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Quantifying morphological adaptations using direct measurements: The carnivoran appendicular skeleton as a case study

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Abstract

Here, I study whether locomotor adaptations can be detected in limb bones using a univariate approach, and whether those results are affected by size and/or shared evolutionary history. Ultimately, it tests whether classical papers on locomotor adaptations should be trusted. To do that, I analyzed the effect of several factors (size, taxonomic group, and locomotor habit) on limb bone morphology using a set of 43 measurements of the scapula, long bones, and calcaneus, of 435 specimens belonging to 143 carnivoran species. Size was the main factor affecting limb morphology. Size-corrected analyses revealed artifactual differences between various locomotion-related categories in the analyses of raw data. Additionally, several between-group differences were new to the size-corrected analyses, suggesting that they were masked by the size-effect. Phylogeny had also an important effect, although it only became apparent after removing the effect of size, probably due to the strong covariation of both factors. Regarding locomotor adaptations, locomotor type was used to represent locomotor specialization, and utilized habitat as an indicator of the capacity to adopt different modes of locomotion (running, swimming, climbing, and digging) and thus maximize resource exploitation by being capable of navigating all the substrates in the habitat they use. Locomotor type produced better results than utilized habitat, suggesting that carnivorans use locomotor specialization to minimize locomotion costs. The characteristic limb bone morphology for each locomotor type studied is described, including several adaptations and trends that are novel to the present study. Finally, the results presented here support the hypothesis of a "viverrid-like", forest-dwelling carnivoran ancestor, either arboreal or terrestrial.

KEYWORDS

adaptation, Carnivora, limb bones, locomotor type, phylogeny, size

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1 | INTRODUCTION

Since the early descriptive studies of H. F. Osborn's students (Dublin, 1903; Lull, 1904; Osburn, 1903; Shimer, 1903), there have been many studies on the adaptations of mammalian limb bones to different locomotor types. Most of those studies either describe anatomical characteristics that are typical of a certain locomotor type (Cartmill, 1974, 1985; English, 1977; Hildebrand, 1985a, 1985b; Maynard Smith & Savage, 1956) or compare the scaling of those characteristics, either within mammals that adopt a particular locomotor type (mainly terrestrial mammals; e.g., Bertram & Biewener, 1992; Christiansen, 1999), or between different locomotor types (e.g., Bou, Casinos, & Ocaña, 1987; Cubo, Ventura, & Casinos, 2006; Godfrey, Sutherland, Boy, & Gomberg, 1991; Schmidt, 2008). There are only a few studies that compare limb bone measurements (bone lengths or diameters; or indices with functional significance) between locomotor types using a univariate approach (i.e., that compare raw measurements instead of allometric coefficients or deviations from a general scaling pattern). This is probably due to the expected size differences between mammals with different locomotor types (Cartmill, 1974, 1985; Eisenberg, 1981; van Valkenburgh, 1987; Wolff & Guthrie, 1985), and to the significant effect of size on most limb bone measurements (Alexander, Jayes, Maloiy, & Wathuta, 1979; Bertram & Biewener, 1990, 1992; Bou et al., 1987; Christiansen, 1999; Gálvez-López & Casinos, 2012), which leads to the hypothesis that most morphological differences between locomotor types are related to size (e.g., Bertram & Biewener, 1990). Finally, in recent decades, both univariate and scaling approaches have been slowly replaced with multivariate methodologies (e.g., Day & Jayne, 2007; Elissamburu & Vizcaíno, 2004; Meachen, Dunn, & Werdelin, 2016; Meloro, 2011; Meloro, Elton, Louys, Bishop, & Ditchfield, 2013; Samuels, Meachen, & Sakai, 2013; van Valkenburgh, 1987), particularly since the advent of geometric morphometrics in the early 1990s (e.g., Adams, Rohlf, & Slice, 2004; Martín-Serra, Figueirido, & Palmqvist, 2014a, 2014b; Martín-Serra, Figueirido, Pérez-Claros, & Palmqvist, 2015; Monteiro & Abe, 1999; Morgan, 2009; Schutz & Guralnick, 2007; Taylor & Slice, 2005). These methodologies focus on the study of bone shape as a whole (especially true in the case of geometric morphometrics), which in turn allows a deeper understanding of how bone morphology is related to function and size. All these types of study, however, tend to refer to "classic" literature when discussing results. Thus, the question remains on whether raw, individual bone measurements with functional significance can be used to identify locomotor adaptations (i.e., whether they represent a valid basis for more complex approaches on functional morphology). This is particularly concerning in studies in which limb bone measurements of extant species are used to infer the ecomorphology of extinct species (e.g., Argot, 2001; Fujiwara, 2009; Marchi, 2015; Meloro, 2011; Pierce, Clack, & Hutchinson, 2011; Samuels et al., 2013; Schutz & Guralnick, 2007; Spaulding & Flynn, 2009; van Valkenburgh, 1987). If the locomotor adaptations described in those "classic" studies proved to be inaccurate, the locomotor habits of several extinct species could have been misinterpreted.

Most studies that compare limb bone measurements using a univariate approach focus on adaptations either to fossoriality, especially in Rodentia (Elissamburu & Vizcaíno, 2004; Lehmann, 1963), or to arboreality (Gonyea, 1976; Iwaniuk, Pellis, & Whishaw, 1999; Argot, 2001; Sargis, 2002; with special emphasis on primate locomotion: Ashton, Oxnard, & Spence, 1965; Larson, 1995; Lemelin, 1999; Polk et al., 2000; Ruff, 2002; Marchi, 2015). Very few studies include both arboreal and fossorial species (Casinos, 1994; Meachen et al., 2016; Polly, 2010; Samuels et al., 2013; van Valkenburgh, 1987). Furthermore, of those studies only Polly (2010) tested the strength of the phylogenetic signal in carnivoran limb bone morphology, but none described whether or how phylogenetic relatedness affects the results of ecomorphological studies. Finally, recent multivariate studies concur on a strong phylogenetic signal in the carnivoran appendicular skeleton (Martín-Serra et al., 2014a, 2014b; Meachen et al., 2016; Meloro, 2011; Samuels et al., 2013).

The main aims of the present study are therefore: (a) to assess whether locomotor adaptations can be detected in limb bones using a univariate approach; (b) to determine whether the size differences observed between animals with different locomotor types allow this kind of approach; and (c) to test the effect of phylogenetic relatedness, since the existence of a shared evolutionary history might obscure differences between locomotor types.

In order to test the influence of locomotion, size, and phylogenetic relatedness on limb bone morphology, a widely-distributed, monophyletic clade, whose species span a wide size range and present highly diverse locomotor capabilities, is needed. The order Carnivora is such a group (Nyakatura & Bininda-Emonds, 2012; Wilson & Mittermeier, 2009), since carnivorans span a size range of four orders of magnitude (from less than 0.1 kg in the least weasel (*Mustela nivalis*) to well over two tonnes in elephant seals (*Mirounga* spp.)) and present one of the widest locomotor diversities among mammals, lacking only flying and truly fossorial species (Bertram & Biewener, 1990; Meachen et al., 2016; van Valkenburgh, 1987; Wilson & Mittermeier, 2009).

Previous studies have suggested that the Carnivora is an evolutionarily conservative group regarding locomotor type and limb morphology (Alexander et al., 1979; Bertram & Biewener, 1990; Day & Jayne, 2007; Flynn,

TABLE 1 Species measured

Species	*n*	Loctyp	Habitat	M_b	Species	*n*	Loctyp	Habitat	M_b
Canidae									
Canis aureus	6	Runner	Variable	1	*Lycalopex gymnocercus*	4	Terrestrial	Open	1
Canis latrans	3	Runner	Variable	1	*Lycaon pictus*	3	Runner	Mosaic	1
Canis lupus	5	Runner	Variable	2, 3	*Nyctereutes procyonoides*	3	Terrestrial	Forest	1
Cerdocyon thous	2	Terrestrial	Mosaic	1	*Otocyon megalotis*	1	Terrestrial	Open	1
Chrysocyon brachyurus	6	Terrestrial	Open	4	*Speothos venaticus*	6	Semiaquatic	Forest	1
Cuon alpinus	3	Runner	Forest	1	*Urocyon cinereoargenteus*	1	Scansorial	Mosaic	1
Dusicyon australis	1	Terrestrial	Open	5	*Vulpes chama*	1	Terrestrial	Open	1
Lupulella adusta	4	Runner	Mosaic	1	*Vulpes lagopus*	3	Terrestrial	Open	1
Lupulella mesomelas	7	Runner	Open	1	*Vulpes vulpes*	12	Terrestrial	Variable	6
Lycalopex culpaeus	3	Terrestrial	Variable	1	*Vulpes zerda*	2	Terrestrial	Desert	1
Mustelidae									
Amblonyx cinereus	2	Semiaquatic	Freshwater	1	*Martes foina*	23	Scansorial	Mosaic	9
Arctonyx collaris	1	Semifossorial	Forest	1	*Martes martes*	8	Semiarboreal	Forest	9
Eira barbara	2	Semiarboreal	Forest	1	*Martes zibellina*	1	Scansorial	Forest	1
Enhydra lutris	1	Aquatic	Marine	1	*Meles meles*	5	Semifossorial	Mosaic	10
Galictis cuja	2	All-terrain	Variable	1	*Mellivora capensis*	2	Semifossorial	Variable	1
Galictis vittata	2	All-terrain	Mosaic	1	*Melogale moschata*	1	Scansorial	Mosaic	1
Gulo gulo	2	Scansorial	Mosaic	1	*Melogale orientalis*	1	Scansorial	Mosaic	1
Ictonyx lybicus	2	All-terrain	Desert	1	*Mustela erminea*	8	All-terrain	Mosaic	9
Ictonyx striatus	1	All-terrain	Variable	1	*Mustela eversmannii*	1	All-terrain	Open	1
Lontra felina	3	Semiaquatic	Marine	1	*Mustela lutreola*	1	Semiaquatic	Freshwater	1
Lontra longicaudis	2	Semiaquatic	Freshwater	1	*Mustela nivalis*	5	All-terrain	Variable	9
Lontra provocax	1	Semiaquatic	Freshwater	7	*Mustela nudipes*	2	All-terrain	Forest	1
Lutra lutra	5	Semiaquatic	Freshwater	8	*Mustela putorius*	6	All-terrain	Mosaic	1
Lutrogale perspicillata	1	Semiaquatic	Freshwater	1	*Neovison vison*	2	Semiaquatic	Freshwater	1
Lyncodon patagonicus	2	All-terrain	Open	1	*Pteronura brasiliensis*	2	Semiaquatic	Freshwater	1
Martes americana	1	Semiarboreal	Forest	1	*Vormela peregusna*	3	Semifossorial	Variable	1
Mephitidae									
Conepatus chinga	2	Semifossorial	Open	1	*Spilogale gracilis*	2	All-terrain	Mosaic	1
Conepatus humboldti	1	Semifossorial	Variable	1					
Otariidae									
Arctocephalus australis	1	Aquatic	Marine	11	*Otaria flavescens*	2	Aquatic	Marine	12
Arctocephalus gazella	1	Aquatic	Marine	11	*Zalophus californianus*	2	Aquatic	Marine	12
Phocidae									
Hydrurga leptonyx	1	Aquatic	Marine	12	*Phoca vitulina*	2	Aquatic	Marine	13
Mirounga leonina	1	Aquatic	Marine	13					
Ailuridae									
Ailurus fulgens	7	Semiarboreal	Forest	14					
Procyonidae									
Bassaricyon gabbii	1	Arboreal	Forest	1	*Potos flavus*	4	Arboreal	Forest	1
Bassariscus astutus	1	Semiarboreal	Mosaic	1	*Procyon cancrivorus*	3	Scansorial	Freshwater	1
Nasua narica	4	Scansorial	Forest	15	*Procyon lotor*	5	Scansorial	Freshwater	1

(Continues)

TABLE 1 (Continued)

Species	*n*	Loctyp	Habitat	M_b	Species	*n*	Loctyp	Habitat	M_b
Nasua nasua	6	Scansorial	Mosaic	16					
Ursidae									
Ailuropoda melanoleuca	2	Scansorial	Forest	1	*Ursus americanus*	2	Scansorial	Mosaic	1
Helarctos malayanus	1	Scansorial	Forest	1	*Ursus arctos*	6	Scansorial	Variable	1
Melursus ursinus	1	Scansorial	Mosaic	1	*Ursus maritimus*	4	Semiaquatic	Marine	1
Tremarctos ornatus	2	Scansorial	Mosaic	1					
Viverridae									
Arctictis binturong	4	Arboreal	Forest	1	*Genetta tigrina*	1	Semiarboreal	Mosaic	1
Arctogalidia trivirgata	2	Arboreal	Forest	1	*Hemigalus derbyanus*	4	Semiarboreal	Forest	1
Civettictis civetta	4	Terrestrial	Mosaic	21	*Paradoxurus hermaphroditus*	2	Arboreal	Forest	1
Cynogale benettii	1	Semiaquatic	Freshwater	1	*Poiana richardsoni*	1	Semiarboreal	Forest	1
Genetta felina	5	Scansorial	Mosaic	1	*Viverra tangalunga*	4	Terrestrial	Forest	1
Genetta genetta	7	Scansorial	Mosaic	1	*Viverra zibetha*	2	Terrestrial	Forest	1
Genetta maculata	3	Semiarboreal	Mosaic	1	*Viverricula indica*	4	Scansorial	Mosaic	1
Herpestidae									
Atilax paludinosus	2	Semiaquatic	Freshwater	1	*Herpestes ichneumon*	4	Terrestrial	Open	1
Crossarchus obscurus	2	Terrestrial	Forest	9	*Ichneumia albicauda*	2	Terrestrial	Mosaic	1
Cynictis penicillata	4	Terrestrial	Open	1	*Suricata suricatta*	4	Semifossorial	Open	1
Galerella pulverulenta	4	All-terrain	Forest	1	*Urva brachyura*	1	Terrestrial	Forest	1
Galerella sanguinea	1	All-terrain	Mosaic	1	*Urva edwardsii*	2	Terrestrial	Mosaic	1
Helogale parvula	2	Terrestrial	Mosaic	1	*Urva javanica*	1	Terrestrial	Mosaic	1
Eupleridae									
Cryptoprocta ferox	2	Semiarboreal	Forest	1	*Mungotictis decemlineata*	1	Scansorial	Forest	1
Fossa fossana	2	Terrestrial	Forest	1	*Salanoia concolor*	2	Scansorial	Forest	1
Galidia elegans	4	All-terrain	Forest	1					
Hyaenidae									
Crocuta crocuta	2	Runner	Mosaic	9	*Parahyaena brunnea*	1	Runner	Variable	1
Hyaena hyaena	3	Runner	Variable	1	*Proteles cristatus*	2	Terrestrial	Open	9
Felidae									
Acinonyx jubatus	3	Runner	Mosaic	1	*Lynx pardinus*	4	Scansorial	Mosaic	13
Caracal aurata	1	Scansorial	Forest	1	*Lynx Rufus*	1	Scansorial	Variable	1
Caracal caracal	5	Scansorial	Mosaic	1	*Neofelis nebulosa*	1	Semiarboreal	Forest	18
Felis chaus	1	Scansorial	Variable	1	*Otocolobus manul*	2	Scansorial	Open	1
Felis nigripes	2	All-terrain	Mosaic	17	*Panthera leo*	7	Scansorial	Open	1
Felis silvestris	15	Scansorial	Mosaic	1	*Panthera onca*	2	Scansorial	Forest	1
Herpailurus yagouaroundi	3	Scansorial	Mosaic	1	*Panthera pardus*	8	Scansorial	Variable	13
Leopardus colocola	2	Scansorial	Variable	1	*Panthera tigris*	9	Scansorial	Mosaic	19
Leopardus geoffroyi	2	Scansorial	Mosaic	1	*Panthera uncia*	4	Scansorial	Open	20
Leopardus pardalis	2	Scansorial	Forest	1	*Pardofelis marmorata*	1	Arboreal	Forest	1
Leopardus tigrinus	2	Scansorial	Forest	1	*Prionailurus bengalensis*	1	Scansorial	Mosaic	1
Leopardus wiedii	1	Arboreal	Forest	1	*Prionailurus planiceps*	1	Scansorial	Freshwater	1
Leptailurus serval	6	Scansorial	Mosaic	13	*Prionailurus viverrinus*	1	Scansorial	Freshwater	1
Lynx canadensis	1	Scansorial	Mosaic	1	*Puma concolor*	5	Scansorial	Variable	1

TABLE 1 (Continued)

Species	*n*	Loctyp	Habitat	M_b	Species	*n*	Loctyp	Habitat	M_b
Lynx lynx	3	Scansorial	Mosaic	1					
Prionodontidae									
Prionodon linsang	1	Arboreal	Forest	1					
Nandiniidae									
Nandinia binotata	5	Semiarboreal	Forest	1					

For each species, the table shows the number of specimens measured (*n*), the category assigned for both locomotor type (loctyp) and preferred habitat (habitat), and the references from which the mean body mass value for that species was taken (M_b). References: Wilson & Mittermeier (2009); Blanco, Saénz de Buruaga, & Llaneza (2002); Mech (2006); Dietz (1984); Brook & Bowman (2004); Cavallini (1995); Reyes-Küppers (2007); Yom-Tov, Heggberget, Wiig, & Yom-Tov (2006); Grzimek (1988); Virgós et al. (2011); Perrin, Würsig, & Thewissen (2002); MacDonald (2001); Silva & Downing (1995); Roberts & Gittleman (1984); Gompper (1995); Gommpper & Decker (1998); Sliwa (2004); Sunquist & Sunquist (2002); Mazák (1981); IUCN Cat Specialist Group (2011); Ray (1995). See Table 3 for a description of locomotor type and utilized habitat categories.

Neff, & Tedford, 1988). Furthermore, Bertram and Biewener (1990) stated that, owing to this supposed conservative design of carnivoran limbs, morphological differences between terrestrial, scansorial, and arboreal carnivorans are mostly the result of size differences among these groups; whereas adaptations to swimming and digging should be independent of size. However, Iwaniuk et al. (1999) and Iwaniuk, Pellis, & Whishaw (2000) found a significant correlation between several functional indices and the degree of arboreality, thereby suggesting that size is not the only determining factor correlated with differences in limb bone morphology among terrestrial, scansorial, and arboreal mammals. Thus, regarding the aims listed above, a significant size effect is expected on limb bone measurements; but it is also expected for both semifossorial and aquatic carnivorans to be significantly different from other locomotor types; and that, at least for some of the studied variables, a gradation exists related to the degree of arboreality. Finally, a significant phylogenetic effect is expected, but its relationship to locomotor adaptations and size in carnivorans remains unclear.

2 | MATERIALS AND METHODS

The sample consisted of 435 specimens from 143 species of Carnivora (Table 1). For each specimen, measurements were taken on the scapula, humerus, radius, ulna, third metacarpal, femur, tibia, and calcaneus, as described in Figure 1 and Supporting Information—Database. Although anatomically the scapula is an element of the shoulder girdle, previous studies show that functionally it acts as the main propulsive segment of the forelimb, thus being analogous to the femur in the hind limb (Boczek-Funcke, Kuhtz-Buschbeck, & Illert, 1996; Fischer et al., 2002; Fischer & Blickhan, 2006; Martín-Serra et al., 2015). Therefore, in the present study, the scapula is considered the most proximal segment of the forelimb. Table 2 lists the 43 variables analyzed in this study.

The studied specimens are housed in the collections of the Phylogenetisches Museum (Jena, Germany), the Museum für Naturkunde (Berlin, Germany), the Museu de Ciències Naturals de la Ciutadella (Barcelona, Spain), the Muséum National d'Histoire Naturelle (Paris, France), the Museo Nacional de Ciencias Naturales (Madrid, Spain), the Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" (Buenos Aires, Argentina) and the Museo de La Plata (La Plata, Argentina; Table S1). Only adult specimens (judged by epiphyseal fusion) were sampled and where possible only the limb elements of the left side were measured.

Since body mass values were missing from most specimens, mean values for each species were obtained from the literature (taking into account the sex of the specimen when available, as described in Supporting Information—Database; Table 1). Taxonomy follows Wilson and Mittermeier (2009), except for a few species for which the synonyms in Wozencraft (2005) are preferred. Additionally, *Lupulella* is used for both African jackals following Atickem et al. (2018), *Herpestes* is reserved for the Egyptian mongoose (Veron et al., 2015), and felid nomenclature follows Kitchener et al. (2017). Locomotor adaptations were studied using two separate sets of categories, adapted from previous ecomorphological studies on Carnivora (Eisenberg, 1981; Gittleman, 1985; Meloro et al., 2013; Ortolani & Caro, 1996; Samuels et al., 2013; van Valkenburgh, 1985, 1987): locomotor type and utilized habitat (Table 3). The "locomotor type" categories represent locomotor specialization, that is, the main locomotor habit of each species. Meanwhile, "utilized habitat" was used as a broader ecological correlate,

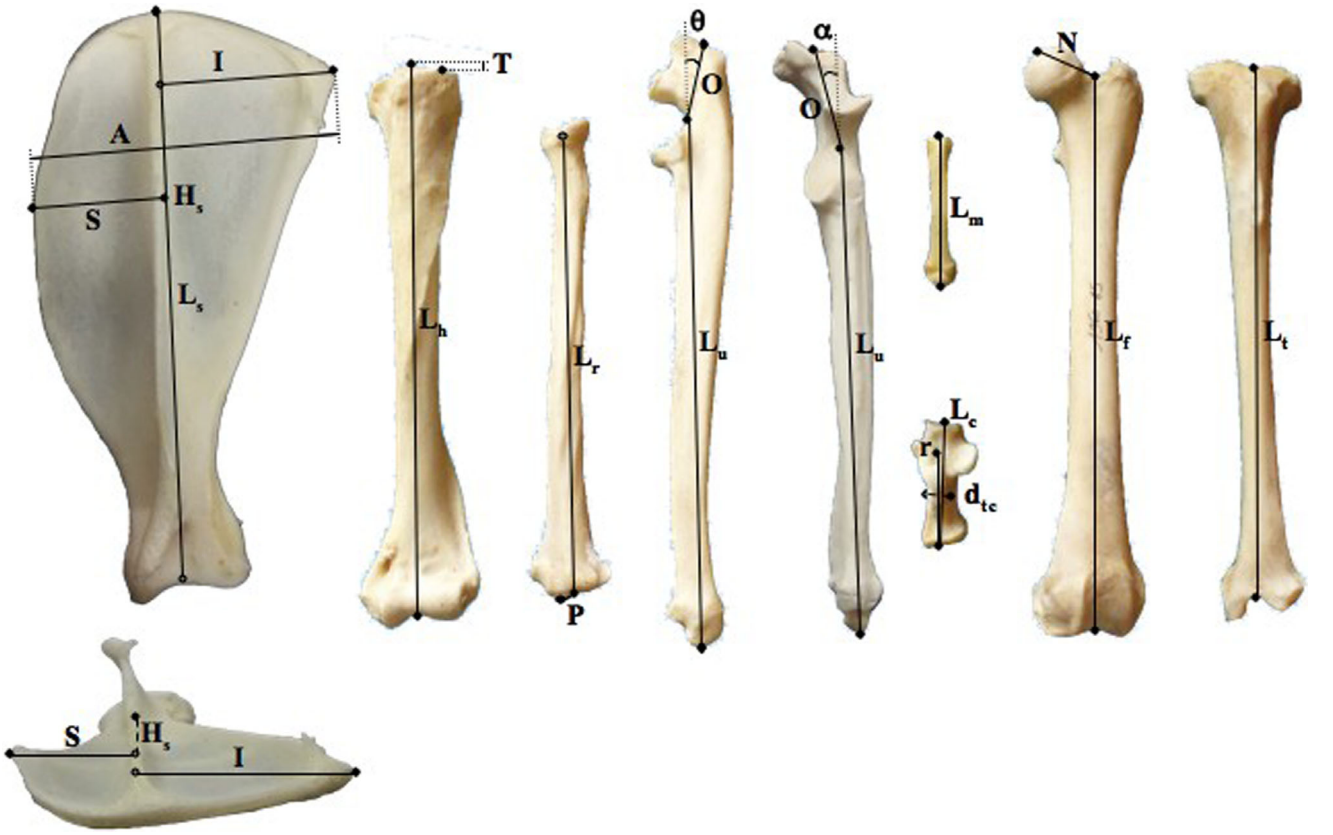

FIGURE 1 Bone measurements. All other variables were calculated from these measurements. See Supporting Information—Database for a more detailed definition of each variable, and an assessment of measurement error. Variable names are listed in Table 2

representing the animal's capacity to use several modes of locomotion besides the one defining its locomotor type, in order to exploit all the available resources within its home range (e.g., a semiaquatic carnivoran might also be capable of digging proficiently). In this way, carnivorans inhabiting more complex habitats are considered more likely to use several modes of locomotion (e.g., while desert-dwelling carnivorans are only likely to run or dig, forest-dwelling carnivorans may be capable of running, climbing, digging, and even swimming). Each species was thus assigned a locomotor type category and a utilized habitat category, based on the literature (Dietz, 1984; Roberts & Gittleman, 1984; Grzimek, 1988; Poglayen-Neuwall & Toweill, 1988; Frandsen, 1993; Gompper, 1995; Ray, 1995; Gommpper & Decker, 1998; Storz & Wozencraft, 1999; MacDonald, 2001; Perrin et al., 2002; Sliwa, 2004; Beisiegel & Zuercher, 2005; Reyes-Küppers, 2007; Wilson & Mittermeier, 2009). Since previous studies have shown that the capacity to adopt several modes of locomotion comes at the expense of increased costs of locomotion (e.g., semiaquatic mammals: Williams, 1983a, 1983b, 1989; Williams et al., 2002), the carnivoran appendicular skeleton is expected to be optimized for a particular locomotor type, instead of presenting a less specialized morphology in order to perform several locomotor modes (i.e., better results are expected using locomotor type than using utilized habitat).

In order to better understand the possible influence of each factor on limb bone morphology, a sequence of analyses was performed.

1 One-way fixed-factor analyses of variance (ANOVA) were carried out on each variable (raw data) to determine whether significant differences existed between the mean values of the different locomotor types, utilized habitats, or carnivoran families (phylogenetic effect proxy). All analyses were carried out on $\log_{10}$-transformed values, since preliminary tests showed that this transformation enhanced the resolution of the analyses, particularly among the categories with the smallest individuals. Similar findings were also reported by Meloro et al. (2013).
While ANOVA is robust against violations of the normality assumption (Kirk, 1995), violations of the homoscedasticity assumption can cause serious problems with type I errors, especially in unbalanced designs, such as the present study. Consequently, the Welch procedure

TABLE 2 Variable names and abbreviations

Name	Abbreviations
Body mass	M_b
Scapular length	$\boldsymbol{L_s}$
Maximum width of supraspinous fossa	$\boldsymbol{S}$
Maximum width of infraspinous fossa	$\boldsymbol{I}$
Maximum scapular width	$\boldsymbol{A}$
Scapular spine height	$\boldsymbol{H_S}$
Humerus functional length	$\boldsymbol{L_h}$
Humerus sagittal diameter	$\boldsymbol{d_{sh}}$
Humerus transverse diameter	$\boldsymbol{d_{th}}$
Projected height of greater tubercle	T
Humerus robusticity	*HR*
Radius functional length	$\boldsymbol{L_r}$
Radius sagittal diameter	$\boldsymbol{d_{sr}}$
Radius transverse diameter	$\boldsymbol{d_{tr}}$
Styloid process length	$\boldsymbol{P}$
Radius robusticity	*RR*
Ulna functional length	$\boldsymbol{L_u}$
Ulna sagittal diameter	$\boldsymbol{d_{su}}$
Ulna transverse diameter	$\boldsymbol{d_{tu}}$
Olecranon process length	$\boldsymbol{O}$
Olecranon angle	α
Olecranon abduction angle	θ
Ulna robusticity	*UR*
Indicator of Fossorial ability	*IFA*
Third metacarpal functional length	$\boldsymbol{L_m}$
Third metacarpal sagittal diameter	$\boldsymbol{d_{sm}}$
Third metacarpal transverse diameter	$\boldsymbol{d_{tm}}$
Third metacarpal robusticity	*MR*
Femur functional length	$\boldsymbol{L_f}$
Neck–head length	$\boldsymbol{N}$
Femur sagittal diameter	$\boldsymbol{d_{sf}}$
Femur transverse diameter	$\boldsymbol{d_{tf}}$
Femur robusticity	*FR*
Tibia functional length	$\boldsymbol{L_t}$
Tibia sagittal diameter	$\boldsymbol{d_{st}}$
Tibia transverse diameter	$\boldsymbol{d_{tt}}$
Tibia robusticity	*TR*
Calcaneus length	L_c
Ankle extensors moment arm	r
Calcaneus sagittal diameter	d_{sc}
Calcaneus transverse diameter	d_{tc}
Relative length of the proximal segment of the forelimb	$\%_{prox}$
Relative length of the middle segment of the forelimb	$\%_{mid}$
Relative length of the distal segment of the forelimb	$\%_{dist}$

Note: Two subsamples can be defined within the studied variables: linear measurements (bold) and ratios and angles (italic).

was used instead of the F statistic to test for significant differences between groups (Cohen, 2001). Since robust analysis cannot be performed if the sample contains groups with only one individual, monotypic families (Ailuridae, Nandiniidae) and Prionodontidae were not included in any of the ANOVAs. In parallel, in the ANOVAs for calcaneal variables, aquatic and desert-dwelling carnivorans were not included because only one specimen was measured for each group. However, the values of each variable for all these groups are presented in the corresponding tables for the sake of comparison. Additionally, pairwise comparisons were carried out to search for significant differences between the mean values of each pair of groups. Games–Howell's test was used because group sizes were unequal. No multiple test correction was applied to pairwise comparisons. As others have noted (Johnson et al., 2008; Moran, 2003), the cost in reduced statistical power largely exceeded the benefit from Type I error protection. As an example, nine locomotor type categories imply 36 post hoc pairwise comparisons. At a p-value of .05, we might expect to obtain less than two false significant differences by chance. However, when correcting for multiple tests, in most cases 7–10 comparisons switched from significant to nonsignificant.

All ANOVAs and pairwise comparisons were performed using the R version 3.3.3 (R Core Team, 2017).

2 General linear models (GLMs) were used to assess the possible interactions between size, phylogenetic relatedness, locomotor type, and utilized habitat. The full model included taxonomic group (family), locomotor type and utilized habitat as fixed effects; whereas the size effect was accounted for by including body mass (M_b) as a covariate. Starting with the default full factorial model (i.e., intercept plus all factors, the covariate, and all possible interactions), nonsignificant effects were successively removed one at a time until only significant effects remained in the final model. The criterion for effect removal was based both on effect significance (p-value) and on effect size (partial eta squared, η^2).

GLMs were carried out using SPSS for Windows (release 15.0.12006; SPSS Inc., Chicago, IL).

TABLE 3 Description of locomotor type and utilized habitat categories

Locomotor type	Description
Arboreal	Species that spend most of their life in trees (over 75%), rarely descending to the ground
Semiarboreal	Species that spend a large amount of their time in the trees (between 50 and 75%), both foraging and resting, but also on the surface of the ground
Scansorial	Species that, although mostly terrestrial (over half their time is spent on the ground), can climb well and will readily do so to chase arboreal prey or escape
Terrestrial	Species that rarely or never climb or swim, and that may dig to modify a burrow but not regularly for food
Runner	Species that rely on running to catch their prey, including both endurance and high-speed hunters
All-terrain	Species that, although rarely seen in trees, present good climbing skills, probably because, for them, overcoming obstacles such as fallen logs usually involves some climbing. Furthermore, most of these species are also capable swimmers and may dig to modify a burrow.
Semifossorial	Species that dig regularly for both food and shelter, but that still show considerable ability to move about on the surface
Semiaquatic	Species that forage regularly underwater and usually plunge into the water to escape, but must spend time ashore to groom, et cetera
Aquatic	Species that carry out most of their life cycle in water, although some part of it can be confined to land (parturition, mating, and rearing the young)
Utilized habitat	**Description**
Desert	Open habitats with an extremely low amount of precipitation; they are separated from other open habitats due to the additional adaptations required to live in these harsh conditions. Carnivorans inhabiting deserts should rarely perform any other locomotor habit other than ground locomotion.
Open	Areas with low to nonexistent tree cover (e.g., grasslands, steppes, tundra...). Carnivorans inhabiting open habitats could probably be good diggers, maybe also capable swimmers, but should lack climbing skills.
Mosaic	This category was created for species that either live in forested areas with scarce tree cover (e.g., savannah), or require the presence of both forested and open areas within their home range, thus, they are expected to be good climbers, while also could be capable diggers or swimmers.
Forest	Areas with a high density of trees (e.g., rain forest, taiga, deciduous forest...). Carnivorans inhabiting forested areas should probably be adept climbers, even though not completely arboreal, to be able to chase prey that flee to the canopy. They can also be capable swimmers and diggers.
Freshwater	This category was created for species that dwell in or near freshwater systems (e.g., rivers, lakes, swamps,...). Carnivorans inhabiting freshwater habitats are expected to be capable swimmers, while also can present some ability to climb or dig.
Marine	Saltwater systems and their coastal regions. Marine carnivorans are expected to be very good swimmers, rarely dig, and possess an almost nonexistent ability to climb.
Variable	This category includes all species that appear indistinctly in two or more of the other categories and thus probably contains species with highly variable locomotor skills.

Note: Most locomotor type categories were adapted from previous work on the relationship between locomotor behavior and forelimb morphology (e.g., Eisenberg, 1981; Gittleman, 1985; Samuels et al., 2013; van Valkenburgh, 1985, 1987), although some species are placed here in different categories than some of the cited studies given that there is no consensus in their placement. The all-terrain locomotor category, newly defined in this work, addresses the fact that locomotion in small mammals is different to that of large mammals, and presents a series of common traits across mammalian orders (Fischer, Schilling, Schmidt, Haarhaus, & Witte, 2002). Utilized habitat categories were adapted from previous ecomorphological studies on Carnivora (e.g., Meloro et al., 2013; Ortolani & Caro, 1996).

3 If the size effect in the GLMs was significant, a second set of ANOVAs was carried out on the regression residuals of each variable on M_b using ordinary least squares and the power regression model ($y = a \cdot \cdot x^b \rightarrow \log y = \log a + b \cdot \cdot \log x$). A strong size effect could mask the effect of locomotor type, utilized habitat and phylogeny. Thus, differences between the raw and the size-corrected data would reveal size-related artifacts in the first test. Two possible size-related artifacts could be expected: a, between-group differences that were significant only due to size-differences between those groups, that is, false

positives (e.g., a seal's femur is larger than that of a weasel); or b, between-group differences whose significance was masked because both groups had similar measurements even though their sizes were not, that is, false negatives (e.g., both civets and sea lions have similar-sized femora).

4 GLMs were fitted to the regression residuals to reassess the effect of locomotor type, utilized habitat, phylogenetic relatedness, and their interactions, on the studied variables, once the size effect had been removed. The full model also included M_b as a covariate to verify that there was no size effect in the data.

5 If the GLM on the raw data indicated that phylogeny (taxonomic group) had a significant effect in the variables, the effect of locomotor type and utilized habitat was also assessed using phylogenetically informed comparisons. These methods also account for the potential correlation of the error terms that could arise in interspecific studies, like the present one, due to the lack of independence among species, which can be arranged in a hierarchical sequence (i.e., a phylogenetic tree; Felsenstein, 1985; Harvey & Pagel, 1991).

Phylogenetic ANOVAs by locomotor type and utilized habitat were performed on each variable (Garland, Dickerman, Janis, & Jones, 1993). This procedure first calculates the test statistic and then obtains its null distribution by simulating new sets of dependent variables on the phylogenetic tree. Simulations are run under a Brownian-motion model. The analyses were carried out using the package phytools in R (Revell, 2012), which also performs pairwise comparisons of means among groups obtaining the *p*-values by phylogenetic simulation. The phylogeny used in these analyses is discussed and detailed in Supporting Information—Phylogeny and is presented in Figure S1. When comparing results of traditional and phylogenetic ANOVAs, pairwise differences not recovered on the latter would indicate that they were actually related to evolutionary changes along carnivoran phyletic lines.

6 Finally, if the interaction between phylogeny (taxonomic group) and body mass (Fam*M_b) was significant in the GLMs, phylogenetic ANOVAs by locomotor type and utilized habitat were also conducted on the size-corrected data (regression residuals).

These results can be compared both to the traditional size-corrected ANOVAs and to the phylogenetic ANOVAs on the raw data. Pairwise differences not recovered when comparing with the former would suggest that they describe size-independent changes along carnivoran evolutionary lines. On the other hand, the comparison with the latter should mirror that between the traditional ANOVAs on raw and size-corrected data.

Once the influences of size and phylogenetic relatedness on limb bone morphology have been addressed, a simple approach was used to test the validity of using regression residuals to infer locomotor adaptations in extinct species. Locomotor adaptations of bone morphology in extant species are often used to infer the ecology of extinct species (e.g., Argot, 2001; Fujiwara, 2009; Pierce et al., 2011; Samuels et al., 2013; van Valkenburgh, 1985, 1987). However, if it is shown that size creates artifactual differences between locomotor groups in Carnivora, some size correction would be required prior to identifying morphological indicators of locomotor behavior. Here, regression residuals for each variable to body mass are used as a size correction, since the body mass of extinct species can be estimated using different techniques (e.g., Anyonge, 1993; Egi, 2001; Figueirido, Pérez-Claros, Hunt Jr., & Palmqvist, 2011). The validation approach will consist in first calculating mean residuals for each variable for each locomotor type, utilized habitat and family. Calcaneal variables will not be included because there are no data for some subgroups. Then, for each variable and factor, subgroups will be ordered from lowest to highest mean residual values and their position relative to zero and to other subgroups recorded. It will be assumed that positions close to zero represent those groups that have deviated the least from the theoretical carnivoran ancestor, while those furthest away from it represented the most extreme adaptations. Finally, the relative positions of each subgroup in each variable will be added together and the frequencies with which each subgroup occurred in each relative position will be calculated. If regression residuals are a good indicator of locomotor adaptations in extant species, the positions closest to zero should be occupied by subgroups matching the current assumptions on the theoretical carnivoran ancestor (e.g., myacids, Wesley-Hunt & Flynn, 2005).

3 | RESULTS

Mean values and standard deviations for each variable by locomotor type, utilized habitat, and family are shown in Supporting Information—Results (Table SR1).

3.1 | Analyses on raw data

3.1.1 | Locomotor type

Significant differences between locomotor types were found for all the variables. Pairwise significant differences in body mass indicated that aquatic carnivorans were larger than all other locomotor groups. Runners were the largest from the remaining groups, presenting

significant differences from all other categories except scansorial and semiaquatic. Finally, all-terrain carnivorans were the smallest, although significant differences were not found between them and both semiarboreal and semifossorial carnivorans. Pairwise comparisons produced similar results in most of the other variables (i.e., all-terrain carnivorans had the smallest values, aquatic the largest). Remarkable deviations from that pattern were observed for several ratios and angles (olecranon abduction angle, indicator of fossorial ability (IFA), and ulna, third metacarpal and femur robusticity: runners < rest; olecranon angle, relative length of forelimb proximal segment: arboreal < rest; relative length of forelimb middle segment: rest < arboreal). Additionally, runners presented the largest values for most bone lengths (all except tibia length), scapular spine height, olecranon angle, ankle extensors moment arm, and relative length of forelimb distal segment.

3.1.2 | Utilized habitat

Significant differences between habitats were found for all variables except scapular spine height, humerus and third metacarpal length, relative length of forelimb distal segment, femur length, tibia robusticity, and all calcaneal variables. Pairwise differences in body mass indicated that marine carnivorans were significantly larger than all other habitat categories. Similar results were obtained in almost all other variables, although species inhabiting freshwater habitats had the largest values of olecranon abduction angle. Desert-dwelling carnivorans presented the smallest values of body mass and most other variables, although only for styloid process length, and ulna and third metacarpal sagittal diameters, were these differences significant. Species of open habitats had the smallest values of humerus and ulna robusticity, while forest-dwelling carnivorans presented the smallest olecranon angle values. Finally, marine carnivorans showed the smallest values of relative length of forelimb middle segment.

3.1.3 | Taxonomic group (phylogeny)

Significant differences between families were found for all the variables. Pairwise significant differences in body mass indicated that pinnipeds and ursids were larger than all other carnivoran families, whereas mustelids, mephitids, euplerids, and herpestids were the smallest groups. Pairwise comparisons produced similar results in most of the other variables. In fact, when considering only the subsample of linear measurements (Table 2), pairwise comparison results can be summarized as follows: (a) a clear size separation exists between small and large carnivoran families and (b) a marked size gradient also exists within those two groups. This can be represented as:

[Mephitidae < (Herpestidae, Mustelidae, Eupleridae) < Viverridae < Procyonidae] < [Canidae < Felidae < Hyaenidae < (Otaridae, Phocidae, Ursidae)]

Ratios and angles followed a similar pattern. However, remarkable deviations existed. Canidae had the lowest values for most bone robusticities and the largest for relative length of forelimb distal segment (together with Hyaenidae). Mephitidae presented one of the largest values of IFA (second only to pinnipeds). Finally, regarding relative length of forelimb middle segment, mustelids had the highest values and pinnipeds the lowest.

3.1.4 | GLMs

A total of 18 different models summarized the effects of locomotor type, utilized habitat, phylogenetic relatedness, body size and their interactions, on the observed variability of the 43 variables studied (Table S2). The phylogenetic effect (Fam) was present in all the models, indicating a strong phylogenetic signal in all the studied variables. Similarly, the effect of size was significant in most of the models, but mostly as an interaction with other factors (e.g., Fam*M_b; loctyp*M_b). Neither the direct effect of locomotor type nor utilized habitat were significant in any of the models, appearing instead in most models as significant interactions with size (loctyp*M_b), phylogeny (Fam*loctyp, Fam*hab) or both (Fam*hab*M_b; Table S2). It is also interesting to note that utilized habitat seemed to have a more significant effect than locomotor type on carnivoran limb morphology, since habitat was included in more terms and in more models.

3.2 | Size-corrected analyses

3.2.1 | Locomotor type

In the size-corrected ANOVA, significant differences between groups were found for all variables except both calcaneal diameters. Figure 2 presents an excerpt of the results to avoid overwhelming the reader, while results for the remaining variables can be found in Supporting Information—Results (Figure SR1). After removing the size effect, pairwise comparisons confirmed that it was confounding the results, since significantly different results were found for most of the

linear measurements and some ratios and angles. Particularly, the following findings were size-related artifacts:

1 Aquatic and all-terrain carnivorans were falsely assigned as the extreme values in most variables. In the size-corrected analyses, aquatic carnivorans presented the highest values only for all bone robusticities except the tibia, and also for maximum width of supraspinous fossa, relative length of the forelimb proximal segment, IFA, and radius transverse diameter, while the opposite was true for all bone lengths except the tibia, some diameters (radius sagittal, third metacarpal sagittal and transverse, femur and tibia sagittal), and scapular spine height, relative length of forelimb middle segment, styloid process length, olecranon length, femur neck–head

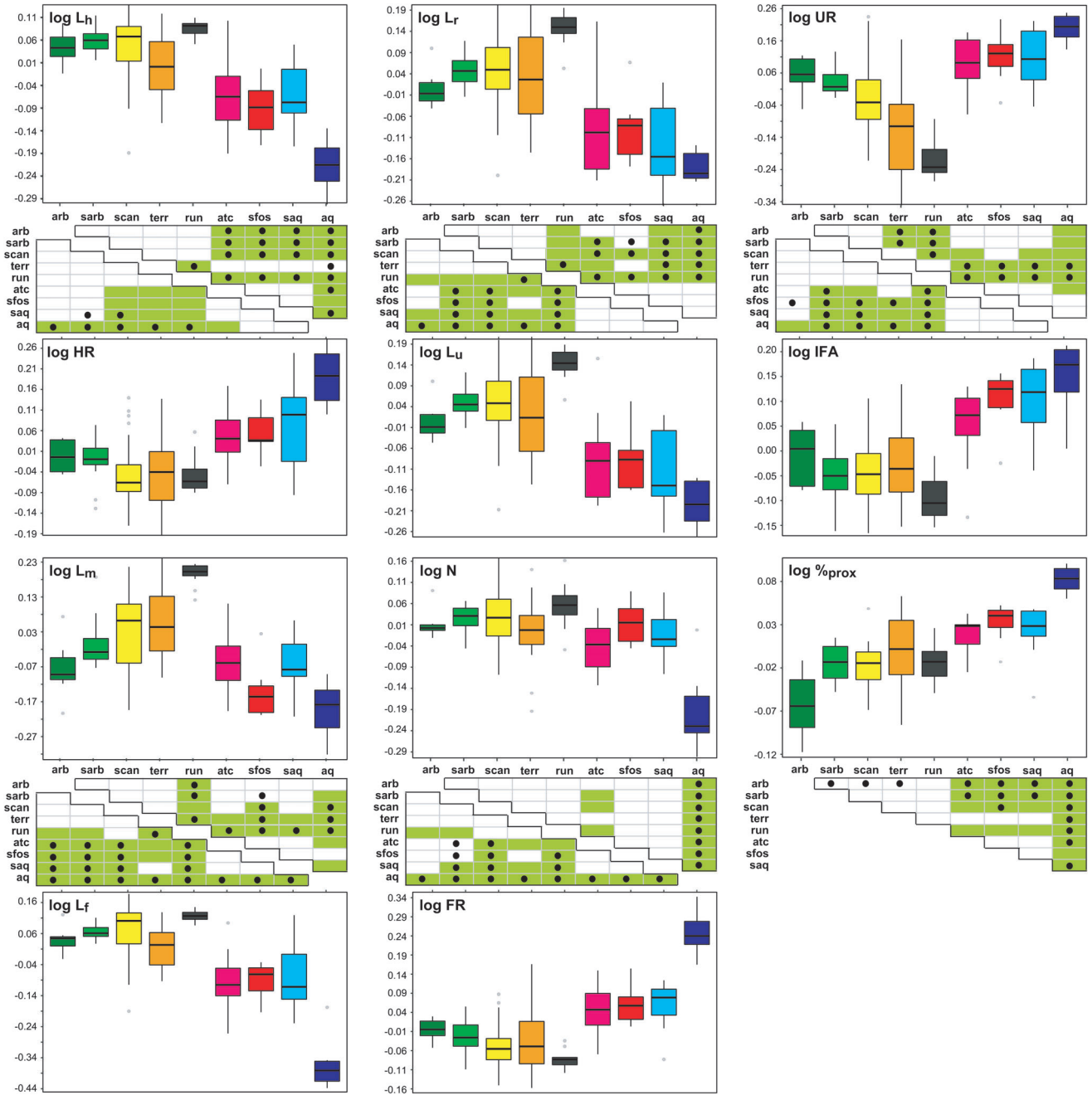

FIGURE 2 Box plots and pairwise differences by locomotor type for some selected variables. Shadowed cells indicate significant differences between a pair of subgroups in the traditional ANOVA for that variable, while a dot represents the same for the corresponding phylogenetic ANOVA. Abbreviations: aq, aquatic; arb, arboreal; atc, all-terrain; run, runner; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial. Variable names are listed in Table 2

length, and tibia robusticity. Similarly, all-terrain carnivorans presented the smallest values only for maximum width of the infraspinous fossa, calcaneus length, and ankle extensors moment arm.

2 All differences between semiarboreal and scansorial carnivorans and between all-terrain and semiaquatic species were size-related artifacts. In the ratios and angles subsample, the same was true for the differences between runners and terrestrial carnivorans, and between all-terrain and semifossorial species.

3 The size effect masked significant differences between subgroups in several variables, particularly among semifossorial and semiaquatic carnivorans and other groups in the linear measurements subsample.

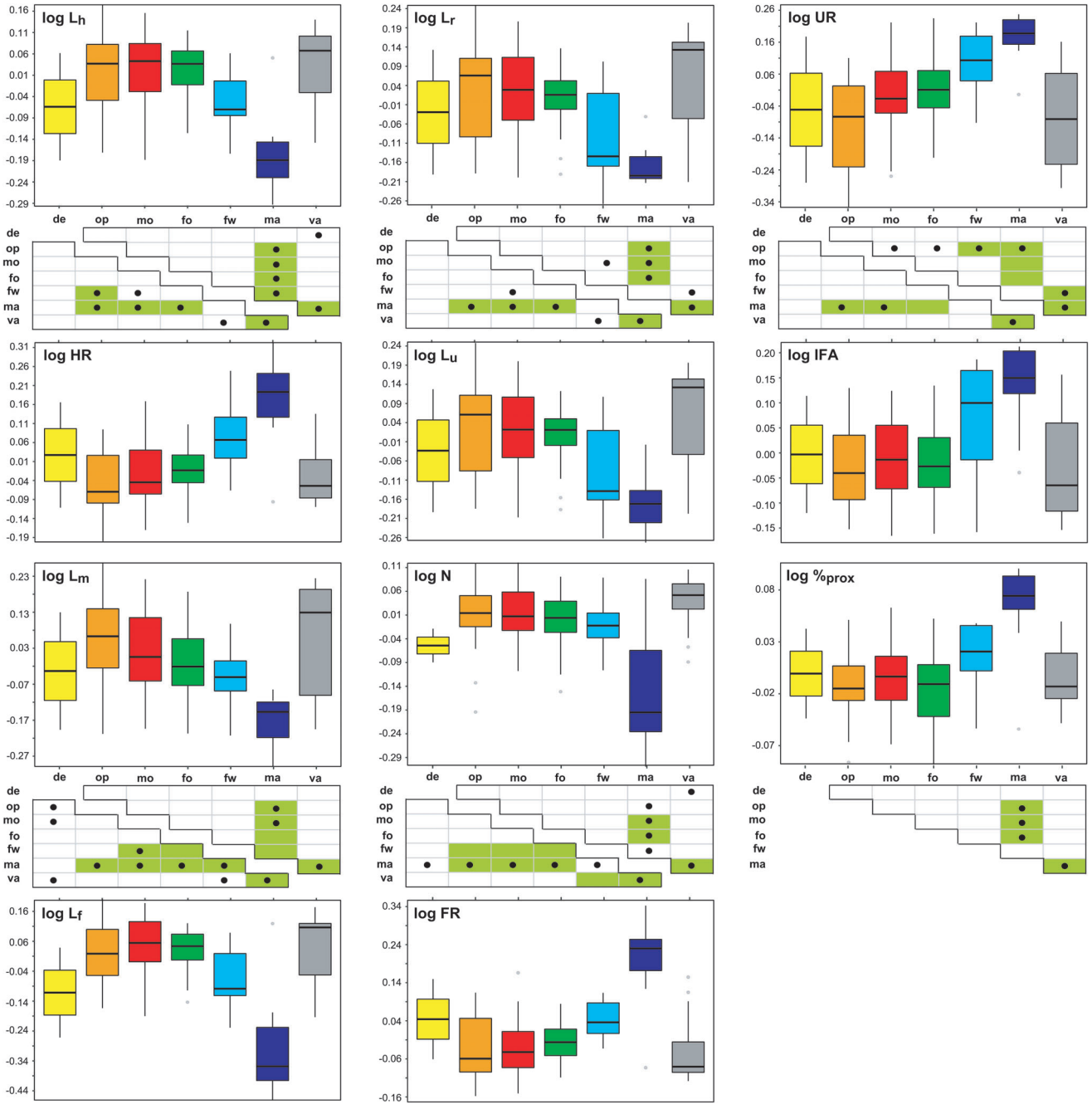

FIGURE 3 Box plots and pairwise differences by utilized habitat for some selected variables. Shadowed cells indicate significant differences between a pair of subgroups in the traditional ANOVA for that variable, while a dot represents the same for the corresponding phylogenetic ANOVA. Abbreviations: de, desert; fo, forest; fw, freshwater; ma, marine; mo, mosaic; va, variable. Variable names are listed in Table 2

Finally, it is also interesting to note that all the remarkable deviations from the body mass pattern described in the analyses on raw data held after removing the size effect.

3.2.2 | Utilized habitat

After the size correction, significant differences between habitats were only found for scapula length, relative length of forelimb proximal segment, humerus length and robusticity, relative length of forelimb middle segment, radius length and robusticity and transverse diameter, ulna length and robusticity, both olecranon angles, IFA, third metacarpal length and robusticity and transverse diameter, femur length and robusticity and neck–head length, and tibia length (Figures 3 and SR2). As in the analysis by locomotor type, removing the size effect had a minor impact on the results of ratios and angles. It did reveal, however, that differences between marine species and carnivorans inhabiting freshwater and desert habitats were a size-related artifact, as were differences between the open and forest categories. Additionally, size masked the differences between desert-dwelling carnivorans and freshwater species, and between the variable and forest categories. Regarding linear measurements, only in a third of the variables were significant differences between utilized habitats still detected. In all of them except radius transverse diameter, marine carnivorans now presented the smallest values instead of the largest. Furthermore, all differences between the variable habitat category and species of open, mosaic and forest habitats were size-related artifacts.

3.2.3 | Taxonomic group (phylogeny)

In the size-corrected ANOVA, significant differences between families were found for all the variables except calcaneus transverse diameter (Figures 4 and SR3). Again, removing the size effect had a small impact on the results of ratios and angles. However, it did reveal that differences between phocids and mustelids, and between mephitids and herpestids were size-related artifacts, while size masked the differences between several pairs (e.g., Canidae vs. Hyaenidae and Eupleridae). As with other factors, significantly different results were found for most of the linear measurements, confirming that the size effect was confounding the results. Particularly, the clear separation between small and large families was no longer recovered. This could be mainly attributed to pinnipeds now presenting the lowest values for many variables, but also to "small" families like Procyonidae and Eupleridae now having above-average values in most variables. Finally, all differences between mephitids and mustelids and between procyonids and herpestids were size-related differences.

3.2.4 | GLMs

A total of 22 different models was obtained (Table S3), but none could explain the residual variability found in radius sagittal diameter. The models obtained for maximum scapular width, maximum widths of supraspinous and infraspinous fossae, humerus transverse diameter, radius robusticity, olecranon process length, olecranon abduction angle, and tibia sagittal diameter, were the same regardless of the data analyzed (raw measurements or residuals). As expected, size (M_b) was not a significant effect in any of the models. However, its interactions with other factors were still significant; particularly with phylogeny and locomotor type. As in the GLMs of the raw data, phylogenetic relatedness (Fam) was the main factor explaining the observed residual variability. As a final note, once the size effect was removed, the effect of locomotor type on carnivoran limb morphology was similar to that of habitat, since both factors were included in a similar number of model terms.

3.3 | Phylogenetically informed comparisons

3.3.1 | Locomotor type

In the phylogenetic ANOVAs on raw data, significant differences between groups were found for all variables except scapular spine height, radius robusticity, ulna transverse diameter, both olecranon angles, femur neck–head length, tibia robusticity, and all calcaneal variables. Thus, previously recovered locomotor type differences in these variables were actually reflecting evolutionary differences among carnivoran lineages. Aside from that, the results were similar to those described for the corresponding nonphylogenetic ANOVAs, although for some linear measurements the differences between runners and aquatic carnivorans with other groups were no longer significant.

In the size-corrected phylogenetic ANOVAs, significant differences between locomotor types were only found for all relative lengths of forelimb segments, humerus length and robusticity, radius length, ulna length and robusticity, IFA, third metacarpal length, femur length and neck–head length and robusticity, and tibia length

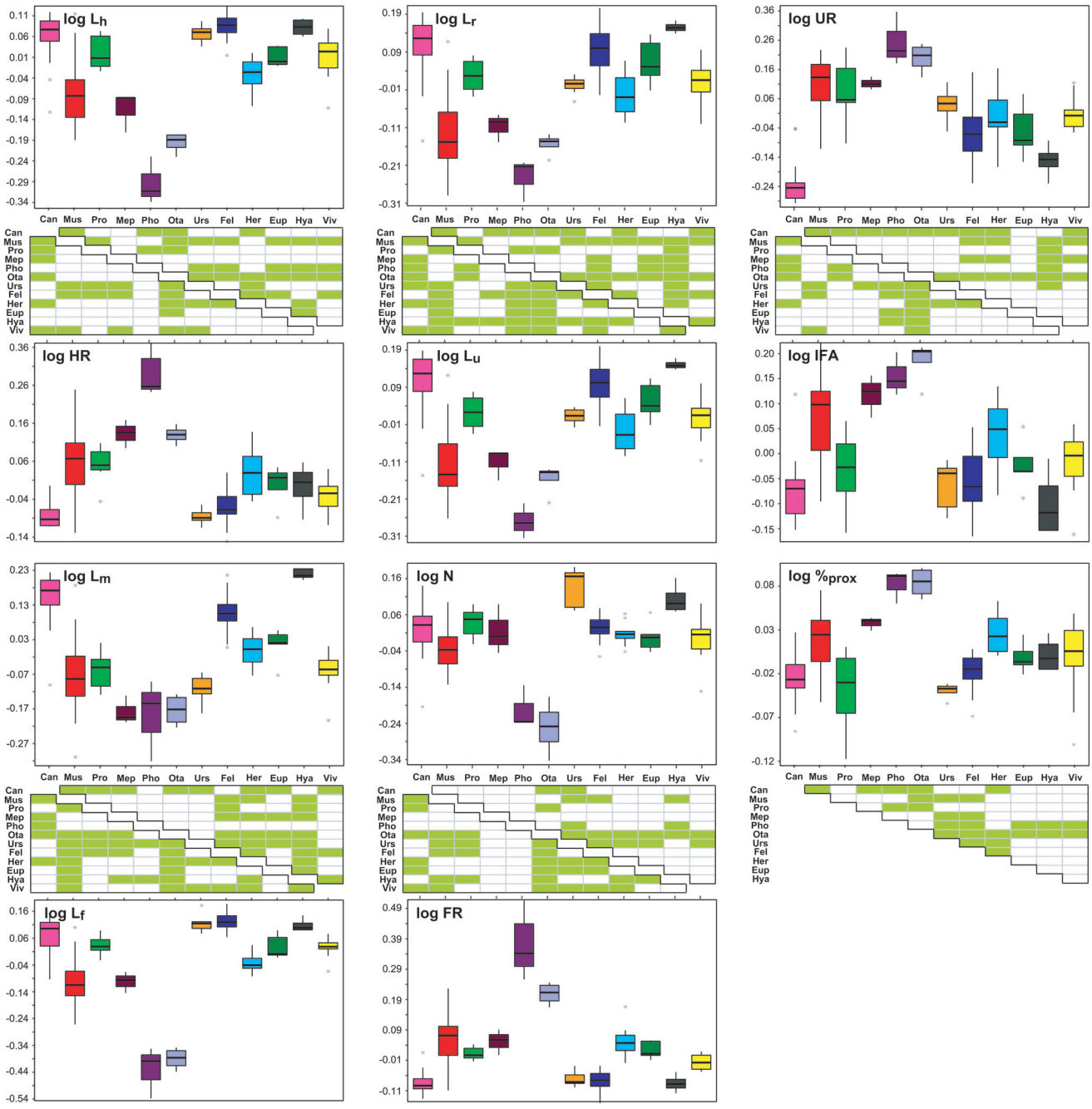

FIGURE 4 Box plots and pairwise differences between carnivoran families for some selected variables. Shadowed cells indicate significant differences between a pair of subgroups in the traditional ANOVA for that variable, while a dot represents the same for the corresponding phylogenetic ANOVA. Abbreviations: Can, Canidae; Eup, Eupleridae; Fel, Felidae; Her, Herpestidae; Hya, Hyaenidae; Mep, Mephitidae; Mus, Mustelidae; Ota, Otariidae; Pho, Phocidae; Pro, Procyonidae; Urs, Ursidae; Viv, Viverridae. Variable names are listed in Table 2

(Figures 2 and SR1). Thus, it would seem that the differences among locomotor types found in the size-corrected ANOVAs for scapular and calcaneal variables, all diameters, styloid process length, olecranon length and both angles, and robusticities of radius, third metacarpal and tibia, were actually reflecting size-independent changes along carnivoran evolutionary lines. All the size-related artifacts described when comparing raw data and size-corrected ANOVAs were also recovered in the corresponding comparison of phylogenetic ANOVAs. Additionally, all differences between all-terrain and semi-fossorial carnivorans, and those between terrestrial and all-terrain species in linear measurements, were size-related artifacts. Regarding pairwise comparisons, they

indicated that aquatic carnivorans had the largest relative length of forelimb proximal segment, bone robusticities, and IFA (together with semifossorial species); and the shortest relative length of forelimb middle segment, all bone lengths (except for the tibia, which was the shortest in semifossorial carnivorans), and femur neck–head length. Runners presented the longest bones and relative length of forelimb distal segment, and the lowest values for IFA and ulna and femur robusticity. As in all previous analyses, arboreal carnivorans had the longest relative length of forelimb middle segment and the shortest of the forelimb proximal segment.

3.3.2 | Utilized habitat

In the phylogenetic ANOVAs on raw data, significant differences between groups were only found for body mass, maximum width of supraspinous fossa, maximum scapula width, relative length of forelimb proximal and middle segments, humerus robusticity and sagittal and transverse diameters, radius sagittal and transverse diameters, styloid process length, ulna sagittal diameter and robusticity, olecranon length, IFA, third metacarpal sagittal and transverse diameter, and femur robusticity. In these variables, pairwise comparison produced similar results to those of the nonphylogenetic ANOVAs. However, the differences between several pairs of categories were not recovered (e.g., between variable and open, mosaic and forest), which suggested that they were actually related to evolutionary changes along carnivoran phyletic lines.

In the size-corrected phylogenetic ANOVAs, significant differences between habitats were only found for scapular spine height, relative length of forelimb proximal segment, humerus length and robusticity, radius length, ulna length and robusticity, IFA, third metacarpal length, femur length and robusticity and neck–head length, and tibia sagittal diameter (Figures 3 and SR2). This was a surprising result, since none of the linear measurements in which significant differences among habitats were found in the phylogenetic ANOVAs on raw data presented similar differences after size correction. That is, all those differences were size-related artifacts, while the actual differences between utilized habitats were masked by the size effect. In the case of ratios, all differences between forest-dwelling carnivorans and species of the mosaic, freshwater and variable categories were also size-related artifacts. Finally, pairwise comparisons indicated that marine carnivorans had the lowest values on all linear measurements and the highest on all ratios, while species dwelling in open habitats had the lowest ulna robusticity values. Carnivorans in the variable category presented the highest values of humerus, radius and ulna lengths, and femur neck–head length.

3.4 | Validation of results

The simple approach used to test the validity of regression residuals is represented in Figure 5. Mean residual frequencies for locomotor types suggest that the carnivoran ancestor was either arboreal or a small terrestrial mammal that climbed small obstacles regularly (Figure 5a), maybe with some digging and swimming capabilities (all-terrain carnivoran). Utilized habitat mean residual values were closest to zero in forest-dwelling carnivorans (Figure 5b), while the same was true for Viverridae in the case of family mean residual values (Figure 5c).

Thus, the results of the present study suggest a forest-dwelling "viverrid-like" ancestor for Carnivora, which agrees with the placement of "miacids" at the branch leading to extant Carnivora (Wesley-Hunt & Flynn, 2005). It is unclear whether that forest-dwelling "viverrid-like" ancestor spent most of its time in the canopy or on the ground. However, this ambiguous result also agrees with a "miacid" ancestor of Carnivora, since recent studies report a mixed set of adaptations to arboreality and high-speed running for these fossil species (Spaulding & Flynn, 2009). Furthermore, the small sizes estimated for basal carnivorans support all-terrain habits if they spent most of their time on the ground (Finarelli & Flynn, 2006).

In conclusion, regression residuals can be used to infer locomotor traits of extinct species, provided that several variables are measured in the most diverse possible sample of extant species.

4 | DISCUSSION

4.1 | Size differences, phylogenetic inertia, or locomotor adaptations?

For all the studied variables, size was the main factor determining limb bone morphology; since for most variables, differences between locomotor types, utilized habitats and taxonomic groups tended to separate the groups with the largest mean body masses from the rest. Furthermore, pairwise differences for most of the variables mirrored those obtained for body mass (M_b), particularly in the case of linear measurements. Finally, all the models summarizing the variability observed in the studied variables included M_b in their factorization; mostly as a significant interaction with another factor (Table S2). As would be expected, the use of regression residuals revealed that most group differences were size-related

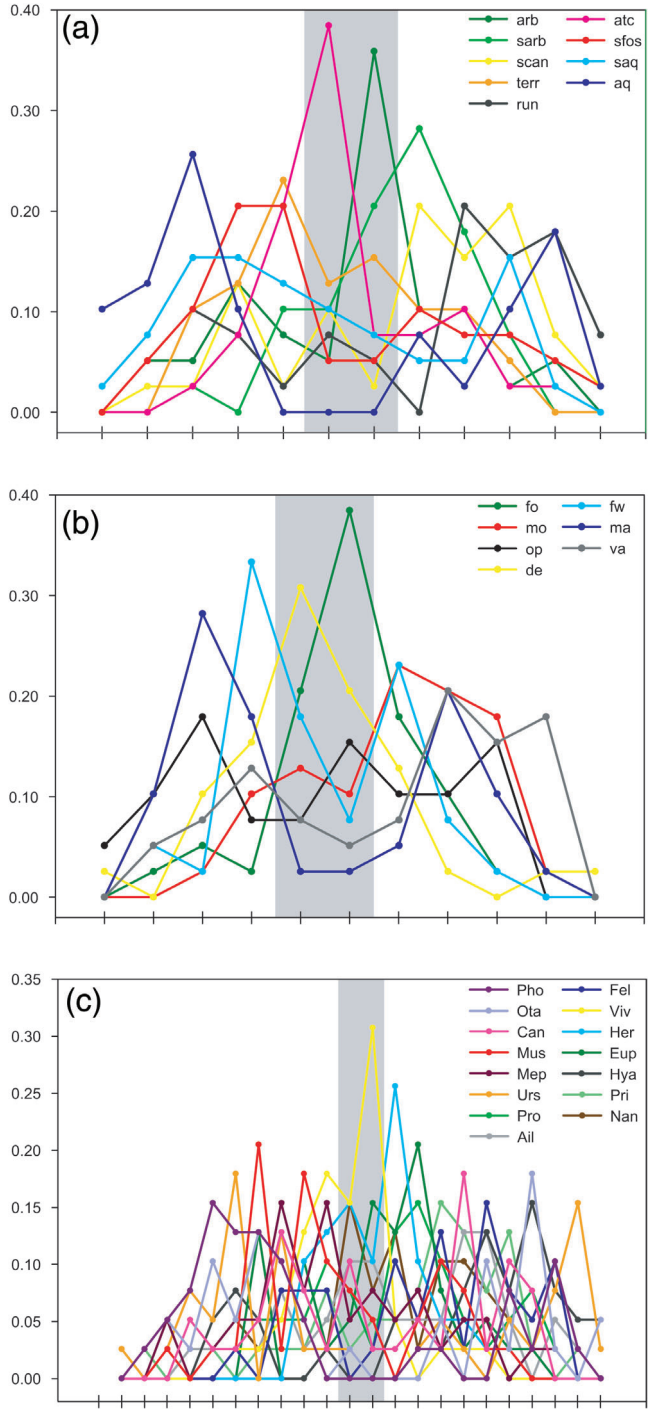

FIGURE 5 Distribution of mean residual values. The distribution of the relative frequencies of the mean residual values in the variables studied is presented for locomotor type (a), utilized habitat (b), and family (c). The grey area represents the positions closest to zero (above and below), relative to the values of all the categories for each factor. Abbreviations: Ail, Ailuridae; Nan, Nandiniidae; Pri, Prionodontidae. All other abbreviations as in Figures 2 to 4

artifacts, since they either were not recovered, or changed their polarity, after removing the size effect, especially in the analyses by utilized habitat.

In agreement with previous studies on carnivoran limb morphology (Bertram & Biewener, 1990; Day & Jayne, 2007; Flynn et al., 1988), the present study shows that shared evolutionary history has a significant effect on the morphology of the carnivoran appendicular skeleton. Not only were significant pairwise differences between families recovered for all variables (Figure SR3), but also all GLMs included the phylogenetic effect (Fam) in their factorization (Tables S2 and S3). It is interesting to note, however, that results from the traditional ANOVA and phylogenetic ANOVA produced similar results when using raw data, which could be interpreted as locomotor adaptations being mostly independent of shared evolutionary history. This is another size-related artifact, as evidenced by the vast differences between sets of ANOVAs on the size-corrected variables. Consistent with this, the interaction between size and shared ancestry (Fam*M_b) had a significant effect in most of the GLMs (Tables S2 and S3), indicating that size changes along phyletic lines explain a significant amount of the variability of the studied variables. Additionally, the size-corrected phylogenetic ANOVAs revealed that many of the putative locomotor adaptations were instead reflecting size-independent changes along carnivoran evolutionary lines. These include most of the differences between utilized habitats.

Summarizing, carnivoran limb bone morphology is mainly determined by size. Once the size effect is accounted for, shared evolutionary history explains most of the remaining observed variation in the majority of the studied variables. That being said, locomotor adaptations in the carnivoran appendicular skeleton can still be identified.

4.2 | Implications for previous assumptions on locomotor adaptations

Contrary to the expectations of Bertram and Biewener (1990), differences between terrestrial, scansorial, and arboreal carnivorans were not mainly caused by size differences between those groups. In fact, most of the significant pairwise differences in the analyses on raw data proved to be size-related artifacts, since they were not recovered after removing the size effect. Furthermore, several significant differences between terrestrial, scansorial and arboreal carnivorans could only be detected in size-corrected analyses, especially those between terrestrial and (semi)arboreal carnivorans. Also according to Bertram and Biewener (1990), adaptations to swimming were expected to be independent of size, while in the present study most differences between aquatic carnivorans and the other locomotor types were size-related artifacts: In the analyses on raw data aquatic

carnivorans had the largest values for most variables, but they turned out to be the smallest after correcting for size differences. It must be said, however, that adaptations in both aquatic carnivorans (generally large) and semiaquatic carnivorans (generally small) were quite similar after removal of the size effect (see below).

In a study on the scaling of relative functional segment lengths in primates and other mammals, Schmidt (2008) obtained a fairly constant set of forelimb proportions for the carnivoran species that she studied: 26%, 40%, and 34% for the proximal, middle, and distal segments (i.e., scapula, humerus, and radius). Furthermore, these proportions seemed to be independent of size in Carnivora. In the present study, similar functional segment proportions were found for most families and utilized habitat subsamples; only Canidae (27%, 37%, and 36%), Hyaenidae (29%, 34%, and 37%), Pinnipedia (37%, 30%, and 33%), and marine species (35%, 33%, and 32%) deviated considerably from Schmidt's values. That was not the case, however, for the locomotor type subsamples, since only terrestrial, scansorial, and semiarboreal carnivorans had functional segment proportions close to 26%, 40%, and 34%. Additionally, different sets of significant differences were obtained prior to and after the size correction; especially in the middle segment. Thus, the size-independence of functional limb proportions proposed by Schmidt (2008) is not supported by the present study. Similar results were obtained by Schmidt and Fischer (2009), who reported similar deviations for Canidae and Hyaenidae, and also a significant allometric effect in the relative length of the scapula in Felidae and in the relative length of the humerus in Carnivora (mainly Felidae + Mustelidae). Unfortunately, the different measurements for limb bone lengths used to calculate segment proportions in Pike and Alexander (2002) prevents any comparison of those results with this study's.

Delving further into functional relative segment lengths, according to Fischer and Blickhan (2006), equal proportions for each segment (33%, 33%, and 33%) increase the self-stability of crouched limbs, which are characteristic of small mammals (Fischer et al., 2002; Jenkins, 1971). Meanwhile, a more extended limb posture requires "asymmetrical limb segment proportions" for self-stability (Seyfarth, Günther, & Blickhan, 2001). In this way, large carnivorans would have been expected to present highly "asymmetrical" functional relative segment lengths and small carnivorans to approach equal proportions. However, this is never the case, as all carnivorans present "asymmetrical" limb segment proportions (Tables SR1–SR3). In fact, the values closest to equal proportions belong to the larger carnivorans: aquatic/marine carnivorans and pinnipeds. Thus, either small carnivorans do not present a crouched posture, which is probably not the case (Horner & Biknevicius, 2010), or more likely small mammals retain the limb segment proportions of an ancestor with more extended limbs, which supports the morphological conservativeness of carnivoran limbs (see below for further evidence).

Finally, regarding the use of ratios to avoid size-related issues in interspecific comparisons, in the present study the same differences prior to and after correcting for size were only obtained for radius robusticity and IFA between utilized habitats. In all other cases, different results were obtained in the raw-data and size-corrected analyses. As pointed out by Aiello (1981), a ratio between two variables will only be independent of size if both variables scale to body mass with the same exponent. These results, plus the artifactual differences detected by the size-corrected analyses, suggest not using limb bone measurements, whether they are distances or ratios, to infer behavioral traits of extinct taxa using univariate methods, at least not without previously employing some sort of size correction. For instance, the ANOVAs and post hoc tests conducted on raw data indicated that aquatic carnivorans had longer limb bones than other locomotor groups. Thus, if we were to find a new carnivoran fossil with exceptionally long limb bones, it would be logical to think of it as an aquatic species. However, the analyses on regression residuals showed that this finding was an artifact caused by the larger body size of aquatic carnivorans, and that these species actually had the shortest limb bones. Consequently, the hypothetical fossil species was probably not adapted to swimming, but more probably to running (see below, and also Hildebrand, 1985*b*; van Valkenburgh, 1987). A similar example using ratios could be found in tibial robusticity (TR), for which the analysis on raw data indicated that terrestrial carnivorans had the most gracile tibiae, but after the size correction aquatic carnivorans had the lowest values of TR. With this in mind, I recommend that in any study in which a sample of extant species is used for ecomorphological inference of fossil taxa, some variable is used first to estimate body mass (and then left out to avoid circularity), and then the regression residuals of each other variable on the estimated body mass can be used to infer the unknown behavioral traits.

4.3 | Locomotor specialization or resource maximization?

In the ANOVAs on raw data, using locomotor type to define morphologically different groups within Carnivora produced slightly better results than using utilized habitat; even though the latter appeared in more GLMs than

the former. However, when using residuals to remove the size effect, locomotor type was a better factor for differentiating subgroups, since significant pairwise differences were recovered for all the variables except calcaneal diameters (cf., with less than half of the variables using utilized habitat). Furthermore, both factors had a similar weight in the size-corrected GLMs. Locomotor type also produced better results than utilized habitat in the phylogenetic ANOVAs (both prior to and after correcting for size). Thus, it could be argued that locomotor type is a better criterion for defining morphologically different groups within Carnivora using univariate analyses. Therefore, since locomotor type was used to represent locomotor specialization and utilized habitat as an indicator of the capacity to perform different modes of locomotion (running, swimming, climbing, and digging), these results suggest that the carnivoran appendicular skeleton is optimized to perform a specific mode of locomotion over maximizing resource exploitation by being able to navigate all substrates in their utilized habitat. Surely this is a result of competition and niche specialization in most carnivoran species. This finding is consistent with the higher costs of locomotion for mammals which perform conflicting modes of locomotion, as demonstrated by the work of Williams and colleagues on the energetics of locomotion in semiaquatic mustelids (Williams, 1983a, 1983b, 1989; Williams et al., 2002). Thus, the general trend for carnivorans would be to specialize in one locomotor mode and hence minimize the cost of locomotion, probably related to the low success rate of prey capture of most carnivoran species (Wilson & Mittermeier, 2009). However, if coping with the increased locomotion costs of having several locomotor modes is possible thanks to a significant increase in prey availability, then such optimal performance of multiple locomotor modes would be selected for through evolution (as in the American mink; Williams, 1983a, 1983b).

4.4 | Morphological adaptations to the different locomotor types

Following the above findings, all subsequent discussion of group differences and descriptions of particular groups is therefore based on the size-corrected analyses. When appropriate, the results of the phylogenetic ANOVAs are discussed, but some relevant results of the non-phylogenetic analyses are also included.

In agreement with previous anatomical studies (English, 1977; Maynard Smith & Savage, 1956; Osburn, 1903), aquatic carnivorans characteristically have the shortest and most robust limb bones, as well as the lowest scapular spines. Short limbs both reduce the resistance arms of drag forces (increasing streamlining) and increase the capacity of limb muscles to produce backward thrust to propel the body forward, while increased robusticities accommodate the greater muscle forces and hydrodynamic forces associated to moving in a medium denser than air (i.e., water; English, 1977; Fish, 2004). Both the low scapular spine and having the shortest femur neck–head length (newly described in this study) could be related to increasing streamlining too, although reorienting the moment arms of shoulder and hip flexors and extensors seems a more plausible explanation (see e.g., Dewaele, Amson, Lambert, & Louwye, 2017 for an in-depth review of muscle function during swimming and ground locomotion in aquatic carnivorans). The flattened limb bones of aquatic carnivorans serve both to increase the surface area of flippers (i.e., fin-like limbs) and to increase muscle attachment areas (Dewaele et al., 2017; Mori, 1958): those studied here present the smallest sagittal diameters for the radius, third metacarpal, femur and tibia. Aquatic carnivorans also present the highest values of the IFA, which indicates an enlarged olecranon process relative to ulna length. In this case, however, it obviously does not correlate with frequency of digging, but just indicates very powerful elbow extensors, which is again related to the greater muscle forces required to move in a dense medium, and could also be related to supporting their heavy body on land. This is particularly true in otariids, in which, as pectoral oscillators (see below), forelimb retractors are the main producers of forward thrust to propel the body while swimming (Pierce et al., 2011; Williams et al., 2002). Aquatic carnivorans also present the widest supraspinous fossae and one of the most medially bent olecrana (i.e., high θ; second only to semiaquatic carnivorans), while the projected height of the greater humeral tubercle (T) is only larger in runners. Some of these adaptations were already observed by English (1977), who related them to the particular swimming style of otariids. The enlarged fossa supraspinata provides a larger insertion area for the serratus ventralis and supraspinatus muscles, while the brachiocephalicus, supraspinatus and infraspinatus insert in the robust greater tubercle. All these muscles play an important role in protracting and abducting the forelimb during the recovery phase of the forelimb cycle while swimming, while the supraspinatus and infraspinatus also contribute as shoulder stabilizers (English, 1977). In addition, a medially bent olecranon would maximize triceps leverage in an adducted position (as in the end of the propelling phase during swimming). Otariids are pectoral oscillators, that is, they swim propelling themselves forward with thrust produced by the enlarged foreflippers, while phocids swim by pelvic oscillation, generating thrust with horizontal undulations of the spine combined with hindflipper paddling (Pierce et al., 2011). Thus, all these adaptations would be of little

use for phocids, and indeed, phocids present the second narrowest supraspinous fossae and intermediate values for T and θ, while IFA is higher in otariids than in phocids. Aquatic carnivorans also present the shortest styloid processes (P), which allows wide mediolateral movements of the wrist, probably related to increased manoeuvrability when swimming. Finally, regarding limb segment proportions, aquatic carnivorans have the largest proximal segments and the smallest middle and distal segments, which is again related to the development of flippers (i.e., shorter elements to increase mechanical advantage, reduce resistance arms of drag forces, decrease surface: volume ratio to improve thermoregulation, and so on; Fish, 2004; Pierce et al., 2011). Since the proximal segment does not protrude from the body like the middle and distal segments, its shortening is less pronounced, which results in a longer relative length of the scapula relative to the humerus and the radius. Similar results were also reported by English (1977).

Most of the adaptations described for aquatic carnivorans, namely wider supraspinous fossa than infraspinous fossa, high bone robusticities, large IFA and θ values, streamlining (i.e., short limb bones, scapular spine and femur neck–head length), short styloid processes, and relatively longer proximal than distal segments, can also be found in semiaquatic carnivorans (which present mean residual values similar to those of aquatic carnivorans, although not so extreme). High IFA and short femora in this group were also reported by Samuels et al. (2013). In contrast to aquatic carnivorans, however, semiaquatic carnivorans present narrow scapulae, have the lowest values of T and their proximal limb bones are not flattened. The first two characters, narrow scapula and a greater tubercle of the humerus not protruding from the humeral head, were also observed in phocids (pelvic oscillators), which suggests a similar swimming style for semiaquatic carnivorans. However, semiaquatic carnivorans propel themselves underwater either with alternate, cyclic thrusts involving all four limbs, or using a combination of hind-paw strokes and dorsoventral body undulations, depending on their commitment to swimming (Williams, 1983a, 1983b; Williams et al., 2002). Thus, the similarity with phocids is probably due to the abundance of highly committed swimmers (otters) in the semiaquatic sample. The lack of limb bone flattening probably represents the compromise between being able to swim well and being able to move on land (Williams et al., 2002).

Regarding semifossorial carnivorans, in agreement with studies on fossoriality in mammals (Elissamburu & Vizcaíno, 2004; Lehmann, 1963; Samuels et al., 2013; van Valkenburgh, 1987), IFA is large, although smaller than in aquatic carnivorans. Furthermore, they have amongst the longest olecrana (only longer in runners). By having long moment arms (i.e., olecrana), the triceps can produce the large forces at the manus required for digging with the forelimbs (Hildebrand, 1985*a*; van Valkenburgh, 1987). Similar to aquatic and semiaquatic carnivorans, semifossorial carnivorans have relatively longer scapulae (high $\%_{prox}$ values), and remarkably robust and short limb bones (particularly the tibia), which provide a twofold advantage: they are strong enough to produce the power required for digging (Hildebrand, 1985a), and they are an advantage for moving through narrow tunnels while chasing prey (Gambaryan, 1974; Shimer, 1903). These findings agree with previous studies on fossoriality in rodents, which did not include aquatic species and thus concluded that fossorial species had the shortest limb bones (Bou et al., 1987; Casinos, 1994; Lehmann, 1963) and more robust forelimb bones (Elissamburu & Vizcaíno, 2004). It must be said, however, that the higher values of aquatic and semiaquatic carnivorans could also be attributed to the lack of truly fossorial species in the sample. Finally, contrary to what would be expected according to Maynard Smith and Savage (1956), semifossorial carnivorans present the narrowest scapulae (particularly the supraspinous fossa).

Regarding adaptations to arboreality, in agreement with previous studies on arboreality (Argot, 2001; Iwaniuk et al., 1999, 2000; van Valkenburgh, 1987), an association between several variables and arboreality was observed. Bertram and Biewener (1990) suggested that significant differences in limb bone morphology between terrestrial, scansorial, and arboreal carnivorans would be scarce. In the present study, this is only true if we just focus on these three categories; including runners in the comparison as the least arboreal carnivorans raises considerably the number of significant differences related to arboreality (Figures 2 and SR1). As the degree of arboreality increases (i.e., from runners to arboreal carnivorans), so does scapular width (A), most bone robusticities (contrary to the results of Iwaniuk et al., 1999, but in agreement with those of Polk et al., 2000; Samuels et al., 2013), some bone diameters (d_{th}, d_{su}, d_{tf}; see also Polk et al., 2000), and the relative length of the humerus ($\%_{mid}$) and the olecranon (IFA). Meanwhile, the values of several variables increase with decreasing arboreality: most bone lengths (particularly that of the third metacarpal), height of the scapular spine (H_S), projected height of the greater tubercle (T), length of the radial styloid process (P), olecranon length and orientation (O, α; in agreement with the results of van Valkenburgh, 1987), femur neck–head length (N), moment arm of the ankle extensors (r), some bone diameters (e.g., d_{sm}, d_{tm}), and relative length of the proximal and distal segments ($\%_{prox}$, $\%_{dist}$). Both the decrease in T values and the increase in A values reflect the compromise between the benefit of having increased mobility at the shoulder in the three-dimensional arboreal environment (a low greater tubercle of the

humerus allows a wider range of forelimb abduction) and the need to prevent shoulder dislocation (a wider scapula allows for the development of larger shoulder stabilizer muscles; Maynard Smith & Savage, 1956). In runners, however, which present high *T* and *P* values, these processes act as physical buttresses against mediolateral movements (Johnson & Dunning, 2005). Thus, motion at the joints is mostly reduced to the parasagittal plane, which stabilizes the joints against mediolateral collapse during running (Polly, 2007). As discussed elsewhere (Fujiwara, 2009; van Valkenburgh, 1987), the orientation of the olecranon relative to the ulnar shaft (α) determines the forelimb position in which the triceps muscle has its greatest leverage. A cranially bent or straight olecranon (low α values) maximizes triceps leverage in a crouched position, which is generally used in clawed arboreal mammals, including carnivorans (but note some arboreal carnivorans use their toes and foot pads to grasp branches; Cartmill, 1974). In contrast, a caudally bent olecranon (high α values) provides maximum triceps leverage when the limb is extended, as in most terrestrial carnivorans specialized in running (Day & Jayne, 2007; Howell, 1944). Furthermore, a long olecranon (i.e., triceps moment arm) increases the force produced by the elbow extensors and hence the force exerted on the support during terrestrial locomotion. This also applies to the ankle extensors and their moment arm (*r*). Increasing ground reaction forces, together with higher stride length and frequency, are required to increase the speed of locomotion (Dutto, Hoyt, Cogger, & Wickler, 2004), which agrees with the higher values of *O* and *r* found in runners. The increase of both scapular spine height and femur neck–head length, from arboreal carnivorans to runners, results in a lateral displacement of the attachment sites of several forelimb protractors, shoulder flexors and hip extensors (hind limb protractors), increasing their moment arms. This could also be related to increased speed: shoulder flexors contribute to pushing the body forward during the late stages of the stance phase, while more powerful limb protractors would allow shorter swing phases (see for example, English, 1978; Deban, Schilling, & Carrier, 2012, for timing and intensity of muscle activation at different speeds). Another adaptation to running in terrestrial mammals is limb elongation, especially of the distal segments (Hildebrand, 1985*b*; Iwaniuk et al., 1999; Lull, 1904), which would explain the increase in bone lengths, $\%_{prox}$ and $\%_{dist}$ as arboreality decreases. Additionally, short limbs (as found in arboreal carnivorans) have been reported to be an adaptation that increases stability during arboreal locomotion for claw-climbing mammals, like carnivorans (Cartmill, 1985). The observed increase in robusticity of the distal forelimb elements (ulna and third metacarpal) as the degree of arboreality increased, is probably related to the development of more powerful muscles in the forearm and manus (pronators, supinators, and deep digital flexors), as already described for rodents with increasing degree of fossoriality (Elissamburu & Vizcaíno, 2004; Hildebrand, 1985a). In the present study, no association between arboreality and IFA was found, contrary to the results of Iwaniuk et al. (1999), which seems to confirm their hesitations about their results being an artifact caused by the predominance of digging and swimming species in their nonarboreal sample. Finally, it should be noted that, although the gradient arboreal–semiarboreal–scansorial–runner was found in most of the variables discussed above, the position of terrestrial carnivorans was highly variable. However unexpected, since they were expected to present intermediate values between runners and scansorial carnivorans, these findings were not surprising. On the one hand, categorizing locomotor type based on the degree of arboreality is tricky, particularly for the less arboreal species. Thus, some species considered here scansorial could be considered terrestrial by other researchers, and vice versa (Meachen-Samuels & van Valkenburgh, 2009; Samuels et al., 2013). On the other hand, the term ambulatory, generalized or unspecialized, has often been used to refer to terrestrial species that are not particularly adept at running, digging, climbing, or swimming, probably as a compromise for using more than one mode of locomotion (e.g., Jenkins & Camazine, 1977; Polly, 2007). The odd positioning of the terrestrial species on the arboreal–runner gradient in the present species seems to support this unspecialized morphology. Thus, it could be argued that these species should not be included in comparative studies, since their lack of marked adaptations just adds noise instead of acting as a baseline for comparisons.

Finally, regarding all-terrain carnivorans, as expected, they presented a mix of the adaptations described for the other locomotor types. In particular, all-terrain carnivorans showed most of the adaptations common to arboreality, swimming, and digging (e.g., short and robust limb bones, relatively long proximal segment, and short distal segment), although they rarely if ever climb trees, dig for food or shelter, or spend time in or near water masses. In this case, those adaptations reflect the challenges of carnivorans so small that they are likely to have to overcome a wide variety of different obstacles which larger carnivorans do not face, with the caveat that the occurrence of the former is far more frequent. On the other hand, all-terrain carnivorans also presented one of the most caudally bent olecrana (high α; second only to runners) and particularly short femora and calcanei. These traits cannot be easily related to the locomotor requirements previously discussed, neither do they agree with the characteristic kinematics of locomotion in small mammals (Fischer et al., 2002). Thus, the results of the present study suggest that indeed these small terrestrial

carnivorans present a set of adaptations that allow them to perform all sorts of modes of locomotion. Nevertheless, it would be interesting to carry on further studies to assess whether other groups of small mammals present similar adaptations, and how these relate to their alleged characteristic kinematics.

4.5 | Thoughts on the inclusion of Pinnipedia

Traditionally, pinniped species are not included in studies on the locomotor adaptations in the carnivoran appendicular skeleton. The rationale behind this is that their adaptations are believed to be so extreme that cannot be compared with the trends found in terrestrial carnivorans. However, if we are to understand how these extreme adaptations came to be during carnivoran evolution, the wider picture of the whole order should be examined. Furthermore, the largest carnivorans happen to be pinnipeds, so their inclusion allows for a deeper understanding of how size affects the results.

In any case, the inclusion of pinnipeds in this study raises some concerns:

1 *Aquatic and marine carnivorans are composed of roughly the same species, which in turn mainly belong to the same monophyletic clade, Pinnipedia.*
It could be argued, then, that the adaptations described above for aquatic/marine carnivorans only represent the particular response of Pinnipedia to the requirements of an aquatic lifestyle, and not a general trend for aquatic/marine carnivorans. However, this is unlikely because, not only do nonpinniped species in those categories present similar (residual) values to pinniped species, but similar adaptations have also been found in semiaquatic carnivorans, which are only distantly related to pinnipeds. Furthermore, results of the ANOVAs by locomotor type and utilized habitat were not completely replicated in the ANOVAs by family. For instance, while aquatic carnivorans as a whole presented the largest values for most variables related to scapular width (A, S), Phocidae presented the lowest values for these variables, while aquatic carnivorans presented the shortest olecrana (O) and Otariidae the longest.
2 *Pinnipeds represent such an extreme specialization that their inclusion could affect the results. Furthermore, their extreme size could also be the cause for the appearance of size-related artifacts.*
To address this, all the analyses were repeated excluding Pinnipedia from the sample to check whether the same patterns were derived for the remaining carnivorans. The results are presented grouped by factor (locomotor type, utilized habitat, and taxonomic group) to emphasize the observed differences.

4.5.1 | Locomotor type

Excluding Pinnipedia meant removing aquatic carnivorans from the comparison, since only the sea otter (*Enhydra lutris*) was left in that category. In the analyses of raw data, the results for the remaining categories were fairly similar after removing Pinnipedia. In fact, in a few of the variables there was a slight increase in the resolution of the post hoc tests (i.e., more significant pairwise comparisons).

As expected, removing Pinnipedia altered the regression lines on body mass, which resulted in different residual values for all categories in all variables. Consequently, post hoc comparison also varied: some pairwise differences lost significance, some were new to the analyses without Pinnipedia, but most of them remained unaltered. These changes, however, had a minimal impact on the trends described for the analyses of the whole order, as follows:

- Significant differences between locomotor types were no longer recovered for the lengths of the styloid process and the olecranon. Additionally, no significant pairwise differences were recovered for scapular spine height even though the ANOVA indicated significant differences between means.
- All-terrain carnivorans no longer had the lowest values of maximum width of the infraspinous fossa, semiaquatic carnivorans did (i.e., their positions were switched).
- Semiarboreal carnivorans now presented the largest values for the lengths of the humerus, femur, and tibia instead of runners (again the positions of both categories were switched).

Finally, regarding the phylogenetic ANOVAs, differences between locomotor types in about half the variables were no longer significant in the analyses of raw data. For the remaining variables, significant pairwise differences were almost exactly the same with and without Pinnipedia. In the residual analyses significant differences were only found for radius length, ulna robusticity, relative length of the forelimb middle and distal segments, and femur length, with the resolution of the post hoc tests slightly reduced in all variables except for the relative lengths. However, it is interesting to note that in both phylogenetic analyses, in all the variables whose significance was lost after removing Pinnipedia the *p*-values

were very close to being significant (most under .10) and significant pairwise differences could still be found in all of them.

4.5.2 | Utilized habitat

The marine habitat category was reduced to two members after removing Pinnipedia. Thus, the resolution of the post hoc comparisons involving this category was expected to decrease. The analyses of raw data were only significant for styloid process length, olecranon angle and sagittal diameter, third metacarpal sagittal diameter, and relative length of forelimb middle segment. Since for most variables the only significant pairwise differences in the analyses with Pinnipedia were between marine mammals and the other groups, these results were not surprising. Most other trends described in the analyses with the whole sample were recovered without Pinnipedia, the exception being those trends described for humerus and ulna robusticity, and olecranon abduction angle, which were no longer significant.

The new residual values after removing Pinnipedia produced quite different results in the ANOVAs by utilized habitat. Again, differences between habitats were no longer recovered for most of the variables. Mainly because pairwise differences between marine carnivorans and other habitats were no longer significant, but in this case, it also affected to pairwise differences between freshwater carnivorans and other habitats. Surprisingly, in the few variables for which significant differences between habitats were new to the analyses without Pinnipedia, all the significant pairwise differences were between marine carnivorans and other habitats.

Finally, in both sets of phylogenetic ANOVAs, raw data and residuals, significant differences were only found for the robusticity of the humerus, femur and ulna, and the relative length of the forelimb distal segment (plus femur length in residuals). Additionally, the significant pairwise differences recovered in both sets were practically the same. These results, however, are very different from those obtained for the whole order.

4.5.3 | Taxonomic group (phylogeny)

Otariidae and Phocidae were excluded from the analyses. Other than that, as with locomotor type, removing Pinnipedia slightly increased the resolution of the post hoc tests.

The analyses on the new regression residuals produced similar results to those obtained previously in the analyses of the whole order. Several pairwise differences ceased to be significant in all variables, and only a few were new to the analyses without Pinnipedia. However, as in the analyses by locomotor type, these changes had little to no effect on the patterns described for the residual analyses including Pinnipedia.

4.5.4 | GLMs

Removing Pinnipedia dramatically altered the models summarizing the effect of locomotor type, utilized habitat, phylogenetic relatedness, body size, and their interactions, on the observed variability of the variables studied: the number of individual models increased, all variables produced different models to those in the previous analysis, the phylogenetic effect (Fam) lost half its presence as an independent factor (but was still highly significant in its interaction with other factors), and both locomotor type and utilized habitat appeared as direct effects in some models. Size (M_b) was still the most significant factor and was present in all the models (either as an independent factor or as an interaction with other factors). Surprisingly, by removing Pinnipedia the effect of locomotor type was clearly more significant than that of utilized habitat, since the first was present in 23 out of 28 models, while the latter was significant in less than half the models (and then mostly as an interaction with other factors).

GLMs for the residual variability were also more numerous and completely different to those obtained for the whole order. Additionally, size continued to appear as an independent factor in several models, not only as part of an interaction with other factors. This suggests that the new regressions were not able to remove the effect of size, probably due to reduced correlation between some variables and body mass after removing Pinnipedia. This phenomenon should be more deeply explored in the future. Finally, as in the GLMs on raw data without Pinnipedia, the effect of locomotor type was clearly more significant than that of utilized habitat.

In summary, removing Pinnipedia emphasized that carnivorans exhibit locomotor specialization, since significant differences between utilized habitats were rarely found in the studied variables after excluding Pinnipedia from the analyses. On the other hand, the results of the comparisons between locomotor habits were mostly the same with and without Pinnipedia in the sample (particularly in the phylogenetic ANOVAs). Finally, the analyses by taxonomic group were largely unaffected by the inclusion or exclusion of Pinnipedia.

5 | CONCLUSIONS

Regarding the aims of this work, it has been demonstrated that locomotor adaptations in the carnivoran

appendicular skeleton can be detected using univariate methods. However, since both size and shared evolutionary history have a strong effect on limb bone morphology in Carnivora, I would recommend performing such analyses only after applying some sort of size correction and always using phylogenetically informed comparisons. In this regard, it is interesting to note that locomotor adaptations and mere changes along phyletic lines can only be correctly distinguished after removing the size effect (i.e., both traditional and phylogenetic ANOVAs produce similar results on data not corrected by size), which is probably related to the strong covariation detected between size and phylogeny. Additionally, it has also been proven that using ratios instead of raw measurements does not avoid size-related artifacts, since they are not size-independent. All these findings caution the use of classic literature to establish starting hypotheses on comparative studies, at least in carnivoran limb morphology, since in those studies no size correction was performed (using ratios is not a valid size correction), nor was shared evolutionary history taken into account. As a final note on comparative studies, I doubt the utility of including unspecialized categories (here terrestrial carnivorans) as a baseline for comparisons, or even at all, since in some cases they can add more noise than results.

The results of this study suggest that carnivorans exhibit locomotor specialization (i.e., optimizing the performance of a specific mode of locomotion) over maximizing resource exploitation by being able to navigate all substrates in their utilized habitat. Finally, this work supports the hypothesis of a "viverrid-like", forest-dwelling carnivoran ancestor, either arboreal or with mixed adaptations (presented here as all-terrain: a small terrestrial mammal that climbs small obstacles regularly and can show digging and swimming capabilities).

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CONFLICT OF INTEREST

I have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available on request from the author.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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