ONE

LEARNING FROM LIFE ON EARTH IN THE PRESENT DAY

The only known habitat for life is the planet we call Earth. The only place we know the life experiment has been carried out is this planet Earth. We do not know how life originated here, however. Nevertheless, we understand a great deal about the physical and chemical conditions, the environments, and some of the spontaneous ('self-organising') mechanisms that the physics and chemistry of this Universe make possible, so there is no difficulty in formulating reasonable models for the emergence and onward evolution of living things. One of the best existing books about this topic starts like this:

> The main assumption held by most scientists about the origin of life on Earth is that life originated from inanimate matter through a spontaneous and gradual increase of molecular complexity. This view was given a well-known formulation by Alexander Oparin [Oparin, 1957a], a brilliant Russian chemist who was influenced both by Darwinian theories and by dialectical materialism. A similar view coming from a quite different context was put forward by J. B. Haldane [Haldane, 1929]. By definition, this transition to life via prebiotic molecular evolution excludes panspermia (the idea that life on Earth comes from space) and divine intervention. (Luisi, 2006, chapter 1, p. 1)

Although I intend to discuss here the notion of panspermia (see Chapter 5, below), I will not discuss the other mechanism that Pier Luigi Luisi says is excluded by prebiotic molecular evolution in the quotation above, namely divine intervention. I choose not to include this because personally I see no need to invoke divinely magical or mythological processes in the *scientific* story I wish to tell: basic physics and chemistry are enough. If you want to round out your reading on the topic then I suggest you start with chapter 1 in Luisi (2006) and chapter 6 of Lurquin (2003). For the real hard-core discussion you don't need to go much further than Dawkins (1986, 2006) and Scott (2009). If you put the words 'dawkins' and 'god' together in Amazon's search window, the software will display publications on both sides of the argument, and from the number of items offered you may get an inkling of why I decided not to venture into this part of the arena!

Having indicated what I will not discuss, let me indicate what I will describe here. This book examines the most likely mechanisms by which life arose and progressed on Earth as we understand it from the most recent research. In many ways this book is a tourist guide in which I will escort you, the reader/tourist, through more than 4 billion years of the historical journey experienced by this planet. Because the only known habitat for life is planet Earth, we will start by examining how the habitat that has cradled the life we know about was formed. Among others, we will visit the following intellectual places:

- The formation of the Earth, in context of the origin of the Solar System, and how the basic chemistry, physics and geology of the early Earth influence the search for the origins of life.
- From this argument I will advance the view that the origin of life may be a logical inevitability of chemical evolution in a wide range of environmental conditions and I will account for the origin of biological building blocks on a prebiological world from a wide range of sources.
- Although it is most frequently argued that the primitive Earth's ocean was the one and only location in which prebiological chemical evolution could have occurred, I will develop the notion that for very extensive periods of time, billions upon billions of aerosol droplets existed all over the protoplanet Earth within which billions upon billions of different chemical reactions *might* have taken place, forming molecules and reaction trains that *might* have contributed to the origin of life.
- This leads naturally to speculations about evolution of almost-living protocells of all sorts: those without a genetic apparatus, those comprised of autocatalytic chemical cycles, the RNA-world and protein-world precursors of living things, and those exploiting advantages of existing within lipid envelopes –with all of these existing at the same time but in different aerosol droplets.
- Bring those aerosols down to earth in rain or spindrift and they will form slime upon the sterile solidified volcanic lava. Where that slime is protected from hostile solar radiation by tephra or in lava bubble caves something like a prebiological biofilm will form, within which all

pathways were effective (if they *could* happen, they *did* happen) and where they coexisted and were coextensive they could work together, creating ever more integrated and interconnected chemical systems.

- Life emerged from non-enzymatic systems of autocatalytic chemical cycles which later acquired the capacity of enzymatically controlled metabolism.
- The characteristics expressed by the earliest living, or even pre-living, things (their 'lifestyle') were those that today would be categorised as being ***heterotrophic***. The first chemical machines used readily available nutrients. As these were exhausted, selective advantage was gained by those chemical machines able to release chemical catalysts into the environment to degrade the tars and other polymers accumulated by hundreds of millions of years of abiotic chemical reactions.
- Much of current biology is dependent on symbiosis, so 'symbiotic associations' *must* have also been important in prebiology.
- This will lead logically to the idea that different types of protocells, each good at one particular process, must have coexisted. Some might have found selective value in collaborating, or in symbiotically absorbing and using other protocells, or in exuding factors (primitive enzymes and/or toxins) that targeted other protocells to open them up and make use of their constituents.
- The first living things arose on Earth as soon as conditions allowed and within a relatively short time the Earth became a planet dominated by primitive bacteria, with the majority still in biofilms.
- Further levels of collaboration within those biofilms allowed the higher organisms (eukaryotes) to emerge, initially as a one-celled organism that possessed a mixture of characteristics from which evolved the animal, fungal and plant lineages that we know today.

There are a great many publications in the literature that deal with these topics, particularly among those published in the last ten to twenty years. So, why add yet another one? Well, I would claim that the unique feature of the argument I wish to present here is that it is based on appreciation of the central role of the fungal grade of organisation in the evolution of higher organisms. This has never been done as far as I am aware, which is a pretty remarkable omission, but I believe the main reason for this is that most writers on the topic of the origin and early evolution of life have been, and still are, essentially ignorant of the distinctive features of fungal cell biology that set them apart from plants and animals, with little more knowledge of fungi than that revealed to them in primary school.

And fungi are very different from both plants and animals. Despite this, for most of the early period of the science of biology, the fungi were thought to be plants, peculiar and non-photosynthetic perhaps, but plants nevertheless. Generally speaking 'fungi' in this context means mushrooms and toadstools, and the fact that they appear on the ground among green plants in nature accounts for their association with plants. Indeed, fungi were initially firmly classified as plants and were even given an evolutionary history that derived them from algae by loss of photosynthesis. In the early part of the twentieth century it became increasingly clear that there are a great many fungi in the world. Beyond the most obvious mushrooms and toadstools, which are themselves incredibly diverse and numerous, there are enormous numbers of filamentous moulds: microscopic and soil fungi that have colonies, called mycelia, where the main body of the fungus is made up of thin, cottony, thread-like filaments that are called hyphae. There are also a great many yeasts: single-celled organisms that are specialised for growth in liquids, particularly small volumes of liquids like the sugary fluid in flower nectaries, or raindrops and dew drops on fruits and flowers, as well as the fluid circulation streams of both animals and plants in parasitic or pathogenic species. Yeasts are perfectly respectable fungi, though their specialism to a particular habitat has made them reduced in their form and structure, so their relationship to the overwhelming majority of other fungi, which are characteristically filamentous (or 'hyphal'), is in many respects similar to the relationship of flightless birds to the majority of other birds.

Most books about the origin of life have been written by physicists, cosmologists, astronomers and molecular biologists, all of whom, for some reason, think that biology is a lesser science than their own. For example: 'physics and chemistry, possibly more than biology, held clues to [the origin of life and the cosmos itself]', which is a quotation from the first paragraph of the preface to Lurquin (2003), who is a plant chemist/molecular biologist. Other authors apologise for their shortcomings but proceed undaunted; for example, the physicist Dyson (1999) quotes this from Schrödinger (1944) (yes, the one with the cat):

> . . . some of us should venture to embark on a synthesis of facts and theories; albeit with second-hand and incomplete knowledge of some of them, and at the risk of making fools of themselves. So much for my apology.

And Freeman Dyson adds:

> This apology for a physicist venturing into biology will serve for me as well as for Schrödinger, although in my case the risk of the physicist making a fool of himself may be somewhat greater. (Dyson, 1999, chapter 1, p. 2)

A properly modest standpoint, except that, save for photosynthesis, Dyson's view of biology is narrowed to include only animals, which leads him to worry about aspects like encephalopathic prions and embryonic development of animals; neither of which have much relevance to the origins of life.

Similarly, while there is a great deal to admire in the chemoton theory of the chemical engineer Tibor Gánti (Gánti, 2003) he is extremely animal-centred, as is Conway Morris (2003); and Lane (2010) reveals his bias with the phrase 'so many creatures, even plants, indulge in sex' (chapter 1, p. 3).

Animal centricity is one of the two common failings of many of the 'origin of life' publications: plants often get a mention, but a strong impression remains that they are mentioned only because their photosynthesis provides the essential oxygen for the important organisms, animals, to get on with the business of being real living creatures. James R. Griesemer (in Gánti, 2003) refers to the 'vertebrate bias' with these words:

> Hull (1988) pointed out that there is a substantial 'vertebrate bias' in the types of features that biologists, who are all vertebrates, take to be 'typical' of organisms, even though vertebrates are very 'atypical' organisms (see also Buss 1983, 1987). Modern genes may be just as atypical of replicators in general as vertebrates are of organisms in general; it is an empirical question with implications ... (Gánti, 2003, chapter 5, p. 172)

It's worth noting that even Charles Darwin was close to suffering this animal bias in his work on the insectivorous higher plants known as sundews (Latin generic name *Drosera*). His wife, Emma Darwin, in a letter to Lady Lyell, August 1860, said:

> At present he [Charles] is treating *Drosera* just like a living creature, and I suppose he hopes to end in proving it to be an animal. (Darwin & Litchfield, 1915, p. 177)

Just like a living creature? Is a plant not a living being? Many of the papers and books that have been published recently, as well as the majority of biology and natural history programmes broadcast on radio, TV and Internet reinforce this animal bias.

The second common failing is that fungi, if mentioned at all, are dealt with in a perfunctory and sometimes indifferent manner. In Tom Fenchal's book, *The Origin & Early Evolution of Life*, the Introduction starts promisingly enough:

> This book is about the development of life from its origin and until multicellular plants, fungi, and animals arose ... (Fenchel, 2002)

Unfortunately, fungi are acknowledged to be one of the crown groups of eukaryotes in this way:

> Plants, animals and fungi are relatively closely related, but they derived independently from different protists. The fungi are more closely related to animals than to plants (which should be noted especially by botanists and vegetarians). (Fenchel, 2002, chapter 12, p. 122)

The recognition is satisfying, and is more than most books manage, but I find the closing phrase unnecessarily dismissive.

I respect these various sources for the contributions they have made to discussion of the origin of life, and (as you must have realised by now) I will be quoting from them where appropriate, with all due reference and acknowledgement, even though I consider their lack of appreciation of fungi a severe disappointment. Their understanding of the physical sciences may be enviable, but their appreciation of biology and living systems is frequently naive and sometimes banal. It seems that the biologists too, even the eminent ones, are no better informed and I trace the cause to severe flaws in our educational system. As I have commented before, with various colleagues (Moore & Pöder, 2006; Moore *et al.*, 2006; Moore, Robson & Trinci, 2011, preface, pp. ix–x) this partial view of biology afflicts the school curriculum and results in most current biology teaching, from school-level to university, concentrating on animals, with a trickle of information about plants and bacteria. This results in the majority of school and college students (and, since they've been through the same system, most current university academics) being ignorant of fungal biology and of their own dependence on fungi in everyday life. Allow me to explain.

I think it's likely that the lack of a proper appreciation of the fungal lifestyle is a severe limitation to understanding the origin and early evolution of life on Earth because, as I will argue below, the first eukaryotes had the nutritional and cell-biological attributes of fungi as well as features that later emerged in plants and animals. From this primitive, almost protofungal, stem the first to diverge were the plants. This left what are known as opisthokonts, ancestors of both animals and fungi, which are organisms with a single posterior flagellum. Finally the animals diverged from these, leaving their sister ancestral opisthokonts to evolve into fungi. That is, animals are the last of the crown group of eukaryotes to diverge and are therefore least informative about the point of origin of eukaryotes; and although they diverged early, plants are narrowly channelled into a specific way of life and are therefore less informative than fungi about the point of origin. Known fungal evolution 'is not marked by change and extinctions but by conservatism and continuity' (Pirozynski, 1976); an observation comparing very ancient fossil fungal spores to modern fungi, which implies that the fungal lifestyle will be informative about the point of origin. I should explain here that I am using the word 'lifestyle' as a synonym for 'body plan' as used by Cavalier-Smith (2006, 2010a):

> It cannot be coincidental that the largest expansion of protist diversity in Earth history immediately followed these global glaciations. The pump was primed by the earlier origin of eukaryotes. Glacial melting did not initiate cellular innovation; it just released the pent-up potential for

> innovation and rapid radiation that major new body plans themselves create. (Cavalier-Smith, 2010a, p. 127)

It is clear that Tom Cavalier-Smith includes physiological features under the same phrase:

> . . . adaptive zones for the new phyla were created for the first time by their novel body plans, e.g. water splitting (oxygenic) photosynthesis by cyanobacteria and their immediate ancestors, phagotrophy by eukaryotes. (Cavalier-Smith, 2006, figure 8 legend)

Indeed, the fungal nutritional lifestyle/body plan has been at the essential centre of the evolution of life on this planet from its very start. To remind ourselves about this it is worth extracting some quotations from Robert Harding Whittaker's original 'New concepts of kingdoms of organisms' paper (Whittaker, 1969). With regard to nutritional modes, Whittaker wrote:

> There are, however, not two principal modes of nutrition [photosynthetic and ingestive] but three – the photosynthetic, absorptive, and ingestive. The three modes largely correspond to three major functional groupings in natural communities, the producers (plants), reducers (saprobes, that is, bacteria and fungi), and consumers (animals) . . . The importance of the reducers in the cycling of materials in ecosystems appears to exceed that of the consumers. In evolution ingestive nutrition was a development secondary to the absorptive nutrition of most monerans and many eucaryotic unicells. Both protozoans with food vacuoles and metazoans with digestive tracts have probably evolved from absorptive flagellates, and in this evolution internalized the process of food absorption and added to it the process of ingestion. One may consider that the eucaryotic plants also have internalized the absorption of food through a membrane, that surrounding the chloroplast as symbiont and organelle. The three modes of nutrition imply different logics on which the evolution of structure in higher organisms was based . . . (Whittaker, 1969, p. 152)

The relevance of this to discussion of the origin of life is that even in discussions of prebiotic chemistry a common notion is that some sort of compartment would absorb material from its outside to convert to more of the substance of its inside (an 'absorptive protonutrition').

> The taking in of organic substances dissolved in the surrounding aqueous medium and their transformation into parts of its own body is, obviously, the absolutely indispensable form of metabolism in a living body which arises by the incorporation of polymeric organic compounds into multimolecular systems. (Oparin, 1957a, chapter IX, p. 400)

I will show below that there is good reason to believe that the prebiotic primeval Earth was well supplied with a wide range of organic compounds varying from simple sugars and amino acids to peptides, carbohydrate polymers and polyaromatic hydrocarbons (PAHs) made up of several to many rings of carbon atoms – all these being the results of abiotic synthesis in locations as different as the surface of the Earth itself or other objects in the Solar System, through to interstellar space. Most arguments see the need for the prebiotic compartment (Oparin's coacervate; see Chapter 9) to first take up simple compounds from its medium and then, as these are exhausted, to release catalytic materials (reactive ions or metabolites/peptides/ribozymes) into the medium to break down larger molecules into simple compounds that the compartment can continue to absorb.

This is a step on the way to life; a prebiotic stage which depends on an evolutionary logic (using the phrase coined by Whittaker, 1969) that is the principal nutritive mode (saprotrophism) among modern-day bacteria and fungi; and it is the shared evolutionary logic which is the important point. The fungal grade of cellular organisation is a eukaryotic grade of organisation, but the strands of evolutionary logic that gave rise to it apply just as much to the primeval (prebiotic) period as to the later periods of cellular evolution of prokaryotes and eukaryotes alike. It is perhaps worth mentioning that despite recent antipathy to use of the word 'prokaryote' the prokaryote–eukaryote dichotomy 'reflects a profound evolutionary truth' (see discussion in Cavalier-Smith, 2010a, p. 113) and is one that I will continue to use.

Fungi, which today form a gigantic and diverse group of organisms, were all classified as plants right up to the middle of the twentieth century. This is when the notion began to crystallise that fungi might form a group of higher organisms different from both plants and animals. That is, that in their own right fungi might form a distinct kingdom of eukaryotes (organisms whose cells contain complex membrane-surrounded structures, in contrast to the mainly bacterial prokaryotes that generally do not have membranous structures within their cells). A classic publication on this topic is the paper, from which I have already quoted, entitled 'New concepts of kingdoms of organisms' (Whittaker, 1969) that contributed, with many other publications, to the present situation where fungi are not classed as animals or plants, but have a kingdom of their own to which they belong. This 'Kingdom Fungi' is amazingly diverse and includes organisms that range from being just a single cell, like the yeasts, to others that cover hundreds of acres of land. Indeed, some fungi are among the largest organisms on the planet (Arnaud-Haond *et al.*, 2012). One individual mycelium of the tree pathogen *Armillaria ostoyae* has been found in the mixed-conifer forest of the Blue Mountains of northeast Oregon in the USA that covers 965 ha (2384 acres; equivalent to 1355 Premiership football fields, or seven times the size of London's Hyde Park and three times the size of New York's Central Park). This mycelium is estimated to be 1900 to 8650 years old (Ferguson *et al.*, 2003).

To date, 100 000 species of fungi have been discovered but it is thought that there are over one and a half million species still to be found. Fungi can live in many habitats from polar regions to temperate and tropical forests, and in both fresh and salt water. However, most fungi live in soil. The fungi that most people are familiar with are those that form mushrooms and toadstools (there's no technical difference between a mushroom and a toadstool, essentially the words are synonyms). But mushrooms are not organisms in their own right, they are the fruiting bodies of a much larger and more extensive mycelium growing beneath the ground within the soil (mushrooms are analogous to the apples on an apple tree). The Kingdom Fungi is extremely diverse; in the British Isles there are 15 000 known species of fungi, 4500 of which are mushrooms (200 edible and only about 50 being poisonous to some degree), yet the British Isles can claim only 48 known species of mammal, 210 species of birds, and 1500 species of higher plant. The number of fungal species in Britain rivals the known species of insects (22 500 British species), but that comparison might misleadingly underestimate the diversity of the fungi as virtually every individual insect carries a load of parasitic fungi, many of which are species-specific, so in Britain (and the rest of the world) there may be many as yet unnamed entomogenous (which means 'growing on or in the bodies of insects') fungi.

Fungi are not able to produce their own food directly as plants do; rather, fungi recycle dead organic matter by discharging a full range of digestive enzymes into their surroundings. These enzymes degrade organic material outside the mycelium and then the hyphae ingest the soluble nutrients produced by that external digestion. Organisms like this are said to be saprotrophs, which means 'decomposer' because they live by digesting debris left by other organisms. A saprotroph is a specific kind of heterotroph, or consumer, which gets its nutrients ready-made from its environment. This distinction will become important when we have to start thinking about how the first organisms made a living a few billion years ago. Those that were literally 'the first' must have got their nutrients from their surroundings, but by definition, those nutrients could not have been left as debris by other organisms (because there hadn't been any); so the first organisms were heterotrophs, just consuming what was available (and as we will see, quite a wide range of organic compounds was available). But as soon as some of those organisms died, the second generation of organisms that came along would have been able to evolve ways of using the dead debris of the first; that is, they could have been saprotrophs, recycling debris like modern-day fungi. They would not have been fungi in those distant days, but they would have shared the characteristic fungal lifestyle.

In most soil environments of the present day, the bulk of the debris is made up of plant litter, such as leaves, plant stems and woody branches. But fungi are able to produce a complete range of digestive enzymes and are equally able to digest the protein, cartilage and bone of animal cadavers, and the chitinous exoskeletons of insects. They can also extract nutrients, like metal ions, phosphorus and sulphur, from inorganic minerals. But it is in the digestion of woody plant cell walls that the fungi demonstrate their unique abilities to recycle. Only fungi can degrade woody lignin, and without fungal wood decay the world would fill up with dead timber – as it did in Carboniferous days, 360 million years ago (mya), when the thickest coal seams were laid down because at that time the fungi had not yet evolved the ability to recycle dead timber so the wood just accumulated until it fossilised into coal.

The cell walls of plants are very strong. The components that provide the strength are cellulose (the sugar-based molecule from which the first, or primary, plant cell wall is made) and lignin (the phenol-based molecule that is characteristic of the plant cell's secondary cell wall). Fungi are very important for the decay of wood because they are the only organisms capable of breaking down both cellulose and lignin. Cellulose is a polymer of glucose that forms fibres that are incredibly strong. Brown rot fungi break down cellulose. Brown rot fungi are so called because the lignin remains intact and the wood keeps its brown colour. The enzymes released by brown rot fungi break the cellulose chains into single molecules of the sugar glucose that can be absorbed and used by the fungus. Lignin is the other strong polymer. It is the second most abundant natural polymer on Earth after cellulose. Fungi that break down lignin are called white rot fungi; this is because as it is digested and the content of lignin is decreased, the wood becomes lighter in colour. White rot fungi degrade lignin by producing oxidising enzymes that are released from their hyphae; in a very real sense they 'burn' the wood in an enzyme-controlled way. Lignin contains phenols and the white rot fungi are the only organisms that can deal with them (the fungi open up the carbon rings to form open chain molecules that can be metabolised). These two types of fungi have important roles in the recycling of nutrients. Without them, old plant material would not decay and the soil nutrients would be locked into an accumulating mass of undegradable lignin-based biomass. So, today, it is entirely thanks to the fungi that all the leaves that fall from the trees, the branches, and even the whole dead trees that fall to the ground in storms are broken down and recycled into nutrient-rich humus that can be used by plants for their growth.

This lifestyle, based on their ability to exude digestive enzymes that are able to recycle most of the organic (and some of the inorganic) matter in their environment, is a major contribution that fungi make to life on this planet, but it is not their only contribution. Fungi form a crucial part of the food web in most natural habitats; snails and slugs, mice, voles, squirrels and deer regularly eat lichens, mushrooms, toadstools and truffles as a major part of their diets, while millipedes, insects, insect larvae and beetle grubs eat the hyphae of mycelia in the soil. Throughout their existence, fungi have formed