

varieties of *A. majus*. The next, more difficult step, is to find out what it is that interacts with the altered sequence to modulate the gene expression.

Flower pigmentation obviously has a great advantage as a system for signalling gene expression; its self-indicating property makes unnecessary such complicated manoeuvres as fusing the gene under investigation to *Escherichia coli lacZ* and staining tissue preparations for β -galactosidase activity. The flower pigment is sufficiently cell-limited to indicate rather precisely the cells in which transcription of the pigmentation gene is switched on. We may expect soon to know

a good deal about the quantitative and developmental controls of both *pal* and *niv*, which are examples of unlinked genes whose activities are closely coordinated. Similar information may be expected on analogous systems in maize, where the genes *C₂* and *A₁*, homologous to *niv* and *pal*, respectively, exhibit a rich diversity of effects of inserted transposable elements, all documented in great detail by McClintock and now ripe for molecular analysis. □

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Host-parasite coevolution

The mite pockets of lizards

Michael J. Benton

THE study of parasite evolution, and in particular the coevolution of parasites and their hosts, is fraught with problems. The fossil record is patchy^{1,2} and it is hard to reconstruct the evolutionary story from living forms alone. An intriguing recently described example³, the case of chiggers and mite pockets in lizards, illustrates some of these problems and paradoxes.

Many lizards are infested by chiggers, the larvae of trombiculid mites, which feed on tissue fluid and cell debris. Surprisingly, lizards seem to go out of their way to attract the chiggers — they have special mite pockets that provide a protected, warm and humid site. In many cases, the skin of the lizard also has smaller scales than normal and a good blood supply in the pocket, which enables the parasites to feed more readily.

Arnold⁴ finds that chiggers are the most

common inhabitants of mite pockets, although ticks are occasionally found. The chigger is 0.25–0.5 mm long when it enters the pocket (see figure) and its size increases considerably after feeding on the host. It then drops to the ground where it metamorphoses into the adult form. Feeding involves the piercing of the skin and the injection of saliva through the stylostome, a tubular structure that develops in the skin of the host. The saliva causes cell breakdown and an increase in tissue fluid as a result of the inflammation reaction. The parasite may become fully engorged in a single day, or in a period of time of up to several weeks. Chiggers can cause severe damage to their hosts: lesions in the skin, allergic reactions to the saliva, secondary infection and transmission of disease organisms.

Mite pockets have been found in more

than 150 species and in 5 distinct families of lizard, which suggests that they have evolved independently many times. The pockets occur typically on the side of the neck, in the armpit region, high on the side of the chest, in the groin area and at the side of the base of the tail. Most species have pockets at only one location, but a few have two types of pockets. The pockets themselves range from slight folds in the skin to well-developed invaginations with a thick skin covering, often with reduced scales on the inside.

There are various models for the coevolution of parasites and their hosts. Brooks⁴ has divided the process in this context into two phenomena: co-accommodation, where parasite and host mutually adapt

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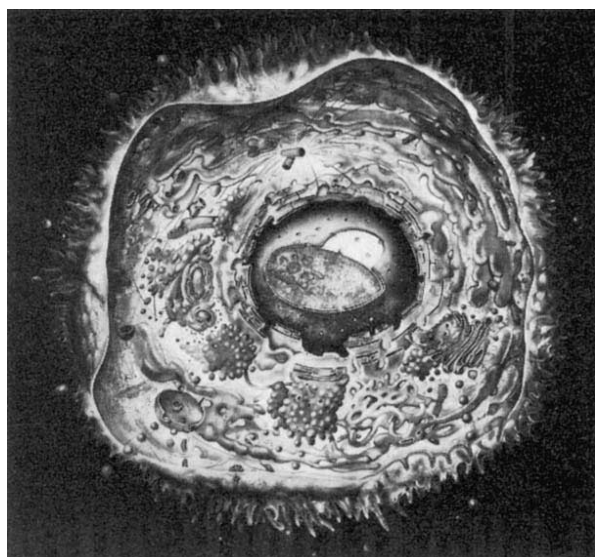
Chiggers in the axial mite pocket of the dwarf chameleon *Rhampholeon brevicandatus*. The hairy abdomens of the chiggers are about 0.5 mm in diameter (from ref. 3).

through time, and co-speciation, where a new parasite species arises either when speciation of the host occurs or when the parasite occupies a new host or takes on a new role in an old host. The relative importance of these two modes of host-parasite coevolution is not certain. In some groups, co-speciation seems to be the norm, particularly where parasites have specific host requirements and where co-accommodation is very narrow. If the host undergoes speciation, then the parasite probably speciates at the same time.

The chigger-lizard relationship seems to support another model of parasite-host coevolution in which co-speciation is of minor importance. Several ecologists⁵⁻⁸ argue that host-parasite relationships are largely the result of chance, analogous to the colonization of islands by free-living organisms. This approach suggests that the parasite load of any host is the result of a random 'first-come-first-served' process that depends on the rate of arrival of parasites and the rate at which they are rejected or die off.

Chiggers infest amphibians, birds and mammals as well as lizards; indeed, a single species of chigger can be found on members of three or four distinct host groups. *Trombicula (Eutrombicula) alfreddugesi*, for example, has been observed⁹ infesting 32 mammals, 52 birds, 39 reptiles and 3 amphibians. There is thus little evidence of close parasite-host specificity, nor of co-speciation. Chiggers seem to infest their

THE fascinating and complex world of the cell forms the basis of the newly opened Biochemistry Gallery at the Science Museum, South Kensington, London. The main attraction of the introductory exhibition *Cells, Molecules and Life* is a specially commissioned painting of the ultrastructural organization of the cell (right), the work of John Barber and Cynthia Clarke, which is linked to models illustrating various cellular processes. The gallery opened on 17 December 1986 and is sponsored by the Biochemical Society, now celebrating its 75th anniversary; over the coming years the feature will expand to cover much of the biochemical basis of life. □



vertebrate hosts effectively at random.

This case raises another evolutionary problem: why should so many species of lizards apparently create structures to attract chiggers? Arnold³ finds that lizards with mite pockets are more likely to be infested with chiggers than closely related forms that lack pockets. This is unsurprising from the chigger's point of view, but why do lizards develop such structures?

Arnold's survey excludes the idea that the association of the chiggers with the mite pockets is fortuitous. The pockets are not a direct response to chigger infestation either, as they occur in newly hatched, uninfested individuals. But chiggers do apparently have several direct effects on lizards, including thickening of the skin around the stylostome and movement of lymphoid cells to the vicinity.

Arnold's best explanation for the mite pockets is that they are a form of damage limitation for the lizards. The pockets provide optimum conditions for chiggers and infestations are concentrated locally. The problem is contained, avoiding large-scale

disruption of skin and superficial organs. The skin in the pockets is resilient and recovers rapidly after the chiggers drop out.

There are parallels in other organisms — many plants have specialized galls or clumps of hairs where mites feed, and these structures apparently prevent the mites from damaging the photosynthetic surfaces of the leaves. Nevertheless, these kinds of structures seem to be an odd response to parasitism, and the risk arises that the parasites will take advantage of the superior feeding stations to such an extent that the host is overwhelmed. □

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Geophysics

Mapping the mantle and core

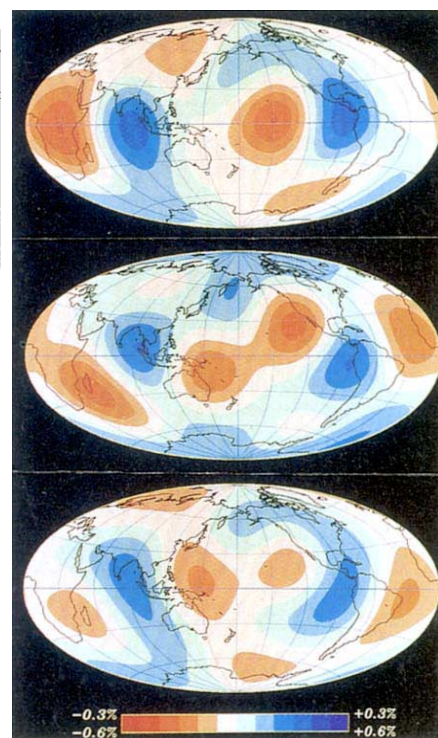
David Gubbins

It is common to talk of the effects of the plate tectonic revolution on geology; less so to speak of its effects on geophysics. It has left two obvious avenues of study open to the geophysicist interested in the study of the Earth's deep interior — either to view plate tectonics as a purely kinematic theory, describing only the convective motions of the Earth's mantle without addressing the question of why the plates move, and to try to supply a theory for the underlying dynamics of mantle convection; or to try to find new geophysical methods to map the deeper convective motions, again in a purely kinematic description. Several forthcoming papers, beginning with that by D. Giardini, Xiang-Dong Li and J.M. Woodhouse in this issue (*Nature* **325**, 405–411; 1987) suggest this latter approach is about to bear fruit.

The main tool for mapping the mantle is seismology. Seismic waves sample the elastic parameters, mainly the speed of compressional and shear waves, but also the density. However, a little knowledge of the properties of the material that constitutes the Earth's mantle and core can be used to convert seismic velocity into density and temperature provided the material is of uniform composition. Density, temperature and geoid (the equipotential surface of the Earth's gravitational field) anomalies can be combined with a model of mantle properties to determine the flow pattern, at least in principle (Hager, B.H. *et al.* *Nature* **313**, 541–545; 1985).

Adam Dziewonski (Harvard University) recently gave the Harold Jeffreys lecture to the Royal Astronomical Society. His theme was mapping the elastic parameters of the interior of the Earth — all the way from the central solid inner core to the surface — just as Jeffreys himself, with K.E. Bullen, had done almost 50 years ago. We can now map lateral changes in the elastic parameters, whereas Jeffreys was confined to a spherical Earth, layered like an onion. The long delay in progressing from the spherically symmetrical to the laterally varying model is a tribute to the careful work of Jeffreys and Bullen, and also an indication of just how difficult the extension has been.

Tomography, imaging of the interior of the Earth using seismic waves, should provide better information about shallow than deep regions, as earthquakes, the sources of the waves, are confined to shallow depths. Imaging the deep interior is like trying to look through frosted glass — the image is blurred by refraction in the glass. Seismic tomography attempts to remove the effects of the glass — the Earth's crust and lithosphere — using detailed models of the refractive index which has in turn been determined from tomography. The major pitfall is to map shallow structures into deep ones. Virtually all deep earthquakes occur in subducted plates, structures which exhibit the sharpest lateral temperature and consequent seismic velocity changes that exist anywhere in the



Three models of lower mantle structure of spherical harmonic degree 2 and 4. Top, P-velocity model V3 based on travel time residuals (± 0.3 per cent; Morelli and Dziewonski, 1986). Middle, P-velocity model based on splitting in free oscillation spectra (± 0.3 per cent; Giardini *et al.*, this issue). Bottom, S-velocity model based on SH waveforms (± 0.6 per cent; Woodhouse and Dziewonski, 1986).

Earth. This effect could dominate the true signal from the deep interior of the Earth, and the fear that this is the case has led many seismologists to be sceptical about the results from tomography.

In this issue, however, Giardini and colleagues present independent seismological evidence that is in broad agreement with the tomographic results. After a large earthquake the Earth rings like a bell. These elastic free oscillations have only been observed since 1960 but many of them have now been identified and their frequencies measured with great accuracy. Each frequency contains many modes, a degeneracy resulting from the spherical symmetry of the Earth analogous to the degeneracy of spectral lines from an atom. Departures from either spherical symmetry or isotropy will split the degeneracy and allow measurement of the fine structure of the spectrum. Observations of splitting are even more recent but can now be made routinely using the International Deployment of Accelerometers network of gravimeters run by the University of California at San Diego.

The new splitting measurements are directly sensitive to lateral heterogeneity and relatively insensitive to small-scale structure such as the subducted plates. It would be nice to report that Giardini *et al.* obtained the same solution for deep Earth structure from two quite distinct datasets,