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A Möbius strip of single crystals

A crystalline ribbon of niobium and selenium can be coaxed into a novel topology.

Möbius strip is produced by twisting a ribbon of material through 180° and joining its two ends, resulting in a distinct, one-sided topology[1-4]. Here we describe a Möbius structure formed by crystals of a compound of niobium and selenium, $NbSe_3$. It is surprising that a crystalline ribbon should adopt this exotic topology in view of its inherent rigidity, which would be expected to prevent it from either bending or twisting.

$NbSe_3$ is a typical low-dimensional inorganic conductor, which shows charge-density-wave (CDW) phase transitions at 58 K and 145 K. Its crystals are synthesized by chemical-vapour transport and assume fibrocrystalline ribbon and whisker shapes. We have been able to create a Möbius strip of single $NbSe_3$ crystals by modifying the conventional growth conditions.

We soaked a mixture of Se and Nb powder at 740 °C in an evacuated quartz tube for a period varying from a few hours to a few days. The growth conditions differed from those that are typically used, in that they relied on a furnace that had a large temperature gradient; this creates a crucial non-equilibrium state inside the quartz tube in which selenium circulates through vapour, mist and liquid (droplet) phases.

Figure 1 shows scanning electron microscopic (SEM) images of different topologies that are assumed by $NbSe_3$ crystals produced under these conditions. Ring diameter and width are typically 100 μm and 1 μm, respectively (Fig. 1a); Möbius crystals are typically around 50 μm in diameter and less than 1 μm in width (Fig. 1b); and 'figure-of-eight' crystal strips (Fig. 1c), with a double twist, have a circumference of about 200 μm and a width of 1 μm. We confirmed by X-ray diffraction and transmission electron microscope diffraction that the ring and Möbius structures are equivalent to a conventional crystalline ribbon with single-phase and monoclinic properties.

The mechanism of ring formation by the ribbon-shaped $NbSe_3$ crystals depends on their being bent by the surface tension of the viscous selenium droplet on which they have grown. The ribbon grows along the equator of the droplet to minimize bending energy, finally meeting its own tail to form a perfectly seamless ring (Fig. 1d).

Growth of the Möbius strip is difficult by comparison because of the twisting involved. Bending of a bar or beam is accompanied by twisting, and the low symmetry in a monoclinic crystal also promotes bending with twisting[5], as shown
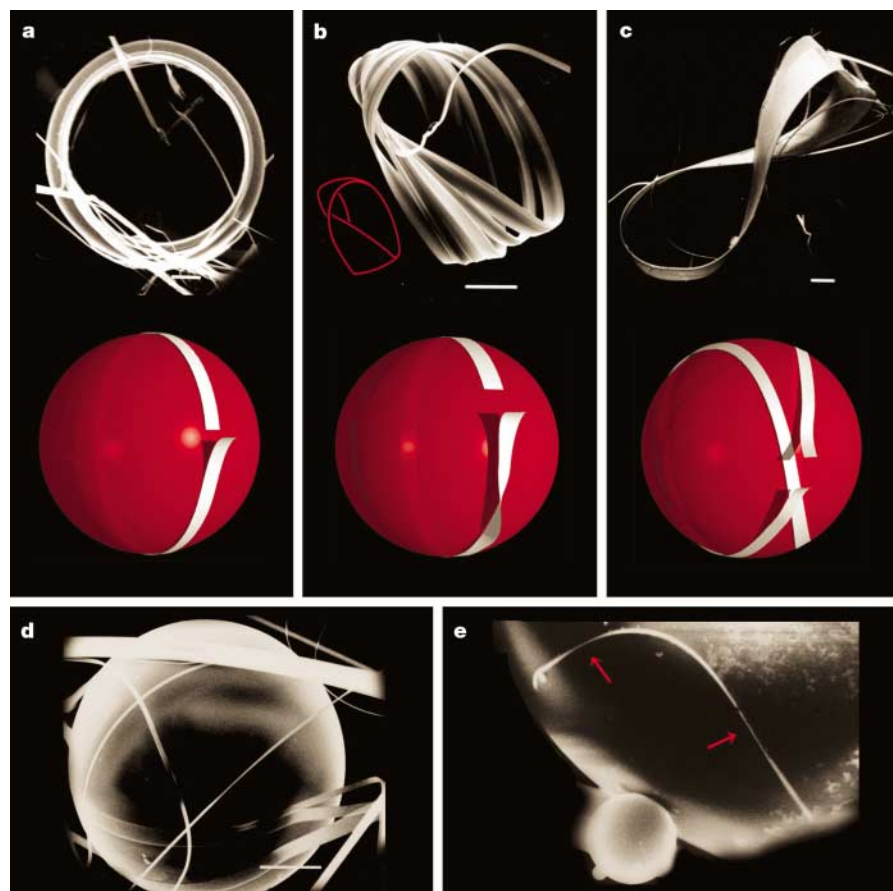
Figure 1 Scanning electron microscopic images of $NbSe_3$ crystal topology. **a–c,** The three types of topology, classified by the nature of their twisting (shown schematically beneath images; white ribbons represent $NbSe_3$ crystals, red spheres represent selenium droplets). **a,** Ring structure (0π twist). **b,** Möbius strip (1π twist). **c,** Figure-of-eight strip (2π twist). **d,** $NbSe_3$ fibres (white streaks) bend into rings around a selenium drop of diameter about 50 μm. The $NbSe_3$ ribbon is spooled onto a selenium droplet by surface tension until its ends bind together. **e,** High-magnification image showing a twist in a ribbon of $NbSe_3$ crystals; spooling of the ribbon can produce a twist, as in the formation of a Möbius crystal, owing to its anisotropic elastic properties. Scale bars, 10 μm.

in Fig. 1e. Droplet rotation, which we observed frequently, could also help to produce the twist.

The figure-of-eight crystal strips arise as a result of either double encircling or double twisting. According to White's theorem[6], a doubly encircling loop is topologically equivalent to a 2π-twisted loop, which is analogous to a ring conformer of DNA[7].

These different topological arrangements of $NbSe_3$ all show the characteristic CDW phase transitions, indicating that the samples are crystalline and relatively ordered, and that the CDW displacements are identical to those in conventional, untwisted crystals[8,9]. This was demonstrated by satellites in the electron-diffraction patterns (CDW wave vector $Q_1 = 0.24 \pm 0.01$), by anomalies due to CDW phase transitions in the temperature dependence of the resistivity at 145 K and 54 K, and by non-linear conduction due to CDW sliding.

We have developed a new growth technique for topological crystals by using a spherical droplet as a spool. This technique could be extended to a wide range of materials, and we have already obtained topological variants of tantalum compounds with selenium and sulphur ($TaSe_3$ and TaS_3). It may also be possible to grow crystals to a desired size by controlling the non-equilibrium conditions inside the furnace and thus the size of the droplets. Our crystal forms offer a new route to exploring topological effects in quantum mechanics[10-13], as well as to the construction of new devices.

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Endosymbiotic bacteria

GroEL buffers against deleterious mutations

GroEL, a heat-shock protein that acts as a molecular chaperone[1], is over-produced in endosymbiotic but not in free-living bacteria[2–4], presumably to assist in the folding of conformationally damaged proteins. Here we show that the overproduction of GroEL in *Escherichia coli* masks the effects of harmful mutations that have accumulated during a simulated process of vertical transmission. This molecular mechanism, which may be an adaptation to the bacterium's intracellular lifestyle, is able to rescue lineages from a progressive fitness decline resulting from the fixation of deleterious mutations under strong genetic drift[5,6].

Endosymbiotic bacteria have small population sizes, do not undergo recombination, and are maternally transmitted through tight population bottlenecks[7], causing the fixation of deleterious mutations due to genetic drift and hence an irreversible decline in fitness[8]. However, endosymbiosis is surprisingly stable and persists over long periods[9], which has led to the suggestion[5] that *groE* (the GroEL-encoding operon) could be buffering the mutational loss of functionally active proteins because, unlike other endosymbiont genes, it is subject to strong purifying selection[5].

To test this idea, we investigated the effects of overexpression of *groE* in a set of *E. coli* strains (a free-living bacterium close to several endosymbionts[9]) with mutations randomly accumulated throughout the genome. These spontaneous mutations were fixed by random genetic drift in a process that simulated the vertical transmission of a single endosymbiont between hosts.

We studied the accumulation of mutations in 12 replicate lines of two *E. coli* B genotypes, one of which had a 3.3-fold-increased mutation rate[10]. These genotypes had already adapted to a simple environment (DM25 medium) for 10,000 generations[11], suggesting that mutation accumulation might result in a decline in fitness. After 3,240 generations of mutation accumulation, we measured the fitness of the strains evolved on DM25 relative to their respective ancestors. As expected, the
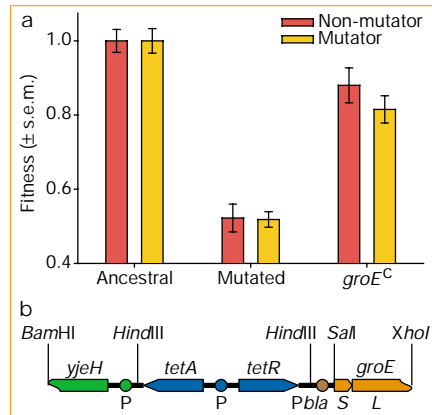
Figure 1 Effect of the overexpression of the *groE* operon on the fitness of randomly mutated strains of *Escherichia coli*. **a**, The fitness values for the ancestral strains of mutators and non-mutators are the same (left); 'mutated', fitness loss after 3,240 generations of mutation accumulation; '*groE*ᶜ', fitness recovery of strains in which *groE* is overexpressed. Culture conditions, fitness assays and phenotypic markers are described elsewhere[11], as is the mutation-accumulation protocol[12]. **b**, The regulated *E. coli groE* operon was changed to a constitutive form (*groE*ᶜ) by putting the structural genes under the control of the β-lactamase gene promoter (P*bla*). Recombinant genotypes were obtained by transduction using P1*vir* (ref. 13). The *groE*ᶜ construct contains part of the flanking *yjeH* gene, the inducible tetracycline-resistance operon (*tetA/R*) for transductant selection, the P*bla* promoter, and the *groE* coding regions (S and L). Restriction-enzyme cutting sites are indicated; P, promoter. Further details are available from the authors.

mutated strains lost fitness (Fig. 1a) as a result of the accumulation of deleterious mutations ($\bar{W}=0.5168\pm0.0159$ for mutators; $\bar{W}=0.5208\pm0.0087$ for non-mutators; paired *t*-tests, $P<0.0001$).

We then replaced the regulated *groE* operon of the mutated strains with a constitutive allele (*groE*ᶜ; Fig. 1b). To estimate the fitness of the *groE*ᶜ strains, we ran competition experiments against the corresponding ancestors on DM25. Surprisingly, none of the *groE*ᶜ strains reached the expected cell density during growth overnight. A simple explanation could be that an overproduction of GroEL of about 86 ± 16-fold is deleterious because it diverts amino acids away from other cellular functions.

To test this, we grew each *groE*ᶜ strain and its ancestor in DM25 supplemented with increasing concentrations of tryptone (a mixture of peptides and amino acids). We found that *groE* overexpression was deleteri-

ous in the presence of small amounts of tryptone, but that there were no significant differences in cell density between *groE*ᶜ strains and their non-mutated ancestors at tryptone concentrations of 0.1% or higher. In endosymbionts, amino acids are not limiting because these are abundant in their intracellular environment[9].

To determine whether fitness estimates depend on the environment, we estimated fitness on DM25 and on DM25 + 0.1% tryptone. Both fitness estimates were correlated (partial correlation test, $P<0.0001$).

Figure 1a shows that the average fitness of the *groE*ᶜ strains derived from non-mutator strains ($\bar{W}=0.8801\pm0.0214$) was 75.9% greater than that of the mutated strains (paired *t*-test, $P<0.0001$), but was 12% less than that of the ancestors ($P=0.0002$); the average fitness of the *groE*ᶜ strains derived from evolved mutators was $\bar{W}=0.8152\pm0.0167$, which is 61.6% greater than that of the mutated strains (paired *t*-test, $P<0.0001$) but 18.48% less than that of the ancestral strains ($P<0.0001$).

Is fitness recovery a result of the buffering of deleterious effects by GroEL, or is it simply a general benefit associated with increased concentrations of GroEL? In favour of the first possibility, the advantage of GroEL overproduction is evident only in an amino-acid-rich environment; also, if mutation compensation is occurring, we would expect a positive correlation between the extents of fitness loss and recovery, as evidenced by their partial correlation (1-tailed test, $P=0.0089$). We conclude that GroEL overexpression is likely to be of help in maintaining these endosymbionts by protecting them against the harmful effects of accumulated mutations.

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