



## A novel series of forepaw muscles for mammals observed in the Patagonian weasel *Lyncodon patagonicus*

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The intrinsic autopodial musculature of mammals is composed of a relatively stable number of muscular groups. Here, we present the first myological studies of *Lyncodon patagonicus*, a South American mustelid that is morphologically and ecologically poorly known. The typical intrinsic muscles of the manus of *Lyncodon* are similar to those of its sister taxon *Galictis*, although there exist few variations, including additional subdivisions and relatively more distal insertions in some muscles. A striking feature is the presence of a novel series of forepaw muscles never before described for mammals. These muscles, named here mm. flexores digitorum proprii manus, are represented by a medial and a lateral belly for each digit and are located immediately distal to the mm. flexores breves profundi. They are located distally alongside the tendons of the latter, along the palmar aspect of the phalangeal series, and they insert onto the flexor tubercle of the distal phalanx of each digit. We propose that the incorporation of these muscles in the forepaw musculature of *Lyncodon*, in addition to some other osteo-myological features, imply a distinctive morpho-functional adaptation to increase the force of flexion and independence of digital movements likely used to grasp prey during hunting. This hypothesis should be confirmed by future ecological and behavioral studies on this species.

La musculatura intrínseca del autopodio de los mamíferos está compuesta por un número de grupos musculares relativamente estable. En este trabajo nosotros presentamos el primer estudio miológico de *Lyncodon patagonicus*, un mustélido de América del Sur pobremente conocido tanto en aspectos morfológicos como ecológicos. Los músculos intrínsecos típicos de la mano de *Lyncodon* son similares a los presentes en el taxón hermano *Galictis*, aunque presenta algunas variaciones, incluyendo la presencia de subdivisiones adicionales y algunas inserciones relativamente más distales. Una característica distintiva fue la presencia de una novedosa serie de músculos nunca antes descrita para un mamífero. Estos músculos, aquí denominados mm. flexores digitorum proprii manus, están representados por un vientre medial y uno lateral para cada dígito, ubicados inmediatamente distales a los mm. flexores breves profundi. Distalmente, estos se ubican a los lados de los tendones de estos últimos, en el aspecto palmar de la serie falangeal, insertándose en los tubérculos flexores de las falanges distales de cada dígito. Nosotros proponemos que la incorporación de estos músculos a la musculatura de la mano de *Lyncodon*, sumado a otras características osteo-miológicas, podría implicar una adaptación morfo-funcional distintiva, posibilitando una mayor fuerza de flexión e independencia en los movimientos digitales, posiblemente utilizada por el taxón durante la manipulación de presas durante la caza. Esta función debe ser confirmada por futuros estudios ecológicos y comportamentales para esta especie.

Key words: dexterity, forelimb, intrinsic forepaw musculature, *Lyncodon*, Mustelidae

The arrangement of the flexor forepaw musculature of mammals is typically composed of muscles originating directly or indirectly from the medial epicondyle of the humerus and the

radius and ulna, and by many intrinsic muscles of the manus. Topographically linked to the intrinsic manus musculature, and typically considered as part of them (Diogo and Abdala 2010;

but see [Cunningham 1878](#); [Young 1880](#)), are the mm. lumbricales and m. palmaris brevis ([Cunningham 1878](#); [McMurrich 1903](#); [Diogo and Abdala 2010](#)). The mm. lumbricales run from the tendons of the m. flexor digitorum profundus to the medial aspect of the lateral digits; they are typically represented by 4 muscles, one for each of the 4 lateral digits (e.g., [Kanagasuntheram and Jayawardene 1957](#); [Jouffroy 1971](#); [Woods 1972](#); [Diogo and Abdala 2010](#)). However, a pair of mm. lumbricales for each digit (occurring this arrangement in one or more digits) occurs in some mammals ([Galton 1870](#); [Windle and Parsons 1899](#); [McMurrich 1903](#); [Diogo and Abdala 2010](#)). In several mammal lineages, they are reduced in number (e.g., *Canis*, *Proteles*, hippopotamids and some other artiodactyls, perissodactyls, many xenarthrans, many rodents and lagomorphs—[Mivart and Murie 1866](#); [Humphry 1869](#); [Windle and Parsons 1897, 1899](#); [Woods 1972](#); [Kesner 1986](#); [Fisher et al. 2007](#)) or absent (e.g., *Crociodura*, *Talpa*, *Chrysochloris*, some arvicolines, some xenarthrans, many artiodactyls—[Windle and Parsons 1899](#); [Jouffroy 1971](#); [Kesner 1986](#); [Fisher et al. 2007](#) and citations therein). The m. palmaris brevis runs transversally through the hypothenar region; it is variably present, being typically present in carnivorans (but see [Windle and Parsons 1897](#)), rodents, marsupials, and many primates, and absent in some lemurids and xenarthrans ([Mivart and Murie 1866](#); [Parsons 1894](#); [Windle and Parsons 1899](#); [McMurrich 1903](#); [Kanagasuntheram and Jayawardene 1957](#); [Jouffroy 1971](#); [Kesner 1986](#); [Fisher et al. 2009](#); [Diogo and Abdala 2010](#); [Ercoli et al. 2015](#)).

Regarding the deeper intrinsic musculature (deep to the mm. lumbricales and m. palmaris brevis), although there is wide variation among the different mammalian clades, there is a relatively constant arrangement ([Cunningham 1878](#); [Young 1880](#)) that consists in the presence of 3 layers: palmar, intermediate, and dorsal. The palmar layer (= “first layer of deep hand-muscles” of [Windle and Parsons 1897](#)) is composed of the mm. adductores digitorum (= mm. contrahentes, mm. adductores breves). These muscles typically run from the deep carpal ligament, the ventral aspect of the carpals, and/or the bases of the metacarpal bones to the proximal phalanx of some digits, being highly variable in the number of these insertions. The belly of digit III is typically absent in most mammals (e.g., [Young 1880](#); [McMurrich 1903](#); [Kanagasuntheram and Jayawardene 1957](#); [Jouffroy 1971](#); [Fisher et al. 2007](#)). Besides the absence of this belly, the belly for digit IV is also missing in many mammals, e.g., many carnivorans, some primates, tree-shrews, colugos, macroscelids, cricetids and some other rodents ([Parsons 1894](#); [Haines 1950](#); [Jouffroy 1971](#); [Kesner 1986](#); [Diogo and Abdala 2010](#); [Diogo et al. 2012](#)). Furthermore, the belly for digit I may also be absent or reduced in some rodents (e.g., most cavioids, most microtines—[Windle 1897](#); [Kesner 1986](#); [Rocha-Barbosa et al. 2007](#)), some ungulates (e.g., hippopotamids and some artiodactyls—[Fisher et al. 2007](#) and citations therein), *Orycteropus*, and *Manis* ([Windle and Parsons 1899](#)), and some carnivoran clades (e.g., most canids and hyaenids—[Windle and Parsons 1897](#)). As extreme cases, in some rodents and some ungulates (e.g., most ruminants), all of the mm.

adductores digitorum are absent or reduced ([Jouffroy 1971](#); [Fisher et al. 2007](#)). These muscles are highly modified in many primates and xenarthrans, both groups displaying a wide range of variants ([Windle and Parsons 1899](#); [Kanagasuntheram and Jayawardene 1957](#); [Jouffroy 1971](#); [Diogo and Abdala 2010](#); [Diogo and Wood 2011](#); [Diogo et al. 2012](#)).

In a deeper position are the intermediate and dorsal layers. The homologies and identification of these muscles are more difficult to discern across mammal species. The mm. interossei sensu lato (see [Diogo and Abdala 2010](#)) are composed of bellies belonging to both layers, while the mm. opponens ([Cunningham 1878](#); [Lewis 1989](#); [Diogo and Abdala 2010](#)) and abductor of digits I and V ([Cunningham 1878](#) contra [Lewis 1989](#)) are considered to be part of some of these layers, or, in the case of the abductors, an independent origin for them has been proposed (see below; and see [Diogo and Abdala 2010](#) for a discussion of their homologies). In his study of primates, [Lewis \(1989\)](#) proposed that opponens muscles and specific flexors for these digits (i.e., flexor pollicis brevis and flexor digiti minimi brevis) are modified bellies from the mm. flexores breves profundi, resulting this modification in a reduced number of the bellies of the latter muscles. However, for other mammalian lineages (e.g., carnivorans—[Fisher et al. 2009](#)), it has been described the presence of the abductor and opponens without reduction of the number of bellies of the mm. flexores breves profundi (including under this denomination the specific flexors above mentioned). The mm. interossei are located immediately palmar or at the level of the metacarpal bones, connecting their bases or those of adjacent elements (i.e., carpal bones and/or carpal ligament) with the metacarpal sesamoids (of the same digit or that of an adjacent digit). Eventually, additional insertions or bellies continue beyond this point and surround the phalanges to reach the extensor tendons (e.g., primates, some carnivorans and marsupials, hippopotamids, and xenarthrans—[Galton 1870](#); [Humphry 1869](#); [Young 1880](#); [Reighard and Jennings 1901](#); [Haines 1950](#); [Jouffroy 1971](#); [Fisher et al. 2007](#); [Julik et al. 2012](#); [Evans and de Lahunta 2013](#); see m. interossei accessorii of hylobatids in [Susman et al. 1982](#)). In this regard, the different arrangement of the origins and insertions of these bellies was the trigger that led [Cunningham \(1878\)](#) to differentiate these muscles into 2 basic, theoretically ancestral layers: the intermediate layer that consists of the mm. interossei palmares (= “second layer of hand-muscles” of [Windle and Parsons 1897](#) and “flexor breves profundi” of [Lewis 1989](#); see also [Cunningham 1878](#); [Young 1880](#); [McMurrich 1903](#); [Haines 1950](#); [Jouffroy 1971](#); [Diogo and Abdala 2010](#); [Diogo et al. 2012](#)) and the dorsal layer that consists of the mm. interossei dorsales (= “third layer of hand-muscles” of [Windle and Parsons 1897](#) and “intermetacarpales” + “flexores breves profundi” of [Lewis 1989](#); [Diogo and Abdala 2010](#); but see below). Recent researchers ([Cihák 1972](#); [Lewis 1989](#); [Diogo and Abdala 2010](#); [Diogo et al. 2012](#)) also supported the idea of 2 ancestral layers, suggesting that the m. palmar interossei derived from an ancestral layer named mm. flexores breves profundi, while the muscles considered as mm. interossei dorsales in many lineages are actually the result of the fusion of some bellies ancestrally corresponding to the 2

ancestral layers, i.e., the mm. flexor breves profundi and the mm. intermetacarpales of these authors.

The mm. flexores breves profundi are commonly present in mammals, although reduced in number or size in some lineages (e.g., macropodids, some rodents, *Manis*, most xenarthrans, and many ungulates—Humphry 1869; Galton 1870; Young 1880; Windle and Parsons 1899; Kesner 1986; Fisher et al. 2007; Rocha-Barbosa et al. 2007). Their ancestral arrangement consists of a pair per digit (Lewis 1989), located superficial to the dorsal layer, and with flexor functions. The mm. intermetacarpales may be absent, reduced, or fused with the mm. flexores breves profundi in many mammal lineages (Diogo and Abdala 2010), such as carnivorans (Young 1880; Windle and Parsons 1897; McMurrich 1903). There are 4 in the ancestral condition (Lewis 1989), located between adjacent metacarpals, with abductor functions, which are functionally linked with the more palmar abductors and opponens muscles of digits I and V.

In addition to the variant mentioned above, there exist at least 2 particular modifications that affect the general scheme of the mm. interossei. The first occurs when a group of fibers slips off and spans transversally between the insertions of the other mm. interossei deriving in, for example, the “palmaris transversus” of *Arborimus* (Kesner 1986), the “transversus” of *Manis* (Humphry 1869), the “transverse adductor indicis” of *Dasyopus* (Windle and Parsons 1899), and an innominate muscle in *Hystrix* (Parsons 1894:272). A second kind of modification was described by Humphry (1869) in sloths, in which an additional and secondary set of mm. interossei named “phalangeal interossei” originates from the second phalanges and inserts together with the other mm. interossei onto the extensor tubercles.

The m. flexor digitorum brevis manus (= flexor brevis manus) and the abductors of the peripheral digits have been considered to be derived from the dorsal layer despite their relatively superficial position (sensu Cunningham 1878:434), but recent studies suggest the possibility that this muscles could be derived from the m. flexores breves superficiales of other tetrapods (e.g., Lewis 1989; Diogo and Abdala 2010). The former muscle originates from the pisiform bone, the annular ligament, and/or the palmar aponeurosis. Although the m. flexor digitorum brevis manus can be represented by bellies for all digits (e.g., Kanagasuntheram and Jayawardene 1957), it usually consists of a single belly extending to digit II (*Rhynchocyon*), IV (some tenrecids), or V (macroscelids, some marsupials and rodents, and many carnivorans—Mivart and Murie 1866; Parsons 1894; Windle 1897; Windle and Parsons 1897; Jouffroy 1971). On occasion, it may reach 2 digits (digits IV and V in most feliforms and *Myrmecophaga*—Mivart and Murie 1866; Windle and Parsons 1897, 1899; Jouffroy 1971; Julik et al. 2012). On the other hand, this muscle is absent in many mammal clades (e.g., some marsupials, bats, most ungulates, talpids, mephitids, canids, and most mustelids—Windle and Parsons 1897; Jouffroy 1971; Fisher et al. 2007, 2009; Ercoli et al. 2015 and citations therein). The m. abductor pollicis brevis (= abductor digiti I) and the m. abductor digiti minimi (= abductor digiti V) connect proximal carpal elements with the external aspect

of the corresponding proximal phalanges, metacarpals, and/or metacarpal sesamoids. More or less differentiated, a m. opponens pollicis (= opponens digiti I) and a m. opponens digiti minimi (= opponens digiti V) are frequently present and often tightly associated with each of the 2 abductor muscles (described above), respectively. These abductors and opponens muscles are typically present in mammals (e.g., Galton 1870; Young 1880; Windle 1897; Windle and Parsons 1897, 1899; Kesner 1986; Rocha-Barbosa et al. 2007; Diogo and Abdala 2010; Diogo et al. 2012) but reduced or absent in some lineages (e.g., in those with an atrophied pollex—Parsons 1894; Windle and Parsons 1897; Fisher et al. 2007).

Among carnivorans, the principal variants described by previous authors affect most of the manus intrinsic musculature, mainly related to: reduction in number or size of bellies (in relation to cursorial adaptations) and reduction of external digits (e.g., canids, felids, and hyaenids—Reighard and Jennings 1901; Jouffroy 1971; Spoor and Badoux 1986; Julik et al. 2012; Evans and de Lahunta 2013), and subdivision and enlargement of the muscles that allow dexterity of the digits and grasping, especially related to the pollex and the radial sesamoid (e.g., Davis 1964; McClearn 1985; Antón et al. 2006; Fisher et al. 2009; Abella et al. 2015). Regarding the representation of each layer, the palmar and intermediate ones are typically well represented, while the dorsal one is not described (but is surely fused with the intermediate layer—Cunningham 1878; Young 1880) or only represented by few distinct elements (e.g., Reighard and Jennings 1901; Davis 1964; abductor digiti II and abductor digiti IV of Ercoli et al. 2015 and citations therein). Mustelids demonstrate a typical carnivoran arrangement, although the m. flexor digitorum brevis manus is absent or reduced in derived mustelids (Windle and Parsons 1897; Ercoli et al. 2015).

The Patagonian weasel, *Lyncodon patagonicus* (Fig. 1), is a small South American ictonychine weasel, and one of the most poorly known mustelids (Prevosti et al. 2009; Wilson and Mittermeier 2009; Sato et al. 2012). It inhabits arid



**Fig. 1.**—*Lyncodon patagonicus*, living specimen photographed in Chubut, Argentina, by Darío Podestá. Note the slender and gracile digits of the forepaw.



environments of southern Argentina and Chile (Cabrera and Yepes 1940; Schiaffini et al. 2013), and its natural history remains entirely anecdotal (e.g., Doering 1881; Koslowsky 1904; Cabrera and Yepes 1940; Prevosti and Pardiñas 2001; Wilson and Mittermeier 2009). The scant information about its ecology and behavior suggests *Lyncodon* is nocturnal–crepuscular and hypercarnivorous (supported by its craniodental morphology—Ewer 1973:177), mainly preying on fossorial caviomorph rodents (e.g., *Ctenomys* and *Microcavia*—Cabrera and Yepes 1940; Cicchino and Castro 1998; Teta et al. 2008; Wilson and Mittermeier 2009). It can perform agile gaits, pursue prey actively, and display aggressive behaviors (Doering 1881; Koslowsky 1904; Cabrera and Yepes 1940). The particular forelimb autopodial morphology (e.g., relatively developed interdigital webs, high proximal phalanx/metacarpal length ratio, and long and narrow unguis phalanges) has led some previous authors to propose digging abilities (Pocock 1921, 1926) or, in contrast, grasping abilities (Ercoli 2015). The information concerning the morphology of this species is limited to Koslowsky (1904), Pocock (1921, 1926), Cabrera (1929), Pascual (1958), Prevosti and Pardiñas (2001), and Ercoli (2015).

In line with prior contributions about the myology of South American mustelids (Ercoli et al. 2013, 2015), we carried out exhaustive dissections on *L. patagonicus*, a species for which myological studies are lacking. Here, we describe the intrinsic muscles of the forepaw, and identify a strikingly novel series of forepaw muscles, not present in any other carnivoran species and, as far as we know, in any other mammal.

## MATERIALS AND METHODS

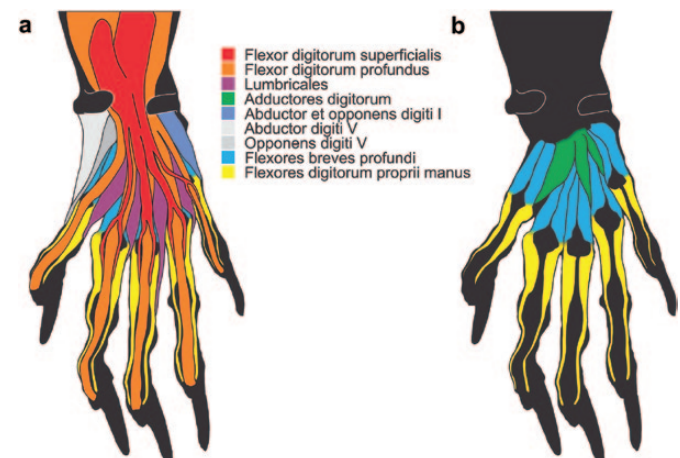
For the present study, we had access to a unique fresh wild-caught specimen of *L. patagonicus* (corresponding to the subspecies *L. p. patagonicus*, see Cabrera 1929). This material was kindly provided on loan to us by the staff of the National Mammal Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN, Buenos Aires, Argentina). Materials of this species are extremely rare in mammal collections and, as far as we know, the specimen dissected is the only fresh specimen in any public scientific collection that is suitable for myological studies. The specimen, field number MACN-MASTO-198, is a female weighing 135 g (total length = 338 mm) collected by Dr. Never Bonino in Bariloche (Río Negro province, Argentina) in 2014. The presumed cause of death was injuries inflicted by a domestic dog, without major damage to the specimen except in some regions of the trunk. The specimen was fixed in a solution of 1 part formalin to 18 parts water saturated with NaCl (see Ercoli et al. 2013) for 3 days and later stored in 70% ethanol. Only the right forepaw could be studied, leaving the left one intact as required by curatorial procedures. In addition, the dehydrated left forepaw preserved within an embalmed skin of a second specimen (MACN Ma 23.21; from Aguada Grande, Santa Cruz province, Argentina; collected by A. Pozzi in 1920) was rehydrated and dissected, but only principal tendons (e.g., m. palmaris longus, m. flexor digitorum superficialis, and m. flexor digitorum

profundus) could be observed due to the poor preservation of muscular tissues of the whole intrinsic musculature. For reference during dissection, we used osteological specimens of *Lyncodon* and comparative musteloid species (see Appendix I) from the recent mammal collections of MACN, Museo de La Plata (MLP, Buenos Aires, Argentina), and the Field Museum of Natural History (FMNH, Chicago, Illinois).

For each intrinsic muscle of the forepaw, general features, origin, and insertion were recorded and illustrated. To confirm the tissue type of the novel series of muscles, we obtained histological slides following a 3-color staining technique. We carried out a progressive dehydration of the tissues via an ascending series of ethanol, cleared in toluene, and then embedded in Paraplast. All samples were sectioned using a microtome at 5–10  $\mu\text{m}$ , mounted on glass slides, rehydrated, and stained with hematoxylin and modified Masson’s Trichrome (see Taboada et al. 2013). The procedure was carried out and kindly supervised by Lic. Agustín Elías-Costa and Dr. Carlos Taboada from the Division of Herpetology of the MACN; the access to equipment, work spaces, and supplies used were kindly provided by Dr. Cristián Ituarte and the Divisions of Herpetology, Ichthyology, and Invertebrates of the MACN. In order to enrich the discussion of the osteological modifications of the manus related to the fossorial/manipulation abilities of *Lyncodon*, we calculated the ratio between the length of the metacarpal III and the length of the proximal phalanx of the third digit (McIII/PhIII) for *Lyncodon* and other musteloid species.

## RESULTS

The detailed muscular anatomy of the forepaw of *Lyncodon* is similar in many aspects to that described for *Galictis cuja* (Ercoli et al. 2015; Fig. 2), which is expected because *Galictis* and *Lyncodon* are sister genera (Sato et al. 2012). As in *G. cuja*, *Lyncodon* possesses the same set of intrinsic musculature of the manus (i.e., m. palmaris brevis, 4 mm. lumbricales, m. abductor



**Fig. 2.**—Drawing showing the muscles of the manus, before a) and after removal b) the m. flexor digitorum superficialis, m. flexor digitorum profundus, m. abductor et opponens digiti I, m. abductor digiti V, m. opponens digiti V, and the mm. lumbricales.

digiti V, m. opponens digiti V, m. abductor et opponens digiti I, 3 mm. adductores digitorum, 10 mm. flexores breves profundi, m. abductor digiti II, and m. abductor digiti IV, while the m. flexor digitorum brevis manus is absent). Next, we describe these muscles, highlighting the distinctive features of *L. patagonicus*, while the features not detailed here should be considered as identical to those described for *G. cuja* (Ercoli et al. 2015).

*Palmaris brevis*.—The m. palmaris brevis presents a different configuration compared to *Galictis*. As usual, it originates from the fascia that covers the carpus at the level of the accessory carpal bone, but this muscle inserts at the level of the metacarpal I, via 2 tendons, onto an additional belly of the m. palmaris longus that corresponds to digit I.

*Lumbricales*.—The 4 mm. lumbricales (Fig. 2a) are represented by independent bellies that originate from the tendons of the m. flexor digitorum profundus at the level of the carpus instead of the metacarpals, as was described for *Galictis*. They insert via thin tendons onto the medial surface of the base of the proximal phalanges or the middle one (for the case of digit III).

*Opponens digiti V*.—The m. opponens digiti V (Fig. 2a) originates from the ligament distal to the accessory carpal bone, the medial surface of the accessory itself, and from metacarpal V and its proximal sesamoid, as was described for most of the cases of *Galictis*, but these origins were purely aponeurotic (versus mixed fibers). The insertion occurs on the lateral side of digit V, but its exact location could not be described due to some damage in the autopodium.

*Abductor digiti V*.—The m. abductor digiti V (Fig. 2a) originates from the accessory carpal bone and inserts onto the lateral sesamoid of digit V and the lateral aspect of metacarpal V, as was described in *Galictis*, but the differentiation in 2 bellies (denoted for *Galictis*) could not be checked in *Lyncodon* due to damage.

*Abductor et opponens digiti I*.—The m. abductor et opponens digiti I (Fig. 2a), as in *Galictis*, extends from the radial sesamoid to the proximal phalanx of digit I. In *Lyncodon*, the presence of an extra insertion onto the ventromedial aspect of metacarpal I (observed in some specimens of *Galictis*) was confirmed.

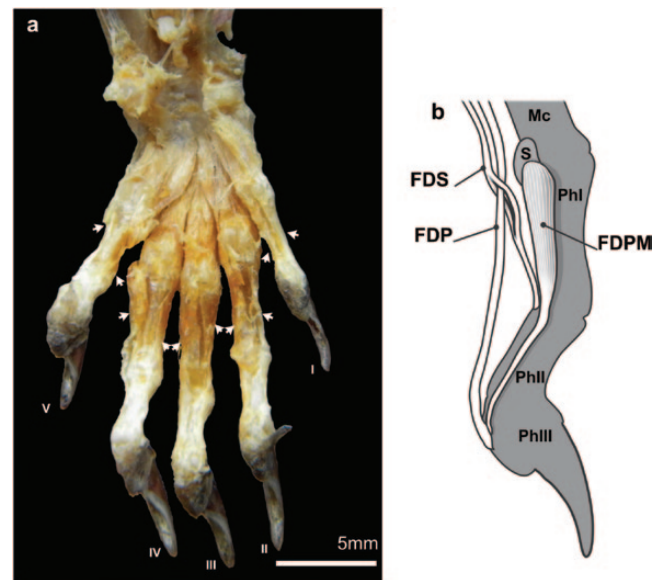
*Adductores digitorum*.—The mm. adductores digitorum (Fig. 2b) extends from the transverse carpal ligament to the proximal end of the proximal phalanx of digits I, II, and V, similar to that described for *Galictis*. However, in *Lyncodon*, the 3 muscles are independent from each other at their origins, the muscle for digit I is the smaller (versus II), and the insertion on digits I and II are tendinous (instead of fleshy, as occurs in digit V, and all cases for *Galictis*).

*Flexores breves profundi*.—The 10 mm. flexores breves profundi (Fig. 2b) originate from the proximal area of the corresponding metacarpal of each digit, the plantar process of carpal bone III, and the distal ligament of the accessory carpal bone, as in *Galictis*. They insert via fleshy fibers onto the corresponding metacarpal sesamoids, as usual, but there is an additional insertion onto the base of the middle phalanx of digit III.

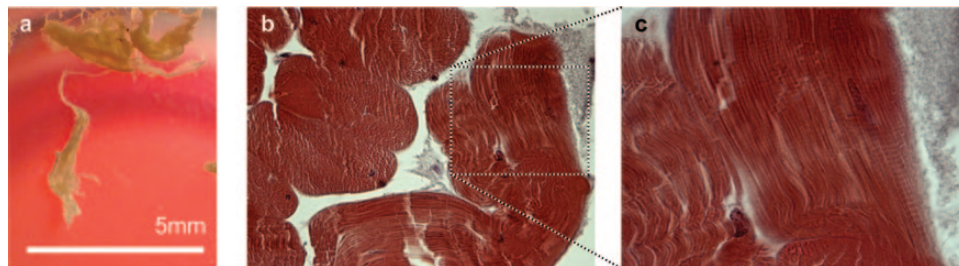
*Abductor digiti II*.—The m. abductor digiti II, differing with respect to *Galictis*, is composed of 2 bellies instead of only 1; one originates exclusively from the proximal sector of the lateral margin of metacarpal I (not reaching the middle of this bone, as in *Galictis*), and the other originates from carpal II (not observed in *Galictis*). On the other hand, the insertion of both bellies occurs on the medial area of the proximal phalanx of digit II instead of the medial sesamoid of metacarpal II.

*Abductor digiti IV*.—The m. abductor digiti IV extends from the base of metacarpal V to the lateral aspect of the lateral sesamoid of metacarpal IV and metacarpal IV itself (as in *Galictis*), but the fibers of origin are mixed (medially tendinous and laterally fleshy) instead of only fleshy.

*Flexores digitorum proprii manus*.—In addition to the usual set of muscles and the variants recorded for *L. patagonicus*, a novel and intriguing series of 10 bellies, arranged as a pair per digit lying over the palmar aspect of the forepaw, was detected and is described here (Figs. 2b and 3). The muscular nature of the fibers that compose these bellies was confirmed by histological analysis (Fig. 4). This series of muscles, henceforth named mm. flexores digitorum proprii manus, is represented by a medial and lateral belly for each digit. They present a similar arrangement to that of the mm. flexores breves profundi and are located immediately distal to them. The bellies of this series run along the sides of the tendons of the mm. flexor digitorum profundus and the mm. flexor digitorum superficialis, on the



**Fig. 3.**—Morphology of the mm. flexores digitorum proprii manus of *Lyncodon patagonicus*. a) Arrangement and location of the bellies (arrows) in palmar view of the left forepaw. The lateral belly for digit V was already removed and the arrow indicates the origin area of this belly. See Fig. 2b for a diagram indicating each muscle observed in the picture. b) Scheme of a single belly of the mm. flexores digitorum proprii manus (FDPM), and its topographic relationships with the tendons of the mm. flexores digitorum superficialis (FDS), the mm. flexores digitorum profundus (FDP), and osteological elements of a digit (Mc = metacarpus; PhI = first phalanx; PhII = second phalanx; PhIII = third phalanx; S = metacarpal sesamoid).



**Fig. 4.**—Appearance of the some loose bellies of the mm. flexor digitorum proprij manus in an ethanol 70° solution a), histological slides of muscle tissues at 400× b) and 1,000× c) in the highlighted frame; note muscular fibers cut near to transverse and longitudinal planes, showing the expected red staining, striations, and general structure for muscular fibers.

palmar aspect of the phalangeal series. For each digit, the lateral and medial bellies originate via fleshy fibers from the distal end of the corresponding metacarpal sesamoid, and some tendinous fibers take origin from the distal end of the corresponding belly of the mm. flexores breves profundi, to which they are loosely attached. All of the bellies become tendinous at the level of the distal end of the proximal phalanx and insert onto the flexor tubercle of the distal phalanx, immediately lateral and medial to the insertion tendons of the m. flexor digitorum profundus (Figs. 2 and 3).

*Ratio McIII/PhIII comparison.*—The mean values of the ratio McIII/PhIII (Table 1) indicate that *L. patagonicus* possesses the relative longest proximal phalanx (i.e., 1.32; the lowest value of the ratio) in comparison with other weasel-like musteloids and the whole sample. The length of the proximal phalanx of digit III of *L. patagonicus* is equivalent to the 76% of the length of the metacarpal III, a very different condition to the sister taxa, *Galictis* spp. (ranging 56–63%).

## DISCUSSION

From our literature review and our previous knowledge about the intrinsic musculature of mammals, the mm. flexores digitorum proprij manus of *L. patagonicus* appear to be unique. The absence of these muscles in representatives of the sister group, *Galictis*, is particularly interesting, highlighting the distinctiveness of *L. patagonicus*. The disposition of a pair per digit is very similar to that observed for the mm. flexores breves profundi, but the mm. flexores digitorum proprij manus are clearly independent, although distally contiguous with the former, and located along the palmar aspect of the phalangeal series instead of the metacarpal series. The presence of these muscles represents a major modification of the typical mammalian autopodial arrangement. Functionally, each pair of mm. flexores digitorum proprij manus seems to act as a flexor of the interphalangeal joints without accompanying flexion of the metacarpophalangeal joints, an exclusive function of these mover muscles. The incorporation of these muscles in the forepaw musculature would result in an increase of the total intrinsic flexor mass (and surely the force for digital flexion) and a greater degree of independence of digital movements (i.e., dexterity) during grasping (see also Kesner 1986). Furthermore, some of the distinctive features highlighted for the other forepaw muscles of *L. patagonicus* support the possibility of enhanced grasping

**Table 1.**—Values of the ratio between the length of the metacarpal III and the length of the proximal phalanx of the third digit (McIII/PhIII) for musteloid species. See Appendix I for measured specimens in this study.

Species	McIII/PhIII
<i>Lyncodon patagonicus</i>	1.322
<i>Lontra longicaudis</i>	1.393 <sup>a</sup>
<i>Potos flavus</i>	1.409 <sup>a</sup>
<i>Taxidea taxus</i>	1.409 <sup>a</sup>
<i>Poecilogale albinucha</i>	1.426
<i>Mustela nivalis</i>	1.478
<i>Eira barbara</i>	1.513 <sup>a</sup>
<i>Mustela frenata</i>	1.528
<i>Bassariscus astutus</i>	1.551 <sup>a</sup>
<i>Ictonyx striatus</i>	1.589
<i>Galictis cuja</i>	1.598 <sup>a</sup>
<i>Mustela nigripes</i>	1.610
<i>Mustela vison</i>	1.626
<i>Mustela erminea</i>	1.659
<i>Mellivora capensis</i>	1.661
<i>Martes pennanti</i>	1.665
<i>Martes americana</i>	1.689
<i>Spilogale gracilis</i>	1.742 <sup>a</sup>
<i>Galictis vittata</i>	1.759
<i>Lontra canadensis</i>	1.792 <sup>a</sup>
<i>Nasua nasua</i>	1.835 <sup>a</sup>
<i>Nasua narica</i>	1.887 <sup>a</sup>
<i>Procyon lotor</i>	1.959 <sup>a</sup>
<i>Arctonyx collaris</i>	2.008 <sup>a</sup>
<i>Gulo gulo</i>	2.009 <sup>a</sup>
<i>Meles meles</i>	2.057 <sup>a</sup>
<i>Conepatus chinga</i>	2.339 <sup>a</sup>
<i>Mephitis</i> sp.	2.428 <sup>a</sup>

<sup>a</sup>Data from bibliography (Van Valkenburgh 1987; Iwaniuk et al. 1999; Ercoli 2015).

abilities for this species. These traits include an extra belly for the m. abductor digiti II; extra insertions for the mm. flexores breves profundi and m. palmaris brevis; relatively more distal insertions of some mm. lumbricales, mm. flexores breves profundi, and m. abductor digiti II, as well as independent origins of the bellies of the mm. adductores digitorum.

The only other intrinsic phalangeal series of muscles of a mammal was described in sloths by Humphry (1869) under the name of “phalangeal interossei,” but these muscles differ in origins, insertions, and functions compared to the mm. flexores digitorum proprij manus of *L. patagonicus*. Humphry’s



description indicates that those muscles originate from the apposed sides of the middle phalanges and insert together with the other mm. interossei into the apposed sides of the extensor tendons, near the extensor expansions (Humphry 1869:49). Due to the common insertion, Humphry considered them as a secondary set of the mm. interossei (sensu lato) and assigned them a lateral stabilization function, in relation to the autopodial specialization of sloths to suspensory postures.

The dissection of the dehydrated forepaw extracted from an old embalmed skin of a second specimen did not allow us to check any feature of the intrinsic musculature of *L. patagonicus*, due to poor preservation; therefore, further studies to corroborate this issue are necessary. The presence of these muscles, confirmed in only a single specimen and no knowledge of the innervation pattern, limits the interpretation about homologies and ecological inferences. In the case of *L. patagonicus*, the presence of the mm. flexores digitorum proprii manus is difficult to explain due to the paucity of behavioral data for this species. However, from an ecomorphological perspective, Pocock (1921, 1926) suggested digging abilities for the species based on the external morphology of the autopodia and the long ungual (distal) phalanges, in comparison with both the rest of the forepaw and the ungual phalanges of the hind limb. In contrast, Ercoli (2015) proposed that the morphology of this species agrees more closely with grasping abilities instead of digging specializations, based on several osteological characters. One of the most remarkable traits of *Lyncodon* is the notable low value for the metacarpal/first phalanx length ratio (1.32, measured for digit III), a condition very different from *Galictis* spp. (*G. cuja* = 1.60; *G. vittata* = 1.67—Ercoli 2015), and being the lowest value for Musteloidea (Table 1). This feature, in combination with the markedly gracile autopodial elements (i.e., shaping a slender autopodium) and the particular myological features discussed above, among others traits discussed by Ercoli (2015), distinguishes *Lyncodon* from *Galictis* spp. Furthermore, these features are unexpected in a specialized powerful digger (Ercoli 2015), as has been discussed for other taxa (Yalden 1970; Quaife 1978; Salton and Sargis 2008; Morgan and Verzi 2011). The only scratch-digger musteloid with a relatively low value for this ratio is *Taxidea taxus* (1.41; Table 1), a species that combines digging specialization with the ability to grasp prey (see Quaife 1978). However, *T. taxus* bears extremely robust forepaw elements and a scoop-like manus (Quaife 1978), which are common features of digging mammals conspicuously absent in *L. patagonicus*. Thus, although the *Lyncodon* morphology leaves open the possibility that the species could dig in loose soil, it seems mismatched with possibility of powerful excavation. Conversely, the features of *Lyncodon* agree more closely with a refined ability to grasp either prey or substrate (i.e., locomotion over slender branches—Van Valkenburgh 1987; Hildebrand 1988; Taylor 1989; Iwaniuk et al. 1999), and only the former option seems credible in relation to what we know about the natural history of the Patagonian weasel (Ercoli 2015).

Future studies are needed to confirm the presence of the mm. flexores digitorum proprii manus as a common feature

of *L. patagonicus*. It is reasonable to think that these muscles, together with the other myological and osteological modifications discussed, could represent an adaptation of the forepaw for fine digital control and for firmly grasping prey. Hunting behavior data from future ecological studies of the Patagonian weasel are needed to support this inference.

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## APPENDIX I

Musteloid specimens measured for the calculation of the ratio between the length of the metacarpal III and the length of the proximal phalanx of the third digit (McIII/PhIII).

*Lyncodon patagonicus*: MACNMa 21982, MLP 6.III.36.32. *Mustela erminea*: FMNH 122025, 122630. *Mustela frenata*: FMNH 25626, 25625, 49372. *Mustela nigripes*: FMNH 25621, 25622. *Mustela nivalis*: FMNH 129331. *Mustela vison*: FMNH 135301, 122031. *Poecilogale albinucha*: FMNH 36045, 149354. *Ictonyx striatus*: FMNH 177232, 177231. *Martes americana*: FMNH 72956, 151035. *Martes pennanti*: FMNH 165360, 153812. *Galictis vittata*: FMNH 127293, 123657. *Mellivora capensis*: FMNH 43298.