Palaeontology

New fossil finds in old rocks

from S. M. Awramik

THE well-preserved stromatolites from 3,300–3,500-Myr-old rocks in South Africa described on page 489 of this issue[1] are not the first report of stromatolites from the Early Archaean, but these structures are by far the best preserved and morphologically convincing examples of such stromatolites that can be interpreted as microbial in origin. This discovery reinforces the notion[2,3] that the Earth's earliest biota was much more advanced morphologically, and presumably metabolically, than has previously been thought.

Dealing with Archaean fossils is a tricky business. First, you have to convince the scientific community that the objects in question are really fossils; then demonstrate that the rocks in which the fossils were found are of the proposed Archaean age; and finally show that the fossils were coeval with the rocks. With almost every claim for the discovery of an Archaean fossil there are counterclaims proposing alternative non-biological origins, or that the rock or fossil in question is not of Archaean age[4]. Such prudence is justifiable because, in addition to extending the known record of life, Archaean fossils provide information on the diversity and relative abundance of early life, and lead to interpretations of metabolic characteristics and affinities of the microbes concerned. They also have significant bearing on evolutionary models that include the origins of life, its early diversification, phylogenetic relationships, rates of evolution and evolutionary events leading to the appearance of eukaryotes, animals and plants.

The general model for the early history of life used to be one of sluggishly evolving prokaryotes that took some 2,000 Myr to reach the eukaryotic grade and another 800 Myr before the animal level of organization evolved. The picture of life on the early Earth has become sharper in recent years as a result of important discoveries of fossils in the Early Archaean, 3,800–3,400 Myr ago. These discoveries have been made mainly in two regions: the Pilbara Block in Western Australia; and the Barberton Mountain Land in South Africa, areas that have excellent exposures of the oldest known relatively unmetamorphosed sedimentary rocks.

In rocks from the Swaziland Supergroup in the Barberton Mountain Land, solitary spheroidal microfossils, several micrometres across, that are interpreted as bacteria, have been detected in chert[5,6]. Although these are currently regarded as 'dubiofossils', because there are doubts about their cellular microbial origin[7], they were headline news in the 1960s as they extended the first appearance of life by more than 1,000 Myr. Such small roundish microfossils were what most scientists would have predicted the Earth's oldest cells should have looked like. More convincing reports of spheroidal microfossils[8] and the discovery of paired cells in the South African rocks soon followed[9]. The dyads suggested that these prokaryotes reproduced by binary fission and they made a stronger case for the biogenicity of the microfossils.

In 1980, two reports appeared[10,11] on the discovery of stromatolites in the 3,400–3,500-Myr-old Warrawoona Group sediments from the Pilbara Block. Stromatolites present a very different picture when reconstructing the Early Archaean biosphere. They suggest more advanced microbial life. Stromatolites are conventionally viewed as biosedimentary structures produced by communities of photoresponsive microbes that trap and bind sediment. At times, these microbes can generate layered domed and columnar structures centimetres to metres in size. Cyanobacteria (in particular filamentous cyanobacteria) and microbes that behave like cyanobacteria, are the dominant stromatolite builders today and were probably responsible for most fossil stromatolites. We do not know whether cyanobacteria existed in the Early Archaean but the stromatolites imply that proto-cyanobacteria, cyanobacteria-like microbes or some other prokaryote with stromatolite-building capabilities had already evolved the ability to live in shallow, agitated waters and cope with sediment and sunlight.

It is not surprising that the biological nature of the Warrawoona stromatolites has been questioned[12,13]. Their morphology is simple, evaporites are associated with them and no microbial fossils were detected in their laminae. The growth of the evaporite minerals could have produced the simple doming. But this also occurs in modern evaporitic mat environments, where the shape of microbial mats (incipient stromatolites) is modified by the growth of evaporites.

Independent support for a microbial origin comes from the discovery of filamentous microbial fossils in Warrawoona chert[3]. Tubular fossil filaments suggest that the sheathed filamentous habit of prokaryotes, a highly successful stromatolite-building characteristic, has already evolved by the latter part of the Early Archaean. Unfortunately, these microfossils were not found in domed stromatolites. In summary, although the evidence is strong, the jury is still out on the biogenicity of the Warrawoona stromatolites.

The focus for the oldest remains of life on Earth now returns to South Africa, to the Swaziland Supergroup, where the lowest part, the Onverwacht Group, is approximately the same age as the Warrawoona Group. Members of the research team at Louisiana State University that discovered stromatolites in the Warrawoona[10] and microfossils in the Onverwacht[14] now describe morphologically complex, biogenically convincing stromatolites from the Fig Tree Group, another part of the Swaziland Supergroup[1]. These stromatolites are significant partly because their morphology is much more complex than the simple dome shapes found in the Warrawoona. The complex pseudocolumnar shape, good preservation, mode of occurrence, well-defined laminae and laminar microstructure are a combination of features that are difficult to explain by abiogenic processes. The closest abiogenic analogue would be geyserite. Furthermore, they are strikingly similar to other less ancient stromatolites, including early Proterozoic (2,500–1,600 Myr) biogenic stromatolites from the Gunflint Iron Formation and superficially similar to some modern non-marine cyanobacterial stromatolites. Combined with all the microbial fossil and organic geochemical data from the Early Archaean, the discovery adds to an impressive array of palaeobiological information on the biosphere of the early Earth.

It is unfortunate that stromatolites have played a relatively minor part in unravelling the early history of life. In many ways, the presence of stromatolites in such ancient rocks as the Swaziland Supergroup can reveal more about the degree of microbial evolution than microbial fossils preserved in chert, the common palaeobiological standard for the level of evolution in the Precambrian. Early Archaean stromatolites have interesting, if highly speculative, implications for the microorganisms that built them. First, as early as 3,500 Myr ago, microbes must have evolved that were benthic through-

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out most or all of their life cycle and were either fast-growing or motile — otherwise they could not have maintained their position at or near the sediment/fluid interface and would have been buried. A positive photoresponsive behaviour would enhance this ability, and presumably the microbes were photoautotrophic. Second, because the stromatolites formed in very shallow waters, they must have had some minimum resistance to high-energy solar radiation and finally, it is probable that some of the builders were filamentous forms with sheaths around the trichomes.

No longer can the evolutionary history of Precambrian life be viewed as slowly changing microbial biota that gradually increased in diversity and complexity until the appearance of eukaryotes. The Swaziland stromatolites and the other Archaean fossil data indicate that by 3,300–3,500 Myr ago, diverse microbial life existed on Earth, some of which was organized into microbial ecosystems. Once life appeared on the early Earth, it diversified rapidly and in all probability explored and occupied most if not all habitable ecological zones. □

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Developmental genes

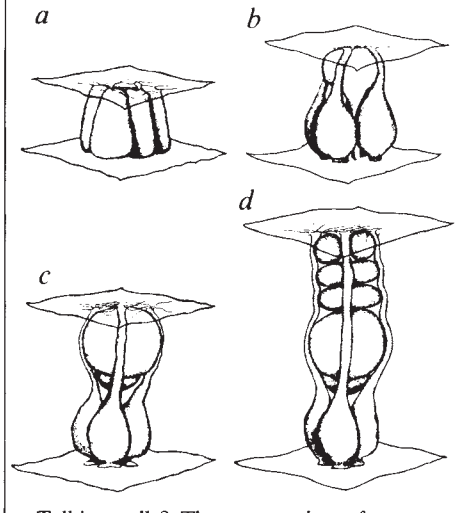
Mediators of cell communication?

from Michael Akam

THE control of development operates at many different levels. In recent months this has become easy to forget, with the nucleus the focus of attention and the DNA-binding properties of the homoeo box taking much of the limelight. Now the sequencing of two other 'controlling' genes, one from insects and the other from nematodes, has revealed homology with mammalian proteins of very different function. The *lin-12* gene of *Caenorhabditis*, which controls patterns of cell lineage[1], and the *Notch* gene of *Drosophila*, which plays a role in the early development of the nervous system[2], both encode proteins homologous with epidermal growth factor (EGF) and the structurally related family of mammalian proteins. Other members of this family are all membrane-bound or secreted proteins, suggesting that *Notch* and *lin-12* act at or beyond the cell membrane, perhaps to mediate cell communication.

The family of EGF-related proteins all share a characteristic cysteine-rich peptide of 40 – 50 amino acids. This sequence occurs nine times in the membrane-bound precursor of EGF; the terminal copy of the repeat, cleaved from the precursor, is the EGF peptide itself[3]. The *Notch* and *lin-12* genes also encode multiple copies of this peptide motif. The complete structure of the lin-12 protein is not yet clear, but I. Greenwald[1] finds eleven copies of the EGF motif within the four exons that have been sequenced. *Notch* seems to encode an enormous protein of some 2,700 amino acids in a 10.5-kilobase-long transcript. K. Wharton and colleagues[2] have sequenced all but a few hundred bases of this transcript from overlapping complementary DNA clones. In the amino-terminal half of the derived protein they predict 36 tandem repeats of a 40-amino-acid motif that shares the conserved cysteine spacing of EGF, and shows limited homology at other sites within the repeat. This region is followed by a putative transmembrane sequence of hydrophobic amino acids, followed by a large carboxy-terminal region which, except for a polyglutamine stretch, bears no close homology with other known proteins.

The structure of the Notch protein predicted by this sequence, which includes an extracellular EGF-like domain, resembles that of the membrane-bound protein in the EGF family, for example, the low-density lipoprotein (LDL) receptor and the precursors of several growth hormones (EGF, tumour growth factor and vaccinia virus growth factor). But the EGF family also includes secreted proteins with diverse functions, including the blood-clotting factors urokinase and plasminogen activator. The role of the EGF domain within these secreted proteins is not known.



Talking cells? The segregation of neuroblasts is an early step in the formation of the insect nervous system, in this case the grasshopper, and one which requires adjacent cells to communicate. The *Notch* mutations of *Drosophila* disrupt this process (see text). In insects, neuroblasts segregate from a sheet of apparently equivalent cells in the embryonic ectoderm (*a*). The first sign that a cell will become a neuroblast is the dorsal shift of its nucleus and cell body towards the interior of the embryo (*b*). Several cells in each region may initiate this process but only a single cell completes it. This cell will undergo the characterisitic pattern of divisions which generate neurones (*c,d*). (Redrawn from ref. 9.)

At first sight, the effects of *lin-12* and *Notch* mutations have little in common with one another or with the functions of the EGF protein family. The *lin-12* mutations cause losses and duplications of a range of structures in the animal, which result from alterations in the normally precise control of cell lineage during embryogenesis[4]. Recessive lethal *Notch* mutations (which cause notching in the adult wing when heterozygous) result in overgrowth of the nervous system in embryos[5]. There are, however, close parallels in the cellular phenomena underlying these different phenotypes. Both mutations alter the way in which equivalent cells choose between alternative developmental pathways. In both cases the decisions affected may depend on local interactions between neighbouring cells.

A functioning *lin-12* gene is needed for the normal development of several groups of cells during embryogenesis and maturation of *Caenorhabditis*. Cells of each affected group are characterized by analogous positions in the cell-lineage tree. In normal development, cells within each of these groups adopt two or more different fates (say A and B), each fate being defined by subsequent patterns of cell division and differentiation. When the *lin-12* gene does not function, all cells within a group are forced to adopt the same fate (fate A), or a subset of their normal fates. However, when mutation results in overexpression of the *lin-12* gene, all cells of the group are forced to adopt the alternative fate (B). Thus mutations that modulate *lin-12* activity switch the development of cells in a way that parallels the choices made during normal development. This suggested that the role of the *lin-12* gene in normal development was analogous to that of the homoeotic selector genes in *Drosophila*[6].

Several experiments where individual cells are killed show that the groups of cells affected by *lin-12* have the special properties of 'equivalence groups'[7]. In such a group, all cells seem to have the same intrinsic developmental potential; the fate adopted by each cell is specified by its location and by the interactions it makes with neighbours. One of the possible fates of a cell in an equivalence group is usually dominant; when a cell that will fulfill the dominant fate is killed, another member of the group alters its own behaviour to replace the dead cell.