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## Commentary

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# Sailing the skies: the improbable aeronautical success of the pterosaurs

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### Summary

**Pterosaur wings bore a striking resemblance to sails, having a bony spar at the leading edge, formed by the forelimb and one enormously elongated digit, and an elastic wing membrane. Such simple wings would be expected to have performed badly due to excessive deformation, membrane flutter and poor control characteristics. Here I discuss how certain anatomical features, specifically a forewing membrane in the inner part of the wing and a system of fibres embedded in the distal part, may have countered these shortcomings. The forewing, supported by the unique pteroid bone, would**

**have reduced the wings' geometric twist, and has been shown in wind tunnel tests to improve membrane stability at low angles of attack and dramatically increase the maximum lift coefficient at high angles of attack. The function of the fibres is poorly understood, but it is suggested that they improved membrane stability and optimised twist nearer the wingtips.**

Key words: actinofibrils, aerodynamics, aeroelasticity, propatagium, pteroid, pterosaur flight, sails, wing membrane.

### Introduction

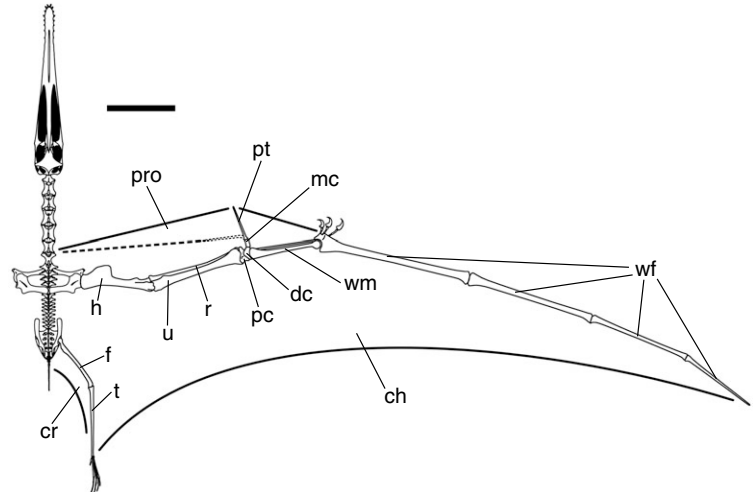
The remarkable nature of the extinct pterosaurs – flying reptiles that lived between 220 and 65 million years ago – was instantly recognised when they were first discovered in the late eighteenth century (Collini, 1784). The great comparative anatomist and father of vertebrate palaeontology Georges Cuvier, the man who correctly identified the first documented specimen, affectionately wrote that it resembled more “*le produit d'une imagination malade plutôt que des forces ordinaires de la nature*” (the product of a sick imagination rather than the ordinary forces of nature) (Cuvier, 1824). Pterosaurs (formally the Pterosauria) are conveniently divided into two groups: a paraphyletic assemblage of basal forms that spanned the Late Triassic and Jurassic periods called the ‘Rhamphorhynchoidea’, characterised by their long, stiff tails (with the exception of the short-tailed anurognathids), and a monophyletic group called the Pterodactyloidea that arose some time in the Jurassic and continued until the end of the Cretaceous period (Wellnhofer, 1991a). These all had short tails, and generally had longer skulls and necks than the ‘rhamphorhynchoids’. We currently recognise about 100 species (Unwin, 2003), many of these being putative piscivorous forms (e.g. the toothed ‘rhamphorhynchoid’ *Rhamphorhynchus* and toothless pterodactyloid *Pteranodon*), but also including some apparently adapted for insect feeding (e.g. *Anurognathus*), filter-feeding (e.g. the pterodactyloid *Pterodaustro*), and for crushing the hard shells of molluscs

and/or crustaceans (e.g. the pterodactyloid *Dsungaripterus*) (Wellnhofer, 1991a).

With regard to terrestrial locomotion, there is a consensus that the smaller pterosaurs were habitually quadrupedal, thanks to a large number of trackways consisting of both hand- and footprints that are unquestionably pterosaurian in origin on account of certain diagnostic characteristics: e.g. in many cases the left and right handprints are more widely spaced than the footprints (Mazin et al., 2003). The mode of terrestrial locomotion of the larger pterodactyloids is still debated: it has been argued that these could not have used quadrupedal locomotion because of the great disparity in length between the fore- and hindlimbs, and it has been suggested instead that these forms adopted an erect, upright, bipedal posture (Bennett, 1990; Bennett, 2001). This stance would have circumvented problems of front-heaviness that would have arisen if the vertebral column were horizontal or near-horizontal due to the (usually) large skull and long neck. It would, however, have rendered these pterosaurs top-heavy with only marginal postural stability due to the relatively small legs, which would have defined a very small polygon of support. Additionally, quadrupedal trackways made by large pterosaurs have been found (Hwang et al., 2002), whereas there are no known bipedal pterosaur trackways.

The chief skeletal adaptation for flight in the pterosaurs was the greatly elongated fourth finger of each hand which, together with the proximal arm bones, constituted a spar that supported

Fig. 1. Skeletal reconstruction of the Cretaceous pterosaur *Anhanguera santanae* in dorsal view, showing the elongated wing-finger (wf) supporting the cheiropatagium (ch), the unique pteroid bone (pt) supporting the propatagium (pro) and the cruropatagium (cr) medial to the leg. Two possible reconstructions of the pteroid are shown, with corresponding outlines of the propatagium: a forward-pointing orientation (solid line), and a medial orientation (broken line). Scale bar, 200 mm. Additional abbreviations: dc, distal carpal; f, femur; h, humerus; mc, medial carpal; pc, proximal carpal; r, radius; t, tibiotarsus; u, ulna; wf, wing-finger; wm, wing-finger metacarpal.



a sail-like wing membrane or cheiropatagium (Fig. 1). This membrane is superbly preserved in several specimens (Padian and Rayner, 1993), and a number of recent finds indicate that its trailing edge ran from the wingtip to the distal end of the lower leg, probably in all pterosaurs (Unwin and Bakhurina, 1994; Lu, 2002; Frey et al., 2003). There are no other rigid or semi-rigid support structures in the cheiropatagium, in marked contrast to bird and bat wings, with their keratinous feather shafts and additional elongated digits, respectively. Nevertheless, despite the superficial simplicity of their wings, pterosaurs successfully exploited the aerial environment for 150 million years, and the pterodactyloids became, during the Cretaceous period, the largest flying animals that have ever lived. *Quetzalcoatlus northropi*, one of the last of its kind, had a wingspan estimated at about 12 m (Lawson, 1975; Wellnhofer, 1991a). Incidentally, it is now almost universally accepted that, while these later, giant forms were secondarily adapted for soaring (Hankin and Watson, 1914; Bramwell and Whitfield, 1974; Brower, 1983), the 'rhamphorhynchoids' and smaller pterodactyloids were fully capable flapping flyers (Padian, 1983; Padian and Rayner, 1993).

Without rigid supports, it is likely that the high aspect ratio cheiropatagium was subject to significant deformation in flight, particularly flapping flight. The problems that this may cause were made starkly apparent in a wind tunnel study of a life-size model of a wing of the Late Jurassic pterosaur *Pterodactylus*, with a wing semi-span of 0.27 m (Sugimoto, 1998). The model consisted of a metal spar and a latex rubber membrane with an unloaded tension of zero. As a fixed wing, the model performed very badly, fluttering severely at relative air velocities above  $3 \text{ m s}^{-1}$ , and achieving maximum lift:drag ratios of only 1.6–1.7. These compare unfavourably with measured lift:drag ratios of birds: for instance, the highest reported value for bird wings is 36.3, calculated from wind tunnel data of a live laggar falcon and black vulture (Tucker, 1987). In fact, a best lift:drag ratio of 1.6–1.7 is roughly equivalent to that of some gliding mammals (i.e. entire gliding mammals, not just the gliding membranes) (Jackson, 1999), despite the fact that the flight surfaces in these forms have

much lower aspect ratios than pterosaur wings, and also that the pterosaur lift:drag ratios were derived from tests of the wings alone, and do not account for the additional 'parasite drag' caused by the body. When the model *Pterodactylus* wing was flapped the deformation was so extreme – the wing membrane turned inside out during the downstroke – that the lift coefficient, averaged over the wingbeat, was negative unless the angle of attack at the base of the wing exceeded  $10^\circ$ .

The severity of the problems apparent in these wind tunnel tests stems mainly from the fact that the model wing membrane was initially slack, in all likelihood an unrealistic state (Bramwell and Whitfield, 1974; Pennycuik, 1988). For a membranous wing to be at equilibrium, the aerodynamic forces must be balanced by tension in the membrane. If the unloaded tension is zero, the strain (i.e. deformation) of the wing membrane must be large for this condition to be met unless the Young's Modulus is very high, i.e. the elasticity very low, which is certainly not the case for latex rubber. In addition, the model did not include any representation of a trailing edge tendon, for which there is now tentative fossil evidence (Frey et al., 2003), which may have constrained deformation. The poor performance of the model wings may therefore be partly regarded as a result of unrepresentative material properties. There are, however, several problems unique to sail-like wings that a simple tensioning of the membrane would not have alleviated.

Firstly, unless membrane tension were infinite, the trailing edge of the cheiropatagium would have lifted when an aerodynamic load was applied (either in gliding or flapping flight), and the membrane, being strongly tapered, would therefore have twisted in a nose-down sense from root to tip, a morphology known as geometric wash-out. This would not have been entirely detrimental. By reducing the angle of attack at the wingtips, the wash-out would have reduced the risk of tip stall, a particular problem for highly tapered wings (Simons, 1978; Marchaj, 1996). A geometric wash-out is also important for optimising the angle of attack along the wing during the downstroke of flapping flight (Norberg, 1990). However, excessive twist is undesirable, as it diminishes the maximum

lift coefficient and the lift:drag ratio (Marchaj, 1988). Indeed, it was probably this factor more than any other that caused the poor performance of the model *Pterodactylus* wing described above. Some workers have therefore suggested that the shape of the wing spar limited membrane wash-out in pterosaurs. Three-dimensionally preserved fossil material shows that the wing-finger curved posteriorly and ventrally from root to tip (Bramwell and Whitfield, 1974; Wellnhofer, 1991a; Bennett, 2001). It has been argued that the ventral curvature of the spar could have approached that of the trailing edge of the cheiroptagium, thus reducing twist (Short, 1914; Brower, 1983; Bennett, 2000). Experiments on spar-and-membrane parawings, precursors of the first hang gliders, have indeed demonstrated the benefit in terms of the lift:drag ratio of curving the spar in this fashion (Polhamus and Naeseth, 1963). However, it must be remembered that the pterosaur wing-finger was not as rigid as the tubular metal leading edges of these parawings. The wing-finger phalanges were slender, somewhat dorso-ventrally flattened bones separated by synovial joints. These joints are widely believed to have been immobile, i.e. not under muscular control, largely because the joints are buttressed in the plane of the wing, which is also the plane in which flexion and extension of the phalanges would be expected to occur (Bramwell and Whitfield, 1974; Wellnhofer, 1991b; Bennett, 2001). Nevertheless, given the low rigidity of the joint capsule connective tissue in comparison with bone, they probably could not have prevented interphalangeal bending when the wing was loaded, and of course they could not have prevented bending of the bones themselves. It thus seems quite likely that the wing-finger would have curved dorsally in flight, not ventrally, and the shape of the wing spar would in reality have done relatively little to reduce excessive twist in the cheiroptagium.

Secondly, theoretical and experimental work on sail profiles (Thwaites, 1961; Nielsen, 1963; Greenhalgh et al., 1984; Newman and Low, 1984; Newman, 1987; Sugimoto and Sato, 1991) has shown that, owing to the mutual interdependence of shape and aerodynamic loading, multiple profile shapes are simultaneously possible at low angles of attack, a phenomenon that can cause serious instabilities (Fig. 2). At high angles of attack only a simple convex shape is possible (Fig. 2, shape 1); as incidence is reduced, the only significant effect at first is a rearward migration of the chordwise position of maximum camber. Eventually, a specific angle of attack is reached at which the incoming flow attaches smoothly to the profile, i.e. the dividing streamline runs to the leading edge. This is termed the ideal incidence (Theodorsen, 1930), at which the sail profile has fore-and-aft symmetry about the mid-chord (Fig. 2, shape 2). It should theoretically occur at an angle of attack of zero (Thwaites, 1961; Nielsen, 1963). In reality, however, ideal incidence is usually slightly positive, and increases in magnitude with sail camber, because of flow separation ahead of the trailing edge (Newman and Low, 1984; Cyr and Newman, 1996). If the angle of attack is reduced below ideal incidence, a point of inflexion appears at the leading edge that migrates rearward as the angle of attack is reduced (Fig. 2,

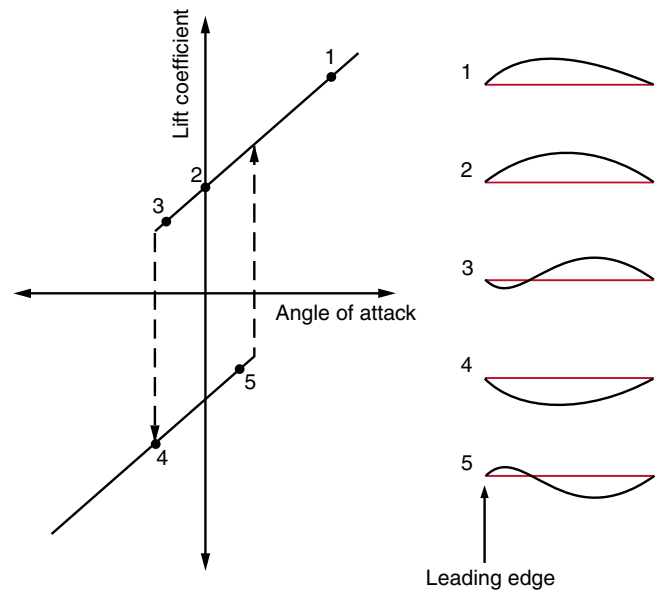


Fig. 2. Theoretically predicted hysteresis behaviour of an inextensible sail profile of given slackness in inviscid flow, showing changes in sail shape and the lift coefficient as angle of attack is decreased from a high value (1) through ideal incidence (2) and beyond, when the sail becomes S-shaped (3) and finally pops through (broken line), adopting a wholly convex shape with negative camber (4). A subsequent increase in the angle of attack from this point causes the profile to become S-shaped again (5) before positive camber is restored. Profile chord lines are indicated in red.

shape 3). While the sail is in this state it becomes susceptible to a frequently severe fluttering instability called luffing (Greenhalgh et al., 1984; Newman and Low, 1984; Newman, 1987; Sugimoto and Sato, 1991). The lift is still positive at this stage, but if incidence is reduced still further, a point is eventually reached when an S-shaped profile is no longer tenable, and the sail 'pops through', adopting an entirely convex shape, but lying beneath the chord line (Fig. 2, shape 4). Unsurprisingly, the lift is now negative. This pop-through generally occurs at a small negative angle of attack, the precise value depending on camber and the extent of flow separation (Greenhalgh et al., 1984; Newman, 1987). If the angle of attack of the upside-down sail is now increased, the profile will not cross the chord line again instantly, but must once again pass through ideal incidence and an S-shaped phase (Fig. 2, shape 5) before it pops through and attains positive camber once more. In other words, sail profiles exhibit hysteresis behaviour around ideal incidence (Greenhalgh et al., 1984; Newman, 1987; Sugimoto and Sato, 1991).

It is important to note that the behaviour described above concerns inextensible sail profiles with constant slackness, in all likelihood quite different to pterosaur wing profiles which, as has already been argued, would probably have been elastic and pre-tensioned. For such profiles, membrane camber increases with the angle of attack, all other factors being equal. Should membrane camber disappear at an angle of attack of zero, such that the profile becomes a flat plate, there would

logically be no S-shaped profile solution and no hysteresis, and the membrane would undergo a smooth transition between positive and negative camber. It must be remembered, however, that in flight, all other factors bar the angle of attack are not equal. Taking the simple case of equilibrium gliding, for example, a reduction in the angle of attack is accompanied by an increase in the relative airspeed, such that the total aerodynamic force remains constant: equal and opposite to body weight (Norberg, 1990). If one ignores changes in the spanwise lift distribution, one could therefore argue that the excess length of a profile at a given spanwise station of the wing would in fact remain constant in this case unless the material properties of the membrane were altered. The situation is different for flapping flight, in which the magnitude of the aerodynamic forces is time-variant: in this case the elasticity of the wing may have been important in avoiding luffing and camber-reversal if the angle of attack was reduced during the upstroke, as is the case in birds and bats (Norberg, 1990). Clearly, however, membrane elasticity did not prevent these occurring during flapping of the model *Pterodactylus* wing (Sugimoto, 1998), as described above. Inextensible sail profiles therefore seem to be reasonably good models for pterosaur wing profiles, at least to a first approximation. Needless to say, their tendency to luff or turn inside out, and then remain inside out even at small positive angles of attack, could have had disastrous consequences. Indeed, the notorious unrecoverable 'luffing dive' has been known to cause fatal hang glider crashes (LaBurthe, 1979; Kroo, 1981).

A final potential drawback of sail-wings is that they offer relatively little scope for control. Significant flexion at any of the forelimb joints, as used by birds and bats to adjust wing span and area in gliding flight to alter the equilibrium gliding speed (Tucker and Parrott, 1970; Pennycuik, 1971), or in flapping flight to reduce the magnitude of the aerodynamic forces generated during the upstroke in order to maximise net positive thrust (Norberg, 1990), would have caused a drop in tension in the cheiropatagium and a concordant increase in the geometric twist. Furthermore, pronation or supination of the wing spar at the shoulder would have had only a minor effect on the angle of attack because there were no rigid members linking the spar to the trailing edge. Elevation and depression of the leg would have been more effective in this regard. However, given the high aspect ratio, the legs would only have been able to modify the angle of attack of the proximal part of the wing.

On the evidence of the foregoing discussion one could get the impression that pterosaurs were barely capable of flight at all, with excessively twisted, unstable, scarcely controllable wings. The fact that this was manifestly not the case reveals the degree to which they were able to escape the historical constraints of their simple wing form. It should be noted at this juncture that modern sails and hang gliders are not good analogies for pterosaur wings, as they are generally made of nearly inextensible fabric supported by rigid spars, and are provisioned with battens, high-tension wires and other structures to limit deformation as much as possible (Kroo,

1981; Marchaj, 1988; Marchaj, 1996; Gratton, 2001). The pterosaurian solution was necessarily quite different and is currently poorly understood: investigations into the aerodynamics and aeroelasticity of pterosaur wings are still in their infancy. Nevertheless, recent palaeontological and aeronautical studies have highlighted a number of anatomical features that may have been of critical importance in rendering the pterosaurs airworthy.

Firstly, the cheiropatagium was not the only pterosaur wing membrane. There was also a membrane between the legs called the uro- or cruropatagium and one in front of the proximal region of the arm called the propatagium (Fig. 1). The role of the cruropatagium is poorly understood, and is not relevant to the present discussion, but the propatagium is likely to have been a vitally important component of the wing. It was supported by a modified wrist bone called the pteroid, whose function is a controversial topic. For many years it was widely believed that the pteroid was simply a passive element that pointed towards the body, forming the distal part of the leading edge of the propatagium (Bramwell and Whitfield, 1974; Wellnhofer, 1985; Wellnhofer, 1991a). This is indeed how the bone appears to be oriented in several articulated (but flattened) fossils (Padian and Rayner, 1993). However, my analysis, with colleagues, of exceptionally well preserved three-dimensional wrist bones from the Santana Formation (Lower Cretaceous) of Brazil indicated otherwise (Wilkinson et al., 2006). We proposed instead, on the basis of the 3D morphology of the supposed articular surfaces of the relevant bones, that the pteroid pointed forwards in flight, and could be depressed through a wide arc before swinging towards the body, eventually coming to lie within a transverse vertical plane, but deflected beneath the horizontal (Fig. 3A) (n.b. in the traditional reconstruction the pteroid is typically oriented horizontally). The propatagium would thus have acted as a ventrally deflectable leading edge flap that could have been conveniently furled away when the pterosaur was on the ground (Fig. 3B,C). We argued that it is this furled configuration that is visible in articulated fossils (Wilkinson et al., 2006).

This reconstruction rests on an oft-made assumption that the pteroid articulated with the so-called medial or pre-axial carpal (Fig. 4A,B), within a deep concavity or fovea located on its anterior face (Fig. 4B). However, in no three-dimensionally preserved specimen is the pteroid actually preserved in articulation with the fovea of the medial carpal (Bennett, 2006). In many such fossils, a small oval sesamoid bone is located there instead, which has been regarded by Bennett (Bennett, 2001; Bennett, 2006) as evidence that the fovea was not a true articular surface at all, but a groove for a tendon, specifically the wing-finger metacarpal extensor tendon. The sesamoid would in this case have developed within this tendon at the point where it passed through the fovea, and the pteroid would have articulated on the medial side of the medial carpal (Fig. 4C), and would thus have pointed towards the body. It would not, however, have necessarily been a passive element: it would instead have been free to elevate and depress, and

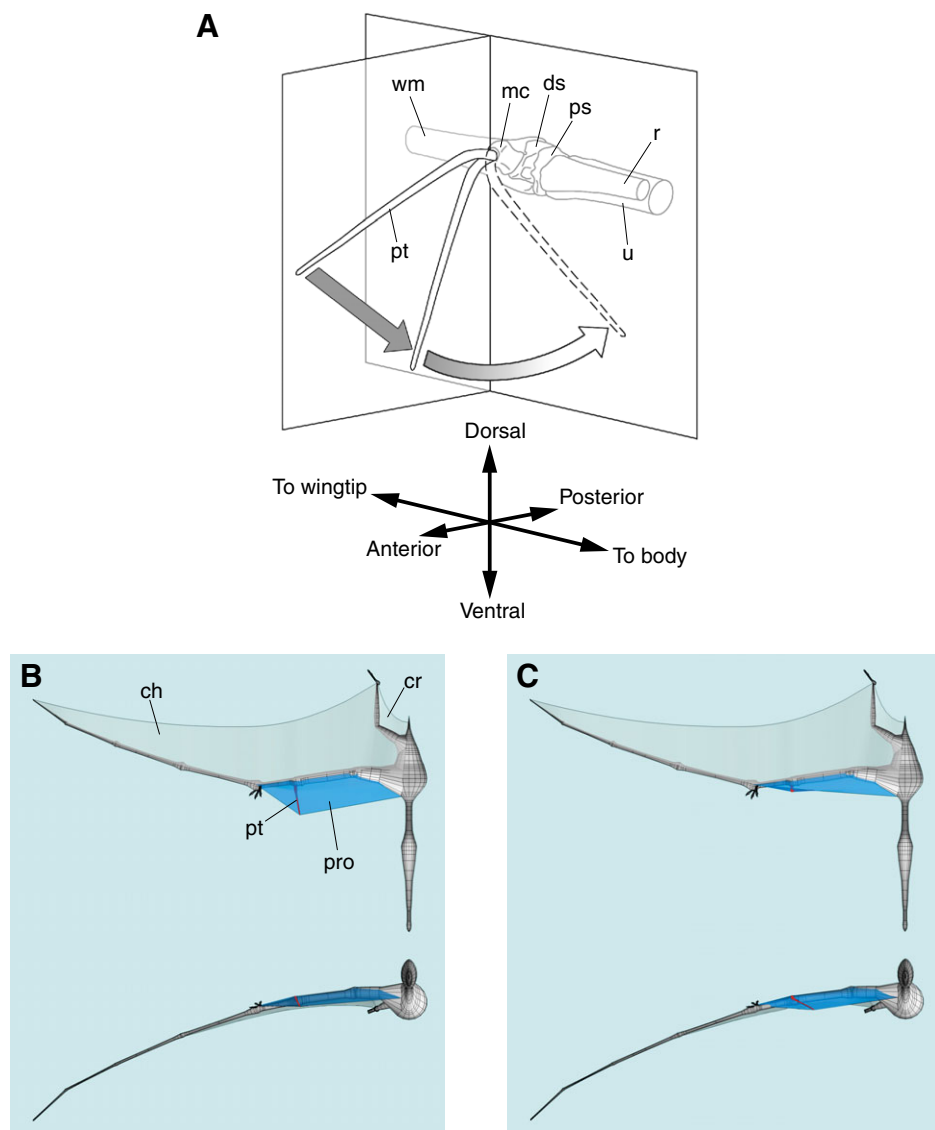


Fig. 3. (A) Articular movement of the right pteroid as reconstructed by Wilkinson et al. (Wilkinson et al., 2006). From the forward-pointing orientation, flexion at first takes the form of pure depression, so that the pteroid is confined to the indicated vertical plane that lies perpendicular to the wing spar. Depression then gives way to adduction, and the pteroid swings towards the body, eventually coming to occupy a plane parallel to the wing spar at the limit of flexion (broken outline). (B) Dorsal (top) and anterior (bottom) views of a virtual model of *Anhanguera*, with an extended propatagium (indicated in dark blue) and forward-pointing pteroid (indicated in red). (C) As in B, but with the pteroid fully flexed and the propatagium furled. Abbreviations as in Fig. 1.

therefore could still have enabled the propatagium to act as a leading edge flap (Bennett, 2006), although considerably narrower than in our alternative reconstruction (Wilkinson et al., 2006).

I find the reconstruction of Bennett (Bennett, 2001; Bennett, 2006) a little difficult to accept, mainly because there is no obvious articular surface on the side of the medial carpal (Wilkinson et al., 2006). It is instead possible that the sesamoid was embedded within a pteroid extensor tendon, and was closely associated with the pteroid–carpal joint (Fig. 4D). It could thence have been pulled into apparent articulation with the fovea of the medial carpal during *post-mortem* dislocation of the pteroid, just as the sesamoids of the human hand and foot can be pulled into their associated joint capsules following dislocation (Del Rossi, 2003). Nevertheless, the current lack of a known specimen in which the pteroid is preserved in articulation with the fovea of the medial carpal is a significant blow to the idea of a broad propatagium, and it thus seems safest at this juncture to focus on the common aspects of the

two opposing reconstructions: the dorso-ventral mobility of the pteroid and concordant potential for deflection of the propatagium.

A ventrally deflected propatagium would have had a number of important benefits. Given that it extended only part-way along the semi-span, probably terminating at the knuckle (Wilkinson et al., 2006), it would have reduced the angle of attack of the proximal wing with respect to that of the distal wing, more so for a given pteroid deflection angle if the propatagium were broad. This twist in a nose-up sense from root to tip is opposite to the wash-out described above, and is termed a geometric wash-in. This arrangement would have partly cancelled the inherent wash-out of the cheiropatagium.

Secondly, wind tunnel tests of sail profiles with and without a broad propatagium indicate that it would also have acted as a very effective high lift device (Wilkinson et al., 2006). Deflection of the broad propatagium caused the flow to remain attached near the leading edge even at an angle of attack of 20° (the maximum attainable with the experimental set-up). By

preventing stall in this way, the maximum section lift coefficient was increased by nearly 45% to 2.4 (Fig. 5). Of key importance is the fact that a movable propatagium can set the profile's entry angle (the angle between the chord line and the tangent at the profile's leading edge). In standard sail profiles the entry angle is a function of the camber and the position of maximum camber, and the latter cannot be directly controlled. To achieve high entry angles on such a profile, the camber would have to be very large indeed. On the evidence of previous wind tunnel tests of slack sail profiles (Greenhalgh et al., 1984; Newman and Low, 1984; Sugimoto and Sato, 1991), excessive flow separation would probably prevent the attainment of very high lift in this case. As yet, there are no

wind tunnel data available for a deflected narrow propatagium, but given that this configuration would also increase the entry angle of the profile, the possibility remains that the high lift effect would also occur in this case. Wind tunnel tests of profiles with an undeflected narrow propatagium performed very badly, such that its removal increased the best lift:drag ratio and the maximum lift coefficient (Wilkinson et al., 2006). It therefore appears that it would have been detrimental for the pteroid to have been directed horizontally in flight.

The high lift function of the propatagium would have been of great benefit to the giant pterosaurs when taking off or landing. These manoeuvres are generally problematic for large flying animals thanks to the well-known adverse scaling of the

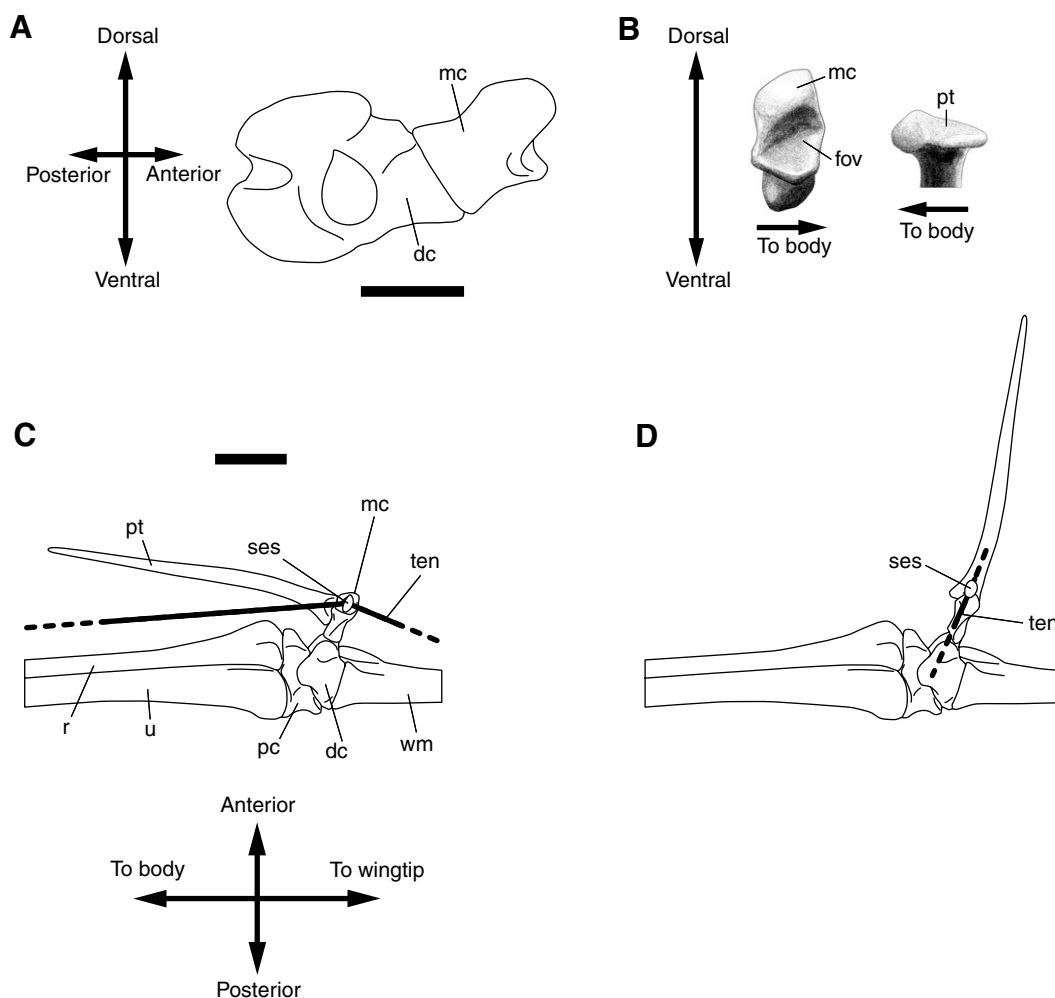


Fig. 4. (A) Lateral view of the right medial carpal in articulation with the distal carpal of the Cretaceous pterosaur *Coloborhynchus robustus*. Scale bar, 25 mm. (B) Traditionally recognised articular surfaces of the right carpal-pteroid joint of *Coloborhynchus*, the medial carpal in distal (anterior) view showing the fovea (fov), and the head of the pteroid in proximal view. Specimen details can be found in Wilkinson et al. (Wilkinson et al., 2006). Scale as in A. (C) Reconstruction of the right wrist of *Coloborhynchus* in dorsal view according to descriptions provided by Bennett (Bennett, 2001; Bennett, 2006), with a sesamoid bone (ses) within the fovea, and the pteroid articulating on the side of the medial carpal. Note that the medial carpal has been rotated about its long axis by 180° with respect to A and B. The postulated trajectory of the wing-finger metacarpal extensor tendon (ten), in which the sesamoid is embedded, is also shown. Scale bar, 50 mm. (D) Reconstruction of the right wrist in dorsal view according to Wilkinson et al. (Wilkinson et al., 2006), with the pteroid at maximum elevation, and an alternative reconstruction of the sesamoid, which is shown in close association with the carpal-pteroid joint, embedded within a putative pteroid extensor tendon (origin and insertion points unknown). Scale as in C. Abbreviations as in Fig. 1. Broken line indicates a continuation of the extent of the tendon.

minimum gliding speed with mass (Alexander, 1998). Wing loading (weight divided by wing area) generally increases with size because, while mass scales with the cube of the linear dimension, wing area scales only with the square of the linear dimension. Hence large flying animals are expected to be, relative to their mass, less well endowed with lift-generating flight surfaces, and must fly faster to support their weight, as indicated by the following equation derived from classical aerodynamics:

$$V_{\min} = \sqrt{2WL / \rho C_{L,\max}}$$

where  $V_{\min}$  is the minimum gliding speed in  $\text{m s}^{-1}$ ,  $WL$  is the wing loading in  $\text{N m}^{-2}$ ,  $\rho$  is air density [currently about  $1.2 \text{ kg m}^{-3}$  at sea level but a little higher in Late Cretaceous times (Dudley, 1998)] and  $C_{L,\max}$  is the maximum lift coefficient.

The essential outcome of this line of reasoning is that, as size and wing loading increase, it becomes progressively more difficult to achieve sufficient relative airspeed to take off or to avoid mortal injury upon landing. The disproportionately large wings and ultra-lightweight skeletons of the giant pterosaurs would have partially offset the trend in wing loading (Bramwell and Whitfield, 1974; Alexander, 1998), but the very high  $C_{L,\max}$  that on current evidence was provided by the propatagium was

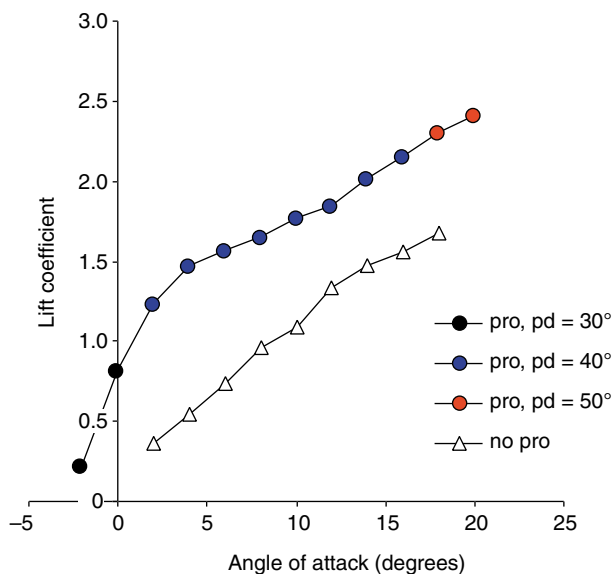


Fig. 5. Lift coefficients of spar-and-membrane profile models, with (pro) and without a propatagium (no pro), measured in a wind tunnel at a Reynolds number of  $1.2 \times 10^5$ , an appropriate value for large pterosaurs (Wilkinson, 2002). Data re-plotted from Wilkinson et al. (Wilkinson et al., 2006). Measurements were nominally made at angles of attack from  $-2^\circ$  to  $20^\circ$ , but below  $2^\circ$  the model without a propatagium luffed so severely that readings could not be taken. Above  $18^\circ$  the same model stalled, and again became too unstable for the lift to be measured. For the model with a propatagium, the best performance was obtained if propatagium deflection (pd), measured with respect to the chord line of the cheiropatagium, was increased from  $30^\circ$  to  $50^\circ$  as indicated.

clearly advantageous, particularly for *Quetzalcoatlus northropi*, the largest known pterosaur. Unlike most other large pterosaurs that have been found in marine deposits, its remains were found far from contemporary seas (Lawson, 1975). This suggests that, while its ocean-going relatives were able to use gravity-assisted take-offs from cliffs, *Quetzalcoatlus* was land-based and may have had to take off from more-or-less level ground. Furthermore, a fast running take-off would have been extremely problematic, regardless of whether large pterosaurs were habitually quadrupedal or bipedal: all pterosaurs must have become transiently bipedal to enable deployment of the wings prior to take-off. The chief problem is that the cheiropatagia were attached to the legs, which means that running would have caused the angle of attack and camber of the inner wings to oscillate asymmetrically as the legs moved back and forth, with concordant stability problems. A means of substantially reducing the minimum relative airspeed for flight in these giants must therefore have been vital.

In wind tunnel tests, the broad, deflected propatagium was shown to be useful not only as a high-lift device. It also greatly improved profile stability at low angles of attack. Without a propatagium, the model profile luffed severely at angles of attack below  $2^\circ$ , such that force measurements could not be taken. If the propatagium was present, positive lift was still obtained at an angle of attack of  $-2^\circ$  (Fig. 5). This stabilising effect was a simple geometric consequence of there being a deflected forewing: its presence meant that the point where the membranes were anchored to the spar always lay above the chord line, which made a full pop-through physically impossible and ameliorated luffing.

Finally, the propatagium would have acted as a useful control surface. If pteroid depression were coupled with leg depression, the result would have been an increase in camber of the inner wing and a concordant increase in lift. If, however, the pteroid were depressed alone, the increase in camber would have been coupled with a decrease in the angle of attack, which may have caused only an increase in drag. Used asymmetrically, the propatagia could therefore have controlled roll or yaw by respectively increasing either the lift or drag of one wing. Qualitatively, these conjectures should hold regardless of whether the reconstructions of Bennett (Bennett, 2001; Bennett, 2006) or Wilkinson et al. (Wilkinson et al., 2006) prove to be correct, as both treat the pteroid as a mobile element, capable of altering the ventral deflection angle of the propatagium.

The propatagium, thanks to the function of the pteroid, was undoubtedly a tremendously important feature, and its absence from the distal part of the wing could be regarded as a drawback, especially as the local angle of attack was likely to have been lower here due to twist, and the membrane consequently more susceptible to luffing and pop-through. However, the distal part of the cheiropatagium was qualitatively different from its proximal part. It was invested with a system of long, thin, closely spaced fibres or actinofibrils, probably composed of either collagen or keratin (Bennett, 2000), that ran almost parallel to the wing spar near the bones, but radiated postero-distally, curving to meet the

trailing edge at a high angle (Padian and Rayner, 1993; Bennett, 2000). Fibres of similar apparent histology are present in the proximal cheiropatagium, but they are much shorter and diffusely scattered (Unwin and Bakhurina, 1994). It has been suggested that the actinofibrils of the distal cheiropatagium were stiff structural elements, able to transfer aerodynamic loads directly to the wing bones or to spread the distal cheiropatagium in the chordwise direction when the wing was extended (Padian and Rayner, 1993; Bennett, 2000). However, it seems most unlikely that the actinofibrils, which had an average diameter of 0.05 mm (Padian and Rayner, 1993), possessed sufficient bending stiffness or compression resistance to have had these functions, quite apart from the fact that the fibrils make no direct contact with the wing bones (Bennett, 2000). Tension in the cheiropatagium was responsible for the transfer of aerodynamic loads, and the putative trailing edge tendon (Frey et al., 2003) could have prevented its excessive chordwise contraction.

The form and likely composition of the actinofibrils strongly suggests that they were resistant neither to bending nor to compression, but to extension. They would thus have altered the equilibrium of profile shape and aerodynamic loading in the distal cheiropatagium. At the very least, the fibrils would have limited the strain of the membrane and therefore reduced camber along their respective lengths relative to that of a fibril-less membrane. Due to the radiating pattern of the fibrils, this constraining action would have occurred more in the chordwise direction proximally, but more in the spanwise direction distally. Near the tip, the fibrils may therefore have limited the deflection of the trailing edge and thus reduced the overall geometric twist.

Additionally, the diminishing chordwise constraint of membrane excess length towards the tip could have caused a spanwise increase in profile camber. This would have caused the local zero-lift angle of attack to decrease from root to tip, thereby giving rise to an aerodynamic wash-in (a nose-up twist of the angle of attack as measured from the zero-lift angle) that would have opposed the geometric wash-out of the cheiropatagium and improved the spanwise lift distribution (Simons, 1978). Finally, in limiting the deformation of the distal cheiropatagium as a whole, the fibrils would have narrowed the range of angles of attack within which there are multiple profile solutions, and could thus have reduced the risk of luffing. The fibrils may therefore have fulfilled the roles that one would expect, bearing in mind the potential problems of sail-like wings, but it will take physical models or a coupled finite element/computational fluid dynamic analysis to confirm these suppositions. As a further complication, it is known that the cheiropatagium contained muscle fibres, following the discovery and subsequent study with a scanning electron microscope of a three-dimensionally preserved wing membrane fragment from the Santana Formation of Brazil (Martill and Unwin, 1989), but as yet the global distribution of these muscles within the cheiropatagium is largely unknown, as is the likely effect of their contraction on the shape of the membrane.

## Conclusions

The paradoxical aerial proficiency of pterosaurs rested on the fact that their wings were not simple sails. Instead, there was a clear functional division between the proximal part, that was relatively elastic, bore the pteroid-controlled propatagium, and could be manipulated by the leg, and the distal part, that was stiffened by actinofibrils. Much more research in several disciplines is required if we are to find out exactly how this arrangement solved the many inherent problems of sail-like wings. It is clear, however, that the pterosaurian adaptive solution to flight was unique, and highly successful.

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