THE BIOGENIC TRANSFORMATION OF THE EARTH
(Part 2: The Role of Life)
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Except for its ocean cover, Hadean Earth would have presented a landscape totally alien to a human observer. Really it would have had no landscape deserving the term. High winds would make for a choppy ocean surface, with lots of spray. Increased evaporation where winds were strongest at the equator would increase salinity and density to drive deep-ocean circulation. Giant storm clouds would rush upwards for perhaps a hundred kilometres, carrying both water vapour and droplets of spray. Dominated by a carbon dioxide-rich atmosphere, rain and sea would be mildly acid, rather than alkaline as now. Periodically this strange world would experience the aftermath of giant impacts, with huge masses of vaporized rock and sea water hanging in the atmosphere. Strong acids might form from combinations of nitrogen, oxygen, sulphur, chlorine and hydrogen freed in the plasma of the impact fireball. They would rain out to change the ocean's chemistry for a period. Beneath all this weather, high heat production would generate magmas at perhaps five times modern rates, and much more when comets delivered their motion energy. The whole oceanic crust would be in chemical interaction with sea water, surface lava breaking down to muds and dissolved compounds, and deeper parts reacting with circulating water to release dissolved products at hydrothermal vents. I paint a complex and strange picture, but the summary is one word, ***reactive****. For whatever the processes that generated the chemical complexity of life and its precursors, a wealth of opportunities for reactions of many different kinds was the only way to open a window of opportunity to transform that alien world. A landscape for life is inaccurate; more like a busy laboratory.—Stephen Drury*[1]

At the end of Part 1 we concluded by drawing a picture of the post-Hadean Earth of 3,900 million years ago: "The period of heavy bombardment has ceased; the oceans have formed; a strongly reducing atmosphere believed rich in carbon dioxide blankets the planet and through the greenhouse effect keeps temperatures from plummeting while an early, weaker sun produces insufficient radiation to cause a run-away Venusian hothouse effect. Hundreds of millions of years go by while minerals leach from the first proto-continents, lightning flashes through the air billions of times, and strong doses of ultraviolet radiation excite a growing suite of complex molecules forming in Earth's aqueous environments."

The biogenic transformation of this hostile world environment to the benign and nourishing biosphere that we take for granted hinges on seven crucial developments: (1) the early origin of life, its expression in the prokaryotic (bacterial) cell, and its widespread dispersal; (2) the conversion of Earth's atmosphere through the drawdown of carbon-dioxide and the production of oxygen by biological means; (3) the development of the 'modern' eukaryotic cell with all its ramifications; (4) the colonization of the land by plants; (5) the evolution of seed plants; (6) the explosive radiation of flowering plants from the Cretaceous to the present; and (7) the rise of the grasses and their dominant role in the food chain.

(1)The Early Rise and Spread of Life. Life seemingly permeates every pore of the Earth. Organisms are found beneath permanently frozen lakes in the Antarctic, in boiling hot springs, at superheated water vents in the dark abyss of the oceans, in highly acidic pools and among salt crystals on the surfaces of desert playas, even inside of pipes in nuclear reactors. Snow banks of the High Sierra are coated red by algae adapted to live on ice, providing a food source for ice worms eking out their livelihoods in the interstices between ice crystals. Microbes have been pulled out of oil-well bore-holes more than two kilometers below the surface of our planet.

With the exception of the insides of solid crystalline rocks and the molten material from which rocks are formed, there are probably no naturally occurring habitats in our terrestrial or marine environments where life does not exist. To lava and solid rock, man has added a few artificial sterile environments—the combustion chambers of engines, rockets, and blast furnaces, the cores of nuclear reactors, vats of concentrated and purified chemicals, and autoclaves where surgical instruments are sterilized.[2] Indeed, from a systems engineering point of view, it takes a great expenditure of energy to maintain a system free of living organisms for any significant amount of time.[3]

Scientists still have not been able to replicate that mystery of mysteries—the origin of life. But biochemistry has vastly advanced our knowledge of the transformation of simple compounds that were undoubtedly present on early Earth to ever-more complex organic compounds via common physical processes. Hydrocarbon molecules, once thought to be the rare stuff of biogenic activities, have been found in meteorites and in interstellar clouds. The basic building blocks of life seem to be a common feature of our physical universe.[4]

We also know that certain classes of molecules tend to be self-organizing and are able to form primitive membranes (even a soap bubble is a membrane). Biologists concur that a critical step in the formation of life was the development of the membrane, of an inside vs. an outside environment. Cocoon self-organizing molecules away from the disruptive effects of the open environment where random forces are constantly at work, add an energy source, and only the step of molecular self-replication is required to begin life.[5]

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[1] Drury, p. 182.

[2] Apparently even the insides of rocks are not immune from life. In the Dry Valleys of Antarctica scientists have found green algae that grow in a layer just beneath the surface of rocks, obtaining sunlight through translucent rock crystals. Amazingly, a form of so-called endolithic fungi has co-evolved to live off the algae. See Margulis (1995), pp. 146-147.

[3] On the surface, life apparently violates one of the key principles of physics known as the Second Law of Thermodynamics, which states that entropy always increases. For 'entropy' read randomness. The entropy of my desk seems to always increase as more mail gets piled on it. But life by its very nature is self-organizing. A tree breathes in passing CO2, which is randomly scattered in the atmosphere, and combines it with water and randomly scattered nutrients within reach of its roots to create a fantastically organized arboreal plant. This is the essence of life and why organism and organize share the same root meaning. Of course life doesn't really violate the Second Law. Just as it takes energy to sort through my mail and clean off my desk, a tree expends energy to organize itself. In each case the net effect of the organizing activity is the release of less-organized by-products (we often call them 'pollution') and energy resulting in an overall increase in entropy. In the case of my desk, the physical activity of my reading and sorting the mail requires the expenditure of energy which heats the air in the room, and I pass the by-products out of my system (office) to the nearest recycling center after expending additional energy grinding some of the mail through the shredder. Thus, even though the entropy of my office has decreased, the overall entropy of the encompassing Earth system has increased. The first axiom of an astrobiologist on the prowl for extraterrestrial life is to look for signs of a local reversal of the Second Law of Thermodynamics.

[4] No one has been able to spontaneously create life in a test tube. The most famous experiment was carried out by Harold Urey and Stanley Miller in 1953, in which they sealed the raw chemicals representative of the early Earth into a glass vial and subjected the contents to cycles of heat and lightning. No one expected much to happen, yet the yellow-brown sludge that formed in their mini-world was full of surprises; most notably the formation of organic molecules, including amino acids, the building blocks of proteins and life. Schopf (1999)(pp. 122-128) provides a detailed description of the experiment, with photographs and diagrams.

[5] This sounds easy when rattled off in three brief sentences. However, the simplest self-replicating molecule that we know of (RNA: ribonucleic acid) is extremely

For those of us schooled in the 1950s or earlier, the most fundamental basis of life hinged upon plants and their ability to produce food through photosynthesis. The photosynthetic process was considered the root of all life, and the photosynthetic autotrophs ("self-feeders") were recognized as being at the base of the food chain upon which all other organisms depended. Life, it seemed, could only have originated in the lineage of photosynthesizing bacteria, most likely the ancestors of what were then called the blue-green algae (now properly identified as the cyanobacteria).

While cyanobacteria have not been completely ruled out as the Last Universal Common Ancestor (LUCA) from which all other living species descended, that likelihood has become increasingly dubious as more knowledge has accrued about the microbial world. We now know that the organisms of Kingdom Bacteria exhibit the largest diversity of metabolisms of any of the kingdoms of life, and include many species exhibiting non-oxygenic (anaerobic) and non-photosynthetic food-producing capabilities.

In particular, paleobiologists are keenly interested in the sub-Kingdom called Archea or the archeabacteria, characterized today by many "extremophiles", organisms living in extreme environments of heat and cold, acidity or salinity, such as may have existed on the early Earth. Some archeabacteria are anaerobic, some are also chemolithoautotrophic (able to produce food purely from available raw non-biogenically-derived nutrients—the raw chemicals spewed from deep ocean vents, for example).

From our inference that the early atmosphere contained little free oxygen, we can conclude that the first life forms must have been anaerobes. It seems likely that life arose in the "primordial soup" created from hundreds of millions of years of chemical leaching from the continents into the oceans, and as modified by naturally-occurring electrical and thermal energy sources, as well as by radiation from various sources. The primitive archaebacteria, with their capabilities to function as anaerobes in extreme environments, seem to fit the bill for being among life's earliest forms[6]. But did life originate in a boiling hot spring, or a slushy salt flat, or by photosynthesizing organisms floating in shallow bodies of water, or by chemolithoautotrophs propelled by the energy and chemical resources issuing from deep ocean vents? This question may never be answered, but the fact that we can ask it demonstrates that the science of paleobiology has come a long way indeed.

We do not know exactly when or where this remarkable event took place. Some scientists think life may have evolved more than once, only to have been exterminated by the sterilizing effect of major impact events during the Earth's early period of heavy bombardment. But there are bounds on the origin of life, albeit rather broad. The oldest confirmed fossils are from the 3,465-million-year-old Apex chert of northwest Australia[7]. These remains of ancient bacteria appear quite advanced—in fact they look nearly identical to existing species— so the guess is that life arose at a much earlier date.

Tantalizing hints of that earlier life have been found in the 3,800 million-year-old Isua Supracrustal Group from southwestern Greenland, the oldest sedimentary rocks yet found. Because of exposures to high temperatures and pressures, any true fossils that may have been present in these rocks would have been destroyed. There are, however, deposits of carbon. Isotopic analysis points toward a biogenic source, however the carbon could also have accumulated through purely physical means, so the jury is still out.[8] For our purposes, we will assume that bacterial life was present and widespread on Earth by at least 3,500 million years ago, and probably was around for several hundreds of millions of years before then.[9]

What is crucial to our story is not how nor where life began, fascinating as those conjectures are, but the fact that science has pushed its origins back so far. Instead of life having a scant 600 million years to work on the Terran environment (concluded from the old fossils of the Cambrian era), the recent fossil finds in Australia, South Africa, and Greenland have increased the span seven-fold. Within this staggering amount of time, life processes that would only minutely influence Earth's environment on a yearly-, decades-, or even millennial- scale can now be seen to result in huge change when acting over billions of years. According to paleobiologist William Schopf:

> . . . the Precambrian encompasses such an enormous sweep of time that even accumulated minor changes can have a telling effect. For example, the 21% oxygen of today's atmosphere would have been generated by the steady addition of only a tiny amount (0.000000006% O2 per year) from the time of the Apex fossils to the present.[10]

Life was here early, but was it widespread? After all, the first land masses were quite small, and the plants and animals which cover our continents today were totally absent from terrestrial environments, such as there were.[11] We must look to the geological record.

Because of geologic recycling processes, rocks older than 3,500 million years are rare and those that represent unaltered sediments that could successfully preserve fossils are exceedingly so. Thus the record by which we can judge the extent of life's dominion on the early Earth is sparse. But by 2,500 million years ago, bacterial mats seem to have been widespread, leaving a fossil record of domed, layered structures, called stromatolites, on every continent.[12] The filamentous bacterial fossils contained in the stromatolites are quite advanced, being virtually identical to the living forms found in bacterial mats around the world today. Similar filamentous forms are present in the 3,465 million-year-old fossils from Australia.[13] The presence of advanced forms at such early dates seems indicative of a very early and widespread dispersal of bacterial-based life forms. This premise is further backed up by the dates of Precambrian geological features called banded iron formations (BIFs) which are attributed to biological origins.

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complex, while DNA, the molecular basis of all life as we know it, lies at another order of magnitude of complexity. According to Drury (p. 214), the "transition or leap to DNA-based life, and the multifarious machinery for translation that entails, means diversification into at least three kinds of RNA and the adoption of some complexly functional proteins . . ." Also see Drury, pp. 208-209, for a discussion on possible origins of self-replicating molecules. Refer to Margulis (1995), pp. 58-66, for a full discussion of the Urey-Miller-type experiments and theories about the origin of life.

[6] The Archaea are so named because they are characterized by classes of microbes that live in hostile of environments similar to those believed to have dominated the early Earth. Indeed, these 'extremophiles', found today in the boiling hot springs of Yellowstone, growing on salt crystals in Death Valley, tinting the alkaline wastes of Owens Dry Lake, clustered in highly acidic environments, and thriving around chemically-enriched super-heated water vents of the deep ocean, may be direct descendants of the earliest life on Earth. Most importantly, they all live in anoxic conditions, the prerequisite for life in earliest times. However, for a contrasting view in which the archaebacteria are proposed to be later derivatives of more complicated cells, see Ridley's article, *The Search for LUCA*, in the November, 2000, issue of Natural History Magazine (p. 82).

[7] For age of the Apex chert, see Schopf, Cradle of Life, pp. 85-89.

[8] Regarding the interpretation of the Greenland Archean-age rocks, see Schopf (1999), pp. 166, 177; Drury, pp. 199-200, 203.

[9] For a discussion of bounds on the beginning of life, refer to Schopf (1999), pp. 166-169, 177.

[10] Quote on rate of O2 production, see Schofp (1999), p. 170.

[11] The Archean proto-continents were really just chains of islands. Stanford University researcher Don Lowe estimates that prior to 3,000 million years ago land comprised less than 5 percent of the Earth's total surface area [Ward (p. 262)].

[12] The oldest stromatolites found to date occur in a deposit reported to extend over "tens of square" kilometers in a horizon of the Western Australia Pilbara sequence, dated to be 3,450 million years old [Schopf (1999), p. 196]. Schopf devotes a whole chapter to stromatolites, complete with many photos and drawings [Schopf (1999), Chapter 7: Stromatolites: Earth's First High-Rise Condos].

[13] Schopf identifies eleven species of organisms from the Apex chert and provides a discussion of their characteristics and similarities to living forms, particularly the cyanobacteria [Schopf (1999), pp. 96-99].

(2) The Conversion of the Earth's Atmosphere. As described in Part 1, Earth's original atmosphere was very much like that of Venus, dominated by carbon-dioxide with little or no free oxygen.[14] If the atmosphere had remained the same from that time, the increasing solar output of the sun would have eventually resulted in an unlivable hot-house world just as we see on our sister planet. Something happened to draw down the level of CO2 to today's fraction of a percent, not only overcoming the original huge reservoir of that gas, but also the billions of tons emitted by volcanic eruptions over the eons. It happened on a microscopic scale working over immense time.

The stromatolites and banded iron formations (BIFs) provide key evidence in this story. Photosynthesizing filamentous cyanobacteria are a key component of most bacterial mats, and as discussed earlier, the same type of filamentous structures are found in the fossil stromatolites.[15]. Paleobiologists theorize that cyanobacterial organisms thrived in the CO2-rich primal atmosphere, taking in the hot-house gas and expelling oxygen as a 'pollutant' for hundreds of millions of years.[16]

The highly reactive oxygen was ejected into the waters surrounding the bacterial communities, just as we discharge sewage into the waters surrounding our towns and cities. The evidence for this comes from the widely-distributed pre-Cambrian BIFs from which most of the world's iron supply has been extracted. With little or no oxygen in the environment, iron washed out of continental rocks and ran to the sea dissolved as divalent ferrous ions instead of immediately rusting in place to form insoluble iron oxide (rust) as it does in today's oxidizing atmosphere. Thus the seas became enriched in ferrous iron, forming a near-inexhaustible sink for the lethal oxygen. Encountering the stromatolite effluent in offshore troughs, which geologists call by the wonderful name of miogeosynclines, the ferrous iron was oxidized to the trivalent ferric state, forming precipitates of insoluble iron oxides that rained down on the seabed. The bands in BIFs are interpreted as representing seasonal variations in available iron or oxygen.

It is estimated that over 20,000 million trillion grams of oxygen was absorbed in this manner, nearly 20 times the amount of oxygen currently in the atmosphere. The conclusion is that only a wide scale photosynthetic process could accomplish such a feat.[17]

The heyday for stromatolites lasted for more than a billion years, until the ferrous sink saturated. This appears to have occurred about 2,200 million through 1,900 million years ago, when the last BIFs were laid down. By that time other oxygen-producing organisms were on the scene to take over. In effect, the stromatolites fouled their own nests, eventually poisoning themselves through the continued production of oxygen.[18]

The advent and flourishing of true algae provided a final boost in oxygen, which with a saturated ocean now entered the atmosphere. Here too was another great sink for this most active of elements; in the form of whole mountains of raw iron. The oxidation of terrestrial iron resulted in the world-wide formation of red beds, beginning about 2,200 million years ago when the ocean sink became saturated. The rusting of the Earth continues to this day. [19]

After thousands of millions of years of slow-but-steady biogenic conversion of CO2 to O2 through the process of photosynthesis, the oxygen sinks afforded by BIFs and the red beds became saturated. Free oxygen could at last accumulate in the atmosphere. A vital consequence of an oxygen-rich atmosphere, aside from providing the 'air' we breathe (the oxygen that powers our metabolism), was the concomitant formation of the ozone layer and the mitigation of deadly levels of ultra-violet radiation upon the surface of the planet.[20] A whole new terrestrial environment became available for life to exploit.

(3) The Rise of the Eukaryotic Cell. The 'other oxygen-producing organisms' that provided the 'final boost' were composed of a new and different type of cell, with a metabolism centered on the highly efficient oxidizing potential that could be utilized only when a dependable supply of O2 became available.

From a microscopic viewpoint, there are really only two kingdoms of life. All living cells, from single-celled bacteria to multi-celled plants and animals, fall into one of two categories: prokaryotes or eukaryotes. Human beings and all 'higher' organisms (including plants) are composed of eukaryotic cells—big cells that contain specialized bodies of which the most extraordinary is the nucleus that houses the DNA-containing genes tightly coiled around strands of protein to form discrete chromosomes that are the basis for transmitting inherited traits from generation to generation.[21] All bacteria, on the other hand, are single-celled prokaryotes. The prokaryotic cell is much smaller than its eukaryotic cousin and is structurally less complex, appearing to be little more than a bag of chemicals containing one or more simple closed loops of DNA.

This lack of complexity (primitiveness) of the prokaryotic cell, combined with its earlier appearance in the fossil record, leads most evolutionary biologists to conclude that prokaryotes, and specifically the sub-kingdom of archaebacteria, to be the lineage most closely related to the earliest life on Earth.[22]

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[14] Carbon dioxide constitutes 96.6 percent of the Venusian atmosphere. Contrast this with a CO2 level of only 0.03 percent on Earth. The Martian atmosphere, thin as it is, is also dominated by CO2 (95%). [Margulis (1995), p. 27]

[15] The living versions of stromatolites are subject to predation from more lately-evolved organisms and are greatly reduced in size and distribution, growing only in special isolated habitats. The largest surviving community appears to be in Shark Bay, Australia, a remote super-salty lagoon about 1000 km north of Perth, where one can hop from one calcareous domed structure to another, at least at low tide [see Schopf (1999), p. 198 for photograph of Shark Bay colony compared to a photograph of fossil stromatolites]. I have observed domed bacterial mats in salt-making lagoons in Costa Rica. Simple flat bacterial mats grow in almost every salt-water estuary in the world. Cyanobacteria are also commonly found in desert environments where they are a key constituent of cryptogamic (or cryptobiotic) soils that sometimes form a delicate crust on top of the nutrient-poor soils generated in arid regions.

[16] Oxygen, the third most common element in the Universe, is one of the most reactive and dangerous substances in our environment. Oxygen is at the heart of toxic scavenging molecules—the 'free radicals'—that are damaging to all kinds of cells. A visit to the health food store reveals shelves of antioxidant supplements one can consume in hopes of mitigating this effect. If atmospheric oxygen level rose from its present value of 21% to a level of 35%, plants would spontaneously combust from their own metabolic processes. The global conflagration at the end of the Cretaceous, perhaps induced by an asteroid impact, may have been exacerbated by higher O2 levels. For a discussion of the effects of oxygen in the environment, see Drury, pp. 139-143.

[17] The interpretation of BIFs and their probable biogenic origins are covered in almost every book on life and deep time. See especially Schopf (1999), pp. 171-173.

[18] On the dominance of stromatolites until approximately 2,200 millions years ago, and their supercession by other oxygen-producing microbes, see Drury, p. 231.

[19] In the United States the red beds manifest themselves in the great rusty expanses of the American Southwest, particularly in the canyon country of the Colorado Plateau. The red interior of Australia is another classic example. Red beds are continuing to be formed, most notably in the Arabian Peninsula and in parts of the Sahara. See Drury, pp. 130-131.

[20] The ozone barrier to ultraviolet radiation is comprised of oxygen combined in a three atom molecule (O_3). If this protective shield was removed, virtually all terrestrial life would be exterminated. Even 20 meters of water would be insufficient against these lethal Solar emissions [Drury (p. 181)].

[21] Humans have 23 pairs of chromosomes in each cell (diploid cells), except for reproductive cells in which the chromosome pairs have divided by meiosis so that each resultant haploid cell contains a single set of 23 unpaired chromosomes.. Some organisms have more than 16,000 chromosomes in a single nucleus at times! On the structure of DNA/genes/chromosomes, see Margulis (1997), pp.14-15.

[22] The primitiveness of the prokaryotes should not be construed as a lack of sophistication, for in terms of metabolic capabilities and free interchange of genetic information, the prokarya far outstrip the eukarya. Within the prokarya are families of organisms characterized by a wide range of chemical pathways, many of which do not involve the intake or production of free oxygen. Basically, there are the photoautotrophs (photo: light; autotrophs: self-feeders), the photosynthesizers which may or may not produce oxygen, and the chemolithoautotrophs, a group of free-wheeling self-sustaining organisms that drive their metabolisms independent of the light reactions characterized by the photosynthesizers. The names given to chemoautolithotroph families hint at their

In a theory most recently promulgated by biologist Lynn Margulis and now gaining wide acceptance, it appears that the eukaryotic cell originated through an amalgamation of prokaryotic organisms. In this Theory of Endosymbiosis, a larger prokaryote ancestor engulfed one or more of its cousins, perhaps originally as food. But once inside the host cell, the new bodies proved to be highly useful. Some were efficient energy producers and in their derived forms have come down to us as mitochondria. Others were particularly good at producing food through photosynthesis; we see their modified forms as chloroplasts in algae and plants. Perhaps another type of prokaryote was particularly adept at organizing and maintaining genetic information—the basis for the nucleus.[23] The oldest eukaryotic cell fossils date from about 1,700 million years ago.

Certainly the most important property to emerge from the eukaryotic cell was its eventual capability to group together in a coherent structure in which specialized cells began to differentiate to take on special functions. All eukaryotic cells are dependent on an oxygen-based metabolism (even plants which produce oxygen), which would seem to make them inherently less robust than their prokaryote cousins with their cosmopolitan metabolisms and associated lifestyles.[24] After all, you'll never find eukaryotic organisms living in oxygenless peat bogs or in sulfur pools where the Archea thrive. However, the capability of the eukaryotic cell to form true multicellular organisms opened completely new environments that could at best be only marginally occupied by the prokaryotes.

(4) Plants Creep Out of the Water World. Plants are believed to have derived from single-celled eukaryotic algae. They evolved in the water world, and getting them out of the aqueous environment and onto land poses severe problems. Imagine hauling a water-lily out of a pond and trying to make it grow in your rose garden. It lies there in a shapeless mass because it has no proper structure to support it, whereas in water it was aided by the force of buoyancy. In a few minutes our transplanted water-lily begins to shrivel up and die, its tissues sucked dry by the air around it. Many water plants have no roots as we know them, so getting at the nutrients in the soil presents another problem. And plants by-and-large reproduce by sex—getting male and female gametes together in the dry terrestrial environment is much more difficult than simply releasing sperm into water to swim or drift to their targets. Yet once ultraviolet radiation levels dropped due to the formation of the ozone layer, a tempting new terrestrial world beckoned.

Plants appear to have made their first tentative steps onto land about 450 million years ago.[25] Scientists believe they resembled a class of plants whose living progeny are the bryophytes—the liverworts, mosses and their kin. None of these plants are much taller than a couple of centimeters and most to this day still require moist environments. This earliest invasion would have seen the greening of estuaries and the borders around permanent sources of water.

But once out of the water the race for the sun was on. Getting your photosynthesizing organs higher and spread out over those of your neighbors was a definite evolutionary advantage. So a number of advances seem to have developed in concert with one another. Plants developed lignin to provide strong support structures.[26] The vascular plants evolved, in which specialized tubes provided a way to transport vital products through the plant, such as soil nutrients to the upper parts of the plant and photosynthate products back down to the roots and branch structures. The new building materials enabled leaves to develop, increasing the photosynthesizing capability many times over. To prevent dehydration, plants coated their leaves with waxy resins and evolved a special breathing apparatus, the stomate, a leaf pore that can be closed shut to minimize water loss by transpiration.

Obtaining nutrients in the terrestrial environment was a more difficult matter, a problem plants couldn't solve on their own. It's doubtful that plants would have moved onto the land proper without having developed symbiotic relationships with members of the fungi and bacterial kingdoms. Roots can only do so much; they are limited in surface area and in their ability to tap certain elements, particularly phosphorus and nitrogen, both vital to plant growth. The roots of almost all plants are surrounded or intruded by a network of mycorrhizal fungi that greatly extends the range and surface area for absorption of needed soil nutrients. The rhizosphere, as it is called, is what really enabled plants to set foot on the land. The fungi absorb and pass on critical minerals, particularly phosphorus, while the plant provides nourishment to the fungi—a truly mutualistic form of symbiosis.[27]

Nitrogen surrounds us, forming 79 percent of the atmosphere, where it combines with itself forming inert $N2$ molecules.[28] Plants cannot grow without nitrogen, but require it in the form of soluble compounds. Fortunately, the amazing prokaryote world of diverse metabolizing organisms provides a group that 'fixes' nitrogen, i.e., captures gaseous nitrogen and turns it into soluble nitrogen-containing compounds, such as the ammonium radical, as a metabolic by-product. Many plants, most notably members of the pea family, incorporate these organisms in root structures called rhizobial nodules that do the trick.[29]

It took millions of years to incorporate all these features. The culmination of all this effort is a tree, and the first true tree (Archaeopteris) doesn't appear in the fossil record until 370 million years ago.[30]

Where autotrophic plants went, heterotrophic feeders were sure to follow. Colonization of the land by plants was accompanied by grazers and the whole gamut of secondary feeders, primarily denizens of the lineage that gave rise to the insect world.

(5) Seeds Change the World. Advances in structure, protection from dehydration, and symbiotic partnerships carried plants onto the land, but without changes in reproductive techniques, they would have remained restricted to watery margins and the dampest of climes.

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cosmopolitan metabolic life-styles: methanogens, hydrogen-oxidizing pseudomonads, nitrosomonads, methylotrophs, manganese oxidizers, and sulfide oxidizers, among others. Bacteria freely interchange pieces of genetic code among themselves (even between species) without recourse to the timely process of sexual reproduction. In terms of information sharing, the eukaryotes are the pony express compared to the bacterial Internet. We humans, although technically 'more advanced' than the 'primitive' bacteria, are in reality less sophisticated in our abilities to cope with the environment than our humble cousins. The meek shall not inherit the Earth, they've never surrendered it! For types of prokarya metabolisms, consult Margulis (1997), p. 47. For discussions on genetic transfer capabilities, see Margulis (1995), pp. 73-76, and Tudge, p. 108.

[23] For Theory of Endosymbiosis, see chapter five of Margulis (1995); also Tudge, pp. 131-139. Drury, p. 196, presents a much shorter summary. For a lengthy and technical discussion of the differences between prokaryotes and eukaryotes, consult Margulis (1997), pp. 9-16, and Tudge, pp. 128-131.

[24] Except for a few odd archaeprotist organisms, all eukaryotes derive their basic energy through the oxidation of three-carbon organic acids inside membrane-bound mitochondria within the cell. See Margulis (1997), p. 12.

[25] Algae appear to have first ventured on to land in the late Ordovician, about 450 million years ago. Non-algal fossils don't appear until the Silurian, about 430 million years ago. See Tudge, p. 561.

[26] Lignin is "a complex macromolecule that stiffens the plant, impregnates xylem, and strengthens the wood of woody trees and shrubs." Margulis(1997), p. 372.

[27] According to Tudge (p. 561), "it now seems that the very first land plants formed mycorrhizal associations with fungi, living symbiotically in their roots; and perhaps—who knows?--their terrestrial algal precursors also lived symbiotically with fungi, so they would qualify as primitive lichens. One way and another, mycorrhizal fungi clearly played a crucial part in the passage on to land." Margulis (1995), pp. 147-149, contains an excellent discussion of the important roles fungi have played in the development of plants.

[28] N2 component of Earth's atmosphere, see Margulis (1995), p. 27.

[29] For nitrogen fixation, see Tudge, p. 108.

[30] For a news release on the recent discovery of fossils of the first tree, visit website: http://forestry.about.com/science/forestry/gi/dynamic/offsite.htm?site=http://204.202.137.112/sections/science/DailyNews/ancienttree990421.html (This is left as an exercise for the Internet student!)

The situation is analogous to amphibians that remain bound to water because of their method of reproduction. Amphibians only evolved into reptiles with the evolution of the amniotic egg, in which the developing embryo is sheltered from the harsh outside environment by the egg shell. Not only did the amniotic egg provide the means to liberate reptiles from water (other than drinking), it was a way to pack and preserve more nutrients for the embryo, ensuring a higher survival rate.

Early plants, just like the bryophytes of today, require a water medium to reproduce. Male gametes must encounter their female counterparts by swimming to them in an aqueous environment provided by the outside world. Thus even mosses and ferns that have developed toleration for drought and live in arid surroundings ultimately must depend on the occasional downpour to provide the means for their sexual unions. Such plants could never dominate the temperate and arid regions of the world. That had to wait until the first truly successful seed plants, the gymnosperms ("naked seeds"), came on the scene.

Around the end of the Devonian period, about 360 million years ago, trees started packaging their male gametes into little packets that could be dispersed by the wind.[31] Those of us with pollen allergies may not fully agree that this was such a good idea, but for plants it was a giant advance. Of course at the same time the female counterparts became modified to accept the windblown grains. Not only that, but the resulting embryo was provided with a protective covering and a large stock of nutritious food to help it get under way when it landed in the right location.

Finally freed from watery surroundings, the gymnosperms must have erupted like a green explosion, with vegetation rapidly spreading over every corner of the Earth. Of course descendants of these plants are still very much with us in the familiar forms of pines, junipers, cypress and their Southern Hemisphere araucaurian relatives. The great conifer forests still dominate the harsh northern temperate zones, a living testament to the power of the seed.[32]

(6) Flowers—More Than Meets the Eye. With the spread of the gymnosperms, the world finally begins to look like home. Flying low over the land a couple of hundred millions years ago, observing plains and mountains covered with vegetation, you would not feel too out of place. But stop for a closer look and you might notice something is missing—walk as far as you like, there's not a flower in sight. The angiosperms have not arrived.

Flowers represent the latest big evolutionary leap in the reproduction of plants.[33] Making pollen is expensive for a plant. And what could be more wasteful than casting it to the wind? About 225 to 140 million years ago, while dinosaurs ruled the Earth, magnolia-like plants began to produce the first flowers.[34] While there is still some controversy attached to the interpretation of this event, it appears that flowers quickly diverted the attention and modified the evolution of insects, resulting in more efficient plant pollination. What we know for sure is that a new plant order, the flowering angiosperms, appeared on the scene, rapidly shoved the Gymnosperms aside over most of the world, while at the same time the Class Insecta grew into the most diverse and widespread group of animals on Earth.[35]

Another important aspect of flowers is that the seeds are usually enveloped in protective tissues (the ovary), as opposed to the naked seeds of the Gymnosperms.[36] In many cases, these protective tissues have developed into fruits that are consumed by various animals, the seeds themselves passing through the digestive track and eventually distributed far and wide in fertile dung deposits.

By rewarding creatures with nectar, pollen and fruit, the Angiosperms have claimed most of the Earth. Of the more than 250,000 species of plants that have been identified, over 95 percent produce flowers.[37] Almost every item found in the produce section of the market is harvested from this remarkable group of plants. Our wildflowers of hill and dale and desert flat are not only beautiful, they represent one of the most successful reproductive stratagems ever deployed on Earth.[38] But evolution never rests, and the vegetable world made one more major advance that has affected the lives of all of us.

(7) Grass. The word usually connotes either a lush freshly-mown green lawn, which is usually composed of true grasses, or, in the slang parlance of the day, marijuana, which is definitely not a member of the grass family. Neither connotation does justice to this important group of plants. Most of the food grown for human consumption is derived from grasses: wheat, rice, barley, corn. Sugar cane and sorghum are grasses. So, in effect, are the hamburgers at McDonalds, or the lamb chops you might have for dinner, since all major stock animals are grazed on grasses. Bamboo shoots are harvested from some of the largest members of the grass family.

The grasses entered the world stage about 64 million years ago, so dinosaurs didn't have the opportunity to munch on them. They must have spread quickly, like weeds (most of the plants we call weeds are fast-growing grasses[39]). They came to dominate the steppes and prairies, which led to a great burst in mammalian herbivore numbers and diversity. The great herds of zebra and antelope that forage the African veldt are but pale reflections of this time, as are the few remaining herds of American bison. Grasses and herbivores evolved together, and many grasses are unique in their ability to grow at the base of the leaf blades so

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[31] For date of first flowering plants, see Bernhardt, p. 221.

[32] The spread of conifers during the Carboniferous laid down the great coal and oil deposits that have powered the Industrial Revolution and upon which all modern economies depend.

[33] What makes a flower a flower? Botanical, it is not the colorful petals and sepals that we lay-folk admire in the fields and flower shops; it is the closed carpel, the special protective and nourishing tissue that completely envelops the growing seed-embryo. Thus all flowering plants fall under the broad classification of angiosperms, derived from the Greek words for seeds (*sperma*) inside a vessel (*angeion*). Bernhardt, p. 21.

[34] The earliest fossil fruit that shows seeds developing inside an enclosing carpel was discovered in 1997 in Late Jurassic strata located east of Beijing, China. *Archaefructus* ("ancient fruit") appears to have had a stem structure like that of an extinct seed fern tree, but the simple fruit is similar to that produced by some modern members of the houseleek (Crassulaceae), magnolia (Magnoliaceae), and buttercup (Ranunculaceae) families. See Bernhardt, p. 222.

[35] Flowers have not interacted exclusively with insects. Many species of bats have evolved into a nectar-eating way of life, becoming efficient pollinators in the process. The agave plants of our American Southwest are almost exclusively pollinated by long-nosed bats. And think how much drabber the world would be without hummingbirds and honeycreepers.

[36] Fertilization and seed development is quite different between angiosperms and their cone-bearing cousins. Each angiosperm seed is the product of two sperm and three female cells. Per botanist Peter Bernhardt, "One sperm cell unites with an egg to start the seed embryo. The second sperm cell usually fuses with two 'polar' cells in the same [embryo] sac. This odd triple union makes all the cells that will become the starchy food tissue that supports the young embryo. A cell containing a tripled nucleus grows and divides rapidly, which explains why the seeds of most flowering plants mature within a couple of weeks or months after fertilization. This means that throughout history, all the great civilizations supported by the cultivation of grasses with edible seeds (wheat, corn, rice) have depended ultimately on one sperm cell uniting with two polar cells." In cone-bearing plants, a single sperm cell unites with the egg cell, while the food tissue goes it alone and matures slowly. Pinyon seeds thus take two years to ripen. As Bernhardt points out, "Pine seeds are tasty, but no large civilization has ever depended on the contents of tree cones to support its citizens." Bernhardt, p. 104.

[37] Contrast the 250,000-plus angiosperms against fewer than 800 living species of gymnosperms. Bernhardt, p. 22.

[38] The reader is referred to Eiseley's *How Flowers Changed the World* for a lovingly written version of the advent of the angiosperms and their impact on the world. See Eiseley (1996)

[39] Many tropical grasses, especially the ones that 'grow like weeds' utilize a different type of photosynthesis, called C4 because of the number of carbon atoms that take place in a key chemical reaction (vs. most plants which are C3). The C4-based metabolism is much more efficient, hence the reason bermuda grass is such a successful invader of domestic lawns. Grass crops such as corn and sorghum can be grown as far north as they are only due to their C4 metabolisms that allow them to reach maturity in relatively short growing seasons. Glimn-Lacy, p. 24.

that cropping by grazers doesn't destroy the growing part of the plant but actually stimulates more growth. One problem in trying to restore native prairies in the United States is the requirement to provide this cropping, so bison are brought in to do their timeless duty.

Evolution is a continuous process—the plants and animals of today continue to change, affected by and affecting the world environment. One of the latest plant groups to appear, the Asteraceae, has rapidly radiated to all parts of the world, forming one of the largest plant families. Almost all are small ephemerals or perennial shrubs. However in the Galapagos Islands I stood in a forest of forty-foot-tall sunflower trees. Who knows?, in another hundred million years the inhabitants of this planet may roam forests composed mainly of huge sunflower trees, sprinkled here and there with 'living fossils' of pine, hemlock, larch and oak. And if Man does his worst and poisons the atmosphere and the oceans, there will always be the resilient bacteria, huddled around ocean vents or deep underground, ready to go forth and reform the Earth again.[40]

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Next Installment: Kingdom Bacteria

Timeline of Events in the Biogenic Transformation of the Earth
(Time is in millions of years before the present.)[41]

Time	Events
4,600	Beginning of Hadean Eon. Origins of Earth-Moon system & other planetary bodies. Sun producing only 70% of today's output.
4,300	Oldest zircon crystals from Australia; first land masses.
3,900	Beginning of Archean Eon. Probable origin of life as first bacterial cells. Appearance of first kingdom (Monera). Anaerobic prokaryotes, metabolisms and reproduction have evolved.
3,800	Isua Supracrustal Belt (present-day Greenland), indicating possible biologically produced carbonate and reduced carbon.
3,700	First appearance of Banded Iron Formations (BIFs), suggesting local sources of oxygen at sediment-water interfaces.
3,600	Pilbara Block (present day Western Australia), containing evidence for anoxygenic communities.
3,500	South African strata containing abundant reduced carbon in shales,. Implies widespread occurrence of photosynthetic bacterial communities. Oldest confirmed microfossils from Apex chert of present northwest Australia.
3,000	Oldest evidence for life in present-day North America: Steep Rock, Ontario. Diversification of bacteria—probably all major metabolic modes evolved by now (e.g., chemoautotrophy, oxidation, oxygenic photosynthesis, reduction of iron and manganese oxides to metals).
2,700	Stromatolites abundant and cosmopolitan on ancient continents in parts of present-day Africa, North and South America, Australia, and Asia.
2,500	Beginning of Proterozoic Eon. Oxygen gas begins to seasonally accumulate; banded iron formations (BIFs) conspicuous and abundant; carbonate platforms, indicating biogenic reef-like structures made by bacterial communities in marine settings. First super continent of Rodinia (pre-Pangaea).
2,400	Beginning of worldwide age of BIFs: 90% of Earth's current mineral iron deposits in present-day southern Africa, Brazil, Central America, western Ontario, northern Michigan, and Minnesota formed between 2,400 and 1,800 million years ago.
2,200	Widespread occurrence of prokaryotic plankton in world's oceans.
2,100	Increasing UV absorbing ozone shield (O3 derived from O2 accumulating in atmosphere).
2,000	Free O2 abundant in atmosphere, indicating dominance of aerobic organisms. Mitochondira, ancestors to most eukaryotes, acquired by symbiosis as purple bacteria.
1,800	Replacement of BIFs by red beds (oxidized iron sediments), indicating worldwide transition to an atmosphere rich in oxygen.
1,700	Appearance of second kingdom (protoctista). Earliest eukaryotes documented in the fossil record, indicating cell evolution by symbiosis.
1,400	Appearance of terrestrial cyanobacterial life (desert crust and soil microbial communities).
600	Appearance of third kingdom (animals). Inferred origins of egg, sperm, embryo. Appearance in fossil record of soft-bodied animals (sponges, coelenterates, arthropods, and others.)
570	Beginning of Phanerozoic Eon and Paleozoic ("ancient life") Era. Appearance of fourth and fifth kingdoms (plants and fungi).
500	(Ordovician Period) Colonization of land surfaces by algae and insects
440	(Silurian Period) Appearance of terrestrial plants. Rhyniophytes with fungi in plant roots. Beginning of widespread life on land.
408	(Devonian Period) Land extensively covered by first forests. First appearance of plants with seeds.
323	(Pennsylvanian [Carboniferous] Period) Widespread large trees in swamps lead to coal forests.
225	(Triassic Period) Appearance of flowering plants (angiosperms).
65	(Late Cretaceous Period) Appearance of grasses.
0.01	(Holocene Epoch) Appearance of agricultural urban centers based on agricultural cultivation of grasses (wheat, rice, etc.)

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[40] In an essay of this brevity, I have touched only upon the contributions of 'living' biota to the genesis of the environment. Thus I have deliberately omitted the effects of viruses, which technically are not considered members of any of the kingdoms of life. However, their effect on organisms and life processes can be enormous. The oceans, for example, form a huge reservoir of viruses (from 10 to 100 million in a teaspoonful), which may be critically involved in regulating the largest biome on the planet. See Suttle (1999).

[41] Table modified from timeline presented in Margulis (1995), pp. 54-64.