A study of *Pteranodon*

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A specimen of *Pteranodon* from the Niobara Chalk, Kansas, is described. Although not complete, the limbs and the anterior part of the skull are well preserved, enabling careful study. No specific name has been assigned to the specimen since it was collected in 1920. Comparing data from Eaton (1910), the name *Pteranodon* cf. *ingens* is ascribed to this specimen. The very small size may indicate that this may be a new species. A proposal regarding the function of the crest of *Pteranodon* is put forward. It is suggested that the crest (not preserved in the specimen described) may have acted as a muscle attachment projection to assist counteraction of the forces occurring during a suggested method of feeding.

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Introduction

Late in the first quarter of this century, Ch. Sternberg collected three reptiles from the Niobara Chalk (Upper Cretaceous) in Kansas and sold them to the Palaeontological Institute, Uppsala. Wiman (1920) gave a very brief account of these three: *Pteranodon* sp., *Platecarpus coryphæus*, and *Clidastes sternbergii.* All three specimens lie in the original calcareous matrix. The following account is a more detailed description of *Pteranodon* sp.

A comparison with the figures of the Marsh Collection given by Eaton (1910) shows that the present specimen is very well preserved. It has however, lost its original skeletal configuration so the identification of the individual bones has been largely by the characters of each, and not by the position within the skeleton. This specimen is by no means complete with the main part of the vertebral column and the rib cage missing. The limbs are near complete: the rear limbs are present, but only the left wing can be seen.

Systematics

Order PTEROSAURIA
Suborder PTERODACTYLOIDEA
Family PTERANODONTIDAE
Genus PTERANODON Marsh 1876
       P. cf. *ingens* Marsh 1876

The skull

The skull has been well preserved anteriorly although the rostrum is slightly splintered. There is no evidence of teeth along the border of the premaxillae. On the dorsal side of the nasal vacuity, the prefrontal can be seen to meet the premaxilliae; just posterior to this junction, the right facial part of the skull has been broken away, thus leaving the inner surface of the left face exposed (Text-fig. 1). Of this, part of the nasal and lachrymal can be seen. Below the lachrymal, which separates the nasal foramen from the orbital cavity, lies a triradiate bone, which on preliminary inspection was very puzzling; by looking at photographs of other specimens of *Pteranodon*, it is clear that this bone is the right jugal (Pl. 1 fig. 2). It would seem that not all of this bone was exposed to the surface when the skull was in its original state, the post-orbital partially obscuring the upper part.
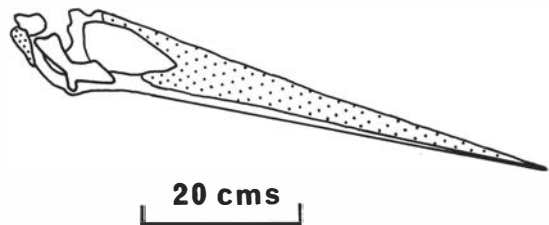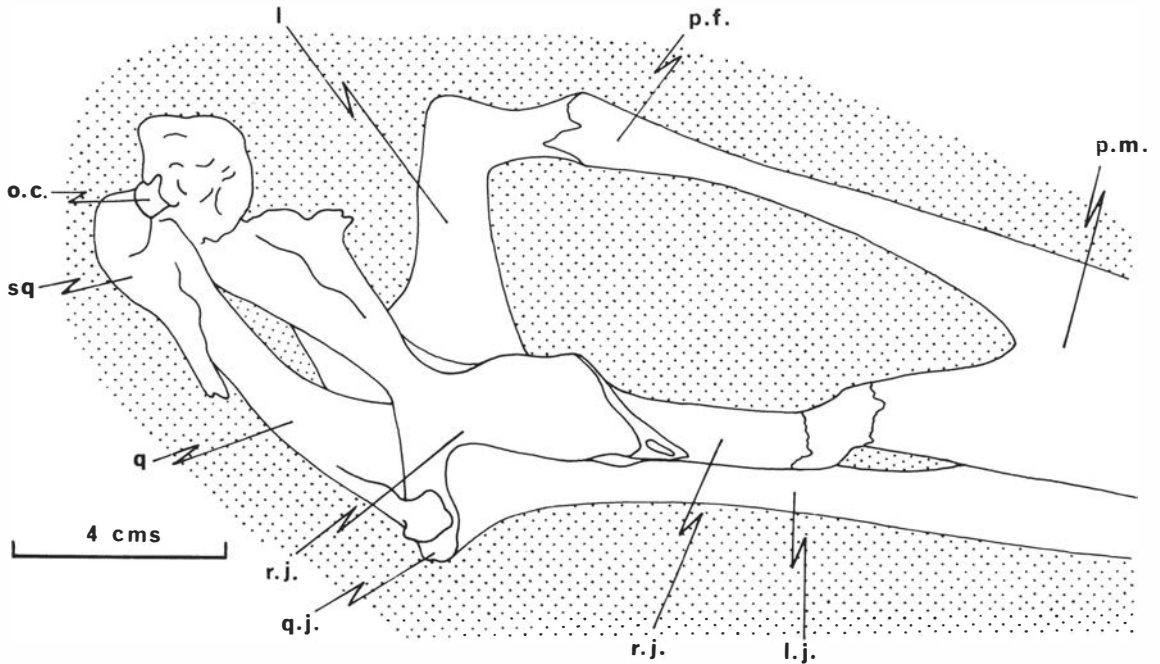

20 cms

Fig. 1. Skull. The dotted region shows the right face of the skull.

Fig. 2. Posterior region of the skull. Dotting indicates the rock matrix. j — jugal; l — lachrymal; o.c. — occipital condyle; p.f. — prefrontal; p.m. — premaxilliae; q — quadrate; q.j. — quadrato-jugal; sq squamosal.

The left jugal is partly seen lying beneath the right jugal. The left quadrate is clearly exposed lying between the squamosal and the quadrato-jugal. The fact that it is the inner surface of the left jugal, is seen by the occipital condyle being on the distal side (from the observer) to the quadrate. The left squamosal can be identified although it is not well preserved; only a small part of the anterior projection of this bone is seen because it has been fractured anteriorly and is missing.

To the right of the squamosal (with respect to the specimen) lies the occipital condyle and the exoccipital (Text-fig. 2). The former is very well preserved, but the latter is only just definable. Part of the problem with the identification of the right jugal, is that it lies on the same plane as the occipital condyle thus giving the impression that it was an internal bone. However, the right jugal contributes to the formation of the characteristic "screw joint" for jaw articulation with the quadratojugal.

Apart from the occipital condyle and the squamosal, no identifiable bones are to be seen in the posterior part of the skull. Unfortunately, there is no evidence for a crest.

Mandibles

Only the ventro-posterior part of the lower jaw is exposed, showing where the rami meet ventrally (Pl. 1 fig. 4). The posterior extremities of the rami are well preserved and the underside of the codylar cavities can be seen. The horizontal axis of these was measured with respect to the main shaft of the rami, and after correcting for slight distortion, they were found to lie at 28° (actually measured at 32° and 26°) (Text-fig. 3). There is also a slight vertical inclination to the codylar cavities but this could not be determined. The rami have a pronounced ridge on their ventral surface which
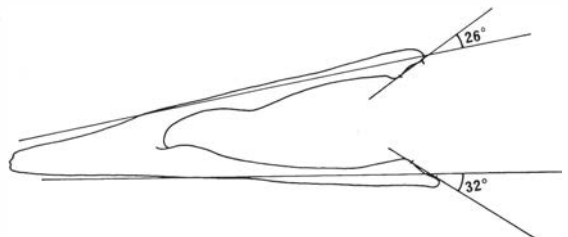
Fig. 3. Lower mandible showing angle of the hinge sockets in relation to the posterior of the jaw rami.

runs from the outer side, posteriorly, to the inner side, anteriorly, thus crossing over the shaft of the rami about half way along its length.

Vertebrae

Most of the vertebral column is lost. Only three clearly definable vertebrae are preserved, of which two have some of the original characters visible. The first of these (Pl. 1 fig. 3; Text-fig. 4) exposes its posterior surface as indicated by the facets of the posterior zygapophyses which can be clearly seen. The neural spine is broken at the base and "leans" heavily to the right; otherwise, this structure is complete. Only one of the transverse processes has been preserved well: the left process has the distal extremity missing. Both processes have their bases well above the centrum, diverging at a slightly inclined angle from the position of the base of the neural spine. The neural canal is very clear and seemingly undamaged, although filled with sediment. The centrum has a gently concave posterior surface. The outline in cross-section is almost circular except for a deep indentation by the neural canal on the dorsal surface. The centrum shows its length, and thus it can be seen to have expanded ends with a constricted centre. From the characters of this vertebra, it would seem that it belonged to the dorsal part of the column.

In *Pteranodon*, the distal ends of the neural spines of the dorsal vertebrae are connected by
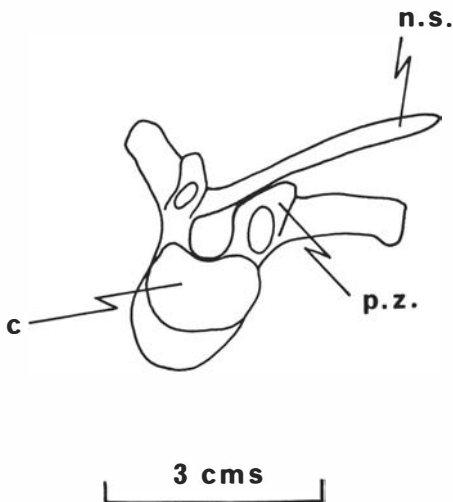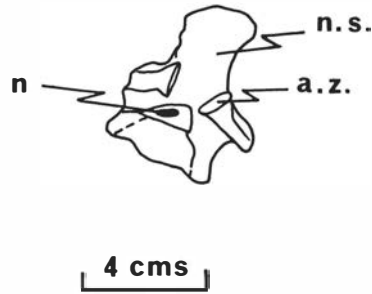

Fig. 5. ? Cervical vertebra. a.z. — anterior zygapophysis; n — neural canal; n.s. neural spine.

a bone running parallel to, and above, the vertebral column. It appears that the vertebra in question was one of these, although the extreme distal part is missing.

The other well preserved vertebra (Text-fig. 5) is considerably less well preserved than that just described. However, the neural spine is seen although the form is not distinct. The anterior zygapophyses are more clearly seen, but only the actual facets are well preserved. Unfortunately, the transverse processes are absent. Just below these anterior zygapophyses lies the neural canal which is badly distorted. Only the upper part of the centrum is seen. This vertebra has a short, broad neural spine, and the neural canal is relatively large; the anterior zygapophyses are quite pronounced although small. Thus it would appear that this vertebra was from the posterior cervical region.

The remaining vertebra is very poorly preserved exposing the lateral view only. This is considerably larger than the vertebrae already described. Since compression has affected this bone a great deal, it is difficult to determine what is missing and what is present. Two very subdued processes can be seen projecting posteriorly, and beneath, the remains of the centrum. The anterior end can not be seen because it is obscured by the rostrum of the skull. This vertebra is probably one of the cervical vertebrae, particulary regarding the subdued nature of the lateral processes.

Fig. 4. Dorsal vertebra. c— centrum; n.s. — neural spine; p.z. — posterior zygapophysis.

Pectoral girdle

The left and right coracoid and scapula are present and are quite well preserved (Pl. 2 figs. 7, 8; Text-figs. 6 a, b). They are firmly fused at their distal
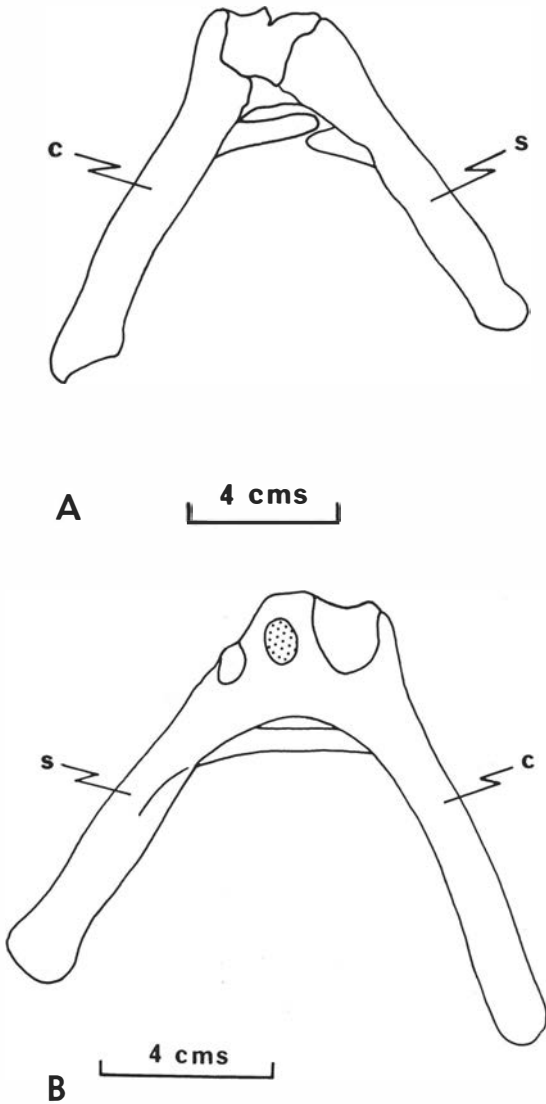
pressure on the sternum and the dorsal vertebrae facets. The lengths of the respective bones, left and right, are:

Scapula	11,9 cm	11,4 cm
Coracoid	12,2 cm	12,4 cm

Pectoral limb

The bones preserved are those from the left wing only. Because the left wing is almost complete, an estimate of the total wing span can be made. The third and fourth phalanges are missing, but proportions from other large flying reptiles were taken, thus a quick calculation can be made: the total length of the wing bones is 94,1 cm; the distance from the distal point of the pectoral girdle to a line midway between the proximal ends of the coracoid and scapula is 10,0. Doubling this up for the left and right wing, a figure of 208,2 cm is obtained, and when the width of the vertebrae are accounted for, a total wing span of about 210 cm is reached. This, by *Pteranodon* standards, is rather small: the largest on record is a specimen measuring about 9 m from wing tip to wing tip.

The *humerus* (Pl. 2 fig. 1; Text-fig. 7) is completely preserved; Eaton (1910 p. 28) discusses the forms of distortion found in various humeri of this genera. The bones that the figures in his paper (Pl. XIX figs. 1, 2, 9, 10; Pl. XX figs. 1—6) appear not to be in such a good state of preservation as the Uppsala specimen even though they are free from the matrix. The radial crest is well developed and clearly seen, but it is interesting to note that this bone is the opposite way round to that shown in Eaton's reconstruction of *Pteranodon* (Pl. XXXI). The expanded end of the humerus, with the radial crest, articulates with the radius but the reconstruction shows the ex-
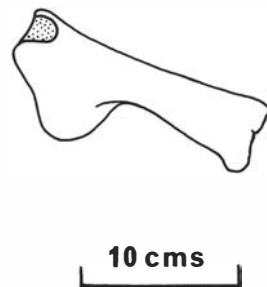

Fig. 6. The scapula and coracoid: (A) from the right side, and (B) from the left side.

Fig. 7. The humerus.

extremities. Both bones have their posterior sides exposed, thus the facets for articulation with the humeri are clearly visible. The articular facet for the accommodation of the dorsal vertebrae and the sternum lie on the extreme distal ends of the bone; since these bones are still in the original matrix, these facets are difficult to see. The fusion line between the coracoid and the scapula is not seen in either case, but a strut joins both bones posterior to where they fuse. This has presumably formed as a strengthener to the fusion, which during flight must have had to accommodate considerable stress. Also, the added rigidity would ease the

panded end articulating with the coracoid. However, the reconstruction seems to be quite correct in this respect, thus it seems that the humerus of the Uppsala specimen has shifted from its original position.

The facets for articulation with the radius and ulna are clearly visible and the large facet for accommodating the coracoid at the proximal end is almost perfectly preserved.

The *radius* is completely preserved. It appears to be in its original position with the humerus. There is a fracture across the shaft just below the head but the two ends have not parted. The proximal end has a greater expansion than the distal end with two convexities for accepting the humerus. The shaft is not absolutely straight having a slight curve towards the proximal end. The distal articular surface is quite flat as is the opposing face of the proximal carpal.

The *ulna* (Pl. 2 fig. 2; Text-fig. 8) is well preserved although the ventral surface has collapsed. It has shifted from its original position slightly. The two ends expand asymmetrically (see Table 1), the proximal end being the larger. The articular facets are not well exposed because they lie at the extremity and are partly hidden in the matrix.

The *carpalia* are for the most part present but difficult to define since only one face is exposed. The proximal carpal can be identified by the double receptacle for the radius and ulna, thus the other element is assumed to be the distal carpal. This latter bone is almost square in outline with a large median ridge running almost the whole length; the height of the ridge in proportion to the length is about 30 %. The positioning of the carpalia is almost as it was during life, lying between the radius and the metacarpal IV. Anteriorly to these bones, lies the *Pteroid* which has not been damaged apart from the collapsing of the shaft. The length of the proximal shaft (before the "kink") is 20 % of the length of the shaft after the "kink" to the distal end.

The *metacarpal IV* typically tapers distally from an expanded proximal head. The shaft is quite straight but has been compressed; it is difficult to
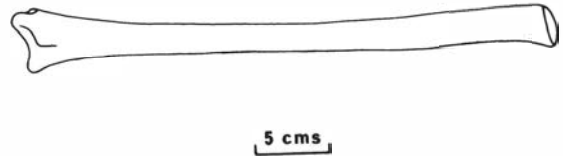

5 cms

Fig. 9. The phalange IV₁.

discern whether scars marking the attachment of the other metacarpals are visible due to the splintering from collapse. The distal end shows only a slight expansion to a rounded head with a distinct groove for articulation with the phalange IV₁.

The *metacarpal II* has been figured as the 'metacarpal' in the diagram accompaning the specimen in the museum. Comparing the specimen figured by Eaton (1910 Pl. XXII fig. 3), the Uppsala metacarpal is most similar to the metacarpal II, thus on this basis, I have named it as such. The bone lies a long way from its original position. It also has collapsed, but only proximally where the expansion has been greatest; the distal end appears to be not quite complete.

The *phalange IV₁* (Pl. 2 fig. 3; Text-fig. 9) is also in the same state of preservation as the metacarpals. The proximal head shows the characteristic concavity for accommodating the distal end of the metacarpal IV; the plane of the opening of the receptacle does not lie parallel with the perpendicular plane to the main shaft. This means that this bone lay at an angle to the metacarpal IV, thus giving the wing a curved aspect to the posterior (Text-fig. 10). The expansion is, as one would expect, greater at the proximal end, and, this is relatively sudden compared with the gradual and subtle increase towards the distal end. The distal facet is very nearly flat having a very slight convexity. Presumably, there was no great flexibility in this joint with the phalange IV₂.
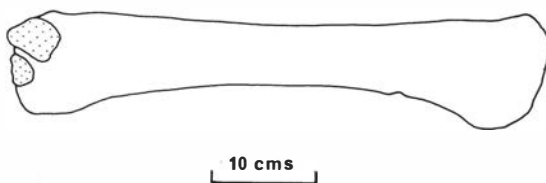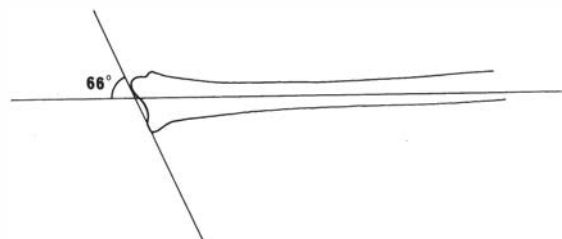

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Fig. 8. The ulna.

66°

Fig. 10. The phalange IV₁ showing the angle of the distal socket in relation to the main shaft.

The *phalange IV$_2$* is not fully exposed: the distal end is partially missing, and half of the proximal surface is hidden beneath the premaxillae. It has been fractured across the centre of the shaft but the two ends have not separated. The shaft has completely collapsed leaving two ridges running along the outer border. There is no curvature in the shaft and there is only a slight distal tapering. The articulation surface of the proximal end, although partially hidden, does indicate a flat surface, similar to that of the opposing surface of the phalange IV$_1$, as one would expect.

Pelvic limb

The pelvic girdle is absent. Only the femora and tibiae and a number of tarsals are present. The femora of both rear limbs are present and show the principal features of the posterior surface (the anterior surface being face down in the matrix).

The left femur (Pl. 2 fig. 4; Text-fig. 11), which lies at the bottom of the specimen, has a straight shaft with a slightly diverging distal extremity. The distal articulation facet is rather flat like the proximal facet of the tibia. The shaft has been compressed thus is flat with two ridges running along the sides; this is particularly marked at the distal end. The proximal end shows the head clearly and the greater trochanter. The head lies on a relatively short constricted shaft leading from the main part of the femur at a slight angle (which can not be measured in this case). The head appears to be more than hemispherical, but this is a false impression due to the constricted nature of the shaft. The Uppsala specimen has a considerably reduced articulation facet for the acetabular compared with those shown by Eaton (1910 Pl. XXVII, XXVIII).
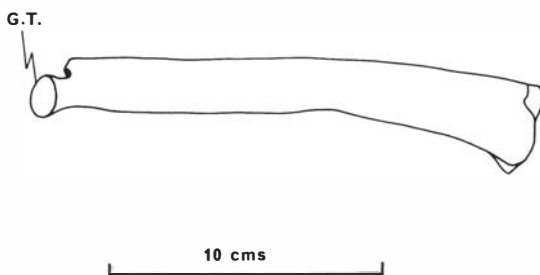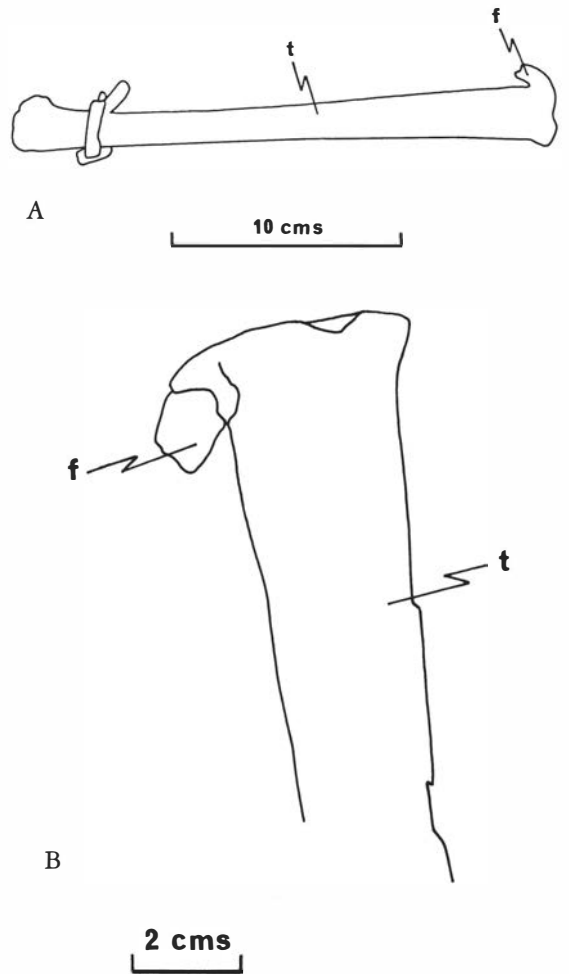

A

B

Fig. 12. The tibia and fibula. (A) whole tibia, (B) enlarged view of the proximal end of the tibia showing the remains of the fibula.

The right femur, although partly obscured in the centre, shows both ends quite clearly. A curvature is apparent (concave facing inwards) although it is very slight. The neck of the greater trochanter can be seen more clearly in relation to the main part of the femur: the distal part of the neck runs sub-parallel with the main shaft, then curves inwards toward the shaft. The distal end of the femur expands to form a flat articular surface for the tibia, very similar to the left femur.

The tibiae (Pl. 2 figs. 5, 6; Text-fig. 12 a, b) are present and are both typically long slender bones with only a slight proximal expansion, which is continuous along the length of the shaft. The left tibia has been fractured near the centre but

Fig. 11. The femur. G.T. — Greater Trochanter.

the two halves have not parted. The distal end lies against the radius thus the facet can not be seen, although the groove accommodating the tarsals does project back. The distal end of the right tibia, where the facet is exposed better, shows two grooves which give a subdued tri-lobate condition; the central lobe passes proximally into a long furrow, which has been emphasized by the collapse of the shaft due to compression. This is not seen in the left tibia because the position is at a slight angle thus the compression has obliterated any such structure.

The proximal articular facets are typically flat in both cases; fused to one side of the facet of the right tibia, is a small process which Wiman (1920) correctly observed as being a fragment of the fibula. There is a slight initial curving to this bone as though it would meet with the tibia distally if it were complete; there is no evidence on the tibia to support this.

Discussion

Although this specimen has been disturbed from its original configuration, the preservation has been remarkably good. The record of all specimens of *Pteranodon* has come from the marine environment. Vertical compression has had its effects on every bone, but this has not been so great as to inhibit an accurate study.

Since so little work has been done on the genus *Pteranodon*, a specific name for this specimen is difficult to apply. However, by closely correlating data published by Eaton (1910), the Uppsala specimen would seem to be *Pteranodon ingens* Marsh. The evidence for this determination lies with all bones common to both the type specimen

(No. 1175) and the Uppsala specimen: the hume-rus, quadratojugal, femur, and the shape of the nasal vacuity principally. The coracoid and scapula do not closely follow the type specimen, but rather that of *Pteranodon* sp. (No. 2616, Eaton 1910 Pl. XVIII). In each of the former bones, the similarity to *P. ingens* is striking with respect to *P. longiceps* and *P. occidentalis*. The evidence against ascribing this specimen to *P. ingens* is the absolute size, and the coracoid and scapula. Proportions of mea-surements from the type specimen and the Uppsala specimen show a very consistent trend, suggesting that if the larger, type specimen is an adult, then the Uppsala specimen must be also. (As with most vertebrates, proportions of the skeleton alter during the individuals' life). The Uppsala specimen is some 25 % smaller than the type, and almost 80 % smaller than the largest found having a wing span of 9 m.

From a study of Eaton's monograph and the Uppsala specimen, it is quite clear that a thorough revision of the genus *Pteranodon* is required, and only when this is complete can the systematics of the Uppsala specimen be elucidated. Meanwhile, the determination *P.* cf. *ingens* is ascribed to this specimen. Although the crest is missing, there is no question of this specimen belonging to the genus *Nyctosaurus*: the post-cranial skeleton of these two genera is quite distinct (Williston 1902, 1905, 1911).

The function of the crest has been the subject of much discussion, and will continue to do so. Bramwell & Whitgift (1974) give a short history of the speculations about the function of the crest. As they so rightly point out, such a skeletal modi-fication is bound to affect the animal's way of life, particularly flying. This crest has apparently evolved in order to serve a particular purpose. It
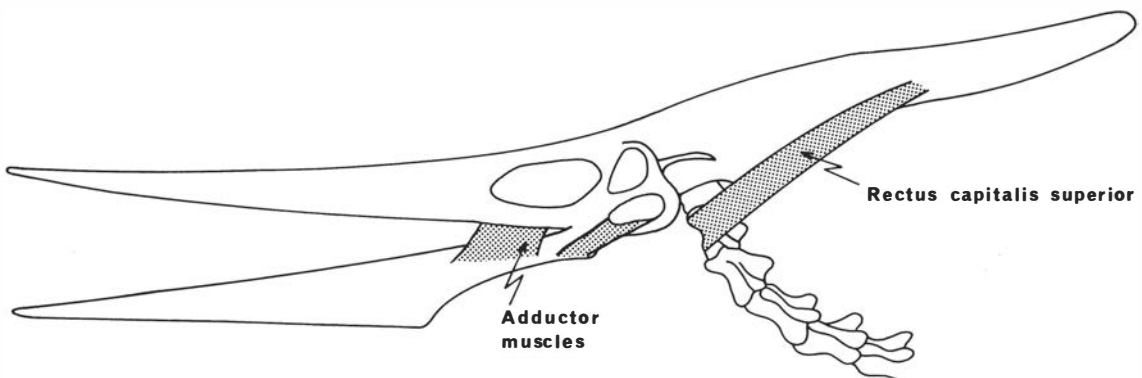

Fig. 13. Suggested musculature of *Pteranodon* accommodating the scooping method of feeding.

has been strongly held that the crest served as a rudder, but as Bramwell's aerodynamic experiments show, the crest contributes little to the steering abilities (although the head does). Also, all birds, bats and apparently other pterosaurs do not require such a structure for flight in that they are able to turn by banking which they do by reducing the air pressure beneath the relevent wing. There is no reason to suppose that *Pteranodon* was not able to do this also.

It was Eaton who first put forward the idea of the crest having evolved for the purpose of muscle attachment. He suggested that to increase the power of the jaws, a muscle could have extended from the mandible to the tip of the crest. This seems rather unlikely if one considers the weight of muscle and the geometry of the skull. Bramwell & Whitgift reached the conclusion that the prime function of the crest was for weight saving by enabling a reduction in the amount of muscle required to turn the head to a sufficient angle for it to serve as an efficient aerodynamic brake. Because the skull is so thin, the rectus capitalis muscles would not only have a powerful turning ability, but also a powerful vertical pull. If one considers why a vertical force would be required, one can look to the animal's possible feeding habits. Since *Pteranodon*, unlike other pterosaurs, has no teeth, it is probable that it fed on plankton and other small organisms that lived near the surface of the sea. To obtain this food it would had to have glided down and scooped up the food with its lower jaw. This would have exerted a considerable stress pulling the mandible down, (it is probable that this animal was not able to fly very slowly). The adducter muscles that would counteract this force need not be enlarged greatly, or require any particular skeletal modification, to bear this added stress. In this way, the stress would be transferred to the skull as a whole, and the leverage that the crest gave the capitalis muscles would counteract this stress, (Text-fig. 13). This then would correlate the fact that *Pteranodon* is the only pterosaur with a crest and no teeth.

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Explanation of plates

Plate 1

Fig. 1. The specimen as it is mounted in the museum of the Palaeontological Institute. $\times$ 0,1.

Fig. 2. Showing the posterior region of the pre-orbital part of the skull. The nasal fenestra is marked 'n'. $\times$ 0,2.

Fig. 3. Showing a dorsal vertebra viewed from the posterior. $\times$ 1,0.

Fig. 4. Showing the mandible with only the ventral side of the posterior rami visible. $\times$ 0,25.

Plate 2

Fig. 1. Showing the left humerus; note the expansion of the whole of the distal end. $\times$ 0,7.

Fig. 2. Showing the left ulna. $\times$ 0,5.

Fig. 3. Showing the left phalange IV; note the distal concavity for reception of the metacarpal IV. $\times$ 0,3.

Fig. 4. Showing the left femur with pronounced greater trochanter on the left. $\times$ 0,2.

Fig. 5. Showing the complete right tibia. $\times$ 0,5.

Fig. 6. Showing the proximal end of the right tibia and the fragmentary fibula. $\times$ 1,0.

Fig. 7. Showing the left part of the pectoral girdle; note the strengthening 'strutt' bridging the coracoid and scapula. $\times$ 0,5.

Fig. 8. Showing the right part of the pectoral girdle; here the 'strutt' has snapped. $\times$ 0,5.

Plate I

Pteranodon
Niobrara Group Krita
12 miles S om Russel Springs
Logan Co Kansas
Sternbergs Expedition 1918

Plate II