

MYOLOGICAL RECONSTRUCTION OF THE PELVIC GIRDLE OF *ANHANGUERA PISCATOR* (PTEROSAURIA: PTERODACTYLOIDEA) USING THREE-DIMENSIONAL VIRTUAL ANIMATION

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ABSTRACT – Despite muscular reconstructions of fossil vertebrates that have been performed for many years, sites of origin and attachment of muscles are rarely visible because their preservation on bones relies upon favorable circumstances. Limited attempts at reconstructing the pelvic muscles of pterosaurs have been made, but there is no report in the literature concerning a full detailed description of the pelvic girdle musculature of these flying reptiles. Thus, the aim of this study is to perform the reconstruction of the pelvis and hind limb myology in *Anhanguera piscator* Kellner & Tomida using the Extant Phylogenetic Bracket Method and advanced three-dimensional computer graphics, a methodological approach that has not yet been used for this purpose. Each muscle from the dorsal and ventral groups was individually reconstructed and outlined in the osteological model as lines whose ends represent their sites of origin and attachment in the bone. The authors used the Extant Phylogenetic Bracket Method to study these muscles in a more detailed way considering their divisions, such as Mm. *iliotibiales* 1-3, M. *iliofemoralis externus*/M. *iliotrochantericus caudalis*, and Mm. *flexores tibiales internus* 1-4.

Key words: myology, 3D reconstruction, *Anhanguera piscator*, Romualdo Formation, Brazil.

RESUMO – Apesar da reconstrução muscular em vertebrados fósseis vir sendo realizada há muitos anos, locais de origem e inserção dos músculos nos ossos são raros porque a preservação depende de circunstâncias particulares (e.g. material osteológico excepcionalmente bem preservado). Tentativas limitadas de reconstrução da musculatura pélvica de pterossauros têm sido feitas, mas não há registro na literatura de uma descrição detalhada da musculatura da cintura pélvica destes répteis voadores. Assim sendo, este estudo teve por objetivo a reconstrução miológica da pelve e membro posterior de *Anhanguera piscator* Kellner & Tomida a partir do método “Extant Phylogenetic Bracket” e de computação gráfica tridimensional avançada, sendo esta uma abordagem metodológica inédita para este propósito. Cada músculo dos grupos dorsal e ventral foi individualmente reconstruído e desenhado em um modelo osteológico na forma de linha cujas terminações representaram seus pontos de origem e inserção no osso. O método “Extant Phylogenetic Bracket” permitiu estudar estes músculos de um modo mais detalhado, considerando suas divisões, tais como Mm. *iliotibiales* 1-3, M. *iliofemoralis externus*/M. *iliotrochantericus caudalis*, e Mm. *flexores tibiales internus* 1-4.

Palavras-chave: miologia, reconstrução 3D, *Anhanguera piscator*, Formação Romualdo, Brasil.

INTRODUCTION

Muscles are the most often reconstructed aspect of the soft anatomy of a fossil vertebrate, but their sites of origin and attachment in bones are quite rare in the geological record because its preservation depends on special circumstances (Dilkes, 2000) that include exceptional preservation of osteological material. Several attempts to reconstruct the musculature of fossil vertebrates have been performed for many years (e.g. Romer, 1923a,b,c, 1927; Milner, 1925;

Galton, 1969), and have been somewhat controversial (Bennett, 2003) since in many cases there is no modern analog to compare or to be used as a model. This is particularly true for pterosaurs, an extinct clade of volant creatures, and the first group of vertebrates to develop powered flight.

The study of pterosaur muscles can be drawn back to the early 20th century, with the spots of attachment of some pectoral muscles being discussed by Fürbringer (1900). Thereafter, more studies about muscle reconstructions of the pectoral girdle in a limited number of pterosaur

species, including the ones of Kripp (1943), Padian (1983), Wellnhofer (1991) and Bennett (2003), were accomplished. The latter provided an extensive description of the pectoral musculature of a non-pterodactyloid (“rhamphorhynchoid”, *Campylognathoides* Strand, 1928) and a large pterodactyloid (*Anhanguera* Campos & Kellner, 1985), shedding light on the functional consequences of the “advanced” pectoral girdle (Bennett, 2003).

Two attempts to reconstruct the pelvic muscles have been done. The first study was the one of Bennett (2001) on *Pteranodon* Marsh, 1876 (see Kellner, 2010 for taxonomic comments on the Pteranodontidae), who inferred the placement of some pelvic muscles based on evidences of muscle scars. The second study was published by Fastnacht (2005), who used the Extant Phylogenetic Bracket Method (EPB; Witmer, 1995) and comparisons with reconstructions in other archosaurs (*e.g.* Wellnhofer, 1978; Hutchinson, 2001a) to reconstruct the pelvic musculature of an unidentified species of the clade Dsungaripteridae. However, there is no record in the literature regarding a full detailed description of all muscles of the pelvic girdle in any pterosaur species.

According to Dilkes (2000), one line of evidence for the restoration of musculature in an extinct vertebrate concerns the use of myological patterns in one or more extant models. A widely used method for reconstructing the soft anatomy in extinct vertebrates using extant analogs is the already mentioned EPB of Witmer (1995), which provides a metric of the level of speculation inherent in a soft tissue reconstruction (Carrano & Hutchinson, 2002). This method is based on the inference on soft tissue homologies from osteological landmarks, and has the advantage of being applied to virtually any unpreserved trait of a fossil taxon with little or no modification (Witmer, 1995). A similar general approach was previously outlined by Bryant and Russell (1992).

A second line of evidence followed by Dilkes (2000) concerns the identification of osteological features such as rugose scars and prominent projections. These topographic indicators can reveal many (but not all) muscle attachment sites (Carrano & Hutchinson, 2002). Osteological evidence depends, therefore, on well-preserved external surfaces of fossilized bones in order to allow the recognition of soft tissue scars. Notwithstanding, pterosaur material is rare and frequently fragmentary due to the fragile nature of its hollow-boned skeletons that tend to be crushed, hindering the identification of anatomical features (Kellner, 1996). Thus, it is difficult to have a specimen complete enough to allow studies of this kind. However, *Anhanguera piscator* Kellner & Tomida, 2000 (Aptian-Albian, Romualdo Formation, NE Brazil) is a noteworthy exception. This large pterodactyloid is considered the most complete anhanguerid described so far, showing exceptionally well-preserved bones that can provide abundant information regarding its anatomical features, which allow a more accurate and complete myological study to be accomplished.

Plenty of works have been performed to reconstruct the musculature of extinct archosaurs (*e.g.* Romer, 1923a;

Coombs, 1979; Langer, 2003; Hutchinson *et al.*, 2005; Maidment & Barrett, 2011; Bates & Schachner, 2012; Bates *et al.*, 2012; Hutchinson, 2012). Recently, new technologies, such as advanced three-dimensional computer graphics, have been used in paleontology to reconstruct fossil models. These tools enable the model to be reconstructed from its disassembled parts and manipulated in a virtual space to simulate all kinds of movements, and are very helpful in the case of extinct organisms (Costa *et al.*, 2010) to interpret them as living, functioning animals.

The aim of this study is to perform the myological reconstruction of the pelvic girdle of *Anhanguera piscator* using EPB to associate muscles and their osteological correlates, and advanced three-dimensional computer graphics to outline the muscles on a three-dimensionally reconstructed osteological model of pelvis, femur and tibia. The latter methodological approach has until now not been used for myological reconstructions of the pelvic girdle of *A. piscator*. **Institutional abbreviations.** DFMMh, Dino-Park Münchehagen/Verein zur Förderung der niedersächsischen Paläontologie, Germany; MN, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; YPM, Yale Peabody Museum of Natural History, Yale University, New Haven, USA.

MATERIAL AND METHODS

Construction of the osteological model

The construction of an osteological model (*i.e.* an overall model comprising articulated pelvis, femur and tibia) was performed and each step followed the methodology used by Grillo & Azevedo (2011). This construction required an extensive review on the osteology of pelvis, femur and tibia of *Anhanguera piscator*. The construction of the model regarded the image capture process of the pelvic girdle bones (right pelvis, femur and tibia) undertaken by the Next Engine Desktop 3D Scanner (Next Engine Inc., Santa Monica, CA) together with the software ScanCore Studio (Next Engine Inc., Santa Monica, CA). This process produced a virtual model of each bone alone. These models were aftermost manipulated with the software Autodesk 3D Studio Max 5.0 (3DS MAX) in the sense of having its broken parts reconstructed (*e.g.* the preacetabular process of the ilium), as well as its articulation points (pelvis-femur, femur-tibia) established. Concerning the pelvis-femur articulation, these points were determined from the positioning of centroids at the articular region. The center of rotation of tibia was placed between the femoral condyles. Then, the models were integrated into one overall model comprising articulated pelvis, femur and tibia (Figure 1).

Construction of the myological model

The muscles of the pelvic girdle of *Anhanguera piscator* (cast MN 5023-V) were reconstructed by using the EPB method. This method, as already been pointed out, concerns to an outgroup-based phylogenetic methodology in which extant taxa are used as outgroups to be compared with an extinct taxon in order to formulate hypotheses with different confident levels to infer about the presence or absence of a

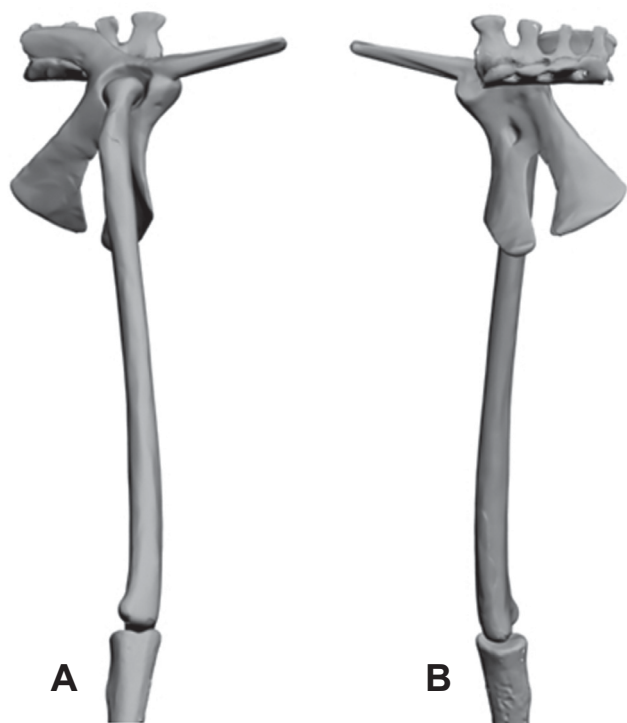


Figure 1. Osteological model of *Anhanguera piscator* by three-dimensional modeling in lateral (A) and medial (B) views.

particular character in the extinct taxon (Witmer, 1995). The intrinsic level of speculation in a soft tissue reconstruction was termed “levels of inference”, which is an established hierarchy of inference concerning three possible assessments at the outgroup node: (I) both extant taxa present the soft tissue and its osteological correlate, giving an unequivocally support to the reconstruction of a given muscle; (II) one of the taxa lacks both the soft tissue and the osteological correlate, or the osteological correlate is present in only one of the extant taxa and in the fossil taxon, with the presence of the soft tissue in both extant taxa, which gives an equivocal support for reconstructing the muscle; (III) both extant taxa lack the soft tissue and its osteological correlate, which unequivocally supports the absence of a given muscle in the extinct taxon. If inferences lack conclusive data from the osteological correlates of soft tissues, they are called Levels I', II' and III'. These ones have less support than Levels I, II and III, but more than one at the next overall level (Carrano & Hutchinson, 2002). This study considered Levels I, I', II and II' to the myological reconstruction of *A. piscator* pelvic muscles, and avoided Levels III and III' because of them being overly speculative. Although the phylogenetic position of pterosaurs is disputed, we followed most authors that regard those flying reptiles as the sister group of the Dinosauromorpha (e.g. Gauthier, 1984; Padian, 1984; Benton, 1999; Kellner, 2004; Nesbitt, 2011) and, thus, Crocodylia and Aves were considered as outgroups.

Each muscle from the dorsal (*Triceps femoris* and Deep Dorsal) and ventral (*Flexor cruris*, Mm. *adductores femores*, Mm. *puboischiofemorales externi*, M. *ischiotrochantericus*

and Mm. *caudofemorales*) groups were individually reconstructed. The inferred muscles were then depicted in the osteological model as lines whose ends represent their sites of origin and attachment in the bone. Comparisons with previous works (Bennett, 2001; Fastnacht, 2005) are also addressed in order to give support to the muscular arrangement determined in *Anhanguera piscator* by the use of EPB.

RESULTS AND DISCUSSION

Once the osteological model was constructed, the muscles were placed according to the arrangement of their spots of origin and insertion. Muscles were outlined in the osteological model as lines whose ends represent their sites of origin and attachment in the bone (Figure 2).

Dorsal Group

M. triceps femoris

Triceps femoris muscle is comprised by M. *iliotibialis*, M. *ambiens*, M. *femorotibialis* and M. *iliofibularis*.

M. *iliotibialis* (IT) is a large, blade-like superficial muscle in Crocodylia and Aves, with three heads usually numbered 1-3 from anterior to posterior that originate from the dorsolateral margins of the ilium (Carrano & Hutchinson, 2002). M. *iliotibialis* 1 is also termed M. *iliotibialis cranialis* (IC) in Aves, with M. *iliotibialis lateralis* (IL) being homologous to M. *iliotibialis* 2+3 (Carrano & Hutchinson, 2002). These heads, together with M. *ambiens* and Mm. *femorotibiales*, are responsible for extending the femorotibial joint. The knee extensor tendon formed by this convergence is inserted in the cnemial crest of the tibia (Romer, 1923c; Carrano & Hutchinson, 2002).

Bennett (2001) draw the attention to the anterior preacetabular process of the ilium being weakly rugose along the lateral margins in *Pteranodon* (YPM 1175) probably for the origin of M. *iliofemoralis* and *iliotibialis*. Moreover, he associated the rugose area of the cnemial crest at the tip of the proximal tibia to the insertion of *Triceps femoris*, which comprises Mm. *iliotibiales* 1-3. Fastnacht (2005) also placed these muscles as a single unity in the anterior surface of the preacetabular process of the ilium, though rather proximally displaced.

Regarding the origin of these muscles in *Anhanguera piscator*, most of the preacetabular process of both ilia is broken, which does not allow the recognition of scars in this region. However, we can estimate from the preserved, proximal portion that this process was long and slender but massively built (Kellner & Tomida, 2000), which could have functioned as an attachment site to the pelvic musculature. Besides, *A. piscator*, similar to *Pteranodon*, has a relatively well-developed cnemial crest that could have functioned as an insertion spot to this muscle. Thus, M. *iliotibialis* is inferred for *A. piscator* to have its origin along the lateral margin of the preacetabular process of the ilium, with M. *iliotibialis* 1 more anteriorly placed (to the edge of the process), M. *iliotibialis* 2 between Mm. *iliotibiales* 1 and 3, at the median portion of

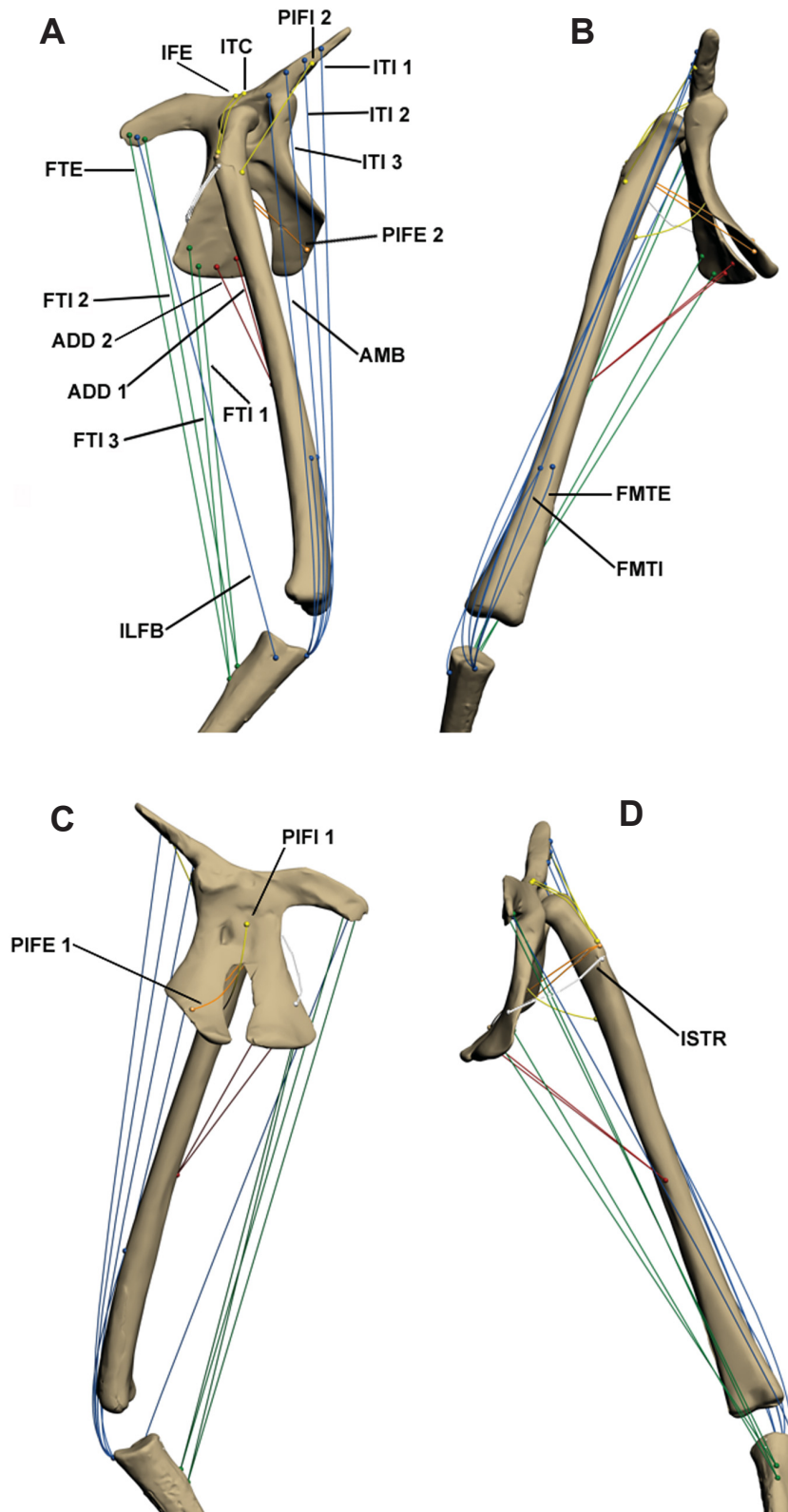


Figure 2. Muscles of the right pelvic girdle of *Anhanguera piscator* in lateral (A), anterior (B), medial (C) and posterior (D) views. Dorsal Group: Deep dorsal (yellow), *Triceps femoris* (blue). Ventral Group: *Flexor Cruris* (green), *Puboischiofemoralis externus* (orange), *Adductor femoris* (red) and *Ischiotrochantericus* (white). **Abbreviations:** ADD 1-2, Mm. *adductores femores* 1-2; AMB, *M. ambiens*; FMTE, *M. femorotibialis externus*; FMTI, *M. femorotibialis internus*; FTE, *M. flexor tibialis externus*; FTI1-3, Mm. *flexores tibiales interni* 1-3; IFE, *M. iliofemoralis externus*; ILFB, *M. iliofibularis*; ISTR, *M. ischiotrochantericus*; ITC, *M. iliotrochantericus caudalis*; ITI1-3, Mm. *iliotibiales* 1-3; PIFE1-2, Mm. *puboischiofemorales externi* 1-2; PIFI1-2, Mm. *puboischiofemorales interni* 1-2.

the process, and *M. iliotibialis* 3 more posteriorly placed, and all of them being inserted in the cnemial crest of the tibia. As previously highlighted, as the ilium lacks this process almost completely, it had to be digitally reconstructed.

Neither Bennett (2001) nor Fastnacht (2005) detailed the positioning of the three muscle heads of *Mm. iliotibiales*. Both authors have mentioned these muscles as if they would form a single unity that has a common origin. Comparisons with Crocodylia and Aves provided by the use of EPB showed that these heads have specific origin spots along the lateral margin of the preacetabular process, though they share a common insertion area (cnemial crest) at the tibia.

M. ambiens (AMB) is a double-headed muscle in Crocodylia that originates from the lateral and medial sides of the contact between the pubis and *pars acetabulus* (Dilkes, 2000). Aves share with all other extant Reptilia the single-headed condition, which is the most parsimonious character state (Dilkes, 2000). In all extant Reptilia *M. ambiens* arises from the pubic tubercle or it is more dorsally placed regarding this structure, which is absent or reduced in Crocodylia (Hutchinson, 2001a). The reduction of the pubic tubercle to a small roughness area shows the reduction of the pubo-ischiadic ligament (and *Mm. flexor crures*) in basal Archosauriforms (Hutchinson, 2001a). *M. ambiens* in both Crocodylia and Aves is inserted in the cnemial crest (Romer, 1923a; Carrano & Hutchinson, 2002). In the former it extends the femorotibial joint, and in the latter it contributes to the extension of the tibiotarsus and adducts the leg (Otero & Vizcaíno, 2008).

Bennett (2001) pointed to the presence of rugose tubercles in *Pteranodon* at the margin of the acetabulum: the first near its anterior margin, at the base of the anterior blade of ilium (e.g. YPM 1175, 2456, 2535), the second posterior to it and an adjacent rough area, and a third one directly below it. The former tubercle is associated to the origin of *M. ambiens*, and the others are not specifically related to any muscle. According to Fastnacht (2005), in the dsungaripterid this origin shifted onto the anterior edge of the pubis, not being associated to a tubercle, which is a more similar condition to Crocodylia. However, once the double-headed condition of *M. ambiens* is only known for Crocodylia, it is more parsimonious to consider this muscle in *Anhanguera piscator* with a single head and originating from the pubic tubercle as in *Pteranodon* and Aves, being inserted in the cnemial crest. Thus, Fastnacht's (2005) positioning regarding the origin of this muscle is controversial because it was inferred based on a more derived and, thus, less parsimonious condition. Once the myological reconstruction of Fastnacht was not detailed in his study, there is no argument in his work to support this hypothesis. Moreover, though a pubic tubercle in *A. piscator* cannot be recognized due to its ontogenetically immature condition (Kellner & Tomida, 2000), the evidence of this structure in *Pteranodon* can determine this positioning in a more accurate way.

M. femorotibialis (FMT) comprises two heads (*M. femorotibialis internus*/FMTI and *M. femorotibialis externus*/FMTE) in Crocodylia, and three in Aves (*M. femorotibialis*

medialis/FMTM, *M. femorotibialis intermedius*/FMTIM and *M. femorotibialis lateralis*/FMTL), which means that Aves have increased the number of heads of this muscle. *M. femorotibialis externus* is homologous to *M. femorotibialis lateralis*, and *M. femorotibialis internus* to *M. femorotibialis medialis* and *intermedius* (Dilkes, 2000; Romer, 1923c; Carrano & Hutchinson, 2002). Having a fleshy origin, it mostly originates from the available surface of the anterior femoral shaft, between the femoral head and trochanters (proximally) and the condyles (distally) (Romer, 1923c; Carrano & Hutchinson, 2002; Hutchinson, 2001b). These limits are marked by three intermuscular lines: *linea intermuscularis cranialis, caudalis* and *lateralis*, which run along the anterior, posterior and lateral surfaces in the femur, respectively (Otero & Vizcaíno, 2008). *M. femorotibialis* is anterolaterally inserted in the cnemial crest of the tibia in both Crocodylia and Aves.

The positioning of the origin area of this muscle in *Anhanguera piscator* is problematic because of the absence of the pubic tubercle previously pointed out in this specimen. The division of *M. femorotibialis internus* in Aves (*M. femorotibialis medialis* and *intermedius*) cannot be assessed in *A. piscator* and, thus, this condition remains unknown. Therefore, it is considered that *A. piscator* displays the same condition as in Crocodylia (with *M. femorotibialis* comprising two heads). Moreover, there are no signs of intermuscular lines that could help in the positioning of the *M. femorotibialis* heads, which leads us to place both heads regarding their positioning in Crocodylia (distal half of the femoral shaft), being inserted in the cnemial crest of the tibia.

Bennett (2001) noted extensive areas of thin muscle scars in *Pteranodon* placed at the proximal half of the femoral diaphysis, distal to the great and internal trochanters, which are generally associated to the origin of *M. femorotibialis* and other muscles. The former would be inserted at the cnemial crest of the tibia, together with the other muscles that form the *triceps femoris*. Fastnacht (2005) did not consider this muscle in his myological reconstruction.

In extant archosaurs, *M. iliofibularis* (ILFB) originates from the lateral surface of the ilium posterior to the origin of *M. iliofemoralis externus* and ventral to *M. iliotibialis* 1-3 (Dilkes, 2000; Carrano & Hutchinson, 2002) and is inserted in a tubercle placed on the anterolateral proximal fibular shaft (Dilkes, 2000; Carrano & Hutchinson, 2002; Otero & Vizcaíno, 2008). It seems, therefore, to have tapered from a large, fleshy origin with about one-fourth of the lateral iliac surface to a small, tendinous insertion on the fibula (Dilkes, 2000). In *Anhanguera piscator*, the posterior tip of the postacetabular process of the ilium is slightly turned outward and has a rough surface possibly related to muscle attachments. On the lateral side, the lower part of the posterior postacetabular process also has a slightly rough bone texture (Kellner & Tomida, 2000). This area is interpreted as related to the origin of the *M. iliofibularis*. A prominent, rounded tubercle on the anterolateral surface of the proximal fibular shaft is consensually considered the insertion area of *M. iliofibularis* in Archosauria (Carrano &

Hutchinson, 2002), which would be the same for *A. piscator*. However, no fibula is preserved in this specimen, although a lateral emargination on the proximal articulation of the tibia, leading to a shallow groove prolonged down the shaft seems to be the contact between tibia and fibula (Kellner & Tomida, 2000). Therefore we consider that *M. iliofibularis* was inserted in this contact surface.

Regarding *Pteranodon*, Bennett (2001) pointed to a rough sub-horizontal plate of the postacetabular process of the ilium and associated it to the likely area of origin of epaxial muscles and *M. caudofemoralis*. This same condition would probably be found in an adult specimen of *A. piscator* by the ontogenetic increase of the slightly rough bone texture of the ilium, as observed in the immature specimen. Fastnacht (2005) placed *M. iliofibularis* at the lateral surface of the medial region of this same structure on the ilium in the dsungaripterid studied by him.

Deep Dorsal Group

Deep Dorsal Group is formed by *M. iliofemoralis* and *M. puboischiofemoralis internus*.

M. iliofemoralis (IF) does not present divisions in Crocodylia and originates from the ilium, just above the acetabulum. In Aves it has typically two heads: *M. iliofemoralis externus* (IFE) and *M. iliotrochantericus caudalis* (ITC), which arise from virtually the entire lateral surface of the ilium (Dilkes, 2000). The single head of this muscle in Crocodylia is inserted along the lateral surface of the femoral shaft, and in Aves both heads are inserted together onto the lateral surface of the femur close to its head (Dilkes, 2000; Carrano & Hutchinson, 2002).

Kellner & Tomida (2000) pointed out to a well-developed great trochanter with a rough surface for muscle insertion placed lateral to the femoral neck, which would be associated to the insertion of the *M. iliofemoralis*. The division of *M. iliofemoralis* is observed by the presence of the lesser trochanter at the insertion area of this muscle (trochanteric shelf of the femur), which is homologous to the insertion area of *M. iliotrochantericus caudalis* in Aves (Hutchinson, 2001b). Since *Anhanguera piscator* presents this structure, the division of this muscle is considered (the same condition as in Aves). Therefore the positioning of both heads followed the arrangement observed in Aves, with *M. iliofemoralis externus* being placed ventrally to *M. iliotibialis* 1-3, anteriorly to *M. iliofibularis*, posteriorly to *M. iliotrochantericus caudalis* and dorsally to the acetabulum and the acetabular shelf (Dilkes, 2000), being both inserted in the greater trochanter of the femur.

Neither Bennett (2001) nor Fastnacht (2005) considered *M. iliofemoralis* divided into two heads, with its origin being referred only generally at the lateral surface of the ilium, above the acetabulum. Bennett (2001) related the anterior blade of the ilium of *Pteranodon* to the likely area of origin of *M. iliofemoralis* and *M. iliotibialis* 1-3, which is slightly rough along the lateral borders. The insertion is referred to the rough greater trochanter and, thus, the proximal region of insertion

of *M. iliofemoralis* (Hutchinson, 2001b). Fastnacht (2005) placed this muscle at the lateral surface of the ilium, just above the acetabulum, as in Crocodylia and Aves, and inserted it at the lesser trochanter. As in *Anhanguera piscator* the greater trochanter is well developed, this structure was considered the insertion area of this muscle (*contra* Fastnacht, 2005).

M. puboischiofemoralis internus (PIFI) has two divisions in Crocodylia: *M. puboischiofemoralis internus* 1-2. In Aves this number increases to three: *M. iliofemoralis internus* (IFI), *M. iliotrochantericus cranialis* (ITCR) and *M. iliotrochantericus medius* (ITM). The former is homologous to *M. puboischiofemoralis internus* 1, and the others to *M. puboischiofemoralis internus* 2 (Romer, 1923b; Rowe, 1986). These homologies suggest that the evolution of the bipedalism in Aves was followed by few myological changes, along with profound changes in the skeleton (Rowe, 1986). The origin of *M. puboischiofemoralis* 1 in Crocodylia is the medial surface of the ilium and the medio-proximal surface of the ischium, as well as the ventral surface of the sacral ribs (Romer, 1923c; Hutchinson, 2001a; Carrano & Hutchinson, 2002; Hutchinson, 2002). In Aves, *M. iliofemoralis internus* originates from the lateral surface of the ilium, at the reduced preacetabular fossa (“cupedicus” fossa) (Hutchinson, 2001a, 2002). This change in the position of *M. puboischiofemoralis internus* 1 shows that the origin of this muscle moved laterally in Aves, with the reduction of this fossa at the lateral surface of the ilium (Hutchinson, 2002; Norell *et al.*, 2001). In Crocodylia, this muscle is inserted onto the proximal surface of the femur, more antero-medially positioned concerning the origin of *M. puboischiofemoralis internus* 2 (Romer, 1923c; Hutchinson, 2001b, 2002). The insertion of *M. iliofemoralis internus* in Aves is the medio-proximal surface of the femur, at a rounded mark (Hutchinson, 2001b, 2002).

Reconstruction of the *M. puboischiofemoralis internus* 2, together with its avian homologs (*Mm. iliotrochanterici cranialis* and *medius*), is difficult because it sits at the core of the controversy surrounding the deep dorsal homologs (Carrano & Hutchinson, 2002). It is not known whether *M. puboischiofemoralis internus* 2 was transformed into *Mm. iliotrochanterici cranialis* and *medius* (Romer, 1923b; Rowe, 1986), or if it was completely lost during the evolution of Theropoda (Carrano & Hutchinson, 2002). As the former hypothesis has more support from anatomical data and ontogeny of extant groups (Rowe, 1986), it is more parsimonious and is therefore favored. In Crocodylia, *M. puboischiofemoralis internus* 2 originates from the lateral surfaces of the last six dorsal vertebral centra, being inserted onto the antero-lateral surface of the proximal femur by a large tendon (Romer, 1923c; Carrano & Hutchinson, 2002). This muscle had its posterior part possibly lost in Aves (Dilkes, 2000). The avian homologs of *M. puboischiofemoralis internus* 2 originate from the ventro-lateral surface of the preacetabular process of the ilium, anteriorly to the origin of *M. iliofemoralis internus*, and are inserted in the medial (*M. iliotrochantericus medius*) and distal (*M. iliotrochantericus lateralis*) surfaces of the trochanteric crest of the femur (Dilkes, 2000).

Since *Anhanguera piscator* does not present a preacetabular fossa, which is related to the origin of *M. puboischiofemoralis internus 1* in Aves (Hutchinson, 2001a, 2002), the present authors consider that it displayed the same condition found in Crocodylia. Concerning the insertion area of this muscle, it followed the consensually established proximal surface of the femur (Dilkes, 2000; Romer, 1923c; Hutchinson, 2001b, 2002) although its accurate position may vary within the different groups. Regarding *M. puboischiofemoralis internus 2*, the change in the position of its origin from the lateral surfaces of the dorsal vertebral centra in Crocodylia to the ventro-lateral surface of the preacetabular process of the ilium in Aves is related to the formation of the preacetabular fossa and the expansion of the preacetabular process in the latter group (Hutchinson, 2001a, 2002). Pterosaurs lack a preacetabular fossa; therefore the present authors consider that the origin of *M. puboischiofemoralis internus 2* would be at the preacetabular process of the ilium. This process is mostly broken in *A. piscator*, but appears to be long and slender (Kellner & Tomida, 2000), which turn it to be possibly associated to the origin of this muscle whose arrangement would follow the one of *M. iliotrochanterici cranialis* and *medius* in Aves.

There is no accurate reference in pterosaur literature concerning the origin of *M. puboischiofemoralis 1*. In regard to *Pteranodon*, Bennett (2001) highlighted a series of muscle scars at the proximal half of the femoral diaphysis, distal to the greater, lesser and internal trochanters, and associated it to the origin of *M. femorotibialis* and other muscles. Hutchinson (2001b) placed *M. puboischiofemoralis 1* at the same position of pterodactyloid pterosaurs. The scars reported by Bennett (2001), which were referred to *M. femorotibialis* and others, can, thus, include *M. puboischiofemoralis 1*, once they are placed in a consensual area to the origin spot of this muscle (proximal femur). Consequently, the reconstruction of this muscle in *Anhanguera piscator* in this same position was corroborated.

Cooper (1981), Gauthier (1986), Rowe (1989) and Novas (1996) inferred that the lesser trochanter was primarily the insertion of *M. puboischiofemoralis 2*. On the contrary, Hutchinson (2001a) deduced that the insertion was at the distal base of the trochanter for this muscle. This author claims that the reconstruction of *M. puboischiofemoralis 2* as inserted at the lesser trochanter is more speculative than the insertion of *M. iliotrochantericus caudalis* in the distal base of the trochanter because this muscle occupies a great part of the proximal trochanteric shelf in Aves. However, this same author relates the lesser trochanter in pterodactyloid pterosaurs as occupying the same position of the insertion of *M. puboischiofemoralis 2* in other Reptilia, which is the cranio-lateral region of the femoral diaphysis. The lesser trochanter in *Anhanguera piscator* is indeed a rough surface (Kellner & Tomida, 2000), which turns this area to be a likely area of muscle attachment. In this case, this attachment could be thoroughly referred to *M. puboischiofemoralis 2* in an equivalent position to its insertion in Crocodylia that, in turn, corresponds to a topological area that is equivalent to the avian homologues (*M. iliotrochantericus cranialis* and *M. iliotrochantericus medius*).

The reconstructed muscles of the Dorsal Group of *Anhanguera piscator* can be seen in Tables 1 and 2.

Ventral Group

Flexor cruris Group

This Group comprises *M. puboischiotibialis*, *M. flexor tibialis internus* and *M. flexor tibialis externus*. Their homologies remain poorly resolved, but as Crocodylia presents five muscle heads (and at least four in other extant groups) whereas Aves has two, it can be stated that this muscle group was reduced on the line to extant birds (Carrano & Hutchinson, 2002).

M. puboischiotibialis (PIT) is present in basal reptiles, reduced in Crocodylia and absent in Aves (Dilkes, 2000;

Table 1. Muscles of *Anhanguera piscator* reconstructed (Dorsal Group – *Triceps femoris* and Deep Dorsal Group), with the levels of inference in parentheses.

Group/Muscle	Origin	Insertion
Dorsal Group - <i>Triceps femoris</i>		
<i>M. iliotibialis 1</i>	lateral margin of the preacetabular process (more anteriorly displaced) (I')	cnemial crest of the tibia (I')
<i>M. iliotibialis 2</i>	lateral margin of the preacetabular process (intermediate position) (I')	cnemial crest of the tibia (I')
<i>M. iliotibialis 3</i>	lateral margin of the preacetabular process (more posteriorly placed) (I')	cnemial crest of the tibia (I')
<i>M. ambiens</i>	pubic tubercle (I')	cnemial crest of the tibia (I')
<i>M. femorotibialis internus</i>	proximal half of the femoral shaft (I')	cnemial crest of the tibia (I)
<i>M. femorotibialis externus</i>	proximal half of the femoral shaft (I')	cnemial crest of the tibia (I)
<i>M. iliofibularis</i>	posterior postacetabular process (I)	proximal tibial articulation (I')
Deep dorsal Group		
<i>M. iliofemoralis externus</i>	lateral surface of the ilium (I')	greater trochanter of the femur (I')
<i>M. iliotrochantericus caudalis</i>	lateral surface of the ilium (I')	greater trochanter of the femur (I')
<i>M. puboischiofemoralis internus 1</i>	medial surface of the ilium (I')*	proximal surface of the femur (I')
<i>M. puboischiofemoralis internus 2</i>	proximal surface of the femur (I')	lesser trochanter of the femur (I)

* Also at the medio-proximal surface of the ischium and at the ventral surface of the sacral ribs.

Table 2. Muscles of *Anhanguera piscator* reconstructed (Dorsal Group – *Flexor cruris* Group and *M. adductor femoris*), with the levels of inference in parentheses.

Group/Muscle	Origin	Insertion
<i>Flexor cruris</i> Group		
<i>M. puboischiotibialis</i>	inferred absent	inferred absent
<i>M. flexor tibialis internus</i> 1	postero-lateral surface of distal ischium (II')	postero-medial surface of the proximal tibia (II')
<i>M. flexor tibialis internus</i> 2	lateral surface of the postacetabular process of the ilium (II)	postero-lateral surface of the tibia (II')
<i>M. flexor tibialis internus</i> 3	lateral surface of the ischial tuberosity (I')	postero-medial surface of the proximal tibia (I')
<i>M. flexor tibialis internus</i> 4	ilio-ischiadic fascia (II')	medial surface of the tibia (II')
<i>M. flexor tibialis externus</i>	lateral surface of the postacetabular process of the ilium (II')	medial surface of the tibia (II')
<i>M. adductor femoris</i>		
<i>M. adductor femoris</i> 1-2	lateral surface of the ischium (I')	medial shaft of the femur (I')

Romer, 1923c; Carrano & Hutchinson, 2002; Hutchinson, 2002). This muscle in Crocodylia originates from the proximal tip of the obturator process of the ischium (Carrano & Hutchinson, 2002), and is inserted in the postero-medial surface of the proximal tibia (Romer, 1923c; Hutchinson, 2002). Bennett (2001), Kellner & Tomida (2000), Hutchinson (2001b) and Fastnacht (2005) do not mention this muscle, and once there is no evidence of this muscle scar in *Anhanguera piscator*, it is considered absent.

M. flexor tibialis internus (FTI) has four heads in Crocodylia: *M. flexor tibialis internus* 1 (FTI 1), *M. flexor tibialis internus* 2 (FTI 2), *M. flexor tibialis internus* 3 (FTI 3) and *M. flexor tibialis internus* 4 (FTI 4). *M. flexor tibialis internus* 1 has its origin on the postero-lateral surface of the distal ischium, and its insertion in the postero-medial surface of the proximal tibia (Romer, 1923c; Hutchinson, 2002). *M. flexor tibialis internus* 2 originates from the lateral surface of the postacetabular process of the ilium, and is inserted in the postero-lateral surface of the tibia (Dilkes, 2000; Carrano & Hutchinson, 2002; Hutchinson, 2002). The origin of *M. flexor tibialis internus* 3 is on the lateral surface of the ischial tuberosity, with its insertion in the postero-medial surface of the proximal tibia (Carrano & Hutchinson, 2002; Hutchinson, 2002). *M. flexor tibialis internus* 4 originates from the ilio-ischiadic fascia and shares a common tendon with *M. flexor tibialis internus* 3 (thus without any muscle scars) (Dilkes, 2000; Carrano & Hutchinson, 2002). In Aves, just the *M. flexor cruris medialis* (FCM), which is the homolog of *M. flexor tibialis internus* 3, is present, and originates from a similar position regarding this muscle, though more distally placed (Carrano & Hutchinson, 2002; Hutchinson, 2002). It is inserted in the proximal tibia as in Crocodylia (Carrano & Hutchinson, 2002; Hutchinson, 2002).

Once the posterior tip of the postacetabular process in *Anhanguera piscator* has a rough surface that might have served for muscle attachments (Kellner & Tomida, 2000), it is possible to associate this area to the origin of *M. flexor tibialis internus* 2. *Mm. flexores tibiales interni* 1 and 4 were considered having the same origin as in Crocodylia (the former in the postero-lateral surface of distal ischium, and the latter in the ilio-ischiadic fascia). *M. flexor tibialis internus* 3, which has its origin at the ischium in both Crocodylia and

Aves, was reconstructed with a more distally placed origin concerning its position in Crocodylia (as in Aves) because the ischial tuberosity (present in Crocodylia) is absent in *A. piscator*. Regarding the insertion of these heads in *A. piscator*, *Mm. flexores tibiales interni* 1, 2 and 4 were reconstructed about the same place as in Crocodylia, and *M. flexor tibialis internus* 3 as in Crocodylia and Aves. In Figure 2 these muscles are inserted in the posterior portion of the proximal tibia. Since *M. flexor tibialis internus* 4 leaves no muscle scar as abovementioned it was not depicted in Figure 2. However, it is considered to share a common tendon with *M. flexor tibialis internus* 3 in *A. piscator*, at the posterior portion of the proximal tibia.

The only reference regarding the origin and insertion of *M. flexor tibialis internus* in pterosaurs is presented by Fastnacht (2005). However, this author reconstructed this muscle without considering its divisions. The area of origin is the same as that of *M. flexor tibialis internus* 2 in Crocodylia (lateral surface of the postacetabular process of the ilium) and, thus should be referred just to the origin of *M. flexor tibialis internus* 2 and not to the other heads of *M. flexor tibialis*. The insertion area is at the tibia, but without an accurate positioning. Due to the lack of accuracy of Fastnacht (2005), his reconstruction of this muscle in a dsungaripterid species was not considered for the myological reconstruction in this study.

M. flexor tibialis externus (FTE) in Crocodylia originates from the postero-lateral side of the ilium and is inserted on the proximal end of the tibia and the lateral head of *M. gastrocnemius* (Dilkes, 2000). The avian homologue is *M. flexor cruris lateralis* (FCLP) (Dilkes, 2000; Carrano & Hutchinson, 2002) and its typical origin, although highly variable, is on the postero-lateral side of the postacetabular process of the ilium and proximal caudals (Dilkes, 2000). This muscle has various insertions in different birds. However, a small slip (*M. accessories semitendinosus*) is occasionally present and attaches to the popliteal region of the femur (Dilkes, 2000).

There is no evidence of the origin of *M. flexor tibialis externus* on the ilium of *A. piscator*. The reconstruction was made with its origin on the lateral surface of the postacetabular process of the ilium and its insertion on the medial surface of

the tibia, sharing a tendon with *M. flexor tibialis internus* 3, as in extant archosaurs (Carrano & Hutchinson, 2002).

As already mentioned, Fastnacht (2005) only referred to *M. flexor tibialis*, determining for *M. flexor tibialis externus* the same position as the origin of the heads of *M. flexor tibialis internus* (lateral surface of the postacetabular process of the ilium). Despite the fact that the position of the heads of *M. flexor tibialis internus* varies concerning their origins, which was not considered in the myological reconstruction of Fastnacht (2005), the origin of *M. flexor tibialis externus* in Crocodylia is close to the origin of *M. flexor tibialis internus* 2. Thus, the origin of this muscle in *A. piscator* was inferred to be in this area.

M. Adductor femoris

M. adductor femoris (ADD) has two heads in Crocodylia: *M. adductor femoris* 1 (ADD1) and *M. adductor femoris* 2 (ADD2), each with a separate origin on the lateral side of the ischium (Dilkes, 2000; Carrano & Hutchinson, 2002). In Aves these muscles are termed *M. puboischiofemoralis pars medialis* (PIFM) and *M. puboischiofemoralis pars lateralis* (PIFL), respectively, and their origin can also include the pubis (Dilkes, 2000). Insertion of these muscles is on the posterior surface of the femur (Dilkes, 2000; Carrano & Hutchinson, 2002). *M. adductor femoris* 1 and *M. puboischiofemoralis pars medialis* have their origin near the anterior tip of the ischium (Romer, 1923c; Carrano & Hutchinson, 2002). *M. adductor femoris* 2 and *M. puboischiofemoralis pars lateralis* originate on the same area, though more anteroventrally placed in Aves. In Crocodylia *M. adductor femoris* 2 is separated from *M. adductor femoris* 1 by *M. puboischiofemoralis externus* 3 (Hutchinson, 2001a). According to Carrano & Hutchinson (2002), the displacement of the origin of the *M. puboischiofemoralis pars lateralis* in Aves might be related to the reduction of the obturator process and the movement of *M. iliotrochantericus* towards the lateral surface of the ischium. *M. adductor femoris* 2, such as *M. adductor femoris* 1, runs ventrolaterally to insert on the second (lateral) rugosity of the posterior side of the femur (Carrano & Hutchinson, 2002).

Once *Mm. adductores femores* shared close areas of origin and insertion, they were reconstructed sharing the same spot for insertion in *Anhanguera piscator*. Moreover, no evidence of the obturator process is observed, which might lead to the displacement of the origin of these muscles as in Aves. Thus, *Mm. adductores femores* were reconstructed with their origin on the lateral surface of the ischium, near the anterior tip and anteroventrally positioned, being inserted on the medial shaft of the femur with a displacement to its posterior region.

Fastnacht (2005) did not determine the origin of these muscles. Their insertion is reconstructed at the medial surface of the diaphysis, but without outlining the extension of the adductor crest. Bennett (2001) argued that scars at the ischial symphysis and the caudal margin of the ischium would be associated with the origin of pelvic muscles even though not specifically mentioning any particular muscle. The author also highlighted the presence of a long and slender scar

beginning half way down the medial surface of the femoral diaphysis, and extending to the medial surface of the distal half, which forms the adductor crest. Both studies confirm the medial position of the insertion of these muscles at the femoral diaphysis.

M. puboischiofemoralis externus

M. puboischiofemoralis externus (PIFE) has three heads in Crocodylia: *M. puboischiofemoralis externus* 1 (PIFE1), *M. puboischiofemoralis externus* 2 (PIFE2) and *M. puboischiofemoralis externus* 3 (PIFE3), and two in Aves: *M. obturatorius medialis* (OM) and *M. obturatorius lateralis* (OL). Hutchinson (2001a) and Hutchinson & Gatesy (2000) state that the tripartite division of *M. puboischiofemoralis externus* in Crocodylia is plesiomorphic for archosaurs based on the presence of a long pubic apron in these taxa (Carrano & Hutchinson, 2002). The origin of *M. puboischiofemoralis externus* 1 in Crocodylia is the antero-medial surface of the pubic shaft and apron (Romer, 1923c; Carrano & Hutchinson, 2002; Hutchinson, 2002). In Aves, its homologue (*M. obturatorius lateralis*) was reduced owing to the loss of the pubic symphysis, with its origin on the proximo-lateral surface of the pubis (Hutchinson, 2002). The origin of *M. puboischiofemoralis externus* 2 in Crocodylia is the postero-medial surface of the pubic shaft and apron (Romer, 1923c; Carrano & Hutchinson, 2002; Hutchinson, 2002). With the loss of the pubic symphysis in Aves, its homologue (*M. obturatorius medialis*) moved posteriorly onto the pubo-ischiadic membrane (Hutchinson, 2002). *M. puboischiofemoralis externus* 3 originates from the obturator process of the ischium in Crocodylia, between *Mm. adductores femores* 1-2 origins (Romer, 1923c; Carrano & Hutchinson, 2002; Hutchinson, 2002). The retention of this structure suggests the presence of this muscle (Hutchinson, 2001a), which in Aves is reduced or lost (Hutchinson, 2001a,b). In archosaurs, the insertion of these heads is in the greater trochanter (Hutchinson, 2001b).

As in Crocodylia, *Anhanguera piscator* does not present a pubic symphysis, and therefore *Mm. puboischiofemoralis externi* 1-2 has a similar condition to this group, with the insertion at the greater trochanter. *A. piscator* does not have an obturator process, but an obturator foramen in the medial pubis (Kellner & Tomida, 2000). Because this process is also absent in Aves, *M. puboischiofemoralis externus* 3 was inferred to be absent in *A. piscator*.

Fastnacht (2005) placed the origin of *M. puboischiofemoralis externus* on the ventral surface of the pubis in dsungaripterids, and its insertion in the greater trochanter of the femur. Bennett (2001) associated the insertion of this muscle on the lesser trochanter in *Pteranodon*. However, the reconstruction of the relationships determined by the topology of the phylogenetic tree of Hutchinson (2001b) that presented the femoral trochanter evolution in Archosauria showed that the attachment spot for the insertion of *M. puboischiofemoralis externus* 1 is the greater trochanter. Therefore, we followed Hutchinson (2001b) and Fastnacht (2005).

M. ischiotrochantericus

M. ischiotrochantericus (ISTR) in Crocodylia originates from the medial surface of the ischium (Romer, 1923c; Carrano & Hutchinson, 2002; Hutchinson, 2001a, 2002), whereas in Aves its homologue, *M. ischiofemoralis* (ISF), had shifted its origin onto the lateral surface of the ischium and to the ilioischial membrane with the loss of the ischial symphysis in this group (Carrano & Hutchinson, 2002; Hutchinson, 2001a, 2002). Insertion is on the posterior femur in Crocodylia, and on the proximo-lateral surface of the femur in Aves (Dilkes, 2000).

Anhanguera piscator presents an ischial symphysis and, thus, *M. ischiotrochantericus* has its origin reconstructed at the medial surface of the ischium, without the lateral displacement observed in Aves (see Dilkes, 2000), being inserted on the proximo-lateral surface of the femur which is an area of muscle insertion to other muscles.

Bennett (2001) called the attention to a series of scars on the ischial symphysis of *Pteranodon* probably related to muscle insertion, as well as to the caudal border of the ischium being rough. Once an ischial symphysis is also present in *Anhanguera piscator* and based on the abovementioned scars position at this area in *Pteranodon*, the laterally displaced muscle spot of Aves is not followed.

M. caudofemoralis

M. caudofemoralis (CF) has two heads in Crocodylia: *M. caudofemoralis brevis* (CFB) and *M. caudofemoralis longus* (CFL). Their homologues in Aves are *Mm. caudofemorales pars pelvica* (CFP) and *pars caudalis* (CFC), respectively. *M. caudofemoralis brevis* and its avian homologue consist of a short head that arises from the ilium and the anterior caudals (Crocodylia) or just from the ilium (Aves), whereas *M. caudofemoralis longus* and its homologue comprise a long head that originate entirely from the posterior axial skeleton (Gatesy, 1990). Both *Mm. caudofemorales* are inserted onto the posterior surface of the femoral shaft, with *M. caudofemoralis longus* usually slightly distal and medial to *M. caudofemoralis brevis* (Carrano & Hutchinson, 2002).

According to Gatesy (1990), *M. caudofemoralis longus* has an important role on the femoral retraction during the locomotion (stance phase) of extant saurian reptiles, being considered the hip extensor. This muscle decreased

in importance for the locomotion of extant birds, with its homologue being consequently reduced. As stated by Gatesy (1990), the flexion/extension of patellar articulation has increased its relevance in avian locomotion, whereas the tail and the femoral fourth trochanter, which were the spots of insertion of these muscles, gradually decreased in size. Thus, it can be inferred that walking was primarily hip-driven for basal archosaurs and has changed to a knee-driven gait typical of Aves (Gatesy, 1990), which shows that this muscle influence the locomotion differently among many groups.

The presence of the fourth trochanter at the femur of *Anhanguera piscator* indicates the insertion of *Mm. caudofemorales*. As in Aves, *A. piscator* shows a reduced tail; it is therefore inferred that the origins of these muscles are on the lateral iliac surface (*M. caudofemoralis brevis*) and on the caudal vertebrae (*M. caudofemoralis longus*).

In *Pteranodon*, Bennett (2001) placed the insertion of *M. caudofemoralis* at the fourth trochanter, a large and very rugose tuberosity on the posterior to posteromedial surface of the femoral shaft, but without regarding its division. This placement corroborates the positioning of this muscle in *A. piscator*. *Pteranodon* also shows a short tail, a condition observed in pterodactyloids. This raises the possibility of assuming the division of this muscle in *Pteranodon* and other pterodactyloid pterosaurs, which have the same features of *Anhanguera piscator* (reduced tail, presence of femoral fourth trochanter).

The reconstructed muscles of the ventral group of *Anhanguera piscator* can be seen in Table 3. The reconstructed pelvic girdle muscles were integrated in the osteological model. Once the tail was not represented in the model, *Mm. caudofemorales* were not depicted in Figure 2, but their spots of origin and insertion can be seen in Table 3.

CONCLUSIONS

In this study we performed for the first time the myological reconstruction of the pelvic girdle of *Anhanguera piscator* using the Extant Phylogenetic Bracket (EPB) method. The EPB proved to be a more accurate method in defining muscle attachments and reducing speculation by correlating the osteological structures of the fossil form with that of extant archosaurs (Aves and Crocodylia). Moreover, many muscles with divisions in both extant taxa imply that

Table 3. Muscles of *Anhanguera piscator* reconstructed (Ventral Group), with the levels of inference in parentheses.

Group/Muscle	Origin	Insertion
<i>M. puboischiofemorlis externus</i>		
<i>M. puboischiofemorlis externus</i> 1	antero-medial surface of the pubic shaft and apron (I')	greater trochanter of the femur (I)
<i>M. puboischiofemorlis externus</i> 2	postero-medial surface of the pubic shaft and apron (I')	greater trochanter of the femur (I)
<i>M. puboischiofemorlis externus</i> 3	inferred absent	inferred absent
<i>M. ischiotrochantericus</i>	medial surface of the ischium (I')	proximo-lateral surface of the femur (I')
<i>M. caudofemoralis</i>		
<i>M. caudofemoralis brevis</i>	lateral iliac surface (I')	fourth trochanter at the femur (I')
<i>M. caudofemoralis longus</i>	caudal vertebrae (I')	fourth trochanter at the femur (I')

the same divisions were represented in *A. piscator*. However, these muscles were considered only in a general way in pterosaur literature, without discussion of muscle divisions. The method allowed us to consider the division of muscles, such as Mm. *iliotibiales* 1-3, M. *iliofemoralis externus*/M. *iliotrochantericus caudalis*, and Mm. *flexores tibiales internus* 1-4. A more complete muscular reconstruction in this sense would lead to a better understanding on the stance and locomotion of *A. piscator*. This kind of approach permits a more confident mapping of muscle attachments, and as a consequence, the reconstruction of a more accurate musculoskeletal complex that leads to the formulation of well-based biomechanical assumptions.

Based on this reconstruction it was possible to test the hypothesis on the optimal stance of *Anhanguera piscator* and state that this species had a quadrupedal mode of locomotion when grounded rather than an upright stance (Costa *et al.*, 2013). Such a biomechanical approach could only be accomplished by testing the optimal position of each hind limb muscle in a limited range of motion when the muscle was previously outlined. This was the first time a quadrupedal stance for a pterosaur was tested using this methodology. This method can thus be applied to other pterosaurs including giant species (e.g. Kellner *et al.*, 2013) in order to shed light on other questions regarding the biomechanics of this group.

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REFERENCES

- Bates, K.T. & Schachner, E.R. 2012. Disparity and convergence in bipedal archosaur locomotion. *Journal of the Royal Society Interface*, **9**:1339-1353. doi: 10.1098/rsif.2011.0687
- Bates, K.T.; Maidment, S.C.R.; Allen, V. & Barrett, P.M. 2012. Computational modeling of locomotor muscle moment arms in the basal dinosaur *Lesothosaurus diagnosticus*: assessing convergence between birds and basal ornithischians. *Journal of Anatomy*, **220**:212-232. doi: 10.1111/j.1469-7580.2011.01469.x
- Bennett, S.C. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description of osteology. *Palaeontographica Abteilung A*, **260**:1-112.
- Bennett, S.C. 2003. Morphological evolution of the pectoral girdle of pterosaurs: myology and function. In: E. Buffetaut & J-M. Mazin (eds.) *Evolution and Palaeobiology of Pterosaurs*, Geological Society of London, p. 191-215.
- Benton, M.J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society B*, **354**:1423-1446. doi: 10.1098/rstb.1999.0489
- Bryant, H.N. & Russell, A.P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society B*, **337**:405-418. doi: 10.1098/rstb.1992.0117
- Carrano, M.T. & Hutchinson, J.R. 2002. The pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology*, **253**:207-228. doi: 10.1002/jmor.10018
- Coombs, W.P. Jr. 1979. Osteology and myology of the hindlimb in the Ankylosauria (Reptilia, Ornithischia). *Journal of Paleontology*, **53**:666-684.
- Cooper, M.R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museum of Southern Rhodesia B*, **6**:689-840.
- Costa, F.R.; Rocha-Barbosa, O. & Kellner, A.W.A. 2010. Stance Biomechanics of *Anhanguera piscator* Kellner & Tomida, 2000 (Pterosauria, Pterodactyloidea) Using Tridimensional Virtual Animation. *Acta Geoscientica Sinica*, **31**:15-16.
- Costa, F.R.; Rocha-Barbosa, O. & Kellner, A.W.A. 2013. A biomechanical approach on the optimal stance of *Anhanguera piscator* (Pterodactyloidea) and its implications for pterosaur gait on land. *Historical Biology*. doi: 10.1080/08912963.2013.807253
- Dilkes, D.W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Transaction of the Royal Society of Edinburgh - Earth Sciences*, **90**:87-125. doi: 10.1017/s0263593300007185
- Fastnacht, M. 2005. The first dsungaripterid pterosaur from the Kimmeridgian of Germany and the biomechanics of pterosaur long bones. *Acta Palaeontologica Polonica*, **50**:273-288.
- Fürbringer, M. 1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift für Naturwissenschaft*, **34**:215-718.
- Galton, P.M. 1969. The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia). *Postilla*, **131**:1-64.
- Gatesy, S.M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology*, **16**:170-186.
- Gauthier, J. 1984. *A cladistic analysis of the higher systematic categories of the Diapsida*. University of California, Ph.D. thesis, 564 p.
- Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, **8**:1-55.
- Grillo, O.N. & Azevedo, S.A.K. 2011. Pelvic and hind limb musculature of *Staurikosaurus pricei* (Dinosauria: Saurischia). *Anais da Academia Brasileira de Ciências*, **83**:73-98. doi: 10.1590/s0001-37652011000100005
- Hutchinson, J.R. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society*, **131**:123-168. doi: 10.1111/j.1096-3642.2001.tb01313.x
- Hutchinson, J.R. 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society*, **131**:169-197. doi: 10.1111/j.1096-3642.2001.tb01314.x
- Hutchinson, J.R. 2002. The evolution of hindlimb tendons and muscles on the line to crown-group birds. *Comparative Biochemistry and Physiology Part A*, **133**:1051-1086. doi: 10.1016/s1095-6433(02)00158-7

- Hutchinson, J.R. 2012. On the inference of function from structure using biomechanical modeling and simulation of extinct organisms. *Biology Letters*, **8**:115-118. doi: 10.1098/rsbl.2011.0399
- Hutchinson, J.R. & Gatesy, S.M. 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology*, **26**:734-751. doi: 10.1666/0094-8373(2000)026<0734:AAATEO>2.0.CO;2
- Hutchinson, J.R.; Anderson, F.C.; Blemker, S.S. & Delp, S.L. 2005. Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: implications for stance, gait, and speed. *Paleobiology*, **31**:676-701. doi: 10.1666/0094-8373(2005)031[0676:AOH MMA]2.0.CO;2
- Kellner, A.W.A. 1996. Reinterpretation of a remarkably well preserved pterosaur soft tissue from the early Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, **16**:718-722. doi: 10.1080/02724634.1996.10011360
- Kellner, A.W.A. 2004. The ankle structure of two pterodactyloid pterosaurs from the Santana Formation (Lower Cretaceous), Brazil. *Bulletin of the American Museum of Natural History*, **285**:25-35. doi: 10.1206/0003-0090(2004)285<0025:c>2.0.co;2
- Kellner, A.W.A. 2010. Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with the description of two new species. *Anais da Academia Brasileira de Ciências*, **82**:1063-1084. doi: 10.1590/s0001-37652010000400025
- Kellner, A.W.A.; Campos, D.A.; Sayão, J.M.; Saraiva, A.A.F.; Rodrigues, T.; Oliveira, G.; Cruz, L.A.; Costa, F.R.; Silva, H.P. & Ferreira, J.S. 2013. The largest flying reptile from Gondwana: a new specimen of *Tropeognathus* cf. *T. mesembrinus* Wellnhofer, 1987 (Pterodactyloidea, Anhangueridae) and other large pterosaurs from the Romualdo Formation, Lower Cretaceous, Brazil. *Anais da Academia Brasileira de Ciências*, **85**:113-135. doi: 10.1590/s0001-37652013000100009
- Kellner, A.W.A. & Tomida, Y. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), northeastern Brazil. *National Science Museum Monographs*, **17**:1-135.
- Kripp, D. von. 1943. Ein Lebensbild von *Pteranodon ingens* auf flugtechnischer Grundlage. *Nova Acta Leopoldina, Neue Folge*, **12**:16-32.
- Langer, M.C. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *PaleoBios*, **23**:1-39.
- Maidment, S.C.R. & Barrett, P.M. 2011. The locomotor musculature of basal ornithischian dinosaurs. *Journal of Vertebrate Paleontology*, **31**:1265-1291. doi:10.1080/02724634.2011.606857
- Milner, R.W. 1925. The pectoral limb of *Eryops* and other primitive tetrapods. *Bulletin of the American Museum of Natural History*, **51**:145-312.
- Nesbitt, S.J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**:1-292. doi:10.1206/352.1
- Norell, M.A.; Clark, J.M. & Makovicky, P.J. 2001. Phylogenetic relationships among coelurosaurian theropods. In: J. Gauthier & L.F. Gall (eds.) *New perspectives on the origin and early evolution of birds*, proceedings of the International Symposium in Honor of John H. Ostrom, Peabody Museum of Natural History/Yale University, p. 49-67.
- Novas, F.E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology*, **16**:723-741. doi:10.1080/02724634.1996.10011361
- Otero, A. & Vizcaíno, S.F. 2008. Hindlimb musculature and function of *Neuquensaurus australis* Lydekker (Sauropoda: Titanosauria). *Ameghiniana*, **45**:333-348. doi:10.4202/app.2009.0099
- Padian, K. 1983. A functional analysis of flying and walking in pterosaurs. *Paleobiology*, **9**:218-239.
- Padian, K. 1984. The origin of pterosaurs. In: SYMPOSIUM ON MESOZOIC TERRESTRIAL ECOSYSTEMS, 3, 1984. *Proceedings*, Tübingen, Attempto Verlag, p.163-168.
- Romer, A.S. 1923a. The pelvic musculature of saurischian dinosaurs. *Bulletin of the American Museum of Natural History*, **48**:605-617.
- Romer, A.S. 1923b. The ilium in dinosaurs and birds. *Bulletin of the American Museum of Natural History*, **48**:141-145.
- Romer, A.S. 1923c. The pelvic musculature of ornithischian dinosaurs. *Bulletin of the American Museum of Natural History*, **48**:605-617.
- Romer, A.S. 1927. The pelvis musculature of ornithischian dinosaurs. *Acta Zoologica*, **8**:225-275.
- Rowe, T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other reptilian. *Journal of Morphology*, **189**:327-346. doi: 10.1002/jmor.1051890310
- Rowe, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, **9**:125-136. doi:10.1080/02724634.1989.10011748
- Wellnhofer, P. 1978. Pterosauria. In: P. Wellnhofer (ed.) *Handbuch der Palaeoherpetologie Part 19*, Gustav Fischer, p. 1-82.
- Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. London, Salamander, 192 p.
- Witmer, L.M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: J.J. Thomason (ed.) *Functional Morphology in Vertebrate Paleontology*, Cambridge University Press, p. 19-33.

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