Anatomy of the hindlimb musculature in the cursorial caviomorph *Dasyprocta azarae* Lichtenstein, 1823 (Rodentia, Dasyproctidae): functional and evolutionary significance

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Abstract

The musculature of the hindlimb of the cursorial caviomorph *Dasyprocta azarae* is described and functionally evaluated, together with osteological associated traits. Our results show that several features are indicative of emphasized parasagittal movements and stabilized joints. Mm. glutei are relatively well developed, in agreement with an enhanced extension of the hip joint. The relative elongation of the ischium indicates an improved mechanical advantage of the hamstring muscles, required for powerful extension of the hip. M. iliopsoas would act mainly as a protractor of the femur rather than as a rotator. M. peroneus brevis, an evertor and plantarflexor of the foot, is absent. The inversion of the pes would be reduced, such as expressed by the marked reduction of the m. tibialis caudalis. Osteological characters are arranged to facilitate parasagittal movements and to restrict joint mobility. Some features of *Dasyprocta* (e.g., presence of a gluteal tongue of m. gluteus medius, reduction in number of m. lumbricales, presence of a gluteal crest of the ilium) are interpreted as potential synapomorphies of cavioids. Other features associated to cursoriality (absence of mm. peroneus brevis, reduction of m. tibialis caudalis) would have been acquired independently in the extreme cursorial cavioids *Dasyprocta* and *Dolichotis*.

Keywords: Cavioidea; character mapping; *Dasyprocta azarae*; functional morphology; hindlimb musculature.

Introduction

The caviomorph rodents (or South American Hystricognathi) constitute a monophyletic group (e.g., Huchon and Douzery 2001) representative of the oldest rodent radiation in South America, with the earliest fossils dating to the Late Eocene?-Early Oligocene (Wyss et al. 1993, see also Frailey and Campbell 2004). Caviomorphs evolved in isolation during most of the Cenozoic, reaching an important morphological

disparity and taxonomical diversity (Vucetich et al. 1999), currently expressed by the existence of 12 extant families in South America (Honeycutt et al. 2007). In terms of ecology and lifestyles, caviomorphs display a diverse array of locomotor behaviors and use of substrate, ranging from cursorial, saltatorial, semifossorial, fossorial, to arboreal and swimming forms (e.g., Nowak 1991, Elisamburu and Vizcaíno 2004), occupying a broad variety of habitats (Redford and Eisenberg 1992, Emmons 1997).

Among extant caviomorphs, the family Dasyproctidae is represented by the genera *Dasyprocta* (agoutis) and *Myoprocta* (acouchis), comprising several species that inhabit mainly forested habitats at tropical and subtropical areas. Agoutis and achouchis, together with maras [*Dolichotis patagonum* (Zimmermann, 1780) and *Pediolagus salinicola* (Burmeister, 1876), Caviidae], are the caviomorphs best specialized to cursorial habits (e.g., Weisbecker and Schmid 2007), showing the ability to trot, gallop, jump vertically, and move with remarkable speed and agility (Nowak 1991). Families Dasyproctidae and Cavidae (including *Hydrochoeris,* sensu Rowe and Honeycutt 2002) together with family Agoutidae are grouped in the Superfamily Cavioidea, a clade of caviomorphs with cursorial adaptations, such as reduction of the clavicle and digit number (Rocha-Barbosa et al. 2005).

Analyses of the postcranial musculature in caviomorphs are relatively scarce and most of them are mainly descriptive approaches (e.g., Wood and White 1950, Woods 1972, McEvoy 1982, Parsons 1894), or restricted to a specific portion of the postcranial musculature (Rocha-Barbosa et al. 2002, Rocha-Barbosa et al. 2007). With the exception of the significant contribution of Parsons (1894), there is no integrative comparative study of hindlimb musculature in these rodents. Particularly in the case of *Dasyprocta*, there are few contributions on the myology of this genus (Mivart and Murie 1866, Parsons 1894, Windle 1897). It should be noted that *Dasyprocta* has not previously been evaluated to explore if their cursorial adaptations are reflected in their muscular features.

In this contribution we make a detailed study of the musculature of the hindlimb of *Dasyprocta azarae* Lichtenstein, 1823, one of the species that reaches the most austral distribution in South America, and analyze their main hindlimb traits from a functional perspective. We also examine some anatomical features of *Dasyprocta* in the phylogenetic context of the Cavioidea (Rowe and Honeycutt 2002) to gain an understanding of the evolution of the cursorial specializations within this group of caviomorphs.

We expect that myological and osteological associated characters analyzed here, which are not yet available for

most caviomorphs, can be useful in future ecomorphologic and evolutionary studies on these rodents.

Materials and methods

We dissected two male individuals of *Dasyprocta azarae* that had died at the Zoológico de La Plata (La Plata, Argentina). The specimens were preserved in a solution composed of one part formalin to 18 parts water saturated with NaCl (Rinker 1954, Woods, 1972). All dissections were done under a magnifying glass (2×) or under a binocular microscope using magnifications of 7×, 10×, and 15×.

Dissected specimens were deposited at Museo de Ciencias Naturales ''P. Scasso'', San Nicolás, Argentina (MPS-Z 181 and 182). For osteological observations, and to recognize the precise areas of attachments of each muscle during dissections, we used the skeletons of *Dasyprocta* specimens contained at the Centro Nacional Patagónico (CENPAT, Puerto Madryn, Argentina; see Appendix 1) as reference. Osteological features of *Dasyprocta* spp. were also examined in specimens housed at the Museu Nacional (MN, Rio de Janeiro, Brazil; see Appendix 1). Drawings of the muscles and areas of origin and insertion were made. We analyzed the musculature of the hindlimb in *D. azarae* and compared our results with those previously provided by Mivart and Murie (1866), Parsons (1894), and Windle (1897). It should be noted that these contributions on the musculature of this genus presented a purely descriptive approach that include a few comparative illustrations of the muscles analyzed. We mainly followed the myological nomenclature and system arrangement of McEvoy (1982), because it is in agreement with those used by other authors in studies on rodent musculature (e.g., Rinker 1954, Klingener 1964). Muscle function was inferred from the literature and by manipulating the specimens dissected. In particular, we discussed those muscular and associated osteological features of the hindlimb in *D. azarae* that are relevant for functional interpretations. Most of the osteological characters of cavioids used in the comparisons have been previously discussed by Candela and Picasso (2008).

Identified morphological disparity among cavioids was coded into eight hindlimb characters (see below), the evolution of which was mapped on a molecular phylogeny of the Cavioidea presented by Rowe and Honeycutt (2002). Cavioids for which myological information was available are *Agouti* (Agoutidae), *Cavia*, and *Dolichotis* (Beddard 1891, Parsons 1894). *Coendou* (Erethizontidae) and *Chinchilla* (Chinchillidae) were used as out-groups (myological data from Wood and White 1950, McEvoy 1982). Osteological characters mapped on the molecular phylogeny were observed on the caviomorph specimens listed in Appendix 1 and state of characters listed in matrix (Appendix 3).

Cladistic mapping was done using the computer program TNT 1.0 (Goloboff et al. 2003). The tree was edited with the program WINCLADA (Nixon 1999).

Character description is as follows:

1. Gluteal tongue of m. gluteus medius: 0=absent; 1=present.
2. M. tibialis caudalis: 0=belly and tendon well developed with respect to the remaining muscles of the flexor group of the leg; 1=belly and tendon very poorly developed with respect to the remaining muscles of the flexor group of the leg.
3. M. peroneus brevis: 0=present; 1=absent.
4. Extra-head of m. tibialis cranialis: 0=absent; 1=from tendon of origin of m. extensor digitorum longus; 2=from lateral condyle of femur.
5. Mm. lumbricales of the hindfoot: 0=four; 1=two.
6. Tibia length respect to femur length: 0=equal or less than femur length; 1=longer than femur length.
7. Third metatarsal length respect to femur length: 0=less than half femur length; 1=equal or longer than half femur length.
8. Fossa glutea: 0=undivided; 1= divided by gluteal crest.

Results

Muscular anatomy

No significant myological variation was observed between the two specimens dissected in this study. Nevertheless, muscular differences between our data and those reported by previous authors on *Dasyprocta* (Mivart and Murie 1866, Parsons 1894, Windle 1897) are mentioned in Appendix 2.

Extensor system

Iliacus group

M. iliacus (Figures 1, 2B, 6 and 8)
M. iliacus arises from the cranial ventral iliac spine and the iliac fossa of the ilium, extending caudally to the level of the tuberosity for the origin of m. rectus femoris; it also takes origin from the fibrous sheet that covers m. gluteus medius. Insertion is made by a strong tendon, onto the lesser trochanter of the femur, in common with m. psoas major. M. iliacus flexes the hip joint.

M. psoas major (Figures 2B, 7 and 8)
M. psoas major takes origin from the ventral aspect of the bodies of the third to sixth lumbar vertebrae. It inserts via a strong tendon, onto the lesser trochanter of the femur, in common with m. iliacus. M. psoas major flexes the hip joint; when the leg is fixed in position, it flexes the vertebral column.

M. pectineus (Figures 1, 2B and 8)
M. pectineus lies cranial and deep to m. adductor longus. It originates from the iliopubic eminence of the pubis and inserts onto the pectineal line, on the caudal surface of the femoral shaft, distal to the lesser trochanter and medial to
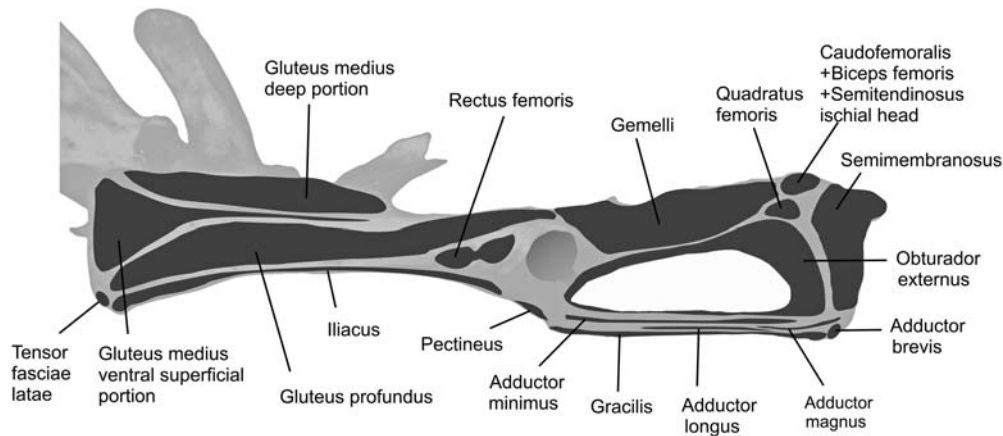
Figure 1 Lateral view of left pelvis of *D. azarae* showing areas of muscle attachment. All areas represent origins of muscles.

the insertion of m. adductor longus. M. pectineus adducts the hip joint.

Gluteal group

M. tensor fasciae latae (Figures 1, 5 and 7)
M. tensor fasciae latae originates from the ventral cranial iliac spine and lumbodorsal fascia. It inserts onto the fasciae latae, which inserts onto the proximal aspect of the patella. M. tensor fasciae latae flexes the hip joint and extends the knee joint.

M. gluteus superficialis (Figures 2A,B,D and 5)
M. gluteus superficialis arises from the lumbodorsal fascia; its most caudal and dorsal fibers take origin from the spinous processes of the third and fourth lumbar vertebrae, intermingling with cranial fibers of m. femorococcygeus. Insertion is made by a strong flat tendon onto the third trochanter of the femur and by fleshy fibers onto the fasciae latae. M. gluteus superficialis extends the hip joint.

M. femorococcygeus (Figures 5 and 6)
M. femorococcygeus lies between m. gluteus superficialis and m. biceps femoris, superficial to m. caudofemoralis. This muscle is subtriangular in transversal section and has a long triangular shape in lateral view. It arises from the spinous processes of the fourth and fifth sacral vertebrae. Insertion is made by a narrow tendon onto the lateral border of the patella. M. femorococcygeus abducts the hip joint.

M. gluteus medius (Figures 1, 2B,D, 5 and 6)
M. gluteus medius is a very large muscle that takes origin from the lumbodorsal fascia, the fascia over the erector spinae musculature beginning at the level of the last two lumbar vertebrae, the spinous processes of the first to third sacral vertebrae, and also from the iliac crest, the gluteal crest, and the dorsal portion of the gluteal fossa (see below) of the ilium. It inserts onto the greater trochanter of the femur and the caudal aspect of the proximal end of the femoral shaft. M. gluteus medius extends the hip joint.

M. gluteus profundus (Figures 1, 2A,D and 6)
M. gluteus profundus originates from the ventral portion of the gluteal fossa of the ilium, extending caudally onto the body of the ilium dorsal to the tuberosity for the origin of m. rectus femoris and the acetabular fossa. Insertion is made by a wide tendon onto the lateral aspect of the greater trochanter of the femur, proximal and distal to the origin of m. vastus lateralis. M. gluteus profundus extends the hip joint.

M. piriformis (Figures 2D and 6)
M. piriformis is triangular in shape lying caudal to the deep portion of m. gluteus medius. It originates from the ventral aspect of the transverse processes of the second and third sacral vertebrae. It inserts onto the proximal end of the greater trochanter of the femur, in common with the deep portion of m. gluteus medius. M. piriformis abducts and extends the hip joint.

Quadriceps femoris group

M. rectus femoris (Figures 1, 6 and 8)
M. rectus femoris lies between mm. vasti lateralis et medialis. It takes origin by two very short strong tendons, from an area that comprises the tuberosity for the origin of m. rectus femoris and the adjacent surface of the ilium cranial to the acetabulum. Insertion is made by a strong tendon onto the proximal border of the patella. M. rectus femoris flexes the hip joint and extends the knee joint.

M. vastus lateralis (Figures 2A,D, 5, 6 and 8)
M. vastus lateralis is the largest of the muscles that constitute m. quadriceps femoris; their proximal fibers lie deep to m. gluteus medius and superficial to m. gluteus profundus. It originates from the proximal half of the lateral aspect of the femur. It inserts onto the proximal and lateral aspects of the patella. Mm. vasti lateralis, medialis et intermedius extend the knee joint.

M. vastus medialis (Figures 2A–C and 8)
M. vastus medialis arises from a narrow area on the craniomedial aspect of the femoral shaft, extending from the great-
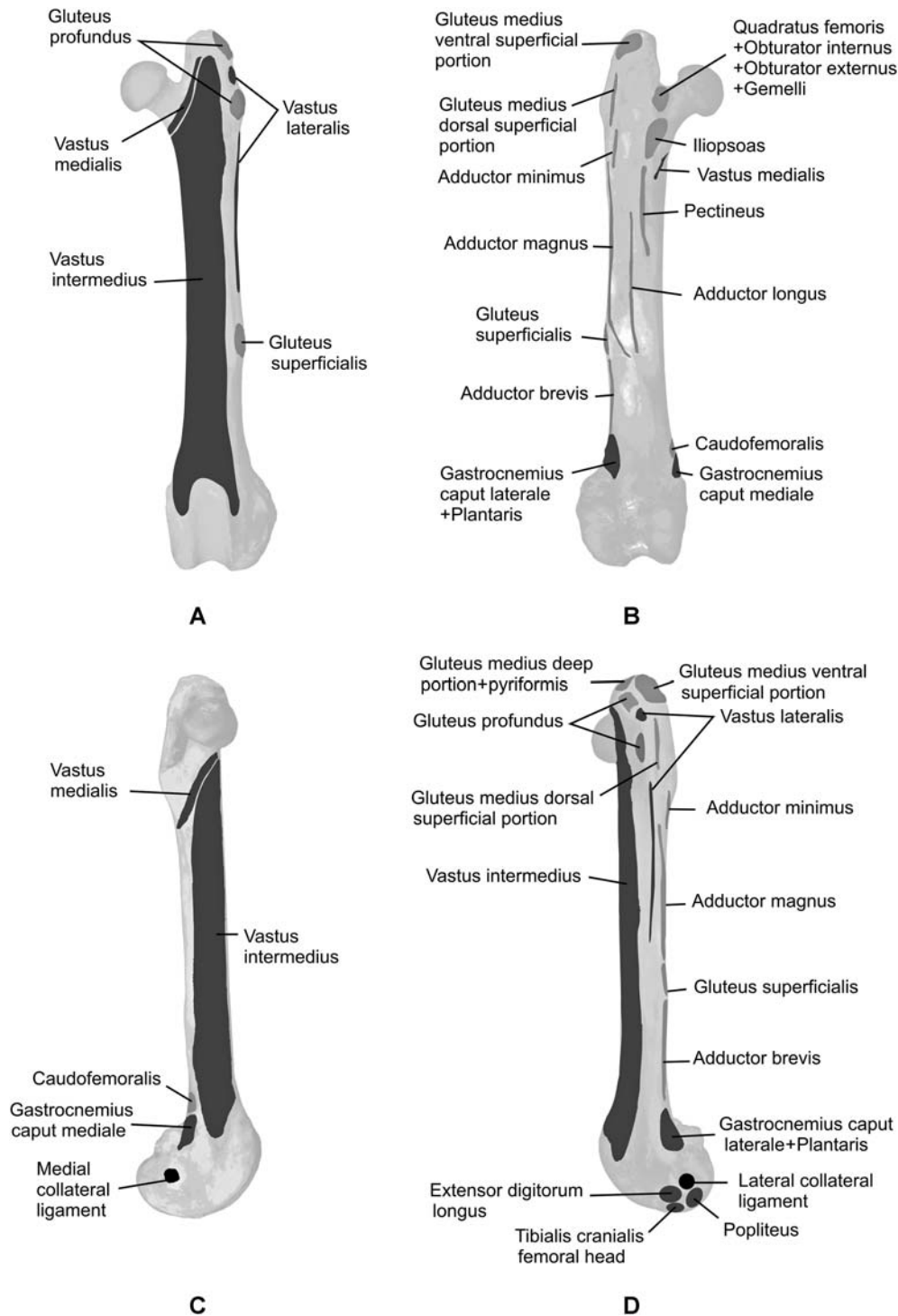
Figure 2   Left femur of *D. azarae* showing areas of muscle attachment. (A) Cranial; (B) caudal; (C) medial; (D) lateral views. Dark gray: areas of muscle origin; pale gray: areas of muscle insertion.

er trochanter to the level of the lesser trochanter, proximal to the origin of m. vastus intermedius. It inserts onto the proximal and medial aspects of the patella. Mm. vasti lateralis, medialis et intermedius extend the knee joint. Some of the proximal fibers of this muscle blend with those of m. vastus intermedius.

M. vastus intermedius (Figure 2A,C,D)
This muscle is the deepest of the muscles that constitute m. quadriceps femoris. It originates from the cranial and medial surfaces of the femoral shaft, extending from the greater trochanter to the distal end of the femur. It inserts onto the lateral, medial, and proximal borders of the patella. Mm. vas-

ti lateralis, medialis et intermedius extend the knee joint. Some of the proximal fibers of this muscle blend with those of m. vastus medialis.

Tibial extensor group

M. extensor digitorum longus (Figures 2D, 4B, 6, 9 and 11A)
M. extensor digitorum longus lies lateral to m. tibialis cranialis and superficial to m. extensor hallucis longus. It takes origin by a broad tendon from a small pit, the extensor fossa, located on the lateral condyle of the femur, proximal to the origin of the femoral head of m. tibialis cranialis. The tendon of insertion passes deep to the proximal extensor retinaculum, lying lateral to the tendons of mm. tibialis cranialis and extensor hallucis longus; distally it is independently fastened by the distal extensor retinaculum. After passing the distal retinaculum, it splits into three digital tendons that course on the dorsal aspect of the pes to end onto the distal phalanges of all digits. M. extensor digitorum longus dorsiflexes the ankle joint and extends the joints of all digits.

M. extensor hallucis longus (Figures 3A, 4B, 9 and 11A)
M. extensor hallucis longus lies lateral to the distal portion of m. tibialis cranialis and deep to m. extensor digitorum longus. It arises from the distal third of the cranial aspect of the tibia and fibula, and from the interosseus membrane between these bones. The tendon of insertion passes deep to the proximal extensor retinaculum, lying deep to the tendon of m. tibialis cranialis and medial to that of m. extensor digitorum longus. Distally, it shares a loop of the distal extensor retinaculum with the m. tibialis cranialis tendon. Then, it courses onto the dorsolateral aspect of metatarsal and digit II to insert onto the mediodistal aspect of the second phalanx of digit II. M. extensor hallucis longus dorsiflexes the ankle joint and extends digit II.

M. tibialis cranialis (Figures 2D, 3A,C, 4B, 6–11A)
At its origin, m. tibialis cranialis is composed of two heads: the femoral head takes origin by a narrow tendon from a small pit on the lateral condyle of the femur, close to the lateral lip of the femoral trochlea and distal to the origin of m. extensor digitorum longus; the tibial head arises by fleshy fibers from the lateral fossa of the tibia. The tendon of the femoral head passes in a groove located between the tibial tuberosity and medial condyle. The tendon of insertion of m. tibialis cranialis passes deep to the proximal extensor retinaculum, lying superficial to the tendon of m. extensor hallucis longus and medial to that of m. extensor digitorum longus. Distally, it shares a loop of the distal extensor retinaculum with the m. extensor hallucis longus tendon. There, it courses to the medial side of the foot to end onto the entocuneiform and the proximomedial aspect of metatarsal II. M. tibialis cranialis dorsiflexes the ankle joint and inverts the foot.

M. extensor digitorum brevis (Figures 4B and 11A)
M. extensor digitorum brevis is a small muscle that lies deep to the tendons of insertion of m. extensor digitorum longus.

It is composed of two bellies that originate from the dorsal aspect of the calcaneus. The bellies give rise to two tendons that course on the lateral aspect of digits II and III; at the level of the medial interphalangeal joint, the tendons join those of m. extensor digitorum longus, to end onto the distal phalanges of digits II and III. M. extensor digitorum brevis extends the joints of digits II and III.

Peroneal group

M. peroneus longus (Figures 3C, 6 and 9)
M. peroneus longus lies superficial to m. peroneus digiti quarti. It arises from the lateral aspect of the fibular head and from the lateral collateral ligament. Its belly gives rise to a tendon about the midshaft of the fibula; at the distal end of this bone, it curves around the sulcus for m. peroneus longus, located on the lateral surface of the lateral malleolus. Distally, the tendon runs superficial to that of m. peroneus digiti quarti, passes in a groove in the trochlear process of the calcaneus and in the sulcus for the m. peroneus longus, located on the lateral aspect of the cuboid, to turn under the tarsus. From there, the tendon travels toward the medial aspect of the foot into a perpendicular canal, deep to the plantar process of the navicular and the plantar sesamoid, to finally insert onto the ventral aspect of the proximal end of metatarsal II and lateral aspect of the entocuneiform. M. peroneus longus everts the foot and plantarflexes the ankle joint.

M. peroneus brevis
As noted by Mivart and Murie (1866), Parsons (1894), and Windle (1897), m. peroneus brevis is absent in *Dasyprocta*.

M. peroneus digiti quarti (Figures 3C, 4B, 6, 9 and 11A)
M. peroneus digiti quarti lies deep to m. peroneus longus. It arises from the lateral aspect of the distal three quarters of the fibular shaft, and fibrous sheet separating this muscle from m. flexor digitorum fibularis. At the distal end of the fibula, m. peroneus digiti quarti gives rise to a tendon that courses into the sulcus for the m. peroneus digiti quarti, on the caudal border of the lateral malleolus. Distally it passes deep to the tendon of m. peroneus longus to end onto the dorsolateral aspect of the metatarsal IV and digit IV. M. peroneus digiti quarti extends the joints of digit IV.

Flexor system

Adductor group

M. gracilis (Figures 1 and 7)
M. gracilis is composed of two heads that originate from the symphysis pelvis, extending from the iliopubic eminence to the ventral ischial tuberosity (*sensu* Hill 1937). Cranial head inserts onto the medial edge of the patella; caudal head inserts onto the medial aspect of the crural fascia. M. gracilis adducts the hip joint and flexes the knee joint.

M. adductor longus (Figures 1, 2B and 8)
In medial view, m. adductor longus lies deep to m. gracilis and superficial to mm. adductor minimus, adductor magnus
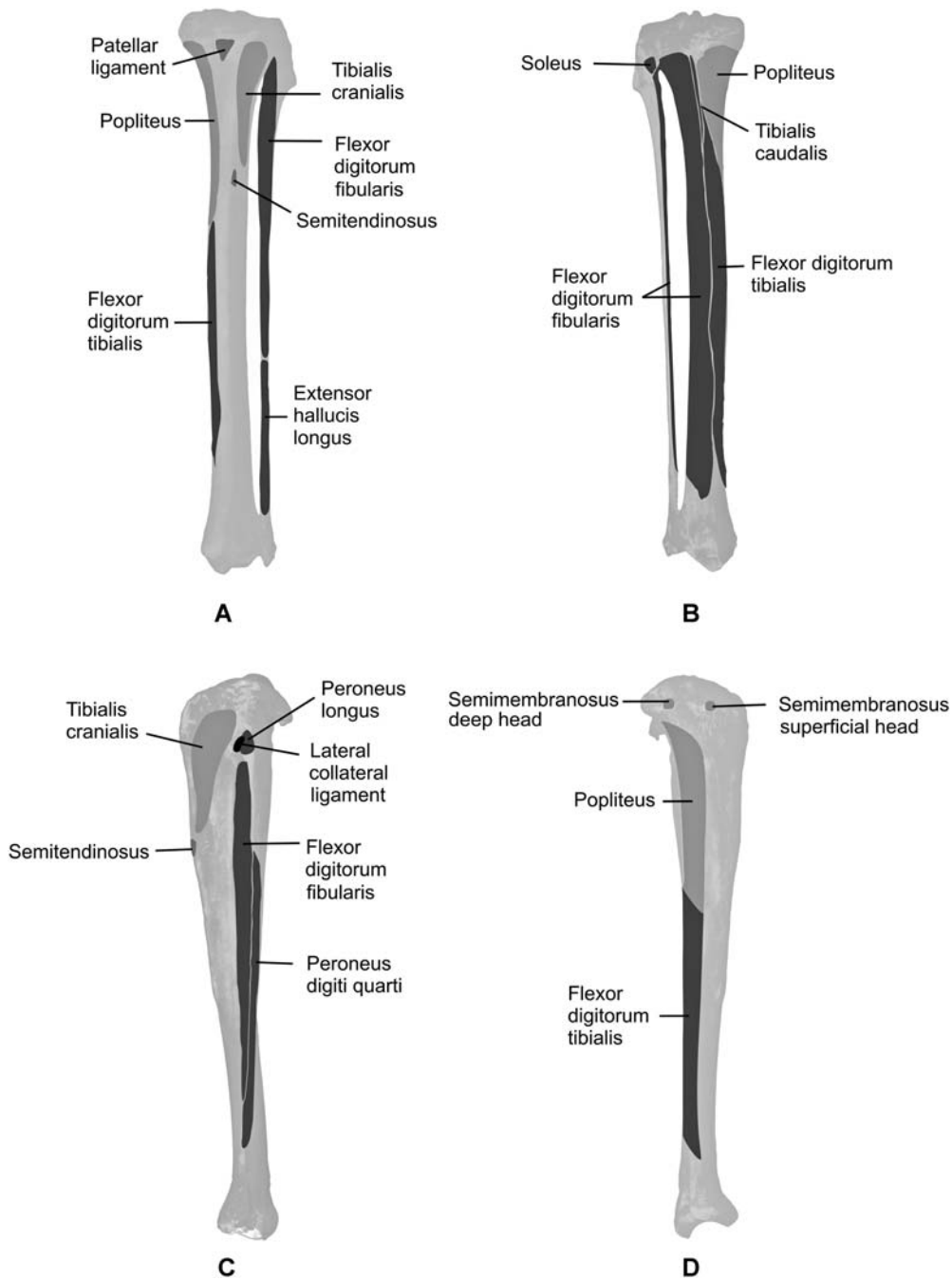
Figure 3   Left tibia and fibula of *D. azarae* showing areas of muscle attachment. (A) Cranial; (B) caudal; (C) lateral; (D) medial views. Dark gray: areas of muscle origin; pale gray: areas of muscle insertion.

and pectineus. It arises from the two middle quarters of the symphysis pelvis. Insertion is onto the caudal aspect of the femoral shaft, lateral to the insertion of m. pectineus, extending from about the midpoint of the pectineal line to the level of the third trochanter. M. adductor longus adducts the hip joint.

M. adductor brevis (Figures 1, 2B,D and 8)
M. adductor brevis is the narrowest of the adductor muscles. In lateral view, it is the most superficial of this group, along with m. adductor magnus, lying distal to the latter. This mus-

cle takes origin by a strong and relatively long tendon from the ventral ischial tuberosity. It inserts onto the distal third of the lateral border (lateral crest) of the femoral shaft, from the distal end of the third trochanter to the origin of m. gastrocnemius caput laterale. M. adductor brevis adducts the hip joint.

M. adductor magnus (Figures 1, 2B,D, 6 and 8)
In lateral view, m. adductor magnus is triangular in shape, lying superficial to m. adductor minimus and proximal to m. adductor brevis. In medial view, m. adductor magnus lies
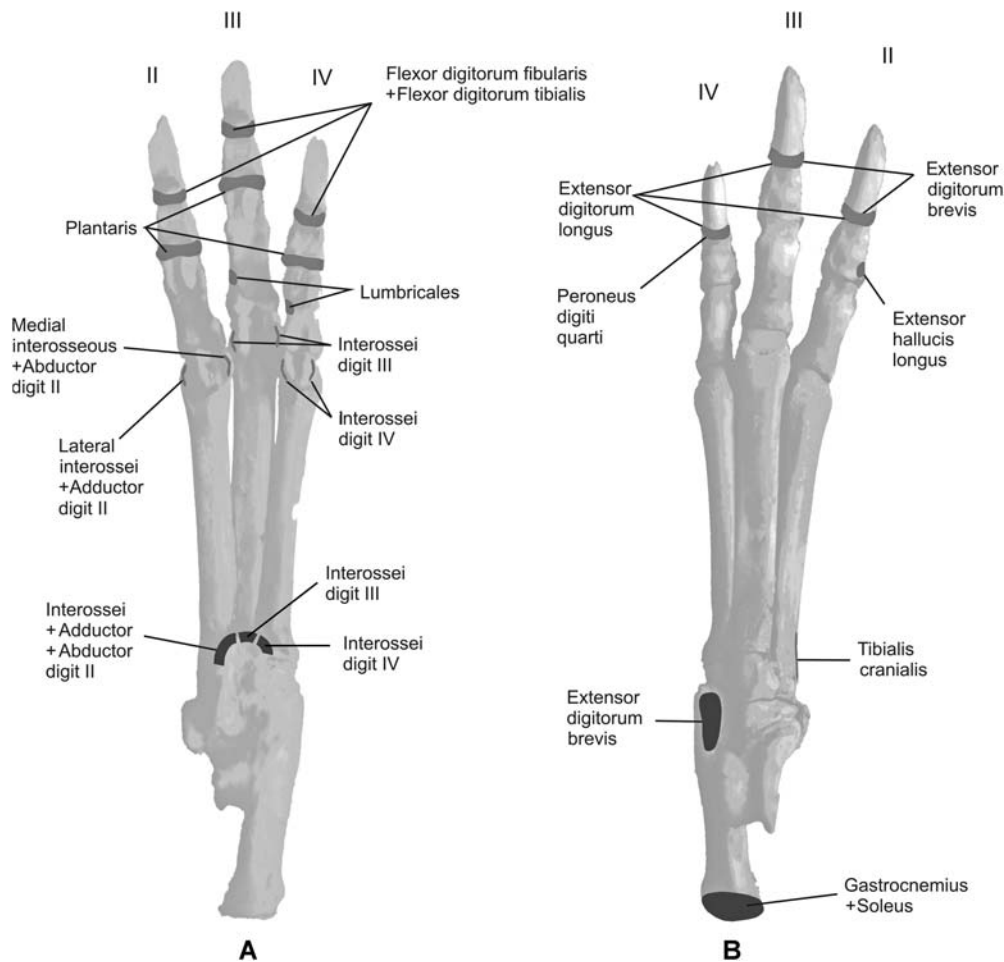
Figure 4 Left foot of *D. azarae* showing areas of muscle attachment. (A) Ventral; (B) dorsal views. Dark gray: areas of muscle origin; pale gray: areas of muscle insertion.

deep to m. adductor longus. The origin of this muscle is from the caudal third of the pubis, extending distally to the level of the ventral ischial tuberosity. It inserts onto the lateral border of the femoral shaft (lateral crest), from the level of the insertion of m. adductor minimus to the third trochanter. At this point, the most distal fibers insert onto the caudal surface of femoral shaft. M. adductor magnus adducts the hip joint.

M. adductor minimus (Figures 1, 2B,D and 6)
In lateral view, m. adductor minimus lies deep to m. adductor magnus and superficial to m. obturator externus. Its origin is from the pubis, extending from a point caudal to the iliopubic eminence to the ventral ischial tuberosity. Insertion is made by a wide tendon onto the caudolateral aspect of the femoral shaft, at the level of the lesser trochanter, and slightly medial to the insertion of m. adductor magnus. M. adductor minimus adducts the hip joint.

M. obturator externus (Figures 1 and 2B)
M. obturator externus lies deep to mm. adductor minimus and quadratus femoris. It takes origin from the superficial borders of the obturator foramen and superficial surface of

the obturator membrane. It inserts into the trochanteric fossa of the femur. M. obturator externus adducts the hip joint and laterally rotates the femur.

Ischiotrochanteric group

M. quadratus femoris (Figures 1, 2B and 6)
M. quadratus femoris runs almost horizontal from the ischium to the femur, lying superficial to m. obturator externus. It arises from a relatively small area of the ischium, ventral to the ischiatic tuberosity and between the origins of mm. gemelli, obturator externus, and semimembranosus. It inserts into the trochanteric fossa of the femur. M. quadratus femoris extends the hip joint and laterally rotates the femur.

Mm. gemelli (Figures 1, 2B and 6)
Mm. gemelli originate from the lateral aspect of the body of the ischium, between the acetabulum and the ischiatic tuberosity. Insertion is onto the tendon of m. obturator internus, and by this tendon into the trochanteric fossa of the femur. Mm. gemelli laterally rotates the hip joint. Both mm. gemelli are intimately united; m. obturator internus tendon passes between them.

M. obturator internus (Figure 2B)

M. obturator internus takes origin from the pelvic surfaces of the borders of the obturator foramen and obturator membrane. Insertion is made by a strong flat tendon that lies between mm. gemelli and runs through the lesser isquiatic notch, to end into the trochanteric fossa of the femur. M. obturator internus laterally rotates the hip joint.

Hamstring group

M. caudofemoralis (Figures 1, 2B,C, 6 and 8)

M. caudofemoralis is a strap-like muscle that lies deep to m. femorococcygeus. It originates from the ischiatic tuberosity, cranial to the origin of m. biceps femoris. It inserts onto the medial aspect of the distal femoral shaft, proximal to the origin of m. gastrocnemius caput mediale; some distal fibers insert onto this latter muscle. M. caudofemoralis extends the hip joint.

M. semitendinosus (Figures 1, 3A,C, 5, 7 and 8)

M. semitendinosus is the most caudal of the hamstring muscles. At its origin, this muscle is composed of two heads: dorsal head arises from the spinous processes of the first to third caudal vertebrae; ischial head takes origin from the ischiatic tuberosity. The ischial head is much smaller than the dorsal head, lying deep to the latter. Both heads fused immediately distal to the origin of the ischial head. Insertion is made by a long tendon onto the cranial border of the tibia; distally to this tendon, insertion is made by aponeurosis onto the medial aspect of the crural fascia. M. semitendinosus extends the hip joint and flexes the knee joint.

M. biceps femoris (Figures 1, 5 and 6)

M. biceps femoris is the largest of the hamstring muscles. It lies between mm. fermorococcygeus and semitendinosus. It takes origin by a stout tendon from the ischiatic tuberosity. Insertion is made by aponeurosis onto the crural fascia on the lateral aspect of the leg, extending from the knee to the ankle. M. biceps femoris extends the hip joint and flexes the knee joint.

M. semimembranosus (Figures 1, 3D, 6–8 and 10)

In medial view, m. semimembranosus lies deep to the caudal head of m. gracilis and superficial to m. semitendinosus. It originates from the caudolateral aspect of the ramus of the ischium, between the ischiatic and ventral ischial tuberosities. Insertion is made by two heads onto the medial condyle of the tibia. The superficial head inserts by a tendon that runs superficial to the medial collateral ligament, to reach the medial condyle of the tibia cranially to that ligament. The deep head inserts by a tendon onto the medial condyle of the tibia, deep to the medial collateral ligament. M. semimembranosus extends the hip joint and flexes the knee joint.

Flexor group of the leg

M. gastrocnemius (Figures 2B,D, 4B, 6–10)

M. gastrocnemius is composed of two heads: caput laterale arises by a stout tendon from the caudolateral aspect of the lateral epicondyle of the femur and adjacent area of the distal femoral shaft, superficial to and in common with the origin of m. plantaris; caput mediale takes origin by a stout tendon from the caudomedial aspect of the medial epicondyle of the femur and adjacent area of the distal femoral shaft, distal to the insertion of m. caudofemoralis. Both heads of m. gastrocnemius along with m. soleus constitute the m. triceps surae. A sesamoid bone is present in the tendon of origin of each head. Distally, the tendons of insertion of both heads, along with that of m. soleus, join and fuse to form a strong common tendon (tendon calcaneus communis), which inserts onto the proximal end of the calcaneal tuberosity. M. gastrocnemius flexes the knee joint and plantarflexes the ankle joint.

M. plantaris (flexor digitorum superficialis, Figures 2B,D, 4A, 8–11B)

M. plantaris lies deep to m. gastrocnemius, been completely covered by it. It takes origin by a stout tendon from the caudolateral aspect of the lateral epicondyle of the femur, deep to and in common with the origin of m. gastrocnemius caput laterale. This muscle gives rise to a strong tendon that runs medial to the tendo calcaneus comunis; distally, it courses caudal and superficial to that tendon, wrapping around the proximal end of the calcaneal tuberosity to become a wide thin plantar fascia at the sole of the foot. There, the plantar fascia splits into three tendinous slips that constitute the perforated tendons for the passage of the tendons of mm. flexor digitorum tibialis et fibularis. The three tendinous slips attach to the middle phalanges of all digits. M. plantaris plantarflexes the ankle joint, assists in flexing the knee joint, and flexes the metatarsophalangeal and proximal phalangeal joints of all digits.

M. soleus (Figures 3B, 4B, 9 and 10)

M. soleus lies deep to the lateral head of m. gastrocnemius and superficial to m. flexor digitorum fibularis. It originates from the caudal aspect of the head of the fibula and inserts onto the proximal end of the calcaneal tuberosity. The tendon of insertion joins those of m. gastrocnemius to constitute a common tendon. M. soleus plantarflexes the ankle joint.

M. popliteus (Figures 2D, 3A,B,D, 8–10)

M. popliteus is a triangular muscle that courses from lateral to medial side of the crus. It originates by a strong tendon from a small pit on the lateral condyle of the femur, caudal to the origins of mm. extensor digitorum longus and tibialis cranialis (femoral head), and distal to the origin of the lateral collateral ligament. The tendon of origin passes deep to the lateral collateral ligament. The distal end of the medial collateral ligament is covered by fibers of m. popliteus, some of them originating from it. This muscle inserts onto the caudal and medial aspects of the proximal two-fifths of the tibial shaft, proximal to the origin of m. flexor digitorum tibialis. M. popliteus medially rotates the tibia and flexes the knee joint.
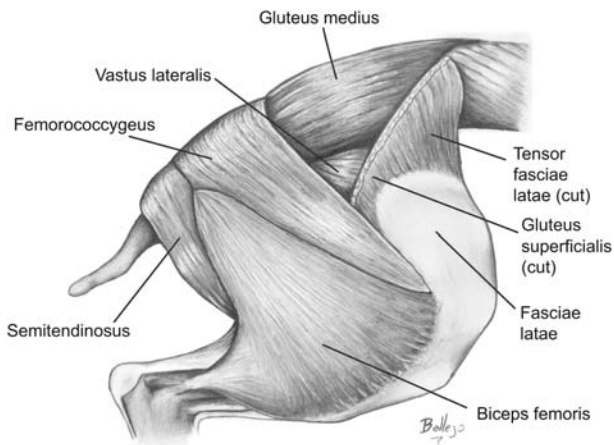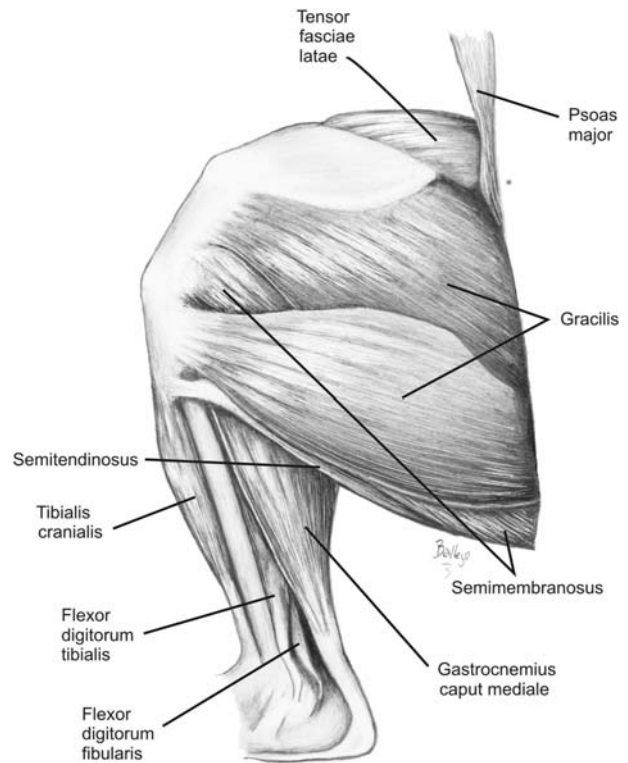
Figure 5 Lateral superficial view of the right hindlimb of *D. azarae*.
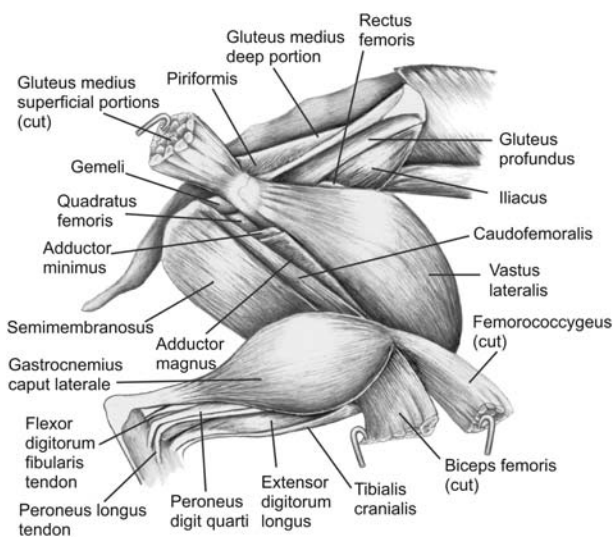
Figure 6 Lateral deep view of the right hindlimb of *D. azarae*.

Figure 7 Medial superficial view of the right hindlimb of *D. azarae*.

M. flexor digitorum tibialis (medialis, Figures 3A,B,D, 4A, 7, 8, 10, 11B)

M. flexor digitorum tibialis lies distal to m. popliteus. It arises from the caudal and medial aspects of the tibial shaft, distal to the insertion of m. popliteus. Distally, it gives rise to a tendon proximal to the medial malleolus of the tibia; there, the tendon courses into the sulcus malleolaris, on the caudal aspect of the malleolus, lying superficial to the tendon of m. tibialis caudalis. Distally, the tendon of m. flexor digitorum tibialis curves around the medial tarsal bone, passing between this bone and the sustentaculum of the calcaneus to course into a groove on the ventral aspect of the foot, limited by the plantar process of the navicular, laterally, and the medial tarsal and entocuneiform, medially. Cranial to the plantar process of the navicular, the tendon fuses with that of m. flexor digitorum fibularis to form a strong common tendinous plate which splits into three branches that insert

onto the distal phalanges of all digits. Nevertheless, in the branch to digit II a longitudinal division, the lateral part representing the m. flexor digitorum tibialis tendon, could be observed. M. flexor digitorum tibialis plantarflexes the ankle joint and flexes the joints of all digits.

M. flexor digitorum fibularis (lateralis, Figures 3B,C, 4A, 6–10)

M. flexor digitorum fibularis lies deep to m. soleus and lateral to mm. popliteus and flexor digitorum tibialis. It arises from the caudal surfaces of the fibula and tibia, and the interosseus membrane. Distally, this muscle gives rise to a 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 ventral aspect of the foot, limited by the plantar process of the navicular, medially, and the cuboid and plantar sesamoid, laterally. Cranial to the plantar process of the navicular, the tendon fuses with that of m. flexor digitorum tibialis to form a strong common tendinous plate which splits into three branches that insert onto the distal phalanges of all digits. M. flexor digitorum fibularis plantarflexes the ankle joint and flexes the joints of all digits.

M. tibialis caudalis (Figure 3B)

M. tibialis caudalis is composed of a thin small belly that lies deep to mm. flexor digitorum fibularis and flexor digi-
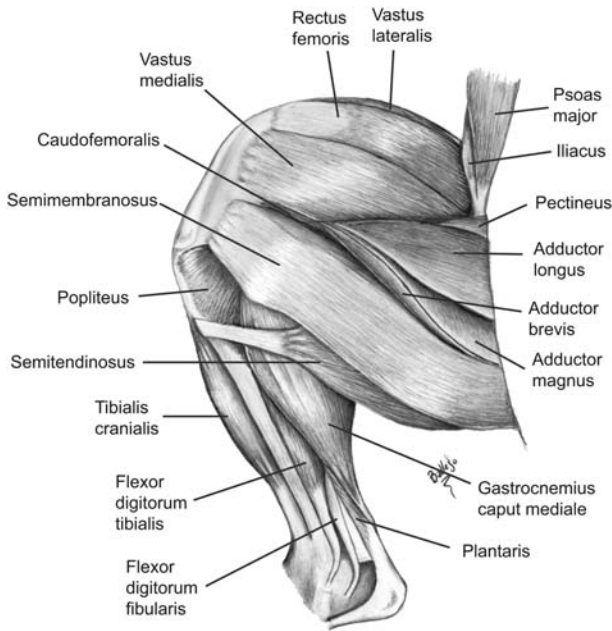
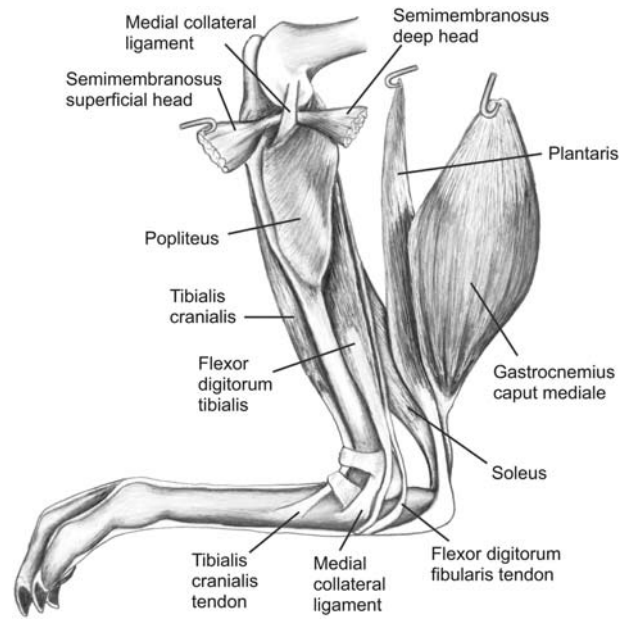**Figure 8**   Medial deep view of the right hindlimb of *D. azarae*.

Figure 10   Medial view of the right leg of *D. azarae*.
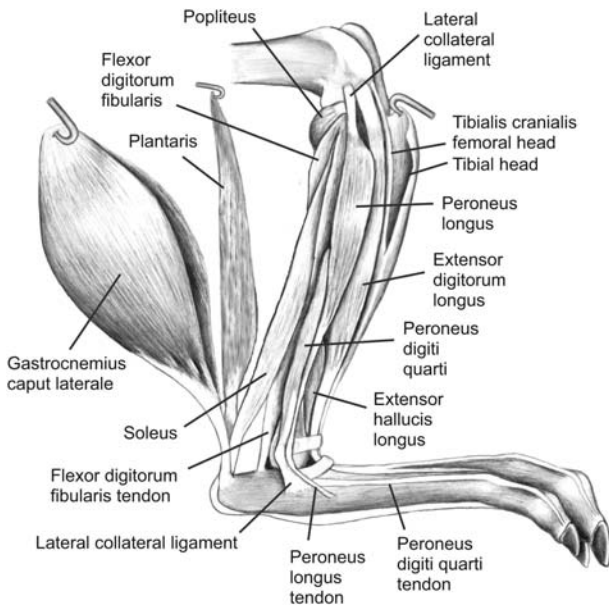

Figure 9   Lateral view of the right leg of *D. azarae*.
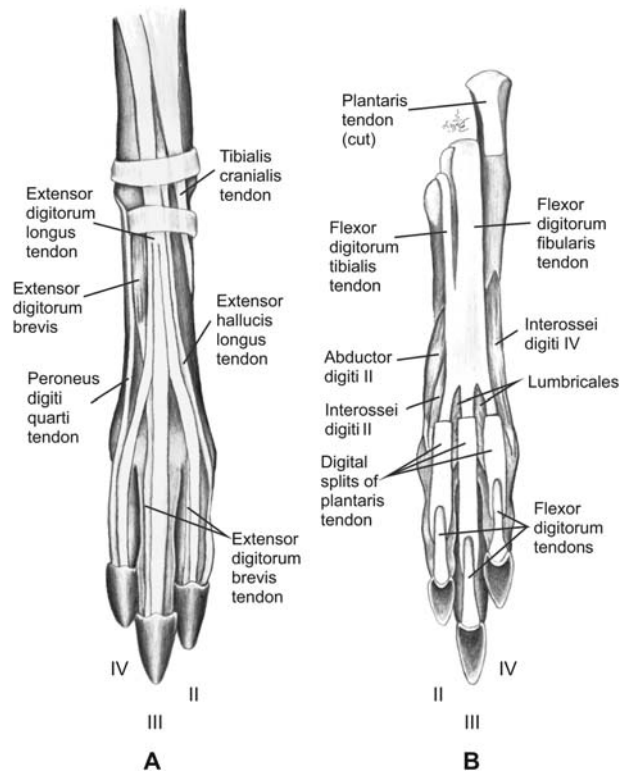

Figure 11   Right foot of *D. azarae*. A, dorsal; B, ventral views.

torum tibialis. It arises from the caudal surface of the proximal shaft of the tibia, between the origins of mm. flexor digitorum fibularis, flexor digitorum tibialis, and popliteus. It gives rise to a very thin long tendon that travels along the three distal quarters of the tibial shaft. Distally, it curves around the sulcus malleolaris, lying deep to the tendon of m. flexor digitorum tibialis, to insert onto the caudal border of the medial tarsal bone. M. tibialis caudalis helps to plantarflex the ankle joint.

Flexor group of the pes

M. flexor digitorum brevis
This muscle could be represented by the tendinous slips that arise from the superficial plantar fascia formed by m. plantaris. Insertion is onto the middle phalanges of the digits.
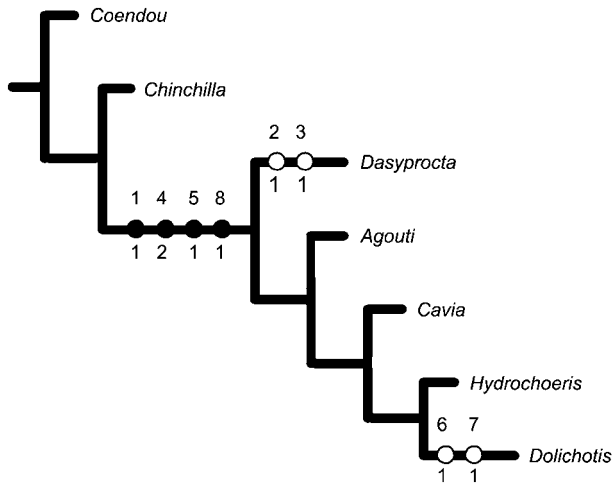
Figure 12   Mapping of eight anatomical characters, as reconstructed using parsimony, onto the phylogeny of Cavioidea (Rowe and Honeycutt 2002) and outgroup taxa. Only unambiguous character state optimizations are shown. Ambiguous optimizations are discussed in the text. Numbers above branches indicate character number whereas those below are character states.

Mm. lumbricales (Figures 4A and 11B).

In *Dasyprocta*, there are two mm. lumbricales, located between the digital tendons of mm. flexor digitorum fibularis and flexor digitorum tibialis. They take origin from the common tendinous plate formed by mm. flexor digitorum tibialis and flexor digitorum fibularis. Lateral m. lumbricalis inserts onto the medial aspect of the proximal phalanx of digit IV; medial m. lumbricalis inserts onto the medial aspect of the proximal phalanx of digit III. Mm. lumbricales flex digits III and IV.

Mm. interossei (Figures 4A and 11B)

Mm. interossei of digits III and IV arise from the dorsal aspect and cranial border of the plantar sesamoid; mm. interossei of digit II arise from the dorsal aspect and cranial border of the navicular. Mm. interossei of each digit insert onto the medial and lateral sesamoids at the metatarsophalangeal joints of the digits.

M. abductor digiti II (Figures 4A and 11A)

M. abductor digiti II lies lateral to the lateral interosseous of digit II. It originates from the lateral border of the navicular. It inserts onto the lateral aspect of the lateral sesamoid at the metatarsophalangeal joint of digit II. M. abductor digiti II abducts digit II. This muscle was not observed by Mivart and Murie (1866).

Adductor digiti II (Figure 4A)

Adductor digiti II lies medial to the medial interosseous of digit II. It originates from the proximal border of the navicular. It inserts onto the medial aspect of the medial sesamoid at the metatarsophalangeal joint of digit II. M. adductor digiti II adducts digit II. This muscle was not observed by Mivart and Murie (1866).

Character mapping (Appendix Table 1)

Optimization of the examined characters on the phylogeny of Rowe and Honeycutt (2002); Figure 12) revealed that, in a cavioid phylogenetic context, the reduction of m. tibialis caudalis (character 2) and absence of m. peroneus brevis (character 3) arose independently in *Dasyprocta*. It is worth noting that both conditions, here associated with cursorial specializations (see discussion), were also present in *Dolichotis*. Ambiguous optimization of these features preclude us from inferring if these character states were also independently acquired by *Dolichotis* or by the ancestor of *Dolichotis-Hydrochoeris* clade.

Presence of a gluteal tongue of m. gluteus medius (character 1), an extra-head of m. tibialis cranialis originating from the lateral condyle of the femur (character 4), reduction in number of mm. lumbricales of the hindfoot (character 5), and a gluteal fossa divided by a gluteal crest (character 8) are potential synapomorphies of cavioids.

Elongation of the hindlimb was observed in the cursorial *Dasyprocta* and *Dolichotis*, and the saltatorial *Chinchilla*. In the phylogenetic context of cavioids, elongation of the distal elements of the hindlimb (characters 6 and 7) was a condition independently acquired by *Dolichotis* (unambiguous autopomorphies of this taxon). Ambiguous optimization of characters 6 and 7 at most basal nodes prevent us to infer the evolution of these characters at this level of the tree. Nevertheless, we can state that, as in other mammals, the elongation of the hindlimb was acquired at least more than once in caviomorph rodents.

Discussion

Species of the genus *Dasyprocta* are characterized by their cursorial habits and their ability to leap and run with remarkable speed and agility (Nowak 1991). According to Gambaryan (1974), only the limbs work during the gallop in *Dasyprocta*, the spine remaining rigid, a similar condition to that observed in the ungulates. This mode of running has been named dorsostabile dilocomotory (Gambaryan 1974). Most of the muscular and osteological traits of the hindlimb observed in *Dasyprocta azarae* are indicative of emphasized parasagittal movements and stabilized joints, compatible with those habits.

In *Dasyprocta azarae* mm. glutei medius and profundus are relatively well developed. The gluteal fossa of the ilium is divided by the gluteal crest in dorsal and ventral portions. The deep portion of m. gluteus medius takes origin from the dorsal gluteal fossa, whereas m. gluteus profundus arises from the ventral gluteal fossa (Figure 1). Therefore, as with other cavioids, m. gluteus profundus takes origin from a distinct fossa of the ilium, a potential synapomorphy of this group (Figure 12). This musculoskeletal arrangement is difficult to evaluate from a functional perspective.

The relatively high mechanical advantage of mm. glutei medius and profundus is indicated by the proximally projected greater trochanter of the femur (Figure 2). As it occurs in other cavioids (Candela and Picasso 2008, Figure 13), a

proximally projected greater trochanter increases the moment arm of these muscles and their mechanical advantage (Maynard Smith and Savage 1956). Therefore, in *Dasyprocta* the high mechanical advantage 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). The development of a gluteal tongue of m. gluteus medius, as observed in some ungulates and rodents (Rinker 1954, Klingener 1964), is a potential synapomorphy of cavioids (Figure 12). Although the presence of a gluteal tongue (and a relatively great development of the gluteal muscles) was interpreted as an anatomical feature that could potentially enhance the angular range of the lumbosacral joint (Gál 1993), more data are necessary to infer the precise function of this trait in relation to different types of locomotion in caviomorph rodents.

As with mm. glutei medius et profundus, m. gluteus superficialis has craniocaudally oriented fibers, an adequate arrangement to allow the extension of the hip joint, resembling that of m. gluteus medius. Conversely to cursorial forms, in arboreal caviomorphs such as porcupines, the fibers of m. gluteus superficialis are more vertically oriented, an arrangement that would emphasize the abduction and lateral rotational actions versus extension (Candela and Picasso 2008).

As in other cavioids (Candela and Picasso 2008, Figure 13) accentuated parasagittal movements of the femur are also depicted in the configuration of the hip joint, which indicates a relatively elevated congruence at this joint, necessary to stabilized flexion/extension movements (Argot 2002, Salton and Sargis 2009). Acetabular cavity in *Dasyprocta* is deep and limited by well-extended walls, which partially restrict rotational movements. The proximally projected greater trochanter also could restrict the mobility of the hip joint, limiting the movements of abduction of the femur, a condition observed in other terrestrial mammals (Taylor 1976, Gebo and Sargis 1996, Argot 2002, Sargis 2002, Salton and Sargis, 2009).

The hamstring muscles of *Dasyprocta* are relatively well developed (Gambaryan 1974: Table 33). Some osteological features, such as a prominent ischiatic tuberosity (Figure 1), are related to extensive origin areas for mm. caudofemoralis, biceps femoris, and semitendinosus (ischial head). The robust area caudally located to this tuberosity indicates a strong origin for m. semimembranosus. The relative elongation of the ischium with respect to total pelvic length (Figure 1), situates the areas of origin of these muscles far from the hip joint, thus improving their mechanical advantage, a condition required for powerful extension of the hip at the beginning of propulsion, and for the flexion of the knee during the recovery stroke (Elftman 1929, Maynard Smith and Savage 1956, Argot 2002).

The lesser trochanter in *Dasyprocta* is relatively small and caudally located, as found in other cursorial caviomorphs, a condition that would improve the function of m. iliopsoas as a protractor rather than as a rotator of the femur (Gebo and Sargis 1994, Argot 2002, Candela and Picasso 2008, Salton and Sargis 2009). As Gambaryan (1974) pointed out, the relative weight of m. iliopsoas increases in proportion to the increase in cursorial specialization.

As occurs in other cavioids (Candela and Picasso 2008, Figures 13, 17), *D. azarae* has a deep knee, characterized by a long and relatively narrow femoral trochlea, delimited by sharp crests, cranially projected patella and tibial tuberosity, which increases the mechanical advantage of m. quadriceps femoris (mm. rectus femoris, vasti lateralis, medialis, et intermedius) in the extension of the knee (Gebo and Sargis 1994, Fostowicz-Frelik 2007, Salton and Sargis 2009). In agreement with the necessary stability required for the ability to run or eventually to leap, the knee joint has prominent tibial spines and concave tibial condyles. These features increase the congruence at the knee, restricting movility and rotation of the tibia (Salton and Sargis 2009).

With regard to the muscles of the crus, Gambaryan (1974) showed that the weight of m. tibialis cranialis in *Dasyprocta* is relatively less than in sciurids. This author pointed out that, among different lineages of mammals, the relative development of this muscle is not dependent on their locomotor abilities. It is possible that in *Dasyprocta* m. tibialis cranialis acts principally as an extensor rather than as an invertor of the pes, in agreement with the limited rotational movements at the cruro-astragalar joint (see below). Action of this muscle as an invertor was indicated for arboreal porcupines (McEvoy 1982). Presence of an extra-head of m. tibialis cranialis originating from the lateral condyle of the femur constitutes a potential synapomorphy of cavioids (Figure 12).

In *D. azarae*, the belly and tendon of m. tibialis caudalis are greatly reduced, a condition that might be indicative of the reduced function of this muscle in the inversion of the foot. Hildebrand (1978) observed that the size of the tendon of m. tibialis caudalis is medium to very small in cursorial species of rodents. In agreement with this interpretation, among cavioids, this feature would have evolved independently in the extreme cursors *Dasyprocta* and *Dolichotis* (Figure 12). Conversely to this condition, this muscle is well developed in species with a marked ability for the inversion of the pes, as seen in arboreal porcupines (McEvoy 1982). In *D. azarae*, m. tibialis caudalis could assist in the plantarflexion of the pes.

M. peroneus brevis, an evertor and plantarflexor of the foot, is absent in *D. azarae*. The same condition was observed in the cursor *D. patagonum* (Beddard 1891). The reduced ability for eversion of the foot in these species could be interpreted as a feature associated with cursorial specializations. In the context of cavioids, loss of m. peroneus brevis evolved independently in the extreme cursors *Dasyprocta* and *Dolichotis* (Figure 12).

Reduction in the number of mm. lumbricales in *Dasyprocta* is associated with reduction of digits I and V, a character shared by all cavioids, interpreted here as a possible synapomorphy of this group (see Figure 12). Reduction of digits and associated musculature is a typical condition of cursorial forms (Weisbecker and Schmid 2007).

Among examined cavioids, elongation of the tibia and third metatarsal, a feature functionally associated with cur-

sorial or saltatorial habits (Gambaryan 1974), was solely observed in the extreme cursors *Dasyprocta* and *Dolicthotis*. This was acquired more than once in this group (Figure 12).

Emphasized parasagittal and limited rotational movements are expressed at cruroastragalar (=tibioastragalar), calacaneoastragalar and transverse joints. As in *D. patagonum* (Candela and Picasso 2008, Figures 17, 19 and 21), the tibial articular surface is deep and concave, in congruence with symmetrical crests of the astragalar trochlea. These features indicate that the cruroastragalar joint in *D. azarae* restricts the movements mainly to plantarflexion-dorsiflexion, typical of cursorial locomotion (Gebo and Sargis 1994, Fostowicz-Frelik 2007). As in other cavioids, the astragalar head in *Dasyprocta* is oriented parallel to the parasagittal plane, which restricts the movement to flexion-extension. The distal portion of the calcaneus and the metatarsals are long (outlever), a condition that would increase speed at the expense of force (Carrano 1997, Candela and Picasso 2008, Figure 21).

In sum, several features of *D. azarae*, such as the strong development of extensors and flexors of the thigh, crus, and foot, reduction of some evertors and invertors of the pes, and reduction in number of mm. lumbricales indicate that the musculature of the hindlimb as a whole is particularly devised to emphasize parasagittal movements and to limit lateral and rotational ones. In agreement with the musculature, osteological characters of the hindlimb, specially displayed in the features of the articular joints, limit the rotational ability of the femur, tibia, and autopodium. These features, together with the lengthening of the ischium, elongation of the hindlimbs (tibia, metatarsals), and the relatively long distal calcaneum, are necessary to achieve the stability and agility to run and leap observed in this species.

Some of the above-mentioned hindlimb features of *Dasyprocta* are shared with the remaining cavioids, and are interpreted as cursorial adaptations. By contrast, other features also functionally related to cursoriality (absence of m. peroneus brevis, reduction of m. tibialis caudalis) evolved independently in the more extreme cursorial taxa *Dasyprocta* and *Dolichotis*.

The information provided herein will be effectively applied to the study of fossil dasyproctids and their relatives, which are well represented in the Cenozoic of Argentina, particularly in the Miocene of Patagonia (e.g., Candela and Vizcaíno 2007). The study of these fossils should shed light on the evolution of cursoriality in this group of caviomorph rodents.

Acknowledgements

Appendix 1

List of specimens examined to construct the data matrix of hindlimb anatomical features. Abbreviations: CNP, Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MACN, Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia'', Buenos Aires, Argentina; MN; Museu Nacional, Rio de Janeiro, Brazil.

Agouti paca (MN 4871, MN 4878, MN 5631); *Cavia aperea* (MLP 15.II.96.49, MLP 2.IV.02.9, MLP 29.XII.00.15, MLP 30.V.02.7); *Chinchilla* sp. (MLP 24.VIII.98.4, MLP11.VIII.99.41, MLP 31.XII.02.37); *Coendou prehensilis* (MN 4923, MN 4925, MN 4936); *Dasyprocta* sp. (CNP 896, CNP 790, MN 4847, MN 4848, MN 4854, MN 4664, MLP 10.VI.98.1); *Dolichotis patagonum* (MLP 236, MLP 249, MLP 250, MLP 642); *Hydrochoeris hydrochaeris* (MACN 43.43, MACN 31.18).

Appendix 2

Remarks on some of the hindlimb muscles analyzed in this study.

M. iliacus: as in *Cavia*, and unlike other caviomorphs (e.g., *Erethizon*, *Chinchilla*, *Lagidium*, *Agouti*), the iliac fossa of *Dasyprocta* (ventrally located to the lateral crest) is very narrow, and it is restricted to the ventral edge of the ilium.

M. psoas major: Mivart and Murie (1866) observed an origin of this muscle from all lumbar vertebrae.

M. tensor fasciae latae: caudally, this muscle is continuous with and inseparable from m. gluteus superficialis. It lies superficial to the lateral, cranial, and medial aspects of m. vastus lateralis.

M. gluteus superficialis: as in other rodents, m. gluteus superficialis is cranially continuous with m. tensor fasciae latae, forming one muscular sheet (Parson, 1894). The tendon of insertion of m. gluteus superficialis is cranially continuous with the fasciae latae.

M. femorococcygeus: caudal fibers of this muscle are not easy to separate from those of m. biceps femoris. At its origin, some fibers intermingle with those of mm. gluteus superficialis and semitendinosus. This muscle has been described as a cranial part of m. biceps femoris by Mivart and Murie (1866) and Parsons (1894) but, as Hill (1937) and Rinker (1954) stated, it is a member of the gluteal complex not related to m. biceps femoris.

M. gluteus medius: as in other rodents (McEvoy 1982, Rinker 1954), three intimately related portions of m. gluteus

medius can be recognized. The dorsal superficial portion takes origin from the lumbodorsal fascia and the fascia over the erector spinae musculature. Their fibers pass over the proximal end of the greater trochanter of the femur to insert onto the caudolateral aspect of the proximal femoral shaft. The ventral superficial portion arises from the dorsal border of the wing of the ilium, the iliac crest and adjacent area of the wing of the ilium, extending caudally onto the crest that divides the gluteal fossa, here called gluteal crest. This portion of m. gluteus medius completely covers and encloses the deep portion of this muscle (dorsally located to the gluteal crest) and m. gluteus profundus (ventrally located to the gluteal crest). The ventral superficial portion inserts, by a strong wide tendon, onto the caudolateral aspect of the greater trochanter of the femur, superficial to the origin of m. vastus lateralis. The deep portion of m. gluteus medius takes origin from the dorsal portion of the gluteal fossa to insert onto the proximal end of the greater trochanter, in common with m. piriformis. This portion is intimately associated with the cranial fibers of the latter muscle. Deep portion corresponds to m. gluteus minimus *sensu* Mivart and Murie (1866) and Parsons (1894); nevertheless, as stated by Rinker (1954) and Klingener (1964), deep portion of m. gluteus medius and m. gluteus minimus can be identified because of their separation by the passage of cranial gluteal nerve. M. gluteus medius extends cranially to the iliac crest as far as to the level of the last two lumbar vertebrae, forming a ''gluteal tongue'' over the fascia that covers the erector spinae musculature. This gluteal tongue was also observed in some ungulates, as well as in other rodents (Rinker 1954, Klingener 1964).

M. gluteus profundus: the ventral portion of the gluteal fossa of the ilium lies ventral to the gluteal crest and dorsal to the lateral crest, which separates it from the iliac fossa. As noted above, the same condition was observed in cavids (e.g., *Cavia*, *Dolichotis*), whereas in other caviomorphs (e.g., erethizontids, chinchillids) the gluteal fossa is not clearly divided into ventral and dorsal portions. This muscle corresponds to m. scansorius *sensu* Mivart and Murie (1866) and Parsons (1894; see remarks above on the identification of mm. glutei medius and profundus).

M. piriformis: the cranial fibers of m. piriformis are continuous with the caudal ones of the deep portion of m. gluteus medius.

M. rectus femoris: it was somewhat difficult to clearly differentiate both heads of origin of this muscle; the same condition was observed in some caviomorphs but in others both heads were distinct (Parsons 1894). The tendons of insertion of mm. vasti join that of m. rectus femoris, constituting the m. quadriceps femoris tendon, which includes the patella in it, continuing distally to insert onto the tibial tuberosity (Figure 3A).

M. tibialis cranialis: this muscle is the largest of the extensor muscles of the foot. In rodents, it usually has a single origin from the proximal portion of the tibia, but in some caviomorphs the origin is double. In Dasyproctidae, it has, in addition, a femoral origin by a tendon, as described here and elsewhere (Mivart and Murie 1866, Parsons 1894, Windle 1897); in Chinchillidae, fleshy fibers arise from the tendon of origin of m. extensor digitorum longus (Wood and White 1950, Parsons 1894); in Caviidae, both conditions were observed, in addition to some specimens which possessed solely the tibial origin (Mivart and Murie 1866, Parsons 1894). In rodents, this muscle usually has two insertions (onto the entocuneiform and metatarsal I) but, in those cases in which digit I is absent or rudimentary, only a single tendon of insertion was observed (Parsons 1894).

M. gracilis: M. gracilis is a very wide muscle. In medial view, it is the most superficial muscle of the thigh. Proximally, the cranial border of the caudal head slightly overlaps the caudal portion of the cranial head. Mivart and Murie (1866) recognized the cranial head as m. sartorius.

Mm. adductores: the names applied to the adductor muscles of rodents and the interpretation of their synonymies by different authors have been a matter of controversy, as it has been exemplified by Klingener (1964).

M. adductor brevis: Mivart and Murie (1866) recognized this muscle as m. adductor magnus.

M. adductor magnus: it seems that Mivart and Murie (1866) recognized this muscle as m. adductor brevis.

M. adductor minimus: neither Mivart and Murie (1866), nor Parsons (1894), nor Windle (1897) recognized this muscle in *Dasyprocta*. Among other caviomorphs, it was either not described in *Cavia* (e.g., Cooper and Schiller 1975) or *Chinchilla* (Wood and White 1950), but it was observed in *Erethizon* and *Coendou* (McEvoy 1982), and probably was recognized but not named in *Dolichotis* (Windle 1897).

M. caudofemoralis: this muscle has been identified as a part of m. semimembranosus by Mivart and Murie (1866) and Parsons (1894). The origin of this muscle in some rodents is from the caudal vertebrae (e.g., Rinker 1954, Parsons 1984).

M. soleus: Mivart and Murie (1866) observed a tibial origin for this muscle.

M. flexor digitorum tibialis: union of both flexor digitorum tendons has been observed in all the caviomorphs studied (e.g., Hildebrand 1978, Dobson 1883).

M. flexor digitorum fibularis: Mivart and Murie (1866) did not observe a tibial origin for this muscle.

M. tibialis caudalis: Mivart and Murie (1866: 415) stated that the insertion of this muscle is onto ''the proximal end of the plantar surface of the naviculare''. This observation was probably made by the fact that ''early writers…seem

not to have distinguished the medial tarsal bone from the navicular'', as Hildebrand (1978) pointed out.

M. abductor digiti II: this muscle was not observed by Mivart and Murie (1866).

Appendix 3

Appendix Table 1 Matrix of coded hindlimb anatomical features used in character mapping. Cases of polymorphism are coded ''/''; unknown character conditions are coded ''?''.

Taxa/character	1	2	3	4	5	6	7	8
Coendou	0	0	0	0	0	0	0	0
Chinchilla	0	0	0	1	0	1	1	0
Agouti	1	0	0	2	1	0	0	1
Dasyprocta	1	1	1	2	1	1	1	1
Hydrochoeris	?	?	?	?	1	0	0	1
Cavia	1	0	0	0/2	1	0	0	1
Dolichotis	1	1	1	2	1	1	1	1

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