



Anais da Academia Brasileira de Ciências

ISSN: 0001-3765

aabc@abc.org.br

Academia Brasileira de Ciências

Brasil

GRILLO, ORLANDO N.; AZEVEDO, SERGIO A.K.

Pelvic and hind limb musculature of *Staurikosaurus pricei* (Dinosauria: Saurischia)

Anais da Academia Brasileira de Ciências, vol. 83, núm. 1, marzo, 2011, pp. 73-98

Academia Brasileira de Ciências

Rio de Janeiro, Brasil

Available in: <http://www.redalyc.org/articulo.oa?id=32717681004>

- How to cite
- Complete issue
- More information about this article
- Journal's homepage in redalyc.org

redalyc.org

Scientific Information System

Network of Scientific Journals from Latin America, the Caribbean, Spain and Portugal

Non-profit academic project, developed under the open access initiative



Anais da Academia Brasileira de Ciências (2011) 83(1): 73-98
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
www.scielo.br/aabc

Pelvic and hind limb musculature of *Staurikosaurus pricei* (Dinosauria: Saurischia)

ORLANDO N. GRILLO and SERGIO A.K. AZEVEDO

Departamento de Geologia e Paleontologia, Museu Nacional/UFRJ
Quinta da Boa Vista, s/n, São Cristóvão, 20940-040 Rio de Janeiro, RJ, Brasil

Manuscript received on January 15, 2010; accepted for publication on June 21, 2010

ABSTRACT

The study of pelvic and hind limb bones and muscles in basal dinosaurs is important for understanding the early evolution of bipedal locomotion in the group. The use of data from both extant and extinct taxa placed into a phylogenetic context allowed to make well-supported inferences concerning most of the hind limb musculature of the basal saurischian *Staurikosaurus pricei* Colbert, 1970 (Santa Maria Formation, Late Triassic of Rio Grande do Sul, Brazil). Two large concavities in the lateral surface of the ilium represent the origin of the muscles *iliotrochantericus caudalis* plus *iliofemoralis externus* (in the anterior concavity) and *iliofibularis* (in the posterior concavity). Muscle *ambulatorius* has only one head and originates from the pubic tubercle. The origin of *puboischiofemoralis internus 1* possibly corresponds to a fossa in the ventral margin of the preacetabular iliac process. This could represent an intermediate stage prior to the origin of a true preacetabular fossa. Muscles *caudofemorales longus* et *brevis* were likely well developed in *Staurikosaurus* is unique in bearing a posteriorly projected surface for the origin of *caudofemoralis brevis*.

Key words: extant phylogenetic bracket, locomotion, muscular reconstruction, Saurischia, *Staurikosaurus pricei*.

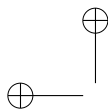
INTRODUCTION

Bipedalism is a form of locomotion adopted by few groups of animals (Alexander 2004, Gatesy and Biewener 1991, Hutchinson and Gatesy 2006, McGowan 1999). Dinosaurs first evolved as bipedal animals and all living representatives of this clade are bipeds. The evolution of this type of locomotion is associated with several modifications in posture, orientation of the hind limbs, as well as correlated osteological and myological modifications. Understanding bipedal locomotion in dinosaurs requires multidisciplinary approach.

According to Lockley and Gillette (1989), studies of trackways dating from the 19th century allowed the estimate of velocity (Alexander 1976, Farlow 1981, Day et al. 2002) and posture (Coombs 1980, Ishigaki 1989,

Thulborn 1989, Wade 1989, Jones et al. 2000, Delfino 2002) of dinosaurs. Comparisons with living animals have often been used (e.g. Paul 1988, 1998, Coombs 1999, 2001, Jones et al. 2000, Hutchinson 2000). New studies using advanced graphic computational and engineering principles (e.g., Gatesy et al. 1999, Thulborn 2001, Hutchinson and Garcia 2002, Wilhite 2002) and computed tomography (e.g., Carrier et al. 2001, Rayfield et al. 2001) also revealed important aspects of posture and locomotion, such as mass and center of mass position (e.g., Henderson 1999, Seebacher 2000). In addition, muscle reconstructions have led to new positions about dinosaur locomotion (e.g., Hutchinson et al. 2005).

The first reconstruction of dinosaur pelvis



(Romer 1923a, b, Colbert 1964, Coombs 1979). More recent works (e.g., Dilkes 2000, Hutchinson 2001a, b, 2002, Carrano and Hutchinson 2002, Langer 2003) made more extensive use of avian data, resulting in reconstructions that are consistent with the phylogenetic positions of the studied taxa.

Witmer (1995, 1997) proposed a methodology (Extant Phylogenetic Bracket, EPB) based on phylogenetic relationships and parsimony that allows the reconstruction of soft tissue features in extinct animals using an accurate approach (see also Bryant and Russell 1992 for an independently-devised but similar approach). EPB is suitable for muscle reconstructions, requiring a minimal level of speculation, and can be improved if associated with data from extinct species with close phylogenetic affinities. This association can reveal important osteological transformations that sometimes are not clear when the study relies only on data from extant species (Hutchinson 2001a). Several works on dinosaur limb muscle reconstruction have used the EPB (Dilkes 2000, Gatesy 1990, Hutchinson and Gatesy 2000, Hutchinson 2001a, b, 2002, Carrano and Hutchinson 2002, Langer 2003, Jasinoski et al. 2006). Most of these studies focused mainly on questions related to the origin and evolution of avian locomotion (Gatesy 1999, Hutchinson 2001a, b, 2002). Some authors presented simplified propositions for musculature and locomotion in basal dinosaurs (Carrano 2000, Hutchinson and Gatesy 2000, Hutchinson 2001a, b, 2002), but no detail on the locomotion in the earliest dinosaurs was provided.

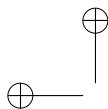
The evolutionary success of Dinosauria, including birds, has often been attributed to their bipedal and erect posture that freed their hands from a locomotor function, allowing their use for capturing and manipulating prey (Paul 1988) and later for flight. Accordingly, the study of the locomotion on the early evolution of Dinosauria is very important for understanding its success of more than 225 million years. A detailed muscular reconstruction of given taxa may help to resolve specific points and may also contribute to understanding major transformations that took place between basal

provided for only two species: *Tyrannosaurus rex* (see Carrano and Hutchinson 2002) and *Saturnalia tupini-quim* (see Langer 2003). The work of Langer (2003) represents the most detailed muscular reconstruction for a basal dinosaur, and the results were presented as representative of a general condition shared by basal dinosauriforms (e.g., *Marasuchus* and *Pseudolagosuchus*) and basal dinosaurs, such as *Herrerasaurus*, *Staurikosaurus*, *Guaibasaurus* and basal species of the groups Theropoda, Ornithischia and Sauropodomorpha (Langer 2003).

Remains of basal dinosaurs are often very incomplete or poorly preserved, which may lead to uncertainties when muscular reconstructions are attempted. Therefore, it is important to evaluate muscle arrangement in other basal dinosaurs in order to complement previous works. Also, the study of the pelvic and hind limb musculature in other basal dinosaurs may confirm the hypothesis of Langer (2003) of a shared general construction in several basal members of the group. In this work we propose a detailed reconstruction of the pelvic and hind limb musculature of the basal Saurischian *Staurikosaurus pricei* Colbert, 1970. This taxon represents one of the most complete basal dinosaurs found in south Brazil (Santa Maria Formation, Late Triassic, Rio Grande do Sul), and its remains may reveal important features for understanding the early evolution of locomotion in Dinosauria.

ABBREVIATIONS

ar	adductor ridge (= <i>linea aspera</i>)
bs	brevis shelf
C1-25	1 st to 25 th caudal vertebra
D11-15	11 th to 15 th dorsal vertebra
dris	dorsal ridge of ischium
EPB	Extant Phylogenetic Bracket
ir	ischial ridge
is	ischium
it	ischial tuberosity
lia	<i>linea intermuscularis cranialis</i>
lip	<i>linea intermuscularis caudalis</i>
M.	muscle
Mm.	muscles
mr1	first medial iliac ridge



PELVIC AND HIND LIMB MUSCLES OF *STAURIKOSAURUS*

pf	preacetabular fossa
pib	preacetabular iliac border
pst	<i>processus supratrochantericus</i>
pt	pubic tubercle
pu	pubis
rea	rough expanded area
S1-2	1 st and 2 nd sacral vertebra
str	striations

MATERIALS AND METHODS

In order to determine the areas of origin and insertion of the pelvic and hind limb muscles of *Staurikosaurus pricei*, the holotype MCZ 1669, deposited at the Museum of Comparative Zoology (Harvard University), as well as its cast (MN 6104-V), deposited at the Museu Nacional (Universidade Federal do Rio de Janeiro), were examined.

Firstly, based on recent studies on the evolution of the archosaur pelvic and hind limb osteology (Gatesy 1990, Hutchinson 2001a, b, 2002), the homologies between bone surfaces correlated with muscle attachments, were traced between extant taxa (Crocodylia and Aves) and *Staurikosaurus*. In this study we accept the general conclusion that *Staurikosaurus* was a herrerasaurid, which is considered as a basal saurischian (Fig. 1A) according to most recent works (Yates 2003, Langer 2004, Leal et al. 2004, Bittencourt and Kellner 2009). Additional osteological data were obtained from the direct examination of specimens from the osteological collection of the Museu Nacional, namely: *Tupinambis* sp. (Squamata, Teiidae; 04AC), *Caiman yacare* (Crocodylia, Crocodylidae; 05AC, 06AC and 07AC) and *Dendrocygna viduata* (Aves, Anseriformes, Anatidae; 14AC). Data was also gathered from the literature for the following taxa: fossils and living Crurotarsi (Gregory and Camp 1918, Romer 1923c, Troxell 1925, Parrish 1987, Long and Murry 1995, Galton 2000, Schwarz and Salisbury 2005), Dinosauromorpha and basal dinosaurs, including Herrerasauridae (Novas 1992, 1993, 1996, Sereno and Arcucci 1993, 1994, Long and Murry 1995, Bonaparte 1996, Hunt et al. 1998, Bonaparte et al. 1999), non-avian Theropoda (Osborn 1905,

man 1990, Raath 1990, Rowe and Gauthier 1990, Sereno 1993, Makovicky and Sues 1998, Sampson 1998, Norell and Makovicky 1999, Currie 2000, Carrano and Hutchinson 2002, Carrano et al. 2002, and Chen 2001, Ji et al. 2003, Kobayashi and Li 2003, Calvo et al. 2004, Huang et al. 2004, Naish et al. 2004, Coria and Currie 2006, Xu et al. 2006), Sauropodomorpha (Osborn 1904, Galton 1984, Ostrom and Madsen 1999, Langer 2003, Yates 2003, Leal et al. 2004), other extinct and extant sauropsid taxa, including Ankylosauria (Romer 1922, 1956, Goodrich 1958, Zaaf et al. 2004), Russell and Bels 2001, Paul 2002, Sen 2003, and 2004).

The phylogenetic framework adopted here (Fig. 1A) is congruent with the tree used by Hutchinson (2001a, b, 2002) and those of Benton and Clark (1999), Benton (1999), Sereno (1997, 1999), Holtz (1994), Gauthier et al. (1999), Norell et al. (2001), Huang et al. (2004), Leal et al. (2004), Lloyd et al. (2008), and other phylogenies presented in several of the works cited in the previous paragraph.

In order to define the correlations between bone surfaces and muscle origins and insertions we used the Extant Phylogenetic Bracket (EPB) method (Witmer 1997). EPB allows the use of data from one (or more) extant taxa, which represent the sister groups to a given extinct taxon, in order to infer the relationships of the latter with minimal speculation, i.e., with parsimony (Fig. 1B). One of the extant taxa needs to be the living sister group of the extinct taxon, and this taxon needs to have the other extant taxon as the living sister group. EPB was applied to verify the congruence of the reconstruction for each muscle of *Staurikosaurus*. As for any non-avian dinosaur, its closest extant taxa are Crocodylia and Aves (Fig. 1B). EPB was applied to the use of an extensive phylogenetic framework of extant taxa, which facilitates the identification of homologies when the extant taxa are highly divergent, as in the case with Crocodylia and Aves.

We adopted the “levels of inference” of the EPB as a metric of the level of speculation in the phylogenetic reconstruction, according to Witmer (1995, 1997).

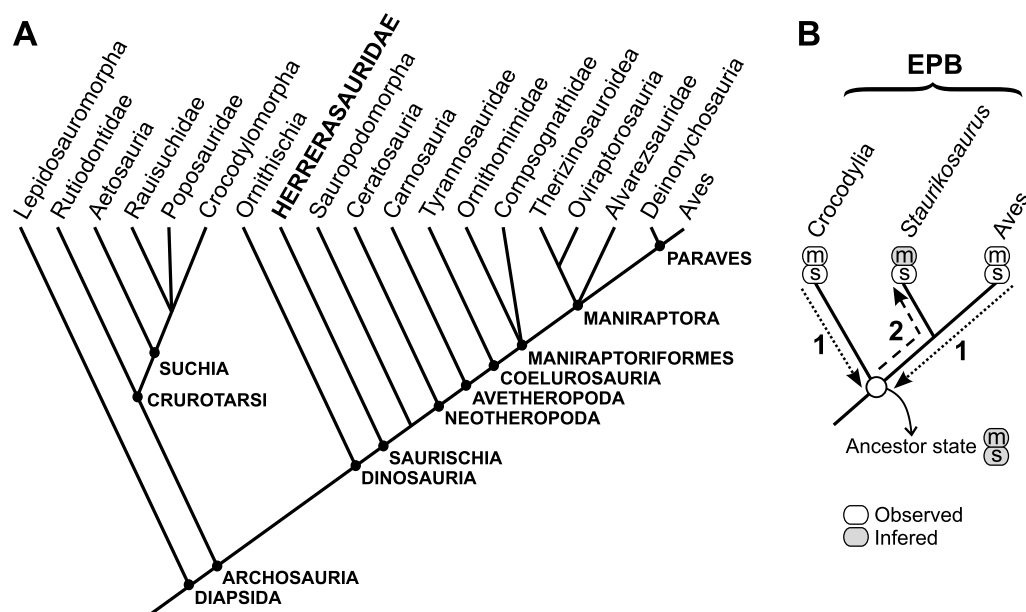


Fig. 1 – Phylogenetic framework adopted in this study, depicting the position of Herrerasauridae (A) and the application of the EPB to *Staurikosaurus* muscle reconstruction (B): (1) Inference of the status of the osteological structure (s) and muscle (m) in the closest common ancestor of the extant taxa from the observation of the extant taxa; (2) if the inference indicates that the muscle was present in the ancestor, the most parsimonious condition indicates that it was also present in the extinct taxon (*Staurikosaurus*). Inferences are shown in gray circles (adapted from Witmer 1997).

spond to a revision of the work of Gadow (1880), Romer (1923c) and Rowe (1986).

RESULTS

The reconstruction of the pelvic and hind limb musculature of *Staurikosaurus* will be presented following the order on Table I. For each muscle, the condition observed in Crocodylia and Aves will be presented along with the preserved osteological evidence that supports the inferences for *Staurikosaurus*. The final reconstruction is presented in Table II and Figure 2.

TRICEPS FEMORIS

Mm. iliotibiales (IT1, IT2 and IT3) – Muscle (M.) *iliotibialis* is a superficial, thin, large lamina in Crocodylia and Aves, and is composed of three heads that originate along the anterior and dorsal margins of the lateral ilium (Romer 1923c, Carrano and Hutchinson 2002). Superfi-

in *Saturnalia* that he supposed to be homologous with an expanded area in *Herrerasaurus*, *Caseosaurus*, and other dinosaurs (Fig. 2 and 3F). This is continuous with the dorsal border of the ilium and was reconstructed as the origin of IT1 (Langer 2003).

This rough expanded area is also present, although less expanded, in other Diapsida, including Lepidosauromorpha. It seems correlated with the preacetabular iliac border (*pib*) because it is always adjacent to the dorsal extremity of that structure (Fig. 3). In some Suchia (Poposauridae and Raulisuchidae), the rough expanded area and the preacetabular iliac border are posteriorly dislocated along the lateral surface of the ilium, projecting over the supra-acetabular crest (Fig. 3D-F). Apparently, this condition is also present in Crocodylomorpha, as can be observed in the material from extant crocodiles, although an analysis of basal crocodiliforms is necessary to confirm the series of transformations between these taxa. In living crocodiles this rough area is



PELVIC AND HIND LIMB MUSCLES OF *STAUROKOSAURUS*

TABLE I

Homologies of the hind limb muscles in extant archosaurs (Modified from Hutchinson [2001a, 2002] and Carrano and Hutchinson [2002]). Although some variability exists within birds and crocodilians regarding muscle size, shape, and even presence, the condition listed represents the inferred condition for the common ancestor of each group (Carrano and Hutchinson 2002).

Crocodylia	Aves
DORSAL GROUP	
1. Triceps femoris	
M. iliotibialis 1 (IT1)	M. iliotibialis cranialis (IC)
Mm. iliotibiales 2, 3 (IT2, IT3)	M. iliotibialis lateralis (IL)
M. ambiens (AMB)	M. ambiens (AMB)
M. femorotibialis externus (FMTE)	M. femorotibialis lateralis (FMTL)
M. femorotibialis internus (FMTI)	M. femorotibialis intermedius (FMTIM) and M. femorotibialis medialis (FMTM)
M. iliofibularis (ILFB)	M. iliofibularis (ILFB)
2. Deep Dorsal	
M. iliofemoralis (IF)	M. iliofemoralis externus (IFE) and M. iliotrochantericus caudalis (ITC)
M. puboischiofemoralis internus 1 (PIFI1)	M. iliofemoralis internus (IFI)
M. puboischiofemoralis internus 2 (PIFI2)	M. iliotrochantericus cranialis (ITCR) and M. iliotrochantericus medius (ITM)
VENTRAL GROUP	
3. Flexor cruris	
M. puboischiotibialis (PIT)	[absent]
M. flexor tibialis internus 1 (FTI1)	[absent]
M. flexor tibialis internus 2 (FTI2)	[absent]
M. flexor tibialis internus 3 (FTI3)	M. flexor cruris medialis (FCM)
M. flexor tibialis internus 4 (FTI4)	[absent]
M. flexor tibialis externus (FTE)	M. flexor cruris lateralis pars pelvica (FCLP)
4. Mm. adductores femores	
M. adductor femoris 1 (ADD1)	M. puboischiofemoralis pars medialis (PIFM)
M. adductor femoris 2 (ADD2)	M. puboischiofemoralis pars lateralis (PIFL)
5. Mm. puboischiofemorales externi	
M. puboischiofemoralis externus 1 (PIFE1)	M. obturatorius lateralis (OL)
M. puboischiofemoralis externus 2 (PIFE2)	M. obturatorius medialis (OM)
M. puboischiofemoralis externus 3 (PIFE3)	[absent]
6. M. ischiotrochantericus (ISTR)	M. ischiofemoralis (ISF)
7. Mm. caudofemorales	
M. caudofemoralis brevis (CFB)	M. caudofemoralis pars pelvica (CFP)
M. caudofemoralis longus (CFL)	M. caudofemoralis pars caudalis (CFC)

and the preacetabular iliac border are also adjacent to the anterior limit of the M. *iliofemoralis* (Fig. 3F), as seen in Lepidosauromorpha (Fig. 3A).

terior part of the origin of this muscle should be to IT1 in dinosaurs, as occurs in *Alligator* (Fig. 3). The rough area is preserved in both ilia

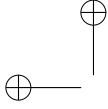


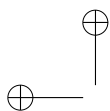
TABLE II
Muscles inferred as present in *Staurikosaurus pricei* and levels of inference required.

Muscle	Origin	Insertion
IT1	anterodorsal border of the ilium (I), in a rough expanded area (<i>are</i>)	tibial cnemial crest (I)
IT2	dorsal border of the ilium (I); posterior limit undefined	tibial cnemial crest (I)
IT3	dorsal border of the ilium (I); posterior limit between ILFB and FTE (I')	tibial cnemial crest (I)
AMB	pubic tubercle (I)	tibial cnemial crest (I)
FMTE	lateral surface of femoral shaft, between <i>lia</i> and <i>lip</i> (I)	tibial cnemial crest (I)
FMTI	lateral surface of femoral shaft, between <i>lia</i> and <i>ar</i> (I)	tibial cnemial crest (I)
ILFB	concavity on the lateral postacetabular surface of the ilium (I')	crest in the anterolateral margin of the fibula (I)
IFE	subtriangular concavity on the lateral surface of the ilium (I), posterior to ITC (II)	femoral trochanteric shelf (II)
ITC	subtriangular concavity on the lateral surface of the ilium (I), anterior to IFE (II)	anterior trochanter (II)
PIF1	? – medial surface of the ilium and in the sacral ribs (II) or in the iliac “preacetabular fossa” (II)	medial surface of the anteromedial proximal keel of the femur (II)
PIF2	last five (six?) dorsal vertebrae (II)	lateral surface of the anteromedial proximal keel of the femur (II); posterior tendon absent?
PIT	[probably absent]	[probably absent]
FT1	if present, in the distal ischial tubercle (not preserved; II')	if present, on a mark in the proximal caudomedial surface of the tibia (II)
FT2	lateral postacetabular surface of the ilium, posterior to FTE (II')	scar in the proximal caudomedial surface of the tibia (II)
FT3	ischial tuberosity (II) and adjacent concavity (?)	scar in the proximal medial surface of the tibia (I)
FT4	?	?
FTE	lateral postacetabular surface of the ilium, posterior to ILFB (I')	scar in the proximal medial surface of the tibia (I)
ADD1	? – anterior margin of the ischial obturator process (I')	posterior surface of the femoral shaft, between <i>lip</i> and <i>ar</i> (I)
ADD2	scar on the lateral surface of the ischium, dorsal to the ischiadic border (II)	posterior surface of the femoral shaft, between <i>lip</i> and <i>ar</i> (I)
PIFE1	anterior surface of the pubic apron (II)	femoral greater trochanter (I)
PIFE2	posterior surface of the pubic apron (II)	femoral greater trochanter (I)
PIFE3	caudoventral to the ischiadic border, between ADD1 and ADD2, on the lateral surface of the obturator process (II)	femoral greater trochanter (I)
ISTR	medial and dorsal surfaces of the ischium, adjacent to ADD2 (II)	proximal lateral surface of the femur (I), in a groove proximal to the trochanteric shelf
CFB	expanded medial surface of the iliac brevis fossa (II)	posterior lateral surface of the femur, between the fourth trochanter and <i>lip</i> (I)
CFL	caudal vertebral centra and transverse processes (at least from 1 to 25; I)	medial surface of the fourth trochanter (I); secondary tendon absent (II)

Herrerasaurus, differently, this area is larger in the ventral part, a condition also seen in *Marasuchus*. In *Staurikosaurus*, the origin of IT1 is supposedly located in the anterolateral margin of the cranial iliac process (Level I inference), in the dorsal portion of the rough area. The origin of IT2 extends along the ventral portion of this surface and continues to the dorsal margin of the ilium. The dorsal iliac border is not preserved in *Staurikosaurus*, so it is impossible to determine the exact limit between IT2 and IT3. Likewise, the posterior limit of IT3

In Aves, the posterior limit of *M. iliotibialis lateralis* (IL = IT2+3) is located between the areas of origin of *M. flexor cruris lateralis pars pelvica* (FCLP = FTE) and ILFB (Fig. 2C). Accordingly, it is possible to infer the posterior limit of IT3 in *Staurikosaurus* from the position of ILFB and FTE (Level I' inference).

In living archosaurs, the three heads of *M. iliotibialis* converge together with *M. ambiens* and *Mm. femorotibiales*, forming a common extensor tendon that inserts onto the tibial cnemial crest (Romer 1923c,



PELVIC AND HIND LIMB MUSCLES OF *STAURIKOSAURUS*

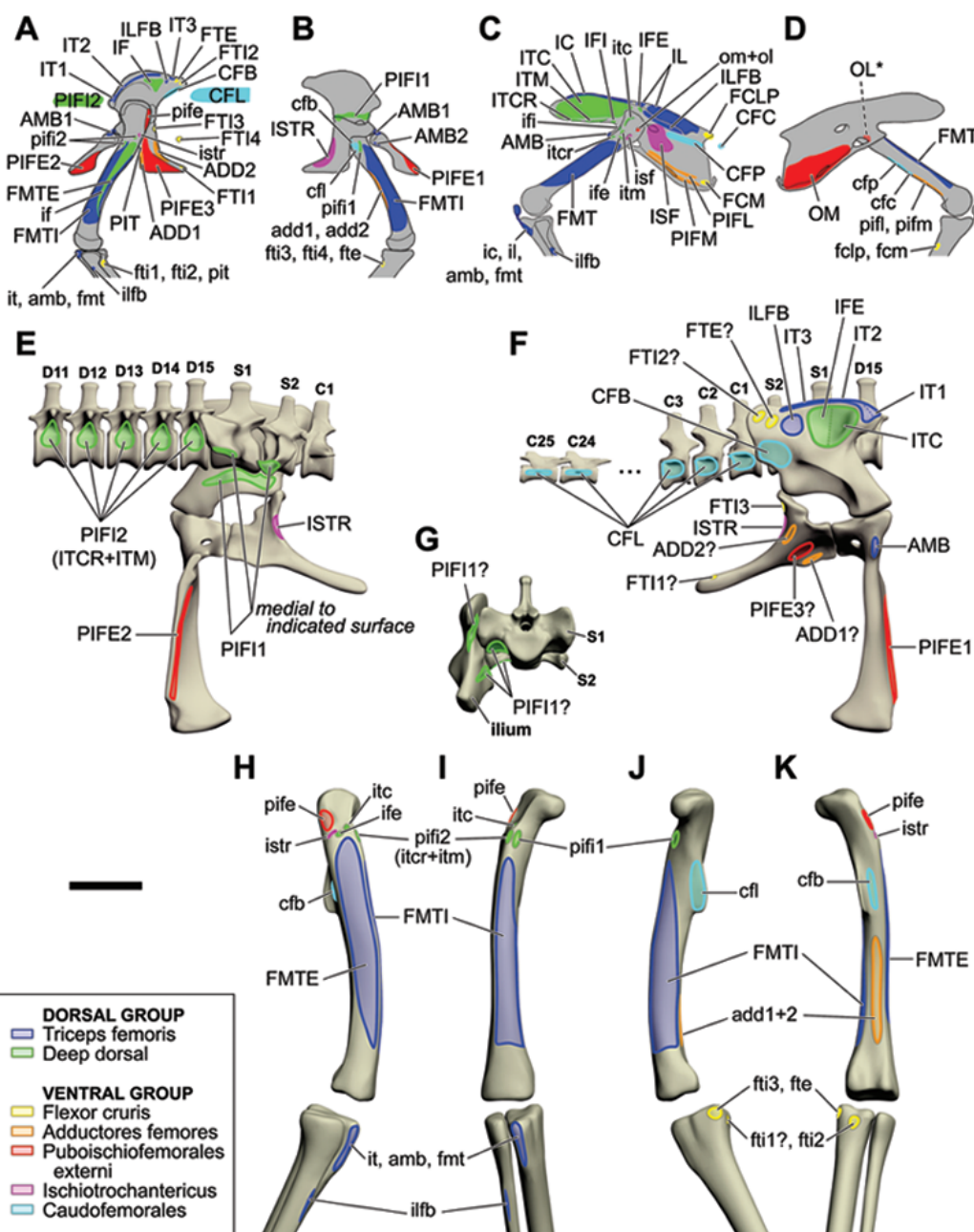


Fig. 2 – Areas of muscle origin (upper case) and insertion (lower case) in extant Crocodylia (A and B) and Aves (C and D), and reconstruction for *Staurikosaurus* indicated over a 3D reconstruction of the pelvis and vertebrae (E-G) and hind limb (H-K). Lateral view (A, C, F, H), medial view (B, D, E, J), anterior view (G, I) and posterior view (K). In G, it is shown the two possibilities for the origin of the muscle. Abbreviations followed by question mark indicate uncertain presence of the muscle or uncertain position on the area indicated (no clear evidence).



M. *ambiens* (AMB) – In extant Reptilia (including Aves), the origin of the *M. ambiens* is anteroventral to the acetabulum, often from a pubic tubercle (*pt*; Hutchinson 2001a). In Crocodylia, this structure is absent or reduced (Hutchinson 2001a), and *M. ambiens* is divided in two heads that originates on the cranial portion of the preacetabular cartilage and in the medial proximal region of the proximal pubis, but this condition is derived in relation to other Reptilia (Romer 1923c, Hutchinson 2002). The pubic tubercle of *Staurikosaurus* is preserved only on the left pubis (Fig. 5A) and is similar in shape to that of *Herrerasaurus*, *Saturnalia*, and *Lagerpeton*. The right pubis of *Staurikosaurus* has often been used to illustrate this bone in the taxon, but it is damaged in the region of the pubic tubercle. This leaded several authors (e.g., Colbert 1970, Galton 1977, Novas 1993) to propose that this structure was absent in *Staurikosaurus*. AMB inserts in the tibial cnemial crest, together with the Triceps *femoris* group (Romer 1923c, Hutchinson 2002). In extant archosaurs, AMB also has a secondary tendon that perforates the extensor tendon (Carrano and Hutchinson 2002, Hutchinson 2002). This tendon was probably also present in *Staurikosaurus*.

Mm. *femorotibiales* (FMTE and FMTI) – *M. femorotibialis* has two divisions in Crocodylia (*femorotibialis externus*, FMTE; *femorotibialis internus*, FMTI) and three in Aves (*femorotibialis lateralis*, FMTL; *femorotibialis intermedius*, FMTIM; *femorotibialis medialis*, FMTM), which originates from the main part of the femoral shaft between the trochanteric region and the condyles (Romer 1923c, Hutchinson 2002, Carrano and Hutchinson 2002). Three ridges (*linea intermuscularis cranialis*, *lia*; *linea intermuscularis caudalis*, *lip*; *linea aspera* = adductor ridge, *ar*) indicate the limits between these muscles, defining three adjacent areas around the femoral shaft: FMTE (= FMTL) is delimited by *lia* and *lip*, and FMTI (= FMTIM + FMTM) is limited by *lia* and *ar* (Hutchinson 2001b). In *Staurikosaurus* these three ridges are not complete, but the right femur and the proximal part of the left femur have the major part of the *lip* and its distal part respectively preserved. An irregular border is seen on the middle anterior portion

Staurikosaurus, but most of its dorsal extension is obliterated due to distortions of the fossil. In the left femur, this portion of the shaft is concealed by the dorsal vertebrae. Accordingly, it is possible to determine the areas of origin of FMTE and FMTI with some precision, but their exact distal extension is uncertain.

In Aves, FMTI is divided in two parts (FMTIM and FMTM). Langer (2003) observed in *Saturnalia* a tenuous line that extends proximally from the medial condyle along the medial surface of the femur that could indicate a rudimentary division of FMTI. Due to poor preservation, this structure is not observable in *Staurikosaurus*.

As in extant Archosauria, Mm. *femorotibiales* of *Staurikosaurus* extended anterolaterally down to the proximal tibia, where they inserted onto the anterolateral cnemial crest, forming the knee extensor tendon (Romer 1923c, Carrano and Hutchinson 2002).

M. *iliofibularis* (ILFB) – *M. iliofibularis* originates on the lateral surface of the ilium, between Mm. *iliofemorialis* and *flexor tibialis externus* (Hutchinson 2002, Carrano and Hutchinson 2002), slightly ventral to *iliofibialis* (Romer 1923c). Bittencourt and Kellner (2009) indicated that *Staurikosaurus* has one large concavity on the lateral surface of the ilium, but, this concavity appears to be divided in two by a smooth elevation (Fig. 4A-B), so that two concavities are present. The anterior one is large and deep and is located just dorsal to the acetabulum. The shallower posterior concavity probably corresponds to the ILFB origin because it is topographically equivalent to the surface where this muscle originates in extant Archosauria. A smooth arc-shaped scar in the dorsoposterior limit of the posterior concavity may indicate the limits of ILFB origin (Fig. 4C), whereas its ventral limit is indicated by the brevis shelf (Fig. 4C).

The anterolateral surface of the proximal part of the fibula of *Staurikosaurus* has an elongated crest that corresponds to the ILFB tubercle (Bittencourt and Kellner 2009), i.e., the insertion area of ILFB, as seen in extant Archosauria.



PELVIC AND HIND LIMB MUSCLES OF *STAIKOSAUROS*

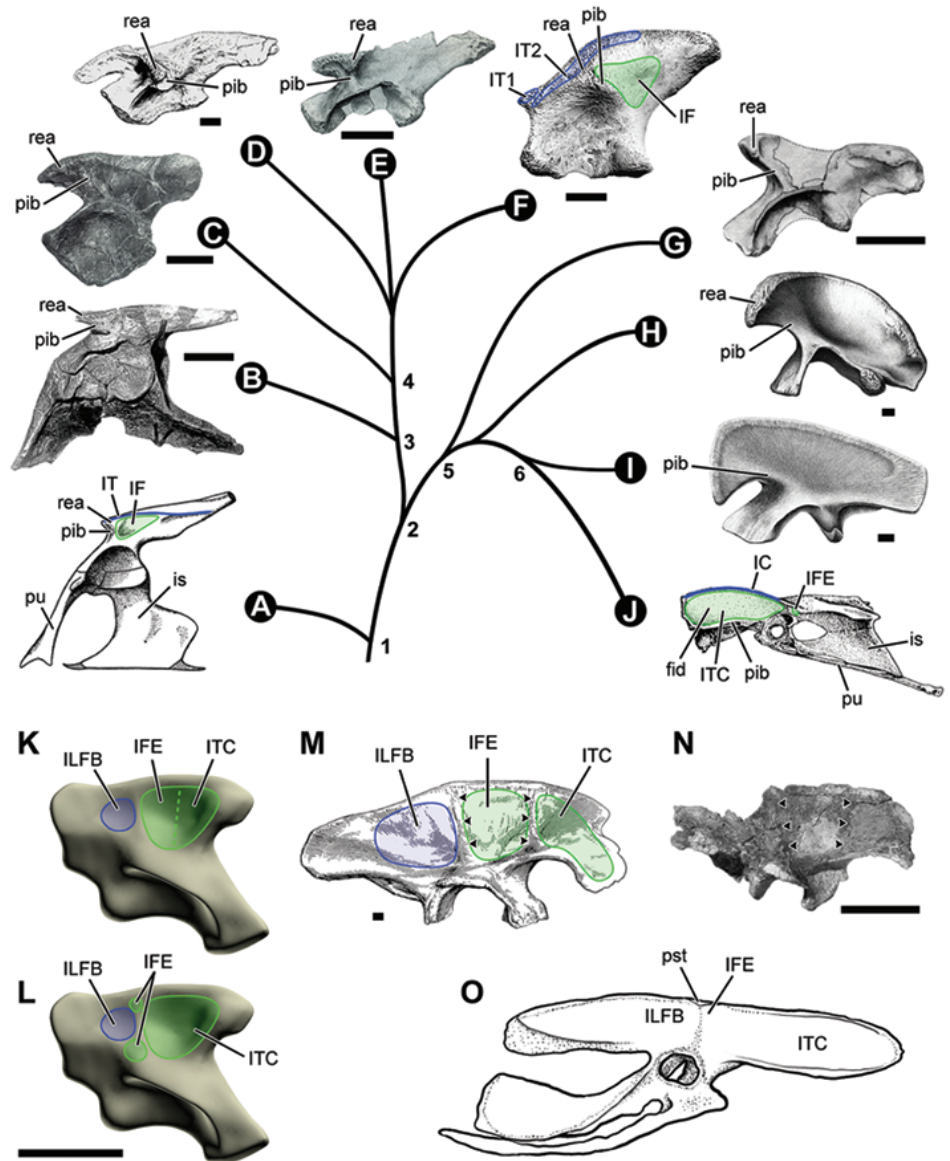


Fig. 3 – Iliac structures associated with muscle origin. A-J: Evolution of the preacetabular iliac border (*pib*) and the associated rough area (*rea*) in Diapsida and its relationship with the origin of the muscles IT, IC (blue areas in A, F and J) and IF, IFE and ITC (green area in A, F and J). Number and letters correspond to the following taxa: (1) Diapsida (A – *Iguana*, Lepidosauromorpha), (2) Archosauria, (3) Crurotalia (4) Suchia (C – *Stagonolepis*, Aetosauria; D – *Lythrosuchus*, Poposauridae; E – *Postosuchus* [juvenile], Rauisuchia), (5) Saurischia (F – *Caiman*, Crocodylomorpha), (6) Avetheropoda (G – *Caseosaurus*, Basal Saurischia [right ilium reversed]; H – *Apatosaurus*, Sauropodomorpha) and (6) Avetheropoda (I – *Allosaurus*, Carnosauria; J – *Meleagris*, Aves). K-O: Relationship between the position of the areas of ITC, IFE and ILFB in *Staurikosaurus* (K, hypothesis adopted in this work; L, two hypothesis proposed by Langer 2003), *Tyrannosaurus* (M), *Sinornithomimus* (N) and *Crypturellus* (O, indicating the relationship of IFE and the processus supratrochantericus, *pst*). Arrowheads in



iliofemoralis externus (IFE) and *iliotrochantericus caudalis* (ITC) (Carrano and Hutchinson 2002). This subdivision is reflected on a differentiation in the area of insertion of IF in the femoral trochanteric shelf: in Dinosauriformes, the trochanteric shelf has a cranial protuberance (anterior or lesser trochanter) that is homologous to the area of insertion of ITC in Aves, which suggests that IF was divided in this taxon (Hutchinson 2001b). This structure is present in *Staurikosaurus*, but is reduced in size (Bittencourt and Kellner 2009), so we can infer the presence of both IFE and ITC and indicate the area of insertion of ITC.

According to Hutchinson (2002), the insertion of IFE occurs in a rough area of the trochanteric shelf, on the lateral surface of the femur. In the left femur of *Staurikosaurus* there are some rough scars with undefined limits that may correspond to muscle insertion areas (Fig. 5D). One of these is located on the trochanteric shelf, exactly posterior to the anterior trochanter, and is interpreted here as the insertion area of IFE.

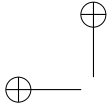
IFE and ITC origins are located on the lateral surface of the ilium, but there is generally no scars that indicate the exact limits of their areas (Hutchinson 2001a, Carrano and Hutchinson 2002). As already mentioned, the ilium of *Staurikosaurus* has a large subtriangular concavity on the anterior lateral surface of the ilium. This is dorsal to the acetabulum, bound anteriorly by the preacetabular iliac border (Fig. 4C). This concavity could hold a large muscle, similar to the condition observed in *Tyrannosaurus* by Carrano and Hutchinson (2002) and in *Saturnalia* by Langer (2003). A Level I inference indicates that this area corresponds to the origin of both parts of the *iliofemoralis* (IFE and ITC), contrary to the proposition of Langer (2003). According to Langer (2003), ITC would occupy this entire concavity and IFE would originate from the dorsal border of the acetabulum, immediately posterior to the supraacetabular crest or from a small surface in the dorsal limit between this large anterior concavity and the concavity of origin of ILFB (Fig. 3L). The first hypothesis is not congruent with the position of the origin of IFE in Aves because it is located between ITC and ILFB

areas in *Tyrannosaurus*, and they interpreted this as the division of IF in IFE and ITC (Fig. 3M). The similar size of these two muscles is corroborated by the size of their insertion areas in the femur. According to the propositions of Langer (2003), ITC would be a very large muscle and IFE would be a very small one, and this is not congruent with the size of their insertion areas in the femur of *Staurikosaurus*: the anterior trochanter is reduced and, although the limits of the insertion area of IFE are not clear, the rough area appears to be equal in size to the anterior trochanter (Fig. 5D).

The anterior limit of ITC may be indicated by the preacetabular iliac border that is adjacent to the anterior limit of the area of IF in lepidosaurs and Crocodylia, and of ITC in Aves (Fig. 3A, F, J). In *Staurikosaurus*, the preacetabular iliac border has striations (*str*) parallel to its long axis (Fig. 4C) that may be related to the origin of ITC.

M. puboischiofemoralis internus 1 (PIFI1)—*M. puboischiofemoralis internus 1* of Crocodylia (= *iliofemoralis internus*, IFI, in Aves) is homologous to the muscles PIFI1 and PIFI2 of other Reptilia (Rowe 1986, Hutchinson 2002).

In Crocodylia, PIFI1 originates from the medial surface of the ilium, in the medial proximal surface of the ischium, and sacral ribs (Romer 1923c, Hutchinson 2001a, 2002, Carrano and Hutchinson 2002). In Aves, IFI originates on the lateral surface of the ilium, from a reduced preacetabular (“cuppedicus”) fossa (*pf*; Hutchinson 2001a, 2002). The change in position of the origin area of PIFI1 can be observed along the evolution of Archosauria and is related to the expansion of the cranial iliac process (Carrano 2000, Hutchinson 2001a). The appearance of the preacetabular fossa and the reduction of the ventral portion of the pelvis also indicate this transition (Hutchinson 2001a, 2002). These changes probably produced the dorsolateral displacement of PIFI1 origin in tetanuran theropods (as indicated by the appearance of the preacetabular fossa). The lateral displacement in Aves is indicated by the reduction of this fossa (Norell et al. 2001, Hutchinson 2002).



PELVIC AND HIND LIMB MUSCLES OF *STURIKOSAURUS*

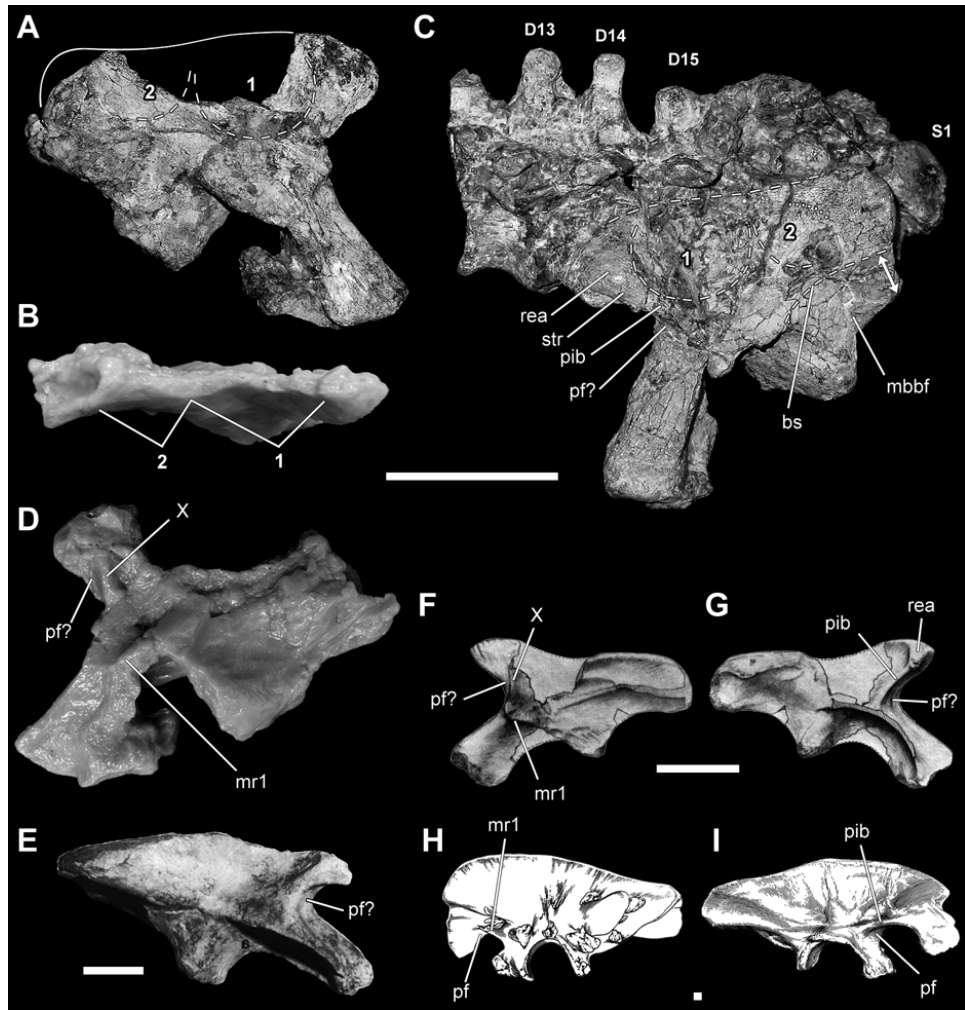


Fig. 4 – Right (A-B) and left (C) ilium of *Sturikosaurus* in lateral (A, C) and dorsal (B) views indicating the existence of two concavities (1 and 2) on the lateral surface and the expansion of the posterior part of the medial blade of the brevis fossa (mbbf), indicated by the two directional arrows (C). The dorsoposterior limit of ILFB origin (concavity 2) is indicated by a smooth border (dotted line in C). Right ilium of several taxa (A-I) indicating the presence of a preacetabular fossa (pf) or a similar structure (pf?) on the ventral surface of the cranial iliac process: *Sturikosaurus* (medial view [D]), *Sellosaurus* (lateral view [E]), *Caseosaurus* (medial [F] and lateral [G] views) and *Tyrannosaurus* (medial [H] and lateral [I] views). The first medial iliac ridge (mr1) delimits the preacetabular fossa medially in *Tyrannosaurus*. In *Sturikosaurus* and *Caseosaurus* the preacetabular fossa is delimited medially by a border (X) connected, but not equivalent to the mr1. Scale bars: 50 mm (E – from Galton 1984; F-G – from Galton and Murry 1995; H-I – from Osborn 1916).

developed and the cranial process of the ilium is not expanded. Hutchinson (2001a) considers the preacetabular fossa as an Avetheropoda character formed by the expansion of the first medial iliac ridge (articulation ridge

rikosaurus the first medial iliac ridge is in similar relation to this border in Crocodylia, i.e., horizontal and dorsal to the acetabulum (Fig. 4D, F, H). However, two forms have been another medial ridge in the ilium



tebra articulation (X in Fig. 4D, G). This ridge bounds a shallow fossa, topographically equivalent to the preacetabular fossa, i.e., it is located in the ventromedial surface of the cranial process of the ilium (Fig. 4). Despite the topographical equivalence, the homology between these structures is not clear because this fossa is medially limited by a ridge that cannot be certainly homologized with the first preacetabular medial ridge of the ilium. Accordingly, the origin of PIFI1 in *Staurikosaurus* is uncertain (Fig. 2G): it could be equivalent to that of Crocodylia (Level II inference), or may have shifted into the aforementioned fossa (also Level II inference).

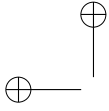
The PIFI1 of Crocodylia inserts at the proximal part of the femur, anteromedially to the insertions of PIFI2 (Romer 1923c, Hutchinson 2001b, 2002), on a keel that separates the insertion of PIFI2 and FMTI (Hutchinson 2001b). In Aves, IFI inserts on a rounded mark at the medial proximal portion of the femur (Hutchinson 2001b, 2002). *Herrerasaurus* (Novas 1993, Hutchinson 2001b) and *Staurikosaurus* possess a crest on the anterior surface of the femur, distal and anterior to the anterior trochanter, that is similar to that of Crocodylia, indicating a similar insertion of PIFI1 (Level II inference).

M. puboischiofemoralis internus 2 (PIFI2) – There are two homology hypothesis for the archosaur PIFI2 (Carrano and Hutchinson 2002, Hutchinson 2002): PIFI2 of Crocodylia may be homologous to Mm. *iliotrochantericus cranialis* (ITCR) and *medius* (ITM) of Aves (Romer 1923b, Rowe 1986), with M. *iliofemoralis* (IF) of Crocodylia divided in two avian parts: *iliofemoralis externus* (IFE) and *iliotrochantericus caudalis* (ITC); and PIFI2 may have been lost in Aves, and IF was divided in four parts: IFE, ITC, ITCR and ITM (Gadow 1880). Because the first hypothesis has more support from anatomical and ontogenetic data and requires fewer transformations in the number and position of muscles (Rowe 1986), we will treat PIFI2 of Crocodylia as homologous to ITCR and ITM of Aves. PIFI2 of Crocodylia should not be confused with the homonymous muscle of other Reptilia, but is homologous to their PIFI3 (Rowe 1986,

bar vertebrae; Romer 1923c). In Aves, the origins of the homologous ITCR and ITM are located on the ventrolateral surface of the preacetabular iliac process, anteriorly to the origin of IFI. As previously presented, this transition is associated with the expansion of the preacetabular iliac process and with the origin of the preacetabular fossa (Hutchinson 2001a, 2002). In *Tyrannosaurus*, the centra of the dorsal vertebrae have large pleurocels and little area for the attachment of muscles, and the preacetabular fossa is present (Carrano and Hutchinson 2002). *Staurikosaurus*, on the other hand, has large areas for the attachment of PIFI2 on the dorsal vertebrae that lack pleurocels. Also, the last five dorsal vertebrae of *Staurikosaurus* have shallow depressions below the infradiapophyseal fossae that could correspond to part of PIFI2 origin. The eighth and ninth dorsal vertebrae are partly covered by sediments and rib fragments, so it is impossible to verify the presence of these depressions, which are absent from the seventh to the more anterior dorsal vertebrae. Accordingly, as for Crocodylia, PIFI2 of *Staurikosaurus* probably originated from the last five (maybe six) dorsal vertebrae (Level II Inference).

In Crocodylia, PIFI2 inserts on the lateral surface of a keel extending along the proximal femur, lateral to the PIFI1 insertion, and its tendon is partly divided by the proximal part of the origin of FMTI (Romer 1923c). In Tetanurae, PIFI2 inserts on a large process (accessory trochanter), which is reduced to a small scar in basal Aves (Hutchinson 2002). Despite this difference, the positions of these structures are the same. Bittencourt and Kellner (2009) proposed that, in *Staurikosaurus*, PIFI2 inserted on a proximodistally extended and narrow crest located on the posterolateral surface of the proximal femur, but it is not congruent with the position observed in Crocodylia and Aves. In fact, this crest corresponds to the medial limit of the insertion of Mm. *puboischiofemorales externi*.

In *Staurikosaurus*, the surface of the anterior keel of the femur is damaged and partly covered by sediments, and it is impossible to identify muscle scars. However, the same condition seen in Crocodylia, with PIFI2 inserting on the lateral surface of this keel, is



PELVIC AND HIND LIMB MUSCLES OF *STAUROKOSAURUS*

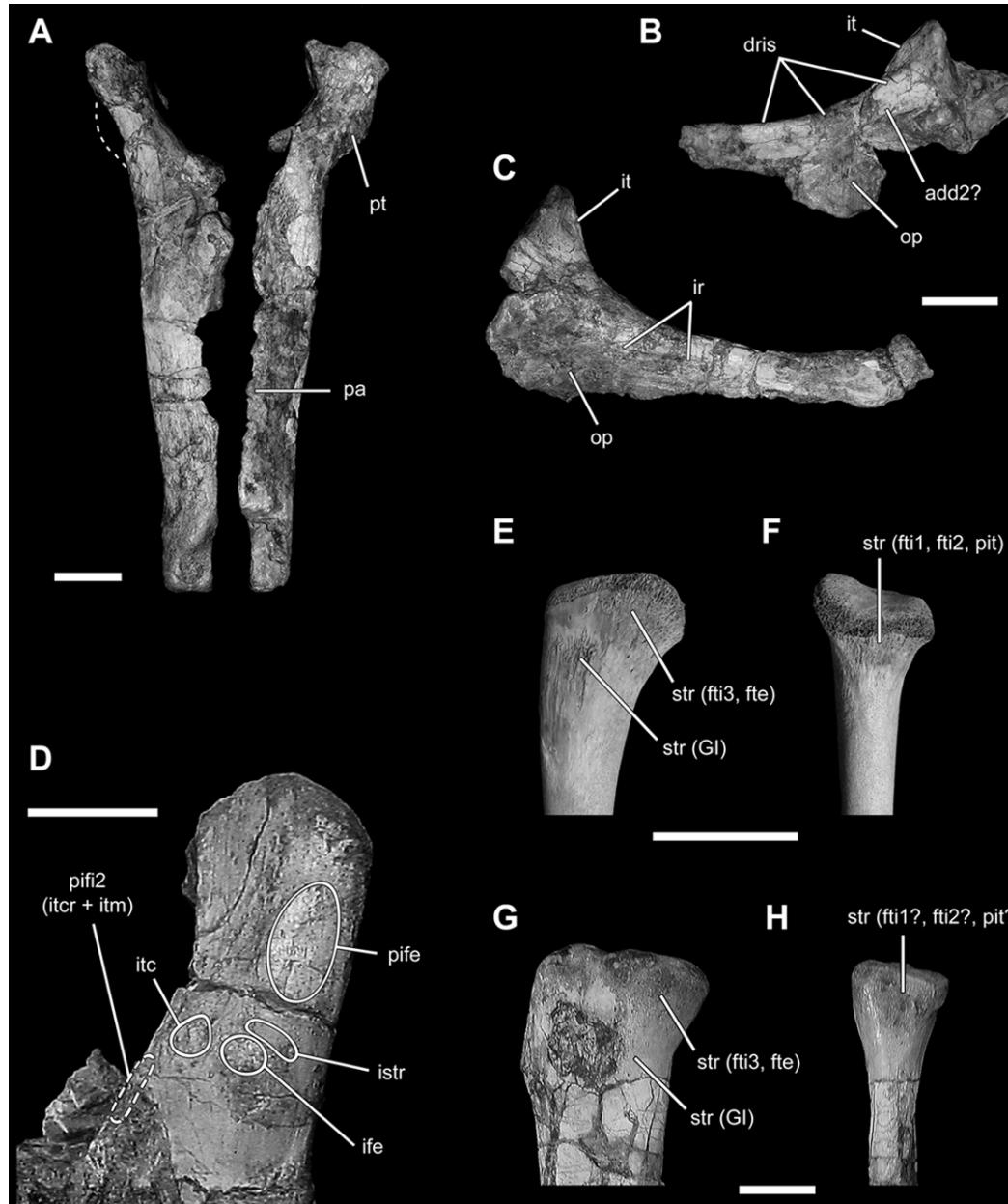


Fig. 5 – Right and left pubis in anterior view (A) indicating the pubic tubercle (*pt*) and the pubic apron (*pa*). Dashed line indicates the position of the unpreserved *pt* in the right pubis. Right (B) and left (C) ischium in lateral view. The dorsal ridge of the ischium (*dris*), ischial tuberosity (*it*) and obturator process (*op*) are indicated, along with a scar that may indicate the origin of ADD2. Lateral view of the proximal part of the left femur (D) indicating the approximate areas of insertion of the muscles ITC (on the anterior trochanter), IFI (on the trochanteric shelf), ISTR (on a groove proximal to the trochanteric shelf) and PIFE (on the greater trochanter). The probable insertion of the muscles STR (fti1, fti2, pit) and STR (fti3, fte) are indicated on the proximal part of the right femur (E) and the proximal part of the left femur (F). The probable insertion of the muscles STR (fti1?, fti2?, pit) and STR (fti3, fte) are indicated on the proximal part of the right femur (G) and the proximal part of the left femur (H).



insertion tendon in the currently available material of *Staurikosaurus*; the muscle scars on the trochanteric region of the femur are not well defined.

FLEXOR CRURIS

Homologies of the *Flexor cruris* group are not well resolved (Romer 1923c, Hutchinson 2002). Here we follow the hypothesis of Romer (1942). See Hutchinson (2002) for a revision of different hypothesis and nomenclature.

The *Flexor cruris* muscles share two insertion tendons in Crocodylia: FTI1 shares a tendon with FTI2 that connects to the tendon of PIT, and inserts on the caudomedial surface of the proximal tibia (Romer 1923c, Hutchinson 2002), whereas FTI3, FTI4 and FTE share a tendon that inserts on the posteromedial surface of the proximal tibia, as occurs with the avian homologues of these muscles (Hutchinson 2002, Carrano and Hutchinson 2002). The proximal portion of the right tibia of *Staurikosaurus* bears several striations that are similar to the scars observed in extant *Caiman tibiae* (Fig. 5E-H), which correspond to the insertion of FTI3 and FTE (posteromedially), and of FTI1, FTI2 and PIT (posterolaterally). Accordingly, the same condition is inferred for *Staurikosaurus*. Considering the proposed absence of PIT in *Staurikosaurus* (see below), the posterolateral striations seen on its tibia may correspond to the insertion of FTI1 (if present) and FTI2.

On its medial side, the proximal tibia of *Staurikosaurus* also bears a scar (partly lost due to fragmentation of the bone surface) distal to that of FTI3 and FTE (Fig. 5G), which can be attributed to the *M. gastrocnemius internus* (that will not be treated here).

***M. puboischiotibialis* (PIT)** – *M. puboischiotibialis* is present in basal reptiles, reduced in Crocodylia and absent in Aves (Romer 1923c, Hutchinson 2002, Carrano and Hutchinson 2002). In Crocodylia, there is only one branch of PIT originating on a scar located on the proximal tip of the obturator process (*op*) of the ischium (Carrano and Hutchinson 2002), ventral to the acetabulum (Romer 1923c). PIT inserts on the caudomedial

the ischium of *Staurikosaurus* in not preserved, and it is impossible to determine the presence of PIT. Yet, Hutchinson (2002) points that the scar for PIT is absent in all basal archosaurs and that there is no evidence of one or more parts of PIT in Dinosauromorpha. Accordingly, it was probably also absent in *Staurikosaurus*.

***M. flexor tibialis internus 1* (FTI1)** – *M. flexor tibialis internus 1* is absent in Aves and originates from the caudolateral surface of the distal ischium of crocodiles (Romer 1923c, Hutchinson 2002). Some theropods (e.g., *Allosaurus*, *Piatnitzkysaurus*, and *Therizinosauroides*) and *Herrerasaurus* possess a structure (distal ischial tuberosity) on the caudolateral surface of the distal ischium that is topographically equivalent to FTI1 origin in Crocodylia (Hutchinson 2001a, 2002, Carrano and Hutchinson 2002). The distal part of the ischium of *Staurikosaurus* is not preserved, and the presence of the distal ischial tuberosity cannot be confirmed. Yet, it is present in *Herrerasaurus* and *Saturnalia* (Langer 2003), suggesting the presence of FTI1 in *Staurikosaurus* (Level II' inference).

***M. flexor tibialis internus 2* (FTI2)** – *M. flexor tibialis internus 2*, absent in Aves (Hutchinson 2002, Carrano and Hutchinson 2002), originates from the lateral surface of the postacetabular iliac process of crocodiles, ventral to the origin of FTE (Romer 1923c, Hutchinson 2002, Carrano and Hutchinson 2002). Langer (2003) indicated a division of muscle scars on the lateral surface of the postacetabular iliac process in *Saturnalia* and other dinosaurs (*Herrerasaurus*, *Caseosaurus*, basal ornithischians and 'prosauropods') that is topographically equivalent to the origins of FTI2 and FTE in Crocodylia. One of these marks is an extension of the dorsal iliac margin (origin of IT3) that corresponds to the origin area of FTE (Langer 2003). Posterior to this scar, on the caudal most part of the ilium, there is another scar probably associated with FTI2 (Langer 2003). These scars are not visible in *Staurikosaurus*, but a Level II' inference indicates the presence of FTI2 and FTE originating from its postacetabular iliac process, dorsal to the brevis shelf.

***M. flexor tibialis internus 3* (FTI3)** – *M. flexor tibialis*



PELVIC AND HIND LIMB MUSCLES OF *STURIKOSAURUS*

on the ischial tuberosity (*it*; Hutchinson 2001a, 2002), at the posterior margin of the ischium, proximal to the origin of ADD2 (Romer 1923c). It is homologous to the avian *M. flexor cruris medialis* (FCM), which originates from a similar (but distal) position, while the ischial tuberosity is absent (Hutchinson 2001a, 2002, Carrano and Hutchinson 2002). The ischium surface is not well preserved in *Staurikosaurus*, with fractures hampering the identification of muscle scars. However, both ischia bear a crest (Fig. 5 B-C) near the articular surface of the ilium that is slightly proximal in relation to the ischial tuberosity of other dinosaurs, but may be a homologous structure. Along with a depression lateral to the crest, these structures could correspond to the origin area of FTI3 as proposed by Langer (2003).

M. flexor tibialis internus 4 (FTI4) – This division of the *flexor tibialis internus* is only present in Crocodylia, and is equivalent to the superficial part of FTI2 of other Reptilia (Romer 1942, Hutchinson 2001a, 2002). FTI4 originates on the fascia around the caudoventral ilium and the caudodorsal ischium (Hutchinson 2002). Accordingly, its origin cannot be verified in *Staurikosaurus* because it is not correlated to any bone scar. Its presence is also equivocal, since it is absent in Aves.

M. flexor tibialis externus (FTE) – *M. flexor tibialis externus* (= *flexor cruris lateralis pars pelvica*, FCLP, in Aves) originates on the lateral surface of the ilium of crocodiles, posterior to *Mm. iliofibularis* and *iliofemoralis externus* (Romer 1923c, Carrano and Hutchinson 2002). As already mentioned, the ilium of *Staurikosaurus* has no preserved muscle scar posterior to the origin of ILFB. The shape of the posterodorsal limit of ILFB in *Staurikosaurus* suggests the posterior extension of the dorsal border of the ilium (Fig. 4C), as seen in other taxa (e.g., in *Saturnalia* and *Herrerasaurus*, Langer [2003]). Accordingly, it is assumed that the origin of FTE in *Staurikosaurus* was posterior to ILFB and in continuity to that of IT3. FTI2 origin may be posterior to that of FTE, but their exact positions cannot be confirmed with current available material.

are homologous to, respectively, *M. puboschioidalis pars medialis* (PIFM) and *pars lateralis* (PIFL) in Aves (Romer 1923c, Hutchinson 2002). The two muscles originate from the lateral surface of the ischium (near the cranial border of the bone) and are separated in Crocodylia, by the origin of PIFE3 (Romer 1923c). In Aves, the position of PIFL origin is anteroventral in relation to its crocodilian homologue, ADD2 (Hutchinson 2001a). This is probably related to the reduction of the obturator process, and the change of the origin of *ischiotrochantericus* to the lateral surface of the ischium (Carrano and Hutchinson 2002).

According to Hutchinson (2001a), the ischiofemoralis (*ir*) is located cranioventrally to the origin of FTI4 and ventrally to ADD2. The bone surface of both ischia of *Staurikosaurus* is damaged, and no muscle scar can be safely identified. The ischial ridge is better preserved on the left bone (Fig. 5C). On the right ischium, distal to the ischial ridge, in a well-preserved small area, there is a depression (Fig. 5B) topographically equivalent to the origin of ADD2 in Crocodylia may correspond to the origin of this muscle. The origin of ADD1 is probably located on the anterior margin of the obturator process in extant archosaurs, but this structure is not preserved in the holotype of *Staurikosaurus*.

The two ADD heads converge to a long, narrow insertion area, on the caudal surface of the distal femur (Romer 1923c), located between the *intermuscularis caudalis* and the *linea aspera* (obturator ridge, Hutchinson 2001b). These structures, already mentioned, are partly preserved in the femur of *Staurikosaurus* and indicate the approximate position of ADD insertion. Unfortunately there is no distinction for either of the branches, as Carrano and Hutchinson (2002) observed in *Tyrannosaurus*.

MM. PUBOISCHIOFEMORALES EXTERNI

Mm. Puboischiofemorales externi originate on the lateral surface of the pubo-ischiadic plate in basal archosaurs, and is divided in two pubic parts, PIFE1 and PIFE2. These are homologous to the avian *Mm. obturatorius lateralis*, *obturatorius medialis*, and *obturatorius*.



2002) and the modifications seen in Aves are attributed to the division of the pubo-ischiadic plate and loss of the obturator process (Hutchinson and Gatesy 2000).

The three heads of PIFE in Crocodylia shares an insertion tendon that attaches to the greater trochanter of the femur, as occurs with the avian homologues OL and OM (Hutchinson and Gatesy 2000, Hutchinson 2001b, Carrano and Hutchinson 2002). In *Staurikosaurus*, the greater trochanter is a S-shape crest located on the cranio-lateral region of the proximal region of the femur (Fig. 5D; Bittencourt and Kellner 2009). Galton (1977, 2000) previously identified this structure as the anterior trochanter (see Bittencourt and Kellner 2009, for a discussion).

M. puboischiofemoralis externus 1 (PIFE1) – In *Staurikosaurus*, PIFE1 originates on the anterior surface of the pubic apron (*pa*; Fig. 5A), as seen in Crocodylia (Romer 1923c, Hutchinson 2002, Carrano and Hutchinson 2002). The apron corresponds to the dorsoventrally expanded surface of the pubic symphysis (Hutchinson 2001a). In Aves, which lack a pubic symphysis, PIFE1 originates from the proximal lateral surface of the pubis (Hutchinson 2002). Accordingly, the reconstruction proposed for *Staurikosaurus* corresponds to a Level II inference. Langer (2003) suggests the lateral surface of the distal part of the pubis of *Herrerasaurus* (as probably in *Staurikosaurus*) as equivalent to the anterior surface of the pubis of *Saturnalia* because it has a series of striations that continues from the anterior surface of the apron. These striations could indicate the origin of PIFE1 (Langer 2003). Extant archosaurs do not have any part of PIFE1 originating from the distal lateral surface of the pubis. As this supposition requires a Level III inference, it was not considered here.

Langer (2003) noted the laterally expanded lateral border of the pubis of *Saturnalia*, *Herrerasaurus*, and prosauropods, which gives the pubis a sinuous shape in anterior view. Novas (1993) erroneously (see Fig. 5A) indicated that *Staurikosaurus* retains the primitively straight dinosauiromorph condition for the lateral border of the pubis. Langer (2003) proposed that the proximal

more dorsal if compared to the other basal Saurischia, and the origin of PIFE1 could be more dorsally expanded.

M. puboischiofemoralis externus 2 (PIFE2) – PIFE2 originates on the posterior surface of the pubic apron (Romer 1923c, Hutchinson 2002, Carrano and Hutchinson 2002). In Aves, the homologue OM has moved caudally to the pubo-ischiadic membrane (Hutchinson 2002). We consider (Level II inference) that *Staurikosaurus* has the same plesiomorphic condition of Crocodylia because the pubic apron is well developed.

M. puboischiofemoralis externus 3 (PIFE3) – PIFE3 originates from the lateral surface of the ischial obturator process, between the origin areas of ADD1 and ADD2 (Romer 1923c, Hutchinson 2002, Carrano and Hutchinson 2002). It is limited anterodorsally by the ischial ridge (Hutchinson 2002). In Aves, this muscle was lost together with the obturator process (Hutchinson 2001a, 2002). The obturator surface of the ischium of *Staurikosaurus* is not well preserved and no muscle scar is preserved. Accordingly, the origin of PIFE3 was tentatively reconstructed based on the position of the ischial ridge, PIFE3, ADD1, and ADD2 in Crocodylia.

M. ISCHIOTROCHANTERICUS (ISTR)

M. *ischiotrochantericus* (ISTR) of crocodiles originates on the medial surface of the caudal part of the ischium (Romer 1923c, Hutchinson 2001a, 2002, Carrano and Hutchinson 2002). In Aves, with the reduction of the ischial symphysis, the origin of the homologue M. *ischiofemoralis* (ISF) was displaced to the lateral surface of the ischium and to the ilio-ischiadic membrane (Hutchinson 2001a, 2002, Carrano and Hutchinson 2002).

In Aves, ISF is more cranial than in Crocodylia, in which ISTR is located on the caudal extremity of the ischium (Romer 1923c). But the distal part of the ischium in Aves corresponds to a caudoventral elongation of the distal part of the ischial symphysis (Hutchinson 2001a). Besides, the avian ISF is located near the origin of PIFM (= ADD1) and PIFL (= ADD2), as occurs in Crocodylia, and ISTR origin is medial to that of ADD2 (Carrano and Hutchinson 2002).



PELVIC AND HIND LIMB MUSCLES OF *STAURIKOSAURUS*

Langer (2003) suggest that the dorsal surface of the dinosaur ischium was laterally displaced, so that the dorsal ridge of the ischium (*dri*), which separates the origins of ISTR and ADD2, is placed on the lateral surface of the ischium (Langer 2003). In *Staurikosaurus*, the ridge that separates ISTR from ADD2 is visible and helps to define the approximate position of ISTR origin, which is near and dorsal to the scar that supposedly indicates the origin of ADD2.

In Crocodylia, ISTR inserts on a scar on the caudolateral surface of the proximal femur (Romer 1923c, Hutchinson 2002), in a position almost equal to that seen in Aves (Hutchinson 2002). Dinosauromorphs have a sigmoid structure (trochanteric shelf) that corresponds to the insertion of IFE. A groove proximal to the trochanteric shelf corresponds to the insertion of ISTR (Hutchinson 2001b, 2002, Carrano and Hutchinson 2002). The trochanteric shelf of *Staurikosaurus* is reduced (Bittencourt and Kellner 2009), but the groove where ISTR is inserted is present and clearly seen on the left femur (Fig. 5D).

MM. CAUDOFEMORALES

M. caudofemoralis brevis (CFB) – *M. caudofemoralis brevis* of crocodiles (= *caudofemoralis pars pelvica*, CFP, in Aves) originates on a shallow fossa on the medioventral surface of the ilium, from the posterior sacral ribs and the first caudal vertebra (Romer 1923c, Carrano and Hutchinson 2002). In Aves, CFP originates only from the caudolateral surface of the ilium (Hutchinson 2002). Changes in the origin of CFB/CFP are apparently related to modifications of the medial and lateral regions of the postacetabular ilium, which include the transversal widening and deepening of both the iliac blade and the medial shelf, forming the brevis shelf (*bs*) and the brevis fossa of Dinosauria (Novas 1996, Hutchinson 2001a, 2002). Accordingly, CFB of dinosaurs would have its origin from the brevis fossa, which is reduced in taxa proximally related to Aves (Hutchinson 2001a, 2002).

According to Novas (1992), Herrerasauridae retains the plesiomorphic condition of basal Ornithomiridae

(1993, 1996) considered herrerasaurids as basal Theropods and suggested that a groove on the lateral surface of the posterior part of the ilium of *Herrerasaurus* represents a reduced brevis fossa. Hutchinson (2001) treats Herrerasauridae as basal Theropoda and suggests that the most parsimonious condition would be the reduction of the brevis fossa in this group. Even if we consider Herrerasauridae as basal Saurischia (Yates and Langer 2004, Leal et al. 2004), the reduction hypothesis is more parsimonious since ornithischians also have a well-developed fossa (Novas 1992, 1996).

The reduction of the brevis fossa appears to be more pronounced in *Staurikosaurus* than in *Herrerasaurus*, because just a shallow depression on the lateral surface of the acetabular surface of the ilium is present. This depression is dorsally delimited by an elongated elevation that starts at the dorsoposterior margin of the supra-acetabular crest, finishing on the posterior margin of the ilium. This structure is interpreted as homologue to the brevis ridge that bounds the groove of the posterior ilium in *Herrerasaurus*, and the brevis shelf. Accordingly, the surface ventral to this shelf (posteroventral margin of the ilium) corresponds to the medial blade of the ilium, which bounds the brevis fossa medially (medial blade of the brevis fossa, *mbbf*, Fig. 4C) in other Dinosaurs. Therefore, the lateral surface of this blade would represent the origin of CFB in *Staurikosaurus*. Despite the reduction of the brevis fossa, *Staurikosaurus* possesses a marked dorsoventral expansion of the posterior ilium on the posteroventral margin of the ilium (Fig. 4C), which does not occur in *Herrerasaurus*. In both taxa, the medial blade (posteroventral margin of the ilium) corresponds to 29% of the length of the ilium, but the posterior ilium in *Herrerasaurus* is not dorsoventrally expanded, suggesting that the posterior part of CFB was enlarged in *Staurikosaurus*.

CFB inserts on the posterolateral surface of the femur, between the fourth trochanter and the line of insertion of *muscularis caudalis* (Hutchinson 2001a, b, 2002, Carrano and Hutchinson 2002) in a position slightly medial and lateral to the insertion of *M. caudofemoralis longus* (Romer 1923c). In Aves, the fourth trochanter



linea intermuscularis caudalis, but no muscle scars are observed. Accordingly, the inferred position of CFB insertion is approximate.

M. caudofemoralis longus (CFL) – *M. caudofemoralis longus* (= *caudofemoralis pars caudalis*, CFC, in Aves) originates on the centra and ventral surfaces of the caudal vertebra transverse processes (Romer 1923c, Gatesy 1990, Hutchinson 2001b), approximately from the third to the fifteenth element (Romer 1923c, Gatesy 1990). In Aves, CFC was reduced along with the reduction of the tail and the evolution of the pygostyle, and its origin is restricted to this structure (Gatesy 1990, Hutchinson 2002). The presence of transverse processes would be an indication of the minimal extension of the origin of CFL in the tail of archosaurs, as are specializations of the vertebrae and chevrons (Gatesy 1990). In Theropoda, the tail has a transition point where the caudal vertebrae lose the transverse processes (Russell 1972), so that the origin of the CFL is restricted to the area anterior to this point. The transition is also marked by the elongation of the prezygapophyses and dorsoventral compression of the chevrons on the vertebrae posterior to the point (Gauthier 1986, Gatesy 1990).

The holotype of *Staurikosaurus* does not have the complete caudal series preserved: there are six proximal vertebrae; a block containing six articulated vertebrae from the middle part of the tail; two blocks with two vertebrae each, also from the middle of the tail; and the last 19 caudal vertebrae (Bittencourt and Kellner 2009). Vertebrae from one of the median blocks with two vertebrae bear transverse processes. But the 19 terminal vertebrae lack these structures and have elongated prezygapophyses (Gauthier 1986, Bittencourt and Kellner 2009). Based on regression equations obtained from data collected from the preserved caudal vertebrae (height and length of the centrum), and considering that *Staurikosaurus* had the same number of caudal vertebrae of *Herrerasaurus* (i.e., 47 vertebrae), it was possible to estimate the position of the middle blocks of vertebrae. This method also allowed estimating the length of the non-preserved vertebrae and indicated that

25 caudal vertebrae of *Staurikosaurus* have transverse processes, and this is the minimal extension of CFL origin (Grillo and Azevedo 2011).

CFL of crocodiles inserts on the medial surface of the fourth trochanter, on an associated depression (Romer 1923c, Gatesy 1990, Hutchinson 2001b, 2002). In Aves, the reduction of CFC was accompanied by the reduction of the fourth trochanter to a roughed area (Gatesy 1990, Hutchinson 2001b, 2002). *Staurikosaurus* possesses a well-developed crest-shaped fourth trochanter (Colbert 1970, Galton 1977, 2000, Bittencourt and Kellner 2009) that indicates that the CFL was a large and powerful muscle. This condition is congruent with the expanded area of origin of this muscle in the tail.

In extant crocodiles the CFL has a secondary tendon that extends from the distal part of CFL to the caudal region of the knee (Romer 1923c, Hutchinson 2001b, 2002), contributing to the origin of the *M. gastrocnemius lateralis* (Hutchinson 2002). In Theropoda, the fourth trochanter is pendant and has a process ventrally directed that could be an indication of the presence of this secondary tendon (Hutchinson 2002, Carrano and Hutchinson 2002). *Staurikosaurus* has a pendant fourth trochanter, although its margin is damaged and the ventral process cannot be observed, so that the secondary tendon was probably present (Level II' inference).

DISCUSSION

Reconstructions of the pelvic musculature of saurischian dinosaurs have been attempted for more than a century (Romer 1923b, c), but recent works (e.g. Hutchinson 2001a, b, 2002) clarified several aspects of the evolution of the hind limb muscles in archosaurs. Some studies (e.g. Coombs 1979, Dilkes 2000, Carrano and Hutchinson 2002, Langer 2003) did not focus on higher level taxa, but on particular species. This approach may reveal exclusive adaptations, contributing to understand the different locomotion adaptations of each species.

The muscle reconstruction of *Staurikosaurus* allowed the identification of both modifications that differentiate this taxon from other closely related species, and of a series of osteological structures not observed



PELVIC AND HIND LIMB MUSCLES OF *STAURIKOSAURUS*

specimen, which has several problems of preservation that hampered the observation of muscle scars. However, the comparison with other proximally related taxa and the use of bones from both sides of the body, associated to the EPB methodology, allowed to construct a map of origin and insertion for the majority of the hind limb muscles. The result is consistent to muscle arrangement in extant archosaurs and other extinct dinosaurs that have already been studied (see Carrano and Hutchinson 2002, Langer 2003).

Some muscle associated structures were described for the first time for *Staurikosaurus*, complimenting previous descriptions and studies about this taxon (Colbert 1970, Galton 1977, 2000, Bittencourt and Kellner 2009): the pubic tubercle (associated to AMB origin), the *lineae intermusculares* on the femur (associated to FMTE, FMTI, ADD1-2 and CFB), the two concavities on the lateral surface of the ilium (associated to ITC, IFE and ILFB origin), the concavities on the posterior dorsal vertebrae (associated to PIFI2 origin) and the fossa on the ventral margin of the cranial iliac process (probably associated to PIFI1 origin). The pubic tubercle has been figured as absent in *Staurikosaurus* (e.g., Colbert 1970, Galton 1977, Novas 1993), and a recent revision (Bittencourt and Kellner 2009) did not recognize this tubercle, perhaps as a result of taphonomic damage. All these studies were based on the right pubis, but the pubic tubercle is preserved only on the left pubis (Fig. 5A).

The concavities on the lateral surface of the ilium described here are different from those mentioned by Bittencourt and Kellner (2009). These authors indicate that the ilium of *Staurikosaurus* has two concavities on the lateral surface, the caudal one being interpreted as a reduced *brevis fossa*. The cranial concavity indicated by Bittencourt and Kellner (2009) was interpreted here as comprising two concavities associated to the origins of IFE, ITC, and ILFB (concavities 1 and 2, Fig. 4A-C).

The muscle reconstruction of *Staurikosaurus* may be compared to that presented by Langer (2003) for another basal Saurischian, *Saturnalia tupiniquim*. Langer (2003) indicated that the hind limb and pelvic anatomy of *Saturnalia*, and hence muscle arrangement and func-

rerasaurus, *Staurikosaurus*, *Guaibasaurus*, and sauropodomorphs. Most of the results presented are very similar to those of Langer (2003). Differences are mainly conceptual, rather than anatomical.

As proposed by Langer (2003), we consider the tenuous convexity that separates the two main concavities on the lateral surface of the ilium indicates the anterior limit of ILFB origin. However, Langer proposed that the anterior concavity corresponds to the origin of ITC, so that the origin of IFE would be located on the surface immediately caudal to the acetabular crest or close to the dorsal margin of the ilium, over the dorsal extremity of the convexity that separates the two main lateral iliac concavities (Fig. 4A). The first hypothesis is congruent with the arrangement seen in Crocodylia, in which the origin of IF borders the dorsoposterior margin of the acetabulum. In this context, IFE would have originated as a posteroventral extension of IF. This is not congruent with the origin of IF in Aves, which is located on the dorsal margin of the ilium on the *processus supra-trochantericus* (*pst*; Figs. 1 and 2; Hutchinson 2001a). This indicates that IFE represents a dorsoposterior separation of IF, which is congruent with the second hypothesis of Langer (2003). If this hypothesis is accepted, it is also necessary to infer that ITC was split into a reduced IFE and a large ITC. Yet, no logical evidence suggests that ITC was initially of similar size to IFE, enlarging only along theropod evolution until it was reduced again in Aves, and restricted to the dorsal margin of the ilium. This is supported by the enlargement of the anterior trochanter and cranial iliac process in basal theropods, and by the later reduction of the former in taxa closely related to Aves (Hutchinson 2000, Gatesy 2000, Hutchinson 2001b). Another indication that IFE and ITC had similar sizes in non-maniraptorian theropods is the presence of a dorsoventrally directed convexity on the lateral surface of the anterior iliac process, which divides the anterior concavity of the ilium separating the origins of ITC and IFE in *Tyrannosaurus* (Carrano and Hutchinson 2002), as well as in the ornithomimosaur *Sinornithomimus dongi*. In this context, the most parsimonious scenario for the evolution of



Another difference between the proposition of Langer (2003) for *Saturnalia* and the one presented here for *Staurikosaurus* is related to AMB. Langer (2003) proposed that this muscle, as in Crocodylia, would have two heads originating from the pubic tubercle and from the dorsal margin of the pubis. On the contrary, we consider that the AMB of dinosaurs, as in Aves, would have just one head, originating from the pubic tubercle. According to Carrano and Hutchinson (2002), the presence of two heads in Crocodylia represents an apomorphy of this clade because both Aves and Lepidosauria have just one AMB head (Romer 1922, 1923c).

Other differences relative to the reconstruction presented by Langer (2003) are related to insufficient information retrieved from the holotype of *Staurikosaurus*. The smooth division on the femur of *Saturnalia* that could indicate the separation of FMTI in two parts (FMTM and FMTIM) was not preserved or is absent in *Staurikosaurus*. The phylogenetic positioning of Herrerasauridae is still uncertain. Some works (e.g. Yates 2003, Leal et al. 2004, Bittencourt and Kellner 2009) place Herrerasauridae basal to Eusaurischia, but others (e.g., Novas 1993, Sereno 1997, Sereno and Novas 1992, Benton 1999) suggest a closer relation to Theropoda. Accordingly, the presence of an initial division of FMTI in *Saturnalia* does not bring additional evidences for its division in Herrerasauridae until more stable phylogenetic hypotheses are obtained.

We restricted the origin of PIFE3 to the obturator process, as in Crocodylia, because the obturator process is not completely preserved and no muscle scar could be observed. Yet, Langer (2003) observed striations on the ventrolateral surface of the ischium of *Saturnalia*, which were associated to PIFE3. This could also be the case for *Staurikosaurus*, but new material is necessary to confirm this hypothesis. Besides, Langer (2003) reconstructed ISTR as originating from the entire mediadorsal surface of the ischium, but the distal part of that bone forms an elongated symphysis (Hutchinson 2001a). Moreover, in Crocodylia, ISTR origin is restricted to the obturator process and does not extend into the symphysis. In Aves, the homologue ISF is also restricted to the proximal portion

bic peduncle to the origin of PIFI1 or the dorsal part of AMB. In the prosauropod *Sellosaurus gracilis* there is a depression on the ventral margin of the cranial iliac process that extends to the pubic peduncle (Fig. 4E). This is equivalent to the fossa observed on the cranial process of the ilium of *Staurikosaurus* (Fig. 4C-D) and *Caseosaurus* (Fig. 4F-G), which are in the same position of the preacetabular fossa of Avetheropoda (Fig. 4H-I). The preacetabular fossa of Avetheropoda was attributed to the origin of PIFI1, since it is the condition of the avian homologue IFI (Hutchinson 2002). Accordingly, it is possible to infer that early on dinosaur evolution PIFI1 changed its origin from the medial surface of the ilium, as is the case for Crocodylia, to the ventral margin of the cranial iliac process and the dorsal part of the pubic peduncle of the ilium. Later on Theropod evolution, the incorporation of dorsal vertebrae to the sacrum led to the rearrangement of the first medial iliac ridge and to the development of the preacetabular fossa as defined for Avetheropoda by Hutchinson (2001a).

In conclusion, disregarding the differences pointed above, it is possible to confirm that basal dinosaurs shared a similar muscle arrangement as proposed by Langer (2003).

In the following paragraphs, this arrangement is compared with that of extant Crocodylia and Aves and to the reconstruction presented by Carrano and Hutchinson (2002) for *Tyrannosaurus*, in the intent to discuss some aspects of hind limb muscle evolution in Saurischia.

Relative to Crocodylia, *Staurikosaurus* differs in various aspects: (1) the iliac surface for muscle origins is proportionally larger, especially on the anterior portion of the bone, due to the expansion of the cranial iliac process; (2) the origin of ILFB is also enlarged, occupying a large concavity on the lateral surface of the ilium; (3) IF is divided; (4) AMB has just one head; and (5) PIFI1 apparently moved from the medial surface of the ilium to a fossa on the ventral margin of the cranial iliac process and dorsal part of the pubic peduncle. Other muscles in *Staurikosaurus*, such as CFB, CFL, PIFE1-2, and PIFI2, have origin and insertion areas in positions equivalent to Crocodylia.



PELVIC AND HIND LIMB MUSCLES OF *STURIKOSAURUS*

these two taxa is the existence of a true preacetabular fossa on the ventral margin of the cranial iliac process of *Tyrannosaurus*, but *Staurikosaurus* also bears other dissimilarities including: (1) reduced anterior trochanter; (2) the femoral head in its plesiomorphic orientation, rotated 45° posteriorly; (3) a more proximal insertion of FTI3 and FTE and origin of ADD2 and FTI3; (4) more posterior origin of IFE; (5) reduced brevis fossa; and (6) a CFB origin extending to the posterior margin of the ilium and with its posterior part dorsoventrally expanded. The arrangement of other muscles are similar in both taxa or is uncertain in *Staurikosaurus* (e.g., origins of ADD1 and PIFE3) or in *Tyrannosaurus* (presence or absence of FTI1 and FTI2). Other differences are related to the proportionately larger bone surfaces of *Tyrannosaurus* due to the expansion of the cranial and caudal processes of the ilium.

Differences in muscle position observed between *Staurikosaurus* and *Tyrannosaurus* are related to changes in muscle function, as is the case of ADD2, FTI3, and FTE, which have their origins in a more distal position. This makes ADD2 to change its primary function from adductor to extensor and increases the moment arm of FTI3 and FTE (Carrano and Hutchinson 2002).

Based on the comparison between *Staurikosaurus* and *Tyrannosaurus*, it is possible to infer that the main features of the avian musculature present in *Tyrannosaurus* were also present early on saurischian evolution, e.g., a divided IF (Hutchinson 2001b) and the origin of PIFI1 from the ventral surface of the cranial process of the ilium. Modifications not present early on the evolution of Saurischia, but present in *Tyrannosaurus*, include: (1) the expanded anterior trochanter (Hutchinson and Gatesy 2000); (2) the expansion of the cranial and caudal iliac processes (Carrano 2000), which is less evident in basal dinosaurs; and (3) the rotation of the femoral head, the lateral surface of which moved to a more anterior position (Carrano 2000, Hutchinson 2001b).

The reconstruction of pelvic and hind limb musculature of *Staurikosaurus* also revealed a specific adaptation unknown to other taxa: the posterior part of the

Herrerasaurus, this expansion characterizes a v increase of CFB, since the length of the medial b the brevis fossa corresponds to 29% of the total of the ilium in both taxa.

ACKNOWLEDGMENTS

The Museum of Comparative Zoology is thankful for the loan of the *S. pricei* holotype to Alexander K Museu Nacional/UFRJ. Jonathas de Souza Bitt is thanked for providing the photographs of the S holotype and Riccardo Mugnai is thanked for providing the casts of the holotype. This research is part of the MSc thesis of one of the authors (ONG) at the Museu Nacional of Universidade Federal do Rio de Janeiro, funded by a fellowship of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ). The holotype was examined by the doctors Max Langer, Alexander K and Oscar Rocha-Barbosa, who are thanked for providing useful comments that greatly improved the final version of this paper.

RESUMO

O estudo da musculatura pélvica e do membro posterior dos dinossauros basais é importante para entender a evolução do bipedalismo em dinossauros Saurischia. Empregando uma metodologia que tem como base dados obtidos de táxons vivos e extintos posicionados em um contexto filogenético, foi possível fazer inferências bem suportadas relativas à maior parte dos músculos do membro posterior do dinossauro Saurischia basal *Staurikosaurus pricei* Colbert (Formação Santa Maria, Triássico Superior do Rio Grande do Sul, Brasil). Duas grandes concavidades na superfície do ílio correspondem à origem dos músculos *iliotrochantericus caudalis* e *iliofemoralis externus* (compartilhando a concavidade anterior) e para o músculo *iliofibularis* (na concavidade posterior). O músculo *ambiens* apresenta apenas um ramo e se origina no tubérculo púbico. A origem provável do músculo *puboischiofemoralis internus 1* está localizada numa margem ventral do processo pré-acetabular do ílio, representando um estágio anterior à formação da verdadeira fossa acetabular. Os músculos *caudofemorales longus et brevis*



Palavras-chave: “extant phylogenetic bracket”, locomoção, reconstrução muscular, Saurischia, *Staurikosaurus pricei*.

REFERENCES

- ALEXANDER RMCN. 1976. Estimates of speeds of dinosaurs. *Nature* 261: 129–130.
- ALEXANDER RMCN. 2004. Bipedal animals, and their differences from humans. *J Anat* 204: 321–330.
- BARSBOLD R AND OSMÓLSKA H. 1990. Ornithomimosauria. In: WEISHAMPEL DB ET AL. (Eds), *The Dinosauria*, Berkeley: University of California Press, p. 225–244.
- BENTON MJ. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philos T R Soc B* 354: 1423–1446.
- BENTON MJ AND CLARK JM. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: BENTON MJ (Ed), *The phylogeny and classification of the Tetrapods*, Vol. 1: Amphibians, Reptiles, Birds, Systematics Association Special 35 A: 295–338.
- BITTENCOURT JS AND KELLNER AWA. 2009. The anatomy and phylogenetic position of the Triassic dinosaur *Staurikosaurus pricei* Colbert, 1970. *Zootaxa* 2079: 1–56.
- BONAPARTE JF. 1996. *Dinosaurios de America del Sur*. Buenos Aires: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, 174 p.
- BONAPARTE JF, FERIGOLO J AND RIBEIRO AM. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul State, Brazil. In: TOMIDA Y ET AL. (Eds), *Proceedings of the Second Gondwanaland Dinosaur Symposium*, Tokyo: National Science Museum Monographs 15: 89–109.
- BONAPARTE JF, NOVAS FE AND CORIA RA. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contrib. Sci Nat Hist Mus Los Angeles Co* 416: 1–42.
- BRINKMAN DB AND SUES H-D. 1987. A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. *Palaeontology* 30: 493–503.
- BRYANT HN AND RUSSELL AP. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philos T R Soc B* 337: 405–418.
- CARRANO MT. 1999. What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. *J Zool (London)* 247: 29–42.
- CARRANO MT. 2000. Homoplasy and the evolution of dinosaur locomotion. *Paleobiology* 26: 489–512.
- CARRANO MT. 2001. Implications of limb bone scaling, curvature and eccentricity in mammals and non-avian dinosaurs. *J Zool (London)* 254: 41–55.
- CARRANO MT AND HUTCHINSON JR. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *J Morphol* 253: 207–228.
- CARRANO MT, SAMPSON SD AND FORSTER CA. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *J Vert Paleontol* 22: 510–534.
- CARRIER DR, WALTER RM AND LEE DV. 2001. Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *J Exp Biol* 204: 3917–3926.
- CLARKE JA. 2004. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). *Bull Am Mus Nat Hist* 286: 1–179.
- COLBERT EH. 1964. Relationships of the Saurischian Dinosaurs. *Am Mus Novit* 2181: 1–24.
- COLBERT EH. 1970. A saurischian dinosaur from the Triassic of Brazil. *Am Mus Novit* 2405: 1–60.
- COLBERT EH. 1989. The Triassic dinosaur *Coelophysis*. *Bull Mus N Arizona* 57: 1–160.
- COOMBS JR WP. 1979. Osteology and myology of the hindlimb in the Ankylosauria (Reptilia, Ornithischia). *J Paleontol* 53: 666–684.
- COOMBS JR WP. 1980. Swimming ability of carnivorous dinosaurs. *Science* 207: 1198–1200.
- CORIA RA AND CURRIE PJ. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28: 71–118.
- CURRIE PJ. 2000. Theropods from the Cretaceous of Mongolia. In: BENTON MJ, SHISHKIN MA, UNWIN DM AND KUROCHKIN EN (Eds), *The age of dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press, p. 434–455.
- CURRIE PJ AND CHEN P-J. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Can J Earth Sci* 38: 1705–1727.



PELVIC AND HIND LIMB MUSCLES OF *STAUROSAURUS*

- DILKES DW. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiaasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Trans R Soc Edinb, Earth Sci* 90: 87–125.
- FARLOW JO. 1981. Estimates of dinosaur speeds from a new trackway site in Texas. *Nature* 294: 747–748.
- GADOW H. 1880. *Zur vergleichenden Anatomie der Muskulatur des Beckens und der hinteren Gliedmasse der Reptilien*. Jena: G. Fischer.
- GALTON PM. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from The Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. *Paläontol Z* 51: 234–245.
- GALTON PM. 1984. An early prosauropod dinosaur from the upper Triassic of Nordwürttemberg, West Germany. *Stuttgarter Beitr Naturkd, ser B*, 106: 1–25.
- GALTON PM. 2000. Are *Spondylosoma* and *Staurikosaurus* (Santa Maria Formation, Middle-Upper Triassic, Brazil) the oldest saurischian dinosaurs? *Paläontol Z* 74: 393–423.
- GATESY SM. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* 16: 170–186.
- GATESY SM. 1999. Guinea fowl limb function. I: Cineradiographic analysis and speed effects. *J Morphol* 240: 115–125.
- GATESY SM AND BIEWENER AA. 1991. bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J Zool (London)* 224: 127–147.
- GATESY SM, MIDDLETON KM, JENKINS JR FA AND SHUBIN NH. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature* 399: 141–144.
- GAUTHIER J. 1986. Saurischian monophyly and the origin of birds. In: PADIAN K (Ed), *The origin of birds and the evolution of flight*, *Mem California Acad Sci* 8: 1–55.
- GOODRICH ES. 1958. *Studies on the structure and development of vertebrates*. New York: Dover Publications 1: 485.
- GREGORY WK AND CAMP CL. 1918. *Studies in comparative myology and osteology*. III. *Bull Am Mus Nat Hist* 38: 447–563.
- GRILLO ON AND AZEVEDO SAK. 2011. Recovering missing data: estimating position and size of caudal vertebrae of mass of extinct animals by 3-D mathematical models. *Paleobiology* 25: 88–106.
- HOLTZ JR TR. 1998. A new phylogeny of the carnosaurs. *Gaia* 15: 5–61.
- HUANG SH, NORELL MA AND KEQIN G. 2004. A new Compsognathid from the Early Cretaceous Yixian Formation of China. *J Syst Palaeont* 2: 13–30.
- HUENE F VON. 1908. *Die Dinosaurier der Europaica*. 1. Abhandlung, mit Berücksichtigung der Ausseren Erscheinungen vorkommnisse: Geologische und Palaeontologische Abhandlung, Supp band 1: 1–419.
- HUNT AP, LUCAS SG, HECKERT AB, SULLIVAN R AND LOCKLEY MG. 1998. Late Triassic dinosaurs from the western United States. *Geobios* 31: 511–531.
- HUTCHINSON JR. 2001a. The evolution of pelvic osseous and soft tissues on the line to extant birds (Neornithes). *Zool J Linn Soc* 131: 123–168.
- HUTCHINSON JR. 2001b. The evolution of femoral osseous and soft tissues on the line to extant birds (Neornithes). *Zool J Linn Soc* 131: 169–197.
- HUTCHINSON JR. 2002. The evolution of hindlimb osseous and muscles on the line to crown-group birds. *Comparative Biochem Physiol A* 133: 1051–1086.
- HUTCHINSON JR. 2004a. Biomechanical modeling and sensitivity analysis of bipedal running ability. II. Extinct taxa. *J Morphol* 262: 441–461.
- HUTCHINSON JR. 2004b. Biomechanical modeling and sensitivity analysis of bipedal running ability. I. Extant taxa. *J Morphol* 262: 421–440.
- HUTCHINSON JR, ANDERSON FC, BLEMKER S AND DELP SL. 2005. Analysis of hindlimb muscle function in arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: implications for gait, and speed. *Paleobiology* 31: 676–701.
- HUTCHINSON JR AND GARCIA M. 2002. *Tyrannosaurus* was not a fast runner. *Nature* 415: 1018–1021.
- HUTCHINSON JR AND GATESY SM. 2000. Adductor muscles, and the evolution of archosaur locomotion. *Paleobiology* 26: 734–751.
- HUTCHINSON JR AND GATESY SM. 2006. Beyond the bones. *Nature* 440: 292–294.
- ISHIGAKI S. 1989. Footprints of swimming sauropterygians from Morocco. In: GILLETTE DD AND LOCKLEY MG (Eds), *Dinosaur Tracks and Traces*, Cambridge: Cambridge University Press.



- the reconstruction of dromaeosaur (Theropoda: Eumaniraptora) shoulder musculature. *Zool J Linn Soc* 146: 301–344.
- JI Q, NORELL MA, MAKOVICKY PJ, GAO K-Q, JI SA AND YUAN C. 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. *Am Mus Novit* 3420: 1–19.
- JONES TD, FARLOW JO, RUBEN JA, HENDERSON DM AND HILLENUS WJ. 2000. Cursoriality in bipedal archosaurs. *Nature* 406: 716–718.
- KOBAYASHI Y AND LÜ J-C. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica* 48: 235–259.
- LANGER MC. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *PaleoBios* 23: 1–40.
- LANGER MC. 2004. Basal Saurischia. In: WEISHAMPEL DB ET AL. (Eds), *The Dinosauria*, 2nd ed., Berkeley: University of California Press, p. 25–46.
- LEAL LA, AZEVEDO SAK, KELLNER AWA AND DA ROSA AAS. 2004. A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Paraná Basin, Brazil. *Zootaxa* 690: 1–24.
- LLOYD GT, DAVIS KE, PISANI D, TARVER JE, RUTA M, SAKAMOTO M, HONE DWE, JENNINGS R AND BEN-TON MJ. 2008. Dinosaurs and the Cretaceous terrestrial revolution. *Proc R Soc B* 275: 2483–2490.
- LOCKLEY MG AND GILLETTE DD. 1989. Dinosaur tracks and traces: an overview. In: GILLETTE DD AND LOCKLEY MG (Eds), *Dinosaur Tracks and Traces*, Cambridge: Cambridge University Press, p. 3–10.
- LONG RA AND MURRY PA. 1995. Late Triassic (Carnian and Norian) Tetrapods from the Southwestern United States. *New Mexico Mus Nat Hist Sci Bull* 4: 1–254.
- MADSEN JR JH. 1993. *Allosaurus fragilis*: A revised osteology, 2nd ed., Utah Geol Survey Bull 109: 1–163.
- MAKOVICKY PJ AND SUES H-D. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *Am Mus Novit* 3240: 1–27.
- MCGOWAN C. 1999. A practical guide to vertebrate mechanics. Cambridge: Cambridge University Press, 301 p.
- MOLNAR RE, KURZANOV SM AND ZHIMING D. 1990. NAISH D, MARTILL DM AND FREY E. 2004. Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Hist Biol* 16: 57–70.
- NORELL MA, CLARK JM AND MAKOVICKY PJ. 2001. Phylogenetic relationships among coelurosaurian theropods. In: GAUTHIER JA AND GALL LF (Eds), *New Perspectives on the Origin and Early Evolution of Birds*, New Haven: Yale University Press, p. 49–67.
- NORELL MA AND MAKOVICKY PJ. 1999. Important features of the dromaeosaurid skeleton II: Information from newly collected specimens of *Velociraptor mongoliensis*. *Am Mus Novit* 3282: 1–45.
- NORMAN DB. 1990. Problematic Theropoda: “Coelurosaurians”. In: WEISHAMPEL DB ET AL. (Eds), *The Dinosauria*, Berkeley: University of California Press, p. 280–305.
- NOVAS FE. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Paleontology* 35: 51–62.
- NOVAS FE. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *J Vert Paleontol* 13: 400–423.
- NOVAS FE. 1996. Dinosaur monophyly. *J Vert Paleontol* 16: 723–741.
- OSBORN HF. 1904. Manus, sacrum, and caudals of sauropoda. *Bull Am Mus Nat Hist* 20: 181–190.
- OSBORN HF. 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bull Am Mus Nat Hist* 21: 259–265.
- OSBORN HF. 1916. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *Bull Am Mus Nat Hist* 35: 733–771.
- OSTROM JH. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Peabody Museum of Natural History, *Bull Peabody Mus Nat Hist* 30: 1–165.
- OSTROM JH AND MCINTOSH JS. 1999. *Marsh’s dinosaurs: The Collections from Como Bluff*. New Haven: Yale University Press, 388 p.
- PADIAN K, HUTCHINSON JR AND HOLTZ JR TR. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria



PELVIC AND HIND LIMB MUSCLES OF *STAUROKOSAURUS*

- PAUL GS. 1988. Predatory dinosaurs of the world: A complete illustrated guide. New York: Simon and Schuster, 464 p.
- PAUL GS. 1998. Limb design, function and running performance in ostrich-mimics and tyrannosaurs. *Gaia* 15: 257–270.
- PAUL GS. 2002. Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds. Baltimore: The Johns Hopkins University Press, 472 p.
- RAATH M. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: CARPENTER K AND CURRIE PJ (Eds), *Dinosaur systematics: Approaches and perspectives*, Cambridge: Cambridge University Press, p. 91–105.
- RAYFIELD EJ, NORMAN DB, HORNER CC, HORNER JR, SMITH PM, THOMASON JJ AND UPCHURCH P. 2001. Cranial design and function in a large theropod dinosaur. *Nature* 409: 1033–1037.
- ROMER AS. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bull Am Mus Nat Hist* 46: 517–606.
- ROMER AS. 1923a. The pelvic musculature of saurischian dinosaurs. *Bull Am Mus Nat Hist* 48: 605–617.
- ROMER AS. 1923b. The ilium in dinosaurs and birds. *Bull Am Mus Nat Hist* 48: 141–145.
- ROMER AS. 1923c. Crocodilian pelvic muscles and their avian and reptilian homologues. *Bull Am Mus Nat Hist* 48: 533–552.
- ROMER AS. 1942. The development of tetrapod limb musculature – the thigh of *Lacerta*. *J Morphol* 71: 251–298.
- ROMER AS. 1956. Osteology of the reptiles. Chicago: University of Chicago Press, 772 p.
- ROWE T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other reptilian. *J Morphol* 189: 327–346.
- ROWE T AND GAUTHIER J. 1990. Ceratosauria. In: WEISHAMPEL DB ET AL. (Eds), *The Dinosauria*, Berkeley: University of California Press, p. 151–168.
- RUSSELL DA. 1972. Ostrich dinosaurs from the late Cretaceous of western Canada. *Can J Earth Sci* 9: 375–402.
- RUSSELL AP AND BELS V. 2001. Biomechanics and kinematics of limb-based locomotion in lizards: review, synthesis and prospectus. *Comp Biochem Physiol A* 131: 1–10.
- Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science* 280: 1048–1051.
- SCHWARZ D AND SALISBURY SW. 2005. A new crocodylomorph, *Theriosuchus* (Atoposauridae, Crocodylomorpha), from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. *Geobios* 38: 779–802.
- SEEBACHER F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *J Vert Paleontol* 21: 51–60.
- SEN K. 2003. *Pamelaria dolichotrachela*, a new proleptid reptile from the Middle Triassic of India. *J Asian Earth Sci* 21: 663–681.
- SERENO PC. 1997. The origin and evolution of dinosaurs. *Annu Rev Earth Planet Sci* 25: 435–489.
- SERENO PC. 1999. The evolution of dinosaurs. *Science* 285: 2137–2147.
- SERENO PC AND ARCUCCI AB. 1993. Dinosaurian remains from the Middle Triassic of Argentina: *Lagania chanarensis*. *J Vert Paleontol* 13: 385–399.
- SERENO PC AND ARCUCCI AB. 1994. Dinosaurian remains from the Middle Triassic of Argentina: *Mariloriculus lilloensis* gen. nov. *J Vert Paleontol* 14: 53–73.
- SERENO PC AND NOVAS FE. 1992. The complete skeleton of an early dinosaur. *Science* 258: 1137–1141.
- STOKSTAD E. 2001. Did saurian predators fold up on themselves? *Science* 293: 1572.
- THULBORN RA. 1989. The gaits of dinosaurs. In: GILLETTE DD AND LOCKLEY MG (Eds), *Dinosaur Tracks and Traces*, Cambridge: Cambridge University Press, p. 50.
- TROXELL EL. 1925. *Hyposaurus*, a marine crocodilian. *J Sci*, 5th Series 9: 489–514.
- WADE M. 1989. The stance of dinosaurs and the Dancer Syndrome. In: GILLETTE DD AND LOCKLEY MG (Eds), *Dinosaur Tracks and Traces*, Cambridge: Cambridge University Press, p. 73–82.
- WILHITE R. 2003. Digitizing large fossil skeletal elements for three-dimensional applications. *Palaeontologia Electronica* 5(2):10, 619KB; http://palaeo-electronica.org/palaeo/issue2_02.htm
- WITMER LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossil dinosaurs. *Palaeontologia Electronica* 1(1):1–10.



- 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. *J Vert Paleontol* 17: 1–73.
- XU X, CLARK JM, FORSTER CA, NORELL M, ERICKSON GM, EBERTH DA, JIA C AND ZHAO Q. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature* 439: 715–718.
- YATES AM. 2003. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *J Syst Palaeontol* 1: 1–42.
- ZAAF A, HERREL A, AERTS P AND DE VREE F. 1999. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria). *Zoomorphology* 119: 9–22.