‘subgame perfection’ — the assumption that people pursue their own interests from each point in a game onwards. In particular, players will not avenge or reward the actions of another player if doing so hurts their own interests at that time. People will never reciprocate kindness unless doing so brings further advantages to themselves. Nor will rational people avenge wrongs if the revenge will be costly to themselves. A great deal of evidence supports subgame perfection and the rationality hypothesis. For instance, in the workplace an employee’s performance can be improved by offering financial incentives — or by disciplinary action.

But there is striking evidence against subgame perfection, in the form of experimental work on ultimatum games[2]. In these, one player (the leader) makes an offer to another (the follower) on how to split a sum of money. If the follower accepts, the split is made according to the leader’s offer. But if the follower refuses the offer, neither player gets anything. According to the principle of subgame perfection, the leader should get almost the whole amount, because the follower gains nothing by refusing any offer that gives him something. In practice, however, small offers are almost always refused.

Fehr and Rockenbach’s experiments[1] are more subtle. The subjects of their study (a sample of more than 200 students at the University of Bonn) played a game involving two players, an investor and a trustee, each of whom was given an equal sum of money. The investor decided on an amount of money to give to the trustee and specified the amount that he wanted the trustee to return. The experimenter tripled the amount offered by the investor and passed it on to the trustee. The trustee then chose how much to return to the investor. In a second version of the game, the investor, when making the gift to the trustee, could commit to imposing a fine of a fixed size on the trustee if he returned less than the amount requested. Each investor and trustee interacted only once (they were recruited for the experiment on the spot in the university canteen), so that no player could reward or punish a partner’s behaviour in future rounds of play.

On average, trustees reciprocated investors’ generosity by making payments that increased with the size of investors’ transfers. Trustees were least generous when the fine was imposed, more generous when there was no possibility of a fine, and most generous when the investor could impose a fine but chose not to do so. Fehr and Rockenbach’s close examination of their evidence indicates that perceptions of fairness influenced the trustees’ negative reactions to imposition of the fine. The earnings of the trustee and investor are equalized if the trustee returns two-thirds of the investor’s transfer. Trustees apparently made this calculation, for the imposition of a fine had less effect on what trustees returned when investors requested that the trustee return less than two-thirds of their transfer than when they requested that more than two-thirds be given back.

An explanation of the authors’ findings is obvious — people are insulted and angered by threats that constrain their actions. Most of us want the freedom to choose. Nevertheless, the fairness that the authors emphasize may be crucial. Evidence from many sources indicates its importance[3]. People do seem to have in mind norms of behaviour for themselves and others, and try to enforce them. This vital topic of human motivation certainly deserves more experimental exploration. ■

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**Planetary science**

# The core of planet formation

Bill Minarik

The rocky bodies from which the Earth formed may have already separated into a metal core and silicate shell. Innovative experiments exploring the behaviour of molten metal trapped between silicate grains suggest how.

Roughly speaking, the Earth is a metallic core surrounded by a silicate shell. Understanding the mechanisms that caused this separation, or differentiation, is one of the outstanding questions of Solar System science. Most of the Earth’s volume is inaccessible to researchers, so information about its core must be gleaned indirectly. It comes from four main sources: remote sensing techniques using, for example, gravity and seismic waves; the study of core material from other Solar System bodies found on Earth as meteorites; inferences from the geochemistry of rocks formed from magmas that originated deep below the Earth’s surface; and laboratory experiments at high pressures and temperatures, to simulate conditions approaching those at the core. This last is the approach taken by Takashi Yoshino and colleagues[1], who, on page 154 of this issue, present new constraints on the mechanism and timing of core formation.

Core formation probably occurred early in the history of the Solar System. Evidence for this comes, for example, from the decay of short-lived isotopes: decay of the hafnium isotope $^{182}$Hf to tungsten ($^{182}$W) constrains the timing of core formation to the first 30 million years of the Solar System for all four bodies for which we have samples — Earth, the Moon, Mars and the asteroid Vesta[2,3]. Earth formed from a nebula of dust and gas, as material clumped together to form kilometre-sized planetesimals, which then rapidly accreted into larger bodies (Fig. 1), ranging up to thousands of kilometres in diameter. The end point of the accretion process involved energetic collisions of large planetesimals. The ejected material from one such collision re-accreted in the proto-Earth’s orbit to form the Moon.

Chemical data require that both the proto-Earth and the object with which it collided had already formed metallic cores. But data from meteorites are less clear. Samples of undifferentiated materials (such as from the chondritic meteorites) suggest that some planetesimals reached sizes of tens to hundreds of kilometres without substantial melting (and hence without separation); but other samples (from iron meteorites)

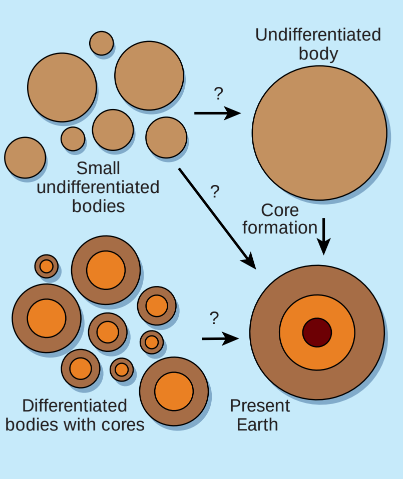

Figure 1 **Timing of core formation. The Earth formed through accretion, absorbing planetesimals (lumps of rock and ice) through collisions. Did the Earth accrete undifferentiated material that then separated into shell and core — in which case, did the planet reach its present mass before differentiating, or was it a more gradual process? Alternatively, core formation might have happened rapidly inside growing planetesimals, so that the Earth’s core is a combination of these previously formed cores. Isotopic evidence supports the latter model, and now Yoshino *et al.*[1] demonstrate a mechanism for the physical process.**

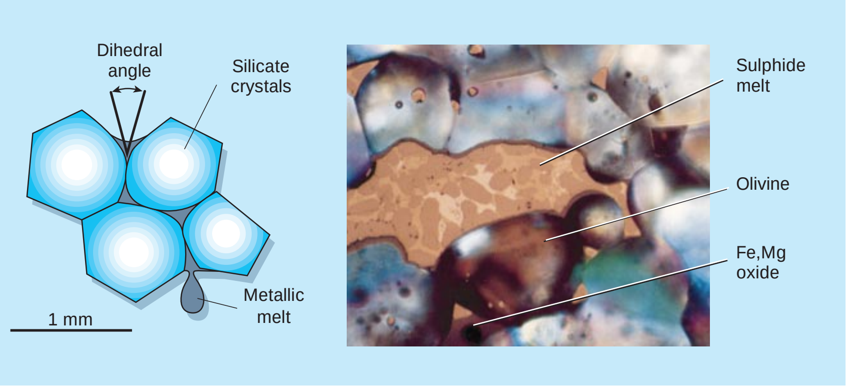

Figure 2 **Degrees of separation. Metal alloys with a lower melting point than silicate minerals form a melt between the grain boundaries of silicate crystals. The dihedral angle (left) is a measure of how likely it is that pockets of melt will connect and separate from the silicate matrix. The photomicrograph (right) shows sulphide melt trapped in a matrix of Fe,Mg oxide and olivine (the silicate that makes up most of the Earth's upper mantle). The dihedral angle is near 90° and, if the melt makes up a sufficiently large fraction of the sample volume, the melt pockets start to interconnect. The field of view of the photomicrograph is about 500 $\mu$m.**

record differentiation into mantle and core.

The melting points of alloys of iron, nickel, sulphur and oxygen (900–1,000 °C) are lower than those of silicate minerals (1,100–1,400 °C), so when a cold planetary body is heated a metallic melt forms but the silicate and oxide minerals remain solid. Whether this metallic melt can segregate from the silicate matrix — and eventually form a metallic planetary core — depends on its microstructure, which is in large part determined by the interfacial energies of melt and minerals. These energies can be parametrized in terms of the dihedral angles made by the silicate grain boundaries around the pockets of metallic melt (Fig. 2). Systems with large melt–solid interfacial energies (relative to solid–solid grain-boundary energies) have large dihedral angles, resulting in isolated melt pockets surrounded by melt-free grain boundaries. In such systems, the melt is unlikely to separate from the matrix.

Constraints on this core-forming process mostly come from experiments, as meteorites have lost much of their crucial textural information by the time they reach Earth. Olivine — $(Fe,Mg)_2SiO_4$ — makes up much of the Earth's upper mantle, and presumably made up much of the silicate fraction of accreting planetesimals. Metallic melts within an olivine matrix have large dihedral angles. This implies that, in a matrix that does not deform, core-forming melts would be trapped at grain boundaries. So for the melt to migrate towards the core, higher temperatures are needed to melt a matrix made of olivine and other silicate minerals. This process would produce a different trace-element chemistry in the melt than if the molten metal had percolated through a solid silicate matrix to the core.

Characterizing the permeability of a system using dihedral angles poses several difficulties. First, there are theoretical assumptions. For instance, a single dihedral-angle value for a sample implies that the interfacial energies are isotropic (which is not generally true in a system containing many different, anisotropic minerals); we must assume that the microstructure is dominated by surface reaction kinetics, not by mechanical deformation. In experiments, the system geometry must remain stable during the transition from high temperature and pressure to ambient conditions. Finally, with increasing melt fraction, even a system of isolated melt pockets will start to interconnect, but the 'percolation threshold' — the minimum melt fraction required for interconnection — has been modelled numerically only for simple systems[4].

To overcome these limitations, Yoshino *et al.*[1] have performed the first high-temperature, high-pressure experiments that determine the interconnectivity of metallic melt in an olivine matrix through observed changes in electrical conductivity. Conductivity was measured after the samples were brought to a pressure of 3 gigapascals and a temperature of 1,200 or 1,300 °C, corresponding to a depth of about 100 km in the present Earth or of about 700 km in the Moon. The authors find that about 6% by volume of iron–sulphur melt is sufficient to form highly conductive pathways, representing interconnected (and therefore permeable) melt channels in the olivine matrix. Interestingly, although the formation, in systems with high dihedral angles, of a heterogeneous distribution of larger melt pockets surrounded by many melt-free grain boundaries has been predicted theoretically, and shown experimentally for other systems, Yoshino *et al.* saw no evidence for this in their experiments. This discrepancy is unresolved, and further experiments are needed.

If these high electrical conductivities

NATURE

## 100 YEARS AGO

**In Campbell Island, south of New Zealand, the breeze-fly (*Helophilus campbellicus*), one of the Syrphidae, so closely resembles a blow-fly (*Calliphora eudypti*) that when, in 1901, I captured a specimen of the first, which is rare, I thought it was the blow-fly, which is common… Now in any other locality this resemblance could be put down to mimicry. The blow-fly is common and offensive. The breeze-fly is rare and feeds on flowers. Everything favours this explanation except that in Campbell Island there are no insect-eating birds and no lizards, and consequently mimicry would be useless.** **F. W. Hutton**

**Accidental resemblances between insects are to be expected… With regard to Captain Hutton's special instance, however, there appear to be certain points which require consideration before accepting the conclusion that the resemblance is merely a coincidence:— (1) The possible coexistence of the two species in other localities where the resemblance has a meaning; (2) the possible change of conditions in the struggle for life in the locality itself; (3) our possibly imperfect knowledge of the struggle which is waged there now.** **B. Poulton**

**From *Nature* 12 March 1903.**

## 50 YEARS AGO

**The Nutrition Society held a symposium on 'The Role of Vitamins in Metabolic Processes' in the Biochemistry Department of the University of Sheffield on December 20, 1952… . In the final paper, Dr. L. J. Harris (Dunn Nutritional Laboratory, Cambridge) examined the literature which, despite its bulk, still leaves us without evidence for a specific metabolic role of vitamin C. Among older hypotheses was one associating ascorbic acid with collagen formation, and also the more general theory that certain formative cells, such as osteoblasts, show reduced activity; in these cells the vitamin has been found to be concentrated in the Golgi apparatus… The great majority of animals can synthesize vitamin C, but, although glucose is known to be its precursor, it is still not known whether synthesis is a property of all cells of the body, or whether certain tissues are specialized for this purpose; similarly, the function of the vitamin in plants is still obscure.**

**From *Nature* 14 March 1953.**

correspond directly to the permeability of the olivine matrix to metallic-melt percolation, the separation of a core from silicate mantle could happen very quickly in a planetesimal. The high temperatures required could result from the heat produced by the decay of short-lived isotopes present at the birth of the Solar System. More complete calculations of the thermal evolution of growing planetesimals (which include, for example, latent heat of melting, release of gravitational potential energy and impact kinetic energy) point to many sources of heat in the early Solar System that probably led to core formation and magma oceans in many growing planetesimals[5].

But heating in a static environment may not be the whole answer. Deforming systems can have higher permeabilities than static systems, and impact-induced melting or differential stress may connect isolated melt pockets and produce pools of metal[6] that may then sink through unmelted material. Each of these processes will tend to shorten the interval between accretion and core formation, so core formation should be ubiquitous once an accreting rocky planetesimal reaches a radius of 50–100 km. But then the existence of large bodies that do not seem to have differentiated (including some large asteroids such as Ceres, and Jupiter's moon Callisto) is puzzling: is there some mechanism that prevented these bodies heating sufficiently to produce a core?

Building on the success of Yoshino *et al.*[1], future experiments may be able to determine melt connectivity through conductivity measured *in situ* and monitor dynamically evolving microstructure, such as during deformation or reactions. Synchrotron X-ray microtomography[7] is another promising technique, which enables three-dimensional imaging with resolution approaching $1\ \mu m^3$. These experimental advances will help us to understand the processes that have shaped the Solar System. ■

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Evolutionary biology

# Teeth as tools

Anne Weil

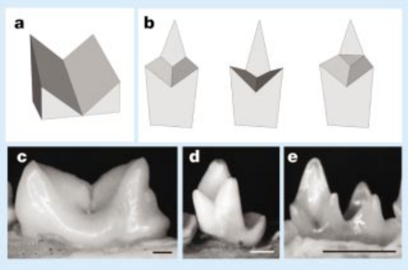
What determines the shapes of mammalian teeth? When tools are designed to cut to the meat of the question, form follows function rather than developmental or evolutionary constraints.

Very different groups of mammals have teeth of similar shapes. One obvious explanation for this is that the greatest efficiency in chewing similar foods is strongly favoured by natural selection. But other reasons could include the constraints imposed in the process of development, or the historical limitations imposed within mammal lineages, and each of these factors might act against or in concert with the demands of optimizing function.

Writing in the *Biological Journal of the Linnean Society* (**78,** 173–191; 2003), Alistair R. Evans and Gordon D. Sanson describe how they have taken an engineer's approach to this question. They have carried out a computer-modelling exercise, designing tools to cut tough substances, and find that the most efficient tools closely resemble the molars of carnivorous and insectivorous mammals. They conclude that in many cases developmental and evolutionary factors have not strongly influenced molar shape, and that function is indeed the primary determinant.

Most mammals use differentiated cheek teeth for chewing, to divide food into small pieces that can be swallowed easily and digested efficiently. Mammalian teeth are replaced at most once in an individual's lifetime, so exact positioning of them is possible, allowing the cutting edges and points of upper and lower teeth to meet in a precise way. The hands, tongue and facial muscles are variously used to position food between the teeth. Tough (as opposed to brittle or soft) foods are divided by an initial puncture (or punctures), which is then extended into a longer cut. Chewing tough foods can thus be envisaged as a mechanical task in which the teeth act as simple, edged tools.

Evans and Sanson considered six functional factors used by engineers in tool design: sharpness of points; sharpness of blades; the angle between the blade and the substance cut; the angle between the blade and a line perpendicular to the cut; the entrapment of substance between blades; and the movement of substance away from the blade that prevents the implement from becoming clogged up. They considered these factors for tools with single blades (which are rectangular in horizontal cross-section, and can resemble a chisel, scissors or a guillotine), as well as for tools with two blades that meet at an angle (which are triangular in cross-section). Not surprisingly, they found that some shapes work better than others. The field of optimal shapes narrowed further when true-to-life criteria were applied: a serial arrangement for the blades, like that of teeth in the jaw, and a degree of lateral as well as vertical movement, as commonly occurs in chewing.



BIOL. J. LINN. SOC. **78,** 184 (2003)

Figure 1 **Efficient model cutting tools, and some similarly shaped mammalian cheek teeth. The single-bladed** (a) **and double-bladed** (b) **models optimize eight efficiency factors considered by Evans and Sanson. On that evidence, real mammalian molars** (c, **single-bladed;** d, e, **double-bladed) may approach a functional ideal. Scale bars, 1 mm.**

In the case of the single blades, the most efficient is a symmetrical, notched blade (Fig. 1a), strikingly similar to 'carnassial' teeth that have evolved in several mammal lineages (Fig. 1c). The optimal double-bladed models have three points and two high crests (Fig. 1b), forming a 'protoconoid' that closely resembles the trigonid of simple mammalian lower molars (Fig. 1d, e). This notched triangle is a familiar shape to any student of mammalian evolution, because it evolved early and possibly more than once in mammalian history and is present in many living groups, such as opossums and bats.

Evans and Sanson's study did not address the significant role of crushing in chewing. Their modelling therefore did not produce a 'tribosphenic' tooth shape, characterized on the lower molars by a low basin behind the high trigonid (Fig. 1d, e) into which the largest cusp of the upper tooth fits. Tribosphenic molars perform both slicing and crushing functions, and were present in the ancestors of all living mammals. Although Evans and Sanson focused on cutting alone, the superior efficiency of their protoconoid models, and the evident supremacy of function in determining tooth form, may support the arguments of those who believe that tribospheny evolved two or even three times within early mammals. ■

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