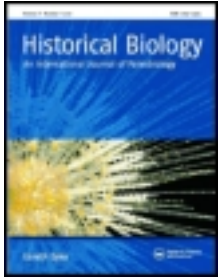


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The influence of caudofemoral musculature on the titanosaurian (Saurischia: Sauropoda) tail skeleton: morphological and phylogenetic implications

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The influence of caudofemoral musculature on the titanosaurian (Saurischia: Sauropoda) tail skeleton: morphological and phylogenetic implications

Lucio M. Ibric^{a*}, Matthew C. Lamanna^b and Kenneth J. Lacovara^c

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Due to their abundance, taxonomic and morphological diversity, wide range of body sizes and broad geographical distribution, titanosaurian sauropods were one of the most important Cretaceous herbivorous dinosaur groups. Consequently, titanosaurs constitute one of the best samples in which to evaluate the relationship between bony structures and unpreserved soft-tissues within Sauropoda. We reconstruct the morphology and interpret the implications of selected soft-tissues associated with the titanosaurian caudal skeleton. These tissues, especially the *M. caudofemoralis longus* (CFL), exerted a considerable influence on the anatomy of the caudal vertebrae and haemal arches. In all studied titanosaurian taxa, the reconstructed caudofemoral musculature corresponds to one of three principal morphotypes that accord with previously recognised phylogenetic patterns within the clade. Basal titanosaurians had an elongate *M. CFL* that extended for much of the proximal half of the tail; in saltasaurines, this muscle was much shorter. Non-saltasaurine lithostrotians exhibited an intermediate condition. Furthermore, the differing position of the fourth trochanter, and therefore, the insertion of the caudofemoral muscles, among various titanosaurian taxa suggests distinctions in the locomotor function of these animals.

Keywords: Sauropoda; Titanosauria; caudal vertebrae; soft-tissues; caudofemoral musculature

Introduction

Sauropod dinosaurs reached body sizes never achieved by any other terrestrial animal group, living or extinct (McIntosh 1990; Upchurch et al. 2004; Hone et al. 2005; Sander et al. 2010). The evolutionary increase of sauropod body sizes entailed a change to a quadrupedal posture from the bipedality exhibited by early dinosaurs (Sereno 1997), as well as a reorganisation of the basal sauropodomorph body plan (Dodson 1990; Bonnan 2003; Yates and Kitching 2003; Carrano 2005; Wilson 2005). The tail and its associated soft-tissues must have been an important factor in this anatomical transformation.

Titanosaurian sauropods were one of the most abundant and widespread herbivorous dinosaur groups, having been discovered on all continents, including Antarctica (Cerdeña et al. 2012). Based in part on the occurrence of their characteristic wide-gauge trackways, the temporal range of titanosaurs is thought to have extended from the Middle Jurassic to the end of the Cretaceous (Curry Rogers 2005). Titanosaurs include truly enormous taxa such as *Argentinosaurus huinculensis* (Bonaparte and Coria 1993) as well as much smaller-bodied forms (e.g. *Saltasaurus loricatus*; Bonaparte and Powell 1980). With more than 50 species discovered to date, titanosaurs currently represent more than one-third of known sauropod diversity (Curry Rogers 2005; González Riga 2011).

Owing to a number of factors, including their considerable taxonomic and anatomical diversity, lengthy evolutionary history, relative abundance, extraordinary range of body sizes and widespread geographic distribution, titanosaurs constitute one of the best samples in which to evaluate the relationship between soft-tissues and morphological patterns within Sauropoda. Skeletal elements throughout the tails of titanosaurs exhibit a complex of highly variable characters.

The *M. caudofemoralis longus* (CFL), the largest and one of the most important caudal muscles, in tandem with the *M. caudofemoralis brevis* (CFB), must be considered in any attempt to understand the evolution of caudal vertebral function and morphology in titanosaurian sauropods (Salgado and García 2002; Gallina and Otero 2009; Otero et al. 2012). Evidence of unpreserved soft-tissues on the caudal vertebrae provides an opportunity to analyse and interpret the influences of such tissues on the caudal series in titanosaurs.

Caudal vertebrae are important structures within the axial skeleton, useful for interpreting associated soft-tissues as well as whether or not such tissues influenced the morphology of these bones. Moreover, although no rigorous analysis has yet been performed, Salgado and García (2002) discussed the important role that musculature may have played in the evolution of titanosaurian caudal morphology. Therefore, an interpretive study of

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soft-tissues constitutes an excellent opportunity to gain insight into the morphology and evolution of the caudal series within Titanosauria.

Along these lines, a detailed analysis of caudal skeletal characters and bony soft-tissue correlates of taxa within Titanosauria will enhance our understanding of the evolution and palaeobiology of this sauropod group. Furthermore, an interpretive study of titanosaurian caudal soft-tissues provides an opportunity to understand the influence of these tissues on the morphology of the caudal series within this sauropod clade, what selective pressures may have driven morphological changes, and possible phylogenetic patterns that these modifications may have followed.

Institutional abbreviations

CM, Carnegie Museum of Natural History, Pittsburgh, USA; MCS, Museo Regional de Cinco Saltos, Cinco Saltos, Argentina; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MPCA, Museo Provincial Carlos Ameghino, Cipolletti, Argentina; MUC, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco Colección de Paleovertebrados, Comodoro Rivadavia, Argentina.

Specimens examined

Andesaurus delgadoi (holotype), MUCPv 132, a partially articulated partial skeleton that includes, among other elements, two sacral vertebrae, 25 proximal, middle and distal caudal vertebrae, and the fragmentary left femur (Calvo and Bonaparte 1991; Mannion and Calvo 2011); *Baurutitan britoi* (holotype), MCT 1490-R, an articulated vertebral series consisting of the last sacral and the proximal-most 18 caudals (Kellner et al. 2005); *Epachthosaurus sciuttoii*, UNPSJB-PV 920, a nearly complete, articulated postcranial skeleton that includes the complete sacrum, the first 29 caudal vertebrae and both femora (Martínez et al. 2004); *Laplatasaurus araukanicus*, MPCA 1501, an articulated caudal sequence consisting of 27 proximal, middle and distal vertebrae (Salgado and García 2002; Powell 2003); *Neuquensaurus australis*, MCS-5, a partially articulated partial skeleton that includes the sacrum and 15 proximal and middle caudal vertebrae (Salgado et al. 2005); *Pellegrinisaurus powelli* (holotype), MPCA 1500, a partial skeleton that includes a continuous sequence of 26 proximal, middle and distal caudal vertebrae, and the shaft of the right femur (Salgado 1996); and an undescribed, nearly complete skeleton of an as-yet unidentified giant titanosaur that includes a partial sacrum, numerous caudal vertebrae (including an articulated sequence of 17 proximal and middle caudals) and the left femur. Most of these specimens (MCS-5, MPCA 1500, MPCA 1501, MUCPv 132, UNPSJB-PV 920 and the

undescribed specimen) were examined directly in their respective institutions.

Materials and methods

The study and interpretation of soft-tissues in extinct taxa is a discipline of palaeobiology that has seen expansive growth over the last several years (e.g. Farlow 1987; Witmer 1997; Tsuihiji 2004; O'Connor 2006; Holliday 2009; Wedel 2009). Witmer (1995) described a technique, the Extant Phylogenetic Bracket (EPB) method, to make inferences regarding unpreserved soft-tissues in extinct organisms. The EPB (Witmer 1995) of Titanosauria includes Crocodylia, which retains many ancestral archosaurian traits, and Aves (= Neornithes of some authors), which exhibits numerous derived traits (Hutchinson 2001a, 2001b) (Figure 1). Dinosaurs present features throughout their skeletons which have been shown to be osteological correlates of rarely preserved soft-tissues such as tendons, ligaments, muscles and cartilage. These correlates typically take the form of processes, tuberosities, scars or traces on bones. The EPB concept is based on anatomical comparisons of homologous structures, and as applied to non-avian dinosaurs, works with the two extant archosaur clades, Crocodylia and Aves. This method has been successfully employed by many other authors (e.g. Hutchinson 2001a, 2001b, 2002; Jasinowski et al. 2006; O'Connor 2006; Organ 2006; Schwarz-Wings 2009; among others).

Phylogenetic framework of muscular inferences

The anatomical framework used herein was generated through detailed observations of extant archosaurs.

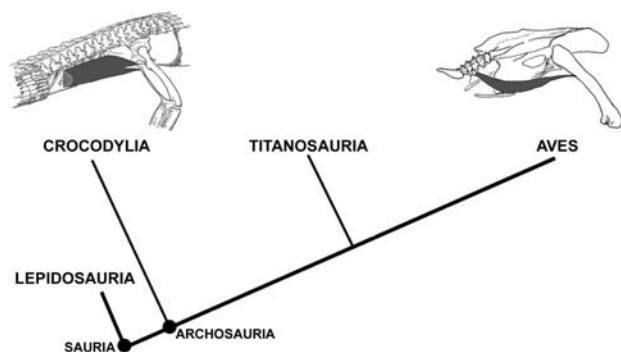


Figure 1. Simplified phylogeny of Sauria showing position of Titanosauria, both components of the titanosaurian EPB (Crocodylia and Aves) and Lepidosauria. Schematic drawing above Crocodylia depicts M. CFL (shaded area) and associated skeletal elements in right caudolateral view. Schematic drawing above Aves depicts M. CFC (the avian homologue of M. CFL; shaded area) and associated skeletal elements in right caudolateral view. Phylogeny modified from Otero and Vizcaíno (2008), after Gauthier (1986); drawings after Gatesy (1990, figs. 3a and 4a).

Soft-tissue data for Crocodylia were compiled through dissections of two subadult specimens of *Alligator mississippiensis* (American Alligator; Figure 2) and the literature (see, for example, sources in Table 1). Soft-tissue information for Aves was taken from the literature (see, for example, sources in Table 2). Additional anatomical data were gleaned from dissections of two taxa outside the titanosaurian EPB: the lepidosaurs (specifically, iguanid lizards) *Cyclura cornuta* (Rhinoceros Iguana) and *Iguana iguana* (Green Iguana). All dissected specimens were provided by Clyde Peeling's Reptiland (Allenwood, PA, USA) and the dissections were performed at Drexel University (Philadelphia, Pennsylvania, USA).

The EPB approach (Witmer 1995, 1997) allows for the inference of soft-tissue morphologies in extinct taxa through the documentation of osteological correlates of such morphologies in extant taxa that phylogenetically 'bracket' the fossil in question. This is followed by the identification of these osteological correlates in the extinct taxon. Because the inferred soft-tissues are based on osteological correlates of these same tissues in the closest extant relatives of the fossil under investigation, speculation is decreased to a minimum (Witmer 1995).

Witmer (1995) proposed three levels of soft-tissue inference, depending on whether or not the osteological

correlate for that tissue is present in both taxa that comprise the EPB of the fossil taxon in question, in only one of these extant taxa, or in neither of them. These levels are termed Level I (decisive and positive), Level II (equivocal) and Level III (decisive and negative), respectively. Moreover, when a level of inference is followed by a prime symbol (e.g. Level I'), this indicates that bony correlates are not known for the soft-tissue under consideration; the presence of this tissue must therefore be inferred (or not) solely on phylogenetic grounds (Witmer 1995).

The archosaurian tail: muscle nomenclature, attachment and function

Two main hypaxial muscles are present in the tails of living archosaurs, the M. CFL and the M. CFB (Frey et al. 1989; Gatesy 1990, 1995, 1997; Hutchinson et al. 2005; see Figure 2). In Aves, when these muscles are present, their homologues are the M. caudofemoralis pars caudalis (CFC) and the M. caudofemoralis pars pelvica (CFP), respectively (Hutchinson 2001b; Gangl et al. 2004; Otero and Vizcaíno 2008). The precise origins and insertions of these muscles differ between Crocodylia and Aves (Tables 1–3). These differences are mainly related to the anatomy of the tail (i.e. the fusion of the caudal vertebrae into a pygostyle in birds) in addition to changes in the morphology of the proximal femur on the evolutionary line to birds (Hutchinson 2001a, 2001b).

In crocodylians, because of the loss of the internal trochanter present in lepidosaurs, the fourth trochanter constitutes the osteological correlate of the insertion of the caudofemoralis musculature (CFB + CFL; Gatesy 1990) (Table 3). The origins of these muscles are more controversial in the literature, but there is general consensus that the CFB originates from the last sacral and/or first caudal vertebrae as well as the ventral surface of the iliac postacetabular process (Romer 1923; Hutchinson 2002; Wilhite 2003; Otero and Vizcaíno 2008; Otero et al. 2010) (except in *Gavialis gangeticus* [Indian Gharial], where this muscle is apparently absent; Frey et al. 1989). The origin of the CFL is similarly contentious, but all previous works agree that it arises, at least in part, from a subset of the first 15 caudal centra (Tables 1 and 3). Furthermore, several recent works (Wilhite 2003; Otero et al. 2010; Persons and Currie 2010) concur that the CFL also originates from the first 11–13 haemal arches (Wilhite 2003; Otero et al. 2010), and that its attachment to the vertebral transverse processes is minimal (Otero et al. 2010) or non-existent (Wilhite 2003; Persons and Currie 2010).

Where present, the avian homologues of the crocodylian CFB and CFL – the CFP and CFC, respectively – typically insert on different, though closely comparable, anatomical structures. In general, however, extant birds lack the broad and well-marked bony processes for the origin and insertion of these muscles that are present in crocodylians and

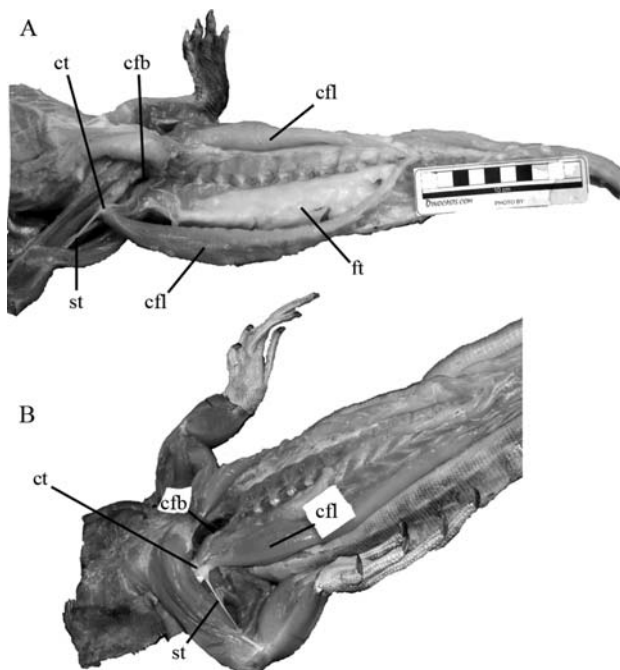


Figure 2. Dissection of *A. mississippiensis* (American Alligator) (A) and *I. iguana* (Green Iguana) (B), showing morphology of soft tissue structures associated with the caudal skeleton in ventral view. Scale equals 10 cm. *Abbreviations*: cfb, M. caudofemoralis brevis; cfl, M. caudofemoralis longus; ct, common tendon; ft, layer of fat; st, secondary tendon.

Table 1. Osteological origin and insertion sites of Mm. caudofemorales in selected extant Crocodylia, arranged by taxon.

Taxon (source)	CFB		CFL	
	Origin	Insertion	Origin	Insertion
Alligatoridae: <i>A. mississippiensis</i> (Romer 1923)	Last sacral and first caudal vertebrae; ilium (caudal edge)	Femur (dorsal to insertion of CFL)	Caudal vertebrae ~3–15 (centra and ventral surfaces of transverse processes)	Femur (fourth trochanter)
Alligatoridae: <i>A. mississippiensis</i> (Tarsitano 1981)	Last sacral and first caudal vertebrae; ilium (ventral rim, caudal to acetabulum)	Femur (fourth trochanter, caudal aspect)	Caudal vertebrae 3–13 (centra and ventral surfaces of transverse processes)	Femur (mainly fourth trochanter)
Alligatoridae: <i>A. mississippiensis</i> (Wilhite 2003)	Last sacral vertebra (rib); ilium (caudo-ventral surface)	Femur (fourth trochanter)	Caudal vertebrae 2–8 (ventral surfaces of centra); haemal arches (lateral surfaces of first 11–13)	Femur (fourth trochanter)
Alligatoridae: <i>A. mississippiensis</i> (this paper)	First and ? second caudal vertebrae; ilium (postacetabular region)	Femur (fourth trochanter, joined tendinously to CFL)	Caudal vertebrae 1–14 (ventrolateral surfaces); haemal arches 1–12 (lateral surfaces)	Femur (fourth trochanter, joined tendinously to CFB)
Alligatoridae: <i>A. mississippiensis</i> and <i>Caiman crocodyllus</i> (Gatesy 1990)	Not described	Not described	Caudal vertebrae 3–15 (centra, in sulcus between transverse processes and haemal arches)	Femur (fourth trochanter and shallow pit medial to fourth trochanter)
Alligatoridae: <i>C. crocodyllus</i> (Persons and Currie 2010)	First caudal vertebra; ilium	Femur (fourth trochanter)	Caudal vertebrae (lateral surfaces of centra); haemal arches (lateral surfaces, becoming increasingly dorsal distally)	Femur (fourth trochanter)
Alligatoridae: <i>C. latirostris</i> (Otero et al. 2010)	First caudal vertebra (lateral surfaces of centrum and bases of transverse processes); ilium (caudoventral portion)	Femur (proximomedial, near fourth trochanter, proximal to CFL insertion)	Caudal vertebrae ~1–13 (ventral surfaces of centra in all; ventromedial regions of transverse processes in ~5–13 only); haemal arches ~1–13 (lateral surfaces)	Femur (fourth trochanter)
Gavialidae: <i>G. gangeticus</i> (Frey et al. 1989)	Not applicable (muscle absent)	Not applicable (muscle absent)	Caudal vertebrae 1–10	Femur (fourth trochanter)

Notes: CFB, M. caudofemoralis brevis; CFL, M. caudofemoralis longus.

Table 2. Osteological origin and insertion sites of *M. caudofemoralis* in selected extant Aves, arranged phylogenetically by taxon (with phylogeny following Livezey and Zusi [2007]).

Taxon (source)	CFP			CFC		
	Origin	Insertion	Origin	Insertion	Origin	Insertion
Apterygiformes: <i>A. mantelli</i> (McGowan 1979)	Synsacral caudal vertebrae (lateral surfaces); ilium (caudal 3/4 of postacetabular wing); ilioischadic membrane	Femur (caudolateral surface of majority of shaft)	Caudal vertebrae (lateral surface)	Femur (caudolateral surface of shaft)	Caudal vertebrae (lateral surface)	Femur (caudolateral surface of shaft)
Struthioniformes: <i>S. camelus</i> (Gangl et al. 2004)	Ilium (lateral surface of postacetabular wing); ilioischadic membrane	Femur (caudomedial surface; linear, roughened area on proximal shaft)	Caudal vertebrae 1–4 (ventrolateral surfaces)	Not applicable (insertion on medial surface of muscular belly of caput caudate of CFP)	Caudal vertebrae 1–4 (ventrolateral surfaces)	Not applicable (insertion on medial surface of muscular belly of caput caudate of CFP)
Anseriformes: <i>Anseranas semipalmata</i> (Schulin 1987)	Ilium; ischium (caudolateral surface of both elements)	Femur (caudal intermuscular line on proximal half)	Pygostyle (ventral edge)	Femur (caudal surface of proximal half)	Pygostyle (ventral edge)	Femur (caudal surface of proximal half)
Anseriformes: Anatidae, multiple species (Raikow 1970)	Ilium; ischium (caudolateral surface of both elements, near ilioischadic synchondrosis)	Femur (caudal surface of shaft, near distal end of proximal third)	Pygostyle (ventral edge, near proximodistal midpoint)	Femur (caudal surface of shaft, near distal end of proximal third)	Pygostyle (ventral edge, near proximodistal midpoint)	Femur (caudal surface of shaft, near distal end of proximal third)
Galliformes: <i>Dendragapus obscurus</i> (Hudson et al. 1959)	Ilium (narrow line along ventral edge of dorsolateral iliac crest); ischium (narrow line on caudolateral surface)	Femur (caudal surface of shaft, near distal end of proximal third)	Pygostyle (ventrolateral surface of base)	Femur (caudal surface of shaft, near distal end of proximal third)	Pygostyle (ventrolateral surface of base)	Femur (caudal surface of shaft, near distal end of proximal third)
Galliformes: <i>N. meleagris</i> (Gatesy 1999)	Ilium (lateral lamina); ischium (lateral lamina)	Femur (caudolateral aspect of proximal shaft)	Pygostyle (ventral surface, via connective tissue)	Femur (caudal surface)	Pygostyle (ventral surface, via connective tissue)	Femur (caudal surface)
Sphenisciformes: Multiple species (Schreweits 1982)	Ilium (ventrolateral surface of dorsolateral iliac crest)	Femur (caudal surface, between about 1/2 and 3/4 length of femur)	Caudal vertebrae (distal-most one or two free caudals); pygostyle (proximal half)	Femur (caudal surface, between about 1/2 and 3/4 length of femur)	Caudal vertebrae (distal-most one or two free caudals); pygostyle (proximal half)	Femur (caudal surface, between about 1/2 and 3/4 length of femur)
Ciconiiformes: <i>Eudocimus albus</i> (Vanden Berge 1970)	Ilium (ventral edge of dorsolateral iliac crest, along narrow line extending caudally from ilioischadic foramen)	Femur (caudomedial surface of shaft)	Pygostyle (ventrolateral surface)	Femur (caudomedial surface of shaft)	Pygostyle (ventrolateral surface)	Femur (caudomedial surface of shaft)
Columbiformes: <i>Columba livia</i> (George and Berger 1966)	Ilium (ventral surface of dorsolateral iliac crest)	Femur (caudal surface, near distal end of proximal third)	Pygostyle (ventral surface)	Femur (caudal surface, near distal end of proximal third)	Pygostyle (ventral surface)	Femur (caudal surface, near distal end of proximal third)
Columbiformes: <i>C. livia</i> (Bauemel 1988)	Ilium (sulcus immediately ventral to dorsolateral iliac crest)	Femur (caudal surface, linear tuberosity on proximal part)	Pygostyle (ventral third of caudal border, on crest)	Femur (caudal surface, linear tuberosity on proximal part)	Pygostyle (ventral third of caudal border, on crest)	Femur (caudal surface, linear tuberosity on proximal part)

Table 2 – *continued*

Taxon (source)	CFP		CFC	
	Origin	Insertion	Origin	Insertion
Coliiformes: <i>Colinus striatus</i> and <i>C. leucocephalus</i> (Berman and Raikow 1982)	Not applicable (muscle absent)	Not applicable (muscle absent)	Pygostyle (ventrolateral surface of caudal end of base)	Femur (caudal surface, approximately at midshaft)
Passeriformes: <i>Agelaius phoeniceus</i> (George and Berger 1966)	Not applicable (muscle absent)	Not applicable (muscle absent)	Pygostyle (ventrolateral corner of base)	Femur (caudal surface of proximal end)
Passeriformes: <i>P. pica</i> (Verstappen et al. 1998)	Not applicable (muscle absent)	Not applicable (muscle absent)	Pygostyle (ventrolateral surface)	Femur (caudolateral surface, immediately distal to trochanter)

Notes: See Vanden Berge and Zweers (1993) for synonymies of *M. caudofemoralis* in older literature. CFC, *M. caudofemoralis* pars caudalis (homologue of *M. CFL* in Crocodylia); CFP, *M. caudofemoralis* pars pelvica (homologue of *M. CFB* in Crocodylia).

Table 3. Origin, insertion, and function in the caudofemoral musculature of Crocodylia and Aves (origin and insertion summarised from data in Tables 1 and 2).

Muscle	Origin	Insertion	Function
Crocodylia			
CFB	First caudal and/or last sacral vertebrae; ilium (ventral part of postacetabular region)	Femur (fourth trochanter)	Hind limb retraction
CFL	Proximal caudal vertebrae (lateral and ventral surfaces); proximal and proximal-most middle haemal arches (lateral surfaces)	Femur (fourth trochanter)	Hind limb retraction; long axis rotation and adduction of hind limb; lateral tail flexion
Aves			
CFP	Ilium (lateral surface); often ilioischadic membrane or ischium (lateral surface); occasionally caudal vertebrae (lateral surfaces)	Femur (caudal surface, usually within proximal half)	Control of tail feathers; coactivation of proximal hind limb musculature (hamstrings and quadriceps)
CFC	Caudal vertebrae (ventral and/or lateral surfaces of free caudals and/or pygostyle)	Femur (caudal surface, usually within proximal half)	Control of tail feathers; coactivation of proximal hind limb musculature (hamstrings and quadriceps)

Notes: CFB, *M. caudofemoralis brevis*; CFC, *M. caudofemoralis pars caudalis*; CFL, *M. caudofemoralis longus*; CFP, *M. caudofemoralis pars pelvica*.

lepidosaurs. The origins and insertions of the caudofemoralis muscles differ slightly among various avian taxa (Table 2). For example, in the ratite *Struthio camelus* (African Ostrich), the CFC inserts on the medial surface of the muscular belly of the caudal head of the CFP, whereas the CFP itself inserts on the caudomedial surface of the femur, at a linear, roughened area on the proximal shaft (Gangl et al. 2004). The CFC originates from the ventrolateral surfaces of the first four caudal vertebrae, whereas the CFP attaches to the lateral surface of the iliac postacetabular wing and the ilioischadic membrane. In the galliform *Numida meleagris* (Guinea Fowl), the CFC originates from connective tissue on the ventral surface of the pygostyle and inserts via a tendon on the caudal face of the femur, whereas the CFP originates from the lateral aspect of the ilium and ischium and inserts on the caudolateral section of the proximal femoral shaft (Gatesy 1999). Finally, in the passeriform *Pica pica* (Black-Billed Magpie), the CFC originates from a narrow tendon attached to the ventrolateral surface of the pygostyle and, as in *Numida*, inserts tendinously on the caudolateral surface of the femur; the CFP is absent (Verstappen et al. 1998).

In crocodylians, both the CFB and CFL contribute to limb retraction, whereas the latter also functions in the longitudinal rotation and adduction of the leg (Gatesy 1995). These muscles probably also serve to move the tail laterally (Schwarz-Wings et al. 2009). By contrast, when present in birds, the functions of these muscles differ from those interpreted for crocodylians. The role of the tail as a whole differs due to most birds' ability to fly (Gatesy 1995). In addition, the decrease in the length of the tail, due to a reduction of the number of caudal vertebrae as well as the fusion of the distal caudals into a pygostyle,

directly affects the development and function of the caudal musculature (Hutchinson and Gatesy 2000). In birds, the main function of the caudal musculature is the control of tail feathers (Gatesy 1995; Gatesy and Dial 1996). Moreover, at least in *Numida*, during walking, the caudal musculature has a coactivation function with the hamstring and quadriceps muscles (Gatesy 1995). The acquisition of flight also appears to have affected the evolution of the avian tail, decoupling its morphological and functional relationship with the hind limb and trunk (Gatesy and Dial 1996). Conversely, in crocodylians, the tail remains functionally connected with the hind limb.

Description

Caudal vertebrae of titanosaurian sauropods

Titanosaurian sauropods are one of the most important groups of herbivorous dinosaurs in terms of diversity and abundance. As a result of the discovery and description of nearly complete skeletons of several taxa (e.g. *Epachthosaurus*, Martínez et al. 2004; *Rapetosaurus krausei*, Curry Rogers 2009), the postcranial osteology of this sauropod clade has become much better known in recent years. Caudal vertebrae are particularly abundant in the titanosaurian fossil record; indeed, a number of taxa (e.g. *Adamantisaurus mezzalirai* [Santucci and Bertini 2006a]; *Aeolosaurus colhuehuapensis* [Casal et al. 2007]; *Baurutitan* [Kellner et al. 2005]; *Pellegrinisaurus* [Salgado 1996]) are based largely or entirely on this part of the axial skeleton. Unfortunately, articulated and nearly complete caudal series of titanosaurs are not frequently recovered. Nevertheless, in specimens of *Andesaurus* (MUCPv 132

[Calvo and Bonaparte 1991; Mannion and Calvo 2011]), *Baurutitan* (MCT 1490-R; Kellner et al. 2005), *Epachthosaurus* (UNPSJB-PV 920; Martínez et al. 2004), *Laplatasaurus* (MPCA 1501; Powell 2003), *Pellegrinisaurus* (MPCA 1500; Salgado 1996), *Neuquensaurus* (MCS-5; Salgado et al. 2005) and a few other titanosaurs, at least the proximal and middle sections of the tail are present and fully or partially articulated.

Phylogenetic relationships within Titanosauria are controversial (see, for example, Salgado et al. 1997a; Upchurch 1998; Wilson 2002; Curry Rogers 2005; González Riga 2011). However, the systematic positions of several titanosaurs that preserve nearly complete caudal series are relatively well established. *Andesaurus* and *Epachthosaurus* are widely regarded as basal representatives of Titanosauria (Calvo and Bonaparte 1991; Martínez et al. 2004; Mannion and Calvo 2011), whereas *Neuquensaurus* is placed within the highly derived clade Saltosaurinae (Powell 2003; Salgado et al. 2005). Although the precise systematic positions of *Baurutitan*, *Laplatasaurus* and *Pellegrinisaurus* remain unresolved, characters evident in their skeletons strongly suggest that all three taxa are non-saltosaurine lithostrotians; in other words, they are neither basal titanosaurs nor saltosaurines (see Upchurch et al. 2004; Kellner et al. 2005; Salgado and Bonaparte 2007). Consequently, these six genera collectively encompass a broad phylogenetic range of Titanosauria, and therefore, their caudal sequences constitute a dataset that is well suited to evaluating the influence of soft-tissues on this region of the skeleton.

Caudal vertebrae of basal titanosaurs such as *Andesaurus* (Calvo and Bonaparte 1991; Mannion and Calvo 2011) and *Epachthosaurus* (Powell 1990; Martínez et al. 2004) possess two distinct types of intercentral articulations. All caudal centra are strongly procoelous in *Epachthosaurus*; on the contrary, in *Andesaurus*, the proximal-most caudals are very shallowly procoelous, whereas the remainder are amphicoelous (Mannion and Calvo 2011). Moreover, caudal centra of *Andesaurus* are proximodistally short and transversely narrow (i.e. 'V-shaped' in proximal view, although they have been somewhat distorted in transverse dimension by taphonomic processes; see Mannion and Calvo 2011), particularly in the proximal section of the tail. However, caudal centra of *Epachthosaurus* are robust, proximodistally elongate and dorsoventrally tall throughout the entire sequence. In both of these basal titanosaurs, the neural arches are located on the proximal parts of the centra and the transverse processes are distally projected. The prezygapophyses of both taxa are proximodorsally oriented, becoming more proximally projected distally. The neural spines of *Andesaurus* and *Epachthosaurus* are wider proximodistally than transversely.

One of the features that distinguishes *Andesaurus* from most other titanosaurs (with the exception of *Saltasaurus*

and perhaps a few other taxa) is the persistence of a rudimentary transverse process through the preserved middle caudal sequence. However, although a well-developed transverse process is absent in middle caudals of *Epachthosaurus*, these latter vertebrae exhibit a pronounced lateral ridge that might correspond to a vestige of this process. This ridge is present until at least caudal 21 of *Epachthosaurus* (LMI personal observation).

In the lithostrotian titanosaurs *Baurutitan* (Kellner et al. 2005), *Laplatasaurus* (Huene 1929; Salgado and García 2002; Powell 2003) and *Pellegrinisaurus* (Salgado 1996), the caudal vertebrae are strongly procoelous with a prominent distal condyle and a fairly deep proximal concavity. The neural arches are located over the proximal halves of the centra. The transverse processes are distolaterally projected and, where this can be observed, they disappear between caudals 8 and 10. Where preserved, the neural spines are distally inclined in the proximal-most caudals. This inclination decreases further distally in the proximal part of the caudal sequence. The proximal caudal neural spines exhibit well-developed pre- and post-spinal laminae.

Some of the caudal vertebral features exhibited by these lithostrotians are particularly significant for the goals of this study. In these taxa, the most proximal caudal centra are also the widest transversely; subsequent centra in the proximal caudal series gradually become narrower. This condition confers a transversely narrow ventral surface to all centra in this part of the sequence. The proximal caudal centra are relatively tall dorsoventrally. Furthermore, the morphology of their lateral faces changes as one moves distally through the sequence. In *Baurutitan*, the lateral surfaces of the proximal (excluding the biconvex first) caudal centra are slightly concave dorsoventrally (Kellner et al. 2005). Conversely, in the articulated tail referred to *Laplatasaurus* (MPCA 1501), the proximal-most caudal centra display dorsoventrally convex lateral surfaces (Salgado and García 2002; Powell 2003); the remaining centra are slightly concave. Both of these lithostrotians exhibit well-marked ridges on the lateral aspect of the distoventral margins of selected proximal caudal centra. In *Baurutitan*, this ridge is present in caudal vertebra 8, whereas in *Laplatasaurus*, it occurs in caudals 9 and 10. Furthermore, both taxa lack or display a reduction of the transverse processes in this region of the caudal sequence. The same morphologies can be extrapolated to *Pellegrinisaurus* (Salgado 1996) and the nearly complete proximal and middle caudal sequence of an undescribed gigantic lithostrotian from southern Patagonia (LMI personal observation).

The saltosaurine titanosaur *Neuquensaurus* has traditionally been regarded as having a biconvex first caudal centrum (Huene 1929; Salgado et al. 1997a). Nevertheless, recent work indicates that this biconvex vertebra is actually the last (i.e. seventh) sacral, which is not always fused to the remainder of the sacrum (Salgado et al. 2005;

D'Emic and Wilson 2010; LMI personal observation). Unquestionable proximal caudal centra of *Neuquensaurus* are strongly procoelous with a deep proximal cotyle and a well-developed distal condyle. They are proximodistally and dorsoventrally compressed with convex lateral faces. Furthermore, ridges or rims (probably vestiges of the transverse processes) are present on the lateral surfaces of the proximal caudal centra; these lateral protuberances migrate ventrally as one moves distally through the proximal and proximal-most middle caudal sequence (Salgado and García 2002; Otero and Vizcaíno 2008; LMI personal observation). Asymmetrical lateral (possibly pneumatic) fossae also occur in the proximal caudal centra of *Neuquensaurus*, as does a well-marked ventral depression. All known caudal centra of this saltasaurine exhibit camellate (= 'cancellous' or 'spongy') tissue structure.

In *Neuquensaurus*, the neural arches are placed on the proximal margin of the centrum. The transverse processes of the proximal-most caudal vertebra are dorsoventrally deep, extending from the centrum to the neural arch. These processes are distally projected in the remainder of the proximal caudal sequence. The zygapophyses are relatively short and the neural spines are strongly inclined distally. As observed in proximal and lateral views, *Neuquensaurus* proximal caudal neural spines exhibit several fossae or cavities that are most pronounced near the prespinal lamina. Comparable cavities also occur in the proximal-most middle caudals.

Results

Crocodylian caudal myology

Although previous studies (e.g. Romer 1923; Frey et al. 1989; Gatesy 1990; Otero et al. 2010) have investigated the soft-tissues present in the tails of crocodylians, the dissections performed for this study added information pertinent to our objectives (Figure 2). The smaller CFB is present as a thin sheet that laterally overlaps the femoral end of the CFL. The origin of the CFB is on the proximal-most caudal vertebrae (the first and possibly the second) and the postacetabular region of the ilium. This muscle inserts on the femoral fourth trochanter, joined tendinously to the CFL. The larger muscle, the CFL, is tube-shaped. Its femoral end is wider than its caudal end; the latter gradually narrows to an acute terminus beginning at approximately caudal vertebra 5 or 6. In the two dissected alligators, the origin of the CFL is on the first 14 caudal vertebrae. More specifically, this muscle is firmly attached to the ventrolateral aspect of these vertebrae (to the centra and [minimally] the ventral portions of the first few transverse processes) as well as to the lateral surfaces of the first 12 haemal arches. Moreover, the CFL is covered throughout its extent by a thick layer of fat. At the point of union between the CFB and CFL, very close to the fourth trochanter, an auxiliary tendon connects these muscles

Table 4. Measurements of tail and M. CFL in dissected specimens.

Individual	Tail-TL (cm)	CFL-TL (cm)	% TL (CFL/tail)
A1	80.5	29.6	36.8
A2	50.2	19.1	38.1
IG	67.4	18.4	27.3

Notes: A1, *Alligator mississippiensis* (larger individual); A2, *Alligator mississippiensis* (smaller individual); CFL-TL, total length of M. caudofemoralis longus; cm, centimetre; IG, *Iguana iguana*; Tail-TL, total length of tail.

(particularly the latter) to the distal end of the femur, contributing to the origin of the M. gastrocnemius lateralis (Gatesy 1990) (see Figure 2).

Both of the dissected alligators are juveniles; however, they are of distinct body sizes and degrees of maturity, and therefore, they have different tail and CFL lengths. Nevertheless, the relative extent of the CFL along the tail is closely comparable in both individuals (~37.5%; Table 4). Moreover, the tails of both individuals exhibit extensive cartilage, particularly in the spaces between the bony vertebral elements. Cartilage is present throughout the tail; however, a particularly thick layer separates the 14th and 15th caudals, which is also the area of the caudal terminus of the CFL.

Lepidosaurian caudal myology

Lepidosaurians are not part of the sauropod EPB. Nevertheless, due to their gross morphological similarities with non-avian archosaurs, study of the soft-tissues in lepidosaur tails may provide insights into titanosaurian caudal anatomy. Therefore, as noted above, two lepidosaurs were dissected for this study: the iguanid lizards *I. iguana* and *C. cornuta*. *Iguana* exhibits both caudofemoralis muscles, the CFB and CFL. As in the alligator, the smaller, sheet-like CFB overlaps the CFL laterally. The origin of the CFB is on the ventral aspect of the first caudal vertebra, whereas its insertion is via a tendon onto the internal trochanter of the femur (which is homologous to the major trochanter of Testudines and perhaps also to the fourth trochanter of Archosauria; see Hutchinson 2001b). The *Iguana* CFL is large and tubular but less robust than that of *Alligator*. This size difference may be related to the differing thickness of the bony tail elements in these two diapsids. As with the CFB, the CFL inserts tendinously on the femoral internal trochanter, whereas its origin lies on the lateral aspect of the proximal-most 12 to 13 caudal centra and haemal arches. The tendon for insertion of the CFL on the internal trochanter penetrates deeply into this muscle, extending more than half its total length. The insertion area of both the CFB and CFL on the femur is surrounded by a thin, well-defined layer of connective tissue. Moreover, as in *Alligator*, the auxiliary tendon that connects the CFB and

CFL with the distal end of the femur is present in *Iguana*. The CFL extended 27.3% the length of the tail in this *Iguana* individual (Table 4). Although some fat and cartilage are present in the tail of *Iguana*, these tissues are less extensive than in *Alligator*.

The majority of the caudal soft-tissue morphologies observed in *Iguana* are also present in the closely related *Cyclura*. However, the tails of these two iguanids differ in a few aspects. In *Cyclura*, the CFL is longer and more robust than in *Iguana*. Moreover, although the shape, origin and insertion of the CFB are the same in the two iguanids, in *Cyclura*, this muscle is joined at its origin by an auxiliary tendon to the proximal femur, at the junction of this bone with the pelvic girdle. Finally, the connective tissue that envelops parts of the CFB and CFL and their tendon of insertion in *Iguana* is also present in *Cyclura*. However, this tissue is much more abundant and clearly distinguishable in the latter taxon.

Discussion

Soft-tissue inferences in titanosaurian sauropod tails

The M. CFL is present in extant Crocodylia (Tables 1 and 3). It is also present in modified form as the M. CFC in most modern birds (Aves), including representatives of basal lineages such as Ratitae and Galloanserae (Tables 2 and 3). Crocodylia and Aves comprise the EPB of titanosaurian sauropods and other non-avian dinosaurs. Therefore, based on their EPB, the presence of the CFL in titanosaurs is regarded as a decisive and positive inference (Witmer 1995).

The dissections conducted for this study demonstrate that, in *A. mississippiensis*, the origin of this hypaxial muscle is on the proximal-most 14 caudal vertebrae and the first 12 haemal arches (the first two vertebrae lack associated haemal arches, i.e. in *A. mississippiensis*, the proximal-most haemal arch articulates between the second and third caudals [Erickson et al. 2005]). This result is consistent with those of most previous studies (Table 1). It has long been recognised that, in most crocodylians, the CFL originates on the proximal ~13–15 caudal vertebrae (e.g. Romer 1923; Galton 1969; Frey et al. 1989; Gatesy 1990); moreover, Wilhite (2003) argued that this muscle attaches to the first ~12 haemal arches as well. Based on their dissections of *Caiman latirostris*, Otero et al. (2010) indicated that the CFL originates on the proximal-most 13 caudal vertebrae and haemal arches. Taken together, the data indicate that the crocodylian CFL originates on the lateral and ventral surfaces of the first ~14 caudal centra and the lateral surfaces of the first ~12 haemal arches, with minor variations possible between different taxa and/or individuals. The insertion of this muscle is on the fourth trochanter of the femur (Table 3).

In Aves, the origin of the homologue of the CFL (the CFC) is on the ventral and/or lateral aspect of the caudal vertebrae, either the free (i.e. proximal) caudals (e.g. *Apteryx mantelli*, *S. camelus*), the pygostyle (most other birds) or both (e.g. penguins; Schreweis 1982). Its insertion is on the proximal half of the caudal surface of the femur, usually within the proximal one-third (Tables 2 and 3). When considered in light of the condition in Crocodylia, these data indicate that, in Titanosauria, the

Table 5. Caudofemoral muscle origins and insertions inferred for *A. delgadoi* (basal Titanosauria), *L. araukanicus* (non-saltasaurine Lithostrotia) and *N. australis* (Saltasaurinae).

Taxon	CFB origin
<i>A. delgadoi</i>	Last sacral vertebrae and first caudal vertebra
<i>L. araukanicus</i>	Last sacral vertebrae and first caudal vertebra
<i>N. australis</i>	Last sacral vertebrae and first caudal vertebra
Taxon	CFB insertion
<i>A. delgadoi</i>	Femur (via tendon on fourth trochanter)
<i>L. araukanicus</i>	Femur (via tendon on fourth trochanter)
<i>N. australis</i>	Femur (via tendon on fourth trochanter)
Taxon	CFL origin
<i>A. delgadoi</i>	First ~17 caudal vertebrae and haemal arches (lateral surfaces)
<i>L. araukanicus</i>	First ~9–10 caudal vertebrae and haemal arches (lateral surfaces)
<i>N. australis</i>	First ~8 caudal vertebrae and haemal arches (lateral surfaces)
Taxon	CFL insertion
<i>A. delgadoi</i>	Femur (via tendon on fourth trochanter)
<i>L. araukanicus</i>	Femur (via tendon on fourth trochanter)
<i>N. australis</i>	Femur (via tendon on fourth trochanter)

Notes: CFB, M. caudofemoralis brevis; CFL, M. caudofemoralis longus.

origin of the CFL was on the ventral and/or lateral surfaces of the caudal vertebrae and its insertion was on the proximal half of the femur. As per Witmer (1995, 1997), we regard this as a Level I inference (Table 5).

The M. CFB and its homologue the M. CFP are also present in many extant crocodylians and birds. Accordingly, although the CFP is lost in some neoavian taxa (e.g. colliiforms, passeriforms; see Table 2, also George and Berger 1966), as proposed by Otero and Vizcaíno (2008), the presence of the CFB in Titanosauria may be regarded as a decisive and positive inference. In Crocodylia, the origin of the CFB is on the proximal-most caudal vertebrae (the first and possibly the second) and the postacetabular region of the ilium. This muscle inserts on the femoral fourth trochanter, joined tendinously to the CFL. A closely similar situation was probably the case in Titanosauria.

In addition, the presence of a tendon for the insertion of the CFL and CFB is another soft-tissue structure that may be regarded as present in Titanosauria via a Level I inference. However, several soft-tissue features, such as the auxiliary tendon to the distal femur (possibly lost in birds as a result of the reduction of the CFC and fourth trochanter; Hutchinson 2001b), the connective tissue at the CFL/CFB insertion point, the thick layer of fat covering the CFL and the large amount of cartilage require more speculation (i.e. Level II inferences), owing to the fact that these soft-tissues occur in only one component of the titanosaurian EPB, Crocodylia. Nevertheless, because of the gross similarity of the crocodylian caudal and proximal hind limb skeletons to those of titanosaurs, those tissues may well have been present in these dinosaurs as well.

Morphological implications

The proximal and proximal-most middle caudal sequences of *Andesaurus*, *Baurutitan*, *Epachthosaurus*, *Laplatasaurus*, *Pellegrinisaurus* and *Neuquensaurus* exhibit morphological variations in the lateral and ventral surfaces of the centra. Such variations are evident, for example, in the section of the articulated caudal series referred to *Laplatasaurus* (MPCA 1501) that has been regarded as corresponding to vertebrae 2 through 10. In this section of the tail, the 'primary lateral surface' (*sensu* Salgado and García 2002) is dorsoventrally wide in the proximal centra but becomes progressively narrower distally. By approximately caudals 9–10, the primary lateral surface is restricted to the ventrolateral corner of the centrum, and has been largely replaced by a nearly vertical 'secondary lateral surface' (*sensu* Salgado and García 2002) (Figure 3). As a result, in this section of the tail, the centra are less proximodistally concave and more quadrangular in distal view. The same morphological pattern is also present in the undescribed southern Patagonian titanosaur (LMI personal observation) and may be inferred for *Baurutitan* as well. Nevertheless, in

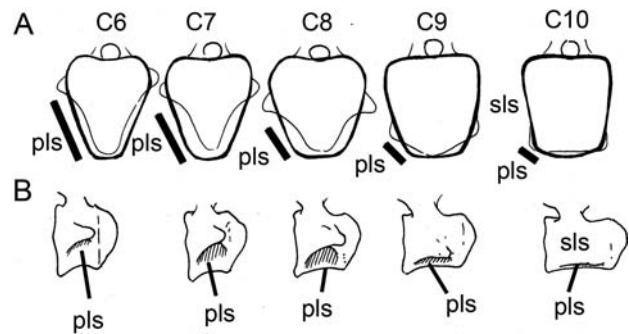


Figure 3. Line drawings of centra and ventral neural arches of caudal vertebrae 6–10 of a representative non-saltasaurine lithostrotian titanosaur (e.g. *Laplatasaurus* [MPCA 1501], *Baurutitan*) in proximal (A) and left lateral (B) views, showing the primary lateral surfaces of the centra (black lines in (A) and hatched areas in (B)) and their progressive replacement by the secondary lateral surfaces. Based on Salgado and García (2002, fig. 1) and an undescribed southern Patagonian titanosaur (LMI personal observation). *Abbreviations*: C, caudal vertebra; pls, primary lateral surface; sls, secondary lateral surface.

Laplatasaurus, the primary lateral surfaces of centra 7–10 are strongly dorsolaterally inclined, rendering the centra more 'heart-shaped' in distal view than in, for example, *Baurutitan*. These variations of the lateral surfaces of the caudal centra are interpreted as a consequence of the morphology and attachment of the caudal hypaxial musculature, particularly the M. CFL.

However, the morphology of the lateral surfaces of the caudal centra in *Neuquensaurus* differs from that seen in *Baurutitan* and *Laplatasaurus*. Centra in the proximal section of the tail of *Neuquensaurus* show a well-marked rim. Placed ventral to the transverse processes, this rim migrates to the ventral aspect of the proximal caudals before disappearing at approximately caudal 8. The disappearance of this rim may correspond to the distal end of the CFL in this taxon (Figure 4). Furthermore, both *Baurutitan* and *Laplatasaurus* have ventrally narrow centra through the proximal section of the tail, in contrast to the relatively wide ventral surfaces of *Neuquensaurus*. The proximal caudal sequences of these three titanosaurs do resemble one another in that the rim (in *Neuquensaurus*) and the ventrolaterally positioned primary lateral surface (in *Baurutitan* and *Laplatasaurus*) co-occur with the loss of the transverse processes.

Gatesy (1995) described the 'transition point' as a skeletal indicator of the distal terminus of the CFL in theropod dinosaur tails. This caudal region is characterised by the disappearance of the transverse processes, the elongation of the prezygapophyses and the presence of proximally and distally projected processes at the ventral ends of the haemal arches. Furthermore, this proposed theropod 'transition point' corresponds relatively well to the condition in crocodylians (Gatesy 1995). Recently,

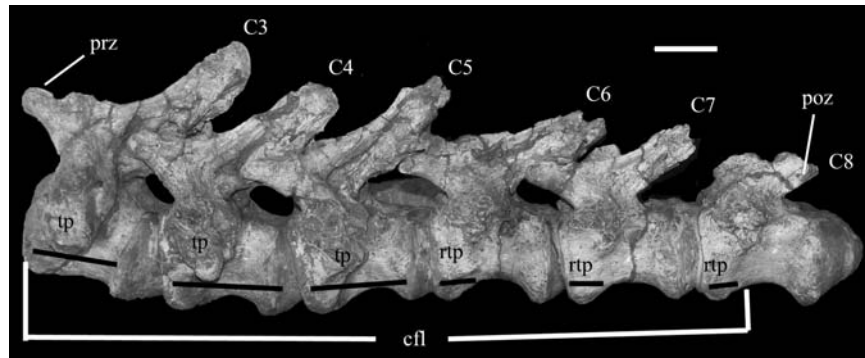


Figure 4. Caudal vertebrae 3–8 of the saltosaurine titanosaur *N. australis* (MCS-5/3–8) in left lateral view, showing proposed dorsal extent of the M. CFL (indicated by horizontal/subhorizontal black lines) in this taxon. Scale equals 5 cm. Abbreviations: C, caudal vertebra; cfl, origin of M. caudofemoralis longus; poz, postzygapophysis; prz, prezygapophysis; rtp, rudimentary transverse process (i.e. ‘rim’); tp, transverse process.

Otero et al. (2012) inferred a similar condition for a wide range of sauropod taxa. Therefore, all of the osteological correlates for the distal end of the CFL hypothesised for theropods and later for sauropods in general are probably also applicable to titanosaurs, including *Baurutitan* and potentially *Laplatasaurus* and *Neuquensaurus* as well.

In the basal titanosaurian *Andesaurus*, the aforementioned features that are thought to be correlated with caudal musculature are not present. However, the proximal and middle caudal vertebrae of this taxon display features that may be related to the hypaxial muscles. The proximal caudals exhibit relatively tall lateral surfaces that are inclined dorsolaterally, resulting in a narrow ventral surface, a feature that may be at least partly due to diagenetic alteration. The transverse processes are well developed until approximately caudal 14, and vestiges of them (the ‘circular bulges’ of Mannion and Calvo 2011) remain throughout much of the rest of the preserved caudal sequence (LMI personal observation). Furthermore, in the distal middle caudal vertebrae, longitudinal rims or ridges are present that may also represent a distal continuation of the transverse processes.

Following the interpretation described above, it is likely that the CFL of *Andesaurus* originated on the lateral aspect of the caudal centra and haemal arches. Thus, the rims or ridges could represent the dorsal limit of the CFL in the distal-most preserved vertebrae. Comparable ridges are present until at least caudal 21 of *Epachthosaurus* (LMI personal observation). As such, in basal titanosaurians, or at least in *Andesaurus* and *Epachthosaurus*, the CFL may have been proximodistally longer than in, for example, *Baurutitan*, *Laplatasaurus*, *Pellegrinisaurus* and *Neuquensaurus*. These results concur with those of Salgado and García (2002), who argued that the distal end of the CFL in *Neuquensaurus* and *Pellegrinisaurus* occurred at approximately caudal vertebra 6–7 and at approximately caudal 9 in *Laplatasaurus*. Salgado and García (2002) further suggested that the extent of the CFL in the North American titanosaur *Alamosaurus sanjuanensis* was more distal (caudal ?19) than in any of these three taxa. In addition, we interpret that the CFL may have reached caudal 9–10 in *Baurutitan*, and, as above, that it extended beyond caudal 17 in *Andesaurus* and *Epachtho-*

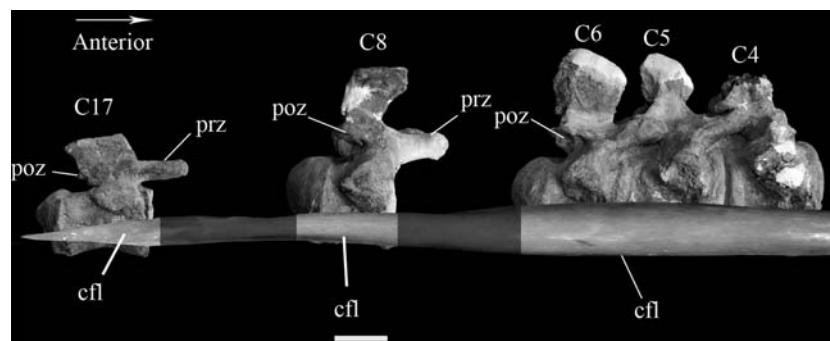


Figure 5. Representative proximal (4th–6th), proximal middle (8th) and distal middle (17th) caudal vertebrae of the basal titanosaurian *E. sciuttoii* (UNPSJB-PV 920) in right lateral view, showing hypothesised morphology of M. CFL in these three sectors of the tail of this taxon. Shaded areas of M. CFL indicate morphologies inferred from preceding and succeeding caudal sectors. Scale equals 10 cm. Abbreviations: C, caudal vertebra; cfl, M. caudofemoralis longus; poz, postzygapophysis; prz, prezygapophysis.

saurus (Figure 5). The apparent variations in the robustness and proximodistal length of this muscle in titanosaurs may hold important morphofunctional and phylogenetic implications (see below).

Gallina and Otero (2009) discussed the possible relationship of the morphology of sauropod caudal vertebrae, particularly the proximal caudal transverse processes, to the Mm. caudofemorales group. These authors argued that the variation of the first caudal transverse processes exhibited by some macronarians (e.g. *Epachthosaurus*, *Neuquensaurus*) is intimately related to the origin of the CFB. However, it is important to add that, in *Epachthosaurus* and *Neuquensaurus*, although morphologically slightly different, the transverse processes extend broadly across the centrum and neural arch. Their extent renders the lateral surface of the centrum – here interpreted as a surface of origin for the CFB – very short dorsoventrally. Therefore, we consider that, on the proximal-most caudal vertebra of titanosaurs, the dorsal attachment of the CFB was on the transverse process, whereas the ventral attachment was on the lateral surface of the centrum.

Both *Epachthosaurus* and *Neuquensaurus* display proximal (excluding the proximal-most) caudal transverse processes that taper in dorsoventral dimension and become more dorsally placed as one move distally through the caudal sequence. As a consequence, the lateral surfaces of the centra become wider, generating a broad surface for the attachment of the CFL. According to the proximodistal extent of this muscle, in the proximal sector of the tail, the ventral attachment surface of the CFL is the lateral surfaces of the centra and haemal arches; in the distal sector, it is the lateral surfaces of the centra only. However, as is the case for the CFB, the dorsal attachment of the CFL was on the transverse processes, specifically in the proximal portion of the caudal sequence. All of these attachments of the Mm. caudofemorales group strongly influenced the morphology of titanosaurian caudal vertebrae. In addition, as mentioned by Otero et al. (2012), the morphological variability of sauropod haemal arches may also have been related to the caudal musculature.

As mentioned above, proximal caudal vertebrae of *Neuquensaurus* exhibit several asymmetrically developed cavities or fossae on the proximal and lateral aspects of the neural spines and the lateral surfaces of the centra (LMI personal observation). Based on the EPB approach, soft-tissue inferences for these fossae and cavities are decisive and negative (Level III). Therefore, their anatomical function requires more speculation. In sauropods, the taxonomic significance of asymmetrical cavities, fossae and laminae is controversial (Curtice 1999; Wilson 1999; Santucci and Bertini 2006b; Casal and Ibiricu 2010). However, the asymmetrical osteological structures of *Neuquensaurus* may be related to the presence of caudal soft-tissues; therefore, these bony features may potentially have morphological, functional and/or taxonomic implications. Nevertheless, because comparable structures do

not occur in Crocodylia, and in some cases, in Aves, soft-tissues that may have been associated with them may only be reconstructed with inferences that range from Level II' to Level III'. Lastly, although this is only a Level II' inference, the caudal vertebrae of titanosaurs may have been bordered by cartilage as in extant crocodylians.

Phylogenetic implications

The sauropods analysed herein collectively represent three general evolutionary grades within Titanosauria and therefore encompass a broad phylogenetic range of this clade. *Andesaurus* and *Epachthosaurus* are regarded as basal titanosaurs, whereas *Neuquensaurus* is highly derived (i.e. within Saltosaurinae). Based primarily on their caudal vertebral morphology, *Baurutitan*, *Laplata-saurus* and *Pellegrinisaurus* are considered non-saltosaurine lithostrotians.

Salgado and García (2002) hypothesised that musculature influenced caudal vertebral morphology in titanosaurs, a hypothesis that is supported herein. However, the detailed phylogenetic implications of these morphologies remain unclear. Two main points must be considered when interpreting the phylogenetic significance of the caudal musculature, particularly the CFL: the morphological variation of the lateral surfaces of the caudal centra and the

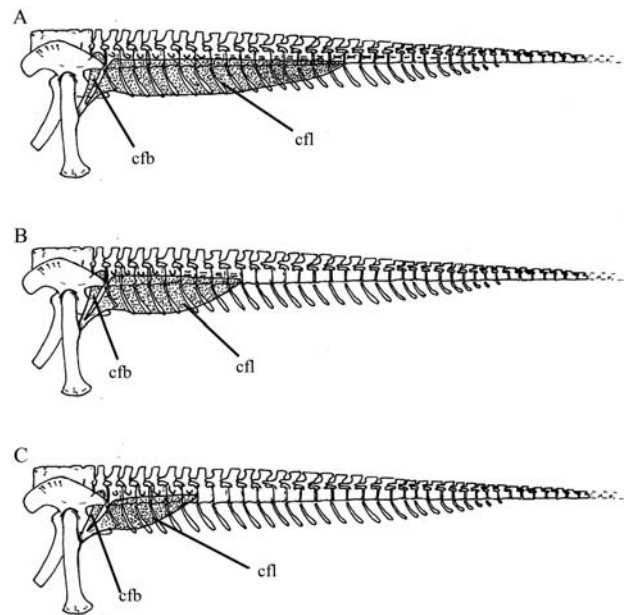


Figure 6. Schematic titanosaurian sacral, caudal, pelvic and proximal hind limb skeletons in left lateral view, showing reconstructed caudofemoralis musculature for three evolutionary grades of this sauropod group. (A) Basal Titanosauria (e.g. *A. delgadoi*, *E. sciuttoi*), (B) non-saltosaurine Lithostrotia (e.g. *B. britoi*, *L. araukanicus*) and (C) Saltosaurinae (e.g. *N. australis*). Abbreviations: cfb, M. caudofemoralis brevis; cfl, M. caudofemoralis longus.

length and attachment of this muscle (Figure 6). The presence of ridges or rims that migrate ventrally as one move distally in the caudal sequence, as in *Neuquensaurus*, may represent a derived state within Titanosauria. However, there are two distinct titanosaurian caudal morphotypes in which such lateral rims are absent. Caudal centra with a primary lateral surface that is subsequently replaced by a secondary lateral surface at approximately vertebra 9–12 (as in, for example, *Laplataosaurus*) constitute one of these morphotypes. Centra with a longitudinal lateral ridge or protuberances that probably correspond to the distal continuation of the transverse processes (as in *Andesaurus* and *Epachthosaurus*) represent the second morphotype.

Accordingly, we propose the existence of three general evolutionary states in titanosaurian proximal caudal vertebrae: (1) a protuberance on the lateral aspect of the vertebrae that persists until at least caudal 20 (considered state 0), (2) a primary lateral surface that becomes dorsoventrally narrow distally and is replaced by the secondary lateral surface at approximately caudal 9–12 (considered state 1) and (3) a rim that migrates across the lateral aspect of the centrum, becoming situated on its ventrolateral corner at about caudal 8 (considered state 2). These three states may easily be rephrased as a character statement for use in phylogenetic analysis, as follows: ‘morphology of lateral aspect of proximal and middle caudal vertebrae: transverse process or rudimentary transverse process persists until at least caudal 20 (0); primary lateral surface replaced by secondary lateral surface at approximately caudal 9–12 (1); low rim migrates ventrally across lateral surface of centrum, terminating on ventrolateral corner at approximately caudal 8 (2).’ All of these structures are herein interpreted as osteological correlates for the attachment of the CFL. Moreover, having dorsoventrally compressed proximal caudal centra with slightly convex lateral surfaces is a synapomorphic condition that characterises saltasaurine titanosaurs such as *Neuquensaurus* and *Saltasaurus* (Salgado et al. 1997a). On the contrary, as mentioned above, in most basal titanosaurians, the lateral morphology of the caudal centra differs from that of saltasaurines. This variation in centrum morphology is also interpreted as a consequence of the differing anatomy of the caudofemoral musculature in these titanosaurs.

In Aves, the evolutionary trend of the caudofemoral musculature is its reduction, and in some cases its loss. Conversely, crocodylians exhibit a large and well-developed CFL. These divergent morphologies of the caudofemoral musculature may be related to the differing functions of the tail in these two archosaur clades (see below). The proximodistal extent of the caudofemoral musculature is herein considered to be a phylogenetically significant character within Titanosauria. As mentioned above, in the two alligators we dissected, the origin of the

CFL is on the first 14 caudal vertebrae and the first 12 haemal arches. According to our analysis, in *Neuquensaurus*, the CFL extends until caudal 8, whereas in *Baurutitan* and *Laplataosaurus* it extends to a point between caudals 9 and 12. Conversely, in basal titanosaurians such as *Andesaurus* and *Epachthosaurus*, the CFL extends more distally than caudal 12. In caudal centra of these titanosaurian taxa, the distal termination of the CFL is variously determined by the occurrence of a ventrolaterally placed rim (*Neuquensaurus*), the complete replacement of the primary lateral surface by the secondary lateral surface (*Baurutitan*, *Laplataosaurus*) or the presence of a longitudinal ridge at the approximate dorsoventral midline (*Andesaurus*, *Epachthosaurus*). This point also corresponds to the disappearance of transverse processes (in, for example, *Baurutitan* and *Neuquensaurus*) or their putative continuation as vestiges (e.g. *Andesaurus*). Changes in the size and shape of the haemal arches also occur at this point in the tail (see Otero et al. 2012). Therefore, three evolutionary states for the distal termination of the CFL may be inferred in Titanosauria: at caudal 17 or more distally (state 0); between caudals 9 and 12 (state 1) or at caudal 8 (state 2). This hypothesis may be tested in other titanosaurian taxa for which the caudal sequence is well represented (e.g. *Gondwanatitan faustoi*, see Kellner and de Azevedo 1999, p. 118, fig. 6; *Trigonosaurus pricei*, see Campos et al. 2005, p. 585, figs. 25 and 26; two Brazilian titanosaurians that we regard as exhibiting state 1).

Finally, although a detailed reconstruction of the caudofemoral musculature in non-titanosaurian macronarians is outside the scope of this study, we will briefly comment on the condition in the basal macronarian *Camarasaurus* spp. to help place our conclusions for Titanosauria into a broader phylogenetic context. In *Camarasaurus*, significant morphological changes in the tail skeleton are observed at approximately caudals 12–14. Specifically, at this point in the tail, the transverse processes disappear, but a well-defined ridge or protuberance divides the lateral aspect of the centrum into two convex surfaces (Gilmore 1925; McIntosh et al. 1996; LMI personal observation). In caudals 12–13 of the nearly complete juvenile *Camarasaurus lentus* CM 11338, this ridge is placed at the approximate dorsoventral midline of the centrum, whereas in caudal 14, it is situated near the ventral margin. Immediately distal to this latter vertebra (i.e. on caudals 15–16), the ridge rises dorsally to a position adjacent to the neurocentral suture. Taking this series of morphological changes into account, we preliminarily consider that the CFL may have terminated at approximately caudal 14 in *Camarasaurus*. If so, the distal extent of the CFL past caudal 12 may represent the plesiomorphic condition for Macronaria. The persistence of the lateral protuberances – possibly rudimentary transverse processes – distal to this portion of the tail may also represent a plesiomorphic state for this clade. These

hypotheses are consistent with our interpretation of the caudal morphologies of the basal titanosaurs *Andesaurus* and *Epachthosaurus*.

Morphofunctional implications

An in-depth analysis of the biomechanical function of the titanosaurian caudal soft-tissues reconstructed herein is beyond the scope of this study. However, we will discuss some functional implications of these soft-tissues, particularly the caudofemoral musculature. In extant crocodylians, the principal function of the caudofemoral muscles (the CFL and CFB) is to retract the femur (Bonnar 2004). The function of this musculature is modified in birds, where it has been decoupled from terrestrial locomotion and is instead adapted for flight control and a bipedal stance. Two main factors should be considered when reconstructing the function of the caudofemoral musculature in non-avian dinosaurs: the evolution of the fourth trochanter and the insertion angle of the CFL. In non-avian theropods, the fourth trochanter is prominent in basal taxa (e.g. Ceratosauria, Allosauroidea), whereas in derived forms (e.g. Maniraptora) it is weakly developed or absent (Gatesy 1995; Hutchinson 2001b). In titanosaurian sauropods, as in crocodylians and lepidosaurs, the fourth trochanter is strongly developed for the insertion of the caudofemoral musculature. However, its position on the femoral shaft varies within the group. Unfortunately, the femur of *Andesaurus* is not completely preserved (Calvo and Bonaparte 1991; Mannion and Calvo 2011); however, in another basal titanosaur, *Epachthosaurus* (UNPSJB-PV 920), the total length of this bone is 110 cm (Martínez et al. 2004). In the latter taxon, the proximodistal midpoint of the fourth trochanter is placed some 49.5 cm from the proximal end of the femur (i.e. at 45.0% of femoral length) (Figure 7(A)). Conversely, in the saltasaurine *Neuquensaurus*, the femur MCS-9 is 81 cm in length (Salgado et al. 2005), whereas the fourth trochanter is placed ~33 cm from the proximal end (40.7%) (Figure 7(B)). These measurements indicate that, in *Neuquensaurus*, the fourth trochanter is relatively closer to the femoral head than it is in *Epachthosaurus*.

The differing positions of the fourth trochanter, and therefore the insertion of the caudofemoral musculature, between these two titanosaurian taxa suggest differences in their locomotor function. Bonnar (2004) stated that the relative position of the fourth trochanter on the sauropod femoral shaft may have influenced the functional aspects of this bone; specifically, he argued that a more proximally positioned fourth trochanter would increase the range of femoral retraction, although simultaneously decreasing the torque (i.e. the turning moment of the shaft) about the femoral head. Therefore, the more proximal fourth trochanter of *Neuquensaurus* suggests that, relative to *Epachthosaurus*, this Patagonian saltasaurine had a greater range of femoral retraction but experienced less torque on its femoral head. Moreover, the effectiveness of a joint is a

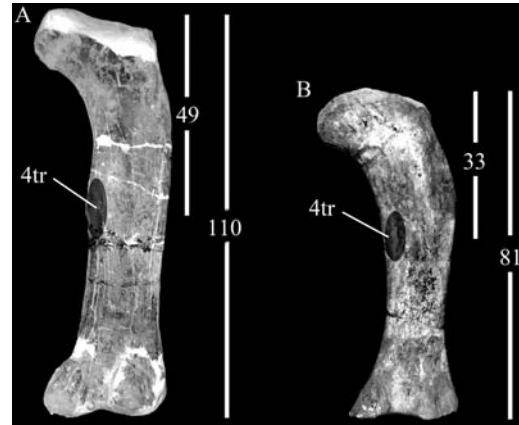


Figure 7. Right femora of basal titanosaurian *E. sciutoi* (UNPSJB-PV 920) (A) and saltasaurine *N. australis* (MCS-9) (B) in caudal view, indicating position of the fourth trochanter and the distance (in cm) of this structure from the proximal extreme of the femur. Total proximodistal length of the femur is also indicated (in cm). *Abbreviation*: 4tr, fourth trochanter.

function of the distance of the tendon of insertion (in this case the common tendon that united the CFB and CFL and inserted on the fourth trochanter) from the axis of movement (in this case the femoral head). Therefore, the closer the ‘pull angle’ (i.e. the angle between the action line of the muscle and the mechanical axis of the femur) to 90°, the greater the effectiveness. Our analysis suggests that, because the CFL is reconstructed as much shorter in *Neuquensaurus* than it is in *Epachthosaurus*, the femoral pull angle was closer to a right angle in the former taxon than it was in the latter (Figure 6(A),(C)).

In addition to their relationships to soft-tissues, the morphofunctional aspects of a given vertebrate taxon are tightly correlated with its osteological features as well. For example, although hyposphene–hypantrum articulations are present in the dorsal vertebrae of most saurischian dinosaur clades, these accessory intervertebral articulations are absent in saltasaurid titanosaurs (Wilson and Carrano 1999; Apesteguía 2005). Although the caudal dorsal vertebrae of selected titanosaurian taxa (e.g. *Epachthosaurus*; Martínez et al. 2004) combine a convex cranial centrum surface with accessory articulations, the evolution of strongly opisthocoealous caudal dorsals in Titanosauria was generally accompanied by the loss of hyposphene–hypantrum articulations. Wilson and Carrano (1999) suggested that this adjustment increased the range of trunk motion in Saltasauridae. Because a similar ball-and-socket morphology is present in the caudal vertebrae of many titanosaurs, comparable flexibility probably extended into the tail as well. Dorsal tail motion was also enhanced by the biconvexity of the first caudal vertebra present in several derived titanosaurian taxa such as *Alamosaurus* (Gilmore 1946), *Baurutitan* (Kellner et al. 2005), *Pellegrinisaurus* (Salgado 1996) and possibly *Aeolosaurus* (Salgado et al.

1997b). Combined with the procoelous centra of successive vertebrae, this conferred far more flexibility to the tails of derived titanosaurs than in other sauropods (Wilson and Carrano 1999). Therefore, although this hypothesis must be evaluated by detailed studies, based on the aforementioned morphofunctional inferences, the tail of *Neuquensaurus* and probably other saltasaurines may have been more functionally effective than those of more basal titanosaurs. *Neuquensaurus* could potentially attain a tripod position by using its tail as a prop; conversely, this stance might have been biomechanically or functionally difficult for a basal titanosaurian such as *Andesaurus* or *Epachthosaurus*.

One of the most notable aspects of the titanosaurian radiation is the diversity of body sizes that its constituent species attained; indeed, some titanosaurs reached sizes that have never been surpassed by any other continental vertebrate taxon. As mentioned by Otero and Vizcaíno (2008) and Gallina and Otero (2009), in titanosaurs, the CFL originated on the lateral and ventral surfaces of the caudal vertebrae as well as the lateral sides of the proximal haemal arches. With regard to this last feature, in the very large diplodocid sauropod *Seismosaurus* (= *Diplodocus*?; Lucas 2000) *hallorum*, the ventral extremes of the proximal haemal arches are proximodistally broad and paddle-shaped (see Gillette 1991, p. 428–429, figs. 9 and 10). This feature is not unique to that diplodocid, however: a closely comparable morphology is also present in the aforementioned undescribed gigantic titanosaur from southern Patagonia (LMI personal observation). Given that these taxa are not closely related, the resemblance of their haemal arches is clearly the result of homoplasy. We propose that these ventrally broad haemal arches may correspond to an increased surface of attachment for the CFL in these very large sauropods. Titanosaurs are recognised as possessing a ‘wide-gauge’ stance, a posture that influenced the line of action of the femoral retractor musculature (i.e. the adductor component of the CFL; Gallina and Otero 2009). Therefore, the broad surface of the haemal arches for the origin of the CFL present in large titanosaurs may have played an important role in femoral adduction. Finally, the aforementioned implications are being proposed without considering other aspects of titanosaurian skeletal and soft-tissue anatomy, such as cartilage, ligaments and internal bone texture. However, when the goal is to interpret morphofunctional patterns, simplifying the number of variables can be beneficial (Bonnar 2004).

Conclusions

The well-known caudal sequences of the titanosaurian sauropods *Andesaurus*, *Epachthosaurus*, *Baurutitan*, *Laplatasaurus*, *Pellegrinisaurus*, and *Neuquensaurus* constitute an excellent dataset for the reconstruction of musculature and other soft-tissues in this part of the titanosaurian body, and for interpreting the implications of these tissues for the

anatomy, phylogeny and functional morphology of this non-avian dinosaur clade. The EPB is a well-supported approach for the identification of osteological correlates of soft-tissues in extant titanosaurian relatives, limiting the level of speculation. Comparisons of the caudal skeletal morphology of various titanosaurian taxa reveal differences in characters that are herein interpreted as osteological correlates for the presence of soft-tissues, particularly the hypaxial musculature. The varying conditions of these correlates indicate that, in the taxa under investigation, the M. CFL had three distinct morphotypes that correspond to previously recognised grades in titanosaurian evolution (basal titanosaurs, non-saltasaurine lithostrotians and saltasaurines). As proposed by Salgado and García (2002) and later by Gallina and Otero (2009), the caudofemoral musculature probably played an important role in the evolution of titanosaurian caudal vertebral morphologies. Furthermore, the position of the fourth trochanter as well as the angle formed by the insertion of the common caudofemoralis tendon on this structure may have had important morphofunctional implications for titanosaurs. Finally, based on the osteological and inferred soft-tissue anatomy of the saltasaurine *Neuquensaurus*, the tail of this taxon may have had greater flexibility and capacity for withstanding stress than those of basal titanosaurians (e.g. *Andesaurus*, *Epachthosaurus*) and non-saltasaurine lithostrotians (e.g. *Baurutitan*). More detailed studies and future fossil discoveries may shed light on the soft-tissue interpretations proposed herein.

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References

- Apesteguía S. 2005. Thunder-lizards: the sauropodomorph dinosaurs. In: Tidwell V, Carpenter K, editors. Evolution of the hyposphene–hypantrum complex within Sauropoda. Chapter 12. Bloomington: Indiana University Press. p. 248–267.

- Baumel JJ. 1988. Functional morphology of the tail apparatus of the pigeon (*Columba livia*). *Adv Anat Embryol Cel.* 110:1–115.
- Berman SL, Raikow RJ. 1982. The hindlimb musculature of the mousebirds (Coliiformes). *Auk.* 99:41–57.
- Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la provincia de Neuquén, Argentina. *Ameghiniana.* 30(3):271–282.
- Bonaparte JF, Powell J. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda–Coelurosauria–Carnosauria–Aves). *Bull Soc Geol Fr.* 59:19–28.
- Bonnan MF. 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. *J Vertebr Paleontol.* 23(3):595–613.
- Bonnan MF. 2004. Morphometric analysis of humerus and femur shape in Morrison sauropods: implications for functional morphology and paleobiology. *Paleobiology.* 30(3):444–470.
- Calvo JO, Bonaparte JF. 1991. *Andesaurus delgadoi* gen. et sp. nov. (Saurischia–Sauropoda), dinosaurio Titanosauridae de la Formación Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. *Ameghiniana.* 28(3–4):303–310.
- Campos DA, Kellner AWA, Bertini RJ, Santucci RM. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arq Mus Nac Rio de Janeiro.* 63(3):565–593.
- Carrano MT. 2005. The sauropods: evolution and paleobiology. In: Curry Rogers K, Wilson JA, editors. *The evolution of sauropod locomotion: morphological diversity of a secondarily quadrupedal radiation.* Chapter 8. Berkeley: University of California Press. p. 229–251.
- Casal GA, Ibricic LM. 2010. Materiales asignables a *Epachthosaurus* Powell, 1990 (Sauropoda: Titanosauria), de la Formación Bajo Barreal, Cretácico Superior, Chubut, Argentina. *Rev Bras Paleontol.* 13(3):247–256.
- Casal G, Martínez R, Luna M, Scitutto JC, Lamanna M. 2007. *Aeolosaurus colhuehuapensis* sp. nov. (Sauropoda, Titanosauria) de la Formación Bajo Barreal, Cretácico Superior de Argentina. *Rev Bras Paleontol.* 10(1):53–62.
- Cerda IA, Paulina Carabajal A, Salgado L, Coria RA, Reguero MA, Tambussi CP, Moly JJ. 2012. The first record of a sauropod dinosaur from Antarctica. *Naturwissenschaften.* 99:83–87.
- Curry Rogers K. 2005. The sauropods: evolution and paleobiology. In: Curry Rogers K, Wilson JA, editors. *Titanosauria: a phylogenetic overview.* Chapter 2. Berkeley: University of California Press. p. 50–103.
- Curry Rogers K. 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *J Vertebr Paleontol.* 29(4):1046–1086.
- Curtice BD. 1999. Proceedings of the Southwest Paleontological Symposium. In: McCord RD, Boaz D, editors. *A report on the utility of sauropod caudal vertebrae for generic identification and of the first occurrence of Apatosaurus in Arizona.* Mesa: Mesa Southwest Museum and Southwest Paleontological Society. p. 39–48.
- D’Emic MD, Wilson JA. 2010. New remains attributable to the holotype of the sauropod dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics. *Acta Palaeontol Pol.* 56(1):61–73.
- Dodson P. 1990. The Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. *Sauropod paleoecology.* Chapter 17. Berkeley: University of California Press. p. 402–407.
- Erickson GM, Lappin AK, Larson P. 2005. Androgynous rex – the utility of chevrons for determining the sex of crocodylians and non-avian dinosaurs. *Zoology.* 108(4):277–286.
- Farlow JO. 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs. *Paleobiology.* 13(1):60–72.
- Frey E, Reiss J, Tarsitano SF. 1989. The axial tail musculature of Recent crocodiles and its phyletic implications. *Am Zool.* 29(3):857–862.
- Gallina PA, Otero A. 2009. Anterior caudal transverse processes in sauropod dinosaurs: morphological, phylogenetic and functional aspects. *Ameghiniana.* 46(1):165–176.
- Galton PM. 1969. The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia). *Postilla.* 131:1–64.
- Gangl D, Weissengruber GE, Egerbacher M, Forstenpointner G. 2004. Anatomical description of the muscles of the pelvic limb in the ostrich (*Struthio camelus*). *Anat Histol Embryol J Vet Med C.* 33(2):100–114.
- Gatesy SM. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology.* 16(2):170–186.
- Gatesy SM. 1995. Functional morphology in vertebrate paleontology. In: Thomason JJ, editor. *Functional evolution of the hindlimb and tail from basal theropods to birds.* Cambridge: Cambridge University Press. p. 219–234.
- Gatesy SM. 1997. An electromyographic analysis of hindlimb function in *Alligator* during terrestrial locomotion. *J Morphol.* 234(2):197–212.
- Gatesy SM. 1999. Guineafowl hind limb function. II: electromyographic analysis and motor pattern evolution. *J Morphol.* 240:127–142.
- Gatesy SM, Dial KP. 1996. Locomotor modules and the evolution of avian flight. *Evolution.* 50(1):331–340.
- Gauthier J. 1986. The origin of birds and the evolution of flight: memoirs of the California Academy of Sciences, no. 8. In: Padian K, editor. *Saurischian monophyly and the origin of birds.* San Francisco: California Academy of Sciences. p. 1–55.
- George JC, Berger AJ. 1966. *Avian myology.* New York City: Academic Press.
- Gillette DD. 1991. *Seisimosaurus halli* gen. et sp. nov., a new sauropod dinosaur from the Morrison Formation (Upper Jurassic/Lower Cretaceous) of New Mexico, USA. *J Vertebr Paleontol.* 11(4):417–433.
- Gilmore CW. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. *Mem Carnegie Mus.* 10(3):347–384.
- Gilmore CW. 1946. Reptilian fauna of the North Horn Formation of central Utah. *USDI Prof Paper.* 210-C:1–53.
- González Riga BJ. 2011. Paleontología y dinosaurios desde América Latina: Proceedings del III Congreso Latinoamericano de Paleontología. In: Calvo J, Porfiri J, González Riga BJ, Dos Santos D, editors. *Paleobiology of South American titanosaurs.* Mendoza: Universidad Nacional de Cuyo. p. 125–141.
- Holliday CM. 2009. New insights into dinosaur jaw muscle anatomy. *Anat Rec.* 292:1246–1265.
- Hone DWE, Keesey TM, Pisani D, Purvis A. 2005. Macroevolutionary trends in the Dinosauria: Cope’s rule. *J Evol Biol.* 18(3):587–595.
- Hudson GE, Lanzillotti PJ, Edwards GD. 1959. Muscles of the pelvic limb in galliform birds. *Am Midl Nat.* 61(1):1–67.
- Huene F von. 1929. Los saurisqueos y ornitisqueos del Cretáceo Argentino. *An Mus La Plata.* 3:1–196.
- Hutchinson JR. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zool J Linn Soc.* 131:123–168.
- Hutchinson JR. 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zool J Linn Soc.* 131:169–197.
- Hutchinson JR. 2002. The evolution of hindlimb tendons and muscles on the line to crown-group birds. *Comp Biochem Phys A.* 133:1051–1086.
- Hutchinson JR, Anderson FC, Blemker SS, Delp SL. 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(4):676–701.
- Hutchinson JR, Gatesy SM. 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology.* 26(4):734–751.
- Jasinowski SC, Russell AP, Currie PJ. 2006. An integrative phylogenetic and extrapolatory approach to the reconstruction of dromaeosaur (Theropoda: Eumaniraptora) shoulder musculature. *Zool J Linn Soc.* 146(3):301–344.
- Kellner AWA, Campos DA, Trotta MNF. 2005. Description of a titanosaurid caudal series from the Bauru Group, Late Cretaceous of Brazil. *Arq Mus Nac Rio de Janeiro.* 63(3):529–564.
- Kellner AWA, de Azevedo SAK. 1999. Proceedings of the Second Gondwana Dinosaur Symposium. In: Tomida Y, Rich TH, Vickers-Rich P, editors. *A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil.* Chapter 7. Tokyo: National Science Museum of Tokyo. p. 111–142.
- Livezey BC, Zusi RL. 2007. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II: analysis and prospects. *Zool J Linn Soc.* 149(1):1–95.
- Lucas SG. 2000. Dinosauria of New Mexico. In: Lucas SG, Heckert AB, editors. *The gastromyths of ‘Seisimosaurus,’ a Late Jurassic dinosaur from New Mexico.* Bulletin 17. Albuquerque: New Mexico Museum of Natural History and Science. p. 61–67.

- Mannion PD, Calvo JO. 2011. Anatomy of the basal titanosaur (Dinosauria, Sauropoda) *Andesaurus delgadoi* from the mid-Cretaceous (Albian–early Cenomanian) Río Limay Formation, Neuquén Province, Argentina: implications for titanosaur systematics. *Zool J Linn Soc.* 163(1):155–181.
- Martínez RD, Giménez O, Rodríguez J, Luna M, Lamanna MC. 2004. An articulated specimen of the basal titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciuttoi* from the early Late Cretaceous Bajo Barreal Formation of Chubut Province, Argentina. *J Vertebr Paleontol.* 24(1):107–120.
- McGowan C. 1979. The hind limb musculature of the brown kiwi, *Apteryx australis mantelli*. *J Morphol.* 160(1):33–73.
- McIntosh JS. 1990. The Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. *Sauropoda*. Chapter 16. Berkeley: University of California Press. p. 345–401.
- McIntosh JS, Miller WE, Stadtman KL, Gillette DD. 1996. The osteology of *Camarasaurus lewisi* (Jensen 1988). *Brigham Young U Geol Stud.* 41:73–115.
- O'Connor PM. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *J Morphol.* 267(10):1199–1226.
- Organ CL. 2006. Thoracic epaxial muscles in living archosaurs and ornithomimid dinosaurs. *Anat Rec A.* 288(7):782–793.
- Otero A, Gallina PA, Canale JI, Haluza A. 2012. Sauropod haemal arches: morphotypes, new classification and phylogenetic aspects. *Hist Biol.* 24(3):1–14.
- Otero A, Gallina PA, Herrera Y. 2010. Pelvic musculature and function of *Caiman latirostris*. *Herpetol J.* 20(3):173–184.
- Otero A, Vizcaíno SF. 2008. Hindlimb musculature and function of *Neuquensaurus australis* Lydekker (Sauropoda: Titanosauria). *Ameghiniana.* 45(2):333–348.
- Persons WS, Currie PJ. 2010. The tail of *Tyrannosaurus*: reassessing the size and locomotive importance of the M. caudofemoralis in non-avian theropods. *Anat Rec.* 294(1):119–131.
- Powell JE. 1990. *Epachthosaurus sciuttoi* (gen. et sp. nov.) un dinosaurio saurópodo del Cretácico de Patagonia (Provincia de Chubut, Argentina). *Congr Argentino Paleontol Bioestrat Tucumán Actas.* 1:123–128.
- Powell JE. 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. *Rec Queen Victoria Mus.* 111:1–173.
- Raikow RJ. 1970. Evolution of diving adaptations in the stiff-tail ducks. *U Calif Pub Zool.* 94:1–52.
- Romer AS. 1923. Crocodylian pelvic muscles and their avian and reptilian homologues. *B Am Mus Nat Hist.* 48:533–552.
- Salgado L. 1996. *P. powelli* nov. gen. et sp. (Sauropoda, Titanosauridae) from the Upper Cretaceous of Lago Pellegrini, northwestern Patagonia, Argentina. *Ameghiniana.* 33(4):355–365.
- Salgado L, Apesteguía S, Heredia SE. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. *J Vertebr Paleontol.* 25(3):623–634.
- Salgado L, Bonaparte JF. 2007. Patagonian Mesozoic reptiles. In: Gasparini Z, Salgado L, Coria RA, editors. *Sauropodomorpha*. Chapter 8. Bloomington: Indiana University Press. p. 188–228.
- Salgado L, Coria RA, Calvo JO. 1997a. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. *Ameghiniana.* 34(1):3–32.
- Salgado L, Coria RA, Calvo JO. 1997b. Presencia del género *Aeolosaurus* (Sauropoda, Titanosauridae) en la Formación Los Alamitos, Cretácico Superior de la Provincia de Río Negro, Argentina. *Rev U Guarulhos – Geociências.* 2(6):44–49.
- Salgado L, García R. 2002. Variación morfológica en la secuencia de vértebras caudales de algunos saurópodos titanosaurios. *Rev Esp Paleontol.* 17(2):211–216.
- Sander PM, Christian A, Clauss M, Fehner R, Gee CT, Griebeler E-M, Gunga H-C, Hummel J, Mallison H, Perry SF, et al. 2010. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biol Rev.* 86(1):117–155.
- Santucci RM, Bertini RJ. 2006a. A new titanosaur from western São Paulo state, Upper Cretaceous Bauru Group, south-east Brazil. *Palaeontology.* 49(1):59–66.
- Santucci RM, Bertini RJ. 2006b. A large sauropod titanosaur from Peirópolis, Bauru Group, Brazil. *Neues Jahrb Geol P M.* 2006(6):344–360.
- Schreweis DO. 1982. A comparative study of the appendicular musculature of penguins (Aves: Sphenisciformes). *Sm C Zool.* 341:1–46.
- Schulin R. 1987. Hind limb myology and phylogenetic relationships of the Australian magpie goose *Anseranas semipalmata* (Latham). *Zool Jahrb Anat Ontog.* 116(2):217–243.
- Schwarz-Wings D. 2009. Reconstruction of the thoracic epaxial musculature of diplodocid and dicraeosaurid sauropods. *J Vertebr Paleontol.* 29(2):517–534.
- Schwarz-Wings D, Frey E, Martin T. 2009. Reconstruction of the bracing system of the trunk and tail in hyposaurine dyrosaurids (Crocodylomorpha; Mesoeucrocodylia). *J Vertebr Paleontol.* 29(2):453–472.
- Sereno PC. 1997. The origin and evolution of dinosaurs. *Annu Rev Earth Pl Sci.* 25:435–489.
- Tarsitano SF. 1981. Pelvic and hindlimb musculature of archosaurian reptiles. Unpublished Ph.D. thesis. New York: The City University of New York. 191 pp.
- Tsuihiji T. 2004. The ligament system in the neck of *Rhea americana* and its implication for the bifurcated neural spines of sauropod dinosaurs. *J Vertebr Paleontol.* 24(1):165–172.
- Upchurch P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zool J Linn Soc.* 124:43–103.
- Upchurch P, Barrett PM, Dodson P. 2004. The Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. *Sauropoda*. Chapter 13. 2nd ed. Berkeley: University of California Press. p. 259–322.
- Vanden Berge JC. 1970. A comparative study of the appendicular musculature of the Order Ciconiiformes. *Am Midl Nat.* 84(2):289–364.
- Vanden Berge JC, Zweers GA. 1993. Handbook of avian anatomy: Nomina Anatomica Avium. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, editors. *Myologia*. Chapter 23. 2nd ed. Cambridge: Nuttall Ornithological Club. p. 189–250.
- Verstappen M, Aerts P, De Vree F. 1998. Functional morphology of the hindlimb musculature of the black-billed magpie, *Pica pica* (Aves, Corvidae). *Zoomorphology.* 118:207–223.
- Wedel MJ. 2009. Evidence for bird-like air sacs in saurischian dinosaurs. *J Exp Zool.* 311A(8):611–628.
- Wilhite R. 2003. Biomechanical reconstruction of the appendicular skeleton in three North American Jurassic sauropods. Unpublished Ph.D. thesis. Baton Rouge: Louisiana State University. 185 pp.
- Wilson JA. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *J Vertebr Paleontol.* 19(4):639–653.
- Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zool J Linn Soc.* 136(2):217–276.
- Wilson JA. 2005. Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. *Paleobiology.* 31(3):400–423.
- Wilson JA, Carrano MT. 1999. Titanosaurs and the origin of 'wide-gauge' trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology.* 25(2):252–267.
- Witmer LM. 1995. Functional morphology in vertebrate paleontology. In: Thomason JJ, editor. *The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils*. Chapter 2. Cambridge: Cambridge University Press. p. 19–33.
- Witmer LM. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Soc Vertebr Paleontol Mem.* 3:1–73.
- Yates AM, Kitching JW. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proc R Soc B.* 270(1525):1753–1758.