species have reached different localities.

Hotspots of species richness have variously been argued as representing cradles of diversity exhibiting high origination rates, museums of diversity exhibiting low extinction rates, or some combination of the two. For reef fish, the IPR seems to function as the first of these, constituting a major (but not exclusive) centre of speciation (new species formation) in the Indian and Pacific oceans, from which species disperse to more peripheral locations. Other major marine centres of origin, functioning for other organisms, seem more obviously to have served as museums, as well as cradles, of diversity[8].

The high levels of speciation in the IPR may result from the high number and density of islands (and hence reefs; Fig. 1). This would theoretically enhance allopatric speciation (the differentiation of geographically isolated populations into distinct species) and perhaps other forms of speciation, resulting in the IPR also being a hotspot of endemism.

In addition, a negative relationship has recently been demonstrated, both theoretically and empirically, between the size of a species' geographical range and its probability of speciation[9,10]. This finding raises the intriguing possibility that hotspots of origination experience positive feedbacks, in which to some degree the restricted species ranges that result from high levels of speciation encourage more speciation. This is because species with small ranges are characterized by reduced dispersal between different populations and by lower local densities, which reduce levels of gene flow[9] and hence enhance the likelihood of genetic isolation. Positive correlations between range size and dispersal ability have been reported for other groups of marine organisms, and would fit with the findings of Mora *et al.*[4] for reef fish in the Indian and Pacific oceans. Positive correlations between range size and local abundance are very general, and might also apply to reef fish: although there is little evidence of this at present, insufficient data are available for most families[11]. So the very reasons for the existence of the centre of diversity in the IPR may also be responsible for its importance in the structuring of reef assemblages across the Indian and Pacific oceans.

Kipling sent his honest serving men "east and west" and "over land and sea". In seeking to understand patterns of species richness, such a broad-scale view was undoubtedly the correct one. ■

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Geochemistry

Lost terrains of early Earth

Stein B. Jacobsen

Isotope data provide insight into the earliest phases of terrestrial evolution. The latest reappraisal supports the view that the early Earth had a cratered crust which crystallized from a magma ocean.

Unlike Earth, several bodies such as the Moon, Mercury and Mars have a clear record of their surface history dating back almost to the origin of the Solar System. This early crust is now no longer evident on Earth, where the oldest rocks are 3.8–4.0 billion years old and thus date to about 600–700 million years after the planet's formation. Studies[1–3] in which neodymium (Nd) isotopes were used as a window into these lost terrains concluded that the Earth probably had a magma ocean from which a proto-crust and a layered mantle crystallized about 4.47 billion years ago. But the interpretation was challenged by reports[4–7] that there was no evidence of an expected corollary of that conclusion — a specific signature of another isotope, hafnium (Hf). In particular, it was proposed[6,7] that before 4.0 billion years ago the crust was similar to the continental crust we see today.

On page 931 of this issue, however, we have a reversal of perspective. In a new study of Hf isotopes in meteorites, Bizzarro *et al.*[8] point out that the data used up to now for a crucial parameter, the evolution of the lutetium (Lu)–Hf isotopic system in 'bulk' planetary material[9,10], were incorrect. With their new data, the Hf and Nd information fall into line, thus supporting the earlier inferences drawn from the Nd isotopes. Appropriately enough, the discovery of Hf was announced in these pages 80 years ago, almost to the month (see Box 1).

Chondritic meteorites — aggregates of

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100 YEARS AGO

A few weeks ago we described some of the excellent results obtained by Messrs. Heraeus, of Hanau, in their attempts to produce apparatus of "silica glass," and Prof. Dewar had added point to our remarks by exhibiting at the Royal Institution a "liquid air holder" made of silica, which had been made to order and sent by return of post, almost, from Hanau to London a few days before. Similar apparatus could have been made in England, it is true, but it could not have been produced by any means so quickly as at Hanau… Truly, as Prof. Dewar said the other evening, there will soon be another "lost industry" if our practical men do not wake up. Silica glass making as an industry no doubt is still in earliest infancy, but though so young, it already shows signs of growth. Everyone who has worked with silica, and knows its properties and how comparatively easy it is to work with, foresees that soon silica glass will replace ordinary glass in many of its most important applications.

From *Nature* 26 February 1903.

50 YEARS AGO

G. Notini and S. Forselius discuss the methods which have been undertaken to exterminate the wild rabbits on Gotland Island. The wild rabbit was introduced into Sweden with the object of providing a new game animal of commercial value. Vigorous stock was selected and care was taken to ensure the proper environmental conditions, based on European accumulated experience in parts where the stock had become more or less stabilized, excess numbers being kept down by small predatory animals and also disease. As has occurred in other parts of the world where mammals, birds and plants have been introduced outside their own habitat, the rabbits in Gotland increased rapidly in numbers. None of their ordinary checks was present, the only one being the occasional severe winters experienced in the island. The ordinary methods of man-shooting, poisoning, snaring, etc. — but not poison, have proved ineffective; poison is regarded as too dangerous… The rabbit to-day in Gotland constitutes such a menace to sylviculture and agriculture that it is ranked with the small rodents. Work is now being undertaken on the introduction of the virus disease *Myxomatosis cuniculi* into the Gotland rabbit population.

From *Nature* 28 February 1953.

Box 1 Hafnium history

Not only is 2003 the eightieth anniversary of the identification of hafnium but, like the paper by Bizzarro *et al.*[8], news of the discovery came from Copenhagen — hence the element's name, which derives from *Hafniae*, the Latin for Copenhagen. The paper appeared in *Nature* on 20 January 1923 (**111,** 79; 1923) under the title "On the missing element of atomic number 72".

The discovery was made by Dirk Coster (a Dutchman) and George de Hevesy (a Hungarian) working in Niels Bohr's laboratory. Initially, the nature of element 72 was a little controversial — some claimed that it had been found among the rare earth metals. But Bohr believed that it should lie not there but among the group 4 elements with zirconium; and so it turned out. Following X-ray spectroscopy of zirconium minerals, Coster and de Hevesy concluded that: "It seems to be very probable that ordinary zirconium contains at least from 0.01 to 0.1 per cent. of the new element. Especially the latter circumstance proves that the element 72 is chemically homologous to zirconium."

De Hevesy had a peripatetic career, working not only in Copenhagen, but in Manchester (with Rutherford), Vienna, Budapest, Freiburg, Cornell and Ghent. In 1943, he won the Nobel Prize in Chemistry for his research on the use of isotopes as tracers for studying chemical processes. **Tim Lincoln**

material from the primitive Solar System that have not undergone planetary differentiation — are central to studies such as these. They provide the best estimate of the starting composition of the terrestrial planets except for the most volatile elements (such as hydrogen, helium and nitrogen). Therefore it is commonly accepted that the average evolution of the chondritic Lu–Hf and samarium (Sm)–Nd systems also represent their evolution in the terrestrial planets as a whole. Deviation from the chondritic evolution of these isotopic systems is thus a measure of planetary differentiation processes such as mantle melting and solidification of these melts into crustal or mantle layers.

The basis for modelling planetary evolution with isotope systems such as Lu–Hf or Sm–Nd is a good estimate of the bulk planetary isotope evolution of such a system. These parameters have long been well established for the Sm–Nd system[11,12]. But because of the difficulty of making precise Lu/Hf isotopic measurements on meteorites, the parameters used for this system[9,10] were of inferior quality. Bizzarro and colleagues' study[8] of chondritic meteorites rectifies this situation and is also in agreement with a Lu/Hf study of a group of meteorites called eucrites[13] (eucrites are thought to be the product of lava flows from the surface of the asteroid Vesta, formed as partial melts of its interior).

The decay of ^{176}Lu (half-life 36 billion years) into ^{176}Hf is a good clock for tracing the evolution of planetary crusts and mantles, because the behaviour of these elements during melting and crystallization is well understood and produces variations in concentration that can be quantitatively predicted. The process gives a crust and mantle of different chemical compositions. Compared with the primordial, well-mixed Earth, the composition of which is also known from the analysis of meteorites, the crust has a higher proportion of some elements than the mantle. Lutetium and Hf are preferentially extracted from the mantle and enriched in the crust, Hf more so than Lu. The Sm–Nd isotopic system has an entirely analogous behaviour.

The Moon has a distinctive signature for the Nd and Hf systems, and it is well accepted that it was produced by a particular evolutionary pattern — an early magma ocean gave way to crust overlying accumulated mineral layers of the lunar mantle, the main differentiation occurring around 4.4 billion years ago. Similar events had been inferred from Nd isotopes for the early Earth. But this view was challenged by studies of Hf isotopes, on the grounds that the Nd data had been altered by metamorphism whereas the Hf data were more robust and gave the true signature of early differentiation.

Bizzarro *et al.*[8] have now found a clear Hf isotope record of the Earth's primordial crust. From Hf isotope data of 3.1–4.1-billion-year-old zircons — resistant mineral grains that have survived from the time of the parent rock's formation, even when that rock has not — they conclude that the early differentiation between crust and mantle occurred 4.33 ± 0.10 billion years ago (about the time of early differentiation of the Moon). Although this early terrestrial crust no longer exists, it left a clue behind in that the zircon Hf isotope ratios are much higher than the bulk planetary Lu–Hf isotopic evolution as inferred from meteorites — that is, much higher than in the primordial mantle. So the host rocks of the ancient zircons did not emerge from mantle that had never given birth to crustal rocks before. Rather, the mantle source of the rocks containing the zircons had already supplied some Hf to an even earlier crust. This is in line with what has been observed for two Sm/Nd isotopic clocks: the decay of ^{147}Sm (half-life of 106 billion years) to ^{143}Nd, and of ^{146}Sm (half-life of 103 million years) to ^{142}Nd.

Today, Earth's crust forms mainly at mid-ocean ridges where crustal spreading occurs, and is recycled into the mantle where tectonic plates collide. The Earth's early crust was probably not formed by this mechanism. If plate tectonics had been active then, the isotopic effect observed in Hf and Nd isotopes would not have survived. So the early crust must have been relatively stable, and any recycling to the mantle must have started relatively late. The most likely cause of the total destruction of Earth's early crust is the late meteorite bombardment in the inner Solar System, which occurred about 3.9 billion years ago and is clearly preserved in the lunar crustal record as the 'terminal lunar cataclysm'[14]. Other planetary crusts from this time are heavily cratered (as shown for the Moon in Fig. 1), and this must also

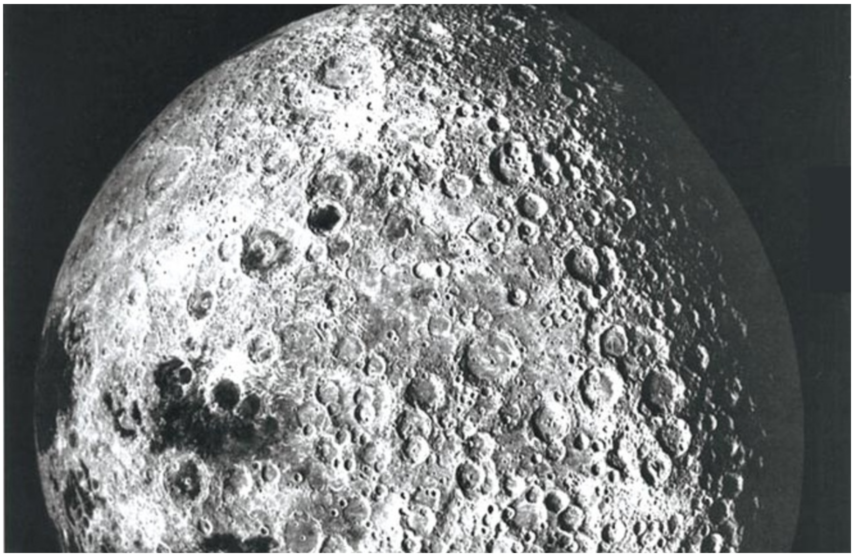
NASA

Figure 1 **Lunar analogy. These heavily cratered highlands on the Moon show what the crust on the early Earth might have looked like. Later terrestrial processes, including plate-tectonic movement, have destroyed any direct information of this initial phase of Earth evolution.**

have been true of the early Earth. This crust was later destroyed by further impacts and possibly by the onset of the plate-tectonic cycle some 3–4 billion years ago.

The early age of the proto-crust, as determined with Hf isotopes, requires that the now-extinct ^{146}Sm was common and enriched in the most ancient rocks compared with chondritic meteorites, and should give a signature of a high ^{142}Nd abundance. To add to the descriptions of ^{142}Nd anomalies in rocks from the 3.8-billion-year-old rocks in west Greenland[2,3], there are now reports that such anomalies are relatively common in samples from this area[15,16]. From the size of the ^{142}Nd anomaly, one can infer that Earth's most ancient crust must have started forming before Earth was 100 million years old — that is, 4.47 billion years ago.

Bringing the Nd and Hf data into agreement is a great step forward. With that done, we can expect further, exciting results about the earliest crust on Earth to be forthcoming. ■

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Developmental biology

A twist in a mouse tale

Nick Dyson

Studies of the retinoblastoma gene can still deliver surprises, and enlightenment. Several of the abnormalities in mice lacking this gene are, it seems, the indirect consequence of a placental defect.

On page 942 of this issue, Wu *et al.*[1] describe a surprising new observation about the function of *Rb*, the gene that is mutated in retinoblastoma cancers. *Rb* is often described as a prototype for tumour suppressors — that priceless category of genes that, among other tasks, protect us from developing cancers — as it was the first gene of this type to be identified. The biochemical and cellular properties of its protein product have been investigated in great detail, and the characteristics of *Rb*-deficient mice have been studied for over a decade. One might think that there is little left to be learned. But how wrong that would be! The results reported by Wu *et al.* force us to view the abnormal development of *Rb*-deficient mice from a completely new perspective.

Identifying the function of a gene is a tough challenge. A classic strategy is to inactivate the gene in model organisms such as mice, then sit back and see what happens. This approach has particular value when applied to tumour suppressors. Many genes that have an effect on the proliferation of cancer cells also influence normal cellular behaviour during animal development — and the tumour suppressors are no exception. Changes in the physical and behavioural characteristics (the phenotype) of an organism after the inactivation of a tumour suppressor show where the gene is essential, and give insights into events that are important for animal development. The mutant phenotypes also provide clues to the types of biological processes that might be affected by loss of the tumour suppressor during cancer development.

Mice that lack both copies of the *Rb* gene are highly abnormal, and die between days 14 and 15 of embryonic development[2–4]. The embryos show defects in the cell-division cycle and in cell differentiation, as well as high levels of cell death. Severely affected tissues include the central nervous system and liver. *Rb*-deficient embryos also have defects in red-blood-cell development, and it was originally suggested that anaemia was a likely cause of death.

Experiments with cell culture have further revealed that the lack of Rb protein can compromise the normal control of cell-cycle exit, cell differentiation and cell survival, as well as the control of 'checkpoints' by which the cell monitors the fidelity of cell-cycle progression. Because the Rb protein is broadly expressed and is normally present in the tissues that are affected in *Rb*-deficient animals, many have assumed that the phenotypes of these animals were caused simply by the loss of Rb protein from the affected tissues.

Wu *et al.*[1] now characterize a placental abnormality in *Rb*-mutant mice that was overlooked in earlier studies. Placental architecture depends on cells derived from both mother and developing embryo. Wu *et al.* find that the defect in *Rb*-deficient placentas seems to be caused by the overproliferation of extra-embryonic trophoblast stem cells. This affects the labyrinth layer — a layer in the mouse placenta that contains the fetal–maternal interface and is morphologically different from the human placenta[5] — and results in an over-representation of trophoblasts and a decrease in blood spaces. The consequence, as measured by the accumulation of essential fatty acids in normal and mutant embryos, is decreased nutrient transport from mother to embryo across the placenta.

This finding might have been dismissed as simply another tissue that requires the Rb protein. But Wu *et al.* take our understanding of *Rb*-mutant mice to a higher level, by showing the significance of the defect that they have found. They use two different genetic tools that make it possible to generate an *Rb*-deficient embryo supplied with a normal placenta containing wild-type extra-embryonic cells. Remarkably, embryos prepared by both methods develop to term, and many of the defects previously described for *Rb*-deficient embryos (including the defects in the central nervous system and in red-blood-cell differentiation) are suppressed. So, the placental abnormalities seem to be the primary reason why the *Rb*-mutant mice die at such an early embryonic stage. Several of the defects that were thought to reflect the loss of Rb function in specific tissues are instead indirect effects of a more systemic change.

Interestingly, however, several abnormalities still occur. These include defects in muscle and bone, cataracts, and inappropriate cell proliferation in several tissues. These residual abnormalities might reflect a specific requirement for the Rb protein in each of these tissues, but further experiments are needed to be sure.

This result sheds light on a long-standing puzzle. Several years ago the analysis of chimaeric mice, composed of random mixtures of wild-type and *Rb*-deficient cells, led to the surprising observation that the mutant cells can make a substantial contribution to a wide assortment of apparently normal tissues[6,7]. This showed that many of the abnormal features of *Rb*-deficient embryos could be prevented by the presence of wild-type cells — but the reason for this effect was unclear. The placental defect described by Wu *et al.*, and its consequences, might finally explain why animals composed entirely of *Rb*-deficient (embryonic and extra-embryonic) cells are so much more severely affected than mosaic animals.

The findings also have an impact on studies of compound mutants in which the