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Occurrence and morphometrics of the brachioradialis muscle in wild carnivorans (Carnivora: Caniformia, Feliformia)

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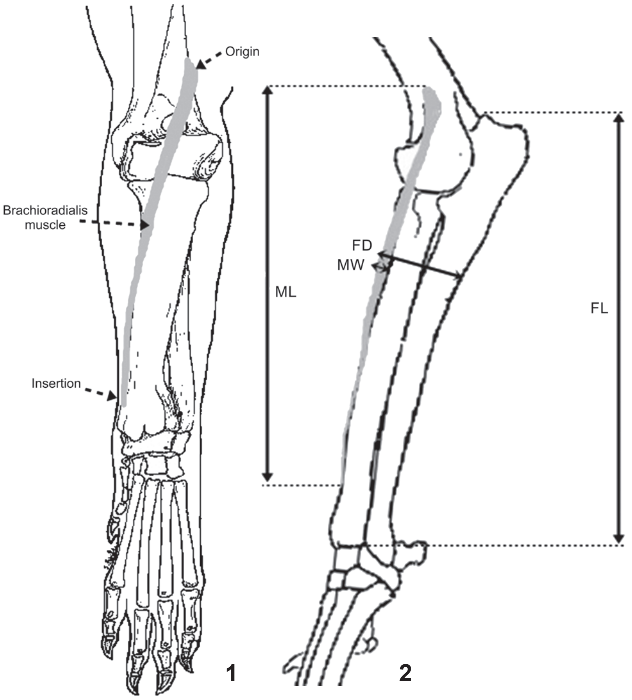
ABSTRACT. The brachioradialis is an important muscle that acts in the external rotation of the forearm (supination). However, its occurrence is controversial and little studied in the order Carnivora. Thus, this study investigates the occurrence and anatomo-functional arrangement of this muscle in wild carnivorans species. Fifty-eight thoracic limbs of specimens from species of Canidae, Procyonidae, Mustelidae and Felidae were dissected. Measurements of the length of the muscle (ML), the length of the forearm (FL), latero-medial width of the muscle (MW) and the lateral-medial diameter of the forearm (FD) were obtained to establish the ratios MW/FD and ML/FL in order to investigate the relative proportion of the muscle in relation to the forearm of each species. The brachioradialis muscle was identified in all species, although it was unilaterally or bilaterally absent in some canid individuals. The ratios demonstrated significant differences in the anatomical proportions among the families, with greater functional importance in the mustelids, procyonids, and felids because of a set of elaborate movements in the thoracic limb of representatives of these families when compared to canids.

KEY WORDS. Comparative anatomy; forelimb; myology.

Since thoracic limbs are not only used in locomotion, but also in prey capture and grooming and mating behavior, their morphology can be a good predictor of numerous ecological variables, such as the size and kind of prey, the variety of movements, the role in supporting body mass (Andersson 2004a, Fabre et al. 2013a) and the habitat (Davis 1964, Ewer et al. 1973, Taylor 1989, Polly 2007, Meachen-Samuels & Van-Valkenburgh 2009, Fabre et al. 2013a, et al. 2013b, Meloro et al. 2013, Martín-Serra et al. 2014). Together with cranio-dental data, data on thoracic limbs are also used to extrapolate the predatory behavior of extinct species (Iwaniuk et al. 1999, Andersson & Werdelin 2003). Most ecomorphology studies have prioritized the osteological characteristics of the humerus, whereas the shape and other features of the radio-ulnar joint remain largely unstudied (Fabre et al. 2013a, b, 2014). Moreover, the muscular arrangement is rarely taken into account. Knowledge about muscular disposition associated with some biomechanical findings can better elucidate the function of some important bone structures that would otherwise be neglected (Julik et al. 2012). Several studies in this field have biases because of misunderstanding of the muscular topography. Thus, the addition of quantitative and qualitative data on muscular anatomy would contribute to improve the capacity to characterize forelimb morphology in the context of locomotion, grasping ability and dexterity of the species (Iwaniuk et al. 2001, Fabre et al. 2013b). By homology, soft tissue information from extant species can help making well-founded or even speculative inferences about extinct species (Witmer 1995).

The musculoskeletal system forms an arrangement based on levers in which the joints act as fulcra (Hermanson 2013). The mechanical benefits of its configuration depend on the positions of the muscle attachments (relative to the fulcrum) and the usage of the load. A muscle attached close to a fulcrum is less powerful than a comparable muscle inserted at a greater distance, although the former produces its effects faster. This reflects a conflict between the requirements of speed and power (Dyce et al. 2010).

The brachioradialis muscle (formerly called the supinator longus) usually consists of a narrow muscular band situated at the flexor angle of the humerus-radius-ulna joint (Fig. 1) (Budras et al. 2012, Hermanson 2013). It is positioned between the superficial and deep layers of antebrachial fascia and adheres to the surface of the deep fascia's leaflet (Mills 2003, Dyce et al. 2010, Hermanson 2013), together with the cephalic vein



Figures 1-2. (1) Schematic representation of the basic arrangement of brachioradialis muscle in the domestic dog. (2) Schematic representations of the measurement points. ML: muscle length; FL: forearm length; MW: muscle width; FD: forearm diameter.

and the superficial branch of the radial nerve (Saint Clair 1986, Sebastiani & Fishbeck 2005), therefore being the most cranial and superficial muscle of the craniolateral group of the forearm (Bohensky 2002, Sebastiani & Fishbeck 2005).

In domestic carnivorans, this muscle has its origin at the proximal extremity of the humeral lateral supracondylar crest, immediately proximal and superficial to the extensor carpi radialis muscle (Schwarze 1984, Mills 2003, Liebich et al. 2011, Hermanson 2013). The muscle extends cranially over the proximal part of the extensor carpi radialis muscle, crosses the forearm medially, and extends distally in the groove between the extensor carpi radialis muscle and the radius (Schwarze 1984, Liebich et al. 2011, Hermanson 2013). It ends in the periosteum of the radius at the level of the third or fourth distal parts, by a thin aponeurosis (Bohensky 2002, Mills 2003, Budras et al. 2012, Hermanson 2013). Some authors describe its insertion into the styloid process of the radius (Leach 1976, Sebastian & Fishbeck 2005, Liebich et al. 2011, Moore et al. 2013, Ercoli et al. 2014).

The function of the brachioradialis muscle is to perform the craniolateral rotation of the radius (supination) (Bohensky 2002, Sebastiani & Fishbeck 2005, Hermanson 2013).

Supination is a movement of flipping the distal radius over the distal ulna, rotating the radius craniolaterally around its long axis (Andersson 2004b). The movement starts with the contraction of forearm muscles (supinator and brachioradialis), transmitting external rotation also to the manus. Cursorial mammals often have restricted pronation-supination, whereas scansorial mammals can usually completely supinate the manus (Polly 2007). Thus, the brachioradialis functionally belongs to the group of muscles that act on the radio-ulnar joint, and is expected to be well developed only in carnivorans. In domestic ungulates, this muscle is vestigial or absent due to the reduced or lost capacity of movement between these two bones (Polly 2007, Liebich et al. 2011).

In domestic dogs, the occurrence and antimeric distribution of the brachioradialis muscle has been well documented by Wakuri & Kano (1966), Santos Junior et al. (2002), and Pestana et al. (2009). There are no reports in the literature, as far as we know, about the occurrence of the brachioradialis muscle in wild carnivorans, although there are studies with variable contexts containing references to the presence of the muscle in Carnivora (Davis 1964, Arlamowska-Palider 1970, Julik et al. 2012, Sánchez et al. 2013, Ercoli et al. 2014).

Carnivorans form a successful and functionally diverse clade, with close to 300 living species (Ewer 1973, Wilson & Mittermeier 2009, Hunter 2011). Despite this diversity, the accumulated knowledge of myological variation within the order is still incomplete (Macalister 1873a, Mackintosh 1875, Windle & Parsons 1897, Hall 1926, 1927, Howard 1973, Leach 1976, Fischer et al. 2009, Moore et al. 2013, Ercoli et al. 2014). Hence, these animals provide a good model for this study, as they represent one of the most successful cases of repeated and independent evolution of similar morphologies in a great range of ecologies (Andersson 2004a, b, 2005, Nowak 2005, Sato et al. 2009, 2012, Slater et al. 2012, Fabre et al. 2013a, 2014, Samuels et al. 2013, Martín-Serra et al. 2014). The locomotor range of movements of carnivorans includes, to varying extents, climbing, digging, running and swimming (Andersson & Werdelin 2003). Furthermore, carnivorans species show different degrees of supination and some species cannot even use the forelimbs for grappling with or handling prey (Ewer 1973, Andersson & Werdelin 2003). We hypothesized that the life style of carnivorans, including cursoriality and food procurement strategies, should be reflected in changes in brachioradialis muscle arrangement. This muscle is expected to be frequently found and to be relatively larger in species that need to rotate the forelimbs. Thereby, the aim of this study is to verify the occurrence, anatomo-functional arrangement and sexual dimorphism of the brachioradialis muscle in wild carnivoran species, thus contributing to studies in ecomorphology.

MATERIAL AND METHODS

This study was carried out with 29 carnivorans cadavers of Canidae: *Cerdocyon thous* (Linnaeus, 1766) (three males and six females) and *Lycalopex gymnocercus* (G. Fischer, 1814) (four males and one female); Mustelidae: *Galictis cuja* (Molina, 1782) (three males and two females) and *Lontra longicaudis* (Olfers, 1818) (one female); Procyonidae: *Procyon cancrivorus* (G.[Baron] Cuvier, 1798) (one male and two females) and *Nasua nasua* (Linnaeus, 1766) (one female); and Felidae: *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) (four females) and *Leopardus colocolo* (Molina, 1782) (one female). These specimens were collected dead from highways in the southwest region of the state of Rio Grande do Sul (Pampa biome) between July 2012 and November 2013 (IBAMA/SISBIO authorization number 33667-1). Only adult individuals were included, based on inspection of permanent dentition.

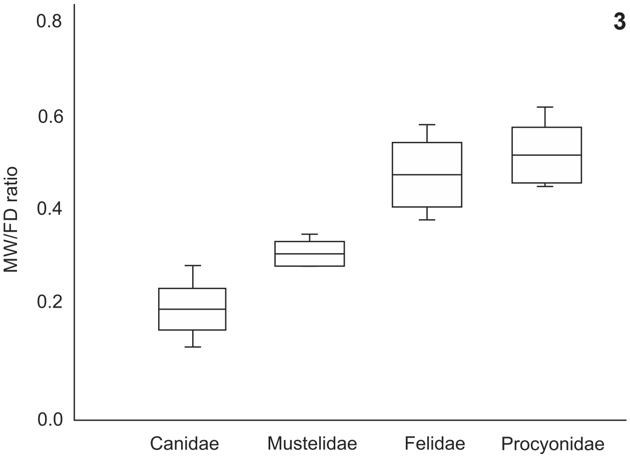
After collection, the specimens were fixed in a formaldehyde solution (50%) and conserved in opaque polyethylene tanks with the same solution at 10% for at least 14 days, until they were dissected. The skin and fascia of the thoracic limbs were carefully removed and the superficial intrinsic muscles identified. The brachioradialis muscle, whenever present, was dissected until its origin and insertion were exposed. Then measurements were taken (Fig. 2) of the length of the brachioradialis muscle from its origin until its insertion (ML) and the length of the forearm from the olecranon tuberosity until the radiocarpian joint (FL). Also, lateral-medial width of the brachioradialis muscle (MW) and the lateral-medial diameter of the forearm (FD) were obtained at the level of their middle thirds. The measurements were performed by a single examiner using a digital pachymeter (resolution 0.01mm, accuracy ±0.02 mm, ZAAS Precision Amatools®). Thereafter, two ratios were calculated: MW/FD and ML/FL. The MW/FD ratio was calculated to reflect the relative proportion of the functional participation of the brachioradialis muscle in the forearm region of the specimens. The ML/FL ratio represents the proportion of muscle length in relation to the forearm length and can be associated with added speed during contraction. The 29 specimens are deposited in the Laboratory of Animal Anatomy of the Universidade Federal do Pampa, Uruguaiana, RS, Brazil. The deposit numbers of the specimens analyzed are available in the appendix.

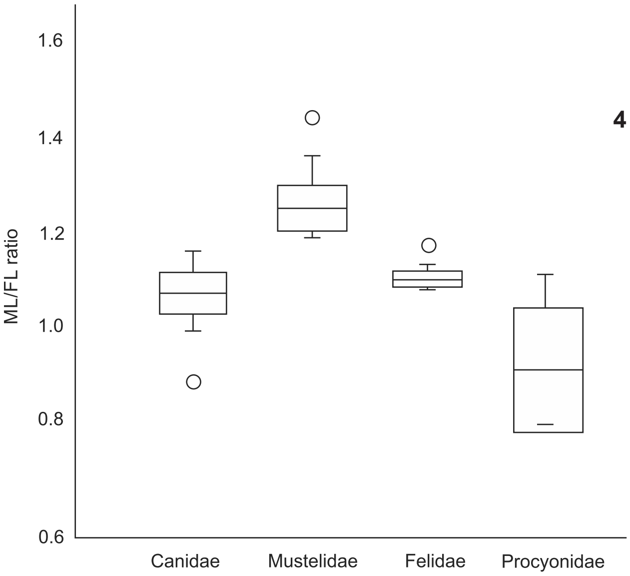
Descriptive statistical data (mean, standard deviation, variance and coefficient of variation) were calculated. The ratios were compared among species and families using analysis of variance (one-way ANOVA) and significant differences between the means were determined by using the Tukey test at 99% probability. In species with enough samples for comparison of the ratios between genders (*C. thous*, *G. cuja* and *P. cancrivorus*), the t-test was performed at 99% probability. These tests were executed by the BioEstat 5.3® program. Photomacrographs were taken with a Sony Cybershot DSC-TF1® camera with 16.1 MP and the images were treated with the Photoscape® v.3.5 software.

RESULTS

Except for two specimens of *L. gymnocercus*, in which one male only had the muscle on the right antimere and a female only on the left, along with a female of *C. thous* that did not have the muscle in any antimere, all the other specimens (26) had the brachioradialis muscle in both antimeres. Therefore, among all 58 thoracic limbs analyzed, 54 presented the muscle (Table I).

The results of the MW/FD and ML/FL ratios grouped by family (Canidae, Mustelidae, Procyonidae and Felidae) are presented in Table II and in Figs. 3 and 4.





Figures 3-4. Box-plots showing the mean ± SD of the MW/FD ratio (3) and ML/FL ratio (4) grouped by families of carnivorans analyzed.

In canids, felids and procyonids, the brachioradialis muscle originated on the lateral supracondylar crest of the humerus and its insertion was on the medial surface of the radial distal extremity (medial styloid process) in every specimen analyzed (Figs. 5-12), except one male specimen of *L. gymnocercus*, in which

Table I. Means and standard deviations (mm) of the measurements and MW/FD and ML/FL ratios obtained from the forelimbs (n = 54) of carnivorans specimens that presented the brachioradialis muscle.

Family	Species	n	Male	Female	ML	MW	FL	FD	MW/FD Ratio	ML/FL Ratio
Canidae	*L. gymnocercus*	8	7	1	125.65 ± 8.05	3.46 ± 0.98	123.72 ± 3.59	22.54 ± 1.77	0.15 ± 0.04 ^{d}	1.01 ± 0.06 ^{c}
Canidae	*C. thous*	16	6	10	127.43 ± 11.7	4.93 ± 0.77	117.42 ± 11.94	24.60 ± 2.49	0.20 ± 0.03 ^{cd}	1.08 ± 0.04 ^{bc}
Mustelidae	*L. longicaudis*	2	0	2	92.69 ± 0.75	11.66 ± 0.24	76.87 ± 0.71	40.43 ± 0.60	0.29 ± 0.00 ^{bc}	1.21 ± 0.21 ^{ab}
Mustelidae	*G.cuja*	10	6	4	63.81 ± 2.65	6.83 ± 0.53	50.13 ± 3.59	22.28 ± 1.99	0.31 ± 0.02 ^{b}	1.27 ± 0.07 ^{a}
Felidae	*L. geoffroyi*	8	0	8	112.32 ± 3.60	11.63 ± 1.65	102.39 ± 3.38	25.63 ± 1.73	0.45 ± 0.06 ^{a}	1.09 ± 0.01 ^{bc}
Procyonidae	*N. nasua*	2	0	2	110.94 ± 0.49	15.73 ± 0.46	100.52 ± 0.82	32.89 ± 0.42	0.48 ± 0.02 ^{a}	1.11 ± 0.01 ^{bc}
Procyonidae	*P. cancrivorus*	6	2	4	112.78 ± 4.64	13.72 ± 1.47	134.54 ± 7.88	25.97 ± 0.73	0.53 ± 0.06 ^{a}	0.84 ± 0.05 ^{d}
Felidae	*L. colocolo*	2	0	2	123.59 ± 1.31	11.99 ± 0.07	107.61 ± 1.43	21.79 ± 0.30	0.55 ± 0.04 ^{a}	1.15 ± 0.03 ^{abc}

Values followed by different letters in the same column show statistically significant differences according to the Tukey test ($p < 0.01$). Brachioradialis muscle length (ML); brachioradialis muscle width (MW); length of the forearm (FL); diameter of the forearm (FD).

Table II. Descriptive statistics regarding the MW/FD and ML/FL ratios obtained for the thoracic limbs (n = 54) of carnivorans specimens grouped by families (SD) Standard deviation, (CV) Coefficient of variation.

Family	MW/FD ratio							ML/FL ratio						
	n	Mean	Variance	SD	CV (%)	Minimum	Maximum	n	Mean	Variance	SD	CV (%)	Minimum	Maximum
Procyonidae	8	0.51^{a}	0.0036	0.06	11.62	0.45	0.62	12	1.27 ^{a}	0.0050	0.07	5.62	1.19	1.44
Felidae	10	0.47^{a}	0.0048	0.07	14.58	0.38	0.58	10	1.11 ^{b}	0.0008	0.02	2.48	1.08	1.17
Mustelidae	12	0.30^{b}	0.0005	0.02	7.44	0.28	0.35	24	1.06 ^{b}	0.0031	0.05	5.28	0.88	1.16
Canidae	24	0.18^{c}	0.0020	0.45	24.22	0.11	0.28	8	0.91 ^{c}	0.0171	0.13	14.38	0.79	1.11

Values followed by different letters in the same column show statistically significant differences according the Tukey test ($p < 0.01$).

the right brachioradialis muscle was shortened and joined to the middle third of the extensor carpi radialis muscle. In mustelids, the muscle originated from the caudal surface of the humeral neck and caudomedially to the brachial muscle point of origin, and also was inserted in the styloid process of the radius, being very fleshy in its course. In procyonids, especially in *P. cancrivorus*, the muscular part was restricted until the middle third of the forearm, where it narrowed into a thin insertion tendon (Fig. 7). In every specimen it was the most superficial muscle in the forearm, transiting near the cephalic vein, and was innervated by branches of the radial nerve.

The t-test ($p < 0.01$) for comparison of means of the MW/FD ratios revealed similarity between genders in *C. thous* ($p = 0.2219$), *G. cuja* ($p = 0.7273$) and *P. cancrivorus* ($p = 0.0986$). The same test for comparison of means of the ML/FL ratios revealed similarity between genders in *C. thous* ($p = 0.4026$) and *G. cuja* ($p = 0.1743$) and difference in *P. cancrivorus* ($p = 0.0024$).

DISCUSSION

The presence in nearly all the specimens assessed in this study reflects the functional relevance of the brachioradialis muscle to the order Carnivora. Its occurrence is expected in species that require significant mobility in the radius-ulnar joint, especially in external rotation (supination) of the hand (paw) and forearm, which does not happen, for instance, in ungulates (Nickel et al. 1986, Liebich et al. 2011). According to Saladin (2010), the brachioradialis muscle also acts as a synergist in the flexion of the humerus-radio-ulnar joint, but by itself it is not able to generate enough strength because its insertion is far from the fulcrum.

Only among canids were individuals identified that did not present the muscle unilaterally or bilaterally (one *C. thous* and two *L. gymnocercus*). Besides this, in one male specimen of *L. gymnocercus* the brachioradialis muscle was not long enough to be inserted in the radius, joining the extensor carpi radialis muscle in a clearly accessory position. The absence or presence, unilaterally or bilaterally, of the brachioradialis muscle has also been reported in *C. familiaris* by Wakuri & Kano (1966), Santos Junior et al. (2002) and Pestana et al. (2009). Considered together, these three studies reveal that the brachioradialis muscle is absent in 46 to 62% of dogs, appearing unilaterally in 15 to 20% of cases. In running dogs of the greyhound breed, the muscle was not found in ten individuals dissected by Williams et al. (2008). These findings corroborate the well-recognized observation that canids have lost some of the ability to supinate their manus (Ewer 1973, Andersson & Werdelin 2003). Therefore, in a superficial analysis considering the canids, the brachioradialis muscle seems to be more frequent in wild ones than in domestic ones, perhaps because

Figures 5-12. Photomacrographs showing the comparative anatomic arrangement of the brachioradialis muscle (white arrow) in the forearm region of: (5) *Cerdocyon thous*, right forearm; (6) *Lycalopex gymnocercus*, left forearm; (7) *Procyon cancrivorus*, right forearm; (8) *Nasua nasua*, right of forearm; (9) *Leopardus geoffroyi*, left forearm; (10) *Leopardus colocolo*, right forearm; (11) *Lontra longicaudis*, left forearm; (12) *Galictis cuja*, left forearm. Scale bars: 20 mm.

the former animals retain a greater need to perform supination movements to capture prey. Nevertheless, the unilateral and even bilateral absence of this muscle in some individuals suggests that it may no longer perform a useful function and instead is a rudimentary muscle that is on its way out. The apparent absence of this muscle in greyhound dogs could reflect the increased intensity of artificial selection to eliminate a useless muscle, since it can interfere with a desirable running ability in wild canids.

After examining some specimens, W.J. Gonyea (unpubl. data) noted that the brachioradialis muscle was present in arboreal and fossorial taxa and absent in cursorial ones. In support of this hypothesis, the muscle was not identified in the cursorial canids *Canis latrans* (Say, 1823) (n = 1), *Urocyon cinereoargenteus* (Schreber, 1775) (n = 4) and *Vulpes vulpes* (Linnaeus, 1758) (n = 5) (S.A. Feeney unpubl. data). The appearance of the brachioradialis muscle in almost all cursorial canids *C. thous* (n = 8/9) and *L. gymnocercus* (n = 5/5) analyzed in this study contrasts with previous observation (W.J. Gonyea, unpubl. data). Until there are more investigations, we can propose that the presence of this muscle in canids may be a characteristic shared by Neotropical species with close phylogenetic relationship rather than just a morphofunctional issue. Supporting this hypothesis, the presence of the brachioradialis muscle was also mentioned by Vaz et al. (2011) in an adult female *Atelocynus microtis* (Sclater, 1883) and in an adult male *C. thous*. Indeed, *C. thous*, *L. gymnocercus* and *A. microtis* inhabit the Neotropics and have the same number of chromosomes (74) (Pessutti et al. 2001), unlike *C. latrans*, *U. cinereoargenteus* and *V. vulpes* (S.A. Feeney, unpubl. data).

Despite disagreement over the cursorial canids, observations of the presence of the muscle in arboreal and fossorial carnivorans are compatible with the findings of this study. In fact, the mustelids, procyonids and felids analyzed here have scansorial, arboreal and fossorial habits (Reis et al. 2010, Hunter 2011). Mustelids and procyonids in particular can display great ability to perform different kinds of movements such as grasping, swimming and food manipulation (McClearn 1992, Iwaniuk et al. 1999, Fabre et al. 2013b), and their lack of cursorial adaptation means that none of them have lost the ability to supinate their paws, in contrast to other carnivorans such as canids and some hyaenids (Iwaniuk et al. 1999, Polly 2007, Fabre et al. 2014). Although with different purposes and small samples, some other studies have mentioned the occurrence of this muscle in species of these families, for instance in the mustelids *Aonyx cinerea* (Illiger, 1815) (Macalister 1873b), *Lutra lutra* (Linnaeus, 1758) (Windle & Parsons 1897), *Enhydra lutris* (Linnaeus, 1758) (Howard 1973), *Martes pennanti* (Erxleben, 1777) (n = 1) (S.A. Feeney, unpubl. data) and *G. cuja* (n = 3) (Ercoli et al. 2014); in the procyonid *Procyon lotor* (Linnaeus, 1758) (n = 2) (S.A. Feeney, unpubl. data); and in the felids *Puma concolor* (Linnaeus, 1771) (n = 2) (Concha et al. 2004), *Acinonyx jubatus* (Schreber, 1775) (n = 8) (Hudson et al. 2011), *Leopardus pardalis* (Linnaeus, 1758) (n = 1) (Julik et al. 2012) and *Panthera onca* (Linnaeus, 1758) (n = 2) (Sánchez et al. 2013).

The superficial location in the forearm, the proximity of the cephalic vein and innervation by branches of the radial nerve were common to all specimens analyzed, resembling the description of domestic carnivores (Sebastiani & Fishbeck 2005, Budras et al. 2012).

The MW/FD ratio was calculated to reflect the relative proportion of its participation in the forearm region of the specimens. This way, when comparing species and/or families, those with the highest ratios should be the ones in which the brachioradialis muscle has greater relative contribution through the group of antebrachium muscles. Although calculation of physiological cross-section area (PCSA) has been used to estimate the maximum isometric force of muscles (Williams et al. 2008), in this study we considered this determination to be less important since it generates an absolute value which is highly influenced by the body size of the individuals. For example, the brachioradialis of a crab-eating fox (*C. thous*) would exhibit both higher absolute PCSA and maximum isometric force values than the muscle in a lesser grison (*G. cuja*). However, the muscle is proportionally weaker in the former. Since the brachioradialis has parallel fibers, determination of the ratio between cross section widths (MW) to the forearm diameter would give a more proportional estimate of functional relevance, at least in its topographic region (forearm). In fact, the results of MW/FD ratio reflected observations from the usage of the forelimbs in each species.

The significantly lower MW/FD ratio in canids compared to the other three families used in this study can be explained by the fact that canids are essentially terrestrial and have developed a highly specialized lifestyle among carnivorans. In more cursorial taxa, the functional adaptations prioritize, among other aspects, the movements of the limbs in the sagittal plane, disfavoring supination or pronation (Ewer 1973). In contrast to felids, canids have a limited ability to subdue and grapple with other animals by using their forelimbs. Instead they engage in sustained pursuit predation, an activity whose success depends on the number of animals participating in the hunt (Andersson 2005). In addition, canids rarely climb or manipulate prey to a higher extent. These habits are correlated to a less functional, or even absent, brachioradialis muscle.

In the mustelids *G. cuja* and *L. longicaudis* the MW/FD ratio, significantly higher only than in the canids, comparatively reflects greater recruitment of the muscle to help in specific swimming movements and fossorial habits. At times, they also use their thoracic limbs to drag prey out of the water (Reis et al. 2010).

The felids and procyonids of this study showed the highest MW/FD ratios, with no differences among them. The repertoire of manual movements of these two families is more complex because, besides being fast runners, they are also able to swim, climb trees and remain balanced at tall heights (Reis et al. 2010, Hunter 2011). Undeniably, scansorial habits and grasping requires accurate three-dimensional movements, which demand morphofunctional adaptations and higher recruitment and precision in muscular contraction (Ewer 1973, Fabre et al. 2013b). Procyonids even use their hands to precisely bring food into their mouths, requiring a greater capacity for supination (Paranaíba et al. 2012). Species showing well-developed grasping ability potentially have a wide range of pronation-supination movements, which can confer greater mobility to the forearm and the hand (Fabre et al. 2013b). This was the case of *P. cancrivorus*, which exhibited a high MW/FD ratio. In felids, essentially carnivores, rotation movements are even more necessary to capture, overwhelm and manipulate prey extensively (Hudson et al. 2011).

These functional correlations are coherent with those previously proposed for domestic carnivorans. According to Saint Clair (1986), the distal muscles of the thoracic limbs are more developed in cats than in dogs to assure the greater rotation of the distal portion of the limb. The brachioradialis muscle presents a correlation not only with the forelimb usage in carnivorans. ANDERSSON (2004b) stated that manipulation and locomotion are conflicting functions, since elbow-joint morphology supports a division between grapplers (i.e., ambushers) and nongrapplers (i.e., pursuers). Joints of the former are relatively wide, while in the latter they are relatively narrow and box-like with pronounced stabilizing features. Concerning forepaw dexterity, IWANIUK et al. (2001) considered that manus and carpal shape and myology may play a more critical role than manus proportions. According to them, behavioral observations also suggest that manus proportions correlated more closely with locomotion than non-locomotory forepaw usage.

The ML/FL ratio represents the proportion of muscle length in relation to the forearm length. This ratio was significantly higher in mustelids. Longer muscles, especially with parallel fibers (which is the case of the brachioradialis), have more sarcomeres in series, which means added speed during contraction (KARDONG 2011). Therefore, in the mustelids one can assume that the brachioradialis muscle has a higher shortening speed than in the other families, an aspect that may be functionally important during swimming. This relatively longer length is a reflection of a more proximal level of origin in the humerus than in the other families, in other words, on the caudal surface of the humeral neck instead of the lateral supracondylar crest. Strengthening this hypothesis, in procyonids the ratio was significantly lower, because these animals have the slowest movements among the analyzed families. This shorter length was determined by the fact that its muscular part extends only until the forearm's middle third. This trait was also verified in two specimens of *P. lotor* (S.A. Feeney, unpubl. data).

From a mechanical point of view, it can be supposed that the arrangement of the mustelid brachioradialis muscle raises the power leverage, creating a low power ratio, which increases the strength and becomes important in fossorial habits. In felids, in contrast, the origin at a more distal level makes the power leverage lower, creating a higher power ratio, which increases speed, an important aspect for chasing prey. This confirms the findings of HUDSON et al. (2011) for *A. jubatus*, that the internal architecture with long fibers of the brachioradialis muscle is an adaptation that allows the muscle to contract at high speeds and extensively rotate the radio-ulnar joint.

In the mustelids of the subfamily Lutrinae *A. cinerea*, *L. lutra* and *E. lutris* (MACALISTER 1873b, WINDLE & PARSONS 1897, HOWARD 1973), the brachioradialis muscle has its origin proximal to the humeral diaphysis, which also happened with *L. longicaudis*, a member of the same subfamily analyzed in this study. The origin at a proximal level could be a synapomorphy of Lutrinae. In the *Lontra canadensis* (Schreber, 1777), a representative species of the most basal lineage of otters, FISHER (1942) described the brachioradialis muscle as originating from the proximal region of the humerus and running to the lateral supracondylar crest. From an evolutionary perspective, this condition may reflect an intermediate position between the mustelids of the ferret type (Mustelinae) and lineages like otters (Lutrinae). Based on Bayesian inference methods, KOEPFLI et al. (2008) stated these two subfamilies diverged in the late Miocene (10 MYA) during the first burst of diversification among Mustelidae.

Among the mustelids of Mustelinae, in the five specimens of ferrets (*G. cuja*) dissected in this study, the muscle extended from the proximal part of the humerus to the lateral supracondylar ridge. However, in six ferrets of the same species dissected by ERCOLI et al. (2014), the muscle had proximal origin in one-half (similar to the findings of this study) and in the other half the origin was restricted to the supracondylar crest. In four individuals of the species *M. pennanti*, the origin of the muscle occurred just proximally to the lateral humeral supracondylar ridge (S.A. Feeney, unpubl. data).

In fact, a great number of morphologic characteristics shared between the subfamilies Lutrinae and Mustelinae can be understood as favorable for both aquatic habits and locomotion in tunnels (ERCOLI et al. 2014). This peculiar arrangement, elongated and wide, of the brachioradialis muscle in this family reinforces this observation. Furthermore, a more proximal origin means the levers are more equilibrated. Thus it can be assumed that the muscle also acts as an important flexor of the humerus radio-ulnar joint.

SCHWARZE (1984) and DYCE et al. (2010) reported that the muscle is small and almost never identified in dogs, especially in small ones. In *L. gymnocercus*, a canid slightly smaller than *C. thous*, the averages of the MW/FD and ML/FL ratios were also lower (significantly at 95% probability). However, the body size should not be a condition to predict the occurrence or functional relevance of the brachioradialis muscle in carnivorans, since small specimens such as *G. cuja* and felines exhibited a bilaterally well developed muscle.

In species with enough samples for comparison of the ratios between genders (*C. thous*, *G. cuja* and *P. cancrivorus*), only ML/FL ratio was significantly lower ($p = 0.024$) in female (0.81) than male (0.92) *P. cancrivorus*. Though it would be desirable to study a larger number of specimens, this may reflect the need for more developed skills for pray chasing in males.

Finally, the study allowed establishing that the brachioradialis muscle occurs in individuals of the eight carnivorous species analyzed. This muscle originated on the lateral supracondylar crest of the humerus and was inserted in the medial surface of the radial distal extremity in canids, felids and procyonids, while its origin was on the caudal humeral neck in mustelids. Signs of sexual dimorphism were only detected in the relative length of the muscle in male *P. cancrivorus*. Overall, the mustelids, procyonids and felids have a proportionally more developed muscle than canids. As expected, these findings are consistent with the complexity and diversity of movements executed by the forelimbs of these species in the wild.

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Appendix. The specimens analyzed are deposited in the Laboratory of Animal Anatomy of Universidade Federal do Pampa, Uruguaiana, RS, Brazil, with the following numbers:

Cerdocyon thous: 5139, 5144, 5267, 5273, 5275, 5717, 8503, 8504, 8505
Lycalopex gymnocercus: 5134, 5261, 5269, 5274, 5603
Procyon cancrivorus: 5136, 5268, 8517
Galictis cuja: 5142, 5146, 5599, 5714, 5720
Leopardus geoffroyi: 5138, 5145, 5147, 5150
Nasua nasua: 8527
Lontra longicaudis: 8507
Leopardus colocolo: 5137

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