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Forelimb proportions and the evolutionary radiation of Neornithes

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Analysis of a comprehensive dataset demonstrates that the brachial index (BI = humerus length/ulna length) of modern birds (Neornithes) varies significantly between clades at all taxonomic levels, yet is strongly correlated with recent phylogenetic hypotheses. Variance in BI at the infraclass level is low, but increases rapidly during the proposed major radiation of neornithines in the Palaeocene and Eocene. Although a BI of greater than 1 is primitive for Neornithes, more basal groups of Mesozoic birds (Confuciusornithidae and some members of the diverse Enantiornithidae) had BIs comparable with those of 'higher' modern clades. It is possible that occupation of ecological niches by these Mesozoic clades precluded the divergence of some groups of neornithines until after the Cretaceous–Tertiary boundary. We suggest that with further analysis and data collection the relationships between flight behaviour, ecology and BI can be determined. Hence, BI may provide a useful tool for characterizing the ecology of fossil birds.

Keywords: birds; flight; phylogeny; systematics; wing morphology

1. INTRODUCTION

Flapping flight is a central and constraining adaptation in birds. Strong correlations between form and function indicate that bird wing morphology is subject to strong selective pressures associated with aerodynamic performance (Rayner 1988). To a large extent, the proportions of wing bones determine planform and wing deformations during flight. Early anatomists noted variations in the relative proportions of proximal wing elements (humerus, radius and ulna), and remarked on the distribution of this variation within birds (Beddard 1898; Steiner 1917; Böker 1927; Marples 1930). Subsequently, proportions of the proximal wing elements have been used in the morphological classification of Aves (Verheyen 1961) and employed as discrete characters in determining phylogenetic relationships of Mesozoic birds (Chiappe 1995, 1996; Forster *et al.* 1998; Ji *et al.* 1998; Padian & Chiappe 1998). Recently, Rayner & Dyke (2002) concluded that the brachial index (BI) correlated well with neornithine phylogeny and varied little within orders or families; however, they did not apply rigorous statistical analysis. Consequently, whether differences in BI among clades are statistically robust is unclear. If BI is clade specific, particularly at the species or genus level, it could be related directly to flight ecology and could provide further insights into the evolution and radiation of modern birds. In this paper, a more rigorous analysis was used to determine at what taxonomic level, if any, clade-specific values of BI exist. In addition, variation in BI over time was estimated.

2. MATERIAL AND METHODS

The dataset used here is part of an ongoing project and currently comprises 1305 recent and fossil bird species across 682 genera (see electronic Appendix A). BI measurements were collated from skeletal specimens and measurements taken from the literature (Murie 1871; Magnan 1922; Böker 1927, 1935; Kälin 1942; Middleton & Gatesy 2000). Data for all 23 orders and 129 of the 151 families listed in the taxonomy of Sibley & Ahlquist (1990) are included. Measurements include at least one representative taxon for all but one (Pedionomidae) of the non-passerine families of Sibley & Ahlquist (1990). Coverage of the Passeriformes is slightly less comprehensive. Owing to a lack of available specimens, the families Oxyruncidae, Prionopidae, Vangidae, Dulidae, Remizidae, Rhabdornithidae, Climacteridae, Epithanuridae, Artamidae and Paradisaeidae were not included in the dataset.

The distribution of BI was compared with three different phylogenetic hypotheses. The first was that of Sibley & Ahlquist (1990), which remains the 'only' comprehensive morphologically independent molecular hypothesis. The second was the recent phylogeny of Cracraft *et al.* (2004), which is speculative (in places) and represents a compromise among the (14) authors. The third was the phylogeny of Wetmore (1960). We are not arguing for the validity of the hypotheses (a unanimous consensus on the validity of a phylogeny is difficult to achieve), but instead argue that the extreme differences between them provide a rigorous test of BI variation among taxa. At this stage, we are concerned with determining broad patterns of variation among categories at different taxonomic levels (i.e. nested clades within Neornithes) and variation of BI over time. Therefore, a fully nested ANOVA was used to analyse the dataset (Bell 1989; Sokal & Rohlf 1995). In addition to determining differences between clades at a taxonomic level, a nested ANOVA provides an estimate of the variance of a character attributable to a particular taxonomic level independent of other levels (Bell 1989). Expansion of the already extensive dataset would be required for an investigation of more specific questions about the ecological factors that influence BI using a phylogenetically independent contrasts method of analysis.

3. RESULTS

A fully nested ANOVA showed that, regardless of which phylogeny was used, significant differences (all $p < 0.005$) in BI exist between clades at all taxonomic levels within Neornithes (table 1). Therefore, as argued by Rayner & Dyke (2002) BI varies significantly between orders and families, but contrary to Rayner & Dyke (2002) BI also varies within orders and families (i.e. between genera and species). The conditions required to use the Satterthwaite approximation for the calculation of F-values for nested ANOVA with unequal sample sizes were violated. Therefore, p-values were calculated using approximate F-values ($MS_{subgr}/MS_{subsubgr}$; MS, mean square) after Sokal & Rohlf (1995). Infraclass, order, family and genus are responsible for similar amounts of variation (table 1). Although there are significant differences in BI between species, most of the total variation in BI is accounted for by generic level and lower (i.e. infraclass + order + family + genus = 96% of the total variation in BI), and the contribution of the taxonomic level species to total variation in BI is trivial (table 1).

4. DISCUSSION

Finding that most variation in BI is accumulated by generic level is not surprising because species within genera tend to have similar morphologies and ecologies.

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Table 1. Fully nested ANOVA for the brachial index in neornithines, using three different phylogenetic hypotheses.
(SCV, the cumulative variance (sum of variance components up to and including that level) divided by the total variance; it represents an intraclass correlation coefficient (Bell 1989). For each phylogeny $p < 0.005$ for each taxonomic level.)

	Sibley & Ahlquist (1990)			Cracraft *et al.* (2004)			Wetmore (1960)		
level	d.f.	variance component	SCV	d.f.	variance component	SCV	d.f.	variance component	SCV
infraclass	1	0.016 (24.37%)	0.244	1	0.017 (25.82%)	0.258	1	0.015 (23.94%)	0.239
order	21	0.012 (18.23%)	0.426	27	0.017 (26.50%)	0.523	27	0.023 (35.54%)	0.595
family	111	0.018 (28.07%)	0.707	106	0.012 (17.94%)	0.703	136	0.013 (19.58%)	0.791
genus	533	0.016 (25.01%)	0.957	532	0.017 (25.39%)	0.957	502	0.011 (16.54%)	0.956
species	639	0.001 (0.81%)	0.965	635	0.001 (0.80%)	0.965	635	0.001 (0.81%)	0.964
within species	1472	0.002 (3.51%)	1.000	1476	0.002 (3.55%)	1.000	1476	0.002 (3.59%)	1.000
total	2777	0.065		2777	0.065		2777	0.064	

Indeed, most variation in many life-history variables is accounted for at ordinal and family levels (Bennett & Owens 2002). It is encouraging that variation in BI at higher levels (Eoaves/Neoaves) is relatively low (24.37%), because it suggests most variation in BI (the remaining 75%) has arisen concomitantly with the proposed major radiation of Neornithes during the Palaeocene and Eocene (Feduccia 1995, 2003). If the opposite was true and most variation in BI was already accounted for at the infraclass level, BI would be less likely to provide an insight into Neornithine radiation and evolution.

Distribution of BI among Neornithine phylogeny has already been discussed at length by Rayner & Dyke (2002) (also see electronic Appendix B). Figures 1 and 2, however, show mean BI plotted onto the ordinal-level phylogenies of Sibley & Ahlquist (1990) and Cracraft *et al.* (2004). BIs of less than unity occur within the higher landbird terminals. This trend towards a reduction in BI culminates in the Apodiformes and Trochiliformes. Swifts, such as the extant *Apus apus*, have the lowest BI of any birds (0.48) and the ostrich *Struthio camelus* the highest BI (3.30).

Contrary to current consensus (Groth & Barrowclough 1999; García-Moreno & Mindell 2000; van Tuinen *et al.* 2000; Cracraft *et al.* 2004), Sibley & Ahlquist (1990) group Galloanserae with Palaeognathae (ratites and tinamous) in Eoaves. Re-rooting Galloanserae between Palaeognathae and Neoaves (Galloanserae as a sister group of Neoaves), however, does not significantly change the results or conclusions presented here. Furthermore, re-running the nested ANOVA using the most recent phylogeny proposed for avian higher taxa (Cracraft *et al.* 2004) and the hypothesis of Wetmore (1960) produces fundamentally the same results as found using the phylogeny of Sibley & Ahlquist (1990), i.e. clade specific BIs and the same taxonomic distribution of variation in BI. The fact that our conclusions remain the same whichever phylogeny is used is testament to their robustness.

A number of workers have listed the character 'humerus longer than ulna' as primitive for basal birds (such as *Archaeopteryx*), and have noted that the opposite state is seen above the node Ornithothoraces (Padian & Chiappe 1998). Although BI is less than 1 in some clades of Mesozoic birds (Enantiornithidae, Confuciusornithidae), the original primitive condition (BI > 1) is seen basally within Neornithes (Rayner & Dyke 2002). The presence of modern birds in the Mesozoic is debated (Benton 1999; Feduccia 2003), but a number of clades (i.e. Enantiornithidae and Confuciusornithidae) were certainly present that had similar wing proportions (BI < 1) to 'higher' modern clades (Rayner & Dyke 2002). Perhaps the absence of 'higher' modern bird clade fossils from the Mesozoic (Dyke 2001) is as a result of the occupation of niches for fast and manoeuvrable fliers (BI < 1; Rayner & Dyke 2002) by other, already abundant and morphologically diverse taxa, such as the enantiornithine birds. Extinction of confuciusornithine and enantiornithine lineages prior to the Cretaceous–Tertiary boundary may have vacated niches, which were subsequently filled by the radiation of Neornithes during the Palaeocene and Eocene.

It is possible that major changes to the phylogeny used could alter any conclusions made about the distribution of BI within Neornithes. By contrast, and as shown in

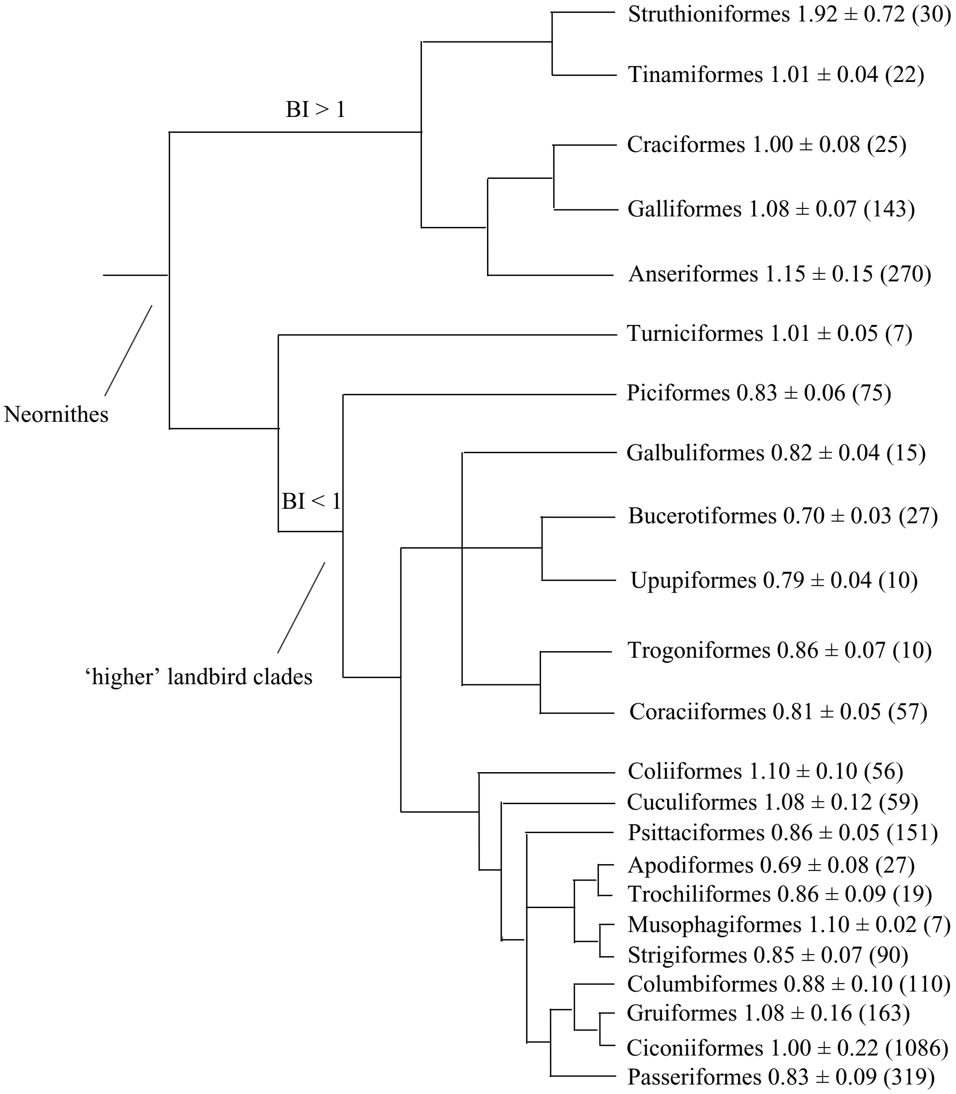

Figure 1. The distribution of the brachial index on the ordinal-level phylogenetic hypothesis presented by Sibley & Ahlquist (1990). Values displayed are means ± s.e. (n).

table 1, conclusions about the accumulation of variation in BI through geological time and the finding that BI varies significantly between clades at all taxonomic levels are likely to be robust. We conclude that BI potentially provides insights into the evolution and radiation of neornithines and may, with further analysis and integration with ecological variables, provide a useful tool for characterizing fossil specimens where only oesteological characters have been preserved.

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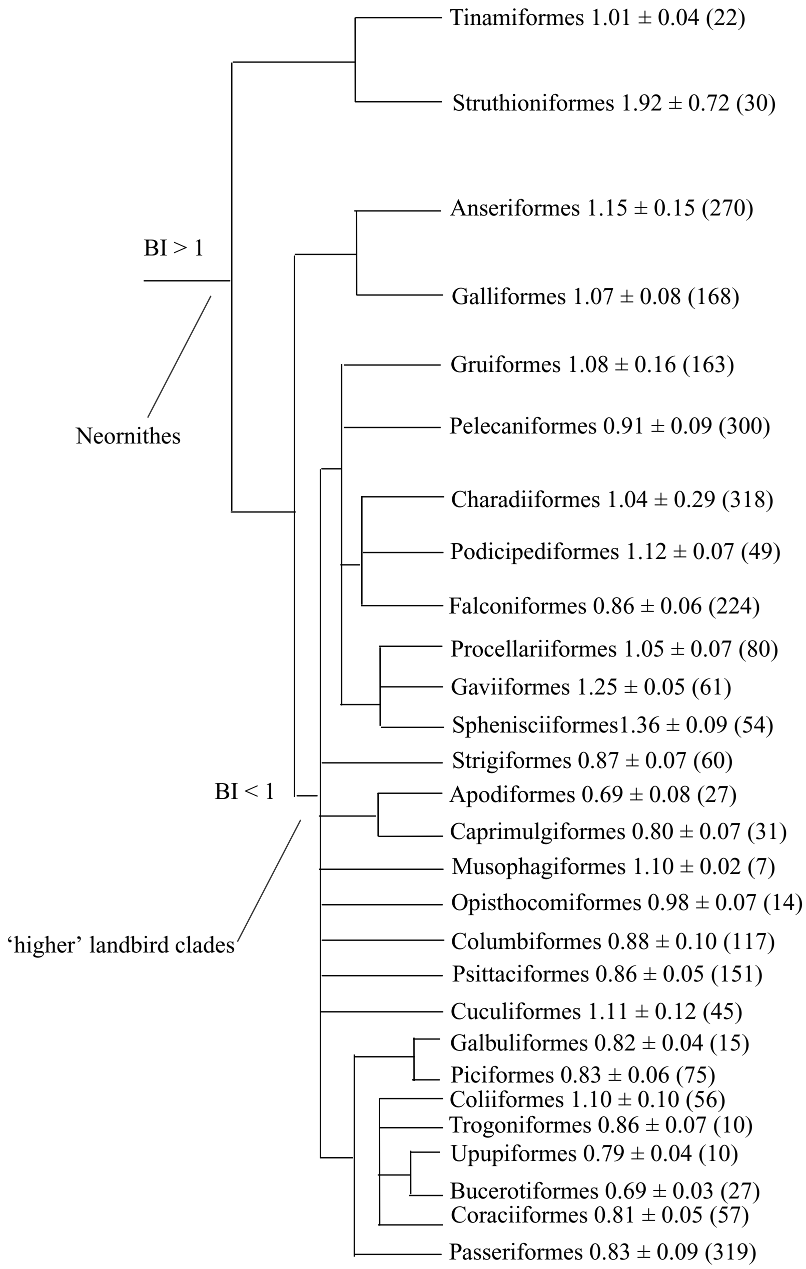

Figure 2. The distribution of the brachial index on the ordinal-level phylogenetic hypothesis presented by Cracraft *et al.* (2004). Values displayed are means ± s.e. (*n*).

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