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Abstract: The study has used a multivariate analysis of morphometric data to define and attempt to explain the differences and similarities between *Acinonyx* and *Panthera*. Despite being a highly specialized cat, the cheetah still follows the generalized large felid form in 21 out of 34 variables analyzed. The dental differences seen are adaptations to capturing and killing prey that have occurred in the genus *Acinonyx* alone. In addition, the cheetah retained some cranial features of the smaller cats, despite increasing its overall size. In view of this, it is not so much that cheetahs have altered that is surprising, but how apparently conservative the feline cranial shape has been over the last few million years.

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Defining Cheetahs, a multivariate analysis of skull shape in big cats

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INTRODUCTION

The 'big cats' are a group of large felids comprising the five members of the genus *Panthera* (Lion *P. leo*, Leopard *P. pardus*, Jaguar *P. onca*, Snow Leopard *P. uncia* and Tiger *P. tigris*) and the Cheetah (*Acinonyx jubatus*). Molecular phylogenies have been used to date the Cheetah's divergence from the main cat lineage (including *Panthera*) to between 16.2 Ma (Bininda-Emonds, Gittleman & Purvis, 1999) and 8.2 Ma (Mattern & McLennan, 2000). Whichever is right, it is apparent that the Cheetah has evolved separately for several million years.

In behaviour the Cheetah is an atypical felid. It commonly chases its prey at high speeds and kills by strangulation, although it is capable of stalking like a typical felid (Ewer, 1973). This study has used a multivariate analysis of morphometric data to define and attempt to explain the differences and similarities between *Acinonyx* and *Panthera*.

METHODS

A total of 390 skulls of all six species were measured to the nearest 0.1 millimetre (see the Appendix for a list of museum collections). Thirty-four measurements were taken on each; these are summarized in Table 1. Only cats with complete data sets were included, reducing the total to 152 specimens consisting of 34 Cheetahs, 26 Jaguars, 36 Leopards, 41 Lions, 10 Tigers and five Snow Leopards.

Principal components analysis (PCA) was used to highlight differences in shape between the species; this technique creates new axes that are orthogonal to each other and combines the variables to show the maximum variation between individuals (Fowler, Cohen & Jarvis, 1998).

RESULTS AND DISCUSSION

The results of the PCA are shown in Table 2. Only two axes were produced with eigenvalues greater than 1 and these encompassed 93.6% of the variation. All variables showed a high positive loading on axis 1 (PC1), suggesting that these are size-related differences. Only 13 of the original 34 variables had values greater than 0.1 on PC2, these are shown in Table 3. The majority of these were related to dentition or measurements of the brain case. Although the

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Table 1. Description and abbreviations of measurements used in this study. Those marked with an asterisk are highlighted on PC2

Measurement abbreviation	Description of measurement
CSL *	Upper canine, greatest anteroposterior length at cemento-enamel (C-E) junction
CSB *	Upper canine, greatest mediolateral breadth at C-E junction
UP2B *	Upper 2nd premolar, greatest mediolateral breadth
UP3L	Upper 3rd premolar, greatest anteroposterior length
UP3B *	Upper 3rd premolar, greatest posterior mediolateral breadth
UP4L	Upper 4th premolar, greatest anteroposterior length
UP4Ba *	Upper 4th premolar, anterior mediolateral breadth
UP4BBL	Upper 4th premolar, mediolateral breadth at carnassial notch
UP4Lp	Upper 4th premolar, anteroposterior length of the protocone
UP4Lm	Upper 4th premolar, anteroposterior length of the metastyle
UM1B	Upper 1st molar, mediolateral breadth
BL	Basal length, from anterior of incisors to the foramen magnum
PL	Palate length, from buccal edge of incisors to the farthest edge of the palate
RB	Rostral breadth, greatest distance between buccal edges of the upper canines
MB	Muzzle breadth, greatest distance between posterior buccal edge of upper P^4s
ZB	Zygomatic breadth, greatest width of the zygomatic arches
IO *	Least distance between the orbits
PP *	Greatest breadth of the postorbital process
PC *	Least width of the postorbital constriction
CONDB	Breadth of the occipital condyles, from the outer edges, across the foramen magnum
CIL *	Lower canine, greatest anteroposterior length at C-E junction
CIB *	Lower canine, greatest mediolateral breadth at C-E junction
P3L	Lower 3rd premolar, greatest anteroposterior length
P3B	Lower 3rd premolar, greatest posterior mediolateral breadth
P4L	Lower 4th premolar, greatest anteroposterior length
P4B *	Lower 4th premolar, greatest posterior mediolateral breadth
M1L	Lower 1st molar, greatest anteroposterior length
M1B	Lower 1st molar, greatest mediolateral breadth
C-cd	Length from buccal edge of lower canine to mandibular condyle
HPC *	Height of the coronoid process
P3-M1	Distance from anterior edge of lower P_3 to the posterior edge of lower M_1.
A	Anterior depth of the mandible, anterior to P_3
P	Posterior depth of the mandible, posterior to M_1
Bp/4	Greatest mandibular breadth below lower P_4

Table 2. Principal components extracted. Two have eigenvalues above 1, accounting for 93.6% of the variance

	Initial eigenvalues			Extraction sums of squared loadings		
Component	Total	% of variance	Cumulative %	Total	% of variance	Cumulative %
1	30.582	89.948	89.948	30.582	89.948	89.948
2	1.230	3.617	93.565	1.230	3.617	93.565
3	0.645	1.896	95.461			
4	0.281	0.826	96.287			
5	0.211	0.620	96.906			
6	0.150	0.440	97.346			
7	0.139	0.407	97.754			

Table 3. Results of PCA. Only those measurements with values above 0.1 are shown

Variable	PC1	PC2
CSL	0.972	–0.138
CSB	0.951	–0.183
UP2B	0.922	–0.135
UP3B	0.957	–0.187
UP4BA	0.941	–0.283
ZB	0.956	0.101
IO	0.933	0.288
PP	0.804	0.522
PC	0.643	0.707
CIL	0.967	–0.199
CIB	0.916	–0.249
P4B	0.971	–0.132
HPC	0.939	0.144

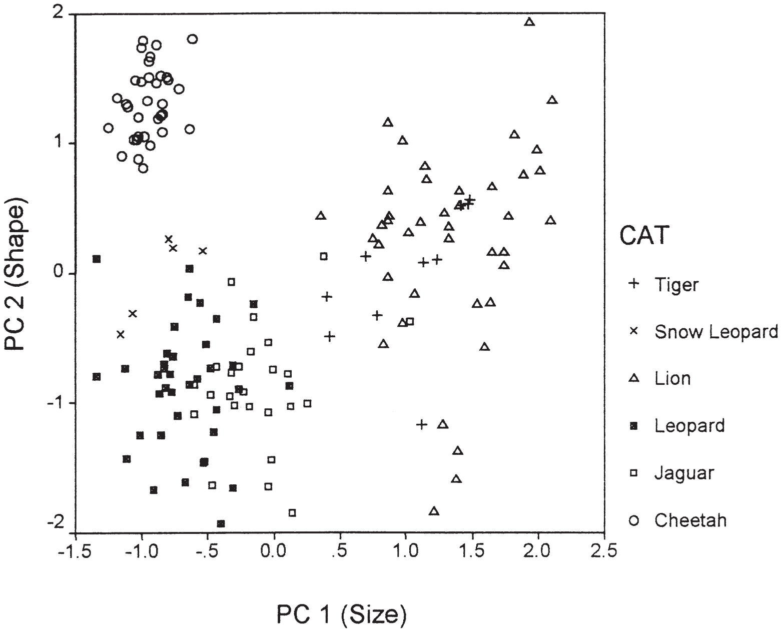

Fig. 1. Scatterplot of the first two PCA axes. PC1 is defined by size, with larger cats to the right and smaller cats to the left. PC2 shows shape changes, with the Cheetah forming a distinct cluster in the top left-hand corner.

second axis contains only 3.6% of the total variance, it clearly separates *Acinonyx* from *Panthera* when these axes are plotted with species labels (Fig. 1).

This analysis shows that the major difference between the pantherine cats is on PC1. The cats fall into two groups, with the Snow Leopard, Leopard and Jaguar clustering to the left of the graph as a smaller sized group in comparison with the Lion and Tiger group that forms a cluster on the right. In 21 out of 34 measurements there were no obvious differences between any of the species, other than size.

The second axis is related to shape and it is here that the greatest difference between the smaller *Panthera* group and the Cheetah can be seen. The Cheetahs form a discrete cluster in the top left-hand corner and examination of the values in Table 3 shows that this is because the teeth of a Cheetah are narrower than would be predicted from its cranial breadth (PP and PC). These changes may be related to the Cheetah's running adaptations and felid biomechanics. The Cheetah is built for speed and any adaptation that would increase this would be of benefit. Its teeth have lost the crushing function that many of the other cats still retain (Ewer, 1973). This can be seen in the P^4 which has a greatly reduced protocone (Martin, Gilbert & Adams, 1977), and is highlighted in Table 3 where the anterior breadth of the P^4 (UP4Ba) has a high negative loading on PC2. Teeth are heavy and dense and a reduction in tooth size would reduce the weight of the skull. In comparison with similar sized Leopard teeth, the mean P^4 breadth (UP4B) in Cheetahs is 0.3 mm smaller. The teeth of both cats are made of the same materials, dentine and enamel, therefore a decrease in overall size must result in a reduction in weight. In all cases the breadths of the teeth have altered more than the anteroposterior lengths, with the exception of both the upper and lower canines. The reduction in both the anteroposterior and mediolateral diameters of the canines is due to the fact that they are used to bite and hold struggling prey. A tooth that is circular in cross-section is more resistant to damage than a laterally compressed one when the stresses are unpredictable (Biknevicius & Van Valkenburgh, 1996). Therefore, to minimize the possibility of breakage in felid canines, a reduction in the mediolateral breadth requires a corresponding decrease in the anteroposterior length. In addition, *Acinonyx* has reduced canine height which may make a throat bite more effective than a neck bite, as the teeth are not large enough to penetrate the vertebral column (Eaton, 1974: 143).

The brain case measurements are those variables that are least related to size on axis 1. The interorbital breadth is greater than would be predicted from the tooth size. This is related to the inflation of the nasal bones in the Cheetah, which allows the cat to breathe rapidly whilst prey is being strangled (Kingdon, 1997). This adaptation may also prevent the brain overheating during and after a sprint (Taylor & Rowntree, 1973). A similar inflation is seen in the Snow Leopard, which clusters towards the Cheetah on PC2; in this case it is interpreted as an adaptation to cold climates (Hemmer, 1972). The Cheetah shows increased breadth of the postorbital process (POP) and postorbital constriction (POC) in comparison with the pantherines. The greater breadths of these dimensions are typical of small felids (Werdelin, 1983). It appears that despite increasing its size to that of a pantherine, the Cheetah has retained small-cat cranial proportions. This retention of cranial shape, despite an increase in overall size, has also been observed in the Puma (*Puma concolor*) (Werdelin, 1983).

CONCLUSIONS

On the basis of this study, a Cheetah can be defined as a cat with narrow teeth, small canines and a wide brain case for its size. Despite being a highly specialized cat, it still follows the generalized large felid form in 21 out of 34 variables analysed. The dental differences seen are adaptations to capturing and killing prey that have occurred in the genus *Acinonyx* alone. In addition, the Cheetah has retained some cranial features of the smaller cats, despite increasing its overall size. In view of this, it is not so much that Cheetahs have altered that is surprising, but how apparently conservative the feline cranial shape has been over the last few million years.

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APPENDIX 1

UK: British Museum (Natural History), London; Liverpool Museum, Liverpool; Manchester Museum, Manchester; University Museum of Zoology, Cambridge; National Museums of Scotland, Edinburgh. Europe: Hungarian Natural History Museum, Budapest; Natural History Museum, Vienna. South Africa: Mammal Research Institute, Pretoria; Transvaal Museum, Pretoria; Bernard Price Institute, Johannesburg; Zoology Museum, University of the Witwatersrand, Johannesburg; South African Museum, Cape Town. USA: Smithsonian Institute, Washington, DC. Mexico: Institute of Biology, Mexico City; Polytechnic, Mexico City; INAH, Mexico City.