

Basal Sauropodomorpha (Dinosauria, Saurischia) of Gondwana

Alejandro OTERO^{1,2*}, Cecilia APALDETTI^{1,3} & Diego POL^{1,4}

¹Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). ²División Paleontología de Vertebrados (Anexo), Facultad de Ciencias Naturales y Museo, Avenida 60 y 122, La Plata (1900), Argentina; alexandros.otero@gmail.com. ³Universidad Nacional de San Juan, Museo de Ciencias Naturales, Av. España 400 (norte), San Juan, 5400 Argentina; capaldetti@unsj.edu.ar. ⁴Museo Paleontológico Egidio Feruglio, Av. Fontana 140, Trelew, Chubut 9100, Argentina; dpol@mef.org.ar

Abstract: Basal sauropodomorphs include the non-sauropod portion of Sauropodomorpha, which lived in all continental landmasses between the Late Triassic and Early Jurassic. The early evolution of the group is well recorded in Carnian beds of Argentina and Brazil, achieving a rapid diversification during Norian and Rhaetian, adding records from South Africa, India and Europe. After the Triassic/Jurassic extinction, most lineages of Rhaetian sauropodomorphs continued into the Early Jurassic, extending to North America, China, and Antarctica. Carnian sauropodomorphs were not diverse, abundant or morphologically disparate. During the Norian they notably diversified both taxonomically and ecologically, became abundant and dominated terrestrial ecosystems. By the Early Jurassic, Sauropodomorpha achieved their broadest geographical distribution and morphological disparity, ranging from small-medium size and facultatively bipedal forms to giant quadrupedal sauropods. The diversity and disparity of Sauropodomorpha changed radically at the end of the Early Jurassic when all lineages became extinct, except for the gravisaurians, which subsequently gave rise to Eusauropoda becoming the dominant megaherbivores during the rest of the Mesozoic.

Key words: Evolution, Upper Triassic, Lower Jurassic, Gravisauria, Diversity, Disparity.

Resumen: Sauropodomorfos basales de Argentina. Los sauropodomorfos basales incluyen a los sauropodomorfos no saurópodos, que habitaron todos los continentes entre el Triásico Superior y el Jurásico Inferior. La evolución temprana de este grupo está bien documentada en el Carniano de Argentina y Brasil, alcanzando una rápida diversificación durante el Noriano y Retiano, incluyendo el registro de África, India y Europa. Luego de la extinción triásico/jurásica, la mayoría de los linajes rhaetianos continuaron en el Jurásico temprano, extendiéndose a Norteamérica, China y Antártida. Los sauropodomorfos carnianos no fueron diversos, abundantes o morfológicamente dispares, aunque durante el Noriano alcanzaron una gran diversidad tanto taxonómica como ecológica, gran abundancia y dominaron los ecosistemas terrestres. Para el Jurásico temprano, Sauropodomorpha alcanzó su mayor distribución geográfica y disparidad morfológica, desde formas pequeñas a medianas y facultativamente bípedas, hasta formas cuadrúpedas graviportales. La diversidad y disparidad de Sauropodomorpha cambió radicalmente en el Jurásico temprano, cuando todos sus linajes se extinguieron, con la excepción de los gravisáuridos, quienes dieron origen a Eusauropoda, convirtiéndose en los megaherbívoros dominantes por el resto del Mesozoico.

Palabras clave: Evolución, Triásico Superior, Jurásico Inferior, Gravisauria, Diversidad, Disparidad.

INTRODUCTION

During the Late Triassic, a major faunal restructuration occurred in continental environments, though which archosaurs, and particularly dinosaurs, displaced synapsids as the dominant elements within tetrapod assemblages (e.g., Bonaparte, 1971; Benton, 1983; Charig, 1984; Brusatte *et al.*, 2010; Martínez *et al.*, 2011). During that period the origin and early diversification of main dinosaurian groups have occurred, most notably the Sauropodomorpha.

Traditionally, sauropodomorph dinosaurs have been categorized in two distinctive body plans. On the one hand, the basal forms (previously known as “prosauropods”) of small to medium body size (1.5 to 10 m), interpreted as omnivorous to herbivorous, relatively long necks, bipedal to facultative quadrupedal, and the presence of large manual digit I with a medially deflected claw (Galton & Upchurch, 2004). On the other hand, the derived sauropods that achieved colossal sizes (up to 40 meters), extremely long necks, fully herbivorous diet with adaptations to bulk feeding, and obligate quadrupedal locomotion (Upchurch *et al.*, 2004).

Sauropodomorpha has been diagnosed by several synapomorphies, which represent the character states found in basal members of the group and only a few of them have been preserved unchanged in the entire group (Figure 1), including relatively small skulls, lanceolate teeth with coarsely serrated crowns, ten or more moderately elongate cervical vertebrae, humerus less than 55-65% the length of the femur, transverse width of distal humerus greater than 33% of the total length, robust pollex with an enlarged ungual, hindlimb equal to or shorter than trunk, tibia shorter than femur, and ascending process of the astragalus keyed into the descending process of the tibia (Gauthier 1986; Galton & Upchurch, 2004; Yates, 2007b).

Basal sauropodomorphs include the non-sauropod portion of Sauropodomorpha, which inhabited all continental landmasses in a range of time between Late Triassic (Carnian, 225 mya) and Early Jurassic (*ca.* 180 mya, Toarcian) (Upchurch *et al.*, 2004; Langer *et al.*, 2010). Although not significantly abundant compared to other late Triassic groups of tetrapods (e.g., therapsids), the first record of the Sauropodomorpha is well documented in the late Carnian to early Norian beds of Argentina and Brazil (e.g., Langer *et al.*, 1999; Martínez & Alcober, 2009; Ezcurra, 2010; Cabreira *et al.*, 2011). This group achieved a great diversification by the end of Norian, and a global distribution by the Early Jurassic.

Although some cladistics analyses depicted non-sauropod sauropodomorphs as monophyletic (“Prosauropoda” *sensu* Sereno, 1999; Benton *et al.*, 2000; Galton, 1990; Galton & Upchurch, 2004), there has been a growing consensus on the paraphyly of Prosauropoda in recent years (Gauthier, 1986; Upchurch *et al.*, 2007; Yates, 2007a; Ezcurra, 2010; Rowe *et al.*, 2010; Sertich & Loewen, 2010; Apaldetti *et al.*, 2011, 2012; Pol *et al.*, 2011; Otero & Pol, 2013; Otero *et al.*, 2015; McPhee *et al.*, 2014, 2015a, b; Peyre de Fabrègues & Allain, 2016). Most recent studies (Rowe *et al.*, 2010; Sertich & Loewen, 2010; Pol *et al.*, 2011; Apaldetti *et al.*, 2012; Otero & Pol, 2013; McPhee *et al.*, 2014) only recognize smaller monophyletic groups within the paraphyletic grade of successive sister groups to Sauropoda (e.g., Plateosauridae, Massospondylidae, Riojasauridae) (Figure 2).

Sauropodomorpha was defined by Salgado *et al.* (1997) as “the clade including the most recent common ancestor of Prosauropoda and Sauropoda and all of its descendants”. Such definition considers Prosauropoda as monophyletic, allowing a node-based definition. However, considering the paraphyletic nature of basal forms, it is preferable a stem-based definition for Sauropodomorpha, as follows: “the most inclusive clade containing *Saltasaurus* Bonaparte & Powell, 1980 but not *Passer o Triceratops* Marsh, 1889” (Sereno, 2007). Within non-sauropod sauropodomorphs, two main clades can be distinguished: Massopoda and Sauropodiformes. The former is defined as “the most inclusive clade containing *Saltasaurus loricatus* but not *Plateosaurus engelhardti*” (Yates, 2007b). Such stem-based definition basically encloses most sauropodomorphs, except for its basalmost forms (including Plateosauridae). Sauropodiformes was node-based defined by Sereno (2007) as “the least inclusive clade containing *Mussaurus patagonicus* but not *Saltasaurus loricatus*”. As depicted by its name, Sauropodiformes includes sauropodomorphs closely related to Sauropoda. McPhee *et al.* (2014) argued for a modified definition of

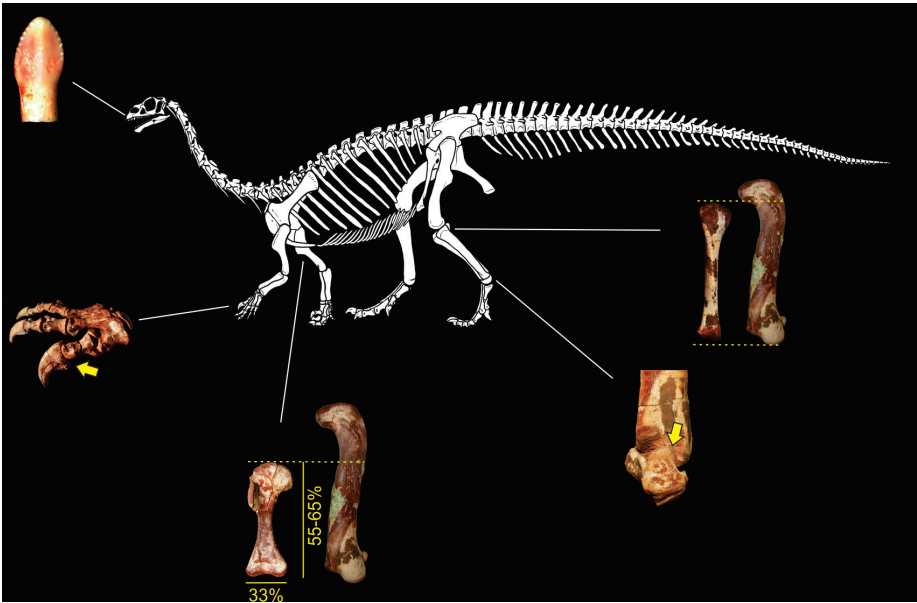


Figure 1. Skeleton of a typical basal sauropodomorph depicting sinapomorphies of Sauropodomorpha.

this clade, which points to a clade slightly more inclusive and similar in taxonomic content to Anchisauria.

In this contribution we present an updated review of the events that highlights the evolution of early sauropodomorphs in Gondwana. This includes body fossil record, major diversifications and distribution patterns, as well as key anatomical innovations within a phylogenetic context.

Sauropodomorphs of the early Late Triassic—Origin and diversification

The oldest record of sauropodomorph body fossils came from Ischigualasto (northwestern Argentina) and Santa María (southern Brazil) formations, with an estimated age of *ca.* 231 Ma (Martínez *et al.*, 2011). Nonetheless, until recently only *Saturnalia tupiniquim*, from the later unit, was indisputably recognized as the basalmost member of Sauropodomorpha (Yates, 2007a; Upchurch *et al.*, 2007; Pol *et al.*, 2011), apart from its original assignment (Langer *et al.*, 1999). *Eoraptor lunensis*, from the Ischigualasto Formation, was considered for a long time as a theropod (e.g., Sereno, 1999; Ezcurra, 2010), and even as a basal saurischian (Langer, 2004; Brusatte *et al.*, 2010). However, after a re-preparation of the original material and its inclusion in new phylogenetic data matrices, *Eoraptor* has been recently considered as a basal member of Sauropodomorpha (Martínez *et al.*, 2011, 2012; Sereno *et al.*, 2012; McPhee *et al.* 2015b) adding to the diversity of basal sauropodomorphs from the earliest Late Triassic. Furthermore, *Panphagia protos* and *Chromogisaurus novasi*, both from Ischigualasto Formation (Martínez & Alcober, 2009; Ezcurra, 2010; Martínez *et al.*, 2012), and *Pampadromaeus barberani*, from Santa María Formation (Cabreira *et al.*, 2011) complete the late Carnian–early Norian scenario of early sauropodomorphs. Although most basal forms of Sauropodomorpha are mainly reported for the Carnian–Norian of Gondwana, at least two other basal forms are known from Rhaetian of England, *Thecodontosaurus* and *Pantydraco* (e.g., Benton *et al.*, 2000; Galton *et al.*, 2007).

Basalmost forms of Sauropodomorpha can be differentiated from Norian and more advanced forms by the presence of simpliomorphies, reminiscent to their basal saurischian relatives. These include their small size, bipedality, distally recurved tooth crowns, elongated forelimb (particularly humerus and manus), deep extensor pits on distal end of metacarpals I-III, narrow metacarpal IV, narrow proximal width of metatarsal V, relatively short cervical centra, two sacral vertebrae, partially open acetabulum (shared with *Guaibasaurus*), extremely long postacetabular process of the ilium (also present in Neotheropoda), and short and curved femoral shaft.

Sauropodomorphs of the Late Triassic–Radiation

During Norian and Rhaetian, sauropodomorphs became more diverse and abundant, which is reflected in the great number of occurrences in different regions of the world, with a main focus in southern Pangea, particularly, in the current regions of Argentina, South Africa, and to a lesser extent, Brazil. In continental Europe, basal sauropodomorphs records a great number of occurrences, although less diverse (e.g., Riley & Stutchbury, 1836; Huene, 1908, 1932; Galton, 1973, 2001; Yates, 2003)

The Norian–Rhaetian sauropodomorph record from of Argentina mainly come from the Los Colorados Formation (La Rioja Province), with the occurrences of *Riojasaurus*, *Coloradisaurus*, *Lessemsaurus*, and other unnamed taxa (Bonaparte, 1967, 1978, 1999; Martínez *et al.*, 2004; Ezcurra & Apaldetti, 2012). With much more restricted occurrences, the Brazilian record is composed by *Unaysaurus*, from the Caturrita Formation (Rio Grande do Sul state) (Leal *et al.*, 2004). At least other four new taxa of Sauropodomorpha have been found in the Late Triassic of Quebrada del Barro Formation (San Juan Province), although they are until undescribed (Martinez *et al.*, 2015). Finally, Upper Triassic record of Gondwana is completed with the South African forms found in the Lower Elliot Formation, composed by *Eucnemesaurus*, *Plateosaurus*, *Blikanasaurus*, *Euskelosaurus*, *Melanorosaurus*, and *Antetonitrus* (Haughton, 1924; Galton & van Heerden, 1985; Yates, 2007; Barrett, 2009; Yates & Kitching, 2010) and *Nambalia* and *Jaklapallisaurus*, from India (Novas *et al.*, 2011).

Norian sauropodomorphs can be distinguished from Carnian representatives by several key innovations related to size increase: fully herbivorous diet, at least three sacral vertebrae, facultative quadrupedal locomotion, femur with more elliptical cross-section and straighter shaft, and a more robust manus.

Sauropodomorphs of the Early Jurassic–Global distribution

With the exceptions of the basalmost branches, most lineages of Rhaetian sauropodomorphs continued into the Early Jurassic, achieving a worldwide distribution, extending to regions such as North America, China, and Antarctica. Unlike Triassic forms, the Early Jurassic sauropodomorph record from Argentina has been reported from several localities. In this sense, this period witnesses a notably diversification of massospondylids, reporting *Adeopapposaurus* and *Leyesaurus*, from Cañón del Colorado and Quebrada del Barro Formations, respectively (San Juan Province; Martinez, 2009; Apaldetti *et al.*, 2011). Records of this family also occur in South Africa, with *Massospondylus* (Upper Elliott Formation) (Cooper, 1981), Antarctica, with *Glacialisaurus* (Smith & Pol, 2007), and also outside Gondwana, with *Lufengosaurus* reported from China (Young, 1941). The affinities of the latter two taxa within Massospondylidae, however, have been recently challenged (Peyre de Fabrègues & Allain, 2016).

In Argentina, basal sauropodiforms begin to dominate in Patagonia, with the records of *Mussaurus patagonicus* (Laguna Colorada Formation) at Santa

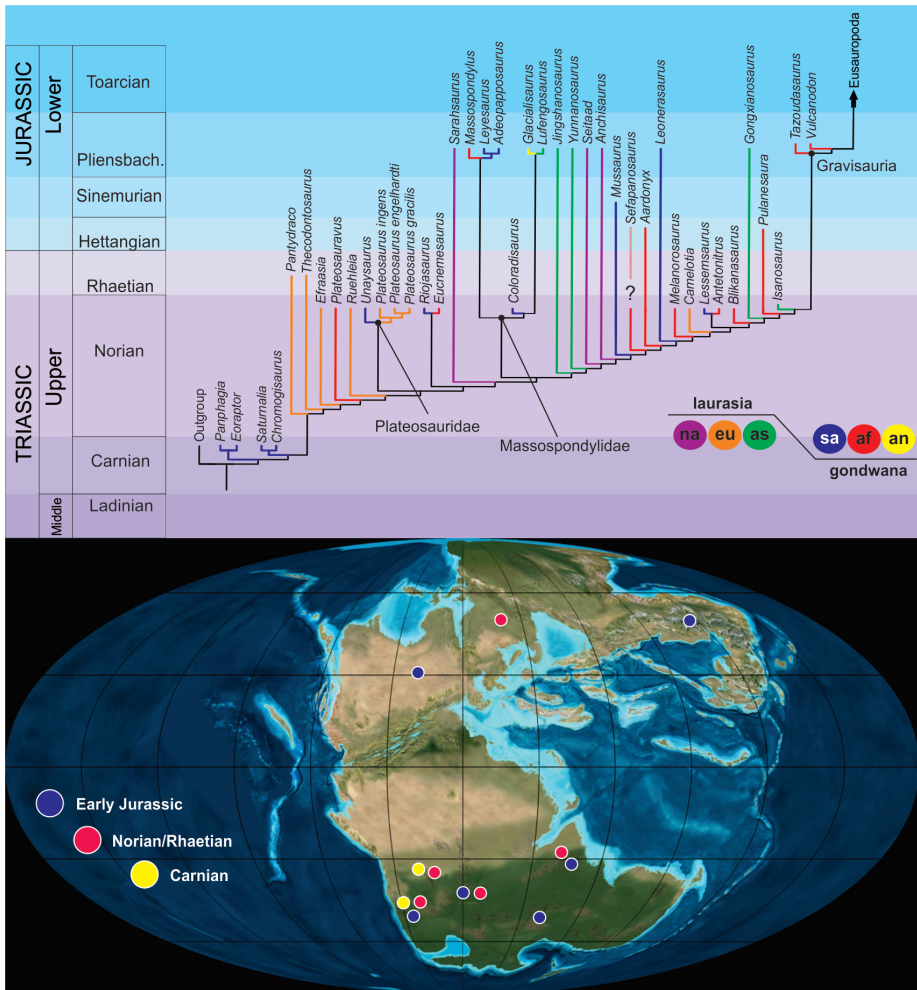


Figure 2. Calibrated phylogeny of basal sauropodomorphs (Modified from Otero *et al.*, 2015). The phylogenetic position of *Panphagia*, *Eoraptor* are taken from McPhee *et al.* (2015a), and *Pulanesaura* are taken from McPhee *et al.* (2015b). Abbreviations: af, Africa; an, Antarctica; as, Asia; eu, Europe; na, North America; sa, South America. Below, paleogeographic reconstruction of the Triassic/Jurassic boundary showing basal sauropodomorph occurrences (map taken from www.cpgeosystems.com).

Cruz Province (Bonaparte & Vince, 1979; Smith *et al.*, 2014), and *Leoneriasaurus taquetrensis* (Las Leoneras Formation) at Chubut Province (Pol *et al.*, 2011). In addition, *Aardonyx celestae* from the South African Upper Elliot Formation (Yates *et al.*, 2010), and new records from southeastern Gondwana are reported from India (*Lamplughsa* and *Pradhania*) (Kutty *et al.*, 2011).

Key anatomical features of Early Jurassic sauropodomorphs from Gondwana are related to the establishment of the graviportal quadrupedalism and fully herbivory refinement, started in the Late Triassic with the lineage of *Lessemisaurus* and *Antetonitrus*, and continued with *Blikanasaurus*, *Pulanesaura*, and *Vulcanodon* in the Early Jurassic. In this regard, *Pulanesaura* display interesting innovations

such as tooth with wrinkled enamel and “D” shaped cross-section and lack of flexor pit on the humerus (McPhee *et al.*, 2015b). In general terms, the anatomical features that changed from the small herbivorous, even possible omnivorous and bipedal forms to those giant fully herbivorous and obligate quadrupedal forms are, in fact, mainly related to the new requirements for feeding and locomotion (Salgado *et al.*, 1997; Upchurch, 1998; Wilson & Sereno, 1998). In general those changes tended to a decreasing of the relative skull size with an increasing and translation of the external nares, an elongation of the neck, a straightening of the limbs reducing the distal limb elements, and a relative lengthening of the forelimb in comparison to the hindlimb (Rauhut *et al.*, 2011). All those changes led to an increase of the body size in most of the lineages, turning to Sauropoda as the largest animals that once inhabited the terrestrial ecosystems.

DISTRIBUTION PATTERNS AND MORPHOLOGICAL DISPARITY

The early evolution of Sauropodomorpha, including the rise of sauropods, is perhaps one of the most fascinating events in the evolutionary history of dinosaurs. This represents the first 40 out of the 165 million years of the history of the group, and concentrates the most dramatic anatomical changes, mainly related to the acquisition of graviportal locomotion and refinement of herbivory (Barrett & Upchurch, 2007; Rauhut *et al.*, 2011). Such transformations took place within Carnian–Rhaetian ages in the early stages of basal sauropodomorph evolution.

Although far from being resolved, the current phylogenetic scenario of basal sauropodomorphs shows some interesting biogeographic patterns that deserve considerations. Despite the fact that there are some reports of fragmentary primitive dinosaur with sauropodomorph affinities in the Cabora Bassa Basin (India) and lower Zambezi Valley (Zimbabwe) (Raath, 1996; Langer *et al.*, 2010) the definitive oldest record of Sauropodomorpha came from South America (Langer *et al.*, 1999; Cabreira *et al.*, 2011; Martínez *et al.*, 2012). During Norian and Rhaetian times, a rapid sauropodomorph diversification occurred, reflected in abundant records from South Africa, South America, and Europe (e.g., von Meyer, 1837; Bonaparte, 1978; Yates, 2007a). During this radiation the sauropod lineage must have arisen, generating some of the adaptations to quadrupedal gigantism that remained almost unchanged throughout the evolution of Sauropoda (e.g., elliptical femoral cross-section). Two main lineages of sauropodomorphs surpass the Triassic: the sauropodiform lineage (which includes Sauropoda) and Massospondylidae.

After the Triassic/Jurassic extinction, sauropodomorph diversity decreased worldwide (Barrett, 2000; Upchurch & Barrett, 2005; Mannion & Upchurch, 2010; Mannion *et al.*, 2011), but their morphospace occupation increased during the Early Jurassic (Apaldetti *et al.*, 2013). Massospondylidae are first recorded in the Norian (*Coloradisaurus*) but are only widely distributed by the Early Jurassic (e.g., Young, 1941; Martínez, 2009; Apaldetti *et al.*, 2011). Except for *Lufengosaurus* from China, all massospondylids are known from Gondwana. This clade includes the most gracile forms of Jurassic sauropodomorphs, characterized mainly for their relative short skulls, great elongation of their cervical vertebrae, and short forelimb. These features denote massospondylids occupied a differentiated region of the morphospace in comparison to other members of Sauropodomorpha (Apaldetti *et al.*, 2013). On the other hand, the sauropodiform lineage that survives the Triassic/Jurassic limit includes several basal branches of the clade and Sauropoda (e.g., Houghton, 1924; Yates *et al.*, 2010; Otero & Pol, 2013; McPhee *et al.* 2014). Most of them are robust and show the acquisition of quadrupedal locomotion, such as *Leoneerasaurus* and more derived forms. These sauropod close relatives (including *Lessemsaurus* and

Antetonitrus) exhibit morphologies that progressively approached the condition of Sauropoda, occupying regions of the morphospace closer to the derived eusauropods (Apaldetti *et al.*, 2013).

In sum, at the beginning of their evolution in the Carnian–Norian boundary, basal sauropodomorphs were not diverse, abundant or morphologically disparate. Later, during the Norian they notably diversified both taxonomically and ecologically, became abundant and dominated terrestrial ecosystems (e.g., South America, South Africa, India, and Europe). During the Early Jurassic, Sauropodomorpha achieved their broadest geographical distribution, morphological disparity, ranging from small-medium size and facultatively bipedal forms (massospondylids) to giant quadrupedal gravisaurian sauropods. Their taxonomic diversity at this point, however, was lower than in their initial radiation in the Late Triassic. The diversity and disparity of Sauropodomorpha changed radically at the end of the Early Jurassic (Allain & Aquesbi, 2008; Rauhut *et al.*, 2011; Cúneo *et al.* 2013) when all lineages of sauropodomorphs became extinct, except for the gravisaurians, which subsequently gave rise to Eusauropoda which became the dominant megaherbivores during the rest of the Mesozoic.

ACKNOWLEDGEMENTS

The committee of the XXX JAPV is thanked for the invitation to participate in the special volume “Evolución y Paleobiogeografía de los vertebrados del Mesozoico y Cenozoico de Argentina”. Paleogeographic map on Figure 2 was made freely available by Ron Blakey (NAU Geology).

BIBLIOGRAPHY

- Allain, R., & N. Aquesbi. 2008. Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas* 30: 345-424.
- Apaldetti, C., R.N. Martínez, O.A. Alcober & D. Pol. 2011. A new basal sauropodomorph (Dinosauria: Saurischia) from Quebrada del Barro Formation (Marayes-El Carrizal Basin), Northwestern Argentina. *PLoS ONE* 6: e26964.
- Apaldetti, C., D. Pol & A. Yates. 2012. The postcranial anatomy of *Coloradisaurus brevis* (Dinosauria: Sauropodomorpha) from the Late Triassic of Argentina and its phylogenetic implications. *Palaeontology* 56: 277-301.
- Apaldetti, C., D. Pol, & R.N. Martínez. 2013. Evolution patterns and morphological disparity on Sauropodomorpha during Triassic-Jurassic boundary. *73 Annual Meeting of the Society of Vertebrate Paleontology*. Los Angeles, USA. pp. 79.
- Barrett, P.M. 2000. Prosauropod dinosaurs and iguanas: speculations on the diets of extinct reptiles. In: H-D. Sues (ed.), *Evolution of herbivory in terrestrial vertebrates. Perspective from the fossil record*, pp. 42-78. Cambridge University Press.
- Barrett, P.M. 2009. A new basal sauropodomorph dinosaur from the upper Elliot Formation (Lower Jurassic) of South Africa. *Journal of Vertebrate Paleontology* 29: 1032-1045.
- Barrett, P.M. & P. Upchurch. 2007. The evolution of feeding mechanisms in early sauropodomorph dinosaurs. *Special Papers in Palaeontology* 77: 91-112.
- Benton, M.J., L. Juul, G.W. Storrs, & P.M. Galton. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southern England. *Journal of Vertebrate Paleontology* 20: 77-108.
- Bonaparte, J.F. 1967. Dos nuevas “faunas” de reptiles triásicos de Argentina. *II International Symposium of Gondwana* (Mar del Plata), Actas 1: 286-306.
- Bonaparte, J.F. 1971. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina. *Opera Lilloana* 22: 1-183.
- Bonaparte, J.F. 1978. *Coloradia brevis* n. g. et n. sp. (Saurischia Prosauropoda), dinosaurio Plateosauridae de la Formación Los Colorados, Triásico superior de La Rioja, Argentina.

- Ameghiniana* 15: 327-332.
- Bonaparte, J.F. 1999. Evolución de las vértebras presacras en Sauropodomorpha. *Ameghiniana* 36: 115-187.
- Bonaparte, J.F. & M. Vince, 1979. El hallazgo del primer nido de dinosaurios triásicos (Saurischia, Prosauropoda), Triásico superior de Patagonia, Argentina. *Ameghiniana* 76: 173-782.
- Brusatte, S.L., S.J. Nesbitt, R.B. Irmis, R.J. Butler, M.J. Benton, & M.A. Norell. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews* 101: 68-100.
- Cabreira, S.F., C.L. Schultz, J.S. Bittencourt, M.B. Soares, D.C. Fortier, L.R. Silva & M.C. Langer. 2011. New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. *Naturwissenschaften* 98: 1035-1040.
- Charig, A.J. 1984. Competition between therapsids and archosaurs during the Triassic Period: a review and synthesis of current theories. *Symposium of the Zoological Society of London* 52: 597-628.
- Cooper, M.R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums and Monuments of Rhodesia*, Serie B, 6: 689-840.
- Cúneo, R., Ramezani, J., Scasso, R., Pol, D., Escapa, I., Zavattieri, A.M., & Bowring, S.A. 2013. High-precision U–Pb geochronology and a new chronostratigraphy for the Cañadón Asfalto Basin, Chubut, central Patagonia: Implications for terrestrial faunal and floral evolution in Jurassic. *Gondwana Research* 24: 1267-1275.
- 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 Palaeontology* 8: 371-425.
- Ezcurra, M.D. & Apaldetti, C. 2012. A robust sauropodomorph specimen from the Upper Triassic of Argentina and insights on the diversity of the Los Colorados Formation. *Proceedings of the Geologists' Association* 123: 155-164.
- Galton, P.M. 1990. Basal Sauropodomorpha-Prosauropoda. En: D. Weishampel, P. Dodson, & H. Osmólska (eds.), *The Dinosauria*, pp. 320-344. University of California Press, Berkeley.
- Galton, P.M. 1973. The cheeks of ornithischian dinosaurs. *Lethaia* 6: 67-89.
- Galton, P.M. 2001. The prosauropod dinosaur *Plateosaurus* Meyer, 1837 (Saurischia: Sauropodomorpha; Upper Triassic). II. Notes on the referred species. *Revue de Paléobiologie* 20: 435-502.
- Galton, P.M., J. van Heerden. 1985. Partial hindlimb of *Blikanasaurus cromptoni* n. gen. and n. sp., representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. *Geobios* 18: 509-516.
- Galton, P.M. & Upchurch, P. 2004. Prosauropoda. In: D. Weishampel, P. Dodson, & H. Osmólska (eds.), *The Dinosauria*, pp. 232-258. University of California Press, Berkeley.
- Galton, P.M., A.M. Yates, & D. Kermack. 2007. *Pantydraco* n. gen. for *Thecodontosaurus caducus* Yates, 2003, a basal sauropodomorph dinosaur from the Upper Triassic or Lower Jurassic of South Wales, UK. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 243: 119-125.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. In: Padian (ed.), *The origin of Birds and the Evolution of Flight*, pp. 1-55, Memoir of the California Academy of Science 8.
- Haughton, S.H. 1924. The fauna and stratigraphy of the Stormberg Series. *Annals South African Museum* 12: 323-497.
- Huene, F. von. 1914. Beiträge zur Geschichte der Archosaurier. *Geologie und Paläontologie Abhandlungen* (Neue Folge) 13: 1-53.
- Huene, F. von. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Paläontologie* 4: 1-361.
- Kutty, T.S., S. Chatterjee, P.M. Galton, & P. Upchurch. 2007. Basal sauropodomorphs (Dinosauria: Saurischia) from the Lower Jurassic of India: their anatomy and relationships. *Journal of Paleontology* 81: 1218-1240.
- Langer, M.C., F. Abdala, M. Richter & M. Benton. 1999). A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Académie des Sciences* 329: 511-517.
- Langer, M.C. 2004. Basal Saurischia. In: D. Weishampel, P. Dodson, & H. Osmólska (eds.), *The Dinosauria*, 2nd edition, pp. 25–46, University of California Press, Berkeley.

- Langer, M.C., M.D. Ezcurra, J.S. Bittencourt & F.E. Novas. 2010. The origin and early evolution of dinosaurs. *Biological Reviews* 85: 55-110.
- Leal L.A., S.A.K. Azevodo, A.W.A. Kellner & A.A.S. da Rosa. 2004. A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Paraná Basin, Brazil. *Zootaxa* 690: 1-24.
- Mannion, P.D. & P. Upchurch. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology* 36: 283-302.
- Mannion, P.D., P. Upchurch, M.T. Carrano, & P.M. Barrett. 2011. Testing the effect of the rock record on diversity: multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biology Reviews* 86: 157-181.
- Martínez, R.N. 2009. *Adeoposaurus magnai* gen. et sp. nov. (Dinosauria: Sauropodomorpha) with comments on adaptations of basal Sauropodomorpha. *Journal of Vertebrate Paleontology* 29: 142-164.
- Martínez, R.N., O.A. Alcober, G. Heredia & C.E. 2004. Nuevos prosaurópodos de la Formación Los Colorados (Triásico Superior-Noriano), La Rioja, Argentina. *XX Jornadas Argentinas de Paleontología de Vertebrados*, La Plata, Argentina, pp. 42.
- Martínez, R.N. & O.A. Alcober. 2009. A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS ONE* 4: e4397.
- Martínez, R.N., P.C. Sereno, O.A. Alcober, C.E. Colombi, P.R. Renne, I.P. Montañez, & B.S. Currie. 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science* 331: 201-210.
- Martínez, R.N., C. Apaldetti & D. Abelín. 2012. Basal Sauropodomorpha from the Ischigualasto Formation. *Society of Vertebrate Paleontology Memoir* 12: 51-69.
- Martínez, R.N., Apaldetti, C., Correa, G., Colombi, C., Fernandez, E., Santi Malnis, P., Praderio, A., Abelín, D., Benegas, G., Aguilar, A., & Alcober, O. 2015. A new Late Triassic Vertebrate Assamblage from Northeastern Argentina. *Ameghiniana* 52, 379-390.
- McPhee, B.W., A.M. Yates, J.N. Choiniere & F. Abdala. 2014. The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda. *Zoological Journal of the Linnean Society* 171: 151-205.
- McPhee, B.W., J.N. Choiniere, A.M. Yates & P.A. Viglietti. 2015a. A second species of *Eucnemesaurus* Van Hoepen, 1920 (Dinosauria, Sauropodomorpha): new information on the diversity and evolution of the sauropodomorph fauna of South Africa's lower Elliot Formation (latest Triassic). *Journal of Vertebrate Paleontology* 35. DOI: 10.1080/02724634.2015.980504
- McPhee, B.W., M.F. Bonnan, A.M. Yates, J. Neveling & J.N. Choiniere. 2015b. A new basal sauropod from the pre-Toarcian Jurassic of South Africa: evidence of niche-partitioning at the sauropodomorph-sauropod boundary? *Scientific Reports* 5: 13224.
- Meyer, von. H., 1837. Mitteilung an Prof. Bronn (*Plateosaurus engelhardti*). *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie* 1837: 817.
- Novas, F.E., M.D. Ezcurra, S. Chatterjee & T.S. Kuttly. 2011. New dinosaur species from the Upper Triassic Upper Maleri and Lower Dharmaram formations of Central India. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101: 333-349.
- Otero, A., & D. Pol., 2013. Postcranial anatomy and phylogenetic relationships of *Mussaurus patagonicus* (Dinosauria, Sauropodomorpha). *Journal of Vertebrate Paleontology* 33: 1138-1168.
- Otero, A., Krupandan, E., Pol, D., Chinsamy, A., & Choiniere, J. 2015. A new basal Sauropodiform from South Africa and the phylogenetic relationships of basal sauropodomorphs. *Zoological Journal of the Linnean Society* 174: 589-634.
- Peyre de Fabrègues, C. & R. Allain. 2016. New material and revision of *Melanorosaurus thabanensis*, a basal sauropodomorph from the Upper Triassic of Lesotho. *PeerJ* 4:e1639.
- Pol, D., A. Garrido & I.A. Cerda. 2011. A new Sauropodomorph dinosaur from the Early Jurassic of Patagonia and the origin and evolution of the Sauropod-type sacrum. *PLoS ONE* 6: e14572.
- Raath, M. 1996. Earliest evidence of dinosaurs from central Gondwana. *Memoirs of the Queensland Museum* 39: 703-709.
- Rauhut, O.W.M., R. Fechner, K. Remes & K. Reis. 2011. How to get big in the mesozoic: the evolution of the sauropodomorph body plan. In: N. Klein, K. Remes, C.T. Gee, P.M. Sander

- (eds.), *Biology of the sauropod dinosaurs: understanding the life of giants*, pp. 119-149, Bloomfield, Indiana University Press.
- Riley, H. & S.Stutchbury. 1836. A description of various fossil remains of three distinct saurian animals discovered in the autumn of 1834, in the Magnesian Conglomerate on Durdham Down, near Bristol. *Proceedings of the Geological Society of London* 2: 397-399.
- Upchurch, P. & P.M. Barrett. 2005 A taxic and phylogenetic perspective on sauropod diversity. In: K.A. Curry-Rogers & J.A. Wilson (eds.), *The Sauropods, Evolution and Paleobiology*, pp. 104-124. Berkeley and Los Angeles: University of California Press.
- Rowe, T.B., H-D. Sues, & R.R. Reisz. 2010. Dispersal and diversity in the earliest North American sauropodomorph dinosaurs, with a description of a new taxon. *Proceedings of the Royal Society B* 278: 1044-1053.
- Salgado, L., R.A. Coria, & J.O. Calvo. 1997. Evolution of titanosaurid sauropods I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3-32.
- Sereno, P.C. 1999. The evolution of dinosaurs. *Science* 284: 2137-2147.
- Sereno, P.C. 2007. Basal Sauropodomorpha: historical and recent phylogenetic hypotheses, with comments on *Ammosaurus major* (Marsh, 1889). *Special Papers in Palaeontology* 77: 261-289.
- Sereno, P.C., R.N. Martínez, O.A. Alcober. 2012. Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). *Society of Vertebrate Paleontology Memoir* 12: 83-179.
- Sertich, J.J.W., M.A. Loewen. 2010. A New Basal Sauropodomorph Dinosaur from the Lower Jurassic Navajo Sandstone of Southern Utah. *PLoS ONE* 5: e9789.
- Smith, N.D, & D. Pol. 2007. Anatomy of a basal sauropodomorph dinosaur from the Early Jurassic Hanson Formation of Antarctica. *Acta Palaeontologica Polonica* 52: 657-674.
- Smith, R.M.H., C.A. Marsicano, D. Pol & A.C. Mancuso. 2014. Ichnology of sauropodomorph nests from Patagonia indicates Early Jurassic origin of herd-living and herding site fidelity. *4th International Paleontological Congress* (Mendoza), Actas, pp. 227.
- Upchurch, P. & P.M. Barrett. 2005 A taxic and phylogenetic perspective on sauropod diversity. In: K.A. Curry-Rogers & J.A. Wilson (eds.), *The Sauropods, Evolution and Paleobiology*, pp. 104-124. Berkeley and Los Angeles: University of California Press.
- Upchurch, P., P.M. Barrett & P. Dodson. 2004. Sauropoda. In: D.B. Weishampel, P. Dodson, y H. Osmólska (eds.), *The Dinosauria* 2nd edition, pp. 259-322, University California Press, Berkeley.
- Upchurch, P., P.M. Barrett & P.M. Galton. 2007. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. *Special Papers in Palaeontology* 77: 57-90.
- Yates, A.M. 2003. The species taxonomy of the sauropodomorph dinosaurs from the Löwenstein Formation (Norian, Late Triassic) of Germany. *Palaeontology* 46: 317-337.
- Yates, A.M. 2007a. The first complete skull of the Triassic dinosaur *Melanorosaurus* Hughton (Sauropodomorpha: Anchisauria). *Special Papers in Palaeontology* 77: 9-55.
- Yates, A.M. 2007b. Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. *Historical Biology* 19: 93-123.
- Yates, A.M. & J.W. Kitching. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London B* 270: 1753-1758.
- Yates, A.M., M.F. Bonnan, J. Neveling, A. Chinsamy, & M.G. Blackbeard. 2010. A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism. *Proceedings of the Royal Society B* 277: 787-794.
- Young, C.C. 1941. A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.) from Lufeng, Yunnan, China. *Palaeontologica Sinica*, Series C 7: 1-53.
- Wilson, J.A. & P.C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* 5: 1-68.