hexagonal tube-like cavities, with diameters in the sub-micrometre to few-micrometre range, that develop parallel to the *c*-axis of the hexagonal structure (which is the common direction of crystal growth). They are the most harmful defects in SiC.

Intensive work on various aspects of the PVT growth technique — reactor design, growth conditions, seed orientation and surface preparation — has led to a considerable reduction in the number of these defects in SiC ingots and wafers. The best commercially available 3-inch-diameter wafers (of the 4H polytype) have micropipe densities of 10–100 cm^{-2} and dislocation densities of 10^3–10^4 cm^{-2}. This quality of crystal is good enough for use in some commercial SiC devices, such as Schottky diodes[3], but not for others. For instance, in high-power bipolar devices, there is a degradation in the material's electrical properties that seems to be related to the development of extended stacking faults, originating from in-plane dislocations in the SiC (ref. 4).

So reducing the density of dislocations in an SiC wafer, and in the epitaxial layer on top of it that forms the active part of the device, is an absolute necessity for the development of high-power SiC technology. Nakamura *et al.*[1] have succeeded: their new process produces SiC crystals with a dramatically lower dislocation density — although, perversely, the first step of the process actually creates a high density of stacking faults.

Most SiC crystals are grown on the *c*-faces (perpendicular to the *c*-axis) of other crystals. In fact, it has already been shown that growing SiC crystals on surfaces with a different crystal orientation — the *a*-faces — fully suppresses the formation of micropipes. However, crystals made in this way are affected by basal-plane stacking faults. Nevertheless, Nakamura *et al.* started with a SiC single crystal that had been grown on an *a*-face, inheriting a high density of dislocations from its seed crystal. Then, taking a section of the crystal along the *a*-axis of that face, they allowed the crystal to develop on the other *a*-face (Fig. 2), afterwards continuing with classic growth on the *c*-face. Nakamura *et al.* call this the repeated *a*-face (RAF) growth process. It is the repetition of the *a*-face step that ensures that stacking faults are eliminated and dislocations suppressed. The ingots of SiC produced are, say the authors, "virtually dislocation-free".

These results are spectacular: the RAF process is a major innovation in materials science. Silicon carbide has become, at last, a contender for silicon's crown. ■

Roland Madar, of CNRS, is in the Department of Physics, Institut National Polytechnique de Grenoble, Grenoble 38402, France.
e-mail: roland.madar@inpg.fr

1. Nakamura, D. *et al. Nature* **430,** 1009–1012 (2004).
2. Tairov, Yu. M. & Tsvetkov, V. F. *J. Cryst. Growth* **43,** 209–212 (1978).
3. Peters, D., Friedrichs, P., Schörner, R. & Stephani, D. *Mater. Sci. Forum* **389–393,** 1125–1128 (2002).
4. Lendenmann, H., Dahlquist, F., Bergman, J. P., Bleichner, H. & Hallin, C. *Mater. Sci. Forum* **389–393,** 1259–1264 (2002).

Social evolution

Kinship is relative

David C. Queller

Kinship fosters the evolution of cooperation. However, a once-heretical theory and an unconventional social organism show that the cooperation-enhancing effect of kinship is sometimes negated.

As evolutionary biologist W. D. Hamilton showed more than 40 years ago, selfish genes can lead to cooperation and altruism[1]. A gene can spread by helping other individuals that carry copies of the gene. This extension of individual selection, called kin selection, works best with the recognition of close relatives, but Hamilton also thought that if the dispersal of individuals is limited, this might build up enough local genetic similarity to favour a less targeted kind of altruism towards neighbours in general. Because local dispersal is very common, this mechanism might greatly expand the range of cooperation in nature. However, later models[2–4] suggest that this is not necessarily so: when limited dispersal makes neighbours close relatives, it also makes them close competitors, and this can negate the effect of kinship. On page 1024 of this issue[5], Griffin and colleagues provide the first experimental test of this effect, confirming that both kinship and the scale of competition matter.

The study is part of a growing trend towards using microorganisms to study social evolution[6]. Sociobiologists have been slow to recognize that microorganisms have social interactions worthy of study. However, any reader of John Bonner's work on cellular slime moulds[7] will realize that these single-celled amoebae interact in interesting ways; some give up their lives to form a stalk that furthers the dispersal of others. Analogous behaviour occurs in Myxobacteria[8]. And interesting behaviour is not limited to the exotica of the microbial world; the old laboratory workhorse *Escherichia coli* has strains that aid their own type by wielding poison–antidote systems to destroy other strains that lack the same system[9]. Perhaps the most common form of microbial cooperation is the secretion of substances outside the cell to do various kinds of work, such as digestion. The work provides a public good, in which the benefits are available not just to the secretor, but to anyone in the neighbourhood. This puts individuals into a social bind. Why work to help others when you can be lazy and freeload off your neighbours? The obvious answer is kin selection. If your effort helps others with the same genes, it is not wasted.

Once it is recognized that microbes have interesting social behaviour, two clear advantages can be exploited. First, many microbes are well understood biochemically and genetically. Second, it is easy to manipulate entire populations of microbes over space and to select them over time. Griffin *et al.*[5] made full use of these advantages in their study of a freeloading mutant of the bacterium *Pseudomonas aeruginosa*. This 'cheater' mutant is deficient in production of a public benefit called siderophores. Siderophores are synthesized and excreted in response to iron deficiency. They then bind iron, making it available for uptake — either by the secretor or by its neighbours. The mutant saves on the cost of producing siderophores but can still obtain iron if it has secretor neighbours.

Griffin *et al.* selected populations, starting with equal numbers of cheaters and secretors, over six cycles of group interaction, each lasting about seven generations (Fig. 1, overleaf). In natural populations with limited dispersal, neighbours tend to be both relatives and competitors, but Griffin *et al.* were able to vary the relatedness and scale of competition independently. High or low relatedness was imposed by allowing bacteria to grow and interact in groups derived from a single bacterium (a cheater or a secretor) or from two bacteria (initially in a ratio of one cheater to one secretor), respectively. The scale of competition was manipulated during the transfers to form each next cycle of groups. Global competition was allowed by mixing the groups and then choosing random individuals to start the next cycle. The more productive groups thus contributed more to the next cycle. Local competition was imposed by taking an equal number of individuals from each group, without mixing between the cycles. Crossing the relatedness and competition treatments yields a simple two-by-two design that permits the study of both factors and their interaction.

As expected, at the end of the experiment the high-relatedness treatments yielded higher frequencies of the cooperative secretors than the low-relatedness treatments, demonstrating the importance of kinship in the evolution of cooperation. But the greater novelty of the study comes from another theory-

©2004 Nature Publishing Group

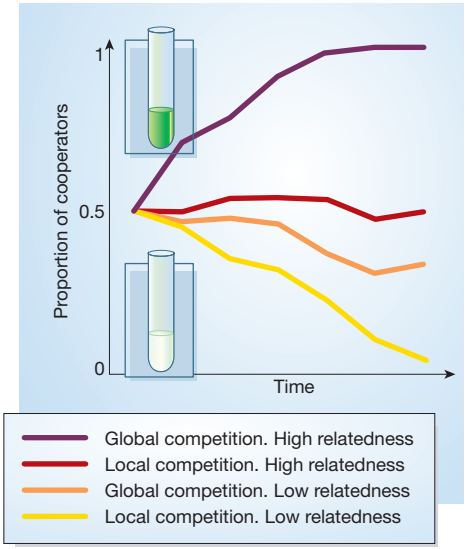

Figure 1 **Cheaters and secretors. Cooperator *Pseudomonas aeruginosa* secrete a green siderophore, pyroverdin, which makes iron available for uptake by all cells. Cheaters save on the expense of producing pyroverdin but can exploit the siderophores of nearby secretors. Griffin *et al.*[5] tested how the proportion of each varied over time in response to relatedness (high or low) and scale of competition (global or local). As these results show, relatedness is crucial but it is modulated by the scale of competition. (Simplified from ref. 5.)**

confirming result: the local-competition treatments yielded more cheaters than the global-competition ones. Kinship is crucial, but it is modulated by the scale of competition. Local competition exactly cancelled out the effect of high relatedness, such that neither type was favoured (Fig. 1).

There is an interesting history behind the theories tested here. The first study to challenge Hamilton's ideas about limited dispersal was a computer simulation based on group-selection theory[2]. This theory divides selection into within-group and between-group components, with the latter favouring cooperation. Group selection has a shady past. At one time, some biologists saw group-selected cooperation everywhere in nature, even though the process was unsupported by rigorous models, and consequently the whole idea was brought into disrepute. But there has been growing agreement that group selection, properly applied, is a roughly equivalent way of understanding social selection — not so much an alternative theory as an alternative means of slicing up the way in which selection occurs. Thus, kin-selection theorists took the computer-simulation results[2] seriously and quickly found two different ways of squaring them with their theory. First, one can add in the indirect effects for the cases where helping a neighbour takes away fitness from another, perhaps equally related, neighbour[3]. Alternatively, relatedness can be rescaled so that it measures genetic similarity relative to the locally competing individuals, rather than to the global population[4].

It is the relativistic effect of kinship that Griffin *et al.* set out to show, and they have succeeded. Curiously, however, their experiment is perhaps more easily understood from a group-selection standpoint. The conditions of low and high relatedness correspond exactly to the presence and absence of within-group selection. The conditions of global and local competition correspond exactly to the presence and absence of between-group selection. The two-by-two crossing of these treatments therefore leads to the most basic group-selection experiment possible. The results confirm that cooperation is favoured by between-group selection and disfavoured by within-group selection.

Does all this mean that we should discard kin selection in favour of the simpler group-selection approach? Hardly. Kin selection has yielded far more insights into the complex behaviours of animals such as social insects. For example, elegant theories of sex-ratio conflict in social insects emerge naturally from kin-selection models, whereas the corresponding group-selection models are so complex that they have not been developed. But this history does suggest that group selection has matured enough for it to become a partner with kin selection in contributing insights, though the story is not without some irony. Once, group selectionists saw cooperation everywhere but were brought down to earth by individual selectionists. Now group selection is being used, not to show the ubiquity of cooperation but to rein in theories on an important form of cooperation envisaged by individual selectionists. ■

David C. Queller is in the Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005, USA.
e-mail: queller@rice.edu

1. Hamilton, W. D. *J. Theor. Biol.* **7,** 1–52 (1964).
2. Wilson, D. S., Pollock, G. B. & Dugatkin, L. A. *Evol. Ecol.* **6,** 331–341 (1992).
3. Taylor, P. D. *Evol. Ecol.* **6,** 352–356 (1992).
4. Queller, D. *Evol. Ecol.* **8,** 70–73 (1994).
5. Griffin, A. S., West, S. A. & Buckling, A. *Nature* **430,** 1024–1027 (2004).
6. Crespi, B. J. *Trends Ecol. Evol.* **16,** 178–183 (2001).
7. Bonner, J. T. *The Cellular Slime Molds* (Princeton Univ. Press, 1967).
8. Velicer, G. J., Kroos, L. & Lenski, R. E. *Proc. Natl Acad. Sci. USA* **95,** 12376–12380 (1998).
9. Riley, M. S. & Gordon, D. M. *Trends Microbiol.* **7,** 129–133 (1999).

Chemical biology

Green fluorescent RNA

Michael Famulok

The future for intracellular imaging looks bright with the development of fluorescent probes made entirely of RNA. The cunning design exploits structural attributes of RNA to detect a variety of small molecules.

Green fluorescent protein (GFP) has proven tremendously useful as a method of creating intense visible fluorescence by entirely molecular biological steps[1]. Generally, the gene encoding GFP is fused with a gene of interest so that the resultant protein is tagged with the fluorescent module. It can then be followed in real time by optical imaging, to decipher spatio-temporal information on gene expression or protein localization within living cells or tissues[2]. Such information is crucial for understanding complex cellular processes that depend on when, where and how much of a protein is present. The challenge now is to devise similar methods to reveal other molecules involved in cellular functions, such as small-molecule messengers, drugs, metabolites and short functional RNAs. Stojanovic and Kolpashchikov[3], writing in the *Journal of the American Chemical Society*, report a considerable advance in this area with the development of RNA-based probes that can detect small organic molecules by fluorescence.

The new concept relies on aptamers — short RNA sequences that can bind specifically to particular ligands[4]. These molecules are fairly recent discoveries, but already they have been adapted to make probes for various molecules[5]. However, current aptamer probes are generated and labelled with fluorescence or radioactivity outside the cell, and a delivery mechanism is needed to get them inside — a procedure that is potentially disruptive to the very processes under observation. Stojanovic and Kolpashchikov have sidestepped this problem by creating an aptamer probe that can be genetically encoded and produced inside the cell, and that is able to generate marked fluorescence by itself.

The basis of their probe is an aptamer that can bind to the dye malachite green[6] (MG). The dye itself is not fluorescent, but its structure is such that when it binds to the aptamer it is forced into a rigid conformation that is highly fluorescent[7]. This, however, is only half the story. Stojanovic and Kolpashchikov's probe has a second module — another aptamer that binds to whatever small molecule is to be detected.

To form the final probe, the authors take advantage of an intrinsic property of

©2004 Nature Publishing Group