The precise temporal calibration of dinosaur origins

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Dinosaurs have been major components of ecosystems for over 200 million years. Although different macroevolutionary scenarios exist to explain the Triassic origin and subsequent rise to dominance of dinosaurs and their closest relatives (dinosauromorphs), all lack critical support from a precise biostratigraphically independent temporal framework. The absence of robust geochronologic age control for comparing alternative scenarios makes it impossible to determine if observed faunal differences vary across time, space, or a combination of both. To better constrain the origin of dinosaurs, we produced radioisotopic ages for the Argentinian Chañares Formation, which preserves a quintessential assemblage of dinosaurian precursors (early dinosauromorphs) just before the first dinosaurs. Our new high-precision chemical abrasion thermal ionization mass spectrometry (CA-TIMS) U–Pb zircon ages reveal that the assemblage is early Carnian (early Late Triassic), 5- to 10-Ma younger than previously thought. Combined with other geochronologic data from the same basin, we constrain the rate of dinosaur origins, demonstrating their relatively rapid origin in a less than 5-Ma interval, thus halving the temporal gap between assemblages containing only dinosaur precursors and those with early dinosaurs. After their origin, dinosaurs only gradually dominated mid- to high-latitude terrestrial ecosystems millions of years later, closer to the Triassic–Jurassic boundary.

dinosaur origins | Chañares Formation | geochronology | Triassic | biostratigraphy

The Triassic Period (252.2–201.3 Ma) is a key interval of earth history that witnessed the origin of many faunal and floral components of modern terrestrial ecosystems, and was punctuated by at least two large-scale environmental perturbations, the end-Permian and end-Triassic mass extinctions (1). These events frame the evolutionary history of nonmarine tetrapod communities during the Triassic, resulting in a long-recognized threefold division: (*i*) lineages that survived the end-Permian mass extinction; (*ii*) a wide variety of new Triassic lineages that did not survive the end-Triassic mass extinction; and (*iii*) the first representatives of lineages that dominated later Mesozoic and Cenozoic ecosystems (2, 3). Among the third group is arguably the most contentious of Mesozoic macroevolutionary events: the origin and rise of dinosaurs (4–8).

Although dinosaurs have often been cited as a classic case of an evolutionary radiation, many disparate hypotheses have been proposed for their origin and subsequent rapid rise to global dominance (4–8). One of the major difficulties with testing these hypotheses has been the lack of precise biostratigraphically independent age constraints for early dinosaur-bearing assemblages, which would provide a firm temporal basis for comparing origin scenarios across time and space (9).

Robust analysis of macroevolutionary patterns requires well-documented assemblages with fossil specimens examined in a phylogenetic context, as well as an independent, accurate, and precise geochronologic framework. As recently pointed out, analyses of the origin and early diversification of dinosaurs have suffered from an overreliance on low-resolution (both stratigraphic and taxonomic) vertebrate biostratigraphy that obscures real faunal differences in time and space (10). This situation is particularly problematic for Triassic nonmarine communities, where tetrapod composition across Pangea appears to be particularly heterogeneous (11–13). Without precise independent age control (other than vertebrate biostratigraphic correlations), it is impossible to determine if these faunal differences vary across time, space, or a combination of both.

Among the many uncertainties regarding dinosaur evolution is the timing of the origin and subsequent radiation of this clade and their closest relatives (early dinosauromorphs). Contrasting hypotheses suggest they appeared anywhere between soon after the end-Permian extinction (~252 Ma) to very close in time to the first dinosaurs (~231 Ma) (14). This question has been put to the fore by recent discoveries of African dinosauromorphs (15) from strata thought to be early Middle Triassic in age, ~245–242 Ma. Nonetheless, the significance of these fossils for understanding the early evolutionary history of the group is unclear as they lack a precise time framework, with the age of the strata based solely on vertebrate correlations among unconnected Gondwanan basins. This problem has been exacerbated by the recent recognition that these vertebrate index taxa may differ in age across Gondwana (16). To resolve these outstanding major issues, we examined the Agua de la Peña succession of the Ischigualasto–Villa Unión Basin in northwestern Argentina, which contains an extensive dinosaur and dinosaur-precursor record for investigating the timing of the origin and early diversification of dinosauromorphs (Fig. 1).

The Chañares Formation

The Triassic Ischigualasto–Villa Unión Basin of northwest Argentina was filled with up to ~4,000 m of predominantly alluvial, fluvial, and lacustrine deposits. The base of the Agua de la Peña Group

Significance

Many hypotheses have been put forth to explain the origin and early radiation of dinosaurs, but poor age constraints for constituent fossil assemblages make these scenarios difficult to test. Using precise radioisotopic ages, we demonstrate that the temporal gap between assemblages containing only dinosaur precursors and those with the first dinosaurs was 5–10 million years shorter than previously thought. Thus, these data suggest that the origin of dinosaurs was a relatively rapid evolutionary event. Combined with our synthesis of paleoecological data, we demonstrate there was little compositional difference between the dinosaur precursor assemblages and the earliest dinosaur assemblages, and thus, the initial appearance of dinosaurs was not associated with a fundamental shift in ecosystem composition, as classically stated.
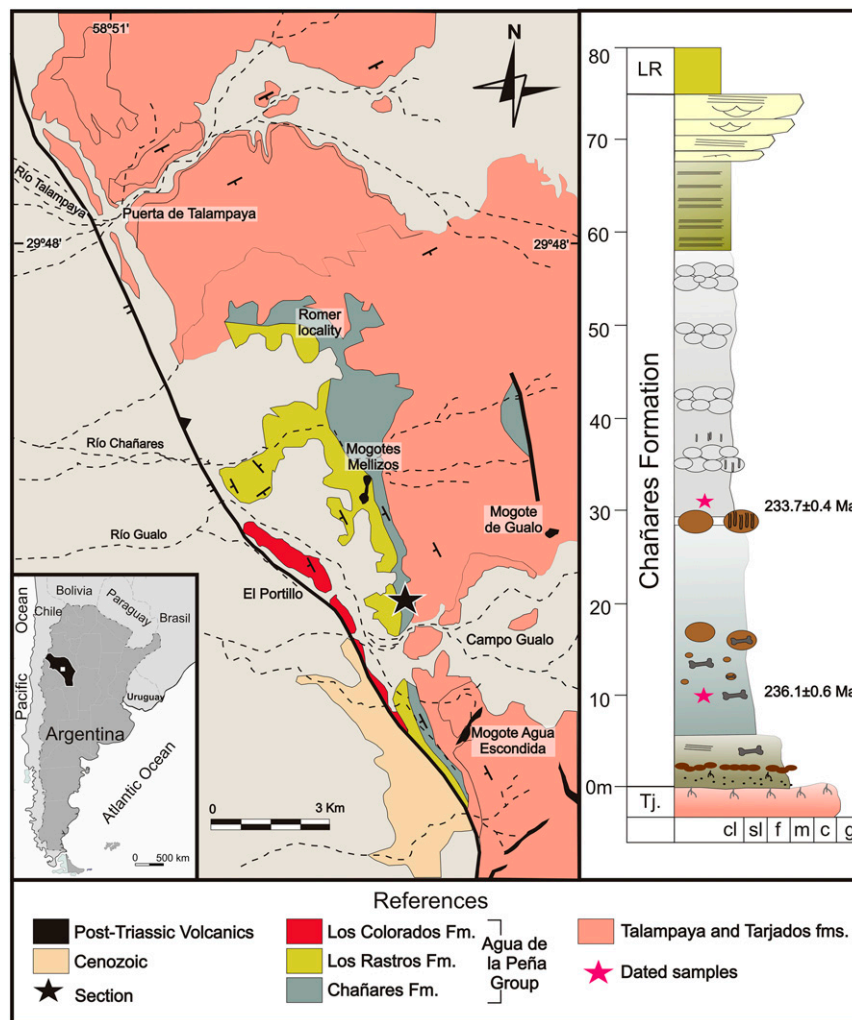
Fig. 1. Geological map of the Chañares–Gualo area in Talampaya National Park (La Rioja Province). The main fossiliferous localities are the Romer locality and Río Gualo. The latter locality is where the detailed section (*SI Appendix*) was measured. (*Right*) Generalized stratigraphic column from Río Gualo showing the sampled levels. For additional references, see *SI Appendix*.

comprises the fluvial–lacustrine tuffaceous deposits of the Chañares Formation, which is conformably overlain by the lacustrine–fluvial organic-rich shales, siltstones, and sandstones of the Los Rastros Formation. The top of this unit is unconformably covered by the fluvial sandstones, mudstones, and tuffs of the Ischigualasto Formation. This unit is, in turn, conformably overlain by the thick fluvial "redbed" siltstone and sandstone deposits of the Los Colorados Formation (17–20) (*SI Appendix*, Fig. S1). The Triassic succession of the Agua de la Peña not only preserves the earliest dinosaur fossils of all three major clades (Ornithischia, Sauropodomorpha, and Theropoda) in the Ischigualasto Formation (21), but it also contains a remarkably diverse assemblage of early dinosauromorphs in the underlying Chañares Formation; this includes nearly complete skeletons of the lagerpetid *Lagerpeton chanarensis* and early dinosauriforms *Marasuchus lilloensis*, *Pseudolagosuchus*, and *Lewisuchus* (2, 20, 22). Overlying the Ischigualasto Formation are the redbeds of Los Colorados Formation, representing the first Triassic ecosystem that is dominated by dinosaurs (12, 21, 23, 24). Whereas the chronostratigraphy of the Ischigualasto and Los Colorados strata is now studied in detail (21, 24, 25), the age of the Chañares Formation has remained poorly constrained to the Middle Triassic by vertebrate biostratigraphy and lithostratigraphic relationships (20, 26–29), with age estimates ranging from Anisian to Ladinian (247–237 Ma).

To constrain the age of the Chañares dinosauromorph assemblage, we produced what are to our knowledge the first precise radioisotopic ages for the tetrapod-bearing levels using reconnaissance laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) U–Pb zircon analyses followed by chemical abrasion thermal ionization mass spectrometry (CA-TIMS) U–Pb zircon dating with permil level precision.

The Chañares Formation is a ~75-m-thick package of siliciclastic fluvial and lacustrine deposition (20, 28, 29). All reported tetrapod fossils have been found in the lower third of the unit; the most articulated and complete specimens, including nearly all dinosauromorphs, are preserved in diagenetic concretions that erode out of a thick siltstone interval 15–20 m above the base of the formation (20, 29). Our two U–Pb-dated horizons bracket the main fossiliferous interval and include (*i*) a siltstone containing abundant volcanic detritus directly underlying the base of the fossiliferous concretion horizon from a locality preserving skeletons of the classic (and biostratigraphically important) Chañares cynodont synapsid *Massetognathus*; and (*ii*) a complexly interbedded white tuff that is ~10 m above the top of the fossiliferous concretion horizon (Fig. 1). Crucially, both the concretion horizon and the white tuff were sampled from a single locality and stratigraphic succession, and can be continuously traced throughout all of the main fossil localities in the area, where they maintain the

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same stratigraphic relationships in terms of thickness and relative stratigraphic position (*SI Appendix*).

Results

The new chemical abrasion thermal ionization mass spectrometry (CA-TIMS) U–Pb zircon ages obtained (Fig. 2) indicate that the base of a redeposited zircon bearing fossiliferous concretion horizon yields a maximum age of 236 Ma, and the overlying white tuff is no older than 235 Ma, and possibly as young as 234 Ma (*SI Appendix*). This new temporal framework assigns the Chañares dinosauromorph assemblage to the Late Triassic, specifically the early Carnian (236–234 Ma), because available age constraints from marine sequences indicate that the Middle–Late Triassic boundary (i.e., the Ladinian–Carnian boundary) is older than 236 Ma (30–32). This new date is 5–10 million years younger than the Middle Triassic ages previously ascribed to the Chañares strata based mainly on vertebrate biostratigraphy. Although both samples contain complex age inventories, they are maximum age constraints for each stratum. Thus, any difference between these ages and the true depositional age would only skew younger in age, placing the fossil assemblages further into the Carnian.

Discussion

Age of Middle Triassic Units in Gondwana. The new dates for the Chañares Formation vertebrate assemblage call into question the age of other classic Gondwanan Middle Triassic assemblages whose ages are based solely on vertebrate correlations. In this context, the new early Carnian age of the Chañares tetrapods suggests a similarly young age for the lower Santa Maria Formation in nearby southern Brazil, because it shares with the Chañares assemblage a variety of tetrapod genera and species unknown from anywhere else (27, 28). The same may also be true for the Omingonde Formation of Namibia, which is also thought to be Middle Triassic by correlations based on the tetrapod taxa shared with southern Brazil (26). The new dates also imply greater uncertainty for the ages of other putative Middle
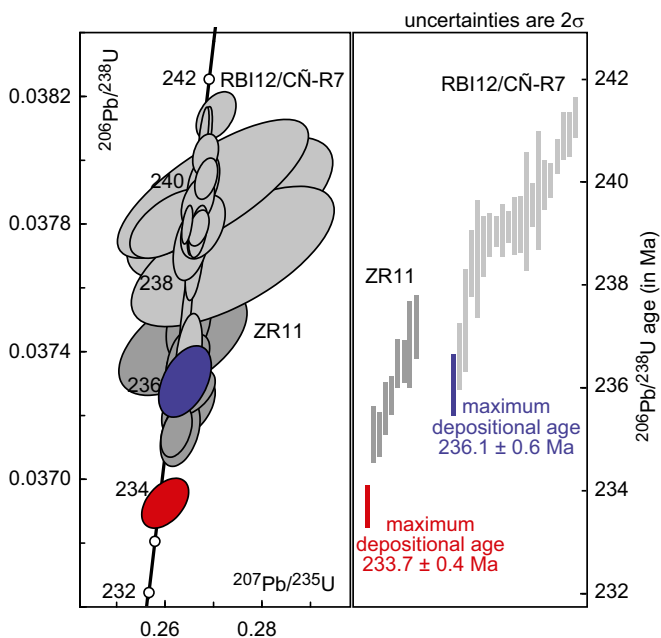

Fig. 2. ID-TIMS U–Pb single-zircon analyses for samples RBI12/CN-R7 (light gray/blue) and ZR11 (dark gray/red). Panels show concordia plot (*Left*) and age-ranked representation (*Right*), including age interpretation considering the youngest age of each sample as maximum depositional age. Data and further discussion of these analyses can be found in *SI Appendix*.
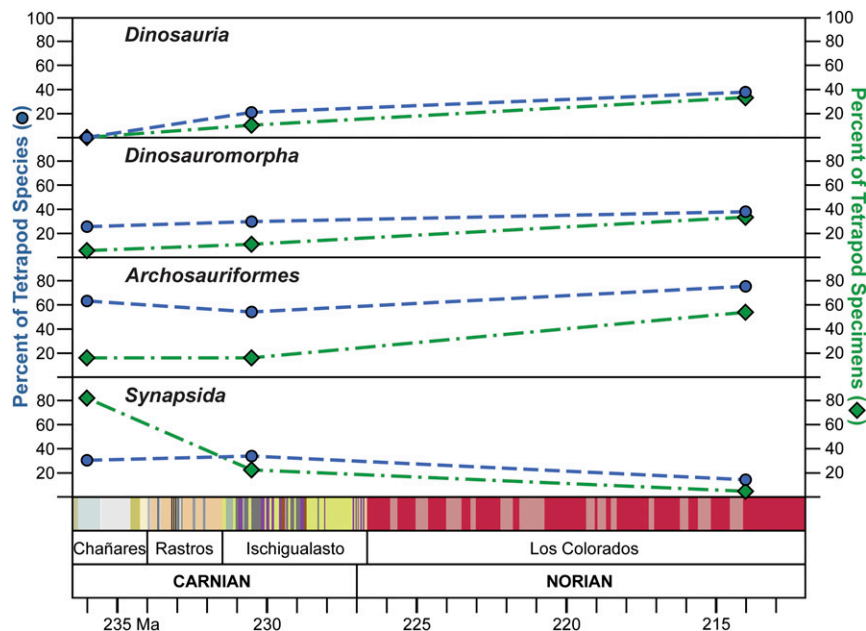
Triassic vertebrate assemblages from South Africa (*Cynognathus* Assemblage Zone), Zambia (Ntawere Formation), Tanzania (Manda Formation), and Antarctica (upper Fremouw Formation). These assemblages have been particularly influential in the discussion of the origin of dinosauromorphs (15, 33), and Triassic biotic provincialization after the end-Permian mass extinction in southern Pangea (13). The Zambian, Tanzanian, and Antarctic assemblages are all correlated to the South African Karoo Basin record using vertebrate biostratigraphy, yet all of these sequences (including the Karoo Basin) are devoid of both published radio-isotopic dates and other independent criteria for assessing their age. The Carnian age for the Chañares fauna increase the likelihood that some or all of these assemblages are erroneously dated, and may actually be Carnian in age. This scenario is supported by the recent case of the Argentinian Puesto Viejo Group, traditionally considered to be early Middle Triassic (*Cynognathus* Assemblage Zone) in age based on biostratigraphic correlations with the Karoo Basin, where a new sensitive high-resolution ion microprobe (SHRIMP) U–Pb age suggests the vertebrate assemblages are, instead, early Carnian in age (16), and thus approximately equivalent to that of the Chañares Formation. If supported by future additional dating of other putative Middle Triassic strata, such as the Manda and Ntawere formations, these new data suggest that evidence for biotic provinciality in Gondwana (13) may instead reflect either different ages across the basins, or that all are Late Triassic in age and have little to do with documenting the recovery from the end-Permian mass extinction in southern Pangea. Accordingly, our new high-precision ages highlight the great uncertainty involved in fine-scale stratigraphic correlations of disjunct regions when relying only on biostratigraphic data. Biostratigraphically independent age constraints are essential for robust testing of macroevolutionary and biogeographic hypotheses in the fossil record.

The Origin of Dinosaurs in Gondwana. The new age constraints for the Chañares Formation, along with existing age data for the overlying dinosaur-bearing Ischigualasto and Los Colorados formations (21, 24, 25), provide the basis for the first attempt to construct a robust framework for calibrating the timing of macroevolutionary patterns related to the origin and early diversification of dinosaurs in Gondwana. The new results presented herein suggest that the closest relatives of dinosaurs had diversified by the start of the Late Triassic, ~236 Ma, as represented by the basal dinosauriforms *Marasuchus*, *Pseudolagosuchus*, and *Lewisuchus*. The transition to communities containing the first dinosaurs occurred in less than a 5-million year interval, based on unambiguous dinosaur body fossils dated to 231.4 Ma from the lower part of the Ischigualasto Formation (21, 25). Possible early dinosaur footprints from the intervening Los Rastros Formation suggest that the origin of dinosaurs could have been even older (34). Footprints attributed to early dinosauromorphs from the Early–Middle Triassic of Poland were used to pull the origin of the group to the beginning of the Triassic (35). Nevertheless, the positive identification of dinosauromorph derived character states (i.e., apomorphies) in these footprints is controversial (5, 14), and in any case, these strata have not been radioisotopically dated. In the present context, robust geochronologic and paleontologic evidence does not currently exist to extend the fossil record of dinosauromorphs beyond the base of the Late Triassic, but additional precise radioisotopic age constraints from different basins across Pangea are necessary to confirm this.

The new scenario presented herein suggests a relatively rapid origin of dinosaurs in the high latitudes of Gondwana, thus halving the temporal gap between assemblages containing only dinosaur precursors and those with early dinosaurs. This temporal framework, combined with our new synthesis of paleoecological data (Fig. 3; *SI Appendix*), suggests there was little compositional difference between the Chañares assemblage and the earliest dinosaur assemblage from the lower part of the Ischigualasto succession; in both, dinosauromorphs (including

Fig. 3. The record of early dinosauromorph evolution in the Ischigualasto–Villa Union Basin as calibrated by biostratigraphically independent geo-chronology. Relative abundance of specimens and relative richness of species for the tetrapod clades Synapsida, Archosauriformes (including Dinosaur-omorpha), Dinosauromorpha (including Dinosauria), and Dinosauria are plotted vs. time in millions of years. The *Exaeretodon* biozone of the upper Ischigualasto Formation is excluded from these plots because of its low sample size, poor sampling, and taphonomic biases against vertebrate preservation (data sources in *SI Appendix*).

dinosaurs) are a minority in terms of both species richness and relative abundance, with synapsids still dominant. Only ~15 million years later, during the deposition of the upper section of the Los Colorados Formation, do dinosaurs begin to domi-nate, where they are both numerically abundant and taxo-nomically and morphologically diverse (24, 36). Nonetheless, dinosaurs did gradually diversify and take over in these areas during the Late Triassic, which is in striking contrast to low-latitude Laurasian faunas, where dinosaurs were rare and species poor until the start of the Jurassic Period (4, 10, 37). Accord-ingly, the origin of dinosaurs did not immediately cause a major shift in ecosystem composition and function at least in the high-latitude tetrapod communities of Gondwana, where they first became dominant. Moreover, these results, along with the de-layed rise of dinosaurs in the tropics (38), would reinforce the conclusion that it is unlikely that there was one cause for di-nosaurian success and their subsequent dominance. After their origin and rapid initial diversification, dinosaurs were likely part of a gradual evolutionary process that involved several other contingencies, such as climatic change and the end-Triassic extinction of other tetrapod clades, which led to the ultimate global success of the group for the rest of the Mesozoic Era.

Methods

All samples were taken from fresh and unweathered in situ rock in strati-graphically extensive exposures that are directly correlative to previously published stratigraphic work (*SI Appendix*). Zircons were isolated using standard mineral separation techniques. Sample ZR11 was first analyzed using the LA-ICPMS technique; the youngest crystals in this analysis were subsequently analyzed using isotope dilution (ID)-TIMS (*SI Appendix*). Sam-ple RBI12/CN-R7 was only analyzed using ID-TIMS. Before ID-TIMS analysis, zircons were chemically abraded and thermally annealed to remove potential zones of Pb loss (*SI Appendix*). Detailed analytical data for the LA-ICPMS and ID-TIMS analyses are presented in *SI Appendix*, Tables S2 and S3. Paleoecological data in Fig. 3 were compiled from the peer-reviewed literature; data and sources are presented in *SI Appendix*.

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