

Pelvic musculature and function of *Caiman latirostris*

Alejandro Otero^{1,3}, Pablo A. Gallina^{2,3} & Yanina Herrera^{1,3}

¹División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina

²Área de Paleontología, Fundación de Historia Natural Félix de Azara, CEBBAD, Universidad Maimónides, CABA, Argentina

³CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Argentina

The musculoskeletal hindlimb anatomy of the alligatorid *Caiman latirostris* Daudin is presented. The description includes origin and insertion sites as well as anatomical function of the pelvic and proximal hindlimb musculature. The hindlimb anatomy of *C. latirostris* described here is rather conservative when compared to that of other extant crocodylians studied. Nonetheless there is some inter-specific variation between *C. latirostris* and other Crocodylia, such as the well known *Alligator mississippiensis*. *Caiman latirostris* and other alligatorids have many differences between each other concerning the origin and insertion sites as well as the extent and relative development of the muscular masses involved, such as the absence of *M. flexor tibialis internus* 4, the addition of one dorsal vertebra to the origin of PIFI 2, totalling seven vertebrae, the exclusion of sacral vertebrae in the origin site of CFB, and the inclusion of transverse processes, as well as haemal arches in the origin site of CFL, among others. Regarding muscle function, hindlimb agonist–antagonist movements in *Caiman latirostris* are not performed by a sole muscle, but instead by a principal muscle and others that complete the action. These anatomical variations could be correlated with a particular locomotor behaviour and phylogenetic landscape.

Key words: Alligatoridae, anatomy, Crocodylia, function, hind limb, myology

INTRODUCTION

The broad-snouted caiman, *Caiman latirostris* Daudin, is an alligatorid crocodile endemic to the tropical and subtropical regions of South America (Densmore & Owen, 1989; Hrbek et al., 2008; for ecological studies see Prado & Moreno, 2000, 2001; Verdade et al., 2002; Borteiro et al., 2009). However, compared to its North American relative *Alligator mississippiensis*, which has been subject of many anatomical studies since early in the 19th century (Romer, 1923a; Hoffstetter & Gasc, 1969; Rowe, 1986; Blob & Biewener, 2001; Reilly & Blob, 2003; Meers, 2003), information on the anatomy of *C. latirostris* is limited. The pelvic and hindlimb anatomy of crocodylians is of particular interest because it provides not only the possibility of studying the associations between form and function, but also their implications for the evolution of archosaurian locomotion (Hutchinson, 2001a,b, 2002; Hutchinson & Gatesy, 2000).

The first edited crocodylian soft anatomy studies date from the early 1800s (Buttman, 1826; Stannius, 1854), followed by more detailed work by Reese (1915) and Romer (1923a,b). However, there is no consensus on the homology of certain hindlimb muscles (e.g. *Flexor cruris* group, deep dorsal group, *M. caudofemoralis longus*), and all descriptions have hitherto only focused on northern alligatorids (e.g. *Alligator mississippiensis*: Reese, 1915; Romer, 1923a; Rowe, 1986) as well as African (*Crocodylus niloticus*) and Asian crocodiles (*Gavialis gangeticus*: Göüye, 1688; Buttman, 1826; Meckel, 1828, Meers, 2003).

The structure and function of the archosaurian pelvic region has adopted diverse successful configurations that

allowed the clade to live in both terrestrial as well as aquatic environments (Romer, 1956). The crocodylian hind limb has a wide range of posture configurations, varying along a continuum from crouched to fully erect (Parrish, 1986; Blob, 2000, 2001; Blob & Biewener, 2001). Therefore, knowledge of the pelvic structure and muscular arrangement of living crocodylians allows us to understand major patterns of musculoskeletal hindlimb evolution, and to formulate hypotheses about archosaurian locomotion (Galton, 1969; Hutchinson, 2001a,b; Hutchinson & Gatesy, 2000; Gatesy, 2002; Otero & Vizcaíno, 2008). The aim of this paper is to give a detailed description of the pelvic and proximal hindlimb musculature of the South American alligator *C. latirostris*, providing comprehensive illustrations and comments on the hindlimb muscle function.

MATERIALS AND METHODS

The present study is based on dissections of two specimens donated by the Granja La Esmeralda, a crocodile breeding station in Santa Fe Province, performed at the Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICyTTP), in Diamante, Entre Ríos Province, Argentina. The specimens were provided devoid of skin and dissected a few hours after death in order to enable recognition of soft-tissue attachments (Fig. 1a). Each muscle was removed, from the most superficial layers to the inner ones, in order to determine muscle origin, insertion, and spatial relationships. We focused mainly on the pelvic muscular arrangement, but the proximal hindlimb musculature was also considered because muscles that originate in the pelvis actually insert

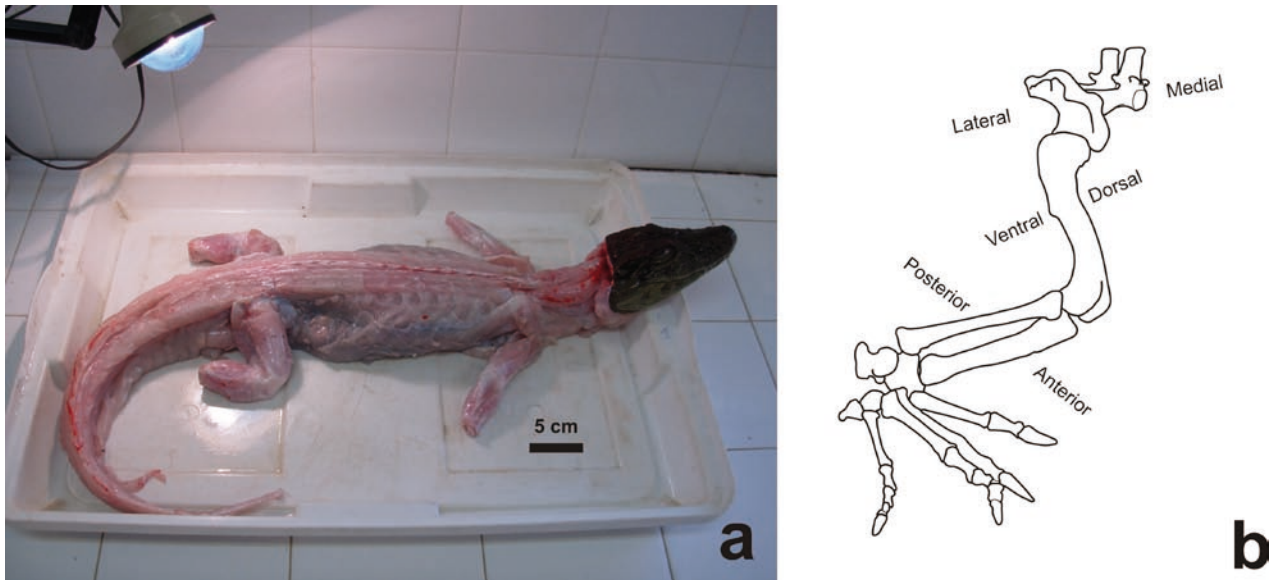


Fig. 1. The broad-snouted caiman, *Caiman latirostris*. a) Photograph of one of the specimens dissected. b) Spatio-anatomical nomenclature used in this study, adapted from Reilly & Elias (1998).

on the proximal hind limb. The insertion site of *Mm. gastrocnemii* was assumed from the literature, since the *C. latirostris* specimens were provided without the pes.

The organization and homologies of reptilian pelvic muscles are still a matter of discussion (Romer, 1942; Rowe, 1986). For practical reasons we used functional criteria for muscular organization, i.e. dividing muscular masses according to their actions, such as protractor, retractor, adductor or abductor. Nevertheless, we followed the arrangement proposed by Carrano & Hutchinson (2002) for the general organization of the crocodylian pelvic and hindlimb muscles as well as Rowe's (1986) scheme for the dorsal thigh musculature. Muscle nomenclature has been a subject of confusion since homologies are not fully established and because of different terminologies for the same muscle, as well as due to non-described or misinterpreted variation (Romer, 1923a). We adopted a terminology describing the origin and insertion attachment points (Romer, 1923a; Wilhite, 2003) (Appendix A). For example, the *caudofemoralis* muscle originates from the caudal region and inserts on the femur. Muscle nomenclature used herein follows Reese (1915), Romer (1923a), Rowe (1986), Hutchinson (2001a,b, 2002), Carrano & Hutchinson (2002) and Wilhite (2003) (Appendix B).

For spatial-anatomical nomenclature (e.g. dorsal, ventral, anterior, posterior) we follow the terminology presented by Reilly & Elias (1998) based on the sprawling posture of the crocodylian hind limb. Consequently, the ilium is oriented with its major axis facing antero-posteriorly, the femur is oriented nearly transversal to the spine, and the tibia and fibula are oriented perpendicular to the latter (Fig. 1b). Finally, muscle function was analysed based on the lines of action of muscles observed and compared with previous work on archosaurian locomotion (Hutchinson & Gatesy, 2000; Wilhite, 2003; Otero & Vizcaino, 2008).

RESULTS

Triceps femoris group

Mm. iliotibiales (IT). This is a large and sheet-like superficial muscle of parallel fibres. It is composed of three separated heads; all of them have tendinous origins and they cover the anterolateral portion of the femur (Fig. 2a). The three heads arise from the dorsal margin of the iliac blade. The *M. iliotibialis cranialis* (IT1) originates from the anteriormost surface of the ilium. It is a small portion that is not distinguished from the second head. The middle and largest head, *M. iliotibialis medialis* (IT2), originates from the dorsolateral edge of the ilium, covering, in part, the tibial extensor muscles. The posterior head, *M. iliotibialis caudalis* (IT3), is the smallest head and arises immediately posterior to IT2. The three heads converge with *M. ambiens* (AMB) and *M. femorotibialis* (FMT) to generate the knee extensor tendon that inserts on the entire surface of the cnemial crest of the tibia.

The principal function of *Mm. iliotibiales* is to extend the femorotibial joint. However, this muscle also helps *M. iliofemoralis* in abduction, flexes the leg and extends the hip (J. Hutchinson, pers. comm.).

Mm. femorotibiales (FMT). This muscle is composed of two heads (*M. femorotibialis externus*/FMTE and *M. femorotibialis internus*/FMTI) with pinnate fibres and fleshy origins that cover almost the entire femoral diaphysis. These portions are laterally separated by *M. iliofemoralis* (IF, Fig. 2b). The medial and largest portion (FMTI) originates from the anterior surface of the femur – deep with respect to IT2 – including the medial portion of the diaphysis, up to the femoral distal margin. The minor head (FMTE) originates on the posterior surface of the femur just behind the attachment site of *M. iliofemoralis*. Both heads insert on the tibial cnemial crest, through a common tendon with *Mm. iliotibiales* and *M. ambiens*.

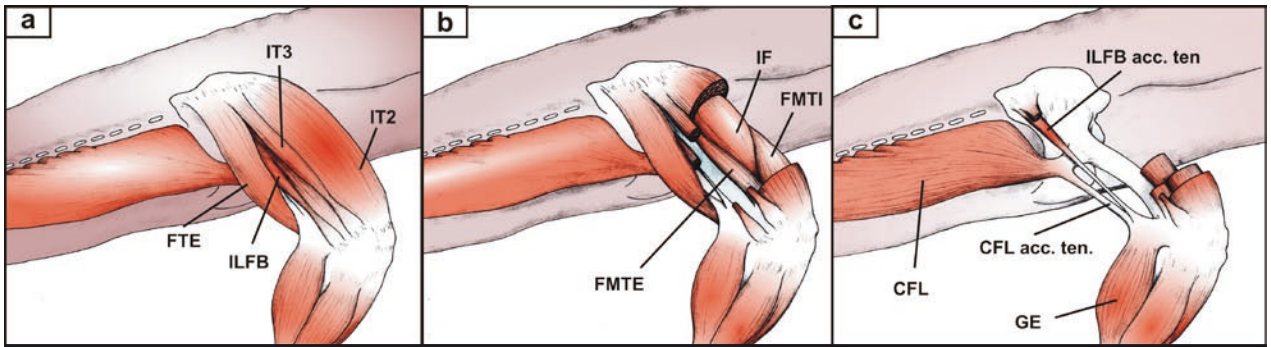


Fig. 2. Dissection of lateral thigh of *Caiman latirostris* showing muscle arrangement from superficial layers to inner ones (a–c). Note the secondary tendon of *M. iliofibularis* and *M. caudofemoralis longus* both contacting *M. gastrocnemius externus* (c).

Muscle *femorotibiales* is part of the knee extensor group. Its action is to extend the femorotibial joint.

M. ambiens (AMB). In basal Reptilia and Neornithes, *M. ambiens* is composed of a single head that originates at the pubic tubercle (Vanden Berge & Zweers, 1993; Hutchinson, 2001a; Carrano & Hutchinson, 2002). Extant crocodylians present two distinctive heads of this muscle; however, in the specimens of *Caiman latirostris* dissected herein the AMB has only one recognizable head that arises anteriorly to the acetabulum from the surface around the ambiens process of the pubis. It inserts together with *Mm. iliotibiales* and *Mm. femorotibiales* onto the cnemial crest. There is a second tendon that passes through the knee extensor tendon and joins the external head of *M. gastrocnemius*.

Muscle *ambiens* extends the femorotibial joint.

M. ischiotrochantericus (ISTR). In basal Reptilia and crocodylians, *M. ischiotrochantericus* is a single muscle that arises from the medial surface of the ischial blade, whereas in Neornithes its homologue – the *M. ischiofemoralis* (ISF) – originates from the lateral surface of the ischium, the ilio-ischiadic membrane, the ischio-pubic membrane, and sometimes from the ventral surface of caudal vertebrae of the synsacrum (Vanden Berge, 1982; Hutchinson, 2001a; Lecuona, 2007). In *C. latirostris*, the *M. ischiotrochantericus* originates on the posteromedial surface of the ischium, behind the origin of the *M. adductor femoris* 2. It inserts on the proximo-posterior femoral shaft, over the *M. caudofemoralis longus* (CFL) insertion scar.

Muscle *ischiotrochantericus* extends and laterally rotates the femur.

M. iliofibularis (ILFB). Muscle *iliofibularis* is a thin and fusiform muscle with parallel fibres that are placed behind *Mm. iliotibiales* and ahead of the *Flexor cruris* group. Its fleshy origin runs from the dorsolateral surface of the ilium, below the IT2 and above the *M. iliofemoralis* origins (Fig. 2a). It inserts by means of a tendon on the anterolateral surface of the fibula, over a tenuous scar. A

secondary tendon inserts on the origin region of *M. gastrocnemius internus*, next to the secondary tendon of CFL (Fig. 2c).

Muscle *iliofibularis* flexes the knee articulation, and also extends and abducts the hip (Gatesy, 1997).

Flexor cruris group

Homologies of this group (“long flexors” *sensu* Romer 1923b) are not well resolved (Romer, 1923b; Hutchinson, 2001a, 2002). However, it is well established that crocodylians exhibit the most complete scheme for this muscular group (Reese, 1915; Romer, 1923b; Hutchinson, 2001a, 2002; Wilhite, 2003; Lecuona, 2007). The *Flexor cruris* group is composed by fusiform, elongated and parallel fibres at the posterior portion of the leg. Six heads are present in most crocodylians, extending from the pelvis to the femorotibial joint, arranged in two quite distinctive groups (*sensu* Romer, 1923b): an external group, composed of the *M. puboischiotibialis* (PIT) and two heads of *M. flexor tibialis internus* (*M. flexor tibialis internus* 1/FTI1 and *M. flexor tibialis internus* 2/FTI2); the internal group, composed of the other two heads of *M. flexor tibialis internus* (*M. flexor tibialis internus* 3/FTI3 and *M. flexor tibialis internus* 4/FTI4), and the *M. flexor tibialis externus* (FTE). The *C. latirostris* specimens dissected herein lack the *M. flexor tibialis internus* 4 (*contra* Lecuona, 2007).

M. puboischiotibialis (PIT, Fig. 3). This is a small muscle that arises from a muscle scar placed on the anterolateral surface of the ischium, over the proximal end of the obturator process. It inserts on the proximomedial aspect of the tibia. The *M. puboischiotibialis* aids in adducting the leg (Hutchinson & Gatesy, 2000).

M. flexor tibialis internus (FTI, Fig. 3). Three of the five heads of the *Flexor cruris* group present in *C. latirostris* correspond to FTI. The first head (FTI1) originates from a slight muscle scar located on the posterodorsal surface of the ischium. It inserts on the posteromedial face of the proximal tibia, after joining with the FTI2 and PIT. Muscle FTI2 originates on the posterolateral aspect of the ilium

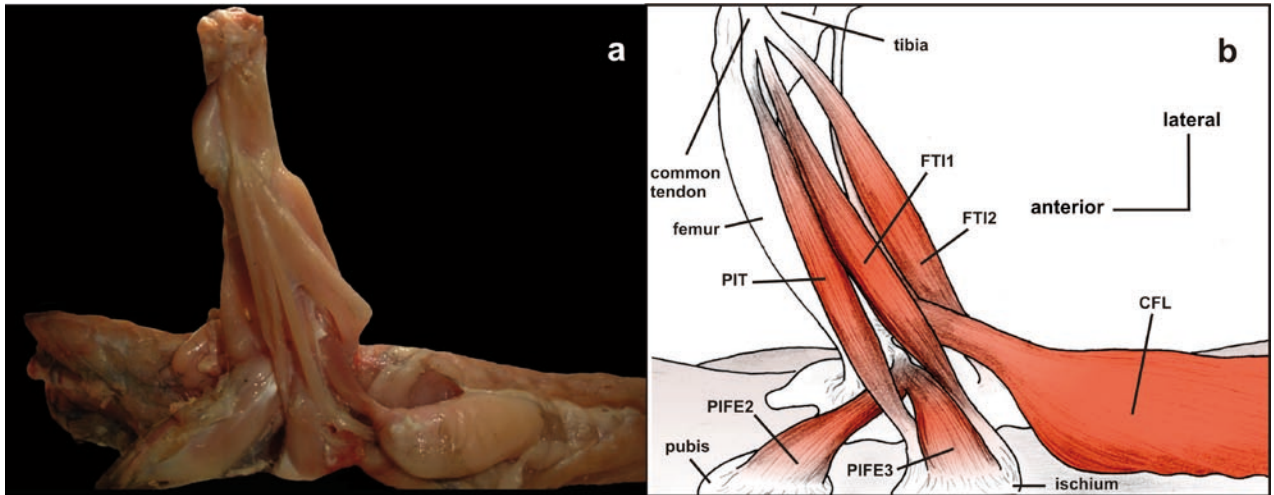


Fig. 3. Ventral view of the pelvic region of *Caiman latirostris* showing the medial arrangement of the *Flexor cruris* group as well as the origin sites of PIFE2, PIFE3 and CFL. a) Photograph; b) schematic drawing. Other pelvic muscles have not been drawn to facilitate recognition.

and inserts together with FTI1 and PIT on the postero-medial surface of the tibia. The third head of this group (FTI3) arises on the ischial tuberosity (see also Lecuona, 2007). It inserts through a common tendon of insertion with the FTE onto a small scar over the proximomedial region of the tibia. The *flexor tibialis interni* are the most important femorotibial joint flexor muscles. In *C. latirostris*, the line of action of this muscle is anteroposterior and also adds an adductor component (see Discussion).

M. flexor tibialis externus (FTE). This originates from the lateral face of the ilium, behind the site of origin of IT3 and above the origin of FTI2. It inserts onto the proximomedial aspect of the tibia, sharing a common tendon with FTI3. Muscle *flexor tibialis externus* aids in the femorotibial flexion action.

Mm. adductores femores (ADD). The *adductores femores* group is composed of two recognizable heads with longitudinal fibres and a triangular shape. Both portions originate from the lateral surface of the ischium and insert on the caudal surface of the femoral shaft.

Muscle *adductor femoris* 1 (ADD1) arises by means of a fleshy origin over the anterolateral surface of the ischium, over or close to the obturator process. Muscle *adductor femoris* 2 (ADD2) has its origin on the posterolateral portion of the ischium and separated from the ADD1 by *M. puboischiofemoralis externus* 3 (PIFE3). In both cases, it inserts along the posterior surface of the femoral shaft up to the beginning of the distal condyles. These muscles are the main femoral adductors and also contribute to limb retraction.

Mm. caudofemorales

M. caudofemoralis brevis (CFB). Muscle *caudofemoralis brevis* is the smaller of the two major femoral retractors. It is placed anterior to the *M. caudofemoralis longus* (CFL)

and joins the latter at the base. It has two origin sites, from the ilium and from caudal vertebrae as in *Alligator* (Romer, 1923a). The first origin site arises from the postero-ventral portion of the ilium. The caudal origin is from the lateral sides of the first caudal centrum and the base of the transverse processes, in which it leaves noticeable scars. It inserts on the femur, proximomedially, close to the fourth trochanter, proximally to the CFL insertion scar. Muscle CFB helps CFL in retraction of the femur.

M. caudofemoralis longus (CFL, Figs. 2–4). This is the noteworthy hindlimb muscle of *Caiman latirostris* and occupies almost the entire anterior tail region, reaching its maximum volume proximally. Muscle *caudofemoralis longus* is placed just beneath the epaxial musculature and is entirely covered by the latter and the hipaxial musculature. As in lepidosaurs (Gatesy, 1990), it originates from lateral sides of haemal arches, the base of proximal caudal vertebral centra, as well as the proximal portion of the ventral surface of the transverse processes (see also Gatesy, 1990; Wilhite, 2003) (Fig. 4). In the first four caudal vertebrae, the origin area does not include the most proximal portion of the transverse processes, but only the centrum and haemal arches. From the fifth caudal, its origin also includes the base of the processes and extends up to the disappearance of the processes (Gatesy, 1995). In one of the dissected specimens the muscle reaches the thirteenth caudal. This muscle runs anteroventrally, increasing its volume and joining CFB to insert via a tendon onto the fourth trochanter of the femur. This tendon bifurcates and continues downwards parallel to the leg and inserts on to the proximoventral area of the fibula, where it joins the tendon of *M. gastrocnemius externus* as well as the secondary tendon of ILFB. Muscle *caudofemoralis longus* is the main retractor of the hind limb (Gatesy, 1995) and also contributes to adduction and rotation of the axis of the leg.

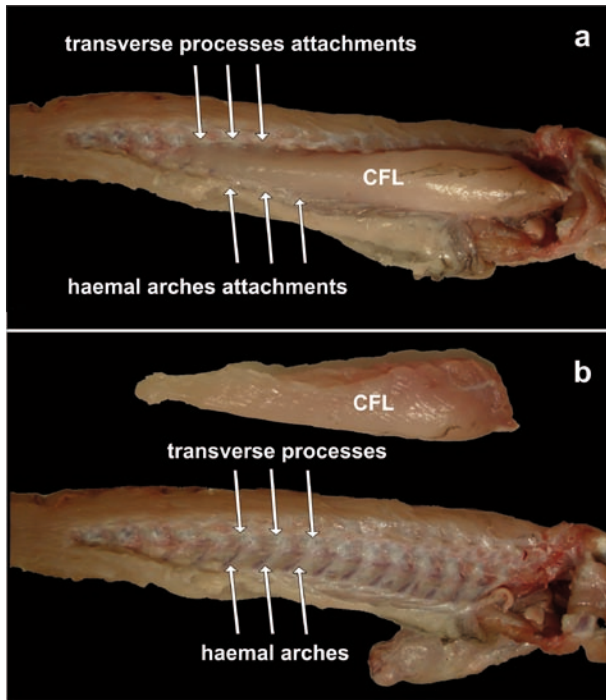


Fig. 4. The tail of *Caiman latirostris* in right lateral view. a) Muscle *caudofemoralis longus* placed *in situ*. b) Muscle *caudofemoralis longus* removed. Note the origin site of CFL from haemal arches and caudal transverse processes.

M. ilioischiocaudalis (ISC). This muscle is placed in the tail immediately beneath the skin. It originates from the ventral surface of the transverse processes, then runs externally to the CFL and inserts on the tips of the haemal arches.

***Mm. puboischiofemorales externi* (PIFE)**

In non-archosaurian reptilians this muscle is undivided (Hutchinson, 2001a), although archosaurs exhibit multiple splitting of this muscular group, reaching three heads in crocodylians and two in Neornithes (Reese, 1915; Romer, 1923a; Hutchinson, 2001a; Wilhite, 2003), which originate fleshy from the pelvic region and insert via tendons onto the proximal surface of the femur.

M. puboischiofemoralis externus 1 (PIFE1). This fan-shaped muscle originates along the anteromedial (dorsal) surface of the pubis and prepubic cartilage. It inserts on the major trochanter of the femur, via a common tendon with *M. puboischiofemoralis externus* 2 and 3.

M. puboischiofemoralis externus 2 (PIFE 2, Fig. 3). This originates from the lateral (ventral) surface of the pubis and prepubic cartilage and shares insertion with PIFE1 and PIFE3.

M. puboischiofemoralis externus 3 (PIFE 3, Fig. 3). This muscle originates from the lateral aspect of the ischium ("obturator process" *sensu* Hutchinson, 2001a; Carrano &

Hutchinson, 2002) between ADD1 and ADD2. It shares its insertion with PIFE1 and PIFE2.

Muscle *puboischiofemoralis externi* 1 and 2 protract and anterolaterally rotate the femur, also aiding in adducting the leg. Muscle *puboischiofemoralis externi* 3 contributes to the adduction action.

Deep dorsal group

Muscles derived from the deep dorsal group have had a controversial history as their homologies are not well resolved (Rowe, 1986; Carrano & Hutchinson, 2002). The presence of two embryonic masses of this group within Reptilia has been well established (Rowe, 1986). Nonetheless, controversy remains about the homologies of the muscles derived of those embryonic masses. On one hand, non-archosaurian reptilians and crocodylians exhibit one single division for the *M. iliofemoralis*, whereas Neornithes present two muscles derived from that embryonic mass (*M. iliofemoralis externus*/IFE and *M. iliotrochantericus caudalis*/ITC). On the other hand, the second mass is divided into three heads in non-archosaurian Reptilia (*M. puboischiofemoralis internus* 1/PIFI1, *M. puboischiofemoralis internus* 2/PIFI2 and *M. puboischiofemoralis internus* 3/PIFI3), and two in crocodylians (PIFI1 and PIFI2) (Rowe, 1986; Hutchinson, 2001a; Carrano & Hutchinson, 2002).

M. iliofemoralis (IF). This is a single tear-shaped muscle, with longitudinal fibres and no head divisions. It has a fleshy origin on the lateral surface of the ilium, below the second head of IT, above the *Flexor cruris* group and the acetabulum. It inserts fleshy onto the lateral surface of the femur between FMTI and FMTE. Muscle *iliofemoralis* abducts the leg.

M. puboischiofemoralis internus 1 (PIFI1). This is a triangle-shaped muscle that arises from the medioventral surface of the ilium. From there, it surrounds the ilium cranially and it is oriented parallel to *M. puboischiofemoralis internus* 2. It inserts onto the medial surface of the proximal region of the femur, anteromedially to the fourth trochanter.

M. puboischiofemoralis internus 2 (PIFI2). This is a broad triangular muscle with longitudinal fibres. It originates in the proximal ventral face of the transverse processes as well as in the lateral faces of the last seven dorsal vertebrae. It inserts at two separated points onto the dorsal and anteroproximal region of the femur.

Muscles PIFI 1 and 2 protract the leg and help in adduction.

Mm. gastrocnemii (G). This muscular complex is composed of two fusiform heads not easily differentiable from one another. The lateral portion (*M. gastrocnemius externus*, GE) originates from the posterior and distal surfaces of the femur (Fig. 2c). The medial head (*M. gastrocnemius internus*, GI) originates from the tibial proximomedial surface. Both heads insert via a tendon on the plantar surface of the pes (Lecuona, 2007). This muscle extends the metatarsus and flexes the toes.

DISCUSSION

Comparison with previous studies

Many contributions concerning crocodylian musculoskeletal anatomy have become available since Gouye (1688) offered the first published dissection of *C. niloticus* (African and Asian crocodiles: Buttman, 1826; Stannius, 1854; American alligator: Reese, 1915; Romer, 1923a; Rowe, 1986; Wilhite, 2003). However, the musculoskeletal anatomy of South American crocodylians has been neglected, and musculoskeletal patterns remained obscure. Because of the scarcity of information on crocodylian hindlimb soft anatomy, we will focus the discussion on the comparison with *A. mississippiensis*, despite their relatively short phylogenetic distance (Brochu, 1999).

The first difference between *C. latirostris* and *A. mississippiensis* concerns the number and extent of muscle heads present within crocodylians. Muscle *iliotibialis* is composed of three heads in specimens of both species as dissected by Romer (1923a) and Wilhite (2003). However, according to Reese (1915) two heads of that muscle were reported in *A. mississippiensis*; the anterior head, well developed, and a posterior one, less developed. The anterior-most head of Reese's specimens should include the first and second head of *C. latirostris*. The same author describes two portions of the *M. iliofibularis*, but the secondary tendon of this muscle does not correspond to the one observed in *C. latirostris*. It seems to correspond to one of the *Flexor cruris* group, maybe the FTI1 or FTE. A similar situation occurs with the single head of the *M. adductor femoris* of *A. mississippiensis* mentioned by Reese (1915), which corresponds by position to ADD1 of *C. latirostris*. Muscle *ambiens* has a single head in Chelonia and lepidosaurs, although crocodylians have two quite distinct heads; however, in the dissected *C. latirostris* specimens there is only one, showing a primitive situation. The single head of *M. ambiens* in *C. latirostris* specimens could be related to individual variation, or to the sub-adult condition of the specimen (A. Lecuona, pers. comm.).

The differences between the attachment sites of *C. latirostris* and other Crocodylia is striking. In the dissected specimens as well as in *Alligator* specimens (Wilhite, 2003), the ISTR insertion scar is placed over the posteroproximal region of the femur, not proximolaterally as pointed out by Carrano & Hutchinson (2002). On the other hand, there is no consensus among authors regarding the precise origin of the CFB within crocodylians. In *C. latirostris* it originates over the posterior edge of the ilium and caudal vertebrae, while in *A. mississippiensis* CFB originates on the last sacral vertebra (Reese, 1915; Romer, 1923a; Carrano & Hutchinson, 2002; Wilhite, 2003). The exact origin of CFL in extant and extinct archosaurs is an issue of discussion (Reese, 1915; Romer, 1923a; Galton, 1969; Borsuk-Bialynicka, 1977; Carrano & Hutchinson, 2002; Wilhite, 2003; Meers, 2003; Otero & Vizcaíno, 2008). In *C. latirostris* it originates from the proximal caudal vertebral centrum and transverse processes, as well as from the haemal arches, as noted by Gatesy (1990) for lepidosaurs and archosaurs. Some authors agree that in *A. mississippiensis* CFL originates from

the sides and ventral surface of proximal caudal vertebrae (Romer, 1923a; Galton, 1969, Carrano & Hutchinson, 2002), and also from the sides of the haemal arches (Wilhite, 2003).

Regarding the *Flexor cruris* group, Reese (1915) describes a muscle for *A. mississippiensis* similar to PIT in *C. latirostris*; however he interpreted it as FTI1. The fourth head of FTI, which is present in *A. mississippiensis* (Romer, 1923a), is absent in *C. latirostris* (but see Wilhite, 2003). There are only three heads for this muscular group in *A. mississippiensis*, which correspond to FTI1, FTI2 and PIT (Reese, 1915; *contra* Romer, 1923; Carrano & Hutchinson, 2002; Wilhite, 2003). Moreover, there are some differences concerning the insertion of the FTE when compared to *A. mississippiensis*. In the latter there are two insertion sites (Reese, 1915); one corresponds to the insertion seen in *C. latirostris*, and the other runs along the leg to contact the tendon of *M. gastrocnemius* (see also Wilhite, 2003).

The configuration and names of the *Mm. puboischiofemorales externi* group diverge depending on the author. For *A. mississippiensis* only two heads of this muscle group are described, corresponding by position to PIFE2 and PIFE3 of *C. latirostris* (Reese, 1915), or to PIFE1 and PIFE2 (Wilhite, 2003). Only Romer (1923a) describes three heads, as in *C. latirostris*. There are certain discrepancies, in turn, concerning the PIFI1 and PIFI2. *Alligator mississippiensis* has three heads for this muscle (Reese, 1915). Two of them arise in the pubis and contact the PIFE; the other head corresponds to the PIFI2 seen in *C. latirostris*. Other authors only describe the PIFI1 for *Alligator* (Wilhite, 2003). There is a wide consensus with respect to the origin of PIFI2 in crocodylians from the last six dorsal vertebrae (Reese, 1915; Romer, 1923a; Carrano & Hutchinson, 2002). *Caiman latirostris* adds one dorsal vertebra, totalling seven vertebrae for the origin of this muscle. Nevertheless, the insertion site is the core of controversy, varying from the ventral surface of the transverse processes (Rowe, 1986), or from the lateral faces of the centra (Carrano & Hutchinson, 2002), as well as from both structures (Romer, 1923a; present study).

Functional aspects

Crown group crocodylians (Crocodylia) are, together with birds (Neornithes), the sole survivors of the clade Archosauria (Gauthier, 1986). The hindlimb posture of extant crocodylians resembles those of primitive archosaurs in having a sprawling or "abducted" limb posture (limbs held lateral to the body), although crocodylians are capable of achieve more upright or "adducted" postures (limbs held beneath the body) in certain situations (Blob, 2000; Blob & Biewener, 2001). As a consequence, the hindlimb muscle control depends on the posture adopted and the orientation of the ground reaction force (GRF), which is the substrate opposite force (Biewener, 1989).

Adduction–abduction (Fig. 5a). It has been demonstrated for *A. mississippiensis* that during the stance phase, muscle control is governed mainly by abduction–adduction actions (Hutchinson & Gatesy, 2000). In the American alligator, during the stance phase the foot is lateral to the

acetabulum; thus the GRF exerts an abduction moment about the hip joint (Hutchinson & Gatesy, 2000). As in *A. mississippiensis*, the abduction moment in *C. latirostris* is countered by the ADD1 and also aided by other ventral adductor muscles such as the PIFE3, PIT, and ADD2 (Hutchinson & Gatesy, 2000). Other muscles that exert an adduction action are FTI1+2+3, PIFE1+2, PIFI 1 and also CFL. These muscles originate from sites placed along the sagittal plane of the body (e.g. ischium, pubis, tail). In a sprawled stance phase, the femur is almost perpendicular to the sagittal plane of the body; hence the insertion sites of the muscles mentioned above display a mediolateral

line of action. As a result, an adductor action is exerted whenever they contract. On the other hand, the principal abductor muscle of the leg acting on the swing phase in *A. mississippiensis* is the *M. iliofemoralis* (Hutchinson & Gatesy, 2000). Because of the similar muscular attachments and leg posture, that could be the action it has in *C. latirostris* too. Moreover, IT2, IT3 and ILFB also help in leg abduction during the swing phase.

Extension–flexion (Fig. 5b). Leg extension and flexion become more important in locomotor control during the swing phase (Reilly & Blob, 2003). In *C. latirostris*, the most important muscle group acting on the hip and femorotibial extension are the *Mm. iliotibiales*. However, their heads have different importance for these actions with respect to the relative development of each one. The principal extensor component and most developed head of this muscle group is the IT2, while IT1 and IT3 have an auxiliary task as in *A. mississippiensis* (Wilhite, 2003). Other muscles that aid in femorotibial extension are the *Mm. femorotibiales* and *M. ambiens*.

The principal knee flexor muscle is the *M. iliofibularis*. In spite of the fact that this muscle is relatively thin in *C. latirostris*, it is the main flexor muscle of the leg. Muscle *iliofibularis* is noteworthy and powerful taking into account that it is the antagonist of four extensor muscles (i.e. IT, FMT, AMB and ISTR). Other muscles that contribute to knee flexion are the three heads of muscle FTI and the FTE. In *A. mississippiensis*, the flexion action is also helped by the FTI4, which is not present in any of the dissected specimens of *C. latirostris*. The ILFB and the FTI muscles could achieve their antagonist power by inserting on the proximal portion of the fibula, generating its greatest force in the contraction phase.

Retraction–protraction (Fig. 5c). Many muscle groups collaborate in femoral retraction. The most important is the *Mm. caudofemorales*, CFL being the major femoral retractor, aided by CFB. Muscles adductor 1 and 2 and PIFE 3 also contribute to femoral retraction. During the swing phase, the PIFI1+2 and PIFE1+2 are the principal femoral protractors (Hutchinson & Gatesy, 2000).

CONCLUSIONS

This hindlimb anatomical description of *C. latirostris* shows a rather conservative muscular arrangement with respect to other studies on extant crocodylians. Nonetheless *C. latirostris* differs from other Crocodylia. The dissections described herein demonstrate that the pelvic and proximal hindlimb musculature of *Caiman latirostris* display many differences with respect to that observed in its well known relative *A. mississippiensis*. The results presented here reflect differences in the interpretations of muscle origins, insertions and actions. The arrangement of the pelvic and proximal hindlimb musculature is summarized below:

1) *M. iliotibialis* 1 + 2 of *C. latirostris* corresponds in position to *M. iliotibialis* 1 of *A. mississippiensis*.

2) The secondary tendon of *M. iliofibularis* of *C. latirostris* does not correspond to that of *A. mississippiensis*.

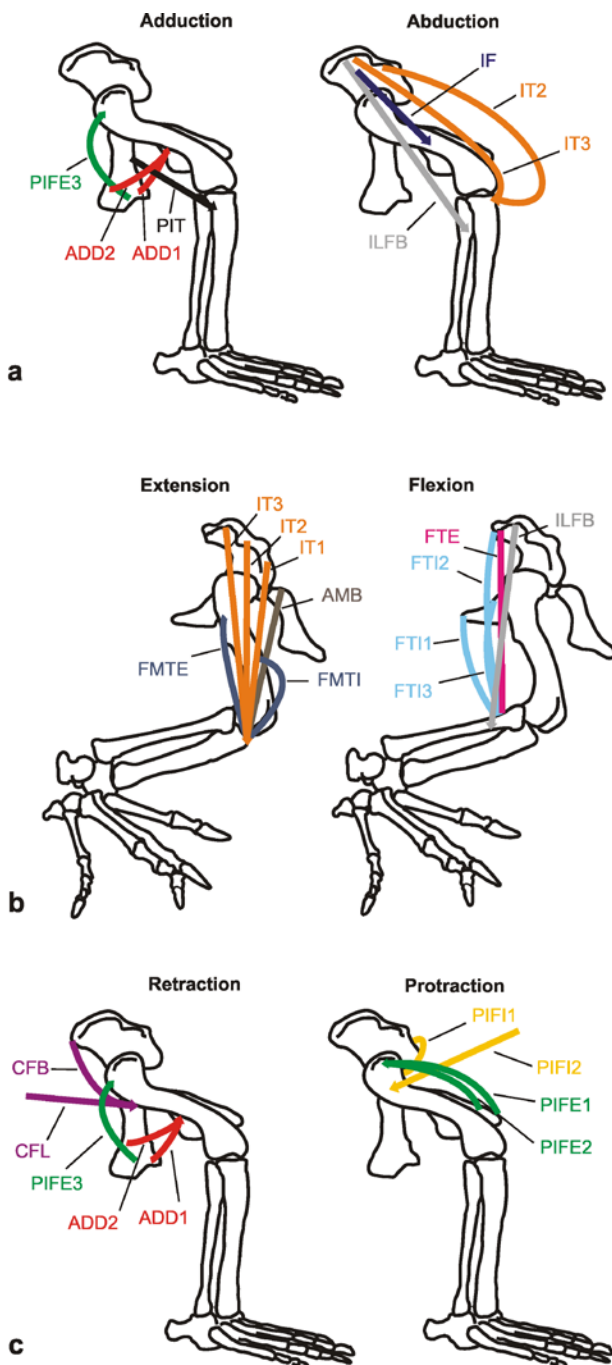


Fig. 5. Pelvic girdle and hind limb of *Caiman latirostris* showing principal muscles acting during locomotion.

In this sense, the secondary tendon of *A. mississippiensis* seems to correspond to the *M. flexor tibialis internus* 1 or *M. flexor tibialis externus* of *C. latirostris*.

3) The *M. adductor femoris* 1 of *C. latirostris* corresponds in position to the single head of *Mm. adductor femores* of *A. mississippiensis*.

4) *Caiman latirostris* does not present the *M. flexor tibialis internus* 4. There is no evidence in *C. latirostris* of a secondary tendon joining the external head of *M. gastrocnemius*, nor the secondary insertion site of FTE, as seen in *A. mississippiensis*. Muscle *ambiens* presents only one head.

Attachment sites in *C. latirostris* and other Crocodylia can be summarized as:

1) In the dissected specimens, the insertion scar of *M. ischiochantericus* is placed above the posteroproximal femur, not proxilaterally as observed in *A. mississippiensis*.

2) In *C. latirostris* the CFB originates on the ilium and caudal vertebrae, excluding sacral vertebrae, while the CFL originates from proximal caudal vertebral centrum and transverse processes, as well as from the haemal arches.

3) *Caiman latirostris* adds one dorsal vertebra to the origin of PIFI 2, totalling seven vertebrae.

4) There is no consensus among authors regarding the configuration and names of many hindlimb muscles. The discrepancies are focused on the *Mm. puboischiofemorales externi* and *Mm. puboischiofemorales interni* groups.

We also conclude that the hindlimb agonist–antagonist movements in *C. latirostris* are not performed by only one muscle, but instead by a system that includes a principal muscle that fulfills the action with the help of other muscles. In this sense, the adduction–abduction action is mainly performed by the ADD1 and the IT respectively. The extension–flexion action is mainly exerted by the pair IT2–ILFB, respectively. Finally, the PIFI 1+2 and PIFE 1+2 act mainly on protraction, whereas the CFL are the principal retractors of the leg.

ACKNOWLEDGEMENTS

We thank the authorities of the CICyTTP-Diamante (CONICET) where the dissections were made, C. Piña for providing the specimens of *C. latirostris* and J. González for his helping in the dissections. J. Desojo and an anonymous reviewer are thanked for useful comments on the manuscript. N. Toledo is thanked for the skilful drawings and M. Griffin for checking the English spelling. S. Apes-teguía and A. Lecuona are thanked for useful comments on the manuscript.

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Accepted: 21 April 2010

APPENDIX A

Sites of origin, insertion and function of pelvic and proximal hindlimb muscles present in *Caiman latirostris*

Muscle	Abbreviation	Origin	Insertion	Action
<i>M. iliotibialis 1</i>	IT1	anteriormost surface of ilium	tibial cnemial crest	knee and hip extension
<i>M. iliotibialis 2</i>	IT2	dorsolateral edge of the ilium	tibial cnemial crest	knee and hip extension + abduction
<i>M. iliotibialis 3</i>	IT3	dorsolateral edge of the ilium, above IF	tibial cnemial crest	knee and hip extension + abduction
<i>M. femorotibialis internus</i>	FMTI	anteromedial surface of femoral shaft	tibial cnemial crest	femorotibial joint extension
<i>M. femorotibialis externus</i>	FMTE	posterolateral surface of femoral shaft	tibial cnemial crest	femorotibial joint extension
<i>M. ambiens</i>	AMB	ambiens process of the pubis	tibial cnemial crest	femorotibial joint extension
<i>M. ischiochantericus</i>	ISTR	posteromedial surface of the ischium, behind ADD 2 origin	proximoposterior femoral shaft, over the CFL insertion scar	extension + lateral rotation of the femur
<i>M. iliofibularis</i>	ILFB	dorsolateral surface of the ilium, behind IT2 and over the origin of IF	anterolateral surface of the fibula	knee articulation flexion + hip extension and abduction

Cont...

Appendix A (cont.)

Muscle	Abbreviation	Origin	Insertion	Action
<i>M. puboischiotibialis</i>	PIT	antrolateral surface of the ischium	proximomedial aspect of the tibia	aids in adducting the leg
<i>M. flexor tibialis internus 1</i>	FTI1	posterodorsal surface of the ischium	posterolateral face of proximal tibia	femorotibial joint flexor and adductor
<i>M. flexor tibialis internus 2</i>	FTI2	posterolateral aspect of the ilium	posterolateral surface of the tibia	femorotibial joint flexor and adductor
<i>M. flexor tibialis internus 3</i>	FTI3	ischial tuberosity	proximomedial tibia	femorotibial joint flexor and adductor
<i>M. flexor tibialis externus</i>	FTE	lateral face of the ilium, behind the origin site of IF and over the origin of FTI2	proximomedial aspect of the tibia	aids femorotibial flexion
<i>M. adductor femoris 1</i>	ADD1	anterolateral surface of ischium	posterior surface of femoral shaft	adduction + femoral retractor
<i>M. adductor femoris 2</i>	ADD2	posterolateral portion of ischium	posterior surface of femoral shaft	adduction + femoral retractor
<i>M. caudofemoralis longus</i>	CFL	lateral sides of haemal arches + the base of proximal caudal vertebral centra + proximal portion of the ventral surface of transverse processes	femoral fourth trochanter	femoral retractor + contributes to adduction and rotation of the axis of the leg
<i>M. caudofemoralis brevis</i>	CFB	posteriormost region of the ilium, ahead ISC + lateral sides of the centrum and the base of transverse processes	close to the femoral fourth trochanter	aids CFL in retraction
<i>M. ilioischiocaudalis</i>	ISC	ventral surface of transverse processes	tips of haemal arches	
<i>M. puboischiofemoralis externus 1</i>	PIFE1	anteromedial (dorsal) surface of the pubis and prepubic cartilage	major trochanter of the femur	femoral protractor + rotates anterolaterally the femur + aids in adducting the leg
<i>M. puboischiofemoralis externus 2</i>	PIFE2	lateral (ventral) surface of the pubis and prepubic cartilage	major trochanter of the femur	femoral protractor + rotates anterolaterally the femur + aids in adducting the leg
<i>M. puboischiofemoralis externus 3</i>	PIFE3	lateral aspect of the ischium, between ADD1 and ADD2	major trochanter of the femur	femoral retractor + rotates anterolaterally the femur + aids in adducting the leg
<i>M. iliofemoralis</i>	IF	lateral surface of the ilium, under the second head of IT, above the flexor cruris group and the acetabulum	lateral surface of the femur between FM TI and FM TE	leg abduction
<i>M. puboischiofemoralis internus 1</i>	PIFI1	medioventral surface of the ilium	medial surface of proximal femur, cranio-medially to the fourth trochanter	protracts the leg + helps in adduction
<i>M. puboischiofemoralis internus 2</i>	PIFI2	proximal ventral face of transverse processes + lateral faces of the last seven dorsal vertebrae	dorsal, proximal and cranial femur	protracts the leg + helps in adduction
<i>M. gastrocnemius internus</i>	GI	posterior and distal surface of the femur	plantar surface of pes	metatarsus extension + toes flexion
<i>M. gastrocnemius externus</i>	GE	tibial proximomedial surface	plantar surface of pes	metatarsus extension + toes flexion

APPENDIX B

Pelvic and proximal hindlimb musculature nomenclature of *Caiman latirostris* presented in this work compared with previous studies on *Alligator mississippiensis* (Reese, 1915; Romer, 1923a; Rowe, 1986; Hutchinson, 2001a, b, 2002; Carrano & Hutchinson, 2002).

Triceps femoris group

	<i>Mm. iliotibiales</i>		
Reese, 1915	M. iliotibialis 1	M. iliotibialis 1	M. iliotibialis 2
Romer, 1923a	M. iliotibialis 1	M. iliotibialis 2	M. iliotibialis 3
Hutchinson, 2001a,b, 2002	M. iliotibialis 1	M. iliotibialis 2	M. iliotibialis 3
Carrano & Hutchinson, 2002	M. iliotibialis 1	M. iliotibialis 2	M. iliotibialis 3
This work	M. iliotibialis 1	M. iliotibialis 2	M. iliotibialis 3

	<i>M. iliofibularis</i>	<i>M. ambiens</i>
Reese, 1915	M. iliofibularis	M. ambiens
Romer, 1923a	M. iliofibularis	M. ambiens 1 + 2
Hutchinson, 2001a,b, 2002	M. iliofibularis	M. ambiens 1 + 2
Carrano & Hutchinson, 2002	M. iliofibularis	M. ambiens 1 + 2
This work	M. iliofibularis	M. ambiens

	<i>Mm. femorotibiales</i>		<i>M. ischiochantericus</i>
Reese, 1915	M. femorotibialis anterior	M. femorotibialis posterior	not mentioned
Romer, 1923a	M. femorotibialis internus	M. femorotibialis externus	M. ischiochantericus
Hutchinson, 2001a,b, 2002	M. femorotibialis internus	M. femorotibialis externus	M. ischiochantericus
Carrano & Hutchinson, 2002	M. femorotibialis internus	M. femorotibialis externus	M. ischiochantericus
This work	M. femorotibialis internus	M. femorotibialis externus	M. ischiochantericus

Flexor cruris group

	<i>M. flexor tibialis internus</i>		
Reese, 1915	M. flexor tibialis internus 1	M. flexor tibialis internus 2	M. flexor tibialis internus 3
Romer, 1923a	M. puoischiotibialis	M. flexor tibialis internus 1	M. flexor tibialis internus 2
Hutchinson, 2001a,b, 2002	M. puoischiotibialis	M. flexor tibialis internus 1	M. flexor tibialis internus 2
Carrano & Hutchinson, 2002	M. puoischiotibialis	M. flexor tibialis internus 1	M. flexor tibialis internus 2
This work	M. puoischiotibialis	M. flexor tibialis internus 1	M. flexor tibialis internus 2

	<i>M. flexor tibialis internus</i>		<i>M. flexor tibialis externus</i>
Reese, 1915	not mentioned	not mentioned	M. flexor tibialis externus
Romer, 1923a	M. flexor tibialis internus 3	M. flexor tibialis internus 4	M. flexor tibialis externus
Hutchinson, 2001a,b, 2002	M. flexor tibialis internus 3	M. flexor tibialis internus 4	M. flexor tibialis externus
Carrano & Hutchinson, 2002	M. flexor tibialis internus 3	M. flexor tibialis internus 4	M. flexor tibialis externus
This work	M. flexor tibialis internus 3	absent	M. flexor tibialis externus

	<i>Mm. adductores femores</i>	
Reese, 1915	Ischiofemoralis?	Ischiofemoralis?
Romer, 1923a	M. adductor femoris 1	M. adductor femoris 2
Hutchinson, 2001a,b, 2002	M. adductor femoris 1	M. adductor femoris 2
Carrano & Hutchinson, 2002	M. adductor femoris 1	M. adductor femoris 2
This work	M. adductor femoris 1	M. adductor femoris 2

Cont...

Appendix B (cont.)

	<i>Mm. caudofemorales</i>		<i>M. ilioischiocaudalis</i>
Reese, 1915	<i>M. caudi-femoralis</i> 1	<i>M. caudi-femoralis</i> 2	<i>M. ilioischiocaudalis</i>
Romer, 1923a	<i>M. coccigeo-femoralis longus</i>	<i>M. coccigeo-femoralis brevis</i>	<i>M. ilioischiocaudalis</i>
Carrano & Hutchinson, 2002	<i>M. caudofemoralis longus</i>	<i>M. caudofemoralis brevis</i>	not mentioned
This work	<i>M. caudofemoralis longus</i>	<i>M. caudofemoralis brevis</i>	<i>M. ilioischiocaudalis</i>
	<i>Mm. puboischiofemorales externi</i>		
Reese, 1915	<i>M. puboischiofemoralis externus</i> 1	<i>M. puboischiofemoralis externus</i> 2	not mentioned
Romer, 1923a	<i>M. puboischiofemoralis externus</i> 1	<i>M. puboischiofemoralis externus</i> 2	<i>M. puboischiofemoralis externus</i> 3
Hutchinson, 2001a,b, 2002	<i>M. puboischiofemoralis externus</i> 1	<i>M. puboischiofemoralis externus</i> 2	<i>M. puboischiofemoralis externus</i> 3
Carrano & Hutchinson, 2002	<i>M. puboischiofemoralis externus</i> 1	<i>M. puboischiofemoralis externus</i> 2	<i>M. puboischiofemoralis externus</i> 3
This work	<i>M. puboischiofemoralis externus</i> 1	<i>M. puboischiofemoralis externus</i> 2	<i>M. puboischiofemoralis externus</i> 3
Deep dorsal group			
	<i>M. iliofemoralis</i>	<i>Mm. puboischiofemoralis interni</i>	
Reese, 1915	<i>M. caudali-ilio-femoralis</i>	<i>M. puboischiofemoralis internus</i> 1+2	<i>M. puboischiofemoralis internus</i> 3
Romer, 1923a	<i>M. iliofemoralis</i>	<i>M. puboischiofemoralis internus</i> 1	<i>M. puboischiofemoralis internus</i> 2
Rowe, 1986	<i>M. iliofemoralis</i>	<i>M. puboischiofemoralis internus</i> 1	<i>M. puboischiofemoralis internus</i> 2
Hutchinson, 2001a,b, 2002	<i>M. iliofemoralis</i>	<i>M. puboischiofemoralis internus</i> 1	<i>M. puboischiofemoralis internus</i> 2
Carrano & Hutchinson, 2002	<i>M. iliofemoralis</i>	<i>M. puboischiofemoralis internus</i> 1	<i>M. puboischiofemoralis internus</i> 2
This work	<i>M. iliofemoralis</i>	<i>M. puboischiofemoralis internus</i> 1	<i>M. puboischiofemoralis internus</i> 2
	<i>Mm. gastrocnemii</i>		
Reese, 1915	<i>M. gastrocnemius caput tibiale</i>	<i>M. gastrocnemius caput femorale</i>	
Romer, 1923a	not mentioned	not mentioned	
Hutchinson, 2001a,b, 2002	<i>M. gastrocnemius medialis</i>	<i>M. gastrocnemius lateralis</i>	
Carrano & Hutchinson, 2002	<i>M. gastrocnemius internus</i>	<i>M. gastrocnemius externus</i>	
This work	<i>M. gastrocnemius internus</i>	<i>M. gastrocnemius externus</i>	