

Timing of mammal-like reptile extinctions across the Permian-Triassic boundary in South Africa

Kenneth G. MacLeod Department of Geological Sciences, University of Missouri, Columbia, Missouri 65211, USA

Roger M. H. Smith South African Museum, P.O. Box 61, 8000 Cape Town, South Africa

Paul L. Koch Earth Sciences Department, University of California, Santa Cruz, California 95064, USA

Peter D. Ward Department of Geological Sciences, Box 351310, University of Washington, Seattle, Washington 98195, USA

ABSTRACT

The rate, timing, and pattern of change in different regions and paleoenvironments are critical for distinguishing among potential causes for the Permian-Triassic (P-T) extinction. Carbon isotopic stratigraphy can provide global chronostratigraphic control. We report a large $\delta^{13}\text{C}$ excursion at the P-T boundary and no long-term Permian $\delta^{13}\text{C}$ trends for samples from the interior of Pangea. Stratigraphic gaps between available samples limit the resolution of our $\delta^{13}\text{C}$ curve, but the excursion is within a 15-m-thick zone of overlap between Permian and Triassic taxa. Sedimentological and taphonomic observations demonstrate that this 15 m interval does not represent geologically instantaneous deposition. Together these data support a rapid and globally synchronous P-T event, but suggest that it occurred over a geologically resolvable interval of time.

Keywords: Permian-Triassic extinction, carbon isotopes, chemostratigraphy, therapsids, Karoo basin, South Africa.

INTRODUCTION

The Permian-Triassic (P-T) extinction event was the largest of the Phanerozoic and a variety of causal mechanisms have been proposed (e.g., impact: Bowring et al., 1998; Retallack et al., 1998; environmental shifts: Thackery et al., 1990; Smith, 1995; Retallack, 1999; oceanic anoxia: Wignall and Twitchett, 1996; oceanic overturn: Knoll et al., 1996; volcanism: Renne et al., 1995; and synergistic combinations among these; Erwin, 1994; Morante, 1996). Different mechanisms predict different global-scale patterns, but correlation with adequate resolution is difficult to achieve. Many areas lack independently dated material, and lithostratigraphic and biostratigraphic techniques are often inappropriate due to the physical and environmental separation between sections. Carbon isotope stratigraphy is one of the few means of consistently providing global chronostratigraphic control. The surface ocean mixes on time scales of 10^4 yr and, because its carbon isotopic composition is in dynamic equilibrium with the much more rapidly mixing atmosphere, global $\delta^{13}\text{C}$ excursions should be geologically simultaneous in continental and shallow-marine environments (Koch et al., 1992).

A rapid, negative $\delta^{13}\text{C}$ excursion has been documented at the P-T boundary in both organic and inorganic samples from a number of globally distributed marine sections (e.g., Baud et al., 1989; Magaritz et al., 1992; Wang et al., 1994). The reported excursion ranges from $\sim 3\text{‰}$ to $>10\text{‰}$, but the most negative values are consistently associated with P-T extinctions. Thus, in the marine realm P-T extinctions appear to have been temporally coincident and were associated with a rapid, large-scale input of ^{12}C to, or removal

of ^{13}C from, the surficial carbon pool. Differences in the size of the reported P-T excursion(s) make further interpretation difficult; comparisons among studies show no apparent pattern across environments, regions, or sample types.

In nonmarine sections, the relationship between $\delta^{13}\text{C}$ changes and the P-T boundary is not well established. In inland deposits from South Africa $\delta^{13}\text{C}$ values gradually decline by $\sim 10\text{‰}$ through the Upper Permian (Thackery et al., 1990); however, the tusks analyzed are composed entirely of dentin (King, 1981; Hotton, 1986), which is relatively susceptible to alteration (Koch et al., 1997). In coastal sections from Australia, $\delta^{13}\text{C}_{\text{org}}$ values appear constant through the Permian and show a large excursion at the boundary (Morante, 1996), but this excursion may reflect a mixing signal rather than an isotopic excursion within one phase (Foster et al., 1999). Documenting the

$\delta^{13}\text{C}$ relative to other events in a nonmarine section would provide important information on global patterns and possible diachroneity at the continental end of ecological gradients. To date, though, uncertainties in the continental record have relegated inland data to a minor role in P-T discussions (Knoll et al., 1996; Wignall and Twitchett, 1996; Bowring et al., 1998).

P-T INTERVAL IN THE STUDY AREA

The Karoo basin of South Africa contains excellent sections preserving an apparently complete stratigraphic record of the Permian through the Triassic in the interior of southern Pangea (e.g., King, 1991; Rubidge, 1995; Smith, 1995). Fossiliferous strata crop out extensively in the basin, high sedimentation rates yield excellent stratigraphic resolution, and mammal-like reptiles (therapsids) provide a biostratigraphic framework for regional correlation (Fig. 1). However, no consensus exists regarding patterns of faunal change. Rubidge (1995) reported that 17 of 26 reptilian genera (13 of the 21 therapsids) found in the *Cistecephalus* assemblage zone are among the 44 genera (36 therapsids) found in the *Dicynodon* assemblage zone, but only 3 of these 44 (2 of 36 therapsids) are among the 20 genera (12 therapsids) in the *Lystrosaurus* assemblage zone. King (1991) reported a peak in diversity of at least 85 reptilian

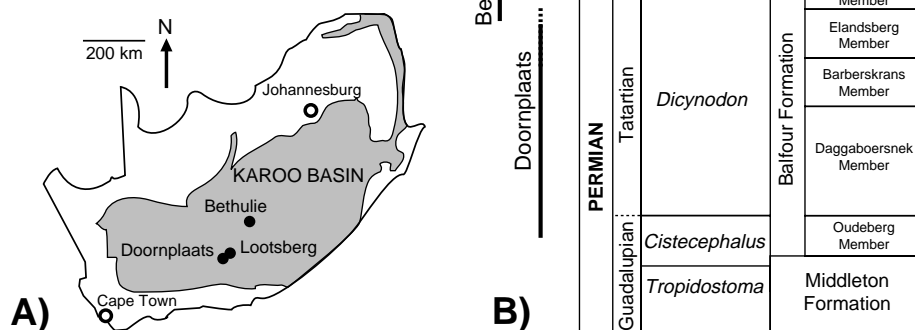


Figure 1. A: Map of South Africa showing extent of Karoo basin and approximate position of localities discussed. **B:** Time, therapsid assemblage zones, and stratigraphic subdivisions of Beaufort Group for interval represented by Bethulie and Doornplaats sections. *Lystrosaurus* has been reported in float from Doornplaats locality, but *Lystrosaurus* assemblage zone strata were not recognized in this study. Correlations are after King (1991) and Rubidge (1995).

Data Repository item 200026 contains additional material related to this article.

genera in the *Cistecephalus* assemblage zone and 16 and 23 genera in the *Dicynodon* and *Lystrosaurus* assemblage zones, respectively.

At the subzonal level, the stratigraphic distribution of only two taxa, Permian *Dicynodon* and Triassic *Lystrosaurus*, are known in detail, and their ranges overlap (Hotton, 1967; Smith, 1995; King and Jenkins, 1997). At Lootsberg Pass the two taxa apparently cooccurred during deposition of ~60 m of sediment, *Dicynodon* preferentially occurring in green beds and *Lystrosaurus* in red beds (Hotton, 1967). At Bethulie, several hundred kilometers farther from the sediment source, the ranges of the two taxa overlap by 15 m in an interval where sandstones become more prevalent, mudrocks change from being dominantly green to dominantly red, and sedimentary architecture suggests a decrease in the sinuosity of local streams (Smith, 1995). The Bethulie observations were interpreted as indicating that a *Lystrosaurus*-dominated upland fauna (Triassic) replaced the *Dicynodon*-dominated lowland fauna (Permian) as an alluvial apron prograded northward from the then active Cape fold belt (Smith, 1995). This model explains regional change and requires no global forcing. In dentin from *Diictodon* tusks collected at localities spread across the Karoo basin and over a composite stratigraphic thickness of ~1 km (comprising the *Tropidostoma*, *Cistecephalus*, and most of the *Dicynodon* assemblage zones), $\delta^{13}\text{C}$ values showed a negative shift of >10‰ which was attributed to long-term, gradual changes in global primary productivity (Thackery et al., 1990), but diagenetic alteration could also explain the results.

MATERIALS AND METHODS

To better document the pattern of isotopic change within the Karoo basin, to examine the relationship between isotopic curves and local faunal and sedimentological change, and to improve correlation between the Karoo basin and other P-T sections, we measured carbon and oxygen isotope composition of soil nodules, dicynodont tusks, and diagenetic calcite collected from ~350 m of strata spanning the upper *Cistecephalus* assemblage zone through the *Dicynodon* assemblage zone at Graaff Reinet, Cape Province, and from ~150 m of strata from the upper *Dicynodon* assemblage zone into the lower *Lystrosaurus* assemblage zone (i.e., across the P-T boundary) at Bethulie, Orange Free State (Fig. 1).¹ Correlating zonal boundaries with standard stage boundaries is problematic because radiometric and paleomagnetic data are lacking and biostratigraphic correlation is indirect, but the interval studied represents much of the Tartarian-Induan stages and may extend down into the Guadalupian stage (King,

1991; Rubidge, 1995). Regardless, previously reported changes among Karoo fauna and $^{13}\text{C}/^{12}\text{C}$ ratios occur within the interval studied.

Nodules and tusks were sectioned and then abraded to expose a fresh surface. Sparry calcite occurred as veins within nodules or in voids (e.g., pulp cavities) of fossil material. Powders for each sample were generated using a low-speed drill and analyzed with a VG Optima mass spectrometer. For soil nodules and diagenetic calcite, ~100 μg of powder was heated under vacuum to remove any organic contaminants. Samples were run using an Isocarb automated carbonate system with CO_2 generated by dissolution of sample powders in 100% H_3PO_4 at 90 °C. Tusk samples were run manually; ~25 mg of powder was collected and most samples were treated sequentially with dilute NaOHCl and buffered 1M acetic acid to remove organic contaminants and diagenetic calcite (Koch et al., 1997). Samples were reacted off-line for 15 min in a stirred reaction vessel containing 100% H_3PO_4 at 90 °C. Water was stripped from the evolved gas cryogenically. The gas was collected in a fused quartz tube containing silver foil and was then heated to 500 °C to remove sulfur-bearing contaminants. Carbon results are reported in standard delta (δ) notation relative to the Vienna Peedee belemnite (V-PDB) standard, and oxygen results are shown relative

to both the V-PDB and the Vienna standard mean ocean water (V-SMOW) standards.

RESULTS

The majority of the nodules from the Doornplaats locality exhibit $\delta^{13}\text{C}_{\text{V-PDB}}$ of ~-7‰ without any apparent stratigraphic trends (Fig. 2). Several nodules from Doornplaats exhibit anomalously low $\delta^{13}\text{C}$ values (one ^{13}C -depleted nodule was collected near the *Cistecephalus-Dicynodon* zonal boundary and two are from within the *Dicynodon* zone). However, other nodules collected from the same stratigraphic horizons yield $\delta^{13}\text{C}$ values similar to those of nodules from the rest of the section. The $\delta^{13}\text{C}$ of diagenetic calcite is low in every sample we analyzed and matches the values in ^{13}C -depleted nodules; $\delta^{18}\text{O}$ values are similar among all samples.

At Bethulie a negative $\delta^{13}\text{C}$ excursion in both soil nodules and dicynodont tusks is coincident with the stratigraphic overlap between *Dicynodon* and *Lystrosaurus* (Fig. 3). The $\delta^{13}\text{C}$ of diagenetic calcite in this section does not match excursion values, and the $\delta^{18}\text{O}$ values of nodules, tusks, and diagenetic calcite are all distinct.

DISCUSSION

Low $\delta^{13}\text{C}$ values in isolated nodules at Doornplaats appear to be diagenetic artifacts (Fig. 2).

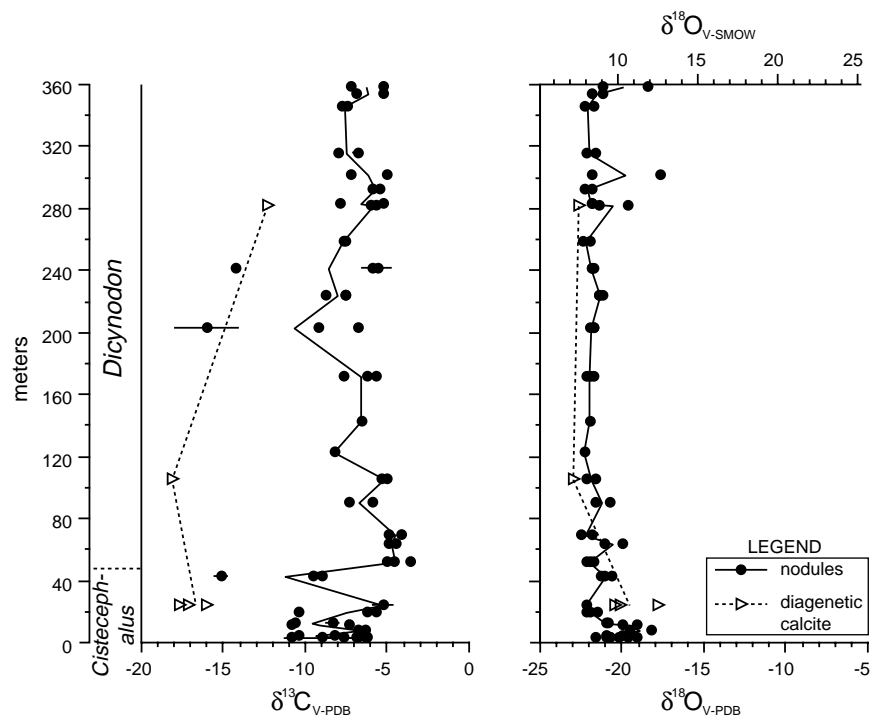


Figure 2. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of nodules and diagenetic calcite plotted against stratigraphic level for Doornplaats locality. Analytical error is less than symbol size, but horizontal bars indicate range of observed within-nodule variability ($n = 2$ or 3). For these replicates, circle represents average within nodule value. Stratigraphic trends in isotopic data are drawn through average of samples from each stratigraphic horizon. *Cistecephalus-Dicynodon* boundary is placed at top of Oudeberg Member of Balfour Formation (Rubidge, 1995). Results suggest relatively constant $\delta^{13}\text{C}$ values throughout *Cistecephalus* and *Dicynodon* zones. Negative $\delta^{13}\text{C}$ values in several nodules are considered diagenetic artifacts. V-PDB is Vienna Peedee belemnite; V-SMOW is Vienna standard mean ocean water.

¹GSA Data Repository item 200026. Data from Bethulie and Doornplaats, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, editing@geosociety.org, or at www.geosociety.org/pubs/drpint.

Oxygen isotopic ratios in nodules and diagenetic calcite are similar, suggesting some alteration of nodule calcite. More important, low $\delta^{13}\text{C}$ values are not found in all nodules from a given horizon, arguing against a paleoenvironmental signal, and low nodule values match values measured on diagenetic calcite, arguing for a diagenetic source. Relative to variation among nodules from the same horizon, differences between horizons is small and there is no statistically significant trend in $\delta^{13}\text{C}$ values through the section. The stability of $\delta^{13}\text{C}$ values in the majority of Doornplaats nodules suggests that $\delta^{13}\text{C}$ ratios were relatively constant during the last several million years of the Permian, contradicting the previously reported gradual decline of $\sim 10\text{‰}$ across this interval (Thackery et al., 1990).

Unlike results from Doornplaats, low $\delta^{13}\text{C}$ values at Bethulie seem to reflect primary variation. Low values are observed in all nodules and tusks from the stratigraphic interval containing the excursion, and $\delta^{18}\text{O}$ ratios of nodules, tusks, and diagenetic calcite form distinct populations (Fig. 3). Diagenetic calcite samples were not found from below ~ 80 m at Bethulie, but analysis of a split of a *Dicynodon* sample from 57 m shows that the boundary excursion is unlikely to

be a stratigraphically focused diagenetic artifact. Most tusk powders were treated with dilute acetic acid to remove diagenetic carbonate, but this split was washed with NaOHCl and H_2O only. Thus, the CO_2 evolved should have contained a mixture of carbon from dentin and carbon from diagenetic calcite. Because the gas had a higher $\delta^{13}\text{C}$ than the acid-treated split from the same sample, we conclude that diagenesis was not the cause of low $\delta^{13}\text{C}$ values at the boundary. Finding a $\delta^{13}\text{C}$ excursion at Bethulie that is associated with the independently defined P-T boundary and that is similar to excursions reported from different environments simultaneously supports a paleoenvironmental signal in the Bethulie results and confirms the excursion as a truly global feature.

If Bethulie values were pristine, nodules and tusks should exhibit parallel trends with a small offset ($\sim 3\text{‰}$) between sample types (Koch et al., 1992). The two curves show a reasonable separation through much of the section (Fig. 3) but nodules show a much larger shift at the P-T boundary ($\sim 10\text{‰}$) than tusks (3‰ – 4‰). Soil formation proceeds over thousands of years, and the sampled portions of the tusks were presumably formed in at most a few years. We would expect the samples formed over longer intervals (soil

nodules) to average out high-frequency secular variation, but the tusks we sampled from the excursion interval could have been formed during short intervals when local carbon reservoirs were enriched in ^{13}C . An alternative hypothesis we favor is that the difference in peak heights reflects subtle differences between nodules and tusks in diagenetic alteration. The dentin that makes up dicynodont tusks (King, 1981; Hotton, 1986), is relatively susceptible to alteration (Koch et al., 1997). If original isotopic ratios in the tusks were modified by diagenesis, all tusk values would have been shifted toward the $\delta^{13}\text{C}$ value of diagenetic calcite (i.e., toward higher values), but the tusks that originally had the lowest isotopic ratios would be shifted by the greatest amount. In this scenario the size of the excursion is reduced, but its stratigraphic position is not affected.

Excursion values were found in 8 samples from 4 stratigraphic horizons spanning 10 m of section (Fig. 3). Within the resolution of these data, the initiation of the $\delta^{13}\text{C}$ excursion coincides with the first appearances of *Lystrosaurus* and values began to return to background levels after the last appearance of *Dicynodon*. However, the 3 nodule samples all come from a single horizon and 3 of 4 sampled horizons are separated by ~ 1 m. Stratigraphic gaps between occurrences of Bethulie nodules and the preservational issues just discussed limit our ability to directly access the rate of $\delta^{13}\text{C}$ change, but rate is a critical factor in evaluating different extinct mechanisms.

Recent radiometric dates from Chinese marine sections indicate a maximum duration of $\sim 10^6$ yr for changes across the P-T boundary (Bowring et al., 1998). Bowring et al. applied average sedimentation rates between bracketing model ages to estimate the duration of the $\delta^{13}\text{C}$ spike as 165 k.y., but discussed how the interval could have been less than 10 k.y. Other studies have also used average sedimentation rates to suggest that the boundary event was geologically rapid (≤ 54 k.y.; Eshet et al., 1995; ≤ 30 k.y.; Rampino and Adler, 1998). Average sedimentation rate calculations applied to the 15 m overlap zone at Bethulie give similar results. At Bethulie the *Dicynodon* and *Lystrosaurus* assemblage zones are ~ 250 and ~ 400 m thick, respectively, and each zone represents millions of years (King, 1991; Rubidge, 1995). The overlap interval contains numerous beds of lithologies that occur commonly in the subjacent and superjacent strata and no major stratigraphic breaks were recognized (Smith, 1995); however, unremarkable bedding contacts could conceivably represent significant amounts of time such that the boundary interval represents the entire $\sim 10^6$ yr permitted by the radiometric dates (Bowring et al., 1998). Thus, the most significant aspect of Bethulie overlap zone is its implication for the minimum duration of the P-T event.

One of the more intriguing aspects of the P-T boundary is the cooccurrence in a number of sections of Permian and Triassic organisms (Erwin,

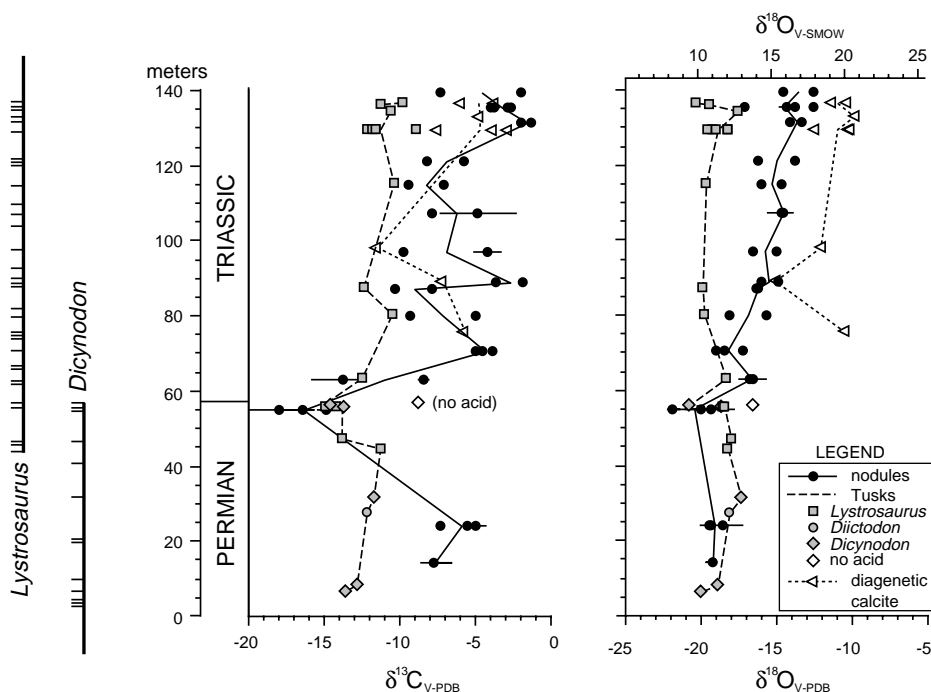


Figure 3. Stratigraphic pattern of *Dicynodon* and *Lystrosaurus* occurrences (Smith, 1995, and new data) and $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of nodules, tusks, and diagenetic calcite at Bethulie. Isotopic plots and abbreviations as in Figure 2. Tick marks indicate stratigraphic horizon where *Dicynodon* or *Lystrosaurus* were observed; many of these horizons contained multiple individuals. Permian-Triassic (P-T) boundary is placed at last occurrence of *Dicynodon* (Smith, 1995), and large number of individuals observed minimizes statistical uncertainty in stratigraphic position of this datum as well as in first appearance datum of *Lystrosaurus*. Nodules and tusks both show negative $\delta^{13}\text{C}$ excursion at P-T boundary, with lowest $\delta^{13}\text{C}$ values corresponding to the stratigraphic interval in which *Dicynodon* and *Lystrosaurus* cooccur. *Lystrosaurus* and *Dicynodon* tusks exhibit similar values in overlap zone, arguing against artifacts introduced by vital effects. At 57 m, split of *Dicynodon* not treated with acetic acid yielded $\delta^{13}\text{C}$ value of -8.7‰ , $\sim 6\text{‰}$ higher than split treated with acid, suggesting that diagenetic carbon in excursion interval is comparable to diagenetic calcite higher in section.

1994; Smith, 1995; Wignall and Twitchett, 1996; Bowring et al., 1998). These have often been dismissed as the result of reworking, but the Bethulie section allows this feature to be critically examined. Several of the highest *Dicynodon* occurrences are scattered skeletons, and all occur in overbank deposits. The lowest occurrences of *Lystrosaurus* (skulls with articulated jaws) also occur in overbank deposits. Local channels have a maximum relief of <1 m, so the stratigraphic cooccurrence of the taxa can not be attributed to taphonomic artifacts that mixed temporally distinct faunas. In addition, the 15 m overlap zone contains several paleosol horizons, each of which would have required >1 k.y. to form. Therefore, the Bethulie overlap zone represents a geologically resolved interval of time. It is possible that the first occurrence of *Lystrosaurus* shortly before the last occurrence of *Dicynodon* is coincidental and unrelated to P-T boundary event. Similarly, the low $\delta^{13}\text{C}$ of the tusk from 47 m could represent diagenetic smearing of a sudden isotopic excursion coincident with the extinction of *Dicynodon*. The generation of a better resolved $\delta^{13}\text{C}$ tied to detailed biostratigraphic data could resolve these questions, but we believe that available data suggest that the P-T boundary event in the Karoo basin was not geologically, let alone biologically, instantaneous.

CONCLUSIONS

The coincidence between faunal change (the replacement of the *Dicynodon* assemblage zone fauna by the *Lystrosaurus* assemblage zone fauna as estimated from the ranges of the nominate taxa) and the $\delta^{13}\text{C}$ excursion argues that biological and paleoenvironmental change in the Karoo basin was temporally coincident with the P-T boundary in other regions and environments. Thus, any ultimate explanation for the P-T transition should explicitly include discussion of how the forcing mechanism would cause changes in continental interiors. Furthermore, whereas the proximate cause of the replacement of *Dicynodon* by *Lystrosaurus* may be a shift to drier conditions (Smith, 1995), an ultimate forcing mechanism beyond a prograding alluvial wedge must be sought to explain why changes in the Karoo basin are synchronous with turnover elsewhere. The synchronous biological and geochemical change among disparate environments suggested by $\delta^{13}\text{C}$ stratigraphy seems more consistent with a single dominant forcing mechanism rather than a synergistic accumulation of stressful ecological events over time (Erwin, 1994; Morante, 1996; Bowring et al., 1998). Using data from the Cretaceous-Tertiary boundary as a guide, the faunal overlap and apparent duration of the $\delta^{13}\text{C}$ excursion does not match the expected geological record of a biologically rapid event such as an asteroid impact (Bowring et al., 1998; Retallack et al., 1998) or a catastrophic overturn of a stratified ocean (Knoll

et al., 1996). However, the excursion is geologically rapid enough and large enough to require export of readily exchangeable carbon from strongly ^{13}C -depleted reservoirs, such as remineralized organic carbon in the deep ocean or methane stored in gas hydrates. The rapid release to the atmosphere of methane or CO_2 from such sources could have paleoclimatic effects in continental interiors consistent with the observed sedimentological changes across the boundary.

ACKNOWLEDGMENTS

We thank Y. Maestas and G. Retallack for comments on this manuscript; M. de Wit, K. Hoppe, G. Koehler, and J. Zachos for discussion and analytical assistance; the Brodies and Claassens for access to their farms; A. Crean and P. October for field work; and the Royalty Research Fund (University of Washington) for financial support.

REFERENCES CITED

- Baud, A., Magaritz, M., and Holser, W. T., 1989, Permian-Triassic of the Tethys: Carbon isotopic studies: *Geologische Rundschau*, v. 78, p. 649-677.
- Bowring, S. A., Erwin, D. H., Jin, Y. G., Martin, M. W., Davidek, K., and Wang, W., 1998, U/Pb zircon geochronology and tempo of the end-Permian mass extinction: *Science*, v. 280, p. 1039-1045.
- Erwin, D. H., 1994, The Permo-Triassic extinction: *Nature*, v. 367, p. 231-236.
- Eshet, Y., Rampino, M. R., and Visscher, H., 1995, Fungal event and palynological record of the ecological crisis and recovery across the Permian-Triassic boundary: *Geology*, v. 23, p. 967-970.
- Foster, C. B., Logan, G. A., and Summons, R. E., 1999, The Permian-Triassic boundary in Australia: Organic carbon-isotopic anomalies relate to organofacies, not a biogeochemical "event": Ninth Annual V. M. Goldschmidt Conference: Lunar and Planetary Institute Contribution no. 971, p. 87-88.
- Hotton, N., III, 1967, Stratigraphy and sedimentation in the Beaufort Series (Permian-Triassic), South Africa, in Teichert, C., and Yochelson, E. L., eds., *Essays in paleontology and stratigraphy*, R. C. Moore Commemorative Volume: Lawrence, University of Kansas Press, p. 390-428.
- Hotton, N., III, 1986, Dicynodonts and their role as primary consumers, in Hotton, N., III, et al., eds., *The ecology and biology of mammal-like reptiles*: Washington, D.C., Smithsonian Institution Press, p. 71-82.
- King, G. M., 1981, The functional anatomy of a Permian dicynodont: *Royal Society of London Philosophical Transactions, ser. B, Biological Sciences*, v. 291, p. 243-322.
- King, G. M., 1991, Terrestrial tetrapods and the end Permian event; a comparison of analyses: *Historical Biology*, v. 5, p. 239-255.
- King, G. M., and Jenkins, I., 1997, The dicynodont *Lystrosaurus* from the Upper Permian of Zambia: Evolutionary and stratigraphic implications: *Palaeontology*, v. 40, p. 149-156.
- Knoll, A. H., Bambach, R. K., Canfield, D. E., and Grotzinger, J. P., 1996, Comparative Earth history and Late Permian mass extinction: *Science*, v. 273, p. 452-457.

- Koch, P. L., Zachos, J. C., and Gingerich, P. D., 1992, Correlation between isotopic records in marine and continental carbon reservoirs near the Paleocene/Eocene boundary: *Nature*, v. 358, p. 319-322.
- Koch, P. L., Tuross, N., and Fogel, M. L., 1997, The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite: *Journal of Archaeological Science*, v. 24, p. 417-429.
- Magaritz, M., Krishnamurthy, R. V., and Holser, W. T., 1992, Parallel trends in organic and inorganic carbon isotopes across the Permian/Triassic boundary: *American Journal of Science*, v. 292, p. 727-739.
- Morante, R., 1996, Permian and Early Triassic isotopic records of carbon and strontium in Australia and a scenario of events about the Permian-Triassic boundary: *Historical Biology*, v. 11, p. 289-310.
- Rampino, M. R., and Adler, A. C., 1998, Evidence for abrupt latest Permian mass extinction of foraminifera: Results of tests for the Signor-Lipps effect: *Geology*, v. 26, p. 415-418.
- Renne, P. R., Zichao, Z., Richards, M. A., Black, M. T., and Basu, A. R., 1995, Synchrony and causal relations between Permian-Triassic boundary crises and Siberian flood volcanism: *Science*, v. 269, p. 1413-1416.
- Retallack, G. J., 1999, Postapocalyptic greenhouse paleoclimate revealed by earliest Triassic paleosols in the Sydney basin, Australia: *Geological Society of America Bulletin*, v. 111, p. 52-70.
- Retallack, G. J., Seyedolali, A., Krull, E. S., Holser, W. T., Ambers, C. P., and KYTE, F. T., 1998, Search for evidence of impact at the Permian-Triassic boundary in Antarctica and Australia: *Geology*, v. 26, p. 979-982.
- Rubidge, B. S., 1995, Biostratigraphy of the Beaufort Group (Karoo Supergroup): Pretoria, South Africa, Council for Geoscience, 46 p.
- Smith, R. M. H., 1995, Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 117, p. 81-104.
- Thackeray, J. F., van der Merwe, N. J., Lee-Thorpe, J. A., Sillen, A., Lanham, J. L., Smith, R., KETSER, A., and Monteiro, P. M. S., 1990, Changes in carbon isotope ratios in the Late Permian recorded in therapsid tooth apatite: *Nature*, v. 347, p. 751-753.
- Wang, K., Geldsetzer, H. H. J., and Krouse, H. R., 1994, Permian-Triassic extinction: Organic $\delta^{13}\text{C}$ evidence from British Columbia, Canada: *Geology*, v. 22, p. 580-584.
- Wignall, P. B., and Twitchett, R. J., 1996, Oceanic anoxia and the end Permian mass extinction: *Science*, v. 272, p. 1155-1158.

Manuscript received June 21, 1999

Revised manuscript received November 16, 1999

Manuscript accepted November 24, 1999