Page Back: Earth - Glossary	Unit Up: Cosmic Evolution	Unit Up: Cosmos	Unit Home (you are here)	Page Next: Glossary (subcategory)
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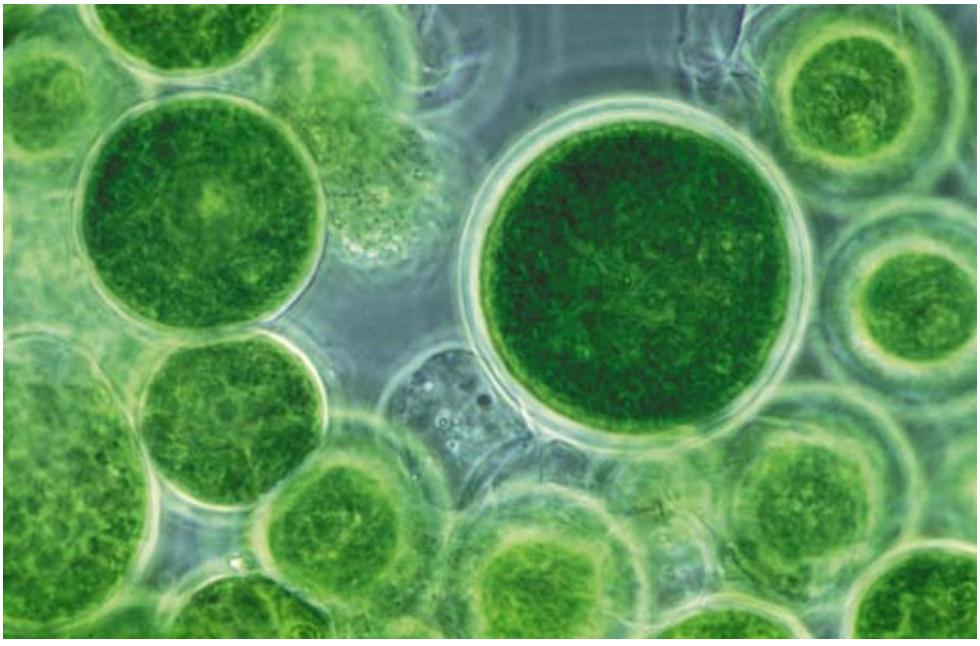
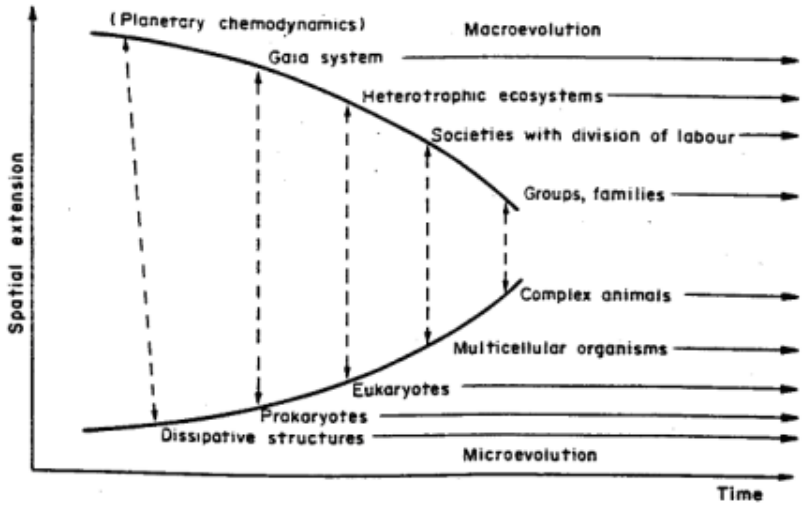
Life



The Green Algae, *Chlorella* sp. (Division Chlorophyta, Order Chlorellales. Family Chlorellaceae). This photo is found at a number of places online, e.g. Integrated Algae Production in Built Environments, Algae Research, HFood: Chlorella, This hardy freshwater organism has a number of uses (food, medicinal, wastewater treatment, biofuel, etc).

Life as Emergent Evolution



The above shows the second of a series of three integrative diagrams on Cosmic evolution by Erich Jantsch. In his book ***The Self Organizing Universe***, Jantsch, an astronomer and futurist influenced by systems theorist Illya Prigogine, unifies the various fields of science and human knowledge in a single evolutionary framework. The above diagram, entitled "Socio-biological evolution", continues the same events and processes shown inthe previous diagram. As the name indicates, evolution is here not only about life but about communities of organisms and social behaviour. Here, following the development of the Earth, life appears and evolves through feedback between the micro- and macro- scales. On the macro- or more properly collective scale, there is the evolution of the prebiotic Earth (macro) and dissipative structures (micro) into planetary biosphere (Gaia - macro) and prokaryote organisms (micro). The evolution of eukaryotes makes possible diversified ecosystems, while multicellular organisms and more complex nervous systems and intelligence levels enable intraspecific societies and group and family behaviour (ethology, sociobiology). MAK110907. (diagram copyright, Erich Jantsch, Pergamon Press).

Previous diagram | Next diagram

The science of Evolution

A number of specialised fields of biology contribute methodologies and tools for mapping out and understanding the history and evolution, and building the family tree of, life on Earth. Because each is as useful as the other, they are arranged here in chronological sequence of their first articulation as a proper science:

Taxonomy Although the philosopher Aristotle organised the animal kingdom in a linear scale according to a "natural ladder", and so, in a sense, was the first biologist, it wasn't until the 18th century, the Swedish botanist Carl von Linné, an heir to the age of enlightenment, developed a method of classifying the natural world in a formal manner, called binomial nomenclature. This enabled every species, living or extinct, to be be scientifically identified, described, and placed in a category with similar organisms. Without being able to formally identify, name, and reference species in this way, biology would not be possible. Almost two and a half centuries later, Linnaeus (the Latinised version of his name under which he is better known)'s taxonomic system is still an essential part of biology.

Paleontology : Although since classical times travellers and philosophers would observe shells in rocks at the sides of mountains, or discover the skeletons of prehistoric elephants or dinosaurs and believe them to the the remains of fabulous mythical creatures, Paleontology, as a science of the study of ancient life via fossil remains, only dates back to end of the 18th century. Fossil shells and plants were thought of as curiosities formed under the Earth by inorganic means, perhaps representing the way in which the "great chain of being" bridged the mineral and plant and animal kingdoms. Natural philosophers of the time had difficulty making sense of the growing number fossil bones

uncovered in mines and quarries until the great French naturalist Georges Cuvier showed that they were the petrified remains of animals anatomically similar to those found today, but different enough to belong to different genera and families of organisms. Fossils could thus be understood and explained biologically, rather than as miraculous curiosities. As evolution was not yet understood, Cuvier explained the succession of life in terms of repeated local extinctions, with new species migrating to fill the gaps. He was thus the first person to show that species once alive could become extinct. Up until that time this was thought impossible, because it would create a gap in the God's perfect creation, the Great Chain of Being. Cuvier never explained where species came from in the first place, as he considered this beyond the capacity of science (he was totally opposed to the proto-evolutionary theory of Lamarck). Catastrophism, the idea of repeated global catastrophes, after which God repopulated the world with different species, is often wrongly attributed to Cuvier, and belongs to later scientists such as Alcide d'Orbigny in France and William Buckland in England. Even with the many scientific discoveries made since, uncovering and understanding the fossil record remains an essential part of mapping the history of life on Earth.

Evolution: In the mid 19th century Charles Darwin established a naturalistic theory of evolution, one that still serves as the foundation for evolutionary biology today. Although scientists had already aquired a concept of geological processes over vast eras of time, and Cuvier, Owen, and other naturalists had identified fossils and even named many kinds of prehistoric organisms, and that species could become extinct, the idea that ***life itself could change*** was still new, although gaining in popularity, tied in with the general idea of social progress and spiritual themes of the temporalisation of the Great Chain of Being. What was radicallyt new however was to explain evolutrion in pureely naturalistic terms, Darwin being only the second scientist to do so, after Lamarck. It is hard for us in the modern world to imagine the importance of Darwin's discovery, and his introduction of dynamism and progressive change in a literalist biblical theistic or deistic worldview.

Without evolution, there would only be a stifling sameness, no rise and fall of vendobionts, anomolocarids, trilobites, sea scorpions, weird armoured paleozoic fish, primordial coal swamps, dinosaurs, and all the other incredible denizens and ecosystems that have populated and shared our planet through the ages. About the most we could hope for in a static universe would be dinosaurs on Noah's Ark. Nor would we have an idea of where we are going (which may or may not be an optimistic one, depending on your perspective).

Darwinism (natural selection) and Lamarckism (acquired characteristics) would continue as rivals for half a century and more; there would even be a totally independent Lamarckian-like Americxan theory called Orthogenesis, developed by Cope and later by Osborne. In the end the weight of experimental evidence favoured Darwin, especially when Mendellian inheritance provided the missing mechanism by which inherited traits could be incorporated into Darwinian selectionism, the result being the early to mid twentieth century "modern synthesis" (sometimes called "neo-Darwinism" although this technically refers to an earlier phase of Darwinian theory)

Phylogeny and Systematics. If paleontology reveals the remains of organisms from past ages, and evolution shows that these various species came about through natural rather than supernatural processes, ***Phylogeny*** is the piecing together of the family tree of life on Earth, tracing the path which evolution took. Phylogeny was developed by the german scientist, illustrator, and evolutionary populariser Ernst Haeckel in the second half of the 19th century. Nevertheless it was not till the mid 20th century that ornithologist and biological systematist Ernst Mayr, vertebrate paleontologist George Gaylord Simpson, and evolutionary biologist Arthur James Cain developed evolutionary systematics, seamlessly integrating the taxonomic system of Linnaeus with the evolutionary "Modern Synthesis" science of Darwin and Mendel to create the new science of ***Systematic Biology***, which is concerned with the classification of life according to its phylogeny (its evolutionary history). Palaeontologist Alfred Sherwood Romer, popularised phylogenetic trees that were incorporated into evolutionary systematics. Several decades later, the German entomologist Willi Hennig developed the second great phylogenetic science, Cladistics, as a means of empirically testing phylogenetic hypotheses, although it would not be until the 1980s that his ideas were accepted in the English-speaking world, where they had a revolutionary impact, especially in vertebrate paleontology, thanks to the work of Jacques Gauthier and others. Cladistic hypotheses are graphically represented in the form of a type of phylogenetic tree called a cladogram, which is totally distinct from Romer's trees. During the 1960s, the biochemist Walter M. Fitch developed molecular phylogeny, by which the evolutionary history of a group can be traced through studying molecular sequences (proteins, RNA, and DNA). As with cladistics, the statistical results can be represented in the form of a branching tree. In the 1970s and 80s Carl Woese expanded this

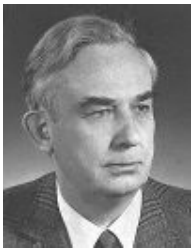
methodology to study the family tree of all life on Earth, discovering the three great domains of life. Modern phylogenetics is mostly a synthesis of cladistics and molecular phylogeny. Especially in vertebrate paleontology, paleoherpetology, and dinosaurology, the Linnaean system has been challenged by the new cladistic system of phylogenetic nomenclature. Nevertheless the utility and robustness of the Linnaean scheme make its abandonment unlikely any time soon. Both classification schemes use a system of nested hierarchies to show how organisms are related, and only recognise "natural" groups (groups that share a common ancestor).

Great names in phylogeny:

Ernst Haeckel, who first defined phylogeny

George Gaylord Simpson, mammalologist and co-founder of evolutionary systematics

Alfred Sherwood Romer, the most influential paleontologist of the 20th century



Willi Hennig, the father of cladistics

Carl Woese who developed molecular phylogeny and discovered the three domains of life

As with geneology diagrams that map the ancestry of a human family, phylogenetic diagrams that trace the origin, descent, and evolutionary relationships of groups of organisms, or even of all life on earth, are presented in terms of tree-like diagrams, called dendrograms or cladograms which together map out the family relationship of all of life on Earth, putting it all together in one big evolutionary tree. Along with the geological timescale, phylogeny constitutes the central focus of ***Palaeos***.

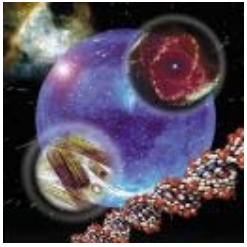
Even so, phylogenetic science has yet to realise its full crossdisciplinary potential; today evolutionary systematics is neglected, whilst new promising developments such as stratocladistics are ignored, leading to irresolvable conflicts between "morphology" (cladistics) and "molocules", with the latter generally being given preference over the former whenever there is any contradiction between the two. MAK120320

Ecology : Just a holding page at the moment.

Life in the Universe

There is no reason why Life should be limited to Earth alone. Hence this page should perhaps be titled "Life in the Universe", rather than just Life. In any case, as shown below, we have purely informally divided life into two categories - Life on Earth ("Tellurobiota") and LIfe elsewhere in the Universe (Astrobiology). wherever life appears however, and whatever form it takes, it is likely to be governed by the same rules of evolution, ecological guilds and niches, and so on. Also central to the topic at hand is paleontology, the study of ancient life via fossil remains (which raises also the possibility of exopaleontology, the study of fossil lifeforms from other worlds, currently only the province of science fiction, apart from controversial Martian meteorite fossils), and phylogeny and systematics, putting it all together in one big evolutionary tree (so far only applicable to Earth, but who knows in the future what science will uncover). MAK110905

Astrobiology : Of course life is certainly not limited to this planet alone, hence we have a page on the very speculative but also very cool science of ***astrobiology***.



Life on Earth : Here is our basic introduction to Life on Earth; which we have informally christened "Tellurobiota". This unit covers such topics as the Meaning of Life, the Facts of Life, and the Purpose of Life, Kingdoms of Life, and the Tree of Life and serves as a springboard to more detailed consideration of the phylogeny (evolutionary tree) of Life on Earth.

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page by MAK110905, edited RFVS111204, last modified MAK120329

Life

A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z

A.

Autotroph: an organism which makes its own food from inorganic materials. using sunlight or chemical reactions for energy. Wikipedia glossary, MAK

B.

Benthic: Used to describe aquatic organisms that are bottom dwelling. (USGS Paleontology glossary)

Big Five: five mass extinctions identified by Jack Sepkoski and David M. Raup in a paper published in 1982. These are:

- ***Ordovician–Silurian extinction event*** (End Ordovician or O-S) – 440–450 Ma at the Ordovician-Silurian transition. Two events occurred that killed off 27% of all families and 57% of all genera. Together they are ranked by many scientists as the second largest of the five major extinctions in Earth's history in terms of percentage of genera that went extinct.
- ***Late Devonian extinction*** – 360–375 Ma near the Devonian-Carboniferous transition. At the end of the Frasnian Age in the later part(s) of the Devonian Period, a prolonged series of extinctions eliminated about 19% of all families, 50% of all genera and 70% of all species. This extinction event lasted perhaps as long as 20 MY, and there is evidence for a series of extinction pulses within this period.
- ***Permian–Triassic extinction event*** (End Permian) – 251 Ma at the Permian-Triassic transition. Earth's largest extinction killed 57% of all families and 83% of all genera[5] (53% of marine families, 84% of marine genera, about 96% of all marine species and an estimated 70% of land species) including insects. The evidence of plants is less clear, but new taxa became dominant after the extinction.[8] The "Great Dying" had enormous evolutionary significance: on

land, it ended the primacy of mammal-like reptiles. The recovery of vertebrates took 30 million years, but the vacant niches created the opportunity for archosaurs to become ascendant. In the seas, the percentage of animals that were sessile dropped from 67% to 50%. The whole late Permian was a difficult time for at least marine life, even before the "Great Dying".

- ***Triassic–Jurassic extinction event*** (End Triassic) – 205 Ma at the Triassic-Jurassic transition. About 23% of all families and 48% of all genera (20% of marine families and 55% of marine genera) went extinct.[5] Most non-dinosaurian archosaurs, most therapsids, and most of the large amphibians were eliminated, leaving dinosaurs with little terrestrial competition. Non-dinosaurian archosaurs continued to dominate aquatic environments, while non-archosaurian diapsids continued to dominate marine environments. The Temnospondyl lineage of large amphibians also survived until the Cretaceous in Australia (e.g., ***Koolasuchus***).
- ***Cretaceous–Tertiary extinction event*** (End Cretaceous or K-T extinction) – 65.5 Ma at the Cretaceous.Maastrichtian-Paleogene. Danian transition interval. The K–T event is now called the Cretaceous–Paleogene (or K–Pg) extinction event by many researchers. About 17% of all families, 50% of all genera and 75% of species became extinct. In the seas it reduced the percentage of sessile animals to about 33%. The boundary event was severe with a significant amount of variability in the rate of extinction between and among different clades. Mammals and birds emerged as dominant land vertebrates in the age of new life.

More recently it has been argued on statistical evidence that the "Big Five" represent the largest (or some of the largest) of a relatively smooth continuum of extinction events. See also sixth extinction. (Wikipedia)

Bauplän: The concept of a body plan, ***Bauplän*** (pl. Baupläne), is critical to understanding the most fundamental evolutionary radiations. What is a body plan? This is a difficult question to define, and it is usually answered with examples: the insect body plan, the jellyfish body plan, or whale body plan. Loosely defined, a body plan is primarily morphological, involving the shared structural homologies of upper taxa. For example, the vertebrate bauplän might be described as comprising a "cephalised, sensate, bilaterally symmetrical, motile, coelomate gnathostome having a segmented endoskeleton, a dorsal hollow nerve chord, and a ventral gut" (Ostrom 1992, p. 119). Body plans, or baupläne, affect development at its most basic level, thus developmental constraints strongly influence the range of body plans possible. Even in simple animals, axes of symmetry are so fundamental that significant internal co-adaptation is required for viable body plan mutations to occur. (Chris Clowes 2002)

Belief: The position of affirming the truth of a proposition. Belief, if asserted as true in a debate, bears a burden of proof (as does disbelief). See also: unbelief. (W.J. Hudson)

Bilateral symmetry: Symmetry in only one plane, called the sagittal plane, that divides an organism into roughly mirror image halves (note that in nature and biology, symmetry is approximate. For example, plant leaves, while considered symmetric, will rarely match up exactly when folded in half). Thus there is approximate reflection symmetry. Often the two halves can meaningfully be referred to as the right and left halves, e.g. in the case of an animal with a main direction of motion in the plane of symmetry. Contrast radial symmetry. (Wikipedia)

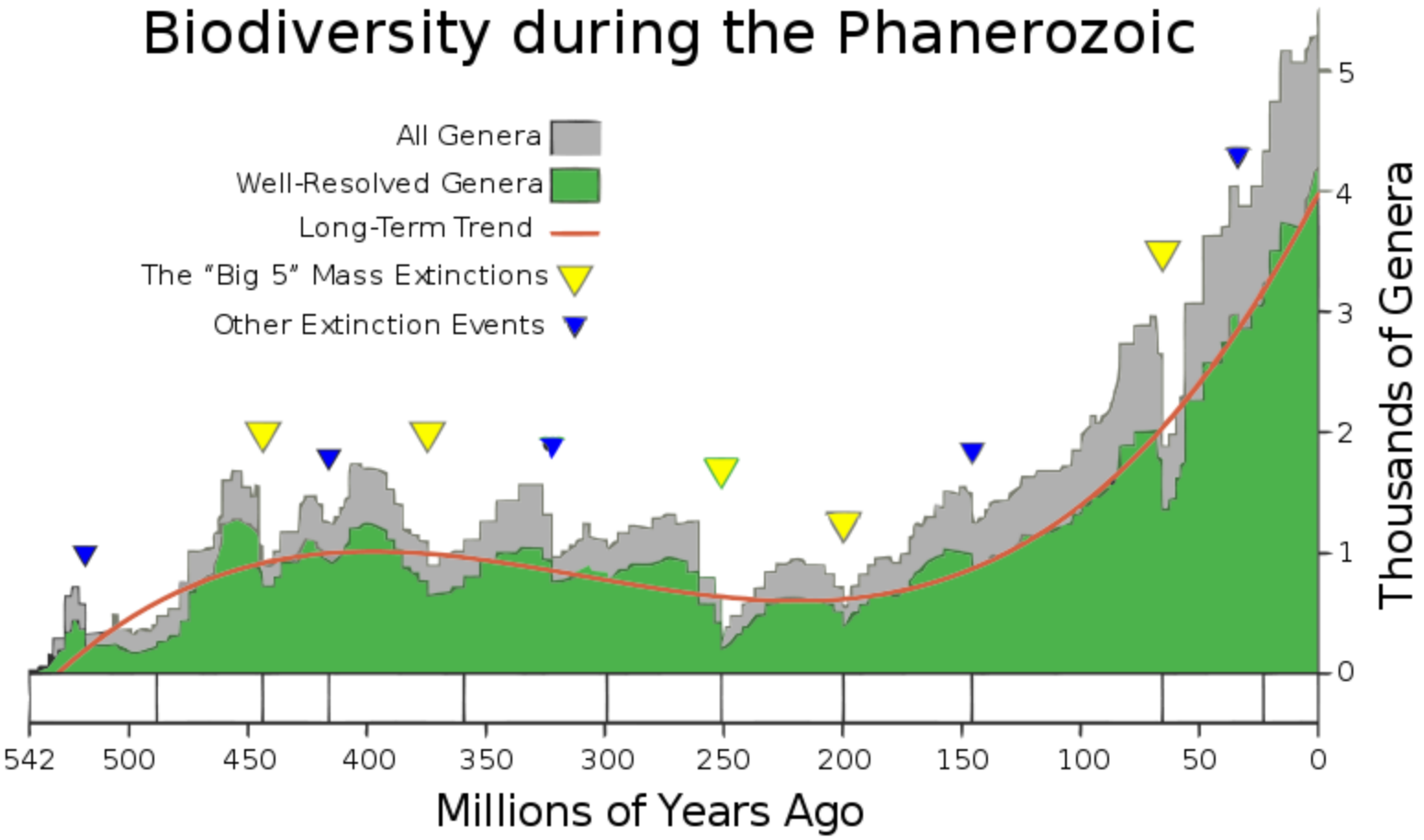
Biocenose: see Community.

Biocentrism : Centered on life as a whole, rejecting the idea that man is the summit of creation, or has greater moral worth or ontological value than other species. Contrast anthropocentrism. (MAK, Wikipedia glossary)

Biochemistry: Chemical reactions that occur within or are associated with living organisms. (UCMP Understanding Evolution Glossary)

Biodiversity: In biology, the degree of variety of the Earth's animal, plant, and microbial lineages within a given ecosystem, biome, or an entire planet. Used to describe species richness, ecosystem complexity, and genetic variation. Different measures of biological diversity (biodiversity) include number of species, number of lineages, variation in morphology, or variation in genetic characteristics. In terrestrial habitats, tropical regions are typically rich whereas polar regions support fewer species. Biodiversity is also a measure of the health of ecosystems. Greater biodiversity implies greater health. The term biological diversity was used first by wildlife scientist and conservationist Raymond F. Dasmann in the 1968 lay book ***A Different Kind of Country*** advocating conservation. The term was widely adopted only after more than a decade, when in the 1980s it came into common usage in science and environmental policy. Global biodiversity has fluctuated through time (see following diagram), being diminished by mass extinctions

(including the current anthropogenic extinction) and after several million years following such dips, increasing through evolutionary radiation (from UCMP Understanding Evolution Glossary, Allaby 1998, and Wikipedia, A Glossary of Terms Related to Basic Ecology)



From Wikipedia. This image shows the biodiversity during the Phanerozoic. Note that this is a result of changes in both the rate of extinctions and the rate of new originations. The Dresbachian extinction event in particular is obscured by nearly immediate replacement with new genera. Colour code:

- grey = total known genera from Sepkowski's catalogue (cited by Rohde & Muller)
- green = "well-defined genera", i.e. known genera excluding those represented by "single occurrences" and those whose dates are uncertain.
- red = trend for "well-defined genera". Derived by fitting a third-order polynomial to the data.
- yellow = the "Big Five" mass extinctions.
- blue = other extinction events.

Reference: Rohde, R.A., and Muller, R.A. (2005). "Cycles in fossil biodiversity". *Nature* 434: 208-210. pdf.
(this version of diagram by Albert Mestre)

Biogenetic law: see recapitulation.

Biogeochemistry: effect of biota on global chemistry, and the cycles of matter and energy that transport the Earth's chemical components in time and space. Wikipedia glossary

Biogeochemical cycle: the pathway through which a chemical, element, or molecule moves through the atmosphere, hydrosphere, lithosphere, and biosphere. Wikipedia glossary

Biogeography: the study of the distribution of organisms and species, past and present, and of diverse processes that underlie their distribution patterns. The patterns of species distribution at this level can usually be explained through a combination of historical factors such as speciation, extinction, continental drift, glaciation (and associated variations in sea level, river routes, and so on), and river capture, in combination with the area and isolation of landmasses (geographic constraints) and available energy supplies. Wikipedia

Bioluminescence: The production of light by living organisms. (USGS Paleontology glossary)

Biomass: the sum of all living living organisms in an area; a measure of the quantity of living matter in a given unit area or volume. Wikipedia glossary

Biome: The total complex of biotic communities occupying and characterizing a particular area or zone, classified according to its climate and type of vegetation. More Wikipedia glossary

Biophilia: The term "biophilia" literally means "love of life." coined by psychologist Erich Fromm to describe a psychological orientation of being attracted to all that is alive and vital. Edward O. Wilson introduced and popularized the hypothesis in his book entitled ***Biophilia***. He proposed the possibility that the deep affiliations humans have with nature are rooted in our biology. Unlike phobias, which are the aversions and fears that people have of things in the natural world, philias are the attractions and positive feelings that people have toward certain habitats, activities, and objects in their natural surroundings. (Wikipedia)

Biota: The plants and animals of a specific region or period, or the total aggregation of organisms in the biosphere (Allaby 1998); the total collection of organisms of a geographic region or a time period. (A Glossary of Terms Related to Basic Ecology) More

Biotic factors: The living environmental influences that affect organisms, such as predators, competitors, prey. Wikipedia glossary

Biosphere: life as a planetary phenomenon, the global ecosystem, the totality of life on Earth, or on other planets in the universe. See also Gaia hypothesis.

C.

Cambrian explosion, Cambrian radiation: The abrupt appearance of a diverse and highly derived fauna in the brief Tommotian and Atdabanian Stages of the Early Cambrian is widely known as the 'Cambrian Explosion,' one of the most, if not the most, dramatic evolutionary radiations in the history of life. Although that particular phrase only came into common usage in the early to mid 1970s, the event itself has long been recognized as a phenomenon demanding some accommodation from evolutionary theory. As early as 1859, Charles Darwin drew attention to the matter in ***Origin of Species***, and it is probable he had considered the matter for many years prior to that.

The paleontological evidence does not, generally corroborate molecular clock studies (contrary to the almost bizarre view expressed in Ayala ***et al***. 1998). Bruce Runnegar (1982, p. 397) notes: "Few of the known late Precambrian animals have been closely related to Cambrian organisms, and none of the associated or coeval trace fossils has been thought to have been produced by the animals observed more directly. ... What the trace fossil record does tell us, is that there were few large, mobile, bottom-dwelling animals before the end of the [Vendian]." (Chris Clowes 2002-2003)

The long-running puzzlement about the appearance of the Cambrian fauna, seemingly abruptly and from nowhere, centers on three key points: whether there really was a mass diversification of complex organisms over a relatively short period of time during the early Cambrian; what might have caused such rapid change; and what it would imply about the origin and evolution of animals. Interpretation is difficult due to a limited supply of evidence, based mainly on an incomplete fossil record and chemical signatures left in Cambrian rocks.

The "Cambrian explosion" can be viewed as two waves of metazoan expansion into empty niches: first, a co-evolutionary rise in diversity as animals explored niches on the Ediacaran sea floor, followed by a second expansion in the early Cambrian as they became established in the water column. The rate of diversification seen in the Cambrian phase of the explosion is unparalleled among marine animals: it affected all metazoan clades of which Cambrian fossils have been found. Later radiations, such as those of fish in the Silurian and Devonian periods, involved fewer taxa, mainly with very similar body plans. Although the recovery from the Permian-Triassic extinction started with about as few animal species as the Cambrian explosion, the recovery produced far fewer significantly new types of animals.

Whatever triggered the early Cambrian diversification opened up an exceptionally wide range of previously-unavailable ecological niches. When these were all occupied, there was little room for such wide-ranging diversifications to occur again, because there was strong competition in all niches and incumbents usually had the advantage. If there had continued to be a wide range of empty niches, clades would be able to continue diversifying and become disparate enough for us to recognise them as different phyla; when niches are filled, lineages will continue to resemble one another long after they diverge, as there is limited

opportunity for them to change their life-styles and forms.

There were two similar explosions in the evolution of land plants: after a cryptic history beginning about 450 million years ago, land plants underwent a uniquely rapid adaptive radiation during the Devonian period, about 400 million years ago. Furthermore, Angiosperms (flowering plants) originated and rapidly diversified during the Cretaceous period. (Wikipedia)

Further reading (giving two diametrically opposite perspectives): ***Wonderful Life*** by Stephen J. Gould; ***The Crucible of Creation*** by Simon Conway Morris

Community: Any grouping of populations of different organisms that live together in a particular environment (Allaby 1998), including plants, animals, micro-organisms. Each population is the result of procreations between individuals of same species and cohabitation in a given place and for a given time. When a population consists of an insufficient number of individuals, that population is threatened with extinction; the extinction of a species can approach when all biocenoses composed of individuals of the species are in decline. In small populations, consanguinity (inbreeding) can result in reduced genetic diversity that can further weaken the biocenose. Biotic ecological factors also influence biocenose viability; these factors are considered as either intraspecific and interspecific relations. (Wikipedia, A Glossary of Terms Related to Basic Ecology)

D.

E.

Ecological species concept: A definition of a species as a set of organisms adapted to a particular, discrete set of resources (or "niche") in the environment. Compare with biological species concept, cladistic species concept, phenetic species concept, and recognition species concept. See other species definitions. (Fossil Mall glossary)

Ecology: The study of the interactions of organisms with their environment and with each other. (Wikipedia glossary)

Ecomorphology or ***Ecological Morphology*** is the science of the relationship between morphological and ecological variation, for example by measuring the performance of traits (i.e. sprint speed, bite force, etc.) associated behaviors, and fitness outcomes of the relationships. See also Functional Morphology. (Wikipedia

Ecosystem: A discrete unit, or community of organisms and their physical environment (living and non-living parts), that interact to form a stable system (Allaby 1998). (A Glossary of Terms Related to Basic Ecology)

Ectotherm: ("outer warmth") colloquially, "cold blooded"; an animal that regulates body temperature through external means; e.g. basking in the sun to become warmer, or sitting in the shade to become cooler. Includes most invertebrates, most fish, and all amphibians and reptiles (apart from endothermic pterosaurs and some or perhaps all dinosaurs). ***Poikilothermy*** (body temperature varies considerably) is similar. The Permian sail backed pelycosaurs such as ***Dimetrodon*** were classic ectotherms which used their sails as temperature regulation devices. (MAK)

Endemic, Endemism: Present within or limited to a particular geographic or local area. A species or taxonomic group that is restricted a to particular area because of such factors as isolation or response to soil or climatic conditions; this species is said to be endemic to the place and would be native. Compare with Cosmopolitan (Allaby 1998) (A Glossary of Terms Related to Basic Ecology)

Endotherm: ("outer warmth") colloquially, "warm blooded"; an animal that regulates and maintains a constant body temperature and can generate internal heat for maximal metabolic efficiency, regardless of external (environmental, ambient) temperature. ***Homeothermy*** (body temperature remains more or less the same) is similar. Thermoregulation includes cooling through panting or sweating (evaporation) and warming through shivering. Birds, mammals, some fish (tuna), some insects (bees) and quite likely feathered bird-like dinosaurs are all examples of endothermy. (MAK)

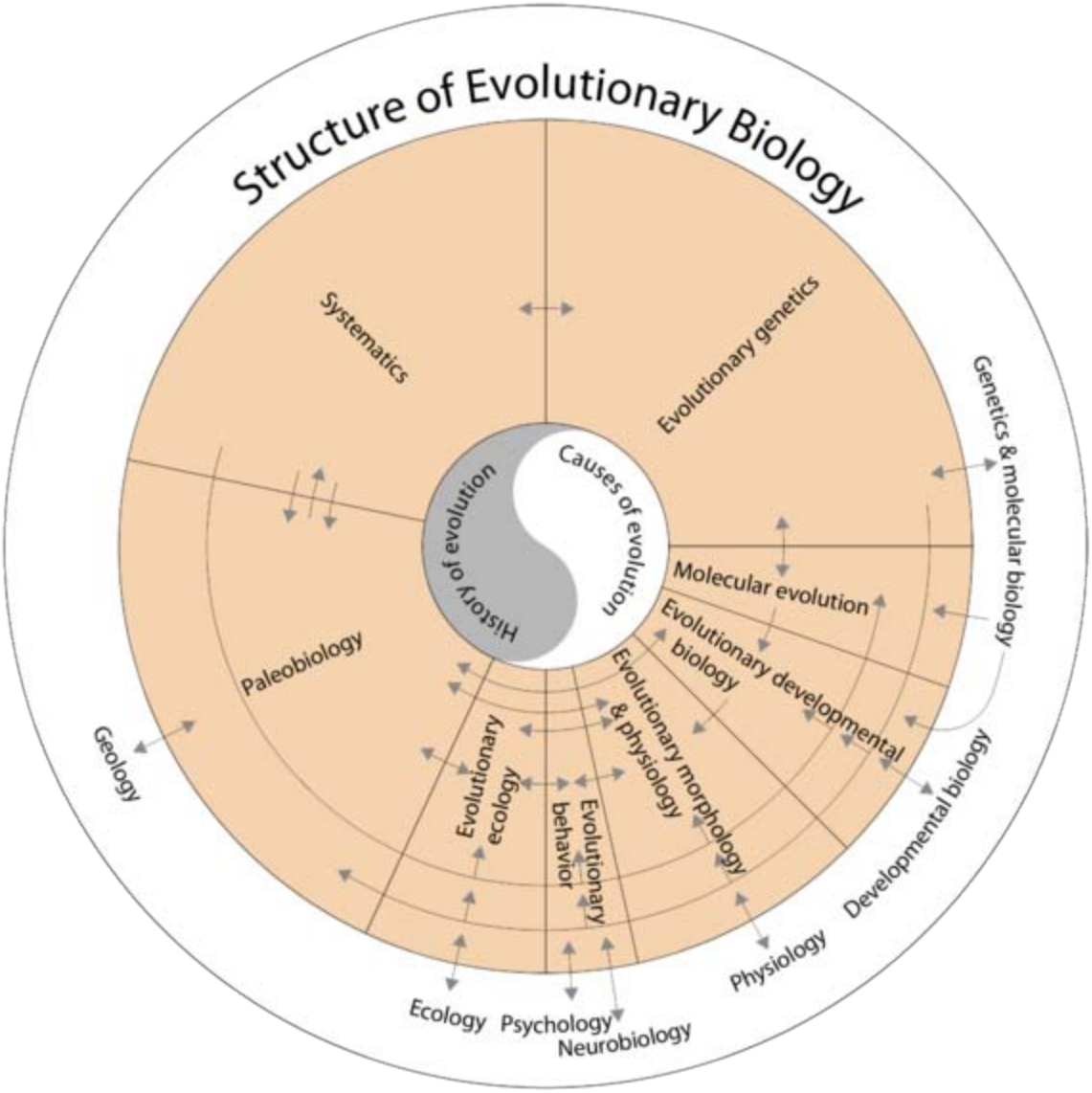
Endosymbiosis: A relationship in which one organism lives inside another, to the mutual benefit of both

(these are called ***endosymbionts***). Examples are nitrogen-fixing bacteria (called rhizobia) which live in root nodules on legume roots, single-celled algae inside reef-building corals, and bacterial endosymbionts that provide essential nutrients to about 10%–15% of insects. It is generally accepted that early in the evolutionary history of Eukarya, eukaryote cells engulfed bacteria, forming a symbiotic relationship, which became so mutually interdependent, that they behaved as a single organism; these include mitochondria and chloroplasts. (from Wikipedia and UCMP Understanding Evolution Glossary)

Eubacteria: the majority of extant bacteria; one of the three domains of life on Earth, prokaryotes that are metabolically and morphologically distinct from Archaea. Woese et al 1990 replaced "Eubacteria" with "Bacteria " as the taxon name; in order to avoid ambiguity we have avoided following this course. **More**

Eukarya, Eukaryote: an organism whose cells contain complex structures enclosed within membranes (called organelles), and in which genetic material is contained within a nucleus, in contrast to prokaryotes. Cell division in eukaryotes is also distinct, involving separating the duplicated chromosomes by means of microtubules. There are two types of division processes. In mitosis, one cell divides to produce two genetically identical cells. In meiosis, which is required in sexual reproduction, one diploid cell (having two instances of each chromosome, one from each parent) undergoes recombination of each pair of parental chromosomes, and then two stages of cell division, resulting in four haploid cells (gametes). Each gamete has just one complement of chromosomes, each a unique mix of the corresponding pair of parental chromosomes. Lynn Margulis argues that some of these structures, for example mitochondria and chloroplasts, were originally distinct organisms, and that the eukaryote cell itself is the result of endosymbiosis between several different types of prokaryote organisms, an event or events of great evolutionary significance. In Carl Woese's molecular phylogeny-based classification, the third domain of life on Earth. Woese rejects the prokaryote-eukaryote distinction. Relative to prokaryotes, eukaryotes represent only a small proportion of life on Earth, Steven Jay Gould refers to this when arguing for nondirectionality. (MAK, incorporates material from Wikipedia) **More**

Evolutionary biology: sub-field of biology concerned with evolution



From Wikipedia. The structure of evolutionary biology and its relationship to other biological disciplines. The history and causes of evolution (center) are the subject of the various subdisciplines of evolutionary biology (inner ring), which grade into one another and, as shown by the arrows, are related both to one another and to other disciplines (outer ring). The areas of the segments in the diagram convey an impression of the historical contributions of the subdisciplines to the literature of evolutionary biology. (Diagram and text by Andrew Colvin)

Extant : A species or taxon that is still in existence, recent, living, surviving now. The opposite of extinct.

Extinct: A species or taxon that has died out and hence is no longer found on Earth. Extinction may be recent, the result of human activity, or it may have occurred millions of years ago. The opposite of extant. When extinction occurs simultaneously across many taxa it is known as a mass extinction.

Extremophile: an organism that favours extreme conditions (relative to what is optimal to most life on Earth), such as very high or very low temperature, or lack of oxygen. Most life in the universe would almost certainly be extremophile.

F.

Fauna: The animal life of a region or geological period (Allaby 1998). (A Glossary of Terms Related to Basic Ecology)

Fish: A rather taxonomically meaningless assemblage of vertebrates defined only by their non-tetrapod nature. The traditional term is disliked by cladists because it does not constitute a natural clade.

Flora: Plant or bacterial life forms of a region or geological period Allaby 1998 (A Glossary of Terms Related to

Basic Ecology)

Food chain: a group of organisms interrelated by the fact that each member of the group feeds upon on the one below it. (Wikipedia glossary)

Food web: a set of interconnected food chains by which energy and materials circulate within an ecosystem. (Wikipedia glossary)

Fungi: Moulds and mushrooms. Not quite animals and not quite plants (though phylogenetically more closely related to the former than the latter). One of the threekingdoms of multicellular life in the Whittaker-Margulis classification scheme. **Fungi**

G.

Gaia hypothesis: The theory, formulated by the environmentalist James Lovelock and co-developed by the microbiologist Lynn Margulis in the 1970s, that all life on Earth, as well as their inorganic surroundings form a single and self-regulating complex system, maintaining the conditions for life in the planet. The scientific investigation of this hypothesis focuses in the observation of how the biosphere and the evolution of life forms contribute to the stability of global temperature, ocean salinity, oxygen in the atmosphere and other factors of habitability. Remains a controversial topic in some areas of the scientific community, although basically accepted in fields like geophysiology and Earth system science. (from Wikipedia)

Generalist: Jack of all trades, master of none. Highly adaptable, but not able to compete well with more advanced organisms in specialised roles. Tends to be cosmopolitan, generally morphologically primitive. Like R-selected species, good at surviving unstable environments and situations. (MAK)

Gigantotherm: ("giant warmth") an animal that maintains a constant body temperature through simply being so large that it takes a long time for its temperature to rise or fall. Gigantothermy is a form of Homeothermy (having a constant body temperature); it may be arrived at either through ectothermic (giant cold-blooded animal) or endothermic (giant warm-blooded animal) means. Dinosaurs are classic examples of gigantothermy. (MAK)

Guild: Group of organisms having a similar morphology, and exploiting the same food resources, living the same life-style and in the same environment, but which are not necessary related. Because no two types of organisms can occupy the same ecological niche (one will inevitably outcompete the other, and push it aside), comparable guilds have to be separated by geographical or chronological distance. A good example of the same guild is the modern crocodile and the phytosaurian thecodont (Parasuchia) of the late Triassic. Both are astonishingly similar in size, appearance, and life-style, and indeed modern crocodiles only appeared after the phytosaurs had become extinct. But they are only distantly related (both are archosaurian reptiles, but their common ancestor lived millions of years before the first phytosaur appeared). (MAK)

Gymnosperm: "naked seeds", after the unenclosed condition of their seeds (called ovules in their unfertilized state). Their naked condition stands in contrast to the seeds or ovules of flowering plants (angiosperms) which are enclosed during pollination. Includes conifers, cycads, Ginkgo, Gnetales, and extinct groups such as "seed ferns". (Wikipedia)

H.

Habitat: 1. The place, including physical and biotic conditions, where a plant or an animal usually occurs (Allaby 1998). 2. The physical conditions that surround a species, or species population, or assemblage of species, or community (Clements and Shelford, 1939). (A Glossary of Terms Related to Basic Ecology)

Hierarchy: Biological organisation, or the hierarchy of life, is the hierarchy of complex biological structures and systems that define life using a reductionistic approach. Each level represents an increase in organisational complexity, with each "object" being primarily composed of the previous level's basic unit. The basic principle behind the organisation is the concept of emergence: the properties and functions found at a hierarchical level are not present and irrelevant at the lower levels. The usual scheme, from the lowest level (below) to the highest level (top), is as follows (note: the following modifies the table taken

from Wikipedia by differentiating organisms and communities and so on):

Ecological level	• The biosphere, the complete set of ecosystems • The ecosystem, a grouping of organisms from all biological domains in conjunction with the physical (abiotic) environment • The biocoenosis or community, an interspecific grouping of populations • The population, a grouping of organisms of the same species
Organism level (obviously, if unicellular this is the same as the cellular level, below)	• The organism, the basic living system, a functional grouping of the lower-level components, including at least one cell
Super-cellular or Multicellular level	• The organ system, a functional grouping of organs • The organ, a functional grouping of tissues • The tissue, a functional grouping of cells
Cellular level	• The cell, the basic unit of all life and the grouping of organelles
Sub-cellular level	• The organelle, a functional grouping of biomolecules; biochemical reactions and interactions
A-cellular and Pre-cellular level	• The molecule, a grouping of atoms • The atom

Each level can also be broken down into its own hierarchy, and specific types of these biological objects can have their own hierarchical scheme. For example, genomes can be further subdivided into a hierarchy of genes (Wikipedia). The hierarchy can also extend beyond the biosphere to the cosmos as a whole; such arrangements being common in Transpersonal Psychology and the New Age/New Paradigm/New Consciousness movement. Philosopher and author Arthur Koestler, in association with (more) suggested a holarchy, a hierarchy of "holons", in which each part is the whole of those unites below it. This idea was adapted by New Age/New Consciousness philosopher Ken Wilber who applied it in an evolutionary context.

Homeostasis: the property by which a system, especially a living organism, regulates its internal environment so as to maintain a stable, constant condition. According to James Lovelock, the planet Earth as a whole is homeostatic system (Gaia Hypothesis). (MAK, Wikipedia glossary)

I.

J.

K.

K-selected species: species that produce fewer but stronger offspring and dedicate more care to their upbringing. K-selected species are better suited for, and better able to compete with strong competitors in a crowded environment. (Wikipedia glossary)

Keystone species: keystone species is a species that has a disproportionate effect on its environment relative to its abundance. Such species affect many other organisms in an ecosystem and help to determine the types and numbers of various others species in a community. (Wikipedia glossary)

L.

M.

Mass extinction: Event involving higher extinction rates than the usual degree of background extinction. See Big Five for diagram of extinction rates, and synopsis of five major extinctions.

Megafauna: animal life, generally specifically applied to terrestrial vertebrate, of exceptionally large size. Dinosaurs and large mammals such as proboscideans (mastodons, elephants, etc), rhinos, and so on are classic examples. Because they are so striking and charismatic, megafauna often feature in nature documentaries, books and artwork on the history of life, and so on.

Metazoa: a multicellular animal, whose cells are organized into tissues and organs. One of the three kingdoms of multicellular life in the Whittaker-Margulis classification scheme. They are rather anthropocentrically divided into Vertebrates and Invertebrates. **More**

Mimicry: imitative behavior, one species resembling one another, and gaining advantages as a result. For example harmless flies that have the same colouration as bees and wasps. Because predators know that wasps sting they tend to avoid anything that looks like them. See Batesian mimicry and Müllerian mimicry. Wikipedia glossary

Morphospace: a representation of the possible shape, structure, or form of an organism, usually with two or three variables plotted on a grid or diagram. More technically, an n-dimensional space, which each of the n axes corresponds to a variable which describes a particular aspect or character of the organism's morphology. The location in that space represents the specific morphology. So in the diagram at the right, the three axes or dimensions of morphospace each represent a particular variable in shell coiling (here translation rate, expansion rate, and distance of generating curve from coiling axis); together they can describe every possible spiral shaped shell. Adaptive radiation spreads out in morphospace along one or several dimensions. Note that in this diagram only a small proportion of possible morphospaces are occupied, most are impractical for adaptive or anatomic reasons. (MAK, AK's Rambling Thoughts, Mark Ridley; diagram from Raup 1966 via Mark Ridley - Evolution - A-Z morphospace)

Müllerian mimicry: A form of mutually beneficial mimicry in which two or more poisonous species resemble each another.Contrast with Batesian mimicry

Multicellular organism: an organism consisting of a hierarchical assemblage of cells, or in complex multicellular organisms, systems (for example circulatory, digestive, or reproductive) themselves collections of organs; these are, in turn, collections of tissues, which are themselves made of cells. (from Wikipedia)

Mutualism: In ecological and biological science today, mutualism is synonymous with the original scientific and current colloquial term symbiosis, an interaction between individuals of two different species where both benefit. (MAK)

N.

Nekton: Used to describe aquatic organisms that swim, as opposed to plankton which drift. (USGS Paleontology glossary)

Niche: In ecology, the role the species plays in the functioning of the ecosystem: the "functional status of an organism in its community" (Charles Elton, in Odum, 1959). The part of the environment occupied by a particular species along with the resources it uses and produces. A species' niche includes such factors as energy consumed, time of consumption, space occupied, temperature required, mode of reproduction, and behavior. (UCMP Understanding Evolution Glossary)

Nitrogen cycle: a continuous cycle by which nitrogen from the atmosphere and compounded nitrogen keeps getting exchanged through the soil into substances that can be taken up and used by green plants, what is left returns to the air as a result of denitrification. Wikipedia glossary

Nitrogen fixation: A chemical process by which nitrogen in the atmosphere is assimilated into organic compounds. Only certain bacteria are able to fix atmospheric nitrogen, which then becomes available to other organisms through the food chains. (PBS evolution Glossary)

Nucleotide: the building block of DNA and RNA; consists of a sugar and phosphate backbone with a base attached. (PBS evolution Glossary)

Nucleus: a membrane-enclosed central region of the eukaryotic cell, which contains the genetic material.

O.

Oxygen crisis: being a crisis for the earlier mentioned Archaea (one of the three domains of life), in that photosynthetic blue-green algae totally transformed the Earth by changing the atmosphere from reducing to oxygenating, thus paving the way for eukaryote life.

P.

Paleobiogeography: The branch of paleontology that deals with the geographic distribution of plants and animals in past geologic time, especially with regard to ecology, climate, and evolution.

Paleoecology: the study of the relationships between species in fossil assemblages.

Paleoenvironment: Environment in the geologic past. (USGS Paleontology glossary)

Paleoclimate: The climate of a given period of time in the geologic past. (USGS Paleontology glossary)

Parthenogenesis: Development from an egg cell that has not been fertilized. The term for a certain form of asexual reproduction that is found in some lizards, insects (notably among aphids), and certain other organisms. (PBS evolution Glossary)

Pelagic: Referring to open water marine habitats free of direct influence of the shore or ocean bottom. Pelagic organisms are generally free-swimming (nektonic) or floating (planktonic). (USGS Paleontology glossary)

Phanerozoic: the most recent, and current, of the four eons of the geological timescale, the time of diverse and complex life, complex ecosystems, and an oxygen-rich atmosphere. Divided into Paleozoic, Mesozoic, and Cenozoic. The Phanerozoic begins with the start of the Cambrian period, and continues to today. **More**

Population: A group of potentially inter-breeding individuals of the same species found in the same place at the same time (Booth et al. 2003). A group of organisms, typically a single species, and typically isolated from other members of its species in some manner. (W.J. Hudson)

Pheromone: chemical substance produced by some organisms and emitted into the environment to communicate with others of the same species.. (PBS evolution Glossary)

Philosophy of biology: subfield of philosophy of science, which deals with epistemological, metaphysical, and ethical issues in the biological and biomedical sciences. Although philosophers of science and philosophers generally have long been interested in biology (e.g., Aristotle, Descartes, and even Kant), philosophy of biology only emerged as an independent field of philosophy in the 1960s and 1970s. Philosophers of science then began paying increasing attention to biology, from the rise of Neodarwinism in the 1930s and 1940s to the discovery of the structure of DNA in 1953 to more recent advances in genetic engineering. Other key ideas include the reduction of all life processes to biochemical reactions, and the incorporation of psychology into a broader neuroscience. (Wikipedia)

Phosphorus cycle: the biogeochemical cycle that describes the movement of phosphorus through the environment. (Wikipedia - Glossary of ecology)

Pioneer species: species that first inhabit an environment which was previously unoccupied. (Wikipedia - Glossary of ecology)

Plankton: Aquatic organisms that drift, or swim weakly. Hence ***Planktonic*** describing aquatic organisms that float. (USGS Paleontology glossary)

Plant: traditionally and taxonomically meaninglessly used to include all photosynthetic organisms and fungi. In the Whittaker-Margulis scheme one of the three kingdoms of multicellular life, include the land plants and (in later classifications) green algae. more

Predation: the interaction among populations when one organism kills and consumes another one. (Wikipedia glossary)

Primary producer: an autotroph that obtains energy directly from the nonliving environment through photosynthesis or less commonly through chemosynthesis. (Wikipedia glossary)

Primary production: production of organic compounds from carbon through photosynthesis. This effects all life on Earth either directly or indirectly. (Wikipedia glossary)

Prokaryote: also Bacteria, Monera (the terminology differs) are organisms that lack a cell nucleus (pro ***before***, ***karyon*** kernel), or other membrane-bound organelles. They include the simplest and oldest forms of life, such as the various types of bacteria and blue-green algae, which don't have a distinct cellular nucleus or other intra-cellular membranes, in contrast to eukaryotes. But they are also very metabolically diverse, and able to survive extreme conditions (which make them good candidates for extraterrestrial life; i.e. if there is life elsewhere in the cosmos, of which the answer must surely be that, the vast majority of it, just like on Earth, will quite likely be prokaryote, or else something equivalent). The prokaryote-eukaryote distinction is rejected by Carl Woese, who, using molecular phylogeny proposes instead three domains of life, two of which - the Bacteria and Archaea, are prokaryote. **More**

Protozoa: originally "protist" or wastebasket taxon for animal-like (motile, heterotrophic) unicellular eukaryotes; Cavalier-Smith's system one of the six kingdoms of life, including the first eukaryotes, flagellate, and amoeboid forms.

Q.

R.

R-selection, R-selected species: A species that produces a large number of off-spring, each of which receives little care (quantity rather than quality). R-selected species are better suited for variable or unpredictable environments. (Wikipedia glossary)

Resource partitioning: when two or more species share, and compete for a resource in different ways in order for both species to coexist. (Wikipedia - Glossary of ecology)

Rhizaria: corresponds mostly to the old class ***Rhizopoda*** (which is invalid due to being polyphyletic), protozoa or protists that have pseudopodia. (MAK)

S.

Sixth extinction: the on-going anthropogenic mass-extinction, so called because it is comparable in impact to the preceding big five. The term was coined or popularised by Richard Leakey and Roger Lewin in their 1996 book ***The Sixth Extinction: Patterns of Life and the Future of Humankind***. In his book ***The Future of Life*** (2002), E.O. Wilson calculated that, if the current rate of human disruption of the biosphere continues, one-half of Earth's higher lifeforms will be extinct by 2100. (MAK, Wikipedia)

Snowball Earth: hypothesis that the Earth's surface became entirely or nearly entirely frozen one or more times during the Precambrian. The most recent snowball was about or earlier than 650 million years ago (Neoproterozoic era, during the appropriately named Cryogenian period). Evidence includes glacial deposits found at what at the time were tropical paleolatitudes, It is not known whether the Earth was a full snowball, or a "slushball" with a thin equatorial band of open (or seasonally open) water. (MAK, Wikipedia)

Social behavior: behavior of an individual towards society and members of the same species as a whole. Wikipedia - Glossary of ecology

Subtropical: Bordering on the tropics or nearly tropical. (USGS Paleontology glossary)

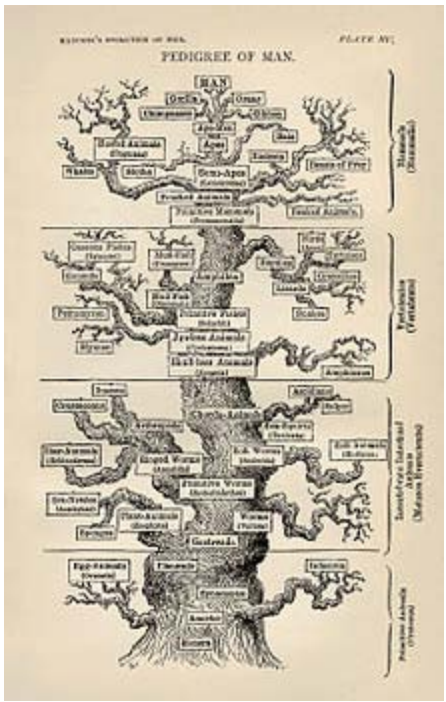
Suspension feeder - aquatic or marine organisms which capture food suspended in the water column. Suspension feeders that use a filter to capture food (e.g. brachiopods, crinoids, etc.) are called ***filter feeders***. Suspension feeders were more predominant in Paleozoic ecosystems, where they often would form tiers. (MAK, University of Arizona Geosciences 308 Paleontology glossary)

Superorganism: an organism consisting of many (sometimes thousand, in some cases even millions) individuals working together as a single functional somatic or social unit, e.g. a jellyfish (where individual organisms fulfill the role of different organs) or an ant colony (where the superorganism is more dispersed in space, but also more intelligent). (MAK)

T.

Terrestrial: organisms living mostly or entirely on dry land, in contrast to aquatic or marine; land habitats as distinction from aquatic habitats.

Thermoregulation: the ability of an organism to keep its body temperature within certain boundaries, even when the surrounding temperature is very different. This process is one aspect of homeostasis: a dynamic state of stability between an animal's internal environment and its external environment. See also ectotherm, endotherm, gigantothermy. (from Wikipedia)



Tree of Life: poetic term for an evolutionary tree that (ideally) includes all life on Earth. The earliest tree-like diagram was the Tree of Porphyry which classified categories in a branching series. Beginning in the 19th century branching diagrams were used by the French botanist Augustin Augier in 1801, the French evolutionist Jean-Baptiste Lamarck (1744-1829), who produced the first branching tree of animals in his ***Philosophie Zoologique*** (1809) based on the Great Chain of Being, and the American geologist Edward Hitchcock (1763–1864), who in 1840 published the first Tree of Life based on paleontology. Charles Darwin also drew abstract trees; Darwin's being the first evolutionary tree of life. It was Ernst Haeckel however who enthusiastically constructed several Trees of Life. Shown on the right is a famous illustration published in ***The Evolution of Man*** (1879), which shows a Great Chain of Being model with ***Homo sapiens*** at the top. Although this would seem an anthropocentric step backwards in relation to his earlier but more contemporary-looking three-kingdom model, it should be remembered that for Haeckel, as for many 19th century evolutionists, humans were considered the pinnacle of evolution. Teilhard de Chardin serves as a 20th century example. Since then a number of sophisticated trees have been drawn. In evolutionary systematics, trees were generally spindle diagrams that mapped geologic time (vertical axis) against taxonomic diversity (horizontal width) and emphasised monophyletic ***sensu*** Haeckel taxa (i.e. both monophyletic (***sensu*** Hennig) and paraphyletic groups). Sometimes width did not reflect diversity but was simply artistic license. For an example of such a tree see the diagram at evolutionary systematics. Supplanting evolutionary systematics in the 1980s, phylogenetic systematics placed great emphasise on tree diagrams, called cladograms, which are based either on gross morphology, molecular phylogeny, or both. Some of these diagrams can be incredibly detailed. (Wikipedia, MAK). ***Tree of Life*** also refers to a valuable reference website (albeit still very incomplete, although some taxa, e.g. Agnatha, Ankylosauria, are well represented) with an interactive presentation of the full "tree of life". Detailed references are

supplied on each page about particular organisms. It is not entirely up to date with latest ideas; for example, the tree of Eutheria fails to reflect the recent classification into Laurasiatheria, Afrotheria, Euarchontoglires, and Xenarthra. Link. (EvoWiki)

U.

Unicellular Organism: a living system consisting of only a single cell. May be simple, as with bacteria, or complex, as with protists. In the case of protists, different parts of the cell takes on the functions that organs and other systems fulfill in multicellular (many-celled) organisms. (MAK)

V.

W.

X.

Y.

Z.

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page last modified MAK111012, edited RFVS111204

Life : References

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archaea, bacteria, eubacteria

Life

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LIFE ("Tellurobiota")
|
Bacteria (Crown Group Life)
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia (incl. Vertebrata)
            `--Protostomia
```


Plants in the Ruwenzori Mountains, SW Uganda, Bujuku Valley, at about 3700 m altitude. Photo by Manuel Werner, Creative Commons Attribution-Share Alike, Wikimedia

Introduction

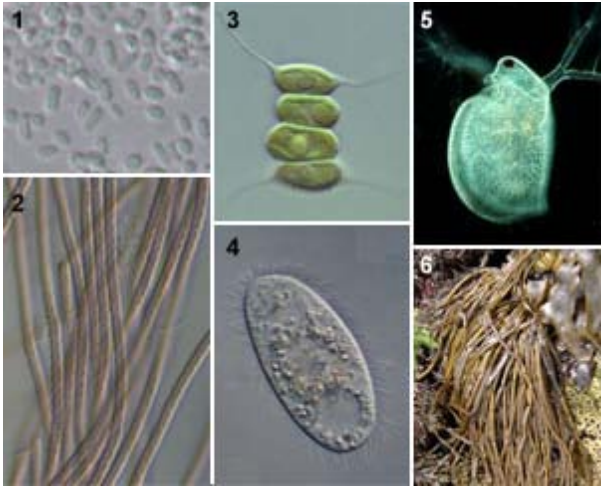
Whilst life is no doubt widespread in the cosmos, all we know of it at present is its terran (Earth)-based form. Therefore we have "Tellurobiota", an informal name for Life on Earth, hence the quotation marks, which was coined by one of us (RFVS, ca. 2000). Which brings us to the following pages:

Life on Earth : Basic introduction to Life on Earth; which covers such essential topics as the Meaning of Life, the Facts of Life, and the Purpose of Life (or not, depending on your perspective).

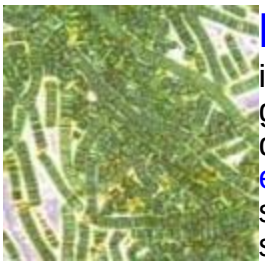
Kingdoms of Life : While the number and details of kingdoms of life differ, we have decided as far as main categories go to follow an informal approach that broadly follows the The Five Kingdom paradigm of Robert Whittaker and Lynn Margulis, except that the non-technical (and by now pretty much systematically meaningless) 19th Century distinction of the animal kingdom into vertebrates and invertebrates are used.

Tree of Life : Beginning with the Master Dendrogram - more commonly but less correctly called a cladogram, although we follow cladistic principles - you can follow the evolutionary relationship of the past and present organisms, up to the major categories of life, domains and kingdoms. This brings us to the following main categories (Kingdoms of Life):

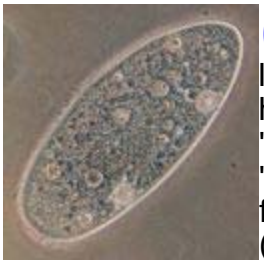
Kingdoms of Life



Diversity of "Tellurobiota" (Life on Earth) 1: unidentified bacteria (Bacteria). 2: *Phormidium* (Bacteria, NIES-507). 3: *Desmodesmus* (Eukarya). 4: *Tetrahymena* (Eukarya). 5: *Ceriodaphnia* (Eukarya). 6: *Scytosiphon* (Eukarya).
Original url (includes phylogeny and basic intro) - SHIGEN; see also the Tree of Life Page



Bacteria : Bacteria (or Monera, the terminology differs, Prokaryotes is another synonym) include the simplest and oldest forms of life, such as the various types of bacteria and blue-green algae, which don't have a distinct cellular nucleus. But they are also very metabolically diverse, and able to survive extreme conditions (which make them good candidates for extraterrestrial life; i.e. if there is life elsewhere in the cosmos, of which the answer must surely be yes, the vast majority of it, just like on Earth, will quite likely be prokaryote, or else something equivalent). This section therefore is about the root and stem of the tree of life. Expect to find some good basic technical discussion, but so far not much in the way of systematic detail. It is hard to get excited by such simple life-forms. We have however adopted Carl Woese's three domain theory of life, which divides life on Earth into three primary branchs or domains: Bacteria or Eubacteria (most bacteria), Archaea (remnants from the earlier history of the earth), and Eukarya (everything else).
(image, Blue-Green Algae, Wikipedia, from NOAA



(mostly) Unicellular Eukarya : Eukarya constitutes the third domain of life on Earth, and here again for the sake of organisational simplicity and informality we have made an artificial distinction between mostly unicellular eukaryotes, including "algae", these being the more plant-like (non-motile, photosynthetic) forms, and "protozoa" which are more animal-like (motile, heterotrophic). Unfortunately or fortunately, as with the prokaryotes, the real situation regarding unicellular eukaryotes (the Protista of Whittaker and Margulis) has turned out to be far from simple, and subsequent experts in the field such as Thomas Cavalier-Smith and others have proposed various phylogenies and taxonomic schemes. The remaining Eukarya make up the three kingdoms of multicellular life of the the Whittaker-Margulis scheme.
image, *Paramecium*, Wikipedia, photo by Barfooz

Kingdom Plantae : the coverage of the more advanced Plant taxa (gymnosperms and flowering plants) is still quite basic at the time of writing).
image,Ferns, Wikipedia, photo Sanjay ach

Fungi : the fungi are not quite animals and not quite plants (again we don't have that much on them, though hopefully this will change).
(image, Giant Mushroom, Wikimedia

Kingdom Metazoa (Animals): Invertebrates : the Metazoa or animals are divided anthropocentrically and totally colloquially into Vertebrates and Invertebrates. Invertebrates is another way of saying all metazoa (multicellular animals) except for higher chordates. That this outmoded classification is retained is because paleontology, biology, and popular understanding still refers to animal life in terms of vertebrate and invertebrate. Mostly small, they are often overlooked in favour of their backboned brethren, although a microscope or even a hand lens will reveal creatures as astonishing as those that one might imagine would inhabit an alien world. Marine forms with hard parts have a very good fossil record, and a few these groups are covered here.
image, Ladybird Beetle, *Coccinella septempunctata*, Wikipedia, photo by Thomas Moertel

Kingdom Metazoa (Animals): Vertebrates : Vertebrates include all those large charismatic animals. Much as Palaeos started out as Toby White's ***Vertebrate Notes***, and anyway who doesn't love ichthyosaurs, dinosaurs and other exotic Mesozoic critters? So not surprisingly this is the clade is given the most detailed coverage on these pages. image, Giant Grouper, *Epinephelus lanceolatus*, Wikipedia, photo by Diliff

Links

Life on Earth - the Highlights - 3 part very basic intro and overview of the evolution of life on Earth. (more to be added...)

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LIFE  ("Tellurobiota")
|
Bacteria (Crown Group Life)
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia (incl. Vertebrata)
            `--Protostomia
```


The Meaning of Life

But natheless, whil I have tyme and space,
Er that I ferther in this tale pace,
Me thynketh it acordaunt to resoun
To telle yow al the condicioun
Of ech of hem, so as it semed me,
And whiche they weren, and of what degree,
And eek in what array that they were inne ...

Chaucer, **Canterbury Tales**: Prologue.

This section is the heart of Palaeos. We have to begin this section somewhere, and so this is also the Beginning of Life. If time permits, we will one day add sections on the definition of "life" and the ways it may have begun. For a recent review, see Robinson (2005). However, that kind of systematic treatment is not exactly what this site is all about (see, ***infra***, the Purpose of Life). So instead, we'll get right to business.

Broadly speaking, we will follow the "Three Domains" model of evolution, at least for organizational purposes. In this model, the earliest and most basic life forms are the Archaea: relatively simple, mostly chemoautotrophic single-celled organisms. Today, these organisms are still often found as "extremophiles," living in harsh, toxic environments using a remarkable diversity of metabolic tricks and adaptations to survive under apparently impossible conditions.

From the Archaea developed two, quite different groups, the Eubacteria and the Eukarya. The Eubacteria are also single-celled organisms, but with complex cell walls, involving peculiar biochemicals which allow us to conclude, with moderate confidence, that they are a natural group. They include the organisms we normally think of as bacteria and also the blue-green algae. The Eukarya include all organisms made up of

cells with nuclei. That is, their DNA is walled off in a separate compartment of the cell. Again, this feature is striking enough that we can be reasonably sure that the Eukarya all derived from a single common ancestor, probably within Archaea. Eukaryotes may be single-celled organisms (such as ***Amoeba*** or ***Paramecium***), multi-celled organisms (such as oak trees or humans), or at some intermediate stage of organization (like sponges or slime molds).

From the Eukarya evolved three sorts of multi-celled organisms: plants (Chlorobionta), Fungi, and Animals (Metazoa). Animals were originally radially symmetrical, like a simple jellyfish, or lacked any symmetry, like sponges. However, at some point, six or seven hundred million years ago, some animals (Bilateria) evolved bilateral symmetry. This sounds trivial, but it was a very significant breakthrough. Most importantly, it allowed segmentation of body sections, so that different segments of the body could specialize for different functions. This required the evolution of an entirely different type of genetic regulation because genes had to operate differently depending on which segment they might be in. This is substantially more complicated than sponge or jellyfish-style development.

From the basic bilaterian plan, two developmental styles evolved. This gets a bit further into developmental biology than we wish to go at the moment. It is sufficient to note that these are the deuterostomes (echinoderms and chordates) and the protostomes (almost everything else). The chordates include the vertebrates, which includes us. Because we are vertebrates, this group has always had a special place, and we refer to all non-vertebrate metazoans as "invertebrates." We will retain this bit of phylogenetic chauvinism in Palaeos for some organizational purposes, until we hear objections from any brachiopods or priapulid worms who might have occasion to offer their comments.

Finally, its important to remember that this site, like life, was not planned. It grew and evolved. It began and, one day, we will become bored and it will die. It may be useful, but it has no overriding mission other than the fun of creating it. So, if you need something thoroughly vetted and organized, try the **Shrub of Life**. Palaeos is... different.

References:

Robinson R (2005), ***Jump-starting a cellular world: Investigating the origin of life, from soup to networks***. **PLoS Biol** 3: e396.

The Facts of Life

Cladograms, or "trees of life," are appropriate phylogenetic schemes for metazoans (multi-celled eukaryotes) but sometimes misleading in other organisms. Nonetheless, we have to have some kind of roadmap, and cladograms at least have the virtue of being testable. The following map is roughly equivalent to a three-color map of the world with just some the major continents sketched in. Although we pretend to start with basal "Life," we know so little of the very first forms that we actually start with LUCA, the Last Universal Common Ancestor. LUCA, whatever it was, is everybody's great-great-great- ... grandparent. Like the Biblical Adam & Eve, LUCA (presumably a single-celled, asexual organism) had at

least two offspring, one of which gave rise to the Eubacteria (the usual run of bacteria), and one of which produced the Archaea (peculiar, extremophile bacteria) and the Eukarya (organisms with cells having separate nuclei — like us). This is, of course, a vast oversimplification. However, we have to start somewhere. A very much simplified diagram of the scheme looks like this:

```
LIFE
|
Bacteria (LUCA)
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta (green plants)
      `--+--Fungi
         `--Metazoa (animals)
            |--Deuterostomia
            |  |--Echinodermata
            |  `--Vertebrata
            `--Protostomia
               |--Mollusca
               `--Arthropoda
```

At this level there are many uncertainties. Are the Fungi more closely related to animals (Metazoa) than to plants? Quite likely. Are eukaryotes really more closely related to Archaea, or do they derive from Eubacteria, or from some fusion of the two? Anybody's guess at this point. We look forward to changing our minds at frequent intervals.

The Purpose of Life

Frankly, we're less worried about being wrong than about missing the show completely. The discussions on this site are of quite variable quality, format, accuracy, and style. We're not worried by that, either. As this site has developed, we've learned that the paleo web is dominated by two groups: educators and academic scientists. The educators tend to want everything boiled down to colorful, but tasteless and insubstantial uniformity. The academic scientists tend to be paralyzed by detail. We aim to steer a middle course, avoiding neither the difficult and technical problems, nor the uncertainty inherent in saying anything meaningful about deep time. Truthfully, we scarcely steer at all, but proceed from subject to subject in the manner of a bumper car ride or a destruction derby. We have no overriding mission to educate or provide definitive guidance. Rather, our's is a more self-indulgent attempt to explore the world and to pick up rocks just to see what's under them.

Then again, maybe that ***is*** the purpose of life.

Page Back (Life on Earth) | Page Up (Life) | Page Top | Page Next (Kingdoms of Life)

The Classification of Living Organisms

```
LIFE ("Tellurobiota")
|
Bacteria (Crown Group Life)
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia (incl. Vertebrata)
            `--Protostomia
```


En Français!

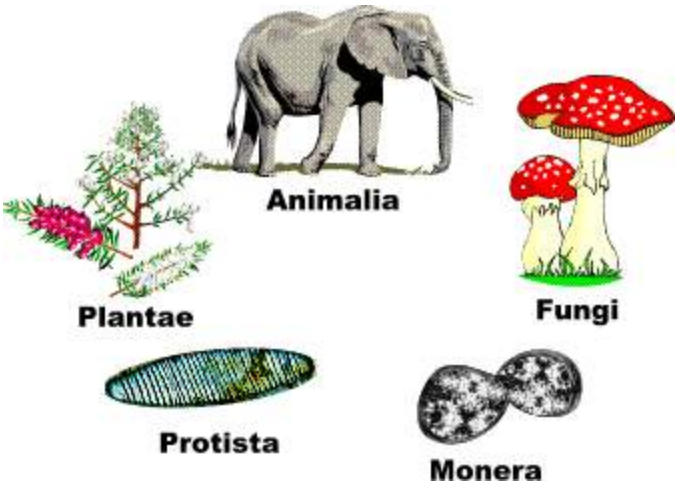
The Kingdoms of Life

Up until the 1950s and 60s, textbooks only referred to two kingdoms of living beings, Animals (including protozoa) and Plants (including bacteria). These are the same two suggested by Linnaeus, and retained by some occultist systems of thought, such as Theosophy and Anthroposophy, and unified systems of science and metaphysics like those of Arthur Young and Edward Haskell, all of whom added inanimate (e.g. mineral) and - in the case of the theosophists non-physical ("elemental") kingdoms on, giving all of them the same grade as Animals and Plants.

Now, on the macroscopic level it is quite easy to see the distinction between a plant and an animal. A plant sits in one place and makes glucose from sunlight, carbon dioxide and water, whereas an animal roves about and needs to find its food outside of itself. But on a microscopic level this situation breaks down. Not only are there single-celled organisms that sometimes act like plants and sometimes like animals (***Euglena*** for example photosynthesis food from sunlight but also can feed by consuming organic matter like an animal). Then there are bacteria and blue-green algae, which differ structurally from higher organisms far more than plants differ from animals. A paradigm shift was required. This culminated in the

Five Kingdoms hypothesis.

The Five Kingdom paradigm



graphic from the former "Five Kingdoms page"

The progress of scientific knowledge has meant the increasing divergence of science from metaphysics, and in 1959 R. H. Whittaker replaced the unwieldy dichotomy of plant and animal kingdoms: animals, plants, Fungi, Protista or Protoctista, and Monera (bacteria and blue-green algae, with only a very simple, prokaryote, cellular structure). The five kingdom paradigm was further developed by Lynn Margulis. This very useful system is still retained in many text books today. But it has recently been shown to be inadequate (e.g. the tremendous metabolic and structural diversity of Monera and Protista, and the fact that those two taxa are paraphyletic and not viable under the modern cladistic scheme). Hence the (currently preferred) "three domain" model.

Five Kingdoms : An Illustrated Guide to the Phyla of Life on Earth
by Lynn Margulis, Karlene V. Schwartz (Contributor), Stephen Jay Gould

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The Three Domains Paradigm

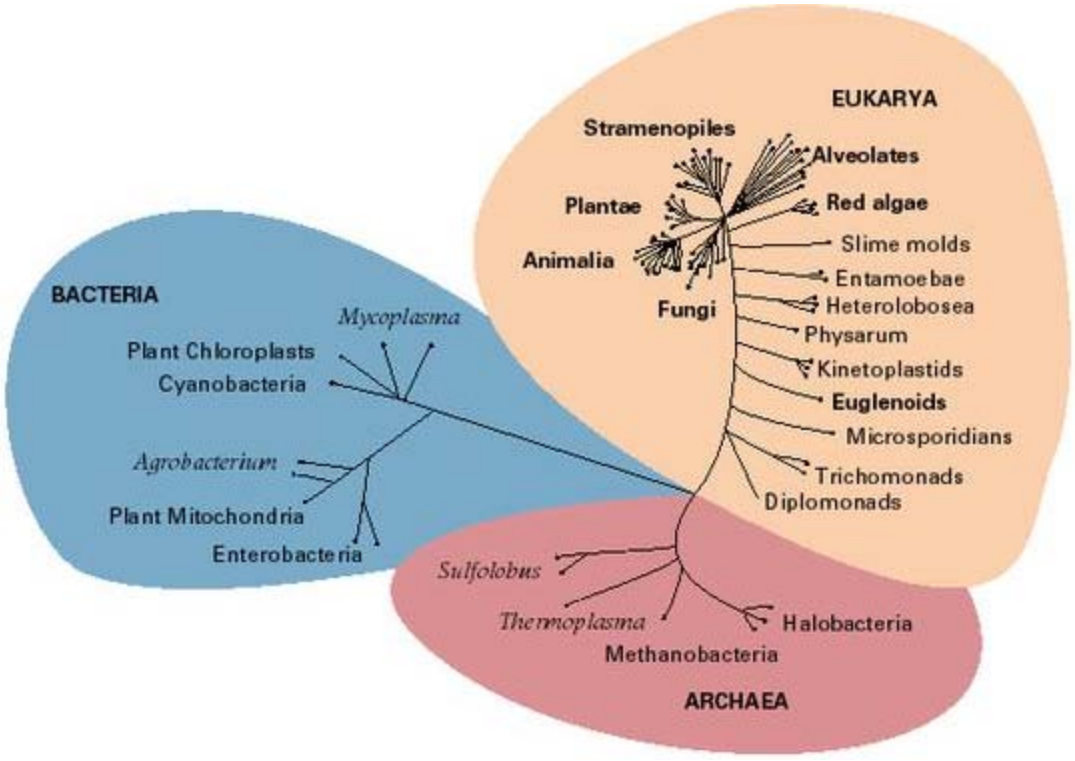
Modern genetic research over the last decade or so has revealed that anaerobic bacteria found in harsh oxygen-free conditions are genetically and metabolically completely different from other, oxygen-breathing organisms. These bacteria, called Archaeobacteria, or simply Archaea, are said to be "living fossils" that have survived since the planet's very early ages, before the Earth's atmosphere even had free oxygen. DNA and RNA analysis have suggested to some workers that, instead of five kingdoms, there are actually three "Domains": Archaea, Bacteria, and Eukarya (Eukaryota). This last group refers to organisms whose genetic material is contained in a special membrane, the nucleus, and includes all higher organisms from protists to humans. Rather than just four kingdoms it would seem to include over a dozen. So much so that the term "Kingdom" has become (in this usage) meaningless. So we have:

two kingdoms	five kingdoms	three domains and who knows how many "kingdoms"	
Animalia (all Metazoans)	**Animalia**		**Animalia**

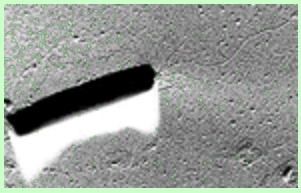
Plantae	Fungi	Eukarya	Fungi
	Plantae		Plantae
either Protozoa (=Animal) or Algae (=Plant)	Protoctista		Alveolata
			Stramenopiles
			etc...
			Sporozoa
			Mycetozoa
			Euglenozoa
			etc...
			Archezoa
Plant (bacteria and blue-green algae)	Monera	Eubacteria	(kingdoms not specified)
		Archaea	Euryarchaeota Korarchaeota Crenarchaeota

Thus the diversity of life is seen to be far more complex than was envisaged, and familiar organisms like animals and plants are just a tiny proportion of all of the many different forms.

The following diagram illustrates the relationship between the Three Domains, and the various branches of each.



The Three Domains

 **Domain Archaea** (formerly "Archaeobacteria")	 **Domain Eubacteria**	 **Domain Eukarya**

Our Organizational Scheme

We follow -- to the extent possible -- a cladistic model without fixed ranks. However cladograms, with their continual bifurcations, do not lend themselves to the kind of ranked hierarchical structures necessary to keep a web site organized. Accordingly, we have adopted a modified five-kingdom model for organizational purposes. Actually we use six categories, as follows:

Bacteria: This section covers both the the Eubacteria and Archaea.

Eukarya: This section covers almost exclusively single-celled forms, ***i.e.*** the Protista or Protoctista. For historical reasons, the basal Plantae and red algae (Rhodophyta) are also in this group.

Plants: It might be more accurate to call this section Chlorobionta. As mentioned, the clade Plantae is a bit more inclusive and also includes Rhodophyta and certain "green algae" which are treated in the Eukarya section.

Fungi: As we define Fungi, this section probably ought to include the Microsporidia. It doesn't. Other than the Microsporidia, this section covers the Fungi.

Invertebrates: Here we take up all metazoans except the chordates.

Vertebrates: Finally, the largest single section of Palaeos covers the chordates, with about 99% of this material devoted to the Vertebrata.

Links

The Biosphere: Life on Earth - Three Domains of Life

The Tree of Life Project Root Page - The Tree of Life project adopts the three domain model.

Natural History - General - Phylogeny

Classification of the Earth's Biosphere - by W B Leatham - an interpretation of high order systematics, incorporating recent discoveries of new taxa into a modified Linnean hierarchy (replacing "Domain" with "Superkingdom"). Also provides a useful summary of each phylum of organism, together with known geological time range.

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Master Dendrogram

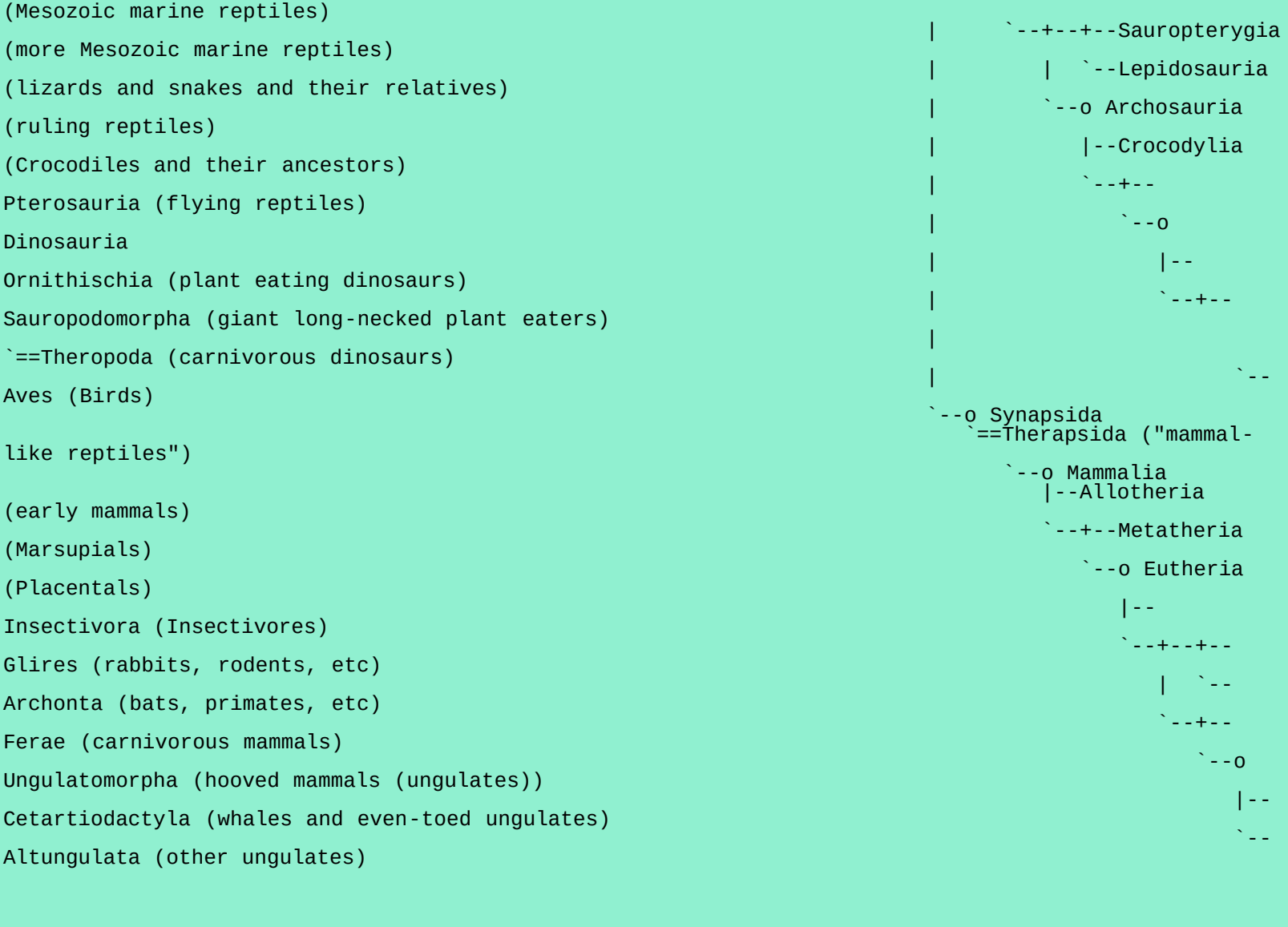
```
LIFE ("Tellurobiota")
|
Bacteria (Crown Group Life)
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia (incl. Vertebrata)
            `--Protostomia
```

Life
"Tellurobiota" - Life on Earth
The Meaning of Life
Kingdoms of Life (more)
Tree of Life

The following provisional dendrogram (more about dendrograms or "cladograms" here) is included until we have a more complete one ready. No hyperlinks added yet, sorry.

```
Tellurobiota (Life on Earth)
|
o Bacteria (LUCA)
|--o Eubacteria ("True" bacteria; note - phylogenetic relationships controversial!)
|  |--Actinobacteria (Gram positive bacteria)
|  `--+--+--Thermotogae (a small group of extremophiles)
|     |  `--Firmicutes (Gram positive bacteria)
|     `--o Didermata
|        |--Cyanobacteria (Blue-Green algae)
|        `--+--Sphingobacteria
|           `--Proteobacteria (most bacteria)
`--o Neomura
   |--o Archaea (anaerobic "archaic" bacteria)
   |  |--Crenarchaeota
   |  `--Euryarchaeota
   `--o Eukarya (organisms with a cell nucleus - note: conflicting phylogenies)
      |--Metamonada (includes symbiotes with termites)
      `--+--Discicristata (euglena, a plant-animal like form, and similar)
         `--+--Rhizaria (amoeba-like forms, often with shells)
            |  |?--Vendobionta (enigmatic Precambrian forms, the first large animals)
            |  |--Radiolaria
            |  `--+--Foraminifera
            |     `--Cercozoa
            `--+--+--o Chromalveolata
               |  |  |--o Alveolata
               |  |  |  |--Ciliophora (Ciliates)
               |  |  |  `--o Miozoa
               |  |  |     |--Dinozoa (Dinoflagellata)
               |  |  |     `--Apicomplexa (Sporozoa)
               |  |  `--Chromista (diatoms and related types ("Golden algae"))
```


`--o Plantae (Plant Kingdom)
|--Rhodophyta (Red algae)
`--o Chlorobionta (Green plants)
|--Chlorophyta (green algae in part)
`--+--Charophyta (green algae in part)
|==(various green algae)
`--o Embryophyta (land plants)
|--Bryophyta (mosses)
`--o Tracheophyta (vascular plants)
|=="Rhyniophytes"
`--+--Lycophyta (club mosses and their tree-like ancestors)
`--o Euphyllophyta
|--Monilophyta (horsetails and ferns)
`--Spermatophyta (seed plants)
`--+--Apusomonadida
`--+--Amoebozoa (amoebas)
`--o Opisthokonta
|--+--Microsporidia
| `--o Fungi
| |--Chytridiomycota (aquatic forms)
| `--+--Zygomycota (bread mold, etc)
| `--+--o Basidiomycota
| | |--Ustilaginomycetes
| | `--Hymenomycetes
| `--o Ascomycota
| |==Taphrinomycotina
| `--+--Saccharomycotina (yeasts)
| `--Pezizomycotina
`--o Metazoa (animals)
|--Choanoflagellata
`==Porifera (sponges)
|--Ctenophora (comb jellies)
`--+--Cnidaria (jellyfish, corals, etc)
`--o Bilateria
|--o Protostomia
| |--o Ecdysozoa
| | |--+--Chaetognatha (arrow worms)
| | | `--Nemata
| | `--+--Tardigrada
| | `--o Arthropoda (phylogeny controversial)
| | |== Lobopoda
| | `--+--Anomalocarida
| | |--Trilobita
| | `--+--Myriapoda
| | `--+--Chelicerata
| | `--+--Crustacea
| | `--Insecta
| |?--Bryozoa
| `--o Lophotrochozoa
| `== Halkieriids and other "coat of mail" animals
| |--o Mollusca (snails, clams, squid, etc)
| | |--Polyplacophora (chitons)
| | `--+--Bivalvia
| | `--+--Gastropoda (slugs and snails)
| | `--Cephalopoda (squids and octopii)
| `--+--Annelida (segmented worms)
| `--+--Scalidophora
| `--Brachiopoda
`--o Deuterostomia
|--Vetulicolia
`--+--o Ambulacraria
| |--Hemichordata
| `--+--Vetulocystidae
| `== Homalozoa
| `--Echinodermata (starfish, sea urchins, etc)
`--o Chordata
|--Cephalochordata
`--o Vertebrata (backboned animals)
`--+--Conodonta (ancient eel-like animals)
`--+--Pteraspidomorphi (early armoured
vertebrates)
`--o Gnathostomata (jawed vertebrates)
|--Placodermi (early armoured fish)
`--+--Chondrichthyes (sharks and rays)
`--+--Actinopterygii (ray-finned fish)
`==Sarcopterygii (lobe-finned fish)
`--o Tetrapoda (land vertebrates)
|--Temnospondyli (early
amphibians)
| `--Lissamphibia (modern
amphibians)
`--o Reptilomorpha (reptile-
like amphibians)
|--+--Anapsida (turtles and
others)
| `--o Eureptilia
| |--Ichthyosauria



Page Back | Page Top | Unit Home | Page Next: Bacteria

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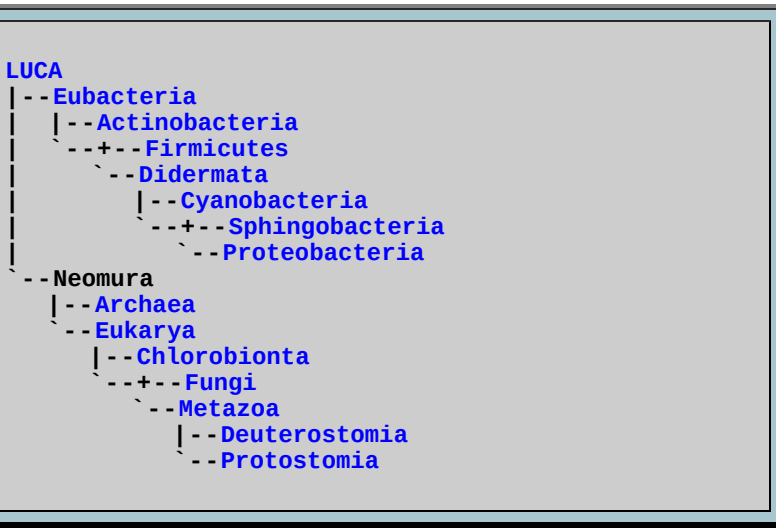
The Bacteria (Crown Group Life)



Lists

A. Glossary of terms and abbreviations.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

B. Taxon Index: alphabetical list of taxa.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

C. References: literature citations by author.

A B C D E F G H I K L M N O R S T U V W X Y Z

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The Bacteria

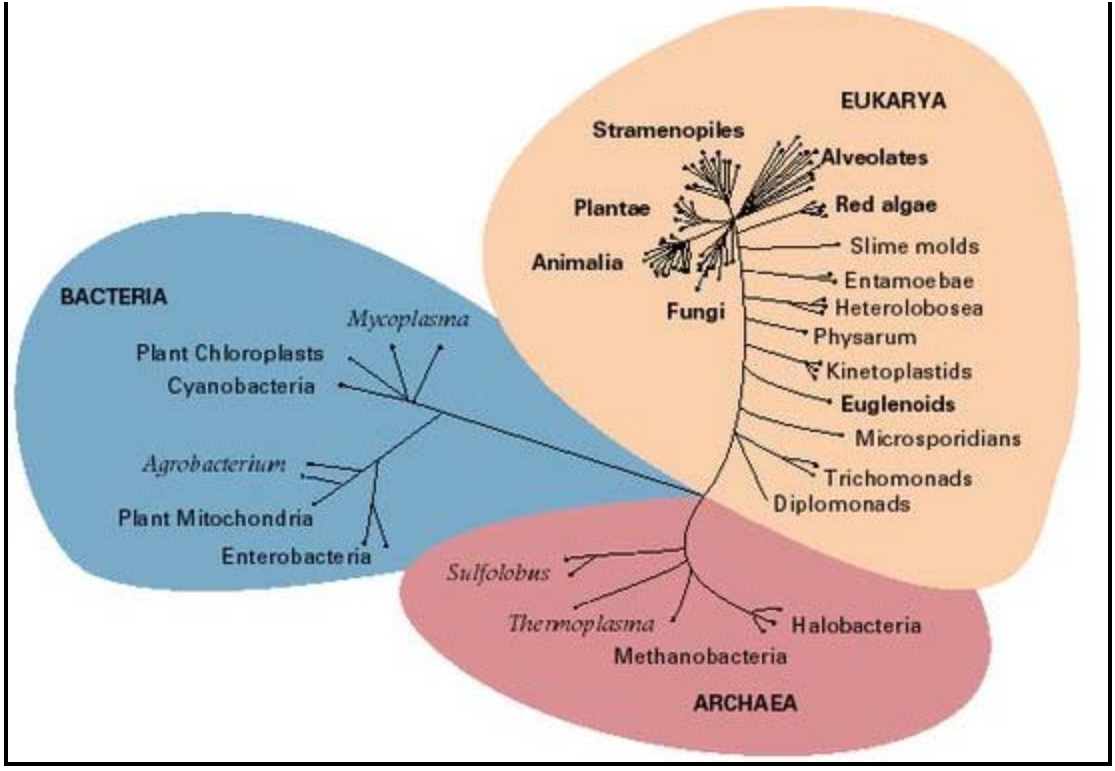
(Crown Group Life)

```
LUCA
|--Eubacteria
|   |--Actinobacteria
|   `--+--Firmicutes
|      `--Didermata
|         |--Cyanobacteria
|         `--+--Sphingobacteria
|            `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```

Looking for LUCA Without a Map

Bacterial phylogenetics and systematics are areas that are fraught with controversy, confusion and very little concordance. To attempt to fit some sort of analysis of them within the confines of a single web-page, and without years of study to give oneself authority, would be the height of folly. With that in mind, feel free to read on,

as we strive to raise ourselves to greater heights than ever before. If any of the arguments presented seem somewhat circular and self-contradictory, they probably are – you have been warned.



Undoubtedly the most influential work in modern higher-level prokaryote systematics was conducted by Carl Woese and associates in the 1970s and 1980s. This led to the much-popularised *SSU rRNA* tree in which life was divided into three "domains" separated from each other by long branches – the Eukaryota, the Archaebacteria, and the Eubacteria (later named by Woese as Eucarya, Archaea and Bacteria – Pace, 1997). The Archaea were the unexpected factor in this. They were found to possess a number of characters, particularly those relating to transcription of genes, in common with eukaryotes rather than other prokaryotes (Eubacteria), plus a few features entirely of their own. News headlines like 'New third form of life discovered' began appearing, and Woese's redefinition of the term 'Bacteria' to include Eubacteria only, together with the unfamiliar extremophile nature of most of the cultured archaebacteria, lead to the establishment of the idea that Archaea were different in some fundamental way from Eubacteria.

Looked at from a more phylogenetic rather than a purely phenetic viewpoint, it becomes difficult to see what all the hyperbole is about. While Archaea have DNA-processing genes that resemble those of Eukarya, their metabolic genes are more like those of Eubacteria. Cavalier-Smith (2002). This only appears as a conflict if one assumes that all parts of the genome in all organisms are evolving at the same rate. This assumption is often made in molecular biology due to the influence of Kimura & Ohta's (1974) Neutral Mutation Hypothesis, which suggests that the majority of genetic mutations are more or less selectively neutral in effect, so should happen randomly with respect to time. However, this theory only applies to mutations in non-coding parts of the genome, or other mutations that do not affect the resulting phenotype.

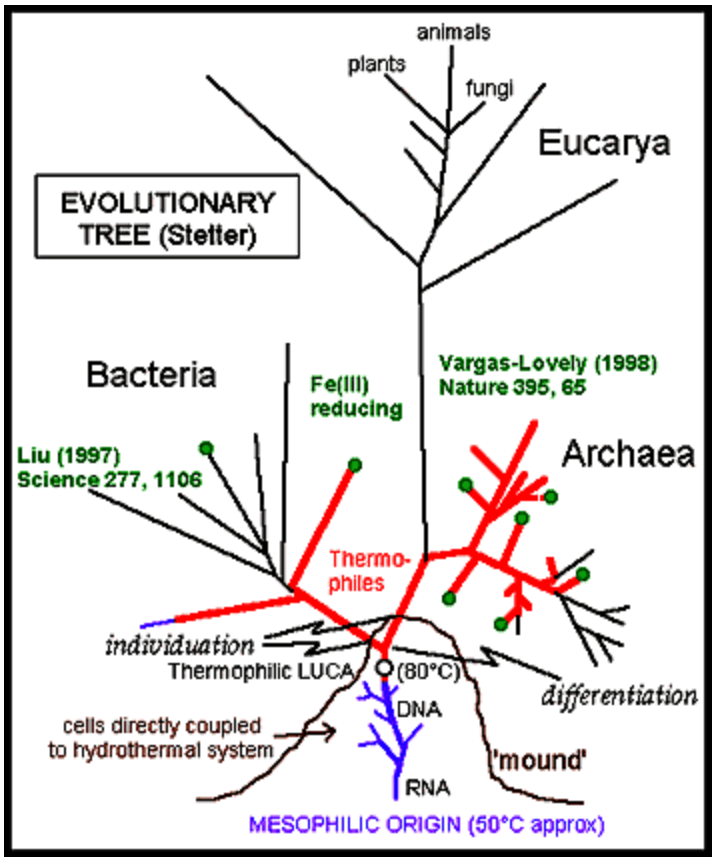
When it comes to alterations in phenotype, different selective pressures on different parts of the genome and/or organism mean that evolution is not uniform for all characters of the organism – the principle known as 'mosaic evolution'. Compare crocodiles and birds to their common reptilian ancestor – one is more distinct from the ancestor than the other, and within each, some features have changed more from the ancestor than others.

Under this principle, the supposedly 'inexplicable' combination of characters possessed by Archaea is entirely explicable. Some of the features shared with one domain will represent plesiomorphies that have been lost in the remaining domain, while features shared with one or the other domain may be apomorphies of a larger clade.

To make any sense of this requires us to establish which domains are more closely related, and which is the most

basalmost domain. This is where the real fun and frustration begins. The*rRNA* tree is, like all phylogenetic trees when they are first calculated, un-rooted. Normally the position of the root of a tree is established by inclusion of an outgroup, a taxon that is definitely known to be outside the group of interest. Unfortunately, somewhat by definition, no suitable outgroup exists for the totality of life. Obviously, a more inventive approach was needed.

The approach used was to select genes that had duplicated before the Last Universal Common Ancestor of modern life (referred to by the catchy acronym '*LUCA*'). The trees of these genes should be able to be used to root each other and indicate the point where LUCA was to be found. The first two gene pairs used by independent researchers in 1989 were *elongation factors* (*EF-Tu* vs. *EF-G*) and catalytic vs. regulatory subunits of eubacterial *F-ATPases* with V- or *V-like-ATPases* of Eukarya and Archaea. Both these studies found the root to be on the branch separating Eubacteria from the other two domains. Philippe & Forterre (1999). Studies using other genes also found this pattern, and it became accepted as the standard view.

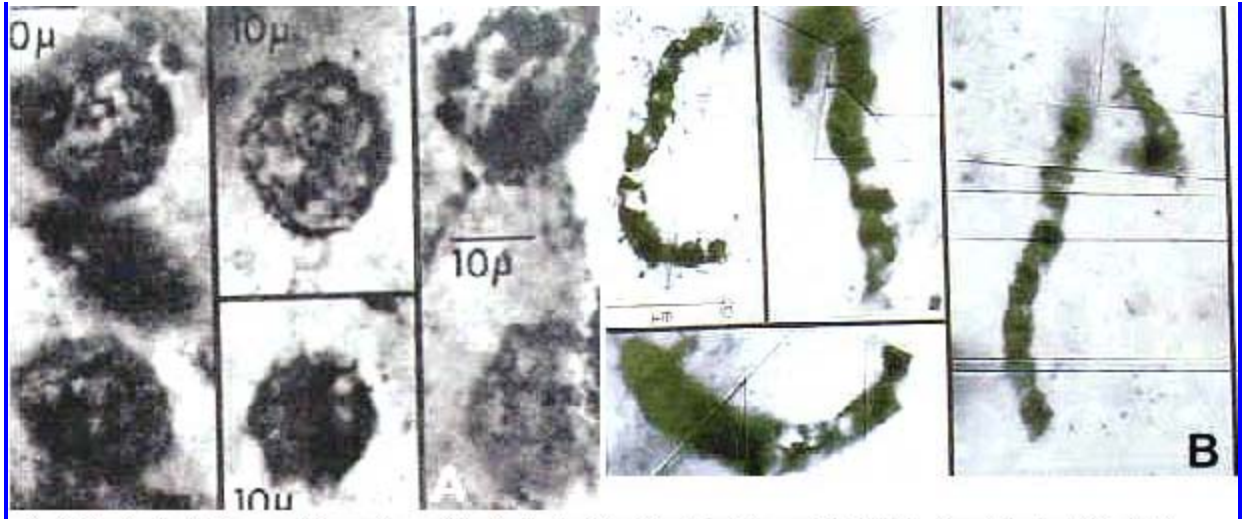


This picture of the evolution of life sat well with the supposed greater complexity of the DNA-processing systems in Eukarya and Archaea than in Eubacteria. Like all popular pictures, though, critics soon materialised to complain about it. Further gene studies failed to always retrieve the same branching order, and often didn't even recognise monophyly for the separate domains. Philippe & Forterre (1999); Cavalier-Smith (2002). Also, many of the genes used appeared to be mutation-saturated at the level used, so that the points of intersection of the paralogous trees were potentially the result of long-branch attraction. Philippe & Forterre (1999). For various reasons, most researchers in bacterial systematics continue to use rRNA trees exclusively, despite suggestions they may be unreliable (see below) and increased recognition in systematics of other organisms that phylogenetic evidence should be drawn from as many sources as possible. Division into three domains, with Eubacteria sister to Archaea + Eukarya, remains the norm, though a few alternative suggestions will be examined here.

The suggestion has been made that the common ancestor of all three domains was not yet a properly developed, integrated cell, but a 'progenote.' Woese (2002). Cell design was held to be shaped largely by rampant lateral gene transfer, with genetic components functioning as interchangeable modular units. Eventually, a 'Darwinian Threshold' was passed where genetic components of individual cells became integrated enough that lateral gene transfer was no longer able to occur enough to blur genealogical lines, and standard vertical descent became predominant. This threshold was passed separately in each of the three domains. The supposed sister status of Eukarya and Archaea is actually an artefact of analysis resulting from Eubacteria crossing the threshold earlier than the other two domains.

Support for this concept supposedly came from the wide divergence between the three domains, with completely different *translation* systems in Eukarya + Archaea vs. Eubacteria, plus the lack of phylogenetic resolution between domains and at the base of domains in trees for many genes. Translation systems were thought to have evolved independently in the two branches, thus removing the need to explain how one system replaced another. Multiple gene trees for Eubacteria show concordance at more recent nodes, but lower resolution at older nodes, potentially compatible with a 'Darwinian Threshold.' Creevey *et al.* (2004).

On the whole, though, this theory makes little sense. That LUCA lacked a translation system is not possible – it must have

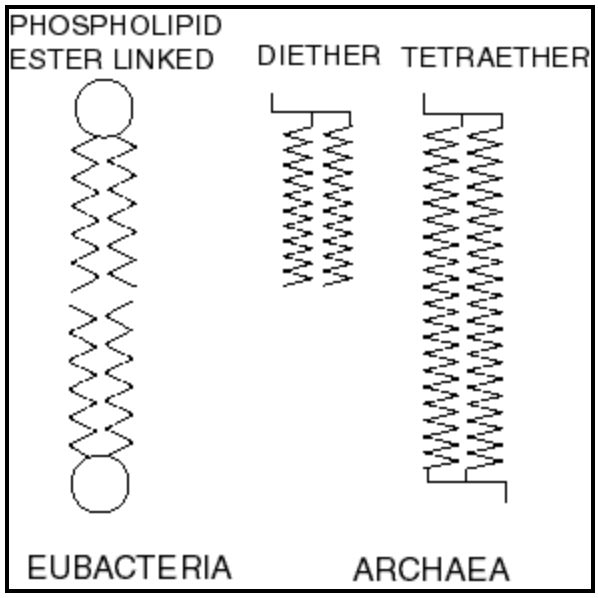


A. Spherical cells from a thin section of black chert of the Fig Tree Group (3.1-3.2 Bya from South Africa). B. Filamentous cells from a thin section of black chert of the Warrawoona Group (3.5 Bya from western Australia).

possessed one to have functioned as an organism. Characters such as the genetic code remain reasonably constant between domains, which would not be expected if it was independently derived in them. Therefore, a separate origin for the eukaryal and bacterial translation systems does not remove the need to explain the change of translation system – instead, we have to explain the replacement of the ancestral system by each of the derived systems. Also, as noted before, Archaea actually share many features with Eubacteria rather than Eukarya, and the differences are not as completely all-encompassing as often thought. The existence of a 'Darwinian Threshold' seems similarly tenuous – if lateral gene transfer was common in the past, there seems to be little reason why it should not still be so. The reasonable resolution in recent branches of gene trees argues against this – if anything, one would expect gene transfer to be more common between closely related organisms than distantly related ones, as there would be less chance that the newly-acquired genes would overly disrupt the genome of the recipient organism. It seems much more likely that the lack of resolution at more ancient levels is due as much to time eroding phylogenetic signal combined with rapid radiation of basal branches, as much as lateral gene transfer obscuring it. After all, Neoaves (the clade containing most modern birds) is also almost completely unresolved as to basal relationships, but no-one is suggesting lateral gene transfer between birds as the cause.

Philippe & Forterre (1999) suggested that Eukarya might be basal, with prokaryotes derived from eukaryotic ancestors by 'genetic streamlining.' This suggestion was based on gene trees of slowly evolving positions of elongation factors. It was felt that this rooting 'would best explain the presence of many more eubacterial-like genes than eukaryotic-like ones in completely sequenced archaebacterial genomes.' But, as explained before, there is no problem with this fact even if Archaea are sister to Eukarya. Archaea would then have simply retained mostly plesiomorphic features that have been lost in their sister group. A basal position for eukaryotes is also at odds with the fossil record. The earliest unequivocal eukaryotes are from the Late Proterozoic, about 850 My ago, though more doubtful examples are known from 1200 My ago. Either date is considerably younger than the earliest Eubacteria, which had appeared by 3.4 Gy ago at the latest (Cavalier-Smith, 2002).

Archaea are often thought of as paraphyletic with regard to one or both of the other domains, with LUCA assumed to be archaebacterial in nature. Paraphyly with regard to Eubacteria, however, seems unlikely in light of the aforementioned greater complexity of DNA-processing systems in Archaea + Eukarya than in Eubacteria, probably due to DNA in the former group usually being contained by *histones* rather than *DNA topoisomerases* in Eubacteria (the former requiring more energy to disassociate than the latter – Cavalier-Smith, 2002). That these systems have not been 'genetically streamlined' in Eubacteria is supported by the fact that Eukarya and Archaea which lack or have reduced histones, such as Crenarchaeota and Dinoflagellata, retain the advanced processing systems rather than developing more eubacterial-like ones. Cavalier-Smith (2002).



Paraphyly of Archaea with regard to Eukarya often appears in gene trees, but if Eubacteria is basal to Archaea + Eukarya, there is quite

strong 'morphological' **[1]** evidence against it. Archaea possess a cell membrane composed of prenyl ether lipids, as opposed to acyl ester lipids in Eubacteria and Eukarya. Cell membrane characters are evolutionarily extremely stable, and this makes it much more likely that Archaea are a monophyletic sister-group to Eukarya. Cavalier-Smith (2002).

Also worthy of consideration is the suggestion that Eubacteria is actually paraphyletic with regard to Archaea + Eukarya. Cavalier-Smith (2002). Prokaryotes can be divided into two groups on the basis of cell membrane structure. The Monodermata or Unibacteria, containing Archaea and mostly Gram-positive Eubacteria, possess a single cell membrane. Didermata or Negibacteria, containing mostly Gram-negative Eubacteria, have a double membrane – the inner cytoplasmic membrane, and the more porous outer membrane. Cavalier-Smith made the argument that Didermata must be ancestral as loss of the outer membrane by hypertrophy of the murein wall between membranes was more probable than gain of a new membrane. While this theory is mechanistically plausible, the problem in evaluating phylogenies with mechanistic models is that Life has often proven to be more ingenious than researchers in coming up with pathways by which evolution may occur.

For now, I cravenly cower to the popular vote, and organise this page with the basalmost division on life between Eubacteria and Archaea + Eukarya. The tree for Archaea is taken from Cavalier-Smith (2002); *see* under Eubacteria for the rationale for the tree used for that domain. Names and information for divisions in Archaea are taken from Cavalier-Smith (2002), while names for Eubacteria are mostly taken from Garrity & Holt (2001), with some names taken from Cavalier-Smith (2002) for clades not recognised or named in the former source.

A few comments need to be made on the use of names for taxa. I have consistently used the name 'Eubacteria' instead of the recent (Woese *et al.*, 1990) restriction of the name 'Bacteria' to this taxon only, despite the popularity of the latter usage. Archaea were previously universally regarded as bacteria, and terms such as 'bacteriology' and 'bacterial' are still often used to cover both Eubacteria and Archaea. The redefinition of 'Bacteria' was unnecessary as the name 'Eubacteria' is well-recognised, and doesn't have the same potential for double meaning.

The name 'Archaebacteria' was altered to 'Archaea' at the same time, to lose the implied connection to Bacteria. This also appears to be an unnecessary name-change. Names should not be changed merely because they are felt to be unsuitable for some reason – not only is it potentially confusing, but unsuitability is often (as in this case) a subjective matter that different researchers may disagree on. Despite the priority of Archaebacteria, the name Archaea has become more commonly used, and at least doesn't have the same potential for confusion as 'Bacteria.' I therefore cave to popular pressure once more, and accept the name 'Archaea'.

I have no pressing reason for using the name 'Eukarya' rather than 'Eucarya' or 'Eukaryota', other than personal preference.

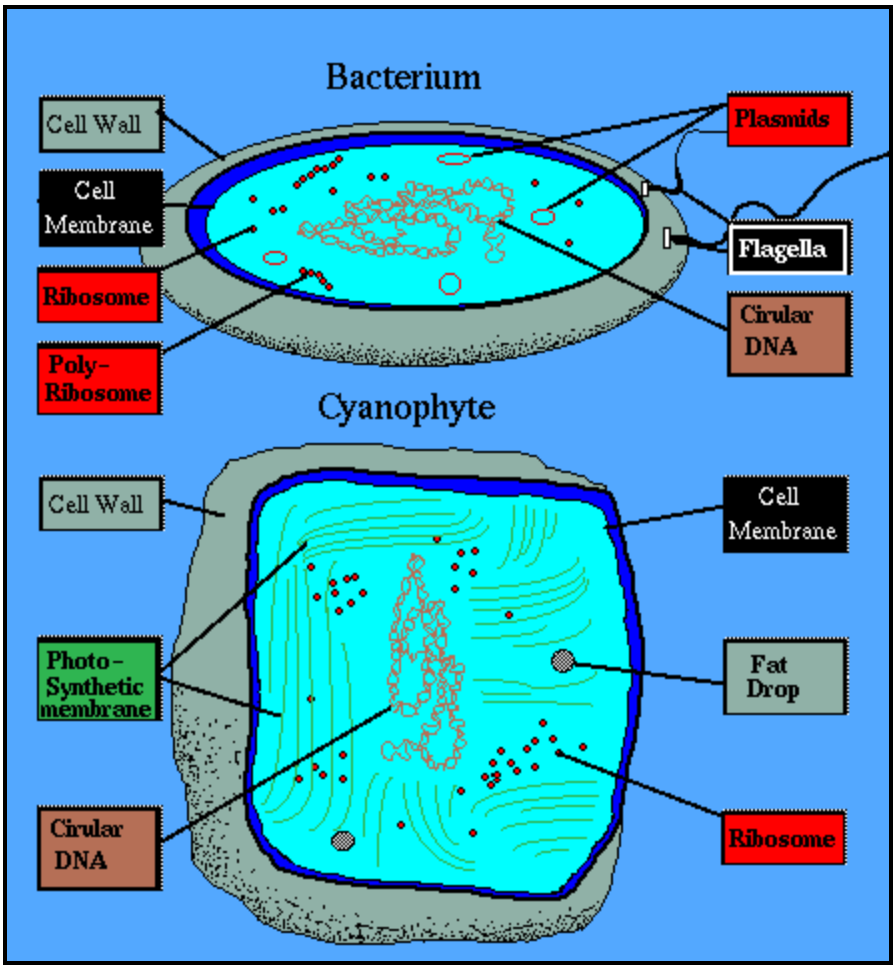
The Diversity of Bacteria

Our tentative cladogram of the bacteria may be found, oddly enough, on the Cladogram page. Not to belabor the obvious, but the bacteria have been around a ***lot*** longer than anything else. Living species tend to be at the tail end of very long evolutionary chains; and, with rare exceptions, our knowledge is limited to living species. Consequently, there are pockets of diversity everywhere in the bacteria that don't seem to be very closely related to anything else. This makes it unreasonably difficult to summarize bacterial diversity. For the moment, we will have to make do with only the largest and most conspicuous groups

```
LUCA
|--Eubacteria
|   |--Actinobacteria
|   `--+--Firmicutes
|      `--Didermata
|         |--Cyanobacteria
|         `--+--Sphingobacteria
|            `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
```

Eubacteria

See **Eubacteria**: Cell wall of *peptidoglycan* (or murein); cell membrane of acyl ester lipids. Flagellar shaft (if present) composed of *flagellin*. DNA replicative *sliding clamp* part of a *type C DNA polymerase holoenzyme*. Four *RNA polymerase* holoenzyme subunits. *Hsp60 chaperonins* with sevenfold symmetry and co-chaperonin *Hsp10*. CCA 3'- terminus of *tRNA* encoded by the gene. Protein synthesis initiated by *N-formyl methionine*. The main *DNA helicase* used in DNA replication is *DnaB*.



Relationships within Eubacteria are extremely uncertain at almost all levels of divergence, and many of those that have been suggested make little obvious sense. A number of factors have resulted in this situation – one is the general reliance on rRNA trees to the exclusion of other data sources. *rRNA* trees have been shown in recent years to be sensitive to variations in evolutionary rates in eukaryotes, leading to such errors as the placing of Microsporidia low down in the eukaryote tree, instead of in or near the Fungi. rRNA trees also show low resolution between most branches at high levels.

The other major issue with tree construction which has received a lot of attention is lateral or horizontal gene transfer (LGT), the direct transfer of genes from one species to another. The occurrence of LGT in prokaryotes between unrelated species is undoubted – however, opinions differ as to just how prominent it is. Some regard its occurrence as minimal (e.g. Cavalier-Smith, 2002), others feel that LGT may be so common as to render the construction of an organismal phylogeny for prokaryotes effectively impossible. This page tends away from the latter view, of course – if for no other reason than that otherwise we might as well give up and go home. Cases of LGT might even be potentially used as characters to support clades.

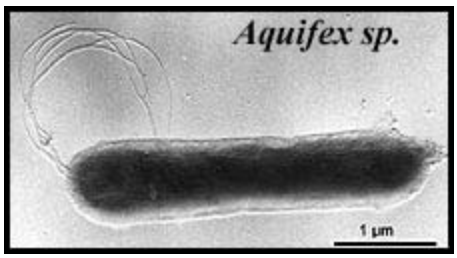
I have rather arbitrarily selected the rRNA tree in Miroshnichenko *et al.* (2003) to represent the general trend of current eubacterial phylogeny:

```
LUCA
|--Neomura
`--+--Aquificae
   `--+--Thermotogae
      `--+--Dictyoglomus
         `--+--+--Firmicutes
            |  `--Cyanobacteria
            `--+--Actinobacteria
               `--+--+--Caldithrix
                  |  `--+--Deferribacteres
                  |     `--+--Nitrospina
                  |        `--Thermodesulfobacterium
                  `--+--+--Sphingobacteria
                     |  `--+--Spirochaetes
                     |     `--+--Fusobacteria
                     |        `--Proteobacteria
                     `--+--+--Acidobacteria
                        |  `--Nitrospirae
                        `--+--Eobacteria
                           `--Planctobacteria
```

Compare this to the tree in Cavalier-Smith (2002), constructed using mostly 'morphological' or physiological characters:

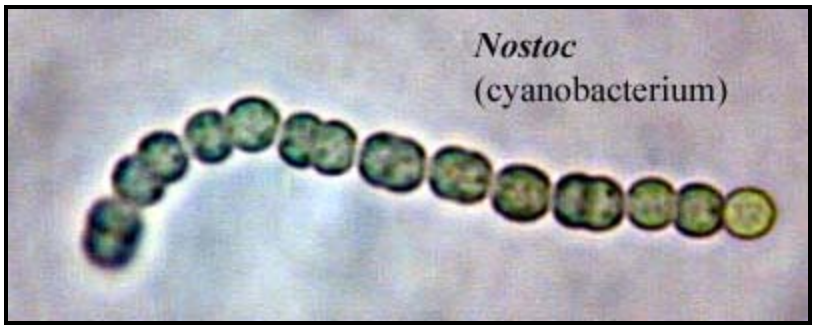
```
LUCA
|--Eobacteria
`--+--+--Cyanobacteria
   |   `--+--+--Firmicutes
   |      |  `--Thermotogae
   |      `--+==Actinobacteria (paraphyletic)
   |         `--Neomura
   `--+--Spirochaetes
      `--+--Sphingobacteria
         `--+--Planctobacteria
            `--Proteobacteria
```

As different as these two trees are, there are some similarities. Most notably, if both trees are unrooted, the Gram-positive bacteria (Actinobacteria, Firmicutes and Thermotogae) are close to Neomura (corresponding to the Monodermata); the Didermata are mostly further away. The relationships within Didermata are more contradictory, but seem poorly supported in both papers (though neither paper actually gives any real measure of support). The exception is Cyanobacteria, which are closest to Monodermata in both trees.



The differences in positions of the Aquificae and Thermotogae are the most significant differences between the trees. *Aquifex* has been widely accepted as the basalmost eubacterium due to its position in rRNA trees. However, *Aquifex* has a double membrane, suggesting a position within Didermata. Some protein trees place it within the ε-proteobacteria, and this was the position accepted by Cavalier-Smith. As placing *Aquifex* in its position on the rRNA tree implies multiple gains or losses of the outer membrane, I here tentatively accept the Cavalier-Smith position.

Thermotogae is the second-most basal major branch in rRNA trees, but is grouped with Firmicutes on many protein trees, by comparison of indels, and by the gene-content tree. As such, I accept the latter position on this page. The differences in position of the Thermotogae and Aquificae are probably due to long-branch attraction in the rRNA tree, and a high proportion of G+C in the genomes of these two taxa and Archaea.



The reposition of these two taxa has significant implications for one of the conclusions drawn from the rRNA tree of life – the supposed hyperthermophilic nature of Luca. This theory was supported by two of three domains having hyperthermophiles as basalmost members. With the eubacterial tree shown here, Archaea is the only domain that is still potentially basally hyperthermophilic, and a mesophilic Luca seems more likely. A hyperthermophilic origin of life, while thought to be consistent with widespread conditions on the young, newly-formed earth, is not consistent with the reduced stability of RNA at high temperatures.

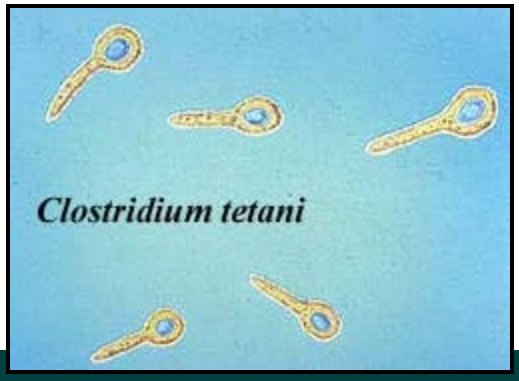
In the tree used here, the order of branches between the base and Cyanobacteria is based on the Cavalier-Smith tree, while relationships within the Didermata exclusive of Cyanobacteria are, for now, based on the more familiar rRNA tree in light of their greater uncertainty. Most of the taxa are based on clusters in gene trees, and may be lacking in morphological apomorphies.

Actinobacteria

Actinobacteria are Gram-positive and almost exclusively aerobic. Their DNA is biased toward high G+C content. Actinobacteria contain 20S *proteasomes*. Such proteasomes are otherwise known only from Archaea and eukaryotes. Nagy *et al*. (1998). Often with *snapping division* or branching filaments; spores if present usually exospores. Filamentous members of this clade are often referred to as 'fungi'. *Actinomyces, Streptomyces, Mycobacterium, Propionibacterium, Corynebacterium, Nocardia, Micrococcus*.

Firmicutes

Mostly with thick rigid *murein* walls containing *teichoic acids* and *lipoteichoic acids*; often forming *endospores*. *Clostridium, Bacillus, Lactobacillus, Streptococcus, Staphylococcus*. In contrast, one subclade, the Mollicutes, has lost the cell wall, and is mostly intracellular parasites or symbionts (Mycoplasma). The name 'Firmicutes' was originally coined to include all Gram-positive bacteria (including Actinobacteria and Togobacteria) and excluding Mollicutes, so its restriction to a subsection of its original content is somewhat unfortunate. It seems to have been accepted, however, so tough.



Didermata

As mentioned above, these are mostly Gram-negative Eubacteria have a double membrane – the inner cytoplasmic membrane, and the more porous outer membrane.

Cyanobacteria

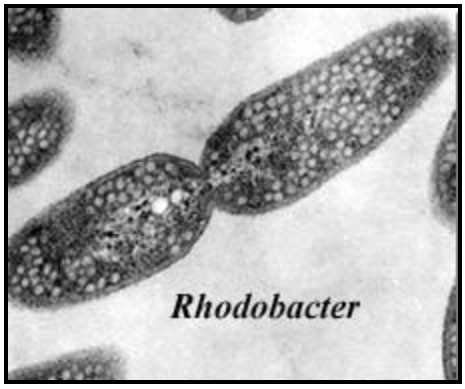
The blue-green 'algae', probably the most familiar bacterial clade, and one of the few to be recognised before the advent of molecular data (the other was the Spirochaetes). Characterised by *oxygenic photosynthesis* with *chlorophyll a*. Flagella absent. A single genus, *Gloeobacter*, is recognisably basal to all others in lacking *thylakoids*. The clade Phycobacteria contains all other cyanobacteria, and has the chlorophyll contained in thylakoids. Phycobacteria have traditionally been divided into five orders on the basis of morphological colony characters. Chloroplasts are derived from Phycobacteria, though from which subclade is still unknown.

Sphingobacteria

Cytoplasmic membrane with *sphingolipids*; outer membrane with lipopolysaccharide; flagella absent.

Proteobacteria

The largest bacterial clade – well-recognised by molecular data, but short on morphological synapomorphies. Large insertion in *RNA polymerase* and *DnaK*. While the genus *Proteus* is included within Proteobacteria, the division is not named after the gen us. Instead, both are named after the Greek shape-changing god Proteus – in the case of Proteobacteria, to reflect the wide range of morphologies covered by the clade. Includes photosynthetic purple sulphur (e.g. *Rhodocyclus*) and non-sulphur (e.g. *Rhodobacter*) bacteria, intracellular parasites (*e.g. Rickettsia*), colonial formers of fruiting bodies (Myxococcales), and a wide range of heterotrophs, such as probably the most well-known bacterium of all, *Escherichia coli*. Divided by molecular data into five large clades, the α-, β-, γ-, δ-, and ε-proteobacteria. Examples – [Alphaproteobacteria] *Rhodobacter, Rhizobium, Rickettsia*; [Betaproteobacteria] *Neisseria, Spirillum*; [Gammaproteobacteria] *Pseudomonas, Vibrio, Escherichia*; [Deltaproteobacteria] *Bdellovibrio, Myxococcus*; [Epsilonproteobacteria] *Helicobacter*.



Archaea

The Archaea, or Archaebacteria have cell membrane of prenyl ether lipids. Flagellar shaft of acid-insoluble

glycoproteins related to pilin. DNA binding protein 10b. tRNA modifications, including archaeosine in D-loop and absence of queuine. Tiny large subunit ribosomal protein, LX. No Hsp90 chaperone. RNA polymerase A split into two proteins. Glutamate synthetase split into three proteins. Divided by rRNA trees into two major clades, Crenarchaeota and Euryarchaeota.

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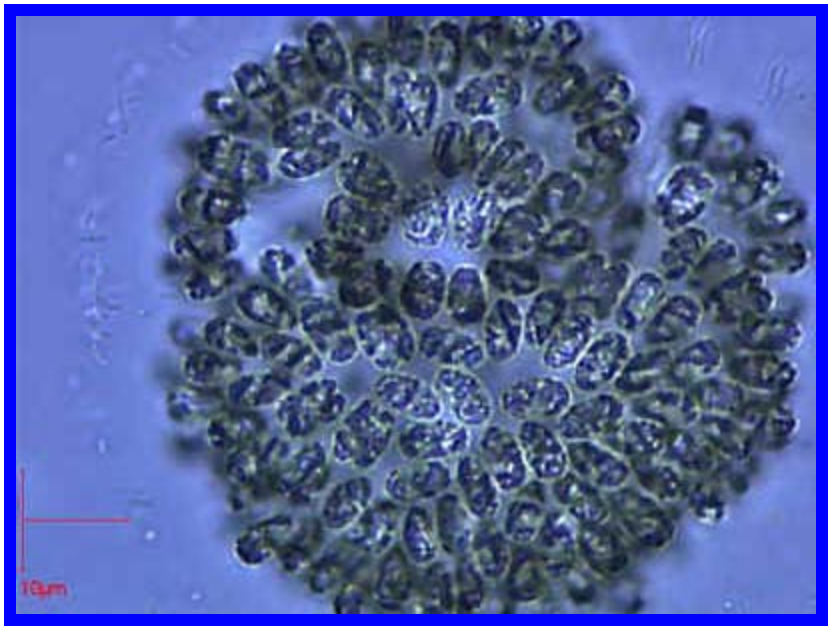
Eubacteria

```
LUCA
|--Eubacteria
|  |--Actinobacteria
|  `--+--Firmicutes
|     `--Didermata
|        |--Cyanobacteria
|        `--+--Sphingobacteria
|           `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
```

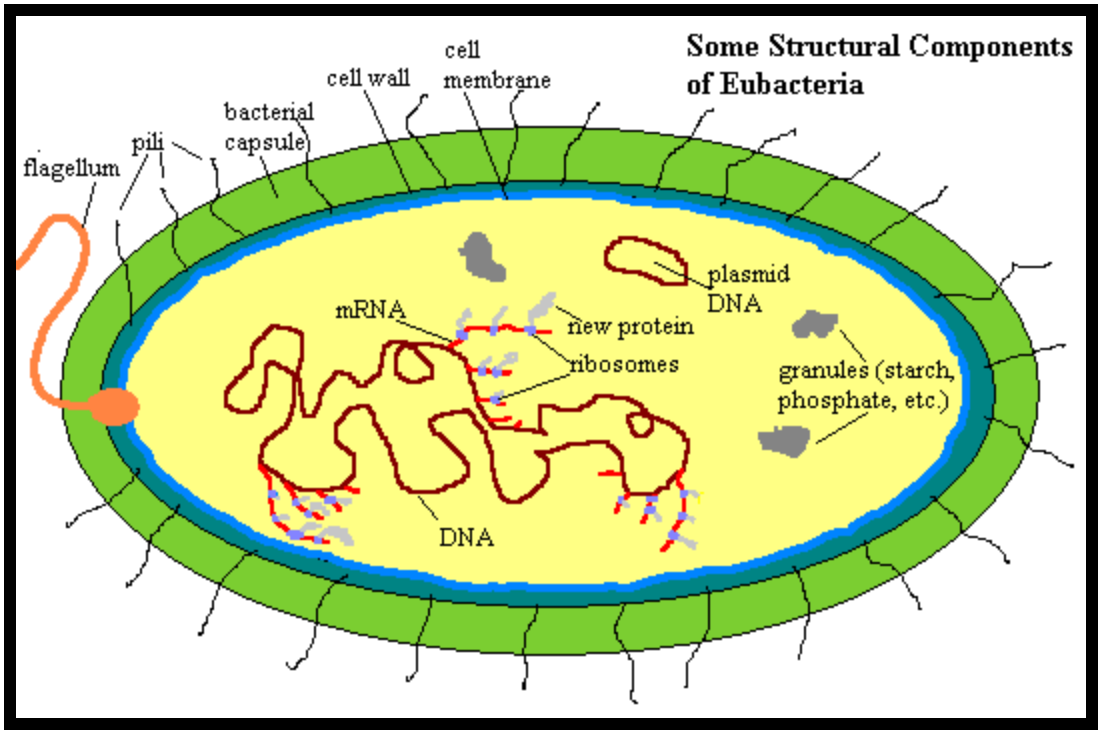

Introduction to Bacterial Anatomy and Physiology

This is the Domain of the Germs. The Eubacteria, in their hundreds of trillions, are the reasons you weren't allowed to pick up the candy you dropped on the floor or eat that egg salad that looked so good a week ago. They are behind every torture you have ever suffered at the hands of the dentist, and they are the root cause of childhood afflictions from antiseptics to acne. They have a ***lot*** to answer for. Then again, they're probably not too happy with us, either. Its hard to tell, since bacteria don't go in much for light conversation or email rants. They grow, or they don't, just as they have for the last three or four billion years, and without making much fuss about it. Bacterial psychology is thus a rather limited field. But such simplicity has its advantages. We are never tempted to paint human thoughts and



emotions onto a 4 µ long pill-shaped blob of protoplasm. We can safely view the bacterium for what it is, a small biochemical machine, without having to steer the usual narrow passage between the twin perils of anthropomorphism and reductionism.

However, to say that the Eubacteria are biochemical machines is not to belittle them. Consider ***Gomphosphaeria*** Kützing 1836, the somewhat larger than average, but otherwise undistinguished, phytoplanktonic cyanobacterium **[1]** on the right. If we allowed a single cell of ***Gomphosphaeria*** to grow and divide under optimum conditions for only about 4.5 days we would be up to our armpits in ***Gomphosphaeria*** over the entire surface of the Earth **[2]**. Even man's most perfect machines, for example the 1976 Toyota Corolla, couldn't come close to matching this kind of performance.



This page will be devoted to considering the basic structural and functional units of the Eubacteria as biological machines. More specific matters, as well as considerations of ecology, phylogeny and evolution will be taken up in connection with more the specific groups to which these matters pertain. So, how are these machines put together? Some of the basic parts are shown in the figure on the left. Look at it carefully, because we have a good bit to cover, starting from outside.

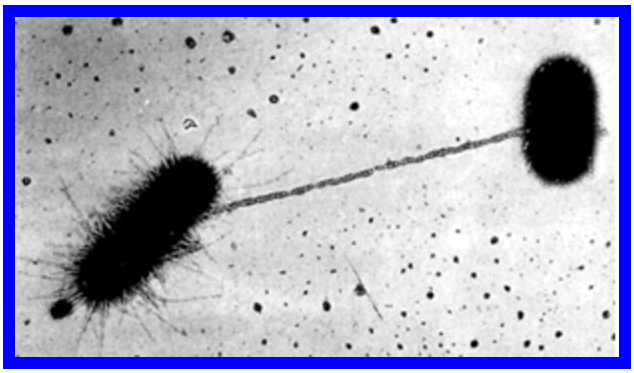
This survey also takes us into some rather dense discussion of cell biology, a little biochemistry, and even a smidgen of thermodynamics. In fact, **this page will serve, for the present, as a very condensed introduction to cell biology for the entire site**. If you don't want to hear about that stuff, you probably shouldn't be reading about bacteria—or single-celled organisms of any kind.

Geometry and mechanics dictate that the first structures we encounter in any cell—and most multicellular organisms, for that matter—are structures dealing with movement, sensation, and interaction with the world outside. In our model eubacterium, these include a flagellum and a system of pili.

The bacterial **flagellum** looks a bit like the eukaryotic organelle of the same name, but it is an entirely different structure. The "tail" portion has no microtubules and consists more or less of an extended filament of a single protein, ***flagellin***. The tail is anchored on what amounts to a rotor. The rotor extends through the outer layers of the cell into the cytoplasm. The system actually works something like a propeller, with the rotor forcing the flagellum to turn in a spiral. The motive force is supplied by sodium or hydrogen ions flowing down a concentration gradient from the outside.

This ion gradient system is the same basic mechanism which is used in a number of other well-known systems, for example in some of the "light reactions" of photosynthesis. It is worth knowing reasonably well. The usual currency of energy in the cell is adenosine triphosphate (ATP). When the cell has ATP to spare, it uses ATP to pump certain ions (here, sodium) out of the cell. Since the sodium concentration is higher outside the cell, the pumps have to pump against the gradient using the energy of ATP. This makes the entire cell a sort of storage battery. To use that stored energy, the cell merely allows some of that sodium to flow back in by means of specialized sodium channels. These channels span the cell membrane and cell wall. When the sodium channel proteins are activated by signals inside the cell and come in contact with a sodium ion outside the cell, they change shape, allowing the ion into the cell and, at the same time, performing some useful work, such as turning the "rotor" of a flagellum **[3]**. The key concept is that the ion channel system takes small bits of energy (ATP molecules) which are all the same and are dispersed throughout the cell, and ultimately concentrates the energy for use at a time and place controlled by ***specific*** "signal" molecules that open ***specific*** ion channels linked to ***specific*** mechanical

tasks—a very elegant system!



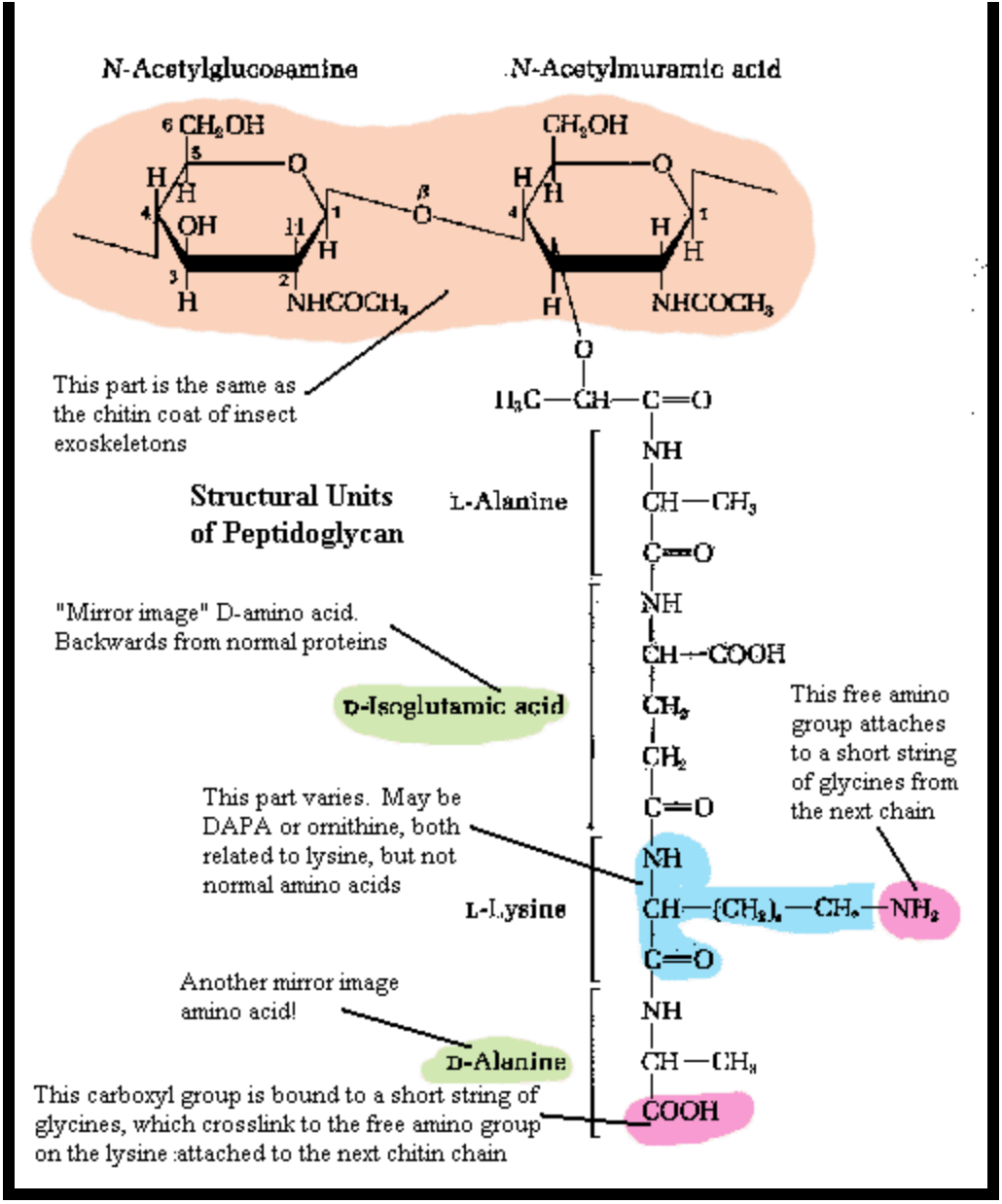
The **bacterial pili** are the bug's equivalent of hands, both as tactile, sensory structures and as tools for grabbing onto and manipulating things at a distance. Our diagram is a bit misleading, since the pili can be quite long. See image (~20,000X) at right from Le revêtement cellulaire des cellules procaryotes. As this image shows, the pilus can serve as a guide for the formation of a cytoplasmic bridge, as for the exchange of DNA. This is a rare, but important event with profound implications for bacterial evolution. Bacteria are not terribly fastidious about who they exchange DNA with. Thus genes can be acquired from unrelated bacteria, and even from non-bacteria. For example, DNA is being exchanged between ***Escherrichia*** and a virus in the image. For this reason, "lateral inheritance" of genes from unrelated organisms is quite frequently observed in bacteria.

Pili perform a great many functions, and consequently are structurally quite diverse. Typically the backbone of the pilus is made up of a long chain protein or polysaccharide (sugar chain) with some type of functionally specific arrangement at the tip. One function of considerable clinical interest is cell-to-cell recognition. The complex array of carbohydrates in and on the pili are the method by which bacteria recognize other cells, and are recognized by them. So, for example, one strain of a germ may be harmless to us while another, differing only in a few sites, may be a deadly pathogen if it recognizes our cells as food, or has surface features which our cells do not recognize as dangerous. Shorter pili, usually referred to as **fimbriae**, are a structurally distinct group of extrusions which operate mostly in bacterial attachment to substrate or to other cells.

The next structure we may encounter is the **bacterial capsule**. The composition, nature, and even existence of the capsule are highly variable, even within a species. It may be composed of polysaccharide or protein, may be tightly or loosely bound, or it may not be found at all. The capsule may be best thought of as an extremely dense layer of short pili. It functions in cell attachment, resistance to desiccation, and as a defense to being swallowed (***phagocytosed***) by other cells. ***Streptococcus pneumoniae*** is a case in point. The R strain of ***Streptococcus*** has no capsule and will not cause disease. It is readily engulfed by human cells. The bacterium is then encased within the membranes of a "vacuole" (a membrane-bound bubble inside the cell) and digested by lysozymes within the vacuole. The S strain has a capsule which prevents digestion. It uses the normally lethal environment of the phagocytic vacuole to grow, replicate and prepare to devour the cell from inside.

Within the capsule is the relatively rigid **cell wall [4]**. The fundamental scaffolding of the cell wall is **peptidoglycan**. See, generally, The Cell Wall. Peptidoglycan is an absolutely bizarre material. As this is not a biochemical essay, we will have to skip over much of the good stuff.

The first element of peptidoglycan is a chain of repeating sugar molecules (a slightly modified glucose, N-acetylglucosamine). This part of the structure is precisely the same as chitin, the material which makes up the exoskeleton of insects and, in more or less modified form, in almost all arthropods. Significantly, it is also found in the radular "teeth" of molluscs,



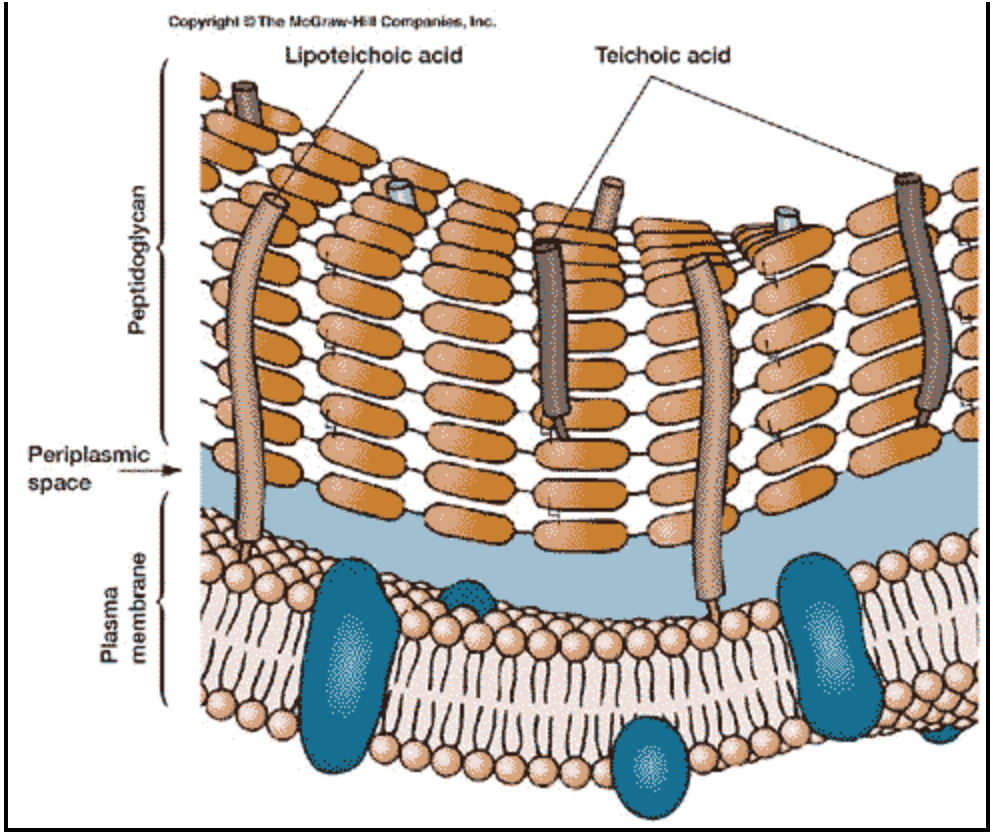
the setae (bristles) and jaws of annelid worms, and the cell walls of Fungi. So, this is exceedingly ancient stuff, possibly predating the split between bacteria and metazoans.

However, in the Eubacteria, every second sugar residue is linked at the 3-position with an amino acid, threonine, which in turn leads on to a strange and unique chain of amino acids (i.e., a peptide chain). The ordinary amino acids which make up all proteins are asymmetrical. That is, they can occur in left-handed (L) or right -handed (D) forms (***racemers***). All higher organisms use only the L-racemers. In fact, even bacteria use only L racemers for ordinary proteins. But they also use certain D-racemers in peptidoglycan. Does this suggest that the bacterial cell wall is older than the standard machinery of protein synthesis and harks back to a time when life wasn't so picky about which racemers it used? It could mean this. Certainly some scientists have thought so. But, since there are no similar structures in the Archaea or the Eukaryota, the more likely explanation is that this is a specialized feature of Eubacteria.

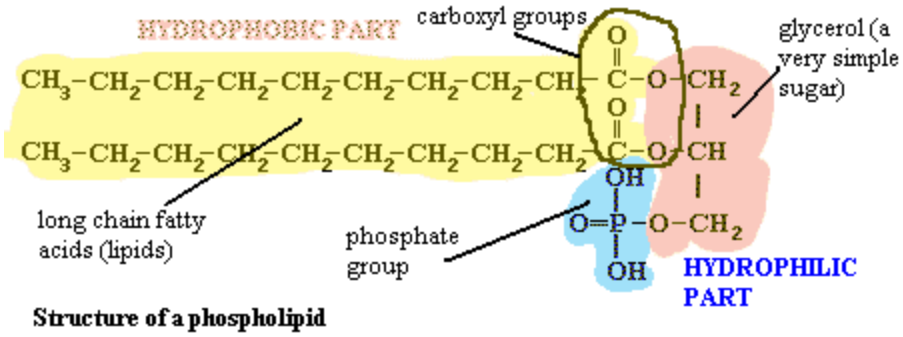
Perhaps, instead, these weird amino acids evolved as an ancient defense against attack by protein-digesting enzymes (***proteases***) which are efficient only in cutting ordinary peptide bonds. Notice the sequence of amino acids here: L-D-L-D. The region around the peptide bond **[5]** between amino acids will be neither left-handed nor right-handed, but a mixture likely to "confuse" proteases which are adapted to digest ordinary proteins. This kind of attack is most like to occur when a bacterium has been engulfed by a eukaryotic cell. So, the moral of this story may be that Eubacteria are not primitive forms at all, but specialized organisms which have been co-evolving with the eukaryotes for a very long time.

Bacterial cell walls contain a number of other typical components. However all of these are somewhat variable between different groups of bacteria; and we will defer discussion of these components for now. Briefly, the usual cell wall materials include **teichoic acids**, polysaccharides of various types, proteins and various derived lipids (fats). Teichoic acids may be of particular evolutionary interest, because they have elements of ***all*** of the major types of biomolecules. However, teichoic acids are found only in certain bacteria, and are not encountered outside the Eubacteria.

Moving inward from the cell wall,



we encounter the **plasma membrane**. The bacterial cell membrane is, like virtually every other cell membrane, internal or external, based on a **phospholipid bilayer**. This basic structure of the membrane and wall together is shown in the figure on the left. To see why it forms a bilayer, we need only refer to the structure of a phospholipid. A phospholipid looks something like this:



Structure of a phospholipid

The "head" of the molecule contains a phosphate group, glycerol, and the carboxyl groups from two long-chain fatty acids. The details need not concern us, but it is important to recognize that these are all polar groups, groups that bind water tightly. That is, the head is ***hydrophilic***. The long chain of carbons on the two "tails" of the molecule has no polar groups and so cannot bind water. These chains are ***hydrophobic***. We might say that they are like oil in water. However, they are not simply ***like*** oil in water. That long featureless run of carbons is chemically ***identical*** to oil. With this kind of dual nature, the hydrophilic part will face the water and the hydrophobic part will exclude water. The most natural way to accomplish both tendencies is to form a bilayer, as shown in the image. See the footnote for a bit more detail **[6]**.

The bacterial plasma membrane is a bit simpler than the plasma membrane of most eukaryotes. Eukaryotic cells have, in addition to phospholipids, cholesterol and other big, flat, mostly non-polar molecules which tend to stabilize the membrane and make it stiffer. Bacteria don't have cholesterol. Eukaryotes also frequently have a good many elaborate lipoproteins (proteins with fats attached) and glycoproteins (proteins with sugars attached). These derivatized proteins do many of the same jobs which are performed by the cell wall and capsule in bacteria. Eukaryotes also have an extensive internal membrane system including the Golgi apparatus, endoplasmic reticula, vesicles, mitochondria, and a nuclear membrane. The Eubacteria have none of these. Some bacteria have small folds in the plasma membrane, in which some specialized functions may occur—notably the ATP-driven active transport of ions discussed above, as well as photosynthesis in the blue-green algae. However, there are no cytoplasmic membranes.

The cytoplasm itself is thus a rather uniform solution without a lot of structure. It does contain **cytoplasmic inclusions** of various kinds for storage of various critical metabolites. These include ***metachromatic granules*** of phosphate, glycogen (a polymer of glucose), grains of starch and salts, and poly(3-hydroxyalkanoate), the bacterial equivalent of fat.

In addition, the cytoplasm may contain **plasmids**. These are small, circular pieces of DNA derived from

bacterial viruses (***bacteriophages***), other bacteria, or perhaps even other organisms. The genes carried on the plasmid may simply be dead weight, which continues to reproduce with the bacterium only because it happens to contain a working site for DNA polymerase. Thus, when this enzyme is active in the cell preparing the bacterial DNA for cell division, it tends to make a copy of the plasmid as well, even though the plasmid serves no biological function. On the other hand, plasmids can be of great practical importance, to humans as well as the bacterial host. Antibiotic-resistant disease bacteria often carry the extra genes which confer resistance on plasmids acquired from some completely different species. Plasmids may also contain other ***virulence factors***, genes which code for proteins which can turn a harmless symbiotic species into a lethal disease vector.

As a starting point for comparison, let's briefly discuss DNA and what it does in metazoans—you, for example. We won't worry about the structure of DNA for now. Its enough to know that DNA is a polymer made of billions of ***nucleotides***. Each nucleotide contains one of 4 bases. The sequence of bases is precisely the same in each cell of your body (with some exceptions for special cells), even though you have about 6 billion DNA nucleotides in each cell. Mitochondria and chloroplasts **[7]** have a bit of their own DNA. All of the rest is contained in a membrane-bound nucleus. This nuclear DNA is encased in ***chromatin***,i.e., a regular coat of basic structural proteins (***histones***). The sequence of bases on the DNA is critical because it specifies a code for making proteins, as we'll discuss in a minute. However, eukaryotic DNA also contains very large stretches of DNA which serve other purposes: binding sites for regulatory proteins, recognition sequences for ligases, and many other functions, some unknown.

In the typical eukaryotic cell, ***RNA polymerases*** use DNA as a template to make long strands of RNA—a very similar polymer which has almost the same nucleotide/base structure. The process of making RNA from DNA is called ***transcription***. The transcribed RNAs are spliced, recombined and "edited" in various steps in the nucleus, before being transported to the cytoplasm as mature messenger RNA (***mRNA***). In the cytoplasm, typically on the surface of an internal membrane system (the ***endoplasmic reticulum***), the mRNA associates with **ribosomes**. Ribosomes are complex structures of protein and two molecules of ***ribosomal RNA***, or rRNA. Ribosomes, and the rRNA molecules in them, are extremely conservative. The ribosomes of all eukaryotes are very similar. Because rRNA changes very slowly, rRNA is a good tool for looking at evolutionary relationships over huge lengths of time.

The ribosomes attach to the mRNA and use the sequences of RNA bases to make proteins according to the "genetic code." Proteins are polymers of amino acids. There are 20 amino acids commonly found in all organisms, and the sequence of amino acids determines what the protein is. Each run of three nucleotides on mRNA (each ***codon***) specifies a particular amino acid. Since there are 4x4x4 = 64 possible codons, the code is redundant. That is, more than one codon sequence may specify a particular amino acid. This code is almost unbelievably conservative. Every living thing uses essentially the same code, with only a few, minor variations. See Table of Standard Genetic Code. This process of assembling proteins from the genetic code in mRNA is called ***translation***. Translation is performed by the ribosomes using another type of RNA, transfer RNA or ***tRNA***. There are 61 different tRNAs. Three codons are ***termination codons*** which signal the end of a coding sequence. Naturally, these have no tRNA. Each tRNA molecule has an ***anticodon*** at one end that binds to a specific mRNA codon. At the other end of the tRNA is the corresponding amino acid. The ribosomes move along the mRNA molecule, matching up the codons with tRNA anticodons, popping off the amino acid from the tRNA's far end, and adding the amino acid to the growing protein chain.

The **bacterial chromosome** is a single, circular molecule of DNA, vastly larger than any naturally occurring plasmid, but much smaller than almost all eukaryotic chromosomes. Bacterial DNA contains relatively few regulatory sites, by comparison with eukaryotic DNA, and has no extensive non-coding regions. Bacteria have no chromatin and, as mentioned above, there is no nucleus. The DNA is simply suspended in the cytoplasm. The Eubacteria use the same genetic code as metazoans. However, the bacterial ribosome, and ribosomal RNA, is considerably different. This may reflect a sharp functional difference. Bacterial DNA is not "edited" and transported. The ribosomes attach to the RNA even as it is being synthesized, so that transcription and translation are simultaneous and closely coupled.

This more or less concludes our whirlwind tour of cell biology and the bacterial cell. It is conventional to have lots of pictures and diagrams of transcription and translation. We have deliberately chosen to depart from this tradition in the interests of getting these painful necessities over quickly and without visual distraction. For good or evil, we will have plenty of opportunities for graphics later.

[1] ***Phytoplankton*** is an ecological term referring to any photosynthetic microorganism normally found in water, including forms (like ***Gomphosphaeria***) that are often found attached to some substrate. The Cyanobacteria are the large group of very basal photosynthetic Eubacteria traditionally called "blue-green algae" because they use phycocyanin (a bluish pigment), as well as chlorophyll a (a green pigment), for photosynthesis of carbohydrates.

[2] Try it. Assume each cell is a cylinder 4 µ long, with a radius of 1 µ (1 µ = 10^{-6} m). Further assume a generation time of 1 hour and that the radius of the earth is 6.35 X 10^{6} m. You can assume what you like about armpit height. It doesn't make much difference to the result.

[3] **DO NOT** get the idea that the bacterial cell has a net electrical charge. It doesn't. For every sodium (Na^{+}) the cell pumps out, it must let some other positive charge in, typically potassium (K^{+}). This "battery" works by entropy, not enthalpy. I'll try to explain in a few sentences as follows. The pore cells are symmetrical. They grab onto any sodium—inside or outside the cell—change shape, then release the sodium and return to their original shape. There is no net gain or loss of potential chemical or electrical energy (or ***enthalpy***). However, if there is much more sodium outside than inside, the net effect is that the transport works only one way, and can therefore perform useful work. How can this be? We seem to be getting work energy from nowhere!

In thermodynamics, at constant temperature, **$\Delta G = \Delta H - T\Delta S$**. **$\Delta G$** is the change in ***free energy***, energy that performs work. Doing work means that **ΔG decreases**. **ΔH** is the change in ***enthalpy***, or (roughly) potential energy, including the energy stored in chemical bonds. If we break bonds, the **ΔH decreases**. T is the temperature measured from Absolute Zero, and **ΔS** is the change in ***entropy*** or the amount of disorder in the system. So, we can get useful work out of a system by reducing enthalpy (i.e. breaking bonds or discharging an electrical potential) or by increasing entropy (increasing the amount of disorder). By breaking down a concentration gradient, we increase entropy. The bacterial cell breaks down high-energy ATP molecules to create a sodium gradient, and so uses enthalpic potential energy to reduced entropy. Then it recovers its investment by letting the sodium back in, so increasing entropy, and converting that change in entropy to free energy used to turn the rotor.

[4] If you're familiar with plant cell walls, try to forget what you know. This is a completely different, and only distantly related, structure.

[5] The ***peptide bond*** is the -CONH- part that links two amino acids.

[6] Actually, the water excludes the long carbon chains, rather than the reverse. This turns out to be another entropy effect. In a bilayer, the non-polar lipid tails are do not interact with water and are free to be very disordered with respect to each other. The polar water molecules, like tiny temporary magnets, form temporary, shifting structures with their nearest neighbors. However, if a lipid molecule is forced into water solution, the water molecules still have no way to interact with the nonpolar tail. Instead, the water molecules form a sort of cage around the lipid, interacting with each other and creating a structure which has a good deal of long-range order. Worse, each water molecule near the tail has fewer neighbors, reducing the randomness of the interactions. Thus entropy strongly favors the bilayer. Even though it looks more ordered, the entropy of the entire system, including the water, is much higher when the long chains are only in contact with each other.

[7] Don't worry about what these are in detail either, if you aren't familiar with these organelles. Mitochondria are small, convoluted membranous structures in the cell which perform oxidative metabolism. That is, they use oxygen to break down sugars and related nutrients into water and carbon dioxide, using the energy released to create ATP for future use as en energy resource. Chloroplasts are layered membranous structures that perform photosynthesis. That is, they use energy from sunlight to build up sugars from carbon dioxide and water, releasing oxygen in the process. In essence, mitochondria and chloroplasts are opposites.

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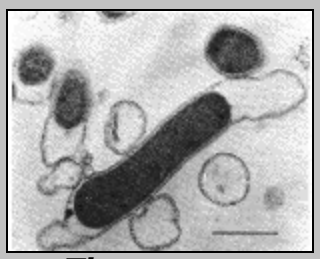
rewritten ATW030228
Last revised ATW030228
checked ATW060201, edited RFVS111214

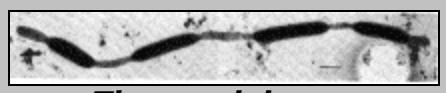
Thermotogales

Thermotogales is a relatively minor branch of the Eubacteria consisting of only three genera: ***Thermotoga***, ***Thermosipho***, and ***Fervidobacterium***. Other genera which may fall into this group include ***Caldotoga***, ***Geotoga***, ***Petrotoga***, ***Thermopallium***, and ***Marinotoga***. All of these organisms are extremophiles. ***Fervidobacterium*** grows at relatively moderate temperatures. The other members of the group are all hyperthermophiles who flourish at 60–90° C.



Thermotoga maritima

Fervidobacterium islandicum



***Thermosipho* sp.**

The "toga" motif in the genus names derives from an unusually prominent cell envelope which can be seen most clearly in the image of ***Thermotoga*** on the right. This "toga" is apparently a reasonably ordinary outer membrane of a Gram-negative-type cell envelope.

The Thermotogales make their living by scavenging biomolecules, including amino acids, glucose, sucrose, starch, cellulose, and xylan. They are found in marine geothermal vents and non-marine hot springs, both at very high temperature but moderate pH and salinity. The Thermotogales use sulfur, rather than oxygen as an electron acceptor in metabolism, thus generating hydrogen sulfide (H_2S) rather than water, as a by-product of metabolism. If the available sulfur is organically bound, considerable hydrogen gas may be

produced by some species. Thermotogales are anaerobic, but can tolerate oxygen to some degree. Their ability to generate hydrogen from organic waste products, while tolerating oxygen, has encouraged some interest in the commercial use of these bacteria. van Ooteghem ***et al***. (2001).

Adapting to Life in Hell

The environment in which these bacteria live thus bears an unfortunate resemblance to some classic descriptions of the Underworld:

The dismal Situation waste and wilde,
A Dungeon horrible, on all sides round
As one great Furnace flam'd, yet from those flames
No light, but rather darkness visible
Serv'd only to discover sights of woe,
Regions of sorrow, doleful shades, where peace
And rest can never dwell, hope ne'er comes
That comes to all; but torture without end
Still urges, and a fiery Deluge, fed
With ever-burning Sulphur unconsum'd
Such place Eternal Justice had prepar'd
For those rebellious, here their Prison ordain'd
In utter darkness, and their portion set
As far remov'd from God and light of Heav'n
As from the Center thrice to th' utmost Pole.

John Milton (1667), **Paradise Lost**, 1: 60–69.

What does an organism have to do to live on scraps, at near the boiling point of water, with little or no light or air, and in the continuous presence of active and toxic sulphur compounds? The following are some of the problems, and the strategies adopted by Thermotogales and other hyperthermophiles.

At high temperature, fat melts; and this is as true of phospholipid membranes as of lard or butter. Some fluidity is good, but it has to be balanced by the necessity for maintaining the important difference between inside and outside. (Recall, for example, the ion gradients discussed in connection with the Eubacteria). Thermotogales incorporate unusual high melting-point lipids in the cell membrane. They also make use of unusual long-chain ***di***carboxylic fatty acids in their membrane lipids. One possible function of these molecules is to create a tightly bound polar layer ***within*** the membrane.

At higher temperature, DNA denatures. That is, the two strands of the double helix fall apart. Hyperthermophiles use a mixture of three strategies to stabilize their DNA against thermal denaturation. (1) the amount of free water in the cell is minimized. DNA can melt because water molecules compete for the hydrogen bond interactions which hold the two strands of DNA together. By reducing the amount of free water, the Thermotogales reduce the rate of meltdown. Note that this is ***free*** water. The amount of total water in the cell is not much reduced. Rather, the ionic strength of the cytoplasm is increased, so that water in the cell is bound up in hydration shells around these ions. (2) Most mesophiles use DNA gyrases, enzymes which help uncoil DNA when it needs to be open for RNA synthesis. Hyperthermophiles have the opposite problem, and have evolved reverse gyrases that effectively tie the DNA up in knots (actually supercoils, not literal knots) so that it can't melt. These enzymes are characteristic of the Archaea. Thermotogales actually have both gyrases and reverse gyrases. (3) Eukaryotic cells use special, arginine-rich proteins called histones and protamines to fold up DNA compactly when it is not in use. Hyperthermophiles use analogous proteins simply to keep the DNA together.

Some important RNA species are also partially double-stranded, for example transfer RNAs and the structural RNAs that are incorporated into ribosomes. These also denature at high temperature. Hyperthermophiles eliminate all mismatches, bulges, and other irregularities that, in mesophiles, lead to flexibility in the RNA. Hyperthermophile RNAs are also usually as short as possible, with no extra sequences, since shorter sequences have fewer nonfunctional folding possibilities. Additional base

modifications and changes in protein binding may also be used to stabilize double-stranded regions.

Proteins also denature, but making them resistant to temperature appears to be a relatively simple. However, enzymes are only active over a particular temperature range. Adaptation to high temperature necessarily means that the enzyme will ***only*** work at high temperature.

Perhaps the most challenging problem of high temperature is not the effect on macromolecules, but the instability of small, high-energy molecules. As we have mentioned previously, ATP is basic to the energy budget of the cell. Other nucleotide triphosphates (GTP, UTP, CTP, etc) are essential to nucleic acid synthesis, as well as specialized enzyme reactions. But these molecules are quite unstable at high temperatures, and it is simply unknown how hyperthermophiles are able to deal with this challenge.

Image: ***Hell*** by Hans Memling (1485) from It's The End Of The World As We Know It...Again

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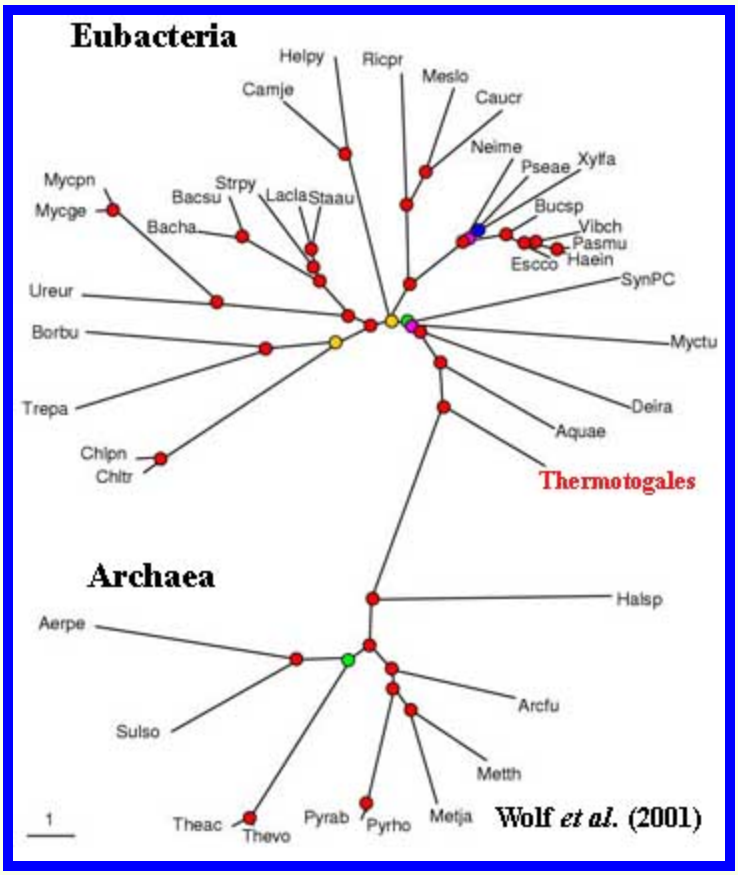
Adaptation or Cooptation?

The Thermotogales are often cited as one of the most basal clades of the Eubacteria. Indeed, even using the most sophisticated techniques, involving statistical analysis of completely sequenced genomes, Thermotogales consistently scores close to the base of the Eubacteria, not far from its presumed origin in the Archaea. Wolf ***et al***. (2001).

The problem is that we can't be sure that those Archaean genes are "native" to the Thermotogales. ***Thermotoga*** is one of the relatively few organisms in which we have really good evidence for large amounts of lateral gene transfer. That is, some genes in ***Thermotoga*** have not simply been passed on from parent to daughter cell, they have somehow been acquired from other species. In fact, it has been estimated that 25% of the ***Thermotoga*** genome has been co-opted, rather than inherited, from the Archaea. Nesbo ***et al***. (2001). Similar studies have revealed gene transfer and extensive genomic diversity across different strains of ***Thermotoga***. The authors of the current crop of phylogenetic studies express confidence that their results are sufficiently robust not to be misled by lateral gene transfer. Yet, it is difficult to see where this confidence comes from.



A Different Kind of Evolution?

If we may be permitted a speculative leap here, the Thermotogales may be close to the boundary between Darwinian, organismal evolution and an entirely different model of genetic transmission. This model, admittedly, has disturbing resonances in the thoroughly discredited ideas of Trofim Denisovich Lysenko (1898–1976), notably bad scientist and champion of the inheritance of ***acquired*** characteristics. **[1]**

Fortunately, the resonance is misleading. What we are suggesting is not that ordinary evolutionary processes are inapplicable. Rather, we suggest that they are applicable at a different level. If genes can be transmitted separately from genomes, then the

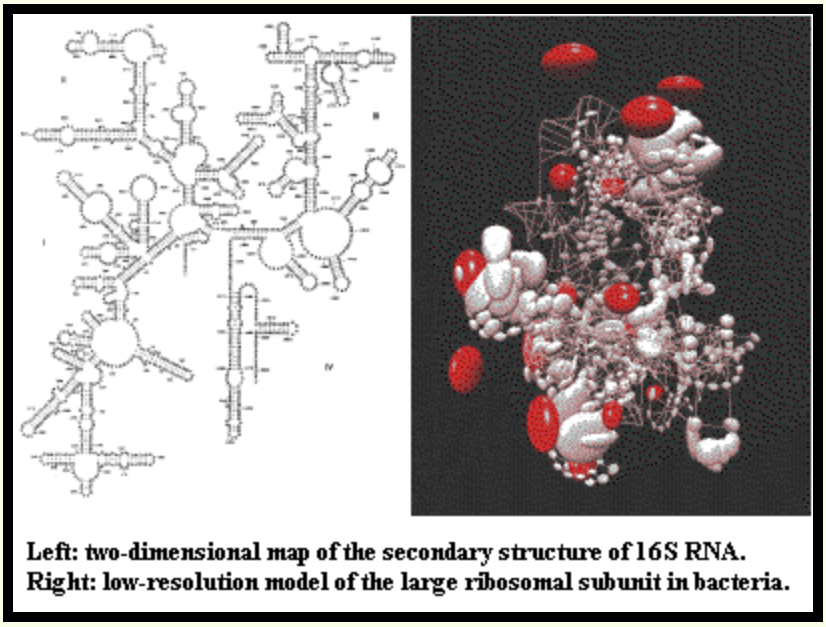
appropriate unit of evolutionary change is the gene and not the genome.

Taken to its logical extreme, one may imagine a stromatolite, bacterial mat or biofilm of the deep Proterozoic, in which cells are essentially empty husks, while various genes migrate between them, sorting themselves out into functional communities by natural selection. If a cell happens to contain a complement of genes which work well together, those genes will flourish, multiply, and those genes will be transmitted and enter into other combinations, just as if each gene were an independent species in an evolving ecosystem.

Things could never have been quite that simple; but we are constructing a paradigm here, not a complete picture. Yet recent studies of bacterial ecology in hyperthermophiles suggest that we're not that far off, either. Hot springs and geothermal vents are places of violent activity. Since enzymes and membranes are "tuned" to work best in a particular temperature range, a prudent hyperthermophile will find a location which is frequently at the right temperature and lock itself to some substrate. Thus bacteria in these environments are normally found in tightly bound bacterial mats. What's interesting is that these mats experience both horizontal and vertical gradients of important environmental variables. Horizontally, the average temperature changes quickly with distance from the heat source. Vertically, the availability of light and circulating nutrients varies enormously with depth in the bacterial mat. All of these variables are subject to both cyclic (daily or seasonal) and stochastic (random) fluctuations.

Conventional organismal ecology would lead us to make three predictions in this scenario: (1) the horizontal gradients would lead to species sorting, with successive populations of more thermophilic bacteria being found in a concentric pattern as we approach the heat source; (2) the vertical gradients would lead either to species sorting or to cyclic cell migrations during daily or seasonal cycles; and (3) populations would be relatively similar in similar environments near different springs.

The third prediction is sometimes true. The first two are untrue. ***See, e.g.***, Miller & Castenholtz (2000); Ramsing ***et al.*** (2000). What seems to happen instead is that one, or perhaps two, species come to occupy the entire gradient. Yet genetic variability within that species exceeds, by a considerable degree, what would normally be expected in a limited population. For example, Miller & Castenholtz identified four different types of 16S (large subunit) ribosomal RNA along a thermal gradient in a hot spring population of ***Synechococcus***. Ribosomal RNA, as we have mentioned, is one of the most conservative biomolecules in all of life. Because it is extensively folded, and must maintain very precise interactions with numerous ribosomal proteins, viable mutations are exceedingly rare. The possibility that a single population (of anything, much less a bacterium) has independently evolved 4 different alleles of this RNA species seems remote. Even if statistically possible (and it might be), consider



Left: two-dimensional map of the secondary structure of 16S RNA. Right: low-resolution model of the large ribosomal subunit in bacteria.

how much more likely it is that some other species, already adapted to this temperature zone, would colonize the region and out-compete the evolving ***Synechococcus***. We are almost forced to the conclusion that, in this environment, "***Synechococcus***" is at most a rather vague phenotypic context and that several rRNA "species", probably acquired from immigrants, are undergoing species sorting independent of this context.

And, speaking of sorting, we have wandered a long way from our brief introduction to an obscure Eubacterial clade. The implications of this mode of life are something we will have to sort out elsewhere—perhaps when we reach into the depths of the Archaea. (ATW030330)

Notes

[1] On this site, we go to some lengths to avoid anything related to politics. Accordingly, we won't talk about Lysenko's politics. We note simply that his story is an interesting one and that, on a personal note, it is one of the very reasons we do not permit politics on this site. (ATW050729)

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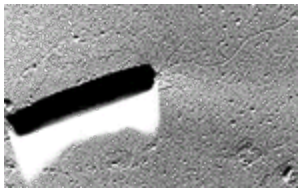
Wolf YI, IB Rogozin, NV Grishin, RL Tatusov & EV Koonin (2001), ***Genome trees constructed using five different approaches suggest new major bacterial clades***. **BMC Evol Biol.** 1: 8.

Archaea

```
LUCA
|--Eubacteria
|  |--Actinobacteria
|  `--+--Firmicutes
|     `--Didermata
|        |--Cyanobacteria
|        `--+--Sphingobacteria
|           `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```

```
<==o ARCHAEA (archaeobacteria, archeans)
   |-- KORARCHAEOTA
   |--o CRENARCHAEOTA
   |  |  |--+-- Thermofilum
   |  |  |  `--+-- Pyrobaculum
   |  |  |     `-- Thermoproteus
   |  |  `--+--+-- Sulfolobus
   |  |     |  `--+-- Metallosphaera
   |  |     |     `-- Acidianus
   |  |     `--+--+-- Pyrolobus
   |  |        |  `--+-- Hyperthermus
   |  |        |     `-- Pyrodictium
   |  |        `--+--+-- Thermodiscus
   |  |           |  `-- Igneococcus
   |  |           `--+-- Staphylothermus
   |  |              `--+-- Desulfurococcus
   |  |                 `-- Thermosphaera
```

```
`--o EURYARCHAEOTA
   |-- Thermococcales
   |-- Thermoplasmales
   |-- Archeoglobales
   |-- Methanopyrales
   |-- Methanococcales
   |-- Methanobacteriales
   `--+-- Methanomicrobiales
      `-- Halobacteriales
```

Reference(s):

—iNet: Tree of Life: http://phylogeny.arizona.edu/tree/phylogeny.html

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Pieces

```
LUCA
|--Eubacteria
|  |--Actinobacteria
|  `--+--Firmicutes
|     `--Didermata
|        |--Cyanobacteria
|        `--+--Sphingobacteria
|           `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```

Pieces
- GroEL

This section contains discussions of individual proteins, organelles or other subcellular components. To put the matter plainly, we frequently get side-tracked by brief discussions of non-germane topics. For the most part, these random remarks are shunted off into the glossary, where they can be safely ignored and forgotten. Sometimes, however, we not only get off-topic, but ramble on for several hundred words about some dull and completely inconsequential point. Eventually, we run out of steam and realize we've blundered far off the path; but, by then, the screen is full of words and pictures. Like so many clay objects made by small children, we're reluctant to simply discard the results of such earnest effort, however inartful and misguided. We have instead chosen to pack them away in this deep recess where they are unlikely to be found. Thus far, we have pondered:

GroEL

---

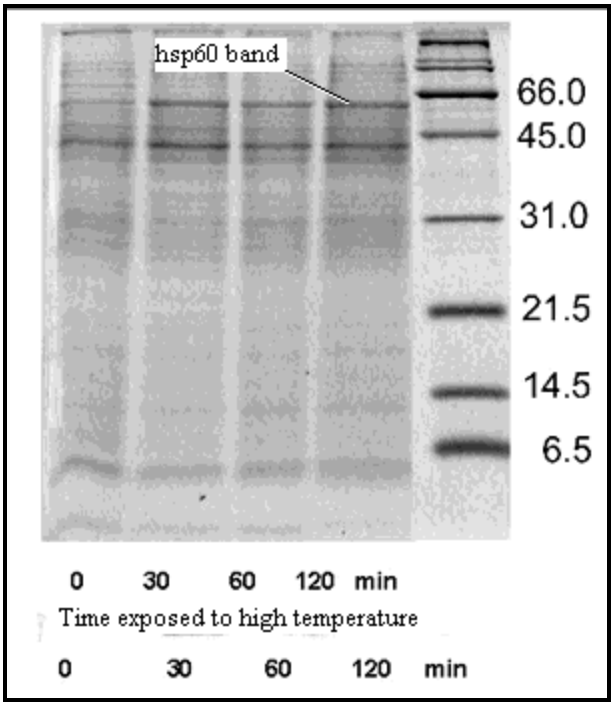
page last modified ATW050122, edited RFVS111214

GroEL

```
LUCA
|--Eubacteria
|   |--Actinobacteria
|   `--+--Firmicutes
|      `--Didermata
|         |--Cyanobacteria
|         `--+--Sphingobacteria
|            `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```


Bad-Tempered Introduction

Despite the name, GroEL is not some childhood friend of Superman. GroEL is a ***chaperonin***. If you are unfamiliar with that term, then you need to read the glossary entry first. Return here only if you are unusually stubborn or really can't find a better source of information. In the latter case, we might tactfully suggest that you take up hopscotch, or some less intellectually demanding activity, as more suited to your research skills. This is only a brief entry designed to remind us of a few aspects of chaperonin structure and function which are relevant to our broader phylogenetic purposes.

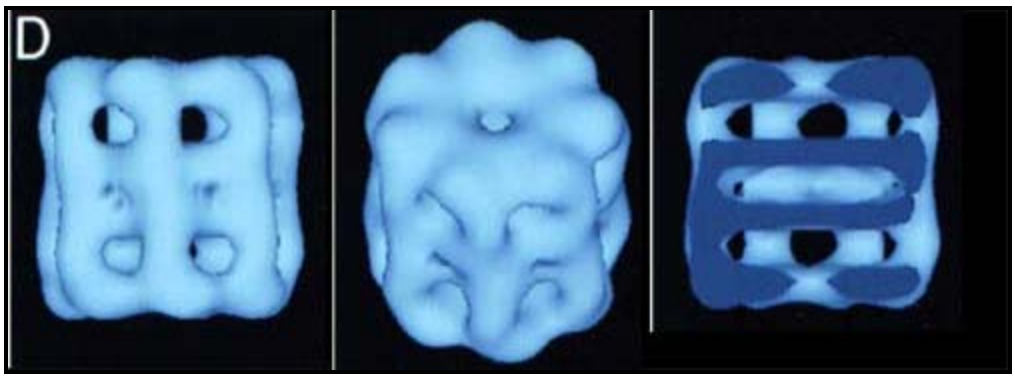


Why Chaperonins?

Chaperonins were originally characterized as a subpopulation of "heat-shock proteins," proteins whose synthesis was promoted by heat stress. This is the reason that GroEL and its homologues, for example, are often referred to as "Hsp60" proteins. GroEL is a 60D (actually 59D) heat shock protein.

It was realized quite early on that chaperonins help to turn polypeptides, fresh from the ribosome, into properly folded proteins. No one knew how the trick was done. In fact, the details are still obscure. However, it was clear that randomly ordered polypeptides passed through the double-ring of the chaperonin molecule and emerged as globular proteins, more or less correctly folded. The chaperonin was thus like a stage magician who runs a scarf through a magic ring, from which it emerges a different color. This illusion is normally created using a scarf that is actually a bag, with the inside covered in cloth of a different color. While feeding the "scarf" through the ring, the magician simply turns the bag inside-out. The analogy is not perfect, but we will see that the chaperonin protein does its job in roughly the same way.

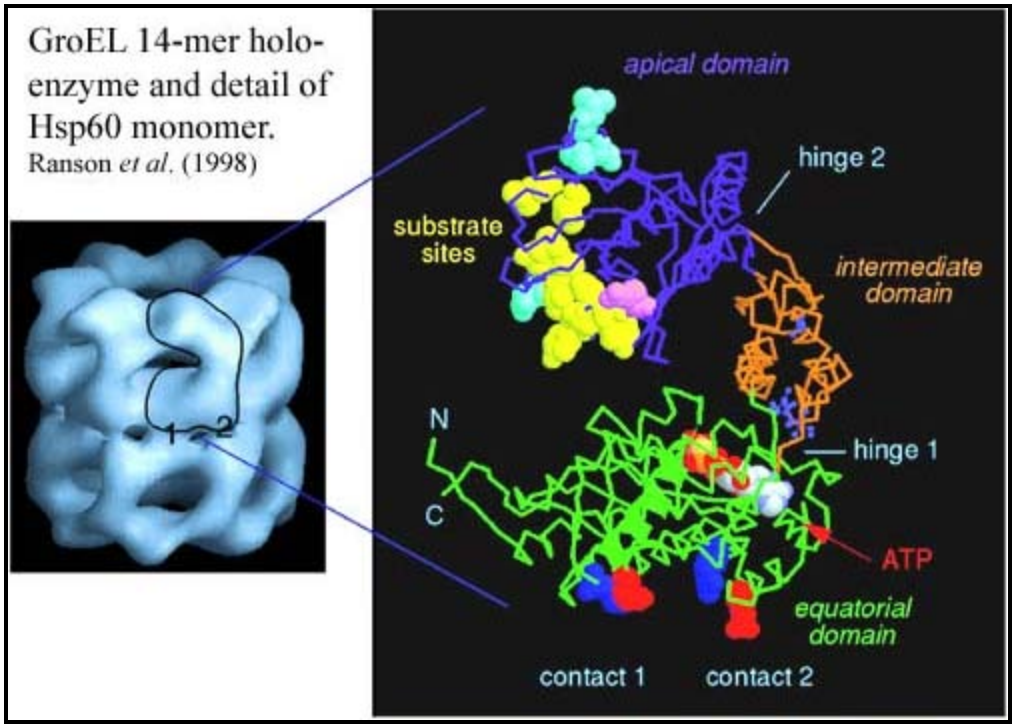
But why bother? A few proteins are absolutely dependent on chaperonins to attain their correct conformation. These proteins are sometimes very important, but they represent a very small proportion of total protein diversity. Why would cells evolve general purpose chaperonins, rather than a few, special purpose types specialized to handle the bulk protein products of the cell? This generality of chaperonins became even more inexplicable when it was found that many proteins which are not chaperonin-dependent fold themselves just fine, and at about the same speed, if they are simply left to themselves in a test tube. So what is the point?



The answer seems to relate to the fact that a cell is ***not*** a test tube. In the test tube, proteins are relatively pure and dilute. In the cell, proteins are at high concentration. Before they can fold properly, they've gotten tangled up with other things and the whole business would become a gooey mess. In fact, in many cases, the function of chaperonins may simply analogous to playpens, evolved to keep untrained infant polypeptides from blundering into other things and getting into trouble.

In addition to folding new proteins, chaperonins also re-fold old proteins which have somehow gotten twisted out of shape. This "personal trainer" function seems to be why chaperonins are induced by heat shock. Heat stress can denature proteins, and the cell mobilizes chaperonins like a small army of physical therapists to twist everything back into its proper conformation.

What does GroEL do?



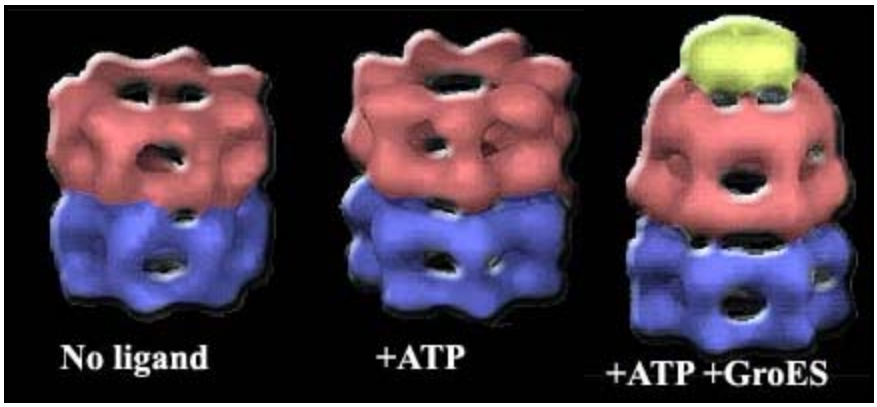
The blue-colored image above shows some low-resolution electron density maps of the holoenzyme. As the top view shows, the top half is a ring made of seven identical monomers. The bottom half is a mirror image. The third picture shows a vertical cross-section. Note the large amount of empty space in the middle of the rings.

The key to the activity of GroEL is in the structure of the monomer, shown in the next image from Ranson ***et al.*** (1998). The Hsp60 monomer has three distinct sections separated by two hinge regions. The apical section contains a large number of hydrophobic binding sites for "native" (unfolded) protein substrate. Note that most sensibly folded globular proteins won't bind to the apical domain because they have their hydrophobic

parts tucked away inside, away from the aqueous medium. This is the thermodynamically optimum conformation. So, these "substrate sites" will only bind to proteins which are ***not*** optimally folded. The apical domain also has binding sites for the Hsp10 monomers of its helper protein, GroES, which we'll get to in a minute.

The equatorial domain has a slot near the hinge point for ATP, as well as two attachment points for the other half of the GroEL molecule. The rest of the equatorial section is moderately hydrophilic.

What happens when we plug in ATP and GroES? The answer is shown in the next set of figures. For purposes of the following discussion, we will refer to the "activated" half of the GroEL molecule as the ***cis*** domain and the other half as the ***trans*** domain.



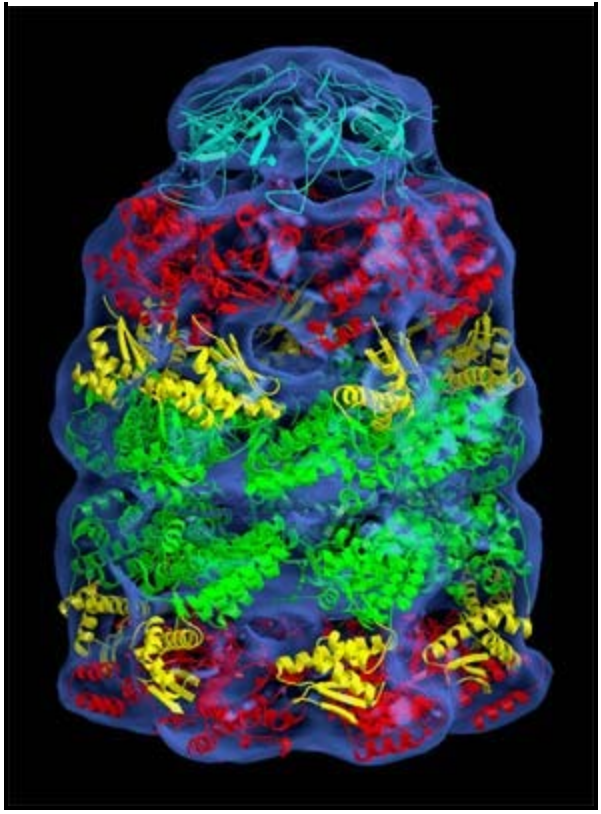
The addition of ATP and GroES has a drastic effect on the conformation of the ***cis*** domain. This effect is caused by flexion and rotation at the two hinge points on the Hsp60 monomers. The intermediate domain folds down and inward about 25° on the lower hinge. This effect, multiplied through the cooperative flexing of all monomers, increases the equatorial diameter of the GroEL cage. But the effect on the upper hinge is far more drastic. The apical domain rotates a full ***60°*** degrees up and out on the upper hinge, and also rotates ***90°*** around the hinge axis. This motion opens the cage very widely at the top of the ***cis*** domain, but the exit is blocked by the GroES cap, and the change in shape completely removes the substrate binding sites from the inside of the GroEL cage. **[3]**

Once More from the Top, with Substrate

Despite all this beautiful work with empty cages, it is not clear what happens when actual proteins are provided as substrate. Plainly, the non-polar, hydrophobic interactions with the inactive state of GroEL select badly folded peptides. In effect, these confused and potentially antisocial proteins are suckered into the GroEL cage by non-polar binding sites. Then the trap is sprung, the door locked by GroES, and they find themselves caught, alone in a relatively polar environment. A second or two later, the ATP is hydrolyzed, and the peptide is pushed out through the trans domain, emerging into the cellular environment once more, but now transformed into a model molecular citizen. How has this rehabilitation taken place?

On this topic a great deal of elegant thermodynamic and kinetic work has been done in the last 5–7 years. Most of this effort, we submit, has been wasted because of a general failure to take account of the phylogenetic framework in which this all occurs. Some thermodynamic generalities are worth emphasis. The constricted nature of the molecular cage strongly favors compact molecular conformations of the substrate protein. Free in solution, long-range, non-polar interactions can only occur at a high cost in entropy **[2]**. In the crowded quarters of the GroEL cage, the relative loss of entropy is much smaller. Thirumalai ***et al.*** (2003); ***see also*** Takagi ***et al.*** (2003). The method of capture also tends to concentrate the non-polar binding sites separately from the polar sites. When the GroEL non-polar surfaces are removed, the chance that any given non-polar group will encounter a nonpolar ***intra***molecular site are much greater than in bulk solution.

Given these generalities, one might well speculate that the transformation works very much like the magician's ring. The hydrophobic sites on the outside of the polypeptide are gathered together at the top of the ***cis*** domain When the



GroEL binding sites are suddenly tucked away, the substrates hydrophobic sites naturally bind each other. In fact, they ***must*** bind each other since the only alternative is to sit next to polar sites or to water. By definition, they don't like to do that. Conversely, the hydro***philic*** sites are now spread out all through the cage. Thus, they surround the clustered non-polar core as the refolded peptide is pushed out the ***trans*** side of the cage. In effect, the GroEL complex, like the magician's ring, simply operates by turning the substrate inside out.

GroEL has no Specific Mechanism

These are just general themes. The real point is that there is no need to invoke any more specific or detailed mechanism. In fact, one of the key observations made by Ranson ***et al.*** in their review is that there seems to be considerable variability in exactly when ATP and GroES bind, exactly how they effect the conformational changes, how the substrate complex forms, and how it is released.

In phylogenetic context it is easy to see why this is so. GroEL and its homologues have not changed much since the basal split between Archaea and Eubacteria. Proteins have been learning how to optimize their reactions with GroEL, or very similar molecules, for about three ***billion*** years. Given this enormous span of time, and the virtual immutability of GroES, as opposed to the huge evolutionary lability of its substrates, it is much more reasonable to conclude that cellular proteins have evolved to make the best possible uses of GroEL—not that GroEL has some magic mechanism which assures optimal results for all proteins.

GroEL is a complicated molecule and, doubtless, there are any number of ways in which a polypeptide can interact with it. Merely by way of example, it is known that certain larger polypeptides, which can't fit inside the ***cis*** chamber, extend into the ***trans*** portion and interact in some (unknown) way with the ***trans*** heptamer. Since GroEL has changed hardly at all over the last several billion years, it seems far more likely that the rest of the genome has adapted to GroEL, and uses it in various specialized ways. GroEL itself cannot specialize. GroEL, like many anatomical and biochemical features at the intersection of many developmental pathways, cannot change significantly without lethal effects. Thus the search for a specific GroEL mechanism will inevitably fail. Aside from qualitative thermodynamic considerations, such as those mentioned above, there is no evidence for a tightly constrained general mechanism, and no need to invoke one. Like the kitchen spoon, GroEL is a device which is both ubiquitous and unspecialized—not part of the recipe, but one of the basic tools around which the whole idea of a recipe is built.

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[3] If you enjoy this sort of thing and have the time, take a look at Suhre ***et al***. (2006). The authors describe free software for playing with protein conformation which comes with the specs for GroEL as a "reference case."

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Bacteria Dendrograms

```
LIFE
|--Eubacteria
|  |--Cyanobacteria
|  `--+--Spirochaetes
|     `--+--Acidobacteria
|        `--+--Eobacteria
|           `--Planctobacteria
`--Neomura
   |--Archaea
   |  |--Eurythermea
   |  `--Neobacteria
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```

Master Dendrogram

Master Dendrogram

```
LIFE
|--Eubacteria
|  |--Actinobacteria
|  `--+--+--Thermotogae
|     |  `--Firmicutes
|     `--Didermata
|        |--Cyanobacteria
|        |  |--Gloeobacter
|        |  `--Phycobacteria
|        |     |--Chroococcales
|        |     |--Pleurocapsales
|        |     |--Oscillatoriales
|        |     `--Hormogoneae
|        |        |--Nostocales
|        |        `--Stigonematales
|        `--+--+--Caldithrix
|           |  `--+--Deferribacteres
|           |     `--+--Nitrospina
|           |        `--Thermodesulfobacterium
|           `--+--+--Sphingobacteria
|              |  |  |--Chlorobi
|              |  |  `--Bacteroidetes
|              |  `--+--Spirochaetes
|              |     `--+--Fusobacteria
|              |        `--Proteobacteria
|              |           |--Rhodobacteria
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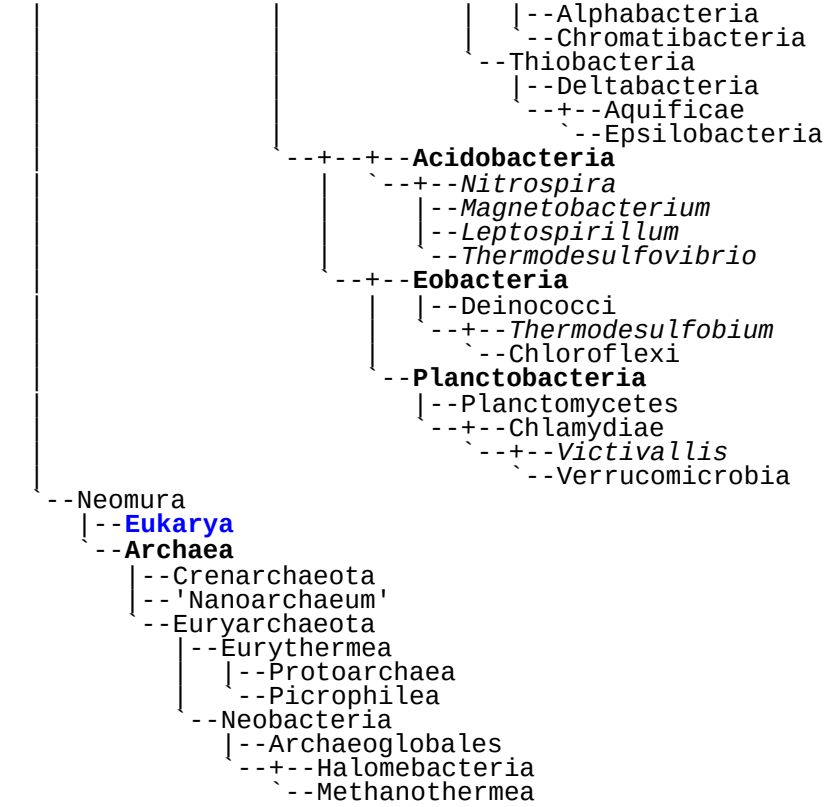

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Glossary A–Z

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LUCA
|--Eubacteria
|   |--Actinobacteria
|   `--+--Firmicutes
|      `--Didermata
|         |--Cyanobacteria
|         `--+--Sphingobacteria
|            `--Proteobacteria
`--Neomura
   |--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```

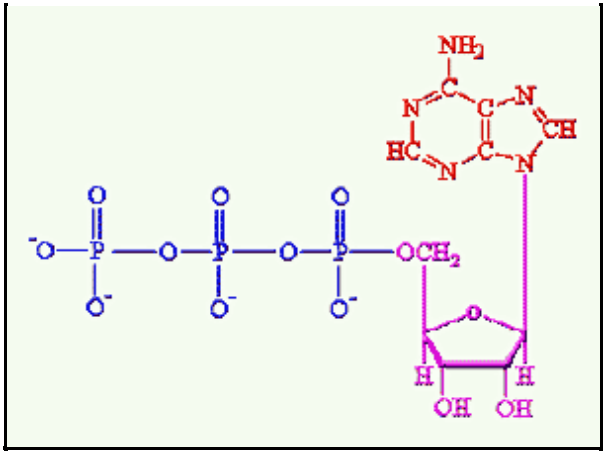

A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z

A

A-ATPase: the name sometimes given to the V-ATPase of Archaea.

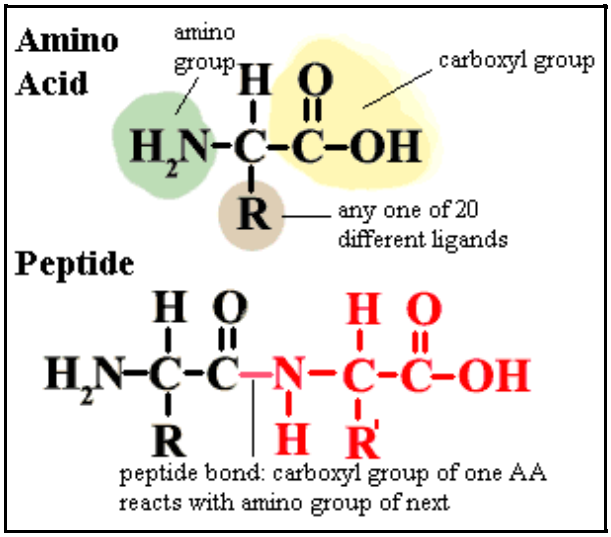
Active transport: transport across a cell membrane which requires energy generated by the hydrolysis of some energy carrier (usually ATP).The selective active transport of ions (usually sodium) out of the cell is often used as a secondary energy storage mechanism. ***See*** ion gradient system.

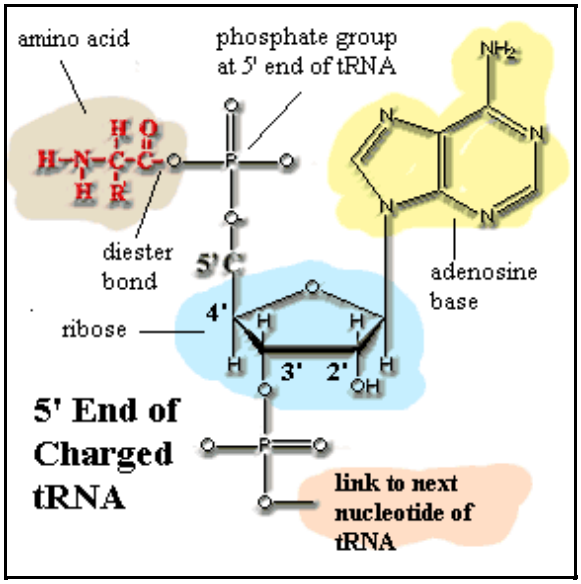
ATP: adenosine triphosphate. This is the common currency of chemical energy in most cells. It is more or less accurate to say that the whole object of metabolizing food, of whatever



kind, is to recover energy to make ATP. Specifically, the energy from the breakdown of food is used to add a third phosphate group onto adenosine ***di***phosphate (***ADP***) to make the ***tri***phosphate. The energy stored in ATP is then used to drive various reactions by cleaving the third phosphate back off (***hydrolysis*** of ATP). This job is done by enzymes (***ATPases***) which couple the ATP hydrolysis with some other reaction which absorbs energy. Chemically, ATP is built from exactly the same chemical unit that supplies the adenosine or "A" monomers to RNA. Now, stop fidgeting and pause a moment to reflect on the evolutionary implications of all this: precisely the same molecule, phosphorylated adenosine, is at the core of (a) most information exchange (b) the vast majority of food metabolism reactions, and (c) most synthetic reactions, in every known organism. Why? No one knows the answer to this question. This is not the sort of molecule you'd expect to form spontaneously—or at least not under the kinds of conditions found today. There are two relatively high-probability implications. (1) We may be missing a lot of hidden evolution—lost diversity—which occurred between the first living organism and the last common ancestor of all organisms alive today. (2) Life may have gotten started at the interface between radically different chemical environments. Notice that the adenosine base in ATP is strongly reduced, non-polar, compact, and basic. The phosphate end is highly oxidized, ionic, has an extended shape, and is quite acidic. The ribose ring in between is intermediate in all four respects. It's hard to see how this molecule could form without either a sophisticated biochemical system already in place (implication "a"), the close juxtaposition of wildly different chemical environments (implication "b"), or both.

Amino acid: the fundamental building block of proteins. There are twenty different amino acids normally found in proteins. All have the general structure shown in the figure. In proteins, the amino acids are joined by peptide bonds as shown in the image. Notice that the central carbon atom has four different ligands. It is therefore asymmetrical and can exist in two mirror image forms (enantiomers), known as **L** and **D** enantiomers. Proteins in living organisms are all made from **L**-amino acids. However bacterial cell walls and a few other structures incorporate some **D**-amino acids. A few naturally occurring amino acids are not normally found in proteins and are not specified in the genetic code. Ornithine (R = $(CH_2)_3NH_2$) is one example. These are non-protein amino acids are common intermediates in a variety of metabolic pathways. Finally, some amino acids may be chemically modified after they have been incorporated into proteins.





amino acyl-tRNA: a "charged" tRNA, ***i.e.*** one with a bound amino acid. The carboxyl group of the amino acid is bound through a diester linkage to the 5' phosphate ligand of a terminal adenine on the tRNA. This leaves the amino group free to form a peptide bond with the growing protein chain on a ribosome. The amino-acyl tRNA for alanine may be abbreviated ala-tRNA, $tRNA^{ala}$, or even ala-$tRNA_{ala}$. Generally, the subscript refers to the tRNA species, and the superscript shows what it is actually charged with.

amino group: a ligand of the form $-NH_2$.

anticodon: the complementary RNA or DNA sequence to that of a codon. Thus, GCG is one of the codons for alanine. ***See*** genetic code. The corresponding anticodon would be CGC.

Apomorphy: a character state which is unique to a single,

terminal taxon. Example: among primates, complex grammar is an apomorphy of human beings. It is quite diagnostic of humans, but useless in determining phylogenetic relationships because it is not a shared, derived characteristic, or synapomorphy, of any larger group.

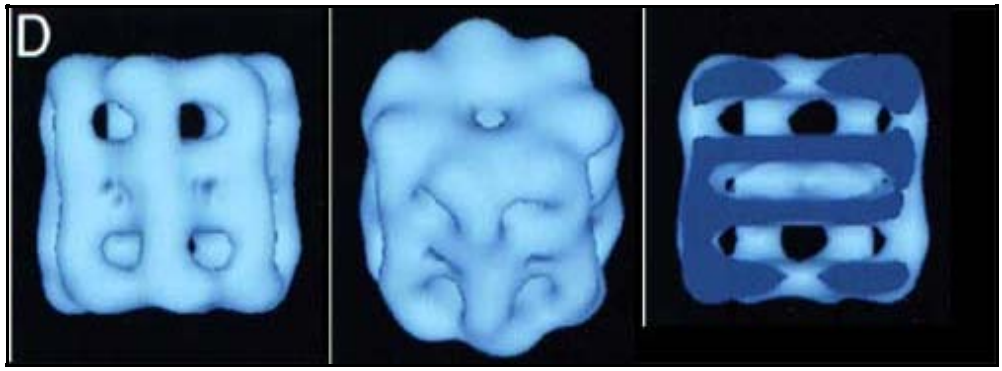
Autotroph: an organism which obtains energy from inorganic sources, sunlight or the oxidation of inorganic chemicals.

Autotrophic nutrition: synthesis of organic food molecules from inorganic compounds such as carbon dioxide.

B

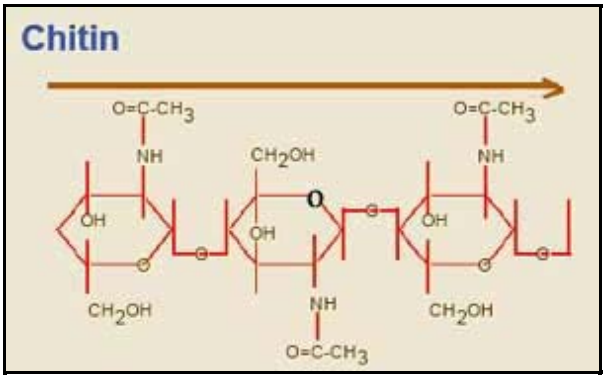
C

carboxyl group: a ligand of the form -COOH, ***i.e.***, a simple organic acid.

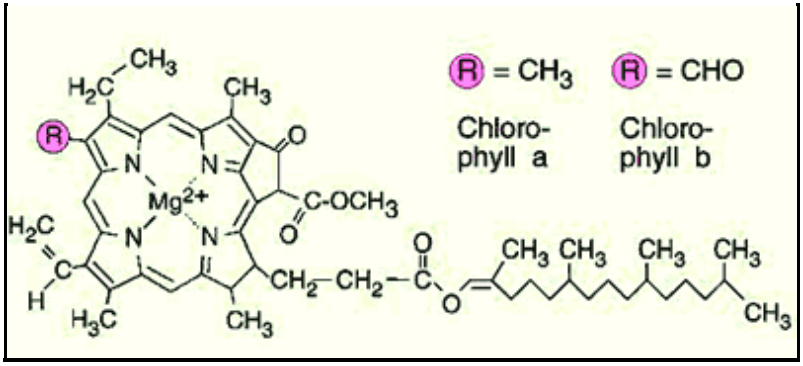


Chaperonin: any of a class of ATP-dependent (***i.e.*** they need chemical energy to do the job) proteins which are responsible for folding polypeptides into the correct conformation. As anyone who has been confronted with a spool of ribbon and a pile of presents knows, the ribbon will not fold itself into an appropriately decorative conformation. Even though the desired conformation is stable and energetically favorable, the ribbon needs energetic guidance to attain this state within some biologically relevant timescale. This is the function of chaperonins. They are composed of two doughnut-shaped subunits. Chaperonins also have a limited ability to "repair" proteins which have been incorrectly folded. **Class I chaperonins** are chaperonins closely related to the ***E. coli*** GroEL protein, and are sometimes referred to as **GroE chaperonins**. The holoenzyme is composed of two heptameric subunits and works in concert with a helper Hsp 10 protein (GroES). Class I chaperonins are found in Eubacteria, mitochondria, and chloroplasts. **Class II chaperonins,** or **TCP1** proteins include both the **thermosomes** or **TF55** proteins of Archaea and the **CCT** proteins of eukaryotes. The eukaryotic species are composed of two octameric rings, while thermosomes may have either 8 or 9-member rings. Class II chaperonins do not have a helper protein. Class II chaperonins are very closely related to Class I chaperonins by structure, but not by sequence. For more information, ***see*** Pieces: GroEL.

Chitin: a polymer of repeating sugar molecules (a slightly modified glucose, poly-N-acetyl-D-glucosamine). See image. Chitin is the material which makes up the exoskeleton of insects and, in more or less modified form, in almost all arthropods. In arthropods, chitin occurs in a crosslinked form, α-chitin. Significantly, it is also found in the radular "teeth" of molluscs, the setae (bristles) and jaws of annelid worms, and the cell walls of Fungi. So, this is exceedingly ancient stuff, possibly predating the split between bacteria and metazoans.



chlorophyll: a widely dispersed photosynthetic pigment, particularly effective in red and blue light (it reflects the mid-range green wavelengths, which is why it appears green to our eyes). Note that **chlorophylls a and b** differ only in the substitution of a methoxy for a methyl ligand in one position.



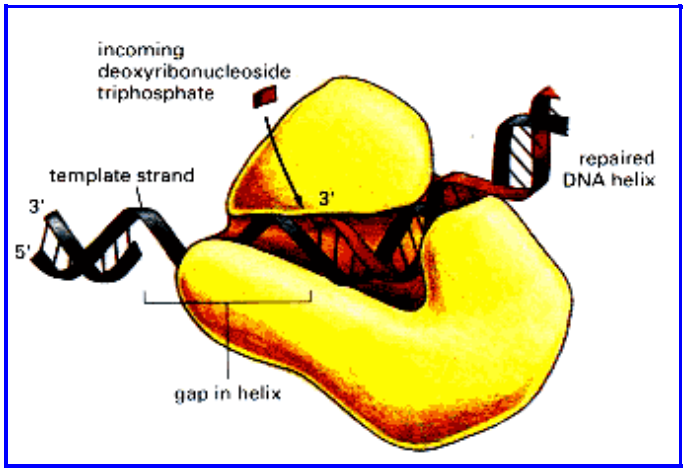
Clade: a group of organisms consisting of an organism and all of its descendants.

Codon: the basic element of the genetic code. A sequence of three nucleotides that specifies a particular amino acid, or serves as a "start" or "stop" signal for translation.

Crista: (pl. ***cristae***) **(1)** of mitochondria, folds in the internal membrane of the mitochondrion which gives the organelle its characteristic appearance. This is the site of the electron transport chain in oxidative metabolism. The cristae, therefore, serve as the physical link between the tricarboxylic acid cycle and oxidative phosphorylation (ATP synthesis). ***See also*** Wikipedia: Mitochondrion. **(2)** more generally, crest (its literal meaning in Latin) or ridge.

D

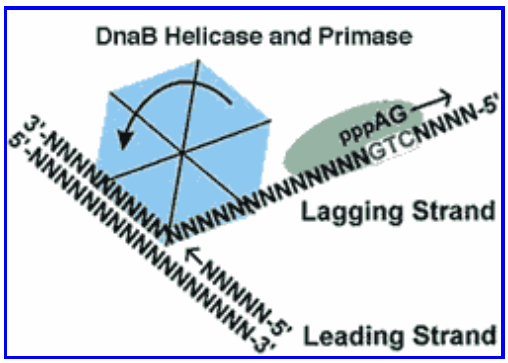
DNA polymerase: an enzyme which replicates DNA, either as a part of cell replication or DNA repair.



DNA polymerase III: The dominant DNA polymerase in ***E. coli***. By extension, similar DNA polymerases in other Eubacteria (***i.e.,*** Type C polymerases) are often referred to by the same name. "DNA Polymerase III is an asymmetrical dimer, composed of 18 subunits, a complex arranged from combination of 10 distinct subunits. Three subunits form the core of the enzyme, these are alpha, epsilon and theta. The holoenzyme is created from other subunits (beta, delta, delta prime, chi, gamma, psi, and tau) variationally binding to this core, and conferring the full functions and characteristics the enzyme needs to carry out the replication of DNA. As a replicative enzymatic mechanism of DNA, the Polymerase replicates with high fidelity. To maintain this level of fidelity, a proofreading mechanism has been included, by evolution, in the enzyme, in the form of its epsilon subunit."DNA Polymerase III. Image from the same page.

DNA polymerase, Type C: DNA polymerases with sequence and structure similar to ***E. coli*** polymerase III. Type C polymerases are restricted to Eubacteria. By sequence they have no detectable relationship to polymerases from Archaea or eukaryotes.

DNA topoisomerase: any of a class of enzymes that alter or maintain the topological structure of DNA, ***e.g.***, in a supercoiled form.



DnaB: a bacterial helicase. There are several helicases, but this is the main one involved in DNA replication in Eubacteria. It works cooperatively with DNA polymerase III to unwind DNA ahead of DNA synthesis on the leading strand (i.e., 5' → 3'). Every 500 or 100 nucleotides, it stimulates primase to create an RNA primer for replication of the lagging strand. DnaB is an ATP-dependent homohexamer. ***See*** DNAB HELICASE HOME PAGE, also the source of the figure.

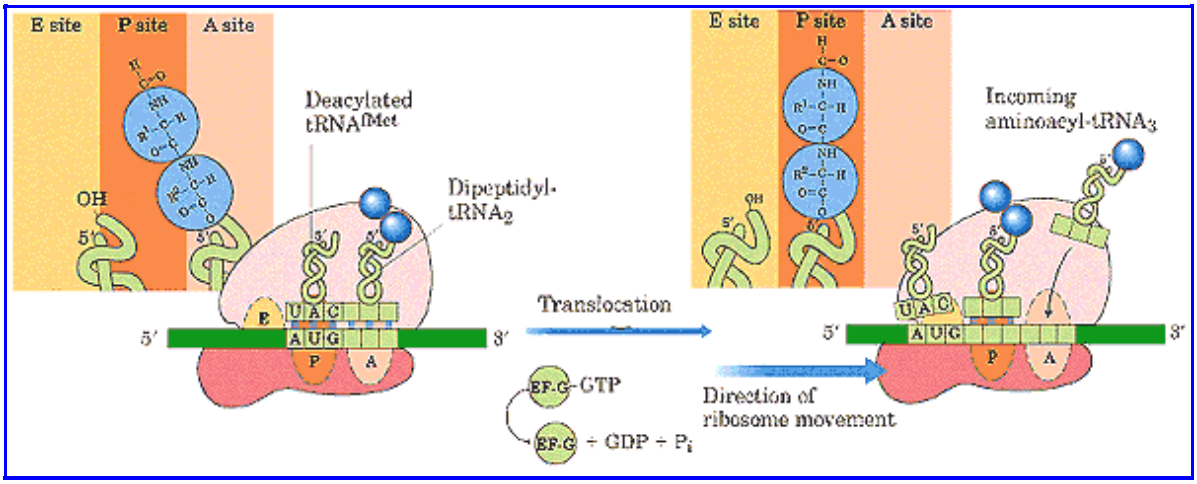
DnaK: a bacterial chaperonin homologous to the Hsp70 of eukaryotes. DnaK works in tandem with DnaJ and GrpE to

accomplish ATP-dependent folding of polypeptides. DnaK is a heat shock protein. However, when not operating under heat shock conditions, DnaK is also present and is involved in the degradation of σ^{32}, an RNA polymerase regulator which detects the promoter sites for transcription of RNA coding for heat shock proteins.

E

EF: elongation factor, ***q.v.***

EF-G: the elongation factor responsible for moving peptidyl-tRNA from the ribosomal A-site to the P-site during translation. Like EF-Tu, it makes use of a ribosomal GTPase to rotate the small (30S) ribosomal subunit with respect to the large (50S) subunit. EF-G is homologous to the EF-2 of eukaryotes.



EF-Tu: the elongation factor responsible for attachment of an incoming amino acyl-tRNA to the ribosomal A-site. Like EF-G, it makes use of a ribosomal GTPase to rotate the small (30S) ribosomal subunit with respect to the large (50S) subunit. EF-Tu is homologous to the EF-1α of eukaryotes.

Elongation Factor: during translation of mRNA on ribosomes, each tRNA binds successively to three sites on the ribosome: the A (acceptor) site, the P (peptide site), and the E (exit) site. Elongation factors are small, GTP-dependent proteins which are instrumental in this process. EF-Tu (homologous to EF-1α of eukaryotes) binds the tRNA into the A site. After the amino acid on the tRNA has been added to the growing peptide chain, EF-G (homologous to EF-2 of eukaryotes) is responsible for moving the peptidyl-tRNA complex to the P site. EF-Tu and EF-G are themselves believed to be homologous. That is, they share sequences which suggest that the genes coding for these proteins derived from a single common ancestral gene, probably before LUCA. The operation of elongation factors is described in a bit more detail in the figure at tRNA.

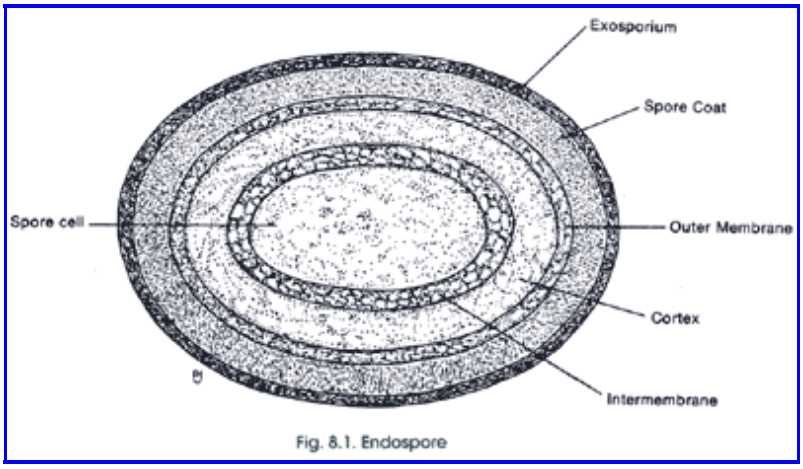
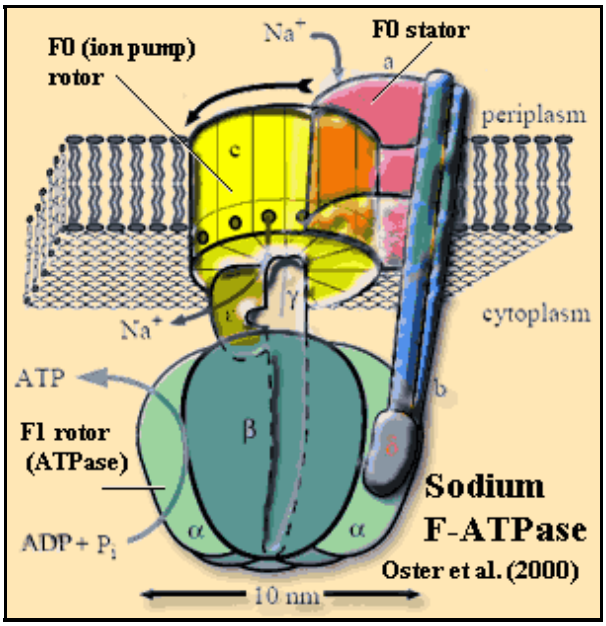


Fig. 8.1. Endospore

endospore: the nearly immortal resting state of some bacteria. Endospores are composed of a central spore cell, which is surrounded by various protective layers. The outermost layer is the exosporium, which is a thin covering made of protein. Below this is the spore coat which is made up of highly cross-linked keratin and layers of spore-specific proteins. The cortex consists of loosely cross-linked peptidoglycan. The innermost spore cell contains the components of the vegetative bacterial cell (the cell wall, cytoplasmic membrane, cytoplasm, nucleoid, etc.). The water content of endospores is only about 10–30% of the water content of vegetative cells; therefore, endospores are capable of surviving at levels of dehydration that would kill vegetative cells. The low water content also provides the endospore with chemical resistance (to chemicals such as hydrogen peroxide) and it causes the remaining enzymes of the spore cell to become inactive. One chemical produced by endospores that is thought to lend to their high resistance is dipicolinic acid. This chemical has been found in the spore cell of all endospores examined. Dipicolinic acid interacts with calcium ions to form calcium dipicolinate, which is the main substance believed to lend endospores their resistance and represents about 10% of the

dry weight of an endospore. The spore cell also contains small acid-soluble spore proteins (SASPs). These function to protect DNA from UV radiation, dessication and dry heat, and they also serve as a carbon and energy source during the germination process (conversion back to a vegetative cell). Another component of endospores that contributes to their resistant to chemical agents is the strong spore coat, which is composed of highly cross-linked keratin. Identification of particular organisms can be aided by the presence, location and size of endospores. Endospores can be located centrally, terminally or subterminally within a cell. Sometimes the endospore is much larger in diameter than the cell, which causes the cell to appear swollen at the location of the endospore." Endospore Structure.

F



F-ATPase: a very ancient, but sophisticated, molecular machine found in Eubacteria, mitochondria, and, in modified form (V-ATPase, A-ATPase, etc.), in all organisms. Very generally, an F-ATPase consists of a rotating ion pump (F_0) coupled by a shaft to an ATPase (F_1). In Eubacteria, the F-ATPase normally runs in "reverse," allowing ions (usually H^+, sometimes Na^+) at high concentration to enter the cytoplasm, driving ATP synthesis. The mechanism has been described as a "Brownian ratchet." It works a little like an old-fashioned coin-operated vending machine. The ion enters a dead end "coin slot" between the stator element and the rotor element of the ion pump. Random thermal motions of the rotor (since there is no hand to turn a crank) align the slot with a series of polar amino acid groups on the lower half of the rotor. The ion drops through into this region, which blocks the rotor from rotating backwards (hence the "ratchet") as well as blocking this lower half of the slot. When the next ion enters the upper slot and the rotor turns again, the first ion is released into the cytoplasm. This creates a net torque on the shaft which rotates the F_1 ATPase, driving ATP synthesis. Free energy calculations suggest that this process is nearly 100% efficient. ***See*** mini-review by Oster ***et al.*** (2000).

flagellin: a fibrous protein which forms most of the shaft in the flagellae of prokaryotes. This is quite different from the 9+2 microtubular rosette which makes up the core of eukaryotic flagellae. Interesting fact: an aberrant inflammatory response to flagellin turns out to be one of, and perhaps ***the*** main causative agent in Crohn's Disease. Lodes ***et al.*** (2004).

fmet: abbreviation for **N**-formyl methionine, ***q.v***.

formyl: a general term for a ligand consisting of a one-carbon organic acid (carboxyl group), based on formic acid, HCOOH. The nomenclature is ambiguous, since the same term is often used to mean any of the following: HCOO-R, HCO-R, and even (wrongly) R-CO-R' (instead of ***keto***) or R-COOH (instead of ***carboxy***).

G

genetic code: the standard code is shown in the table. Each sequence of three nucleotides in DNA or RNA potentially specifies an amino acid. In RNA, all T (thymidine) bases are replaced by U (uracil). Other than this, the DNA and RNA codes are the same. During translation, ribosomes and associated enzymes "read" mRNA containing the code and assemble chains of amino acids (i.e. proteins) according to this blueprint. The code is redundant, in that each amino acid (except tryptophan and methionine) is

	T (or U)	C	A	G
T / U	TTT Phe (F) TTC " TTA Leu (L) TTG "	TCT Ser (S) TCC " TCA " TCG "	TAT Tyr (Y) TAC TAA **Ter** TAG **Ter**	TGT Cys (C) TGC TGA **Ter** TGG Trp (W)
C	CTT Leu (L) CTC " CTA " CTG "	CCT Pro (P) CCC " CCA " CCG "	CAT His (H) CAC " CAA Gln (Q) CAG "	CGT Arg (R) CGC " CGA " CGG "

specified by more than one series of codons (nucleotide bases). The sequences UAA, UAG, and UGA signal the ribosome to terminate translation. There are minor variations in the code. However, exceptions to the standard code are very rare.

A	ATT Ile (I) ATC " ATA " **ATG** Met (M)	ACT Thr (T) ACC " ACA " ACG "	AAT Asn (N) AAC " AAA Lys (K) AAG "	AGT Ser (S) AGC " AGA Arg (R) AGG "
G	GTT Val (V) GTC " GTA " GTG "	GCT Ala (A) GCC " GCA " GCG "	GAT Asp (D) GAC " GAA Glu (E) GAG "	GGT Gly (G) GGC " GGA " GGG "

glycocalyx: a typically loose extracellular layer of polysaccharides.

GroE chaperonin: ***see*** chaperonin.

GroEL: a chaperonin of Eubacteria. For more information, ***see*** Pieces: GroEL.

GroES: a helper protein of the chaperonin GroEL. For more information, ***see*** Pieces: GroEL.

H

heat shock proteins: a distinct population of proteins synthesized under conditions of heat stress. RNA polymerase does not usually recognize the promoter sites for these proteins on the bacterial DNA. This requires a special "sigma factor," σ^{32}. Sigma 32 is produced constitutively by the cell but, normally, is selectively degraded with a half life of about 60 sec. Under heat stress conditions, degradation is suppressed, and σ^{32} binds to RNA polymerase, allowing it to recognize these promoters and to synthesize mRNA coding for the heat shock proteins.

helicase: an enzyme which unwinds and separates the two strands of DNA for repair or replication.

Histones: a family of strongly conserved, highly basic (arginine and lysine-rich) DNA-binding proteins found in eukaryotes and Euryarcheota. Among other functions, histones maintain DNA in a supercoiled form and act as a sort of universal repressor for regions of the genome which do not have to be immediately available for transcription.

Holoenzyme: a fully-assembled enzyme in functional form, including all polypeptides and subunits. Many enzymes function as n-mers (typically dimer or tetramer). In those cases, the holoenzyme includes the entire ***n***-mer.

Hsp: ***see*** heat shock proteins.

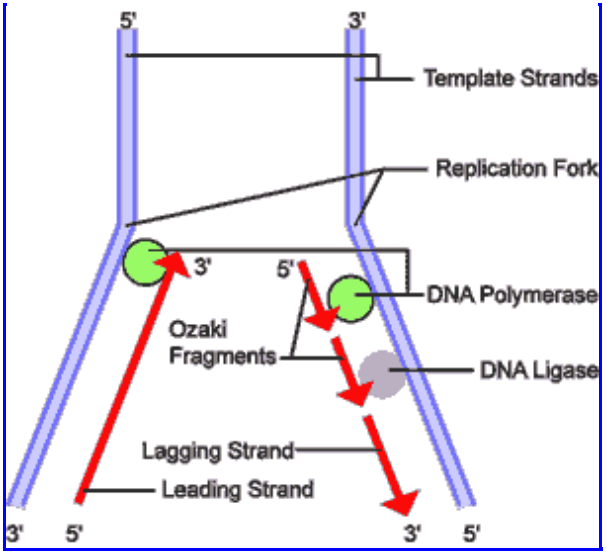
Hsp10: the polypeptide monomer of GroES.

Hsp60: (a) the polypeptide monomer of Class I chaperonins. (b) any Class I chaperonin.

Hsp70: ***see*** DnaK.

L

lagging strand: DNA replication by DNA polymerase requires a short RNA primer sequence and works only in one direction, 5' to 3'. Since the two strands of DNA are antiparallel, this creates a problem. As a DNA helicase separates and unwinds the DNA strands, on one strand, the **leading strand**, the separated strand DNA strand is exposed 3' to 5'. Synthesis of a new antiparallel strand can then proceed from a new 5' end, and follow the helicase without interruption. However, on the other strand, the lagging strand, DNA synthesis must proceed in the reverse direction. This is accomplished by a secondary feature of the helicase. Every 500 or 1000 nucleotides, the helicase stimulates a primase to nick the lagging strand and insert a few RNA nucleotides as a primer. The DNA polymerase then proceeds to replicate that strand—



still 5' to 3' but now in the opposite direction because it is working on the opposite strand of the original DNA. Replication of the lagging strand continues until the polymerase reaches the last point at which the lagging strand was replicated. A DNA ligase then removes the primer from this previous fragment (an **Ozaki fragment**), and zips the two Ozaki fragments together.

leading strand: ***see*** lagging strand.

ligand: a functional group in a molecule. The term usually refers to something relatively small and straightforward, ***e.g.***, a carboxyl group, a phenyl group.

lipoteichoic acid: ***see*** teichoic acid.

LUCA: Last Universal Common Ancestor. The last common ancestor of all extant species: Eubacteria, Archaea, and Eukarya.

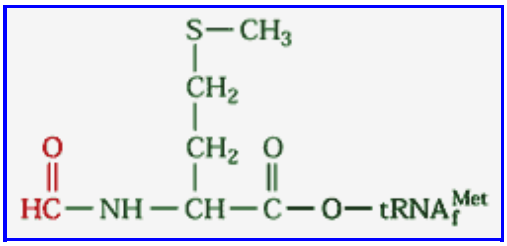
M

mRNA: RNA species which are used as templates to produce proteins (in the process known as ***translation***). Prokaryotic mRNA consists of an unbroken series of nucleotide bases in the triplet genetic code for amino acids.

murein: the cell wall material of Eubacteria, a/k/a peptidoglycan. The structure of murein is discussed here.

N

N-formyl methionine: usually abbreviated fmet, an amino acid derivative used, together with a special $tRNA_f$, to initiate translation. $tRNA_f$ bears the same anticodon as the tRNA for methionine. However, $tRNA_f$ has unique structural features, such as the sequence GCGCGC on the anticodon stem. ***See*** Protein Synthesis: The Ingredients, also the source of the image. fmet is formed from methionine by a specific formyl transferase, using formyl tetrahydrofolate as the formyl group donor. fmet is used only in protein initiation. When the polypeptide translation is complete, fmet is cleaved off. Our understanding is that this occurs in two steps, with the formyl group removed first, then the methionine.



O

Ozaki fragment: ***see*** lagging strand.

P

peptide bond: an amide linkage between two amino acids. ***See***, amino acid.

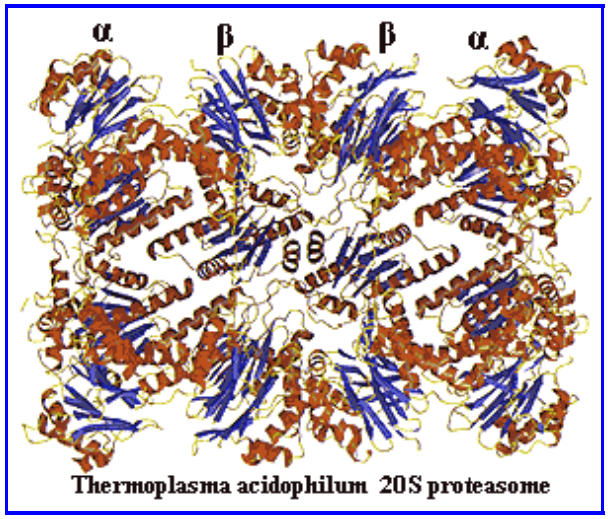
peptidoglycan: the cell wall material of Eubacteria, a/k/a murein. The structure of murein is discussed here.

photosynthesis: a process by which an organism uses energy from light and an (usually) inorganic electron source to reduce organic compounds. There are three major groups of photosynthetic bacteria: cyanobacteria, purple bacteria, and green bacteria. The cyanobacteria carry out **oxygenic photosynthesis**, that is, they use water as an electron donor and generate oxygen during photosynthesis.The photosynthetic system is located in an extensive thylakoid membrane system that is lined with particles called phycobilisomes. The green and purple bacteria carry out anoxygenic photosynthesis. They use reduced molecules such as H_2, H_2S, S, and organic molecules as an electron source and generate NADH and NADPH. In green bacteria, the photosynthetic system is located in ellipsoidal vesicles called chlorosomes that are independent of the cytoplasmic membrane. In purple bacteria, the photosynthetic system is located in spherical or lamellar membrane systems that are continuous with the cytoplasmic membrane. Introduction to Photosynthesis.

polypeptide: any relatively long chain of amino acids linked by peptide bonds. Usually treated as synonymous with "protein," however the term polypeptide is not restricted to structures similar to those produced by organisms.

protease: an enzyme evolved to digest other proteins into their component amino acids.

proteasome: a proteasome is the evil twin of a chaperonin. Like a chaperonin, it is a longitudinally symmetrical series of 7-member rings (but four rings, not two) with a hole through the middle and an affinity for improperly-folded polypeptides. ***Unlike*** a chaperonin, a proteasome does not restore proteins to conformational health and send them on their way. Instead, the proteasome slashes the doomed polypeptide into little 7–13 amino acid oligopeptides so that they may be completely degraded by other proteases. Since its function is reclamation, not rehabilitation, a proteasome lacks any of the bells and whistles of a chaperonin and possesses a much narrower aperture. Thus, only proteins which are more or less completely unfolded can pass into the destructive core of the complex. The basic 20S proteasome is found in Actinobacteria and Archaea. In eukaryotes, the 20S structure forms the core of a 26S proteasome. Image from the Max-Planck-Institut für Biochemie, Abteilung für Strukturforschung.



Thermoplasma acidophilum 20S proteasome

R

ribosomal RNA: ribosomes are the small, but incredibly complex nucleoprotein complexes responsible for protein synthesis. They bind to mRNA molecules from the nucleus and physically move along the molecule, "reading" the code on the mRNA and attaching amino acids to the growing peptide (protein) chain. In eukaryotes there are three, quite distinctive RNA species bound up in the ribosome. These are known by their "Svedberg" numbers, a possibly obsolete measure of relative movement in centrifugation through a density gradient. The three species in prokaryotes are the 5S, 16S and 23S RNAs, ***vide infra***.

ribosomal RNA, 16S or ssu RNA: the RNA molecule associated with the small ribosomal subunit. The secondary structure of typical 16S rRNA is extremely complex. An exhaustive set of maps and sequences can be found at rRNA secondary structure models.

ribosome: the cellular organelle responsible for translating mRNA into protein. Ribosomes are complexes of specialized RNA species and numerous proteins. A really outstanding short explanation of the ribosome can be found at Ribosome Structure and Function.

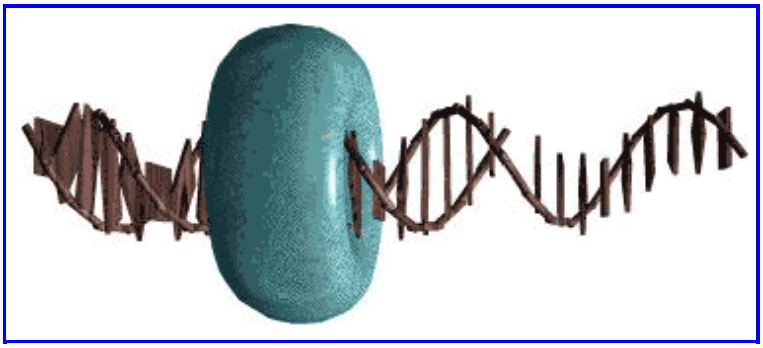
RNA, 4S: ***see*** tRNA.

RNA polymerase: any of the enzyme complexes directly responsible for transcription—the manufacture of

RNA from the DNA template.

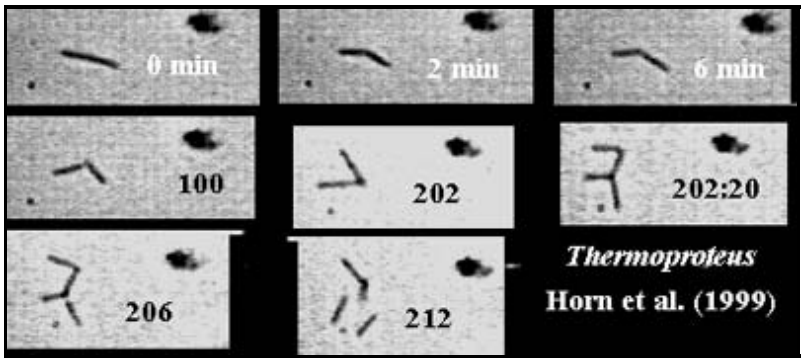
rRNA: ribosomal RNA, ***q.v.***

S

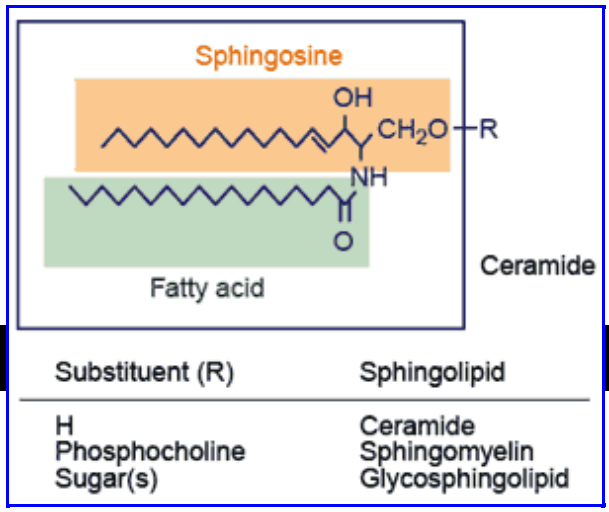


Sliding clamp: the usual toroidal form of the DNA replication complex, including (in Eubacteria) two copies of DNA polymerase III, DNA topoisomerases, and associated proteins. Image from the von Hippel Lab at the University of Oregon.

snapping division: a mode of cell division characterized by rapid horizontal division of an elongated cell with the two daughters finishing at an angle to each other. The daughter cells frequently remain in contact for a period of time. The image shows two rounds of snapping division in ***Thermoproteus***, an archaean, in time lapse photography. From Horn ***et al***. (1999).



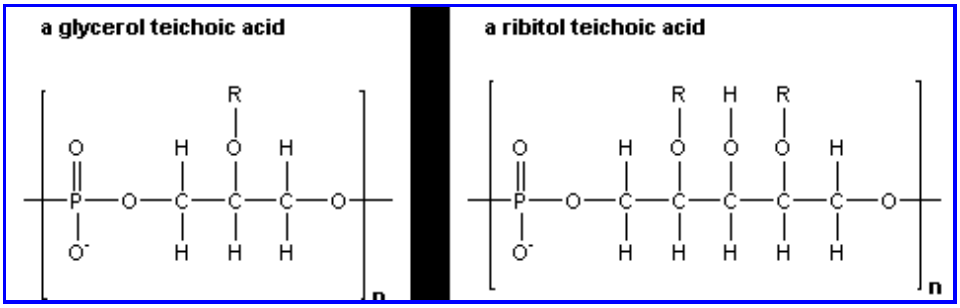
sphingolipid: "All sphingolipids contain a sphingoid long-chain base (***e.g.*** sphingosine) that is linked to a fatty acid molecule through an amide bond, thereby forming the ceramide unit. Addition of phosphocholine or carbohydrates to ceramide leads to sphingomyelin or glycosphingolipids, respectively." General sphingolipid structure.



SSU rRNA: RNA associated with the small ribosomal subunit. "16S" RNA.

T

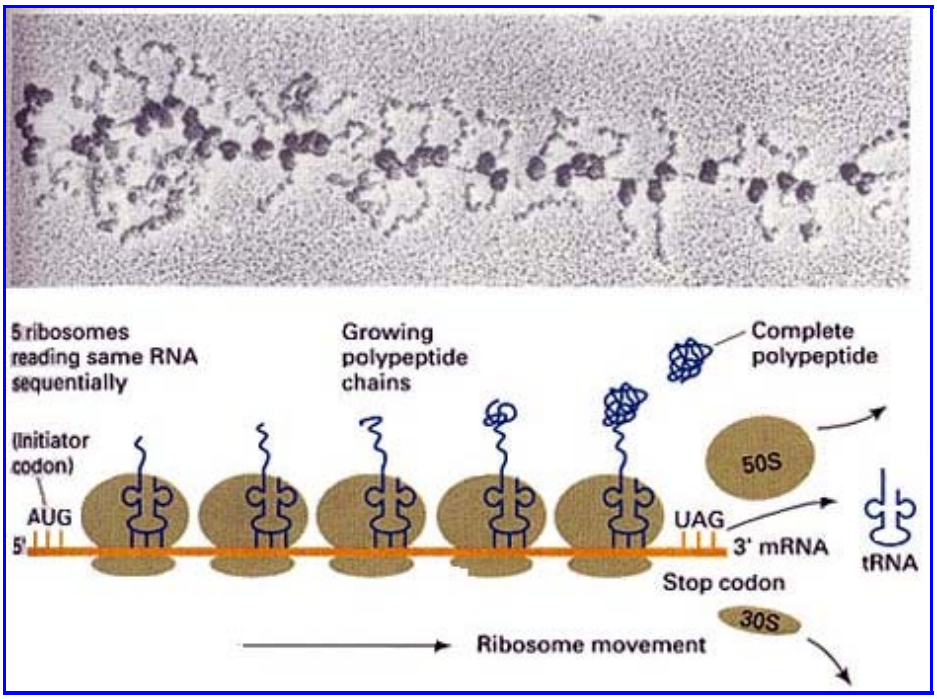
teichoic acid: anionic, phosphate-rich polymers linked to the peptidoglycan of gram-positive bacteria. "They are made up primarily of repeating units of either glycerophosphate or ribitol phosphate molecules that have sugars and D-alanine attached to the glycerol or ribitol backbone. Some teichoic acids are attached to membrane lipids and these are called lipoteichoic acids. All gram-positive organisms contain lipoteichoic acids but some may lack the peptidoglycan bound form." Dr. Stuart Hill's Bios 213 Lecture notes, Lecture 9.



thylakoid: a unit of a stacked, lamellar membrane system in most cyanobacteria on which photosynthesis is carried out.

topoisomerase: ***see*** DNA topoisomerase.

transfer RNA: ***see*** tRNA.

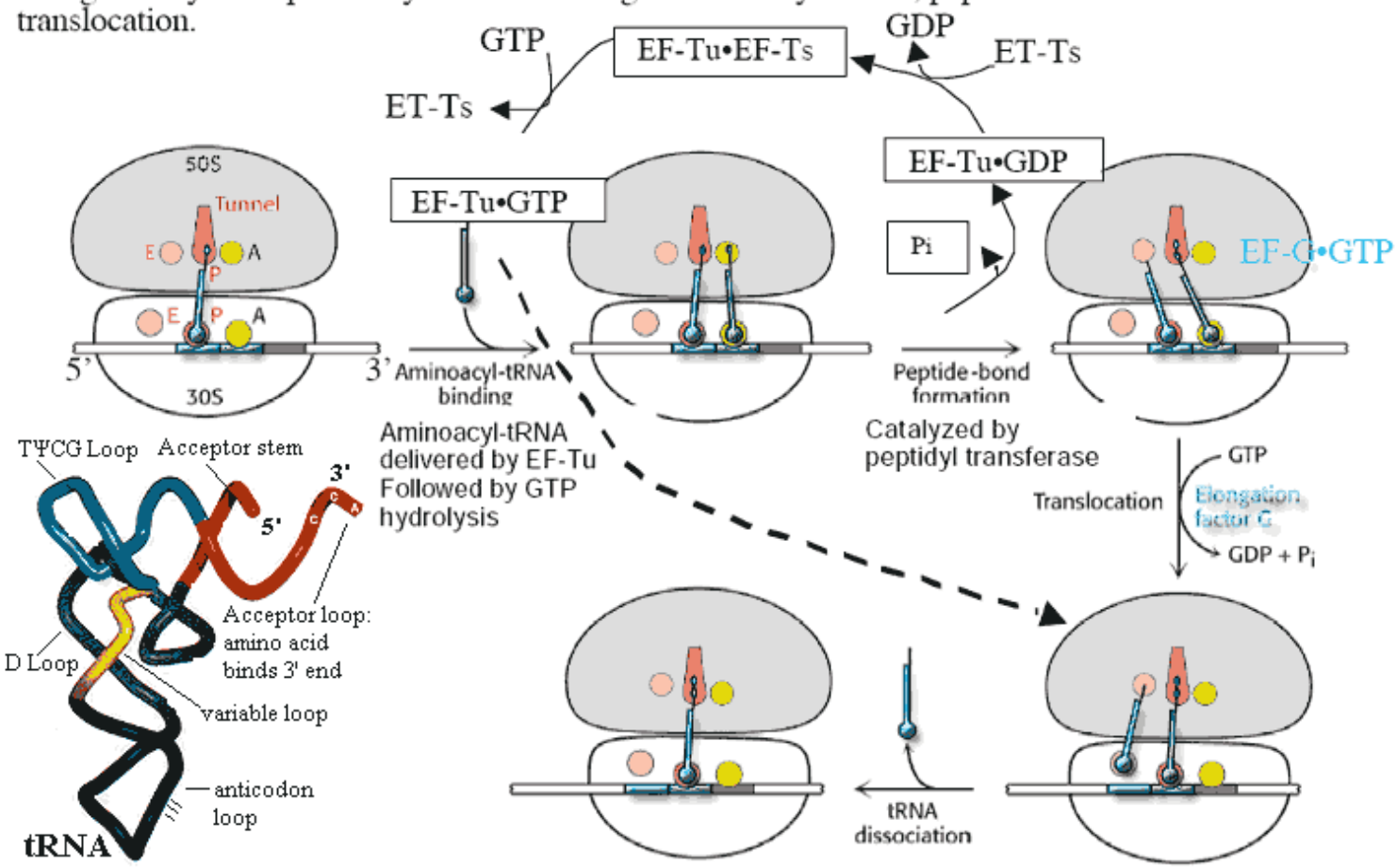


translation: the process whereby the genetic code carried by mRNA is read and used to construct proteins. This process is carried out by ribosomes. The ribosomes recruit appropriate 4S or transfer RNAs (tRNAs) which are (conceptually) molecules with an amino acid at one end and an "anticodon" at the other. The anticodon consists of three nucleotide bases which are the complement of the codon which codes for the tRNA's amino acid. Thus, for example, proline is coded by the sequence CCA. The corresponding $tRNA_{pro}$ would then bear a proline amino acid at one end, and the complementary sequence, ***i.e.*** GGU, at the other. The ribosome sits on the mRNA molecule. If the ribosome detects that the tRNA bases form complementary base pairs with the next mRNA triplet in line, it clips the amino acid off the tRNA and ads it to the growing protein. It then moves up three bases on the mRNA and looks for the next matching tRNA. ***See also*** image at tRNA.

tRNA: 4S RNA. This is the RNA species which actually makes the connection between genetic code and amino acid. There are 61 different tRNA species—one for each of the 64 possible codons except the termination signals. Each tRNA has an anticodon segment, with three exposed bases complementary to a particular codon. Each tRNA can be "charged" with a particular amino acid by a specific amino acyl-tRNA transferase. During translation, the tRNA which bears the appropriate anticodon base pairs with the mRNA which is being translated. The tRNA is then bound to the A-site on the small ribosomal subunit by elongation factor Tu. The ribosome then catalyzes the formation of a peptide bond between the tRNA-bound amino acid and the growing protein chain. Elongation factor G then moves the peptidyl-tRNA complex to the P-site of the ribosome. The tRNA-peptide link is cleaved on arrival of the next tRNA at the A site. The uncharged tRNA then moves to the E site and is released. Specific tRNAs are usually abbreviated with the 3-letter amino acid designation in subscript. Thus the tRNAs for alanine are abbreviated $tRNA_{ala}$. ***See also***, aminoacyl-tRNA.

Elongation Cycle of Protein Synthesis

Elongation cycle of protein synthesis: Binding of aminoacyl-tRNA, peptide bond formation and translocation.



After peptide bond formation, the binding of EF-G•GTP results in an anti-clockwise ratchet-like rotation of the small ribosomal subunit with respect to the 50S subunit. The first step results in the transfer of the peptidyl moiety of the aminoacyl-tRNA from the A site to the P site on the 50S, forming an A/P hybrid state. At the same time the deacylated tRNA in the P site acquires an E/P hybrid state. The second step requires GTP hydrolysis and the 30S subunit reverses in its position, resulting in the placement of the peptidy-tRNA in the P/P site and the deacylated tRNA in the E site. During this movement the mRNA advances so that the next codon is positioned in the A site.

V

V-ATPase: This is the eukaryotic version of the F-ATPase, ***q.v.*** V-ATPase is constructed slightly differently so that the "forward" reaction is favored. That is, it functions as an ATP-dependent ion pump. It is used, for example, to pump protons into digestive vacuoles to maintain very low pH inside the vacuole. V-ATPases are also found in various Archaea and in some Eubacteria which seem to have acquired the archaean species by lateral gene transfer. The archaean version is sometimes referred to as "A-ATPase." Finbow & Harrison (1997)

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References

```
LIFE
|--Eubacteria
|  |--Cyanobacteria
|  `--+--Spirochaeta
|     `--+--Acidobacteria
|        `--+--Eobacteria
|           `--Planctobacteria
`--Neomura
   |--Archaea
   |  |--Eurythermea
   |  `--Neobacteria
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--Metazoa
            |--Deuterostomia
            `--Protostomia
```

References
Notes

A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z

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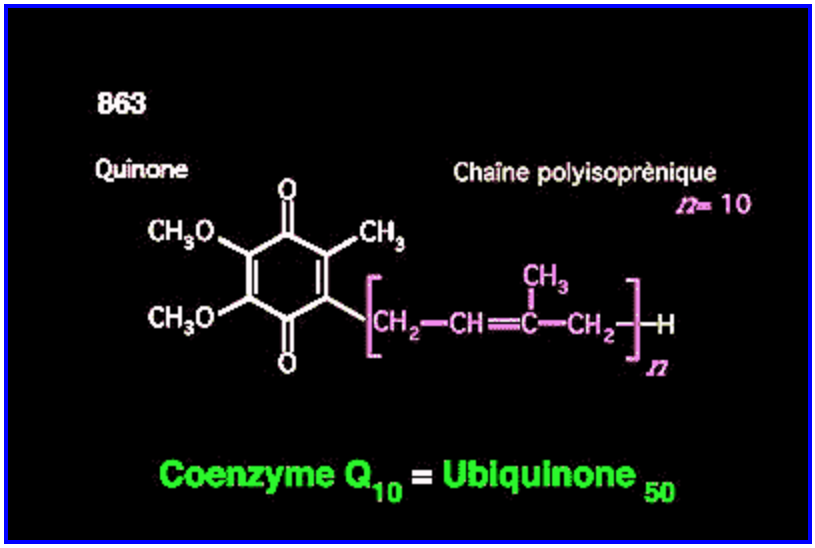
Z

Notes

[1] Where the term 'morphological' characters appears in single quotes, it is used in a broader sense than usual—not just morphological characters ***per se***, but any character that might arguably be used in a phylogenetic analysis the same way as a true morphological character. So synthesis or not of certain proteins, or gene-structural characters such as indels, might also count as 'morphological' characters.

[2] Here's the remedial thermodynamics for those who need it. The magic equation is ΔG = ΔH - TΔS. The free energy (ΔG) needed to get something done at constant temperature is equal to the change in potential energy (enthalpy) between the initial and final states (ΔH) less the absolute temperature multiplied by the change in entropy (TΔS). Entropy is an elegant philosophical and and physical concept which can variously be conceptualized as "disorder" or "randomness," but also "freedom" or "potential number of future states." We pause briefly to allow the philosophical implications to sink in... Ready? Now, consider a simple model of a protein as a chain of paperclips. We know that the final, properly folded state of the protein has low enthalpy because the final state is quite stable. It has to be or the protein could never maintain its useful shape. So ΔH is negative, and the reaction is favored. So far so good. However, if we have to fasten together distant parts of the chain, this drastically reduces the number of states which the chain can assume. This reduces entropy, and the -TΔS term becomes strongly positive, especially under heat stress (higher T), and the conformation change becomes prohibitively expensive in terms of free energy. When the chain is suckered into a small volume, taking due advantage of random fluctuations in shape to accomplish the task, the number of possible conformations is strongly reduced because there is no room to assume extended shapes. Thus the change in entropy needed to make distant parts of the chain interact is no longer so great a problem, and the final state is reached without much grief. (This sounds as if we're getting something for nothing, and reducing total entropy, neither of which happen in thermodynamics. The key is that the GroEL molecule and ATP have to be considered as part of the system.)

[3] c'est-à-dire un alcool avec une longue chaîne composées de plusieurs (une dizaine) unités de 3-mèthyl-2-butene (isoprène). Ça c'est un motif chimique très courrant, par exemple en l'omniprésent co-facteur métabolique ubiquinone. **Image: Faculté de la Pitié Salpêtrière**.



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