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Confuciusornis sanctus stands out among the remarkable diversity of birds of the Jehol biota (Lower Cretaceous, Liaoning Province, China). Its basal position in the phylogenetic tree of birds, combined with the exceptional number of well-preserved, largely complete and articulated specimens, makes it a perfect model system for studying the variation, development and life history of early Mesozoic birds. A comprehensive morphometric study (measurements of humerus, ulna, radius, femur and tibia) previously identified two distinct size classes of *C. sanctus*, while demonstrating the lack of statistical support of the association between this size dimorphism and the characteristic pair of long tail feathers present in some specimens. Four plausible explanations were discussed to account for the resultant size classes: the existence of more than one species in the sample; sexual size dimorphism; two size classes corresponding to attritional death assemblages; and/or a particular growth pattern similar to that inferred for non-avian dinosaurs. Here we present an expanded statistical analysis based on a larger sample of *C. sanctus* that substantiates previous interpretations, but also addresses the statistical association between the presence/absence of tail feathers and fore- and hind-limb allometry. We discuss the implication of the resulting quantitative patterns of morphological variation to understand better confuciusornithid taxonomy and the life history of *C. sanctus*.

Keywords: *Confuciusornis*; life history; Mesozoic birds; morphometrics

Introduction

The Early Cretaceous lacustrine deposits of the Jehol Group in north-eastern China have yielded an enormous number of fossil birds representing stunning taxonomic and ecologic avian diversity (Chang *et al*. 2003; Chiappe 2007; Zhou & Zhang 2007). *Confuciusornis sanctus* stands out not only because its remains are far more abundant than those of other Jehol birds, but also because only some specimens display a pair of long stiff tail feathers, an intraspecific difference that has often been interpreted as evidence of sexual dimorphism (Feduccia 1996; Hou *et al*. 1996, 1999; Martin *et al*. 1998).

Characterized by having a toothless, powerful beak, a large manus with three elongate clawed digits, and an enormous and strongly recurved claw on the alular digit (Chiappe *et al*. 1999), *C. sanctus* and other confuciusornithids have consistently been interpreted as basal pygostylians, some of the most primitive birds in which the abbreviated caudal vertebrae are fused into a pygostyle (Chiappe *et al*. 1999; Clarke *et al*. 2006; Gao *et al*.

2008; O'Connor *et al*. 2009; Bell *et al*. 2010; Fig. 1). The basal position of *Confuciusornis* in the phylogenetic tree of birds, combined with the exceptional number of well-preserved, largely complete and articulated specimens, offers an unprecedented opportunity for studying the variation, development, and life history of early Mesozoic birds.

Species-level multivariate analyses of morphometric datasets have proven useful for assessing a range of life history phenomena in both extinct and extant organisms (Dodson 1976; Chapman *et al*. 1981; Houck *et al*. 1990; Ranta *et al*. 1994; Senter & Robins 2003). A quantitative analysis of a small sample of specimens ($n = 13$) limited to tarsometatarsal lengths of *C. sanctus* was presented by Peters & Ji (1999), showing a lack of correlation between size and the presence/absence of the characteristic long tail feathers of this taxon. However, given the limited sample of that study, the statistical basis for this conclusion was weak. A much larger ($n = 106$) and more comprehensive morphometric study (measurements of the humerus, ulna, radius, femur and tibia) was presented by Chiappe *et al*. (2008). These authors identified two distinct size

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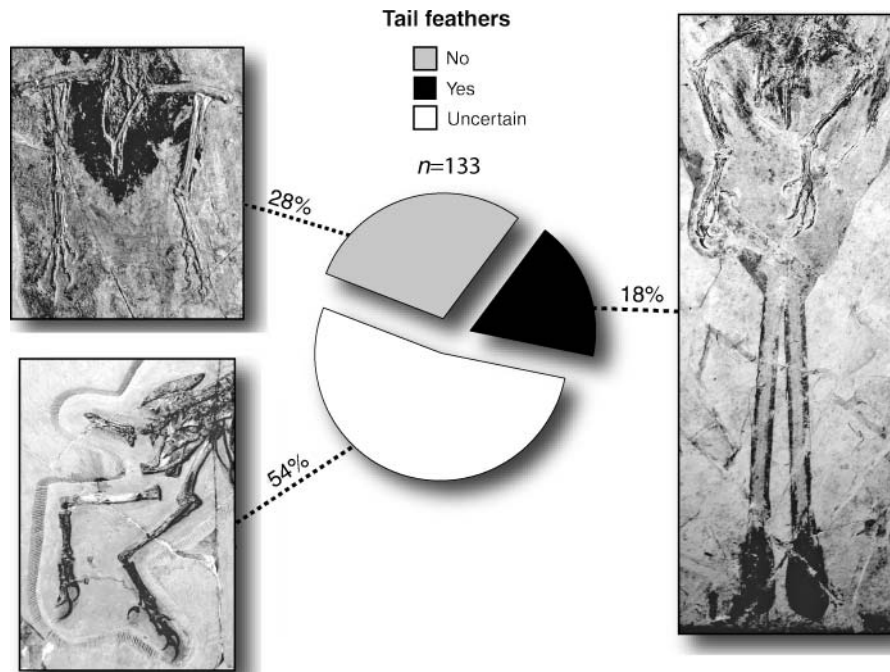*Corresponding author. Email: jesus.marugan@uam.es

Figure 1. Studied specimens and percentages regarding the presence/absence and uncertainty of tail feathers; sample size *n* = 133. Examples are BMNHC₋PH000766-with tail feathers, IVPP 13156-without tail feathers, and PMOL00031-uncertain. See Appendix for institutional abbreviations.

classes in the sample, each containing long-tailed specimens, thus conclusively demonstrating the lack of statistical correlation between size and the presence/absence of long tail feathers. Chiappe *et al*. (2008) concluded that if these feathers were a sexually dimorphic characteristic, as contended in a number of previous studies, their presence was not correlated with sexual size dimorphism. Chiappe *et al*. (2008) also presented four plausible explanations that, individually or together, could account for the resultant size classes of their statistical analysis: (1) the existence of more than one species in the sample; (2) the presence of sexual size dimorphism; (3) two size classes corresponding to attritional death assemblages; and/or (4) a particular growth pattern similar to that inferred for non-avian dinosaurs. Using a sample slightly modified from that of Chiappe *et al.* (2008) – adding only five more specimens – Peters & Peters (2009, 2010) argued that the two size classes identified by Chiappe *et al*. (2008) were nothing more than the expression of sexual size dimorphism, in which the large class was interpreted as female. Chiappe *et al*. (2010), however, suggested that the conclusion of Peters & Peters (2009) was unsubstantiated and largely the result of questionable inferences about the growth patterns of early birds and *ad hoc* statistics. In this paper we present an expanded statistical analysis based on a much larger sample of *C. sanctus*, and discuss the evolutionary significance of understanding the size variation and life history of this basal bird and its implication for confuciusornithid taxonomy.

Material and methods

To date, nine species in four genera have been grouped within Confuciusornithidae: *Confuciusornis sanctus* Hou *et al*. 1995, *C. chuonzhous*, Hou, 1997, *C. suniae* Hou, 1997, *C. dui* Hou *et al*., 1999, *C. feducciae* Zhang *et al*., 2009, *Jinzhouornis zhangjiyingia* Hou *et al*., 2002, *J. yixianensis* Hou *et al*., 2002, *Changchengornis hengdaoziensis* Ji *et al*., 1999 and *Eoconfuciusornis zhengi* Zhang *et al*., 2008. Chiappe *et al*. (1999) demonstrated that *C. chuonzhous* and *C. suniae* were based on anatomical misinterpretations, and regarded these species as junior synonyms of *C. sanctus*. Likewise, Chiappe *et al*. (2008) showed that *Jinzhouornis zhangjiyingia* and *J. yixianensis* were indistinguishable qualitatively and quantitatively from *C. sanctus* and were also junior synonyms of the latter. They also demonstrated that *C. hengdaoziensis* was quantitatively different from *C. sanctus*, in addition to the anatomical differences highlighted by Ji *et al*. (1999). Here we have limited our dataset to *Confuciusornis*, including *C. sanctus* (with its junior synonyms), *C. dui* and *C. feducciae*. We have also included *E. zhengi* given that the morphology of the only known specimen (e.g. non-fused tarsals) demonstrates that it corresponds to a juvenile – but not a hatchling – and therefore makes a worthwhile comparison with *C. sanctus*.

The material studied comprises 130 specimens of *C. sanctus*, in addition to the holotypes of *C. dui*, *C. feducciae*, and *E. zhengi*. These specimens come from several
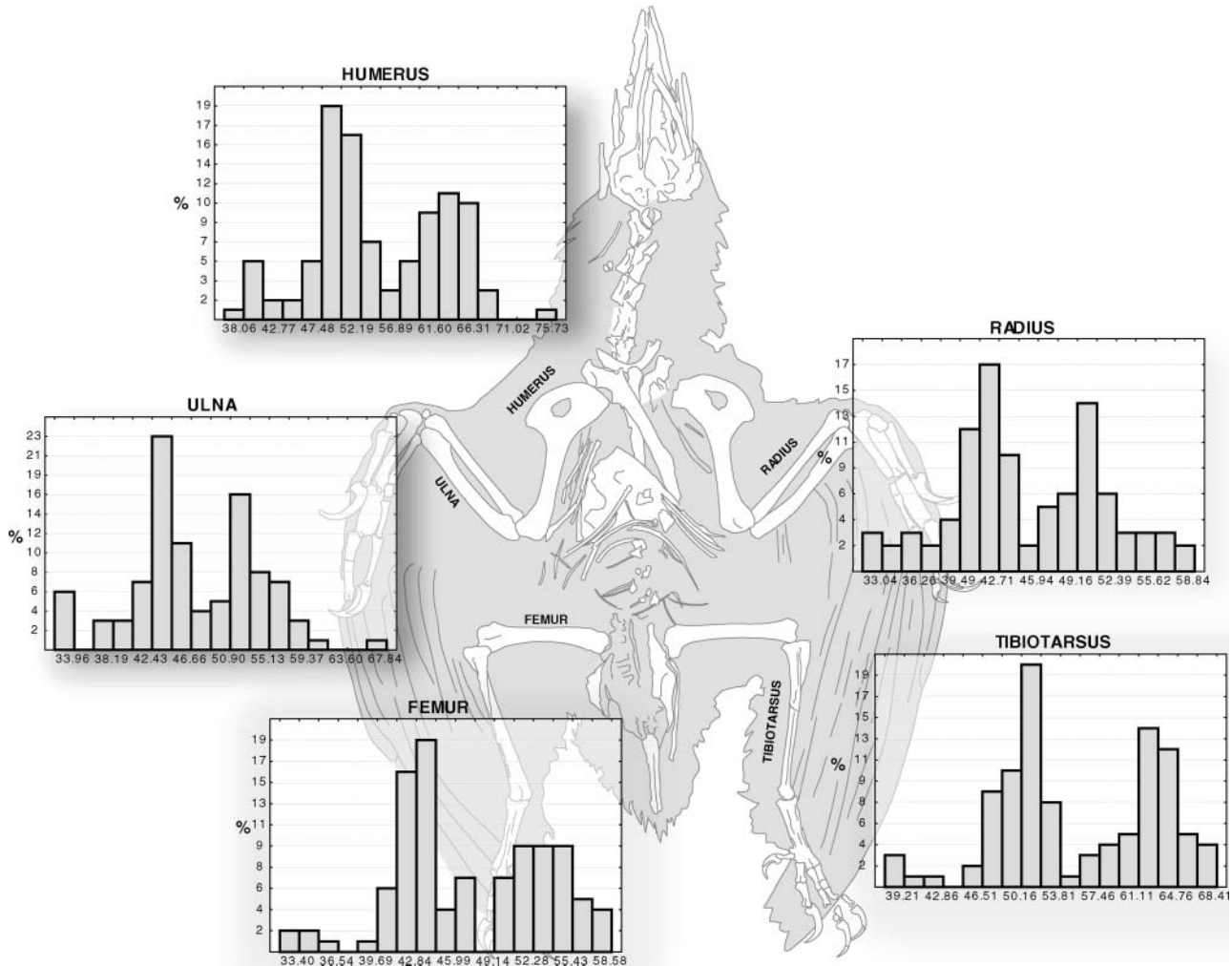
Figure 2. Scheme of *Confuciusornis sanctus* showing the studied bones (measurements are the chord lengths of humerus, ulna, radius, femur and tibiotarsus), and the frequency distributions of the variables.

localities and strata within the Early Cretaceous Jehol Group (Chang *et al*. 2003; Wang & Zhou 2006), which, with the exception of *E. zhengi* (Dabeigou Formation, Hebei Province), are contained within the Yixian Formation of western Liaoning Province (Chang *et al*. 2003). These strata span approximately 10 million years between the Dabeigou Formation (∼131 Ma) and the top of the Yixian Formation (∼121 Ma) (Chang *et al*. 2003; Wang & Zhou 2006; Zhang *et al*. 2008). A complete list of material is given in the Appendix.

Measurements of the humerus, radius, ulna, tibia and femur (Fig. 2) were taken from high-resolution photographs using Sigmascan Pro v. 5 (see Appendix). The existence of the pair of caudal rectrices was coded as a categorical variable that had three entries: presence, absence and unknown. These feathers were considered absent only on specimens in which the outline of the plumage around the pygostyle was well preserved, offering strong evidence that the absence of these feathers was not the result of taphonomy (Fig. 1).

Chiappe *et al.* (2008) focused on analysing the principal trends of size variation of *C. sanctus* with principal components analysis (PCA), and used discriminant analysis to test the association between size and the presence of tail feathers. Here, PCA based on the variance-covariance matrix was also used to characterize overall trends of variation in all the quantitative characters simultaneously. General linear models (homogeneity of slopes and ANCOVA; Mardia *et al.* 1979; Friston *et al.* 1995) were used to test the pairwise association between the variables (bone chord lengths) and the categorical factor that expresses the presence or absence of tail feathers. All the analyses were performed using Statistica v. 6.

Results

Specimens with tail rectrices are outnumbered by specimens without them or those coded as unknown (Fig. 1). The

Table 1. Descriptive statistics.

Bone	Tail feathers	*n*	Maximum length	Minimum length	Mean	Standard deviation
Humerus	No	64	69.93	40.85	57.99	7.11
	Yes	25	70.08	30.06	54.7	10.71
	?	29	68.36	42.5	55.7	7.28
	Total	118				
Ulna	No	53	60.60	33.96	50.23	6.24
	Yes	23	69.96	34.06	48.18	9.37
	?	23	59.7	40.73	48.52	5.5
	Total	99				
Radius	No	45	57.79	33.95	47.37	5.88
	Yes	18	60.45	33.04	45.97	8.13
	?	23	58.19	36.62	45.76	6.05
	Total	86				
Femur	No	61	59.46	33.4	49.06	5
	Yes	19	59.06	35.73	48.92	6.66
	?	29	60.15	34.38	48.07	6.27
	Total	109				
Tibia	No	64	70.24	40.9	58.42	6.79
	Yes	21	68.86	40.4	56.17	8.45
	?	24	69.99	39.21	55.27	7.51
	Total	109				

descriptive statistics are summarized in Table 1. Results are consistent with those presented by Chiappe *et al*. (2008), as discussed in Chiappe *et al.* (2010). The frequency distributions of five measured variables are bimodal (Fig. 2). All length measurements are linearly positively and significantly correlated (Pearson-moment correlations are never lower than 0.91, $p < 0.01$; Table 2). However, the pairwise general lineal model analyses capture a signal of statistically significant association between the presence or absence of tail feathers and the chord lengths of the bones (difference in the intercept and/or slopes; Fig. 3, Table 3). Such an association is captured when the allometry of the hind-limbs is predicted by the fore-limbs; namely, the presence/absence

of tail feathers is associated with significant differences in the slopes and/or the intercepts between the humerus, ulna and radius, predicting the variability of the femur and the tibiotarsus. Although confidence intervals are statistically shared by all the lineal models (95% confidence; Fig. 3), this association for the entire sample remains consistent whether or not the data include the smallest specimens (the ones representing the tail of the size class of smaller individuals) and those described as different species.

Most pairwise linear models suggest nearly isometric scaling between the variables of the entire sample (Table 3), but when the two size classes were examined separately (excluding the smallest specimens at the tail of

Table 2. Correlations between chord lengths of bones.

Paired variables	Pool sample		Small morph		Large morph	
	n	*r*	*n*	*r*	*n*	*r*
Hum-Uln	95	0.95**	43	0.76**	37	0.76**
Hum-Rad	84	0.94**	39	0.67**	30	0.58**
Hum-Fem	99	0.92**	52	0.47**	42	0.42**
Hum-Tib	101	0.94**	48	0.50**	41	0.68**
Uln-Rad	73	0.97**	34	0.91**	29	0.75**
Uln-Fem	87	0.92**	44	0.52**	39	0.52**
Uln-Tib	90	0.93**	43	0.60**	38	0.62**
Rad-Fem	74	0.92**	39	0.41**	31	0.66**
Rad-Tib	74	0.91**	37	0.37*	30	0.70**
Fem-Tib	100	0.95**	52	0.66**	44	0.59**

Notes: Hum = humerus, Uln = ulna, Rad = radius, Fem = femur, Tib = tibiotarsus.
For clusters, the specimens where grouped by femur size (see Fig. 3).
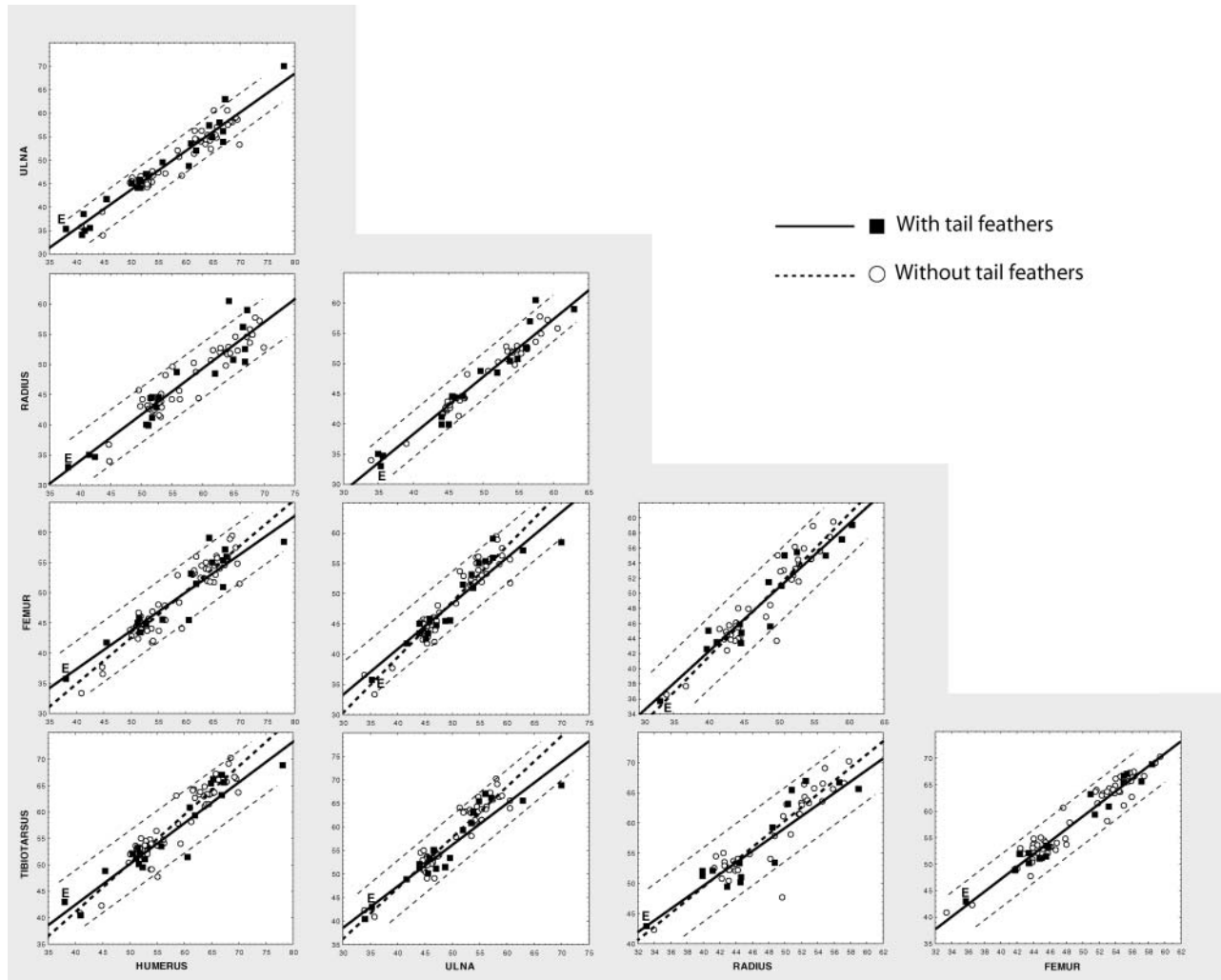*$p < 0.05$; **$p < 0.01$.

Figure 3. Pairwise scatter-plots and linear models among all the measured variables. All regressions are highly significant ($p < 0.01$). Only specimens unambiguously with and without feathers were included in the analyses. A single regression line fit to the whole sample is shown when the analyses did not detect statistically significant differences associated with the presence of tail feathers. Sample size in each model varied depending on the matching between specimens without missing data for that specific comparison (the sample size for each analysis is listed in Table 3). The bold E corresponds to *Eoconfuciusornis*.

the frequency distribution), all the slopes became lower and the intercepts changed (Fig. 4A). The correlations also decreased – although remaining equivalent in both morphs – the exception being the lengths of the radius with the femur and the tibia, in which the correlation is much lower in the smaller size class (Table 2). Likewise, when size classes were examined separately there were differences in the association of the presence/absence of long tail feathers in the intercepts and the slopes (Fig. 4B, C), although the number of individuals with these feathers is too low to be statistically rigorous.

When performing a PCA to analyse the variability of the measurements, the sample was reduced to $n = 62$ because we chose not to estimate missing values. The results of the PCA on the entire sample demonstrate a trend char-

acterized by two different size classes within the sample (Fig. 5). The first PC is clearly dominant (accounting for 95.58% of the total explained variance), and as expected represents size differences (all the strikingly high loadings have the same sign and nearly equivalent values upon this vector, 0.98 – 0.96; see loadings in Table 4). This level of explained variance appears larger than that in most studies of intraspecific variation of living birds, and the PC loadings are more homogeneous (e.g. Johnston & Selander 1971; Johnston 1973, 1992; Baker 1980). The second and third PCs (PC 2 and PC 3) explain only 1.61% and 1.43% of the remaining variance, respectively. When the percentage of explained variance between two PCs is so similar, it is often difficult to treat and plot these dimensions separately since their order may be easily interchanged with the addition

Table 3. General Lineal Models (Homogeneity of Slopes and ANCOVA).

| Sample size | | | | | | | | | Linear Model | | | | | | | | |
x	y	tf	ntf	tot	Effect	F	df	P	R^2_{tf}	b_{tf}	a_{tf}	R^2_{ntf}	b_{ntf}	a_{ntf}	R^2_{tot}	b_{tot}	a_{tot}
Humerus	Ulna	23	52	75	Intercept	2.0025	1	0.1614	–	–	–	–	–	–	0.92	0.80	3.08
					Tail × Humerus	0.5102	1	0.4773									
Humerus	Radius	18	44	62	Intercept	1.7036	1	0.1969	–	–	–	–	–	–	0.88	0.77	2.78
					Tail × Humerus	0.6740	1	0.4150									
Humerus	Femur	17	57	74	Intercept	15.4238	1	0.0002*	0.85	0.64	11.27	0.87	0.76	4.45	0.86	0.82	6.72
					Tail × Humerus	3.2593	1	0.0753									
Humerus	Tibiotarsus	20	60	80	Intercept	14.9858	1	0.0002*	0.89	0.78	10.86	0.88	0.91	4.28	0.88	0.89	5.37
					Tail × Humerus	2.8227	1	0.0970									
Ulna	Radius	17	37	54	Intercept	0.0000	1	1.0000	–	–	–	–	–	–	0.94	0.97	−0.84
					Tail × Ulna	0.5580	1	0.4858									
Ulna	Femur	19	49	68	Intercept	9.7746	1	0.0026*	0.87	0.77	9.73	0.89	0.91	2.77	–		–
					Tail × Ulna	3.4736	1	0.0660									
Ulna	Tibiotarsus	19	51	70	Intercept	12.2781	1	0.0008*	0.88	0.90	11.24	0.90	1.07	3.93	–	–	–
					Tail × Ulna	4.0987	1	0.0469*									
Radius	Femur	15	40	55	Intercept	9.4095	1	0.0034*	0.90	0.82	9.26	0.89	0.94	3.84	–	–	–
					Tail × Radius	1.7308	1	0.1941									
Radius	Tibiotarsus	15	40	55	Intercept	5.0230	1	0.0293*	0.83	1.01	9.16	84.00	1.10	5.34	–	–	–
					Tail × Radius	0.3833	1	0.5385									
Femur	Tibiotarsus	18	59	77	Intercept	0.0210	1	0.9634	–	–	–	–	–	–	0.90	1.17	0.29
					Tail × Femur	0.1219	1	0.7290									

*$p < 0.05$.

x = predictor, y = predicted, N = number of specimens, tf = tail feathers, ntf = no tail feathers, F = F-value, df = degrees of freedom, P = probability $\mathbf{R^2}$ = coefficient of determination, b = slope, a = intercept.

Table 4. PCA loadings of variables.

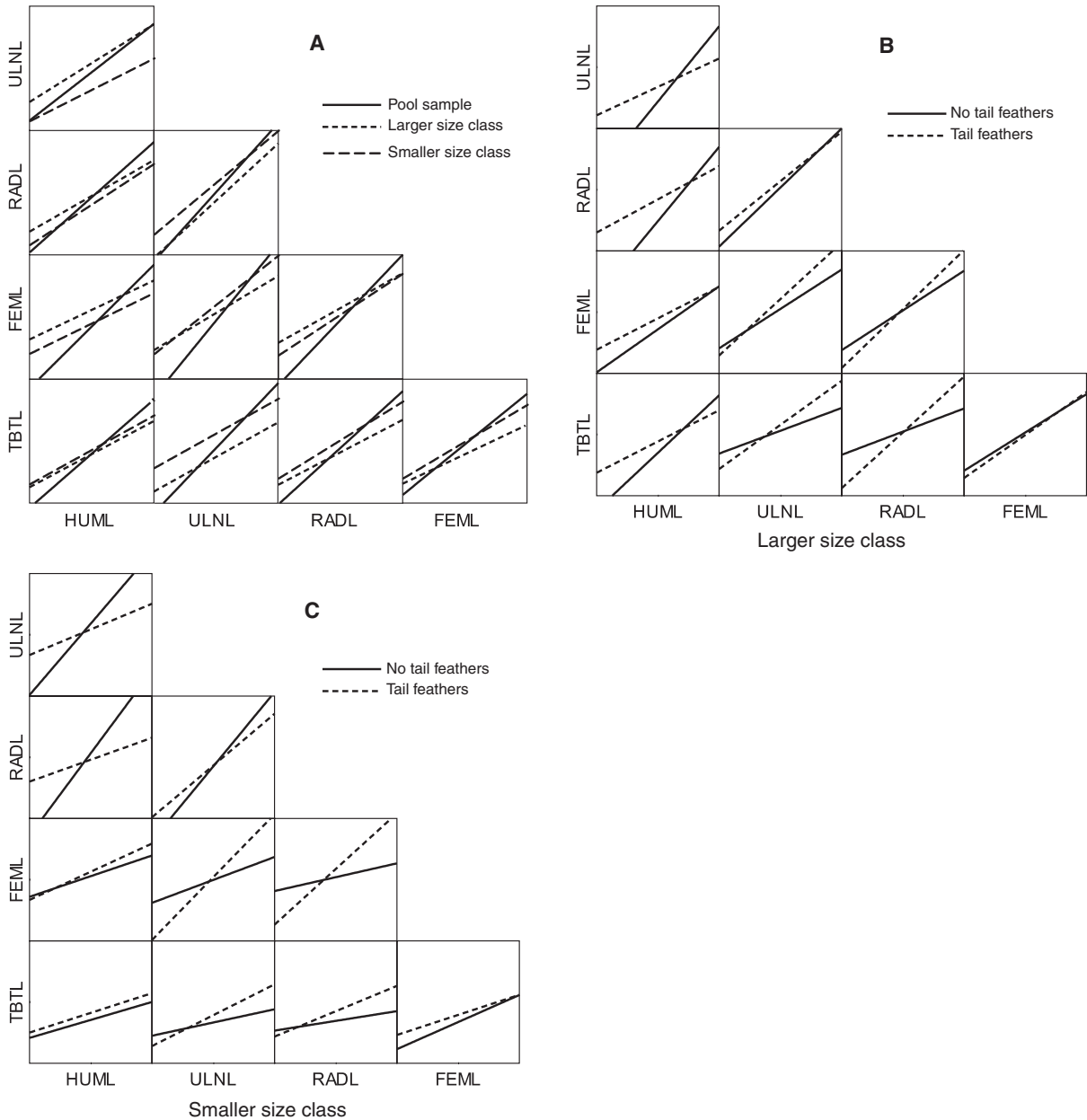| $n = 62$	PC 1	PC 2	PC 3	PC 4	PC 5
HUML	−0.98	0.13	−0.15	−0.05	0.00
ULNL	−0.98	−0.16	−0.01	−0.02	−0.11
RADL	−0.98	−0.17	−0.07	0.07	0.10
FEML	−0.97	0.00	0.19	−0.14	0.05
TBTL	−0.98	0.11	0.10	0.13	−0.02
% Explained variance	95.52	1.67	1.49	0.88	0.42

Figure 4. Combined regression lines compared between the total sample and within size classes. **A,** Pool sample regression line compared with regressions within each cluster separately; **B,** regressions computed for presence/absence of tail feathers within the large size class; **C,** regressions computed for presence/absence of tail feathers within the small size class. In **B** and **C** sample size is too small to be statistically rigorous.
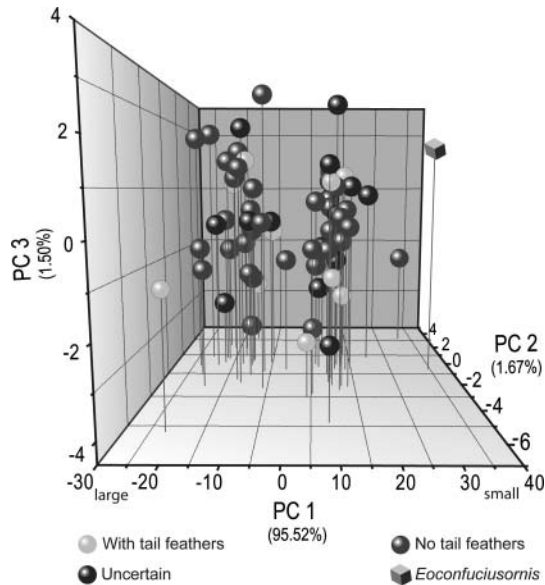
Figure 5. Three dimensional ordination of the PCA (*n* = 62). The three axes are drawn to scale only for aesthetic purposes, but tick marks denote the large-scale differences between PC1 and both PC2 and PC3 (the latter two being nearly identical). The figure of a cube is *Eoconfuciusornis*. Size increases towards the negative scores (see Table 4 for the loadings of the variables on the PCs).

of a few specimens (Marugán-Lobón & Buscalioni 2009). This is why the ordination of the first three PCs is here presented three-dimensionally (Fig. 5). Moreover, given that the scores of PC2 and PC3 are normally distributed (Shapiro-Wilk's W-tests are statistically significant, with $p > 0.01$ in both cases), it is reasonable to assume that both dimensions represent a combined amount of variation in limb proportions between the two size classes.

Discussion

Remarks on confuciusornithid taxonomy

The results of the analyses provide insights into the taxonomy of confuciusornithids. The sample included a number of holotypes of various species. One is *Confuciusornis dui* (IVPP V11553) (Hou *et al*. 1999), which our study included based on the measurements of a cast housed at the Institute of Vertebrate Paleontology and Paleoanthropology (the holotype is apparently lost). Hou *et al*. (1999) diagnosed this species on the basis of a more slender and pointed rostral portion of the mandible and the upper jaw, respectively, the presence of short laterally projected processes and a median notch on the cranial margin of the sternum, and a few differences in either the development or the proportions of other bones including the claw of the alular digit, the tarsometatarsus, and the pygostyle. Our results showed no significant quantitative differences between *C. dui* and the remaining sample: IVPP V11553 clusters with

the smallest size class. However, our study was based on a cast deposited at the IVPP, differing in measurement values from those of Hou *et al*. (1999), and we were unable to obtain a reliable value for the poorly preserved femur (the value used was that of Hou *et al*. 1999). The profile of the skull of *C. dui*, particularly when the impression of the rhamphotheca apparently preserved in the holotype is taken into consideration, is somewhat different from *C. sanctus*, although the rhamphotheca is not well preserved in the latter. The sternum is difficult to compare because it is usually poorly preserved among confuciusornithids. The lateral process and median cranial notch, however, are comparable to those of some specimens of *C. sanctus*. Overall, the holotype of *C. dui* is quantitatively indistinguishable from the small end of the spectrum of *C. sanctus*, although a restudy of the former and of the referred material (Hou *et al*. 1999) needs to be done before regarding these species as synonymous.

Specimen D 2454 was included in the sample of Chiappe *et al*. (2008) prior to being used as the holotype of *C. feducciae* by Zhang *et al*. (2009) who diagnosed this species on the basis of its large size, differential proportions of the wing, the apparent absence of a foramen piercing the deltopectoral crest of the humerus, and more subtle differences of the furcula, sternum and ischium compared to *C. sanctus*. This diagnosis, however, is problematic. Zhang *et al*. (2009) figured the left humerus as lacking a large proximal foramen, but the right humerus of D 2454 clearly shows the presence of an ample foramen piercing the large deltopectoral crest. Despite being one of the largest specimens in our sample, D 2454 is quantitatively indistinguishable from all other specimens of *C. sanctus*, making it difficult to visualize the more subtle differences (e.g. thinner proximal phalanx of alular digit, relatively longer ischium) proposed by Zhang *et al*. (2009) as not resulting from the taphonomic processes and preservational deformation pervasive in the entire sample of confuciusornithids. In light of this, we tentatively regard *C. feducciae* as a junior synonym of *C. sanctus*. Our sample also included the holotype of the older confuciusornithid *Eoconfuciusornis zhengi* (IVPP V11977) (Zhang *et al*. 2008). Our examination of this specimen confirms the assertion of Zhang *et al*. (2008) that it is not a fully grown individual but a juvenile (e.g. unfused compound bones and surface pitting on numerous bones). Quantitatively, IVPP V11977 groups together with the smallest individuals of our sample – similar in size to *C. dui*, both clustering with the smallest size class – and is indistinguishable from other *C. sanctus*. Morphologically, however, there seems to be stronger support for its specific distinction (e.g. the deltopectoral crest of the humerus is definitively not pierced by a foramen). Determining whether or not the much older *E. zhengi* is a synonym of *C. sanctus* may require additional specimens, particularly adults. For the moment, we do not consider *E. zhengi* to be a synonym of *C. sanctus*.

Palaeobiological implications

The biological meaning of size-based polymorphism (two size classes) and its relation to the most notable variable in the sample, the presence/absence of long rectrices, remains difficult to explain. Assuming that all specimens regarded as *Confuciusornis sanctus* belong indeed to a single species, if the long rectrices are interpreted as evidence of sexual dimorphism (Feduccia 1996; Hou *et al.* 1996, 1999; Martin *et al.* 1998), the fact that they are scattered, spanning the entire size cline, is interpreted as indicating that such a sexual trait was not correlated with size differences (Chiappe *et al.* 2008). If the bimodal size distributions are assumed to represent sexual dimorphism (Peters & Peters 2009), the long rectrices would not be a sexually dimorphic trait, and it would be assumed that these feathers were present in both sexes and their absence explained by either taphonomic processes (biostratinomic and/or diagenetic) or moulting (Chiappe *et al.* 1999). However, the results of the expanded sample here analysed reveal an association between the allometry of the fore-limb versus the hind limb (the former predicting the latter) and the tail feathers. Such an association is yet another source of polymorphism in the sample, and though it does not contribute to size difference, it could still be interpreted as evidence of sexual dimorphism. Nevertheless, after screening the literature for the occurrence of pairs of elongated central rectrices, Peters & Peters (2009) pointed out that contrary to widespread belief, the presence of these feathers may not be a reliable sexual character in most extant birds. If such were to be the case, the statistical interaction between long rectrices and limb allometry revealed by our sample could underscore taxonomic differences, indicating two *Confuciusornis* species, with and without long rectrices, each exhibiting size dimorphism.

Interpreting the pattern of size and long tail feather distribution it is further complicated by the fact that other than sexual dimorphism could explain size polymorphism in *C. sanctus*. Such a pattern may be the result of an attritional death assemblage biased against mid-age (and mid-size) individuals and largely composed of the gradual accumulation of smaller juveniles (with higher mortality rate) and larger senescent specimens (Voorhies 1969). Yet the rich death assemblages of the Jehol Biota are assumed to be the result of catastrophic events (Chang *et al.* 2003), a pattern that probably lacked such selectivity. As highlighted by Chiappe *et al.* (2008), the sample may also reflect important differences in growth rates during ontogeny: a specific growth pattern characterized by a multi-year sigmoid growth curve with a mid-development phase of exponential growth, separating earlier (smaller cluster) and later (larger cluster) phases of slower growth (Erickson *et al.* 2001). This interpretation is congruent with inferences supporting the hypothesis that skeletal maturity of *C. sanctus* was reached after several years of growth (Chiappe *et al.* 2010; cf. de Ricqlès *et al.* 2003; Peters & Peters 2009), although these inferences await a more comprehensive histological study sampling the entire size distribution, and an assessment of the relationship between allometry and the characteristics of bone tissue (Erickson *et al.* 2009), to truly ascertain their validity.

In addition to these alternatives, the possibility that the two size classes may each represent morphologically indistinguishable and apparently sympatric species cannot be ruled out either. While this alternative needs to be seriously considered in light of the association between the long tail feathers and the specific allometry of the limbs of each size class, the apparent absence of morphological characters that can diagnose subsets of the entire sample makes it problematic. This notwithstanding, evidence from extant examples (Galapagos and African finches) indicates that although intra-specific multimodal size distributions in birds are rare, such frequencies can emerge by ecological divergence (Smith 1990, 1993; Smith & Girman 2000; Huber *et al.* 2007; Hendry *et al.* 2009) and even in sympatry, where natural and sexual selection can cooperate in favouring ecological differentiation (van Doorn *et al.* 2009). The analytical results of the measurements of *C. sanctus*, either treating the sample as a whole or as two size classes, match those from analyses of both, differently-sized sympatric intra-specific morphs (Smith 1990) and differently-sized closely-related sympatric species (Christiansen 2006). The fact that our analyses underscore scaling differences of long bones associated with the presence of tail feathers—perhaps a sexual character of one or more sympatric species—suggests that the analytical value of the tail feathers should not be dismissed in future studies.

In conclusion, although it is tempting to single out one causal factor to interpret the quantitative aspects of the life history of *C. sanctus* (e.g. sexual dimorphism; Peters & Peters 2009, 2010), the results provide evidence that a much more integrative approach is needed to meet this challenge. Additional studies, incorporating more comprehensive bone histological sampling and analysis of other morphological traits, should help. It is likely that the quantitative variation of *C. sanctus* will continue to require the integration of a number of biological phenomena and the potential adaptive role of a larger number of traits.

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