Hindlimb Musculature of the Largest Living Rodent *Hydrochoerus hydrochaeris* (Caviomorpha): Adaptations to Semiaquatic and Terrestrial Styles of Life

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ABSTRACT The caviomorph species *Hydrochoerus hydrochaeris* (Cavioidea), or capybara, is the largest living rodent. This species is widely distributed, from northern South America to Uruguay and eastern Argentina, inhabiting in a wide variety of densely vegetated lowlands habitats in the proximity of water. *Hydrochoerus hydrochaeris* not only runs with agility, like other members of the Cavioidea, but it can also swim and dive easily. For these reasons, it has been classified as a cursorial as well as semiaquatic species. However, comprehensive anatomical descriptions of the osteology and myology of the capybara are not available in the literature and analyses on its swimming abilities are still required. We hypothesize that some of the characters of the hindlimb of *H. hydrochaeris* could reveal a unique morphological arrangement associated with swimming abilities. In this study, an anatomical description of the hindlimb musculature of *H. hydrochaeris*, and a discussion of the possible functional significance of the main muscles is provided. In addition, we explore the evolution of some myological and osteological characters of the capybara in the context of the cavioids. We concluded that most of the muscular and osteological features of the hindlimb of *H. hydrochaeris* are neither adaptations to a specialized cursoriality, nor major modifications for an aquatic mode of life. *Hydrochoerus hydrochaeris* share several features with other cavioids, being a generalized cursorial species in the context of this clade. However, it shows some adaptations of the hindlimb for enhancing propulsion through water, of which the most notable seems to be the shortening of the leg, short tendons of most muscles of the leg, and a well-developed soleus muscle. These adaptations to a semiaquatic mode of life could have been acquired during the most recent evolutionary history of the hydrochoerids. J. Morphol. 277:286–305, 2016. © 2015 Wiley Periodicals, Inc.

INTRODUCTION

The caviomoph species *Hydrochoerus hydrochaeris* (Cavioidea), the capybara, is the largest living rodent. Within the Caviomorpha clade (i.e., New World Hystricognathi) this species is widely distributed, from northern South America (Ecuador, Colombia, Venezuela and Guianas) to Uruguay and eastern Argentina (Mones and Ojasti, 1986; Moreira et al., 2013). The capybara is a social rodent that lives in a wide variety of densely vegetated lowlands habitats in the proximity of water (Mones and Ojasti, 1986; Nowak, 1991). Without doubt, *H. hydrochaeris* is well known and noticeable because of its large size, about 50 kg (Mones and Ojasti, 1986), exceeding the size of any other extant rodent.

In taxonomy, *H. hydrochaeris* and *H. isthmius* (the other species of the genus) have been assigned to its own family, Hydrochoeridae (e.g., Woods, 1984). More recent phylogenetic analyses based on molecular (Rowe and Honeycutt, 2002; Rowe et al., 2010; Fabre et al., 2012; Upham and Patterson, 2012) and morphological characters (Pérez and Pol, 2012) included *Hydrochoerus* within Caviidae, related to the rock cavy (*Kerodon*). This clade also comprises the cavies (*Cavia, Galea, Microcavia*) and the maras (*Dolichotis* and *Pediolagus*). Caviidae (including the capybara), together with Dasyproctidae and Cuniculidae, belong to the Cavioidea, all of which show a cursorial mode of locomotion (e.g., Woods, 1972; Rocha-Barbosa et al., 2002; Casinos et al., 1996; Candela and Picasso, 2008; García-Esponda and Candela, 2010). Cavioidea is one of the main lineages in which the caviomorphs diversified during the Cenozoic, after their arrival to South America

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(Antoine et al., 2012), occupying a wide spectrum of habitats and substrates. Nevertheless, the capybara not only runs with agility, as other members of the clade, but it can also swim and dive easily. For these reasons, *H. hydrochaeris* has been classified as a cursorial as well as semiaquatic species (e.g., Elissamburu and Vizcaíno, 2004; Samuels and Van Valkenburgh, 2008). The capybara possesses some features related to its semiaquatic mode of life, such as the partial webbing of the digits of the manus and pes, and a dorsal position of the nostrils, eyes, and ears (Howell, 1930). Furthermore, it is the only semiaquatic rodent that has developed a quadrupedal paddling mode of swimming (Howell, 1930; Fish, 1993; Samuels and Van Valkenburgh, 2008). However, the postcranial skeleton of the capybara has been regarded as not particularly adapted for swimming (Mones and Ojasti, 1986), but comprehensive anatomical descriptions of this species are not provided (Mones and Ojasti, 1986, but see Araújo et al., 2012).

Considering its habits and substrate preferences, we hypothesize that at least some of the anatomical features of the hindlimb of *H. hydrochaeris* could reveal a particular or unique morphological arrangement associated with swimming, when compared with other groups of cavioids and other rodents.

Here, we provide a detailed anatomical description of the hindlimb musculature of *H. hydrochaeris* and discuss the possible functional significance of the main muscles analyzed. On this basis, we evaluate the probable relationships of both myological and osteological features of the hindlimb with its locomotor behavior. In addition, we explore the evolution of some of these characters, and its potential value as synapomorphies in the context of the main clades identified. Finally, we interpret the probable evolution of the semiaquatic habits of the living capybara, in the context of the cavioids.

MATERIALS AND METHODS

Dissections of the right and left hindlimbs of two adults (male and female) and one subadult (male) specimens of *Hydrochoerus hydrochaeris* (Linnaeus, 1766) were performed. The specimens died at La Plata Zoo (Jardín Zoológico y Botánico de La Plata, Argentina). With comparative purposes, we also made dissections of the hindlimbs of three adult Guinea pigs [*Cavia porcellus* (Linnaeus, 1758)], donated from the Instituto Biolgico Tomás Perón (La Plata). Guinea pig specimens were preserved in a solution composed of one part formalin to 18 parts water saturated with NaCl (Rinker, 1954; Woods, 1972), whereas capybaras specimens were preserved in a 10% formalin solution. Dissected specimens were deposited at the Museo de Ciencias Naturales "P. Scasso" (MPS-Z), San Nicolás, Argentina (*H. hydrochaeris*: MPS-Z 141-143, *C. porcellus*: MPS-Z 144-146).

Dissections were conducted under a magnifying glass (2×) or under a binocular microscope using magnifications of 7–15×. Areas of origin and insertion of the muscles, as well as their topographic relationships were analyzed. Photographs were taken at each level of dissection and muscle origins and insertions were mapped on hindlimb skeletons of museum specimens. Each muscle was carefully removed and blotted dry. External tendons were then removed and muscle belly mass was recorded to the nearest 0.01 g using an electronic scale. For each muscle and muscle groups (with the exception of the muscles of the pes), the percentage values relative to the total mass of the hindlimb were calculated. Literature data on the anatomy of the hindlimb musculature of other caviomorphs was also reviewed (Mivart and Murie, 1866; Beddard, 1891; Parsons, 1894; Windle, 1897; Wood and White, 1950; McEvoy, 1982; Rocha-Barbosa et al., 2007; García-Esponda and Candela, 2010, 2015).

Osteological features of *Hydrochoerus*, *Cavia*, *Galea*, *Microcavia*, *Dasyprocta*, *Myocastor*, *Ctenomys*, *Lagostomus*, *Chinchilla*, and *Coendou* were examined in specimens housed at the Centro Nacional Patagónico (CENPAT, Puerto Madryn, Argentina), the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Buenos Aires, Argentina), the Museo de Ciencias Naturales "P. Scasso" (MPS-Z, San Nicolás, Argentina), Museo Municipal de Ciencias Naturales "Lorenzo Scaglia"(MMPMa, Mar del Plata, Argentina), and the Museu Nacional (MN, Rio de Janeiro, Brazil; a list of these specimens is provided in supporting information Apendix S1). Number of vertebrae observed in *H. hydrochaeris* was: thirteen thoracic (T1–T13), six lumbar (L1–L6); four sacral (S1–S4), and seven caudal (Cd1–Cd7).

The osteological nomenclature used in this study follows that used by Candela and Picasso (2008) and Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 2005). The myological nomenclature and the muscular system arrangement was that of McEvoy (1982) for erethizontids, which is in agreement with other studies on rodent musculature (e.g., Rinker, 1954; Klingener, 1964). Muscle function was inferred from the literature (e.g., Liebich et al., 2004; Bezuidenhout and Evans, 2005) and by manipulating the specimens dissected. In particular, we discussed those muscular and associated osteological features of the hindlimb of *Hydrochoerus* that we consider relevant for functional interpretations. Most of the osteological characters of cavioids used in the comparisons have been previously discussed by Candela and Picasso (2008). Comparisons with other species of Caviomorpha were centered on intergeneric morphological variation, so, in the text, all the species analyzed are referred to by their generic names. The morphological variation of caviomorphs analyzed correspond to six families (Erethizontidae, Dasyproctidae, Ctenomyidae, Chinchillidae, Echimyidae, and Caviidae), that belong to all (i.e., four) higher taxa nested in this clade (e.g., Fabre et al., 2012; Voloch et al., 2013). In addition, we examined the morphological variation of the hindlimb in the main clades of noncaviomorph rodents, obtained from García-Esponda and Candela (2015, and bibliography therein).

The overall morphological variation observed among rodents was coded in 14 characters using the characters of the hindlimb analyzed in García-Esponda and Candela (2010, 2015) as a basis. Character state definitions are provided in supporting information Appendix S1; the resultant data matrix is provided in supporting information Table S1; sources of information used for coding character states for each taxa analyzed are provided in supporting information Table S2. The evolution of these characters was mapped on a composite molecular phylogeny of Rodentia (Rowe and Honeycutt, 2002; Blanga-Kanfi et al., 2009; Fabre et al., 2012; Upham and Patterson, 2012), including those caviomorphs for which the myological information was available. Cladistic mapping was done with TNT 1.0 software (Goloboff et al., 2003). Character states were considered unordered, except character 3. The tree was edited with WINCLADA (Nixon, 1999). Of the 14 characters analyzed, the character states 1–6 correspond to those described in García-Esponda and Candela (2015), whereas the characters 7–14 correspond to the characters 1–8 of García-Esponda and Candela (2010). Anatomical data of noncaviomorph genera included in
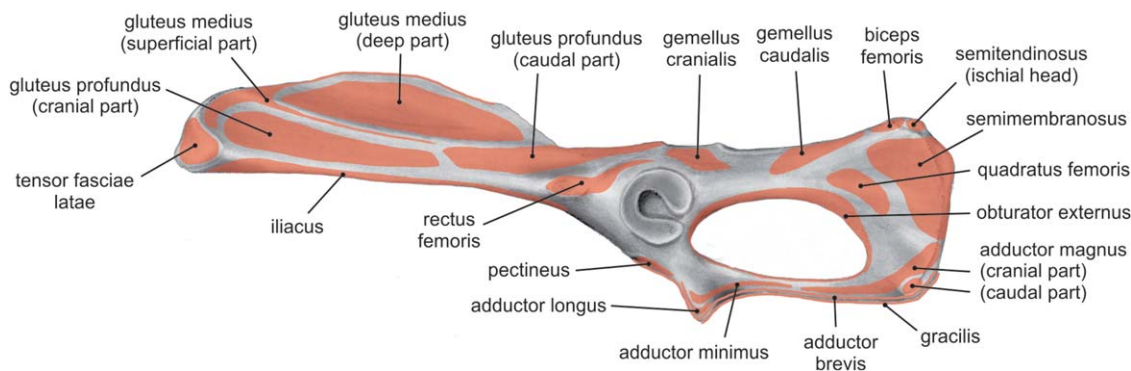
Fig. 1. *Hydrochoeris hydrochaeris*, lateral view of the left coxal bone showing areas of muscle attachment. All areas represent origin of muscles.

the data matrix were taken from García-Esponda and Candela (2015) and completed (characters 7–14) using information from Alezais (1900), Hill (1937), Bryant (1945), Rinker (1954), Fry (1961), Klingener (1964), Ryan (1989; see supporting information Table S2). Character states of myological features of *H. hydrochaeris* were completed with data from this study.

RESULTS
Weighing

Weights for muscle groups of the hindlimb of *H. hydrochaeris* are presented in supporting information Table S3. A comparison with *C. porcellus* indicated that, in spite of their great size disparity, muscle mass distributions showed minor differences between both species.

Myology
Extensor system.
Iliacus group.

Musculus iliacus. The origin of the m. iliacus (Figs. 1, 6, and 7) is from the ventral cranial iliac spine, the iliac fossa, and the broad ventral border of the wing of the ilium, extending distally to the tuberosity for the origin of the m. rectus femoris. A few cranial muscular fibers originate from the proximal part of the inguinal ligament. A fascia from the m. gluteus medius, which inserts on the lateral crest of the ilium, separates this muscle from the m. gluteus profundus. Distally, the muscular fibers of the m. iliacus blend with those of the m. psoas major to constitute the m. iliopsoas (Fig. 2). The m. iliopsoas inserts by a strong wide tendon onto the lesser trochanter of the femur. The m. iliacus flexes the hip joint; when the leg is fixed in position, it flexes the vertebral column.

Musculus psoas major. The m. psoas major (Fig. 7) takes origin from the ventral aspect of the bodies of T13–S1 and from the ventral surface of the transverse processes of L4–S1. This muscle can be divided into two parts: a lateral portion, originating from T13–L4, and a medial portion, originating from L5–S1; the femoral nerve passes between both parts. Distally, the m. psoas major blends with the caudal fibers of the m. iliacus to constitute the m. iliopsoas (Fig. 2). It inserts via a strong wide tendon, onto the lesser trochanter of the femur, extending distally near the common insertion of the mm. pectineus and adductor longus. The m. psoas major flexes the hip joint; when the leg is fixed in position, it flexes the vertebral column.

Musculus psoas minor. The m. psoas minor (Fig. 7) is a slender muscle that lies medial to the m. posas major (Fig. 7). It takes origin from the ventral surfaces of the bodies of L2–L4. It inserts by a thin long tendon onto the iliopubic eminence. The m. psoas minor is a weak flexor of the vertebral column.

Musculus pectineus.   The m. pectineus (Figs. 1, 2B,C, and 8) lies cranial to the m. adductor longus and lateral to the m. adductor brevis. It arises from the iliopubic eminence of the pubis and adjacent area. The m. pectineus inserts onto the caudal surface of the body of the femur, in common with the m. adductor longus. Both muscles insert onto a longitudinal fossa, distally located to the lesser trochanter, which is part of the medial lip of the facies aspera. At the insertion, the cranial and caudal surfaces of the muscle are covered by fibrous aponeuroses. The m. pectineus adducts the hip joint.

Gluteal group.

Musculus tensor fasciae latae. The mm. tensor fasciae latae (cranially, Figs. 1, 5, 7, and 8) and gluteus superficialis (caudally) form a continuous superficial muscular sheet, that partially covers the lateral aspect of the thigh and the ventral portion of the gluteal musculature. This muscular sheet has a triangular outline, with its apex pointing to the knee and its base horizontally oriented, extending from the ventral cranial iliac spine to the greater trochanter. The m. tensor fasciae latae takes origin from the ventral cranial iliac spine and the cranial part of the inguinal ligament. This
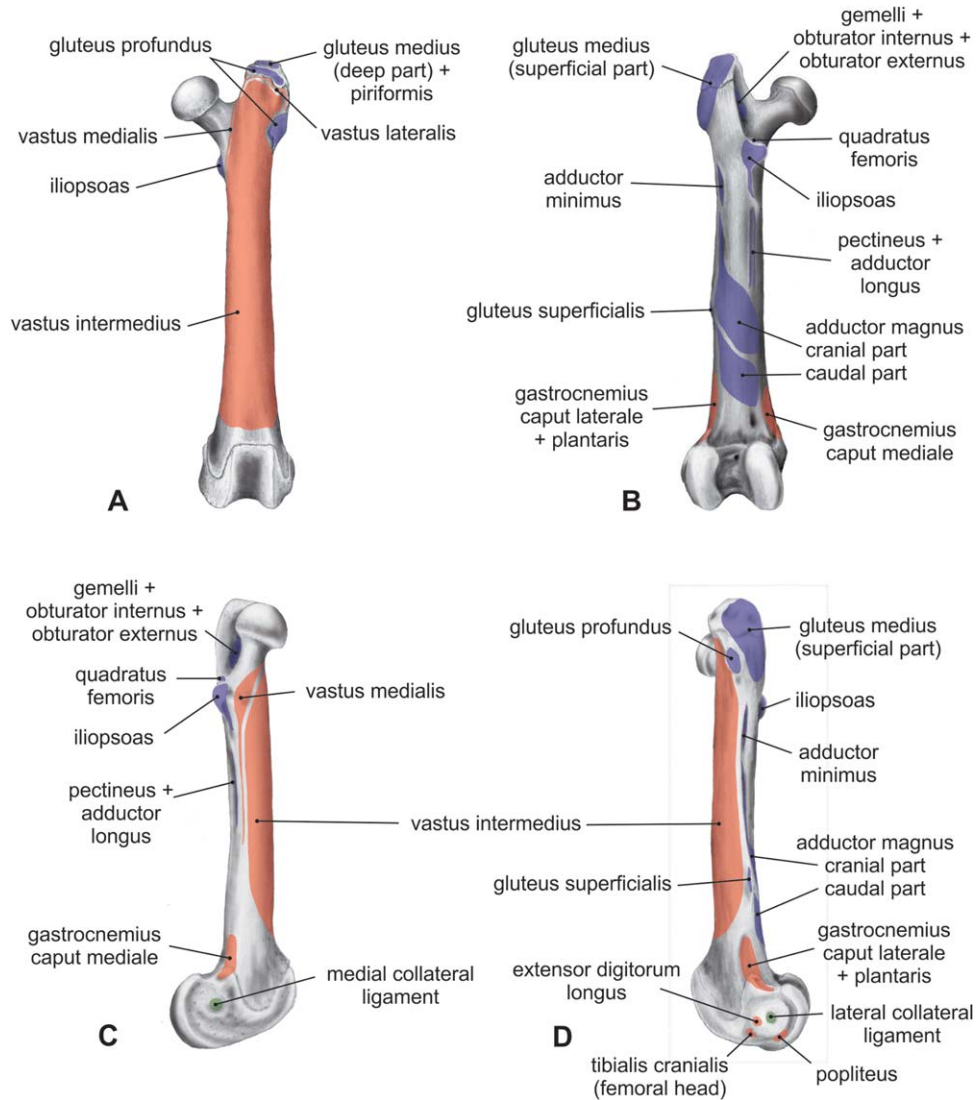
Fig. 2. *Hydrochoeris hydrochaeris*, left femur showing areas of muscle attachment. **A**, cranial; **B**, caudal; **C**, medial; **D**, lateral views. Red, areas of muscle origin; blue, areas of muscle insertion; green, areas of ligament attachment.

muscle covers the laterocranial and cranial portions of the m. quadriceps femoris. The m. tensor fasciae latae inserts onto the fascia lata. Its cranial fibers extend far distally, very close to the patella, also inserting onto its proximal border. The m. tensor fasciae latae tenses the fascia lata, flexes the hip joint and extends the knee joint.

Musculus gluteus superficialis. As stated above, the m. gluteus superficialis (Figs. 2B,D, 5, and 6) constitutes the caudal part of a superficial muscular sheet constituted in common with the m. tensor fasciae latae. The m. gluteus superficialis lies cranial to the m. femorococcygeus and lateral to the mm. quadriceps femoris and gluteus medius. The origin of this muscle is mainly from the lumbodorsal fascia. Its cranial fibers insert onto the fascia lata, while its caudal fibers insert, by a

strong flat tendon, onto the third trochanter of the femur. This tendon of insertion runs in the same direction as the caudal border of the muscle. The m. gluteus superficialis flexes the hip joint.

Musculus gluteus medius. The m. gluteus medius (Figs. 1, 2A,B,D, 5, and 6) is the largest of the muscles of the hindlimb. It takes origin from the iliac and gluteal crests, the dorsal gluteal fossa, and the sacral tuberosity of the ilium; also from the lateral sacral crest, the gluteal fascia, the fascia over the mm. erector spinae and transversospinalis, and the spinous processes of S1–S3. The m. gluteus medius inserts onto the greater trochanter of the femur. This muscle is composed of a larger superficial part and a smaller deep part. The superficial part completely covers the deep part and the mm. gluteus profundus and piriformis.
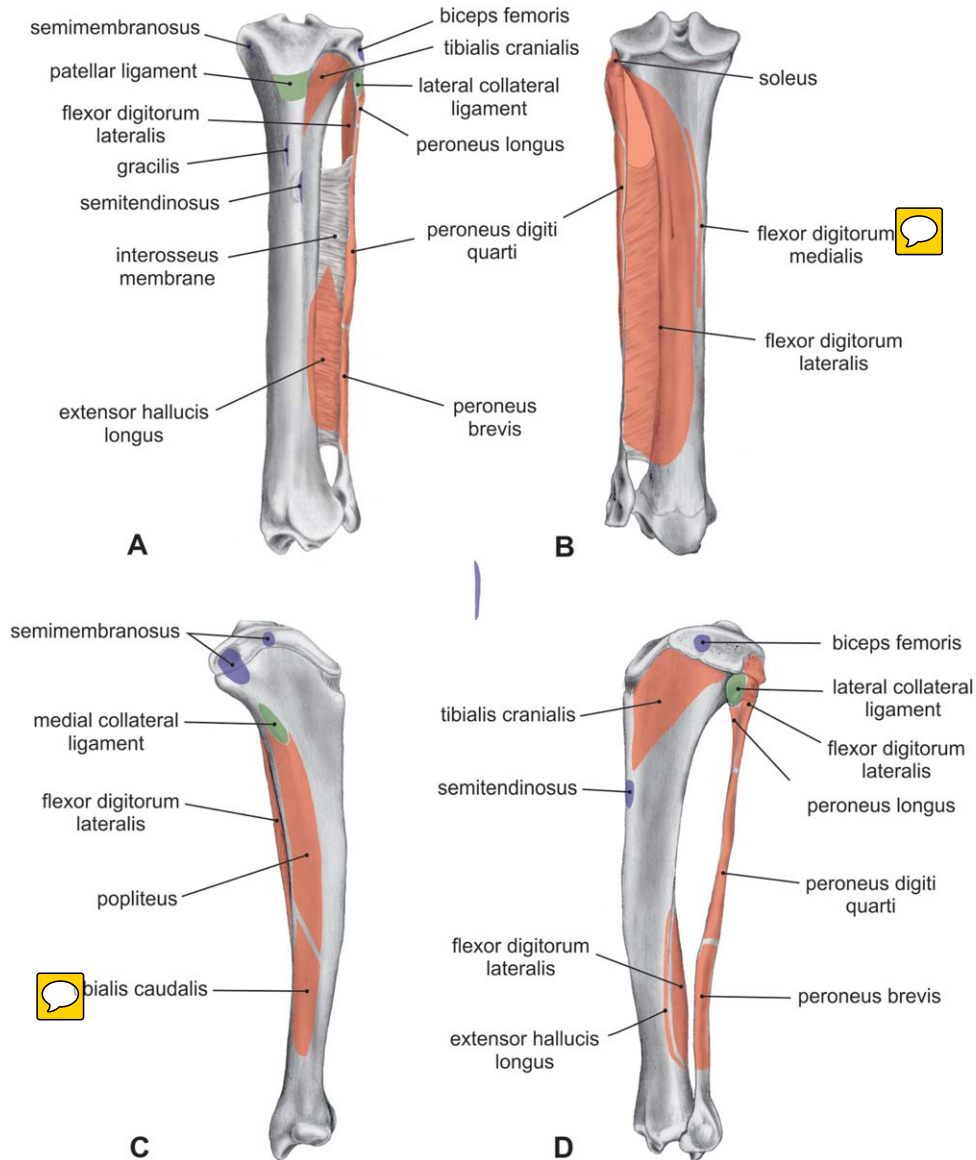
Fig. 3. *Hydrochoeris hydrochaeris*, left tibia and fibula showing areas of muscle attachment. **A**, cranial; **B**, caudal; **C**, medial; **D**, lateral views. Red, areas of muscle origin; blue, areas of muscle insertion; green, areas of ligament attachment.

The deep surface of the superficial part gives rise to a muscular septum, which takes its origin from the gluteal crest of the ilium. This septum separates two deep compartments: a dorsal one, which lodges the deep part of the m. gluteus medius and the m. piriformis, and a ventral one, which lodges the m. gluteus profundus. The dorsal muscular fibers of the superficial part of the m. gluteus medius extend more cranially than the iliac crest, up to the level of L4, forming a "gluteal tongue." This "gluteal tongue" inserts like a wedge among the erector spinae musculature. The deep part of the m. gluteus medius takes origin from the dorsal gluteal fossa of the ilium. This part is intimately related to the m. piriformis, especially at its cau-

dal border, but it is easy to separate from it at their origins. The fibers of the superficial part of the m. gluteus medius pass over the greater trochanter of the femur to insert onto its caudal surface; the deep part of this muscle inserts onto the apex of the greater trochanter, together with the m. piriformis. The m. gluteus medius extends and abducts the hip joint.

Musculus gluteus profundus. The m. gluteus profundus (Figs. 1, 2A,D, and 6) originates from the ventral gluteal fossa of the ilium, extending caudally onto the body of the ilium on an area dorsal to the tuberosity for the origin of m. rectus femoris and to the acetabulum. This muscle is incompletely divided into a cranial part, with its fibers more or
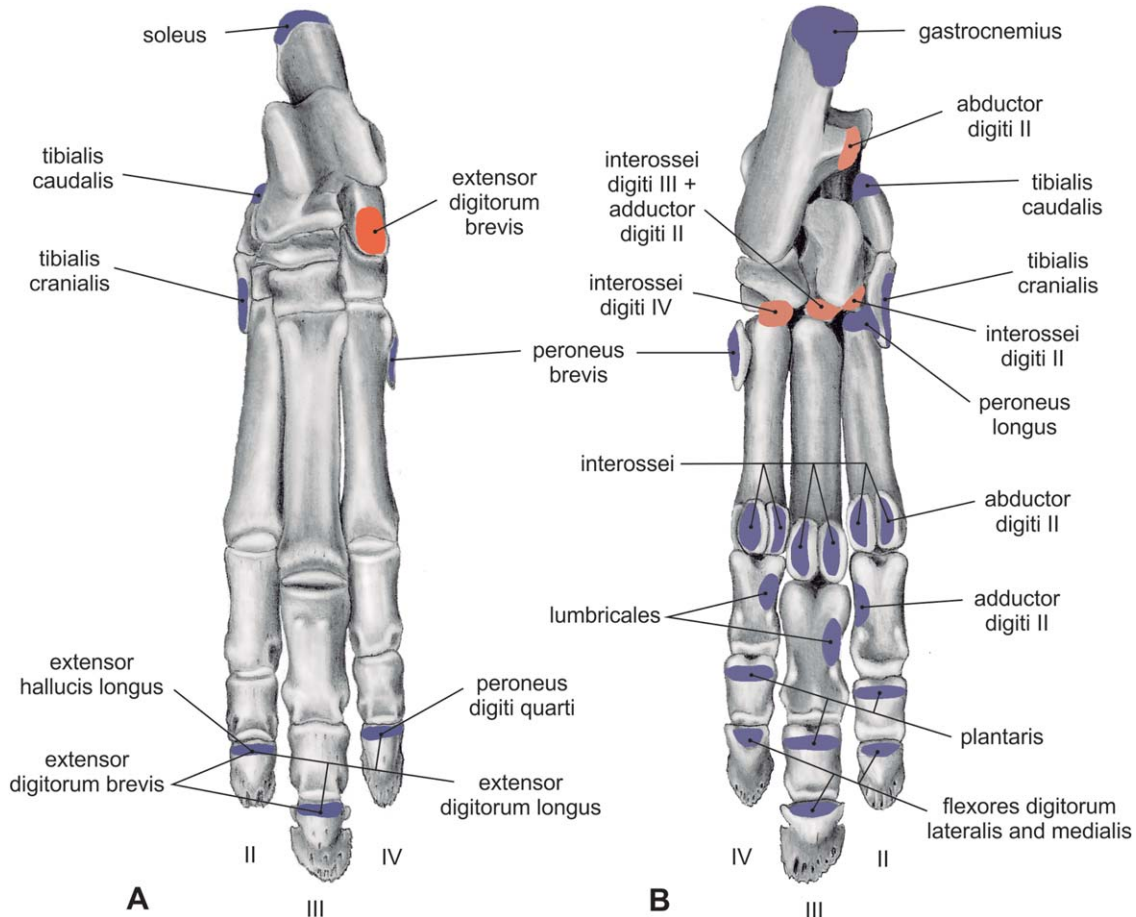
Fig. 4. *Hydrochoeris hydrochaeris*, left foot showing areas of muscle attachment. **A**, dorsal; **B**, plantar views. Red, areas of muscle origin; blue, areas of muscle insertion.

less oriented in a craniocaudal direction, and a caudal part, with its fibers oriented more transversely. A branch of the cranial gluteal nerve pierces this muscle and continues distally to innervate the m. tensor fasciae latae. The ventral border of the m. gluteus profundus develops a very strong tendon that inserts onto the lateral crest of the greater trochanter, passing between the two heads of origin of the m. vastus lateralis (see below). This tendon is continuous with the remaining insertion of the muscle onto the proximal end of the greater trochanter, but in the adult female specimen it was almost independent. The m. gluteus profundus abducts and extends the hip joint.

Musculus piriformis. The m. piriformis (Figs. 2A and 6) has a compressed pyramidal shape, lying medial to the superficial portion of the m. gluteus medius and caudal to the deep portion of this muscle. It originates from the ventral aspect of the transverse processes of the first to third sacral vertebrae. The m. piriformis inserts onto the proximal end of the greater trochanter of the femur, in common with the deep portion of m. gluteus medius. The m. piriformis abducts and extends the hip joint.

Musculus femorococcygeus. The m. femorococcygeus (Figs. 5 and 6) is located at the superficial muscular layer of the hip and thigh. At its origin, it lies between the mm. gluteui superficialis and medius and the m. semitendinosus; distally, it is located between the mm. vastus lateralis and biceps femoris. In lateral view, the m. femorococcygeus has a long triangular outline, with a broad origin at the vertebral column and a thinner distal end. This muscle arises from the spinous processes of S4–C1 and from the gluteal fascia. After its origin, the muscle passes over the greater trochanter of the femur to continue distally down to the knee. Insertion is made by a tendon onto the lateral border of the patella. The m. femorococcygeus abducts and extends the hip joint.

Musculus tenuissimus (abductor cruris caudalis). This muscle is absent in *H. hydrochoeris*.

Quadriceps femoris group.

Musculus rectus femoris. The m. rectus femoris (Figs. 1, 7, and 8) is a spindle-shaped bipinnate muscle located between the mm. vasti lateralis and medialis, and cranial to the m. vastus intermedius. This muscle takes origin by a very strong tendon
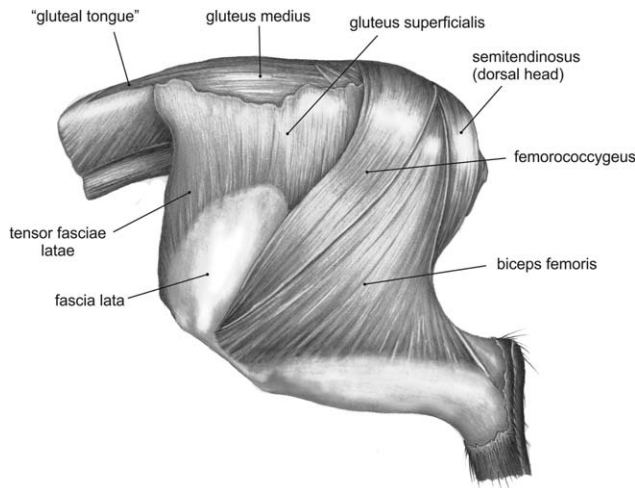
Fig. 5. *Hydrochoeris hydrochaeris*, lateral superficial view of the left hindlimb.

from an area located cranial and dorsal to the acetabulum, which comprises the femoral tuberosity. No clear evidence of a division in straight and reflected heads of origin was observed. The m. rectus femoris is almost entirely covered by the mm. vasti, mainly by the m. vastus lateralis. Insertion is made by a short and strong tendon onto the proximal border of the patella, cranial to the insertion of the m. vastus intermedius. The m. rectus femoris flexes the hip joint and extends the knee joint.

Musculus vastus lateralis.   The m. vastus lateralis (Figs. 2A and 6−8) lies lateral to the m. rectus

femoris, superficially covering the lateral and cranial aspects of this muscle. The m. vastus lateralis originates from the greater trochanter of the femur, between the insertion of the m. gluteus profundus and the proximal origin of the m. vastus intermedius. At its origin, the muscle is divided into two short heads; a larger and more superficial head, and a smaller, more fibrous and deeper head. Between both heads there is a slit, where the tendon of the cranial portion of the m. gluteus profundus passes, to insert on the greater trochanter of the femur (see above). At its distal part, the deep surface of the m. vastus lateralis has a fibrous fascia that blends with that of the mm. vastus intermedius and gastrocnemius and with the tendon of insertion of the m. femorococcygeus. The m. vastus lateralis inserts onto the lateral border of the patella. This muscle extends the knee joint.

Musculus vastus medialis.   The m. vastus medialis (Figs. 2A,C, 7, and 8) is located medial to the m. rectus femoris, partially covering it. This muscle arises from a narrow area at the craniomedial aspect of the femoral shaft. This area of origin extends from the greater trochanter of the femur to the level of the insertion of the m. pectineus. Some of the most proximal fibers of the m. vastus medialis blend with those of the m. vastus intermedius. The m. vastus medialis inserts onto the medial border of the patella. This muscle extends the knee joint.

Musculus vastus intermedius.   The m. vastus intermedius (Figs. 2A,C,D) is the deepest of the muscles that constitute the m. quadriceps femoris.
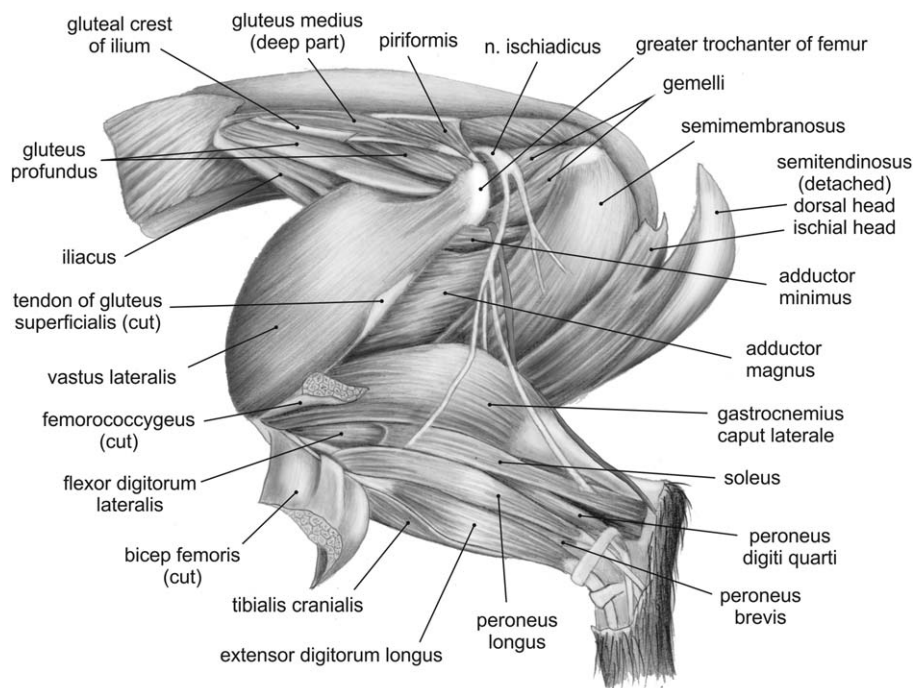

Fig. 6. *Hydrochoeris hydrochaeris*, lateral deep view of the left hindlimb.
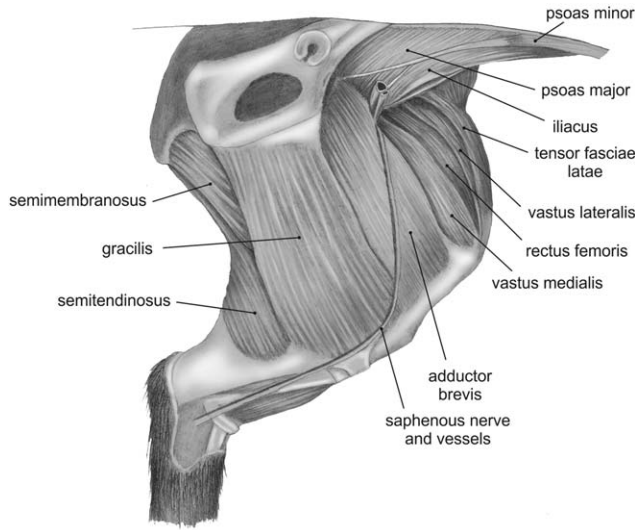
Fig. 7. *Hydrochoeris hydrochaeris*, medial superficial view of the left thigh (part of the right coxal bone is showed without muscles).

This muscle takes origin from the cranial, lateral, and medial surfaces of the femoral shaft, extending from the greater trochanter to the distal end of the femur. Some of the most proximal fibers of the m. vastus intermedius blend with those of m. vastus medialis. It inserts onto the proximal bor-

der of the patella, deep to the insertion of the m. rectus femoris. The m. vastus intermedius extends the knee joint.

Tibial extensor group.

Musculus extensor digitorum longus. The m. extensor digitorum longus (Figs. 2D, 4A, 6, 10, and 11A) lies at the cranial compartment of the leg, lateral to the m. tibialis cranialis and superficial to the m. extensor hallucis longus. It is a fusiform unipennate muscle that takes origin by a strong tendon from the extensor fossa of the lateral condyle of the femur, cranial to the origin of the lateral collateral ligament. This tendon passes lateral to the groove that houses the tendon of the m. tibialis cranialis, running parallel to it. From the distal fourth of the deep medial aspect of the m. extensor digitorum longus, a flat fascicle of muscle fibers separate from its belly and course proximally to insert onto the fascia that covers the proximal lateral aspect of the femoral head of the m. tiabialis cranialis; blending of muscle fibers from both muscles was not observed. The tendon of insertion of the m. extensor digitorum longus originates just proximal to the crural extensor retinaculum, passing deep to it and lateral to the tendons of mm. extensor hallucis longus and tibialis cranialis; distally it is independently fastened by the tarsal extensor retinaculum. Immediately distal to the origin of this tendon, the branch to the digit II is
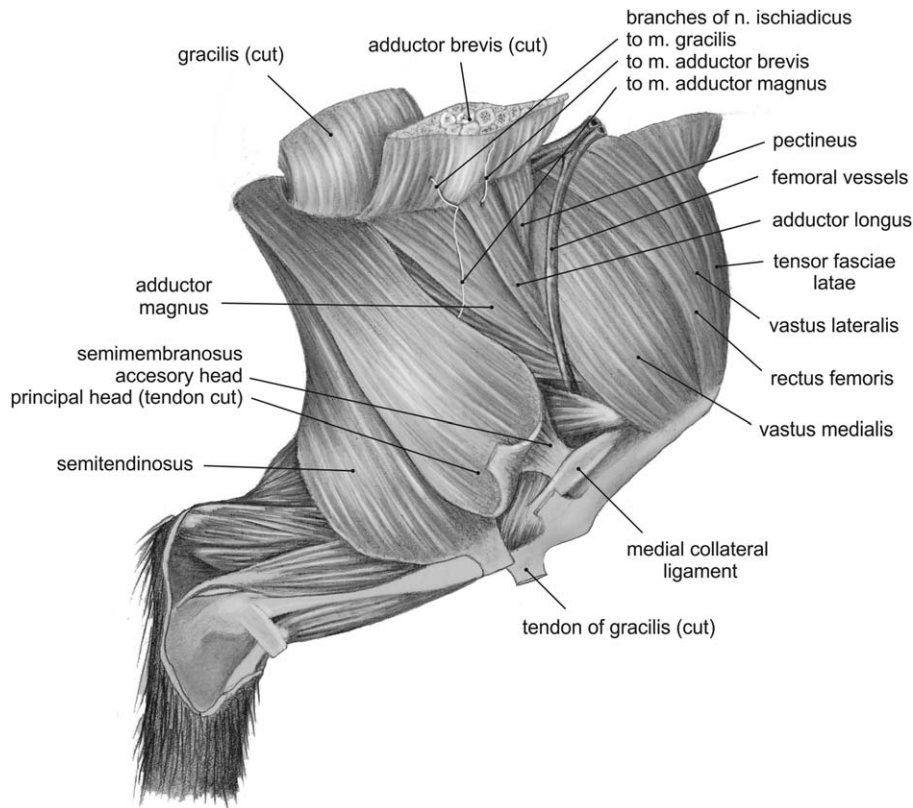

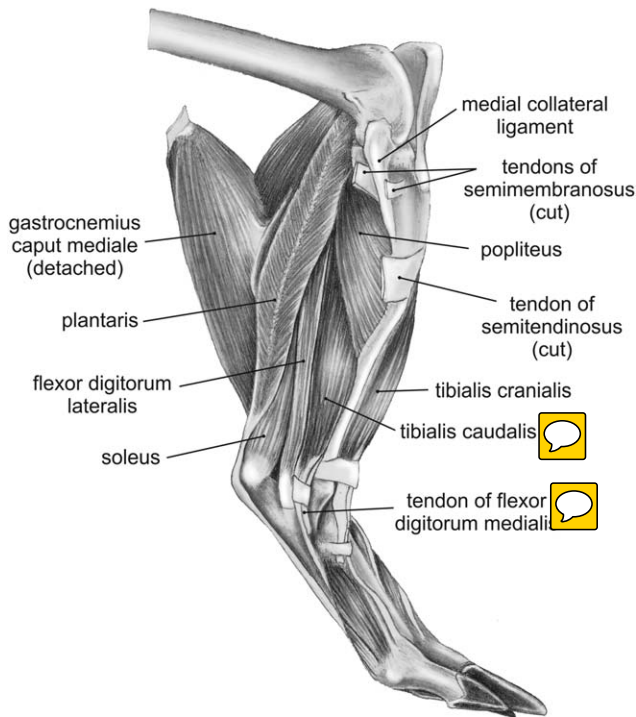Fig. 8. *Hydrochoeris hydrochaeris*, medial deep view of the left thigh.

Fig. 9. *Hydrochoeris hydrochaeris*, medial view of the left leg and foot.

originated, whereas the branches to digits III and IV separate after passing the tarsal extensor retinaculum. All these branches course on the dorsal aspect of the pes to end onto the distal phalanges of the three digits. The m. extensor digitorum longus dorsiflexes the ankle joint and extends the joints of all digits.

Musculus tibialis cranialis. The m. tibialis cranialis (Figs. 2D, 3A,D, 4, 6, 9, 10, and 11A) is located at the cranial compartment of the leg, medial to the m. extensor digitorum longus and cranial to the m. extensor hallucis longus. This muscle is composed of two heads: femoral and tibial. The spindle-shaped femoral head takes origin by a long tendon from a small pit of the lateral condyle of the femur. This tendon passes in the cranial groove of the tibia (extensor fossa?). The tibial head has a fleshy origin from the proximal portion of the lateral fossa of the tibia. At its medial aspect, the femoral head is enfolded by the tibial head; at its lateral aspect, it receives a fascicle of muscular fibers from the m. extensor digitorum longus (see above). Both heads of the m. tibialis cranialis are easily separable from each other from their origins to about their midlengths; from this point, they are intimately united, but even separated by a fascia that is distally continuous with the tendon of insertion of the muscle. The muscle architecture of both heads of m. tibialis cranialis is quite different: the tibial head is composed of muscle fibers that are almost parallel to the line of action of the muscle, whereas those of the femoral head have a bipinnate arrangement. The tendon of insertion of the m. tibialis cranialis passes deep to the crural extensor retinaculum,
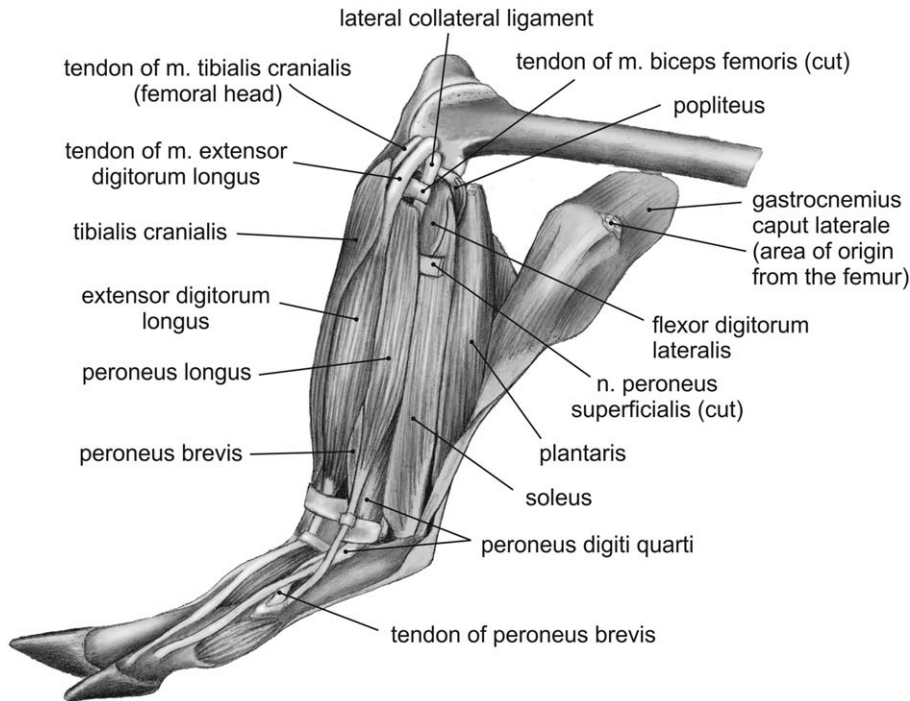

Fig. 10. *Hydrochoeris hydrochaeris*, lateral view of the left leg and foot.
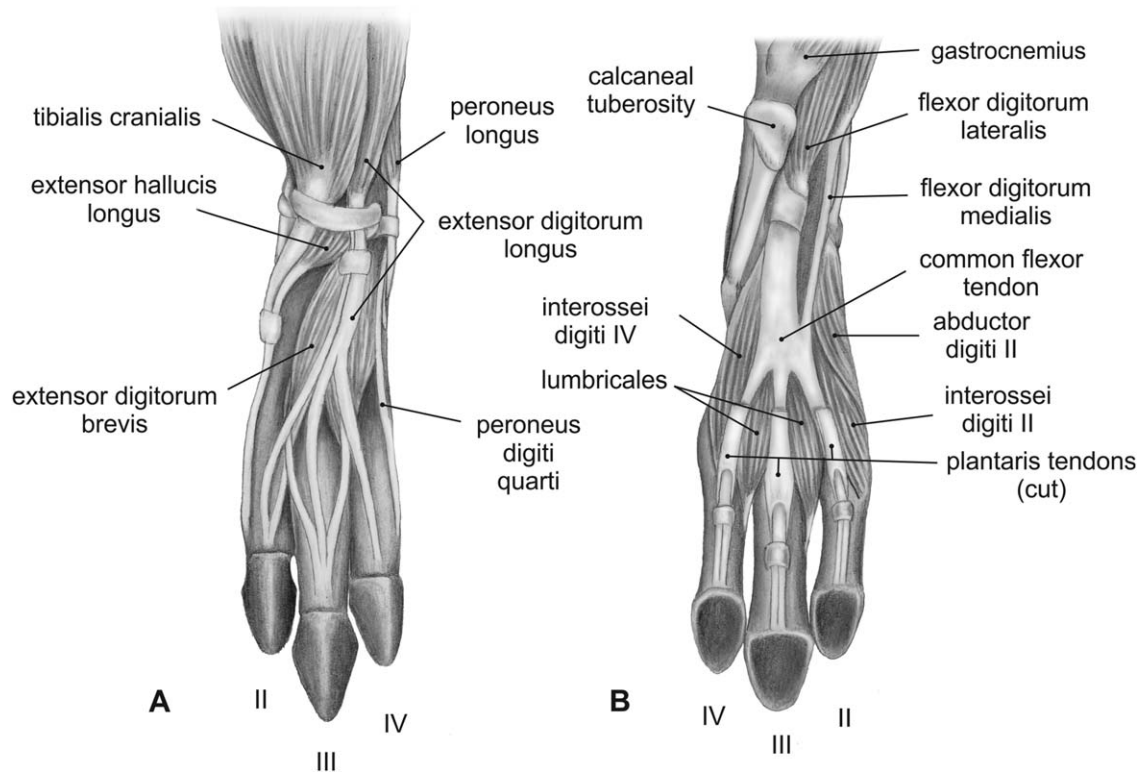
Fig. 11. *Hydrochoeris hydrochaeris*, left foot. **A**, dorsal; **B**, plantar views.

lying medial to the distal fibers of the m. extensor hallucis longus. Distally, the tendons of both muscles share a ligamentous loop, and then, that of the m. tibialis cranialis courses to the medial side of the foot to end onto the medial cuneiform bone. The m. tibialis cranialis dorsiflexes the ankle joint and weakly inverts the foot.

Musculus extensor hallucis (digiti I) longus. The m. extensor hallucis longus (Figs. 3A,D, 4A, and 11A) lies at the cranial compartment of the leg, caudal to the mm. tibialis cranialis and extensor digitorum longus. It is a flat triangular muscle that arises from the distal two thirds of the cranial aspects of the tibia and fibula, and from the interosseus membrane between these bones. Its distal muscular fibers pass deep to the crural extensor retinaculum, between the tendons of the mm. tibialis cranialis and extensor digitorum longus. Distal to this retinaculum, the muscular fibers give rise to the tendon of insertion, which passes through a ligamentous loop along with the m. tibialis cranialis tendon. After passing this loop, the tendon of the m. extensor hallucis longus angles and courses onto the dorsolateral aspect of metatarsal and digit II to insert onto the distal phalanx. The m. extensor hallucis longus dorsiflexes the ankle joint and extends digit II.

Musculus extensor digitorum brevis. The m. extensor digitorum brevis (Figs. 4A and 11A) is a

small muscle that lies on the dorsal surface of the foot, ventral to the tendinous digital branches of the m. extensor digitorum longus. It is composed of two bellies that originate from the dorsal aspect of the calcaneus, cranial to the lateral articular surface for the astragalus; it also arises from the tarsal extensor retinaculum. The lateral belly of the m. extensor digitorum brevis partially covers the fourth metatarsal and gives rise to a tendon that course on the lateral aspect of digit III to join the digital branch of the m. extensor digitorum longus tendon to this digit. The medial belly partially covers the third metatarsal and gives rise to two tendons: one of them courses on the medial aspect of digit III to join the digital branch of the m. extensor digitorum longus tendon to this digit, the other courses on the lateral aspect of digit II to join the digital branch of the m. extensor digitorum longus tendon to this digit. The m. extensor digitorum brevis extends the joints of digits II and III.

Peroneal group.

Musculus peroneus longus. The m. peroneus longus (Figs. 3A,D, 4B, 6, 10, and 11A) is a unipennate muscle that lies at the lateral compartment of the leg, lateral to the mm. peronei digiti IV and brevis. This muscle arises from the craniolateral aspect of the fibular head and from the lateral collateral ligament. Their muscular fibers extend along almost the entire length of the leg,

giving rise to a tendon a few millimeters before reaching the fibular retinaculum, on the lateral malleolus. After passing the retinaculum, the tendon runs to the tarsus, coursing superficial to the tendons of the mm. peronei digiti IV and brevis. Distally, the tendon passes in the grooves for this muscle located at the calcaneus and cuboid bones, to finally turn under the tarsus. There, the tendon travels toward the medial aspect of the foot into a perpendicular canal, cranially located to the cuboid and navicular bones, to finally insert onto the ventral aspect of the proximal end of metatarsal II and ventral aspect of the entocuneiform. The m. peroneus longus plantarflexes the ankle joint and weakly everts the foot.

Musculus peroneus brevis. The m. peroneus brevis (Figs. 3A,D, 4, 6, and 10) is the smallest of the peroneal muscles. It lies medial to the m. peroneus longus and cranial to the m. peroneus digiti quarti, taking origin from the distal third of the fibula. Distally, just before reaching the fibular retinaculum on the lateral melleolus, it gives rise to a tendon that shares the compartment of this retinaculum with the tendon of the m. peroneus digiti quarti, lying caudal to the latter. After passing the retinaculum, the tendon of the m. peroneus brevis runs to the tarsus, coursing deep to the tendons of the mm. peronei digiti quarti and longus, to insert on the lateral aspect of the reduced fifth metatarsal. The m. peroneus brevis assists in plantarflexing the ankle joint and everting the foot.

Musculus peroneus digiti quarti. The m. peroneus digiti quarti (Figs. 3A,B,D, 4A, 6, 10, and 11A) lies at the lateral compartment of the leg, medial to the m. peroneus longus. It is a unipennate muscle that arises from the lateral aspect of the proximal three quarters of the fibular shaft, and from the fascia separating this muscle and the m. flexor digitorum fibularis. At the distal end of the fibula, the m. peroneus digiti quarti gives rise to the tendon of insertion, which passes deep to the fibular retinaculum, coursing into a groove on the caudal border of the lateral malleolus. The most distal muscular fibers of the muscle extend on the caudal aspect of the tendon into the retinaculum. At the fibular retinaculum, the tendon of the m. peroneus digiti quarti lies caudal to that of the m. peroneus brevis; distally, the former becomes superficial to the latter. Finally, the tendon of the m. peroneus digiti quarti runs on the dorsolateral aspect of the metatarsal IV and digit IV to end onto the distal phalanx. The m. peroneus digiti quarti extends the joints of the digit IV.

Flexor system.

Adductor group.

Musculus gracilis. The m. gracilis (Figs. 1, 3A, 7, and 8) forms a rectangular muscular sheet of parallel arranged fibers that lies caudal to the m. adductor brevis, and medial to the mm. semimem-branosus, semitendinosus, and to all other adductor muscles. The m. gracilis has an extensive origin, by means of a symphysial tendon, from the ventral border of the hip bone, from the pubic tubercle to the ventral ischial tuberosity. The cranial origin of the m. gracilis is aponeurotic; lying medial to the caudal half of the m. adductor brevis. The muscular fibers extend distally to the level of the saphenous vessels and nerve. The m. gracilis inserts onto the medial aspect of the crural fascia, and by a tendon onto the proximal tibia. The mm. gracilis and adductor brevis form a muscular sheet that is medial to all the other muscles of the hip adductor group. The distal caudal border of the m. gracilis is connected with a crural aponeurosis, which forms a superficial fibrous sheath that extends from the medial to the lateral side of the leg, distally reaching the heel. This aponeurosis is firmly united to the calcaneal tendon. The m. gracilis adducts the hip joint and flexes the knee joint.

Musculus adductor longus. The m. adductor longus (Figs. 1, 2B,C, and 8) lies caudal to the m. pectineus, cranial and medial to the m. aductor magnus, and lateral to the m. adductor brevis. It originates from the cranial ramus of the pubis, caudal to the origin of the m. pectineus. Insertion is made by muscular fibers, in common with the m. pectineus, onto the medial lip of the linea aspera. The m. adductor longus is perforated by the branch of the obturator nerve that innervates the m. adductor brevis. The m. adductor longus adducts the hip joint.

Musculus adductor brevis. The m. adductor brevis (Figs. 1, 7, and 8) lies cranial to the m. gracilis, forming with this muscle, as stated above, a muscular sheet that is medial to all other adductor muscles of the hip joint. The m. adductor brevis has an extensive origin from the ventral border of the hip joint, from the level of the iliopubic eminence to the ventral ischial tuberosity. The caudal half of this muscle lies lateral to the cranial half of the m. gracilis. At this level, where both muscles overlap, a branch of the obturator nerve pierces the m. adductor brevis to reach the lateral surface of the m. gracilis. The m. adductor brevis inserts onto the fascia of the knee region and onto the patella. The m. adductor brevis adducts the hip joint.

Musculus adductor magnus. The m. adductor magnus (Figs. 1, 2B,D, 6, and 8) lies caudal and lateral to the m. adductor longus, lateral to the mm. adductor brevis and gracilis, and medial to the mm. semimembranosus; it also surrounds caudally the m. adductor minimus. The m. adductor magnus originates from the caudal ramus of the pubis, the ventral ischial tuberosity, and the ischial ramus. This muscle has an extensive fleshy insertion onto the caudal surface of the femur, occupying most of the facies aspera, from a point

distal to the insertion of the m. adductor minimus to the distal end of the femoral shaft; proximally, this insertion is lateral to those of the mm. pectineus and adductor longus. The m. adductor magnus of *H. hydrochaeris* can be divided into proximal and distal parts; nevertheless, these parts are somewhat difficult to separate from one another, especially at it insertional ends. The origin of the distal part is by a flat tendon from the ventral ischial tuberosity. The m. adductor magnus adducts the hip joint.

Musculus adductor minimus. The m. adductor minimus (Figs. 1, 2B,D, and 6) lies lateral to the m. adductor longus, medial to the m. obturator externus, and cranial to the m. adductor magnus. Its origin is by fibers from the cranial and caudal pubic rami. Insertion is made by a wide tendon in a groove located at the proximal lateral border of the femur, distal to the greater trochanter. In a lateral view, the proximal border of the m. adductor magnus overlaps the caudal border of the m. adductor minimus. Close to its cranial origin, the m. adductor minimus is independently pierced by the cranial and caudal branches of the n. obturatorius. This muscle adducts the hip joint.

Musculus obturator externus. The m. obturator externus (Figs. 1 and 2B,C) is the deepest of the muscles of the hip adductor group, lying medial to all of them. This multipennate muscle takes origin from the lateral aspect of the obturator membrane and adjacent margins of the obturator foramen. It inserts by a strong tendon into the trochanteric fossa of the femur, along with the mm. obturator internus and gemelli. The m. obturator externus adducts and laterally rotates the hip joint.

Ischiotrochanteric group.

Musculus quadratus femoris. The m. quadratus femoris (Figs. 1 and 2B,C) has a rectangular outline, running horizontally from the ischium to the femur. It lies caudal to the m. gemellus caudalis and medial to the m. obturator externus. It arises by fleshy fibers from a relatively small area of the ischium, cranioventral to the ischial tuberosity, between the origins of the m. gemellus caudalis, obturator externus, and semimembranosus. It inserts by a narrow tendon onto the distal end of the intertrochanteric crest, proximal to the lesser trochanter. The m. quadratus femoris extends and laterally rotates the hip joint.

Musculi gemelli. The mm. gemelli cranialis and caudalis (Figs. 1, 2B,C, and 6) originate by fleshy fibers from the laterodorsal aspect of the body of the ischium, from an area dorsal to the acetabulum to the ischial tuberosity. Both mm. gemelli are intimately united together and to the tendon of the m. obturator internus, which passes superficially between them. Their tendons fuse with the latter, to insert all together into the trochanteric fossa of the femur. In one specimen, a few fibers of the m. gemellus caudalis insert onto the tendon of

the m. obturator externus. The mm. gemelli laterally rotates the hip joint.

Musculus obturator internus. The m. obturator internus (Fig. 2B,C) is a multipennate muscle that takes origin from the medial surface of the obturator membrane and from almost all the pelvic surfaces of ischium and pubis. Insertion is made by a strong flat tendon that lies between the mm. gemelli and runs through the lesser sciatic notch, in a pulley-like notch caudal to the ischiatic spine, to finally end into the trochanteric fossa of the femur, in common with those muscles. The m. obturator internus laterally rotates the hip joint.

Hamstring group.

Musculus caudofemoralis. The m. caudofemoralis is absent in *H. hydrochaeris*.

Musculus biceps femoris. The m. biceps femoris (Figs. 1, 3A,D, 5, 6, and 10) is located at the superficial muscular layer of the thigh, caudal to the m. fermorococcygeus. It is a thick muscular sheet that has a triangular outline, with its apex taking origin by a stout tendon from the ischial tuberosity. The caudal portion of the muscle is thicker than the cranial one. In addition, the m. biceps femoris considerably reduces its thickness at its distal portion, taking an extensive aponeurotic insertion onto the lateral aspect of the crural fascia. Close to the knee, the deep fascia of the muscle develops a short tendon that inserts onto the lateral condyle of the tibia and the head of the fibula. This tendon runs superficial to the tendon of the m. extensor digitorum longus and deep to the lateral collateral ligament. In addition, the muscular fibers of the distal cranial border of the m. biceps femoris insert onto the tendon of them. femorococcygeus, which ends onto the lateral border of the patella. The muscular fibers of the distal caudal border of the m. biceps femoris are connected with the crural fibrous fascia that extends to the calcaneus, and which is firmly united with the calcaneal tendon. The m. biceps femoris extends the hip joint and flexes the knee joint.

Musculus semitendinosus. The m. semitendinosus (Figs. 1, 3A,D, and 5−9) is the most caudal muscle of the hamstring group. At its origin, it is composed of two heads: the dorsal head arises from the spinous processes of Cd1–Cd3, whereas the ischial head takes origin from the ischial tuberosity and from the tendon of origin of the m. biceps femoris. The ischial head is much smaller than the dorsal one, representing about a third of the length of the latter. Distally, where both heads fuse, a distinct tendinous inscription can be observed. After receiving the ischial head, the muscle runs to the medial aspect of the leg, passing medially to the m. gastrocnemius caput mediale, to insert onto the crural fascia and, by a tendon, onto the cranial border of the tibia. The distal caudal border of the m. semitendinosus is continuous with the medial aspect of the

superficial fibrous sheath of the leg (see above). The m. semitendinosus extends the hip joint and flexes the knee joint.

Musculus semimembranosus. The m. semimembranosus (Figs. 1, 3A,C, and 6−9) lies lateral to the m. gracilis and medial to the m. semitendinosus. It originates from the caudolateral aspect of the ramus of the ischium, and from the ischial and ventral ischial tuberosities. This muscle consists of two heads: a principal head, which represents the m. semimembranosus proper, and a smaller accessory head (ischiotibial, sensu Alezais, 1900). The accessory head is fusiform and is almost completely enfolded by the principal head; it originates from the ventral ischial tuberosity and inserts by a strong tendon onto the medial condyle of the tibia, deep to the medial collateral ligament. The most lateral (deep in medial view) fibers of the principal head insert onto the tendon of the accessory head, whereas the most medial (superficial in medial view) muscular fibers of the principal head insert by a wide tendon, which runs superficial to the medial collateral ligament, onto the medial condyle of the tibia, cranially to that ligament. The m. semimembranosus extends the hip joint and flexes the knee joint.

Flexor group of the leg.

Musculus gastrocnemius. The m. gastrocnemius (Figs. 2B–D, 4B, 6, 9, 10, and 11B) is superficial to all other muscles of the caudal compartment of the leg. It is composed of two heads: lateral head (caput laterale) and medial head (caput mediale). The lateral head arises by a stout tendon from the lateral supracondylar tuberosity of the femur, in common with the origin of the m. plantaris and superficial to it. This tendon contains a sesamoid bone. The proximal part of the lateral head of the m. gastrocnemius is well-developed in a proximal direction, so that its muscular fibers overpass the femoral area of origin of the muscle. Some fibers of this part originate from the tendon of insertion of the m. femorococcygeus. The deep surface of this proximal part develops a fascia that blends with the latter tendon and with fascias of the mm. vasti intermedius and lateralis. So, the lateral head of the m. gastrocnemius indirectly takes origin from the lateral border of the patella. The lateral head ends to a level much proximal than the medial head; nevertheless, both heads have similar masses. The medial head takes origin by a stout tendon from the medial supracondylar tuberosity of the femur; this tendon lacks a sesamoid bone. A common strong and wide tendon for both heads, the calcaneal tendon, inserts onto the proximal end of the calcaneal tuberosity. The m. gastrocnemius flexes the knee joint and plantarflexes the ankle joint.

Musculus plantaris (= flexor digitorum superficialis). The m. plantaris (Figs. 2B,D, 4B, 9, 10, and 11B) lies caudal to the m. soleus and cranial to the m. gastrocnemius. It takes origin by a stout tendon from the lateral supracondylar tuberosity of the femur, in common with the lateral head of the m. gastrocnemius. The cranial surface of this muscle is flat, whereas its caudal surface is bulgy. Distally, a few centimeters proximal to the heel, the m. plantaris gives rise to a strong tendon that first runs medial to the calcaneal tendon, and then courses caudal and superficial to it, wrapping around the proximal end of the calcaneal tuberosity, forming a tendinous cap. At the plantar surface of the foot the tendon continues as a wide thin plantar fascia that splits into three tendinous slips, which end onto the middle phalanx of each digit. At the metatarsophalangeal joints, each tendinous slip forms a sleeve (manica flexoria) for the passage of the digital tendons of the mm. flexores digitorum lateralis and medialis. The m. plantaris plantarflexes the ankle joint, assists in flexing the knee joint, and flexes the metatarsophalangeal and proximal phalangeal joints of all digits.

Musculus soleus. The m. soleus (Figs. 3B, 4A, 6, 9, and 10) is a fusiform, large flat muscle that lies caudal to the m. flexor digitorum lateralis and cranial to the mm. plantaris and gastrocnemius. It originates from the caudal aspect of the head of the fibula; a few fleshy fibers also originate from a small caudal prominence of the lateral condyle of the tibia. The m. soleus inserts onto the calcaneal tuberosity, just cranial to the calcaneal tendon, but independently from it. The tendon of insertion is extremely short because of the great distal extension of the fibers of the muscle. The m. soleus plantarflexes the ankle joint.

Musculus popliteus. The m. popliteus (Figs. 2D, 3C, 9, and 10) has a triangular outline, extending from the lateral to the medial side of the leg, and lying cranial to the m. gastrocnemius and proximal to the mm. flexores digitorum profundi. It originates by a strong tendon from a small pit located near the border of the lateral condyle of the femur. The tendon of origin passes deep to the tendon of the m. extensor digitorum longus and to the lateral collateral ligament, running in a groove, located at the caudal border of the lateral condyle of the femur. The m. popliteus has a fleshy insertion; the most proximal fibers insert on the distal part of the lateral collateral ligament, whereas the rest of the muscle inserts onto the proximal half of the caudal and lateral surfaces of the body of the tibia. The m. popliteus flexes and medially rotates the knee joint.

Musculi flexores digitorum profundi. Comprises the mm. flexores digitorum medialis and lateralis and the m. tibialis caudalis. The tendons of insertion of both first muscles unite to form a common tendon; the tendon of insertion of the m. tibialis caudalis remains independent.

Musculus flexor digitorum medialis. The m. flexor digitorum medialis (Figs. 3B, 4B, 9, and

11B) is a unipennate muscle that lies at the caudal compartment of the leg, between the mm. popliteus and flexor digitorum lateralis, extending from the lateral to the medial side of the leg. The most proximal muscular fibers of the m. flexor digitorum medialis take origin from a fascia that separates the mm. popliteus and tibialis caudalis. This fascia attaches along the popliteal line, from the caudal aspect of the lateral condyle to the lateral border of the tibia. The m. flexor digitorum medialis also has a fleshy origin from the lateral surface of the tibia, distal to the insertion of the m. popliteus. At its distal third, the m. flexor digitorum medialis enfolds the tendon of the m. tibialis caudalis, so that that tendon runs in a groove excavated in the belly of the m. flexor digitorum medialis. Very close to the flexor retinaculum, the m. flexor digitorum medialis gives rise to a tendon that courses caudal to the tendon of the m. tibialis caudalis; both tendons passing together in the malleolar groove of the tibia. Distally, the tendon of the m. flexor digitorum medialis passes between the medial tarsal bone and the sustentaculum of the calcaneus to run into a groove excavated on the plantar aspect of the foot. This groove is limited by the plantar process of the navicular, laterally, and the medial tarsal and entocuneiform, medially. At about the proximal third of the metatarsus, the tendon of the m. flexor digitorum medialis fuses with the tendon of the m. flexor digitorum lateralis to form a strong common tendon. Distally, this tendon splits into three branches that run on the plantar face of each digit, pass through the perforated tendons (manica flexoria), and insert onto the distal phalanges. In one of the limbs of the adult male dissected, the tendon of the m. flexor digitorum medialis inserted onto the entocuneiform and do not fuse with the tendon of the m. flexor digitorum lateralis. The m. flexor digitorum medialis plantarflexes the ankle joint and flexes the metatarsophalangeal joints and the joints of all digits.

Musculus flexor digitorum lateralis. The m. flexor digitorum lateralis (Figs. 3, 6, 9, 10, and 11B) lies cranial to the m. soleus and lateral to the mm. popliteus, tibialis caudalis, and flexor digitorum medialis. This muscle arises from the caudal surfaces of the fibula and tibia, and the interosseus membrane. It is a bipinnate muscle, with a well-developed internal tendon. At the caudal aspect of the head of the fibula, some fibers of the m. flexor digitorum lateralis enfold the origin of the m. soleus. Distally, this muscle gives rise to a very strong tendon that passes into the wide groove of the caudal process of the tibia to curve around the sustentaculum of the calcaneus; there, it courses into a groove on the plantar aspect of the foot, lateral to the plantar process of the navicular. At about the proximal third of the metatar-

sus, the tendon of the m. flexor digitorum lateralis receives the tendon of the m. flexor digitorum medialis to form a strong common tendon, which splits into three branches that insert onto the distal phalanges of all digits. The m. flexor digitorum lateralis plantarflexes the ankle joint and flexes the metatarsophalangeal joints and the joints of all digits.

Musculus tibialis caudalis. The m. tibialis caudalis (Figs. 3C, 4, and 9) lies between the mm. flexores digitorum lateralis and medialis. It arises from the caudal aspect of the lateral condyle of the tibia and from a fascia that separates this muscle from the m. popliteus, which attaches along the popliteal line. The belly of this muscle is completely covered by the m. flexor digitorum medialis. At about the midlength of the body of the tibia, the m. tibialis caudalis gives rise to a thin long tendon that runs along a groove excavated in the belly of the m. flexor digitorum medialis. Distally, at the flexor retinaculum, the tendon curves around the sulcus malleolaris of the tibia, lying cranial to the tendon of the m. flexor digitorum medialis, to finally end onto the caudal border of the medial tarsal bone. The m. tibialis caudalis assists in plantarflexing the ankle joint and inverting the foot.

Flexor group of the pes.

Musculus abductor ossis metatarsi V. The m. abductor ossis metatarsi V is a very small muscle, which has a tendinous origin from the fascia of the lateral aspect of the calcaneus. It has a fleshy insertion onto the caudal border of the reduced fifth metatarsal bone. The length of the belly was about 26 mm long. This muscle was only observed in both foots of the adult male specimen.

Musculi lumbricales. As in other cavioids, the foot of *H. hydrochaeris* has two mm. lumbricales (Figs. 4B and 11B). They are located between the digital branches of the common tendon of the mm. flexores digitorum medialis and lateralis, taking origin from this tendon. The lateral m. lumbricalis inserts onto the medial aspect of the proximal phalanx of digit IV; the medial m. lumbricalis inserts onto the medial aspect of the proximal phalanx of digit III. The mm. lumbricales flex digits III and IV.

Musculi interossei. There are two mm. interossei to each digit (Figs. 4B and 11B). The mm. interossei digiti IV arise from the plantar aspect of the cuboid and metatarsal IV; the mm. interossei digiti III and II arise from the plantar aspect and cranial border of the navicular. The mm. interossei of each digit insert, respectively, onto the medial and lateral sesamoids located at the plantar aspect of the metatarsophalangeal joints.

Musculus abductor digiti II. The m. abductor digiti II lies medial to the medial interosseous muscle of digit II (Figs. 4B and 11B). It originates from the sustentaculum of the calcaneus, courses ventral to the medial tarsal and medial cuneiform bones, and inserts onto the medial aspect of the

medial sesamoid at the metatarsophalangeal joint of digit II. The m. abductor digiti II abducts digit II.

Musculus adductor digiti II. The m. adductor digiti II lies lateral to the medial interosseous muscle of digit II and ventral to the mm. interossei of digit III, originating from the plantar aspect of the navicular (Fig. 4B). This muscle inserts onto the lateral aspect of the proximal phalanx of digit II. The m. adductor digiti II adducts digit II.

DISCUSSION
Functional Interpretations

The capybara as a cursorial species. Several osteological and muscular traits of the limbs of Cavioidea (i.e., Caviidae, Dasyproctidae, and Cuniculidae) have been interpreted as functionally associated with a cursorial mode of locomotion (e.g., Woods, 1972; Rocha-Barbosa et al., 2002; Casinos et al., 1996; Candela and Picasso, 2008; García-Esponda and Candela, 2010). From a functional point of view, some features analyzed in this study are consistent with these interpretations.

The development of a "gluteal tongue" (i.e., a cranial extension of the m. gluteus medius originating from the fascia that covers the erector spinae musculature) is a feature observed in most ungulates (Slijper, 1946; Jouffroy, 1971). Although it is a character rarely described in rodents (e.g., Slijper, 1946; Rinker, 1954, Klingener, 1964), our study indicates that the "gluteal tongue" is a feature shared by all the cavioid species analyzed (see Character evolution). In ungulates, the vertebral column is characterized by its rigidity during locomotion; notwithstanding, the lumbosacral joint has a great mobility and is closely associated with the propulsive apparatus (Gál, 1993). As the "gluteal tongue" crosses the lumbosacral joint, its contraction (together with the entire m. gluteus medius) would produce lumbosacral extension, potentially enhancing the angular range of the lumbosacral joint (Gál, 1993). Since *H. hydrochaeris* has an almost immobile lumbar region (Slijper, 1946, Table 4), it is possible that its "gluteal tongue" has a similar function as that described in ungulates, as it was also interpreted for *Dasyprocta* by García-Esponda and Candela (2010).

The m. tibialis cranialis of *Hydrochoerus* is composed by two heads: tibial and femoral. This singular anatomical arrangement constitutes a unique feature among the Rodentia and a potential synapomorphy of the Cavioidea (see Character evolution). As stated previously, the m. tibialis cranialis of the cavioids has a dual origin, from the femur and from the tibia, and a single insertion on the foot. From a functional perspective, the m. tibialis cranialis of *Hydrochoerus* could play a similar role in the step cycle to that described for the m. peroneus tertius in ungulates. In the latter group, the knee and talocrural joints are intimately linked by the action of the m. peroneus tertius, both joints functioning in a synergistic manner, in such a way that the flexion of the knee produces a simultaneous dorsiflexion of the foot (Jouffroy, 1971; Liebich et al., 2004). Similarly, in *H. hydrochaeris* the femoral head of the m. tibialis cranialis originates from a pit located near the border of the lateral condyle of the femur. Then, when the knee is flexed, the lateral condyle acts mechanically as a cam, pulling eccentrically the tendon of origin of the femoral head of the m. tibialis cranialis in a proximal direction. This action produces a dorsiflexion of the foot, thus preventing the toes to catch the substrate during the swing phase of the step cycle. As it was also interpreted for *Dasyprocta* (García-Esponda and Candela, 2010), the m. tibialis cranialis of *Hydrochoerus* would principally act as a dorsiflexor rather than as an invertor of the foot, in agreement with the observed limited rotational movements at the talocrural joint (see below). Moreover, the function of the m. tibialis cranialis as a dorsiflexor seems to be reinforced by the particular architecture of its femoral head, which has a bipinnate arrangement of its fibers, that increase its effective physiological cross sectional area (Powell et al., 1984). Thus, the lighter femoral head of the m. tibialis cranialis of *H. hydrochaeris* (supporting information Table S3) would produce relatively greater force when compared with the heavier paralleled fiber tibial head, as it was observed in *Cavia* (Powell et al., 1984). As pointed by Rasmussen et al. (1978: 263): "Since the major decrease in step cycle duration as the animal progresses to faster gaits comes from a reduction in the stance phase, it follows that the flexor muscles active during the swing phase would assume a greater proportion of total stride duration." Therefore, it is assumed that the enhanced dorsiflexion function of the m. tibialis cranialis of cavioids could be related with a cursorial mode of locomotion.

As in other cavioids (see Fig. 11; see also García-Esponda and Candela, 2010), the reduction in number of the mm. lumbricales in the capybara is related to the loss of digits I and V. Reduction or loss of digits is a typical condition of cursorial forms (Rocha Barbosa et al., 2007; Weisbecker and Schmid, 2007).

The gluteal fossa of the ilium of *Hydrochoerus* is divided by the gluteal crest in dorsal and ventral portions, a feature also shared with other cavioids. The ventral and dorsal gluteal fossae are occupied by the m. gluteus profundus and the deep part of the m. gluteus medius, respectively. The gluteal crest serves as origin for the deep muscular septum of the m. gluteus medius, which separates the mentioned gluteal muscles in individual compartments. The functional significance of this particular conformation of the gluteal fossa of the ilium

and the arrangement of the mm. glutei of cavioids is difficult to infer. In general, the gluteal musculature has a major role in the extension of the hip joint, propelling the body forward. The important extension action of the gluteal musculature is rather expressed by the important large mass of this muscle group (supporting information Table S3), representing the highest percentage of the mass relative to the total mass of the hindlimb musculature. This feature was also observed by Gambaryan (1974) when comparing *Dasyprocta* with other rodents not specialized in running. Data on the relative mass of the gluteal musculature of non cavioid caviomorph rodents is lacking. Moreover, the gluteal muscles have a relatively high mechanical advantage in all cavioids, indicated by the proximally projected greater trochanter of the femur (see Candela and Picasso, 2008; García-Esponda and Candela, 2010), a feature that increases the moment arm of these muscles (Maynard Smith and Savage, 1956). The improvement of the mm. glutei medius and profundus is compatible with a powerful extension of the thigh during the propulsive phase of locomotion, a characteristic feature of cursorial species (Maynard Smith and Savage, 1956; Taylor, 1976; Gebo and Sargis, 1994; Salton and Sargis, 2009).

Many osteological traits of the hindlimb in *H. hydrochaeris* are indicative of emphasized parasagittal movements and stabilized joints, features that are also compatible with cursorial habits (Candela and Picasso, 2008; García-Esponda and Candela, 2010). For instance, the hip joint is characterized by a deep acetabular cavity limited by well extended walls, a trait that indicates a relatively high congruence, which is required to stabilize flexion/extension movements (Argot, 2002; Salton and Sargis, 2009). The proximally extended greater trochanter of the femur also restricts the movements of abduction of the femur, a condition observed in other terrestrial mammals (Taylor, 1976; Argot, 2002; Sargis, 2002; Candela and Picasso, 2008; Salton and Sargis, 2009). The knee is deep with a long and narrow femoral trochlea, delimited by sharp crests, and a cranially projected tibial tuberosity. These features increase the mechanical advantage of the m. quadriceps femoris (mm. rectus femoris, vasti lateralis, medialis, and intermedius) in the extension of the knee (Gebo and Sargis, 1994; Fostowicz-Frelik, 2007; Salton and Sargis, 2009). The capybara has an upper ankle joint characterized by a set of features similar to that described in other cavioid rodents (see Candela and Picasso, 2008), such as deep and concave tibial facets, separated by a sharp and prominent intercondylar ridge, sharp, and high crests on the astragalar trochlea, well developed distal tibial spine and posterior process. These features would increase the stabilization of the upper ankle joint, restricting lateral movements and the

range of dorsiflexion. As in other cavioids (Candela and Picasso, 2008), the movements of the astragalonavicular joint of *Hydrochoerus* are also restricted to flexion and extension, as indicated by the astragalar head, which is oriented in a parasagittal plane. The calcaneus of *Hydrochoerus* has a strong anteroposteriorly concave and obliquely oriented cuboid facet, which restricts the movements to a parassagital plane. In *H. hydrochaeris*, the calcaneal and astragalar sustentacular facets are anteroposteriorly oriented, a condition that improves parasagittal movements. The calcaneocuboid joint is more distally located with respect to the astragalonavicular joint, thus restricting the movement at the lower ankle joint (Candela and Picasso, 2008).

In sum, in the context of the Cavioidea, *H. hydrochaeris* has myological and osteological features of the hindlimb that are interpreted neither as adaptations to a highly specialized cursoriality, such as those observed in *Dasyprocta* and *Dolichotis* (Candela and Picasso, 2008; García-Esponda and Candela, 2010), nor as specializations to an aquatic style mode of life (see below). *Hydrochoerus hydrochaeriss* exhibits several features typical of cavioids that allow us to consider it as a generalized cursorial species in the context of this clade.

The capybara as a semiaquatic species. The capybara inhabits densely vegetated areas in the proximity of ponds, lakes, rivers, streams, marshes, and swamps (Mones and Ojasti, 1986; Nowak, 1991). Although most of its activity occurs on land, using the water primarily as a refuge (Nowak, 1991), it displays some adaptations related with a semiaquatic mode of life. For example, the nostrils, eyes, and ears are relatively dorsally located on the head, projecting above the water when the capybara is swimming, and the digits of both fore-and hindlimbs are partially webbed (Howell, 1930; Moreira et al., 2013).

Semiaquatic rodents use drag-based propulsion as the main mode of swimming, usually using pelvic paddling (Howell, 1930; Fish, 1993, 1996). The capybara is the only exception since it does not use pelvic paddling, swimming by quadrupedal paddling instead (Howell, 1930; Fish, 1993). Semiaquatic rodents have a well-developed tail, while the capybara has a very short one. Furthermore, as the short tail of the capybara is insufficient in size to act as a rudder or stabilizer, swimming by quadrupedal paddling seems to be a consequence of this restriction, in order to maintain the equilibrium during swimming (Howell, 1930). Quadrupedal paddling, used by terrestrial and a few semiaquatic mammals, is considered a less efficient locomotor mode than pelvic paddling (Thewissen and Taylor, 2007). The mammals that use pelvic paddling usually exhibit distinctive morphological adaptations for swimming (Thewissen and Taylor, 2007). For example, comparisons of the limb

morphology between terrestrial and semiaquatic species of opossums (Stein, 1981) and rodents (Stein, 1988) have elucidated osteological and myological modifications associated with adaptations to a semiaquatic mode of life. On the contrary, mammals that use quadrupedal paddling have a great dependence on land and all four limbs are almost equally developed. When comparing semiaquatic mammals that swim by quadrupedal paddling with their terrestrial relatives, the limb specializations displayed by the former are usually very minor or absent altogether (Thewissen and Taylor, 2007).

In spite of its quadrupedal paddling mode of swimming, a few characters observed in the limbs of the capybara are associated to its semiaquatic life style, when comparing this species with its closest terrestrial relatives (i.e., caviids and other cavioid rodents).

Previous ecomorphological analyses (Elissamburu and Vizcaíno, 2004; Samuels and Van Valkenburgh, 2008; Carrizo et al., 2014) have evaluated the morphology of the appendicular skeleton of extant species of rodents with respect to their locomotor habits. According to Samuels and Van Valkenburgh (2008), the semiaquatic rodents are characterized by relatively robust bones, enlarged muscular attachments, relatively short femora, and elongated hind feet. Particularly, the hindlimb of the capybara differed from that of these semiaquatic rodents in exhibiting lower crural and pes length indices. In addition, when comparing with other cavioid rodents, the limbs of the capybara are characterized by relatively more developed epicondyles of the humerus, a more robust ulna, a longer olecranon, and a more robust tibia (Elissamburu and Vizcaíno, 2004). These authors related the relatively broad distal humerus (which serve for the attachment of well-developed flexors, pronator, and supinator muscles) as well as the long olecranon of the capybara with swimming. These features could be associated with a strong extension of the forearm and flexion of the manus, thus enhancing force during the power phase of the paddling stroke, whereas the robustness of the tibia could be related with the large body mass of this species (Elissamburu and Vizcaíno, 2004). Samuels and Van Valkenburgh (2008) also related the relatively robust bones of the capybara with a large body mass and with stresses acting on them during terrestrial or semiaquatic locomotion.

In addition to these data, the relatively short bones of the leg and foot (expressed as low crural, and pes length indices; see Samuels and Van Valkenburgh, 2008 and supporting information Table S1) could be related with an increment of the outforce (F_o) generated by the foot during swimming. This enhancement is accomplished by the shortening of the out-lever arm (l_o) of the plantarflexor muscles of the foot (mainly the mm. gastrocnemius and soleus), so that the resultant F_o is increased.

Thus, a relatively short foot implies an increment of the thrust force generated during the power phase of the paddling stroke cycle. Similarly, a short leg produces a shorter l_o of the extensor muscles of the hip joint (mainly the mm. glutei and hamstring), thus, also increasing the resultant F_o. In addition, the relatively short leg and foot of the capybara would reduce the induced drag by allowing the hindlimb to move closer to the body during the recovery stroke (see Samuels and Van Valkenburgh, 2008 for the interpretation of a shorter femur in semiaquatic rodents). A high crural index (tibia longer than femur) can be the result of either tibia elongation or femur shortening (Samuels and Van Valkenburgh, 2008). It is worth mentioning that similar scores can result from distinct adaptations for different habits, that is, distal elongation of the tibia for cursoriality or proximal shortening of the femur for swimming via hindlimb paddling. Thus, the shortened tibia of *Hydrochoerus* really constitutes a unique feature among semiaquatic rodents (Samuels and Van Valkenburgh, 2008).

Another noteworthy feature of the hindlimb of the capybara, when comparing with other cavioid rodents, is the relatively greater distal extension of the fibers of the plantar flexor and dorsiflexor muscles of the foot, most of which reach the ankle joint. As a consequence of this disposition, the relative lengths of the insertion tendons of these muscles before reaching the respective retinacula or sites of attachment at the leg are very short, or even they originate at the retinacula (see Figs. 9–11). A quite opposite condition is that found in highly specialized cursorial species, which have very long tendons (García-Esponda and Candela, 2010). So, the particular muscle arrangement observed in the capybara might be related with the accommodation of both large muscular masses (Fi) and stresses placed on the relatively short distal bones of the hindlimb, allowing a powerful plantar flexion of the foot during swimming. It is worth mentioning that adaptations for power and speed are generally opposite (Hildebrand, 1985a,1985b).

Our observations indicate that there are no substantial differences in the overall arrangement and the relative masses of the muscular groups of the hindlimb between *H. hydrochaeris* and the small bodied guinea pig *C. porcellus* (supporting information Table S3), with the exception of the m. soleus, whose relative mass is four times higher than that of the guinea pig (*Hydrochoerus* = 2.37% vs. *Cavia* = 0.60% of the total mass of the hindlimb musculature). The m. soleus is a plantarflexor that is well developed in several species of mammals and absent in numerous cursorial forms (e.g., canids, ungulates; Jouffroy, 1971). It is a slow-twitch muscle involved in maintaining posture, containing a very high proportion of slow oxidative Type I fibers (e.g., Ariano et al., 1973; Dimov and Dimov,

2007). The relatively greater development of the m. soleus of the capybara might be related with swimming habits of this species, considering the high capacity of this muscle to resist the fatigue. In turn, it is possible that the m. soleus acts as a powerful plantarflexor during the power phase of the paddling stroke cycle, a condition possibly associated with the relative shortening of the tendons of this muscle.

Different adaptations of the hindlimb seem to have been developed by different quadrupedal paddling mammals with semiaquatic habits. For example, the hippo, with relatively few hindlimb adaptations to a semiaquatic habitat, can be considered a similar case as the capybara. In fact, the hippo hindlimb shows few functional adaptations to its semiaquatic habitat, a condition that was related to the fact that this ungulate spends, such as the capybara, an appreciable amount of time on land, foraging on terrestrial grasses, thus precluding the development of more restrictive aquatic adaptations (Fisher et al., 2010). Since hippos move through the water by walking, rather swimming, many of the muscular features that characterize them (e.g., robust and power glutei and hamstring muscles extending the hip joint) are adaptations for powerful propulsion. In the case of the capybara, the set of features related to its semiaquatic habits are different from that of the hippo. As noted above, these traits that are interpreted as adaptations to increase the thrust during swimming, include the relative shortening of the leg, relatively short tendons of the leg muscles, and well-developed plantar flexor muscles, especially the m. soleus.

In a recent study, Martin-Serra et al. (2015) found the limbs of cursorial carnivorans to be more integrated than those of noncursorial taxa. If this were also true of cursorial Cavioidea, that might suggest there would be greater constraint on modification of the limb for an additional function (swimming), than would be seen in semiaquatic rodents with noncursorial ancestors (like *Castor* and *Ondatra*). In these latter taxa, the hindlimbs tend to be strongly modified for swimming via hindlimb paddling (Samuels and Van Valkenburgh, 2008), while *Hydrochoerus* remains a quadrupedal swimmer.

Character Evolution

Character mapping (Fig. 12) indicates that in *Hydrochoerus* the presence of a "gluteal tongue" of the m. gluteus medius (character state 7-1), the presence of a femoral head of the m. tibialis cranialis (character-state 10-1), the reduction in the number of the mm. lumbricales of the hindfoot (character state 11-1), and a gluteal fossa of the ilium divided by a gluteal crest (character state 14-1) are features shared with all other cavioids
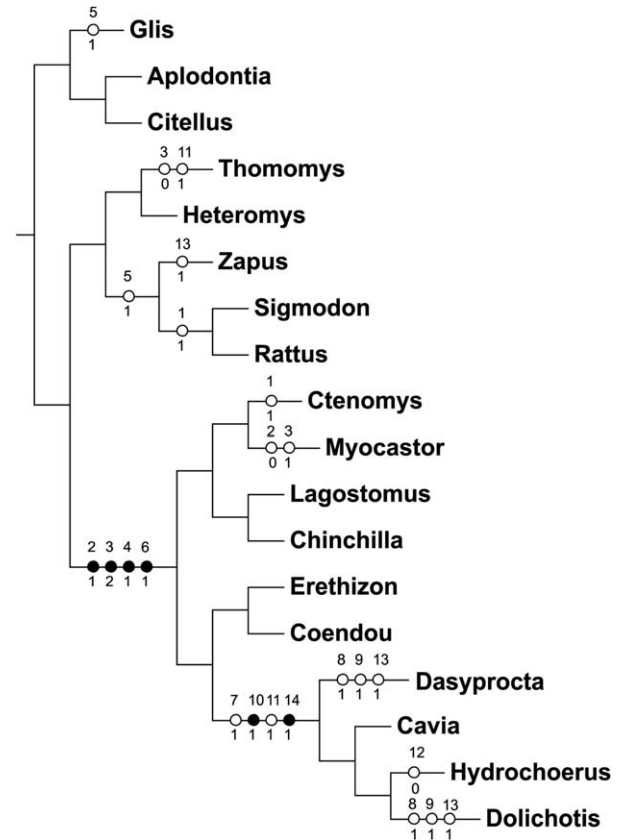

Fig. 12. A. Mapping of 14 anatomical characters, as reconstructed using parsimony, onto a composite phylogeny of Rodentia (Rowe and Honeycutt, 2002; Blanga-Kanfi et al., 2009; Fabre et al., 2012; Upham and Patterson, 2012). Only unambiguous character state optimizations are shown. Numbers above branches indicate character number whereas those below are character states (see supporting information Appendix S2 for characters and character states).

analyzed. Analysis of evolutionary transformation shows that, in the context of Rodentia, these four characters would be potential synapomorphies of the cavioids (Fig. 12).

The reduction of the m. tibialis caudalis (character state 8-1) and the absence of the m. peroneus brevis (character state 9-1), conditions that are associated with highly cursorial specializations (see García-Esponda and Candela, 2010), arose independently in *Dasyprocta* and *Dolichotis* (Fig. 12). Unlike previous results (see García-Esponda and Candela, 2010), the optimization obtained for both features at the *Dolichotis-Hydrochoerus* clade is now resolved. *Hydrochoerus*, having the state 0 of both characters, indicates the generalized condition for the cavioids. Mapping of the length of the tibia with respect to the length of the femur (crural index, character 12) indicates that the relative shortening of the tibia (character state 12-0) was a condition independently acquired by *Hydrochoerus* (unambiguous autopomorphy of this taxon), in the context of the cavioids (compare with results in

García-Esponda and Candela, 2010). Ambiguous optimization of this feature at most basal nodes of cavioids preclude us from inferring a tibia longer than the femur (character state12-1), as a potential synapomorphy of cavioids. Likewise, in the phylogenetic context of cavioids, the elongation of the pes (character state 13-1) was a condition independently acquired by *Dolichotis* and *Dasyprocta* (differing from the results obtained by García-Esponda and Candela, 2010). *Hydrochoerus* (character state 13-0) shows the generalized state of this character. The retention of a short pes in this taxon could be associated with its swimming abilities. The elongation of the pes (character state 13-1) is also observed in the saltatorial clade *Chinchilla-Lagostomus*, and in the semiaquatic *Myocastor*. Ambiguous optimization of this feature prevents us from inferring that the elongation of the pes was independently acquired by these genera or by the ancestor of the Octodontoid-Chinchilloid clade. Nevertheless, we can state that, as in other mammals, the elongation of the pes was acquired more than once in the caviomorphs. Finally, as it was indicated by García-Esponda and Candela (2015), caviomorphs can be characterized by four potential synapomorphies (i.e., characters 2, 3, 4, and 6; see Fig. 12), showing the generalized condition of these characters in *Hydrochoerus*.

CONCLUSIONS

Our results indicate that *Hydrochoerus hydrochaeris* can be considered a generalized cursorial species in the context of Cavioidea. Morphological features supporting propulsion through water seem to have been reached through the shortening of the leg, shortening of tendons of the leg muscles, and by a well-developed soleus muscle.The few adaptations to semiaquatic habitats, keeping most of the features of cavioids, which would reveal relatively high phylogenetic constraints, seems to have occurred more recently in the evolution of the *Hydrochoerus* lineage.

ACKNOWNLEDGMENTS

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