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Osteology of Pteranodon

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GEORGE F. EATON, Ph. D.

CURATOR OF THE OSTEOLOGICAL COLLECTION, AND ASSOCIATE CURATOR  
IN VERTEBRATE PALEONTOLOGY  
PEABODY MUSEUM OF YALE UNIVERSITY

PUBLISHED UNDER THE AUSPICES OF

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WEIMAR : PRINTED BY R. WAGNER SOHN

## OSTEOLOGY OF PTERANODON.

BY GEORGE F. EATON.

(WITH PLATES I—XXXI.)

The collection of North American Cretaceous pterodactyls assembled by Professor Marsh at the Peabody Museum of Yale University is numerically very large, consisting of the remains of 465 individuals of *Pteranodon* as well as seven individuals of the allied genus *Nyctosaurus*, these two genera from the Niobrara Cretaceous of western Kansas being originally placed by Marsh in the order Pteranodontia. For various reasons it has seemed wise to limit the present memoir to the treatment of *Pteranodon*, postponing until a more opportune time the discussion of a few additional facts regarding the structure and affinities of *Nyctosaurus*. Of the great number of examples referred to *Pteranodon*, a few are complete enough to show new generic characters, but the majority of individuals are so incomplete and fragmentary as to be of comparatively little value. Owing to this condition of the material, it has been found inadvisable to treat each species separately, and the present memoir has been accordingly divided into topics based on the principal skeletal parts. As with one exception the specific names have remained unchanged, an elaborate synonymy is obviated, the only species here recognized that has been known under another name being *Pteranodon occidentalis*, which was first described by Professor Marsh as *Pterodactylus Oweni* (*Am. Jour. Sci.*, June, 1871).

As might be expected, in carrying on the work done by Professor Marsh on this group, considerable difficulty was met with at the outset because of the incomplete and fragmentary condition of much of the material first obtained, and from which the types of the species of *Pteranodon* were necessarily chosen. With this fact in view, it need occasion no surprise that of the three individual specimens originally referred to *Pteranodon occidentalis*, only one, No. 1164,<sup>1</sup> is complete enough to be of any value in the present work. This specimen consists of a right humerus peculiarly crushed, three carpals, and the first and fourth phalanges of the wing finger, together with a few barely recognizable fragments presumably belonging to the same wing. Later Professor Marsh observed the form of the jaws of *P. occidentalis* in a fragmentary skull, No. 1179, and from his notes it is evident that he considered this specimen also a type of the species.

*P. ingens*, the second species described by Marsh, was based upon much more satisfactory material. One of the types, No. 1175, is a magnificent but incomplete skeleton, which does not include the fifth digit of the hand, the so-called wing finger. Another valuable type of this species is the large nearly complete skull, No. 2594, to be particularly described in the following pages. The other types of *P. ingens* consist only of a few poor fragments of wing bones, adding nothing to the characters shown by No. 1175 and No. 2594.

When Professor Marsh separated *P. ingens* from *P. occidentalis*, the skull of neither species was known to him. With the exception of the carpals, the humerus was the

<sup>1</sup> The numbers used in the present memoir refer to the Paleontological Catalogue of the Peabody Museum of Yale University.

only entire skeletal element common to the two types, and he evidently distinguished these species by their marked difference in size and by supposedly contrasting characters ascribed to the humeri and to the proximal ends of the ulnæ.

While it might be expected that the great difference in size of *P. occidentalis* and *P. ingens* would be accompanied by some minute but reliable differences in the form of the wing bones, recent careful work by the preparator has not proved such to be the case. On the contrary, the slight differences in the form of the humeri and of the proximal ends of the ulnæ, noted by Professor Marsh, now appear to be due entirely to extraneous causes. To the critical reviewer of Professor Marsh's early work on this subject, it is evident that the two skulls referred by him to *P. ingens* and *P. occidentalis* were specifically identified by their size alone. There can have been no other reason for associating them with the skeletal parts belonging to the original types of the two species.

That such action was arbitrary, can not be disputed, yet it was in accordance with the established usage of Paleontology, and the ultra-critical course of denying the specific identity of these two skulls would be equally arbitrary and would involve the subject in still greater uncertainty. It seems advisable to let this part of Professor Marsh's work stand unchallenged, and to attempt the separation of the Pteranodon material in the collection into three species by slight but fundamental differences displayed by the skulls.

*P. velox* was based upon the distal end of the right metacarpal of the wing finger and the proximal end of the adjoining first phalanx. It now appears that the form of this fragmentary metacarpal is considerably altered by an attached concretion of foreign matter; otherwise it and the proximal end of the first phalanx differ no more in form from the same portions of the types of the foregoing species than is to be expected in view of the crushing they have undergone.

*P. longiceps* is represented by a nearly perfect skull, No. 1177, with atlas and axis, which offers striking similarities to the skull of *P. ingens*, but is only about two-thirds its size. The matrix was not thoroughly removed from the skull of *P. ingens* until after Professor Marsh's death, and it appears that the difference in size recorded by him was the only comparison of these two species possible under the circumstances. Professor Marsh regarded the skull of *P. longiceps* as the type of the genus Pteranodon, and it seems especially desirable that this species be retained. Its distinction from *P. ingens* can be accepted without too great difficulty, in view of the marked contrast in size accompanied by the slight structural differences noted in the following pages. Obviously, it is impossible to differentiate a species represented by the skull only from another species represented by wing bones only, but by accepting Professor Marsh's choice of the fragmentary skull No. 1179 as a type of *P. occidentalis*, it becomes possible to compare that species with *P. longiceps*.

*P. comptus*, which was described in the American Journal of Science, vol. xi, June, 1876, is untenable. It was based upon portions of three skeletons in the Yale Museum, and was defined by Professor Marsh as "the smallest Pterodactyle known from American strata." The types were said to include distal ends of two fifth metacarpals, the distal end of the ulna, and two sacral vertebræ. Of the three supposed individuals referred to this species, No. 2287, marked "*P. comptus*, type in part," consists of two posterior dorsal centra detached from their neural arches. They are smaller than the corresponding parts of any example of Pteranodon known to the writer, and should perhaps be referred to Nyctosaurus. No. 2335, also labeled "*P. comptus*, type in part," comprises

the distal ends of both tibiæ, together with the right tarsus. The skeleton to which they belonged was of about the size of *P. occidentalis*, No. 1164. Associated with these types in the collection is No. 2397, which is clearly composed of parts of two individuals, because the distal end of the femur and the distal end of the tibia, with fragmentary metatarsals included under this number, are of incompatible size. The tibia evidently belonged to an individual of about the size of the type of *P. occidentalis*, No. 1164, while the femur is that of a slightly smaller animal. It is a matter of considerable surprise to find that the measurements of the distal end of this tibia exactly equal those given by Professor Marsh for the distal end of the wing metacarpal, in his specific definition. The peculiarly crushed distal end of the tibia looks wonderfully like the distal end of the wing metacarpal, and Professor Marsh may have confused the two at a time when the osteology of pterodactyls was little understood. The only course open under the circumstances is to regard *P. comptus* as no longer valid.

*P. nanus* clearly does not belong in the genus *Pteranodon* and may be referred to *Nyctosaurus*.

The collection also contains many incomplete specimens of doubtful specific identity, which have proved of considerable value in determining the characters of the genus.

#### SKULL OF PTERANODON LONGICEPS MARSH.

The nearly complete skull of *Pteranodon longiceps* Marsh, No. 1177, which was originally described as the type of the genus<sup>1</sup> and later more fully discussed and figured,<sup>2</sup> is shown in Plate I, figure 1. The result of further investigation has been to reveal new structure rather than to discover inaccuracies in Professor Marsh's preliminary work, which was necessarily somewhat incomplete. The purpose of the present memoir will therefore be best served by making free use of original definitions as far as they have proved correct, while new structure may be properly described in detail.

It should be noted that fusion of the elements has resulted in almost complete obliteration of the cranial sutures in this genus. The terminology of the skull is therefore somewhat lax, and must at times refer to the regions usually occupied by these elements, their exact limits being indeterminable.

The head was remarkably long in proportion to its width, and in this respect *Pteranodon* probably surpassed all other vertebrate animals. The skull is greatly produced in the axial direction, the attenuated jaws continuing forward into long sharp points, while the enormous sagittal crest extended far backward over the cervical region. The margins of the jaws are smooth and thin, though not especially sharp, and no remains of horn sheaths have been observed.

#### *Under Side of Skull.*

The occipital condyle is small, its smooth rounded surface forming more than a hemisphere. It is directed downward and backward at an angle of about 45° with the palatal axis of the skull, and is separated by a slightly constricted neck from the main part of the basioccipital bone, which is represented by an irregularly oval plate about

<sup>1</sup> *Am. Jour. Sci.* (3), vol. xi, p. 507, June, 1876.

<sup>2</sup> *Ibid.*, vol. xxvii, p. 423, pl. xv, May, 1884.

2 cm in length. A slight break, probably occurring along the line of the original suture, separates this from the basisphenoid bone, a long narrow ossification of triangular section underlying the entire bony interorbital septum and terminating anteriorly in the basiptyergoid expansions.

In the crushed specimen, broad and flat paroccipital processes extend outward and a little downward from the occipital condyle. At their outer extremities they are completely fused with the hinder ends of the remarkable elongate bars formed by the united quadrates and squamosals. The foramen magnum appears to have been a round opening about 4 mm in diameter. Above this and separated from the paroccipital processes by narrow elliptical vacuities rises the triangular supraoccipital plate, bearing throughout its entire length a thin but prominent median ridge. At this point the inferior border of the great supraoccipital or sagittal crest originates.

The skulls of the three species recognized in this memoir differ considerably in the pitch of their supraoccipital plates. To express this more definitely, in *P. longiceps* the supraoccipital plate rises less abruptly from the general axis of the basisphenoid than in *P. occidentalis*, while in *P. ingens* the supraoccipital rises so little that its apex is a trifle below the line made by prolonging the axis of the basisphenoid. The varying pitch of the supraoccipital plate may be regarded as a valid difference, for as the three type skulls are crushed laterally the midline ossifications subtending these critical angles have not been subjected to displacement.

The extreme specialization of the American Cretaceous pterodactyls is well shown by the form of the articular portion of the quadrate. Professor Marsh's figure of the type did not sufficiently emphasize this structure, although he stated that the distal end of the quadrate was one of the most characteristic parts of the skeleton. Dr. Plieninger was probably the first to illustrate this peculiar bone correctly, but his monograph does not throw light on its true significance and function. The distal ends of the quadrates, instead of forming simple ginglymal joints with the mandibles, participate with them in the formation of one of the most remarkable mechanical devices to be found in the reptilian class. The articular surface of each quadrate bears 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, their surfaces bearing stout threads exactly corresponding with the quadratic grooves. The left quadrate of the type of *P. longiceps*, No. 1177, with part of the jugal is shown in Plate V, figure 1. As the articular facet of the left mandibular ramus of this skull is wanting, the same portion of another individual, No. 2578, equal in size, has been used for illustration (Plate V, figure 2). Any possible difficulty in the interpretation of these fragments will be removed by comparing them with the quadrate and articular of No. 2476 (Plate V, figures 4, 5, and 6). So perfect is the mutual adjustment of these parts that unless dislocation took place, which is not supposable, opening the mouth must have caused considerable widening of the lower jaws posteriorly. The quadrates being immovably fixed by the supporting bones of the pterygo-palatine arch, an expansion of the posterior parts of the mandible was the only way by which lateral motion caused by the spiral articulations could be taken up mechanically. The fact is of especial interest in its bearing upon the prevailing supposition that the mandibular rami were joined by an immovable symphysis and their component elements firmly anchylosed.

In a preliminary description of this part (*Am. Jour. Sci.*, July, 1903), the writer called attention to the suspensorium of the Pelican, which is mechanically equivalent. Although



this bird lacks the perfect spiral groove and thread characteristic of the quadrate and articular of Pteranodon, the modeling of these bones seen in the prepared cranium forms an effective screw that thrusts apart the mandibular rami when the mouth is opened. That the spiral articulation is directly concerned in the widening of the mouth of both Pteranodon and the Pelican, there can be little doubt. In the Pelican, however, this skeletal modification may have arisen as a result of the peculiar musculature of the lower jaw referred to by Dr. Coues (*Key to N. A. Birds*, p. 721). The reference, which is not original with Dr. Coues but quoted from another author whose name is not given, is repeated here: "When the bill is opened, the crura of the lower mandible separate from each other to a considerable extent [in their continuity—not at the symphysis], by the action of muscles inserted into their base, and the sac is expanded." Possibly the mechanical similarity between the suspensorium of Pelican and Pteranodon should be received as evidence of the possession of a gular sac by the pterodactyl also. This would be in harmony with the views of Mr. F. A. Lucas, who stated (*Ann. Rept. Smithsonian Inst.* for 1901, p. 657): "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).

#### *Maxillary Arch.*

In this skull no demarcation is shown between the premaxillæ and maxillæ, and here as well as in the type of *P. ingens*, to be described later, the maxillo-jugal sutures are entirely obliterated. A skull of Pteranodon sp. in the Museum of the University of Kansas shows a long splintlike development of the jugal overlapping the maxilla on its outer surface and extending forward to a point beneath the anterior end of the nasal vacuity. This is quite in accord with Professor Williston's view as to the position of the suture in question, expressed in his paper: "On the Skull of *Nyctodactylus*." Peculiar breaks occur in the types of *P. longiceps* and *P. ingens*, nearly beneath the centers of the antorbital vacuities. At first glance, these seem to indicate the position of the maxillo-jugal sutures, but it is much more probable that they are merely fractures caused by pressure, this part of the maxillary arch being subjected to an unequal strain, owing to the partial support afforded by the transpalatine bone.

#### *Palato-ptyergoid Arch.*

The extraordinary form of the palatines and pterygoids, together with their associated elements, is one of the most striking characters of Pteranodon, and still further separates the genus from other groups of the Pterosauria.

Although certain important parts are yet wanting in the type skull of *P. longiceps*, careful and persistent work on this specimen has resulted in considerable advance in a knowledge of the palatal region. The complete demonstration of the bony palate will be found on page 9, where the type skull of *P. ingens* is described in detail. The peculiar form of the bones of the palato-ptyergoid arch here described is based on these elements as preserved in the type of *P. longiceps* and also in another skull, No. 2440, of about the same size.

Stout transverse buttresses of bone about 3 cm in length extend outward and slightly downward from the anterior extremity of the basisphenoid, fusing at their distal ends with the quadrates, which they support in the strongest manner. The inner ends of

these buttresses may be termed *basipterygoids*, as they are evidently outgrowths of the basisphenoid. It is impossible to determine to what extent the pterygoids share in the formation of these parts, many of the elements being, as previously stated, so completely fused as to obliterate the original sutures; but it will be in strict agreement with the usual interpretation of the reptilian skull to consider the outer portions uniting with the inner sides of the quadrates as parts of the true pterygoids.

From the middle of the anterior edge of each of these pterygoid buttresses, a thin ribbon of bone about 1 cm in width extends forward and slightly outward, widening a little anteriorly until its outer border becomes confluent with the palatal border or shelf of the maxilla at a point about 5 cm in front of the quadrate. The inner border of this palato-pterygoid ribbon, forming the boundary of the great palatal vacuity or posterior nares, can be traced in skull No. 2440 (which is of similar size to the type skull) to about 10 cm in advance of the quadrate. Other fragmentary skulls of the genus show that in this region the inner margins of the palato-pterygoids converged, but no specimen in the collection indicates whether any posteriorly directed style in the midline separated the posterior nares. From the large palatal vacuity forward to the tip of the beak, the palate extends as a continuous tract of bone, showing no demarcation between premaxillæ, maxillæ, paired vomers, and palatines. In front of the basisphenoid there is a small smooth and curved natural edge of bone, supposed by Professor Marsh to be part of the posterior border of the large and simple oval palatal vacuity including the posterior nares. That the skull of this species bore a most remarkable ossification in the roof of the oral cavity anterior to the basisphenoid, was made evident by the fortunate identification of a fragment of the palato-pterygoid, which had escaped notice when the type was first described. For want of this piece, Professor Marsh was compelled to restore by conjecture the middle third of the palato-pterygoid, and was led to overlook a small but important ossification clearly representing the transpalatine or ectopterygoid of other Reptilia. In Plate V, figures 7 and 8 of the type show the completed palato-pterygoid ribbon with its associated bones, from the under side (figure 7), and the same parts as they would appear from above if the roof of the skull were removed (figure 8). From these figures it is clear that the pterygo-jugal vacuity is bridged across by a small transpalatine whose outer end in the type remains as a conical stub on the inner surface of the posterior end of the maxilla. Not only is the inner end of the transpalatine bone fused with the palato-pterygoid ribbon after the usual manner, but it is continued as an oblique rod backward and inward across the upper surface of the palato-pterygoid, its broken inner extremity actually projecting freely into the posterior part of the large palatal vacuity. Plate V, figure 9, shows the same portions of the palato-pterygoid and transpalatine in skull No. 2440, as seen from above. The precise form of this extraordinary oblique rod at its origin near the midline of the skull is not shown in any specimen of *P. longiceps*, but comparison with the almost identical structure seen in the type of *P. ingens*, No. 2594 (Plate IV, figure 2), demonstrates beyond all possibility of doubt that these remarkable ossifications are lateral outgrowths from the base of the parasphenoid.

It is difficult to compute the true form of the upper margin or ridge of the skull. Specimens crushed laterally at first sight seem to indicate a form quite different from those crushed vertically. Professor Marsh, whose material was mainly of the former description, stated: "A sharp ridge extends from the end of the premaxillaries along the median line to the true cranium, and is continued backward by the thin elevated

crest." An examination of small fragments retaining the natural curvature of this region leads to the conclusion that the ridge was not so marked over the upper jaw as Professor Marsh supposed. On the midline between the orbits, however, the beginning of the upper border of the great sagittal crest is clearly to be seen.

*Side View of Skull.*

The side view of the skull is scarcely less instructive than the palatal view, as it gives an excellent idea of the general proportions of this remarkable type. In front of the large narial vacuity extends an almost unbroken arch of bone formed by the united premaxillæ, maxillæ, and nasals. The outline of the superior border of the upper jaw or snout is continued in a slightly ascending curved line above the narial vacuities and orbits into the upper margin of the sagittal crest. In figuring this strange outgrowth from the parietal and supraoccipital bones, Professor Marsh gave an example of his exceptional shrewdness in working from fragmentary material. As seen in Plate I, figure 1, there remains only the basal portion of the great crest once borne by the type skull. From the evidence offered by this, he was able to anticipate later discovery by figuring and describing an enormous crest that formed about one-third of the entire length of the skull. The only complete large crest known is that of a specimen identified with *P. ingens*, No. 2473 (Plate II, figure 2). Under that species, the form and function of this remarkable part of the skull will be further discussed.

Beneath the antorbital vacuities, the maxillæ are seen extending backward to meet the supposed jugal elements that continue the cutting edges of the jaw almost to the quadrates. From the middle of the jugal arises the flat bar of bone separating the antorbital vacuity or nares from the orbit. In the type, the ossifications forming this bar, supposedly lachrymal, prefrontal, and nasal, can not be distinguished from each other. The orbit is bounded inferiorly by the jugal alone, which apparently united posteriorly with the squamosal and postorbital or postfrontal to form the supratemporal arcade, no demarcation being shown between the two last-named bones in any skull of the genus in the Marsh Collection.

The exact relations and extent of the squamosal remain a vexed problem. In the type skull of *P. longiceps*, as well as in that of *P. ingens*, an unbroken tract of bone, which may be the squamosal, arises from the paroccipital region and after participating with the jugal and postorbital elements in the formation of the supratemporal arcade extends forward and downward in a long splintlike process overlapping the inferior border of the quadrate. This interpretation of the squamosal is slightly at variance with the views of Professor Williston,<sup>1</sup> who regards the inferior outer part of the supratemporal bar of *Nyctosaurus* as a quadrato-jugal articulating with the postorbital, jugal, squamosal, and quadrate. In the types of *P. longiceps* and *P. ingens*, suture-like lines show on the outer sides of the quadrates, and may possibly indicate the position of thin quadrato-jugal plates. Such a hypothetical arrangement of the lateral temporal elements has at least the merit of agreeing with the position of the corresponding bones in the generalized Hatteria skull, and the extreme elongation of basisphenoid, jugal, and quadrate in *Pteranodon* removes any possible lack of harmony in a proportionately long squamosal.

<sup>1</sup> *On the Skull of Nyctodactylus.*

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The largest opening seen in the side view of the skull was originally termed by Professor Marsh "the antorbital vacuity." Professor Williston describes<sup>1</sup> and figures an oval depression or excavation in front of the orbit in *Nyctosaurus*, which in his opinion "clearly corresponds to the antorbital vacuity of the earlier pterodactyls." He concludes: "From this it is evident that the antorbital vacuity is not united with the nares in this genus or *Ornithostoma*" (*Pteranodon*). This depression does not appear in the types of *P. longiceps* and *P. ingens*, and the term "antorbital vacuity" is here retained.

The orbit as seen in the type is pear-shaped, with the elongation forward and downward, in this respect as well as in its position above the infratemporal vacuity differing greatly from the orbit of *Nyctosaurus*, in which genus it is situated much further forward, overlying in fact the anterior end of the quadrate when the line of the jaws is horizontal.

The supraorbital ridge of the frontal projects boldly outward over the orbit and is one of the stoutest parts of the skull. The orbits are without floor and open anteriorly into each other and into the great narial cavity. The interorbital septum as seen in the type rests upon the entire length of the basisphenoid, its anterior edge leading backward and upward until on the level with the center of the orbit, when it curves sharply forward and upward to merge with the under surface of the frontals. The sclerotic circle has been lost in the skull of *P. longiceps*, but is excellently preserved in the type of *P. ingens* (Plate III, figure 1, and Plate V, figure 3).

#### *Lower Jaws.*

The articular part of the mandible has been already described in connection with the remarkable form of the quadrates. As seen in the lateral view of the type skull of *P. longiceps* (Plate I, figure 1), the lower jaws fit closely against the cutting edges of the maxillary arch, which they simulate in general form. In the type, the points of both the upper and lower jaws are wanting, and no specimen in the Marsh Collection is complete in this respect. By fairly carrying out the lines of the remaining portions of the jaws, extremely slender terminal points are indicated. That this was the true form of these parts in the smaller allied genus *Nyctosaurus*, is clearly shown by abundant material, and the wonderful delicacy of other portions of the skeleton of *Pteranodon* renders such a hypothesis tenable.

For a little over two-thirds of their total length, the mandibular rami meet in a firm symphysis. Behind this, the separated rami quickly diminish in depth and increase slightly in transverse diameter, their form becoming oval in section immediately in front of the quadratic articulations. Posterior to the articular facets there are small angular projections.

Professor Williston has given an excellent restored figure of the posterior half of the mandible, seen from above (*Note on the Mandible of Ornithostoma, Kansas Univ. Quart.*, vol. iv, July 1, 1895). The Marsh Collection contains a fragment of this part, No. 2478, which is here figured from the right and left sides (Plate I, figures 2 and 3), so as to show the posterior part of the mandibular symphysis and the bony floor of the oral cavity, which united the parapets of the jaw nearly as far back as the termination of the symphysis. The front end of the fragment can not well be figured, but it demonstrates the presence of a long cavity of triangular section, enclosed between the floor

<sup>1</sup> *Ibid.*

and side walls. Other specimens indicate that this cavity extended nearly or quite to the point of the mandible.

The principal measurements of the type skull of *P. longiceps*, No. 1177, are as follows:—

Length from extremity of sagittal crest to end of premaxillary . . . . .	720.	mm
Length from occipital condyle to end of premaxillary . . . . .	630.	
Transverse diameter of occipital condyle . . . . .	8.4	
Distance from occipital condyle to distal end of quadrate . . . . .	105.	
Length of mandible . . . . .	570.	
Maximum depth of mandible . . . . .	70.	
Depth of mandible immediately in front of articulation . . . . .	26.	

It should be noted that the measurements given by Professor Marsh included the calculated missing portions of the crest and the tip of the jaws. The foregoing measurements are taken directly from the skull as preserved.

#### SKULL OF PTERANODON INGENS MARSH.

The type skull of this species, No. 2594, a preliminary notice of which was published by Professor Marsh in the American Journal of Science and Arts, vol. xi, June, 1876, is shown in Plate II, figure 1, Plate III, figure 1, and Plate IV, figure 2. Not only is it of much larger size than the types of *P. longiceps* and *P. occidentalis*, but it differs materially in the slope or pitch of the supraoccipital. In the side view of this skull (Plate II, figure 1), it will be seen that a line carried out in extension of the basisphenoid passes through the apex of the supraoccipital plate, which rises less abruptly in *P. ingens* than in the type skulls of the other species. The basal portion of the crest is accordingly deeper than in *P. longiceps*.

Another slight difference between the skulls of *P. ingens* and *P. longiceps* is seen in the arrangement of the open network of slender rods of bone forming the lower section of the interorbital septum, where it rests upon the basisphenoid. In *P. ingens*, the solid upper portion of the septum merges into the open fabric of the lower part. In *P. longiceps*, this transition is more abrupt, and there is a stout and well-defined inferior border to the solid upper portion. It is of course impossible to determine whether this minor difference, drawn from the two skulls only, is of taxonomic importance. Additional material may prove it to be merely an individual variation. The anterior border of the septum divides, right and left, into two branches whose upper ends abut against the under side of the frontal or prefrontal region. This structure is apparently similar to that admirably figured and described by Dr. Plieninger, from a fragmentary skull of Pteranodon sp., in his memoir entitled: "Beiträge zur Kenntniss der Flugsaurier," but the complete condition of the overlying elements in the roof of the skull here prevents a thorough examination.

The greatest value of the type skull of *P. ingens* lies in the excellent preservation of the palatal region. The lower aspect of the skull is similar to that of *P. longiceps*, as far as the latter is preserved, so that it is necessary to describe in detail only those structures of *P. ingens* that are lacking in other skulls of the genus.

To demonstrate the palatal region more clearly, a drawing (Plate IV, figure 2) has been prepared from this unique type skull, and every effort has been made to restore the

associated elements to their original form. The anterior border of the large palatal vacuity is the only part of the drawing which is conjectural.

The small curved and natural edge of bone in front of the basisphenoid, which in *P. longiceps* Professor Marsh supposed to be the posterior limit of a large and simple palatal vacuity, is here shown to be merely the rear border of a small oval foramen occupying in part the position of the small median vacuity of *Nyctosaurus*, described and figured by Professor Williston (*Jour. Geol.*, 1902) as the interpterygoid vacuity. In front of this extends a remarkable trident-shaped ossification, the slender and pointed median spindle of which is here identified as the parasphenoid. At the base of this element arises on each side a round and tapering rod, which projects diagonally forward and outward across the palatal vacuity, as shown in the figure. After fusing with the palato-pterygoid ribbon, which it overlies, it becomes continuous with the delicate transpalatine. In the fossil skull, the diagonal of the right side is broken close to its origin at the base of the parasphenoid, and the distal portion has been lost; the diagonal of the left side was broken midway of its length, and owing to the lateral crushing of the specimen the posterior part slightly overlaps its own forward extremity. The pneumatic canals pervading nearly every part of the skull are visible even at the fractures of these slender rods.

Dr. J. Versluys, Jr., of the University of Giessen, who has examined the type skulls of *Pteranodon*, has kindly expressed his satisfaction with the plate showing the form of the palatal region of *P. ingens*, although his views as to the homology of some parts of the skull differ from those of the present writer. Thus Dr. Versluys identifies as "basipterygoid processes of the basisphenoid" the oblique rods arising at the base of the parasphenoid; and accordingly he would apply the name of basioccipital to the ossification in the base of the skull supposed by the writer to represent the united basioccipital and basisphenoid.

There is perhaps no more convenient test for the interpretation of any reptilian cranium than the ease with which its homologies may be traced in the extremely generalized skull of *Hatteria*. The writer is confident, therefore, that when submitted to this test the homologies of *Pteranodon* as understood by Marsh and Williston will prove generally correct.

The sclerotic circle is composed of twelve thin plates of bone arranged with overlapping edges. In Plate III, figure 1, the left orbit of the type is shown as actually preserved. By removing the matrix from the orbit, the circle was exposed, pressed inward against the interorbital septum, the component plates being apparently little displaced from their normal position. As these parts are somewhat indistinctly rendered in the photographic plate, they are again shown in Plate V, figure 3.

#### *Supraoccipital Crest.*

The supraoccipital crest is better preserved than that of the type of *P. longiceps*, but here also an indefinite part has been lost. The form of the complete crest is known only from the fragmentary skull No. 2473, represented in Plate II, figure 2. Enough of the base of this cranium remains to show that it is of almost exactly the same size as the type skull No. 2594, and fragments of the wing bones also prove that the skeleton of which it was a part nearly equaled in size the type skeleton of *P. ingens*, No. 1175. The crest may have been flexible, for in all examples known it is found to be extremely thin, in the type its transverse measurement posterior to the supraoccipital plate

being only 3<sup>mm</sup>. To give a better conception of the complete skull, a composite restoration, based upon the type and No. 2473 jointly, is shown in Plate IV, figure 1.

Since the great supraoccipital crest is one of the most striking characters of the genus, it is of the highest importance to learn what its true function may have been. Professor Seeley in "Dragons of the Air," p. 70, has aptly compared the Pteranodon crest with those borne by the Cormorant and the Chamæleon, stating by way of explanation that the separate and movable crest of the Cormorant (*Phalacrocorax*) is not strictly the equivalent of the fixed crest of the pterodactyl. Although the Pteranodon crest is now known to have been much longer than it was supposed to be when first described, the recent animals referred to by Professor Seeley help greatly toward a satisfactory understanding of its function, especially when they are considered as stages in a developmental series including *Plotus* (the Darter), *Phalacrocorax*, *Chamæleo*, and *Chelydra*. A brief review of the comparative anatomy of these types of vertebrate crania may throw light upon the present discussion.

In *Chelydra serpentina*, the Snapping Tortoise (Y. U. Osteol. Coll., No. 5454), the united supraoccipital and parietals form a strong crest of considerable length (Plate V, figure 10). Dissection of the head shows that the main function of this crest is to furnish the origin of the divisions of the enormous *musculus temporalis*, which gives this tortoise its dreaded power to seize and lacerate its prey. Another noteworthy reptilian example of this structure is offered by the Chamæleon. Plate V, figure 11, of *Chamæleo vulgaris*, shows the remarkable extension of the parietals and supraoccipital, strengthened on each side by the elongated squamosals. The definition of the *temporalis* muscle given by Mivart (*On the Myology of Chamæleon parsonii*, *Proc. Zool. Soc. London*, p. 850, 1870), is quoted here:—

"*Temporalis*. This muscle is of prodigious size; and it would be interesting to know what is the use to the Chameleon of so singularly voluminous a temporal. It springs from the whole surface of the temporal fossa, and from the occipital crest, where it appears on the back of the head, having the most anterior part of the *longissimus dorsi* on its inner side, and the *complexus* on its outer side. It is inserted into the upper border of the mandible, between the coronoid process and the articular surface."

Since the origin of the *temporalis* extends so widely over the lateral surface of the Chamæleon's crest, the inference may be drawn that the principal direct function of the crest is to serve for the attachment of this remarkably powerful muscle. The fact that the animal's feeding habits, as far as known, do not require any such development of the muscles for closing the jaws in no way invalidates this conclusion. As in *Chelydra* so here in *Chamæleo*, the insertions of the *longissimus dorsi* and of the *complexus* are situated so low down on the occipital arch that the crest is not to be considered as a lever to facilitate the elevation of the head. This is equally true of the insertions of the neck muscles in the genera of recent birds to which reference is now made.

The occipital styles seen in two genera of Totipalmate birds, *Phalacrocorax* and *Plotus*, have been the cause of considerable difference of opinion among zoötomists, and many thrusts have been given and parried on the subject of the "xiphoid bone" so aptly named by an early writer. William Yarrell, Esq., F. L. S., etc., whose instructive paper: "On the use of the xiphoid bone and its muscles in the Corvorant" (*Sowerby's Zool. Jour.*, vol. iv, 1828) contains two excellent engravings of the skull of *Phalacrocorax carbo*. Owing to the difficulty of reproducing these engravings, figures (Plate V, figures 13 and 14) have been made from a skull of *P. dilophus* (Y. U. Osteol. Coll.,

No. 538). to show the form and position of the occipital style and the attachment of the temporal muscles, the arrangement of these muscles being adapted from Yarrell's figure. As Yarrell's description of this structure can not be improved upon, it is quoted here:—

“This additional bone [occipital style] is about one inch in length, triangular in shape, somewhat grooved on its surfaces, and from its articulation with the *occiput* tapers gradually to a point. The mode by which this bone is articulated to the *occiput* is similar to that observed in the ribs of serpents, in which the condyle is situated upon each *vertebra*, and the cavity is at the end of the rib: so in the Corvorant, the condyle is upon the occipital bone, the cavity at the triangular end of the xiphoid bone: the joint is therefore hemispherical: admitting great extent of motion, the advantages of which will be hereafter pointed out.

“From the upper edge of this bone to its lateral angle throughout its whole length from the extreme point to the *occiput*, there arises on each side a triangular-shaped long muscle, the fibres of which are directed forwards, downwards and outwards to be inserted by a strong tendon upon the upper edge of the lower mandible. immediately behind the insertion of the tendon of the temporal muscle. The muscles of the upper part of the neck, giving motion to the head, are inserted upon the occipital bone and its elevated crest, over which these additional muscles slide with every movement of the head, the particular articulation of the xiphoid bone only permitting it to become a fixed point of support to its own particular muscles. when both act simultaneously as additional elevators of the lower mandible, thus assisting in prehension, and materially increasing the power of the bird in securing a slippery prey.”

The literature on the anatomy of *Plotus*, the Darter, is equally complete. Professor A. H. Garrod states in his paper: “Notes on the Anatomy of *Plotus anhinga*” (*Proc. Zool. Soc. London*, 1876):—

“In the Society's female specimen there is a fibro-cartilaginous similarly situated process, not more than one sixth of an inch long, which is ossified in the evidently older male. In his notes on the anatomy of the Cormorant, Hunter tells us that ‘a small bone, about an inch long, passes back from the os occipitis and gives origin to the temporal muscle, which is very strong.’ The same bone in the Darter, although comparatively not so long, performs the same function, the superficial temporal muscles meeting behind the skull along the median raphe, which becomes ossified to form the above-mentioned bony style in the adult bird.” Professor Garrod's drawing is exactly reproduced in Plate V, figure 12, although the length of the occipital style as it appears in the figure does not accord with the length given in the text.

In a later paper (*Proc. Zool. Society. London*, 1878). Professor Garrod records that in *P. levaillanti*, the African Darter, the temporal muscles run back beyond the skull, being separated by a median fibrous raphe, which is not ossified into a separate bony style.

In the five recent animals here referred to are seen four different stages in the development of an occipital crest, *Chelydra* and *Chamæleo* representing the same stage as far as the present discussion is concerned.

The first and lowest stage is that ascribed to *Plotus levaillanti* and to the female of *P. anhinga*, in which the enlarged temporal muscles meet behind the cranium and their line of contact has been occupied by a minute “fibro-cartilaginous process.” In the older male of *P. anhinga*, the second stage, the fibro-cartilage has become ossified and the process converted into a true bony style. In the third stage, represented by Phala-



crocorax, the occipital style or "xiphoid bone" has attained such size that it can no longer be overlooked in a hasty examination of the skull. Finally, in Chelydra and Chamæleo, the crest occupies about one-third the entire length of the cranium, and the muscles that are attached to it are the most prominent in the anatomy of the head. With the exception of Chamæleo, these animals are all noted for their skill in capturing fish.

To quote from a letter in which Dr. R. W. Shufeldt has kindly expressed his views, there is at present no doubt on the matter of the physiology of the occipital style: 'Owing to the character of the food (*living, struggling fish*) and the *mode* of feeding of such birds as Cormorants, Plotus, etc., it is undoubtedly a structure that has been developed in time, to afford an increased surface for the origin of the temporal muscles upon either side. The seizing and prehensile power of the jaws is thus manifestly increased.'

This statement applies equally well to the development of the crest in Chelydra and other chelonians, *e. g.*, the quasi-marine Toxochelys from the Upper Cretaceous of Kansas, whose skull in this respect is similar to that of Chelydra.

In all these examples, the relation of the crest to the temporal muscles is regarded as simple, and the function of the crest is supposedly limited to satisfying the need of increased muscular origin; the earlier stages of the development which culminated in the crest of Pteranodon may well have been similar to the developmental stages through which the ancestors of Phalacrocorax among birds and of Chelydra among reptiles have passed.

In Pteranodon, the temporal muscles must have extended from their mandibular insertions through the pterygo-jugal vacuities and so upward and backward to the large supratemporal fossæ. How far their origins spread posteriorly is not shown by the fossil remains; but in the absence of large bladeliike pterygoids, such as are present in the Crocodilia, it is evident that the temporal muscles were the principal elevators of the lower jaws, just as in the genera of recent birds and reptiles referred to above. And, as in these recent animals, the size and power of the temporal muscles could best be increased by extending their origins posteriorly along the sides of a median crest. Such a modification would have been strictly in accord with the general change of form which the skull of Pteranodon had undergone during its specialization.

The occurrence of Pteranodon remains in the chalk deposited in a shallow sea and at a distance of not less than one hundred miles from the probable shore line, also the shape and proportionate size of the jaws, have given rise to the supposition that this pterodactyl lived principally upon small fish taken at the surface in a manner somewhat similar to that adopted by the Skimmer, Rhynchops, which is said to feed as it skims low over the water with the fore parts inclined downward, the under mandible grazing or cutting the surface. If this were true, it would add greatly to the probability that Pteranodon originally developed a crest in the same way that certain piscatorial birds have developed theirs. It is scarcely imaginable, however, that the temporal muscles of the pterodactyl extended backward along the entire length of the fully developed crest, as in Phalacrocorax, Chelydra, and Chamæleo; and in order to account for the complete development of this part it seems necessary to fall back upon the general theory that growth along certain lines may be initiated through the exercise of one function, while further development is dependent upon another totally distinct function. Of what use the posterior part of the crest was to Pteranodon remains largely conjectural. The high crest carried by the head of the male Basiliscus, to which in regard to form and direction Professor Marsh compared the Pteranodon crest, is strictly exoskeletal, and therefore is of little assistance in the present case. The weight of the crest would appear not to

be required as a counterpoise to the long jaws of Pteranodon, for the form of the cervical vertebræ indicates a strong musculature of the upper part of the neck; neither the weight of the crest nor its effect as a vertical aëroplane, however, can be entirely disregarded.

The principal measurements of the type skull of *P. ingens*, No. 2594, are as follows:—

Total length of specimen . . . . .	840 mm
Length from occipital condyle to distal end of quadrate . . . . .	153
Transverse diameter of occipital condyle (approximate) . . . . .	13
Depth of mandible immediately in front of articulation . . . . .	34
Length of occipital condyle to posterior end of imperfect crest . . . . .	515

The length of the complete crest of No. 2473, from the center of the occipital condyle to the tip of the crest, is 784 mm.

#### SKULL OF PTERANODON OCCIDENTALIS MARSH.

The imperfect skull No. 1179 (Plate III, figure 2) is evidently the one referred to as *P. occidentalis* in the definition of *P. longiceps* (*Am. Jour. Sci.*, June, 1876, p. 508), where Professor Marsh stated that the skull of the latter "is somewhat larger than *P. occidentalis* Marsh. which apparently has more slender jaws." His notes also furnish collateral evidence on this point, yet for some reason this specimen was never fully described. No. 1179 may therefore be regarded as one of the types of *P. occidentalis*. Not only is this skull of about the same relative size as the smallest individual of the genus, which fact presumably had much to do with its original reference to *P. occidentalis*, but it differs materially in form from the type skulls of the two other species. The figure shows that the posteriorly directed face of the supraoccipital rises more sharply in this species than in the type of *P. longiceps*, in this regard the difference between *P. occidentalis* and *P. ingens* being even more striking. The supraoccipital crest is smaller than in the type skulls of other known species, and the curved and regular form of its superior margin favors the supposition that it is here practically complete, while in *P. ingens*, No. 2594, and *P. longiceps* more or less of the crest has been lost.

The apparent slenderness of the jaws alluded to by Professor Marsh is not an altogether satisfactory character. While it is true that in its present condition the left mandibular ramus is not so deep immediately behind the symphysis as are the same parts of *P. longiceps* and *P. ingens*, there is some doubt whether the inferior margin of the mandible may not have been broken away at this point. If the rami were no deeper immediately behind the symphysis than this fragment indicates, it would appear impossible for the transverse diameter of the mandible to approximate the corresponding measurement of the maxillary arch. The angular part of the mandible posterior to the articulation is missing, and the connection between the maxillary arch and the basal portion of the skull has been destroyed. With the exception of the points of difference already mentioned, the skull in its general form is similar to those of the other species.

#### *Measurements of Skull No. 1179.*

Distance from occipital condyle to distal end of quadrate . . . . .	75. mm
Distance from occipital condyle to apex of supraoccipital surface . . . . .	46.
Diameter of occipital condyle . . . . .	7.5

## CERVICAL VERTEBRÆ OF PTERANODON.

The cervical vertebræ are nine in number, counting the elementary atlas and axis as the first two units of the column. This is proved beyond all doubt by comparing the cervical series in the type of *P. ingens*, No. 1175 (Plate VI, figures 1–6), which consists of the seven anterior vertebræ, with the parts preserved of the cervical series of a smaller example of *Pteranodon* sp., No. 2692 (Plate VI, figures 7–9), in which the complete seventh, eighth, and ninth vertebræ remain in their natural sequence. Both these series have been slightly restored by the artist. In all examples of the genus found in the collection, the atlas and axis are coössified, and neither in the small type of *P. longiceps*, No. 1177 (Plate VI, figure 11), nor in the much larger *P. ingens*, No. 1175 (Plate VI, figures 1 and 12), is it possible to trace readily the limits of the elements theoretically composing these united vertebræ. As the atlas and axis of *P. longiceps* have been crushed transversely, while the same parts of *P. ingens* have been subjected to pressure in the axial direction only, the true form of these bones may be more easily understood by a comparison of the two figures mentioned. Viewed laterally, these vertebræ have much the same appearance as the corresponding parts of *Nyctosaurus*, figured by Professor Williston (*On the Osteology of Nyctosaurus*). Above the neural arch, which is proportionately smaller than in *Nyctosaurus*, the thin spine extends upward and backward in an easy curve. At its mid-height, the wide-spreading postzygapophyses are given off. The sides of the axial centrum are excavated deeply, thus materially lessening the weight. In the types of *P. ingens*, Nos. 2594 and 1175, pneumatic foramina may be seen leading forward and backward from the lateral excavations. In the posterior view, the convex oval termination of the centrum appears more produced transversely than that of *Nyctosaurus*, and the supplementary articulating processes, termed by Professor Williston the exapophyses, are not confluent, but remain separate and distinct as in the other cervicals. That these vertebræ, in spite of their apparently massive form, were extremely light, is also indicated by the paired fenestræ seen on the posterior wall of the arch, a little above the level of the neural canal. The delicate cancellous structure disclosed within may have been occupied by the pneumatic cells that seem to have pervaded nearly all parts of the skeleton in this genus.

The third, fourth, fifth, sixth, and seventh cervicals are alike in general form, and the slight differences which they offer lie in their comparative lengths. There can be no serious doubt as to the natural sequence of these vertebræ, for in *P. ingens*, No. 1175, they were preserved in so close juxtaposition as to lead to the conclusion that they had been but little disturbed before being covered by the chalk matrix. The measured lengths of the cervical centra of this example are as follows: Third, 61 mm; fourth, 67 mm; fifth, 83 mm; sixth, 76 mm; seventh, 65 mm. From this it would appear that of these five vertebræ, the third cervical was the shortest, the fourth and fifth successively increasing in length, and the sixth and seventh again becoming shorter, the length of the seventh being reduced nearly to that of the fourth. This sequence is substantiated in part by *P. ingens*, No. 2594, where the length of the third cervical is but little greater than that of the united atlas and axis to which it remains attached. The fourth vertebra of No. 1175, anterior and posterior views of which are shown in Plate VI, figures 13 and 14, is very similar to the other long cervicals, and has been already described by Professor Williston (*Restoration of Ornithostoma*) as follows:—

"The centrum is elongated. The ball is much broader than high, and strongly convex in both directions; its upper border is convex, but the inferior margin is emarginate on each side. . . . there is a stout process, jutting downwards and backwards from the side of the centrum on each side, having on the posterior surface a concave articular facet, oval in shape and touching or slightly separated from the articular surface of the ball. The facet looks downwards, backwards, and outwards. . . . The corresponding articular facets on the anterior end of the centrum are somewhat smaller, are convex and distinctly separated from the concavity of the centrum. The articulation of the centra with each other thus depends upon three distinct, or nearly distinct surfaces, the lateral inferior ones convex on the cup end, concave on the ball end. Such a mode of articulation would seem to limit the motion to one in a vertical, antero-posterior plane, while greatly strengthening the joints. I know of no similar arrangement in any other vertebrate animal, and will, for convenience, call the articulations exapophyses. The anterior zygapophyses project distinctly beyond the plane of the cup and are widely separated from each other. From the tip of the processes a ridge runs downward and inward to the outer part of the pre-exapophyses. The post-zygapophyses are concave and oblique. Above them there is a stout metapophysis.<sup>1</sup> The spine is elongate and thin, and apparently only a ridge."

The elongated cervicals all possess distinct tubercular hypapophyses, which project from the anterior ends of the centra beneath the oval articular cups. The vertebræ are lightened by pneumatic canals, which enter the centra midway of the sides, and also by paired canals that under favorable conditions of preservation may be seen at both ends a little above the level of the neural canal. The first seven cervicals are without ribs.

The eighth and ninth vertebræ resemble each other closely, but differ greatly from those preceding them. Their form is well preserved in *Pteranodon* sp., No. 2692 (Plate VI, figures 8 and 9, figure 10 portraying diagrammatically the anterior view of the eighth cervical). The centra are short, their length and breadth being nearly equal. The articular facets of the prezygapophyses and preëxapophyses remain much the same as in the elongated cervicals, but their basal portions are produced laterally to form transverse and capitular processes bearing ribs. The ribs of the eighth cervical somewhat resemble the hatchet ribs characteristic of these vertebræ in certain other groups of Reptilia. but they are little produced anteriorly and posteriorly. They are firmly coëssified with the supporting processes. The right rib of the ninth cervical is of the usual double-headed form (Plate VI, figure 16). Its diameter is comparatively small and its length is only about one-half that of the first dorsal ribs. Evidently it did not reach and connect with the sternum. A pair of short double-headed ribs found with *P. ingens*, No. 1175, the right member of which is shown in Plate VI, figure 15, probably belonged to the missing ninth cervical. From the inferior margin of the articular cup of the eighth cervical projects a small hypapophysis. It is slightly bifid in two examples in the collection; in others, both large and small, the hypapophysis is simple, but because of the incompleteness of the types, it is impossible to make use of these differences as specific charac-

<sup>1</sup> In this instance, Professor Williston evidently uses the term metapophysis in a general sense, just as he does in his paper on the Osteology of *Nyctosaurus*. Another authority informs us that we must apply this term only to the "apophysis developed on the prezygapophysis or anterior articulating process of a vertebra."

ters. The centrum of the ninth cervical bears no hypapophysis. The articular facets of the postexapophyses of the eighth and ninth cervicals remain much the same as in the vertebræ preceding them, but there are no posteriorly directed processes below these facets. Instead of curving backward in the bladelike form characteristic of the third to the seventh cervicals, the neural spines rise straight upward and are abruptly truncated at their full height. When these vertebræ have been crushed in the axial direction and the thin neural spines have been destroyed, the stout processes, termed by Williston metapophyses, assume the appearance of bifid spines.

## DORSAL VERTEBRÆ.

In a short paper entitled: "Note on American Pterodactyls" (*Am. Jour. Sci.*, vol. xxi. April, 1881), Professor Marsh wrote: "To aid the powerful wings [of Pteranodon] in flight, the pectoral arch is strengthened, (1), by the ankylosis of several vertebræ: (2), by the robust scapulæ articulating on opposite sides of the common neural spine of these vertebræ." This brief description was accompanied by a foot-note calling attention to a similar structure in some of the English Cretaceous pterodactyls also. Following this suggestion, Professor Seeley published an instructive paper: "On the Shoulder-girdle in Cretaceous Ornithosauria" (*Ann. Mag. Nat. Hist.*, May, 1891), in which he described the structure in *Ornithocheirus* Seeley, and figured a composite restoration of three dorsal vertebræ united by a "supra-neural ossification," with lateral facets for the scapulæ. The Marsh Collection contains several more or less perfect examples of the anterior dorsal or notarial vertebræ of Pteranodon. These have been carefully prepared in order to ascertain, if possible, the exact number of anchylosed vertebræ and their form. The best preserved notarium is that of Pteranodon sp., No. 2692. Photographic views showing the actual condition of the left and right sides may be seen in Plate VII, figures 1 and 2. Attention should be called to the fact that the last cervical is still in contact with the notarium. The slight dislocation it has suffered is apparent only in the view from the right side. Obviously, to separate this ninth cervical from the notarium would necessitate destroying its delicate rib. While this specimen is by no means complete, it is possible, by supplying the missing portions of one side from those preserved on the other, to reconstruct accurately the original form. Figures 1, 2, 3, and 4, of Plate VIII, have been made in this way to show the notarial vertebræ as seen from the left side, from the front obliquely, from above, and from below, respectively. These diagrams are slightly at fault in that they represent the ribs as issuing nearly at right angles to the vertebral column; the ribs were probably directed a little posteriorly. The most important characters of this series of vertebræ in No. 2692 are as follows:—

The centra of the eight anterior dorsal vertebræ are firmly coössified. The dorsal spines are bound together and surmounted by a thin median ossification, the supraneural plate, which is fused with their upper extremities. The vertical depth of this median ossification is greatest above the interval between the third and fourth dorsal spines, where on each side it presents an oval facet for the lodgment of the upper ends of the scapulæ. These eight vertebræ are also bound together by paired ossifications that extend the length of the notarium, fusing with the ends of the transverse processes in the same manner that the supraneural ossification unites with the dorsal spines. The centrum of the first dorsal is the largest of the series. Its length and breadth are about

equal and the oval articular cup and anterior articulating facets resemble those of the last cervical. The transverse and capitular processes are remarkably large, and are completely fused with the stout ribs which they support. Posteriorly, the centrum of the first dorsal vertebra is so perfectly coössified with that of the second dorsal as to be inseparable and almost indistinguishable from it. The postexapophyses of the first dorsal and the preëxapophyses of the second are only vestigial. The centrum of the second dorsal vertebra is narrower than the first centrum. The transverse and capitular processes are much lighter, as are also the anchylosed ribs which they support. Since the sutures are effaced, it has become impossible to determine accurately where the capitula proper of the ribs begin and the corresponding processes end. This is also true of the preceding vertebra and its ribs. In the second dorsal, however, the capitular processes are given off from the centrum at a slightly higher level. The third centrum is united to the second without the aid of exapophyses. The slender anchylosed rib which it supports is still of the double-headed form, but the capitulum is situated so high up on the centrum that the foramen enclosed by the two branches of the rib is greatly reduced in size. The centra of the five succeeding vertebræ, the fourth, fifth, sixth, seventh, and eighth of the notarium, progressively diminish in breadth until they become nearly circular in section, being constricted in the middle and expanded at the ends. Toward the end of the series, the fusion of the centra is possibly a little less complete, and in one specimen, No. 2699, the fifth and sixth vertebræ were found slightly displaced, the exposed ends showing anteriorly a cup and posteriorly a reciprocal convex articular surface. The zygapophyses, too, which are completely fused anteriorly, appear less thoroughly united toward the rear end of the notarium. In the posterior vertebræ of the series, the transverse processes are a little longer and are given off higher up on the neural arches; in fact, they originate considerably above the level of the neural canal. Both the transverse processes and the neural spines are slighter than those of the anterior dorsals. No ribs are in place behind the third pair, but the indications are that all the posterior dorsal vertebræ carried slender single-headed ribs. With the notarium of No. 2692, one free dorsal vertebra was found which is similar in form and size to the last notarial, and may be accordingly regarded as the ninth of the dorsal series. In another and larger example of *Pteranodon* sp., No. 2616; four dorsals similar to the free dorsal of No. 2692 were found in close contact with each other, though not in perfect articulation (Plate XIII, figure 1; also Plate VI, figures 17-20). Like all the separate precaudal vertebræ, these four free dorsals are procœlous. Judging from the character of the articulating surfaces, both central and zygapophysial, of the three anterior vertebræ of this series, and from the condition of the distal end of their transverse processes and neural spines, which are not modified for attachment with either notarium or pelvis, they are evidently free vertebræ. Front and rear views of the first vertebra of this series are shown in Plate VI, figures 21 and 22. These same figures would equally well portray the characters of the free dorsal found with No. 2692. The fourth vertebra differs from the three preceding in having some further osseous development at the extremity of its neural spine. This may be the vestige of a median longitudinal band uniting the neural spines of the sacral vertebræ. Unfortunately, the anterior portion of the sacrum of No. 2616 is not preserved, so that it is impossible to determine to what extent the vertebra in question may have been connected with the sacral series. Other examples of the genus offer clearer evidence upon the number of free dorsals and are briefly described.

In *Pteranodon* sp., No. 2451, which is a little smaller than No. 2692, there are preserved the last two notarial vertebræ so completely fused that they are as one bone: next, three separate dorsal centra, and following these the four anterior centra of the sacral series inseparably fused together (Plate XII, figure 1). While this sacrum is manifestly incomplete, enough remains to show that ten vertebræ enter into its composition, three of them anterior to that vertebra whose transverse processes share in the formation of the anterior pelvic brim. Without anticipating further the discussion of the sacrum, it seems best to designate in this way one of the sacral vertebræ which will serve as a fixed point in calculating the number of dorsal vertebræ.

Again, in the type of *P. ingens*, No. 1175, there are preserved three dorsal vertebræ. In these, the articular surfaces of the centra and of the zygapophyses indicate a little movement, which of course argues in favor of their supposed location between notarium and sacrum. The sacrum of this type, to be described later, is composed of a thoroughly fused column of ten vertebræ, the fourth member of the series bearing the transverse processes that partly define the anterior pelvic brim. No. 2451 and No. 1175 thus appear to differ from No. 2616 in having only three free dorsals. There is, however, not the slightest evidence that the total number of vertebræ is variable. The possible existence of a fourth free dorsal in No. 2616 is best explained by referring to the fragmentary pelvis of *Pteranodon* sp., No. 2489 (Plate XIII, figure 3), in which the sacral vertebræ number but *nine*, the *third* member of the series giving rise to the transverse processes which enter into the formation of the anterior pelvic brim. This matter will appear more clear after the pelvis has been described in detail.

The series of notarial vertebræ finds its counterpart in the consolidated dorsal vertebræ of many recent birds; and as the musculature of birds and reptiles is also much the same, a study of the avian dorsal region will help toward a better understanding of the notarium of *Pteranodon*. The subject can be best introduced by quoting from Newton's "Dictionary of Birds," p. 854: "In many birds the thoracic vertebræ shew a tendency to more rigid junction, which is often effected in old individuals by the ossification of the various ligaments connecting the processes of adjoining vertebræ, or even by the ossification of the attached tendons of the spinal muscles. In other cases consolidation is carried further by the co-ossification not only of the centra but also of the spinous, transverse and zygapophysial processes of adjoining vertebræ, so that in extreme cases the whole dorsal region may become one continuous mass of bone."

If the eminent writer of the foregoing quotation had been describing the notarium of *Pteranodon*, his words could hardly have been better chosen, so nearly does the pterodactyl resemble the extreme case cited. This coalescence of dorsal vertebræ in the avian skeleton is generally regarded as directly correlated with increased power of flight. Such was clearly the view of Sir Richard Owen when he wrote (*Comparative Anatomy and Physiology of Vertebrates*, Vol. II, p. 17): "The neural spine is a compressed quadrate plate, its truncate summit is often thickened, sometimes produced forward and backward to fix the vertebræ from their highest points: ossified tendons of spinal muscles, also, aid the coalesced spinous and transverse processes in fixing part of the dorsal region, but only in birds of powerful flight, and not in all such. The partial ankylosis of the dorsal region is associated in Falcons with their 'hovering' action." The exception to the rule is happily stated, for in the Frigate-bird, of extremely wide wingspread and noted for its powers of flight, the vertebral column anterior to the pelvis retains its flexibility to advanced age, if not throughout life, the vertebræ remaining

unfettered by ossified tendons and ligaments. On the other hand, the Gallinaceous birds, a group incapable of long-sustained flight, have the anterior dorsal vertebræ rigidly connected by the coössification of the dorsal spines and of the transverse processes, the hypapophyses also being more or less united in the same manner.

Drawings have been made of the dorsal and sacral vertebræ of three representative adult birds, and the writer has attempted to identify the points of attachment of the muscles of the trunk by comparison with the excellent figures and definitions given by Dr. Shufeldt in "The Myology of the Raven." Figure 1, Plate IX, is taken from a skeleton of the Burgomaster Gull, *Larus glaucus* (Y. U. Osteol. Coll., No. 2290). The squarely truncate summits of the dorsal spines are made to appear bifurcated behind by the tendons of origin of the longissimus dorsi, which lie close against the spines of the succeeding vertebræ. Underneath these and hidden by them are other paired tendons, which are directed forward from the summits of the dorsal spines and which presumably afford insertion for the same muscle. Extending forward and backward from the ends of the transverse processes are tendons serving as further points of attachment for the longissimus dorsi and for the sacro-lumbalis. Plate IX, figure 2, shows the dorsum of the Coot or Scoter, *Oidemia nigra* (Y. U. Osteol. Coll., No. 429), in which the tendons arising from the dorsal spines are less developed than those of the previous example, while the tendons of muscles attached to the transverse processes have expanded into broad sheets binding the dorsal vertebræ firmly together in an almost inflexible column. In the dorsum of the Wild Turkey, *Meleagris gallipavo* (Y. U. Osteol. Coll., No. 360), the vertebral coalescence has reached its highest development (Plate IX, figure 3). The centra of four vertebræ are fused into one continuous mass, and their dorsal spines with the attached tendons are represented by a thin median plate of bone. Lateral flexion of this region is rendered equally impossible by the paired ossifications resulting from the fusion of tendons attached to the transverse processes. Since this consolidation of the dorsal vertebræ in birds, though usually associated with increased power of flight, is not brought about by ossification of the tendons of any muscles of the fore limb, but rather by the ossification of the tendinous origins and insertions of muscles of trunk and neck, it seems possible that the extent to which such development is carried may depend in some slight degree upon the physiology of the cervical region. Should this prove to be the case, there will be less difficulty in accounting for the marked variations of this structure in closely related groups of birds.

Comparing the figures of the notarium of Pteranodon with that of *Meleagris* just described, it will be seen that, with the exception of the presence in the pterodactyl of a supraneural plate with oval facets for the scapulæ, these two animals have developed similar and equivalent structures; and, considering the general similarity of avian and reptilian musculature, there can remain little doubt that Pteranodon acquired its remarkable notarium by the same developmental process that may be traced in birds.

It is interesting to note that while in most birds the coalesced anterior dorsals are more or less rigidly connected with the posterior dorsals underlying the blades of the ilia, in *Meleagris* a free dorsal intervenes between the sacral or pelvic series and the anterior group, indicating slight flexibility in the same part of the vertebral column where in Pteranodon the writer supposes three or four free vertebræ to have persisted.



## SACRUM AND PELVIS.

The preservation of the sacrum and pelvis of the type of *P. ingens* Marsh, No. 1175, is remarkable, displaying to advantage the principal characters of these important skeletal parts. Plate X exhibits the slightly distorted form of this specimen, while restored diagrams have also been prepared to show the side, top, and bottom views, respectively (Plate XI, figures 1, 2, and 3).

Ten vertebræ firmly anchylosed together constitute the sacral series, using this term in its broader sense—the “synsacrum” of Professor T. J. Parker. The entire length of the inflexible column so formed is 184 mm. The extremities of the neural spines of all these vertebræ are united by a continuous median longitudinal band about 9 mm wide and about 6 mm in vertical depth. In general form, the three anterior members of this series are similar to the free dorsals which precede them. Their transverse processes arise from the sides of the neural arch above the level of the centra and are fused distally with the anterior blades of the ilia. The first of these vertebræ bears anterior zygapophyses for articulation with the last free dorsal, and the transverse processes of these three anterior vertebræ have on their lower surfaces small facets for the support of ribs, as is frequently the condition in the avian sacrum. These facets are most distally situated on the transverse processes of the first vertebra, least so on those of the third. What appears to be the proximal portion of one of these ribs still lies upon the third vertebra with little displacement from its original position. The distal ends of the transverse processes of vertebra 4 extend downward and backward as stout buttresses, which support the ilia more broadly than do the transverse processes of the preceding and of the following vertebræ. The transverse processes of vertebræ 5, 6, and 7 are separated by much smaller foramina, and they unite distally to form a continuous support for the ilia, as in some herbivorous Dinosaurs. The three remaining vertebræ, numbers 8, 9, and 10 of this series, bear shorter transverse processes arising more nearly at the level of their centra; they are separate at their distal ends, which connect with the ilia. Their neural spines also aid in supporting the pelvis.

The ilia extend forward as broad thin plates resting against the transverse processes of the anterior sacral vertebræ. Posteriorly, they unite with the transverse processes of vertebræ 8, 9, and 10. They also converge medially on the dorsum and fuse with the median longitudinal band over the neural spines of vertebræ 8, 9, and 10. So complete is the anchylosis of these parts that they can not be differentiated with any degree of certainty.

The united pubes and ischia are directed downward and backward, and meet below in a 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 the prepubes. The prepubes of this example have not been preserved, and in no specimen in the Marsh Collection have they been found in place. Plate XVI, figure 3, shows the prepubis belonging to *Pteranodon* sp., No. 2472, which is about the size of No. 1175.

The remarkable similarity of *Pteranodon*'s sacrum to those of many recent birds is distinctly brought out by comparing it with the sacrum of the Wild Turkey, *Meleagris*

*gallipavo*<sup>1</sup> (Y. U. Osteol. Coll., No. 2112), shown in Plate IX, figure 4. Morphologically considered, the fourth synsacral vertebra of *P. ingens*, No. 1175, is clearly the homologue of that vertebra in the avian sacrum here figured, whose transverse processes aid in the formation of the incomplete anterior pelvic brim, and also bound anteriorly the fovea containing the kidneys. The three following vertebræ of *P. ingens*, numbers 5, 6, and 7, occupy precisely the same position as those avian vertebræ which Huxley identified as true sacrals, on the ground that the nerves issuing from their intervertebral foramina form the sacral plexus. It has been already pointed out that vertebræ 8, 9, and 10 of the synsacrum of *P. ingens* support the posterior extensions of the ilia both by their transverse processes and also by their neural spines, in this regard differing from vertebræ 5, 6, and 7, and resembling the "posterior parapophysial vertebræ" of the avian sacrum, to adopt the phrase used by Messrs. Mivart and Clarke, in their treatise: "On the Sacral Plexus and Sacral Vertebræ of Lizards and other Vertebrata" (*Linn. Soc. Trans.*, 2nd series (Zool.), vol. i, p. 513). The following quotation from the scholarly work of these gentlemen is of especial interest in this connection:—

"The determination of the homological relations of the different parts of the post-dorsal part of the spinal column of Birds is a matter of much difficulty. It might be anticipated, however, from the close relations and probable genetic affinity between Birds and Reptiles, that the true sacral vertebræ of the former class might be readily determined by the aid of reptilian characters. But however close may be the morphological affinities, they are so strangely disguised by great physiological differences, that the results of comparison are much too unsatisfactory to justify the anticipation above referred to. The enormous forward prolongation of the iliac bones and the great power and activity of the erect and vigorous legs of birds, compared with the backwardly extending ilia and the sprawling and feebly pushing legs of Saurians, combine to produce in Birds a redundancy of both osseous and nervous structures compared with those of the existing Reptilia. Could we dissect the different forms of *Pterosauria* and *Dinosauria*, these difficulties and obscurities would no doubt disappear; but the hiatus is too great between the most Sauroid of existing Birds and any form of Lizard for the homological relations, in this respect, to be readily and easily solved."

Returning to Pteranodon, certainly no form of reptilian sacrum could be desired by Paleontologists, which should approach more closely the common type of avian sacrum. The difficulty lies not in comparing Pteranodon's sacrum with that of Birds, but in reconciling its peculiar specialized development with the simpler forms known in other Reptilia.

Since the eighth and ninth vertebræ of the synsacrum of *P. ingens* so closely resemble the two "posterior parapophysial vertebræ" of the avian sacrum, it will be instructive to compare the sacrum of *P. ingens* with that of an older and more primitive pterosaur. Quenstedt's plate of *Pterodactylus (Cycnorhamphus) suevicus*, published in 1855 (*Ueber Pterodactylus suevicus*), shows two anchylosed vertebræ whose transverse processes unite distally to support the ilia. Immediately in front of these two sacrals is a somewhat longer vertebra, described by that author in the following words:—

"Nicht minder interessant als das Kreuzbein ist der starke Wirbel Nro. 22, man könnte ihn den Kreuzbeinträger nennen, denn seine überaus kräftigen Querfortsätze gehen plötzlich unter einem Winkel von 60° gegen die Medianlinie nach hinten, ragen die Hälfte

<sup>1</sup> In this case, the sacrum of a young bird has been chosen for illustration. The transverse processes of the avian vertebra referred to appear to be ossified from separate centers.

ihrer Länge über den Wirbelkörper hinaus, um mit ihrer fast vierseitigen Endigung dem Knochenwulste des Kreuzbeins so nahe zu treten, dass dadurch eine besonders feste Verbindung möglich wurde."

That vertebra of Pteranodon's synsacrum whose long backwardly directed transverse processes mark the anterior limits of the renal depressions bears the same relation to the three following vertebræ as does the twenty-second vertebra of Quenstedt's specimen to the two vertebræ which follow it. Obviously, the two united vertebræ of *Pterodactylus suevicus* supporting the iliac bones are true sacrals, for the following vertebræ have no pelvic connection. Applying the terminology of the simpler case to the more complex, it is evident that the fifth, sixth, and seventh vertebræ of Pteranodon's synsacrum are to be considered true sacrals rather than the two following, whose place in the series so closely resembles that of the two "posterior parapophysial vertebræ" regarded by many recent authors as the true avian sacrals. The definition of the sacral vertebræ used by such authors can not then be applied to the extremely birdlike Pteranodon, and it seems best to retain for this highly specialized pterosaur the simpler definition used by Professor Huxley.

Four other fragmentary sacra preserved in the Marsh Collection are figured here. Three of these, Nos. 2451, 2570, and 2616 (Plate XII, figures 1, 2, and Plate XIII, figure 2) closely resemble the sacrum of *P. ingens*, No. 1175, except in their dimensions, which are much smaller. As they are unaccompanied by other skeletal parts of taxonomic value, they may belong to any of the three species of Pteranodon, and no useful ends would be attained by arbitrarily giving them specific names. Two of these specimens have been already alluded to in the discussion of the dorsal vertebræ. Plate XIII, figure 3, shows the sacrum of Pteranodon sp., No. 2489, to which reference has also been made in the preceding pages. Great interest attaches to this specimen because of the reduced number of its vertebral parts. The synsacrum is here composed of only nine vertebræ, and as stated above it is not the fourth vertebra, but the third of the series, which sends out the stout transverse processes forming the anterior bounds of the renal depressions. So little is preserved of the rest of the skeleton of No. 2489 that it is quite impossible to determine the taxonomic value of this marked variation. This condition is of course more primitive than that seen in the other sacra, and indicates how near the sacrum of Pteranodon may approach that of the allied genus *Nyctosaurus*, figured by Professor Williston (*On the Osteology of Nyctosaurus*), where the second synsacral vertebra bears the stout transverse processes.

It is important to note that the anterior synsacral vertebra is in every case firmly anchylosed to the following member, whether there are ten vertebræ in the series or only nine: the first vertebra included in the synsacra of Nos. 1175, 2451, and 2570 can not then be considered as an insecurely attached unit, which may or may not retain its connection with its fellows according as the local conditions at the time of interment were quiet or disturbed. The coalescence of the synsacrals must have taken place early in the development of the individual.

#### CAUDAL VERTEBRÆ.

The number of caudal vertebræ in Pteranodon is not definitely known, but the opinion of Professor Marsh and Professor Williston expressed in various papers, that the tail

was short, is well supported by the material preserved in the Marsh Collection. In *Pteranodon* sp., No. 2489, five free caudal vertebræ have been preserved, and are shown from above, obliquely, in Plate XIII, figure 4. These apparently followed the three primitive caudals or urosacrals forming the posterior division of the synsacrum. They dwindle rapidly in size, and although badly crushed, are supposed to indicate a length of tail of from 12 to 16<sup>mm</sup> in an animal about nine-tenths the size of *P. ingens*, No. 1175. So short a caudal member could have been of little service as a rudder, and the animal must have depended largely or wholly upon other means of guiding its flight. It will be remembered in this connection that other practically tailless forms of flying animals have no apparent difficulty in directing their movements. Plate VI, figure 23, shows the lower surface of four caudal vertebræ of another example of this genus, No. 2546, about the same size as No. 2489. These vertebræ are still contained in the matrix and presumably represent the middle third of the caudal series.

The caudal vertebræ have been described by Professor Williston as amphiplatyan (*Kansas Univ. Quart.*, vol. vi, No. 1, Jan., 1897), while Professor Gadow (*Amphibia and Reptiles*) regards the caudal vertebræ of all Pterosauria as amphicœlous. Some of the larger caudals of *Pteranodon* in the Marsh Collection appear slightly concave at both ends, but their original condition is uncertain, their form having been greatly altered by pressure. It is to be expected that the character of the central articulations would be somewhat obscure in the degenerate tail ascribed to this genus.

#### SHOULDER GIRDLE.

The shoulder girdle, consisting of the scapula, coracoid, and the sternum, has been so fully described by Professor Williston that little further remains to be recorded about the osteology of these parts. Characterizing the sternum of one of the "smaller species" of *Pteranodon* (*Restoration of Ornithostoma, Kansas Univ. Quart.*, vol. vi, No. 1, Jan., 1897), Professor Williston writes: "It is extremely thin and [is] pentagonal in outline. Projecting in front of the articulations for the coracoids is a stout process, obtusely pointed, and evidently directed somewhat ventrally in life. The articular facets [for the coracoids] look dorsad and laterad and are gently convex from side to side and concave antero-posteriorly. Just back of the articulations the moderately thickened borders slope obliquely backward to the full width of the bone. The first articular facet for the ribs begins at the angles and runs backward a half inch. It is of considerable thickness, and may be for the attachment of the stout co-ossified rib attached to the first of the consolidated dorsal vertebræ. The lateral margins of the sternum, back of the angle, are thin, and have three emarginations, separating four articular projections. The three posterior ones are small and pointed, and could have given attachment to only slender ribs. The lateral borders are parallel with the longitudinal axis of the bone. The posterior border is not preserved, but from the general resemblance to the bone in *Nyctodactylus*, I believe that it is nearly straight, although it may have been gently concave or convex. The bone was in all probability concave above in life."

No perfect sternum is known to the writer, and indeed such is the tenuity of the posterior border of the bone that none is likely to be found. Three more or less complete examples have been selected from which a fairly accurate idea of the entire bone may be obtained. Plate XIV, figure 1, shows the lower surface of the vertically crushed

sternum of a large animal, *Pteranodon* sp., No. 2546. Through comparison of other skeletal parts, this individual is known to be about nine-tenths the size of the type of *P. ingens*, No. 1175. Its specific identity, however, remains doubtful, as no skeletal parts of taxonomic value have been preserved. The inner or upper surface of the anterior portion of another sternum of slightly smaller size, No. 2616, is shown in Plate XIV, figure 2, while figures 1 and 2 of Plate XV are taken from the right and left sides, respectively, of a laterally crushed sternum, No. 2692. This last example is especially useful in giving an idea of the natural shape of the bone, which must presumably have been intermediate between the forms of those crushed vertically and those crushed laterally.

The nearly complete restoration of the sternum, No. 2546, shown in Plate XVI, figure 5, has been obtained mainly by replacing missing portions of one side by the corresponding portions preserved on the other side. The form of the manubrium has been determined partly from the impression left upon the matrix by the portion lost by the collector, and partly by recourse to the sternum of No. 2692. The four lateral articular projections described and figured by Professor Williston, and supposed by the present writer to be for the attachment of sternal ribs, are well shown both in this drawing and in the photographic view (Plate XIV, figure 1). There is also a fifth pair of projections that appear to be for articulation with a fifth pair of sternal ribs. A small round vacuity is seen in the midline close to the posterior border of the sternum. (This has been also observed in another specimen in the Marsh Collection.) Immediately in the rear of this vacuity is a pair of closely approximated articular projections, which probably served to connect with the abdominal ribs. There seems to have been another pair of articulations separated from the median pair by shallow emarginations, as shown in the restored figure, but the frail and imperfect margin of the bone here permits of no definite conclusions. On the right side of the sternum (the left in the figure) a small oblong ossicle lies in each of the first two shallow emarginations. Only one of these ossicles remains on the left side. Their significance is not understood by the writer.

The manubrium is evidently much deeper in the vertical direction than wide, and its sharp inferior edge is continued backward to the middle of the broad part of the sternum as a rudimentary keel. This is also the condition in the laterally crushed sternum of No. 2692, but in another example that has been subjected to great vertical pressure, as evidenced by the almost total obliteration of the coracoidal facets, no trace of the keel is to be seen. While it is not desired to convey the idea that *Pteranodon's* sternum bore a prominent keel for the attachment of the pectoral muscles, it would be equally erroneous to describe it as strictly of the ratite type.

The lateral halves of the broad and thin body of the sternum appear to have been of rounded form, so that this part of the bone may have resembled a shallow dish or trough, with the addition of the low keel-like process on the anterior portion. In the restored figure, the transverse measurement is of course somewhat reduced through foreshortening.

A posterior view of the right scapula and coracoid of *P. ingens* (type), No. 1175, is shown in Plate XVII, figure 1. The two united bones are defective behind and below the glenoid, and in order to assemble the fragments it has been necessary to replace the missing portions with plaster of Paris. The general outline will be found fairly correct, but no attempt has been made to restore the bone in detail. In size, this specimen exceeds all other examples preserved in the Marsh Collection. In the left scapula and coracoid of *Pteranodon* sp., No. 2512, a posterior view of which is shown in Plate XVII, figure 2, the general proportions are admirably preserved, although the bones are

slightly incomplete. Across the middle of the glenoid surface can be seen the suture between the component elements. Two views, front and rear, are shown of the left scapula and coracoid belonging to the smaller Pteranodon sp., No. 2616 (Plate XVIII, figures 1 and 2). The articular coracoidal facets of the sternum of this individual have been shown in Plate XIV, figure 2. Upon examination, these figures will be found to agree in the main with Professor Williston's admirable description of this part of the shoulder girdle in his paper entitled: "Restoration of Ornithostoma." In the right scapula and coracoid of Pteranodon sp., No. 1181 (Plate XXIII, figure 1), a deep and narrow depression lies immediately behind the glenoid surface. It is presumably the coracoidal foramen mentioned by Professor Williston. While no other specimen in the collection shows unmistakable evidence of this foramen, there is no reason for supposing that it was wanting in some of the species.

The following quotation is from Professor Williston's description of the "Coraco-scapula":—

"This bone is stout, U-shaped, with the coracoid arm distinctly longer than the scapular. The distal extremity of the scapula has a large oval facet placed obliquely to the long axis, and evidently also obliquely to the transverse axis of the body, indicating that the bone was directed not only outward and downward, but also more or less forward. The shaft in all the known specimens below the articulation is trihedral or flattened, but in life it was evidently round or oval in cross-section. On the lower part the width is greater, due to a projection of the dorsal side before the glenoid articulation, for the attachment of muscles. The glenoid articulation is deeply concave from above downward, convex from side to side and bounded both above and below by a prominent ridge, that on the inferior border being much stronger than the upper one. The surface is markedly oblique to the plane of the bone, doubtless in life directed outwardly and posteriorly in the oblique position of the bone that I have described. The surface is considerably narrower from side to side below than above, and in this direction [side to side] it is convex throughout. A rugose line, indicating the junction of the two bones, passes directly backward near the middle of the articular surface. At the bottom of the U, formed by the conjoined bone, there is a process arising from the scapula and reaching to the anterior surface of the coracoid, to which it is joined; it incloses a small, oval foramen just back of the middle of the glenoid surface. The diameter of the foramen is about twelve millimeters.

"The shaft of the coracoid is flattened antero-posteriorly in all the specimens, though probably in life oval. On its proximal half there is a prominent process on the inferior border for muscular attachment. From beyond the middle the sides of the bone are parallel. The sternal articulation is gently concave in one direction and slightly convex in the other, to agree with that of the sternum, forming a reciprocal joint, which must have had considerable mobility. A little above the sternal end, on the posterior side, there is a narrow rugosity, more than an inch in length, for muscular attachment."

The different skeletal parts comprising the thorax have been described separately and may now be considered in their joint relationship to the act of respiration. The only considerable and essential portion of the thoracic frame remaining in any doubt is the series of sternal ribs. As the writer is not aware that these have ever been positively identified in Pteranodon, it may be well to call attention to a small but seemingly complete bone (Plate XVI, figure 4) found with the skeleton of *P. ingens* (type), No. 1175. While this bone is only 41 mm in length, its form closely resembles that of some of

the sterno-costalia of *Campylognathus zitteli*, figured by Dr. Plieninger in: "Die Pterosauria der Juraformation Schwabens," p. 222.

The quotation from Professor Williston's "Restoration of Ornithostoma," in regard to the sternum, conveys the idea that one or more "coössified" *vertebral* ribs issuing from the anterior dorsal vertebræ were connected directly with the sternum; and the same eminent paleontologist has written concerning the more or less closely allied genus *Nyctosaurus* (*Osteology of Nyctosaurus*, p. 136): "There are apparently four pairs of stout ribs arising from the first four dorsal vertebræ, the first three of which, at least, are anchylosed to the centrum in the adult animal. They were doubtless all attached to the four tubercles on each side of the sternum." And again in the same work, p. 139: "It has been suspected that there are sternal ribs intervening between the vertebral ribs and the sternum, but there is no evidence of such in the present specimen."

The notarium of *Pteranodon* sp., No. 2692, already figured, proves beyond all doubt that the *vertebral* sections of the first three dorsal ribs are anchylosed to their vertebræ. If the lower ends of these vertebral ribs articulated directly with the lateral sternal projections, the sternum would be immovably fixed in its position; and, no account being taken of diaphragmatic breathing, which is at the most but rudimentary and negligible in *Aves* and *Reptilia*, this pterodactyl could have filled its lungs only by gulping air into them as do the *Chelonians* with fixed plastron. On general grounds, such limited respiratory action would seem inadequate in a flying reptile, the pneumaticity of whose skeleton almost or quite equaled that of the most lightly-framed existing bird.

More direct evidence on the question of the fixity or mobility of the sternum is offered by the peculiar saddle-shaped facets at the base of the manubrium sterni, for the articulation of the lower ends of the coracoids, a joint which Professor Williston himself stated "must have had considerable mobility" (see p. 26). There is no doubt whatever that Professor Williston is correct in his statement that the sternum moved upon the coracoids, although such a conclusion appears at variance with his ideas on the structure and connections of the dorsal ribs. The mechanical principle involved is simple, and from the diagram of the thorax (Plate XXXI), it will be readily seen that not only must well-developed sternal ribs have intervened between the anterior vertebral ribs and the sternum, but also that there must have been a slight rotation of the scapulæ upon the supra-neural facets of the notarium; otherwise there could have been no movement of the sternum. Even then the mechanical action of respiration would not be exactly equivalent to that prevailing in many reptiles and in birds, where both the vertebral ribs and the corresponding sternal ribs are free to move when drawn forward by the inspiratory muscles, the main action of these muscles being to straighten the angles between the vertebral and sternal sections of the ribs, and thus by the well-known principle of the "toggle-joint" to force the sternum away from the vertebral column.

In *Pteranodon*, on the other hand, the action of the thoracic mechanism was greatly lessened by the immobility of the anterior vertebral ribs, as well as by the complete anchylosis of the coraco-scapular union, an articulation which permits of considerable movement in almost all carinate birds; and the movement of the sternum was accomplished by swinging it bodily downward and backward about the distal ends of the vertebral ribs, to which points it was united by sternal ribs. Clearly, in this animal, the anterior vertebral ribs being fixed, the levatores costarum and the external intercostals would cease to function as contractile muscles, and in the adult pterodactyl they would probably degenerate into aponeurotic tissue, serving only to close the intercostal

spaces. Similar changes would probably take place in the expiratory muscles attached to the anterior vertebral ribs. On the other hand, those muscles of the thorax and abdomen controlling the movement of the sternum and sternal ribs would be developed in proportion to the respiratory needs of the animal.

#### WING BONES.

Of all the skeletal parts of Pteranodon, the wing bones perhaps offer the least inducement to further investigation. Obtained more abundantly at the outset by collectors, and usually in better preservation than the axial skeleton, they naturally form the subject of much of the earlier contributions to the osteology of this genus, with the result that their study has been carried nearly to completion. It is proposed in this memoir to figure the entire skeleton as far as it is possible to do so from specimens in the Marsh Collection, and some brief comment upon the wing bones may properly accompany their illustration without attempting to paraphrase descriptions, the excellent definitions recorded by Marsh, Williston, and Plieninger being easily accessible.

In the introductory pages of the present memoir, Professor Marsh's separation of the two species *P. occidentalis* and *P. ingens* is shown to have been based partly upon the relative size of the types and partly upon differences in the form of their humeri and of the proximal ends of their ulnæ. It is also stated that further work upon the collection has led the writer to the conclusion that these differences are of no taxonomic value, as they appear to be merely the variant results of unequal pressure in the matrix. It is impossible to record anything more satisfactory in regard to the proximal articulations of the ulnæ in question than the statement that these bones having been so greatly distorted. the wonder is, not that the original investigator gave undue importance to their differences, but rather that he so promptly recognized in them the same skeletal element.

In regard to the supposed specific difference of the two humeri, it is now possible to write more explicitly. When the humerus of *P. occidentalis* (type), No. 1164, was described by Professor Marsh, the "anconal" side alone was entirely exposed to view (Plate XIX, figure 9). He was therefore deceived by the appearance of the radial crest, which then seemed much smaller than the corresponding process of the humerus of *P. ingens*. Upon removing the matrix from the opposite side of *P. occidentalis* (Plate XIX, figure 10), it became evident that the radial crest had been crushed and shortened by pressure, and that no specific difference could be pointed out in these processes of the two types. The humerus of *P. ingens* (type), No. 1175, is somewhat better preserved than that of *P. occidentalis*, which it resembles closely except in size, and although the radial crest is by no means perfect, the generic characters of the bone are well displayed. Two views of this humerus are given, Plate XIX, figure 1, showing the "anconal" or dorsal surface, and figure 2, the palmar or inferior surface.

The vagaries of form assumed by the humerus under pressure in the matrix are surprising, the first result of this perplexing situation being that almost every humerus in the collection seems to represent a distinct species. From an examination of fourteen practically complete humeri of Pteranodon, variously distorted, it appears that pressure in the vertical direction (the vertebral axis of the pterodactyl being supposed to lie in the horizontal plane, with the wings outstretched laterally) usually crushes and shortens the radial crest, while pressure in the horizontal plane not only leaves the



radial crest extended at its full length, but also alters the head of the humerus in such a way that the radial crest appears to originate further from the proximal condyle.

A practical test of this theory has been obtained by performing the following simple experiments, adapted from Professor Daubrée's admirable method of artificial mountain-making: Two models of the humerus were made from soft clay, simulating the original form of the bone as closely as possible. These models were crushed between two flat surfaces, the direction of pressure in one instance being normal to the upper or anconal side, and in the other instance being normal to the radial side of the bone. The result of the first experiment was that the crushed model assumed the form of the humerus of *P. occidentalis* (type), while the result of the second experiment was that the model assumed the form of the humerus of *Pteranodon* sp., No. 2302, shown in Plate XX, figures 4 and 5. While these simple ossifragous experiments obviously failed to comply with the exact conditions prevailing in nature, they add considerable weight to the writer's opinion that the different forms of humeri shown in Plate XX are due solely to the varying conditions of pressure to which the bones were subjected. All doubt upon this matter would be removed if the humeri belonging to one individual were found differently crushed; unfortunately, in not one of the 465 examples of *Pteranodon* in the collection are the proximal portions of both humeri preserved.

In Plate XIX, figures 3, 4a, and 4b, the left ulna and the ends of the left radius of *P. ingens*, No. 1175, are shown, the palmar or inferior surface of the ulna being toward the observer. The proximal ends of the radius and ulna and the distal end of the radius, all three fragments belonging to the right wing of No. 1164, type of *P. occidentalis*, are shown in Plate XIX, figures 11, 12a, and 12b. Some of the bones of the left wing of *Pteranodon* sp., No. 2425, are figured in Plate XXI, just as they are preserved in the matrix. The radius and ulna are here practically entire, and appear to have retained their natural positions relative to each other, although their articulations with the humerus and carpus are dislocated. This specimen is also valuable for the excellent state of preservation of the two larger carpals, usually distinguished by the terms "proximal" and "distal." A view of the inferior or palmar surface of these bones, on a larger scale, is shown in Plate XXII, figure 1. A small slender bone of doubtful identity occupies the place of the third or lateral carpal in this specimen, but the process for the support of that carpal, arising from the radial side of the distal carpal, is admirably preserved. The reverse side of the slab containing this specimen has been excavated so as to permit Plate XXII, figure 2, to be made, which shows the dorsal side of the carpus. Three views of the left carpus of *P. ingens*, No. 1175, are given in Plate XIX, figures 6, 7, and 8. In figure 6, showing the proximal surface of the carpus, the distal carpal is nearly concealed, but the greater part of the lateral carpal is visible. Figure 7 is taken from the dorsal view of the carpus, all three bones being compressed in the direction of the axis of the wing. In figure 8, the distal view of the carpus, the outlines of the distal and lateral carpals are clearly seen, the latter borne by a process extending from the radio-palmar angle of the distal carpal. In assembling the carpus for illustration, it was found impossible to maintain a perfect contact between the distal and lateral carpals without rotating the lateral carpal slightly from that position in which it would best support the first metacarpal or "pteroid bone." The carpus of *P. occidentalis* No. 1164, shown in Plate XIX, figures 13 and 14, appears to be precisely similar to that of *P. ingens* just described, except that the lateral carpal of *P. occidentalis* is differently crushed and makes a better contact with the distal

carpal, when in the supposed natural position. The lateral carpal of this example has two foramina on opposite sides of the bone.

In another example of *Pteranodon* sp., No. 2683, the two larger carpals of the right wing are preserved with but little distortion, and the lateral carpal, although found in two separated fragments, has been restored well enough to be photographed in its supposed natural position relative to the main body of the carpus. The writer is not aware that the three carpals have yet been found in true contact in any example of the genus, and until either this is done or the lateral carpal is found in contact with the pteroid bone, it will remain an open question which end of the lateral carpal is rightly supported by the process arising from the radio-palmar angle of the distal carpal. Comparison with the European pterodactyls offers little aid toward the solution of this problem. In support of the position of the lateral carpal in the accompanying figures, it may be said that the articular sockets characterizing the ends of the bone are of unequal size, and the end of the bone bearing the larger socket may be reasonably supposed to be turned toward the distal carpal, inasmuch as the articular process of the distal carpal is considerably larger than the proximal head of the pteroid. In Plate XXII, figure 4, the main body of the carpus of No. 2683 is seen from the palmar side, as found in contact with the proximal end of the large fifth metacarpal. In figure 5, the carpus has been removed from the matrix so as to exhibit the dorsal side.

The form of the great metacarpal, recognized by most paleontologists as the fifth, is shown in Plate XXI, taken from the wing bones of *Pteranodon* sp., No. 2425. The dorso-radial surface of the bone is here presented to view. It will appear at a glance that all the sections of this wing are more or less dislocated. The characteristic forms of metacarpals II, III, and IV may be learned from such parts of these bones as are preserved, all three appearing to consist of extremely slender rods of bone closely pressed to the great metacarpal and expanding distally into rounded condyles for the articulation of the phalanges of the short clawed fingers. The greater part of the pteroid bone remains with its proximal head almost in contact with the carpus. Its shaft, however, has been turned from its normal position. In most specimens, the pteroid is directed nearly toward the head of the humerus. A complete pteroid may be seen in Plate XXIII, figures 1 and 2, showing the wing bones of *Pteranodon* sp., No. 1181. The bone bears a slight resemblance to the distal parts of the lateral metacarpals, next to which it lies in the matrix. It is, however, easily distinguished by its greater curvature at the articular end and by its stouter shaft. The question whether or not the so-called pteroid should be properly identified as the metacarpal of the first digit of the manus need not be entered into here, as there is no new evidence to be offered in support of either view.

Previous attempts to assemble the phalanges of the three clawed fingers of the hand, viz., digits II, III, and IV, have not been entirely successful. The best diagrammatic reconstruction of these parts was given by Professor Williston in his paper: "On the Osteology of *Nyctosaurus*." p. 145. In explanation of the figure, he states: "I give herewith a diagrammatic figure of these parts in *Pteranodon*, based on a specimen in which nearly all the bones were present and in position, some of the terminal phalanges only being misplaced, and one or two of the fourth finger missing. In a former paper I stated that the phalanges of the hand were of two kinds, long and short. Possibly this is the case in some of the smaller species, but I think not. I doubt not that the small phalanges there described were from the foot, and had become misplaced and

associated with the hand phalanges in the specimen described." In an article entitled: "The Fingers of Pterodactyls" (*Geol. Mag.*, February, 1904), Professor Williston gives the number of phalanges of the three clawed digits in the hand of Pteranodon, as two, three, four, respectively, but he does not discuss further the occurrence of the very short phalanx which he had previously noted.

No complete manus of Pteranodon with the parts in their natural position is found in the Marsh Collection, yet the specimens preserved afford conclusive evidence as to the number and arrangement of the phalanges. Figure 2, Plate XXIII, has been prepared to show to better advantage the phalanges of the right manus of Pteranodon sp., No. 1181. Although the bones are disarticulated, it is clear that there are here preserved five phalanges of moderate length, one very short phalanx, and three terminal claws. One of the longer phalanges has a deep process at the proximal end on the lower side. Judging from other material, this process appears to be characteristic of the first phalanx of the fourth digit.

In another specimen of Pteranodon sp., No. 2428, the greater part of the right manus is preserved; in fact, the claw-shaped distal phalanges only are wanting. In this manus, as well as in that of No. 1181, there is one very short intermediate phalanx whose length is but a trifle greater than its diameter. Plate XVI, figure 2, based upon No. 2428, presents the writer's mature views of the phalanges of the manus, which, it will be seen, are in accordance with the recognized general formula for the digits of the reptilian hand. The forms of the bones actually preserved are shaded, while the missing claws and the distal end of metacarpal II are represented in outline. The short phalanx already mentioned has been identified as the second phalanx of the fourth digit, thus agreeing perfectly with the condition generally prevailing in the older pterodactyls, where the second phalanx is considerably shorter than its proximal and distal neighbors. Professor Williston's doubt as to whether the short phalanges which he found associated with the manus might not have been interpolated from the foot is removed by comparing the diameter of the phalanges of the manus with those of the podials. The digits of the foot are so much more slender than those of the hand that they may be readily distinguished by their size alone. Three nearly complete digits of the right manus of Pteranodon sp., No. 2493, are shown in Plate XXII, figure 3. The arrangement of the phalanges is evidently unnatural, although these parts are said to occupy the same order as when discovered by the collector. The short phalanx of digit IV, which lies near the distal end of the metacarpal, has clearly been dislodged from its true position, and one of the long phalanges of digit III is wanting. The same forces that moved backward the short phalanx of digit IV may have removed one of the phalanges of the adjacent digit, and closed the gap so formed.

Reverting again to the large metacarpal V (that of the wing finger), six figures are especially introduced to show its distal articulation with the first phalanx. The adjacent ends of these two bones belonging to the left wing of a large example of Pteranodon sp., No. 2628, are shown in Plate XXIV, figures 1 and 2, taken from the ulnar and radial sides, respectively. Figures 3 and 4 portray the corresponding portions of the left wing of a smaller example of *P. occidentalis* (Marsh's own identification), No. 1165, at the angle of extreme flexure, though there is some reason to suppose that slight dislocation has here been effected.

The articulation of metacarpal V with the first phalanx of digit V has been figured, in the examples cited, from bones crushed transversely. To demonstrate better the form

of this joint viewed from the palmar side, figure 5 has been made from the conjoined fragments of the left metacarpal and the first phalanx of *Pteranodon* sp., No. 2660, which are crushed vertically. The bones are here represented in actual contact, with the joint extended just as preserved in the matrix. Figure 6 shows these same parts when separated.

The distal end of the first phalanx of the wing finger, as described by Marsh, "presents an elliptical, convex, articular face, which does not entirely cover the distal surface. The second phalanx has its proximal extremity adapted to this articular face by a shallow elliptical cup, which does not extend over the most proximal portion of the extremity. The distal end resembles in everything but size the corresponding part of the first phalanx. The next or third phalanx is quite similar to that which precedes it, except that it is more attenuated. The slender terminal phalanx appears to have been more nearly circular at its proximal end, although apparently compressed toward its other extremity. The articular surfaces of all the bones preserved are smooth and well defined, like those of mammals and birds. All the bones of the wing, moreover, even the carpals, appear to have been pneumatic." The shafts of the wing bones generally are of extreme tenuity, fragments from some of the larger specimens having only a thickness of one millimeter.

From the form of the articulation, it is evident that the flexion of these phalanges upon each other was limited to an angle of about 45°. When the wing was fully extended, it is probable that the flexion of these bones upon each other was very slight. In Plate XXV, figures 1-7, the wing bones preserved in *Pteranodon* sp., No. 2452, have been arranged so that the relative lengths of the phalanges may be seen. The wing bones preserved in another individual, No. 2774, are displayed in Plate XXVI, figures 1, 2, and 3. The fourth or terminal phalanx is missing in this example, but is preserved in No. 2470 (Plate XXVI, figures 4-7) and No. 2591 (Plate XXVI, figures 8 and 9). The curvature of the fourth phalanx of the wing finger, which is clawless, varies slightly in different individuals, and indeed is not precisely the same in the right and left wings of one of the few examples in which both members are preserved. In no specimen in the Marsh Collection is this bone straight. The pteroid bone, lacking its proximal articulation, might easily be mistaken for a terminal phalanx. In face of this evidence, it would appear unwise to attempt to separate species on slight differences of curvature in the terminal phalanx of digit V.

From twenty-five examples of *Pteranodon* in the collection, linear measurements of various wing bones have been taken, and are presented in Table A. In Table B, each of the first five sections of the wing has been taken in turn as the unit of length, the lengths of the other bones being expressed as percentages. The original purpose of these tables — to aid in separating the species — is in large measure foiled by the imperfection of the material. Perhaps their greatest value lies in the indications they afford as to the size attained by the genus.

For convenience, the measurements of the femur and tibia have been included in these tables; and at the bottom of Table B, the comparative measurements of the wing bones of *P. ingens* given by Professor Williston in his paper: "On the Osteology of *Nyctosaurus*" have been entered. These measurements, as stated in a letter from Professor Williston, were "taken from a life-sized drawing made of the mounted specimen in the Kansas Museum." It now seems impossible to prove positively that the wing bones referred to belonged to a single individual; for the Curator having charge of the collection writes: "I find that in some cases the bones have been mounted on wires, etc., and that the catalogue number must have been either erased or is underneath." On

the supposition that they are taken from a single individual, it is instructive to note that the ratio of the ulna to the humerus is 136, which is only a trifle greater than the ratio of the corresponding bones of Professor Marsh's type of *P. ingens*, No. 1175. In all other examples of Pteranodon in the Yale Collection, the length of the ulna is still greater in comparison with that of the humerus.

TABLE A.  
Lengths of long bones of the wing and leg in millimeters.

Cat. No.	Hum.	Ra.	Ul.	Mc. V.	1st Phal.	2d Phal.	3d Phal.	4th Phal.	Femur	Tibia
1164	167	...	...	...	430	...	...	...	...	...
2616	180	260	...	...	510	...	...	...	190	...
1175	290	...	384	...	...	...	...	...	270	...
2425	155	217	223	360	...	...	...	...	...	...
2692	170	...	...	...	453	358	...	125+	...	...
2767	...	...	...	400	...	...	240	...	175	...
2493	202	284	296	454	550	474	...	...	192	290
1181	144	205	210	...	...	...	...	...	...	...
2348	...	283	290	455	...	470	322	165+	...	...
2591	...	...	...	...	...	...	323	193	...	...
2738	...	...	...	...	670	500	...	...	260	353
2499	...	...	338	...	...	480	330	...	...	...
2662	...	...	...	...	...	...	325	185	...	...
2452	...	...	315	550?	623	460	301	160+	...	...
2680	...	242	250	...	...	370?	260	...	...	...
2451	173	...	...	382	452	...	...	...	...	248
2730	230	...	325	...	...	445+	...	...	...	...
2689	...	...	...	...	705	...	358	...	...	...
2470	...	...	...	...	495	380	260	152	...	...
2414	...	...	355	572	...	...	...	...	...	...
2774	...	...	...	...	454	372	263	...	...	...
2708	...	...	...	...	476	...	255	...	...	...
2403	...	...	...	...	...	490	315	170	...	...
2473	...	...	...	600	...	...	...	...	...	...
2496	...	...	...	...	...	...	...	206	...	...

TABLE B.  
Proportional lengths of long bones of the wing and leg.

Cat. No.	Hum.	Ra.	Ul.	Mc. V.	1st Phal.	2d Phal.	3d Phal.	4th Phal.	Femur	Tibia
1175	100	...	132	...	...	...	...	...	93	...
2730	100	...	141	...	...	193+	...	...	...	...
2425	100	140	144	232	...	...	...	...	...	...
2493	100	141	147	225	272	235	...	...	95	144
1181	100	142	146	...	...	...	...	...	...	...
2616	100	141	148 <sup>1</sup>	...	283	...	...	...	106	...
1164	100	...	...	...	257	...	...	...	...	...
2451	100	...	...	221	261	...	...	...	...	143
2692	100	...	...	...	266	212	...	74+	...	...
2493	...	...	100	153	186	160	...	...	65	94
2348	...	...	100	157	...	162	111	57+	...	...
2414	...	...	100	161	...	...	...	...	...	...
2452	...	...	100	174	194	147	95	51+	...	...
2730	...	...	100	...	...	137+	...	...	...	...
2499	...	...	100	...	...	142	98	...	...	...
2680	...	...	100	...	...	148 <sup>2</sup>	104	...	...	...
1175	...	...	100	...	...	...	...	...	70	...
2452	...	...	...	100 <sup>2</sup>	113	84	55	29+	...	...
2451	...	...	...	100	118	...	...	...	...	63
2493	...	...	...	100	121	104	...	...	42	63
2348	...	...	...	100	...	103	71	36+	...	...
2767	...	...	...	100	...	...	60	...	44	...
2452	...	...	...	...	100	74	48	26+	...	...
2738	...	...	...	...	100	75	...	...	40	53
2470	...	...	...	...	100	77	53	31	...	...
2692	...	...	...	...	100	79	...	28+	...	...
2774	...	...	...	...	100	81	57	...	...	...
2493	...	...	...	...	100	86	...	...	35	53
2689	...	...	...	...	100	...	51	...	...	...
2708	...	...	...	...	100	...	54	...	...	...
2451	...	...	...	...	100	...	...	...	...	55
2403	...	...	...	...	...	100	64	35+	...	...
2452	...	...	...	...	...	100	65	35+	...	...
2470	...	...	...	...	...	100	68	40	...	...
2348	...	...	...	...	...	100	69	35+	...	...
2499	...	...	...	...	...	100	69	...	...	...
2680	...	...	...	...	...	100	70	...	...	...
2774	...	...	...	...	...	100	71	...	...	...
Average	100	142	143	226	268	...	...	...	...	...
"	...	...	...	...	100	79	53	31	...	...
<sup>2</sup>	100	...	136	210	268	172	...	...	106	150
"	...	...	100	154	197	126	...	...	...	...

<sup>1</sup> Calculated.<sup>2</sup> Taken by S. W. Williston, from a specimen in the Museum of the University of Kansas.

## LEG BONES.

The femur of *Pteranodon ingens* has been amply described by Professor Williston in the following paragraph (*On the Osteology of Nyctosaurus*, p. 150), which will be found to agree well with the form of the bone as shown in Plates XXVII, XXVIII, and XXIX:—

“The convexity of the head is regular, covering nearly half of a circle transversely, probably a little less in the conjugate diameter, the surface thus forming an oval or ovate figure, the plane of whose base is nearly at right angles to the long diameter of the bone. The convex surface is sharply limited from the neck. The neck is cylindrical, rather stout, and is directed nearly vertically downward. The rounded and moderately prominent trochanter is placed over the middle of the shaft, descending into the concavity at the side of the neck, and externally separated from the margin of the bone. The shaft is nearly of equal width throughout: doubtless in life it was nearly cylindrical, with a strong anterior curvature, and a flattening in the popliteal region. The sharp margin of the inner condyle encompasses nearly half a circle. The outer condyle, though extending further, is much less in extent. The inner distal articular surface is the larger, and is separated from the inner surface by a distinct ridge, especially posteriorly.”

Professor Williston's description of a tibia of *Nyctosaurus* immediately following the above quotation applies equally well to the tibia of *Pteranodon*, showing how closely the leg bones of these two genera resemble each other. His words are as follows:—

“The tibia is a slender, straight bone, moderately expanded at the upper extremity. The margin of the articular surface above is nearly transverse to the longitudinal axis. The width contracts chiefly at the expense of the posterior margin to the lower part of the upper fourth of the bone, the shaft below being of nearly uniform width. The trochlear surface at the distal extremity is pulley-shaped, covering about half of a circle, perhaps more, and has a moderately deep groove.” Professor Williston adds: “There is no trace of any fibula, either in the preserved remains or in any tibial articulation.” This is also true of the *Pteranodon* material contained in the Marsh Collection.

Of the leg bones of *P. ingens* (type), No. 1175, only the right femur (entire), the proximal end of the left femur, and the proximal and distal ends of the right tibia are preserved; the bones of the right leg are shown in Plate XXVII, figures 4, 5a, and 5b. The two femora and their tibiæ of a slightly smaller individual of *Pteranodon* sp., No. 2738 (Plate XXVIII), will be found similar to those of *P. ingens* (type), as are also the leg bones of *Pteranodon* sp., No. 2489, which are figured on Plate XXVII, figures 1, 2, and 3, together with the partially complete set of podials found with them. The leg bones of a still smaller individual of *Pteranodon* sp., No. 2493, are shown in Plate XXIX, with the nearly perfect right tarsus and metatarsus. The state of preservation of the two tarsals is such that it is now impossible to fit these bones accurately together in contact with the tibia and metatarsus. In this plate, they are shown as found in the matrix, a little removed from their natural position. The stout claw-shaped bone associated with them is supposed to be the rudimentary fifth metatarsal. In the illustration of the right foot of No. 2502 (Plate XVI, figure 1), the tarsals are figured from the proximal surface. The claw-shaped fifth metatarsal is preserved, and distinctly shows the articular facet on its proximal end. Unfortunately, these three bones are so badly

distorted that they can not be accurately assembled.<sup>1</sup> The metatarsals and phalanges of this example, although fractured and separated, are yet capable of being fitted together so as to form a nearly complete member, perhaps the most complete foot that has been observed in material of this genus. In addition to the four long metatarsals, Nos. I-IV, and the claw-shaped rudimentary metatarsal V, there are preserved six long phalanges, the proximal end of a long phalanx, three extremely short phalanges, and four small claw-shaped terminal phalanges. In the figure, these parts have been arranged in what seems to the writer to be their natural order, assuming that metatarsal II is the longest and metatarsal IV the shortest. The number of phalanges forming each digit is thus calculated to be: Digit I, 2 phalanges; digit II, 3 phalanges; digit III, 4 phalanges; digit IV, 5 phalanges. It will be seen that this foot agrees closely with that described by Professor Williston in "Osteology of Nyctosaurus," p. 152. The number and order of the long and extremely short intermediate phalanges are the same as stated by Professor Williston, and the only departure from the arrangement of podials proposed by that author is that four terminal claw-shaped phalanges, instead of two, are called for by the present scheme. That the four small claw-shaped phalanges found together belong to the same foot, is sufficiently proved by the fact that the four long slender penultimate phalanges of the foot terminate in small but distinct trochlear articulations. In No. 2489 (Plate XXVII, figure 3) and also in No. 2554, which is not figured here, the distal termination of the penultimate phalanx of digit I is known to be of the same form.

#### RESTORATIONS OF PTERANODON.

Only a very imperfect conception of the entire skeleton of Pteranodon can be obtained from the detailed description, of its component parts, and a restoration with the wings outspread as in flight (Plate XXX) is here introduced in the attempt to show to better advantage the general proportions of this most highly specialized and grotesque animal. The drawing is virtually a composite restoration, the cranial characters being based mainly on the type skull of *P. longiceps*, No. 1177, while the pelvis and the greater part of the vertebral column are copied from the type of *P. ingens*, No. 2594. As the utmost care has been taken to reduce all the skeletal parts of the examples consulted to the same relative size, the figure should have considerable value in its portrayal of the generic characters.

Hardly less instructive is the lateral view of the skeleton shown in Plate XXXI. In making this diagram, it was found advisable to figure the bones of the left wing and leg only, as it seemed impossible to represent the limbs of both sides in true perspective in the lateral view without giving an erroneous idea of their length. In these two plates, sternal ribs are figured, also short curved ribs borne by the free posterior dorsal vertebræ. As stated in the foregoing pages, the form of these ribs is not known from any example in the Marsh Collection; neither is it possible to represent with certainty the gastralia and the cartilaginous structure which doubtless connected the prepubes with the sternum.

The bizarre aspect of the great supraoccipital crest of the skull, extending backward

<sup>1</sup> The anterior surface of the distal end of the tibia is also figured in order to show the relative size of the foot.



over the dorsal region, is most striking. And the appearance of the hind limbs in the complete restoration well sustains the truth of Professor Seeley's contention that the "slender toes of many birds, and even the two toes of the ostrich, may be thought to give less adequate support for those animals than the metatarsals and digits of Pterodactyles." The small size of the pelvis compared with the rest of the skeleton will at once arrest the attention of a biologist in whose mind the question arises how the females of this genus could have produced their young. Were it not for the greatly elongated wings and the supraoccipital crest, the pelvic diameters would not seem so disproportionate; for compared with the size of the thorax of the adult animal, the channel enclosed by the ischio-pubes is not relatively much smaller than that observed in some of the Crocodilia and Chelonia. That this character is perhaps a little more pronounced in Pteranodon than in the earlier pterosaurs, need cause no surprise, inasmuch as Pteranodon is in nearly every respect more specialized than the other genera. The seemingly immoderate proportions of the head and wings were probably due entirely to postnatal growth; and while difficulty of parturition might ultimately have become a factor in exterminating the genus, it should be remembered that the proportions of the axial skeleton and limb girdles figured in the restorations are taken from well-preserved specimens and therefore can not be regarded absurd. There is as yet no definite evidence to show whether the animals were viviparous or produced soft-shelled eggs.

Like many another extinct group of American vertebrates described as being of "gigantic size," Pteranodon seems in this respect to have surpassed its Old-World congeners. The wing-spread of any example — a dimension that perhaps conveys a more definite idea of size than do other measurements — may be calculated by assuming that the wing bones missing in any individual were of average proportions, and by computing their lengths from the averages given in Table B; but it is obvious that the resultant calculation is approximate only. Allowance must also be made for the diameter of the thorax and for the carpus. Contrary to precedent, the wing-spread is here estimated as the distance from the tip of one terminal phalanx to that of the opposite limb, with all the joints slightly flexed, especially the elbow and the carpus, this position of the wings affording a more natural measurement than the total length of the same bones stretched in a straight line from shoulder to wing-tip, although by the latter method the size would be made to appear about five per-cent. greater.

The wing-spread of several of the examples referred to in the foregoing pages may be approximately stated, as follows:—

	m.	ft.	in.
No. 1164, type of <i>P. occidentalis</i> . . . . .	3.855	= 12	8
No. 1175, type of <i>P. ingens</i> . . . . .	6.803	= 22	3
No. 2493, Pteranodon sp. . . . .	4.902	= 16	0
No. 1181, Pteranodon sp. . . . .	3.390	= 11	1

The wing-spread of the type of *P. longiceps*, No. 1177, was probably nearly equal to that of No. 2493; the type skull of *P. occidentalis*, No. 1179, belonged to an individual of about the same size as No. 1164, while the two types of *P. ingens*, Nos. 1175 and 2594, apparently had about the same wing-spread. Perhaps the largest example of Pteranodon sp. in the Marsh Collection is No. 2514, represented by the right quadrate and the proximal ends of the radius and ulna. The quadrate exceeds in size that of *P. ingens*, No. 2594, by one-fifth. If this proportion remained constant throughout the entire skeleton,

the wing-spread of No. 2514 would be about 8.163 m, or 26 feet, 9 inches. The proximal ends of the radius and ulna, however, do not appear so robust as those of *P. ingens* (type), No. 1175, supposed to be of the same size as No. 2594, a comparison that argues against the extreme size computed above. It would seem quite as reasonable to conclude that the proportionate size of the skull and limbs may have varied considerably in Pteranodon, just as in other genera of recent and fossil vertebrates.

Important data concerning the types and other valuable examples of Pteranodon are given below. As previously stated, all the material in the Marsh Collection referred to this genus was obtained from the Niobrara Cretaceous beds of western Kansas. The color of the matrix seems to be affected to some extent by exposure to the elements, and can not at present be relied upon as a criterion of age.

*Pteranodon occidentalis* (type), No. 1164, was collected by Professor O. C. Marsh, July, 1871, from the "Gray Shale" of the Niobrara Cretaceous, on the north side of the Smoky River in western Kansas. It comprises the following bones of the right wing: The humerus; the proximal end of the ulna: the proximal and distal ends of the radius; the carpus; the greater part of the fifth metacarpal, including both ends; the first phalanx, both ends of the second phalanx, both ends of the third phalanx, and the greater part of the fourth phalanx, of the fifth digit.

*Pteranodon ingens* (type), No. 1175, was collected by E. W. Guild, alias E. S. Field, May 17, 1876, from the "Yellow Chalk" of the Niobrara Cretaceous, in Wallace County, Kansas. It comprises the following bones: The basioccipital, the left quadrate, the articular portions of the mandibular rami; cervical vertebræ 1, 2, 3, 4, 5, 6, and 7; three dorsal vertebræ; the pelvis, with series of ten vertebræ; the right scapula and coracoid; the right humerus, ulna, proximal and distal ends of the radius; the carpus, proximal and distal ends of the fifth metacarpal; the right femur, and the proximal and distal ends of the right tibia; the proximal part of the left femur.

*Pteranodon longiceps* (type), No. 1177, was collected by Professor S. W. Williston, May 2, 1876, from the "Yellow Chalk" of the Niobrara Cretaceous, near the Smoky River in western Kansas. The type consists of the skull, together with the atlas and axis.

*Pteranodon occidentalis* (type skull), No. 1179, was collected by E. S. Field, alias E. W. Guild, 1875, from the "Yellow Chalk" of the Niobrara Cretaceous, near Castle Rock in Trego County, Kansas. The specimen is imperfect.

*Pteranodon ingens* (type), No. 2594, was collected by Professor S. W. Williston, July 20, 1877, from the "Yellow Chalk" of the Niobrara Cretaceous, in Wallace County, Kansas. The skull, with atlas and axis, is preserved.

*Pteranodon* sp., No. 1181, was collected by Professor B. F. Mudge, April 24, 1875, from the "Yellow Chalk" of the Niobrara Cretaceous, in Trego County, Kansas. It comprises: The right scapula and coracoid; the right humerus, radius, and ulna; lateral carpal and pteroid; fragments of the fifth metacarpal; fragments of the second, third, and fourth metacarpals, and most of the phalanges of the manus.

*Pteranodon* sp., No. 2493, was collected by E. S. Field, alias E. W. Guild, September 4, 1876, from the "Yellow Chalk" of the Niobrara Cretaceous, in Trego County, Kansas. It comprises the following bones: The anterior part of the sternum, the right scapula and coracoid, and fragments of the left scapula and coracoid; the right humerus, radius, and ulna; two carpals; the right fifth metacarpal and portions of the lateral metacarpals; the first, second, and third phalanges of the fifth digit; two femora; two tibiæ, and most of the right podials.

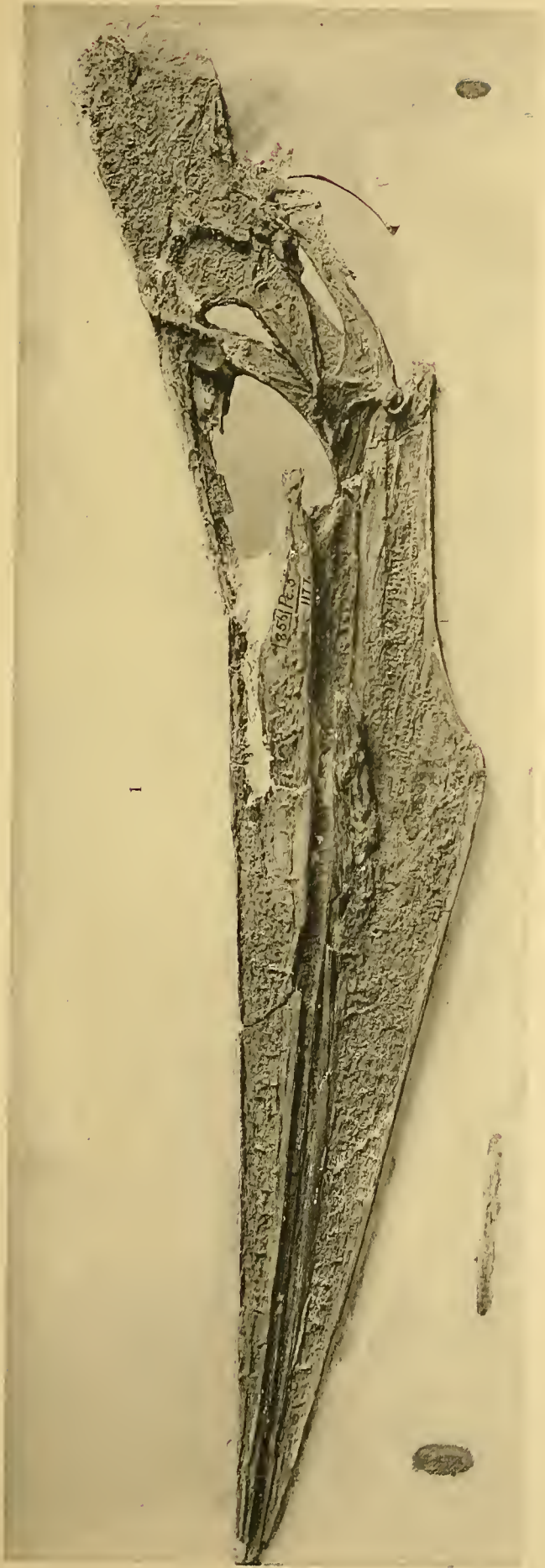


**Plate I.**

Figure 1.—Skull of the type of *P. longiceps* Marsh, No. 1177; seen from the left side.  
× 0.34

Figure 2.—Fragmentary mandible of *Pteranodon* sp., No. 2478; seen from the right side.  
× 0.64

Figure 3.—The same specimen; seen from the left side. × 0.64



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2



3



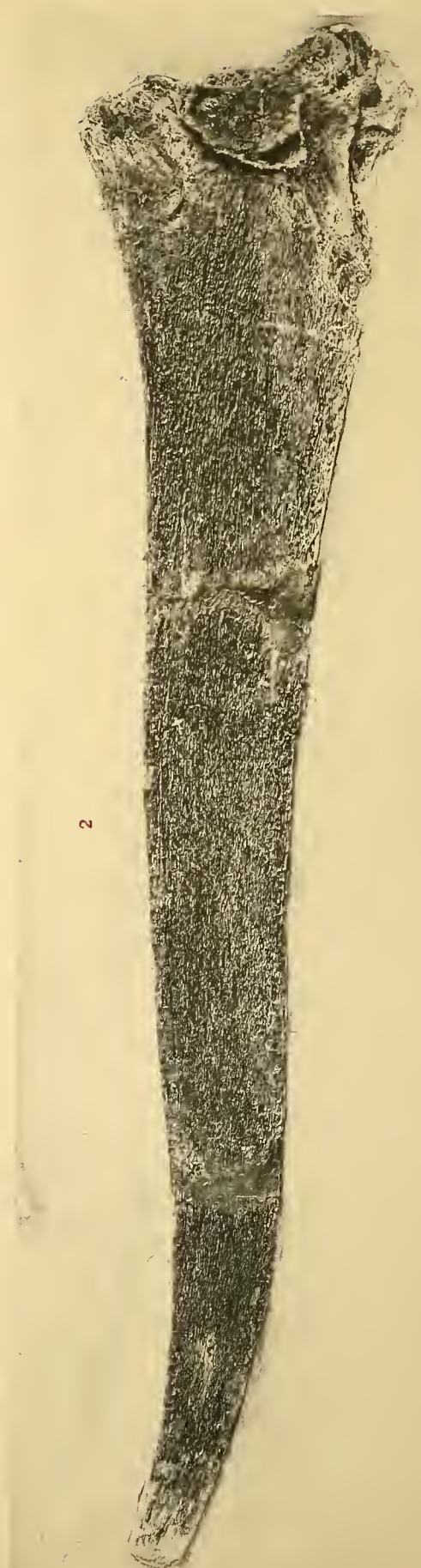


**Plate II.**

Figure 1.—Skull of the type of *P. ingens* Marsh, No. 2594, with the anterior cervical vertebrae; seen from the right side.  $\times 0.28$

Figure 2.—Complete supraoccipital crest of the fragmentary skull of *Pteranodon* sp., No. 2473; seen from the right side.  $\times 0.29$









**Plate III.**

Figure 1.—Skull of the type of *P. ingens* Marsh, No. 2594; middle section; seen from the left side. × 0.42

Figure 2.—Skull of the type of *P. occidentalis* Marsh, No. 1179; seen from the right side. × 0.58





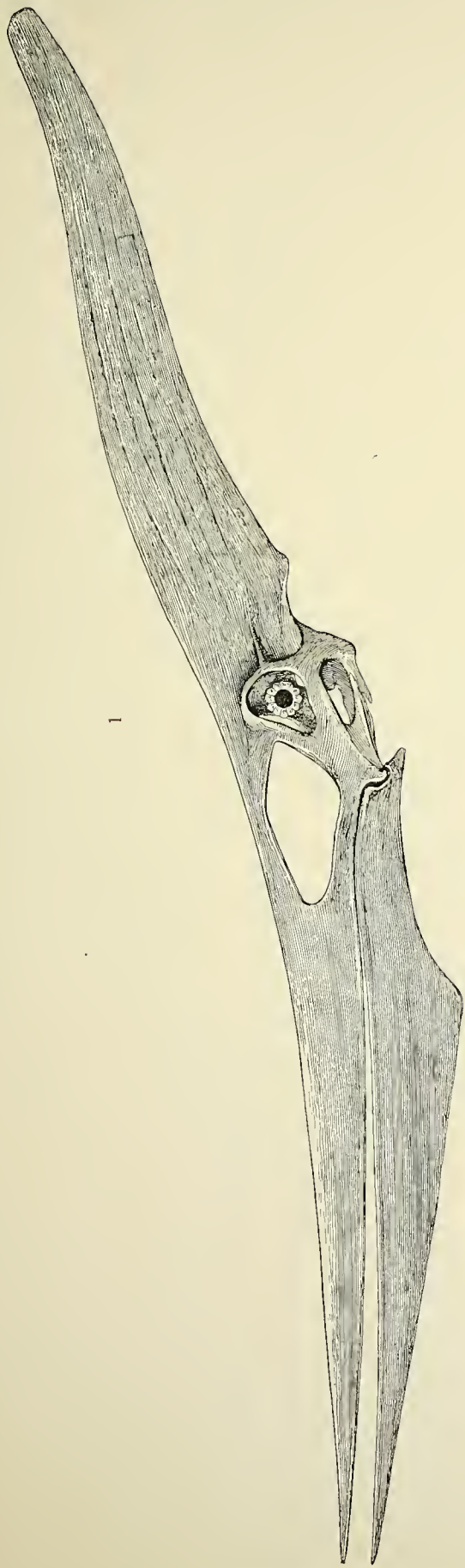


**Plate IV.**

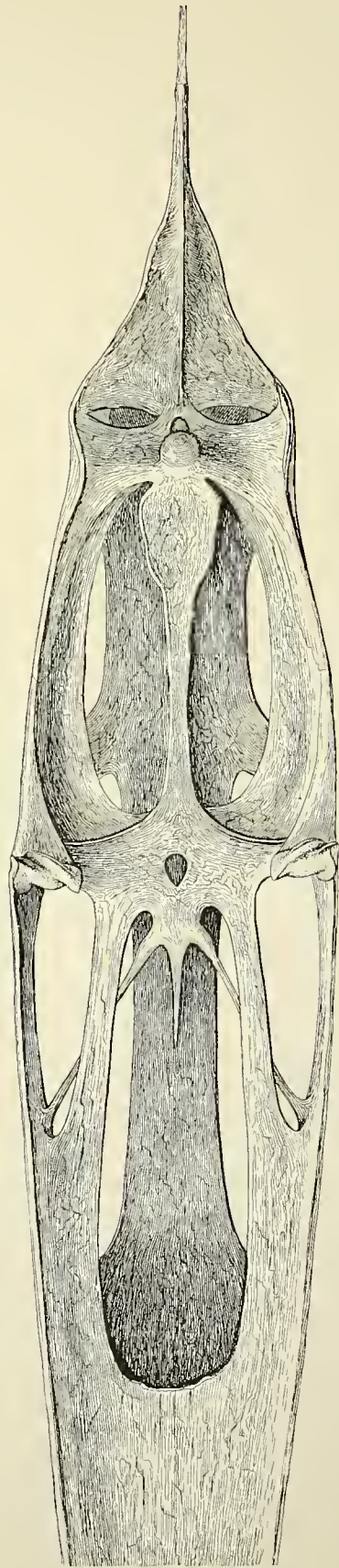
Figure 1.—Composite restoration of the skull of Pteranodon, based on the type of *P. ingens* Marsh, No. 2594, and on Pteranodon sp., No. 2473; seen from the left side.  $\times 0.14$

Figure 2.—Restoration of the skull of the type of *P. ingens* Marsh, No. 2594; palatal view.  $\times 0.50$





2

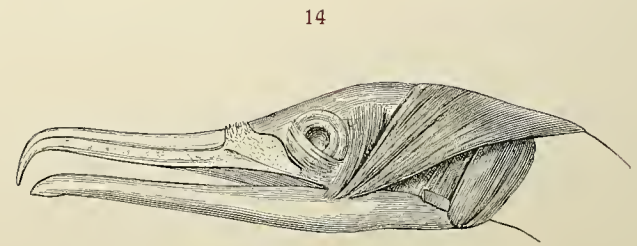
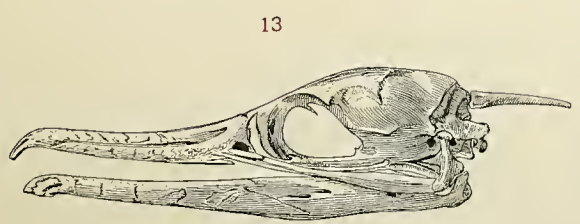
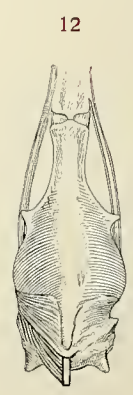
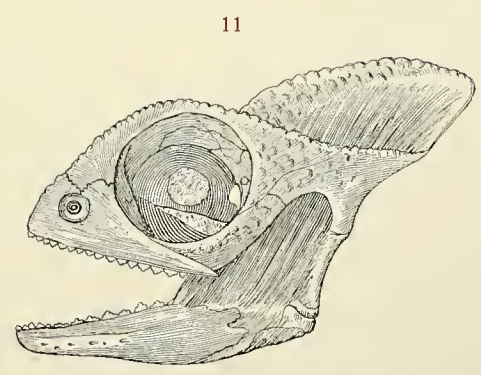
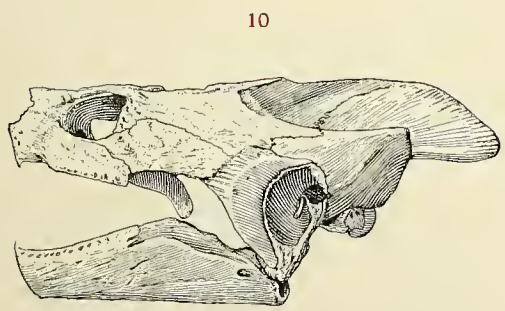
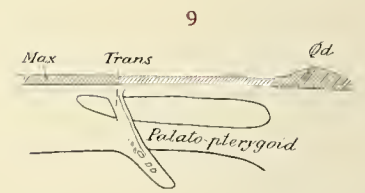
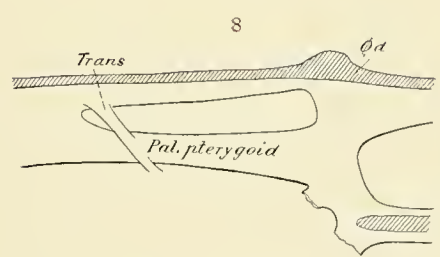
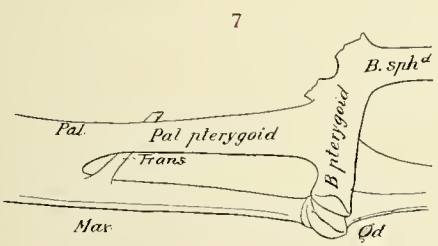
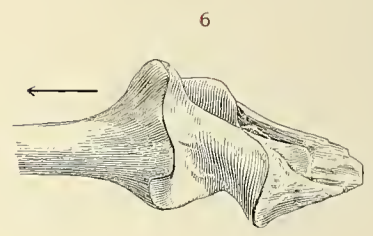
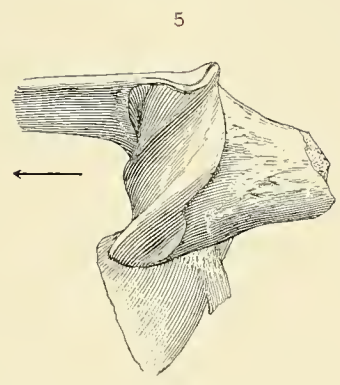
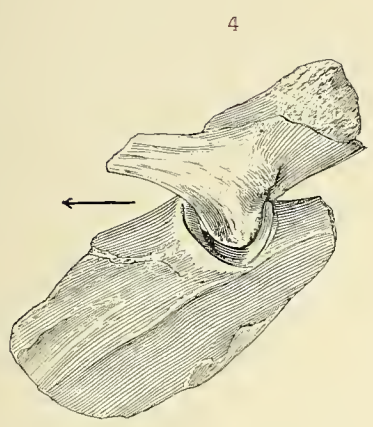
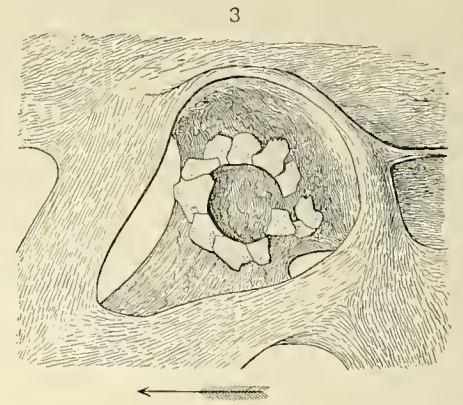
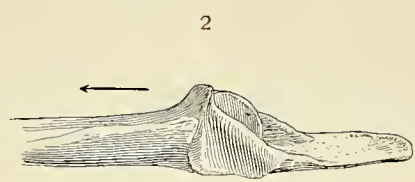
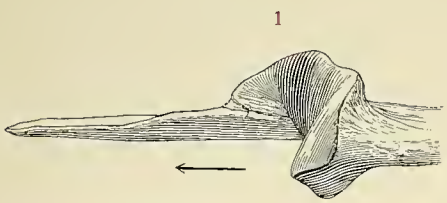






## Plate V.

- Figure 1.—Left quadrate of the type of *P. longiceps* Marsh, No. 1177, with part of the jugal; seen from below.  $\times 1.0$
- Figure 2.—Articular facet of the left mandibular ramus of *Pteranodon* sp., No. 2578: seen from above.  $\times 1.0$
- Figure 3.—Left orbit of the skull of the type of *P. ingens* Marsh, No. 2594, as actually preserved.  $\times 0.50$
- Figure 4.—Left quadrate and articular of *Pteranodon* sp., No. 2476; seen from the left side.  $\times 0.75$
- Figure 5.—Left quadrate of the same specimen; seen from below.  $\times 1.0$
- Figure 6.—Left articular of the same specimen; seen from above.  $\times 1.0$
- Figure 7.—Diagram of the palato-pterygoid ribbon in the type of *P. longiceps* Marsh, No. 1177, with the associated bones of the right side; seen from below.
- Figure 8.—The same elements; seen from above.
- Figure 9.—Restored palato-pterygoid and transpalatine of the right side in *Pteranodon* sp., No. 2440; seen from above.
- Figure 10.—Skull of *Chelydra serpentina* (Snapping Tortoise; Y. U. Osteol. Coll., No. 5454): left side.  $\times 0.66$
- Figure 11.—Skull of *Chamaeleo vulgaris*; left side; to show the temporal muscles. (After Dollo.)
- Figure 12.—Skull of *Plotus anhinga*; superior view: showing the occipital style and the origin of the temporal muscles. (After Garrod.)
- Figure 13.—Skull of *Phalacrocorax dilophus* (Y. U. Osteol. Coll., No. 538): left side; showing the occipital style.  $\times 0.50$
- Figure 14.—Skull of the same; showing the mandibular musculature. (After Yarrell.)  $\times 0.50$







## Plate VI.

Figures 1-6.—Seven anterior cervical vertebræ of the type of *P. ingens* Marsh, No. 1175; seen from the left side; slightly restored.  $\times 0.50$

Figure 1.—Atlas and axis.

Figure 2.—Third cervical.

Figure 3.—Fourth cervical.

Figure 4.—Fifth cervical.

Figure 5.—Sixth cervical.

Figure 6.—Seventh cervical.

Figure 7.—Seventh cervical vertebra of *Pteranodon* sp., No. 2692; seen from the left side.  $\times 0.66$

Figure 8.—Eighth cervical vertebra of the same individual; seen from the left side; showing rib.  $\times 0.66$

Figure 9.—Ninth cervical vertebra of the same individual; seen from the left side.  $\times 0.66$

Figure 10.—Eighth cervical vertebra of the same individual; anterior view.  $\times 0.66$

Figure 11.—Atlas and axis of the type of *P. longiceps* Marsh, No. 1177; seen from the left side.  $\times 1.0$

Figure 12.—Atlas and axis of the type of *P. ingens* Marsh, No. 1175; seen from the rear.  $\times 0.66$

Figure 13.—Fourth cervical vertebra of the type of *P. ingens* Marsh, No. 1175; anterior view.  $\times 0.50$

Figure 14.—The same specimen; posterior view.  $\times 0.50$

Figure 15.—Right rib of the ninth cervical vertebra of the type of *P. ingens* Marsh, No. 1175; posterior view.  $\times 0.50$

Figure 16.—Right rib of the ninth cervical vertebra of *Pteranodon* sp., No. 2692; anterior view.  $\times 0.66$

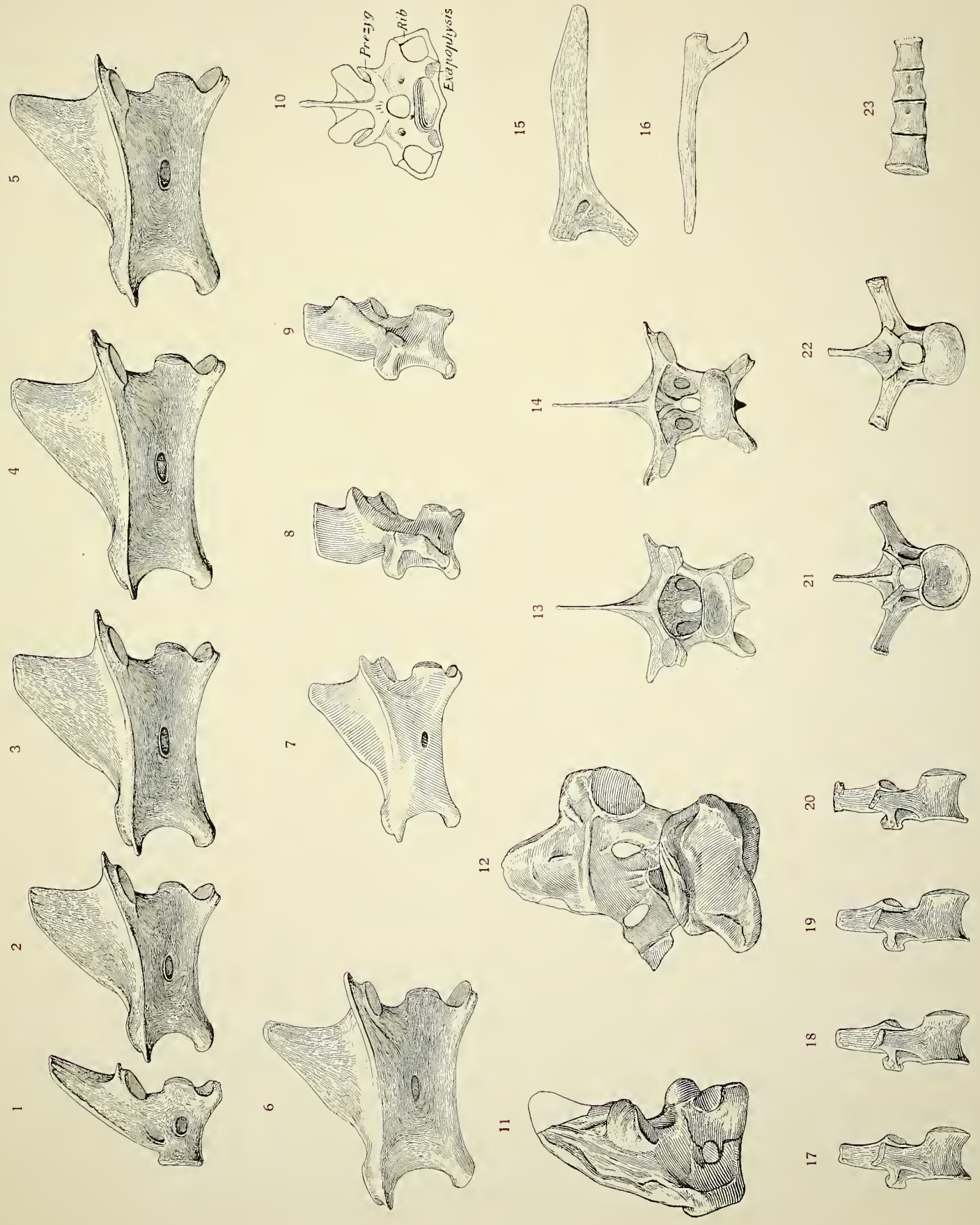
Figures 17-20.—Four free dorsal vertebræ of *Pteranodon* sp., No. 2616; seen from the left side; slightly restored.  $\times 0.66$

Figure 21.—First free dorsal vertebra of the foregoing series; anterior view.  $\times 0.66$

Figure 22.—The same vertebra; posterior view.  $\times 0.66$

Figure 23.—Four caudal vertebræ of *Pteranodon* sp., No. 2546; seen from below.  $\times 0.66$







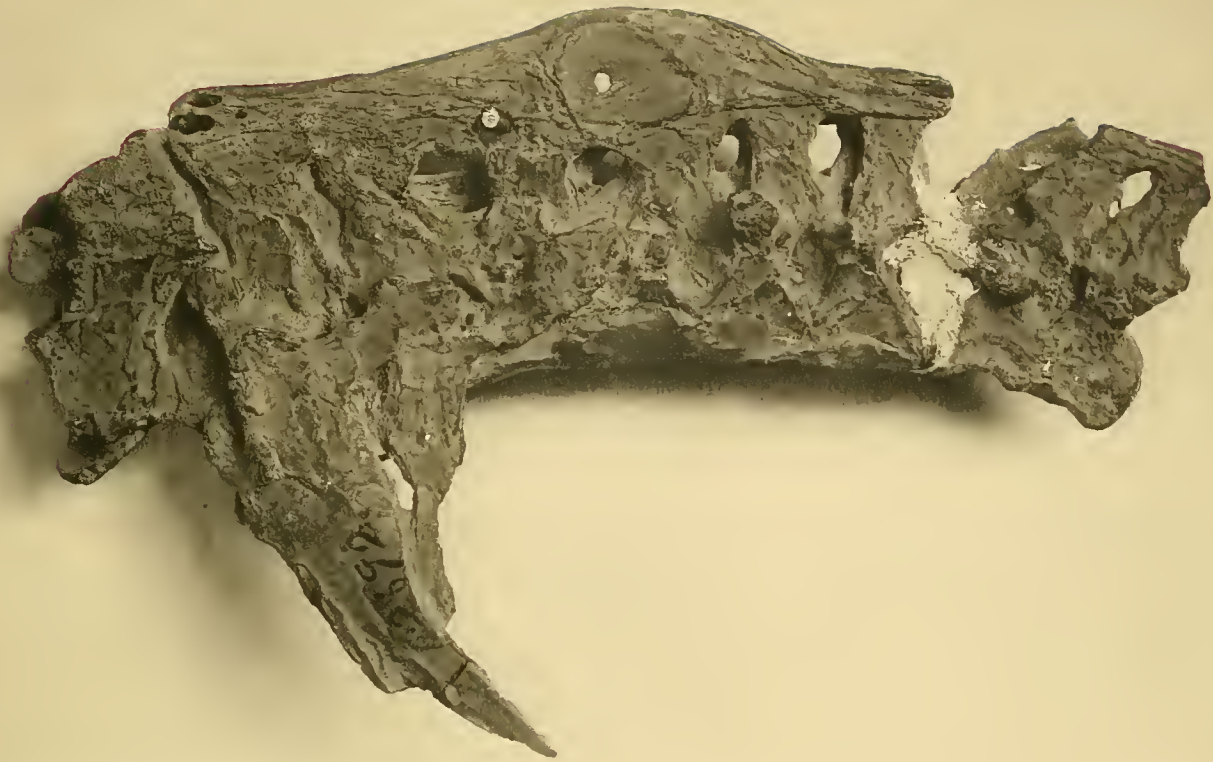


**Plate VII.**

Figure 1.—Notarium of *Pteranodon* sp., No. 2692, with the ninth cervical vertebra attached; seen from the left side.  $\times 1.04$

Figure 2.—The same specimen; seen from the right side.  $\times 0.98$

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2







### Plate VIII.

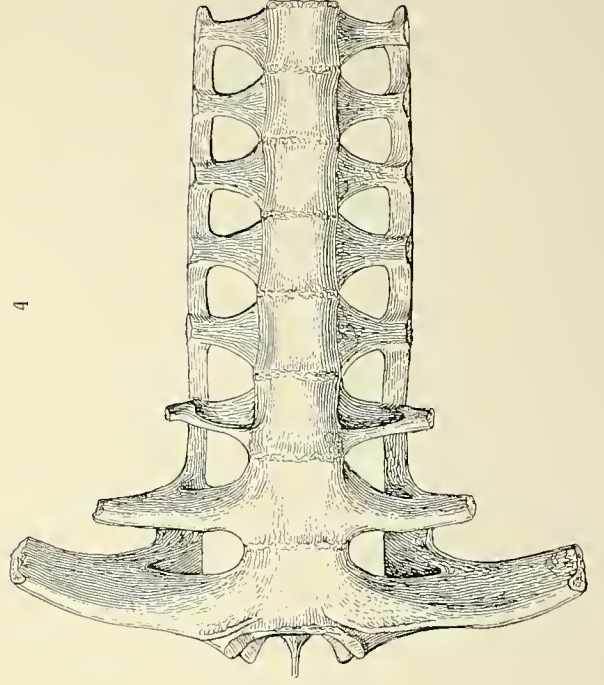
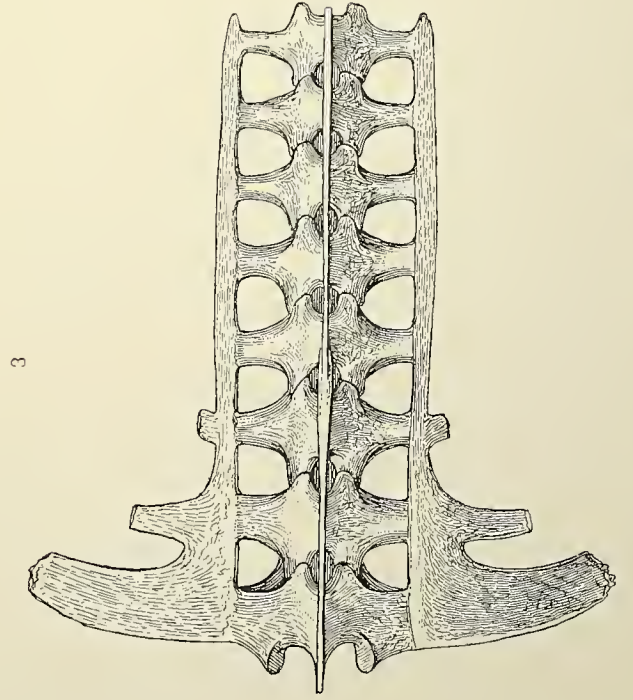
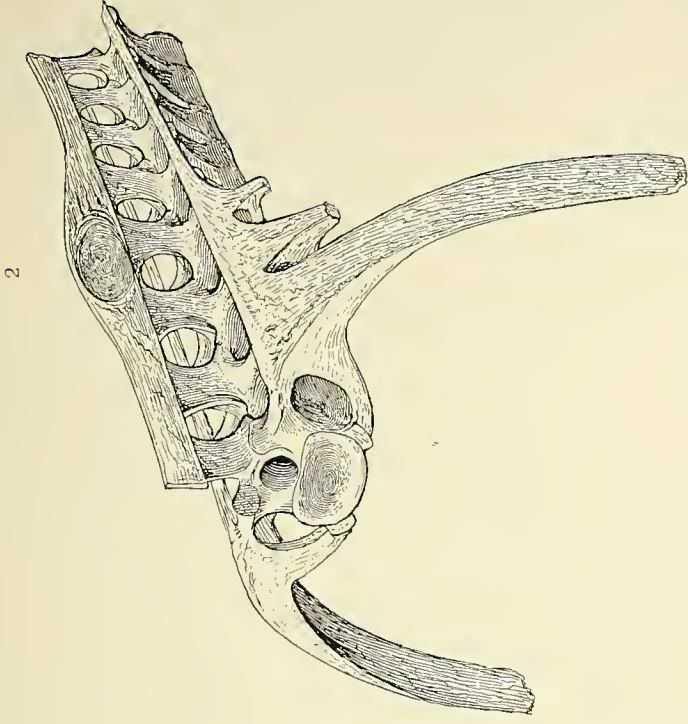
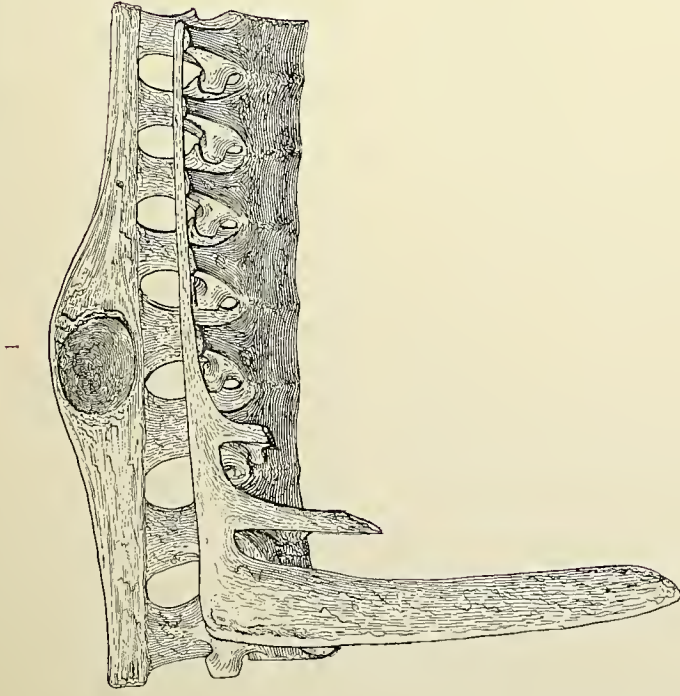
Figure 1.—Restoration of the notarium of *Pteranodon* sp., No. 2692; seen from the left side.  $\times 0.75$

Figure 2.—The same specimen; seen from in front, obliquely.  $\times 0.75$

Figure 3.—The same specimen; superior view.  $\times 0.75$

Figure 4.—The same specimen; inferior view.  $\times 0.75$









**Plate IX.**

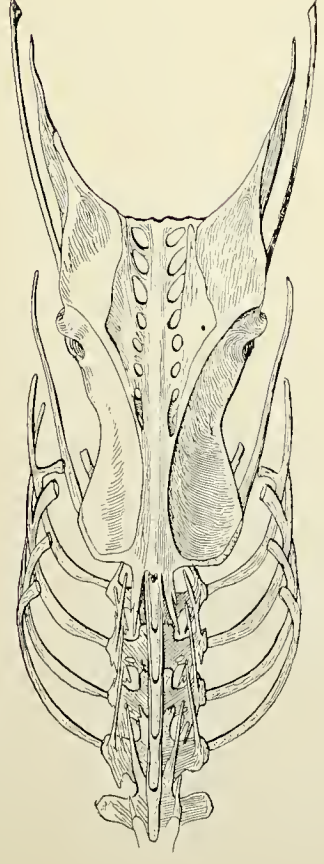
Figure 1.—Dorsum of *Larus glaucus* (Y. U. Osteol. Coll., No. 2290); seen from above.  
× 0.62

Figure 2.—Dorsum of *Oidemia nigra* (Y. U. Osteol. Coll., No. 429); seen from above.  
× 0.67

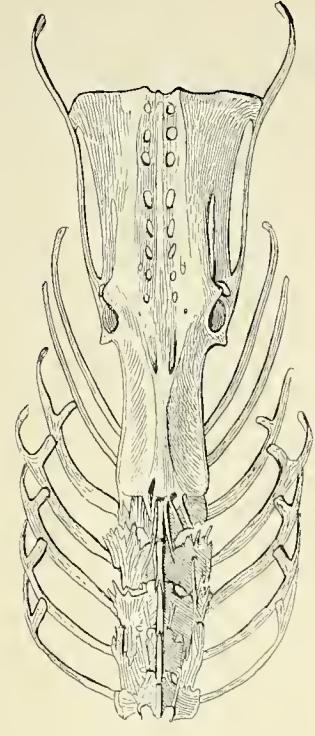
Figure 3.—Dorsum of *Meleagris gallipavo* (Y. U. Osteol. Coll., No. 360); mature individual;  
seen from above. × 0.50

Figure 4.—Sacrum of *Meleagris gallipavo* (Y. U. Osteol. Coll., No. 2112); young individual;  
seen from below. × 0.50

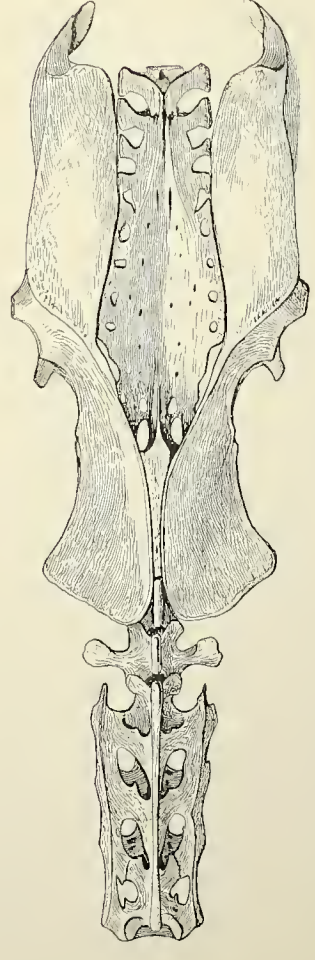
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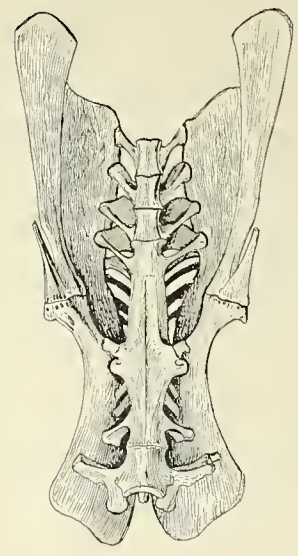
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**Plate X.**

Sacrum and pelvis of the type of *P. ingens* Marsh, No. 1175; seen from below. × 0.96









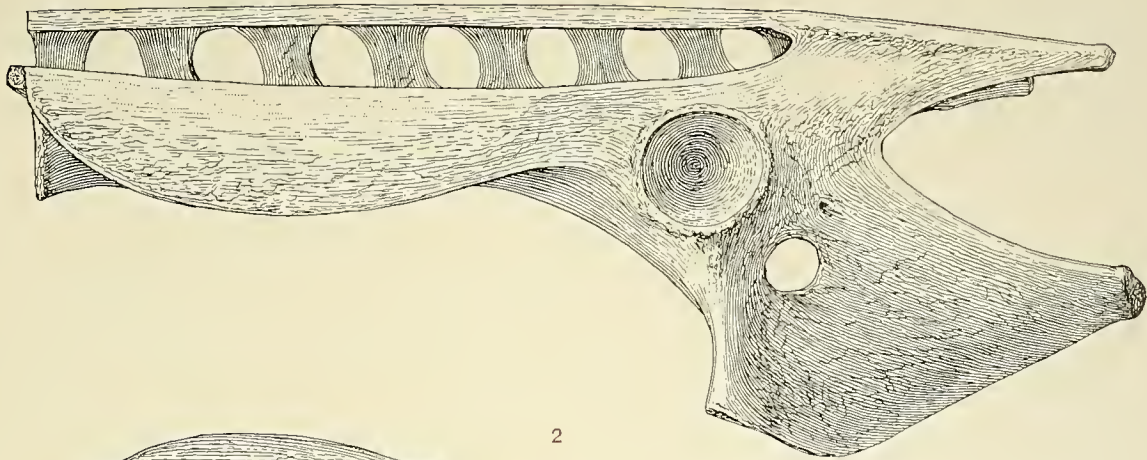
**Plate XI.**

Figure 1.—Sacrum and pelvis of the type of *P. ingens* Marsh, No. 1175; seen from the left side.  $\times 0.75$

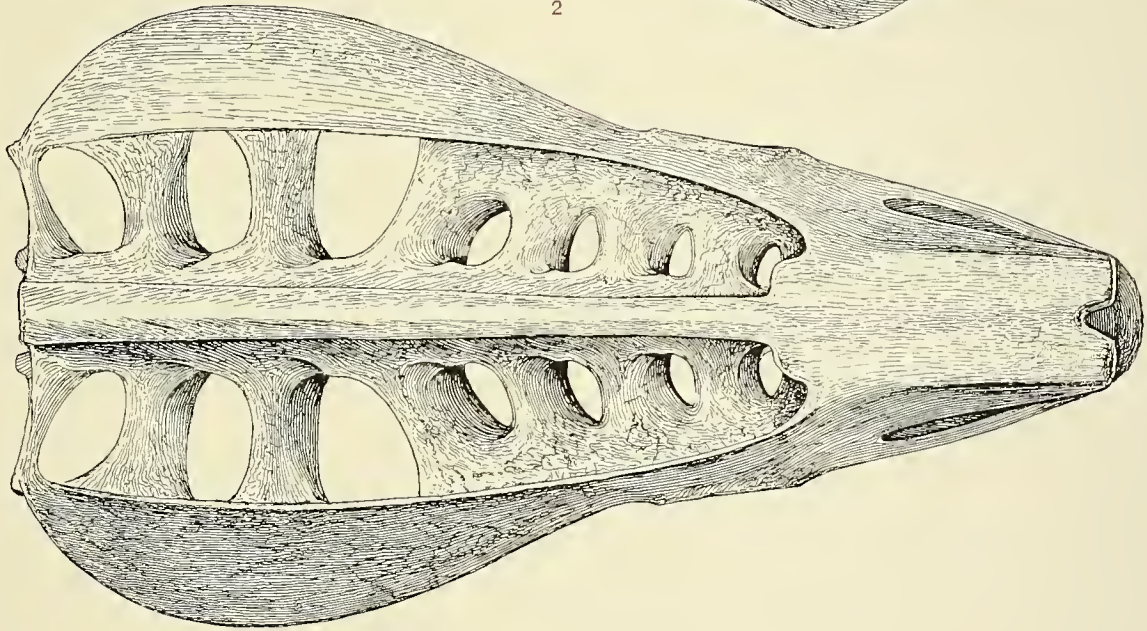
Figure 2.—The same specimen; seen from above.  $\times 0.75$

Figure 3.—The same specimen; seen from below.  $\times 0.75$

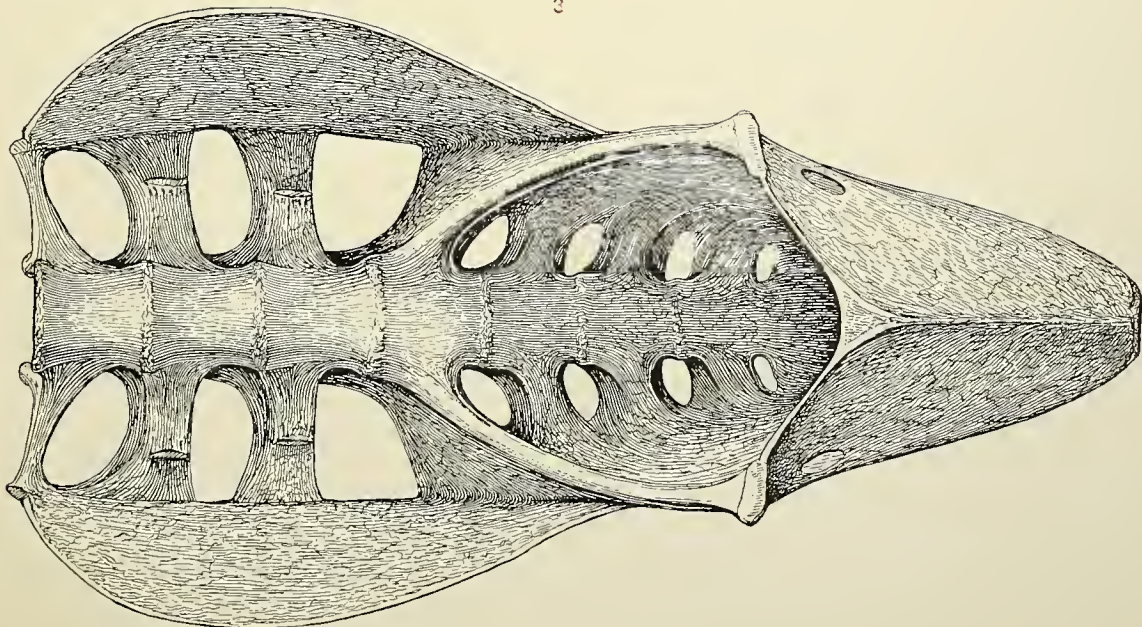
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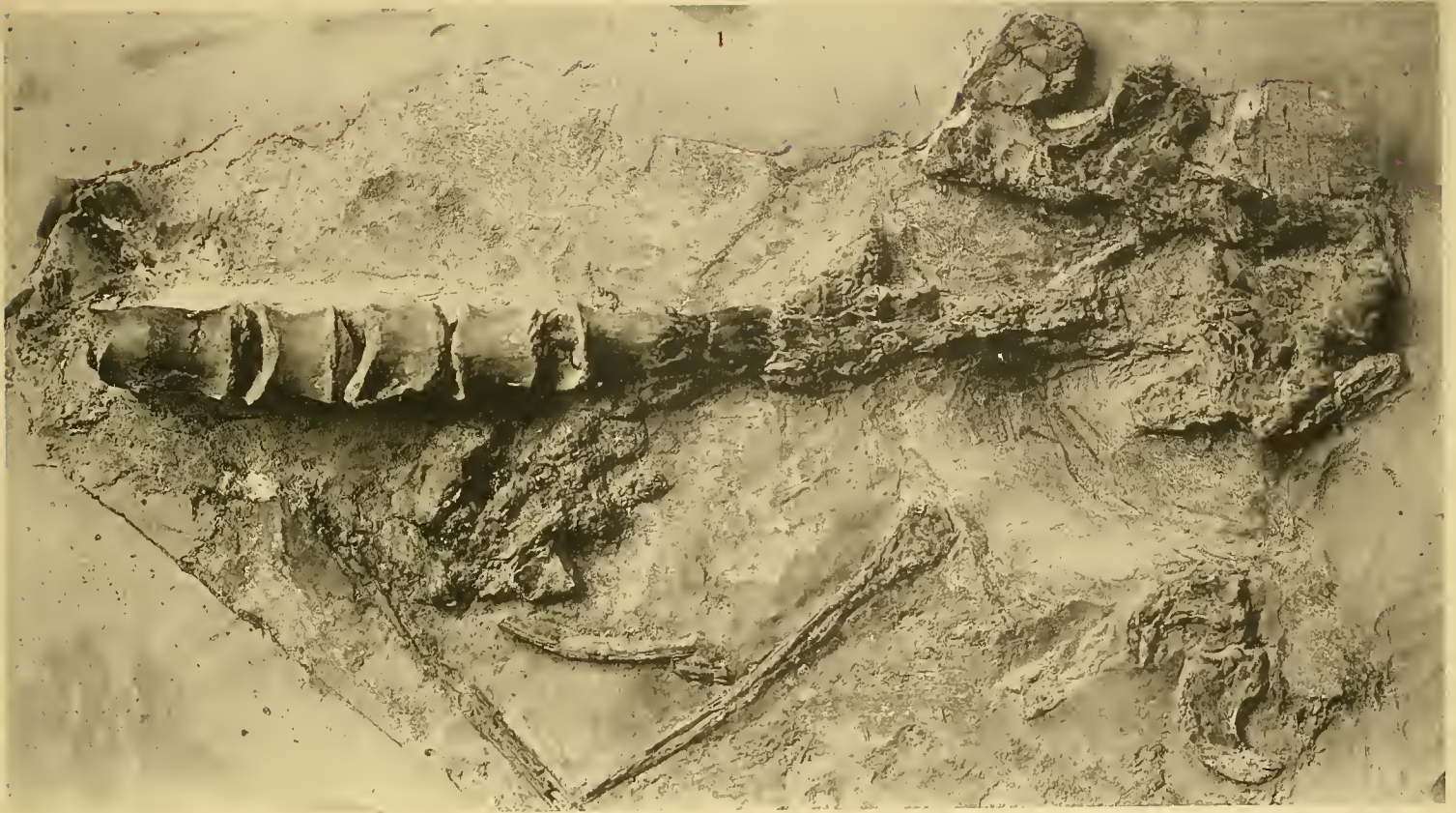


**Plate XII.**

Figure 1.—Two notarial vertebræ, three free dorsal vertebræ, and the anterior sacral vertebræ of *Pteranodon* sp., No. 2451; seen from below.  $\times 0.85$

Figure 2.—Sacrum of *Pteranodon* sp., No. 2570; seen from below.  $\times 1.0$









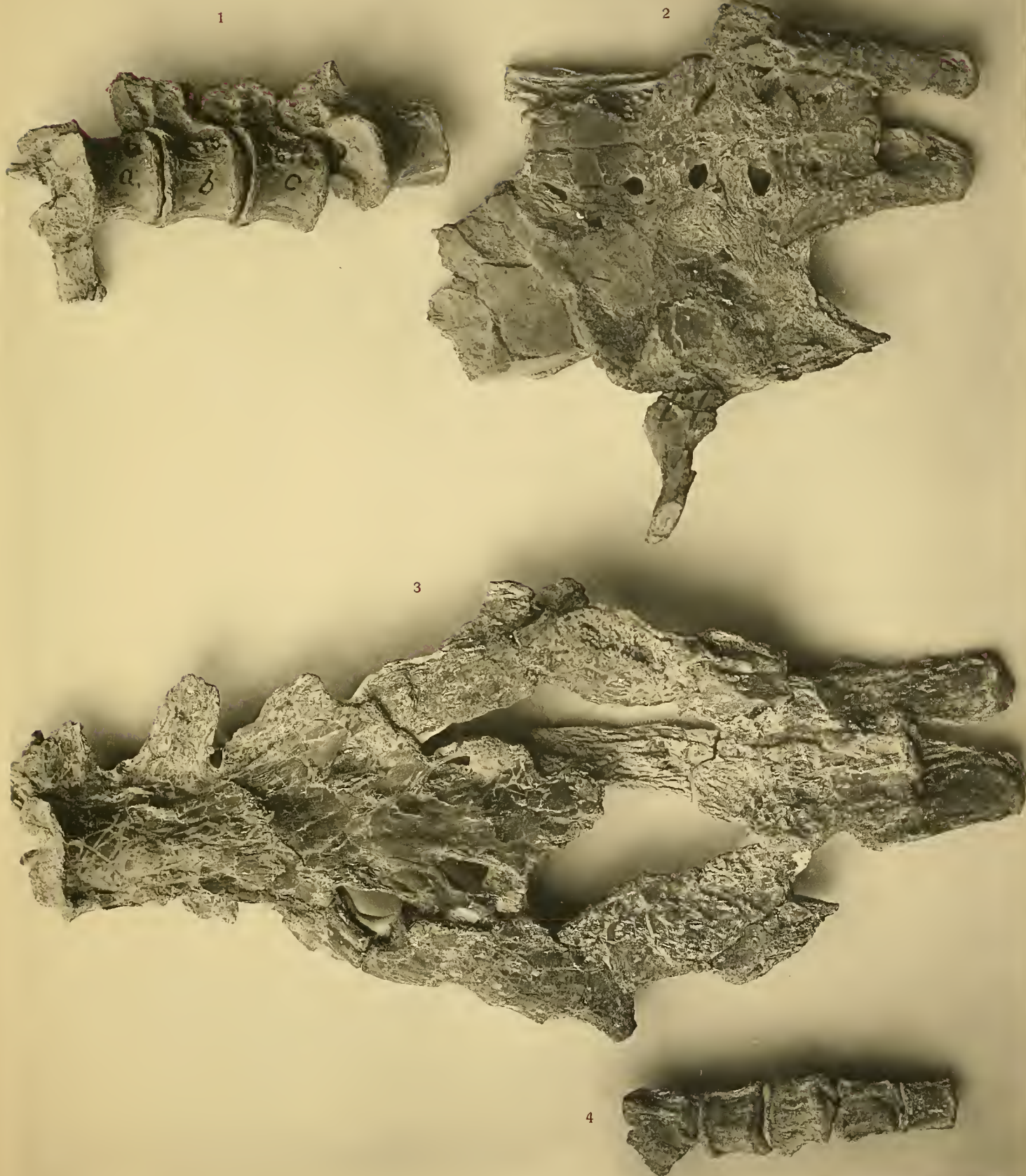
**Plate XIII.**

Figure 1.—Four free dorsal vertebræ of *Pteranodon* sp., No. 2616; seen from below.  
× 1.0

Figure 2.—Fragmentary sacrum of *Pteranodon* sp., No. 2616; seen from below. × 1.0

Figure 3.—Sacrum of *Pteranodon* sp., No. 2489; seen from below. × 1.0

Figure 4.—Five caudal vertebræ of the same individual; seen from above, obliquely.  
× 1.0







**Plate XIV.**

Figure 1.—Sternum of *Pteranodon* sp., No. 2546; seen from below.  $\times 0.60$

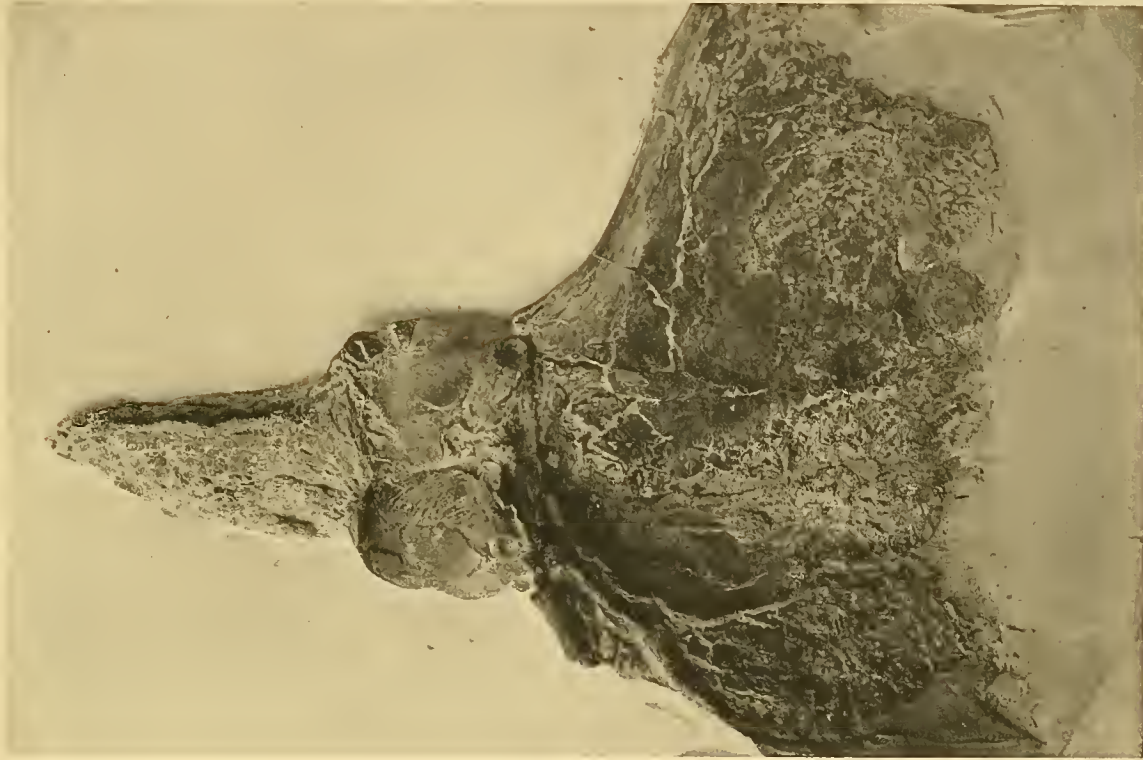
Figure 2.—Anterior portion of the sternum of *Pteranodon* sp., No. 2616; inner or upper surface.  $\times 1.0$



1



2





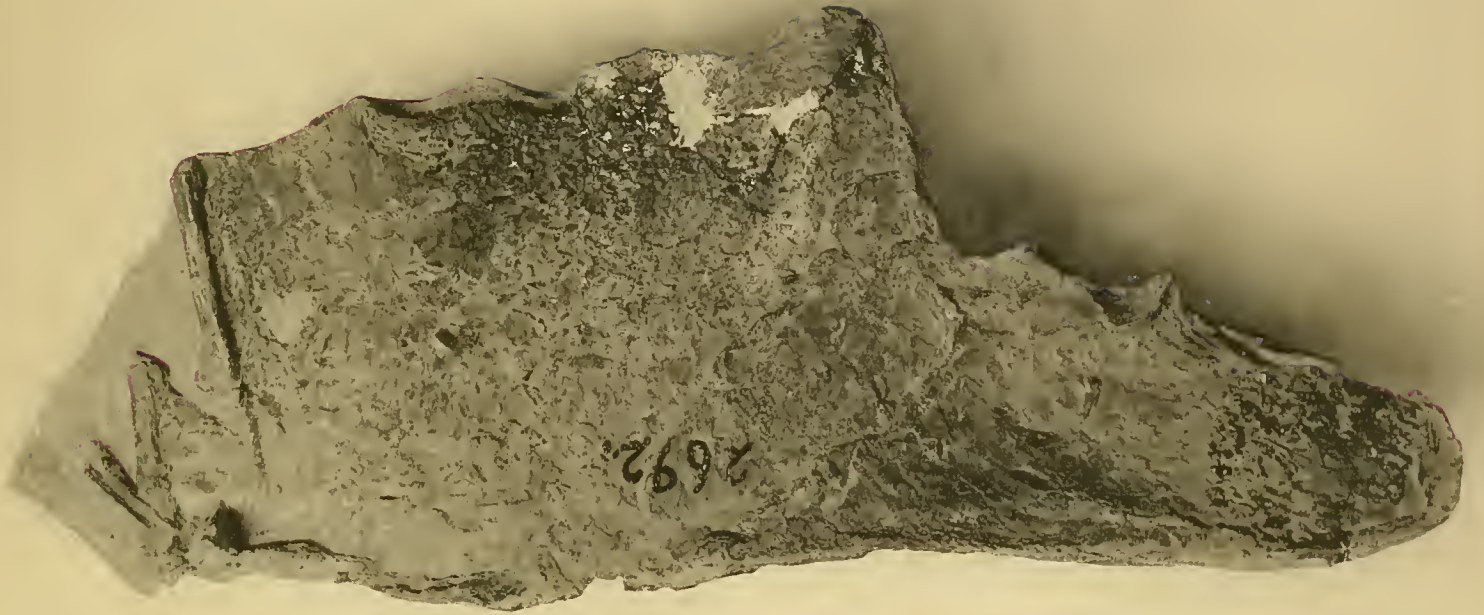


**Plate XV.**

Figure 1.—Sternum of Pteranodon sp., No. 2692; right side.  $\times 1.0$

Figure 2.—The same specimen; left side.  $\times 1.03$

1



2







### Plate XVI.

Figure 1.—Distal end of the right tibia, and the podial bones of *Pteranodon* sp., No. 2502; dorsal view.  $\times 0.66$

Figure 2.—Digits II, III, and IV of the right manus of *Pteranodon* sp., No. 2428; missing parts are represented in outline.  $\times 0.66$

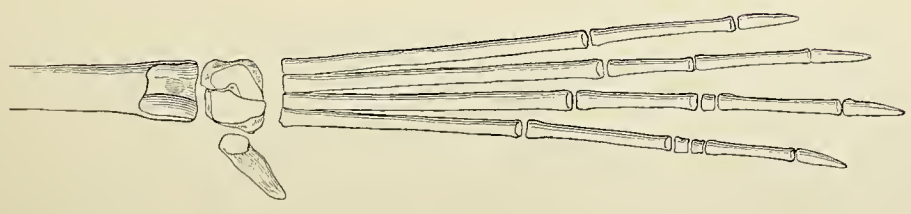
Figure 3.—Prepubis of *Pteranodon* sp., No. 2472.  $\times 1.0$

Figure 4.—Supposed sternal rib of the type of *P. ingens* Marsh, No. 1175.  $\times 1.0$

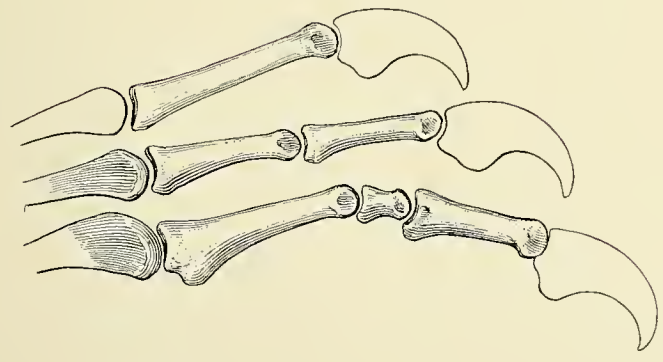
Figure 5.—Nearly complete restoration of the sternum of *Pteranodon* sp., No. 2546; seen from below.  $\times 0.66$



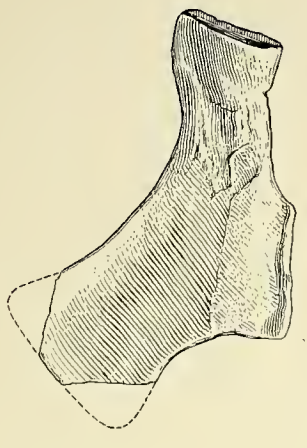
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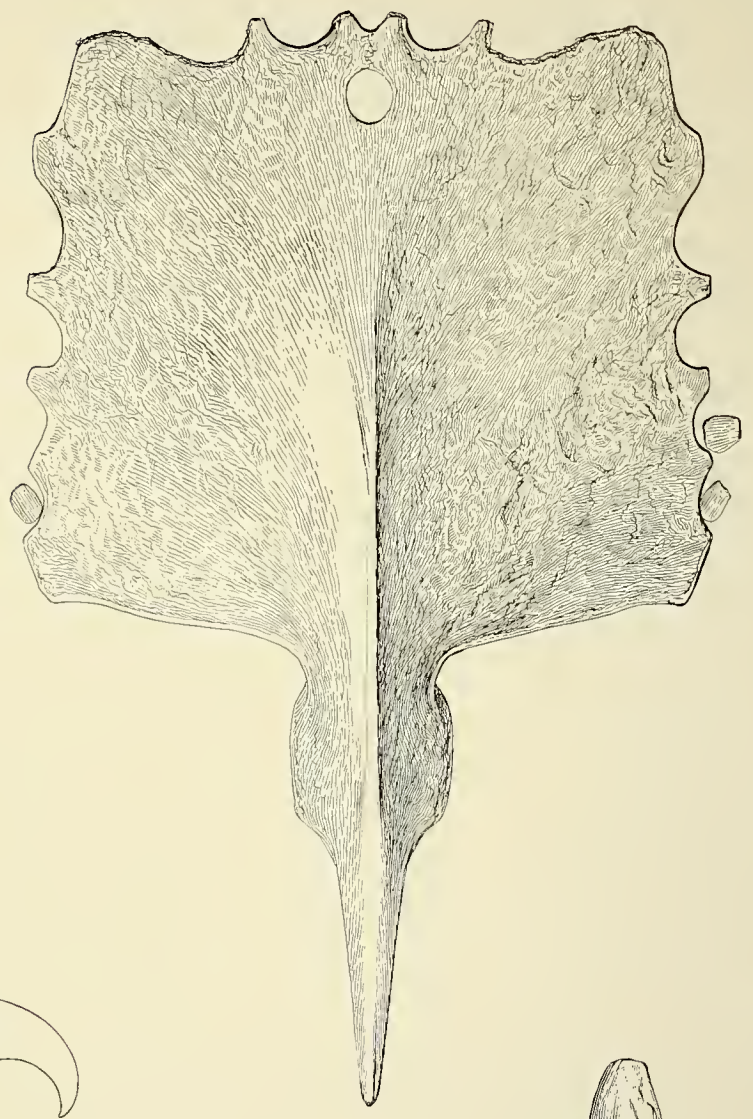
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4







**Plate XVII.**

Figure 1.—Right scapula and coracoid of the type of *P. ingens* Marsh, No. 1175; posterior view.  $\times 0.75$

Figure 2.—Left scapula and coracoid of *Pteranodon* sp., No. 2512; posterior view.  $\times 0.75$







**Plate XVIII.**

Figure 1.—Left scapula and coracoid of *Pteranodon* sp., No. 2616; seen from in front.  
× 0.88

Figure 2.—The same specimen; seen from the rear. × 0.89









## Plate XIX.

Figures 1–8.—Bones of the left wing preserved in the type of *P. ingens* Marsh, No. 1175.  
× 0.30

Figure 1.—Humerus; superior or anconal surface.

Figure 2.—The same bone; inferior surface.

Figure 3.—Ulna; inferior surface.

Figures 4a, 4b.—Proximal and distal ends of the radius; inferior surface.

Figures 5a, 5b.—Proximal and distal ends of metacarpal V.

Figure 6.—Carpus: proximal surface.

Figure 7.—Carpus; dorsal view.

Figure 8.—Carpus; distal view.

Figures 9–19.—Bones of the right wing preserved in the type of *P. occidentalis* Marsh,  
No. 1164. × 0.30

Figure 9.—Humerus; superior or anconal surface.

Figure 10.—The same bone; inferior surface.

Figure 11.—Ulna; proximal end; superior surface.

Figures 12a, 12b.—Proximal and distal ends of the radius; superior surface.

Figure 13.—Carpalia; proximal surface.

Figure 14.—Carpalia; distal surface.

Figures 15a, 15b.—Fragmentary metacarpal V.

Figure 16.—First phalanx of digit V (wing finger); radial side.

Figures 17a, 17b.—Proximal and distal ends of the second phalanx of digit V;  
radial side.

Figures 18a, 18b.—Proximal and distal ends of the third phalanx of digit V;  
radial side.

Figure 19.—Fourth phalanx of digit V: radial side.







**Plate XX.**

Figure 1.—Left humerus of *Pteranodon* sp., No. 2709; inferior view.  $\times 0.39$

Figure 2.—Left humerus of *Pteranodon* sp., No. 2831; superior view.  $\times 0.39$

Figure 3.—Left humerus of *Pteranodon* sp., No. 2589; inferior view.  $\times 0.39$

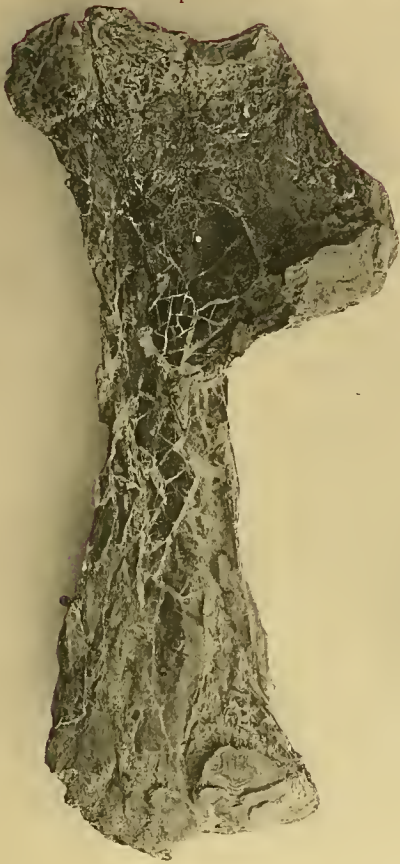
Figure 4.—Left humerus of *Pteranodon* sp., No. 2302; anterior view.  $\times 0.39$

Figure 5.—The same bone; posterior view.  $\times 0.39$

Figure 6.—Right humerus of *Pteranodon* sp., No. 2730; superior view.  $\times 0.39$



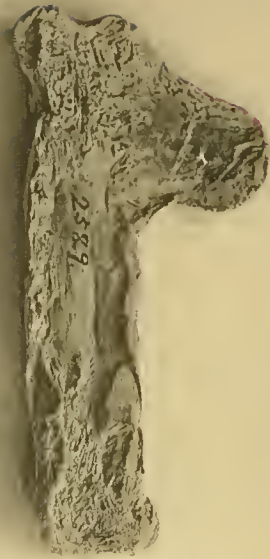
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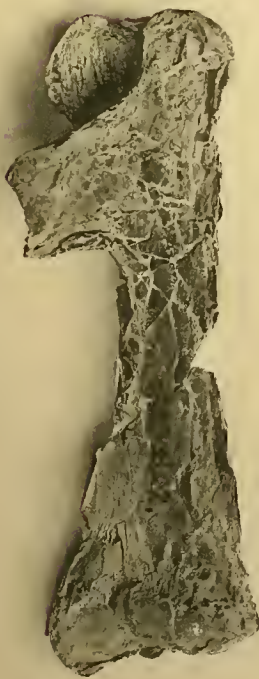
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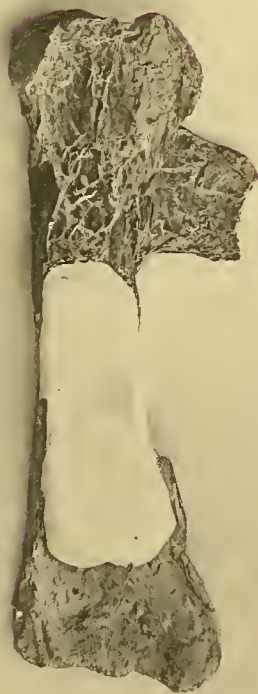
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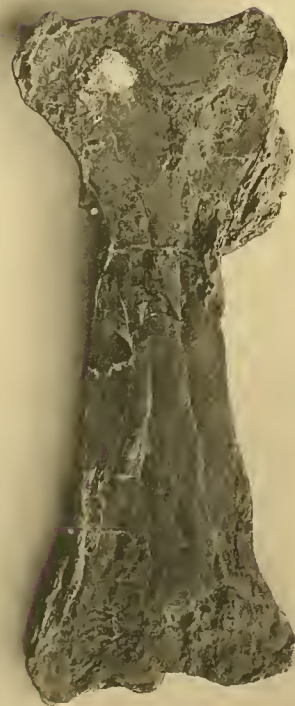
4



5



6







**Plate XXI.**

Bones of the left wing of Pteranodon sp., No. 2425, as preserved in the matrix; namely, the humerus, radius and ulna, the proximal and distal carpals, the metacarpals, pteroid bone, and the fragmentary proximal phalanges.  $\times 0.43$







**Plate XXII.**

Figure 1.—Left carpus of *Pteranodon* sp., No. 2425; palmar surface.  $\times 0.64$

Figure 2.—The same specimen; dorsal surface.  $\times 0.58$

Figure 3.—Distal ends of metacarpals II, III, and IV, of *Pteranodon* sp., No. 2493, with three nearly complete digits of the right manus, the number and order of the phalanges in two of these digits being incorrectly preserved.  $\times 0.78$

Figure 4.—Right carpus of *Pteranodon* sp., No. 2683, with the proximal end of metacarpal V; palmar view.  $\times 0.82$

Figure 5.—The same carpus removed from the matrix; dorsal view.  $\times 0.82$



1



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4



5







**Plate XXIII.**

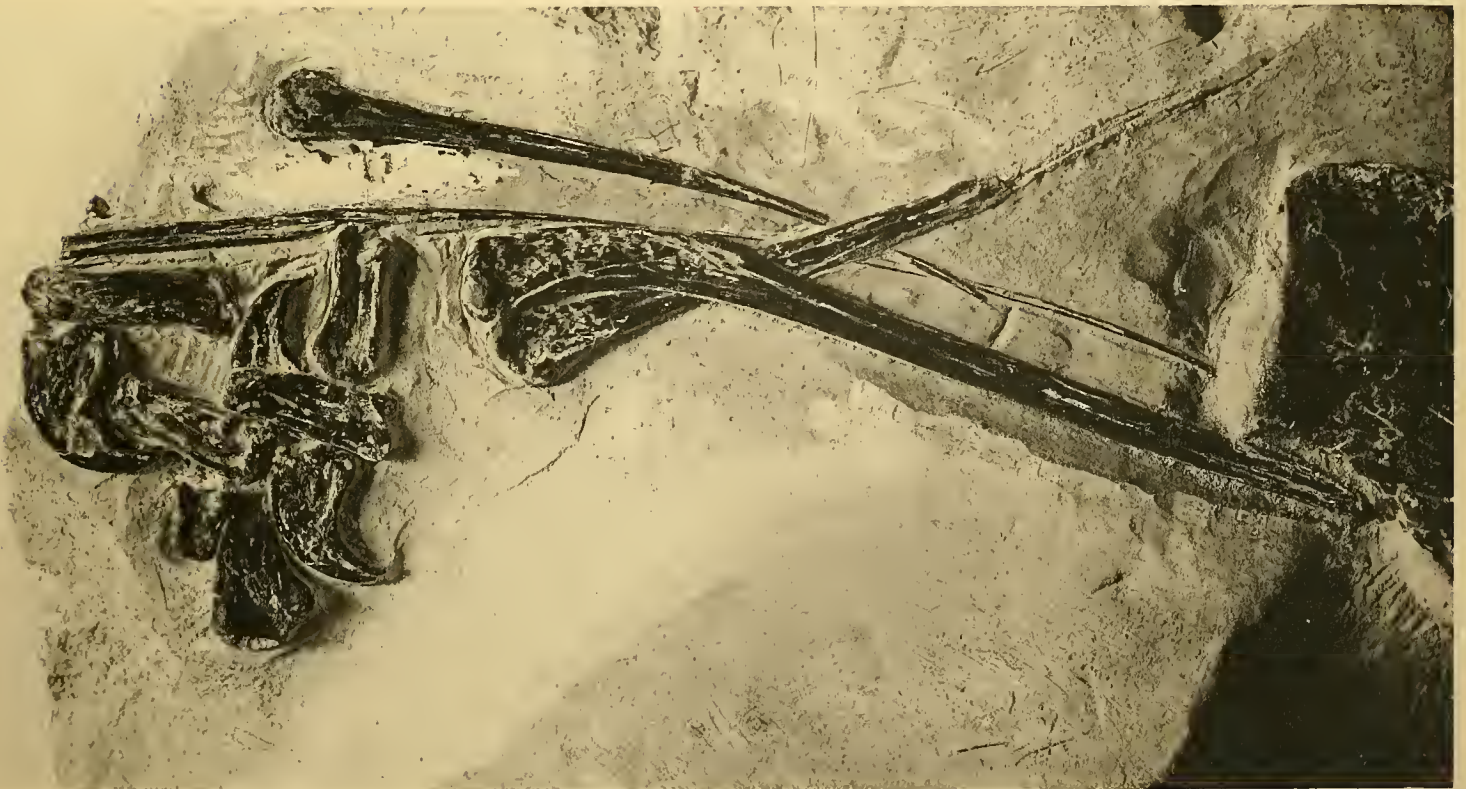
Figure 1.—Right scapula and coracoid and bones of the right wing of *Pteranodon* sp.,  
No. 1181, preserved in the matrix.  $\times 0.45$

Figure 2.—Pteroid bone, metacarpals II, III, and IV, and phalanges of the same specimen.  
 $\times 1.11$

1



2







### Plate XXIV.

Figure 1.—Adjacent ends of metacarpal V and the first phalanx of the left wing of *Pteranodon* sp., No. 2628; ulnar side.  $\times 0.50$

Figure 2.—The same specimen; radial side.  $\times 0.50$

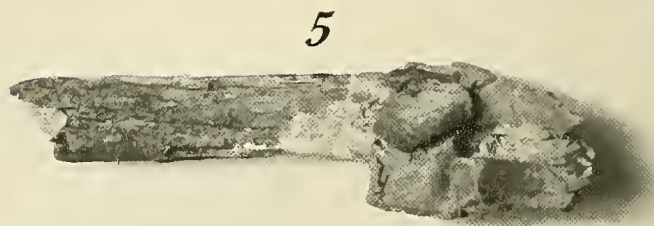
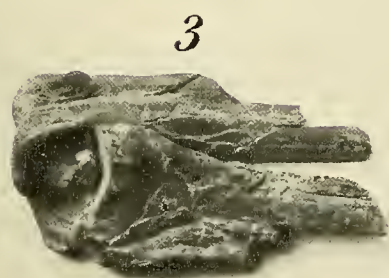
Figure 3.—Adjacent ends of metacarpal V and the first phalanx of the left wing of *P. occidentalis* Marsh, No. 1165 (identification of O. C. M.), at the angle of extreme flexure; ulnar side.  $\times 0.50$

Figure 4.—The same specimen; radial side.  $\times 0.50$

Figure 5.—Conjoined fragments of the left metacarpal V and the first phalanx of *Pteranodon* sp., No. 2660; palmar surface.  $\times 0.67$

Figure 6.—The same fragments separated; palmar surface.  $\times 0.67$









**Plate XXV.**

Figures 1-7.—Wing bones preserved in *Pteranodon* sp., No. 2452.  $\times 0.35$

Figure 1.—Right ulna; palmar view.

Figure 2.—Right radius; palmar view.

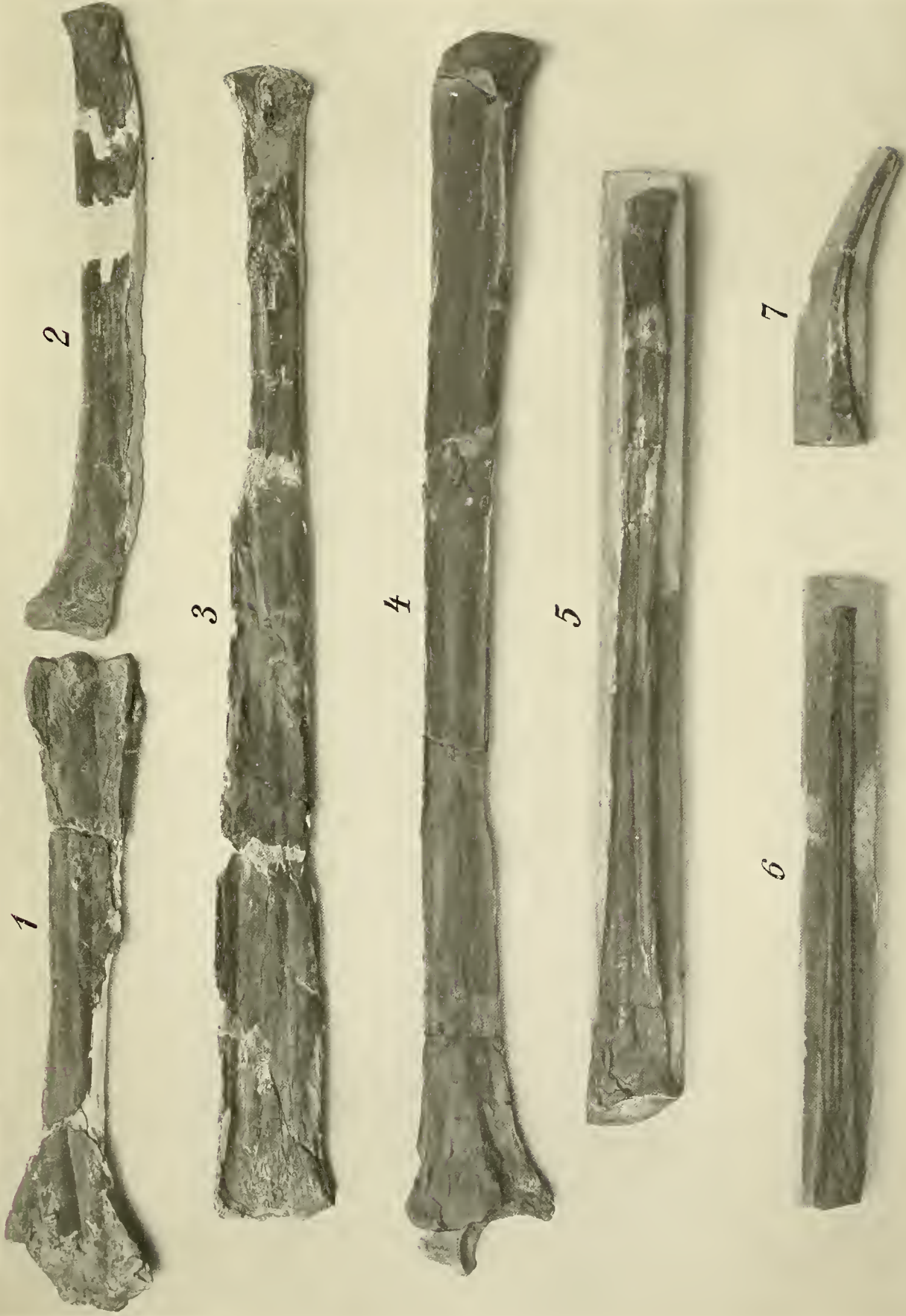
Figure 3.—Left metacarpal V.

Figure 4.—First phalanx of the left digit V (wing finger); radial side.

Figure 5.—Second phalanx of the left digit V; radial side.

Figure 6.—Third phalanx of the left digit V; radial side.

Figure 7.—Fourth or terminal phalanx of the left digit V; radial side.







## Plate XXVI.

Figures 1-3.—Bones of the left wing preserved in *Pteranodon* sp., No. 2774; radial side.  
× 0.35

Figure 1.—Distal end of the metacarpal and first phalanx of digit V.

Figure 2.—Second phalanx of digit V.

Figure 3.—Third phalanx of digit V.

Figures 4-7.—Bones of the right fifth digit of *Pteranodon* sp., No. 2470; radial side.  
× 0.35

Figure 4.—First phalanx.

Figure 5.—Second phalanx.

Figure 6.—Third phalanx.

Figure 7.—Fourth phalanx.

Figures 8, 9.—Third and fourth phalanges of the fifth digit of the wing of *Pteranodon* sp., No. 2591. × 0.35









**Plate XXVII.**

Figures 1-3.—Bones of the right leg and foot of *Pteranodon* sp., No. 2489.  $\times 0.57$

Figure 1.—Femur; inner and posterior view.

Figure 2.—Tibia; inner and posterior view.

Figure 3.—Nearly complete pes.

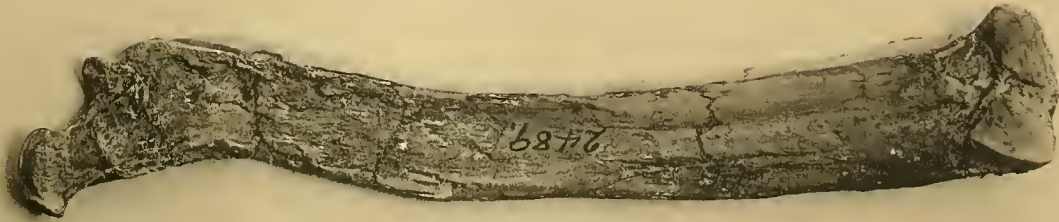
Figures 4, 5a, 5b.—Bones of the right leg of the type of *P. ingens* Marsh, No. 1175;  
posterior view.  $\times 0.57$

Figure 4.—Femur.

Figure 5a.—Proximal end of the tibia.

Figure 5b.—Distal end of the tibia.

1

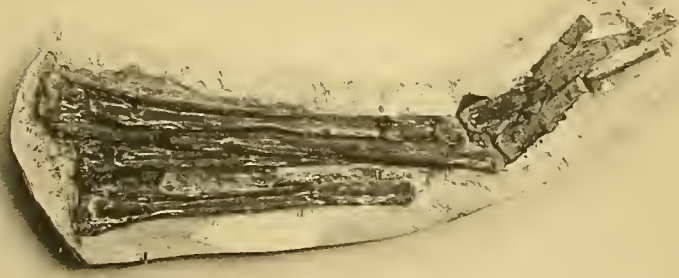


27489

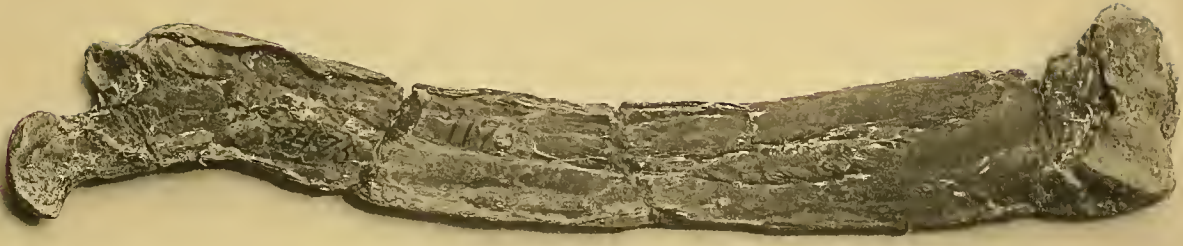
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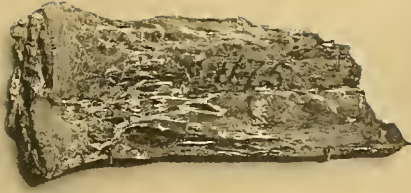
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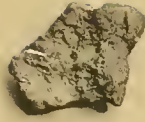
4



5 a



5 b







**Plate XXVIII.**

Figures 1-4.—Leg bones of *Pteranodon* sp., No. 2738.  $\times 0.64$

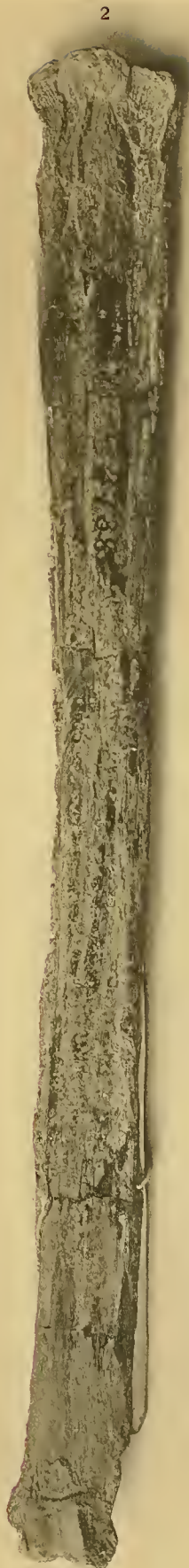
Figure 1.—Left femur; anterior view.

Figure 2.—Left tibia; anterior view.

Figure 3.—Right femur; inner and posterior view.

Figure 4.—Right tibia; posterior view.









**Plate XXIX.**

Figures 1-4.—Bones of the hind limbs preserved in *Pteranodon* sp., No. 2493.  $\times 0.65$

Figure 1.—Right femur: from the right side.

Figure 2.—Right tibia (from the right side), tarsus, and metatarsus.

Figure 3.—Left femur; posterior view.

Figure 4.—Left tibia; posterior view.



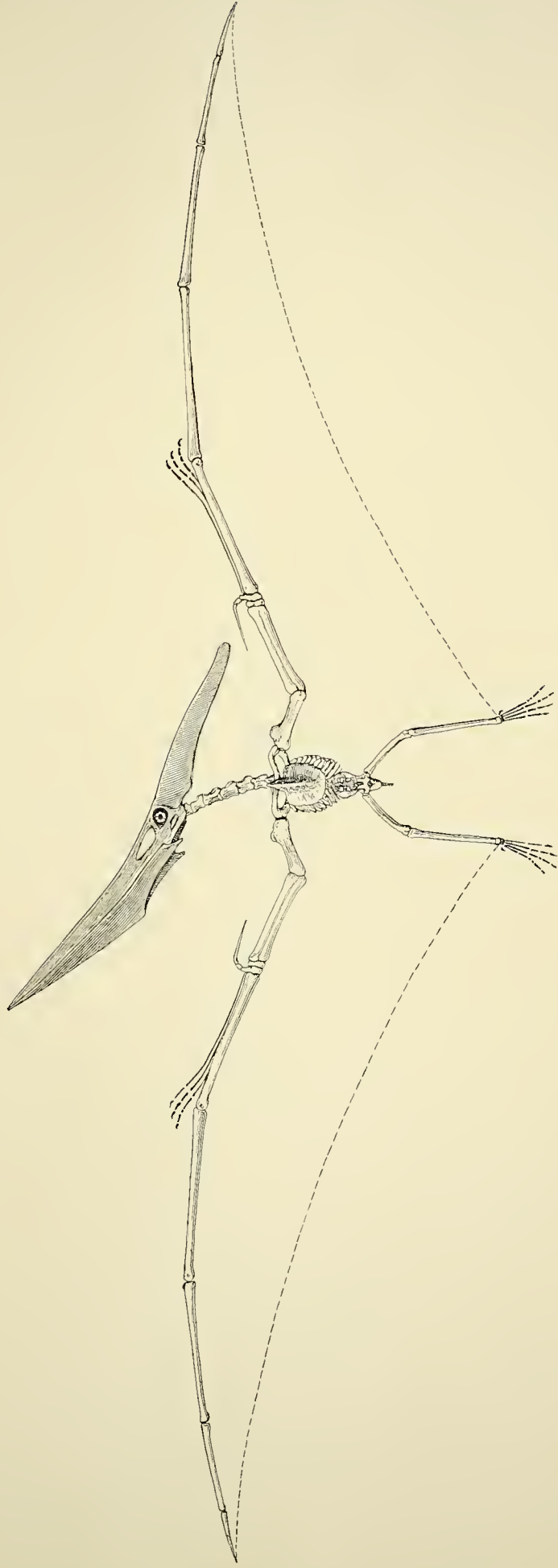




**Plate XXX.**

Restoration of Pteranodon Marsh, based on various individuals of the genus, including the types of *P. longiceps*, No. 1177, and of *P. ingens*, No. 2594.





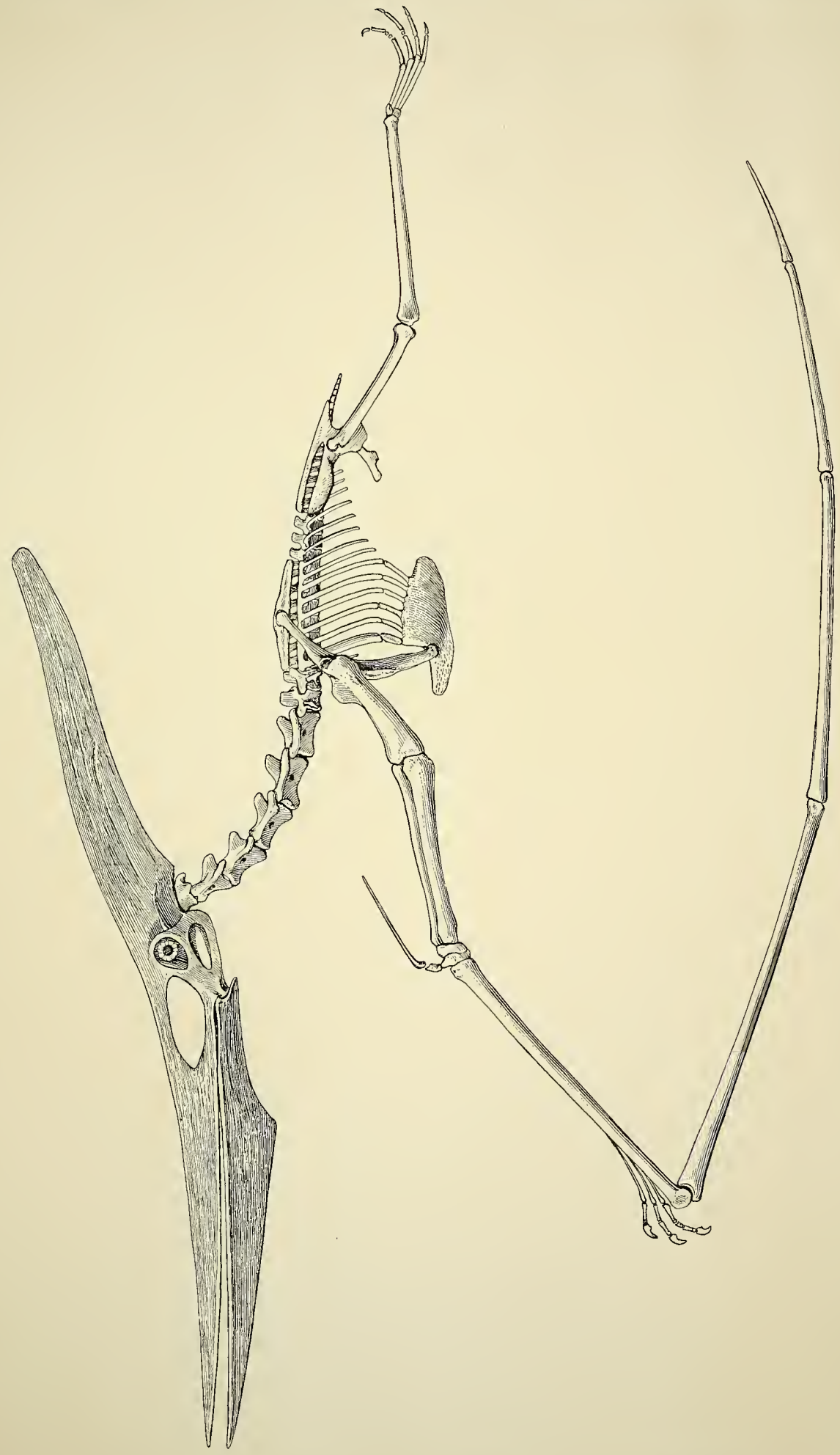
Restoration of Pteranodon Marsh.





**Plate XXXI.**

Restoration of Pteranodon Marsh: from the left side; based upon various individuals of the genus. For convenience of representation, the right limbs are omitted and the left wing is more sharply flexed than would be the case in actual flight.



Restoration of Pteranodon Marsh.















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