

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

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 M³ (or last molar) alveolus.
10. Length of jaw: greatest length of the mandible from the anterior edge of I₁ 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	$s.e._m$	$s.e._y$
<i>Felis caracal</i>	0.989	-0.539	0.030	2.976
<i>Felis nigripes</i>	1.007	-0.649	0.037	2.096
<i>Felis libyca</i>	0.988	-0.754	0.045	3.484
<i>Panthera leo</i>	0.987	1.541	0.019	4.481
<i>Hyaena brunnea</i>	0.979	-1.037	0.024	5.209
<i>Galago crassicaudatus</i>	1.009	0.604	0.045	2.520
<i>Galago moholi</i>	0.992	-2.508	0.049	1.500
<i>Cercopithecus mitis</i>	0.996	-2.227	0.054	4.473
<i>Cercopithecus aethiops</i>	1.026	-0.232	0.027	2.185
<i>P. ursinus</i>	1.029	-2.357	0.047	7.105
<i>Otomys irroratus</i>	0.969	-0.754	0.048	1.382
<i>Otomys angoniensis</i>	1.031	-3.631	0.038	0.983
<i>Pronolagus rupestris</i>	0.958	3.280	0.036	0.250
<i>Aethomys chrysophilus</i>	1.012	-1.870	0.020	0.468
<i>Aethomys ineptus</i>	1.004	-0.289	0.056	1.256
<i>Lepus saxatilis</i>	0.999	-0.174	0.010	0.067
<i>Procavia capensis</i>	0.978	-0.607	0.040	2.828
<i>Damaliscus lunatus</i>	0.990	-0.269	0.012	4.849
<i>Taurotragus oryx</i>	1.028	-1.696	0.067	16.950
<i>Bos taurus</i>	1.004	-2.381	0.050	16.730
<i>Kobus ellipsiprymnus</i>	0.996	1.187	0.034	9.496
<i>Tragelaphus scriptus</i>	0.965	0.117	0.025	5.998
<i>Hippotragus niger</i>	1.013	0.463	0.027	11.650
<i>Potamochoerus porcus</i>	0.992	-0.178	0.026	9.464
<i>Phacochoerus aethiopicus</i>	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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ABSTRACT

Systematic excavations at Buffalo Cave in the Makapan Valley were begun in October 1993. This paper presents our preliminary analysis of the faunal assemblage from this site, including new *in situ* fossils and the collections which have been housed at the Bernard Price Institute, Palaeontology since the 1940's. Our palaeoecological reconstruction suggests that the local environment at Buffalo Cave at the time of deposition was an open country grassland or savanna, including a high proportion of acedaphine bovids and other grazing fauna. However, the presence of other taxa, particularly of trachelophines, hippotragines, and reduncines, may indicate that a more wooded habitat including a local water source, could also have been part of the Buffalo Cave environment during some part of its depositional history. The fauna overall indicates that deposition occurred during the Pleistocene, rather than the Pliocene. Thus, the environmental and temporal information presently available suggests that the Buffalo Cave fauna represents an environmental and time period distinct from other sites in the Makapan Valley (i.e., the Lineworks and Cave of Hearths).

INTRODUCTION

Knowledge of bone breccia deposits from the Makapan Valley probably dates back to the turn of the century, as a result of the extensive lineworks mining operations throughout the region (Mason 1962, 1988). At the very least, amateur palaeontologists had learned of these fossiliferous beds by about 1920 from locals employed by the lineworks operations (Eitzman 1958).

Although the Makapan Lineworks site has been the major focus of palaeoanthropological research in this region (e.g., Cadman & Rayner 1989; Dart 1925, 1948, 1952, 1957; Ewer 1956, 1958; Gentry 1970; Kitching 1953, 1965, 1980; Maguire B. 1980a; Maguire J.M. *et al.* 1980, 1985; Partridge 1979, 1986; Rayner *et al.* 1992; Torren 1952; Vrba 1982, 1987; Wells & Cooke 1950; and others), other fossil-bearing sites are present in the valley, and have drawn the interest of palaeontologists, as well as archaeologists (e.g., Broom 1937; Cooke 1962; Mason 1971, 1988; van Riet Lowe 1948). In 1937, from another former mining operation across the valley from the Lineworks, Broom (1937) discovered and described a fossil which he believed to represent an extinct dwarf buffalo. He named the species *Bos makapani*, and the site has become known as 'Buffalo Cave'. No systematic excavations were ever undertaken there, and the site has only a few mentions in palaeontological literature (Bosch *et al.* 1982; Broom and Jensen 1946; Gentry 1978; van Riet Lowe 1948). Periodic excursions by the University of the Witwatersrand since the 1940's (J.W. Kitching and

P.V. Tobias *pers. comm.*) have resulted in a modest collection of bone breccia blocks which are stored at the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand.

Beginning in October 1993, a systematic palaeontological excavation has been conducted at Buffalo Cave under the auspices of the Homimid Palaeoecology Research Programme (HPRP) at the University of the Witwatersrand. The objective of the HPRP, and therefore of the excavations at Buffalo Cave and elsewhere, is the analysis of evolutionary changes in the faunas and ecosystems of southern Africa during the time period in which early hominids were evolving. The palaeontological remains recovered are thus an important part of an ever-growing database, and have the potential to fill in important temporal gaps in our knowledge concerning environmental changes during the more recent evolutionary history of the southern African region. This report is our preliminary assessment of the Buffalo Cave fauna, including our initial interpretation of the ecological and temporal setting of the site in relation to other South African Plio-Pleistocene localities. Obviously, our interpretation of the palaeoecological conditions at Buffalo Cave is subject to modification following the future recovery of *in situ* materials during our ongoing excavations.

CONTEXT OF BUFFALO CAVE FOSSILS

Buffalo Cave is located in the Makapan Valley at approximately 24°08'S 29°11'E, 19 km east-northeast of Pongolacrus in the Northern Transvaal (Figure 1).