

## Aerodynamic characters of the cranial crest in *Pteranodon*

By

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### Abstract

Perhaps the most iconic of pterosaurs is the Late Cretaceous *Pteranodon*, known for its large wing span of up to 5.6 m or more and a remarkable long bony crest at the back of the head. The function of this crest has been the subject of much controversy, having been interpreted as an aerodynamically beneficial structure, perhaps acting as an airbrake, a forward rudder, or a counterbalance to the beak. In this paper these hypotheses are tested by experimenting on cranial models of both *P. longiceps* and its close relative *P. sternbergi* in a wind tunnel and comparing the results against a crestless control model. The results show that, while a crest assists in lowering the yawing moment of the head and limiting the movement of the centre of pressure, the overall aerodynamic effect is modest. The crest most probably evolved independently of any aerodynamic function, other than to maintain their streamlined profile for reducing drag, and presumably served primarily in either intraspecific sexual displays and/or species recognition.

**Key words:** pterosaurs, aerodynamics, flight, Cretaceous, biomechanics.

### Zusammenfassung

Mit seiner Flügelspanne von bis zu 5,6 m und dem markanten knöchernen Hinterhauptskamm gehört *Pteranodon* aus der Oberkreide zu den bekanntesten und beliebtesten Flugsauriern. Die Funktion des Scheitelkammes war Gegenstand vieler Kontroversen: Er wurde als aerodynamisch nützliche Struktur betrachtet, die möglicherweise als Luftbremse wirkte oder als Frontruder oder auch als Gegengewicht zum Schnabel.

Hier werden diese Hypothesen mit Hilfe von Kopfmodellen von *P. longiceps* und seinem nahen Verwandten *P. sternbergi* in Winkalversuchen überprüft und mit einem kammlosen Kontrollmodell verglichen. Die Ergebnisse zeigen, dass der Kamm dazu beiträgt, das Giermoment zu senken und die Verschiebung des Druckzentrums zu begrenzen, obgleich der generelle aerodynamische Effekt eher gering ist. Die Kämmen entstanden höchst wahrscheinlich außerhalb des aerodynamischen Funktionsregimes außer dass die ein stromlinienförmiges Profil zur Reduktion des Luftwiderstandes zeigen. Die Kämmen waren entweder intraspezifische Sexualmerkmale oder dienten der Arterkennung.

**Schlüsselwörter:** Pterosauria, Aerodynamik, Flug, Kreide, Biomechanik

### 1. Introduction

Extinct organisms offer many challenges to functional interpretation, especially if there is no living animal that can act as a comparative model. The pterodactyloid pterosaur *Pteranodon* is an example of this – a flying reptile from the Late Cretaceous (100–65 million years ago) of North America, whose adult wingspan varied from 3.8–5.6 m depending on its gender, but might also have reached sizes of over 6 m (BENNETT 2001).

*Pteranodon* was named by MARSH (1876) on the basis of an isolated skull from shallow marine limestones of the Niobrara Chalk Formation (Late Cretaceous) of Kansas, USA. This pterosaur, as one of the largest animals ever to fly, has been the subject of several aerodynamic studies (HANKIN & WATSON 1914; BRAMWELL 1971; BRAMWELL & WHITFIELD 1974; BROWER 1983; CHATTERJEE & TEMPLIN 2004). The head crest has often been interpreted as an aerodynamically useful structure that may

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have functioned as: an airbrake to slow speeds while landing (BRAMWELL & WHITFIELD 1974), a forward rudder to provide steering (HEPTONSTALL 1971; STEIN 1975), or an aerodynamic counterbalance to correct cranial movements, reducing the need for heavy neck muscles (EATON 1910; HEPTONSTALL 1971; BRAMWELL & WHITFIELD 1974). Others have postulated non-aerodynamic functions for the head crest including: a site of muscle attachment (EATON 1910), a heat loss vane (KELLNER & CAMPOS 2002; CHATTERJEE & TEMPLIN 2004), or a display structure (SHORT 1914; BENNETT 1992, 2001; CHATTERJEE & TEMPLIN 2004).

While some previous workers (BRAMWELL & WHITFIELD 1974; STEIN 1975; BROWER 1983; WILKINSON et al. 2006) have performed wind tunnel experiments on model pterosaurs, most work so far has focused on wing design and function. These earlier studies are also of limited use owing to inaccurate reconstructions of the animal, wing shape and properties, and a complete lack of taxonomic diversity. *Pteranodon longiceps* has thus commonly been used as a standard for all pterodactyloids. This is not appropriate for several reasons including: it's unusually large size, highly derived anatomical features, large crest variations among different *Pteranodon* species, and because recent finds have revealed pterosaurs with an even more remarkable array of head crests (CAMPOS & KELLNER 1997; KELLNER & CAMPOS 2002; FREY et al. 2003).

Recent studies that highlight the variability in size and shape between species (FREY et al. 2003), sexual dimorphism (BENNETT 1992, 2001) and ontogenetic variability (BENNETT 2003; MARTILL & NAISH 2006) have tended to interpret the primary function of the pterosaur crest as for display, even though experimental tests to determine the aerodynamic characteristics of different types of crested forms have never been carried out. The aim of this paper is to investigate the aerodynamic characteristics of the cranial crest of the well-studied pterosaur *Pteranodon longiceps* and its closest relative *P. sternbergi*. Calculated aerodynamic results can then be compared with theoretical assumptions to determine whether the crest acted in some aerodynamically useful manner, or was primarily a structure for display.

Institutional Abbreviations: FHSM, Fort Hays Sternberg Museum, Fort Hays State University, Hays, Kansas; KUVV, Museum of Natural History, University of Kansas; UALVP, Geology Museum, University of Alberta, Edmonton; YPM, Yale Peabody Museum.

## 2. Methodology

### 2.1 Model construction

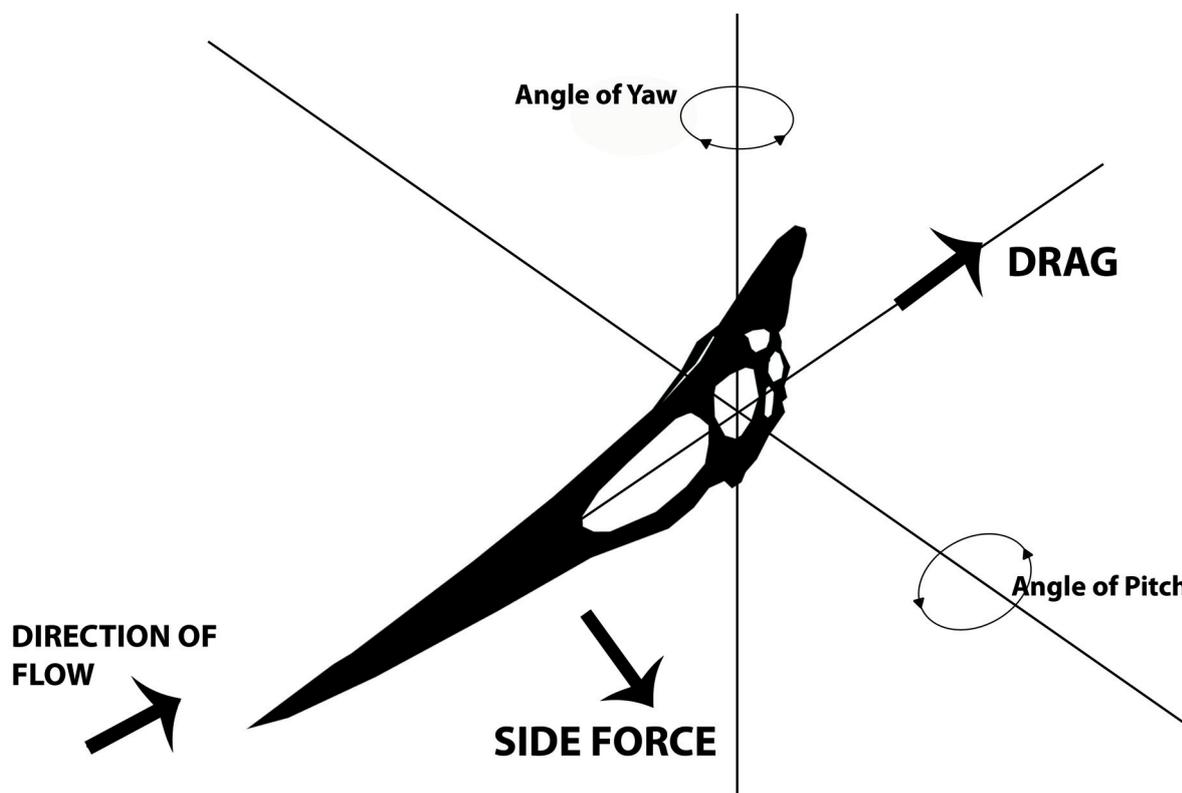
While *Pteranodon* is one of the best-known pterosaurs, represented by hundreds of specimens, it is difficult to use these as a basis for accurate three-dimensional models because the bones are usually fragmentary and crushed (BENNETT 2001). Here the composite cranial reconstructions of *Pteranodon* by BENNETT (2001), based on specimens of *P. longiceps* (KUVV 976, 2212; YPM 1177, YPM 2473) and *P. sternbergi* (FHSM VP 339; UALVP 24238), were used to generate two-dimensional templates in both dorsal and lateral profiles. These two templates were then joined together to produce a three-dimensional structure

that, when bulked up with modelling clay, resulted in a three-dimensional model of the head. Additional bulking due to the presence of soft tissue was very limited as no heavy neck muscles could be attached to the free head and much of the rest of the skull formed the beak. For use in wind tunnel experiments, the sculpted models were then cast in polyurethane, and the crest was cut from a thin aluminium sheet (3 mm thick based on data from BRAMWELL & WHITFIELD 1974) so that it would remain rigid under load. Three scale models were built: large, crested versions of *P. longiceps* and *P. sternbergi*, and a crestless control. By using models with almost identical head shapes (excluding the crests), all aerodynamic differences can therefore be attributed to the shape and presence or absence of a cranial crest. The control model was based on BENNETT's (2001) composite reconstruction, but was scaled to around half life size because the wind tunnel was not large enough for a full-sized model (around 727 mm in this case). While the skulls of old adult males greatly exceed the size of this composite reconstruction (~1138 mm for the head of a presumed male *P. longiceps*, excluding a crest, and 1090 mm for *P. sternbergi*), the models were subject to the same requirements of space and were scaled down appropriately. Thus for large adult animals the model of *P. sternbergi* can be considered to be one third life size while the *P. longiceps* model is between half and one third life size.

As the object of these experiments was to measure the aerodynamic forces produced by the head crest configurations, it was only necessary that the models had external forms that were broadly representative of the real animals. Other characteristics such as mass and mass distribution did not have to be replicated as the model was not free flying. It was fixed to a central strut and dynamic stability was not a study variable. It was also unnecessary to attempt to reproduce the fine detail of the skin over the heads and crests as the lift and drag characteristics are insensitive to the precise form and patterns of roughness over the range of conditions of interest (HOERNER 1965). Similarly, the section shape of a thin aerofoil (the crest in these experiments) has very little effect on the profile drag at low Reynolds numbers (HOERNER 1965). However, the maximum lift coefficient achieved before stall is somewhat sensitive to the fine details of the section shape and also the Reynolds number. In our experiments these restrictions did not affect the conclusions because our main objective was to investigate the sub-stall performance characteristics.

### 2.2 Wind tunnel testing

The models were mounted in a low-speed wind tunnel in the Handley Page Wind Tunnel Laboratory at City University, London, on custom-made brackets positioned on the occipital condyle. The brackets allowed the models to be fixed in a range of 'beak down' (pitch) orientations (Fig. 1) as well as a range of yaw angles (to represent the head being turned to the side). The wind tunnel force-measuring balance and electronic data-acquisition system recorded the three principal forces produced by the models under aerodynamic loading: side force (laterally acting forces), yawing moment (the moment of the side force about the vertical axis), and drag (the force acting backwards). The balance was calibrated so as to cancel out the tare drag of the attachment strut and bracket as well as the weight of the models.



**Figure 1:** Schematic diagram of a *Pteranodon* cranium and movement about the major axes. The pitch and yaw were constantly altered to test the varying effect of model orientation on force generation while the third axis, roll, was not used in this study. The thick arrows here show the major forces acting on the model.

Experiments were run at a speed of 20 m/s, approximately twice the flight speeds calculated in previous studies for *Pteranodon*: 7 m/s (HEPTONSTALL 1971), 8 m/s (BRAMWELL & WHITFIELD 1974), 9.51 m/s (BROWER 1983), 15 m/s (STEIN 1975), or 10–15 m/s (CHATTERJEE & TEMPLIN 2004). The doubling of the tunnel velocity in this way was required to achieve dynamic similarity of the half-sized models. At this speed, the Reynolds number was 400,000 for the complete model and approximately 130,000 for the crests, both of which were expected to be below the transition point from a laminar to a turbulent flow regime. Preliminary tests at a range of air speeds confirmed the insensitivity of the non-dimensional aerodynamic characteristics to flow velocity, so a single speed could be adopted for the tests. The results were reduced to non-dimensional form, from which actual forces could then be predicted for any likely flight speed.

An examination of the osseous labyrinth from an endocast of Anhanguera by WITMER et al. (2003) indicated that pterodactyloid pterosaurs, such as *Pteranodon*, would probably have flown with a somewhat inclined cranium. As a result, side force and yawing moments were calculated for each model at head inclinations (itches) of 0°, 20° and 40° along with yaw angles ranging from -10° to 40°. While it would have been desirable to test our models at up to 90° yaw and greater degrees of pitch, the model attachment, position of the strain gauges and other aspects of the working section of the tunnel prevented this from being a possibility. At 40° pitch the range of yaw was further restricted because of interference from the

central mounting strut.

The resulting forces were then converted into their dimensionless coefficients for comparison and analysis, as follows:

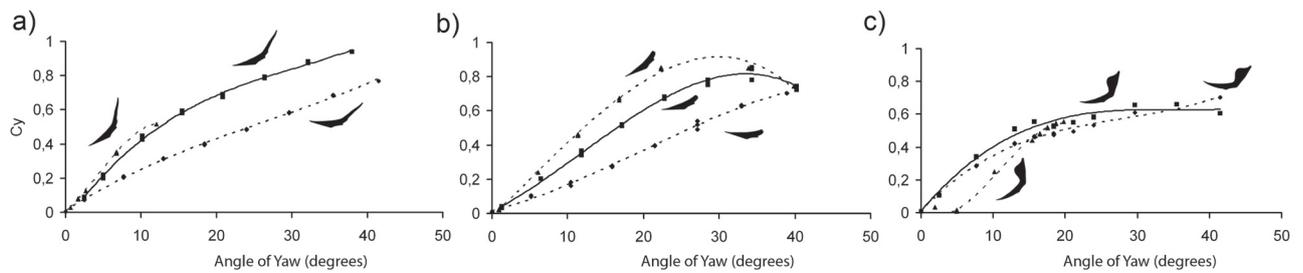
- 1) Side force coefficient ( $C_Y$ ) =  $Y / q * S$ , and
- 2) Yawing moment coefficient ( $C_N$ ) =  $N / q * S * c$ ,

Where:  $Y$  = side force,  $q$  = dynamic pressure,  $S$  = Surface area (m<sup>2</sup>),  $N$  = moment, and  $c$  = reference length (m).

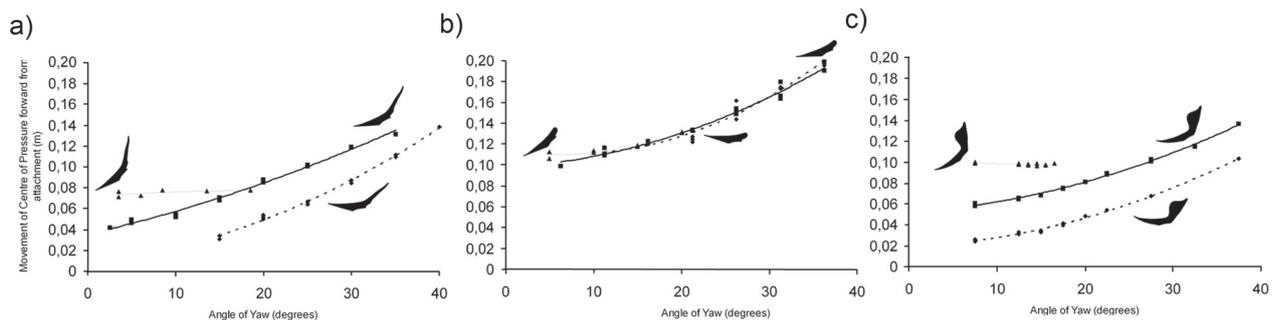
Owing to the unusual shape of the crest, the total head length (tip of beak to most caudal part of the cranium) was used as the model's reference length rather than the more traditional chord in the case of a wing. The yawing moment data were used to calculate the point of action of the side force (the centre of pressure), from which the turning couple applied to the heads was calculated.

### 3. Results

Results of the wind tunnel tests for each model show how variations in model pitch and yaw angle affect the side force up to a yaw angle of 40°. It is important to note that the coefficients presented are dimensionless and represent the aerodynamic characteristics of the model shape rather than any potential differences in size.



**Figure 2:** Wind tunnel results showing the lateral force ( $C_y$ ) generation characteristics of the three models over angle of yaw. The models *P. longiceps* (a), the crestless form (b), and *P. sternbergi* (c) were mounted at varying angles of cranial pitch,  $0^\circ$ ,  $20^\circ$  and  $40^\circ$ , indicated by the icons on the figure.



**Figure 3:** Wind tunnel results showing the displacement of the aerodynamic centre of pressure from the attachment bracket of the three models: *P. longiceps* (a), the crestless model (b), and *P. sternbergi* (c). Varying angles of cranial pitch,  $0^\circ$ ,  $20^\circ$  and  $40^\circ$  are indicated by the icons on the figure.

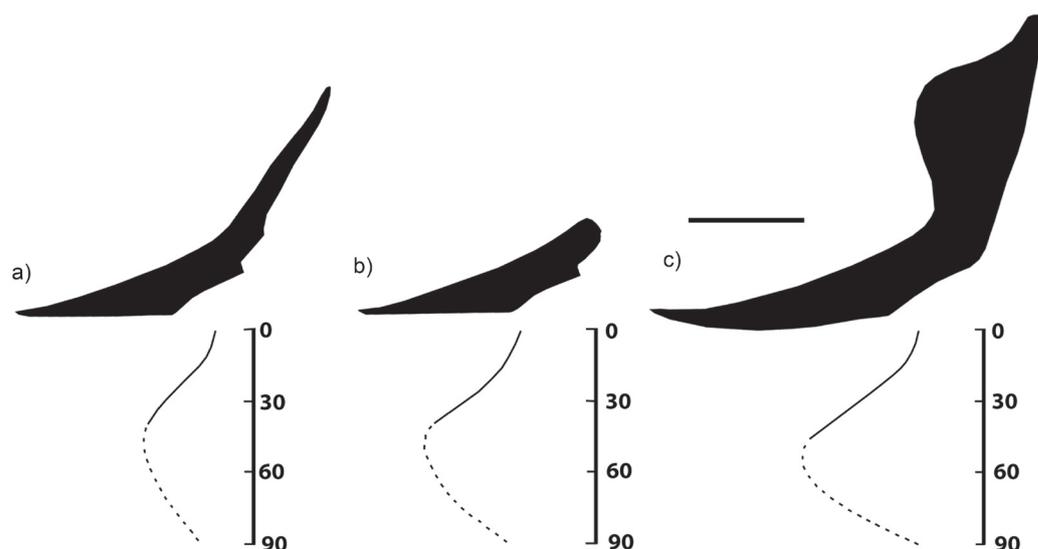
As was expected, there is a general trend of increasing side force with yaw angle (Fig. 2). For *P. longiceps*, (Fig. 2a) with the head horizontal, the side force coefficients increase almost linearly with angles of yaw up to the maximum value tested ( $40^\circ$ ). When the head is pitched downwards, the rate of increase of side force with yaw angle (the lift-curve slope) is initially greater, but becomes the same as for the horizontal orientation at angles of yaw greater than  $15^\circ$ . This result probably arises because the crest acts as a high aspect ratio aerofoil, which initially increases the lift-slope curve, but then experiences stall at a yaw angle of  $10^\circ$  to  $15^\circ$ . At the same time, the low aspect-ratio head, which is of greater area than the crest, can be expected to have a lower lift slope and a far less marked stall point. The combination of these two characteristics is the most likely explanation of the knee in the curve.

The crestless model (Fig. 2b) displays a similar lift slope to the crested *P. longiceps* when both are horizontal. When the head is pitched down, the lift slope increases and at  $40^\circ$  it is almost the same as for the head with a crest at the same pitch orientation. In this case, it appears that the head itself is becoming an increasingly efficient aerofoil as it is pitched down, most probably because of the increase in effective aspect ratio. With this model it was possible to test the  $40^\circ$  pitch case at yaw angles up to  $40^\circ$ , and a clear stall occurred. The angles

of stall reduce with increasing pitch angle, which is commensurate with the changing aspect ratio. However, because of the lower surface area of the crestless model, the actual forces produced will be less.

The *P. sternbergi* model (Fig. 2c) showed less variation of lift slope with pitch angle than the *P. longiceps* model. Apart from a localised reflex in the  $40^\circ$  pitch case around the zero angle of yaw, all three curves more or less collapsed into one another. They all had lift curves with a marked knee inflection at  $15^\circ$  to  $20^\circ$  angle of yaw, with maximum lift being reached by  $40^\circ$ . This is probably because the crest is a relatively large proportion of the total area of the profile of the head and crest, so tends to dominate the aerodynamic characteristics. As the head was pitched down, the effective aspect ratio did not change greatly, thus limiting the change in lift-curve slope. The marked knee inflection in the curve at an angle of yaw of approximately  $15^\circ$  most probably reflects the point at which the flow over the crest becomes stalled, while the flow around the low-aspect-ratio head remains attached and allows the lift to continue to rise with yaw angle, albeit much less rapidly.

The centres of pressure in all three models are anterior to the point of attachment (Figs 3 & 4). In the case of *P. longiceps* the centre of pressure at  $0^\circ$  and  $20^\circ$  pitch angle moves anteriorly, almost linearly with increasing yaw angle, up to the limit of the



**Figure 4:** The three models: *P. longiceps* (a), the crestless model (b), and *P. sternbergi* (c) are drawn in proportion to full size along with the displacement of the aerodynamic centre of pressure off the occipital condyle for varying angles of yaw. The solid lines represent experimental data while the broken line is the predicted movement of the centre of pressure to the centre of the projected area of the head/crest at 90°. Scale bar 300 mm.

tests at 40°. The position is more anterior at 20° pitch, which may be because the model's rostrum becomes a more effective aerofoil as pitch angle increases. At 40° pitch, movement of the centre of pressure has become mostly insensitive to yaw (Fig. 3a). When the crest is removed, the results collapse onto one another and the position of the centre of pressure becomes the same regardless of the cranial pitch (Fig. 3b).

The model of *P. sternbergi* exhibits similar results to *P. longiceps*. The results for 0° and 20° pitch show almost linear increase with yaw angle, the curve for the higher pitch angle being the more anterior of the two. At 40° pitch, the centre of pressure is again constant with yaw angle (Fig. 3c).

The wind tunnel results were recorded for yaw angles up to 40°, which for the 20° and 40° pitched models was approaching the stall point, and thus the maximum side force. BRAMWELL & WHITFIELD (1974) measured similar results for *P. longiceps*, but were able to make their tests over a wider range of yaw angles. They found that stall occurred at a yaw angle of around 50° for a model in a horizontal (zero pitch) orientation.

If the model was turned to a yaw angle of 90°, the flow became fully separated and the centre of pressure coincident with the centre of area. By interpolation, this allows a good approximation of the position of the centre of pressures position for the missing angles of yaw, between 40° and 90° (Fig. 4).

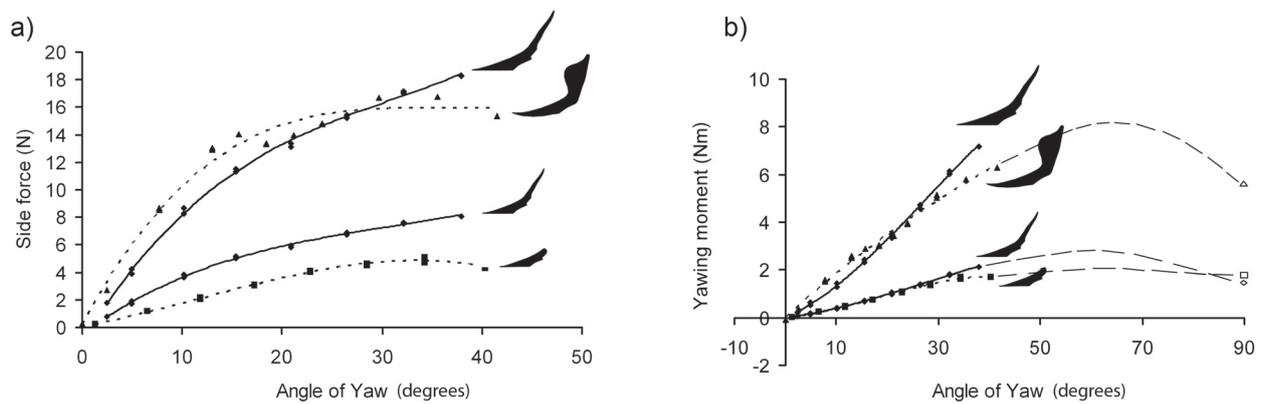
The results described above show the location of the centre of pressure. However, the yawing (or twisting) moment on the attachment of the head to the neck is the product of the distance of the centre of pressure from the attachment and the actual side force being produced. Typical values of side force and yawing moment were calculated and are shown in Figure 5. As previously stated, the independence of the coefficients

from velocity allows aerodynamic forces, which are a function of the square of the flight speed, to be calculated for any desired velocity. Here, a flying speed of 14 m/s was used to facilitate direct comparison with BRAMWELL & WHITFIELD's results. The maximum value for *P. longiceps* found here was 2.5 Nm as compared to a value of 9.0 Nm reported by BRAMWELL & WHITFIELD (1974), who assumed a relatively larger head size. If the *P. longiceps* results were 'scaled up' to the size proposed by BRAMWELL & WHITFIELD (1974) a moment of 15.9 Nm is predicted – a clear disagreement between the two studies. This may be in part due to differences in the shape of the models, position of the model attachment or tunnel calibration however, in the absence of the original test data, it is not possible to comment further on this difference.

The locations of the centres of pressure in the models are shown in Figure 4. In each case the yaw scale is positioned to be in line with the neck attachment. The solid parts of the curves represent the locations calculated from the present tests. As described above, the location at a yaw angle of 90° is coincident with the centre of area and thus it is possible to construct the likely shape of the curve between yaw angles of 40° and 90°.

## 4. Discussion

Having tested our three models, we may now consider the validity of the generally assumed aerodynamic functions of the cranial crest. The depression of the head outlined by WITMER et al. (2003) tends to increase the lift-curve slope, which results in a rapid increase in lateral force with yaw angle. This force



**Figure 5:** Calculated full-scale forces produced by the three models. (a) Side force over the range of tested yaw angles; and (b) yawing moment derived from the wind tunnel tests and calculation of the result at 90° yaw. The larger *P. longiceps* represents the results produced assuming the model was one third its life size. A flight speed of 14m/s was selected for ease of comparison with BRAMWELL & WHITFIELD'S (1974) results.

is, however, limited by stall, which occurs at lower yaw angles when the head is depressed, although a more abrupt stall may itself be a potential source of aerodynamic instabilities. Depression of the head also has the effect of limiting the anterior movement of the centre of pressure, which in turn limits the yawing moment acting on the attachment of the head. Thus the least destabilizing position for the head of *Pteranodon*, by which early or abrupt stall (and the associated sudden change in applied forces) can be avoided, is horizontal, while the yawing moment can be reduced by depressing the head, at the possible expense of flight stability.

#### 4.1 Airbrake

The idea that the crest acted as an airbrake, proposed by BRAMWELL & WHITFIELD (1974), relied on the generation of a large drag force as a result of turning the head through 90° in flight. While our models lacked the range of movement tested by BRAMWELL & WHITFIELD (1974), at a horizontal pitch and a maximum angle of attack of 44°, *P. longiceps* and *P. steinbergi* respectively produced around 25% and 50% more drag than the crestless model because of their crests. As the cranium was pitched down to 40°, however, the drag characteristics of the three models became much more similar. This effect is caused as the model of *P. steinbergi* generates little to no additional lift as the head is pitched downwards. In contrast, the other two models actually become better airfoils as the head is depressed and thus generate not only more lift but also additional lift-induced drag which causes the various drag profiles to converge.

Physiological arguments, as much as aerodynamic evidence, indicate that turning the head to act as an airbrake would have been a dangerous and inefficient method of slowing the animal. Turning the head fully broadside to the airflow would result in the binocular vision being diverted from the animal's flight path, a risky manoeuvre when landing. Deploying the head as an airbrake would also have required a large turn of both the head and neck and placed additional stress on to the neck muscles. It is likely that the wings would have provided a more

effective airbrake both during flight and landing in addition to the, as yet untested, braking performance of the uropatagium and webbed feet. As WILKINSON et al. (2006) have shown, the highly cambered wing membrane is capable of producing a combination of high lift and drag, a far more effective and controllable means of slowing flight than turning the head 90° to one side. The crest is thus poorly designed for an airbrake and indeed a crestless model is itself capable of producing similar values of drag compared with a crested model, provided the head could be pitched downwards during flight. The study of WITMER et al. (2003) suggests that this was the case and thus a crest is not required and, at larger values of pitch, does not enhance the production of drag.

#### 4.2 Forward Rudder

STEIN'S (1975) argument that the crest acted as a forward rudder for steering was based on the belief that a membrane joined the crest to the neck. The idea is weakened by the fact that no fossil evidence for such a membrane has been found in any pterosaur, and most significantly no evidence has been found even in specimens that preserve a gular pouch and other soft tissue structures around the head including soft-tissue crests. While a lack of evidence does not disprove the existence of such a membrane, it remains unlikely for several reasons: the dorsally, rather than caudally, directed crest of *P. steinbergi* is a poor shape to support such a membrane, neck mobility would have been hampered to an unknown degree, and large wings along with additional flight control surfaces (e.g. propatagium [WILKINSON et al. 2006] or foot rudders [FREY et al. 2003]) would almost certainly be better suited for steering.

A related idea was that the large cranium alone might have acted as a flight-control mechanism (HEPTONSTALL 1971) by generating the forces required to turn the animal. A crest would certainly have assisted in such a role, as the crested *P. longiceps* produced around twice as much side force as its crestless counterpart. It remains difficult, however, to understand why such a design would have been more efficient than the use of the animal's large wings under the control of its complex

neuroanatomy (WITMER et al. 2003). The total lift produced by the wings must equal the weight of the animal. BRAMWELL & WHITFIELD (1974) estimated a mass of 16.6 kg, so using the scaling factor deduced from the difference in head size between their reconstruction and that used for the present work, the mass of *P. longiceps* was 4.3 kg. Thus, if the animal banked at 45°, it would have produced a turning force of 30 N, more than three times the maximum generated by the head and crest at an angle of yaw of 40°, and six times that generated at 15° yaw, the probable upper limit before the onset of a potentially destabilizing stall of the crest. Thus by comparison to the wing the crest is a substantially less useful structure for generating lift. It is relevant that extant soaring bats, which do not have crests and rely on wings alone for turning, achieve tight turning circles when circling in thermal lift (NORBERG et al. 2000), as do many species of birds in same conditions.

### 4.3 Counterbalance

The final suggestion was that the crest functioned as an aerodynamic counterbalance to reduce the mass of the muscles required to resist the yawing moments of the head, by shifting the centre of pressure caudally from the attachment (EATON 1910; HEPTONSTALL 1971; BRAMWELL & WHITFIELD 1974). This reduction in the mass of the neck muscles would have had evolutionary significance through reducing the weight of the animal.

Wind tunnel experiments on *P. longiceps* by BRAMWELL & WHITFIELD (1974) showed that the crest acted as a complete counter balance only at angles of yaw greater than 70°. While this may be aerodynamically correct, it is difficult to accept that this characteristic was actually exploited by the animal. Not only is it highly unlikely that an animal in flight would ever have turned its head to such a degree, but according to BRAMWELL & WHITFIELD (1974) the margin between the aerodynamic yawing moment of the head and the restoring moment available from the neck muscles at 45–50° angle was extremely small. In practice this gives the very real possibility that the slightest increase in moment, caused for example by fluctuating air speeds (or indeed errors in their estimates), may have broken the animal's neck. This extremely low margin of safety appears implausible for a large flying animal.

While our experiments lacked this range of movement, they confirm that below a 45° turn of the head, neither crest acted as a full counterbalance, and the calculation of the result at 90° yaw indicates that even at this angle the crested forms were not fully counterbalanced. When compared to the crestless form, the *P. longiceps* model only produced a 20% higher yawing moment despite having almost 50% more total area. Thus the addition of the crest did not result in substantial increases in the yawing moment, despite increased aerodynamic forces due to its greater area.

Such an effect would have been significant since controlling lateral movements of the head was clearly important to pterosaurs, as suggested by anatomical observations. The cervical vertebrae of *Pteranodon* show a combination of condylar-cotylar, zygapophyseal, and exapophyseal articulations designed to resist twisting motions of the neck (BENNETT 2001). The location of the centre of pressure (Figs 3 & 4) in all results however suggests that the crest's primary function was not as

a full aerodynamic counterbalance.

If the crest is regarded as a sexually dimorphic feature (BENNETT 1992), the apparent absence of a major aerodynamic function might then suggest that males did not suffer a major adaptive penalty by carrying a large crest compared with the smaller-crested females. From the point of view of a sexually selected characteristic it is key that the feature impose some kind of penalty on the animal carrying it (DARWIN 1871). Although the aerodynamic effects of the crest may not have hindered the animal, a penalty, in the form of the energy devoted to both developing and carrying such a heavy structure on such a lightweight animal, must be considered. Thus the neutral aerodynamic results obtained from this study cannot rule out a sexually selective origin or function of the cranial crests in *Pteranodon*.

### 5. Conclusion

Many studies of function in animals contrast adaptations for physical activities and those for display (FARLOW & DODSON 1975; HOEFS 2000). In the case of the head crest of *Pteranodon*, and perhaps of other pterosaurs, the crest is aerodynamically streamlined, so that it does not impede flight by creating excessive drag. However our wind tunnel experiments suggest that previously proposed specific aerodynamic functions (airbrake, forward rudder, and counterbalance) are unlikely to have applied to any great extent. It is more likely that the wings could have performed any steering and balancing functions adequately, particularly with the aid of the animal's complex neuroanatomy (WITMER et al. 2003) and complex membrane (FREY et al. 2003), without the need for additional mechanical assistance from the head and its crest. A behaviour demonstrated by extant soaring bats. Our experiments suggest, in fact, that were *Pteranodon* to try to use its head to assist in steering, braking, or manoeuvring, it would have created aerodynamic instability and imposed substantial twisting loads on the neck attachment.

Sexually dimorphic traits in pterosaurs are apparently evident in the pelvic and other postcranial characters of a number of species including *Rhamphorhynchus* (WELLNHOFER 1975), *Pterodactylus* (MATEER 1976), *Quetzalcoatlus*, *Dsungaripterus* and *Anhanguera* (BENNETT 1992). The work of BENNETT (2001, 2003) has demonstrated that sexual selection and ontogenetic age are the most likely influences in determining the size and shape of the crest. In apparent male specimens of *Pteranodon* the head crest is greatly enlarged against the females, around 50% larger than in putative females (BENNETT 1992). Species could also grow through several variable crest forms throughout their development (MARTILL & NAISH 2006) and rapidly sprout massive structures upon reaching maturity (BENNETT 2003).

Palaeobiologists, and perhaps most evolutionary biologists, might feel that interpreting a complex structure as 'merely' for display is a weak line of argument. Surely something as evolutionarily costly and astounding as the head crest of *Pteranodon* must have offered some hard, biomechanical advantage? And yet, similar recent studies of the dorsal plates of *Stegosaurus* and other extinct reptiles (MAIN et al. 2005) have shown that these elaborate structures perhaps served

more for communication than for thermoregulation. A key point in understanding those animals, as here, is that many (or most) congeners seemed to survive perfectly well without the elaborate structure, be it a head crest or a dorsal plate. Animals today often sport astonishing structures for display purposes (e.g. peacock, lyrebird, red deer): providing the structure does not represent an overwhelming encumbrance, the riotous functioning of sexual selection may far outweigh the common sense of natural selection.

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## 6. References

- BENNETT, S. C. (1992): Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. – *Journal of Vertebrate Paleontology*, **12**: 422–434.
- BENNETT, S. C. (2001): The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part 1. Part I. General description of osteology. – *Palaeontographica*, Abt. A, **260**: 1–112.
- BENNETT, S. C. (2003): New crested specimens of the Late Cretaceous pterosaur *Nyctosaurus*. – *Paläontologische Zeitschrift*, **77**: 61–75.
- BRAMWELL, C. D. (1971): Aerodynamics of *Pteranodon*. – *Biological Journal of the Linnean Society* **3**: 313–328.
- BRAMWELL, C. D. & WHITFIELD, G. R. (1974): Biomechanics of *Pteranodon*. – *Philosophical Transactions of the Royal Society London B*, **267**: 503–581.
- BROWER, J. C. (1983): The aerodynamics of *Pteranodon* and *Nyctosaurus*, two large pterosaurs from the Upper Cretaceous of Kansas. – *Journal of Vertebrate Paleontology*, **3**: 84–124.
- CAMPOS, D. A. & KELLNER, A. W. A. (1997): Short note on the first occurrence of Tapejaridae in the Crato Member, (Aptian), Santana Formation, Araripe Basin, Northeastern Brazil. – *Anais da Academia Brasileira de Ciências* **69**: 83–87.
- CHATTERJEE, S. & TEMPLIN, R. J. (2004): Posture, locomotion, and paleoecology of pterosaurs. – *Geological Society of America, Special Papers*, **376**: 1–64.
- DARWIN, C. (1871): *The Descent of Man and Selection in Relation to Sex*; New York (Appleton), 864 pp.
- EATON, G. F. (1910): Osteology of *Pteranodon*. – *Memoirs of the Connecticut Academy of Arts and Science*, **2**: 1–38.
- FARLOW, J. O. & DODSON, P. (1975): The behavioural significance of frill and horn morphology in ceratopsians dinosaurs. – *Evolution*, **29**: 353–361.
- FREY, E., TISCHLINGER, H., BUCHY, M.-C. & MARTILL, C. M. (2003): New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. – In: E. BUFFETAUT & J.-M. MAZIN (Eds), *Evolution and Palaeobiology of Pterosaurs*. – Geological Society, London, Special Publications **217**: 233–282.
- HANKIN, E. H. & WATSON, D. M. S. (1914): On the flight of pterodactyls. – *Aeronautical Journal*, **18**: 324–335.
- HEPTONSTALL, W. B. (1971): An analysis of the flight of the Cretaceous pterodactyl *Pteranodon ingens* (Marsh). – *Scottish Journal of Geology*, **7**: 61–78.
- HOEFS, M. (2000): The thermoregulatory potential of *Ovis* horn cores. – *Canadian Journal of Zoology* **78**: 1419–1426.
- HOERNER, S. F. (1965): Fluid-dynamic drag. *Hoerner Fluid Dynamics*.
- KELLNER, A. W. A. & CAMPOS, D. A. (2002): The function of the cranial crest and jaws of a unique pterosaur from the early Cretaceous of Brazil. – *Science* **297**: 389–392.
- MAIN, R. P., RICQLÉS, A. DE, HORNER, J. R. & PADIAN, K. (2005): The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. – *Paleobiology* **31**: 291–314.
- MARSH, O. C. (1876): Notice of a new sub-order of Pterosauria. – *American Journal of Science*, **11**: 507–509.
- MATEER, N. J. (1976): A study of *Pteranodon*. – *Bulletin of Geological Institutions of the University of Uppsala*, N.S., **6**: 23–33.
- MARTILL, D. M. & NAISH, D. (2006): Cranial crest development in the azhdarchoid pterosaur *Taupuxuara*, with a review of the genus and tapejarid monophyly. – *Palaeontology*, **49**: 925–41.
- NORBERG, U. M. L., BROOKE, A. P. & TREWHELLA, W. J. (2000): Soaring and non-soaring bats of the Family Pteropodidae (flying foxes, *Pteropus* spp.): Wing morphology and flight performance. *The Journal of Experimental Biology*, **203**: 651–664.
- STEIN, R. S. (1975): Dynamic analysis of *Pteranodon ingens*: a reptilian adaptation to flight. – *Journal of Paleontology*, **49**: 534–548.
- WELLNHOFER, P. (1975): Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands. – *Palaeontographica*, Abt. A, **148**: 1–33.
- WILKINSON, M. T., UNWIN, D. M. & ELLINGTON, C. P. (2006): High lift function of the pteroid bone and forewing of pterosaurs. – *Philosophical Transactions of the Royal Society London B*, **273**: 119–126.
- WITMER, L. M., CHATTERJEE, S., FRANZOSA, J. & ROWE, T. (2003): Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. – *Nature*, **425**: 950–953.