Comment on "Abrupt and Gradual Extinction Among Late Permian Land Vertebrates in the Karoo Basin, South Africa"

In a groundbreaking paper, Ward *et al.* (*1*) provided both the stratigraphic context and a quantitative description of the terrestrial vertebrate fossil record across the Permian-Triassic (P-T) boundary from the Karoo basin in South Africa. They drew three primary conclusions: (i) that there was an accelerated gradual decline in diversity prior to the P-T boundary (in the *Dicynodon* Zone); (ii) that this was followed by a pulse of extinction at, or near, the boundary itself; and (iii) that the taxa that first appear in the Triassic most likely originated in the Permian—that is, the origin of the Triassic fauna was not a response to vacated niches caused by the P-T extinction pulse. Thus, the authors conclude that there is little evidence for a single catastrophic extinction mechanism such as might be expected from a large bolide impact.

These conclusions were based on the application of confidence intervals on the ends of the stratigraphic ranges, an approach designed to compensate for the incompleteness of the fossil record (*2*). Ward *et al.* (*1*) augmented their field data with qualitative data from outside their study area, which they used to extend the stratigraphic ranges of the taxa found within the study area. However, confidence interval lengths are a function both of the observed stratigraphic ranges and of the number of fossiliferous levels from which each taxon is known. Although Ward *et al.* (*1*) were able to extend the stratigraphic ranges of the taxa in their study, they were unable to provide a measure of how rich those extraneous fossil records are, and thus their confidence intervals are for the most part too long.

Here, I have reanalyzed the data of Ward *et al.* (*1*), restricting my analysis to just their own high-precision data. This analysis suggests a rather different set of conclusions from those drawn by Ward *et al.* (*1*).

First, for each taxon, I cannot reject the hypothesis that it became extinct before the P-T boundary (Table 1). In contrast, Ward *et al.* (*1*) argue that *Pristerodon*, *Aelurognathus*, and *Diictodon* became extinct before the deposition of Unit II, which marks the base of the Triassic (Fig. 1). Thus, the field data of Ward *et al.* do not support the claim that there was an accelerated background rate of extinction before the P-T boundary, although some taxa may have become extinct in the Permian. The apparent drop in diversity as one approaches the P-T boundary appears to be due to the Signor-Lipps effect (*3*).

Second, the data are consistent with the simultaneous extinction of all seven taxa restricted to the Permian that are known from at least two fossiliferous horizons. The 91% confidence band on the position of the mass-extinction horizon (assuming that there was one) is very narrow, extending only 1 to 2 meters into Unit II (Fig. 1), although the width of this type of confidence band can be sensitive to new data. Thus, the data are consistent with a sudden catastrophic extinction, although there is insufficient data to rule out a wide range of gradual extinction scenarios.

Figure S4 of Ward *et al.* shows a broader scale synoptic data set where many taxa disappear in the *Dicynodon* Zone well before the P-T boundary, which they use to support the notion of accelerated background rates before the P-T boundary. However, without quantitative data it is hard to test this scenario, so the question of whether there was an accelerated gradual decline (over normal turnover rates) leading up to the P-T boundary must remain open until data of the quality collected by Ward *et al.* (*1*) are collected more widely. However, noting the taxa held in common between their figure S4 and their high-precision field data, it appears that the Signor-Lipps effect extends through at least half of the *Dicynodon* Zone: The high-precision field data suggest that all the taxa that became extinct in this zone may have become extinct at the P-T boundary and not before—an observation that further undermines the argument for an accelerated background extinction rate close to the boundary.

Turning to the eight taxa that first appear in the Triassic, the data do not strongly support the claim that these taxa originated in the Permian (that is, before the deposition of Unit II); indeed, the data provide stronger support for a Triassic origin of these taxa (Table 1). For example, if one assumes that these taxa all arose simultaneously, we can be confident at the 78% level that this mass origination occurred in the Triassic, with only 22% confidence that this horizon was in the Permian (Fig. 1).

It is important to recognize that the use of confidence intervals on stratigraphic ranges here depends on two aspects of the data that have not been fully established. The first is accuracy of the relative positions of the fossil horizons depicted in the composite section. To make the problem tractable, Ward *et al.* (*1*) had to make the simplifying assumption that the relative rates of deposition between their correlation tie points was constant. The second simplifying assumption is that the fossils are distributed randomly within the true stratigraphic ranges of the taxa. Violations of this assumption may have a significant impact on the lengths of the computed confidence intervals. Bearing in mind these caveats, the data in Ward *et al.* (*1*) are not

Table 1. Confidence (C) that vertebrates became extinct in the Permian (prior to the deposition of Unit II) or originated in the Triassic (after the deposition of Unit I) calculated using $C = 1 - (G/R + 1)^{-(H-1)}$ (*4*). G is either the interval between the last occurrence of a Permian taxon and the base of Unit II or the interval between the first occurrence of a Triassic taxon and the base of Unit II. R is the stratigraphic range, and H the number of fossiliferous horizons. Using a Bonferroni correction, the critical value for a Permian extinction is 0.993 (a value exceeding 0.993 indicates that the taxon became extinct in the Permian at a significance level of 0.05). The critical value for a Permian origination is 0.006 (a value less than 0.006 indicates that the taxon originated in the Permian at a significance level of 0.05). This analysis indicates that one cannot rule out extinction at the Permian-Triassic boundary for any of the taxa that disappear in the Permian, nor can one rule out a Triassic origin for any of the eight taxa that first appear in the Triassic.

Taxon	C extinction in Permian	C origination in Triassic
Pristerodon	0.980	
Aelurognathus	0.591	
Dinanomodon	–	
Rubidgea	0.552	
Diictodon	0.534	
Theriognathus	0.273	
Pelanomodon	–	
Dicynodon	0.000	
Lystrosaurus A	0.000	
Moschorhinus	0.000	0.000
Lystrosaurus B	0.000	0.000
Owenetta	0.000	0.000
Ictidosuchoides	0.000	0.000
Proterosuchus		0.639
Lystrosaurus C		0.690
Micropholis		0.171
Thrinaxodon		0.885
Galesaurus		0.691
Lystrosaurus D		0.884
Lydekkerina		0.958
Procolophon		0.472

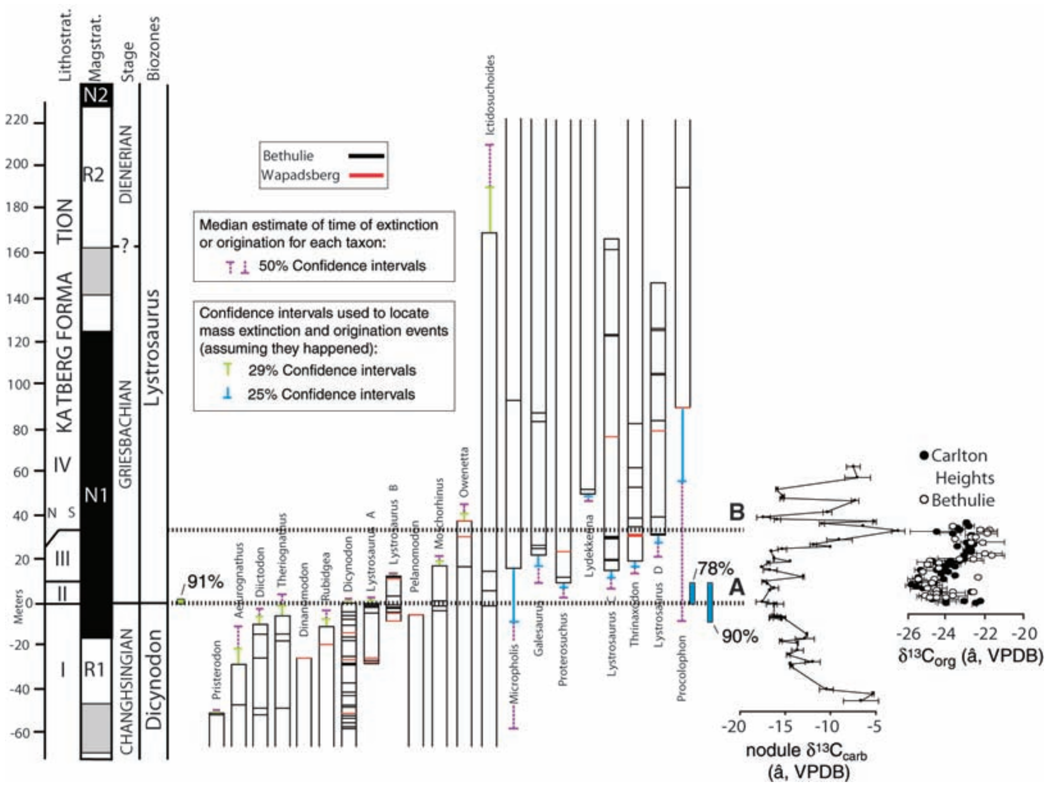

Fig. 1. Redrafting of figure 3 of Ward *et al*. (*1*), showing new confidence intervals on the stratigraphic ranges of taxa based only on the data given in the figure. Following (*5*) and with the 29% confidence intervals indicated in green, the very short vertical green line on the left shows the 91% confidence band for the extinction of all Permian taxa (assuming that there was such an extinction). With 25% confidence intervals, the longer blue line on the right shows the 90% confidence band for the Triassic taxa originations, assuming that originations were synchronous (which may not have been the case). The shorter blue line at the right shows the confidence (78%) that a sudden reemergence of the taxa found in the Triassic occurred in the Triassic and not in the Permian. Also indicated (in dashed purple) are the 50% confidence intervals on each of the stratigraphic ranges. If the assumption of randomly placed fossil horizons is met, we can be 50% confident that the true time of origin or extinction lies between the end of the observed stratigraphic range and the end of the 50% confidence interval. Concomitantly, we can be 50% confident that the true time of origination or extinction lies beyond the end of the confidence interval.

sufficient to reject the hypothesis of a catastrophic (local) extinction at the P-T boundary with a rapid recovery/replacement thereafter, even though there are some taxa that survive the event. The data are also consistent with a range of more gradual turnover hypotheses.

Charles Marshall
Museum of Comparative Zoology
Harvard University
26 Oxford Street
Cambridge, MA 02138, USA
E-mail: cmarshal@oeb.harvard.edu

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