

## THE ASSESSMENT OF SIZE IN FOSSIL FELIDAE

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### ABSTRACT

Estimations of body size in fossil vertebrates depend on establishing the relationships between body mass, overall length or some measure of stature and measurements taken on skeletal elements in living relatives or close proxies. However, most osteological collections lack information on body size for individual specimens, and published investigations usually fall back on summary data derived from the literature to plot against measurements taken directly on the skeletal material. The utility of such approaches beyond very general indications of size is open to question. In an effort to reduce these problems we attempt to establish some objective basis for using skeletal elements for the purpose of size estimation in the larger Felidae of the genus *Panthera*, using data for the jaguar, *Panthera onca*. We show that cranial length offers a good indication of overall size in the living animal, and that various other cranial dimensions correlate closely with that measurement, while individual teeth, despite their frequent occurrence in assemblages, show a looser relationship and therefore appear less useful for size estimations of fossil material than has been thought.

**Key words:** *Carnivora, Felidae, Panthera onca, pantherine cats, size.*

### RESUMEN

Las estimaciones de la talla corporal en vertebrados fósiles depende de las relaciones establecidas entre el peso corporal, la longitud total o alguna medida de estatura tomada de los elementos esqueléticos de animales actuales emparentados o muy afines. Sin embargo, en muchas colecciones osteológicas falta información sobre la talla corporal de los ejemplares, de forma que las investigaciones publicadas usualmente recurren a datos sintetizados de la literatura que se relacionan con medidas tomadas directamente del material esquelético. La utilidad de estas aproximaciones más allá de indicaciones generales sobre la talla es discutible. En un esfuerzo de minimizar estos problemas intentamos establecer bases objetivas para el uso de los elementos esqueléticos con el propósito de estimar la talla de los grandes Felidae del género *Panthera*, utilizando los datos obtenidos del jaguar, *Panthera onca*. Se muestra que la longitud craneal ofrece una buena indicación de la talla total en los animales actuales, y que otras dimensiones craneales se correlacionan estrechamente con esta medida, mientras que los dientes aislados, a pesar de su hallazgo frecuente en las asociaciones fósiles, muestra una menor correlación y por lo tanto es menos útil para la estimación de la talla en formas fósiles de lo que anteriormente se había pensado.

**Palabras clave:** *Carnivora, Felidae, Panthera onca, tamaño*

### Introduction

Size is an important piece of information about an animal. The effect of herbivores on vegetation or the impacts of predators on prey depend on size in some measure, and without it no ecological overview could be complete. In the fossil record, size of

an animal often appears to be one of the things we can talk about with some certainty, so that for the palaeontologist its importance is perhaps even greater. But what do we mean by size, and just how do we assess, and if necessary quantify, the size of fossil animals? Most palaeontologists would probably take size to mean a measure of shoulder height or

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body weight or mass, and estimate one or other by reference to living relatives or morphologically most similar forms. But it may be more difficult to make such assessments than we imagine, particularly if we try to place an actual figure on the estimate of size in terms of body weight. The literature on studies of human evolution is full of discussions of the best estimator to apply to reconstruction of body mass in australopithecines, paranthropines and early members of the genus *Homo* (McHenry, 1991; Ruff, Trinkaus and Holliday, 1997), and controversy still seems to surround the subject. In our own work on the Carnivora we have at times sought some measurement, usually of relative rather than absolute size, as a means of comparing species and variations within species (Turner, 1984, 1987, 1997; Andrews and Turner, 1992, Turner and O'Regan in prep.). In the usual absence of complete skeletons we have, like others, used measurements of commonly occurring items such as teeth as indicators of size, but often without any formally established basis for so doing.

Others authors (Legendre and Roth, 1988; Van Valkenburgh, 1990; Anyonge, 1993; Egi, 2000) have sought more specific information on the relationship between size in skeletal and dental elements and body mass in Carnivora. These studies have usually aimed to provide estimates for typical size in species rather than of individual animals, but even at this lower scale of resolution the methodologies employed are, in our view, open to question. In particular we believe that the basis for extrapolations from size or body mass of living taxa is simply not secured. Our purpose in this paper is therefore to examine the matter a little further and try to establish some objective basis for using skeletal elements for the purpose of size estimation in the larger Felidae of the genus *Panthera*, using data for the jaguar, *Panthera onca*. In the discussion that follows we refer only to fully adult animals.

## Previous studies

### *Size and living species*

We speak very readily of one animal, or better still a species, being larger or smaller than another, but what do we mean when we talk of size? If we compare elephants with mice we have no problems in understanding the differences, but what of animals of broadly more comparable size, or individuals within a species? We may employ measurements such as mass, height at some convenient point such as the shoulder or greatest length from snout to tip of the tail. Horses, at least in the English-speaking world,

are still measured in the archaic system of hands at the shoulder, where a hand is four inches or approximately 10 centimetres, the approximate width of an average human hand at the palm. In such a system a horse that reaches 12 hands is obviously taller than one reaching 11 hands; but is it necessarily larger? One individual or an entire breed of horse may be shorter in stature but much more massive, and therefore heavier, than another. In such circumstances the plain description of one as larger than the other is likely to involve at least a degree of confusion.

If we confine our allocation of size to measurements of height or length we perhaps have some general basis for agreement. Even then we should have to specify very clearly what we meant for the population or species. A single average height or length plus range and standard deviation would hardly adequately cover the adults of a sexually dimorphic population, so we would have to deal with the sexes separately. But the difficulties of specifying linear dimensions tend to pale when we move to specifications of body weight or mass. Pooled and averaged heights or lengths of individuals to agreed points are one thing, but what is the appropriate body mass to measure on each animal in the sample of a species in order to say something meaningful about either the individuals themselves or the population as a whole? We still of course face problems of inter-sexual differences, but in addition we must deal with complications of the definition of body mass. We could simply weigh everything in the sample and derive the relevant statistics and infer population parameters, but that would ignore obvious causes of potentially wide discrepancy. To overcome these we should immediately have to specify whether the individuals weighed were obese, well-nourished or emaciated (perhaps a seasonal variation), whether all body fat had been removed to give a lean carcass mass, whether the bodies were cleaned (gutted) or entire and especially whether the stomach contents were included or excluded — a male lion, *Panthera leo*, weighing around 190 kg may eat up to 34 kg of meat at a sitting (Schaller, 1972: 270) — and so forth. Something of the complications may be seen in the brief discussion given by Smuts, Robinson and Whyte (1980: 367) for dealing with sizes of lions in the Kruger National Park of South Africa, or in the more general discussion by Alexander (1989). Intuitively, one might suppose that lean body mass of an entire carcass from an animal in good condition would be the desired figure, but that is probably not the one that is commonly available in the literature.

One should put this uncertainty into some perspective. To stay with the lion, Schaller (1972: 210) quotes average body masses of 120 kg for eastern

African females and 190 kg for males, while Kingdon (1997: 284) quotes ranges of 122-182 kg and 150-260 kg respectively for African ones in general. Neither author specifies the basis for these figures, particularly whether lean body mass is used or not, but by any standards the lion is a very large cat and we all know what is meant by that. The problem comes when we seek greater accuracy or precision. As Gingerich (1990) has shown using data from Alexander *et al.* (1979), plots of body mass against long bone lengths and parasagittal midshaft diameters for one individual from each of 36 mammalian species ranging in size from shrew to elephant appear to produce an acceptable predictor of general body mass - at least in the sense that a log-log plot of the data produces a straight line. However, as he also points out the prediction is effectively only for average body mass of species and the variation may be considerable. We shall return to Gingerich's study in the next section.

#### *Size and fossil species*

If the problems of specifying sizes for individuals or species that we can measure directly are more complex than they might seem at first sight, it is clear that attempts to do the same thing for fossil animals present us with a fresh set of difficulties. In most cases we have only bones, and often incomplete skeletons of any one individual. However, it is often not too difficult to reconstruct the general appearance and stance of the skeleton, and to go on to measure or estimate things like length or shoulder height with suitable allowances made for missing items like inter-vertebral discs, hooves, and so on. In human populations the requirements for such predictors in anthropology and forensic pathology have led to numerous studies using known material, although accuracy still seems to be elusive (see summary by White, 2000). A range of individuals will then give an idea of the range of variation in the population or species. But if we want a measure of body mass then we have to go about it by a rather more circuitous route. We could reconstruct the musculature, measure the body volume by displacement and calculate a figure for mass based on average tissue density in related species (Alexander, 1989), but while that is fine for a typical representative of a species we would hardly want to do that for a range of individuals. Alternatively, we could seek some way of estimating body mass from some or other aspect of skeletal dimensions.

Such estimates use a predictor based on relationships between known body mass and skeletal dimensions in modern analogues, and there we arrive

straight back at the problem of specifying the desired body mass in living taxa. It is perhaps significant that although anthropologists concerned with human ancestors seek such answers for their material, as we pointed out in the introduction, forensic pathology appears to avoid the topic despite the fact that body masses and skeletal sizes can be determined from dissection room cadavers, perhaps because the range of mass in people of similar skeletal size is so obviously high. Those problems are heightened when we deal with non-human material in most cases because such predictors are usually based on body mass figures taken from the literature, where few attempts are made to deal with the difficulties of variation within the species, and the skeletal and body mass figures usually derive from quite distinct data sets (see below). In addition, attempts to apply the predictor to fossil data show up considerable discrepancies when different body parts are used, as Gingerich (1990: 84) in the study cited in the previous section has pointed out. Interestingly enough, one of his examples, based on the giant Oligocene rhinocerontid *Baluchitherium* (now referred to the genus *Indricotherium*), represents attempt to estimate size using various skeletal elements for material now known to have been both reconstructed and wrongly extrapolated from several animals of differing sizes (Fortelius and Kappelman, 1993). As the latter authors point out, although Gingerich found problems with the method, he seems rather ironically to have come closer to a realistic estimate of the size of the animal than previous workers.

When we turn to the Carnivora we see some of the problems of jumping from measurement of skeletal elements to body mass in the work of Legendre and Roth (1988), Van Valkenburgh (1990), Anyonge (1993) and most recently Egi (2000). Legendre and Roth used lower carnassial crown area for 162 species. Van Valkenburgh used four measurements, head-body length, cranial length from posterior edge of occipital condyles to prostethion (condylobasal length), occipital condyles to anterior edge of orbit and alveolar margin length of  $M_1$  for 72 living species, emphasising cranial and dental items on the basis that they are more frequently recovered. One might add that they also tend to be more readily identifiable to species. Anyonge's analysis employed cross-sectional and joint surface measurements of long bones for 28 living species, based on the reasonable argument that the morphology and proportions of such weight-bearing elements, and in particular cross-sectional area, should reflect body mass as stressed by Gingerich (1990). Egi used various measurements taken on long bones of modern Carnivora.

The logic in all these applications is clear, but the problems arise from the data sources then employed. Legendre and Roth took body masses from a wide literature and plotted them against the lower carnassial areas measured on specimens also obtained from the literature. Van Valkenburgh averaged body masses and head-body lengths for each sex of each species from a similarly diverse literature, using an overall estimate of mass for the species if separate sex data were not available: indeed as she acknowledged (1990: 181) «in most cases the estimates... represent the average of midpoints of published ranges of mass and lengths; thus they are not sample means». The estimated mean body masses for each species were then plotted against estimated mean head-body lengths and against measurements of cranial length, length of occipital to orbit and length of  $M_1$  for one specimen of each sex of each species. In Anyonge's study (1993: 343) the postcranial skeletal measurements taken by the author were again plotted against mean body weights taken from the literature, apparently without regard to sexual dimorphism and using mid points of published ranges in cases where mean data were unavailable. Egi (2000: 500) managed to find body masses for 58 measured individuals in 12 of 47 species (318 individuals in all) used in the analysis, but still derived most of the body mass data from the literature while taking skeletal measurements on a separate pool of specimens. All authors went on to use the relationships established from the analyses on living taxa to predict body mass in fossil species of Carnivora or the archaic mammalian carnivore order Creodonta.

How useful and reliable are such estimates? It would be unreasonable to expect any generalised predictor to give an accurate estimate of body mass in the case of any particular individual, as Gingerich (1990) pointed out, and none of the authors offers any examples of use of those derived from their studies to estimate independently known body masses of individuals of modern species for which the necessary skeletal and dental measurements are known. As we pointed out in the case of living lions above, we should put uncertainty into perspective, and as Alexander (1989: 26) stresses for mass estimates of dinosaurs the sauropods are large by any standard. But are the published relationships meaningful in any wider sense? Only Van Valkenburgh (1990: 197) and Egi (2000: 505) provide any discussion of sources of error and variation. Van Valkenburgh notes the difficulties posed by uncertainties about the nature of true body mass in a species, but then goes on to consider which of the skeletal variables used in her study offer the best estimate of body mass in extinct species. That discussion

makes the implicit assumption that the relationships derived are meaningful even if inaccurate and makes the point that questions of relatively broad scope should be addressed. However, given the nature of the data on body masses employed in both studies it is hard to see how even such a generalised conclusion can be drawn. In her own words (1990: 201) the means for living species are «probably poor estimates» and those estimated for extinct species a «rough approximation», and it seems clear that the data employed are really simply too full of confounding variables to offer more than such approximations. Moreover, the assessment of accuracy is essentially confined to departure of individual mass estimates from the line of best fit derived from the overall data set, hardly the point at issue for reconstruction of fossil body masses. Egi similarly confines the discussion to sources of error within the scaled data sets rather than to questions of the utility of the data compiled.

Larger and smaller measurements of the skeletal variables employed point to respectively larger and smaller animals, and one should probably leave the matter at that. If the fossil material is of a cat, and the bone lengths and cross-sectional areas are similar to those of say a large lion, then we have a large, lion-sized animal. To take widely diverse published measurements of body mass for species and plot them against skeletal dimensions of completely different animals that lie at unknown points on the size ranges of the species surely cannot produce more meaningful results. We are not denying the intuitively obvious relationship between measures of skeletal size and measures of body mass at a general level, simply questioning our abilities to obtain an accurate figure for the latter from the former in such a way.

### Relative sizes

If our argument that previous efforts to estimate body mass from skeletal material are flawed is correct, we still face the need to know something about size, and in particular about variations in size, when we deal with fossil assemblages. For reasons outlined at the beginning of this paper, the reconstruction of linear dimensions is probably not too difficult where we have sufficiently complete materials, and we can of course compare cross-sectional areas of weight-bearing limbs to add an element of relative body mass to the investigation without necessarily bothering about absolute values. However, fossil remains are often of incomplete individuals, and we would usually like to include as many as possible in any analysis in order to obtain a more

representative picture of the population from which they are drawn. Ideally, we would like to include a diverse array of skeletal parts, or at least to use those most commonly found.

Among the Carnivora, teeth are a commonly found item, recognisable and often of taxonomic significance as pointed out above and frequently employed as indicators of size and in particular of sexual dimorphism (Kurtén, 1955, 1963; Turner, 1984; Andrews and Turner, 1992). Sexual dimorphism, especially in the upper and lower canine teeth, is well attested in animals such as bears and cats in such studies, but the question of correlations between absolute size of the individuals and the various elements of their dentition is less clearly established. However, assessing such correlations is less than easy for precisely the reasons gone into above. In the absence of any clearly-defined absolute reference dimension of body size based on weighing carcasses we have therefore sought to return to measurable properties of the skeleton itself, and to the use of cranial size as a reference against which to judge the distribution of sizes in the dentition.

Gould (1974) adopted such an approach in his well-known study of antler size in the giant deer or so-called Irish Elk, *Megaloceros giganteus*. He sought to place the giant deer on a graph of antler size against body size for cervids, and rejected body weight itself as the reference dimension for many of the reasons stated here. Instead, he used basal cranium length, basion-prosthion, a measurement known to have a slightly negative allometric relationship to body length in Cervidae, and we have elected to use the same measurement for the Felidae. Of course such a decision raises once more the question of the relationship between a cranial measure of size and the actual size of the animals involved. Fortunately, we have been able to locate one source of data on felid body masses where condylobasal cranial length is available for the *same* animals, the study by Hoogesteijn and Mondolfi (1996) on the living jaguar, *Panthera onca*. Such data do not completely overcome the problem of precisely what measure of body mass has been employed in recording, and of course refer only to one species, but the authors stress their general reliability and they do go a long way to providing a baseline for comparison.

## Results

We begin by establishing the general relationship between size of the living animal and the length of the cranium in jaguars using the data of Hoogesteijn and Mondolfi (1996). Figure 1 shows the plot of

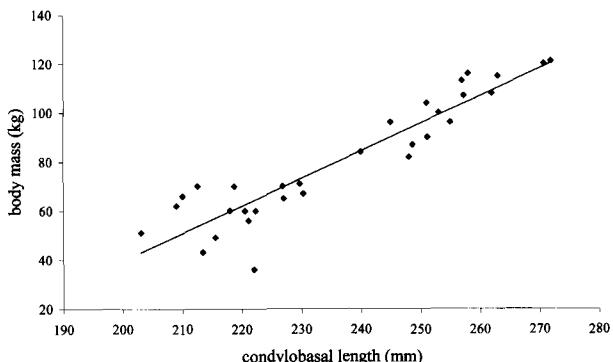


Fig. 1.—Modern jaguar: condylobasal length of cranium vs body mass (data from Hoogesteijn and Mondolfi, 1996).

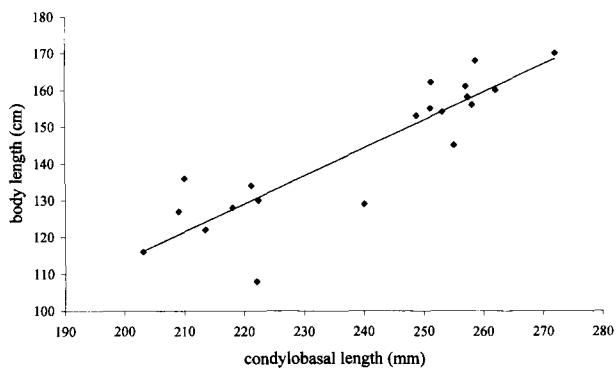


Fig. 2.—Modern jaguar: condylobasal length of cranium vs body length (data from Hoogesteijn and Mondolfi, 1996).

condylobasal length against body mass, for which a least-squares linear regression has been performed giving the equation.

$$\text{body mass} = 1.122 \text{ condylobasal length} - 184.88, \quad \text{with } r = 0.93 \text{ and } r^2 = 0.86.$$

We have used a linear regression rather than a reduced major axis regression because while there are arguments for the latter based on the fact that both variables in the analyses that follow are strictly random entities, with the *x* variable in particular not under the control of the observer, in practice we are seeking to estimate *y* given *x* rather than simply fit a line to the scatter (Fowler and Cohen, 1990).

Two points emerge. First the relationship is encouragingly close; larger, heavier animals have longer crania. Second, the relationship is linear but it is also allometric. There appears to be some dispute in the literature over whether such a result can properly be taken to describe an allometric relationship or whether only a power function will suffice (Reiss, 1989), but clearly any function where

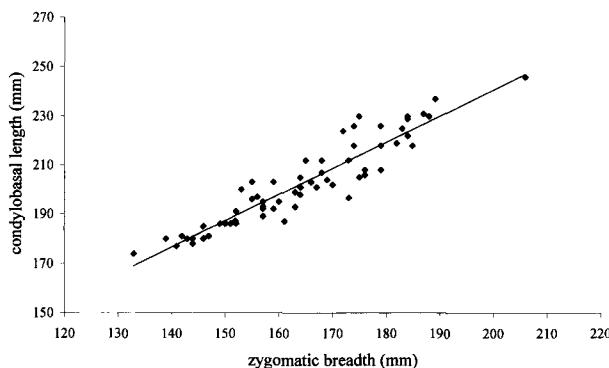


Fig. 3.—Modern jaguar: condylobasal length of cranium vs zygomatic breadth (data authors).

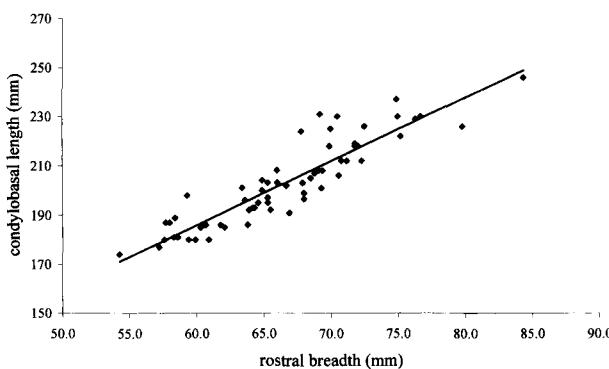


Fig. 4.—Modern jaguar: condylobasal length of cranium vs rostral breadth (data authors).

the  $y$  intercept is so far from zero must produce an allometric result in the literal sense of the term, as Gould (1966) has argued. The issue is not one of restricting the term allometry but of deciding what function best expresses the relationship when, as in this case, the two variables are allometrically connected. In Figure 2 we show a second plot again based on the data of Hoogesteijn and Mondolfi (1996), this time for a measure of body length against condylobasal cranial length. The authors state that such body length measurements must be considered inherently less reliable than the body mass figures, but again we see a generally good, allometric relationship between the two variables where

$$\text{body length} = 0.7597 \text{ condylobasal length} - 38.063, \\ \text{with } r = 0.89 \text{ and } r^2 = 0.79$$

On the basis that both body mass and a linear measurement of size show such good relationships to cranial length we conclude that the latter may be taken as a good proxy for body size in jaguars. If this result can be extrapolated to other pantherine felids then we may take it as a general predictor of

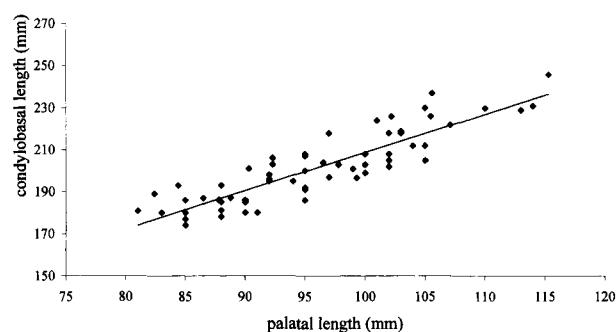


Fig. 5.—Modern jaguar: condylobasal length of cranium vs palatal length (data authors).

Table 1.—Modern jaguars. Linear regression equations of condylobasal length of cranium versus cranial, mandibular and dental measurements (data authors). N = 68

Measurement (x axis)	Equation	R <sup>2</sup>
Zygomatic breadth	$y = 1.0694x + 26.857$	0.8749
Rostral breadth	$y = 2.5909x + 30.495$	0.8293
Palatal length	$y = 1.8227x + 26.57$	0.7844
Lower canine-condyle	$y = 1.2272x + 10.987$	0.9489
Upper carnassial length	$y = 7.1052x + 14.827$	0.6285
Lower carnassial length	$y = 8.5215x + 33.224$	0.4979
Upper canine length	$y = 6.9312x + 80.08$	0.5813
Lower canine length	$y = 7.115x + 80.217$	0.5909
Lower P3 - carnassial	$y = 3.504x + 21.748$	0.6918
Lower canine-carnassial	$y = 2.4752x - 12.123$	0.8522

body size at least *within* species. Our next task is to ask whether more commonly recovered items such as cranial fragments, complete or semi-complete dentitions and individual teeth are closely correlated in size with cranial length in jaguars. Since Hoogesteijn and Mondolfi provide little information on this point we have used our own large comparative data set for this purpose.

Figures 3, 4 and 5 show respectively the relationships between condylobasal cranial length and the width across the zygomatic arches, the rostral breadth measured across the buccal surfaces of the upper canines and the length of the palate. All give good relationships with high  $r^2$  values, as listed in Table 1 together with the equations of the linear regressions. An even higher correlation is seen in Figure 6 when we consider the canine to articular condyle length of the mandible, with an  $r^2$  value of 0.95 (Table 1). This latter measurement can be closely approximated in a mandible even when the canine is missing, since the anterior surface of the crown base that forms the anterior landmark for this measurement is reasonably represented by the anterior edge of the canine alveolus.

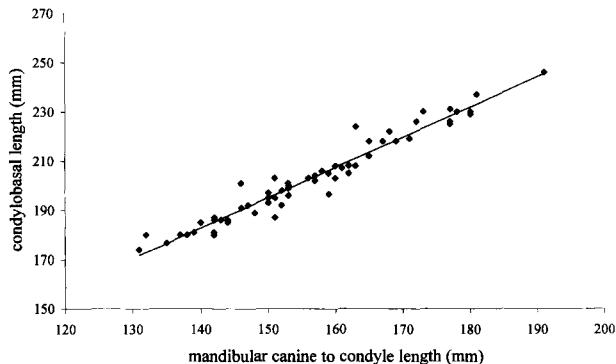


Fig. 6.—Modern jaguar: condylobasal length of cranium vs mandibular canine-condyle length (data authors).

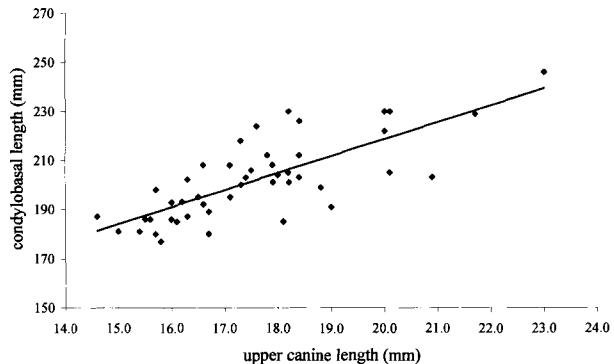


Fig. 9.—Modern jaguar: condylobasal length of cranium vs upper canine length (data authors).

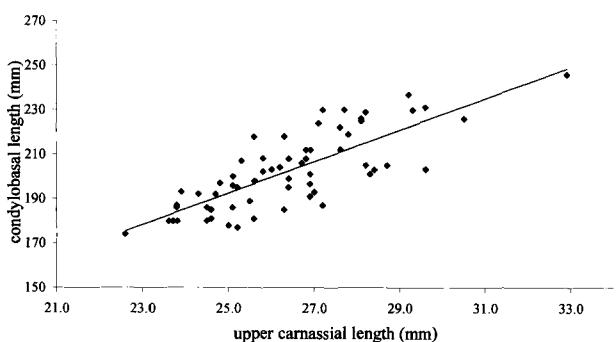


Fig. 7.—Modern jaguar: condylobasal length of cranium vs upper carnassial length (data authors).

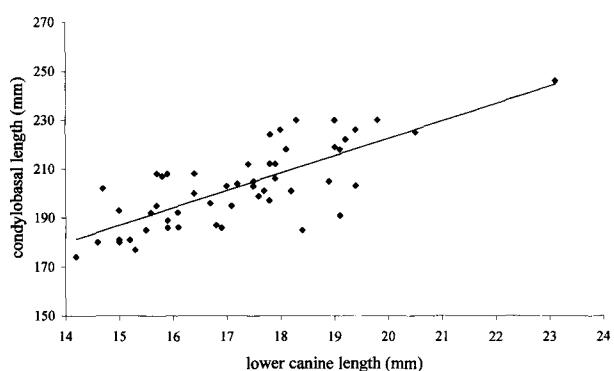


Fig. 10.—Modern jaguar: condylobasal length of cranium vs lower canine length (data authors).

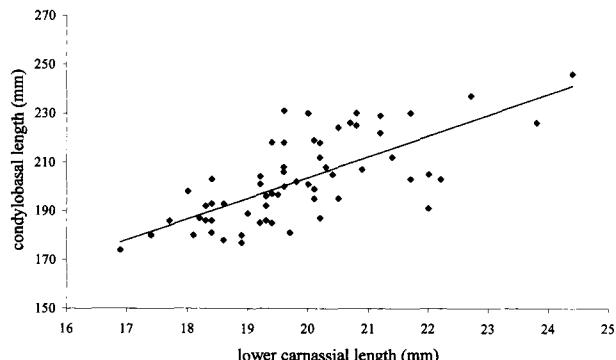


Fig. 8.—Modern jaguar: condylobasal length of cranium vs lower carnassial length (data authors).

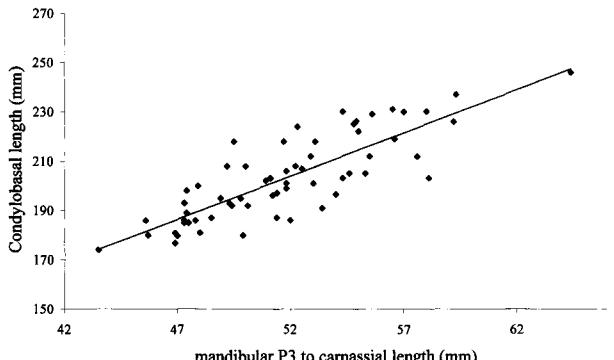


Fig. 11.—Modern jaguar: condylobasal length of cranium vs mandibular P<sub>3</sub>-carnassial length (data authors).

However, when we turn to the dentition the relationships become less close. Figures 7-10 show respectively the patterns for antero-posterior lengths of upper and lower carnassial and upper and lower canine crowns, all measured at the base of the enamel, and it is apparent that the correlations, while always positive, are less significant than those for cranial measurements with  $r^2$  values that never

exceed 0.63 (Table 1). The lower toothrow measurement from the anterior edge of  $P_3$  to  $M_1$  (Figure 11) is a little more useful, with an  $r^2$  value of 0.69, but it is only with the longer dental measurement from lower canine to  $M_1$  (Figure 12) that we see an increase in the  $r^2$  value to 0.85 (Table 1). Like the lower canine to articular condyle measurement shown in figure 6, this measurement can be closely approxi-

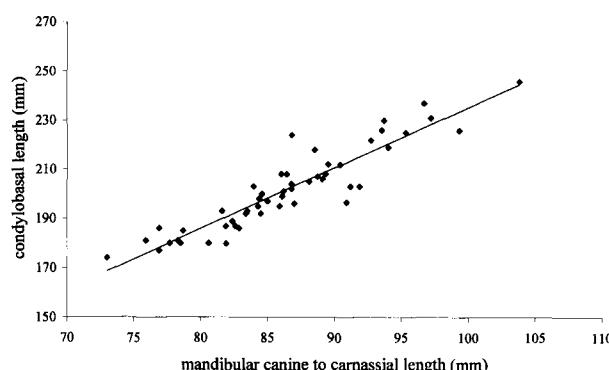


Fig. 12.—Modern jaguar: condylobasal length of cranium vs mandibular canine-carnassial length (data authors).

Table 2.—Modern lions. Linear regression equations of condylobasal length of cranium versus cranial, mandibular and dental measurements (data authors). N = 94

Measurement (x axis)	Equation	R <sup>2</sup>
Zygomatic breadth	$y = 1.101x + 39.295$	0.8550
Rostral breadth	$y = 2.991x + 7.9095$	0.8336
Palatal length	$y = 1.5962x + 43.323$	0.8660
Lower canine-condyle	$y = 1.2113x + 13.821$	0.9382
Upper carnassial length	$y = 7.4493x + 5.3483$	0.2946
Lower carnassial length	$y = 8.7179x + 39.834$	0.3283
Upper canine length	$y = 7.9184x + 86.184$	0.5674
Lower canine length	$y = 8.9822x + 75.229$	0.5495
Lower P3 - carnassial	$y = 4.492x + 38.487$	0.5358

Table 3.—Modern leopards. Linear regression equations of condylobasal length of cranium versus cranial, mandibular and dental measurements (data authors). N = 95

Measurement (x axis)	Equation	R <sup>2</sup>
Zygomatic breadth	$y = 1.1552x + 26.272$	0.7719
Rostral breadth	$y = 3.1742x + 11.563$	0.8288
Palatal length	$y = 1.6963x + 21.683$	0.8913
Lower canine-condyle	$y = 1.2368x + 12.384$	0.9790
Upper carnassial length	$y = 6.8768x + 11.071$	0.5080
Lower carnassial length	$y = 8.9258x + 17.593$	0.4831
Upper canine length	$y = 9.5065x + 49.005$	0.6789
Lower canine length	$y = 10.605x + 39.504$	0.6820
Lower P3 - carnassial	$y = 4.3481x + 24.091$	0.6726

mated by the alveoli even in the absence of the teeth.

To examine whether this pattern of relationships holds more generally within the pantherine cats we performed similar assessments on data sets of lion, *Panthera leo*, and leopard, *Panthera pardus*. Results for these are presented in Tables 2 and 3 again in the form of equations of the linear regression line with  $r^2$  values, although in neither of these were we able to include the lower canine-carnassial

length. In the lion (Table 2) the pattern is broadly similar to the jaguar, with cranial dimensions and the lower canine to mandibular condyle showing strong correlations with condylobasal length and the individual teeth showing much weaker relationships. However the relationship with the lower tooththrow measurement from the anterior edge of  $P_3$  to  $M_1$  is even smaller than in the case of the jaguar. For the leopards the pattern again holds good (Table 3), and the relationship with  $P_3$  to  $M_1$  is again similar to that of the jaguar. One interesting point of the leopard pattern, however, is in the somewhat higher correlation with the lengths of both the upper and lower canines.

## Discussion

We conclude from the results obtained in our study that the condylobasal length of the cranium in adult jaguars is strongly correlated with the overall size of the animal, whether based on body mass or on a relatively crude measure such as body length, and may be taken as a good proxy indicator of size. When other cranial dimensions are then plotted against condylobasal length it is apparent that several taken along the central axis of the cranium, as well as those that record width, in turn show good correlations with the basal length. This close relationship extends to measurements that include several teeth, or take their starting point from dental landmarks such as the anterior surface of the canines or even the tooth alveoli. It is thus apparent that parts of the skull likely to be frequently preserved in fossil specimens, such as the snout and the robust zygomas as well as the horizontal ramus of the mandible, can give useful data on cranial length and hence the size of the living animal. Even in more fragmented specimens, it is often possible to obtain measurements between say one zygomatic arch and the midline of the frontal or palate, from which the complete width may be estimated.

In contrast, individual teeth, particularly those in the middle portion of size ranges, do not show a particularly close relationship with condylobasal length, and may therefore be taken to show a less close relationship to overall size of the animal. This is unfortunate, given the frequent abundance of such teeth in fossil assemblages and the part they often play in determining abundance of taxa and the potential that they therefore seem to hold for investigation of size variation within a species. However, such a result is perhaps not surprising. The size of the individual teeth in a population is unquestionably positively correlated with the size

of the animals, as demonstrated here and commented on in previous studies of the wider pattern seen in the Carnivora by Kurtén (1967). Nevertheless, the formation of the dentition takes place at an early stage in development and does so largely under genetic control, while the size to which the animal may actually grow in normal circumstances is determined by many environmental factors that may produce an end result across a wide range limited only at one end by genetic potential. So while we may presume that the genetic potential for large body size within a population would correlate with a large dentition, the closeness of the actual relationship may differ considerably and a high level of uncertainty surrounds inferences of body size. Males can in all probability be assumed to cluster in a group of larger individuals than females, but within each the correlation will be less close. To take one concrete example, Figure 7 shows the relationship of upper canine length to condylobasal length in jaguars. At the extremes, larger or smaller teeth clearly represent respectively longer or shorter crania and thus probably males or females, but in the centre, a carnassial length of say 27 mm may come from an animal with a cranium of around 180 mm to around 230 mm in length. Figure 1 shows the equally wide divergence in body masses to be expected from such a range of cranial lengths in the data of Hoogesteijn and Mondolfi (1996).

When we extend the analysis to include lions and leopards we see essentially the same relational patterns emerging in the cranial and dental data. Unfortunately, we do not have information on the relationship between condylobasal cranial length and body size for these two species, and while it would appear reasonable to expect a similarly close correlation *within* each taxon we do not know if all three would fall on or close to a single trend line. Thus we cannot at this stage use condylobasal length in pantherine cats as a group in order to provide a general predictor of body size, an unfortunate situation since it prevents us from using the measurement to refine estimates of body size in unidentified or problematic fossil taxa beyond saying lion-like or jaguar-like. But if the relationship within each taxon is indeed close, then it would seem unlikely that individual teeth of pantherine cat species will correlate particularly closely with the size of the animals, and could certainly give a misleading impression of both relative and absolute body mass in any fossil sample. That conclusion may very well prove to be even more widely applicable to the relationship between tooth size and body size in other Felidae, other Carnivora and perhaps even to other mammalian families.

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