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# ON THE SKELETON OF NYCTODACTYLUS, WITH RESTORATION.

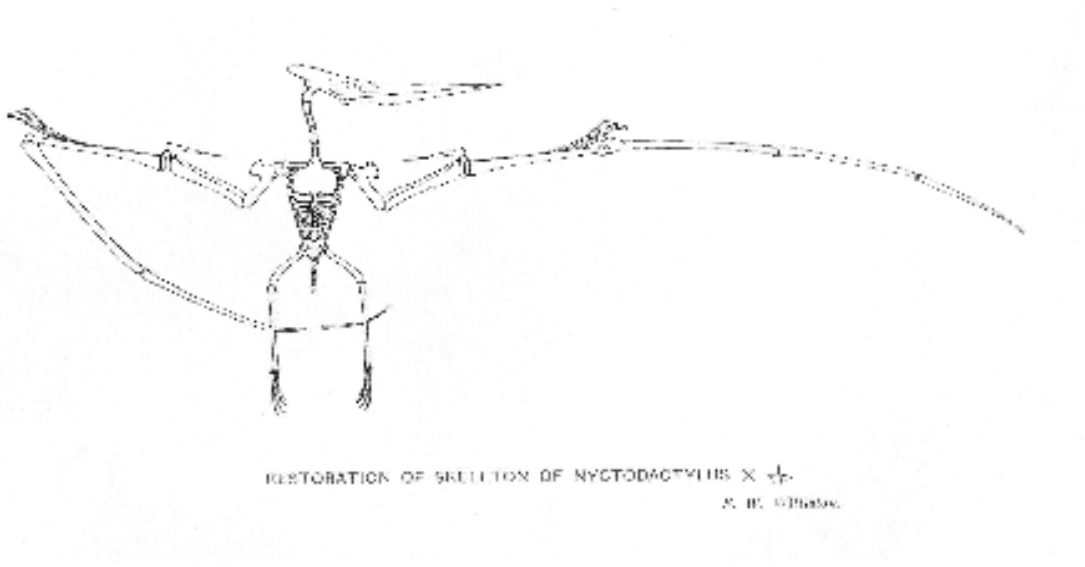
by
S.W.WILLISTON, M.D., PH.D.
*The University of Kansas*.
With 1 Text Figure.

The genus *Nyctodactylus* was proposed by Marsh, in 1879, for a pterodactyl from the Niobrara cretaceous of Kansas. Though very inadequately described, the single distinctive character given by him - the non-articular distal extremity of the scapula - permitted its recognition with certainty, and, in 1892,(1) I gave additional characters placing the genus on a secure foundation. A specimen of this genus, of unusual perfection, recently collected by my assistant, Mr. H. T. Martin, in his usual skilful manner, presents so many interesting new features that I give herewith a brief description of its more important characters in advance of a monographic study of the group, which I hope to find time to undertake soon. The specimen is very nearly complete, lacking only the two distal phalanges of the wing finger in part, and many of the small bones of the digits and of the tail. The skeleton lies upon its back, with but little distortion or disarrangement of the bones; the right wing is folded across the abdomen, the neck vertebrae are partly dislocated, and the legs have been drawn a short distance away from the pelvis. The head lies obliquely to the long axis of the skeleton, with its palatal surface uppermost; and the bones of the pelvis have been separated at the sutures, lying flattened out with the sacrum in the middle. The outlines of the different parts have been, for the most part, made from tracings; that of the skull has been taken in part from a specimen of *Ornithostoma* [Pteranodon] in the museum, since the skull of the specimen is too delicate to remove from the matrix; its anterior portion, however, has been examined on both sides, as also the mandible, and I do not think that the shape as given can depart much from reality. I may further add that the feet and small fingers have been completed from specimens of *Ornithostoma*. Because the bones of these pterodactyls are so exceedingly thin they have been invariably flattened out in fossilization; the first phalange of the wing finger, the longest bone in the skeleton, has the thickness at its middle, as crushed, of less than one and a half millimeters. On account of this flattening, it is difficult to estimate accurately the real width that the bones had in the living skeleton; possibly they are represented in the drawing, for the most part, too broadly.

A brief resume of the more important osteological characters of this pterodactyl may now be given as follows:

Head long and slender, toothless; antorbital opening confluent with the nares; atlas and axis partly or entirely coossified; seven true cervical vertebrae present, without free ribs, and with non-articular exapophyses.(2) Eighth vertebrae apparently ribless, much shorter than the seventh, with the posterior zygapophyses much prolonged; ninth, tenth and eleventh vertebrae, that is, the second, third and fourth dorsal, coossified, and each with stout coossified ribs, or much elongated diapophyses, articulating with the sternum; fifth to ninth dorsals, inclusive, short, stout, procoelous, with elongated diapophyses; tenth, and perhaps also the ninth (which is partly concealed beneath the radius), coossified with the sacrum; sacrum composed of six firmly fused vertebrae, all united with the ilium, and tapering much distally; caudal

vertebrae amphiplatyan, probably about twelve in number (the first one and the three distal ones, only, so far discovered in the specimen). Ilium projecting far in front of the sacrum, narrow; ischium (or conjoined ischium and pubis) with a long, somewhat arcuated median symphysis, and with a large obturator foramen; acetabulum imperforate, situated far dorsad [sic.]; prepubis (pubis?) band like, with an anterior projection, U-shaped in life. Sternum very broad and thin, evidently deeply concave above, without keel, but with a stout presternal process; with four costal articulations on each side, and a median, flattened, xiphisternal process. First three or four dorsal ribs stout, coossified with the vertebrae, and articulating with the sternum; posterior ribs very slender, almost threadlike, probably articulating in front with the extremities of the abdominal ribs, single headed; abdominal ribs at least four in number on each side; arranged very much as the costal cartilages of the sixth to the tenth ribs in man, but joined in front and attached to the xiphisternal process.



RESTORATION OF SKELETON OF NYCTODACTYLUS × ¼.

Coracoid and scapula coossified (imperfectly so in another specimen of the same species), the former articulating by the usual saddle-shaped joint with the sternum, the latter terminating in a free, spatulate extremity, without union with the notarium. Humerus with its deltoid process very long, helmet-shaped and with a constricted neck; remaining bones of the extremities very much as they have been described in *Ornithostoma*.

In the restoration given herewith, in which the measurements have been made with great care by myself, one is struck with amazement at the extraordinary development of the head and wings as compared with the rest of the skeleton. While the wings gave a spread of very nearly eight feet [244 cm], the body proper was less than four inches [10.2 cm] in diameter and not more than six in length [15.3 cm], exclusive of the small tail; the pelvis is less than five-eighths of an inch [1.5 cm] in diameter at its outlet, and the entire body was smaller than one's closed hand! One wonders where sufficient surface was present for the attachment of the strong muscles necessary for the control of the wings. When it is remembered, however, that even the largest bones of the skeleton had walls less than a millimeter in thickness, and that many of the smaller ones were almost like cylinders of writing paper, he will perceive that, notwithstanding the extraordinary development of the anterior extremities and head, the creature, when alive, must have weighed but little. I doubt whether the living animal attained a weight of five pounds [2.27 Kg]. How and where such a creature could have reared their young is to me inexplicable. No evidences have been found in many species of these animals that have been exhumed from the Kansas chalk that they were viviparous, and from the high degree of ossification of the bones in the adult, it is quite sure that the foetus must have had a bony skeleton, and that evidences of such would have been forthcoming before now had the young really been born alive, unless, indeed, in the immature condition of marsupials. If eggs were laid, they could not have been more than a centimeter in diameter, and even if much elongated to accommodate the long bones

of the wings, the newly hatched pterodactyl could hardly have been of sufficient size to have cared for itself.

A number of other interesting conclusions - or speculations - are suggested by the present specimen. The acetabulum is placed far back, nearly over the edge of then sacrum; so far back, indeed, that it would have been impossible for the knees to have met in the middle, when the thighs were flexed to a right angle. Furthermore, the femora have a peculiar mesial convexity, whereby the tibiae were directed at a marked angle outwards, with the thigh in the normal human position. The convexity of the head of the femur, covering a little more than a third of a circle, is at right angles to the long axis of the shaft, making articulation impossible, except in a strongly abducted condition. Similar evidence is presented by the glenoid articulation of the humerus, demonstrating, I think, the improbability of an ordinary quadrupedal position in ambulation, as Seeley has restored some of the European forms. I am convinced that the thigh was rotated outwards, through an angle of thirty or forty degrees, and was directed outwardly nearly in a coronal plane at an angle of thirty or forty degrees from the mesial line. I am not sure, indeed, but that the knees may have been turned at times more or less backward. The condylar surface of the femur is such that the knees could not have been flexed much, if any, more than a right angle. The tibiae might easily have been brought parallel with each other, while the femora were outwardly rotated and abducted.

This normal outward rotation of the femora is shown in an excellent specimen of the hind extremities of Ornithostoma ingens [Pteranodon ingens] preserved in matrix. The head of the femora occupy their normal relation to each other in connection with the remains of the pelvis, but both were directed outwards with the trochanters turned inwards. I may add that in removing one of these femora for further study of its shape, I was greatly surprised to find on the under surface - the ventral - very vivid markings of the integument. Photographs of these will be given later. I may say here that there is no direct evidence of either scales or feathers, but the numerous, regular placed patches of darker material are such as might have been produced by the skin of a bird where there are many feathers. Since we have hitherto been entirely ignorant of the covering of the body of these animals, the discovery is one of great interest. I am convinced that the integument was not a simple smooth membrane over the body, though what it really was I am not prepared to say. I expect to find further evidence, that I hope will solve the question, when the remaining bones of the specimen have been removed from the matrix.

So far, then, as the evidence of the legs goes, the animal may have stood erect upon its feet with the thighs rotated outward and the tibiae far apart. Of the clawless character of the feet in these animals there can be no question. A specimen collected by me nearly ten years ago has the bones all intact and in position. The feet were not in the least prehensile.

The articulation of the humerus with the coraco-scapula was nearly perfect saddle-shaped, with its axes nearly in the planes of the body. Unlike the legs, there was little or no rotation of the upper extremity, either in the shoulder joint or elsewhere. This, it will be seen, must have detracted not a little from the ability to control the direction of flight by the wings, while giving greater strength to them as parachutes. The wing membranes could never have have [sic.] assumed any form, except that of an approximate plane when distended, bellied out, perhaps, like the sail of a yacht antero-posteriorly. The joints of the wing are all ginglymoidal, unless indeed a slight lateral flexibility was possible at the closely united compact wrist, which is doubtful; nor could the anterior or radial curvature of the phalanges be much, if any, greater than I have indicated in the restoration. Because of this lack of rotary power of the anterior extremity, I doubt not that the caudal membranous expansion in Rhamphorhynchus served as a compensatory steering organ, and the same function was subserved, in a somewhat different way, by the legs in the short-tailed forms. But there are much better reasons for supposing that the wing membranes continued to the legs or ankles of these animals. The peculiar structure and evident position of the legs would have been inexplicable under any other assumption, but if the membrane was restricted to the sides of the body the patagial surface must have been a mere ribbon, five or six inches wide [12.7 - 15.2 cm] and nearly four feet long [122 cm], scarcely serviceable as a wing or parachute even!

If the animal stood erect when upon the ground, with the knees rotated outwards and the tibiae parallel, the wings, drooped at the side, which may have been possible, would have reached the surface at the

metacarpophalangeal joint, with the phalanges trailing or partly folded; and it is possible that in such a position, partly stooped, partly creeping, the creature might have laboriously got about on land. But I do not think that they often voluntarily sought the ground for ambulation. Their home was in the air, and they rested suspended by the flexible, sharply-clawed middle fingers. The elongated zygapophyses of the first dorsal vertebra, a functional cervical, though structurally a dorsal, indicate, not a marked backward curvature of the neck at this place, but rather the possibility of a marked anterior curvature. Perhaps the neck was sufficiently flexible to permit a strong sigmoid curvature, bringing the head in a forward direction when in a prone position.

It is commonly believed that the small, slender bone articulating with the wrist and directed backwards toward the shoulder - the so called pteroid or thumb metacarpal - was for support of the membrane in front of the elbow.

I am satisfied that this was not its function, for the simple reason, as I believe, that there was no membrane there, unless it extended on the side of the neck broadly towards the skull! This may seem a mere assumption, but there are evidences in favour that give this idea some weight. The strongly developed deltoid process shows attachments for several muscles. One occupies the whole distal anterior face, as indicated by an oblique line running from near the distal lower extremity inwards and upwards. This was doubtless for the insertion of the supracoracoid muscle, the origin of which is shown by a strong tuberosity on the upper part of the coracoid, and whose tendon was guarded in part, apparently, by a sesamoid bone found near the glenoid articulation. On the distal convex border, near its upper extremity, there is a small facet for muscular attachment, looking outward and forward in the extended position of the arm. This may have been for the attachment of the pectoralis, as Plieninger seems to believe, but of which I am very doubtful. Certainly the pectoralis must have been a very weak muscle to have terminated in so small a tendon, and the extensive surface of the sternum calls for a larger one. It would furthermore have acted as a powerful muscle of inward rotation, of which the joint was incapable. Lying in front of the arm and adjacent thereto, there are a number of long, thin, striated ossified tendons, with somewhat fimbiated extremities, some of them eighty millimeters in length by four or five in width. I am satisfied that the most of the space in front of the elbow was filled during life by strong muscles, controlling the movement of the arm and wrist, the anterior brachial and carpal flexors, whose origins were high up on the humerus. On the upper distal extremity of the radius there is an articular surface extending backward, and, lying near it in the specimen, there is a small sesamoid bone, doubtless belonging to a carpal flexor. The pteroid bone has a rounded convex articular surface on one side of its broad carpal extremity that evidently fitted into a depression in the lateral carpal bone lying near it. The joint seems to have a permitted considerable enarthroidal movement, with but little gliding motion; it clearly permitted considerable oscillation of its free extremity in the plane of the wing. The distal extremity reached nearly to the deltoid process in the ordinary flight position of the wing. There certainly was not sufficient membrane in front of the elbow to need such an elaborate structure for its support if the membrane ceased at the shoulder. On the assumption that this bone is a reversed thumb metacarpal, an altogether probable theory, one cannot conceive how it could have assumed its present position, unless it had been reversed and brought toward the shoulder by the action of a membrane that originally extended along the sides of the body over the outstretched fingers like that of a bat. By the gradual development of the little finger, as is shown, indeed, by the more elongated metacarpal of the later forms and the greater proportional development of the middle fingers in the early forms, the end of the thumb was drawn backward and rendered tense, until its position became directly opposite to the original one.

We must assume then that the membrane originally was developed to a greater or lesser extent in front of the arm as well as behind it. Had the membrane finally disappeared here, it is only natural to suppose that the bone controlling it would become vestigial - assuming Lamarckian views! On the contrary, it has evidently increased in size, for it seems to be larger in this one of the most specialized of all pterodactyls than in the earlier ones. What then could be its function, unless as the support of a membrane that extended over the shoulder to the side of the neck? I can not say that I am convinced that this really was the case in our *Nyctodactylus*, but I think it not improbable.

The attachment of what I believe to be the pectoral muscle was by a stout and prominent process on the inner proximal side of the humerus. [3]

In an earlier communication I stated that the upper part of the bill or beak in Ornithostoma was not produced in a sharp ridge as Marsh stated, but that it was rounded. Plieninger (l. c.), however, thinks that I was mistaken and that Marsh was right. "Die Medianine des Schadels ist im vordered Theile in eine scharfe Kante ausgezogen, welche allmahlick nach hinten, gegen die Nasopraeorbital Offnung hin, in eine sanfte, stumpfe Rundung ubergeht; allem Auscheine nach ist die scharfe Kante im vordersten Theil nicht durch Druch hervorgerufen, sondern war ursprunglich vorhansen." In the present specimen the skull is in a most admirable state of preservation, and an examination of it proves beyond shadow of doubt that the median part above was rounded, evenly and smoothly convex, at least as far back as the narial opening. "Die Oberflache der Schadelknocken ist fast durchwegs mit verschieden deformten, meist annahernd ovalen Grubchen bedeckt. Williston glaubt, dass nur der Abdruck der in der spongiosen Masse befindlichen Hohlraume sei, eine Ansicht, welche ich nicht theilen kann." - Plieninger (l. c.). The upper surface of the beak does not show the slightest indication of such a depression, but is perfectly smooth and plane. This condition I have seen so often in *Ornithostoma* that I feel sure that the depressions were always the result of the compression to which the bones were subjected.

At present our knowledge of the skeleton of *Nyctodactylus* is nearly complete, more complete perhaps than that of any other pterodactyl known.

Its structure demonstrates the comparative unimportance of the scapular articulation as a diagnostic or classificatory character. The structure of the skeleton throughout, even of the notarium or consolidated dorsal vertebrae, is very much like that of *Ornithostoma* save in the scapula. From this it follows that the genus must be placed in the same family with *Ornithostoma* and *Ornithocheirus*. In my own opinion, there is not even a subfamily difference.

I still believe that the genus *Pteranodon* is identical with *Ornithostoma*, and that the former term must be abandoned. Plieninger (l. c.), however, concludes that even if the two terms be synonyms, the name *Ornithostoma* has no claims for recognition, because it was not adequately described or figured before March described *Pteranodon*. Were this true, and it may be, it would not be sufficient justification for the rejection of *Ornithostoma*. Were the rule applied to Marsh's own names, a large part of them would be rejected, as he rarely gave characters substantiating his terms. But there is a far weightier reason for the abandonment of the term *Pteranodon*. Prof. Seeley, according to his statement,[4] pointed out to Prof. Marsh the toothless character of *Ornithostoma* and showed him evidence before *Pteranodon* was known!

On every principle of nomenclature and justice the name Ornithostoma must take precedence over Pteranodon if these genera are found to be identical, as I believe will be the case.

NOTE: - Since the foregoing has been typed, the skull of the specimen described has been nearly wholly freed from the matrix. It has no occipital crest, and the occiput is a little less pronounced than in the figure; otherwise the outline is nearly correct. The fossil skull, thirty one centimeters in length, inclusive of the mandible, weighs less than thirty nine grams!

1. Kansas Univ. Quart., Vol. I, p. 12.
2. Plieninger, (Paleontographica, XLVIII, 82, 1901) objects to this term, and identifies the processes with the parapophyses. Assuming that they are morphologically identical with the real parapophyses, which is by no means proven, and is to me very doubtful, their very different position and function necessitates a distinctive name, for which I propose that of exapophyses (Kans. Univ. Quarterly, 1896).
3. Plieninger rightly objects to the use by me of the term "bicipital crest" for this process, by saying that it was not for the attachment of the biceps muscle, which never arises from the humerus. That so unpardonably an error may not be attributed to one who has had taught human anatomy for many years, I may say that I use the term, inadvertently, in the anthropotomic sense of the "anterior bicipital ridge" and as such I believe it to be correct, though not a proper term here.
4. Dragons of the Air. London, 1902. p. 182.