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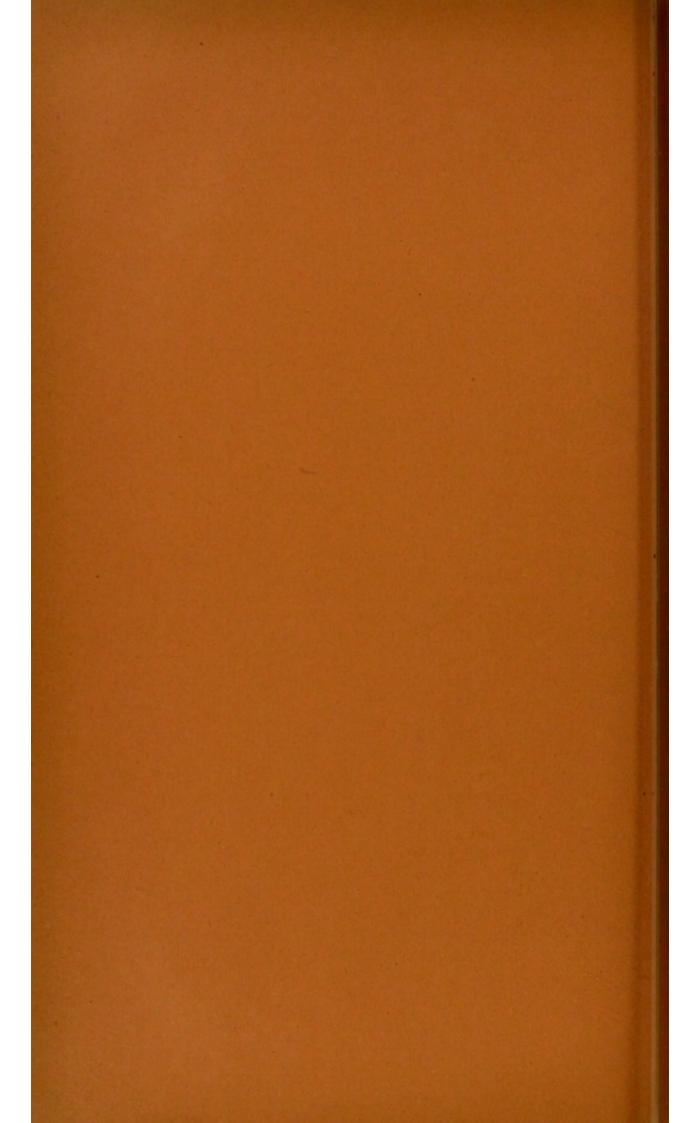
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On the Shoulder-girdle in Cretaceous Ornithosauria. By Professor H. G. Seeley, F.R.S., &c., King's College, London.

In 1882* Professor Marsh published the remarkable discovery that the American Cretaceous Ornithosaurs are characterized by the anchylosis of the anterior thoracic vertebræ into a structure resembling a sacrum, to which the scapulæ are said to articulate. No figure has been given of this singular condition of the shoulder-girdle. But it appears to me probable that the character is common to all the Cretaceous Ornithocheiroidea, and is a distinctive condition of that ordinal group.

Sir Richard Owen in 1859 published in the 'Transactions of the Palæontographical Society,' pl. iv. figs. 6, 7, 8, figures of a symmetrical bone from the Cambridge Greensand which was interpreted as probably frontal. The discovery of a more perfect specimen did not elucidate its nature; and in the 'Ornithosauria,' 8vo, 1870, p. 88, I placed over my account of it the twofold description "? Neural Arch of Sacral Vertebra, ? Vomer," remarking that there is no proof that it is a skull-bone, but that if from the skull it might have been the vomer. This specimen I drew in pl. xii. figs. 15, 16. I go on to remark that "A specimen collected by the Rev. T. G. Bonney is preserved on the sacral side of a left os innominatum with the keel downward. It appears to show a sutural

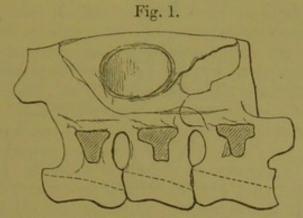
^{* &}quot;Wings of Pterodactyles," Am. Journ. Sci., April 1882, p. 254.

surface from which an anterior part has come away. And if this specimen is compared with the neural arch of the sacral vertebra (pl. x. figs. 8, 9) it will be found to correspond entirely." The vertebra referred to is singular in the circumstance that the transverse process has a higher position relatively to the neural canal than is usual, the infra-neural articulation preserves the concavo-convex articulations, while the neural spine shows a vertical suture with the arch next it. The neural spine of this vertebra is not absolutely the same in character with the bones already referred to. It is a remarkably thick wedge, forming more than half the height of the vertebra. Its sides are smooth, vertical, and flattened, with a defining ridge above the transverse neural platform. I believe this vertebra to be one of three which I suppose to have been anchylosed by their neural arches in Ornithocheirus, to form the articulation for what is usually the free extremity of the scapula. And it follows that the other specimens to which I have referred are portions of separated neural arches of this structure, in which three consecutive neural spines are blended together.

This difference of condition from an ordinary pelvic sacrum is exactly what might have been anticipated, for the ordinary transverse processes evidently carried costal ribs, though they are not shown in English specimens of dorsal vertebræ of Ornithocheirus, and therefore the mechanical stimulus to ossification was necessarily absent from the infra-neural parts of the vertebræ, which in the pelvic sacrum has blended the vertebræ together. All these bones are in the Woodwardian

Museum of the University of Cambridge.

If the interpretation of them which I offer is legitimate, it is probable that the portion of the neural arch which is impressed with the vertical, parallel, transversely ovate facets, concave from front to back, for the scapular articulation, is a distinct ossification imbedded in the neurapophyses, comparable to the neural spines of lower Vertebrates, which have not usually a separate existence in the Ornithosaurian skeleton. It has every appearance of being a separate bone, but it is manifest that the evidence of its relation to the vertebræ is imperfect. I have published figures of all the materials, and offer a restoration of the scapular ossification on which I have drawn the outline of the most complete supra-neural bone which has been found separate (fig. 1). My reason for including three vertebræ is based upon a comparison of my figures in the 'Ornithosauria,' pl. x. figs. 8, 9, and pl. xii. fig. 17, with pl. xii. figs. 15, 16, and the figure of 1859 already quoted in Owen's Palæontographical Monograph. This seems to indicate that two vertical sutures must have divided a mass like that outlined on the restoration. I have no knowledge whether

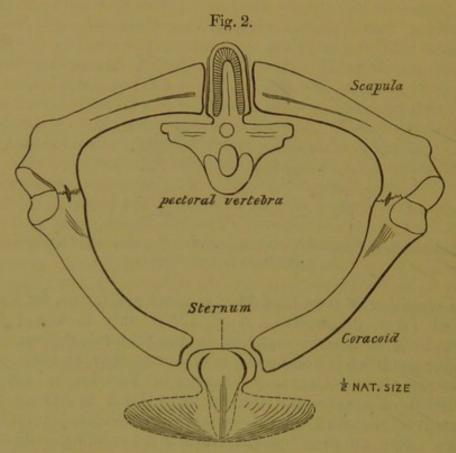


Restoration of Pectoral Vertebræ, showing Supra-neural Ossification with Ovate Articulation.

this condition is paralleled by American specimens, for Prof. Marsh (Am. Journ. Sci., April 1882) only mentions the anchylosis of several vertebræ in the pectoral region. A similar condition is well known to characterize many birds, and Professor Owen instances ('Anatomy of Vertebrates,' vol ii. p. 16) the Flamingo and the Sparrow-Hawk as having the second to the fifth dorsal vertebræ consolidated into one piece. But no bird has the scapula articulating with the neural arch.

I have figured the scapula in Ornithocheirus and some allied genera ('Ornithosauria,' pl. i. figs. 2-12, and 'Geological Magazine,' Jan. 1881, pl. i. fig. 1). It is a short stout bone which widens and thickens to what is usually the free end, where it terminates in a broad, ovate, truncate, flattened surface, which is smooth, vertically flat, and a little convex in length. This extremity, which has every character of an articular surface, exactly corresponds in form and size with the impressions on the sides of the bone which I regard as part of the neural arches of pectoral vertebræ. The conclusion therefore seems to follow that the scapulæ extended transversely outward, curving a little downward from the neural spine which divided their extremities from each other. Though this condition is dissimilar to anything seen among birds, the scapulæ approximate dorsally in some mammals, as do the supra-scapulæ among lizards and amphibians. Since the scapula and coracoid are anchylosed together in most species of Ornithocheiroidea, an arch is thus made between the vertebra and the sternum, which is almost as firm as the arch

of the pelvis, which no other fossil group of animals parallels. I accordingly make a restoration of this structure of the shoulder-girdle (fig. 2).



Restoration of the Shoulder-girdle in *Ornithocheirus*.

Posterior aspect.

The only hypothetical element is the posterior transverse expansion of the sternum, which is never preserved in Cambridge-Greensand specimens. I have also completed the transverse processes of the vertebra; but no specimen shows the form of the articulation for the rib or the length of the process. In some species the coracoids may have been relatively longer; but I believe this form of shoulder-girdle is substantially the same in all the Cretaceous group. It will be interesting if a similar structure is found in the American species.

I have long been aware of a very close affinity between these fossils from Cretaceous Rocks of England and America. The publication by Professor Marsh (Am. Journ. Sci., May 1884) of figures of the skull of *Pteranodon* made that affinity more manifest. Sir Richard Owen figured in the 'Palæontographical Monograph of Cretaceous Pterosauria,' pl. iv. figs. 4, 5, a fragment described as part of the proximal end of the metacarpal of the fifth or wing-finger. I regarded this fossil as part of the premaxillary of a toothless Pterodactyle, and in the Ann. & Mag. Nat. Hist. for January 1871, p. 35, remarked:—"A new genus appears to be constituted by some (three) portions of jaws from the Cambridge Greensand. Unfortunately, the extremity is not preserved. They have the ordinary dagger-shaped snout, but appear to be entirely destitute of teeth. I provisionally name the genus Ornithostoma." It was only after this publication that anything was heard of Pterodactyls in America, and not till 1876 that the toothless character of their jaws was known and the

name Pteranodon proposed.

Professor Marsh's material is evidently incomparably superior to that which was before me; but there is, so far as I can discern, no evidence of generic difference between Ornithostoma and Pteranodon. If any one will turn to the figure of my type (Pal. Soc. 1859, pl. iv. figs. 4, 5) already quoted, and compare either the lateral aspect, fig. 4, or the palate, fig. 5 (from which the matrix there shown is now removed), with Prof. Marsh's figures reproduced in the 'Geological Magazine,' August 1884, p. 347, the only difference found will be that the American toothless Ornithosaur is twice the size of that from the Cambridge Greensand. There is perfect correspondence between them in the dagger-shaped form of the jaw, in the relation between the height of the jaw and the breadth of the palate, in the flattened sides of the snout and their convergence superiorly into a rounded ridge, in the thin rounded margin to the jaw which represents the alveolar border, and in the smooth palate formed by a single wide concave channel. No palæontologist will fail to appreciate the significance of these absolute coincidences of structure; and, so far as they go, they seem to me to indicate that Pteranodon is a synonym of Ornithostoma. I record the British species as O. Sedgwicki.

There is some other evidence which points towards the same conclusion. In the 'Ornithosauria' I figured the quadrate bone and quadrato-jugal of *Ornithocheirus* (pl. xi. figs. 13, 14, &c.). The form of the quadrato-jugal was then unparalleled; but Prof. Marsh's figures show substantially the same type (loc. cit.) in the American toothless

Ornithosaur.

Further, Professor Marsh figures an extraordinary development of the occipital crest in this type, and the Ornithocheirus of the Cambridge Greensand gives evidence of a crest having been worn away. Mr. J. F. Walker's specimen of natural mould of the Ornithosaurian brain

('Ornithosauria,' pl. xi. figs. 10-12, and Journ. Linn. Soc. vol. xiii. pl. xi.) was only laid bare after I had removed a great thickness of open cellular investing bony tissue from above it. The skull figured pl. xi. figs. 1, 2 of the 'Ornithosauria' shows traces of an eroded crest above the foramen magnum, and superiorly the external tissue of the parietal region is worn away; but there is nothing to show how much has been worn away. When, however, the form of the receding neural arches of the atlas and axis is compared with the back of the skull, the vertebræ slope backward as though an occipital crest extended backward from the skull; but it may not have been so much developed as the nuchal bone in the Cormorant.

In my theoretical restoration of the skull of *Ornitho-cheirus*, given in the Ann. & Mag. Nat. Hist., January 1871, pl. iii. fig. 3, there is no antorbital vacuity in the skull, and this condition was found to characterize the American toothless Ornithosaurs when Prof. Marsh figured the complete skull in 1884.

There is therefore, as it seems to me, a close correspondence between the skulls of the American edentulous Cretaceous Ornithosaurs from Kansas, and the dentigerous genera from the Upper Greensand and other Cretaceous rocks of Europe in all points which can be compared; and this I take as evidence that they are closely allied and belong to the same ordinal group. Mr. E. T. Newton (Proc. Geol. Assoc. vol. x. no. 8, p. 421) places Pteranodon and Nyctodactylus in Prof. Marsh's Pteranodontia, while Ornithocheirus and Ornithostoma are placed in a division of the Pterosauria. But if Pteranodon is Ornithostoma, and if the skull of Ornithocheirus is in essential points on the same plan as in the American genus, I fail to see how Mr. Newton's grouping can be sustained.

There is another point of identity between the American and English types in the structure of the carpus. It was no easy matter to determine the mutual relations of these bones in Cambridge specimens, for the structure was unlike anything previously known. They were described and figured in the 'Ornithosauria,' their relations to each other were first figured in the Ann. & Mag. Nat. Hist., August 1870, in "Remarks on Dimorphodon," and some further details were supplied in the Linnean Society's Journal, December 1876, pl. xi. The carpus consists of a proximal carpal, a distal carpal, and a lateral carpal, formed as in birds. It was this evidence of the structure of the hand which led me in 1869 to form the genus Ornithocheirus for animals which had previously been referred to the genus Pterodactylus. Professor Marsh finds

the carpus to have the same structure in the toothless Ornithosaurs from Kausas, and discussed it fully in April 1882 (Am. Journ. Sci.), though without mentioning memoirs in which the structure had been figured, and from which the

interpretation appears to be taken.

If, then, the resemblances in the bones which led Professor Cope to refer the early discoveries of American Ornithosaurs to Ornithocheirus have to be transferred to Ornithostoma, it does not affect the organic identity of the type; and it is by means of the excellent contributions to knowledge made by Professor Marsh that I am able to establish the conclusion that the dentigerous and edentulous Ornithosaurs of the Cretaceous rocks of Europe and America belong to the same subordinal group. I long ago pointed out (Ann. & Mag. Nat. Hist., August 1870) how small is the classificational importance to be attached to presence or absence of teeth in Ornithosaurs and in Birds; and while the discovery of Ichthyornis by Prof. Marsh demonstrated that generalization among birds, the discovery of these Ornithosaurs, which mainly differ in their teeth, while they agree in the typical parts of the skeleton, gives it a parallel justification among the Ornithosauria. Whether the name Pteranodontidæ can be retained for a family to include the genus Ornithostoma remains to be established; for it is not improbable that animals will be found in which there is a partial development of teeth, and that Ornithosauria will eventually parallel Cetacea in the development and suppression of dentition.

I have used the name Ornithocheiroidea for the order (Journ. Linn. Soc. vol. xiii. p. 96), and that name may be found convenient as indicative of characters of skull, shouldergirdle, carpus, vertebræ, and other bones in which the Cretaceous modification of the group differs from the Pterodactylia, which is chiefly characteristic of the Middle Secondary

rocks, though I believe not absolutely limited to them.

Professor Zittel ('Handbuch der Palæontologie') has referred to my early proposal to name the fossil flying animals Saurornia (Rep. Brit. Assoc., Bath, October 1864, Sections, p. 69, and Ann. & Mag. Nat. Hist., February 1865). The new facts then brought forward necessitated a new name for the subclass. When I afterwards found that Prince C. L. Bonaparte, adopting von Meyer's view that the group formed an order, proposed to name the order Ornithosaurii in 1838, I adopted the name Ornithosauria, though it seemed a less suitable name, and was originally given to only one division of the animals comprised in Saurornia.

De Blainville had suggested Pterodactylia and J. J.

Kaup had used Pterosaurii previously for the genus Ptero-dactylus, not for the group as now known *. The merit of recognizing that order clearly rests with von Meyer, and the suggestion of a name for it cannot be important unless the name is suitable. Recognition of avian affinities in the bones of Pterodactyles in 1864 proved the starting-point of work among fossil reptiles which ended in the recognition of similar avian characters in portions of skeletons of other orders previously regarded as entirely reptilian. And on that account the name Ornithosauria is convenient, as

expressing a new and truer point of view.

The Pterosauria of Owen and Zittel is not the Pterosaurii of J. J. Kaup any more than the Ornithosauria of 1869 is the Ornithosaurii of Fitzinger and Bonaparte; but while the former name appears to me to perpetuate a fundamental error, the latter is based on important truths of organic and osteological structure, which are becoming generally recognized. I proposed (Journ. Linn. Soc., Dec. 1876) to limit de Blainville's Pterodactylia to the Jurassic Pterodactyles as an order comparable to the Ornithocheiroidea. And if the name Pterosauria were retained, it could only be as a substitute for Pterodactylia, indicating the short-tailed animals with long hind limbs, of which Pterodactylus is the type. And in any case the name must be limited to the group for which it was originally proposed, as in the classification given in the Ann. & Mag. Nat. Hist. for March 1891.

^{*} Ann. & Mag. Nat. Hist., August 1870.