Papéis Avulsos de Zoologia
Museu de Zoologia da Universidade de São Paulo

Volume 52(29):341-347, 2012 www.mz.usp.br/publicacoes
http://portal.revistasusp.sibi.usp.br
www.scielo.br/paz
ISSN impresso: 0031-1049
ISSN *on-line:* 1807-0205

Biomechanical comments about Triassic dinosaurs from Brazil

Rafael Delcourt[1]
Sergio Alex Kugland de Azevedo[2,3]
Orlando Nelson Grillo[2,4]
Fernanda Oliveira Deantoni[2,5]

ABSTRACT

*Triassic dinosaurs of Brazil are found in Santa Maria and Caturrita formations, Rio Grande do Sul state, Brazil. There are three species known from the Santa Maria Formation (*Staurikosaurus pricei, Saturnalia tupiniquim *and* Pampadromaeus barberenai*), and two from Caturrita Formation (*Guaibasaurus candelariensis *and* Unaysaurus tolentinoi*). These dinosaur materials are, for the most part, well preserved and allow for descriptions of musculature and biomechanical studies. The lateral rotation of the* Saturnalia *femur is corroborated through calculations of muscle moment arms. The enhanced supracetabular crest of* Saturnalia, Guaibasaurus, Staurikosaurus, Herrerasaurus ischigualastensis, Efraasia minor *and* Chormogisaurus novasi *suggests that basal dinosaurs may have maintained an inclination of the trunk at least 20° on the horizontal axis. The pectoral girdle articulation of basal sauropodomorphs (*Saturnalia *and* Unaysaurus*) was established using a new method, the Clavicular Ring, and the scapular blade remains near 60° on the horizontal axis. This is a plesiomorphic condition among sauropodomorphs and is also seen in the articulated plateosauridae* Seitaad ruessi. *The Brazilian basal dinosaurs were lightweight with a body mass estimated around 18.5 kg for* Staurikosaurus, *6.5 kg for* Saturnalia, *and 17 kg for* Guaibasaurus. Pampadromaeus *probably weighed 2.5 kg, but measures of its femur are necessary to confirm this hypothesis. The Triassic dinosaurs from Brazil were diversified but shared some functional aspects that were important in an evolutionary context.*

Key-Words: Dinosaurs; Triassic; Biomechanics; Articulation; Mass.

INTRODUCTION

Knowledge of Brazilian dinosaurs increased substantially with the description of new species, and referred materials have been registered annually (Bittencourt & Langer, 2011; Cabreira *et al.,* 2011; Delcourt & Grillo, 2011; Kellner *et al.,* 2011; Santucci & Arruda-Campos, 2011; Zaher *et al.,* 2011). Triassic dinosaurs of Brazil were found in the Santa Maria and Caturrita formations in central Rio Grande do

1. Museu de Zoologia, Universidade de São Paulo. Caixa Postal 42.494, 04218-970, São Paulo, SP, Brasil. E-mail: E-mail: rafaeldelcourt@usp.br
2. Museu Nacional, Universidade Federal do Rio de Janeiro. Quinta da Boa Vista, São Cristóvão CEP 20940-040, Rio de Janeiro, RJ, Brasil.
3. E-mail: sazevedo@mn.ufrj.br
4. E-mail: ongrillo@gmail.com
5. E-mail: fer.deantoni@gmail.com

Sul, belonging to the Rosário do Sul Group (Langer *et al.,* 2007a; Bittencourt & Langer, 2011). They represent the oldest Brazilian strata in which dinosaur remains were found. The basal condition of some taxa even confuses their positioning in the phylogenetic context (Bittencourt & Kellner, 2009; Langer *et al.,* 2011). On the other hand, some materials are so well preserved as to allow reconstructions of the musculature (Langer, 2003; Langer *et al.,* 2007b; Grillo & Azevedo, 2011) and biomechanical studies (Langer, 2003; Grillo, 2007; Grillo & Azevedo, 2006, 2010; Delcourt *et al.,* 2011a, b; Delcourt, 2012).

Triassic dinosaurs of Brazil have been given and important role in the evolutionary scenario, but not as much as Argentine dinosaurs like *Eoraptor lunensis* Sereno, Forster, Rogers & Monetta, 1993, *Herrerasaurus ischigualastensis* Reig, 1963, and *Eodromaeus murphi* Martinez, Sereno, Alcober, Colombi, Renne, Montañez & Currie, 2011. However Brazilian stem-sauropodomorphs (*i.e., Saturnalia tupiniquim* Langer, Abdala, Richter & Benton, 1999 and *Pampadromaeus barberenai* Cabreira, Schultz, Bittencourt, Soares, Fortier, Silva & Langer, 2011) help us to understand Sauropodomorph evolution since its most basal forms (Langer *et al.,* 1999; Langer & Benton, 2006; Cabreira *et al.,* 2011). Here we aim to enrich the current state of knowledge on the biomechanics of Triassic dinosaurs from Brazil, with comments on sauropodomorph pectoral girdle articulation and mass prediction.

Dinosaur Biomechanics

Biomechanical studies have increased understanding of the biology of the dinosaur in recent years (Alexander, 2006; Hutchinson & Gatesy, 2000; Hutchinson, 2005; Hutchinson *et al.,* 2005; Hutchinson & Gatesy, 2006; Hutchinson *et al.,* 2011). *Staurikosaurus* and *Saturnalia,* Triassic dinosaurs from Brazil, have contributed to this knowledge (Grillo, 2007; Grillo & Azevedo, 2006, 2010; Delcourt *et al.,* 2011a, b).

Langer (2003) proposed that the *Saturnalia* femur turned laterally during the retraction phase of the leg. In this scenario the distal femoral condyles turned laterally and the femoral head turned medially. This occurred because the main retractor muscle of the femur (*i.e., caudofemoralis longus*) was inserted into the medial surface of the femur (Langer, 2003). Delcourt *et al.* (2011b) corroborated that some muscles (*flexor tibialis externus, flexor tibialis internus* 2, *ischiotrochantericus, puboischiofemorales externi* 1-3, *puboischiofemoralis internus* 1, anterior portion of *caudofemoralis longus,* and *caudofemoralis brevis*) had a reduced moment arm for lateral rotation of the *Saturnalia* femur.

The moment arm about a given joint is the major determinant of skeletal muscle function in vertebrates (Hutchinson *et al.,* 2005). It is measured as the smallest distance between the line of action (*i.e.,* force) of a muscle-tendon complex and the center of rotation of a join (Hutchinson *et al.,* 2005). According to Nagano & Komura (2003) smaller moment arms are not favorable for muscle contraction, but during fast locomotion, the opposite occurs: when muscles reach maximum contraction velocity, longer moment arms result in smaller joint moment, power, and work outputs. So it is possible that the lateral rotation increased the locomotive performance of *Saturnalia* during fast locomotion (Delcourt *et al.,* 2011b), corroborating with Langer's (2003) hypothesis, but more studies are necessary to confirm this hypothesis.

Furthermore on the subject of locomotion, some authors (Molnar & Farlow, 1990; Carrier *et al.,* 2001) suggested that theropods had strength in some regions of the supracetabular crest, as well as the pubic peduncle. This condition allowed the femur head to fit below the strength if the ilium remained inclined beyond the horizontal position. Molnar & Farlow (1990) suggested that this configuration of the ilium allowed the pelvic girdle and the trunk to be oriented at a substantial angle relative to the horizontal during locomotion.

Some basal saurischians like *Saturnalia, Guaibasaurus, Staurikosaurus, Herrerasaurus, Efraasia minor* Galton, 1973 and *Chromogisaurus novasi* Ezcurra, 2010 possessed an enlargement of the supracetabular crest that was inclined relative to the line of the vertebral column by 20° to 25°, approximately (Fig. 1). It is possible that this inclination corresponded to the trunk inclination at least during fast locomotion, as proposed by Carrier *et al.* (2001). If this hypothesis is correct, even stem-sauropodomorphs (*i.e., Saturnalia, Pampadromaeus*) were fully bipedal and during the evolution of sauropodomorphs the quadruped stance was adopted depending on the weight increase and proportion of forelimbs and hind limbs, as noted by Upchurch (1997). Some authors proposed that basal sauropodomorphs were facultative bipedal/quadrupedal (Langer, 2003; Galton & Upchurch, 2004; Langer *et al.,* 2010). However, further analyses that involve considerations about the center of mass position (see Hutchinson & Gatesy, 2006; Hutchinson *et al.,* 2007) and muscle force, as well as a better understanding on the relation between muscle moment arms and posture in extant taxa are necessary to confirm stem-sauropodomorph bipedalism and the trunk inclination of basal saurischians.

Pectoral Girdle Articulation

Pectoral girdle articulation and position relative to the ribcage is hard to determine (Mallison, 2010; Delcourt *et al.,* 2011c). According to Mallison (2010), the pectoral girdle should be U-shaped in the sauropodomorph *Plateosaurus,* allowing little or no rotation of the scapula against the ribcage. This restriction in rotation was caused by the fusion of the clavicles (Mallison, 2010), which was observed in some dinosaurs (Currie & Madsen, 1996; Makovicky & Currie, 1998; Yates & Vasconcelos, 2005; Lipkin *et al.,* 2007). Remes (2008) figured that the pelvic girdle changed orientation during the evolution of the Sauropodomorpha: the angle of the scapula, relative to the horizontal axis, ranged from 45° to 65° in sauropodomorphs. However, more inclined angles, near 60°, are plesiomorphic and are seen in basal sauropodomorphs.

Delcourt *et al.* (2011c) developed a simple method to articulate the pectoral girdle in stem-sauropodomorphs. They observed that, in articulated skeletons of several dinosaur taxa (*e.g.,* Yates & Vasconcelos, 2005, fig. 1A; Xu *et al.,* 2006, fig. 1), the distance

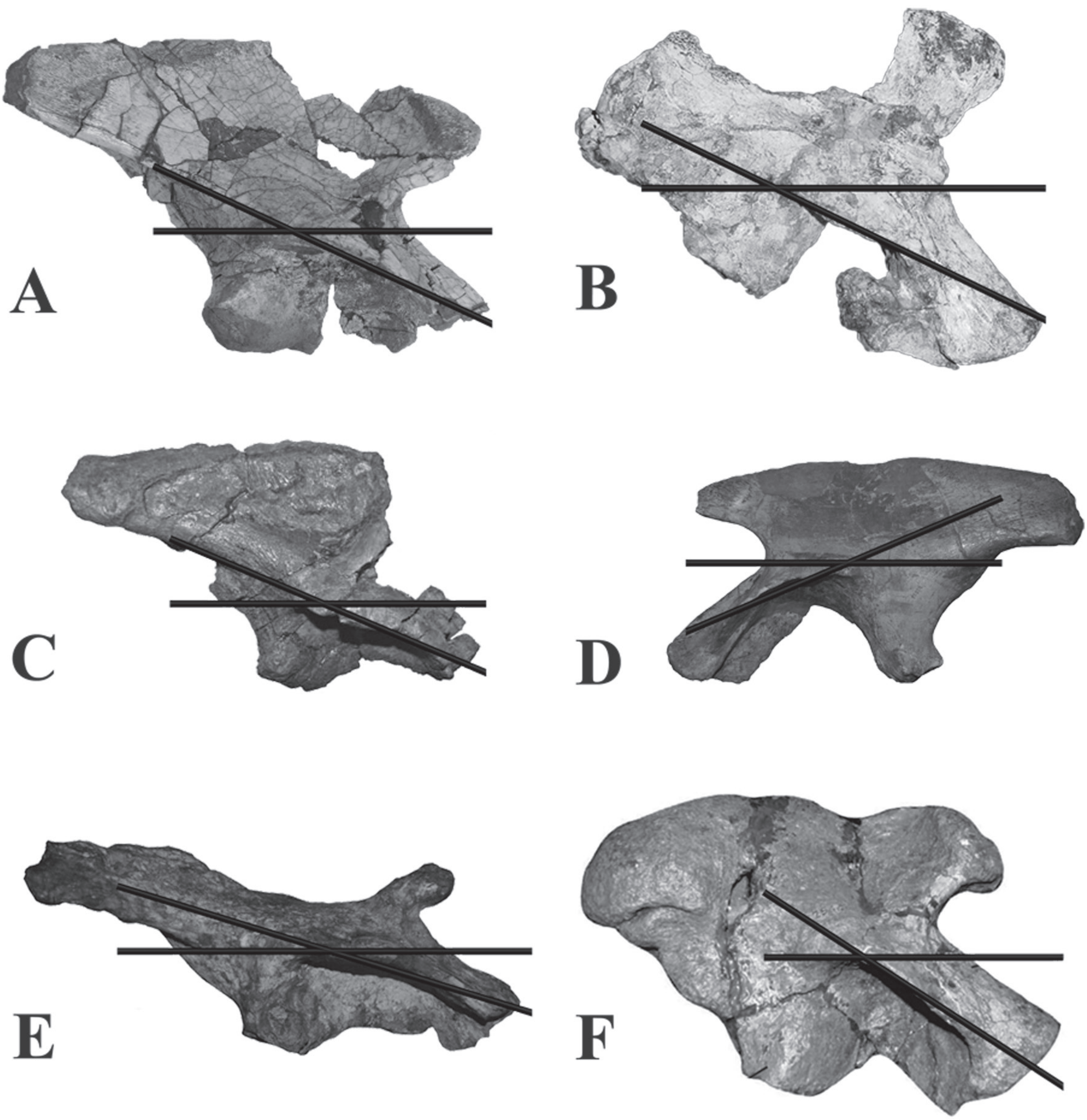

FIGURE 1: Ilium in lateral view of Triassic dinosaurs showing the angles of enlargement of the supracetabular crest. In **A,** *Saturnalia* with 25°; **B,** *Staurikosaurus* with 26°; **C,** *Chromogisaurus* with 23° (modified from Ezcurra (2010)); **D,** *Efraasia,* with 23° (modified from Langer *et al.* (2011)); **E,** *Guaibasaurus* with 17° (modified from Langer *et al.* (2011)) and **F,** *Herrerasaurus* with 33°.

from the ventral surface of the first dorsal vertebra to the acromion process (that corresponds to the articulation point for the clavicle) is roughly equivalent to the largest length of the coracoid. They proposed that this length could be used as the diameter of a circle (the Clavicular Ring) that, when positioned tangent to both acromia and the ventral surface of the first dorsal vertebra, would indicate the anterior position of the pectoral girdle. For determining the position of the scapula, it was necessary to determine the width of the ribcage and of the U-shaped pectoral girdle and rotate it (using the acromia as pivot axis) till the scapula contacted the ribs. The Clavicular Ring, is oriented on the vertical plane, and as it is connected to both acromia, the dorsal part of the ring should touch the ventral surface of the first vertebra to articulate the pectoral girdle. In *Saturnalia,* after articulating the pectoral girdle using the Clavicular Ring (diameter of 40.72 mm), the main axis of the scapula formed an angle of 60.13 degrees with the horizontal axis, which corresponds to the inclination proposed for the scapular blade in sauropodomorphs (Delcourt *et al.,* 2011c)

In this paper, the same method was applied to the plateosaurid *Unaysaurus* (Leal *et al.,* 2004; Lloyd *et al.,* 2008). The *Unaysaurus* Clavicular Ring has a diameter of 102.2 mm, and the orientation of the pectoral girdle is 60 degrees to the horizontal, according to this method (Fig. 2). Interestingly, this condition is similar to the one found in *Seitaad ruessi* Sertich & Loewen, 2010, probable plateosauridae from Kayenta Formation, Arizona, USA. There is an articulated pectoral girdle preserved for this dinosaur, and it suggests that the scapula blade formed an angle of approximately 60° (Sertich & Loewen, 2010). This orientation confirms the Remes (2008) proposition as explained above.

Mass Prediction in Basal Dinosaurs

The mass of extinct animals has been measured by different methods by some authors (Motani, 2001; Christiansen & Fariña, 2004; Hutchinson *et al.,* 2007; Gunga *et al.,* 2007). The method that uses a correlation between mass and the dimensions of long bones, developed by Christiansen & Fariña (2004), had high correlation coefficients (= 0.975) in extant taxa, and within the measured bones (*e.g.,* femur, tibia and fibula) the femur was more representative (correlation coefficients = 0.995). From this method, the masses of the basal Brazilian dinosaurs could be easily estimated, as seen in Table 1. These values correspond to the approximated mass, because the formula proposed by Christiansen & Fariña (2004) was based on theropod data only. Since *Staurikosaurus* and *Guaibasaurus* are considered basal theropods according to the most recent phylogenetic studies (Langer *et al.,* 2011; Martinez *et al.,* 2011), the use of this formula is justified. *Saturnalia* is not a theropod, but a stem-sauropodomoph. However, according to their basal position, which was close to the theropod-sauropodomorph dichotomy (Langer *et al.,* 1999; Langer & Benton, 2006; Martinez *et al.,* 2011), the estimated mass might be not far from reality.

TABLE 1: Relationships between femur length and prediction mass of *Guaibasaurus, Pampadromaeus, Saturnalia* and *Staurikosaurus* from Christiansen & Fariña (2004) formula.

Taxon	Femur Length (mm)	Approximate Mass (kg)
Guaibasaurus	214 ~	17
Pampadromaeus	117 (?)	2.5 (?)
Saturnalia	157	6.5
Staurikosaurus	220	18.5

There is no published information about the measures of the femur of *Pampadromaeus,* so we couldn't predict its mass. If the scale of fig. S2 (Cabreira *et al.,* 2011) is correct, *Pampadromaeus* may have reached approximately 2.5 kg in body mass. The mass of *Unaysaurus* was not predicted for two reasons: first it is not a preserved femur; and second, even if the tibia was preserved, the method used here is appropriate for theropod dinosaurs. The use of this method for *Saturnalia* and *Pampadromaeus* was justified above.

CONCLUSION

As seen above, among other Brazilian dinosaurs, the Triassic forms are well preserved, allowing studies in biomechanics and muscular reconstruction. Based on the osteological evidence, the basal saurischian probably had its trunk erected at least 20° relative to the horizontal, and basal sauropodomorphs (*i.e., Saturnalia* and *Pampadromaeus*) perhaps were fully bipedal.

The Clavicular Ring methodology provides a new approach for reconstructing the scapular blade orientation relative to the horizontal axis. The plesiomorphic condition of the articulate pectoral girdle (*i.e.,* 60°; Remes, 2008) is found using the Clavicular Method in *Saturnalia* and *Unaysaurus* and it is confirmed by *Seitaad ruessi.*

The basal dinosaur from Brazil (*i.e., Saturnalia, Staurikosaurus* and *Guaibasaurus*) were lighter than most derived dinosaurs, as seen in several species of theropods (Christiansen & Fariña, 2004), and the bipedal condition was very important for the evolutionary success of dinosaurs (Langer *et al.,* 2010).

Some functional aspects help us to understand basal dinosaur paleoecology and evolution beyond the phylogenetic framework. The high-quality preservation of the fossils of the Santa Maria and Caturrita formations allows for morphological, biomechanical and phylogenetic studies. Based on the information above presented, we conclude that the different Brazilian species of Triassic dinosaurs were diversified, but at the same time shared some functional aspects that were important for their evolutionary context as a group.

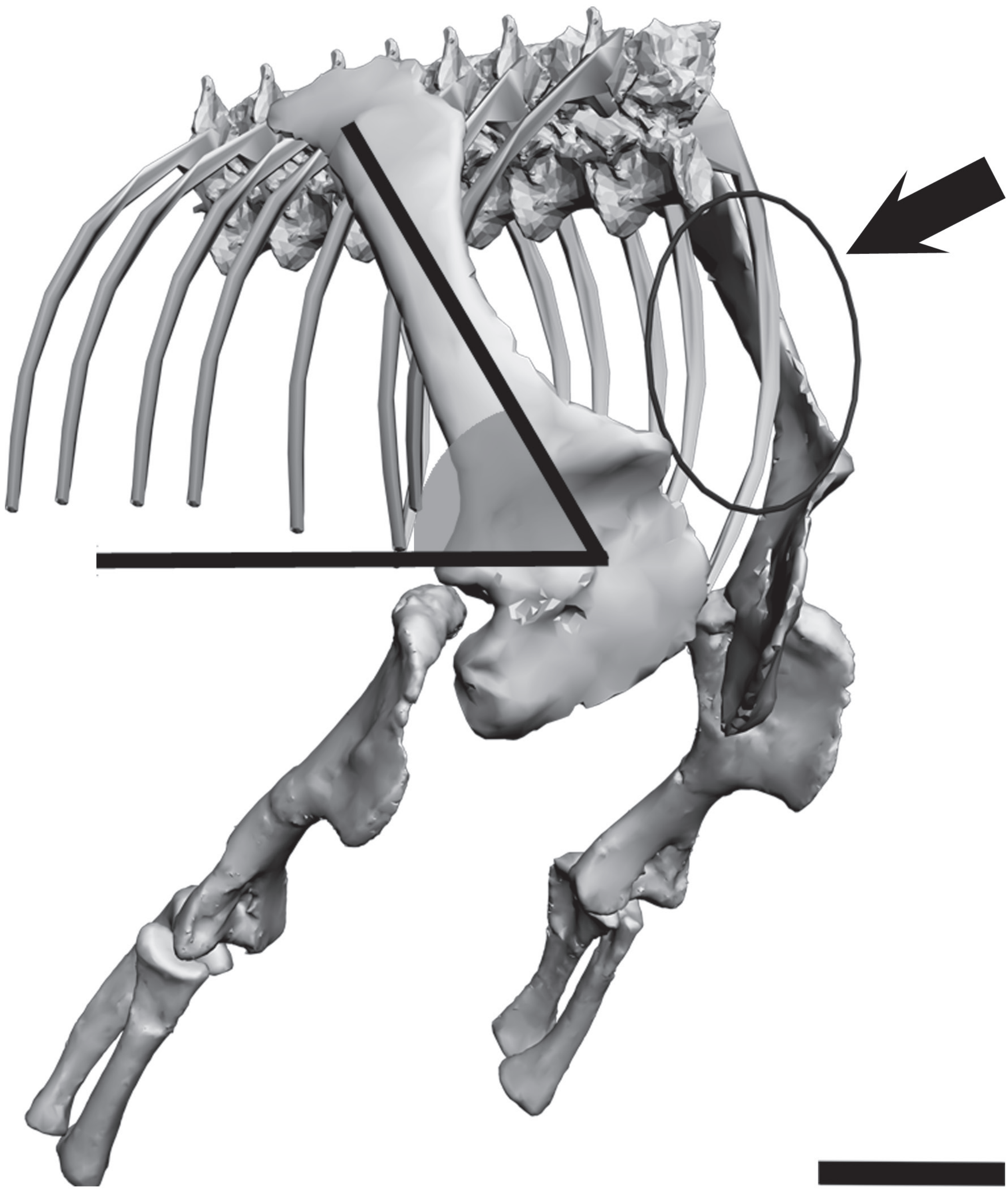

FIGURE 2: *Unaysaurus* Pectoral girdle articulated using Clavicular Ring. The black arrow shows the ring that contacts the ventral surface of the first dorsal vertebra to the acromion process. The angle is approximately 60°. Scale bar = 50 mm.

RESUMO

*Dinossauros do Triássico brasileiro foram encontrados nas formações Santa Maria e Caturrita, Rio Grande do Sul, Brasil. São conhecidas três espécies da Formação Santa Maria (*Staurikosaurus pricei, Saturnalia tupiniquim *e* Pampadromaeus barberenai*) e duas da Formação Caturrita (*Guaibasaurus candelariensis *e* Unaysaurus tolentinoi*). Os materiais associados a esses dinossauros encontram se muito bem preservados, permitindo descrever a musculatura e realizar estudos biomecânicos. A rotação lateral do fêmur de* Saturnalia *é corroborada pelos cálculos de biomecânica, e o reforço da crista supra-acetabular de* Saturnalia, Guaibasaurus, Staurikosaurus, Herrerasaurus ischigualastensis, Efraasia *e* Chromogisaurus novasi *sugere que dinossauros basais possivelmente mantivessem o tronco inclinado ao menos 20° em relação ao eixo horizontal. A articulação da cintura peitoral de sauropodomorfos basais (*Saturnalia *e* Unaysaurus*) foi estabelecida utilizando a metodologia de "Clavicular Ring" e a lâmina escapular permanece próxima a 60° em relação ao eixo horizontal, uma condição plesiomórfica para sauropodomorfos e também encontrada no plateossaurídeo articulado* Seitaad ruessi. *Os dinossauros basais do Brasil eram leves e as estimativas de massa foram de 18,5 kg para* Staurikosaurus, *6,5 kg para* Saturnalia *e 17 kg para* Guaibasaurus. *Provavelmente* Pampadromaeus *tinha 2,5 kg, mas medidas do fêmur são necessárias para confirmar essa hipótese. Os dinossauros do Triássico brasileiro foram diversificados, mas compartilham alguns aspectos funcionais que foram importantes dentro do contexto evolutivo.*

Palavras-Chave: Dinossauros; Triássico; Biomecânica; Articulação; Massa.

ACKNOWLEDGEMENTS

We thanks Max C. Langer (Departamento de Biologia, FFCLRP, Universidade de São Paulo) and the Museu de Ciências e Tecnologia (PUC/RS) for loan of the *Saturnalia* materials; Jonathas S. Bittencourt for the *Herrerasaurus* and *Staurikosaurus* photos; and Autodesk Inc. for providing free licenses for the 3DS Max software through their Education Community program. This research is part of the MSc thesis of one of the authors (RD) at the Museu Nacional of the Universidade Federal do Rio de Janeiro, funded by a fellowship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

REFERENCES

Alexander, R.M. 2006. Dinosaur biomechanics. *Proceedings of the Royal Society of London Series B – Biological Sciences,* 273:1849-1855.

Bittencourt, J.S. & Kellner, A.W.A. 2009. The anatomy and phylogenetic position of the Triassic dinosaur *Staurikosaurus pricei* Colbert, 1970. *Zootaxa,* 2079:1-56.

Bittencourt, J.S. & Langer, M.C. 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. *Anais da Academia Brasileira de Ciências,* 83(1):23-60.

Cabreira, S.F.; Schultz, C.L.; Bittencourt, J.S.; Soares, M.B.; Fortier, D.C.; Silva, L.R. & Langer, M.C. 2011. New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. *Naturwissenschaften,* 98(12):1035-1040.

Carrier, D.R.; Walter, R.M. & Lee, D.V. 2001. Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *Journal of Experimental Biology,* 204:3917-3926.

Christiansen, P. & Fariña, R.A. 2004. Mass prediction in theropod dinosaurs. *Historical Biology,* 16(2-4):85-92.

Currie, P.J. & Madsen, J.H. 1996. On the Presence of Furculae in Some Non-Maniraptoran Theropods. *Journal of Vertebrate. Paleontology,* 16(3):573-577.

Delcourt, R. 2012. *Biomecânica dos membros anteriores e posteriores de Saturnalia tupiniquim Langer, Abdala, Richter & Benton, 1999.* (Dissertação de Mestrado). Museu Nacional/ Universidade Federal do Rio de Janeiro. Rio de Janeiro.

Delcourt, R. & Grillo, O.N. 2011. A probable Maniraptora (Dinosauria: Theropoda) from Vale do Rio do Peixe Formation; Bauru Basin. *In:* Jornada de Zoologia. Zoologia no Brasil, passado, presente e futuro. 3ª. *Resumos.* Rio de Janeiro, UNIRIO. Resumo n. 10.

Delcourt, R.; Grillo, O.N.; Azevedo, S.A.K. & Langer, M.C. 2011a. Forelimb muscle's moment arm in *Saturnalia tupiniquin. In:* Congreso Latinoamericano de Paleontologia de Vertebrados, 4º. *Resumos.* San Juan, Argentina, Sociedade Brasileira de Paleontologia. (1 CD-ROM)

Delcourt, R.; Grillo, O.N.; Azevedo, S.A.K.; Langer, M.C. & Belmonte, S.L.R. 2011b. Hindlimb muscle's moment arm in *Saturnalia tupiniquin. In:* Congreso Latinoamericano de Paleontologia de Vertebrados, 4º. *Resumos.* San Juan, Argentina, Sociedade Brasileira de Paleontologia. (1 CD-ROM)

Delcourt, R.; Grillo, O.; Azevedo, S. & Romano, P. 2011c. Clavicular Ring: A new method to articulate the pectoral girdle in stem-sauropodomorphs. *In:* Annual Meeting Society of Vertebrate Paleontology, 71º. *Program and abstracts.* Las Vegas, Nevada, Society of Vertebrate Paleontology. (Supplement to the on line Journal of Vertebrate Paleontology, Nov. 2011 – Poster session – p. 31).

Ezcurra, M.D. 2010. A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. *Journal of Systematic Paleontology,* 8(3):371-425.

Galton, P.M. & Upchurch, P. 2004. Prosauropoda. *In:* Weishampel, D.B.; Dodson, P. & Osmolska, H. *The Dinosauria.* 2. ed. University of California Press, Berkeley. p. 232-258.

Grillo, O.N. 2007. *Miologia e biomecânica do membro posterior de Staurikosaurus pricei Colbert, 1970 (Dinosauria, Saurischia).* (Dissertação de Mestrado). Museu Nacional/Universidade Federal do Rio de Janeiro. Rio de Janeiro.

Grillo, O.N. & Azevedo, S.A.K. 2006. Modificações funcionais na musculatura caudofemoral de *Staurikosaurus pricei* Colbert, 1970 (Dinosauria, Saurischia). *In:* Simpósio Brasileiro de Paleontologia de Vertebrados, 5º. *Livro de resumos.* Santa Maria, RGS, Sociedade Brasileira de Paleontologia.

Grillo, O.N. & Azevedo, S.A.K. 2010. Hind limb muscle moment arms and its implications on the locomotion and posture in *Staurikosaurus pricei. In:* International Congress of Vertebrate Morphology, 9º. *Abstracts.* Punta del Este, Uruguay, International Society of Vertebrate Morphologists. (1 CD-ROM).

Grillo, O.N. & Azevedo, S.A.K. 2011. Pelvic and hind limb musculature of *Staurikosaurus pricei* (Dinosauria: Saurischia). *Anais da Academia Brasileira de Ciências,* 83(1):73-98.

Gunga, H.C.; Suthau, T.; Bellman, A.; Friedrich, A.; Schwanebeek, T.; Stoinski, S.; Trippel, T.; Kirsch, K. & Hellwich, O. 2007. Body mass estimations for *Plateosaurus engelhardti* using laser scanning and 3D reconstruction methods. *Naturwissenschaften,* 94:623-630.

Hutchinson, J.R. & Gatesy, S.M. 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology,* 26(4):734-751.

Hutchinson, J.R. & Gatesy, S.M. 2006. Beyond the bones. *Nature,* 440:292-294.

Hutchinson, J.R. 2005. Dinosaur Locomotion. *In: Encyclopedia of Life Sciences.* Macmillan, London. 7 p. Disponível em: www.rvc.ac.uk/aboutus/staff/jhutchinson/documents/JRH16.pdf.

Hutchinson, J.R.; Anderson, F.C.; Blemker, S.S. & Delp, S.L. 2005. Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: implications for stance, gait, and speed. *Paleobiology,* 31(4):676-701.

Hutchinson, J.R.; Bates, K.T.; Molnar, J.; Allen, V. & Makovicky, P.J. 2011. A Computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *Plos ONE,* 6(10):1-20.

Hutchinson, J.R.; Ng-Thow-Hing, V. & Anderson, F.C. 2007. A 3D interactive method for estimating body segmental parameters in animals: Application to the turning and running performance of *Tyrannosaurus rex. Journal of Theorical Biology,* 246:660-680.

Kellner, A.W.A.; Azevedo, S.A.K.; Machado, E.B.; Carvalho, L.B. & Henriques, D.D.R. 2011. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. *Anais da Academia Brasileira de Ciências,* 83(1):99-108.

Langer, M.C. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *PaleoBios,* 23(2):1-30.

Langer, M.C. & Benton, M.J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Paleontology,* 4(4):309-358.

Langer, M.C.; Abdala, F.; Richter, M. & Benton, M.J. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l' Academie des Sciences Paris,* 329:511-517.

Langer, M.C.; Bittencourt, J.S. & Schultz, C.L. 2011. A reassessment of the basal dinosaur *Guaibasaurus candelariensis,* from the Late Triassic Caturrita Formation of south Brazil. *Transactions of the Royal Society of Edinburgh-Earth Sciences,* 101:301-322.

Langer, M.C.; Ezcurra, M.D.; Bittencourt, J.S. & Novas, F.E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews of the Cambridge Philosophical Society,* 85:55-110.

Langer, M.C.; Ribeiro, A.M.; Schultz, C.L. & Ferigolo, J. 2007a. The continental tetrapod-bearing Triassic of south Brazil. *New Mexico Museum of Naural. History and Science Bulletin,* 41:201-218.

Langer, M.C.; França, M.A.G. & Gabriel, S. 2007b. The pectoral girdle and forelimb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Upper Triassic, Brazil). *Special Papers in Paleontology,* 77:113-137.

Leal, L.A.; Azevedo, S.A.K.; Kellner, A.W.A. & DaRosa, A.A.S. 2004. A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Paraná Basin, Brazil. *Zootaxa,* 690:1-24.

Lipkin, C.; Sereno, P.C. & Horner, J.R. 2007. The furcula in *Suchomimus tenerensis* and *Tyrannosaurus rex* (Dinosauria: Theropoda: Tetanurae). *Journal of Paleontology,* 81(6):1523-1527.

Lloyd, G.T.; Davis, K.E.; Pisani, P.; Tarver, J.E.; Ruta, M.; Sakamoto, M.; Hone, D.W.E.; Jennings, R. & Benton, M.J. 2008. Dinosaurs and the Cretaceous Terrestrial Revolution. *Proceedings of the Royal Society of London Series B-Biological Sciences,* 275:2483-2490.

Makovicky, P.J. & Currie, P.J. 1998. The presence of a Furcula in Tyrannosaurid Theropods, and its phylogenetic and functional implications. *Journal of Vertebrate Paleontology,* 18(1):143-149.

Mallison, H. 2010. The digital *Plateosaurus* II: An assessment of the range of motion of the limbs and vertebral column and of previous reconstructions using a digital skeletal mount. *Acta Palaeontologica Polonica,* 55(3):433-458.

Martinez, R.N.; Sereno, P.C.; Alcober, O.A.; Colombi, C.E.; Renne, P.R.; Montañez, I.P. & Currie, B.S. 2011. A basal Dinosaur from the Dawn of the Dinosaur Era in Southwestern Pangaea. *Science,* 331:206-210.

Molnar, R.E. & Farlow, J.O. 1990. Carnosaur paleobiology. *In:* Weishampel, D.B.; Dodson, P. & Osmolska, H. *The Dinosauria.* University of California Press, Berkeley. p. 210-224.

Motani, R. 2001. Estimating body mass from silhouettes: testing the assumption of elliptical body cross-sections. *Paleobiology,* 27(4):735-750.

Nagano, A. & Komura, T. 2003. Longer moment arm results in smaller joint moment development, power and work outputs in fast motions. *Journal of Biomechanics,* 36:1675-1681.

Remes, K. 2008. *Evolution of the pectoral girdle and forelimb in Sauropodomorpha (Dinosauria, Saurischia): osteology, myology and function.* (Doktorarbeit). Fakultät für Geowissenschaften der Ludwig-Maximilians Universität München. München.

Santucci, R.M. & Arruda-Campos, A.C. 2011. A new sauropod (Macronaria, Titanosauria) from the Adamantina Formation, Bauru Group, Upper Cretaceous of Brazil and the phylogenetic relationships of Aeolosaurini. *Zootaxa,* 3085:1-33.

Sertich, J.W. & Loewen, M.A. 2010. A New basal Sauropodomorph Dinosaur from the Lower Jurassic Navajo Sandstone of Southern Utah. *Plos ONE,* 5(3):1-17.

Upchurch, P. 1997. Prosauropoda. *In:* Currie, P.J. & Padian, K., *Encyclopedia of Dinosaurs.* Academic Press, San Diego. p. 599-607.

Xu, X.; Clark, J.M.; Forster, C.A.; Norell, M.A.; Erickson, G.M.; Eberth, D.A.; Jia, C. & Zhao, Q. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature,* 439:715-718.

Yates, A.M. & Vasconcelos, C.C. 2005. Furcula-like clavicles in the prosauropod dinosaur *Massospondylus. Journal of Vertebrate Paleontology,* 25(2):466-468.

Zaher, H.; Pol, D.; Carvalho, A.B.; Nascimento, P.M.; Riccomini, C.; Larson, P.; Juarez-Valieri, R.; Pires-Domingues, R.; Silva Jr, N.J. & Campos, D.A. 2011. A complete skull of an early Cretaceous Sauropod and the evolution of advanced Titanosaurians. *Plos ONE,* 6(2):1-10.

Aceito em: 20.08.2012
Publicado em: 28.09.2012

Publicado com o apoio financeiro do Programa de Apoio às Publicações Científicas Periódicas da USP

Seção de Publicações do MZUSP