Microbiology

Crossroads for archaebacteria

from D.P. Kelly

Two extraordinary new microorganisms are described as independent reports in this issue of *Nature*. They are extraordinary not only for living in hot acidic mud holes but also, and more importantly, for seeming to represent a crossroad in the evolution of archaebacteria — an ancient line of bacteria which is distinct from other bacteria (eubacteria) and eukaryotes.

Karl Stetter and his colleagues have obtained their archaebacterium from solfataric craters in Italy. As reported on page 787, it grows best at *p*H2 and at 90° C, but its outstanding claim on scientific attention is its ability to grow either as an aerobic autotroph, oxidizing sulphur with the production of sulphuric acid, or as an anaerobe, by the reduction of sulphur with hydrogen to hydrogen sulphide at very low redox potentials. Such metabolic versatility, alternatively oxidizing or reducing sulphur, has never before been reported or even thought to exist.

Many biologists are familiar with the activities of sulphate reducing bacteria (like *Desulfovibrio*) and sulphur-oxidizing bacteria (like *Thiobacillus*), the respective activities of which sustain a large part of the anaerobic and aerobic phases of the global sulphur cycle. While some enzymes and reactions in the reduction and oxidation of sulphur in these two types of bacteria are similar, the organisms themselves are physiologically, ecologically and phylogenetically very distinct from each other. In recent years, two seemingly distinct groups of thermophilic archaebacteria have been isolated from very hot natural environments. These are the extremely thermoacidophilic Sulfolobales, which can synthesize their organic requirements from inorganic precursors, obtaining energy from the aerobic oxidation of elemental sulphur even at *p*H 1.0, and the Thermoproteales, which grow at higher *p*H under anaerobic conditions and obtain energy from the oxidation of hydrogen coupled to the reduction of elemental sulphur to hydrogen sulphide. Although it has been reported that the anaerobic oxidation of sulphur is coupled to molybdate reduction in *Sulfolobus brierleyi*, it has not been considered that there might be any physiological 'overlap' between the activities of the sulphur-oxidizing *Sulfolobus* and the sulphur-reducing *Thermoproteus* species.

The isolation by Stetter's group of an organism that readily switches between such extremely different biochemical and physicochemical conditions for growth has many implications in biochemistry and phylogeny. By various means Stetter and his colleagues have proved that the switch is a phenotypic adaptation of the whole population and not a result of multiplication of selected individuals within the cultures. By the criterion of DNA hybridization, the genomes of cultures growing anaerobically and aerobically are identical but are not significantly similar to the genomes of conceivably related bacteria, such as *Sulfolobus brierleyi*.

If one takes the view that the evolutionary sequence was from anaerobic sulphur-reducing energy conservation (as seen in present day Thermoproteales) to aerobic sulphur-oxidizing processes (as in the Sulfolobales) following the appearance of the oxygen atmosphere, then the new organisms represent a relict of the branch point in evolution from which the two extant groups arose. The metabolic versatility and complexity of the newly discovered organism is such that it cannot be regarded as a metabolically 'primitive' ancestor of the modern day Sulfolobales. Indeed, it could well represent an evolutionary line from the Thermoproteales that is parallel to that of Sulfolobales.

The bacterium described by Wolfram Zillig and his colleagues on page 789 comes from a solfatara in Iceland which also yielded *Thermoproteus* in the enrichment cultures. It is similar to Stetter's, growing best at *p*H 2.5 and 85°C. The most exciting observation so far from this strain is that although its DNA-dependent RNA polymerases are identical whether it is growing aerobically or anaerobically, there are electrophoretic differences in the cellular proteins and a plasmid of 7,700 base pairs seems to be amplified five-fold during anaerobic sulphur-reducing growth.

The discovery of these remarkably versatile archaebacteria may thus have provided material not only for comparative biochemistry and phylogeny, but also for the development of a cloning vector to study information transfer and metabolic regulation in the Sulfolobales. □

D.P. Kelly is in the Department of Environmental Sciences, University of Warwick, Coventry CV4 7AL, UK.

Macroevolution

The Red Queen put to the test

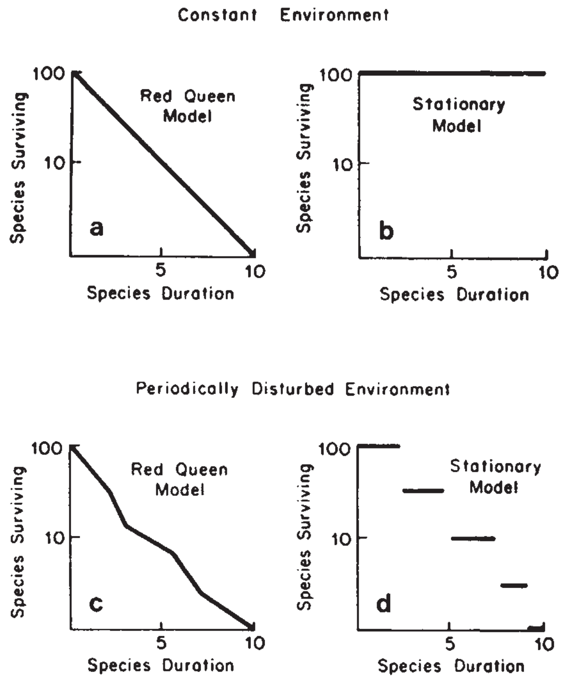
from Michael J. Benton

VAN Valen's Red Queen hypothesis[1] has attracted a great deal of interest since it was first proposed, and it has also been the subject of some controversy. Hitherto, discussions of the validity of the Red Queen have often been rather inconclusive because of the lack of an adequate test of the hypothesis. Now, Stenseth and Maynard Smith[2] have proposed a test, and two groups have already attempted to apply it[3,4].

The Red Queen hypothesis was based on the observation that, within any particular group of organisms, the probability of the extinction of any species or other taxon is constant through time (the Law of Constant Extinction). Thus, a species might disappear at any time, irrespective of how long that species has existed. Van Valen's explanation for this observation is that the various species within a community maintain constant relationships relative to each other, but that these interactions are constantly evolving. Thus, the antelope evolves greater speed in order to escape from the lion, but the lion evolves greater speed in order to catch its dinner, and so the status quo is maintained. Or, as the Red Queen put it in Lewis Carroll's *Through the Looking Glass*, "Now here, you see, it takes all the running you can do, to keep in the same place". Thus, species evolve continuously as a result of biotic interactions, and changes in the physical environment are not needed in order to propel evolution.

Several authors have questioned whether the Red Queen hypothesis is the only explanation of the Law of Constant Extinctions[5,6]. There certainly seems to be a paradox if we consider that organisms may be continuously evolving and adapting, yet this process does not improve their overall chances of survival: the probability of extinction is independent of the age of a species.

Stenseth and Maynard Smith[2] contrast the Red Queen model, in which evolution is driven principally by biotic interactions, with a Stationary model, in which evolution is driven mainly by abiotic factors (for example, climatic change, or topographic change). The Stationary model is probably in better accord with traditional assumptions about evolution, and it predicts that evolution will cease in the absence of changes in abiotic parameters. Translated into practical terms, the two models should give quite different patterns of species evolution, and Stenseth and Maynard Smith suggest that an examination of the fossil record might provide a resolution between the two. The Red Queen model predicts constant rates of speciation, extinction and phyletic evolution in ecosystems, even when they are at equilibrium diversity, whereas the Stationary model predicts zero rates of evolution at equilibrium, interrupted by bursts of evolution, extinction and speciation in response to changes in the physical environment (see top pair of figures).



Predictions of the Red Queen and Stationary models for species, survivorship in constant (a,b) and periodically-disturbed (c,d) environments. Modified from ref.3.

The main problem in applying the palaeontological test is to find an example in which no environmental change has occurred. Because such an example would be hard to demonstrate (if, indeed, one exists), Hoffman and Kitchell[3] have allowed for the effects of a periodically disturbed environment in their application of the test by modifying the simple predicted patterns (see bottom pair of figures). The patterns are still distinctive: the Red Queen model gives an approximately straight line, while the Stationary model gives a distinctly stepped pattern. Their test uses data from detailed sampling of microfossils (coccoliths, foraminifera, radiolaria, diatoms, and others) from 111 deep-sea boreholes that sample the past 50 million years of sediments on the Pacific sea floor. The simple speciation and extinction curves obtained from these data are more or less smooth, rather than stepped, and so seem to support the Red Queen. An analysis of the cumulative appearance of new species also gives general support to the Red Queen although there is some evidence of stepping.

Further analysis shows there to be considerable variation in the probability of extinction over geological time: for example, there seem to have been particular periods in which all the microfossil groups had high extinction rates. These indicate plankton extinction events which would normally be attributed to sharp changes in the environment. When Hoffman and Kitchell make allowance for these events, the various analyses again point to the validity of the Red Queen model. On the other hand, Wei and Kennett[4], who have also used the planktonic record as a test, regard their own results as weak evidence for the Stationary model. Over the past 22 Myr, the diversity of planktonic organisations has changed sharply at times that correspond to evironmental changes.

There are, however, several problems in applying these kinds of test. One problem concerns the difficulty of separating biotic from abiotic factors in order to assess their relative significance: it is probably impossible to pigeonhole both kinds of phenomena as independent factors. Second, in many real situations the test would be inconclusive. For example, it would be hard to distinguish the two predicted patterns if both curves were stepped as a result of rapid changes in the physical environment. At the other extreme, continuous small changes in environmental conditions might give similar gently sloping graphs for both models. Another problem concerns the assumption that species diversity reaches an equilibrium level, where speciation rate equals extinction rate. The possibility of non-equilibrium models also has to be considered.

The debate between the two models should not be confused with that between gradualism and punctuated equilibrium. The Red Queen hypothesis is often seen as a gradualist interpretation of evolution, but neither viewpoint implies the other. The question of whether evolution is driven mainly by biotic interactions or by the physical environment is of great importance to all evolutionists and we may hope to see a great deal of palaeontological work in the next few years that addresses this problem. It is important to know if the Red Queen or the Stationary model has generality in all kinds of situations, or whether one model prevails in particular groups or in particular kinds of environments. Let us hope that palaeontological data are better suited to testing these two models than they have been for distinguishing gradualism from punctuated equilibrium. □

1. Van Valen, L. *Evol. Theory* **1**, 1 (1973).
2. Stenseth, N.C. & Maynard Smith, J. *Evolution* **38**, 870 (1984).
3. Hoffman, A. & Kitchell, J.A. *Paleobiology* **10**, 9 (1984).
4. Wei, K-Y. & Kennett, J.P. *Paleobiology* (in the press).
5. McCune, A.R. *Evolution* **36**, 610 (1982).
6. Krimbas, C.B. *Evol. Biol.* **17** (in the press).

Michael J. Benton is in the Department of Geology, The Queen's University of Belfast, Belfast, BT7 1NN, Northern Ireland.

Planetary science

Volcanic sulphur flows on Io

from Michael H. Carr

ON PAGE 778 of this issue, J.A. Naranjo describes the flow of molten sulphur at Lastarria volcanco in Chile[1] and sulphur flow on the flanks of Mauna Loa in Hawaii has also recently been described[2]. Although it is common to find sulphur in volcanic fumes, sulphur flows are rare on Earth and are of special interest for understanding volcanic activity on Io, innermost of Jupiter's four large satellites. Sulphur seems to play a prominent role in the intense volcanic activity of Io, but precisely how prominent is the subject of current debate.

Io is by far the most volcanically-active body in the Solar System. Its largest volcano, Loki, has been dissipating energy at a rate of over 10^{13} watts over the past few years[3], equivalent to the Earth's total rate of loss of heat. Tidal energy drives Io's volcanism. Because of a resonance of its orbital motions with those of the other large jovian satellites, Io has an eccentric orbit, which results in changes in the sizes of the tides raised on its surface. The theory that this continuous flexure generates frictional heat, which could drive volcanism, was suggested just before the discovery of Io's volcanism during the Voyager encounters[4]. The original suggestion was that all the tidal energy is dissipated within a thin elastic lithosphere, but it now seems that significant amounts of the energy are dissipated by visco-elastic deformation below the rigid lithosphere. Part of the generated heat is conducted outward through the crust but most is carried to the surface in molten rock.

A controversial issue is the relative role of sulphur and silicates in Io's volcanism. Shortly after the Voyager encounters, two models were put forward. In one, it was suggested that the surface is covered with a largely molten layer of sulphur, some kilometres thick, resting on a silicate subcrust, which is visible only as occasional high mountains[5]. In this model, almost all the flows and volcanic constructs are composed of sulphur. In the alternative model, both silicate and sulphur volcanism occur, and the surface consists of interbedded sulphur and silicates[6].

Why, despite recognizing the strong likelihood of some form of sulphur volcanism on Io, did the group who suggested the second model doubt that the satellite's surface is composed entirely of sulphur? After all, sulphur has been detected in the trail of neutral and ionized particles that Io leaves behind in its orbit; sulphur dioxide