Locomotor evolution in the Carnivora (Mammalia): evidence from the elbow joint

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List of Papers

This thesis is based on the following papers, referred to by their roman numerals

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Paper I Predicting carnivore body mass from a weight bearing joint. *Andersson, Unpublished manuscript.*

Paper II Elbow joint morphology as a guide to locomotor behaviour in the order Carnivora, with examples from Miocene Mustelidae. *Andersson, Unpublished manuscript*.

Paper III The evolution of cursorial carnivores in the Tertiary: implications of elbow joint morphology. *Andersson & Werdelin, Unpublished manuscript*.

Introduction

In the absence of direct observations, paleontologists have to infer ecological and behavioural traits from dental and skeletal morphology. Functional analysis of structures and morphologies among recent relatives forms the basis of such studies. Because of the nature of the fossil record, much attention has been paid to dental morphology (e. g., Crusafont-Pairó and Truyols-Santonja, 1956; Van Valkenburgh, 1988), which has proven to be a useful indicator of diet (Van Valkenburgh, 1989). However, traits such as locomotor adaptations are equally important indicators of the mode of life of individual taxa, and these have to be inferred from the appendicular skeleton (e. g., Van Valkenburgh, 1987). The locomotory repertoire of most carnivores includes, to varying extents running, climbing, digging and swimming, however.

A general observation is that Carnivora use their forelimbs differently during food procurement and threat avoidance (e. g. Ewer, 1973). Felids often climb trees and are known to manipulate their prey extensively. Canids, on the other hand rarely climb and manipulate prey to a lesser extent. This thesis aims to develop a locomotor habit indicator for terrestrial carnivores that does not directly rely on allometric assumptions. By measuring forearm usage, complex behaviours such as hunting strategies can be inferred and their evolution studied. Carnivorans are characterised by combining estimates of body size (Paper I) with forearm utilization inferred from the shape of the humeral articular surface of the elbow joint (Paper II). The observed pattern characteristic of modern day Carnivora is compared to that of extinct carnivorans (Paper III).

Forearm function

The mammalian elbow joint complex is designed to transfer loads between the upper and lower portion of the arm. The elbow joint has to provide stability while at the same time allowing for mobility (Jenkins, 1973; Evans, 1993). At the elbow, the humerus articulates with the radius and ulna. Flexion-extension of the elbow involves movement in the humeroulnar and humeroradial articulations and the elbow can functionally be regarded as a compound joint with a uniaxial hinge-like movement. Pronation-supination of the hand is primarily achieved through movement in the wrist. However, movement in the elbow complex increases the range of pronation-supination. Such movement involves the proximal radioulnar articulation, whereby the radius is rotated around its long axis.

While at the same time allowing for movement, the joint has to withstand internal and external forces during activity without dislocation. Elbow joint stability and integrity are maintained through a series of ligaments and bony features, including the medial trochlear flange and the trochlea furrow (e. g., Evans, 1993).

Skeletal scaling in mammals

Scaling refers to the relative growth of traits (Huxley, 1924) and allometry to the rate by which this growth occurs. Huxley formalized the study of scaling by formulating the model of simple allometry: $y = bx^a$, where a is the allometric coefficient (Huxley, 1932; Huxley and Teissier, 1936). Basic geometry predicts that linear change of a cube will result in an area increase by a factor 2 and volume increase by a factor 3. In animals, the model of geometric similarity predicts that mass (M) will scale to a linear dimension (l) by $l \propto M^{0.333}$. Simple geometric similarity therefore predicts that skeletal safety factors cannot remain constant through a broad range of sizes, since body mass increase exceeds that of linear dimensions. Nevertheless, Alexander et al. (1979) reported that the long bone length of a wide range of mammals, from shrews to elephants, scales as $l \propto M^{0.360\text{-}0.390}$, close to what is predicted from geometric similarity. The limbs of large and small mammals seem to suffer the same stresses during locomotion (Alexander, 1977, 1979), and long bones withstand the peak forces exerted during normal activity without breaking. This indicates that bending moment and peak forces in long bones during the support phase are reduced by other mechanisms. This was later confirmed by Biewener (1983), who showed that decreasing longitudinal curvature and reorienting the bone so that loading forces are directed along the longitudinal axis results in compression rather than in bending forces, thus allowing scaling according to geometric similarity, while, at the same time, safety factors remain constant in small and large mammals. To predict body mass or assess cursoriality using skeletal elements known to scale geometrically is questionable, since their allometry depends on compensatory factors.

Not all mammals scale according to geometric similarity. Several aspects of the limbs of the posturally extreme bovids scale with an allometric coefficient significantly lower than that predicted by geometric similarity (McMahon, 1973; Alexander, 1977; see also Alexander et al., 1979). To explain this, McMahon (1973) proposed an alternative scaling model, in which bones scale so as to retain elastic, rather than geometric, similarity. Under elastic similarity, linear dimensions increase in proportion to the diameter, which predicts a mass to linear dimension scaling of $l \propto M^{0.25}$ and a mass to diameter (D) scaling of $D \propto M^{0.375}$. Under elastic similarity, bones scale so as to withstand elastic buckling and bending forces, and thus skeletal safety factors remain similar in small and large animals. It has become clear that scaling in mammals is differentiated and scaling over a broad size range cannot be successfully explained by one model only (e. g., Christiansen, 1999; Iriarte-Díaz, 2002). The implication is that lifestyle indicators that are based on allometry, i.e., limb proportions and metatarsal-femur length ratio, should be used with caution until better knowledge of their scaling is available.

Body mass estimation

Body size is the point of entry to many biological, ecological and evolutionary studies (e. g., Damuth and MacFadden, 1990; Peters, 1993). Paleontologists are forced to rely on predictive models for obtaining the body mass of extinct animals. These models generally assume scaling according to Huxley's model of simple allometry (see above) where body mass is regressed on a predictor (e. g., all mammals: Gingerich, 1990; carnivores: Legendre and Roth, 1988; Van Valkenburgh, 1990; Anyonge, 1993; Egi, 2001). This procedure has limitations, and relies on a few basic assumptions.

A causal relationship between body mass and the predictor is assumed and the predictor is treated as an independent variable. A second assumption is that the sample population is a random representation of the global population. Large samples that comprise a broad spectrum of the existing morphologies is one way to assure a representative sample. Another way is to break down the sample into subsets that are analysed separately, e. g., subsets based on taxonomy (Van Valkenburgh, 1990; Anyonge, 1993), function (Conroy, 1987; Egi, 2001) or size, i. e., the "narrow allometry" of Smith (1980). Control of within-group variation and the effects of systematic scaling, as well as increased accuracy in the regression lines, is gained, but sample sizes are often dramatically reduced. The usefulness of such a predictive model is further impaired by loss of generality. Predictions are limited to animals within the extant size range, since extrapolation beyond the domain of a data set is theoretically questionable. Thus, body mass predictions of extinct animals that are beyond the range of modern relatives or functional equivalents require further assumptions about scaling.

Long-bone length and surface area of the humerus and femur head of terrestrial carnivores, traits that are widely used as body mass predictors, scale in accordance with what is predicted by geometric similarity ($l \quad M^{0.37\text{-}0.39}$, Alexander et al., 1979; $A \propto M^{0.634\text{-}0.642}$, Godfrey et al., 1991). This suggests that scaling of these parts of the long bone is not directly dependent on body mass and that compensating mechanisms are in effect (e. g., those proposed by Biewener, 1983). Carnivore limb structure and posture need to be further explored to determine under which circumstances humerus and femur length, midshaft circumference and midshaft cross-sectional area are reliable body mass predictors.

Carnivore hunting strategy and cursoriality

Among the hunting strategies employed by members of the order Carnivora, two, stalk and ambush and sustained pursuit, are particularly prevalent among larger species of the order. It has, however, been difficult to identify morphological traits that support this distinction, and ecological observations have shown that Carnivora adopt a continuum of strategies, depending on available habitat and prey. Identifying pursuit predators through traditional measurements of cursoriality has failed, since cursoriality is based on running ability, while pursuit predation is a hunting strategy.

The concept of cursoriality was originally developed for ungulates adapted to sustained running in open spaces (Gregory, 1912), which represent the fast-running end-members in a four step classification scheme for ungulates. Hildebrand (1985, 1988) defined cursors as animals “that travel far and fast on ground” (Hildebrand (1988, p. 473) Others have defined cursoriality using morphological traits, including muscle mechanics and limb proportions (Maynard Smith and Savage, 1956) or through stance and limb excursion pattern during locomotion (Jenkins, 1971). A biomechanical concept of cursoriality emerged though the work of Alexander and Jayes (1983), who proposed a dynamic similarity model for mammalian quadrupedal locomotion.

Today there is no widely accepted consensus regarding how to define cursoriality in mammals (Stein and Casinos, 1997), and even the existence of such a biological entity has been questioned (Biewener, 1989). Mammals maintain similar peak stress in bone and muscles during body mass scaling by changing limb posture during locomotion to an upright stance (Biewener, 1989). Thus, the upright stance found among fast runners (Jenkins, 1971) may be determined by other factors than running speed.

Fast runners tend to have longer limbs and a high Metatarsal/Femur (MT/F)-ratio, also referred to as the “cursorial index ” (e. g., Gregory, 1912; Maynard Smith and Savage, 1956; Bakker, 1983). A survey of maximum running speed in 49 species, ranging from 2.5-2000 kg, showed that hind limb proportions and limb length are correlated. However, the “cursoriality index” appears not to be correlated with maximum running speed when only cursorial ungulates and carnivores are considered (Garland and Janis, 1993). At equal body size ungulates generally tend to have longer limbs and feet than carnivores, yet they are not significantly faster (Garland and Janis, 1993).

Pursuit predators in the past

Ungulates in the past responded to selective pressure for locomotion and speed by evolving “cursorial” (sensu Gregory, 1912) adaptations, e. g., elongated limbs (Gregory, 1912; Maynard Smith and Savage, 1956). The selective pressure driving the shift to increased running abilities in mammals has been suggested to be an arms race between predator and prey (Dawkins and Krebs, 1979; Bakker, 1983). However, the empirical evidence for such scenario assumes cursoriality inferred from the MT/F-ratio. “MT-F-Cursoriality” appears during the early Eocene and increases step-wise during the early Miocene. Among carnivores, the

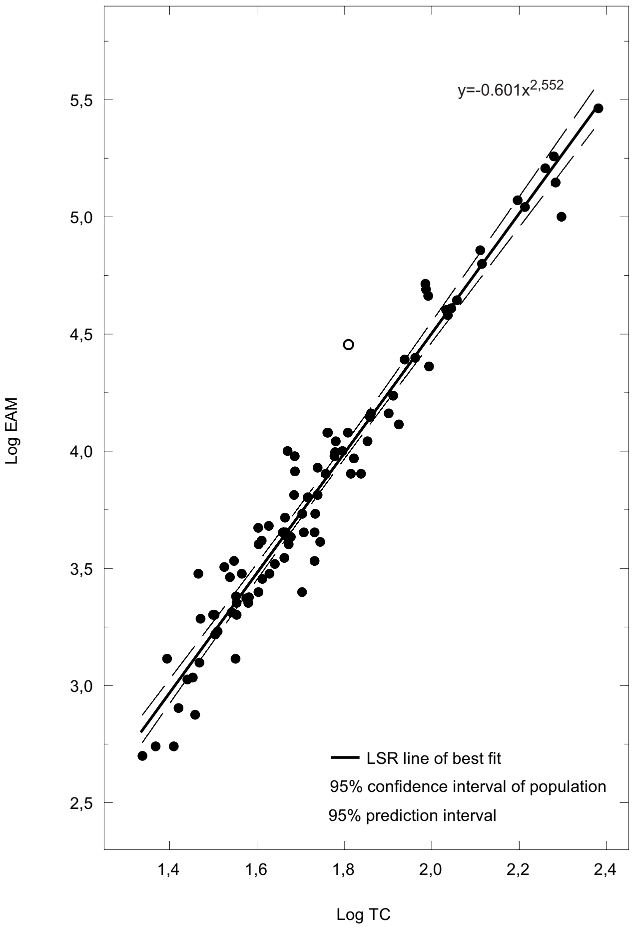

Figure 1. *Scatterplot of untransformed estimated average body mass (EAM) in grams and trochlea circumference (TC) in centimetres with 95% confidence and prediction levels (n=92, R^2=0.952. P<0.001). Sea otter* (Enhydra lutris) *identified as an outlier (open circle).*

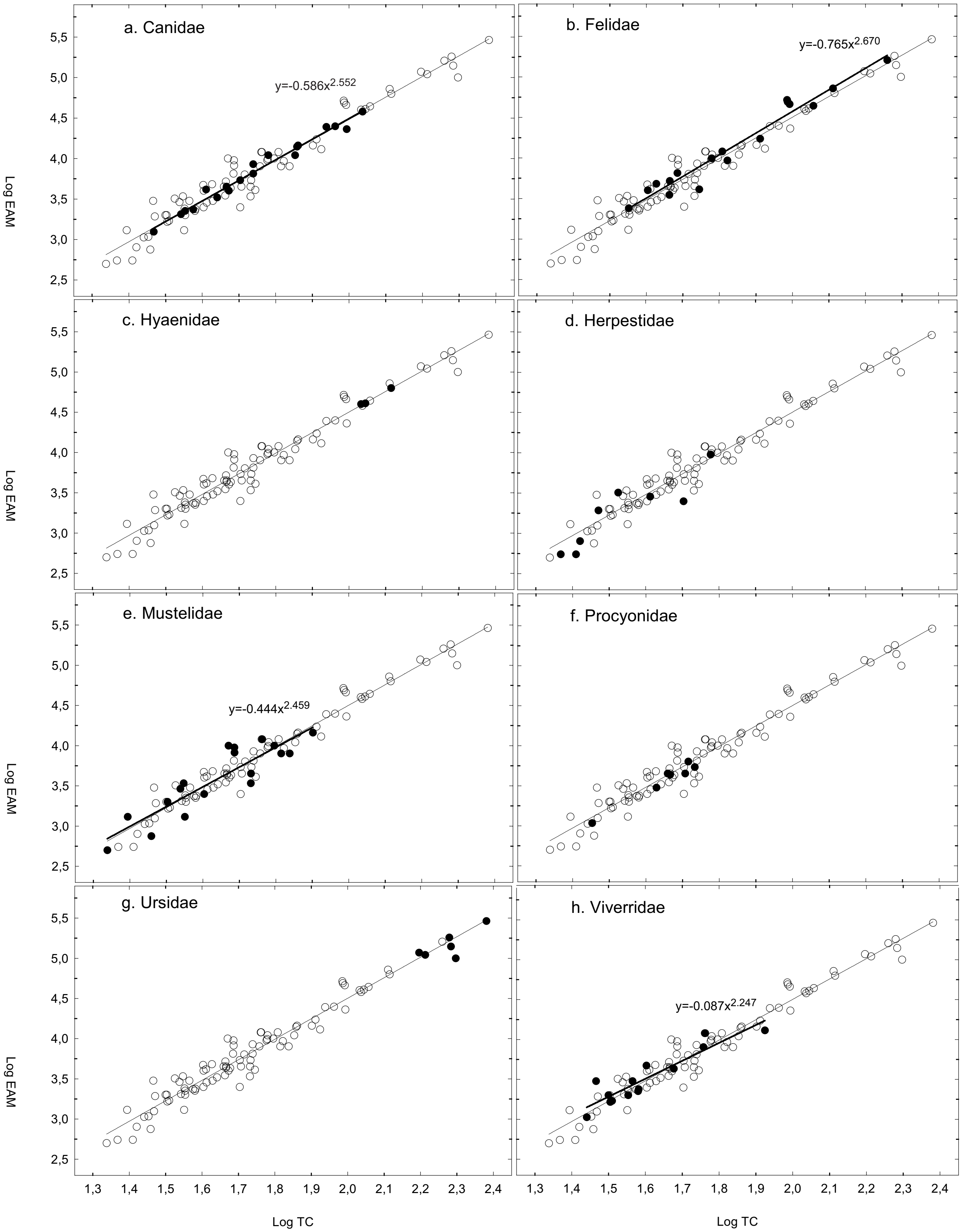

Figure 2. *Scatterplot of log_{10}-transformed estimated average body mass (EAM) and trochlea circumference (TC). Thin line; least squares regression line of best fit for total Carnivora. Thick line and filled circles; least squares regression line of best fit and data points for each family: Canidae, n=19, R^2=0.979. P<0.001; Felidae, n=17, R^2=0.954. P<0.001; Mustelidae, n=18, R^2=0.799. P<0.001; Viverridae, n=14, R^2=0.844. P<0.001.*

same increase occurs during the Middle Miocene, about 20 million years later, while pursuit-predation, does not appear until the Plio-Pleistocene (Bakker, 1983; Janis and Wilhelm, 1993). The coevolutionary hypothesis does not account for the observed time lag and Janis and Wilhelm (1993) proposed an alternative hypothesis, by which "cursoriality" in ungulates evolved to minimize energy expenditure during foraging at average speeds.

Shape analysis

Analysing the shape of the humeral part of the elbow articulation poses several problems. The first is to capture the undulating and highly complex shape of the articular surface. A three-dimensional analysis would be ideal because of the highly convex nature of the articulation. However, such procedure involves a 3D-digitizer, generally in the form of a fixed set-up. Here, ease of data collecting was chosen over precision. The articulation was captured (in 2D) by high-resolution digital photography and landmarks were placed on the outline of the articular surface. For the analysis, distance methods were chosen over direct landmark analysis procedures, e. g., relative warp (Bookstein, 1991 and references therein) and outline methods, e. g., radius function (Rohlf and Bookstein, 1990).

Thin plate spline analysis was used to graphically visualize differences between the wolverine (Gulo gulo) and the wolf (Canis lupus) (Fig.3). Redundancy in the data set was kept to a minimum by using a truss approach, whereby Euclidean distances connecting the landmarks and forming a truss network were calculated (Strauss and Bookstein, 1982). For the analysis of a globally redundant distance matrix see, e. g., Lague & Jungers (1999).

The untransformed data matrix containing the 11 unweighted Euclidean distances was analysed by Principal Components Analysis of the Variance-Covariance matrix. The information in the 11 variables was thereby reduced to a set of principal components. The geometric information in the principal components was then discussed in a functional and biological context.

Summary of papers

Paper I

Body mass prediction in extinct mammals generally follows Huxley's model of simple allometry. Body mass is regressed on the predictor, assuming a causal relationship between the two. A second assumption is that scaling is uniform between the sample population and in the individuals being estimated. Scaling of the distal humerus articular circumference appears to be uniform throughout the order Carnivora, regardless of foot posture. Articular circumference is found to be highly correlated with body mass in carnivores (r^2=0.952, SEE=0.136, p<0001, n=92) (Figure 1). The statistical properties of the regression line for the total sample of Carnivora are good for a regression analysis. By using this taxonomically and morphologically, "broad" model, a minimum number of assumptions need to be made, allowing average body mass estimates to be predicted. Some degree of differential scaling between carnivore families and between animals of large and small size cannot be ruled out, but this result is inconclusive (Figure 2). There are no reasons to believe that humerus trochlea circumference cannot, after necessary adjustments, successfully be used as a body mass predictor, not only for carnivores, but also for a broad range of quadrupedal mammals. Body mass for eight extinct carnivoran species are calculated and these generally conform to earlier mass predictions

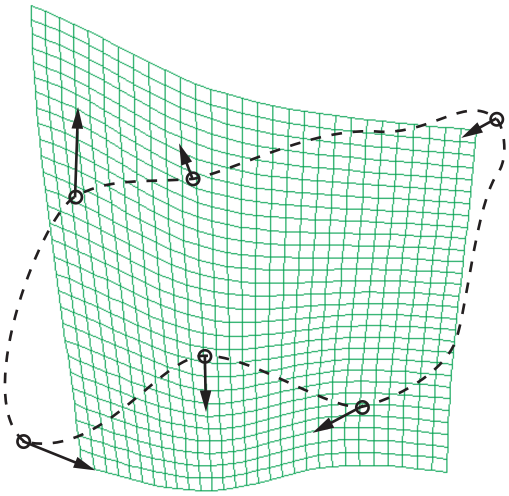

Figure 3. *Thin-plate spline comparison of wolverine* (Gulo gulo) *against grey wolf* (Canis lupus)*, graphically illustrating the difference in shape of the distal humerus articulation between carnivores scoring high* (C. lupus) *on the second principal component (PC2) and low* (G. gulo)*. Broken line, hand fitted, indicate the outline of the articulation of* C. lupus*. The thin-plate spline is calculated from the consensus configurations of the two species (*G. gulo*, reference species, n=6; C. lupus, n=5; Bookstein, 1991), generated through generalized least squares (GLS) orthogonal procrustes analysis (Rohlf and Slice, 1990).*

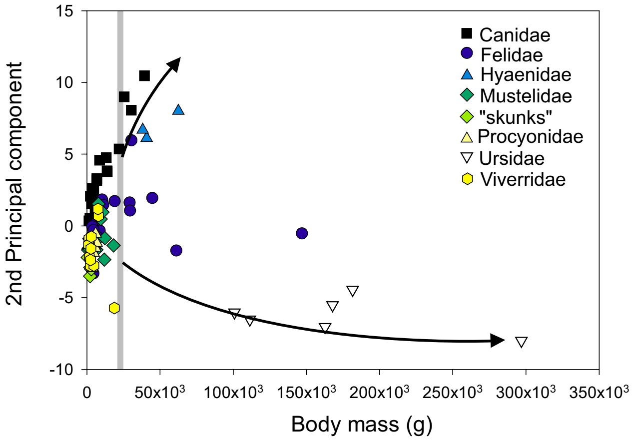

Figure 4. *Second principal component (PC2, trochlea shape component) of recent carnivores plotted against calculated body mass. The postulated threshold at 21.5-25 kg (shaded grey) where carnivores shifts diet from small to large prey (Carbone et al., 1999). Around and above this threshold carnivorans are strongly dichotomised into grapplers and non-grapplers. Hand-fitted arrows mark the two morphological trajectories.*

Paper II

In this paper I test if the degree of manual manipulation and locomotor adaptations can be traced through elbow joint morphology. Due to the nature of the fossil record it would be most desirable if a single articulation, such as the humeral part of the elbow, could provide a proxy for hunting strategies, including predation by stalk-and-ambush and predation by sustained pursuit.

The results suggest that manual manipulation and locomotion are conflicting functions, and that there is a trade-off between the two. Elbow joint morphology thus supports the division between ambushers (grapplers) and pursuers (locomotors). Joints of the latter are characterized by being relatively narrow and box-like, having pronounced stabilizing features, such as a medial flange that projects mediodistally and a relatively deep mid-trochlea furrow (Figure 3). At large body sizes, carnivorans show a strongly dichotomised pattern, a shift coinciding with a postulated threshold in predator-prey size ratio (Carbone et al., 1999), suggesting mutually exclusive lifestyles involving either grappling of prey or pursuit (Figure 4). The former allows for large body sizes, as, e. g., in pantherine felids and ursids, while the latter group includes species of no more than moderate size, e. g., hyenids and canids. Elbow joint morphology is closely linked to phylogeny (Figure 5),

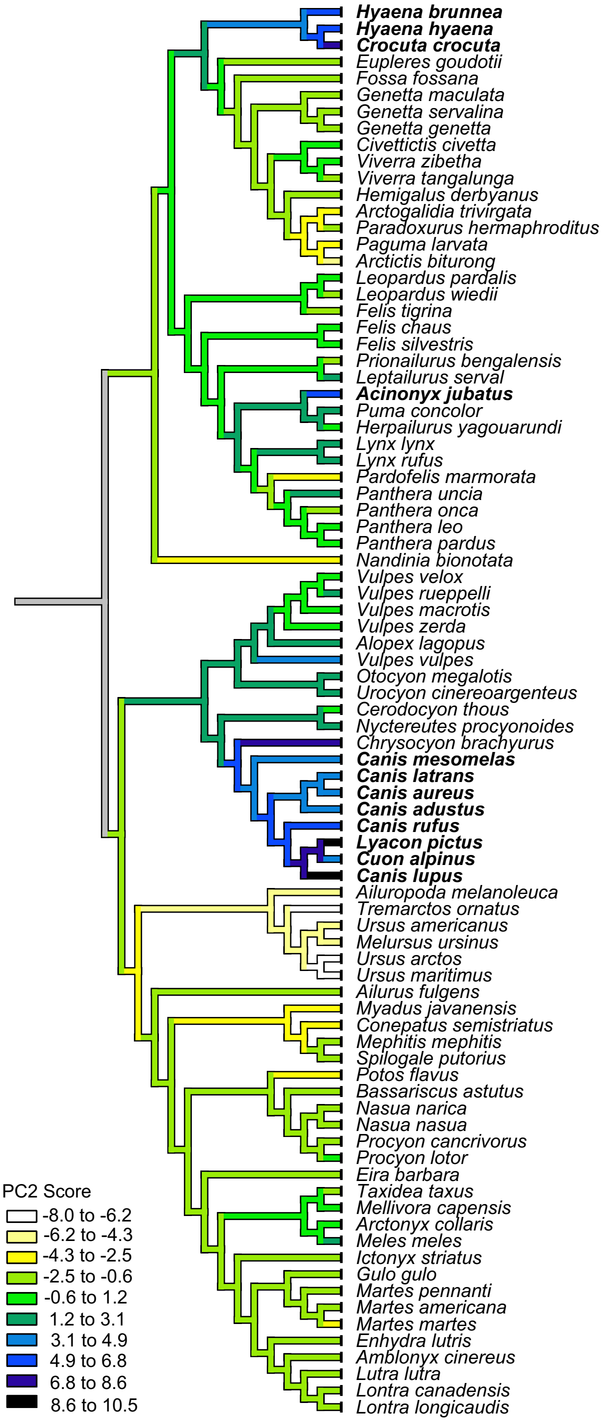

Figure 5. *Second principal component (PC2, trochlea shape component) mapped onto a composite phylogeny for the Carnivora. Carnivores traditionally regarded as primarily using their forelimbs for locomotion (non-grappling, locomotors) are shown in bold typefaces. PC2 largely follows the phylogeny. Transitions are rare, although present e.g., the cheetah (Acinonyx jubatus). Ancestral stages are reconstructed by minimizing the sum of squared changes. The value for the root is not reconstructed.*

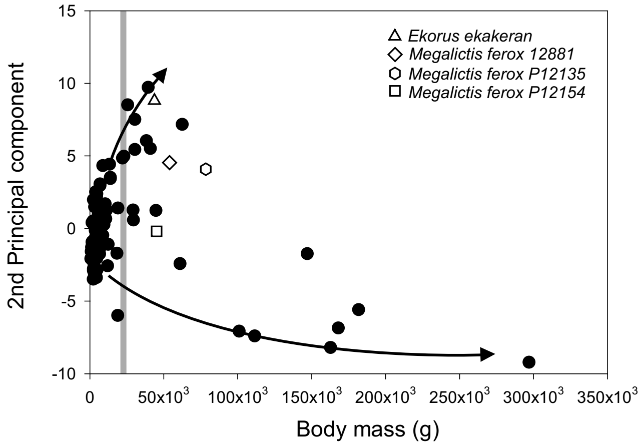

Figure 6. *Second principal component (PC2, trochlea shape component) of extinct giant mustelids and extant carnivora plotted against body mass. The postulated threshold at 21.5-25 kg where carnivore shift from small to large prey (Carbone et al., 1999) is shown (shaded grey).*

but the morphology of the cheetah converges with that of locomotors, showing that strong selective forces may override the phylogenetic component.

Two taxa of giant mustelids from the Miocene were analysed (Figure 6). The African late Miocene species *Ekorus ekakeran* has a joint morphology comparable to that of modern day locomotors. Two joint morphologies where found in the North American late Oligocene-early Miocene *Megalictis ferox*, indicating that this taxon may be in need of revision. The first morphology is comparable to that of modern Pantherine cats and the second forms an intermediate between locomotors and grapplers that is not present in the recent carnivoran fauna.

Paper III

The pattern of elbow joint morphology in modern carnivora is compared to that of carnivoran faunas from the Tertiary. Two time-slices for which there were adequate data on fossil carnivores were analysed using multivariate landmark-based morphometrics: one from the Oligocene (33.7-23.8 Myr BP) and one from the early-middle Miocene (23.8-11.2 Myr BP) (Figure 7). At intermediate and large body sizes the extant carnivoran fauna is characterised by a strongly dichotomised pattern. Scoring high are locomotor species, with reduced supinatory abilities, and scoring low are carnivore species that manually manipulate prey and food items.

In the Oligocene, the overall patterns are remarkably similar to that observed for extant Carnivora. Most taxa are small and retain supinatory abilities. Larger species tend towards the same extremes as extant species. *Hyaenodon horridus* is by far the most cursorially adapted Oligocene carnivore available to us. Daphoenine amphicyonids and the mustelid *Megalictis ferox* are moderately cursorial, while all nimravids are comparable to modern pantherine cats.

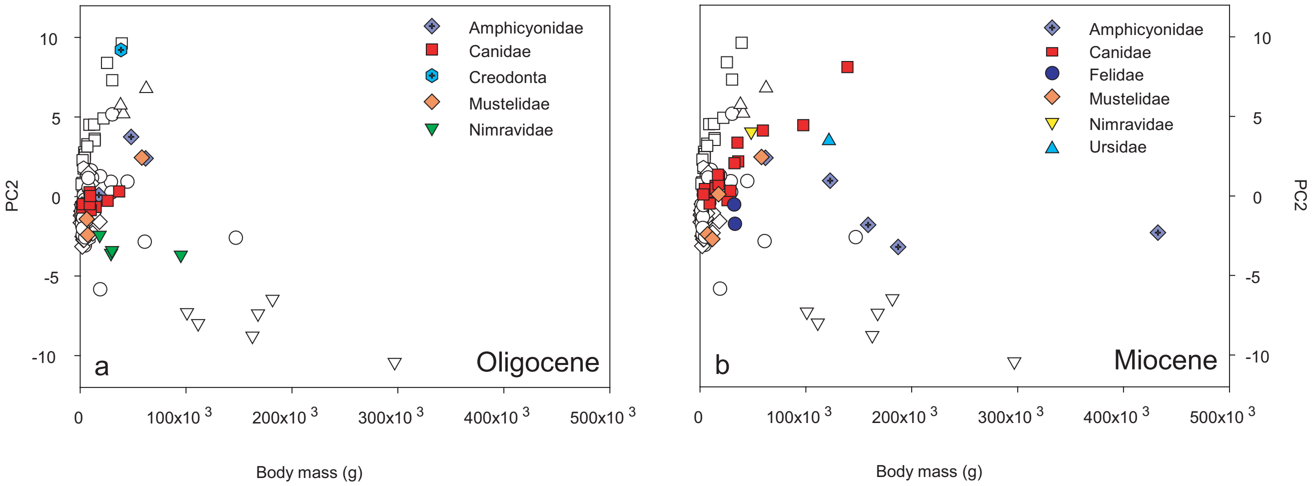

Figure 7. *a. Diagram of PC 2 (trochlea shape component) against body mass for a sample of 22 species of Oligocene carnivora. b. The same as in a but including a sample of 31 Miocene carnivora. The overall patterns are similar to that of extant carnivora (see Figure 4), However, for the Miocene the whole pattern is shifted towards larger taxa with an intermediate elbow joint morphology compared to either the Oligocene or Recent.*

Miocene carnivores show overall similarities in pattern to the Oligocene and Recent, but also some notable differences (Figure 7). The overall pattern, with an axis of moderately large, cursorial species and an axis of non-cursorial species of increasing size, remains. However, the whole pattern is shifted to the right, with the result that in the Miocene there were larger taxa with an intermediate elbow joint morphology than in either the Oligocene or Recent. We suggest that this difference is a reflection of the extraordinary species richness of browsing ungulates in the early Miocene of North America (Janis et al. 2000). Such an increase in prey spectrum in a mixed environment would create a unique situation, in which large carnivores need not commit to a cursorial habitus in order to fill their nutritional requirements.

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Paper I

Predicting carnivore body mass from a weight bearing joint

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Abstract

The use of humerus distal trochlea circumference as a body mass predictor for carnivores is explored. Trochlea circumference is found to be highly correlated with body mass in carnivores, (r^2=0.952, SEE=0.136, p<0001, n=92). Scaling appears to be uniform throughout the order Carnivora, regardless of foot posture. Some degree of differential scaling between carnivore families and between animals of large and small size cannot be ruled out, but this result is inconclusive. A predictive model that allows mass predictions for a broad range of carnivores with a minimum of assumptions is presented. Detransformation bias is corrected by a Maximum Likelihood Estimate. Body mass for eight extinct carnivore species are calculated and these generally conform to earlier mass predictions.

Key words: Carnivora, Mammalia, humerus, trochlea circumference, joint scaling.

INTRODUCTION

Body size is the point of entry to many biological, ecological and evolutionary studies (e.g., Damuth and MacFadden, 1990; Peters, 1993). While body masses for extant species are usually, if not always, available, paleontologists are forced to rely on predictive models for obtaining the body mass of extinct animals. These models generally assume scaling according to Huxley's model of simple allometry and are normally constructed as follows: 1) A measurement (or set of measurements) that scales directly to body mass is selected; 2) A data set, comprised of living carnivore species of known body mass, is gathered; 3) Body mass is regressed on the variable and the resulting equation is used in future predictions (for predictive models see, e.g., mammals: Gingerich, 1990; carnivores: Legendre and Roth, 1988; Van Valkenburgh, 1990; Anyonge, 1993; Egi, 2001). This procedure has limitations, and relies on a few basic assumptions.

The predictor is treated as an independent variable assuming a causal relationship between body mass and the predictor. Correlation may occur for the wrong reasons and body mass causality needs to be confirmed *a priori*. The second assumption is that the sample population is a random representation of the global population. This assumption may be difficult to meet in small samples.

The absolute cornerstone of these models are the body mass data used to generate the predictive equation. In the literature body mass is commonly given as the range of extreme records, particularly of the greater extreme (e.g. Nowak, 1999; Macdonald, 2001. Simply calculating the arithmetic mean of this range tends to exaggerate average body mass for a species. The inaccuracy that stems from uncertain body masses feeds through predictive models and extra caution must be taken not to violate the assumption of a representative sample.

Large samples that comprise a broad spectrum of the existing morphologies is one way to assure a representative sample. Another way is to break down the sample into subsets that are analysed separately, e.g, subsets based on taxonomy (Van Valkenburgh, 1990; Anyonge, 1993), function (Conroy, 1987; Egi, 2001) or size, i.e. the "narrow allometry" of Smith, (1980). Control of within group variation, the effects of systematic scaling, as well as increased accuracy in the regression lines is gained, but sample sizes are often dramatically reduced. The usefulness of such a predictive model is further impaired by loss of generality. Predictions are limited to animals within the extant size range, since extrapolation beyond the domains of a data set is theoretically questionable. Thus, body mass predictions of extinct animals that are beyond the range of modern relatives or functional equivalents require further assumptions about scaling.

Body mass has been shown to be one of the major factors determining humerus distal trochlear area in anthropoid primates (Swartz, 1989; Godfrey et al., 1991) and carnivores (Godfrey et al., 1991,). Capturing the area of the asymmetric and topologically complex trochlea involves making latex molds (Gomberg and Morbeck, 1983) geometric modelling (Egi, 2001) or 3D-digitization. As an alternative, trochlear circumference is a direct measurement related to area. It can therefore be expected to be a good body mass predictor and *post hoc* interpretation of correlation is thus avoided.

Here, the relationship between body mass and humerus trochlear circumference is explored, in the hope of finding a variable that allows us to predict body mass over a broad range of carnivores with a minimum of assumptions.

Body mass as predicted by the model presented herein is calculated for a number of extinct carnivore species, which allows comparison of estimates from earlier published models (Legendre and Roth, 1988; Van Valkenburgh, 1990; Egi, 2001).

Table 1. Estimated average body mass (EAM) in grams and foot posture of the Recent carnivore species (see text for sources) used in the regression analysis.

Estimated average species body mass (EAM) and foot posture of recent carnivores

Species	EAM	Fp	n=	Source
Canidae		D		
Alopex lagopus	3300	D	5	Prestrud and Nilssen, 1995;Heptner et al., 1998
Canis adustus	11000	D	4	Kingdon, 1977
Canis aureus	11000	D	4	Kingdon, 1977
Canis latrans	14000	D	4	Bekoff, 1977; Thurber and Peterson, 1991
Canis lupus	38000	D	5	Heptner et al., 1998; Mech, 1974
Canis mesomelas	8500	D	3	Kingdon, 1977
Canis rufus	24600	D	1	Paradiso and Nowak, 1972
Cerodocyon thous	5400	D	2	Sundquist et al., 1989; Nowak, 1999
Chrysocyon brachyurus	23000	D	6	Nowak, 1999
Cuon alpinus	14500	D	1	Cohen, 1978
Lyacon pictus	25000	D	4	Kingdon, 1977
Nyctereutes procyonoides	4000	D	2	Ward and Wurster-Hill, 1990
Otocyon megalotis	4150	D	2	Kingdon, 1977
Urocyon cinereoargenteus	4500	D	3	Fritzell and Haroldson, 1982
Vulpes macrotis	2050	D	2	McGrew, 1979
Vulpes rueppelli	2250	D	1	Nowak, 1999
Vulpes velox	2350	D	1	Kilgore 1969 in Egoscue, 1979; Nowak, 1999
Vulpes vulpes	6500	D	4	Heptner et al., 1998; Haltenorth and Roth, 1968; Nowak, 1999
Vulpes zerda	1250	D	2	Nowak, 1999
Felidae				
Acinonyx jubatus	46000	D	4	Kingdon, 1977, Nowak, 1999
Prionailurus bengalensis	4000	D	1	Nowak, 1999
Felis chaus	6500	D	2	Heptner and Sludskii, 1992
Puma concolor	51800	D	3	Nowak, 1999
Pardofelis marmorata	3500	D	1	Nowak, 1999
Leopardus pardalis	9900	D	6	Emmons, 1988; Konecny, 1989; Kiltie, 1984; Murray and Gardner, 1997
Leptailurus serval	12000	D	1	Kingdon, 1977
Felis silvestris	4800	D	2	Kingdon, 1977; Heptner and Sludskii, 1992
Felis tigrina	2400	D	2	Kiltie, 1984
Leopardus wiedii	4100	D	1	Konecny, 1989; Kiltie, 1984; de Oliviera, 1998b
Herpailurus yagouarundi	5200	D	1	Konecny, 1989; de Oliviera, 1998a
Lynx lynx	17250	D	5	Haglund, 1966; Heptner and Sludskii, 1992; Tumlison, 1987
Lynx rufus	9300	D	4	Young, 1958; Larivière and Walton, 1997
Panthera leo	161000	D	3	Smuts, 1976; Kingdon, 1977
Panthera onca	72000	D	3	Schaller and Vasconcelos, 1978; Rabinowitz and Nottingham, 1986
Panthera pardus	49000	D	2	Bailey, 1993; Kingdon, 1977
Panthera uncia	44000	D	1	Nowell and Jackson, 1996
Herpestidae				
Atilax paludinosus	3200	D	1	Baker, 1992
Bdeogale nigriceps	2500	D	1	Kingdon, 1977
Galida elegans	800	P	2	Nowak, 1999; Macdonald, 2001
Galidictis faciata	550	P	2	Garbutt 1999, Mammals of Madagascar, Yale University Press
Herpestes ichneumon	2850	D	1	Kingdon, 1977
Herpestes sanguineus	550	D	1	Kingdon, 1977
Mungos mungo	1925	D	1	Kingdon, 1977
Cryptoprocta ferox	9500	P	2	Nowak, 1999
Hyaenidae				
Crocuta crocuta	63000	D	2	Mills, 1990; Kingdon, 1977
Hyaena brunnea	40700	D	1	Mills, 1990; Mills, 1982; Kingdon, 1977
Hyaena hyaena	40000	D	2	Rieger, 1981; Kingdon, 1977
Mustelidae				
Amblonyx cinereus	2000	P	1	Nowak, 1999
Arctonyx collaris	10000	P	1	Nowak, 1999
Conepatus semistriatus	3400	P	1	Nowak, 1999
Eira barbara	4500	P	2	Nowak, 1999
Enhydra lutris	28500	P	1	Nowak, 1999
Gulo gulo	14500	P	6	Nowak, 1999
Ictonyx striatus	1300	P	1	Kingdon, 1977
Lontra canadensis	8200	P	3	Nowak, 1999 Nowak, 1999
Lontra longicaudis	10000	P	2	Nowak, 1999
Lutra lutra	9500	P	5	Nowak, 1999
Martes americana	750	P	1	Nowak, 1999
Martes martes	1300	P	1	Helldin, 1999; Nowak, 1999
Martes pennanti	3400	P	1	Powell, 1981
Meles meles	12000	P	4	Nowak, 1999
Mellivora capensis	8000	P	2	Kingdon, 1977
Mephitis mephitis	2900	P	2	Nowak, 1999
Myadus javanensis	2500	P	1	Nowak, 1999
Spilogale putorius	500	P	2	Kinlaw, 1995; Nowak, 1999; Macdonald, 2001
Taxidea taxus	8000	P	2	Long, 1973; Nowak, 1999
Procyonidae				
Ailurus fulgens	4500	P	2	Nowak, 1999
Bassariscus astutus	1080	P	3	Armstrong et al., 1972; Poglayen-Neuwall and Toweill, 1988
Nasua narica	4500	P	2	Gompper, 1995
Nasua nasua	4350	P	1	Nowak, 1999
Potos flavus	3000	P	2	Nowak, 1999; Ford and Hoffmann, 1988
Procyon cancrivorus	5400	P	1	Emmons, 1990
Procyon lotor	6350	P	3	Lotze and Anderson, 1979
Ursidae				
Ailuropoda melanoleuca	117500	P	2	Chorn and Hoffmann, 1978
Melursus ursinus	100000	P	1	Nowak, 1999
Tremarctos ornatus	110000	P	1	Nowak, 1999
Ursus americanus	140000	P	1	Macdonald, 2001
Ursus arctos	181000	P	3	Heptner et al., 1998; Nowak, 1999
Ursus maritimus	290000	P	3	DeMaster and Stirling, 1981; Cattet et al., 1997; Derocher and Wiig, 2002
Viverridae				
Arctictis biturong	13000	P	1	Nowak, 1999
Arctogalidia trivirgata	2250	P	1	Nowak, 1999
Civettictis civetta	12000	D	1	Kingdon, 1977
Eupleres goudotii	3000	D	1	Albignac, 1974
Fossa fossana	1700	D	1	Nowak, 1999
Genetta genetta	2000	P	1	Kingdon, 1977
Genetta maculata	1650	P	3	Macdonald, 2001
Genetta servalina	1060	P	2	Kingdon, 1977
Hemigalus derbyanus	2375	P	2	Nowak, 1999
Nandinia bionotata	2000	P	2	Kingdon, 1977
Paguma larvata	4300	P	1	Nowak, 1999
Paradoxurus hermaphroditus	3000	P	1	Nowak, 1999
Viverra tangalunga	4700	D	2	Nowak, 1999
Viverra zibetha	8000	D	1	Nowak, 1999

MATERIAL AND METHODS

Sample

The sample population comprises representatives of almost the entire extant size range of the Order Carnivora, with the exception of the very smallest (weasels: Mustelidae, body mass <500g). A total of 199 specimens from 94 species distributed over 57 genera and 8 families (19 canids, 17 felids, 8 herpestids, 3 hyaenids, 19 mustelids, 7 procyonids, 6 ursids, 14 viverrids) are included (Table 1). Sample sizes for each species range from 1 to 6 individuals. If available, equal numbers of male and female specimens were included. All individuals are wild captured, adult, museum specimens housed at the Swedish Museum of Natural History, Stockholm, Sweden, the Zoological Museum, Copenhagen, Denmark and the Field Museum of Natural History, Chicago, USA.

Body mass is predicted for three Nimravid species, *Hoplophoneus occidentalis* (n=1; AMNH 1407), *Hoplophoneus primaevus* (n=1; AMNH 38980) and *Dinictis felina* (n=1; AMNH 9763); three creodonts, *Hyaenodon horridus* (n=5; AMNH 1375, AMNH 1381, F:AM 75623, F:AM 75692, F:AM 75701), *Limnocyon versus* (n=1; AMNH 12155) and *Machaeroides eothen* (n=1; AMNH 92803); one hyaenid, *Adcrocuta eximia* (n=1) (AMNH 140301); and one felid, *Homotherium serum* (n=1 F:AM 128069). All individuals are adult specimens housed in the American Museum of Natural History, New York, USA.

Trochlea circumference

Outlines may be effectively captured by, e.g., a radial function (Rohlf, 1990). This method is, however, inapplicable to the humerus distal trochlea, because of the absence of an obvious internal reference point. Humerus trochlear circumference is here taken as the distance along the outline enclosing the articular surface, as seen in anterior view. It is calculated via a set of eight landmarks and 18 intermediate helping points (Fig. 1), digitised from high resolution digital images, using TPSdig32 written by F. J Rohlf (http://life.bio.sunysb.edu/morph/index.html). The landmarks are defined as maxima of curvature, (type 2 landmarks of Bookstein, 1991) and the helping point placed so as to best capture the outline.

Trochlear circumference (TC) is calculated as the sum of the distances between the landmarks and the helping points along the trochlea outline (Equation 1), multiplied by a scale factor (***f***).

$$TC = \sum_{i=1}^{j} \sqrt{(X_i - X_{i+1})^2 + (Y_i - Y_{i+1})^2} \times f \qquad (1)$$

Body mass

Body mass is among the easiest variables to obtain from living animals. Nevertheless, to produce an average body mass of a species is a complex undertaking. Sexual dimorphism, seasonal variation and variation over geographic range, are all natural sources of variation in a species' body mass (see references in table 1). Reasonable estimates of average body mass (EAM) based on information taken from the literature were entered into the model (Table 1). Average species mass is preferred even when associated body weight exists. In using associated body mass, the status of individuals at one instance in time (time of death), is emphasized, rather than the existing variability within the species as a whole.

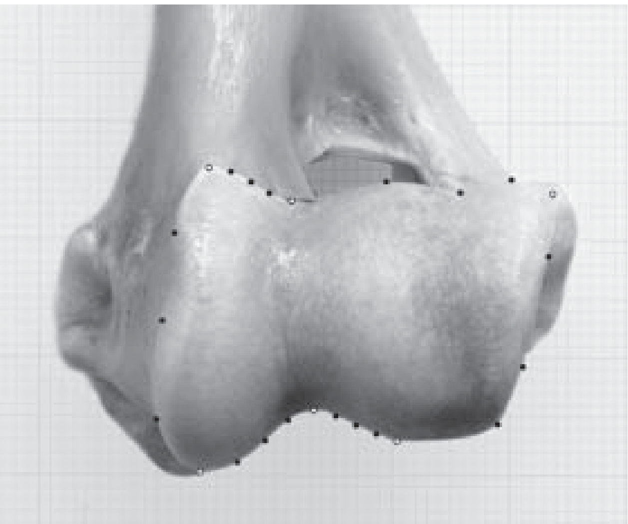

Figure 1. Distal humerus of grey wolf (*Canis lupus*) in anterior view. Landmarks (open circles) and helping points (filled circles) used to capture trochlea circumference.

Foot Posture

In a recent analysis of foot posture in mammals (Carrano, 1997), the traditional classification into plantigrade and digitigrade foot posture is supported, but intermediate stages based on fine morphology and hind foot mechanics are also recognized. Here, species are assigned to either plantigrade or digitigrade foot posture and intermediate stages are not recognized.

Information on foot posture was taken from the literature. (Canidae: Carrano, 1997; Felidae: Carrano, 1997; Herpestidae: Carrano, 1997; Mustelidae: Pocock, 1920; Pocock, 1921; Carrano, 1997; Procyonidae: McClearn, 1992; Carrano, 1997; Ursidae: Carrano, 1997; Viverridae: Taylor, 1988; Pocock, 1915a; Pocock, 1915b; Carrano, 1997).

Statistical Analysis

A scatter plot of the raw data (Fig. 2a) confirms the expected power function relationship between humerus trochlear circumference and body mass. Transformation of both variables into $\log_{10}$ effectively straightens the scatter (Fig. 2b). Thus, body mass and humerus trochlea circumference

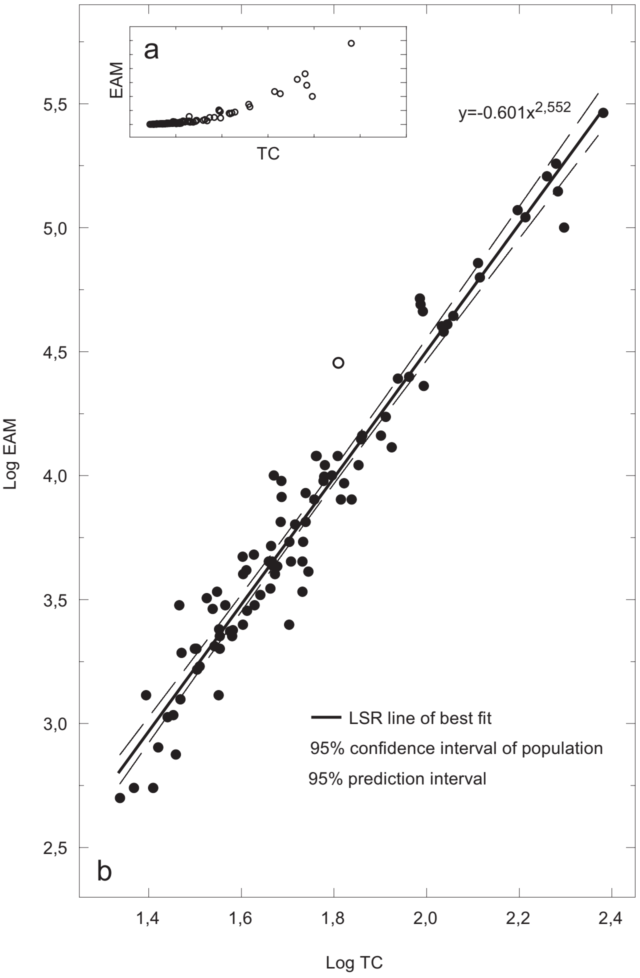

Figure 2. a. Scatterplot of untransformed estimated average body mass (EAM) in grams and trochlea circumference (TC) in centimetres. **b.** Scatterplot of $\log_{10}$-transformed estimated average body mass (EAM) and trochlea circumference (TC), with 95% confidence and prediction levels. Sea otter (*Enhydra lutris*) open circle.

is assumed to scale according to Huxley's (1932) model of simple allometry (Equation 2),

$$(2) \quad Y = aX^b \Leftrightarrow \log y = \log a + b \log x$$

where *a* is the y-axis intercept and *b* the slope.

Test for normality and outliers

Statistical evaluation of bivariate normality was carried out via the stabilized normality plot (SNP; Michael, 1983), wherein arcsine-transformed, normally distributed variables will form a 45° straight line. This test is analogous to the standard nonparametric Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1997). The distribution is graphically presented in a delta stabilized probability plot (Δ SNP; Fig. 3). In the Δ SNP variables are standardized $(y_{i-j} - x_{i-j})$, and a perfect normal error distribution will be horizontal (y=0).

Enhydra lutris (sea otter) was identified as an outlier, violating the 90% confidence limit, and was excluded from further analysis. No other terrestrial or aquatic carnivore is as closely bound to life in water as the sea otter. Feeding, resting, sleeping and even mating occur in water (Fisher, 1939). It is therefore not surprising that the humerus distal trochlea of *E. lutris* should scale differently from that of terrestrial carnivores.

After removal of *E. lutris* all data points fall within the 95% confidence limit for a normal distribution (Fig. 3). The distribution is positively skewed (Fig 4) as is expected under lognormal distribution (Aitchison and Brown, 1957).

Regression analysis

Body mass was regressed on trochlea circumference in a least squares regression. The choice of regression model has been subject to lively debate and no general consensus has been reached, for further discussion, see Smith (1994).

In reality, both body mass and trochlea circumference are independent variables, each with its own measurement errors and distributions that are beyond the control of the investigator. In other words, this is a clear type II situation (Bartlett, 1949). If the aim were to explore the functional relationship between these variables, a type-II regression model might prove to be the appropriate choice. However, because the aim is to produce a predictive model, in which body mass can be predicted from trochlea circumference, I accept the assumption of variable dependency, and thus body mass (dependent variable) is regressed on trochlea circumference (independent variable, without error). The sampling unit / predictor ratio is kept to a ratio greater than 10:1, to meet the general recommendation in multiple regression (e.g., Darlington, 1990). A set of 7 equations (equation 1) was generated, one for the total sample of Carnivora, one for each family represented by >10 species (Fig. 5) and one each for plantigrade and digitigrade taxa (Fig. 6). For each equation, the intercept (*a*), the slope (*b*), the standard error of the estimate (SEE) and the coefficient of determination (r^2) are presented (Table 2). The significance of the best lines of fit is determined by t-tests (Sokal and

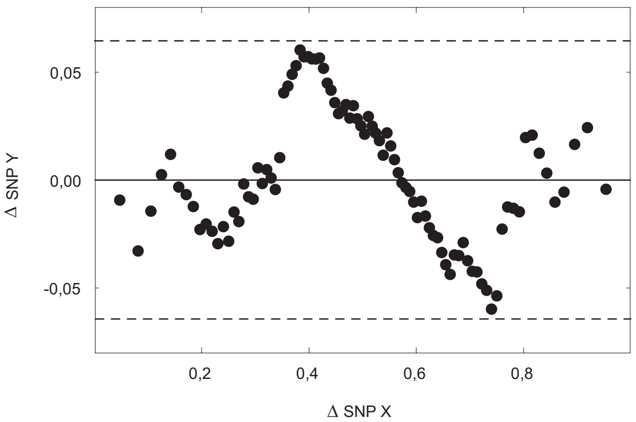

Figure 3. Delta Stabilized Normality Plot (Δ SNP) after removal of the outlier *Enhydra lutris*. The dotted line represents the 95% confidence limit, at ± 0,064241.

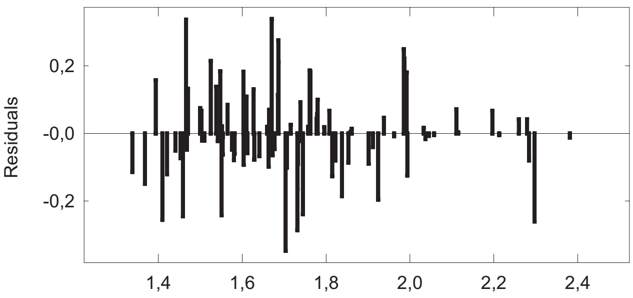

Figure 4. Residuals plot after removal of the outlier *Enhydra lutris*.

Rohlf, 1997), where significant deviation from zero of the slope is being tested. The t-values and p-values (two-tailed at df= n - 2) are presented in Table 2.

The strength of the independent variable (TC) as predictor of the dependent one (EAM) is indicated by the percent standard error of the estimate (%SEE) (equation 3), where *SEE* is the standard error of the estimate (Brody, 1945; Smith, 1984).

$$(3.)\ \%SEE = 10^{(2+SEE)} - 100$$

Subsample differences

Lines of best fit are subjected to pairwise comparison. Two null hypotheses are tested. $H_0(1)$: The difference between the lines of best fit for families is caused by random errors in the samples. If trochlea circumference is affected by habitual adaptations, some degree of differential scaling is expected. $H_0(2)$: The difference between lines of best fit for digitigrades and plantigrades is caused by random errors in the sample.

$$QMLE = \exp\frac{\ln 10 \times s^2}{2}$$

The slopes (b) of the regression lines are tested pairwise for differences, using the Student t-test. The t-statistics and p-values (at df=$n_1 + n_2$-2) are presented in Table 3.

Detransformation bias

A systematic bias is introduced during detransformation of predicted body mass values from log-space back into arithmetic-space. The slope, the y-intercept and the SEE may be affected but neither the r^2 nor t-values (Zar, 1967).

Since the bias is a constant proportion of the predicted value and can be corrected by multiplication with a correction factor. A commonly used correction factor is the Quasi Maximum Likelihood Estimator (QMLE; equation 4). The QMLE is calculated as the natural antilog of the error variance (s^2) divided by two (Sprugel, 1983). For calculations in $\log_{10}$-space a further adjustment of the error variance is needed (Sprugel, 1983). This adjustment is done by multiplying the error variance with the natural logarithm of 10 (ln10).

(4.)

The global population error is estimated from the sample error variance by introducing a maximum likelihood predictor to the QMLE equation thus producing a maximum likelihood estimator (MLE; equation 5).

$$(5.)\ MLE = \exp\frac{(N-(p-1)/N)\ln 10 \times s^2}{2}$$

Where (N-(p-1)/N) is the maximum likelihood predictor, N is the number of observations, p is the degrees of freedom (in bivariate regression df=2), and s^2 the residual mean variance. The QMLE and MLE for each of the regression equations are presented in table 2.

RESULTS

Inspection of the scatters in Fig. 2b suggest a linear relationship between the $\log_{10}$ of body mass and trochlea circumference. Data points are evenly distributed around the line of best fit for Carnivora (Fig 5a-h) and no systematic bias is present in the carnivore families. All of the generated lines of best fit are highly significant ($p<0,001$). The high correlation is seen in the high r^2 and relatively low SEE (table 2). However, some variation does occur. The r^2 ranges between 0.799-0.979 and the SEE between 0.064-0.202.

The regression line for the total sample of Carnivora has an r^2 of 0.952 and an SEE of 0.136, a rather high correlation, comparable to those presented by Van Valkenburgh (1990, r^2=0.690-0.920, SEE=0.185-0.377) and Anyonge (1993, r^2=0.880-0.960, SEE=0.028-0.214) for "total" carnivore best lines of fit.

Canids have the highest r^2 at 0.979, followed by felids at 0.953. Mustelids have the lowest r^2 at 0.799 and the highest SEE at 0.202. Regression lines of plantigrades and digitigrades have r^2 of 0.956 and 0.949 and SEE of 0.147 and 0.123, respectively.

The slopes of the regression lines all indicate strong positive allometry ($b > 1$) in the body mass and trochlea circumference relationship. Felids have the steepest slope at 2.670 ± 0.123 and viverrids the flattest at 2.247 ± 0.136. The line of best fit for the total sample of Carnivora has an intermediate slope of 2.552 ± 0.136, which is similar to that of plantigrades at 2.527 ± 0.471 and digitigrades at 2.560 ± 0.233.

The results of the pairwise comparison between the regression lines are presented in table 3. The first null hypothesis, $H_0(1)$ is rejected for the canid-viverrid regression ($p<0.001$). The canid family is characterized by medium- to large-sized species and viverrids by small- to medium-sized ones. This might suggest scaling differences between small and large carnivores. However, for the canid-mustelid comparison, the null hypothesis cannot be rejected and thus they are, statistically speaking, equal. Mustelids are also characteristically small- to medium-sized species and the null hypothesis is rejected for the mustelid-viverrid comparison, suggesting that there is no consistently different scaling in trochlea circumference between large

Table 2. Results of the least squares regression analysis (LSR). Equations of the best lines of fit; *a*, intercept; *b*, slope; SEE, standard error of estimate; r^2, coefficient of determination; t, Student-t value; p, p-value for slope significance; %SEE, percent standard error of estimate; n, sample size; MLE, $\log_{10}$ adjusted maximum likelihood estimate; QMLE, $\log_{10}$ adjusted quasi maximum likelihood estimate.

LSR best lines of fit of body mass on trochlea circumference

	Intercept (*a*)	Slope (*b*)	SEE	r^2	t	p	%SEE	n=	MLE	QMLE
Carnivora	-0.601	2.552	0.136	0.952	42.234	<0.0001	36.8	92	1.049	1.050
Canidae	-0.586	2.539	0.064	0.979	27.950	<0.0001	15.9	19	1.009	1.011
Felidae	-0.765	2.670	0.123	0.954	17.529	<0.0001	32.7	17	1.034	1.041
Mustelidae	-0.444	2.459	0.203	0.799	7.968	<0.0001	59.4	18	1.095	1.115
Viverridae	-0.087	2.247	0.136	0.844	8.044	<0.0001	36.7	14	1.039	1.050
Digitigrade	-0.590	2.560	0.123	0.949	29.559	<0.0001	32.8	49	1.039	1.041
Plantigrade	-0.586	2.527	0.147	0.956	27.721	<0.0001	40.3	43	1.055	1.059

and small carnivores. This is further supported by the largest carnivores, the ursids. Ursids are represented in the data set by too few species to allow a separate regression analysis to be carried out, but as can be seen in Fig. 5g they fall along the trajectory expected for carnivores. The first null hypothesis is rejected for all the remaining pairwise tests.

Comparisons between highly correlated lines of best fit with small SEE may result in rejection of the null hypothesis even for small differences in slopes. This effect, in combination with a low species count, may in part be the reason for the outcome of the pairwise comparisons of family-specific equations.

The second null hypothesis, $H_0(2)$ cannot be rejected and trochlea circumference scales equally in plantigrade and digitigrade carnivores. This suggests that the size of the distal humerus articulation and trochlea circumference are determined by the weight-bearing function, rather than by locomotor adaptations.

The systematic bias introduced during detransformation ranges from 1% to 12%, where the MLE is 0.2%-2% lower than the QMLE. The greatest difference between the QMLE and the MLE is found for mustelids. The lowest correction factor, 1.009, is that for the canids. The total Carnivora regression equation needs to be corrected by a factor of 1.049 (MLE)-1.050 (QMLE). Mustelids require the highest factor, 1.095-1.115. The plantigrade regression line needs to be corrected by 1.039-1.041 and the digitigrade one by 1.055-1.059.

Prediction of body mass in fossil taxa

Body mass was calculated for a number of extinct carnivores. Average body mass and 95% confidence range is calculated in logarithm-space using the total Carnivora equation, then detransformed into arithmetic-space. The detransformation bias was corrected by the maximum likelihood estimator (MLE = 1.049) and the result is presented in table 4.

The predicted average body mass of a single individual of *Hoplophoneus occidentalis* is slightly lower, and for *Hoplophoneus primaevus* and *Dinictis felina* slightly higher, that that reported by Van Valkenburgh (1990). In all cases the mass presented by her is well within the range predicted herein.

The body mass of *Hyaenodon horridus* is estimated to be 40.3 kg (average of five individuals). Van Valkenburgh (1990) reported body mass ranging from 31-131 kg. The mass presented herein is very close to that reported by Egi (2001) for this species.

The mass predicted for *Limnocyon versus* is slightly higher and that of *Machaeroides eothen* lower than that reported by Egi (2001).

Legendre and Roth, 1988 presented body mass estimations of *Adcrocuta eximia* with an average of 49 kg, which is considerably lower than the 73 kg (52.1-97.4) predicted herein.

DISCUSSION

Because of the nature of the fossil record craniodental measurements have been the logical entry for body mass predictions. Legendre and Roth (1988) presented a model based on the area of the lower first molar. Correlation between body mass and first lower molar length, skull length and occiput to orbit length is relatively poor for the Carnivora as a whole, but becomes stronger if families are analysed separately (Van Valkenburgh, 1990). A series of postcranial predictors were explored by Anyonge (1993). These predictors generally correlate better with body mass. Proximal and distal humerus and femur articulations, modelled as partial spheres, partial cylinders and partial cones, as predictors were explored by Egi (2001). She presented %SEE at an exceptionally low and homogeneous 8.1%-12.6%. No r^2, nor SEE was presented, and therefore I have been unable to reproduce these results.

The coefficient of determination, equal to the squared correlation coefficient, and the standard error the of estimate, are statistical indicators of the strength of the bivariate relationship. Given satisfactory regression statistics, the reliability of a predictive model is determined only by the strength of the underlying assumptions. Even a regression equation with perfectly correlated variables may be unsuitable as a predictive model, if the initial assumption of random representation of the global population is violated.

Small sample sizes may strongly affect the reliability of equations generated by regression analysis. The family-

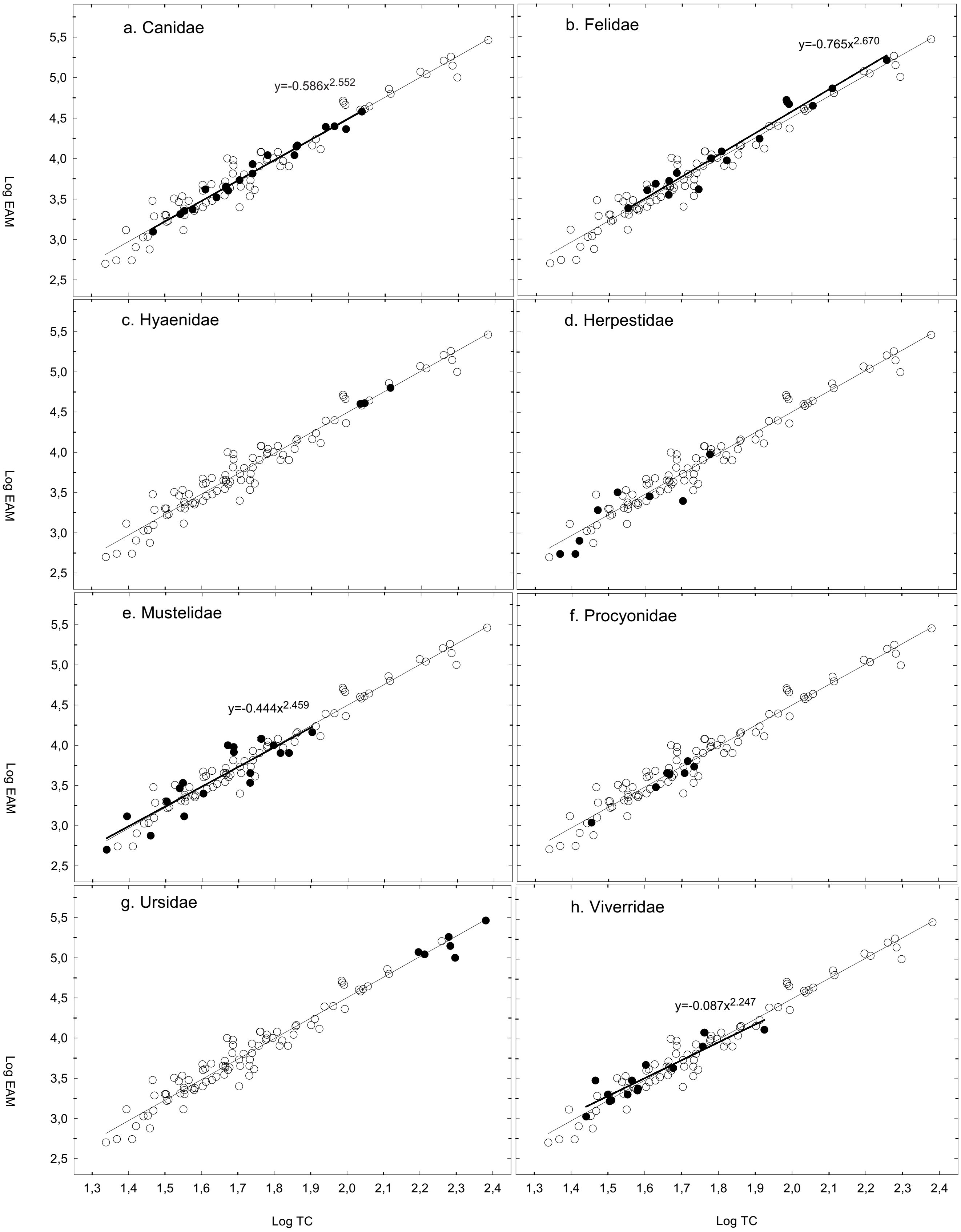

Figure 5. Scatterplot of $\log_{10}$-transformed estimated average body mass (EAM) and trochlea circumference (TC). Thin line; least squares regression line of best fit for total Carnivora. Thick line and filled circles; least squares regression line of best fit and data points for each family.

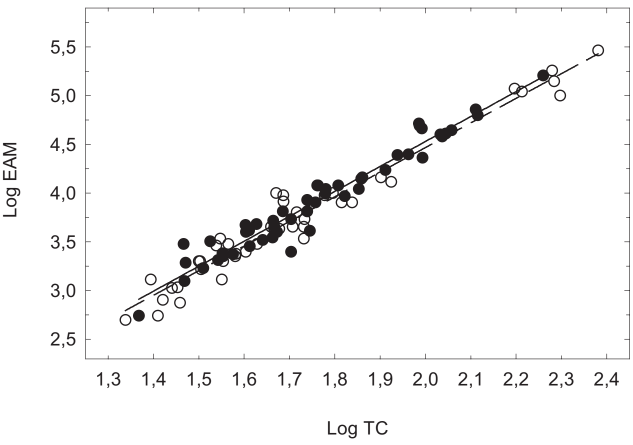

Figure 6. Scatterplot of $\log_{10}$-transformed estimated average body mass (EAM) and trochlea circumference (TC). Filled circles, digitigrades; open circles, plantigrades. Filled line, least squares regression line of best fit for digitigrades; broken line, least squares regression line of best fit for plantigrades.

specific equations presented herein are based on sample sizes ranging from 14–19 species, a near minimum required for a reliable regression analysis (e.g., Darlington, 1990).

By pooling all families into one equation for the order Carnivora, increased reliability is obtained, since the equation now is based on the information contributed by all 92 species. As discussed above, the average body mass of a species is very difficult to estimate, because of all the sources of natural variation that exist. By using a model based on 92 carnivore species, the effects of the body mass estimate of an individual species is reduced. Since no systematic bias is thought to exist, the sample variation may be regarded as representative of the variation in carnivores, and allows body mass and variance (at the 95% level) to be predicted.

An important factor in all body mass prediction is scaling, as clearly illustrated by Van Valkenburgh (1990). *Hyaenodon horridus* (Creodonta) is known from several complete skeletons (Scott and Jepsen, 1936) and has a skull and body that scale entirely differently from any living carnivore. Body mass predicted from cranial measurements is greatly overestimated, while the reverse seem to be true for body mass predicted from postcrania (Van Valkenburgh, 1990). Knowing the effects of scaling, as in the case of *H. horridus*, allows us to recognize and evaluate discrepancies in the results. However, for less well known taxa, one may be forced to actively choose which prediction model is to be trusted, a potentially *ad hoc* approach.

Scaling will inevitably affect the outcome of body mass predictions. Minor discrepancies in predicted mass due to naturally occurring variation are expected, but caution must be used in evaluating highly conflicting mass predictions. These may be evidence of uncontrolled effects of scaling, i.e., the scaling of the individual is different from that of the sample population, and thus the assumption of random representation of the global population is violated. It may also indicate that the variable is not directly dependent on body mass and may therefore be unsuitable as a body mass predictor.

In the absence of better solutions, conflicting outcomes are commonly resolved by calculation of the arithmetic mean of mass predictions (e.g. Van Valkenburgh, 1990; Anyonge, 1993; Egi, 2001). This approach might make intuitive sense, but is from a theoretical perspective only marginally better than guesswork.

Anyonge, (1993) presented 11 equations based on femora and humeri predictors. Femur-based mass predictions are on an average 24%, and as much as 60% higher than those predicted from the humerus, The sample on which the equations are based, is strongly biased towards cats (50% felids) with body mass ranging between 5-181 kg. The difference between the slopes of the total and felid regression lines is 0-9%, reflecting the cat bias. Non-felid like scaling in the animals that are being investigated may offer a partial explanation for the conflicting body masses reported.

Scaling by simple geometric similarity predicts mass (M) to scale to a linear dimension (l) by $l \quad M^{0.333}$, and to area (A) by $A \propto M^{0.667}$. Simple geometric similarity therefore predicts that skeletal safety factors cannot remain constant through a broad range of animals, since body mass increase exceeds that of linear dimensions. Limbs of large and small mammals seem to suffer the same stresses during locomotion (Alexander, 1977; Alexander, 1979), and long bones do withstand the peak forces exerted during normal activity without breaking.

Bending moment and peak forces in long bones during the support phase may be lowered by reducing longitudinal

Table 3. Result of the pairwise comparison between slopes of least squares regression lines of best fit (H_o: $b_i=b_j$). t-values (two-tailed). NS, not significant; * significance at 5.0% limit; **, significance at 1.0% limit; ***, significance at 0.1% limit.

Regression lines pairwise tested for difference

	Canidae	Felidae	Mustelidae	Viverridae	Digitigrade	Plantigrade
Canidae		***	NS	***		
Felidae	-4.0676		***	***		
Mustelidae	1.6583	3.7172		**		
Viverridae	8.1971	9.0760	3.3472			
Digitigrade						NS
Plantigrade					1.1703	

Table 4. Predicted body mass of extinct carnivores. Average and 95% confidence range. Average estimates taken from the literature. [1], Legendre and Roth, 1988; [2], Van Valkenburgh, 1990; [3],Anyonge, 1993; [4], Egi, 2001. [juv]., range including both juveniles and adults.

Predicted body mass of extinct carnivores

	Species	Average	Range	n=	Body mass from the literature
Nimravidae	*Hoplophoneus occidentalis*	60.0	(43.9 - 82.1)	1	66-69[2]
	Hoplophoneus primaevus	19.1	(14.0 - 26.1)	1	13-19[2]
	Dinictis felina	24.0	(17.5 - 32.8)	1	17-20[2]
Creodonta	*Hyaenodon horridus*	40.3	(29.5 - 55.1)	5	31-131[2]; 38.22[4]; 24.9-43.3 [4, juv]
	Limnocyon versus	8.2	(6.0 - 11.2)	1	6.87[4]; 5.1-8.4 [4, juv]
	Macheiroides eothen	8.3	(6.1 - 11.4)	1	11.54[4]; 7.6-13.9 [4, juv]
Hyaenidae	*Adcrocuta eximia*	71.2	(52.1 - 97.4)	1	49[1]
Felidae	*Homotherium serum*	142.9	(104.5 - 195.5)	1	146-220[3]

curvature and by reorienting the bone so that loading forces are directed along the longitudinal axis, thus resulting in compression rather than in bending forces (Biewener, 1983). These mechanisms may allow scaling according to geometric similarity while, at the same time, safety factors remain constant in small and large mammals (Biewener, 1983).

McMahon (1973) proposed an alternative scaling model, in which bones scale so as to retain elastic similarity and thus withstanding elastic buckling and bending forces, and thus skeletal safety factors remain similar in small and large animals. Under elastic similarity, linear dimensions increases in proportion to the diameter which predicts a mass to linear dimension scaling of $l \quad M^{0.25}$ and a mass to diameter (D) scaling of $D \propto M^{0.375}$.

$\propto$

Scaling in antelope (Bovidae) limbs is largely as predicted by elastic similarity (Alexander, 1977). The lengths of the humerus and femur scale as as $l \propto M^{0.262\text{-}0.263}$ and the humerus midshaft diameter as $l \propto M^{0.381}$ (Alexander, 1977, see also Alexander et al., 1979). However, femoral midshaft diameter scales according to the prediction of geometric similarity ($l \propto M^{0.330}$ Alexander, 1977).

Long bone length of a broad range of mammals, from shrews to elephants (except bovids), scales as $l \propto M^{0.360\text{-}0.390}$ and that of terrestrial carnivores as $l \propto M^{0.37\text{-}0.39}$ (n=8; Alexander et al., 1979), which is in accordance with geometric similarity scaling (Alexander et al., 1979). The surface area of the humerus and femur heads in carnivores scale to body mass according to the model of geometric similarity ($A \propto M^{0.634\text{-}0.642}$ Godfrey et al., 1991).

This suggests that scaling of these parts of the long bone is not directly dependent on body mass and that compensating mechanisms are in effect (e.g., those proposed by Biewener, 1983). Carnivore limb structure, and posture need to be further explored to determine under which circumstances humerus and femur length, midshaft circumference and midshaft cross-sectional area are reliable body mass predictors.

The humerus trochlea circumference scales according to the prediction of under elastic similarity (Andersson, in prep.), thus suggesting a direct body mass dependency. The circumference is highly correlated with body mass, and scaling appears to be uniform throughout the order Carnivora, regardless of foot posture (H_o(2): not rejected). Some degree of differential scaling between large and small carnivores cannot be ruled out, but this is inconclusive, since canids and mustelids scale equally (H_o(1) Canids-Mustelids; rejected).

The statistical properties of the regression line for the total sample of Carnivora are good for a regression analysis (p<0001, r^2=0.952, SEE=0.136). By using this model, a minimum number of assumptions need to be made and it allows average body mass estimates to be predicted, along with a confidence interval that is a good representation of the existing interspecific variation. There are no reasons to believe that humerus trochlea circumference cannot, after necessary adjustments, successfully be used as a body mass predictor, not only for carnivores, but also for a broad range of quadrupedal mammals.

Prediction of body mass in fossil taxa

The QMLE has a tendency to overcorrect the detransformation bias when sample variance is high and when residuals are not normally distributed (see Smith, 1993 and references therein). By using the MLE the effect of the systematic overcorrection is reduced. For the mustelid equation, the family specific equations with highest variance (SEE 0.203) and the highest detransformation bias, the MLE is 2% lower than the QMLE. For the total Carnivora equation the detransformation bias is about 5% and the MLE is only 0.1% lower than the QMLE.

The mass predictions are generally consistent with earlier published estimations. All deviations from earlier estimated body masses are well within the confines of natural variation, except that for *Adcrocuta eximia*. The model presented by Legendre and Roth (1988) is based on the area of the first lower molar, as calculated by the smallest rectangle surrounding the crown, and systematically overestimates body mass for felids and ursids and underestimates that of hyaenids and canids (Legendre and Roth, 1988, fig. 1, p. 88). The body mass for *Adcrocuta eximia* presented herein greatly exceeds that presented by Legendre and Roth (1988), which is consistent with the bias suggested for their method.

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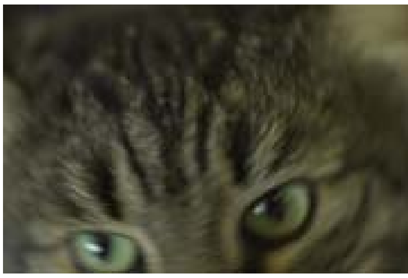

Paper II

Elbow joint morphology as a guide to locomotor behaviour in the order Carnivora, with examples from Miocene Mustelidae

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Among the hunting strategies employed by members of the order Carnivora, two, stalk and ambush and sustained pursuit, are particularly prevalent among larger species of the order. It has, however, been difficult to identify morphological traits that support this distinction, and ecological observations have shown that Carnivora adopt a continuum of strategies, depending on available habitat and prey. In this paper, the shape of the distal humerus articulation is analysed, with the aim of exploring the use of the forearm in prey procurement, and as a guide to such behaviour among extinct Carnivora. The elbow joint complex is designed to transfer loads between the upper and lower segment of the forelimb, to provide stability and at the same time allow mobility. The results suggest that manual manipulation and locomotion are conflicting functions, and that there is a trade-off between the two. Elbow joint morphology thus supports the division between ambushers (i. e., grapplers) and pursuers (i. e., locomotors). Joints of the latter are characterized by being relatively narrow and box-like, having pronounced stabilizing features, such as a medial flange that projects mediodistally and a relatively deep mid-trochlea furrow. At large body sizes, carnivores show a strongly dichotomised pattern, suggesting mutually exclusive feeding strategies that involve either grappling of prey or pursuit. The former allows for large body sizes, e. g., pantherine felids and ursids, but the latter includes species of only moderate size, e. g., hyenids and canids. Elbow joint morphology is closely linked to phylogeny, but the morphology of the cheetah converges with that of locomotors, showing that strong selective forces may override the phylogenetic component.

Two taxa of giant mustelids from the Miocene were analysed. The African late Miocene species *Ekorus ekakeran* has a joint morphology comparable to that of modern-day locomotors. Two joint morphologies were found in the North American late Oligocene-early Miocene *Megalictis ferox*, indicating that this taxon may be in need of revision. The first morphology is comparable to that of modern pantherine cats and the second forms an intermediate between locomotors and grapplers that is not present in the recent carnivoran fauna.

ADDITIONAL KEY WORDS: Ambush predation, pursuit predation, cursoriality, morphometrics, Multivariate statistics, Principal component analysis.

INTRODUCTION

Assessing locomotor habits of terrestrial carnivores and studying their evolution, traditionally involves measurement of limb lengths (Van Valkenburgh 1987, Bakker 1983, Janis & Wilhelm 1993). Van Valkenburgh (1987) showed a correspondence between a series of morphological indices and a set of predetermined locomotor categories, chosen to emphasize foraging and escape behaviours, e. g., arboreal, fossorial, semi-fossorial and terrestrial. Arboreal and scansorial carnivores tend to have strongly curved claws, shorter metatarsals and a lower Metatarsal/Femur (MT/F) ratio than do their non-climbing relatives. The latter ratio is widely used as a measure of locomotor performance and cursoriality in mammals (e. g., Gregory 1912, Maynard Smith & Savage 1956, Bakker 1983, Janis & Wilhelm 1993). A detailed analysis of this "cursoriality index" shows, that it does not correlate with maximum running speed when only fully cursorial ungulates and carnivores are considered (Garland & Janis 1993). At equal sizes, ungulates generally tend to be more "cursorial" than carnivores, yet they do not achieve significantly higher running speeds (Garland & Janis 1993). The total length of the hind limbs, however, correlates significantly with maximum running speed over a wide range of mammals, indicating a discrepancy in the scaling of limb length and its proportions.

Scaling of limbs has attracted great interest among researchers, especially in the search for models that allows predictions of scaling. Simple geometric similarity predicts that mass (M) should scale with a factor three to linear (l) dimensions ($l \propto M^{0.333}$). Despite the problem that body mass increases at a relatively greater rate than other dimensions, many mammals appear to scale according to this model (Alexander et al. 1979). McMahon (1973) formulated an alternative model, by which scaling works so as to withstand elastic buckling during loading ($l \quad M^{0.25}$). Scaling according to the model of elastic similarity has been confirmed for bovids (McMahon 1975, Alexander 1977). Rubin & Lanyon (1984) proposed that safety factors are kept constant, not by allometric scaling of the bones but rather by allometric scaling of the forces applied to them.

This failure to explain mammalian design with a single allometric model indicates that size-differential scaling (e. g., Iriarte-Díaz 2002) or other causative factors may be present. One such factor was identified by Biewener (1989), who suggested that mammals maintain similar peak stress in bone and muscles by changing limb posture during locomotion, from a crouched to an upright posture, as size increases.

Apropriate use of allometric models to predict behaviours and habits of extinct animals assumes that the allometric model fully compensates for any deviations caused by differential scaling.

Here an alternative approach is taken. I will test if the function of the forelimbs can be traced through the morphology of the elbow joint, and whether this can be quantified and used together with body size as an indicator of feeding strategies among carnivores. By analyzing the shape of the humerus part of the elbow through landmark based multivariate morphometrics, no direct assumptions are made about regression-based allometry and scaling, although body mass is estimated from a predictive regression (LSR) model. Using a single articulation rather than articulated specimens has great potential because of the nature of the fossil record. The elbow joint complex has further proved to be indicative of feeding strategy and locomotor strategies in primates (Rose 1988).

The mammalian elbow joint complex is designed to transfer loads between the upper and lower arm segments and to provide stability, while at the same time allowing for mobility (Jenkins 1973, Evans 1993). At the elbow, the humerus articulates with the radius and ulna. Flexion-extension of the elbow involves movement in the humeroulnar and humeroradial articulations and the joint can functionally be regarded as a compound joint with a uniaxial hinge-like movement. Pronation-supination of the hand is primarily achieved through movement in the wrist. However, movement in the elbow complex may increase the range of pronation-supination that is possible. Forearm rotation involves movement in the proximal radioulnar articulation, whereby the radius is rotated around its long axis (Evans 1993).

While at the same time allowing for movement during activity, the joint has to withstand internal and external forces without dislocation. Elbow joint stability and integrity is maintained through a series of ligaments and bony features. In mammals that use their forelimbs primarily for locomotion, movement in the elbow is hinge-like and movement parasagittal. This articular configuration is found among recent ungulates (Sisson & Grossman 1938) and similar function and morphology is expected among cursorially adapted carnivorans. If present, it may provide a useful tool to identify cursoriality among Carnivora.

Large canids and hyaenids are generally regarded as more cursorially adapted than other carnivores (Maynard Smith & Savage 1956, Hildebrand 1954, Ewer 1973, Spoor & Badoux 1986). Prey is run down, grabbed by the mouth and rarely stalked (Kruuk 1972, Mills 1990). Many of the fastest carnivores today are found among this group. Endurance is, however, often equally as important as maximum speed. The spotted hyaena (*Crocuta crocuta*) attacks large prey and may engage in a sustained pursuit, commonly for 1-3km. A group of 20 Eland antelopes where observed being chased for 24km (Mills 1990). Canids normally respond to threats by running or hiding in burrows, although the grey fox (*Urocyon cinereoargenteus*) has been observed to climb trees (Terres 1939).

Cursoriality was originally defined for ungulates adapted to sustained running in open spaces, and cursorial animals represent the fast-running end-members in a four stage classification scheme for ungulates (Gregory 1912). Other definitions have followed: A cursor is any animals "that travel far and fast on ground" (Hildebrand 1988, p. 473). Others have defined cursoriality using morphological traits, including muscle mechanics and limb proportions (Maynard Smith & Savage 1956) or by stance and limb excursion pattern during locomotion (Jenkins 1971). A biomechanical concept of cursoriality emerged though the work of Alexander & Jayes (1983). They proposed a dynamic similarity model for mammalian gaits, that enabled prediction of the relations between size, speed, stride length and duty factor. According to this model, most mammals greater than five kg are cursorial (*sensu* Jenkins 1971). At present there is no widely accepted consensus regarding how to define cursoriality in mammals (Stein & Casinos 1997).

MATERIAL AND METHODS

Material

Representatives of nearly all extant carnivoran families were included in the analysis, with the exception of the Herpestidae and the aquatic pinnipeds (families Otariidae, Odobenidae and Phocidae). The former group was excluded because at present its phylogeny is poorly known (e. g., Taylor 1988; Taylor et al. 1991) and the latter because their forelimbs are used in a way that is non-comparable to their terrestrial relatives. However, semi-aquatic carnivores, including the otters (Lutrinae, Mustelidae) are included. A total of 188 individuals distributed over 87 species, with 1-6 individuals per species, are analysed, representing almost the entire size range found within the order today (Fig. 1). Species with multiple individuals in the data setwere averaged before analysis. See appendix for a list of species and the number of individuals included.

The taxonomy for the recent Carnivora follows that of Wilson & Reeder (1993), with a few exceptions. The kit fox (*Vulpes macrotis*) is here treated as a separate species.The

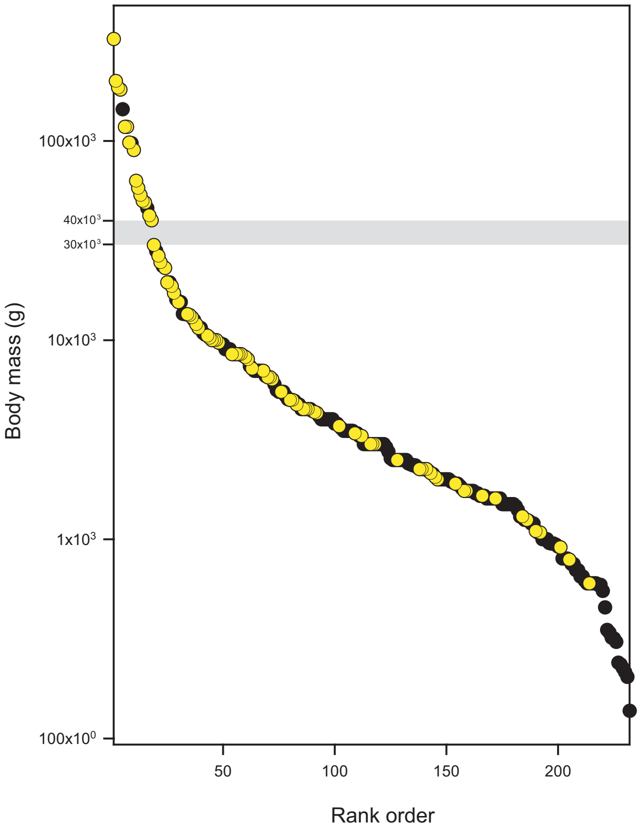


Figure 1. Cenogram showing the distribution of recent carnivores over body mass. A total of 238 species are recognized within the order Carnivora (Wilson & Reeder 1993). There is a marked absence of carnivores at the 30 to 40kg interval (area shaded grey). Yellow circles represent species included in this study, for species list see Appendix. Species are ranked by size and rank is plotted against average species body mass taken from the literature (Harris 1968, Banfield 1974, Lekagul & McNeely 1977, Kingdon 1977, Heptner et al. 1998, Heptner & Sludskii 1992, Nowak 1999 and Macdonald 2001 unless otherwise is stated). For the following species, average species body mass was estimated from the first lower molar using equations given by Van Valkenburgh 1990, *Ducisyon australis* (n=1), *Mustela africana* (n=1), *Mustela felipei* (n=1), and *Diplogale hosei* (n=2).

systematic position of the fossa (*Cryptoprocta ferox*) is debated. DNA/DNA-hybridisation suggests affinities with the herpestids (Veron & Catzeflis 1993), while morphological traits suggests it to be closer related to Felidae than any aeluroid carnivore (Veron 1995). The fossa is excluded from this study because of its uncertain phylogenetic position.

Recent molecular phylogenetic analyses suggest that the family Mustelidae is paraphyletic (e. g., Dragoo & Honeycutt 1997). Evidence from mitochondrial-DNA (cytochrome *b*), ribosomal-DNA (12S, 16S) and morphological characters indicates that skunks (*Conepatus, Mephitis, Spilogale, Myadus*) form a monophyletic clade, which in turn is the sister-group to a monophyletic Procyonidae + reduced Mustelidae (encompassing weasels, badgers and otters) (Dragoo & Honeycutt 1997).

Controversies about the phylogenetic position of the lesser panda (*Ailurus fulgens*) involve its sister-group status to either ursids, procyonids or mustelids. Analysis of mithochondrial-DNA and one nuclear intron suggested a close relationship with musteloid carnivores (Flynn et al. 2000). Despite ongoing controversies, the lesser panda is included in this study.

Data on the elbow joint was collected from museum collections at the Field Museum of Natural History (FMNH), Chicago, USA; Zoological Museum (ZMUC), University of Copenhagen, Denmark and Swedish Museum of Natural History (NRM), Stockholm. Information on locomotor strategies, ecology and evolution was taken from the literature.

Shape analysis

The shape of the distal articulation surface of the humerus was captured and analysed using landmark-based morphometric methods. Shape variables were created from six, two-dimensional coordinate landmarks, digitised from high-resolution digital photographs using the TPSdig32 software written by F. J. Rohlf, (http://life.bio.sunysb.edu/morph/index.html). Efforts were made to ensure a consistent orientation, where the axis around which the ulna rotates on humerus was parallel to the film plane. A set of 11 Euclidean distances (Fig. 2), forming a truss network with minimum redundancy, was calculated (Strauss & Bookstein 1982). The untransformed data matrix containing the 11 unweighted Euclidean distances were analysed by principal components analysis of the variance-covariance matrix. The 11 variables were thereby transformed into a set of principal components. The loadings for the first three principal components are presented in Figure 2 and scores for each species are graphically presented in Figures 3 and 4 (see also appendix).

Body mass

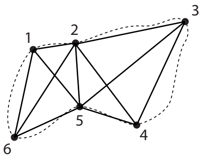
Body mass was estimated using trochlea circumference and the equation given in Andersson (MS). Several predictive equations for estimation of carnivore body mass are available (e. g., Van Valkenburgh 1990, Anyonge 1993). Body mass for each extant carnivoran species is calculated as the average of the included individuals. Calculated average body mass was chosen over average species body mass from the literature. The average body mass is thus expected to differ slightly from that given in the literature.

RESULTS

The cumulative explanatory power of the first three principal components is 99,3% of the total sample variance.

The first principal component accounts for 97.0% of the variance (Fig. 2). Components loadings are positive, but not all variables contribute equally to the vector, as indicated by the range of the component loadings, between 4.356 and

Figure 2. Component loadings for PC1 to PC3 of the principal components analysis of recent carnivores.



Distance	PC1	PC2	PC3
2 - 6	9.265	0.210	-0.699
2 - 5	4.356	1.359	0.185
3 - 5	11.151	-0.647	0.771
1 - 5	7.118	1.087	0.101
2 - 4	7.632	0.451	-0.255
5 - 6	6.733	-1.274	-0.936
4 - 5	5.331	-1.247	-0.548
3 - 4	8.495	0.431	0.854
2 - 3	9.377	-1.117	0.580
1 - 2	4.596	-0.887	0.040
1 - 6	8.123	1.760	-0.659
Variance explained	659.036	12.189	3.871
% of total variance explained	96.961	1.793	0.570

11.151. Distances 3-5 and 2-3 of the capitulum contribute most to the component, closely followed by 2-6 of the trochlea, while distance 2-5 contributes the least. The first principal component (PC1) generally reflects overall size, but here it also includes allometric information. This allometry is clearly seen when PC$_1$ is plotted against body mass (Fig. 3). The best line of fit is a 3rd order power equation ($PC1 \propto M^{0.31}$, r^2=0,991, SEE=2,4196, P<0.001).

The second principal component (PC2) accounts for 1.8% of the total variance. Distances 1-6, 2-5 and 5-6 of the trochlea contribute most to this component, followed by 4-5 and 2-3 of the capitulum (Fig. 2).

The morphological changes indicated by an increase in scores on the second principal component can be summarized as follows. The distal humeral articulation becomes mediolaterally narrower, with a more box-like outline. Medially, the trochlear part becomes narrow and the relative depth of the mid-trochlea furrow increases. The relative displacement of landmarks, when moving from low towards high scores on PC2 is illustrated graphically in Figure 4.

All carnivores traditionally regarded as non-grappling cursors are found among those scoring high on PC2: the grey wolf (*Canis lupus*), African hunting dog (*Lyacon pictus*), maned wolf (*Chrysocyon brachyurus*), spotted hyaena (*Crocuta crocuta*), striped hyaena (*Hyaena hyaena*) and brown hyaena (*hyaena brunea*) (Fig 5).

Scoring intermediate or low on PC2 are carnivores that use their forelimbs to subdue, manipulate or excavate food items. Among these are, ursids. mustelids, procyonids and felids. Small canids are characterized by intermediate scores.

The fast running cheetah (*Acinonyx jubatus*) has an elbow joint morphology comparable to that of other cursorial carnivorans, and scores nearly as high as the striped- and spotted hyaenas. Three families that do not form a monophyletic group are represented among the species with high-scores on PC2, which indicates the presence of a functional signal and iterative processes.

The third component accounts for 0.6% of the variance. Distance 5-6 of the trochlea, and 3-4 and 3-5 of the capitulum contribute the most in explaining this component (Fig. 2). Felids generally score lower than the other carnivore families. This is true also of the cheetah, which in PC2 is distinctly separated from the other felids (Fig. 5b).

The score of the second principal component is mapped onto a composite phylogeny of Carnivora in Figure 6. Visual examination clearly shows that the distribution of PC2-scores largely follows the phylogeny and that switching between grappling and locomotion is rare, although it has occurred in the cheetah.

All canids score relatively high on PC2, higher than other carnivores of the same body mass. The rarity of transitions and the high scoring Canidae indicate the presence of a strong phylogenetic signal. Attempts to test for phylogenetic indepencence (e. g., Felsenstein 1985) between the shape variable PC2 and forearm utility (grapplers and locomotors, see Fig. 10), yields three contrasts only, one for the cheetah, one for the hyaenas and one for the canids. The limited number of transitions does not make calculation of contrast statistics meaningful.

Measurement of the morphological variability of the elbow joint complex through PC2 is ultimately measurement of functional and behavioural disparity. The disparity pattern at the family level is illustrated by box-plots in Figure 7. For the canids, variation in elbow morphology is higher than in any of the other clades tested and is skewed to the right. It is the presence of highly evolved locomotors that results in the high variance. Among the felids, the cheetah falls far to the positive side and disregarding this extreme outlier, the relatively long box, combined with short whiskers, indicates a highly uniform elbow morphology, despite the great size range represented by the felids The median is lower than that of any canid and the family is characterized by being skewed to the right.

Morphological variability among the viverrids is relatively high. The box is short and whiskers long compared

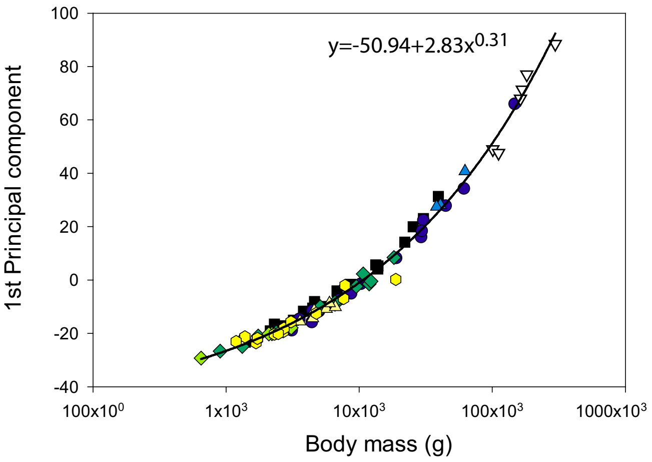


Figure 3. First principal component (PC1) plotted against body mass (g). X-axis log transformed. Best line of fit (LRS, r^2=0,991, SEE=2,4196, P<0.001).

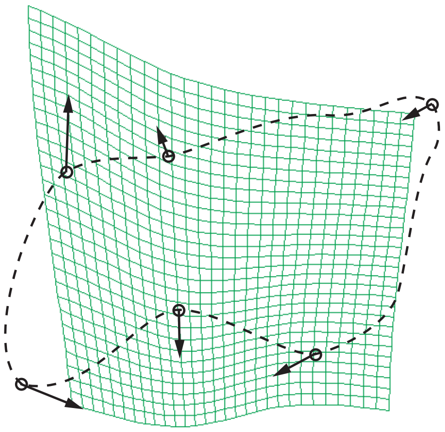


Figure 4. Thin-plate spline comparison of wolverine (*Gulo gulo*) against grey wolf (*Canis lupus*). Graphically illustrating the difference in shape of the distal humerus articulation between carnivores scoring high (*C. lupus*) and low (*G. gulo*) on the second principal component (PC2). The broken line, hand fitted, indicates the outline of the articulation of *C lupus*. The thin-plate spline is calculated from the consensus configurations of the two species (*G. gulo,* reference species, n=6; *C. lupus,* n=5; Bookstein 1991), generated through generalized least squares (GLS) orthogonal procrustes analysis (Rohlf & Slice 1990).

to that of the felids. The distribution is slightly skewed to the left.

Small carnivorans (<10 kg) are morphologically relatively uniform, as indicated by overall low and uniform scores on PC2 (Figs. 8, 9). At intermediate sizes (10-80 kg), morphological disparity tends to increase with size. At the onset of the increase, the relatively high-scoring jackals (*Canis mesomelas*, *C. adustus* and *C. aureus*) are found alongside the low-scoring binturong (*Arctictis binturong*) and mustelids, including the American badger (*Taxidea taxus*), sea otter (*Enhydra lutris*) and wolverine (*G. gulo*).

The trend is interrupted by a marked drop in variation at the 30-40 kg interval. At large body sizes (>80 kg), variance decreases with increasing body size in a stepwise fashion and the largest carnivores (ursids) are characterized by uniform elbow morphology (Fig. 7). At body sizes of approximately 20 kg and above, species distribution is strongly dichotomised, with a gap separating those scoring high from those scoring low (Fig. 10).

DISCUSSION

The structural changes captured by the shape analysis of the distal humerus articulation, reflect a functional shift in load bearing, joint stability and forearm supination that is connected with differences in forearm use. To some extent, manual manipulation and locomotion appear to be mutually exclusive functions, and thus, the structural complex is indicative of feeding strategies.

The high percentage explained by the first principal component is not unexpected, since the ranges in body mass of the carnivores analysed is between approximately 0.5 and 300 kg. The first principal component indicates that the humeroradial part of the joint scales with a relatively higher positive allometry than the humeroulnar part. This indicates differential scaling between the humerus and radius in carnivores. As body size increases, so does the effect of gravity and consequently the need for weight support. Increased weight support might offer an explanation for the relative increase in the lateral portion of the joint, as seen in PC1. It is suggested that, as size increases, the relative weight-bearing role of the joint is shifted towards the lateral portion. Functional and structural analysis of the lower portion of the forearm generally focuses on either the ulna or the radius (e. g., Jenkins 1973, Rubin & Lanyon 1982, Biewener 1983). However, to what extent the scaling of bone

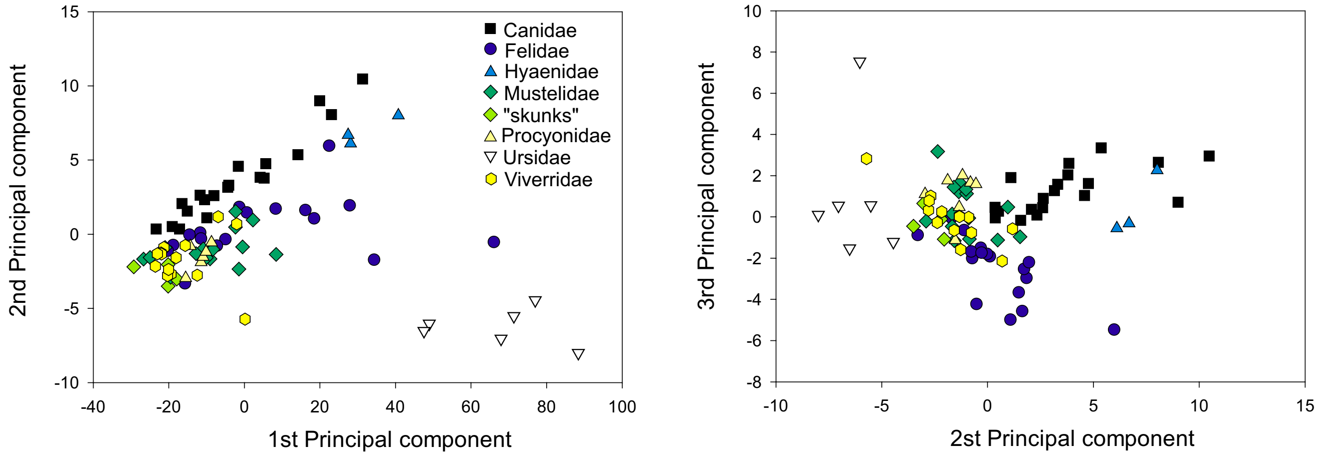


Figure 5. Results of the principal component analysis of recent carnivores. PC1 plotted against PC2 (a), PC2 against PC3 (b). For species scores see appendix.

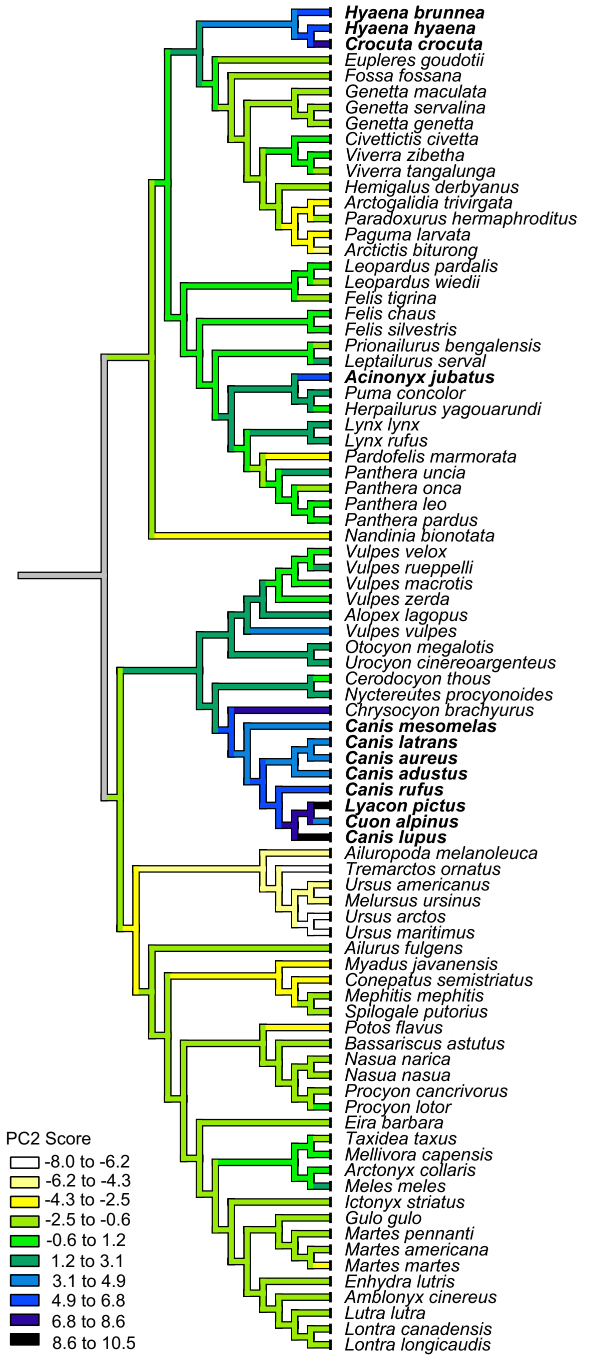


Figure 6. Second principal component mapped onto a composite phylogeny for the Carnivora. Carnivores traditionally regarded as primarily using their forelimbs for locomotion (non-grappling, locomotors) are written in bold typefaces. PC2 largely follows the phylogeny. Transitions are rare, but have occurred, e.g., the cheetah (*Acinonyx jubatus*). Ancestral stages are reconstructed by minimizing the sum of squared changes. The value for the root is not reconstructed. The topology is constructed using the following sources: Decker & Wozencroft 1991; Bryant et al. 1993; Tedford et al. 1995; Veron 1995; Masuda et al. 1996; Talbot & Shields 1996; Dragoo & Honeycutt 1997; Wayne et al. 1997; Flynn & Nedbal 1998; Seymour 1999; Flynn et al. 2000; Veron & Heard 2000; Gaubert et al. 2002; Wang, pers. com.

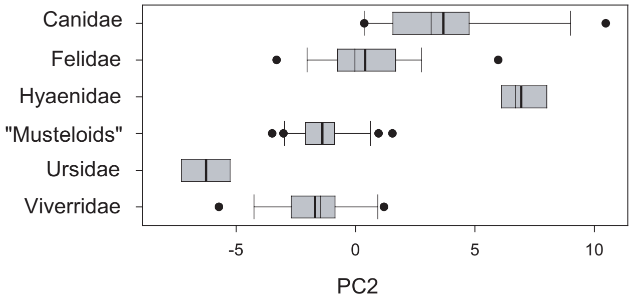


Figure 7. Box-plots of PC2 for recent carnivores. The largest dispersion is found among the canids, followed by felids and viverrids. The former two are right skewed and the latter left. The cheetah (Felidae) forms an extreme upper outlier. “Musteloids” comprise a monophyletic clade including mustelids (weasels, badgers and otters), skunks, lesser panda (*Ailurus fulgens*) and procyonids. Box-plots include information on location, dispersion, skewness and tail-shape (McGill et al. 1978**,** Benjamin 1988). Box lengths represent the interquartile range, which comprise 50% of the observations. Boxes are divided by medians (thin lines) and means (thick lines). Whiskers connect boxes to the extremal most points within 1.5 interquartile ranges. Points outside these ranges are plotted individually. Dispersion of observation is indicated by box height and skewness by box and whisker asymmetry.

and limb mechanics is affected by the proposed functional shift is unclear.

The second principal component is the main shape variable. The hinge-like movement of the elbow joint during flexion and extension is assured by the shape of the humeroulnar articulation. The ulnar notch of the ulna articulates with the trochlea furrow of the humerus and ensures a uniaxial rotation around the humeral articulation. Additional lateral stability is achieved by the size and projection of the medial trochlear flange. The importance of the humeroulnar part of the elbow is indicated by the fact that two out of three of the variables most influential for PC2 relate to this part of the joint. Carnivores scoring low on PC2, i. e., grapplers, have relatively shallow trochlear furrows and relatively large and distally projecting medial trochlear flanges. These features provide extra stability against forces acting in a non-parasagittal plane, and are especially prominent among large felids.

As expected, the elbow morphology of carnivores whose forelimbs are used primarily for locomotion is hinge-like and optimised for parasagittal movements. The joints are snugly fitted and the humeroulnar part is relatively narrow. The medial trochlear flange is of moderate size and the mid-trochlea furrow relatively deep. This articular configuration bears clear resemblances to that found among recent ungulates (Sisson & Grossman 1938).

Small carnivorans generally have a high degree of forearm supination, as they use their forelimbs for various activities ranging from digging and swimming to climbing. The binturong (*A. binturong*) scores considerably lower than others species of equal size. This species is, however, known

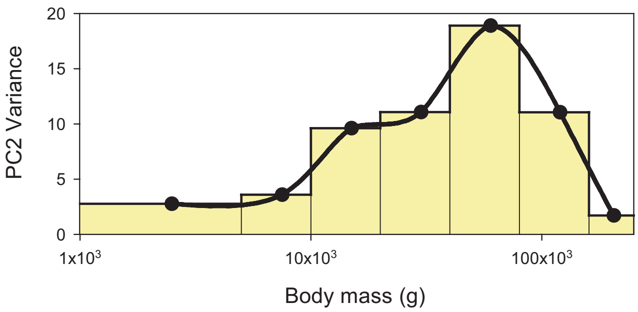


Figure 8. Species arranged in seven bins according to size and plotted against the variance of PC2 for each bin. Geometric midpoints are connected by a spline curve. Small carnivores are characterized by low variability. The variability increases with size at intermediate body sizes. This increase is truncated. At large sizes variability decreases. Size-bin intervals (kg): 1>1st<5 (n=38); 5>2nd<10 (n=17); 10>3rd<20 (n=11); 20>4th<40 (n=8); 40>5th<80 (n=4); 80>6th<160 (n=3); 160>7th<240 (n=3). Carnivores >240 kg are not plotted, since only one species represented in the sample falls within this range.

to be fully arboreal and to move ”slowly and deliberately” (Lekagul & McNeely 1977).

The elbow joint of the long-legged maned wolf (*C. brachyurus*) is directly comparable to that of other highly cursorial pursuit predators like the African hunting dog (*L. pictus*) and the spotted hyaena (*C. crocuta*). This is also true for other aspects of its skeletal anatomy (Hildebrand, 1954). Yet the maned wolf is not known to prey substantially on large vertebrates (Aragona & Setz 2001), although it has been observed to pursue such prey (Bestelmeyer & Westbrook 1998). Its diet consists mainly of plants, invertebrates, reptiles and small mammals caught by digging or by adopting a pounce-pin technique (Kleiman 1972). The evolution of the long legs of the maned wolf has been suggested as an adaptive response to “overlook tall grass” (Hildebrand 1954). An alternative explanation that cannot be ruled out is that it evolved for a pursuit-predatory lifestyle, which it now has abandoned.

Large cats ambush their prey by an initial stalking phase, followed by a fast but relatively short dash at maximum speed. When captured, prey is often subdued using the forepaws (e.g., Kitchener 1991). This technique is taken to its extreme in the cheetah (*A. jubatus*), which has been clocked at speeds approaching 100 km/h (Hildebrand 1959). The cheetah scores considerably higher than that of any other felid analysed on PC2. This species is one of the rare exceptions, where extreme selective pressures, i. e., for maximum running speed, have overridden the phylogenetic pattern.

The rarity of transitions between grapplers and locomotors observed among recent carnivores suggests, either phylogenetic niche conservatism, constrained by forearm utility, or selective extinctions in the past. Conservatism appears to be particularly strong in canids, which are less supinatory than other carnivores at equivalent sizes. The ecological significance of grappling and locomotor abilities is unclear. It is, however, expected that increased locomotor capabilities are likely to influence parameters such as, e. g., foraging behaviour and home range size.

From ecological observations it has become clear that carnivores often use a range of hunting strategies and foraging behaviours, depending on habitat and prey. However, at a general level the prey size selected for is related to the size of the predator. For recent carnivores, Carbone et al. (1999) suggested that a major dietary shift occurs around 21.5-25 kg. Below this threshold, the mass of individual food items is less than half the size of the predator and the diet is often omnivorous. Prey is generally excavated or pounced on and subsequently pinned down or chased for some distance (Ewer 1973).

Above the threshold the diet is generally comprised of prey near or above the body mass of the predator and is strongly shifted towards vertebrates. This generalisation holds true for most carnivores, with a few exceptions, including the insectivorous sloth bear (*Ursus ursinus*) and the hypercarnivorous weasels (Mustelidae), indicating that energy expenditure rather than size is the determining factor (e.g., McNab 2000).

Given the presence of a marked dietary shift around the postulated threshold, an equally marked shift in selective

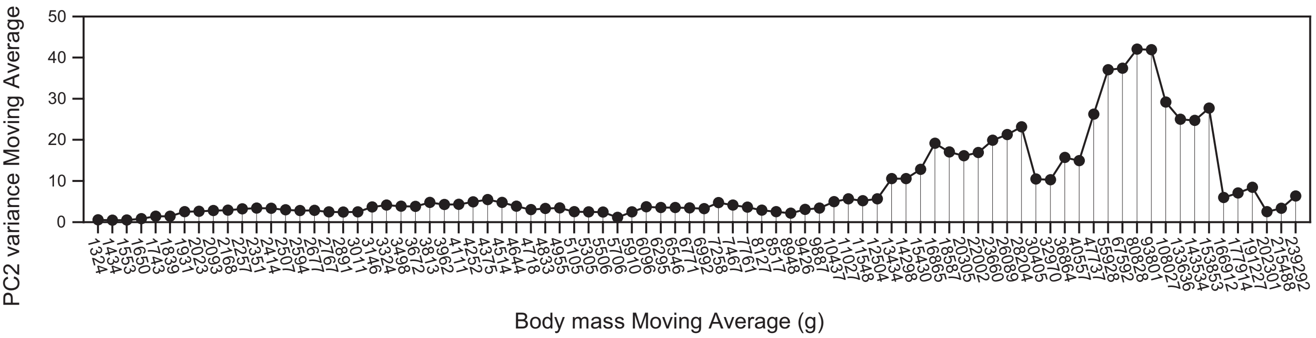


Figure 9. Moving average of PC2 variance body mass. Variation is low and uniform at small sizes. At around 10 kg variation starts to increase with size. There is a marked decrease in variation around 30-40 kg. The species are ranked according to body size and the average over a moving succession of 10 increments is calculated.

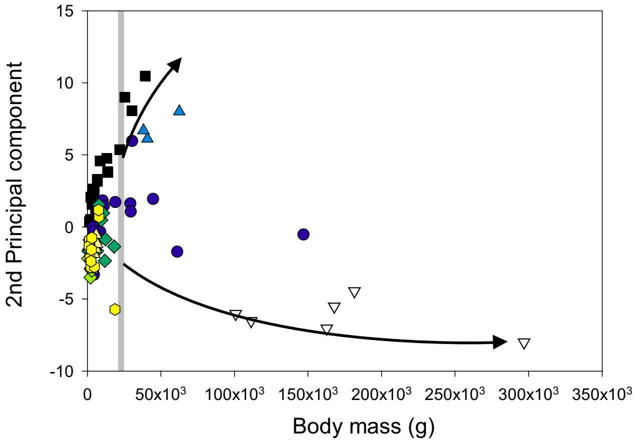


Figure 10. Second principal component (PC2) of recent carnivores plotted against calculated body mass. The postulated threshold at 21.5-25 kg where carnivorans shift diet from small to large prey (Carbone et al. 1999) is shown shaded grey. Around this threshold carnivores are strongly dichotomised. Hand-fitted arrows mark the two morphological trajectories, the top one, grapplers and the lower one, non-grapplers. For legend see Figure 5.

regime is expected and indeed present. Large carnivores are distributed in a strongly dichotomized pattern, into those with retained and those with restricted forearm supination. The shift coincides closely with the postulated threshold (Figure 10). Retaining forearm supination allows for large body sizes, as seen in ursids, while locomotor adaptations allow for moderate sizes only.

The extant Carnivora scoring highest on PC2 are found at intermediate sizes. Localization of these in a "cursorial window" is not unexpected, since body size and locomotor performance are strongly correlated.

During locomotion, energy is expended at higher rates in small than in large animals (e. g., Taylor et al. 1982) and long strides make running more economical (Kram & Taylor 1990). It is the inverse relation between time spent in contact with the ground and metabolic energy consumed that makes running more economical in large than small animals (Kram & Taylor 1990). Thus, a fast and able runner should, theoretically, have a long stride and relatively low body mass, the cheetah being a typical example of such design.

The fastest mammals found today weigh around 50 kg (Coombs 1978, Garland 1983). However, among mammals 119 kg is suggested as the optimal size regarding running abilities (Garland 1983). This far exceeds that of the fastest or the most enduring runners present among the extant Carnivora. Locomotor performance of terrestrial mammals was analysed by Iriarte-Díaz (2002), who found that maximum relative running speed (body length s^{-1}) decreases with size and that scaling is differentiated between small and large animals. The point of change in curvature is suggested to be around 30 kg Iriarte-Díaz (2002). This size falls roughly within the "cursorial window" suggested here by the second principal component.

Surprisingly, the canid family was found to include the greatest morphological disparity (Fig. 7). When regressing body mass on skull and body length Van Valkenburgh (1990) obtained much smaller prediction errors for canids than for felids and mustelids. Since canids are almost entirely terrestrial, little variation in body shape and general morphology is expected within the family. However, in the elbow joint the morphological differences between large and small canids are substantial, a difference also expected to be observed in other parts of the locomotor apparatus.

At small sizes, carnivore diversity, in terms of the number of species, is high, yet morphological disparity is low (Fig. 9). Around 10-13 kg morphological disparity starts to increase. At around this size, carnivores that are dynamically cursorial (Alexander & Jayes 1983), with a fully upright position (*sensu* Jenkins 1971) are expected to appear. The observed pattern might be caused by the presence of relative locomotors, including jackals, along with grapplers, including mustelids.

The marked drop in morphological disparity observed at around 30-40 kg (Fig. 9) is not caused by biased sampling. Today, there is a marked absence of carnivore species in this particular interval, as is clearly seen in Figure 1. The drop in morphological disparity follows the postulated dietary threshold (Carbone et al. 1999). From empirical observations, it is suggested that carnivores at body sizes above the dietary threshold, experience strong selective forces for an increase in body mass to above 40kg. How such a pattern relates to the hypothesis of a "cursorial window" around 50 kg and the inverse relation between body size and locomotor cost (e .g., Taylor et al. 1982, Kram & Taylor 1990) remains to be tested.

Besides biomechanical considerations, physiological and ecological factors may influence such a pattern. Carnivore population density is related to the productivity of their prey, and ultimately to primary productivity. Carbone & Gittleman (2002) developed a simple scaling model that predicts the predator (P) mass supported by prey mass (p) (*p* (*Px008.91)*))). At some level, prey and primary productivity are also expected to influence carnivore diversity and disparity, but the provisions of such a relationship remain to be formalized.

MIOCENE GIANT MUSTELIDS: A CASE STUDY

From the Miocene, several lineages of large-bodied mustelids are known. Of these, the North American *Megalictis* (Hunt & Skolnick 1996) and the African *Ekorus* (Werdelin 2003) are known from crania and nearly complete skeletons. Extant terrestrial mustelids are, with a few exceptions, characterized as small omnivorous - hypercarnivorous carnivores with short legs, elongated body and body mass less than 10 kg. The boreal wolverine (*G. gulo*), with a body mass usually ranging between 10-20 kg, forms a clear exception (Pasitschniak-Arts & Larivière 1995). However, the wolverine is much smaller than some mustelids known from the fossil record.

Megalictis ferox Matthew, 1907 is known from the Late Oligocene-Early Miocene of North America. The general morphology appears to be that of an up-scaled wolverine, "Limbs short and stout, feet plantigrade, short and spreading… phalanges short, claws large , non retractile little curved and not compressed…" (Matthew 1907 p. 196). *M. ferox* was about twice the size of the modern wolverine. Hunt & Skolnick (1996) joined the three formerly used genera *Megalictis* Matthew, 1907, *Aelurocyon* Peterson, 1907 and *Paroligobunis* Peterson, 1910 under *Megalictis*, which has priority. The taxonomic history of *M. ferox* is given in greater detail by Hunt & Skolnick (1996). The 19 individuals referred to the taxon exhibit a vast size range. An estimation of the body mass of *M. ferox*, using the measurements of the first lower molar provided by Hunt & Skolnick (1996) and the predictive equation of Van Valkenburgh (1990) indicates a range of about 20-60 kg.

Three specimens are included in the present study 1.) *AMNH 12881*- Vertebrae, limbs and footbones. Referred to *M. ferox* by Matthew (1907). Found in the Upper Rosebud formation (early Miocene). 2.) *FMNH P12154* – Known from a skull, part of the mandible, vertebrae, limbs and foot bones. Originally referred to *A. brevifacies* by Riggs (1945). From the Upper Harrison Formation (early Miocene). 3.) *FMNH P12135* – Humerus, femur, partial ulna and vertebrae. Originally referred to *M. ferox* by Riggs (1945). Exact origin unknown, "found in a small residual deposit of the Upper Harrison beds…" (Riggs 1945 p. 95) but is likely to have originated from the Upper Harrison Formation.

Ekorus ekakeran, Werdelin, 2003, KNM-LT 23125 is known from a near complete skeleton from Lothagam, a locality of Late Miocene age (Leakey et al. 1996) and housed in the Kenya National Museums (KNM), Nairobi, Kenya. *E. ekakeran* is dentally highly derived and feloid-like. The limbs are relatively long, ca. 20% longer than those of *M. ferox*. The feet are stout and the foot posture plantigrade.

Using the predictive equation of Van Valkenburg (1990) indicates a body mass of the single individual of *Ekorus ekakeran*, of about 40 kg.

The results of a new principal component analysis, this time including the extinct "giant" mustelids is presented in Figure 11. *E. ekakeran* (KNM-LT 23125) scores high on the second principal component, comparable in magnitude to that of the highest scoring extant locomotors. The humeri AMNH 12881 and FMNH P12135 of *M. ferox* score higher than those of any of the recent felids of equivalent size, with the exception of the cheetah. Their scores are comparable to those found among modern hyaenas. Thus, at this score they are unmatched in size by any of the extant carnivorans.

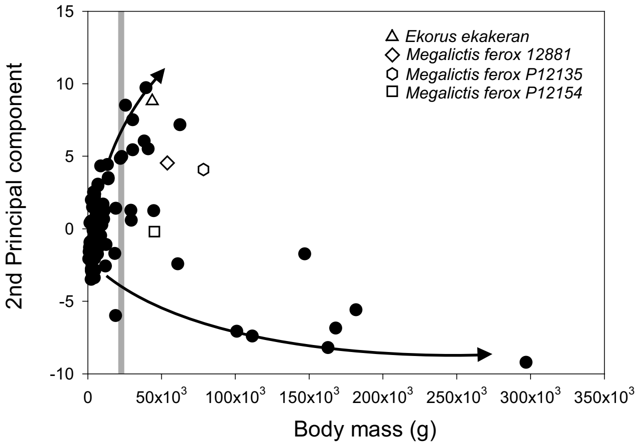


Figure 11. Second principal component (PC2) of extinct giant mustelids and recent carnivorans plotted against body mass. Hand-fitted arrows mark the two trajectories for grapplers and non-grapplers. The postulated threshold at 21.5-25 kg where carnivore shift from small to large prey (Carbone et al. 1999) is shown shaded grey.

However, the humerus FMNH P12154 scores distinctly lower, somewhere between the jaguar (*Panthera onca*) and the snow leopard (*Panthera uncia*).

The African radiation, represented by *E. ekakeran*, appears to have evolved under selective pressure for increased locomotor abilities, with a feeding strategy possibly comparable to that of hyenas and large canids. Cranially and dentally *E. ekakeran* is highly derived, with a shortened face and a felid-like dentition. In the limbs, however, a mosaic of features is expressed. The limbs are relatively long compared to those of other mustelids, yet the feet are short and stout. This combination may seem odd, since recent locomotor carnivorans tend to have long and slender feet (Spoor 1985; Carrano 1997). Evidence from the elbow joint, however, suggests that the opposite may well have been possible in the Miocene.

The North American radiation of large body size among mustelids appears to have responded to different selective pressures and there are indications of evolution in two directions. In the first, forearm supination is partly reduced and, in combination with a relatively large body size, places such forms as ecomorphs without any modern analogue. In the second, forearm supination is fully retained, suggesting a locomotor strategy comparable to that of modern pantherine cats.

Sexual dimorphism in Megalictis

Individuals referred to *M. ferox* by Hunt & Skolnick (1996) constitute a taxon with a considerable variation in size, as illustrated by the length of the first lower molar, which ranges in length from 16.9-23.2 cm, as reported by them. The great variation in size observed is explained by sexual dimorphism, "The possibility that more than one morphologically uniform chronospecies of these large mustelids existed in the midcontinent during the same brief time interval within the Early Miocene seems to us unlikely" (Hunt & Skolnick 1996, p. 42). They reject the hypothesis of multiple species, sympatric through resource partitioning, since no significant morphological differences were found by them.

The data presented here, however, suggest that two different morphologies are present in the material. These data impy a considerable difference in forearm use, indicating a possible difference in prey procurement strategy. Sexual dimorphism is expected to involve a shift in size, not a major shift in shape. For *M. ferox* to be a single species, one has to explain the observed difference as characteristic of a taxon with extreme ecological partitioning between males and females or, alternatively, throughout its temporal or geographical range. Further analysis of this taxon is needed to confirm or reject the hypothesis of sexual dimorphism and formally revise the taxon. The results presented here, one species or not, indicate the presence of multiple large bodied mustelids in the Upper Harrison formation.

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Appendix. List of recent carnivore sample. Number of individuals for species and scores of the first to third principal component.

Family	Species	N=	PC1	PC2	PC3
Canidae	*Alopex lagopus*	5	-11.706	2.627	0.901
	Canis adustus	4	-1.622	4.583	1.036
	Canis aureus	4	5.652	4.759	1.619
	Canis latrans	4	4.150	3.839	2.602
	Canis lupus	5	31.291	10.470	2.951
	Canis mesomelas	3	-4.103	3.308	1.583
	Canis rufus	1	14.151	5.366	3.354
	Cerdocyon thous	2	-9.918	1.103	1.911
	Chrysocyon brachyurus	6	23.049	8.063	2.649
	Cuon alpinus	1	5.256	3.789	2.039
	Lyacon pictus	4	19.936	8.997	0.716
	Nyctereutes procyonoides	2	-8.057	2.603	0.445
	Otocyon megalotis	2	-15.111	1.560	-0.162
	Urocyon cinereoargenteus	3	-10.518	2.334	0.088
	Vulpes rueppelli	1	-16.509	2.070	0.367
	Vulpes velox	1	-17.139	0.356	0.468
	Vulpes macrotis	2	-19.101	0.520	0.277
	Vulpes vulpes	4	-4.417	3.162	1.280
	Fennecus zerda	2	-23.315	0.359	-0.051
Felidae	*Acinonyx jubatus*	4	22.420	5.969	-5.472
	Felis chaus	2	-11.722	0.105	-1.917
	Felis silvestris	2	-14.591	-0.032	-1.790
	Herpailurus yagouarundi	1	-11.504	-0.295	-1.739
	Leopardus pardalis	6	-5.037	-0.334	-1.502
	Leopardus tigrinus	2	-20.301	-1.118	-0.642
	Leopardus wiedii	1	-7.303	-0.777	-1.675
	Leptailurus serval	2	-1.372	1.835	-2.957
	Lynx lynx	5	8.262	1.721	-2.528
	Lynx rufus	4	0.602	1.462	-3.657
	Prionailurus bengalensis	1	-18.875	-0.733	-2.002
	Puma concolor	3	16.122	1.633	-4.572
	Panthera leo	3	66.020	-0.531	-4.226
	Panthera onca	3	34.329	-1.713	-0.047
	Panthera pardus	2	18.416	1.072	-4.982
	Pardofelis marmorata	1	-15.743	-3.312	-0.874
	Uncia unica	1	27.862	1.943	-2.195
Hyaenidae	*Crocuta crocuta*	2	40.742	8.006	2.261
	Hyaena hyaena	2	27.483	6.687	-0.312
	Parahyaena brunnea	1	28.090	6.109	-0.552
Musteloids	*Amblonyx cinereus*	1	-20.979	-0.891	-0.054
	Enhydra lutris	1	-1.456	-2.356	3.176
	Lontra canadensis	3	-10.849	-0.995	1.133
	Lontra longicaudis	2	-12.782	-1.307	1.651
	Lutra lutra	5	-10.039	-1.587	1.445
	Arctonyx collaris	1	-2.374	0.478	-1.120
	Meles meles	4	-2.296	1.535	-0.970
	Myadus javanensis	1	-17.889	-3.021	0.656
	Mellivora capensis	2	2.271	0.958	0.481
	Conepatus semistriatus	1	-20.154	-3.496	-0.448
	Mephitis mephitis	2	-20.190	-2.048	-1.083
	Spilogale putorius	2	-29.277	-2.204	-0.104
	Eira barbara	2	-9.080	-1.670	0.140
	Gulo gulo	6	8.431	-1.356	1.218
	Ictonyx striatus	1	-26.656	-1.675	-0.457
	Martes americana	1	-24.937	-1.567	-1.156
	Martes martes	1	-19.527	-2.900	-0.201
	Martes pennanti	1	-8.337	-1.018	1.333
	Taxidea taxus	2	-0.486	-0.859	-1.076
Procyonidae	*Potos lavus*	2	-15.533	-2.957	1.109
	Bassariscus astutus	3	-22.747	-1.334	0.473
	Nasua narica	2	-10.893	-1.528	-1.124
	Nasua nasua	1	-14.322	-0.806	1.658
	Procyon cancrivorus	1	-10.135	-1.182	2.017
	Procyon lotor	3	-8.714	-0.549	1.595
Ailurus	*Ailurus fulgens*	2	-11.466	-1.881	1.774
Ursidae	*Ailuropoda melanoleuca*	2	48.973	-6.034	7.541
	Melursus ursinus	1	76.992	-4.447	-1.211
	Tremarctos ornatus	1	47.573	-6.517	-1.532
	Ursus americanus	1	71.337	-5.521	0.562
	Ursus arctos	3	67.958	-7.045	0.542
	Ursus maritimus	3	88.416	-7.999	0.105
Viverridae	*Eupleres goudotii*	1	-21.308	-0.895	-0.017
	Fossa fossana	1	-22.037	-1.269	-1.588
	Hemigalus derbyanus	2	-18.083	-1.575	-0.653
	Arctictis biturong	1	0.167	-5.724	2.823
	Arctogalidia trivirgata	1	-19.408	-2.679	1.014
	Paguma larvata	1	-12.489	-2.764	0.788
	Paradoxurus hermaphroditus	1	-20.071	-2.379	-0.275
	Civettictis civetta	1	-2.019	0.689	-2.137
	Genetta genetta	1	-23.553	-2.165	0.252
	Genetta maculata	3	-21.936	-1.336	0.043
	Genetta servalina	2	-23.033	-1.324	0.012
	Viverra tangalunga	2	-15.658	-0.762	-0.772
	Viverra zibeth	1	-6.950	1.182	-0.583
Nandinia	*Nandinia bionotata*	2	-20.323	-2.784	0.325

Paper III

The evolution of cursorial carnivores in the Tertiary: implications of elbow joint morphology

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The evolution of cursorial adaptations in Tertiary carnivores has been contentious[1,2]. Most such studies have focused on the relationship between hindlimb proportions and running speed[3]. Here we show that in extant carnivores, the elbow joint has evolved in two distinct directions with mutually exclusive implications for locomotor ability and prey procurement. Some carnivores retain supinatory ability, allowing them to manipulate prey and other items with the forepaws. Such carnivores can become very large. Other carnivores lose the ability to supinate and become cursors. This allows for only moderate size increase. Modern carnivores above ca. 20 kg body mass are committed to either of these strategies, a threshold that coincides with a postulated fundamental threshold in carnivore physiology[4]. The biaxial pattern mostly follows phylogenetic lines, but a strong selective regime can override this signal, as shown by the extant cheetah. Oligocene and early-middle Miocene carnivores follow the same pattern, though in the Miocene the pattern is shifted towards larger body mass, which may be due to the extraordinary richness of browsing ungulates at this time[5].

The evolution of cursorial predators in the Tertiary has been the subject of continued discussion, with varying suggestions regarding controlling factors and even the very existence of such carnivores[1,2]. These studies have mainly focused on running speed, through the correlation between this and certain morphological features. In particular, the metatarsal/femur (MT/F) ratio has been used as a speed index and guide to the predatory behaviour of extinct terrestrial carnivores[3]. Although the MT/F is correlated with speed, however, a recent review shows that the relationship between this ratio and maximal running speed is not a strong one and that caution should be exercised in using hindlimb proportions to predict locomotor performance of extinct carnivores[3]. On the other hand, it has been observed[6,7] that the structure of the elbow joint is indicative of the degree of supinatory ability in mammals. Since cursorial carnivores require an elbow joint that provides stable, close-packing in full pronation, leaving minimal supinatory ability, it should be possible to use this anatomical region to identify cursorial carnivores in the fossil record. Further, the loss of supination means that such carnivores cannot use their forelimbs for grappling or manipulation of prey items, suggesting a trade-off between cursoriality and prey procurement strategies[8,9]. For this study, we analysed the shape of the posterodistal articular surface of the humerus by principal components analysis of a truss network[10]. The resultant shape vectors were then related to body mass. The results show that extant Carnivora (Fig. 1A) can be separated into three groups: small species with intermediate supinatory ability, taxa with increasingly reduced supinatory ability and moderate size increase and taxa of increasingly large size and moderate increase in supinatory ability. The first group includes taxa up to a size of ca. 20 kg. The second group includes canids and hyenids with a body mass of more than 20 kg. In these taxa, the elbow joint has been strongly modified for running, and allows only fore-aft movement, with little supination. To this group can be added the cheetah, the only pursuit predator among the Felidae. The third group includes the remaining Felidae, larger Mustelidae, all Ursidae, and a single viverrid, the binturong. The shape of the posterodistal articular surface of the humerus thus clearly distinguishes Carnivora that are strong forelimb supinators from Carnivora with strong cursorial adaptations in the elbow joint.

Overall, grouping seems to be by family, suggesting that phylogeny is the dominant determinant of the pattern (Fig. 1A). A closer look at the smaller Carnivora shows how strong the effect of phylogeny is. Fig. 1B shows all Carnivora smaller than 30 kg. With the exception of the slender mongoose, small canids have higher scores on PC 2 than other carnivores of similar size. Thus, at least among extant species, canids

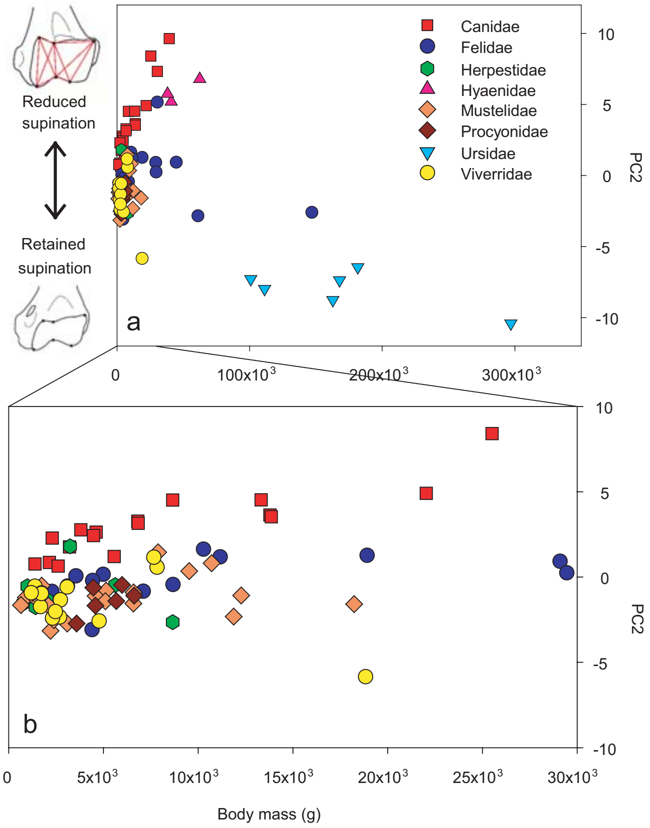

Figure 1: **a**. Diagram of PC 2 (trochlea shape component) against body mass for 93 species of extant carnivores. **b**. The same as a. for carnivores up to 30 kg body mass. Trochlear shape, with the truss network indicated in red, is exemplified at the far left.

are more cursorially adapted than other carnivores at all sizes. However, the separation between the cheetah and the other felids indicates that a strong adaptive component is also present in the pattern.

The relationship between MT/F ratio and elbow joint morphology is complex. The former relates to running speed, while the latter relates to range of motion. Both features are relevant to cursoriality, however. Previous work[2] has concluded that the evolution of limb length in ungulates represents an adaptation to decrease energy expenditure during transport.

High MT/F ratios are characteristic of carnivores adapted to open habitats. Far from all of these are pursuit predators in the sense of being high-speed distance runners, but all would benefit from reduced energy expenditure during long-distance travel. Similar reasoning can be applied to the loss of supinatory ability in carnivores, since this reduced lateral excursion during leg swing rather than necessarily affecting maximal running speed. This is corroborated by Fig. 1A, which shows that reduced supinatory ability coincides with high-speed distance pursuit in only a few species. Instead, many taxa that show reduced supinatory ability are such that would benefit from reduced energy expenditure in foraging, such as striped and brown hyenas, which cover very great distances in order to find food. In the cheetah, on the other hand, any reduction in energy expenditure means increased potential attack distance and greater potential success rate. That the evolution of elbow structure in carnivores is related to energy expenditure is further indicated by the fact that, up to a body mass of ca. 20 kg, all carnivore are bunched at an intermediate humerus articulation shape (Fig. 1B). At larger sizes, there is an increasingly rapid separation of the two main adaptive groups. This is close to the size that has been suggested[4] as the point where predators shift from large to small prey (21.5 kg). Our results suggest that above this size, energy requirements in modern environments can no longer sustain an intermediate strategy of moderate supinatory ability and moderate cursoriality.

To test whether the pattern observed in the modern world is also characteristic of Tertiary faunas, we selected two time-slices for which we had adequate data on fossil carnivores. The first is the Oligocene (33.7-23.8 Myr BP). The position of 22 carnivores from this time period is shown in Fig. 2A. Mean articular surface shape lies more toward the lower end of PC 2 than in extant taxa, but the overall patterns are remarkably similar. Most taxa are small and have intermediate values for PC 2. Larger species (no very large Oligocene carnivores were available) tend towards the same extremes as extant species: some highly cursorial, moderately large species, and some large species with a high degree of supinatory ability. The latter are all Nimravidae, whilst the former include daphoenine amphicyonids, the mustelid *Aelurocyon brevifacies* and the creodont *Hyaenodon horridus*. Judging by elbow joint morphology, the latter is by far the most cursorially adapted Oligocene carnivore available to us.

The results for 31 early-middle Miocene (23.8-11.2 Myr BP) carnivores show overall similarities in pattern to the Oligocene and Recent, but also some notable differences (Fig. 2B). The overall pattern, with an axis of moderately large, cursorial species and an axis of non-cursorial species of increasing size, remains. However, the whole pattern is shifted to the right, with the result that in the Miocene there were larger taxa with an intermediate elbow joint morphology than in either the Oligocene or Recent. The best examples of such intermediate taxa are the amphicyonid *Pliocyon* sp. (123 kg reconstructed body mass) and the ursid *Hemicyon ursinus* (122 kg). This is in strong contrast to the Recent or the Oligocene, where no carnivore above ca. 20 kg takes such an intermediate position. We suggest that this difference is a reflection of the extraordinary species richness of browsing ungulates in the early Miocene of North America[5]. Such an increase in prey spectrum in a mixed environment would create a unique situation, in which large carnivores need not commit to a cursorial habitus in order to fill their nutritional requirements. Among individual taxa, the position

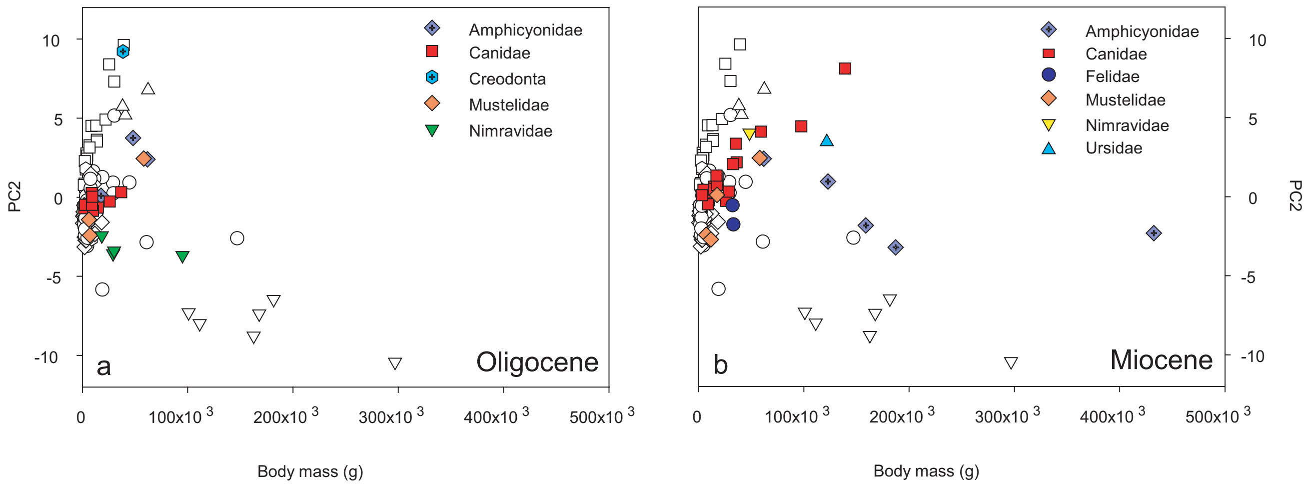

Figure 2: **a**. Diagram as in Figure 1a but including a sample of 22 species of Oligocene carnivore species. **b**. The same as in a. but including a sample of 31 Miocene carnivore species.

of *Barbourofelis whitfordi* among cursorial taxa is in marked contrast to the nimravids of the Oligocene, which retain full supinatory ability (Fig. 2A).

Our work shows that the carnivore elbow joint evolves in two well defined directions that have mutually exclusive implications for the functional morphology of locomotion. They can either retain their supinatory ability, which allows the forepaw to be used for manipulation of prey and other objects, or they can lose their ability to supinate and become cursors and in some cases pursuit predators. Retention of supination allows for great increase in body mass, while cursorial carnivores rarely reach 100 kg. In the extant fauna, carnivores of less than ca. 20 kg body mass can remain intermediate between these extremes, while carnivores above this threshold are committed to one of the two adaptive pathways. This threshold coincides with the point where carnivores shift from small to large prey[4] and this may represent a fundamental functional threshold in carnivore evolution.

Material and Methods

Material. Data on elbow shape and body mass were compiled for extant and extinct terrestrial carnivores. The sample includes representatives of a diversity of lifestyles and almost the entire extant size range of the Order Carnivora, with the exception of the very smallest (weasels, body mass <500g). Semi-aquatic carnivores such as otters are included, while the fully aquatic Pinnipeds are not. All calculations are made on averages of individuals within species or genera (1-17 individuals). A total of 199 extant specimens from 93 carnivore species in 57 genera and 8 families were included: Canidae (19), Felidae (17), Herpestidae (8), Hyaenidae (3), Mustelidae (19), Procyonidae (7), Ursidae (6), Viverridae (14). A total of 147 fossil specimens from 25 species and 21 genera were used, all from North America.

Shape analysis. To assess the movements in the elbow, the shape of the posterodistal articular surface of the humerus was captured. Euclidean distances forming a truss (Fig. 1A)[10] were calculated from six landmarks, digitised from high-resolution digital photographs. The untransformed variable-set of 11 Euclidean distances was reduced by Principal Components Analysis of the variance-covariance matrix. Component 1 accounted for 97.7% of the total variance. It has all positive loadings and can be regarded as a size component. Component 2 accounts for 1.2% of the total variance.

Body mass reconstruction. Body mass was reconstructed using a predictive equation where humerus trochlea circumference (TC) served as a predictor. TC is calculated as the total sum of the Euclidean distances between 24 landmarks placed along the margin of the posterodistal articular surface. Independent contrasts[14-16] indicate that TC and body mass are phylogenetically independent and covary significantly ($r^2=0.733$, $p < 0.001$).

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Competing interests statement

The authors declare that they have no competing financial interests.

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