



## Larger wild felids exhibit longer dental skeletons

<sup>1</sup>Pere M. Parés-Casanova and <sup>2</sup>Sara de la Cruz

<sup>1</sup>Department of Animal Production, University of Lleida, Catalunya (Spain)

<sup>2</sup>Av. Alcalde Rovira Roure 191, E-25198 Lleida, Catalunya (Spain)

Correspondence: [peremiquelp@prodan.udl.cat](mailto:peremiquelp@prodan.udl.cat)

(Received: 23/10/14)

(Accepted: 18/11/14)

### ABSTRACT

Extant members of the cat family (*Felidae*) have been considered morphologically skull conservative, i.e., despite great differences in size, there is relatively little variation in the cranial shape. Consequently, felids tend to show isometry (skull shape scales in a linear fashion with the skull size). However, although other researches have considered the role of shape, the allometry on the different cranial anatomical points has not normally been investigated. Here, we apply geometric morphometric methods in a sample of 40 skulls from adult specimens of different wild species belonging to the family *Felidae*, basing the study on 14 homologous landmarks on the lateral aspect of the skull, to assess the significance of allometry. No allometric effect of skull size on general skull shape could be discerned, but based on individual analysis of the different landmarks analysed, it was evident that variables on *splanchnocranium* -and specially those related to teeth series- did show a positive allometry with skull size. These facial landmarks are those related to feeding and acquiring prey and, thus, bigger skulls (larger wild cats) will tend to present longer dental skeletons.

**Key words:** allometry, isometry, *Felidae*, neurocranium, *splanchnocranium*

### INTRODUCTION

The skeleton, more than any other phenotypic features, provides phylogenetic links between vertebrates, revealing the course of their evolution. Because of its basic supportive and protective roles, we can understand in broad terms how different bone morphologies might be adaptive in different environments and for different life history traits and, hence, how natural selection might influence the evolution of these different morphologies.

In particular, morphological and morphometric studies of the skull reflect the contributions of genetic and environmental components to the individual's development and describe genetic and ecophenotypic variations [1]. Most of these studies have been undertaken from a "classical" point of view, that is by using lineal measurements (for instance [2, 3], but there are many others) in which total lengths, widths and perimeters are used as variables. In these cases, the measurement of shape has classically been from these linear distance measurements. Geometric morphometrics (GM) can be defined as the quantitative representation and analysis of morphological form using geometric coordinates instead of measurements. One of the most powerful components of GM analysis is the visualization of shape variability. Another advantage of GM is that size and shape can be mathematically separated.

In the skull, which has multiple functions, it is difficult to relate the proportions of its different parts to structure performance. In this case, the significance of allometry (the pattern of covariation among several morphological traits or between measures of size and shape) can be investigated by examining how anatomical variables impact on its different parts. Our approach to this study focuses on covariation of shape *versus* size.

Despite great differences in size between species, modern members of the cat family (*Felidae*) are highly specialized for a predatory and purely carnivorous lifestyle, and are obligate hypercarnivores, mostly from killed as opposed to scavenged prey [4]. Preferred prey size is correlated with the size of the felid itself, i.e. large cats take proportionately larger prey than small cats, prey mass often exceeding predator mass in the largest felids [5].

Differences in size aside, the morphology and predatory behaviour of extant cats is considered to be conservative, in that there is relatively little variation regarding the shape of cranio-mandibular structures. Consequently, it is thought that differences in felid skull shape may largely be attributable to the influence of size, making felids appropriate candidates for studies of allometry [6]. Many previous studies have studied cranio-dental morphology and biomechanics (see [7] for a revision). This study has been specifically performed to investigate the allometry of cranial form on splanchno and neurocranium separately, using techniques of geometric morphometrics. The hypothesis of this research is that general variation in skull form for felids is size-based and mainly focused on splanchnocranium (facial skeleton), because dietary differences must reflect shape variation on most functional areas—that is those related to feeding and acquiring prey and, thus, organismal performance-. Christiansen's researches [6, 8] are among the few studies on felid skull morphology to employ a GM approach, although his studies do not encompass the same species considered for this research.

## MATERIALS AND METHODS

### Material examined

Forty adult specimens (*i.e.* individuals with fully erupted upper cheek teeth series) of different wild species belonging to the cat family (*Felidae*, G. Fischer 1817), that span the full range of felid body sizes and skull shapes, were sampled. The specimens are listed in Table 1. The skulls were deposited in the Natural History Museum of Barcelona (Catalonia). Sex was not available for all specimens, but this variable was not taken into account for our research.

Table 1. Specimens studied (N=40).

	Vernacular	♂	♀	Unknown	TOTAL
<i>Acinonyx jubatus</i> (Schreber, 1775)	Cheetah	1	0	0	1
<i>Felis silvestris</i> (Schreber, 1775)	Wildcat	2	1	3	6
<i>Leopardus pardalis</i> (Linnaeus, 1758)	Ocelot	0	0	1	1
<i>Leptailurus serval</i> (Schreber, 1776)	Serval	0	1	0	1
<i>Lynx lynx</i> (Linnaeus, 1758)	Eurasian lynx	1	1	1	3
<i>Panthera leo</i> (Linnaeus, 1758)	Lion	1	1	1	3
<i>Panthera onca</i> (Linnaeus, 1758)	Jaguar	2	2	2	6
<i>Panthera pardus</i> (Linnaeus, 1758)	Leopard	1	1	4	6
<i>Panthera tigris</i> (Linnaeus, 1758)	Tiger	1	0	3	4
<i>Profelisaurata</i> (Temminck, 1827)		0	0	1	1
<i>Puma concolor</i> (Linnaeus, 1771)	Puma	0	1	5	6
<i>Uncia uncia</i> (Schreber, 1775)	Snow leopard	0	2	0	2

### Geometric morphometrics

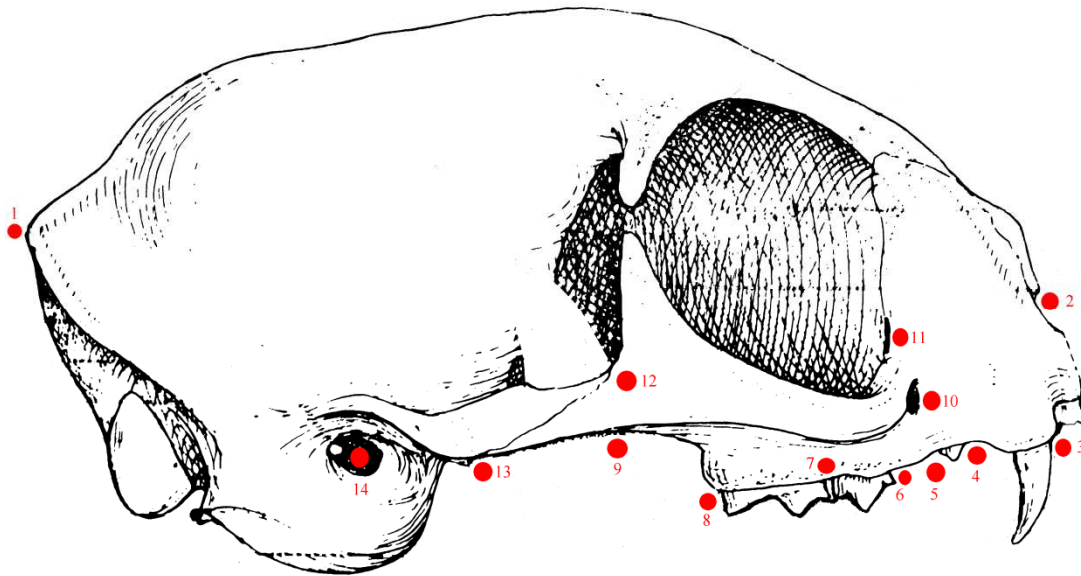
The GM technique, which has been shown to be objective and efficient compared to traditional methods (Rohlf, 1998), was used to analyze the variation in the skulls of the specimens. GM allows the comparison of geometrical forms of a structure as described by a set of topographically corresponding points (landmarks). The technique provides a powerful tool for studying the evolutionary forces modelling biological forms. See [9, 10 and 11] for more details. Landmark-based morphometric methods were chosen as they are more effective in capturing information about the shape of an organism and lead to powerful statistical procedures for testing differences in shape. Moreover, they provide accurate tools for visualizing shape changes in a way that is both quantitatively correct and extremely suggestive [10].

### Image acquisition

Image capture was performed with a Nikon® D70 digital camera (Nikon Inc., Tokyo, Japan) (image resolution 2240 x 1488 pixels) equipped with a Nikon AF Nikkor® (Nikon Inc., Tokyo, Japan) 28 to 200-mm telephoto lens. The focal axis of the camera was parallel to the right lateral aspect of each skull. A scale bar was used in this process. Fourteen landmarks, assumed to be homologous and topologically equivalent, were plotted on the skull in order to describe the size and shape of skull variations (Figure 1). Landmarks used in this study were primarily chosen to describe major cranial and facial regions as well as parts of particular morpho-functional or sensory interest. They referred to the: (1) most nuchal part of the external occipital protuberance (*protuberantia occipitalis externa*); (2) most rostral part of the incisivo-nasal suture; (3) most rostral part of the base of the canine, at the maxillar bone; (4) most rostral part of the base of the 2<sup>nd</sup> premolar, at the maxillar bone; (5) most nuchal part of the base of the 2<sup>nd</sup> premolar, at the maxillar bone; (6) most rostral part of the base of the 3<sup>rd</sup> premolar, at the maxillar bone; (7) most rostral part of the base of the 4<sup>th</sup> premolar, at the maxillar bone; (8) most nuchal part of the base of the 1<sup>st</sup> molar, at the maxillar bone; (9) ventral part of the palatinum bone (*lamina perpendicularis ossis palatini*); (10) midpoint of the infraorbital foramen (*foramen infraorbitale*); (11) midpoint of the fossa of lachrymal sac (*fossa sacrilacrimalis*);

(12) dorsal part of the temporo-zygomatic suture at the zygomatic arch (*arcus zygomaticus*); (13) ventral part of the temporo-zygomatic suture at the zygomatic arch; (14) midpoint on the foramen of the tympanic foramen (*porus acusticus externus*).

**Figure 1.** The 14 landmark locations (right lateral aspect of the skull), morphologically homologous, used to capture shape from the lateral right view of the skull. See text for anatomical locations of landmark definitions.



Landmarks were digitized twice using TpsDig, v. 2.16 software [12] and converted to scaled x and y coordinates and centroid size (CS, the square root of the sum of the squared distances among the landmarks in a configuration and their extracted centre of mass), and standardized after removing artefactual variation due to different positions of the specimens using CoordGen6f (H. D. Sheets, [www.canisius.edu/sheets](http://www.canisius.edu/sheets)). Size information was retained as CS. A Mantel test between the two replicates reflected  $R=1$ ,  $p < 0.00001$ , which suggested that the matrix entries were positively associated and therefore digitizing error was considered negligible.

After the standardization has been performed, each specimen corresponds to a point in the curved shape space and the metric that defines the shape space is the Procrustes distance [9]. In order to perform traditional statistical analyses on the matrix of shape coordinates, the specimens in the shape space must be projected to a tangent Euclidean space: the distance relationship between points is, thus, approximated as occurs in a flat map approximation of a small region of the earth's surface [13]. For the smallest shape variation around the point of tangency, the best point of tangency is the sample mean form. TpsSmall, v. 1.20 software [14] was used to assess this correlation between the 2D Procrustes distances to the Euclidean distances in that tangent space. The correlation was very close to linear for all of the data ( $r=0.999$ ; slope,  $b=0.984$ ), suggesting that tangent space was an adequate approximation to Kendall and that no specimens deviated appreciably from the linear regression line. Thus, although the lateral view of the skull is not a flat object, authors considered that the two-dimensional approach implies a limited loss of information, and we proceeded with the morphometric analyses.

#### Statistical treatment

Multivariate regression analysis was performed between size (expressed as  $\ln$  CS) and the  $x$  and  $y$  uniform components. An overall MANOVA test of multivariate regression significance was provided, where the Wilks'  $\lambda$  test statistic was computed as the ratio of determinants. The significance level was 0.05%.

Data were analysed using PAST - Paleontological Statistics Software Package for Education and Data Analysis [15]. Tps series and PAST are available over the Internet by FTP from the "morphmet" directory at [life.bio.sunysb.edu](http://life.bio.sunysb.edu) or via the WWW at <http://life.bio.sunysb.edu/morph/>.

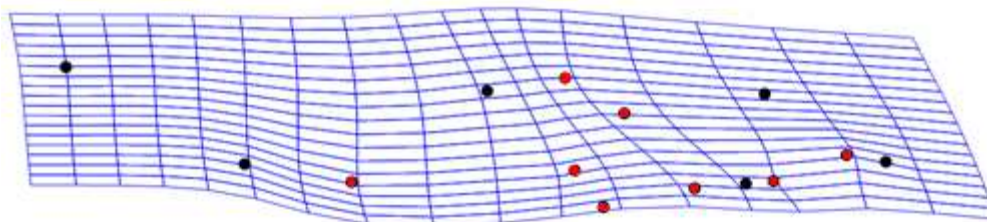
## RESULTS AND DISCUSSION

A regression of  $\ln CS$  versus  $x$  and  $y$  uniform components was non-significant ( $R^2=0.339$ , Wilk's  $\lambda=0.032$ ,  $F_{28,11}=11.7$ ,  $p<<<0.0001$ ), so no allometric effect of size on general shape could be discerned. Based on individual analysis of the landmarks (Table 2), it was evident that variables X10 -midpoints of the infraorbital foramen (*foramen infraorbitale*) and X11,Y11 -midpoint of the fossa of lachrymal sac (*fossa sacrilacrimalis*)- appeared as the most responsible for the overall correlation between size and shape (Figure 2). Other variables, such as X3, X4, X6, X7 and Y8, related to teeth series, and Y13 -ventral part of the temporo-zygomatic suture at the zygomatic arch- would signal an allometry of splachnocranium. Variables X3, X4, X6, X7 showed a positive allometry, while the others (X10, X11, Y11, Y8 and Y13) showed a negative one.

Table 2. Slopes and intercepts for each Procrustes. Significant values are shown in bold. Those with  $|r|>0.6$  appear in box.

Variable	Slope	Error	Intercept	Error	r	P
X1	<b>0.031</b>	<b>0.008</b>	<b>-0.797</b>	<b>0.041</b>	<b>0.543</b>	<b>0.0003</b>
Y1	<b>0.025</b>	<b>0.006</b>	<b>-0.018</b>	<b>0.032</b>	<b>0.549</b>	<b>0.0002</b>
X2	<b>-0.022</b>	<b>0.005</b>	<b>0.345</b>	<b>0.026</b>	<b>-0.585</b>	<b>0.0001</b>
Y2	0.006	0.006	0.058	0.030	0.160	0.3236
X3	<b>0.024</b>	<b>0.005</b>	<b>0.180</b>	<b>0.025</b>	<b>0.626</b>	<b>0.0000</b>
Y3	-0.004	0.004	-0.003	0.023	-0.153	0.3455
X4	<b>0.021</b>	<b>0.003</b>	<b>0.153</b>	<b>0.014</b>	<b>0.782</b>	<b>0.0000</b>
Y4	0.007	0.005	-0.064	0.026	0.226	0.1609
X5	0.005	0.004	0.179	0.019	0.213	0.1875
Y5	<b>-0.010</b>	<b>0.003</b>	<b>0.003</b>	<b>0.017</b>	<b>-0.455</b>	<b>0.0031</b>
X6	<b>0.018</b>	<b>0.003</b>	<b>0.058</b>	<b>0.018</b>	<b>0.652</b>	<b>0.0000</b>
Y6	<b>-0.010</b>	<b>0.003</b>	<b>-0.003</b>	<b>0.015</b>	<b>-0.513</b>	<b>0.0007</b>
X7	<b>0.022</b>	<b>0.004</b>	<b>-0.022</b>	<b>0.022</b>	<b>0.648</b>	<b>0.0000</b>
Y7	<b>-0.006</b>	<b>0.003</b>	<b>-0.039</b>	<b>0.015</b>	<b>-0.340</b>	<b>0.0320</b>
X8	<b>0.016</b>	<b>0.005</b>	<b>-0.089</b>	<b>0.024</b>	<b>0.498</b>	<b>0.0011</b>
Y8	<b>-0.014</b>	<b>0.003</b>	<b>-0.021</b>	<b>0.015</b>	<b>-0.618</b>	<b>0.0000</b>
X9	<b>0.011</b>	<b>0.005</b>	<b>-0.090</b>	<b>0.024</b>	<b>0.376</b>	<b>0.0169</b>
Y9	<b>-0.016</b>	<b>0.004</b>	<b>0.062</b>	<b>0.019</b>	<b>-0.595</b>	<b>0.0001</b>
X10	<b>-0.045</b>	<b>0.004</b>	<b>0.342</b>	<b>0.020</b>	<b>-0.888</b>	<b>0.0000</b>
Y10	<b>0.012</b>	<b>0.003</b>	<b>-0.020</b>	<b>0.015</b>	<b>0.574</b>	<b>0.0001</b>
X11	<b>-0.062</b>	<b>0.003</b>	<b>0.387</b>	<b>0.014</b>	<b>-0.966</b>	<b>0.0000</b>
Y11	<b>0.023</b>	<b>0.004</b>	<b>-0.027</b>	<b>0.020</b>	<b>0.702</b>	<b>0.0000</b>
X12	-0.005	0.010	-0.083	0.051	-0.077	0.6382
Y12	0.011	0.007	0.026	0.039	0.240	0.1354
X13	-0.010	0.008	-0.200	0.041	-0.208	0.1979
Y13	<b>-0.030</b>	<b>0.006</b>	<b>0.134</b>	<b>0.031</b>	<b>-0.643</b>	<b>0.0000</b>
X14	-0.004	0.003	-0.362	0.014	-0.245	0.1271
Y14	<b>0.008</b>	<b>0.003</b>	<b>-0.090</b>	<b>0.017</b>	<b>0.381</b>	<b>0.0152</b>

Figure 2. Linear regression as warp. Variables X10 -midpoint of the infraorbital foramen (*foramen infraorbitale*), X11, Y11 -midpoints of the fossa of lachrymal sac (*fossa sacrilacrimalis*), X3, X4, X6, X7 and Y8, related to teeth series, and Y13 -ventral part of the temporo-zygomatic suture at the zygomatic arch- (all as red dots) appeared to be the most responsible for the overall correlation between size and shape.



Although felids' morphology and ecological role as hypercarnivores are quite constant, and the cat-like ecomorph suggested by Martin [16] is consistent throughout the species, body size variation is considerable [17, 18]. Extant felids are characterized by being anatomically derived for predation with a powerful precision killing bite [19], and there is ample evidence that the skull is optimized to function as a coherent mechanical unit [20]. As a general rule, when animals increase in body size, either through ontogeny or phylogeny, they tend to change in shape [21]. But skull shape in felids seems to be not linked to global size modifications but to splachnocranium size. Therefore, this detected allometry must be related to other causes than mere differences in body size between felids. We propose that it could be related to performance requirements, and, in particular, to differences in prey size as well as differences in how they capture and kill prey. In this study, large felids exhibit longer dental skeletons than small felids, and this would be congruent with the fact that different bite forces are required from small to large wild cat. This fact has been stated by Slater and van Valkenburgh [20].

Although geometric morphometric tools seem to depict facial shape allometry accurately, it should be mentioned that the comparison made here did not involve a complete description of skulls (landmarks are a mere choice of the authors, no semi-landmarks were studied, and nothing was obtained from mandibles). Validation, including a wider range of wild felids, will clearly be needed to test this hypothesis fully.

### CONCLUSION

- The detected allometry must be related to other causes than mere differences in body size between felids. It is proposed that it could be related to performance requirements, and, in particular, to differences in prey size as well as differences in how they capture and kill prey.
- Large felids exhibit longer dental skeletons than small felids, and this would be congruent with the fact that different bite forces are required from small to large wild cat.

### Acknowledgements

Authors are indebted to the staffs at the Natural History Museum of Barcelona (Catalunya), especially its Curator of Mammals, Dr Javier Quesada, and also to Olga Boet for loaning the specimens and the associated information. The authors declare no conflict of interest related to this work.

### REFERENCES

- [1] Wehausen, J.D., Ramey, R.R. *Journal of Mammalogy*, **2000**, 81, 145-161.
- [2] Karimi, I., Onar, V., Pazvant, G., Hadipour, M. Mazaheri, Y. *Global Veterinaria*, **2011**, 6, 2, 111-117.
- [3] Özcan, S., Aksoy, G., Kürtül, I., Aslan, K., Özüdogru, Z. *Kafkas Üniversitesi Veteriner Fakültesi Dergisi*, **2010**, 16, 1, 111-114.
- [4] Van Valkenburgh, B. *Paleobiology*, **1998**, 14, 155-173.
- [5] Radloff, F.G.R., du Toit, J.T. *Journal of Animal Ecology*, **2004**, 73, 410-423.
- [6] Christiansen, P. *Biological Journal of the Linnean Society*, **2008**, 95, 766-778.
- [7] Chamoli, U., Wroe, S. *Journal of Theoretical Biology*, **2011**, 283, 217-226.
- [8] Christiansen, P. *Biological Journal of the Linnean Society*, **2007**, 91, 573-592.
- [9] Bookstein, F.L. *Morphometric Tools for Landmark Data*. New York: Cambridge University Press, **1991**.
- [10] Rohlf, F.J., Marcus, L.F. *Tree*, **1993**, 8, 129-132.
- [11] Monteiro, L.R., Reis, S.F. *Princípios de morfometria geométrica*. Ribeirão Preto, Brazil: Holos Editora, **1999**.
- [12] Rohlf, F.J. *TpsDig version 2.16*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York: Stony Brook, **2010**.
- [13] Rohlf, F.J. *Systematic Biology*, **1998**, 47, 147-158.
- [14] Rohlf, F.J. *TpsSmall version 1.20*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York: Stony Brook, **2003**.
- [15] Hammer, Ø., Harper, D.A.T., Ryan, P.D. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, **2001**, 4, 1: [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm).
- [16] Martin, L.D. *Fossil History of Terrestrial Carnivora*. In: Gittleman JL, ed. *Carnivore Behavior, Ecology, and Evolution*. New York: Cornell University Press, **1989**, 536-568.
- [17] Sunquist, M., Sunquist, F. *Wild Cats of the World*. Chicago: University of Chicago Press, **2002**.
- [18] Lencastre, F., Flamarion, L. *Zoological Journal of the Linnean Society*, **2001**, 161, 2, 414-462.
- [19] Christiansen, P., Wroe, S.M. *Ecology*, **2007**, 88, 347-358.
- [20] Slater, G.J., Valkenburgh, B. van. *Paleobiology*, **2008**, 34, 403-419.
- [21] Wayne, R.K. *Evolution*, **1986**, 40, 243-261.