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New information on the scapular musculature of *Saturnalia tupiniquim* (Dinosauria, Saurischia)

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ABSTRACT

A new feature to the scapulocoracoid of the basal dinosaur *Saturnalia tupiniquim* is here proposed based on new analysis of paratypic material. A shallow pit on the medial portion of the scapula blade seems to represents the scapular origin of the muscle *triceps longus caudalis*. The presence of this feature suggests that *S. tupiniquim* had three heads to the triceps muscle: *triceps longus caudalis, triceps longus cranialis,* and *triceps brevis cranialis*, indicating a more close anatomical resemblance with lepidosaurs and crocodilians, than to birds. Further analysis on other basal dinosaur scapulae is required to confirm the existence of those three heads of the triceps in the basal dinosaur lineage or to determine whether this feature is unique to *S. tupiniquim*.

Key words: *Saturnalia tupiniquim*, Dinosauria, scapula blade, triceps, Upper Triassic.

RESUMO

NOVAS INFORMAÇÕES SOBRE A MUSCULATURA ESCAPULAR DE SATURNALIA TUPINIQUIM (DINOSAURIA, SAURISCHIA). Uma nova feição é identificada na escápula-coracóide do dinossauro basal *Saturnalia tupiniquim*, a partir da análise de um dos materiais componentes do parátipo. Nesse elemento, foi registrada uma fossa rasa sobre a porção medial da lâmina escapular, interpretada aqui como a origem escapular do músculo triceps *longus caudalis*. A confirmação de sua presença sugere que *S. tupiniquim* possuía três cabeças de origem para os músculos que compõem o tríceps: *triceps longus caudalis* e *cranialis*, e *triceps brevis cranialis*, condição que o aproxima mais dos lepidossauros e dos crocodilianos do que das aves. É importante salientar, contudo, que somente a análise de novos materiais e de lâminas escapulares de outros dinossauros basais permitirá confirmar se esse caráter foi comum à linhagem de dinossauros, ou se representa uma autapomorfia em *S. tupiniquim*.

Palavras-chave: *Saturnalia tupiniquim*, Dinosauria, lâmina escapular, tríceps, Triássico Superior.

INTRODUCTION

The reconstruction of dinosaur musculature is essential for understanding both dinosaur biomechanics and ecology and is usually approached through comparison with extant animals, especially those which are phylogenetically related. Over the past century many reconstructions of dinosaurs musculatures have been published based in crocodilians (Romer, 1923a, 1923b, 1956; Colbert, 1964; Coombs, 1978). Witmer (1995) developed a method for soft tissue reconstruction on the basis of phylogenetic approaches known as the "Extant Phylogenetic Bracket" (EPB). This method traces bone homology between fossil organisms and a minimum of two phylogenetically close extant taxa, allowing the inference of the musculature in fossil form. Several authors have used this method to confidently reconstruct soft tissue of archosaurs using Crocodylia and Aves as the extant basal and derivate taxa, respectively (e.g., Witmer, 1997; Dilkes, 2000; Carrano and Hutchinson, 2002; Langer, 2003; Langer *et al.*, 2007; Costa, 2010; Grillo and Azevedo, 2011; Maidment and Barret, 2011). Other notable studies of muscle reconstruction involved a basal dinosaur (*Staurikosaurus pricei*) (Grillo and Azevedo, 2011) and a basal ornithischian (Maidment and Barret, 2011).

Saturnalia tupiniquim represents a good example of soft tissue reconstruction using the EPB method. This small dinosaur, recovered from the Santa Maria Formation in the State of Rio Grande do Sul, Brazil, was first described by Langer *et al.* (1999). There exist three well-preserved partial skeletons of *S. tupiniquim* that exhibit tuberosities and a variety of muscle traces (Langer, 2003). Descriptions of the pelvic girdle/hindlimb and pectoral girdle/forelimb musculature of *S. tupiniquim* can be found in Langer (2003) and Langer *et al.* (2007), respectively. In this study, we report an osteological feature found in the area of the triceps head insertion of *S. tupiniquim*. Although this feature was not mentioned in Langer *et al.* (2007), our results suggest that it has significant implications to the anatomy of *S. tupiniquim*.

MATERIALS AND METHODS

To this research materials stored in the MCP (*Museu de Ciências e Tecnologia da Pontifícia Universidade Católica de Porto Alegre*, Porto Alegre, Brazil) and in the MZUSP (*Museu de Zoologia da Universidade de São Paulo*, São Paulo, Brazil) were examined in order to determine the area where the triceps originates. The right scapulocoracoid of the first paratype (MCP 3845-PV) presented an exceptionally well preserved scapula in relation to the other two *S. tupiniquim* skeletons. In the scapular blade of the holotype (MCP 3844-PV) the middle portion is missing being impossible the observation of the origin of the scapular muscle, and in the second paratype (MCP 3846-PV) none of the scapulocoracoid is preserved.

The EPB method was used to infer the triceps of *S. tupiniquim* and location of *S. tupiniquim* in the previous phylogenetic frameworks (Figure 1).

RESULTS

The *triceps brachii* in crocodilians is a complex muscle consisting of five heads: *triceps longus lateralis* and *caudalis*, and *triceps brevis cranialis*, *intermedialis,* and *caudalis*. The origins of those heads are over the scapula (*triceps longus*) and humerus (*triceps brevis*) (Meers, 2003; Jasinoski *et al.*, 2006; Maidment and Barret, 2011). The tendon associated with triceps *longus caudalis* attaches to the scapula and the coracoid, immediately overlying the insertion of the subscapularis (Meers, 2003).

In birds the scapulotriceps (*triceps longus lateralis*) originates from the lateral and ventral scapular blade, caudal to the glenoid, and the humerotriceps (*triceps brevis cranialis*) originates from the caudal humeral shaft and bicipital crest (Hudson *et al.*, 1972; Jasinoski *et al.*, 2006; Maxwell and Larsson, 2007; Maidment and Barret, 2011). The tendon of the triceps; however, is completely absent (Jasinoski *et al.*, 2006; Maidment and Barret, 2011).

Langer *et al.* (2007) described the origin of muscles in the scapulocoracoid of *S. tupiniquim* proposing that the *triceps longus* arises together with the sternocoracoideus from an oval pit, cranial to the glenoid (coracoidal head of the triceps) and from another oval pit, caudal to the glenoid (scapular head of the triceps). However, in MCP 3845-PV, there is a shallow pit in the medial portion of the scapular blade, caudal to the glenoid, that are here interpreted as the scapular part of the *triceps longus caudalis* tendon (Figure 2A). In fact, this tendon is found in the same place on the scapula of the crocodilians (level II of EPB). The shallow pit is anterior to the expansion of the scapular blade in medial view, as in *Caiman latirostris*, and other crocodilians (Meers, 2003, Figure 2B). Moreover, the scapular head of the triceps discussed by Langer *et al.* (2007) is here interpreted like representing the *triceps longus lateralis* (Figure 3), a condition similar to that also found in the crocodilians (Figure 4). Also in *S. tupiniquim* the *triceps brevis* has only one head (*cranialis*) on the lateral shaft of the humerus (Langer *et al.*, 2007).

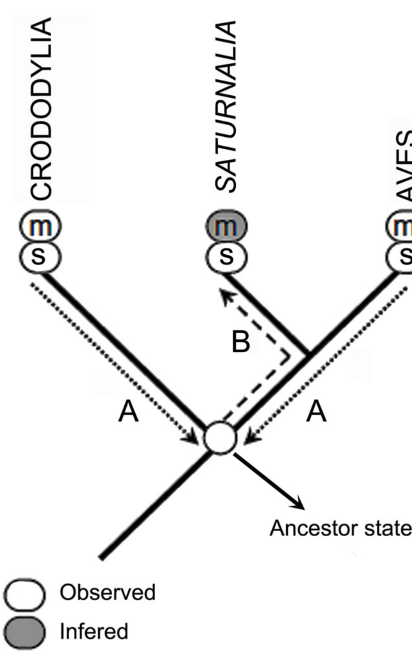

Figure 1. Application of the EPB in the reconstruction of *S. tupiniquim* muscle by Langer *et al.* (2007). **A**. inference of the osteological structure (s) and muscle (m) in the closest common ancestor, based in the observation of extant taxa; **B**. inference from the osteological structure (s) and muscle (m) of extinct taxa (adapted from Grillo and Azevedo, 2011). Phylogenetic frameworks from Sereno (1999), Hutchinson (2002), Langer (2004) and Langer and Benton (2006).

FINAL COMMENTS

The reanalysis herein presented, based in a better preserved scapulocoracoid of *S. tupiniquim,* indicates that his triceps complex is composed by three heads: *triceps longus caudalis* and *cranialis* and *triceps brevis cranialis* (Figures 2-3). This attest that *S. tupiniquim* actually had a muscle configuration closer to that observed in lepidosaurs and crocodilians, which have four (Dilkes, 2000) and five triceps heads, respectively (Meers, 2003; Jasinoski *et al.*, 2006; Maidment and Barret, 2011).

Dilkes (2000) proposed that dinosaurs have just two triceps heads, a condition similar to that of birds. However, the triceps scar (a shallow pit) on the medial portion of the scapular blade in *S. tupiniquim* shows that the triceps complex is more similar to what is found in basal dinosaur, and allows suggesting that the *triceps longus caudalis* was lost during the evolution of birds. Future analyses involving comparisons with

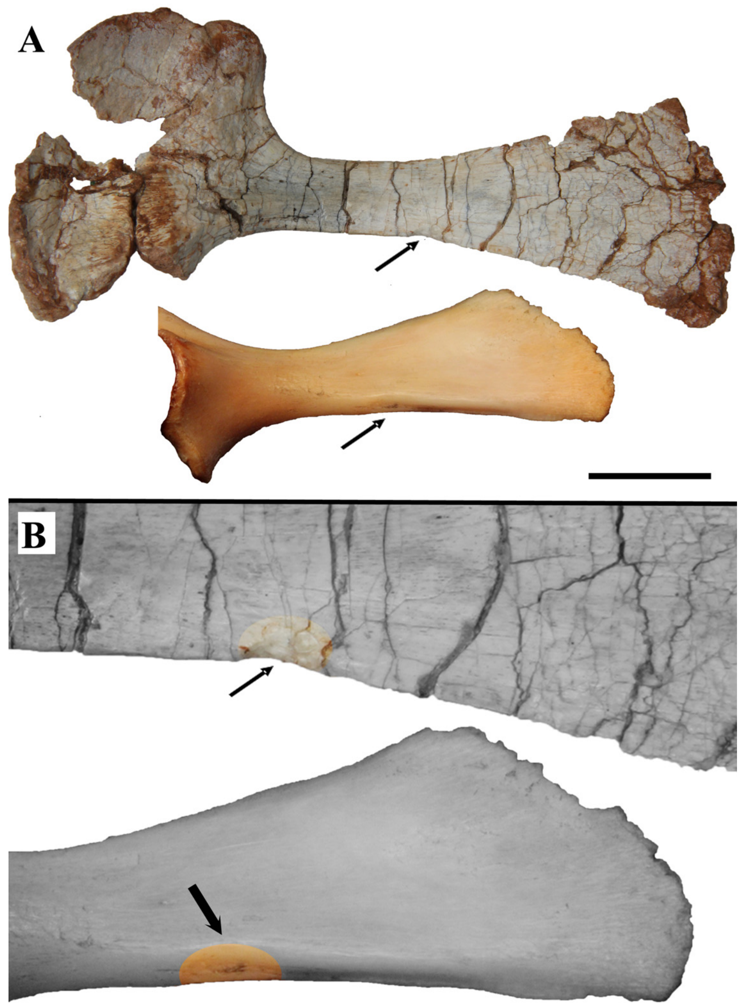

Figure 2. A. Comparison between the right scapulocoracoid (medial view) of *Saturnalia tupiniquim* (above, MCP 3845–PV) and *Caiman brevirostris* (below, MZUSP 2137–R), highlighting the scar of the scapular origin of the *triceps longus caudalis* (black arrows). Scale bar 2 cm; **B.** Detail of **A.**

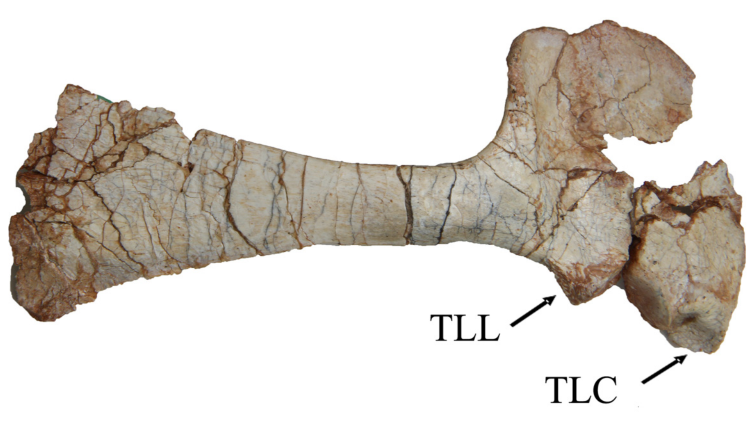

Figure 3. Right scapulocoracoid of *S. tupiniquim* (MCP 3845–PV) in lateral view. Arrows indicate the origins of the *triceps longus lateralis* (TLL) and the coracoidal head of the *triceps longus caudalis* (TLC). Scale bar 2 cm.

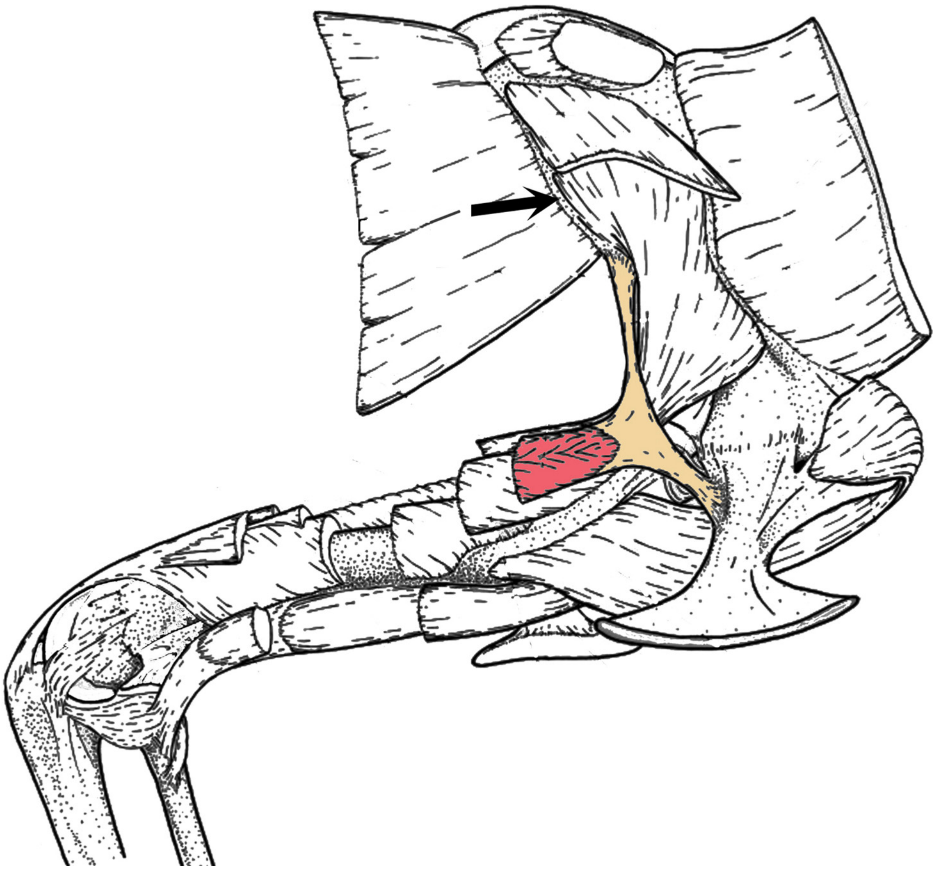

Figure 4. Dissection of shoulder and brachium of a crocodilian (medial view) showing the triceps *longus caudalis* tendon arising from the scapular blade and coracoids (in yellow). The arrow points scapulacoracoid and associated muscles (adapted from Meers, 2003, Figure 7).

additional fossils could probably furnish more elements to a better understanding of the significance of this condition in *S. tupiniquim* and other basal dinosaurs.

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