

# Climatically driven biogeographic provinces of Late Triassic tropical Pangea

Jessica H. Whiteside<sup>a,1</sup>, Danielle S. Grogan<sup>a</sup>, Paul E. Olsen<sup>b,1</sup>, and Dennis V. Kent<sup>b,c</sup>

<sup>a</sup>Department of Geological Sciences, Brown University, 324 Brook Street, Box 1846, Providence, RI 02912; <sup>b</sup>Lamont-Doherty Earth Observatory, Columbia University, 61 Route 9W, Palisades, NY 10964; and <sup>c</sup>Department of Earth and Planetary Sciences, Rutgers University, Piscataway, NJ 08854

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Although continents were coalesced into the single landmass Pangea, Late Triassic terrestrial tetrapod assemblages are surprisingly provincial. In eastern North America, we show that assemblages dominated by traversodont cynodonts are restricted to a humid 6° equatorial swath that persisted for over 20 million years characterized by “semiprecessional” (approximately 10,000-y) climatic fluctuations reflected in stable carbon isotopes and sedimentary facies in lacustrine strata. More arid regions from 5–20°N preserve procolophonid-dominated faunal assemblages associated with a much stronger expression of approximately 20,000-y climatic cycles. In the absence of geographic barriers, we hypothesize that these variations in the climatic expression of astronomical forcing produced latitudinal climatic zones that sorted terrestrial vertebrate taxa, perhaps by excretory physiology, into distinct biogeographic provinces tracking latitude, not geographic position, as the proto-North American plate translated northward. Although the early Mesozoic is usually assumed to be characterized by globally distributed land animal communities due to a lack of geographic barriers, strong provinciality was actually the norm, and nearly global communities were present only after times of massive ecological disruptions.

biotic provinciality | Cynodontia | orbital forcing | Procolophonidae | latitudinal gradient

Geographic and climatic barriers are among the main constraints on the distribution of organisms. During the Late Triassic, Pangea lacked significant geographic barriers nearly pole-to-pole, and was warm and equable without glaciation or sea ice (1). Nonetheless, when correlated temporally by nonbiostatigraphic means, diverse Late Triassic continental faunal and floral assemblages display dramatic differences across paleolatitude (e.g., refs. 2–4) (Fig. 1). Although the equator-to-pole temperature gradients may have been relatively weak, Milankovitch-type climatic variability expressed in precipitation and evaporation was nonetheless very important (5–8). Then, as now (9,10), this scale of temporal variability may have played a critical role in structuring terrestrial communities, and thus early Mesozoic sequences provide a unique window into the link between climate variability and biotic provinciality.

Here, we focus on the tropical regions of Late Triassic central Pangea and the role of traversodont cynodonts (basal synapsids) and procolophonids (parareptiles) as possible ecologically equivalent herbivores (Fig. 2) under different climatic regimes. We test the correlation between climate variability and biotic provinces within narrow swaths of time constrained by astrochronology, paleomagnetic polarity stratigraphy, and paleomagnetically determined plate position from long [ $>5$  million years (My)] lacustrine and associated fluvial records spanning 30° of paleolatitude. We show that faunal composition tracks different modes of orbitally forced climate variability that maintained Pangean faunal provinces and suggest that this may be a common feature of continental ecosystems.

## Geologic, Climatic, and Biotic Context

Exposed eastern North America rift basins, formed during the incipient breakup of Pangea, comprise a northeast-southwest transect across the paleo-equator and tropics (Fig. 1). Best known is the Newark basin that, during the approximately 32 My. covered by its continuously cored record (11, 12), translated northward with central Pangea, transecting zonal climate belts from the equator to 20°N (8, 13, 14). The astrochronologic and paleomagnetic polarity constraints on this sequence allow tight temporal calibration and correlation to other basin sections in eastern North America (Fig. 1). Perhaps because of the extreme continentality of the climate of Pangea or elevated temperatures associated with high atmospheric CO<sub>2</sub> concentrations (15, 16), these lacustrine records were extremely sensitive to insolation changes driven by celestial mechanics (6, 7, 17) as exemplified by the tropical (5–20°N) Newark basin lacustrine record displaying lake-level cycles with periods of approximately 20 thousand years (ky) (precession), approximately 100 ky (short eccentricity), and 405 ky (long eccentricity) (6). This record also reveals longer periods of climatic precession modulation of approximately 1.8 My and approximately 3.5 My cycles (7), but it notably lacks convincing obliquity periods (6), indicating that precession and eccentricity controlled lake-level cyclicity at these latitudes.

To examine the links between the expression of cyclical climate mode and biotic provinciality, we analyzed cores and measured outcrop sections in seven eastern North American rift basins from Nova Scotia to South Carolina, which together with the 20° of northward translation of the Newark basin extend the latitudinal transect an additional 5° south and 5° north, spanning a total of 30° of latitude (Fig. 1).

Many terrestrial vertebrates have been found in these rift basin sequences, including rich assemblages of hitherto unexpected composition (18). Most surprising are assemblages containing abundant small (skull length, 3–10 cm) traversodont cynodonts from multiple localities and levels within the Richmond and Deep River basins (Figs. 1 and 2) (e.g., refs. 18–20). Such assemblages were previously known exclusively from Gondwana (e.g., refs. 21, 22), and are still unknown from the American Southwest (23). Coeval strata from other eastern North America basins have produced assemblages of more familiar aspect, where procolophonid parareptiles of similar size to the cynodonts are abundant (24, 25). In these strata, traversodont cynodonts are either absent or very rare.

Traversodont cynodonts and procolophonids have dentitions that display at least superficially similar specializations for herbivory (25–27), consistent with a diet of tough, fibrous plant material (28, 29) (Fig. 2). Their mutually exclusive abundance patterns

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<sup>1</sup>To whom correspondence may be addressed. E-mail: Jessica\_Whiteside@Brown.edu or polsen@ldeo.columbia.edu.

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mechanisms. Biotic provinciality driven by zonal climate belts coupled with ecological incumbency, priority, or niche preemption effects (e.g., ref. 57) that develop as a consequence of the basic climatic structure may be prevalent when geographic barriers are minimal except at times of extreme ecological reorganization, such as the end-Permian (2, 58), and end-Triassic mass extinctions (2, 16) and the Paleocene-Eocene Thermal Maximum (59, 60) hyperthermal.

## Methods

**Depth Rank and Color.** Depth rank, a proxy of relative lake depth, is a classification of facies by suites of sedimentary structures in which facies are assigned a value of 0 to 5 in order of increasing relative water depth (7, 17). Color is related to the reduction-oxidation state of the sedimentary environment.

**Carbon Isotopic Analyses.** From each section of interest, we took samples at submeter intervals for bulk carbon isotopic ( $\delta^{13}\text{C}_{\text{org}}$ ) and TOC analyses. Samples were weighed into methanol-rinsed Ag boats, acidified in a desiccator over concentrated HCl for 72 h at 60–65 °C, dried for 24 h at 60–65 °C, and dried for an additional 24 h at 60–65 °C in a desiccator with silica gel. Samples were wrapped in Sn immediately prior to analysis.  $\delta^{13}\text{C}_{\text{org}}$  and TOC measurements were made on a Costech 4010 Elemental Analyzer (EA) with a Zero-Blank carousel coupled to a Thermo DeltaVPlus stable light isotope ratio mass spectrometer (IRMS) at Brown University. Samples were flash-combusted in the EA at 1020 °C in a pure oxygen pulse, with resulting products being fully oxidized to  $\text{CO}_2$  in a metal oxide bed, subsequent reduction of  $\text{NO}_x$  to  $\text{N}_2$  in a copper bed, and chromatographic separation prior to admission to the IRMS. Standardization with reference pulses resulted in isotopic accuracy and precision better than 0.3% for  $\text{CO}_2$ .

**Time Series Analysis.** Time series analysis was performed using Analyseries 2.0.4.2 (61). The age models were developed either by direct correlation to the Newark-APTS by paleomagnetic polarity stratigraphy or by identification of one of the thickness periodicities as the 405-ky cycle of eccentricity (see *SI Text* for details).

**Daily Insolation Model.** For this model, daily solar insolation averaged over 24 h at latitude  $\varphi$  and day  $\lambda$  (rad, independent of calendar date) is given by (62, 63)

$$W = (S_0/\pi) \cdot [1 + e \cos(\lambda - \omega - \pi)]^2 / (1 - e^2)^2 \cdot (H_0 \sin \varphi \sin \delta + \cos \varphi \cos \delta \sin H_0), \quad [1]$$

where  $S_0$  is the solar constant (1,365 W/m<sup>2</sup>),  $H_0$  is the hour angle, and  $\delta$  is the declination angle. The orbital parameters of eccentricity  $e$ , obliquity  $\varepsilon$ , and precession  $\omega$  are given by Laskar et al. (64) (abbreviated below as La2004) and provide

$$\sin \delta = \sin \varepsilon \sin \lambda \quad [2]$$

and

$$\cos H_0 = -\tan \varphi \tan \delta. \quad [3]$$

At the equator, maximum insolation occurs approximately at the equinoxes (vernal equinox,  $\lambda = 0$ ; autumnal equinox,  $\lambda = \pi$ ), and minimum insolation occurs approximately at the solstices (summer solstice,  $\lambda = \pi/2$ ; winter solstice  $\lambda = 3\pi/2$ ), although the exact values of maximum and minimum  $\lambda$  vary slightly over time (37). Moving away from the equator, maximum and minimum  $\lambda$  vary with increasing magnitude.

To find the magnitude and day of maximum and minimum insolation at latitude  $\varphi$ , we use a MATLAB program that implements Eq. 1 and the La2004 orbital parameter solution (*SI Text*). The program iteratively calculates daily solar insolation for  $\lambda_{\text{max}} \pm d$  rad and  $\lambda_{\text{min}} \pm d$  rad with steps of 0.02 rad, where  $\lambda_{\text{max}}$  and  $\lambda_{\text{min}}$  are the equinoxes and solstices, respectively. For  $\varphi < 10^\circ$ ,  $d = 0.8$  is sufficient. For  $\varphi > 10^\circ$ ,  $d$  must increase with  $\varphi$ .

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# Supporting Information

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## SI Text

**Age Models and Explanation of Spectra for Sections in Main Text Fig. 3, Vago no. 1, Vinita Formation, Richmond Basin.** The upper Vinita Formation of the Richmond basin has produced the second-richest traversodont-dominated assemblage (1, 2) known from the Newark Supergroup. The Richmond basin section is coal-bearing, but unlike the Deep River basin, most of the preserved basin section is lacustrine, and the markedly cyclical portion of the section (the Vinita Formation) is older than the Cumnock Formation, approximately the same age as the Pekin Formation.

The Vinita Formation differs dramatically from most other formations of the eastern North American rifts in that much of the lacustrine section lacks signs of subaerial exposure, indicating that the lakes rarely dried out. The Vago no. 1 (Fig. S1) core from the middle part of the Vinita Formation lacks any evidence of subaerial exposure. The observed cyclicity consists of alternating intervals of black microlaminated mudstone and interbedded graded sandstones (turbidites) with intervals of less well laminated mudstone.

The exact position of the Vago no. 1 core (Table S1) within the Vinita Formation is uncertain, but based on its overall black shale lithologies in comparison with the industry wells drilled in the basin, especially the Horner no. 1 well (Fig. S2 and Table S1), it appears to come from the lower third of the Vinita Formation, in the Manakin Member of ref. 3.

The accumulation rate in the Horner no. 1 well in the Richmond basin (Table S1) can be used to constrain that in the Vago no. 1 core (Fig. S2). We performed Fourier analysis of the pollen data displayed in ref. 4 (Dataset S1, A). We normalized and then averaged the individual spectra of pollen counts to produce an average spectrum (Fig. S2). The scale of the largest cycle, with a period of 832 m (2,731 ft), is comparable to the 1.75 million year (My) cycle identified in the Newark basin astronomically tuned geomagnetic polarity time scale (Newark-APTS) (5, 6). If this is correct, the cycle with a period of around 178 m (585 ft) should be the 405 thousand year (ky) eccentricity period with a corresponding inferred accumulation rate of 0.440 m/ky (1.5 ft/ky).

Fourier analysis of depth ranks from the entire Vago no. 1 core (Fig. S1; Table S2; Dataset S1, B; and Fig. 3 of the main text) shows prominent frequencies with periods at 9.38 m (31 ft) and 203.2 m (667 ft). Assuming that the higher frequency is the 20-ky cycle of climatic precession, the 203.2-m period corresponds to the 405-ky cycle. The small peak at 38.1 m (125 ft) probably represents the approximately 100-ky cycle. The inferred accumulation rate of 0.469 m/ky is close to that derived from the Horner no. 1 core (0.440 m/ky).

We sampled an interval from 26.8 to 64.5 m (88.0 to 211.7 ft) in the Vago core for bulk organic carbon isotopic analysis (Dataset S1, B and Fig. S1). Sixty-four samples were recovered amounting to 1 sample/0.4 m or 1 sample/900 y based on our accumulation rate model. The overall pattern of the relationship between depth ranks, total organic carbon (TOC), and  $\delta^{13}\text{C}_{\text{org}}$  is that more  $^{13}\text{C}$ -enriched values tend to be present in the deep water units, and values more depleted in  $^{13}\text{C}$  are present in the shallower water units, consistent with the pattern seen in the Lockatong Formation. However, Fourier analysis of this interval shows the same peaks as the depth rank data from the entire core, but also a prominent peak at around 4.5 m (15 ft). Based on setting the 9.3-m peak to 20 ky, this peak should be about 10 ky. This semiprecessional peak corresponds in the time domain to a return to higher depth ranks about half way through the 20-ky cycle. Malinconico (7) looked at this same interval using organic

petrographic techniques and noted that the mudstones with higher depth ranks have more algal material, whereas the mudstones with more poorly developed laminations tend to lack algal material. The latter units in our analyses correspond to the deeper water phase of the semiprecessional cycle and tend to have values more enriched in  $^{13}\text{C}$  than the microlaminated units, which are the deepest water phase of the 20-ky climatic precession cycle. Ediger (8) also identified a double cycle in organic petrology and reasoned that it corresponded to the combined effect of the 20-ky precession and 40-ky obliquity cycles. At that time there was no expectation that a 10-ky cycle should be present at equatorial latitudes, and it was not known that the Vinita Formation was deposited at the equator. The “double cyclicity” observed by Ediger (8) and Malinconico (7) is more parsimoniously explained as an expression of the 10-ky cyclicity caused by local forcing at the equator.

**MO-C-2-81 Core, Cumnock Formation, Deep River Basin.** The Deep River basin is the most southerly exposed Pangean rift in eastern North America. The three nominal subbasins (Durham, Sanford, and Wadesboro) contain important cyclical lacustrine strata. The best-known of the lacustrine units, the coal-bearing Cumnock Formation of the Sanford basin, is comprised of Milankovitch-forced cycles (9, 10) and is represented by a series of 30.5- to 152.4-m (100- to 500-ft) cores taken for hydrocarbon exploration during the 1980s.

The MO-C-2-81 core (Figs. S1 and S3 and Table S1) recovered nearly the entire Cumnock Formation, although only the upper portion of the core was suitable for  $\delta^{13}\text{C}_{\text{org}}$  analysis because of an igneous sill at the core bottom. We took 104 samples amounting to a rate of 1 sample/0.3 m or 1 sample/1,500 y based on the age model described below. Fourier analysis of the color proxy data (Fig. 3 of the main text and Dataset S1, B) reveals that the most prominent frequencies in the core are at periods of 3.8 m (12.5 ft) and 4.3 m (14.0 ft), and at 24.3 m (79.8 ft) and 82.1 m (269.4 ft).

We constrained the accumulation rate of the MO-C-2-81 core by paleomagnetic correlation to the Newark-APTS (Dataset S1, C). Because of the sill at the bottom of MO-C-2-81, this core could not be used for paleomagnetic analysis. The core MO-C-4-81 (Table S1 and Fig. S3) was selected instead for paleomagnetic analysis because it consists largely of red strata, whereas gray strata of the Cumnock tends not to produce interpretable paleomagnetic results. Correlation to MO-C-2-81 is based on cyclostratigraphy (Fig. S3). We took 49 2.5-cm-diameter plugs of MO-C-4-81 for paleomagnetic analysis following the sampling procedure and analytical methods described by Kent et al. (11) (processed by M. Et-Touhami and P.M. LeTourneau) (Dataset S1, C). Plugs were drilled perpendicular to the core axis (assumed vertical) and where bedding dips were discernable, in the down-dip direction to assist in the interpretation of polarity in these azimuthally unoriented cores. Vector endpoint diagrams of thermal demagnetization of the natural remanence in 10 or more steps to 575 °C for gray samples (expected to have a magnetite remanence carrier) and 675 °C for red samples (expected to have a hematite carrier) were used to interpret magnetization components and to infer the polarity of the characteristic magnetization as gauged with respect to a normal polarity overprint that is commonly present according to fully oriented outcrop samples. The polarities could not be determined for samples with scattered (mainly gray) or even univectorial demagnetization trajectories. In the case of MO-C-4-81, both normal and reverse polarities are present, comprising an upper reverse polarity zone and a lower

mainly normal polarity zone, with a thin but distinct reverse polarity interval toward the base (Fig. S3).

To gain greater stratigraphic scope, we also recovered 47 plugs from the Deep River basin core CH-C-1-81 (Dataset S1, C). This core intersects red beds at the bottom (nominal Peking Formation) and a significant thickness of Sanford Formation at the top. Both in terms of gross lithology and detailed cyclostratigraphy, CH-C-1-81 is much more similar to MO-C-2-81 than it is to MO-C-4-81. Again, both normal and reverse polarities were present and as predicted for a basinal core, compared to MO-C-481, a much larger proportion of gray strata with nearly the full extent of the Cumnock Formation being represented. A transition from predominately normal to reverse polarity is apparent in the middle of the formation. There is a normal fault near the bottom of the core, which unfortunately cuts out strata in the position of the small reverse interval in the lower part of MO-C-4-81. Another small reverse interval is present at the base of the core, however. Both of these polarity zones would have a duration less than 40 ky based on our assessments of the cyclicity and the independently derived accumulation rate.

There is a prominent diabase sill in the upper part of the Cumnock Formation in CH-C-1-81. This sill is of normal polarity, and the surrounding aureole is also of normal polarity, surrounded by strata of reverse polarity. We omit this normal polarity interval from the composite stratigraphy because it is clearly an overprint from the sill intrusion. Finally, at the top of the core there is a short but distinct interval of normal polarity. Because it is represented by only three closely spaced samples, we do not regard it as a likely candidate for the base of a major normal polarity zone.

The Cumnock Formation cores barely penetrate into underlying red strata, and having only two main polarity zones, a unique correlation is not possible. To capture greater stratigraphic context and to place the Cumnock cores into the Newark-APTS, we sampled the SO-C-2-81 core in the Dan River basin, which recovered the basal part of the lower member of the Cow Branch Formation (Fig. S3), with 60 2.5-cm plugs for paleomagnetic analysis. The detailed stratigraphy of the lower member of the Cow Branch Formation is nearly identical to that of the Cumnock Formation including the position of coal beds, despite the fact that the two sites are 145 km apart in separate basins. Fourier analysis of the upper 122 m (400 ft) of the SO-C-2-81 core shows a hierarchy of frequencies similar to that seen in the Cumnock Formation (Fig. S4 and Dataset S1, B), except that the spectrum is noisier and the accumulation rate is higher in the lower member of the Cow Branch Formation, compared to the Cumnock Formation. The ratios of the homologous thickness periods corresponding to the approximately 100-ky cycles in the Cumnock and lower Cow Branch (23.8 m/33.9 m) is 0.702.

Polarities could not be determined for most samples from the Lower Cow Branch member because the lithologies are gray to black and the samples usually alter during thermal demagnetization. The exceptions occur near the very base of the formation where red beds are intercalated with gray, in which case all determinable samples were of normal polarity. Normal polarities were also seen in the mostly red Pine Hall Formation in SO-C-2-81, consistent with a close correlation of the lower Cumnock Formation. Although only two polarity zones are present in the composite section, the lower member of the Cow Branch lies stratigraphically below the long polarity stratigraphy described by Kent and Olsen (12) and thus has a well-constrained correlation to the Newark-APTS. Based on placing the SO-C-2-81 core in context with the rest of the Dan River basin polarity stratigraphy (Fig. S4), the normal-reverse couplet seen in the Cumnock is most simply correlated to polarity chron E8 of the Newark-APTS (Figs. S3 and S4), although there is a thin but well-defined (in terms of demagnetization behavior) reverse polarity interval in samples 187.70, 192.02, and 194.65 m (615.8, 630.0, and 638.6 ft). This reverse zone is most simply correlated to the

reverse polarity zone at the base of CH-C-1-81. The two thin reverse zones were not observed in E8n in the Princeton core, which may be due to much lower temporal resolution and/or continuity in those fluvial sediments.

Based on this correlation (Fig. S3), the Cumnock Formation comprises only two 405-ky cycles, the period of which corresponds to the cycle thickness of 82.1 m (Fig. S3). The accumulation rate of the lower member of the Cow Branch based on this correlation is 0.312 m/ky. When this accumulation rate is multiplied by the ratio between the Cumnock and lower Cow Branch formations the accumulation rate for the Cumnock Formation is 0.219 m/ky.

Assuming this average accumulation rate for the Cumnock, data on rock color have periods of 3.8, 4.3, and 24.3 m that correspond in time to periods of 17.4, 19.6, and 110.0 ky, respectively, which match well the predicted period of the two modal precessional periods and the short eccentricity cycle. Less well-defined peaks exist at 2.8 m (12.8 ky) and 7.3 m (33.3 ky).

Periods indistinguishable from those in the rock color data are observed in the portion of the core we sampled for  $\delta^{13}\text{C}_{\text{org}}$  (Fig. 3 in the main text and Dataset S1, B), although, because this is a subsample, all of the peaks are more spread out. TOC concentration variations are nearly identical to the color periods.  $\delta^{13}\text{C}_{\text{org}}$  values tend to be more enriched in  $^{13}\text{C}$  in the deeper-water, more organic-rich units and more  $^{13}\text{C}$ -depleted in the organic-poor units, following the pattern seen in the Lockatong Formation of the Newark basin (13, 14), typical of broad rifts of eastern North America where the enhanced efficacy of the biological pump during deep-water times overwhelmed other effects. Fourier analysis of the  $\delta^{13}\text{C}_{\text{org}}$  data indicates a strong shift toward the 24.3-m (111.0-ky) cycle and as much power at the semiprecessional period 2.2 m (10.1 ky) as at the precessional periods around 4.2 m (19.2 ky) (Fig. 3 in the main text). Interestingly, both rock color and the geochemical data have periods very similar to those seen in Fourier analysis of gamma ray data from the Butler no. 1 exploration well described by Hu and Textoris (10).

Based on available paleomagnetic data (Fig. S3), the Cumnock Formation was deposited beginning at 226 Ma at the equator. Traversodonts are known from the shallow water facies of the Cumnock Formation (15, 16), the underlying Peking Formation (16), and the overlying Sanford Formation (17) in the Sanford subbasin as well as from Lithofacies association II the Durham basin (18). Extrapolating from the correlation to the Newark-APTS, Fig. S3 and biostratigraphic correlation (19), the upper Peking Formation was deposited at 2°S latitude at approximately 231 Ma. The youngest traversodont-producing strata in the Sanford subbasin are in the lower Sanford Formation, deposited at approximately 1°N latitude at approximately 224 Ma. The traversodonts from Lithofacies Association II in the Durham subbasin are the same age as the middle Sanford Formation of the Sanford subbasin and were deposited at approximately 3°N at 222 Ma (20). In total, the Deep River basin traversodont-bearing strata were deposited in a 5° swath around the Triassic paleoequator, over at least a 9-My interval, during which time the climate responded to the semiprecessional cycle.

**Solite Quarry, Upper Member of the Cow Branch Formation, Dan River Basin.** The Cow Branch Formation of the Dan River (Danville) basin is a thick, (+2 km) cyclical gray and black lacustrine unit comprised of two members informally termed the lower and upper members (Figs. S1, S3, and S4). A very rich aquatic assemblage has been recovered from this formation (21, 22), and the paleomagnetic reversal stratigraphy of the basin section is known in more detail than any other southern basin (12) (Fig. S4). As yet, no traversodonts or procolophonids are known from this basin; however, there has been no prospecting in the more terrestrial strata in which they would be expected. The lacustrine



strata do show the strongest semiprecessional cyclicity of all units in this study (Fig. S1).

The lacustrine record of the upper member of the Cow Branch Formation is best displayed in the three quarries of the former Virginia Solite Corporation in Leaksville Junction, North Carolina. We measured depth ranks for all three quarry sections and computed their fast Fourier transform (FFT) power spectra (Fig. S4 and Table S1). All three sections have significant periods in their spectra at around 46, 11, and 6 m that are highly coherent (Fig. S4). By correlating the magnetic polarity stratigraphy of the Dan River basin with the Newark basin time scale, we determined an average accumulation rate for the Solite sections of 0.463 m/ky (Fig. S4). Using this accumulation rate, the main periods in the Solite depth rank sections are roughly 100, 24, and 13 ky (Figs. S1 and S4). In addition, section 2 is just long enough to begin to have resolvable power at 405 ky (175 m, 378 ky). Field mapping confirms that the sedimentary expression of the 400-ky cycle is a prominent part of the Dan River section in general (12).

The Dan River basin lacustrine record thus shares with the Newark basin periodic lake level cycles of roughly 400, 100, and 20 ky. The characteristic two peaks that average approximately 100 ky are also present, as seen in the Newark basin power spectra (Fig. S1). However, unlike the Newark basin record, the most prominent cycles in all three Dan River basin sections are of 10- to 15-ky duration. Visual examination of the Solite quarry outcrops reveals that well-developed cycles comparable to those attributed to the approximately 20-ky cycles in the Newark basin are present, and these correspond to the approximately 20-ky cycles seen in the power spectra (Fig. 3 in the main text). However, each of these cycles tends to have two deep-water intervals, rather than just one as seen in the Newark basin. The two deep-water intervals are responsible for the approximately 10-ky peaks in the power spectra.

We analyzed 15 samples of the uppermost two cycles in section 2 of the Solite Quarry for  $\delta^{13}C_{org}$ . The upper cycle produces the lagerstätten described in refs. 21 and 22 (Fig. S3 and Dataset S1, B). Sampling density amounted to about 1 sample/0.6 m or 1 sample/1,600 y, using our age model. These samples had been collected in the early 1980s and analyzed for TOC, carbonate, and sulfur at that time (23). Both cycles preserve a pattern comparable to that seen in the narrow rift basins of eastern North America, with relatively negative values in the deeper water units and relatively more positive values in the shallow water units. This pattern differs from that seen in the Cumnock Formation in which the more important process for the isotopic ratios of organic matter seems to have been the efficacy of the biological pump (Fig. S1). As expected from the Fourier analysis of depth ranks, there are two zones of relative negative values per cycle due to preferential preservation of lignin-derived organic matter in the shallow water units. We note that the Dan River basin, at least as presently preserved, is the narrowest of all the exposed rift basins (Fig. 1 in the main text), and the strata were deposited at a paleolatitude of 4° (Fig. 1 in the main text) (24).

**Nursery No. 1 Core, Lockatong Formation, Newark Basin.** Newark basin cyclicity has been understood in broad outline for almost half a century (25), and nearly the entire cyclostratigraphy has been recovered in core and described (5, 6, 11). For this study we selected the middle Lockatong Formation from about the middle of the Byram Member to the middle of the Skunk Hollow Member in the Nursery no. 1 core (Fig. S1). Based on magnetostratigraphic polarity correlation (Fig. S4), we analyzed depth ranks from the interval that is directly contemporaneous with section 2 of the Solite Quarry section (Dataset S1, B). The most prominent period is at 4.6 m corresponding to the 20-ky cycle, and there are two other strong periods at 20 m (90 ky) and 100 m (approximately 400 ky) based on the FFT consistent with the results of Olsen and Kent (26). Although there is a minor

period at 2.8 m (12 ky), it is obvious that there is far less of a semiprecession signal in the Lockatong compared to the Solite sections. The paleolatitude of Nursery no. 1 core is 7° (Fig. 1 in the main text) (27).

**Andrus no. 1 and Lenn Bros. no. 1 cores, Balls Bluff Formation, Culpeper basin.** We examined two cores from the largely red Balls Bluff Formation of the Culpeper basin recording depth ranks and color (Dataset S1, B). The two cores stratigraphically overlap with an unambiguous cyclostratigraphic correlation (Fig. S1) and were reported on briefly and figured with the polarity stratigraphy by Olsen and Kent (27). Correlation with the Newark basin section is straightforward. The paleolatitude of these cores was 13° N (Fig. 1 in the main text). Based on correlation to the Newark-APTS, the accumulation rate averages 0.2225 m/ky. The prominent thickness periods at 18.7 ky (4.2 m), 22.0 ky (4.9 m), and 23.4 ky (5.2 m) represent climatic precession, the periods at 86.7 ky (19.3 m) and 112.3 ky (25.0 m) represent short eccentricity, and the cycle at 380.6 ky (84.7 m) is the 405-ky long eccentricity cycle. Other prominent thickness periods at 7.3 and 11.4 m may be smeared-out 20-ky cycles, although similar periods occur in the Nursery core. There are only hints of semiprecessional periods at approximately 12.5 ky (2.8 m), similar to the Nursery core. The paleolatitude of this sequence is 12°N.

**Somerset no. 1 Core, Passaic Formation, Newark Basin.** This core (Fig. S1) was studied as part of the original series of papers on the Newark basin coring project (e.g., refs. 11 and 26), and the FFT of this specific part of the Nursery core (Dataset S1, B) is closely comparable to that of the contemporaneous Andrus and Lenn Bros. cores. Here we use the Newark-APTS the same way we did for the latter and calculate an average accumulation rate of 0.1647 m/ky. The untuned spectrum of this part of the Somerset core has prominent periods at 21.6 ky (3.6 m), 26.4 ky (4.4 m), 108.8 ky (17.9 m), and 411.2 ky (67.7 m). As in the Andrus and Lenn Bros. cores, there is a hint of semiprecession at approximately 12 ky (2.0 m). Kent and Tauxe (24) corrected the paleolatitudes originally determined for the Newark basin cores (11) for inclination error, and this forms the basis of all the paleolatitudes used here, extrapolated from the time-space nomogram of Fig. 1 in the main text. Consequently, the paleolatitude for this part of the Somerset core is 15°N.

**Methods and Background for Insolation Model.** At the equator, the sun passes overhead twice a year, once at the vernal equinox ( $\lambda = 0$ ) and once at the autumnal equinox ( $\lambda = \pi$ ). This leads to two potential times of maximum daily insolation during the year, and a complementary twice yearly minimum daily insolation at the summer solstice ( $\lambda = \pi/2$ ) and winter solstice ( $\lambda = 3\pi/2$ ).

Daily solar insolation averaged over 24 h at latitude  $\phi$  and day  $\lambda$  (rad, independent of calendar date) is given by (28, 29)

$$W = (S_0/\pi) \cdot [1 + e \cos(\lambda - \omega - \pi)]^2 / (1 - e^2)^2 \cdot (H_0 \sin \phi \sin \delta + \cos \phi \cos \delta \sin H_0), \quad [S1]$$

where  $S_0$  is the solar constant (1,365 W/m<sup>2</sup>),  $H_0$  is the hour angle, and  $\delta$  is the declination angle. The orbital parameters of eccentricity  $e$ , obliquity  $\epsilon$ , and precession  $\omega$  are given by Laskar et al. (30) (abbreviated below as La2004) and provide

$$\sin \delta = \sin \epsilon \sin \lambda, \quad [S2]$$

$$\cos H_0 = -\tan \phi \tan \delta. \quad [S3]$$

Eq. S1 can be simplified for the equatorial case (31–33):

$$W_{eq} = (S_0/\pi) \cdot [1 + e \cos(\lambda \cdot \omega \cdot \pi)]^2 / (1 - e^2)^2 \cdot \cos \delta. \quad [S4]$$

As shown by Ashkenazy and Gildor (33), because  $e \ll 1$  and  $\sin(\varepsilon) \approx \varepsilon$ , Eq. S4 can be approximated by

$$W_{\text{eq}} \approx (S_0/\pi(1 - e^2)^2) \cdot \left(1 - 2e \cos(\lambda \cdot \omega) - \frac{1}{2}e^2 \sin^2 \lambda\right). \quad \text{[S5]}$$

Earth's precession ( $\omega$ ) dictates which equinox receives greater daily insolation at the equator each year. As shown by Berger et al. (32), if we assume eccentricity ( $e$ ) and obliquity ( $\varepsilon$ ) constant over an approximately 21-ky precession period, then

Vernal equinox ( $\lambda = 0$ ) is maximum for  $\pi/2 \leq \omega \leq 3\pi/2$

Autumnal equinox ( $\lambda = \pi$ ) is maximum for  $3\pi/2 \leq \omega \leq 2\pi$ ,

$$0 \leq \omega \leq \pi/2$$

Summer solstice ( $\lambda = \pi/2$ ) is minimum for  $0 \leq \omega \leq \pi$

Winter solstice ( $\lambda = 3\pi/2$ ) is minimum for  $\pi \leq \omega \leq 2\pi$ . [S6]

Precession has an approximately 21-ky cycle, and so the maxima (and minima) switch between the equinoxes (and the solstices) twice every 21 ky. This can be seen as an approximately 11-ky cycle in the spectral analysis of maximum and minimum equatorial insolation (see figure 4c and d in ref. 33). As illustrated by Eq. 6, switching between equinoxes and switching between solstices as the insolation extremes is out of phase by  $\pi/2$  in the precessional index. Therefore, one of the two extremes switches seasons approximately every 5 ky, as can be seen by the 5-ky cycle in the spectral analysis of maximum-minimum insolation (figure 5 in ref. 32). The approximately 100-ky and approximately 405-ky cycles are also observed in the spectral analyses due to the modulation of equatorial insolation by eccentricity.

Maximum and minimum insolation do not always occur precisely on the equinoxes and solstices. The roots of differentiating Eq. 5 with respect to  $\lambda(\delta W_{\text{eq}}/\delta \lambda = 0)$  gives a better approximation of the days ( $\lambda$ , in rad) of maximum and minimum insolation. Let the expected days of maxima (equinoxes,  $\lambda = 0$  and  $\lambda = \pi$ ) and minima (solstices,  $\lambda = \pi/2$  and  $\lambda = 3\pi/2$ ) be called  $\lambda_e$  and the approximated days of maxima and minima be called  $\lambda_a$ . Then, using the approximations given by Ashkenazy and Gildor (33),

$$\cos \lambda_e \approx \cos \lambda_e - \sin \lambda_e (\lambda_a \cdot \lambda_e) \quad \text{[S7]}$$

$$\sin \lambda_e \approx \sin \lambda_e + \cos \lambda_e (\lambda_a \cdot \lambda_e), \quad \text{[S8]}$$

a solution for the days of maxima and minima insolation is found to be (33)

$$\lambda_0 = \sin \omega / [(-\varepsilon 2/2e) + \cos \omega] \quad \text{for } \lambda \approx 0 \quad \text{[S9]}$$

$$\lambda_\pi = \sin \omega / [(\varepsilon 2/2e) + \cos \omega] + \pi \quad \text{for } \lambda \approx \pi \quad \text{[S10]}$$

$$\lambda_{\pi/2} = -\cos \omega / [(\varepsilon 2/2e) + \sin \omega] + \pi/2 \quad \text{for } \lambda \approx \pi/2 \quad \text{[S11]}$$

$$\lambda_{3\pi/2} = -\cos \omega / [(-\varepsilon 2/2e) + \sin \omega] - \pi/2 \quad \text{for } \lambda \approx 3\pi/2. \quad \text{[S12]}$$

These adjustments to the timing of insolation extremes do not reduce the strength of the approximately 11-ky cycle, and they have been shown to enhance the strength of the eccentricity cycles seen in frequency analysis (see figure 4 in ref. 33).

Moving away from the equator, the timing of insolation extremes,  $\lambda$ , vary with increasing magnitude. To find the magnitude and day of maximum and minimum insolation at nonequatorial latitude  $\varphi$ , we use a MATLAB program that implements Eq. 1 and the La2004 orbital parameter solution (see below and Dataset S1, D). The program iteratively calculates daily solar insolation for  $\lambda \text{ max } \pm d$  rad and  $\lambda \text{ min } \pm d$  rad with steps of 0.02 rad, where  $\lambda \text{ max}$  and  $\lambda \text{ min}$  are the equinoxes and solstices, respectively. For  $\varphi < 10^\circ$ ,  $d = 0.8$  is sufficient. For  $\varphi > 10^\circ$ ,  $d$  must increase with  $\varphi$ .

Because of chaotic diffusion of planetary orbital motions and uncertainties in initial condition, the La2004 solution for the orbital parameters is not reliable beyond 50–60 Ma. However, the 405-ky eccentricity cycle is more stable than the others and deviates by only two periods by 250 Ma (30), and the frequencies of approximately 20 ky, approximately 40 ky, approximately 100 ky, and approximately 405 ky have been observed in cyclic sedimentary sequences through the Phanerozoic (34, 35). Although differences from Cenozoic values are to be expected in deep time, we find it reasonable to use the La2004 solution in these calculations to characterize the cyclicity in low-latitude insolation during the Late Triassic because the basic geometry problem will not have changed.

**Matlab Script (See Dataset S1, D).**

---

```

%This program inputs values of eccentricity, obliquity and
%precession angle to calculate annual maximum and minimum insolation at a
%given latitude. To call this function, type MMInsol(latDeg) into the
Matlab command prompt,
%replacing the term "latDeg" with the latitude, in degrees, at which you
%want to calculate maximum and minimum annual insolation.

%To run this program, you must use a text file containing the following
%information in columns:
    %Time in kyr at 0.1 kyr intervals
    %the Laskar 2004 solution to Eccentricity for the correct time range
    %the Laskar 2004 solution to Obliquity (in radians) for the correct time range
    %the Laskar 2004 solution to Precession Angle (in radians) for the
    %correct time range

% A text file containing this information for the past 100kyr is provided
% along with this program. The text file is called
Dataset_S4_Orb_param.xlsx
% same as a text file and rename it Orb_param.txt
% Information in this text file was obtained from the Laskar's
% downloadable program at
% http://www.imcce.fr/Equipes/ASD/insola/earth/earth.html
% This program can be used to download similar information for periods of
% time other than the past 100kyr. To use newly downloaded information,

```

---



```

        end
    end
end

Table(:,1)=MinInsol(:,1);
Table(:,2)=MinInsol(:,2);
Table(:,3)=MaxInsol(:,1);
Table(:,4)=MaxInsol(:,2);
Table(:,5)=Time;

figure;plot(Time,MinInsol(:,1),Time,MaxInsol(:,1))

%To compare this solution to potential maximum and minimum solutions at
the
%solstices and equinoxes, uncomment the below calculations and plots:

%Lambda = 0 is the vernal equinox
%Lambda = Pi is the autumnal equinox
%Lambda = Pi/2 is the summer solstice
%Lambda = 3Pi/2 is the winter solstice

%name all variables same as above, but with _new to differentiate

%Uncomment below for loop to calculate insolation at equinoxes and
solstices:

Lambda_new=[0,Pi,Pi/2,3*Pi/2];

for k=1:4;
    Del_new(:,k)=asin(sin(Oblig).*sin(Lambda_new(1,k)));
    H_new(:,k)=acos(-tan(lat).*tan(Del_new(:,k)));

    z_new(:,k)=H_new(:,k).*sin(lat).*sin(Del_new(:,k))+cos(lat).*cos(Del_new(
    ,k)).*sin(H_new(:,k));
    Cos_new(:,k)=cos(Lambda_new(1,k)-Prec-Pi);
    Denom_new=(1-Eccen.^2).^2;

    Insol_new(:,k)=(S/Pi)*z_new(:,k).*((1+Eccen.*Cos_new(:,k)).^2)./Denom_new;
end

%the first column of Insol_new is insolation at Lambda = 0
%the second column of Insol_new is insolation at Lambda = Pi
%the third column of Insol_new is insolation at Lambda = Pi/2
%the fourth column of Insol_new is insolation at Lambda = 3Pi/2

%Uncomment any of the plots below to view

%To plot the equinoxes against MaxInsol (recommended for low lat):
%figure;plot(Time,Insol_new(:,1),Time,Insol_new(:,2),Time,MaxInsol(:,1))

%To plot solstices against MinInsol (recommended for low lat):
%figure;plot(Time,Insol_new(:,3),Time,Insol_new(:,4),Time,MinInsol(:,1))

%To plot the equinoxes against MinInsol (recommended for high lat):
%figure;plot(Time,Insol_new(:,1),Time,Insol_new(:,2),Time,MinInsol(:,1))

%To plot solstices against MaxInsol (recommended for high lat):
%figure;plot(Time,Insol_new(:,3),Time,Insol_new(:,4),Time,MaxInsol(:,1))

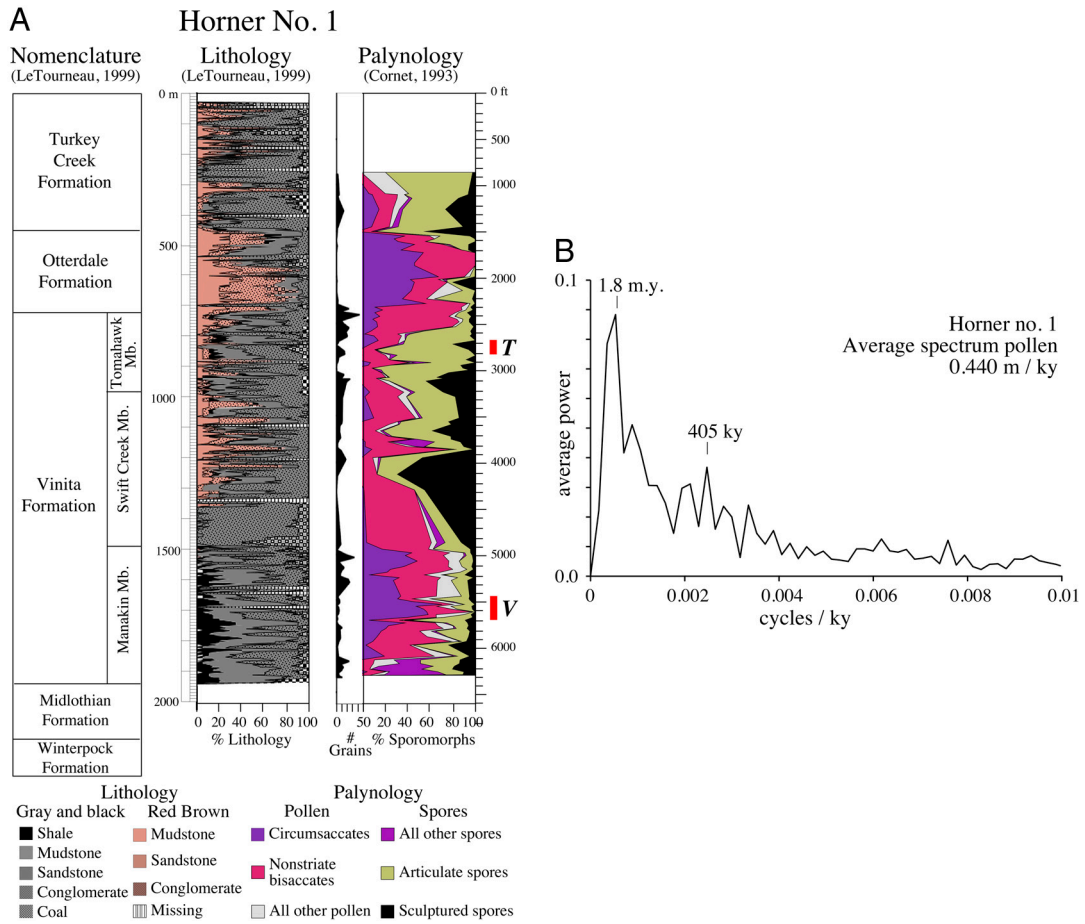
```

**Phylogeny and Nitrogen Excretion.** We reconstructed the ancestral states of nitrogen secretion for procolophonids and traversodonts using squared-change parsimony in Mesquite v.2.5 (36) (Fig. S5). Two ancestral state reconstructions of the excretory physiology of amniotes were examined: with turtles as archosauromorph diapsids (e.g., refs. 37 and 38) or nested within parareptiles (e.g., refs. 39 and 40). With either alternative, traversodont cyno-

donts are unequivocally urea excreters. With turtles as parareptiles, procolophonids are unambiguous uric acid excreters. With turtles within Diapsida the character state is ambiguous, but it is a reasonable hypothesis that parareptiles would have uric acid excretion, as do all living sauropsids. Backbone phylogeny follows refs. 41–43 for basal amniotes, and refs. 44–46 for synapsids.

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**Fig. S2.** (A) Lithology and sporomorph data from the Horner no. 1 well in the Richmond basin from refs. 3 and 4. Red bars show the projected position of the Vago no. 1 core (V) and traversodonts (Table S1) (T). (B) Average of spectra of pollen morphotypes shown in Fig. S2. Peak at 0.00560 m/cycle is set at 405 ky.

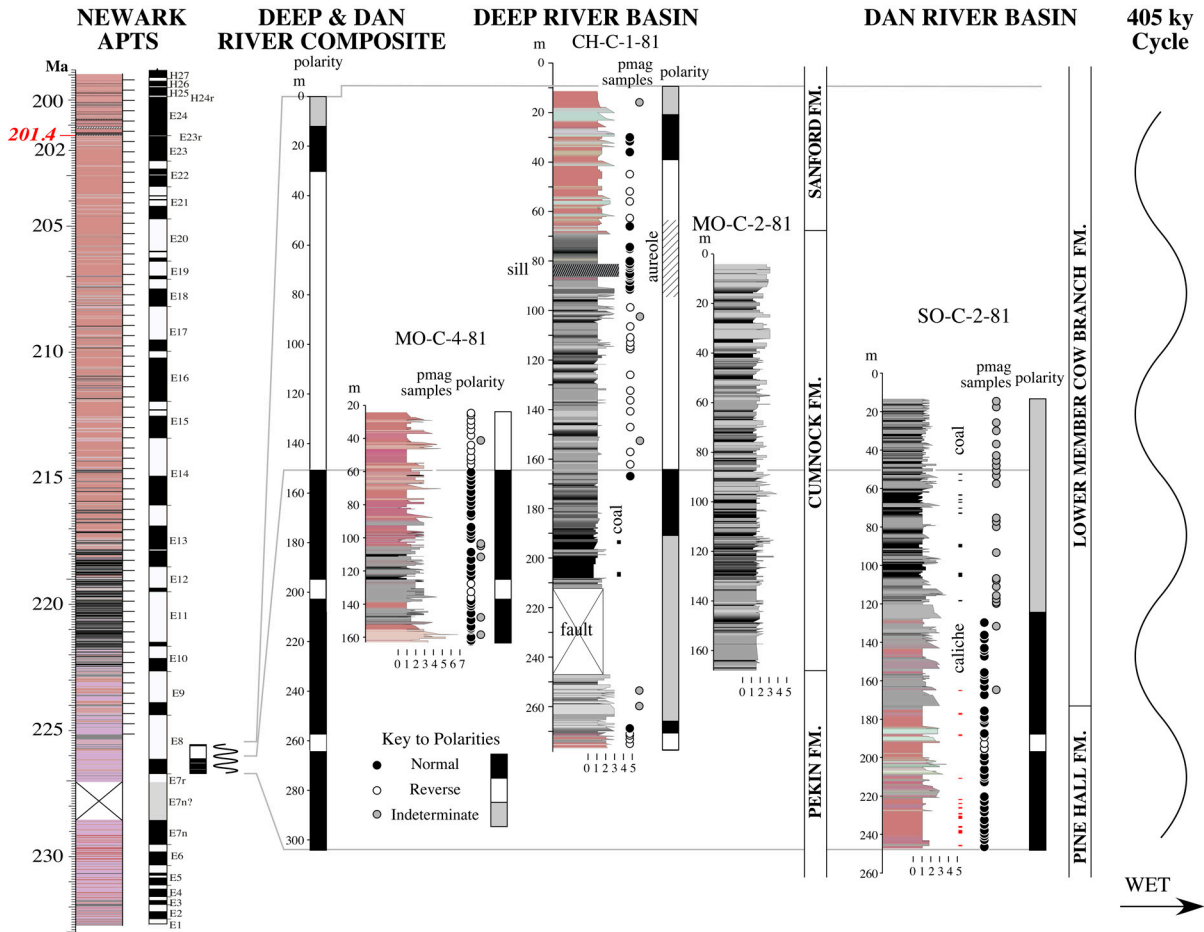
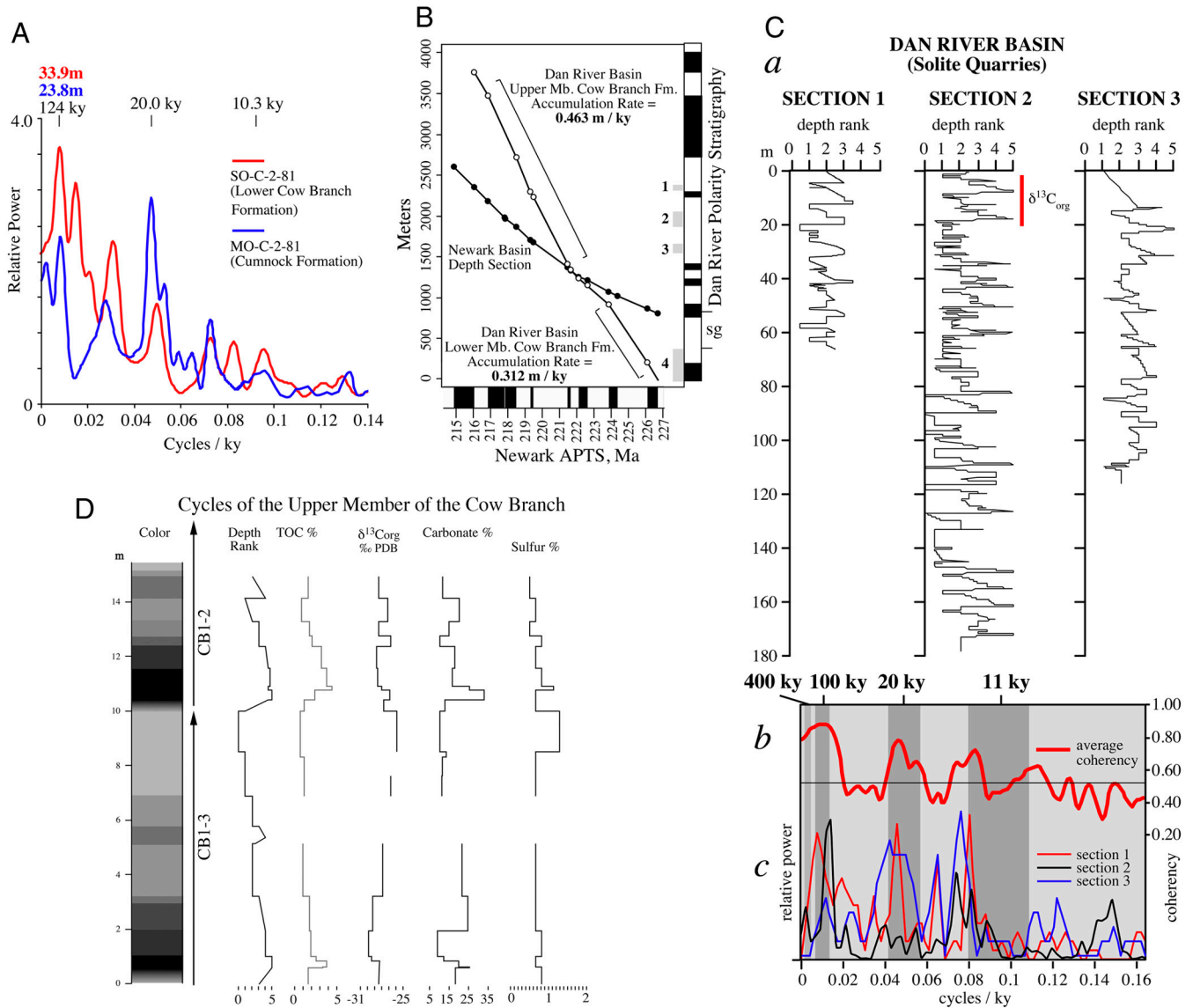
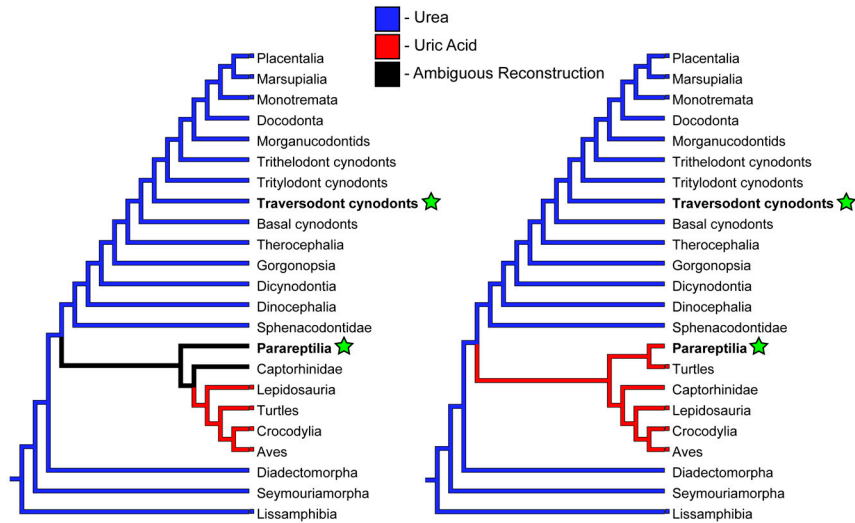


Fig. S3. Correlation between the Cumnock Formation of the Deep River basin in Cores MO-C-4-81, MO-C-4-81, and CH-C-1-81, the lower member of the Cow Branch in core SO-C-2-81 and the Newark-APTS.





**Fig. 54.** (A) Blackman–Tukey spectra of Cumnock and lower Member of the Cow Branch Formation. (B) Correlation between the Newark-APTS and the Dan River section (gray bars 1, 2, and 3 show the positions of Solite Quarry sections 1, 2, and 3; gray bar 4 is the lower member of the Cumnock Formations as seen in core SO-C-2-81 in Fig. 53. “sg” is position of a gap in sampling of outcrop and core). (C) Data from the upper member of the Cow Branch Formation of the Dan River basin at the Solite quarry. [(a) Depth ranked sections from the three Solite quarry sections; red bar labeled  $\delta^{13}\text{C}_{\text{org}}$  is section of 2 cycles shown in D (depth ranks increase in value with interpreted lake depth; see ref. 26). (b) Coherency between all three Solite sections (see Table S1 for locations); coherencies above the horizontal line are significant at the >95% level; all three pairwise coherency analyses were performed and the results averaged; (c) FFTs of all three sections. Note the consistent set of peaks between 12 and 8 ky.] (D) Detailed geochemical and depth rank data from the uppermost two cycles in section 2 of the Solite Quarry (see C) that correspond to cycles CB1-3 and CB1-2 described in ref. 21. CB1-2 is the source of the main lagerstätte described in refs. 21 and 22 (carbon, sulfur, and carbonate data are from ref. 23).



**Fig. S5.** Ancestral state reconstruction of the excretory physiology of amniotes with alternate phylogenetic hypotheses based on the position of turtles as diapsids or nested within parareptiles (see *S1 Text*). The two extinct taxa of interest, traversodont cynodonts and parareptiles, are highlighted by green stars.

**Table S1. Metadata for cores and sections**

Core or section	Formation	Age	Age, Ma	N Latitude	W Longitude
Vago no. *	Vinita	Carnian	approximately 230–235	37.60333	77.69111
Horner no. 1 †	Vinita, Otterdale	Carnian	approximately 230–235	37.451178	77.740343 †
MO-C-2-81 ‡	Cumnock	E. Norian	226	35.451944	79.384722
CH-C-1-81 ‡	Cumnock	E. Norian	226	35.558333	79.215000
MO-C-4-81 ‡	Cumnock	E. Norian	226	35.334722	79.466111
SO-C-2-81 ‡	lower Cow Branch	E. Norian	226	36.286389	80.140833
Solite Quarry 1	upper Cow Branch	E. Norian	220	36.543739	79.675194
Solite Quarry 2	upper Cow Branch	E. Norian	220	36.539083	79.671929
Solite Quarry 3	upper Cow Branch	E. Norian	220	36.538088	79.664241
Nursery no. 1 §	Lockatong	E. Norian	220	40.289594	74.823437 ¶
Lenn no. 1	Balls Bluff	L. Norian	209	38.460657	77.906449
Andrus no. 1	Balls Bluff	L. Norian	209	38.462522	77.923172
Somerset no. 1 §	Passaic	L. Norian	209	40.505763	74.565385 **

\*Virginia Department of Mines, Minerals, and Energy Division of Geology and Mineral Resources, Charlottesville, VA.

†Lamont-Doherty Earth Observatory, Eastern United States onshore repository.

‡North Carolina Geological Survey, Raleigh Field Office and Repository, Raleigh, NC.

§Rutgers/New Jersey Geological Survey Rift-Drift Core Repository, Piscataway, NJ.

¶Nursery location given as 40° 18' 03"N, 74° 49' 27"W in refs 1 and 2, corrected here.

||US Geological Survey Herndon Warehouse.

\*\*Somerset location given as 40° 30' 31"N, 74° 33' 58"W in Table S2: Metadata for traversodont and procolophonid specimens.

1 Kent DV, Olsen PE (1999) Astronomically tuned geomagnetic polarity time scale for the Late Triassic. *J Geophys Res* 104:12831–12841.

2 Olsen PE, Kent DV, Cornet B, Witte WK, Schlichte RW (1996) High-resolution stratigraphy of the Newark rift basin (Early Mesozoic, Eastern North America). *Geol Soc Am* 108:40–77.

**Table S2. Metadata for traversodont and procolophonid specimens**

Taxon and species no. (T = traversodont P = procolophonid)	Basin	Formation	Age, Ma	N Latitude	W Longitude
cf. <i>Hypsognathus</i> (P) <sup>a</sup>	Dunbarton	unnamed	approximately 211	33.1348	81.3549
<i>Boreogomphodon jeffersoni</i> (T) 21371 <sup>b c</sup>	Deep River	Pekin	approximately 231	35.637730	78.996560
Traversodontia sp. (T) 24722 <sup>b</sup>	Deep River	Cumnock	225	35.597481	79.017703
Traversodontia sp. (T) 25570 <sup>b</sup>	Deep River	Sanford	223	35.574844	79.015673
<i>Boreogomphodon herpetairus</i> (T) 15576 <sup>d</sup>	Durham	Lithofacies association II	approximately 220	35.871660	78.898939
<i>Boreogomphodon jeffersoni</i> (T) 448632 <sup>e</sup>	Richmond	Vinita	approximately 233	37.462504	77.672058
<i>Gomphiosauridion baileyae</i> , (P) 448630 <sup>e</sup>	Richmond	Vinita	approximately 233	37.462504	77.672058
cf. <i>Hypsognathus</i> (P) <sup>f</sup>	Newark	Passaic	215	40.579146	75.080242
<i>Hypsognathus fenneri</i> (P) VP-2160 <sup>g</sup>	Newark	Passaic	210	40.416325	75.514066
<i>Hypsognathus fenneri</i> (P) 1676 <sup>h</sup>	Newark	Passaic	208	40.862694	74.141998
<i>Hypsognathus fenneri</i> (P) 11643 <sup>e</sup>	Newark	Passaic	202	40.893738	74.168146
<i>Hypsognathus fenneri</i> (P) <sup>i</sup>	Newark	Passaic	202	40.308980	75.834927
<i>Hypsognathus fenneri</i> (P) 55831 <sup>j</sup>	Hartford	New Haven	approximately 203	41.543594	72.822859
<i>Arctotraversodon plemmyridon</i> (T) 990GF89.1 <sup>k</sup>	Fundy	Wolfville	approximately 233	45.316	63.782
<i>Acadiella psalidodon</i> (P) 19190 <sup>l</sup>	Fundy	Wolfville	approximately 233	45.137537	64.324608
<i>Haligonia bolodon</i> (P) 996GF74.1 <sup>k</sup>	Fundy	Wolfville	approximately 233	45.311538	63.806942
<i>Scoloparia glyphanodon</i> (P) 996GF83.1 <sup>k</sup>	Fundy	Wolfville	approximately 233	45.145533	64.273762
<i>Hypsognathus</i> cf. <i>fenneri</i> (P) 998GF45.1 <sup>k</sup>	Fundy	Blomidon	215	45.193205	64.358524

<sup>a</sup>Core from Savannah River Plant Deep Rock Boring number 11 (SRP DRB-11) at 641.4 m (2,015.7 ft) archived at the Savannah River Site.

<sup>b</sup>North Carolina Museum of Natural Sciences, Raleigh, NC.

<sup>c</sup>Fig. 2 *Upper Left* in the main text.

<sup>d</sup>Department of Geology, University of North Carolina, Chapel Hill, NC.

<sup>e</sup>United States National Museum, Washington, DC.

<sup>f</sup>Private collection of Jack Boyland.

<sup>g</sup>State Museum of Pennsylvania, Harrisburg, PA.

<sup>h</sup>American Museum of Natural History, New York, NY.

<sup>i</sup>Reading Public Museum, Reading, PA (specimens).

<sup>j</sup>Yale Peabody Museum, New Haven, CT (specimen found in rubble rock wall).

<sup>k</sup>Nova Scotia Museum, Halifax, NS, Canada.

<sup>l</sup>Yale Peabody Museum, New Haven, CT (Princeton Collection).

## Other Supporting Information Files

[Dataset S1 \(XLS\)](#)