



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

Peter D. Ward, *et al.*  
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## Response to Comment on “Abrupt and Gradual Extinction Among Late Permian Land Vertebrates in the Karoo Basin, South Africa”

We welcome the examination by Marshall (1) of our study (2), particularly his corrected statistical analysis of confidence intervals on stratigraphic ranges, which we accept. We believe, however, that in the process he has misinterpreted both our original data and his own reanalysis. We argued for both gradual and abrupt aspects to the Permian-Triassic (P-T) extinction, whereas Marshall suggests that only an abrupt pattern is present, with no heightened extinction rate prior to the boundary nor any pre-Triassic contributions to the postextinction fauna. We discuss these points below.

First, Marshall is mistaken that we have augmented ranges based on discoveries outside our field area. All of the data that we presented comes from one of our measured sections. Figure S4 simply extends the coverage to lower levels of the same stratigraphic sections (for the *Dicynodon* Zone).

Regarding previous extinction rates, we specifically stated that it was the data in figure S4 that showed enhanced extinction in the upper *Dicynodon* Zone. By limiting his reanalysis and reinterpretation to the “high-precision data” from the topmost 60 m of the ~400-m-thick *Dicynodon* Zone, where only a few species become extinct, Marshall misses the pronounced general trend that we were in fact talking about. In our sections of the upper *Dicynodon* Zone (excluding the boundary interval), there are 10 extinctions and 2 originations. Other regional studies have noted the same trend. In the Karoo Basin as a whole, Rubidge (3) observed that 11 of the 32 genera listed in the *Dicynodon* Zone disappear before

the end of the zone; Kitching (4) listed 44 genera occurring in this zone, of which 18 do not make it to the boundary. This can be contrasted with the fauna of the Hell Creek Formation which, at least for its dinosaur content, has no such background extinction over its duration, in a unit that is similar, both sedimentologically and in temporal duration, to the *Dicynodon* Zone. Hence, we still contend that a substantially enhanced extinction took place prior to the P-T boundary, with an even higher rate of extinction at the boundary.

Marshall also questions our conclusion that the originations of some typical members of the “Triassic fauna” may have preceded the boundary. Although his reanalysis suggests that a Permian origination of *Galesaurus* is unlikely, that still leaves *Lystrosaurus* B and probably *Micropholis* as Permian originators. Given that *Lystrosaurus* has been named zonal index for the first Triassic land animal zone, both in the Karoo and elsewhere in the world, the clear occurrence of this most typical member of the early Triassic terrestrial vertebrate fauna in Permian rocks robustly validates our contention. Moreover, phylogenetic analyses of P-T tetrapods from the Karoo, which suggest that numerous Triassic lineages probably originated before the extinction (5, 6), independently support this conclusion. Finally, the revised analysis by Marshall does not prove a synchronous radiation any more than our original data did, so there is no strong evidence for a rapid radiation into vacated niches after a catastrophic vertebrate extinction.

We thus conclude that Marshall’s reanalysis does not preclude a period of enhanced gradual extinction leading into the main pulse of abrupt extinction at the Permian-Triassic boundary, nor does it preclude Permian origination of some of the key elements of the postextinction Triassic fauna. The extinction event was therefore not simply the result of an instantaneous catastrophic event that caused a single abrupt extinction pulse, followed by synchronous radiation into an empty ecospace, but a complex and staged process in which each phase was qualitatively and quantitatively different. This points to an extinction mechanism (or mechanisms) that was prolonged, variable in intensity, and probably environmental in origin.

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