function of temperature. Similar studies (with neutrons) on uranium led to the discovery of a series of complex charge-density waves in that material (*5*).

The two studies (*1, 2*) provide important insights into some of the basic elastic and thermodynamic properties of plutonium. Furthermore, both the DFMT method and the microbeam method used in the experiment open up new avenues for investiga-

tion, not only of the actinides but also of many other interesting materials.

Plutonium emerges as a fascinating element. Last year, we learned that some compounds of plutonium superconduct at surprisingly high temperatures (*6*). Now that we understand more about the vibrations in the element itself, there will be many new efforts to solve some of the riddles of the past 60 years. Hopefully, these studies will

help to convince those weaned on its controversial nuclear properties that there is another side to plutonium.

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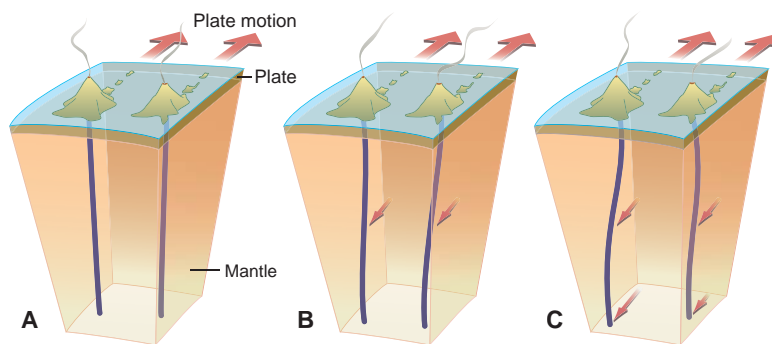**GEOPHYSICS**

Hotspots Come Unstuck

Joann Stock

Volcanic hotspots such as Hawaii and Iceland are believed to be caused by fixed volcanic sources deep in Earth's mantle. As a tectonic plate drifts over such a hotspot, age-progressive island chains and seamounts—such as the Hawaiian-Emperor seamounts—are created. But how do we know that the hotspots are fixed relative to one another and that their tracks reflect only the plate motions above them? New paleomagnetic data from drill holes into the Emperor seamounts, reported by Tarduno *et al.* on page 1064 of this issue (*1*), show that the story is not that simple.

The ages of the Emperor seamounts indicate rapid (>5 cm/year) relative motion between the plate and the hotspot source from 81 to 47 million years ago. This could mean that the Pacific plate was moving northward over a stationary hotspot source, carrying the volcanic record of the Emperor seamounts with it. Alternatively, the Pacific plate could have been stationary, underlain by a southward-moving source of hotspot volcanism.

Paleomagnetic data can reveal the original latitude of the seamount eruptions and the history of latitudinal motion of the Pacific plate. These data can thus distinguish between these two extreme possibilities, which have very different implications for mantle dynamics (see panel A of the figure). If all Emperor seamounts were at 19°N when they erupted, this would suggest that the hotspot

source was fixed at 19°N with respect to the North Pole and that there was northward motion of the Pacific plate. Conversely, if all seamounts had paleolatitudes equivalent to their modern latitudes, the Pacific plate would have been stationary, but the hotspot plume would have moved southward.

Paleomagnetic results (*1, 2*) show that the truth lies somewhere in between. The latitude of the volcanic centers was not constant with time, but was south from their

Different views of hotspot plumes. (A) The plumes are stationary and vertical. As the plate moves over them, the only control on the hotspot tracks is the plate velocity. **(B)** The plume bases are fixed relative to one another, but the plumes are at an angle due to mantle flow, with the plate moving over them. Thus, there are two controls on the hotspot tracks: mantle flow and plate motion. **(C)** The hotspot tracks are due to the sum of three effects: relative motion between the two plume sources, change in geometry of the plume conduits due to mantle flow, and plate motions at the surface.

modern latitudes for seamounts north of Koko Seamount. Earlier data showed that the Pacific plate had a northward component of motion (*3, 4*). The Emperor Seamount drilling results (*1, 2*) reveal that there was also southward drift of the hotspot plume beneath the Pacific plate, contrary to the fixed-hotspot hypothesis (*5*).

If the hotspots are all fixed relative to each other, then continental hotspot tracks could be used to reconstruct plate positions for times older than the seafloor spreading record (before 150 million years ago); kinks in hotspot tracks such as the Hawaiian-Emperor bend could be linked to

major changes in plate motion. However, the fixed-hotspot hypothesis has never been universally accepted, because the criteria for hotspot volcanism are ambiguous and the tracks and eruptive history of many of these features are difficult to define.

Hotspot fixity can be tested by computing past relative plate positions under the fixed-hotspot assumption and comparing these with reconstructions based on marine magnetic anomalies, which record seafloor spreading in the ocean basins. This method requires a reliable chronology of the hotspot traces, which is not always available, and a good knowledge of the seafloor spreading history of the plates. Furthermore, it can only be applied to plates connected to each other through a "plate circuit" of mid-ocean ridges.

For some Indo-Atlantic hotspots, the relative plate motions from magnetic anomalies and those from hotspot traces are similar. There thus appears to be a self-consistent set of plate motions in which this subgroup of hotspot sources was fixed (*6*). However, conclusions differ on whether all major Pacific plate hotspots fit a single reference frame (*7, 8*). Comparisons of these two hotspot groups through the plate circuit reveal relative motion between individual Pacific hotspots and the Indo-Atlantic hotspots (*9, 10*).

A mistake in the plate circuit assumptions, such as an unrecognized plate boundary, could account for this misfit, but no suitable boundary has yet been found (*11*). The new data of Tarduno *et al.* (*1*) explain why a missing plate boundary cannot completely account for the hotspot misfit: The latitude of the hotspot volcanism in the Emperor seamounts was changing with time, while the latitudes of the Indo-Atlantic hotspots did not change.

What does this result imply for processes deep in the mantle? The plates are the

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surface expression of mantle convection. We cannot directly image the three-dimensional flow deeper in the mantle, but can infer it from dynamic models based on plate velocities and mantle density anomalies inferred from seismic data. If a rising hotspot plume becomes advected by the mantle flow, the plume may tilt, displacing the hotspot-related eruptions laterally from the deeper hotspot source (panel B). Such an effect may have tilted the Hawaiian-Emperor hotspot conduit, causing the latitudinal variations in the Emperor seamounts (*1*, *12*). Additional latitudinal change might be caused by relative motion of the bases of the hotspot plumes (panel C), but with present data it is difficult to determine the magnitude of this effect.

Many aspects of hotspots remain controversial. The criteria for identifying hotspot volcanism vary greatly from study to study, and there is disagreement regarding the depth at which the sources originate (*13*, *14*). The volcanic histories of some linear island chains formerly used as examples of hotspot traces are incompatible with linear age progressions (*15*). Even if two hotspot plumes originate at the base of the mantle, there is no theoretical reason for them to be fixed relative to one another, although the relative motion of their sources may have been slow.

The Hawaiian-Emperor seamount chain is the best-characterized hotspot trace to date, with numerous high-precision ages and significant paleomagnetic data from ocean drilling. Similar paleomagnetic data and detailed ages on other hotspot traces worldwide are needed to constrain the likely influence of mantle flow on the pattern of volcanism at Earth's surface.

To understand the forces driving plate tectonics, we need a physical model of mantle flow based on plausible rheologies and consistent with a reliable history of past plate motions in a well-defined reference frame. Paleomagnetic observations of hotspot tracks are crucial for validating any such reference frame and constraining the integrated effects of mantle flow. Ultimately, we may be able to reconstruct the past velocity history of Earth's mantle and surface, including plate motions, mantle flow history, and their effects on hotspot tracks.

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MOLECULAR BIOLOGY

RNAi Extends Its Reach

Marjori Matzke and Antonius J. M. Matzke

The discovery of RNA interference (RNAi) and a vast new world of tiny regulatory RNAs has profoundly changed the way we think about gene regulation in animals, plants, and many fungi. The tiny RNAs are termed "short interfering RNAs" (siRNAs) or "microRNAs" (miRNAs) depending on their origin. They down-regulate gene expression by binding to complementary messenger RNAs (mRNAs) and either triggering mRNA elimination (RNAi) or arresting mRNA translation into protein (*1*, *2*) (see the figure). Recently we have learned that the RNAi pathway extends beyond silencing mRNA to act on the genome. For example, in the fission yeast *Schizosaccharomyces pombe*, the RNAi machinery is required for assembly of silent condensed heterochromatin at centromeres and at the mating-type region (*3*–*6*). Results reported by Schramke and Allshire on page 1069 of this issue (*7*) broaden the role of RNAi. They show that normally euchromatic (decondensed) genes can be direct targets of RNAi-dependent heterochromatin formation. In addition, they find that the same silencing pathway acts on dispersed endogenous DNA repeats to repress genes involved in the sexual cycle.

RNAi induced by synthetic hairpin RNAs (shRNAs) has been used extensively to study gene function in plants and animals. Schramke and Allshire (*7*) showed that a *ura4*+ shRNA encoded on an extrachromosomal plasmid could silence a *ura4*+ marker gene in *S. pombe* and that this was coupled to heterochromatin formation. The silencing was dependent on components of the RNAi machinery: Dicer (Dcr1), which cleaves double-stranded RNA (dsRNA) precursors to give miRNA or siRNA, Argonaute (Ago1), and RNA-dependent RNA polymerase (Rdp1). This could be consistent with classic RNAi silencing (see the middle of the figure), but would not explain the coupling between silencing and heterochromatin formation, and thus the requirements for two known chromatin factors were also tested.

The enzyme Clr4, which methylates histones (the major proteins of chromatin), was essential for *ura4*+ silencing and *ura4*+ siRNA production. In addition, chromatin immunoprecipitation experiments showed that the pattern of modifications at the silenced *ura4*+ locus was identical to the pattern at centromeric repeats (*3*–*5*) and the silent mating-type region (*6*). Thus, silencing by RNAi is coupled to chromatin modifications at the *ura4*+ target locus. The *S. pombe* ortholog of heterochromatin protein 1, Swi6, was not required for *ura4*+ silencing and siRNA production, but was needed for heterochromatin to spread from the *ura4*+ nucleation site. Swi6 also recruited the protein cohesin, another constituent of heterochromatin. Thus, all hallmarks of authentic heterochromatin were established at the *ura4*+ locus by an RNAi-mediated pathway (see the figure).

The *ura4*+ experiments showed that RNAi could silence a normally expressed gene and initiate a patch of heterochromatin that spread laterally from the silenced locus. However these experiments involved an shRNA encoded on an introduced plasmid. Do naturally occurring siRNAs silence genes by RNAi-dependent chromatin modifications? To answer this question, Schramke and Allshire looked to transposons, sequence elements that can invade and colonize genomes. In plants, these genome interlopers are controlled by DNA methylation, histone methylation, and RNAi (*8*, *9*). Drawing on the influential ideas of Barbara McClintock, who won a Nobel Prize in 1983 for the discovery of transposons, Schramke and Allshire postulated that these elements might fortuitously provide regulatory sequences for adjacent host genes. This concept echoes an early model of gene regulation formulated by Britten and Davidson (*10*). They proposed that networks of dispersed DNA re-

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