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SHORT COMMUNICATION

Limb disparity and wing shape in pterosaurs

G. J. DYKE,*† R. L. NUDDS† & J. M. V. RAYNER†

*School of Biology and Environmental Science, University College Dublin, Dublin, Ireland
†School of Biology, University of Leeds, Leeds, UK

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Abstract

The limb proportions of the extinct flying pterosaurs were clearly distinct from their living counterparts, birds and bats. Within pterosaurs, however, we show that further differences in limb proportions exist between the two main groups: the clade of short-tailed Pterodactyloidea and the paraphyletic clades of long-tailed rhamphorhynchoids. The hindlimb to forelimb ratios of rhamphorhynchoid pterosaurs are similar to that seen in bats, whereas those of pterodactyloids are much higher. Such a clear difference in limb ratios indicates that the extent of the wing membrane in rhamphorhynchoids and pterodactyloids may also have differed; this is borne out by simple ternary analyses. Further, analyses also indicate that the limbs of *Sordes pilosus*, a well-preserved small taxon used as key evidence for inferring the extent and shape of the wing membrane in all pterosaurs, are not typical even of its closest relatives, other rhamphorhynchoids. Thus, a bat-like extensive hindlimb flight membrane, integrated with the feet and tail may be applicable only to a small subset of pterosaur diversity. The range of flight morphologies seen in these extinct reptiles may prove much broader than previously thought.

Introduction

Pterosaurs were one of the most distinctive groups of all the archosaurian reptiles, characterized by a membranous wing, supported along its leading edge by the forelimb and elongated fourth finger (wing finger). Pterosaurs lived alongside the dinosaurs throughout the Mesozoic and were the first true flying vertebrates – their mode of flight was first discussed by Cuvier (1801). However, despite a generally good fossil record, both temporally and stratigraphically (Benton, 1993), the precise construction and shape of the pterosaur wing remains disputed (Padian & Rayner, 1993; Unwin & Bakhurina, 1994; Unwin, 1999). In particular, the extent of the flight membrane in these reptiles has been considered as either 'bird-like' (narrow wing attached only to the forelimbs) or 'bat-like' (broad membrane attached to both the forelimbs and hindlimbs): an apparently clear-cut dichotomy with clear implications for pterosaur flight styles, ecology and aerodynamics. Direct fossil evidence for the flight membrane in pterosaurs is, however, extremely rarely preserved. Most recently, it has been suggested that the flight membrane shape in *all* pterosaurs must have been 'bat-like' (i.e. integrated with the legs and tail) because of soft tissue preservation seen in one exceptionally well-preserved taxon, *Sordes pilosus* from the Jurassic of Kazakhstan (Unwin & Bakhurina, 1994; Unwin, 1999, 2006). Because the wing membrane is associated with the hindlimb and tail in this small pterosaur, its shape and extent has been used to bolster a model for the wing morphology and flight style of pterosaurs in general (Unwin & Bakhurina, 1994; Unwin, 1999, 2006). Can exceptional preservation in one kind of pterosaur be used as inference for the morphology of all? Interpretation of soft tissue morphology is difficult and open to some subjectivity (Padian & Rayner, 1993; Unwin, 1999) and although soft tissue is preserved in other pterosaur specimens (Frey & Martill, 1998; Frey *et al.*, 2003) its extent and preservation remains equivocal (see Padian & Rayner, 1993 and Unwin, 1999, 2006 for discussion of some specimens). In contrast, bone lengths and proportions are more easily identified especially in fossil taxa,

Correspondence: Gareth Dyke, School of Biology and Environmental Science, University College Dublin, Belfield Dublin 4, Ireland.
Tel.: 353 1 716 2195; fax: 353 1 716 1152;
e-mail: gareth.dyke@ucd.ie

they are repeatable as specimen measurements and have been shown to reflect wing morphology and flight styles in vertebrate taxa (Rayner & Dyke, 1998; Nudds *et al.*, 2004). Thus, if the wing morphology of *Sordes* is to be considered typical of all pterosaurs we would predict its wing bone proportions are also typical of all pterosaurs.

To address this prediction in this study, we investigate trends, similarities and differences in the forelimb and hindlimb proportions of pterosaurs. The forelimb and hindlimbs (in bats) are part of the flight apparatus and therefore we would predict that flight mode and flight morphology should be reflected in limb proportions and ratios. We specifically address the question of whether pterosaurs were more 'bird-like' or 'bat-like' in their limb proportions. We determine whether the limb proportions of *Sordes* are representative of pterosaurs in general, and therefore whether the 'bat-like' model (Unwin, 1999) can be universally applied to encompass all diversity within this clade.

Material and methods

The data we use here were taken from sets of measurements in the literature, as well as directly from bird, bat and pterosaur specimens (Hazlehurst, 1991; Nudds *et al.*, 2004). For analyses (Appendix), data are included for 24 valid species of pterosaurs, 216 species of bats and 447 species of birds (Nudds *et al.*, 2004). Forelimb and hindlimb sets were divided into three elements for this analysis: humerus, radius or ulna and hand (metacarpals), alongside femur, tibia or tibiotarsus (birds) and foot (metatarsals). The tarsal contribution to the tibia was included for all taxa; in pterosaurs and bats, which have nonfused feet, we measured the length of metatarsal III and considered this equivalent to the avian tarsometatarsus (Gatesy & Middleton, 1997). All linear relationships were analysed using a Model II or reduced major axis (RMA) regression, which accounts for variation in both x and y variables and should minimize error when the error distributions of the variates are unknown (Rayner, 1985; Sokal & Rohlf, 1995). The RMA slope was calculated as the ordinary least squares (OLS) slope (regression coefficient) divided by the OLS correlation coefficient and 95% confidence limits were calculated following Sokal & Rohlf (1995). Standard error of the RMA slope was taken to be equal to that of the OLS slope (Sokal & Rohlf, 1995). Because ANCOVA assumes that the independent variable is measured without any error (Sokal & Rohlf, 1995) – not the case here – differences in the forelimb to hindlimb length ratio were investigated using a common line approach. The estimated bat RMA regression line was taken as the common line and then the slopes and intercepts of the RMA regressions for the other groups were tested against it using t-tests. Mean values of species were calculated for all data; the pterosaur sample was further divided following recent phylogenetic hypotheses (Kellner, 2003; Unwin, 2003, 2006) into clades of derived pterodactyloids (short-tailed, long-necked taxa) and rhamphorhynchoids (basal, long-tailed, short-necked taxa).

Results

The slopes of the RMA regressions describing the relationship between hindlimb length and forelimb length (Fig. 1) for pterodactyloids and rhamphorhynchoids did not differ from that of bats ($t = -0.972$, $P > 0.05$ and $t = 0.069$, $P > 0.05$ respectively). This, however, was not the case for birds where the regression slope was significantly lower than that of bats ($t = -9.049$, $P < 0.001$). The intercept of the regression describing the hindlimb to forelimb length ratio of rhamphorhynchoids did not differ significantly from that of bats ($t = -0.341$, $P > 0.05$). In contrast, the intercepts of the pterodactyloids and bird regressions were significantly higher than that of bats ($t = 5.386$, $P < 0.001$ and $t = 510.807$, $P < 0.001$ respectively). Therefore, the relationship between hindlimb and forelimb length in rhamphorhynchoids is not discernable from that of bats. In contrast, although the slopes of the relationships between limb lengths are similar, pterodactyloids have longer hindlimbs relative to their forelimbs than bats (Fig. 1). Birds also have longer hindlimbs relative to their

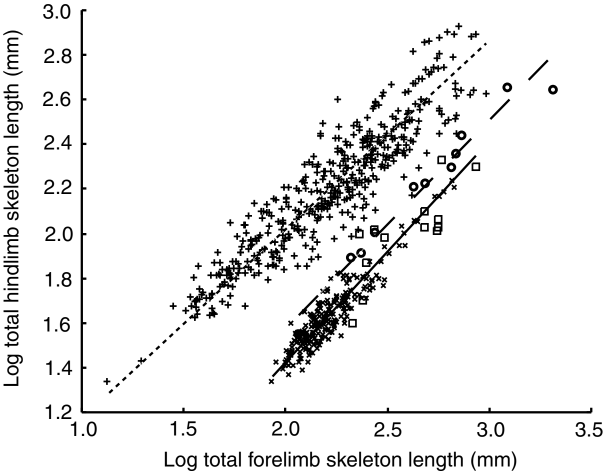

Fig. 1 Reduced major axis regressions of total hindlimb length against total forelimb length for each of the four taxa: birds ($y = 2.19x^{0.84}$, $t = 51.20$, $n = 447$, $r^2 = 0.84$, $P < 0.001$, dotted line), pterodactyloids ($y = 0.51x^{0.93}$, $t = 15.39$, $n = 11$, $r^2 = 0.96$, $P < 0.001$, large dashed line), bats ($y = 0.28x^{0.99}$, $t = 39.50$, $n = 216$, $r^2 = 0.87$, $P < 0.001$, solid line) and rhamphorhynchoids ($y = 0.25x^{1.00}$, $t = 5.20$, $n = 13$, $r^2 = 0.64$, $P < 0.001$, solid line). The regression lines for bats and rhamphorhynchoids are represented by a single line as they are not distinguishable on the scale of this figure. Tests of the intercepts and slopes of the regression lines suggested that both birds (plus signs) and pterodactyloids (circles) differ in their limb length ratios to that of bats (crosses), but the limb length ratios of rhamphorhynchoids (squares) and bats are similar (see Results).

forelimbs than bats, but the scaling relationship (slope) between the hindlimbs and forelimbs of birds also differs from that of bats.

Our data are also sufficient to demonstrate that the three taxonomic groups of flying vertebrates (birds, bats and pterosaurs) can easily be distinguished on the basis of their forelimb proportions (Fig. 2a). Intuitively, because of their elongated wing fingers, the hand of pterosaurs is much longer than that of either birds or bats; this is correlated well with a relative reduction in the lengths of the proximal bones of the wing (Fig. 2a). The rhamphorhynchoid *Sordes*, the principal basis for some wing membrane reconstructions, has intermediate forelimb proportions between pterosaurs and bats (Fig. 2a).

In their forelimb proportions, pterosaurs were conservative: a relatively longer hand, for example, is matched by a correlated reduction in the relative length of the humerus, radius and ulna (Fig. 2b). There is no marked difference between the pterodactyloid and rhamphorhynchoid taxa, with the exception of *Sordes* – the only pterosaur included in our data set that has a hand <80% of its total forelimb length (Fig. 2b). Conversely, pterosaur hindlimb proportions are much more variable than are their forelimbs (Fig. 2b). In this case, *Sordes* falls away from the other rhamphorhynchoids, although within the range of the entire clade (Fig. 2b).

Discussion

Two critical aspects of pterosaur limb proportions are bourne out by our simple analyses: a clear difference between pterodactyloids and clades of rhamphorhynchoids; and the unusual nature of the limbs of *Sordes*. Our data suggest that *Sordes* is neither a typical pterosaur, nor a typical rhamphorhynchoid. Given that the phylogenetic placement of this taxon also remains controversial (Kellner, 1995, 1996; cf. Kellner, 2003; Unwin, 2003, 2006), the wing morphology of *Sordes* may not be representative of all pterosaurs, as previously suggested (Unwin, 1999, 2006).

Further, clear differences in the reduction of the forelimb and hindlimb segments between pterodactyloid and clades of rhamphorhynchoid pterosaurs may reflect differences in the degree of wing membrane involvement with the hindlimbs. The forelimb to hindlimb ratio in rhamphorhynchoids is similar to that of bats (Fig. 2a); bats and *Sordes* have flight membranes integrated with their hindlimbs and tail (Unwin & Bakhurina, 1994; Unwin, 1997, 1999, 2006). Functional integration of both the forelimb and hindlimbs with the flight apparatus means that correlated changes in forelimb proportions would likely be mirrored in the hindlimbs. It thus remains possible that the 'bat-like' model may prove applicable to all rhamphorhynchoids, especially those that prove closely related to *Sordes*, in the absence of any further evidence of soft tissue preservation. Conversely, pterodactyloids have longer hindlimbs relative to their forelimbs than do either rhamphorhynchoids or bats (Fig. 2a).

Of course, primary feathers contribute part of the functional length of bird wings. We are, however, interested in what the skeleton can tell us, because as argued in the introduction, bone dimensions are more easily interpreted in fossil specimens than the extent of soft tissue or feathers. Furthermore, differences in external structure and flight behaviour are correlated well with the underlying skeletal morphology (Gatesy & Middleton, 1997; Rayner & Dyke, 1998; Nudds *et al.*, 2004). Birds have relatively small hand-wings and a relatively short forelimb to hindlimb ratio and feathers, whereas bats, rhamphorhynchoids and pterodactyloids have longer hand-wings and longer forelimbs relative to their hindlimbs and have membranous wings. Hence, our argument that skeletal lengths indicate differences in external morphology is corroborated further. We do not have wing lengths for the bird specimens used in this

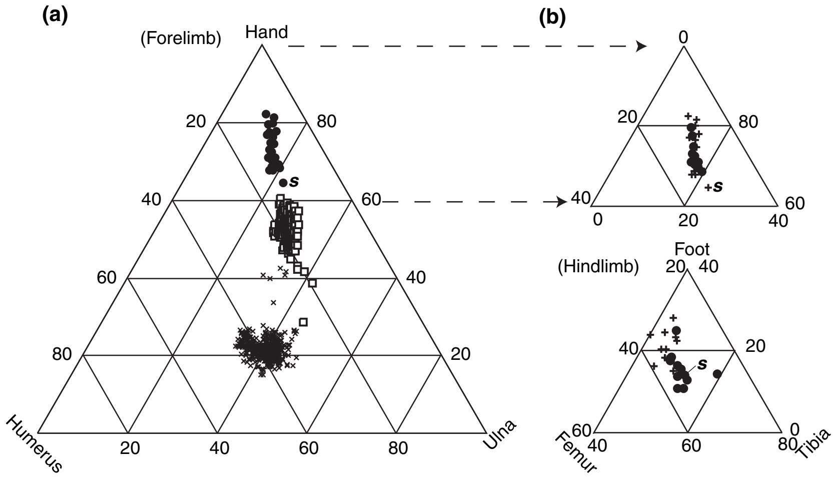

Fig. 2 Ternary plots to show limb variation in flying vertebrates: (a) forelimb segments in birds (crosses), bats (squares) and pterosaurs (circles); (b) forelimb and hindlimb segments in pterosaurs (circles denote pterodactyloids, crosses rhamphorhynchoids). The position of *Sordes* is indicated by an 'S'.

study. If, however, we double the forelimb lengths of the birds (an extreme estimate of the primary feathers contribution to wing length), then although the regression line for birds in Fig. 1 is moved to the right (changes from $y = 2.19x^{0.84}$ to $y = 1.21x^{0.84}$) nearer the bat line, the regression equation still remains markedly and significantly different from that of the other three taxa.

Differences in forelimb to hindlimb proportions and ratios or ratios nearer to an extant, but unrelated vertebrate clade suggests clear differences in membrane shape. Because the limb ratios vary, even if the membrane attachment sites are the same for each pterodactyl taxa, membrane shape must differ. Conversely, if membrane shape is similar between the two pterodactyl taxa, then because the limb ratios are different the attachment sites of the membranes must differ! It does not, of course, necessarily mean that a 'bat like' model is not applicable to all pterosaurs. However, since there is as yet no convincing fossil evidence for the extent of the flight membrane in these pterosaurs relative to the legs and feet, we argue that application of the *Sordes* morphology to pterodactyloids in general is perhaps premature. Although it is tempting to extrapolate far-reaching conclusions when presented with exceptionally well-preserved fossil specimens, extrapolating across all pterosaur diversity based on just a few wing membranes should be performed with caution.

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Supplementary Material

The following supplementary material is available for this article online:

Appendix S1: Bird, bat and pterosaur species data used for the purposes of this analysis.

This material is available as part of the online article from http://www.blackwell-synergy.com

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