



## U-Pb age constraints on dinosaur rise from south Brazil

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### ABSTRACT

Triassic dinosaurs from South Brazil are considered as some of the oldest known worldwide, but their precise correlation to other early dinosaur occurrences have proven difficult. The problem of such long-distance faunal correlations has been exacerbated by reliance on an equivocal tetrapod biostratigraphy and the lack of palynomorphs and other age-bearing microfossils. Here, we present new high-precision U-Pb zircon geochronology (CA-ID-TIMS method) from two classical dinosaur-bearing fossil sites in south Brazil; a weighted mean  $^{206}\text{Pb}/^{238}\text{U}$  date of  $233.23 \pm 0.73$  Ma ( $2\sigma$  complete uncertainty) from the Santa Maria Formation and a single zircon  $^{206}\text{Pb}/^{238}\text{U}$  date of  $225.42 \pm 0.37$  Ma representing the maximum age of the Caturrita Formation. The new age results, combined with available geochronology from other Triassic dinosauromorph occurrences, allow establishing a chronostratigraphic framework for the Late Triassic appearance of dinosaurs in western Pangea. Within this context, the major macroevolutionary events associated with the rise of dinosaurs can be recognized and their possible links to coeval paleoenvironmental and biotic shifts can be examined.

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### 1. Introduction

Our knowledge of dinosaur rise has been largely based on fossil evidence gathered from South American deposits of putative Late Triassic age (Sereno, 2012; Da Rosa, 2015). All uncontroversial oldest dinosaurs were found either in NW Argentina or in south Brazil, from the Ischigualasto (*Herrerasaurus*, *Pisanosaurus*, *Eoraptor*, *Panphagia*, *Sanjuansaurus*, *Chromogisaurus*, *Eodromaeus*) and Santa Maria (*Staurikosaurus*, *Saturnalia*, *Pampadromaeus*, *Buriolestes*) formations, respectively (Langer et al., 2010; Martinez et al., 2011; Cabreira et al., 2016). Some of the better-known dinosaur precursors also come from the same Triassic continental basins (Langer et al., 2013). Yet, such fossil-rich deposits are notorious for being poorly understood in terms of depositional history (Irmis, 2010), a knowledge gap only partially filled by the more recent radioisotopic age investigations of several Triassic rock units of NW Argentina (Martinez et al., 2011, 2012; Ottone et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017), which confirmed an end-Carnian age for the oldest dinosaur records. Yet, no reliable age data have so far been reported from the presumed coeval deposits of south Brazil. In addition, recent age calibration of the earliest dinosauromorph occurrences of the North American Southwest (e.g., Ramezani et al., 2014) and dinosauriform records from Europe (e.g., Niedzwiedzki et al., 2014) have challenged conventional models for the rise of dinosaurs. Here, we provide the first radioisotopic age

data, based on detrital zircon U-Pb geochronology by the CA-ID-TIMS method, for two of the most relevant Brazilian rock successions for the study of early dinosaurs; the upper Santa Maria Formation, which yielded *Staurikosaurus pricei* and *Saturnalia tupiniquim* (Langer, 2003), and the Caturrita Formation, which yielded *Guaibasaurus candelarensis* (Langer et al., 2011).

### 2. Geological settings

In Brazil, Triassic deposits with tetrapod remains are only found in Rio Grande do Sul, at the southern margin of the Paraná Basin (Zerfass et al., 2003; Langer et al., 2007), where the Sanga do Cabral and Santa Maria supersequences were deposited in response to the Gondwanides orogenesis within two distinct depositional settings: (1) a broad alluvial basin during the Early Triassic and (2) more restricted extensional depocenters during Middle and Late Triassic (Zerfass et al., 2004). The Mid-Late Triassic extension in south Brazil resulted in the development of intracontinental rift basins, generated by transtensional stresses within a dextral shear zone in response to oblique convergences along the southern Gondwanides branch (Zerfass et al., 2004). In this context, deposits of the Santa Maria supersequence are divided into four third-order sequences, reflecting changes in fluvial style (Horn et al., 2014). The Santa Cruz and Pinheiros/Chiniquá sequences represent low-energy fluvial systems, with distal and proximal floodplain environments, as well as levees, crevasses, and low to middle sinuosity channels. The Candelária sequence includes two different subsystems, one mostly composed of floodplain deposits (distal and proximal, levees,

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crevasses, minor channels) and another represented by channel-crevasse facies within a high-energy fluvial system. The overlying Mata sequence is composed of higher energy channels. The latter sequence lacks vertebrate fossils, whereas the other three encompass four Assemblage-Zones (Soares et al., 2011), supposedly spanning the Ladinian to the Norian (but see Martinelli et al., 2017a). In general, the Triassic rocks of south Brazil have sporadic outcrops, exposed mainly in erosional gullies or along road cuts. The lack of continuous exposures hampers direct correlation, which until now has relied on tetrapod biostratigraphy. The two geochronology sample sites are spaced ca. 35 km from one another and occur within two separate post-Triassic structural blocks (Da Rosa and Faccini, 2005), i.e. the Santa Maria and the Faxinal do Soturno blocks. Both sites expose beds related to the Candelária sequence, although belonging to different depositional subsystems and tetrapod Assemblage-Zones (see below).

The Cerro da Alemaoa site (Da Rosa, 2015), also historically known as Waldsanga (Langer, 2005a), is located in the eastern outskirts of Santa Maria ( $29^{\circ}41'51''S$ ;  $53^{\circ}46'25''W$ ). It is the type-section of the Alemaoa Member of the Santa Maria Formation (Andreis et al., 1980), with a 20 meters-thick sequence of massive reddish mudstones, intercalated with fine sandstones (Fig. 1). The presence of calcareous concretions is the most remarkable feature of the Alemaoa Member at this site, sometimes forming carbonaceous crusts of restricted lateral expression (Da Rosa et al., 2004). The uniformly fine-grained deposits are occasionally disrupted by minor channels, only few meters wide and thick. These lithologies grade laterally into floodplain deposits, with increasing degrees of pedogenesis, evidence of phreatic oscillations, and variable types of vertebrate fossil preservations. In general, fossils are better preserved in the upper 10 m of the Alemaoa Member at Cerro da Alemaoa; below which they are heavily distorted by calcitic cementation (Holz and Schultz, 1998). The floodplain facies of this site yields fossils of the *Hyperodapedon* Assemblage Zone (Langer et al., 2007). This includes the type-series of the sauropodomorph *Saturnalia tupiniquim*, which comes from about 3 to 7 m below the top of the Alemaoa Member, whereas traversodontid and rhynchosaur remains, as well as the newly described probainognathian cynodont *Alemoatherium huebneri* (Martinelli et al., 2017b), were collected even higher in the section (Langer, 2005a). The collected geochronology sample represents the typical Alemaoa Member mudstone and comes from 5 m below its top. The overlying Caturrita Formation in the site consists of a basal, 50 cm-thick fossiliferous conglomerate, which grades upwards into about 10 m of medium-grained sandstones with planar and trough cross-stratification (channel facies) and climbing ripples (crevasse splays). Less than 0.5 km east of Cerro da Alemaoa, about 3 m of the Alemaoa Member is exposed along small ravines that most probably correspond to what remains of the type-locality (Sanga Grande) of *Staurikosaurus pricei* (Colbert, 1970), correlating with the lower portion of the unit at Cerro da Alemaoa (Fig. 1).

The Linha São Luiz site (Bonaparte et al., 2010) is located to the north of Faxinal do Soturno ( $29^{\circ}33'45''S$ ;  $53^{\circ}26'48''W$ ) and exposes a ca. 20 m section of the Caturrita Formation (Fig. 1). Its basal portion consists of a) medium to fine sandstones at the base, with large and medium trough cross-stratification, representing channel facies, and b) medium- to fine-grained, massive sandstones, with root structures and bioturbation, characteristic of crevasse facies. The collected geochronology sample is from the latter beds, which are extraordinarily rich in fossil remains representative of the *Riograndia* Assemblage Zone, i.e. the Faxinal do Soturno local fauna of Bonaparte et al. (2010), including *Guaibasaurus candelariensis* and a plethora of small tetrapods such as procolophonids, cynodonts, and lepidosaurs. A 2.5 meters-thick interval of brownish mudstones with intercalated fine-grained and rippled sandstones characteristic of lacustrine facies occurs in the middle part of the section. This is a highly fossiliferous horizon that has yielded insect wings, fish scales, conchostracans, and plant remains such as conifer shoots, impressions of leaves and associated reproductive parts, as well as fossil wood (Barboni and Dutra, 2013). The top of the section

exposes 7 m of medium- to fine-grained sandstone, with plane-parallel stratification, mud cracks, and climbing ripples. These correspond to crevasse splay facies and preserve large dinosaur footprints (Silva et al., 2012). Contrary to the typically Triassic vertebrate fauna of the lower sandstone sampled here for geochronology, the plant (Barboni and Dutra, 2013), microfossil (Rohn et al., 2014), and ichnological (Silva et al., 2012) remains from the upper part of the section appear to be more consistent with a Jurassic age.

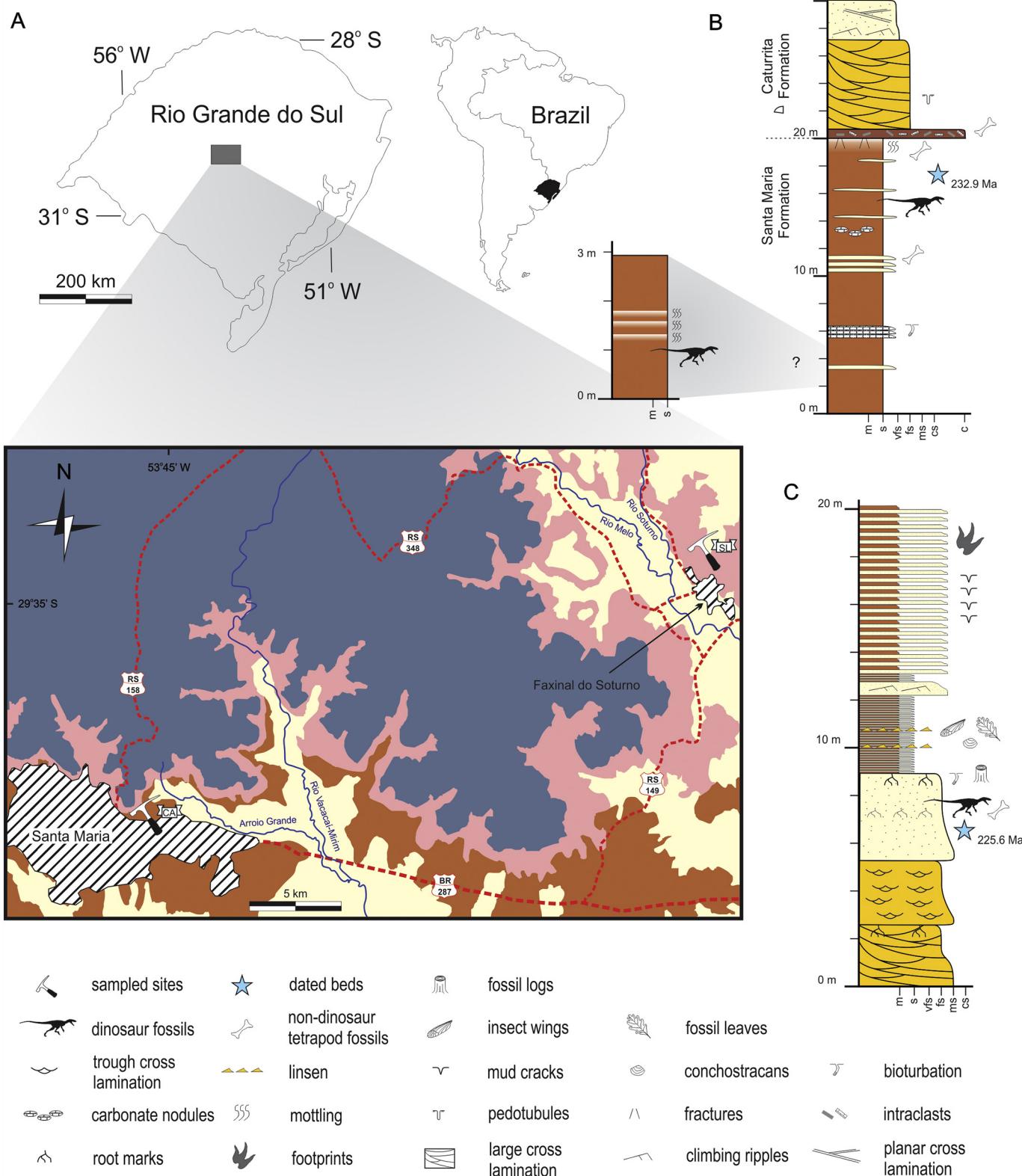
### 3. U-Pb geochronology

Zircons were isolated from two ca. 0.7 kg samples of red mudstone and fine-grained sandstone, respectively, from the Cerro da Alemaoa and Linha São Luiz sites, using standard crushing, as well as magnetic and density separation techniques. Selection of individual zircon grains and their analysis by the U-Pb CA-ID-TIMS technique follow the criteria and detailed analytical procedures described in Ramezani et al. (2011). Zircons were pre-treated by a chemical abrasion method modified after Mattinson (2005) involving thermal annealing at  $900^{\circ}\text{C}$  for 60 h and leaching in concentrated HF at  $210^{\circ}\text{C}$  for 12 h in order to mitigate the effects of radiation-induced Pb loss in zircon. The EARTHTIME ET535 mixed  $^{205}\text{Pb}$ - $^{233}\text{U}$ - $^{235}\text{U}$  tracer (Condon et al., 2015; McLean et al., 2015) was used in the analyses and isotopic measurements were made on either a VG Sector 54 or an Isotopx X62 multi-collector, solid-source, mass spectrometer equipped with Daly photomultiplier ion-counting systems at the Massachusetts Institute of Technology. Reduction of mass spectrometric data, as well as calculation of dates and propagation of uncertainties were done using the Tripoli and U-Pb\_Redux software and associated algorithms (Bowring et al., 2011; McLean et al., 2011).

Complete ID-TIMS U-Pb data are given in Table S1 (Supplementary Information). A separate set of 85 selected zircon grains from both samples were analysed first by laser-ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) for U-Pb dating on a Thermo Scientific ELEMENT 2 high-resolution sector-field ICP-MS instrument coupled with an ANALYTE.G2 excimer laser at the University of Kansas, following the procedures described in Cioffi et al. (2016) and the results are given Table S2 (Supplementary Information). Zircons identified to most likely comprise the youngest population were subsequently removed from the grain mount and analysed by the CA-ID-TIMS method described above (Table S1). The results are illustrated in the date distribution plot of Fig. 2.

Reported ages for the dated samples are derived from either the weighted mean  $^{206}\text{Pb}/^{238}\text{U}$  date of three or more youngest analyses that overlap within  $2\sigma$  analytical uncertainty (*Saturnalia* sample), or the  $^{206}\text{Pb}/^{238}\text{U}$  date of the single youngest analysis where overlapping dates could not be obtained (*Guaibasaurus* sample), and interpreted as maximum estimates for the age of deposition of the corresponding beds and associated fauna. All uncertainties are reported at the 95% confidence level ( $2\sigma$ ) and follow the notation  $\pm X/Y/Z \text{ Ma}$  (Fig. 2), where X is the internal (analytical) uncertainty in the absence of all external errors, Y incorporates the U-Pb tracer calibration error and Z includes the latter as well as the decay constant errors of Jaffey et al. (1971). We follow the recommended Triassic time scale of Ogg (2012; option 2) and Cohen et al. (2013; updated) involving a short Carnian duration (c. 237–228 Ma) in the following discussion.

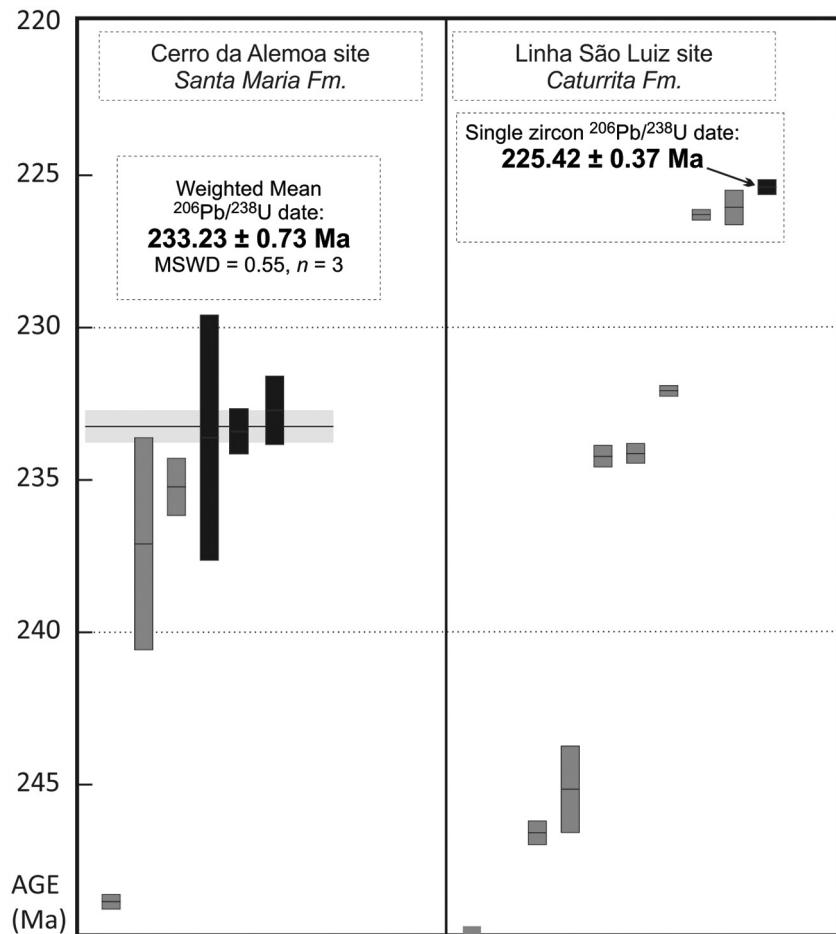
Sixteen zircon U-Pb analyses by the CA-ID-TIMS method from the *Saturnalia* sample, including four zircons pre-screened by LA-ICP-MS, range in  $^{206}\text{Pb}/^{238}\text{U}$  date from  $575.4 \pm 1.5 \text{ Ma}$  to  $232.7 \pm 1.1 \text{ Ma}$  (Table S1). The three youngest analyses (z4, z38\* and z44\*) form a statistically coherent cluster yielding a weighted mean  $^{206}\text{Pb}/^{238}\text{U}$  of  $233.23 \pm 0.61/0.69/0.73 \text{ Ma}$  with a mean square of weighted deviates (MSWD) of 0.55. The latter date serves as the best maximum estimate for the depositional age of the bone bed near the top of the Santa Maria Formation. Fourteen zircon CA-ID-TIMS analyses from *Guaibasaurus* sample (including 5 by LA-ICP-MS) range in  $^{206}\text{Pb}/^{238}\text{U}$



**Fig. 1.** A: Location map of the geochronology sample sites (CA – Cerro da Alemao, SL – Linha São Luiz), within Rio Grande do Sul state, south Brazil, and the surface distribution of the geologic units in the area. Santa Maria Formation in brown, Caturrita Formation in pink, the superimposed Botucatu and Serra Geral formations in blue, and Cenozoic alluvial deposits in yellow. B: Stratigraphic column of the Santa Maria and Caturrita formations at Cerro da Alemao, with the auxiliary section at Sanga Grande. C: Stratigraphic column of the Caturrita Formation at Linha São Luiz. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

date from  $526.11 \pm 0.39$  Ma to  $225.42 \pm 0.25$  Ma with only limited overlap among the three youngest analyses, such that no statistically meaningful weighted mean date can be calculated. The single youngest

analysis from this sample (z24\*) with a  $^{206}\text{Pb}/^{238}\text{U}$  date from  $225.42 \pm 0.25/0.285/0.37$  Ma places a maximum limit on the age of deposition of the fossil-rich beds of the Caturrita Formation.



**Fig. 2.** Date distribution plot of analysed zircon by the CA-ID-TIMS method from the dinosaur-bearing Santa Maria and Caturrita formations of Rio Grande do Sul, south Brazil (see Fig. 1 for sample locations). Vertical bar height is proportional to  $2\sigma$  analytical uncertainty of individual zircon analyses; solid bars are data used in age calculation. See Table S1 for complete U-Pb data. Older analyses beyond the plot area are not shown. Shaded horizontal band and its thickness represent the weighted mean  $^{206}\text{Pb}/^{238}\text{U}$  date and its  $2\sigma$  confidence interval, respectively. Reported dates include external sources of uncertainty.

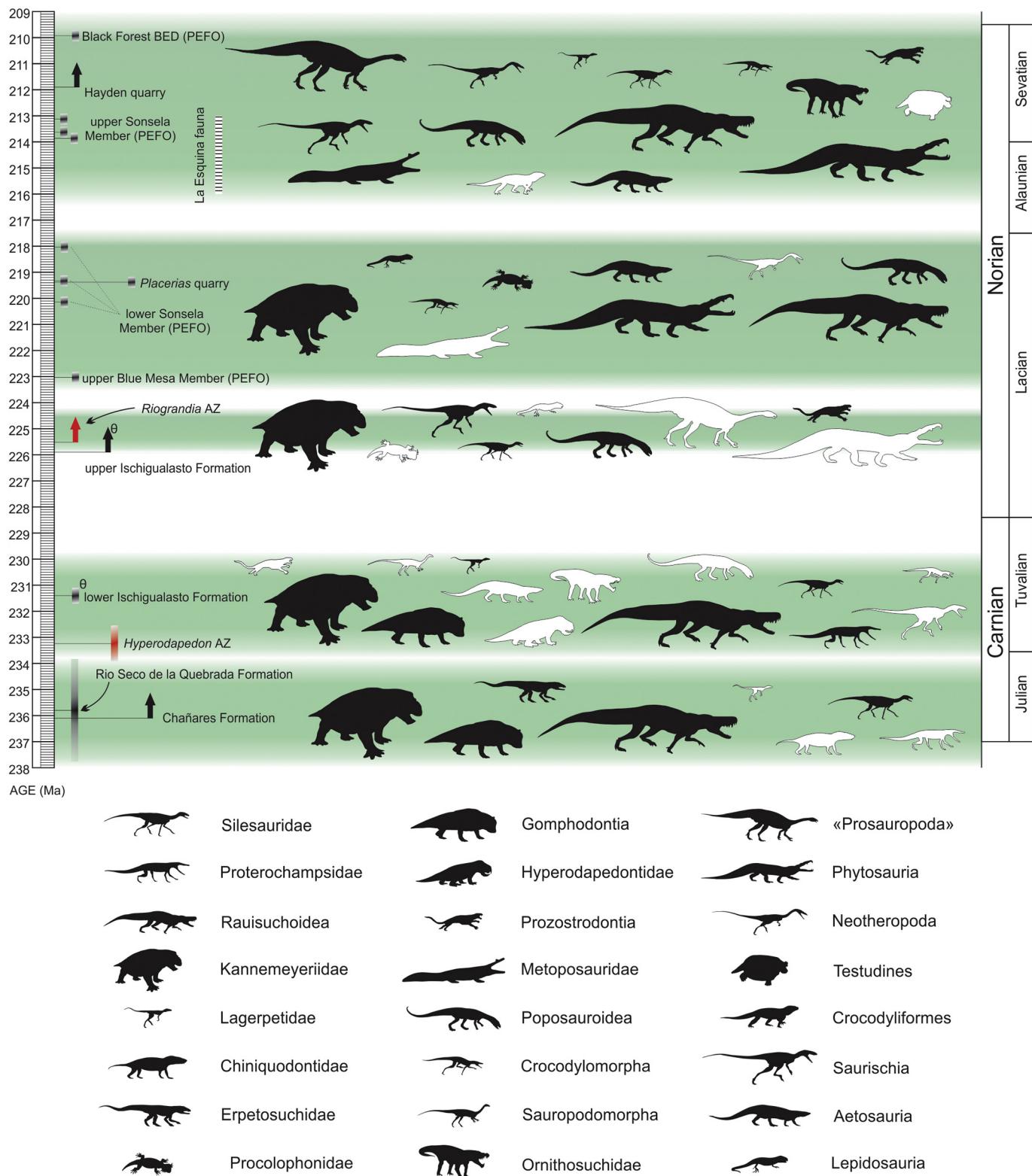
#### 4. Discussion

Recent radioisotopic geochronology from several Late Triassic strata in both North and South America (Martinez et al., 2011, 2012; Irmis et al., 2011; Ramezani et al., 2011, 2014; Ottone et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017), coupled with new magnetostratigraphy (Olsen et al., 2010; Kent et al., 2014), has begun to unravel the tempo of dinosaur rise in western Pangaea. The independent radioisotopic data helped in moving past the “transcontinental land vertebrate biochronology” conundrum (Langer, 2005b; Rayfield et al., 2009; Irmis, 2010; Irmis et al., 2011), where the tetrapod record is used to establish the relative ages of the strata, which are in turn used to infer patterns of tetrapod evolution through time. Yet, this advance didn't come painlessly, as exemplified by the unexpected Carnian U-Pb zircon age (Ottone et al., 2014) yielded by the putative early Middle Triassic Río Seco de la Quebrada Formation, Argentina, calling for an extensive revision of the therapsid biozonal models (Martinelli et al., 2017a).

Our new  $233.23 \pm 0.61$  Ma U-Pb maximum depositional age for the Santa Maria Formation at Cerro da Alemao (type-locality of *Saturnalia tupiniquim*) brings it to the age proximity of the base of the Ischigualasto Formation in Argentina with a ca. 231.5 Ma age based on  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology (Rogers et al., 1993; recalculated by Martinez et al., 2011). The apparent c. 1.5 Myr difference between the two dates may not be of significance, but simply due to the fact that the age of the Santa Maria Formation comes from detrital zircon. This age relation supports the correlation of the *Hyperodapedon* Assemblage-Zone (AZ) of the

Santa Maria Formation to the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone of the Ischigualasto Formation (Martinez et al., 2012), as previously proposed by Lucas (1998) and Langer et al. (2010), and is consistent with a late Carnian (Tuvalian) age for their associated fauna. The younger than 225.5 Ma age for the Caturrita Formation at Linha São Luiz (containing *Guaibasaurus candelariensis*) is more difficult to put in regional context due to the lack of robust geochronology elsewhere. Our date is significantly older than a reported  $^{40}\text{Ar}/^{39}\text{Ar}$  date of  $217.0 \pm 1.7$  Ma from near the top of the Ischigualasto Formation (Currie et al., 2009), but is more consistent with another reported  $^{40}\text{Ar}/^{39}\text{Ar}$  date of  $225.9 \pm 0.9$  Ma (Martinez et al., 2011) for the same horizon. This corresponds to the lower boundary of the *Jachaleria* biozone (Martinez et al., 2011), which extends to the base of the overlying Los Colorados Formation (La Chilca fauna; Caselli et al., 2001; Arcucci et al., 2004). Our Caturrita Formation maximum age is early Norian (Lacian) and hints at a significant hiatus between the dated layer at Linha São Luiz and the putatively Jurassic (Rohn et al., 2014) overlying beds with plant, microfossil, and ichnological remains.

The oldest known dinosauromorph body fossils and archosauriform-dicynodont assemblages with radioisotopic age constraints (Fig. 3) presently cluster around ca. 236 Ma, i.e. early Carnian (Julian), and include the faunas of the Chañares and Río Seco de la Quebrada formations in Argentina (Ottone et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017), and possibly the Santacruzodon Assemblage-Zone in Brazil (Philipp et al., 2013). Previous tetrapod-based correlations predicted those units to be temporally disparate; the Río Seco de la Quebrada Formation was presumed Anisian and the Chañares



**Fig. 3.** Carnian-Norian time line for the appearance of dinosaurs among major groups of terrestrial tetrapods based on available radioisotope geochronology from western Pangaea fossil sites (USA, Argentina, and Brazil). PEFO – Petrified Forest National Park, Arizona, USA. Triassic time scale based on Ogg et al. (2016). Tetrapods are grouped into generalized time slices (green), with open silhouettes representing first occurrence of taxa in the sampled faunas. Species-level splits and single-taxon occurrences such as *Promastodontosaurus*, *Pelorocephalus*, *Marasuchus*, *Doswellia*, *Vancleavea*, and *Trilophosaurus*, are not represented. Geochronology based on Rogers et al. (1993), Irmis et al. (2011), Ramezani et al. (2011, 2014), Martinez et al. (2011), Ottone et al. (2014), Marsicano et al. (2016) and this study (in red). Age of the La Esquina fauna inferred from Kent et al. (2014).  $^{40}\text{Ar}/^{39}\text{Ar}$  dates are shown with  $2\sigma$  confidence intervals; others signified by an arrow indicating the high possibility of representing a detrital (old) age. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Formation Ladinian, whereas the *Santacruzodon* AZ was placed near the Ladinian-Carnian boundary (Lucas, 2010; Abdala and Ribeiro, 2010). The clustering in time of these contrasting fossil assemblages from adjacent basins suggests high levels of endemism among the South American tetrapod faunas of the time (but see Martinelli et al., 2017a), at least compared to the late Carnian assemblages. Better age constraints on the *Dinodontosaurus* Assemblage-Zone in Brazil, which is supposed to be coeval with the Chañares fauna, but older than the *Santacruzodon* AZ (Abdala and Ribeiro, 2010), will shed more light at these unexpected temporal relationships.

At present, the best calibrated post-Carnian dinosauromorph records belongs to the Chinle-Dockum Basin of the North American southwest in Arizona and New Mexico. Modern re-evaluation of the Chinle tetrapod record (Nesbitt et al., 2007; Nesbitt, 2011), combined with high-precisions U-Pb geochronology of its key fossil-bearing intervals in Arizona (Ramezani et al., 2011; Atchley et al., 2013) and New Mexico (Irmis et al., 2011; Ramezani et al., 2014) revealed serious limitations to the “Adamanian” and “Revueltian” land-vertebrate faunachron scheme of Lucas (1998, 2010), despite the recognition of assemblages potentially fitting that framework in a biostratigraphic revision of the Chinle Formation at the Petrified Forest National Park, Arizona (Parker and Martz, 2011). The revised chronostratigraphy of the Chinle Formation elucidated an extensive, ca. 16 Myr depositional and fossil preservational gap in the North American record that spans almost the entire Ladinian, Carnian and early Norian (Ramezani et al., 2014). As such, the oldest documented Chinle dinosauromorphs occur immediately succeeding the above gap at ca. 223 Ma. Age uncertainties associated with the Triassic dinosaur record of Argentina do not allow a robust correlation with the Chinle Formation. Yet, magnetostratigraphic correlation of upper Los Colorados Formation strata, coeval with those yielding the La Esquina fauna (Caselli et al., 2001), to the Newark astrochronological polarity time scale (Olsen et al., 2010) places them between ca. 213 and 216 Ma (Kent et al., 2014), i.e. within the temporal limits of the dated tetrapod-bearing strata of the Chinle Formation.

A compilation of the presently available geochronology, including those presented here, can be used to establish a basic chronostratigraphic framework for the Late Triassic tetrapod evolution in western Pangea, within which dinosaur rise can be more comprehensively depicted. Indeed, the sequence of dated fossil assemblages as a function of time (Fig. 3) allows the inference of local taxon ranges and broad-scale faunal variations. Accordingly, early Carnian faunas were devoid of dinosaurs (Fig. 3), although dinosaur precursors were prevalent in the Chañares Formation. Those faunas are dominated by therapsids such as small- to medium-sized herbivorous and carnivorous cynodonts and large herbivorous dicynodonts. Non-dinosauromorph archosaurs are absent from the Rio Seco de la Quebrada Formation, but occur in the *Santacruzodon* AZ and the Chañares Formation, mainly represented by proterochampsids and rauisuchoids (Martinelli et al., 2009, 2017a; Lacerda et al., 2013; Ezcurra et al., 2017).

Dinosaurs made their western Pangea appearance in the late Carnian faunas of Argentina (base of the Ischigualasto Formation) and Brazil (*Hyperodapedon* AZ of the Santa María Formation), already with a high diversity of saurischians (Ezcurra, 2010), including small-sized omnivores (e.g., *Buriolestes*, *Chromogisaurus*, *Eoraptor*, *Panphagia*, *Saturnalia*) and medium to large carnivores (e.g., *Herrerasaurus*, *Sanjuansaurus*, *Staurikosaurus*). These very similar faunas are dominated by rhynchosaurs, particularly the genus *Hyperodapedon*, which are absent or much less abundant in both older and younger deposits (Montefeltro et al., 2010; Ezcurra et al., 2013). Apart from rhynchosaurs and dinosaurs, the faunas also include large herbivorous dicynodonts (absent in Brazil), small carnivorous and medium-sized herbivorous cynodonts, large- to medium-sized carnivorous rauisuchoids, poposauroids, ornithosuchids, and proterochampsids, small crocodylomorphs and non-dinosaur dinosauromorphs (lagerpetids and silesaurids), as well as the omnivorous/scavenger aetosaurs and temnospondyl aquatic carnivores (Langer et al., 2007; Martinez et al.,

2012). The appearance of *Hyperodapedon*, dinosaurs, ecteniniid and prozostrodontid cynodonts, aetosaurs, poposauroids, crocodylomorphs, and ornithosuchids, with almost no extinction of major tetrapod groups already present in older strata, indicate a higher level of niche partitioning compared to that of early Carnian faunas.

The early Norian fauna of Faxinal do Soturno in Brazil includes the saurischian *Guaibasaurus*, but is otherwise heavily biased towards small-sized tetrapods, such as procolophonids, tritheledontid and brasilotontid prozostrodontians, and lepidosaurs (Bonaparte et al., 2010). This is part of the *Riograndia* Assemblage Zone (Soares et al., 2011) that also encompasses outcrops of the Caturrita Formation yielding the dicynodont *Jachaleria*, the “prosaupropod” *Unaysaurus*, poposauroid and phytosaur remains, and possibly the silesaurid *Sacisaurus* (Bittencourt et al., 2013; Müller et al., 2016). *Jachaleria* allows correlation to the depauperate La Chilca fauna (Arcucci et al., 2004), at the boundary between the Ischigualasto and Los Colorados formations, in Argentina. The absence of aetosaurs and crocodylomorphs in such early Norian faunas is most likely a collection bias, as these taxa are known from older and younger deposits in South America (Fig. 3). Overall, the early Norian record in western Pangea is characterized by the appearance of “prosaupropods”, tritheledontids, brasilotontids, phytosaurs, procolophonids, and lepidosaurs.

The timeline presented here (Fig. 3) highlights an important gap in both the North and South American records near the Carnian-Norian boundary. This gap corresponds to the lack of fossil preservation in the mid- to upper levels of the Ischigualasto Formation (e.g., Martinez et al., 2011), as well as in the basal Shinarump and Mesa Redondo members of the Chinle Formation (Ramezani et al., 2014). At present, this Carnian-Norian gap is perhaps the largest missing piece in the early dinosaur evolution puzzle. The filling of this such gap may rest on a better exploration of some poorly sampled South American sites, such as the *Exaeretodon*-rich localities of the Santa María Formation (Langer et al., 2007; Oliveira and Schultz, 2007), and the Cerro las Lajas exposures of the Ischigualasto Formation (Von Baczkó et al., 2014), in La Rioja, Argentina, both of which may be slightly younger than the typical faunas of the *Hyperodapedon* AZ of Brazil and the base of the Ischigualasto Formation, in Argentina, and respectively yielded the dinosaurs *Pampadromaeus barberenai* and *Pisanosaurus mertii*.

The Norian faunas of the North American southwest (Fig. 3) typically consists of aetosaurs, phytosaurs, crocodylomorphs, rauisuchoids, poposauroids, silesaurids, lagerpetids, dicynodonts, metoposaurs, and saurischian dinosaurs, including neotheropods, as recorded in the Chinle-Dockum continental deposits of eastern Arizona, New Mexico, and western Texas (e.g., Long and Murry, 1995; Heckert et al., 2005; Irmis et al., 2007; Parker and Martz, 2011; Nesbitt et al., 2007). The fauna of the highly fossiliferous *Placerias* Quarry in eastern Arizona also includes procolophonids, lepidosaurs, and the eponymous dicynodont (Jacobs and Murry, 1980; Fiorillo et al., 2000; Irmis, 2005), with a depositional age no distinct from that of the typical mid-Chinle assemblages of the Petrified Forest National Park (Ramezani et al., 2014). The novelties of the Chinle-Dockum and La Esquina faunas, compared to earlier Norian faunas of western Pangaea (e.g., *Riograndia* AZ), include metoposaurs, neotheropods, turtles, and crocodyliforms. At this point, an important degree of latitudinal provincialism is observed. Poposauroids, phytosaurs, and metoposaurs are found only in North America, whereas only the La Esquina fauna bears crocodyliforms, ornithosuchids, tritheledontids, and “prosaupropods”.

## 5. Conclusions

The Late Triassic tetrapod chronostratigraphy presented here (Fig. 3) reflects the presently available geochronology from limited western Pangean tetrapod-bearing deposits. Additional radioisotopic geochronology with a broader paleogeographic scope will undoubtedly refine (perhaps alter) the picture portrayed here. Macroevolutionary patterns drawn from Fig. 3 should be taken as general, as they deal with major

faunal groups only, but are considered largely accurate in the sense that they are derived exclusively from dated or reliably correlated sites. They should not be interpreted as temporal ranges for the corresponding taxa, as older or younger records may occur outside the scope of the studied sites. Nonetheless, an increase in the major taxon diversity suggests that the first stages of the main Late Triassic turnover in tetrapod assemblages of western Pangea has been recorded in late Carnian deposits, already with high levels of niche partitioning. Given the large gaps in the fossil record and ambiguous ages of most putative Middle Triassic tetrapod faunas of south Pangea, it is not straightforward which taxa are novel to the early Carnian faunas. However, the small ratio of new major taxa in the middle Norian faunas indicates a more stable composition from those times onwards. Indeed, post-early Carnian ecosystem rebuilding may have lasted up to 10 Myr, crossing the Carnian–Norian boundary and encompassing early Norian faunas of both North and South America. A late Carnian faunal turnover affecting terrestrial tetrapods has long been advocated (Benton, 1983; Benton et al., 2014; but see Sues and Fraser, 2010), and is partially supported by the model proposed here.

The late Carnian faunal diversification in southwestern Pangaea may have been climatically driven, as the fossil-bearing successions in south Brazil indicate more arid conditions relative to those of the early Carnian (Zerfass et al., 2003). This apparently follows a more humid phase recorded over lower latitudes and the northern hemisphere known as the mid-Carnian “Wet Intermezzo” (Ogg, 2015) in the context of a warming climate (Trotter et al., 2015), but the precise onset and duration of such events are still unclear (Furin et al., 2006). In turn, a later return to wetter conditions has been recorded in the Norian tetrapod-bearing terrestrial deposits of South America (Holz and Scherer, 2000; Pierini et al., 2002; Colombi and Parrish, 2008). Accordingly, a peculiar ecological scenario seems to characterize the appearance of dinosaurs in the region, matching dryer and warmer conditions, the dominance of rhynchosaurs as first level consumers, and overall faunal diversification. It is tempting, although conjectural, to correlate such dryer and possibly more homogenous late Carnian landscapes of southwestern Pangea to the disruption of previously prevailing early Carnian endemisms, leading to faunal interchange and biodiversity increase. Future research should definitely focus on the calibration of major macroevolutionary events, by integrating extensive faunal and floral inventories with high-precision geochronology of key Triassic successions.

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