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Article

Craniolateral forearm muscles of the crab-eating raccoon (*Procyon cancrivorus*) and a comparative review with other carnivorans

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ABSTRACT. The crab-eating raccoon *Procyon cancrivorus* (Cuvier, 1798) is a species of the order Carnivora and family Procyonidae with a geographical distribution in Central and South America. Although crab-eating raccoons use scansorial locomotion, they also have aquatic habits, displaying greatly developed skills when handling their food. This species can frequently be found in wildlife care centers due to injuries caused by domestic dogs, humans, and car collisions. Having knowledge of the species' gross anatomy and anatomical bases is imperative to perform the most appropriate medical and surgical procedures. Thus, the objective of this investigation was to analyze the interspecific and intraspecific differences of the craniolateral forearm muscles of *Procyon cancrivorus*. Gross dissections were performed in four specimens describing the origin, insertion, shape, innervation, and arterial supply of the craniolateral forearm muscles. There is a constant and well development of brachioradialis muscle comparatively to that described in strictly cursorial species; the extensor carpi radialis muscle has two bellies that are fused proximally; the extensor digitorum communis muscle can also extend a tendon to the digit I as an anatomical variant, and the extensor digiti I and II muscle also extends the tendon to digit III. All are innervated by the deep branch of the radial nerve, and their arterial supply is mainly by the radial collateral, cubital transverse, and cranial interosseous arteries. The anatomical characteristics observed in this study complement the previous descriptions for *Procyon cancrivorus*, and the anatomical variants found in this species can also be in other carnivorans. Thus, the intraspecific anatomical variations of the digital extensor muscles in *P. cancrivorus* are phylogenetic traits that can occur as a common pattern or as anatomical variants in other species of the order Carnivora.

KEYWORDS. Function, innervation, insertion, myology, origin.

RESUMEN. Músculos cráneo-laterales del antebrazo del mapache cangrejero (*Procyon cancrivorus*) y una revisión comparativa con otros carnívoros. El mapache cangrejero *Procyon cancrivorus* (Cuvier, 1798) es una especie del orden Carnivora y familia Procyonidae con distribución geográfica en América Central y del Sur. Esta especie tiene hábitos arbóreos y acuáticos. Tiene una alta frecuencia en los centros de rehabilitación de fauna silvestre debido a las lesiones causadas por perros, humanos y colisiones de automóviles, por esto, tener conocimiento de la anatomía macroscópica de la especie es imprescindible para realizar los procedimientos médicos y quirúrgicos más adecuados. Por lo tanto, el objetivo de esta investigación fue analizar las diferencias inter e intraespecíficas de los músculos cráneo-laterales del antebrazo de *Procyon cancrivorus*. Se realizaron disecciones macroscópicas en cuatro especímenes donde se describió el origen, inserción, forma, inervación y la irrigación arterial de la musculatura cráneo-lateral del antebrazo. Entre los principales hallazgos se pueden mencionar: el músculo braquiorradial es constante y bien desarrollado comparativamente a lo descrito en especies estrictamente cursoriales; el músculo extensor radial del carpo presenta dos vientres fusionados proximalmente; el músculo extensor común de los dedos también puede formar un tendón al dedo I como una variante anatómica, y el músculo extensor de los dedos I y II también extiende un tendón al dedo III. Todos están inervados por el ramo profundo del nervio radial y su irrigación arterial es principalmente por las arterias colateral radial, transversa cubital e interósea craneal. Las características anatómicas encontradas en este estudio complementan las descripciones anteriores para *Procyon cancrivorus*, y las variantes anatómicas encontradas en esta especie también pueden encontrarse en otros carnívoros. Así, las variaciones anatómicas intraespecíficas de los músculos extensores digitales en *P. cancrivorus* son rasgos filogenéticos que se puede presentar en el patrón común o como variante anatómica en otras especies del orden Carnivora.

PALABRAS CLAVE. Función, inervación, inserción, miología, origen.

Procyon cancrivorus (Cuvier, 1798) is commonly known as the crab-eating raccoon and it has a wide geographic distribution that ranges from Costa Rica to Uruguay (Cubas *et al.*, 2006; Wilson & Mittermeier, 2009). It belongs to the order Carnivora, suborder Caniformia and family Procyonidae (Nyakatura & Bininda-Emonds, 2012). Phenotypically, *P. cancrivorus* is a medium-sized animal (2-6 kg, Labate *et al.*, 2001), with a wide tail which is approximately 50% of its total body length and is marked by five to ten dark and yellowish rings (Cubas *et al.*, 2006). One of the main facial characteristics of the species is a dark mask around the eyes (Labate *et al.*, 2001). The species also portrays elongated limbs including hands without hair (Nowak, 1999; Cubas *et al.*, 2006). Within the family Procyonidae, the species of the genus *Procyon* are semipalmigrades with five functional digits in its hands, providing skills to climb and handle food (Mcclearn, 1992).

It is a solitary species, with nocturnal and twilight habits that lives in shrubby areas close to rivers, swamps, or similar sources of water (Nowak, 1999; Pellanda *et al.*, 2010). This is possibly due to its diet consisting of crab, and its ability to swim (Cubas *et al.*, 2006; Martinelli & Volpi, 2010). Although *P. cancrivorus* is a species with few studies due to its nocturnal and crepuscular habits, it frequents the terrestrial substratum, and climb trees in search of refuge (Massoia *et al.*, 2012). Therefore, this species characterizes its locomotion for being mainly terrestrial (Wilson & Mittermeier, 2009; Massoia *et al.*, 2012), but also having arboreal and swimming abilities (Indrusiak & Eizirik, 2003; Martinelli & Volpi, 2010; Pellanda *et al.*, 2010). This can lead to changes in the shape and arrangement of the muscles (Diogo & Abdala, 2010), such as has been reported in the flexor digitorum superficialis and palmaris longus muscles in carnivorans (Perdomo-Cárdenas *et al.*, 2021). For example, some mustelids and species of the genera *Procyon*, *Nasua*, *Ailurus* and *Ailuropoda* have one m. palmaris longus evolutionarily derived from the m. flexor digitorum superficialis (Mackintosh, 1875; Davis, 1964; Mcclearn, 1985; Fisher *et al.*, 2009; Perdomo-Cárdenas *et al.*, 2021). While the genus *Potos* has developed two palmaris longus muscles, from which it is inferred that it may have occurred due to *Potos* has higher manual abilities than other carnivoran species (Mcclearn, 1992; Perdomo-Cárdenas *et al.*, 2021). However, the presentation of a m. palmaris longus in carnivorans is also associated to a palmigrade or semipalmigrade locomotion (Perdomo-Cárdenas *et al.*, 2021). On the other side, the rotators muscles are functionally more developed in arboreal carnivorans, while the humeral adductors and scapular adductor and protractors are more developed in terrestrial carnivorans (Taverne *et al.*, 2018). Therefore, possible anatomical variations can also be found in species with different locomotion habits.

The movements of the different types of locomotion are generated by the contraction of the different muscle groups and the functioning of the peripheral nervous system. This innervates the muscles, providing the opportunity for chemical energy to be transformed into mechanical energy, resulting in the production of various movements (Paranaiba *et al.*, 2012). The function of the thoracic limb muscles is fundamental to the animal capturing food, mating, and defending itself. These needs vary according to their habits of life, showing how fundamental is the study of the functional anatomy of different species (Aversi-Ferreira *et al.*, 2005). The thoracic limbs, specifically the craniolateral muscles of the forearm, have functions of supination of the manus, extension of digits, and adduction and abduction of the carpus (Hermanson *et al.*, 2013). Although, there are three studies about the thoracic limb muscles in *P. cancrivorus* (Windle, 1888; Lima *et al.*, 2010; Santos *et al.*, 2010a), these do not contain a detailed description of the craniolateral forearm muscles. Among these studies, someone did not report the m. brachioradialis (Santos *et al.*, 2010b), the m. supinator (Lima *et al.*, 2010), and the m. extensor digiti I et II (Lima *et al.*, 2010; Santos *et al.*, 2010a,b). The detailed knowledge of these muscles will give an anatomical basis allowing the performance of surgical procedures of the distal part of the humerus, and the entire length of the radius and the ulna. Also, this knowledge would be useful to evolutionary studies, such as muscular reconstructions in fossil procyonids (Tarquini *et al.*, 2019; Vélez-García *et al.*, 2022). Thus, the main objective was to analyze the intra- and interspecific differences of the craniolateral forearm muscles of *P. cancrivorus*.

MATERIAL AND METHODS

Specimens and fixation process. Four specimens of *P. carnivorous* (two juvenile females and two adult males) that died of natural causes were used. These specimens remain at the amphitheater of Veterinary Anatomy of the Universidad del Tolima. One male with skin and one female without skin were donated by CORPOCALDAS (Corporación Autónoma Regional de Caldas, environmental authority of Caldas-Colombia) to the Universidad de Caldas; and two necropsied specimens (a juvenile female and an adult male) were donated by CORTOLIMA (Corporación Autónoma Regional del Tolima environmental authority of Tolima-Colombia). The specimens were fixed with intramuscular and subcutaneous infiltrations of a solution of 10% formaldehyde and 20% glycerin, and then submerged in a solution of 5% formaldehyde. In one of the females, arterial repletion was performed with latex dyed with red vinyl through the axillary arteries. This study was approved by the bioethics committee of the Universidad del Tolima (2.3-059).

Dissection and documentation. Gross dissections of both thoracic limbs were performed base on Evans & De Lahunta (2017). The origin, insertion, innervation, and arterial supply of each muscle were described according to the *Nomina Anatomica Veterinaria* (Icvgan, 2017). Photographic records of dissections were taken with a Canon EOS Rebel T5i 18 MP camera associated with a macro lens of 60 mm and a Canon 6D associated with a macro lens of 100 mm.

RESULTS

The m. brachioradialis was fusiform and flattened, with a fleshy origin from the proximal extreme of the lateral supracondylar crest of the humerus, and it was inserted by a tendon onto the proximal part of the styloid process of the radius (Figs 1, 2 and 4). It was innervated by the deep branch of the radial nerve (Fig. 5) and supplied by the collateral radial and transverse cubital arteries.

The m. extensor carpi radialis (Figs 1-3) had a fleshy origin from the two distal thirds of the medial aspect of the lateral supracondylar crest of the humerus and the proximal fifth of the intermuscular septum with the m. extensor digitorum communis, which covered superficially the origin of the m. extensor carpi radialis. Two muscular bellies (cranial and caudal; Fig. 2) were formed from the proximal third of the forearm, the cranial belly was fusiform, and the caudal belly was bipennate. The cranial belly formed a tendon from the middle third of the forearm, whilst the caudal belly was free of muscle fibers from the distal third of the forearm. Both tendons passed deep to the tendon of the m. abductor digiti I longus. The tendon of the cranial belly inserted onto the dorsal surface of the base of metacarpal bone II, and the caudal belly onto the dorsal surface of the base of metacarpal bone III (Fig. 3). It was innervated by two branches of the deep branch of radial nerve (Fig. 5). Both bellies were supplied by the transverse cubital artery (Fig. 5), and the caudal belly also by a branch of the cranial interosseous artery.

Fig. 1. Cranial view of a left forearm (a), and lateral view of a left forearm (b). 1, m. brachioradialis; 2, m. extensor carpi radialis; 2’, cranial belly; 2”, caudal belly; 3, m. extensor digitorum communis; 3’, tendon of the m. extensor digitorum communis; 4, m. extensor digitorum lateralis; 4’, tendon of insertion of the m. extensor digitorum lateralis; 5, m. extensor carpi ulnaris; 5’, tendon; 6, m. abductor digiti I longus; 7; extensor retinaculum.

Fig. 2. Lateral views of a left forearm where the m. extensor digitorum communis had been retracted toward caudal to see the bellies of the m. extensor carpi radialis. 1, m. brachioradialis; 2, m. extensor carpi radialis; 2’, cranial belly; 2”, caudal belly; 3, m. extensor digitorum communis; 4, m. extensor digitorum lateralis; 5, m. extensor carpi ulnaris; 6, m. abductor digiti I longus.

The m. extensor digitorum communis (Figs 1, 2 and 5) originated via fleshy and tendinous fibers from the lateral aspect of the distal third of the lateral supracondylar crest of the humerus, the lateral epicondyle of the humerus, and the adjacent intermuscular septa (m. extensor carpi radialis and m. extensor digitorum lateralis). This muscle formed a deep common tendon with the m. extensor digitorum lateralis, which originated from the lateral epicondyle of the humerus. In two specimens, muscle fibers originating from the antebrachial fascia were observed. In the middle of the forearm, four tendons were formed, but these were only free of fleshy fibers from the distal quarter of the forearm. Each tendon was inserted onto the extensor process of the distal phalanges of the digits II-V (Fig. 3). In one thoracic limb of two specimens, the medial tendon sent a fascicle to the digit I (unilaterally), which joined to the medial tendon of the m. extensor digiti I et II. The muscle was innervated by the deep branch of radial nerve and supplied by the cranial interosseous and transverse cubital arteries (Fig. 5).

The m. extensor digitorum lateralis had a fleshy and tendinous origin from the lateral epicondyle of the humerus, intermuscular septum with the m. extensor digitorum communis, antebrachial fascia, and lateral collateral ligament of the elbow. It also had a common deep origin tendon with the m. extensor digitorum communis, which originated from the lateral epicondyle of the humerus (Fig. 1). In one specimen, the origin from the antebrachial fascia was not observed. Distally, the muscle formed three tendons that extended to the digits III-V, which joined the extensor digitorum communis tendons (Fig. 3). It was innervated by the deep branch of the radial nerve and was supplied by the cranial interosseous artery (Figs 1, 5).

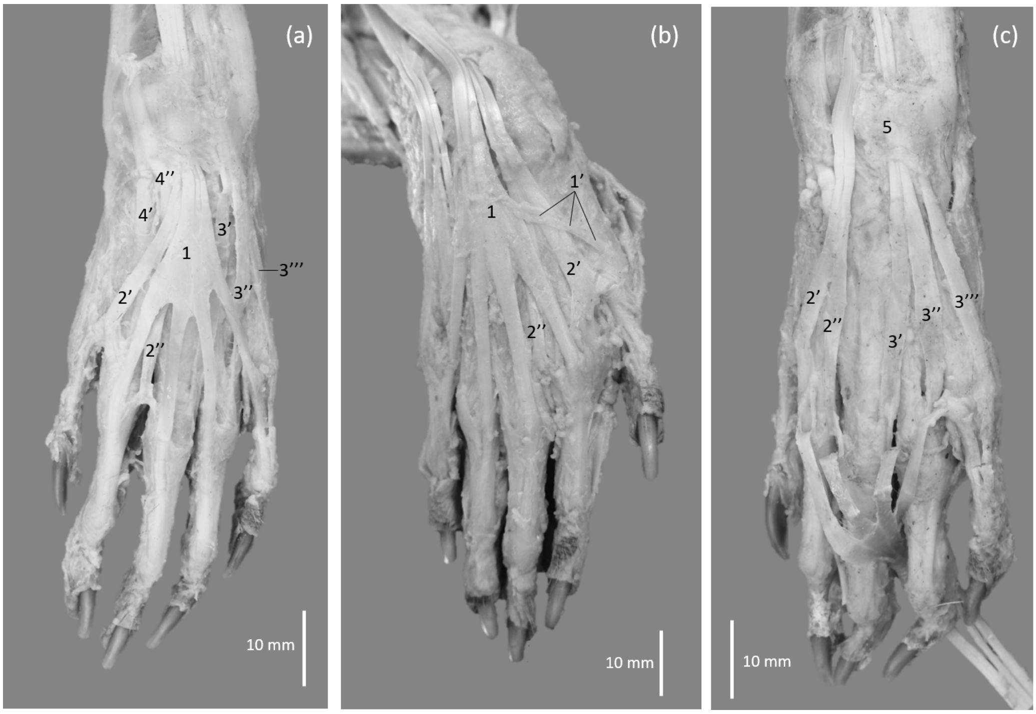

Fig. 3. Dorsal view of a left hand, dorsal view of a right hand (b), deep dorsal view of a left hand (c). 1, Extensor digitorum communis tendon; 1’, tendon to the digit I; 2, extensor digiti I et II tendons; 2’, medial tendon, 2”, lateral tendon; 3, extensor digitorum lateralis tendons; 3’, medial; 3”, intermediate; 3”’, lateral; 4, extensor carpi radialis tendon; 4’, tendon of the cranial belly; 4”, tendon of the caudal belly; 5, Extensor retinaculum.

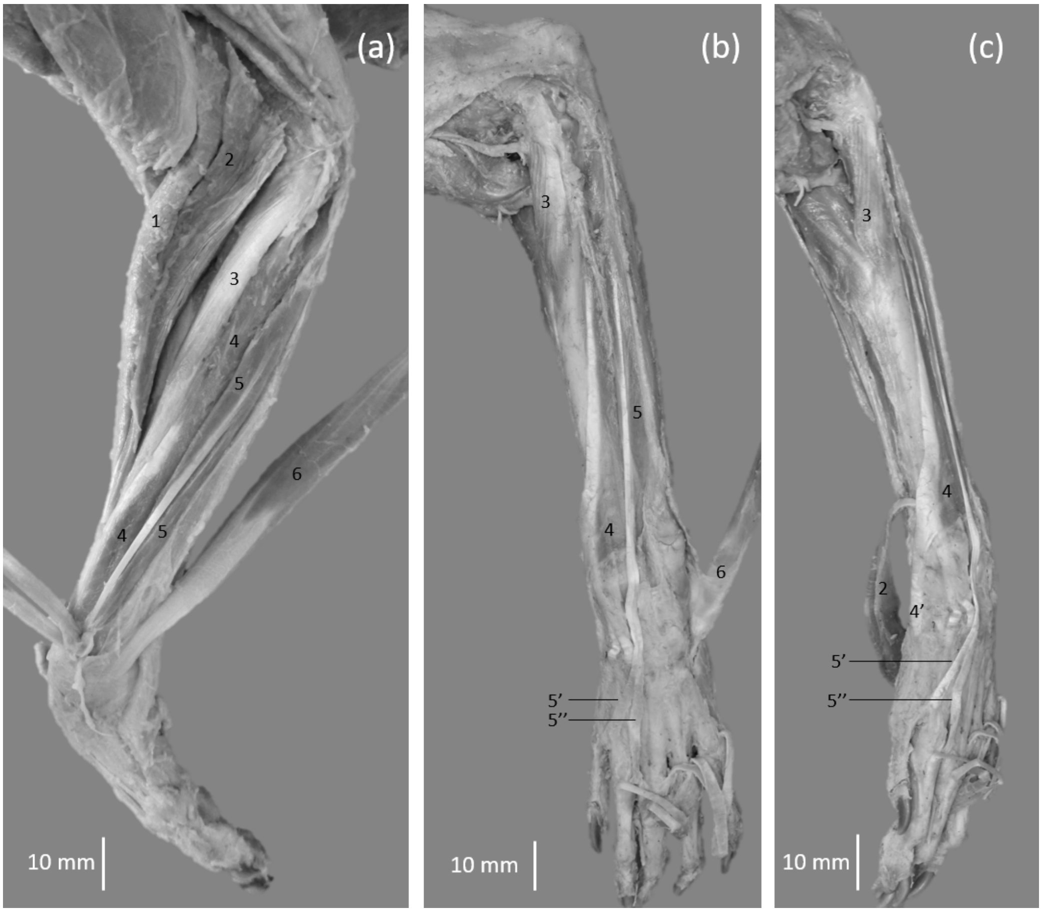

Fig. 4. Deep lateral views of a two left forearms (a-b), and deep cranial view of a left forearm (c). 1, m. brachioradialis; 2, m. extensor carpi radialis; 3, m. supinator; 4, m. abductor digiti I longus; 4’, tendon; 5, m. extensor digiti I et II; 5’, medial tendon; 5”, lateral tendon; 6, m. extensor carpi ulnaris.

The m. extensor carpi ulnaris was fusiform, originated via a tendon from the distal extreme of the lateral epicondyle of the humerus. It formed a flat tendon in the distal third of the forearm (Figs 1, 2), which inserted onto the base of the metacarpal V and the accessory carpal bone (Figs 4, 5). There was a synovial bursa at the level of the cranial surface of the styloid process of the ulna, which protected its tendon. In a left forearm, the muscle presented an ulnar head, which originated from the three middle fifths of the caudal part of the lateral surface of ulna (just caudal to the ulnar origin of the m. abductor digiti I longus) (Fig. 6). It was innervated by the deep branch of the radial nerve and was supplied by the cranial interosseous artery (Fig. 5).

The m. abductor digiti I longus (Figs 1, 2, 4) was bipennate and had a wide fleshy origin from the middle third of the lateral margin of the radius, along the antebrachial interosseous ligament, the antebrachial interosseous membrane, and the lateral surface of the ulna. In two specimens, its origin was also observed from the lateral collateral ligament of the elbow. It inserted by a tendon onto the medial surface of the base of the metacarpal I and the sesamoid bone (Fig. 4). Its tendon passed superficially to the tendons of m. extensor carpi radialis. It was innervated by the deep branch of the radial nerve and was supplied by the cranial and caudal interosseous arteries.

The m. extensor digiti I et II had two bellies, which originated from the caudal part of the lateral surface of the ulna and the epimysium of the m. abductor digiti I longus (Fig. 4). It formed two tendons, one medial and one lateral, the medial tendon extended to the digit I and the abaxial surface of the digit II; and the lateral tendon extended to the axial surface of the digit II and the abaxial surface of digit III. Both tendons joined with the extensor digitorum communis tendons at the level of the metacarpophalangeal joint (Figs 3, 4). It was innervated by the deep branch of the radial nerve and was supplied by the cranial interosseous artery.

The m. supinator was fusiform with a tendinous origin from the lateral epicondyle of the humerus, the annular radial ligament, and the lateral collateral ligament of the elbow. It had a fleshy insertion onto the proximal third of the cranial surface, lateral, and medial margins of the radius (Fig. 4). It was innervated by the deep branch of the radial nerve (Fig. 5) and supplied by the transverse cubital and cranial interosseous arteries.

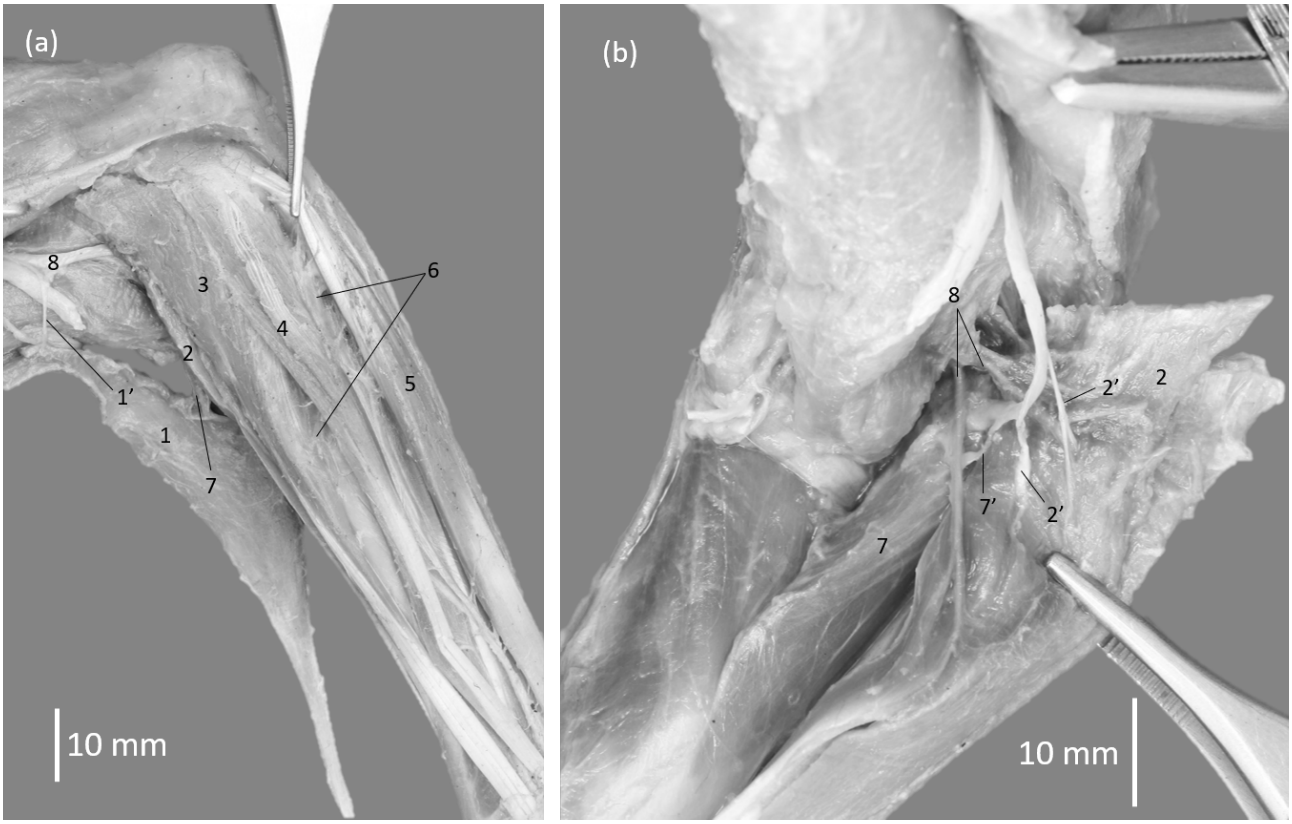

Fig. 5. Lateral view of a left forearm where the m. brachioradialis had been retracted toward medial (a), and lateral view of a left forearm (b). 1, m. brachioradialis; 2, m. extensor carpi radialis; 3, m. extensor digitorum communis; 4, m. extensor digitorum lateralis; 5, m. extensor carpi ulnaris; 6, cranial interosseous artery; 7, m. supinator; 8, transverse cubital artery; 1', 2', 7', branches of the deep branch of radial nerve to the respective muscle.

Fig. 6. Lateral view of a left forearm where the m. extensor carpi ulnaris had been retracted toward cranial. 1, m. extensor carpi ulnaris; 1", ulnar head (variant accessory head) of the m. extensor carpi ulnaris; 2, M. extensor digiti I et II; 3, M. abductor digiti I longus.

DISCUSSION

Comparative myology. The m. brachioradialis of the specimens of *P. cancrivorus* in the current study had the same attachments reported by other authors (Windle, 1888; Lima *et al.*, 2010; Souza-Junior *et al.*, 2015). Although Santos *et al.* (2010a,b) did not mention the m. brachioradialis, this muscle was present on their figures. Therefore, the brachioradialis is a common muscle in *P. cancrivorus* as in other procyonids (Mackintosh, 1875; Allen, 1882; Windle & Parsons, 1897; Julitz, 1909; Mcclearn, 1985; Souza-Junior *et al.*, 2015, 2021; Vélez-García *et al.*, 2022), mustelids (Macalister, 1873; Mackintosh, 1875; Windle & Parsons, 1897; Leach, 1976; Moore e*t al.*, 2013; Ercoli *et al.*, 2015; Souza-Junior *et al.*, 2015; Böhmer *et al.*, 2020), ailurids (Fisher *et al.*, 2009), ursids (Haughton, 1864; Shepherd, 1883; Kelley, 1888; Windle & Parsons, 1897; Davis, 1964), herpestids (Taylor, 1976), felids (Beswick-Perrin, 1871; Windle & Parsons, 1897; Barone, 1967; Concha *et al.*, 2004; Julik *et al.*, 2012; Cuff *et al.*, 2016; Viranta *et al.*, 2016; Nazem *et al.*, 2017; Vargas *et al.*, 2017; Ari *et al.*, 2019; Sánchez *et al.*, 2019), and viverrids of the genera *Genetta* (Taylor, 1976) and *Paradoxurus* (Beswick-Perrin, 1871). Whilst, it is a small or absent muscle in canids (Haughton, 1864; Vaz *et al.*, 2011; Hermanson, 2013; Echeverry *et al.*, 2015; Souza-Junior *et al.*, 2015, 2018; Böhmer *et al.*, 2020; Smith *et al.*, 2020), felids of the genus *Acynonix* (Windle & Parsons, 1897; Taverne *et al.*, 2018; Böhmer *et al.*, 2020), hyaenids (Watson & Young, 1879; Watson, 1882; Spoor & Badoux, 1986; Böhmer *et al.*, 2020), and viverrids of the genus *Civettictis* (Devis, 1868; Young, 1880; Macalister, 1873; Windle & Parsons, 1897). In mustelids of the family Ictonychidae and subfamily Lutrinae, the origin is from the proximal third of the humerus (Windle & Parsons, 1897; Howard, 1973; Ercoli *et al.*, 2015; Souza-Junior *et al.*, 2015), while it originates only from the middle third in *Galictis cuja* (Ercoli *et al.*, 2015), or from the cranial aspect of the lateral epicondyle in *Taxidea taxus* (Moore *et al.*, 2013). In the ailurid *Ailurus fulgens*, it has two heads, in which one originates from the lateral supracondylar crest and the other from the m. brachialis (Fisher *et al.*, 2009). In ursids, it can also have two heads similar to *Ailurus*, such as *Ursus maritimus* (Kelley, 1888) and *Ailuropoda melanoleuca* (Davis, 1964), whereas *Ursus americanus* only has one head from the lateral supracondylar crest (Haughton, 1864; Shepherd, 1883). The origin of the m. brachioradialis in felids reaches the middle third of the humerus (Julik *et al.*, 2012; Concha *et al.*, 2004; Viranta *et al.*, 2016; Vargas *et al.*, 2017; Ari *et al.*, 2019; Dunn *et al.*, 2022), however, it could originate from the proximal third in *Panthera* and *Leopardus* (Barone, 1967; Sánchez *et al.*, 2019; Smith *et al.*, 2021) or only from the lateral supracondylar crest in *Caracal*, *Acynonyx* and *Leopardus* (Beswick-Perrin, 1871; Hudson *et al.*, 2011; Souza-Junior *et al.*, 2015). Carnivorans present few variants in the insertion of m. brachioradialis, however, there are some differences, such as in herpestids (*Ichneumia albicauda* and *Herpestes* *ichneumon*), since the m. brachioradialis inserts onto the cranial surface of the distal extreme of the radius (Taylor, 1976); in *Ailurus* it also inserts onto the m. pronator teres (Fisher *et al.*, 2009); in *Leopardus pardalis*, *Leopardus. geoffroyi* and *Panthera onca* it also inserts onto the proximal row of the carpus (Sánchez *et al.*, 2019) or in *Lynx lynx* only onto the radial carpal bone (Ari *et al.*, 2019); and in *L. pardalis* onto the flexor retinaculum (Julik *et al.*, 2012). In the euplerid *Cryptoprocta ferox*, the muscle was only described as a muscle well developed (Böhmer *et al.*, 2020).

The m. extensor carpi radialis in *P. cancrivorus* has been described as a single muscle (Lima *et al.*, 2010; Santos *et al.*, 2010a), such as occurs in other procyonid as *Nasua nasua* (Santos *et al.*, 2010b), some mustelids (Haughton, 1864; Macalister, 1873; Howard, 1973; Leach, 1976; Moore *et al.*, 2013), canids (Haughton, 1864; Vaz *et al.*, 2011; Hermanson, 2013; Echeverry *et al.*, 2015; Souza-Junior *et al.*, 2015, 2018; Smith *et al.*, 2020), hyaenids (Watson & Young, 1879; Watson, 1882; Spoor & Badoux 1986), herpestids (Taylor, 1976), viverrids (Devis, 1868; Macalister, 1873; Young, 1880; Taylor, 1976), and some felids, such as *Caracal caracal* (Beswick-Perrin, 1871), *Acynonyx jubatus* (Hudson *et al.*, 2011; Nazem *et al.*, 2017; Böhmer *et al.*, 2020), and *L. lynx* (Viranta *et al.*, 2016). However, we observed two muscle bellies in the m. extensor carpi radialis of *P. cancrivorus*, one cranial and one caudal, which corresponded respectively to the m. extensor carpi radialis longus and m. extensor carpi radialis brevis described independently in other procyonids (without fusion), such as *Procyon lotor* (Allen, 1882; Mcclearn, 1985), *N. nasua* (Mackintosh, 1875; Mcclearn, 1985; Böhmer *et al.*, 2020), and *Potos flavus* (Beswick-Perrin, 1871; Julitz, 1909; Böhmer *et al.*, 2020; Vélez-García *et al.*, 2022). Therefore, based on the findings in *P. cancrivorus*, these muscles were not considered as independent muscles because they had intermixed fleshy fibers between them. Mackintosh (1875) in *Nasua narica* describes that both muscle bellies are partly fused, similar to our findings in *P. cancrivorus*. In *P. flavus*, both muscles can have intermixed fibers as an anatomical variant, but in a very low proportion (Vélez-García *et al.*, 2022). Some mustelids can have both independent muscles, such as *Martes foina*, *Martes martes*, *Meles meles* and a specimen of *G. cuja* (Ercoli *et al.*, 2015; Böhmer *et al.*, 2018, 2020). Although, both muscle bellies can be partly fused as in *M. foina* (Mackintosh, 1875), *Eira barbara* (Macalister, 1873), and *Enhydra lutris* (Howard, 1973). Ursids such as *U. americanus* and *U. maritimus*, present a single muscle (Shepherd, 1883; Kelley, 1888), although it was described as two independent muscles in *Ursus* sp. (Haughton, 1864) and *A. melanoleuca* (Davis, 1964). In *Ailurus* both muscle bellies are only separated on the middle of the forearm, but both can be completely separated as an anatomical variant (Fisher *et al.*, 2009). In felids, it was divided into two muscles (Concha *et al.*, 2004; Icvgan, 2017; Sánchez *et al.*, 2019; Dunn *et al.*, 2022), but both muscle bellies can be fused proximally in *Felis catus* (Barone, 1980), *L. pardalis* (Julik *et al.*, 2012), *Panthera leo* (Barone, 1980; Vargas *et al.*, 2017), *Panthera uncia* (Smith *et al.*, 2021), *Panthera tigris* (Dunn *et al.*, 2022), and *L. lynx* (Ari *et al.*, 2019); even the brevis belly may be fused with the m. extensor digitorum communis in *L. pardalis* (Julik *et al.*, 2012). Although, in *P. leo* both muscles were reported independently, similar to that described in the hyaenid *Hyena hyaena* and the herpestid *H. auropunctatus* (Böhmer *et al.*, 2020).

The origin of the m. extensor digitorum communis of *P. cancrivorus* was similar to that observed by Lima *et al.* (2010), however these authors did not report the origin from the intermuscular septa. Other authors only reported the origin from the lateral epicondyle of the humerus (Santos *et al.*, 2010a), similar to that observed in other procyonids such as *N. nasua* (Santos *et al.*, 2010b), *N. narica* (Mackintosh, 1875), and *P. flavus* (Julitz, 1909; Vélez-García *et al.*, 2022). Although in *P. flavus*, origins from the adjacent intermuscular septa have also been reported (Vélez-García *et al.*, 2022). Other studies in procyonids reported a restricted origin from the lateral supracondylar crest of the humerus in *P. lotor* (Allen, 1882; Mcclearn, 1985), *N. nasua* and *N. narica* (Mcclearn, 1985). In mustelids, it can originate only from the lateral supracondylar crest (Leach, 1976; Böhmer *et al.*, 2018) or from lateral epicondyle (Mackintosh, 1875; Moore *et al.*, 2013), whereas *G. cuja* and *E. lutris* has both origins (Howard, 1973; Ercoli *et al*, 2015), similar to that observed in *P. cancrivorus*. In *A. fulgens*, it only originates from the lateral epicondyle, however, it can originate from the m. extensor carpi radialis brevis or be fused with the m. extensor digitorum lateralis as anatomical variants (Fisher *et al.*, 2009). In *Ursus*, the m. extensor digitorum communis originates from the lateral epicondyle (Shepherd, 1883; Kelley, 1888), while in *Ailuropoda* it originates from the lateral supracondylar crest and it is proximally inseparable to the adjacent muscles (Davis, 1964). In canids, it originates from the lateral epicondyle (Vaz *et al.*, 2011; Hermanson, 2013; Souza-Junior *et al.*, 2018; Liebich *et al.*, 2020; Smith *et al.*, 2020), however it also originates from the intermuscular septum with the m. extensor carpi radialis and antebrachial fascia in *Canis lupus familiaris* (Hermanson *et al.*, 2013) and also from the articular capsule of the elbow in *Cerdocyon thous* (Echeverry *et al.*, 2015). In most felids, it originates from the lateral epicondyle, while in some species it originates from the lateral supracondylar crest, such as in *L. pardalis* (Julik *et al.*, 2012), *A. jubatus* (Hudson *et al.*, 2011; Nazem *et al.*, 2017), *P. leo* (Barone, 1967; Vargas *et al.*, 2017), *P. uncia* (Smith *et al.*, 2021), and *P. tigris* (Dunn *et al.*, 2022). In *L. lynx*, the muscle can originate from the lateral epicondyle of the humerus (Viranta *et al.*, 2016) and lateral supracondylar crest (Ari *et al.*, 2019), and it also has other origins either from the lateral margin of the radius (Viranta *et al.*, 2016), or from the ulna and olecranon (Ari *et al.*, 2019), which is uncommon in carnivorans. In hyaenids and viverrids it originates from the lateral epicondyle (Devis, 1868; Watson & Young, 1879; Young, 1880; Watson, 1882;

Spoor & Badoux 1986). In *C. crocuta*, it also originates from the intermuscular septum (Watson & Young, 1879), whereas Taylor (1976) observed in the viverrid *Genetta* and herpestids an origin from the lateral supracondylar crest. The m. extensor digitorum communis extends tendons to the digits II-V in most carnivorans, however it also extends a tendon to the digit I in *M. foina* (Böhmer *et al*., 2020), and *L. lynx* (Viranta *et al.*, 2016). Although in *L. lynx* that tendon can be absent (Ari *et al.*, 2019), thus the tendon for the digit I is an anatomical variant in this species, being similar to that reported in *P. leo* (Vargas *et al.*, 2017) and the findings of this study in *P. cancrivorus*.

The origin of the m. extensor digitorum lateralis in *P. cancrivorus* has been reported from the lateral ligament of the elbow and the lateral tuberosity of the radius (Lima *et al.*, 2010), or from the lateral epicondyle of the humerus (Santos *et al.*, 2010a). This partially agrees with our findings, since the origin from the radius was not found, and the origins from the intermuscular septum and the antebrachial fascia was not reported by those studies. In *P. flavus*, the muscle also originates from the lateral collateral ligament of the elbow and intermuscular septum (Vélez-García *et al*., 2022), similar to *P. cancrivorus*. In other procyonids, it only originates from the lateral epicondyle (Mackintosh, 1875; Mcclearn, 1985; Santos *et al.*, 2010b) or the lateral supracondylar crest in *P. lotor* (Allen, 1882). However, the muscle sends tendons to the digits III to V in all procyonids (Mackintosh, 1875; Allen, 1882; Mcclearn, 1985; Lima *et al.*, 2010; Santos *et al.*, 2010a,b; Böhmer *et al.*, 2020; Vélez-García *et al.*, 2021). In *N. narica*, it can form two muscles, one lateral that only extends to the digit V, and one medial that extends to the digits III and IV (Mackintosh, 1875). This disposition of *N. narica* can also occur in some mustelids, such as *Aonyx* (Macalister, 1870), *G. cuja* (Ercoli *et al.*, 2015), and *T. taxus* (Moore *et al.*, 2013), whereas one muscle extends tendons to the digits III-V in *E. barbara* (Macalister, 1873), *M. foina* and *M. meles* (Böhmer *et al.*, 2020). In *Martes americana* and *Pekania penannti*, it originates from the lateral epicondyle and the lateral proximal side of the radius (Leach *et al.*, 1976); whereas in *M. foina* and *M. martes*, it originates from the lateral supracondylar crest and only extends to the digits IV and V (Böhmer *et al.*, 2018). In *E. lutris*, it originates from the lateral supracondylar crest and lateral epicondyle, and extends tendons to the digits IV and V (Howard, 1973). In *A. melanolueca*, it originates from the lateral epicondyle and condyle and only extends to the digits IV and V (Davis, 1964), whereas in *Ursus*, it only originates from the lateral epicondyle and extends to the digits III-V (Haughton, 1864; Shepherd, 1883; Kelley, 1888), being similar to *Ailurus* (Fisher *et al.*, 2009). In canids, it originates from the lateral epicondyle (Vaz *et al.*, 2011; Echeverry *et al.*, 2015; Souza-Junior *et al.*, 2018; Smith *et al.*, 2020), however, it also originates from the lateral collateral ligament of the elbow in *C. l. familiaris* (Hermanson, 2013), *C. thous* (Echeverry *et al.*, 2015), and *Lycaon pictus* (Smith *et al.*, 2020). Even it also originates from the intermuscular septum with the m. extensor digitorum communis in *C. thous* (Echeverry *et al.*, 2015). In some canids as *Cuon alpinus and Vulpes vulpes*, the tendon to the digit III is absent (Böhmer *et al.*, 2020). In felids, it originates from the lateral epicondyle (Beswick-Perrin, 1871; Barone, 1986; Concha *et al.*, 2004; Hudson *et al.*, 2011; Nazem *et al.*, 2017; Viranta *et al.*, 2016; Vargas *et al.*, 2017; Smith *et al.*, 2021; Dunn *et al.*, 2022), or the lateral supracondylar crest (Julik *et al.*, 2012; Sánchez *et al.*, 2019; Liebich *et al.*, 2020), however in *L. pardalis* it also originates from the m. supinator (Julik *et al.*, 2012). On the other side, the muscle sends tendons to the digits III to V in all felids (Beswick-Perrin, 1871; Barone, 1986; Concha *et al.*, 2004; Hudson *et al.*, 2011; Julik *et al.*, 2012; Nazem *et al.*, 2017; Viranta *et al.*, 2016; Vargas *et al.*, 2017; Ari *et al.*, 2019; Sánchez *et al.*, 2019; Böhmer *et al.*, 2020), although in *F. catus*, it can also extend a tendon to the digit II (Barone, 1980; Liebich *et al.*, 2020), similar to *L. pardalis* (Julik *et al*., 2012) and *P. tigris* (Dunn *et al*., 2022). In herpestids, viverrids, and hyaenids, it originates from the lateral epicondyle (Devis, 1868; Watson & Young, 1879; Watson, 1882; Taylor, 1976; Spoor & Badoux, 1986), and extends tendons to the digits IV-V (Devis, 1868; Watson & Young, 1879; Watson, 1882; Spoor & Badoux, 1986; Böhmer *et al.*, 2020). Although, it may also originate from the radius, near the insertion point of the lateral collateral ligament of the elbow in *Hyaena hyaena* (Spoor & Badoux, 1986), and it can also extend a tendon to the digit III in the viverrid *Civettictis civetta* (Macalister, 1873; Young, 1888), the herpestid *Herpestes auropunctatus* and the euplerid *C. ferox* (Böhmer *et al*., 2020).

The origin and insertion of the m. extensor carpi ulnaris observed in *P. cancrivorus* agree with other studies (Windle, 1888; Santos *et al.*, 2010a), whereas other authors did not report an insertion onto the accessory carpal bone (Lima *et al.*, 2010). In other procyonids, it can have an origin from the olecranon, such as in *N. narica* (Mackintosh, 1875) and *P. flavus* (Julitz, 1909); or from the body of the ulna in *P. cancrivorus* as an anatomical variant. Even the muscle also originates from the articular capsule of the elbow in *P. flavus* (Vélez-García *et al*., 2022). The muscle also inserts onto the accessory carpal bone in *P. lotor* (Allen, 1882) and *P. flavus* (Vélez-García *et al*., 2022), similar to our findings in *P. cancrivorus.* Although Mcclearn (1985) only reports the insertion onto the metacarpal V in *P. lotor* and *Nasua*. The origin and insertion in *P. cancrivorus* are also similar to mustelids (Macalister, 1870; Howard, 1973; Leach *et al.*, 1976; Moore *et al.*, 2013; Ercoli *et al.*, 2015), ursids (Haughton, 1864; Shepherd, 1883; Kelley, 1888), *Ailurus* (Fisher *et al.*, 2009), canids (Haughton, 1864; Vaz *et al.*, 2011; Hermanson, 2013; Echeverry *et al.*, 2015; Souza-Junior *et al.*, 2015; Souza-Junior *et al.*, 2018; Smith *et al.*, 2020), felids (Beswick-Perrin, 1871; Barone, 1986; Concha *et al.*, 2004; Hudson *et al.*, 2011; Viranta *et al.*, 2016; Nazem *et al.*, 2017; Vargas *et al.*, 2017), herpestids

(Taylor, 1976), and viverrids (Devis, 1868; Watson, 1882; Taylor, 1976). However, there are some differences with some mustelid species, such as in *G. cuja*, where the m. extensor carpi ulnaris originates from the articular capsule of the elbow (Ercoli *et al.*, 2015). On the other hand, there was no carpal insertion in *T. taxus* (Moore *et al.*, 2013), *M. martes* and *M. foina* (Böhmer *et al.*, 2018). In the ursid *A. melanoleuca*, it also originates from the condyle and its fibers are inseparable from the anconeus and extensor digitorum lateralis muscles, and it does not insert onto the accessory carpal bone (Davis, 1976). In felids, such as *L. pardalis* it fuses with the articular capsule of the elbow and m. anconeus, and it does not insert onto the accessory carpal bone (Julik *et al.*, 2012). In *L. lynx*, it can also originate from the ulna and insert onto the extensor retinaculum (Viranta *et al.*, 2016), but does not insert onto the accessory carpal bone (Viranta *et al.*, 2016; Ari *et al.*, 2019). In *P. uncia* and *P. tigris*, it does not insert onto the accessory carpal bone (Smith *et al.*, 2021; Dunn *et al.*, 2022), but in *P. tigris*, it inserts onto the accessory carpal ligament ("pisometacarpal ligament" Dunn *et al.*, 2022). In viverrids of the genus *Genetta*, it also originates from the ulna (Taylor, 1976). In hyaenids, it does not insert onto the carpus (Watson & Young, 1876; Spoor & Badoux, 1986), although in *Proteles* inserts onto the retinaculum extensor (Watson, 1882).

The radial and ulnar origins of the m. abductor digiti I longus observed in *P. cancrivorus* has been previously described (Lima *et al.*, 2010), while it was also reported originated from the ulna and the interosseus membrane (Santos *et al.*, 2010). Therefore, both studies differ from our findings in *P. cancrivorus*, where the origin reaches both bones and the interosseus ligament, and an insertion onto the sesamoid bone was found. In other procyonids, such us in *P. lotor*, *Nasua* and *P. flavus*, the origin from the radius, the interosseus ligament and the ulna is common (Allen, 1882; Julitz, 1909; Mcclearn, 1985; Vélez-García *et al.*, 2022). Although in *Nasua*, the radial origin can be absent (Mackintosh, 1875; Santos *et al.*, 2010b). However, an insertion onto the sesamoid bone can occur (Mackintosh, 1875), similar to *P. flavus* (Vélez-García *et al.*, 2022), and *P. cancrivorus*. In *P. flavus*, it can also insert onto the radial carpal bone (Beswick-Perrin, 1981), similar to *P. lotor* (Windle & Parsons, 1897). In mustelids, such as *Martes* and *P. pennanti*, the m. abductor digiti I longus originates from the radius and the ulna, and inserts onto the metacarpal bone I (Leach, 1976; Böhmer *et al.*, 2018). Although in *M. foina*, it can originate from the interosseous antebrachial ligament, and inserts onto the sesamoid bone (Mackintosh, 1875). In *E. barbara*, this muscle only originates from the ulna and inserts onto the metacarpal bone I, the sesamoid bone and carpal I (Macalister, 1873). In *G. cuja*, *Aonyx*, and *E. lutris*, it originates from the radius and the ulna, and inserts onto the sesamoid bone and the metacarpal I (Macalister, 1870; Howard, 1973; Ercoli *et al.*, 2015). In *T. taxus*, it is described as "extensor pollicis brevis", which only originates from the radius and inserts onto the metacarpal bone I (Moore *et al.*, 2013). In ursids, it originates from the radius, the ulna, and the interosseous membrane, and inserts onto the metacarpal I (Haughton, 1864; Shepherd, 1883; Kelley, 1888), although in *A. melanoleuca*, it only inserts onto the sesamoid bone (Davis, 1964). In *Ailurus*, it has the same origins, but fuses with the m. supinator and inserts onto the sesamoid bone and the metacarpal bone I (Anton *et al.*, 2006; Fisher *et al.*, 2009). In canids, it only originates from the radius and the ulna (Vaz *et al.*, 2011; Souza-Junior *et al.*, 2018; Smith *et al.*, 2020), although, it can also originate from the interosseus membrane and inserts onto the sesamoid bone and metacarpal bone I in *C. l. familiaris* (Hermanson, 2013) and *L. pictus* (Smith *et al.*, 2020). In felids, it originates from the radius, the ulna, and the interosseus membrane (Julik *et al.*, 2012; Sánchez *et al.*, 2019; Dunn *et al.*, 2022), however, it is reported to only originate from the radius and the ulna in *L. lynx* (Viranta *et al.*, 2016; Ari *et al.*, 2019), *P. leo* (Barone, 1986; Vargas *et al.*, 2017) and *P. uncia* (Smith *et al.*, 2021). Whereas in *Puma concolor*, it only originates from the ulna and only inserts onto the metacarpal bone I (Concha *et al.*, 2004). In *L. pardalis*, *P. leo* and *P. tigris*, it also inserts onto the sesamoid bone (Barone, 1986; Julik *et al.*, 2012; Dunn *et al.*, 2022), and in *L. lynx* onto the carpal bone I (Ari *et al.*, 2019). In herpestids and viverrids of the genera *Genetta* and *Civettictis*, it originates from the radius and the ulna (Young, 1880; Taylor, 1976). However, in *C. civetta,* it has been reported to only originate from the ulna, and insert onto the metacarpal bone I and the sesamoid bone (Mackintosh, 1875). In hyaenids, it originates from the ulna, the radius, and the interosseus membrane, and inserts onto the metacarpal bone I (Watson & Young, 1876; Spoor & Badoux, 1985). In *H. hyaena*, it can also have an insertion onto the sesamoid bone, similar to *H. aurupunctatus* (Böhmer *et al.*, 2020).

The m. extensor digiti I et II was not reported by Lima *et al.* (2010) and Santos *et al.* (2010a) in *P. cancrivorus*, whereas Windle (1888) reported this muscle as a deep digital extensor that originated from the radial border of the ulna with tendons to the digits I and II. However, this last author did not report a tendon extending to the digit III as our findings in four specimens did. In other procyonids, it also extends a tendon to the digit III, such in *P. lotor*, *N. nasua,* and *N. narica* (Mackintosh, 1875; Allen, 1882; Mcclearn, 1985), being similar to our findings in *P. cancrivorus*. Although, the tendon to the digit III can be absent in *N. nasua* (Mackintosh, 1875; Böhmer *et al.*, 2020) and *P. lotor* (Windle & Parsons, 1897), while in *P. flavus* the absence of this tendon is normal (Beswick-Perrin, 1871; Windle & Parsons, 1897; Julitz, 1909; Vélez-García *et al.*, 2022). Interestingly, in *P. flavus* has been found an independent muscle to the digit III, but as an anatomical variant (Vélez-García *et al.*, 2022). Böhmer *et al.* (2020) only reported the tendon to the digit II in *P. flavus*, which may also be interpreted as an anatomical variant since it was always present in other studies (Beswick-Perrin, 1871; Windle & Parsons, 1897; Julitz, 1909; Vélez-García *et* *al.*, 2022). Mackintosh (1875) reported that this muscle is one-headed in *Nasua*, while Mcclearn (1985) describes it as two separate bellies in *P. lotor* and *Nasua*, similar to *P. cancrivorus*. In mustelids, it originates from the ulna and extends tendons to the digits I and II (Macalister, 1870, 1875; Howard, 1973; Moore *et al.*, 2013; Böhmer *et al.*, 2018, 2020), however, in *M. americana*, *P. pennanti*, and *G. cuja*, it also originates from the m. abductor digiti I longus (Leach, 1976; Ercoli *et al.*, 2015), which is similar to *Ailurus* (Fisher *et al.*, 2009), and *P. cancrivorus*. Although in *G. cuja*, it also originates from the septum of the m. flexor digitorum profundus (Ercoli *et al.*, 2015), and the case of *Lutra vulgaris*, it only goes to the digits II and III (Haughton, 1864). In *Ursus* it can be absent or fused with the m. abductor digiti I longus (Shepherd, 1883; Kelley, 1888), although when it is present, only extends the tendons to the digit I (Haughton, 1864); whereas in the genus *Ailuropoda*, it extends tendons to the digits I and II (Davis, 1964). In canids, the muscle originates from the ulna, but it has different distribution of the tendons. In *C. l. familiaris*, *C. thous*, and *L. gymnocercus*, it forms two tendons to the digits I and II, and sometimes to the digit III, where the tendon to the digit I goes to the head of the metacarpal bone I and the other to the extensor digitorum communis tendon for digit II (Hermanson, 2013; Vélez *et al.*, 2015; Souza-Junior *et al.*, 2018). In. *C. thous*, it also originates from the m. abductor digiti I longus and interosseous ligament (Vélez *et al.*, 2015). In *L. pictus*, the medial tendon inserts onto the base of the metacarpal bone II (Smith *et al.*, 2020). In *C. alpinus* and *V. vulpes*, the tendons to the digits I and II insert onto the distal phalanxes (Böhmer *et al.*, 2020). In felids, it originates from the ulna and extends tendons to the digits I and II (Barone, 1967; Concha *et al.*, 2004; Julik *et al.*, 2012; Vargas *et al.*, 2017; Sánchez *et al.*, 2019; Böhmer *et al.*, 2020; Smith *et al.*, 2021). However, the lateral tendon can send a small fascicle to the tendon for digit III of the m. extensor digitorum lateralis in *P. tigris* (Dunn *et al.*, 2022). In hyaenids, the m. extensor digiti I et II only goes to the digit II (Watson & Young, 1879; Spoor & Badoux, 1985; Böhmer *et al.*, 2020) or digit III in *Proteles* (Watson, 1882). In viverrids, herpestids and euplerids the origin is also from the ulna and the muscle extends tendons to the digits I and II (Watson, 1882; Taylor, 1976; Böhmer *et al.*, 2020).

The m. supinator in *P. cancrivorus* has been described as originating only from the orbicular ligament (Windle, 1888) or only from the lateral epicondyle (Santos *et al.*, 2010a; Silva *et al.*, 2015). We found a wide origin including the lateral collateral ligament of the elbow and the radial annular ligament, similar to *P. flavus* (Vélez-García *et al.*, 2022). Whilst the insertion onto the proximal third of the radius was similar to that previously reported (Silva *et al.*, 2015). In *P. lotor*, it originates from the orbicular ligament and inserts onto the proximal third (Allen, 1882) or proximal half (Windle & Parsons, 1897) of the body of the radius. In procyonids of the genus *Nasua*, it originates from the lateral epicondyle and inserts onto the proximal two-thirds of the radius (Mackintosh, 1875; Santos *et al.*, 2010b), whereas in *P. flavus* it inserts onto the proximal half or proximal two-thirds (Windle & Parsons, 1897; Julitz, 1909; Vélez-García *et al.*, 2022). In mustelids, there are several origins and insertions, such as in *M. foina*, where it inserts onto the proximal half (Mackintosh, 1875); in *T. taxus* it originates from the humeral condyle and the radius, and inserts onto length of the radius (Moore *et al.*, 2013); in *G. cuja*, it originates from the articular capsule and the lateral collateral ligament of the elbow, and inserts onto the proximal two-thirds (Ercoli *et al.*, 2015); in *M. americana* and *P. pennanti*, it originates from the lateral epicondyle and the lateral collateral ligament, and according to the figures inserts onto the proximal third of the radius (Leach, 1976); while in *M. foina* and *M. martes* it originates from the humerus and inserts until the distal third of the radius (Böhmer *et al.*, 2018); in *Mustela putorius*, *L. vulgaris* and *Aonyx cinereus*, it reaches the third quarter of the radius (Windle & Parsons, 1897); in *E. lutris* it originates from the lateral epicondyle and inserts onto the proximal three fourths of the radius (Howard, 1973); and in *Aonyx*, it can inserts onto the distal third of the radius (Macalister, 1870). In *Ailurus*, it only originates from the lateral collateral and the radial annular ligament, and inserts onto the proximal half of the radius, fuses with the m. abductor digiti I longus (Fisher *et al.*, 2009). In ursids, the origin is similar to that of *Ailurus*, but it inserts onto the proximal three-quarters of the radius (Shepherd, 1883; Kelley, 1888; Windle & Parsons, 1897; Davis, 1964). In canids, it originates from the lateral epicondyle and lateral collateral ligament, and inserts onto the proximal quarter of the radius (Hermanson *et al.*, 2013; Smith *et al.*, 2020); in *L. gymnocercus* and *C. thous*, it only originates from the lateral epicondyle and inserts onto the proximal third (Silva *et al.*, 2015). In felids, it originates from the lateral epicondyle and inserts onto the middle third (Vargas *et al.*, 2017), until the distal third of the radius (Barone, 1967). In *L. lynx*, it originates from the lateral epicondyle and lateral collateral ligament, and inserts onto almost length of the radius (Viranta *et al.*, 2016); in *P. concolor* onto the middle third (Concha *et al.*, 2004); in *A. jubatus* onto the quarter proximal (Hudson *et al.*, 2011; Nazem *et al.*, 2017). In *L. pardalis*, it originates from the radial annular and lateral collateral ligaments, and inserts onto the proximal two-thirds (Julik *et al.*, 2012; Sánchez *et al.*, 2019), while in *P. onca*, it inserts onto the distal third (Sánchez *et al.*, 2019). In *P. uncia*, it originates from the lateral epicondyle of the humerus and inserts onto the proximal two thirds of the radius (based on the figures of Smith *et al.*, 2021). While in *P. tigris*, it originates from the elbow articular capsule and adjacent ligaments, and inserts onto the proximal half of the radius and m. abductor longus digiti I (Dunn *et al.*, 2022). In herpestids, it inserts onto the proximal two-thirds, while in viverrids, it inserts onto the proximal third of the radius (Windle & Parsons, 1897; Taylor, 1976) (Tab. I).

Tab. I. Main differences of the craniolateral forearm muscles among carnivorans based on the literature review and the results of this study (O: origin, I: insertion).

Muscle	Main differences	Species
Brachioradialis	O: lateral supracondylar crest of the humerus	Procyonids, mustelids, a ursid (*U. americanus*), and felids (*Caracal*, *Acynonyx* and *Leopardus*)
	O: proximal third of the humerus	Mustelids (Family Ictonychidae), and felids (*Panthera* and *Leopardus*)
	O: middle third of the humerus	Mustelid (*G.* cuja) and felids
	O: lateral epicondyle of the humerus	Mustelid (*T. taxus*)
	Two heads	*Ailurus* and ursids (but *U. americanus*)
	I: cranial surface of the radius	Herpestids (*I. albicauda* and *H. ichneumon*)
	I: proximal row of the carpus	Felids (*L. pardalis*, *L. geoffroyi* and *P. onca*)
	I: flexor retinaculum	A felid (*L. pardalis*)
	Absent or vestigial	Canids, hyaenids, viverrids (*Civettictis*), and a felid (*Acynonyx*)
Extensor carpi radialis	Single muscle	A mustelid (*G. cuja*), *Ailurus*, ursids (*Ursus*), canids, hyaenids, herpestids, viverrids, and felids (*C. caracal*, *A. jubatus* and *L. lynx*)
	Partly fused	Procyonids (*P. cancrivorus* and *N. nasua*) and felids (*F. catus, L. pardalis, P. leo*, *P. uncia*, *P. tigris,* and *L. lynx*)
	Double muscle (Extensor carpi radialis longus and extensor carpi radialis brevis)	Procyonids (*P. lotor*, *P. flavus* and *N. narica*), mustelids (*M. foina*, *M. martes, M. meles* and as anatomical variant in *G. cuja*), *Ailurus* (only as an anatomical variant), and a ursid (*A. melanoleuca)*
	O: adjacent intermuscular septum	Procyonids (*P. cancrivorus* and *P. flavus*) and canids (*C. l. familiaris* and *C. thous*)
	O: articular capsule of the elbow joint	A canid (*Cerdocyon thous*)
	O: Fused with the m. extensor digitorum communis	Felids (*L. pardalis* and as an anatomical variant in *P. tigris*) and mustelids (*M. americana* and *P. pennanti*)
Extensor digitorum communis	O: lateral supracondylar crest of the humerus	Procyonids (*P. lotor*, *N. nasua* and *N. narica*), mustelids *(M. foina*, *M. martes*, *M. americana* and *P. pennanti*), a ursid (A. *melanoleuca*), felids (*L. pardalis*, *A. jubatus*, *P. leo*, *P. uncia*, and *P. tigris*), herpestids and viverrids (*Genetta*)
	O: lateral epicondyle of the humerus	A procyonid (*P. flavus*), a mustelid (*T. taxus*), *Ailurus*, ursids (*Ursus*), canids, felids, hyaenids and viverrids (*Civettictis*)
	O: lateral supracondylar crest and epicondyle of the humerus	A procyonid (*P. cancrivorus*), and mustelids (*G. cuja* and *E. lutris*)
	O: antebrachial fascia	A procyonid (*P. cancrivorus*) and canids (*C. l. familiaris* and *C. thous*)
	O: intermuscular adjacent septa	Procyonids (*P. cancrivorus* and *P. flavus*), canids (*C. l. familiaris* and *C. thous*), and a hyaenid (*C. crocuta*)
	O: fused with the m. extensor carpi radialis brevis	Felid (*L. pardalis* and as an anatomical variant in *P. tigris*) and mustelids (*M. americana* and *P. pennanti*)
	Tendon to the digit I as an anatomical variant	Procyonid (*P. cancrivorus*), mustelid (*M. foina*), and felids (*P. leo* and *L. lynx*)

Tab. I. Cont.

Muscle	Main differences	Species
Extensor digitorum lateralis	O: lateral epicondyle of the humerus	Procyonids (*P. lotor* and *Nasua*), mustelids (*M. foina* and *M. martes*), ursids (*Ursus*), a canid (*L. gymnocercus*) and felids
	O: lateral supracondylar crest	Felids (*C. caracal*, *L. pardalis*, *P. onca* and *P. concolor*)
	O: lateral epicondyle of the humerus and lateral collateral ligament	Procyonids (*P. cancrivorus* and *P. flavus*), and canids (*C. l. familiaris*, *C. thous*, and *L. pictus*)
	Double muscle	A procyonid (*N. narica*), and mustelids (*Aonyx*, *G. cuja*, and *T. taxus*)
	O: lateral epicondyle of the humerus and radius	Mustelids (*M. americana* and *P. penannti*) and a hyaenid (*H.hyaena*)
	O: lateral epicondyle and condyle of the humerus	Ursid (*A. melanoleuca*)
	O: antebrachial fascia	A procyonid (*P. cancrivorus*) and a canid (*C. thous*)
	O: intermuscular adjacent septum	Procyonids (*P. cancrivorus* and *P. flavus*) and a canid (*C. thous*)
	Absence of the tendon to the digit III	Mustelids (*M. martes, M. foina* and *E. lutra*), ursid (*A. melanoleuca*), canids (*C. alpinus*, *V. vulpes*, and as anatomical variant in *L. gymnocercus*), herpestids, viverrids (but *C. civetta*), and hyaenids
	Presence of a tendon to the digit II	Felids (*F. catus*, *P. tigris* and *L. pardalis*)
Extensor carpi ulnaris	O: lateral epicondyle of the humerus	Procyonids (*P. cancrivorus*), mustelids, ursids, *Ailurus*, canids, felids, herpestids, hyaenids, and viverrids
	O: lateral epicondyle of the humerus and articular capsule of the elbow	Procyonid (*P. flavus*), mustelid (*G. cuja*), and a felid (*L. pardalis*)
	O: lateral epicondyle of the humerus and the ulna	Procyonids (*N. narica*, as an anatomical variant in *P. cancrivorus* and *P. flavus*), felid (*L. lynx*), viverrids (Genetta)
	I: metacarpal bone V and accessory carpal bone	Procyonids (*P. cancrivorus,* and *P. flavus*, and as anatomical variant in *P. lotor*), mustelids (but *T.* taxus, *M. martes* and *M. foina*), *Ailurus*, canids , felids (but *L. lynx, L. pardalis*, *P. uncia* and *P. tigris*), herpestids, and viverrids
	I: metacarpal bone V and extensor retinaculum	Felid (*L. lynx*) and a hyaenid (*Proteles*)
Abductor digiti I longus	Absence of the origin from the radius	Procyonid (*Nasua* as an anatomical variant), a mustelid (*E. barbara*), and a felid (*P. concolor*)
	Absence of the origin from the ulna	A mustelid (*T. taxus*), and a viverrid (*C. civetta*)
	I: sesamoid bone and metacarpal bone I	Procyonids (*P. cancrivorus, Nasua, P. flavus*), mustelids (*G. cuja*, *Aonyx*, *E. lutris, E. barbara* and *M. foina*), *Ailurus*, canids, felids (*L. pardalis, P. leo* and *P. tigris*), hyaenids and a viverrid (*C. civetta*)
	I: only onto sesamoid bone	A ursid (*A. melanoleuca*) and a mustelid (*M. foina* as an anatomical variant)
	I: carpal bone I	A mustelid (*E. barbara*) and a felid (*L. lynx* as an anatomical variant)
	I: radial carpal bone	Procyonids (as an anatomical variant in *P. flavus* and *P. lotor*)

Tab. I. Cont.

Muscle	Main differences	Species
Extensor digiti I et II	Presence of a tendon to the digit III	Procyonids (*P. cancrivorus*, *N. nasua* and *P. lotor*), canids (as an anatomical variant in *C. l. familiaris*, *C. thous*, and *L. gymnocercus*), and a felid (*P. tigris*)
	A unique tendon to the digit II	Hyaenids
	A unique tendon to the digit III	Hyaenid (*Proteles*)
	Tendons only to the digits II and III	A mustelid (*L. vulgaris*)
	Absent or fused to the abductor digiti I longus and sending tendon only to the digit I	Ursids (*Ursus*)
	I: metacarpal bone I and tendon of the extensor digitorum communis to the digit II	Canids (but *C. alpinus* and *V. vulpes*)
	I: distal phalanges of the digits I and II	Canids (*C. alpinus* and *V. vulpes*)
Supinator	O: only from the lateral epicondyle	A mustelid (*E. lutra*), canids (*L. gymnocercus* and *C. thous*), and felids
	O: lateral epicondyle and lateral collateral ligament	Mustelids (*M. americana,* and *P. pennanti,*), canids and felids (*L. lynx*, *A. jubatus*, *P. concolor*)
	O: lateral epicondyle, lateral collateral and radial annular ligaments	Procyonids (*P. cancrivorus*, *P. flavus* and *P. lotor*)
	O: lateral collateral and radial annular ligaments	A felid (*L. pardalis*), *Ailurus* and ursids
	O: articular capsule of the elbow joint and lateral collateral ligament	Mustelid (*G. cuja*)
	I: proximal third of the radius	Procyonids (*P. cancrivorus* and *P. lotor*), canids (*L. gymnocercus* and *C. thous*) and viverrids
	I: proximal two thirds of the radius	Procyonids (*Nasua*, *P. flavus* and *P. lotor*), mustelids (*M. americana, P. pennanti, G. cuja*), felid (*L. pardalis*), herpestids
	I: proximal half of the radius	Procyonid (*P. flavus* and *P. lotor*), mustelids (*M. foina)*
	I: Along the radius	Mustelid (*T. taxus*)
	I: distal third of the radius	Mustelids (*M. foina*, *M. martes* and *Aonyx*), felid (*P. onca*)
	I: middle third	Felid (*P. concolor*)
	I: proximal three quarters of the radius	Mustelids (*Mustela putorius, L. vulgaris A. cinereus*, and *E. lutris*), and ursids
	I: proximal quarter of the radius	Canids (*C. l. familiaris* and *L. pictus*), and a felid (*A. jubatus*)

Functional analysis. Within the craniolateral forearm muscles of *P. cancrivorus*, the brachioradialis and supinator muscles are two muscles that should act as lateral rotators of the antebrachium and manus (supinators). Based on Kardong (2012), when the muscle is inserted proximally, it acts for fast movements, while when it is inserted distally, it acts for strong movements. Therefore, in *P. cancrivorus*, the proximal insertion of the m. supinator should give it more velocity to supination, while the m. brachioradialis due to its distal insertion gives it more force to supination. The proximal insertion of the m. supinator also is present in other carnivorans mainly with cursorial habits, such as canids, hyaenids, viverrids, and the felid *A. jubatus*. However, the permanent presence of a well-developed m. brachioradialis in *P. cancrivorus* has allowed it to perform more activities, such as manipulating its food with its hands, swimming, and climbing trees. Since carnivoran species with a well-developed m. brachioradialis can perform more activities with their thoracic limbs than just walking and running (Indrusiak & Eizirik, 2003; Martinelli & Volpi, 2010; Pellanda *et al.*, 2010; Souza *et al.*, 2015; Souza-Junior *et al.*, 2015; Taverne *et al.*, 2018). Additionally, this muscle contributes to elbow flexion in carnivorans, but this action is secondary due to its insertion onto the distal part of the forearm (Saladin, 2010; Souza *et al.*, 2015, 2020). Interestingly, other mammals as Primates with similar attachments to *P. cancrivorus*, the primary function of the m. brachioradialis is to flex the elbow (Myatt *et al.*, 2012) and stabilize the elbow during flexion tasks (Boland *et al.*, 2008). Therefore, the m. brachioradialis should flex and stabilize the elbow together to the extensor carpi radialis and extensor digitorum communis muscles in *P. cancrivorus* since these also originate from the lateral supracondylar crest. Thereby, procyonid species have a pronounced lateral supracondylar crest to give origin to these muscles (Taverne *et al.*, 2018; Tarquini *et al.*, 2019; Vélez-García *et al.*, 2022), which is a characteristic of carnivorans with arboreal abilities (Taylor, 1976; Argot, 2001; Fabre *et al.*, 2015; Taverne *et al.*, 2018). On the other hand, the proximal origins of brachioradialis, extensor carpi radialis and extensor digitorum communis muscles could be associated with the feeding habits of *P. cancrivorus* when the individual needs to be flexing the elbow to bring food to its mouth with its hands.

The m. extensor carpi radialis is mainly an extensor of the carpus and can be present as a single or double muscle in a common or variant manner in carnivorans. Therefore, there should be no functional differences among carnivorans, but the constant arrangement as a single muscle in *P. cancrivorus* allows to differentiate it of *P. lotor*. Thus, during the phylogenetic divergence of both species, the muscles extensor carpi radialis longus and brevis were separated in *P. lotor* (based on the descriptions of Allen, 1882, Mcclearn, 1985 and Taverne *et al.*, 2018) and remained partlty fused in *P. cancrivorus*.

The m. extensor carpi ulnaris in *P. cancrivorus* should act as an abductor of the carpal joint and extensor or flexor of the carpus when the carpal joint is already extended or flexed respectively, such as occur in other carnivorans (Singh, 2018; Smith *et al.*, 2020; Vélez-García *et al.*, 2022). The extensor carpi radialis and the abductor digiti I longus muscles could counteract the action of the m. extensor carpi ulnaris abducting the carpus in *P. cancrivorus*. Thereby, these actions allow more movements of its hands due to the high handling habilities of the genus *Procyon* (Mcclearn, 1992).

The m. extensor digitorum communis extends the digits II to V and in some variant cases in *P. cancrivorus*, it also extends the digit I similar to *M. foina* (Böhmer *et al.*, 2020) and some felids (Viranta *et al.*, 2016; Vargas *et al.*, 2017). Therefore, that tendon is a characteristic that could have had the common ancestor of the carnivorans when the digit I was more functional, and thus it can appear in species with high use of the digit I, such as musteloids and felids. However, the extension of the digit I in all carnivorans is always performed by the abductor digiti longus I and extensor digiti I et II muscles. This latter muscle, in the case of *P. cancrivorus* also supports the extension of the digit III, although this support is not always necessary since the tendon to this digit can be absent (Windle, 1888). However, the higher proportion of presentation of this tendon in *P. cancrivorus* allows us to infer that the common ancestor of the caniformes had it, therefore it may be present in other caniformes species as an anatomical variant and a phylogenetic trait. On the other side, the extension of the digits III to V is supported by the m. extensor digitorum lateralis, such as occur in most carnivorans.

This study confirms that *P. cancrivorus* has intraspecific variations that anatomically are related to other carnivorans, such as the tendon for the digit I from the m. extensor digitorum communis, the origin from the ulna of the m. extensor carpi ulnaris, the origins from the antebrachial fascia and the intermuscular septa of the extensor digitorum communis and lateralis muscles. In contrast, another intraspecific variation was not related to other carnivorans, such as the origin of the m. abductor I digiti longus from the lateral collateral ligament of the elbow. Therefore, it could be a proper anatomical variation of *P. cancrivorus* based on the comparative review. On the other side, the brachioradialis, extensor carpi radialis, supinator, and extensor digiti I et II are the most anatomically variant muscles among carnivoran species. However, there are only functional differences when there is a well-developed m. brachioradialis, and when the distribution of tendons is different from the digital extensor muscles.

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