

spontaneous retro-translocation. They categorized these structures into eight main classes, five in the pre-translocation state (pre1–pre5) and three in the post-translocation state (post1–post3).

The authors' main criterion for pre- or post-translocation categorization was the position in the 30S subunit of a region in the peptidyl-tRNA called the tRNA anticodon stem loop — when this region was in the A site, the sub-state was categorized as pre-translocation, and when in the P site it was given post-translocation status. The authors note that, irrespective of the incubation time, the relative numbers of ribosomes in the five pre- and three post-translocation states remained constant. They therefore conclude that the sub-states in the two states are all in equilibrium and are kinetically separated by a rate-limiting step.

But how do the two ribosome-bound tRNAs move sequentially through their five pre-translocation states to the rate-limiting translocation event? And why, as the authors find, is the post-translocation peptidyl-tRNA stable in the P site, whereas the E-site tRNA becomes progressively less stably bound on its way to dissociating from the ribosome?

Fischer *et al.*¹ report strong correlations between the various ribosome conformations and the positions of the tRNA molecules, but they also find that any given position of the tRNAs is associated with a broad range of ribosome structures. It therefore seems that there is a complex landscape of diverse ribosomal conformations and tRNA-binding modes that have similar standard free energies and that are separated by low-energy barriers.

When the authors raise the incubation temperature to 37 °C — the optimal temperature for *E. coli* growth — cryo-EM cannot detect distinct ribosome structures. This suggests that, at this temperature, the ribosome is rapidly 'diffusing' between a large number of conformational sub-states. The authors therefore describe the ribosome as a "Brownian machine", in that forward and backward translocations in the absence of EF-G depend on selective sampling of a large set of rapidly interconverting ribosome conformations.

As Fischer and colleagues point out, the main question now is whether EF-G-catalysed forward translocation can also be understood in terms of the ribosome as a Brownian machine, existing in a conformational spectrum of sub-states similar to that seen in spontaneous retro-translocation. Alternatively, it could be that GTP-bound EF-G rapidly drives the ribosome into a ratcheted state with little room for conformational excursions, and that, after GTP hydrolysis, it guides the ribosome to the completion of translocation along a structurally well-defined reaction path. It could, in fact, be that the mechanism behind rapid EF-G-catalysed translocation is pre-organization of the ribosome in a structure that leads from the ground state to a transition state in the translocation reaction with a small loss

in entropy (a small entropy of activation)¹².

The key to understanding how EF-G promotes such rapid and precise translocation therefore remains unclear. Will the key be the conformational fluctuations described by Fischer *et al.*¹, or analysis of a small number of high-resolution structures of the ribosome that clarify the transition state of EF-G-catalysed translocation? Either way, Fischer and colleagues' seminal cryo-EM work has revealed important and intriguing aspects of the interplay between rapidly inter-converting ribosomal conformations and elongation-factor-driven ribosome function. ■

Måns Ehrenberg is in the Department of Cell and Molecular Biology, BMC, Uppsala University, Uppsala S-75124, Sweden.

e-mail: ehrenberg@xray.bmc.uu.se

1. Fischer, N., Konevega, A. L., Wintermeyer, W., Rodnina, M. V. & Stark, H. *Nature* **466**, 329–333 (2010).
2. Schmeing, T. M. & Ramakrishnan, V. *Nature* **461**, 1234–1242 (2009).
3. Schmeing, T. M., Huang, K. S., Kitchen, D. E., Strobel, S. A. & Steitz, T. A. *Mol. Cell* **20**, 437–448 (2005).
4. Trobro, S. & Åqvist, J. *Proc. Natl Acad. Sci. USA* **102**, 12395–12400 (2005).
5. Ogle, J. M. & Ramakrishnan, V. *Annu. Rev. Biochem.* **74**, 129–177 (2005).
6. Weixlbaumer, A. *et al. Science* **322**, 953–956 (2008).
7. Laurberg, M. *et al. Nature* **454**, 852–857 (2008).
8. Sund, J., And er, M. & Åqvist, J. *Nature* **465**, 947–950 (2010).
9. Valle, M. *et al. Cell* **114**, 123–134 (2003).
10. Moazed, D. & Noller, H. *J. Nature* **342**, 142–148 (1989).
11. Rodnina, M. V. *et al. Nature* **385**, 37–41 (1997).
12. Kamerlin, S. C. L. & Warshel, A. *Proteins* **78**, 1339–1375 (2010).

EARTH SCIENCE

Proposal with a ring of diamonds

David A. D. Evans

Plate reconstructions show that ancient eruptions of diamond-bearing rocks occurred consistently above a ring-like region of plume-generation zones deep in Earth's mantle. Do such zones remain stationary?

Diamonds are formed only at great depths within Earth's mantle, enduring there for billions of years until they are brought to the surface in explosive 'kimberlite' volcanic eruptions¹ — named after the spectacularly diamond-rich Kimberley region of South Africa (Fig. 1). Kimberlite emplacement has been relatively rare during the past 50 million years, and no modern kimberlite eruption has ever

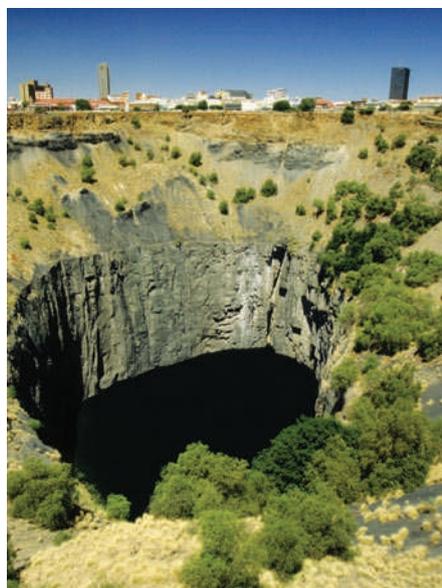


Figure 1 | The Big Hole at Kimberley, South Africa. Here, one hundred years of mining for diamonds, largely by hand pick and shovel, have hollowed out the original funnel-like geometry of the kimberlite eruptive pipe that extends deep below the present water table.

been observed. But such events were relatively common during the Mesozoic era of 250 million to 65 million years ago, when the Pangaea supercontinent was breaking apart. On page 352 of this issue, Torsvik *et al.*² report an intriguing pattern of ancient kimberlite fields in time and space, a pattern that they show has persisted for at least 200 million years, and is rooted to the bottom of Earth's mantle, nearly 3,000 km beneath the planet's surface.

Torsvik *et al.* combine state-of-the-art tectonic-plate reconstructions, using palaeomagnetic data³, with a stacked suite of tomographic images of the planet's deep interior⁴. They show that kimberlite eruptions have been consistently located above the edges of an enormous body of chemically distinct rock in the lowest 500 km of the mantle. This large, low-shear-wave-velocity province (LLSVP) located under Africa is one of two such regions on opposite sides of the world that dominate lowermost-mantle global seismic structure. Most of the world's large igneous provinces (LIPs) of the past 200 million years are localized along their edges^{5,6}. Torsvik *et al.* refer to those edges as 'plume-generation zones' in reference to the narrow mantle upwellings⁷ that give rise to many LIPs.

The LLSVPs are not completely understood. Nonetheless, Torsvik *et al.*² consider the hypothesis that they can be used as fixed markers of absolute palaeolongitude in the mantle. Their success in reconstructing LIPs and kimberlites to the LLSVP edges for the past 200 million to 250 million years shows that the hypothesis is viable. Extending the

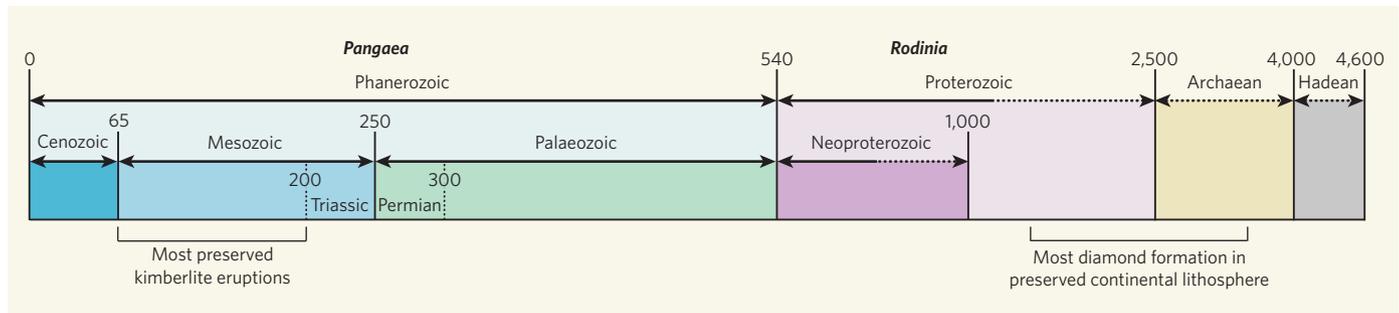


Figure 2 | Kimberlites, diamonds and supercontinents in time. Numbers are ages in millions of years. Most of the world's natural diamonds were formed deep within the continental lithosphere during Archaean and early Proterozoic time, and were brought to the surface much later by kimberlite volcanic eruptions. Torsvik *et al.*² show that the most common incidence of preserved kimberlites, which erupted during an interval starting about 200 million years ago, can be linked to plume-generation zones arising from the ring-shaped margin of a large,

low-shear-wave-velocity province (LLSVP) lying deep in the mantle. Torsvik and colleagues' proposal is that the African and Pacific LLSVPs have been stationary in the mantle for at least the past 540 million years, if not longer. An alternative explanation of this pattern, discussed here, is that supercontinents such as Pangaea and Rodinia caused a reorganization of mantle flow, and that LLSVPs are created and disintegrate in each supercontinental cycle, with no necessary palaeogeographic connection from one to the next.

hypothesis to greater ages, Torsvik *et al.* use the assumed-fixed LLSVPs to likewise reconstruct Palaeozoic continents into an absolute palaeogeographic framework, constrained in both palaeolatitudes and palaeolongitude throughout the past 540 million years of Phanerozoic time (see Fig. 2 for a timeline).

Another possible interpretation of the LLSVPs, however, is that they are a legacy of the most recent supercontinent, Pangaea, and were created only about 200 million years ago when most of the preserved kimberlites and LIPs began erupting. Such a scenario is consistent with models of mantle convection that include supercontinents^{8,9} as large caps at Earth's surface that organize subduction zones to their peripheries and create stable, long-wavelength upwellings on the same scale as upwellings of the Mesozoic–Cenozoic Earth. Torsvik and colleagues' palaeogeographic correlations of LIPs, kimberlites and LLSVPs for ages greater than 200 million years are not particularly strong; the Permian–Triassic Siberian traps (one of the largest preserved LIPs on Earth) reconstruct to a position more than 3,000 km from the nearest edge of an LLSVP, and the early–middle Palaeozoic reconstructions to fixed-longitude LLSVPs are tenuous, with only a handful of data constraining the models.

The almost complete lack of known LIPs between 500 million and 300 million years old can be neatly explained by the fact that Pangaea hadn't yet formed. However, Torsvik *et al.* present an alternative explanation — that the LIP record is biased by preservation. They argue that the early–middle Palaeozoic continents were simply not well situated over the LLSVPs, and that any oceanic LIPs formed above the plume-generation zones would now be lost from the geological record by subduction.

However, large oceanic volcanic plateaus can resist subduction and become preserved¹⁰, so the remarkable gap in the current global LIP database between 500 million and 300 million years ago probably reflects a true paucity of such magmatism. Furthermore, despite the numerous late-Palaeozoic traverses of the

LLSVP edges by the supercontinent Gondwanaland's richest diamond-bearing areas (such as western Africa and the Congo region), there is an impressive dearth of kimberlites and LIPs in those regions through that time interval. The same observation holds for the middle–late Cenozoic era, which is almost completely lacking in kimberlites, even in Africa, lying astride its namesake LLSVP.

By contrast, the LIP record from about 800 million to 550 million years ago is globally abundant (although kimberlites of that antiquity have only rarely been found). This can readily be interpreted as the legacy of LLSVPs formed by organization of mantle convection under the earlier supercontinent Rodinia, and associated with its break-up in Neoproterozoic time. Those more ancient LLSVPs might have existed, but there is no guarantee that they occupied the same locations — in terms of an 'absolute' mantle reference frame — as their post-Pangaeian counterparts.

Whether the LLSVP-related plume-generation zones, like the proverbial diamonds they exhume, are 'forever' fixed in the mantle has implications for understanding planetary convection through the aggregation and break-up of supercontinents. If today's LLSVPs formed only 200 million years ago, resulting from Pangaea's organization of global mantle flow, then they can be interpreted as the loci of large-scale upwellings complementary to long-lived subduction systems¹¹. However, if the African LLSVP preceded formation of Pangaea, as interpreted by Torsvik *et al.*², then it seems, oddly, to have attracted the supercontinent's lateral motion so that, just before it broke up, the landmass lay precisely atop the mantle anomaly.

Torsvik *et al.* instead attribute that apparent attraction to coincidence, and speculate that the LLSVPs remain isolated from mantle convection on billion-year timescales. However, viscous entrainment should have eroded their edges through the aeons, creating the conundrum of why they are so large today. In the more conventional 'Pangaea-legacy' model of LLSVPs, there

is no need for such isolation; they are an integral part of a two-upwelling convection system that is expected to be stable until assembly of the next supercontinent around Eurasia, creating new LLSVPs in perhaps entirely different locations in the mantle^{12,13}.

Torsvik and colleagues² have thus made a provocative proposal — that of the existence of a stationary palaeogeographic 'ring' of regions in the mantle containing most of the world's diamond-bearing kimberlites. They propose that mantle convection's engagement with such a ring has endured for as long as 500 million years, and perhaps even longer, through Earth's history. The alternative proposal, espoused here, is that the global convection system breaks its engagement with the ring of plume-generation zones every 500 million years or so, through each supercontinental cycle. Regardless of which model survives further scrutiny, global palaeogeography is advancing to a new stage of kinematics — and consequent implications for dynamics — marrying palaeolatitudes with palaeolongitude in deep time. ■

David A. D. Evans is in the Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06511, USA.
e-mail: dai.evans@yale.edu

1. Wilson, L. & Head, J. W. III *Nature* **447**, 53–57 (2007).
2. Torsvik, T. H. *et al.* *Nature* **466**, 352–355 (2010).
3. Torsvik, T. H., Müller, R. D., Van der Voo, R., Steinberger, B. & Gaina, C. *Rev. Geophys.* doi:10.1029/2007RG000227 (2008).
4. Becker, T. & Boschi, L. *Geochem. Geophys. Geosyst.* doi:10.1029/2001GC001688 (2002).
5. Torsvik, T. H., Smethurst, M. A., Burke, K. & Steinberger, B. *Geophys. J. Int.* **167**, 1447–1460 (2006).
6. Burke, K., Steinberger, B., Torsvik, T. H. & Smethurst, M. A. *Earth Planet. Sci. Lett.* **265**, 49–60 (2008).
7. Montelli, R., Nolet, G., Dahlen, F. A. & Masters, G. *Geochem. Geophys. Geosyst.* doi:10.1029/2006GC001248 (2006).
8. Zhong, S., Zhang, N., Li, Z.-X. & Roberts, J. H. *Earth Planet. Sci. Lett.* **261**, 551–564 (2007).
9. Phillips, B. R. & Coltice, N. *J. Geophys. Res.* doi:10.1029/2009JB006600 (2010).
10. Richards, M. A., Jones, D. L., Duncan, R. A. & DePaolo, D. J. *Science* **254**, 263–267 (1991).
11. Richards, M. A. & Engebretson, D. C. *Nature* **355**, 437–440 (1992).
12. Evans, D. A. D. *Tectonophysics* **362**, 303–320 (2003).
13. Li, Z.-X. & Zhong, S. *Phys. Earth Planet. Inter.* **176**, 143–156 (2009).