alkali metal, caesium. The classic experiments of Bridgman in the 1940s revealed an anomalous volume discontinuity under pressure. As early as 1950, Sternheimer[7] interpreted this as an '*s*–*d*' transition in which the electronic *d*-states became lower in energy relative to the *s*-states under pressure (see also refs 8,9). Sternheimer attributed the general idea to Fermi (without a citation) saying, "In order to explain the phase transition, Fermi proposed that the valence electron is forced into a vacant internal orbit".

Neaton and Ashcroft[3] find that changes in electronic structure also lead to remarkable changes in the crystal structure, including distorted and paired hydrogen-like structures that may even be insulating. Up to now theorists have considered only high-symmetry 'simple' structures; within the confines of such structures the only phase transitions are between bcc and close-packed structures that must have simple metallic behaviour.

Neaton and Ashcroft have offered an alternative interpretation for the transition in Li under pressure. They propose that in any element the valence electrons are excluded from the ion core regions by the Pauli exclusion principle, which prevents any two electrons from occupying the same state. This effect grows with pressure as the volume available to the valence electrons decreases, and Neaton and Ashcroft propose that this effect is especially pronounced in Li because of its large core (the size of the core decreases as the nuclear charge increases). This also leads to a strong repulsive pseudopotential that can cause a distortion of the lattice. In high-symmetry structures there will be multiple electronic states with the same energy that are split by the distortion, with the electrons occupying only the lowest-energy state. This is the solid-state analogue of the Jahn–Teller effect in molecules, which can always lower their energy by such a distortion. As shown in their Fig. 5 on page 143, Neaton and Ashcroft find that in the molecular-like state the valence electrons are excluded from the region between the pairs of nuclei and instead occupy states with maximum density in the interstitial regions. This picture could be viewed as a different interpretation of Fermi's idea[7] that under pressure the valence electron is forced into a vacant internal orbit.

There are many experimental consequences of the calculations of Neaton and Ashcroft and experimental tests are already underway[10]. Among the predicted observable effects are large changes in the optical behaviour of Li from a silvery metallic appearance to a transparent or black colour, as expected for an insulator or semimetal. Preliminary measurements to be announced this month by V. V. Struzhkin at the *International Conference on High Pressure Science and Technology* in Honolulu, Hawaii, suggest new evidence for such effects. If the structures have low symmetry like those in molecular hydrogen, then there may also be strong infrared absorption as has been discovered in hydrogen[2].

Part of the excitement over this work is that if Li does form molecular analogues of hydrogen under pressure, then there is the possibility of superconductivity at a relatively high temperature for an element, and other interesting phenomena long sought for hydrogen. Because the effects occur at a much lower pressure than in hydrogen, perhaps Li can point the way to creating the Holy Grail of metallic hydrogen under pressure. Finally, such behaviour will clearly move Li and other alkalis away from being 'simple metals' in the minds of condensed-matter physicists and towards the category of 'interesting metals'.

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Chloroplasts

Ever decreasing circles

Geoff McFadden

If there is life on Mars, it may be disappointingly ordinary compared to some bizarre earthlings. Consider the genetic blueprint of dinoflagellates. The nucleus of these marine algae has DNA with non-standard bases, lacks typical histones (DNA packaging proteins common to all other nucleated cells) and has permanently condensed DNA, as if perpetually poised for division. But if the dinoflagellate nucleus is peculiar then, as we find on page 155 of this issue[1], the chloroplast is even more so. There Zhang *et al.* present the first analysis of the structure and gene content of the dinoflagellate chloroplast genome, one of the last frontiers in understanding chloroplast evolution.

Chloroplasts constitute the photosynthetic machinery of eukaryotes. They derive from endosymbiotic cyanobacteria and bear hallmarks of that prokaryotic ancestry[2]. The chloroplast genome is smaller than that of a cyanobacterium, but is still circular with a single replication origin and genes assembled into operons (expression units incorporating numerous, often related, genes). Until now, all known chloroplast genomes adhered to this uniform architecture, but dinoflagellates buck the trend.

Zhang *et al.*[1] show that, despite a common origin with other chloroplasts, dinoflagellate chloroplasts have adopted a unique genome architecture in which each gene has its own minicircle. In other words, dinoflagellate chloroplasts contain a small family of plasmid-like molecules, each carrying a gene for a protein or ribosomal RNA. The authors[1] find that all minicircles in a given dinoflagellate species have a repeat region that appears to participate in inter-circle gene conversion, thereby maintaining identity between circles, and they propose that this region contains a replication origin and an anchor point for circle segregation during chloroplast division. This repeat region could be a key to development of a genetic transformation system for dinoflagellate chloroplasts — it should be easy to introduce a plasmid-type construct, incorporating the repeat and a selectable marker, into them.

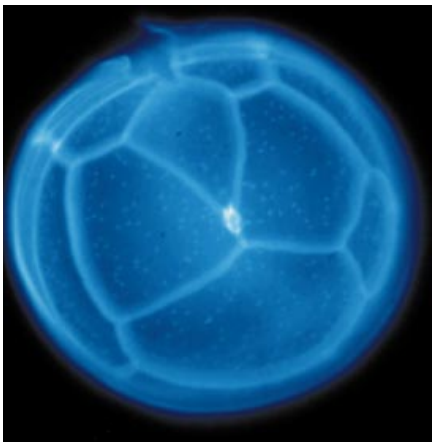

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Figure 1 **The dinoflagellate *Diplopelta bomba*. The chloroplast genome of dinoflagellates is like no other, and long defied characterization, but its genetic blueprint has now been revealed by Zhang *et al.*[1].**

How dinoflagellates developed minicircles from a large, multigenic circle (the ancestral state for chloroplasts) is not apparent. But there is an intriguing similarity in another endosymbiotic organelle, the mitochondrion. Mitochondrial genomes typically resemble chloroplast genomes (and their respective bacterial progenitor genomes) in being circular[3]. However Watanabe *et al.*[4] find that the single-gene minicircles in mitochondria of a little-known group of miniature parasitic animals, known as mesozoa, do not share a common non-coding region, although the mitochondrial circles do possess stem loop structures that may function in replication/segregation. There is no evidence for a canonical master circle in either the dinoflagellate chloroplast or the meso-

zoan mitochondrion, but neither group[1,4] can rule out its existence.

Gene content of the dinoflagellate chloroplast seems minimal. Normal chloroplasts retain some 100–200 genes[2], but Zhang *et al.*[1] found only nine genes among all the minicircles they examined. Other, less abundant circles probably await discovery, but we can expect the gene catalogue to be impoverished. Where are the missing genes? In the nucleus, no doubt. A pervasive trend in endosymbiosis is confiscation of the chloroplast's genes by the nucleus (the host), which is estimated to hold 800–900 plastid protein genes[2]. Why then has the dinoflagellate nucleus asserted even more control over its photosynthetic slave than other hosts? Minicircles may be the key. Transfer of DNA may have been expedited by each gene being packaged on a discrete, compact unit better able to make the journey from one part of the cell to another. In dinoflagellates, the products of these vagrants must be copious, so tracing them might be as simple as randomly sequencing active nuclear genes (an expressed sequence tag approach).

A revelation of molecular phylogeny was that dinoflagellates are close relatives of human parasites such as *Plasmodium* (which causes malaria) and *Toxoplasma*[5] — and here the plot really thickens. These parasites have a relict chloroplast[6–8], so could the chloroplasts in *Plasmodium* and dinoflagellates have the same origin? Zhang *et al.*[1] provide the data from dinoflagellates to help answer that question, but all is not yet clear. Ironically, the *Plasmodium* chloroplast genome (which is circular and encodes 68 genes[6]) is more conventional than that of dinoflagellates, preventing whole-genome comparison. Scrutiny of individual chloroplast genes shared by *Plasmodium* and dinoflagellates can reveal little more. *Plasmodium* chloroplast genes are highly divergent[6], and the dinoflagellate chloroplast genes are even more so. Because divergent genes tend to be grouped artificially in the calculations involved in building phylogenetic trees[9], any grouping of *Plasmodium* and dinoflagellate chloroplast genes must be treated with scepticism.

So we still cannot tell if dinoflagellates and *Plasmodium* have the same chloroplast. But we do have further insight into the origin of dinoflagellate chloroplasts, which are suspected to have been acquired by a process known as secondary endosymbiosis[9]. Zhang *et al.* provide strong supporting evidence for that view. The endosymbiosis of a cyanobacterial-like cell within a eukaryote to create the original chloroplast is referred to as the primary endosymbiosis (and in another paper in this issue, on page 159, Tomitani *et al.*[10] provide compelling evidence that a single primary endosymbiosis is ultimately the source of all chloroplasts). Secondary endosymbiosis is the subsequent purloining of chloroplasts by non-photosynthetic eukaryotes that engulf and retain a (primary) chloroplast-containing cell; the process occurred frequently in eukaryotic evolution and leaves a tell-tale clue in the form of multiple chloroplast membranes[9].

By analysing chloroplast genes, Zhang *et al.* show that dinoflagellates, whose plastids have three membranes, probably engulfed a red-algal-like cell. An independent study comes to the same conclusion[11]. Nonetheless these exciting results do not solve the origin of the *Plasmodium* chloroplast, which has four membranes and was also acquired secondarily[8,12], and there is vigorous debate over whether it derived from a red alga[13] or a green alga[8]. This issue is of more than academic interest because the *Plasmodium* chloroplast could be an ideal target for drug therapies. Many drugs that inhibit chloroplast activities kill *Plasmodium* and *Toxoplasma*[14], so increased understanding of chloroplasts could ultimately help combat malaria and related infections. □

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Evolutionary biology

Dirty eating for healthy living

Jared M. Diamond

As babies, we are warned by our mothers not to eat dirt, but as adults some of us do it anyway and dignify it with the name of geophagy. The regular and intentional consumption of soil, by itself or mixed with food, has been recorded from traditional human societies on all continents, especially among pregnant women[1–4]. Geophagy has also been documented in many species of mammals, birds, reptiles, butterflies and isopods, especially among herbivores[5–9]. Why do they and we do it? Proposed biological functions of geophagy have now been tested by James Gilardi and coworkers[10], who uncover a fascinating evolutionary arms race between plants and their would-be animal consumers.

The dirt-eaters studied were Peruvian Amazon rainforest parrots, of which a thousand or more individuals of 21 species gather early each morning at certain sites with exposed bare soil on river banks or cliff faces (Fig. 1). Because these sites are ideal for viewing and photography, they attract 4,000 bird-watching tourists each year, support 500 jobs in the local ecotourism industry, and earn Peru about US$1,000 per year per individual wild macaw. The birds' taste in dirt is highly specific: for instance, they congregate not just at one particular bend of the Manu River but at one soil band running hundreds of metres horizontally along that bend, spurning the dirt in bands one metre above or below the preferred band. Gilardi *et al.* tested possible functions of geophagy by comparing the physical and chemical properties of soil samples from the preferred and rejected bands.

The commonest explanation for geophagy in birds is to provide grit[8]. Because birds lack teeth, many ingest pebbles or coarse soil with which to grind food in their gizzards. Preferred particle sizes of grit increase with bird size, from 0.5 mm for sparrows to 2.5 cm for ostriches. However, Gilardi *et al.* found that the soil preferred by Peruvian parrots is very fine: only 5% of it by volume is coarse sand exceeding even 0.05 mm in particle diameter. Most of it is clay less than 0.2 μm in particle diameter, and preferred soils contain only a quarter as much coarse sand and nearly twice as much fine clay as rejected soils. So parrots are not eating soil to get grit. On reflection, this is not surprising: parrots have no need for grit because their strong, sharp bills can shred the hardest nuts.

A second function of geophagy, suggested for livestock, wild ungulates, rabbits, butterflies and pregnant women, is to provide essential minerals[6,7]. Soils sold in Ghanaian markets to pregnant African women are richer in iron and copper than the dietary supplement pills made by pharmaceutical companies specifically for prenatal use. But Gilardi *et al.*[10] found that soils preferred by parrots contain lower available quantities of most biologically significant minerals than non-preferred soils, and much lower quantities than the parrots' preferred plant foods. Hence, unless the parrots are making a big mistake in their taste preferences, they are not selecting soils for mineral content.

A third function of geophagy, proposed for ungulate livestock, is to buffer the rumen contents[6]. Because parrots lack a rumen, it will come as no surprise that their preferred soils have no more buffering capacity than distilled water.

What, then, do the parrots actually gain from ingested soil? It turns out that they regularly eat seeds and unripe fruits whose con-