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The pelvic and hindlimb myology of the basal titanosaur *Epachthosaurus sciuttoi* (Sauropoda: Titanosauria)

Lucio M. Ibiricu[a], Rubén D. Martínez[b] and Gabriel A. Casal[b]

[a]Instituto Patagónico de Geología y Paleontología (IPGP), CCT CENPAT-CONICET, Chubut, Argentina; [b]Laboratorio de Paleontologia de Vertebrados, Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina

ABSTRACT

Epachthosaurus sciuttoi is a basal titanosaur from the early Late Cretaceous of central Patagonia, Argentina. Here, we present the reconstruction of the pelvic and hindlimb musculature of this titanosaur, based on the soft tissue data of extant archosaurs. The majority of the pelvic, hindlimb and pes muscles are within a decisive and positive level of inference. Comparison with a derived titanosaur such as *Neuquensaurus*, shows several morphological differences which are directly related with the muscular attachments, supporting differences about the musculature arrangement between these two sauropod dinosaurs. For example, the anterior projection of the preacetabular process of *Neuquensaurus* extends more laterally, whereas in *Epachthosaurus* the preacetabular process is laterally less extended. The fibular lateral tuberosity in *Neuquensaurus* is closer to the fibular head than it is in *Epachthosaurus*. The femoral fourth trochanter in *Neuquensaurus* is closer to the femoral head than it is in *Epachthosaurus*. Likewise, the caudofemoralis longus may have extended more distally in the tail in *Epachthosaurus*. These differences, among others, may have influenced the muscular arrangement and, therefore, the locomotor function abilities of these titanosaurs. Finally, this myological description of *Epachthosaurus*, where twenty one muscles were reconstructed, constitutes useful data for researches interested in functional anatomy.

Introduction

The titanosaurians are the most abundant, morphologically diverse and geographically widespread group of sauropod dinosaurs. The record of this group is present on all continents (Cerda et al. 2012), however, in South America the Titanosauria are by far the most abundant herbivorous dinosaurs, and include more than 40 genera (González Riga 2011; Faria et al. 2015). Continental deposits of the Bajo Barreal Formation (Early Cenomanian - Late Turonian, Casal et al. 2016) exposed in central Patagonia, Argentina preserve a rich and important fossil record (Martínez et al. 1986; 2016; Martínez & Novas 2006; Ibiricu et al. 2013a, Ibiricu et al. 2015; among others).A well preserved, and articulated skeleton of *Epachthosaurus sciuttoi* was found in this Cretaceous unit, along with other dinosaur specimens. *Epachthosaurus* was briefly described by Martínez et al. (1988, 1989) supporting its inclusion within Titanosauria. Consequently, Martínez et al. (2004) provide a detailed description of *E. sciuttoi*.

The study of soft tissue in extinct taxa is always a difficult task, particularly in sauropod dinosaurs, because the absence of proportional extant forms and biomechanics correlatives. Nevertheless, the 'Extant Phylogenetic Bracket' (Witmer 1995, 1997) had been an interesting and frequently used methodology when reconstructing soft tissue of extinct dinosaurs (Hutchinson and Gatesy 2000; Hutchinson 2002; Jasinoski et al. 2006; O' Connor 2006; Schwarz-Wings 2009; Sander et al. 2011; among others). The musculoskeletall system in

extant crocodylians and birds is well documented (McGowan 1979; Rowe 1986; Meers 2003; Reilly and Blob 2003; Gangl et al. 2004; Carril et al. 2014).

Although, Romer (1923) was the first to analyze the pelvic musculature in *Camarasaurus* and all saurischians, Borsuk-Bialynicka (1977) was the first author which focused in the appendicular musculature in titanosaurs (i.e. *Opisthocoelicaudia*). Nevertheless, the only comprehensive study of musculature and functional morphology in a South American titanosaurian to date is that of Otero and Vizcaino (2008). These authors performed a hindlimb musculature reconstruction in order to interpret appendicular muscle arrangements and function in *Neuquensaurus australis* (Lydekker 1893) and its implications within saltasaurines. This titanosaur, is one of the most derived forms within Titanosauria (Wilson 2002; Salgado and Bonaparte 2007). On the other hand, *Epachthosaurus* is one of the basal forms within the group (Salgado et al. 1997; Salgado and Bonaparte 2007). This situation is particularly interesting, because it establishes an opportunity to evaluate the musculature within two different evolutionary stages. An interpretative study of the musculature system of *Epachthosaurus* constitutes an excellent opportunity to gain insight into the morphology and function of the appendicular bones within Titanosauria. Although *Epachthosaurus* is a medium-size titanosaur, the increase in body size observed in sauropods entailed an evolutionary change to quadrupedal posture from the early

CONTACT Lucio M. Ibiricu ✉ ibiricu@cenpat-conicet.gob.ar

bipedality in dinosaurs (Sereno 1997) as well as a reorganization of the body plan (Bonnan 2003). Therefore, the musculature may have been played an important role in this reorganization (Salgado and García 2002; Ibiricu et al. 2013b). Along these lines, a detailed analysis of appendicular skeletal features and bony soft tissue correlates in *Epachthosaurus* will enhance our knowledge of the paleobiology and comparative morphofunctional implications of this sauropod dinosaur. Finally, this study will be a useful source of information for different other studies regarding the functional anatomy, morphology and biomechanical titanosaurs modelling.

Institutional abbreviations

UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco Colección de Paleovertebrados, Comodoro Rivadavia, Argentina.

Specimens examined

Epachthosaurus sciuttoi (Lectotype), UNPSJB-PV 920 is represented by: an articulated skeleton lacking the skull, neck, four anterior dorsal vertebrae and distal caudal vertebrae. The pelvic girdle and appendicular bones, focus of this study, include: ilium, ischium, pubis (pelvic bones recovered slightly displaced but articulated, but see below), femora, tibia, fibula and metatarsals (the pes are complete and articulated). *Neuquensaurus australis*, a Late Cretaceous sauropod, is one of the most well preserved sauropods, including both the axial and appendicular skeleton (Salgado et al. 2005; Otero 2010), condition shared with *Epachthosaurus*. Because *Neuquensaurus* represents one of the better preserved and is among the most derived titanosaur, this sauropod is currently used in this analysis, based on the study of Otero and Vizcaíno (2008) as well as it was examined directly for one of us.

Materials and methods

Research on soft tissues in extinct taxa has been the focus on an increasing number of studies in the, particularly, last decade. (Tsuihiji 2004; Wedel 2009; Liparini and Schultz 2013; Ibiricu et al. 2017; among other). However, the inference and interpretation of soft tissues in sauropods is particularly difficult, in part, because of the absence of extant analogous organisms. Witmer (1995, 1997)) proposed the Extant Phylogenetic Bracket (EPB) be applied in non-avian dinosaurs, based on anatomical comparison of homologous structures. This methodology works for non-avian dinosaurs with the two extant archosaurian clades [i.e. Crocodylia (which retains many ancestral archosaurian traits) and Aves = Neornithes of some authors (which retains many
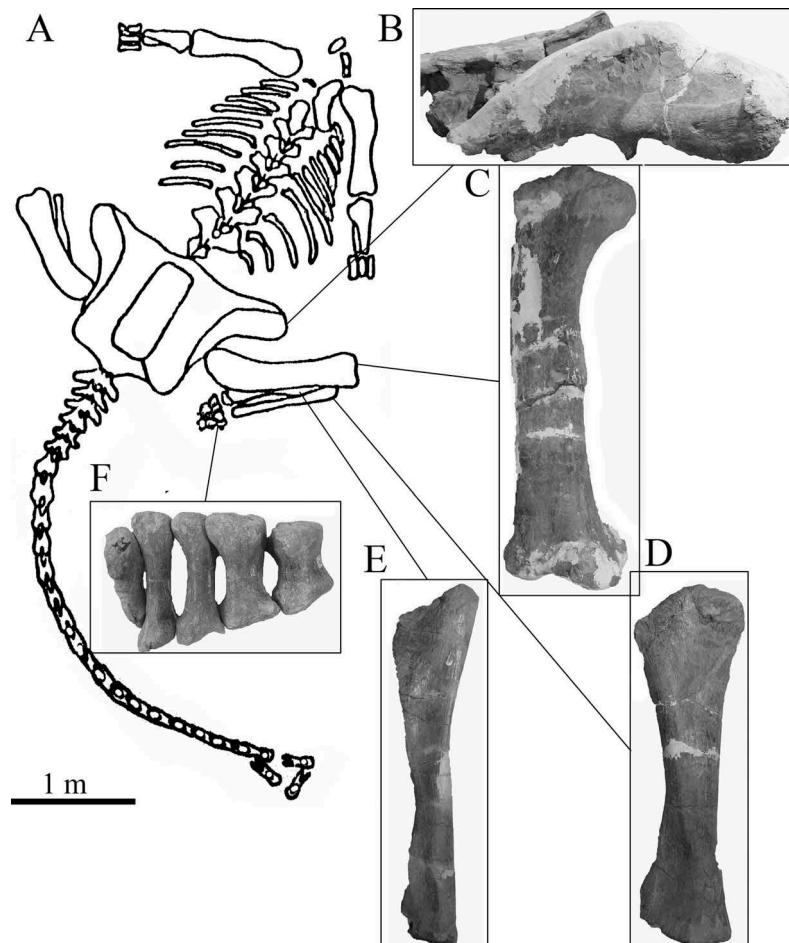

Figure 1. (A) Skeletal disposition, in dorsal view, of *Epachthosaurus sciuttoi* (UNPSJB-PV 920, modified from Martínez et al. 2004), (B) lateral view of the right ilium, (C) posterior view of the right femur, (D) medial view of the right tibia, (E) medial view of the right fibula, (F) lateral view of the right pes.
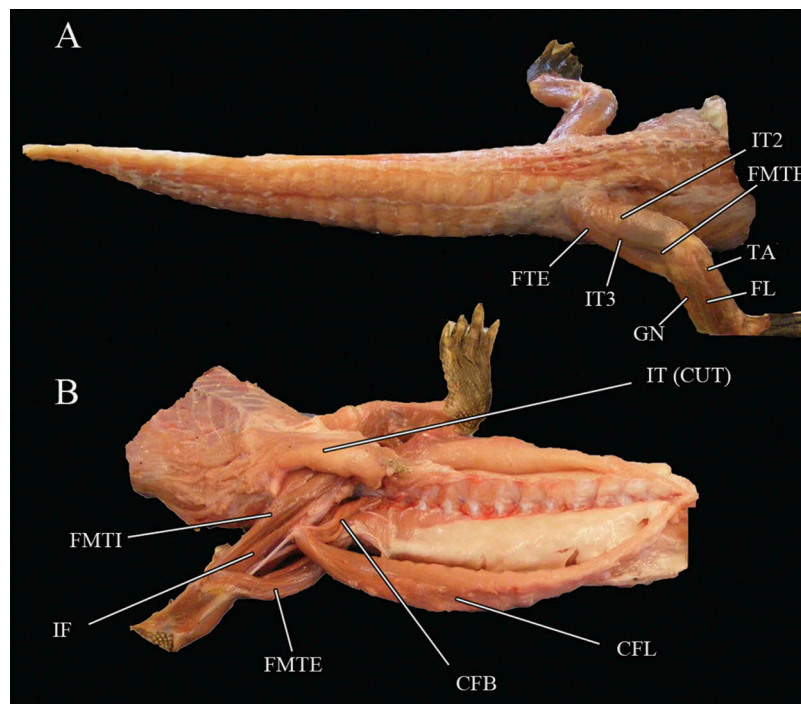
Figure 2. (A) Dissection of *A. mississippiensis* (American Alligator, taken/modified from Ibiricu et al. 2013b) showing some selected muscles (A) in dorsolateral view, (B) in ventral view. *Abbreviations*: CFB, M. caudofemoralis brevis; CFL, M. caudofemoralis longus; FDL, M. flexor digitorum longus; FL, M. fibularis longus; FTE, M. flexor tibialis externus; FTI, M. femorotibialis internus; GN, M. gastrocnemius; IF, M. iliofemoralis; ILFB, M. iliofibularis; IT, M. iliotibialis (IT2, IT3, see text).

derived traits)] as an anatomical framework for non-avian dinosaurs. This frequently employed method is used in this study (see for more detail about EPB and its applications to Witmer 1995). The bones of *E. sciuttoi* were observed and described first hand in its respective collection. The musculature terminology, bony correlates, homology, origin and insertion described follows that of Romer (1923); Hutchinson (2001a, 2001b); Carrano and Hutchinson (2002); and Otero and Vizcaíno (2008). The soft tissue data for Crocodylia was taken from Wilhite (2003); Reilly et al. (2005); Otero et al. (2010) and Klinkhamer et al. (2017). Additionally, we compiled data from previous dissection (taken from Ibiricu et al. 2013b; see Figure 2). Although the information recovered in these dissections was focused in the analysis of the caudal musculature, it is used as support of the present study. The Avian information was taken directly from literature review in order to place the muscles studied in an evolutionary framework (e.g. McGowan 1979; Rowe 1986; Gatesy 1999; Gangl et al. 2004). We also referred to previous works on basal dinosaurs (Grillo and Acevedo 2011), sauropod no-titanosaurs (Wilhite 2003), ornithischians (Dilkes 2000; Maidment and Barrett 2011), and basal archosaurs (Schachner et al. 2011; Liparini and Schultz 2013).The orientation of the limb elements differ in the extant archosaurs and in non-avian dinosaurs. Thus, the morphologic modifications of the avian forelimb, in other words, into the wings, are a challenge for musculature reconstructions (e.g. absence of some muscles) of a quadrupedal titanosaur. The pelvis (ilium) and hindlimb bones (femur, tibia and fibula, including the pes) selected are those, mainly, belonging to the right side of the *Epachthosaurus*. The skeleton was found in tuffaceous sandstone and its left side is slightly deformed. The ischium and pubis are excluded in this study because both appendicular elements are partially preserved and, therefore, origin and/or insertion of the musculature would be speculative and cannot be discerned

with exactitude. The muscles selected for analysis in this study are summarized in Table 1.

Osteological correlates

Soft tissue is rarely preserved in the fossil record. However, the bones and specifically some of the structures present, allow the identification of the presence of the soft tissue (e.g. tendons, ligaments, and muscles, see Jasinoski et al. 2006; Petermann and Sander 2013). Indicators of origin or insertion of muscles are preserved as: pits or rugose scars (tendinous or aponeurotic attachments); crest; smooth bone surfaces, striations (fleshy attachments) and ridges (fleshy attachments). Nevertheless, there is variable visibility in fossil bones depending on the morphology of the organism, in other words, more gracile individuals bear less visible bony correlates (Jasinoski et al. 2006). In addition, bones, particularly appendicular, exhibit several well marked rugosities, these traces on the bones may indicate the presence of cartilage, specifically close to or on the articular surfaces (see Holliday et al. 2010). In the selected bones analyzed in *Epachthosaurus*, several of these osteological correlates are clearly identifiable (Figure 3) and are observed as bony indicators of the presence of pelvic and appendicular musculature.

Results and description

Muscular reconstruction in Epachthosaurus

Superficial dorsal muscles of the upper hindlimb

M. Iliotibialis (IT). In extant crocodylians the IT is a large and superficial muscle composed of three heads (IT1, IT2, IT3). The origin, via fleshy attachment, of these heads is alongside of the dorsal margin of the ilium. The three muscular heads insert, via a

Table 1. Selected muscles, homologies in extant archosaurs (based on Carrano and Hutchinson 2002) and muscles, origin and insertion inferred as present in *Epachthosaurus sciuttoi*. *Abbreviations*: in, insertion; or, origin.

Crocodylia (Muscle)	Aves (Muscle)	*E. sciuttoi* (inferred)	Levels
Iliotibialis 1	Iliotibialis cranialis	Iliotibialis 1 (IT1)	
Iliotibialis 2	Iliotibialis lateralis	Iliotibialis 2 (IT2)	or: LI/in: LI
Iliotibialis 3	Iliotibialis lateralis	Iliotibialis 3 (IT3)	
Iliofemoralis	Iliofemoralis externus Iliotrochantericus caudalis	Iliofemoralis (IF)	or: LI'/in: LI'
Flexor tibialis externus	Flexor cruris lateralis pars pelvica	Flexor tibialis externus (FTE)	or: LI/in: LI'
Iliofibularis	Iliofibularis	Iliofibularis (ILFB)	or: LI'/in: LI
Caudofemoralis brevis	Caudofemoralis pars pelvica	Caudofemoralis brevis (CFB)	or: LI/in: LI
Caudofemoralis longus	Caudofemoralis pars caudalis	Caudofemoralis longus (CFL)	or: LI/in: LI
Femorotibialis externus	Femorotibialis lateralis	Femorotibialis (FMT)	or: LI'/in: LI
Femorotibialis internus	Femorotibialis medialis/ intermedius		
Gastrocnemius externus	Gastrocnemii pars lateralis intermedia	Gastrocnemius (GN)	or: LI'/in: LI'
Gastrocnemius internus	Gastrocnemius pars medialis		
Tibialis anterior	Tibialis cranialis	Tibialis anterior (TA)	or: LI'/in: LI
Fibularis (peroneus) longus & brevis	Fibularis longus & brevis	Fibularis longus (FL) & brevis (FB)	or: LI/in: LI
Extensor digitorum longus	Extensor digitorum longus	Extensor digitorum longus (EDL)	or: LI'/in: LI
Extensor digitorum brevis	Absent	Extensor digitorum brevis (EDB)	or: LII/in: LII
Extensor hallucis longus	Extensor hallucis longus	Extensor hallucis longus (EHL)	or: LI/in: LI'
Flexor hallucis longus	Flexor hallucis longus	Flexor hallucis longus (FHL)	or: LI'/in: LII'
Flexor digitorum brevis	Absent	Flexor digitorum brevis (FDB)	or: LII'/in: LII'
Flexor digitorum longus	Flexor digitorum longus	Flexor digitorum longus (FDL)	or: LI'/in: LI'
Fibularis longus	Fibularis longus	Fibularis longus (FL)	or: LI/in: LI
Fibularis brevis	Fibularis brevis	Fibularis brevis (FB)	or: LI/in: LI
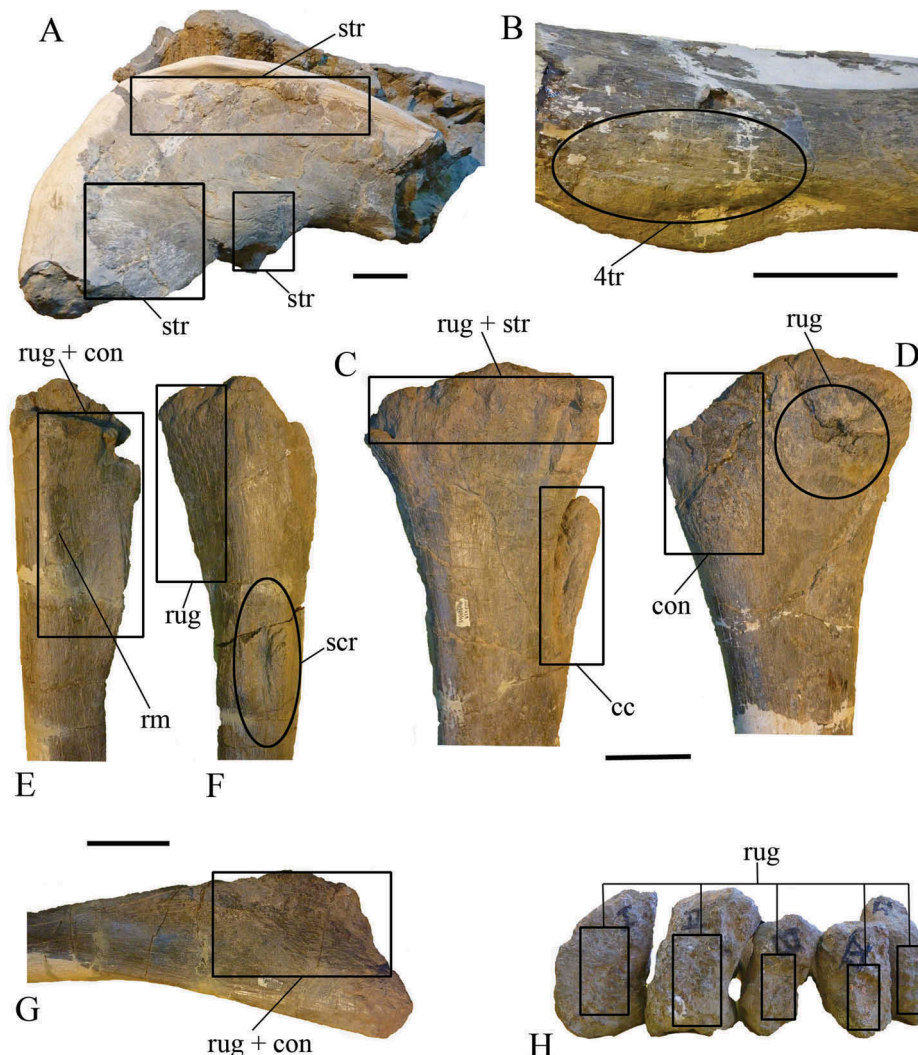
Figure 3. Detailed bony correlates (morphological structures associated to the soft tissue) of selected bones of *E. sciuttoi*. (A) ilium in lateral view, (B) femur in medial view, (C) tibia in lateral view, (D) tibia in medial view, (E) fibula in posterior view,(F) fibula in lateral view, (G) fibula distal end in medial view, (H) pes in dorsal view. Scale equals 10 cm. *Abbreviations*: 4tr, fourth trochanter; cc, cnemial crest; con, concavity; rm, rim; rug, rugosities; scr, scar; str, striations.
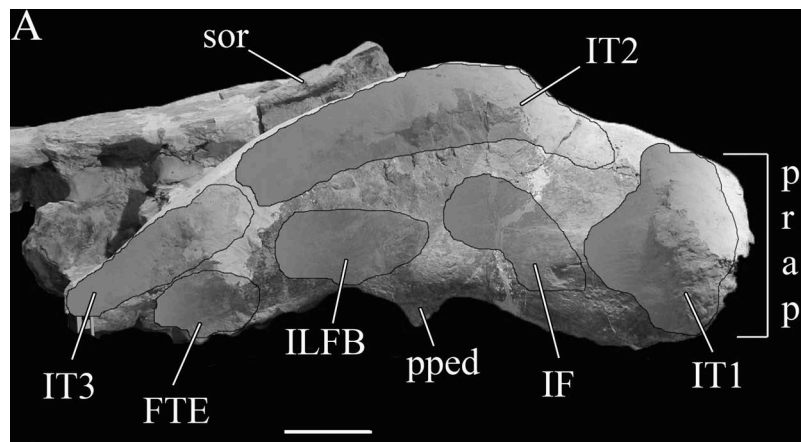
Figure 4. Ilium of *E. sciuttoi* in lateral view. Scale equals 10 cm. *Abbreviations*: FTE, M. flexor tibialis externus, IF, M. iliofemoralis, ILFB, M. iliofibularis, IT, M. iliotibialis, pap, postaetabular process, pped, pubic penduncle, prap, preacetabular process, sor, supraspinous rod. Note: the capitalized abbreviations refer to muscles and the lowercased abbreviations to morphological elements in this as well as in all figures.
the capitalized abbreviations refer to muscles and the lowercased abbreviations to morphological elements in this as well as in all figures.

common extensor tendon, onto the cnemial crest of the tibia. In extant birds, the IT 'complex', as well as crocodylians, also split in three muscular heads. The origin in birds is in the preacetabular process and acetabulum, whereas its insertion is onto the cnemial crest.

In *Epachthosaurus* there is not a clear division of the origin IT heads, therefore it is not possible to discriminate, with accuracy, the origin and division of the muscular heads on the ilium. However, a series of well-marked striations are present on the preserved portion of the dorsal border (anteroposteriorly directed) of the ilium. This suggest the site of a fleshy origin of the tripartite superficial IT, as observed in crocodylians (Figure 4). The insertion of these three heads in living archosaurs, is via a common extensor tendon, probably together with the M. ambiens and Mm. femorotibiales (see Otero and Vizcaíno 2008). Therefore, the robust and rugose cnemial crest observed in *Epachthosaurus* may have been the site of insertion for the IT.

M. Iliofibularis (ILFB). The ILFB in crocodylians arises from the lateral surface of the ilium, slightly ventral to the M. iliotibialis, specifically between IT 2 and IT3 (Liparini and Schultz 2013). This muscle, inserts in a well-defined scar in the lateral surface of the fibula via tendinous attachment. In Aves the ILFB originates from the postacetabular iliac crest (=ala postacetabularis illi, Lamas et al. 2014) whereas its insertion, by a tendon, is on the anterolateral surface of the fibular shaft (Otero and Vizcaíno 2008; Carril et al. 2014).

In the preserved portion of the ilium (postacetabular portion) of *Epachthosaurus*, a series of striations are observed in the lateral surface of the postacetabular process (Figure 4). These striations, well-marked and rugose, may have been the fleshy site of origin of the ILFB. In other words, in *Epachthosaurus*, the ILFB would have originated in the posterolateral portion of the ilium, ventrally to the IT 3. The insertion, as in crocodylians and extant birds, may have been in the fibula, specifically in the lateral tuberosity (Figure 5). This fibular structure is well developed in *Epachthosaurus* and it is located in the proximolateral aspect of the fibula (see above). The insertion was probably via a tendon as is the case for other sauropods (Wilhite 2003).
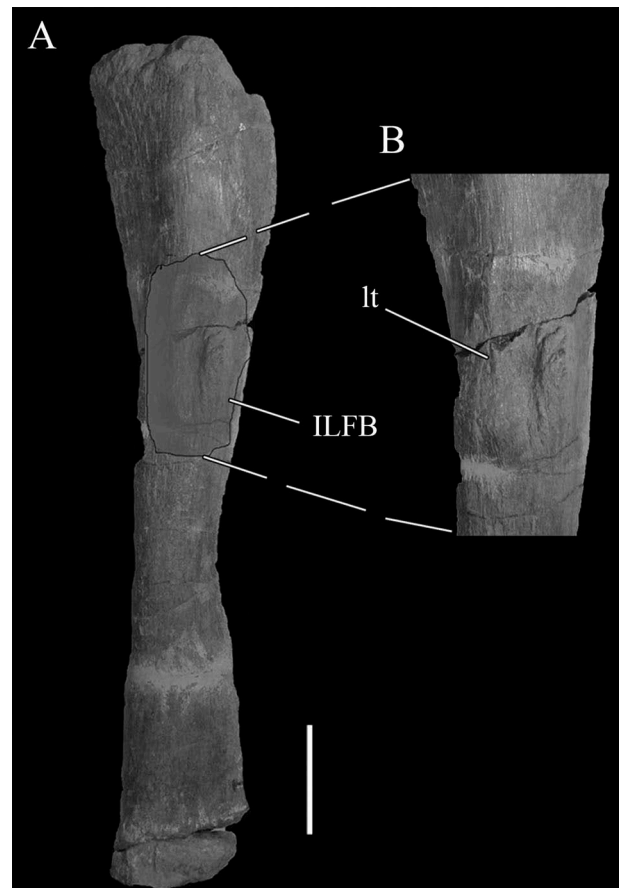

Figure 5. Fibula of *E. sciuttoi* in (A), in lateral view, (B) detailed of the lateral tuberosity (= lateral trochanter). Scale equals 10 cm. *Abbreviations*: ILFB, M. iliofibularis, lt, lateral tuberosity.

Deep dorsal muscles of the upper hindlimb

M. Iliofemoralis (IF)

In crocodylians the IF originates on the lateral surface of the ilium, dorsal to the acetabulum, and inserts onto a broad proximolateral surface of the femur. In extant birds, the IF is fragmented into the two muscular heads (M. iliotrochantericus caudalis and M. iliofemoralis externus; Carrano and

Hutchinson 2002). The M. iliofemoralis externus originates on the lateral surface of the ilium and inserts on the lateral femoral shaft. The M. iliotrochantericus caudalis arise from the lateral surface of the preacetabular ilium, whereas its insertion is onto the lesser trochanter.

The ilium of *Epachthosaurus* is anteroposteriorly and dorsoventrally concave (i.e., a rugose 'fossa-like' is present at the center of the ilium blade). This could represent a site of origin for the IF (Figure 4), and may have originated deep to the muscular head of the IT 2. On the other hand, if this muscle was divided into two heads, similar to extant birds, is an equivocal state, but possible (see Maidment and Barrett 2011). The IF probably inserts on the proximal surface of the femur. In this portion of the femur, there is a shallow sulcus, which could represent the insertion site of the IF.

M. Femorotibialis (FT)

The FT is composed of two distinct heads in crocodylians [M. femorotibialis externus (FMTE) and M. femorotibialis internus (FMTI)]. These heads are separated, proximately, for the M. iliofemoralis (Wilhite 2003). The smaller of these muscles, the FMTE, originates from the entire surface of the anterior femoral shaft (i.e. between the trochanteric region and distal condyles; Carrano and Hutchinson 2002). The FMTI arises from the posterior surface of the shaft, between the insertions of the M. iliofemoralis and M. ischiofemoralis. The intermuscular lines present on the femur shaft indicate the fleshly boundaries between these muscles (see Grillo and Azevedo 2011). The heads of the FT inserts, via a broad tendon, to the anterior surface of the tibia. In extant birds the FMTE corresponds to M. femorotibialis lateralis and the homologous of the FMTI is the M. femorotibialis medialis and intermedius, therefore, this muscle shows three heads (Liparini and Schultz 2013). However, in few ratites, this muscle is divided in four heads (Schachner et al. 2011). The FMT arises from the femoral shaft occupying most of this limb bone, whereas its insertion is via a tendon onto the cnemial crest as in crocodylians.

The FT may have originated in the lateral (i.e. Femorotibialis externus = FME) and the anteriomedial (i.e. Femorotibialis internus = FMI) femoral shaft, probably covering most of the femoral shaft (Figure 6). However, the femoral shaft of *Epachthosaurus* does not present an intermuscular line, contrary to derived titanosaurs, which is the putative site of origin and division of the two heads of the FT (see above in discussion). Therefore, the origin and number of muscular heads in *Epachthosaurus* remain unresolved, however, its presence in a phylogenetic framework is certainly unequivocal. On the other hand, the well-marked cnemial crest of *Epachthosaurus* tibia may have been the attachment
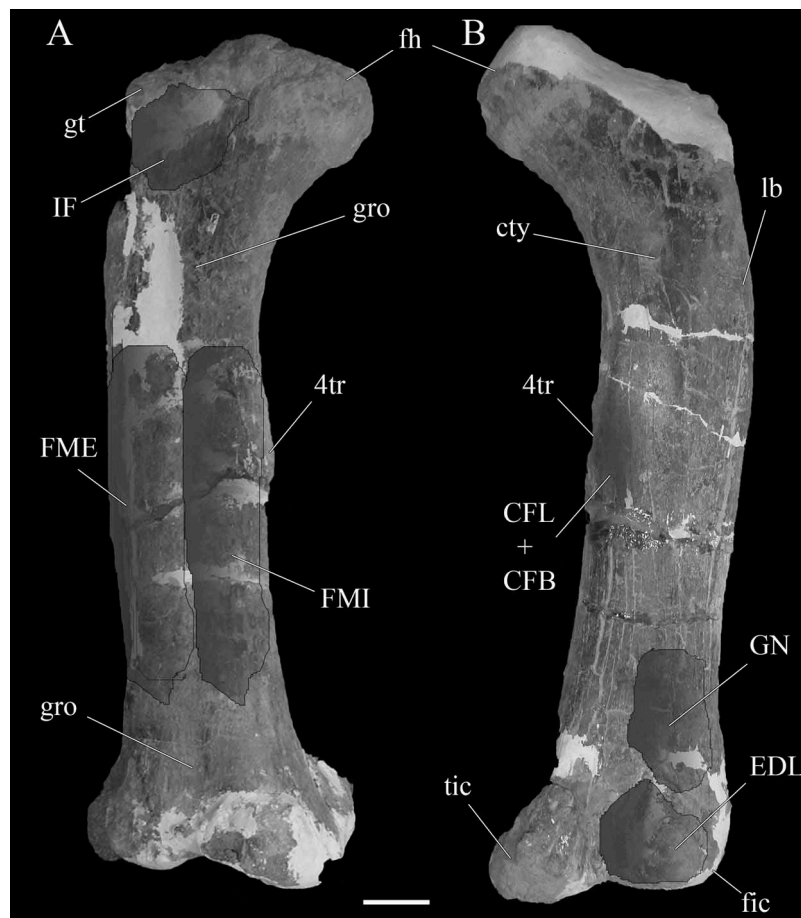

Figure 6. Femur of *E. sciuttoi* in (A) anterior view, (B) posterior view. Scale equals 10 cm. *Abbreviations*: CFB, M. caudofemoralis brevis, CFL, M. caudofemoralis longus, cty, concavity, EDL, M. extensor digitorum longus, fh, femoral head, fic, fibular condyle, FME, M. femorotibialis externus, FMI, M. femorotibialis internus, ft, fourth trochanter, GN, M. gastrocnemius, gro, groove, gt, greater trochanter, lb, lateral bulge, tic, tibial condyle.

for the probably robust FT, via a tendon, similar to the insertion described in extant archosaurs.

M. Flexor tibialis externus (FTE)

In crocodylians, the FTE, is a large muscle which originates by a tendon from the posterolateral aspect of the iliac blade, posterior to the IT 3 (Klinkhamer et al. 2017). It inserts on the posteroproximal surface of the tibia and on the tendon of M. gastrocnemius . The avian homologous is the M. flexor cruris lateralis. It is divided in birds into two components, pars pelvica and pars accessoria.

In the lateral surface of the ilium on the postacetabular process of *Epachthosaurus* there is a shallow depression bearing longitudinal and well-marked striations (Figure 4). This area is proposed to be the origin site, probably via a tendon, whereas its proposed insertion is on the posteroproximal surface of the tibia (Figure 7).

Deep ventral muscles of the upper hindlimb

M. Caudofemoralis longus (CFL)

The tube-shaped CFL in crocodylians arises from the first caudal vertebrae (the number of vertebrae depends of the taxon) on the ventrolateral aspect of the vertebral body and the ventral portion of the transverse processes as well as the lateral surface of haemal arches. The insertion of the CFL is via a robust tendon on the fourth trochanter of the femur (Ibiricu et al. 2013b). The CFL is present, but modified, in most modern birds (M. caudofemoralis pars caudali),

particularly regarding to the fusion of the caudal vertebrae into a pygostyle and changes in the morphology of the proximal portion of the femur.

Gatesy (1995) described the 'transition point' as an indicator of the distal end of the CFL in theropod dinosaurs. Later, Otero et al. (2012) inferred the same condition in sauropod dinosaurs. This putative end of the muscle is directly correlated with the disappearance of the caudal transverse processes, the elongation of the prezygapophyses, and the presence of anteriorly and posteriorly projected processes at the ventral ends of the haemal arches. These osteological correlates can potentially be applied to *Epachthosaurus*. In this taxon, the transverse processes disappear in caudal vertebra 17 and at this vertebral section the anterior zygapophyses are longer (see Ibiricu et al. 2013b). Therefore, this caudal region is interpreted as the origin and area the attachment of the CFL in *Epachthosaurus*. The fourth trochanter in *Epachthosaurus*, as in crocodylians, is strongly developed (Martínez et al. 2004; Ibiricu et al. 2013b). This site is interpreted as the area of insertion for the CFL in *Epachthosaurus*, probably via a strong tendon (Figure 6).

M. Caudofemoralis brevis (CFB)

The origin of the CFB in crocodylians (depending on the taxon) is in the anterior-most caudal vertebrae and/or last sacrals and the postacetabular region of the ilium . The tendinous insertion of this thin caudal muscle is on the femoral fourth trochanter, just slightly dorsal to the insertion of the CFL. In birds the M. femoralis pars pelvica = CFP
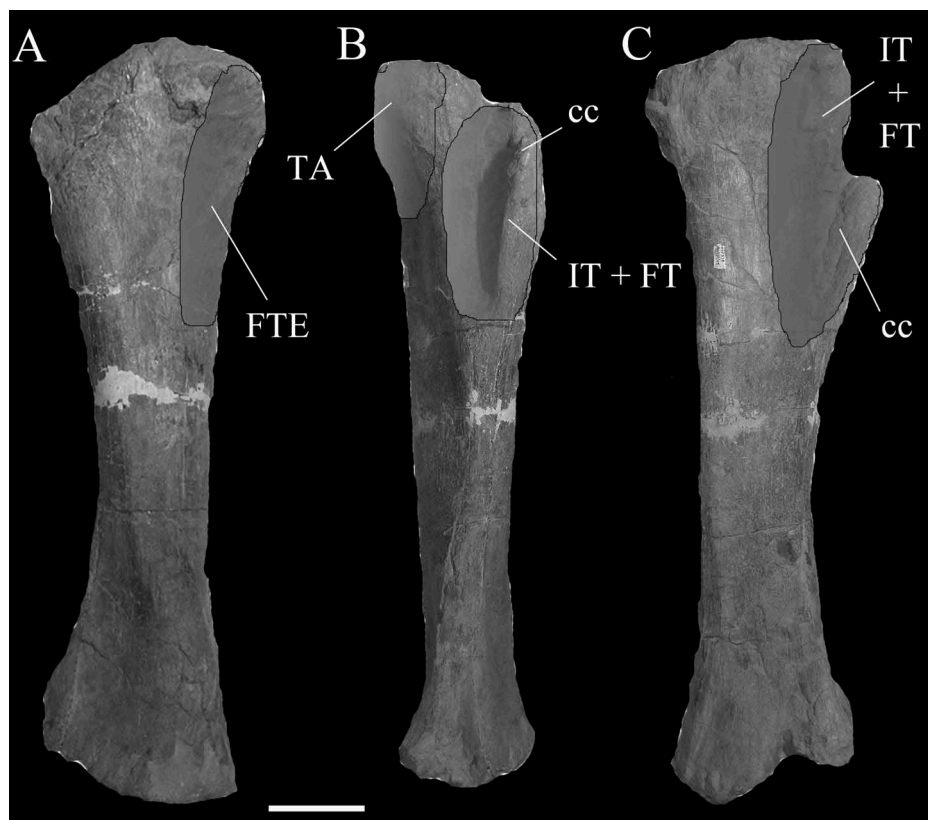

Figure 7. Tibia of *E. sciuttoi* in (A) medial view, (B) anterolateral view, (C) lateral view. Scale equals 10 cm. *Abbreviations*: cc, cnemial crest, FT, M. femorotibialis, FTE, M. flexor tibialis externus, IT, M. iliotibialis, TA, M. tibialis anterior.

arises only from the lateral surface of the ilium and occasionally the caudal vertebrae (lateral surfaces). The CFP inserts on the posterior surface, usually within the proximal half, of the femoral shaft.

Phylogenetic reconstruction of the CFB in *Epachthosaurus* is unequivocal. The CFB may have originated on the last sacral and first caudal vertebra of *Epachthosaurus* whereas its insertion was probably via a well-developed and common tendon on the femoral fourth trochanter (Figure 6).

Muscles of the Pes

Superficial dorsal muscles of the lower hindlimb

M. Gastrocnemius (GN). In crocodylians this muscle includes two muscular heads [M. gastrocnemius externus (GNE) and M. gastrocnemius internus (GNI). The external head arises from the distal posterior surface of the femur, whereas the internal head arises from the posteromedial surface of distal femur and the medial side of the proximal tibia. The external head, exhibits a long tendon that runs over the calcaneum and inserts on the ventral surface of the metatarsals and variably on the pedal phalanges. The internal muscular head displays the same pattern, inserting on the base of metatarsal I extending to metatarsal V (Schachner et al. 2011). The avian homologous of the GN is composed, generally, by three muscular heads or parts (lateralis, intermedia, and medialis). These heads originated either from lateral or medial part of the proximal portion of the tibia and from the distal portion of the femur, all the heads inserting, via common tendon, onto the base of the tarsometatarsus.

In *Epachthosaurus* there is no a clear division of the GN, however, the external head may have originated from the posterior surface of the femur (Figure 6, there are rugosities in this portion of the femur) and the internal head from the lateroproximal portion of the tibia (a slightly marked depression is present in the medial surface of the proximal surface). The insertion, probably via a tendon, is located in the distal portion of the posterior surfaces of metatarsals. The metatarsals of *Epachthosaurus* displays well marked rugosities and rim-like markings that could have been the site of insertion of the two muscular heads of the GN (Figure 8).

M. Tibialis anterior (TA). In crocodylians, the TA arises from the proximal third of the anterior surface of the tibia. This muscle, via a tendon, linked with the M. extensor digitorium longus, inserts onto the dorsal surface of the Metatarsals I, II and III. The avian homologous (M. tibialis cranialis, although there is discussion about it, see Schachner et al. 2011) is composed of two heads. The larger of these two distinctive muscular heads, originates from the lateral portion of the cnemial crest and the smaller arising from the femoral condyle. Both heads, insert via a common tendon, into the proximal portion of the tarsometatarsus.

The number of heads of the TA in *Epachthosaurus* is ambiguous, but it is interpreted to have retained one head as in crocodylians. The origin via fleshy attachment appears to be on the anteroproximal surface of the tibia (Figure 7), and its insertion in the metatarsals (Mt I to Mt IV). The
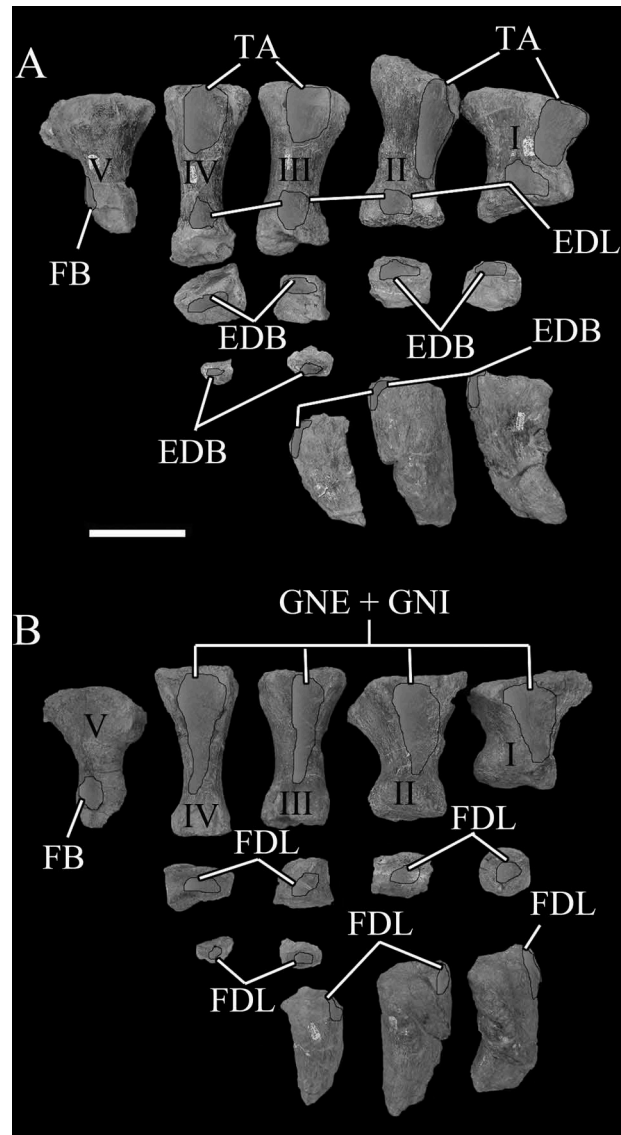

Figure 8. Right pes of *E. sciuttoi* in (A) anterior view, (B) posterior view. Scale equals 10 cm. *Abbreviations*: EDB, M. extensor digitorum brevis, EDL, M. extensor digitorum longus, FB, M. fibularis brevis, FDL, M, flexor digitorum longus, GNE, M. gastrocnemius externus, GNI, M. gastrocnemius internus.

proximal end of the first metatarsals (including also the Mt IV) of *Epachthosaurus* show clear rugose depressions (fossa-like depressions), which may represent the site of insertion, probably by a tendon, for the TA (Figure 8).

Superficial dorsal/extensor muscles of the lower hindlimb

M. Extensor digitorum longus (EDL)

In crocodylians the EDL takes its origin from the anterior surface of the lateral (external) femoral condyle. The insertion of the EDL is onto the dorsal surface of metatarsals I-III in tandem with the TA (Schachner et al. 2011). In birds, the EDL arises from the tibial crest (crista cnemialis; Gangl et al. 2004). This muscle in extant birds runs along the Retinaculum extensorium tibiotarsi and the Retinaculum extensorium tarsometatarsus, and it inserts, via tendon, on the dorsal surface of the distal pedal phalanges.

In *Epachthosaurus* the femoral lateral condyle (=fibular condyle) is well developed and it could have been the origin of the EDL (Figure 6), however, there is not a distinctive scar. The metatarsals I through IV display, in the anterodistal surfaces, slightly marked concavities. These bony correlates, as in crocodylians, could represent the site of insertion of the EDL (Figure 8) along with the TA. On the other hand, in the pedal digits the scars are not clear, and the inference about the insertion of this muscle as crocodylians appears to be equivocal.

M. Extensor digitorum brevis (EDB)

In crocodylians, the EDB arises from the dorsal surface of the tarsal, whereas their insertion is on the dorsal surfaces of the distal pedal phalanges. In birds this muscle is absent (the EDB has been lost in the line of Aves).

The presence of the EDB in *Epachthosaurus* in a phylogentic framework is equivocal. Nevertheless, the dorsal portion of metatarsals (I to IV) of *Epachthosaurus* exhibit well marked rugose surfaces and the laterodorsal portion of the claws have well-developed sulci. These bony correlates could have been the insertion surface for the EDB (Figure 8).

M. Extensor hallucis longus (EHL)

The EHL in crocodylians originates from the anterior surface of the distal portion of the fibula and inserts, dependent on taxa, on the dorsal surface of the tarsal or metatarsal I (Carrano and Hutchinson 2002). In Aves, the EHL originates from the anteriomedial portion of the tibiotarsus. The EHL inserts on the dorsal surface of the hallucal ungula (i.e. on the ungula of the hallux = digit I).

The distal end of the *Epachthosaurus* fibula exhibits a concavity and a well-developed rim, these structures could represent the site of origin of the EHL. The insertion, running distally, of this muscle could have been in the metatarsal I, however, there are no muscle scars that indicate clearly its insertion location.

Deep ventral/flexor muscles of the lower hindlimb

M. Flexor hallucis longus (FHL)

The FHL shares origin with the GN on the posterior surface of the distal end of the femur in crocodylians. The FHL runs distally to insert on the ventral surfaces of the phalanges and ungual of digit I. In Aves, the FHL arises from the lateral femoral condyle and it inserts on the ungula of the hallux.

The distal end of the femoral surface of *Epachthosaurus* displays several osteological correlates, including an intercondylar sulcus, rims and ventral rugose articular surface, all which could represent the site of origin of the FHL. The insertion appears to be more uncertain, particularly because there is not a clear muscular scar and/or scars. However the FHL may have inserted in the distal surface of pedal phalanges of digit I (probably including the claw). Nevertheless, plantar aponeurosis is a soft tissue present in extant archosaurs. This soft tissue does not leave osteological scars. Therefore, it is highly possible that this structure was present in the pes of *Epachthosaurus*.

M. Flexor digitorum longus and brevis (FDL & FDB)

The FDL in crocodylians arises from the lateral (external) femoral condyle with an accessory origin from the fibula shaft (proximal third portion and/or posteromedial surface; Dilkes 2000). These muscular heads inserts converging via a common tendon and passed posterodistally, onto the ventral surfaces of the metatarsals (Klinkhamer et al. 2017). In crocodylians, the FDB originates from tarsals and inserts in the distal pedal phalanges (Dilkes 2000). The origin of the FDL in birds varies depending of the extant taxa (Schachner et al. 2011). Nevertheless, in the majority of birds the FDL arises from the tibitarsus and fibula, with an additional origin to the lateral condyle of the femur (Dilkes 2000). This muscle inserts on the ventral surface of the unguals. The FDB has been lost in Aves.

There are several putative muscle scars in the distal condyle of the femur of *Epachthosaurus* and the posteromedial surface of the fibula, which could represent the origin of the FDL. Conversely, the insertion is unclear, although it may have been on the dorsal surface of the pedal phalanges and claws (see Bonnan 2005). Because birds lack the FDB, we cannot determine its putative presence as decisive and positive in *Epachthosaurus* based on the extant phylogenetic approach.

Deep ventral muscles of the lower hindlimb

M. Fibularis (peroneus) longus and brevis (FL & FB)

In crocodylians two heads of this muscle, longus and brevis (=Mm. fibulares longus et brevis), are present. Both components arise from the fibular shaft and a portion of the tibia with the brevis head positioned more laterally and distally than the longus head. The FL inserts on the calcaneum, whereas the brevis head inserts on the anterolateral surface of the proximal metatarsus and distal tarsus. In extant birds, the FL has variable origin including the lateral aspect of the cnemial crest, the knee capsule and fleshy the fibula and tibiotarsus. This muscle inserts on the posterior surface of the tibiotarsus. Likewise, via an accessory tendon, withthe M. flexor, it perforates digit III. The FB originates from the lateral aspect of the tibiotarsus and fibula, inserting on the lateral aspect of the tibiotarsus.

The origin of the fibularis heads in *Epachthosaurus* could have been just posterior to the M. iliofibularis, in that site well marked striations and rugosities are present. The insertion of the FL would have been in the surface of the proximal metatarsus owing to the fact the apparently absence of an osseous calcaneum (see below), whereas the insertion of the FB in the posterolateral surface in metatarsal V, where a rugose-fossa- like is present (Figure 8).

Discussion

Soft tissue inferences in Epachthosaurus pelvis and hindlimb

As mentioned above, the crown group crocodylians together with birds, are a good framework to infer muscular

arrangement of non-avian dinosaurs. However, crocodylians appear be a better 'model' when the aim is to infer the soft tissue in sauropod dinosaurs (Dodson 2003). This is in part because extant birds show highly modified postcranial anatomy, including fusion of the hindlimb along avian evolution [e.g. fusion of the caudal vertebrae into a pygostyle and changes in the morphology of proximal end of the femur (Hutchinson 2001b)]. Moreover, the hindlimb of extant birds includes a mix of ancestral dinosauromorph, theropod features and avian synapomorphies (Carrano and Hutchinson 2002). On the other hand, crocodylians are more conservative regarding the soft tissue anatomy that is more similar to the condition hypothesized in sauropod dinosaurs (Meers 2003; Wilhite 2003; Fletchner 2009). In addition, through evolution of extant birds the origin and insertion is highly variable and, in some cases, several muscles have been lost (Maidment and Barrett 2011; Carril et al. 2014). Moreover, there are differences in the number (e.g. increasing the muscular heads) and attachment (e.g. absence of some morphological features such as absence of the fourth trochanter) of muscles and bony correlates in birds. This is directly associated with the dissimilar locomotor and function patterns of those archosaurians (Gatesy 1995). Conversely, in crocodylians, the tail remains functionally connected with the hindlimb as in non-avian dinosaurs and *Epachthosaurus* in particular. Nevertheless, the muscular arrangement in extant crocodylians differs among the representatives of the clade (Klinkhamer et al. 2017; Otero et al. 2010). For example the musculature, although conservative in some aspects, is different between *Alligator mississippiensis* and *Caiman latirostris* (Otero et al. 2010). Therefore, the same pattern within Titanosauria is probably expected. In this regard, *Epachthosaurus* differs in the muscular arrangement within the group, particularly with more derived forms (see below).

The appendicular bones of *Epachthosaurus* display a suite of clear bony correlates (see Figure 3), for example, the ilium shows several rugosities. However, in some cases, they are influenced by the presence of cartilaginous epiphyses (see Holliday et al. 2010), and striated areas which are indicators

of muscular insertion and/or origin. These rugose scars are indicative of fleshy attachment (Hutchinson 2001b; Hieronymus 2002). Additionally, in *Epachthosaurus*, the femur (e.g. fourth trochanter), tibia (e.g. cnemial crest), and fibula (e.g. lateral tuberosity) display pits or rugose scars which indicate the presence of tendinous or aponeurotic muscular attachments (Jasinoski et al. 2006). Other surfaces of the hindlimb and pelvis, although there are not visible scars (i.e. smooth bone surfaces), may represent the fleshy attachment of musculature. In phylogenetic frameworks, the pelvic and hindlimb musculature of *Epachthosaurus* is well supported and described here confidently (based on the EPB, Witmer 1995; decisive and positive inference; Figure 9). In this regard, 21 pelvic and hindlimb bones were recognized and consequently reconstructed in *Epachthosaurus*. Eighteen of the 21 muscles analyzed were present in both extant bracket of Archosauria (i.e. crocodylians and birds) and inferred as decisive and positive (Level I according to Witmer 1995). However, in some of the reconstructed muscles in the pelvic and hindlimb bones of *Epachthosaurus* (either insertion or origin), the bony correlates are not clearly identified for the muscle under consideration. Therefore, the presence of these muscles must be considered solely on phylogenetic grounds.

The tarsi in sauropod dinosaurs in general and titanosaurs in particular are mostly dominated by the astragalus. Within macronarian sauropods, ossified calcaneum is reported in few taxa (e.g. *Brachiosaurus, Camarasaurus* and *Neuquensaurus*, see Bonnan 2000). There is no ossified calcaneum in *Epachthosaurus*, whether the absence of the calcaneum is an artifact of taphonomy is impossible to determine. However, probably a 'cartilaginous' calcaneum could have filled the gap between the metatarsals and the fibula in *Epachthosaurus*. The Fibularis (peroneus) longus, a flexor of the ankle joint, in crocodylians insert on the calcaneum, the putative absence of this bone in *Epachthosaurus* could have affected its effectiveness (see below).

In the majority of the studies of muscular reconstruction of sauropod dinosaurs, the pes (hind foot) is dismissed
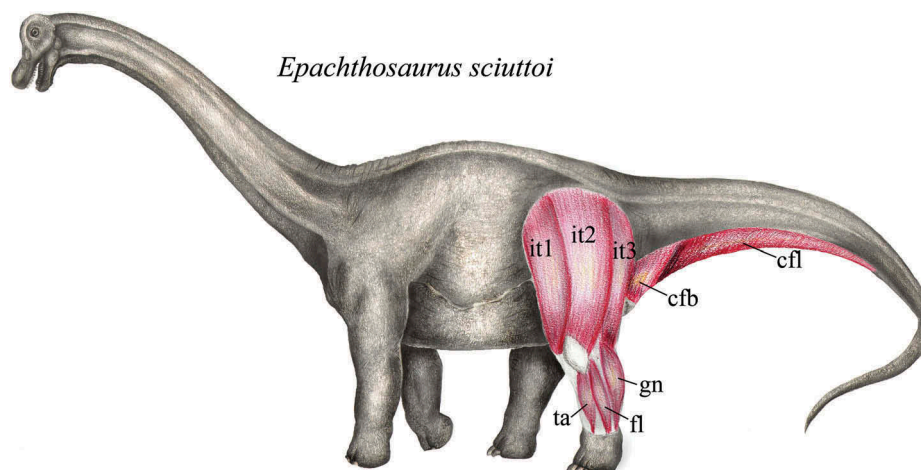

Figure 9. Hypothetical reconstruction of *E. sciuttoi* showing some of the muscles described in this study. *Abbreviations*: CFB, M. caudofemoralis brevis; CFL, M. caudofemoralis longus; FDL, M. flexor digitorum longus; FL, M. fibularis longus; GN, M. gastrocnemius; IT, M. iliotibialis (IT1, IT2, IT3, see text). Ilustration by Guadalupe Vilchez Barral.

Table 2. Morphological differences between *Neuquensaurus* and *Epachthosaurus*, muscles involved and function inferred following Otero and Vizcaíno (2008). Muscles abbreviations as those described above.

Morphological feature	Neuquensaurus	Epachthosaurus	involved	Function
Pre and postacetabular process of the ilium	More laterally projected	Less laterally projected	IT	Extends the femorotibial joint
Fourth trochanter distance to the femoral head	Closer	Further	CFB + CFL	Retracts the limbs and contributes to the long axis rotation and adduction
Femora intermuscularis line	Present	Absent	FT	Extends the femorotibial joint
Tibia lateral transverse lenght	about 49% total tibia lenght	about 30% total tibia lenght	IT/FT	Extends the femorotibial joint
Fibular lateral tuberosity	Well-developed	Less-developed	ILFB	Flexes the knee joint and abducts the the hip
Fibular lateral tuberosity distance to the fibular head	Closer	Further	ILFB	Flexes the knee joint and abducts the the hip
Calcaneum	Ossified	No ossified	FL	Flexors of the ankle joint

because it does not contribute significantly to the range motion of the hindlimb. Overall, the pes morphology remained conservative during sauropod evolution (Bonnan 2005). Nevertheless, *Epachthosaurus* display metatarsals with different length, in contrast, other titanosaurs where the pes was articulated and well preserved, for example, *Notocolossus gonzalezparejasi* (Gonzalez Riga et al. 2016), display metatarsals with similar length (i.e. short and robust metatarsals showing approximately the same length). Although many of the muscles attaching to the pes leave no clear osteological correlates, the reconstruction of the musculature is important because the muscles there attached contributes to the flexion and extension of the metapodials and digits. Therefore, the pes muscular reconstruction in *Epachthosaurus*, may constitute a source of information for future comparative studies within Titanosauria, where at least, two different pes morphologies could have been present. The acquisition of a semi-plantigrade posture in sauropods may have been a mechanical advantage to the flexor muscles. For example, it may have retained the appropriate insertion angle for the M. gastrocnemius (Bonnan 2005). This posture may have been an advantage for *Epachthosaurus* in particular increasing the angle for the insertion of the M. gastrocnemius. The presence of an elastic plantar pad was inferred in sauropod dinosaurs (Bonnan 2005). This pad probably acted to alleviate the weight transmitted through the pes, probably in tandem with the Metatarsals I to III, the most robust elements in the pes of *Epachthosaurus*. Additionally, it may support the pes posteriorly and it may unite the metatarsals into a cohesive 'block' as in elephant, although the reduction of pedal bones (phalanges) in *Epachthosaurus* differs with those large-bodied graviportal mammals (see Gonzalez Riga et al., 2016). If this pad was present in *Epachthosaurus* is speculative, but possible.

Muscular comparison with Neuquensaurus: morphofunctional implications

An in-depth analysis of the biomechanical function of the *Epachthosaurus* hindlimb is beyond the scope of this study. However, there are some significant considerations regarding the morphofunctional implications of the comparison between *Epachthosaurus* and *Neuquensaurus*. Throughout sauropod evolution there were several shifts in the pelvis and hindlimbs. For example, in titanosaurian sauropods, the preacetabular and postacetabular processes of the ilium are expanded anteroposteriorly and dorsoventrally. Additionally, the blade of the preacetabular process is strongly curving (Carrano 2005). The femur increase its midshaft eccentricity and the trochanteric shelf (anterolateral buttress) differentiated into a crest on the lateral surface of the femur. Likewise, the tibial cnemial crest is reduced. On the other hand, the morphology of the sauropod pes displays a generally conserved morphology (Bonnan 2005). These morphological changes are mainly related with locomotor specializations (Wilson and Carrano 1999), however, it also includes a rearrangement of the sites of muscular attachments in the pelvis and hindlimb affecting the lines of actions and moment arms (Otero & Vizcaino 2008). Although these anatomical pelvic and hindlimb modifications throughout sauropod evolution are present in Titanosauria as a whole, within the member of the group there are differences, an example of this, are *Epachthosaurus* (a medium sized basal member) and *Neuquensaurus* (a small sized derived member) (Table 2). In this regard, the most important morphological difference between the ilium of *Neuquensaurus* and *Epachthosaurus* is the strong lateral projection of the preacetabular process of the former (Figure 10(a, b)). Archosauriforms display an expanded anterior process of the ilium (Hutchinson 2001b). Additionally, when the expansion is more anterior of the preacetabular process (iliac blade), the more anterior the origin of the muscles there attached (e.g. M. iliotibialis = anterior head = IT1 and M. iliofibularis). This muscular arrangement increases the moment arm (i.e. increasing the force of action) for protraction and femoral medial rotation (Lijima and Kobayashi 2014). The anterior projection of the preacetabular process of *Neuquensaurus* is greater than that seen in *Epachthosaurus*, therefore an increasing of the force of action is expected in the saltasaurine titanosaur. In other words, *Neuquensaurus* have more distal attachment for the IT and ILFB, therefore, it saltasaurine would have had a moment arm about the hip greater than *Epachthosaurus*. Additionally, the preacetabular process of *Neuquensaurus* is dorsoventrally narrower than it is in *Epachthosaurus* (Figure 10a, b). This morphological difference is also linked with the origin of the IT1 and the IF. Therefore, in *Neuquensaurus*, it may have granted a biomechanical advantage, increasing the extending of the femorotibial joint as well as the abduction of the hip.
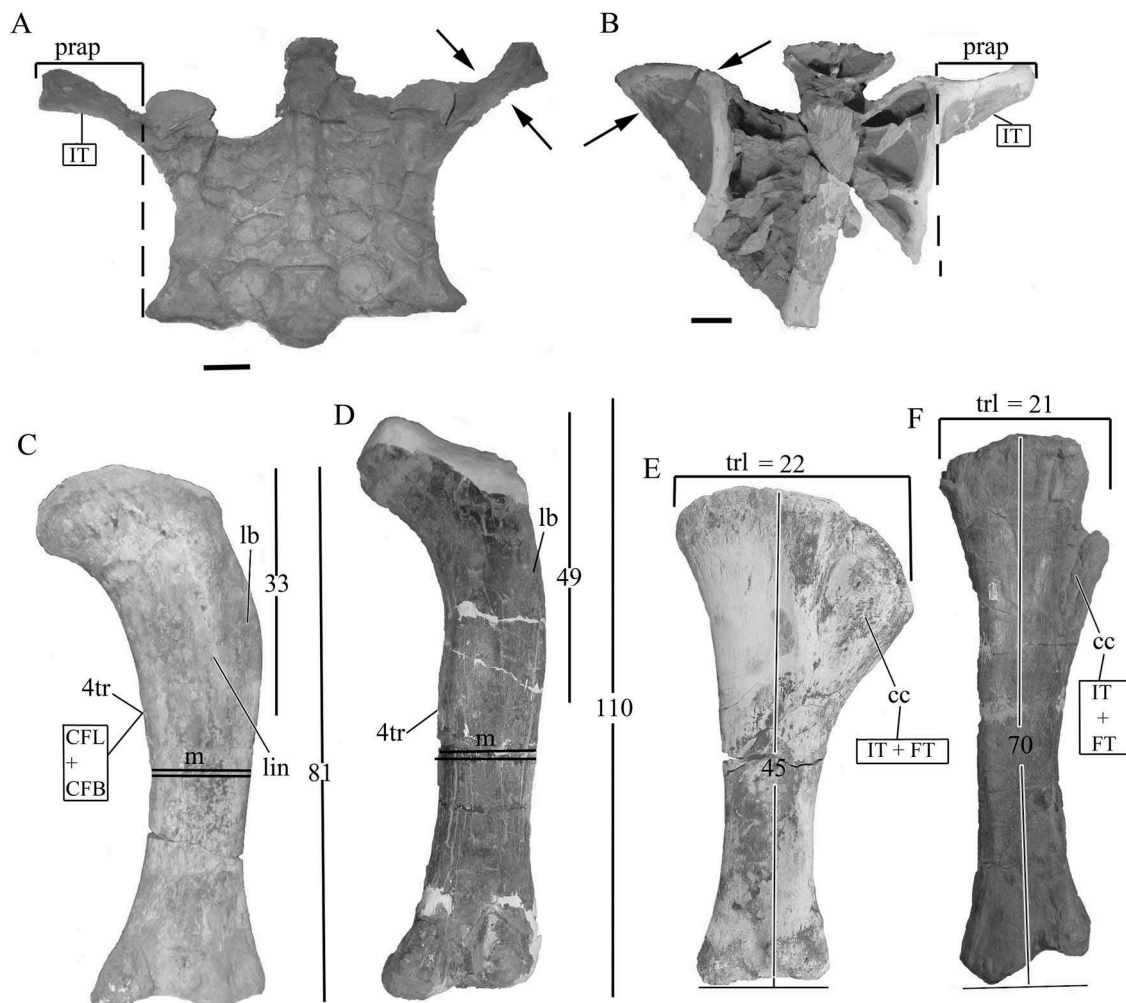
Figure 10. Morphological comparison between selected pelvic and hindlimb bones of *Neuquensaurus australis* and *Epachthosaurus sciuttoi*. Ilia in ventral and dorsal view respectively of (A) *N. australis* (MCS-5/16), (B) *E. sciuttoi*, showing the development of the preacetabular process. Scale equals 10 cm. Right femora in posterior view of (C) *N. australis* (MCS-9), (D) *E. sciuttoi*, indicating position of the fourth trochanter and distance (in cm) of this from femoral head. Tibiae in lateral view of (E) *N. robustus* (MCS-6) and (F) *E. sciuttoi*, indicating the difference in the lateral width (in cm) and the development of the cnemial crest. *Abbreviations*: 4tr, fourth trochanter; cc, cnemial crest; CFB, M. caudofemoralis brevis, CFL; M. caudofemoralis longus; FT, M. femorotibialis; IT, M. iliotibialis; lb, lateral bulge; lin, linea intermuscularis; m, femoral minimum transverse width; prap, preacetabular process; trl, transverse lateral width. The black arrows indicate the dorsoventral development of the preacetabular process. Total proximodistal length of the femora and tibiae are also indicated in cm.

The lateral tuberosity is a well-marked and defined fibular scar for the insertion of the IF. This muscle scar is placed more closely to the proximal end and is more developed in *Neuquensaurus* than it is in *Epachthosaurus* (Otero and Vizcaíno 2008; Figure 11). Thus, the development as well as the location of the lateral tuberosity on the fibular shaft observed in those titanosaurs differs, among other members of Titanosauria (e.g. *Bonitasaura, Laplatasaurus, Saltasaurus, Uberabatitan*, see Gilardhi et al. 2016; Figure 4 and Table 3). Therefore, the location and development suggests mechanical differences of the IF among the titanosaur taxa.

The location of the fourth trochanter on the femoral shaft varies in the diplodocid dinosaurs *Diplodocus* and *Apatosaurus* (Bonnan 2004). The fourth trochanter is the site of insertion of the caudofemoral musculature. This suggests mechanical differences between these sauropods (Bonnan 2004). The same pattern could be extrapolated to *Neuquensaurus* and *Epachthosaurus*. In both titanosaurs the fourth trochanter is strongly developed. However, its position on the femoral shaft varies (Figure 10(c, d)) as well as with other member of Titanosauria (Table 3). In other words, in

Neuquensaurus, the site of insertion of the caudofemoralis musculature (CFL and CFB, via a common tendon) on the fourth trochanter is closer to the femoral head than it is in *Epachthosaurus* (at 40.7 and 45.0% of femoral length respectively). This position may have increased the range of femoral retraction, decreasing torque about the femoral head, in *Neuquensaurus* (see Bonnan 2004; Ibiricu et al. 2013b; Ullmann et al. 2017). The morphology of the lateral surfaces of the caudal centra (site of attachment of the CFL) in *Neuquensaurus* exhibit well-marked rim. This rim, placed below the transverse processes, migrates ventrally disappearing about caudal vertebrae eight. The disappearance of this rim may correspond to the end of the CFL (Ibiricu et al. 2013b; Figure 12). On the other hand, in *Epachthosaurus* (based on the disappearance of the transverse processes) the elongation of the caudal prezygapophyses and the lateral morphology of the centra and haemal arches (the 'transition point' in theropod dinosaurs, according to Gatesy 1995) may correspond to the distal end of the CFL, about caudal vertebra 17 or further (Figure 12). Thus, although the origin and insertion of the tail musculature in both titanosaurs is the same, the extension of the
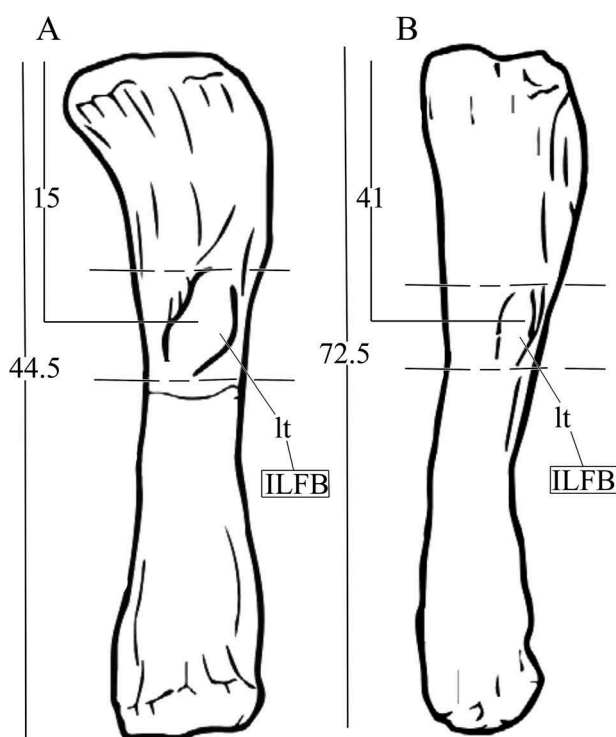
Figure 11. Fibulae comparison in lateral view of (A) *N. robustus* and (B) *E. sciuttoi* (redrawing from Ghilardi et al. 2016), indicating position of the lateral tuberosity and distance (in cm) of this structure from the proximal extreme of the fibula. Total proximodistal length of the fibulae is also indicated (in cm). *Abbreviations:* ILFB, M. iliofibularis, lt, lateral tuberosity.

present in titanosaurs is related to large body sized animals acting as support of its own weight (Carrano 2001) where the femur is broader mediolaterally that anteroposteriorly. This condition offers resistance to increase bending moment which offsets the lateromedial forces created by the weight of the animal (Wilson 2005; García et al. 2015). Additionally, in *Neuquensaurus* the standing poses is typically wider (Otero 2010). In this regard, the femoral eccentricity of this derived titanosaur is greater than in *Epachthosaurus*, which is related to the support of medio-lateral bending. The linea intermuscularis is present through the evolution of archosaurians (Hutchinson 2001b). This structure is represented by a crest on the femoral shaft of saltasaurines, running vertically on the anterior surface of the femoral shaft (Otero 2010). On the contrary, in non-saltasaurines sauropods this line is absent. In concordance with Otero and Vizcaíno (2008), there, is the area of the origin of the two heads of the FT, acting as a divisor or boundary between both femorotibialis heads. In *Epachthosaurus*, the presence of the FT in a phylogenetic framework is undeniable, because the muscle is present in both extant brackets of Archosauria. However, contrary to *Neuquensaurus*, in *Epachthosaurus* the number of heads and a clear osteological correlate, remain unclear.

Unlike the absence of an osseous calcaneum in *Epachthosaurus*, this ankle bone was present in *Neuquensaurus* (MLP-CS 1233, see Otero 2010; Bonnan 2004). The ossified calcaneum may provide advantages to the foot of *Neuquensaurus*. For example, the ossified calcaneum may have contributed to the pes stability and appropriate plantar muscle (fibularis) alignment. This would not have been an advantage only of *Neuquensaurus* on *Epachthosaurus* but also on other titanosaurs where the absence of an ossified calcaneum is not an artifact of taphonomy (i.e. no ossified 'cartilaginous?' calcaneum).

In sum, *Epachthosaurus* and *Neuquensaurus* pelvic and hindlimb bones, display several morphological differences. These morphological differences are directly related with the site of muscular attachment, suggesting that the muscles there involved arranged in different ways. Future in depth biomechanical analysis, for example applying morphometry and 3D reconstructions, may test the implications of these morphological variations. Nevertheless, this

CFL differs between these sauropod dinosaurs (Figure 12). Consequently *Epachthosaurus* may have displayed a greater rigidity of the tail, due to a major extension of the CFL.

Likewise, the tibia proximal transverse width of *Neuquensaurus* is larger than it is in *Epachththosaurus* (see Figure 10(e,f) and Table 3). In this site attaches the IT and FMT, both muscles related to the extension of the femorotibial joint. This suggests that the former could have had a greater muscular cross-sectional area. The muscle with the greater physiologic cross-sectional area will produce the most force (Josephson, 1975).

Within saltasaurines, *Neuquensaurus* displays the highest values of femoral eccentricity (Otero 2010). The eccentricity

Table 3. Measurements (in cm) of the elements from the hindlimbs of several titanosaur taxa. Abbreviations: D4Tr, distance of the fourth trochanter from the femoral head; DFs, distance of the fibular lateral tuberosity from the fibular proximal end; F, femur; Fi, fibula; PDL, proximodistal length (total length); T, tibia; TLW, transverse lateral width. * denote measurements taken from the literature figures, ** denote bones partially preserved. *Diamantinasaurus* (Poropat et al. 2014); *Rapetosaurus* (Curry Rogers 2009); *Lohuecotitan* (Diez Díaz et al. 2016); *Dreadnoughtus* (Lacovara et al. 2014).

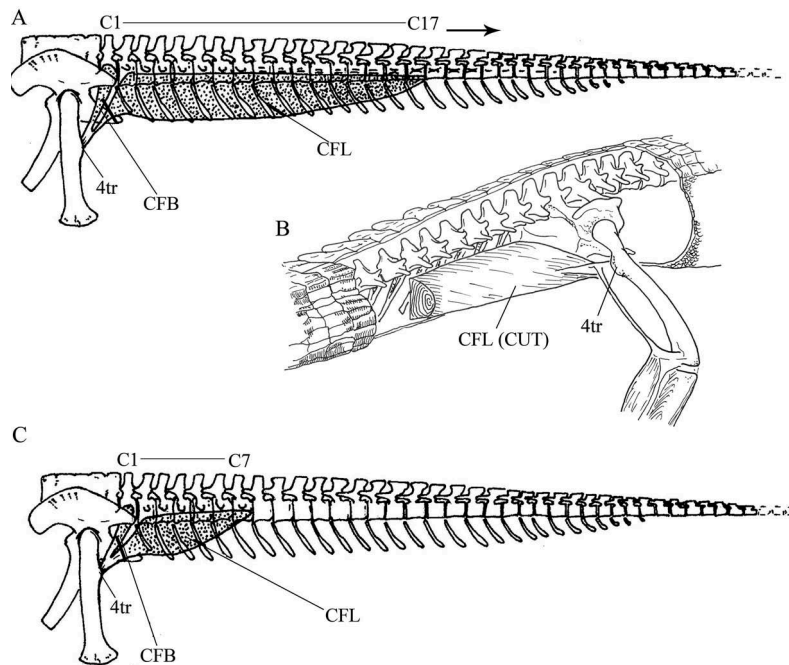|					Muscles				
Taxon	Element	PDL	D4Tr	Element	PDL	TLW	Element	PDL	DFs
Opisthocoelicaudia	F	139.5	76	T	81	26	Fi	83	42*
Neuquensaurus	F	81	33	T	45	22	Fi	44.5	15*
Epachthosaurus	F	110	49	T	70	21	Fi	72.5	41
Diamantinasaurus	F	134.5	44	T	79.5	28	Fi	76.9	35*
Rapetosaurus	F	65.7	22.5*	T	50**	12*	Fi	46.6	15*
Lohuecotitan	F	101.8	50*	T	66	22*	Fi	64.3	28*
Dreadnoughtus	F	191	89	T	109	38	Fi	103	34

Figure 12. Schematic titanosaurian sacral, caudal, pelvic and posterior hindlimb skeletons in left lateral view, showing reconstructed caudofemoralis musculature for (A) *Epachthosaurus* and (B) *Alligator* and (C) *Neuquensaurus* (modified from Ibiricu et al. 2013b; Figures 1 and 6). *Abbreviations*: 4tr, fourth trochanter; C, caudal vertebrae; CFB, M. caudofemoralis brevis, CFL; M. caudofemoralis longus.

study constitutes a potential source of information in order to infer the putative locomotor differences abilities between these titanosaurs in particular and among titanosaurs in general.

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