Biomechanics of the unique pterosaur pteroid

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Pterosaurs, flying reptiles from the Mesozoic, had wing membranes that were supported by their arm bones and a super-elongate fourth finger. Associated with the wing, pterosaurs also possessed a unique wrist bone—the pteroid—that functioned to support the forward part of the membrane in front of the leading edge, the propatagium. Pteroid shape varies across pterosaurs and reconstructions of its orientation vary (projecting anteriorly to the wing leading edge or medially, lying alongside it) and imply differences in the way that pterosaurs controlled their wings. Here we show, using biomechanical analysis and considerations of aerodynamic efficiency of a representative ornithocheirid pterosaur, that an anteriorly orientated pteroid is highly unlikely. Unless these pterosaurs only flew steadily and had very low body masses, their pteroids would have been likely to break if orientated anteriorly; the degree of movement required for a forward orientation would have introduced extreme membrane strains and required impractical tensioning in the propatagium membrane. This result can be generalized for other pterodactyloid pterosaurs because the resultant geometry of an anteriorly orientated pteroid would have reduced the aerodynamic performance of all wings and required the same impractical properties in the propatagium membrane. We demonstrate quantitatively that the more traditional reconstruction of a medially orientated pteroid was much more stable both structurally and aerodynamically, reflecting likely life position.

Keywords: flight; wing membrane; ornithocheirids; *Coloborhynchus*; *Anhanguera*; aerodynamics

1. INTRODUCTION

Of the three groups of vertebrates to evolve flapping flight, the extinct pterosaurs were arguably the most unusual (Wellnhofer 1991a; Unwin 2006). Unlike living bats and birds, these archosaurian reptiles supported an elastic wing membrane with their arm bones and a single elongate fourth finger. We know that the pterosaur wing membrane extended distally from the posterior edge of the forelimb, from the distal end of the wing finger and that it was also present proximally, on the anterior side of the antibrachium, forming a propatagium supported in part by a bone called the pteroid (figure 1). Although the anatomy and evolutionary relationships of pterosaurs have been studied in detail and thousands of fossils are known (Wellnhofer 1991a; Bennett 1996, 2001; Unwin 2003; Barrett *et al.* 2008; Butler *et al.* 2009; Dyke *et al.* 2009), the functional morphology of their flight has been debated for decades (e.g. Hankin & Watson 1914; Heptonstall 1971; Bramwell & Whitfield 1974; Stein 1975; Sneyd *et al.* 1982; Pennycuick 1988; Padian & Rayner 1993; Chatterjee & Templin 2004; Wilkinson 2008).

In particular, the articulation and orientation of the pterosaur pteroid have proved highly contentious. In most pterosaurs, this bone was slender and rod like (Bennett 2007), probably articulating with one of the syncarpals (figure 1), although even the precise location of this articulation is debated (Marsh 1882; Hankin & Watson 1914; Frey *et al.* 2006; Wilkinson *et al.* 2006; Bennett

2007). Irrespective of its articulation point, however, debates have centred on whether, or not, the pteroid supported the propatagial region of the pterosaur wing in flight by projecting forward in an anterior orientation (e.g. Hankin 1912; Frey & Riess 1981; Unwin *et al.* 1996; Wilkinson *et al.* 2006; Wilkinson 2007, 2008; Unwin 2006) (figure 1a), or was orientated more parallel to the edge of the wing in a medial orientation (e.g. Wagner 1858; Hankin & Watson 1914; Padian 1984; Wellnhofer 1991a; Padian & Rayner 1993; Bennett 2007; Prondvai & Hone 2008) (figure 1b). These alternative pteroid orientations, based either on anatomical (Bennett 2007) or aerodynamic evidence (Frey & Riess 1981; Wilkinson *et al.* 2006), have significantly different implications for the control and surface area of the propatagium and thus pterosaur flight performance.

Hypotheses for pteroid function have been based on anatomical interpretations of well-preserved fossils (Pennycuick 1988; Unwin *et al.* 1996; Frey *et al.* 2003; Bennett 2007), theoretical consideration of aerodynamic performance advantages (Frey & Riess 1981) and on aerodynamic experiments using models (Wilkinson *et al.* 2006). An anteriorly orientated reconstruction for the pteroid (Wilkinson 2007, 2008) means that the propatagium must have extended distally from the pteroid to form, in dorsal profile, an elongate triangle to an attachment at the distal end of the wing metacarpal (figure 1c). Proximal to the pteroid, the anterior edge of the propatagium is reconstructed subparallel to the radius/ulna, terminating in the region where the shoulder joins the body (Wilkinson 2007) (figure 1c). On the other hand, a medially orientated pteroid would imply a much

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Figure 1. Competing reconstructions of pterosaur wing outline and pteroid orientations: (a) anteriorly orientated pteroid (e.g. Unwin *et al.* 1996; Wilkinson *et al.* 2006); (b) medially orientated pteroid (e.g. Bennett 2007); (c) the membrane shape implied by an anteriorly orientated pteroid (Wilkinson 2008) and the pteroid-supported triangle of the propatagium.

narrower, shallow triangular propatagial shape (cf. figure 1b). Recent, detailed reconstructions of an anteriorly orientated pteroid have been based on ornithocheirid pterosaurs and they remain contentious (cf. Wilkinson *et al.* 2006; Bennett 2007).

Here we adopt a biomechanical approach to the question of pteroid orientation, considering four different, but related, aspects of pteroid function in the ornithocheirid pterosaur *Coloborhynchus*: (i) ability to resist applied bending loads, (ii) bone shape and suitability for reacting to these loads, (iii) shape and suitability for creating a lifting surface, and (iv) articulation effects on associated areas of the propatagium. We suggest that our results can be generalized across pterodactyloid pterosaurs and show that while no single characteristic can conclusively support one, or the other, pteroid orientation, the four lines of evidence we present, when taken together, provide very strong support for a medial orientation.

2. MATERIAL AND METHODS

Bending moments for an anteriorly orientated pteroid were calculated using the wing bone geometry of Wilkinson (2008) (figure 1c) and two different estimates for body mass (see below).

(a) Pteroid shape and length

Although the shape of the pterosaur pteroid varied considerably between species (Bennett 2007), this bone tended towards a slender, tapering, rod-like shape in the pterodactyloid clades Ornithocheiridae and Pteranodontidae. To provide a representative example for our analyses, we chose the Lower Cretaceous ornithocheirid *Coloborhynchus robustus* that had a 5.8 m wingspan (Wellnhofer 1991b; Unwin 2006; Wilkinson 2008). The pteroid of *C. robustus* (SMNK 1133PAL) is unusually well described (Unwin *et al.* 1996) (figure 2a); we modelled its mechanics using a propatagium shape based on Wilkinson (2008) (figure 1c).

Although the pteroid of SMNK 1133PAL is preserved in three dimensions, it lacks its distal end (Unwin *et al.* 1996) (figure 2a). We measured the length of the preserved section of this bone from Unwin *et al.* (1996) as 184 mm, while Wilkinson *et al.* (2006) reported this length as 178 mm from the specimen. Wilkinson *et al.* (2006) showed that pteroid length is isometric with ulna length (47% of the ulna length for ornithocheirid pterosaurs), which implies a length of 187 mm for SMNK 1133PAL. This is only slightly more than the preserved length and if correct would require an unusually blunt end to this bone, at variance with the reconstruction of Unwin *et al.* (1996) who show the pteroid tapering to a sharp point. Thus, the dotted lines in figure 2a show a possible extension of the pteroid to a similar pointed shape, resulting in the overall length of 238 mm (figure 2a) used here.

(b) Membrane tension and pteroid bone properties

Tensile forces in the plane of the pterosaur wing membrane must have existed because it needed to be stretched tight to operate effectively as a lifting surface. Between the wrist and the body, these forces would have been reacted by attachments to the body and wing bones (indicated by the lighter-shaded region in figure 1c), so tension in the wing must have increased as the elbow joint extended. With an anteriorly directed pteroid (Wilkinson *et al.* 2006; Wilkinson 2008), a large part of the propatagium would have extended in front of this region, held in tension between the wing bones and body (the darker-shaded region in figure 1c). At its proximal end, the tension in this anterior region of the membrane would also have been reacted by body attachment, but distally could only have been reacted by tension in the distal triangle of membrane between the pteroid and the metacarpal. These tensile forces would apply compressive load to the pteroid while the lift forces on the propatagium would have loaded it in bending, which would have necessitated a firm constraint at the base of the pteroid.

Maximum bending moment before pteroid failure depends upon the breaking strength of this bone and its cross-sectional shape. Loaded in bending, a pteroid would be subject to tensile and compressive stresses; because bone is significantly stronger in compression than in tension, the ultimate tensile strength (in the absence of buckling) will determine the maximum bending moment. However, because post-yield behaviour of bone is very variable (Currey 2004), ultimate properties are unreliable for structural analysis. More reliable, and consistent, is strain (and hence stress if Young's modulus (E) is known) at yield: Currey (2004) demonstrated a close relationship between E and yield strain (yield strain = $0.11E^{-0.13}$), one in which yield strain does not vary rapidly with E . Thus, at an E of 20 GPa, the yield strain is predicted to be $7500 \mu\epsilon$ and at 15 GPa, $7700 \mu\epsilon$, implying stresses of 150 and 116 MPa, respectively.

Although we cannot know Young's modulus of a pteroid, because these elements were made of dense, laminar bone (Unwin *et al.* 1996), they were probably at the higher end of the range for vertebrates. In terms of modern analogues, Currey (2004) gives E values for the bones of cranes of 23 GPa and for King Penguins of 21.7–22.2 GPa; from these data, we selected an average value of 22 GPa for E , providing a tensile yield strain of $7360 \mu\epsilon$ and a yield stress in tension of 162 MPa.

(c) Body weight and wing loading

In steady flight, the total lift on the wings equals body weight, which allows us to calculate estimates for propatagium lift

Figure 2. Pteroid morphology and lift distribution: (a) tracings of the well-preserved pteroid of *Coloborhynchus* (Staatliches Museum für Naturkunde, Karlsruhe (SMNK 1133PAL)) redrawn from Unwin *et al.* (1996, fig. 2). Top tracing shows the pteroid outline in the ventral view, the lower tracing is in the medial view. Dotted lines show extension of the pteroid to a likely pointed shape; (b) wing section (black outline, above) and pressure distribution (grey outline, below) used for analysis.

and thus pteroid bending moment. However, estimating the body mass of pterosaurs is problematic. Most early methodologies (e.g. Bramwell & Whitfield 1974; Brower & Venius 1981) used similar morphometric scaling relationships and arrived at very low values, resulting in an average predicted mass for a 5.8 m wingspan pterosaur of 13.9 kg. Witton (2008) presented new estimates based on dry skeletal mass resulting in much higher estimates for pterosaurs. Since ornithocheirid pterosaurs are consistently lighter than other pterosaurs (Witton 2008), we took a subset of closely related ornithocheirid species (*Nurhachius*, *Nyctosaurus*, *Pteranodon*, *Anhangura*) from Witton's (2008) dataset and using the same curve-fitting approach recovered the relationship $M = 0.4526 \times S^{2.4232}$, where M is the body mass and b is the wingspan; this gives a predicted mass of 32 kg for a 5.8 m wingspan. These two sources provide upper and lower bounds for our wing loading calculations.

(d) Wing area

We scaled wing area measured from Wilkinson's (2008) reconstruction of *Anhangura* to a 5.8 m wingspan *Coloborhynchus*. Wilkinson (2008) showed that allometric

coefficients for ornithocheirids are very close to unity, so this area scales isometrically, giving an area of 1.845 m² for the cheiro- and uropatagia (figure 1c). The area of each propatagium was thus estimated as 0.22 m² using the wing bone reconstructions of Wilkinson (2008) (figure 1c), and gives a total membrane area of 2.285 m².

(e) Lift distribution

Wilkinson *et al.* (2006) proposed that the broad pterosaur propatagium acted as a high lift flap on the front of the wing (figure 1c). Although no measured aerodynamic pressure distribution data exist for such a section shape, it is possible to estimate the pressure distribution across the wing and the propatagium using numerical methods (e.g. the JavaFoil program; Hepperle 2008). A possible pterosaur wing cross section (figure 3a) was analysed with JavaFoil, and results show lift concentrated in the anterior region of the section when operating at a lift coefficient of 0.8, representative of soaring flight (Pennycuik 1983; Chatterjee *et al.* 2007) (figure 2b). We used this pressure distribution to calculate the proportion of lift generated by the

Figure 3. Results: (a) load distribution of pteroid and location of tissue required to react to bending moment produced by aerodynamic lift forces in an anterior orientation, based on *Anhanguera* but scaled to a 5.8 m wingspan *Coloborhynchus* (after Wilkinson 2008); (b) predicted membrane strain as pteroid flexion increases.

propatagium and the centre of that lift; from these, we estimated the pteroid bending moment.

Pressure distribution was integrated using numerical techniques (<http://mathworld.wolfram.com/NumericalIntegration.html>) over 20 ordinates. Because lift is the integral of the pressure distribution, we apportioned lift between the anterior (i.e. pteroid supported) and posterior regions of the propatagium. The propatagium supported 56 per cent of the total lift (the shaded area of the pressure curve), and the centroid was 18.6 per cent of the chord from the leading edge.

We also modified our calculations to account for dynamic flight conditions such as a pitch-up landing manoeuvre. Under soaring conditions, the steady-state lift coefficient is approximately 0.8 (Pennycuik 1983; Chatterjee *et al.* 2007), but near to stall this coefficient can be much greater. Wilkinson (2007) reported a peak lift coefficient of 2.5 at stall for a pterosaur wing cross-section with a wide propatagium; this means that in a dynamic, pitch-up landing, the transient lift force could have been as much as three times that of the steady state. Note that our estimate for lift is conservative because: (i) although pressure may have been further concentrated on the propatagium owing to separation, this effect was not included and (ii) we assume

span-wise wing loading to be proportional to the local chord even though in practice lift was probably concentrated towards the root with the wing tips unloaded owing to twist (Wilkinson 2008).

(f) *Bending moment*

We calculated bending moments on the pteroid using steady-state and dynamic stall lift conditions for two wing loading cases based on high- and low-weight estimates. The bending moments were calculated as the product of the lift on the pteroid-supported triangle of the propatagium (30.92 N, figure 1c) and the distance of the centroid from the region of greatest narrowing of the pteroid near the attachment to the articulation (where the cross-section is 11.7×12.2 mm) (figure 2a). To calculate section properties of the pteroid, we assumed that the pteroid bone wall thickness was between 0.47 and 0.70 mm. Unwin *et al.* (1996) did not provide a cortical thickness but noted that the *Coloborhynchus* pteroid comprised parallel fibred bone and was pneumatized and contained trabeculae, a common feature of thin-walled pterosaur long bones. Wellnhofer (1985) described the pteroid of *Santanadactylus spixi*: 75 mm long with a missing distal end (reconstructed total length, 100 mm), an oval cross-section and a wall thickness of

0.5 mm. Witton (2008) undertook an analysis of cortical thickness published by Steel (2008; L. Steel 2005, unpublished data) and presented the regression of cortical thickness with diameter. A diameter of 12 mm is associated with a mean thickness of 0.47 mm, and we adopted a somewhat arbitrary but conservative maximum of 0.70 mm to give an indication of the sensitivity of our results.

Bending stress was calculated using the standard beam bending formula, $\sigma = M \times y/I$, where σ is the stress, y , the distance from the neutral axis of the cross-section, M , the applied moment and I , the second moment of area of the section. The second moment of area for an elliptical section is $\pi/4 \times a \times b^3$, where a and b are the radii.

(g) Pteroid loading in a medial orientation

If the ornithocheirid pteroid was orientated medially, the area of the propatagium would have been much smaller, estimated from the geometry shown in figure 1c, less than 0.10 m² for *Coloborhynchus*. Consequently, not only would the loads be much reduced, but the different geometries would also change the type of loading. Held medially, the pteroid is not subject to any bending loads at all as it would be a tension member along the anterior edge of the propatagium (figure 1c). Since the propatagium is thought to have been elastic and no more than 2 mm thick (Frey *et al.* 2006), any tensile loads it transmitted to the pteroid must have been small compared with the tensile strength of the bony pteroid.

(h) Membrane strain

Wilkinson (2008) provided a series of diagrams showing stages in a proposed pteroid articulation, from a flexed or 'furled' position (pointing medially and subparallel to the radius and ulna), to fully extended (pointing anteriorly and slightly dorsally). This geometry requires an extensible triangle of the propatagium distal to the pteroid, extending to the end of the metacarpal. The distance from the tip of the pteroid to the distal end of the metacarpal (distal termination of the propatagium) was calculated using Euclidean geometry for each of Wilkinson's (2008) three stages to estimate the change in length and hence strain in the anterior edge of the membrane triangle.

3. RESULTS

Calculated bending stresses for the *Coloborhynchus* pteroid are shown in table 1. During dynamic stall, all reconstructions result in very high, unsafe stresses on this bone (figure 3a); low wall thickness and high weight give a value 120 per cent of yield stress, reducing to 96 per cent with high wall thickness (applied stress: yield stress ratios of 0.83 and 1.04, respectively) (table 1); using the lower weight estimate (13.9 kg) results in ratios of 1.89 and 2.39. Under steady lift conditions, using the high body weight estimate, ratios are 2.58 and 3.26, while with low body weight these are 5.91 and 7.48 (table 1).

Note that our calculations are for conservative loading cases; compressive loading on the pteroid is not taken into account, which, when combined with the bending moment, would increase the possibility of buckling failure. It is also likely that aerodynamic loading would be more concentrated on the proximal part of the wing especially during dynamic stall, the situation in which the broad propatagium is expected to be most effective.

Table 1. Calculated variation in pteroid tensile bending stress and stress ratios for different cortical thicknesses of bone and body weights.

cortical thickness (mm)	0.47	0.7	0.47	0.7
weight (N)	314	314	137	137
steady stress (N m ⁻²)	63	50	27	22
steady stress ratio	2.58	3.26	5.91	7.48
dynamic stress (N m ⁻²)	196	155	86	68
dynamic stress ratio	0.83	1.04	1.89	2.39

Note also that our calculations were carried out on *Coloborhynchus* since reliable information is available on the size and cross-section of the pteroid. However, other pterodactyloids have proportionally longer (*Cycnorhamphus*), and in some cases more slender, pteroids (*P. kochi*) (Wellnhofer 1968; Wellnhofer 1991a; Bennett 2007), implying that they too were structurally incapable of resisting the bending loads of an anterior orientation.

Indeed, our reconstruction shows that if the pteroid was orientated anteriorly, the length of the anterior edge of the distal triangle of the propatagium would increase by 40 per cent (figure 3b) as the pteroid moved from its anterior ('flight') position to its fully flexed (furled) position. This introduces a substantial additional strain in the propatagial material since it must have been under initial load in order to balance the tension required to keep the proximal region taut and stable in flight.

4. DISCUSSION

A number of lines of evidence suggest that the pteroid of ornithocheirid pterosaurs was held in a medial orientation during flight. Further, our mechanical analyses show that this bone would have been very highly stressed in flight if orientated anteriorly, particularly if the larger weight estimates proposed for these pterosaurs (Witton 2008) are correct. Although calculated stresses do not exceed yield stress in all cases, ratios of calculated stresses to yield stress (so-called safety factors) are generally less than 3, lower than *in vivo* measurements of extant bats and birds (Pennycuik 1967; Biewener & Dial 1995; Swartz *et al.* 1996; *contra* Kirkpatrick 1994), which fall in the range 4.8–5.1. Although Kirkpatrick (1994) measured breaking stresses of bird and bat bones, the large standard deviation range recorded in this study (up to 50% of mean values in some cases) and other inconsistencies in results render conclusions problematic (C. Palmer 2009, unpublished data).

While it could be argued that, under very specific conditions (i.e. steady flight, calm air and low body mass), the ornithocheirid pteroid was sufficiently strong to resist the applied bending loads when held anteriorly, its proximal articulation requires the presence of soft tissue to resist the applied moment. Suitable attachment sites for counteractive muscles or tendons on pterosaur wrist bones have never been described, lending further support to our generalized medial model for the orientation of the pterosaur pteroid. In addition, and also contrary to an anterior orientation, the ornithocheirid pteroid has a significant curvature towards its wrist attachment (Unwin *et al.* 2006; Bennett 2007; Wilkinson 2008) and is

reconstructed with this curvature orientated convex dorsally, an unsuitable shape for the attachment of the restraining ligaments required to prevent rotation. Their lever arm (distance between the insertion point on the pteroid and its articulation) would have been greatly reduced by this direction of pteroid curvature (figure 3a); from a purely mechanical point of view (not implying a realistic anatomical reconstruction), if the pteroid were inverted, its shape would be much better suited to resisting dorsal bending. Thus, even if this bone were deployed anteriorly (Wilkinson *et al.* 2006; Wilkinson 2008), it is curved in the wrong direction to resist the bending that must have occurred. The pteroid of another pterodactyloid, *Nyctosaurus* (Frey *et al.* 2006; Bennett 2007), has an even sharper curvature in this region, rendering an anterior orientation even more unlikely because of constraints at the wrist.

The likely alternative configuration, a medially orientated pteroid (e.g. Frey *et al.* 2006; Bennett 2007), would not have suffered these geometric constraints, would have experienced negligible bending loads and would thus have functioned within safe structural limits. In such an orientation, depression of the pteroid could have deflected the propatagium and increased camber in the wing section, providing an increase in the maximum lift coefficient. It is also notable that available pteroid cross sections from across Pterosauria (Wellnhofer 1985; Unwin *et al.* 1996) show that this bone had a suboval cross-section with the major axis in the mediolateral plane—the opposite of what might be expected from a bone that is loaded in dorsoventral bending. Such proportions might however be expected in a bone that is directed medially and forms the leading edge of the propatagium as this would minimize drag, a result that certainly applies across all pterodactyloid pterosaurs.

In some pterodactyloids, known pteroids are gently curved dorsally towards the distal end when orientated anteriorly (figure 3a) (Wellnhofer 1968, 1991a; E. Frey 2009, personal communication). One proposed justification for an anteriorly orientated pteroid has been that it functioned to provide a high lift wing section (Wilkinson *et al.* 2006), with the propatagium deflected ventrally by the pteroid to increase camber in the local wing section. A pteroid curved dorsally towards its tip would counteract this effect and reduce (rather than increase; *contra* Wilkinson *et al.* 2006) the maximum achievable lift. In addition, the shape of the propatagium implied by an anterior orientation also requires a sharp discontinuity in the anterior (leading) edge of the wing (Wilkinson *et al.* 2006) (figure 1c). This shape would have generated vortices from the sharply angled edge; a characteristic that would have increased induced drag and reduced the effectiveness of the wing membrane region affected by the shed vorticity (Hoerner 1985).

Our results show that in order for the ornithocheirid pteroid, around 50 per cent of the ulna length, to exhibit the degree of movement proposed by Wilkinson (2008), the outer region of the propatagium must have stretched by about 40 per cent or more between its 'flying' and furled positions (figure 3b). Although this might have been possible if the wing membrane were very flexible, this very degree of flexibility would make the membrane ill-suited to provide the stability and tension needed in the anterior edge of a lifting surface. For this distal area

of the membrane to exert tension in the broad, proximal section of the propatagium (figure 1c), it would have had to increase, or at least keep constant, the in-plane tension as the pteroid was deployed and the length of its anterior edge was reduced. This is the exact opposite of the stress–strain relationship for the skin of flying vertebrates (Swartz *et al.* 1996), so to be anatomically and mechanically feasible the distal region of the pterosaur propatagium would have needed to contain muscles attaching to both the pteroid and the wing metacarpal. Locations for such muscles attachments have never been described. It is also notable that the pteroid of *Cycnorhamphus* was proportionately much longer (75% of ulna length; Bennett 2007), which would have required even greater extension in this region of the wing membrane.

In conclusion, while none of our arguments might be individually conclusive, when taken together they provide a very strong biomechanical case against an anteriorly orientated ornithocheirid pteroid, and are complemented by the anatomical conclusions of Bennett (2007). Our argument for a medial orientation does not rely upon precise details of articulation but on the more general issues of the structural strength of the pteroid bone, its shape with respect to the applied loading, its interaction with the propatagium and resultant aerodynamic performance. More generally, we demonstrate that basic aerodynamics can be used to predict 'envelopes of performance' when discussing what pterosaurs could, and could not, do with their wings.

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