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ON THE OSTEOLOGY OF NYCTOSAURUS (NYCTODACTYLUS),

WITH NOTES ON

AMERICAN PTEROSAURS.

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In previous papers* I have given a summary of the principal characters of the genus *Nyctosaurus*,† with more or less complete descriptions of certain parts of the skeleton. In the present paper I give a more detailed description of the skeleton, based upon the unusually well-preserved and nearly complete specimen collected by Mr. H. T. Martin, together with some remarks upon the relationships and habits of the American pterosaurs, and the description of a new genus and species from the Lower Cretaceous of Kansas.

The specimen herewith described is of unusual importance, as throwing much light upon the structure, not only of the American pterodactyls, but also upon certain characters of the European ones. It is, I believe, for purposes of study the most complete specimen of this order of reptiles now known, comprising as it does nearly every bone in the skeleton, for the most part associated in their natural relations. The specimen now forms a part of the collections of the Field Columbian Museum.

SKULL.

A full description, with illustrations, of the skull has been given in the Journal of Geology, vol. x, 1902, p. 520. I give herewith illustrations of the mandible, not there figured. A careful measurement of the sides of this bone a little in front of the posterior end of the symphysis, where they are the broadest, obtained by measuring each fractured portion, gives a width for each side of twenty-four millimeters. The corresponding width of the palate is twenty-eight millimeters. This would give, as the greatest depth of the mandible, near the end of the symphysis, about twenty millimeters.

*Kansas University Quarterly, vol. i, p. 5, 1892.
American Journal of Anatomy, vol. 1, p. 297, 1902.
Journal of Geology, vol. x, p. 520, 1902.
Text Book of Paleontology, Zittel (Eastman), vol. ii, p. 255, f. 361.

†This genus has generally been known as *Nyctodactylus*. (See synonymy beyond.) Marsh changed the name because of the supposed preoccupation of the name *Nyctosaurus*. In this he was not justified. The name has never been used otherwise for a genus of animals. Doubtless he thought the term conflicted with Nyctisauria, used for a group of sauria. It does not, however, according to the accepted canons of nomenclature, and the original name should not be displaced.

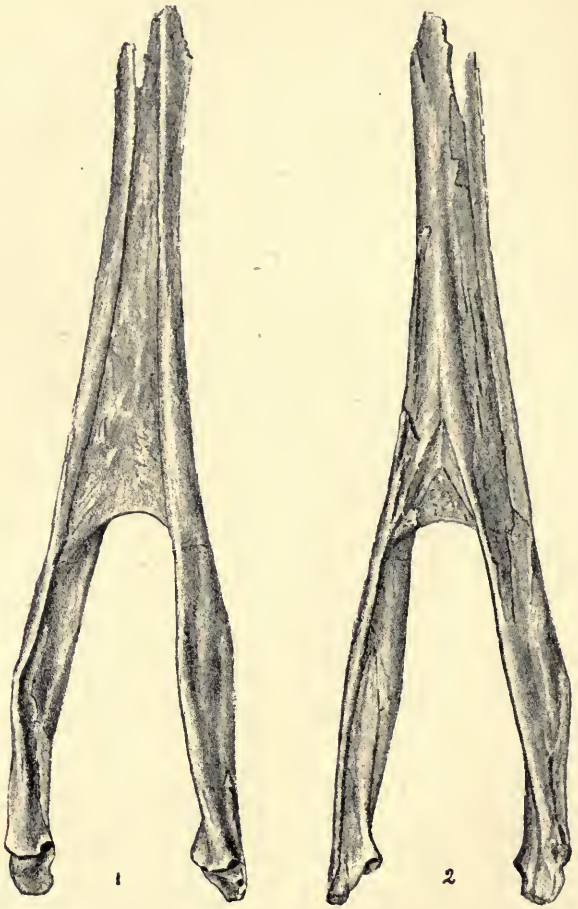


FIG. 1. Mandible of *Nyctosaurus gracilis*, x ⅔. 1, from above; 2, from below.

MEASUREMENTS OF MANDIBLE.

	mm.
Length, as preserved	168
Lengths of rami to hind margin of floor	78
Width between condyles	39

HYOIDS.

Two slender, cylindrical, gently curved bones, about thirty millimeters in length, were found lying side by side beneath the anterior part of the skull. They are sufficiently well shown in Plate I of the paper cited in the Journal of Geology. Lying near the occiput in the same plate, is seen a small, triangular, or V-shaped bone which I then thought might be

a proatlas, said by Zittel to occur in the pterodactyls, but of which there is no other evidence in this specimen. Since the removal of this bone from the matrix, it seems quite surely to be, rather, the anterior, median element of the hyoidean apparatus. One view, which I take to be the superior, is shown in Pl. XLI, Fig. 6, three times the natural size, and, in Fig. 7 of the same plate, is shown one of the articular extremities (*a*) from the side, much more enlarged. The bone is nearly flat, with the pointed extremity curved upward, and with the two articular extremities much more massive than the remainder of the bone; they are also directed upward. Each has a smooth, synovial articular surface, doubtless for the articulation of the cylindrical rods. On the opposite surface, near the articulations, there is a slight longitudinal ridge, and near the middle of the bone on each side, there is an elongated, oval surface, apparently for muscular attachment. The slender rods seem to agree quite with the hyoidean bones of other pterodactyls, but I cannot find that the triangular bone has ever been described.

VERTEBRÆ.

Seven has usually been accepted as the number of vertebræ in the neck of pterodactyls. If, however, we consider that vertebra which bears the first rib articulating with the sternum to be the first dorsal, then I believe that the prevailing number of cervicals in pterodactyls is eight. Fürbringer has already expressed the opinion that there are eight vertebræ instead of seven:* "Falls die Patagiosaurier zum Theil nur sieben Halswirbel besitzen, wie algemein behauptet wird, aber meines Erachtens erst noch zu erweisen ist, so wäre eventuell anzunehmen, das dieselben durch eine geringgradige, kranial gerichtete Wanderung der vorderen Extremität ihren ursprünglich aus acht Wirbeln bestehenden Hals um einen in das thorakale Gebiet übergehenden Wirbel verkürzten." He further expressed the opinion that the vertebra which I had considered to be the first dorsal in *Pteranodon* was really the eighth cervical. In a later paper I stated that the eighth vertebra in the neck of *Nyctosaurus* was a functional cervical, though a structural dorsal. . . . I have usually assigned this vertebra to the dorsal series because of its great structural differences from the anterior cervicals; but these differences are scarcely greater than those of the last cervical in the turtles. Owen† correctly located it in the neck. In his description of this vertebra in *Dimorphodon* he says: "At the base of the neck or the beginning of the back, the vertebræ suddenly decrease in length; the hypapophysis disappears, or is represented only by a slight projection of

* Jena. Zeitschr. f. Naturwissenchaft, vol. xxxiv, p. 665, 1900.
† Paleontograph. Soc., 1869, p. 69.

the lower border of the anterior cup; parapophyses [i. e., exapophyses] are less produced. The lower surface of the centrum is flattened and quadrate in form. The parapophysis, diapophysis and rudimental rib coalesce around the vertebrarterial canal; an oblique ridge is continued from the anterior zygapophysis downward and outward upcn the pleurapophysis and behind the zygapophysis. Above these developments the neural arch contracts from before backward to an extent of five lines, compared with a total vertebral breadth anteriorly of one inch, eight lines; it then rapidly expands, rising vertically at its fore part, and developing at its back part the posterior zygapophysis, the articular facets of which look more directly outward than in the long cervical vertebræ; the superincumbent tubercle is more distinct from the facet; the posterior zygapophyses are also much more approximated than in those vertebræ."

It would seem evident from this description, which applies in the main to the corresponding vertebra of the Kansas forms, that the eighth postcranial vertebra is really a cervical. Certainly we can hardly put a vertebra with rudimentary ribs at the beginning of the dorsal series! Owen afterwards ascribed eight vertebræ to the neck, or seven, counting the united axis and atlas as one. Quenstedt, also, in 1855, gave the number as eight. O. Fraas (Paleontographica, 1878, p. 166) found eight vertebræ in the neck of *Pterodactylus suevicus*, but mistook the third for the axis, thus counting only seven.

In my earliest paper* on *Nyctosaurus* I said: "The centra of twelve vertebræ are preserved from the region back of the neck. Three of these are evidently anterior thoracic, judging from their structure and the position in which they lie. The shortest of them, to which was attached a very large rib, and which was lying in front of the scapula, may represent the first thoracic vertebra." This specimen I have figured in Pl. XLIII, Fig. 7, of the present paper. The specimen is fortunately preserved with little or no distortion, though a part of the spine is wanting. As seen from the front (the view figured), the transverse, shallowly concave cup is straight or gently concave on its upper margin, and convex below. Arising from the front end of the centrum there is, on each side, a very stout parapophysis, with which the head of the rib referred to was in apposition. On the anterior side of this process, and continuous, or nearly so, with the outer side of the cup, there is an oval, convex articular surface for union with the exapophysis. Above this process, separated by a notch, there is a long, flattened diapophysis, for articulation with the well-developed tubercle of the rib. The anterior zygapophyses are much more approximated than in the long cervical verterbræ. Their articular

*Kansas University Quarterly, vol. i, p. 9.

surface is oval, the plane of each nearly at right angles with that of its mate. The spine is broad and transverse; from the front it presents a median ridge. On the under side the centrum is flat, the flatness reaching nearly to the extremity of the parapophysis; the width is considerably greater than the length. The posterior surface of the centrum in this specimen is distinctly roughened for sutural union with the following centrum; the posterior zygapophyses also unite with the succeeding ones suturally. This vertebra is very clearly the first of the notarium, as Seeley has happily called the united dorsal vertebræ. "Two other vertebræ found close by the one described, and possibly one or the other contiguous with it, differ remarkably in having no or a rudamentary parapophysial process, and in having the diapophysis much shorter." "In *Pteranodon* there are at least four vertebræ with dia- and parapophyses." "In two other centra there is a long, recurved, parapophysial process, as though formed by an anchylosed rib, on each side; they are probably lumbar vertebræ." It is very clear, however, that these last two vertebræ are not lumbars, but separated elements of the notarium. Of the two other vertebræ mentioned, one is probably the eighth cervical, described below, while the other may be the fourth dorsal.

In *Pteranodon*, I thought there might be two vertebræ intervening between the elongated cervicals and the notarium. "The centrum is short and broad, so different from the preceding one that it is possible there may be an intervening one lost. The ball is more than four times as broad as high, concave on the upper margin, convex below. The post-exapophyses are large, and confluent with the articular faces of the ball, but are concave. The convex pre-exapophyses, at the outer side of the cup are at the base of the lower root (that is the parapophysis) of the elongated transverse process."* This vertebra corresponds with the eighth post-cranial vertebra of the present specimen, but an "imperfect vertebra, evidently following the one described, has the centrum very similar, save that the spine appears to be less stout." I cannot at the present time examine this specimen, but it is probable that it is the first separated vertebra of the notarium.

From the foregoing, then, it seems assured that there is a free, short vertebra in front of the notarium, in both *Pteranodon* and *Nyctosaurus*, bearing a free, small rib, which does not unite with the sternum. This vertebra is the eighth cervical, and is probably present in all pterodactyls. It is strange that authors, in the description of the neck bones of the pterodactyls should have so often spoken of the united atlas and axis as one vertebra, thus reckoning seven instead of eight vertebræ in this part of the

*Williston, Kansas University Quarterly, vol. vi, p. 40.

column. Von Ammon* thus describes the neck vertebræ of *Rhamphorhynchus longicaudatus:*

"Es sind sieben Halswirbel vorhanden. Atlas and Epistropheus werden hierbei als ein Wirbel gerechnet. Beide miteinander zusammenhangen, ihre Gliederung und Form sind undeutlich; die Knochen sind durch späthige Masse entstellt. Es folgen nun nach rückwarts fünf gleichgestaltete, deutlich von einander abgegrenzte Wirbel, dann kommt (der VII in der Reihe) ein von diesen etwas verschieden aussehender, weil anders gestellte Wirbel der den abschluss des Halses bildet; der unter letzterem befindliche Wirbel (der achte, [in reality the ninth]) besitzt bereits eine grössere Rippe, so dass mit ihm die Reihe der Brustwirbel zu beginnen ist."

Atlas and axis, Pl. XLI, Figs. 3–5. The atlas is coössified with the axis for the most part in the adult specimen, though leaving a distinct sutural line of division in the more immature specimen. In the younger specimen, the coössification is less complete, and the axial intercentrum is also apparent, though indistinguishable in the older specimen. The atlas is composed of the usual number of parts, though the centrum, or odontoid must be small. The intercentrum forms the lower third or more of the cup; it is deeply and smoothly concave, with a sharp cotylar rim, which is nearly semicircular in outline. Its upper border in front has three parts: the middle one, concave in outline, joins the odontoid; the lateral borders, oblique in position, join the bodies of the neurapophyses. The posterior surface is probably flat, or but slightly concave; the sutural line with the axial intercentrum is nearly parallel to the rim, and the width is slight, though a little greater on the ventral side, where the under border slopes somewhat ventrad toward the axial intercentrum.

The bodies of the lateral pieces, or neurapophyses, of the atlas complete the rim of the cup, each forming a little less than one-third of the circumference. Their lower border unites with the atlantal intercentrum; the inner, lower border, joins the odontoid; while the inner, upper border, thinner and less in extent, unites with its mate in the middle. The dorsal processes or arches are slender, somewhat oblique, and but slightly dilated at the distal extremity, which appears to be free. They apparently curve backward, to be applied throughout the whole of their extent, to the thin neural border of the axis. The bottom of the cup is formed by the odontoid. Its anterior surface has three convex borders of nearly equal extent, ending more acutely above. How deep or thin this bone is cannot be said, and it is not impossible that the surface appearing in the cup is really the anterior face of the body of the axis, the odontoid being obsolete. The inner ends of the lateral pieces are thin, and it is impos-

*Correspondenzblatt des Naturw. Ver. in Regensburg, 38 Jahrg., 1884, p. 151.

sible to say whether the odontoid appears on the floor of the neural canal or not.

The axial intercentrum is a large, wedge-shaped piece intervening between the atlantal intercentrum and the body of the axis. It is scarcely keeled in the middle below and reaches as high on the sides as does the atlantal intercentrum.

The body of the axis is short and much expanded posteriorly. Its ball is small and widened transversely. Below the ball the body is expanded into a very large, flaring rim, inclosing a deep concavity, having a broad articular surface transversely. This surface evidently corresponds to the united postexapophyses of the later vertebræ—the "posterior parapophyses" of Owen and Plieninger. Nothing quite similar to this structure seems to have been observed in any of the European pterodactyls, though an axis figured by Owen,* as also Seeley, seems to approach this structure. Nor do I find a corresponding adaptation of structure in any of the following vertebræ.

The arch of the axis is broad and relatively high. The neural rim in front, to which are applied the dorsal neurapophyses of the atlas, is thin, forming a heart-shaped opening. The spine is broad, low in front, where there is a thin margin, for a short distance, and is highest behind. The sloping border is thickened, the posterior border thin. Below, on each side, there projects backward a strong process, on the under side of which, before its termination, is the small, oval zygapophysis.

In the figures given in Pl. XLI, I have partially restored the axis and atlas after two specimens, both complete, but compressed in different ways. The length of the atlanto- axis is 14 mm.

Plieninger† describes the atlas in *Pterodactylus kochii* as consisting of a "ziemlich massiven Körper, sowie aus einem Nervenrohr umschliessenden Bogenpaar, welches aussen und oben jederseits einen Fortsatz trägt, der wohl zur Anheftung von Muskeln diente." He also identifies the bone considered by Fraas‡ as a "Schlundring" as the atlas. From the description and figure it would seem that the atlas of *Pterodactylus* is of a very different structure from that in *Nyctosaurus* and *Pteranodon*. (I have seen the united axis and atlas in a species of the latter genus; they resemble the same bones in *Nyctosaurus*.)

Third—seventh cervical vertebræ, Pl. XLIII, Figs. 7–8. The cervical vertebræ were lying close together between the back of the skull and the top of the thorax, but they were dislocated and disassociated, so that nothing can be told of their sequence from their position. Three are

* Brit. Fos. Rept. iv. Pl. viii, fig. 2.
† Paleontographica, 1901, p. 17.
‡ Paleontographica, xxv, Pl. xxii g

lying upon their ventral surface, that is, compressed dorso-ventrally, and two were more or less crushed laterally or obliquely. There is less difference in the lengths of the five following the axis than is the case in *Pteranodon;* I am therefore somewhat in doubt as to the precise position of some of them. Those that are depressed have the under surface irregularly plane or concave, with the lateral margins rounded and concave, formed by the ridge which reaches from the anterior zygapophysis and exapophysis on each side to the corresponding posterior exapophysis. At the front margin there is an oval fossa, or depression, on each side, separated by a convex surface; this convexity seems often to be produced into a distinct hypapophysis in the European pterodactyls. In a previous paper I stated that the exapophyses are non-articular in this genus. This statement, after a more careful examination of the specimens removed from the matrix, I know to be erroneous, at least so far as the processes of the posterior vertebræ are concerned. Owen has identified these processes with the parapophyses, and Plieninger prefers to adopt this name for them. As will be seen by an inspection of Fig. 7, Pl. XLIII, the true parapophysis—that is the process for the articulation of the head of the rib, for which the term was originally introduced by Owen, and in which sense it is now used—is always situated at the anterior end of the vertebra, close to the rim of the cup. This process bears on its anterior face, close to the rim of the cup, a convex, articular surface for union with the corresponding concave surface of the "posterior parapophyses" of the preceding vertebra. One might with as much propriety call these posterior prominent articular processes the diapophyses, or posterior inferior zygapophyses, as "posterior parapophyses." There is no such thing as a posterior parapophysis, nor can there be. Nor could these posterior "parapophyses" ever have arisen as processes for rib articulation. They are very characteristic of the pterodactyl vertebræ, taking the place of the lateral or double articulation of the cryptodire testudinate cervical vertebræ. I have given these articulations a distinctive name of exapophyses in order to save much circumlocution in their description; in any event they should not be called "parapophyses," since they have nothing to do with these processes, either morphologically or functionally.

The cup and ball are widened transversely; in the depressed specimens very much so, and this is not due to their crushing, since those lying upon their sides, though mutilated, still preserve evidence of a lateral elongation of the articular surface. The convexity of the ball is marked dorso-ventrally, more so near the neural side. The posterior border between the exapophyses is thin and concave, nearly concealing the ball, when seen from below. The anterior zygapophyses project much in front of the cup;

they are widely separated from each other. A ridge extends downward and posteriorly from the outer side of the zygapophysial process to the outer side of the convex exapophysis or parapophysis. I find no foramen inclosed between these processes, and can see no vestige of a cervical rib, such as is described in certain European pterodactyls. The posterior zygapophyses are concave and oblique, and above them, there is a more or less prominent process, a sort of "metapophysis." They do not extend as far back as the ball, leaving a wide space between and back of them in which the floor of the neural canal is visible. The laminæ are broad, thin, and roof-like, meeting in the middle and forming a very thin, neural spine. The length of the base of this spine varies not a little in the different vertebræ, from twelve to sixteen millimeters. In only one vertebra is there a long spine, the one figured in Pl. XLIV, Fig. 17, which I take to be the seventh cervical. In the others, the free, thin border slopes slightly upward and forward, forming a rounded spine but a few millimeters in height.

Eighth cervical vertebra. Pl. XLIII, Fig. 8. The eighth vertebra, which, as already explained, is a real cervical and not a dorsal, was lying close to the first notarial vertebra, and near the presternal process of the sacrum. It has been so much compressed that all of its characters cannot be made out with clearness. A figure of it is given as it lay in the matrix. It differs greatly from the vertebra preceding it in the shortness of its centrum, the character of its spine, and in the presence of diapophyses. The ball is transversely widened, and has, at each extremity, a large, concave, articular exapophysis. The post-zygapophyses are situated much posteriorly to the ball, differing therein remarkably from those of the preceding vertebræ. The spine above the zygapophyses is very short and thick; seen from behind, it is concave, and ends obtusely nearly over the zygapophyses. On each lateral expansion, near the upper extremity, there is an oval, rounded, smooth surface, forming a sort of process corresponding to the "metapophyses" of the earlier vertebræ. The front border of the spine is concave in outline, and is rounded. There is a rather slender and moderately long diapophysis, springing high up on the arch. In the specimen it has been compressed against the vertebra, but seems to end in an articular process. On the under side of the vertebra, near the mutilated diapophysis, there is a fragment of a rib, more slender than those of the notarium, which probably belongs with this vertebra. In the much confused anterior end of this vertebra, there is a small process on each side, evidently the exapophysis, which may also have served for the articulation of the head of the rib; if so, however, the head must have been small. In the specimens of the *Pteranodon* vertebræ already described, this parapophysis seems either rudimentary or

wanting. I suspect that the rib was single-headed here. Because of the small size of this rib, the large size of the exapophyses, and the very free union of the vertebra, as also because of the position of the notarium in the specimen, apparently in articulation with the first tubercle of the sternum, I feel confident that this vertebra does not articulate with the sternum, and that it is a cervical.

Plieninger, l. c., considers the eighth shortened vertebra in *Pterodactylus* as the first dorsal, because it bears a diapophysis. No rib was preserved in his specimen, and he does not state whether there is a parapophysial process for the rib. If a rib was present, it was doubtless small, since the next three pairs of ribs are found in place, and are "besonders kräftig." The next three or four pairs are also strong. The posterior ribs are slender.

Dorsal vertebræ. Pl. XLI, Fig. 1; Pl. XLIII, Fig. 7. The three firmly united vertebræ of the notarium, which are visible, lie with their ventral side uppermost, directed a little obliquely toward the left side, and are partly concealed beneath the sternum. The front end lies about ten millimeters back of the front end of the presternal process of the sternum. The first two centra are visible nearly wholly, the third only in part. The centra are flat below, concave on the lateral margins. The first has a concave cup margin, and on each side a stout parapophysis is continued into a strong rib, without clear indications of sutural union. This vertebra in the Kansas University specimen has the ribs free, and it was itself separable from the following centrum through its suture; it is figured in Pl. XLIII, Fig. 7, and has already been described. The parapophysis of the second notarial vertebra seems to be given off somewhat further back, and there are indications of its sutural union with the rib about seven millimeters from the body. The rib is four millimeters in width beyond its proximal part, and a length of about thirty millimeters was preserved. A specimen of a notarial rib, probably the first, preserved with the Kansas University specimen, has a length of forty-five millimeters and a width of five. The corresponding rib in this specimen must have been not less than fifty millimeters in length, and probably about sixty. Whether the third vertebra bears similar anchylosed ribs in this specimen cannot be said, as they are covered by the sternum, but since the third vertebra in the Kansas University specimen has such, it is undoubtedly also the case in this. The end of a flattened rib, about twenty-five millimeters in length and three or four in width, is lying by the articular margin of the sternum, and may belong to this vertebra.

Lying in the axis of the notarium, a convex rim of a dorsal vertebra has partly protruded through the thin sternum. This vertebra is doubtless either in direct articulation with its preceding vertebra, or but very

slightly removed. The length of the series is about fifty millimeters, showing that five vertebræ are associated in it, and that the protruding one is the fifth. Whether the fourth and fifth are both suturally united in the notarium cannot be said, but in all probability the fifth at least is free, since its convexity shows it to be of the nature of the following ones, and because one of the small posterior ribs seems to have been articulated with it. The sixth, seventh, eighth, and ninth vertebræ are nearly in relation with each other, behind the sternum, lying upon their dorsal side, but are pushed somewhat to the left. They are cylindrical in cross-section, with smooth, evenly concave sides and inferior border, with a deep cup and a prominent ball. They are a little longer than broad, of nearly equal length, though a little more slender posteriorly. The anterior zygapophyses extend in front of the cup. The elongated and slender diapophyses arise high up on the arch from near the anterior part of the vertebra, and are directed horizontally outward. These vertebræ are quite similar to those of *Pteranodon*, and are doubtless quite like that figured by Seeley in his Dragons of the Air, p. 86, Fig. 26. The last dorsal (or first sacral) (Pl. XLI, Fig. 1, *dv*), the tenth back of the neck, is flat on its inferior surface, and its transverse process I think arises from the centrum as in *Pteranodon*. It is firmly united with the sacrum by suture in both genera, and is quite as properly counted with the sacrum as with the dorsal or lumbar vertebræ. It is probable that its transverse process unites with, or reaches to, the anterior projection of the ilium, as seems also to be the case in *Pteranodon*.

The position in which the skeleton is lying indicates that the right coraco-scapula and the pelvis are in the positions in which they were as regards each other while yet held together by the ligaments. The right arm, falling across the abdomen, has caused a slight dislocation of the dorsal vertebræ, the notarium held by the ribs has been turned somewhat obliquely, and the sternum has settled down a little to the left. The ends of the scapulæ, however, are nearly in the relative position to each other which they must have held during life, and the axis of the sacrum is in line nearly with the presternum.

Now, by bringing all the vertebræ back into a straight line, the ten vertebræ fill the entire space between the neck and the true sacrum, proving almost incontestably that there were neither more nor less than ten, a number found in no other reptiles except the turtles and *Pareiasaurus;* indeed, if we call the last a sacral, then there are fewer presacral vertebræ in *Nyctosaurus* than in any other known reptile.

The sacrum proper, as described below, is composed of six vertebræ, the lines of sutural union of which are clearly visible in the specimen.

Four caudal vertebræ are preserved, lying close to the proximal end

of the left femur. The largest of these (Pl. XLIII, Fig. 11), that evidently immediately succeeding the sacrum, is flat at each end, and has neither distinct processes nor zygapophyses, and only a small, low spine on the posterior part; its width posteriorly is much less than that anteriorly. The other three vertebræ are in a series, slightly separated from each other, and are mere nodules of bone, without processes of any kind, about four millimeters in length by three in width; the last one ends in a conical point. From the tapering of the first, and the association of the last three close by the side of the femur it seems very probable that the tail was short and slender.

MEASUREMENTS OF VERTEBRÆ.

	Length, mm.	Width, mm.	Expanse, mm.
Atlanto-axis	14	----	----
Third cervical	24	----	----
Seventh cervical	21	----	----
Eighth cervical (about)	9	----	----
First dorsal	9	11	----
Second dorsal	10	11	----
Third dorsal	10	11	----
Length of first five dorsals (about)	53	----	----
Sixth dorsal	9	8	31
Seventh dorsal	9	8	30
Eighth dorsal	9	7.5	29
Ninth dorsal	9	8	----
Lumbar (tenth)	10	9	32
First true sacral	9	7.5	35
Second sacral	9	7.5	37
Third sacral	7.5	7.5	32
Fourth sacral	7	7	28
Fifth sacral	6	6.5	21
Sixth sacral	6	6.5	15
First caudal, or caudo-sacral	7	10(8)	----
Distal caudals	4, 4, 4,	3, 3, 3	----

RIBS.

Thoracic. Pl. XLI, Fig. 1, *r,r.* 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.

Beginning with the fifth dorsal, the ribs are single-headed, and are very slender and delicate. Four pairs are discernible in the specimen, and a fifth seems to be indicated by a fragment. The largest of these, that apparently belonging with the fifth dorsal, is gently curved. It meas-

ures about 75 mm. in length, 2 across its somewhat expanded head, .8 across the shaft a little beyond the capitular thickening, and but .4 near its distal extremity. The sixth vertebra has its rib on the left side in relation with the extremity of the diapophysis; it is a little shorter, .75 in width near its proximal extremity, and .3 distally. The seventh also has a rib in relation with the left diaphophysis; it is yet shorter, and nearly straight; measures .6 in width proximally, and .2 distally. The next rib is straight, and yet more slender, and shorter. The tenth vertebra, that connected with the sacrum, I do not think bore a free rib.

In a former paper I stated my belief that the slender, posterior, single-headed ribs did not inclose the abdominal cavity, but were directed more or less outwardly in the patagial membrane. In support of this belief it is seen that all these ribs are remarkably slender, and but slightly if at all curved. Their free and loose connection with the vertebræ, and their delicacy prevented them from being of use as a support to the abdominal contents; certainly not if the animal walked in a quadrupedal position. Furthermore, if they extended in the walls of the abdomen, the abdomen must have been exceedingly voluminous, and widely unprotected in front.

A better support for my contention is afforded by the position of the various bones in this specimen as they are preserved. All these ribs lie directed outwardly or obliquely backward, and none of them are mutilated or broken in the least, save as may have happened in the preparation of the specimen. The right arm lies obliquely across the abdomen; it was evidently sustained by the soft parts until after the ligaments connecting the forearm bones had partly decomposed, since these two bones and the carpals only are slightly disassociated from the remainder of the wing bones. The radius and ulna fell to the back part of the abdominal cavity while yet the pelvis was held together, permitting the left innominate bone to fall outward over the end of the ulna and carpal. Furthermore, the ventral ribs have fallen upon the radius. Now, under these conditions, had the ribs curved forward in the abdominal walls to meet the ventral ribs, they surely would have been entangled and doubled up beneath the forearm. But this is not at all the case, and it seems highly improbable that the fleshy walls of the abdomen could have fallen apart, and spread out laterally with the wing folded across them. From all of which evidence, I believe that the ribs were directed laterally, supporting the patagial membrane, perhaps as in *Draco*, and that they did not inclose the abdominal cavity.

Further evidence of the same tenor is furnished by the type specimen of *Rhamphorhynchus phyllurus* Marsh, which I have recently examined. In this specimen, the right arm had also fallen across the abdomen, while yet having the patagial membrane attached to it. Nevertheless, the very

slender ribs are spread outwardly, and were not doubled up below the wing bones. They cannot be ventral ribs, since these are large and broad in this species of *Rhamphorhynchus*, according to Zittel.

In *Pterodactylus spectabilis*, as figured in the books, a number of very delicate abdominal ribs are shown, as depicted by Von Meyer. "An die unteren Hälfte des Rumpfes kommen fünf fadenförmige Abdominalrippen. Sie sind fadenförmige, ohne sich gegen die Mitte her zu verstarken, und bei ihre Länge und dünnen Beschaffenheit etwas verbogen. Die erste Rippe, die längste, ergiebt 0.026."* Is it possible that the abdominal and vertebral ribs have been confused in this description?

Ventral ribs or *parasternum*. Pl. XLI, Fig. 2. The ventral ribs were, for the most part, lying in position nearly contiguous with the xiphisternal process. There appear to be four pairs, the first three lying together and united. The first pair is somewhat uncertainly shown, broken on the left side and partly concealed on the right below the border of the sternum. The second pair is very distinct. They are somewhat V-shaped, co-ossified and thickened in the middle, and terminating outwardly in a slender point. The third pair was in position, co-ossified with the margins of the second pair, but not united in the middle. Another pair is seen by the right side of the tenth vertebra, partly beneath the ulna; their whole form cannot be made out, but they are wider and longer, apparently, than the third pair, to which they could have had no ossific union. These ribs are all thin. In the restoration it seems evident that the last pair of these ribs would approach, if not actually meet at their ends, the anterior ends of the prepubic processes. I am very much inclined to believe that the prepubis is really not a part of the pelvis, but rather a part of the parasternal ossifications.

One of the best descriptions extant of the ribs of pterodactyls is that of von Ammon (op. ct.):

"Die hintersten dreizehnte Rippe stellt einen zarten Knochenstreifen vor. Das untere Ende der Rippen ist verdickt und bildet ein kleines Gelenkköpfchen, an welchem der obertste Theil einer Gürtelrippe der Bauchwand befestigt ist. . . . Durch ihre Verbindungen [d. h. der Abdominalrippen] mit den oberen Rippen bestehen also vollständige Gürtel in der Bauchwand. Es schliessen sich immer zwei Bauchrippen zu einem formlichen Halbkreis zusammen. Am Vereiningungspunkte ist eine mediane Verdickung vorhanden, die eine nach unten Spitz auslaufendes langes Köpfchen bildet." The ventral ribs of this pterodactyl (*Rhamphorhynchus longicaudatus*) are very thin and simple, in contrast with the broad ventral ribs of the larger forms of *Rhamphorhynchus*, according to Zittel.

* Paleontographica, vol. x, p. 4, 1868.

Owen* says that "the ribs of *Dimorphodon* acquire a characteristic tenuity beyond the sixth pair," and Seeley mentions the fact that the posterior ribs of the pterodactyls are slender. In current restorations of the pterodactyls, the posterior ribs are often shown as long and strong bones, inclosing a large and deep abdomen, the outlet of which must have been through the narrow pelvis. 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.

PECTORAL GIRDLE AND EXTREMITY.

So far as is definitely known, the pectoral girdle comprises the sternum, coracoid and scapula only. No clavicles (unless the ossification hereinafter described is a clavicle), inter-clavicle, epicoracoids, or precoracoids, even, are known. Furthermore, the bones present are so strangely modified that they present very little resemblance to the same elements in other reptiles, agreeing rather better with those of birds, an agreement, however, that I believe to be homoplastic in nature.

Sternum. Pl. XLII, Fig. 1. The sternum is a broad and thin bone, with a stout anterior projection, and a thin, spatulate xiphisternal process posteriorly. The presternal process is narrowed and rounded on the under surface, and may have projected somewhat ventrad. The saddle-shaped articular surfaces for the coracoids look dorsad and laterad. The anterior borders at the sides of the presternal projection are thickened, concave slightly in outline on the inner part, straight and more oblique on the outer ends. The lateral margins are thin, and are nearly parallel with the median axis of the bone. These borders have three emarginations, separated by four rounded projections, the anterior one longer and thicker than the others, which are thin and small. The posterior border is convex on either side, ending in a short and deep concavity at each side of the flat xiphisternal process. This process is spatulate, with the distal end rounded or very slightly emarginate, and doubless gave attachment to the series of abdominal ribs, which lie in the specimen nearly in connection with it. The sternum is somewhat thickened in the middle anteriorly, or back of the base of the anterior process. On the sides and behind the bone is very thin, almost paper-like; this thinner part in the specimen shows numerous small crinkly fractures, doubtless caused by the flattening of the concave bone; similar crinkles are visible in the thin prepubic bones. The sternum lies nearly in its normal position in the skeleton. In falling backward it has been displaced a little obliquely to the long axis of the body, as have the dorsal vertebræ, perhaps caused by

* Paleontographica Soc., 1869, p. 69.

the weight of the right arm lying across the body. The presternal process extends about half an inch in front of the notarium.

MEASUREMENTS OF STERNUM.

	mm.
Length in middle	88
Greatest width, across attachments of first rib	80
Length of rib margins	28
Width at coracoidal articulations	40
Length of presternal process in front of coracoids	16
Width of xiphisternal process	9
Length of xiphisternal process	11

Coraco-scapula. Pl. XLIII, Fig. 6. This conjoined element is a moderately stout, U-shaped bone, with the coracoid branch stouter and a little longer than the scapular. The distal extremity of the scapula is slightly expanded and flattened spatulate; the shaft is flattened and somewhat constricted in width. There is a rounded protuberance on the outer or upper margin, just beyond the glenoid rim, for the attachment of muscles. This process appears to be wanting in the specimen previously described by me of this genus, but it is possible its absence is due to some postmortem compression. The glenoid articulation is deeply concave from above downward, convex from side to side, and is bounded both above and below by a prominent ridge, that on the inferior border being much stronger than the upper one. The glenoid surface is placed obliquely to the shaft of the bones, doubtless in life looking outward and somewhat backward. The surface, from side to side, is narrower below than above. A line indicating the sutural union of the two bones passes directly through the middle of the articular surface transversely. At the bottom of the U formed by the conjoined bones there is a process, rather slender, arising from the inner surface of the scapula, and reaching to the inner face of the coracoid, which it joins. It incloses a small foramen between it and the coracoid, back of and below the glenoid surface. A precisely similar process is found in the coraco-scapula of *Pteranodon*, and in neither genus does the suture dividing the coracoid from the scapula cross this process; it is, apparently without doubt, either a separate ossification joined to the two bones, or else a process from the scapula. I cannot at present examine the under surface of this scapula, and have none of *Pteranodon* for comparison. In *Nyctosaurus*, however, the process seems to be separated from the scapula throughout a large part of its extent. If it really belongs with the scapula, the inclosed foramen cannot be the usual supracoracoid foramen of the reptilian coracoid.

A similar foramen, though of larger size, is shown by Owen in the coraco-scapula of *Ornithocheirus sedgwicki* (Paleontograph., 1857), which

he calls doubtfully a pneumatic foramen. Whether the part is an acromion process of the scapula, or possibly a vestigial clavicle, must be left for future research.

The coracoid has a flattened shaft, oval in cross-section near its middle, and flattened at either extremity. The sternal articular surface is convex in its greater diameter, gently concave in the opposite direction. Near the outer extremity of the shaft, on the inferior border, there is a strong process, gradually arising from the shaft but with a deep concavity between it and the articular rim. A small sesamoid ossicle was found lying near it. The shaft at its middle is narrowed and smooth; it seems to lack the strong muscular rugosity on the external part which occurs in the *Pteranodon* coracoid; the process on the outer inferior border is also larger than in *Pteranodon*. It will be observed also in the figure that the glenoid articular surface does not extend to the inferior margin of the coracoid, resembling in this respect somewhat the European forms of this bone. The scapula of course differs markedly from that of *Pteranodon* in the non-articular distal end.

MEASUREMENTS OF CORACO-SCAPULA.

	mm.
Extent of coraco-sternal articulation	10
Least width of shaft, below middle of coracoid	7
Length of coracoid	55
Dorso-ventral diameter of glenoid surface	19
Length of scapula	49
Least width of shaft of scapula	14
Width at distal extremity	16

Humerus. Pl. XLII, Fig. 7. The humeri both lie with the inner side uppermost. The proximal articular surface is distinctly saddle-shaped, the convexity directed from behind forward and inward. The curve of the concavity is greater than that of the convexity in the specimen. The ulnar or median process is very stout, reaching as high as the articular surface. It is broad above, with apparently two faces for muscular attachment, separated by a narrow, free space. Its rounded distal border sinks into the surface of the shaft at about its middle third. The deltoid, radial, or lateral process is very large. It is directed forward and a little downward, its lower margin uniting with the shaft at about the middle third. Both upper and lower borders are deeply concave, the upper one the longer. Its distal extremity is expanded, and has an evenly convex border from above downward. Near the upper end of this border, on the inner side, there is a small, oval, oblique surface, looking inward, for muscular attachment; and, beginning near the middle of the upper border, there is a slender, but well-

marked ridge, also for muscular attachment, traversing the anterior face obliquely, and terminating near the lower, outer angle of the process. Fürbringer says of these processes in the pterosaurs: "Proc. lateralis und Proc. medialis, namentlich aber der erstere sind sehr kräftig entwickelt und prominieren insbesondere proximal so stark, dass das zwischen ihnen befindliche Caputhumeri sogar theilweise gegen sich zurücktreten kann; dagegen ist — sehr im Unterschiede zu den meisten Sauropsiden, namentlich aber den Theromorphen und Dinosauriern — der Proc. lateralis wenig in die Länge entwickelt, indem er gewöhnlich nur das proximal ¼ bis ⅓ des Humerus einnimmt. Diese Konfigurationen lassen darauf schliessen, dass die Mm. supracoracoideus (supracoracoscapularis, scapulohumeralis posterior und subcoracoscapularis) eine relativ hohe Entfaltung besassen, der M. pectoralis dagegen keine so abnorme Stärke darbot, wie es von vornherein von einem fliegenden Thiere erwartet werden konnte, und der M. deltoides nur mittelstark entwickelt war."*

The shaft below the lateral process is of nearly uniform width. A little above the middle of each bone, on the inner or ventrolateral side, starting from precisely the same place, and lying transversely, there is a slender bone, less than a millimeter in width, and about twelve millimeters in length, preserved. I do not know what it is, nor whether it really belongs in this position, though the similarity of the bone on the two sides suggests that it does. It may be an ossified tendon. . . Because of the position in which both humeri are lying, the distal extremity has been transversely compressed, effacing the articular surfaces to a great extent. There seems to be a small depression on the inner epicondyle.

MEASUREMENTS OF HUMERUS.	mm.
Length	87
Least width of shaft	5
Least width of lateral process	17
Width of lateral process distally	25
Width of humerus through lateral process	42
Width of median process	5

Ulna. Pl. XLII, Fig. 2. The bones of the left forearm lie nearly in position, and in contact with the distal end of the humerus; those of the right side have been slightly separated, the radius detached and removed proximally. The left ulna is lying nearly upon its outer side, partly overlapping the radius; that of the right forearm has been compressed dorsoventrally. The bone is slightly expanded at the extremities. There are two, nearly confluent, articular surfaces at the proximal end, the smaller, nearly circular one, on the inner side, nearly confluent with the large, less

*Jenas. Zeitschrift, 1900, p. 363.

deeply concave surface on the inner side. Just in front of this, near the middle of the bone, transversely, there is a pneumatic foramen on the flexor side. The inner side of the bone, at this extremity is expanded into a thin, convex process. The articulation at the distal extremity cannot be made out, as it is largely concealed by the carpals. The shaft is nearly straight, curved forward gently at the distal extremity.

MEASUREMENTS.

	mm.
Length	144
Width of proximal extremity	44
Width of shaft	24

Radius. Pl. XLI, Fig. 2, Pl. I. The radius is a more slender and slightly shorter bone than the ulna. On the left side it lies partly concealed beneath the ulna and there would seem to have been no pronation of the bone. The bone is more slender than the radius, somewhat concave along its inner or upper border as it lies in relation with the ulna; nearly straight as it lies compressed from above downward. The bone is more expanded distally than proximally. The proximal articular surface is rounded and concave. Lying near the roughened distal surface shown in the figure there was a small sesamoid bone.

MEASUREMENTS OF RADIUS.

	mm.
Length	140
Width of shaft middle third	18
Width distal extremity	24

Carpals. Pl. XLII, Figs. 2, *cd*, 3, Pl. XLIV, Fig. 8. The two chief carpals of the left wrist are in relation with each other and the wing metacarpal, and but slightly displaced from the forearm bones. On the right side they are separated, and the proximal one is partly concealed beneath the ischium, the distal one having its proximal surface obliquely exposed. In the figure (Pl. XLIV, Fig. 10), the one shown obliquely is that of the other carpus figured. The wing metacarpal of the left side (Pl. XLIV, Fig. 2), lying articulated with the distal carpal, has the under side uppermost, from which it would appear that the view given is of the anterior side of the carpus. The proximal carpal is much the larger, extending on the under side either to articulate with the metacarpal, or nearly so. A subangular space is left between the two bones on the radial side, for the articulation of the lateral carpal or metacarpal of the first digit. This latter bone, of the right side, is shown in Pl. XLII, Fig. 3. It is a small, elongate bone, with an articular emargination on one side, which I had supposed was for the pteroid. I give, also, a good figure of this bone of *Pteranodon*, copied from Cope (Cretaceous Vertebrata, Plate VII,

Fig. 3). It resembles that of *Nyctosaurus*, though having a less elongated process beyond the articular lateral emargination. The figures of the carpal bones of *Ornithocheirus* given by Seeley (Ann. Mag. Nat. Hist. Aug. 1870, and Dragons of the Air, p. 124) closely resemble these bones. Professor Seeley says of the "lateral carpal": "It is a flat, oblong bone, attached to the inner side of the distal carpal, and, instead of being prolonged distally in the same direction as the other metacarpal bones, is turned round and directed upward, so that its upper edge is flush with the base of the radius, and gives attachment to the pteroid." I had supposed that the larger end, as shown in the present figure, fitted into the interval between the two carpals, and that the emargination was for the articulation of the rounded head of the pteroid, though perhaps the position assigned to it by Seeley is the correct one. The bone is thin on the sides shown in the figure, so that the articulation of the pteroid must have been either in the emargination or with the broader end. Marsh says* that it "stands nearly at right angles with the wrist," and I am inclined to think he was right. The structure of these wrist bones is almost identical with what it is in *Pteranodon*.

MEASUREMENTS OF CARPAL BONES.

	mm.
Length of articulated carpus	15
Greatest diameter of distal carpal	24
Lesser diameter of same	14
Greatest diameter of proximal carpal	26
Length of "lateral carpal"	17
Width of same	8

Metacarpals. The first metacarpal, or pteroid (Pl. XLII, Figs. 4, 5), is an elongated, pointed, styliform bone, with an enlarged articular carpal extremity. In both arms this bone has been displaced, though so closely associated with the corresponding extremity that the position is assured. Its articular end is broad, its margin nearly at right angles with the long axis of the bone. The articular surface is nearly at right angles with the transverse diameter, in life nearly circular in outline, and decidedly convex. It is separated from the bone by a slight constriction. The dorsal border of the bone is very gently concave throughout, and the inferior border is correspondingly convex for the greater part of its extent. The pteroid of the right arm is lying close to the lateral carpal, as though its articular surface fitted into the lateral emargination of that bone in life. Oscar Fraas was the first, so far as I can learn, to recognize the real nature of this bone as belonging to the first digit,† a view afterwards adopted by Marsh and Zittel.

*Amer. Journ. Sci., 1882, p. 255.
†Paleontographica, 1878, p. 170.

MEASUREMENTS OF PTEROID.

	mm.
Length	104
Greatest width (at proximal end)	15
Diameter of articular surface	8

The next three metacarpals are, for the most part, wanting in this specimen, a single complete one lying near the distal extremity of the right wing metacarpal (Pl. XLII, Fig. 6). It is a very small, splint-like and slightly curved, pointed bone, measuring about twenty-four millimeters in length by two in greatest width. Its resemblance to the corresponding metacarpals of *Pteranodon* is so great that the whole structure of the hand is doubtless the same in the two genera. I give herewith a diagrammatic figure of these parts in *Pteranodon*, based on a

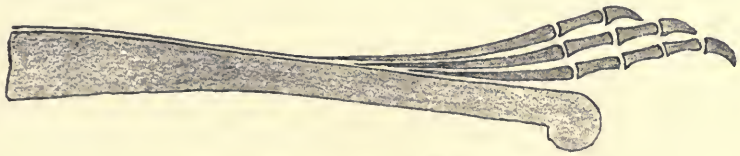


FIG. 2. Metacarpals of *Pteranodon ingens*.

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 displaced and associated with the hand phalanges in the specimen described.

In the specimen of *Pteranodon* the small metacarpals seemed to lie, not as they are diagrammatically figured, one above the other, but more side by side. The second metacarpal is continued, as already stated by Marsh, to the carpus, as a thin, thread-like bone. It was not continued along the dorsal side of the bone, but seems to pass to the radial side, where it belongs. From this it seems also probable that the position of all three bones in life was along the radial dorsal margin of the fifth metacarpal.

Both of the wing metacarpals (Pl. XLIV, Fig. 2) lie upon the dorsal surface, a position in which they are seldom found. The bone is much broader at the base, tapering to beyond the middle, whence the shaft has nearly parallel sides. The proximal articular surface cannot be made out, though there appears to be a division into two facets. The condyles, as in *Pteranodon*, are placed obliquely, the posterior one the larger.

MEASUREMENTS.

	mm.
Length	224
Width at proximal end	18, 23
Width of shaft at middle	11, 12

First phalange of wing finger. Pl. XLIV, Fig. 1. The first phalange, as usual, lies upon the side in both wings. As in *Pteranodon*, it is the longest bone of the body. Its under margin is concave throughout, the concavity greater near each end. The proximal expanded extremity has a deep articular concavity, extending through an arc of about one-third of a circle, with its radius directed at an angle about 45° with the long axis. The upper, olecranon-like projection has a marked emargination of the border above, between which and the proximal end the convexity is greater, with the corresponding deeper concavity of the under border.

There are two articular facets, separated by a median ridge, which fits into the trochlear depression of the metacarpal. The posterior surface extends throughout the whole length of the arc, while that on the anterior side reaches but little more than one-half of the distance, and its upper part is narrower than is the other surface. The pneumatic foramen is on the anterior side, just beyond the end of the articular surface. The dorsal border of the bone is gently and evenly convex from a little beyond the proximal extremity, and the width on the distal three-fifths is nearly uniform. The distal extremity of the bone is curved downward; the articular surface in life was doubtless a vertical oval.

MEASUREMENTS.

	mm.
Length	283
Greatest width at proximal end	27
Chord of proximal articulation	17
Width of shaft, proximal third	14
Width of shaft, distal third	14
Width distal extremity	18
Thickness of shaft at middle as compressed	1.7

The *second wing phalange* (Pl. XLIV, Fig. 5) lies in position in the right wing, but is somewhat displaced in the left. It is much smaller and more slender than the first phalange. Its proximal border is nearly straight and transverse to the axis of the shaft; it is much broader than the shaft. The under border of the bone is gently concave throughout, except on the proximal part, where the concavity is deeper. The upper border, gently concave at the proximal end, is nearly straight thence to near the extremity. The distal extremity is quite like that of the first phalange, though smaller.

MEASUREMENTS.

	mm.
Length	211
Width proximal extremity	17, 18
Width at proximal third	9, 10
Width at distal third	8, 9
Width of distal end	9, 10

The *third phalange* has the proximal extremity preserved, compressed from above. The surface seems to have been only slightly concave. This phalange, like the preceding one, seems to have been proportionally more slender than in *Pteranodon*.

PELVIC GIRDLE AND EXTREMITY.

Pelvis. Pl. XLI, Fig. 1. The pelvis lies with the bones nearly in position, the sacrum with its ventral surface uppermost, the innominate bones separated at their sutures and in juxtaposition with the sacrum, the visceral surface also uppermost.

There was in the sacrum (Pl. XLI, Fig. 1, *s*) in life evidently a considerable concavity transversely, and possibly a slight concavity longitudinally. It is composed of six firmly united vertebræ, the sutural lines between the centra clearly distinguishable. The vertebræ decrease in length from the first to the fifth; the sixth is slightly longer than its predecessor. The centra are flattened in the preserved specimen, though possibly in life they may have been slightly convex transversely. The sacral ribs show no indications of sutural connections anywhere, and are broadly united distally. Between them the oval foramina decrease rapidly in size, and slightly approach the middle line, the last, that between the fifth and sixth vertebræ, being almost punctiform, while the first is of considerable size.

The first process is broad, with a broad, oblique surface, terminating distally in a free, rounded margin. The pelvic brim is indicated by an angular line passing outward and downward obliquely to the upper border of the articular surface for the innominate bone. This surface is oval, and encroaches obliquely on the front surface of the sacrum; beyond it the thin margin of the sacrum does not present a sutural surface on the ventral side. The lateral margins approach each other until at the hind border the distance between them is less than half that at the brim of the pelvis.

The *ilium* (Pl. XLI, Fig. 1, *il*) has a long, flattened or somewhat prismatic anterior process, reaching as far forward as the second presacral vertebra. The process is apparently curved somewhat backward in life, and also outward; it has an obtuse anterior extremity. Posteriorly the

ilium extends a short distance beyond the end of the sacrum as a short, obtuse process. It sends an angular expansion upward and inward opposite the end of the sixth sacral vertebra, which extends five or six millimeters above the margin of the sacrum, possibly forming a sort of roof over the last sacral and the first caudal, and approaching, or possibly meeting, its mate in the middle. The flattened or ventral portion (Pl. XLI, Fig. 1, *ip*) of the ischio-pubis is somewhat trapezoidal in shape with the symphysial line slightly oblique to the sacral border. Both bones, separated at the median suture, lie with the visceral surface uppermost, and both present a considerable concavity. The anterior border begins at the upper margin of the process, which articulates with the sutural surface described on the lateral margins of the sacrum opposite the first intercostal foramen. The margin is thin and concave as far as the angular process for the attachment of the prepubis. This process is everted from the brim of the pelvis, and is tipped with a small, oval, cartilaginous or articular surface. From this surface the margin, somewhat thicker, recedes in a straight line to the beginning of the median symphysis. The symphysial margin is thin and nearly straight. For the first fourth of its length it seems to meet its mate, if at all, in an harmonious suture, and the symphysis in front may have been somewhat rounded or subangular; beyond this, however, the two bones meet in a very oblique surface, attaining a width of four or five millimeters posteriorly, and the two bones must have formed a thin and sharp keel when conjoined. The posterior border is somewhat thicker than the anterior one. It begins in a rather acute rounded angle at the base of the posterior process of the ilium, and is directed backward and ventrad to the angular extremity of the symphysis. The large rounded ischiadic (obturator) foramen is situated in front of the middle of the bone, almost directly ventrad to the acetabulum; its borders are smooth and thin. Between this foramen and the margin of the ilium, there is a considerable convexity, representing the floor of the acetabulum. Its dorsal margin must be nearly over the line of the sacrum. The junction of the innominate with the sacrum is by a narrow concave sutural surface, fitting on the margin of the sacrum; in front there is a considerable oval surface on the anterior part of the bone, which fits into the depressed surface already described, on the sides of the sacrum. Posteriorly, also, the projection of the ilium has a little broader attachment. Dorsad to this junction the ilium seems to have projected beyond the margin of the sacrum slightly in the middle, expanding in the angular process already described.

Prepubes. Pl. XLI, Fig. 1, *pp*. The prepubes are very nearly as they are in *Pteranodon*, consisting of a flat, transverse ribbon-like band meet-

ing in a somewhat angularly expanded median symphysis, which is thoroughly co-ossified, and with an anteriorly directed, somewhat divergent, flat, and obtusely pointed anterior process at each side, the continuation of the posterior flattened portion which joins the pectineal process on the everted margin of the pelvis. This process is somewhat thickened at its posterior extremity, and is of about the same width as the other parts of the bone. The bone in the specimen had been torn apart at the symphysis, each half remaining in partial juxtaposition with the corresponding half of the pelvis. As flattened out the conjoined bone is much too wide transversely to articulate with the surfaces on the margin of the pelvis; too wide even in the flattened-out position of these parts. It seems certain that the extremities must have articulated with the processes described, quite as I have already described the conditions in the pelvis of *Pteranodon*, and it therefore follows that the bone in life must have had a considerable convexity, in a broad, U-shaped form.

There are no indications of any sutural connection in the bones of the pelvis, except such as I have described with the sacrum and between the two halves. Nevertheless, the presence of the large foramen, the general shape of the bone and the position of the acetabulam would be as one would expect were there really the three elements present. A suture between the ischium and pubis is scarcely to be expected, in consideration of the obliteration of the sutures elsewhere in the skeleton. I am therefore inclined to look with favor upon the view, long held by Seeley, that the pelvis is of the normal reptilian structure, and that the bones in front really do not belong to it. It seems very probable that the anterior prolongations of the prepubes come in contact with the posterior ends of the parasternum, and that the whole bone is merely a continuation of the abdominal armature. However, I must admit that the persistence of the sacral and symphysial sutures, permitting the pelvis to drop apart without distortion, and the utter obliteration of any ischio-pubic suture is inexplicable.

"Naturalists have been uncertain as to the number of bones in the pelvis of pterodactyls, because the bones blend together early in life, as in birds. Some follow the Amphibian nomenclature, and unite the ischium and pubis into one bone, which is then termed ischium, when the prepubis is termed the pubis, and regarded as removed from the acetabulum. There is no ground for this interpretation, for the sutures are clear between the three pelvic bones in the acetabulum in some specimens, like *Cycnorphamphus Fraasii*, from Solenhofen and some examples of *Ornithocheirus* from the Cambridge Greensand."*

By modeling in cardboard and clay the bones of the pelvis and

*Seeley, Dragons of the Air, p. 94.

uniting them in a complete basin, with the necessary curvatures, it transpires that the opening of the pelvis had a diameter of about seven-eighths of an inch, while the outlet could have measured but a trifle more than half an inch.

Femur. Pl. XLIII, Figs. 4, 5. Both femora are preserved, separated by a short distance from the pelvis. The neck is directed upward and at a slight angle inward; it is cylindrical, the head only a little dilated and with its convexity only a little oblique to the axis of the bone; that is, the plane of the rim is nearly, but not quite, rectangular to the axis of the shaft. The trochanter stands a little to the outer side of the middle axis of the bone. From its upper angle a ridged process runs backward for a short distance, to the inner side of which, a little below the free, upper concave margin of bone, there is a small pneumatic opening. On the outer side, the margin of the shaft is convex for a short distance, and is then concave throughout to the extremity. On the inner side above, the margin is correspondingly concave; below this to the condyle it is convex. The upper part of the bone was evidently, in life, nearly cylindrical; below it seems to have been wider and somewhat flattened. Near the middle behind, beginning a little above the condylar surface, there is a narrow, elongated, longitudinal ridge for the attachment of a muscle. The distal articular surface cannot be clearly made out in the crushed specimens. The bone had in life, apparently, a marked anterior curvature, as in *Pteranodon*.

MEASUREMENTS OF FEMUR.

	mm.
Length	81
Diameter of neck	6
Diameter of shaft, upper third	7
Diameter through condyles as crushed	13

Femur of *Pteranodon ingens* Marsh, Pl. XLIII, Figs. 1–3. 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.

Tibia. Pl. XLIV, Fig. 3. 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. The sutural union between the tibia proper and the proximal tarsal bone, or bones, is entirely obliterated. The bones of the two sides are compressed in different positions, the left one from the side, the right one from nearly in front; the width above is considerably greater in the former than in the latter, indicating but comparatively little expansion of the upper part from side to side.

There is no trace of any fibula, either in the preserved remains or in any tibial articulation.

MEASUREMENTS OF TIBIA.

	mm.
Length	133 (132)
Width above	15 (11)
Width of shaft at upper end of middle third	7 (6)
Width, lower third	6 (6)
Antero-posterior diameter of trochlea	6 (6)

Foot. But a single metatarsal and one phalange are present in this specimen. These, however, agree so well with the corresponding bones of *Pteranodon* that I doubt not the foot was quite similar to that of the former genus. This metatarsal is expanded at its proximal end and gently convex on the trochlear end. It measures 35 mm. in length, 2 mm. in width at the upper fourth and 4 mm. at either extremity. The bone is compressed from side to side. The phalange, flattened on the side, has a length of 14 mm. The distal end has the extremity convex, its chord rectangular to the long axis of the bone; its width is 3 mm. The proximal end is truncated or gently concave; its width is about 4 mm. The shaft in the middle is scarcely narrowed from the proximal end. I repeat here, briefly, the description of the foot of *Pteranodon*, from my paper in the Kansas University Quarterly, vol. vi, page 50, with some changes.

The first four metatarsals are very slender, straight, and contiguous with each other, each having a flattened proximal articular surface and a rounded trochlear distal extremity. The metatarsal of the fifth toe is

rudimentary, subtriangular in shape, with the obtusely pointed distal part curved, altogether resembling an obtuse claw. The first toe has a single phalange, which is long, cylindrical, gently curved, and obtusely pointed. The second toe has two phalanges, the first of which is elongate and grooved with a distal trochlear articulation. The second phalange resembles the first of the first toe, but is shorter. The third toe has four phalanges, the proximal one of which is like that of the second toe, but is elongate; the second is broader than long; the third is like the first, but is shorter; the fourth is a short, scarcely curved and obtusely pointed claw. The fourth toe has five phalanges, of which the first, fourth, and fifth resemble the first, third, and fourth of the third toe, the second and third the second of the same toe. This toe is the longest. The fifth has no phalanges. I may add that the foot from which these measurements were taken was found together, with the bones in place or but little displaced, and has been so mounted in the University of Kansas Museum. I have repeatedly examined these bones, and am confident that the number of phalanges are as I have given them; that is, there is an absence of the claws on the first and second toes. The measurements of this specimen are as follows:

	mm.
Femur, length	260
Diameter of head	20
Width of condyles	30
Tibia, length	362
Metatarsals, length	101, 105, 95, 80, 25
Phalange, first digit, length	41
Phalanges, second digit, length	25, 31
Phalanges, third digit, length	35, 4, 27, 12
Phalanges, fourth digit, length	40, 3, 3, 26, 12

Ossified tendons. Numerous thin, flat, striated bones are lying on the matrix associated with the anterior extremity, which can only be regarded as tendinous ossifications. One of these on each side is lying by the side or upon the pteroid bone, with its pointed extremity near its proximal end. They measure one hundred to one hundred and twenty millimeters in length, with a greatest breadth of twelve millimeters. Two others are lying by the side of the proximal end of the right wing metacarpal; they are somewhat shorter and have the flattened fimbriated end distad. Another is lying by the side of the distal end of the same bone. There is a shorter, more fan-shaped one by the right humerus, and fragments of others are scattered about the arms. Altogether there are seven of these of about one hundred millimeters in length. Their texture is striate, as though composed of slender, ossified, tendinous fibers,

altogether reminding one very much of similar tendinous ossifications in the legs of many birds.

A number of other slender, rib-like, more or less fragmentary bones are observed scattered about the slab near the body of the specimen, of which I am not at all certain, though I suspect that some of them are ventral ribs, perhaps attached during life to the extremity of the flat parasternal structures already described. One of these bones, lying by the lateral margin of the sacrum is about forty millimeters in length and is gently curved. It is flattened at one end, measuring nearly three millimeters in width, cylindrical at the other, and not more than one millimeter wide. Another, lying back of the pelvis, of about the same length is also slightly curved, one millimeter wide at one end and about three-tenths of a millimeter in width at the other end. There are also parts of several other bones which seem to be similar to these.

SYSTEMATIC POSITION.

Three specimens ascribed to *Nyctosaurus* are now known — the type described briefly by Marsh, the one in the University of Kansas Museum described by me in 1892, and the present one. Marsh must have known more than one specimen, however, in which additional specimens he later recognized the essential generic characters. The three specimens differ materially in size, that described by Marsh being the largest, and the Kansas University specimen the smallest. In the smallest specimen the coracoid and scapula are still distinguished by a separable suture. Furthermore, the separated arches of the dorsal vertebræ, and the distinction of the elements of the atlas all indicate a young animal. On the other hand, the present specimen has all of its sutures obliterated, except that between the atlantal intercentrum and the axial intercentrum, characters which may be ascribed to an adult condition. Among the characters given by Marsh, is the separated coracoid and scapula, but I suspect that this was derived from a smaller specimen than the one which he originally named *Pteranodon gracilis*. I do not think that the absolute differences in size are sufficient to separate the specimens specifically, in that we know that similar differences are ascribed to other pterodactyls by some authors. In order, however, to make the comparative differences between these specimens clearer I have reduced them to a common standard, using the humerus as 100 in each. In addition, I give like comparative measurements of certain species of *Pterodactylus*, derived from figures given by Zittel:

	Nyctosaurus F. C.	Nyctosaurus K. U.	Nyctosaurus type.	Pteranodon ingens.	Pterodactylus Kochii.	Pterodactylus.
Humerus	100	100	100	100	100	100
Ulna	165	165	---	136	148	153
Metacarpal	257	275	---	210	106	105
First Phalange	324	327	---	268	161	160
Second Phalange	241	---	---	172	142	129
Femur	93	93	---	106	109	107
Tibia	151	151	---	150	153	144
Metacarpal	100	100	100	---	---	---
Ulna	64	60	62	---	---	---
First Phalange	126	119	115	---	---	---

It is observed that there is a striking agreement in these specimens, except in the metacarpals, the differences elsewhere being scarcely more than one might expect in the measurement of bones differently affected by the compression to which they have been subjected. Now, we may consider this variation of specific value and give to each of these three specimens a different name; or we may, as is far more reasonable, consider the metacarpal as a variable bone in the individual, as it is in the species and groups, and refer them all to one species. This I have no hesitation in doing. There is, then, but a single species of *Nyctosaurus* now known among the specimens referred to the genus; it should be called *Nyctosaurus gracilis* Marsh.

In specimens of *Pteranodon ingens* there is not a little variation in size, especially in the length of the wing metacarpal, which I have observed to vary from 580 to 615 millimeters, the longest that I have ever known from the Kansas chalk. It is very certain, I think, that absolute identity of size cannot be relied upon to distinguish the different species of pterodactyls, nor do I think that the relative or proportional lengths of the finger bones should receive too much weight; the different species evidently varied individually within certain limits.

In my first paper on *Nyctosaurus*, I discussed briefly the so-called species of *Pteranodon*, *P. nanus*, and *P. comptus*, suspecting that one or both of them belonged with *Nyctosaurus*.

A wider acquaintance with Kansas pterodactyls, both in the laboratory and in the field strengthens my belief that both of these names are synonyms of *N. gracilis*.

No small species from the Kansas chalk can be referred definitely to *Pteranodon*, so far as my own knowledge goes, and I have seen hundreds of specimens. *P. nanus* presents the strong lateral crest of the humerus which I am satisfied is a diagnostic characteristic of *Pteranodon*. Al-

though the author expressly stated that the "coracoid and scapula were firmly anchylosed" a character seen in the present specimen of *Nyctosaurus*, I feel pretty confident that the type of *P. nanus* does not have the articular extremity of the scapula so characteristic of *Nyctosaurus*. The description of *P. comptus* might apply, except in size, to either *Nyctosaurus* or *Pteranodon*. I refer the species to the former genus because of its small size, but its synonymy is not assured. That a better basis for an opinion may be given the reader, I here reproduce all that Marsh has written upon *Nyctosaurus* and the two small species which he referred to *Pteranodon*.

"One of the smallest American species yet found is represented in the Yale Museum by several bones of the wing, a number of vertebræ and the nearly complete pelvis. The wing bones preserved are elongated and very slender. The pelvis is unusually small, and there are five vertebræ in the sacrum. The last of the series indicates that the tail was short. The following are the principal dimensions of this specimen:

	mm.
Length of ulna	187
Length of metacarpal of wing finger	300
Antero-posterior diameter of outer condyle at distal end	15
Tranverse diameter of shaft, above condyles	13
Length of first phalanx of wing finger	347
Extent of five vertebræ of sacrum	57

"This species, which may be called *Pteranodon gracilis*, was about two-thirds the size of *P. velox* Marsh. It probably measured about ten feet between the tips of the expanded wings."*

"*Pteranodon comptus*, sp. nov. The smallest Pterodactyle known from American strata is indicated by portions of three skeletons in the Yale Museum. Among these remains are two distal ends of the characteristic metacarpal of the wing finger, other portions of the wing bones, and two sacral vertebræ. The large metacarpal is very slender and elongated, and its outer distal condyle has its superior margin elevated above the shaft, and terminated proximally in a point. The ulna is comparatively large, and the proximal carpal has an oval air cavity on its radial side. The sacral vertebræ have their centra short, and medially constricted.

"The principal measurements of the remains of this species are as follows:

	mm.
Greatest diameter of ulna at distal end	15
Transverse diameter of proximal carpal	17
Antero-posterior diameter of outer distal condyle of wing metacarpal	12.8
Longitudinal extent of condyle	11.6
Transverse diameter of shaft above condyle	11.5
Length of medial sacral vertebra	9
Transverse diameter of centrum	8.4

*Marsh, Amer. Journ. Sci. June, 1876, p. 508.

"The above specimens are all from the Upper Cretaceous of Western Kansas."*

"*Nyctosaurus*, gen., nov." A second genus of American Pterodactyls is represented in the Yale Museum by several well-preserved specimens. This genus is nearly related to *Pteranodon*, but may be readily distinguished from it by the scapular arch, in which the coracoid is not co ossified with the scapula. The latter bone, moreover, has no articulation at the distal end, which is comparatively thin and expanded. The type of this genus is *Pteranodon gracilis* Marsh, which may now be called *Nyctosaurus gracilis*. It was a Pterodactyl of medium size, measuring about eight to ten feet between the tips of the expanded wings. Its locality is in the Upper Cretaceous of Western Kansas. The type specimens of all the above species are preserved in the Museum of Yale College."†

"In the same geological horizon with the gigantic forms (Pteranodon beds) the remains of a single small Pterodactyl have been found. This animal was more diminutive than the Jurassic species [*Dermodactylus montanus*], having a spread of wings not more than three or four feet. The jaws were proportionally more slender than in the larger Cretaceous species, and no teeth have been found with them. The humerus had a small head and an enormous radial crest, which curved downwards. The scapula and coracoid were firmly ankylosed. Some of the trunk vertebræ have very long transverse processes, or ankylosed ribs, curved backward. Some dimensions of this specimen are as follows:

Length of humerus	62
Greatest diameter of head	12
Transverse diameter across radial crest	30
Greatest diameter of distal end	16
Vertical diameter of humeral glenoid cavity	13
Transverse diameter	6

"This species may be called *Pteranodon nanus*. Its known remains were found by Mr. S. W. Williston, in the Middle Cretaceous of Western Kansas."‡

"The name *Nyctosaurus*, applied by the writer to this group, appears to have been preoccupied, and hence may be replaced by *Nyctodactylus*. The only species known is *Nyctodactylus gracilis*."‖

It is seen that but five vertebræ are referred to the sacrum of the type of *Nyctosaurus gracilis*; if this be a real character one would not question the distinctness of the species. Inasmuch as *Pteranodon* has six vertebræ in the sacrum and one or more lumbars or false sacrals, as in

*Marsh, l. c., p. 509.
† Marsh, Amer. Journ. Sci. Dec., 1876, p. 480.
‡ Marsh, Amer. Journ. Sci. April, 1881, p. 343.
‖ Marsh, Amer. Journ. Sci. April, 1881, p. 343, footnote.

the present specimen of *Nyctosaurus*, I believe that this number will be found common to all the Kansas pterodactyls. I think that Marsh must have been in error in ascribing but five to the sacrum. Should he, however, be correct I would suggest the name *N. leptodactylus* for the present species.

In view of the foregoing I offer the following as the synonymy of this genus and species :

NYCTOSAURUS.

Marsh, Amer. Journ. Sci., xii, p. 480, Dec., 1876. *Nyctodactylus* Marsh, Amer. Journ. Sci., xxii, p. 343, April, 1881 ; ibid., xxvii, p. 423, May, 1884. Williston, Kans. Univ. Quart., i, p. 2, 5, 1893; Journ. Anatomy, i, p. 297, 1902 ; Journ. Geology, x, p. 520, July–Aug. 1902.

NYCTOSAURUS GRACILIS.

Pteranodon gracilis Marsh, Amer. Journ. Sci., xi, p. 508, June, 1876.

Nyctosaurus gracilis Marsh, Amer. Journ. Sci. xii, p. 480, Dec. 1876.

Nyctodactylus gracilis Marsh, Amer. Journ. Sci. xxi, p. 343, April, 1881; Williston, Kans. Univ. Quart., i, p. ii, 1893; Zittel's Paleontology (Eastman), vol. ii, p. 255, Fig. 361, 1902.

(?) *Pteranodon comptus* Marsh, Amer. Journ. Sci. xi, 508, June, 1876; Williston, Kans. Univ. Quart. i, p. 11, June, 1893.

(?) *Pteranodon nanus* Marsh, Amer. Journ. Sci., April, 1881, p. 343; Williston, Kans. Univ. Quart. i, p. 11, June, 1893.

Of the remaining species of Kansas pterodactyls, six have been described, two of which, *P. umbrosus* and *P. harpyia* Cope, are admittedly identical with previously described forms, leaving *ingens*, *occidentalis*, *velox*, and *longiceps* Marsh. No real attempt was made to separate *P. longiceps* from those previously named, nor could there have been, since only the skull was known in this species to the describer, while the skull was not known in either of the other species. It may be identical with either *occidentalis* or *velox*. possibly with both. The characters given by Marsh to distinguish the species have little value, though I believe there are three distinct ones of the genus, known from the Kansas chalk. Two of these species are at once distinguishable by the structure of the humerus, especially of its radial or lateral crest. In *P. ingens* this crest is rounded and obtuse; in one or the other of the smaller forms it is more elongate and of a different shape. Furthermore, among the smaller specimens there appear to be two different types of terminal wing phalange, one nearly straight and the other curved falciform, as in *P. ingens*. If the smaller form with the curved phalange should prove not to be the

young of *P. ingens*, as is not likely, then we have at least three distinctly different species of the genus, perhaps a fourth in *P. comptus*.

A much more interesting question is: What relation do the genera, *Nyctosaurus*, *Ornithocheirus*, and *Pteranodon* (*Ornithostoma*) bear to each other and to *Pterodactylus?*

The classification which has hitherto seemed the best to display the relationship of these forms is the following:

Suborder Pterodactyloidea. Tail short; wing metacarpal, at least as long as the bones of the antebrachium; fifth digit of pes vestigial, without phalanges.

Family Pterodactylidae. Scapula not articulating with supraneural facet.

Genus *Pterodactylus*. Teeth present.

Genus *Nyctosaurus*. No teeth.

Family Ornithocheiridæ. Scapula with an articular facet united with neural facet of the notarium.

Genus *Ornithocheirus*. Jaws with teeth.

Genus *Pteranodon* (*Ornithostoma*). Jaws without teeth.

However, a better knowledge of the genus *Nyctosaurus* convinces me that its relationship is closer with *Ornithocheirus* than with *Pterodactylus;* that it has gone much further in specialization in the same direction with *Ornithocheirus* and *Pteranodon*. Very little now remains to be known of the osteology of both these genera, and not much of *Ornithocheirus*. Their characters as a group may be summed up as follows. While some parts of the skeleton of *Ornithocheirus* are yet unknown, I am confident that future discovery will produce nothing very discrepant.

Ornithocheiridæ. Head elongate, slender; no antorbital vacuity; internal nares large; eight cervical, ten dorsal (*Pteranodon?*), six sacral, and ten to twelve caudal vertebræ present, the last dorsal co-ossified with the sacrum; first three or four dorsal vertebræ united into a notarium, with stout, anchylosed ribs articulating with the sternum; posterior dorsal ribs very slender, single-headed, and nearly straight; three or four pairs of flattened V-shaped ventral ribs present. Ilium much elongated; ischio-pubis with an obturator foramen; prepubes band-like, co-ossified, with an anterior, flattened projection on each side. Coracoscapula with only a slight projection below the glenoid cavity, co-ossified in the adult; scapula but little longer than the coracoid, not narrowed distally. Three carpals present; forearm much longer than humerus; third and fourth metacarpals very short, pointed proximally, not articulating with carpus; second metacarpal thread-like proximally; fifth metacarpal

much longer than forearm; phalanges proportionally long. No fibula present; two tarsals only; fifth digit without phalanges.

Ornithocheirinæ. Upper end of scapula thickened, articulating with a supraneural plate. Head with a prominent parieto-occipital crest.

Ornithocheirus. Jaws with teeth.

Pteranodon (*Ornithostoma*). Jaws wholly edentulous.

Nyctosaurinæ. Scapula flattened spatulate above, not articulating with supraneural plate. Humeral crest constricted; humerus proportionally short, the digit long; no sagittal crest.

Nyctosaurus, *Ornithodesmus* (?).

In contradistinction to these characters I would define the *Pterodactylidæ* as follows: I have never seen any specimen of this genus, and must, therefore, rely entirely upon the descriptions and figures. The characters hence are in a measure provisional.

Pterodactylidæ. A distinct antorbital foramen present, sometimes partly confluent with the nares; occiput not produced, jaws always with teeth. No consolidation of the thoracic vertebræ or anchylosis of the sternal ribs, the posterior ribs less slender. More than ten vertebræ in the dorsal region and less than six in the sacrum. Prepubes never co-ossified in the middle, and without anterior prolongation. Scapula longer than the coracoid, more or less narrowed distally. Humerus and legs relatively large, the forearm and wing finger relatively small; all the metacarpals articulating with the carpus. A fibula present.

I am sure that all these characters are generalized ones, even as the genus is older than those placed in the first group. It seems to me especially that the shortening of the back, the consolidation of the early dorsal vertebræ, and the elongation of the sacrum, with the greater elongation of the wing digit, are better evidences of relationships than is the presence of the peculiar scapular articulation.

Certain conclusions as to the habits of the *Ornithocheiridæ*, as I here define the family, seem inevitable from a better knowledge of their structure. Some of these conclusions I have already presented in a former paper, and a further study only strengthens my belief in their justness.

The neck was strong, with limited torsion, but with great power and effectiveness in the antero-posterior flexion, thus rendering the beak very effective in striking.* The marked posterior projection of the hind zygaphophyses of the last cervical vertebra, quite unlike those of any other vertebræ in the column, indicates, not that the neck turned back-

*Plieninger (op. cit.) misquotes me in saying that "Williston glaubt, dass diese Art der Articulation die Bewegung des Halses in verticaler Richtung von vorne nach hinten eingeschrankt hat." What I said was: "Such a mode of articulation would seem to limit the motion to one in a vertical, antero-posterior plane, while greatly strengthening the joints."—Kans. Univ. Quart., vi, p. 39.

ward at this place, but that it curved forward more after the way of birds, a position compatible with the upright attitude. The whole structure of the neck, the elongated vertebræ, the transverse centra, and lateral exapophysial articulations, the absence of transverse processes, all remind one of the neck in the cryptodire testudinates, where the neck is capable of much and effective antero-posterior flexion.

The articulation of the head of the femur, with the basal plane of its convexity nearly at right angles to the long axis of the bone, and the posterior position of the acetabulum, carry conviction to me that the femora could not have been brought parallel in the same direction without dislocation from the sockets, whatever attitude the animal may have assumed. The articulation of the distal end of the tibia furthermore shows that the metatarsus could not have been extended to a right angle; that is, *Pteranodon* could not have been plantigrade. The greater extension must have been between the metatarsus and phalanges; in other words, the creature must have been digitigrade in ambulation. The flattened proximal ends of the metatarsals indicate a compact and closely united foot, and the bones have been so found in specimens of *Pteranodon*. The toes in *Pteranodon*, and doubtless in this genus also, were practically clawless, and the outer toes were much the longer. The animal was incapable of seizing or holding with the feet.

Nor could a very great flexion at the knee have been possible, as I think the figures of the femur of *Pteranodon ingens* will indicate. If the animal was quadrupedal, it must have been in a crawling attitude, with both legs and arms widely extended.

APATOMERUS MIRUS, GEN. ET. SP. NOV.

In the University of Kansas Quarterly, vol. iii, p. 3, I described and figured a remarkable bone from the Lower Cretaceous of Clark County, Kansas, which I hesitatingly referred to some crocodile-like animal, because I was at a total loss where else to place it, my knowledge of the pterodactyl anatomy then being less than at present. The figure and description are reproduced in vol. iv of the University Geological Survey of Kansas, p. 90, as follows: "The upper end of a femur found in the same region appears to belong to the same kind of an animal, as does the vertebra described above. The shape is not unlike that of a human femur, with the trochanters evidently small and placed much below the level of the head. The neck is stout, the head gently convex, with an angular border. The shaft below the trochanters is somewhat flattened from before backward, but becomes more cylindrical below. The shaft is hollow, with firm walls not more than one-third of an inch in thickness. The portion preserved measures 210 mm."

I am now satisfied that the femur in question belongs to a heavy-boned pterodactyl or some allied, hitherto unknown, animal. The very peculiar head of the bone with its articular convexity directed upward, the position of the trochanter, the hollow shaft and its curvature are characters all found in pterodactyls and in no other animals of which I have any knowledge. The entire length of the bone must have been about 350 or 400 mm., and while the walls are unusually thick, they are not proportionally much more so than in *Dermodactylus*, the type of which I distinctly remember. *Dermodactylus* is from the so-called fresh-water beds of the Wyoming Jurassic, which I have long believed to be contemporaneous with the Comanche beds of Kansas, and which I correlate with the Wealden of Europe. The forms cannot be the same, since this is very much larger.

MAY 14, 1903.

In an article by Mr. F. A. Lucas in the Report of the Smithsonian Institution for 1901, there is given an excellent drawing of a skull of *Pteranodon* (*Ornithostoma*), made "from a specimen in the Yale University Museum." From my recollection of various peculiarities shown in the figure, as also from certain accidental peculiarities, such as the fracture of the infra-narial bar, faithfully reproduced in Professor Marsh's drawings, I have very little hesitation in saying that the specimen there illustrated is the type of the genus *Pteranodon*, upon which was based the figure so long current in text-books. Should I be in error in this identification, I shall be glad to be corrected, hoping, however, in that case, that a true figure of the type specimen may be published.

In the summer of 1891, Professor E. C. Case and myself uncovered from the firm yellow chalk of western Kansas, the uninjured posterior part of a skull of *Pteranodon*, with its sagittal-crest entire and evenly rounded. A figure of this specimen was given in Pl. I, Vol. I, of the Kansas University Quarterly, to which I beg to refer the reader. The specimen is now preserved on a slab in the museum of the University of Kansas, and I doubt not that the crest as disclosed from the matrix and as represented in the figure, is all that the animal possessed in life. Mr. G. F. Eaton, however, in the July number of the American Journal of Science takes me to task for criticising the original figures of *Pteranodon*, which he admits were faulty, and for my "restoration" of the skull, asserting that I was wrong. He now adds to the type a much longer crest than did the author. The basis for Professor Marsh's restoration is shown in Mr. Lucas's plate, if my identification is correct, and the drawing has been faithfully made.

I do not criticise Professor Marsh for making the restoration as he did; he was perhaps justified, though it might have been better had he stated how much of the restoration was conjectural, and had also published a figure of the specimen as it actually was.

In his present paper Mr. Eaton says: "At the present time of writing an incomplete Pterodactyl skull is being worked out at the Yale Museum, which will, in all probability prove to be that of *Nyctodactylus* Marsh. The crest, which is apparently entire, is of small size compared with that of *Pteranodon*, the measurement from occipital condyle to tip of crest being only 49 mm., while the length from occipital condyle to tip of beak was approximately 45 cm. In general the skull compares favorably with that shown in Williston's restoration of *Nyctodactylus*, given in the American Journal of Anatomy, Vol. I, No. 3, May 26, 1902, where he states that the outline is taken in part from a specimen of *Pteranodon* Marsh, or *Ornithostoma* Seeley, as the genus was then called. It is therefore fair to infer that the apparent similarity of the two genera led Williston to draw inadvertently upon the characters of *Nyctodactylus* in making his restoration of *Pteranodon*."

Had Mr. Eaton done me the honor to have read more attentively the article which he quotes; or had he examined the extended article on the skull of *Nyctodactylus* with plates, published in the Journal of Geology for August, 1902; or even had he examined the figure of the skull in Zittel's text-book of Paleontology, published last autumn, of all of which he seems strangely ignorant, he would have learned that *Nyctodactylus has no crest whatever*, not even a vestige of one! It is very evident, therefore, that Mr. Eaton has made the very error which he so freely suggests I have made, and that his specimen is in reality a *Pteranodon!* I am pleased to learn that its "apparently entire" "crest" compares favorably with that which I have assigned to the same genus.

Now, since his own observations show that *Pteranodon* may have a short crest, very much as I have figured it, it will be of interest to learn more fully his reasons for attaching the elongated crest he has to the skull as shown in Mr. Lucas's figure. I furthermore note that Mr. Eaton continues, in his "restoration" of the skull of *Pteranodon*, the gravest of the inaccuracies of the original figures, the absence of the supratemporal fossa and arch. If he is correct in this, the original reference of the genus to a distinct order of reptiles was justified. But we will await further evidence before assuming that he is, and meanwhile, it will be unfortunate if his restoration finds currency.

Inasmuch as Mr. Eaton has so clearly shown his ignorance of recent and very accessible literature on the subject, it is too much to expect that he would have mentioned the fact that the pelvis of *Pteranodon* has been

described and partly figured without certain errors into which he has fallen, and that the peculiar "spiral" condyles of both *Pteranodon* and *Nyctodactylus* have likewise been described and figured, without, however, their having suggested to any one the probability that the animals dislocated their jaws in deglutition.

PLATE XL.

NYCTOSAURUS GRACILIS.

View of part of specimen, showing sternum, pelvis, dorsal vertebræ, ribs and arm bones. Natural size.

Nyctosaurus gracilis Marsh.

PLATE XLI.

NYCTOSAURUS GRACILIS.

Fig. 1. Dorsal vertebræ, ribs, and pelvis; about three-fifths natural size. *r*, ribs; *sy*, lumbar or false sacral; *s*, sacrum; *is*, ischio-pubis; *ob*, obturator foramen; *il*, ilium; *pp*, prepubes.

Fig. 2. Abdominal ribs. About three-fifths natural size.

Fig. 3. Atlanto-axis, from the side. Twice natural size.

Fig. 4. The same from behind, partly restored.

Fig. 5. The same from in front. *a*, atlantal neurapophysis; *ac*, axial centrum; *at*, atlantal intercentrum; *ax*, axial intercentrum; *b*, hull of axis; *o*, odontoid; *ps*, postzygapophysis.

Fig. 6. Hyoid bone. Three times natural size.

Fig. 7. Extremity *a* of Fig. 6, more enlarged, from the side.

Plate XLI.

Nyctosaurus gracilis.

Fig. 1. Dorsal vertebræ, ribs, and pelvis; about three-fifths natural size. *r*, ribs; *dv*, lumbar or false sacral; *s*, sacrum; *ip*, ischio-pubis; *ob*, obturator foramen; *il*, ilium; *pp*, prepubes.

Fig. 2. Abdominal ribs. About three-fifths natural size.

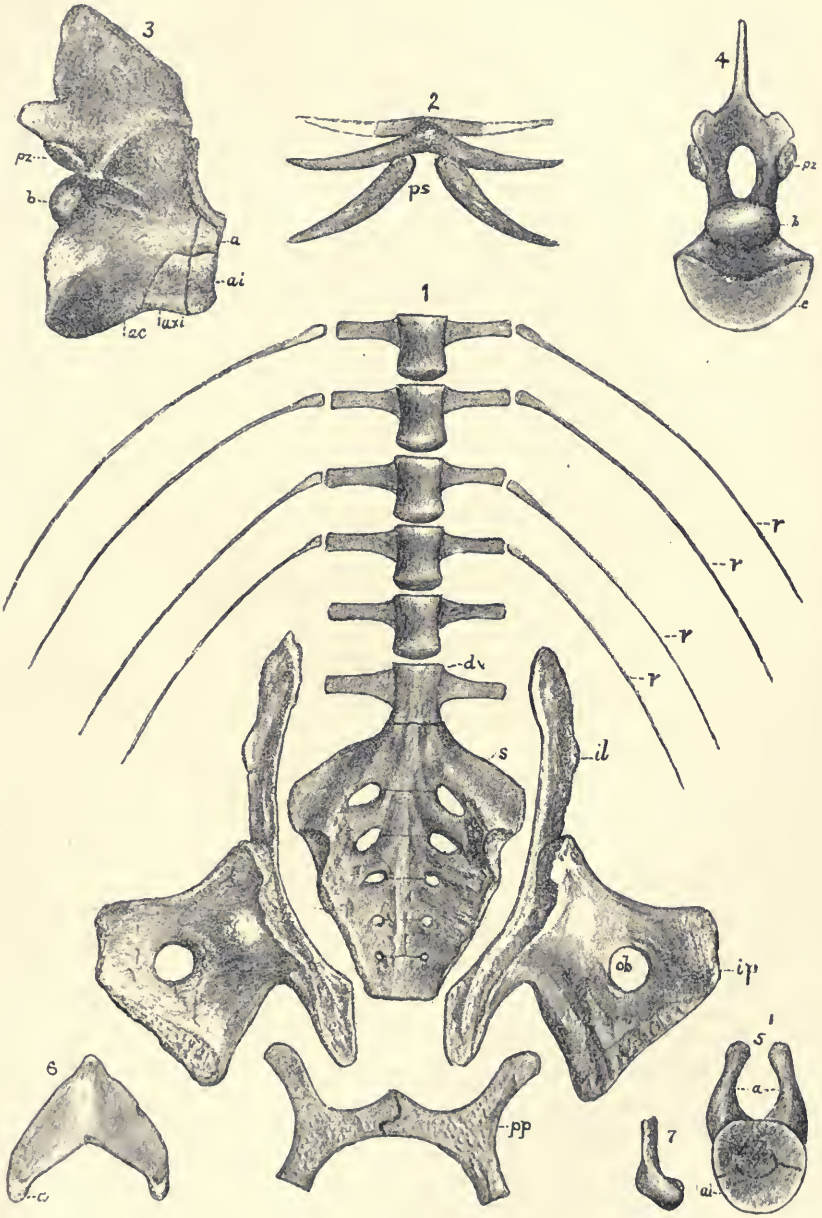
Fig. 3. Atlanto-axis, from the side. Twice natural size.

Fig. 4. The same from behind, partly restored.

Fig. 5. The same, from in front: *a*, atlantal neurapophysis; *ac*, axial centrum; *ai*, atlantal intercentrum; *axi*, axial intercentrum; *b*, ball of axis; *o*, odontoid; *pz*, postzygapophysis.

Fig. 6. Hyoid bone. Three times natural size.

Fig. 7. Extremity *a* of Fig. 6, more enlarged, from the side.



S. W. W. del.

Nyctosaurus.

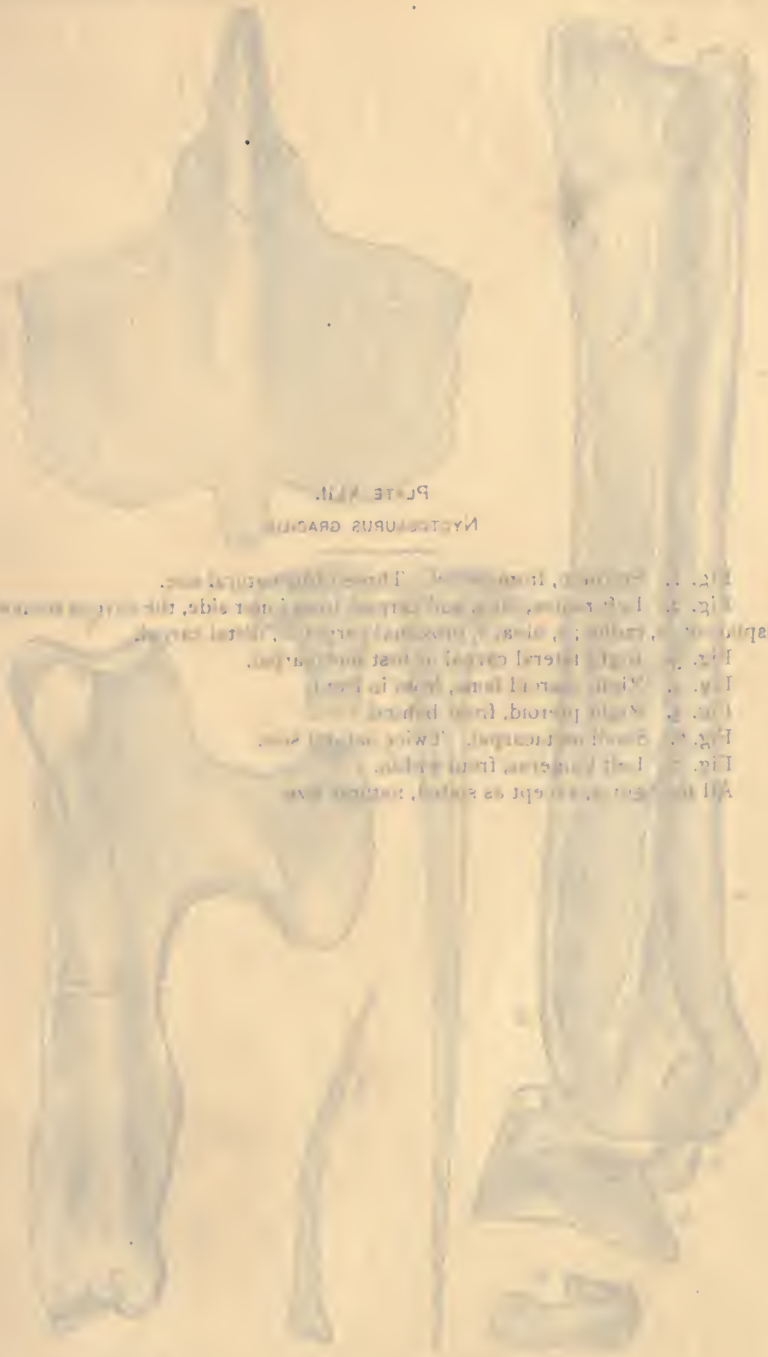


PLATE XLII.

NYCTOSAURUS GRACILIS.

Fig. 1. Sternum, from below. Three-fifths natural size.

Fig. 2. Left radius, ulna, and carpus, from inner side, the carpus somewhat displaced: *a*, radius; *b*, ulna; *c*, proximal carpal; *d*, distal carpal.

Fig. 3. Right lateral carpal or first metacarpal.

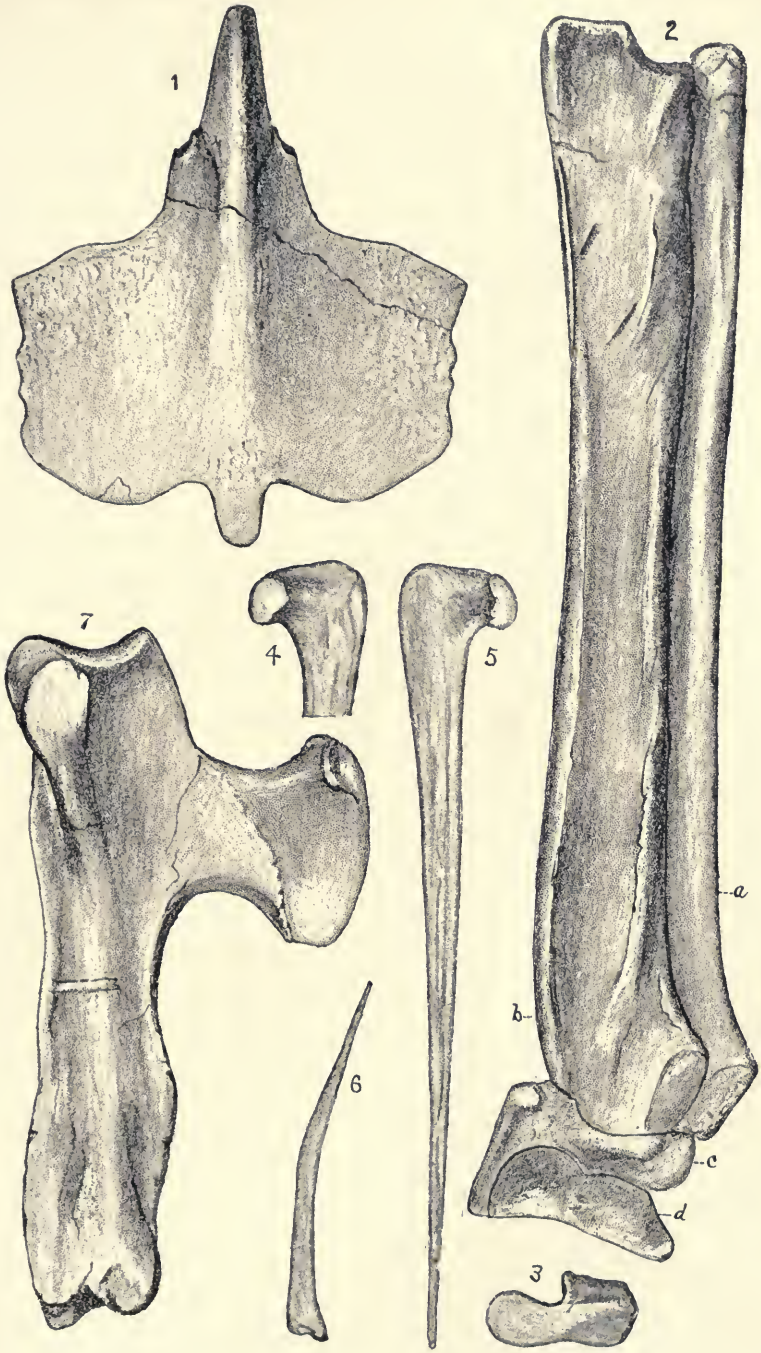
Fig. 4. Right pteroid bone, from in front.

Fig. 5. Right pteroid, from behind.

Fig. 6. Small metacarpal. Twice natural size.

Fig. 7. Left humerus, from within.

All the figures, except as stated, natural size.



S. W. W. del.

Nyctosaurus.

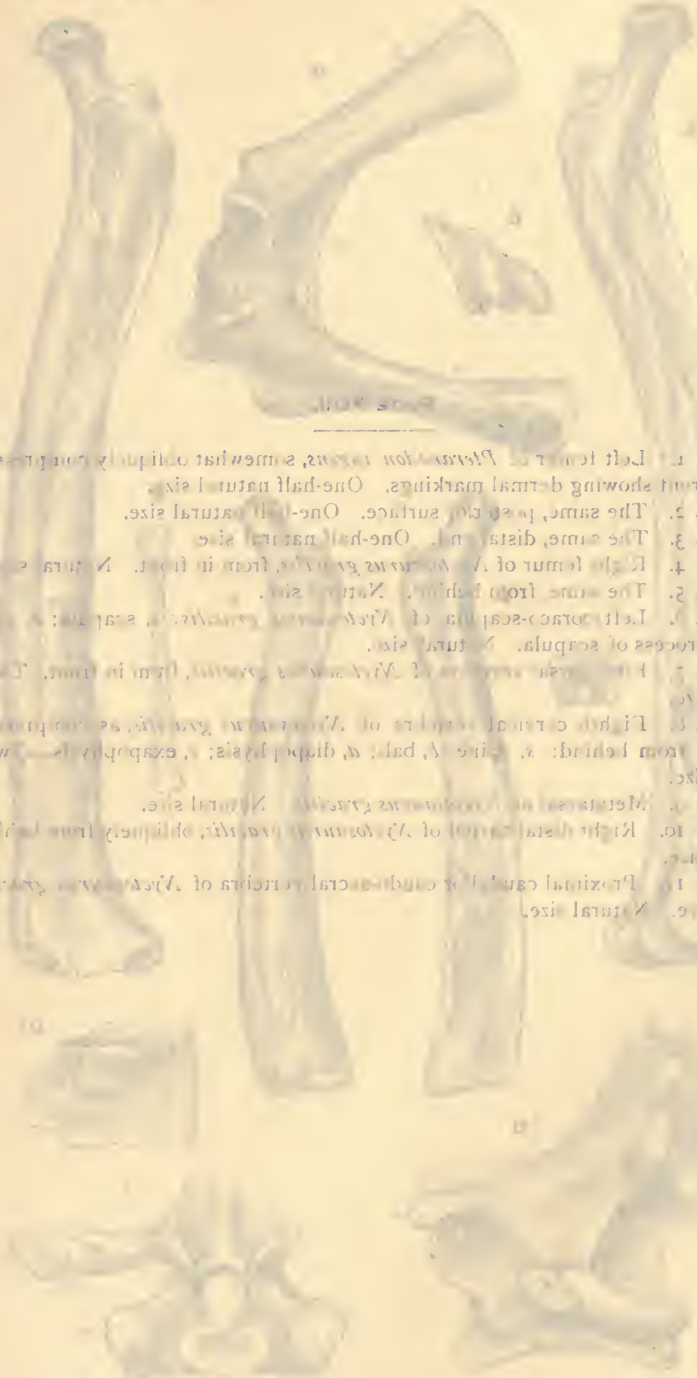


PLATE XLIII.

Fig. 1. Left femur of *Pteranodon ingens*, somewhat obliquely compressed, from in front showing dermal markings. One-half natural size.

Fig. 2. The same, posterior surface. One-half natural size.

Fig. 3. The same, distal end. One-half natural size.

Fig. 4. Right femur of *Nyctosaurus gracilis*, from in front. Natural size.

Fig. 5. The same, from behind. Natural size.

Fig. 6. Left coraco-scapula of *Nyctosaurus gracilis; s*, scapula; *c*, coracoid; *a*, process of scapula. Natural size.

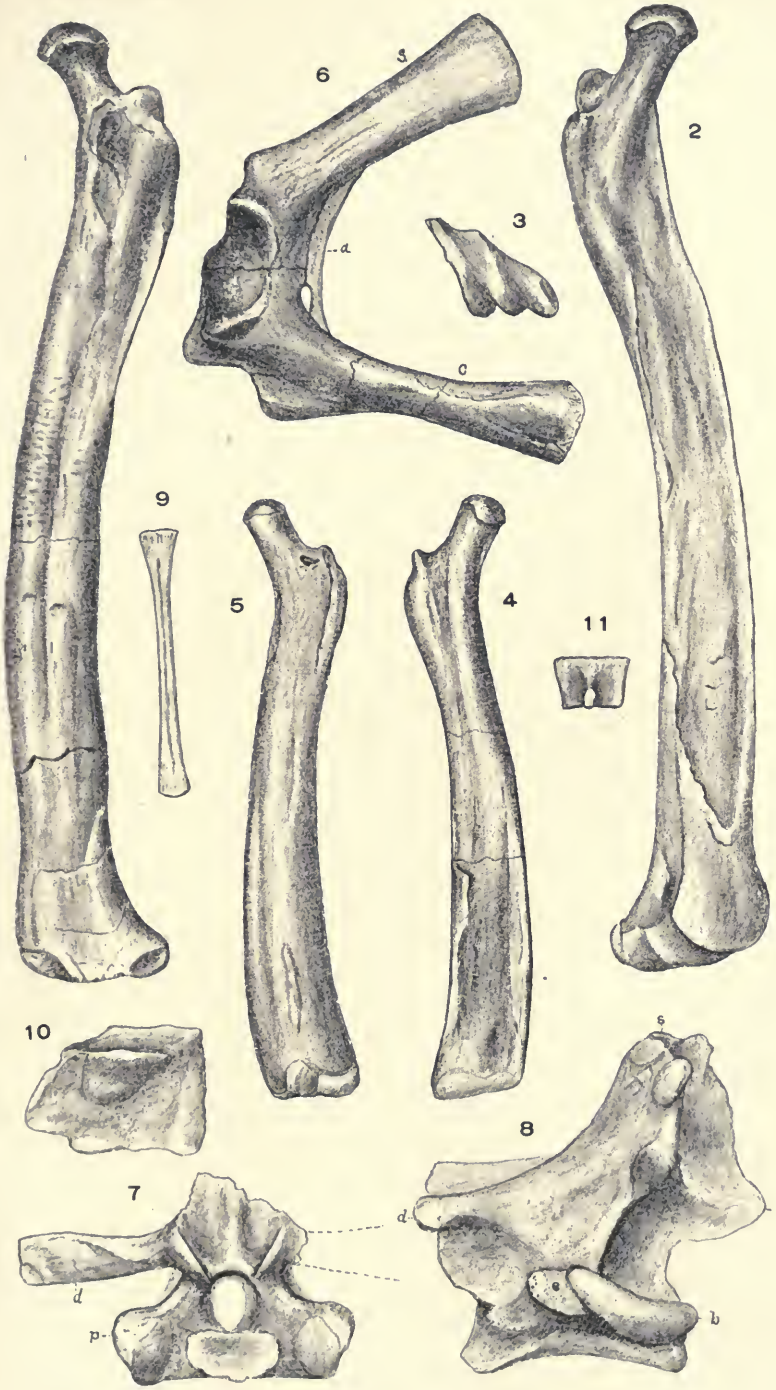
Fig. 7. First dorsal vertebra of *Nyctosaurus gracilis*, from in front. Twice natural size.

Fig. 8. Eighth cervical vertebra of *Nyctosaurus gracilis*, as compressed, obliquely from behind: *s*, spine; *b*, ball; *d*, diapophysis; *e*, exapophysis. Twice natural size.

Fig. 9. Metatarsal of *Nyctosaurus gracilis*. Natural size.

Fig. 10. Right distal carpal of *Nyctosaurus gracilis*, obliquely from behind. Natural size.

Fig. 11. Proximal caudal or caudo-sacral vertebra of *Nyctosaurus gracilis*, from above. Natural size.



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Pteranodon, Nyctosaurus.

PLATE XLIV.

Fig. 1. Right wing phalanx of Pteranodon ingens. One-half natural size.

Fig. 2. Right ring metacarpal of Pteranodon ingens, from below. One-half natural size.

Fig. 3. Tibia of Pteranodon ingens, from the side. Natural size.

Fig. 4. Left femur of Pteranodon ingens, from behind. One-half natural size.

Fig. 5. Right second wing phalanx of Pteranodon ingens, from behind. One-half natural size.

Fig. 6. Penultimate cervical vertebra of Pteranodon ingens, from the side. Two-thirds natural size.

Fig. 7. Fifth cervical vertebra of Pteranodon ingens, from above. Two-thirds natural size.

Fig. 8. Lateral carpus of Pteranodon ingens, after Cope. One-half natural size.

PLATE XLIV.

Fig. 1. Right first wing phalange of *Nyctosaurus gracilis*. One-half natural size.

Fig. 2. Right wing metacarpal of *Nyctosaurus gracilis*, from below. One-half natural size.

Fig. 3. Tibia of *Nyctosaurus gracilis*, from the side. Natural size.

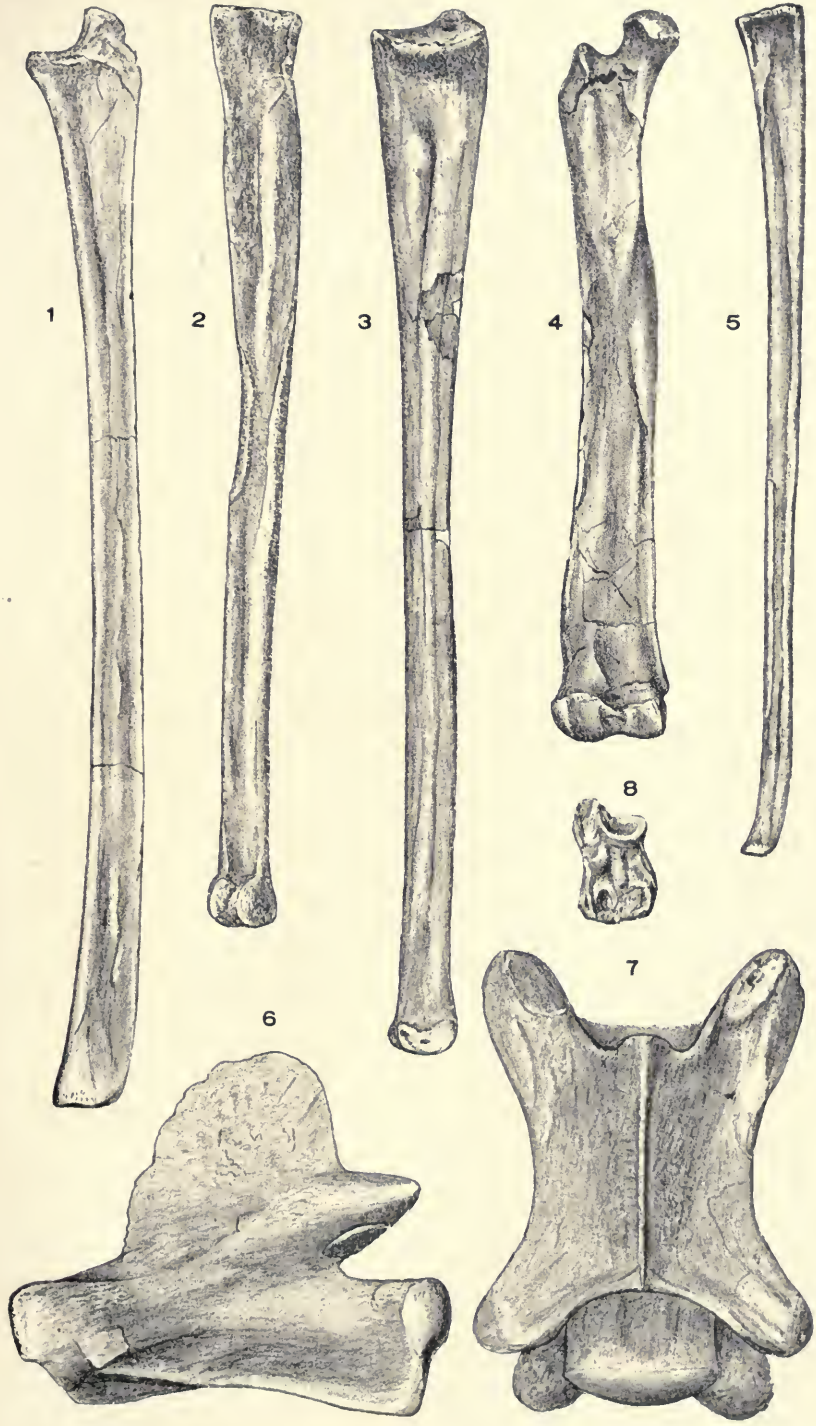
Fig. 4. Left femur of *Pteranodon occidentalis*(?) Marsh, from behind. One-half natural size.

Fig. 5. Right second wing phalange of *Nyctosaurus gracilis*, from behind. One-half natural size.

Fig. 6. Posterior cervical vertebra of *Nyctosaurus gracilis*, from the side. Twice natural size.

Fig. 7. Fifth cervical vertebra of *Nyctosaurus gracilis*, from above. Twice natural size.

Fig. 8. Lateral carpal of *Pteranodon ingens*, after Cope. One-half natural size.



S. W. W. del.

Pteranodon, Nyctosaurus.