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Correlates between calcaneal morphology and locomotion in extant and extinct carnivorous mammals

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Short Title: **Carnivoran calcanea and locomotion**

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Abstract

Locomotor mode is an important component of an animal's ecology, relating to both habitat and substrate choice (e.g., arboreal versus terrestrial) and in the case of carnivores, to mode of predation (e.g., ambush versus pursuit). Here we examine how the morphology of the calcaneum, the "heel bone" in the tarsus, correlates with locomotion in extant carnivores. Other studies have confirmed the correlation of calcaneal morphology with locomotion behaviour and habitat. The robust nature of the calcaneum means that it is frequently preserved in the fossil record. Here we employ linear measurements and 2D geometric morphometrics on a sample of calcanea from eighty-seven extant carnivorans and demonstrate a signal of correlation between calcaneal morphology and locomotor mode that overrides phylogeny. We used this correlation to determine the locomotor mode, and hence aspects of the palaeobiology of, forty-seven extinct carnivorous mammal taxa, including both Carnivora and Creodonta. We found ursids (bears), clustered together, separate from the other carnivorans. Our results support greater locomotor diversity for nimravids (the extinct "false sabertooths") usually considered to be arboreal), than previously expected. However, there are limitations to interpretation of extinct taxa because their robust morphology is not fully captured in the range of modern carnivoran morphology.

Research Highlights

Calcaneal morphology correlates with locomotor grade in Carnivora, largely distinct from phylogenetic signal. Ursid calcaneal morphology is distinct from all other Carnivora. *Nimravus brachyops*' calcaneal morphology indicates a more cursorial locomotion than other nimravids.

Introduction

Placental mammalian carnivores today mostly comprise species in the globally distributed order Carnivora. These mammals are characterised by the possession of a pair of carnassial teeth (upper fourth premolar and lower first molar) (Nowak, 2005; Goswami, 2010). Carnivorans exhibit a wide array of diets, including carnivores, omnivores, and some herbivores, and locomotor types such as tree-dwellers, runners, swimmers, diggers and ambulators (Goswami, 2010). Their evolutionary history stretches back to the generalized paraphyletic assemblage of "Miacoidea" of the Palaeocene of the Northern Hemisphere (Wesley-Hunt and Flynn, 2005; Eizirik et al., 2010; Smith and Smith, 2010). Many modern carnivoran families first appear in the late Eocene, 37-34 mya, and the carnivoran fossil record comprises three times as many extinct species as extant ones (Goswami, 2010), making this a rich order for palaeontological research.

Until the late Eocene the dominant large carnivorous mammals were the Creodonta, traditionally comprising two families: Hyaenodontidae (generally more dog-like forms) and Oxyaenidae (generally more cat-like forms). However, doubts have been cast on the monophyly of this grouping, and Solé (2013) proposed that they should be considered as two separate orders: Hyaenodontida and Oxyaeonodonta. Creodonts are distinguished from carnivorans by more posteriorly positioned, multiple carnassial pairs. They were predominantly scansorial to terrestrial, and appear to have occupied similar ecological niches as today's carnivorans, with later taxa exhibiting increasing specialisation towards hypercarnivory (Friscia and Van Valkenburgh, 2010).

Locomotion is one of the key components to understanding the ecology of a mammal, as an animal's movement strongly correlates with other aspects of its behaviour, such as habitat preference. Specialisations for certain locomotor behaviours lead to changes in musculature, limb proportions and osteology, and this correlation between function and form (ecomorphology) can be quantified (Polly, 2007, 2010; Polly and Sarwar, 2014). Examination of the morphology of extant taxa for which locomotor behaviour is known, allows the inference of the ecomorphology of extinct species (Figueirido et al., 2016).

Previous work has identified distinct locomotor grades in carnivorans (Van Valkenburgh, 1985; Taylor, 1989): arboreal, spending most of their time moving among trees; scansorial, spending a lot of time on the ground yet also able climbers (many felids are scansorial); and terrestrial, spending most of their time on the ground and rarely climbing. Some derived locomotor grades for Carnivora include: cursorial, specialist runners; semi-fossorial, animals that habitually dig for food and/or shelter; and semi-aquatic, animals that spend time, and locomote, both on land and in water. Early carnivorans are understood to have been arboreal to scansorial (Heinrich and

Houde, 2006; Solé et al., 2014). The gait of ursids has been termed “ambulatory”, although other ambulators are smaller carnivorans, such as raccoons (Taylor, 1989). Large bears with plantigrade feet (Ursinae) are not known until the late Miocene (Hunt, 1998a), and the derived gait of modern bears probably dates from around this time.

Carnivorous mammals vary in their stance along a continuum from plantigrade – the primitive mammalian condition - where the entire foot is contact with the ground, to digitigrade, where the carpus and tarsus are raised off the ground and the animal stands on the digits alone (Polly, 2007). Stance relates to locomotion: plantigrade mammals can propel themselves forwards with greater force, whereas a digitigrade stance facilitates speed by increasing the effective length of the distal limb (Polly, 2007). Arboreal forms are generally plantigrade in stance (Taylor, 1989), while an increasingly digitigrade stance is seen in terrestrial and cursorial forms. Many carnivorans are semi-digitigrade.

Various features of the appendicular skeleton have been used to understand locomotion in carnivoran mammals, including metatarsal to femur ratios (Garland and Janis, 1993), forelimb shape (Janis and Figueirido, 2014; Meachen-Samuels, 2012; Meachen-Samuels and Van Valkenburgh, 2009; Fabre et al., 2015; Taylor 1974), and forelimb elements such as the distal humerus (Andersson, 2004; Figueirido et al., 2015, 2016) While fore and hind limb morphology are both influenced by ecological behaviours including locomotion, prey capture and feeding, hind limb morphology provides key information on lever mechanics and forward propulsion during such behaviours. Ankle morphology has been proven to be well correlated with locomotion and stance, particularly the degree of flexion and inversion-eversion of the foot (Taylor, 1970; Polly, 2008), and is less influenced by secondary ecological factors (Polly, 2007; Schutz and Guralnick, 2007; Samuels et al., 2013; Martín-Serra et al., 2014).

The main foot flexion is at the crurotarsal joint between the tibia and the astragalus. Some movement within the tarsus itself – inversion, eversion and flexion - is the generalised condition for mammals (Szalay, 1984); however the degree of movement and correlated morphology is clearly useful in understanding locomotion, making it an ideal focus for study. Being arboreal requires considerable mobility in the hind limb for locomotion in the trees, including increased inversion-eversion of the foot (Jenkins and McClearn, 1984; Polly, 2008). However, terrestrial locomotion requires more stability in the hind limb (Taylor, 1989). The influence of size on ankle mobility appears to be less important than previously suspected (Polly, 2008), although larger body size restricts an animal's ability to climb and move in trees and has implications for the robustness of skeletal elements due to increased loading (Biewener, 1989).

The calcaneum is located in the tarsus (Figure 1) where it articulates with the astragalus and cuboid; the generalised tetrapod condition is for the calcaneum to have an articulation with the fibula, but this is not the usual condition in placentals, and is not seen in carnivorans. The calcaneum is an ideal bone for study as it is robust and easily identified, with high preservation potential. Biomechanically, it is one of the key bones for hind limb movement. The gastrocnemius and soleus muscles attach to the distal end of the calcaneal tuber via the Achilles tendon, and so constitute the main in-lever for plantar-flexion in the hind limb, a motion that produces forward thrust in locomotion when the foot is on the ground. As a result, increased length of the calcaneal tuber increases the lever arm of the gastrocnemius and soleus, and a long tuber is associated with terrestrial locomotion (Polly, 2010), especially cursorial locomotion . The peroneus brevis and peroneus longus attach on the peroneal tubercle of the calcaneum and control flexion and inversion of the foot (Chester et al., 2015), and so the peroneal tubercle is usually broader (mediolaterally) in arboreal taxa.

The articulation of the calcaneum and astragalus forms the lower ankle joint (LAJ), and the range of movement in this joint varies considerably in relation to locomotion. Terrestrial and cursorial taxa have a more tightly locked LAJ, while scansorial and arboreal taxa have a LAJ that allows inversion and rotation of the foot (Jenkins and McClearn, 1984).

Although ideally locomotion and ecology should be assessed using multiple osteological proxies and taking the entire hind and forelimb into account, this is often not possible due to the fragmentary fossil record. The calcaneum is robust and often preserved in the fossil record. While there has been research on correlations between the calcaneum and locomotion in various mammal groups including marsupials (Bassarova et al., 2008), armadillos (Jasinski and Wallace, 2014), and apes (Youlatos, 2003), our research examines calcaneal morphology across much of the order Carnivora, with an almost global distribution, and with the inclusion of a wide range of fossil carnivoran and carnivorous taxa.

Morphometrics, the quantitative study of shape, provides a rigorous approach to understanding the form and variation of living structures that goes beyond simple anatomical observation (Webster and Sheets, 2010). Linear measurements have traditionally been used to capture osteological shape and relative dimensions (Van Valkenburgh, 1985). While the usefulness of this methodology is undoubted, limitations are also recognised: for example the difficulty in capturing complex shapes and angles, and the tendency for linear measurements to be influenced by size (Zelditch et al., 2004). Geometric morphometrics, based on 2D digital landmarking, captures a constellation of osteological points and makes it possible to quantify shape in an inherently multidimensional analysis (Bookstein, 1991; Dryden and Mardia, 1998). Geometric morphometrics removes size variables (although it does not account for the effects of allometry), leaving shape as the only remaining variable for analysis. This landmarking technique is particularly suited to the investigation of the relationship between form and function, such as locomotor grade (Fabre et al., 2015), and exploring the role of phylogeny in shape variation (Monteiro and Abe, 1999).

This study investigates how calcaneal morphology relates to locomotion in extant Carnivora and how it can be used to understand the locomotion and ecology of fossil Carnivora and other carnivorous mammals. Carnivoran families can often be distinguished by their locomotor mode - all procyonids are arboreal or scansorial, most canids are terrestrial and some cursorial. While there is phylogenetic influence on morphology, we are looking for an overriding signal of function in the morphology of the calcaneum. If we can establish such an overriding signal, we have the basis for determining the locomotor mode of extinct taxa by their placement within the morphospace generated by the living ones. This is especially useful for taxa belonging to families where there are no extant members for direct comparison. We then evaluate whether predictions based on the calcaneal morphology of extinct taxa are consistent with previous hypotheses about their locomotor modes.

Geometric morphometrics can only be applied to one bone at a time due to the limitations of Procrustes superimposition. For this and the reasons outlined above, we argue the robust and often preserved calcaneum is an excellent single bone to use for geometric morphometric analysis of ecomorphology.

Materials and Methods

A photographic dataset of 164 calcanea was collected from 132 species of carnivores, including 87 extant Carnivora, 38 extinct Carnivora, and five Hyaenodontida and two Oxyaenida (Table 1). This includes duplicate representatives of some species, depending on availability of specimens. Duplicate specimens are referred to with a numbered suffix (e.g. *Neofelis nebulosa* 2). Where specimens are only identified to genus level, they are referred to with the suffix “sp.” (e.g. *Dinictis* sp.), and where specimens are identified to sub-species level this is also indicated (e.g. *Acinonyx jubatus venaticus*). Calcanea were photographed with a scale bar in dorsal, ventral, medial and lateral views. The extant dataset includes members of all of the terrestrial carnivoran families sampled from a broad geographic distribution. Marine Carnivora (pinnipeds) were excluded. For full details of where photographs were obtained see Table 1 and Acknowledgements.

A supertree was assembled informally for use in comparative phylogenetic methods (Figure 2). This was based primarily on Martín-Serra et al. (2014) and Agnarsson et al. (2009).

Dorsal and lateral view photographs were used for analysis (only dorsal views were used for digital landmarking), and dorsal images were flipped as necessary so that the sustentacular facet was on the left of the photograph, effectively making all specimens left calcanea. Damaged specimens and photographs of low pixel quality were discarded.

Fourteen linear measurements were chosen to capture the relative dimensions of the calcaneum and the ectal and sustentacular facets that form the articulation with the astragalus (Figure 1E). Measurements *a* and *l* capture the length of the calcaneal tuber, forming the lever arm of the pes, and *a* also captures the position of the ectal facet, along with *b*. Measurement *b* also reflects the length of the calcaneal head along with *n*, and the latter also relates to the position of the sustentacular facet. Measurements *d*, *c* and *m* capture the breadth of the calcaneal head. The width of the calcaneal tuber is measured mediolaterally and anteroposteriorly using measurements *f* and *g* respectively. Finally the length and width of the sustentacular and ectal facets are measured by *h*, *i*, *j* and *k*, while the width of the cuboid facet is measured by *e*. All of these relate to the degree of movement and rotation possible in the ankle.

The linear measurements were taken using ImageJ (Abramoff et al., 2004) and measurements for each specimen were taken in the same order. The linear measurements were Z-transformed ((*x*-mean)/stdev) to standardise and remove size so that the results would primarily reflect shape. The transformed data were imported into R (R Core Team, 2013), for the conduction of the principal components analysis (PCA).

For the digital landmarking, 162 dorsal photographs representing 123 species were selected. Eleven landmarks were chosen (Figure 1F) to reflect the length and breadth of the calcaneum, the shape of the calcaneal head, the placement of the sustentacular and ectal facets, and the shape of the groove for the attachment of the Achilles tendon. Landmarks were digitised in the same order for every specimen using tpsDIG2 (Rohlf, 2004). The landmark data was superimposed using generalised Procrustes analysis, translating and rescaling the landmarks and rotating them into an optimal least-squares alignment (Rohlf and Slice, 1990). This removes variables of translation, orientation and scale, leaving only differences in shape for analysis.

Principal components analysis was carried out on the landmark data in R (R Core Team, 2013) using the geomorph package (Adams and Otarola-Castillo, 2013) and moments package (Asquith, 2015). Thin-plate splines were generated using the geomorph package (Adams and Otarola-Castillo, 2013) for the mean of taxa loading at each end of the PC axes (positively and negatively), and to illustrate shape-change between the overall mean shape and the mean calcaneal shape for each locomotor grade.

We carried out MANOVA with posthoc tests in IBM SPSS Statistics v.20 statistical package to determine if there was a statistically significant relationship between principal component scores and locomotor grade.   The post hoc analyses were performed for identifying which locomotor categories were significantly separated by each PC (See Supporting Information 1 and 2). Either the Bonferroni's test (parametric) or Dunnett's T3 (non-parametric) were used for those PC's that showed homogeneity of within-group variances or not, respectively (Quinn and Keough, 2002). Using the information provided by these tests and the morphological changes associated with each PC, we made the ecomorphological interpretations of the differences among locomotor categories.

Linear discriminants analysis (LDA) was also employed using the MASS package (Venebles and Ripley, 2002) in R. This let us assess the ability of our PCA to distinguish locomotor types, and assign taxa to their most probable locomotor grades based on these data.

Results

The results of our principal components analysis are found in Table 2. The first two principal components (PCs) of the landmark data explain a higher percentage of variance than the first two PCs of the linear measurement data. The first two landmark PCs account for 53% of the variance (PC 1 = 29%, PC2 = 24%) whereas the first two linear PCs only account for 40% (PC 1 = 22%, PC2 = 18%).

Results of the MANOVA indicate 46.2% of the variation in the linear dataset, and 49.1% of the variation in the landmark dataset are explained by locomotor grade (Table 3). The MANOVA results show the first 4 PCs yield significant results that distinguish between locomotor groups in the landmark data (Table 3). In the linear data only the first 2 PCs yield significant results.

In the linear data (Figure 3A) scansorial and terrestrial taxa are distributed throughout the morphospace, while cursorial taxa score slightly more positively on the PC1 axis. Arboreal taxa score more negatively on PC1 axis, and most score more negatively than cursorial taxa on PC2. The morphospaces generated by both linear and landmark data are generally similar in taxon distribution, but in the linear data extant bears fall into a distinct phylogenetic cluster scoring more negatively on PC1 and positively on PC2, while in the landmark data ursids cluster by scoring positively on the PC1 axis and positive on the PC2 axis (Figure 3 and Supporting Information 5 and 6).

For the linear dataset the length from the base of the sustentacular facet to the bottom of the calcaneal head (*n*), and tuber length (*a, l*) load positively on PC1 (Figure 4A). The width of the calcaneal head, especially spanning the sustentacular facet and LAJ (*m*), loads negatively on PC1. Variables loading positively on the PC2 axis are for a longer, wider and deeper calcaneal tuber (*a, f, g, l)*, with a wider LAJ (*m*) and projecting sustentacular facet (*d*) (Figure 4B) - these calcanea are more robust. Loading negatively on the PC2 axis are length of the calcaneal head (*b*), and length of the ectal and sustentacular facets (*h*, *j*).

For the landmark data (Figure 3B) scansorial and terrestrial taxa are distributed throughout the morphospace, while cursorial taxa score slightly more negatively on the PC1 axis. Arboreal taxa score more positively on the PC1 axis and negatively on the PC2 axis, whereas cursorial taxa score more positively on PC2. There is very little overlap between arboreal and cursorial taxa (Figure 3 and Supporting Information 5 and 6).

The thin plate splines in Figure 3B indicate that in the landmark dataset, reduction of the calcaneal head length and increase in calcaneal head width (with a wide and flat cuboid facet) load positively on PC1. Calcanea scoring negatively on the PC1 axis have a proportionally long calcaneal head, with a narrow cuboid facet. Taxa with positive scores on PC2 have a longer calcaneal tuber, while in those scoring negatively on PC2 the ectal facet appears to sit higher on the tuber, leading to the effective shortening of the calcaneal tuber. The cuboid facet in taxa scoring negatively on PC2 is more W-shaped than in the rest of the morphospace.

Thin plate splines generated from the extant taxa with known locomotor grades highlight the main anatomical differences between the mean for each grade from the mean for the whole dataset (Figure 4C). The splines for scansorial and terrestrial taxa do not differ greatly from the mean, as may be expected for these generalist grades. The splines for arboreal and semi-fossorial taxa share some features, with a broader calcaneal head and wider sustentacular facet. This effectively shortens the length of the distal part of the calcaneal head, which exhibits a more W-shaped cuboid facet. This feature is shared with taxa scoring negatively on PC2 in the morphospace. In the arboreal taxa the top of the ectal facet is located more distally on the calcaneal tuber, effectively shortening the lever arm of the calcaneal heel and increasing the articulation surface with the rest of the ankle. The cursorial spline has a more V-shaped cuboid facet and a dorsoventrally compressed sustentacular facet. In the spline for the cursorial taxa the lever arm of the calcaneal tuber is effectively lengthened by the lowering of the ectal facet.

The most obvious result in our morphospaces is that the extant bear species (Ursidae) cluster separately in morphospace. In both morphospaces there is overlap between arboreal, semi-aquatic and semi-fossorial taxa. Semi-aquatic taxa do not have a clearly defined morphospace occupation, with taxa falling entirely within the morphospace of other grades.

Figure 5 shows the placement of the fossil taxa within the convex hulls of the locomotor types of the extant taxa. Some fossil taxa fall outside of the morphospace generated by the extant taxa, more so in the landmark data than the linear. Almost all of the outliers score positively on PC2 in both datasets, and more negatively on the PC1 axis in the linear dataset, but positively on PC1 in the landmark dataset. These taxa are mostly amphicyonids and large machairodontine felids. The fossil taxa do not fall with the bears, with the exception of *Amphicyon galushai* (landmark data) and *Ischyrocyon* sp. (linear data). However, in the landmark morphospace most fossil taxa fall into the space between the ursids and the rest of the extant taxa (Figure 3, Figure 5 and Supporting Information 5 and 6). While most members of Nimravidae included in this analysis fall within the arboreal/scansorial convex hull, *Nimravus brachyops* appears distinctly more terrestrial than its relatives. This is particularly evident in the landmark PCA morphospace (Figure 5B). The creodonts mostlyl fall inside the morphospace generated by the extant taxa, except the hyaenodontid *Apterodon gaudryi*, which has scores similar to the extinct felid *Amphimachairodus coloradensis*. The hyaenodonts cluster mostly with terrestrial/cursorial extant taxa such as *Canis lupus dingo*, *Lynx canadensis* and *Panthera leo*, while the two oxyaenids appear more scansorial and semi-fossorial.

Discussion

The findings of this study regarding form and function in the carnivore calcaneum expand upon previous research, which concentrated mainly on the length of the lever arm (Polly, 2008; Polly and MacLeod, 2008). The principle component analyses (PCAs) indicate a measurable distinction between ursid ambulators and all other grades. There was also a clear distinction between arboreal and semi-fossorial versus cursorial morphospaces (Figure 3), although these spaces were all overlayed by the scansorial and terrestrial morphospace. The loadings for the linear PCA suggest that this reflects breadth versus length in the calcaneum (Figure 4). Increased length in the calcaneal tuber correlates with more terrestrial and cursorial locomotion due to the resultant increased lever-arm for movement of the foot in a parasagittal plane, while a broader calcaneal head correlates with arboreal, semi-fossorial and ambulatory grades by relating to greater amount of muscle attachment on the peroneal tubercle for increased movement in the lower ankle joint to allow inversion-eversion and rotation. This is in line with previous research (Polly, 2007, 2008 and 2010; Polly and MacLeod, 2008). Results of ANOVA suggest these distinctions in morphology between locomotor grades are significant and not artefacts of random noise. However phylogeny should always be taken into account when considering calcaneal morphology in Carnivora.

Comparing thin-plate splines for PC1 and PC2 axes (Figure 3B) with those for mean locomotor modes (Figure 4C), it is apparent that morphologies with negative loadings on PC2 are close to the mean arboreal spline, and morphologies with positive loading on PC2 and, to a lesser extent, negative loadings on PC1, are similar to the mean cursorial spline. The mean spline for taxa scoring positively on PC1 in the landmark data identical to that for ambulating bears – which is not a surprise as these taxa cluster so distinctly at the end of the axis. Terrestrial and cursorial mean splines are very similar, but in the cursorial spline the sustentacular facet is narrower dorsoventrally. This could reflect a difference in orientation of the facet, to produce a slightly different hinge-like joint in these locomotor grades, but such a change would not be effectively captured in two dimensional analyses. A three-dimensional analysis may make this clearer.

Most extant Felidae score more positively than Canidae on PC1 in the linear morphospace, and negatively on the PC1 axis in the landmark data (Figure 3 and Supporting Information 5 and 6). This is probably a reflection of heel length in relation to the rest of the calcaneum. Polly (2010) found felids have a higher ratio of calcaneal tuber length than canids. While this would seem to suggest felids are more cursorial than canids, it is probably that the increased length is related to leaping on prey from an ambush position in cats, requiring more “push-off” than running. This distinction between running and leaping may be seen along the PC2 axis in the landmark morphospace - in general canids and felids score differently on this axis.

Many families remain conservative in their range of locomotor types. This is probably linked to body size, particularly for arboreal taxa which must remain small enough to move among trees. Pursuit predators are all larger than 20kg (Carbone et al., 1999), limiting their efficiency as climbers. However, canids and felids exhibit greater locomotor grade diversity than other families in the Carnivora and also have a wider range of body sizes. This implies that body size is an important factor to consider in further analysis of phylogeny and locomotor grade.

The widening of the sustentacular facet in arboreal forms is linked to the increased movement in the joint to allow inversion, eversion and rotation in the lower limb, and so arboreal and semi-fossorial taxa both have a wider calcaneal head reflecting the attachment of musculature to the peroneal tubercle. No meaningful inferences can be drawn from the semi-aquatic taxa included in this analysis. Almost all of the semi-aquatic taxa fall within the morphospaces for other locomotor grades, and the mean thin-plate spline is similar to those for arboreal and semi-fossorial grades. This is possibly due to small sample size, but also, despite being proficient in an aquatic environment, it is possible that none of the semi-aquatic carnivoran families in this dataset (predominantly otters) have become sufficiently aquatic that their calcaneal morphology is radically altered, as seen in marine carnivores (Polly, 2008).

Locomotor grades are a somewhat subjective means of classifying locomotion and may fail to identify more specific traits in an animal’s movement. Complexity in movement was recognised by some of the earliest (and commonly cited) work on carnivore locomotion by Taylor (1970, 1976). Taylor (1976) employed primary and secondary locomotion categories that included “climbing arboreal walking”, and “arboreal and terrestrial walking and jumping”, as primary categories, and “climbing walking”, and “running walking jumping”, as secondary categories. It is worth noting that including too many locomotor grades may leave too few taxa in each grade to allow for meaningful statistical analysis.

Overall, the linear discriminants analysis (LDA) was successful in assigning extant taxa to their locomotor grade (Supporting Information 3). Other than ambulatory, the most accurately assigned locomotor grade in both datasets was arboreal (82% in linear data, 81% in landmark data). Scansorial locomotor grades were least effectively assigned among extant taxa, (only 43% of taxa correctly assigned in the linear data, 54% in the landmark data). This suggests that generalist grades are less easily distinguished using LDA.

When applying to LDA to fossil taxa, many taxa were assigned grades that seem unlikely from anatomical observation, especially robust and/or plantigrade fossil taxa, such as *Smilodon* species, *Megantereon cultridens,* the amphicyonids, *Mesocyon* sp. and *Hoplophoneus*. Many of these taxa were assigned as semi-fossorial or semi-aquatic in the LDA. Some taxa may be assigned incorrectly because their phylogeny constrains calcaneal shape, placing them closer to the mean for their ancestral shape. It is also probable that some fossil taxa moved in a manner unlike extant taxa, explaining why they fall outside the convex hulls of extant grades. The relatively lower occupation of cursorial morphospace by fossil taxa, particularly in the linear data, supports the suggestion by Anyonge (1996) and Janis and Wilhelm (1993) that few extinct Carnivora were pursuit predators. Digging species usually exhibit a more robust morphology, so it is likely that some extinct taxa place near them because they are also more robust for reasons other than digging, including larger body size. It is worth noting that as fossorial taxa dig using their forelimbs, it is not altogether surprising that this ecological mode should be poorly correlated with their calcaneal morphology, and therefore lead to less informative predictions. Robustness, phylogeny and other factors such as stance cannot be not accounted for in the results of the LDA. We therefore do not consider it to be a useful method for assigning fossil taxa to their locomotor grade using calcaneal morphology.

The New World cat *Miracinonyx trumani*, known as the “American cheetah”, and its probable ancestor *M. inexpectatus* (Van Valkenburgh et al., 1990), occupy similar morphospace to the extant Old World cheetah *Acinonyx jubatus* (Figures 3 and 5 and Supporting Information 5 and 6). All of these taxa score positively on PC1 in the linear data and negatively on PC1 in the landmark data. The puma (*Puma concolor*) is also thought to be closely related to *M. inexpectatus* (possibly sharing a common ancestor**;** Van Valkenburgh et al., 1990). This phylogenetic relationship may explain the placement of these taxa in morphospace, where *M. inexpectatus*, *M. trumani* and *P. concolor* cluster together, especially in the landmark morphospace. Both morphospaces support the assertion that *M. trumani* was more cursorial than its closest relative, *M. inexpectatus*. A study of the sacral morphology implies that *M. trumani* did not use its tail for balance during changing direction in locomotion, as seen in the extant cheetah (Harris, 2014), so it may not have been as cursorial as its modern relative.

The systematic position of the Nimravidae, the “false sabre-toothed cats”, is uncertain, with some authors suggesting they are closely related to Felidae (Martín-Serra et al., 2014), others that they are an outgroup to the feliform carnivorans (Wesley-Hunt and Flynn, 2005), or that they may even fall outside of crown Carnivora (Spaulding & Flynn, 2009). We follow Martín-Serra et al., (2014) and place them as the sister-group to Barbourofelidae and Felidae. As their common name suggests, they were superficially cat-like, but generally had shorter legs and shorter tails than extant felids (Martin, 1998a). They are known primarily from the late Eocene and Oligocene, but survived into the late Miocene in Eurasia. Nimravids have previously been considered as terrestrial or arboreal in their habits. The members of the family with the longer sabers (the dirk-toothed forms) have been interpreted as plantigrade in foot posture, while those with shorter sabers (the scimitar-toothed forms) have been interpreted as digitigrade (Martin, 1998a).

In our study, *Nimravus brachyops* (a scimitar-toothed form) falls in a more cursorial morphospace than the other nimravids in our dataset on both landmark and linear PC1 axis (Figure 5). This suggests *N. brachyops* was more cursorial than previously suspected; possibly a pounce-pursuit predator rather than an ambusher. While previous studies, using data from several forelimb and hindlimb elements, have suggested that this younger nimravid (late Oligocene, as opposed to *Dinictis* and *Holophoneus* which were late Eocene-early Oligocene) was more terrestrial (Meachen-Samuels, 2012; Samuels et al., 2013), our analyses reflect this more strongly.

The Machairodontinae were an extinct subfamily within Felidae, known primarily from the Plio-Pleistocene but with origins in the Miocene. They include the “true” sabre-toothed cats such as the North American *Smilodon populator* and *S. fatalis*, and the

Old World *Amphimachairodus coloradensis* and *Megantereon cultridens*. These cats were robust, and considered to be muscular ambush predators (Martin 1998b). In our analyses, the machairodontine felid *Nimravides* sp. also scores positively on the PC1 axis for linear and landmark data. It falls close to taxa such as *Miracinonyx* and *Acinonyx jubatus*, suggesting that it was also a capable runner. *Megantereon cultridens* falls alongside the extant lion and tiger (*Panthera leo, Panthera tigris sumatrae*) in the linear morphospace (Figure 5 and Supporting Information 5 and 6), suggesting a similar ecology to these large extant terrestrial cats - a result supported by previous analyses of the postcrania (Christiansen and Adolfsen, 2007). *Megantereon* scores more positively on both PC1 and PC2 in the linear PCA than any other felid except *Acinonyx* and *Miracinonyx,* due to the proportionally long calcaneal tuber, the low upper limit of the ectal facet, and the longer length of the calcaneal head to the base of the sustentacular facet, all of which load heavily for these axes. In the landmark PCA, *M. cultridens* is in the middle of the generalised terrestrial and scansorial morphospace (Figure 5). The difference in placement between taxa in the different PCAs highlights the differences in results taken using these two different methods to answer the same question.

Amphimachairodus coloradensis scores positively in both datasets, and does not cluster near *Smilodon* in the landmark data, although it does in the linear. Previous studies found *A. coloradensis* was longer-limbed than other machairodontids (Anyonge, 1996) and it has been distinguished from *Smilodon fatalis*, which has been interpreted as an ambush predator (Anyonge, 1996). In this analysis however, *S. fatalis* falls very near *A*. *coloradensis* in the PCA of the linear data. Again, this difference between datasets may reflect the detection of a whole shape in landmark analysis, versus linear measurement.

Previously placed within Nimravidae, barbourofelids were cat-like carnivorans known from the Neogene, and now considered to comprise their own family, more closely related to true felids than were nimravids (Morlo et al., 2004). *Barbourofelis morrisi* has been described as “ambulatory”, a category including slow walking or trotting taxa, and in our dataset represented by extant ursids. Anyonge (1996) generated a morphospace by analysis of limb cross-sections: he showed that *B. morrisi* fell close to ursids, and suggested this was due to *B. morrisi*’s large size and limb proportions. The close position of *B. morrisi* to ursids in the landmark dataset supports this finding. It also falls near the wolverine (*Gulo gulo*) and badger (*Meles meles*)(Supporting Information 5 and 6) which suggests that these extant taxa may be useful comparisons for aspects of the locomotion and ecology of *B. morrisi.*

Extant ursids clustered phylogenetically as well as by locomotor grade (ambulatory) (Figure 3 and Supporting Information 5 and 6). The mean splines for each PC axis in the PCA (Figure 3B) show how their inclusion dominates the quadrant of the morphospace they occupy. This distinction in morphospace probably reflects the distinct ursid plantigrade condition. It does not prove useful for understanding morphology and ecology of most of the rest of Carnivora according to the linear dataset, but in the landmark data many fossil taxa fall between bears and the extant taxa, suggesting placement may be related to robustness. These fossil taxa include Amphicyonidae, commonly known as “bear-dogs”: an important group of carnivorans with their origins in the middle Eocene, persisting into the Pleistocene (Hunt, 1998b). They evolved into a wide range of sizes, and were obligate carnivores: they were mostly plantigrade in their foot posture but some smaller forms may have been digitigrade. Amphicyonids are usually considered to be caniforms, although recent phylogenetic reappraisal suggests they may be a basal carnivoran outgroup to Caniformia (Tomiya and Tseng, 2016). In addition to “bear-dogs” there were also “dog-bears”, in the extinct subfamily Hemicyoninae within the Ursidae, known primarily from the Miocene. Hemicyonines were carnivorous, and differed from modern bears in their digitigrade foot posture (Hunt, 1998a), implying a more cursorial form of locomotion. *Hemicyon ursinus* is morphologically distinct from extant Ursidae (likely due to its digitigrade stance) and in this analysis it did not cluster with them. The LDA assigned only two species to the ambulatory grade: *Smilodon populator* and *Ischyrocyon* sp.

Miacoids are considered polyphyletic, including a number of stem carnivoraforms previously assigned to the genus *Miacis*, but many have been reassigned into distinct separate genera or as basal members of previously described families such as Amphicyonidae (Solé et al., 2014; Tomiya and Tseng, 2016). Like many other “miaciods”, *Dormaalocyon latouri* from the early Eocene of Belgium is a small, long-bodied carnivore (Solé et al., 2014). *Dormaalocyon latouri* falls among arboreal taxa in our analysis (Figure 5, Table 4), which agrees with anatomical observation by Solé et al. (2014), who noted the possibility for a wide range of movement between the calcaneum and astragalus, and the well-developed peroneal tubercle, which they likened to the morphology of the extant arboreal palm civet, *Nandinia binotata*. However, *D. latouri* is placed closer to more robust fossil and extant taxa than to

Nandinia. This is significant as *D. latouri's* morphology should be close to the ancestral morphology of crown Carnivora.

Most creodonts display morphologies that indicate they were scansorial or terrestrial (Morlo, 1999; Friscia and Van Valkenburgh, 2010). This is somewhat supported by these analyses, but although creodont locomotion can be somewhat understood through comparison with that of extant carnivorans, most fell into generalist areas of morphospace. Morlo (1999) includes “ambulatory” as a sub-category of terrestrial locomotion for some creodont taxa, but this category did not prove useful to our understanding of creodont locomotion in these analyses.

Morphology linked to locomotor grade provides a meaningful ecometric trait that can be subject to statistical analysis. Care must be taken to include relevant locomotor categories to capture the variation within the dataset, but it is important to ensure the dataset is large and diverse enough to make further subcategorization statistically meaningful. Any quantitative method for assigning locomotion will only be as successful as the dataset and groupings permit; it is always possible that further inclusion of taxa, changes to categorisation, or more detailed analysis of other elements of the skeleton, may provide a more accurate categorization.

The coupling of linear measurement with landmark analysis may help address potential shortcoming of each methodology, for example where complex shapes may be difficult to capture with linear measurements. This methodology also addresses instances where relative lengths may result in misleading morphospace placement, such as the extremely cursorial placement for *Megantereon cultridens* in our linear morphospace. However, 2D landmarking also has its limits, and 3D analysis – such as 3D landmarks (Martín-Serra et al., 2014) or eigensurface analysis (Polly and MacLeod, 2008) - may capture better shape data for analysis, such as changes in facet orientation (for example the sustentacular facet in *Acinonyx*).

Phylogeny influences locomotor grade, but there can still be meaningful assessment of locomotion in fossil taxa through principle component analysis so long as legacy of phylogeny is carefully considered. The link between body size and phylogeny – namely the larger body size in some families, such as Ursidae, Felidae and Canidae, should also be considered when examining the diversity of locomotor grades in different carnivore families.

The low number of fossil taxa falling within the PCA convex hulls created by extant taxa implies the range of extant taxa does not fully capture the range of morphologies in extinct ones. Plantigrade stance is not clearly captured by this study, which may explain why many plantigrade fossil taxa with robust morphologies were not clearly resolved in terms of their locomotion, being assigned as semi-fossorial and even semi-aquatic, despite this being unlikely based on anatomical observation. The inclusion of secondarily plantigrade extant Ursidae did not resolve this, as they clustered phylogenetically.

These analyses show that the calcaneum can provide a useful single indicator of locomotion in fossil taxa. The large size of the dataset in this analysis including both extant and fossil taxa, and the exploration of various statistical and empirical methods to classify fossil taxa into locomotor type, contribute meaningfully to our understanding of the calcaneum within the field of functional morphology.

Author contributions

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Figure 1: Position of the calcaneum, anatomical nomenclature, and measurements and landmarks used in this study. In (A), (B) and (C) the position of the calcaneum is shaded grey. (C) Dorsal view of the calcaneum with anatomical nomenclature as used in this study, abbreviations: a = astragalus, cu = cuboid. (E) The linear measurements used in this analysis: ***a*** = calcaneal tuber length from top of ectal facet to most uppermost point of calcaneal tuberosity; ***b*** = length from top of ectal facet to base of cuboid facet; ***c*** = projection of peroneal tubercle from midline; ***d*** = projection of sustentacular facet from midline; ***e*** = width of cuboid facet; ***f*** = mediolateral width of calcaneal tuber; ***g*** = anteroposterior width of tuber; ***h*** = length of ectal facet; ***i*** = width of ectal facet; ***j*** = length of sustentacular facet; ***k*** = width of sustentacular facet; ***l*** = tuber length

from uppermost projection of sustentacular facet; ***m*** = width of calcaneal head at widest point including sustentacular facet; ***n*** = length from cuboid facet to bottom of sustentacular facet. (F) Landmarks used in this analysis: **1**, uppermost medial point of the calcaneal tuber; **2**, uppermost lateral point of the calcaneal tuber; **3**, point of maximum curvature in groove for attachment of Achilles tendon; **4**, uppermost point of the sustentacular facet; **5**, medial-most point of the sustentacular facet; **6**, lowermost point of the sustentacular facet; **7**, lowermost medial point of the calcaneal head; **8**, lowermost lateral point of the calcaneal head; **9**, mid-point between landmarks 7 and 8 on the dorsal edge of the cuboid facet; **10**, lowermost lateral point of the ectal facet; **11**, uppermost point of the ectal facet. Felid by Mauricio Anton with permission. Anatomical images by author.

Figure 2: Informal supertree of Carnivora and Creodonta with estimated branch lengths. Includes only the taxa featured in this study (subspecies specified where known). Image and animal silhouettes by author, geological timeline adapted from Cohen et al., 2015.

Figure 3: Principal components analyses. (A) linear measurements, (B) landmarks, entire dataset. Extant taxa colour and shape coded by locomotor grade (for colour see online edition, for full labelling of extant taxa see the Supporting Information 4-6). Bears are circled with dashed line. Calcanea pictured for each axis in linear PCA from taxa scoring most positively/negatively for each axis: (A) PC1- = *Tremarctos ornatus 2*, PC1+ = *Acinonyx jubatus*, PC2- = *Leopardus*

wiedii, PC2+ = *Ursus americanus 2*. Splines on landmark PCA axes are mean of five taxa scoring most positively/negatively for each axis. Splines and calcanea outlines are not to scale.

Figure 4: Loadings for measurements in linear PCA, and thin-shape splines for mean locomotor grades in landmark PCA. See Figure 3 for morphospaces. (A) PC1 loadings for linear PCA. (B) PC2 loadings for linear PCA. Measurements loading positively and negatively for each PC illustrated above and below relevant PC. Highest loading measurements have dashed (red) outline. (C) Thin-plate splines showing relative warp for each locomotor grade from mean.

Figure 5: PCAs with labelled fossil taxa and convex hulls of extant taxa locomotor grade morphospace occupation. (A) Linear measurement PCA. (B) Landmark PCA. Abbreviations for fossil species: Aelf = *Aelurodon ferox*; Amac = *Amphimachairodus coloradensis*; Ampf = *Amphicyon frendens*; Ampg = *Amphicyon galushai*; Ampl = *Amphicyon longiramus*; Ampm = *Amphicyon major*; Aptg = *Apterodon gaudryi*; Barf = *Barbourofelis fricki*; Barm = *Barbourofelis morissi*; Borp = *Borophagus pugnator*; Cyns = *Cynelos sinapius*; Dap = *Daphoenus* sp.; Dest = *Desmocyon thomsoni*; Din = *Dinictis* sp.; Dinf = *Dinictis felina*; Dinsq = *Dinictis squalidens*; Dips = *Dipsalidictis platypus*; Dorl = *Dormaalocyon latouri*; Eucd = *Eucyon davisi*; Epih = *Epicyon haydeni*; Hemu = *Hemicyon ursinus*; Hop = *Hoplophoneus* sp.; Hopp = *Hoplophoneus primaevis*; Hya = *Hyaenodon* sp.; Hyac = *Hyaenodon crucians*; Hyam = *Hyaenodon montanus*; Isch = *Ischyrocyon* sp.; Meg = *Megantereon* sp.; Megc = *Megantereon cultridens*; Mes = *Mesocyon* sp.; Miri =

Miracinonyx inexpectatus; Mirt = *Miracinonyx trumani*; Mlic = *Megalictis* sp.; Nim = *Nimravides* sp.; Nimb = *Nimravus brachyops*; Not = *Nothocyon* sp.; Paco = *Pachyaena ossifraga*; Pare = *Paratomarctus euthos*; ; Pat = *Patriofelis* sp.; Phl = *Phlaocyon leucosteus*; Pse = *Pseudailurus* sp.; Smif = *Smilodon fatalis*; Smip = *Smilodon populator*; Tepr = *Tephrocyon rurestris*; Thiv = *Thinocyon velox*.

Table 1: Dataset used in this analysis. Gender of specimen included where known. Museum abbreviations: MCZ = Museum of Comparative Zoology, USA; NHM = Natural History Museum London, UK; AMNH (FAM is Frick collection within the AMNH) = American Museum of Natural History; NMB = Natural History Museum Basel, Switzerland; UCMP = University of California Museum of Palaeontology, Berkeley USA; UNSM = University of Nebraska State Museum, USA; RNSB = Institut Royal des Sciences Naturelles de Belgique, Belgium; YPM Yale Peabody Museum, USA. Locomotor grades for extant taxa from Samuels *et al.* (2013) except: *[1] Meachen-Samuels (2010); *[2] Nowak (2005); *[3] Christiansen & Adolfssen (2007); *[4] Solé *et al.* (2014); *[5] Van Valkenburgh (1987); *[6] Larviére and Seddon (2001).

Table 2: Distribution of Principle Component axes for PCA carried out on linear measurement and landmark data. *Percentages rounded up.

Table 3: Results of MANOVA.

Table 4: Results of LDA in allocating locomotor group to fossil taxa. A = arboreal, S = scansorial, T = terrestrial, C = cursorial, F = semi-fossorial, W = semi-aquatic, B = Ambulatory. Taxa not included in analysis indicated by a hyphen.