

Marine anoxia and delayed Earth system recovery after the end-Permian extinction

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Delayed Earth system recovery following the end-Permian mass extinction is often attributed to severe ocean anoxia. However, the extent and duration of Early Triassic anoxia remains poorly constrained. Here we use paired records of uranium concentrations ([U]) and $^{238}\text{U}/^{235}\text{U}$ isotopic compositions ($\delta^{238}\text{U}$) of Upper Permian–Upper Triassic marine limestones from China and Turkey to quantify variations in global seafloor redox conditions. We observe abrupt decreases in [U] and $\delta^{238}\text{U}$ across the end-Permian extinction horizon, from ~ 3 ppm and -0.15% to ~ 0.3 ppm and -0.77% , followed by a gradual return to preextinction values over the subsequent 5 million years. These trends imply a factor of 100 increase in the extent of seafloor anoxia and suggest the presence of a shallow oxygen minimum zone (OMZ) that inhibited the recovery of benthic animal diversity and marine ecosystem function. We hypothesize that in the Early Triassic oceans—characterized by prolonged shallow anoxia that may have impinged onto continental shelves—global biogeochemical cycles and marine ecosystem structure became more sensitive to variation in the position of the OMZ. Under this hypothesis, the Middle Triassic decline in bottom water anoxia, stabilization of biogeochemical cycles, and diversification of marine animals together reflect the development of a deeper and less extensive OMZ, which regulated Earth system recovery following the end-Permian catastrophe.

paleoredox | uranium isotopes | biogeochemical cycling | carbon isotopes | Early Triassic

The end-Permian mass extinction—the most severe biotic crisis in the history of animal life—was followed by 5 million years of reduced biodiversity (1, 2), limited ecosystem complexity (3), and large perturbations in global biogeochemical cycling (4, 5). Ocean anoxia has long been invoked both as a cause of the extinction (6–8) and as a barrier to rediversification (9). Numerous lines of evidence demonstrate widespread anoxic conditions around the time of the end-Permian mass extinction (e.g., refs. 6 and 10–12). In contrast, the prevalence of anoxia during the 5- to 10-million-year recovery interval remains poorly constrained (13, 14).

Reconstructing paleoredox conditions is challenging because some indicators of anoxia characterize only the local conditions of the overlying water column, whereas other indicators may be influenced by confounding factors, such as weathering rates on land. Here, we use paired measurements of [U] and $\delta^{238}\text{U}$ in marine carbonate rocks to differentiate changes in weathering of U from variations in global marine redox conditions. Microbially mediated reduction of U(VI) to U(IV) under anoxic conditions at the sediment–water interface results in a substantial decrease in uranium solubility and a measureable change in $^{238}\text{U}/^{235}\text{U}$ (15–18). Because ^{238}U is preferentially reduced and immobilized relative to ^{235}U , the $\delta^{238}\text{U}$ value of seawater U(VI) decreases as the areal extent of bottom water anoxia increases (Fig. S1). Consequently, a global increase in the extent of anoxic bottom waters will cause simultaneous decreases in [U] and $\delta^{238}\text{U}$ of carbonate sediments. A previous study of $\delta^{238}\text{U}$ variations at one

stratigraphic section through the immediate extinction interval ($\sim 40,000$ y) (11) suggested a rapid onset of anoxia coincident with the loss of marine diversity. However, with only a single site, it is unclear if the signal is globally representative; moreover, the lack of data for all but the lowest biostratigraphic zone of the Triassic leaves the pattern and timing of environmental amelioration during the recovery interval unconstrained.

To develop a quantitative, global reconstruction of seawater redox conditions for the entire 15-million-year interval of mass extinction and subsequent Earth system recovery, we measured 58 Upper Permian (Changhsingian) through Upper Triassic (Carnian) limestone samples from three stratigraphic sections (Dajiang, Dawen, and Guandao) arrayed along a depth transect on the Great Bank of Guizhou (GBG), an isolated carbonate platform in the Nanpanjiang Basin of south China (eastern Tethys). To test the extent to which variations in [U] and $\delta^{238}\text{U}$ within the GBG reflect global uranium cycling, we also analyzed 28 limestone samples from the Taşkent section, Aladag Nappe, Turkey, located in the western Tethys (Fig. S1). We focused our measurements on samples deposited in shallow marine environments (<100 m water depth, i.e., Dajiang, Dawen, and Taşkent) likely to have remained oxygenated. Variations in [U] and $\delta^{238}\text{U}$ in these samples should reflect changes in global, rather than local, redox conditions.

Significance

The end-Permian mass extinction not only decimated taxonomic diversity but also disrupted the functioning of global ecosystems and the stability of biogeochemical cycles. Explaining the 5-million-year delay between the mass extinction and Earth system recovery remains a fundamental challenge in both the Earth and biological sciences. We use coupled records of uranium concentrations and isotopic compositions to constrain global marine redox conditions across the end-Permian extinction horizon and through the subsequent 17 million years of Earth system recovery. Our finding that the trajectory of biological and biogeochemical recovery corresponds to variations in an ocean characterized by extensive, shallow marine anoxia provides, to our knowledge, the first unified explanation for these observations.

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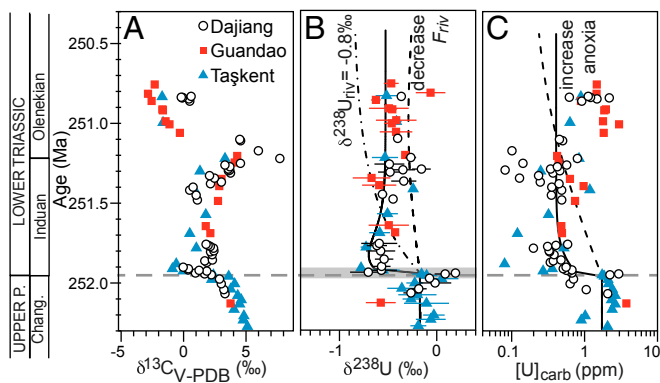


Fig. 1. Late Permian (P.) to early Early Triassic (A) $\delta^{13}\text{C}$, (B) $\delta^{238}\text{U}$, and (C) [U] data and box model results. Gray dashed line indicates end-Permian extinction horizon. Shaded box in *B* represents the temporal extent of data reported in ref. 11. Model results are as follows: increased extent of anoxia (f_{anox}) from modern value of 0.2% to 20% for the first ~30,000 y and to 5% thereafter (solid line); decreased input [U] by an order of magnitude (dashed line); and decreased input $\delta^{238}\text{U}$ value to -0.8‰ (dot-dashed line). The $\delta^{13}\text{C}$ data are from ref. 4 (Dajiang and Guandao) and this study (Taşkent). Error bars on $\delta^{238}\text{U}$ are 2σ of replicate analyses and are reported relative to CRM-145. Data from Dawen are shown in Fig. S2, and details of age model are shown in Figs. S2–S4. Chang., Changhsingian.

Results

The $\delta^{238}\text{U}$ composition of the shallow marine sections averages -0.15‰ in the Upper Permian and abruptly decreases at the extinction horizon to a minimum value of -0.77‰ (Fig. 1, Figs. S2–S4, and Dataset S1). Synchronously, [U] decreases from 3 ppm to ~ 0.3 ppm. In the Induan strata, representing the first ~ 0.7 My after the extinction, [U] and $\delta^{238}\text{U}$ values remain low (0.4 ppm and -0.55‰) in both shallow marine (Dajiang and Taşkent) and slope (Guandao) environments. Lowermost Induan $\delta^{238}\text{U}$ data from Dawen have a mean of -0.57‰ (Fig. S2). In the Olenekian strata, representing the subsequent ~ 4 My, [U] and $\delta^{238}\text{U}$ values gradually increase to 1 ppm and $\sim 0.35\text{‰}$ (Fig. 2). In the uppermost Olenekian strata (~ 247.5 Ma), [U] and $\delta^{238}\text{U}$ decrease to 0.6 ppm and -0.65‰ at Guandao and Taşkent (Dajiang strata are dolomitized and are not considered). In limestones above the Olenekian–Anisian boundary (~ 247 Ma), [U] and $\delta^{238}\text{U}$ increase to 1.2 ppm and -0.23‰ .

Three lines of evidence indicate that these general trends in [U] and $\delta^{238}\text{U}$ reflect secular changes in global seawater redox conditions rather than local or diagenetic effects. First, shallow marine uranium records exhibit consistent trends and similar absolute values between China and Turkey, despite vast differences in geographic settings and burial histories. In our records, differences in [U] and $\delta^{238}\text{U}$ across time intervals are statistically significant both within individual stratigraphic sections and across the entire dataset, whereas the values between sections are statistically indistinguishable (Table S1 and Statistical Analysis: Interpretation). Local or diagenetic controls would likely produce differences among sites rather than differences expressed across time. Second, our uranium data are not significantly correlated with indicators of diagenetic alteration such as $\delta^{18}\text{O}$, Mn/Sr, Mg/Ca, or organic carbon content, and do not covary with proxies for detrital contribution (normalization with Al or Th) or indicators of mineralogy (Sr/Ca) (Fig. S5 and Diagenetic Alteration and Dolomitization and Statistical Analysis: Interpretation).

Finally, the trends in [U] from our stratigraphic sections agree with published records from shallow marine carbonates spanning the Permian–Triassic boundary interval in Saudi Arabia, Iran, Italy, and China (8, 11–13, 26, 27). Although local and diagenetic processes affect all samples of this age and undoubtedly account for some of the variation in our dataset, the most parsimonious

explanation for the statistically supported trends in [U] and $\delta^{238}\text{U}$ is that the dominant signal in the dataset is a primary signature reflecting the uranium composition of seawater.

Discussion

Statistically Significant Temporal Trends. To determine whether the temporal trends we observe in $\delta^{238}\text{U}$ and [U] are statistically significant, we used analysis of variance (ANOVA) (function *avov* in R) for our data categorized by general time intervals (Late Permian, Induan, Olenekian, and Middle–Late Triassic) (Table S1). Both [U] and $\delta^{238}\text{U}$ data from shallow marine records differ significantly among time intervals (P values ≤ 0.01). We then used Dennett’s modified Tukey–Kramer Post-Hoc Test (function *DTK.test* in R) to run pair-wise comparisons between time intervals for all our data. The results for the combined dataset show that for both [U] and $\delta^{238}\text{U}$, the Induan is significantly different from the Late Permian, Olenekian, and Middle–Late Triassic compositions (Fig. 3).

In addition, we applied one-way ANOVA and Dennett’s modified Tukey–Kramer Post-Hoc test to the [U] and $\delta^{238}\text{U}$ records for the shallow marine stratigraphic sections (Table S1). For both Dajiang and Taşkent, the Induan $\delta^{238}\text{U}$ values are significantly different from the Late Permian and Middle–Late Triassic, whereas [U] values are only significantly different between the Induan and the Middle–Late Triassic for Taşkent. The results from Dawen (combined with data from ref. 11) also indicate a significant difference between the Late Permian and Induan $\delta^{238}\text{U}$ data. However, the Olenekian [U] and $\delta^{238}\text{U}$ results are not consistent, and differ in whether or not they are significantly distinguishable from the Induan (Taşkent) or not (Dajiang).

In contrast, data from Guandao did not show significant differences between the various time intervals, suggesting that Guandao sediments on the platform slope may have been impacted by local anoxia/suboxia. These conditions could result in locally more negative $\delta^{238}\text{U}$ if a greater proportion of ^{238}U relative to seawater was reduced into proximally deposited sediments, which would not be captured in our measurements. Therefore, the presence of local anoxia may result in $\delta^{238}\text{U}$ compositions that deviate from global seawater.

From these statistical results, we conclude that the Induan had significantly lower [U] and $\delta^{238}\text{U}$ values than the uppermost Permian and the Middle–Upper Triassic at all sites, whereas the Olenekian is a transitional period. The uppermost Permian and Middle–Upper Triassic data are statistically indistinguishable, implying a recovery in [U] and $\delta^{238}\text{U}$ to preextinction values.

Modeling Implications for Seafloor Anoxia. A mass balance box model of seawater uranium and its isotopes (Fig. 1 and Fig. S6) demonstrates that the observed decreases in [U] and $\delta^{238}\text{U}$ require an increase in bottom water anoxia in the global ocean. Scenarios involving a decrease in either [U] or $\delta^{238}\text{U}$ of riverine uranium would account for a decrease in one metric but not both. Even simultaneous decreases in riverine [U] and $\delta^{238}\text{U}$ would not reproduce the rapid observed decreases (Fig. S6). In contrast, expanding the area of seafloor impacted by anoxia efficiently removes and fractionates U, causing large, rapid, and sustained decreases in [U] and $\delta^{238}\text{U}$, consistent with the magnitude and rate of change of the negative shifts in [U] and $\delta^{238}\text{U}$ at the extinction horizon.

The extent of Early Triassic anoxia implied by our box model calculations is substantial. Our model predicts an increase in the anoxic sink for uranium from 15% of the total removal flux in the latest Permian to 94% in the Induan, similar to the factor of 6 increase in the flux of U to anoxic facies calculated in ref. 11. However, the magnitude and rate of decrease in [U] and $\delta^{238}\text{U}$ also require a factor of 100 increase in the extent of seafloor anoxia (f_{anox}) across the extinction horizon, from 0.2% (28) to 20% of the seafloor during the extinction interval, followed by a

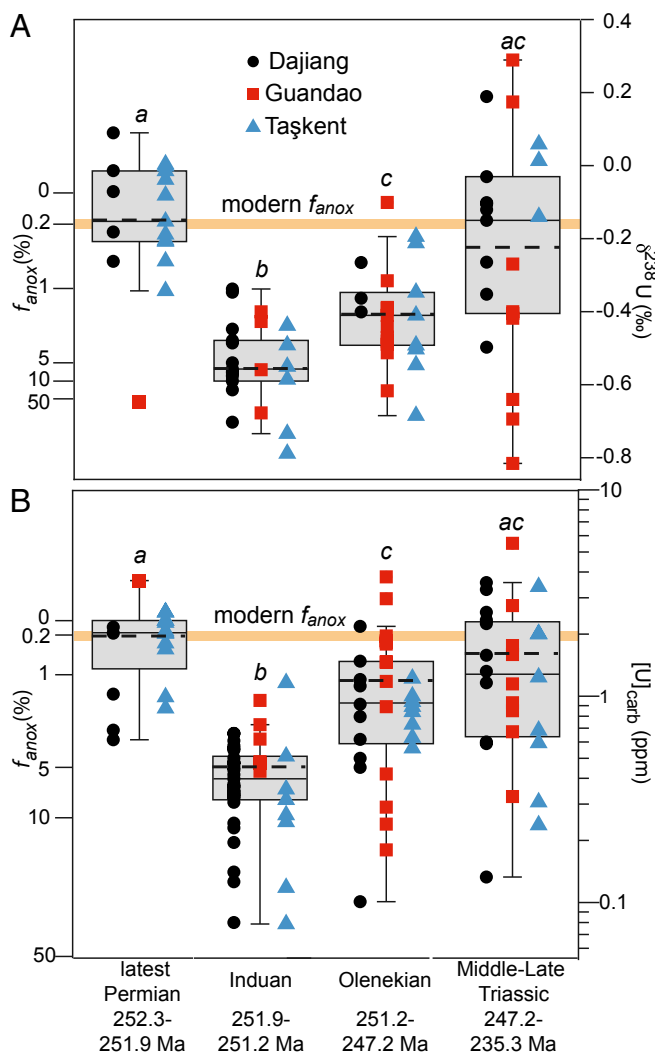


Fig. 3. (A) The $\delta^{238}\text{U}$ and (B) $[\text{U}]$ boxplots. Whiskers denote the minimum and maximum of data within 1.5 times the interquartile range from the median. The mean is marked by the dashed line. Steady-state model predictions for the extent of anoxia, f_{anox} , are calculated for the best-estimate input $\delta^{238}\text{U}_{\text{riv}}$ composition of -0.05‰ (Middle Triassic $\delta^{238}\text{U}$ Composition), and suggest that, in the Late Permian and Late–Middle Triassic, the extent of anoxia was near the modern value, whereas, in the Early Triassic, the extent was larger. Statistical analyses show that latest Permian $\delta^{238}\text{U}$ and $[\text{U}]$ data (a) are significantly distinct from the Induan (b) but similar to the Middle–Late Triassic, whereas the Olenekian data represent a transitional period (c).

Early–Middle Triassic carbon cycle, with large, rapid excursions giving way to smaller and more prolonged variations. Importantly, we are able to produce the $\delta^{13}\text{C}$ excursions without varying the magnitude of the forcing (variation in Z_{UB}) or requiring any large external perturbation to the Earth system. This effect could account for the magnitude and persistence of Early Triassic $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ excursions after the initial negative excursion associated with Siberian Traps volcanism (4, 5, 32) (Fig. 2).

In summary, uranium data confirm a central role for marine redox conditions in modulating Earth system recovery following the end-Permian extinction. The return of marine redox conditions to a preextinction state in the Middle Triassic was concurrent with stabilization of $\delta^{13}\text{C}$ and $\delta^{34}\text{S}_{\text{CAS}}$ values and a return to baseline genus richness, ecological diversity, and animal body size (2, 3, 25). We propose that, as the redox gradient in the upper few hundred meters of the water column diminished due

to a deepening of the OMZ and, perhaps, a reduction in total primary productivity (e.g., ref. 20), benthic communities recovered, and the sensitivity of organic carbon burial to subsequent variations decreased, stabilizing the global carbon and sulfur cycles (Fig. 4). Combined with the long-term trend of increasing seawater oxygenation during the Phanerozoic, long-term deepening of the OMZ and an associated decrease in the sensitivity of global biogeochemical cycles may also explain the trends toward greater taxonomic diversity and ecological complexity, as well as the reduced frequency of large carbon and sulfur isotope anomalies.

Materials and Methods

Uranium Box Model. In the modern ocean, where the extent of anoxia is small ($\sim 0.2\%$) (28) relative to conditions over most of Earth’s history, seawater $\delta^{238}\text{U}$ is invariant at about -0.4‰ (15–17). If carbonates faithfully record seawater chemistry with no postdepositional effects (refs. 15–17 and 34, but see further discussion in ref. 34), then the $\delta^{238}\text{U}$ of carbonates should decrease as regions of anoxic marine bottom waters expand. Because uranium has a residence time ($3.2\text{--}5.6 \times 10^5 \text{ y}$) (35) significantly longer than ocean mixing time (10^3 y), global seawater variations in $[\text{U}]$ and $\delta^{238}\text{U}$ should be reflected within local sediments.

The unique sensitivity of both $\delta^{238}\text{U}$ and uranium concentrations to the extent of bottom water anoxia can be described by differential mass balance equations for the seawater uranium inventory and its isotopic composition, respectively,

$$\frac{dN_{\text{sw}}}{dt} = J_{\text{riv}} - J_{\text{anox}} - J_{\text{other}} \quad [1]$$

$$\frac{N_{\text{sw}} * d\delta^{238}\text{U}}{dt} = J_{\text{riv}} * (\delta^{238}\text{U}_{\text{riv}} - \delta^{238}\text{U}) - J_{\text{anox}} * \Delta_{\text{anox}} - J_{\text{other}} * \Delta_{\text{other}} \quad [2]$$

where N_{sw} is the oceanic uranium inventory in moles, $\delta^{238}\text{U}$ is the value of seawater, $\delta^{238}\text{U}_{\text{riv}}$ is the value of the riverine source, $\Delta_{\text{anox}} = +0.6\text{‰}$ is the effective fractionation factor associated with anoxic sediment deposition (17), and Δ_{other} is the effective fractionation factor associated with the remaining other sinks ($+0.03\text{‰}$, calculated to maintain isotopic steady state in the modern ocean (e.g., refs. 11 and 36)]. We simplify the inputs to J_{riv} , the riverine flux [modern value is $0.4 \times 10^8 \text{ mol U/y}$ (37)]. The outputs are assumed to consist of the anoxic sediment sink (J_{anox}) and the sum of the other

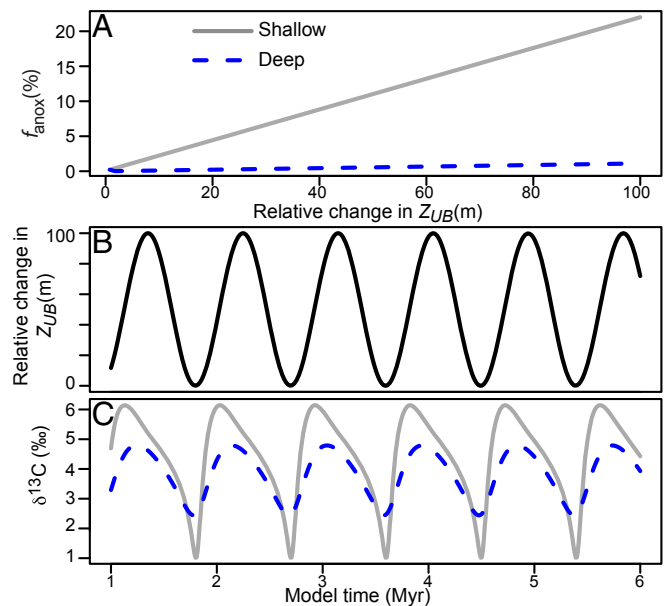


Fig. 4. Sensitivity of $\delta^{13}\text{C}$ to changes in the depth of the upper boundary of the OMZ, Z_{UB} . (A) Relationship between f_{anox} and the depth of the upper boundary of the OMZ relative to the continental shelf–slope break, Z_{UB} , for scenarios with a shallow OMZ (gray line) and deep OMZ (dashed blue line). (B) Temporal change in Z_{UB} used in model. (C) Model output for $\delta^{13}\text{C}$. Model results are shown starting at 1 My, after the system has reached a quasi-steady state. Refer to Supporting Information for model details.

sinks (J_{other}), where $J_{anox} = 0.06 \times 10^8$ mol U/y (37) and J_{other} is calculated by mass balance to an initial steady-state value of 0.34×10^8 mol U/y. We further define the output flux terms J_{anox} and J_{other} as

$$J_{anox} = K_{anox} * N_{sw} * f_{anox} \quad [3]$$

$$J_{other} = K_{other} * N_{sw} * (1 - f_{anox}) \quad [4]$$

where f_{anox} is the fraction of seafloor impacted by bottom water anoxia, and K_{anox} and K_{other} are rate constants calculated for the modern uranium system. We assume a constant K_{anox} , reflecting similar mechanisms of U reduction at the sediment–water interface (SWI) throughout the studied time intervals. Similarly, K_{other} is also assumed to be constant. The concentration of uranium in carbonates is estimated by converting the moles of U in the seawater reservoir, N_{sw} , and assuming constant seawater calcium concentrations and a distribution coefficient of 1.4 (38). The sensitivity of the model to varying [Ca] is evaluated in *Uranium Biogeochemical Cycling and Model Sensitivity*. The model was first evaluated with parameters for the modern ocean, and then the $\delta^{238}\text{U}_{riv}$ term was adjusted to -0.05% to reflect a steady-state baseline value equal to the average Late Permian–Middle/Late Triassic seawater value as inferred from our data (*Middle Triassic $\delta^{238}\text{U}$ Composition*). A detailed description of the uranium cycle is provided in *Uranium Biogeochemical Cycling and Model Sensitivity*, and additional box model results are presented in Fig. S6. An evaluation of model sensitivity is presented in *Uranium Biogeochemical Cycling and Model Sensitivity* and in Fig. S9. R code used in our analysis can be accessed at <https://purl.stanford.edu/mr858s1453>.

To determine the [U] and $\delta^{238}\text{U}$ relationships with f_{anox} shown in Fig. 3, we assume steady-state behavior and solve Eqs. 1 and 2 for N_{sw} and $\delta^{238}\text{U}$, respectively, as a function of f_{anox}

$$N_{sw} = \frac{J_{riv}}{K_{anox} * f_{anox} + K_{other} * (1 - f_{anox})} \quad [5]$$

$$\delta^{238}\text{U} = \delta^{238}\text{U}_{riv} - \frac{N_{sw} * [K_{other} * \Delta_{other} + f_{anox} * (K_{anox} * \Delta_{anox} - K_{other} * \Delta_{other})]}{J_{riv}} \quad [6]$$

Geologic Setting. Our sample set includes three stratigraphic sections from the GBG, south China, and one stratigraphic section from the Aladag Nappe, Turkey (Fig. S1). Three of these sections were so shallow as to be oxygenated even if deeper waters (>100 m) were anoxic, and thus are less likely to have been impacted by diagenesis resulting from local redox conditions. From the GBG, we analyzed a suite of 86 samples for [U] and 55 samples for $\delta^{238}\text{U}$ from Dajiang and 32 samples for [U] and $\delta^{238}\text{U}$ from Guandao. We also analyzed three samples from the Dawen section, allowing us to compare our

measured values across the Permian–Triassic boundary interval to those reported previously in a high-resolution $\delta^{238}\text{U}$ and Th/U record for the 15 m spanning the extinction horizon at the same site (11). To determine whether variations in [U] and $\delta^{238}\text{U}$ are globally reproducible, we also analyzed a suite of 36 samples for [U] and 31 samples from Tashtkent, the Aladag Nappe, Turkey. We correlate the Tashtkent section to the GBG using lithostratigraphy, conodont and foraminiferan biostratigraphy, and $\delta^{13}\text{C}$ chemostratigraphy (4, 20, 42). Detailed description of the stratigraphic sections is provided in *SI Materials and Methods* (Figs. S2–S4).

Uranium Isotopic Analysis. At least 4 g of sample powder was digested using 0.25 N Optima HCl, determined to be the optimal dissolution procedure (see *SI Materials and Methods* and Fig. S10). A ^{238}U : ^{236}U sample to spike ratio of 10:1 was used to maximize both the internal precision and the external reproducibility of the $\delta^{238}\text{U}$ measurements. Uranium was purified by a two-step ion exchange chromatography procedure using UTEVA resin (Eichrom), following procedures adapted from refs. 16, 43.

Uranium isotopic compositions were measured in the ICP-MS/TIMS Facility at Stanford University on a Nu Plasma multicollector-inductively coupled plasma mass spectrometer (MC-ICP-MS). The ^{238}U : ^{235}U ratios were corrected using an exponential law for mass bias assuming the certified spike ^{233}U : ^{236}U ratio of 1.01906 (44), followed by correction for contribution of ^{238}U from the spike. The ^{238}U : ^{235}U ratios are reported relative to reference standard CRM-145 in standard delta notation. Internal precision (2 SE) of measurements of standards was typically 0.07‰. Average measurement reproducibility (2 σ), assessed by replicate measurements of the same sample solution, is 0.11‰ ($n = 83$). Additionally, we processed four samples twice to evaluate external reproducibility, where one limestone sample had a reproducibility of <0.01‰ and three dolomitic samples had an average reproducibility of 0.4‰ (*Dataset S1*; discussed in *Diagenetic Alteration and Dolomitization*). We evaluated reference materials BCR-2 (Columbia River Basalt), HU-1 (Harwell Uraninite), CRM-129a, and an internal carbonate standard to track reproducibility and agreement with previously published values; a summary is provided in *Supporting Information* and Fig. S11. A full description of analytical methods is included in *Supporting Information*, and the data from this study are presented in *Dataset S1*.

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