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ORIGINAL PAPER

In the Pursuit of the Predatory Behavior of Borophagines (Mammalia, Carnivora, Canidae): Inferences from Forelimb Morphology

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Abstract Here, we perform an ecomorphological study on the major bones (humerus, radius, and ulna) of the carnivoran forelimb using three-dimensional geometric morphometrics. More specifically, we test the association between forelimb morphology and predatory behavior. Our results suggest that the main morphological adaptions of carnivorans to different predatory behaviors relate to: (*i*) the capacity to perform long and efficient runs as in pounce/pursuit and pursuit predators; (*ii*) the ability to maneuver as in occasional predators; and (*iii*) the capacity to exert and resist large loads as in ambushing predators. We used borophagine canids as a case study, given the controversy on the predatory behavior of this extinct subfamily. Our results indicate that borophagines displayed a limited set of adaptions towards efficient running, including reduced joint mobility in both the elbow and the wrist, aspects in which they resemble the living canids. Furthermore, they had forelimbs as powerful as those of the extant ambushing carnivorans (i.e., most felids). This combination of traits suggests that the predatory behavior of borophagines was unique among carnivorans, as it was not fully equivalent to any of the living species.

Keywords Ecomorphology · Forelimb · Predatory behavior · Carnivora · Borophaginae

Introduction

One recurrent topic in mammalian ecomorphology is the search for an association between the shape of the major appendicular bones and the ecology of locomotion, which may be used to derive inferences for extinct taxa. As a result, several researchers have proposed that different skeletal traits of living mammals can be interpreted as ecomorphological indicators of their locomotor behavior (e.g., Maynard-Smith and Savage 1955; Taylor 1974, 1976, 1989; Garland and Janis 1993; Anyonge 1996; Harris and Steudel 1997; Iwaniuk et al. 1999; Salton and Sargis 2008, 2009; Meachen-Samuels and Van Valkenburgh 2009; Walmsley et al. 2012; Fabre et al. 2013). These morphological correlates have been in turn applied to estimate the paleoautoecology of extinct species and, based on these estimates, to derive paleosinecological inferences for past communities (e.g., Van Valkenburgh 1985, 1987; Munthe 1989; Janis and Wilhelm 1993; MacLeod and Rose 1993; Argot 2001, 2003, 2004; Palmqvist et al. 2003; Andersson and Werdelin 2003; Mendoza et al. 2005; Andersson 2005; Schutz and Guralnick 2007; Samuels and Van Valkenburgh 2008; Figueirido and Janis 2011; Polly 2010; Lewis and Lague 2010; Meloro 2011; Janis et al. 2012; Ercoli et al. 2012; Meachen-Samuels 2012; Samuels et al. 2013; Janis and Figueirido 2014).

Mammalian carnivorans are particularly interesting because their predatory behavior has presumably influenced the morphological evolution of their appendicular bones. For this reason, a number of researchers have searched for ecomorphological indicators in the appendicular skeleton of carnivorans that relate to their predatory strategies and prey size preferences (e.g., Van Valkenburgh 1985; Harris and Steudel 1997; Figueirido and Janis 2011; Meachen-Samuels and Van Valkenburgh 2009; Janis and Figueirido 2014; Figueirido et al. 2015). Here, we use three-dimensional

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geometric morphometrics to explore in greater depth the association between predatory behavior of carnivorans and the morphology of their appendicular skeleton. Further, this approach is used to infer the predatory behavior of some species of the extinct Borophaginae (Mammalia, Carnivora, Canidae), which dominated the carnivoran guilds of North America during most of the Cenozoic (Van Valkenburgh 1999). This carnivoran subfamily reached a substantial taxonomic diversity (Wang et al. 1999), displayed a wide range of body sizes, and showed a high degree of morphological disparity (Munthe 1989). Concerning their paleoecology and behavior, there is a consensus that their diet ranged from hypocarnivory to hypercarnivory, and even bone-cracking specialization (Werdelin 1989; Valkenburgh et al. 2003; Tseng and Wang 2010). However, their locomotion mode and predatory behavior remain controversial, as they do not seem to have shared the adaptations of the living canines (Munthe 1989; Van Valkenburgh et al. 2003; Andersson 2005). In this respect, in a recent article, Figueirido et al. (2015) provided interesting results by analyzing the elbow joint shape as a “taxon-free” proxy for predatory behavior in borophagines. Here, we go one step further regarding the search for “taxon-free” traits in the carnivoran appendicular skeleton. Our purpose is to find multiple traits that can be interpreted from a biomechanical and functional point of view to be used later as indicators of predatory behavior in extinct carnivorans and, more specifically, in borophagines.

Given that forelimb anatomy is especially informative of carnivoran predatory behavior (see Andersson and Werdelin 2003; Andersson 2005; Meachen-Samuels and Van Valkenburgh 2009; Figueirido and Janis 2011; Samuels et al. 2012; Fabre et al. 2013; Janis and Figueirido 2014), we have focused this study on the morphometric analysis of the forelimb bones (i.e., humerus, radius, and ulna). However, a similar study focused on the hind limb is currently in progress.

Our specific objectives are: (*i*) to explore the association between forelimb bone morphology and those functional aspects related to predatory behavior; and (*ii*) to derive inferences on the predatory behavior of borophagines according to these functional aspects.

Material and Methods

Sample

The sample of living carnivorans analyzed comprises the humerus, radius, and ulna of 115 individuals distributed among 37 species (Table 1). The sample of extinct species includes 66 fossil specimens –sum of humeri, radii, and ulnae– from ten borophagine species (Table 2). The sample of living species was selected in order to cover the highest variability as possible in body size and ecology. However, special attention was paid to those families that show a body size range comparable to the extinct species analyzed. Effects of ontogenetic variation were avoided by selecting only adult specimens, as indicated by complete ossification of the epiphyseal growth plates. All specimens analyzed are housed in the following institutions: American Museum of Natural History (AMNH, New York) and Natural History Museum (NHM, London). Museum numbers and specific locations of the specimens

Table 1 Living species included in this study (N: number of individuals for each species). The predatory category of each species is also indicated (see the main text for the specific bibliographic sources)

Family	Species	N	Predatory behavior
Canidae	*Canis adustus*	1	Pounce/pursuit
Canidae	*Canis aureus*	2	Pounce/pursuit
Canidae	*Canis latrans*	5	Pounce/pursuit
Canidae	*Canis lupus*	5	Pursuit
Canidae	*Canis mesomelas*	4	Pounce/pursuit
Canidae	*Canis simensis*	1	Pounce/pursuit
Canidae	*Cerdocyon thous*	5	Pounce/pursuit
Canidae	*Chrysocyon brachyurus*	2	Pounce/pursuit
Canidae	*Cuon alpinus*	4	Pursuit
Canidae	*Lycaon pictus*	2	Pursuit
Canidae	*Nyctereutes procyonoides*	2	Pounce/pursuit
Canidae	*Speothos venaticus*	2	Pounce/pursuit
Canidae	*Urocyon cinereoargenteus*	4	Pounce/pursuit
Canidae	*Vulpes lagopus*	2	Pounce/pursuit
Canidae	*Vulpes velox*	2	Pounce/pursuit
Canidae	*Vulpes vulpes*	3	Pounce/pursuit
Felidae	*Acinonyx jubatus*	5	Pursuit
Felidae	*Leptailurus serval*	2	Ambush
Felidae	*Lynx rufus*	4	Ambush
Felidae	*Panthera leo*	5	Ambush
Felidae	*Panthera onca*	4	Ambush
Felidae	*Panthera pardus*	6	Ambush
Felidae	*Panthera tigris*	4	Ambush
Felidae	*Puma concolor*	4	Ambush
Felidae	*Uncia uncia*	4	Ambush
Hyaenidae	*Crocuta crocuta*	5	Pursuit
Hyaenidae	*Hyaena brunnea*	1	Occasional
Hyaenidae	*Hyaena hyaena*	2	Pounce/pursuit
Procyonidae	*Nasua nasua*	1	Occasional
Procyonidae	*Procyon lotor*	3	Occasional
Ursidae	*Ailuropoda melanoleuca*	4	Occasional
Ursidae	*Helarctos malayanus*	1	Occasional
Ursidae	*Melursus ursinus*	3	Occasional
Ursidae	*Tremarctos ornatus*	1	Occasional
Ursidae	*Ursus americanus*	3	Occasional
Ursidae	*Ursus arctos*	4	Occasional
Ursidae	*Ursus thibetanus*	3	Occasional

Table 2 List of extinct taxa of the subfamily Borophaginae studied. The number of specimens for each taxon is indicated for humerus (H), radius (R) and ulna (U). See also Table S2 for specific museum numbers of the fossils studied

Species (abbreviation)	H	R	U
Aelurodon ferox (*Afe*)	1	5	2
Aelurodon taxoides (*Ata*)	3	2	2
Borophagus pugnator (*Bpu*)	0	1	0
Borophagus secundus (*Bse*)	0	2	0
Carpocyon tagarctus (*Cta*)	0	1	0
Epicyon haydeni (*Eha*)	2	4	1
Epicyon saevus (*Esa*)	1	3	2
Paratomarctus euthos (*Peu*)	1	0	0
Paratomarctus temerarius (*Pte*)	1	1	1
Tomarctus (*Tom*)	10	13	7

are provided in Table S1 for the extant species and in Table S2 for the extinct ones.

Morphometrics

The shape of the forelimb bones was recorded by digitizing a set of three-dimensional homologous landmarks (LK) using a Microscribe G2X. LK coordinates (x, y, z) were collected with software Immersion Inc. We digitized the same LK's used in a previous article (see Martín-Serra et al. 2014a), in which the criteria for homology and specific locations of the LK's selected are further explained (see also Fig. S1 and Table S3). In addition, the bone surfaces of the humerus, radius, and ulna of one individual of *Panthera onca* (AMNH-139,959) were scanned with a 3D-mobile surface scanner (Nextengine HD) using the software ScanStudio Pro. The same LK's digitized on the bones of the specimens analyzed were also digitized on these 3D-scannings with software Landmark from the Institute of Data Analysis and Visualization (IDAV 2002-2006). In this way, the three-dimensional surface of the shape changes accounted for by the statistical analyses was modeled by morphing (Wiley et al. 2005; Martín-Serra et al. 2014a, 2014b, 2015), which facilitated their morphological interpretation.

Scaling, translation, and rotation effects were removed from the LK's coordinates by performing a Procrustes fit for each bone (Rohlf and Marcus 1993; Dryden and Mardia 1998) using software MorphoJ (Klingenberg 2011). Once the specimens were aligned, a Principal Component Analysis (PCA) of the Procrustes coordinates (Pco) was performed separately on the covariance matrix for each limb bone using MorphoJ (Klingenberg 2011). The morphological changes accounted for by each PC were discussed independently.

Grouping Taxa According to Predatory Behavior

The first step of this study was to explore how differences in the shape of the forelimb bones are reflected by differences in predatory behavior. For this reason, the living taxa were classified into four categories of predatory behavior, following Van Valkenburgh (1985): (*i*) ambushers (e.g., all felids except the cheetah, *Acinonyx jubatus*): predators that usually stalk and chase their prey for short distances, using the forelimbs to grapple with it; (*ii*) occasional predators (e.g., most ursids): species that hunt only occasionally and are not specialized for a particular predatory behavior; (*iii*) pounce/pursuit predators (e.g., most canids): species that usually pounce or chase their prey for short distances and do not use their forelimbs to grapple with it; and (*iv*) pursuers (e.g., pack hunting canids and hyaenids): predators adapted to endurance running that chase their prey for relatively long distances and do not use their forelimbs to grapple with it. See Table 1 for the classification of each species. The only exception to the criteria used by Van Valkenburgh (1985) was the cheetah, a sprinter not adapted to endurance running, which was also classified as a pursuit predator following Figueirido and Janis (2011) and Janis and Figueirido (2014). In addition, the brown hyena, not included in Van Valkenburgh (1985), was considered as an occasional predator following the ecological description of Wilson and Mittermeier (2009).

Shape Variation and Predatory Behavior

The first method selected to test for differences between predatory categories was a multivariate analysis of variance (MANOVA) on the scores obtained by each bone on a principal components analysis (PCA). These scores were used as dependent variables and predatory category as the independent factor. Those PC's that jointly accounted for at least 90 % of the original variance were included in the MANOVA's (of course, extinct species were excluded). These PC's were selected for avoiding the inflation of variables in the analysis, as all PCA's yielded more than 48 eigenvectors for each limb bone (i.e., the number of LK's digitized on each). Canonical variate analysis (CVA) was not used in this step because it can yield misleading results when the number of morphometric variables (three-dimensional coordinates of LK's in this study) is higher than the number of cases (i.e., specimens) per group compared (Mitteroecker and Bookstein 2011), as happens in our case. All MANOVA's and associated analyses (see below) were performed using IBM SPSS Statistics v.15.

The next step was to explore the morphological aspects accounted for by those PC's that better characterize each category of predatory behavior. To accomplish this, we first performed Levene's tests for each PC to evaluate the homogeneity of within-group variances, because the MANOVA F-test is very sensitive to differences in within-group variances (Quinn and Keough 2002). For those PC's that showed homogeneity of variances, the F-statistic was used to test if they allowed discrimination between predatory categories. In contrast, when heterogeneity of variances was noted, a single-factor robust ANOVA computing Welch's test for the level of significance (Quinn and Keough 2002) was performed, because this test does not require the assumption of homogeneity of variance. Subsequently, the partial eta squared (η^2) was calculated for each PC, as this parameter measures the proportion of the total variance of each dependent variable (PC) that is accounted for by between-groups differences. In this way, those PC's that yielded significant results of the F-statistic (or Welch's test) and higher values for partial η^2 were selected for subsequent interpretations.

Together with the MANOVA's, post hoc analyses were also performed for identifying the predatory categories that were significantly separated by each PC. 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 (see Quinn and Keough 2002 and references therein). Using the information provided by these tests and the morphological changes associated with each PC, we made the ecomorphological interpretations of the differences among categories of predatory behavior for each bone.

Ecomorphological Inferences for Borophagines

Although the fossil specimens were not included in the MANOVA's, they were previously included in the PCA's. Therefore, after deciphering the functional and ecological meaning of each PC, special attention was paid to the scores of borophagine specimens along these eigenvectors. The main objective was to extend the functional interpretations obtained from the living taxa to the extinct ones, which would allow in turn deriving paleoautecological inferences on their predatory behavior.

A series of CVA's were also performed with the Procrustes coordinates using software IBM SPSS Statistics v15. Given that this type of analysis can provide misleading results if there are more variables than cases per group, as noted above, dimensionality was reduced using a stepwise procedure for selection of variables. However, given that the variables used are 3D LK's, this procedure often precludes the morphological interpretation of the functions obtained (as the x-, y-, or z-coordinate of a given LK can be removed). In any case, these CVA's were performed to confirm the results obtained with the MANOVA tests and not to make new functional interpretations. The stepwise procedure was performed using the Wilk's lambda method available. The variables were selected according to F-probability values of <0.05 to be included and >0.1 to be removed.

Results

Shape Variation and Group Separation

The PC's obtained for each bone were included as dependent variables in the MANOVA's, following the criterion exposed above (PC 1 to PC 15 for the humerus and the radius, and PC 1 to PC 11 for the ulna; see Table S4).

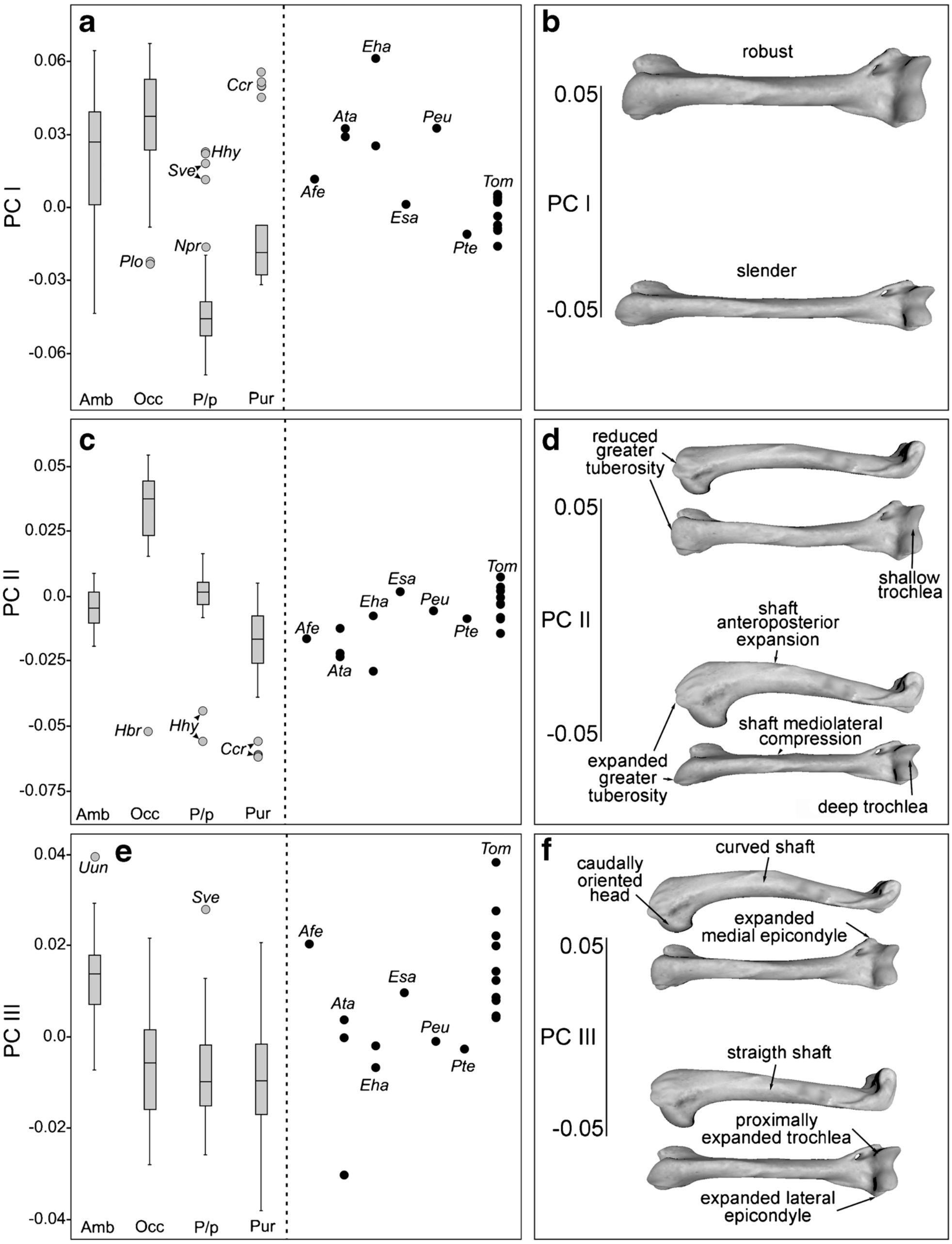
The MANOVA's of the three forelimb bones showed F-statistics that were significant for predatory categories in all cases. Those morphological features that showed an association with predatory behavior were explored for each forelimb bone.

Humerus The *P*-values and partial η^2 values of each PC obtained for humeral morphology (Table S4) indicate that the first three PC's account for the majority of the between-group separation (Table 3). Therefore, these PC's were selected for subsequent functional interpretations. Ambushers and occasional predators show positive scores on the first component (Figs. 1a, S2a), which is associated with a robust humerus (Fig. 1b), and both groups do not differ statistically from each other according to a Bonferroni's test. Pursuit predators have intermediate scores (Figs. 1a, S2a) and, hence, show an intermediate degree of robustness (Fig. 1b). Finally, pounce/pursuit predators have the most negative scores (Figs. 1a, S2a) associated with a slender humerus (Fig. 1b). Both pursuit and pounce/pursuit predators are statistically different from each other, and also from ambushers and occasional predators (Table S5).

Table 3 Results obtained in the MANOVA's performed with the PC's of each bone. The partial η^2 used to select the most important PC's are indicated. The values for the PC's finally selected are in bold

Components	Partial η^2 Humerus	Radius	Ulna
PC 1	**0.511**	**0.567**	**0.575**
PC 2	**0.548**	0.263	**0.448**
PC 3	**0.383**	**0.610**	**0.452**
PC 4	0.127	0.271	0.101
PC 5	0.059	0.180	0.111
PC 6	0.113	0.059	0.067
PC 7	0.014	0.086	0.036
PC 8	0.126	0.012	0.030
PC 9	0.062	0.071	0.032
PC 10	0.048	0.038	0.089
PC 11	0.104	0.023	0.046
PC 12	0.002	0.020	
PC 13	0.023	0.018	
PC 14	0.036	0.003	
PC 15	0.023	0.024	

Fig. 1 Scores and shape changes for the first three PC's for the humerus. Box plots (**a, c, e**) are accompanied by their associated shape changes (**b, d, f**) for each P*c. humerus* models are shown in cranial and lateral views. For each predatory group, the bar displays the median, the box shows the 25–75 % interquartile range of the distribution and, the whisker encloses 5–95 % of cases (grey circles indicate outliers; *Ccr*: *Crocuta crocuta*, *Hbr*: *Hyaena brunnea*, *Hhy*: *Hyaena hyaena*, *Npr*: *Nyctereutes procyonoides*, *Plo*: *Procyon lotor*, *Sve*: *Speothos venaticus*, *Uun*: *Uncia uncia*). Amb, ambushers; Occ, occasional predators; P/p, pounce/pursuit predators; Pur, pursuers. Black circles represent fossil specimens of borophagine species (see Table 2 for species labels)



Occasional predators have the highest scores on the second PC (Figs. 1c, S2a), as their humeri show a reduced greater tuberosity as well as a shallow and wide trochlea (Fig. 1d). In contrast, pursuit predators have the lowest scores on this axis (Figs. 1c, S2a), which reflect that their humeri have an expanded greater tuberosity and a shaft that is compressed mediolaterally and expanded anteroposteriorly, showing a narrow and deep trochlea (Fig. 1d). Both ambushers and pounce/pursuit predators have intermediate scores on this axis (Figs. 1c, S2a) and, thus, show an intermediate morphology between pursuit and occasional predators. In fact, these two groups are not statistically different from each other (according to Dunnett's T3), but both differ from occasional and pursuit predators (Table S5).

Ambushers have positive scores on the third PC (Figs. 1e, S2c), which separates them well from the remaining groups (Table S5). Their humeri show a caudally oriented head, a curved shaft, and an expanded medial epicondyle (Fig. 1f). Occasional, pounce/pursuit, and pursuit predators all have negative scores (Figs. 1e, S2c), related to a straight humeral shaft, an expanded lateral epicondyle, and a proximally expanded trochlea (Fig. 1f). The projections of the three predatory groups on this PC are not statistically different (Table S5).

Radius The *P*-values and partial η^2 values for radius shape (Table S4) indicate that the first and third PC's account for a large proportion of the between-group separation (Table 3). Pounce/pursuit predators have the most positive scores on the first PC (Figs. 2a, S3a) and occupy a portion of the morphospace that is associated with the presence of a slender radius that shows an oval-shaped radial head whose major axis is parallel to the mediolateral plane (Fig. 2b). Pursuers have low positive values on this eigenvector (Figs. 2a, S3a), but they are statistically different from pounce/pursuit predators (Table S5). In contrast, both ambushers and occasional predators show similar scores, which do not differ significantly, on the negative portion of the morphospace (Fig. 2a, S3a; Table S5). This is associated with a robust radius and an oval-shaped radial head whose major axis is rotated with respect to the mediolateral plane (Fig. 2b).

Ambushers differ statistically from the remaining groups in their projections on the third PC, an axis on which they have the most positive scores (Figs. 2c, S3a). This is related to the presence of a radial shaft that is anteroposteriorly compressed and a bicipital tuberosity that is proximally shifted (Fig. 2d). In contrast, occasional predators have the most negative scores (Figs. 2c, S3a), as their radii show an anteroposterior thickening in the shaft and in the distal epiphysis, and also a distally shifted bicipital tuberosity (Fig. 2d). Pursuit and pounce/pursuit predators have similar intermediate scores and radial morphology (Figs. 2c, S3a; Table S5), and both are statistically different from ambushers and occasional predators (Table S5).

Ulna As indicated by the partial η^2 and *P*-values for ulna shape (Table 3, S4), the first three PC's account for the most important fraction of the between-groups variance. For the first PC, both ambushers and occasional predators occupy the positive portion of the morphospace (Figs. 3a, S4a) characterized by the possession of a robust ulna (Fig. 3b). The scores of both groups on this eigenvector do not differ statistically (Table S5). Pounce/pursuit predators have the most negative scores (Figs. 3a, S4a), related to extremely slender ulnae (Fig. 3b). In contrast, pursuers show slightly negative scores (Figs. 3a, S4a) and, accordingly, their ulnae are not as slender as those of pouncers. The scores on this eigenvector of both pursuit and pounce/pursuit predators differ statistically from each other, and also from the remaining groups (Table S5).

Ambush predators have the most positive scores on the second PC (Figs. 3c, S4a), which reflects that their ulnae have a long olecranon process and a straight shaft (Fig. 3d). This group is statistically different from the others. Occasional predators occupy the opposite extreme on this axis (Figs. 3c, S4a), related to a short olecranon process and a caudally curved shaft (Fig. 3d). Pounce/pursuit predators have

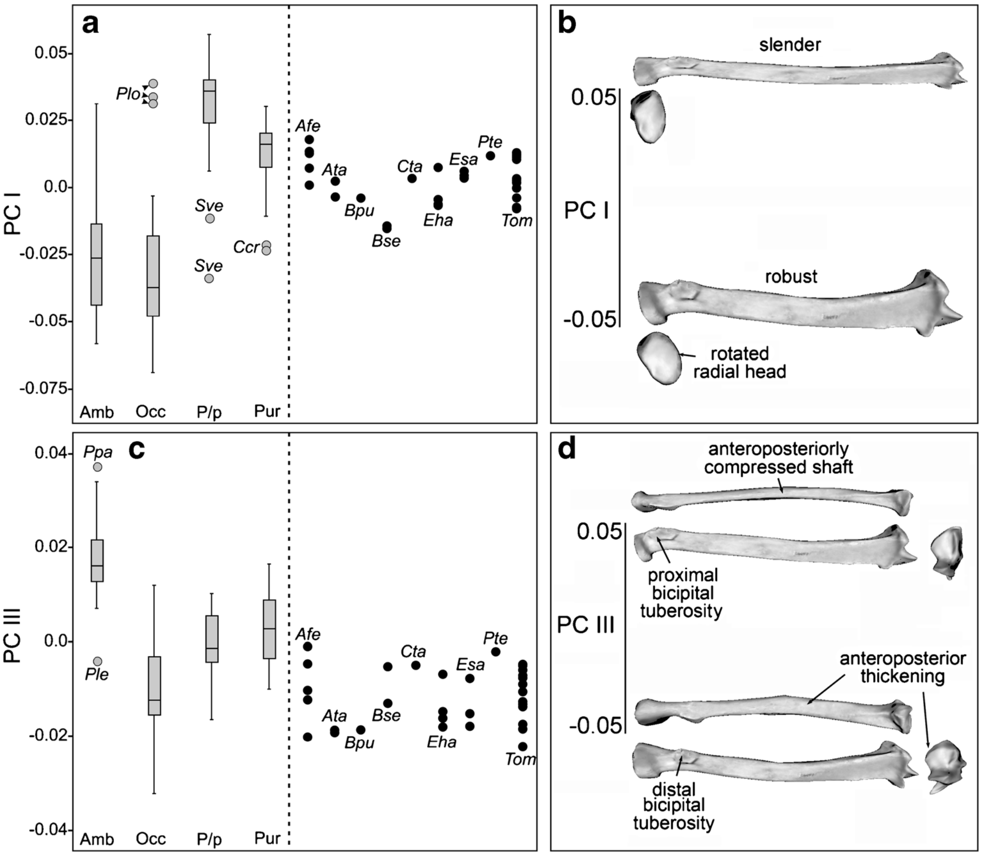


Fig. 2 Scores and shape changes for the first and third PC's for the radius. Box plots (**a, c**) are accompanied by their associated shape changes (**b, d**) for each PC. Radius models are shown in caudal, lateral, proximal, and distal views. For each predatory group, the bar displays the median, the box shows the 25–75 % interquartile range of the distribution, and the whisker encloses 5–95 % of cases (grey circles indicate outliers; *Ccr*: *Crocuta crocuta*, *Ple*: *Panthera leo*, *Plo*: *Procyon lotor*, *Ppa*: *Panthera pardus*, *Sve*: *Speothos venaticus*). Amb, ambushers; Occ, occasional predators; P/p, pounce/pursuit predators; Pur, pursuers. Black circles represent fossil specimens of borophagine species (see Table 2 for species labels)

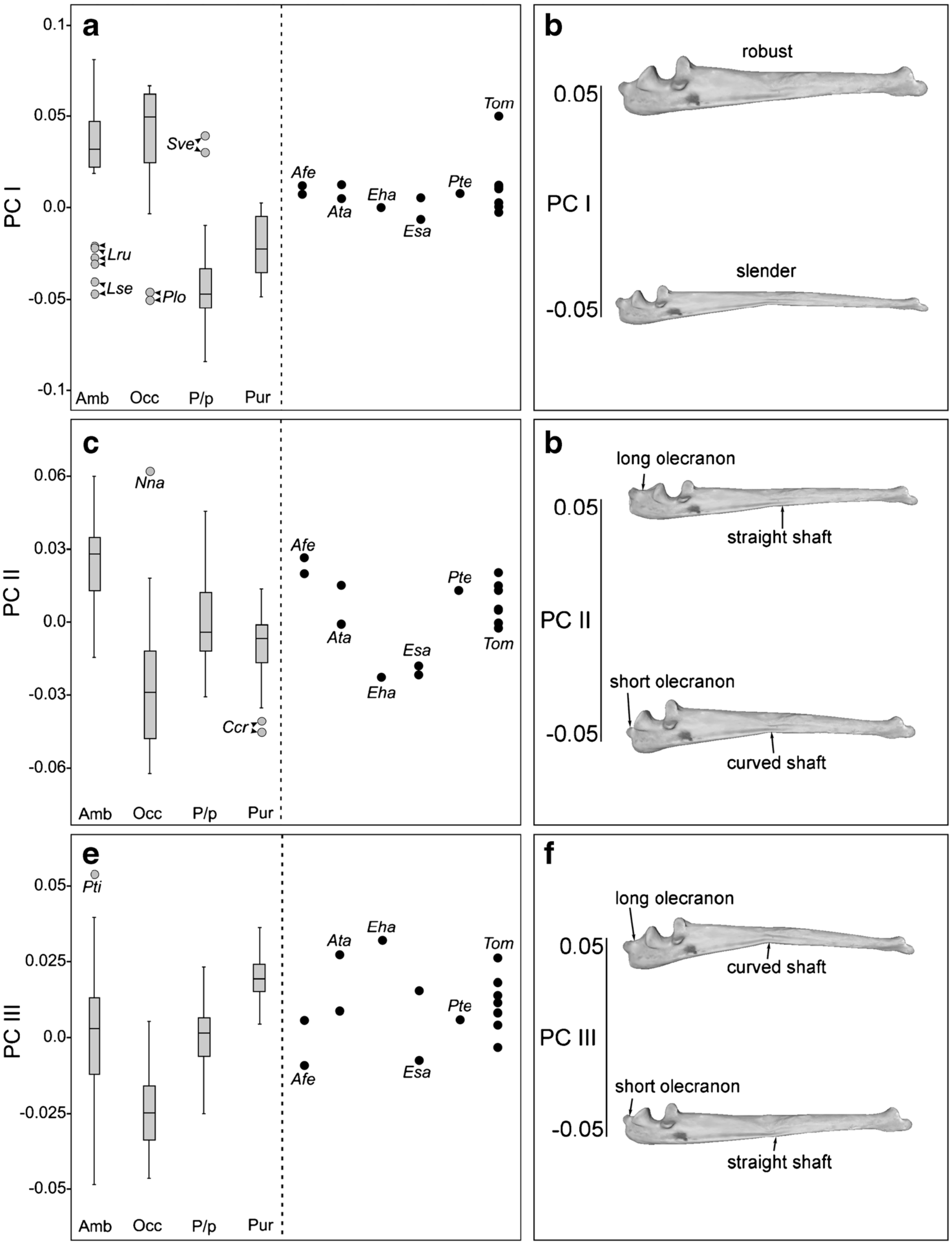


Fig. 3 Scores and shape changes for the first three PC's for the ulna. Box plots (**a, c, e**) are accompanied by their associated shape changes (**b, d, f**) for each Pc. *ulna* models are shown in lateral view. For each predatory group, the bar displays the median, the box shows the 25–75 % interquartile range of the distribution, and the whisker encloses 5–95 % of cases (grey circles indicate outliers; *Ccr*: *Crocuta crocuta*, *Lru*: *Lynx rufus*, *Lse*: *Leptailurus serval*, *Nna*: *Nasua nasua*, *Plo*: *Procyon lotor*, *Pti*: *Panthera tigris*, *Sve*: *Speothos venaticus*). Amb, ambushers; Occ, occasional predators; P/p, pounce/pursuit predators; Pur, pursuers. Black circles represent fossil specimens of borophagine species (see Table 2 for species labels)

intermediate scores and morphologies (Figs. 3c, S4a). Although the scores of occasional and pounce/pursuit predators on this eigenvector are significantly different, pursuers score between both groups and cannot be distinguished from any of them (Figs. 3c, S4a; Table S5).

Pursuit predators show the highest scores on the third component (Figs. 3e, S4c) and are characterized by an ulna with a long olecranon process and a caudally curved shaft (Fig. 3f). In contrast, occasional predators take the lowest ones (Figs. 3e, S4c), which indicates that their ulna has a short olecranon process and a straight shaft (Fig. 3f). Both groups differ statistically from each other, and also from the remaining groups. However, ambushers and pounce/pursuit predators have intermediate scores (Figs. 3e, S4c) and do not differ between them (Table S5).

Paleobiological Inferences for Borophagines: PCA and CVA

The distribution of borophagine taxa along these PC's varies among the three bones studied. For example, for the first PC of humeral shape, *Tomarctus*, *Paratomarctus temerarius*, and *Epicyon saevus* have intermediate scores, which overlap to a great extent with those of ambush predators (Figs. 1a, S2a, b), but also with some occasional predators, as in the case of *Epicyon haydeni*, which shows extremely positive scores

(Figs. 1a, S2a, b). In contrast, borophagines group on the second PC near the average shape of carnivorans (Figs. 1c, S2a, b), occupying the same area as pursuit and ambush predators. *Aelurodon ferox* and several specimens of *Tomarctus* have the most positive scores on the third PC, which is also the case of ambush predators among the living carnivorans (Figs. 1e, S2c, d). In the opposite direction, *E. haydeni*, *Paratomarctus euthos*, and *P. temerarius* show intermediate scores, similar to those of occasional, pursuit and pounce/pursuit predators (Figs. 1e, S2c, d).

In the case of the first PC of radius shape, most borophagines overlap with pursuit predators (Figs. 2a, S3), although *Borophagus secundus* is closer to ambushers and occasional predators (Figs. 2a, S3). Borophagines tend to overlap with occasional predators on the third PC (Figs. 2c, S3), with the exception of *Carpocyon tagarctus*, *Paratomarctus temerarius*, and some specimens of *A. ferox*, which are closer to pursuers or pounce/pursuit predators (Figs. 2c, S3).

The PCA performed for ulna shape shows that most borophagines cluster around the average carnivoran shape on the first PC (Figs. 3a, S4a, b) and are not clearly associated with any of the predatory groups compared (Figs. 3a, S4a, b). They also have intermediate scores on the second PC (Figs. 3c, S4a, b), but the specimens of *A. ferox* show the most positive values and are closer to ambushers. In contrast, *E. saevus* and *E. haydeni* have the most negative ones and are closer to occasional and pursuit predators (Figs. 3c, S4a, b). In the case of the third PC, borophagines show, in general, positive scores (Figs. 3e, S4c, d). The most positive projections are those of *Aelurodon taxoides*, *E. haydeni*, and some specimens of *Tomarctus*, which overlap mainly with pursuers (Figs. 3e, S4c, d). In contrast, *A. ferox* and one specimen of *E. saevus* have the most negative scores and coincide with both ambushers and pounce/pursuit predators (Figs. 3e, S4c, d).

The stepwise CVA performed for humeral shape yielded highly significant results for the discrimination of predatory groups (Table 4). The percentage of specimens correctly classified after cross-validation was 94.8 %. According to the probability of pertinence to a given predatory group, borophagines are classified within the following groups (Table 5): *Aelurodon ferox* is mainly classified as a pursuer, while *E. haydeni*, *E. saevus*, *P. euthos*, and *P. temerarius* are all classified as ambushers (Table 5). However, *A. taxoides* and *Tomarctus* are not clearly assigned to a single group, as they have similar probabilities of belonging to ambush and pursuit predators (Table 5).

The CVA for the radius also showed significant results (Table 4), with 85.2 % of correct classifications after cross-validation. The probabilities for borophagines of belonging to one of these groups are shown in Table 5. Most specimens of *Aelurodon ferox*, *Borophagus pugnator*, *E. saevus*,

Table 4 Results obtained in the stepwise CVA for the three bones. The Pco included in the analysis and their standardized coefficients for each CV are shown. The eigenvalue, percentage of variance explained, Wilks' λ, χ^2 and *P*-value for each CV are also shown

	CV1	CV2	CV3
Humerus			
Pco 2	0.8896	0.6895	0.1277
Pco 5	−0.0305	−0.6629	−0.0871
Pco 7	−0.6504	0.5260	−0.4494
Pco 10	0.0168	−0.7805	−0.3172
Pco 12	0.7193	−0.2277	0.5938
Pco 14	−0.6169	0.0163	−0.6292
Pco 15	−0.0115	−0.5308	1.3856
Pco 24	0.2039	0.3837	0.8079
Pco 27	1.3979	−0.4143	0.1771
Pco 38	1.2487	0.0308	−0.5046
Pco 40	−0.1995	0.7509	0.1908
Pco 41	0.3796	0.1788	−0.6404
Pco 42	0.5640	0.3026	0.1102
Pco 43	0.2788	−0.3595	−0.3189
Pco 45	0.3468	0.5845	−0.1909
Pco 46	−0.0780	0.4478	−0.5265
Pco 51	0.5357	−0.0937	0.4970
Eigenvalue	16.53	5.89	1.1
% variance	70.3	25	4.7
Wilks' λ	0.004	0.069	0.477
X^2	572.84	276.42	76.68
P-value	< 0.001	< 0.001	< 0.001
Radius			
Pco 8	0.0717	−0.4498	0.6046
Pco 14	0.0193	−0.4660	0.6512
Pco 19	0.5208	−0.2767	0.2315
Pco 21	−0.2918	0.5928	−0.0259
Pco 22	0.5024	0.3388	0.1559
Pco 23	0.3278	−1.0574	−0.4041
Pco 31	0.7470	−0.0851	0.0904
Pco 32	0.5302	−0.1644	0.0462
Pco 33	−1.1109	0.8180	−0.4117
Pco 37	0.2380	−0.3019	0.0931
Pco 41	−1.0222	0.4736	0.0301
Pco 45	0.3797	0.3132	−0.3515
Pco 48	−0.7589	0.4371	−0.4445
Eigenvalue	6.67	3.78	0.678
% variance	60	33.9	6.1
Wilks' λ	0.016	0.125	0.596
X^2	434.51	219.55	54.61
P-value	< 0.001	< 0.001	< 0.001
Ulna			
Pco 3	1.0090	0.2711	0.4172
Pco 16	0.0418	0.6672	−0.2442
Pco 20	−0.1876	0.0174	0.5407

Table 4 (continued)

	CV1	CV2	CV3
Pco 28	0.0890	0.6930	0.3473
Pco 29	−0.1076	0.3906	−1.1632
Pco 30	0.7520	0.4878	0.1543
Pco 39	−0.3293	−0.4404	0.3471
Pco 40	0.5464	0.0396	0.1133
Pco 47	−1.0632	0.6670	0.7506
Pco 52	0.6444	−0.1168	0.4177
Pco 56	0.6549	0.3823	−0.0215
Pco 58	0.7527	−0.1411	0.4316
Pco 60	−0.7647	−0.3087	−0.1243
Eigenvalue	11.75	3.42	0.539
% variance	74.8	21.8	3.4
Wilks' λ	0.012	0.147	0.65
X^2	470.9	202.35	45.48
P-value	< 0.001	< 0.001	< 0.001

Table 5 Probabilities of pertinence to predatory categories obtained in the CVA's for borophagine species. Humerus, radius and ulna. Amb, ambushers; P/p, pounce/pursuit predators; Pur, pursuers; Occ, occasional predators. See Table 2 for species labels

	Amb	P/p	Pur	Occ
Humerus				
Afe	0.36	0.00	**99.63**	0.00
Ata	36.40	1.18	**62.41**	0.00
Eha	**90.19**	0.12	9.70	0.00
Esa	**99.98**	0.01	0.01	0.00
Peu	**99.94**	0.05	0.01	0.00
Pte	**89.39**	1.16	9.45	0.00
Tom	**51.83**	13.48	34.69	0.00
Radius				
Afe	19.27	**78.25**	2.44	0.04
Ata	0.02	31.75	**68.23**	0.00
Bpu	0.02	**93.66**	6.32	0.00
Bse	**48.98**	2.25	3.32	45.46
Cta	40.34	**55.09**	4.57	0.00
Eha	1.98	27.82	**70.19**	0.00
Esa	0.97	**76.55**	22.48	0.00
Pte	1.13	**98.71**	0.16	0.00
Tom	3.81	**86.26**	2.41	7.52
Una				
Afe	35.27	**49.56**	0.22	14.95
Ata	**50.43**	0.25	49.18	0.14
Eha	0.00	**96.30**	3.70	0.00
Esa	2.10	35.92	4.20	**57.78**
Pte	0.03	**85.91**	1.29	12.76
Tom	13.28	**34.43**	18.45	33.84

The highest values of each species highlighted in bold

P. temerarius, and *Tomarctus* are classified as pounce/pursuit predators, while those of *A. taxoides* and *E. haydeni* are classified as pursuers (Table 5). In contrast, both *B. secundus* and *Carpocyon tagarctus* have uncertain classifications, although they group with ambushers and with occasional predators or with pounce/pursuit predators, respectively (Table 5).

As with the case of the analyses performed for the humerus and radius, the CVA computed from ulna shape separates the predatory groups fairly well (Table 4), with 86.1 % of correct classifications after cross-validation. Table 5 shows the probabilities of pertinence obtained for borophagine species to each predatory group. Both *E. haydeni* and *P. temerarius* are unambiguously classified as pounce/pursuit predators (Table 5). However, this analysis classifies many species with similar probabilities for different predatory groups. For example, *A. taxoides* may be interpreted as an ambusher or as a pursuer, and *E. saevus* as a pounce/pursuit or as an occasional predator (Table 5). The cases of *A. ferox* and *Tomarctus* are the most extremes, as they have similar probabilities to belong to each of the three predatory groups (Table 5).

Discussion

Morphological Variation and Function

In the three bones analyzed, the morphological variation accounted for the first eigenvector is essentially the same. These morphologies involve a change in the degree of bone robustness (Figs. 1b, 2b and 3b), which is probably associated with a trade-off between maintaining resistance to stresses and keeping energetic efficiency during locomotion (Pasi and Carrier 2003; Kemp et al. 2005; Martín-Serra et al. 2014a, 2014b). As such, the robust bones of ambush predators and occasional predators indicate that locomotor efficiency is not a key factor for these groups. While occasional predators do not usually perform long or fast runs (Van Valkenburgh 1985), in which energetic efficiency is crucial, ambushers are adapted to perform short bursts of speed when hunting, although they do not chase their prey for long distances (Van Valkenburgh 1985; Anyonge 1996). Therefore, both predatory strategies require the possession of robust bones for resisting the high peaks of bending stress generated during acceleration or deceleration, changes of direction, and also when grappling with prey (Anyonge 1996; Kemp et al. 2005). As a result, the radii of ambushers and occasional predators show a round-shaped and rotated head (Fig. 2b), which gives more freedom to the rotational movements of this element with respect to the ulna (Gonyea 1978; MacLeod and Rose 1993; Argot 2001; Fabre et al. 2013). This trait is advantageous for both predatory groups, which use their forelimbs to grapple with prey or manipulate food

(Van Valkenburgh 1985; Anyonge 1996; Anton et al. 2004; Fabre et al. 2013). In contrast, pounce/pursuit and pursuit predators, which are adapted to perform long travels for foraging or long chases after prey, respectively, have slender forelimb bones that increase energetic efficiency during locomotion (Van Valkenburgh 1985; Taylor 1989). The anatomical difference observed between these two groups could result from size differences: pounce/pursuit predators tend to be smaller than pursuit predators and thus, their forelimb bones are comparatively slender due to allometric effects (see Martín-Serra et al. 2014a).

The shape changes associated with the second PC of humeral shape mainly account for differences in mobility that result in more efficient movements in the parasagittal plane. In this sense, the shallow trochlea of occasional predators (Fig. 1c, d) indicates a high degree of freedom for the rotation of the elbow joint and increased ability to supinate the forearm (Andersson 2004; Figueirido and Janis 2011; Janis and Figueirido 2014). This is further accomplished by a round-shaped cross-section of the shaft and a reduced greater tuberosity (Fig. 1d), which indicates that limb movements are not restricted to the parasagittal plane in this predatory group (Anyonge 1996; Figueirido and Janis 2011; Janis and Figueirido 2014; Martín-Serra et al. 2014a). Accordingly, the forelimbs of occasional predators can be used for different tasks, including food manipulation, climbing, or grappling with prey (Fabre et al. 2013), rather than being specialized to perform long and/or fast runs. In contrast, the deep and narrow trochlea of pursuers (Fig. 2c, d) decreases their ability to rotate laterally the elbow joint and thus, improves efficiency for parasagittal movements (Andersson 2004; Figueirido and Janis 2011; Janis and Figueirido 2014). In addition, the greater tuberosity is expanded in these carnivorans, which increases the mechanical advantage of the supraspinatus muscle for humeral protraction (Spoor and Badoux 1986), and the shaft is expanded anteroposteriorly and compressed mediolaterally (Fig. 1d). These traits suggest that the main direction of movement of the humerus -and thus the main loads exerted on it during locomotion- is in the anteroposterior (parasagittal) plane (Anyonge 1996), which is advantageous for animals that perform fast and/or continued runs pursuing their prey (Janis and Wilhelm 1993).

The third PC for humeral shape separates ambush predators from other groups (Fig. 1e). The morphology associated with this axis reflects the ability of ambushers to subdue their prey with the forelimbs. In these predators, the humeral head is oriented caudally and the shaft is curved anteroposteriorly (Fig. 1f), which suggest that the humerus functions in a partially flexed position when the prey is grappled with the forelimb. In addition, the medial epicondyle is expanded, which provides a larger surface for the origin of the flexor muscles of the Manus. This indicates the presence of well-developed flexor muscles to grasp with prey using the forepaw (Meachen-Samuels and Van Valkenburgh 2009).

The third PC for radius shape allows the identification of the anatomy typical of ambushers, which show a bicipital tuberosity that is more proximally positioned than in other predators (Fig. 2d). This indicates a lower mechanical advantage for the biceps brachii, which results in less powerful flexion of the forearm but allows flexion to occur more quickly (Taylor 1974; Homberger and Walker 2004). However, the position and development of the bicipital tuberosity is not always consistent with other indicators of flexion capability (Argot 2001). In any case, the presence of a bicipital tuberosity placed in a proximal position is associated with a distal epiphysis that is concave and anteroposteriorly compressed (Fig. 2d), which reflects a more restricted movement of the manus (Gonyea 1978). This trait helps to prevent dislocation at this joint, which could be advantageous for ambushers when hunting, as they have to exert large forces to subdue their prey. In contrast, the bicipital tuberosity of occasional predators, which is more distally located (Fig. 2d), seems to increase the power of the biceps brachii to flex the forearm. However, this trait is not always reliable, as discussed above. In addition, the square-shaped and less concave distal epiphysis of occasional predators (Fig. 2d) may allow them to develop less restricted movements with the wrist, which relates to manipulating abilities (Gonyea 1978).

The morphological traits described by the second and third PC's of ulna shape are striking, as they account for similar, although opposite, changes (Fig. 3d, f). The long olecranon process and the straight ulnar shaft of ambushers (Fig. 3c, d) are probably associated with their need to exert large forces with the forelimbs when grappling with prey, as indicated before, because this ulnar shape provides a high mechanical advantage for the triceps brachii when the forearm is partially flexed. This result agrees clearly with those obtained in previous studies: for example, Iwaniuk et al. (1999) associated the presence of a long olecranon with predatory abilities and a crouched posture in felids and mustelids; similarly, Meachen-Samuels and Van Valkenburgh (2009) correlated this trait with predation over large prey in felids. In contrast, the short olecranon process of occasional predators (Fig. 3c-f), which decreases the mechanical advantage for the triceps brachii in comparison with the anatomical condition of ambushers, probably relates to the fact that they do not usually exert large forces with their forelimbs when manipulating food items, or even when hunting prey that are usually small relative to them. The curved ulnar shaft of pursuit predators (Fig. 3e, f) is clearly associated with a more upright posture (Martín-Serra et al. 2014a). This trait increases functional limb length, and hence stride length (Janis and Wilhelm 1993), which is advantageous for reducing the costs of locomotion during a long chase after prey (Heglund et al. 1974; Strang and Steudel 1990; Janis and Wilhelm 1993).

Paleobiological Inferences for Borophaginae

Depending on the bone analyzed, the forelimb morphology of borophagines combines features that are typical of different predatory categories among modern carnivorans. In general, they have a robust humerus (Fig. 1a, b), which is not as mobile as in occasional predators and many ambushers (Fig. 1c, d). However, *A. ferox* and *Tomarctus* seem to have been able of some degree of interaction with their prey using their forelimbs (Fig. 1e, f). In addition, the hypercarnivorous canid *Speothos venaticus* plots close to the position of ambushers and borophagines (Fig. S2b, d). This species also has a robust humerus that provides a certain ability to exert forces with it, which is probably related to grappling with prey or swimming (Deutsch 1983; Kleiman 1972; Beisiegel and Zuercher 2005). These results agree in general with those obtained from CVA's, as they also classify borophagines as either ambush or pursuit predators, or place them between both types (Table 5). This evidences that the movements of the forelimb of borophagines were somewhat restricted to the parasagittal plane (i.e., those species classified as pursuers), but with a certain ability to interact with their prey using the forelimbs (i.e., those species classified as ambushers).

The radius of borophagines is relatively slender, similar to those of the living pursuers, and its rotational movement with respect to the ulna is partially restricted (Fig. 2a, b). However, the morphology of the radial distal epiphysis (Fig. 2c, d) indicates a certain degree of movement for the wrist. This combination of features is not shared with any living carnivoran, which suggests that, whatever the predatory behavior of borophagines was, the function of the radius was not fully comparable with any of the living groups. Even if we compare borophagines with the bush dog (*S. venaticus*), the latter has a more robust radius, which is closer to the anatomy of ambushers than borophagines (Fig. S3b). Therefore, in contrast with the case of the humerus, the bush dog is not a good analog of borophagines. These results are corroborated by those obtained with CVA, as this multivariate analysis provides also uncertain classifications for the borophagines.

The ulna has an intermediate degree of robustness in all borophagines (Fig. 3a, b), which suggests they were not as extremely adapted for energetic efficiency as modern pursuit or pounce/pursuit predators. However, the length of the olecranon process and the curvature of the shaft both show a high variability. For example, those species with a straight shaft and a long olecranon process (e.g., *A. ferox*; Fig. 3c, d) have a high mechanical advantage for the triceps brachii and the ability to develop a more flexed posture. This indicates that they could have used their forelimbs to some extent to grapple with prey. In contrast, those species with a curved shaft and a more upright posture (e.g., *A. taxoides*, *E. saevus*, and *E. haydeni*; Fig. 3c, d) were not clearly adapted to grapple with prey. In contrast, they could have developed a more efficient locomotion (e.g., *A. taxoides* and *E. haydeni*; Fig. 3e, f), although there is always the possibility that they were not secondarily adapted to grapple with prey if a cursorial condition was basal to these groups (e.g., *E. saevus*; Fig. 3e, f). As in the case of the radius, the bush dog is not a good analog for the borophagines, because it has a more robust ulna with a slightly longer olecranon (Fig. S4b, d). This suggests that, compared to borophagines, *S. venaticus* is less adapted to develop an efficient locomotion and to hold an upright posture. The CVA classifications obtained for *E haydeni* point also to an adaptation to develop an efficient locomotion. However, in the case of *E. saevus* and *A. taxoides* their morphology is more ambiguous (Table 5). Other taxa, such as *P. temerarius* and *Tomarctus*, have a more generalized morphology, as they do not show adaptations for manipulating prey or running fast and efficiently (Table 5). This is confirmed by the classification obtained for *Tomarctus*, but not for *P. temerarius*, as the former is assigned clearly to the pounce/pursuit predatory category (Table 5).

These results agree with the inferences derived by Munthe (1989), who showed that borophagines had a certain ability to manipulate prey according to the morphology of several forelimb structures (e.g., scapulohumeral and elbow joints, muscle insertion scars, etc.) and other traits of the postcranial skeleton (i.e., hind limb morphology and vertebral column). In summary, this study concluded that borophagines did not optimize endurance running, as do modern canids. However, Munthe (1989) also recognized several differences among borophagine taxa: for example, *Epicyon* had more slender limbs, and hence was interpreted as more "cursorial" than *Aelurodon*, *Tomarctus*, and *Borophagus*, which showed more robust limbs (Munthe 1989). Although our findings broadly match with these interpretations, we have shown some adaptive differences between *E. haydeni* and *E. saevus*. However, Van Valkenburgh et al. (2003) concluded that although the body size and craniodental morphology of some borophagines suggest that they fed on large prey, they probably did not have the ability to grapple and subdue prey as the living felids do. In addition, compared to the living strict scavengers (e.g., the brown hyena), borophagines seem to have been more abundant in their paleocommunities. For this reason, Van Valkenburgh et al. (2003) proposed that such specialized trophic behavior was unlikely for borophagines. Instead, they concluded that most borophagine species were pack-hunting predators, not scavengers as proposed previously by other authors (e.g., Werdelin 1989; Munthe 1989). Finally, Andersson (2005) pointed to the opposite direction, as he found that borophagines retained the ability to supinate the forearm, which suggests that they could grapple with prey like the living felids. This led him to propose that pack-hunting predation was unlikely for borophagines. In summary, the comparative analysis of the morphological traits of the postcranial skeleton can hardly be conclusive on this aspect. This study is not an exception, but the differences among the three forelimb bones in modern carnivorans that relate to functional adaptions suggest that the predatory behavior of most borophagines is not adequately represented in any of the living categories. For this reason, the speculation about pack-hunting in borophagines should not only be restricted to their comparisons with the living pack-hunting canids, as other predatory strategies may also have been possible for these extinct canids.

Finally, our results also agree with those of Figueirido et al. (2015) on the elbow joint shape, who found that most borophagine taxa had an intermediate shape between pouncers and ambushers, a kind of incipient pounce condition. In addition, looking at some specific taxa, we also coincide when inferring a more ambush-like morphology to, for example, *Borophagus secundus*, which was also classified as ambush predator according to its elbow joint shape (Figueirido et al. 2015).

Conclusions

The main variations of shape of the forelimb bones that are associated with a given predatory behavior are: (*i*) a change in the degree of bone robustness, which relates to a trade-off between energetic efficiency and resistance to stresses (Martín-Serra et al. 2014a); (*ii*) a change in the degree of freedom for rotational movements in the humerus and radius; (*iii*) a change in the length of the olecranon process, and hence in the mechanical advantage for the triceps brachii; and (*iv*) a change in posture (flexed or upright), which is reflected in the humerus and ulna.

The borophagines included in these analyses showed a particular combination of these traits, which suggests that their predatory behavior cannot be unequivocally assigned to any of the modern categories. They were not as well adapted to grapple with their prey as are modern ambushers, but they neither had the cursorial adaptions of modern pounce/pursuit and pursuit predators. Therefore, our hypothesis is that their predatory behavior was not fully comparable to any of those shown by the living carnivorans. However, several differences among borophagine species emerged in this study, which can be functionally interpreted as indicative of cursorial adaptions for some taxa (e.g., *E. haydeni*), while others probably behaved more as ambushers (e.g., *A. ferox*).

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