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. ☐

Geoff McFadden is in the Plant Cell Biology Research Centre, School of Botany, University of Melbourne, Parkville 3052, Australia.
e-mail: g.mcfadden@botany.unimelb.edu.au

1. Zhang, Z., Green, B. R. & Cavalier-Smith, T. *Nature* **400,** 155–159 (1999).
2. Martin, W. *et al. Nature* **393,** 162–165 (1998).
3. Gray, M., Burger, G. & Lang, B. *Science* **283,** 1476–1481 (1999).
4. Watanabe, K. I.*et al. J. Mol. Biol.* **286,** 645–650 (1999).
5. Wolters, J. *Biosystems* **25,** 75–84 (1991).
6. Wilson, R. J. M. *et al. J. Mol. Biol.* **261,** 155–172 (1996).
7. McFadden, G. I. *et al. Nature* **381,** 482 (1996).
8. Köhler, S. *et al. Science* **275,** 1485–1488 (1997).
9. Palmer, J. D. & Delwiche, C. F. *Proc. Natl Acad. Sci. USA* **93,** 7432–7435 (1996).
10. Tomitani, A. *et al. Nature* **400,** 159–162 (1999).
11. Takishita, K. & Uchida, A. *Phycol. Res.* (in the press).
12. Waller, R. F. *et al. Proc. Natl Acad. Sci. USA* **95,** 12352–12357 (1998).
13. Blanchard, J. *J. Euk. Microbiol.* **46,** 367–375 (1999).
14. McFadden, G. I. & Roos, D. S. *Trends Microbiol.* (in the press).

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 co-workers[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-

J. D. GILARDI

Figure 1 **Blue-headed parrots (*Pionus menstruus*) at a clay lick in Manu, Peru. Gilardi *et al.*[10] have shown that minerals in the clay detoxify the birds' plant diet.**

tent of alkaloids and other toxins renders them bitter and even lethal to humans and other animals. Because many of these chemicals are positively charged in the acidic conditions found in the stomach, they bind to clay minerals bearing negatively charged cation-exchange sites[2,3,5,9]. That's why experienced tourists visiting destinations with poor sanitation carry medicines such as kaopectate (high in clay minerals) to adsorb the toxins. That's also why peasant farmers and hunter–gatherers throughout the world often mix bitter but otherwise nutritious plant foods (like acorns and wild potatoes) with selected soils before consumption[1–3].

Peruvian parrots behave like sophisticated human tourists and hunter–gatherers. Their preferred soils were found to have a much higher cation-exchange capacity than adjacent bands of rejected soils — because they are rich in the minerals smectite, kaolin and mica. In their capacity to bind quinine and tannic acid, the preferred soils surpass the pure mineral kaolinate and surpass or approach pure bentonite. Clearly, parrots would be well qualified for jobs as mining prospectors.

Gilardi *et al.* confirmed this hypothesis with two sets of bioassays. First, they exposed brine shrimp (the toxicologist's test animal of choice) to extracts of seeds routinely consumed by macaws. Many of the brine shrimp died, confirming the toxicity of the parrots' diet. But mixing the solutions or extracts with soil preferred by parrots reduced the effective toxin loads by 60–70% and improved shrimp survival. Second, Amazon parrots were given an oral dose of the alkaloid quinidine with or without preferred soil, and quinidine levels were measured in the parrots' blood for three hours as absorption took place from the gut. Providing soil along with the quinidine reduced absorbed quinidine blood levels by 60%.

What is the evolutionary significance of plant toxins and animal anti-toxin behaviour? From a plant's evolutionary perspective, a seed should be high in nutrients to support germination and seedling growth; the ripe fruit around the seed should also be nutrient-rich and attractive to animals, encouraging them to pluck and eat the fruit and disperse the seed. On the other hand, the seed itself should be repulsive to animal consumers, inducing them to regurgitate or defaecate it, and the unripe fruit should be repulsive, lest animals harvest it before the seed is viable. From an animal's evolutionary perspective, an ability to defeat the plant's toxin defences would enable it to obtain the nutrients in the seed as well as those in the ripe fruit, and to outcompete other animal consumers by harvesting the fruit while it is unripe and still unpalatable to them.

Any textbook of animal biology describes the resulting evolutionary arms race, in which plants evolve increasingly potent toxins (such as strychnine and quinine), and animals evolve increasingly potent means of detoxification. While enzymatic detoxification has previously received the most attention, the work of Gilardi *et al.*[10] and the wide distribution of geophagy among animal herbivores suggest an additional important means of detoxification by adsorption on ingested soil minerals.

A host of interesting questions now comes into focus. How do parrots discover the best soils — can they discriminate among soils immediately by texture and taste, or must they experiment with various soils mixed with toxic food and discover which soil assuages their upset stomach? Might the availability of suitable geophagy sites limit herbivore distributions and merit concern from conservation biologists? Only certain species of local herbivores are reported as visiting geophagy sites: why? To return to our youthful dirty habits, do curious dirt-licking babies deserve our encouragement for their experiments with self-medication?

Jared M. Diamond is in the Department of Physiology, University of California Medical School, Los Angeles, California 90095-1751, USA.
e-mail: jdiamond@mednet.ucla.edu.

1. Johns, T. *J. Chem. Ecol.* **12,** 635–646 (1986).
2. Johns, T. *With Bitter Herbs They Shall Eat It: Chemical Ecology and the Origins of Human Diet and Medicine* (Univ. Arizona Press, Tucson, 1990).
3. Johns, T. & Duquette, M. *Ecol. Food Nutr.* **25,** 221–228 (1991).
4. Abrahams, P. W. & Parsons, J. A. *Geogr. J.* **162,** 63–72 (1996).
5. Hladik, C. M. & Gueguen, L. *C. R. Acad. Sci.* **279,** 1393–1396 (1974).
6. Jones, R. L. & Hanson, H. C. *Mineral Licks, Geophagy, and Biogeochemistry of North American Ungulates* (Iowa State Univ. Press, Ames, 1985).
7. Kreulen, D. A. *Mamm. Rev.* **15,** 107–123 (1985).
8. Gionfriddo, J. P. & Best, L. B. *Condor* **97,** 57–67 (1995).
9. Mahaney, W. C. *et al. Primates* **37,** 121–134 (1996).
10. Gilardi, J., Duffey, S., Munn, C. & Tell, L. *J. Chem. Ecol.* **25,** 897–922 (1999).

Daedalus

Creep and anti-creep

Many substances — ice is perhaps the best known — can crystallize in lots of different ways, many of them stable only under high positive pressure. Daedalus is now exploring the converse field, that of crystals stable only under negative pressure, that is, tension. Engineering components are routinely stressed to thousands of atmospheres of tension: usually in one or two dimensions only, but isotropic three-dimensional tension is possible. Even liquids, if clean and degassed, can be tensioned to many hundreds of negative atmospheres. Indeed, the sap in trees taller than ten metres is thought to be under permanent tension.

So DREADCO physicists are melting numerous solids, putting the liquid under strong tension, and letting them resolidify again. They are also submitting crystalline samples to sustained three-dimensional tension, and looking for a slow phase-change to some expanded, negative-pressure crystal habit. The pilot experiments are largely empirical; it is hard to guess which substances form distinctive negative-pressure phases. But Daedalus hopes that at least some of these phases will continue to exist metastably at atmospheric pressure, at least for a while.

His ultimate goal is a new engineering material. Many such materials, he points out, creep under load. For a component in tension this is a dangerous vice. But for one in compression it can be a virtue. If overloaded, it creeps plastically away from the load, thickening as it does so, and sharing its burden with more lightly loaded members nearby. A compression structure is often usefully 'self-designing'.

Metastable expanded materials should bring the same self-optimization to tension structures. While it remains tensioned, a component of such a material will be quite stable. But if the tension slackens, it will become metastable. It will slowly contract to its denser phase, restoring the tension and relieving nearby members of some of their load. In fact it will show 'anti-creep'.

DREADCO's anti-creep alloys will be widely welcomed. Bridges, bicycles, power lines, aerospace frames, all will exploit anti-creep technology for greater safety and efficiency. Self-tightening anti-creep fasteners and connectors will transform the small-scale details of engineering. Over the whole field, designers will gratefully allow self-optimizing anti-creep materials to lift some of their lonely burden.

David Jones