How Much Did *Archaeopteryx* and *Quetzalcoatlus* Weigh?

Estimation of the Mass of Fossil Organisms by Multivariate Analysis of Bone Dimensions

Momchil Atanassov[1] and Richard Strauss[2]

[1]Department of Geosciences and [2]Department of Biological Sciences, Texas Tech University, Lubbock TX

PART I: Evaluation

INTRODUCTION

•**Body mass** is an important aspect of the biology of an organism. Many methods have been proposed to estimate body mass from skeletal measurements. Most have been based on univariate regression of the mass of specimens against single measurements, usually of limb bones, and subsequent use of the regression relationship to predict specimens of unknown mass. Although the measures used are often based on functional criteria (e.g., diameters of weight-bearing bones), typically no attempt is made to compare the degrees of correlation of these measures with body mass against other possible skeletal measures. Another class of body-size estimates has been based on volumetric models of reconstructed body forms. These models are advantageous for fossil organisms having no modern analogs, but require complete skeletons to allow for reconstruction and involve various conjectures about the anatomy of soft tissues.

•This project consisted of two parts. Part I was to evaluate five different methods of predicting body mass from sets of morphometric measurements, for six different data sets of extant and fossil animals for which body masses are known or have been estimated. Part II was to apply the multivariate methods to estimate body sizes of three species of pterosaurs, including the giant *Quetzalcoatlus*, and of *Archaeopteryx*.

COMPARISON METHODOLOGY

For each data set, we predicted the body mass separately for each individual and compared the predicted value with its known mass. The results were then averaged across all individuals, giving a mean error (mean difference between predicted and known masses) and a standard deviation of error. For univariate predictive regression and major-axis regression, this was done separately for each character. For the remaining multivariate methods, it was done simultaneously for all characters

PREDICTION METHODS

Five different univariate and multivariate methods were compared in their ability to predict body mass. Log-transformed data (mass and body measurements) were used with all prediction methods to linearize allometric relationships among characters, standardize variances, and produce scale-invariant covariance matrices. In each case the specimens with known body mass were used to fit regression lines or otherwise calibrate the relationship of mass with other body measurements, and "unknown" masses were predicted from the regression relationship.

(1) **Univariate predictive regression** – body mass (the dependent variable) is regressed against on some univariate measure of body size (such as femur diameter, the independent variable) using predictive (Type I) regression, in which regression "errors" (residuals) are assumed to be concentrated in the dependent variable.

(2) **Major axis regression** – body mass is regressed against some univariate measure of body size (such as femur diameter) using major-axis (Type II) regression, in which regression "errors" (residuals) are assumed to be orthogonal to the regression line.

(3) **Multiple regression** – body mass (the dependent variable) is regressed against a set of body measurements (independent variables) using predictive (Type I) regression.

(4) **Principal components regression** – using predictive (Type I) regression, body mass is regressed against the first principal component (PC1) derived from the covariance matrix of the body measurements. When specimens vary in size, PC1 accounts for general size variation.

(5) **Expectation-maximization (EM) imputation** –covariances derived from all characters (mass + body measurements) are used to predict ("impute") the unknown body masses. The EM algorithm is a commonly used means of estimating missing data, and the estimation of unknown masses is an extension of this use.

	Crocodylus	Pterosaurs	Birds	Falcons	*Larus*	Bats		Mean
Specimens	174	11	268	23	18	68		
Characters	14	15	8	7	16	11		
% missing data estimated	0.0	0.6	0.0	3.3	1.4	0.0		
EM predictions								
All characters								
Mean error	-0.003	0.000	**0.000**	-0.099	-0.135	**-0.001**		**-0.047**
Standard deviation of error	0.341	3.012	**0.393**	0.658	1.082	**0.263**		**1.097**
PC predictions								
All characters								
Mean error	**0.000**	**0.009**	0.000	**0.006**	**-0.004**	0.000		**0.002**
Standard deviation of error	**0.330**	**0.466**	0.494	**0.249**	**0.150**	0.322		**0.338**
Multiple regression								
All characters								
Mean error	**-0.001**	0.134	**-0.001**	-0.005	0.267	0.012		**0.079**
Standard deviation of error	**0.328**	6.613	**0.383**	0.319	2.555	0.272		**2.040**
Univariate regression								
Mean error								
Minimum value	0.000	-0.197	-0.001	0.002	-0.011	-0.007		**-0.041**
Mean value	0.000	-0.006	0.000	0.006	-0.003	0.001		**-0.001**
Maximum value	0.000	0.113	0.000	0.007	0.009	0.003		**0.026**
Standard deviation of error								
Minimum value	0.316	0.315	0.501	0.283	0.098	0.283		**0.303**
Mean value	0.368	0.938	0.659	0.358	0.233	0.520		**0.511**
Maximum value	0.576	2.737	0.958	0.654	0.418	0.699		**1.069**
Major-axis regression								
Mean error								
Minimum value	-15.025	-12.539	-17.136	-11.266	-0.150	-18.999		**-11.223**
Mean value	-6.679	-6.757	-10.617	-13.685	4.664	-11.541		**-6.615**
Maximum value	1.308	-3.157	0.100	-18.700	10.867	3.388		**-1.917**
Standard deviation of error								
Minimum value	0.323	0.242	0.511	0.266	0.088	0.283		**0.286**
Mean value	0.383	0.861	0.701	0.346	0.209	0.587		**0.500**
Maximum value	0.644	1.846	1.095	0.662	0.361	0.836		**0.922**

Table 1. Results from evaluation of prediction methods. Red values indicate the "best" results for each data set.

DATA SETS

Data sets were taken from literature sources, and varied in numbers of specimens and characters and of taxa represented. Individuals with unknown body masses or with excessive number of missing body measurements were omitted. Small numbers of missing data for some data sets were estimated using the expectation-maximization imputation method (Strauss, Atanassov & Oliveira, in press) prior to predicting body masses.

Crocodylus – measurements of individuals of a single species, Crocodylus *porosus*; 197 specimens, of which 174 were used. 14 characters + mass (Webb & Messel 1978).

Pterosaurs – 5 species of *Pterodactylus* (Wellnhofer 1970), 2 species of *Cycnorhamphus (Gallodactylus)* (Fabre 1976; Wellnhofer 1970), *Dsungaripterus weii* (Bramwell & Whitfield 1974), *Nyctosaurus gracilis* (Williston 1902), and *Pteranodon ingens* (crested form; Young 1973) were used to calibrate the regressions based on the volumetric model for mass reconstruction (Hazlehurst 1991) and an estimated density of 0.9g/cm³. 11 specimens and 15 characters.

Birds – average mass and measurements for 380 species of extant birds (Hazlehurst 1991); 268 species were used. 11 characters, of which 8 were used (forelimb and hindlimb measurements).

Falcons – a subset of the Hazlehurst (1991) data set on birds, including only representatives of Falconiformes; 23 species and 11 characters, of which 7 were used (forelimb and hindlimb measurements).

Larus – measurements of an ontogenetic series of a single species, the California Gull *Larus californicus* (Carrier & Leon 1990); 18 specimens and 16 characters.

Bats – average mass and measurements for 233 species of extant bats (Hazlehurst 1991); 68 species were used; 12 characters, of which 11 were used (forelimb and hindlimb measurements, including wingspan).

RESULTS OF COMPARISONS

•1. For all data sets, **multivariate predictions of body mass were more accurate than univariate predictions** (Table 1). The regression estimate for the *best* character was comparable in accuracy to the multivariate predictions, but when applying the methods one generally wouldn't know which is the best single character.

•2. For the univariate methods, the variation in predictive value was comparable, but mean predicted body masses were considerably underestimated by the major axis method.

•3. Among the multivariate methods, the **principal-component method was, on average, clearly the most accurate.**

PART II: Applications

Archaeopteryx

Data

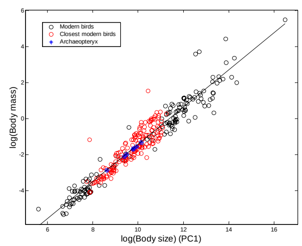
Archaeopteryx measurements taken from Wellnhofer (1974, 1978, 1993), but reduced to 6 limb characters (humerus, ulna, metacarpal, femur, tibiotarsus, tarsometatarsus) in common with data on extant birds. The bird data from Hazlehurst (1991) were reduced to the same 6 characters for 317 species. The 160 bird species that were most similar to the *Archaeopteryx* specimens in terms of the 6 characters were used to individually predict body masses of the *Archaeopteryx* specimens.

Results (Table 2)

The principal-component and multiple-regression methods mostly agreed in the predicted body masses, except that most of the multiple-regression predictions were somewhat greater. However, the EM predictions disagreed with these by three orders of magnitude and so have been ignored here. Based on the results of the comparative evaluations of the methods, we presume that the PC-based estimates are more reliable. Mass estimates range from 57 g for the Eichstatt specimen to 265 g for the Solnhofen specimen, which has recently been renamed *Wellnhoferia grandis* (Elzanowski 2001).

Table 2. Predictions of body mass (g) of *Archaeopteryx* specimens. Red values indicate the "best" results, predictions using the multivariate principal components method.

Archaeopteryx specimen	Principal components predictions	Multiple regression predictions
Eichstatt	**57**	66
Munich (*A. bavarica*)	**123**	119
Berlin	**138**	172
Haarlem	**182**	133
Maxberg	**192**	256
London	**214**	242
Solnhofen (*Wellnhoferia grandis*)	**265**	330



Quetzalcoatlus

Data

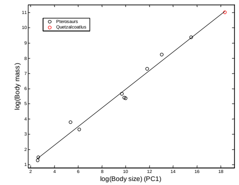
Body measurements (15 characters) and estimated body volumes for 11 species of pterodactyloid pterosaurs were taken from Brower (1980) and Hazlehurst (1991). The same set of body measurements for *Quetzalcoatlus* was taken directly from a cast at the Museum of Texas Tech University of a specimen deposited at the University of Texas (Austin). Body volume of *Quetzalcoatlus* was estimated using the EM, principal-component, and multiple-regression methods, and corresponding estimates of body mass were based on a densities of 0.72 and 0.90g/cm³, which bracket realistic densities for flying animals.

Results (Table 3)

Based on the two density estimates, the principal-component estimates suggest that the body mass of *Quetzalcoatlus* was between 62 and 77 kg. These correspond approximately to the initial estimates at the time of its description, but are considerably less than other more recent estimates. The multiple-regression estimates reported here are an order of magnitude larger and are unrealistic. The EM estimates were several orders of magnitude larger still and so have been ignored.

Table 3. Predictions of body mass (kg) of *Quetzalcoatlus*. Red values indicate the "best" results, predictions using the multivariate principal components method.

Density	Principal components predictions	Multiple regression predictions
0.73	**62**	847
0.90	**77**	1044



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