

The eye in a twinkling

Richard Dawkins

THE creationist's favourite conundrum — "What is the use of half an eye?" — is a lightweight question, a doddle to answer ever since Darwin first anticipated and elegantly solved it in 1859. A more ponderous show of weight seems to lie behind the inevitable supplementary: "Speaking as a physicist [engineer etc.], I cannot believe that there has been enough time for an organ as complicated as the eye to have evolved from nothing". Both questions stem from what I have unkindly called *The Argument from Personal Incredulity*¹. Audiences nevertheless appreciate an answer and I have usually fallen back on the sheer magnitude of geological time. If one pace represents one century, the whole of time *anno Domini* is telescoped into a cricket pitch. But then, to reach the origin of multicellular animals, you'd have to slog it out all the way from New York to San Francisco.

It now appears that the shattering extent of geological time is a steamhammer to crack a peanut. Trudging from coast to coast dramatizes the time available for the evolution of the eye. But a study by Dan Nilsson and Susanne Pelger, published this week in *Proceedings of the Royal Society*², suggests that a ludicrously small fraction of that time would have amply sufficed. When one says 'the' eye, by the way, one implicitly means the vertebrate eye, but serviceable image-forming eyes have evolved between 40 and 60 times,

independently from scratch, in various invertebrate groups³. Among these 40-plus independent evolutions, at least nine distinct design principles have been discovered, including pinhole eyes, two kinds of camera lens eyes, curved-reflector ('Jodrell Bank') eyes, and several kinds of compound eyes⁴. Nilsson and Pelger have concentrated on camera eyes with refracting lenses, such as are well developed in vertebrates and octopuses.

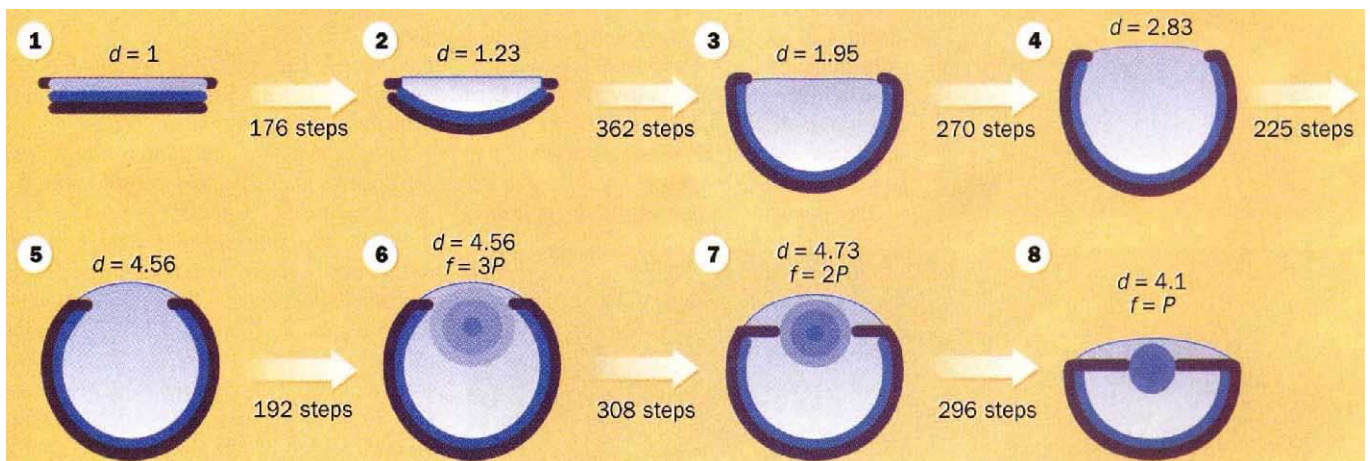
How do you set about estimating the time required for a given amount of evolutionary change? We have to make an assumption about the size of each step and it is sensible to express it as a proportion of an existing measurement (such an assumption underlay J. B. S. Haldane's definition of the Darwin as a logarithmic unit of evolutionary rate). Nilsson and Pelger used the number of successive changes of 1% as a unit for quantifying changes of anatomical quantities. If the change is all in one dimension it is then rather easy. In the unlikely event that natural selection favoured bird-paradise tails of ever-increasing length, how many steps would it take for the tail to evolve from one metre to one kilometre in length? A 1% increase in tail length would not be noticed by the casual birdspotter. Nevertheless, it takes surprisingly few steps to elongate the tail to 1 km — fewer than 700.

Elongating a tail from 1 m to 1 km is all

very well (and all very absurd), but how do you place the evolution of a camera eye on the same scale? The problem is that lots of things have to go on in lots of different parts of the eye, in parallel. Nilsson and Pelger's task was to set up computer models of evolving eyes to answer two questions. First, is there a smooth trajectory of change, from flat skin to full camera eye, such that every intermediate is an improvement? (Unlike human designers, natural selection can't go downhill, not even if there is a tempting higher hill the other side of the valley.) Second, how long would the necessary quantity of evolutionary change take?

Nilsson and Pelger worked at the level of tissue deformations, not the level of cellular biophysics. The existence of a light-sensitive cell was taken as given. Doubtless this could itself be the subject of a later simulation, in which the variables of interest would be molecular. Most of the popular scepticism about the evolution of the eye, however, centres on the tissue level: how could flat skin have invaginated into a smoothly circular cup; how could a lens have appeared at the right distance away from the retina, and with the right refractive index; and so on? Nilsson and Pelger also stopped short of simulating the variable iris and variable focusing, though their methods would lend themselves to these problems and I hope they'll tackle them in the future.

The beauty of simulating an eye as distinct from, say, the leg of a running cheetah, is that its quality can be easily measured, using elementary optics. The eye is represented as a two-dimensional



Stages in Nilsson and Pelger's model sequence of eye evolution. In the initial stage (1) the structure is a flat patch of light-sensitive cells sandwiched between a transparent protective layer and a layer of dark pigment. In stages 2 and 3 the photoreceptor layer and pigment layer (the retina) invaginates to form a hemisphere. The protective layer deepens to form a vitreous body which fills the cavity. The refractive index of the vitreous body is assumed to be 1.35, which is only slightly higher than that of water, and not enough to give the vitreous body any significant optical effect. In stages 4 and 5 the retina continues to grow, but without changing its radius of curvature. This causes a gradual shift from deepening of the retinal pit to constriction of the distal aperture. The aperture size in stage 5 was chosen to reflect the typical proportions in real eyes of this type. In stages 6–8 a graded-

index lens appears by a local increase in refractive index. The central refractive index of the lens grows from an initial 1.35 to 1.52 in the final stage. Simultaneously the lens changes shape from ellipsoid to spherical and moves to the centre of curvature of the retina. As the lens shrinks, a flat iris gradually forms by stretching of the original aperture. The focal length (f) of the lens gradually shortens, and in stage 8 it equals the distance to the retina (P), producing a sharply focused system. The relative change in receptor diameter, required to keep sensitivity constant throughout the sequence, is indicated by the normalized receptor diameter d . The anatomical change between model stages is given as the number of 1% modification steps. (Figure and caption modified from reference 2, with permission).

cross-section, and the computer can easily calculate its visual acuity — that is, spatial resolution — as a single real number. It would be much harder to come up with an equivalent numerical expression of the quality of a cheetah's leg or backbone. Nilsson and Pelger began with a flat retina, atop a flat pigment layer and surmounted by a flat, protective transparent layer (see figure). The transparent layer was allowed localized random mutations of its refractive index. They then let the model deform itself at random, constrained only by the requirement that any change must be only 1% bigger or smaller than what went before. And, of course, in order for a change to be accepted, it had to be an improvement on what went before.

The results were swift and decisive. A trajectory of steadily improving acuity led unhesitatingly from the flat beginning through a shallow cup to a steadily deepening cup. The transparent layer thickened to fill the cup and smoothly

curved its outer surface. And then, almost like a conjuring trick, a portion of this transparent filling condensed into a local, spherical subregion of higher refractive index — not uniformly higher, but a gradient of refractive index such that the spherical region functioned as an excellent graded-index lens. Best of all, the ratio of the focal length of the lens to its diameter settled down at a close approximation to Mattiessen's ratio, long known to be the ideal value for a graded-index lens.

Turning to the question of how long the evolution might have taken, Nilsson and Pelger had to make some plausible population-genetic assumptions. They chose values of heritability, coefficient of variation and intensity of selection from published observations from the field. Their guiding principle in choosing such numbers was pessimism. For each assumption they made, they wanted to err in the direction of overestimating the time taken for the eye to evolve. They even went so far as to assume that any new

generation differed in only one part of the eye: simultaneous changes in different parts of the eye, which would have speeded up evolution, were banned. But even with these conservative assumptions, the time taken to evolve a fish eye from flat skin was under 400,000 generations. Assuming typical generation times of one year for small animals, the time needed for the evolution of the eye, far from stretching credulity with its vastness, turns out to be too short for geologists to measure. It is a geological blink. □

Richard Dawkins is in the Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

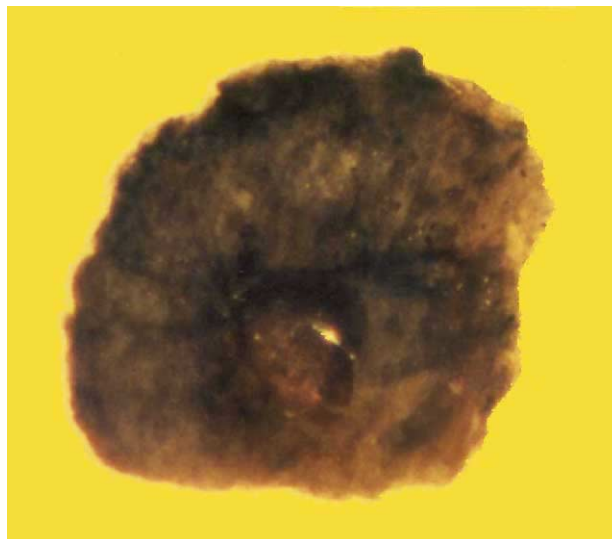
1. Dawkins, R. *The Blind Watchmaker* (Penguin, London/Norton, New York, 1986).
2. Nilsson, D.-E. & Pelger, S. *Proc. R. Soc. B* **256**, 53–58 (1994).
3. Salvini-Plawen, L. v. & Mayr, E. in *Evolutionary Biology* Vol. 10 (eds Heceth, M. K., Steere, W. C. & Wallace, B.) 207–263 (Plenum, New York, 1977).
4. Land, M. F. in *Handbook of Sensory Physiology* (ed. Autrum, H.) 471–592 (Springer, Berlin, 1980).

METEORITICS

Fragments of history preserved

ABOUT 85 per cent of the meteorites observed to fall on the Earth are chondrites. Except for volatile elements such as hydrogen, helium and nitrogen, chondrites have elemental abundances similar to those of the Sun's photosphere; these meteorites preserve the bulk chemistry of the earliest solids to form in the cloud of gas and dust known as the solar nebula. Chondrites that were not greatly altered in their parent asteroids (by water, heat or shock) have heterogeneous mineral compositions and preserve the textures they inherited from the nebula, and typically contain submillimetre igneous spherules with solar compositions (known as chondrules), fine-grained dust of similar constitution, and grains of metallic iron–nickel and sulphide. Carbonaceous chondrites also contain abundant refractory inclusions (also known as Ca, Al-rich inclusions or CAIs), some of which have isotope anomalies suggesting the presence of pre-solar solids.

Chondrules are believed to have formed from clumps of precursor dust by transient heating events. Analyses of chondrule bulk compositions¹ suggest that several chemically discrete components were involved; one was rich in refractory lithophile elements and may have been derived from CAIs. The CAIs themselves also probably formed by high-temperature processes, some from



evaporative residues, others by condensation. The relationship between chondrules and CAIs is a long-standing puzzle: there are compound chondrules (made up of two chondrules stuck together) and there are compound CAIs, but until now there have been no known compound chondrule–CAI objects.

That is why the above chondrule from the Allende meteorite, described on page 723 of this issue² and pictured here about 40 times lifesize, is so important. For the first time we have a chondrule containing a relict (unmelted) precursor grain that appears to be a CAI fragment. The 200- μm grain is spinel (MgAl_2O_4) containing several refractory silicate inclusions (including Al- and Ti-rich pyroxene) and platinum-group metal nuggets; all of

group metal nuggets; all of these phases have compositions within the ranges of those in CAIs in other carbonaceous chondrites.

Although Ca, Al-rich chondrules have been described before³, including some possessing fractionated rare-earth-element patterns similar to those in CAIs^{4,5}, these objects preserve only the chemical signatures of their CAI precursors. The chondrule described by Misawa and Fujita² preserves part of the CAI itself.

Taken to a plausible extreme, the evidence suggests that after CAIs formed in the nebula, some were broken by collisions and entrained in nebular dust before chondrule formation. Flash-heating of such clumps produced chondrules; dust clumps containing a high mass fraction of CAI fragments formed Ca, Al-rich chondrules. In the present case, the heating event was mild enough that part of the CAI survived.

Alan E. Rubin

Alan E. Rubin is at the Institute of Geophysics and Planetary Physics, University of California, Los Angeles, California 90024, USA.

1. Grossman, J. N. & Wasson, J. T. *Geochim. cosmochim. Acta* **46**, 1081–1099 (1982).
2. Misawa, K. & Fujita, T. *Nature* **368**, 723–726 (1994).
3. Bischoff, A. & Keil, K. *Nature* **303**, 588–592 (1983).
4. Rubin, A. E. & Wasson, J. T. *Geochim. cosmochim. Acta* **51**, 1923–1937 (1987).
5. Misawa, K. & Nakamura, N. *Nature* **334**, 47–50 (1988).