

ART. VIII.—*The Characters of Pteranodon*; by G. F. EATON. (With Plates VI and VII.)

A CAREFUL preparation of Pterodactyl material from the Niobrara Cretaceous of western Kansas has been commenced at the Yale University Museum, for the purpose of adding an example of one of the gigantic species of the genus *Pteranodon* Marsh, to the series of restorations of fossil vertebrates recently attempted with success. Preparatory to this work, a critical examination both of the fossils themselves and of the literature based upon them has been made, and an excellent opportunity has been thus afforded to extend our knowledge of the skeleton of *Pteranodon*, in regard to several important points of structure. This, in turn, may be of great value in determining the true position of the genus among the Pterodactyls.

The large collection of these reptiles made by Prof. Marsh and his assistants in the field, during a period including the years 1870 to 1894, and representing, according to Prof. Marsh, the fossil remains of more than six hundred individuals, was never completely examined and described by him. His series of papers upon this unique order, which appeared in this Journal, 1871 to 1882, were, at the time of publication, considered by him as little more than preliminary notices. No detailed work on the American Pterodactyls ever issued from his hands, as his attention was constantly diverted by the acquisition of other and not less valuable vertebrate fossils.

His researches both in field and in laboratory having awakened the interest of the scientific world in the Kansas Pterodactyls, it is not surprising to find other collectors and authors engaged in similar investigations. While part of Prof. Marsh's earlier work on this group was performed in a somewhat hurried manner, the accuracy with which he seized upon important osteological characters is amazing. In one instance, at least, his opinion, after having been disputed almost to the point of ridicule, proves to be much more correct than that advanced by his critic. Considering his great talent and the abundance of material at his command, it is to be regretted that Prof. Marsh did not pursue the study further before laying it aside. Had he done so, he would have prevented the misconceptions which have lately gained credence.

The Sagittal Crest.

The most important correction to the prevailing idea of *Pteranodon* is to be made in regard to the sagittal crest. Prof. Marsh in describing the skull makes use of the follow-

ing words (this Journal, vol. xxvii, May, 1884): "an enormous sagittal crest extends far backward, and somewhat upward." The accuracy of this statement is denied by Prof. S. W. Williston (Kansas Univ. Quarterly, vol. i, No. 1, July, 1892), whose views have been accepted largely because of the fact that he collected the head of Marsh's type of *Pteranodon*. Material in the Yale Museum now shows that, contrary to Williston's opinion, the elongation of the crest, as figured by Marsh, was too conservative. Reference to Plate VI, figure 1, will show its true form, taken from an actual specimen, which is indicated by the continuous line. Marsh's incomplete restoration is shown by the dotted line, while Williston's figure of the skull, shorn of its crest, is reproduced carefully in figure 2. Prof. Marsh laid emphasis on this character, and it is of great importance that this error be corrected at once. Following Williston's lead, Dr. S. P. Langley and Mr. F. A. Lucas, both of the Smithsonian Institution, have perpetuated the error in their respective papers in the Annual Report of that Institution for 1901.

In justice to Williston, it is perhaps only fair to quote him verbatim (loc. cit.): "As stated by me in the American Naturalist, the type specimen of *Pteranodon*, also collected by myself, was incomplete, and the figures of it, as given by Marsh, are faulty." This statement can not be gainsaid. The type suffered through the rough methods of collecting employed in those days; but the following clause has been shown above to be incorrect: "The sagittal crest is large, but not nearly so large as it is figured by Marsh, the outline of whose figure is undoubtedly wrong."

To assign the cause of mistake on the part of another writer may be considered a work of supererogation, yet I am tempted to offer here a possible explanation of Williston's misinterpretation of the sagittal crest of this reptile. At the present time of writing, an incomplete Pterodactyl skull is being worked out at the Yale Museum, which will in all probability prove to be that of *Nyctodactylus* Marsh. The crest, which is apparently entire, is of small size compared with that of *Pteranodon*, the measurement from occipital condyle to tip of crest being only 49^{mm}, while the length from occipital condyle to tip of beak was approximately 47^{cm}. In general, the skull compares favorably with that shown in Williston's restoration of *Nyctodactylus* given in the American Journal of Anatomy, vol. i, No. 3, May 26, 1902, where he states that the outline is taken in part from a specimen of *Pteranodon* Marsh, or *Ornithostoma* Seeley, as the genus was then called. It is therefore fair to infer that the apparent similarity of the two genera led Williston to draw uninten-

tionally upon the characters of *Nyctodactylus* when making his restoration of *Pteranodon*.

The Suspensorium.

Another remarkable character of the skull of *Pteranodon*, which belongs apparently to *Nyctodactylus* also, is the articulation of the mandibles with the quadrates. The distal end of each quadrate has the form of a spiral groove, left-handed in the right quadrate and right-handed in the left. The articular elements of the mandibles have a reciprocal form. So perfect is the mutual adjustment of these parts that, unless actual dislocation took place, the act of opening the mouth must have resulted either in a considerable widening of the lower jaws posteriorly or in the forcing together of the quadrates. Apparently the pterygoids and palatines serve as a rigid and immovable support to the quadrates, a condition which would render movement of the latter impossible. In such case an expansion of the lower jaws is, in my judgment, the only way by which the lateral motion caused by the spiral articulation could be taken up mechanically; and this in the face of the seemingly inflexible mandibular symphysis and the thorough union of the mandibular elements.

The existing vertebrate offering the closest parallel in this respect to *Pteranodon* is the Pelican. A careful inspection of the suspensorium of this peculiar bird reveals a similar spiral articulation between quadrates and mandibles, and it is recorded that in the Pelican the act of opening the mouth results also in the widening of the jaws posteriorly. There has been some speculation in regard to the habits of the American Pterodactyls, but no definite conclusions have yet been reached. Possibly the mechanical similarity between the mandibular suspensorium of the Pelican and that of *Pteranodon* is to be received as evidence of the possession of a gular pouch by this Pterodactyl as well as by the bird.

Mr. Lucas has apparently arrived at the same conclusion along another line of evidence. He says (loc. cit.): "In the peculiar shape of the lower, back portion of the beak there is a suggestion of the former presence of a small pouch, like that found in cormorants, and this would be in accord with the supposed fish-eating habits of *Ornithostoma*" (*Pteranodon* Marsh).

The Pelvis.

A nearly perfect pelvis, recently worked out at the Yale Museum, throws much light on the discussion of the characters of this important part of the skeleton of *Pteranodon*, which has not been thoroughly understood and described by

paleontologists. Three diagrams of this specimen are here given, showing the side, top, and bottom views (Plate VII, figures 1, 2, and 3, respectively). It is not my intention at this time to enter into a detailed description of the pelvic characters. Indeed, at present, it is necessary to publish little more than the diagrams, which may prevent any further serious misinterpretation of the pelvis.

Ten vertebræ firmly anchylosed together form the sacral series, using this term in its broader sense. The upper ends of the neural spines of all these vertebræ are united in a continuous ridge about 9^{mm} wide and about 6^{mm} in vertical depth (Plate VII, figure 1). The general form of the transverse processes of the three anterior vertebræ in this series, and their union with the ilia, are sufficiently well shown in the accompanying diagrams (Plate VII, figures 2 and 3). The first vertebra bears anterior zygapophyses for articulation with the last free dorsal; and the transverse processes of the first three vertebræ have on their lower surfaces small facets for the support of ribs. One of these posterior ribs still lies upon the third vertebra, with little displacement from its original position. The transverse processes of vertebræ 4, 5, 6, and 7, depart widely from the foregoing simple arrangement. They are likewise separated by large foramina, but they unite again laterally and form a continuous support for the ilia. The lower ends of the transverse processes of vertebra 4 extend downward and backward, as stout buttresses, finally becoming confluent with the inferior margins of the ilia. The three remaining vertebræ, numbers 8, 9, and 10 of this series, bear short transverse processes, separate at their distal ends, upon which the ilia rest posteriorly.

The ilia extend forward as broad, thin blades, supported, at their inner margins, by the transverse processes of the anterior sacral vertebræ. Posteriorly they unite over the neural spines of the last three sacrals, and are anchylosed to them as well as to the transverse processes. The united pubes and ischia are directed downward and backward, and meet below in a long median symphysis. The obturator foramina lie just beneath the imperforate acetabula. They are circular in form, of about half the diameter of the acetabula, and may be considered as marking the theoretical line of fusion between the true pubic and ischial elements. On the anterior border of these ischio-pubic expansions are small facets, which undoubtedly served for the attachment of prepubes. In no specimen in the Yale Collection has a prepubis yet been found in place.

Paleontologists will perhaps disagree on the number and position of true sacrals in *Pteranodon*. It will be remembered that Huxley, when confronted with a similar problem in

the avian sacrum, chose the intervertebral foramina as the best criteria for distinguishing true sacrals from sacro-dorsals and uro-sacrals. In the present fossil specimen there are, of course, no nerves to serve as guides, but I hope to show in a subsequent paper that vertebræ 5, 6, and 7, which clearly form a natural division, are the true sacrals. Vertebra 4 may prove to be the homologue of the last lumbar vertebra in the sacrum of recent birds. In closing I should like to state, with due apologies to Prof. Lydekker, that the "parallel" between the sacrum of *Pteranodon* and that of recent birds is striking, though I have no desire to postulate "converging lines" of structure and descent.

Paleontological Laboratory, Yale University Museum,
June 8, 1903.

EXPLANATION OF PLATES.

PLATE VI.

FIGURE 1.—Restoration of skull of *Pteranodon*.

True outline of sagittal crest is shown by continuous line.

Marsh's restoration of sagittal crest is shown by dotted line.

One-sixth natural size.

FIGURE 2.—Enlargement of Williston's diagram of skull of *Pteranodon*.

Approximately one-quarter natural size.

PLATE VII.

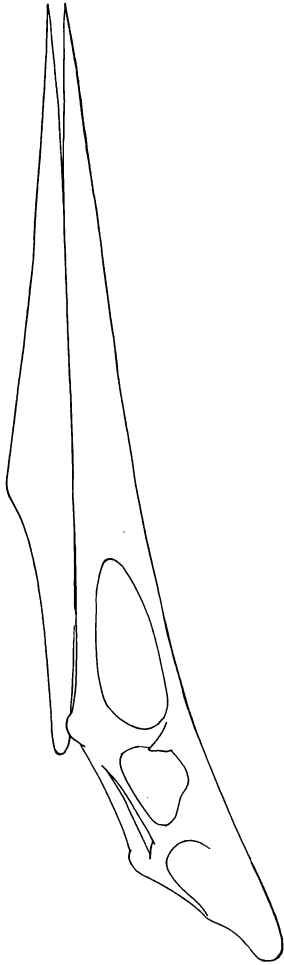
FIGURE 1.—Pelvis of *Pteranodon*; side view.

FIGURE 2.— " " ; top view.

FIGURE 3.— " " ; bottom view.

All three figures are one-half natural size.

SKULL OF PERANODON.

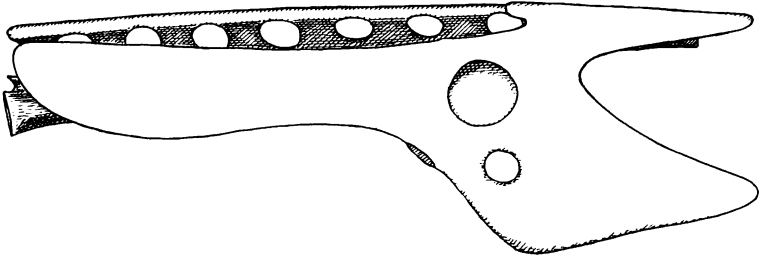


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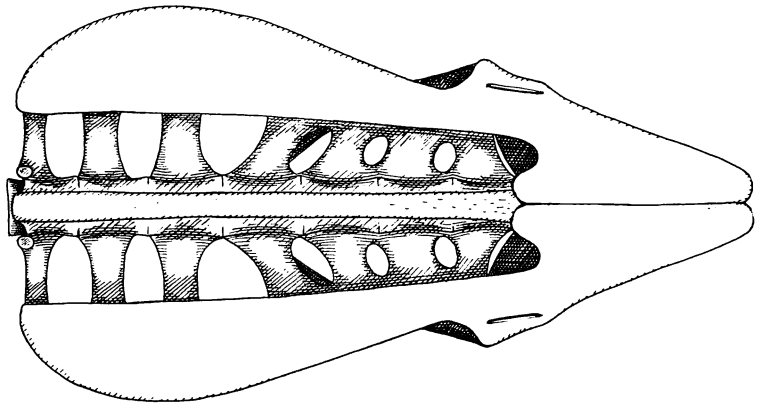


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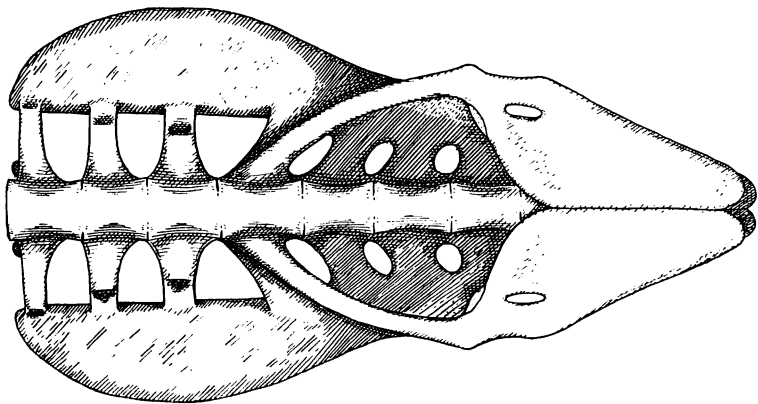
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PELVIS OF PTERANODON.