The paleoclimatic context for South American Triassic vertebrate evolution

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ARTICLE INFO	ABSTRACT
	The Triassic Period was the setting for the origin and early diversification of Mesozoic ecosystems after the end-Permian mass extinction. The study of the Triassic is essential to understand the evolution of non-marine Mesozoic ecosystems, particularly the vertebrate components and their climatic context. During this time, the configuration of the supercontinent Pangea, which was unique (e.g., the only time since the origin of life that a global supercontinent spread across the equator) in the earth's paleobiogeographic history, is one of the factors that characterized the period. This paleogeographic configuration combined with a high global sea level and no polar ice caps would have had an extraordinary effect on the global climate. Multiple sudden climate events occurred during this time, such as large igneous province (LIP) eruptions, including two that had a major part to play in the major mass extinctions that bracket the Triassic Period. Against this backdrop, a number of modern vertebrate clades originated on land, including lissamphibians, lepidosaurs, turtles, dinosaurs, and mammalia-forms. To test the link between climatic and evolutionary events, we compiled paleoclimatic data from Argentinian, Brazilian, Bolivian, and Chilean Triassic non-marine vertebrate-bearing strata to discuss observed paleoclimatic changes and their influence on vertebrate evolution in South America during this time. Fluctuating climate conditions dominated the western Gondwana Triassic, with arid to semiarid conditions during Early Triassic with marked humid seasonal fluctuation in the continental interior, the seasonal semiarid condition of the Middle Triassic shows more humid seasonality than Early Triassic, and the Late Triassic was dominated by seasonal sub-humid conditions with one or more semi-arid intervals, particularly in the continental interior. Comparisons of the Triassic South American vertebrate fossil record and this paleoclimate record show striking patterns; however, better geochronologic control, paleoclimate proxy records, and sample fossil-bearing strata are necessary to understand these trends.

1. Introduction

In the wake of the largest extinction on record, the end-Permian mass extinction, the Triassic Period witnesses the origin and early diversification of many aspects of the biota that persisted for the rest of the Mesozoic Era. In particular, the Triassic is pivotal in our understanding of the evolution of Mesozoic ecosystems on land (e.g., Wing and Sues 1992; Edwin 1994, 1999; Retallack et al., 2003; Benton and Twitchett 2003; Benton et al., 2004; Gastaldo et al., 2005; Irmis and Whiteside, 2010; Fraser and Sues, 2011).

The evolution of these ecosystems was affected by a number of first-order variables. Across Phanerozoic history, the configuration of the supercontinent Pangea was unique in that it comprised a single supercontinent that stretched across the equator terminating at high latitudes in both northern and southern hemispheres (Frakes 1979; Ziegler et al., 1983; Parrish 1993; Torsvik et al., 2012; Torsvik and Cocks 2013; Holz 2015). This, combined with a relatively high global sea level, had an extraordinary effect on global climate. The almost symmetrical position

of Pangea over the equator drove strong seasonality at lower latitudes during the Triassic (Parrish 1993; Sellwood and Valdes 2006; Holz 2015), as well as, a displacement of the arid belt towards the poles (polewards). As result, there was a significant decrease of the precipitation/evaporation rate in the low to mid-latitudes of Pangea's interiors (Fig. 1) (Kent and Tauxe 2005; Sellwood and Valdes 2006; Boucot et al., 2013).

The Triassic Earth was also a hothouse world, with ice-free polar regions (Fig. 1) and elevated atmospheric CO_2 levels (e.g., Schaller et al., 2015; Foster et al., 2017), and therefore intensified climate extremes (e. g., Yonetani and Gordon, 2001). This high CO_2 was partly driven by continental arrangement, as equatorial Pangaea experienced enhanced weathering (e.g. Goddéris et al., 2012, 2014). Based on various paleoenvironmental proxy data, Retallack (2013) hypothesized up to eleven greenhouse climate crises during the Triassic Period. Much of the focus in studying Triassic climate has been on the greenhouse events that bookend the period, the large igneous province eruptions that caused the end-Permian and end-Triassic mass extinctions (e.g., Whiteside et al., 2010; Schaller et al., 2011; Burgess et al., 2017; Black et al., 2018). More recently, attention has turned to other Triassic climate events, such as the "Carnian Pluvial Episode" (CPE) (Simms and Ruffell 1989, 1990), which caused extensive changes in many depositional environments, from non-marine to deep-water ocean settings (e.g., Dal Corso et al., 2012, 2015, 2018; Ogg 2015; Ruffell et al., 2016; Sun et al., 2016; Miller et al., 2017). It has been linked with Wrangellia oceanic LIP eruptions in the eastern Panthalassic Ocean (e.g., Greene et al., 2010; Dal Corso et al., 2012; 2015; Xu et al., 2014), but the CPE also occurred during a time when Pangea was beginning to move northward (e.g., Torsvik et al., 2012), and the Tethys area where most evidence is from was transitioning from the low latitude arid belt to the mid-latitude humid zone (cf. Kent and Tauxe 2005; Whiteside et al., 2011) (Fig. 1). Regardless of cause, the CPE is of particular interest because, like the two mass extinctions, it has been linked with major changes in marine and terrestrial ecosystems (e.g. Flügel 2002; Stanley 2003; Erba 2006; Furin et al., 2006; Goddéris et al., 2008; Bernardi et al., 2018; Benton et al., 2018).

Thus, the dynamic climate of the Triassic Period makes it an ideal case for examining how climate affects ecosystems. Gondwana is a particularly useful area for such studies on land, because it possesses a large number of rich Triassic fossil assemblages preserved in sedimentologically-diverse non-marine strata that span most of the Triassic Period. In particular, South American basins are particularly well-studied, with abundant geochronological age constraints. The Argentinian and Brazilian Triassic sequences are particularly notable for their abundant and diverse vertebrate assemblages that characterized the evolution of the main Mesozoic clades (e.g., Schultz et al., 2000; 2020; Rogers et al., 2001; Arcucci et al., 2004; Schultz 2005; Langer et al., 2007; Martínez et al., 2013; Mancuso et al., 2014; Marsicano et al., 2016). Here, we review available geochronologically-constrained paleoclimatic data from Argentinian, Brazilian, Bolivian, and Chilean Triassic non-marine successions, and compare them with the contemporaneous vertebrate fossil record from the same strata. We then ask how local, regional and global paleoclimatic changes may have influence Triassic biota in South America, and Gondwana as a whole.

2. Geological setting of South American basins

During the Triassic Period, the landmass that is now South America extended from the palaeoequator to subpolar latitudes (Fig. 1) (e.g., Golonka 2007; Golonka et al., 2018). Triassic vertebrate assemblages from this area are largely found in the southern half of the continent (Fig. 2), which during the Triassic Period were areas located between 30 and 60°S paleolatitude (Fig. 3; Torsvik et al., 2012; Torsvik and Cocks, 2013; van Hinsbergen et al., 2015). The western margin of South America was similar to today, in that it was dominated by a convergent subduction-dominated plate boundary, with arc-volcanism creating large mountains along the western coast (e.g., Lovecchio et al., 2020).

Further to the east, sedimentary basins developed as a result of back-arc extension, slab roll-back, and transtensional strain, which resulted in the preservation of thick non-marine sedimentary sequences (e.g., Mpodozis and Ramos 1989; Franzese et al., 2003; Zerfass et al., 2004; Charrier et al., 2015; Spikings et al., 2015; 2016; Oliveros et al., 2018; Lovecchio et al., 2020).

2.1. Argentina

Triassic deposits containing vertebrate fossils in Argentina are distributed in several northwest-southeast trending extensional basins, of which the most prominent are the Cuyana and the Ischigualasto-Villa Unión basins in the northwest of the country (Fig. 2). Each of these basins contains several sub-basins with extensive outcrops whose non-marine infill spans the Late Permian to Late Triassic (Kokogian et al., 2001; Spalletti 2001; Stipanicic 2002). The Triassic vertebrate fossil record Argentina also derives from several smaller basins, such as the San Rafael Basin in western Argentina and Los Menucos Basin in Patagonia. These Argentine basins are dominated by fluvio-lacustrine sedimentary rocks, but also crucially contain volcaniclastic layers with dateable zircons.
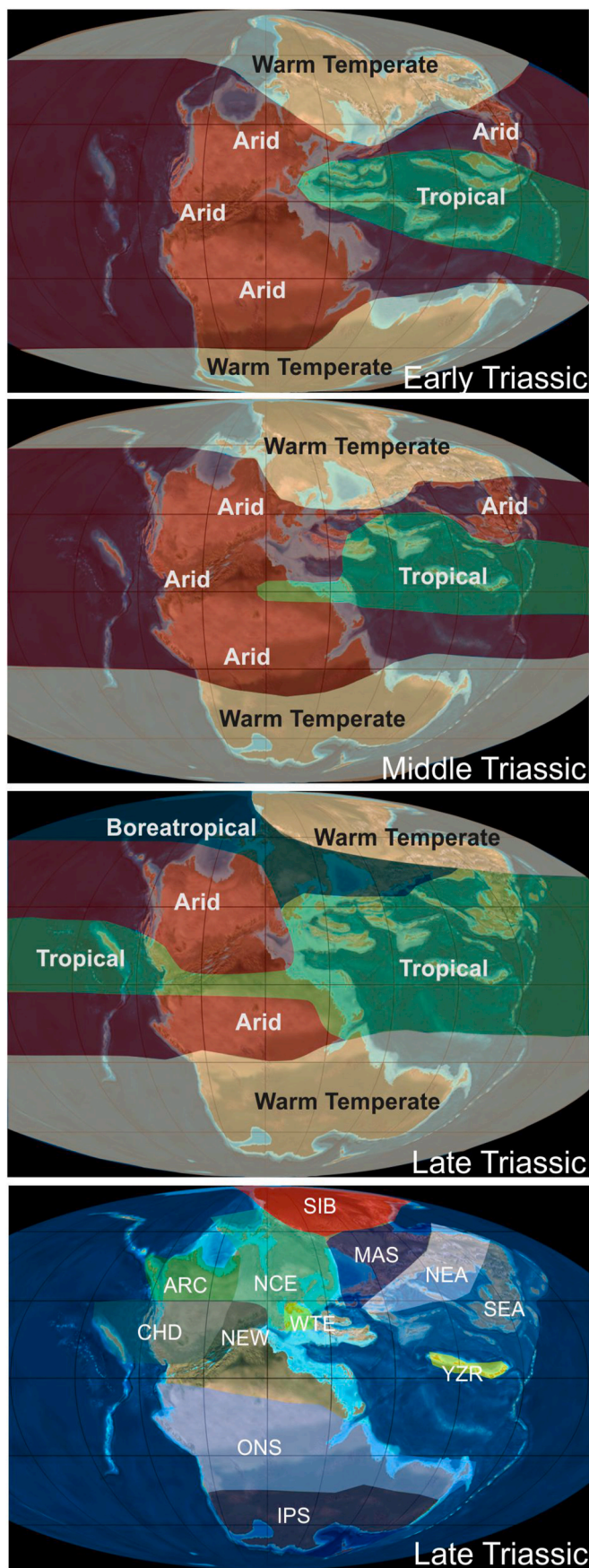
2.1.1. Ischigualasto-Villa Unión Basin

The Ischigualasto-Villa Unión Basin of northwest Argentina (Fig. 2) is expansive, both in terms of its temporal record and areal exposure, in western Gondwana (Stipanicic and Marsicano 2002). It records a nearly continuous Upper Permian to Upper Triassic non-marine succession, with very diverse Triassic Gondwanan terrestrial paleoenvironments and fossils. Vertebrate assemblages include actinopterygian fishes, temnospondyl amphibians, non-mammalian therapsids, turtles, dinosaur precursors (early dinosauromorphs), and early ornithischian, sauropodomorph, and theropod dinosaurs (e.g., Rogers et al., 1993; 2001; Marsicano et al., 2001, 2007; Arcucci et al., 2004; López-Arbarello et al., 2006; Martínez et al., 2013a, 2013b; Mancuso et al., 2014).

Most paleoenvironmental and paleontological data are known from the largest part of the extensional basin, the Ischigualasto-Villa Union Basin that straddles the boundary of San Juan and La Rioja provinces. Here, Ischigualasto-Villa Unión deposits rest unconformably upon thick non-marine Paleozoic deposits (Stipanicic and Bonaparte, 1972; 1979; Caselli 1998; Caselli and Limarino, 2002). The initial infilling of the basin comprises the reddish alluvial fan, ephemeral fluvial and playa-lake deposits of the Talampaya Formation (López-Gamundí et al., 1989; Caselli 1998; Gulbranson et al., 2015). This unit was traditionally assigned to the Triassic based on stratigraphic relationships (e.g., Stipanicic and Bonaparte, 1972, 1979; Milana and Alcober, 1994; Stipanicic and Marsicano 2002), but was recently shown to cross the Permian-Triassic boundary based on CA-TIMS U–Pb zircon age of 252.5 $\pm$ 0.2 Ma obtained from a tuff bed in the upper part of the formation (Gulbranson et al., 2015). The only known vertebrate remains from this formation are manus and pes prints of a non-mammalian therapsid (Bonaparte 1997; Mancuso et al., 2010) (Table 1).

The potentially Lower and/or Middle Triassic Tarjados Formation rests unconformably on the Upper Permian-Lower Triassic Talampaya Formation and is covered by the lower Carnian Chañares Formation (Marsicano et al., 2016). It is dated indirectly by the radioisotopic ages from these overlying and underlying units. The Tarjados Formation comprises largely ephemeral fluvial settings with lesser eolian and playa lake components (Krapovickas et al., 2013). Though not well-sampled, the formation preserves body fossils of dicynodont therapsids, archosauromorphs, tetrapod burrows attributed to small non-mammalian cynodonts, and tetrapod tracks (Table 1) (Cox 1968; Bonaparte 1997; Mancuso et al., 2010; Krapovickas et al., 2013; Ezcurra et al., 2015).

The Chañares Formation is characterized by tuffaceous sandstones and siltstones deposited in fluvial and lacustrine-margin setting in the center and eastern part of the basin, with orthoconglomerates and paraconglomerates deposited in alluvial fans in the northwest part of the

basin (Rogers et al., 2001; Mancuso et al., 2014) transitionally replaced by cyclical lacustrine-deltaic sandstones and black shales of the Los Rastros Formation (Mancuso and Marsicano 2008; Mancuso and Caselli, 2012). Both units are considered as a single conformable sedimentary sequence (Mancuso and Caselli 2012; Mancuso et al. 2014, 2020). Recent radioisotopic ages for the Chañares and Los Rastros formations, which were previously inferred to be Middle Triassic in age, reveal that they are Carnian in age. The CA-TIMS U–Pb zircon dates spanning the Chañares Formation are 236.1 ± 0.6 Ma and 235.2 ± 0.5 Ma (Marsicano et al., 2016) in the northeastern part of the basin, and the date from the lower Los Rastros Formation in the northwestern part of the basin is 234.5 ± 0.9 Ma (Mancuso et al., 2020a, 2020b). The Chañares tetrapod assemblage (Table 1) includes a high diversity of archosauriforms (e.g., proterochampsids, pseudosuchians, and ornithodirans) and high abundance of non-mammalian synapsids (large dicynodonts and smaller cynodonts) (Rogers et al., 2001; Mancuso et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017; Mancuso and Irmis 2020; Ordoñez et al., 2020), as well as rare actinopterygian and sarcopterygian fishes remains (Gouiric-Cavalli et al., 2017). Although the Los Rastros preserves a very diverse plant assemblage (Ottone et al., 2005; Lutz et al., 2011; Pedernera et al., 2020), vertebrate fossils are much rarer, and include actinopterygian fishes (Lopez-Albarello et al., 2006), and a single temnospondyl amphibian (Lopez-Albarello et al., 2006; Mancuso and Marsicano 2008), and dicynodont, cynodont, archosauriform and dinosauriform footprints (Table 1) (Marsicano et al. 2004, 2007, 2010).

The overlying Ischigualasto Formation contains interbedded sandstones, mudstones, and tuffs deposited in channels, levees, and floodplains of a moderate sinuosity fluvial system (Tabor et al. 2004, 2006; Colombi and Parrish 2008; Currie et al., 2009). An $^{40}Ar/^{39}Ar$ age for the base of the Ischigualasto Formation (231.4 ± 2.1 Ma) supports a late Carnian age, whereas the $^{40}Ar/^{39}Ar$ from near the top of the unit (225.9 ± 3.7 Ma) constrains the end of deposition to the latest Canrian or earliest Norian (Rogers et al., 1993; Martínez et al., 2011). Both of these dates are from Ischigualasto Provincial Park in the southeastern part of the basin. The age of the top of the formation is also constrained by magnetostratigraphy from the overlying Los Colorados Formation (also from the southwestern part of the basin), which suggests the contact between the two units is ~227 Ma (Kent et al., 2014). Recent CA-TIMS U–Pb zircon ages from a thicker section at Las Lajas in the northwestern part of the basin (just north of the Cerro Bola area) are consistent with a late Carnian age for the lower part of the formation (dates of 229.3 ± 0.1 and 229.0 ± 0.22 Ma, from ~100 to ~160 m above the base of the formation, respectively), but suggest a significantly younger age for the top of the unit (221.8 ± 0.1 Ma). This implies that either the top of the Ischigualasto Formation is time-transgressive across the basin, or that the overlying Los Colorados magnetostratigraphy correlates differently with the Late Triassic magnetic polarity timescale than originally proposed. The Ischigualasto Formation preserves a very diverse vertebrate assemblage, which not only includes some of the earliest dinosaurs, but as also temnospondyls, dicynodonts, cynodonts, rhynchosaurs, early archosauriforms, pseudosuchians, and early dinosauromorphs (e.g., Martínez et al., 2013a). Plants are also quite diverse in the formation (e. g., Colombi and Parrish, 2008; Césari and Colombi 2013, 2016).

The mudstone and sandstone moderate-sinuosity fluvial red beds of the Los Colorados Formation overlay the Ischigualasto Formation
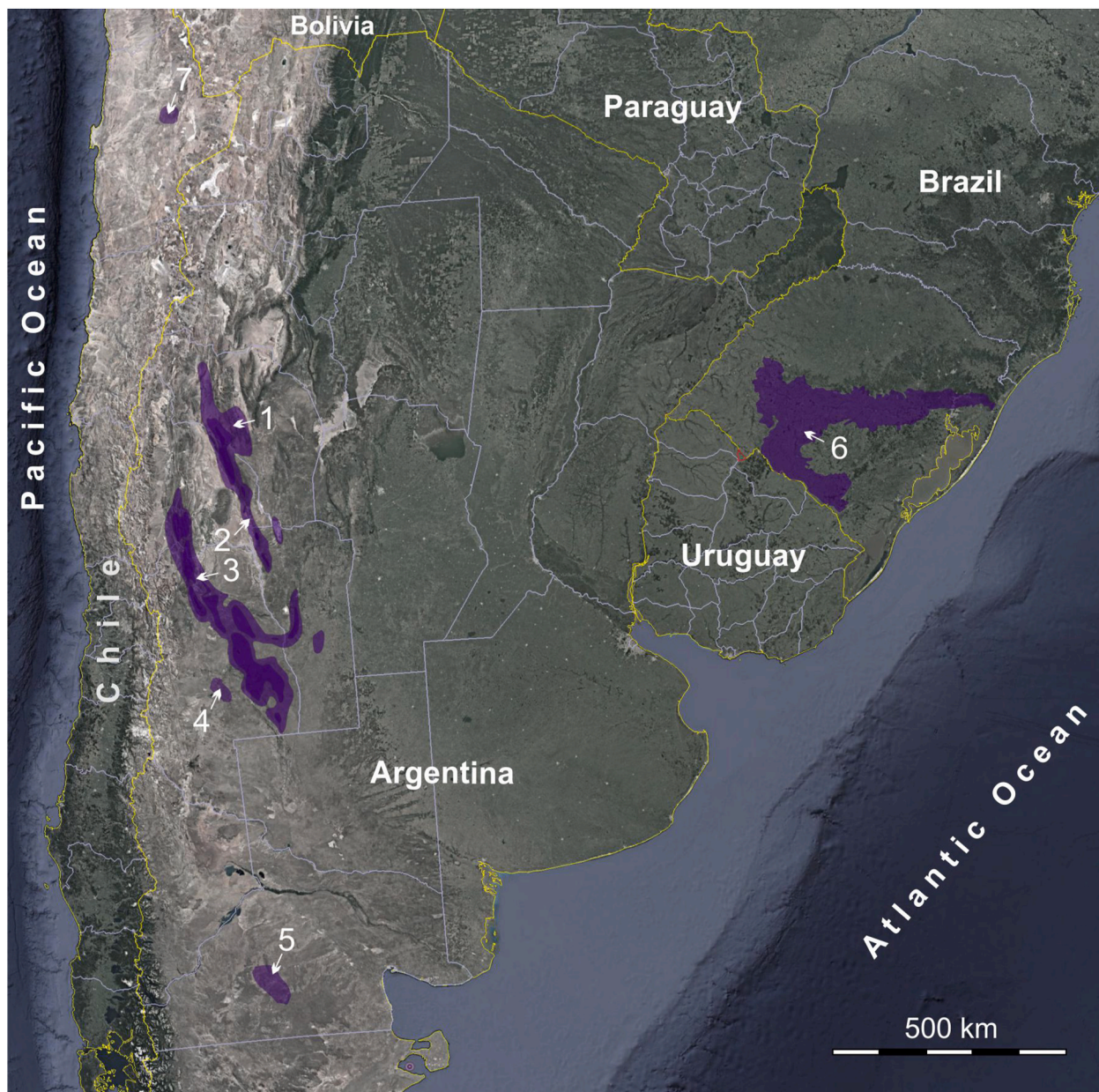
Fig. 2. Location of South American Triassic basins (shaded purple). 1. Ischigualasto-Villa Unión Basin. 2. Marayes-Carrizal Basin. 3. Cuyana Basin. 4. San Rafael Basin. 5. Los Menucos Basin. 6. Paraná Basin. 7. Salar de Atacama Basin.

(Caselli et al., 2001). This uppermost Triassic unit of the basin preserves a well-defined magnetostratigraphy that correlates well to the Newark-Hartford Astrochronostratigraphic Polarity Timescale and U–Pb age constrained Colorado Plateau Coring Project magnetostratigraphy, indicating a Norian age range of ~227 to 213 Ma (Kent et al. 2014, 2018, 2019), though it is important to reiterate the caveats mentioned in the previous paragraph regarding the age of the Ischigualast-Los Colorados boundary. This unit preserves one of the first ecosystems dominated by dinosaurs in terms of abundance (sauropodomorphs, tetanuran theropods), and also includes pseudosuchian archosaurs (aetosaurs, rauisuchids, early crocodylomorphs ("sphenosuchians"), and the earliest crocodyliforms), dicynodonts and cynodonts, and stem turtles (Caselli et al., 2001; Arcucci et al., 2004).

2.1.2. Marayes-El Carrizal Basin

Though considerably smaller in areal extent and exposed stratigraphic thickness, the Marayes-El Carrizal depocenter in southwestern San Juan Province has recently received renewed study (e.g., Spalletti et al., 2011; Apaldetti et al., 2011, 2018; Colombi et al., 2014, 2015a,b; Lutz and Arce 2013; Martínez et al., 2013b, 2015, 2016; Martínez and Apaldetti, 2017). Though the sequence contains a number of Triassic-Lower Jurassic units (Bossi 1976; Spalletti et al., 2011; Colombi et al., 2015b), only the Quebrada del Barro Formation has produced Triassic vertebrate fossils to date (Colombi et al., 2015a; Martínez et al., 2015). This unit comprises a 600–1400 m thick package of conglomerates, coarse sandstones, and sandy mudstones that were deposited by a distributive fluvial system of anastomosing and meandering channels, crevasse splays, playa lakes, and mud-dominated sheet flood deposits (Bossi et al., 1975; Colombi et al. 2014, 2015a; Martínez et al., 2015). Many of these facies are pedogenically-modified into calcisols (Colombi et al., 2015a); these sedimentological data indicate a warm, seasonally well-drained paleoenvironment. No geochonologic age constraints are available for the Quebrada del Barro Formation, but the underlying Carrizal Formation preserves a Middle-Late Triassic macrofloral
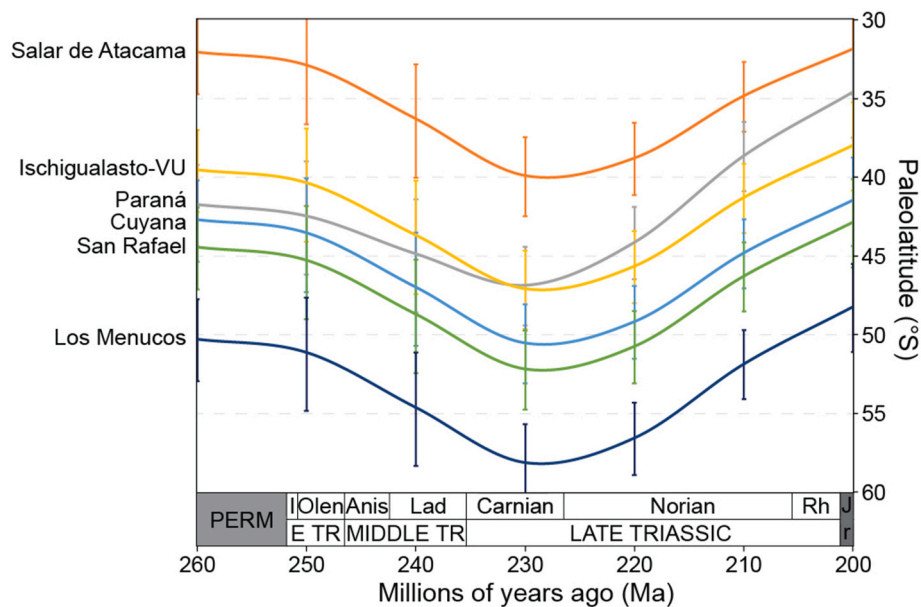
Fig. 3. Approximate Triassic paleolatitudes of key South American basins, with 95% confidence intervals (data from van Hinsbergen et al., 2015).

assemblage (Lutz and Arce 2013), the Quebrada del Barro itself contains a characteristically Late Triassic vertebrate assemblage (Martínez et al., 2015), and it is conformably overlain by the Balde de Leyes Formation, which contains sauropodomorph dinosaurs whose closest relatives are all Early Jurassic in age (Apaldetti et al., 2011; Colombi et al., 2015b). Even though it has received detailed study for less than 10 years, the Quebrada del Barro Formation vertebrate assemblage is already quite diverse, including non-mammalian cynodonts, stem turtles, spheno-dontians, rauisuchid pseudosuchians, early crocodylomorphs and croc-odyliforms, possible pterosaurs, early dinosauromorphs, sauropodomorph dinosaurs, and theropod dinosaurs (Apaldetti et al., 2018; Colombi et al., 2015a; Martínez et al., 2013b; 2015, 2016; Mar-tínez and Apaldetti, 2017).

2.1.3. Cuyana Basin

The Cuyana Basin comprises a series of sub-basins distributed from NNW to SSE in half-grabens that alternate polarity of the master fault (Legarreta et al., 1992) (Fig. 2). Here we focus on those sub-basins and their constituent lithostratigraphic units that meet the following three criteria: i) contain vertebrate fossils; ii) have radioisotopic age con-straints; and iii) preserve published paleoclimate information.

From north to south, the sub-basins are (Fig. 2): a) Cerro Puntudo, the northernmost margin of the basin and filled by the Cerro Puntudo Formation (Mancuso et al., 2010); b) Rincón Blanco, containing the Corral de Piedra Formation within the Rincón Blanco Group (Barredo et al., 2012); c) Paramillos de Uspallata, focusing on the Paramillos and Agua de la Zorra formations that are part of the Cacheuta Group (Har-rington 1971); d) Las Peñas, which preserves the Cerro de las Cabras Formation; and e) Potrerillos, which includes the Río Mendoza, Cerro de las Cabras, Potrerillos, Cacheuta and Río Blanco formations (in ascending order) of the Uspallata Group (Stipanicic 1969; Ávila et al., 2006; Spalletti et al., 2008).

Early studies within the Cuyana Basin proposed the sub-basins were connected during deposition and established lithostratigraphic correla-tions between them using the Uspallata Group lithostratigraphy (Potrerillos sub-basin) for units further north (Strelkov and Alvarez, 1984). Subsequently, other studies provided an accepted chronostrati-graphic framework based on biostratigraphic (Zavattieri 1990a, 1990b; Zavattieri and Arcucci 2007; Brea et al., 2009) and radioisotopic dating (Ávila et al., 2006; Spalletti et al., 2008; Mancuso et al., 2010; Barredo et al., 2012) supporting different ages for deposition intervals within

each sub-basin, therefore indicating it was better to use a separate lithostratigraphic nomenclature for each sub-basin. This temporal and lithostratigraphic framework is followed here and allows us to analyze different paleoclimatic and biotic characteristics of the units through time (Table 1).

2.1.3.1. Cerro Puntudo sub-basin. The Cerro Puntudo Formation pre-serves a typical synrift infill succession with the base of the section formed by coarse alluvial deposits of red conglomerates and pebbly sandstones comprising a basal distal alluvial fan, transitioning to a braided fluvial system with alternating dusky red conglomerates and medium grained to coarse-grained, poorly sorted sandstones. The mid-dle section of the succession is interpreted as a fluvial system of fine-grained to medium-grained sandstones of moderate red color, forming small channels and blackish red mudrocks, interlayered with thin limestones. The uppermost succession is dominated by massive, yellowish grey limestones and stromatolitic limestones, fine-grained very dark red sandstones and mudrocks containing carbonate cement are present with thinner greyish green tuffs. These deposits have been interpreted as sheetfloods in a sandflat and mudflat and gradually transitioning to a carbonate-rich playa lake system (Benavente et al., 2015). The playa lake has been classified as a balanced-fill through flow lake (Benavente et al., 2019). The unit has been U–Pb zircon dated in the lower half section 249.1 ± 9.1 Ma (LA-ICP-MS, Teixeira et al., 2018) and near its top as 243.4 ± 4.0 Ma (SIMS, Mancuso et al., 2010) constraining its deposition to late Early-Middle Triassic (see Irmis et al., this volume for further discussion). The vertebrate assemblage in the Cerro Puntudo Formation is limited to a single pelvic girdle (Mancuso 2009) and footprints from early archosaurs (Benavente et al., 2015).

2.1.3.2. Rincón Blanco sub-basin. The Corral de Piedra Formation con-sists of fine conglomerates and sandstones with trough-cross bedding, lag deposits, and erosive bases that grade upwards into medium fine-grained, moderately to well sorted sandstones/tuffaceous sandstones and reworked tuffs, with thick overbank mudstones at their top and lateral accretion surfaces representing a low energy meandering fluvial system (Barredo et al., 2012) with interspersed ash fall deposits. The unit overlies coarse alluvial fan deposits of the Panul Formation and underlies lacustrine bituminous shale deposits of the Carrizalito For-mation, the latter corresponding to a second reactivation in the sub-basin identified as synrift II (Barredo and Ramos 2010). The Corral

Table 1

Summarized lithostratigraphic, chronostratigraphic, paleoenvironmental, paleoclimatic and vertebrate (body fossil and ichnofossil) data from each South American basin.

Basin	Stratigraphic unit	Age	Depositional environment	Paleoclimate evidence type	Paleoclimate	Vertebrate Assemblage		References
						Body fossil	Ichnofossil	
Argentina								
Ischigualasto-Villa Unión	Talampaya	Lopingian-? Lower Triassic	Ephemeral Fluvial	Sedimentology	Semi-arid		non-mammalian Therapsida	Bonaparte (1997) Caselli (1998) Mancuso et al. (2010) Gulbranson et al. (2015)
	Tarjados	?Lower-Middle Triassic	Ephemeral Fluvial	Sedimentology	Seasonal semi-arid	Dicynodontia Archosauromorpha Archosauria	non-mammalian Cynodontia	Mancuso et al. (2010) Krapovickas et al. (2013) Ezcurra et al. (2015)
	Chañares	lower Carnian	Fluvial Palustrine/ Lacustrine	Sedimentology Clay Mineralogy Stable Isotopes	Seasonal Seasonal sub-humid	Actinopterygii (1) Sarcopterygii (1) Dicynodontia (2) Cynodontia (5) Rhynchosauria (1) Proterochampsidae (3) Pseudosuchia (4) Early Dinosauromorpha(3)		Rogers et al. (2001) Mancuso et al. (2014) Marsicano et al. (2016) Ezcurra et al. (2017) Gouiric-Cavalli et al. (2017) Mancuso and Irmis (2020) Ordoñez et al. (2020) Mancuso et al. (2020a, 2020b)
	Los Rastros	lower Carnian	Lacustrine	Sedimentology Mineralogy Stable Isotopes (lacustrine carbonate $\delta^{18}O$ & $\delta^{13}C$) Paleobotany	Subtropical to temperate seasonal Seasonal sub-humid	Actinopterygii (3) Temnospondyli (1)	Dicynodontia Cynodontia Archosauria (2) Dinosauriformes (3)	Marsicano et al. (2004, 2007, 2010) López-Arbarello et al. (2006) Mancuso and Marsicano (2008) Mancuso and Caselli (2012) Mancuso (2009, 2012) Mancuso et al. (2020a, 2020b)
	Ischigulasto	upper Carnian	Fluvial	Sedimentology (paleosols) Major Element Geochemistry (paleosols) Stable Isotopes (pedogenic carbonate $\delta^{18}O$ & $\delta^{13}C$)	Seasonal sub-humid to semi-arid	Temnospondyli (1) Dicynodontia (2) Cynodontia (7) Rhynchosauria (1) Proterochampsidae (2) Pseudosuchia (1) Early Dinosauromorpha (2) Dinosaur (5)		Moore (2002) Tabor et al. (2004, 2006) Colombi and Parrish (2008) Currie et al. (2009) Colombi et al. (2011) Martínez et al. (2011, 2013a, 2013b) Césari and Colombi (2016)
	Los Colorados	Norian	Fluvial	Sedimentology Paleovertebrate	Seasonal sub-humid	Dicynodontia (1) Cynodontia (1) Testudinata (1) Pseudosuchia (10) Dinosauromorpha (5) Dinosauria (5)	Archosauria	Bossi (1971) Caselli et al. (2001) Arcucci et al. (2004) Kent et al. (2014)
Marayes-El Carrizal	Esquina Colorada Carrizal	Middle Triassic ?Middle and/or Upper Triassic	Alluvial Fan/Fluvial Fluvial	Sedimentology Paleobotany	Seasonal Seasonal subtropical			Bossi (1976) Bossi (1976) Spalletti et al. (2011) Lutz and Arce (2013) Morel et al. (2015)
	Quebrada del Barro	?Norian-Raetian	Distributive Fluvial System	Sedimentology	Seasonal semiarid	Cynodontia (2) Sphenodontia (1) Testudinata (1) Pseudosuchia (3) ?Pterosauria (1) Early Dinosauromorpha (1) Dinosauria (2)		Bossi (1976) Bossi et al. (1975) Colombi et al. (2015a, 2015b) Martínez et al. (2015)
Cuyana	Cerro Puntudo					Pseudosuchia	Archosauria	

Table 1 (*continued*)

Basin	Stratigraphic unit	Age	Depositional environment	Paleoclimate evidence type	Paleoclimate	Vertebrate Assemblage		References
						Body fossil	Ichnofossil	
		Lower-Middle Triassic	Alluvial Fan/Playa Lake	Clay Mineralogy Stable Isotopes (lacustrine carbonate $\delta^{18}O$ & $\delta^{13}C$) Paleobotany	Seasonal semiarid to sub-humid			Sessarego (1988) Mancuso (2009) Mancuso et al. (2010) Benavente et al. (2015, 2019, 2020) Teixeira et al. (2018)
	Corral de Piedra (Portezuelo)	Middle Triassic	Fluvial	Sedimentology	Humid		Dicynodontia (1) Cynodontia (1) Archosauria (1) Dinosauriformes (3)	Marsicano and Barredo (2004) Barredo and Ramos (2010) Barredo et al. (2012)
	Paramillos	Middle Triassic	Alluvial Plain/Fluvial	Paleobotany	Subtropical dry seasonal	Chondrichthyes (1) Temnospondyli (1) Archosauria (1)		Rusconi (1967) Ramos & Kay (1991) Brea (1995) Brea et al. (2009) Johns et al. (2014) Cingolani et al. (2017)
	Agua de la Zorra	Middle-Upper Triassic	Fluvial/Deltaic/ Lacustrine			Actinopterygii (8)		Massabie (1986) Ramos and Kay (1991) Stipanicic and Marsicano (2002) Linares (2007) López-Arbarello et al. (2010) Pedernera et al. (2019)
	Río Mendoza	Lower-Middle Triassic	Alluvial Fan	Sedimentology	Arid Semiarid Humid warm			Strelkov and Alvarez (1984) Spalletti et al. (1999) Artabe et al. (2001) Bellosi et al. (2001) Gallego et al. (2004) Ávila et al. (2006)
	Cerro de las Cabras	Lower-Middle Triassic	Playa Lake	Clay Mineralogy Stable Isotopes (lacustrine carbonate $\delta^{18}O$ & $\delta^{13}C$) Paleobotany	Seasonal semiarid to sub-humid Humid warm	Actinopterygii (4) Dicynodontia (1) Cynodontia (3)	Temnospondyli (1) Dicynodontia (1) Cynodontia (1) Archosauria (2)	Zavattieri (1990a, b, c) Kokogian et al. (1993) Zavattieri and Batten (1996) Marsicano et al. (2004) Ávila et al. (2006) Melchor and de Valais (2006) Zavattieri and Arcucci (2007) Abdala and Ribeiro (2010) López-Arbarello et al. (2010) Domnanovich and Marsicano (2012) Benavente et al. (2015, 2019, 2020) Gouiric-Cavalli et al. (2017) Lagnaoui et al. (2019) Mancuso et al. (2020)
	Potrerillos	Middle-Upper Triassic	Fluvial	Sedimentology Paleobotany	Warm temperate seasonal	Actinopterygii (10) Sarcopterygii (1)		Días and Massabie (1974) Stipanicic (1969) Morel (1991) Brea (1995) Spalletti et al. (1995, 2008) Zavattieri and Batten (1996) Kokogian et al. (2001) Zavattieri and Rojo (2005) Artabe et al. (2007) López-Arbarello et al. (2010) Agnolín et al. (2016)
	Cacheuta	Upper Triassic	Lacustrine	Sedimentology Paleobotany				Stipanicic (1969) Sessarego (1988)

Table 1 (*continued*)

Basin	Stratigraphic unit	Age	Depositional environment	Paleoclimate evidence type	Paleoclimate	Vertebrate Assemblage		References
						Body fossil	Ichnofossil	
					Warm temperate seasonal Humid	Actinopterygii (4) Temnospondyli (3) Archosauriformes (1)		Morel (1991) Brea (1995) Spalletti et al. (1995) Marsicano (1999, 2005) Kokogian et al. (2001) Desojo (2003) Zavattieri and Rojo (2005)
	Río Blanco	Upper Triassic	Lacustrine/Fluvial	Sedimentology Paleobotany	Warm temperate seasonal	Temnospondyli (1)		Stipanicic (1969) Morel (1991) Brea (1995) Spalletti et al. (1995) Marsicano (1999) Kokogian et al. (2001) Artabe et al. (2007)
San Rafael	Quebrada de los Fósiles (Puesto Viejo Group)	Lower-Middle Triassic	Aluvial Fan/ Lacustrine/Fluvial	Sedimentology Paleobotany	Humid to subhumid Warm temperate, strongly seasonal	Dicynodontia (2), Archosauriformes (1)		Bonaparte (1969, 1981, 2000) Valencio et al. (1975) Ramos and Kay (1991) Spalletti et al. (1995, 1997) Abdala et al. (2013) Abdala (1999) Zavattieri et al. (2003, 2020) Domnanovich (2007) Domnanovich and Marsicano (2007, 2012) Ezcurra et al. (2010) Ottone et al. (2014) Monti and Franzese (2016, 2019) Llambías et al. (1993)
	Río Seco de la Quebrada (Puesto Viejo Group)	Middle-Upper Triassic	Fluvial	Sedimentology Paleovertebrate	Humid to subhumid Seasonal	Dicynodontia (2), Cynodontia (3)		Abdala et al. (2013) Domnanovich (2007) Domnanovich and Marsicano (2007 2012) Martinelli et al. (2009) Ottone et al. (2014) Monti and Franzese (2016, 2019) Previtera et al. (2016)
Los Menucos	Vera (Los Menucos)	Lower-Middle Triassic	Ephemeral Fluvial/ Playa Lake/ Volcaniclastic	Sedimentology Paleovertebrate Paleobotany	Seasonal Seasonal subtropical		Temnospondyli (1) Dicynodontia (1) Cynodontia (6) Non-archosaur Diapsida (1) Archosauria (1)	Labudía and Bjerg (2001) Kokogian et al. (2001) Artabe et al. (2001) Domnanovich and Marsicano (2006) Domnanovich et al. (2008) Gallego (2010) Luppo et al. (2018) Citton et al. (2018)
Brazil Paraná	Sanga do Cabral (Sanga do Cabral sequence)	Lower Triassic	Ephemeral Fluvial	Sedimentology (calcretes)	Semi-arid	Temnospondyli (6) Dicynodontia (1?) Cynodontia (1?) Procolophonidae (3) Early Archosauromotpha (1) Early Archosauriformes (2)		Zerfass et al. (2004) Schultz et al. (2020)
	Santa Maria (Pinheiros-Chiniquá sequence)	Middle-Upper Triassic	Ephemeral Fluvial	Sedimentology (calcretes)	Semi-arid with dry predominance	Dicynodontia (2) Cynodontia (11) Procolophonidae (1)		Horn et al. (2014, 2018a, 2018b) Langer et al. (2018)

Table 1 (*continued*)

Basin	Stratigraphic unit	Age	Depositional environment	Paleoclimate evidence type	Paleoclimate	Vertebrate Assemblage		References
						Body fossil	Ichnofossil	
				Major Element Geochemistry (paleosols)		Rhynchosauria (1) Early Archosauriformes (5) Pseudosuchia (2)		Philipp et al. (2018) Schultz et al., (2020)
	Santa Maria (Santa Cruz sequence)	Middle-Upper Triassic	Ephemeral Fluvial			Dicynodontia (1) Cynodontia (5) Early Archosauromorpha (1) Early Archosauriformes (1) Pseudosuchia (1)		Horn et al. (2014, 2018a, 2018b) Langer et al. (2018) Philipp et al. (2018) Schultz et al., (2020)
	Santa Maria (lower Candelária sequence)	Carnian	Lacustrine/Sheet Delta		Semi-arid with marked wet seasons	Actinopterygii (1), Sarcopterygii (1) Temnospondyli (2) Cynodontia (2) Sphenodontia (2) Rhynchosauria (2) Early Archosauriformes (3) Pseudosuchia (5) Early Dinosauromorpha (1) Dinosauria (7)	Sphenodontia	Horn et al. (2014, 2018a, 2018b) Langer et al. (2018) Philipp et al. (2018) Schultz et al., (2020)
	Caturrita (upper Candelária sequence)	lower Norian	Ephemeral Fluvial	Sedimentology (calcretes)	Semi-arid with dry predominance	Temnospondyli (1) Dicynodontia (1) Cynodontia (5) Procolophonidae (1) Sphenodontia (3) Early Archosauromorpha (1) Pseudosuchia (1) Early Dinosauromorpha (1) Dinosauria (5)		Horn et al. (2014, 2018a, 2018b) Langer et al. (2018) Philipp et al. (2018) Schultz et al., (2020)

de Piedra Formation has been dated to 239 ± 16 Ma and the overlying Carrizalito Formation has been U–Pb zircon dated to between 249.5 ± 8.9 Ma and 239.3 ± 3.5 Ma (Barredo et al., 2012). Vertebrate fossils in the Corral de Piedra Formation (in Marsicano and Barredo 2004 in which the unit is named Portezuelo Formation). comprises tracks and trackways from archosaurs (pseudosuchians and dinosauromorphs), cynodonts, and dicynodonts (Marsicano and Barredo 2004).

2.1.3.3. Paramillos de Uspallata sub-basin. The Paramillos Formation is a mainly volcaniclastic unit characterized by conglomerates, and lithic and tuffaceous sandstones with interbedded shales and tuffs (Brea 1995) that represent a fluvial system with an alluvial plain. The unit is most famous for a petrified forest ("Darwin Forest") preserved in growth position by a cooling pyroclastic flow (Brea et al., 2009). The vertebrate paleontological record is limited to teeth of a recent-described hybodontid chondrichthyan species (*Lonchidion paramilloensis*) (Johns et al., 2014). A recent U–Pb zircon (LA-ICP-MS) age of 240 ± 6 Ma was obtained for the lower portion of the Paramillos unit (Cingolani et al., 2017). The overlying Agua de la Zorra Formation consists of bituminous shales and marls with subordinated interbedded fine-grained sandstones and mudstones with interbeded peperitic olivine basalts (Ottone et al., 2011), comprising a fluvial and, lacustrine-deltaic system (Pedernera et al., 2019). The deposits of Agua de la Zorra Formation is interbedded with olivine-rich basalt flows (Ottone et al., 2011) K/Ar dated to 240 ± 10 Ma and 235 ± 5 Ma (Massabie, 1986; Ramos and Kay 1991; Linares 2007), but this age cannot be corrected or re-evaluated because of the complexities of older K/Ar ages (see Irmis et al., this volume). Vertebrate remains of the Agua de la Zorra Formation include the actinopterygian fish of the genus *Guaymayenia* and possible *Gyrolepidoides, Cenechoia, Eurynotus* and *Semionotus* (López-Arbarello et al., 2010), and a possible archosaur (Rusconi 1967).

2.1.3.4. Potrerillos sub-basin. Among the various depocenters of the Cuyana Basin, the stratigraphy of Triassic deposits within Potrerillos sub-basin are the best-studied, having been examined since the early 1900′s (Borrello, 1942; Rolleri and Criado Roqué, 1968; Días and Massabie, 1974; Stipanicic and Bonaparte, 1979; Kokogian and Mancilla, 1989) The currently accepted lithostratigraphic framework places these units in the Uspallata Group, comprising in stratigraphic order the Río Mendoza, Cerro de las Cabras, Potrerillos, Cacheuta, and Río Blanco formations (Stipanicic and Marsicano 2002).

The Río Mendoza Formation unconformably overlies the Permo-Triassic Choiyoi Volcanic Province, and its deposits are mainly red conglomerates with clasts up to boulder size in the lower section and pebble-sized clasts in the upper section. Abundant intrabasinal clasts derive from the underlying Choiyoi Complex (Folguera and Etcheverría, 2004). This unit represents an alluvial fan setting (Kokogian et al., 2001). Radioisotopic dating of what was considered the top of this unit revealed a U–Pb zircon age of 243.5 ± 12.8 Ma (SIMS, Ávila et al., 2006). However, we consider the dated tuff to correspond to the base of the Cerro de las Cabras Formation. The Cerro de las Cabras Formation gradationally overlies the Río Mendoza and consensus is that the lithostratigraphic boundary is placed where finer lithologies dominates over coarse ones (Stipanicic and Marsicano 2002) but both units are part of the same depositional sequence (Kokogian et al. 1993, 2001). The Cerro de las Cabras Formation contains medium and fine greenish sandstones that interfinger with red, green and pink mudstones, siltstones, and limestones, and subordinate conglomerates and pebbly sandstones (Benavente et al., 2015). Tuffs are present throughout the succession but they are more common at the lower and middle part of the section (Stipanicic and Marsicano 2002). The upper part of the section also preserves organic-rich mudstones. These deposits have been interpreted as sheetfloods and ephemeral fluvial system development (Bellosi et al., 2001; Kokogian et al., 2001). The middle section of the unit is dominated by carbonates interbedded with red mudstones and

rarer tuffs that have been interpreted as a sandflat and mudflat subenvironments with development of a carbonate-rich playa lake (Benavente et al., 2015), classified as an underfilled recharge lake (Benavente et al., 2019). Previous biostratigraphic studies suggested a range of ages, with palynomorphs indicating a Middle Triassic age (upper Ansian-Ladinian) (Zavattieri 1990a, 1990b, 1990c, 1991a, 1991b; Zavattieri and Batten 1996) and vertebrates implying an Early Triassic age (Bonaparte 2000; Zavattieri and Arcucci 2007). The only geochronologic age constraint is the previously mentioned U–Pb age from the base of the Cerro de las Cabras Formation (243.5 ± 12.8 Ma). The vertebrate assemblage comprises fish and tetrapods (Table 1), including the actinoperygian genera *Neochallaia, Challaia, Calaichtys* (López-Arbarello et al., 2010; Gouiric-Cavalli et al., 2017), the cynodonts *Cromptodon, Andescynodon* and *Rusconiodon* (Bonaparte 1969, 1971; Abdala and Ribeiro, 2010), indeterminate eucynodonts, and the kannemeyeriid dicynodont *Vinceria andina* (Domnanovich and Marsicano 2012). There are also footprints preserved in the Sierra de las Higueras area (Las Peñas sub-basin) assigned to pseudosuchian archosaurs and non-mammalian therapsids (Marsicano et al., 2004; Mancuso et al. 2020a, 2020b).

The Potrerillos Formation is unconformably separated from the underlying Cerro de las Cabras Formation and comprises conglomerates (Días and Massabie, 1974; Folguera and Etcheverría, 2004; Spalletti et al., 2008), medium to fine grey, yellowish and greenish sandstones, mudstones, coaly to organic-rich mudstones, tuffs, and bentonites. These deposits have been interpreted as braided to meandering fluvial systems grading upwards to deltaic lacustrine systems (Kokogian et al., 2001). The unit has been radioisotopically dated with U–Pb zircon ages of 239.2 ± 8.1 Ma, 239.7 ± 7.2 Ma and 230.3 ± 8.2 Ma from the lower and milddle part of the section (SIMS, Spalletti et al., 2008). The unit preserves actinopterygian fish assigned to the genera *Pseudobeaconia* and *Mendocinichthys*, and possibly *Pholidophorus, Neochallaia, Challaia, Anatoia, Pasambaya, Caminchaia* and *Echentaia* (López-Arbarello et al., 2010). Recently, a dipnoan (sarcopterygian) was reported from this unit for the first time (Agnolín et al., 2016).

The base of the overlying Cacheuta Formation is a gradual transition from the Potrerillos Formation, with alternating fine sandstones, dark mudstones, and tuffs all of light grey color (Stipanicic and Marsicano 2002) that represent a lacustrine system (Kokogian et al., 2001). The palynological assemblage described for the deposits suggests a Late Triassic (Carnian-Norian) age (Zavattieri and Papú 1993). The vertebrate assemblage recorded for the unit include the temnospondyl amphibian *Pelorocephalus*, a brachyopoid temnospondyl (Marsicano 1999, 2005), the archosauriform *Cuyosuchus* (Desojo et al., 2002) and fish the actinoperygian fish genera *Gyrolepidoides, Challaia*, '*Semionotus*', and *Amblypterus* (López-Arbarello et al., 2010).

The Río Blanco Formation is formed by fine grained conglomerates medium grained sandstones, mudstones, tuffaceous mudstones; these sediments are grayish and yellowish color in the lower part of the section and are replaced by pink, purple and red colors higher up. These deposits have been interpreted as a fluvial deltaic lacustrine system (Kokogian et al., 2001). The unit is dated to the Late Triassic because it overlies the Upper Triassic Cacheuta Formation (Stipanicic and Marsicano 2002). Vertebrate remains are limited to the temnospondyl amphibian *Pelorocephalus* (Marsicano 1999).

2.1.4. San Rafael Basin

The Triassic deposits of this basin in southern Mendoza Province (Fig. 2) comprise the Puesto Viejo Group (Stipanicic et al., 2007) divided into the lower Quebrada de los Fósiles and upper Río Seco de la Quebrada formations. The Quebrada de los Fósiles Formation preserves conglomerates interbedded with fine to medium grained sandstones, an ignimbrite, peperitic basalt, mudstones and siltstones in a fining-upward succession. These deposits have been interpreted, in stratigraphic order, as an alluvial fan, fluvial system with alluvial plain development and lacustrine system (Ottone et al., 2014; Monti and Franzese 2016, 2019).

A new LA-ICPMS U–Pb zircon date of 243.5 ± 11.8 Ma from the rhyolitic ignimbrite at the base of Quebrada de los Fósiles Formation suggests a maximum age of Early to Middle Triassic (Monti et al., 2018). The top of the formation is constrained by U–Pb zircon ages of 238.6 ± 4.5 Ma and 235.8 ± 8.8 Ma from an ignimbrite at the boundary between it and the overlying Río Seco de la Quebrada Formation (LA-ICPMS, Domeier et al., 2011; SIMS, Ottone et al., 2014).The paleontological assemblage of this lower unit consists of plant remains and two tetrapods, the dicynodont *Vinceria* and the early archosauriform *Koilamasuchus* (Domnanovich 2007; Domnanovich and Marsicano 2007, 2012; Ezcurra et al., 2010).

The overlying Río Seco de la Quebrada Formation comprises ignimbrites, conglomerates, coarse-grained sandstones, siltstones, andesites, and tuff. The deposits have been interpreted as an alluvial system with floodplain development disrupted by lava flows (Ottone et al., 2014; Monti and Franzese 2016, 2019). The unit's age is constrained by the previously mentioned U–Pb dating of the ignimbrite at its base, suggesting the formation is no older than Middle Triassic. The tetrapod record of this unit is more diverse than the undrerlying formation, and was correlated to the *Cynognathus* AZ based on cynodonts *Cynognathus* and *Diademodon*, and the dicynodont *Kannemeyeria* (Bonaparte, 1969; 2000; Martinelli et al., 2009). The assemblage also includes the dicynodont *Vinceria* and the cynodont *Pascualgnathus* (Martinelli et al., 2009; Domnanovich and Marsicano 2012).

2.1.5. Los Menucos Basin

This basin is located in the northern part of the North Patagonian Massif (Fig. 2). The Triassic deposits of the basin are mainly volcaniclastics dominated by tuffs with subordinate conglomerates, sandstones, and mudstones distributed in two units: the Vera Formation and overlying Sierra Colorada Formation, forming the Los Menucos Group (Labudía and Bjerg 2001; Stipanicic and Marsicano, 2002). The Vera Formation comprises interstratified conglomerates, sandstones mudstones, tuff and pyroclatic flows (Labudía and Bjerg 2001) whereas the Sierra Colorada Formation preserves ignimbrites. The Vera deposits are interpreted as fluvial systems and ephemeral lacustrine systems affected by volcanism (Kokogian et al., 2001). The Vera Formation paleontological record include a very rich palaeofloral assemblage including *Dicroidium* and abundant footprint assemblages made by pseudosuchian archosaurs, temnospondyls, lepidosauromorphs and therapsids (Domnanovich and Marsicano 2006; Domnanovich et al., 2008; Citton et al., 2018). Recently, the lower, middle, and upper Los Menucos Group has been radioisotopically dated with U–Pb zircon ages to 257 ± 6.2 Ma, 251.6 ± 6.1 Ma, and 248.3 ± 5.6 Ma respectively (SIMS, Luppo et al., 2018). A recent stratigraphic review of the Los Menucos Group support their subdividing into Puesto Tscherig Formation, Puesto Vera Formation and Sierra Colorada Formation (Falco et al., 2020). The footprints occur in the Late Permian to Early Triassic Puesto Tscherig and Puesto Vera formations.

2.2. Brazil

2.2.1. Paraná Basin

The Triassic deposits of southern Brazil crop out in the central region of Rio Grande do Sul State, as part of the Paleozoic-Mesozoic Paraná Basin, which is a large intracratonic basin that occupies most of the southern portion of Brazil and parts of Uruguay, Paraguay and Argentina. The basin is divided in five supersequences (Milani et al., 2007), the Rio Ivaí (Silurian), Paraná (Devonian), Gondwana I (Carboniferous-Permian), Gondwana II (Triassic) and Gondwana III (Cretaceous). The rocks of the Gondwana II Supersequence were later divided in two supersequences, the Sanga do Cabral and Santa Maria (Zerfass et al., 2004).

The Sanga do Cabral Supersequence is a tectonically controlled, second-order allostratigraphic unit, whose dominant facies association comprises intraformational massive or trough cross-bedded conglomerate, and horizontal bedded sandstones, sometimes with chute and pool structures and cyclic steps. These facies are interpreted as low-sinuosity, high energy, sheetflow-dominant rivers (Zerfass et al., 2004). This unit is biostratigraphically dated to the Early Triassic by the presence of the parareptile *Procolophon*, and its corresponding lithostratigraphic unit is the Sanga do Cabral Formation. In addition to this taxon, the unit also preserves body fossils of temnospondyl amphibians, dicynodonts, cynodonts, and rhynchosaurian archosauromorphs.

The overlying Santa Maria Supersequence is divided by sedimentological and biostratigraphic data into four sequences, the Pinheiros-Chiniquá, Santa Cruz, Candelária and Mata (Horn et al., 2014). The sedimentation patterns change between the sequences. All sequences began with an ephemeral braided river system (Horn et al., 2018a), probably caused by tectonic rearrangement of the basin (Zerfass et al., 2004, 2005). The Pinheiros-Chiniquá and Santa Cruz sequences have a predominantly eolian depositional environment, mostly comprising meter-scale massive silt layers, interpreted as large dry flats in which loessic sediments are reworked by sparse ephemeral flows.

The overlying Candelária Sequence began with distal sheetfloods laterally deposited with underfilled lacustrine deposits. Towards the top of the sequence, sandstones dominate with the initiation of an ephemeral, mass-flow dominated river system (Horn et al., 2018b). Recent detrital zircon U–Pb ages constrain the age of some of these sequences, with a Santa Cruz Sequence age of 236.3 ± 7.0 Ma (LA-ICPMS, Philipp et al., 2018) and ages of 233.2 ± 0.5 Ma and 226 ± 0.3 Ma for the lower and upper Candelária Sequence, respectively (CA-TIMS, Langer et al., 2018). From a lithostratigraphic viewpoint, the Pinheiros-Chiniquá, Santa Cruz, and lower Candelária sequences correspond to the Santa Maria Formation, the upper Candelária Sequence is equivalent to the Caturrita Formation, and the Mata Sequence is the Mata Sandstone (Schultz et al., 2020: Fig. 1).

The Santa Maria Supersequence preserves a rich vertebrate body fossil assemblage that has been studied for over 100 years. The Middle-Upper Triassic Pinheiros-Chiniquá Sequence contains fossils of dicynodonts, cynodonts, procolophonids, rhynchosaurs, early archosauriforms, and pseudosuchian archosaurs (Schultz et al., 2020, Table 1). This assemblage is formalized as the *Dinodontosaurus* Assemblage Zone, and shares many faunal similarities with the penecontemporaneous Chañares Formation in northwestern Argentina (e.g., Abdala et al., 2013; Mancuso and Irmis 2020). The ?Carnian Santa Cruz Sequence also preserves dicynodonts, cynodonts, early archosauromorphs, early archosauriforms, and pseudosuchian archosaurs and comprises the *Santacruzodon* Assemblage Zone (Schultz et al., 2020, Table 1). The Carnian lower Candelária Sequence is particularly diverse, with both actinopterygian and sarcopterygian fishes, temnospondyl amphibians, cynodonts, sphenodontians, rhychosaurs, early archosauriforms, pseudosuchians, early dinosauromorphs, and some of the earliest dinosaur body fossils in the world (Schultz et al., 2020, Table 1), as well as small reptile footprints (da Silva et al., 2008). This assemblage is known as the *Hyperodapedon* Assemblage Zone, and is very similar in age and faunal content to the lower Ischigualasto Formation of northwestern Argentina (e.g., Langer 2005a,b; Langer et al., 2018). The early Norian upper Candelária Sequence preserves a similar vertebrate assemblage in terms of clades represented, with body fossils of temnospondyl amphibians, dicynodonts, cynodonts, procolophonids, sphenodontians, early archosauromorphs, pseudosuchians, early dinosauromorphs, and dinosaurs (Schultz et al., 2020, Table 1), as well as large dinosauromorph footprints (da Silva et al., 2012). These fossils, which comprise the *Riograndia* Assemblage Zone, appear to overlap in time with the upper Ischigualasto Formation and/or lower Los Colorados Formation in northwestern Argentina (Langer et al., 2018). No vertebrate fossils have been reported from the Mata Sequence/Sandstone.

2.3. Chile

2.3.1. Salar de Atacama Basin

Chile possesses a number of early Mesozoic basins containing non-marine Triassic sedimentary strata, but vertebrate fossils have only been reported from a single location, the Sala de Atacama Basin in the Antofagasta region of northern Chile. Here, in the area surrounding Cerro Químal, a thick sequence (>4500 m) of Triassic volcanics, volcaniclastics, and interbedded sediments comprise the 'El Bordo beds.' These strata were informally divided into four numbered units by Basso and Mpodozis (2012), of which unit 4 represents the uppermost ~300 m and preserves vertebrate remains. This unit preserves fine to medium-grained well-stratified partly laminated multicolored quartz to quartz-feldspar sandstones, alternating with ferrunginous calcareous horizons, grey spary limestones with ostracods and ooids that are sometimes carbonaceous or laminated, fissile grey shales (sometimes silicified) rich in ostracods and pisoids, and dark grey chert (Basso and Mpodozis 2012: pg. 10). The sediments are interstratified with <1 m thick vitric tuffs and andesitic lavas. This sequence is interpreted as a lacustrine depositional system influenced by volcanic activity (Basso and Mpodozis 2012). Breitkreuz and colleagues (Breitkreuz 1991; Breitkreuz et al., 1992; Breitkreuz and Zeil 1994) described similar facies in their studies, but used a different lithostratigraphic scheme, so it's unclear exactly which part of the El Bordo beds their sections correspond to. Plant macrofossil assemblages from units 2 and 4 suggest a Triassic age (Ramírez and Gardeweg 1982; Basso and Mpodozis 2012), and CA-TIMS U–Pb zircon ages date the upper part of unit 1 to 240.8 ± 0.6 Ma and 238.7 ± 0.4 Ma (Basso and Marinovic 2003; Basso and Mpodozis 2012). This suggests that the vertebrate fossils in the stratigraphically higher unit 4 are no older than late Ladinian in age. At least some of these vertebrate fossils are preserved in the pisolitic silicified shales (RBI, personal observation); the assemblage includes the associated skeletons of the putative aetosaur *Chilenosuchus forttae* (a pseudosuchian archosaur) (Casamiquela 1980; Desojo 2003), and a silesaurid dinosauromorph (Rubilar-Rogers et al., 2013).

2.4. Bolivia

2.4.1. Incapampa-Icla Syncline

Previously thought to be Jurassic-Cretaceous in age, new radioisotopic and geochemical age constraints from CAMP volcanics and intrusives indicate the presence of Triassic redbeds in the Incapampa-Icla Syncline of the Chuquisaca Department, southern Bolivia (Sempere et al. 2002, 2004; Bertrand et al., 2014; Davies et al., 2017). This necessitated a relevaluation of various tracksites in the Ipaguazú Formation (Sempere et al., 2004; Apesteguía and Gallina 2011), which are now assigned to the classic Upper Triassic archosaur ichnotaxon *Brachychirotherium* (Apesteguía et al. in press). This sequence is dominated by trough cross-bedded fine-grained sandstones with some ripple laminations and horizontally-bedded layers, and rarer massive mudstones. They are interpreted as an aeolian depositional setting with occasional ephemeral flashy flood deposits (Apesteguía et al. in press). The minimum age of the formation is constrained to latest Triassic by radioisotopic ages ranging from ~202 to 198 Ma for CAMP intrusives and lava flows (Sempere et al., 2004; Bertrand et al., 2014; Davies et al., 2017), but no maximum age constraints are available.

3. Paleoclimate evidence

3.1. Argentina

Paleoclimate evidence for the Triassic of Argentina is mostly based on single proxy studies, particularly paleobotanical (micro- and macrofloral) studies (Zavattieri 1990c; Zavattieri and Batten, 1996; Artabe et al., 2007; Brea 1995; Brea et al., 2009), but also includes evidence from fauna, sedimentology, paleosols, and geochemistry (Krapovickas

et al., 2013; Gulbranson et al., 2015). Only few recent contributions have attempted a multiproxy approach (Benavente et al. 2015, 2019, 2020,2021 ; Mancuso et al. 2020a, 2020b).

3.1.1. Ischigualasto-Villa Unión Basin

The basin developed between 38.2°S to 47.3°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). The widely exposed Upper Permian-Lower Triassic Talampaya Formation displays similar sedimentological characteristics across the basin (Caselli 1998). These sedimentological features, such as mud-cracks, evidence of eolian-fluvial interaction, and carbonate concretions, are interpreted as evidence of arid to semi-arid conditions (Caselli 1998). Particularly in the Cuesta de Miranda area, where the radioisotopic age was obtained, the vertical stacking of facies associations suggests a progressive lowering of the base level and a transition from humid to semiarid or arid conditions (Gulbranson et al., 2015).

The red beds of the overlying Tarjados Formation were deposited in an ephemeral fluvial system interbedded with eolian and playa lake deposits. This interpretation is supported by a variety of sedimentological features, such as desiccation mud-cracks, carbonate nodules, and eolian deposits. Thus, the evidence suggests that water supply in the Tarjados was strongly seasonal, probably under an overall semi-arid climatic regime (Krapovickas et al., 2013).

The Carnian Chañares-Los Rastros succession has a multiproxy paleoclimate interpretation based on sedimentology, clay mineralogy assemblages, paleontological content, and C and O stable isotope of lacustrine limestone data from the same strata. These integrative data suggest warmer and more humid condition than before or after, also provide evidence that the Carnian Pluvial Episode interval in western Gondwana was indeed warmer and more humid than before or after (Mancuso et al. 2020a, 2020b). These data are consistent with inferences from palynofloral assemblages for the two units, both of which suggest a relatively humid climate, but with the Los Rastros implying warmer conditions than in the Chañares Formation (Zavattieri and Batten 1996; Zavattieri and Melchor 1999; Ottone et al., 2005; Perez Loinaze et al., 2018).

The upper Carnian-lower Norian Ischigualasto Formation is interpreted as a moderate sinuosity fluvial system with broad floodplain and paleosol development (Currie et al., 2009; Colombi et al., 2017). Like the underlying Chañares-Los Rastros sequence, this unit has been studied using multiple proxies, including paleontology (mega- and microfloral assemblages), sedimentology and pedogenic (type of paleosols), and geochemistry. These data suggest seasonal semi-arid conditions, with evidence of semi-humid but cooler conditions in the Valle de la Luna Member (Tabor et al. 2004, 2006; Colombi and Parrish 2008; Colombi et al., 2011; Césari and Colombi, 2013; 2016; Perez Loinaze et al., 2018).

Interpretations are more diverse for the uppermost unit of the group, the Norian Los Colorados Formation, with previous authors suggesting a sandy fluvial system with alluvial plains (Bossi 1971; Stipanicic and Bonaparte 1979), ephemeral streams with interbedded eolian dunes (López-Gamundí et al., 1989; Cladera et al., 1998), and general arid climatic conditions (Milana and Alcober 1994). The arid climate previously interpreted for the Los Colorados Formation was mainly based on red color of the sediments rather than any specific sedimentological or geochemical indicators of aridity (López-Gamundí et al., 1989; Milana and Alcober 1994; Cladera et al., 1998). A detailed sedimentological analysis of the Los Colorados Formation supported the interpretation of moderately sinuous fluvial systems, which laterally interfinger with and grade into horizontally-bedded flood-plain deposits, thin-bedded sandstones and silts deposited in ponds and crevasse splays in overbank settings (Caselli et al., 2001; Arcucci et al., 2004). There is no clear evidence of aridity such as intraclast breccias, desiccation cracks, and eolian or evaporite lenses. The presence of thick alluvial deposits that represent episodic flows and high precipitation suggest humid or sub-humid conditions as previously proposed by Bossi

(1971). Moreover, petrographic analysis of the sandstones suggested that their red color is related to oxidation processes during early diagenesis (Caselli et al., 2001; Arcucci et al., 2004), which does at least indicate these sediments were relatively well-drained, and may still be paleoclimatically informative (cf. Lepre and Olsen, 2021).

3.1.2. Marayes-El Carrizal Basin

The basin developed between 39.5°S to 49.0°S paeolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). The Carrizal Formation sedimentology (braided fluvial system with marked changes in discharge and sediment supply) and paleontology (predominance of corystosperms that indicate mesoxerophytic paleocommunities, and dominated by ferns and Equisetales, indicate a paleocommunity formed under mesohydrophytic conditions) data from the unit has been interpreted as an indicator of seasonal climate condition (Bossi 1976; Spalletti et al., 2011; Morel et al., 2015). The Quebrada del Barro Formation sedimentology (calcic-Argillisols in the medial-distal zone of a distributary fluvial system) data suggest seasonality and arid conditions (Bossi 1976; Colombi et al. 2015a, 2015b).

3.1.3. Cuyana Basin

The basin developed between 41.1°S to 50.1°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). Paleoclimate evidence for the Early-Middle Triassic portion of the Cuyana Basin comes from the Cerro Puntudo (Cerro Puntudo sub-basin), Río Mendoza, and Cerro de las Cabras formations (Potrerillos and Las Peñas sub-basins) (Ávila et al., 2006; Mancuso et al., 2010). The Río Mendoza Formation has been interpreted as being deposited in an arid to semi-arid, warm paleoclimate based on its sedimentological characteristics (a strongly seasonal fluvial environment) and paleontological content (fauna and flora living in and around semi-permanent water bodies) (Gallego et al., 2004).

The Cerro Puntudo and Cerro de las Cabras units both record carbonate-rich lacustrine systems with hydrology open to groundwater input. Paleoclimate inferences for these successions are based on the integration of mineralogical, sedimentological, paleontological, and C and O stable isotope data. Clay assemblages are dominated by smectite and Vertisol paleosols have been identified as part of a mudflat subenvironment surrounding paleolake margins (Benavente et al. 2015, 2020). Both features point to an arid seasonal climate regime (Singer 1980). C and O stable isotope values coupled to sedimentological features have revealed that the lacustrine system experienced water level fluctuations controlled by dilution effect due to meteoric water input and evaporation. Nevertheless, the systems record an overall positive hydrologic balance (Benavente et al., 2019). This means that despite the arid seasonal conditions, groundwater input maintained a permanent water body at least at the Cerro Puntudo sub-basin, in which sedimentology reveals no desiccation features for lacustrine facies associations (Benavente et al. 2012, 2015). Even though the lacustrine systems cover a the entire northern area of the Cuyana Basin, the arid seasonal conditions interpreted for these localities may in part reflect a possible rain shadow effect caused by the highlands to the west of the basin (tectonic control) and not simply a regional paleoclimate pattern (Benavente et al., 2015).

Additional information for the Cerro de las Cabras Formation in the Las Peñas sub-basin comes from sedimentology, mineralogy, and tetrapod track taphonomy. In this area, the unit consists of sandstones, siltstones and mudstones interpreted as sandflat and mudflat subenvironments with ephemeral sheetflood water input (Mancuso et al. 2020a, 2020b). The clay assemblages from this unit are dominated by smectite and subordinate illite, also pointing to an arid seasonal climate regime (Singer 1980). This sub-basin is located outside of the inferred rain shadow effect thus implying a regionally arid climate pattern. However, in this area, tetrapod footprint preservation suggests there is also a record of more extended wet periods than drier ones (Mancuso et al. 2020a, 2020b).

These climate interpretations disagree with previous interpretations of a humid and warm climate based on palynofloral assemblages that preserve hygrophytic taxa (Zavattieri 1990c). We suggest that this mismatch could reflect the fact that the floral data are indicators for local sub-environments rather than regional paleoclimate interpretations, or perhaps record the wetter intervals observed from the Las Peñas study area. This reinforces the need to apply multiple proxies to assess paleoclimate patterns.

The Middle-Late Triassic paleoclimate of Argentina is recorded in the Cuyana Basin within the Corral de Piedra Formation (Rincón Blanco sub-basin) (Barredo et al., 2012), the Paramillo Formation (Paramillo de Uspallata sub-basin) (Ramos and Kay 1991; Cingolani et al., 2017), the Potrerillos Formation (Potrerillos sub-basin) (Spalletti et al., 2008). Interpretations for these units are typically supported by single indicators only, therefore reliable paleoclimate conditions for SW Gondwana during this time are lacking.

For the Corral de Piedra Formation, a humid climate has been inferred presumably based in its sedimentological characteristics (meandering fluvial system with thick mud-dominated floodplains) and attributes of the other units of the Rincón Blanco Group (Barredo and Ramos 2010). For the Paramillo Formation, the macrofloral composition of the "Darwin Forest" coupled with sedimentological data (sinuous fluvial system, with channel-filling sand bodies associated with mud-dominated floodplain deposits) and tree growth ring studies have been interpreted as indicators of a warm temperate seasonally dry regime (Brea et al., 2009), with occasional frosts during the cold season (Brea, 1995). The paleofloral composition of the Potrerillos Formation has been characterized and interpreted as representing a monsoonal climate regime (Artabe et al., 2007), whereas the microfloral assemblage has been considered an indicator of warm sub-humid to temperate climate conditions with seasonality (Volkheimer and Zavattieri 1985; Zavattieri 1987; Zavattieri and Rojo 2005). Analysis of freshwater algae from the upper part of the Potrerillos Formation suggests perennially wet, poorly drained conditions (Zavattieri and Prámparo 2006). This interpretation was supported by a recent combined analysis of fossil insect, floral, and sedimentological data (Lara et al., 2017).

The overlying ?Carnian Cacheuta Formation (Potrerillos sub-basin, Cuyana Basin) preserves a microfloral and algal assemblage that has also been interpreted as indicative of a warm temperate paleoclimate regime (Zavattieri and Rojo 2005) with perennially wet, poorly drained conditions (Zavattieri and Prámparo 2006). The Río Blanco Formation, at the top of this sequence, preserves a paleofloral assemblage suggesting a warm temperate climate regime with a dry season (Spalletti et al., 1995; Artabe et al., 2007).

3.1.4. San Rafael Basin

The basin developed between 42.8°S to 52.2°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). The Puesto Viejo Group has been interpreted as accumulation during humid to subhumid paleoclimate conditions based on sedimentological characteristics (fluvial and lacustrine deposits) (Kokogian et al., 2001; Ottone et al., 2014). In particular, the Quebrada de los Fósiles Formation was interpreted developed under warm humid to temperate, strongly seasonal climatic conditions based on the microfloral and algal (Ottone and Garcia 1991; Zavattieri et al. 2003, 2020). A fluctuating water table with alternation of wet/dry conditions was proposed for the overlying Río Seco de la Quebrada Formation based on fossil bone diagenesis (Previtera et al., 2016).

3.1.5. Los Menucos Basin

The basin developed between 48.2°S to 58.1°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). Within the Los Menucos Basin, the Vera Formation sedimentology (fluvial systems associated with marshes and shallow ephemeral lakes) and paleontology (low diversity/high density spinicaudatan assemblage is typical of ephemeral waters with stressed conditions) data has been

interpreted as indicator of seasonal climate conditions with alternating periods of dry and wet conditions (Kokogian et al., 2001; Gallego 2010). The macrofloral record of the Vera Formation is characterized as seasonal and subtropical (Artabe et al., 2001).

3.2. Brazil

3.2.1. Paraná Basin

The basin developed between 34.6°S to 46.9°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). There are no published contributions investigating in detail the paleoclimate of the Lower Triassic Sanga do Cabral Sequence, but sedimentological evidence of ephemeral fluvial channels, eolian sandstones, and calcretes (typically developed under arid to semi-arid climates in the modern), suggest a semi-arid to arid climate (Holz and Scherer 2000), probably with long dry seasons and few wet intervals that activated the river system.

Among earlier work in the basin, Minello (1994) used fossil wood anatomy to infer an arid climate for the Santa Maria and Caturrita formations, and a contribution on the taphonomy and diagenesis of fossil bone from the Pinheiros-Chiniquá Sequence (lower Santa Maria Formation) by Holz and Schultz (1998) inferred a seasonal semi-arid climate with a fluctuating water table. The first explicit paleoclimate work on the Santa Maria Supersequence was Holz and Scherer (2000), which utilized a synthesis of sedimentological and paleontological proxies. They concluded that the presence of ephemeral braided channels, calcretes, and a lack of aquatic fauna were paleoclimatic proxy evidence for semi-arid conditions in the Pinheiros-Chiniquá Sequence. Subsequent work on the calcretes (Silvério da Silva, 1997; Da Rosa et al., 2004; Horn et al., 2013) corroborated this conclusion. Holz and Scherer (2000) inferred gradually more humid, but still seasonal, conditions in the Santa Cruz, lower Candelária, and upper Candelária sequences (middle-upper Santa Maria, Caturrita, and Mata formations), as fluvial architecture transitioned to perennial braided, anastomosing, and meandering channels, with floral evidence of humidity, but noted that most water bodies were likely still seasonal for most of this succession.

More recently, a wider variety of proxies have been applied to understanding the paleoclimate of the Santa Maria Supersequence. Evidence from sedimentology, petrography, clay mineralogy, Chemical Index of Alteration (CIA), fossil wood anatomy, and fossil charcoal all point to a hot, semi-arid and seasonal climate with a fluctuating water table for the Pinheiros-Chiniquá, Santa Cruz, and lower Candelária sequences (Santa Maria Formation) (Pierini et al., 2002; Da Rosa et al., 2004; Bardola et al., 2009; Cardoso et al., 2018; Horn et al. 2018a, 2018b; Rodrigues et al., 2019). New geochemical data obtained by Corecco et al. (2020) suggests evidence for more variability. They showed that there were significant changes from the lower portion of the Santa Maria Supersequence (Pinheiros/Chiniqua and Santa Cruz sequences), which were deposited under more basic and dried environmental conditions as indicated by Ca and Ba concentrations, to the lower portion of the Candelaria Sequence, characterized by more acidic and humid conditions, recorded by an increase in Al, Si, and Sr. Horn et al. 2018a, 2018b observed sedimentological evidence for wetter conditions in the lower-middle part of the Candelária Sequence, perhaps associated with the Carnian Pluvial Episode, but the accompanying CIAm data did not show a shift to more humid values. Paleoclimate data for the upper Candelária Sequence (Caturrita Formation) also suggest warm seasonal conditions, with some evidence of relatively more humid conditions (Pierini et al., 2002; Pires et al., 2005; Crisafulli et al., 2016; Cardoso et al., 2018; Horn et al. 2018a, 2018b).

A review of sedimentary features is also consistent with the idea of seasonal water availability. The presence of mud chips, mud clasts, sometimes with plant fossils and sedimentary structures indicating waning flow (e.g., climbing ripples, Froude transcritical to supercritical structures) are characteristic features of river discharge caused by concentrated rainfall (Allen et al., 2014; Plink-Björklund 2015). The

presence of well-preserved, articulated or semi-articulated fossils along with disarticulated, poorly-preserved, deteriorated bones with insect marks imply distinct burial times (Paes Neto et al., 2016), indicating variable sedimentation rates and, consequently, water supply. Modern examples of riverine systems similar to those in Brazilian Triassic occur where the total annual precipitation falls in a few downpours that lasts from a few hours to a few days intercalated with dry periods that can last for a large portion of the year or even decades (Sneh 1983; Stear 1985; Plink-Björklund 2015).

3.3. Chile

3.3.1. Salar de Atacama Basin

The basin developed between 32.0°S to 40.0°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). No studies have specifically focused on the paleoclimate of the Triassic sediments in the Salar de Atacama Basin. Several workers have inferred a warm and humid tropical paleoclimate for the El Bordo beds on the basis of sedimentological (widespread lacustrine conditions and lack of evaporites) and paleontological data (macrofloral and ostracod assemblages) (Ramírez and Gardeweg 1982; Breitkreuz 1991; Breitkreuz et al., 1992; Breitkreuz and Zeil 1994; Basso and Mpodozis 2012).

3.4. Bolivia

3.4.1. Incapampa-Icla Syncline

The basin developed between 27.5°S to 36.5°S paleolatitude (Fig. 3) (including 95% confidence intervals) (van Hinsbergen et al., 2015). No paleoclimatic studies have been conducted on the track-bearing Ipaguazú Formation in southern Bolivia, but the presence of eolian dune deposits occasionally interrupted by brief flashy flooding events (Apesteguía et al. in press) broadly suggests a seasonal semi-arid to arid climate.

4. Evolution of Triassic climate in western Gondwana

Global studies of Triassic paleoclimate typically take one of two complimentary but separate strategies, either mapping the distribution of proxy data (e.g., Robinson 1973; Parrish et al., 1982; 1986; Golonka 2007; Golonka et al., 2018; Boucot et al., 2013), or using global climate models (GCMs) to infer past climate variables based on our knowledge of modern climate systems (e.g., Parrish and Curtis 1982; Kutzbach and Gallimore 1989; Wilson et al., 1994; Huynh and Poulsen 2005; Péron et al., 2005; Sellwood and Valdes 2006; Winguth and Winguth 2012; Winguth et al., 2015; Harris et al., 2017; Dunne et al., 2021). Most examples of the latter focus on aspects of temperature and precipitation, but there are also classes of models that reconstruct the spatial distribution of weathering fluxes and vegetation and their relationship to atmospheric CO_2 (e.g., Donnadieu et al., 2006; 2009; Goddéris et al., 2008; 2014; Goddéris and Donnadieu 2019). Other studies have applied modern climate zonations to paleolatitudinal data, and the compared them with available proxy data (e.g., Kent and Tauxe 2005; Whiteside et al., 2011).

During the Triassic Period, modeling suggests enhanced monsoonal circulation because of the large exposed land area across the equator (Kutzbach and Gallimore 1989; Parrish 1993; Wilson et al., 1994; Péron et al., 2005; Sellwood and Valdes 2006; Holz 2015; Harris et al., 2017). The monsoonal model predicts three general climatic zones: (1) relatively wet conditions along the northern Tethys and west coast of the Panthalassa Ocean; (2) alternating wet and dry seasons along the coastlines of western Laurasia and Gondwana and the western coast of the Tethys; and (3) arid continental interiors between ~5 and 45° latitude (Parrish 1993; Wilson et al., 1994; Sellwood and Valdes 2006; Preto et al., 2010; Holz 2015; Harris et al., 2017; Dunne et al., 2021). Further model and proxy data for the Late Triassic indicate hot and humid conditions in the equatorial belt, an increasingly hot, arid, and seasonal
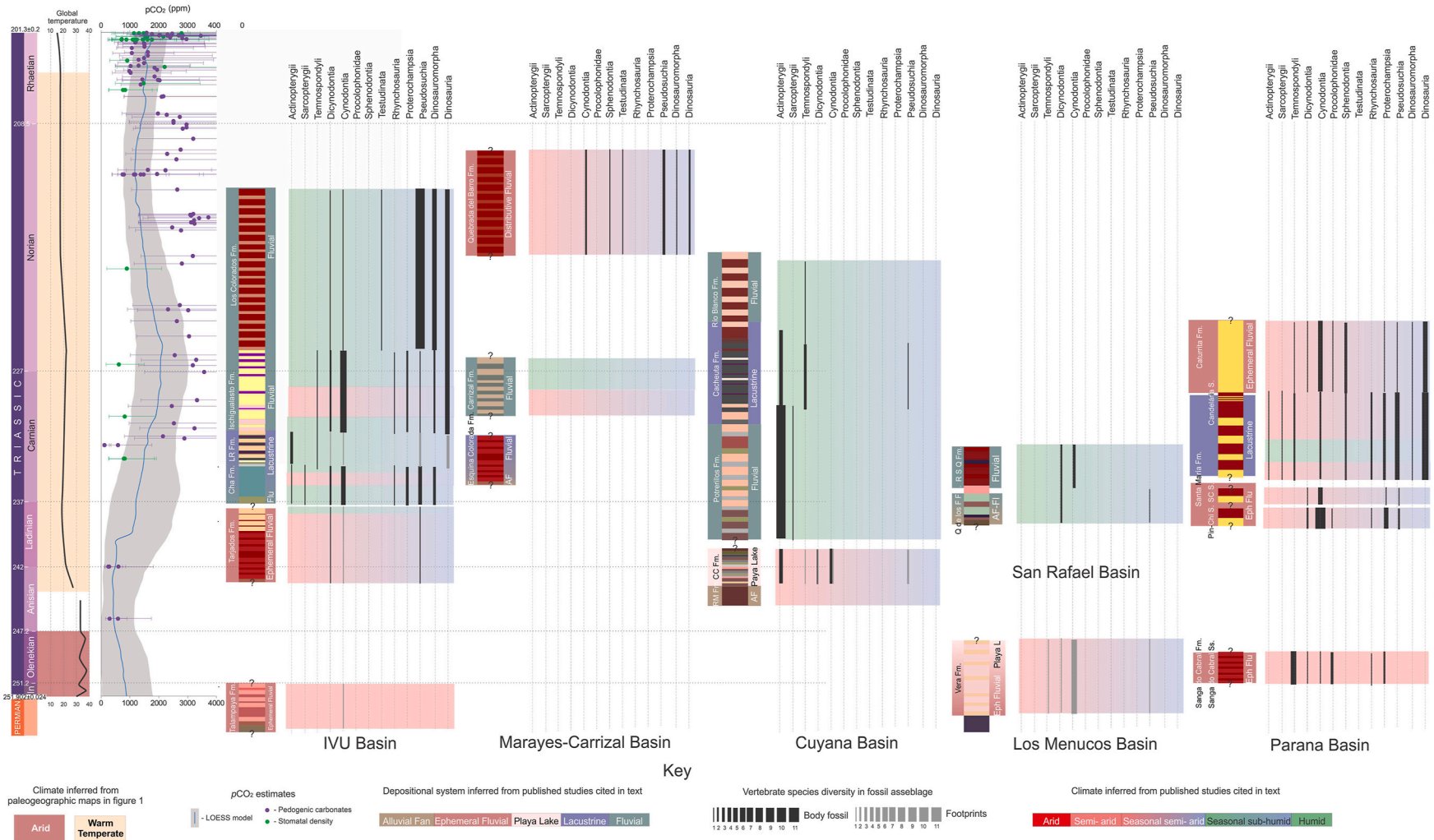
Fig. 4. Summary of Triassic climate and vertebrate assemblages from South America. The global climate inferred from lithological evidence is superposed with relative global temperature (redrawn from Sun et al., 2012 and Veizer et al., 2000). The pCO$_2$ curve includes both proxy data (purple and green points) and the LOESS model curve (blue line with grey 95% confidence interval envelope), re-plotted from Foster et al., (2017). The colored columns for each basin represent the distribution of the units with their characteristic colors. The chronostratigraphic distribution of the basin fill is supported by radioisotopic ages where available (for more detail information see Irmis et al. in the same volume). The depositional system inferred for each basin lithostratigraphic unit is superimposed with colored columns. The climate inferred for each basin lithostratigraphic unit is superimposed with the body fossil and ichnofossil vertebrate fossil record for each major clade.

environment above 5°, and a temperate, more humid climate above 30° (Kent and Tauxe 2005; Whiteside et al. 2011, 2015). These climate predictions correspond well with inferred Triassic floral provinces (Fig. 1; Kustatscher et al., 2018). Overall, these data indicate that the common perception of a globally hot, dry, and seasonal climate during the Triassic Period is largely an artifact of observational bias. In particular, compilations of Triassic paleoclimate in Gondwana usually have poor spatial/temporal resolution that are inadequate for comparison with global interpretations. Once climate patterns are apparent, further difficulties arise in decoupling regional effects and those of continental drift (e.g., Fig. 3) from global changes (e.g., resulting from $p\text{CO}_2$ – see Fig. 4). Here, we integrate available paleoclimate data to provide a broader interpretation of the evolution of Triassic climate in western Gondwana.

During the Early Triassic Epoch, GCMs suggest a strong summer monsoon over much of Gondwana, the development of an extensive arid zone in the interior of Pangea, and areas of high to moderately pluvial discharge restricted to the middle latitudes of the western portion of Pangea (Parrish et al., 1986). In general, these models predict warm and wet conditions in the equatorial region, a zone of particularly hot and dry climate in the low-latitude interior of Gondwana between ~10 and 40°S, and a more temperate climate with moderate precipitation at higher paleolatitudes (Wilson et al., 1994; Kiehl and Shields 2005; Péron et al., 2005; Winguth et al., 2015). Vegetation modeling suggests very distinct biomes, with relatively little vegetation in the hot arid low-latitude zone (Donnadieu et al., 2009). Surprisingly, weathering fluxes are predicted to be quite low, even in the tropics (Donnadieu et al., 2006). Sea surface temperatures from the western Panthalassa Ocean during the Early Triassic oscillated between 30 and 40 °C (Sun et al., 2012), consistent with the atmospheric CO_2 record and tropical sea surface temperatures anomalies(Fig. 4) (Veizer et al., 2000). Retallack (2013, 2021); Retallack et al. (2011) hypothesized a minimum of four greenhouse crises (elevated global atmospheric CO_2) for the Early Triassic based on paleosol, paleobotanical, and carbon isotope data, though there are other potential explanations for some of the carbon isotope excursions (e.g., Kump and Arthur 1999; Whiteside and Ward 2011; Irmis and Whiteside 2012).

Early Triassic fossiliferous units in South America range in estimated paleolatitude from 40.3°S (+3.8/-3.5°) for the Ischigualasto-Villa Unión Basin to 51.1°S (+3.7/-3.5°) for the Los Menucos Basin (Fig. 3; van Hinsbergen et al., 2015). This places these basins south of the hottest and driest parts of Gondwana reconstructed by Early Triassic GCMs, but still in zones with mean annual temperatures between 10 and 20 °C, austral summer temperatures up to ~30 °C, austral winter temperatures between 5 and 15 °C, and relatively low mean annual precipitation rates of 2–4 mm/day (Kiehl and Shields 2005; Péron et al., 2005; Winguth et al., 2015). Proxy data from these basins are largely consistent with these predictions, with evidence of warm, arid, and seasonal conditions in the Talampaya Formation of the Ischigualasto-Villa Unión Basin, Vera Formation of the Los Menucos Basin, and Sanga do Cabral Formation of the Paraná Basin. A number of South American sequences display an Upper Permian-Lower Triassic transition from humid to semiarid or arid climatic conditions, including the Talampaya Formation (Gulbranson et al., 2015), Morro Pelado Member of the Rio do Rasto Formation, Piramboia and Sanga do Cabral formations, the Upper Member of the Yaguarí Formation, and the Buena Vista Formation (e.g., Rohn et al., 2005; Holz et al., 2010). This may have been caused by an increased rain shadow effect from building of the volcanic arc along the western margin of South America (e.g., Lovecchio et al., 2020); alternatively, it may reflect the global rise in atmospheric CO_2 during and after the end-Permian mass extinction (Ekart et al., 1999; Royer et al., 2004; Royer 2006; Berner 2009; Hönisch et al., 2012; Franks et al., 2014; Foster et al., 2017).

Outside of South America, the Katberg Formation of Karoo Basin (South Africa), which has been correlated with Sanga do Cabral Formation of the Paraná Basin (Botha-Brink and Smith, 2020; Schultz et al.,

2020), was located at a higher paleolatitude (59.8°S; +3.7°/-2.5°) than the South American basins (van Hinsbergen et al., 2015). The Katberg succession displays geological and paleontological evidence of a warm, arid regime (Smith et al., 1993, Cateneanu et al., 2005; MacLeod et al., 2017, Retallack et al., 2011), in contrast to the GCM estimates of a temperate climate with moderate precipitation for the Karoo Basin paleolatitudes (Wilson et al., 1994; Kiehl and Shields 2005; Péron et al., 2005; Winguth et al., 2015).

The Middle Triassic Epoch is not particularly well-modeled, but the climate zonation of Gondwana is generally similar to that described for the Early Triassic (Harris et al., 2017). These results are consistent with a low attitude arid belt and a mid-latitude temperate regime inferred from plant remains (Preto et al., 2010). Weathering fluxes are still relatively low compared to the rest of the Mesozoic, but are slightly higher than in the Early Triassic (Donnadieu et al., 2006). Global temperature estimates are still high, between 20 and 30 °C (Veizer et al., 2000; Veizer and Prokoph 2015; Henkes et al., 2018), and three greenhouse crises were proposed by Retallack (2013). Two humid episodes are inferred during the Middle Triassic, based on plant fossil and sedimentological records in the middle Anisian of western Tethys (Kustatscher et al., 2010); and in the Ladinian of the Germanic Basin and the Alps (Mutti and Weissert 1995; Hounslow and Ruffell 2006; Stefani et al., 2010). In Gondwana, most proposed humid episodes are problematic because they are from sediments now known to belong to the Late Triassic Epoch, including those proposed based on plant and insect fossils of the Molteno Formation in southern Africa (e.g., Anderson et al., 1998; Bordy et al., 2005, 2020), and sedimentologic evidence from the lower Santa Maria Formation in Brazil (Holz and Barberena 1994; Langer et al., 2018; Philipp et al., 2018; Irmis et al. this volume), and that of the Los Rastros Formation in northwestern Argentina (Preto et al., 2010; Holz 2015; Mancuso et al. 2020a, 2020b; Irmis et al. this volume).

During the Middle Triassic Epoch, fossil-bearing South American sequences ranged from 43.7°S (+3.7/-3.5°) in the Ischigualasto-Villa Unión Basin to 48.7°S (+3.7/-3.5°) in the San Rafael Basin (Fig. 3; van Hinsbergen et al., 2015). Model-proxy comparisons are difficult for the Middle Triassic because of the lack of GCM results, but those of Harris et al. (2017) suggest relatively cooler winters and wetter summers for this region compared to the Early Triassic, with summer temperatures of 15–30 °C, winter temperatures of 0–10 °C, summer precipitation of 1–7.5 mm/day, and winter precipitation of 2–6 mm/day. The Lower-Middle Triassic Tarjados Formation of Ischigualasto-Villa Unión Basin shows proxy evidence for warm, arid, seasonal conditions similar to the underlying Talamplaya Formation (Krapovickas et al., 2013), but the clay mineralogy assemblage from the top of the Tarjados Formation suggests seasonal conditions with relatively more humid conditions (Mancuso et al. 2020a, 2020b). Middle Triassic carbonate-rich lacustrine sequences (Cerro de las Cabras and Cerro Puntudo formations) developed in the Cuyana Basin are consistent with model predictions of increased precipitation, and also suggest a regional pattern of alternating arid-humid seasons (Benavente et al. 2015, 2019). Similarly, the ?Ladinian units of the Cuyana Basin (Corral de Piedra, Paramillo and Potrerillos) are characterized as seasonal humid warm temperate climate conditions (Brea, 1995; Zavattieri and Rojo 2005; Artabe et al., 2007; Barredo and Ramos 2010), consistent with predictions for cooler winters.

Despite the absence of radioisotopic dates for the Burgersdorp Formation of Karoo Basin (South Africa), its lower section was considered Middle Triassic based on biostratigraphy (Cateneanu et al., 2005; Hancox et al., 2020). During the Middle Triassic, the basin was located at a higher paleolatitude (61.3°S; +3.7°/-3.5°) than the South American basins (van Hinsbergen et al., 2015). The Burgersdorp displays geological and paleontological evidence of a seasonal warm semi-arid regime (Smith et al., 1993, Cateneanu et al., 2005) consistent with the Tarjados, Cerro de las Cabras and Cerro Puntudo formations from South America (Krapovickas et al., 2013; Benavente et al. 2015, 2019).

The Late Triassic Epoch is perhaps the best modeled part of the

Triassic Period; results for Gondwana are again similar to the Early-Middle Triassic, but with a narrower warm and humid equatorial zone, and expanded but more seasonal hot and arid low latitude zone (Wilson et al., 1994; Huynh and Poulsen 2005; Sellwood and Valdes 2006; Dunne et al., 2021). This narrower equatorial zone is reflected in a predicted smaller wet tropical vegetation biome until expansion during the latest Triassic (Donnadieu et al., 2009), when enhanced equatorial runoff is also inferred (Goddéris et al. 2008, 2014). Weathering flux is also inferred to increase slightly during the Late Triassic (Goddéris and Donnadieu 2019). Relatively hot and arid conditions are also predicted for the low latitude of the northern hemisphere, where proxy data indicate intense seasonal fluctuations, alternated humid, sub-humid and even eventually semiarid to arid conditions evidenced by sedimentological, palynological, carbon and oxygen stable isotopic composition of palustrine and pedogenic carbonates, and the global estimations of CO_2 atmospheric levels (e.g., Fowell et al., 1994; Kent and Olsen 2000; Prochnow et al., 2006; Cleveland et al., 2008; Dubiel and Hasiotis 2011; Whiteside et al., 2011; Nordt et al., 2015; Lindström et al., 2016). Retallack (2013) hypothesized three greenhouse crises (early Carnian, early Norian, and early Rhaetian). In contrast, the Carnian Pluvial Episode (CPE) suggests more humid conditions during the middle Carnian at mid- to high latitudes (Simms and Ruffell 1989, 1990; Simms et al., 1994; Dal Corso et al., 2015; Ruffell et al., 2016). After the CPE, a prolonged stage of apparently more stability climate conditions were established for the rest of the Late Triassic (Haas and Demény 2002; Van Houten 1962; Olsen et al., 1978; Olsen 1986; Smoot and Olsen 1988; Simms et al., 1994; Olsen and Kent, 1996, 2000; Kent and Olsen 2000; Reinhardt and Ricken 2000; Vollmer et al., 2008), though there were significant variations in atmospheric CO_2 levels (Fig. 4) (Schaller et al., 2015; Foster et al., 2017).

Pangea rapidly drifted northward during the Late Triassic (e.g., Kent and Olsen, 2000; Torsvik et al., 2012; van Hinsbergen et al., 2015), and therefore South American strata with vertebrate fossil assemblages range from 39.9°S (+2.6/-2.4°) for the Salar de Atacama Basin to 50.5°S (+2.6/-2.4°) for the Cuyana Basin during the Carnian, but those same basins were at 34.8°S (+2.3/-2.1°) and 44.8°S (+2.3/-2.1°), respectively, by the late Norian (Fig. 3; van Hinsbergen et al., 2015). These basins are located in a part of Gondwana where GCMs predict steep gradients in temperature and precipitation (Huynh and Poulsen 2005; Sellwood and Valdes 2006; Dunne et al., 2021), and therefore small differences in estimated paleogeographic position of the sequences have a significant impact on inferred paleoclimate values. These models suggest mean annual temperatures of 15–25 °C, summer temperatures of 20–36 °C, and winter temperatures of 0–16 °C, and mean annual precipitation of 1–6 mm/day, with summer precipitation of <0.5–4 mm/day and winter precipitation of 1–10 mm/day. Depending on the precise paleolatitude, these data suggest slightly warmer summer temperatures for this part of South America compared to Middle Triassic estimates. Conditions for this part of South American are inferred to become warmer and drier during the Norian, as Pangea drifted northward (Dunne et al., 2021).

The aforementioned sensitivity of Late Triassic GCM results to paleogeographic position makes model-proxy comparisons challenging despite an abundance of data. The most complete and best-studied sequence is probably the Agua de la Peña Group in the Ischigualasto-Villa Unión Basin, which preserves a near-continuous record of the Late Triassic from the early Carnian through middle Norian. The Carnian Chañares-Los Rastros sequence is characterized by warm humid- to sub-humid conditions based on multiproxy data with evidence for a warmer and wetter phase that might record the Carnian Pluvial Episode (Mancuso et al. 2020a, 2020b; Benavente et al., 2021). The overlying upper Carnian-lower Norian Ischigualasto Formation was characterized based on paleontological (macro and microflora) and sedimentological evidence as seasonal arid to semi-arid with a semi-humid episode in middle of the unit (Colombi and Parrish 2008; Césari and Colombi 2013), which would be consistent with drier conditions as Pangaea began to drift

northward. That said, paleosol data suggest a more complicated pattern, with an initial humid episode proposed in the lower quarter of the formation, relatively dry conditions in the middle half of the formation, and more humid conditions again in the upper quarter of the formation with cool temperatures (during the season of pedogenic carbonate formation) between ~0 and 10 °C (Tabor et al. 2004, 2006). Finally, the Norian aged Los Colorados Formation was initially interpreted to display an alternation of arid and sub-humid climate conditions (Bossi, 1971), but subsequent detailed sedimentological analysis interpreted the succession as fluvial deposits of mixed charge (suspensive-tractional) with well-developed flood plains and no evidence of aridity (e.g., intraclast breccias, desiccation cracks, eolian lenses, evaporite lenses) (Caselli et al., 2001). This is curious because the age of the formation means it was deposited at a time when northward movement of Pangaea was speeding up, and thus warmer and drier conditions should be most apparent. One possibility is that climate effects of continental drift were partly balanced by a potential long-term decrease in pCO$_2$ during the first half of the Norian (Fig. 4; Foster et al., 2017), though this is not apparent in individual proxy datasets (e.g., Schaller et al., 2015). Carnian-lower Norian units in the Cuyana and San Rafael basins also display evidence of warm to temperate humid seasonal conditions (Zavattieri et al. 2003, 2020; Zavattieri and Rojo 2005; Artabe et al., 2007; Previtera et al., 2016), which is consistent with their higher paleolatitudinal position than the Ischigualasto-Villa Unión Basin (Fig. 3).

Among other South American successions, the Carnian-lower Norian Pinheiros-Chiniquá, Santa Cruz, and lower Candelária sequences (Santa Maria Formation) of the Paraná Basin are interpreted to represent a warm semi-arid seasonal climate (e.g., Holz and Scherer 2000; Horn et al. 2018a, 2018b). These drier conditions in the Paraná Basin compared to penecontemporaneous units in the Ischigualasto-Villa Unión Basin is consistent with the fact that during the Carnian, the two basins switched relative latitudinal position as a result of the rotation of Pangaea, with the former moving north of the latter (Fig. 3). However, the base of Candelária Sequence begins to show more humid conditions (Holz and Scherer 2000) with evidence of a humid pulse in the middle of the Sequence that has been attributed to the Carnian Pluvial Episode (Horn et al. 2018a, 2018b), and persistent wetter conditions in the upper Candelária Sequence (Caturrita Formation). These progressively more humid conditions in the Paraná Basin during the late Carnian and Norian contrast with predictions of drier conditions as Pangaea moved northward; like the Ischigualasto-Villa Unión Basin, this trend might reflect other global changes such as a possible decrease in pCO$_2$. The warm and wet conditions of the El Bordo beds in the Salar de Atacama Basin of northern Chile may seem anomalous given how much further north this basin was located relative to those in Argentina and Brazil, but it is consistent with its proximity to the west coast of Gondwana, where GCMs predict more precipitation than in the interior of the landmass (Sellwood and Valdes 2006; Dunne et al., 2021).

Outside of South America, the Omingonde Formation (Waterberg Basin) of central Namibia has been correlated with Chañares and Santa Maria formations (Abdala et al., 2013; Mancuso and Irmis 2020). Though it was located at a much higher paleolatitude (49.8°S; +2.6°/-2.4°) than the South American units (van Hinsbergen et al., 2015), the Omingonde displays geological and paleontological evidence of a hot to warm seasonally arid regime (Du Toit 1948; Kemp 1982; Hallam 1985; Smith 1995; Abdala et al., 2013). This is again consistent with GCM predictions of drier conditions towards the interior of mid- to high-latitude Gondwana (Huynh and Poulsen 2005; Sellwood and Valdes 2006; Dunne et al., 2021). During the Late Triassic, the Karoo Basin was located at a higher paleolatitude (61.7°S; +2.5°/-2.5° to 46.1°S; +2.9°/-2.7°) than the South American basins (van Hinsbergen et al., 2015).The Molteno Formation of Karoo Basin (South Africa) is considered Carnian in age based on its paleobotanic content, which also suggests cool-temperate humid conditions during the deposition of the unit (Anderson et al., 1998; Smith et al., 1993; Cateneanu et al., 2005).

However, this last climate regime has also been related to local tectonic conditions (Smith et al., 1993; Cateneanu et al., 2005). The Norian-Rhaetian lower Elliot Formation is considered to be deposited under humid to semi-arid climate conditions (Smith et al., 1993; Cateneanu et al., 2005; Bordy et al., 2020). Accordingly, the lower Elliot Formation is more consistent with GCM predictions and those conditions suggested by the South American successions of equivalent age (e.g., Holz and Scherer 2000; Caselli et al., 2001; Tabor et al., 2006; Césari and Colombi 2013; Horn et al. 2018a, 2018b), than the Molteno Formation.

5. Links between climatic and biological events

There is no doubt that vertebrate fossil assemblages can track climate (e.g., Olson 1952; Estes and Hutchison, 1980; Barnosky 2001; Faith and Lyman 2019), but demonstrating a robust correlation is often challenging. Local depositional environment is often a primary taphonomic and ecological filter, and it can be difficult to disentangle the relative controls of local, regional, and global climate as well as biogeographic barriers. One must be especially careful when limited to qualitative comparisons between fossil and paleoclimate data. With these caveats in mind, we can examine whether Triassic vertebrate assemblages in South America show any patterns that might correlate with paleoclimate, both within the continent, and in the broader context of Gondwana and Pangea. Thankfully, there are a rich set of hypotheses to examine, as vertebrate paleontologists began thinking of how climate related to Pangean faunal distributions almost immediately upon their acceptance of continental drift (e.g., Romer 1970; Colbert 1971; Robinson 1971, 1973).

Among available Triassic vertebrate fossil assemblages in South America, those from the Early Triassic have the least available data; the best sample comes from the Sanga do Cabral Formation of the Paraná Basin. This assemblage is similar to others from the Early Triassic of both Laurasia and Gondwana in the abundance and diversity of temnospondyls and procolophonid pararreptiles (e.g., Tverdokhlebov et al., 2002; Nesbitt 2005; Schoch 2011; Irmis and Whiteside 2012; Irmis et al., 2013; Tarailo, 2018; Peecook et al., 2019; McLoughlin et al., 2020; Schultz et al., 2020). Though the Sango do Cabral shares with the earliest Triassic assemblages of South Africa and Antarctica the presence of *Procolophon trigoniceps*, it lacks the dicynodont synapsid *Lystrosaurus* that is so ubiquitous in those two regions and throughout much of Pangea (e.g., Kitching et al., 1972; Cheng 1980; Ray 2005; Surkov et al., 2005; Peecook et al., 2019; Botha-Brink and Smith, 2020; Schultz et al., 2020). The cynodont synapsid *Thrinaxodon* is also present in both South Africa and Antarctica, but absent in Brazil (Peecook et al., 2019; Botha-Brink and Smith, 2020; Schultz et al., 2020). It seems difficult to explain the absence of *Lystrosaurus* in Brazil as an issue of sampling given its remarkable abundance elsewhere. Furthermore, a paleoclimate explanation also seems difficult given that *Lystrosaurus* appears to be specialized for life in highly seasonal warm, arid conditions (e.g., Botha-Brink and Angielczyk 2010; Bordy et al., 2011; Viglietti et al., 2013), and its fossil occurrences span a paleolatitudinal range of ~80°S to ~35°N (van Hinsbergen et al., 2015) across multiple inferred climate zones (e.g., Fig. 1; Kiehl and Shields 2005; Péron et al., 2005; Winguth et al., 2015). The abundance of therapsid footprints (including dicynodonts) in the Los Menucos Basin (Domnanovich and Marsicano 2006; Domnanovich et al., 2008) differentiates it from the Sango do Cabral and suggests similarities with South Africa and Brazil, but further interpretation is unwise given that all known tracks essentially come from a single locality and stratigraphic interval, and thus are not comparable to these much better-sampled assemblages.

Middle Triassic Gondwanan vertebrate assemblages display a higher level of provincialization than those from the Early Triassic (Sidor et al., 2013; Button et al., 2017), but this might reflect in part differing ages across the assemblages (Marsicano et al., 2016). Indeed, the lack of precise and accurate geochronologic age constraints for Middle Triassic Gondwanan assemblages makes interpreting their biogeography and paleoecology very difficult, including any connection to paleoclimate. The high uncertainty associated with radioisotopic ages from South American records means it is currently impossible to evaluate them with respect to specific Middle Triassic climate events observed elsewhere in Gondwana and the Tethys region of Laurasia. The best-sampled assemblage that is confidently Anisian-Ladinian in age is the Cuyana Basin, where the body fossil record comprises exclusively endemic taxa. But it is broadly similar to other Gondwanan assemblages in containing an abundance of synapsids (e.g., Peecook et al., 2019; Hancox et al., 2020), in contrast with the rarity of synapsids and abundance of reptiles (particularly archosauromorphs) in low paleolatitude assemblages from North America and Europe (e.g., Spencer and Storrs 2002; Nesbitt, 2005; Benton 2011; Haque et al. in revision). However, without better sampling of South American assemblages and more precise age control throughout Gondwana, it's unclear if these differences with Laurasia reflect paleobiogeographic, paleoclimatic, or paleoecological (i.e., competitive) effects. One potential clue might come from the higher paleolatitude Ordos Basin of northern China, which is well-dated (Liu et al., 2018) and preserves a Middle Triassic vertebrate assemblage that is more similar to that of southern Gondwana than it is to the aforementioned other assemblages in the northern hemisphere. This might imply that Middle Triassic non-marine ecosystems were sorted latitudinally (and thus also by climate), with mid-high latitude faunas showing more similarity across hemispheres than with lower latitude faunas in their own hemisphere, similar to what is observed during the Late Triassic Epoch (e.g., Whiteside et al., 2011, 2015).

Considerably more paleontological data and geochronologic age constraints are available for the late Ladinian-early Carnian, an interval well-represented by abundant and diverse vertebrate body fossils from South America and southern Africa. The Chañares Formation of Argentina, Pinheiros-Chiniquá Sequence (lower Santa Maria Formation) of Brazil, and Omingonde Formation of Namibia all share a number of dicynodont and cynodont synapsid taxa to the exclusion of other Gondwanan vertebrate assemblages (e.g., Abdala et al., 2013; Mancuso and Irmis 2020). In contrast, the Ladinian-Carnian Río Seco de la Quebrada Formation is more similar to the *Cynognathus* Assemblage Zone (Burgersdorp Formation) of South Africa than it is to aforementioned other South American assemblages. This pattern is intriguing, because paleogeographic data (e.g., Torsvik et al., 2012; van Hinsbergen et al., 2015, Fig. 3) indicate the Chañares, Pinheiros-Chiniquá, and Omingonde all occupied a similar paleolatitude (also see Mancuso and Irmis 2020: Fig. 4), whereas the Río Seco de la Quebrada and Burgersdorp assemblages were located 5–10° further south. This suggests the possibility of paleolatitudinal control of non-marine faunal communities in Gondwana during the Ladinian-Carnian, and is consistent with a similarly positioned boundary between floral provinces (Fig. 1; Césari and Colombi, 2013; Kustatscher et al., 2018; Perez Loinaze et al., 2018). This hypothesized floral and faunal biogeographic boundary is similar in geographic position to an inferred climate boundary in GCM results, where there is a steep gradient from hot temperatures and low precipitation to the north to much cooler temperatures and wetter conditions to the south (e.g., Dunne et al., 2021: Fig. 5). This is broadly consistent with available paleoclimate proxy data, where the Río Seco de la Quebrada Formation appears to be more humid than the Chañares or lower Santa Maria formations (Fig. 4).

More difficult to interpret with respect to these patterns are the Manda beds of Tanzania and Ntawere Formation of Zambia, both in East Africa. They share some synapsid taxa with one or both of the latitudinal zones described above, perhaps reflecting their northern paleolatitude but geographic proximity to southern Africa, but also possess a high diversity of both pseudosuchian and avemetatarsalian archosaurs not observed in other African assemblages, of which only a couple of taxa are closely related to forms from South America (Nesbitt et al., 2017; Peecook et al., 2017). Given that pseudosuchian archosaurs appear to be particularly diverse at low paleolatitudes (e.g., Irmis et al., 2007; 2011; Whiteside et al., 2015; Dunne et al., 2021), it is possible that these East

African occurrences are displaying a mix of low and high paleolatitude signals. Alternatively, unlike the units from South America, these assemblages have not been radioisotopically-dated, so it's possible they are a different age (Marsicano et al., 2016; Peecook et al., 2017).

Well-dated late Ladinian-early Carnian assemblages from the northern hemisphere are sparse; perhaps the best-known assemblage is the upper Ladinian Erfurt Formation (Lettenkeuper) from Germany, which comprises lacustrine and lacustrine-margin vertebrate assemblages from the mid-paleolatitudes (~20–25°N). Tetrapod taxa from this deposit are dominated by temnospondyl amphibians and a high diversity of lepidosauromorph and archosauromorph reptiles (Schoch 2002, 2015a, 2015b; Schoch and Seegis 2016). Temnospondyls are conspicuously absent in penecontemporaneous South American assemblages (likely reflecting depositional setting), and there are virtually no shared reptile lineages. But, without more widespread sampling from the northern hemisphere, this biogeographic difference remains difficult to interpret. The Ladinian-Carnian Badong Formation from the South China Block is constrained by radioisotopic ages, but is poorly sampled, comprising two temnospondyl taxa and the sail-backed pseudosuchian archosaur *Lotosaurus* (Liu 2016; Hagen et al., 2018; Wang et al., 2019), so it is impossible to make further biogeographic or paleoclimatic inferences.

The Carnian displays a local high in pCO_2 (Fig. 4), and contains a major climate event during the middle part of the stage, the Carnian Pluvial Episode. As discussed above, paleoclimatic evidence of the CPE is present in these South American successions, but making links to changes in vertebrate assemblages is more difficult (see discussion in Mancuso et al. 2020a, 2020b). In Brazil, there is a distinct transition in the predominant herbivorous tetrapods, from extremely abundant traversodontid cynodonts in the Pinheiros-Chiniquá and Santa Cruz sequences, to very abundant rhynchosaurian archosauromorphs in the Candelária Sequence, and this is accompanied by an overall increase in tetrapod species diversity (e.g., Azevedo et al., 1990; Schultz et al., 2020); this transition is also present in the Ischigualasto-Villa Unión Basin of Argentina (Mancuso et al., 2014; Martínez et al. 2013a, 2013b). The challenge is that geochronologic age constraints and fossil-bearing levels are disjunct in their stratigraphic distribution in both basins, so it's unclear how sudden this faunal transition was, and whether it is coincident with or post-dates the CPE.

This transition also coincides with the first appearance of dinosaur body fossils in South America (in the Ischigualasto and upper Santa Maria formations), which, in combination with footprint data from South America and Europe, has been used to suggest that the origin of dinosaurs is associated with the CPE climate event. The difficulty here is again the precise timing of these events, and the limitations of the fossil record. Unambiguous dinosaur body fossils do not appear until 1–2 million years after the CPE, but phylogenetic ghost lineages suggest they could be present prior to the CPE, and footprints are only diagnostic to the more inclusive clade Dinosauriformes, which originated well before the CPE (see discussion in Mancuso et al. 2020a, 2020b). This does not rule out a role for the CPE in the origin of dinosaurs, but a better-constrained and better-sampled fossil record is necessary to fully test the hypothesis.

Rhynchosaurs disappear from South America, and perhaps globally, by the early Norian (Fig. 4), but the cause is not clear. Middle Norian vertebrate assemblages from Argentina (upper Los Colorados and Quebrada del Barro formations) typify middle to high paleolatitude faunas from the Norian-Rhaetian of both hemispheres, with abundant and diverse sauropodomorph dinosaurs and the appearance of early turtles, as well as a diversity of non-mammaliaform cynodonts that are closely related to the first mammaliaforms (Whiteside et al. 2011, 2015; Irmis et al., 2011; Irmis et al., 2011; Dunne et al., 2021). These temperate, relatively humid non-marine ecosystems contrast with warmer, more arid low-paleolatitude assemblages where sauropodomorphs and turtles are absent, dinosaurs in general are much rarer, and synapsids are exceptionally rare.

6. Concluding remarks

During the Triassic, western Gondwana was affected by fluctuating climate conditions. The Early Triassic was dominated by arid to semiarid conditions with the most pronounced seasonal fluctuation of humidity in the continental interior. The Middle Triassic of South America comprised prodominentaly seasonal semiarid condition, but shows evidence of significant humid seasonality compared with Early Triassic. During, the Late Triassic, western Gondwana experienced seasonal subhumid conditions with one or more semi-arid intervals, particularly in the interior. A number of intriguing patterns are apparent when comparing the Triassic South American vertebrate fossil record to our understanding of this paleoclimate record. The processes underlying these trends will be further elucidated as we refine the geochronologic control, develop more detailed paleoclimate proxy records, and better sample these fossil-bearing strata.

Authorship contribution statement

ACM: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. BLDH: Investigation, Writing – original draft, Writing. CAB: Investigation, Writing – original draft, Writing. CLS: Investigation, Writing – original draft, Writing RBI: Conceptualization, Investigation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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