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New evidence on the tail of Pterosaur Pteranodon (Archosauria: Pterosauria).

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Introduction

Past reconstructions of pterodactyloid pterosaurs have all considered the tail to be nonfunctional, probably because it was greatly reduced in comparison to the long tail of *Rhamphorhynchus*. Many authors believed that the wing membrane was stretched by the hind legs, and reconstructed a useless short tail embedded in a uropatagium between the legs. Wellnhofer (1985) reconstructed the wing of *Santanadactylus* as stretching down the hind legs almost to the knee, with no uropatagium between the legs so that the small tail was free. Padian (1983, 1985) presented a reconstruction with the wing membrane attached to the end of the tail, but free of the hind legs. Almost all studies of the flight of pterosaurs have been based on Eaton's (1910) description of the osteology of *Pteranodon*. Eaton's knowledge of the tail of *Pteranodon* was based on only two specimens: the five anterior caudal vertebrae of YPM 2489 and the incompletely prepared series of four articulated caudals of YPM 2546. He estimated that a *Pteranodon* with a 7.5 m wingspan would have a tail of 11 to 16 cm, but his plates show a tail of only 8 cm. During a redescription and taxonomic revision of *Pteranodon* I uncovered information that indicates that the tail of *Pteranodon* was longer and more complex than previously thought. This paper presents a reconstruction of the tail of *Pteranodon* and discusses its functional significance.

Description of Materials

No single specimen of *Pteranodon* has preserved a complete tail, but comparison of a number of specimens, YPM 2489, 2546, 2462, and AMNH 6158, allows reconstruction of the entire tail. All specimens are from the Smoky Hill Chalk Member of the Niobrara Formation (Upper Coniacian - Lower Campanian) of Western Kansas. Complete description of these specimens is beyond the scope of this paper, but brief descriptions follow. Measurements are listed in Table 1.

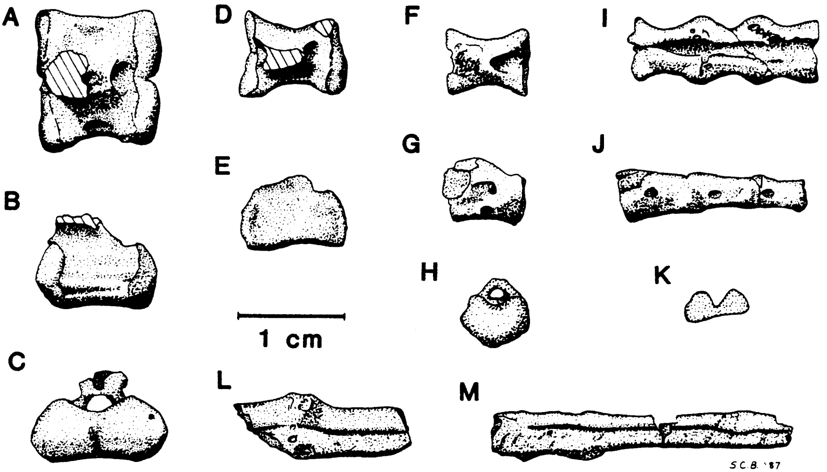

FIGURE 1 - Caudal vertebrae of Pteranodon YPM 2462 in dorsal (A,D,F,I,L,M), left lateral (B,E,G,J), and posterior (C,H,K) views. Second caudal (A-C), fifth caudal (D,E), seventh through tenth caudals (F-K), and distal caudal rod sections (L,M).

Three specimens, YPM 2489, 2546, and AMNH 6158, include series of anterior and middle caudal vertebrae. YPM 2489 includes five vertebrae. The anteriormost vertebra has transverse processes which articulated with the ilia. It is considered the third caudosacral, because in older individuals the centrum, transverse processes, and neural spine fuse to the pelvis. The next vertebra, which is the first without transverse processes, is considered the first true caudal vertebra. The centra of the third caudosacral and first three caudal vertebrae are broad and low, and have unusual duplex articulations. There are shallow vertical grooves down each end of the centra separating the surfaces into two articular facets. This duplex articulation is only slightly developed on the fourth caudal. There is a longitudinal ridge on each side of the centra below the midline. The third caudosacral has small blunt prezygapophyses, but lacks postzygapophyses. None of the caudal vertebrae have zygapophyses. The neural arches and spines are large and tall in the anterior caudals, but they decrease in height and length in the succeeding vertebrae. YPM 2546 includes four articulated caudals from the middle of the tail. The anteriormost caudal of YPM 2546 lacks duplex articulations, and it seems to correspond to the fourth caudal of YPM 2489, but might be more posterior. The centra decrease slightly in size posteriorly. AMNH 6178 is a mounted composite skeleton which includes seven caudal vertebrae. The vertebrae are crushed and have been embedded in plaster. It was not possible to measure the vertebrae directly, but the series was measured from photographs.

YPM 2462 includes uncrushed second and fifth caudals, an articulated series of posterior caudal vertebrae, and two pieces of distal caudal rod. The second caudal (Fig. 1A-C) is low and broad, with an incomplete neural arch. The articular surfaces are strongly convex and divided by a vertical groove into two nearly circular facets. The fifth caudal (Fig. 1D-E) lacks the duplex articulations, is amphiplatyan, and has a small neural arch. At least one vertebra is missing between the fifth caudal and the articulated series of posterior caudals. The anteriormost vertebra of the articulated series (Fig. 1F-H) is similar to the fifth caudal, but the lateral surfaces of the centrum are deeply excavated. It has a neural arch of normal construction, but the fused vertebrae of the articulated series (Fig. 1I-K) do not. The fused vertebrae have small rudiments of the neural arch halves on either side of the neural canal. Posteriorly, the rudiments become progressively smaller and the neural canal forms a deep groove. The two sections of distal caudal rod (Fig. 1L-M) are crushed flat. There are longitudinal grooves on both the dorsal and ventral surfaces, and the pieces appear to consist of two separate rods. A few spots on the distal caudal rod may have been diseased, but the pattern of ankylosis in the posterior vertebrae is symmetrical and does not appear to be pathological.

Reconstruction of the Tail of Pteranodon

The specimens described above provide enough information to reconstruct the tail of Pteranodon. Table 1 includes the measurements of a composite reconstruction scaled to the size of YPM 2489, and Figures 2A-B show the reconstruction of the tail, including the third caudosacral, in dorsal and lateral views. The five anterior vertebrae have broad low centra with duplex articulations and the neural arch and spine decrease in size posteriorly. The next six vertebrae form the transition zone in which the neural arch is completely lost and the centra become deeply grooved by the neural canal. The last section consists of paired rods. The homology of these rods is uncertain. It is possible that the distal caudal rod was cartilaginous and not normally calcified. This might explain why it is rarely preserved. The total length of the tail, excluding the third caudosacral, is estimated to be a minimum of 19 cm and 2.5% of the wingspan in a 7.5 m individual.

Comparisons with other Pterodactyloid Pterosaurs

The many excellently preserved specimens of Pterodactylus from Solnhofen clearly indicate that the tail was long and strong and had simple vertebrae. Based on Wellnhofer (1970) the tail of P. antiquus had 16 vertebrae and was 3.9% of the wingspan, while the tail of P. micronyx had only 12 vertebrae and was 4.2% of the wingspan. The tail of Dsungaripterus (Young; 1964) was opisthocoelous and had large neural arches and transverse processes. The anterior end of the tail did not show any trace of duplex articulations. Nine vertebrae were preserved in two series, and Young (1964) estimated that the tail consisted of 11 to 14 caudal vertebrae, but the posterior end of the tail was not preserved. Based on Young's data the length of the tail was a minimum of 12-15 cm and 3-4% of the wingspan. Despite the fact that Dsungaripterus was much larger than Pterodactylus its tail was of similar relative size as those of Pterodactylus. The tail in Pteranodon differed from both genera in the duplex articulations of the anterior vertebrae, the simplification and ankylosis of the posterior caudal vertebrae, and the presence of distal caudal rods.

The tail of Nyctosaurus is poorly known. FMNH P 25026 has at least four caudals preserved. The first vertebra lies next to the left femur and is similar in shape to the anterior caudal vertebrae of Pteranodon, but it is not clear if it has duplex articulations. Three small caudals lie on the other side of the femur and two more caudals may lie under the femur. A structure which may be a distal caudal rod is preserved near the posterior end of the last caudal. FMNH P 25026

TABLE 1 - Lengths of caudal vertebrae of _Pteranodon_ specimens and composite reconstruction. Numbers in brackets are estimates. All in mm.

VERTEBRA	YPM 2489	YPM 2462	YPM 2546	AMNH 6158	COMPOSITE
CS 1	12.9	-	-	12.7	12.9
C 1	13.7	-	-	13.1	13.7
C 2	12.8	11.4	-	11.1	12.8
C 3	11.9	-	-	11.8	11.9
C 4	10.6	-	10.5	12.2	10.6
C 5	-	9.2	9.4	11.4	9.9
C 6	-	-	8.7	10.6	8.6
C 7	-	6.8	8.3	-	8.5
C 8	-	6.4	-	-	7.2
C 9	-	5.5	-	-	6.2
C 10	-	5.0	-	-	5.6
	-	[10.0]	-	-	[11.2]
	-	16.4	-	-	18.4
	-	[20.0]	-	-	[22.4]
	-	28.7	-	-	32.1
	-	[10.0]	-	-	[11.2]

has preserved tendons which are flat strap-like bundles of filaments, and while the supposed caudal rod may be a tendon, it does not appear to be a bundle of filaments, and unlike the tendons it tapers to a point. The minimum length of the tail including the supposed caudal rod would be 7.5 cm, 3.6% of the estimated 2.1 m wingspan. If the tail of _Nyctosaurus_ was as described above it would have been quite similar to the tail of _Pteranodon_. The major differences are that fewer vertebrae are known in _Nyctosaurus_ than in _Pteranodon_, and the caudal rod of _Nyctosaurus_ would be longer than that of _Pteranodon_. However, the caudal rod of _Pteranodon_ may have been longer than it is reconstructed here.

Functional Significance of the Tail in _Pteranodon_

The structure of the tail was unusual but was not degenerate. The anterior caudals were robust, and although the posterior caudals were simplified, their fusion was a specialization. The duplex articulation of the caudals would have prevented lateral motion, yet allowed dorsoventral flexion. The large size and unusual structure of the anterior caudals might have been an adaptation for the origin of limb muscles such as the caudofemoralis. However, those vertebrae would not provide much area for the muscle origins, and other pterosaurs did not need such adaptations. It is more likely that the anterior caudals formed hinge joints to control the dorsoventral flexion of the tail. Posterior to the hinge joints the tail had only enough flexibility to prevent damage. The reduced lateral motion and flexibility would reduce the mass of muscle necessary to control the tail, because muscles would not be needed to control those motions.

There is no direct evidence in the vertebrae that indicates what function, if any, the tail fulfilled. However, I believe that the tail was embedded in a horizontal membrane that was a continuation of the wing membrane, because that is the only model that can explain the unusual structure of the tail. The tail formed a structure that was comparable in size and strength to the distal phalanx

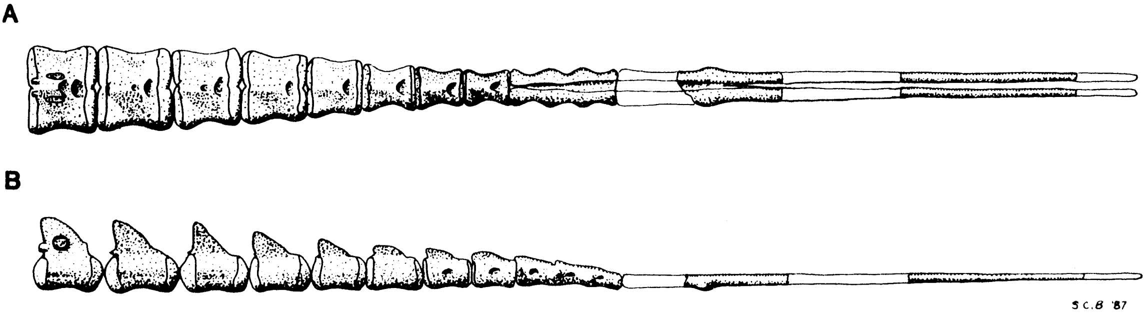

FIGURE 2 · Reconstructions of the tail of Pteranodon in dorsal (A) and left lateral (B) views.

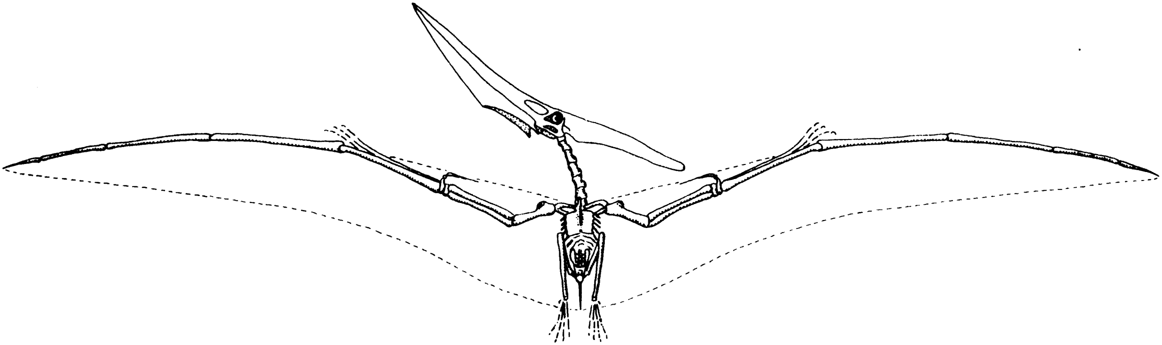

FIGURE 3 · Reconstruction of Pteranodon with wing planform indicated in ventral view.

of the wing finger and thus would be large and strong enough to control the membrane. The vertical hinge joints of the anterior caudals would simplify control of the wing membrane. The posterior margin of the wing membrane was behind the center of gravity, and as the tail moved up and down it would move the membrane and provide pitch control. The short tails of pterodactyloid pterosaurs could not support a rudder structure like that of the long-tailed Rhamphorhynchus, because such a structure would be too close to the center of gravity to be effective. In addition, in Pteranodon the vertical hinge of the tail completely prevents lateral motion and is additional evidence that the tail could not have functioned as a rudder.

Padian (1983, 1985) presented a streamlined model of the pterosaur wing with narrow wings and the hind limbs free of the wing membrane. The model presented above is compatible with Padian's streamlined model. The added strip of wing membrane would not alter the wing area or center of lift significantly from Padian's model, but would provide pitch control. Padian's model with the hind limbs free of the membrane and folded forward is strengthened because the unusual structure of the tail strongly suggests that the tail controlled the posterior edge of the wing membrane, and that the hind limbs were not involved in the wing membrane. The unusual specializations of the tail could not be explained if the wing membrane were stretched by the hind limbs. If the tail were embedded in a uropatagium between the legs, then the legs would control the wing membrane and any movements of the tail would be insignificant. Alternatively, if the tail were free of the wing membrane the specializations would make no sense. Figure 3 is a reconstruction of Pteranodon modified from Eaton (1910, Pl. 30). The tail is longer than the tail Eaton illustrated and is embedded in, and controls the posterior margin of the wing membrane. The legs are completely free of the wing membrane and are folded up toward the center of gravity during flight.

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COMMENT

On "New evidence on the tail of the pterosaur *Pteranodon* (Archosauria: Pterosauria)" by S. C. Bennett

Since this paper was written the description of the tail was incorporated into my dissertation (Bennett, 1991) and my 2001 monograph on *Pteranodon* (Bennett, 2001) and I have come to the conclusion that the interpretation of the distal parts of the tail was incorrect. The interpretation of the tail presented in my dissertation (Bennett, 1991) and subsequently in my 2001 monograph on *Pteranodon* (Bennett, 2001) supercedes the interpretation presented in this paper. Likewise I no longer support the interpretation that the brachiopatagium did not attach to the hindlimb or the interpretation that the hindlimbs were folded up against the body in flight, and my dissertation (Bennett, 1991) and other papers (Bennett, 2000, 2001) supercede the interpretation of the wing and flight posture accepted in this paper.

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