REFERENCES AND NOTES

2 October 1996; accepted 1 November 1996

Response: Rampino (in his letter) and Knoll et al. (in their response) attempt to refute our proposition (1) that Late Permian marine invertebrate mass extinctions coincide with the widespread development of marine anoxia and dysoxia. Their arguments are based on diametrically opposed interpretations of the Permian-Triassic deep sea record of Japan, and both rely heavily on the data from the same paper (2). Thus, neither letter challenges the well-established fact that most Late Permian marine invertebrates disappeared in shallow marine settings at levels marked by the appearance of dysaerobic or anaerobic biofacies (3). Rampino notes that the decline of radiolarians in Japanese sections occurs within a thin, siliceous claystone of latest Permian age immediately beneath a thin, basal Triassic organic-rich mudstone—a dysaerobic facies (2). He therefore argues that the extinction (of radiolarians at least) before the development of oxygen-poor conditions. However, he does not mention the evidence of dysoxic conditions in the claystone, namely, common micronodules of pyrite and discontinuous lamination (2).

Conversely, Knoll et al. acknowledge the oxygen-poor conditions recorded by the claystone (and the several meters of bedded, grey chert developed beneath this level) and argue that the organic-rich mudstone records improved oxygenation. This is counter to Kakuwa’s (and our) interpretation that this layer was a dysaerobic facies (2) and is primarily based on the presence of burrows in the mudstone and the interpretation of pyrite sulphur isotope variations (4). Kakuwa only illustrated millimeter-sized burrows from the claystone and mudstone, but did not document trace fossils from the underlying grey cherts.

Our observations of the chert ichnofabrics reveal them to be pervasively bioturbated by centimeter-sized burrows, testimony to substantially better benthic oxygen values than those of the organic-rich mudstone. The ichnofabrics, therefore, reveal a story of gradually declining benthic concentrations of O in the Late Permian record of Japan, culminating in low dysoxic conditions at the Permian-Triassic boundary. Identical changes are seen in contemporaneous shelf sections (5). Pyrite δ34S variations show a sharp negative swing in the organic-rich mudstone (4), which Knoll et al. interpret as a signature of a fully oxygenated water column. However, strongly negative values of pyrite sulphur (S) can also indicate intensely anoxic conditions such as those pertaining in the present-day Black Sea, where sulphide disproportionating bacteria repeatedly process and lighten elemental S (6). Sulfur isotopes of evaporites provide more conclusive, less equivocal evidence of global changes in the S cycle. These reveal a rapid positive swing beginning in the latest Permian and continuing into the Early Triassic (7), which indicates a major phase of pyrite burial and oceanic anoxia. This evidence alone seems sufficient to rule out the scenario of oceanic overturn and ventilation proposed by Knoll et al. (8).

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REFERENCES

25 October 1996; accepted 1 November 1996

HLA Sequence Polymorphism and the Origin of Humans

In the paper, “The myth of Eve: Molecular biology and human origins” (1), Francisco J. Ayala has made some questionable inferences about the origin of the human species based on analyses of mitochondrial DNA (mtDNA) and human lymphocyte antigen (HLA) sequence polymorphism. Ayala (i) argues that the data on primate HLA class II sequence diversity contradicts the “Mitochondrial Eve” hypothesis (2) about modern human origins, and (ii) estimates that the size of the founding human population was at least 100,000, primarily on the basis of assumptions about the number of DRB1 alleles transmitted to humans from the ancestral species.

It is inherent in the nature of maternal inheritance that all contemporary mtDNA lineages are derived from (or coalesce to) a single founding lineage. The hypothesis as stated by Cann et al. (3) simply postulated that this founding lineage was African and that the coalescence time was on the order of 100,000 to 200,000 years. The identification of a particular founding African mtDNA lineage says nothing about the size of the human population at that time. An estimate of the effective human population size (Nₑ), based on the diversity of mtDNA sequences among contemporary humans, was reported by Wilson and colleagues over a decade ago (4); Nₑ = 6000 females. Other recent estimates, based on classical polymorphisms (5) and Y chromosome–DNA markers (6), are also on the order of 10,000 individuals. Ayala argues that, when one considers various sources of error, these estimates are not inconsistent with his estimate of more than 100,000 individuals from the HLA data. In our view, however, a more realistic appraisal of the HLA class II sequence polymorphism also leads to an Nₑ of about 10,000, in line with Nₑ estimates from other molecular genetic data.

The extensive polymorphism at the HLA class II loci (for example, DRB1) is localized to the second exon, which encodes the peptide binding groove, and, in particular, to those codons encoding amino acids involved in interaction with the peptide and T cell receptor. The crux of the argument relating the contemporary HLA polymorphism to the size of the founding human population is the estimated number of alleles that were transmitted to the human lineage from the ancestral species. Obtain-
Response: Late Permian Extinctions
Paul B. Wignall and Richard J. Twitchett (November 29, 1996)
Science 274 (5292), 1552. [doi: 10.1126/science.274.5292.1552a]

Editor's Summary

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