Age constraints on the dispersal of dinosaurs in the Late Triassic from magnetochronology of the Los Colorados Formation (Argentina)

Dennis V. Kent[a,b,1], Paula Santi Malnis[c,d], Carina E. Colombi[c,d], Oscar A. Alcober[d], and Ricardo N. Martínez[d]

[a]Department of Earth and Planetary Sciences, Rutgers University, Piscataway, NJ 08854; [b]Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964; [c]Consejo Nacional de Investigaciones Científicas y Técnicas, 1033 Buenos Aires, Argentina; and [d]Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan 5400, Argentina

Edited* by Neil D. Opdyke, University of Florida, Gainesville, FL, and approved April 17, 2014 (received for review February 7, 2014)

A measured magnetozone sequence defined by 24 sampling sites with normal polarity and 28 sites with reverse polarity characteristic magnetizations was established for the heretofore poorly age-constrained Los Colorados Formation and its dinosaur-bearing vertebrate fauna in the Ischigualasto–Villa Union continental rift basin of Argentina. The polarity pattern in this ∼600-m-thick red-bed section can be correlated to Chrons E7r to E15n of the Newark astrochronological polarity time scale. This represents a time interval from 227 to 213 Ma, indicating that the Los Colorados Formation is predominantly Norian in age, ending more than 11 My before the onset of the Jurassic. The magnetochronology confirms that the underlying Ischigualasto Formation and its vertebrate assemblages including some of the earliest known dinosaurs are of Carnian age. The oldest dated occurrences of vertebrate assemblages with dinosaurs in North America (Chinle Formation) are younger (Norian), and thus the rise of dinosaurs was diachronous across the Americas. Paleogeography of the Ischigualasto and Los Colorados Formations indicates prolonged residence in the austral temperate humid belt where a provincial vertebrate fauna with early dinosaurs may have incubated. Faunal dispersal across the Pangean supercontinent in the development of more cosmopolitan vertebrate assemblages later in the Norian may have been in response to reduced contrasts between climate zones and lowered barriers resulting from decreasing atmospheric $p\mathrm{CO_2}$ levels.

magnetostratigraphy | paleolatitude | La Esquina | Adamanian

The leading candidate for the oldest known occurrence of dinosaurs is the tetrapod assemblage of the Ischigualasto Formation of Argentina (1–4) where a preferred recalculated ^{40}Ar/^{39}Ar date of 231.4 ± 0.3 Ma (1σ analytical uncertainties) (5) on the Herr Toba tuff from near the base of the formation points to a Carnian age for the dinosaur-bearing fauna. However, two recent studies of high-precision U-Pb zircon dates from the Chinle Formation in the American Southwest, practically the only other Late Triassic strata with radioisotopic age constraints on vertebrate assemblages, arrive at very different interpretations of the timing of the dispersal of dinosaurs depending on the accepted degree of total uncertainty for the Herr Toba ^{40}Ar/^{39}Ar date.

The study by Irmis et al. (6) advocated a diachronous rise of dinosaurs, starting in the Ischigualasto Formation of Argentina in the Southern Hemisphere and appearing only later in the Chinle Formation. They pointed to a new U-Pb zircon date of 211.9 ± 0.7 Ma for a dinosaur-bearing vertebrate assemblage in Hayden Quarry at Ghost Ranch, New Mexico, that was considerably younger than the nominal dates from the Ischigualasto Formation. The *Placerias* Quarry in northeastern Arizona may contain even older dinosaurs from the Chinle Formation (7), and although it was not dated directly, Irmis et al. (6) suggested that a new U-Pb zircon date of 218 ± 0.7 Ma from presumably age-correlative strata in New Mexico would make even the *Placerias* assemblage much younger than the Ischigualastian fauna if the Herr Toba date is taken at face value.

In contrast, Ramezani et al. (8) suggested that the rise of dinosaurs may have occurred at about the same time across the Americas. Their new U-Pb zircon dates for seven tuffaceous horizons in the Chinle Formation at Petrified Forest National Park, Arizona, indicated that the entire succession spans from ∼225.0 to 207.8 Ma (or younger), with the Adamanian–Revueltian faunal transition (9) between 219 and 213 Ma. More pertinently, their assessment of the full dating error envelope for the Ischigualasto Formation, including ^{40}Ar/^{39}Ar data included in a thesis (10), suggested that an age of ∼218 Ma (or younger) cannot be excluded for its contact with the overlying Los Colorados Formation. Such a younger age would allow a closer age correspondence between the geographically separated assemblages, signifying that the Adamanian was effectively the age equivalent of the Ischigualastian (11) and thus that there was virtually parallel development of early dinosaurs across the Americas. Olsen et al. (12) also expressed doubts about the reliability of the dating of the Ischigualastian vertebrate assemblages that would necessarily make them of Carnian age.

There are only two dated levels to formally constrain the numerical age of the Late Triassic epoch: a 230.1 ± 0.06 Ma U-Pb zircon date on a volcanic ash in late Carnian marine strata from southern Italy (13) and an age of 201.3 ± 0.18 Ma calculated for the Triassic–Jurassic boundary from U-Pb zircon dates on volcanic ashes bracketing the boundary in ammonite-bearing sediments

Significance

Uncertainties in reported ^{40}Ar/^{39}Ar dates from the Ischigualasto Formation of Argentina allow its dinosaur-bearing fauna to be Norian in age and possibly contemporaneous with some of the older U-Pb dated dinosaur-bearing units in the Chinle Formation of the American Southwest. Our magnetochronology of the previously undated Los Colorados Formation, which also contains a diverse dinosaur assemblage, constrains its age to the interval from 227 to 213 Ma (Norian) and thereby largely restricts the underlying Ischigualasto Formation to the Carnian. Rise of early dinosaurs was thus diachronous across the Americas with their dispersal from the austral temperate belt blocked until later in the Norian. The breakout may have resulted from critically lowered climatic barriers associated with decreasing atmospheric $p\mathrm{CO_2}$ levels.

Author contributions: D.V.K. and O.A.A. designed research; D.V.K., P.S.M., C.E.C., O.A.A., and R.N.M. performed research; D.V.K. and P.S.M. analyzed data; D.V.K., P.S.M., C.E.C., and O.A.A. participated in fieldwork; O.A.A. initiated and organized field sampling expeditions; R.N.M. verified vertebrate paleontology associations; and D.V.K. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

[1]To whom correspondence should be addressed. E-mail: dvk@rutgers.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1402369111/-/DCSupplemental.

from Peru (14). In the current absence of other reliable radioisotopic age controls on fossiliferous marine strata that are the basis for a global chronostratigraphy, correlations to the Newark astrochronological polarity time scale [APTS (15)] have provided important constraints on ages for standard subdivisions of the Late Triassic (16–18), which have largely been adopted in recently published geologic time scales (19, 20). High-precision U-Pb geochronology on earliest Jurassic volcanics of the Central Atlantic Magmatic Province (CAMP) interbedded with sediments in the upper part of the Newark continental rift sequence strongly affirms the astrochronological methodology (21).

Over the entire ~35-My-long Late Triassic epoch, there are only four land vertebrate biozones recognized in North America and just two in South America (11). The low temporal resolution combined with endemism of faunas for the Late Triassic make it difficult to disentangle temporal and spatial components governing the distribution of dispersed vertebrate assemblages and requires age constraints aside from biostratigraphy. In this regard, dating of the Los Colorados Formation would help determine if the underlying Ischigualasto Formation extends into the Norian or is confined to the Carnian and if the temporal range of the dinosaur-bearing Coloradian fauna actually extends to the end of the Triassic as sometimes supposed (e.g., 11). The apparent absence of volcanic ash layers suitable for radioisotopic dating in the Los Colorados Formation motivated this magnetostratigraphic study of the unit and enabled us to address these objectives.

Magnetochronology of the Los Colorados Formation

The ~600-m-thick Los Colorados Formation occurs in the upper part of the more than 3,500 m of continental deposits in the Triassic Ischigualasto–Villa Union basin of western central Argentina and consists of red-colored, fine- to medium-grain–size fluvial sandstones together with siltstones and ancillary floodplain mudstones with early calcisol development (22, 23) (Fig. 1). The lower contact of the Los Colorados Formation is delineated by a gradational transition from the gray, green, and purple floodplain and fluvial sandstones and overbank mudstones of the underlying ~700-m-thick Ischigualasto Formation (25–27) (Fig. S1). The age of the Ischigualasto Formation and its associated Ischigualastian fauna (28) is bracketed by $^{40}Ar/^{39}Ar$ dates on two volcaniclastic layers: the Herr Toba tuff from near the base of the formation at 231.4 ± 0.3 Ma (1, 5) and an unnamed tuff (sample ISCH-6-611) from its uppermost part at 225.9 ± 0.9 Ma (5). There are no radioisotopically dated horizons in the conformably overlying Los Colorados Formation, whose faunal assemblage (28) is usually considered Norian and even thought to contain elements of both Late Triassic and Early Jurassic aspects (29–31). Fluvial and eolian deposits and interbedded conglomerates of the overlying Cerro Rajado Formation are in erosional contact with the Los Colorados Formation and, although barren of fossils, regarded as Cretaceous or even younger in age (32, 33).

A magnetostratigraphic profile for the entire Los Colorados Formation at the La Sal section was constructed from 52 sites with acceptable data (Table S1) and is delineated by a sequence of 15 geomagnetic polarity intervals labeled LC1r to LC8n in ascending order from the base of the measured section (Fig. 2). Magnetozones LC1 and LC4/LC5 include polarity intervals based on single sites that should thus be regarded as tentative. Nevertheless, available age constraints, including that the 15 polarity intervals should collectively represent roughly 5–15 My according to long-term polarity reversal rates for the Late Triassic (15), lead us to correlate Los Colorados magnetozones LC1r–LC8n to Newark APTS chrons E7r–E15n (Fig. 2). This magnetic correlation requires that only the two shortest chrons in this interval (E11n and E13n.1r) are not represented in the La Sal section dataset, plausibly because of small sampling gaps or depositional hiatuses. With these caveats, and taking the single-site polarity intervals at face value, our magnetic correlation

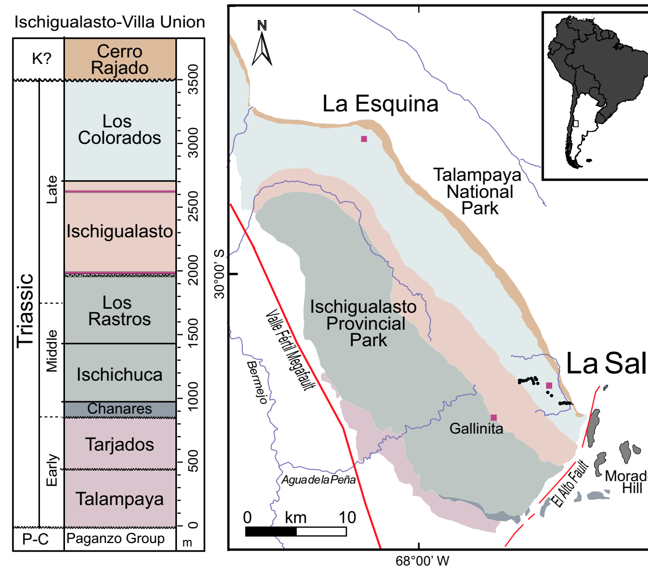

Fig. 1. Columnar section of rock formations (*Left*) and location and geologic sketch map (*Right*) of the Ischigualasto–Villa Union basin where map patterns for formations in the basin are keyed to the columnar section (with basalts near Morado Hill shown as gray fill). The Valle Fertil megafault represents Neogene tectonic inversion activity that exhumed the Mesozoic basin (24). Paleomagnetic sampling sites for the La Sal section are shown by filled circles and listed in Table S1. The starting point of the Gallinita section of the Ischigualasto Formation (25) is indicated by a purple square. The La Esquina fauna of the upper Los Colorados Formation (22) comes from the northern part of the basin as labeled (see also Fig. S2). The dated tuffs from near the base and toward the top of the Ischigualasto Formation (5) are indicated by purple stripes in the stratigraphic column.

produces a remarkably linear plot of sediment thickness versus age (Fig. 3). The correlation indicates an overall sediment accumulation rate of approximately 35 m/My over a total duration of ~14 My from around 227 to 213 Ma. Given that the Carnian–Norian boundary in Tethyan marine sections has been correlated to Newark Chron E7r (16, 17), the base of the Los Colorados Formation in correlative chron LC1r would essentially correspond chronostratigraphically to the Carnian–Norian boundary. The magnetochronological age estimate of ~227 Ma for the base of the Los Colorados Formation is in reasonable agreement with the $^{40}Ar/^{39}Ar$ date of 225.9 ± 0.9 Ma for the tuff (sample ISCH-6-811) in the uppermost Ischigualasto Formation (5), which becomes more strongly constrained to be predominantly Carnian in age. The top of the Los Colorados Formation in the La Sal section extends to latest Norian (chron E15n, ~213 Ma), a few million years before the Rhaetian–Norian boundary that has been correlated to chron E16n (18). Accordingly, the ~600-m-thick sampled section of the Los Colorados Formation falls entirely within the Norian.

Late Triassic Biochronology

The vertebrate fauna in the lower part of Ischigualasto Formation includes a taxonomically diverse group of dinosaurs constituting about 11% of recorded specimens (5). The La Esquina fauna from the upper third of the Los Colorados Formation also contains dinosaurs that are taxonomically diverse, making up about 1/3 of recorded vertebrate taxa (5). Projecting laterally from the La Sal section (Fig. S2), the La Esquina fauna is most probably no younger than ~213 Ma (latest Norian), or ~11 My before the Triassic–Jurassic boundary. This unexpected result, which needs to be verified by direct magnetostratigraphic study of the La Esquina section (30 km along-strike to the northwest traced by cliff exposures; Fig. 1 and Fig. S2), is at variance with

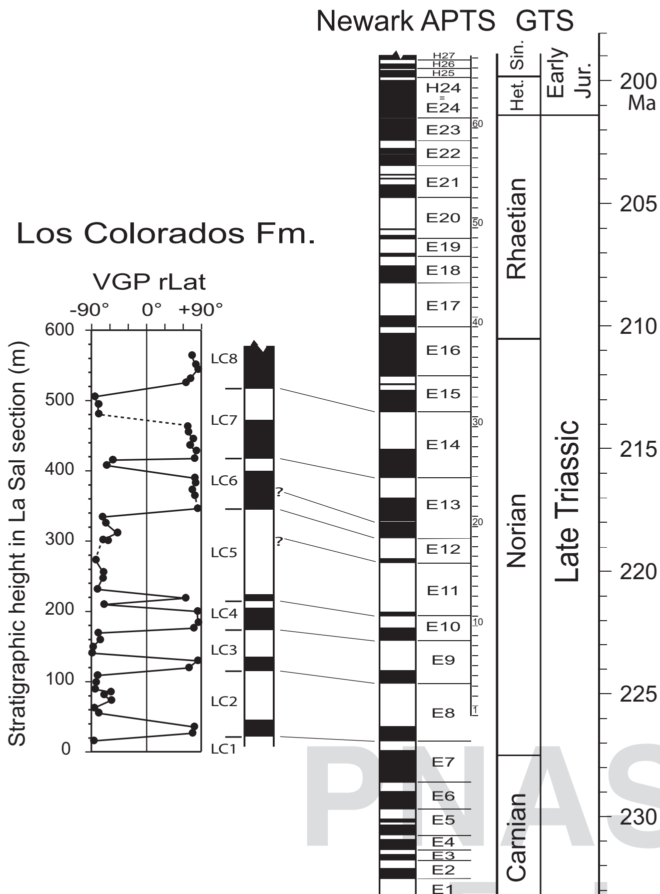

Fig. 2. Magnetic polarity stratigraphy of the La Sal section of the Los Colorados Formation (*Left*) with the preferred correlation to the Newark APTS (15, 34) adjusted to a U-Pb date (rounded to nearest 0.5 My) of 201.5 Ma for the beginning of CAMP volcanism in the Newark basin that is close to the end-Triassic extinction level (21). Magnetic polarity stratigraphy of the Los Colorados Formation section was based on the latitude of the site-mean VGPs with respect to the mean north paleopole (VGP rLat), where rLat approaching +90° is regarded as normal polarity, and rLat approaching −90° as reverse polarity. Filled or open bars in polarity columns denote intervals of normal or reverse polarity; chrons comprised of successive main normal and reverse polarity-paired intervals are designated by LC prefix for Los Colorados, E prefix for Newark, and H prefix for Hartford sequences. Tick marks next to the APTS chron column are for 405-ky Milankovitch cycles used for apportioning durations (12). Geologic time scale (GTS) (20) adjusted for magnetic correlations to Newark APTS (16, 18, 35).

some interpretations of the faunal assemblage as transitional, containing Late Triassic and Early Jurassic elements (e.g., 30).

We can now compare this record with geochronologic data from the Chinle Formation to address the question of a diachronous (6) versus simultaneous (8) rise of dinosaurs across the Americas. Although the Chinle Formation is one of the richest and best studied terrestrial records of Late Triassic biota, dinosaurs are a rare component of most faunas (36). The oldest directly dated dinosaur fauna from the Chinle Formation (or apparently anywhere else outside the Ischigualasto–Villa Union basin) is Hayden Quarry at Ghost Ranch in New Mexico. This is where *Chindesaurus*, the only known example of a herrerasaurid theropod dinosaur from outside South America, has been described (37, 38). High-precision U-Pb zircon dating at Hayden Quarry places a maximum age of 211.9 ± 0.7 Ma for *Chindesaurus* (6), consistent with its occurrence in the Petrified Forest Member in the northern part of Petrified Forest National Park in Arizona (39) whose age is constrained between ~210 and 214 Ma by U-Pb zircon dating (8).

There may be older dinosaurs at *Placerias* Quarry in Arizona, regarded as the oldest Adamanian strata (40) and currently assigned to the upper part of the Blue Mesa Member (39). Irmis et al. (6) obtained a U-Pb zircon date of 218.1 ± 0.7 Ma from a tuffaceous sandstone in the upper part (although previously reported in various abstracts as at the base) of the Blue Mesa Member in the Six Mile Canyon area of New Mexico (39). At about the same time, Ramezani et al. (8) published a U-Pb zircon date of 223.~~185~~ ± 0.027 Ma from the upper part of the Blue Mesa Member at its type locality in Petrified Forest National Park. The discrepancy points to the difficulty in making correlations based on lithology in such widely distributed but discontinuously exposed deposits. Nevertheless, because the Adamanian–Revueltian transition is placed in the upper part of the overlying Sonsela Member (9), the Chinle U-Pb geochronology of Ramezani et al. (8) would place the faunal transition sometime between 219 and 213 Ma, which is not inconsistent with the results of Irmis et al. (6) for the Adamanian.

The earliest documented dinosaur occurrences in North America (Chinle Formation) according to these data are thus demonstrably younger and thus diachronous with respect to

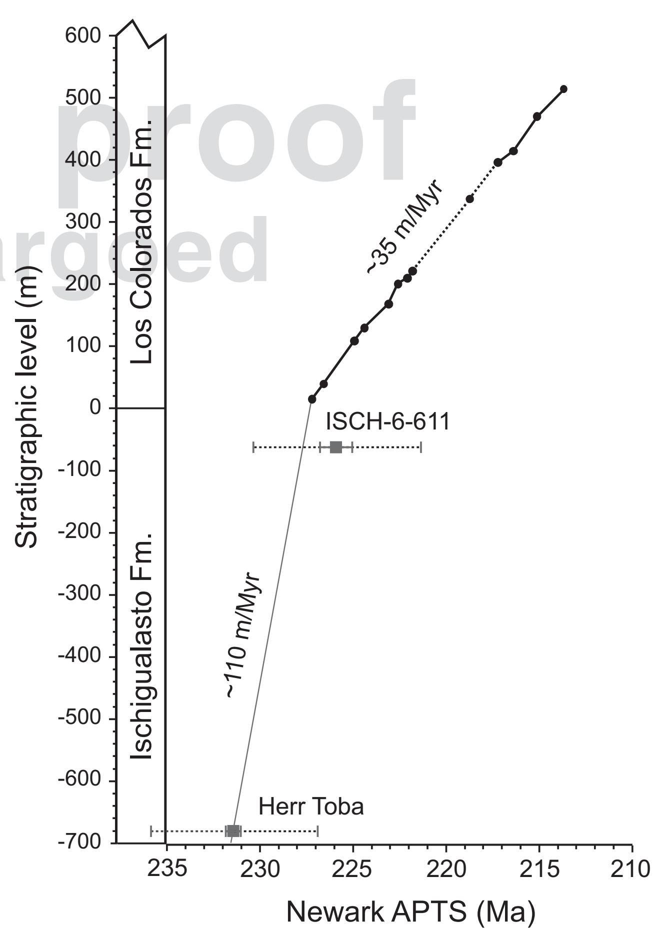

Fig. 3. Stratigraphic level versus age for correlation of magnetostratigraphy of the Los Colorados Formation to the Newark APTS shown in Fig. 2 (solid circles connected by solid lines, dashed over intervals including an unresolved short magnetozone) and $^{40}Ar/^{39}Ar$ dates on two tuffs from the Ischigualasto Formation (labeled ISCH-6-611 and Herr Toba) shown with 1σ analytical (internal) uncertainties [solid error bars (5)] and including external uncertainties (dashed error bars) suggested by ref. 8. Overall sediment accumulation rates implied by these data are indicated for each formation.

those in South America (~231 Ma, Ischigualasto Formation) by minimally ~13 My (using 218 Ma for the *Placerias* Quarry) and as much as 19 My if the more secure ~212-Ma date for *Chindesaurus* from Hayden Quarry ends up as the operative oldest age of Chinle dinosaurs.

Late Triassic Paleogeography

The confirmed earlier rise of dinosaurs in the Ischigualasto Formation and the subsequent provinciality between the abundant and diverse dinosaur fauna from the overlying Los Colorados Formation (5, 30) compared with the very sparse and species-poor dinosaur fauna of the nominally coeval (Norian) Chinle Formation (6) may be related to contrasting paleogeographic settings. Most of the world landmasses in the Late Triassic were assembled in the supercontinent of Pangea with no major internal seaways to act as barriers to dispersal of land vertebrates. So what could have impeded by millions of years the rise of dinosaurs in North America and accounted for the large disparity in their diversity and abundance between South and North America when dinosaurs become more widespread in the Norian? We suggest that an important contributing factor was climate zonation and spatiotemporal changes with continental drift modulated by varying concentrations of greenhouse gases.

Pangea can be reconstructed from relative fits of the now dispersed continental elements (41). However, positioning in latitude requires control from paleomagnetic pole positions in the context of the geocentric axial dipole (GAD) hypothesis. We use the 220-Ma reference pole of the global composite apparent polar wander path (APWP) (42), which is based on the mean of eight entries from igneous rocks and sedimentary rocks corrected for inclination error ranging in age from 211 to 227 Ma. This age window coincides well with our estimated age range of the Los Colorados Formation, and we note that the 220-Ma–mean pole is one of the best defined (A95 = 2.3°) in the global composite APWP for the Mesozoic and early Cenozoic (42). The predicted paleolatitude for the Ischigualasto basin locality (~30°S, 68°W) is 48.4°S, corresponding to a GAD inclination of 68.0°. The characteristic remanent magnetization (ChRM) mean inclination for the Los Colorados Formation (60.4 ± 3.8°) is appreciably shallower (by 7.6 ± 4.7°). This is most probably due to sedimentary inclination error as is often found associated with early-acquired red-bed magnetizations with sufficient data for direct analysis (43, 44).

Pangea was characterized by a nearly pole-to-pole extent of landmass at 220 Ma (Fig. 4). There is no evidence of polar ice caps in the Triassic, a period characterized by generally equable climate (46) whereby latitudinal variations in the difference between precipitation and evaporation (P-E) may have been especially important in defining climate belts. As a leading-order estimate of climate belts, we use the zonal-mean annual values of P-E based on a general circulation model with idealized geography, an annual-mean insolation, and a high (8× preindustrial level) atmospheric pCO_2 concentration (45). More elaborate climate models (e.g., 47) give similar spatial patterns. In this context, the Ischigualasto–Villa Union basin at 48°S paleolatitude would place it in the austral temperate humid belt (Fig. 4). At about the same time (220 Ma), the Chinle depocenter in the North American Southwest (as well as some other important fossil localities like the Newark rift basin in eastern North America and the Argana basin in northern Africa) was migrating into the boreal tropical arid belt while the Keuper (Germanic) basin and Jameson Land of Greenland had entered into the boreal temperate humid belt. Local continental faunas and floras would have become well-adapted to their particular climate regimes whose loci changed slowly as Pangea drifted northward by ~15° over the Late Triassic. At the same time, the terrestrial assemblages would have differed markedly among the climate belts, whose contrasting environments may have presented effective hurdles to dispersal.

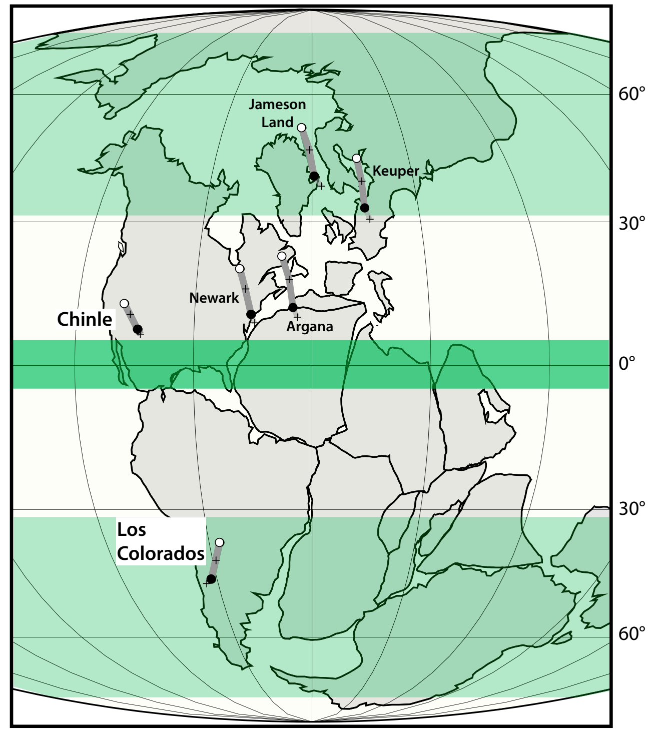

Fig. 4. Reconstruction of Pangea for the Norian based on continental rotation parameters (41) and positioned in latitude using a 220-Ma–mean global pole (42). Some key Late Triassic vertebrate fossil localities are indicated by filled circles connected to their relative positions at 200 Ma by open circles, with relative positions of localities at 230 and 210 Ma indicated by crosses. Idealized zonal belts (45) of precipitation (P) relative to evaporation (E) are indicated by darker green shading for $P > E$ (more humid) and lighter green shading for $P < E$ (more arid).

Prolonged residence within the austral temperate belt seems to be associated with the development of terrestrial vertebrate assemblages that included dinosaurs from their first appearance in the Carnian Ischigualastian fauna to the Norian Coloradian (La Esquina) fauna. In the latter, the first numerical dominance of the herbivorous dinosaurs over other groups is documented and seems to be correlated with their increase in taxonomic diversity and size (48). The breakout of dinosaurs from the austral temperate humid belt to the tropics and beyond may have required lowering of climate barriers; for example, a reduction in P-E contrasts whereby the vast zonal deserts became less arid and perhaps at least intermittently more traversable. Reduced P-E contrasts could have resulted from decreased concentrations of atmospheric pCO_2 (45, 49). Modeling (47) supported by similarly age-registered paleosol carbon isotope analyses (50) points to generally decreasing levels of atmospheric pCO_2 over the Late Triassic and into the Early Jurassic when terrestrial faunas became much more cosmopolitan (51). Interestingly, an interval of particularly low atmospheric pCO_2 values has been reported in the Ghost Ranch section of the Chinle Formation (52) where the early dinosaur *Chindesaurus* was constrained to be no older than ~212 Ma (6). This marked dip in atmospheric pCO_2 speculatively may coincide with a dispersal event of dinosaurs into tropical regions like the Chinle depocenter.

Magnetic polarity stratigraphy of the Ischigualasto Formation and especially the La Esquina section of the Los Colorados Formation and U-Pb zircon dating of tuffaceous layers in these units as well as those more directly associated with dinosaur-bearing

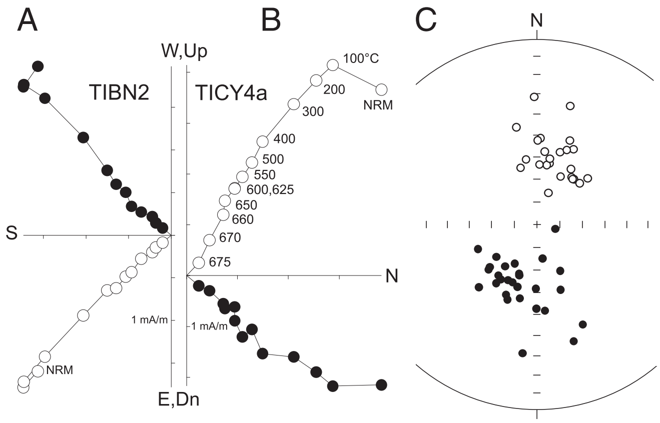

Fig. 5. Paleomagnetic results from Los Colorados Formation. (*A* and *B*) Vector end-point demagnetization diagrams of representative samples with reverse (*A*) and normal (*B*) polarity characteristic magnetizations. Open (closed) circles are projections of the vector end points onto the vertical (horizontal) planes, with thermal treatment steps in degrees Celsius shown next to open symbols in *B*. (*C*) Equal-area plot of 52 site-mean ChRM directions from the Los Colorados Formation, where open/closed symbols are plotted on the upper/lower hemisphere of the projection. Site and formation statistics are given in Table S1.

levels in the Chinle Formation (and elsewhere) would be desirable to confirm the chronology of events outlined here.

Materials and Methods

The La Sal section was chosen for a sampling transect through the Los Colorados Formation on the basis of fresh exposures in a stream cut through the cliff outcrop of strata that are in clear structural continuity and stratigraphic superposition with the Ischigualasto Formation (Fig. 1 and Fig. S1). The La Esquina section with its rich tetrapod fauna from the upper part of the Los Colorados Formation [La Esquina local fauna or Upper Coloradense (30, and references therein)] is about 30 km along-strike to the northwest and linked by essentially continuous cliff exposures; the Los Colorados Formation may be somewhat thicker there than in the La Sal section, but the lower part of the formation is virtually inaccessible at La Esquina to make a complete reference section there. In contrast to the Ischigualasto Formation, which forms a badlands landscape triggered by its drab clay-rich floodplain deposits, the more indurated red siltstones and sandstones of the Los Colorados Formation crop out as prominent cliffs. We attempted to obtain three oriented samples at each site using a cordless drill with a water-cooled 2.5-cm-diameter diamond bit and a magnetic compass for orienting the cores. The finer-grained red mudstone and siltstone facies were preferentially sampled, whereas the coarser-grained sandstones were avoided after measurements on the first sample collection showed that this lithology tended not to yield interpretable results. The various sampling campaigns produced nearly 150 oriented samples from 58 sites that represent most of the lithologic intervals suitable for paleomagnetic analysis in this section.

Thermal demagnetization in a dozen or more treatment steps up to 685 °C using a 2G cryogenic magnetometer and large-capacity ovens in a shielded room was used to identify the ChRM component of each sample's natural remanent magnetism. After removal of generally small spurious or overprint components, demagnetization trajectories typically revealed a high unblocking temperature magnetization that converged toward the origin directed either northerly and up or southerly and down from site to site (Fig. 5 *A* and *B*). Principal component analysis (53) of the last six or more treatment steps between 300 and 600° up to 685 °C anchored to the origin was used to estimate the direction of the ChRM in each sample; component estimates with a maximum angular deviation greater than 15° were rejected as poorly defined except in a few cases where a demagnetization trend was obvious and a stable end-point direction could be identified. We also excluded results from a handful of samples with anomalously shallow directions that may reflect undue influence of depositional processes, especially in the initially sampled medium- to coarser-grained sandstones and a handful of samples with widely aberrant directions that were most probably misoriented. As indicated by the high unblocking temperatures that typically range to 685 °C, the magnetizations are carried predominantly by hematite, which may be of detrital or early diagenetic origin.

In all, 104 of the 142 samples analyzed, representing 52 (88%) of the 58 sites, provided acceptable paleomagnetic data (Table S1). With all directions corrected for a regional stratal tilt with a strike of 320° and dip of 12° to the northeast, the site-mean ChRM directions fall into two nearly antipodal populations (Fig. 5*C*): 24 sites of normal polarity clustered around a mean of Declination, D = 14.8°, Inclination, I = −58.7° (A95 = 5.0°) and 28 sites of reverse polarity with a mean of D = 195.9°, I = 61.9° (A95 = 5.8°). The populations are antipodal at 95% confidence (3.3° departure compared with critical angle of 7.7°) giving a positive reversal test [Class B (54)]. Converted to common (normal) polarity, the 52 ChRM site means are aligned along a mean axis of D = 15.4°, I = −60.4° (A95 = 3.8°).

Virtual geomagnetic pole (VGP) latitudes calculated for the accepted 52 site-mean directions and gauged with respect to the mean (north) VGP position (71.8 °N, 70.8 °E, A95 = 5.0°) delineate a magnetostratigraphic sequence of 15 polarity intervals, which are labeled LC1r to LC8n in ascending order from the base of the measured section (Fig. 2).

ACKNOWLEDGMENTS. This paper benefited from discussions on Late Triassic stratigraphy with Paul Olsen, exchanges on aspects of radioisotopic dating with Sam Bowring and Jahan Ramezani, and constructive comments by Randy Irmis on an earlier version of the manuscript. The authors thank the Jurassic Foundation, the Earthwatch Foundation, and Lamont-Doherty Earth Observatory for financial support of this project. Lamont-Doherty Earth Observatory contribution 7785.

1. Rogers RR, et al. (1993) The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and 40Ar/39Ar dating of dinosaur origins. *Science* 260(5109):794–797.
2. Sereno PC, Forster CA, Rogers RR, Monetta AM (1993) Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* 361(6407):64–66.
3. Brusatte SL, et al. (2010) The origin and early radiation of dinosaurs. *Earth Sci Rev* 101(1-2):68–100.
4. Martínez RN, et al. (2012) Vertebrate succession in the Ischigualasto Formation. *J. Vert. Paleontol.* 32(Suppl 1):10–30.
5. Martínez RN, et al. (2011) A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science* 331(6014):206–210.
6. Irmis RB, Mundil R, Martz JW, Parker WG (2011) High-resolution U–Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. *Earth Planet Sci Lett* 309:258–267.
7. Nesbitt SJ, Irmis RB, Parker WG (2007) A critical reevaluation of the Late Triassic dinosaur taxa of North America. *J Syst Palaeontol* 5:209–243.
8. Ramezani J, et al. (2011) High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): Temporal constraints on the early evolution of dinosaurs. *Geol Soc Am Bull* 123(11-12):2142–2159.
9. Martz JW, Parker WG (2010) Revised lithostratigraphy of the Sonsela Member (Chinle Formation, Upper Triassic) in the southern part of Petrified Forest National Park, Arizona. *PLoS ONE* 5(2):e9329.
10. Shipman TC (2004) Links between sediment accumulation rates and the development of alluvial architecture: Triassic Ischigualasto Formation, northwestern Argentina. PhD thesis (University of Arizona, Tuscon, AZ).
11. Lucas SG (2010) The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology. *Geol Soc Lond Spec Publ* 334:447–500.
12. Olsen PE, Kent DV, Whiteside JH (2011) Implications of the Newark Supergroup-based astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. *Trans R Soc Edinb Earth Sci* 101:201–229.
13. Furin S, et al. (2006) High-precision U-Pb zircon age from the Triassic of Italy: Implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology* 34:1009–1012.
14. Schoene B, Guex J, Bartolini A, Schaltegger U, Blackburn TJ (2010) Correlating the end-Triassic mass extinction and flood basalt volcanism at the 100,000-year level. *Geology* 38:387–390.
15. Kent DV, Olsen PE (1999) Astronomically tuned geomagnetic polarity time scale for the Late Triassic. *J Geophys Res* 104(B6):12831–12841.
16. Muttoni G, et al. (2004) Tethyan magnetostratigraphy from Pizzo Mondello (Sicily) and correlation to the Late Triassic Newark astrochronological polarity time scale. *Geol Soc Am Bull* 116(9-10):1043–1058.
17. Channell JET, et al. (2003) Carnian-Norian biomagnetostratigraphy at Silicka Brezova (Slovakia): correlation to other Tethyan sections and to the Newark Basin. *Palaeogeogr Palaeoclimatol Palaeoecol* 191:65–109.
18. Hüsing SK, Deenen MHL, Koopmans JG, Krijgsman W (2011) Magnetostratigraphic dating of the proposed Rhaetian GSSP at Steinbergkogel (Upper Triassic, Austria): Implications for the Late Triassic time scale. *Earth Planet Sci Lett* 302(1-2):203–216.
19. Gradstein FM, Ogg JG, Schmitz MD, Ogg GM, eds (2012) *The Geologic Time Scale 2012* (Elsevier, Amsterdam), 1st Ed, p 1144.
20. Walker JD, Geissman JW, Bowring SA, Babcock LE (2013) The Geological Society of America Geologic Time Scale. *Geol Soc Am Bull* 125(3-4):259–272.
21. Blackburn TJ, et al. (2013) Zircon U-Pb geochronology links the end-Triassic extinction with the Central Atlantic Magmatic Province. *Science* 340(6135):941–945.

22. Caselli AT, Marsicano CA, Arcucci AB (2001) Sedimentologia y paleontologia de la Formacion Los Colorados, Triasico superior (provincias de La Rioja y San Juan, Argentina). *Rev Asoc Geol Argentina* 56:173–188.
23. Colombi CE, et al. (2012) Large-diameter burrows of the Triassic Ischigualasto Basin, NW Argentina: Paleoecological and paleoenvironmental implications. *PLoS ONE* 7(12):e50662.
24. Suvires GM (2010) Paleosurfaces and relief evolution in cratonic areas of the Western Pampean Ranges (Province of San Juan, Argentina). *Geociências* 29(4):501–509.
25. Colombi CE, Parrish JT (2008) Late Triassic environmental evolution in southwestern Pangea: Plant taphonomy of the Ischigualasto Formation. *Palaios* 23(12):778–795.
26. Currie BS, Colombi CE, Tabor NJ, Shipman TC, Montañez IP (2009) Stratigraphy and architecture of the Upper Triassic Ischigualasto Formation, Ischigualasto Provincial Park, San Juan, Argentina. *J S Am Earth Sci* 27(1):74–87.
27. Milana JP, Alcober OA (1994) Modelo tectosedimentario de la cuenca triasica de Ischigualasto (San Juan, Argentina). *Rev Asoc Geol Argent* 49:217–235.
28. Bonaparte JF (1971) Los tetrapodos del sector superior de la Formacion los Colorados, La Rioja, Argentina (Triasico Superior). *Opera Lilloana* 21:168–183.
29. Benton MJ (1994) Late Triassic to Middle Jurassic extinctions among continental tetrapods: Testing the pattern. *In the Shadow of the Dinosaurs. Early Mesozoic Tetrapods*, eds Fraser NC, Sues H-D (Cambridge Univ Press, New York), pp 367–397.
30. Arcucci AB, Marsicano CA, Caselli AT (2004) Tetrapod association and paleoenvironment of Los Colorados Formation (Argentina): A significant sample from western Gondwana at the end of the Triassic. *Geobios* 37:557–568.
31. Olsen PE, Sues H-D (1986) Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic-Jurassic tetrapod transition. *The Beginning of the Age of Dinosaurs: Faunal Change Across the Triassic-Jurassic Boundary*, ed Padian K (Cambridge Univ Press, Cambridge, UK), pp 321–351.
32. Bossi GE (1977) La Formación Cerro Rajado, Provincia de La Rioja. *Acta Geol Lilloana* 14:19–40.
33. Stipanicic PN, Bonaparte J (1979) Cuenca triásica de Ischigualasto-Villa Unión (Provincia de La Rioja y San Juan). *Geología Regional Argentina*, ed Turner JC (Academia Nacional de Ciencias de Córdoba, Cordoba, Argentina), pp 523–575.
34. Kent DV, Olsen PE (2008) Early Jurassic magnetostratigraphy and paleolatitudes from the Hartford continental rift basin (eastern North America): Testing for polarity bias and abrupt polar wander in association with the Central Atlantic Magmatic Province. *J Geophys Res* 113:B06105, 10.1029/2007JB005407.
35. Ruhl M, et al. (2010) Astronomical constraints on the duration of the early Jurassic Hettangian stage and recovery rates following the end-Triassic mass extinction (St Audrie's Bay/East Quantoxhead, UK). *Earth Planet Sci Lett* 295(1-2):262–276.
36. Parker WG, Irmis RB, Nesbitt SJ (2006) Review of the Late Triassic dinosaur record from Petrified Forest National Park, Arizona. *Museum Northern Ariz Bull* 62:160–161.
37. Irmis RB, et al. (2007) A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. *Science* 317(5836):358–361.
38. Nesbitt SJ, et al. (2009) A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science* 326(5959):1530–1533.
39. Parker WG, Martz JW (2011) The Late Triassic (Norian) Adamanian–Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona. *Earth Environ Sci Trans R Soc Edinb* 101(Special Issue 3-4):231–260.
40. Lucas SG (1997) Upper Triassic Chinle Group, western United States: A nonmarine standard for Late Triassic time. *Late Paleozoic and Early Mesozoic Circum-Pacific Events and Their Global Correlation*, ed Dickins JM (Cambridge Univ Press, Cambridge, UK), pp 209–228.
41. Lottes AL, Rowley DB (1990) Reconstruction of the Laurasian and Gondwanan segments of Permian Pangaea. *Palaeozoic Palaeogeography and Biogeography, Memoir 12*, eds McKerrow WS, Scotese CR (Geol Soc, London), pp 383–395.
42. Kent DV, Irving E (2010) Influence of inclination error in sedimentary rocks on the Triassic and Jurassic apparent polar wander path for North America and implications for Cordilleran tectonics. *J Geophys Res* 115:B10103, 10.1029/2009JB007205.
43. Kent DV, Tauxe L (2005) Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. *Science* 307(5707):240–244.
44. Bilardello D, Jezek J, Kodama KP (2011) Propagating and incorporating the error in anisotropy-based inclination corrections. *Geophys J Int* 187(1):75–84.
45. Manabe S, Bryan K (1985) CO2-induced change in a coupled ocean-atmosphere model and its paleoclimatic implications. *J Geophys Res* 90(C6):11689–11707.
46. Frakes LA, Francis JE, Sykyus JI (1992) *Climate Modes of the Phanerozoic* (Cambridge Univ Press, Cambridge, UK), p 274.
47. Goddéris Y, et al. (2008) Causal or casual link between the rise of nannoplankton calcification and a tectonically-driven massive decrease in Late Triassic atmospheric CO2? *Earth Planet Sci Lett* 267(1-2):247–255.
48. Apaldetti C, Pol D, Martínez RN (2013) Evolución y patrones de ocupación de morfoespacios por dinosaurios Sauropodomorpha a través del límite Triásico–Jurásico. *Ameghiniana* 50(4):R12.
49. Held IM, Soden BJ (2006) Robust responses of the hydrological cycle to global warming. *J Clim* 19:5686–5699.
50. Schaller MF, Wright JD, Kent DV, Olsen PE (2012) Rapid emplacement of the Central Atlantic Magmatic Province as a net sink for CO2. *Earth Planet Sci Lett* 323-324:27–39.
51. Shubin NH, Sues HD (1991) Biogeography of early Mesozoic continental tetrapods: Patterns and implications. *Paleobiology* 17:214–230.
52. Cleveland DM, Nordt LC, Dworkin SI, Atchley SC (2008) Pedogenic carbonate isotopes as evidence for extreme climatic events preceding the Triassic-Jurassic boundary: Implications for the biotic crisis. *Geol Soc Am Bull* 120(11-12):1408–1415.
53. Kirschvink JL (1980) The least-squares line and plane and the analysis of palaeomagnetic data. *Geophys J R Astron Soc* 62:699–718.
54. McFadden PL, McElhinny MW (1990) Classification of the reversal test in palaeomagnetism. *Geophys J Int* 103:725–729.

Supporting Information

Kent et al. 10.1073/pnas.1402369111

Fig. S1. Gradational contact between mauve-colored floodplain and fluvial sandstones and overbank mudstones of the Ischigualasto Formation (lower half of photo) to the predominantly red fluvial siltstones and sandstones of the overlying Los Colorados Formation (cliffs in background) near outlet of Quebrada de la Sal and the base of the sampled section of the Los Colorados Formation.

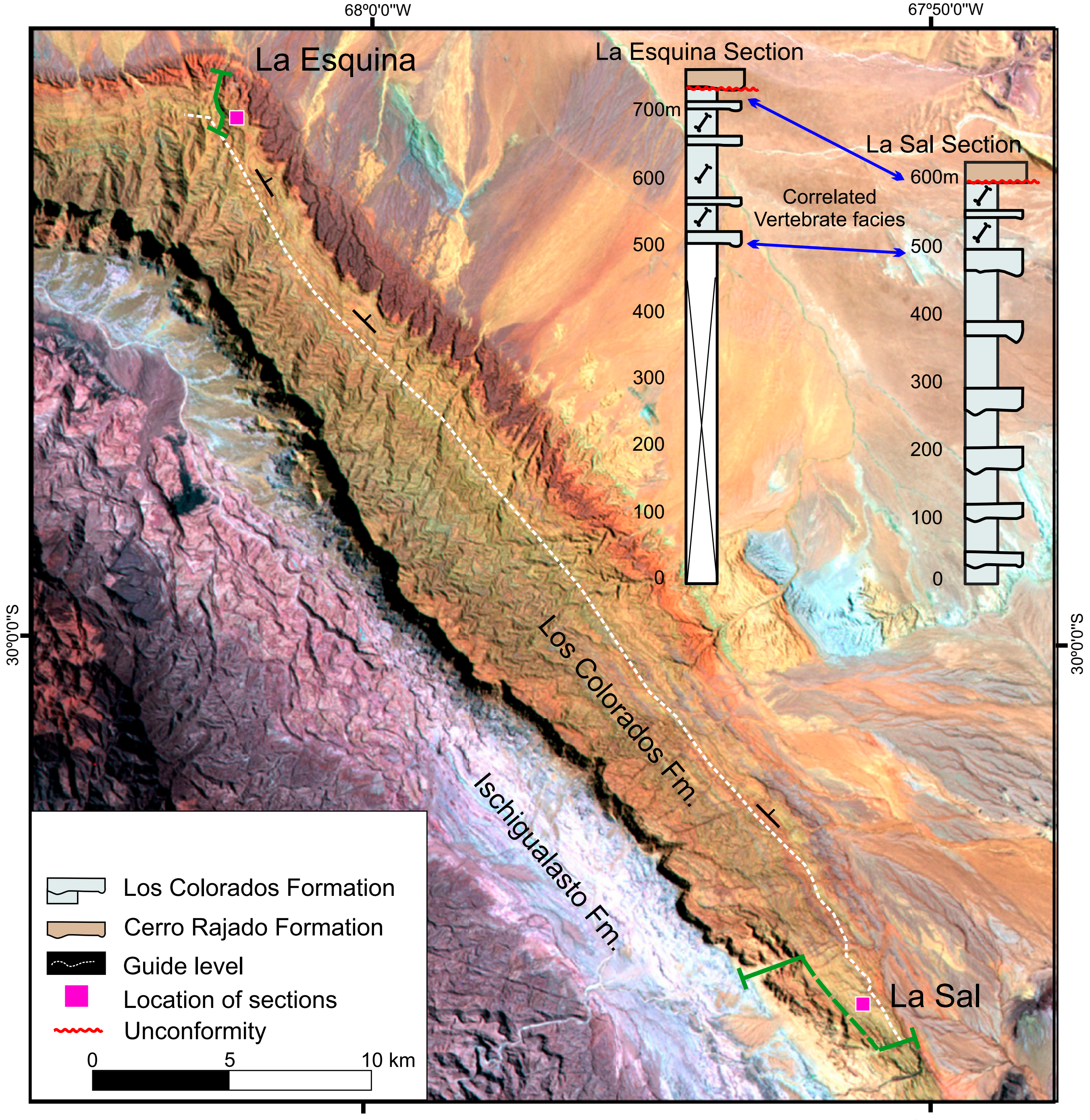

Fig. S2. Satellite image of the southern Ischigualasto–Villa Union Basin showing the continuity of exposures of the Los Colorados Formation between the La Sal section (green lines, dashed where the two subsections were linked), where the paleomagnetic sampling was done, and the La Esquina section (green line), where the La Esquina local fauna was defined. The dashed white line highlights the guide level used to correlate the sections. Lithostratigraphic profiles of each section with dominant sandstone bodies jutting out and finer-grained sediments recessed are shown in the upper right to illustrate how the vertebrate host sedimentary facies were identified and related in both sections, as well as the unconformable contact with Cerro Rajado Formation.

Table S1. Site-mean and formation-mean ChRM directions and corresponding VGPs for La Sal section of the Los Colorados Formation in the Ischigualasto–Villa Union basin (30°S, 68°W)

				ChRM		VGP			
Height (m)	ID	n	k	Dec (°)	Inc (°)	Lon (°)	Lat (°)	rLat (°)	Magzone
10	TIBH	3	33	199.2	66.2	259.2	−66.3	−83.8	LC1r
21	TIBI	3	56	2.3	−51.5	70.1	87.1	74.7	LC2n
30	TIBJ	3	27	21.3	−49.7	29.0	71.6	77.1	LC2n
50	TIEA	2	11	217.2	61.8	236.1	−57.7	−74.7	LC2r
57	TIBL	2	210	200.1	67.0	260.0	−65.2	−82.6	LC2r
68	TIBM	1	1	162.6	34.3	53.3	−70.7	−52.9	LC2r
76	TIBN	2	75	222.8	51.9	217.3	−53.6	−66.8	LC2r
80	TIEQ	2	8	247.4	61.7	235.5	−35.7	−53.1	LC2r
84	TIBO	1	1	193.1	56.4	238.0	−77.1	−83.7	LC2r
94	TIBP	2	33	201.5	54.1	221.9	−71.3	−80.9	LC2r
104	TIBQ	2	500	209.8	70.2	259.1	−57.7	−75.5	LC2r
115	TIBR	1	1	47.6	−59.7	50.7	50.2	66.6	LC3n
125	TIBS	3	65	17.6	−56.3	51.7	73.8	84.0	LC3n
136	TIBT	3	76	197.4	61.1	247.8	−71.5	−89.0	LC3r
145	TIBU	3	291	202.9	62.3	245.1	−67.3	−85.1	LC3r
155	TIBV	2	5	180.5	52.5	284.3	−86.9	−74.3	LC3r
165	TIBW	1	1	181.2	61.6	288.0	−77.2	−78.9	LC3r
172	TIEP	2	176	38.0	−64.6	62.1	56.4	74.1	LC4n
180	TICA	2	19	11.5	−62.5	81.7	73.4	86.3	LC4n
196	TICB	1	1	9.3	−63.4	88.5	73.3	84.5	LC4n
206	TICC	2	467	170.8	74.9	300.2	−57.8	−65.8	LC4r
215	TICD	1	1	358.7	−31.7	286.4	77.1	60.4	LC5n
228	TICE	1	1	213.3	60.9	235.3	−60.8	−77.4	LC5r
243	TICF	3	56	227.9	61.9	234.7	−50.0	−67.0	LC5r
252	TICG	4	21	231.6	67.1	244.4	−46.8	−64.8	LC5r
270	TICH	2	11	203.8	55.9	226.3	−69.1	−81.5	LC5r
298	TICK	2	92	153.5	67.2	329.4	−61.8	−60.0	LC5r
299	TIET	1	1	227.0	60.7	232.5	−50.7	−67.4	LC5r
309	TICL	2	549	103.7	81.8	310.6	−32.5	−40.0	LC5r
323	TICM	2	10	186.4	30.7	136.9	−75.3	−62.5	LC5r
332	TICN	2	131	174.8	51.4	355.9	−85.1	−70.0	LC5r
344	TICO	2	22	26.1	−66.4	72.9	62.7	80.8	LC6n
362	TICQ	2	58	2.2	−63.5	106.1	74.8	79.6	LC6n
371	TICR	2	23	0.4	−52.5	105.8	86.9	74.2	LC6n
381	TICS	2	338	6.0	−57.5	82.2	80.5	80.9	LC6n
388	TICT	1	1	25.8	−52.8	37.5	67.8	78.0	LC6n
406	TICU	2	35	160.1	59.3	344.7	−70.9	−62.9	LC6r
414	TICV	1	1	155.4	40.4	33.7	−67.0	−51.0	LC6r
416	TIEB	2	186	35.9	−64.2	61.9	57.9	75.6	LC7n
427	TICW	3	66	21.7	−54.3	42.5	71.1	81.0	LC7n
435	TICX	2	77	350.4	−60.8	142.6	75.9	70.9	LC7n
444	TICY	2	345	39.2	−64.2	60.8	55.7	73.4	LC7n
454	TICZ	2	6	15.6	−33.9	346.7	71.8	65.8	LC7n
462	TIEC	2	2	343.8	−63.9	146.6	69.9	66.7	LC7n
480	TIEE	2	390	214.9	58.3	229.0	−60.1	−75.5	LC7r
494	TIEF	2	2950	217.3	66.8	247.3	−55.9	−74.0	LC7r
505	TIEG	2	259	207.6	62.3	241.5	−64.2	−81.7	LC7r
525	TIEH	2	12	348.0	−45.4	215.5	79.0	62.1	LC8n
531	TIEI	2	217	45.9	−63.8	58.5	51.2	68.7	LC8n
544	TIEJ	2	243	11.0	−60.3	76.6	75.7	85.8	LC8n
551	TIEK	2	427	31.4	−61.3	57.0	62.0	78.9	LC8n
564	TIEL	2	590	19.8	−75.3	96.0	55.2	70.3	LC8n

Mean characteristic remanent magnetization (ChRM) direction (52 sites): D = 15.4°, I = −60.4° (A95 = 3.8°). Mean virtual geomagnetic pole (VGP) position (52 sites): Longitude (Lon) = 70.8°E, Latitude (Lat) = 71.8°N (A95 = 5.0°). Sampling level in stratigraphic height in meters from base of Los Colorados Formation for each sampling site (ID) at which a ChRM was isolated in number of samples (n) with a Fisher precision parameter (k; assigned 1 for only one sample) for mean direction (Dec, declination; Inc, inclination) in bedding coordinates and corresponding VGP position. rLat is latitude of VGP with respect to mean paleomagnetic north pole; Magzone is magnetic polarity zone where suffix n is for normal polarity and r is for reverse polarity. A95 is radius of circle of 95% confidence about the mean direction.