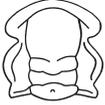# Primary feather lengths may not be important for inferring the flight styles of Mesozoic birds

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LETHAIA

Although many Mesozoic fossil birds have been found with primary feathers preserved, these structures have rarely been included in morphometric analyses. This is surprising because the flight feathers of modern birds can contribute approximately 50% of the total wing length, and so it would be assumed that their inclusion or exclusion would modify functional interpretations. Here we show, contrary to earlier work, that this may not be the case. Using forelimb measurements and primary feather lengths from Mesozoic birds, we constructed morphospaces for different clades, which we then compared with morphospaces constructed for extant taxa classified according to flight mode. Consistent with older work, our results indicate that among extant birds some functional flight groups can be distinguished on the basis of their body sizes and that variation in the relative proportions of the wing elements is conservative. Mesozoic birds, on the other hand, show variable proportions of wing bones, with primary feather length contribution to the wing reduced in the earlier diverging groups. We show that the diverse Mesozoic avian clade Enantiornithes overlaps substantially with extant taxa in both size and limb element proportions, confirming previous morphometric results based on skeletal elements alone. However, these measurements cannot be used to distinguish flight modes in extant birds, and so cannot be used to infer flight mode in fossil forms. Our analyses suggest that more data from fossil birds, combined with accurate functional determination of the flight styles of living forms is required if we are to be able to predict the flight modes of extinct birds. □ *Birds, flight, morphospace, Mesozoic, wing.*

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Modern birds (Neornithes) are the most diverse extant tetrapod group, comprising over 10 400 species (Newton 2003; Gill 2007) and occupying a wide array of ecological niches (del Hoyo *et al.* 1992–2010; Gill 2007). The ecological diversity of modern birds means that they have evolved a huge range of flight techniques, ranging from short bursts for rapid take-off to sustained flapping and soaring (Dial 2003; Gill 2007; Bruderer *et al.* 2010). The many flight modes and speeds in living birds have been shown to be linked to variations in the morphology of the skeletal and non-skeletal (e.g. muscles, feathers) elements that comprise and power the wings (Dial & Biewener 1993; Tobalske *et al.* 2003; Dawson 2005; Nudds *et al.* 2007), as well as to variations in wing loading (weight divided by wing area) and aspect ratio (wing span divided by average wing chord) (Rayner 1988). These latter two factors in particular relate to flight speed and manoeuvrability in all extant flying vertebrates (Norberg & Rayner 1987; Alerstam *et al.* 2007).

It is reasonable to argue that morphological characters that are linked to flight mode in living birds are also likely to have been important to the aerial abilities of extinct taxa. However, previous attempts to compare flight-linked aspects of the forelimb between living and extinct birds from the Mesozoic have focused on the proportions of the skeletal elements (see McGowan & Dyke 2007; Dyke & Nudds 2009), omitting evidence from thousands of Cretaceous bird fossils that preserve the remains, or unequivocal imprints, of flight feathers (but see Wang *et al.* 2011a, b).

Several studies comparing Mesozoic and extant birds have previously been carried out. One of these compared the forelimb proportions of Enantiornithes to those of extant Neornithes, focusing on the proportions of the skeletal wing composed of the three main elements, humerus, ulna and manus (Dyke & Nudds 2009), while others have attempted to compare wing bone and feather proportions between fossil birds and their living counterparts (Wang *et al.* 2011a, b). Differences in the lengths of the longest primary feather relative to total arm length (ta = humerus + ulna + manus) in Mesozoic and extant birds have been used to suggest that the abundant Chinese Cretaceous bird

Confuciusornis (Confuciusornithidae) had a different flight mode from extant birds and may well have been limited to gliding (Wang *et al.* 2011a, b). This conclusion is also consistent with shoulder anatomy (Rayner 2001; Senter 2006) as well as the relative lengths and rachis widths of its primary feathers (Nudds & Dyke 2010; Wang *et al.* 2011b). Several of these studies have also suggested that the enantiornithines as a group probably encompassed a range of flight modes, including at least some used by modern birds. We also know that the relative lengths of the primary feathers are important in determining flight style in extant birds (Nudds 2007; Nudds *et al.* 2011).

In this article, we take a new perspective on this issue by combining measurements of primary feathers and the skeletal arm to investigate further the functional forelimb morphospaces occupied by Mesozoic and extant birds (see also Wang *et al.* 2011a, b). Specifically we test whether, or not, hypotheses that invoke similarities in flight mode, or differences in the relative proportions of wing bone lengths can still be supported when primary feathers are included in an analysis.

Materials and methods

Data

Wing measurements are derived from two sources, for extant birds (Nudds *et al.* 2011) and Mesozoic birds (Wang *et al.* 2011b). Distinct from other studies (see Wang *et al.* 2011a), we made the two data sets directly comparable by including only those Mesozoic birds for which digit measurements were available: this reduced our data set to 50 specimens. In addition, measurements for three specimens of *Archaeopteryx* (Munich, London and Maxberg) (Wellnhofer 2009) were added, and three non-avian theropods with wing feathers were used as an outgroup: *Tianyuraptor ostromi*, *Microraptor gui* and *Anchiornis huxleyi* (Hu *et al.* 2009).

Flight modes

As in previous studies (Nudds *et al.* 2007; Bruderer *et al.* 2010; Wang *et al.* 2011b), extant birds were divided into broad, qualitative categories that describe their flight mode. Here, we divided extant taxa into the following categories; divers, fast flappers, manoeuvring flappers, slow flappers with rapid take-off, and soaring birds, using a standard and widely referenced source (del Hoyo *et al.* 1992–2010). This allows direct comparisons between the forelimb proportions of Mesozoic birds and their extant counterparts where

the flight mode is known, rather than large groupings of extant birds, as in a previous study (Dyke & Nudds 2009). Measurements from four specimens consisting of detached wings (three from *Turdus merula* and one from *Buteo buteo*) provided by Bristol City Museum & Art Gallery were added to the original data set (Nudds *et al.* 2011), expanding the extant data set to 82 specimens from 34 species.

Analyses

Prior to carrying out principal components analysis (PCA), the wing was divided into four elements: humerus (HUM), forearm (FORE), manus (MAN), and longest primary feather (PRI). The lengths in mm of each were $\log_{10}$ transformed and entered into the formula

$$GMw = (\text{lgHUM} \times \text{lgFORE} \times \text{lgMAN} \times \text{lgPRI})^{0.25}$$

GMw is thus an average of the $\log_{10}$ elements, and $\log_{10}$GMw (lgGMw) was subtracted from the log of each element. This method reduces the amount of variation attributable to size by removing a measure of difference between the actual length of each element and an idealized length (the length of each element if all elements in the arm were equal). As average length of each element increases with increasing wing length, so too does GMw and lgGMw, making this idealized length a measure of overall wing length. The results were subjected to PCA using PAST (Hammer *et al.* 2001).

Each fossil specimen was treated as a separate data point. Although we are aware that this artificially inflates sample size, this was necessary as many Mesozoic fossil birds have yet to be fully described and therefore have not been assigned to any particular species or genus (Wang *et al.* 2011b). All specimens awaiting description and included here are identified as indeterminate Enantiornithes. Measurements of specimens of extant taxa were converted to mean values for each species.

To test for the robustness of the data entered into the PCA against any phylogenetic effects, we then employed comparisons by independent contrasts (CAIC; Purvis & Rambaut 1995). All taxa in the dataset were placed in the phylogeny of Livezey & Zusi (2007) with all branch lengths considered equal. Several of the Mesozoic taxa in our dataset are not included in the Livezey & Zusi (2007) study, but we were able to position them phylogenetically (see Fig. 1) according to well resolved published tree topologies (e.g. Chiappe & Dyke 2002; O'Connor *et al.* 2009; Zhou & Li 2010). The specimens identified
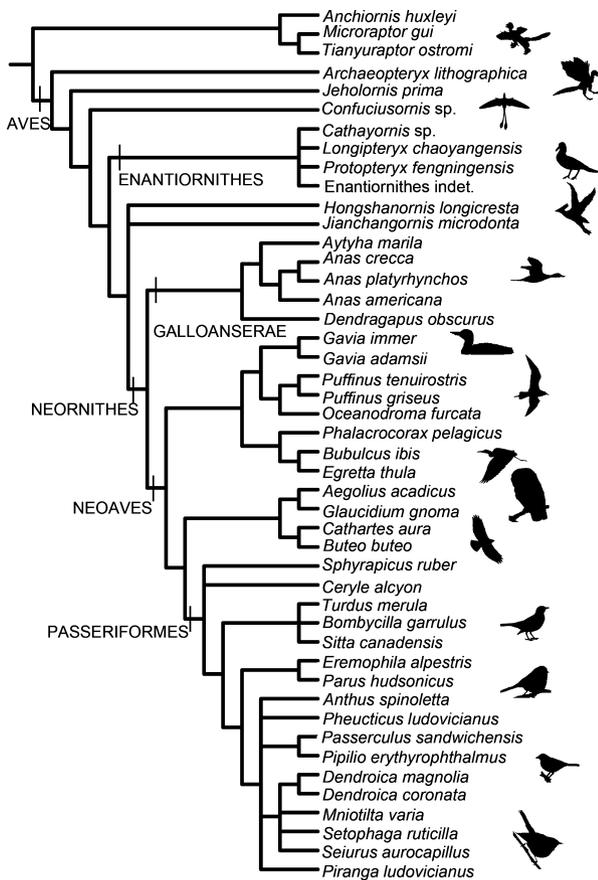
Fig. 1. Composite phylogeny of the taxa used in this study.

	lgGMw	GMw
PC1	88.4	58.7
PC2	6.8	35.4
PC3	4.2	5.8

All four variables load negatively on PC1, indicating that this is a size axis with size decreasing to the right (Fig. 2A). Unsurprisingly, large modern birds, such as *Gavia* (loon) and *Cathartes aura* (Turkey Vulture) lie at the negative-most (left-hand) end of the PC1 axis, whereas small passeriforms such as *Dendroica magnolia* (Magnolia Warbler) plot to the right. As this analysis uses data only from the forelimbs, 'size' is wing length. Some 'shape' data have been incorporated into PC1, as the loadings for the four elements are unequal, becoming more positively loaded from lgHUM to lgPRI. The three non-avian theropods are small (Xu *et al.* 2003; Hu *et al.* 2009), or have relatively short arms (Zheng *et al.* 2010), so they are not the most negative on the PC1 axis (Fig. 2).

On the PC2 axis, lgHUM and lgMAN load negatively whereas lgFORE and lgPRI load positively: the humerus and ulna load weakly, whereas the manus and longest primary load more strongly. Non-avian theropods have the most negative PC2 scores, whereas birds with relatively long primaries compared to the manus, such as *Buteo buteo* (Common Buzzard), plot most positively (Fig. 2). Mesozoic bird groups plot increasingly positively on PC2 with increased phylogenetic closeness to modern birds suggesting a trend of decreasing manus length and increasing primary feather length. A post hoc Spearman Rank Correlation of the $\log_{10}$-transformed manus to primary feather length ratio vs. taxonomic grouping (taxa ranked from 1 to 5: (1) non-avian theropods; (2) *Archaeopteryx* and, *Jeholornis*; (3) *Confuciusornis*; (4) enantiornithines; (5) *Hongshanornis* and *Jianchangornis*), which shows a strong negative correlation (r = −0.63, $P < 0.01$, *df* = 54) and confirms the presence of this pattern.

Both lgHUM and lgFORE load negatively on the PC3 axis, whereas lgMAN and lgPRI load positively. Egrets (Ciconiiformes) – *Bubulcus ibis* and *Egretta thula* – plot most negatively whereas our data show *Confuciusornis* to be most positive on this axis.

Three of the six regressions on the non-phylogenetically controlled data were discarded as residuals were not normally distributed ($P > 0.05$). The remaining regressions were; lgHUM against lgFORE, lgHUM against lgMAN and lgFORE against lgMAN which

as indeterminate Enantiornithes were coded into a polytomy within Enantiornithes (Fig. 1). Variables were analysed in pairs with standardized independent contrasts computed using the CRUNCH algorithm; these contrasts were assessed using ordinary least squares (OLS) linear regression through the origin using R 2.14.0 to find if phylogeny has a substantial effect on the observed patterns in relative wing element lengths. Jarque–Bera tests were used to test for normally distributed residuals and only regressions which produced normally distributed residuals were included in the results. For each slope coefficient, 95% confidence intervals (CIs) were constructed and overlapping limits regarded as indicating no significant difference.

Results

The three first principal components account for 99.4% of the variance, with PC1 accounting for 88.4%, PC2 6.8% and PC3, 4.2% (Table 1). Therefore, results are considered here only with respect to those first three axes.

were compared to their phylogenetically controlled equivalents. Linear regressions of the standardized independent contrasts indicate that with the effects of phylogeny controlled for, all variables retain positive coefficients greater than 0.5 and overlapping CIs (Table 2). All results were significant with *P*-values less than 0.05 (*df* = 35). Note that as contrasts are calculated at the nodes of branches within the phylogeny, the degrees of freedom are reduced when correlating standardized independent contrasts.

As size accounts for the majority of variance in the PCA, we reran the analysis using GMw rather than lgGMw as the size proxy. This effectively removes size as a variable in PCA as it only accounts for 0.09% of the variance. In this analysis PC1, on which both lgHUM and lgMAN load negatively whereas lgPRI loads positively and lgFORE is neutral, accounts for 58.7% of variance. On this axis, non-avian theropods load most negatively whereas the extant *B. buteo* plots most positively (Fig. 2).
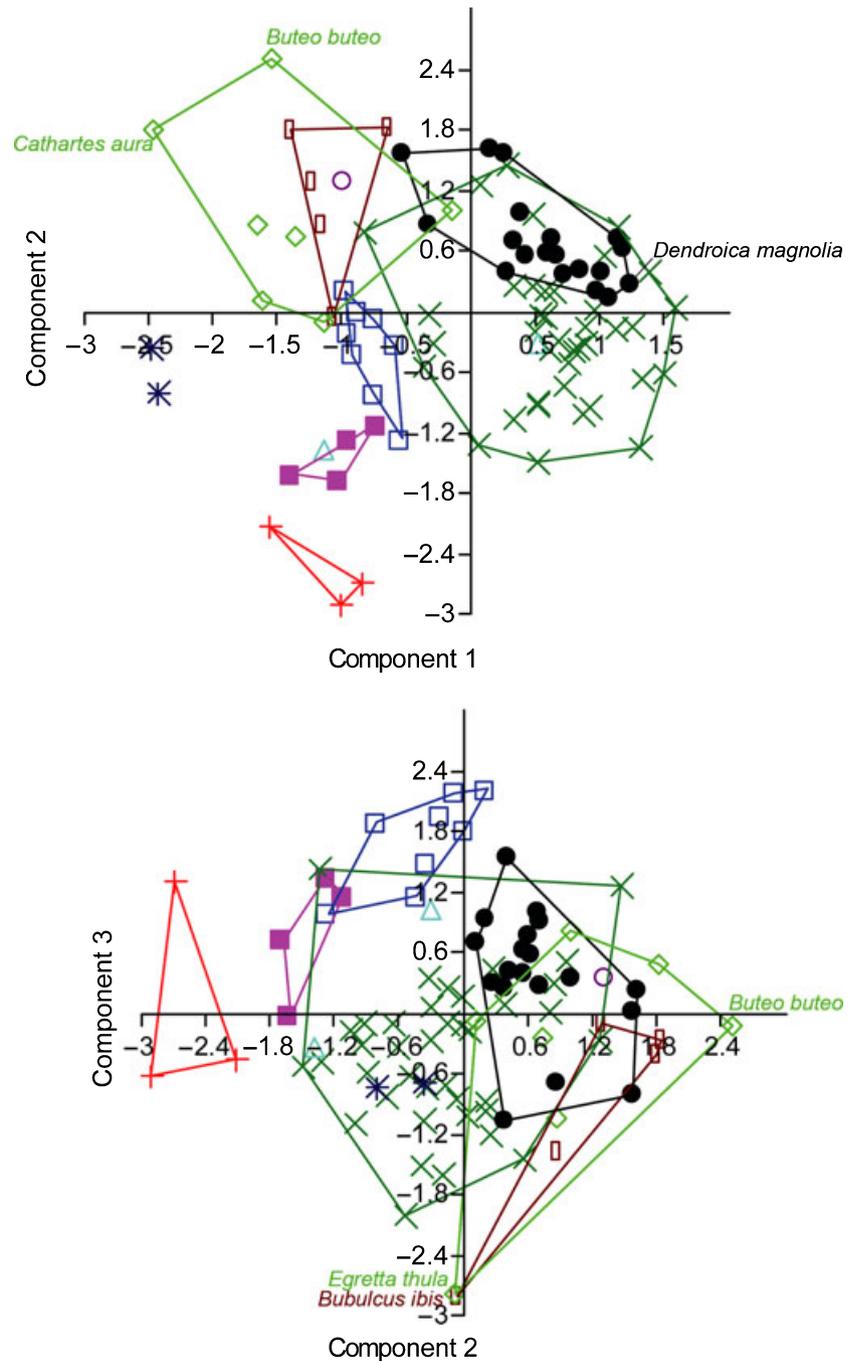

Fig. 2. Principal components analysis (PCA) plots showing the morphospaces occupied by functional groups of Mesozoic avians and neornithines. A, PC1 vs. PC2 plot, PC1 is a size axis in which taxa with longer forelimbs plot more negatively. B, PC2 vs. PC3 plot, the two axes which are independent of limb length. Symbols: red crosses – non-avian theropods; pink filled squares – *Archaeopteryx* and *Jeholornis*; blue hollow squares – *Confuciusornis*; green crosses – enantiornithines; light blue hollow triangles – *Hongshanornis* and *Jianchangornis*; dark blue asterisks – diving birds (*Gavia*); burgundy bars – fast flappers; black filled circles – manoeuvring flappers; purple hollow circles – slow flappers with rapid take off; light green hollow diamonds – soaring birds.

Table 2. Regression coefficients of lgGMw corrected data. All *P*-values were significant at the 0.05 level.

	Before CAIC ± CI	After CAIC ± CI
lgHUM vs. lgFORE	0.974 ± 0.010	0.986 ± 0.093
lgHUM vs. lgMAN	1.018 ± 0.017	1.033 ± 0.155
lgFORE vs. lgMAN	1.043 ± 0.020	0.982 ± 0.171

The PC2 axis accounts for 35.4% of variance. On this axis, lgHUM and lgFORE load positively and lgMAN and lgPRI load negatively (a reversal of the situation on PC3 in the previous analysis) the former of which loads much more negatively. *B. ibis* and *E. thula* plot most positively whereas an enantiornithine indet. specimen (7–293) plots most negatively (Fig. 3).

Both lgHUM and lgPRI load positively on the PC3 axis, whereas lgFORE and lgMAN load negatively. Of these variables lgHUM and lgFORE load strongly whereas lgMAN and lgPRI load weakly. On this axis, *Puffinus tenuirostris* (Aves; Procellariiformes) plots most negatively whereas specimen 7–293 (Enantiornithes indet.) plots most positively (Fig. 3).

The GMw altered data were also entered into CAIC and OLS regressions on the contrasts performed. All but one (lgHUM against lgPRI) of the regressions were retained after testing the residuals for normality. Only the coefficient of lgHUM against lgFORE overlapped with either of its lgGMw-altered equivalents and two of the retained coefficients were negative. After controlling for phylogeny as well as size, only the coefficient between lgHUM and lgFORE remained positive and none of the retained coefficients showed overlap with any of their previous equivalents in spite of the relatively high margins of error. Once again all *P*-values were significant (<0.05).

Discussion and conclusions

Despite the removal of a measure of wing length (lgGMw) in our initial analysis, PC1 still accounted for most of the variance in limb-element lengths in our pooled bird data. Indeed, in the size-independent PC2–PC3 plot (Fig. 2B) there is almost no separation among the functional groups of extant birds, and the only separation is along the size axis (PC1, Fig. 2A). This is consistent with previous studies that have used only skeletal elements, and suggests that most extant volant birds are fairly conservative in terms of variation in the relative lengths of the different elements that make up the wing, including the primary feathers (Dyke & Rayner 2001; Nudds 2007). This was confirmed in our second analysis in which size was effectively removed. In this case, the PC1–PC2 plot (Fig. 3) shows that, with the exception of the positioning of the diving birds along the PC1 axis, there is considerable overlap between extant functional groups.

Mesozoic theropod taxa show a trend of decreasing arm length crownwards in the phylogeny (from non-avian theropods to enantiornithines), although we cannot determine whether this trend continues or not
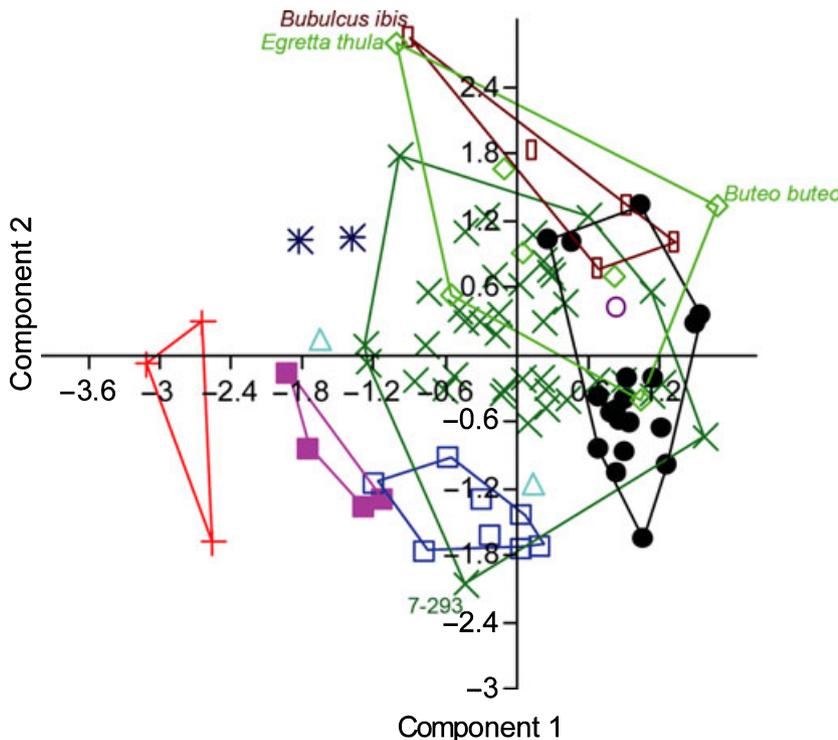

Fig. 3. PC1–PC2 plot from the second principal components analysis. Symbols as in Fig. 2.

in our small sample of non-neornithine ornithurine birds. This trend has been noted before (Dyke & Rayner 2001), and could be interpreted as a decrease in size (*contra* Hone *et al.* 2008), as wingspan scales positively with body mass in extant birds (Nudds 2007); however, previous work has indicated that there is little statistical evidence for any overall trends in the body size of Mesozoic birds (Butler & Goswami 2008).

There also appears to be a trend in the composition of the hand-wing component (manus + primary feathers) through avian phylogeny, with the length of the manus decreasing and primary feather length increasing, from non-avian theropods to enantiornithines. This can be seen on the PC2 axis (Fig. 2A), along which the clusters representing Mesozoic bird groups are distributed from negative to positive values in broad accordance with their phylogenetic positions. Manus and primary feather elements dominate the loadings on this axis, and birds with a longer manus and shorter primaries plot more negatively on the PC2 axis and *vice versa*. The PC1 axis in our second analysis shows a similar pattern, as the primary feather element is the only one to load positively in this analysis, indicating increasing primary feather length relative to the other elements in more derived taxa. However, the enantiornithines overlap with *Confuciusornis* on the PC1 axis and, with the exception of the Enantiornithes indet. specimen 7–293, plot more positively on the PC2 axis (Fig. 3). This separation on the PC2 axis rather than on PC1, and the substantial overlap between enantiornithines and extant birds, suggests that at this point in avian evolution the skeletal elements became modern in their relative lengths with little change in primary feather length. As the hand: primary proportions have been linked to differences in flight mode (Nudds *et al.* 2007; Wang *et al.* 2011a), it is likely that function and phylogeny are intertwined, with more basal birds having reduced flight capabilities (Senter 2006; Nudds & Dyke 2010; Wang *et al.* 2011b).

We cannot determine whether the increase in primary feather length relative to the skeletal elements is a consequence either of the increased importance of primary feathers in the flight of more derived Mesozoic birds, or whether it is linked to a decrease in overall wing length. With regard to the latter suggestion, modern birds show an increase in primary feather length relative to the skeletal arm with decreased size (Nudds 2007; Nudds *et al.* 2011). However, given the lack of any confirmed trend in body size among Mesozoic birds (Butler & Goswami 2008), an increase in the importance of the primary feathers seems more likely. This conforms to previous results showing that the ratio of primary feather length to total arm length

increases with increasing relatedness to Neornithes in Mesozoic birds (Wang *et al.* 2011a, b).

It is also interesting to note that in the size-independent PC2–PC3 plot (Fig. 2B) and the PC1–PC2 plot from our second analysis, none of the earliest-diverging birds in our sample (*Jeholornis*, *Archaeopteryx*, *Confuciusornis*) overlap with any of the extant avian groups. These early birds had limb proportions different from those seen in extant birds: *Confuciusornis*, for example, in the initial analysis has a relatively high positive PC3 value, suggesting a longer hand-wing relative to the proximal arm elements (humerus and forearm) and a negative PC2 value, suggesting a long manus in relation to primary feather length. In the second PCA, a long manus is indicated by the highly negative PC2 value indicating a relatively long hand-wing and a negative PC1 value, suggesting that the primaries are not especially long in relation to the other elements. The separation of the long-tailed basal birds *Archaeopteryx* and *Jeholornis* on the PC2–PC3 plot (Fig. 2B) arises from a more negative PC2 value (only non-avian theropods show more negative values). In the second analysis, separation of basal birds is by virtue of negative PC1 and PC2 values indicating relatively long skeletal elements and short primary feather length (Fig. 3). Recent studies indicate that *Confuciusornis* and *Archaeopteryx* may have been incapable of active powered flight (Senter 2006; Nudds & Dyke 2010; Wang *et al.* 2011a) and the forelimb element proportions as well the pectoral girdle morphology and primary feather structure of these taxa may have contributed to this inability. The PC1–PC2 plot from the initial analysis (Fig. 2A) shows that enantiornithines overlap substantially with manoeuvring flappers, mostly from the high degree of overlap on the size axis, PC1. Enantiornithines overlap substantially with all extant functional groups when size is removed (Figs 2B, 3), as they all do with each other, and this agrees with previous studies, which used either the skeletal elements of the wing only (Dyke & Nudds 2009) or combined skeletal and primary feather length (Wang *et al.* 2011a).

Linear regressions of the data before and after calculation of independent contrasts indicate that controlling for phylogeny does not significantly alter the regression coefficients (Table 2). This suggests that phylogenetic relatedness may contribute little to variation in the relative lengths of the limb elements. With the exception of the the regression between lgHUM-GMw and lgFORE-GMw, the CIs of the GMw altered data coefficients do not overlap with those of the lgGMw-altered data (Table 3), suggesting that differences in overall wing length have a greater effect on the lengths of the limb elements relative to each other. Further changes in the regression coefficients after removal

Table 3. Regression coefficients of GMw corrected data. All *P*-values were significant at the 0.05 level.

	Before CAIC ± CI	After CAIC ± CI
lgHUM vs. lgFORE	0.996 ± 0.216	0.419 ± 0.272
lgHUM vs. lgMAN	0.444 ± 0.120	−0.314 ± 0.290
lgFORE vs. lgMAN	0.115 ± 0.102	−0.581 ± 0.274
lgFORE vs. lgPRI	−0.156 ± 0.037	−0.384 ± 0.175
lgMAN vs. lgPRI	−0.391 ± 0.052	−0.283 ± 0.251

of phylogenetic effects suggests that variation arising from phylogenetic relatedness may be more important when measurements are entirely size independent.

The lack of separation of the different flight modes of extant avians indicates that a proxy for flight mode must be found. Not only should such a proxy distinguish among different avian flight modes, but it should also be applicable to fossil specimens. Until such a proxy is identified, the flight modes of enantiornithine birds will remain uncertain, although differences in pectoral girdle morphology may prove useful in interpretation. Recent work indicates that relative lengths of the forelimb bones combined with their diameters can be used to distinguish different flight modes in Pelecaniformes (Simons 2010). In particular variation in the cross-sectional shape of the carpometacarpus may indicate different loading regimes arising from variation in the attachment angle of the primary feathers (Simons 2010). However, it remains to be seen whether this is true for the majority of volant neornithines. The separation of Aves basal to e-nantiornithines from extant taxa along PC axes 2 and 3 and in the PC1–PC2 plot of the second analysis confirms some earlier suggestions that these basal birds were unable to perform flapping flight, but the small sample of extant neornithines in this study might bias the observation (cf. Wang *et al.* 2011a). In addition, the broad, qualitative nature of the flight categories used in this and previous studies (Nudds *et al.* 2007; Simons 2010) may have led to a perceived lack of separation between the groups defined by flight mode. These broad categories were used because we lack quantitative data on characteristics of wing kinematics such as wing beat frequency and stroke angle and amplitude for the extant species in this study, and it may be that such data would produce better defined, and more widely separated, categories of flight mode (Wang *et al.* 2011a).

Remains of neornithines in the Mesozoic are rare and mostly fragmentary (Chiappe & Dyke 2002; Feduccia 2003; Fountaine *et al.* 2005), despite the large numbers of non-neornithine birds (Fountaine *et al.* 2005; Dyke *et al.* 2007) and molecular evidence for an origin deep in the Cretaceous for at least the most basal neornithine groups (e.g. Cracraft 2001; van Tuinen & Hedges 2001; Paton *et al.* 2002; Dyke &

Van Tuinen 2004). However, the lack of a taphonomic explanation for this scarcity (Fountaine *et al.* 2005; Dyke *et al.* 2007) has led some to suggest that the rarity of neornithines at this time was caused by the occupation of available ecological niches by earlier-originating, non-neornithines (Nudds *et al.* 2004; McGowan & Dyke 2007). After the extinction of non-neornithines at the Cretaceous–Palaeogene boundary, there was a rapid rise in both the number and diversity of neornithine birds (Bleiweiss 1998), perhaps an ecological release following the extinction of potential competitors (Nudds *et al.* 2004; McGowan & Dyke 2007). Comparing forelimb morphology as a proxy for flight mode, an important element of avian ecology, is one possible way of testing this hypothesis of incumbent exclusion.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Measurements of wing elements.

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