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

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The evolution of cursorial adaptations in Tertiary (65–1.65 Myr ago) carnivores has been a contentious issue. Most such studies have focused on the relationship between hind limb proportions and running speed. Here, we show morphometrically 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 one or other of these strategies. This threshold coincides with a postulated threshold in carnivore physiology. The biaxial pattern mostly follows phylogenetic lines, but a strong selective regime can override this signal, as shown by the extant cheetah. Oligocene (33.7–23.8 Myr ago) and early-middle Miocene (23.8–11.2 Myr ago) carnivores follow the same pattern, though in the Miocene the pattern is shifted towards larger body mass, which may be owing to the extraordinary richness of browsing ungulates at this time.

Keywords: carnivore; elbow joint; supination; cursorial; Tertiary

1. INTRODUCTION

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 (Bakker 1983; Janis & Wilhelm 1993). These studies have mainly focused on running speed, through the correlation between this and certain morphological features. In particular, the metatarsal/femur ratio (MT/F) has been used as a speed index and guide to the predatory behaviour of extinct terrestrial carnivores (Garland & Janis 1993). Although the MT/F is correlated with speed, 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 hind limb proportions to predict the locomotor performance of extinct carnivores (Garland & Janis

1993). Alternatively, it has been observed (Jenkins 1973; Rose 1988) that the structure of the elbow joint is indicative of the degree of supinatory ability in mammals. Because cursorial carnivores require an elbow joint that provides stable close-packing of the long bones, leaving minimal supinatory ability, it should be possible to use this anatomical region to identify cursorial carnivores in the fossil record. Furthermore, 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 (Ewer 1973; Lewis 1995, 1997).

2. MATERIAL AND METHODS

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 of less than 500 g). 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 67 genera and eight families were included: Canidae (19 species), Felidae (17), Herpestidae (8), Hyaenidae (3), Mustelidae (19), Procyonidae (7), Ursidae (6), Viverridae (14). A total of 145 fossil specimens from 46 species and 31 genera were used, all from North America. A list of taxa measured for the study is provided in electronic Appendix A (available on The Royal Society's Publications Web site).

To assess morphological correlates of movements in the elbow, the shape of the posterodistal articular surface of the humerus was captured. Euclidean distances forming a truss (figure 1a; Strauss & Bookstein 1982) were calculated from six landmarks, digitized 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 was reconstructed using a predictive equation where humerus trochlea circumference (TC) served as a predictor (Andersson 2003). 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 (Felsenstein 1985; Harvey & Pagel 1991; Purvis & Rambaut 1995) indicate that TC and body mass are phylogenetically independent and covary significantly ($r^2 = 0.733$, $p < 0.001$).

3. RESULTS

For this study, we analysed the shape of the posterodistal articular surface of the humerus by principal components analysis of a truss network (Strauss & Bookstein 1982). The resultant shape vectors were then related to body mass. The results show that extant Carnivora (figure 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, which is the only cursorial 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.

Figure 1. (a) Diagram of principal component 2 (PC2; 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. Trochlea shape, with the truss network indicated in red, is exemplified at the top left.

4. DISCUSSION

Overall, grouping seems to be by family, suggesting that phylogeny is the dominant determinant of the pattern (figure 1a). A closer look at the smaller Carnivora shows how strong the effect of phylogeny is. Figure 1b shows all Carnivora weighing less than 30 kg. With the exception of the slender mongoose, small canids have higher scores on principal component 2 (PC2) than other carnivores of similar size. Thus, at least among extant species, canids 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 the 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 (Janis & Wilhelm 1993) has concluded that the evolution of limb length in mammals represents an adaptation to decrease energy expenditure during transport.

High MT/F ratios are characteristic of carnivores adapted to open habitats. Far from all open habitat carnivores 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

Figure 2. (a) 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 30 Miocene carnivore species.

ability in carnivores, since this reduces lateral excursion during leg swing rather than necessarily affecting maximal running speed. This is corroborated by figure 1a, which shows that only a few of the species that exhibit reduced supinatory ability can be identified as high-speed distance pursuit predators. 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 to find food. In the cheetah, however, any reduction in energy expenditure means a potentially increased attack distance and hence 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 carnivores have an intermediate humerus articulation shape (figure 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 (Carbone *et al.* 1999) 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 ago). The position of 22 carnivores from this time-period is shown in figure 2a. Mean articular surface shape lies more toward the lower end of PC2 than in extant taxa, but the overall patterns are remarkably similar. Most taxa are small and have intermediate values for PC2. Larger species (no very large Oligocene carnivores were available) tend towards the same extremes as extant species: some moderately large, highly cursorial species and some large species with a high degree of supinatory ability. The latter are all Nimravidae, while the former include daphoenine amphiionids, 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 ago) carnivores show overall similarities in pattern to the Oligocene and Recent carnivores, but also some notable differences (figure 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 amphiionid *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 body mass 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 (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 to fill their nutritional requirements. Among individual taxa, the position of *Barbourofelis whitfordi* among cursorial taxa is in marked contrast to the nimravids of the Oligocene, which retain full supinatory ability (figure 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 a great increase in body mass, whereas 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 (Carbone *et al.* 1999) and this may represent a fundamental ecological threshold in carnivore evolution.

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