exactly what happened during the Earth's early history to produce the very fluid lavas called komatiites.

A corollary of this idea is that Io's deeper mantle must be well mixed with the rocks at shallower depths, which implies efficient recycling of the surface layers into the interior. On Earth, partial crustal recycling is accomplished by plate tectonics, which involves the subduction of ocean-floor crust at the margins of continents. But no hint is seen on Io of the topographic features that would be expected if something akin to plate tectonics is taking place there. Instead, some other process, perhaps simply very rapid burial under new eruption deposits, must be at work[10].

Whatever the recycling mechanism, there must be a link between the degree of partial melting of the mantle, the range of depths over which it occurs, and the rate at which the molten rock is extracted from the solid residue and brought to the surface in new eruptions. It is this aspect of the origin of volcanic melts that is still least well understood on Earth, so the comparison of eruptions here and on Io should improve our understanding of volcanism in general. □

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Evolutionary biology

Green beard as death warrant

Alan Grafen

The Gradgrindian view of science — facts come first, ideas later — is rarely true, and there are few more direct demonstrations of that than the discovery of a phenomenon that previously existed only in theory. Genetics is rich in such phenomena, and an example is provided on page 573 of this issue[1], where Keller and Ross describe how they have identified evidence of a 'green-beard' gene. Quibbles over how one defines these genes make it hard to say whether this a 'first', and Keller and Ross themselves cite another candidate[2].

The idea of green-beard genes was invented by Hamilton[3], and named by Dawkins[4]. A basic question about the genetics of social actions is how a gene can spread by recognizing and interacting with individuals carrying copies of itself. The likely way is through kinship, and inclusive fitness theory contains many empirical examples of this. But, to isolate the phenomenon in its starkest form, Hamilton proposed a gene that does three things. It causes its bearer to display an observable and distinctive trait (the 'green beard'); to distinguish between individuals that do not display the trait and those that do; and to be altruistic to those that do. This gene has the capacity to recognize individuals with copies of itself, and helps them, and so helps itself.

This thinking belongs firmly in the 'selfish gene' tradition. It makes many geneticists feel uncomfortable, mutter grimly to each other that these so-called genes are completely hypothetical and wonder why anyone should bother to discuss a gene when it does not really exist. The work of Keller and Ross brings these two worlds into collision.

They have studied the red fire ant, *Solenopsis invicta*, about whose population genetics, behaviour and ecology much is now known. This native South American species is of interest practically as well as scientifically, for it is a recently introduced pest in North America. (I can testify to the pain caused by the pheromonally synchronized bites of workers swarming out of an upturned canoe in a swamp in Georgia.) The ant has many strange features, among them being the existence of two subpopulations that are genetically connected only through males[5]. One subpopulation is monogyne (a single queen per colony), the other is polygyne (several queens per colony).

Figure 1 **Red fire ant queen and workers — here as attendants, not executioners. (Photo courtesy W. Tschinkel.)**

Keller and Ross[1] report only on the polygyne ants, and show that the locus *Gp-9*, which has alleles *B* and *b*, is always heterozygous, *Bb*, in those queens that live long enough to lay eggs. Queens and workers that are *bb* seem to die young from physiological causes, but the remarkable findings concern how *BB* queens meet their fate. They are executed by workers after their emergence from the pupa, and Keller and Ross's experiments suggest that *Bb* workers are particularly incriminated in the deed. Whether the locus responsible is actually *Gp-9* or a very tightly linked locus is not yet known.

The connection with green beards is this. Through the mediation of the bearer, a gene (*b* or a tightly linked allele) induces killing of individuals that do not contain it (*BB* queens) while not inducing killing of individuals that do (*Bb* queens). The green beard in this case seems to be a chemical carried on the queens' cuticle, as Keller and Ross found that rubbing a worker against a *BB* queen causes it to be attacked by other workers, whereas rubbing it against a *Bb* queen does not. This is not exactly what is expected from the classical green-beard principle, in which green-beard wearers would kill non-wearers. Nonetheless, the mechanism of advantage to the gene is impressively similar.

One puzzle is why such a gene should be found at all. Hamilton and Dawkins both emphasized that their theoretical point did not rely on such an unlikely gene actually existing. Biologists didn't used to suppose that organisms had the capacity to detect other individuals' genes and respond accordingly. For one gene to create such a system and manipulate it in a particular way does indeed seem far-fetched, but this capacity no longer surprises us. Genetic discrimination can underlie kin recognition[6], species recognition and individual recognition, and has parallels in immunology. Once such a capacity exists in a species, a mutant that tweaks the existing system could plausibly have the properties of a green-beard gene. In his work, Haig[2] has proposed the existence of green beards in the context of genetic conflicts between parents and their offspring during mammalian fetal development. Now that he and Keller and Ross have stimulated us to reflect on the matter, it is not so surprising that a green-beard gene should be found.

What kind of functional system might the *Gp-9* locus be involved in? Queens in the monogyne subpopulation are all homozygous *BB*, and live to lay eggs, so the locus may be closely involved in maintaining monogyny and polygyny, and genetic separation of subpopulations. It is intriguing to speculate that *BB* queens, if allowed to live, would attempt to make the nest monogynous by attacking the other queens or inciting the workers to do so — this is, after all, presumably how monogyny is maintained in monogynous nests. ▶

Moreover, in the experiment each *BB* queen remained alive while kept in a small colony fragment with a few hundred workers, and was executed only when she was returned to the main colony with its existing queens. This supports the idea that workers in a queenless colony would tolerate a *BB* queen. If this is right, it is possible that genotype-specific execution is a trait evolved by workers to permit polygyny in some nests, in a species in which the monogyny-enforcing mechanism is still active in other nests.

Keller and Ross describe their green-beard gene as an 'outlaw'. Admittedly, the comment is only made in passing, but are they correct? In this context an outlaw is usually defined as a gene whose action favours itself, but opposes the reproductive interests of the individual organism. Where there are outlaws, natural selection at different loci is pulling the organism in different directions. Theoretically speaking, green-beard genes are not, in general, outlaws[7]. Do the effects of *b* harm the interests of the workers or reproductive queens? Does the definition need elaboration for eusocial species, when some notion of colony interest might be invoked?

The interactions between theory and reality are multi-layered. Keller and Ross's study reminds us that scientists who, like Haldane, feel sad when beautiful hypotheses are slain by ugly facts, can draw comfort when beautiful ideas step boldly out into the living world. □

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Earth science

Hot stuff under southern Chile

Julie D. Morris

The isotopes of the uranium decay series are a wonderful tool for exploring geological processes that have taken place on the Earth's surface and in its interior[1]. On page 566 of this issue[2], Sigmarsson and colleagues describe how they have taken advantage of these isotopes to 'image' the melting of a slab of oceanic plate being subducted along a stretch of southwestern South America. The results tell us how melting of the slab relates to volcanism at the surface, and may also bear on our knowledge of the generation of continental crust in the distant past.

The modern history of studies of subduction began in the 1960s with plate tectonics, which showed that chains of active volcanoes around the Pacific rim are underlain by subducting oceanic lithosphere. Earthquakes track the ocean plate, formed at mid-ocean ridges, as it travels beneath the arc of a volcanic chain and into the deep mantle (see Fig. 1). The ubiquitous association of active volcanic arcs and subducting slabs led quite naturally to the belief that lavas erupted at the Earth's surface were formed by melting of the subducting slab about 110 km below the volcanic chain. Hence the consternation when, in the early 1970s, it emerged that most erupting lavas have the wrong chemistry to be the result of slab melting[3].

Since then, a more complex model for the relationship between subduction and modern arc volcanism has been developed. While moving from mid-ocean ridge to subduction trench, the ocean plate incorporates sea water. Water is bound in hydrous minerals in the basaltic layer and in hydrous sediments deposited atop the plate, and also occupies the space between sediment grains. As the oceanic plate (which is usually old and cold) subducts, the water between sediment grains is squeezed out. The hydrous minerals formed at low pressure and temperature transform to minerals that are stable at increasing pressure and temperature, or break down and release their water to the overlying plate. The oceanic plate itself is generally too cold to melt beneath the arc.

The behaviour of water during the subduction cycle may affect a variety of events (the localization of chemosynthetic biota near the trench; the distribution of hazardous inter-plate earthquakes between 0 and about 40 km depth; the explosivity of arc volcanoes; and the formation of ore deposits). Most notably in this context, however, water-rich supercritical fluids or sediment melts released from the slab lower the melting point of the mantle wedge above the slab[4], with the wedge then being the source of the lavas that add to the mass of the continents today. Strikingly, the composition of continental crust forming now does not appear to match the average composition of the crust formed in the past, suggesting that processes today may be different from those that operated when the bulk of the continental crust was formed.

Just occasionally, rocks in active volcanic arcs have a chemical signature which indicates that they were formed by melting of the subducted oceanic plate itself. Such rocks are called 'adakites'[5], and their chemical fingerprint[6,7] shows that modern ones have many features in common with ancient continental crust. This fingerprint is taken to reflect melting of hydrous basalt or its metamorphosed equivalent — although whether melting occurs at the base of the arc crust, or deeper, at the top of the subducting slab, is a matter of debate. Often, adakites are reported from margins where the subducting slab is

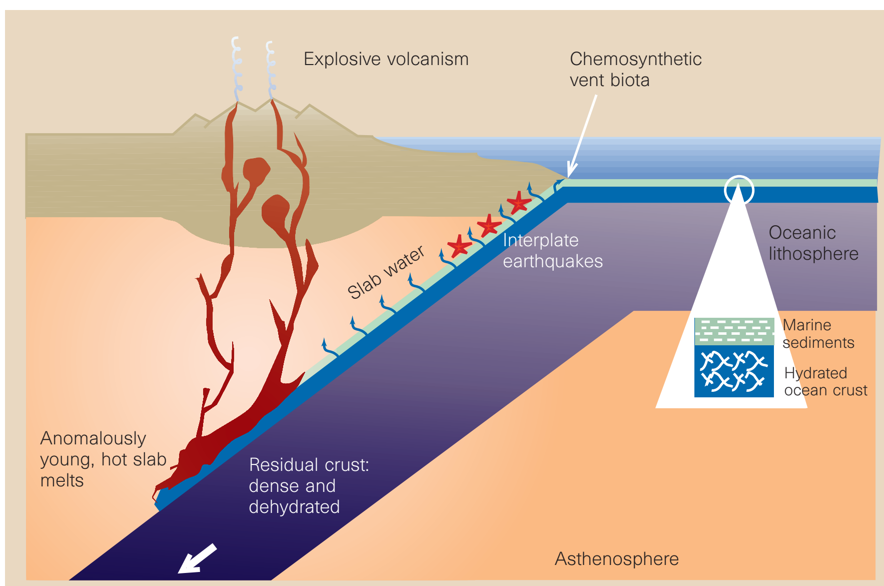

Figure 1 **Slab melting beneath modern volcanic arcs. Many textbooks include diagrams such as this, but the scheme applies only to a few modern arcs, where very young and hot oceanic crust is subducting and melting at depth. The austral Andean volcanic zone studied by Sigmarsson *et al.*[2] is one such setting, and the magmas erupting here stem from the slab itself and have chemical compositions similar to ancient continental crust. At most convergent plate margins, supercritical water-rich fluids move from the slab to the mantle wedge, where they initiate mantle melting. Note that marine sediments often subduct with the plate, and that the slab is subducted past the arc to the deep mantle.**