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## Group Report: Long-term Geosphere–Biosphere Coevolution and Astrobiology

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### ABSTRACT

This discussion group attempted a qualitatively new synthesis of long-term geosphere–biosphere coevolution, with the aim of understanding and presenting to the other groups the broadest possible context in which to consider Earth system analysis for sustainability. This included the prospects for detecting life and intelligence elsewhere in the Universe, as debated by astrobiology. The chemoton model of life comprising three autocatalytic subsystems (boundary, metabolic, genetic) was adopted. The topology of evolution was characterized as a network in the prokaryote realm and as a tree (or bush) in the eukaryote realm. It was agreed that prokaryotic life is common in the Universe but that eukaryotic life is rare and intelligent life is extremely rare. The appearance of intelligent life on a planet might theoretically involve four or five difficult evolutionary transitions along the way. These probably include the origins of the genetic code, of oxygenic photosynthesis, of eukaryotes, and of language. Optimistic and pessimistic scenarios for the long-term coevolution of the geosphere–biosphere were contrasted. A key finding was that dating of the major transitions in evolution and, to a lesser extent, dating of the major transitions in the state of the environment are subject to large error bars that need to be reduced in order to address the causal relationships of coevolution. A major output was a visualization of a time line of coevolution that includes these uncertainties. New suggestions of coevolutionary connections were also made. The feasibility of unequivocal life detection on extrasolar planets was questioned, but it was recognized that astrobiology is already encouraging a useful broadening of Earth system analysis. The failure of the search for extraterrestrial intelligence (SETI) and the apparent difficulty of the transition to natural language support the view that intelligence (or at least natural language) is extremely rare in the Universe. Habitation was defined as a first-order influence of life on the geochemical cycling of a planet, and it may be important for the maintenance of habitability. Theoretical considerations as well as Earth history suggests that there are limits (albeit rather broad ones) on how globally destructive life can become. A proposal was made to extend an existing model of global coevolution to address this and

other Gaia questions. An “autocatalytic Gaia” hypothesis was put forward to suggest that autocatalytic recycling is an almost inevitable planetary phenomenon, once there is life. This is a natural extension of the autocatalytic theory of life (the chemoton model). Some broad lessons of sustainability can be learned from Gaia and the unfolding coevolution of life and its environment on Earth, in particular, the importance of avoiding long time lags for maintaining system stability.

## INTRODUCTION

Co-Causality  
Of Gaia  
You’re the only theory  
I adore  
But save me  
Saints Darwin and Dawkins  
From asking “What is coevolution for?”

— Alison Jolly

The word “evolution” comes from the Latin *evolutio* and means to roll out or unfold. Our group explored the unfolding coevolution of life and the Earth and how things might unfold elsewhere. The discussion was richly nonlinear and followed a quite different order to that imposed in this report. Here we attempt a qualitatively new synthesis rather than a review of the state-of-the-art, which can be found in other chapters of this volume and the recent pertinent literature.

## ORIGINS AND EVOLUTION OF LIFE

Our discussions of the origins and evolution of life focused on three fundamental questions: What is life? What is the topology of life’s evolution? Is life an unavoidable cosmic phenomenon?

### What Is Life?

There is no consensus definition of life; however, there is agreement on the basic characteristics of life. As we know it, all life is based on coupled oxidation–reduction reactions that are far from thermodynamic equilibrium and occur in metastable domains (Schrödinger 1944). As such, on long timescales, biogeochemistry of a planet requires an open, thermodynamic system. Life is self-replicating and adaptive, and contains synthetic machinery that produces polymers. Life-forms are bounded. On Earth, all life-forms catalyze phase-state transitions in which gases in the environment are converted to solutes and vice versa.

A possible strategy to define life is as follows:

1. Assume a tacit (instinctive) knowledge of life.
2. Viruses must be excluded because they do not metabolize or propagate on their own (and hence are not organisms).

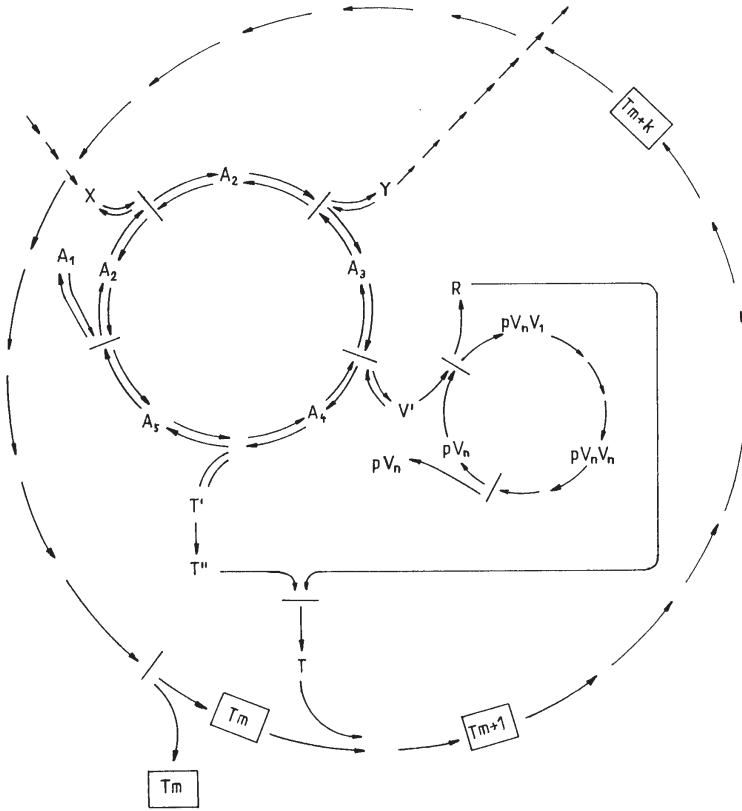
3. Abandon purely verbal criteria for life.
4. Look for minimum models of living *systems*.
5. Abstract essential properties from the simplest living systems of the present day: bacteria.
6. Make the simplest possible abstract model.
7. Ask what kinds of real chemistry can manifest the abstract system.

This strategy hinges on Gánti's seminal contribution to understanding the principles of the living state (Gánti 1979, 2003). He observed that for the living state, reproduction is neither necessary nor sufficient. Many cells and organisms are commonly regarded as being alive even if they cannot reproduce (any longer). So-called potential life criteria must be met only if the population of units is to be maintained and evolved. The correct relation, then, between units of evolution and units of life is that of two, partially overlapping, sets. Gánti's model of a *minimal* living system, satisfying also the potential criteria, is illustrated in Figure 6.1. The chemoton is a chemical supersystem composed of three autocatalytic subsystems: a metabolic network, a replicating template, and a boundary membrane. Stoichiometric coupling among them ensures regulated reproduction of the system as a whole. Spatial reproduction happens because the growth of membrane surface outstrips the increase in mass of internal material, since a doubling of the surface area of a sphere requires more than a doubling in its volume. It is important to emphasize that the membrane is also autocatalytic: building block T, produced by the metabolic network, is spontaneously inserted by virtue of the fact that there is a preexisting membrane surface. It is, however, the presence of the template molecule  $pV_n$  that qualifies this system as a unit of evolution (with unlimited hereditary potential). If one supposes that these templates are the abstract versions of ribozymes (RNA molecules acting as enzymes), then they catalyze steps of the metabolic cycle and membrane growth using their inherited information.

The chemoton model is useful because it combines two traditions: the genetical and the systems theoretical approaches to the problem of defining life. The concept of discrete life rules out “soup” ideas. Our model of what is life affects how we go about detecting life, either on Earth (in the rock record) or elsewhere (astrobiology). Traditionally, the geologist's approach has been to look for morphology (which is potentially flawed), for signs of redox chemistry, and more recently for biomarkers. This is in line with the “order-from-disorder principle” (Schrödinger 1944) for describing the entropy production in the environment of life. Our model of what is life also has implications for what are viewed as the major transitions of life. These issues recur later in the report.

### **Evolutionary Line: Bush, Tree, or Network?**

A productive example of “physics babble” being applied to biology was the question: What is the topology of life's evolution? Although outmoded in



**Figure 6.1** A chemoton model of a minimal living system. The chemoton (Gánti 1979) is a chemical supersystem composed of three autocatalytic subsystems: a metabolic network, a replicating template, and a boundary membrane. The metabolic subsystem, with intermediates  $A_i$ , is an autocatalytic chemical cycle, consuming  $X$  as nutrient and producing  $Y$  as waste material. Template molecule  $pV_n$  is a polymer of  $n$  molecules of  $V$ , which undergoes template replication;  $R$  is a condensation byproduct of this replication, needed to turn  $T'$  into  $T$ , the membranogenic molecule.  $T_m$  represents a bilayer membrane composed of  $m$  units made of  $T$  molecules. Building block  $T$  is spontaneously inserted by virtue of the fact that there is a preexisting membrane surface. The chemoton system can grow and divide spontaneously.

science, some popular conceptions still see evolution as a line, often progressing toward us. This is untenable. At the opposite end of the spectrum is the notion of an evolutionary network or tangle to describe the prokaryote realm. “Down there” frequent transfer of genetic information means that the various lines of descent may often have connections between them. In contrast, in the eukaryote realm, there is little horizontal gene transfer and an evolutionary “tree” or “bush” may reasonably describe the divergence of lineages. A “tree” can appear as a result of bottleneck event(s).

In our discussions, the concept of a Last Universal Common Ancestor (LUCA) was criticized and even described as a “phantom.” A glimpse at a typical tree of life drawn from LUCA at the center can create the erroneous impression that early life was not diverse. However, LUCA is really just an operational idea — the source of all the genetic information today — and it may more realistically represent a community that freely exchanged genetic information. There was much additional genetic diversity in that early population that has just not made it to the present.

### **Is Life an Unavoidable Cosmic Phenomenon?**

The likelihood of the origin of life is difficult to assess, not least because our existence is predicated upon it. This is a problem for Bayesian inference. If the interval to the first prokaryote life on Earth is short, then this suggests that prokaryote life is common in the Universe (Carter 1983). Although suggested morphological evidence for life at 3.8 Ga is no longer accepted, our group agreed that prokaryotic life was present by 3.5 Ga (Westall et al. 2001). This is a relatively short time after the Earth became habitable; hence, prokaryotic life is probably common.

If prokaryotic life is relatively easy to evolve, this raises the question: Did life begin once or many times? There is no clear evidence that life started more than once on Earth (if it did it would of course alter the evolutionary topology); however, absence of evidence is not evidence of absence. There are many extant cases of multiple origins within the network/tangle/bush of life, for example of multicellularity (~20 times) and social organization (in insects ~12 times). However, the simplest life we know of on the planet is very complex, hinting that the origin of such life involved at least one difficult transition.

The sequence of major transitions (Szathmáry and Maynard Smith 1995) is summarized in Table 2.1 (Chapter 2, this volume). Of the three transitions that precede prokaryote life, it is the third — the origin of the genetic code — that is thought to have been particularly difficult. Subsequently, the origin of the eukaryotic cell (cells with a well-formed cell nucleus, such as our cells) and the emergence of language are good candidates for further difficult transitions. A transition can be difficult for either or both of the following reasons: limitation by genetic variation or by natural selection. A variation-limited transition is difficult if the set of the requisite genetic variations is very unlikely to arise. Limitation by selection means that the right conditions for the spread of the appropriate genetic variation is very special and unlikely. A subcategory within selection-limited transitions is the case of “preemption”: though the first transition by itself is not so difficult, it modifies conditions to such an extent that a second, independent trial becomes virtually impossible (Szathmáry 2004).

With the premise that there are certain bottlenecks in evolution that represent “difficult” transitions, one can calculate how many such transitions there might

be in the history of our planet until observers arise. Carter (1983) argued that if observers find themselves arising about half way through the habitable life span of a planet, then there were probably two really difficult transitions to get to observers. Updating this, Andrew Watson noted that humans arise about four-fifths of the way through the habitable region of the planet, suggesting when one follows Carter's reasoning that there are four or five difficult transitions. In addition to the three mentioned above (origins of the genetic code, eukaryotes, and language), the origin of oxygenic photosynthesis may have been a difficult transition.

## LONG-TERM COEVOLUTION OF THE GEOSPHERE–BIOSPHERE

We adopted the basic premise of a coupling between the evolution of the biota and of the global environment. A number of hypotheses for connections between the evolution of life and of the environment are discussed by Lenton, Caldeira, and Szathmáry, Westall and Drake, and Franck and Zavarzin (this volume). A key outcome of this workshop was the realization that dating of the major transitions in evolution and, to a lesser extent, dating of the major transitions in the state of the environment are subject to large error bars. These need to be reduced (see final section) to address the potential causal relationships of coevolution.

A summary diagram of the time line of coevolution, with age error bars and arrows from one side to the other indicating necessary conditions or potential causal connections, is presented in Figure 6.2. Ages are given in billions of years (giga annum: Ga). This forms the basis for the following sections, where we set the geological scene for the emergence of life on Earth. Thereafter we offer two alternative narratives for the development of life and of the environment that highlight the current degree of uncertainty: (a) an optimistic narrative, which takes the earliest dates for various major transitions in the evolution of life; (b) a pessimistic storyline, taking the latest dates for major transitions in evolution.

The Earth system cannot be considered in isolation. Instead it is embedded within the dynamics of our solar system and our galaxy. Examples are impacts by large meteorites, which may result in severe insults to the biosphere with mass extinctions (e.g., the K/T event), or supernova explosions, which may cause a depletion of the stratospheric ozone layer and thus increase the flux of solar UV radiation at the surface of the Earth.

### The Planetary Setting

Planet Earth formed 4.56 Ga ago and the Moon was formed in an impact event 4.52 Ga ago. There are few rocks dating from 4.5–4.0 Ga and those in the range 4.0–3.5 Ga are highly metamorphosed. This meager record, however, tells us

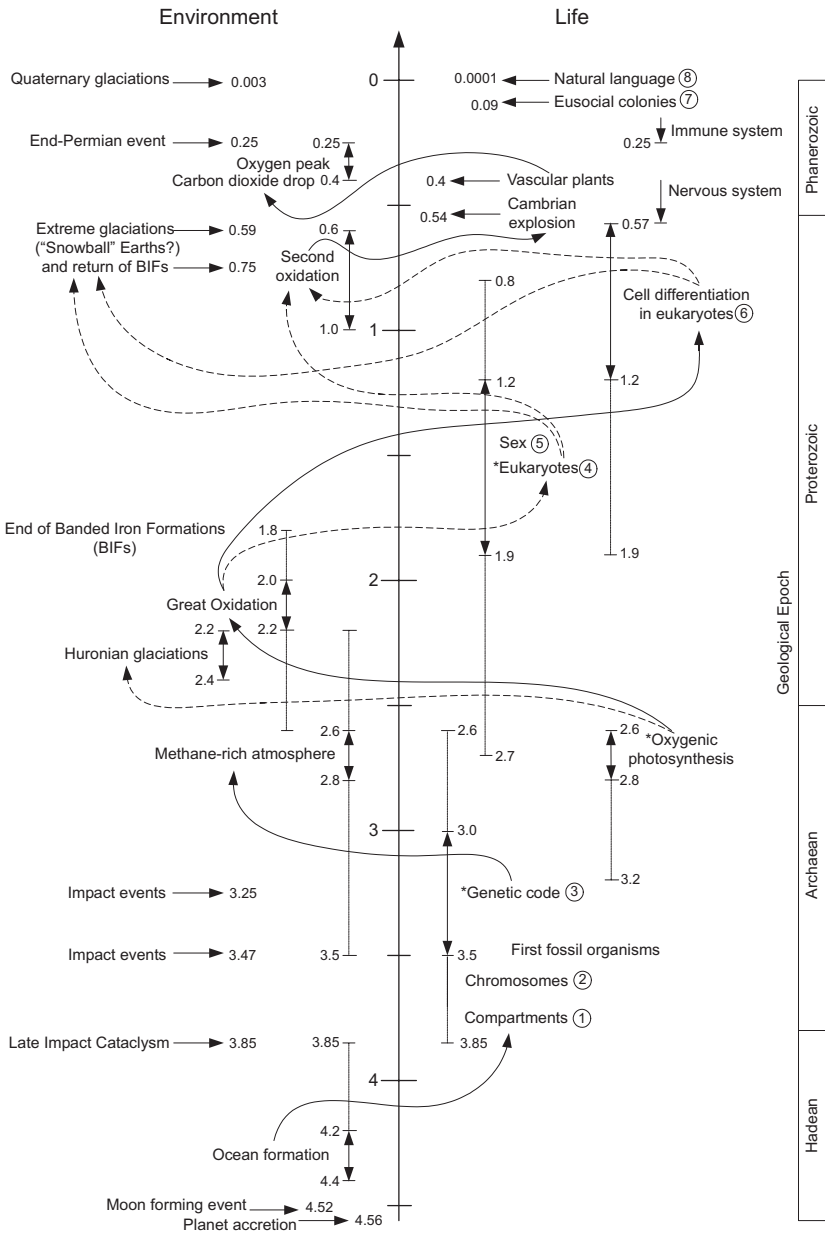
that there was water on the surface of the Earth 4.4–4.2 Ga and that some fractionation of hydrated crust took place to form protogranitic material. The early subaerial portions of the crust probably resembled Iceland and were rapidly recycled. They were not continents with broad continental shelves. Evidence suggests that up until the Moon's Late Impact Cataclysm at ~3.85 Ga, planet-sterilizing impacts repeatedly rendered the surface of the Earth inhospitable for life. However, there is one model that suggests that, even during the largest impacts, only about the uppermost 400 m of water from the oceans were vaporized (Ryder 2003). There were continued impacts after 3.85 Ga, notably at 3.47 Ga and 3.26–3.24 Ga, and these were 10–100 times more massive than the K/T event (Byerly et al. 2002; Kyte et al. 2003). Despite these, the Earth was in a relatively protected position within the Solar System, with Jupiter acting as a “sweeper up” of rogue asteroids. The prebiotic atmosphere was probably composed principally of CO<sub>2</sub> with some N<sub>2</sub>, CH<sub>4</sub>, and H<sub>2</sub>O. Ancient rocks indicate that temperatures, at least close to the seafloor, were very warm, the latest estimate being 70 ± 15°C (Knauth and Lowe 2003). There is still debate about the pH of the early oceans.

The oldest, best-preserved rocks come from the Early Archaean formations of Barberton in South Africa and the Pilbara in NW Australia, aged 3.5–3.2 Ga. These two relatively small areas of supracrustal rocks appear to have survived the ravages of plate tectonics because they represent regions which were underplated by a stabilizing “keel” that protected them from subduction and destruction. Making global extrapolations from just two locations is problematic, but there is no other material available at present. In terms of continental growth, important for providing suitable, stable habitats for the evolution of life, the period to about 3.0 Ga saw the production of a more rigid crust through continued fractionation to produce buoyant granitic material leading to the lateral plate tectonic style that we know. Tectonics caused cratonization whereby supracrustal masses were thrust together, eventually producing true continents with broad continental platforms and shallow shelves.

Carbonate formation in the Early to Late Archaean was related to the alteration of freshly formed lavas (and breccias formed by volcanic explosions and impacts) by seawater, a process called carbonatization, for which there is ample evidence. Carbonates were also deposited as hydrothermal exhalations. However, it was only from the Late Archaean onwards that large-scale carbonate formations started to appear, because this relied on the development of continental platforms.

### **THE OPTIMISTIC VIEW**

The following coevolutionary scenario assumes an early date for each of the major transitions in evolution. The scenario is one of a stable development of life (after the early asteroid bombardment) with occasional environmental crises (of terrestrial or extraterrestrial origin) giving a spurt to evolution.



### Planetary Stability → Evolution of Life

The evolution of life on Earth was contingent on the acquisition of oceans of liquid water and a relaxation of asteroid bombardment, at least to the point that the oceans were no longer being vaporized. This means that the earliest possible date for the emergence of life was 3.85 Ga. The first *bona fide* evidence for life comes from the rocks from Barberton and the Pilbara, 3.5–3.2 Ga (Westall et al. 2001) and shows that life was already highly evolved, having the same characteristics as modern prokaryotes in terms of cell morphologies, colony formation, biofilm formation on sediment surfaces, and carbon and nitrogen isotopic signature (Beaumont and Robert 1999; Westall et al. 2001). Stromatolites were biologically formed at this time (Byerly et al. 1986), but abiogenic stromatolites also existed (Lowe 1994). It is possible that anoxygenic photosynthesis may already have arisen (filamentous microbial mats in shallow water/littoral environments). There is, however, no mineralogical evidence for oxygenic photosynthesis. Pigments, which evolved originally as UV shields, could have been influential in the development of photosynthesis (Nisbet and Sleep 2001).

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**Figure 6.2** Time line of geosphere–biosphere coevolution on Earth. The time line runs from bottom to top, starting with the accretion of planet Earth and ending at the present with numbers indicating ages in billions of years (giga annum: Ga). The major geological epochs are indicated in the scale on the right. Left of the time line are major features of and changes in the state of the environment (geosphere), including some perturbations from outside the system. Right of the time line are major transitions in the evolution of life (biosphere), plus some other significant appearances. The major transitions in evolution are given abbreviated descriptions and numbers in circles following the scheme of Szathmáry and Maynard Smith (1995; see Table 2.1, Lenton, Caldeira, and Szathmáry, this volume), oxygenic photosynthesis is included as an additional transition, and asterisks are used to indicate difficult transitions. Two types of age error bar are used where major changes or transitions took sufficiently long or their timing is sufficiently uncertain to be resolvable at this scale. On the “Environment” side, the double arrowed lines indicate the time range over which we are confident that a feature or change was occurring, whereas the dotted lines indicate wider time ranges over which it may have occurred. On the “Life” side, the doubled arrowed lines indicate the time range over which we are confident a particular transition or group of transitions occurred, whereas the dotted lines indicate the absolute earliest and latest times that a particular transition or group of transitions could have occurred. The first three major transitions in the evolution of life are grouped together with the error bars being for the appearance of prokaryotic life with a genetic code. The fourth and fifth transitions are grouped together because sex is an ancestral trait of eukaryotes (i.e., it appeared at the same time). Arrows from one side of the time line to the other indicate historical contingencies (i.e., necessary conditions) or potential causal connections between the evolution of life and changes in the environment or *vice versa*. Solid arrows indicate connections that are better established and/or less controversial. Dashed arrows indicate less well established and/or more controversial connections. Some further connections are speculated upon in the text. For a full explanation of the various changes, transitions, and interconnections, see the text.

### Evolution of Life → Methane-rich Atmosphere

A methane-rich atmosphere has been proposed in the late Archaean (~2.7–2.8 Ga) on the basis of observed extreme carbon isotope shifts indicative of methanotrophy (biogenic methane consumption) (Hayes 1994), and to counteract the faint young Sun at the time (Pavlov et al. 2000). The greenhouse effect of methane (CH<sub>4</sub>) could have been especially important in the Archaean if one accepts a low limit on CO<sub>2</sub> from paleosols (Rye et al. 1995). In the anoxic Archaean atmosphere, abiotic, volcanic sources could have supported CH<sub>4</sub> < 0.0001 atm, whereas today's biological CH<sub>4</sub> flux would have generated CH<sub>4</sub> > 0.001 atm (Pavlov et al. 2000). The methanogens responsible for this flux today are close to the universal common ancestor. Hence they were probably present soon after 3.5 Ga. Methane could have been a major component of the atmosphere from then on, but methanogens alone would not have left a detectable geochemical signal. That had to wait for the evolution of methanotrophs that oxidize methane with oxygen or sulfate. Their appearance at ~2.7–2.8 Ga, while indicating an abundance of methane, would actually have lowered the methane content of the atmosphere by consuming it.

Oxygen was extremely scarce in the Archaean atmosphere (pO<sub>2</sub> ~10<sup>-11</sup> atm) prior to the origin of oxygenic photosynthesis. This suggests high UV radiation levels reaching the surface of the Earth that would have had a strong influence on mutation rates in early life. However, the flux of UV radiation would have been mitigated by the vast amount of aerosols and dusts in the atmosphere produced by the volcanic activity, as well as a hydrocarbon smog from the photochemical polymerization of CH<sub>4</sub> in the atmosphere (Pavlov et al. 2001). Moreover, early marine life would have been protected by water and the exposed mats were thick, robust polymer sheets where the outer layers would have protected the living organisms beneath, as happens today in exposed environments.

### Oxygenic Photosynthesis → Glaciations and Great Oxidation

The appearance of continental shelves and shallow water platforms over the period 3.2–2.5 Ga provided a suitable environment for the development of oxygenic photosynthesizers. The occurrence of abundant methanotrophy at ~2.7–2.8 Ga indicates that oxygen reached a modest concentration (pO<sub>2</sub> ~0.0005atm) at least locally, which was likely due to the evolution of oxygenic photosynthesis. The first direct evidence for oxygenic photosynthesis comes from chemical biomarkers in the 2.7-Ga Hammersley Basin rocks, Australia (Brocks et al. 1999; Summons et al. 1999). The oldest fossils that strongly resemble colonial cyanobacteria are found in 2.6-Ga formations from the Transvaal in South Africa (Altermann and Schopf 1995; Kazmierczak and Altermann 2002). Large stromatolites, generally thought to be constructed by

cyanobacteria, occur in shallow sea, continental platform settings and are common in the Proterozoic.

Oxygen may have risen sporadically from ~2.7–2.8 Ga onwards, culminating in the Great Oxidation at 2.2–2.0 Ga. At some point the oxygen flux to the atmosphere exceeded twice the methane flux and there would have been a catastrophic decrease in the partial pressure of methane causing global cooling. That may explain the onset of the extreme global (Huronian) glaciations 2.4–2.2 billion years ago. During the glaciation, productivity was suppressed and oxygen should have dropped. If a “snowball Earth” occurred, all nutrient input to the ocean and atmosphere–ocean exchange would have been blocked by the presence of a thick ice crust. Continued volcanic input of CO<sub>2</sub> gas into the atmosphere would have gradually increased temperatures until the ice melted. The vast amount of nutrients suddenly released into the biosphere would have led to a bloom of photosynthetic organisms at the surface of the ocean and a sudden increase in the source of oxygen. Perhaps the Earth went through a series of cycles of rising oxygen triggering glaciation, falling oxygen during glaciation, oxygen rising again afterwards, until the Great Oxidation put the system into a more stable state. Much of the O<sub>2</sub> produced (e.g., after glaciation) was taken up by the oxidation of reduced metal species in solution thus potentially explaining the abundance of banded iron formation (BIFs) at the time.

The evolution of oxygenic photosynthesis was a necessary but not a sufficient condition for the Great Oxidation. In addition, the right environment was required for the burial of organic carbon (which provides a long-term net oxygen source). Kerogen could be buried in sedimentary deposits or subducted to the mantle (Lindsay and Brasier 2002). Furthermore, the net input flux of oxygen had to exceed the input flux of reduced chemical species to the ocean and atmosphere (e.g., from volcanoes and methanogenesis) before oxygen could rise.

### **Oxygenic Photosynthesis, Glaciations, and Great Oxidation → Evolution of Eukaryotes**

The origin of oxygenic photosynthesis and the subsequent rise of oxygen in the atmosphere increased the energy available to the biota, aerobic metabolism being about five times more efficient than anaerobic metabolism. This may have increased the overall rate of mutation, such that there was an increased capacity for evolution. The Great Oxidation has often been portrayed as a disaster for the anaerobic biota. However, in the end it may have been advantageous for them, as it greatly increased their supply of food (organic matter).

The appearance of eukaryote life may be linked to local accumulation of oxygen beginning ~2.7 Ga, to the Huronian glaciations 2.4–2.2 Ga, and/or to the Great Oxidation 2.2–2.0 Ga (Evans et al. 1997; Ward and Brownlee 2000; Lindsay and Brasier 2002). Sterols from 2.7 Ga could indicate the presence of eukaryotes (Brocks et al. 1999) but are no longer accepted as unequivocal

eukaryotic biomarkers. Eukaryotes are mostly aerobic and have a higher oxygen requirement than aerobic prokaryotes, because the mitochondria are encased within a larger cell that limits oxygen diffusion. One hypothesis is that the compartmentalized eukaryote cell is a response to the accumulation of O<sub>2</sub> in the environment, following the evolution of oxygenic photosynthesis. Eukaryotic algae with photosynthesizing chloroplasts appeared later, but in a most optimistic scenario they could have predated and contributed to the Great Oxidation (Lenton, Caldeira, and Szathmáry, this volume). In particular, planktonic algae provide a much greater potential organic carbon sink than cyanobacteria in mats or open water (Paul Falkowski, pers. comm.).

Whether eukaryotes were a cause or a consequence of the Great Oxidation, the rise of oxygen provided a necessary condition for the later transition of cell differentiation in eukaryotes. The timing of this transition is very uncertain. *Grypania* was originally described as a multicellular eukaryotic algae aged 2.1 Ga (Han and Runnegar 1992). However, the age has now been revised to 1.9 Ga and it is unclear whether *Grypania* is a multicellular eukaryote or prokaryote. The oldest eukaryote that can be assigned to an extant phylum is a red alga aged 1.2 Ga (Butterfield et al. 1990; Butterfield 2000). Trace fossils and possible metazoan fecal pellets are widespread from ~1 Ga onwards.

### **Multicellular Eukaryotes → Neoproterozoic Environmental Changes**

A secondary Neoproterozoic rise in oxygen has been linked to either the origin of animals with guts and a consequent change in sedimentology (Logan et al. 1995), or an early evolution of phototrophic communities on the land surface (Lenton, Caldeira, and Szathmáry, this volume). The latter could also be implicated in cooling the Earth, thus priming it for extreme glaciations ~0.75 Ga and ~0.59 Ga (see Lenton, Caldeira, and Szathmáry, this volume).

### **Neoproterozoic Environmental Changes → Cambrian Fauna**

The secondary rise in oxygen was a necessary condition for the evolution of the Cambrian fauna. The contribution of an increase in calcium content of the oceans to the origin of biogenic calcification in the Neoproterozoic was addressed (*Cloudina* being the first calcifying organism). However, calcium seems unlikely to have been a limiting factor, the evolution of hard shells being attributed instead to protection from predation.

### **Vascular Plants → Permo-Carboniferous Environmental Changes**

It is reasonably well established that the rise of vascular land plants triggered a rise in atmospheric oxygen and an order of magnitude drop in carbon dioxide in the Permo-Carboniferous. The evolution of lignin resistant to biodegradation as well as an increased efficiency of phosphorus weathering from rocks may both

have driven a rise in atmospheric oxygen. An amplification of bulk silicate weathering due, for example, to increased depth of the soil profile, rock-splitting by plant roots, and amplification of the hydrological cycle drove a reduction in carbon dioxide.

## **A PESSIMISTIC SCENARIO FOR THE MAJOR TRANSITIONS IN EVOLUTION**

This scenario always assumes the latest possible dating for the appearance of different levels of organization. Such pessimism may be justified by (a) the general underestimation of the difficulty of certain transitions; (b) the contesting of the claim (Schopf 1993) of fossil cyanobacteria 3.5 Ga (a shift of ~1 Ga); and (c) the invalidity of sterols (Brocks et al. 1999) as eukaryotic biomarkers 2.7 Ga (at least 1 Ga shift).

### **Replicators → Compartments**

Fossils from 3.5 Ga indicate that some form of cellular life was present then. A long phase of chemical/replicator evolution is likely to have occurred between late bombardment and this date.

### **Compartments → Linked Genes (Chromosomes)**

Linkage and active segregation of genes is highly advantageous once the mutation rate is low enough. This allows a longer genome with a higher potential for complexity. If 3.5 Ga fossils are genuine, then they are likely to have had chromosomes, even made of DNA.

### **RNA Organisms → Encoded Proteins (Translation)**

It was speculated that many of the earliest fossils could be those of cells without a genetic code, but with actively catalytic genes (Szathmáry, pers. comm.). Whether there was something before RNA (requiring genetic takeover) is unknown, but its existence is possible. If one accepts the earliest unequivocal evidence for cyanobacteria (2.6 Ga), then the divergence of bacteria must have happened before that. Subjectively, the origin of translation is estimated to have happened in cells about 3 Ga (Szathmáry, pers. comm.).

### **Prokaryotes → Eukaryotes**

The major innovation giving a high selective advantage to early eukaryotes was phagotrophy, which also required formation of a cytoskeleton and an endomembrane system, including the nuclear membrane. Thousands of mutations must have been positively selected. Many eukaryotic genes have absolutely no

prokaryotic homologue. Archaeobacteria and eukaryotes are sister groups. Mitochondria came in very early, just after the origin of primitive phagocytosis. The eukaryotic nucleocytoplasm descended from some Gram-positive bacterium, similar to present-day actinobacteria (with sterols, proteasomes, and histon H1). The loss of the eubacterial cell wall triggered the revolution leading to eukaryotes (with a cytoskeleton) and archaeobacteria (with a rigid ether membrane) (Cavalier-Smith 2002).

Eukaryotic fossils must have a clearly identifiable trace of a nucleus, an endomembrane system, and a cytoskeleton (possibly all three together): mere size and shape resemblance to the cell/filament boundaries of present-day eukaryotes do not guarantee anything. The earliest unequivocal eukaryotic evidence is then 0.8 Ga (Porter and Knoll 2000). The eukaryotic revolution may be related to the major glaciations that began  $\sim 0.75$  Ga. Even if the ancestral eukaryotic host cell was aerophilic by itself, the acquisition of mitochondria offered an advantage at a time when oxygen levels would have dropped because of the inhibition of photosynthesis during extreme glaciation.

A corollary to this is that the first major oxidation (2.2–2.0 Ga) was due to cyanobacterial activity; the second (1.0–0.6 Ga) was due to the late arrival of eukaryotic algae.

### **Clones → Eukaryotic Sex**

Sex increases exchange of genetic information within the species level and is a primary character state for all known eukaryotes. It must have been selected for shortly after the origin of cytosis, in the form of an ancient ploidy cycle with incidental recombination. Genes for meiosis are related in all eukaryotes. Thus sex must have emerged at the latest 0.8 Ga.

### **Protists → Plants, Animals, Fungi**

The origin of complex forms of eukaryotic multicellularity was presumably triggered by oxidation (due to the rise of eukaryotic algae) after the extreme Neoproterozoic glaciations. Once again, only fossils clearly of multicellular eukaryote origin can be accepted: anything that can be interpreted as mere colonial protists must be rejected. This leaves us with 0.57 Ga for metazoan origin. These three kingdoms of plants, animals, and fungi have independently evolved a complex epigenetic inheritance system allowing for a large number of cell types and complicated development.

### **Solitary Individuals → Eusocial Colonies (Societies)**

Whereas reproductive skew is common, eusociality is much rarer. It means reproductive division of labor, cooperative brood attendance, and several generations living together. The first social insects date back to  $\sim 92$  million years ago.

**Primitive Societies (Protolanguage) → Complex Society (Natural Language)**

Natural language is unique to humans. It produces a cultural inheritance system with indefinitely large potential. It could have emerged sometime between 100–200 thousand years ago.

**NEW CONNECTIONS**

A couple of tentative new coevolutionary connections were suggested in our discussions:

1. End-Permian Extinction → Immune System: It was speculated whether the evolution of the immune system occurred in the aftermath of the End Permian extinction.
2. Quaternary Environmental Changes → Intelligence and Syntactic Language: The possibility of links between rapid changes in the environment during the Quaternary and the evolution of intelligence in our species was discussed. This includes the most recent difficult transition (the origin of natural language). Intelligence is a costly innovation in terms of the energy demand of the brain. The question is whether the environment may have changed rapidly enough to make it beneficial to have intelligence? Previous links have been made between Quaternary environmental change and human development, including the influence of 23 ka precession cycles on the monsoon region (Africa, Asia). However, any link to language development is unclear at this stage. If there is a link between rapid environmental change and human evolution, it was noted that our current inducing of global change could stimulate our own evolution. We return to discuss the evolution of intelligence in more depth below.

**ASTROBIOLOGY**

Astrobiology is a multidisciplinary approach to study the origin, evolution, distribution, and future of life on Earth and in the Universe, based on the assumption that life is a cosmic phenomenon. This includes the study of the formation of the elements, molecules, and processes that are involved in the formation of habitable planets and life. This holistic approach is based on Earth and terrestrial life as analogues for habitable planets and extraterrestrial life. Research includes:

1. The search for extrasolar planets, including potential signatures of life, such as water and oxygen (ozone).
2. Exploration of our solar system with special emphasis on Mars and Europa (or other moons of the giant planets, e.g., Calypso) that are potential candidates for having hosted or hosting still life.
3. Study of ancient life on Earth and potentially in extraterrestrial materials.

4. Studies on Earth of the strategies of microbial communities to adapt to extreme environments as terrestrial analogues for potential extraterrestrial life.
5. Laboratory studies simulating space conditions or conditions of other planets on chemical processes and the survivability of microorganisms under these conditions.
6. Modeling the habitable zones around stars or galactic centers.

Of the more than 100 extrasolar planetary systems discovered thus far, there are two (47 *Uma* and 55 *Cancri*) that may in some respect (mass of central star, giant planets at larger distances) be good candidates for systems with Earth-like planets in the habitable zone.

### **Is Astrobiology Feasible?**

It is clear that one can do some “astro”-biology on Earth (points 3–6 above), but what is our capability to detect life on other planets? Two missions are currently being designed to try and detect life on extrasolar planets: *Darwin* (ESA) and *Terrestrial Planet Finder* (NASA). Both plan to use a technique of interferometry to cancel out the light from the parent star and thus see any planets in orbit around them. Of particular interest are terrestrial planets (those with hard surfaces, of modest size, in inner orbits). The missions plan to use Lovelock’s technique of looking at the absorption spectrum of infrared light coming from such planets to try and deduce their atmospheric composition (Lovelock 1975). If gases coexisting in extreme thermodynamic disequilibrium (e.g., oxygen and methane) could be detected, this would be evidence for the presence of life. Although the detection of ozone (and thus oxygen) appears feasible, simultaneous detection of methane (which has narrower absorption bands in the infrared) does not, at present. Unfortunately, oxygen/ozone alone is not necessarily indicative of life, whereas extreme atmospheric disequilibrium is. Furthermore, the Earth’s atmosphere has only been oxidizing for approximately half of its history (the past 2.0–2.2 Ga). If we take this as a basis for designing extrasolar life detection, then the missions should equally look for a reducing atmosphere with traces of oxygen as indicative of life.

### **What Can Astrobiology Do for Earth System Analysis? (and vice versa)**

Modeling of potential extrasolar planets is bringing insights to Earth system analysis and the general question of planetary habitability (e.g., the influence of plate tectonics on habitability). The boundaries of the habitable zone in the solar system are mainly influenced by geodynamics (spreading, subduction, continental growth). It may be that the tectonic style of our Earth is an exception and the typical tectonic style for terrestrial planets is that of Mars (stagnant lid tectonics). The sudden stop of plate tectonics on Earth would result in an

interruption of the global volatile cycles on the 100-Ma timescale and in an earlier loss of habitability.

The importance of silicate weathering in the long-term regulation of carbon dioxide and climate (Walker et al. 1981) has become a key mechanism in studying both the Earth system and possible extrasolar planets. It relies on a hydrological cycle and, perhaps not surprisingly, models suggest that water worlds have more chances of being habitable than land worlds. This raised the question of whether water retention on Earth may be tied to atmospheric composition? In particular, is the existence of an effective cold trap and a “dry” upper atmosphere related to the presence of an ozone layer? This is discussed in the section on Gaia below.

### **Terraforming**

While it has the technological capacity, one thing that intelligent life may decide to do is attempt to make other planets or moons habitable. Such activity is usually described as “terraforming,” or more holistically as “ecopoiesis” (Fogg 1995). A favorite candidate planet is Mars. Indeed the seeding of other planetary bodies with life may already have started with incomplete sterilization of Mars landing space capsules (although it is questionable whether any life thus transported could survive on the surface of Mars). In the catalogue of questions generated before the workshop, the possibility of genetically engineering an organism that can be an agent of litho-panspermia was raised (this involves seeding by transport in meteorite fragments). Clearly this must rely on genes from terrestrial organisms, but a novel combination could be produced. One must ask: In which system do you wish to put the organism? Such activities raise considerable ethical questions and, encouragingly in our view, there are already treaties and planetary protection methodologies in place that protect any Mars life and protect the Earth from it (when returning samples).

### **Why Is Space Mute?**

Thus far, the search for extraterrestrial intelligence has failed. At face value, the absence of evidence seems to indicate that intelligence is an extremely rare phenomenon in the Universe. Does this in turn suggest that intelligence is extremely difficult to evolve? Or does it mean that intelligence is very short-lived in the cases where it does evolve? The puzzle is compounded by the recent estimation that most Earth-like planets are on average  $\sim 2$  Ga older than the Earth. If they underwent a similar sequence of major transitions to the Earth at a similar rate, then they could have been emitting detectable signals for  $\sim 2$  Ga. When we equate time with distance across space, this gives a large volume of the Universe from which we might expect to detect a signal.

Frank Drake (pers. comm.) offers, however, a cautionary note: although the Earth has been potentially detectable for the last 50–70 years of radio

transmission, we are currently getting less detectable and may soon become “invisible” in the radio frequency range. The reason is that bandwidth-sharing relies on low energy transmissions (a good example being a mobile phone network), and the resulting signals are not strong enough to be detectable across space (see also Westall and Drake, this volume).

A further intriguing possibility is that sending radio transmissions across the galaxy may not be such an intelligent thing to do. If a civilization makes itself known, it may risk “consumption” by a more aggressive civilization. Thus, the really intelligent thing to do would be to employ a sophisticated technique to hide messages and avoid detection! This science fiction scenario introduces the notion of a population of interacting planetary civilizations subject to some form of selection, in this case for radio-invisibility.

## THE EVOLUTION OF INTELLIGENCE

Is intelligence rare on habitable planets? Or is it a common, indeed probable phenomenon? These questions may be addressed not only by SETI but also from what we have learned about the evolution of life on Earth, where it has taken over three billion years to arrive at intelligent life. This suggests that intelligence is extremely difficult to evolve, and that a planet is quite likely to reach the end of habitability before it emerges (Carter 1983). Human-like intelligence may only appear in social, multicellular creatures. This implies that a planet’s life-forms must first pass through the earlier major transitions in complexity: from naked replicators, to prokaryotes, to something like eukaryotes, to something like metazoans. If the events leading to many or all of these transitions are rare and difficult, then we would expect that there are far fewer planets with eukaryote than prokaryote life, even fewer with large-bodied forms, and fewest with intelligence. In that sense, intelligence must be rare in the Universe, even on the habitable planets. However, *if* a planet has multicellular, social organisms, and *if* it still has a billion years of habitability left, is the transition to intelligence likely or unlikely? Here opinions differ sharply.

It seems that the initial transition to intelligence may have to cross an adaptive valley before it begins to matter. Intelligence has high costs in the energy of brain metabolism, in the vulnerability of the young, the demands of parental care, and the built-in danger of learning maladaptive behavior instead of efficiently following instincts, which have proved right in most cases in the past (Martin 1990). However, benefits are also very high to animals with a particular kind of life history, that is, a niche where environmental changes come often, but not too often. “Too often” means chaotic surroundings, where the experience of the previous generation offers little guidance. In that case, the best strategy is to be *r*-selected and hope that you can breed your way out of disaster by random survival. The benefits of intelligence also dwindle if environmental changes are

so slow that it is possible to evolve innate behavior patterns to cope with the environment in a predictable way (Lumsden and Wilson 1983).

On the right timescale, learning helps (e.g., for innovative omnivores or for seminomadic creatures exploring new habitats). One of the strongest pressures for flexible learning may be competition within the species, each group keeping up with others like intraspecific Red Queens. Any species competes, but the kind of competition we call warfare — where social groups challenge others — means that one must learn rather arbitrary definitions of our-own-group as opposed to the enemy-group. It also exerts intense selection pressure. Thus, chimpanzee tribal war could have been a strong spur to intelligence (Darwin 1871).

Another predisposing factor is fission–fusion societies, as found in chimpanzees, humans, and some cetaceans. In these, individuals of a group have strong social bonds but often forage alone or in subgroups. This means that one individual may possess information which others do not. There is then a value in sharing (or deliberately withholding) information about situations that are distant in space and time. This kind of society can lead to a “theory of mind” (Premack and Woodruff 1978), that is, the realization that another individual may not know what you know, and thus needs to be told. In experimental situations, apes and human four-year-olds demonstrate “theory of mind,” whereas monkeys and three-year-olds do not (Byrne and Whiten 1988, 1997; Whiten and Byrne 1997).

Finally, a tendency to eat embedded food may help. Some foods require a multistep process to open or find them, or even the use of tools. Again, flexibility matters. No primate uses tools as complex as a spiderweb, but the ability to learn food-obtaining behavior, such as termite-dipping, nut-cracking, or fish-net weaving marks both ape and human intelligence (Parker and Gibson 1977; Parker and McKinney 1999).

Our own intelligence depends on grammatical language, the *sine qua non*. It was once widely thought that other animals could not acquire words as symbols. It is now clear that common chimps and bonobos can acquire a 300-word vocabulary (with extensive training) and that dolphins can also learn and combine symbols (Savage-Rumbaugh and Lewin 1994). Laboratory chimpanzees spontaneously develop different food-calls to indicate specific foods (Hallberg et al. 2003).

The new rubicon is grammar. Although other animals combine words, they do not spontaneously produce agent–action–object phrases. Furthermore, attempts to have computer models or robots produce grammar seem to fail (Szathmáry, pers. comm.). This would suggest that grammar is a supremely difficult transition. On the other hand, it seems very odd to think that if animals do not have an agent–action–object view of the world. “You groom me” is different from “I groom you.” “Alpha male thumps Beta” is normal; “Beta thumps Alpha” is headline news. If an animal got as far as regular communication with symbolic words, it should not seem that hard to move on to simple grammar.

Two technical problems make the transition to grammar appear more difficult than it actually might be. One is that we have only one example: our own sophisticated language. It is as though we had to infer the evolution of the eye, given only one species with complex eyes, and nothing with simpler eye-spots. If we still had living *Homo erectus*, or even Neanderthals, we would not find it so hard to understand how the gap was bridged.

The other problem involves the picture of *H. sapiens* having emerged suddenly, around 50,000 years ago in Europe (and Australia), all ready to draw murals on cave walls, presumably commanding an assistant “Pass me the thick paintbrush and some red ochre.” The more Darwinian, gradualist view, precedes this with a 2 million year run-up, via *H. erectus*, grunting “My bone!” or “Handaxe, moron!” (invective enters most trained chimps’ vocabulary), or delightedly reporting, “Mabel baby!” A geometrically scratched stone, a few harpoon-heads, some ochre lumps in Africa suggest 100 thousand years of representation before the cave paintings, but the evidence is still very thin for representation earlier than 40 ka B.P. Still it seems more reasonable than the sudden, simultaneous appearance of artists and linguists in Europe and Australia, with no precursors.

A third, more fundamental, problem concerns the desire to see humanity as separate and special. It is a fair bet that if we did have semi-linguistic species around, we would raise the criterion of intelligence to the ability to tell a good story — including scientific stories of cause and effect. This, in fact, may be a more relevant criterion than grammar for *Pan narrans*, the narrating ape (Pratchett et al. 2002).

In sum: intelligence is rare, taking planets as a whole. Intelligence in the few planets with large creatures may be relatively common, if language can be taken step-by-step, following the logic of the need for communication brought by an innovative, social, competitive lifestyle. If, on the other hand, language is so complex that it is extraordinarily difficult to achieve, we may not be alone in the Universe but we might not have anyone else to talk to.

### **The Origin of Language May Indeed Be Difficult**

The fact that there cannot be too many genes involved in the ape-to-human transition by no means rules out the possibility that language was a genuinely difficult transition. Path-dependence of small populations is one of the key issues (Szathmáry 2004). Theoretical analysis shows that this depends on the relation between population size  $N$  and the rate of beneficial mutations  $u$  (Wahl and Krakauer 2000). If  $Nu > 1$ , then beneficial mutations occur together and can be simultaneously selected for (in sexual populations), whereas if  $Nu < 1$  then replicate populations *cannot* evolve in parallel because each will accumulate a different set of mutations, and even for an overlapping subset the order of incorporation will be different. Note that more complex organisms tend to be bigger, and

they typically have a smaller population size; hence adaptive evolution will be more path-dependent for them. This is especially true for the evolving human lineage.

According to one view (Szathmáry 2001), the largely novel faculty selected for was the ability of the brain networks to process syntactical information. The specific hypothesis is that linguistically competent areas of the human brain have a statistical connectivity pattern that renders them especially suitable for syntactical operations. It is thought that: (a) The origin of human language required genetic changes in the mechanism of the epigenesis in large parts of the brain. (b) This change affected statistical connectivity patterns of the neural networks involved. (c) Due to the selectionist plasticity of brain epigenesis, coevolution of language and the brain resulted in the genetic assimilation of syntactical processing ability as such.

If this is so, why is language not more common? It is hard to assess at the moment why language is unique. Even the “not enough time” case could apply, which would be amusing. But preemption, due to the subsequent cultural evolution that language has triggered, may render further trials very difficult indeed. There is, however, yet another consideration that indicates that language could be variation-limited in a deeper sense.

The habitat of the language amoeba is a large, appropriately connected neural network: most of the information processing within the network elaborates on information coming from other parts of the network. A special type of processing is required: that of hierarchically embedded syntactic structures. This leads to the following difficulties:

1. Neural networks contain a large number of cycles: syntactic structures of language are tree-like. It seems difficult not to process large trees without getting into loops.
2. Overproduction of initial synapses or decreased pruning, both implied in the origin of language, may easily lead to “solipsist” network dynamics, with two consequences: (a) the activity of the network is detached more than optimally from external sources of information; (b) exaggerated internal processing leads to too much “internal talking”: linguistic processing for its own sake.

## GAIA

Having reviewed the geosphere–biosphere coevolution on Earth and introduced astrobiology, we are in a position to address more general Gaia questions.

### **How Important Is Habitation to the Maintenance of Habitability?**

Habitation is contingent on habitability; however, once life is established, can it influence the maintenance of habitability? We broadly define habitation to mean

a first-order influence on the geochemical cycling of a planet. This is a more quantitative definition of life than “abundant life” (Lenton, Caldeira, and Szathmáry, this volume). Thus, life eking out a meager existence in a few localities does not amount to habitation.

The factors required for habitation include a free energy source, essential elements, liquid water, a tolerable temperature, and not too much UV. Recycling of the crust (i.e., plate tectonics) was put forward as a further necessity, and this warrants further theoretical research. Autocatalytic recycling of essential elements is also required for life to achieve a first-order influence on geochemical cycling. This in turn is mediated by life, introducing an element of “boot-straping” to achieve habitability. To retain liquid water, a planet must avoid high rates of H atom loss to space. It was noted that the rate of H loss can be influenced by biology; for example, in a methane-rich atmosphere it will be increased (Catling et al. 2001). Furthermore, H loss depends critically on the thermal structure of the atmosphere, and the existence and effectiveness of a cold trap may ultimately depend on oxygen and thus on life.

Existing studies have mapped out the dynamics of the habitable zone in the future. One study suggests that habitation will prolong the habitability of the Earth system, at least for plants, by maintaining the Earth in cool conditions when otherwise it would be too hot for them (Lenton and von Bloh 2001).

### **How Globally Destructive Could Life Become?**

The habitability question may be inverted to ask: Could the biota force a critical environmental variable to the level that would make the biota extinct? It was generally agreed that this may be possible if there is a long time lag in the system. However, if there are no time lags, the system should be stable, because detrimental effects of life on the environment will become self-limiting.

There is no convincing evolutionary model to argue either way. There are, however, models that could form the basis of future research. The best such model of global coevolution for application to Gaia is that of Stenseth and Maynard Smith (1984). This couples within-species interaction with multi-species dynamics, speciation, and extinction. The population genetic timescale within species is captured by an average lag load ( $L$ ). The lag load of a species is defined as:  $(W_{max} - W) / W_{max}$ , where  $W$  is the average fitness and  $W_{max}$  is the maximum fitness attainable if the evolution of every other species is assumed to be halted. The species number ( $S$ ) captures global biodiversity. The rate of change of each with time is a function of both (an autonomous system). The four possible solutions are: (a) spiraling into an attractor with a constant rate of speciation and extinction (known as the “Red Queen” solution), (b) extinction (of all species), (c) explosion, and (d) stasis (when the species number is constant and maximal, with zero speciation and extinction rates). Only the Red Queen solution and stability are feasible for Earth history. Paleontologists have shown an

interest in the model, for addressing what happens after a major extinction event. The few million years it took for recovery in the aftermath of the K/T extinction event would tend to support the Red Queen solution. Extending this model to include an environment variable is a topic for future research.

The destruction question was made more specific in the form: Can an organism evolve to produce a compound that disrupts the biosphere and nothing can consume it? Looking back into Earth history, a striking example presents itself: the evolution of the production of lignin, causing rising oxygen. After a time delay, fungi evolved the capacity to biodegrade lignin. However, it is unclear whether it was this evolution or simple thermodynamics in the form of fire that prevented oxygen from rising. The “invisible hand” argument (Smith 1776) was put forward and states that for every new waste product there is sufficient variation and creativity in evolution that something will eventually evolve to biodegrade it. This deserves to be tested more thoroughly.

### **Autocatalytic Gaia**

Our group was clearly inclined toward the view that life is an inevitable planetary phenomenon. A rather bolder proposition was also agreed upon: that with life, autocatalytic recycling is an almost inevitable planetary phenomenon. This is a natural extension of the autocatalytic nature of life from the internal environment to the external environment. It was suggested that there is a lock-in effect of recycling. Some of the processes in the recycling loop may be abiotic. However, once closed recycling of essential elements has emerged, it will maintain itself. Such a system is not vulnerable to evolutionary “cheats” because “You can cheat when you are talking about information, but you can’t cheat when you are talking about matter and energy” (Szathmáry, pers. comm.).

### **Can Gaia Be a Role Model for Human Society?**

It was noted with wry humor that humans are currently “terrafouling” Earth rather than terraforming elsewhere. In other words, we are making a mess of our home planet. Our group proposed that Gaia may provide a role model for human society in our quest for sustainability. One way to proceed would be to identify the negative feedbacks that can provide stability to the social system without central control, and the positive feedbacks that can amplify features that are desirable. This was termed a “sociocatalytic” theory. It is irrational, or at least unwise, to assume that humans are rational actors. Game theory was largely unsuccessful in economics because of the assumption of rationality, but successful in evolutionary biology because natural selection is a supremely rational process.

Broad lessons of sustainability can be gained from Gaia. First and foremost, the system has developed and flourished without extra inputs of matter and energy. It is both creative and variant. This undermines the common assumption

that economic growth is necessary for the development of society. We do not need an ever-increasing energy usage to develop as a society! Some cautionary thoughts on globalization also emerged. In particular, one superorganism may be more vulnerable than a population of systems. The bigger the system is, the more vulnerable it is. If the nation state becomes less relevant in the future, we may revert to smaller units that are more stable (there are historical examples to support this). Regarding energy systems, it is clear that the same systems are not appropriate everywhere, and there needs to be diversity to achieve efficiency. This is likely to be a more stable solution than the current drive to make the same energy system work everywhere.

### **THE IMPORTANCE OF AVOIDING TIME LAGS**

We note from our discussion of Gaia that to protect the global system, time lags must be avoided. The reason is that a long delay between cause and effect can allow the cause to reach disruptive proportions before the effect generates any counteracting negative feedback. The introduction of time delays can cause a system to move from a stable domain to a limit cycle (oscillation) and potentially to chaotic behavior. In the Daisyworld model, the original form of which is extremely stable, the introduction of a large heat capacity generates thermal inertia in the system and causes it to oscillate (Nevison et al. 1999), whereas the introduction of discrete generations can lead to deterministic chaos (Jascourt and Raymond 1992). In the real world, long time lags may be caused by the slow response of large reservoirs; for example, atmospheric oxygen at present has a response time of millions of years. One alarming example of the introduction of a potential time lag is the proposal to modify trees genetically to suppress photorespiration in the carbon-fixing enzyme RuBisCO (ribulose biphosphate carboxylase/oxygenase). This has the potential to increase the oxygen source and affect the long-term oxygen balance of the planet. It would take millions of years for changes in atmospheric oxygen to trigger a response, and that response might be quite catastrophic, for example, involving global wildfires.

### **FUTURE RESEARCH AGENDA**

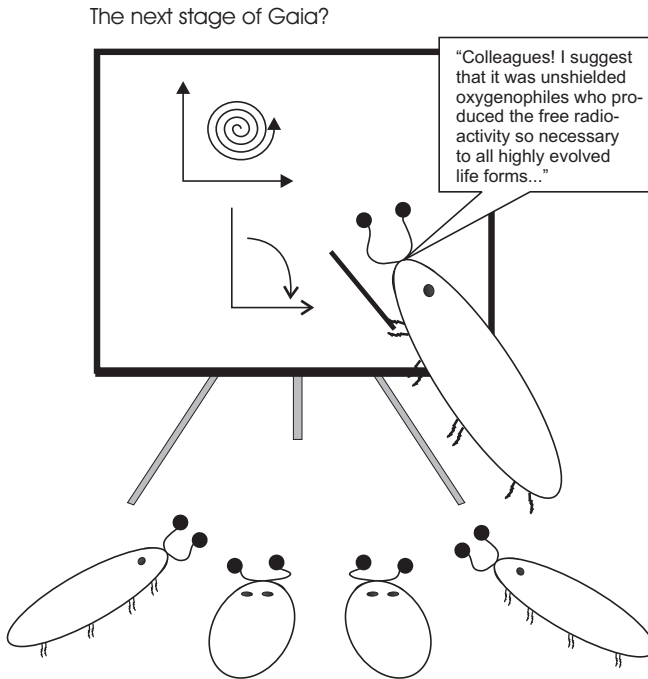
Proposals for future research that emerged during our discussions can be summarized as follows:

1. Origins and evolution of life:
  - a. Given the proposed model of life, the concept of major transitions in evolution should be extended to encompass transitions in all three subsystems of life:
    - i. Boundary system.
    - ii. Metabolic system.
    - iii. Genetic system.

2. Coevolution of the geosphere–biosphere:
  - a. Narrow the error bars in the timing of:
    - i. The major transitions in the evolution of life.
    - ii. The major changes in the state of the Earth system.
  - b. Improve understanding of the causality of coevolution (or is it the co-causality of evolution?):
    - i. Conduct thought experiments *in silico* with generalized (Earth) system models.
    - ii. Is there only one pathway for life through the redox couple sequence?
    - iii. Is there only one pathway for a Gaia system from reducing to oxidizing conditions?
  - c. On specific linkages:
    - i. What was the role of life in the Great Oxidation?
    - ii. What was the role of life in Neoproterozoic environmental changes?
    - iii. Is there a link between environmental change and the evolution of natural language?
3. Astrobiology
  - a. Generalize Earth system models and biological evolution models for use in thought experiments in the search for planetary life:
    - i. If we could stop plate tectonics on Earth, what would happen?
    - ii. If we sterilized the Earth, how long would it remain habitable (e.g., to prokaryotes)?
  - b. Minimum requirements for a sustainable ecosystem on Earth and elsewhere:
    - i. What is the minimum functional diversity required to set up a sustainable ecosystem and what can we learn from terrestrial ecosystems?
    - ii. Are there spatial and temporal limits for the persistence of communities and species?
    - iii. Where and how can we detect habitable and potentially inhabited sites beyond the Earth?
  - c. Extension of human activities beyond the Earth:
    - i. What are the investments required for human migration beyond the Earth (needs, costs, benefits, social and ethical consequences)?
4. Gaia
  - a. Develop generic models to explore the evolutionary dynamics of Gaia systems
    - i. Add dependence on the environment as a third variable to the model of Stenseth and Maynard Smith (1984).
  - b. Gaia as a role model

- i. Develop a systems model of society synthesizing biological, cybernetic and institutional theory.
- ii. Explore the feasibility of a flexible investment framework for achieving the transition to sustainability (highly mobile and available capital  $\sim 1\%$  of global GDP).

In the Dahlem spirit, we offer a humorous final thought on the future of coevolution (created by Alison Jolly during our discussions):



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