# The Functional and Phylogenetic Implications of the Myology of the Lumbar Region, Tail, and Hind Limbs of the Lesser Grison (Galictis cuja)

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## JOURNAL OF MAMMALIAN EVOLUTION

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ORIGINAL PAPER

# The Functional and Phylogenetic Implications of the Myology of the Lumbar Region, Tail, and Hind Limbs of the Lesser Grison (*Galictis cuja*)

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**Abstract** Mustelids are a morphofunctionally diversified group. However, there are no descriptions of the postcranial musculature of South American mustelid species except for some comments from the 19th century. Here, we present the first description of the myology of the hind limbs, and lumbar, sacral, and caudal regions of the lesser grison (*Galictis cuja*), a short-legged South American mustelid, including muscle maps and weight data. We interpret the function and the evolution of several muscular features within a comparative framework and through the optimization of these traits onto a phylogeny. The configuration of the axial musculature (e.g., m. quadratus lumborum with short bundles, heavy iliocostalis, and forward originated sacrocaudalis dorsalis) and the presence of strong ankle musculature are features shared with mustelines and, to a lesser degree, with other musteloids. These could be related to a high mobility of the axial skeleton and strong control of the movement of the ankle joint, in relation to the acquisition of epigean bounding gaits, a crouched locomotion, and enhanced maneuverability inside burrows. We recorded many phylogenetically significant traits, shared with other arctoids (e.g., subdivision of m. gluteus profundus and semimembranosus, presence of a single belly for m. sartorius, and absence of articularis coxae) or exclusively musteloids (e.g., frequent fusion between m. piriformis and gluteus medius). Some features (e.g., restricted origin of the caudal belly of the m. semitendinosus, absence of gluteofemoralis, and unusually complex fibularis brevis) seem to be derived conditions acquired in some mustelid clades. Our results sustain the value of myological data for functional and phylogenetic studies.

**Keywords** *Galictis* · Hind limb · Lumbar region · Mustelidae · Myology · Tail

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## Introduction

The study of the myology and osteology of the mammalian postcranium is relevant in many ways. For example, morphofunctional interpretation allows a better understanding of specific functions and alternative movements related to different locomotor modes and other motor activities (e.g., digging and object manipulation) performed by an individual in its natural environment (Gambaryan 1974; Leach 1977; Hildebrand 1988). Additionally, muscular and osteological anatomy have been considered as potential sources of phylogenetic information (e.g., Windle and Parsons 1897, 1898; Parsons 1898; Fisher et al. 2008, 2009).

Among carnivorans, many myological studies of canids and felids are available in the literature, especially for the domestic dog and cat (e.g., Evans 1993; Williams et al. 2008a, b; Evans and de Lahunta 2010; Hudson et al. 2010,

2011). On the other hand, only a few studies document the myology of other carnivoran families (e.g., Macalister 1873a, b; Davis 1964; Taylor 1974, 1976; Leach 1977; McClearn 1985; Fisher et al. 2008, 2009), which are really diverse in their locomotor adaptations. During the last 150 years, only a few publications have dealt with certain details of the postcranial musculature of some mustelid species (Table 1), most of these focusing primarily on limbs. In addition, a few taxonomically broad comparative studies afforded sparse data about some other mustelid species (e.g., *Gulo gulo*, *Galictis vittata*, *Ictonyx libyca*, *Ictonyx striatus*, *Martes pennanti*, *Mellivora capensis*, *Mustela nivalis*, *Mustela eversmanni*, *Vormela peregusna*; e.g., Meckel 1828; Windle 1889; Windle and

**Table 1** The sources of myological data for the Family Mustelidae. Numbers in parenthesis indicate the specimens examined in the original works, if known. (*) indicates that the reference corresponds to a revision of previous works, and does not include new specimens

| Species | Sources |
| --- | --- |
| **Helictidinae** | |
| *Melogale personata* | Beddard 1905 (1) |
| **Lutrinae** | |
| *Aonyx cinerea* | Macalister 1873a (1); Windle and Parsons 1898 (*); Souteyrand-Boulenger 1969 (1) |
| *Enhydra lutris* | Gambaryan and Karapetjan 1961 (1); Gambaryan 1974 (1); Howard 1975 (1) |
| *Lontra canadensis* | Fisher 1942 (1); Tarasoff 1972 (*) |
| *Lutra lutra* | Cuvier and Laurillard 1849 (1); Haughton 1867c (1); Lucae 1875 (1); Windle and Parsons 1898 (1); Slijper 1946 (1); Gambaryan and Karapetjan 1961 (2–5); Souteyrand-Boulenger 1969 (1); Gambaryan 1974 (3) |
| **Gulolinae** | |
| *Eira barbara* | Macalister 1873b (1); Windle and Parsons 1898 (*); Souteyrand-Boulenger 1969 (1) |
| *Martes americana* | Hall 1926 (1) |
| *Martes foina* | Cuvier and Laurillard 1849 (1); Mackintosh 1875 (1); Windle and Parsons 1898 (*); Gambaryan and Karapetjan 1961 (2–5); Gambaryan 1974 (2) |
| **Melinae** | |
| *Meles meles* | Cuvier and Laurillard 1849 (1); Haughton 1867b (1); Windle and Parsons 1898 (1); Gambaryan and Karapetjan 1961 (2–5); Souteyrand-Boulenger 1969 (1); Gambaryan 1974 (6); Scherling 1989 (6) |
| **Mustelinae** | |
| *Mustela nigripes* | Bisaillon 1976 (2) |
| *Mustela putorius* | Alix 1876; Windle and Parsons 1898 (*); Slijper 1946 (1); Gambaryan 1974 (1); Evans and Quoc An 1980; Moritz et al. 2007 (1) |
| *Mustela vison* | Williams 1955 |
| **Taxidiinae** | |
| *Taxidea taxus* | Hall 1927 (1) |

Parsons 1897, 1898; Slijper 1946; Gambaryan and Karapetjan 1961; Pierard 1965; Souteyrand-Boulenger 1969; Gambaryan 1974; Feeney 1999).

In relation to the use of substrates, mustelids belong to a diverse group that includes species that are frequent climbers (e.g., *Martes*, *Eira*), primarily terrestrial (e.g., *Gulo*), semifossorial diggers (e.g., *Meles*, *Taxidea*), semifossorial non-diggers (e.g., *Mustela*), and aquatic or semiaquatic species (e.g., *Lontra*, *Enhydra*). They are also diverse in mode of locomotion, including trot, gallop, half-bound, and bound among their gaits (Simpson 1945; Tarasoff et al. 1972; Ewer 1973; Gambaryan 1974; Holmes 1980; Van Valkenburgh 1987; Schutz and Guralnick 2007; Horner and Biknevicius 2010). It has been proposed that differences in locomotor styles correspond closely with phylogenetic relationships among species (Simpson 1945; Holmes 1980; Schutz and Guralnick 2007). Also, a number of muscular characters has been considered informative on phylogenetic grounds (e.g., Windle and Parsons 1897, 1898; Fisher et al. 2008, 2009; Julik et al. 2012).

There are no myological anatomical descriptions of the postcranium of South American mustelid species aside from three studies from the ends of the 19th century, which include partial descriptions of specimens of *Eira barbara* and *Galictis vittata* (Macalister 1873b; Windle and Parsons 1897, 1898). In their work, Windle and Parsons (1897, 1898) only mentioned limited comments about *Galictis vittata* and two additional species of the Ictonychinae subfamily (*Ictonyx lybica* and *Ictonyx striatus*), which is at present the only information available for this subfamily.

The lesser grison (*Galictis cuja*) is a mid-sized mustelid (1–2.5 kg; Wilson and Mittermeier 2009). Its range extends through southern South America in Argentina, Chile, Bolivia, Brazil, Paraguay, and Uruguay (Wilson and Mittermeier 2009). It occurs in a variety of habitats, from rainforests to grasslands (Yensen and Tarifa 2003). Primarily carnivorous, lesser grisons prey mostly on rodents, rabbits, birds, reptiles, and amphibians, and secondarily on eggs, fruit, and invertebrates; they are able to track, pursue, scratch, and get into their prey's tunnels to hunt them (Azara 1802; Yensen and Tarifa 2003; Wilson and Mittermeier 2009). Lesser grisons are also able to swim and dig their own burrows, but they are not specialized diggers and do not climb trees (Cabrera and Yepes 1940; Yensen and Tarifa 2003; Wilson and Mittermeier 2009). The locomotor abilities of this species are poorly documented; it has been described as presenting a slow ambulatory gait without a floating phase (Schutz and Guralnick 2007), using walking and trotting (Yensen and Tarifa 2003), although it is also able to run using asymmetrical steps (Dücker 1968) as has been noted for its sister taxa *G. vittata* (Yensen and Tarifa 2003).

The principal goal of this study is to present a detailed myological description of the lumbar and caudal regions and the hind limb of the lesser grison. Obtained data are

interpreted within a comparative, functional, and phylogenetic framework. Our goal is that these new data, together with previously published dissections, will highlight future ecomorphological studies among mustelids, but also will become a new source of characters that help elucidate phylogenetic relationships among fossil and living mustelids.

## Materials and Methods

We studied myological and osteological material of *G. cuja* from the following Argentinean collections: Colección Félix de Azara, Universidad de Maimónides, Buenos Aires (CFA-Ma); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN-Ma); and Museo de La Plata, Buenos Aires (MLP).

The first specimen was an adult male (field number MASTO 92, MACN-Ma) preserved with skin, from kilometer 96 of provincial road 2 near the Samborombón River, Buenos Aires province, Argentina. The total length was 720 mm. This specimen was fixed in a solution of one part of formalin to 18 parts water saturated with NaCl (Woods 1972; see also García-Esponda and Candela 2010) for a week; later it was stored in 70 % ethanol.

The second specimen (MACN-Ma 28.163) was an adult female preserved with no skin and without most distal phalanges, possibly from Jujuy province, Argentina. The total length was 450 mm. The third specimen (MACN-Ma 39.207) was an adult male preserved with damaged lumbar region from Bialet Massé, Punilla Department, Córdoba province, Argentina. The total length of this last specimen was 750 mm. Both specimens were originally fixed in a formalin solution (exact solution is not known), and subsequently stored in 70 % ethanol. Additional observations came from a fourth specimen (CFA-Ma 12837) from General Lavalle, Buenos Aires. We used the following wild-caught specimens: MACN-Ma 23519; MLP 12.V.97.42, 25.IV.01.1, and 674 as osteological references.

Number of vertebrae observed in the lesser grison specimens was: five lumbar (L1 - L5), three sacral (S1 - S3), and typically 21 caudal (C1 - C21) vertebrae. Specimen 1 presents only four lumbar vertebrae and 16 rather than the usual 15 thoracic vertebrae.

For the first three specimens, we weighed the dry mass of each muscle (Supporting Information Table S1). We recorded the principal intraspecific variations (Supporting Information Table S2). During myological description and discussion, we primarily followed Hall (1926, 1927), Evans (1993), and Fisher et al. (2008) and, secondly, other anatomical studies mentioned whenever required. Anatomical terminology follows the Nomina Anatomica Veterinaria (Waibl et al. 2005). We followed the subfamilial taxonomy as presented by Koepfli et al. (2008) and Sato et al. (2012).

Several muscular characters (characters and states definitions in Fig. S1) were mapped onto a phylogeny using the TNT software (Goloboff et al. 2008) to explore their evolution and to obtain ancestral states reconstructions. Character states were considered as ordered, except characters B, C, I, J, L, and Q (Fig. S1). A composite phylogeny was assembled from several sources (Flynn et al. 2005; Koepfli et al. 2007, 2008).

## Results

### Weighing

Muscle weights for each specimen are presented in the Supporting Information Table S1. The percentage values relative to the total mass of the hind limb in *G. cuja* are presented in Table 2. Figure 1 illustrates the muscle mass distribution of *G. cuja* in comparison with other carnivorans.

The dry mass of the muscles of specimens 1 and 3 (male specimens) were typically three times greater than the masses of specimen 2 (female specimen). However, mass percentage values of each muscle relative to the total hind limb weight were similar in most cases. Beyond this, there were marked differences in some muscles between the two male specimens and the female one, such as those observed for the m. iliocostalis lumborum, mm. gemelli, and m. tibialis caudalis (Supporting Information Table S1). Regarding the m. iliocostalis lumborum, specimen 1 (male) possesses a dry mass of this muscle relativized to the leg weight of about 15 %, twice that of specimen 2 (female). The relativized dry mass of mm. gemelli was very variable between legs of the same and among specimens. In the case of m. tibialis caudalis, the female specimen possesses a dry mass of this muscle relativized to the leg weight of 0.77 %, approximately twice the values presented by the male specimens. The curve of mass distribution of hind limbs of *G. cuja* is very similar to some other weasel-like mustelids such as *Mustela*, *Martes*, and *Vormela*, genera that use bounding gaits, but it is different from cursorial (e.g., *Acinonyx*, *Canis*), semi-aquatic (e.g., *Enhydra*, and to a lesser degree *Lutra*), and ambulatory carnivorans (e.g., *Gulo*, *Mellivora*, *Ursus*). *Galictis cuja* presents a weak development of adductors and weak extensors of the hip joint, a moderate to weak development of the extensors of the knee joint, and strong development of heavy extensors of the hip and the ankle, and flexors of the digits (Fig. 1).

### Epaxial Muscles

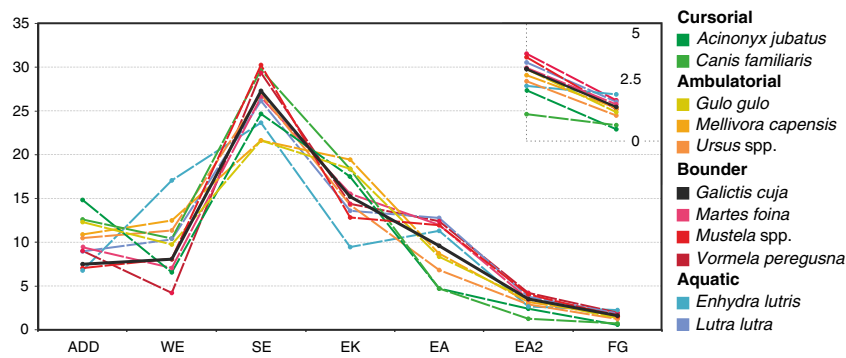#### M. iliocostalis lumborum (Figs. 2a,b, 3 and 4a,c)

This muscle is the lateralmost of the lumbar epaxial muscles. It is robust and has a cylindrical shape; its fibers

**Table 2** Percentage dry mass of each muscle of the hind limb, lumbar region, and tail of *Galictis cuja*, relative to the total muscle mass of the hind limb. Values represent the average percent values of the three specimens analyzed

| Muscles | Mass (%) | Muscles | Mass (%) |
|---|---|---|---|
| *Epaxial* | | Rectus femoris | 6.21 |
| Iliocostalis lumborum | 10.06 | Vastus lateralis | 7.09 |
| Transversospinalis, lumbar sector | 3.33 | Vastus medialis | 1.87 |
| Interspinales (L2-3) | 0.04 | Vastus intermedius | 0.79 |
| Interspinales (L3-4) | 0.08 | Gracilis | 4.22 |
| Intertransversarii lumborum (L4-5) | 0.02 | Pectineus | 0.68 |
| *Tail* | | Adductor longus (proximal) | 0.29 |
| Coccygeus | 0.55 | Adductor longus (distal) | 1.70 |
| Sacrocaudalis ventralis medialis | 1.32 | Adductor brevis | 1.30 |
| Sacrocaudalis ventralis lateralis | 1.92 | Adductor magnus | 2.64 |
| Sacrocaudalis dorsalis medialis | 1.80 | Obturator externus | 0.91 |
| Sacrocaudalis dorsalis lateralis | 6.81 | *Leg* | |
| Intertransversarii ventrales caudae | 0.78 | Gastrocnemius (lateral) | 2.85 |
| Intertransversarii dorsales caudae | 1.79 | Gastrocnemius (medial) | 3.91 |
| *Rectum and urogenital* | | Soleus | 0.95 |
| Levator ani | 0.59 | Flexor digitorum superficialis | 2.84 |
| Pubocaudalis | 0.48 | Popliteus | 0.69 |
| Iliocaudalis | 0.62 | Flexor digitorum lateralis | 2.31 |
| Ischiocavernosus | 0.26 | Flexor digitorum medialis | 0.61 |
| Bulbospongiosus (pair) | 0.76 | Tibialis caudalis | 0.55 |
| Rectococcygeus | 0.08 | Fibularis longus | 0.58 |
| *Sublumbar* | | Fibularis brevis | 0.70 |
| Psoas minor | 0.77 | Extensor digitorum lateralis | 0.34 |
| Iliopsoas | 4.05 | Tibialis cranialis | 2.49 |
| Quadratus lumborum | 2.36 | Extensor digiti I longus | 0.28 |
| *Thigh* | | Extensor digitorum longus | 1.53 |
| Gluteus superficialis | 2.29 | *Foot* | |
| Gluteus medius | 4.47 | Extensor digitorum brevis | 0.41 |
| Piriformis | 0.63 | Abductor digiti V | 0.05 |
| Gluteus profundus | 0.70 | Flexor digitorum brevis | 0.59 |
| Gemelli | 0.26 | Interflexores | 0.06 |
| Obturator internus | 0.46 | Quadratus plantae | 0.21 |
| Biceps femoris | 12.42 | Lumbricales | 0.13 |
| Abductor cruris caudalis | 0.72 | Adductores digitorum | 0.10 |
| Semitendinosus | 3.66 | Flexor breves profundi (I) | 0.13 |
| Semimembranosus (femoral) | 5.50 | Flexor breves profundi (II) | 0.15 |
| Semimembranosus (tibial) | 5.29 | Flexor breves profundi (III) | 0.22 |
| Sartorius | 5.50 | Flexor breves profundi (IV) | 0.22 |
| Tensor fasciae latae | 1.81 | Flexor breves profundi (V) | 0.27 |
| Quadratus femoris | 0.61 | | |

run superficially in lateral and cranial directions from the caudal and medial region (Fig. 2a,b). Cranially, it continues as the m. iliocostalis thoracis, sharing with it a great number of fibers, especially in the superficial aspect. About the L1-2 vertebrae, the m. iliocostalis lumborum is partially covered by a group of fleshy fibers, corresponding to the m. longissimus thoracis, that continue as a superficial fascia in a

caudal direction up to the ilium. This muscle originates mostly through fleshy fibers from the medial surface of the ala ossis ilii (wing of the ilium) and the iliac crest, and via tendinous fibers from the medial aspect of the lumbodorsal fascia. Some of the fibers originate from the body of the last lumbar vertebra, just caudal to its transverse processes. It inserts via a tendinous sheet onto

**Fig. 1** Comparative curves of percent mass relative to the total hind limb mass of principal muscular group in some carnivorans with different locomotor habits. ADD, adductor mass of hip including m. pectineus; WE, weak extensor of the hip (gluteal group including m. piriformis); SE, strong extensor of hip (hamstring group); EK, extensor of the knee (m. quadriceps); EA, principal extensors of the ankle (m. gastrocnemius and m. flexor digitorum superficialis); EA2, other extensor of the ankle (m. flexor digitorum medialis, m. flexor digitorum lateralis, and m. tibialis caudalis); FG, fibular group (m. fibularis longus, m. fibularis brevis and m. extensor digitorum lateralis). Data compiled from Gambaryan (1974), Hudson et al. (2010), and this work (data for *Galictis cuja*)

the caudal edge of the last two ribs, on its angle and dorsal regions. Some of the fibers reach the lateral and caudal aspects of the body of the last thoracic vertebra. This muscle also inserts through numerous fleshy and tendinous fibers on the dorsal surfaces of the transverse processes of the last lumbar vertebra. On other lumbar vertebrae, these insertions are found exclusively at the base and posterolateral ends of the transverse processes, and onto the ventral region of the accessory processes (Fig. 3a).

*M. transversospinalis, lumbar region (Figs. 2a,b and 3b,c)*

It is the most medial series among the epaxial muscles in the thoracolumbar region. It is composed of metameres mostly fused among them and with its thoracic continuation. It corresponds to the cranial continuation of the m. sacrocaudalis dorsalis medialis. It originates through principally fleshy fibers from the lateral surface of the spinous processes and the dorsal surface of the articular processes of all lumbar vertebrae, except the last one (Fig. 3b,c). Also, some fibers originate from the lumbodorsal fascia. The insertion is via fleshy fibers on the mammillary processes of all lumbar vertebrae. The last bundle inserts onto the dorsal area of the intermediate sacral crest of S1-2.

*Mm. interspinales (Fig. 3b,c)*

These muscles are composed of small, sheet-like bellies that are almost indistinguishable from the transversospinalis system, better defined on the caudal end of the lumbar region. They are composed mostly of fleshy fibers that lie on the sides of a tendinous fascia that connects the spinous processes of contiguous vertebrae. The origins and insertions of these muscles are via fleshy and tendinous fibers at the caudal and cranial edges of the spinous processes of contiguous lumbar vertebrae, respectively.

*Mm. intertransversarii lumborum (Fig. 3b,c)*

These are sheet-like muscles that partially differentiate from the m. iliocostalis lumborum. There are some fusing points with the m. quadratus lumborum. Their origins and insertions are through fleshy fibers along the cranial and caudal margin of the transverse processes of adjacent lumbar vertebrae, respectively.
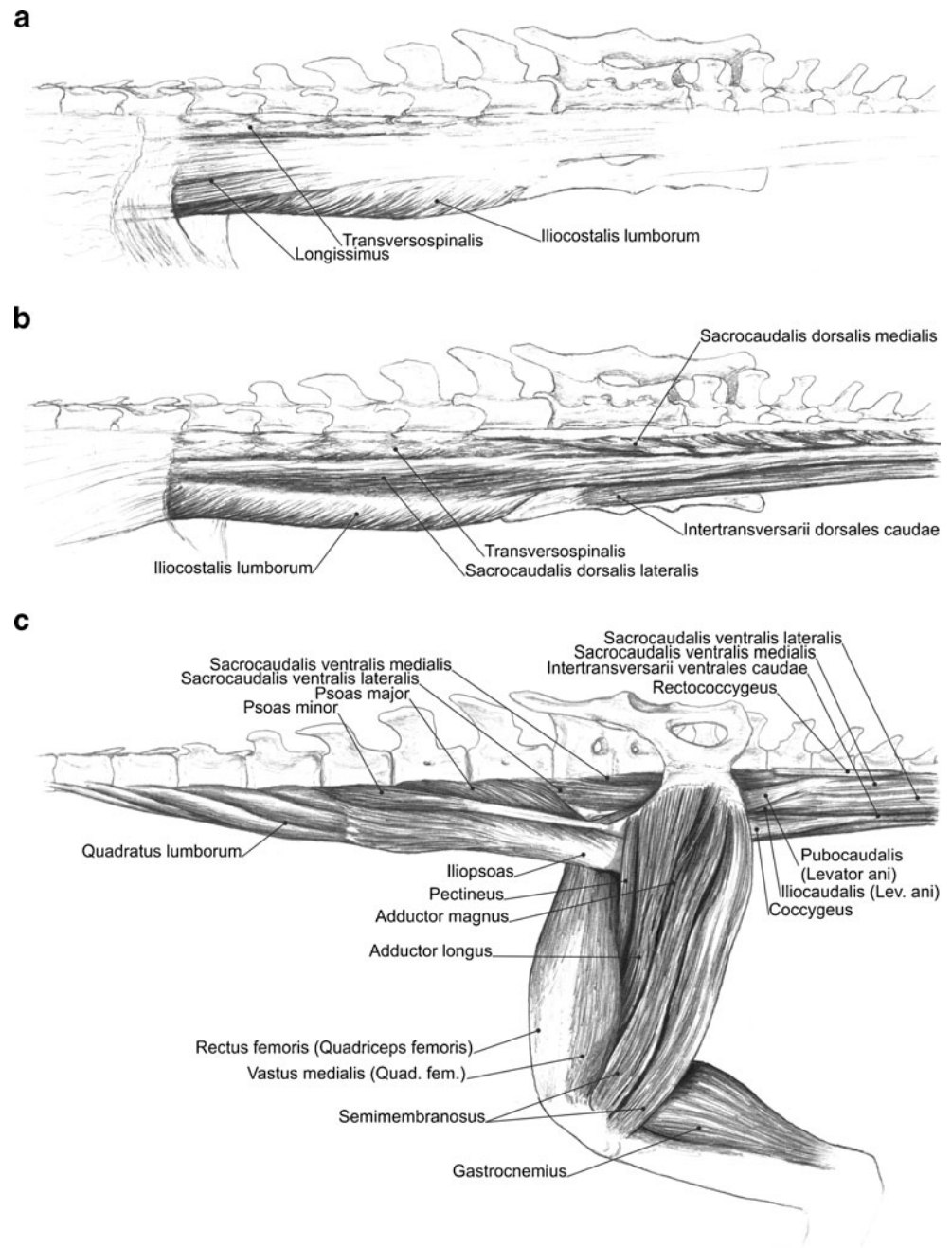
Muscles of the Tail

*M. coccygeus (Figs. 2c, 3a, 4b,c, 5b and 6a)*

This flattened, fan-shaped muscle lies between the mm. intertransversarii dorsales caudae and the m. sacrocaudalis ventralis lateralis. It originates via fleshy fibers from the ischial spine (Fig. 4b,c). It inserts mostly via fleshy fibers, onto the ventral surface of the transverse processes of C2-4, and some fibers reach the caudal end of C1 (Fig. 3a). In the caudal region of insertion, this muscle shares some tendinous fibers with the mm. intertransversarii dorsales caudae.

*M. sacrocaudalis ventralis medialis (Figs. 2c and 3a)*

It is an elongated and thin muscle composed of multiple differentiable metameres. It runs parallel and medial to the m. sacrocaudalis ventralis lateralis and partially fuses with it. In the sacral region, both right and left counterparts do not contact thus leaving a space free of insertion at the midline (Fig. 3a). The first metameres originate mostly via fleshy fibers, while the last ones originate via

**Fig. 2** Axial musculature of *Galictis cuja* in dorsal view before (**a**) and after (**b**) removing m. longissimus and fascias. Axial musculature in ventral view and hind limb musculature in medial view (**c**)



tendinous fibers. They arise from the ventral aspect of the sacral and caudal vertebral bodies. The first bundle originates on the ventral surface of S1. In the cases in which it could be defined (two cases), the remaining metameres originate from C1, C3-4, and C7. Each bundle inserts onto caudal bundles and the ventral midline of every caudal vertebrae.
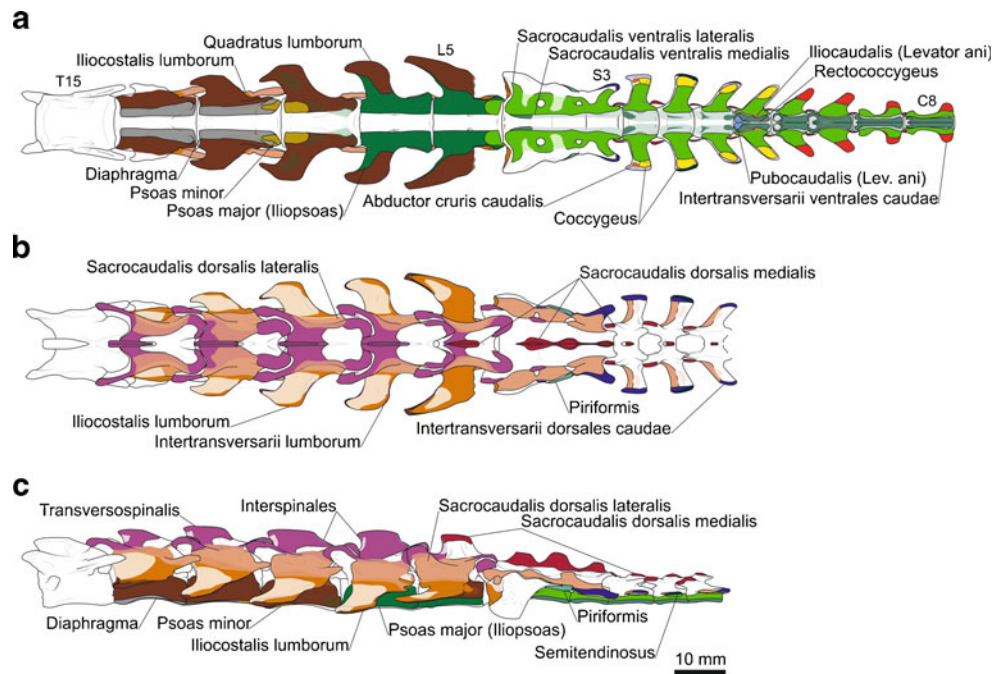
*M. sacrocaudalis ventralis lateralis (Figs. 2c and 3a,c)*

It is robust and cylindrical, and it consists of multiple bundles strongly fused together. The fibers of each bundle

run in ventral and medial directions, generating a series of flattened tendons that run craniocaudally and mediolaterally, and are covered by the lateral surface of the m. sacrocaudalis ventralis medialis, to which this muscle partially fuses. It originates via fleshy fibers, from the caudoventral aspect of the last lumbar vertebra, the ventral surface of the sacrum and its transverse processes, and from the ventral surface of the transverse processes of the caudal vertebrae. The last well differentiable area of origin was recorded on C10. It inserts via elongated tendons that gradually accumulate and become thinner to finally fuse with more caudal bundles in the medial zone.
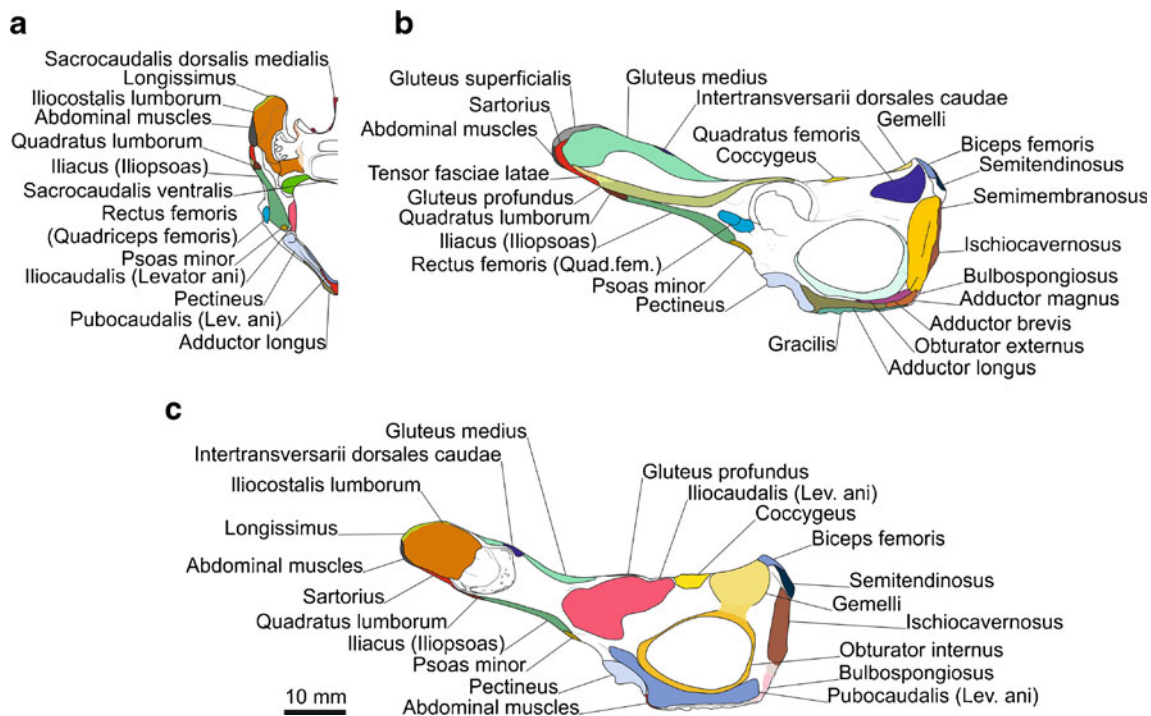
**Fig. 3** Muscular maps of *Galictis cuja*: ventral (**a**), dorsal (**b**), and lateral (**c**) views of axial regions
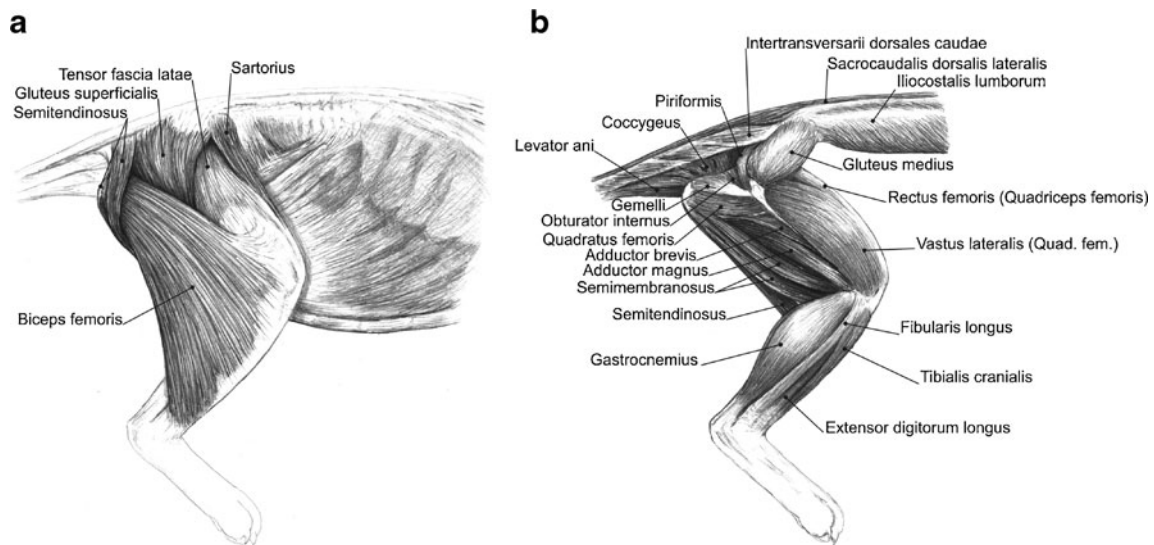
*M. sacrocaudalis dorsalis medialis (Figs. 2b, 3b,c and 4a)*

This muscle represents the caudal continuation of the transversospinalis system. It is elongated and consists of multiple bundles. Each bundle presents fibers that run in caudal and lateral direction, covering approximately three vertebrae between their origin and insertion. The most cranial bundle originates, mostly via tendinous fibers, from the caudal and dorsal aspect of the spinal process of the last lumbar vertebra. Subsequent bundles originate from the spinal processes of the sacral and caudal vertebrae (Fig. 3b,c). It inserts onto the cranial ends of the anterior articular processes of caudal vertebrae. Also, bundles can insert on the mammillary processes if they are present.

**Fig. 4** Muscular maps of *Galictis cuja*: cranial (**a**), lateral (**b**), and medial (**c**) views of the pelvis
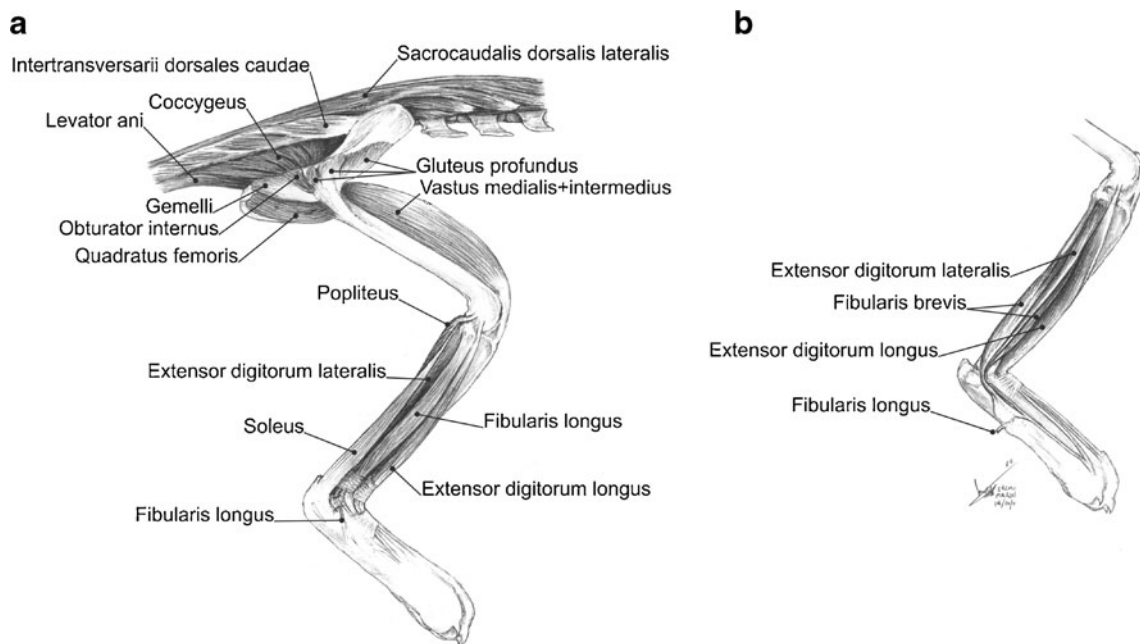
**Fig. 5** Hind limb of *Galictis cuja* in lateral view: superficial (**a**) and intermediate (**b**) musculature

*M. sacrocaudalis dorsalis lateralis (Figs. 2b and 3b,c)*

It is a metameric and flattened muscle located between the m. iliocostalis lumborum and the lumbar muscles of the transversospinalis system. The m. sacrocaudalis dorsalis lateralis can be interpreted as the caudal continuation of the longissimus system. Muscular bundles are elongated and fusiform, and interweaved among each other; each bundle covers five vertebrae. In the caudal lumbar and sacral regions, bundles can be clearly differentiated from the transversospinalis system, from which is separated by a fascia. As it runs caudally, the section of this muscle diminishes continuously, and becomes fully tendinous after the

proximal third of the tail. The first principal bundle originates via a few tendinous fibers from the fascia that covers the thoracic region and via fleshy fibers from the lateral surface of the transversospinalis system, at the level of the last thoracic vertebra. Principal muscular bundles of the lumbar region are progressively more robust towards the caudal region, and originate via tendinous and fleshy fibers from the accessory processes of all lumbar vertebrae and the lateral aspect of the last one (Fig. 3b,c). Some minor bundles originate on the caudolateral aspect of the body of the lumbar vertebrae. Another main muscular bundle originates on the whole dorsal surface of the sacral lateral crest; meanwhile, the remaining smaller bundles, originate in the



**Fig. 6** Hind limb of *Galicitis cuja* in lateral view: deep musculature (**a**, **b**)

anterior area of the transverse and anterior articular processes of the caudal vertebrae. The last distinguishable origin was recorded at C7. These bundles insert via a common tendon that runs over the dorsal aspect of the tail, overlying the transverse processes of the caudal vertebrae to which some fibers attach. Additionally, there are tendinous attachments onto the anterior articular processes and the craniodorsal aspect of the caudal vertebrae.

*Mm. intertransversarii ventrales caudae (Figs. 2c and 3a)*

It is an elongated muscular band composed of a few fused bundles. These small muscles are shorter than the mm. intertransversarii dorsales caudae. They can be interpreted as a caudal continuation of the m. coccygeus (Fig. 2c), and are partially fused with the mm. intertransversarii dorsales caudae. In most cases (five hind limbs) this muscular band presents two bundles located between the m. coccygeus and the seventh or the eighth caudal vertebra. This muscle originates via tendinous and fleshy fibers, from the ventrolateral ends of the transverse processes of C5-7. This muscle originates also via fleshy fibers from the caudal end of the m. coccygeus. It typically inserts via tendinous and fleshy fibers onto the ventrolateral end of the transverse processes of C6-8.

*Mm. intertransversarii dorsales caudae (Figs. 2b and 3b)*

This muscle is located lateral to the m. sacrocaudalis dorsalis lateralis. It presents a tubular shape and it becomes progressively tendinous towards the caudal region. It originates via fleshy and tendinous fibers, from the caudal dorsal iliac spine and the caudal end of the lateral sacral crest (Fig. 3b), and from the dorsal sacroiliac ligament. From C3, a metameric pattern for the attachments is observed onto the lateral ends of the transverse processes of those vertebrae. It inserts mostly via tendinous fibers onto the lateral aspects of the transverse processes from C1 to C13 or C14.

Some Muscles of the Urogenital System and Rectus

*M. levator ani (Figs. 2c, 4a,c, 5b and 6a)*

It consists of two muscular groups (m. pubocaudalis and m. iliocaudalis). It presents an inverted fan-shape and it lies medial to the m. coccygeus.

*M. pubocaudalis (Figs. 2c, 3a and 4a,c)*

It is a fan-shaped and flattened muscle that lies medial to the m. iliocaudalis with which it shares tendinous fibers near its insertion. At the end of its trajectory, it becomes a flattened tendon located medial to the mm. sacrocaudalis ventralis. This muscle originates via fleshy fibers from the internal surfaces of the cranial and caudal ramus of the pubis (Fig. 4a,c). It inserts via tendinous fibers onto the cranial and lateral aspects of C4 (Fig. 3a).

*M. iliocaudalis (Figs. 2c, 3a and 4a,c)*

It is flattened and fan-shaped muscle that is located medial to the m. coccygeus. Near its insertion it becomes tendinous and shares fibers with the m. pubocaudalis. It originates via fleshy fibers, from the internal surface of the acetabulum and the ventral margin of the ilium (Fig. 4a,c). It inserts via tendinous fibers and a flat fascia onto the mm. sacrocaudalis ventralis lateralis at the level of C4 (Fig. 3a) and, in some cases, some fibers reach C3 or C5. Only a few fibers have a bony attachment at these vertebrae.

*M. ischiocavernosus (Fig. 4b,c)*

This short, spindle-shaped muscle originates, via fleshy fibers, from the caudal margin of both ischium and pubis (Fig. 4b,c). It inserts onto the base of the urogenital protuberance.

*M. bulbospongiosus (Fig. 4b,c)*

It is a small muscle; counterparts are strongly fused on the sagittal plane. It originates via a large number of tendinous fibers, from the caudal area of the internal surface of the pelvic symphysis (Fig. 4b,c) and from adjacent muscles and tissues including the ventral surface of C1. It inserts onto the ventral and proximal area of the penis.

*M. retractor penis*

This muscle is absent in the lesser grison.

*M. rectococcygeus (Figs. 2c and 3a)*

This elongated muscle runs medial and ventral between the anus and the proximal end of the tail. It is located between the left and right mm. pubocaudalis and caudal to them. It originates via fleshy fibers from the rectum. It inserts via weak and few tendinous fibers, onto the medial aspect of C4-C6 (Fig. 3a).

Sublumbar Muscles

*M. psoas minor (Figs. 3a,c and 4)*

This muscle lies superficial to the m. iliopsoas. It is slender and flattened; it becomes tendinous at about half of its

**Fig. 7** Muscular maps of *Galictis cuja*: caudal (**a**), medial (**b**), cranial (**c**), and lateral (**d**) views of femur

length. It originates via fleshy and tendinous fibers, on subsequent ventrolateral tubercles of the ventral surface of L2-3 (L1-2 in specimen 1; Fig. 3a,c), sharing fibers with the origin of the diaphragm. This muscle inserts via a tendon onto the ilium, inmediately anteroventral to the acetabulum (Fig. 4).

*M. iliopsoas (Figs. 2c, 3a, 4a,c and 7a)*

This muscle resembles an inverted fan, and is composed of the m. psoas major and the m. iliacus. In ventral view, the origins of the left and right m. psoas major do not contact each other; they are separated by a midline lacking fibers where vertebral bodies can be observed. Near its insertion, the m. psoas major fuses with the m. iliacus and forms the m. iliopsoas. M. psoas major originates mainly via fleshy fibers from the ventrolateral region of vertebral bodies, the ventrolateral tubercles, and the base of the transverse processes of the last two (and some cases three) lumbar vertebrae (Fig. 3a), and on the m. quadratus lumborum at the level of the last three lumbar vertebrae. The m. iliacus originates from the arcuate line and the ventral margin of ilium (Fig. 4a,c). The insertion of m. iliopsoas is mainly via fleshy fibers, onto the lesser trochanter (Fig. 7a), and secondarily onto the femoral neck and the capsule of the hip joint.

*M. quadratus lumborum (Figs. 2c, 3 and 4)*

The m. quadratus lumborum is composed of a series of at least six or seven partially fused fleshy bundles, which run in a caudolateral direction. The series of bundles becomes progressively more robust, independent, fleshy, and short. This muscle originates, with a metameric pattern, along the last four thoracic and all lumbar vertebrae. The first bundles have locally tendinous origins on the ventrolateral tubercles, and through accessory fibers from at least three thoracolumbar vertebrae, and from the ventral margin of the cranial costal foveas. Subsequent metameres originate through fleshy fibers from the whole ventral surface of the vertebral bodies. The first lumbar metamere originates through fleshy fibers from the transverse processes and bodies of L1-3, while each of the two last metameres originates exclusively from transverse processes (Fig. 3). The last bundle is totally independent of the remaining and originates principally through fleshy fibers from the ventral surface of the transverse processes of the last one or two lumbar vertebrae. The insertion is via tendinous and fleshy fibers. The anterior bundles insert onto the anterolateral extremes of the transverse processes of the posterior lumbar vertebrae and onto posterior bundles. The last bundle is the only one that insert directly onto the caudal ventral iliac spine (Fig. 4).

Musculature of the Thigh

*M. gluteus superficialis (Figs. 4b, 5a and 7d)*

This muscle lies on the anteroproximal region of the thigh (Fig. 5a). It is a pennate and inverted fan-shaped muscle, with a more developed caudal portion. In three hind limbs, the caudal portion of the m. gluteus superficialis tends to divide into one or more bellies (see m. gluteofemoralis). It originates via an aponeurosis from the iliac crest (Fig. 4b) and via fleshy and tendinous fibers from the sacrocaudal aponeurosis, covering the first and second caudal vertebrae. It inserts, mainly via fleshy fibers, onto the lateral aspects of the greater trochanter (Fig. 7d) and onto the the insertion of the mm. gluteus medius and tensor fasciae latae.

*M. gluteofemoralis (m. caudofemoralis)*

This muscle is absent. The subdivision of the caudal portion of the m. gluteus superficialis observed in three hind limbs could be a remnant of this muscle.

*M. gluteus medius (Figs. 4b,c, 5b and 7a,d)*

It presents an inverted cone-like morphology. This muscle can be found fused with the m. piriformis to some degree. This muscle originates through fleshy fibers, from the dorsolateral surface of the body and wing of the ilium, including the sacral tubercle (Fig. 4b,c). When it is fused with the m. piriformis, it also originates on the lateral sacral crest. A superficial group of fibers becomes tendinous and reaches the lumbosacral fascia at the level of the sacroiliac joint. The insertion is via both fleshy and tendinous fibers onto the dorsolateral region of the greater trochanter (Fig. 7a,d).

*M. piriformis (Figs. 3, 5b and 7a,d)*

This is a band-like shaped muscle; it sometimes can be fused with the m. gluteus medius. Its origin is via fleshy fibers, from the lateral and ventral aspects of the middle lateral sacral crest (Fig. 3). It inserts mainly through tendinous fibers onto the posterolateral region of the greater trochanter (Fig. 7a,d).

*M. gluteus profundus (Figs. 4b,c, 6a and 7c)*

It presents an inverted cone-morphology. Typically, it presents two bellies (cranial and caudal), but sometimes a third inter-mediate belly is present (Fig. 6a). The cranial belly originates via fleshy fibers from the ilium and the anterodorsal margin of the acetabulum (Fig. 4b,c). The caudal belly originates in a restricted area dorsal to the acetabulum. Some fibers originate from the articular capsule of the hip joint. The insertion is mainly through tendinous fibers onto the dorsal margin of the femoral neck and the dorsomedial region of the greater trochanter (Fig. 7c).

*Mm. gemelli (Figs. 4b,c, 5b, 6a and 7a)*

These short muscles are partially fused at their origins with the m. obturator internus. They originate via fleshy fibers from the cranial, lateral, and dorsal edges of the ischial tuberosity and the body of the ischium (Fig. 4b,c). They insert by tendinous fibers onto the proximal region of the trochanteric fossa (Fig. 7a).

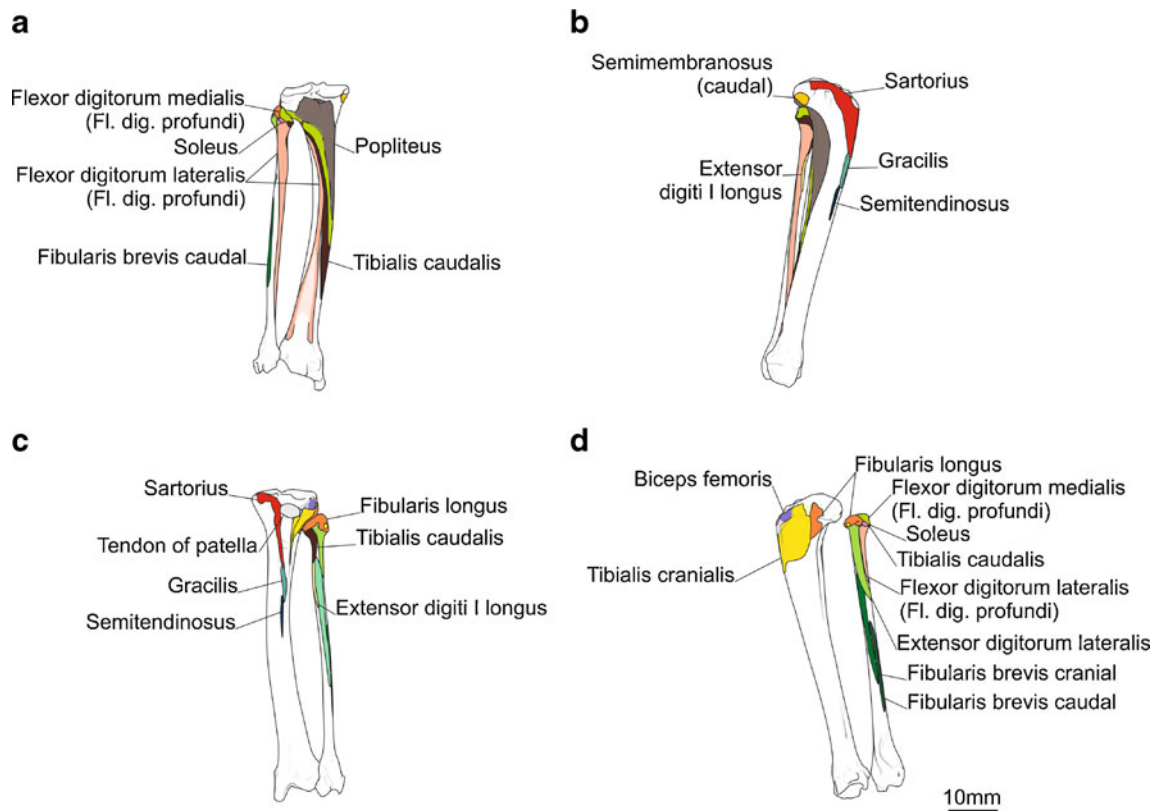*M. obturator internus (Figs. 4c, 5b, 6a and 7a)*

This is an inverted cone-shaped muscle that is frequent-ly partially divided into two bellies near its origin. It originates mainly via fleshy fibers from the medial surface of the obturator foramen (Fig. 4c). This muscle passes and turns over the dorsal margin of the ischium to reach its insertion. The insertion is, via tendinous fibers, onto the proximal region of the trochanteric fossa, near and together with the mm. gemelli and the m. obturator externus (Fig. 7a).

*M. quadratus femoris (Figs. 4b, 5b and 7a)*

It is a thick and short fusiform muscle. It originates via fleshy fibers from the caudal area of the lateral surface of ischium (Fig. 4b). It inserts via fleshy and tendinous fibers onto the caudodistal region of the greater trochanter and the distolateral margin of the trochanteric fossa (Fig. 7a). Some fibers reach the articular capsule of the hip joint.

*M. biceps femoris (Figs. 4b,c, 5a, 7d and 8d)*

The m. biceps femoris is a massive, bilobate, fan-shaped muscle (Fig. 5a) composed of two flat, partially fused bellies. The proximal belly is proximodistally wide, while the distal one is shorter in this direction, but thicker and fleshy. Both bellies present fleshy fibers from their origin until the craniolateral surface of the leg; they continue by means of an aponeurosis that surrounds the cranial and craniomedial region of the leg. The caudal margin of the m. biceps femoris is fused with the m. semitendinosus at its proximal zone. M. biceps femoris originates through a stocky and short tendon and fleshy fibers from a reduced area on the dorsal region of the ischial tuberosity (Fig. 4b,c). Its anterior belly inserts, via an aponeurosis, onto the lateral epicondyle of the femur (sharing fibers with m. vastus lateralis; Fig. 7d), to the proximal two-thirds of the

**Fig. 8** Muscular maps of *Galictis cuja*: caudal (**a**), medial (**b**), cranial (**c**), and lateral (**d**) views of tibia and fibula. Fl. dig. profundi is the abbreviation for flexores digitorum profundi

anterolateral and anteromedial surface of the tibia (Fig. 8d). The distal belly inserts through an aponeurosis on the anteromedial aspect of the distal region of the leg, partially fusing with the m. abductor cruris caudalis. From the fascia that covers the inner surface of m. biceps femoris arises a flat and thin tendon that passes deep to the insertion of the m. abductor cruris caudalis, on the posterolateral surface of the distal leg and inserts on the calcaneus.

*M. abductor cruris caudalis (m. tenuissimus) (Fig. 3a)*

It is a band-like muscle that is located in the lateral and caudal region of the thigh, deep to the m. biceps femoris. Near its insertion, m. abductor cruris caudalis is partially fused with the m. biceps femoris. It originates via tendinous fibers from the bundles of the mm. intertransversarii dorsales caudae, at the level of C1, deep to the m. gluteus maximus. It inserts via tendinous fibers onto the craniomedial surface of the distal region of tibia (Fig. 3a).

*M. semitendinosus (Figs. 3b,c, 4b,c, 5 and 8b,c)*

It is composed of two bellies, fully independent at their origins. Both bellies have a band-like shape and fuse together at their midpoint. The caudal belly originates mainly via fleshy fibers, from the lateral margin of the transverse process of C2 (Fig. 3b,c), and via an aponeurosis from C1 and C3. The ischial belly originates from the ischial tuberosity (Fig. 4b,c). The insertion, via an aponeurosis, is onto the proximodistal line of the central and distal region of the tibia, just distal to the m. gracilis (Fig. 8b,c).

*M. semimembranosus (Figs. 2c, 4b, 5b, 7b and 8b)*

This muscle is partially flattened and is elliptical in its cross-section. It has a single origin, but immediately divides into cranial and caudal bellies (Figs. 2c and 5b). Furthermore, each belly is composed of many partially fused bundles. In three hind limbs, a third group of fibers clearly segregates in an intermediate position. It originates deep to the m. semitendinosus, from the caudal ramus of the ischium (Fig. 4b). The cranial belly (and the intermediate belly if present) inserts via fleshy fibers onto the medial femoral epicondyle, the articular capsule of the knee joint, and the adjacent femoral diaphysis (Fig. 7b). The caudal belly is mostly tendinous and inserts onto the posteroproximal region of the tibia, just below the medial articular condyle (Fig. 8b).

*M. articularis coxae*

This muscle is absent.

*M. sartorius (Figs. 4, 5a, 7b and 8b,c)*

It has a single belly that overlies the anterior and medial aspects of the m. quadriceps femoris. It originates via fleshy and tendinous fibers from the iliac wing (Fig. 4). Some fibers arise from the sacrocaudal aponeurosis, cranial to the m. gluteus superficialis origin. It inserts via an aponeurosis onto the fascia lata, the m. quadriceps femoris, the patella, the medial surface of the cnemial crest, and the fascia cruris, reaching the insertion of the m. gracilis (Figs. 7b and 8b,c).

*M. tensor fasciae latae (Figs. 4b and 5a)*

The m. tensor fasciae latae is a massive muscle. At its origin, it has an elliptical cross-section, but expands and becomes flattened and fan-shaped before continuing as the fascia lata. It originates via tendinous and fleshy fibers from a reduced region of the iliac wing (Fig. 4b). It inserts via the fascia lata onto the gluteus superficialis, the m. biceps femoris, the m. sartorius, and the fascia cruris.

*M. quadriceps femoris (Figs. 2, 3, 4, 5, 6 and 7)*

It is composed of the m. rectus femoris, the m. vastus lateralis, the m. vastus medialis, and the m. vastus intermedius.

*M. rectus femoris (Figs. 2c, 4a,b, 5b and 7c)*

It corresponds to the most cranial belly of the m. quadriceps femoris. It is a bulky, spindle-shaped muscle, circular in cross-section. This muscle originates via tendinous fibers, from the tuberosity for the m. quadriceps femoris (Fig. 4a,b) and from the cranial region of the articular capsule of the hip joint. It inserts via tendinous fibers onto the anterodorsal margin of the patella (Fig. 7c).

*M. vastus lateralis (Figs. 5b and 7c)*

The m. vastus lateralis is subcylindrical in shape, narrowing and flattening toward its insertion. In the last quarter of its length, tendinous fibers begin to dominate. It originates mostly via fleshy fibers, from the cranioproximal end of the femur and from the cranial surface of the femur, medial to the base of the greater trochanter (Fig. 7c). Near its origin it shares fibers with the m. vastus intermedius. It inserts via tendinous fibers onto the lateral margin of the patella and the proximolateral region of the tibia (Fig. 7c), where it fuses

with the insertion of the m. biceps femoris and the fascia cruris.

*M. vastus medialis (Figs. 2c, 6a and 7c)*

It is an elongated and subcylindrical muscle that narrows toward its insertion. This muscle is fused with the m. vastus intermedius in some degree. It originates through fleshy fibers, from the craniomedial margin of the femoral neck and the femoral diaphysis (Fig. 7c). It inserts via tendinous fibers, onto the medial and mediodistal margin of the patella (Fig. 7c).

*M. vastus intermedius (Figs. 6a and 7c)*

It is totally covered by the other bellies of the m quadriceps femoris. This muscle is elongated and partially flattened. It shares fibers with the m. vastus medialis and with the m. vastus lateralis in lesser degree. It originates via fleshy fibers, from the cranial surface of the femoral diaphysis (Fig. 7c). It inserts via tendinous fibers onto the dorsal aspect of the patella (Fig. 7c).
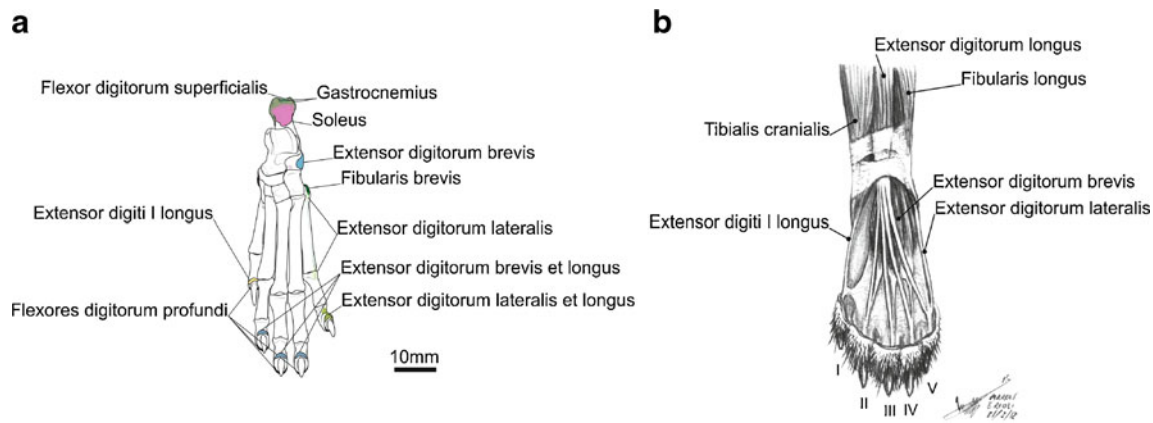
*M. gracilis (Figs. 4b and 8b,c)*

It is a band-shaped muscle that runs over the medial surface of the thigh. It originates mostly via tendinous fibers from the ventral region of the pelvic symphysis (Fig. 4b); it fuses cranially with the fibers of insertion of the abdominal muscles. It inserts via an aponeurosis onto the craniomedial aspect of the tibia, proximal to the insertion of the m. semitendinosus (Fig. 8b,c), covering the most proximal fibers of the latter.

*M. pectineus (Figs. 2c, 4 and 7a)*

It is a fan-shaped muscle that lies on the proximomedial region of the thigh, medial to the m. adductor longus. It originates via fleshy fibers from the cranial region of the pelvic symphysis, pectineal tuberosity, and iliopubic eminence (Fig. 4). It inserts via an aponeurosis and fleshy fibers onto the caudoproximal surface of femur (Fig. 7a).

*M. adductor longus (Figs. 2c, 4a,b and 7a)*

It is located lateral to the m. pectineus and medial to the m. adductor magnus, sharing some fibers with the latter. It has a fan-like shape and is composed of proximal and distal bellies (except in one limb), which differentiate from each other only near their insertion. It originates via fleshy fibers, from the pelvic symphysis and the caudal ramus of the pubis (Fig. 4a,b). The proximal belly inserts via an aponeurosis onto the proximodistal line on the caudoproximal region of

**Fig. 9** Pes of *Galictis cuja* in dorsal view: muscular map (**a**) and illustration of principal musculature (**b**)

the femur (Fig. 7a). The distal belly inserts mostly by fleshy fibers, continuing distally with the proximal belly (Fig. 7a).

*M. adductor magnus (Figs. 2c, 4b, 5b and 7a,b)*

This muscle is located on the medial aspect of the thigh, deep to the m. adductor longus (Fig. 2c). It has a quadrangular morphology, is flat, and slightly widens toward its insertion. Near its insertion it is partially divided into medial and lateral fascicles. It originates via fleshy fibers from a reduced area on the caudal region of the caudal ramus of the pubis and ischial ramus (Fig. 4b). It inserts via fleshy fibers onto the distal end of the caudal surface of the femur in two independent areas just proximal to both femoral condyles (Fig. 7a,b). In the lateral region of this insertion, it shares fibers with the insertion of the m. semimembranosus.

*M. adductor brevis (Figs. 4b, 5b and 7a)*

This muscle lies deep to the m. adductor longus and presents a quadrangular morphology, slightly expanded to its insertion. It originates via fleshy fibers from a reduced area on the caudal region of the caudal ramus of the pubis and ischial ramus (Fig. 4b). It inserts via fleshy fibers onto the proximal third of the lateral surface of the femur (Fig. 7a).

*M. obturator externus (Figs. 4b and 7a)*

It is a thin muscle and presents an inverted fan-shape. It originates via fleshy fibers from the cranial, ventral, and caudal margins of the obturator foramen in the lateral aspect of the pelvic bone (Fig. 4b). It inserts via tendinous fibers onto the central and deeper aspect of the trochanteric fossa (Fig. 7a), partially fusing with the insertion of the m. obturator internus. Some fibers reach the articular capsule of the hip joint.

Musculature of the Leg

*M. gastrocnemius (Figs. 2c, 5b, 7a,d and 9a)*

This muscle is very robust and each head is laterally compressed. In three of the dissected legs, the lateral head of m. gastrocnemius is strongly fused to the m. flexor digitorum superficialis except near their insertion. The lateral head originates via a strong tendon from the lateral epicondyle of the femur, and on the lateral sesamoid of the knee. The medial head originates via another tendon from the medial epicondyle of the femur (Fig. 7a,d). Both heads also originate at the caudal aspect of the femoral diaphysis and the articular capsule of the knee joint. This muscle inserts onto the caudodorsal end of the calcaneal tubercle via a tendinous attachment (Fig. 9a). This tendon fuses partially with the tendons of the m. flexor digitorum superficialis and the m. soleus to give rise to the calcaneal tendon. Also, it inserts on peripheral muscles through an aponeurotic attachment.

*M. soleus (Figs. 6a, 8d and 9a)*

This spindle-shaped muscle is deep to the m. gastrocnemius and the m. flexor digitorum superficialis. It originates via a thin and flat tendon from the caudal aspect of the head of the fibula (Fig. 8d). It inserts onto the fascia that covers the medial aspect of the calcaneus and the distal end of the fibula, and onto the proximal aspect of the calcaneal tubercle via a tendinous attachment (Fig. 9a).

*M. flexor digitorum superficialis (m. plantaris) (Figs. 7a, 9a and 10a)*

It is a robust muscle that lies between the two heads of the m. gastrocnemius. The m. flexor digitorum superficialis

**Fig. 10** Pes of *Galictis cuja* in plantar view: muscular map (**a**), superficial (**b**), intermediate (**c**), and deep (**d**) musculature. Fl. dig. profundi is the abbreviation for flexores digitorum profundi

originates via a tendon from the caudal aspect of the lateral epicondyle of the femur (Fig. 7a). At its distal end, the tendon of this muscle surrounds medially the tendon of the m. gastrocnemius acquiring a caudal position. It inserts via a tendon onto the calcaneus (Figs. 9a and 10a) and the fascia that covers it. In most cases, this tendon is fused with that of the m. gastrocnemius. After the first insertion, it surrounds the calcaneus and fuses with origin of the m. flexor digitorum brevis. In some cases (three legs), it could be observed that some tendinous fibers of m. flexor digitorum superficialis continued distally on the m. flexor digitorum brevis.

### M. popliteus (Figs. 6a, 7d and 8a,b)

It is a triangular-shaped muscle that runs toward the proximal and caudal aspects of the tibia. Along its origin and its inner surface, the m. popliteus presents many tendinous fibers. It originates via a thick and short tendon from the lateral condyle of the femur (Fig. 7d) and the aponeurosis that covers the lateral surface of the distal end of the femur. It inserts via fleshy fibers onto the medial and caudal aspect of the first two-thirds of the tibia (Fig. 8a,b). The attachment between the tibial condyles is strong and tendinous. Some fibers also insert on the m. flexor digitorum medialis.

### Mm. flexores digitorum profundi (Figs. 8, 9 and 10)

This group is composed of the m. flexor digitorum lateralis and m. flexor digitorum medialis. The m. flexor digitorum lateralis, and presumably the m. flexor digitorum medialis (this condition could not be verified), is held in place by two separated retinacula at the level of the ventromedial surface of the calcaneus and the ventral surface of the astragalus. Both muscles fuse at the level of the distal tarsals and the proximal end of the metatarsals, forming a tendinous sheet. This sheet subdivides into five flat and relatively robust tendons. Some fibers are inserted on the distal sesamoids of the metatarsals. Finally, tendons pass through the rings formed by the m. flexor digitorum brevis and insert on the distal phalanges.

### M. flexor digitorum lateralis (m. flexor hallucis longus) (Figs. 8a,d, 9a and 10a,c)

This muscle is markedly bipennate, cylindrical and slightly flattened. Near its origin, it shares fibers with m. tibialis caudalis and m. fibularis brevis. At the level of the ankle, fleshy fibers abruptly become a flat and wide tendon. This tendon passes through the sulcus on the ventral surface of

the sustentacular aspect of the calcaneus before it fuses with the m. flexor digitorum medialis. This muscle originates via fleshy fibers from the interosseous membrane and from the caudal aspects of the tibia and fibula (Fig. 8a,d). It inserts, after fusing with m. flexor digitorum medialis (Fig. 10c), via five separate tendons onto the ventral surface of the distal phalanges of digits I through V (Figs. 9a and 10a,c as Flexores digitorum profundi).

### M. flexor digitorum medialis (m. flexor digitorum longus) (Figs. 8a,d, 9a and 10a,c)

It is a long and bipennated muscle. Only the first quarter presents fleshy fibers; then it becomes a moderately robust and flattened tendon that runs through the sulcus of the medial malleolus, together and superficial to the tendon of the m. tibialis caudalis. This tendon continues through the medial aspect of the tarsal joint toward the tarsus before fusing with m. flexor digitorum lateralis. The m. flexor digitorum medialis shares a retinaculum with the m. tibialis caudalis. This muscle originates via both fleshy and tendinous fibers from the caudal and caudomedial aspects of the head of the fibula (Fig. 8a,d), the interosseous membrane, and via fleshy fibers from the entire lateral margin of the insertion of the m. popliteus on the tibia. After the fusion with the tendon of m. flexor digitorum lateralis (Fig. 10c), it inserts onto the ventral surfaces of the distal phalanges of digits I through V (Figs. 9a and 10a,c as Flexores digitorum profundi).

### M. tibialis caudalis (Figs. 8a–c and 10a)

This muscle lies lateral to and in close contact with the m. flexor digitorum medialis. Both muscles run together through the sulcus of the medial malleolus, where the m. tibialis caudalis becomes internal with respect to the m. flexor digitorum medialis. The m. tibialis caudalis is thin and flattened; it has an inverted fan-shape and is weakly pennate; it becomes a thin tendon at about its midpoint. It originates via fleshy fibers from the caudal aspect of the shaft of the tibia, and the cranial, medial, and caudal aspects of the head of the fibula (Fig. 8a–c). Some fibers originate on adjacent muscles such as the m. flexor digitorum lateralis and the m. flexor digitorum medialis. It inserts via tendinous fibers onto the medial and ventral surfaces of central and tarsal I, and on the sesamoid present between them (Fig. 10a).

### M. fibularis longus (m. peroneus longus) (Figs. 5b, 6a, 8c,d, 9b and 10a)

This muscle is relatively flattened and elongated. It is cranial and superficial in relation to the m. extensor digitorum lateralis (Fig. 6a), and runs through an exclusive sulcus located on the lateral margin of the lateral malleolus. It originates via tendinous fibers from the cranial aspect of the head of the fibula, the lateral aspect of the lateral condyle of the tibia and the adjacent diaphysis of the tibia (Fig. 8c,d). Some fibers originate on the fascia that covers the lateral surface of the knee. Its tendon reaches a first insertion onto the laterodistal end of the calcaneus and the proximal margin of the tubercle of metatarsal V (Fig. 10a); later, it lies internal to the long plantar ligament. The last attachment area is onto the lateral surface of the plantar tubercle of metatarsal I (Fig. 10a). The m. fibularis longus, m. extensor digitorum lateralis, and the m. fibularis brevis are contained by a common retinaculum that is located proximal and lateral to the tarsal joint. Fibers that participate in the construction of the first anterior retinaculum (see above) originate from the medial surface of this retinaculum, superficial to the belly of the m. fibularis longus.

### M. fibularis brevis (Figs. 8a,d and 9a)

This muscle is composed of cranial and caudal bellies. The cranial belly is smaller, bipennate, and with more tendinous fibers. The caudal belly also presents a bipennate condition. These tendons run around the lateral maleolus. In four legs a sesamoid is present within this tendon. In two legs, there is no fusion between the tendons (the condition that actually occurred in the other legs) and the caudal belly formed a ring through which the tendon of the cranial belly passed. The cranial belly originates via fleshy fibers from the anterolateral surface of the middle of the fibula (Fig. 8a,d). The caudal belly originates via fleshy fibers from the caudolateral surface of the middle of the fibula (Fig. 8a,d). It inserts via tendinous fibers onto the dorsolateral aspect of the tubercle of metatarsal V (Fig. 9a), sharing some fibers with the m. extensor digitorum lateralis and m. abductor digiti V. Secondarily, it continues as a flat tendon that inserts on the dorsolateral surface of the whole metatarsal V, the tarso-metatarsal joint of the same digit, and other extensor muscles (tendons of the m. extensor digitorum lateralis and m. extensor digitorum longus, and the aponeurosis of the m. extensor digitorum brevis, if present). It runs deep to the tendon of the m. extensor digitorum lateralis, sharing a great number of fibers with it. In all cases in which the fusion of both bellies of m. fibularis brevis is not complete, distal fibers belonged to the cranial belly.

### M. extensor digitorum lateralis (Figs. 6, 8c,d and 9)

It is an elongated and superficially bipennate muscle, which runs along the cranial and lateral aspects of the fibula (Fig. 6). It becomes tendinous at the level of the distal fifth of the tibia where it lies caudal and parallel to

the m. fibularis longus. Then, it continues through the sulcus of the lateral maleolus, cranial and dorsal with respect to the tendon of the m. fibularis brevis, and through the lateral aspect of the tarsus and metatarsal V. This muscle originates via fleshy fibers from the proximal half of the fibula (Fig. 8c,d) and from peripheral muscles such as m. flexor digitorum lateralis and m. fibularis brevis. It inserts via tendinous fibers onto the proximal surface of metatarsal V (Fig. 9a), where the m. extensor digitorum lateralis shares some fibers with the m. fibularis brevis. Then, it continues as a tendon and presents a second insertion onto the lateral surface of the metatarsal-phalangeal joint and the dorsolateral surface of the proximal phalanx of the digit V (Fig. 9a), where it fuses with the tendon of the m. extensor digitorum longus, and with the m. extensor digitorum brevis and the distalmost fibers of the m. fibularis brevis. Finally, this muscle continues as a wide fascia that covers the dorsal and lateral aspects of intermediate and distal phalanges of digit V (Fig. 9a).

### M. tibialis cranialis (Figs. 5b, 8c,d, 9b and 10a)

It is wide and flattened in its origin. It passes through the ankle joint closely together with the m. extensor digiti I longus. The m. tibialis cranialis is retained together with the m. extensor digiti I longus and the m. extensor digitorum longus by a wide retinaculum in the cranial and proximal aspect of the tarsal joint, and by a second retinaculum at the level of the proximal area of the tarsus (proximal and distal extensor retinacula). M. tibialis cranialis originates via tendinous and fleshy fibers from the craniolateral surface of the proximal quarter of the tibia, including the adjacent surface of the lateral condyle and the lateral margin of the cnemial crest, and from the proximal end of the interosseous membrane (Fig. 8c,d). There is a second tendinous origin in a reduced area of the cranial aspect of the head of the fibula. It inserts via tendinous fibers onto the medial aspect of the ventral tubercle of the base of metatarsal I (Fig. 10a).

### M. extensor digiti I longus (Figs. 8b,c and 9)

It is a thin and moderately flattened muscle that lies deep to the m. tibialis cranialis to which it is very close distally. Then, it continues its path along the medial surface of the digit I as an extremely thin tendon, and is contained by two retinacula (see above). It originates via fleshy fibers from the medial and cranial aspects of the proximal section of the diaphysis of the fibula (Fig. 8b,c) and from the interosseous membrane. It inserts via tendinous fibers onto the extensor tubercle of the distal phalanx of digit I (Fig. 9a). In one dissected leg, the muscle is attached to digit II instead of the digit I as is usual.

### M. extensor digitorum longus (Figs. 5b, 6, 7d and 9)

This muscle is divided into two bellies in its midpoint. Proximally, it lies deep to the m. tibialis cranialis, and distally it lies lateral and caudal to it. This muscle is retained by two retinacula, together with the m. tibialis cranialis and the m. extensor digiti I longus. After this muscle crosses the tarsal joint it becomes totally tendinous and divided into four tendons at the level of the proximal end of the metatarsals. A thin and fragile fascia covers and binds these tendons and those of the m. extensor digitorum brevis and the m. extensor digiti I longus. M. extensor digitorum longus originates via tendinous fibers from the lateral condyle of the femur (Fig. 7d) and from the aponeurosis that covers the m. tibialis cranialis. It inserts via four flat tendons onto the distal phalanges of digits II–V (Fig. 9a), previously being fused the tendons of the m. extensor digitorum brevis and the m. extensor digitorum lateralis (digit V). In most cases, a small bundle of tendinous fibers is observed inserting early on the lateral aponeurosis that covers the first row of tarsals.

### Muscles of the Pes

### M. extensor digitorum brevis (Fig. 9)

This muscle covers the dorsal aspect of the tarsus and the proximal aspect of the metatarsals. It is flattened and imperfectly subdivided into three or four bellies. It originates via an aponeurosis from the dorsolateral surface of the calcaneus (Fig. 9a) and on the fascia that covers the first tarsal row. It inserts via well-defined tendons onto the tendons of the m. extensor digitorum longus, indirectly reaching the extensor tubercles of the distal phalanges of the digits II–IV (Fig. 9a as M. extensor digitorum brevis et longus). In four hind limbs, this muscle attaches via an aponeurosis onto digit V, fusing with its extensor tendons. In two hind limbs this muscle reaches digit I attaching by an aponeurosis to the m. extensor digiti I longus; and in only one hind limb a well-differentiated tendon was present, attaching to the m. extensor digiti I longus.

### M. abductor digiti V (Fig. 10a,c)

This small muscle overlies the m. quadratus plantae and is deep to the m. flexor digitorum superficialis. It is a band-like muscle composed of few fleshy fibers. It originates via a flat tendon from the plantar surface of the calcaneal tubercle. It inserts via tendinous and fleshy fibers onto the lateral and plantar aspects of the tubercle of the base of metatarsal V, where it fuses with the main insertion of the m. fibularis brevis.

*M. flexor digitorum brevis (Fig. 10a,b)*

It is a flattened muscle that consists of four or five bellies strongly fused. From its origin and up to the level of the tarsal-metatarsal joint it is composed of fleshy fibers, and then it continues as aponeurotic tissue and tendons that lie superficial to the m. flexor digitorum profundus. Once they pass the metatarsals, this muscle divides into five tendons that run to the five corresponding digits. On digits II–V, these tendons split into two tendons to each digit (Fig. 10b), forming a ring through which the tendons of the m. flexor digitorum profundus passes, and then attach on the lateral aspects of the phalanges. For digit I, a single tendon is present. This muscle takes origin via an aponeurosis from the principal insertion of the tendon of the m. flexor digitorum superficialis, at the level of the plantar surface of the calcaneal tubercle (Fig. 10a). It inserts via an aponeurosis and five main tendons onto the plantar and proximal aspects of the middle phalanges of digits II–V, and plantar and proximal aspects of the proximal phalanx of digit I.

*Mm. interflexorii (Fig. 10c)*

These muscles are located between the m. flexor digitorum brevis and m. flexor digitorum profundus. These are three small, drop-shaped bellies that finish as delicate tendons. In most cases, the belly that overlies metatarsal V is very reduced and partially fused with the belly that covers metatarsal IV. The lengths of the two bellies that overlie metatarsals III and IV are about a third of the length of the metatarsal that they cover. These muscles originate via fleshy fibers from the plantar and distal aspects of the tendinous platform of the m. flexor digitorum profundus. They insert via tendinous fibers onto the dorsal aspect of the tendons of the m. flexor digitorum brevis that run to the digits III–V, at the level of the distal area of the metatarsals.

*M. quadratus plantae (Fig. 10a,c)*

This flattened muscle runs diagonally from the lateral aspect of pes to the craniocentral area of the plantar surface, deep to the m. abductor digiti V. It originates via tendinous fibers from the lateral surface of the calcaneus (Fig. 10a). It inserts via fleshy fibers onto the surface of the tendinous sheet, which results from the fusion of m. flexor digitorum lateralis and m. flexor digitorum medialis.

*Mm. lumbricales (Fig. 10a,c)*

These muscles are composed of three thin fleshy bands that run between the tendons of the m. flexor digitorum profundus for digits II–V. In one hind limb, a fourth m. lumbrical between digits I and II is present. They originate via fleshy fibers from the lateral and medial surfaces of the tendons of the m. flexor digitorum profundus corresponding to digits II through V (Fig. 10c). They insert via tendons onto the plantomedial and proximal aspects of the proximal phalanges of digits III–V (Fig. 10a).

*Mm. adductores digitorum (Fig. 10a,d)*

These muscles are composed of three muscular bellies partially fused near their origin. They overlie the mm. flexor brevis profundi of digits II, III, and IV. The lateral belly has a triangular shape, while the central and medial ones are thin bands. In one dissected pes, a fourth and much reduced belly is found. These muscles originate via fleshy fibers from the distal surface of the plantar ligaments that cover the distal series of tarsals and the base of the metatarsals. They insert via fleshy fibers onto the lateral surface of the lateral sesamoids of digits I and II, the head of their corresponding metatarsals, and the internal surface of the medial sesamoid of digit V and the head of metatarsal V (Fig. 10a).

*Mm. flexores breves profundi (mm. interossei) (Fig. 10a,d)*

They are the deepest of the plantar muscles. These are fleshy and mediolaterally flattened. There are typically 2 mm. flexor breves profundi (a lateral and a medial one) for each digit. In particular for digits I and V, these parts are totally differentiated in all cases, while the central one are, in some cases, partially fused. Overall, these muscles originate via fleshy fibers from the plantar processes of the tarsal bones, and adjacent areas of the metatarsals and ligaments. The medial part of the m. flexor breves profundi digiti I is more developed than the lateral one and originates from metatarsal I, tarsal I, the aponeurosis and ligament surfaces that cover the calcaneus and the central bone, as well as the ventral surface of the sesamoid that is located between the central bone and the first tarsal. The lateral part of the m. flexor breves profundi digiti I originates via fleshy fibers and via an aponeurosis from the plantar aspects of the proximal area of metatarsal I. The bundles of mm. flexor breves profundi digiti II, III, and IV originate from the proximal and plantar bases and plantar tubercles of the corresponding metatarsals. Both, the medial and the lateral part of the mm. flexor breves profundi digiti V (and the corresponding bellies of digiti IV) originate from the plantar surface of the sesamoid that lies at the base of metatarsal V while some fibers come from the adjacent surface of this metatarsal. All the insertions are via fleshy fibers onto the sesamoid bones of the metatarso-phalangeal joints, and on the distal end of metatarsal of the corresponding digit.

## Discussion

### Lumbar Epaxial Muscles

The degree of differentiation and development of the lumbar epaxial muscular systems is variable among carnivorans (Slijper 1946; Gambaryan and Karapetjan 1961; Davis 1964; Evans 1993; Julik et al. unpublished data) and has important consequences for movement capabilities of the lumbar region and on potential locomotor gaits (Gambaryan and Karapetjan 1961; Gambaryan 1974; Spoor and Belterman 1986; Spoor and Badoux 1988; Feeney 1999; Wroe et al. 2008).

Lumbar epaxial musculature in *G. cuja* is represented by a system of lateral bundles, which we describe as the m. iliocostalis lumborum (see below), and a medial one, the transversospinalis system. The caudal system, mm. sacrocaudalis dorsalis lateralis, gets in between these lumbar systems. Within Mustelidae, the lumbar epaxial musculature was similarly described in mustelines and, although to a lesser degree, in lutrines, varying only on the terminology used. Character optimization (Fig. S1A-C) suggests that these features could be considered as the ancestral condition for the clades Ictonychinae+Lutrinae+Mustelinae. However, some of these traits are modified in some lutrines that are highly specialized for swimming (e.g., reduction and independence of the m. iliocostalis lumborum in *Enhydra lutris*; see Gambaryan and Karapetjan 1961; Tarasoff 1972). In previous works, the lateral system was described as m. sacrospinalis (e.g., *Mustela putorius*; Moritz et al. 2007; see also Alix 1876; Gambaryan and Karapetjan 1961), and as a part of the m. longissimus dorsi (e.g., *Lontra canadensis*; Fisher 1942). In Fisher's description of *L. canadensis*, the "heavy roll muscle" that conforms the lateral muscle of the part III of the "m. longissimus dorsi" (Fisher 1942: 35) seems to be the lumbar part of the iliocostalis system that would be well developed as it was optimized for the clade Ictonychinae+ Lutrinae+Mustelinae (Fig. S1B). Even when lumbar epaxial muscles were not described in detail, a somewhat different organization appears as typical in others musteloids and as the ancestral condition of the superfamily (Fig. S1B,C), with the m. longissimus lumborum as the more developed muscle or the only lateral epaxial system (*Ailurus fulgens*, mephitids, procyonids, and more basal mustelids; Cuvier and Laurillard 1849; Hall 1926, 1927; Julik et al. unpublished data). Some osteological correlates can be proposed in relation to these muscular features: the shape and development of the spinous and transverse processes of the thoracolumbar vertebrae are closely related to the development of the medial systems (longissimus and transversospinalis) and iliocostalis systems, respectively. In particular for *G. cuja*, the cranioventrally oriented and well-developed lumbar transverse processes, and the wide internal face of the wing of the ilium, provide a wide surface for attachment areas and space available for the bundles of m. iliocostalis and sublumbar musculature. These features do not reduce the ability of lateral flexion, as seen as in other short-legged mustelids (Slijper 1946; Gambaryan 1974).

The relatively more developed and differentiated m. iliocostalis lumborum in mustelines and ictonychines (Table 2; Fig. S1B; Gambaryan 1974) could be related to the importance of the axial muscles in attending the execution of both symmetrical (asymmetric contractions) and asymmetrical gaits (symmetrical contractions; Schilling and Carrier 2010). This would compensate for the reduction of limbs that is necessary for entering and enhancing the mobility within the galleries of their prey (Gambaryan 1974; King and Powell 2007). In asymmetrical gaits, at least in epigeal locomotion, maximum running speed depends mostly on the strength of the extension of the column just before the floating phase of extended flight (Gambaryan 1974). Within Carnivora, the opposed tendency can be observed in hyaenids and ursids, which maximize the floating phase of the crossed flight and the participation of the forelimbs during locomotion, in detriment to the length and mobility of the lumbar region (Gambaryan 1974; Spoor and Belterman 1986; Hildebrand 1988; Wroe et al. 2008). These species present fully fused lumbar epaxial musculature (see Fig. S1C); they also present well-developed interspinous ligaments and lumbodorsal fascia, which are related to the enlargement of the dorsal margin of spinous processes, contrary to what is known in mustelids such as *Galictis* (Murie 1871; Davis 1964; Gambaryan 1974; Spoor and Badoux 1988).

During underground locomotion of mustelines and ictonychines, flexibility of the vertebral column becomes more important in order to allow species to pursue their prey within narrow pathways (Alix 1876; Gambaryan 1974; King and Powell 2007; Schutz and Guralnick 2007). This is why epaxial and sublumbar musculature plays such an important role in maneuverability of these species (Alix 1876; Gambaryan 1974; Moritz et al. 2007; Horner and Biknevicius 2010). On the other hand, Horner and Biknevicius (2010) highlighted important postural and motor changes during underground locomotion of the musteline *Mustela putorius* (see also King and Powell 2007). In this species, the function of the m. iliocostalis lumborum (described as m. sacrospinalis) was suggested to be as a stabilizer of the vertebral column in an extended posture during locomotion through narrow galleries (Moritz et al. 2007; Horner and Biknevicius 2010), a function that could be extrapolated to other mustelines and ictonychines of similar habits and morphology.

Ictonychines possess a slightly shorter lumbar region (typically five lumbar vertebrae) and a caudally located anticlinal vertebra (twelfth thoracic vertebra) compared to those found in mustelines and gulolines (typically six

lumbar vertebrae and the eleventh thoracic vertebra as the anticlinal vertebra; Mivart 1885; Leach and de Kleer 1978; Moritz et al. 2007). The traits found in ictonychines can be associated with a relatively more rigid thoracic cage, slower maximum speeds during locomotion when using asymmetrical gaits (Gambaryan 1974), and a lesser vertical oscillation during epigean running. It can also be related to a more regular use of symmetrical gaits (Horner and Biknevicius 2010), frequently described in ictonychines (Cabrera and Yepes 1940; Larivière 2002; Yensen and Tarifa 2003; Schutz and Guralnick 2007).

Caudal Musculature

Although the literature describing caudal musculature of carnivorans is scarce, a great diversity of muscles configurations can still be recognized, especially regarding origins and insertion areas. Morphological configuration of m. intertransversarii dorsales caudae and the m. intertransversarii ventrales caudae of *G. cuja* is very similar to that of other musteloids (e.g., *Lontra canadensis*, *Potos flavus*; Julitz 1909; Fisher 1942). In many carnivoran species, the m. intertransversarii ventrales caudae is not described as independent from the m. intertransversarii dorsales caudae (Reighard and Jennings 1901; Hall 1926; Williams 1955). This opens the possibility for this muscle to be absent or to be fused to the m. intertransversarii dorsales caudae. In *G. cuja*, as in most carnivorans, the m. intertransversarii dorsales caudae originates directly on the posterodorsal portion of the wing of the ilium, although this does not occur in some carnivorans (e.g., *Ailuropoda melanoleuca*, *Canis familiaris*; Davis 1964; Evans 1993).

In *G. cuja*, the origin region of the m. pubocaudalis is similar to other musteloids (Julitz 1909; Hall 1926; Williams 1955), especially to *Lontra canadensis* (Fisher 1942). It includes a small region of the vertical portion of the pubis, and it is independent of the m. iliocaudalis, while in other carnivorans it is usually restricted to the dorsal region of the pelvic symphysis and/or it is fused to the origin of the m. iliocaudalis (Reighard and Jennings 1901; Davis 1964; Evans 1993). Regarding the insertion of these muscles and the m. coccygeus, *G. cuja* is very similar to that previously described for mephitids and mustelids (Macalister 1873a; Hall 1926, 1927; Fisher 1942; Williams 1955); the insertion of these muscles never exceed the fifth caudal vertebra (contrary to other carnivorans such as canids, felids, procyonids, and ursids; Reighard and Jennings 1901; Julitz 1909; Davis 1964; Evans 1993). At least in mephitids and some mustelids such as ictonychines, these traits could be related to a wide range of extension (dorsal flexion) and complex movement of the tail, as well as the "battle flag" behavior, in which these musteloids raise the tail anticipating the secretion of anal musk glands (Hall 1926; Dücker 1968). Another feature shared by

ictonychines, mustelines, lutrines, and *Potos flavus* (Julitz 1909; Fisher 1942; Williams 1955), is the presence of a relatively cranial origin, from the last thoracic vertebra, of the m. sacrocaudalis dorsalis lateralis (Fig. S1C). On the contrary, other musteloids and canids present a more caudal origin, from the first lumbar vertebrae (e.g., Hall 1926, 1927), while in ursids (e.g., Davis 1964) an even more caudal origin was described, without reaching a bony origin neither from thoracic or lumbar vertebrae. This could be related to an increase of the extension strength and a better control of movements of the lumbar and caudal regions. From these comparisons, we believe that caudal musculature is a promising source of characters, even when available data are still limited to a few species.

Lumbar Hypaxial Muscles

Origins and insertions of the m. quadratus lumborum (sometimes described together with the m. psoas major and sometimes with the m. iliopsoas; e.g., Alix 1876; Fisher 1942; Williams 1955) are similar to those described for arctoids (*Ailuropoda melanoleuca*, *Mustela putorius*, *Mustela vison*, *Martes martes*, *Meles meles*, *Spilogale gracilis*, and *Taxidea taxus*; Alix 1876; Hall 1926, 1927; Davis 1964; Scherling 1989; Moritz et al. 2007). The most cranial bundles do not insert directly on the ilium, contrary to the condition observed in hyaenids and at least some canids (Spoor and Badoux 1988; Evans 1993; Feeney 1999). Musteloids (except maybe in *Lontra canadensis*; see "m. iliopsoas, part medial" in Fisher 1942) share the absence of insertions of the m. quadratus lumborum on the ribs, and *G. cuja* is no exception. In this species, each bundle of the m. quadratus lumborum spans over three to five vertebrae between their origin and insertion, similarly as described for *Mustela putorius* (Moritz et al. 2007).

The m. psoas minor of *G. cuja* originates from a reduced area of the bodies of two lumbar vertebrae, the second and third in specimens with five lumbar vertebrae, and the first and second in those with only four of them. A reduced origin was also described for *Mustela putorius* and for *Aonyx cinerea* (Macalister 1873a; Moritz et al. 2007). In the former, it spans the bodies of the third and fourth lumbar vertebra and the transverse processes of the third lumbar vertebra, keeping the same distance with respect to the sacrum as observed in *Galictis*. In the case of *Aonyx cinerea*, the distance is greater (four lumbar vertebrae). Character optimization (Fig. S1D) indicates that a reduced to moderate origin of the m. psoas minor could be the ancestral condition for the clade Ictonychinae+Lutrinae+Mustelinae, while a wide origin of this muscle is reconstructed for the Mustelidae and Musteloidea nodes. A reduced origin doesn't occur in most other carnivorans, including other arctoids (Beswick-Perrin 1871; Macalister 1873b; Mackintosh 1875; Allen 1882;

Hall 1926, 1927; Fisher 1942; Williams 1955; Davis 1964; Scherling 1989; Feeney 1999; Fisher et al. 2008), canids (Evans 1993; Fisher et al. 2008), and feliforms (Mackintosh 1875; Reighard and Jennings 1901; Spoor and Badoux 1988; Fisher et al. 2008), in which this area occupies at least three lumbar vertebrae, typically four, and may be even seven vertebrae (among thoracic and lumbar; Fig. S1D). Regarding the position of the origin of the m. psoas minor, a cranially located origin seems to be the ancestral and typically for most of the Arctoidea species, middle or cranially located for Mustelidae node, but in *Taxidea taxus* and some *Mustela* spp. a derived caudal origin is present (Fig. S1E).

Among musteloids, the origin of the m. psoas major may include the last two lumbar vertebrae (e.g., *Aonyx cinerea*; Macalister 1873a), the last three lumbar vertebrae (e.g., *Enhydra lutris*, *Mustela putorius*, *Martes foina*, *Martes pennanti*, *Meles meles*, *Potos flavus*, *Procyon lotor*, and probably *Lontra canadensis*; Beswick-Perrin 1871; Mackintosh 1875; Allen 1882; Fisher 1942; Howard 1975; Alexander and Jayes 1980; Scherling 1989; Feeney 1999; Moritz et al. 2007) or the last four lumbar vertebrae (e.g., *Ailurus fulgens*, *Nasua nasua*; Cuvier and Laurillard 1849; Fisher et al. 2008). In the case of *G. cuja*, the bony area of origin of this muscle is at the last two lumbar vertebrae, although it also originates directly or indirectly (i.e., on other muscles) on the third lumbar vertebra. In other carnivorans such as canids, hyaenids, and ursids, the m. psoas major originates directly or indirectly on four or more lumbar vertebrae (Shepherd 1883; Davis 1964; Spoor and Badoux 1988; Evans 1993; Feeney 1999). In hyaenids, an accessory origin area was described on the ribs (Spoor and Badoux 1988), which is not the case of any mustelids but *Lontra canadensis* (Fisher 1942). Nevertheless, as we commented above, this could reflect a problem with nomenclatural differences, and it could be a part of the bundles of the m. quadratus lumborum.

The reduction of the amplitude of the origin of the m. psoas major (Fig. S1F) as occurs for the m. psoas minor (Fig. S1D) seems to have been established early in the history of Musteloidea, and to be accentuated in more derived mustelids (e.g., Ictonychinae, Lutrinae, and Mustelinae). The change observed in this clade could be associated with adaptations to locomotion into galleries and the acquisition of a long body and short legged morphology, the requirement of high lumbar movements during epigean bounding gaits, changes in respiratory demands, the reduction of the exploitation of arboreal substrate, and a more frequent exploitation of aquatic substrate, especially in lutrines (Alix 1876; Cabrera and Yepes 1940; Alexander and Jayes 1980; Yensen and Tarifa 2003; Moritz et al. 2007; Wilson and Mittermeier 2009; Horner and Biknevicius 2010). The hypaxial muscles are strikingly very similar in *G. cuja* and *Mustela putorius*. M. quadratus lumborum, m. psoas minor and major are considered to present a double function

in species with elongated bodies: these muscles are flexors of the lumbar region during fast locomotion on the ground, and stabilizers of an extended position during underground locomotion in tunnels (Moritz et al. 2007). Short and partially independent multiple bundles of the m. quadratus lumborum, with their origin and insertions on lumbar vertebrae, and the absence of long bundles of any hypaxial muscle reaching the pelvis or the femur enhance the control and mobility of the lumbar region instead of bringing the legs forward keeping the back straight.

### Biceps Femoris and Abductor Cruris Caudalis

Both muscles possess a relatively constant configuration within Carnivora. Animals that need powerful extension of their hind limbs (e.g., when jumping and paddling) or sustain a backward orientation of them (e.g., when diving) always show insertions of these muscles that reach the distal half of the tibia (Macalister 1873a; Lucae 1875; Windle and Parsons 1898; Fisher 1942; Savage 1957; Gambaryan and Karapetjan 1961; Tarasoff 1972; Tarasoff et al. 1972; Howard 1975). On the contrary, ambulatory or cursorial predators usually use less energetically expensive gaits (e.g., *Nasua*, *Gulo*, *Canis*, *Vulpes*, *Hyaena*), and their m. biceps femoris, m. abductor cruris caudalis, and other knee flexors (e.g., m. gracilis) insert more proximally, reducing the distal muscular mass and inertia, and favoring fast movement (Mackintosh 1875; Savage 1957; Gambaryan 1974; Hildebrand 1988; Spoor and Badoux 1988; McClearn 1992; Evans 1993; Feeney 1999).

The m. abductor cruris caudalis presents a variable origin and it is strongly related to phylogenetic relationships (Fig. S1G). The optimized basal condition of Arctoidea is only present in Ursidae, Canidae, and *Meles meles* (Fig. S1G), and corresponds to an origin restricted to the sacrotuberous ligament, perhaps in relation to a relatively reduced tail. In most of musteloid taxa including *G. cuja*, the origin of m. adbuctor cruris caudalis is more caudal. A reversion to a relative more cranial position of the origin of this muscle is observed for the node Lutrinae+Mustelinae, and in badgers (Hall 1927; Fisher 1942; Williams 1955; Bisaillon 1976; Scherling 1989), or even in the Mustelidae node (ambiguous reconstruction; Fig. S1G).

### Gluteofemoralis

The m. gluteofemoralis is absent, or reduced and fused to the m. gluteus superficialis, in *G. cuja*, *Ictonyx libyca*, *Melogale personata*, *Taxidea taxus*, and some specimens of *Lutra lutra* and *Meles meles*, canids, ursids, and some herpestids (Haughton 1867b; Parsons 1898; Windle and Parsons 1898; Beddard 1905; Hall 1927; Williams 1955; Scherling 1989; Feeney 1999; Fisher et al. 2008; Hudson et

al. 2010). On the contrary, it is present and well-differentiated in gulolines, mustelines, most lutrines, mephitids (but sometimes greatly reduced), procyonids (with the possible exception of *Procyon*; Allen 1882; Windle 1888; Gowell 1897; Feeney 1999), and most feliforms (Haughton 1867c; Macalister 1873b; Lucae 1875; Mackintosh 1875; Alix 1876; Parsons 1898; Beddard 1900; Hall 1926; Fisher 1942; Ray 1949; Williams 1955; Davis 1964; Howard 1975; Bisaillon 1976; Evans and Quoc An 1980; Spoor and Badoux 1988; Fisher et al. 2008; Carlon and Hubbard 2012). The absence or fusion with m. gluteus superficialis of the m. gluteofemoralis have been considered traditionally as a derived character within Carnivora (Fisher et al. 2008). The absence of this muscle is the condition present in Canidae and Ursidae (Fig. S1H). On the other hand, the ancestral condition of Musteloidea corresponds to the presence of m. gluteofemoralis, reverted in the *Procyon* node, and may be in the Mustelidae node (Fig. S1H). In relation to this ambiguity, both the absence or fusion with m. gluteus superficialis of this muscle in ictonychines and the presence in mustelines+lutrines could be resolved as a plesiomorphy or synapomorphy of this group, but new dissections on other species are still necessary.

It is notable that there is shared absence (or reduction) of an independent m. gluteofemoralis in many ambulatory and cursorial carnivorans that do not perform fast direction changes while running, and where the tail is not used as a balancing organ (Taylor 1970; Tarasoff et al. 1972; McClearn 1992; Walker et al. 1998). On the other hand, in the case of ictonychines and some mustelines, the same feature is observed, but important changes of direction during fast running occur (Cabrera and Yepes 1940; Yensen and Tarifa 2003; King and Powell 2007), and are probably more related to the presence of a mobile thoracolumbar region instead of a strong and well-developed tail (e.g., *Mustela erminea*, lyncodontins). This can be linked with the reduction of the adductor-abductor musculature in their limbs (see below).

Regarding the fusion between the m. gluteofemoralis and m. gluteus superficialis, Bisaillon (1976) has already noted different degrees of fusion in mustelids and mephitids. In some limbs of *G. cuja*, the m. gluteus superficialis is particularly subdivided, and presents a caudal portion that resembles in position that of the m. gluteofemoralis. It is possible that these fibers represent a remnant of that muscle, given the recognized fusion in other mustelids.

### Gluteus Group, Piriformis, and Articularis Coxae

In *G. cuja* and other agile and non-cursorial mustelids, the fast extensors of the hip joint (gluteus group) are weakly developed when compared to total hind limb musculature and in relation to other extensor groups (e.g., hamstrings;

Table 2; Fig. 1). This could be related to the capacity of powerful jumping and the absence of cursorial adaptations (Maynard Smith and Savage 1956; Gambaryan 1974).

The degree of fusion observed between the m. piriformis and the m. gluteus medius is variable in *G. cuja* and is a frequent condition within Musteloidea (Fisher et al. 2008; but see also Lucae 1875; Mackintosh 1875; Alix 1876; Hall 1926; Fig. S1I). On the contrary, these muscles are constantly fully separated in other carnivoran groups such as Feliformia, Canidae, and Ursidae (Watson 1882; Davis 1964; Feeney 1999; Fisher et al. 2008; Carlon and Hubbard 2012). Because of the high intraspecific variability, and the small number of specimens analyzed for each taxon, the current reconstruction of the internal nodes of Musteloidea seems unreliable.

The m. articularis coxae is absent in *G. cuja* (Fig. S1J) as reported for most of the Arctoidea species (except for some specimens of *Meles meles*, *Mustela putorius*, and some ursids; Haughton 1867d; Windle and Parsons 1898; Davis 1964; Souteyrand-Boulenger 1969; Bisaillon 1976; Scherling 1989). When it is present it can be associated with proprioception and motor control in animals with a cursorial way of locomotion and with a wide range of flexion and extension movements of the hip joint (Souteyrand-Boulenger 1969; Fisher et al. 2008).

### Sartorius

In *G. cuja*, as in other arctoids (except in some specimens of *Nasua*; Mackintosh 1875; Fig. S1L), the m. sartorius has a single belly. The same condition was described for felids, and many herpestids and viverrids (Lucae 1875; Watson 1882; Windle and Parsons 1898; Hall 1926; Davis 1964; Scherling 1989; Feeney 1999; Fisher et al. 2008; Carlon and Hubbard 2012). In canids and hyaenids, it is always double (Haughton 1867a; Watson 1882; Windle and Parsons 1898; Spoor and Badoux 1988; Evans 1993; Feeney 1999). The presence of two independent bellies within the two most cursorial carnivorans (hyaenids and canids), in which the cranial belly extends and the caudal ones flexes the knee joint, may be understood as a stabilizing system of the movements of this joint during running (Gambaryan 1974; Evans 1993). A single belly for the m. sartorius cannot be clearly stated either as a derived or a primitive condition in carnivorans (Fisher et al. 2008).

### Adductors and Abductors of the Hip Joint

Fisher et al. (2008) suggested that the adductor muscles group should be compared among species as a whole, and they compiled the total number of adductor muscles described in previous works (including the m. pectineus; see Fisher et al. 2008 and citations therein) for different species of Carnivora. They found that the number of adductor

bellies is, in general, constant within families (except in procyonids). The character optimization suggests that this feature is highly variable in Arctoidea, even at the familial level (result not shown). For example, in Mustelidae, four bellies could be the ancestral condition of the family, but in *G. cuja*, as well as in other mustelids (e.g., *Martes foina*, *Mustela putorius*; Cuvier and Laurillard 1849; Mackintosh 1875; Alix 1876), five bellies are present instead of the typical four mentioned by Fisher et al. (2008). Given these, the number of bellies of the adductor mass seems to be poorly informative regarding phylogenetic relationships, especially taking into account the potential interpretative differences between researchers. Fisher et al. (2008) suggested that numerous bundles in the adductor mass could be related to more precise movement needed by procyonids and *Ailurus fulgens* for balancing on branches. This does not agree with the numerous bundles recorded for mostly terrestrial mustelids like *G. cuja* and *Mustela putorius* (Alix 1876), nor with the more moderate number of bundles recorded in highly arboreal species like *Potos flavus* (four bellies; Beswick-Perrin 1871) or *Bassaricyon alleni* (three bellies; Beddard 1900).

Within Musteloidea there are some variants among the adductor muscles that seem to be informative regarding phylogenetic affinities. *Galictis cuja* shows both m. adductor brevis and m. adductor magnus fully independent from each other, with their insertions separated proximodistally on the femoral shaft. This feature is shared with other musteloids (e.g., *Aonyx cinerea*, *Ailurus fulgens*, *Enhydra lutris*, *Lutra lutra*, *Martes foina*, *Mustela putorius*; Macalister 1873a; Lucae 1875; Mackintosh 1875; Alix 1876; Howard 1975; Fisher et al. 2008). On the other hand, *G. cuja* and other musteloids (e.g., *Ailurus fulgens*, *Martes foina*) differ from mustelines and lutrines (and other carnivorans) in the presence of a distal division of the m. adductor magnus (Macalister 1873a; Lucae 1875; Mackintosh 1875; Alix 1876; Howard 1975; Fisher et al. 2008).

The relative mass of adductor and abductor muscles has been directly related to the ability of a fast switch of direction during high-speed locomotion in some mammal groups (e.g., Lagomorpha; Williams et al. 2007). This function is assisted by the tail in those animals with long and robust tails (e.g., many felids, procyonids, and viverrids; Taylor 1970; McClearn 1992; Walker et al. 1998). Even when weasel-like mustelids have been described as able to achieve abrupt changes in direction during fast locomotion (Cabrera and Yepes 1940; Yensen and Tarifa 2003; King and Powell 2007), they have frequently relatively short limbs and tail, and very low relative values of adductor and abductor masses of hind limbs when compared with other agile predators (e.g., foxes, felids, some procyonids; see also Feeney 1999; Fig. 1). Mustelids have a great lateral flexion ability of the vertebral column when compared to other

similar-sized carnivorans (e.g., mephitids and most procyonids). In this way, since most part of the forward propulsion is performed by the epaxial musculature (Gambaryan 1974; Schutz and Guralnick 2007), it is possible that abrupt changes of direction may be achieved by asymmetrical contractions of the lateral axial muscles (e.g., iliocostalis), particularly well developed in mustelids, and only secondarily helped by fast movements of the tail.

Semimembranosus

Within Carnivora, the number of bellies of this muscle varies between one and three in the different families, but important intra- and interspecific variations have been described (e.g., *Ailurus*, Procyonidae; see Fisher et al. 2008). Among the mustelids surveyed by Fisher et al. (2008), m. semimembranosus possessed one belly. However, many mustelids present m. semimembranosus composed of two bellies, such as *G. cuja* (this study), *Gulo gulo*, *Martes* spp., *Meles meles*, *Mellivora capensis*, *Melogale personata*, *Mustela* spp., *Taxidea taxus* (bellies separate near insertion), *Vormela peregusna*, and many otters (*Enhydra lutris*, *Lontra canadensis*, some specimens of *Lutra lutra*) (Beddard 1905; Hall 1926, 1927; Fisher 1942; Gambaryan 1974; Bisaillon 1976; Scherling 1989; Feeney 1999). Mephitidae and Procyonidae (except *Nasua*; Mackintosh 1875) also have two bellies (e.g., Allen 1882; Windle 1888; Gowell 1897; Hall 1926; Feeney 1999). The splitting into two bellies may be related to a subdivision of its function: extension of the hip and flexion of the knee, and the assurance of a wide range and precision of movements. The subdivision of this muscle seems to be an ancestral condition for Arctoidea as well as at the level of the nodes Mephitidae, Mustelidae, Procyonidae, and Ursidae. On the other hand, a single belly of m. semimembranosus is a derived condition only at subfamilial level (Fig. S1M).

It is worth mentioning that some authors use the term "pre-semimembranosus" to refer to the cranial belly of the m. semimembranosus (e.g., Windle and Parsons 1898), while other authors use the same term to refer to a possible subdivision of the m. gluteofemoralis (e.g., Fisher 1942; Scherling 1989). On the other hand, some authors seem to include the cranial belly of the m. semimembranosus within the adductor mass (e.g., Alix 1876).

Semitendinosus

In *G. cuja*, the m. semitendinosus has two bellies, one with its origin at the ischial tuberosity (hereafter ischial belly), and the other which originates from C2 (hereafter caudal belly). The ischial belly is typically present within Carnivora, although in some otters and the American mink it is

strongly reduced (Cuvier and Laurillard 1849; Macalister 1873a; Lucae 1875; Windle and Parsons 1898; Williams 1955) and in other otters is completely absent (some specimens of *Lontra canadensis*, *Enhydra lutris*; Fisher 1942; Howard 1975). The ancestral condition reconstructed for lutrines resulted in a reduced ischial belly (Fig. S1N), while the condition of Lutrinae+Mustelinae resulted ambiguous. The caudal belly is present in some Feliformia (viverrids and herpestids), procyonids (except in *Bassaricyon alleni*; Beddard 1900) (Fig. S1O), and in most mustelids (Windle and Parsons 1898; Taylor 1976; Fisher et al. 2008). Within lutrines and mustelines, it originates from the first or some of the first caudal vertebrae (*Aonyx cinerea*, *Enhydra lutris*, *Lutra lutra*, *Mustela nigripes*, *Mustela putorius*, *Mustela vison*; Macalister 1873a; Alix 1876; Windle and Parsons 1898; Williams 1955; Bisaillon 1976), and it is relatively wide in the formers and reduced in the latter (Fig. S1N,P). In most ictonychines and gulolines, the caudal belly is also present (e.g., *G. vittata*, *Ictonyx libyca*; Windle and Parsons 1898), but its origin is mostly restricted to the second caudal vertebra (*G. cuja*, *Eira barbara* and *Martes americana*; Macalister 1873b; Windle and Parsons 1898; Hall 1926; this study; Fig. S1O). This belly is also known in *Melogale personata* (Beddard 1905), although without precise data about its origin. At the same time, this belly of the m. semitendinosus is absent in *Ailurus fulgens*, canids, felids, hyaenids, mephitids, ursids (Beswick-Perrin 1871; Macalister 1873a; Allen 1882; Watson 1882; Windle 1888; Hall 1926, 1927; Ray 1949; Davis 1964; Bisaillon 1976; Evans 1993; Fisher et al. 2008; Carlon and Hubbard 2012), and some mustelids, including *Ictonyx striatus* (Windle and Parsons 1898), *Meles meles*, and *Taxidea taxus* (Windle and Parsons 1898; Hall 1927; Scherling 1989), and some specimens of *Martes* spp. (e.g., Mackintosh 1875) and *Mustela putorius* (Macalister 1873b; Windle and Parsons 1898; Bisaillon 1976).

Thus, the presence and features related to the origin of the m. semitendinosus seem to be phylogenetically informative at the familial and subfamilial levels (Fig. S1N,P). From a functional point of view, the presence of two bellies in the m. semitendinosus in those groups with more generalized locomotor modes (including bound and half-bound; Gambaryan 1974) leads to an increase of the number of muscular fascicles (and sometimes a mass increase) of hamstring muscles that could be related to more precise movement, a wider range of movements, and perhaps increasing strength (Hildebrand 1988). On the other hand, groups with more specialized locomotor modes (semiaquatic, cursorial, and terrestrial ambulatories), this belly is alternatively present. These variations, as those linked to the origin area of the caudal belly may reflect different capabilities on specific actions, depending on positions and locomotor styles. A wider and exclusively, or mostly exclusively, caudal origin (lutrines)

maximizes the mechanical advantage of the m. semitendinosus in an extended position of the hip joint and a flexed knee, in relation to holding the hind limbs caudally directed and close to the body during swimming in otters (Maynard Smith and Savage 1956; Savage 1957; Gambaryan and Karapetjan 1961; Tarasoff 1972). A restricted ischial origin seems to be an ancestral condition for Arctoidea, and would be related to a typical flexed hip, a more extended knee, and a more vertical position of the hind limb under the body (big predators, cursorial, and ambulatories species).

Fibularis Brevis and Extensor Digitorum Lateralis

In *G. cuja*, the architecture of the m. fibularis brevis and the m. extensor digitorum lateralis is unusual and different from most other carnivorans, but remains similar to that observed in some lutrines, gulolines, and mustelines. The m. extensor digitorum lateralis has many points of interaction with the m. fibularis brevis at the lateral aspect of the hindfoot. The m. fibularis brevis is complex and divided into two bellies that originate from the distal half of the fibula. The tendons of both bellies fuse or cross each other, one of them forming a ring through which the second tendon passes. Within Mustelidae, similar relationships and particular configurations of these two muscles have been described only for *Enhydra lutris* (Howard 1975), *Mustela nigripes* (Bisaillon 1976), *Mustela putorius* (Alix 1876), one specimen of *Martes pennanti* (Feeney 1999), and illustrated but not described for *Martes foina* (Cuvier and Laurillard 1849). In the first two cases, the m. fibularis brevis surrounds the m. extensor digitorum lateralis. In the case of *Martes foina*, Cuvier and Laurillard (1849) showed a distal tendinous projection of the m. fibularis brevis that reaches the m. extensor digitorum lateralis, similar to that described for *G. cuja*. In the case of *Mustela putorius*, Alix (1876) described a typical m. fibularis brevis with an accessory tendon that differentiates at the middle of the zeugopod and cannot be recognized proximally, which seems to belong to the m. extensor digitorum lateralis (that was not described). In the case of *Mustela nigripes*, Bisaillon (1976) linked the observed configuration to a reduction of the capability of flexion and rotation of the ankle, even though, this does not seem applicable, especially in the case of *Enhydra lutris*, given the complex movements of rotation and flexion that this species is capable of during swimming (Tarasoff et al. 1972). The character optimization suggests that these similar conditions evolved independently at least four times within Mustelidae (Fig. S1P). However, given that these features are difficult to record and have been recorded in only a few mustelids studied in detail, it is likely that these traits are present in other mustelid taxa, which would confirm that they are a result of convergence or an inherited condition for the family.

## Musculature of the Tarsal Joint and Digits

In *G. cuja*, most of the extensor muscles of the tarsal joint that originates from the zeugopod, i.e., m. fibularis brevis, m. extensor digitorum lateralis, m. flexor digitorum medialis, m. tibialis caudalis, and especially the m. flexor digitorum lateralis, are greatly developed (Table 2; Fig. 1) and present distally extended origin regions, moderate or marked pinnation, and short tendons. The major tarsal extensors, m. gastrocnemius and m. flexor digitorum superficialis, are greatly developed, reaching a total mass that is about the size of the knee joint extensors (m. quadriceps). These traits, together with those previously described for the gluteal group, the mm. biceps femoris, and abductor cruris caudalis, were also observed in lutrines, gulolines, mustelines, and other ictonychines (Williams 1955; Savage 1957; Gambaryan 1974; Bisaillon 1976). This configuration can be related to motor actions that demand a powerful extension of the tarsal joint (e.g., rapid acceleration, jumping, and swimming) where the muscular power predominates over economy (Gambaryan 1974; Walmsley et al. 1978; Hildebrand 1988; Payne et al. 2005) and the capacity of performing non-sagittal movements (Barnett and Napier 1953). In the case of ictonychines and mustelines, other possible factors may be the effort needed during crouched locomotion within galleries, and secondly, the stabilization of the extra body weight while digging or carrying preys (Van de Graaff et al. 1982; Spoor and Badoux 1988; Gorsuch and Larivière 2005; King and Powell 2007). Given that most mustelids have proportionally short limbs, pinnation could act as a compensatory factor to smaller surfaces available for the origin of muscular fibers, thus maintaining the amount of force that can be exerted by these muscles. In relation to ankle extensors, ambulatory ursids, procyonids, and mustelids like *Gulo gulo* and *Mellivora capensis* have intermediate characteristics between other mustelids and cursorial carnivorans (Fig. 1; Haughton 1867d; Mackintosh 1875; Windle and Parsons 1898; Ray 1949; Gambaryan 1974; Evans 1993; Fisher et al. 2008; Hudson et al. 2010).

We indentified typically three insertion tendons of the m. extensor digitorum brevis for *G. cuja*, for digits II through IV. The same configuration is present in many musteloids and typically in canids, felids, and hyaenids. On the other hand, one hind limb of one specimen of *G. cuja* presented a fourth tendon for the first digit, as it was described for *Galictis vittata* and typically other Arctoidea (Alix 1876; Allen 1882; Watson 1882; Gowell 1897; Windle and Parsons 1898; Howard 1975; Bisaillon 1976; Scherling 1989; Feeney 1999; Fisher et al. 2008). The loss of the tendon for digit I of the m. extensor digitorum brevis seems to have occurred many times in Carnivora (Fig. S1Q), but it cannot always be related to cursorial adaptations.

## Concluding Remarks

The comparative analyses of the musculature of *G. cuja* allowed us to establish functional comparisons and to make a qualitative and quantitative review of possible sources of phylogenetic characters. The morphology and development of the lumbar musculature (and secondarily the sacrocaudal muscles) of *G. cuja* and other weasel-like mustelids are related to the important role of the axial region in propulsion, control of changes of direction, and stabilization during epigean running or locomotion within narrow tunnels. In running, this musculature probably partially replaces or collaborates in these functions with the hind limb muscles, which are relatively reduced. Musculature related to the tarsal joint movement is well developed in *G. cuja*, with several muscles having a distally extended origin area and some degree of pinnation. These characteristics are probably related to the absence of clearly cursorial adaptations and powerful extension of this joint in forward motion during jumping and crouched locomotion, and allow movements outside the parasagittal plane, allowing locomotion on irregular surfaces or with obstacles.

As proposed in previous studies, myology is informative about phylogenetic relationships among species. Complexity and variability of the muscular group m. fibularis brevis+m. extensor digitorum lateralis, is different to the one described for other carnivorans (and proper of *G. cuja*), and must be the focus of future studies. We found certain muscular features in *G. cuja* that are exclusive or typical for arctoids (e.g., absence of the m. articularis coxae), musteloids (e.g., variability in the degree of fusion of the m. piriformis and m. gluteus medius; origin of m. tibialis caudalis; position of the insertion of the pubocaudal flexors), mustelids+procyonids (e.g., caudal belly of the m. semitendinosus typically present), mustelids (e.g., position of the origin of the m. psoas minor), mustelines +lutrines+ictonychines (e.g., many features of epaxial and hypaxial musculature, cranial origin of the m. sacrocaudalis dorsalis lateralis), and mustelines+lutrines setting apart from ictonychines+gulolines (e.g., position of origin of the caudal belly of the m. semitendinosus, position of insertion of the m. adductor magnus). Configuration of the sacrocaudal musculature seems to be potentially informative at a suprafamilial or familial level but there are still very few species for which this information is known. On the other hand, the absence of the m. gluteofemoralis and the frequent absence of the tendon for the digit I of the m. extensor digiti I (*Ictonyx libyca* and *G. cuja*) are shared by some ictonychines, and evolved independently in other clades. The absence or reduction of the ischial belly of the m. semitendinosus (occurring exclusively in lutrines), the absence or reduction of the caudal belly of this muscle, the absence of m. tensor fasciae latae, and the location of the origin of m. abductor cruris caudalis, seems to be informative in low hierarchy relationships whithin arctoids.

The compiled information (particularly the muscular mappings) in this and other myological studies (e.g., Fisher et al. 2008, 2009; Julik et al. 2012) could be considered as a very useful tool for zoologists and palaeontologists that attempt to make morphofunctional or phylogenetic inferences from osteological variation in both extant and extinct species. Several muscular groups leave distinctive scars or delimitable surfaces related to their origin or insertion on bones. In some cases, these features allow knowing, with more or less confidence, the position and the degree of development of the muscles that leave those marks (see Bryant and Seymour 1990). In particular, *G. cuja* is an interesting case of study within Carnivora given that it is an ecologically distinct model compared to well-known carnivorans such as canids and felids.

Future objectives should be the gathering of more myological data on mustelids, and the construction of phylogenies including muscular characters and related osteological features, necessary for a better understanding of the muscular anatomy of these carnivorans.

# References

Alexander RM, Jayes DA (1980) Estimates of the bending moments exerted by the lumbar and abdominal muscles of some mammals. J Zool Lond 194:291–303

Alix ME (1876) Memoire sur la myologie du putois (*Putorius communis*, Cuv.). J Zool Paris 5:153–188

Allen H (1882) The muscles of the limbs of the raccoon (*Procyon lotor*). Proc Acad Nat Sci Philadelphia 34:115–144

Azara F (1802) Apuntamientos para la historia natural de los quadrúpedos del Paraguay y Río de la Plata. La Viuda de Ibarra, Madrid

Barnett CH, Napier JR (1953) The form and mobility of the fibula in metatherian mammals. J Anat 87:207–213

Beddard FE (1900) On the anatomy of *Bassaricyon alleni*. Proc Zool Soc Lond 69:661–675

Beddard FE (1905) Some notes upon the anatomy of the ferret-badger, *Helictis personata*. Proc Zool Soc Lond 75:21–29

Beswick-Perrin J (1871) On the myology of the limbs of the kinkajou (*Cercoleptes caudivolvulus*). Proc Zool Soc Lond 1871:547–559

Bisaillon A (1976) La musculature du membre pelvien du putois d'Amérique (*Mustela nigripes*, Audubon et Bachman). Anat Anz 139:486–504

Bryant HN, Seymour KL (1990) Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. J Morphol 206:109–117

Cabrera A, Yepes J (1940) Mamíferos Sud-Americanos. Historia Natural Ediar, Companía Argentina de Editores, Buenos Aires

Carlon B, Hubbard C (2012) Hip and thigh anatomy of the clouded leopard (*Neofelis nebulosa*) with comparisons to the domestic cat (*Felis catus*). Anat Rec 295:577–589

Cuvier G, Laurillard M (1849) Recueil de Planches de Myologie. Dusacq, Paris

Davis DD (1964) The giant panda: a morphological study of evolutionary mechanisms. Fieldiana: Zool Mem 3:1–339

Dücker G (1968) Beobachtungen am kleinen Grison, *Galictis* (*Grisonella*) *cuja* (Molina). Z Säugetierk 33:288–297

Evans HE (1993) Miller's Anatomy of the Dog. W. B. Saunders Company, Philadelphia

Evans HE, de Lahunta A (2010) Miller's Guide to the Dissection of the Dog. W. B. Saunders Company, Philadelphia

Evans HE, Quoc An N (1980) Anatomy of the ferret. In: Fox JG (ed) Biology and Diseases of the Ferret. Williams & Wilkins, Baltimore

Ewer RF (1973) The Carnivores. Cornell University Press, New York

Feeney S (1999) Comparative osteology, myology, and locomotor specializations of the fore and hind limbs of the North American foxes *Vulpes vulpes* and *Urocyon cinereoargenteus*. PhD Thesis, University of Massachusetts, Amherst

Fisher E (1942) The Osteology and Myology of the California River Otter. Stanford University Press, Stanford

Fisher RE, Adrian B, Elrod C, Hicks M (2008) The phylogeny of the red panda (*Ailurus fulgens*): evidence from the hindlimb. J Anat 213:607–628

Fisher RE, Adrian B, Elrod C, Hicks M (2009) The phylogeny of the red panda (*Ailurus fulgens*): evidence from the forelimb. J Anat 215:611–35

Flynn JJ, Finarelli JA, Zehr S, Hsu J, Nedbal MA (2005) Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. Syst Biol 54:317–337

Gambaryan PP (1974) How Mammals Run. John Wiley & Sons, New York

Gambaryan PP, Karapetjan WS (1961) Besonderheiten im Bau des Seelöwen (*Eumetopias californianus*), der Baikalrobbe (*Phoca sibirica*) und des Seeotters (*Enhydra lutris*) in Anpassung an die Fortbewegung im Wasser. Zool Jahrb 79:123–148

García-Esponda CM, Candela AM (2010) Anatomy of the hindlimb musculature in the cursorial caviomorph *Dasyprocta azarae* Lichtenstein, 1823 (Rodentia, Dasyproctidae): functional and evolutionary significance. Mammalia 74:407–422

Goloboff PA, Farris JS, Nixon K (2008) TNT: a free program for phylogentic analysis. Cladistics 24:774–786

Gorsuch WA, Larivière S (2005) *Vormela peregusna*. Mammal Species 779:1–5

Gowell RC (1897) Myology of the hind limb of the raccoon. Kan Univ Quar 6:121–126

Hall ER (1926) The muscular anatomy of three mustelid mammals, *Mephitis*, *Spilogale*, and *Martes*. Univ Calif Publ Zool 30:7–39

Hall ER (1927) The muscular anatomy of the American badger (*Taxidea taxus*). Univ Calif Publ Zool 30:205–219

Haughton S (1867a) On the muscular anatomy of the Irish terrier, as compared with that of the Australian dingo. Proc R Irish Acad Sci Ser 2 ix:504–507

Haughton S (1867b) On the muscular anatomy of the badger. Proc R Irish Acad Sci Ser 2 ix:507–508

Haughton S (1867c) On the muscular anatomy of the otter (*Lutra vulgaris*). Proc R Irish Acad Sci Ser 2 ix:511–515

Haughton S (1867d) On the muscles of the Virginian bear. Proc R Irish Acad Sci Ser 2 ix:508–511

Hildebrand M (1988) Analysis of Vertebrate Structure. John Wiley & Sons, New York

Holmes T (1980) Locomotor adaptations in the limb skeletons of North American mustelids. Master's Thesis, Humboldt State University, California

Horner AM, Biknevicius AR (2010) A comparison of epigean and subterranean locomotion in the domestic ferret (*Mustela putorius furo*: Mustelidae: Carnivora). Zoology 113:189–197

Howard LD (1975) Muscular anatomy of the hind limb of the sea otter (*Enhydra lutris*). Proc Calif Acad Sci 4th Series 40:335–416

Hudson PE, Corr SA, Payne-Davis RC, Clancy SN, Lane E, Wilson AM (2010) Functional anatomy of the cheetah (*Acinonyx jubatus*) hindlimb. J Anat 218:363–74

Hudson PE, Corr SA, Payne-Davis RC, Clancy SN, Lane E, Wilson AM (2011) Functional anatomy of the cheetah (*Acinonyx jubatus*) forelimb. J Anat 218:375–85

Julik E, Zack S, Adrian B, Maredia S, Parsa A, Poole M, Starbuck A, Fisher RE (2012) Functional anatomy of the forelimb muscles of the ocelot (*Leopardus pardalis*). J Mammal Evol. doi:10.1007/s10914-012-9191-4

Julitz C (1909) Osteologie und Myologie der Extremitäten und des Wickelschwanzes vom Wickelbären, *Cercoleptes caudivolvulus*, mit besonderer Berücksichtigung der Anpassungserscheinungen an das Baumleben. Arch Naturgesch Berlin 75:143–188

King CM, Powell RA (2007) The Natural History of Weasels and Stoats. Oxford University Press, Oxford

Koepfli K-P, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M,Veron G, Wayne RK (2008) Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol 6:10

Koepfli K-P, Gompper ME, Eizirik E, Ho C-C, Linden L, Maldonado JE, Wayne RK (2007) Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange. Mol Phylogenet Evol 43:1076–1095

Larivière S (2002). *Ictonyx striatus*. Mammal Species 698:1–5

Leach D (1977) The forelimb musculature of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben). Can J Zool 55:31–41

Leach D, de Kleer VS (1978) The descriptive and comparative postcranial osteology of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben): the axial skeleton. Can J Zool 56:1180–1191

Lucae JCG (1875) Die Robbe und die otter in ihrem knocken und muskel-skelet. Abh senckenb naturforsch Ges 8:277–378.

Macalister A (1873a) On the anatomy of *Aonyx*. Proc R Irish Acad Sci Series 2 i:539–547

Macalister A (1873b) The muscular anatomy of the civet and tayra. Proc R Irish Acad Sci Ser 2 i:506–513

Mackintosh HW (1875) Notes on the myology of the coati-mondi (*Nasua narica* and *N. fusca*) and common marten (*Martes foina*). Proc R Irish Acad Sci Ser 2 ii:48–55

Maynard Smith J, Savage RJG (1956) Some locomotory adaptations in mammals. Zool J Linn Soc 42:603–622

McClearn D (1985) Anatomy of raccoon (*Procyon lotor*) and coati (*Nasua narica* and *N. nasua*) forearm and leg muscles: relations between fiber length, moment-arm length, and joint angle excursion. J Morphol 183:87–115

McClearn D (1992) Locomotion, posture, and feeding behavior of kinkajous, coatis, and raccoons. J Mammal 73:245–261

Meckel J-F (1828) Traité général d'anatomie comparée. Villeret et cie, Paris

Mivart SGJ (1885) On the anatomy, classification and distribution of the Arctoidea. Proc Zool Soc Lond 23:340–404

Moritz S, Fischer MS, Schilling N (2007) Three-dimensional fibre type distribution in the paravertebral muscles of the domestic ferret (*Mustela putorius* f. *furo*) with relation to functional demands during locomotion. Zoology 110:197–211

Murie J (1871) On the female generative organs, viscera, and fleshy parts of *Hyaena brunnea*, Thunberg. Trans Zool Soc Lond 7:503–512

Parsons FG (1898). The muscles of mammals with special reference to human myology. J Anat Lond 32:721–752

Payne RC, Hutchinson JR, Robilliard JJ, Smith NC, Wilson AM (2005) Functional specialisation of pelvic limb anatomy in horses (*Equus caballus*). J Anat 206:557–574

Pierard J (1965) Note sur l'insertion du muscle fibularis (peroneus) longus chez les mammiferes et particulierement chez le chien et le chat. Can Vet J 6:282–289

Ray LJ (1949) The myology of the inferior extremity of the Malay bear, *Ursus malayanus*. Proc Zool Soc Lond 119:121–132

Reighard J, Jennings HS (1901). Anatomy of the Cat. Henry Holt and Company, New York

Sato JJ, Wolsan M, Prevosti FJ, D'Elía G, Begg C, Begg K, Hosoda T, Campbell KL, Suzuki H (2012) Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). Mol Phylogenet Evol 63:745–757

Scherling A (1989) Zur Anatomie des Bewegungsapparates des Dachses (*Meles meles* L.). PhD Thesis, Universität Gießen, Gießen

Schilling N, Carrier DR (2010) Function of the epaxial muscles in walking, trotting and galloping dogs: implications for the evolution of epaxial muscle function in tetrapods. J Exp Biol 213:1490–1502

Schutz H, Guralnick RP (2007) Postcranial element shape and function: assessing locomotor mode in extant and extinct mustelid carnivorans. Zool J Linn Soc 150:895–914

Shepherd FJ (1883) Short notes on the myology of the American black bear (*Ursus americanus*). J Anat Physiol 18:103–117

Simpson GG (1945) The principles of classification and a classification of mammals. Bull Am Mus Nat Hist 85:1–350

Savage RJG (1957) The anatomy of *Potamotherium*, an Oligocene lutrine. Proc Zool Soc Lond 129:151–244

Slijper EJ (1946) Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Kon Ned Akad Wet Verh (Tweede Sectie) 42:1–128

Souteyrand-Boulenger JD (1969) Le muscle articulaire de la hanche chez les carnivores. Mammalia 33:276–284

Spoor CF, Belterman TH (1986) Locomotion in Hyaenidae. Bijdr tot de Dierk 56: 24–28

Spoor CF, Badoux DM (1988) Descriptive and functional myology of the back and hindlimb of the striped hyena (*Hyaena hyaena*, L. 1758). Anat Anz Jena 167:313–321

Tarasoff FJ (1972) Anatomical observations on the river otter, sea otter and harp seal with reference to those structures that are of known

significance in thermal regulation and diving. PhD Thesis, McGill University, Montreal

Tarasoff FJ, Bisaillon A, Pierard J, Whitt AP (1972) Locomotory patterns and external morphology of the river otter, sea otter, and harp seal (Mammalia). Can J Zool 50:915–929

Taylor ME (1970) Locomotion in some East African viverrids. J Mammal 51:42–51

Taylor ME (1974) The functional anatomy of the forelimb of some African Viverridae (Carnivora). J Morphol 143:307–336

Taylor ME (1976) The functional anatomy of the hindlimb of some African Viverridae (Carnivora). J Morphol 148:227–254

Van de Graaff KM, Harper J, Goslow GE Jr (1982) Analysis of posture and gait selection during locomotion in the striped skunk (*Mephitis mephitis*). J Mammal 63:582–590

Van Valkenburgh B (1987) Skeletal indicators of locomotor behavior in living and extinct carnivores. J Vertebr Paleontol 7:162–182

Waibl H, Gasse H, Hashimoto Y, Burdas K-D, Constantinescu GM, Saber AS, Simoens P, Salazar I, Sotonyi P, Augsburger H, Bragulla H (2005) Nomina Anatomica Veterinaria. International Committee on Veterinary Gross Anatomical Nomenclature, World Association of Veterinary Anatomists, Hannover

Walker C, Vierck CJ, Ritz LA (1998) Balance in the cat: role of the tail and effects of sacrocaudal transaction. Behav Br Res 91:41–47

Walmsley B, Hodgson JA, Burke RE (1978) Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. J Neurophysiol 41:1203–1216

Watson M (1882) On the muscular anatomy of *Proteles* as compared with that of *Hyaena* and *Viverra*. Proc Zool Soc Lond 50:579–586

Williams RC (1955) The osteology and myology of the ranch mink (*Mustela vison*). PhD thesis, Cornell University Press, Ithaca

Williams SB, Payne RC, Wilson AM (2007) Functional specialisation of the pelvic limb of the hare (*Lepus europeus*). J Anat 210:472–490

Williams SB, Daynes J, Peckham K, Payne RC (2008) Functional anatomy and muscle moment arms of the thoracic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). J Anat 213:373–382

Williams SB, Wilson AM, Rhodes L, Andrews J, Payne RC (2008) Functional anatomy and muscle moment arms of the pelvic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). J Anat 213:361–372

Wilson DE, Mittermeier RA (2009) Handbook of the Mammals of the World, Vol. 1. Carnivores. Lynx Editions, Barcelona

Windle BCA (1888) Notes on the limb myology of *Procyon cancrivorus* and of the Ursidae. J Anat Physiol 23:81–89

Windle BCA (1889) The flexors of the digits of the hand. J Anat Physiol 24:72–84

Windle BCA, Parsons FG (1897) On the myology of the terrestrial Carnivora. Part I: muscles of the head, neck, and fore-limb. Proc Zool Soc Lond 65:370–409

Windle BCA, Parsons FG (1898) The myology of the terrestrial Carnivora. Part II. Proc Zool Soc Lond 66:152–186

Woods CA (1972) Comparative myology of jaw, hyoid, and pectoral appendicular regions of New and Old World hystricomorph rodents. Bull Am Mus Nat Hist 147:115–198

Wroe S, Lowry MB, Antón M (2008) How to build a mammalian super-predator. Zoology 111:196–203.

Yensen E, Tarifa T (2003) *Galictis vittata*. Mammal Species 727:1–8