



The hip adductor muscle group in caviomorph rodents: anatomy and homology

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ABSTRACT

Anatomical comparative studies including myological data of caviomorph rodents are relatively scarce, leading to a lack of use of muscular features in cladistic and morphofunctional analyses. In rodents, the hip adductor muscles constitute an important group of the hindlimb musculature, having an important function during the beginning of the stance phase. These muscles are subdivided in several distinct ways in the different clades of rodents, making the identification of their homologies hard to establish. In this contribution we provide a detailed description of the anatomical variation of the hip adductor muscle group of different genera of caviomorph rodents and identify the homologies of these muscles in the context of Rodentia. On this basis, we identify the characteristic pattern of the hip adductor muscles in Caviomorpha. Our results indicate that caviomorphs present a singular pattern of the hip adductor musculature that distinguishes them from other groups of rodents. They are characterized by having a single m. adductor brevis that includes solely its genicular part. This muscle, together with the m. gracilis, composes a muscular sheet that is medial to all other muscles of the hip adductor group. Both muscles probably have a synergistic action during locomotion, where the m. adductor brevis reinforces the multiple functions of the m. gracilis in caviomorphs. Mapping of analyzed myological characters in the context of Rodentia indicates that several features are recovered as potential synapomorphies of caviomorphs. Thus, analysis of the myological data described here adds to the current knowledge of caviomorph rodents from anatomical and functional points of view, indicating that this group has features that clearly differentiate them from other rodents.

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1. Introduction

Caviomorph rodents constitute a monophyletic group (e.g., Fabre et al., 2012; Upham and Patterson, 2012; Voloch et al., 2013) currently represented by numerous species that occupy almost all habitats of the Neotropical region, ranging from rainforest to desert and from sea level to the highest puna (Mares and Ojeda, 1982; Nowak, 1991). This great diversity is a consequence of the explosive adaptive radiation undergone by caviomorphs during the isolation of South America throughout most of the Cenozoic (Vucetich et al., 1999; Antoine et al., 2012). Extant species display a broad range of body size and ecomorphological diversity, reflected in a wide array of locomotor behaviors and substrate preferences (semiaquatic, arboreal, scansorial, fossorial, and terrestrial). However, compared with other clades of the order, studies of caviomorphs that evaluate

the postcranial morphological variation are relatively scarce (e.g., Hildebrand, 1978; Elissamburu and Vizcaíno, 2004; Candela and Picasso, 2008), particularly those focusing on muscular anatomy. Analyses of the myology of caviomorphs were mainly focused on single species (e.g., Alezais, 1900; Wood and White, 1950; Cooper and Schiller, 1975; García-Esponda and Candela, 2010), not involving comparisons that include representatives of all families of the group (but see Parsons, 1894; Woods, 1972; Rocha-Barbosa et al., 2007). Phylogenies of caviomorphs are seldom based on myological characters (but see Rocha-Barbosa et al., 2007); moreover, the systematic implications of myological features of hystricognath rodents were not evaluated since the contributions of Woods (1972) and Woods and Hermanson (1985).

The hip adductor muscles constitute an important group of the hindlimb musculature, having an important function during the beginning of the stance phase of locomotion, adducting, extending and laterally rotating the hip (Rasmussen et al., 1978; Evans, 1993; Palastanga and Soames, 2012). In rodents, this muscular group comprises the mm. gracilis, adductor longus, adductor

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brevis, adductor magnus, and obturator externus (e.g., Hill, 1937). All these muscles are innervated by the obturator nerve and are part of the flexor muscular system of the hindlimb, forming the ventral lumbar group (Hill, 1937; Jouffroy, 1971). The muscles of the hip adductor group take origin from the pelvis and attach onto the femur, with the exception of the m. gracilis, which attaches onto the tibia (Jouffroy, 1971). All of them act in the adduction of the hip joint, whereas those muscles or those parts of the muscles that are located caudally to the hip joint are also involved in the extension of this joint (Elftman, 1929; Rasmussen et al., 1978; Nicolopoulos-Stournaras and Iles, 1984; Evans, 1993; Palastanga and Soames, 2012). The hip adductors play an important function in stabilizing the pelvis during gait when they work with their distal attachments fixed, as they pull the supporting limb into adduction, thereby moving the line of gravity over the supporting foot (Elftman, 1929; McEvoy, 1982; Palastanga and Soames, 2012). In addition, the mm. adductores (longus, brevis and magnus) and the m. obturator externus can also laterally rotate the hip joint.

In many mammals, the hip adductor muscles are subdivided or fused in various different ways; thus, it is not surprising that their homologies and consequent denominations are sometimes hard to establish (e.g., Jouffroy, 1971; Budras, 1972). This is also the case for caviomorph rodents; these muscles have neither been comparatively evaluated among the different genera nor compared with those of other groups of rodents (but see Parsons, 1894).

As mentioned above, caviomorphs have evolved many different locomotion types, associated with a wide range of body sizes. This led to some morphotypes that have no counterparts in other clades of rodents, as, for example, the large semiaquatic capybaras (*Hydrochoerus*), the large terrestrial pacas (*Cuniculus*), or the agile cursorial agoutis (*Dasyprocta*) and maras (*Dolichotis*). In this context, some muscles of the limbs of caviomorphs could present a different morphological arrangement when compared with other groups of rodents, as it was observed for some adductor muscles of the hip (McEvoy, 1982; García-Esponda and Candela, 2010). Thus, we hypothesize that this different morphological pattern could be related to some functional aspects that make possible the many and particular modes of locomotion displayed by this clade.

In the present contribution we provide a detailed description of the anatomical variation of the hip adductor muscle group in caviomorph rodents, deeply discuss the possible hypotheses of correspondence (primary homologies) of each muscle analyzed in different genera of caviomorphs, and identify the homologies of these muscles in the context of Rodentia. On this basis, we identify the unique pattern of the hip adductor muscles in caviomorphs, increasing the knowledge of the morphological features that characterize this clade in the context of Rodentia. In addition, by means of character mapping on a composite molecular phylogeny of rodents, we explore the possible evolution of the analyzed myological characters and the potential synapomorphies of caviomorphs. Finally, we hypothesize about the functional significance of the unique pattern of the hip adductor muscles observed in caviomorphs relative to other rodents.

2. Materials and methods

Anatomical dissections of the hindlimb musculature of seven species of caviomorph rodents were carried out (Table 1). All of the specimens studied were adults. Some of them had died from natural causes at La Plata zoo (Jardín Zoológico de La Plata), while others had been preserved in the mammalogy collection at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. Specimens of *Chinchilla lanigera* were discarded animals from a

Table 1
Species of Caviomorpha analyzed.

Species	N
Cavioidea	
Caviidae	
<i>Cavia porcellus</i>	4
<i>Dolichotis patagonum</i>	3
<i>Hydrochoerus hydrochaeris</i>	2
Chinchilloidea	
Chinchillidae	
<i>Chinchilla lanigera</i>	2
<i>Lagostomus maximus</i>	2
Octodontoidea	
Ctenomyidae	
<i>Ctenomys talarum</i>	3
Echimyidae	
<i>Myocastor coypus</i>	3

local farm; specimens of *Cavia porcellus* came from the Instituto Biológico Dr. Tomás Perón (La Plata). In addition, for the purpose of direct comparison with a group of non-caviomorph rodents, two specimens of the laboratory rat (*Rattus norvegicus*, Muridae) were also dissected.

Specimens were preserved in a 5–10% formalin solution (depending on the size of the species) until dissection; then, they were immersed in a 70% alcohol solution. Dissections were done under a magnifying glass (2×) or under a binocular microscope using magnifications of 7–15×. Areas of origin and insertion of the hip adductor muscles, as well as their topographic relationships to one another and to the branches of the obturator nerve were recorded.

As our objective was to explore the myological variation between different taxa of Caviomorpha, the emphasis was on inter-generic instead of intraspecific anatomical variation. So, in the text, all the species analyzed are referred to by their generic names.

In addition to our observations, data of the hip adductor musculature of *Dasyprocta* (Cavioidea: Dasyproctidae), *Erethizon* and *Coendou* (Erethizontoidea: Erethizontidae) were obtained from García-Esponda and Candela (2010) and McEvoy (1982), respectively. Thus, the myological information on caviomorphs provided in this contribution corresponds to six families (Erethizontidae, Dasyproctidae, Ctenomyidae, Chinchillidae, Echimyidae, and Caviidae) representing all four superfamilies recognized in this clade (Fabre et al., 2012; Upham and Patterson, 2012; Voloch et al., 2013).

The myological nomenclature and system arrangement used is that of McEvoy (1982) for erethizontids, because it agrees with those used by other authors in musculature studies of other groups of rodents (e.g., Rinker, 1954; Klingener, 1964). The topographic position of the obturator nerve was considered a basic landmark in the identification of the adductor muscles, as in previous studies (Hill, 1937; Jouffroy, 1971).

The establishment of primary homology (sensu de Pinna, 1991; for a discussion on the use of primary and secondary homology see Grant and Kluge, 2004; Nixon and Carpenter, 2011; Brower and de Pinna, 2012) or topographical correspondences (Rieppel, 1988) was based on comparative anatomical examinations, following classical criteria of homology, particularly topology and connectivity (see Rieppel, 1988 and bibliography cited therein), and then expressed as characters.

The m. pectineus is topographically related to the hip adductor muscle group, also acting in the adduction of the hip joint. Notwithstanding, it was not included in the present study because it is considered an element of the extensor muscular system of the hindlimb that belongs to the dorsal lumbar group (Hill, 1937; Jouffroy, 1971). The association of the m. pectineus with the dorsal lumbar group is supported by its embryonic development and its

innervation by the femoral nerve (Lance-Jones, 1979). Nevertheless, this muscle is treated with the hip adductor muscles in some functional anatomy studies (e.g., Williams et al., 2007).

The myological and nerve variation identified among rodents was coded into six characters (see below), the evolution of which 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). Cladistic mapping was done with the software TNT 1.0 (Goloboff et al., 2008). Character states were considered unordered, except character 3. The tree was edited with WINCLADA (Nixon, 1999). Hip adductor muscle information provided belongs to the caviomorph genera dissected for the present study (see Table 1), plus literature data on *Erethizon*, *Coendou* (McEvoy, 1982) and *Dasyprocta* (García-Esponda and Candela, 2010). All characters mapped on the molecular phylogeny are listed in Table S1 in the supplementary online Appendix. Anatomical data on non-caviomorph genera included in the data matrix were taken from the literature (see Table S2 in the supplementary online Appendix).

Character descriptions are as follows:

- (1) Morphology of the m. gracilis: 0 = single; 1 = double (cranial and caudal parts).
- (2) Relationship of the m. adductor longus and the obturator nerve: 0 = not perforated by the branch of the obturator nerve that supplies the m. adductor brevis; 1 = perforated by that branch.
- (3) Morphology of the m. adductor brevis: 0 = single (femoral part only); 1 = double (genicular and femoral parts); 2 = single (genicular part only).
- (4) Topographic position of the m. adductor brevis: 0 = lateral to the branch of the obturator nerve that innervates the m. gracilis; 1 = medial to that branch.
- (5) Presence of the m. adductor minimus: 0 = present; 1 = absent.
- (6) Topographic relationship of the branch of the obturator nerve that innervates the m. gracilis: 0 = as a split of the main cranial ramus of the obturator nerve; 1 = as a split of the main caudal ramus of n. obturatorius.

3. Results

3.1. Myology

The anatomical variation observed in the adductor hip musculature of the caviomorph genera analyzed, as well as the comparison with the myology of other groups of rodents, allow us to identify the following muscles: mm. gracilis (cranial and caudal parts), adductor longus, adductor brevis (genicular and femoral parts), adductor magnus, adductor minimus, and obturator externus. The proposed homologies and nomenclature of each muscle in caviomorph rodents, as recognized here and by different authors, are summarized in Table 2 (compare also with the synonyms proposed by Klingener, 1964 for “myomorph” rodents).

3.1.1. *M. gracilis*

The m. gracilis originates from the ventral border of the pubis and ventral ischial tuberosity, mainly by means of the symphyseal tendon. In all genera, the origin extends for most of the length of the symphysis pelvica, except in *Ctenomys* (Fig. 1, and see below). In *Hydrochoerus*, the cranial origin of this muscle is aponeurotic (Fig. 2). The m. gracilis lies caudal to the m. adductor brevis and medial to the mm. semitendinosus, semimembranosus and adductor magnus. At its cranial origin, the fibers of the m. gracilis are medial to the caudal fibers of the m. adductor brevis. The mm. gracilis and adductor brevis form a muscular sheet that is medial to all other muscles of the hip adductor group. In most genera, these two muscles diverge distally, so that, in medial view, a distal portion of the m. semimembranosus can be seen between them (Fig. 1); on the other hand, in *Hydrochoerus*, both muscles do not diverge distally, and the medial muscular sheet formed by them is continuous (Fig. 2). The insertion of the m. gracilis is made by a tendon and by aponeurotic tissue onto the proximal medial surface of the tibia and onto the crural fascia. The distal border of the m. gracilis is connected with a superficial crural aponeurosis that extends to the heel. This aponeurosis extends from the medial to the lateral side of the leg, constituting a superficial fibrous sheath that is firmly connected to the common calcaneal and plantaris tendons.

Table 2
Proposed synonyms of names of hip adductor muscles in caviomorphs.

Alezais (1900) ^a <i>Cavia</i>	Wood and White (1950) <i>Chinchilla</i>	Cooper and Schiller (1975) <i>Cavia</i>	McEvoy (1982) <i>Erethizon</i> and <i>Coendou</i>	García-Esponda and Candela (2010) <i>Dasyprocta</i>	Present study (see Table 1)
Posterior gracilis	Gracilis posticus	Gracilis (caudal head)	Gracilis	Gracilis (caudal head)	Gracilis (cranial and caudal parts only in <i>Ctenomys</i>) Adductor longus
Adductor longus	Adductores longus and brevis (fused)	Adductor longus	Adductor longus	Adductor longus	
Anterior gracilis	Gracilis anticus	Gracilis (cranial head)	Adductor brevis (genicular part)	Gracilis (cranial head)	Adductor brevis (genicular part) Adductor brevis (femoral part, only in <i>Ctenomys</i>) Adductor magnus (proximal part, in cavioids) Adductor magnus (distal part, in cavioids)
Femoral portion of adductor magnus, superior fascicle	Adductor magnus ^b	Adductor magnus	Adductor magnus	Adductor magnus	
Femoral portion of adductor magnus, inferior fascicle		Adductor brevis		Adductor brevis	
Adductor brevis		^c	Adductor minimus	Adductor minimus	Adductor minimus
Obturator externus	Obturator externus	Obturator externus	Obturator externus	Obturator externus	Obturator externus
Condylar portion of adductor magnus					Caudofemoralis ^d

^a The original names of the muscles provided in French by Alezais were translated into English or were replaced by their names in Latin.

^b It is hard to say that m. adductor magnus described by Wood and White completely corresponds to m. adductor magnus of the present study since Wood and White observed that the insertion of their muscle was onto the tuberosity of the tibia.

^c Cooper and Schiller did not mention this muscle in the text, but it was drawn in two figures, where it was erroneously named as m. adductor longus.

^d This muscle actually belongs to the hamstring group of muscles, innervated by a branch of the sciatic nerve.

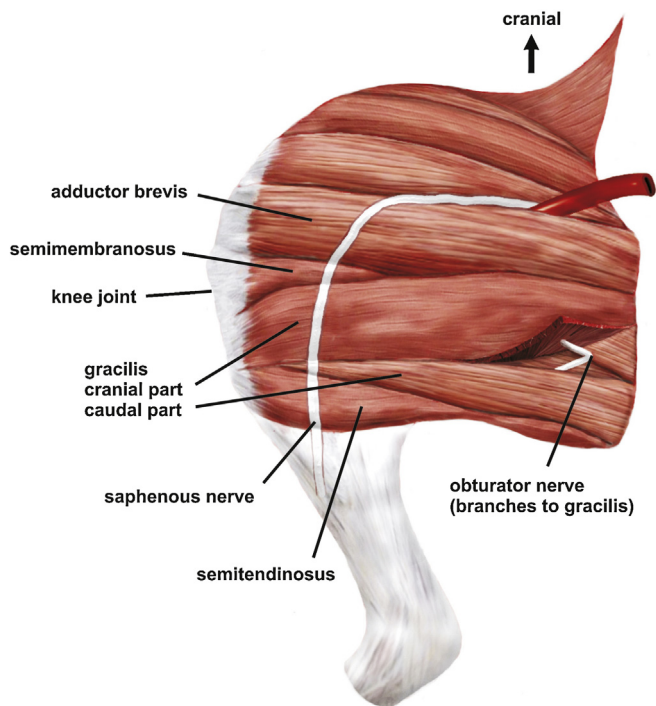


Fig. 1. Medial superficial view of the right hindlimb of *Ctenomys*.

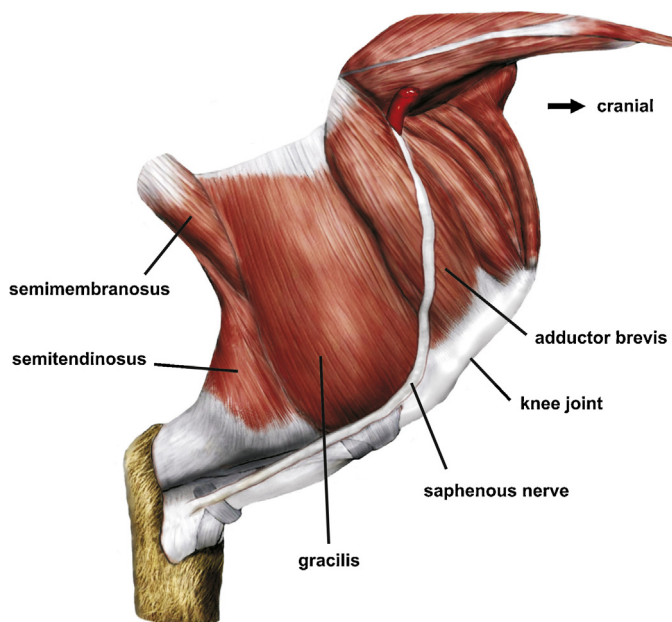


Fig. 2. Medial superficial view of the left hindlimb of *Hydrochoerus*.

It is well developed in all the studied genera, with the exception of *Ctenomys*. The m. gracilis was single in all genera analyzed, with the exception of *Ctenomys* where it was found to be double, and cranial and caudal parts could be observed. In the latter genus, the origin of the cranial part of the m. gracilis is cranial to the symphysis pelvica, whereas the caudal part originates from the ventral ischial tuberosity, caudal to the symphysis (Fig. 1). It is worth mentioning that *Ctenomys*, as other fossorial mammals, has an extremely short symphysis pelvica. At their origins, and for most of their lengths, the cranial and caudal parts of the m. gracilis are separated from one another, but distally both parts become thinner and closer together so that the most distal portion of the cranial part overlaps that of the

caudal one, inserting medially to it (Fig. 1). The cranial part of the m. gracilis inserts onto the crural fascia, whereas the caudal part develops a well-differentiated tendon that ends on the medial surface of the tibia, just proximal to the insertion of the m. semitendinosus.

In *Rattus*, where both cranial and caudal parts of the m. gracilis are also present, a similar arrangement as that described in *Ctenomys* was observed (see Fig. 6).

3.1.2. *M. adductor longus*

The m. adductor longus takes origin from the cranial ramus of the pubis, caudal to the origin of the m. pectineus. It lies caudal to the m. pectineus, cranial and medial to the m. adductor magnus, and lateral to the m. adductor brevis. It is approximately similar in size to the m. pectineus in all genera analyzed, with the exception of *Myocastor*, in which it is smaller than the m. pectineus. In the latter genus, the m. adductor longus lies medial and caudal to the m. pectineus, cranial to the femoral part of the m. adductor brevis, and lateral to its genicular part. In all species, the m. adductor longus inserts onto the caudal surface of the proximal third of the body of the femur, distal to the trochanter minor. The insertion is made by muscular fibers, along with the m. pectineus, onto the linea aspera. Except in *Myocastor*, the m. adductor longus is perforated by a branch of the obturator nerve that innervates the m. adductor brevis (Fig. 3). In *Rattus*, this branch of the obturator nerve does not perforate the m. adductor longus either.

3.1.3. *M. adductor brevis*

With the exception of *Myocastor*, all caviomorphs have a single m. adductor brevis, which lies cranial to the m. gracilis and medial to the mm. pectineus, adductor longus, adductor magnus, the cranial border of the m. semimembranosus, and the caudal border of the m. vastus medialis. As stated above, this muscle forms, along with the m. gracilis, a medial muscular sheet that covers, in medial view, all other muscles of the hip adductor group (Figs. 1 and 2). The m. adductor brevis almost always has a broad origin from the ventral border of the pubis, but some variation was observed: in most genera, it starts from the level of the iliopubic eminence and extends up to the half or most of the length of the symphysis pelvica; in *Hydrochoerus*, the origin extends caudally to the ventral ischial tuberosity; in *Ctenomys* its origin ends where the symphysis pelvica begins. At its origin, the caudal fibers of the m. adductor brevis are lateral to 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. Thus, this branch of the obturator nerve to the m. gracilis lies lateral to the m. adductor brevis for most of its length, but, near its distal border, it pierces this muscle to run medial to its most distal fibers. Insertion of the m. adductor brevis is onto the fascia of the knee region and onto the patella. The insertion onto the patella is made by a narrow tendon which is a continuation of an aponeurosis developed on the cranial border of the muscle. Compared with other rodents (e.g., *Rattus*) in which femoral and genicular parts of the m. adductor brevis were described, it is assumed that the m. adductor brevis of caviomorphs corresponds solely to the genicular part of this muscle (see also McEvoy, 1982). The only recorded exception is *Myocastor*, in which a femoral part of the m. adductor brevis was also observed (Fig. 3). At the origin of the muscle, it is very hard to separate both parts with accuracy, but at about half the longitude of the muscle, they start to separate on their own, the femoral part lying lateral (deep in medial view) to the genicular part. The femoral part inserts onto the caudal surface of the femur, distal to the insertion of the m. adductor longus; the genicular part inserts as in the other caviomorph genera studied.

In *Rattus*, the m. adductor brevis also has both a femoral and a genicular part, but the latter lies lateral to the branch of the

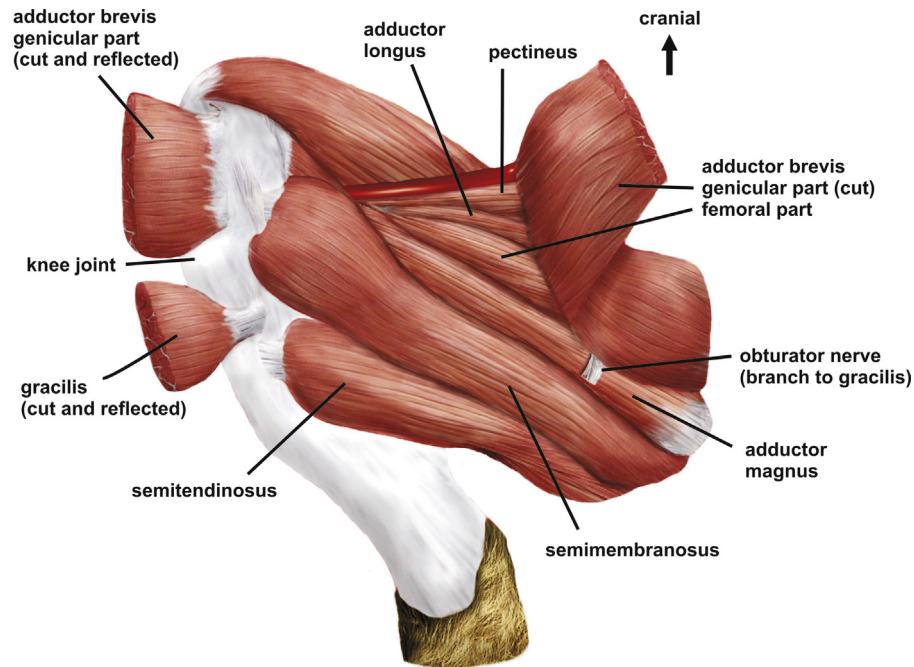


Fig. 3. Medial deep view of the left hindlimb of *Myocastor* (the proximal portions of the mm. adductor brevis and gracilis are detached).

obturator nerve to the m. gracilis, as described for other non-caviomorph rodents (Fig. 6; see Section 4.1).

3.1.4. *M. adductor magnus*

The m. adductor magnus takes origin from the caudal ramus of the pubis, the ventral ischial tuberosity, and the ischial ramus. The area of origin is ventral and caudal to the origin of the m. adductor minimus, dorsal to the origin of the mm. adductor brevis and gracilis, and ventral to the origin of the m. semimembranosus. The m. adductor magnus lies caudal and lateral to the m. adductor longus, lateral to the mm. adductor brevis and gracilis, and medial to the mm. semimembranosus and caudofemoralis. It also lies caudal to the m. adductor minimus, wrapping around it, so that it is superficial to this muscle in both medial and lateral views. In *Myocastor*, the femoral part of the m. adductor brevis interposes between the mm. adductores magnus and longus. The m. adductor magnus has a fleshy insertion onto the caudal surface of the femur, 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. In *Cavia*, *Dolichotis* and *Hydrochoerus* (family Caviidae), proximal and distal parts of the m. adductor magnus can be recognized (Figs. 4 and 5). The distal part comprises the most caudal fibers of the muscle, which form a belly that gradually widens from its origin to its distal end. The origin of this part is attached by a tendon that originates from the ventral ischial tuberosity. This tendon is particularly long and narrow in *Cavia* and *Dolichotis* (as well as in *Dasyprocta*; García-Esponda and Candela, 2010). The remaining cranial fibers constitute the proximal part of the muscle. The proximal part inserts more proximally onto the femur, the caudal part inserts more distally onto this bone. These two portions of the m. adductor magnus are more clearly separable in *Cavia* and *Dolichotis* than in *Hydrochoerus*.

3.1.5. *M. adductor minimus*

The m. adductor minimus originates from the caudal ramus of the pubis, between the origins of the mm. adductor magnus and obturator externus. This muscle lies lateral to the m. obturator externus, medial to the m. adductor longus, and cranial to the m. adductor magnus. The m. adductor minimus is wrapped by this

latter muscle, so that the m. adductor magnus is superficial to it in both medial and lateral views (Fig. 5). The fibers of the m. adductor minimus have a more horizontal orientation than those of most of the other adductor muscles. Insertion is by a flat tendon onto the proximal portion of the lateral crest of the femur, just distal to the greater trochanter. The tendon of insertion is much more evident from the medial surface of the muscle. This muscle was well differentiated from the m. adductor magnus in all the specimens dissected, except in one individual of *Ctenomys*, in which the separation from that muscle was not complete, despite the fact that its tendon of insertion was well developed. The obturator nerve pierces the cranial portion of the m. adductor minimus in *Cavia*, *Dolichotis*, *Hydrochoerus* and *Lagostomus*, but it passes cranial to this muscle in *Chinchilla*, *Ctenomys* and *Myocastor*.

3.1.6. *M. obturator externus*

The m. obturator externus takes its origin from almost the entire border of the obturator foramen and from the external surface of the obturator membrane. This is the deepest of the muscles of the hip adductor group, lying medial to all of them. Insertion is made by a strong tendon into the trochanteric fossa of the femur; its fibers have also a horizontal orientation, as observed in the m. adductor minimus. The m. obturator externus can also act as a lateral rotator of the hip joint.

3.2. Branches of the obturator nerve

In caviomorphs, a general pattern of the obturator nerve and its principal branches can be described. Immediately after passing through the obturator canal, the obturator nerve gives off a branch to the m. obturator externus. The nerve then divides into two main branches: cranial (or medial) and caudal (or lateral). The cranial branch is shorter than the caudal one; it splits into two secondary branches that innervate the mm. adductores longus and brevis. The secondary branch that supplies the m. adductor longus enters its lateral surface. The other secondary branch pierces the lateral surface of the m. adductor longus and runs through this muscle to reach the lateral surface of the m. adductor brevis (Fig. 4). In *Myocastor*, in which genicular and femoral parts of the m. adductor brevis were

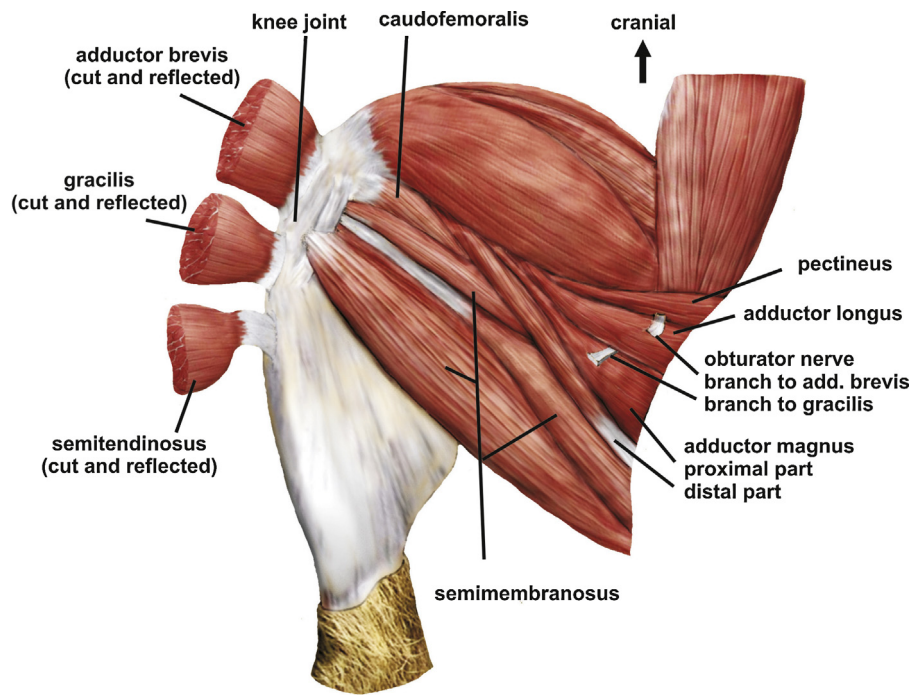


Fig. 4. Medial deep view of the right hindlimb of *Cavia* (the proximal portions of the mm. adductor brevis, gracilis and semitendinosus are detached).

observed (see Section 3.1.3), the branch to this muscle does not pierce the m. adductor longus. The other main division of the obturator nerve, the caudal branch, gives off divisions to the mm. gracilis and adductores minimus and magnus. The secondary branch to the m. adductor minimus is the shorter one of these offshoots. The other two secondary branches are much longer; one enters the medial surface of the m. adductor magnus, while the other enters the lateral surface of the m. gracilis. These two latter branches lie lateral to the mm. adductores longus and brevis (Figs. 3 and 4). Nevertheless, in all genera studied (with the exception of *Myocastor*), the branch to the m. gracilis pierces the most caudal part of the m. adductor brevis, before reaching that muscle; thus, the most caudal fibers of the m. adductor brevis lie lateral to this branch of the obturator nerve. In *Ctenomys*, where cranial and caudal parts of the m. gracilis were observed (see Section 3.1.1), the branch that innervates

this muscle splits into two rami, one for each one of these parts (Fig. 1).

In *Rattus*, the cranial branch of the obturator nerve gives off three secondary divisions to innervate the mm. adductores longus and brevis and the m. gracilis. The latter secondary branch lies medial to the m. adductor brevis (Fig. 6). The caudal branch of the obturator nerve supplies the m. adductor magnus.

3.3. Character mapping

Optimization of the examined characters on the composed phylogeny of the Rodentia is shown in Fig. 7A–G. The interpretation of the evolution of these characters in this phylogenetic context is discussed in detail in Section 4.2.

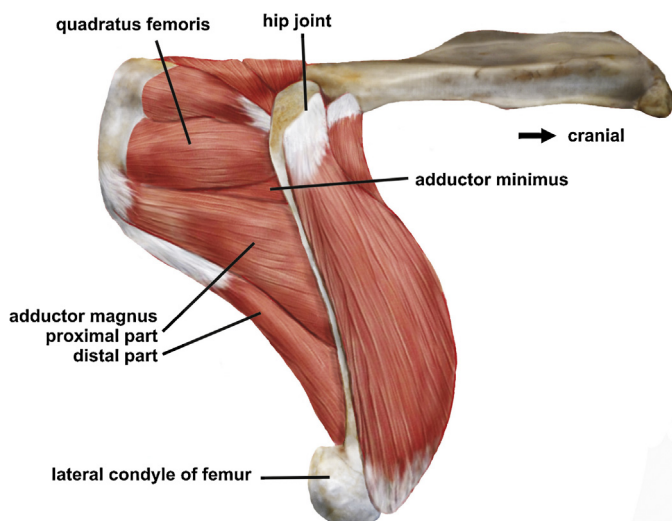


Fig. 5. Lateral deep view of the right hindlimb of *Cavia*.

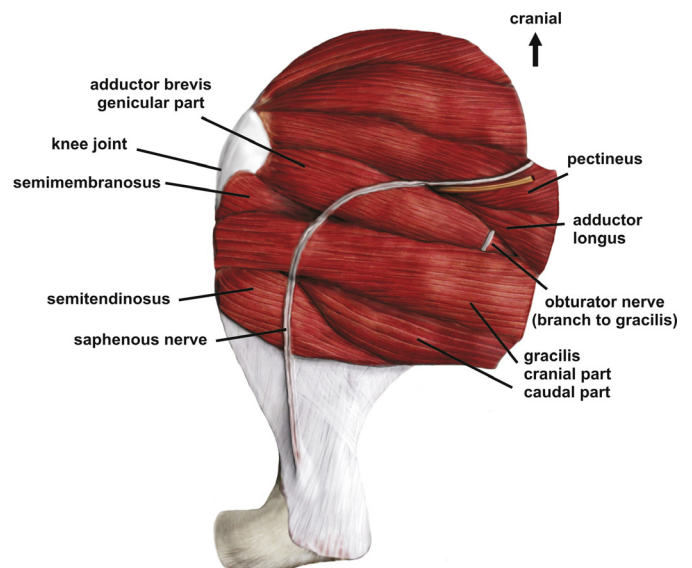


Fig. 6. Medial superficial view of the right hindlimb of *Rattus*.

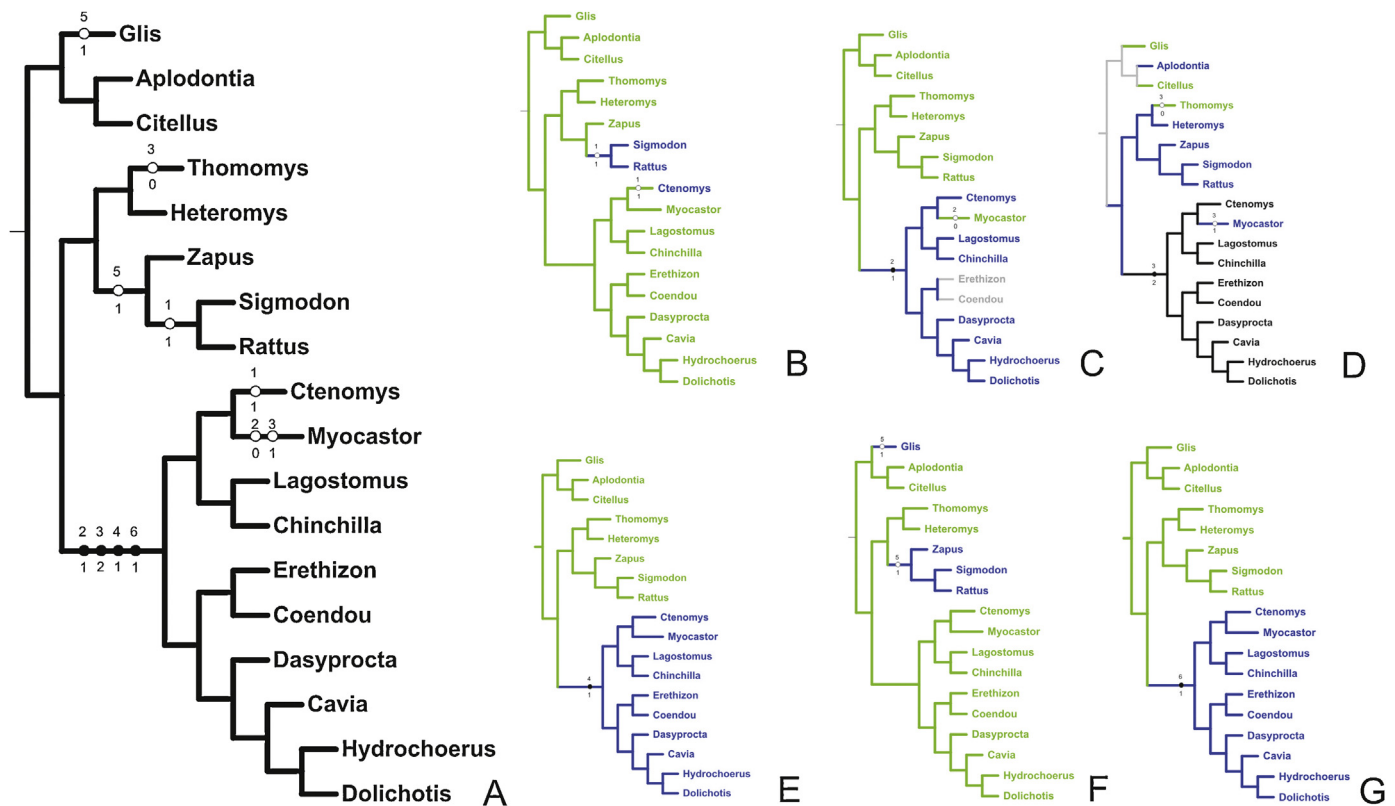


Fig. 7. (A) Mapping of six anatomical characters, as reconstructed using parsimony, onto a composite phylogeny of Rodentia (Rowe and Honeycutt, 2002; Blanda-Kanfi et al., 2009; Fabre et al., 2012; Upham and Patterson, 2012). Only unambiguous character state optimizations are shown. Ambiguous optimizations are discussed in the text. Numbers above branches indicate character numbers whereas those below are character states. (B)–(G) Individual characters mapped onto phylogeny, showing the ancestral character state reconstructions. Character state 0 = green; character state 1 = blue; character state 2 = black; ambiguity = gray.

4. Discussion

Our results indicate that the hip adductor musculature of caviomorphs has a distinctive pattern, characteristic of the group in the context of Rodentia.

4.1. Homologies

The homologies of the hip adductor muscles here identified differ, in some cases, from those previously proposed by other authors (see Table 2).

In Caviomorpha (with the exception of *Myocastor*), the m. adductor brevis is single, represented solely by its genicular part (McEvoy, 1982; present study). This muscle within this group was sometimes misidentified as being the cranial part of the m. gracilis (Table 2). In these cases, the m. gracilis was described as double, having a cranial and a caudal part, when it was actually single. In caviomorphs, this muscle has a singular topographic position, medial to the remaining mm. adductores. Besides this peculiar relationship with the other adductor muscles observed in this group of rodents, we identified this muscle as the genicular part of the m. adductor brevis, and not as the cranial part of the m. gracilis, because of its more cranial origin, its insertion onto the genicular region, enclosing the distal end of the m. caudofemoralis (when it was present), and because of its relationship with the femoral part of the m. adductor brevis in *Myocastor*, the only genus of caviomorphs studied in which this muscle was found to be double. In addition, another important point that supports our interpretation is the fact that, when both parts of the m. gracilis were present, as in *Ctenomys*, they displayed the same morphology, topographic position, and insertion as those of other groups of rodents (e.g., Alezais, 1900; Rinker, 1954). So, in a medial view of the hindlimb of this genus, we can observe,

in a cranial to caudal direction, the m. adductor brevis, the cranial part of the m. gracilis and the caudal part of the m. gracilis (Fig. 1).

In non-caviomorph rodents the genicular part of the m. adductor brevis was also sometimes misidentified as a portion of the m. adductor magnus (Howell, 1926; Jouffroy, 1971).

The misidentification of the m. adductor brevis mentioned above (erroneously identified as the cranial part of the m. gracilis) led some authors to misinterpret the distal part of the m. adductor magnus in *Cavia* and *Dasyprocta* as the m. adductor brevis (Cooper and Schiller, 1975; García-Esponda and Candela, 2010; see Table 2). This fault was due to the division of the m. adductor magnus into a proximal and a distal part, a particular arrangement observed in cavioids.

Other misidentifications were those made by Alezais (1900) (see Table 2), who interpreted the m. caudofemoralis of *Cavia* as a condylar portion of the m. adductor magnus, when the m. caudofemoralis actually belongs to the hamstring group of muscles and is innervated by a branch of the sciatic nerve. This author also interpreted the m. adductor minimus as the m. adductor brevis.

In caviomorphs, two main branches (cranial and caudal) of the obturator nerve have been described, as it was also observed in other rodents or groups of mammals. Our dissections indicate that the secondary branch of the obturator nerve that innervates the m. gracilis is an offshoot of the main caudal (or lateral) branch, and not an offshoot of the cranial (or medial) one, as it was observed in other rodents (e.g., Hill, 1937; Rinker, 1954; Fry, 1961; Klingener, 1964). In addition, the secondary branch of the obturator nerve that supplies the m. adductor brevis (being, as in all rodents, an offshoot of the main cranial branch) pierces and runs through the m. adductor longus to reach that muscle (with the exception of *Myocastor*).

4.2. Morphological variation and evolutionary implications

In non-caviomorph rodents the m. gracilis is a single muscle, as in Aplodontidae (Fry, 1961), Sciuridae (Bryant, 1945), Geomyidae, Heteromyidae, Gliridae (Ryan, 1989), and Dipodidae (Klingener, 1964). It has cranial and caudal parts in Cricetidae (Rinker, 1954; Stein, 1986) and Muridae (Alezaïs, 1900; see Fig. 6). In the Caviomorpha specimens dissected, it has two parts in *Ctenomys* alone (Fig. 1); in all other genera it is a single muscle. It is also single in Erethizontidae (McEvoy, 1982) and Dasyproctidae (García-Esponda and Candela, 2010; see Table 2). Optimization of character 1 (corresponding to the morphology of m. gracilis) in the phylogeny of Rodentia (Fig. 7 B) revealed that caviomorphs retained the plesiomorphic condition for rodents (character state 1-0) represented by a single head (see Lance-Jones, 1979; Ryan, 1989). According to the optimization of this character, a double m. gracilis (with a cranial and a caudal part) would have been acquired independently in *Ctenomys* and in the *Sigmodon–Rattus* clade. Lance-Jones (1979) observed that the m. gracilis in *Mus* begins its development as a single muscle condensation, which later splits into two separate heads.

In non-caviomorphs, the m. adductor longus is not perforated by the branch of the obturator nerve that supplies the m. adductor brevis (character state 2-0), whereas in all caviomorphs examined, except *Myocastor*, this muscle is perforated by that branch (character state 2-1). Optimization of this character in the phylogeny of rodents (Fig. 7C) indicates that a m. adductor longus perforated by the branch of the obturator nerve would have arisen once in the evolutionary history of rodents, and that this character state is recovered as a potential synapomorphy of caviomorphs.

In some rodents, as in most mammals, the m. adductor brevis is single, taking origin from the pelvis and inserting onto the mediocaudal aspect of the femur (Jouffroy, 1971). In other groups of rodents, this muscle also develops a genicular part, which lies medial to the femoral one and inserts onto the knee region. The genicular part of the m. adductor brevis is lacking in Sciuridae (Bryant, 1945), Geomyidae, and Gliridae (Ryan, 1989), whereas both femoral and genicular parts are present in Aplodontidae (Fry, 1961), Heteromyidae (Ryan, 1989), Dipodidae (Klingener, 1964), Muridae (Alezaïs, 1900; Fig. 6), and Cricetidae (Rinker, 1954; Stein, 1986). In the caviomorphs studied, only *Myocastor* has the m. adductor brevis double; in all other genera dissected, as well as in *Erethizon*, *Coendou* (McEvoy, 1982) and *Dasyprocta* (García-Esponda and Candela, 2010), this muscle is single, representing only the genicular part (see Table 2). A double m. adductor brevis was interpreted by some authors as a derived character state for rodents, vs. the primitive single condition of this muscle (Lance-Jones, 1979; Ryan, 1989). However, in the phylogenetic context here considered (Fig. 7D), ambiguous optimization of character 3 (i.e., morphology of the m. adductor brevis) at most basal nodes prevents us from inferring the evolution of this character at this level of the tree. The single condition of this muscle in caviomorphs (i.e., solely the genicular part; character state 3-2) would have been acquired once in this clade. A double m. adductor brevis (consisting of both the femoral and the genicular part; character 3-1) would have been a feature secondarily acquired by *Myocastor*.

Beyond this morphological variation (double in *Myocastor* and single in all other genera), the m. adductor brevis of caviomorphs has a unique configuration in the context of Rodentia. As stated above, in caviomorphs the mm. adductor brevis and gracilis form an almost continuous muscular sheet that is medial to all other muscles of the hip adductor group. The medial position of the m. adductor brevis with respect to the mm. pectineus and adductor longus, completely covering them in medial view, is an arrangement not seen in other rodents (compare with *Rattus*, Fig. 6). In addition, in caviomorphs almost all fibers of the m. adductor brevis

lie medial to the branch of the obturator nerve that supplies the m. gracilis, whereas in non-caviomorphs this muscle lies lateral to that branch (Fig. 6). The medial topographic position of the m. adductor brevis with respect to the branch of the obturator nerve that innervates the m. gracilis (character state 4-1) was observed even in *Myocastor*, in which the m. adductor brevis is double. In a phylogenetic context this relationship of the m. adductor brevis with this branch of the obturator nerve is recognized as a potential synapomorphy of caviomorphs (Fig. 7E).

In rodents, as in other mammals, the most proximal portion of the m. adductor magnus can be differentiated from the rest of the muscle as the m. adductor minimus (Jouffroy, 1971). The presence of a distinct m. adductor minimus is recorded in the Aplodontidae (Fry, 1961), Sciuridae (Bryant, 1945), Geomyidae, and Heteromyidae (Hill, 1937; Ryan, 1989). On the other hand, the m. adductor minimus is not present in Cricetidae (Rinker, 1954; Stein, 1986), Muridae (Alezaïs, 1900), Dipodidae (Klingener, 1964), and Gliridae (Ryan, 1989). The differentiation of the m. adductor minimus is interpreted by Ryan (1989) as a primitive condition in rodents. In the present analysis, all caviomorph genera studied retained the m. adductor minimus (character state 5-0; see Fig. 7F).

In addition, among the caviomorphs dissected, the m. adductor magnus (m. adductor magnus propius sensu Hill, 1937) can be clearly differentiated into a proximal and a distal part in the caviids *Cavia* and *Dolichotis*, a condition that was not observed in the other genera analyzed. This arrangement of the m. adductor magnus was also observed in *Dasyprocta* (García-Esponda and Candela, 2010; but see Table 2), another member of the Caviioidea. Hence, the division of the m. adductor magnus into two parts could be interpreted as a distinctive feature of cavioids. The differentiation of the proximal and distal parts of this muscle in *Hydrochoerus* is very weak, especially at its insertional end. More species of Caviioidea, as well as more details of the intraspecific variation should be analyzed in order to evaluate this character as a possible synapomorphy of this superfamily.

Finally, the secondary branch of the obturator nerve, which innervates the m. gracilis as an offshoot of the main caudal branch (character state 6-1), was optimized as a potential synapomorphy of caviomorphs (Fig. 7G). In all other rodents studied this secondary branch is an offshoot of the cranial branch of the obturator nerve.

4.3. Functional considerations

The m. gracilis is the only double-joint muscle of the hip adductor group since it attaches onto the tibia, thus also acting on the knee joint. In addition to the hip adductor and extensor functions, this muscle can also help the hamstring muscles in the flexion of the knee (Elftman, 1929; McEvoy, 1982; Fisher et al., 2008; Palastanga and Soames, 2012). Moreover, at least in the dog, it was indicated that the m. gracilis can also play a role in the plantar flexion of the ankle joint because of the connection of this muscle with a superficial crural aponeurosis that attaches to the heel via the common calcaneal tendon (Evans, 1993). Interestingly, in caviomorphs our results showed a similar distal attachment of the m. gracilis to the crural aponeurosis, which is in turn connected with the heel. This arrangement indicates a potential plantar flexion function of this muscle, an action not described for the m. gracilis in other rodents.

Taking into account the morphofunctional context of the hip adductor muscle group, we analyze here the possible functional relevance of the hip adductor muscular features that, according to our observations (see Section 3.1), are unique to caviomorphs. In fact, in this group of rodents, the mm. adductor brevis and gracilis form an almost continuous muscular sheet that is medial to all other muscles of the hip adductor group, an arrangement not observed in non-caviomorphs (e.g., *Rattus*, see Fig. 6). Due to the particular configuration of the m. adductor brevis, both muscles

probably act synergistically. During stance phase, the m. gracilis could have an important function, not only on account of the contraction of its fibers, but also due to the tension imparted to it by the m. adductor brevis. This muscular arrangement is similar to that observed by Gambaryan (1974) in ungulates, where the more cranially located m. sartorius is connected with the more caudally located m. gracilis, tightening it during contraction. Since the m. gracilis may act in the adduction and extension of the hip joint, flexing the knee, and plantarflexing the ankle, the m. adductor brevis probably reinforces the multiple functions of the m. gracilis in caviomorphs. Thus, the unique arrangement of the mm. adductor brevis and gracilis and their hypothesized synergistic action would have been of adaptive value during the evolutionary history of this group of rodents, a clade that has undergone a great radiation of locomotion modes associated with a wide range of body sizes not seen in other groups within the order. Nevertheless, detailed information on the individual action of each muscle during the step cycle (e.g., by electromyographic studies) is necessary to test this hypothesis.

5. Conclusion

Our comparative analysis allowed us to identify, in the context of Rodentia, the homologies of the hip adductor muscles in caviomorphs, which partially differ from those proposed by other authors. We conclude that caviomorphs present a singular pattern of the hip adductor musculature that distinguishes them from other groups of rodents. Caviomorphs are characterized by having a single m. adductor brevis, which corresponds solely to its genicular part. This muscle, together with the m. gracilis, composes a muscular sheet that is medial to all other muscles of the hip adductor group. The m. adductor brevis also has a singular topographic position with respect to the branch of the obturator nerve that supplies the m. gracilis, most of its fibers lying medial to it. Due to this particular configuration, the mm. adductor brevis and gracilis probably have a synergistic action. During stance phase, the contractile force of the m. gracilis could be increased by the tension imparted to it by the m. adductor brevis. Thus, the m. adductor brevis probably reinforces the multiple functions of the m. gracilis in caviomorphs.

Mapping of the analyzed myological characters in the context of a phylogeny of Rodentia indicates that several features [the m. adductor longus perforated by the branch of the obturator nerve (character state 2-0), the single condition of the m. adductor brevis, representing only its genicular part (character state 3-2), the medial position of the m. adductor brevis with respect to the obturator nerve (character 4-1), and the branch of the obturator nerve to the m. gracilis as an offshoot of the main caudal branch (character state 6-1)] are recovered as potential synapomorphies of caviomorphs, distinguishing them from other clades of the order.

Studies of comparative anatomy, including myological data, in different lineages of mammals have had a recent resurgence (Diogo et al., 2012). Muscle-based data have shown to be useful as a source of characters in phylogenetic analyses and have demonstrated that they can play an important role in the understanding of evolutionary patterns (e.g., Ercoli et al., 2014). The present contribution provides new myological characters of caviomorphs, until now scarcely known, which may be valuable for future comprehensive morphology-based phylogenetic analyses of these rodents.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2014.12.006>.

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