VIII. *On the Vertebral Characters of the Order* Pterosauria, *as exemplified in the Genera* Pterodactylus (Cuvier) *and* Dimorphodon (Owen).

By Professor Owen, *F.R.S.*, *Superintendent of the Natural History Departments in the British Museum.*

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Although the skeletons of the extinct Flying Saurians of the mezozoic strata have been discovered in a more complete condition than those of any other contemporary Reptiles, they have not, hitherto, owing to the delicate texture and commonly crushed state of the bones, afforded satisfactory observations of the structure of the vertebræ. Yet the vertebral characters of a saurian skeleton are of peculiar interest to the Palæontologist and Comparative Anatomist, on account of the many and strongly-marked differences which they present in the extinct members of the Reptilian class.

In the existing species, the articular terminal surfaces of the centrum, with the exception of those of the Geckos, Rhynchocephalus*, and of some single vertebræ in the column of other Reptiles†, are concave in front and convex behind. But in extinct Reptiles some genera (*Streptospondylus*) show reverse positions of the cup and ball; others (*Ichthyosaurus*) show both surfaces concave; others show both surfaces slightly concave (*Teleosaurus*); others show both surfaces flat (some *Plesiosauri*); others are subconcave behind and flat before (*Cetiosaurus*); with many minor modifications. It is only on arriving at the uppermost of the mezozoic series of rocks in an ascending survey, that we find Lacertian genera (*Mosasaurus* and *Leiodon*‡ of the Chalk) and crocodilians (*Crocodilus basifissus*, from the Greensand of New Jersey§) presenting the procœlian || type of vertebra which prevails in tertiary and modern reptiles.

No fossil vertebra from secondary rocks has come under my observation or knowledge with characters of the articular ends of the centrum which distinguish the vertebræ of birds, viz. a concavity in one direction and a convexity in the other, the directions being reversed at the two ends of the centrum.

All the foregoing considerations have tended to invest the question of the vertebral characters of the Pterodactyles with peculiar interest; and, especially, seeing the adapta-

* Catalogue of the Osteological Series, Museum of the Royal College of Surgeons, 4to. 1853, p. 142.

† Biconcave fifth cervical vertebra in *Chelone Mydas*; biconvex first caudal vertebra, Crocodile.—Catalogue of the Physiological Series, Museum of the Royal College of Surgeons, 4to. vol. i. 1832, pp. 52, 53.

‡ History of British Fossil Reptiles, 4to. p. 188.

§ "Notes on Remains of Fossil Reptiles discovered in Greensand Formations of New Jersey," Quarterly Journal of the Geological Society, vol. v. 1849, p. 380.

|| Report on British Fossil Reptiles, 8vo. 1841, p. 65.

tion of their reptilian type of structure for flight, in reference to carrying out the comparison of their skeleton with that of birds. I have therefore thought the summary of observations might not be unworthy the attention of the Royal Society, which I have made, as opportunities presented themselves, for some years past, on the vertebral characters of different species of the order *Pterosauria.*

Before entering upon such summary, I may briefly allude to the recorded observations on the subject. Baron CUVIER, in his celebrated memoir establishing the reptilian character of the *Ornithocephalus* of SOEMMERING, which he, thereupon, proposed to call 'Pterodactyle,' almost restricts himself to a comparison of the number of the cervical and dorsal vertebræ in the Pterodactyle and Bird*. Five of the cervical vertebræ of *Pterodactylus longirostris* are stated to be "large and prismatic like those of long-necked birds"†. With regard to the dorsal vertebræ, "the spinous processes of the anterior ones are a little longer, those of the posterior ones are short and cut square‡."

The able editors of the posthumous edition of the 'Ossemens Fossiles' found nothing to add, in 1836, to the above-cited brief notices by the Baron on the vertebræ of the Pterodactyle, nor has anything material been with certainty determined and stated since that time.

The *Pterodactylus suevicus* described and figured by Professor QUENSTEDT in 1855, was perhaps in the best condition to have thrown some additional light upon the subject; but the most important remark relates to one of the dorsal vertebræ, in which "the articular surfaces of the body are convex at the back end, as in the Crocodile, concave at the fore part. At least so it seems;" writes the author §.

In regard to the cervical vertebræ, the author says, "they seem not to have the trochlear joints as in Birds, yet a small cavity may be observed on the articular surfaces ||."

Accordingly, Professor PICTET, in the able summary of the characters of extinct reptiles in the last edition of his 'Paléontologie' (8vo, 1857), limits his notice of the vertebral characters of the Pterodactyles to their number in the different regions of the spine.

From observations made on species of *Pterosauria*, extending from the period of the Lias, as exemplified by the *Dimorphodon macronyx*, to the Upper Greensand, as exemplified by the *Pterodactylus Sedgwickii* and *Pter. Fittoni*, I am now able to state that, both

* Ossemens Fossiles, ed. 8vo. tom. x. (1836), p. 215, 222.

† "On y voit cinq vertèbres, grandes et prismatiques comme celles des oiseaux à long cou," tom. cit. p. 232.

‡ "Les apophyses épineuses antérieures sont un peu plus longues; les postérieures sont courtes et coupées carrément," *ib.* p. 233. The figures show that the author is not speaking of two kinds of spinous processes on the same vertebra.

§ "Die Gelenkfläche der Wirbelkörper war auf der Hinterseite convex, vie beim Crokodil, vorn dagegen concav. So scheint es wenigstens."—QUENSTEDT, Ueber *Pterodactylus suevicus* im Lithographischen Schiefer Würtembergs, 4to. 1855, p. 45.

|| "Sie scheinen nicht das Nussgelenk wie bei Vögeln zu haben, obwohl man eine kleine Grube auf der Gelenkfläche wahrnimmt," *ib.* p. 40.

with respect to the cervical and dorso-lumbar vertebræ, the terminal articular surfaces of the vertebral bodies are simply concave anteriorly (Plate X. fig. 1), convex posteriorly (*ib.* fig. 2)*; and that they consequently manifest the earliest known instance of the 'procœlian' type which now prevails in the reptilian class. But in no other reptile are those articular surfaces so narrow vertically in proportion to their breadth as they are in the cervical vertebræ of the *Pterosauria* (*ib.* figs. 1, 2, 12–14, *b*, *c*): in the dorsal series the cup and ball present more ordinary saurian proportions.

This fact, being established, will give new and increased interest to the working out and examination of any detached vertebræ from secondary rocks which resemble in texture and size those of Birds and Pterodactyles. It has been alleged, for example, on microscopic characters of the osseous tissue, that certain pneumatic wing-bones found fossil in Stonesfield slate, are those of birds. But every such vertebra from that lower oolitic bed which I have yet seen, has the simple terminal articular concavity or convexity characteristic of the Pterodactyle. A single specimen showing the interlocking joint, *i. e.* a transverse concavity and vertical convexity, or the reverse, would establish the fact of the existence of birds during the period of deposition of the stratum containing such fossil vertebra. There is but one exception, so far as I know, in the whole class of birds, to the foregoing type of vertebral structure; this occurs in a bird (*Aptenodytes*) which does not fly, but has the wing-bones dense, solid, and modified in form to serve the office of a fin, and is exemplified in but a small part of the vertebral column. In the third to the eighth dorsal vertebræ inclusive, the fore-part of the centrum is simply convex (*ib.* fig. 22, *c*), the hind part concave, and this part is concave in the second dorsal; but the fore-part of this dorsal vertebra is concavo-convex, as in the cervical vertebræ of the Penguin, and in the cervico-dorsal vertebræ of all other birds. But, besides the reverse positions of the cup and ball in the above dorsal vertebræ of the Penguin, as compared with the dorsal vertebræ of the Pterodactyle, the latter might be distinguished by the absence of the large bifurcate hypapophysis (*ib.* fig. 22, *hy*) which projects from the dorsal vertebræ of the Penguin; the inferior surface of the dorsal vertebræ in the Pterodactyle being smooth and simply convex transversely, and slightly concave longitudinally. The anterior cup becomes more shallow in the last lumbar and first sacral vertebræ of the Pterodactyle; the confluent articular surfaces of the sacral vertebræ are flattened. In the caudal vertebræ of the Pterodactyle the anterior transversely-elliptical cup and posterior ball are resumed at the articular end of the centrum; at least in most of the anterior caudal vertebræ of the great *Pterodactylus Sedgwickii* (*ib.* figs. 36, 37).

* VON MEYER was led to believe from the crushed specimen of *Pterodactylus Gemmingi*, described and figured in his 'Palæontographica,' Erster Bd. 4to. 1851, p. 10, that both articular surfaces of the bodies of the cervical vertebræ were concave; and that the hinder surface of a dorsal vertebra was not convex. But this error was due to the state of the specimen. See also his 'Reptilien aus dem Lithographischen Schiefer,' fol. 1859, p. 68.

The cervical vertebræ average seven in number, counting the coalesced atlas and axis as one. They are characterized by their superior size, and especially length, as compared with the other vertebræ in the same skeleton; but differ in different species in this respect, being longest in those Pterodactyles with long, light and slender jaws, shortest in those with shorter, stronger and thicker jaws. The third to the sixth inclusive preserve the same, or nearly the same, length; the seventh becomes shorter, and exhibits other modifications transitional to the dorsal vertebræ.

The ordinary cervical vertebra in *Pterodactylus Sedgwickii* (figs. 1–10) has a long depressed centrum (*b–c*) coalesced with the neural arch (*n*), slightly concave lengthwise at the sides, slightly convex lengthwise below, at least in the fourth or fifth cervical (fig. 5). It developes a pair of short obtuse processes (p'), which form the posterior inferior angles, and between these the under surface is concave transversely; the articular ball (*b*) seems as if tilted up above the level of these processes. There is a low obtuse hypapophysis (*h*) at the fore-part, the base of which is in some cervicals prolonged backward a short way as a rudimental ridge. A large 'foramen pneumaticum' (figs. 5, 7, 8, *o*) perforates the middle of the side of the vertebra at the line of junction of the centrum and neural arch; it conducts chiefly to the large cancelli in the centrum.

The neural arch is low; broader, but shorter, than the centrum. Viewed from above (fig. 9), it presents a subquadrate form, deeply emarginate before and behind, less concave at the sides, and with the four angles produced to form the zygapophyses. The articular surfaces of the anterior pair (*z*) look upward, inward and forward; those of the posterior pair (z') downward, outward and backward: both are flat. The anterior zygapophyses (fig. 10, *z*) project on a level with the sides of the anterior articular cup, some way in advance of it, the base of the process being divided by an oblique notch from the cavity. The posterior zygapophyses (fig. 7, z') do not extend quite to the hinder ball; they project above its level; there is a tuberosity (*m*) above the articular surface in many vertebræ. The neural canal (fig. 6, *n*) is slightly expanded at its outlets, subcylindrical in transverse section, about half the length of the centrum; consequently leaving a large proportion of the spinal cord unprotected by bone at the intervals of the successive neural arches. The neural spine (fig. 8, *ns*) is moderately produced, compressed and truncate; its base is coextensive with the summit of the arch, and it contracts as it rises, with a sharp anterior border. Not any of the cervical vertebræ possess the pleural elements which give the great transverse anterior breadth to the cervicals in the bird, and complete there the large vertebrarterial foramen on each side: nor is the hypapophysis double, forming a transverse pair, as in most of the neck-vertebræ of birds. The processes answering to p' in the Pterodactyle are rudimental, when present, in the bird.

The chief differences in seemingly answerable cervical vertebræ, in different individuals, perhaps species, of large Pterodactyles from the Upper Greensand, are seen in the degree of depth or depression of the centrum, with corresponding differences in the form of the foramen pneumaticum, as shown in figs. 5, 7 and 8; with some slight differences in the hypapophysis affecting the lower contour of the centrum, and in the proportions of the articular surfaces of the zygapophyses.

In the sixth cervical vertebra the centrum becomes flatter below, and an anterior parapophysis (*p*) sometimes extends to the under part of the prezygapophysis (*z*), circumscribing a small arterial foramen, as in fig. 11.

In the last cervical (fig. 12) the centrum becomes much shorter: a diapophysis (*d*) is more distinctly developed behind the prezygapophysis (*z*), and these, with the parapophysis now completing a larger arterial canal, form a protuberance resembling that in the bird, on each side the fore-part of the vertebra.

In the dorsal vertebræ (figs. 13–21) the centrums grow deeper as they shorten, with a proportionate expansion of the articular cup, as in fig. 17, and ball, fig. 20. The posterior zygapophyses (fig. 14, *z'*) are more approximated, project from a higher level, are shorter, with the articular surfaces rather convex and looking more outward, and more distinct from the tubercle above (fig. 15, *z'*, *m'*). The neural spine (*ns*) is thicker. There is a small pneumatic foramen behind the base of each diapophysis. The walls of the neural arch increase in height, expanding as they rise, to send out the diapophyses (*d*) to which the free ribs articulate. These ribs are slender and hollow, as in Serpents (fig. 23, *a*).

In what appears to be a lumbar vertebra (fig. 24) the neural arch again sinks, and the strong diapophysis (fig. 24, *d*) projects far, without supporting a rib. In the first sacral vertebra (fig. 25) the fore-part of the neural arch (*d*) forms a broad transversely extended vertical wall above the small neural canal (*n*), and the strong transverse process (*d*..*p*) sinks or extends its base vertically down to the lower border of the inferiorly flattened centrum (fig. 25, *c* and fig. 26, *c*). Fig. 27 shows parts of the bodies of three anchylosed sacral vertebræ of a neocomian Pterodactyle, the first having an anterior concave articulation (*ib. a*), as in the larger specimen, fig. 25; the groove for the passage of the nerve notches the back part of the parapophysis close to the line of suture with the second sacral vertebra. In this vertebra the corresponding nerve-notch is more advanced, leaving a short sutural surface behind, indicative of a position of the neural arch crossing for a short extent the line of junction of the second with the third sacral centrum. The parapophyses (*p*) of the second vertebra are sent off almost on a level with the lower surface of the centrum, which is almost flat.

Atlas and axis vertebræ of the Pterodactyle (figs. 28–34).

These vertebræ early coalesce with each other, but I have been able to separate them in a young specimen.

The atlas consists of a centrum (figs. 28, 29,30, *c*) and of two styliform neurapophyses (ib. *na*); in one specimen there seemed also to be a very small flattened neural spine. The centrum is so short as to be discoid: it is flat where it joins and becomes anchylosed to the axis, and is concave for the occipital tubercle: this cup is circular (fig. 28, *c*).

The neurapophyses, resting on each side of the upper half of the centrum of the atlas, converge and articulate above with two small tubercles (figs. 31 and 32, *z*) on the fore-part of the neural arch of the axis, almost meeting but not uniting above the neural canal (fig. 28, *n*).

The body of the axis (figs. 29, *cx*) is eight times larger than that of the atlas: it expands posteriorly, and terminates by a transversely elliptical ball (*b*) at the upper part of that end, and in a pair of thick short obtuse diverging apophyses (p') at the lower part. There is a rudimental hypapophysial ridge (fig. 33, *hy*) from the middle and toward the fore-part of the under surface of the centrum. There is no trace of a hypapophysis, free or anchylosed, below the body of the atlas.

The centrum of the axis-vertebra is confluent with the neural arch: at the middle of the side, apparently crossing the line of junction, is a large subcircular aperture (fig. 29, *o*), which leads directly into the widely cancellous structure of the bone below the neural canal. This vacuity, as in the other cervicals, answers to the 'foramen pneumaticum' in the vertebræ of birds, and doubtless admitted a production from the air-cells extending along the neck of the Pterodactyle into the cancelli of the osseous tissue. The neural arch (*nx*) rests upon the three anterior fourths of the centrum; it expands as it passes backward; and there, also, as it rises, until it sends off from each posterior angle the zygapophysis (z'), which has a tubercle above, and a flat articular surface below, looking downward and a little outward and backward. The small tubercles at the fore-part of the neural arch (fig. 31, *z*), to which the neurapophyses of the atlas are ligamentously connected, may be the stunted homologues of anterior zygapophyses. The neural spine begins by a low ridge between those tubercles, increasing rapidly in thickness behind; but it has not been preserved in its full height in any specimen.

In the small atlas and axis (figs. 32—34) the line of suture between the bodies of these two vertebræ is distinct. In a somewhat larger specimen, the centrum of the atlas was separable by a smart blow, and showed the true anterior surface of that of the axis (fig. 31); it is very slightly concave with a submedian prominence. A vertical section of the anchylosed atlas and axis is shown in fig. 30: the neural canal (*n*) expands at its posterior outlet: the large cancelli of the centrum are filled by the matrix.

On comparing the atlas and axis of the Pterodactyle with that of the Bird, the Ostrich for example, the atlas in the bird is represented by the neurapophyses which have coalesced below with a hypapophysis, forming an irregular ring of bone. The centrum has coalesced with that of the axis forming a small prominence convex anteriorly, and filling up the vacuity at the upper part of the cup excavated in the fore-part of the hypapophysis: the neurapophyses are broad in the bird, and overlap the anterior zygapophyses of the axis: they meet above the neural canal, but retain the separating fissure there in the Ostrich. The centrum of the axis is broader before than behind. A short process, like a connate pleurapophysis from the fore-part of the centrum, unites with a diapophysis from the neural arch to form an arterial canal. The pneumatic foramen is behind the diapophysis, and conducts to the cancellous tissue of the neural arch. The centrum is produced into a strong hypapophysis below the posterior articular surface, but not expanded laterally into transverse processes, answering to those marked p' in the Pterodactyle. The hinder articular surface of the centrum of the axis of the bird is convex transversely, but concave vertically, not simply convex, as in the Pterodactyle; thus a portion of the vertebra of that reptile, notwithstanding its pneumatic structure, might be distinguished from the vertebra of a bird.

The caudal region of the spine is that which, in the *Pterosauria*, as in the Bats and most other natural groups, is subject to most variety. In *Pterodactylus* (*Rhamphorhynchus*) *Gemmingi*, v. MEYER, from Solenhofen slate, the tail is very long, and most of the long and slender vertebræ, between thirty and forty in number, seem to have coalesced into a stiff style for supporting an expanded interfemoral membrane. In *Pterodactylus longirostris*, CUV. the tail is short, and the small and short vertebræ are free. In the large Pterodactyles from the Cambridge Greensand, it would seem that the tail was of moderate length and the vertebræ are free. The collections examined by me included fifteen caudal vertebræ.

The largest of these (figs. 35–37) measures $1\frac{1}{2}$ inch in length; it is slightly contracted in the middle; the fore-part of the under surface is a little produced; the back part almost flat between the rudimental processes (p'): the shallow anterior concavity (fig. 36, *c*) has resumed its transversely elliptical shape, and the hinder convexity is defined below by a shallow groove connecting the processes (p'). There is no pneumatic foramen, unless a small hole on each side the hinder outlet of the neural canal have served as such. The neural arch is long and low, of one piece with the centrum, which extends beyond it posteriorly; it sends off short obtuse zygapophyses before and behind: those in front extend beyond the cup of the centrum; the surfaces on those behind look downward and backward. The base of the spine is coextensive with the summit of the arch, but is narrow. The neural canal is much contracted. There is no indication of a hæmal arch, either by articular or fractured anchylosed surfaces. The diameter of the middle of this vertebra is 6 lines.

The next caudal vertebra in size measures 1 inch 5 lines. The base of the neural spine begins two lines behind the fore-part of the arch, but terminates nearer the hind part. The nerve-grooves notch the hinder zygapophyses.

Three more slender caudal vertebræ present each a length of 1 inch 3 lines: the diameter at the middle is 5 lines in one, 4 in a second, and $3\frac{1}{2}$ in the third vertebra, showing that they become more slender without losing length. A caudal vertebra, 3 lines across the middle, appears to have been nearly an inch in length; but both extremities are injured.

The most perfect vertebræ of other species of Pterodactyles from older formations which I have as yet had opportunities of examining, are those of a rather large species from the oolitic slate at Stonesfield. Dr. BUCKLAND kindly transmitted to me, some years ago, two drawings of one of these vertebræ (figs. 38 and 39). They are more slender in proportion to their length than in the larger species from the Greensand. The articular cup and ball of the centrum have the same relative position and transverse breadth. The hypapophysis (*hy*, fig. 39) is further from the anterior border. The neural arch has the same superior breadth, compared with the centrum. There seems to have been rather more development of the process uniting the base of the anterior zygapophysis to the centrum.

The cervical vertebræ of the *Pterodactylus* (*Dimorphodon*) *macronyx*, from the lower lias of Dorsetshire, present the same type of structure.

Explanation of Plate.

PLATE X.

All the figures are of the natural size, and with the exception of fig. 22 (*Aptenodytes patachonica*), belong to the Pterodactyle; and of these, all, save figs. 23, 38, and 39, are from the Upper Greensand, near Cambridge. The details are explained in the text.

Fig. 1. Front view
Fig. 2. Back view
Fig. 3. Under view
Fig. 4. Upper view
Fig. 5. Side view
} of a middle cervical vertebra, *Pterodactylus Sedgwickii.*

Fig. 6. Vertical longitudinal section of a similar but more mutilated vertebra.

Fig. 7. Side view of a middle cervical vertebra, *Pterodactylus Fittoni.*

Fig. 8. Side view of probably fifth cervical vertebra, *Pterodactylus Fittoni.*

Fig. 9. Upper view
Fig. 10. Under view
} of a middle cervical vertebra, *Pterodactylus Fittoni.*

Fig. 11. Front view of sixth cervical vertebra, *Pterodactylus Fittoni.*

Fig. 12. Front view of seventh cervical vertebra, *Pterodactylus Fittoni.*

Fig. 13. Front view
Fig. 14. Back view
} of last cervical or first dorsal vertebra, *Pterodactylus Sedgwickii.*

Fig. 15. Side view
Fig. 16. Front view
} of a dorsal vertebra of a smaller Pterodactyle, with the transverse processes broken off.

Fig. 17. Side view of a more posterior dorsal vertebra.

Fig. 18. Under surface
Fig. 19. Hinder surface
} of centrum of large posterior dorsal vertebra.

Fig. 20. Back view of a middle or posterior dorsal vertebra.

Fig. 21. Under surface of the dorsal vertebra, fig. 16.

Fig. 22. Front view of fourth dorsal vertebra, *Aptenodytes patachonica.*

Fig. 23. A rib of *Pterodactylus Bucklandi*, from Stonesfield Oolite.
Fig. 24. Front view of a lumbar vertebra, *Pterodactylus Sedgwickii.*
Fig. 25. Front view of first sacral vertebra, *Pterodactylus Sedgwickii.*
Fig. 26. Under view of first and second sacral vertebra, *Pterodactylus Sedgwickii.*
Fig. 27. Front and under view of centrums of first three sacral vertebræ of a smaller, probably younger, Pterodactyle.
Fig. 28. Front view }
Fig. 29. Side view } of atlas and axis vertebræ, *Pterodactylus Sedgwickii.*
Fig. 30. Vertical longitudinal section of atlas and axis, *Pterodactylus Sedgwickii.*
Fig. 31. Front view of axis vertebra, *Pterodactylus Sedgwickii.*
Fig. 32. Side view }
Fig. 33. Back view } of atlas and axis vertebræ, *Pterodactylus Fittoni.*
Fig. 34. Under view }
Fig. 35. Under view }
Fig. 36. Front view } of an anterior caudal vertebra, *Pterodactylus Sedgwickii.*
Fig. 37. Upper view } of a cervical vertebra, *Pterodactylus Bucklandi*, from Stonesfield
Fig. 38. Under view } Oolite.

R. Owen & J. Dinkel, del.

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VERTEBRÆ OF PTERODACTYLE.