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Life history of a basal bird: morphometrics of the Early Cretaceous *Confuciusornis*

Luis M. Chiappe^{1,*}, Jesús Marugán-Lobón²,
Shu'an Ji³ and Zhonghe Zhou⁴

¹Natural History Museum of Los Angeles County,
900 Exposition Boulevard, Los Angeles, CA 90007, USA

²Departamento Biología, Facultad de Ciencias,
Universidad Autónoma, Cantoblanco, 28049 Madrid, Spain

³Chinese Academy of Geological Sciences, Beijing 100037, China

⁴Institute of Vertebrate Paleontology and Paleoanthropology,
PO Box 643, 100044 Beijing, China

*Author for correspondence (chiappe@nhm.org).

***Confuciusornis sanctus* stands out among the remarkable diversity of Mesozoic birds recently unearthed from China. Not only is this primitive beaked pygostylian (birds with abbreviated caudal vertebrae fused into a pygostyle) much more abundant than other avian taxa of this age but differences in plumage between specimens—some having a pair of long stiff tail feathers—have been interpreted as evidence for the earliest example of sexual dimorphism in birds. We report the results of a multivariate morphometric study involving measurements of more than 100 skeletons of *C. sanctus*. Our analyses do not show any correlation between size distribution and the presence or absence of blade-like rectrices (tail feathers), thus implying, that if these feathers are sexual characters, they are not correlated with sexual size dimorphism. Our results also provide insights into the taxonomy and life history of confuciusornithids, suggesting that these birds may have retained ancestral dinosaurian growth patterns characterized by a midlife exponential growth stage.**

Keywords: birds; Cretaceous; morphometrics; sexual dimorphism; China

1. INTRODUCTION

Species-level multivariate analyses of morphometric datasets have proven useful for assessing the degree of sexual dimorphism and other life-history phenomena in both extinct and extant organisms (Dodson 1976; Chapman *et al.* 1981; Houck *et al.* 1990; Ranta *et al.* 1994). Among Mesozoic dinosaurs (including birds) these investigations have been rare and, given the paucity of available data, limited to samples of fewer than 25 specimens (Dodson 1976; Chapman *et al.* 1981; Houck *et al.* 1990; Weishampel & Chapman 1990; Currie 2003). In the last decade, hundreds of specimens of the basal pygostylian bird *Confuciusornis sanctus* have been collected from the Early Cretaceous (*ca* 125–120 Myr ago) of northeastern China (Zhou & Zhang 2007). The presence of a pair of very long,

blade-like rectrices in some of these specimens (Chiappe *et al.* 1999) has been consistently interpreted as the earliest evidence of sexual dimorphism in birds (Feduccia 1996; Hou *et al.* 1996; figure 1). Furthermore, specimens with these feathers have been interpreted as males that died during lekking (Feduccia 1996; Hou *et al.* 1996), a mating system involving a reunion of males for the purpose of competitive display. Although most specimens of *C. sanctus* are kept privately and are unavailable for research, we were able to measure 106 specimens housed in public institutions, thus amassing the largest collection of metric data for any Mesozoic dinosaur species to date. Here, we use our metric dataset to determine whether the interpretation of the blade-like rectrices of *C. sanctus* as a sexually dimorphic characteristic is consistent with the presence of sexual size dimorphism.

2. MATERIAL AND METHODS

We measured the maximum lengths of five limb bones (humerus, ulna, radius, femur and tibiotarsus) in a sample of $n=106$ *C. sanctus*, in which the largest specimen is nearly twice the size of the smallest (see electronic supplementary material). When possible, we obtained data from the left and right elements, and then used the log-transformed mean values. Morphometric data were analysed using multivariate exploratory techniques with SPSS software (SPSS Inc. 2005 SPSS v. 14.0.1 for Windows 2005). We conducted a principal component analysis (PCA) based on the variance–covariance matrix for detecting size variability and possible allometric deviations (Jolicoeur & Mosimann 1960; Gould 1966). We also performed a discriminant function analysis (DFA) for testing the probability of assigning a gender (based on presence/absence of blade-like rectrices) by means of a classification function (Chapman *et al.* 1981). In addition, we fitted lines between pairs of different bone data using a reduced major axis (RMA) method (a Model II regression that minimizes the residuals in the x and y directions) in PAST software (Hammer & Harper 2006).

3. RESULTS

Sample sizes for PCA and DFA decreased to $n=59$ (with blade-like rectrices, 39; without blade-like rectrices, 12; uncertain, 8) by pairwise deletion of specimens with missing data (43.5% of the total sample carries missing data). The PCA shows that its first component (PC1) accounts for most covariation among variables and the variability within the sample (95.76% of explained variance; figure 2a); all variables on this component have high positive and nearly identical loadings (table 1). The second component (PC2) explains little variance (1.84%) and it receives positive and negative loadings from the hindlimb (i.e. femur and tibia) and forelimb (i.e. humerus, radius and ulna; figure 2a). Because PC1 and PC2 account for nearly all of the explained variance within the sample (97.6%), the remaining PCA components may concentrate minimal morphological information and therefore are excluded from the present discussion.

The high positive and nearly identical loadings of the first component of the PCA suggest that the entire sample represents a growth series in which the measured bones have nearly isometric scaling. Further support for this conclusion is provided by the major axes of the bivariate scatters (figure 2b; table 1), whose slopes are not significantly different from one. The statistical analysis also reveals no significant differences in the means of bone lengths between specimens with and without blade-like rectrices (ANOVAs; table 1), which explains why the first classification function of the DFA is incapable of

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2008.0409> or via <http://journals.royalsociety.org>.

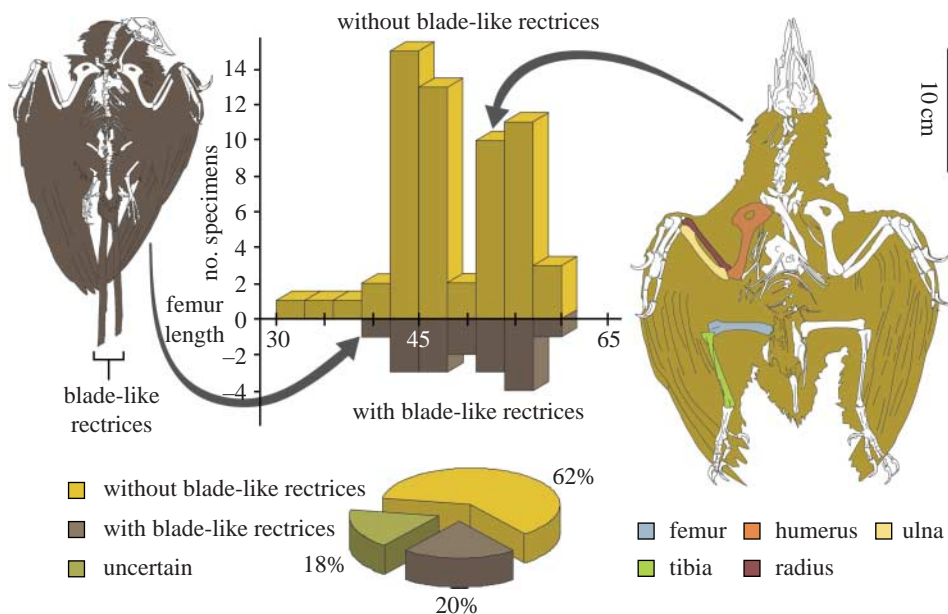


Figure 1. Size distribution (histogram) based on femoral lengths of the analysed specimens of *C. sanctus* with and without blade-like rectrices (scaled left and right skeletons, respectively). The pie chart shows the proportion of specimens in the sample with or without blade-like rectrices and those for which the presence/absence of these feathers is uncertain. Colour coding on the right-hand side skeleton indicates the five bones measured in this study. Note that the percentage of specimens with a pair of blade-like tail feathers (20%) detected in this study is more than twice the ratio previously reported (Martin *et al.* 1998).

Table 1. RMAs for the linear relationship between the log-transformed variables shown in figure 2 (*fem*, femur; *hum*, humerus; *rad*, radius; *tib*, tibiotarsus). (*Changchengornis hengdaoziensis* and *C. dui* were not included in the model. All correlation coefficients (r) are statistically significant ($p < 0.01$). Each confidence interval was bootstrapped to the sample size of each case. Levene tests (at $p < 0.05$) support homoscedasticity in the measured variables, and one-way ANOVAs are not statistically significant ($p < 0.05$). Thus the means of any of the bone lengths are equivalent between specimens with and without caudal rectrices. PCA columns show the loadings (correlation, or r) between each measured variable and the first and second factors of the analysis: note the drop down in amount of explained variance between first and second PCs.)

vars.	n	slope (a)	intercept (b)	err. a	err. b	95% int. a	95% int. b	r
log fem – log hum	83	1.0694	–0.0414	0.0392	0.0660	0.9904; 1.172	–0.2171; 0.0860	0.94
log fem – log rad	71	1.0418	–0.0841	0.0462	0.0780	0.9474; 1.153	–0.2734; 0.0760	0.92
log fem – log ulna	74	1.0688	–0.1084	0.0442	0.0747	0.9609; 1.204	–0.3195; 0.0720	0.93
log fem – log tib	83	1.0352	0.0122	0.0273	0.0460	0.9854; 1.086	–0.0735; 0.0964	0.97
ANOVA				PCA				
F	sig. ($p < 0.05$)					PC1	PC2	
0.479	0.621		log fem	$r =$		0.9717	0.1915	
1.013	0.367		log hum	$r =$		0.9810	–0.0518	
0.442	0.644		log uln	$r =$		0.9825	–0.1389	
1.337	0.268		log rad	$r =$		0.9790	–0.1079	
1.12	0.331		log tib	$r =$		0.9769	0.1625	
			% expl. variance			95.76	1.839	

associating the presence or absence of these rectrices with any combination of variables (Wilks $\lambda = 0.962$, $\chi^2_5 = 1.815$, $p = 0.874$).

4. DISCUSSION

The PCA and the bivariate scatters show a bimodal size distribution (figure 2) whose meaning is not easily explainable. Such a distribution can be hypothesized to be the result of (i) the presence in our sample of an

undetected species closely related to *C. sanctus* or (ii) sexual size dimorphism within *C. sanctus*, (iii) an attritional death assemblage of *C. sanctus* specimens or (iv) important differences in growth rates during the life history of *C. sanctus*. Given that the bivariate plots point at an isometrically scaled growth series (table 1) and that there are no morphologies discriminating between the two size classes, if the bimodal distribution signals the existence of a previously undetected close relative of *C. sanctus* (hypothesis (i)), such a differently

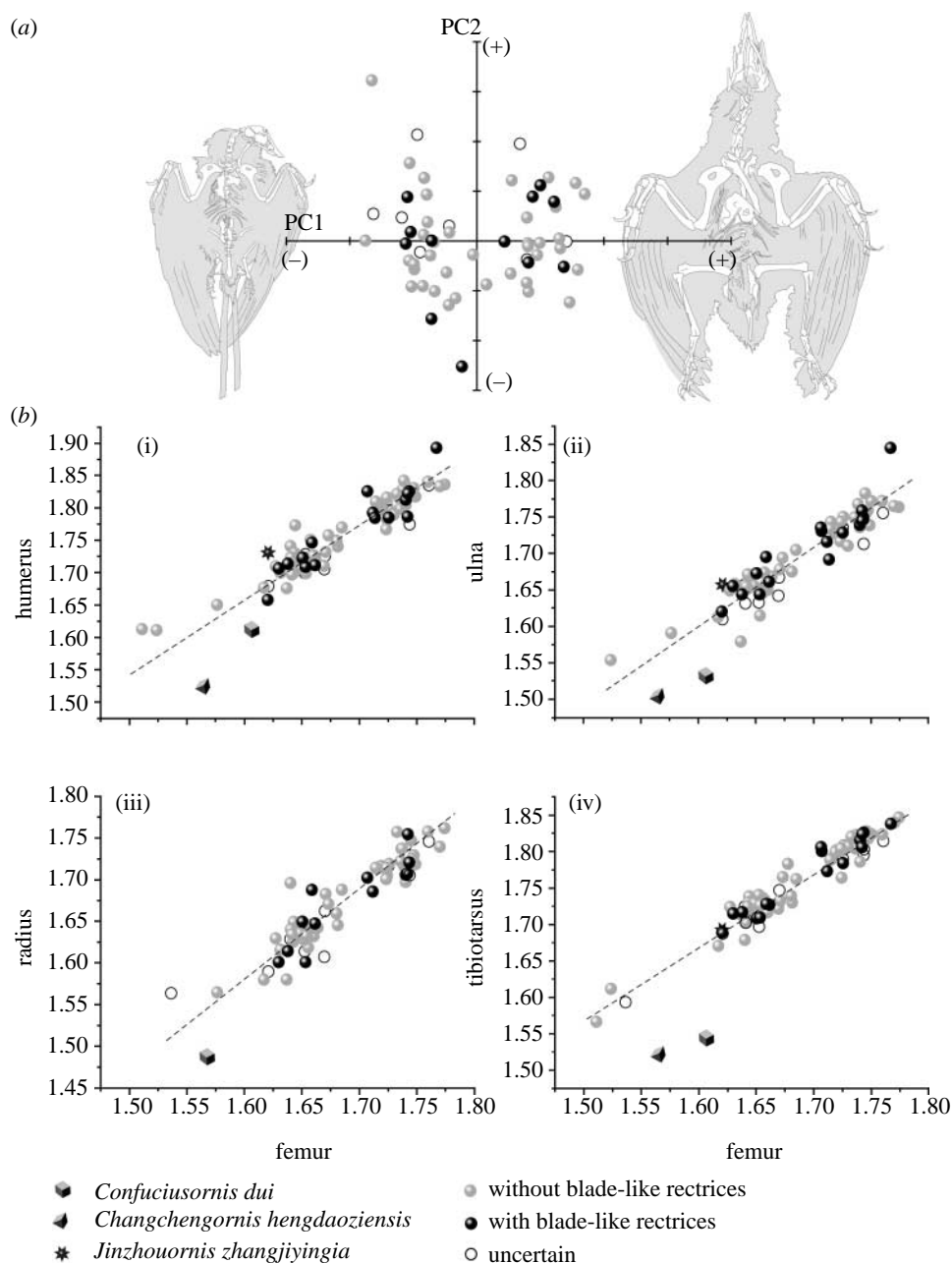


Figure 2. (a) Ordination plot of PCA (see electronic supplementary material for measurements). The scaled silhouettes highlight how the majority of the variation (PC1) is expressed as size differences. There are two separated clusters of size distribution; specimens with blade-like tail feathers are included in the two size classes. The large and homogeneous spread of specimens with these feathers in PC2 reveals no differences in the proportions of the limb bones. The presence/absence of blade-like rectrices was determined by direct observation (see electronic supplementary material) and these conditions were not included in the PCA as variables. (b(i)–(iv)) Bivariate lines of the length of the humerus, ulna, radius, and tibia against the length of the femur of *C. sanctus* (see electronic supplementary material for measurements and table 1 for equations). In addition to the 106 measured specimens of *C. sanctus* we also incorporated in our data the holotypes of the confuciusornithids *Jinzhouornis zhangjiyingia* (Hou *et al.* 2002), *C. dui* (Hou *et al.* 1999) and *Changchengornis hengdaoziensis* (Ji *et al.* 1999). Our examination of the holotype and only known specimen of *J. zhangjiyingia* failed to reveal diagnostic morphologies, and given that this specimen plots near the estimated mean values of *C. sanctus* we consider *J. zhangjiyingia* as a junior synonym of the latter. An alleged relative of *J. zhangjiyingia*, *Jinzhouornis yixianensis* (Hou *et al.* 2002), is also considered to be a junior synonym of *C. sanctus* (see electronic supplementary material), although the very incomplete nature of the only known specimen of *J. yixianensis* prevented us from including it in the morphometric analyses. Unlike *J. zhangjiyingia*, the small *C. dui* and *C. hengdaoziensis* are outliers for the estimated linear regressions of *C. sanctus*, a result that together with the existence of diagnostic characters (Hou *et al.* 1999; Ji *et al.* 1999) lends support to the validity of these taxa.

sized sympatric species would be indeterminable by means of both qualitative and quantitative (distance-based) morphological characters. The bimodal size distribution may reflect the existence of sexual dimorphism (hypothesis (ii)). If that were to be the

case, however, the fact that the morphometric analyses do not result in a statistically significant correlation between size classes and the presence/absence of blade-like rectrices indicates that such dimorphism would be oddly uncorrelated with the most apparent sexual trait.

These results cannot refute the hypothesis that specimens of *C. sanctus* with blade-like rectrices represent lekking males (Feduccia 1996; Hou *et al.* 1996); however, they again highlight the lack of evidence supporting this hypothesis. Further insights into the nature of the resulting bimodality may come from more sensitive geometric morphometric techniques examining potential shape-based differences and fine-tuned morphometric approaches assessing proportional differences in additional skeletal elements (Chapman *et al.* 1997).

The bimodal size distribution of our data could also be posited as the result of taphonomic bias due to normal attritional mortality (hypothesis (iii)), namely, a fossil assemblage composed by the gradual accumulation of juveniles (due to their expected high mortality rate) and senescent individuals (Voorhies 1969). However, the death assemblages of the Jehol Biota are most frequently assumed to be the result of catastrophic events (Chang *et al.* 2003), and consequently they would not reflect the attritional pattern required to support this alternative.

Given that the analysis supports the inclusion of all specimens (except the two outlier taxa: *Confuciusornis dui* and *Changchengornis hengdaoziensis*; see figure 2b) within a growth series, the bimodal size distribution can also be interpreted as evidence of a growth pattern characterized by multi-year sigmoidal growth curve (hypothesis (iv)) similar to those of non-avian dinosaurs (Erickson *et al.* 2001). This explanation conflicts with recent histological interpretations that have reconstructed the growth pattern of *C. sanctus* as similar to those of its modern counterparts, with an estimated growth period shorter than five months (De Ricqlès *et al.* 2003). However, the latter interpretation is at odds with the size distribution of our sample, which cannot be explained if growth were limited to such a short period of time. Simply, the likelihood that the dozens of studied specimens—varying greatly in size and lacking morphologies characteristic of early juveniles—sample only a few months of the life history of this early bird is extremely low (Padian *et al.* 2001; Chiappe 2007). By contrast, our data on *C. sanctus* is better fitted to a multi-year post hatching life history characterized by a mid-development phase of exponential growth that separates earlier and later phases of slower growth (lag and stationary phases of Erickson *et al.* 2001). We therefore believe hypothesis (iv) to be the least implausible explanation for the presence of a bimodal size distribution in our sample. Consequently, we interpret that the gap between the size classes of *C. sanctus* reflects a short exponential growth phase similar to the mid-development stage of the life history of the dinosaurian predecessors of birds (Erickson *et al.* 2001).

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