model of human evolution depends on the demonstration of evolutionarily recent time depths for alleles found in non-African populations. Multiregional model enthusiasts also argue for an African origin, but place this origin at 1 million years before present (Y.B.P.), the approximate time at which *Homo erectus* remains can be identified outside Africa. Thus, for the "Out-of-Africa" model to be accepted, it is critical that allelic time depths be more recent than 1 million Y.B.P.

In support of the recent "Out-of-Africa" model, we (*1*) attempted to show that a single chromosomal segment, a CD4 locus haplotype composed of an Alu(−) allele and an STRP allele of 90 bp separated by 10 kb, had a recent time depth in non-Africans. As we emphasized in the article, in the absence of known recombination between the sites or mutation rates at the STRP marker, it is impossible to estimate an exact time of origin of this haplotype in non-Africans. However, by making certain conservative assumptions, it is possible to place likely upper bounds for this date. We used several methods of analysis to derive an upper bound for the coalescent date for non-Africans. One was based on the variance observed at the STRP on Alu(−) chromosomes outside versus inside Africa; this led to a date of 167,000 Y.B.P. Another analysis was based on the proportion of Alu(−) chromosomes with STRP alleles less than 110 bp outside versus inside Africa that carry the progenitor (90 bp) STRP allele. As an upper bound on this proportion, we examined its variability across five geographically diffuse sub-Saharan African populations that had more than 10 Alu(−) chromosomes. The proportion carrying the 90-bp repeat ranged from 0.25 in the Woloff to 0.53 in the Herero. We used 0.53 as an upper bound for this value across sub-Saharan Africa. For non-Africans, because of the small number of Alu(−) chromosomes not carrying the 90-bp allele, we assumed a Poisson distribution to obtain a lower 95% confidence bound for this number. With these two bounds, we obtained a maximum age of 313,000 Y.B.P. We also performed other conservative analyses [notes 40 and 41 in (*1*)], which gave additional estimates of maximal dates ranging to 450,000 Y.B.P.

All of these estimates of maximum age depend on the *assumption* that the Alu(−) allele has a maximum age of 5 million years and originated in Africa. This upper-bound estimate was used because the allele was not observed in chimpanzees or gorillas. Pritchard and Feldman state that the mutation could technically be even older, but they also agree that it is far more likely that this polymorphism is less than 5 million years old. A younger age seems likely because of the lifetime survival distribution for neutral mutations (*2*). In fact, our data argue for a more recent origin, albeit still ancient [note 42 in (*1*)]. Comparing variation in STRP allele size (calculated by any of several methods) shows that Alu(−) chromosomes have less variation than do Alu(+) chromosomes and are therefore likely to have a more recent coalescent.

Pritchard and Feldman use coalescent theory and a simulation to calculate a lower 95% confidence bound for $N_A\mu$. The sample of chromosomes on which their analysis is based derived from 10 extremely disparate African populations, spanning the entire continent, for which there must have been considerable relative endogamy. Such population structure would make more recent ages for the Alu(−) allele far less likely than would appear in Pritchard's and Feldman's simulation (*3*). Also, it is implausible that the population has been constant in size since the Alu deletion first occurred. Its rather high frequency in Africa suggests a rapid increase in the numbers of this chromosome soon after its introduction. Such growth would lead to a smaller estimate of variance for $N_A\mu$ than that calculated by Pritchard and Feldman.

Still, even under assumptions implausibly more conservative than ours, the upper bound for the estimate of the coalescent date of the Alu(−) chromosome in non-Africans is about 700,000 Y.B.P. (using Pritchard's and Feldman's estimate), still short of the 1 million years speculated by the "Multiregional" model. Their analysis thus supports our conclusion that a more recent date for an exodus of modern humans from Africa is more likely and that the CD4 data argue for the "Out-of-Africa" model rather than for the "Multiregional" model.

We originally stated (*1*) that the data we have obtained for the CD4 locus represent only a single realization of evolutionary history for Africans and non-Africans. As Pritchard and Feldman point out, it is tenuous to derive statistical distributions for coalescent times based simply on theory because of the arbitrary demographic assumptions required. The best way to derive such a distribution is empirically, combining the results of numerous different loci. Examination of linkage disequilibrium patterns for other systems in a fashion similar to what we have presented for CD4 should provide more definitive conclusions regarding the coalescence time for non-Africans.

Neil Risch
Department of Genetics,
Stanford University School of Medicine,
Stanford, CA 94305, USA
Kenneth K. Kidd
Sarah A. Tishkoff
Department of Genetics,
Yale University School of Medicine,
Post Office Box 208005,
New Haven, CT 06520, USA

REFERENCES

1. S. A. Tishkoff *et al.*, *Science* **271**, 1380 (1996).
2. N. Takahata and M. Nei, *Genetics* **124**, 967 (1990); N. Takahata, *Mol. Biol. Evol.* **10**, 2 (1993).
3. N. Takahata, *Genetics* **129**, 585 (1991).

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Late Permian Extinctions

In their article "Comparative Earth history and Late Permian mass extinction" (*1*), A. H. Knoll *et al.* suggest that Late Permian extinctions were caused by the release to the atmosphere of massive quantities of carbon dioxide (CO_2) from the deep ocean; that the CO_2 buildup in the ocean resulted from primary production in the surface layer; and that, despite sluggish ocean circulation rates, the release of phosphorus from decaying organic matter in deep anoxic waters would have been sufficient to further stimulate photosynthesis (*2*), which would in turn have led to further organic decay (that is, positive feedback) before oceanic overturn and release of CO_2.

Knoll *et al.* otherwise deemphasize the role of nutrients in the Permian extinctions, but if ocean circulation had been sufficiently slow in the Late Permian, phytoplankton could have largely stripped the surface mixed layer of nutrients (*3*) so that a "nutrient collapse" could have occurred. Also, the expansion of gymnosperms during this time (*4*) and the greatly increased interior drainage associated with the formation of the Pangean supercontinent (5) could have sequestered large amounts of nutrients on land (*4*, *6*). Greatly decreased nutrient availability during the Late Permian is consistent with the loss of many suspension-feeding invertebrates and nekton and the differential survival of infaunal taxa that fed on organic-rich sediment (*6*, *7*, *8*), as described by Knoll *et al.* Moreover, before Late Permian extinctions, the Permo-Carboniferous was a time of increasing nutrient and food availability in the water column (*6*, *7*). Thus, just as global marine ecosystems were becoming increasingly dependent on greater food availability in the Late Paleozoic, the rug, so to speak, could have been pulled out from under them as nutrients began to reverse toward lower amounts in the Late Permian (*6*).

Turnover of nutrient-rich waters at the end of the Permian during CO_2 release from the oceans could have further exacerbated global ecosystem instability, as Knoll *et al.* briefly discuss. Heightened productivity, as suggested by strong positive excursions in the carbon (C) isotope curve (*9*), may have also greatly augmented rates of extinction in the Late Ordovician, Late Devonian, and Late Cretaceous (*6*); these periods were otherwise characterized by sluggish ocean circulation (*10*) and potential sequestration of nutrients below the photic zone (*6, 11*). Fluctuations in nutrient concentrations were probably an important factor in mass extinctions, whatever the ultimate causal mechanism (*6, 12*), and in the selection of extinction-resistant marine invertebrate taxa according to their life history traits (*13*).

Ronald E. Martin
Department of Geology,
University of Delaware,
Newark, DE 19716, USA
E-mail: daddy@strauss.udel.edu

REFERENCES

1. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *Science* **273**, 452 (1996).
2. P. Van Cappellen and E. D. Ingall, *Paleoceanography* **9**, 677 (1994).
3. T. D. Herbert and J. L. Sarmiento, *Geology* **19**, 702 (1991).
4. H. Tappan, *J. Paleontol.* **60**, 545 (1986).
5. A. R. Wyatt, *Nature* **311**, 370 (1984).
6. R. E. Martin, *Global Planet. Change* **11**, 1 (1995); *Palaios*, in press.
7. R. K. Bambach, *Paleobiology* **19**, 372 (1993).
8. M. C. Rhodes and C. W. Thayer, *Geology* **19**, 877 (1991).
9. M. M. Joachimski and W. Buggisch, *ibid.* **21**, 675 (1993); P. J. Brenchley *et al.*, *ibid.* **22**, 295 (1994); E. Barrera, *ibid.*, p. 877.
10. L. B. Railsback, S. C. Ackerly, T. F. Anderson, J. L. Cisne, *Nature* **343**, 156 (1989); T. J. Bralower and H. J. Thierstein, *Geology* **12**, 614 (1984).
11. P. E. Wilde and W. B. N. Berry, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **48**, 143 (1984); W. B. N. Berry, P. Wilde, M. S. Quinby-Hunt, *ibid.* **74**, 3 (1989).
12. P. Wilde and W. B. N. Berry, in *Global BioEvents*, O. H. Walliser, Ed. (Springer-Verlag, Berlin, 1986), pp. 75–91; P. Wilde, M. S. Quinby-Hunt, W. B. N. Berry, in *Extinction Events in Earth History*, E. G. Kauffman and O. H. Walliser, Eds. (Springer-Verlag, Berlin, 1990), pp. 85–98.
13. E. N. Edinger and M. J. Risk, *Palaios* **9**, 576 (1994); ______, *Paleobiology* **21**, 200 (1995); R. E. Martin, in *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, M. McKinney and J. A. Drake, Eds. (Columbia Univ. Press, New York, in press).

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The changes described by Knoll *et al.* (*1*) can be accounted for if primary production through photosynthesis was curtailed at the end of the Permian for reasons unrelated to ocean dynamics (*2*). The rise in CO_2 in surface waters and the atmosphere could have been a consequence, as well as a cause, of extinction, and symptomatic of a possible extinction cascade.

The triggering event was probably the eruption of the Siberian traps, which occurred at a time indistinguishable from the mass extinction (*3*) and was the largest continental flood-basalt eruption so far known from the Phanerozoic Eon (*3, 4*). The eruption may have released vast quantities of methane (CH_4) that had accumulated on adjacent high-latitude permafrost and continental shelves during the Carboniferous and Early Permian (*5*). A lethal gas, CH_4 would have oxidized rapidly (within 10 years), first to formaldehyde and carbon monoxide, then to CO_2, drawing down oxygen (O) in the process (*5, 6*). Similar but less dramatic releases of CH_4 resulting from flood-basalt eruption at the end of the Paleocene may have led to warming and deep-sea extinctions (*7*). Because hydrate CH_4 and its derivative CO_2 would have been mostly depleted of ^{13}C, the rapid release of CH_4 could account for the observed reduction in changes in ^{13}C ($\delta^{13}C$) at the close of the Permian.

This hypothesis predicts the same pattern of selective extinction as that documented by Knoll *et al.*, namely, that organisms tolerant of high CO_2 concentrations in their tissues preferentially survived. Most survivors would also have been capable of shutting down their metabolism for short intervals during inclement conditions, whereas victims would have been unable to suspend activity despite their generally low per-capita energy use.

At other times in Earth's history, such as the mid-Cretaceous, volcanically erupted CO_2 and perhaps CH_4 may have stimulated evolution instead of bringing on an extinction (*8*). These eruptions differed from the Siberian eruption by occurring principally below the sea surface and may therefore have released gases less dramatically and over a longer interval.

Geerat J. Vermeij
Department of Geology and Center for
Population Biology,
University of California,
Davis, CA 95616, USA
Daniel Dorritie
Department of Geology,
University of California at Davis

REFERENCES

1. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *Science* **273**, 452 (1996).
2. M. Magaritz, *Geology* **17**, 337 (1989); K. Wang, H. H. J. Geldsetzer, H. Krouse, *ibid.* **22**, 580 (1994).
3. P. R. Renne, Z. Zichao, M. A. Richards, M. T. Black, A. R. Basu, *Science* **269**, 1413 (1995).
4. M. R. Rampino and R. B. Stothers, *ibid.* **241**, 663 (1988); P. R. Renne and A. R. Basu, *ibid.* **253**, 176 (1991); I. H. Campbell, G. K. Czamanske, V. A. Fedorenko, R. I. Hill, V. Stepanov, *ibid.* **258**, 1760 (1992).
5. For a review of gas hydrates, see K. A. Kvenvolden [*Rev. Geophys.* **31**, 173 (1993); *U.S. Geol. Surv. Prof. Paper 1570* (1993), p. 279].
6. D. J. Wuebbles and J. S. Tamaresis, in *Atmospheric Methane: Sources, Sinks, and Role in Global Change*, M. A. K. Khalil, Ed. (Springer, Berlin, 1993), pp. 469–513; E. G. Nisbet, *Canad. J. Earth Sci.* **27**, 148 (1990); C. K. Paull, W. Ussler III, W. P. Dillon, *Geophy. Res. Lett.* **18**, 432 (1991).
7. G. R. Dickens, J. R. O'Neill, D. K. Rea, R. M. Owen, *Paleoceanography* **10**, 965 (1995).
8. G. J. Vermeij, *Paleobiology* **21**, 125 (1995).

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Knoll *et al.* (*1*) suggest that the shift in $\delta^{13}C$ measured in marine carbonates, from a maximum of 8 per mil in the Late Permian to slightly more than zero per mil by the Triassic, was the result of a redistribution of C and C isotopes in the ocean and atmosphere. However, such an interpretation runs into difficulties with respect to mass balance.

Even with the increased ocean C concentrations proposed by Knoll *et al.*, the residence time of C in the combined ocean, atmosphere, and biosphere would have been more than 10^6 years. Thus, in time scales greater than this, the flux of C and C isotopes into these reservoirs must have very nearly balanced the flux out of these reservoirs.

The $\delta^{13}C$ value of carbonate sediments diminished from the Late Permian to the Triassic; this means that the flux of ^{13}C, relative to ^{12}C, from the oceans to carbonate sediments, diminished. Without a compensating process, ^{13}C would have accumulated in the atmosphere and oceans, and, in a time scale of more than 10^6 years (*2*), the $\delta^{13}C$ value of carbonate sediments would have increased. However, the C isotope record referred to by Knoll *et al.* shows no such rapid rebound.

To balance the long-term ^{13}C budget, diminished $\delta^{13}C$ in carbonate sediments would have required either diminished organic C burial or enhanced organic C oxidation, relative to inorganic C sedimentation (*3*). Long-term shifts in $\delta^{13}C$ values cannot be explained simply in terms of redistribution of carbon isotopes in the ocean and atmosphere.

Ken Caldeira
Climate System Modeling Group,
Lawrence Livermore National Laboratory,
7000 East Avenue, L-256,
Livermore, CA 94550, USA

REFERENCES

1. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *Science* **273**, 452 (1996).
2. L. R. Kump, *Geology* **19**, 299 (1991).

3. R. A. Berner and D. E. Canfield, *Am. J. Sci.* **289**, 333 (1989).

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In their report "Ocean anoxia and the end Permian mass extinction" (*1*), Paul B. Wignall and Richard J. Twitchett argue that widespread anoxia of the latest Permian oceans contributed to the most severe mass extinction in the geologic record, whereas Knoll *et al.* (*2*) develop a complex scenario in which overturn of deep anoxic waters during the Late Permian led to high atmospheric CO_2 with resultant climatic changes and physiological impact on life.

Studies of Permian-Triassic deep-water sequences in Japan show that a crash in productivity of radiolarians preceded the onset of oxygen-deficient conditions in the earliest Triassic (*3*). Thus, the relative timing of ocean anoxia and extinctions precludes a Late Permian anoxic ocean as a direct cause (as suggested by Wignall and Twitchett) or as an indirect factor (as in the scenario of Knoll *et al.*) in the mass extinction, although the timing raises the question of anoxia as a result of the extinction itself or of whatever caused the massive die-off.

Michael R. Rampino
Earth and Environmental Science,
New York University,
New York, NY 10003, USA, and
Goddard Institute for Space Studies,
National Aeronautics and Space
Administration,
New York, NY 10025
E-mail: rampin@is3.nyu.edu

REFERENCES

1. P. B. Wignall and R. J. Twitchett, *Science* **272**, 1155 (1996).
2. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *ibid.* **273**, 452 (1996).
3. Y. Kakuwa, *Palaeogeog. Palaeoclimaol. Palaeoecol.* **121**, 35 (1996).

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Response: We agree with Caldeira that the mechanism we proposed (*1*) to account for large decreases in the C isotopic composition of surface sea water during Neoproterozoic and Permo-Triassic can work only if the negative excursions lasted for less than 10^6 years. It is likely that the Permo-Triassic boundary excursion persisted no longer than the 10^5-year time scale permitted in Kump's model (*2*). At the proposed Permo-Triassic boundary stratotype at Meishan, China, the stratigraphic interval containing the excursion is 1 meter thick (*3*); an earlier negative excursion described by Jin (*4*) from a Capitanian-Wujiapingian boundary section in southwestern China is confined to a comparably thin stratigraphic interval. For the one Neoproterozoic negative excursion closely constrained by radiometric data, uranium-lead zircon dates on volcanic rocks just below and just above the event are the same to within the measurement error of one million years (*5*).

In reference to Martin's comment, our mechanism does not preclude the possibility that other accompanying effects also played a role in the extinction. Nutrient "shock" from the upwelling of anoxic deep water would be such a subsidiary factor, as would anoxia itself in basinal settings below the mixing zone. However, we advocate elevated CO_2 as a central mechanism in the Permo-Triassic crisis because its expected physiological and climatic effects match well with the observed strong selectivity of extinction and survival. It is this same pattern of selectivity that runs counter to either nutrient deprivation or prolonged surface ocean anoxia being primary kill mechanisms for the bulk of the marine fauna. Broad scenarios for end-Permian nutrient collapse have a long history, but most, including that outlined by Martin, do not include sufficient stratigraphic or mechanistic detail to permit testing. Given the short time scales for the pulses of extinction and the documented selectivity of groups affected, we are left asking what mechanism would produce global nutrient collapse in the time scale indicated and of sufficient intensity to kill nearly everything in the oceans? Why should high exercise capacity correlate with survival rather than extinction in latest Permian marine invertebrates? And why should terrestrial ecosystems have been so strongly affected by oceanographic events conjectured to have locked up nutrients in the deep sea?

Vermeij and Dorritie propose that CH_4 liberated from permafrost by the heat of Siberian flood basalts could account for the geological and paleobiological observations noted in our report. This provides a possible mechanism by which Permo-Triassic boundary volcanism could have triggered extinctions; however, it is unlikely that the quantity of CH_4 liberated in this fashion would have been sufficient to produce the physiological, climatic, or atmospheric effects inferred. The amount of CH_4 currently locked in permafrost is poorly known, but one can make a rough estimate. In Alaskan permafrost, CH_4 concentrations reach maximum values of 400 microatmospheres over depths of about 1 meter. Tundra currently covers an area of 5×10^8 square kilometers, leading to a global estimate of 3.5×10^{13} moles—close to MacDonald's recent estimate (*6*) of 2.5×10^{13} moles. The present atmospheric inventory of CO_2 is 6×10^{16} moles. Thus, CH_4 from a permafrost thaw could not have provided the CO_2 needed for our proposed kill by hypercapnia. Nor can this mechanism account for observed isotopic excursions, the depletion of atmospheric O (currently about 4×10^{19} moles), anomalous carbonate precipitation, or extinction before the Permo-Triassic boundary.

Rampino notes a recent revision in the biostratigraphic placement of Permo-Triassic black shales in Japan (*7*). These studies indicate that the major interval of carbonaceous mudstone sedimentation mentioned in our article began no earlier than the latest Permian; however, the transition from oxidized radiolarian cherts and shales to unoxidized, pyrite-bearing sediments occurs lower in the section in beds thought to be of Capitanian age. In the sections from Japan described by Kakuwa (*7*), bioturbation appears to be confined largely to grey shales at the base of and *within* the black shale interval. Conclusions drawn from lithologic observations of the Japanese sections are of local significance, representing, as they do, a vanishingly small sample of the late Permian ocean floor. This is why we concentrated on the sulfur (S) isotopic data reported by Kajiwara *et al.* (*8*) from the same sections. In principle, such data reflect chemistry through a much larger region of late Permian deep water. The sharp increase in the fractionation of S isotopes in sedimentary pyrite documented by Kajiwara *et al.* (and interpreted by them and us to indicate increasing deep ocean oxygen ventilation) falls at the base of the black shale interval. An attractive explanation for the black shales, then, is that they reflect the congruence of transiently high surface productivity (associated with the overturn of nutrient-rich bottom waters) and the collapse of benthic invertebrate populations. Revised biostratigraphic correlations from Japan are, thus, consistent with and may even strengthen the hypothesis explored in our article.

Although Rampino and Vermeij and Dorritie focus on Permo-Triassic boundary events, available data favor one or more earlier pulses of extinction within a Late Permian interval characterized by geological and geochemical signatures that are unique or unusual in Phanerozoic Earth history (*1*). Any fully satisfying account of boundary extinctions will place them securely in this broader context.

Andrew H. Knoll
Botanical Museum,
Harvard University,
Cambridge, MA 20138, USA
Richard K. Bambach
Department of Geological Sciences,
Virginia Polytechnic Institute
and State University,
Blacksburg, VA 24061, USA

Donald Canfield
Max Planck Institute for
Marine Micropaleontology,
Bremen 28359, Germany
John P. Grotzinger
Department of Earth, Atmospheric,
and Planetary Sciences,
Massachusetts Institute of Technology,
Cambridge, MA 02139

REFERENCES AND NOTES

1. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *Science* **273**, 452 (1996).
2. L. Kump, *Geology* **19**, 299 (1991).
3. D.-Y. Xu and Z. Yan, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **104**, 171 (1993).
4. Y.-G. Jin, *30th Internat. Geol. Congr.* (abstr.) **2**, 4 (1996).
5. J. P. Grotzinger, S. A. Bowring, B. Z. Saylor, A. J. Kaufman, *Science* **270**, 598 (1995).
6. G. MacDonald, *Clim. Change* **16**, 247 (1990).
7. Y. Kakuwa, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **121**, 35 (1996).
8. Y. Kajiwara, S. Yamakita, K. Ishida, H. Ishiga, A. Imai, *ibid.* **111**, 367 (1994).

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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 radiolaria at least) occurred 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 $\delta^{34}S$ 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*).

Paul B. Wignall
Richard J. Twitchett
Department of Earth Sciences,
University of Leeds,
Leeds LS2 9JT, UK

REFERENCES

1. P. B. Wignall and R. J. Twitchett, *Science* **272**, 1155 (1996).
2. Y. Kakuwa, *Palaeogeog. Palaeoclim. Palaeoecol.* **121**, 35 (1996).
3. P. B. Wignall and A. Hallam, *ibid.* **93**, 21 (1992); *ibid.* **102**, 215 (1993); P. B. Wignall, A. Hallam, X. Lai, F. Yang, *Hist. Biol.* **10**, 175 (1995); P. B. Wignall, H. Kozur, A. Hallam, *ibid.* **12**, 39 (1996); P. B. Wignall and A. Hallam, *Palaios*, in press.
4. Y. Kajiwara, S. Yamakita, K. Ishida, H. Ishiga, A. Imai, *Palaeogeog. Palaeoclim. Palaeoecol.* **111**, 367 (1994).
5. R. J. Twitchett and P. B. Wignall, *ibid.* **124**, 137 (1996); R. J. Twitchett, *Pal. Soc. Spec. Publ.* **8**, 400.
6. D. E. Canfield and B. Thamdrup, *Science* **266**, 1973 (1994).
7. G. E. Claypool, W. T. Holser, I. R. Kaplan, H. Sakai, I. Zak, *Chem. Geol.* **28**, 199 (1980); U. Kramm and K. H. Wedepohl, *ibid.* **90**, 253 (1991).
8. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *Science* **273**, 452 (1996).

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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 (N_e), based on the diversity of mtDNA sequences among contemporary humans, was reported by Wilson and colleagues over a decade ago (*4*); N_e = 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 N_e of about 10,000, in line with N_e 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-