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QUANTIFYING MORPHOLOGICAL VARIABILITY WITHIN EXTANT MAMMALIAN SPECIES

by

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ABSTRACT

In this study we attempt to establish a baseline for measuring species variability in the palaeontological record by using linear regression analysis on sets of measurements from extant mammalian species (males and females within species). In particular, this study explores the standard error of the m-coefficient ($s.e._m$), derived from linear regression analyses associated with equations of the form $y = mx + c$, to quantify the degree of morphological variability within extant mammalian species. The slope m generally centres around 1.00. Even though the species in this study range in size from small rodents to large ungulates, $s.e._m$ values show a normal distribution around a mean of 0.035. The approach outlined here has potential application in palaeontological contexts where there is uncertainty about any two specimens being conspecific.

One of the most pressing problems in palaeontology concerns the question whether certain specimens are attributable to a single species. Central to this taxonomic issue is how to quantify morphological variability. Previous attempts to tackle this have included the use of multivariate techniques of the kind that have been used recently by Shea *et al* (1993). Here, a simple technique has been developed whereby the degree of morphological variability in modern species can be quantified, using material that is unquestionably representative of single species. The intention is to compare measurements from a single specimen against a comparable set of measurements from another specimen of the same species; we undertake linear regression analyses for several such comparisons, and determine whether there is any regularity in the standard error of the slope m in equations of the form $y = mx + c$, when dealing with modern mammalian species. The main objective is to explore the potential of using $s.e._m$ to address taxonomic problems.

TABLE 1.
List of species analyzed in this study.

Order	Family	Species
Rodentia	Muridae	*Otomys irroratus*
		Otomys angoniensis
		Aethomys chrysophilus
		Aethomys ineptus
Hyracoidea	Procaviidae	*Procavia capensis*
Lagomorpha	Leporidae	*Lepus saxatilis*
		Prolangus capensis
Carnivora	Hyaenidae	*Hyaena brunnea*
	Felidae	*Felis lybica*
		Felis caracal
		Felis nigripes
		Panthera leo
Primates	Cercopithecidae	*Cercopithecus aethiops*
		Cercopithecus mitis
	Lorisidae	*Galago crassicaudatus*
		Galago moholi
Artiodactyla	Suidae	*Phacochoerus aethiopicus*
		Potamochoerus porcus
	Bovidae	*Damaliscus lunatus*
		Taurotragus oryx
		Tragelaphus scriptus
		Hippotragus niger
		Kobus ellipsiprymnus
		Bos taurus

MATERIALS AND METHODS

Twenty five extant non-hominid mammalian taxa, listed in Table 1, were chosen to represent a broad range of taxonomic groups and body sizes. The taxa encompass 6 mammalian orders (Rodentia, Hyracoidea, Lagomorpha, Carnivora, "Primates", and Artiodactyla), with representatives from 9 families. The species range in average adult body mass from 0.1 to 650 kg, data derived primarily from Skinner and Smithers (1990).

Initially, linear measurements were taken on 5 males and 5 females of each species represented in collections at the Transvaal Museum in Pretoria, South Africa. For each species, only adult individuals of known sex were chosen. Ten measurements per specimen were taken, of which seven were craniofacial and three mandibular (Table 2). These measurements were considered to be generally representative of overall size of the cranium and mandible. For purposes of this exploratory study, data from the largest male and smallest female for each species were used in regression analyses, with data for females on the x axis. By utilizing the extremes rather

TABLE 2.
Measurement definitions

1. Maximum cranial length: greatest length of the skull from the anterior edge of the nasal aperture to the most posterior point on the occiput.
2. Maximum cranial width: greatest width of the braincase at the dorsal root of the squamosals.
3. Interorbital breadth: least breadth between the orbits.
4. Zygomatic arch length: greatest arch length.
5. Greatest cranial height: greatest height of skull perpendicular to the horizontal plane and through the bullae.
6. Mandibular height: measured from the ventral margin of the jaw to the alveolar border between the last two molars.
7. Greatest vertical diameter of the foramen magnum.
8. Length of mandible: from the posterior surface of the condylar process to the anteroventral edge of incisor alveolus.
9. Tooth row length: maximum length of the maxilla, from the anterior edge of incisor alveolus (where present; alternatively, from the most anterior extent of mid-sagittal maxillary bone, as in ruminants without incisors), to the posterior surface of M^3 (or last molar) alveolus.
10. Length of jaw: greatest length of the mandible from the anterior edge of I_1 to the posterior surface of the angular process.

than species means, we hope to document variation within samples for each of the 25 mammalian species ranging in size from small rodents to large ungulates, for purposes of determining whether there is any patterning in the standard error of slope *m* in equations of the form $y = mx + c$, irrespective of variability in body size. The standard error of the slope *m* is designated $s.e._m$.

High $s.e._m$ values can be expected to relate to high morphological variability when comparing any two specimens, reflected also by a high degree of scatter of measurements around a regression line. By contrast, low $s.e._m$ values can be expected to relate to small morphological differences, or very little scatter around a regression line.

RESULTS

As expected when dealing with specimens attributable to the same species, m-coefficients approximate 1,0 (mean for 25 taxa is 0.997 +/- 0.019). Of particular interest is the fact that $s.e._m$ values for 25 taxa approximate a normal distribution around a mean value of 0.035 (+/- 0.014) when data for all species are analysed (Table 3).

The $s.e._m$ values listed in Table 3 do not correlate with body mass (r=0.19). By contrast, the standard error of the *y*-intercept ($s.e._y$) is correlated with body mass (r=0.78).

CONCLUSIONS

This study indicates that morphological variability within mammalian species, as expressed by $s.e._m$, appears to centre around 0.035, irrespective of variability in body size of the mammalian species included in this exploratory analysis. This result applies to craniofacial variables listed in Table 2, for a

TABLE 3

Values for slopes m and constants c in equations of the form y = mx + c, relating two specimens of the same species against each other, in this instance measurements of the largest male (y-axis) against those of the smallest female (x-axis) in samples included for this study.

	m	*c*	$s.e._m$	$s.e._y$
Felis caracal	0.989	-0.539	0.030	2.976
Felis nigripes	1.007	-0.649	0.037	2.096
Felis libyca	0.988	-0.754	0.045	3.484
Panthera leo	0.987	1.541	0.019	4.481
Hyaena brunnea	0.979	-1.037	0.024	5.209
Galago crassicaudatus	1.009	0.604	0.045	2.520
Galago moholi	0.992	-2.508	0.049	1.500
Cercopithecus mitis	0.996	-2.227	0.054	4.473
Cercopithecus aethiops	1.026	-0.232	0.027	2.185
P. ursinus	1.029	-2.357	0.047	7.105
Otomys irroratus	0.969	-0.754	0.048	1.382
Otomys angoniensis	1.031	-3.631	0.038	0.983
Pronolagus rupestris	0.958	3.280	0.036	0.250
Aethomys chrysophilus	1.012	-1.870	0.020	0.468
Aethomys ineptus	1.004	-0.289	0.056	1.256
Lepus saxatilis	0.999	-0.174	0.010	0.067
Procavia capensis	0.978	-0.607	0.040	2.828
Damaliscus lunatus	0.990	-0.269	0.012	4.849
Taurotragus oryx	1.028	-1.696	0.067	16.950
Bos taurus	1.004	-2.381	0.050	16.730
Kobus ellipsiprymnus	0.996	1.187	0.034	9.496
Tragelaphus scriptus	0.965	0.117	0.025	5.998
Hippotragus niger	1.013	0.463	0.027	11.650
Potamochoerus porcus	0.992	-0.178	0.026	9.464
Phacochoerus aethiopicus	0.990	-1.365	0.019	5.667
MEAN:	0.997	-0.653	0.035	4.963
STANDARD DEVIATION:	0.019	1.441	0.014	4.595

range of species listed in Table 1, but can be tested for other variables for other taxa in future analyses. Such results are of potential value for purposes of testing whether particular specimens are conspecific, especially in cases where this is uncertain in palaeontological contexts.

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