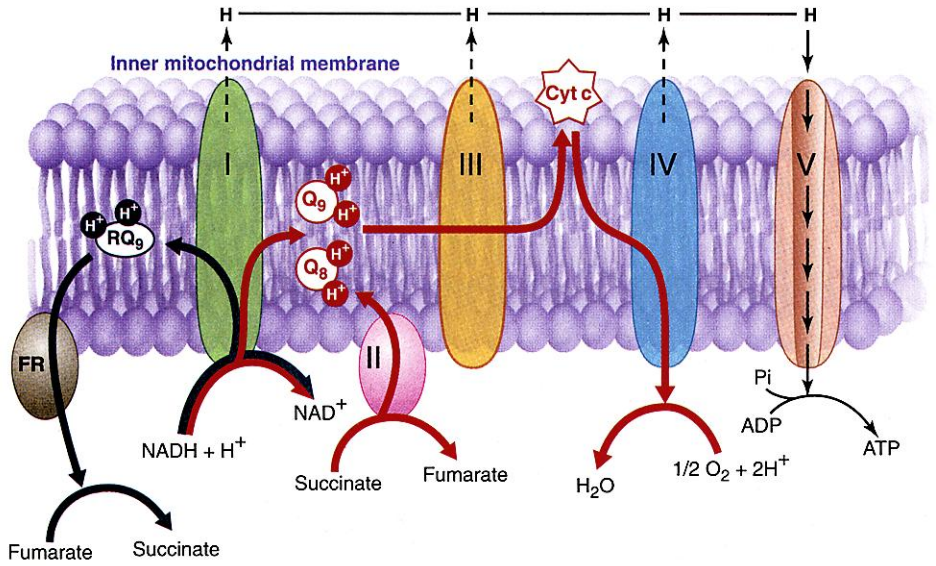

The electron transport chain. Coenzyme Q (Q) is a lipid-soluble factor that is crucial for transport of electrons and protons across the inner mitochondrial membrane, a process that maintains the proton gradient driving ATP synthesis. Q drives electron transport at complexes I, II, and III, and is essential for proton transport at complexes I and III. Worms endogenously synthesize the Q_9 isoform from a DMQ_9 intermediate. They can also obtain Q from feeding on bacteria that synthesize Q_8. Worms also produce RQ_9, an alternate quinone that is involved in anaerobic respiration (blue arrows) rather than aerobic respiration (red arrows). Restricting dietary Q in worms extends longevity perhaps because reduced Q results in the production of fewer oxygen radicals during electron transport.

strongly to a Q-less diet. Interestingly, *daf-2*; *daf-12* double-mutant worms have extended longevity, but do not respond to a Q-less diet. Analysis of these interactions should enable the intersection of insulin signaling with mitochondrial function to be elucidated.

How does Q impact aging? The worm shows an increased reliance on anaerobic respiration (fermentation) for energy production during the nonfeeding dauer larval stage, which occurs in place of larval stage three. Dauer larvae exhibit a number of traits known to slow aging when expressed in adults. Perhaps the balance of Q isoforms—by affecting signaling between mitochondria and the nucleus that results in altered gene transcription (*11*)—induces the longevity-assurance elements of the dauer stage. An attractive alternative is that an abundance of Q_8 and Q_9 may accelerate the rate of electron transport and thus the release of reactive oxygen species from mitochondria. Q is also a cofactor in the activity of uncoupling proteins, which pump protons across the inner mitochondrial membrane. Uncoupling may be an important mechanism to help modulate electron transport efficiency and proton leakage during aging (*12*). These hypotheses await decisive experimentation, and direct measurement of metabolic intermediates and reactive oxygen species. Ultimately, to establish the generality of Q's aging effects, we must also test its impact in organisms such as the fruit fly *Drosophila* and rodents, where the influence of fermentation pathways is likely to be different.

References

1. P. L. Larsen, C. F. Clarke, *Science* **295**, 120 (2002).
2. H. Miyadera *et al.*, *J. Biol. Chem.* **276**, 7713 (2001).
3. P. Stenmark *et al.*, *J. Biol. Chem.* **276**, 33297 (2001).
4. T. Jonassen *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 421 (2001).
5. R. S. Sohal, R. Weindruch, *Science* **273**, 59 (1996).
6. S. Melov *et al.*, *Mutat. Res.* **434**, 233 (1999).
7. B. Lakowski, S. Hekimi, *Science* **272**, 1010 (1996).
8. G. C. Williams, *Evolution* **11**, 398 (1957).
9. C. Kenyon *et al.*, *Nature* **366**, 461 (1993).
10. K. D. Kimura *et al.*, *Science* **277**, 942 (1997).
11. S. M. Jazwinski, *Trends Genet.* **16**, 506 (2000).
12. M. D. Brand, *Exp. Gerontol.* **35**, 811 (2000).

PERSPECTIVES: GEOPHYSICS

Caught Offside

Tim Elliott

Eighty percent of global volcanism occurs out of sight, at submarine volcanoes along the 56,000 km of mid-ocean spreading centers that straddle Earth. This volcanic activity is confined to very narrow (~1 km) zones between two separating tectonic plates. This concentration of volcanic activity is particularly remarkable when the volume of the rock producing the magmatism is considered: a triangular melting region, with a base at least 60 km deep, extends 60 km on either side of the ridge axis (see the first figure).

Several fluid dynamic models have been developed to account for this strong focusing of melts beneath ridges (*1–3*). Yet it has also been noticed that the upper oceanic crust, which consists of the solidified remains of the erupted melts, continues to thicken away from the ridge axis (*4*, *5*). Is the architecture of oceanic crust governed by growth at the ridge crests alone, or is it embellished by off-axis additions?

To answer this fundamental question about the nature of oceanic crust, we require accurate chronometers that can tell us whether all off-axis lavas are older than their ridge crest counterparts, as in a classical plate-spreading model, or whether there are aberrant youngsters. This problem is beyond the resolution of commonly used isotopic dating systems, but is addressed in dramatic fashion by Zou *et al.* on page 107 of this issue (*6*).

The authors use high-precision uranium isotope series measurements to provide a new perspective on this problem. Melting is commonly believed to induce disequilibrium in the short-lived nuclide chains between U and Pb. After eruption, secular equilibrium (in which the decay rates of all intermediate nuclides are equal) is restored on the geologically short time scales of the half-lives of the intermediate nuclides; for example, ^{230}Th has a half-life of 75,000 years. For a fast-spreading ridge, with plates diverging at a rate of 10 cm/year, any melt-produced disequilibrium still present in lavas more than 20 km from the ridge clearly identifies off-axis volcanism.

A finer chronology is possible if the initial disequilibrium is known. Assuming that this has remained constant, Goldstein *et al.* (*7*) have inferred off-axis volcanism 1 to 4 km from the ridge crest. Zou *et al.* now show striking disequilibrium more than 20 km off axis. At these distances, few would have anticipated recent volcanism except at well-defined "seamounts." Yet the samples analyzed by Zou *et al.* are from normal oceanic crust on the flanks of the East Pacific Rise (*8, 9*).

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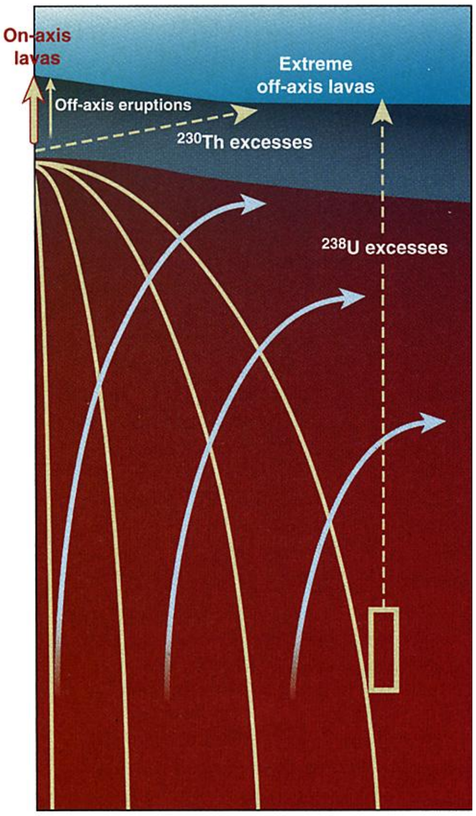


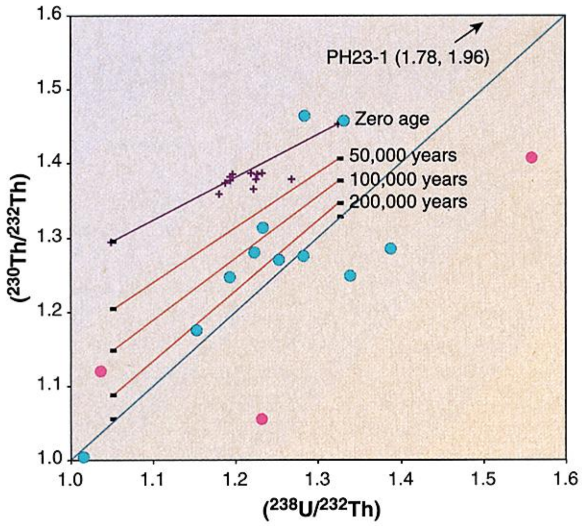
Off-axis volcanism. Melt focusing (yellow curves) as a result of mantle flow (arrowed blue curves) beneath ridges leads to a narrow zone of mid-ocean ridge volcanism. Goldstein *et al.* (*7*) have found "near" off-axis volcanism (thin arrowed yellow line). Zou *et al.* (*6*) identify extreme off-axis eruptions, which they attribute to dyking from the ridge axis (sub-horizontal dashed line) and melting of enriched mantle blebs (vertical dashed line).

Zou *et al.*'s data contain further remarkable features. ^{230}Th-^{238}U disequilibrium at mid-ocean ridges is almost always characterized by ^{230}Th excesses. Indeed, most of Zou *et al.*'s samples show ^{230}Th excesses, including two samples with unexpectedly large ^{230}Th excesses 14 and 21 km off axis. Very few samples with ^{238}U excesses have been reported. It has been argued that these are consistent with melting beneath the deepest (~5 km) parts of the ridge system (*10*) and reflect the smaller, shallower underlying melting region at these locations (*11*). Yet Zou *et al.* document ^{238}U excesses for off-axis lavas from a normal ridge segment less than 3 km deep. Furthermore, the off-axis ^{230}Th and ^{238}U excesses appear to alternate nearly symmetrically on either side of the ridge. Symmetrical features about a ridge are readily explained by sea-floor spreading but are not expected for off-axis magmas.

Accounting for all of Zou *et al.*'s observations within existing paradigms is not easy. The authors attribute off-axis magmas with ^{230}Th excesses to subsurface dikes perpendicular to the dominant direction of fracture propagation at ridges. The source of these lavas is thus the same as at the ridge itself. In contrast, ^{238}U excesses are suggested to result from a distinct magma source that is enriched by material from recycled oceanic crust. This helps to explain the compositions of the lavas with the most extreme ^{238}U excesses, but other samples with ^{238}U excesses do not have such signatures (see the second figure). Moreover, it is not clear why such an enriched source would occur nearly symmetrically on either side of the ridge and show no clear signature of a different source (such as distinct Pb isotope ratios).

It has recently been predicted that the two-dimensional effects of melt transport resulting from (symmetrical) plate spreading can cause systematic variations in melt composition perpendicular to the ridge (*12*). Geochemical variations close to the East Pacific ridge at 12°N seem to be consistent with such a model (*13*). The approach could possibly be extended to account for the off-axis samples in Zou *et al.*'s data set. However, the sense of the variation in their data is opposite to that in (*13*), with anomalously enriched rather than depleted samples found off axis.

U-series disequilibrium measurements are technically demanding, especially at the low concentrations of these nuclides in mid-ocean ridge basalts. The problem is compounded by Mn coatings on sea-floor lavas, which sequester short-lived nuclides from seawater. Leaching techniques have been shown to remove potential contamination from these coatings for on axis samples (*14*). The further off axis, the greater the possible influence of Mn coatings on surfaces and cracks. However, neither insufficient nor overzealous leaching would be expected to preserve near-equilibrium ^{234}U/^{238}U ratios (as documented by Zou *et al.*) or to produce ^{238}U excesses as an artifact of sample preparation, let alone to do so symmetrically on either side of the ridge.



Not treading a fine line? Off-axis samples of Zou *et al.* (circles) (*6*) are compared with on- and near-axis samples of Goldstein *et al.* (crosses) (*7*). Samples in isotopic equilibrium plot on a line with a gradient of 1 (the equiline); those with ^{230}Th excesses plot to the left, and those with ^{238}U excesses to the right. The solid line indicates the range of compositions for on-axis samples. Off-axis samples of different ages would be expected to plot along the red lines. Many of Zou *et al.*'s samples plot where anticipated, but two samples fall on the zero-age line despite being 14 and 21 km off axis. Four samples lie to the right of the equiline. Two of the latter show enriched trace element signatures (pink symbols). One sample is too extreme to fit within the plot.

A couple of problems remain. The off-axis eruptions identified by Zou *et al.* do not have obviously thinner Mn coatings. The nonquantitative nature of Mn thickness chronology makes U-series dating a crucial new contribution, but the qualitative dichotomy for this data set is noteworthy. It is also troubling that one sample of Zou *et al.* shows ^{230}Th/^{232}Th and ^{238}U/^{232}Th ratios much greater than any on-axis sample (see the second figure).

The remarkable features of Zou *et al.*'s data set will doubtless lead to reanalysis of these and other samples. The results are quite reasonably interpreted in terms of eruptions of "normal" and "enriched" lavas some 20 km off axis. The assistant referee's flag is definitely raised.

References

1. M. Spiegelman, D. McKenzie, *Earth Planet. Sci. Lett.* **83**, 137 (1987).
2. W. R. Buck, W. Su, *Geophys. Res. Lett.* **16**, 641 (1989).
3. D. W. Sparks, E. M. Parmentier, *Earth Planet. Sci. Lett.* **105**, 368 (1991).
4. G. L. Christeson, G. M. Purdy, G. J. Fryer, *Geophys. Res. Lett.* **19**, 1045 (1992).
5. A. J. Harding, G. M. Kent, J. A. Orcutt, *J. Geophys. Res.* **98**, 13925 (1993).
6. H. Zou, A. Zindler, Y. Niu, *Science* **295**, 107 (2002).
7. S. J. Goldstein *et al.*, *Nature* **367**, 157 (1994).
8. S. Carbotte, K. Macdonald, *J. Geophys. Res.* **97**, 6959 (1992).
9. R. Batiza *et al.*, *Geophys. Res. Lett.* **23**, 221 (1996).
10. B. Bourdon, A. Zindler, T. Elliott, C. H. Langmuir, *Nature* **384**, 231 (1996).
11. E. Klein, C. H. Langmuir, *J. Geophys. Res.* **92**, 8089 (1987).
12. M. Spiegelman, *Earth Planet. Sci. Lett.* **139**, 115 (1996).
13. ———, J. R. Reynolds, *Nature* **402**, 282 (1999).
14. B. Bourdon *et al.*, *Geochem. Geophys. Geosys.* **1**, paper 2000GC000047 (2000).