

## SAMPLING THE LATE PERMIAN EXTINCTIONS: A PERSPECTIVE USING LAZARUS GENERA

SUTER, Sherman J., Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269–3043, U.S.A., and Department of Paleobiology NHB–121, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

The end–Paleozoic extinctions about 250 million years ago comprise the most severe crisis in metazoan history. Documenting the patterns of disappearances across the Permian–Triassic boundary is a critical step towards understanding the causes of the extinctions. Analysis of such patterns must take into account the Signor–Lipps effect (the backward smearing of true last occurrences due to the failure to discover the latest members of extinct taxa). Evidence for a widespread marine regression and depositional hiatus below the boundary reinforces suspicions that sampling problems may prevent the accurate determination of the extinction patterns. Lazarus taxa, those whose disappearance from the record during the Late Permian is not due to extinction (for they reappear above the boundary), provide one indication of the quality of the Late Permian record. The percentage of genera absent from an interval within their known stratigraphic range provides a minimal estimate of sampling failures. (It does not consider the absence of families known from both sides of the boundary, or of transitional lineages between Paleozoic and Mesozoic genera or families.)

Using Sepkoski's compilation of known generic stratigraphic ranges (with minor corrections and additions), I identified potential Lazarus genera in six clades of skeletonized marine invertebrates. For each genus reported above and below the Permian–Triassic boundary, I searched the literature for Late Permian occurrences and attempted to place these in the Changxingian (= Dorashamian), Djulfian, or Guadalupian (Capitanian and Wordian) intervals. The resulting estimates of the percentage of Lazarus genera are ( $n$  = number of genera crossing the boundary;  $C$  = % missing from Changxingian;  $P$  = % missing from Guadalupian and younger Permian): ammonoids –  $n=3$ ,  $C=33\%$ ,  $P=0\%$ ; nautiloids –  $n=5$ ,  $C=P=30\%$ ; articulate brachiopods –  $n=14$ ,  $C=14\%$ ,  $P=0\%$ ; bivalves –  $n=32$ ,  $C=41\%$ ,  $P=19\%$ ; gastropods –  $n=48$ ,  $C=79\%$ ,  $P=33\%$ ; bryozoa –  $n=9$ , Djulfian= $P=0\%$ . Within the gastropods, Lazarus genera are more common among the opisthobranch orders than among other orders (archaeogastropods, euomphalinids, bellerophonids) – especially in the Changxingian.

Quantitative comparisons among clades are weakened by the substantial differences in numbers of surviving genera, and the approach cannot be applied to clades that were eliminated (fusulinids). But the variations in percentages of Lazarus genera suggest comparable variations in the completeness of the Late Permian records. Although some of the differences may follow from the amount of attention certain taxa have received in recent studies of latest Permian faunas, taphonomic effects are probably more important.

These results (especially the observed percentages of Lazarus genera among the bivalves and gastropods) suggest caution in interpreting the rates and timing of the Late Permian mass extinctions using the final appearances recorded in synoptic taxonomic databases. Determination of the fine structure of mass extinctions requires more refined stratigraphic and geographic data.