stores, potentially promoting afterdepolarizations and arrhythmia[5,6].

However, alterations in Ca^{2+} handling that generate arrhythmias do not generally delay repolarization[6]. Yet abnormalities in repolarization are clearly seen[2] in LQT4 patients. In addition, the conduction slowing seen in ankyrin-B heterozygous mice cannot be attributed simply to Ca^{2+}-handling defects.

Another possibility is that the ankyrin-B mutation in LQT4 patients affects Na^+ channels. Cardiac myocytes from mice lacking both functional copies of ankyrin-B[7] show defects in Na^+ channels: their ability both to carry Na^+ ions and to inactivate upon cellular depolarization is abnormal. Myocytes from ankyrin-B heterozygous mice show similar, if less severe, features[7]. Moreover, mutations in the pore-forming subunits of Na^+ channels that cause similar abnormalities produce conduction slowing, sinus-node dysfunction and repolarization defects[8]. Although the number and distribution of Na^+ channels in ankyrin-B heterozygous mice seem to be normal, their function might still be affected, as might the activity of other channels that control repolarization.

In summary, the work of Mohler *et al.*[1] reveals a new genetic cause for sudden cardiac death, and provides insight into the crucial role of membrane-protein anchors. There is increasing evidence that proteins do not sit randomly in cell membranes, but require precise spatial localization. Mohler *et al.* have shown just how important this spatial organization can be. Although their study deals with a primarily cardiac disease, the ubiquitous distribution of ankyrin-B and related proteins raises the possibility that other tissues and organs are affected in this and similar genetic syndromes. It is also possible that non-genetic alterations in ion-channel function in cardiac diseases might be attributable to changes in ankyrin expression[5]. ■

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Earth science

Ins and outs on the ocean floor

John G. Sclater

Researchers investigating heat exchange between the ocean floor and the ocean have various long-standing issues to tackle. The latest measurements of heat flux in hydrothermally active crust will add to these debates.

Earth loses internal heat in two main ways: in cooling of the ocean lithosphere, originally generated at mid-ocean ridges, and in conduction across the boundary between the mantle and the continental and oceanic lithospheres. Heat exchange between the lithosphere and the oceans then occurs through both the hard but permeable crust at the top of the lithosphere, and the soft but impermeable sediments that cover much of the crust. At the axis of a mid-ocean ridge there are no sediments, and most heat loss is by hydrothermal discharge of sea water through the crust, in places through huge high-temperature geysers[1]. Away from the axes, sediment starts to accumulate, and heat is lost by a combination of advection (water flow) through partially exposed 'basement' rocks, and possibly the sediments, and heat conduction through both rock and sediments. What, though, is the balance between these processes? And how is the hydrothermal outflow of water recharged?

Fisher *et al.*[2] (page 618 of this issue) show that, in one case at least, hydrothermal recharge and discharge occur entirely through the basement rock, and that all the flux through the sediments is conductive. In studies of the Juan de Fuca ridge in the northeast Pacific, they find that an outcrop of permeable basement rock is the recharge point for a hydrothermal outlet more than 50 km away. This discovery adds the finishing touch to a theory originally put forward by Lister[3], and should also reinvigorate research into conductive heat flux through the ocean floor.

In plate tectonics, the intrusion of hot material beneath a mid-ocean ridge creates oceanic lithosphere, which behaves like a plate. As it moves away from the ridge, the lithosphere cools, contracts and is covered in sediment, before finally disappearing into the mantle beneath an oceanic trench. In general, the sedimentary layer thickens with increasing age of the ocean floor, and outcrops of basement rock become sparser before being completely covered by sediment on floor that is more than 60–100 million years old (Fig. 1). According to Lister[3], warm circulating water escapes into the ocean through rock outcrops and the recharge area is a similar outcrop nearby. In an area totally covered by sediment, he believed, hydrothermal circulation occurs within the basement rock but there is no connection to the sea water above.

Geochemical measurements on pore fluids show that thin layers of sediment do permit the passage of upwelling and downwelling fluids[4]. Thus, an alternative view was that, in sedimented regions, recharge occurred through the flow of sea water downwards, through sediments close to the region of discharge. Detailed heat-flux surveys did not always reveal the low and high values in close proximity, however, and seawater flow through the thick, impermeable sediments that cover most of the ocean floor seemed unlikely. Fisher *et al.*[2] now show, in an area almost completely covered by sediment, that outcrops of basement rock can indeed be the source of the return flow. They carried out heat-flux surveys both around and between two outcrops, 50 km apart, in the sediment-filled basin east of the Juan de Fuca ridge. The measurements indicate vigorous discharge at one of them (a narrow outcrop known as Baby Bare), and a substantial recharge through the much larger one (Grizzly Bare), with no evidence for water flow through the sediments in this area.

The bigger picture here concerns various models of the lithosphere. The match between conductive heat flux and age, and subsidence of the mid-ocean ridge with age, initially led to a model of the lithosphere as a flat plate about 125 km thick[5]. Given the lack of a physical justification for that, an alternative proposal was to view the lithosphere as a cooling, rigid, thermal boundary layer that thickens at a rate that is proportional to the square root of time[6] (like ice on a still lake when the temperature is well below freezing). But this model does not account for the 'flattening' of ocean-floor depth with age and predicts a heat flux through the old ocean basins that lies well below that observed. Another suggestion is that oceanic lithosphere consists of a rigid mechanical layer on top of a lower-viscosity, thermal boundary layer[7], with the argument that if both layers increase in thickness with age, the lower one will become unstable after a specific time: this mechanism would have the same effect on the heat-flux and depth measurements as the plate model, and provides a physical justification for it.

Most recently, Nagihara, Lister and I went back to detailed surveys of thermal flux and isostatically corrected depth measurements to show that the data lie on the expected curve for a boundary-layer model, except for being offset in age[8]. This we attribute to varying amounts of 'thermal rejuvenation' of the lithosphere. It is unclear how well this observational approach, relying on the old heat-flow data, is compatible with a two-layer structure for the lithosphere.

Given that the lithosphere marks the upper boundary for convection in Earth's mantle, a quantitative grasp of its behaviour is

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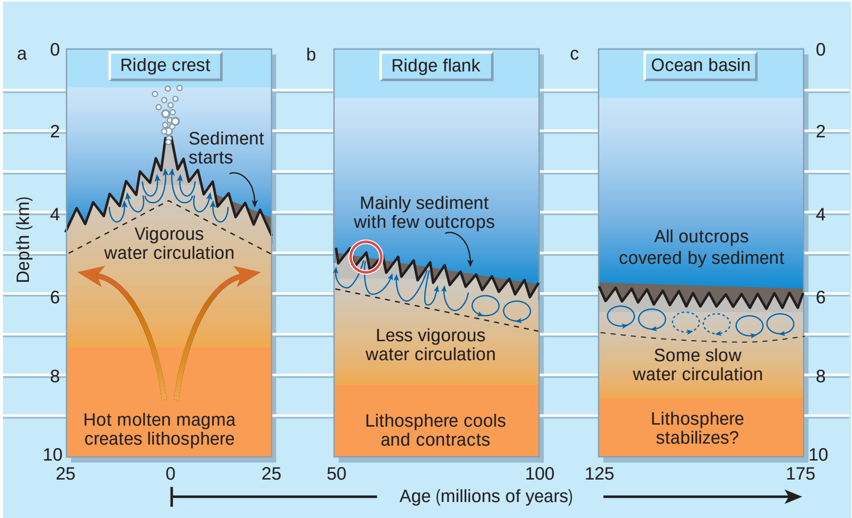

Figure 1 **Changes in ocean-floor depth, sediment thickness and hydrothermal circulation with increasing age of the lithosphere. The ocean floor is depicted in black, sediment in brown and hydrothermal circulation in blue. In** a**, heat loss is by advection; in** b**, by advection and conduction; and in** c **by conduction alone. Fisher *et al.*[2] deal with younger crust than that shown in** b**, but this panel illustrates the flow pattern for the flank of the Juan de Fuca ridge that they surveyed. They find that hydrothermal recharge is occurring through an outcrop of basement rock (red circle) 50 km distant from the point of discharge, and that any heat flow through sediments is by conduction, not advection. (Diagram based on ref. 3.)**

essential for understanding mantle dynamics. A difficulty, however, is that the scatter in the ocean-floor subsidence data increases dramatically for ocean floor more than 80 million years old[9]. The scatter in the conductive heat-flux values is reduced for this age of crust, but lack of knowledge of seawater flow in sedimentary areas with basement outcrops has made it difficult to have confidence in these values. Importantly, then, Fisher *et al.*[2] show that the heat-flux values lie close to those predicted for the age of crust between the outcrops. This implies that there is little deficit in the conductive heat loss, and thus that the flow of sea water must be slow enough to have little or no effect on the conductive flux.

This result, and discovery that the discharge and recharge occur at outcrops, together have major implications for the use of heat-flux measurements to study how the lithosphere changes with age. They explain why most detailed studies on ocean floor more than 60 million years old have little scatter in the values[10]. Relatively thick sedimentary layers cover most ocean crust older than that, and either no heat is lost by advection because there are no outcrops or, if there are, the flow is so slow that it has only a small effect on the conductive flux (Fig. 1).

This is an exciting time to be studying the heat regime of the lithosphere. Now that we are beginning to understand patterns of hydrothermal circulation in the basement rock, it is clear that heat-flux surveys over broad areas well covered by sediment will provide reliable estimates for the conductive flux. Moreover, direct measurements of the density structure of the upper mantle are emerging. Variations in the group velocity of surface waves as they cross the Pacific provide evidence[11] that, on crust 70–100 million years old, the thickening of the Pacific lithosphere flattens relative to that predicted by the cooling boundary-layer model — so constituting evidence for thermal rejuvenation of the lithosphere as it ages.

At a meeting in September last year, the installation of leapfrogging arrays of ocean-bottom seismometers was proposed, with the aim of further refining models of the lithosphere and coupling them to convection patterns in the mantle[12]. Combining the seismic information with new data on heat flux, ocean-floor depth and the gravity field should greatly advance our understanding of global circulation in the mantle. ■

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Ecology

Shady deals with lichens

Peter D. Moore

In tropical forests, many species of lichen gain a place in the sun by living on the leaves of other plants. It seems they can do so without compromising the photosynthetic capacity of their host.

Life can be challenging for a small plant in a tropical rainforest. Most plants of lesser stature solve the problem of light acquisition by being epiphytic — they use taller plants as support systems to gain a place in the sun. Epiphytes include a wide range of plants, from liverworts to orchids, and some, known as epiphyllous species, even adhere to leaf surfaces. Most epiphytes present no direct threat to the host species, although supporting them may impose a burden and, in the case of epiphylls, could interfere with light availability to the host leaves.

Lichens are one of the most common groups of epiphyllous organism. Writing in *Functional Ecology*, Anthony, Holtum and Jackes[1] describe how they assessed the potential shading impact of lichens on their host. The authors show that the host leaves are photosynthetically resilient, and can compensate for the shading effect of lichens, maintaining their overall productivity despite the presence of their uninvited guests.

Epiphylls are abundant in tropical rainforests[2] and have been generally assumed to have an adverse effect on the photosynthetic capacity of a leaf — they both reflect and absorb light, leaving the host leaf in increased shade. Working on a coffee plantation in Mexico, Roskoski[3] found up to 20% of each leaf was covered by epiphylls, but surprisingly, the overall productivity of the crop did not seem to be affected. Studies[4] in the rainforests of Panama, however, revealed that epiphylls reduced the amount of light received by leaves by 55–85%, with an estimated 20% reduction in overall photosynthesis. The precise impact of epiphylls on their host's productivity is thus a matter of debate.

Intuitively, one might suppose that such

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