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ZOOLOGY

Gross anatomy of the craniolateral antebrachial muscles of the Neotropical river otter (*Lontra longicaudis* – Olfers, 1818; Carnivora: Mustelidae)

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ABSTRACT. The Neotropical River otter (*Lontra longicaudis*) is a mustelid primarily characterized by natatorial locomotion, which enables it to inhabit humid forests, swamps, and savannas from Mexico to northern Argentina. Anatomical information on this species remains scarce. Therefore, this study aimed to describe the craniolateral antebrachial muscles of this species. We examined a juvenile specimen fixed in 10% formaldehyde. The brachioradialis muscle was strongly developed and originated from the neck of the humerus. The extensor carpi radialis muscle consisted distally of two bellies inserting onto metacarpal bones II and III. The extensor digitorum communis muscle sent tendons to the digits II-V, whereas the extensor digitorum lateralis muscle sent tendons to digits III-V. The extensor carpi ulnaris muscle had two heads, one humeral and one ulnar. The extensor digiti I et II muscle sent a double tendinous fascicle to the digit II. The anatomical arrangement of the craniolateral antebrachial muscles of *L. longicaudis* suggests adaptations for manus movements necessary for semiaquatic locomotion—primarily natatorial—, and for manipulating its food.

Keywords: Forearm; forelimb; myology; origin; insertion.

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Introduction

The Neotropical river otter (*Lontra longicaudis*) is a member of the order Carnivora, belonging to the family Mustelidae and subfamily Lutrinae (Nyakatura & Bininda-Emonds, 2012). It is geographically distributed between Mexico and northern Argentina (Rheingantz et al., 2022). It inhabits tropical forests, swamps, and savannas, where it feeds mainly on fish (Andrade-Ponce & Angarita-Sierra, 2017; Silva et al., 2012). This species is currently categorized by the International Union for Conservation of Nature (IUCN) as Near Threatened, since various human activities have contaminated and reduced its distribution areas (Rheingantz et al., 2022).

The morphological adaptations of *L. longicaudis* reflect its semiaquatic habits. It has a long and flexible body, interdigital membranes, and a palmigrade stance, which increase the efficiency of the aquatic movements (Ramírez Arango et al., 2024; Trujillo & Mosquera-Guerra, 2018). Specifically, the radius and ulna have a curvature at the midshaft that increases the attachment area for the thoracic limb muscles, whilst the metacarpal bones are shorter than the metatarsal bones to facilitate paddling by the pelvic limbs (Kitchener et al., 2017). Additionally, musteloids tend to have greater muscle mass concentrated in the antebrachium, which contributes to their ability to capture prey as well as to the wide rotation of the antebrachium and manus (Souza-Junior et al., 2021). These adaptations allow both the handling of food and swimming and are also evident in their interactions with the environment, such as building burrows in the water or feeding habits (Trujillo & Mosquera-Guerra, 2018).

Among the muscular structures involved in these adaptations, the craniolateral muscles of the antebrachium play an important role. These muscles are divided into a superficial group that originates from the lateral supracondylar crest and lateral epicondyle of the humerus, and a deep group that originates from the lateral epicondyle or the radius and ulna in most carnivorans (Vélez-García et al., 2022a). Their insertions onto the bones of the antebrachium and manus allow the generation of extension of the carpus and digits, supination, and support for elbow flexion (Böhmer et al., 2019; Hermanson et al., 2020; Vélez-García et al., 2022a; Vélez-García et al., 2022b). The *m. brachioradialis* (BR) and *m. supinator* (S) insert onto the radius, producing craniolateral rotation of the radius and generating supination. The *m. extensor carpi radialis* (ECR) extends the carpal joint and can be divided into one or two muscles inserted onto the metacarpal bones II and

III. Together with the BR, this muscle supports elbow flexion of the tricipital musculature. The *m. extensor digitorum communis* (EDC) extends digits II to V, complemented by the *m. extensor digitorum lateralis* (EDL) for digits III to V and the *m. extensor digiti I et II* (EDI-II) for digits I and II. The *m. extensor carpi ulnaris* (ECU) is an abductor and lateral rotator of the carpal joint and supports carpal extension or flexion depending on whether the carpus is extended or flexed, respectively. The *m. abductor digiti I (pollicis) longus* (AbDIL) extends and abducts digit I and deviates the manus medially (Hermanson et al., 2020). These are essential functions for propulsion in swimming, digging, and prey handling of musteloids (Souza-Junior et al., 2021).

In *L. longicaudis*, there are only two anatomical studies involving craniolateral antebrachial muscles. One of them describes the origin, insertion, and morphometry of the BR compared to other carnivorans (Souza-Junior et al., 2015), and another reports the muscle mass of the thoracic limb compared with that of other carnivorans, without detailed anatomical descriptions (Souza-Junior et al., 2021). For other otter species (subfamily Lutrinae), there are only four studies describing the craniolateral antebrachial muscles from the dissection of a single specimen of each species (Haughton, 1864; Howard, 1973; Macalister, 1870; Windle & Parsons, 1897). However, the only study with a detailed anatomical description of the origin and insertion of these muscles is that of the sea otter (*Enhydra lutris*) (Howard, 1973). In addition, the descriptions of these muscles are not very detailed for the Asian small-clawed otter (*Aonyx cinereus*) (Macalister, 1870) and the Eurasian otter (*Lutra lutra*) (Windle & Parsons, 1897).

Therefore, detailed gross anatomical knowledge of this muscular group will contribute to the understanding of specific anatomical adaptations related to their functions and also serve as a foundation for medical and surgical interventions in the lateral aspect of the brachial and antebrachial regions in *L. longicaudis*. Thus, this study aimed to describe the anatomical characteristics of the craniolateral antebrachial muscles in a *L. longicaudis*.

Material and methods

We used the cadaver of a juvenile male specimen of unknown weight and age, which was donated by CORTOLIMA (Environmental Authority of Tolima, Colombia) to the Veterinary Anatomy Laboratory of the Universidad del Tolima. The cadaver was initially fixed with a solution of 10% formaldehyde and 5% glycerin via subcutaneous and intramuscular infiltrations, then immersed and maintained in a container with 5% formaldehyde. Previous gross dissections of the thorax, neck, and thoracic limbs had been performed to observe the branching of the aortic arch (Vélez-García, 2024) and the origin and distribution of the brachial plexus (Ramírez-Arango et al., 2024). The present investigation aimed to describe the shape, origin, insertion, and arterial supply of the craniolateral muscles of the antebrachium. The superficial and deep fasciae surrounding the muscles were removed to examine their shape and photograph them with a Canon T5i camera equipped with a Canon 60 mm macro lens. Subsequently, each muscle was detached from its origin and insertion to observe and describe the extension of these attachments on the bone and intermuscular septa. The arterial supply was observed according to the distribution of the vessels supplying each muscle. The descriptions were based on the latest version of the *Nomina Anatomica Veterinaria* (NAV) (International Committee on Veterinary Gross Anatomical Nomenclature [ICVGAN], 2017). This study was approved by the Bioethics Committee of the Universidad del Tolima (Code 2.3-059).

Results

The BR is a highly developed fusiform muscle located along the craniolateral aspect of the brachium and antebrachium. It is covered by the *m. triceps brachii caput laterale* (TBLa) at the brachial level, and lies superficially, covering the ECR along the distal two-thirds of the antebrachium. It has a fleshy origin from the surface located distal and caudal to the greater tubercle, between the proximal origins of the *m. triceps brachii caput accessorium* (TBa) and *m. brachialis* (B). It inserts onto the distal three-quarters of the medial margin of the radius and the proximal aspect of the radial styloid process. The radial collateral artery (RCA) supplies this muscle (Figure 1).

The ECR is a single muscle proximally, which divides into two bellies (cranial and caudal) from the middle third of the antebrachium. It originates via fleshy fibers from the proximal two-thirds of the cranial aspect of the lateral supracondylar crest of the humerus and the proximal fifth of the intermuscular septum with the EDC. Both bellies are covered by the AbDIL at the distal end of the antebrachium (Figure 1). The tendons of the cranial and caudal bellies insert onto the bases of the metacarpal bones II and III, respectively (Figure 2). The transverse cubital artery supplies this muscle.

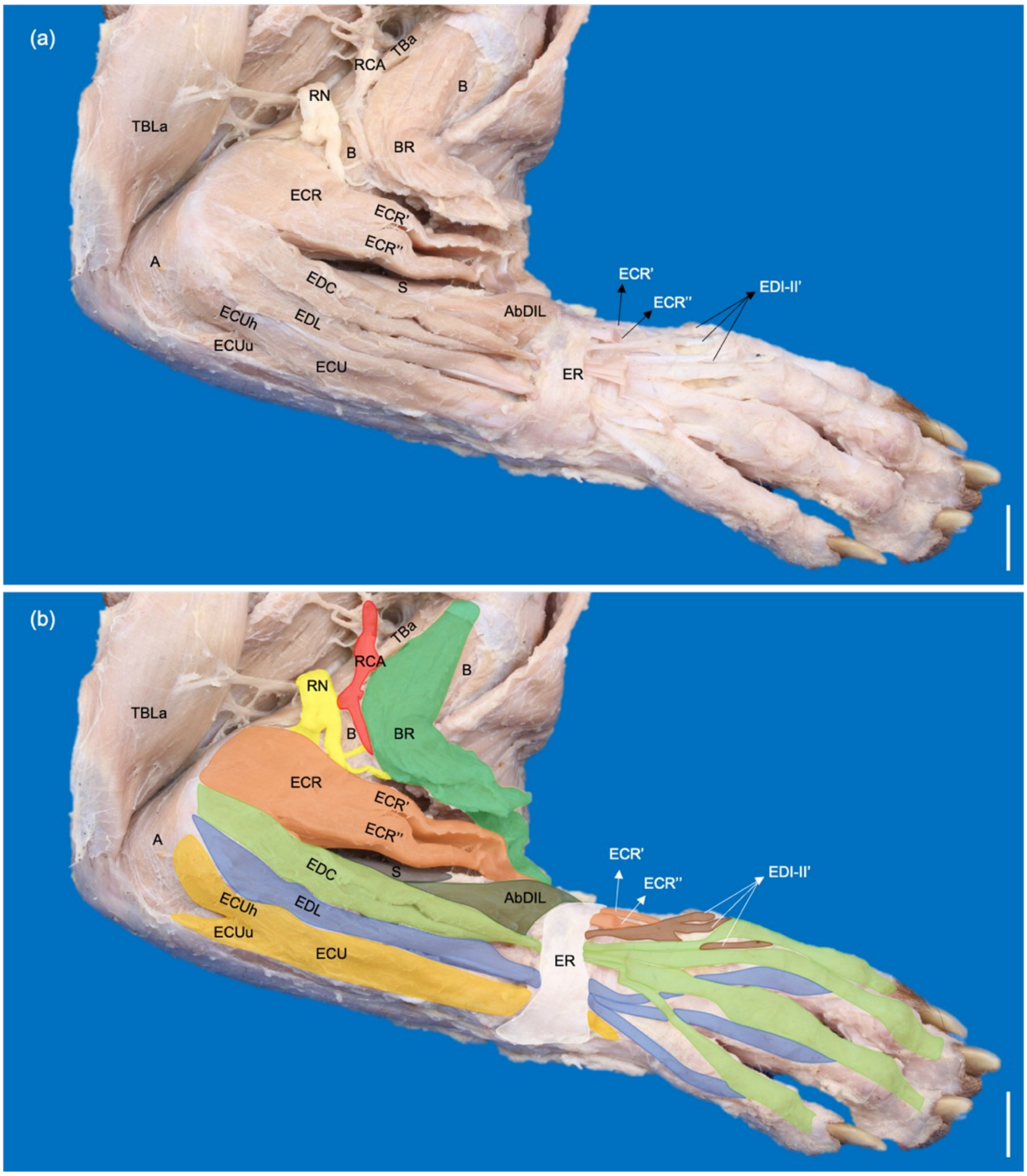

Figure 1. Lateral and superficial photographic view of the right craniolateral antebrachial muscles of *Lontra longicaudis*. Dissection after removal of the superficial and deep fasciae and caudal retraction of the TBLa (a) and the colored structures (b). A: *m. anconeus*; EDI-II': tendons of EDI-II; ECR': cranial belly of ECR (homologous belly to *ECR longus*); ECR'': caudal belly of ECR (homologous belly to the *ECR brevis*); ECUh: humeral head of ECU; ECUu: ulnar head of ECU; RN: radial nerve; RCA: radial collateral artery; ER: extensor retinaculum. White bars: 10 mm

The EDC is a bipennate muscle that develops two bellies from the middle third of the antebrachium. It has a fleshy origin from the distal third of the lateral supracondylar crest, lateral epicondyle, and intermuscular septum with the EDL (Figure 1). The tendons are free of fleshy fibers from the distal third of the antebrachium, forming a broad aponeurosis on the dorsum of the metacarpal region; distally, the four tendons extend to insert onto the bases of the distal phalanges of digits II-V (Figure 2). The cranial interosseous artery supplies the muscle.

The EDL is bipennate and originates via fleshy fibers from the lateral epicondyle of the humerus (Figure 1) and sends tendons to digits III, IV, and V (Figure 2). The muscle is proximally covered by the *m. extensor digitorum communis* and is supplied by the cranial interosseous artery.

The ECU is bipennate and originates via two heads from the humerus and ulna, which join close to their origins. The humeral head (ECUh) originates via a tendon from the lateral epicondyle of the humerus and *m. anconeus* (A). The ulnar head (ECUu) originates from the caudal margin of the ulna at the level of the elbow joint, and from the intermuscular septum formed by the deep fascia between the craniolateral and caudomedial antebrachial muscles (Figure 1). The tendon bifurcates, sending a branch to the dorsolateral aspect of the base of metacarpal bone V, and another branch to the accessory carpal bone. The cranial interosseous artery supplies the muscle.

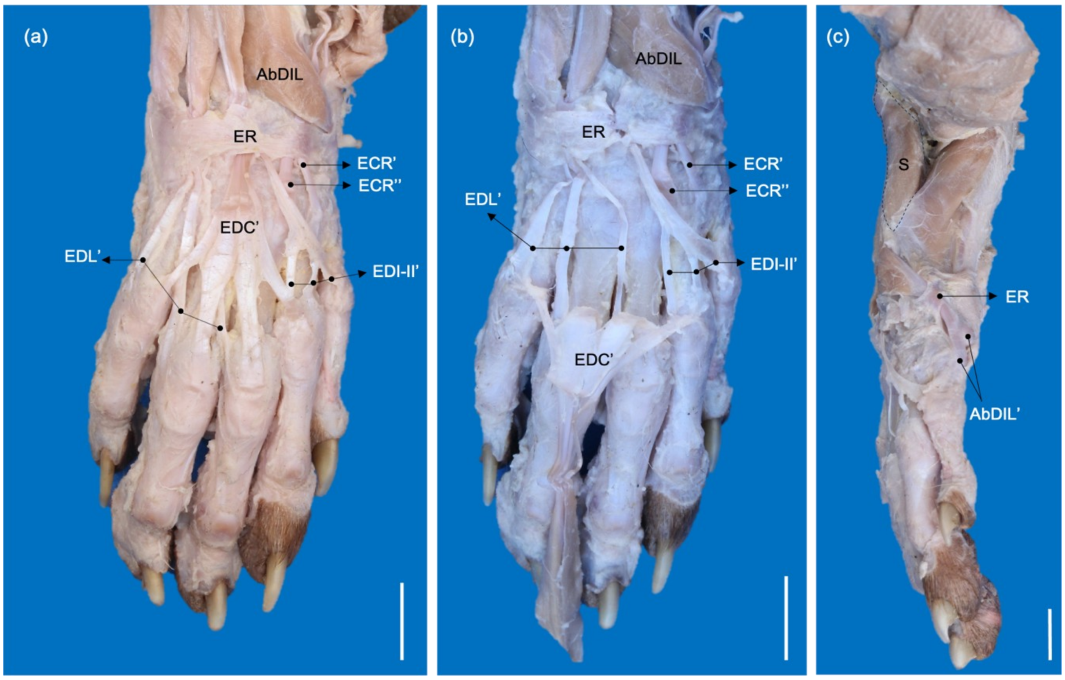

Figure 2. Dorsal views of the right manus (a and b) and medial view of the right antebrachium and manus (c) of *Lontra longicaudis*. AbDIL': tendon of AbDIL; ECR': tendon of ECR cranial belly (homologous to the *ECR longus* tendon); ECR'': tendon of ECR caudal belly (homologous to the *ECR brevis* tendon); EDC': tendons of EDC; EDL': tendons of EDL; EDI-II': tendons of EDI-II; ER: extensor retinaculum. White bars: 10 mm

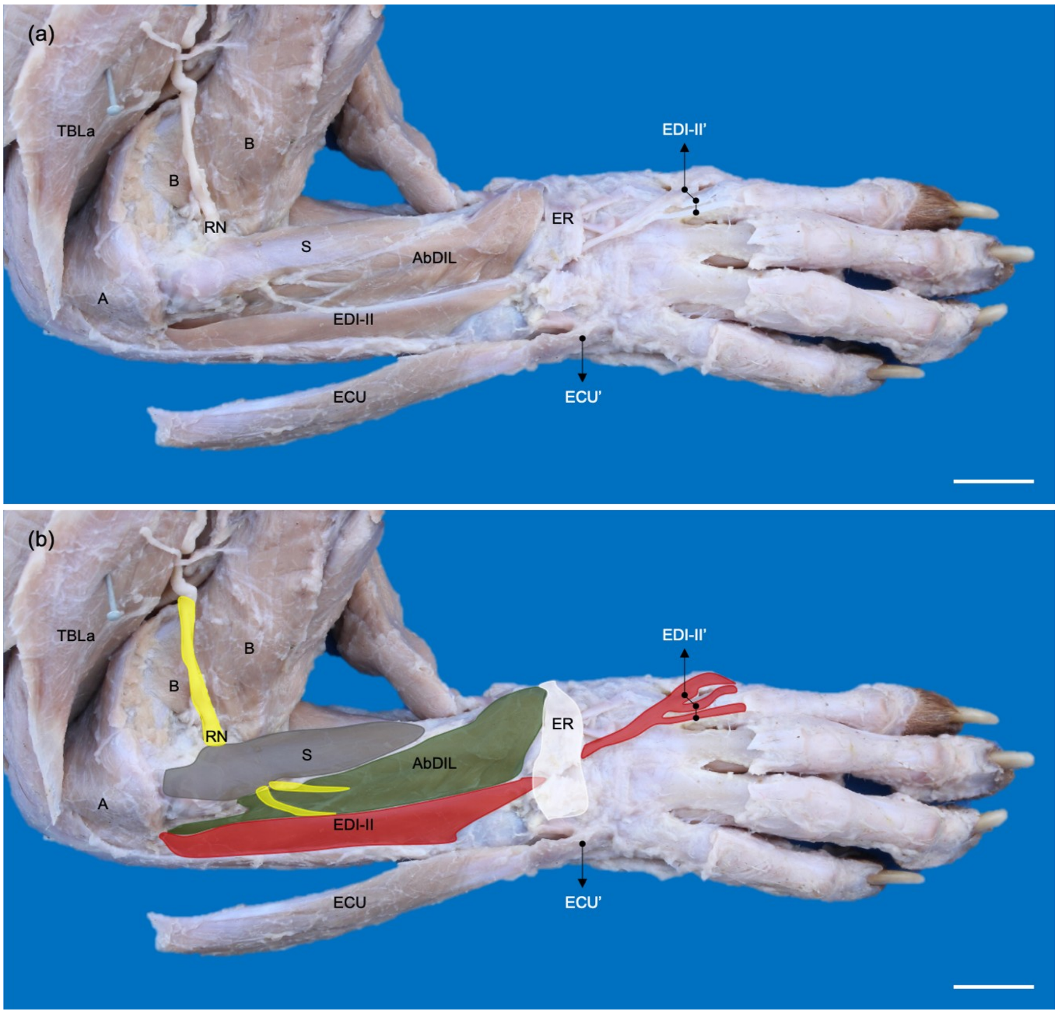

Figure 3. Deep view of the craniolateral aspect of the right antebrachium in a *Lontra longicaudis*. Dissection after removal of the superficial muscles (a) with the colored structures (b). ECU': tendon of ECU; EDI-II': tendons of EDI-II; RN: deep branch of the radial nerve; ER: extensor retinaculum. White bars: 10 mm

The S is fusiform, originating via a tendon from the lateral collateral ligament of the elbow and the lateral epicondyle of the humerus. It inserts onto the proximal half of the radius, reaching the radial neck, medial margin, and caudal and cranial surfaces of the radius (Figures 2 and 3). The cranial interosseous artery supplies the muscle.

The AbDIL is bipennate and originates via fleshy fibers from the cranial surface of the radius—extending from the radial neck—interosseous ligament, and lateral surface of the ulna. It is covered proximally by A (Figure 3). Its tendon bifurcates at the carpal region to insert onto the sesamoid bone (*os sesamoideum m. abductoris digiti I longi*) and the lateral aspect of the base of metacarpal bone I (Figure 2c). The cranial interosseous artery supplies the muscle.

The EDI-II is bipennate, originating via fleshy fibers from the proximal four-fifths of the lateral surface of the ulna, caudal to the AbDIL, and the intermuscular septum with the caudomedial antebrachial muscles. Its proximal portion is covered by A. Its tendons extend to the distal phalanx of digit I, and the axial and abaxial aspects of digit II. The axial tendon joins the tendon of the EDC, while the abaxial tendon inserts onto the base of the proximal phalanx (Figure 2b). The cranial interosseous artery supplies the muscle.

Discussion

Comparative terminology of the craniolateral antebrachial muscles in otters

The anatomical descriptions of the origin and insertion of the craniolateral antebrachial muscles of *E. lutris* (Howard, 1973) closely match our findings in *L. longicaudis*. In the other otter species, some differences could be found based on the few descriptions available for *L. lutra* (Haughton, 1864) and *A. cinereus* (Macalister, 1870). Because these earlier studies date back more than a century, the homologous terms of those muscles are summarized in Table 1. The anatomical terminology used by Howard (1973) most closely aligns with the current nomenclature established by the International Committee on Veterinary Gross Anatomical Nomenclature (2017). Howard (1973) referred to the muscles as *extensor carpi radialis longus* and *extensor carpi radialis brevis,* describing them as proximally fused—consistent with our observations in *L. longicaudis*. However, according to the NAV, the correct designation is simply *m. extensor carpi radialis* (ECR) (ICVGAN, 2017). In contrast, in *A. cinereus,* both muscles are completely separated (Macalister, 1870), thus making the use of both terms more appropriate. According to the NAV, there are two independent muscles for digits I and II since their terms are independent of *m. extensor digiti I* and *m. extensor digiti II*, respectively. Based on recent studies in carnivorans, the term most used is EDI-II, since it is a single muscle with two tendons to both digits (Dunn et al., 2022; Kamali et al., 2023; Vélez-García et al., 2022a).

Table 1. Homologous anatomical terminology of the craniolateral antebrachial muscles in otters (Mustelidae, Lutrinae).

Muscles based on the NAV (ICVGAN, 2017)	Other terms used in former studies
M. brachioradialis	M. supinator radii longus (Haughton, 1864) supinator longus (Macalister, 1870; Windle & Parsons, 1897)
M. extensor digitorum communis	M. extensor digitorum longus (Macalister, 1870)
M. extensor digitorum lateralis	M. extensor digiti minimi and m. extensor tertii et quarti digiti (Macalister, 1870) M. auricularis (Haughton, 1864) M. extensor minimi digiti (Windle & Parsons, 1897)
M. supinator	M. supinator radii brevis (Haughton, 1864) M. supinator brevis (Macalister, 1870; Windle & Parsons, 1897)
M. abductor digiti I [pollicis] longus	M. extensor ossis metacarpi pollicis (Howard, 1973; Macalister, 1870; Windle & Parsons, 1897)
M. extensor digiti I and extensor digiti II	M. indicator (Haughton, 1864) M. extensor pollicis et indicis (Howard, 1973; Macalister, 1870) M. extensor digitorum profundus (Windle & Parsons, 1897)

Comparative anatomy of the craniolateral antebrachial muscles in otters

The BR of *L. longicaudis* is highly developed, with attachments consistent with those previously reported for the same species (Souza-Junior et al., 2015) and other otters, such as *A. cinereus* (Macalister, 1870), *L. lutra* (Windle & Parsons, 1897), and *E. lutris* (Howard, 1973).

The ECR of *L. longicaudis* is similar to that of *E. lutris* (Howard, 1973) and *L. lutra* (Haughton, 1864), although in the latter species there is only a single tendon that bifurcates to insert onto both metacarpal bones. In *A. cinereus,* it is divided into separate *m. extensor carpi radialis longus* and *m. extensor carpi radialis* *brevis*. The former inserts via two tendons onto the metacarpal bone II and forms a slip that joins to the tendon of the latter (Macalister, 1870).

The EDC and AbDIL muscles of *L. longicaudis* are similar to those of other otters (Haughton, 1864; Howard, 1973; Macalister, 1870; Windle & Parsons, 1897).

The EDL of *L. longicaudis* sends tendons to digits III to V, as in *L. lutra* (Haughton, 1864; Windle & Parsons, 1897) and *A. cinereus* (Macalister, 1870). However, in the latter species, it forms two bellies with independent origins from the medial epicondyle; the lateral belly only sends a tendon to digit V, whereas the medial belly sends tendons to digits III-V (Macalister, 1870). In *E. lutris*, it forms tendons only to digits IV and V (Howard, 1973).

The ECU of *L. longicaudis* differs from that of other otters in the presence of an accessory origin from the ulna and an insertion onto the accessory carpal bone. In a *L. lutra*, the muscle inserts near the distal extreme of metacarpal V (Haughton, 1864), whereas in other lutrines it inserts onto the base of that bone (Howard, 1973; Macalister, 1870), similar to *L. longicaudis*.

The S inserts more distally in other otters than in *L. longicaudis*, reaching the proximal three-quarters of the bone in *E. lutris* (Howard, 1973) and *L. lutra* (Windle & Parsons, 1897), and the distal third in *A. cinereus* (Macalister, 1870).

The EDI-II of *L. longicaudis* is similar to that of *A. cinereus* (Macalister, 1870) and *L. lutra* (Windle & Parsons, 1897). It differs from that described in *L. lutra*, in which the tendons extend to digits II and III (Haughton, 1864). In *E. lutris*, the tendon to digit I inserts onto the proximal phalanx (Howard, 1973), and the axial tendon to digit II was not reported.

Functional analysis

The more proximal origin of BR in all otters provides greater force to support elbow flexion performed by the brachialis and biceps brachii muscles. This adaptation is necessary for swimming underwater, as it requires more force to flex the elbow after generating propulsion by the elbow extensors. In other caniforms, the origin of the BR is more distal, ranging from the middle or distal third of the humerus (Ercoli et al., 2015; Tarquini et al., 2023; Vélez-García et al., 2022a). On the other hand, the supination movements are essential to coordinate swimming direction underwater and manipulate food and offspring on the abdomen when the animal is above water (Fabre et al., 2015). Carpal extension is primarily performed by the ECR, supported by the ECU and digital extensors. The ECU may exhibit an additional adaptation to increase the force to move the carpus, mainly during abduction and flexion movements. These are necessary for swimming coordination, together with the carpal adduction that should be generated by the AbDIL. The presence of two heads in the ECU of our *L. longicaudis* specimen could represent an anatomical variant, as the ECUu is absent in other otters and most carnivorans. This ECUu has been found as an anatomical variation in the procyonids *Procyon cancrivorus* (Vélez-García et al., 2022a), *Nasua narica* (Mackintosh, 1875), and *Potos flavus* (Julitz, 1909). Therefore, the presence of the ECUu could be associated with a common ancestor within the superfamily Musteloidea, from which the families *Procyonidae* and *Mustelidae* diverged (Hassanin et al., 2021).

Digit abduction increases the contact area of the manus on the water since the otters have interdigital membranes, which should be performed laterally for digits III-V by the EDL, and medially for digits I-II by the EDI-II and AbDIL (Hermanson et al., 2020).

The innervation to all these muscles in *L. longicaudis* is via the deep branch of the radial nerve (Ramírez Arango et al., 2024). Their arterial supply involves the radial collateral, transverse cubital, and cranial interosseous arteries, as has been described in a few carnivorans, including the procyonids *P. flavus* (Vélez-García et al., 2022b) and *P. cancrivorus* (Vélez-García et al., 2022a), the ursid *Ailuropoda melanoleuca* (Davis, 1964), the canid *Canis lupus familiaris* (Barone, 2021; Hermanson et al., 2020), and the felid *F. catus* (Barone, 2021).

Conclusion

The anatomical arrangement of the craniolateral antebrachial muscles of *L. longicaudis* suggests gross adaptations that enable powerful movements of the elbow and manus underwater, facilitating swimming direction and food manipulation.

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