THE ROYAL
SOCIETY

Life: past, present and future

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Molecular methods of taxonomy and phylogeny have changed the way in which life on earth is viewed; they have allowed us to transition from a eukaryote-centric (five-kingdoms) view of the planet to one that is peculiarly prokarote-centric, containing three kingdoms, two of which are prokaryotic unicells. These prokaryotes are distinguished from their eukaryotic counterparts by their toughness, tenacity and metabolic diversity. Realization of these features has, in many ways, changed the way we feel about life on earth, about the nature of life past and about the possibility of finding life elsewhere. In essence, the limits of life on this planet have expanded to such a degree that our thoughts of both past and future life have been altered. The abilities of prokaryotes to withstand many extreme conditions has led to the term extremophiles, used to describe the organisms that thrive under conditions thought just a few years ago, to be inconsistent with life. Perhaps the most extensive adaptation to extreme conditions, however, is represented by the ability of many bacteria to survive nutrient conditions not compatible with eukaryotic life. Prokaryotes have evolved to use nearly every redox couple that is in abundance on earth, filling the metabolic niches left behind by the oxygen-using, carbon-eating eukaryotes. This metabolic plasticity leads to a common feature in physically stratified environments of layered microbial communities, chemical indicators of the metabolic diversity of the prokaryotes. Such 'metabolic extremophily' forms a backdrop by which we can view the energy flow of life on this planet, think about what the evolutionary past of the planet might have been, and plan ways to look for life elsewhere, using the knowledge of energy flow on earth.

Keywords: biosignature; metabolic evolution; extremophile; metabolic taxonomy; bioenergetics; life detection

1. INTRODUCTION

When invited to contribute to the millennium issue of these *Transactions*, we took it as a challenge to discuss life as it relates to our mission at the Jet Propulsion Laboratory—the connection between life and planetary geochemistry, the interaction between these two forces and the patterns of evolution seen in both. Thus, the ideas that follow may seem somewhat non-conformist: they are meant to stimulate thought and draw reactions rather than to be given truths. The arrival of a new millennium seems a good time for such things; some day we will know if any of the rather simple ideas expressed here had enough merit to stand the test of time, or merely served to stimulate the establishment and the testing of more sophisticated and, perhaps, more useful hypotheses.

Much of the thinking put forward here has been strongly impacted by the fact that during the past two years we have begun a programme to develop methods for life detection. The basic approach we have chosen for this endeavour involves several factors:

(i) the definition of life in measurable terms;
(ii) the development of non-earth-centric biosignatures based on our definition;
(iii) the laboratory fabrication and testing of strategies and instrumentation for life detection;
(iv) field testing of the same methods in extreme environments on earth.

One of the authors (K.H.N.) has spent nearly 30 years studying microbial life in the oceans, lakes, rivers and sediments, in many cases dealing with what can be called extremophilic micro-organisms (e.g. organisms that can tolerate and even prosper in environments regarded as extreme or hostile). An example of such an organism is shown in figure 1, a bacterium called *Shewanella oneidensis* (also known as *Shewanella putrefaciens*). This bacterium, in the absence of oxygen can use a number of 'substitutes' for its respiration (Nealson & Saffarini 1994), including manganese oxide, the solid substrate on which it resides in figure 1. Such a lifestyle would have been regarded as impossible just a few years ago, but is now known to be widespread in low-oxygen environments on earth. This illustrates the key concept that even here on earth, diverse survival mechanisms can be found, and should serve as guideposts for the search for life in extraterrestrial sites (Nealson 1997*b*, 1999). The second author (P.G.C.) has a long-standing interest in the relationships between geochemistry, earth evolution and biology, with specific interest in the relationship between the evolution of the planet and the corresponding coevolution of the biota. With this perspective in mind, we will focus on a new view of life—the relationship between energy flow, minerals and microbes—and introduce the readers of this article to

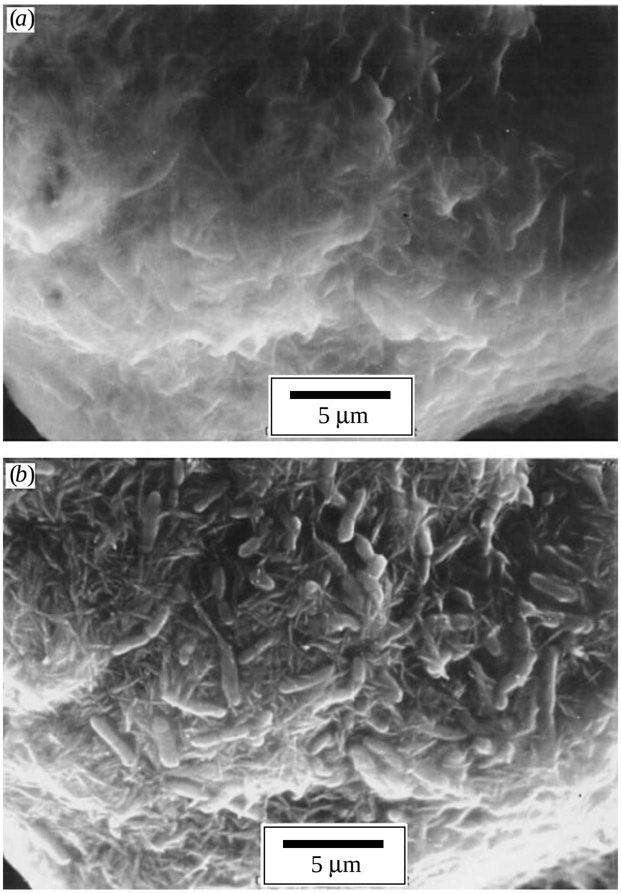

Figure 1. Life in extreme conditions: respiration of rocks. This figure shows the dissimilatory metal reducing bacteria *Shewanella oneidensis* (also known as *Shewanella putrefaciens*) growing under anaerobic conditions. In the absence of molecular oxygen, this bacteria can use either iron oxides or manganese oxides as 'oxygen substitutes' for respiration. It attaches to such oxides, uses them as its respiratory oxidant, eventually dissolving the oxides and producing reduced metals (ferrous or manganous ions) in solution: (*a*) taken with an environmental scanning electron microscope shows what the organism looks like in nature—a particle of metal oxide coated with bacteria that are invisible because of the polysaccharide film produced by the bacteria. (*b*) Taken at the same magnification, but with a high vacuum scanning electron microscope, the bacteria and the metal oxide on which it sits are clearly visible. This image shows the intimate contact between the respiring bacteria and their metal oxidants. Such processes are common in sediments around the world.

the geobiological relationships that may be essential to discovering signals of life off of earth (Banfield & Nealson 1997).

The discussion of past and present life will deal with our own planet. We have some sense of life past; we can read the subtle signs from earth's earliest living days, and follow the effects of life on the planet as it prospered, evolved and moved inexorably towards the present-day biology that we feel (probably incorrectly) we understand reasonably well. In contrast, discussion of the future deals with issues of earthly life moving off our planet as well as the issues of the probabilities and consequences of detecting life in extraterrestrial sites. To attempt to reconstruct some features of past life, or predict those of future life, we will begin with a consideration of present-day life and work in both directions. We will deal here neither with the origin of life nor of its earliest forms. Rather, we will be content to confront the issues surrounding early cellular life: what it may have been like, the problems it faced and a scenario for the evolution of life to the present state. The basic question is whether, by looking at present-day life and the fossil record of the planet, we can recreate a logical flow of events that leads to and is consistent with, today's life. And, if so, does this exercise provide us with insights as to what life might look like in non-earth environments? That is, 'What can we learn from the study of earthly life (both past and present) that will allow us to frame the search for extraterrestrial life properly, to assure that we don't do the unthinkable and miss extraterrestrial life when we encounter it?'

2. PRESENT-DAY LIFE

We begin with the most difficult part of the work, the definition of life. The definition must be sufficiently broad that it would encompass all life with which we are familiar, including life found in extreme environments. It should be sufficiently general that, with it, we would also not miss life that might be fundamentally different from earthly life. The definition must also include properties that are measurable—if it is not measurable we are not interested! With regard to this issue, we hearken back to the words of Lord Kelvin: 'When you can measure what you are speaking about and express it in numbers, you know something about it; but when you cannot express it in numbers, your knowledge is meagre and unsatisfactory; it may be the beginning of knowledge, but you have scarcely advanced to the state of science' (Kelvin 1994). With these caveats in mind, we offer the following.

(i) Life has some structure. It is a machine designed to convert physical or chemical energy to a biologically useful form—to accomplish this end, some kind of 'hardware' for energy conversion is needed (e.g. life has structure).
(ii) Life has unique chemistry associated with its structure. For earthly life, this is a carbon-based chemistry with an elemental ratio that is easily recognizable and distinguishable from the earth's crustal abundance, and from minerals and concretions of abiotic origin.
(iii) Life strives to replicate with fidelity. Copies of complex structures and the molecules that comprise them are made routinely as a part of the life process, and in fact are part of the definition of success of any given group of biota. We proceed from a few copies of many different molecules to many copies of (often very complex) molecules of life.
(iv) Life evolves. Life makes a sufficient number of mistakes during replication that some variability is built into the system, thus allowing for biological evolution of chemistry, structure and behaviour.
(v) Life consumes energy from the environment, using the energy to make the complex chemical structures of which it is composed. It also creates metabolic products as a result of the energy consumption. In many cases, it is possible to recognize life by gradients of reactants and products produced during growth and metabolism, which can be found in the fossil record.

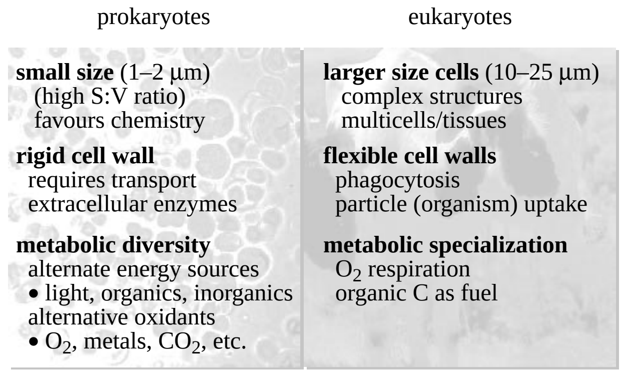

Figure 2. Key properties of prokaryotes and eukaryotes. This figure is meant to point out some fundamental features of the two major forms of life, which may play key roles in dictating the ecological roles and evolution of these groups of organisms. The prokaryotic properties of small size, rigid cell walls and high metabolic diversity all tend to maximize the ability of prokaryotes to do chemistry and compete for chemical niches. Along with this may be a push to remain small, maintaining the 'chemical advantage'. The eukaryotes, on the other hand, have become complex and large, using their ability to uptake large particles and organism fragments to develop many food-gathering strategies. Clearly becoming larger has its advantages for this lifestyle. However, becoming large requires extra energy, and the optimization to an oxygen-requiring respiratory system is consistent with the energy needs of the eukaryotes, even the single-celled organisms.

(vi) Life must develop some means for escaping from its own metabolic end-products. Perhaps one of the first innovations of life would thus be motility, although as life becomes abundant, specific symbioses may be used to achieve the same ends.

(a) *The nature and classification of life on earth*

Today we have a wide array of life forms that are, for the sake of convenience and order, separated into two major groups, the prokaryotes and the eukaryotes (figure 2). Prokaryotic cells are simple and usually small, with few or no intracellular structures, no nuclear membrane surrounding the genetic material (DNA) and (often) rigid cell walls. In contrast, eukaryotic cells are large and complex, with intracellular structures, a nucleus (surrounded by a nuclear membrane) containing two copies of each chromosome and (for the animals) usually non-rigid cell walls. In addition to these cellular distinctions, prokaryotes are primarily unicellular, while eukaryotes can be either unicellular (algae and protists) or multicellular, with complex structures and behavioural features. For the most part, eukaryotes use organic carbon as an energy source and have an oxygen-based respiratory metabolism. Prokaryotes, on the other hand have a great diversity of both energy sources (organic and inorganic) and respiratory oxidants, surviving well in the absence of oxygen and using a wide array of oxygen 'substitutes' for respiration (Gottschalk 1994; Schlegel 1993; Nealson 1977*a*).

Let us look at some of the key prokaryotic properties (figure 2). The prokaryotes are small; they have optimized their surface-to-volume ratio so as to maximize chemistry. On average, for the same amount of biomass, a prokaryote may have 10–100 times more surface area. As a consequence, in environments such as lakes and oceans, where prokaryotes comprise about 50% of the total biomass, they account for 91–99% of the active surface area, and in oxygen-poor (suboxic or anoxic) environments, where the biomass is primarily prokaryotic, the active surface areas are virtually entirely prokaryotic. In essence, if you want to know about environmental chemistry, you must look to the prokaryotes!

The rigidity of prokaryotic cell walls precludes the uptake of large particles and, thus, life as predators. Because they are capable of synthesis of virtually all their own essential vitamins and amino acids, the prokaryotes are excellent prey for the predatory single-celled eukaryotes (protists called flagellates and ciliates), but they are not predators themselves. Instead, they are restricted to life as chemists, and do their metabolism via transport and chemistry. They excrete extracellular enzymes, reduce polymers to monomers and transport the soluble substrates across their membranes. This is in marked contrast to the eukaryotes, which are capable of engulfing (by a process called phagocytosis) other cells, and thus engaging in one of the primary processes of what we think of as biology (e.g. food gathering, foraging or predation). In essence, the prokaryotes spurn life as biologists while optimizing their skills as chemists. The full effect of such evolution is now easily seen in the genomic analyses of prokaryotes, where, in general, high percentages of the identifiable genes are involved with membrane and transport processes. In many cases, up to 25% or more of the total genome deals with the interface between the cell surface and the environment and is involved with uptake, transport or metabolism of environmental chemicals (see the Institute of Genome Research (TIGR) Web site for more information: www.tigr.org/index.html). In eukaryotes on the other hand, much of the DNA is devoted to the more biological concerns, such as regulation, development and cell and organism differentiation.

Finally, the prokaryotes are metabolically very diverse; they are able to use almost any energetically useful chemical energy that is abundant on earth. Evolution and competition have undoubtedly driven these ingenious chemists to develop methods for harvesting virtually every worthwhile corner of the chemical market, including both organic and inorganic energy sources of nearly all kinds. Let us look, for example, at some of the sources of chemical energy available on earth today (figure 3). On the left one sees the energy sources, ranked from the most energy rich at the top to the least energy rich on the bottom. On the right are the oxidants that can be used to 'burn' these fuels, with the best oxidant (oxygen) at the bottom, and the worst one (carbon dioxide) towards the top. Since a fuel needs to be 'burned' to yield energy, we can estimate the amount of energy available simply by connecting a given fuel with an oxidant (these combinations of fuels with oxidants are called redox pairs). If the arrow connecting any redox pair slopes downwards, it indicates that energy is available from this combination, and there is almost certain to be one or more micro-organisms capable of using it. In marked contrast, the eukaryotes use only a few organic carbon compounds as fuels and only molecular oxygen as

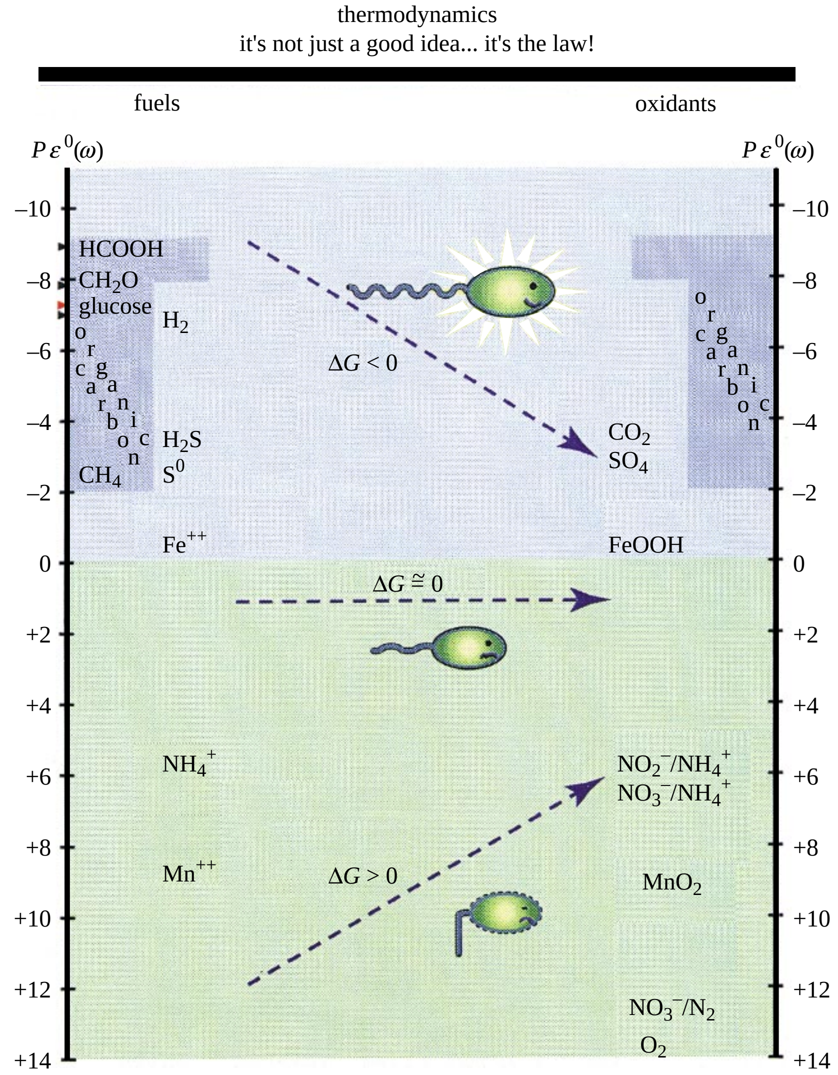

Figure 3. Thermodynamics applied to planetary life. In this diagram, we have illustrated many of the major energetic redox processes that occur on earth in terms of relative energy. On the left are sources of energy: organic chemical or inorganic chemical energy. These are arranged from the most energetic (most reducing) at the top to the least energetic (most oxidizing) at the bottom. On the right side, the oxidants that can be used to burn these fuels are arranged in the same order, with the strongest oxidant (molecular oxygen) at the bottom, and the others in decreasing oxidative strength as one proceeds upwards. If an arrow drawn from a fuel to an oxidant has a negative slope then the reaction will yield energy (and an organism that uses this energy will probably exist).

the oxidant—they sacrifice metabolic diversity for high-energy yield, while the prokaryotes occupy the diverse, lower energy habitats, often recycling the metabolic waste products of the eukaryotes. Such a scheme is consistent with the fact that the prokaryotes dominated the earth for the first two to three billion years, honing their skills as environmental chemists (see below). Indeed, the diversity of prokaryotic metabolism, undoubtedly developed in the past in much less hospitable environments, has resulted in ecologically predictable and stable ecosystems, even to this day.

With regard to our view of the nature of life on earth, major changes have occurred in the past two decades. We have moved from a peculiarly eukaryote-centric view of life to one that openly admits that the small, single-celled creatures that were once ignored play a vitally important role in the metabolism of our planet. The traditional view of life that most of us were taught is commonly referred to as the 'five kingdoms' (figure 4). This model was a logical consequence of the taxonomic system derived by the work of Linnaeus and others in the mid-1700s. This classification scheme relied on observation of the visible features of organisms to give each a name (e.g. *Homo sapiens* for humans), and to group organisms of similar appearance together. The diagram is called a phylogenetic tree; these trees are used to illustrate the evolutionary relationships that may exist among extant (and even fossil) organisms (e.g. to answer the question of which organisms preceded which in time).

Largely because of the nature of the tools then available (human eye, hand lens and, later, simple microscope), it is not surprising that phylogenetic trees were dominated by the macroscopic, multicellular eukaryotes such as the fungi, plants and animals. The tiny eukaryotic protists (amoebae, paramecia, giardia, etc.) being visible but not understood, were relegated to the next-to-the-bottom position in the tree, while the microscopic prokaryotes (also called Monera or Bacteria) were placed at the bottom where they could be acknowledged, although not seriously so. This entire approach was reasonable and useful at the time, in the sense that structural diversity was driving classification, and the single-celled, anucleate prokaryotes have little that could be easily compared with the structurally and behaviourally diverse larger eukaryotic organisms.

This organizational scheme of the biosphere has dramatically changed in the past 15 years with the advent of molecular taxonomy and phylogeny. The basic idea behind this approach is that there are some molecules common to all earthly life, and that by systematic comparison of the sequences of these molecules, it should be possible to derive the taxonomic, and even phylogenetic, relationships

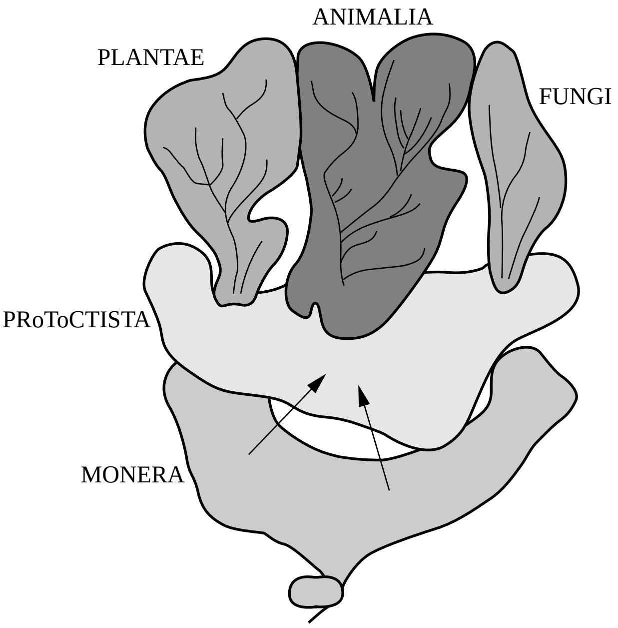

Figure 4. The classical five kingdoms of life. This view of the distribution of life shows in diagrammatic form the major groups of organisms as they were viewed for many decades. The plants, animals and fungi represent the three major kingdoms, with the protists or protoctists (amoebae, Protozoa, slime moulds, etc.) forming a diffuse group below them, and the monera or bacteria. The diagram is meant to convey not only the division of organisms into major taxonomic groups, but some sense of the way in which evolution occurred, from smaller to larger, and from simpler to more complex.

between the organisms that contain them. In effect, the myriad of structures used for taxonomy is replaced by a single, universally distributed molecule whose molecular sequence is used for comparison. Molecular phylogeny has used, up until now, primarily the 16S rRNA, a slowly evolving molecule common to nearly all life on earth, and at the time of writing, there are many thousands of sequences in the international ribosomal data base (RDB). While the germ of this idea is actually decades old, it came to fruition only recently with the development of new techniques in sequencing of nucleic acids, and the use of this information for organismal comparisons (Woese 1987, 1994; Amann *et al.* 1994). From the point of view of the prokaryotes, which lack features that can be used to compare them to each other or to the eukaryotes, this molecular methodology allowed one, for the first time, to have a sense of the phylogeny (a natural history which had been previously lacking) of the various groups (Stahl 1993; Olsen *et al.* 1994). It also allowed direct comparison (on the same scale) of the phylogeny of prokaryotes with that of their eukaryotic counterparts—organisms that may be related only through their chemical (metabolic) roots.

The results of this approach were dramatic: the four eukaryotic kingdoms were found to be a rather homogeneous single group, while the prokaryotes were found to be sufficiently diverse that they were expanded to two separate kingdoms, referred to as Bacteria and Archaea (figure 5). A quick glance at the phylogenetic tree reveals that the major genetic variation among the eukaryotes is seen in the unicellular protists, while the three previously dominant kingdoms (plants, animals and fungi) are clustered at the end of one branch of the eukaryotic assemblage. Apparently, it is possible to achieve structural and behavioural diversity while remaining genetically rather homogeneous. When one considers that multicellular eukaryotes evolved only recently, and that for nearly three billion years the prokaryotes dominated the surface of the earth, one should not be surprised that the bulk of the apparent genetic diversity on the planet resides in this group.

Table 1. *Sources of energy on earth*

source	yearly budget (TW)
solar radiation (incoming)	178 000
heat of evaporation	40 000
energy reflected to space	53 000
reradiated heat from earth	82 000
energy used for photosynthesis	100
geothermal energy	30
tidal energy	3

Another major insight gained through molecular taxonomy and phylogeny arose when the techniques began to be used for analyses of natural populations (Pace 1996). Almost immediately it became apparent that among the prokaryotes, there were many more organism types (as judged by 16S rRNA sequences) than could be cultivated. In fact, it seems clear that less than 1% of all prokaryotic diversity has been successfully grown in the laboratory—in essence, we still have no idea of the true genetic or metabolic diversity of the prokaryotes on our own planet (Pace 1996).

So now we have arrived at a classification scheme that organizes life into two major structural groups comprised of three kingdoms. However, we have yet to define life in a functional sense as we see it on earth today. The problem may be that a focus on structural elements, whether they be organismal, cellular or molecular, does not necessarily lead to an understanding of how life relates to its physical, chemical or geological environment. So, let us view life not in terms of structure, but in terms of energy flow and metabolic capability. For example, with regard to energetics and metabolism, we might divide the living world into functional groups such as physicists, chemists or biologists, as follows:

(i) physicists: those organisms that use physical sources of energy such as light or heat (e.g. on earth, photosynthetic organisms);
(ii) chemists: those organisms that use chemical energy, either organic or inorganic;
(iii) biologists: those organisms that feed on other organisms, using behavioural adaptations to gain organic carbon which they use as chemists.

This view allows us to consider life in terms of energy supply and sources on the planet. What we see with such a treatment is first, that some of the ambiguities of dealing with life on the basis of structures begin to disappear and second, that life on earth is, as expected, very well adapted to the energy sources that are available here. This approach also suggests that before looking for life

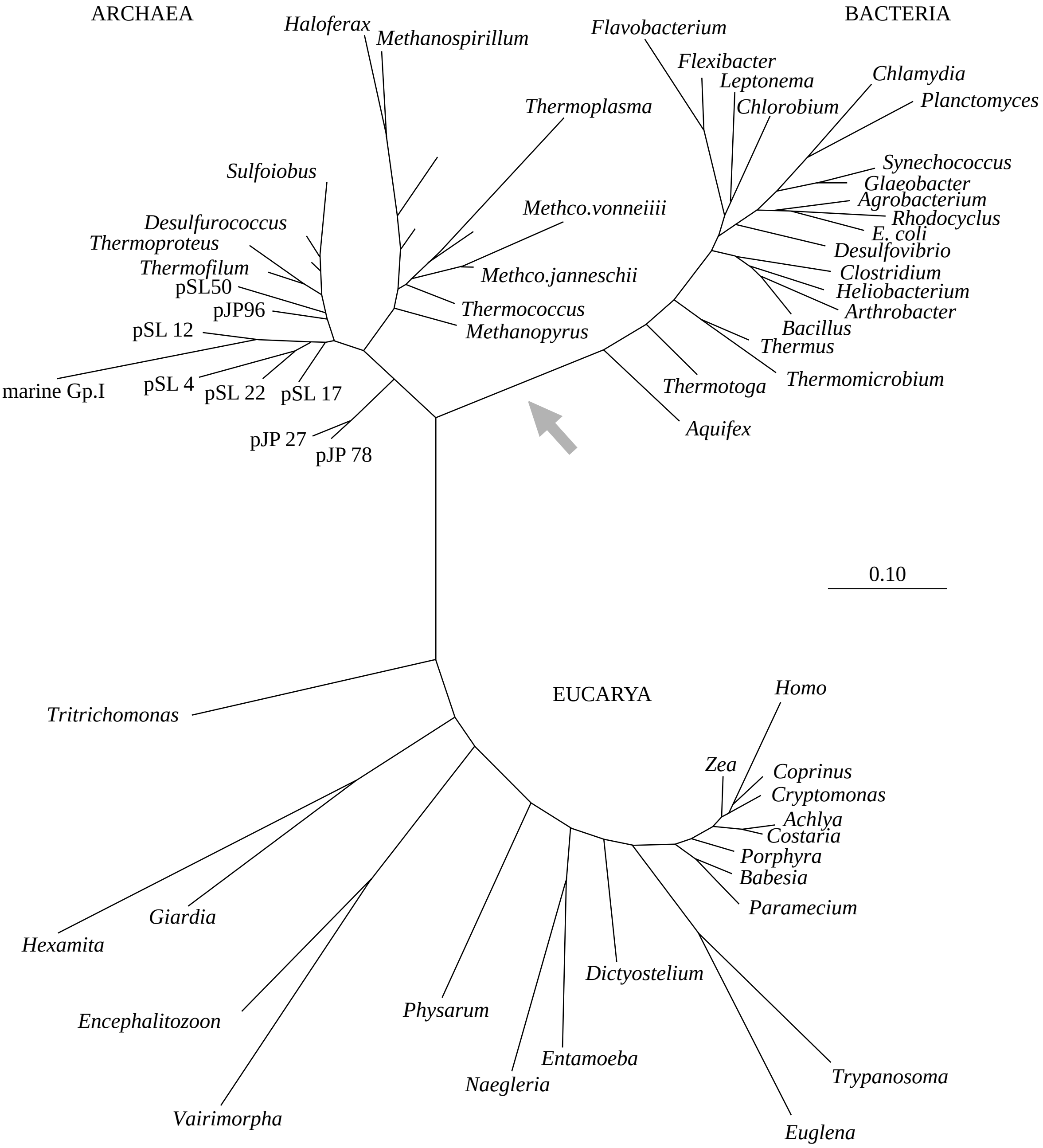

Figure 5. The three kingdoms view of life: the three kingdoms of life, as defined by sequence comparisons of ribosomal RNA (16S rRNA). This view of the tree of life shows three of the previous kingdoms (animals, plants and fungi) clustered at the end of one kingdom, now called the Eucarya. The major genetic diversity in this kingdom is accounted for by the single-celled eukaryotes called the protists. The other two kingdoms are both comprised of single-celled prokaryotes formerly grouped in the Monera (figure 4). These groups, called Bacteria and Archaea constitute a major amount of the genetic diversity as judged by comparison of ribosomal RNA sequences. Diagram provided by N. Pace, University of Colorado, USA.

anywhere, one should spend considerable time in the study of energy sources in the candidate environment.

If such an approach is valid, it must first work with present day life on earth. If so, then one can use it to infer some of the characteristics of past and perhaps extraterrestrial (future) life. So what about the earth? The major source of energy is physical, the light from our sun (table 1), with solar energy accounting for 178 000 terabits (trillion watts), and the next most abundant (geothermal energy), accounting for only 30 terawatts (TW)! Other sources of energy (tidal energy of 3) seem nearly trivial in comparison (Davis 1990). However, to put things in perspective, it is estimated that the yearly global consumption of energy by the entire biota of earth today totals only 100 TW, so that sources such as geothermal energy could, in theory, contribute to the biomass in a significant way if they could be harvested. This would be particularly relevant on early earth, where geothermal fluxes are thought to have been much higher and life was, by definition, much less abundant. However, if life is evolutionarily 'smart' it will not miss the fact that there is a lot of energy available from the sun, and one expects the planet to be dominated by the 'physicists' and their ability to harvest light energy. We should not be surprised

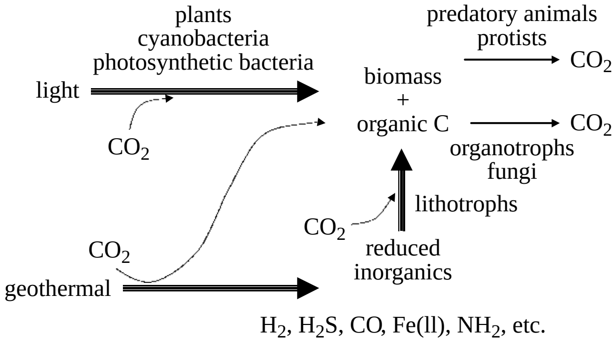

Figure 6. Energy flow on earth. This diagram depicts the energy flow on earth through the various biological reservoirs. Light is used directly by photosynthetic organisms (Bacteria, cyanobacteria and plants) to produce fixed carbon via the reduction of carbon dioxide. Geothermal energy is converted to a variety of reduced inorganic compounds, which are then used by lithotrophic organisms (Bacteria and Archaea) to produce fixed carbon via the reduction of carbon dioxide. In both of these cases, new organisms are created, and organic carbon is added to the environment via excretion or death. The predatory animals and protists complete the cycle by using other organisms as their source of energy, while the organotrophs (heterotrophic Bacteria and fungi) use organic carbon for energy. In both cases the fixed carbon is oxidized to carbon dioxide, allowing the cycle to continue.

to learn that for life on earth today, the physicists (phototrophic, light-using organisms) have the upper hand in terms of energy harvesting (figure 6).

Light energy is used directly by the physicists (phototrophs producing both biomass (more organisms) and excreted organic carbon in the form of waste products (figure 6). In contrast, geothermal energy is used indirectly, being first converted to reduced inorganics such as hydrogen, hydrogen sulphide, ferrous iron, etc., which are used by the inorganic chemists (the so-called lithotrophs) to produce biomass and organic carbon. From this point forward, energy flows through the organotrophs, those organic chemists that live via the consumption of organic matter, and biologists, which specialize in food gathering (predation). As will be discussed below, this simple view is not adequate to explain the cycling of organic matter in anaerobic environments, but it is a good starting point.

Using such an energetic format in which to categorize life liberates one from some of the restrictions that are, by definition, a part of any structural approach. We can ask first what is the chemistry and energy flow of an ecosystem or organism, and then use other cues (such as structure) to do more detailed taxonomy or phylogeny. In a sense, the energetic approach allows us to think of life in a way that embraces the structural and functional differences rather than ignoring or incorrectly cataloguing them. As shown in table 2, it is possible to put all of the known forms of life into one or more of the three categories based on energy usage. We can also call out some of the major constraints on various groups of organisms (table 2). For example, the photosynthetic organisms are evolutionarily limited because they need to be at or near the surface of the planet, they need to interact directly with potentially destructive wavelengths of unfiltered light (e.g. ultraviolet), and they must develop a fairly sophisticated mechanism for harvesting diffuse light energy (e.g. photosynthetic antennae systems and light-absorbing pigments such as chlorophyll). However, given the advantages of such a lifestyle on this planet, it is not surprising that this evolutionary path has proven successful for both prokaryotes and eukaryotes. The chemists consist of both prokaryotes and eukaryotes. Organotrophs include the night-time phototrophs, the fungi and many organotrophic prokaryotes. The ability to grow on organic matter of all sorts is an adaptation peculiar to these groups, and a reason for their widespread success in soil and sedimentary environments. In marked contrast, lithotrophic metabolism (the ability to use inorganic energy sources) is the domain of the prokaryotes; not even fungi are capable of this type of metabolism.

This consideration of present life has focused on energetic issues—an admittedly different approach. It frees us from the constraints of specific morphologies or functions, and even from issues of species diversity, differentiation

Table 2. *Types of organisms by metabolic ability*

(Organisms can also be viewed with regard to the energy sources they use. The physicists use light and are called phototrophs. These include both oxygen-producing plants and cyanobacteria as well as anaerobic photosynthetic bacteria. The chemists include both lithotrophs (those that use inorganic compounds for energy) and organotrophs (those that use organic carbon for energy). Finally, the biologists are all organotrophs, using organic carbon for energy, but obtaining their sources of energy via complex behavioural patterns called predation and feeding.)

organisms			
phototrophs	organotrophs	lithotrophs	predators
photosynthetic bacteria cyanobacteria plants	prokaryotes fungi	prokaryotes	animals protists

constraints		
physical: light	chemical: organic, inorganic	biological: living organic
need antennae to harvest light need mechanism to convert light to biological energy need to be at or near the surface	need mechanism for converting one type of chemical energy into another	need mechanism for converting one type of chemical energy into another need to develop modes of predation and feeding

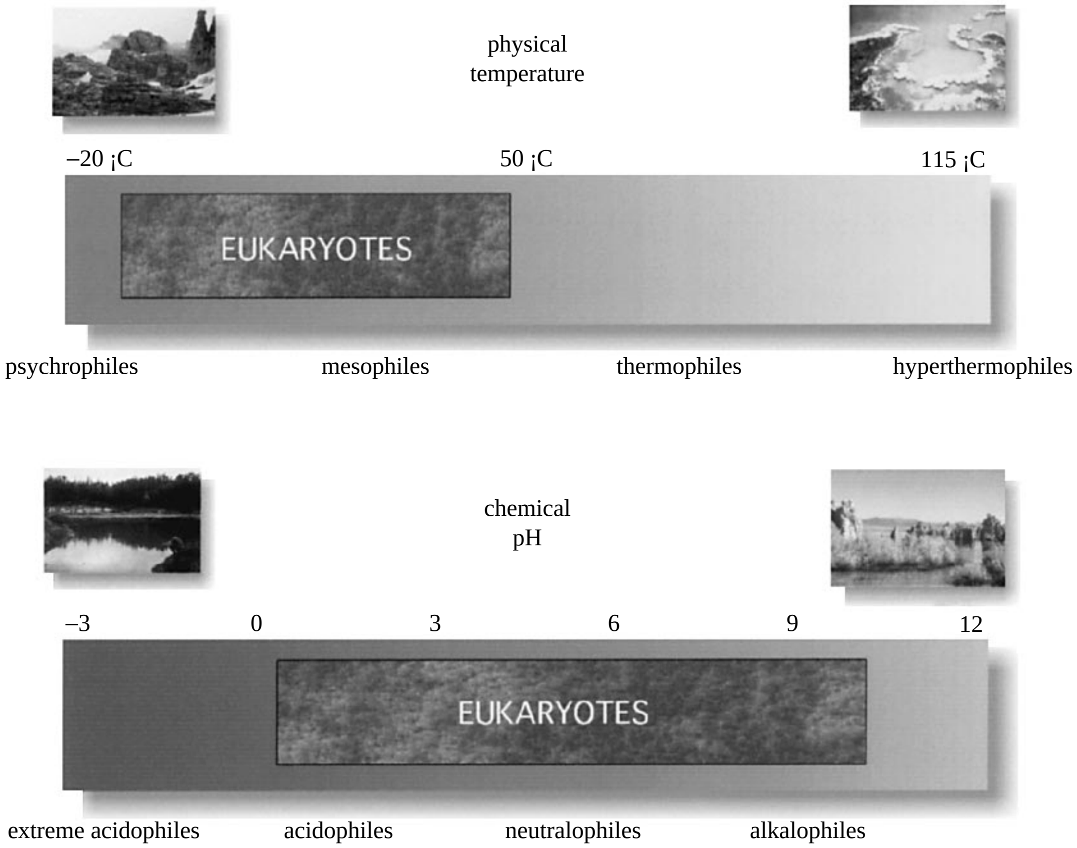

Figure 7. Physical and chemical extremophiles. This diagram shows one physical variable (temperature) and one chemical variable (pH), the ranges that life is now known to tolerate for both eukaryotes and prokaryotes, and some of the names that have been erected to describe the organisms that live over these ranges. Similar profiles can be shown for many other variables, including radiation, dryness and salinity (Nealson 1997*b*). The pictures depict environments on earth: upper left, the Antarctic dry valley; upper right, a thermal pool in Yellowstone Park; lower left, an acidic pond resulting from acid mine drainage; and, lower right, Mono Lake, CA, an alkaline lake of pH approximately 10. Photographs provided by H. Sun, Jet Propulsion Laboratory, USA, and I. Friedmann, Florida State University, USA.

and evolution. Such a consideration ties us tightly to the environment in the sense that understanding the energy flow in an ecosystem may well allow us to predict what the major forms of life might be in a given environment, on earth or beyond it. It warns us to look for evidence of processes rather than specific structures or organisms when searching for new life. We should enter the search with an open mind, knowing that the measurement of processes can yield information that infers life, and then searching for the structures and chemistry relevant to the processes measured.

(b) *Extremophiles*

Having a simple structure confers upon the prokaryotes a degree of environmental toughness not seen in the more complex eukaryotes. The prokaryotes are the environmental 'tough guys'—tolerant to many environmental extremes of pH, temperature, salinity, radiation and dryness. To accommodate such organisms, the word extremophile has crept into our vocabulary in the past decade, invented to describe organisms that are resistant to, and even thrive in, extreme conditions. The prokaryotes have become renowned for their ability to withstand physical and chemical extremes as defined by us fairly non-tolerant *Homo sapiens*. The definition of 'extreme' is, of course, in the eye of the beholder. Our cosy body, maintained at a comfortable 37 °C, is treacherously hot for many psychrophilic (cold-loving) marine bacteria, and too cold for the thermophiles of the Yellowstone ponds! Figure 7 presents a schematic picture of the limits of life for temperature and pH in order to compare the ranges tolerated by life on earth today. This should be regarded as a progress report, not the final truth, as new extremophiles are constantly being found and characterized (e.g. the limits of life are continuously expanding) (Nealson 1997*b*). Extremophiles can be resistant to physical (temperature, dryness, radiation) or chemical (pH, salinity) extremes, but it should be remembered that it is seldom in nature that an organism encounters just one extreme. For example physical extremes of temperature are often associated with high salinity, high radiation or dryness, while high-pressure environments can be either very hot or very cold. As will be discussed below, metabolic stresses, one of the things that prokaryotes tolerate best, are also frequently associated with physical or chemical extremes.

Figure 8 emphasizes an important additional property of prokaryotes, which we refer to here as metabolic extremophily. Given that eukaryotes are almost entirely limited to growth on organic carbon with oxygen as the oxidant, any set of conditions in which organic carbon or oxygen is absent is potentially life threatening to them.

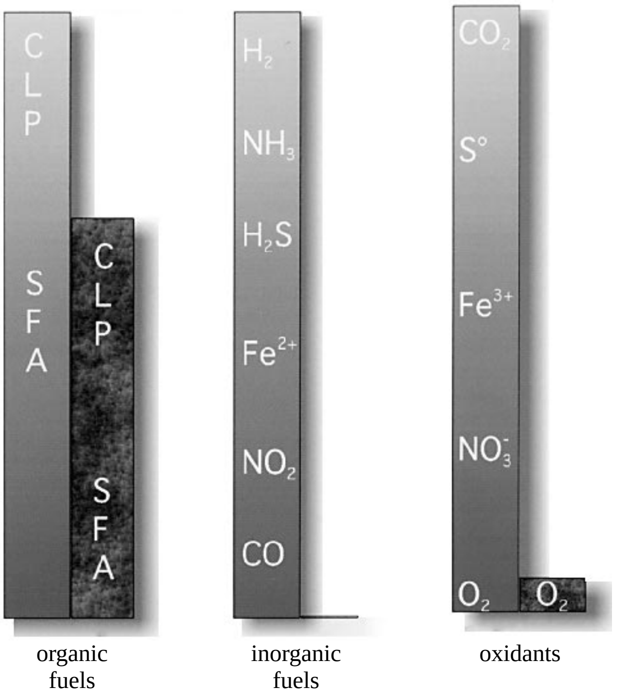

Figure 8. Metabolic extremophily. While physical and chemical extremes are often referred to, metabolic extremes are commonly encountered even on earth. Here we see the comparison of prokaryotes and eukaryotes, demonstrating that the eukaryotes do reasonably well when rich organic carbon is present (C, carbohydrates; L, lipids; P, proteins; S, sugars; F, fatty acids; A, amino acids), although they do not use many organic compounds, such as cellulose, chitin or complex organics. When inorganic energy sources are considered, the eukaryotes can use none of them, while the prokaryotes can use a wide range. Similarly, with regard to oxidants, the absence of oxygen is usually fatal for eukaryotes, while the prokaryotes use a wide range, including Mn^{4+} oxides (see figure 1). This type of extremophily may in fact be the most common encountered.

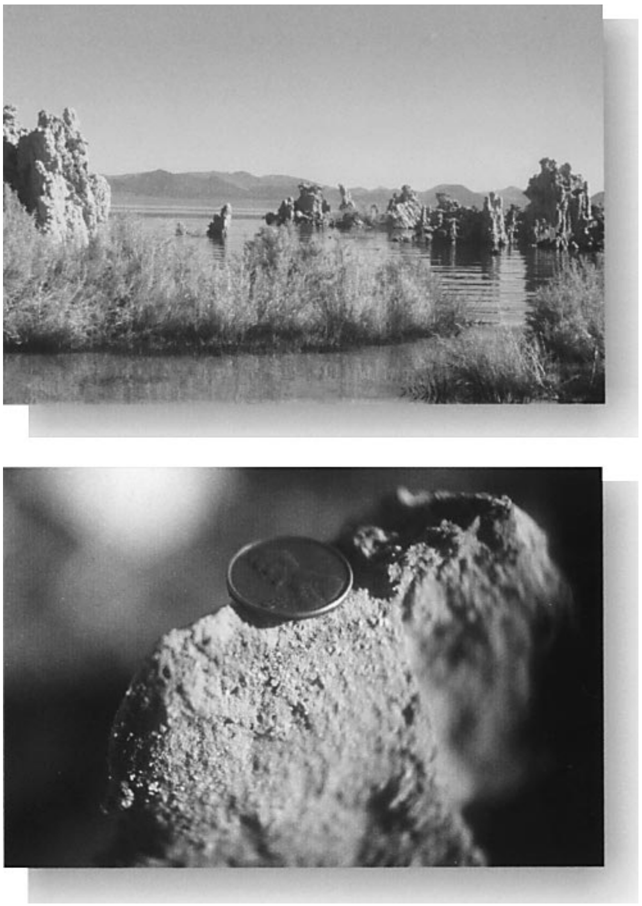

Figure 9. Endolithic organisms. One of the most common strategies adopted by organisms under environmental stress is to move into porous rocks. This is demonstrated here in the high pH environment of Mono Lake, CA. Here, a few millimetres inside the Tufa towers of the lake, a microbial layer, composed primarily of cyanobacteria, has established residence and is clearly visible. This approach is common in desert rocks, sediments and soils throughout the world. Photographs provided by H. Sun, Jet Propulsion Laboratory, USA.

For the prokaryotes, however, such environments simply pose the challenge to continue living with a different metabolic system. While it cannot be said with certainty when such metabolic diversity arose on earth, its very existence forces anyone who is hunting for life to include such 'extreme' habitats in the search, and to broaden the definition of life to include metabolic abilities that, a few years ago, might have been summarily dismissed as impossible. The ability to grow lithotrophically on energy sources such as carbon monoxide, ferrous iron, hydrogen sulphide or even hydrogen gas, implies that bacteria could inhabit worlds not previously considered as candidates for extraterrestrial life. In fact, it may well be that such metabolic plasticity is the biggest adaptation of the prokaryotes. If chemical evolution is the hallmark of prokaryotic evolution, the prediction is that the biochemical diversity (with regard to energy sources and oxidants) should reflect this. To this end, one notes simply that while the prokaryotes and eukaryotes share a common mechanism of energy (ATP) formation, the prokaryotes use almost every redox pair that is in abundance on the planet (figures 3 and 8; Nealson 1997*a*), while the eukaryotes, for the most part, are confined to sugars or organic acids (and then only a few of these) as fuels, and oxygen as the oxidant. Furthermore, prokaryotic life on earth today is characterized by the ability to degrade organic matter under anaerobic conditions, using a wide variety of organic and inorganic oxidants, and to use a remarkable array of organic or inorganic compounds as fuels or energy sources.

One strategy of life that often emerges under extreme conditions is that of adopting an endolithic lifestyle, e.g. to associate with rocks, usually just under the surface (Friedmann 1982, 1993). In California's alkaline, hypersaline Mono Lake, for example, we can see that the tufa mounds (stalagmite-like carbonate pillars) that dominate the lake, and which appear to be dead, are actually teeming with life (figure 9). A few millimetres under the rock surface are populations of cyanobacteria that are geologically shielded from the intense sunlight, and thus position themselves for optimum metabolism and growth. A similar situation occurs in many desert soils, where photosynthetic microbes are found under the surfaces of rock layers (figure 10). These ubiquitous endolithic communities can be found ranging from the very low temperatures of Antarctic rocks to very high temperatures of hot and dry deserts around the world.

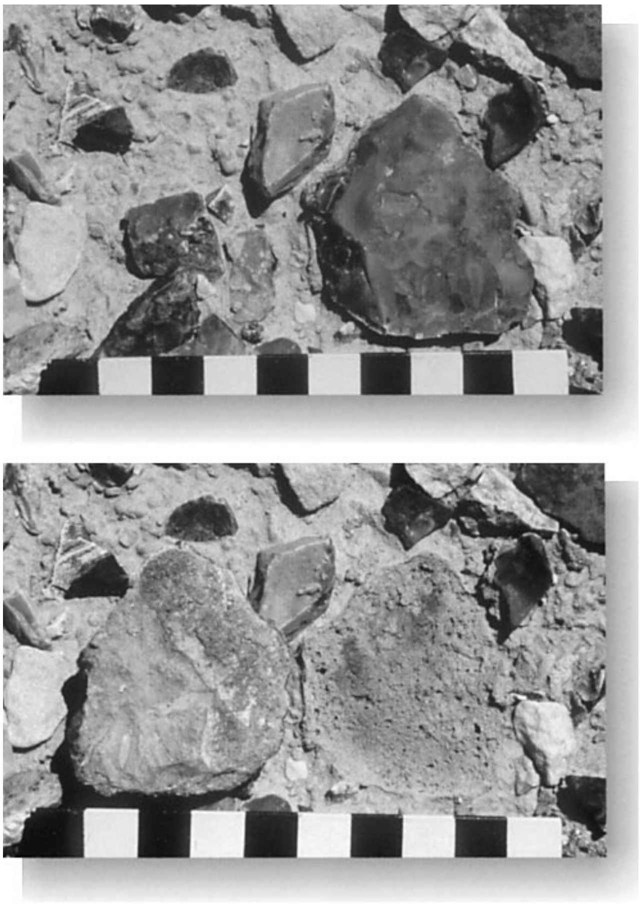

Figure 10. Life in a high-light, low-water environment. Another strategy often employed in desert environments is shown here, in which a small rock is shown to be harbouring abundant cyanobacteria under its surface. The rock acts as a shield from the intense sunlight and a place where water can be sequestered, providing a haven for life in an otherwise very hostile environment. Photographs provided by I. Friedmann, Florida State University, USA.

A final point regarding the prokaryotes relates to their tenacity and ability to survive for long periods of time. There are many examples of bacteria being revived after long-term storage in salt (halite) crystals (Denner *et al.* 1994), amber millions of years in age (Cano & Borucki 1994), and frozen Siberian and Antarctic permafrost (Shi *et al.* 1997). With regard to the latter environment, David Gilichinsky and his colleagues from Puschino, Russia, have been drilling in permafrost sites for many years now, and a number of organisms have been 'revived' from their carefully collected samples. It is not unusual to find between one million and ten million viable bacteria from each gram of permafrost (Shi *et al.* 1997). These are not cold-loving (psychrophilic) bacteria that have adapted to these freezing conditions, but simply mesophilic organisms that have been trapped within this icy storage facility for millions of years. While there is a reasonable amount of healthy skepticism surrounding reports of such biological tenacity (especially in the area of the halite-entombed organisms, where it cannot be said with certainty that no dissolution and reprecipitation occurred), there is good reason to believe that prokaryotes are capable of survival over periods of hundreds of thousands, and probably millions of years.

To recapitulate, on earth today, we observe a remarkably diverse biota. The prokaryotes have diverged to occupy nearly every niche where redox chemistry offers enough energy to drive the synthesis of ATP, while the eukaryotes have diverged (structurally and behaviourally) to become the ultimate predators—losing the capacity to synthesize key vitamins and amino acids while developing the ability to pursue and devour organisms containing these chemicals.

Adding to this biological diversity (and further frustrating those who try to make order out of earthly life), one also sees that to accomplish their ends, almost all organisms on earth engage in symbioses of one kind or another (Margulis 1981). These include the ubiquitous intracellular symbionts of eukaryotic cells (e.g. mitochondria and/or chloroplasts) in which prokaryotic symbionts supply key metabolic needs, prokaryote symbioses, involving intercellular exchange of nutrients such as hydrogen, as well as the complex behavioural symbioses seen among many plants and animals. All add to the complexity of life on earth today, and make its definition and classification under any orderly scheme, including the energetic one proposed here, more challenging.

(c) *Layered microbial communities*

One of the nearly ubiquitous features of life on earth is that in stable environments (e.g. those with little or no physical mixing), one can see predictable layered sequences of metabolites, as shown in figure 11 (Nealson & Stahl 1997). We suggest that such layered sequences are biosignatures of extant life, as they are nearly impossible to create without active chemical catalysis, and will dissipate if the systems are poisoned or killed. Basically, such systems allow us, through the measurement of metabolites that are easily and commonly measured (Nealson & Stahl 1997), to infer the existence of layered prokaryotic communities. Such layered communities are found in sediments around the world, as well as some stratified lakes, fjords and some marine basins. The layers are a function of the production and/or consumption of key metabolites at rates faster than the rates of diffusion, resulting in either the increase or decrease of those particular chemical compounds, e.g. they are the chemical indicators of the catalysis of reactions caused by biological systems. That is to say, that thermodynamics predicts where the energy is available, while kinetics defines where life is active.

As one proceeds downward in the Black Sea, for example, the consumption of organic matter by the organotrophic organisms leads to the rather rapid depletion of oxygen at about 50 m (figure 11). This is followed systematically by the disappearance of nitrate by the nitrate-reducing bacteria, the increase in soluble manganese (the result of the manganese-reducing bacteria), the increase in soluble iron (the result of the iron-reducing bacteria) and the increase in hydrogen sulphide (the result of the sulphate-reducing bacteria). All of these processes are fuelled by organic carbon that sinks into the deep waters, and is oxidized by the anaerobic prokaryotes. As each of these nutrients diffuses upwards in the water column, it can be used by lithotrophic organisms as an energy source, so that cycling of each element occurs within this complex, layered ecosystem.

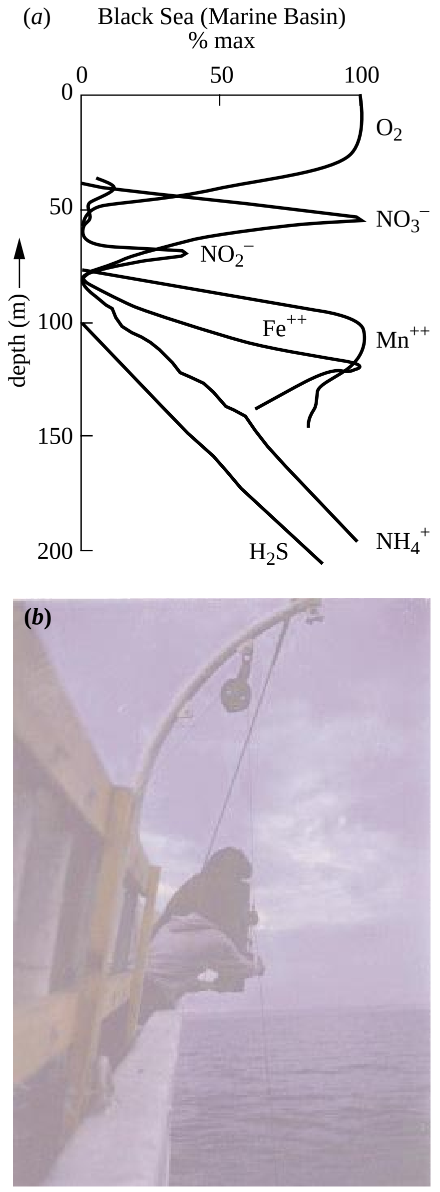

Figure 11. The layered microbial communities of the Black Sea water column. This figure depicts in (*a*), the layered chemical strata as seen in the Black Sea during an expedition in 1988, and in (*b*), a picture of two scientists retrieving a sampling bottle from depth. Such techniques are used to obtain deep-water samples, and the nutrient analyses of such samples as a function of depth reveals the stratified communities as shown in (*a*). Although the Black Sea is 1800 m in depth at this location, only the top 50 m are oxic. The remainder of the profiles reveal a systematic usage of the electron acceptors until all except sulphate are exhausted. Hydrogen sulphide (the product of sulphate reduction) dominates most marine systems because sulphate is so plentiful in seawater.

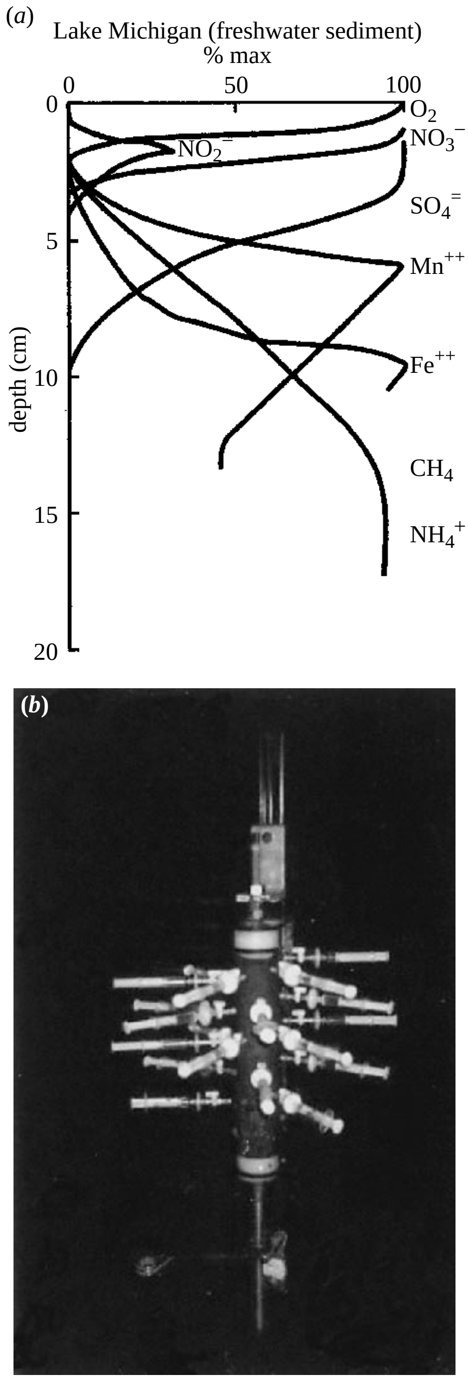

Figure 12. The layered microbial communities of Lake Michigan sediments. In Lake Michigan, the water column almost never becomes anoxic, but anoxia and the accompanying layered chemical strata are seen in the underlying sediments (*a*). In (*b*), is a core sample with sampling syringes inserted. This core is squeezed from both ends, forcing porewater into the syringe collectors, which are then removed and sampled for key redox nutrients. As with the Black Sea, only the surface layer is oxic, with systematic usage of the electron acceptors occurring downward. However, for the Lake Michigan cores, anoxia occurs at 2 cm rather than 50 m. Furthermore, as is true with most lake systems, the low amount of sulphate means that the sulphur cycle is not dominant, and that the deeper layers are dominated instead by carbon dioxide as the oxidant and methane as the major reduced product. Photograph provided by D. Moser, University of Princeton, USA.

Figure 12 shows a similar layered community from a Lake Michigan sediment (MacGregor *et al*. 1997). In this case, the layers are at the centimetre rather than the tens of metres level, four orders of magnitude finer scale than that seen in the Black Sea. But the message is still the same—energy flow from the most to the least energy-rich occurs in an ordered and predictable way leaving easily detectable chemical signatures. One key difference that can be seen between this profile and that of the Black Sea (due mainly to the fact that Lake Michigan is freshwater rather than marine) is that the dominant process in the deepest layer is methane production rather than sulphate reduction, the reflection of the absence of abundant sulphate in freshwater systems. Thus, freshwater ecosystems will be methane dominated, while the marine will be sulphur dominated. The general principles of layered communities remain, however, as one proceeds downwards; the electron acceptors needed for fuel oxidation will be sequentially consumed, resulting in predictable layered communities.

From the work of Jorgensen and his colleagues we know that similar patterns are seen in algal and bacterial mat ecosystems at the submillimetre level (Jorgensen *et al.* 1979), and it seems likely that the same general principles of energy flow will apply to biofilm communities at the micrometre scale (eight orders of magnitude below that seen in the Black Sea). Given these immense scale variations for the same indicator of life, one might well ask whether there are upper bounds for the expression of such 'signals'. The upper size limit that one might expect for such layered communities is not known, but may well be a key question for those searching for life in non-earth environments. In terms of both past and future life, these layered communities offer substantial food for thought. For past life, we suggest that these metabolic layers (or some manifestation of them) may be preserved as records of past life that would be recognizable as fossil communities. As for future life, we suggest that such layered communities might be used as biosignatures of extant life on other planetary bodies—it is, however, our challenge to identify how, and over which scales, to search for them.

To summarize our views of the present, life on earth is remarkably diverse, occupying almost every behavioural and metabolic niche that is available. The eukaryotes have perfected the arts of behavioural diversity and structural diversity (development), and focus on using the best energy sources on the planet (sunlight and organic carbon as fuels and oxygen as an oxidant). Prokaryotes, on the other hand, distinguish themselves not only by their small size, their toughness and their tenacity, but also by their metabolic diversity—their ability to survive in metabolically extreme environments where the energy flow is low by exploiting both electron donors and electron acceptors not available to the eukaryotes. Such prokaryotic abilities led to the widespread existence of layered microbial communities, which are commonly seen in anaerobic niches. Understanding the energy flow of present-day life on this planet leads one to the conclusion that life is energetically opportunistic and efficient. The study of its successful occupation of the planet provides a useful format for understanding past and present life, and for the formulation of strategies for searching for life in environments off of our planet.

3. PAST LIFE

In its early life-compatible stages, the earth was still a fairly inhospitable spot for life as we know it now. It was hot, lacked oxygen in its atmosphere and, consequently, could form little ozone to protect the emerging biota from harmful ultraviolet (UV) light. Yet, it was in such an environment that life arose and left its earliest record(s). From studies of geological sequences of the Issua formation in Greenland (Schidlowski 1988; Mojzsis *et al.* 1996), traces of metabolic activity (carbon metabolism) indicate that life existed on Earth as early as 3.8 Gyr ago. This suggests that the invention of life took place rather rapidly, roughly within 200 Myr of when the planet cooled and thereby became habitable, if not hospitable, for carbon-based life. Such discoveries have triggered speculation about life in general (e.g. the problems associated with the invention of complex living systems), as well as the possibility that similar living systems might have evolved on other planets. For example, it is generally agreed that from the early period of planetary development up until about 3.5 Gyr ago, Mars and Earth shared similar planetary conditions. This has led many to posit that life might have had adequate time and the proper conditions to develop on early Mars. Subsequently, however, Mars lost its magnetosphere, hydrosphere and most of its atmosphere, making the surface of Mars, by earthly standards, an extremely hostile environment. For example, at current subzero temperatures and low atmospheric pressures on Mars, the triple point of water precludes the existence of liquid water on the surface of the planet. However, while the current conditions of high UV light, absence of liquid water and low temperatures seem to eliminate the possibility of extant surface life, the possibility that it may have once existed can not be excluded based on our knowledge of the history of the planet.

The preponderance of evidence of the earliest life on earth is in the form of chemistry, as there are few well-preserved ancient fossils (Knoll 1992; Schopf & Klein 1992; Schopf 1999). The absence of a robust fossil record is due to a combination of rock destruction via plate tectonics, biological recycling and the fact that simple, unicellular life (with no easily preserved hard parts) dominated the early earth. This is consistent with what we know of unicellular life on the planet today, and of conditions necessary for fossil preservation. In fact, until about 2 Gyr ago there was little oxygen on the planet, and the development of complex eukaryotic cells, (which live via oxygenic respiration) was probably not possible. Based on the study of ancient soils, Rye & Holland (1998) concluded that oxygen first appeared (and rose rapidly) in the atmosphere approximately 2 Gyr ago (Holland & Rye 1997; Rye & Holland 1998; figure 13). Given the need for efficient energy metabolism to support complex life, it follows that it was only upon this rise that the development of eukaryotic organisms was possible. The Cambrian explosion of species and complex multicellular eukaryotes (containing tissues, organelles, organs, etc.) did not occur until approximately 500 Myr ago, when oxygen reached current levels (Knoll 1992; Schopf 1999). From that point onwards, the earth began to take on what we would find a familiar appearance: occupied by plants, animals and fungi. However, even before the rise of oxygen, earth was teeming with microbial life—this is the perspective that must be kept in mind when searching for life on other planets of unknown evolutionary age. Indeed, other planets could be in any of these stages, and the search for life can not simply assume that a given stage of life or planetary evolution will have been reached. One should also note that the evolution of earth has been drastically impacted by life. The oxygen we breathe is a product of the evolution of oxygenic photosynthesis. Without this innovation, the planet might well be alive, but its life would look, taste and smell much different from that we see today.

To pursue this further, one might ask how a planet that is generating reduced gases via hydrothermal activity could become more oxidizing with time. While this can be done abiotically to some extent via the loss of hydrogen, if a planet has sufficient gravity to maintain its atmosphere, one of the key inventions of life must be the use of light energy for the production of chemical oxidants that can then be used to maintain an active biota. That is, the invention of photosynthesis is critical to the evolution of large and complex life such as we see on earth today. In addition to the normal role of photosynthesis in the global carbon cycle (e.g. the generation of fixed organic carbon; figure 6), we now imagine a second major role for photosynthesis, namely the generation of oxidants. Because electron donors are needed for charge balance during the photosynthetic reaction, oxidants are generated during photosynthesis (figure 14). For the anaerobic photosynthetic bacteria, a variety of electron donors can be used, including reduced sulphur compounds or ferrous iron, which result in the production of oxidized sulphur compounds (elemental sulphur or sulphate) or even oxidized (ferric) iron. In contrast, for cyanobacteria and the eukaryotic phototrophs (e.g. algae and plants), the electron donor is water and the product is oxygen (figure 14). Once these processes come into play the oxidation level of a planet can increase, and the origin and evolution of respiration should follow, proceeding towards the evolution of more energy-intensive cellular systems.

Given the above discussion, it may be useful to look at the diagram of Rye & Holland (1999) from another perspective: namely that of the appearance of specific oxidants over time, as depicted in figure 13. With the facts we have available today, it is hard to define with accuracy exactly when each oxidant appeared (e.g. the exact times and amounts of reductants). However, such a reconstruction of the redox history of the earth (see DesMarais *et al.* 1992; Canfield & Teske 1996) forms a reasonable backdrop for thinking about the evolution of metabolism and its relationship to the evolution of the earth. There is little doubt that the invention of photosynthesis has had an immense impact on the face of our planet, but what kind of photosynthesis, and when? The geological record of the planet shows that massive iron deposits (banded iron formations or BIFs) accumulated in the billion years before the rise in oxygen, suggesting that the iron was being systematically removed from the ocean. The usual explanation for this is that oxygenic photosynthesis had already evolved, and the iron was being removed by chemical oxidation (to insoluble ferric hydroxide) by molecular oxygen. However, it has also been suggested that iron-based photosynthesis evolved during this time, and that the massive iron accumulations were due to the use of iron as an electron donor, producing massive amounts of oxidized iron under anaerobic conditions (Widdell *et al.* 1993; Ehrenreich & Widdel 1994). It is these kinds of uncertainties that may be cleared up as we learn more about the metabolic evolution of the planet and try to correlate it to the geological record. The exact mechanism aside, it is very likely that in its earliest days, the earth was anoxic, with a redox potential dictated by the abundant reduced iron (ferrous–ferric couple) in the earth's oceans. Given this, it is not difficult to see why iron was the metal of choice for much of our metal-driven biochemistry. Once oxygenic photosynthesis evolved, however, life had played a cruel trick on itself—not only did the toxic oxygen necessitate the invention of mechanisms for protection, but after iron was established as the major cellular transition metal, it became almost inaccessible to life due to the presence of molecular oxygen, which efficiently removed it at the neutral pH values characteristic of the earth's surface.

Oxygen may have played another critical role in evolution in the sense that of all the electron acceptors whose chemistry is compatible with carbon-based life, only it and carbon dioxide are gases. Presumably, if complex animal life was to move on to land, it must either have at its disposal a gaseous oxidant or invent a method for transport of a non-gaseous oxidant on to land. Thus, the invasion of the land by complex multicellular animal life was almost certainly dependent on the invention of oxygenic photosynthesis and the appearance of oxygen as a major component of the atmosphere.

Such an energetic view of the evolution of life is one that, if complete, would allow us to search for life elsewhere over broad temporal scales, e.g. if we knew the sequence of events that led to present-day life, we could look for similar events through analysis of planetary atmospheres. If we continue to learn about our own planetary history and the relationship of life to the evolution of the planet, we may well produce the intellectual framework needed for the interpretation of planetary spectra as they begin to appear through space interferometric methods in the next millennium. It may well be the ability to interpret this spectral information that allows us to make the correct decision(s) as to which planets to send missions to and/or investigate more fully.

4. FUTURE LIFE

For purposes of this discussion we view the future as the attempt to discover life outside of the earthly environment. As we are ready to proceed to other celestial bodies in search of life, we find that our definition of habitability is quite different from that we embraced just a few years ago; it continues to expand physically, chemically and metabolically as we learn more about life on earth. In response to this, we must

(i) consider that the physical and chemical conditions tolerant to life are broader than we once thought;
(ii) examine the potential energy sources available and look carefully for life forms using any such energy;
(iii) be prepared for subtle, single-celled life that may not be obvious at first glance, even looking in places where life might have been preserved as dormant forms.

In fact, the future looks quite exciting. In the near term we see an ambitious and robust series of missions to Mars, beginning with the Mars Surveyor Program of NASA, already in progress. As part of this mission, a series of

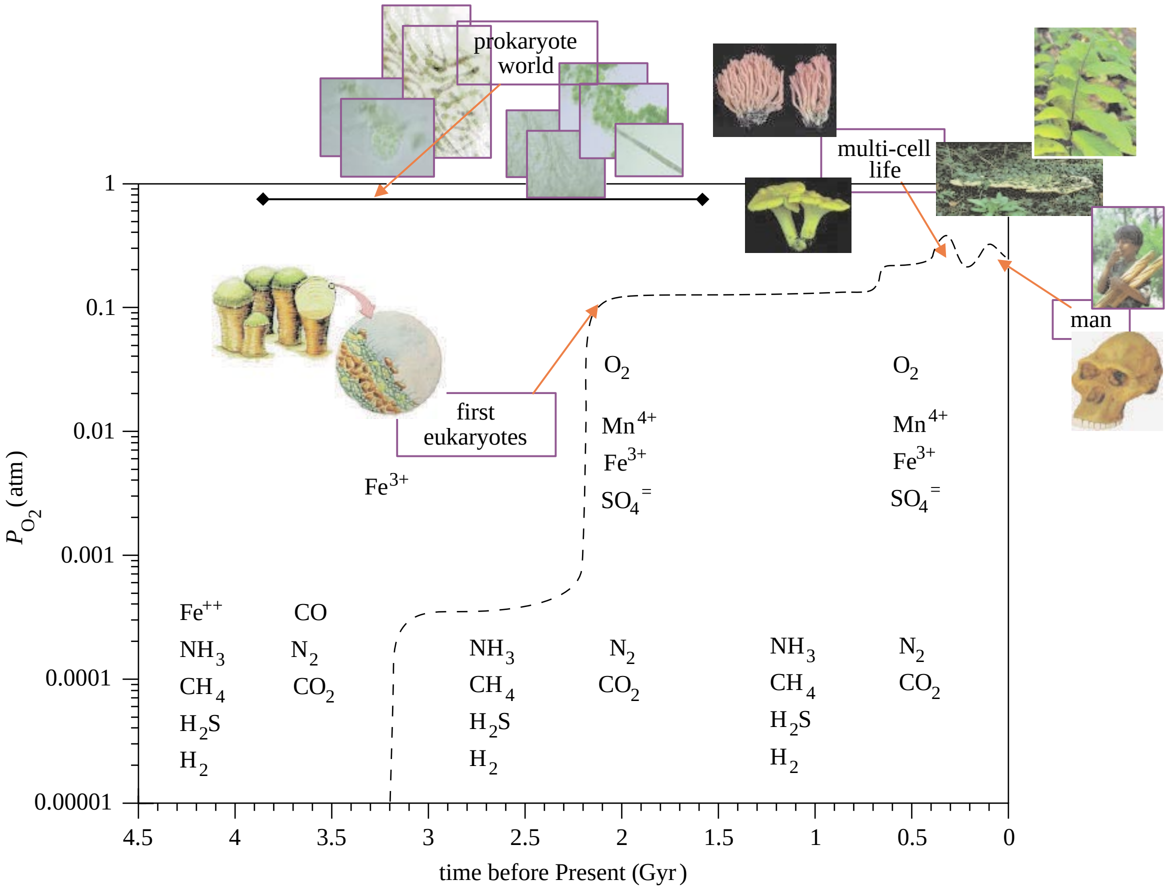

Figure 13. Variation in oxygen concentration over time, and relationship of this to appearance of organisms in the fossil record. This oxygen profile shown in this figure is modelled after that published by Rye & Holland (1999), and has superimposed upon it the estimates of when major groups of organisms appeared. Note that no evidence for complex eukaryotic cells is seen in the fossil record until the major rise in oxygen concentration, approximately 2 Gyr before present. In addition, we have added some speculative points concerning the existence of oxidants and reductants over time. We have superimposed some of the major oxidants and reductants at times that they might have appeared. This part of the diagram is meant to stimulate thought rather than present the facts, as, with the exception of oxidized iron, which is known to be present because of the widespread banded iron formations, little evidence is available as to the appearance of these oxidants on the ancient earth.

sample return missions are planned, which will give us, for the first time, access to selected, pristine samples from another planetary body in our solar system. The architecture for the first set of missions is planned and being executed now, with the first launch planned for 2003 and the return of two samples scheduled for 2008 (figure 15). Although a total of only about 1000 g of sample will be returned, given the sophistication and sensitivity of today's analytical abilities, we stand to gain an almost immeasurable amount of new knowledge about our neighbouring planet.

The Mars missions will also include extensive *in situ* measurements aimed at physical, chemical and (perhaps) biological characterization of Mars. By such studies, we will further develop the methods for life detection off of earth. This is an important issue, as after Mars, it will not be easy to obtain returned samples. Even the next closest candidate, the icy moon of Jupiter called Europa, is four years away and in the intense gravity well of Jupiter, so that sample return with today's propulsion systems is an impossibility. Thus propulsion technologies that allow faster flight and more power must be developed before more far-flung sample returns are likely. However, if we use Mars as a test-bed to develop the methods for *in situ* life detection, it seems likely that we can examine a variety of other sites using both remote and in-situ analyses.

5. BIOSIGNATURES AND SCALE

We began this discussion with the definition of life and the explanation that on the basis of this definition we would develop biosignatures, but what are such biosignatures, and over what scales should they be measured? They must differ with differing scales of view and with different subjects of investigation. For instance, from afar, the only reasonable biosignatures will be those of planetary atmospheres. If our definition of life holds, then we will look for atmospheres that are out of equilibrium—those that contain mixtures of gases that should not be present together. These should be measured as a function of planetary latitude (looking for temperature dependent and/or seasonal processes), and as a function of time (looking for life-driven kinetic effects). One imagines that if spatial and temporal resolution can be achieved, it will be possible to separate those changes that are due to normal geological and chemical evolution of

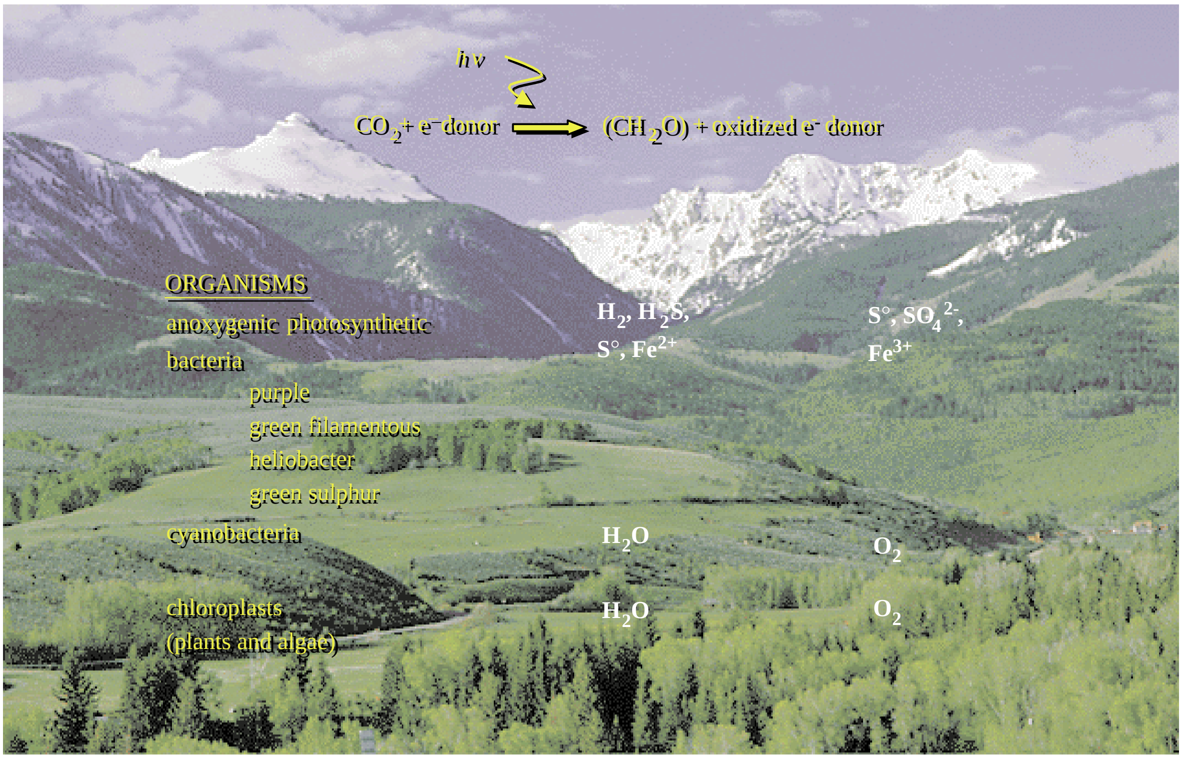

Figure 14. Photosynthesis and the generation of oxidants. This diagram is meant to illustrate that although photosynthesis does indeed result in the production of organic carbon (CH_2O), it also plays an important role in the generation of oxidants. On earth, we know of photosynthetic organisms that use the energy of light to produce oxidized foms of sulphur, iron and water. Without light, or without some other way of generating oxidants, it is not clear how complex life could evolve.

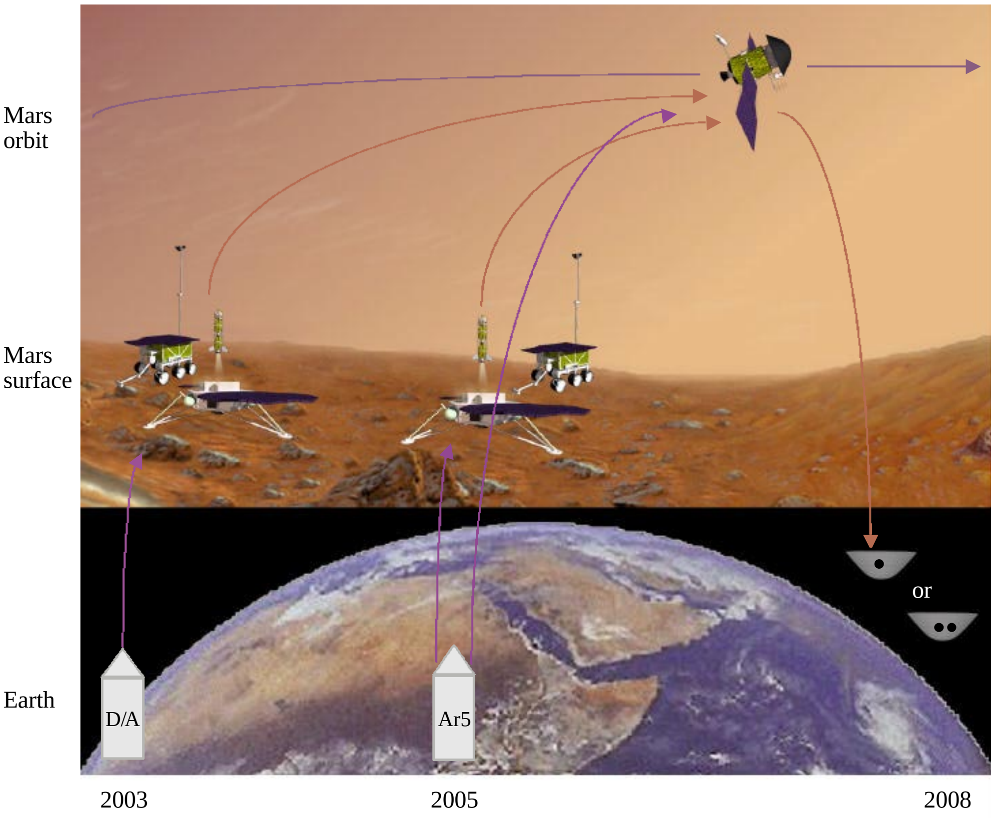

Figure 15. Architecture of a mission. The 2003–2005 joint US–French mission architecture is shown here. In 2003, a lander–rover combination will be launched, arriving to a predetermined site on Mars in 2004. The rover will collect samples, return them to the lander and place them in a sample cannister in the Mars ascent vehicle. This sample cannister will be sealed and then placed into Mars orbit via the ascent vehicle. In 2005, a similar mission will be launched, but using a French launch vehicle (Arianne 5) that is large enough to also launch an orbiter–Earth return vehicle. This mission will also place a sample cannister into Mars orbit, and the orbiting satellite (Earth return vehicle) will locate and retrieve both samples and return them to Earth for scientific studies.

the planet from those catalysed by a metabolically active biota. On earth, nearly every gas is out of equilibrium by orders of magnitude, and these disequilibria are exacerbated by seasonal effects (Lovelock 1979). Of course, if one sees planets with oxygen-rich atmospheres these will become prime candidates for further investigation, but it cannot be forgotten that for most of its history, earth has not had an oxygen-rich atmosphere even though it has been teeming with life. Studies at this scale may well allow us to narrow the 'search space' for potential living planets, using this knowledge to identify the most promising sites to send high-resolution missions for further exploration. Whether or not one supports the Gaia hypothesis developed by Lovelock and Margulis during the mid-1970s, we can all agree that the earth viewed spectroscopically (or even visually) from space would look very different from the other planets in our solar system. With the earth's abundant and reactive oxygen-rich atmosphere, intelligent extraterrestrial scientists would surely suspect that some biotic processes were afoot, feeding gases into the atmosphere in concentrations that would defy the thermodynamic predictions of our extraterrestrial counterparts! So if there is a planetary biosignature, what then of a solar system biosignature? Galactic biosignature? Indeed, would an abiotic universe look different than this one does? These questions, though seemingly imponderable, must be asked in light of the recent discoveries of other planetary systems than our own. The discovery of new potential habitats for life outside our solar system coupled with a deeper understanding of the extent of habitability on this planet cannot help but raise our expectations that life beyond the earth will ultimately be found. As the very definitions of remote and *in situ* sensing are, in fact, dependent on the scale of measurement—not just proximity to investigator and sample—we will need to be prepared with not only microscopes and binoculars, but telescopes as well, because the larger the scale of the biosignature the more distant the observer can be.

6. SUMMARY

As we begin the next millennium, technology has already surpassed the dreams of many, and who is to say where it will lead us. Great opportunities for exploration await us, our children and their children, all of whom can exploit this unique situation. We subscribe to the belief that life will soon be discovered elsewhere, whether it be simple prokaryotic-like life or life advanced far beyond our own. Consider for the moment, for example, that in the past 0.01% of the planet's habitable history, life has moved from the simplest of hominid forms to life so advanced that it can communicate with robotic spacecraft hundreds of millions of miles from our own planet. Given the number of galaxies, solar systems and, probably, habitable planets, why would we not expect a planet somewhere to be a million (or ten or 100 million) years advanced beyond our own system? What would this life be like? What would it know and how would it use that knowledge? The spacecraft and interferometers we struggle to build now would have long since been discarded by this life, and energy might be used in ways we have yet to dream of. Alternatively, we might find planets that mimic earth in its earlier stages, millions to billions of years behind us in evolutionary time—a chance to examine our own history. The study of past and present life on our planet tells us that life has dramatically impacted the geochemical evolution of the planet, and suggests that if we really understood the intimate relationships of these two processes, then it might be possible to locate life by measuring these effects at scales presently not even conceived. This is the challenge, and this is our future.

The research described in this paper was carried out by the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the National Aeronautics and Space Administration (NASA), USA.

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