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Constraints on the wing morphology of pterosaurs

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Animals that fly must be able to do so over a huge range of aerodynamic conditions, determined by weather, wind speed and the nature of their environment. No single parameter can be used to determine—let alone measure—optimum flight performance as it relates to wing shape. Reconstructing the wings of the extinct pterosaurs has therefore proved especially problematic: these Mesozoic flying reptiles had a soft-tissue membranous flight surface that is rarely preserved in the fossil record. Here, we review basic mechanical and aerodynamic constraints that influenced the wing shape of pterosaurs, and, building on this, present a series of theoretical modelling results. These results allow us to predict the most likely wing shapes that could have been employed by these ancient reptiles, and further show that a combination of anterior sweep and a reflexed proximal wing section provides an aerodynamically balanced and efficient theoretical pterosaur wing shape, with clear benefits for their flight stability.

Keywords: Pterosauria; flight; wing shape; morphology; biomechanics; aerodynamics

1. INTRODUCTION

Pterosaurs (extinct Mesozoic flying reptiles) were unique in having a wing formed from an elastic membrane stretched from the edge of a super-elongate finger to the rear limbs. However, based on their fossil record, it is only possible to reconstruct with any certainty the shape of the anterior margin of this wing membrane and its posterior attachment to the ankle [1]. The extent and outline of the posterior membrane margin, between the ankle and the distal end of the wing finger, thus remains subject to considerable speculation (figure 1). Few fossils preserve the soft tissues of the extended pterosaur wing membrane [1], and some of those that do may be subject to damage during preparation or could be morphologically aberrant [7].

In spite of the shortcomings of the fossil record, reconstructing the wing morphology of pterosaurs has a long and contentious history. Among the first to try to take account of both anatomical and mechanical considerations were Hankin & Watson [2], followed by Bramwell & Whitfield [3] and Padian & Rayner [8]. Reconstructions proposed by these authors, however, differ considerably from one another (figure 1); arguably the most comprehensive study to date is the work of Bramwell & Whitfield [3].

The early work of Hankin & Watson [2] was the first to propose that pterosaurs probably possessed narrow wings with a marked concavity along their posterior margin, supported by proximal wing bones held in an elevated cranial position (figure 1*a*). This shape and orientation would have resulted in a scimitar-shaped wing with marked anterior sweep (figure 1*a*), contrasting with some later reconstructions [3,4] of wings with a completely straight anterior margins (figure 1*b,c*), but with differing amounts of anterior sweep in the wing bones. Other subsequent reconstructions ([4], p. 71) invoked a slight convexity to

some wing posterior margins while others ([4], p. 74) were drawn concave. Some workers have even illustrated both concave and convex wing shapes for different pterosaurs (convex: [9], p. 172; concave: [1,6,10]), all with varying degrees of sweep (figure 1).

Marked shape variation in pterosaur wings has largely been illustrated in the context of more general anatomical body reconstructions for these animals; little consideration has been given to the implications of these shapes for aerodynamic balance or the requirement for membrane tension in flight. Further, none of the alternative shapes proposed has been subject to systematic aerodynamic assessment, including (but not limited to) the effects of wing bone geometry, implications of differences in shape of the posterior margin, coincidence between the centre of mass (CG) and centre of pressure (CP), and the forces and effects of wing bone bending.

Here, we synthesize the mechanical and aerodynamic constraints that provide a basis for reconstructing pterosaur wings. With this background in place we are able to predict, for the first time, the likely bounds on possible wing shapes that could have been employed by these ancient reptiles. Our conclusions have implications for understanding the flight and palaeobiology of pterosaurs.

2. MECHANICAL AND AERODYNAMIC CONSTRAINTS

(a) *Static balance: coincidence of centre of mass and centre of pressure*

For steady flight in any system, CM and CP must be coincident so there are no applied moments and the total aerodynamic force—the resultant of lift, drag and total weight—must be equal and opposite (to satisfy Newton's third law of motion; figure 2).

(b) *Surface strain on wing bones*

Structures deflect under load and their failure is the result of complex interactions between the material properties

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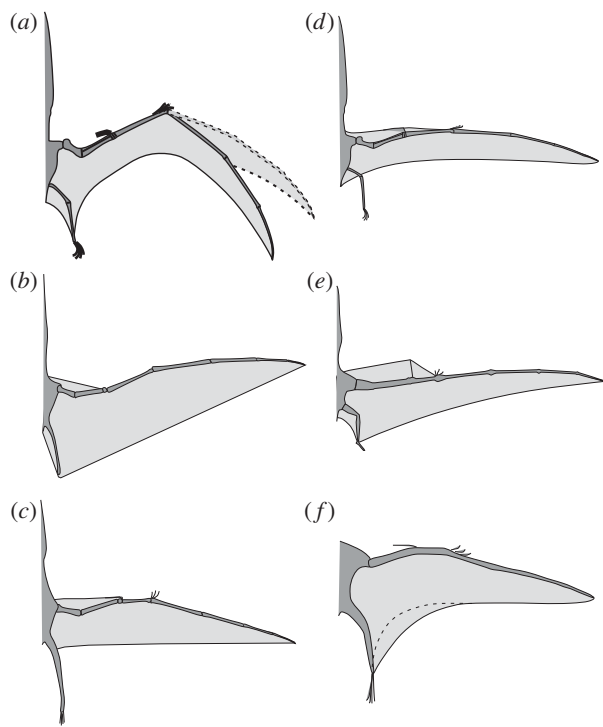


Figure 1. Competing wing shapes for pterosaurs redrawn from published sources: (a) Hankin & Watson [2], (b) Bramwell & Whitfield [3], (c) Wellnhofer [4], (d) Bennett [5], (e) Wilkinson [6], (f) Elgin *et al.* [1].

and geometry. The distal wing bones of pterosaurs were slender, thin-walled beams and thus were likely to fail by either section buckling or rupture, when local strain exceeded the yield strain of the material [11]. Since the tensile strength of bone is significantly less than its compressive strength [11], rupture failure will be tensile. Failure owing to buckling depends primarily on the wall thickness to diameter ratio: Currey ([12], p. 197) showed that for typical pterosaur wing bones, buckling failure will not occur before tensile rupture.

Thus, for our purposes, the structural threshold of a pterosaur wing bone is the point at which surface strain exceeds a limiting tensile strain; because strain is a geometric quantity, this defines the limiting deflection of the wing bones and can be used to make predictions about the likely deflection of bones under load.

(c) Shape of the free margin

We know that the margin of the pterosaur wing membrane was unconstrained posteriorly and attached distally to the ankle and body [1,13] (figure 1). From a purely mechanical point of view, there is thus a very good reason to expect that the posterior membrane margin was concave [6] (figure 1e). This is because, unlike bats, pterosaurs did not have additional fingers to extend across their membrane. The wing membrane did have some internal structures: one [5,8] or possibly more [13] layers of ‘aktinofibrils’—fibres with a higher modulus of elasticity than the surrounding tissue. The most recent fossil evidence indicates that these fibres were of a diameter comparable to human hair (approx. 0.1–0.5 mm) and were most probably composed of collagenous tissue (although this is purely conjectural) [13]. These fibres would have increased the in-plane

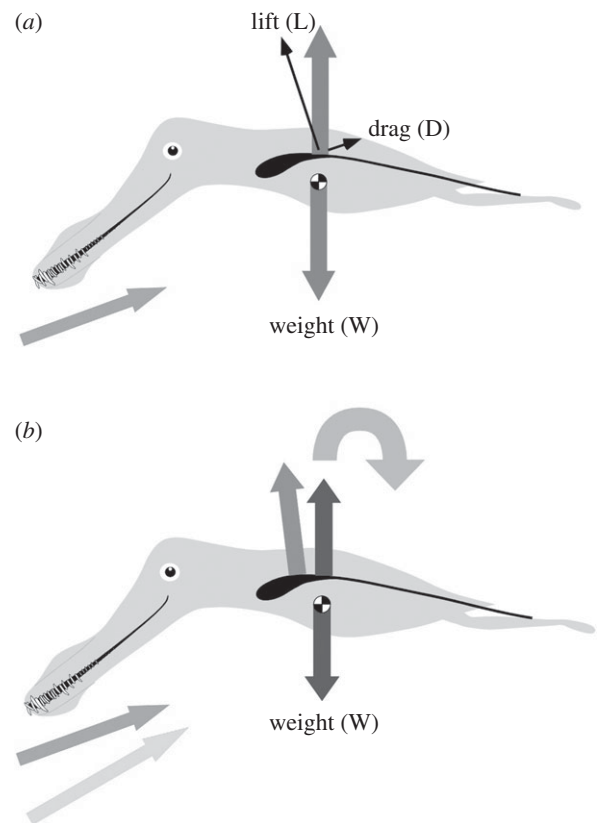


Figure 2. Cartoon to show the balance of forces on a gliding pterosaur. (a) The resultant of the aerodynamic lift and drag forces is equal in magnitude to the weight, opposite in direction and acts along the same line. (b) When a gust is encountered, the aerodynamic force changes in magnitude and location. This effect can be destabilizing (as shown) or, with a different geometry, stabilizing.

tensile strength to the membrane, but in view of the thinness of the membrane (less than 1 mm) [13], they would have contributed very little to its bending or compressive strength (electronic supplementary material).

The free margin of a flexible membrane streaming in an airflow cannot be convex and be stable unless it is supported by stiffening structures capable of resisting bending and compressive loads, like the batten-stiffened regions of yacht sails and hang-glider wings. Without stiffening battens, a thin membrane with no significant out-of-plane bending stiffness can only be constrained from instability by in-plane tension, which is unavoidably absent in a region with a convex margin [14] (electronic supplementary material). This universal requirement for a concave margin to maintain membrane tension is apparent from examination of man-made structures like tents and sails that lack battens, as well as the membranes of bats that use extended fingers to this effect, yet have a very marked concave membrane margin between the fingers [15,16]. Following this line of reasoning, reconstructing a convex wing margin for pterosaurs must be incorrect: without in-plane battens, the membrane would have flapped uncontrollably, greatly increasing the drag [17] and destroying the shape required for flight.

A possible solution to the problem of membrane instability is the suggestion that pterosaurs may have possessed a tendon that ran along the posterior margin of the wing [18]. When tensioned, this tendon could have

stabilized the free margin, allowing an almost straight (but still not convex) edge. However, fossil evidence for such a tendon is equivocal, especially in larger species (wing span greater than a few metres) where preserved membranes are unknown [1], and mechanically it was unlikely to have been present. In order to be effective at stabilizing the membrane edge, a tendon would have had to have been under considerable tension to balance the chordwise (antero-posterior) tension of the wing membrane. Such loading geometry would subject the wing bones to substantially greater bending loads than if the membrane tension was primarily subparallel to the wing bones (i.e. spanwise). Sneyd *et al.* [19] estimated that chordwise membrane tension, reacted by a supporting tendon, would have increased bending moments in the wing bones by a factor approximately equal to the aspect ratio of the wing: a factor of more than 10 in a typical ornithocheirid pterosaur. Bramwell & Whitfield [3] calculated a slightly lower difference factor of 6 for *Pteranodon*, which they estimated to be structurally unsustainable. Simple mechanics (as well as anatomical parsimony) imply that spanwise tension, with no requirement for a tendon, is more likely to have been the case in pterosaur wings. Finally, our argument is also supported by the position of the aktinofibrils, which, when preserved, are orientated to produce anisotropic membrane properties that would have resisted spanwise tension [5,13].

(d) *Aerodynamic efficiency and induced drag*

In sustained unpowered flight, one measure of aerodynamic efficiency is the ratio of lift to drag. Lift is fixed and equal (to a first order) to an animal's body weight, so drag must be minimized to achieve the highest lift: drag ratio and thus maximum aerodynamic efficiency [20, p. 50]. Strictly speaking, although maximizing lift: drag ratio will maximize flight range, for some birds (and perhaps therefore some pterosaurs) flight endurance appears to be a more important parameter. This is maximized by flying at the lowest descent (sink) speed, which does not coincide exactly with the maximum lift: drag ratio. However, in practice, it is generally the case that increases in lift: drag ratio tend also to reduce sink rates [21].

The drag of a wing can be defined as the sum of four components: (i) the frictional drag of the airflow over the wing surface; (ii) the interference drag owing to flow constrictions around the wing body junction; (iii) the profile (pressure) drag produced by regions of flow separation across the wing section, manifested in the wake; and (iv) the drag owing to lift (induced drag). For a wing of a given area and aerofoil section, the frictional, interference and profile drag components are fixed for any given velocity and fluid density, and thus induced drag, which is geometry-dependent, is the only variable that needs to be assessed.

Aerodynamic theory and experimental data have shown that induced drag is primarily determined by aspect ratio (slenderness) and planform shape (especially degree of wing taper), although wing tip shape and distribution of twist along the wing can also be important ([22], p. 435). Theoretical studies ([23], p. 411) have shown that in order to minimize induced drag, the lift distribution along a wing must be elliptical, leading to the 'ideal' Spitfire-like wing shape that is well known in aircraft design. In practice, a simple prismatic wing with

50 per cent taper is very nearly as efficient as this ideal wing, but as taper increases further, it rapidly becomes more and more detrimental to performance ([23], p. 420). A highly tapered wing not only has high induced drag, but is also prone to tip stall ([23], p. 430), which is detrimental to control during low-speed flight. These simple parameters have been used before to explain the relatively conserved number of wing shapes found among flying animals [24], and because we know that some wing shapes work better than others under certain conditions, predictive methods can be used to inform choices between competing wing reconstructions, especially in extinct vertebrates.

(e) *Static stability*

While the most basic requirement for steady flight is that the aerodynamic resultant and weight are equal and opposite, any configuration must also be such that if its flight path is disturbed, the animal (or aeroplane) can return to a stable condition. Arguably, the most demanding stability requirement is in pitch (i.e. rotation in the sagittal plane), because an animal's mass moment of inertia is much less for this axis than for yaw and roll (the other axes in which stability is important), so response rates have to be much faster. Pitch stability is determined by the interaction of aerodynamic and weight forces, and depends on how they move relative to one another under the influence of changes in the airflow over the wing. For example, if an animal encounters a gust that increases the angle of attack on its wings, the aerodynamic resultant increases in magnitude and moves antero-posteriorly.

For a simple cambered wing, this movement is anterior ([20], p. 41), inducing a nose-up pitch rotation, which increases the angle of attack and is thus destabilizing (figure 2*b*). Returning to an original flight path under these conditions can only be achieved by active control, which requires very rapid reaction times and precise manipulation of control surfaces. Such 'active stability' can be provided by computer control in specialized, agile aircraft, but it remains unclear whether it can be achieved by flying animals. Passive pitch stability has been shown to be plausible in large, soaring birds [25,26], and may even confer energetic advantages as it reduces muscular and neurological activity in flight.

If we assume that large, soaring pterosaurs were also statically stable in pitch (a likely assumption), their wing characteristics must be such that not only must CP coincide with CM in a static sense, but when the incident flow direction changes, CP must also move in a direction to stabilize flight.

3. THEORETICAL MODELLING OF WING SHAPES

Taking into account the constraints described above, we tested a number of competing pterosaur wing shapes using theoretical aerodynamic modelling. We used the open source XFLR5 software that implements the vortex lattice method ([27]; [28], p. 331) and was specifically developed for low Reynolds number flight (i.e. for designing model aeroplanes). More details of our methodology and validation of techniques are provided in the electronic supplementary material.

Using these techniques, we quantified the position of the CP and lift distribution in order to investigate the relative

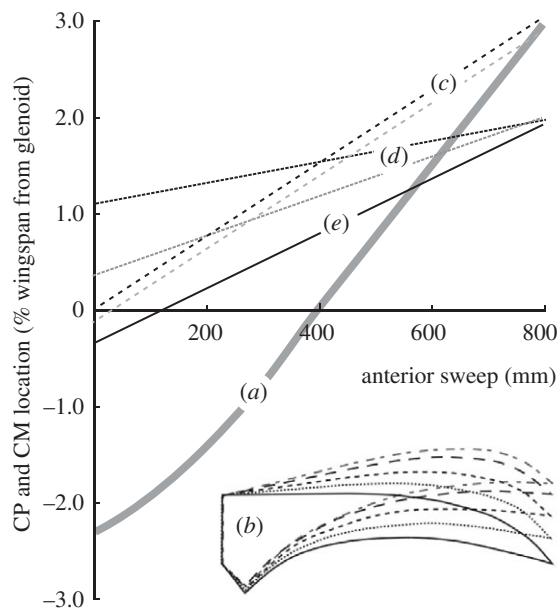


Figure 3. Coincidence of CP and CM with varying reconstructions and wing sweep. (a) Variation of CP position with wing sweep. (b) Morphed wing shapes used to construct the curve of CP location. (c) Movement of CM with wing sweep for reconstructions based on Strang *et al.* [30] mass allocation. (d) Movement of CM with wing sweep for reconstructions based on Henderson mass allocation [29]. (e) Movement of CM with wing sweep for reconstructions based on Bramwell & Whitfield [3] mass allocation.

positions of CP and CM in different pterosaur wing forms. We also assessed the theoretical performance of different wing shapes by comparing calculated induced drag with that of an ideal elliptical wing of the same aspect ratio to yield a ratio that we term 'span efficiency' (e). This ratio is a measure of the aerodynamic efficiency of a particular wing shape (corrected for aspect ratio), and it is important because, for a given wing area, aspect ratio is expensive: long slender wings limit manoeuvrability, are more prone to aeroelastic instabilities and create larger bending moments in proximal supporting structures.

4. RESULTS

(a) Coincidence of centre of mass and centre of pressure

Bramwell & Whitfield [3] and Henderson [29] have provided estimates of mass (and allocation of mass) and CM for a selection of pterosaur species, and Strang *et al.* [30] presented a mass allocation for *Anhanguera*. These data were used to calculate a range of CM location estimates. In the species examined, large pterodactyls *Pteranodon* and *Anhanguera*, CM falls close to the posterior face of the humerus where it articulates with scapulocoracoid, while analysis of Henderson's wing shape [29] shows that the location of the CP was posterior to this location of CM. We morphed the wing shape to give progressively more and more anterior sweep (while also adjusting the CM location to allow for the movement of the mass of the wing membrane and wing bones), and determined the degree of sweep at which the two centres were coincident (figure 3). The resulting wing shape has more than 10° of anterior sweep (figure 4).

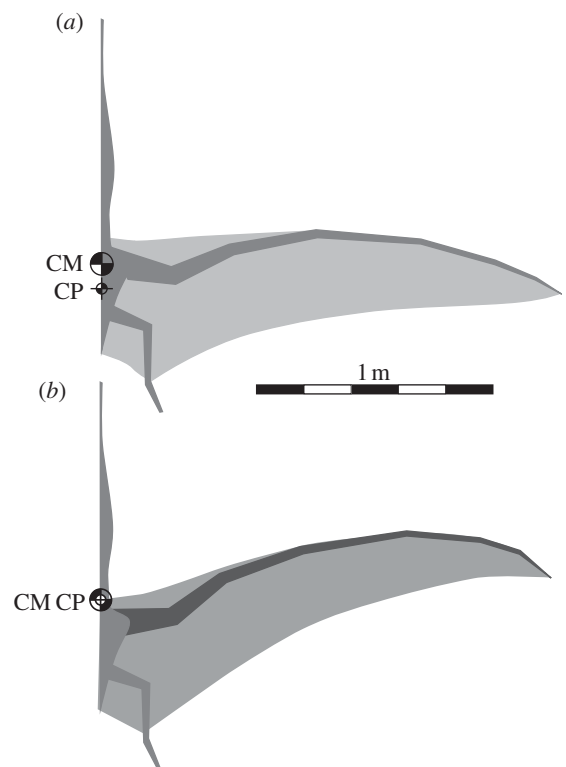


Figure 4. Effect of requirement for aerodynamic balance on wing planform shape. (a) Typical published reconstruction [28] showing relative positions of CM and CP, which are not coincident. (b) The same wing morphed to reflect the effects of membrane tension and the anterior sweep required to bring CM and CP into coincidence.

This approach was also used to show that the CM and CP locations are not coincident in many of the wing shape reconstructions currently in the literature, suggesting that pterosaur wings had more anterior sweep than is shown in almost all modern reconstructions. Interestingly, the relatively early reconstruction produced in Bramwell & Whitfield [3] is very close to being balanced, according to this analysis. In particular, this approach clearly demonstrates the implausibility of shapes with high posterior sweep (e.g. [6,31]) because they would be aerodynamically unbalanced.

(b) Surface strain

We also incorporated bending deflection into pterosaur wing bones (figure 5). While actual wing bone loading cannot be estimated, the possible maximum bone curvature can be calculated on the basis of acceptable strain (§2). Using a yield strain (ϵ_{yield}) of 0.0075 [11] and a safety factor of 3 [32], calculated average deflections are 8° for the first and second wing phalanges (WP1 and WP2), 10° for WP3 and 12° for WP4. It is also apparent from many fossil specimens [1,4,33] that WP4 frequently had natural curvature, typically around 15°. These bone deflections (assuming no flexibility in the interphalangeal joints) were applied to Bennett's [34] reconstruction of *Anhanguera santanae* (which was in turn modified from Wilkinson *et al.* [10]) and also to Wilkinson's later reconstruction [6]. The result produced wings with increased posterior sweep, the opposite direction to that required for aerodynamic balance (§2). However, anatomical reconstruction of bone and joint geometry inevitably

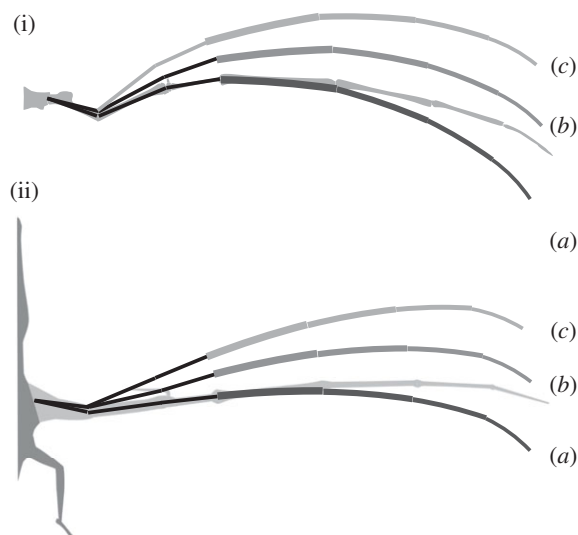


Figure 5. Alternative wing bone reconstructions taking account of bone-bending deflection and possible joint flexion. (i) Wing bones as reconstructed by Bennett [5]. (a) Maximum deflected shape (in response to membrane in plane tension loading) of wing bones retaining joint angles as reconstructed [5]. (b) Effect of 5° humerus and wrist flexion. (c) As in (b), but with additional 10° flexion of the elbow. This wing bone geometry allows the wing shape to be balanced. (ii) The process repeated for the Wilkinson wing reconstruction [6].

contains some imprecision (C. Bennett 2010, personal communication), and it is known [5,6] that the pterosaur elbow joint could flex through a large angle.

A 5° change in the angle of the humeroulnar joint and at the wrist results in moderate anterior sweep: if this is combined with a 10° flexure of the elbow then the forward sweep of the wing can be sufficient to provide aerodynamic balance. An anteriorly swept wing configuration is thus perfectly possible within the bounds of known pterosaur anatomy (figure 5c).

(c) *Lunate planform*

The pterosaur wing has an obligatory highly tapered planform owing to the basic structure of the wing bones and membrane. While there is some evidence [8] of preserved wings having a small, finite width at the tip, the extent is such that the overall wing is still highly tapered (pointed) in an aerodynamic sense. The shape is well into the range where it will exhibit a high induced drag owing to the degree of taper ([23], p. 420). There is, however, a feasible geometry that may have mitigated this disadvantage—a lunate or doubly elliptical crescent-shaped planform, first noted in this context by Hazlehurst & Rayner [35] and found in many bats [15,16]. As Hazlehurst & Rayner [35] observed, this geometry both reduces the tendency to tip stall and lowers the induced drag, observations that have been reinforced by more recent research, which has also shown that ‘lunate’ curvature can be concentrated towards the tip of the wing and still be effective [22].

We further applied our aerodynamic model to calculate variations in lift along the span of the wing, in order to analyse the likelihood of tip stall. Comparisons were

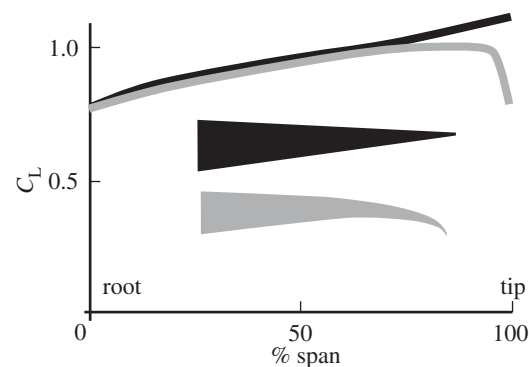


Figure 6. Effect of lunate wing shape on lift distribution and propensity for tip stall. A straight, tapered shape (black) for which the lift coefficient increases progressively towards the distal extremity (tip). The lift coefficient distribution means that the wing tip will be the first region to experience stall, resulting in ‘tip stall’. A lunate shape (light grey) results in a reduction in lift coefficient towards the tip, reducing the likelihood of tip stall.

made between a triangular, tapered wing and the same basic shape, but with the distal regions curved anteriorly to give a lunate shape. In the proximal regions, lift distribution was more or less identical for the two geometries, but in the distal tip regions, lift distributions deviated significantly from each other, with the triangular shape showing an increasing lift coefficient right to the tip. In contrast, the lunate shape exhibited a maximum lift coefficient followed by significant reduction towards the tip (figure 6), indicating that it would be less prone to excessive lift coefficients and thus to local stall propagating from the tip.

(d) *Induced drag*

Next, we investigated the effect of anterior sweep on induced drag using the vortex lattice method (VLM) programme. With a plain untwisted wing, the span efficiency reduced with increasing anterior sweep, suggesting that while an anteriorly swept planform may be required for aerodynamic balance, it is disadvantageous in terms of the induced drag. Another variation was investigated, which represented an anteriorly swept wing where the relatively more elastic proximal regions of the membrane (the cruropatagium between the legs and the membrane that might have been controlled by leg movement [5,13]) were held at a different angle to the rest of the wing. Consequently, the wing sections in this region had reflex—a reversal in the section camber towards the posterior margin. With this reflex applied to the most proximal one-third of the wing, the span efficiency approached a value of one, the highest that is theoretically possible (figure 7).

(e) *Static stability*

The movement of CP with increasing angle of attack depends on the wing section and the wing geometry, but, as noted earlier, this typically moves in an anterior direction for cambered wing section shapes. As angle of attack increases, so does the lift coefficient, and the VLM programme allows the variation of CP location with lift coefficient to be determined (figure 7). This

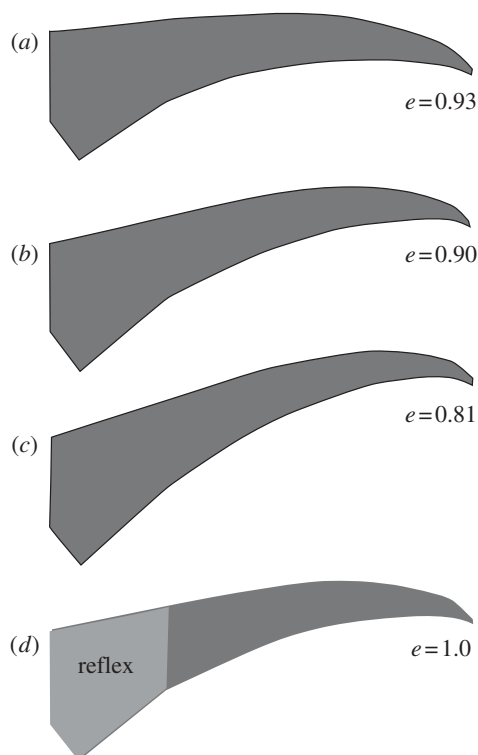


Figure 7. Comparison of the aerodynamic efficiency (as quantified by span efficiency e) for a family of wing geometries. In (a–c) wings have constant sections, but increasing anterior sweep. The span efficiency is reduced with increases in anterior sweep (a–c), while (d) has the same planform as (b) but different, reflexed wing sections in the proximal region. The span efficiency is increased significantly and is the highest of all the variants. This indicates that while anterior sweep can result in reduced efficiency, when applied in combination with reflex in the proximal regions of the wing, a very high efficiency can be secured.

was first calculated for a wing that was assumed to retain its shape as the lift coefficient increased. However, in response to an increase in lift (resulting, for example, from encountering a gust), the wing would in fact deflect owing to changing loading, with the wing bones deflecting dorsally and also being subject to twist along their length. This is because the applied lift force is posterior to the structural neutral axis of the wing bones. In consequence, the wing sections would experience twist along the length of the wing such that the angle of attack of the distal sections would be reduced, a configuration that is called ‘washout’ in aerodynamics. Thus, we ran the aerodynamic analysis for two washout configurations: 2.5° and 5° washout at the wing tip. Variation of CP location with lift coefficient ran almost parallel to that for the rigid wing, but was displaced in a posterior direction (figure 8).

This observation is relevant because of the situation where a flexible, anteriorly swept wing experiences a gust. The overall lift coefficient will increase, but the twisting of the wing will off-load the distal regions, so the total increase is likely to be less than for a rigid wing. Since for any given lift coefficient the location of the CP is shifted posteriorly with increasing washout, instead of CP moving anteriorly with increasing lift coefficient (along a line of constant wing twist), it will move posteriorly, conferring passive pitch stability (figure 8).

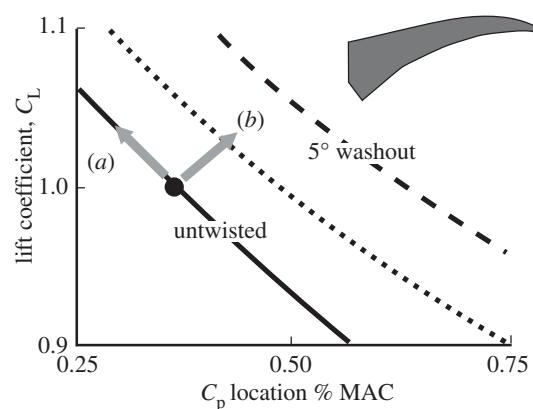


Figure 8. Effect of wing flexibility on pitch stability response. The graph shows the movement of the CP with changes in lift coefficient. The solid line is for an untwisted wing and the dashed lines for increasing amounts of washout (the natural deflection under transient aerodynamic load). When a rigid wing (a) experiences a transient increase in lift (i.e. encountering a gust), the CP moves anteriorly, resulting in pitch instability. However, if the wing flexes in response to this change in loading, the locus of the CP will be along the line (b), resulting in a posterior movement, which confers pitch stability.

This possibility—that wing flexibility actually can provide pitch stability—was first proposed by Sneyd *et al.* [19]. Our application of vortex lattice code shows that it is possible to investigate the likely effect and to confirm a possible mechanism (figure 8). It is also well worth noting that the opposite effect is true for a posteriorly swept wing: wing flexibility reduces pitch stability.

5. CONCLUSION

Animals that fly must be able to do so over a huge range of aerodynamic conditions, determined by weather, wind speed and the nature of their environment, and no single parameter can be used to define optimum flight performance as it relates to wing shape. Reconstructing the wings of pterosaurs has proved especially problematic: they were composed of a soft-tissue membrane, and are thus rarely preserved in the fossil record. As a result, theoretical aerodynamic modelling, combined with mechanical constraints imposed by what we know from fossils, is useful in predicting the likely boundaries of possible wing shapes employed by these extinct flying reptiles. We have applied this approach here, presenting a series of simple theoretical analyses bounded by clear mechanical and aerodynamic constraints.

Our modelling results show that the requirement for the CM and CP to be coincident imposes limits to the wing sweep, and that the need for membrane stability in flight provides very strong arguments in favour of a concave posterior margin. Considerations of minimum induced drag and passive static stability then indicate that a combination of anterior sweep, a lunate wing tip shape and a reflexed proximal wing section provides the most efficient theoretical pterosaur wing shape (figures 4b and 7d). These constraints on wing reconstruction are likely to provide reliable and robust predictions for actual wing shape, because the mechanical and physiological demands of flight place a great premium on aerodynamic and

structural (weight) efficiency. These are the parameters to which the constraints apply.

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REFERENCES

- Elgin, R., Hone, D. W. E. & Frey, E. 2011 The extent of the pterosaur flight membrane. *Acta Palaeontol. Pol.* **56**, 99–111. (doi:10.4202/app.2009.0145)
- Hankin, E. H. & Watson, D. M. S. 1914 On the flight of pterodactyls. *Aero. J.* **18**, 24–335.
- Bramwell, C. D. & Whitfield, G. R. 1974 Biomechanics of *Pteranodon*. *Phil. Trans. R. Soc. Lond. B* **267**, 503–581. (doi:10.1098/rstb.1974.0007)
- Wellnhofer, P. 1991 *The illustrated encyclopedia of pterosaurs*. London, UK: Salamander Books.
- Bennett, S. C. 2000 Pterosaur flight: the role of actinofibrils in wing function. *Hist. Biol.* **14**, 255–284. (doi:10.1080/10292380009380572)
- Wilkinson, M. T. 2008 Three-dimensional geometry of a pterosaur wing skeleton, and its implications for aerial and terrestrial locomotion. *Zool. J. Linn. Soc.* **154**, 27–69. (doi:10.1111/j.1096-3642.2008.00409.x)
- Dyke, G. J., Nudds, R. L. & Rayner, J. M. V. 2006 Limb disparity and wing shape in pterosaurs. *J. Evol. Biol.* **19**, 1339–1342. (doi:10.1111/j.1420-9101.2006.01096.x)
- Padian, K. & Rayner, J. M. V. 1993 The wings of pterosaurs. *Am. J. Sci.* **293**, 91–166. (doi:10.2475/ajs.293.A.91)
- Bennett, S. C. 2001 The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. *Palaeontograph. Abt.* **A260**, 1–153.
- Wilkinson, M. T., Unwin, D. M. & Ellington, C. P. 2006 High lift function of the pteroid bone and forewing of pterosaurs. *Proc. R. Soc. B* **273**, 119–126. (doi:10.1098/rspb.2005.3278)
- Currey, J. D. 2004 Tensile yield in compact bone is determined by strain, post-yield behaviour by mineral content. *J. Biomech.* **37**, 549–556. (doi:10.1016/j.jbiomech.2003.08.008)
- Currey, J. D. 2006 *Bones: structure and mechanics*. Princeton, NJ: Princeton University Press.
- Kellner, W. A., Wang, X., Tischlinger, H., Campos, D., Hone, D. W. E. & Meng, X. 2010 The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. *Proc. R. Soc. B* **277**, 321–329. (doi:10.1098/rspb.2009.0846)
- Jackson, P. S. & Christiet, G. W. 1986 Numerical analysis of three-dimensional elastic membrane wings. *AIAA J.* **25**, 5.
- Norberg, U. M. L. 2002 Structure, form, and function of flight in engineering and the living world. *J. Morph.* **252**, 52–81. (doi:10.1002/jmor.10013)
- Norberg, U. M. L., Brooke, A. P. & Trewheella, W. J. 2003 Soaring and non-soaring bats of the family pterorodidae (flying foxes, *Pteropus* spp.): wing morphology and flight performance. *J. Exp. Biol.* **203**, 651–664.
- Morris-Thomas, M. T. & Steen, S. 2009 Experiments on the stability and drag of a flexible sheet under in-plane tension in uniform flow. *J. Fluids Struct.* **25**. (doi:10.1016/j.jfluidstruct.2009.02.003)
- Pennycuik, C. J. 1988 On the reconstruction of pterosaurs and their manner of flight, with notes on vortex wakes. *Biol. Rev.* **63**, 209–231. (doi:10.1111/j.1469-185X.1988.tb00633.x)
- Sneyd, A. D., Bundock, M. S. & Reid, D. 1982 Possible effects of wing flexibility on the aerodynamics of *Pteranodon*. *Am. Nat.* **120**, 455–477. (doi:10.1086/284005)
- Azuma, A. 2006 *The biokinetics of flying and swimming*, 2nd edn. Reston, VA: AIAA Education Series.
- Palmer, C. 2010 Flight in slow motion: aerodynamics of the pterosaur wing. *Proc. R. Soc. B* **277**, 1881–1885. (doi:10.1098/rspb.2010.2179)
- Marchaj, C. A. 1988 *Aero-hydrodynamics of sailing*. London, UK: Adlard Coles Nautical.
- Anderson, J. D. 2007 *Fundamentals of aerodynamics*. London, UK: McGraw-Hill Int. Ed.
- Rayner, J. M. V. 1987 Form and function in avian flight. *Curr. Ornithol.* **5**, 1–66.
- Krus, P. 1997 *Natural methods for flight stability in birds*. Anaheim, CA: World Aviation Congress and exposition, SAE AIAA.
- Thomas, A. L. R. & Taylor, G. K. 2001 Animal flight dynamics. I. Stability in gliding flight. *J. Theor. Biol.* **212**, 399–424. (doi:10.1006/jtbi.2001.2387)
- DeYoung, J. 1976 *Historical evolution of vortex-lattice methods*. Washington, DC: NASA SP-405, NASA-Langley.
- Katz, J. & Plotkin, A. 2001 *Low-speed aerodynamics*, 2nd edn. Cambridge, UK: Cambridge University Press.
- Henderson, D. M. 2010 Pterosaur body mass estimates from three-dimensional mathematical slicing. *J. Vert. Paleo.* **30**, 768–785. (doi:10.1080/02724631003758334)
- Strang, K. A., Kroo, I., Gerritsen, M. & Delp, S. 2009 Efficient flight of pterosaurs—an unsteady aerodynamic approach. In *47th AIAA Aerospace Sciences Meeting (Proceedings)*, Orlando World Center Marriott, Orlando, FL, 5–8 January. See http://www.aiaa.org/content.cfm?page_id=230&lumeetingid=1811.
- Witton, M. T. 2009 A new approach to determining pterosaur body mass and its implications for pterosaur flight. *Zitteliana* **B28**, 143–159.
- Palmer, C. & Dyke, G. J. 2010 Biomechanics of the unique pterosaur pteroid. *Proc. R. Soc. B* **277**, 1121–1127. (doi:10.1098/rspb.2009.1899)
- Unwin, D. M. 2005 *The pterosaurs from deep time*. New York, NY: Pi Press.
- Bennett, S. C. 2007 Articulation and function of the pteroid bone of pterosaurs. *J. Vert. Paleo.* **27**, 881–891. (doi:10.1671/0272-4634(2007)27[881:AAFO TP]2.0.CO;2)
- Hazlehurst, G. & Rayner, J. M. V. 1992 Flight characteristics of Jurassic and Triassic Pterosauria: an appraisal based on wing shape. *Paleobiology* **18**, 447–463.