Aspects of locomotor evolution in the Carnivora (Mammalia)

BY

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Abstract
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In this thesis, the shape of the distal humerus trochlea is analysed using landmark-based morphometrics and multivariate methods, with the aim of exploring locomotor evolution in carnivorans. Elbow joint morphology is used together with body size and craniodental morphology to characterize past and present carnivorans. Evolutionary implications are studied at the ordinal, familial, and species levels, testing specific hypotheses about scaling, morphological constraints, evolutionary trajectories, and potential for social pack-hunting behaviour. The circumference of the distal humerus trochlea is found to be highly correlated with body mass, and appears to scale similarly throughout the order Carnivora. A general predictive model for carnivoran bodymass is presented (a=0.601; b= 2.552; r2=0.952, SEE=0.136, p<0001, n=92), which removes the need for the investigator to actively choose between the diverging estimates that different predictors and their equations often produce. At the elbow joint, manual manipulation and locomotion appear to be conflicting functions, thus suggesting mutually exclusive lifestyles involving either forelimb grappling or pursuit. At large body sizes, carnivorans are distributed over a strongly dichotomised pattern (grappling or locomotion), a pattern coinciding with the postulated threshold in predator-prey size ratio at 21.5-25 kg. This pattern is compared to that of two carnivoran faunas from the Tertiary. In the Oligocene (33.7-23.8 Myr BP), the overall pattern is remarkably similar to that observed for extant Carnivora. In the Miocene (23.8-11.2 Myr BP) carnivores show a similarly dichotomised pattern as the Oligocene and Recent, although the whole pattern is shifted towards larger body sizes. This difference is suggested to be a reflection of the extraordinary species richness of browsing ungulates in the early Miocene of North America. Such an increase in prey spectrum would create a unique situation, in which large carnivores need not commit to a cursorial habitus in order to fill their nutritional requirements. Finally, the elbow joints and craniodental morphology (14 measurements) of fossil canids were examined with the aim of assessing the potential for pack-hunting in fossil canids. It is clear that small and large members of the Recent Caninae share similar craniodental morphologies. However, this pattern is not present in Borophaginae and Hesperocyoninae. In the latter, large representatives are characterized by being short-faced, with reduced anterior premolars and enlarged posterior premolars, thus approaching a "pantherine-like" craniodental configuration. These traits are interpreted as an adaptation for killing prey with canine bites. It is similarly determined that, unlike recent Caninae, all analyzed species of borophagines and hesperocyonines have retained the ability to supinate their forearms. It is therefore likely that manual manipulation was part of their hunting behaviour, thus removing an essential part of the argument for social pack-hunting in these forms, as the benefits of such a strategy become less obvious.

Keywords: Mammalia, Carnivora, Locomotion, Cranial, Elbow joint, Morphology, Morphometrics, Landmarks, Multivariate statistics, Allometry, Ecomorphology, Dental, Body size

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To my parents Lilian & Christer Andersson and
to all who have been given a second chance

Papers included in this thesis

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I **Andersson, Ki** (*in press*). Predicting carnivoran body mass from a weight bearing joint. Accepted for publication in the *Journal of Zoology, London*.

II **Andersson, Ki** (*in progress*). Elbow joint morphology as a guide to locomotor behaviour in the order Carnivora (Mammalia), with examples from Miocene Mustelidae. Submitted to *Zoological Journal of the Linnean Society*.

III **Andersson, Ki & Werdelin, Lars** (2003). The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. *Biology Letters* (Published online http://www.pubs.royalsoc.ac.uk; 6 August 2003).

IV **Andersson, Ki** (*Manuscript*). Potential for pack-hunting in Tertiary canids (Canidae, Carnivora).

Contents

Abbreviations

CVA	Canonical variates analysis
DFA	Discriminant function analysis
GLS	Generalized least squares
LRS	Least squares regression
MRS	Multiple regression
MT/F	Metatarsal/Femur ratio
PCA	Principal components analysis

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 form the basis for 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 locomotor 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, Gonyea, 1978). 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 explore these differences and 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). The canid family is studied with special reference to the origin of social pack-hunting (Paper IV).

In the papers included in this thesis I examine the evolutionary implications of locomotor habits at the ordinal (Paper III), familial (paper IV) and species (paper II) levels, thereby providing a new framework for future studies and understanding of carnivoran evolution.

Figure 1. Cat showing its full grappling abilities. Grappling is made possible through extensive forearm supination. Photograph by *Ki Andersson*.

Carnivore hunting strategy

Predation on large and powerful prey is a hazardous business and the risk of injury is high. Pantherine felids use their forepaws to subdue large prey and dispatch them through suffocation (e. g., Kitchener 1991). Much of the success of this strategy is attributed to the ability to grasp the prey with the forequarters (Gonyea & Ashworth 1975; Gonyea 1978). However, the forequarters of Recent canids are specially adapted for running and for maximal stability during movements in the parasagittal plane, and their ability to manipulate objects manually is limited (Hildebrand 1954). Hence, they adopt a different strategy, in which they engage in a pursuit that eventually exhausts the prey to the point where it can be brought down and killed with multiple bites.

Ewer 1973 suggested that there was strong selective pressure for communal hunting behavior when a pursuit hunting strategy is adopted.

> "Once the technique of chasing has been adopted and the limbs have become cursorially specialised, they are no longer free to become adapted in other ways. This means that the jaws must now be used not only to kill the prey but also to bring it down. The success rate of a lone hunter using this technique against prey larger than itself would inevitably be low and the advantages of group pursuit are obvious" (Ewer, 1973, p. 226).

It has, however, been difficult to identify morphological traits that support a clear distinction between ambush and pursuit-type of hunting behaviour, and
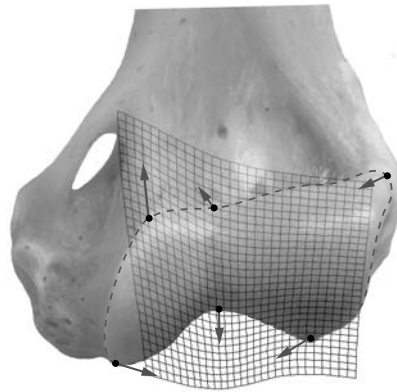
Figure 2. Thin-plate spline comparison of wolverine (*Gulo gulo*) against grey wolf (*Canis lupus*), graphically illustrating the difference in shape of the distal humerus articulation between carnivores with extensive (*G. gulo*) and limited (*C. lupus*) supinatory abilities. The broken line, hand-fitted, 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 and Slice, 1990).

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 elbow joint

The mammalian elbow joint complex is designed to transfer loads between the upper and lower portion of the arm. The joint has to provide stability while at the same time allowing for mobility (Jenkins, 1973; Gonyea 1978; 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

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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 in a cube will result in an area increase by a factor two and volume increase by a factor three. 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 $l \propto M^{0.360-0.390}$, 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.

The concept of cursoriality

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.

There is today 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 factors other than running speed.

Fast runners tend to have longer limbs and a high metatarsal/femur ratio (MT/F), 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 sizes, 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. "MT-F cursoriality" appears during the Early Eocene and increases step-wise during the Early Miocene. Among carnivores, the 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.

Methodological framework

A quantitative approach to problems in bioscience, including character evolution and morphological adaptation involves the use of morphometrics (MacLeod and Forey, 2002) and biostatistics (=biometry, Sokal and Rohlf, 1995). The following chapter is short account of the theoretical framework of some of the numerical methods used in this thesis.

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 are 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 ($l \propto M^{0.37-0.39}$, Alexander et al., 1979; $A \propto M^{0.634-0.642}$, 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.

Multivariate statistics

Multivariate methods were originally developed to analyze highly complex problems in, i. a., economics and psychometrics, such as causal factors determining behavioural traits (e. g., Thurstone, 1947). Multivariate methods allow a large number of variables to be analyzed simultaneously in multidimensional space. In the beginning the use of these methods was hampered by the complex nature of the calculations involved. Following the rapid developments in computer technology, advanced multivariate approaches are available today, where dozens, even hundreds, of variables can be analyzed in standard commercial desktop applications. Being able to use many variables to solve the problems at hand is appealing, although this can be a mixed blessing. Many investigators are tempted to include too much data in their models, hoping that the added input will increase the power of their models. Without properly addressing the theoretical background, such an approach may violate fundamental assumptions of the methods used.

Today, multivariate methods are widely adopted in bio- and earth sciences (e. g., Reyment and Savazzi, 1999), with several refined applications in morphometrics (Bookstein, 1991, Marcus et. al., 1996). The choice of method depends on the nature of the question being addressed.

Multivariate methods can be divided into two main categories, depending on the purpose of the analysis. The first category includes methods that make large and complex problems manageable, by reducing dimensionality. Principal components analysis (PCA) is an example of one such method, extensively used in biometric studies. In principal components analysis the first axis (1st principal component) is aligned with the direction of maximal variance in a sample and is defined by a linear combination of variables. The second axis is placed orthogonal to the first, as are all consecutive axes. In principal components analysis it is assumed that the sample is drawn from a single statistical population. In analyses of measurements from organisms

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the first component generally accounts for most of the variance in the sample, and is typically explained by differences in size.

The second category includes methods that classify objects, such as cluster and discriminant function analysis (DFA). In modern phylogenetic studies, cluster analysis has been specially adapted for the analysis of discrete characthers, and is used to evaluate phenetic and genetic similarities and dissimilarities between species.

A discriminant function analysis identifies the linear combination of variables that produces the maximal separation between two *a priori* determined groups. For discrimination of three or more groups of data canonical variates analysis (CVA) is applied. This method is analogous to the two-dimensional, discriminant analysis, although it involves multidimensional regression (MRS) models rather than linear regression models (LRS).

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 a 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 warps (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*) (Figure 2). 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 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.

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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. Predictors used to calculate the body mass of extinct carnivorans often scale differently between different taxa, thus yielding body mass estimates that diverge considerably depending on which predictive equation is used. This requires the investigator to choose the most appropriate one in each instance, a procedure that is best avoided if possible.

In this paper, the carnivoran elbow joint is explored with the aim of producing a single general body mass predictor that can be used over a broad range of terrestrial and arboreal carnivorans. The circumference of the distal humerus trochlea is found to be highly correlated with body mass, and trochlea circumference appears to scale similarly throughout the order Carnivora (Figure 3). This scaling is clearly not as theoretically predicted by elastic similarity and slightly higher than that predicted by geometric similarity, indicating a slight positive allometry with respect to the latter. Some degree of differential scaling between carnivoran families and between animals of large and small size cannot be ruled out, but this result is inconclusive. A predictive model that allows mass estimations for a broad range of carnivorans is presented (a=0.601; b= 2.552; r^2=0.952, SEE=0.136, p<0001, n=92). Body mass for eight extinct carnivoran species are calculated and these generally conform to earlier mass predictions.

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
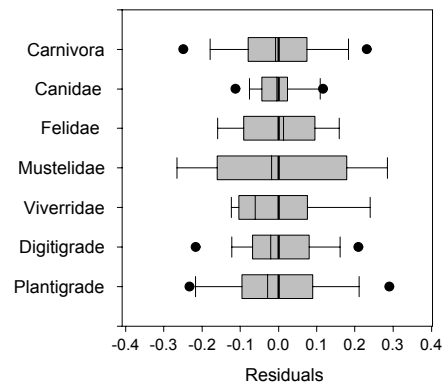
Figure 3. Box-plots of least square regression (LRS) residuals after the removal of *Enhydra lutris*, identified as an outlier. Box-plots include information on location, dispersion, skewness and tail-shape. In a theoretically "ideal" situation, all sub-group boxes would be identical. Here sub-group means are similarly located although some differences in dispersion and skewness are indicated. Thus, the Carnivora model (a=0.601; b=2.552; r^2=0.952, SEE=0.136, p<0.0001, n=92) can be used to estimate body mass for a broad range of carnivorans. Box heights represent the interquartile range, comprising 50% of the observations. Boxes are divided by medians (thin lines) and means (thick lines). Whiskers connect boxes to the extremal points within 1.5 interquartile ranges. Points outside the 5th and 95th percentile of these ranges are plotted. Dispersion of observations is indicated by box height and skewness by box and whisker asymmetry (McGill et al. 1978; Benjamini 1988).

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 2). 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 4b). 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, but the morphology of the cheetah converges with that of locomotors, showing that strong selective forces may override the phylogenetic component.
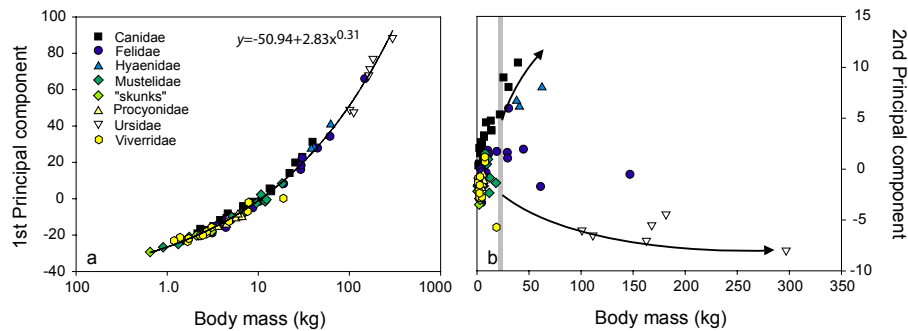
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Figure 4. Results from a principal components analysis (PCA) of the untransformed variance-covariance elbow data matrix. The same symbols are used in graph **a** and **b**. **a**. First principal component (PC1) plotted against body mass (kg). X-axis $\log_{10}$-transformed. The first principal component reflects overall size in the sample, but also includes allometric information. Species are evenly distributed around the least squares regression line of best fit, suggesting that no major systematic differences in allometry are present. **b**. Second principal component (PC2, trochlea shape component) of Recent carnivores plotted against calculated body mass. The area shaded grey represents the postulated prey selection threshold at 21.5-25 kg where carnivores shift 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. See Figure 2 for a graphical illustration of the morphological differences between grapplers and non-grapplers.

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 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; Figure 5a) and one from the early-middle Miocene (23.8-11.2 Myr BP; Figure 5b). At intermediate and large body sizes the extant carnivoran fauna
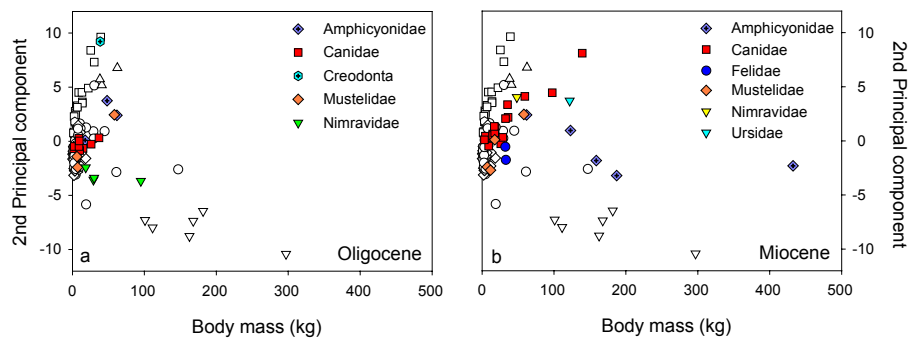
Figure 5. a. Diagram of the second principal component (PC2, trochlea shape component) against body mass for a sample of 22 species of Oligocene carnivorans. **b**. The same as in 6a but including a sample of 30 Miocene carnivorans. The overall patterns are similar to that of extant carnivorans (see Figure 5). However, for the Miocene the whole pattern is shifted towards larger taxa with an intermediate elbow joint morphology as compared to either the Oligocene or Recent. Recent species are represented by open symbols. All fossil species (filled symbols) are from the North American continent.

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.

Miocene carnivores show overall similarities in pattern to the Oligocene and Recent, but also some notable differences (Figure 5). 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.
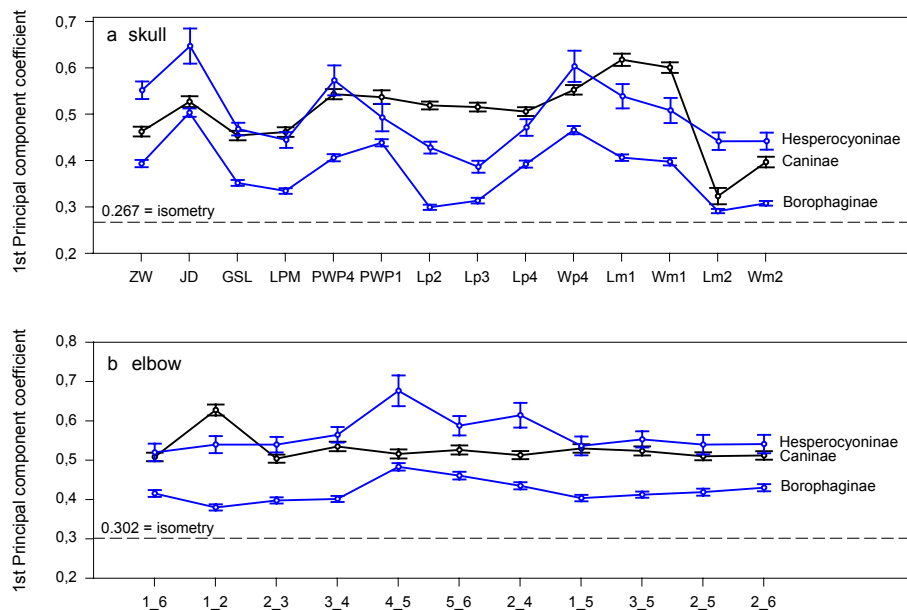
Figure 6. Results of multivariate allometry analyses of the craniodental and elbow joint characteristics of Recent and fossil Canidae. **a**. analysis of the skull; **b** analysis of the elbow. The three Canidae subfamilies, Caninae, Borophaginae and Hesperocyoninae are analysed separately using pricipal components analysis (PCA). The coefficients of the first principal component are reported for each analysed variable. Most variables scale with positive allometry, as indicated by coefficient values higher than those theoretically predicted under isometry. Scaling conforming to isometry would be indicated by all coefficient values equaling the square root of the number of analysed variables p (p=14, skull matrix; p=11, elbow matrix), represented by broken lines in graphs **a** and **b**. Bootstrapped (1000 iterations) error bars are given, marking the upper and lower 99.9% confidence limit.

Paper IV

Communal hunting allows some modern canids to catch large and powerful prey. As opposed to, e. g., felids, Recent canids have a limited ability to grapple and subdue prey using their forelimbs. Instead, they engage in sustained pursuit predation and the success rate during this activity typically increases with the number of individuals participating in the hunt. This paper focuses on the potential for social pack-hunting in large-bodied fossil canids. Clearly, such behaviors do not fossilize directly and have to be inferred from anatomy.

Craniodental adaptations for handling and killing large prey and forearm utility in running and grappling are investigated by principal components (PCA) and canonical variates analyses (CVA). It is tested if fossil canids

responded to predation of large prey by evolving the same morphological traits as their Recent pursuit-type relatives. The analyses show that small and large members of the Recent Caninae share similar craniodental morphologies. However, this pattern is not present in the fossil subfamilies Borophaginae and Hesperocyoninae (Figure 6a). In the latter, large representatives are characterized by being short-faced with reduced anterior premolars and enlarged posterior premolars, thus approaching a "pantherine-like" craniodental configuration. These traits are interpreted as an adaptation for killing prey with felid-like canine bites.

The elbow joints of large canids also do not converge on a single morphotype (Figure 6b). All analyzed species of borophagines and hesperocyonines have retained the ability to supinate their forearms, unlike recent large Caninae. It is therefore likely that manual manipulation was part of their hunting behavior, thus removing an essential part of the argument for social pack-hunting in these forms, as the benefits of such a strategy become less obvious. An association between the origin of pack-pursuit "wolf avatars" and the origin and evolution of grass-dominated ecosystems is hypothesized. The results presented here clearly suggest that Recent large canids are poor ecological, morphological and behavioral analogs for their large fossil relatives.

Conclusions

- ***The elbow-joint can successfully be used to predict body mass over a broad range of extinct carnivorans.*** This removes the need for the investigator to actively choose between a line-up of predictors and equations producing greatly diverging body mass estimates.
- ***The ability to supinate the forearm and thereby manipulate prey items can be traced through the shape of the humerus (upper arm) part of the elbow articulation.*** This provides an additional measure of cursoriality that does not directly depend on allometric assumptions.
- ***Manual manipulation and locomotion appear to be mutually exclusive functions of the elbow joint.*** This dichotomized pattern is especially prevalent above the postulated ecological-physiological threshold at 21.5-25Kg where carnivorans shift diet from small to large prey.
- ***Locomotor evolution in carnivorans appears constrained by unknown ecological and biomechanical constraints.*** Carnivorans with retained ability for forearm supination appear free to evolve large body mass (>100kg). However, carnivorans that have lost this ability appear limited to intermediate sizes.
- ***Fossil faunas show a remarkably similar dichotomized pattern to that observed for extant Carnivora*** though during the early-middle Miocene (23.8-11.2 Myr BP) the whole pattern is shifted towards larger body sizes.
- ***Recent large canids are poor ecological, morphological and behavioural analogs for their large fossil relatives.*** Craniodental morphology of large fossil canids is distinctly different from that of their Recent relatives, approaching the morphology found today in carnivorans that kill by single bites, i. e., ambush-type hunters. Large fossil canids retain the ability to grapple prey.
- ***Combined, the evidence from the skull and the elbow removes an essential part of the argument for social pack-hunting in pre-Pliocene canids.***

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