in part this potential energy which enables the individual to manifest the kinetic energy of its own muscular effort, since in flight, for instance, an animal is projected upwards against gravity. Now, in the manifestation of kinetic energy, the heat, or whatever the force was which did the work against gravity, is obviously converted into motion; hence the difficulty found by Prof. Owen, in animals being sometimes warmer in rest than in motion, is met. And it may be presumed that it is as true of organic as of inorganic matter, that it is arrest of motion which develops heat; but in the case of the increase of temperature of the incubating Boa and the bird, the heat is so obviously due to the arrest of radiation by the contact of the parent's body with the eggs, which are acquiring an independent heat of their own, that it should occasion no more astonishment than that we are warmer with a fire than without one, and certainly should not have

been given as evidence that heat is not dependent upon energy; for here the heat is not generated but only conserved.

In ascending from the lower to the higher groups of the vertebrate province, increase in temperature is found to be associated with perfection of the respiratory system, and not necessarily with a non-conducting covering; and it is to superior respiration and its concomitant superior nutrition that must be attributed, as a chief cause, the grades of organization which divide vertebrate animals into classes. Any modification of the skeleton which throws light on the respiratory function is therefore of great classificational value in palæontology. The avian type of skeleton differs typically from that of other classes in having the respiratory organs prolonged into the bones. It is stated by a good observer, and is, I believe, well known, that if the larynx of a bird be tied, and the humerus broken, and the fractured surface exposed, the animal will breathe feebly through its humerus. Similarly to birds, and unlike all other animals, the bones of Pterodactyles show pneumatic foramina, which, so far as comparable, are placed, as in birds, in the limb-bones and vertebral column. I draw the conclusion, therefore, that the foramina are evidence in Pterodactyles that the respiratory organs extended into the bones; and seeing that from a bird's bone with this pneumatic structure we infer for the animal hot blood and a peculiar kind of respiration, so there is no choice but to make the same inferences from the pneumatic bone of a Pterodactyle, since no other relation of the pneumatic structure is known; it is a law of limb-bones and vertebræ to which there is no exception. To attribute any function to the pneumatic foramina other than that seen in birds would be to discard the only known clue to their interpretation. Prof. Owen admits that the bones are filled with air, and that therein they resemble those of birds; but he does not intimate where the air came from, and makes no mention of the respiratory relation of the foramina, which accordingly have no physiological function assigned to them. And Prof. Owen only finds that "the legitimate if not sole inference from the admission of air to the bones is that it contributes to perfect the mechanism of flight," which is supposed to be achieved by air replacing dense osseous tissue, and so making the bones lighter. If that were the sole or legitimate function, it ought to be manifested in the crocodile and turtle, where the quadrate bone is excavated for a tympanic air-cell; and in the skulls of the Elephant and many mammals air is admitted to several bones, but this justifies no such inference as that drawn by Prof. Owen.

Hence I conclude that Prof. Owen's philosophy will not

bear investigation, and that it cannot replace the old paths of physiology.

It also seems to me that Prof. Owen has done injustice to his subject by ignoring the work of others, by appropriating their discoveries as his own, and by so representing their labours as to asperse their reputation.

Thus, in the 'Comparative Anatomy of the Vertebrates,' vol. i. p. 176, Prof. Owen, in an unobtrusive way, essentially claims the discovery of the pneumatic structure of Pterodactyle bones, referring to his later monographs on Pterosaurs. In this monograph on *Dimorphodon* the claim is essentially repeated (p. 79), reference being made to the Palæontographical volume for 1851 for the demonstration that the larger bones of Pterodactyles were filled with air, while the same character is here inferred for *Dimorphodon*. Prof. Owen has quoted freely from the introduction to Von Meyer's 'Reptilien aus dem lithographischen Schiefer,' 1859; but he has omitted to quote or mention the passage in which Von Meyer claims to have made this discovery in 1837, and gives Prof. Owen credit for having subsequently made known English specimens which show the same character. On turning to the 'Jahrbuch für Mineral.' 1837, p. 316, I find the omission was not made because Von Meyer's claim was groundless; for there is printed this passage:—"Further, I must communicate to you that by examining many united bones of Pterodactyles from the Lias of the neighbourhood of Bayreuth, I have discovered that some of them are furnished with air-holes, like certain birds' bones, whereby an affinity with birds in a new way is given to them."

Then with regard to the name Pterosauria, I am not aware that it has claim to an earlier date in England than 1841. Yet referring to Von Meyer, he quotes Prince C. L. Bonaparte as having named the order Ornithosaurii at the same time. On looking into the matter, I find that in the "Nuovi Annali delle Scienze Naturali, Bologna,' Sept. 24, 1840, vol. iv. p. 91, and previously in 1838, vol. i. p. 391, Bonaparte not only invented the name, but adopted the ordinal group suggested by Von Meyer in 1830, and placed it above all other reptiles, in immediate sequence to birds,—a result possibly due to Von Meyer's discovery of 1837. Accordingly Prof. Owen's name has no claim to usage, either on the ground of priority or fitness, and I have therefore used the name Ornithosauria*.

* Since this was written, six months ago, I find that, in 'Das Thierreich,' vol. ii. part 2. p. 23, published at Darmstadt in 1836, Dr. J. J. Kaup introduced the Pterosaurii as the second order in his second stem of Amphibia. And earlier still (Nouv. Ann. Muséum, 1835, vol. iv. p. 238,

Finally, there are two passages of a kind that are rarely seen in a scientific monograph, one reflecting on Prof. Huxley, the other reflecting, I think, upon myself. The former passage is as follows:—"The tyro, fresh from the lecture-room of his physiological teacher, ambitious of soaring into higher regions of biology than were opened to him at the medical school, impressed with the relations of active locomotion to generation of animal heat, may be pardoned for inferring that the amount of work involved in sustaining a Pterodactyle in the air would make it, physiologically, highly probable that it was a hot-blooded animal. But a competent friend, finding him bent on rushing with such show of knowledge into print, would council him to provide himself with a thermometer adapted to the delicate testing of the internal heat of small animals. So provided, if he should chance to beat down a chafer in full flight, the experiment, made with due care and defence of the fingers guiding the instrument, would teach him how fallacious would be the inference that, because an animal can fly, it must, therefore, be hot-blooded," &c. &c.

The other passage, referring seemingly to myself, concludes as follows:—"An argument in favour of Avian affinity from the joint-structures could only be propounded by one not gifted with the judgment needed to deal with problems of this nature." These passages I leave to the consideration of others. Yet I would express my conviction that it did not fall within the province of the Palæontographical Society to publish such matter.

XI.—*On four new Species of Birds from China.*

By Robert Swinhoe, F.Z.S.

Ephialtes glabripes, sp. nov.

Similar to *Eph. semitorques* (Temm. & Schleg.) of Japan,

De Blainville introduces a scheme of Vertebrates as having been given in his lectures, in which *Pterodactylia* is given as the third class of Vertebrata, intermediate between Birds and Reptiles. I regret not having been aware of this fact at an earlier period, since the name Pterodactylia is in all ways preferable to other names. As, however, it has hitherto remained unknown, I am not prepared to adopt it now, the name Ornithosauria being already in use. De Blainville adds this observation:—"Cette classe ne contient encore que le genre Ptérodactyle connu seulement à l'état fossile, et que nous pensons n'être ni un mammifère de la famille des chauve-souris, comme Sœmmering l'a pensé, ni même un reptile proprement dit, comme G. Cuvier l'a dit, mais un être faisant le passage des oiseaux aux reptiles, et dont le système épidermique n'était peut-être pas squameux."