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Patterns In Palaeontology: The first 3 billion years of evolution.

by Russell Garwood *[1]

Introduction:

Breathe in. Breathe out. It's a good bet that you're currently sitting in front of a computer, reading; I'm going to go ahead and assume that you're breathing, too. In, and out. You probably weren't even thinking about breathing until I mentioned it, but all the same, it's keeping you alive. Oxygen from the air is being transported into the cells of your body, which are using it to create energy. So far, so good. But what you may not realize is that the cellular machinery performing this process so integral to our existence (Fig. 1) has roots buried deep in the geological past. It's a story that begins before the origin of organized cells, in an ancient, alien world. But if we're going back that far, we might as well go all the way back, to the very beginning. After all, to be breathing, you have to be alive. How did that happen? How do we define 'being alive'? Without further ado, let's find out. Breathe in. Breathe out. And back to the origin of life.

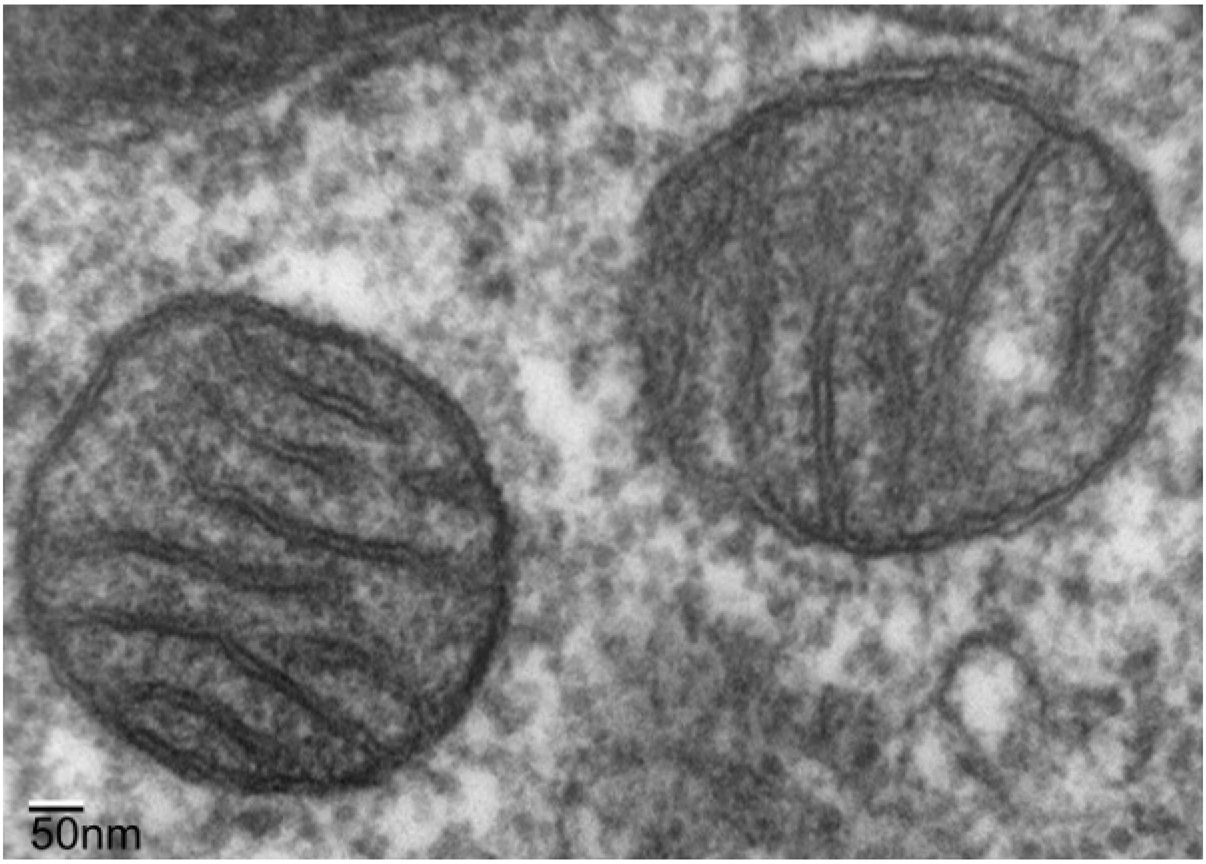

FIGURE 1 — TWO MITOCHONDRIA, THE STRUCTURES WITHIN ANIMAL CELLS THAT ARE RESPONSIBLE FOR PRODUCING THE CELLULAR ENERGY SOURCE ATP IN THE PRESENCE OF OXYGEN. THESE TWO ARE FROM A MAMMAL'S LUNG.

Origins:

In the beginning: The building blocks of life — as we know it, at least — are liquid water (a wonderful solvent that remains liquid at a large range of temperatures) and organic polymers that provide function and structure. Before we can have life, we need these raw materials. Water comes, in part, from Earth's mantle, which in its early history would have contained lots of 'hydrated' minerals — those with molecules of water as part of their crystal structure. It's a surprisingly soggy place. Water would have escaped from the mantle through volcanic eruptions, and got into the atmosphere. Another likely source of water is icy asteroids and comets that stuck the planet. The organic compounds on Earth originated both from Earth-based syntheses — in which they were made by elements reacting in the atmosphere — and from space. Recent research has shown that interplanetary dust particles, comets, asteroids and meteorites are all rich in organic compounds. These include amino acids (the building blocks of proteins) and nucleobases, which are integral to DNA.

Timing: Our little blue dot started forming 4.54 billion years ago (4.54 Ga) — that's 4,540 million years. During accretion, the temperature would have been too high for water to have existed as a liquid, but current geochemical evidence suggests that from 4.4 to 4.0 Ga, extensive oceans could have existed for long periods, allowing simple organic compounds to accumulate. Perhaps it was during this quiet period that key steps in the origin of life occurred. An interplanetary stick in the spokes occurred at around 3.9 Ga: a period lasting between 20 million and 200 million years, called the late heavy bombardment (Fig. 2). During this period, material from space battered Earth, and could have killed any life that existed (we know about this event from craters on the Moon; no rocks on Earth are this old, thanks to the effects of plate tectonics). However, computer models suggest that the late heavy bombardment is unlikely to have sterilized Earth completely, so it remains a distinct possibility that life originated before 3.9 Ga.

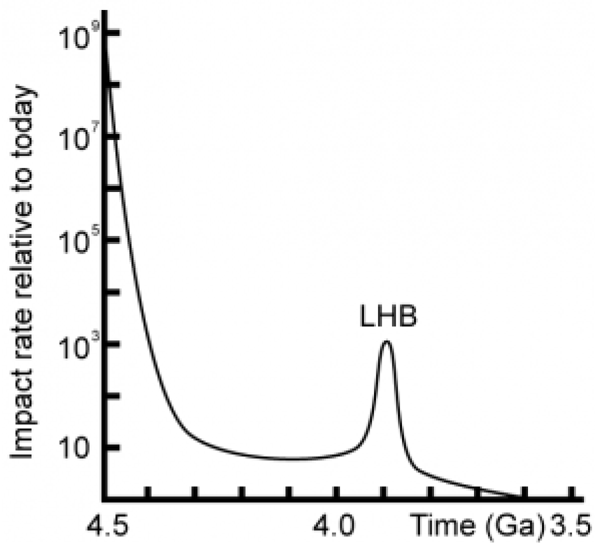

FIGURE 2 — A DIAGRAM SHOWING THE NUMBER OF IMPACTS FROM SPACE ON AN EARLY EARTH.

Abiognesis: If we're looking for the origins of life, first we have to define it, which is where... ahem... life becomes tricky. At their most basic level, living organisms show self-sustaining biological processes, and the ability to replicate imperfectly (that imperfection providing the raw material for natural selection). It's not a perfect definition, because there is something of a grey area between living and non-living — for example viruses, which replicate but can't do many of the other things associated with life on their own — but it will have to do. Defining the point at which we can consider early molecules or systems life is similarly tricky, so we'll just gloss over that and recognize that at some point, abiotic (non-living) chemistry must have acquired the characteristics of living systems, probably in a series of steps. This marks the origin of life: an event called abiogenesis.

We'll cover here just two of the theories currently vying for attention regarding how abiogenesis may have occurred. The first — known as the prebiotic soup hypothesis — posits that life began in a relatively cool aquatic environment. Organic compounds would have accumulated in primordial oceans, and could have been concentrated by freezing or evaporation of the water. Further reactions could have led to increasingly complex molecules, including small polymers. All that would be required from that point is for one molecule, by chance, to develop the ability to catalyse its own replication, and an evolutionary cascade could begin. These molecules would become more and more abundant, and natural selection could mediate their changes. An alternative model, the metabolist hypothesis, posits a hot and volcanic origin for life. This suggests that a self-sustaining chain of reactions could have evolved first, close to mineral-rich hydrothermal systems near the ocean floor (Fig. 3). If this was the case, the first 'life' would not have possessed informational molecules. Once the reactions had increased in complexity, though, these genetic molecules would be needed for modern biochemistry to develop. The two hypotheses aren't entirely mutually exclusive. For example, self-sustaining reaction chains could have caused the prebiotic soup to become enriched in hard-to-synthesize or unstable molecules.

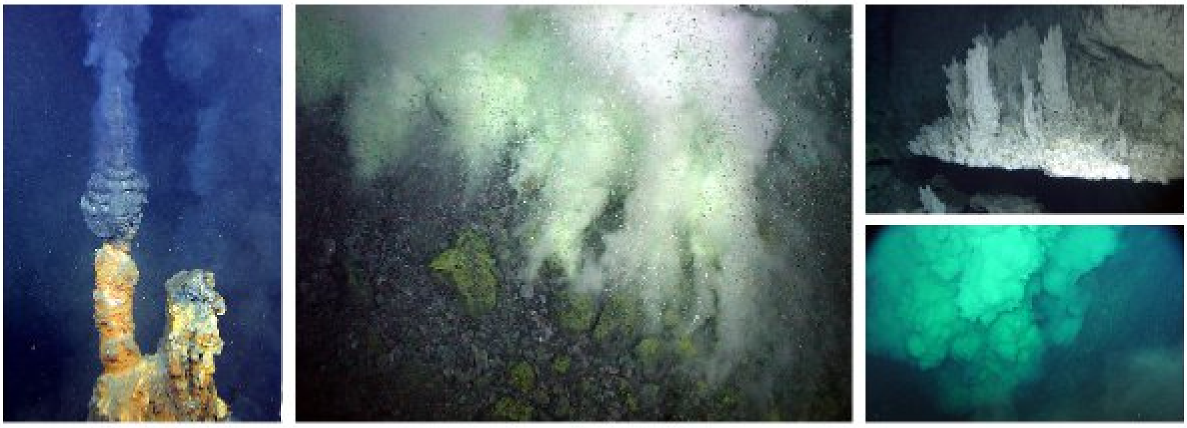

FIGURE 3 — EXAMPLES OF HYDROTHERMAL VENTS ON THE OCEAN FLOOR, SUCH AS THAT POSITED IN THE METABOLIST HYPOTHESIS. LEFT: A TYPICAL BLACK SMOKER. MIDDLE: A DEGASSING EVENT WITH BUBBLES OF CARBON DIOXIDE; YELLOW SULPHUR IS VISIBLE ON THE OCEAN FLOOR. TOP RIGHT: DENDRITIC (BRANCHING) CARBONATE MINERAL GROWTHS, WHICH DEVELOP WHEN HOT MINERAL-RICH FLUIDS HIT COLDER WATER. BOTTOM RIGHT: A SMOKY PLUME FOUND IN THE SAME LOCATION AS THE DEGASSING EVENT (MIDDLE) NEAR THE NORTHERN MARIANA ISLANDS.

Early evolution:

So, that's all very exciting: the first step in our, and everything else's, evolution. By this point we're probably somewhere before 3.8 Ga, and have all the ingredients for life: molecular entities capable of multiplication, heredity and variation. Good stuff. I hope you're still reading and, for that matter, breathing. Again, I'll assume you are and we can move swiftly on, because quite a lot happened over the next billion years.

Cells: Life as we know it involves cells: membrane-bound packets of life (again, we're ignoring those pesky viruses!). Early genetic molecules probably needed some protection from the vagaries of the early oceans, and this may have come in the form of globules of fatty acids (Fig. 4). These long molecules are special in that they have a water-loving (hydrophilic) head, coupled with a water-hating (hydrophobic) tail. Because of this, when in water they can spontaneously join together to form balls with the hydrophilic end outside and the hydrophobic end inside, which can grow and divide, while retaining a portion of their contents. This may well be the origin of cell membranes.

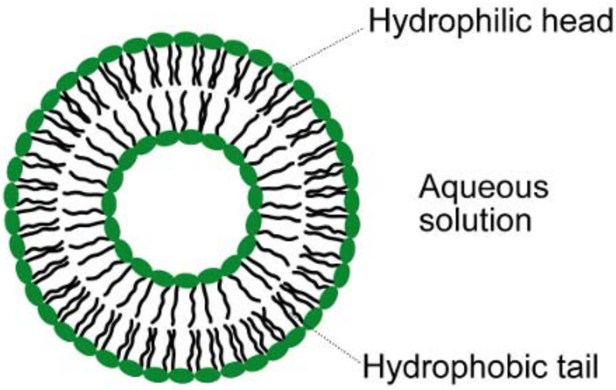

FIGURE 4 — THE PROBABLE ORIGIN OF CELL MEMBRANES: A VESICLE.
THESE SMALL GLOBULES NATURALLY FORM FROM FATTY ACIDS IN WATER.

Early genetic molecules: Life as we know it relies on genetic molecules — long compounds found in cells, which store the information needed for life. In modern cells this is DNA. From DNA, proteins can be created by the molecule RNA, through a process known as protein synthesis (more information). DNA is, however, a horribly complex compound, and it is very unlikely that this was the first genetic molecule. We're fairly sure that before DNA, RNA was the genetic molecule of choice. There could also have been a precursor to RNA — some form of polymerized self-replicating molecule, with the capacity to store and pass on information. The nucleobases and the backbone of any early genetic molecules may have been different from DNA and RNA.

RNA: RNA (Fig. 5) is an all-in-one molecule: it can both store information and catalyse reactions. When it acts as a catalyst we call it a ribozyme, and it has the capacity to carry out a wide range of important biochemical reactions that early life may have needed to survive. For example, it's likely that by the time RNA-based life was established, there was no longer a ready supply of non-biological organic compounds. Because there were no raw materials to sustain life, simple metabolic-like pathways are likely to have appeared to provide the components needed for life. It is during this RNA world that protein synthesis may have become established: four of the basic reactions involved in protein biosynthesis are catalysed by ribozymes. It is possible that viruses are a hangover from an RNA world (although this is quite a can of worms and we probably shouldn't open it here). Viruses don't have cells — they hijack other cells' molecular machinery for their own nefarious ends — but they are large RNA molecules.

DNA and protein world: In autumn — especially if you happen to be in regular contact with university students (trust me on this) — people start coming down with colds and flu. We don't build immunity to these minor ailments because they mutate very quickly. That is because they are RNA-based, and RNA is relatively unstable compared to DNA. Thus RNA-based agents mutate quickly, which is not ideal for healthy self-replication

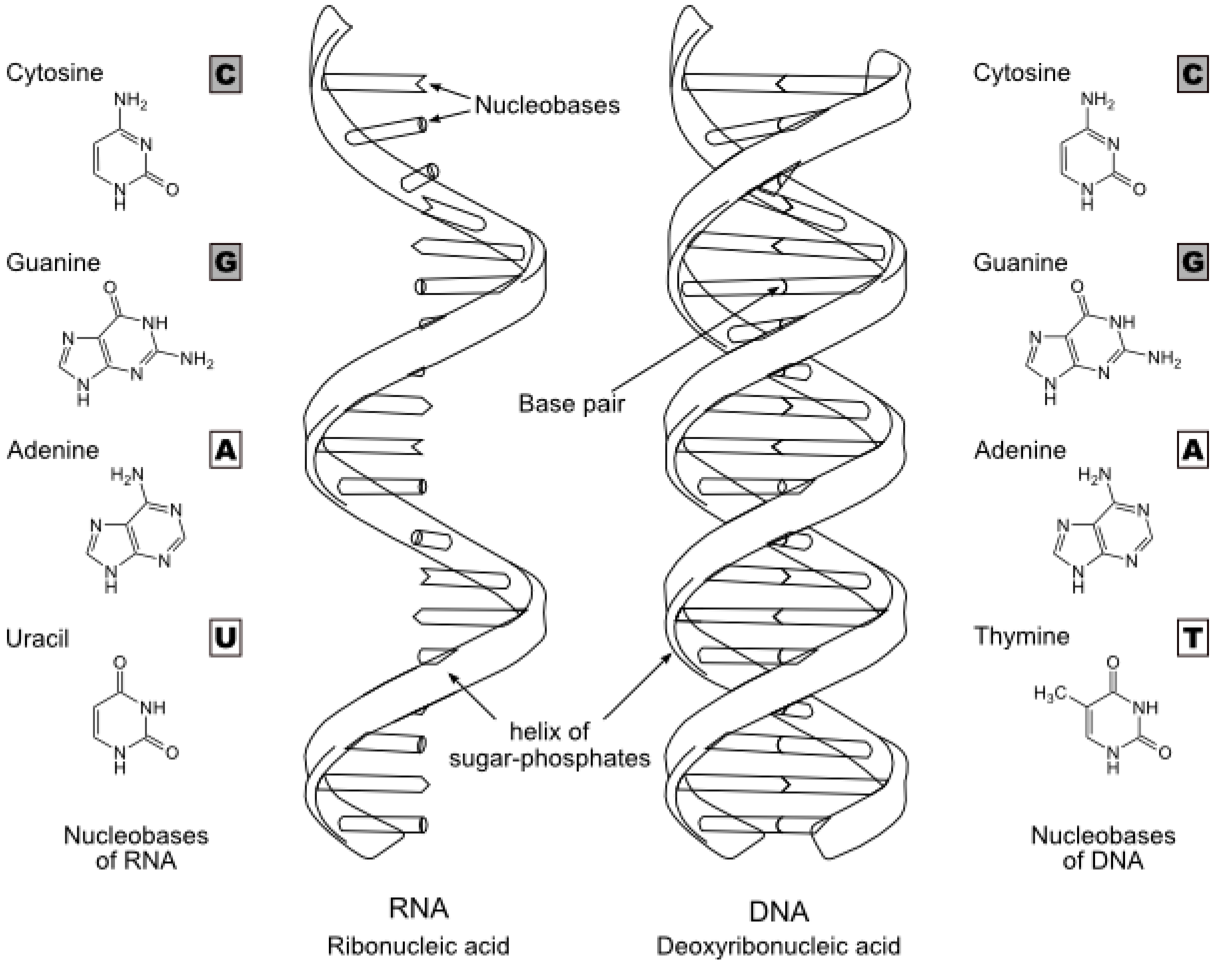

FIGURE 5 — A COMPARISON OF THE GENETIC MOLECULES RNA AND DNA. RNA IS USED DURING PROTEIN SYNTHESIS; DNA IS STORES THE GENETIC INFORMATION OF AN ORGANISM. BOTH HAVE FOUR BASES AND A MOLECULAR BACKBONE, BUT RNA IS OFTEN SINGLE-STRANDED, WHEREAS DNA IS DOUBLE-STRANDED. IMAGE CREDITS.

(or indeed our autumnal/hibernal health). At some point, ribozymes that could catalyse the polymerization of DNA (Fig. 5) must have arisen, and genetic information was transferred to DNA — a much more stable molecule. This enhanced stability would have allowed molecules to get longer and store more genetic information, and to reproduce without as many mistakes. All of this would eventually have allowed more complex organisms to evolve. RNA would then have been demoted to its current role as a messenger and transcriber of DNA.

Milestones:

LUCA: Early in the history of life, probably before 2.5 Ga, the last universal common ancestor (LUCA) of all extant organisms lived. The tree of life seems to be rooted in hyperthermophilic organisms (those adapted to high temperatures), so it has usually been assumed that LUCA was just such a specialist. However, there is currently little conclusive proof of this — indeed, researchers remain uncertain that the tree of life is truly rooted here. Furthermore, it seems that the proteins used by these specialists are heat-adapted versions of those found in other organisms, so they probably didn't arise first in a heat-loving organism. Thus — beyond the fact that it was probably some form of bacteria-like micro-organism that used DNA as its genetic molecules, we have relatively little idea what LUCA was like.

Prokaryotes: Life as we know it is split into two groups with different basic cell structures. One is the 'prokaryotes' — comprising the Archaea and Bacteria, which look similar (Fig. 6). They tend to be smaller than 10 micrometres (one micrometre is one-millionth of a metre) in size, and have no nucleus or internal membrane-bound structures. Their DNA is a single loop sitting freely inside the cell. Generally, Archaea and Bacteria are unicellular, reproduce by simple (asexual) splitting, or fission, and use horizontal gene transfer for genetic recombination. They obtain energy by a wide variety of means, meaning that they can 'breathe' all kinds of elements, from hydrogen sulphide to iron. Although the Archaea and Bacteria are superficially similar, they possess very different biochemistry, suggesting that they split fairly early in the history of life (see also Fig. 8 for a tree).

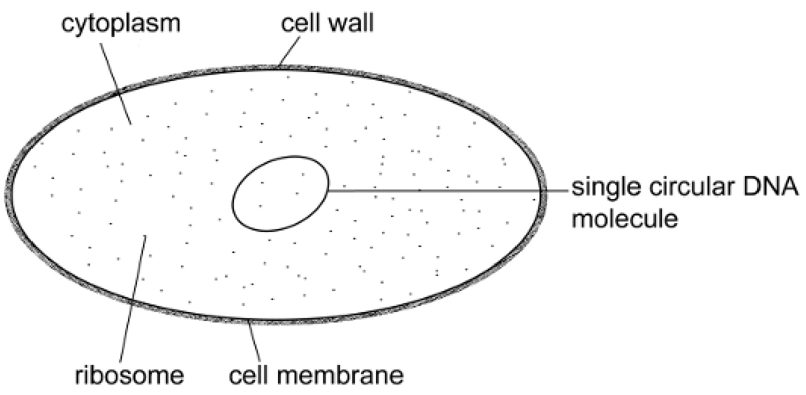

FIGURE 6 — THE BASIC STRUCTURE OF A 'PROKARYOTE' CELL, SUCH AS A BACTERIUM OR ARCHAEAN. THERE IS ACTUALLY NOTABLE MORPHOLOGICAL DIVERSITY WITH THESE SINGLE-CELLED ORGANISMS.

Eukaryotes: Organisms with more complex cells (such as fungi, plants, animals and amoebae), belong to a second group, known as the Eukaryota. Their cells tend to be larger (10–100 micrometres) and they possess organelles (Fig. 7) — membrane-bound structures in the cytoplasm (interior) of the cell. For example, mitochondria process oxygen to provide the cell with energy, and in some organisms chloroplasts are responsible

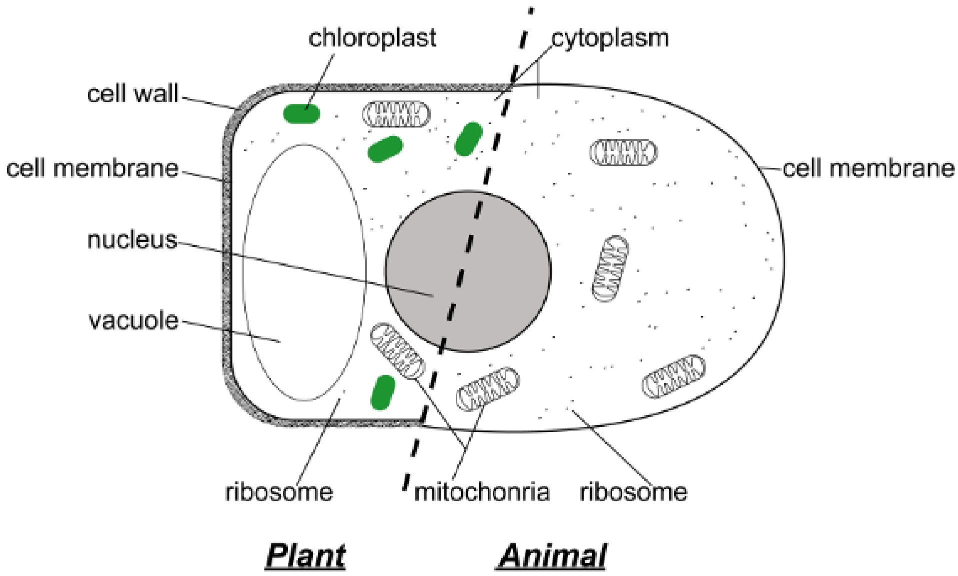

FIGURE 7 — EXAMPLES OF PLANT AND ANIMAL EUKARYOTE CELLS. A NUMBER OF OTHER ORGANELLES ARE OMITTED, BUT THE DIFFERENCE BETWEEN THESE AND PROKARYOTE CELLS IS CLEAR

for photosynthesis. The nucleus houses the DNA, which is found in long molecules that form chromosomes, and organisms are often multicellular with differentiated cells doing specialized jobs. Cell reproduction occurs by mitosis, with meiosis for sexual reproduction, which is the norm for genetic recombination

Endosymbiosis: One of the key theories for the origin of the complex structures in the cells of eukaryotes is an idea called endosymbiosis. It's all kinds of awesome. Central to this idea is that the organelles come from the long-term cooperation, or symbiosis, of two prokaryotes. The earliest internal structure, and by far the hardest to tie down, is the nucleus. This could be the result of an endosymbiotic relationship, or it could have evolved without this process (an autogenous origin). However, the story for mitochondria and organelles such as chloroplasts (a type of plastid) has far less ambiguity. Mitochondria retain portions of their own DNA, and were originally bacteria with the ability to respire oxygen. At some point — perhaps owing to a failed attempt at predation — they started to live inside a larger organism. Current theories are split over whether this was a eukaryote, with nucleus already present, or another prokaryote. If the former, the mitochondria could have had a role in making oxygen less toxic for an anaerobic host. If the latter, the host may have been an archaen, within which primitive mitochondria could have produced hydrogen as a source of energy and electrons for the host cell. In both scenarios, over time, the organisms would have come to rely on each other totally, and mitochondria would have lost their cell walls and transferred some, but not all, of their genetic material to the hosts. So all the time you've been reading this you have been burning oxygen because of cellular heritage more than 1 billion years old: a lasting tryst between two early unicellular organisms. Neat, huh?

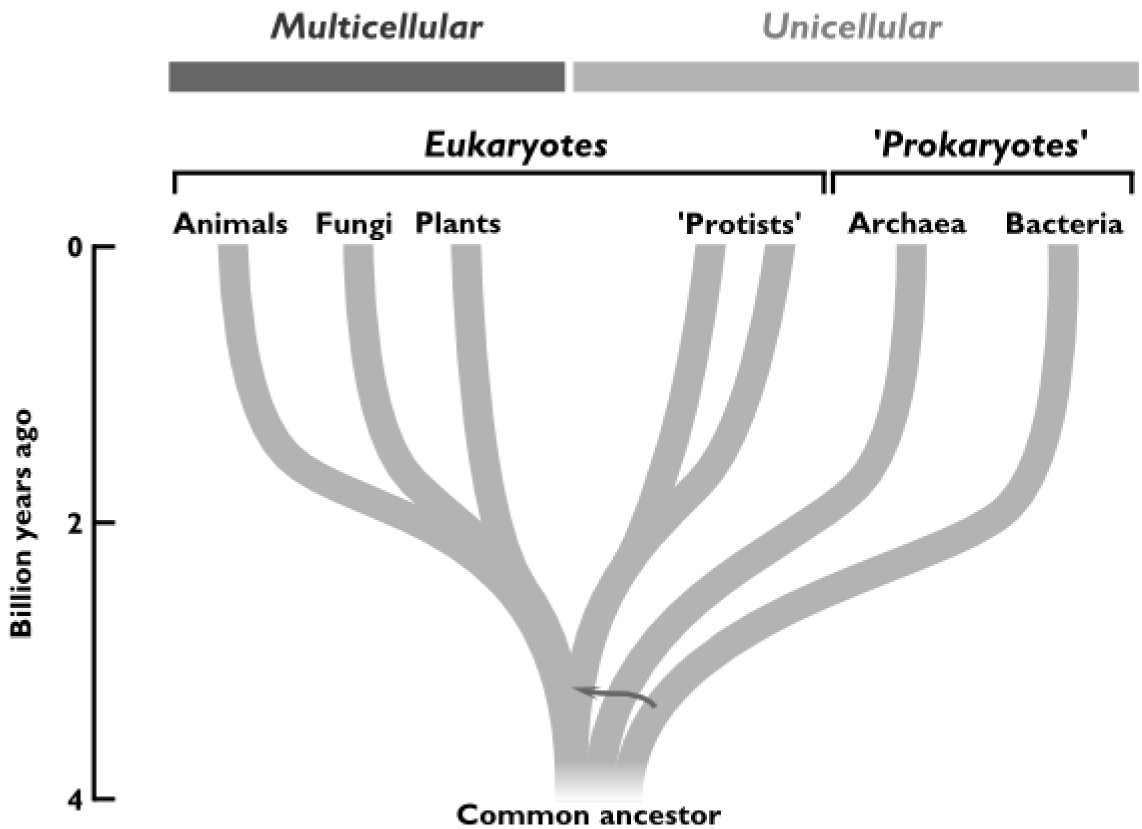

FIGURE 8 — A SIMPLIFIED TREE OF LIFE. MANY OF THE MAJOR BRANCHES ARE OMITTED, BUT A SPLIT BETWEEN PROKARYOTES AND EUKARYOTES IS SHOWN. THE DARK-GREY ARROW REPRESENTS THE ENDOSYMBIOTIC ORIGIN OF EUKARYOTE CELLS. ALSO MARKED ON THE TREE ARE THE 'PROTISTS', A GROUPING OF SINGLE-CELLED EUKARYOTES SUCH AS AMOEBAE AND MALARIA (SEE BELOW).

Plastids and malaria: Like mitochondria, plastids are membrane-bound organelles, but they are a little more independent of their host than mitochondria. Chloroplasts, which allow plants to photosynthesize, are one example. Plastids have evolved numerous times in the history of life, and often resemble cyanobacteria. In symbiosis, the cyanobacteria would provide carbon compounds to the host, and the host would provide mineral nutrients to the cyanobacteria. Another, independently evolved, plastid is that found in *Plasmodium falciparum* — the parasite responsible for the most virulent and prevalent form of malaria. This parasite is a nasty little unicellular eukaryote. It has a nucleus and organelles, so conventional antibiotics (which kill prokaryotic bacteria) can't be used to fight it. In each malarial parasite there is a plastid that probably began life as a eukaryotic red alga. This — and the resulting plastid — was at one point photosynthetic. The organelles have four membranes, and have either lost their nuclei, or as we see in some lineages related to malaria, have a dramatically reduced remnant called a nucleomorph. These plastids are also no longer photosynthetic — ancestors of the group probably converted into parasitism early in the evolution of animals, more than 500 million years ago. Nevertheless, it seems that the plastids are integral to survival in a number of the life stages of the *Plasmodium falciparum* parasite, facilitating the biosynthesis of important compounds such as fatty acids. This, and the fact that they aren't found in human cells, makes them a good target for drugs to fight malarial infection.

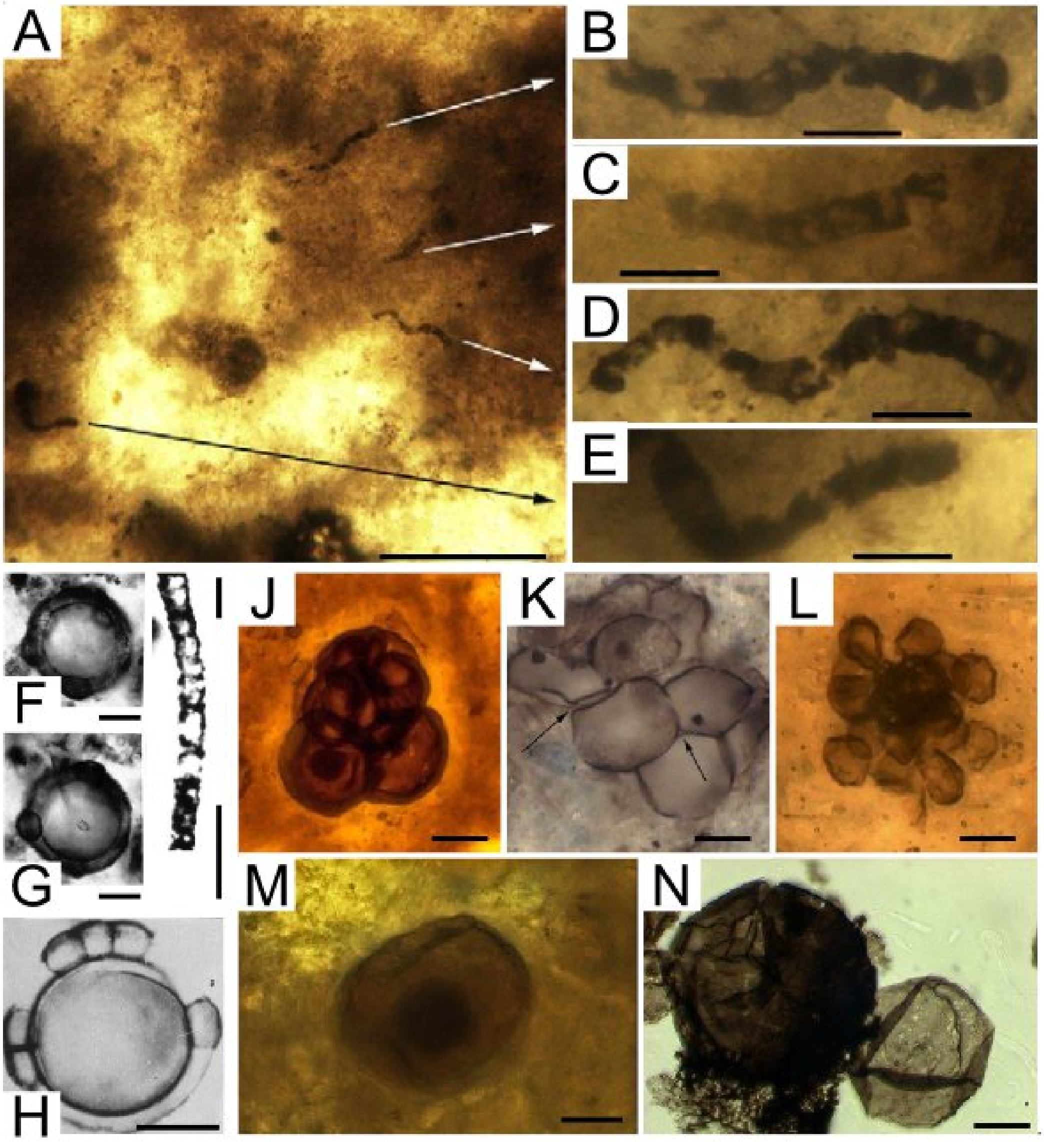

FIGURE 9 (PREVIOUS PAGE) — A–E: EXAMPLES OF FOSSILS FROM THE APEX CHERT. IF THEY ARE BIOLOGICAL IN ORIGIN, THEY ARE CONTENDERS FOR THE EARLIEST KNOWN FOSSILS. MODIFIED FROM THIS SOURCE. F–I: THE EARLIEST UNIVERSALLY ACCEPTED FOSSILS, FROM THE GUNFLINT CHERT. MODIFIED FROM THIS SOURCE. J–N: CELLULAR FOSSILS FROM THE TORRIDONIAN ROCKS OF NORTHERN SCOTLAND — WHICH INCLUDE THE EARLIEST PRESERVED FRESHWATER EUKARYOTES. MODIFIED FROM THIS SOURCE. SCALE BAR IN PANEL A: 100 MICROMETRES. ALL OTHERS 10 MICROMETRES.

Fossils: So, this is Palaeontology [online] and not biology 101; it would be nice to look at some fossils. The earliest specimens that might be fossils are from around 3.4 Ga: one rock called the Apex Chert in Australia contains possible traces of life, in the form of carbon-rich structures shaped like hairs, called filaments (Fig. 9A–E). However, proving that such traces are biological in origin is very difficult, and these particular structures have been called into doubt, and the argument currently continues. The similarly aged Hoogenoeg Formation of South Africa also has possible traces of life, which could represent hyperthermophile prokaryotes. By around 3 Ga, stromatolites — layered rocks that, in many cases, may have been laid down by cyanobacteria — became common. By the time of the 1.88-Ga Gunflint Cherts, today found in Minnesota, USA, and Ontario, Canada, a wide range of prokaryotes existed; they are preserved as fossilized cells, colonies of small round bacteria (coccoidal colonies) and filaments(Fig 9F–I). Possible multicellular fossils have been described from 2.1-Ga rocks in Gabon, but exactly where these fall on the tree of life is far from settled. The oldest unequivocal eukaryotes date from 1.5 Ga, and freshwater or terrestrial eukaryotes have been described from 1 Ga rocks in Northern Scotland (Fig. 9J–N).

Sex: Sex is a little bit weird — and not just the noises animals make when doing it (especially foxes). For any sexually reproducing species, there is a two-fold cost: only half the species can bear young, and males must be able to find females. Nevertheless, it is a common method of reproduction, especially in animals and plants, where it has evolved repeatedly. Thus, it must improve the fitness of any offspring. It seems that sex is preferable to asexuality when there is a threat that changes rapidly between generations, is sensitive to genetic variation and kills a large proportion of species populations. The most likely suspects to meet these criteria are parasites and disease-causing pathogens, which co-evolve with their hosts, changing rapidly between generations. Sex helps to fight this constant bombardment through increasing genetic variation, and helps to spread favourable traits quickly. This battle between organisms and disease is a race, very similar to that of the Red Queen in Lewis Carroll's *Through the Looking Glass*, who said, "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!" So this idea is called the Red Queen hypothesis. An alternative (well, complementary) idea is that replication through sex is often imperfect, allowing beneficial mutations, which can then be spread. There are two copies of every gene, which minimizes the expression of harmful mutations. Sexual reproduction may date back to the origin of Eukaryotes, but there is an evolutionary radiation at 1.2 Ga that could also have resulted from the advent of sex.

Multicellularity: Building a body from multiple cells is another complicated and — I think — downright amazing adaptation. All the information needed to build every single cell in your body must be stored in the DNA that they all share. Furthermore, your entire body forms from a single cell: the genetic bottleneck that is a fertilized egg. Despite the ferocious complexity of this task, there are more than 20 independently evolved instances of multicellularity — including plants, fungi and animals, to name just three of the most familiar. Multicellularity allows cells of different types to form, and so labour is divided within an organism, encouraging increased specialization. When the system goes wrong and cell-growth gets out of control, cancer is the result. Multicellularity is most likely to have evolved through the symbiosis of unicellular organisms of the same species that work together, creating colonies with specialized roles for the different individuals. This process been observed numerous times in the living world, and the boundary between colonial organisms and a multicellular entity is rather diffuse. The first convincing evidence of multicellularity in the fossil record dates from about 1.7 Ga, with a possible contender at 2.1 Ga. The first reliable cellular differentiation is placed at about 1.2 Ga (the red algae *Bangiomorpha pubescens*, Fig. 10).

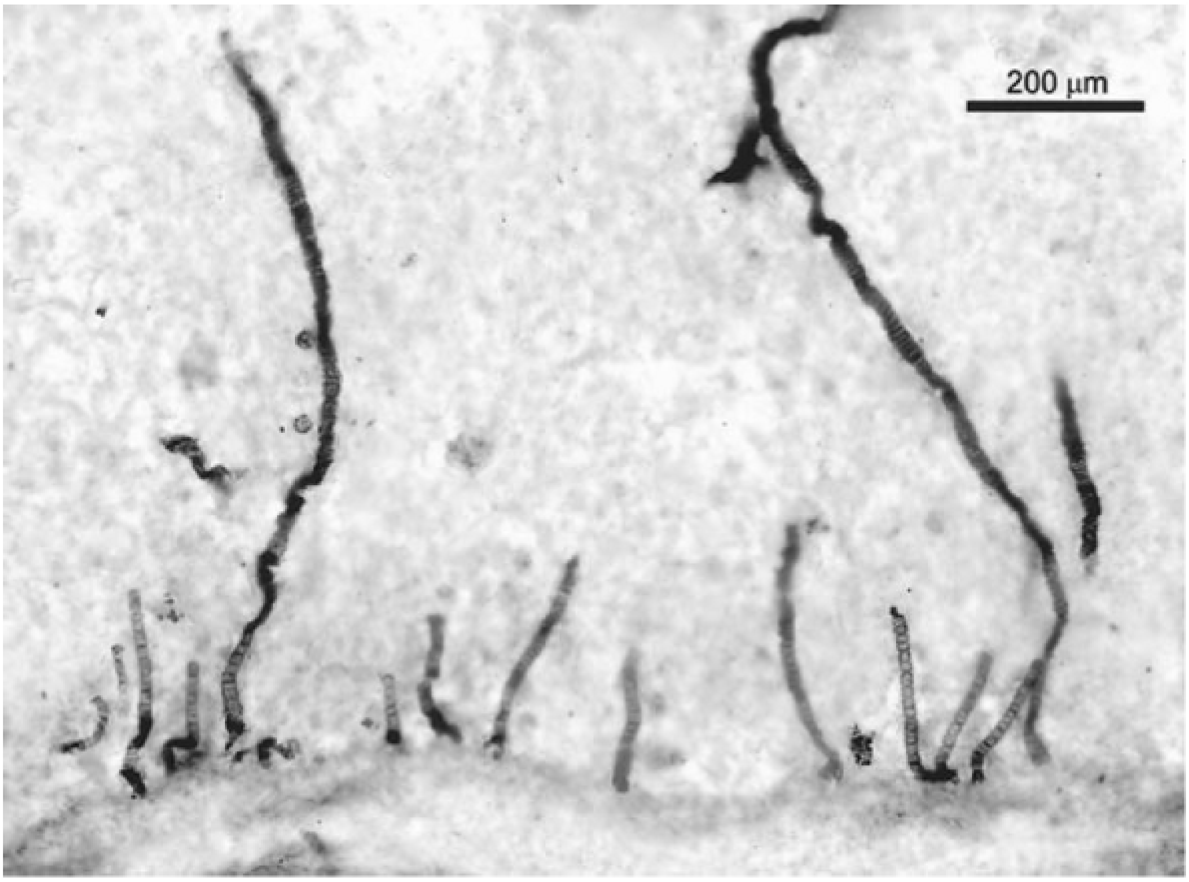

FIGURE 10 — THE 1.2-GA RED ALGAE *BANGIOMORPHA PUBESCENS*, WHICH DISPLAYS CELLULAR DIFFERENTIATION. SOURCE.

Sponges, slime moulds and the Portuguese man o' war: We need look no further than some of these special creatures to see how flexible, and sometimes inflexible, multicellular life can be. On the side of flexibility, can I introduce you to the common sponge? This is a creature made of layers of specialized cells, so it shows functional differentiation and a division of labour (Fig 11A). However, if you put one through a sieve — breaking the cells apart and making them, in effect, unicellular — the cells show individual, amoeba-like behaviour. Eventually, they can group together to form cell agglomerations, and finally whole new sponges. If you do this with two different species, and mix the resulting mush, eventually the separated cells will mix only with their own species. This survival is unusual for multicellular creatures — normally, if you chop a bit off, or indeed push it through a fine sieve, the disaggregated bits die.

Inflexibility can be seen in the Portuguese man o' war (Fig 11B). This creature, which looks like a jellyfish, is in fact a colonial member of the same phylum, in a group called the siphonophores. We know from their anatomy and evolutionary relationships that Portuguese man o' wars are colonies of individual zooids, and they share a unicellular common ancestor which is more closely related to them than it is to, say, true jellyfish. However, if you chop bits off, they cannot survive on their own — thus the Portuguese man o' war is, to all intents and purposes, part of an independently evolved multicellular animal line. Awesome, huh?

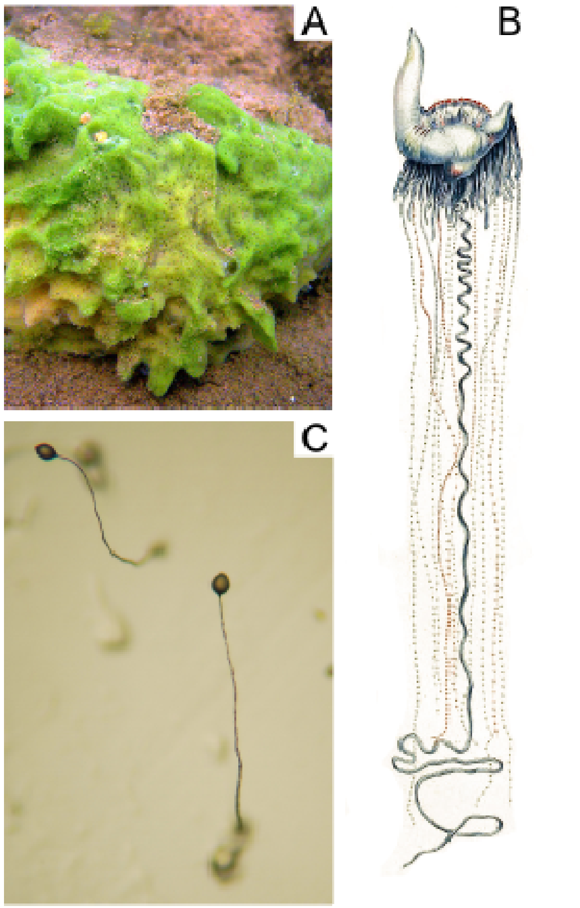

FIGURE 11 — THE FRESHWATER SPONGE, *SPONGILLA LACUSTRIS*, COURTESY OF KIRT L. ONTHANK. B. THE PORTUGUESE MAN O' WAR. C. THE FRUITING BODYOF THE SLIME MOULD DICTYOSTELIUM DISCOIDEUM.

A final example of just how creatively confusing life can be when it comes to multicellularity are the slime moulds. *Dictyostelium*, is a kind of slime mould. Members of this genus are singularly unprepossessing things that live in soils, most of the time as haploid social amoebae. They eat bacteria in soil, and divide asexually. However, if there is a lack of food, the single cells can do one of two things: in the first, two cells can fuse sexually, and attract other cells that are then eaten. Some of these (before being devoured) leave a protective barrier around a giant diploid cell that can, at a later date, hatch amoebae for the cycle to begin again. As if that wasn't cool enough, the other option is that a social life cycle can kick off. The amoebae aggregate to form a small free-moving slug that acts like a single multicellular organism. This seeks out light, and eventually forms a fruiting body: some of the cells die to form a trunk-like extension, to lift up the remaining cells (Fig 11C). These are then better placed to release spores that can be dispersed and hatch out into further amoebae in the correct conditions. Some colonies even farm bacteria, and carry these during spore dispersal to maximise their chances of survival. Aren't they just the coolest?

Conclusion:

In the last 20 minutes or so, we've covered a few of the major things that happened in the first 3 billion years of evolution (still breathing? Oh good!). It has been a wild ride from the origins of life, somewhere before 3.5 billion years ago, to the organization of cells through endosymbiosis, the advent of sexual reproduction and the development of multicellularity (speaking of, isn't Fig. 12 awesome? More respect to the slime moulds!). By necessity, I have left quite a lot out, for which I can only apologize. I can't pretend that the missing bits are not pertinent or interesting. Some of what we're missing is factual, but I have also glossed over more than a little of the uncertainty and conflict inherent to palaeontology and life sciences in the murky depths of geological time. To compensate for these shortcomings, there are suggestions for further reading below, which outline aspects of the above in more detail. No doubt our understanding of much of this will change in the near future. Nevertheless, I hope that you have enjoyed reading as much as I enjoyed writing this.

No sponges were harmed in the creation of this article.

Further reading:

Coté, G. and De Tullio, M. 2010. Cell Origins and Metabolism. *Nature Education* 3(9). *An excellent, freely available overview of a number of these topics from Nature Education's online teaching/learning portal, Scitable. Good job,* Nature*!*

Eldredge, N. & Eldredge, G. 2012 Introducing "The Origin of Life". *Evolution: Education and Outreach* 5, 333. doi:10.1007/s12052-012-0451-9 *A special issue of this excellent journal, aimed at a wide audience, exploring a number of these themes. Good job, all involved! Note: Until the end of 2012 access to this journal requires an institutional subscription, or is eye-wateringly expensive. If you can't access the papers, please drop me an email.*

Ruse, M. & Travis, J. 2011. *Evolution: The First Four Billion Years.* Harvard University Press. ISBN:0674062213 *A lengthy but great overview of evolution in all its forms and guises. Any similarities to the title of this article are entirely coincidental. And all that jazz.*

Brusca, R. C. & Brusca, G. J. 2003. *Invertebrates,* 2nd edn. Sinauer. ISBN:0878930973 *An introductory invertebrate-zoology textbook, which gives a clear picture of the context and biology of the animals mentioned above.*

And finally, some cool, more technical stuff:

Abramov, O. & Mojzsis, S. J. 2009. Microbial habitability of the Hadean Earth during the late heavy bombardment. ***Nature*** **459,** 419–422. doi:10.1038/nature08015

Gargaud, M., Lopez-Garcia, P. & Martin, H. 2012. Origins and Evolution of Life: An Astrobiological Perspective. Cambridge University Press. ISBN:052176131X

Kalanon, M. & McFadden, G. I. 2010. Malaria**,** *Plasmodium falciparum* **and** its apicoplast. *Biochemical Society Transactions* **38,** 775–782. doi:10.1042/BST0380775

Kumala, M. 2010. The never-ending story — the origin and diversification of life**.** *Evolution: Education and Outreach* doi:10.1007/s12052-010-0278-1

Strother, P. K., Battison, L., Brasier, M. D. & Wellman, C. H. 2011. Earth's earliest non-marine eukaryotes. *Nature* **473,** 505–509. doi:10.1038/nature09943

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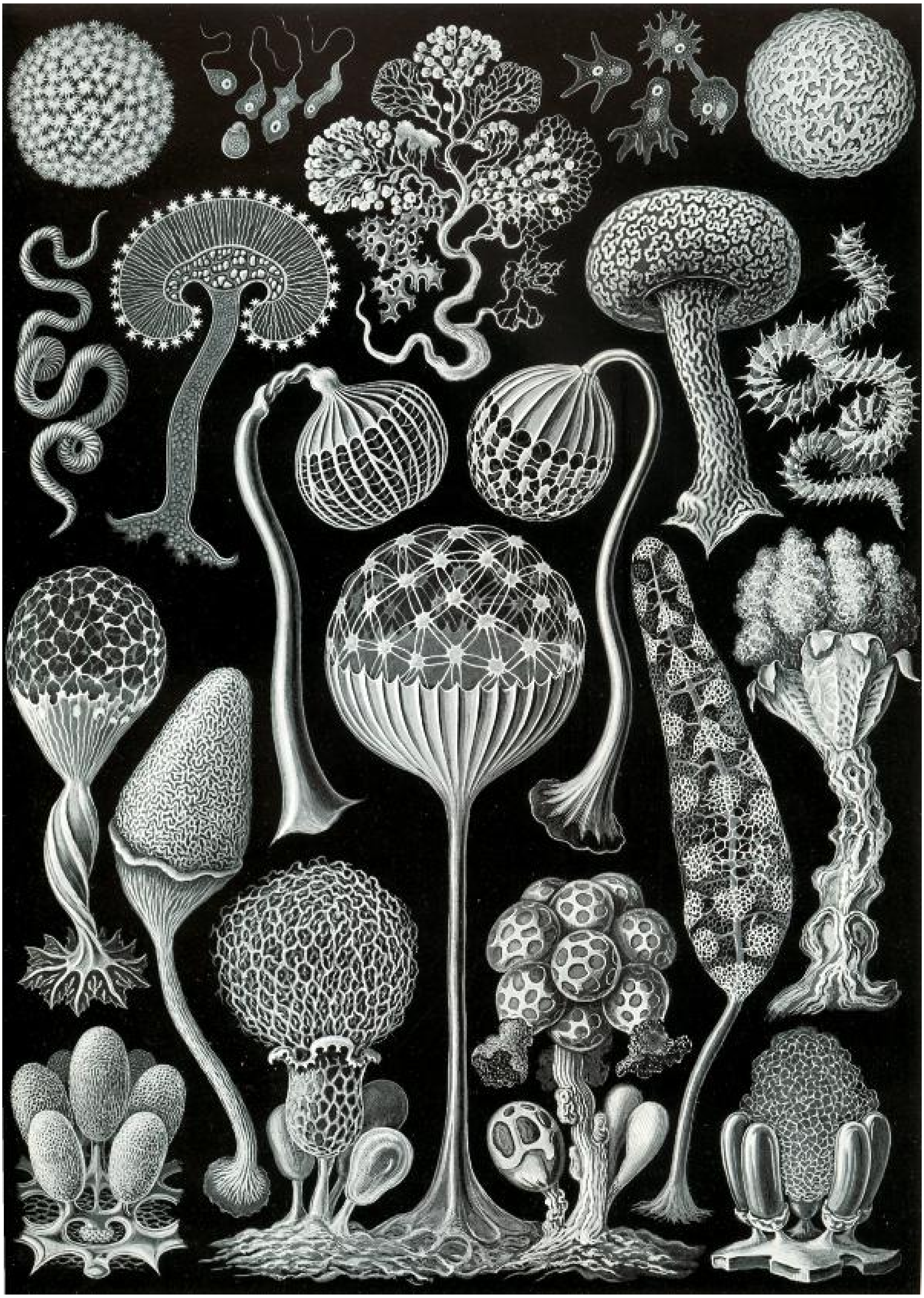

FIGURE 12 — ERNST HAECKEL'S REPRESENTATION OF THE MYCETOZOA, OR SLIME MOULDS, FROM HIS 1904 WORK KUNSTFORMEN DER NATUR (ARTFORMS OF NATURE).