

# **Part 1**

## **General Aspects and Documentary Resources**



# 1

## Systems of Classification of Living Organisms: Great Steps in Chemical and Biological Evolution

We start by describing the general principles of the classification of living organisms. The taxonomic system is arranged as a hierarchy going from the kingdom (the most general) down to the species level (the most particular), which comprises the following main groupings, illustrated by the example below (the succession should be read from left to right):<sup>1</sup>

Kingdom	Phylum	Class	Order	Family	Genus	Species
Animal	Chordata	Mammals	Primates	Hominoidea	<i>Homo</i>	<i>sapiens</i>

Considering the biodiversity of life forms on this planet, it is sometimes necessary to consider intermediate groupings as well. Thus, one may sometimes refer to a “superclass” (or subphylum), “superorder” (or subclass), and subspecies (sometimes called a race).

This latter concept is especially useful in chemotaxonomy, which is the study of the relationship between the membership of a species in a given biological group and the chemical composition of this same species in relation to other members of the taxonomic group; one may then speak of a “chemical race”.<sup>2</sup> This concept makes it possible to distinguish between species that are indistinguishable in terms of traditional systematics but which nevertheless exhibit different biochemical, and often biological, characteristics. On the other hand, sometimes a thorough chemical analysis of an organism permits it to be “repositioned” in the traditional taxonomic system. This process would seem to have great potential in the search for various specific chemical structures which it would be fruitless to seek in groups of organisms in which they are lacking; but one should nevertheless be cautious in the use of these relationships – it should always be remembered that in the majority of cases “one only finds what one is looking for”.

### Whittaker’s five kingdoms system (1959)

The traditional dichotomy between the animal kingdom and the plant kingdom has been completely abandoned since the 1960s. Systems of classification have not stopped evolving in the face of advances in microbiology and molecular biology, and it is probable that an “absolute classification system”, based on the genome, will be available before the end of this century.

The merit of Whittaker was to construct a coherent classification system based on two fundamental criteria: the degree of cellular evolution and the mode of reproduction. A study of the first criterion makes it possible to divide the living world into two great “groups”: Monera and Eukaryotes. Monera consist only of primitive cells without a true nucleus, and for this reason they are also called Prokaryotes. Monera are thus almost exclusively represented by unicellular organisms or by certain colonial forms of these primitive cells; the most well-known of these aggregated forms being the Cyanobacteria (Cyanophyceae or blue-green algae). In contrast, Eukaryotes always consist of “advanced” cells containing a nucleus and, unlike Monera, they can be either uni- or multicellular organisms.

After the distinction between prokaryotes and eukaryotes has been made, the second criterion can be applied. According to their mode of reproduction, the eukaryotes can be divided into three separate “groups”: Fungi, Plantae, and Animalia. Fungi have only non-flagellate cells and reproduce by spores, sexually or asexually. Plantae develop from an embryo with alternation of generations: a haploid gametophyte and a diploid sporophyte. As for the Animalia, they have sexual

<sup>1</sup> The Latin “genus–species” unit is always written in italics; the name of the genus always takes a capital initial letter whereas the name of the species never does (e.g. *Homo sapiens*).

<sup>2</sup> However, several different terms are used, such as cohort, suborder, superfamily, tribe or subgenus.

**Tab. 1** Summary of the main characteristics of prokaryote and eukaryote cells\*

Characteristic	Prokaryotes	Eukaryotes
Dimensions	1–10 µm; almost all are unicellular organisms	10–100 µm; uni- and multicellular organisms
DNA	Included in a nucleoid, without a membrane or nucleus; no chromosomes	The presence of a nucleus equipped with a membrane. The nucleus contains chromosomes made of DNA, RNA and proteins (histones)
Cellular organelles	Absent	Present
Cytoskeleton	No	Yes, with microtubules and actin
Enzymes for photosynthesis	Associated in chromatophores bound to the cell membrane. Photosynthesis may be anaerobic or aerobic	Gathered in structures equipped with a membrane: the chloroplasts
Anaerobic/Aerobic**	The majority are anaerobic	Almost all are aerobic
Nitrogen-fixing activity	Yes	No

\* Adapted from Margulis & Schwartz (1998) and Nelson & Cox (2000).  
 \*\* Obligate or facultative.

reproduction, with two haploid gametes giving rise to a diploid zygote, and develop from a blastula (a cluster of cells equipped with a central cavity).

The fifth kingdom of Protocista, is defined only by exclusion. Protocista are uni- or multicellular eukaryotes which are not fungi, plants or animals; it is in this kingdom that the marine algae reside. This fifth kingdom, defined by exclusion rather than having a clear definition, is the weak point of Whittaker's system, which was to evolve into a new system, based on the ternary concept, which is currently used. Whittaker's five kingdoms system was slightly modified by the American biologist Stephen Jay Gould in the mid-1970s. The first criterion remains unchanged, but the second criterion, based on the mode of reproduction, is replaced by a "degree of cell complexity" criterion, which consists simply in separating unicellular from multicellular eukaryotes. The first group are then called Protista<sup>3</sup> and the second group remains divided into fungi, plants and animals.

The third edition of *Five Kingdoms* by Margulis & Schwartz (1998) gives an excellent presentation of the

<sup>3</sup> In order to avoid any confusion with the "Protocista" of Whittaker.

evolution of the concepts underlying various systems for the classification of living organisms.

### Discovery of Archaea (Archaeobacteria): ternary model of living organisms (Woese & Fox, 1977)

In the early 1970s, biologists discovered an unusual group of prokaryote organisms living in "extreme" habitats, such as underwater and terrestrial hydrothermal vents or in hypersaline water. It soon became apparent that certain biochemical characteristics of these new bacteria, in particular the structure of their membrane lipids, were very different from those of "traditional" prokaryotes, and in 1977 the biochemist Carl Woese described them as Archaeobacteria.<sup>4</sup> A ternary classification of the living world therefore became possible by considering only one criterion: the fundamental characteristics of the cell. There thus remain two kingdoms of Prokaryotes and a single kingdom of Eukaryotes. Thanks to the techniques of molecular biology, and hence the study of the nucleotide sequences of ribosomal RNA 16S,<sup>5</sup> very reliable results are being obtained on the evolutionary relationships of the organisms of the three kingdoms. It is generally agreed that there was an "ancestor" common to all of the organisms now living – LUCA (Last Universal Common Ancestor) – which led to the first separation between the Eubacteria and a second "ancestor", which later diversified into Archaeobacteria on the one hand, and Eukaryotes on the other (see Fig. 1).

Within these three kingdoms, biologists currently agree that the following principal divisions can be distinguished, which all have marine representatives.

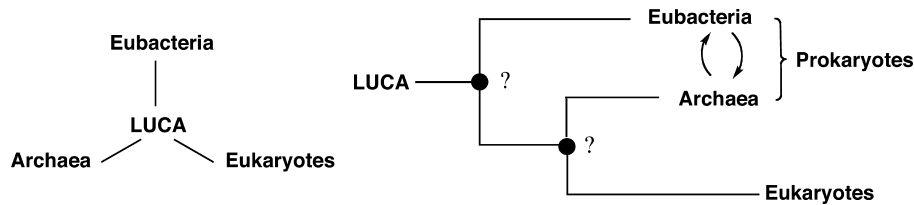
*Archaeobacteria:* Methanogens, Extreme Halophiles, Hyperthermophiles

*Eubacteria:* Proteobacteria, Cyanobacteria, Prochlorophyta

*Eukaryotes:* Protista, Fungi, Plantae, Animalia

<sup>4</sup> The term Archaea is currently preferred to Archaeobacteria, Archaeobacteria, Archeobacteria or Archeobacteria, but all five terms can be found in the literature.

<sup>5</sup> S stands for Svedberg unit of sedimentation velocity by ultracentrifugation (1 S = 10<sup>13</sup> second). Theodor Svedberg (1884–1971), won the Nobel Prize in Chemistry in 1926 for his invention of the ultracentrifuge.



**Fig. 1** Evolutionary diagrams of the three “kingdoms of life”; the right-hand diagram illustrates certain uncertainties about the paraphyly of Archaea (see Chapter 2).

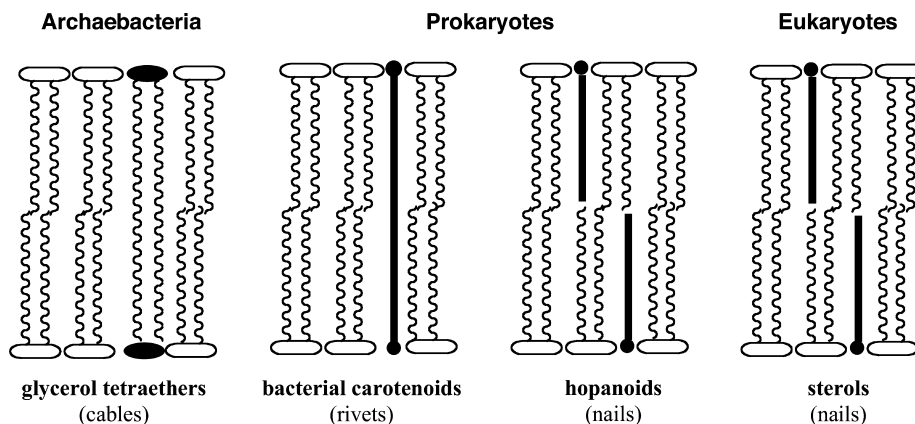
## Characteristics of cell membranes

At the physical interface between the living and non-living, cell membranes are essentially composed of phospholipids, which globally exhibit a structure with a polar hydrophilic end and a non-polar hydrophobic end. The assembly constitutes a kind of “bi-dimensional liquid”, sometimes called a “fluid mosaic model”. The hydrophilic “heads” are immersed in the aqueous medium (water) on each side of the double layer, and the hydrophobic “tails” congregate inside the membrane. The thermodynamic stability of such a “liquid” is maximal for a thickness of 40 Å (4 nm) and the mechanical properties of the membranes result from the combination of the lipids with stabilizing elements, which maintain the cohesion of the assembly. The chemical study of these stabilizing elements allows a clear distinction between the cell membranes of the three fundamental types of organisms.

For archaean membranes, the stabilizing elements are glycerol ethers, mostly tetraethers, with the hydrophobic central part being terpenic, and thus branched out (twice times four units bound “head to head”). For the membranes of other prokaryote cells (Eubacteria) and all eukaryote cells, the hydrophilic part of the stabilizing elements is in this case bound to the hydrophobic part by ester bonds. The stabilizing element of Eu-

bacteria is either a carotenoid – the central part is thus always terpenic, but formed by twice times four units bound “tail to tail” – or a hopanoid. These polycyclic triterpenes are considered to be ancestors of the sterols, which we find as stabilizing elements in all the eukaryote cell membranes. More than 100 sterols are known, which all derive from hopane, a pentacyclic hydrocarbon found in all the sediments, coals and fossil hydrocarbons, everywhere on Earth (Ourisson, 1984, 1986; Ourisson *et al.*, 1994). Therefore, the three fundamental types of cells: Archaeobacteria, Eubacteria and Eukaryotes, whose membranes are entirely formed by a bilayer of phospholipids, differ chemically by the nature of the stabilizing elements of these double layers. There is however a “chemical constancy” in all this: isoprenic units which we find associated in different arrangements, but which are present from archaebacterial lipids to sterols, by way of hopanoids and carotenoids. Figure 2 summarizes the role of these membrane-stabilizing elements.

The membrane phospholipids of Archaea are very complex and contain structural elements unknown in the other membranes such as gulose, aminopentanetrol, sulfuric esters and sulfonic acids, among others (Koga & Morii, 2005). Some more detailed information on these aspects is presented in Chapter 6, which deals with the Archaea.



**Fig. 2** Stabilizing elements of the three fundamental models of cell membranes (according to Ourisson, 1986).

Chemists know how to extract membrane phospholipids in order to study their diverse constituents: which include classes of phospholipids, fatty acids and unsaponifiable elements. The chemical study of membrane phospholipids thus allows confirmation, in a multicellular organism, of the presence of cells characterizing prokaryotic or archaeobacterial symbionts. This is particularly the case for benthic organisms, which live anchored to the seabed or submerged structures and whose nutrients come from the circulation of seawater through their bodies; these include all the sponges and a large number of cnidarians (for example corals). Glycerol ethers and hopanoids have thus been pinpointed

in sponges – the most primitive pluricellular eukaryotes; it is therefore possible to deduce from their presence that these sponges are accommodating Archaeobacteria and/or Eubacteria. It is, on the other hand, more complicated to determine the origin of these substances, which could be a symbiotic relationship or could result from the food web. Figure 3 presents some examples of these various membrane stabilizers.

Let us remember that the isoprene unit is traditionally represented according to the diagram below, with two “heads” and one “tail”, although some authors adopt the reverse convention (one “head” and two “tails”).

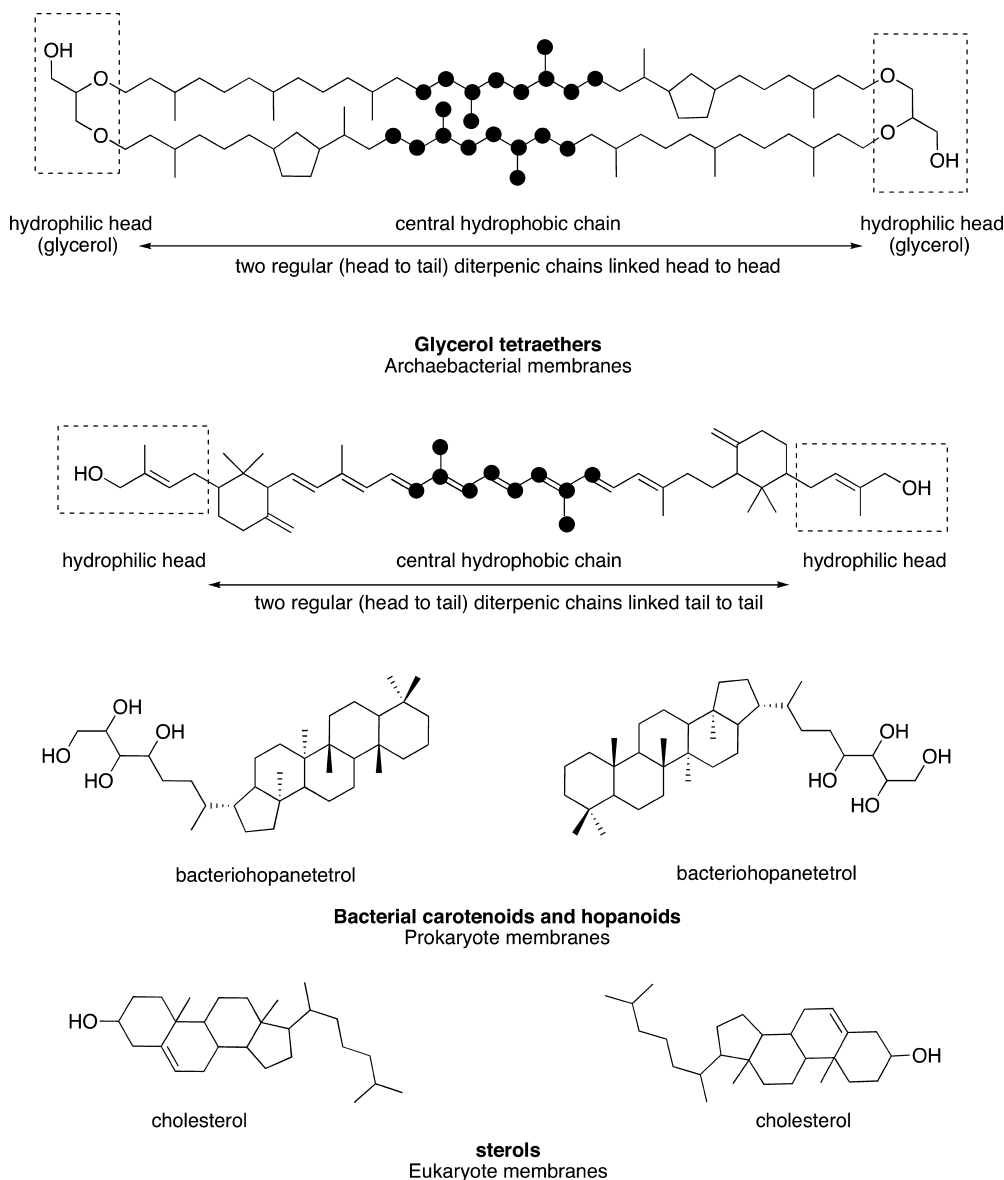
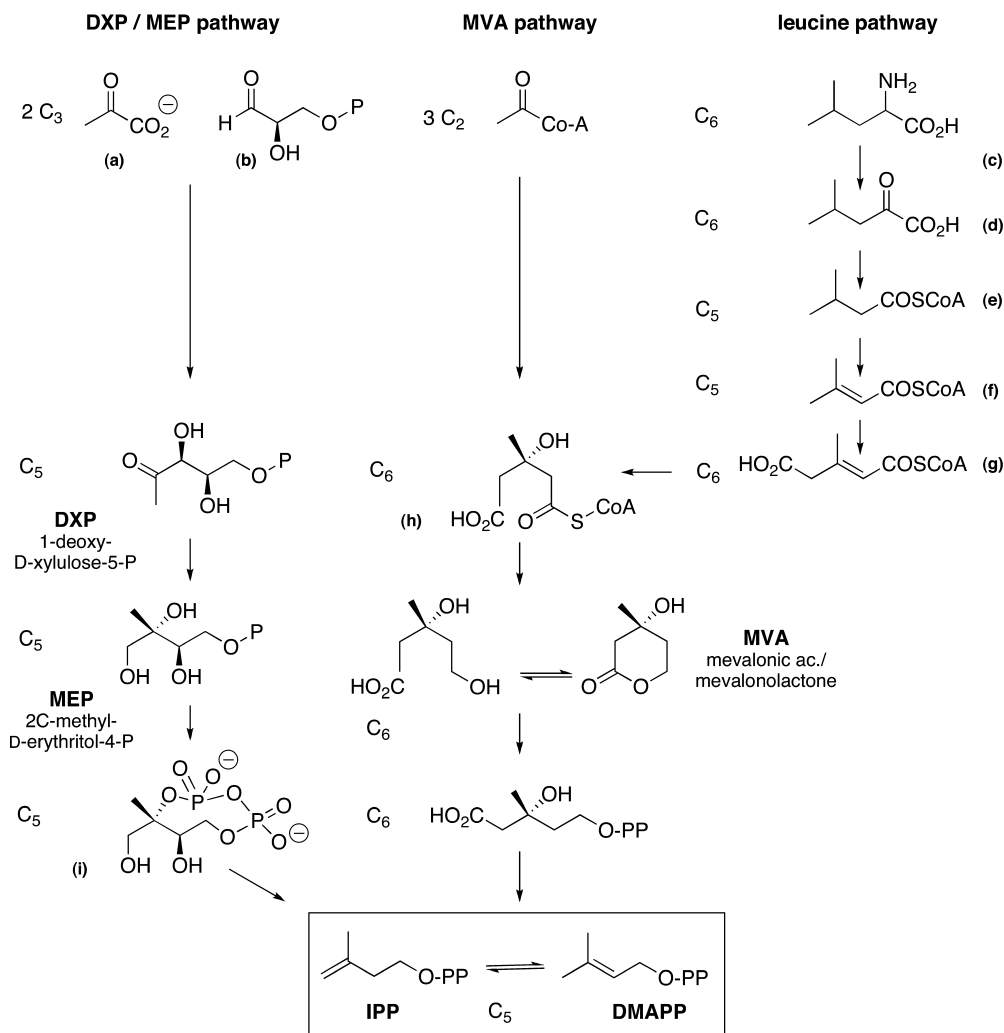


Fig. 3 Examples of various stabilizers of cell membranes.



(a): acetylcoenzyme A ; (b): glyceraldehyde-3-phosphate ; (c): leucine ; (d) α-ketoisocaproic acid  
 (e): isovalerylcoenzyme A ; (f): 3-methylcrotonylcoenzyme A ; (g): 3-methylglutaconylcoenzyme-A  
 (h): 3-methyl-3-hydroxy-glutarylcoenzyme A ; (i) 2-C-methyl-D-erythritol-2,4-diphosphate

Fig. 4 Biosynthetic pathways for terpenes.



## Some recent data on terpenes

Terpenes (i.e. all the components formed starting from isoprene units) are very numerous in nature and their number is estimated at approximately 23,000. Terpenes are still defined as products of the metabolism of isopentenyl diphosphate (formerly pyrophosphate), which

comes from acetylcoenzyme-A by means of a metabolic pathway that has been studied in great detail: the mevalonic acid pathway (MVA). This definition has become ambiguous since 1988, when Rohmer and his team showed that another pathway of biosynthesis of biological isoprene units – isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP)<sup>6</sup> – was carried out by certain Eubacteria by way of pyruvic acid and 3-phosphate D-glyceraldehyde. The condensation of these two

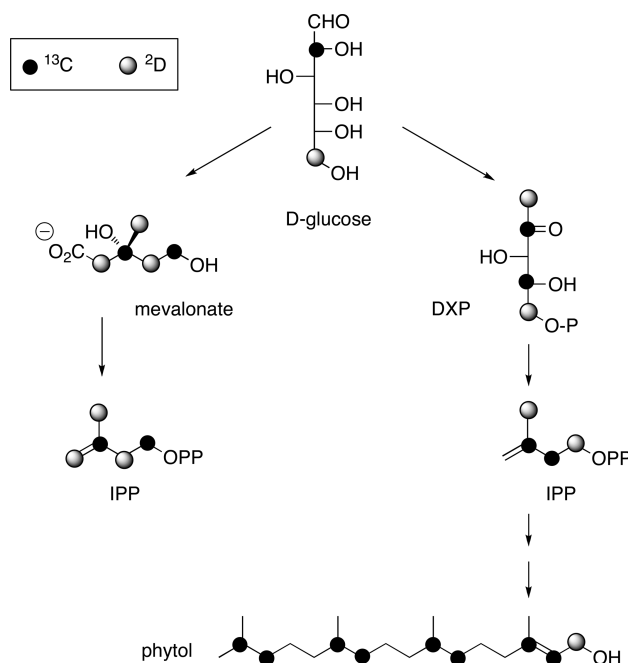
<sup>6</sup> The acronyms IPP and DMAPP are well known and are still used, although they refer to the term pyrophosphate instead of diphosphate.

precursors, followed by the loss of a carbon dioxide molecule, leads to an intermediate with five carbon atoms, 1-deoxy-D-xylulose-5-phosphate (DXP or DOXP). This is later transformed into another five-carbon derivative, 2-C-methyl-D-erythritol-4-phosphate (MEP), which finally gives isopentenyl diphosphate. This new pathway for the biosynthesis of terpenes is summarized by the initials DXP/MEP or DOXP/MEP, and is now simplified as MEP.

During the last decade of the 20th century, this new biosynthetic pathway has been intensively studied and it is now established that it is not limited to Eubacteria (Prokaryotes), but that it also occurs in many eukaryote organisms such as *Plasmodium falciparum*, the agent of malaria. The MEP pathway is present in the majority of bacteria, and some of them, such as *Streptomyces* sp., have both the MEP and the MVA pathways, which are expressed differently from each other. The MEP pathway leads to the production of menaquinone prenylated chains, and the MVA pathway leads to the prenylated chains of the secondary metabolites, which have antibiotic activity (Rohmer, 2003). In the algae and higher plants, the MVA pathway is localized in the cytoplasm and leads to ubiquinones, to triterpenes, and to sterols, whereas the MEP pathway is localized in the chloroplasts. Among the non-photosynthetic organisms, the MEP pathway has been shown to occur in some Api-complexa such as *Plasmodium falciparum*, which makes it reasonable to suppose that the search for enzyme inhibitors of the stages of the MEP pathway could lead to new antimalarial compounds (Cassera *et al.*, 2004). Several articles and developments on these two biosynthetic pathways of terpenes have been published (in particular those of Rohmer *et al.*, 1993; Rohmer, 1999, 2003, 2008; Bochar *et al.*, 2001; Eisenreich *et al.*, 2001; Fellermeier *et al.*, 2001; Rohdich *et al.*, 2001; Dubey *et al.*, 2003; Kuzuyama & Seto, 2003; Meyer *et al.*, 2003; Kashman & Rudi, 2004; Dudareva *et al.*, 2005).

Lastly, a third pathway leading to the biological isoprene units starting from leucine is highlighted in the parasitic Protozoan *Leishmania mexicana* and in both Myxobacteria, *Myxococcus xanthus* and *Stigmatella aurantiaca*. For euglenobionts, leucine is a constituent of sterols (Ginger *et al.*, 2001) and, for the two bacteria, leucine labelled with deuterium was found to be a component in a sesquiterpene and one of its degraded derivatives, geosmin (Dickschat *et al.*, 2005; see also Chapter 8, p. 151). Myxobacteria also incorporate leucine, isoleucine and valine in *iso*- and *anteiso*- long-chain fatty acids, which are frequent in sponges (Bode *et al.*, 2005; see also Chapter 19).

These three biosynthetic pathways leading to terpenes and sterols are summarized in Figures 4 and 5, which show, as a concrete example, the biosynthesis of phytol



**Fig. 5** Biosynthesis of phytol by the non-mevalonic pathway in the cyanobacterium *Synechocystis* sp. UTEX 2470<sup>7</sup> (according to Proteau, 1998).

following the MEP pathway by the Cyanobacteria *Synechocystis* sp.

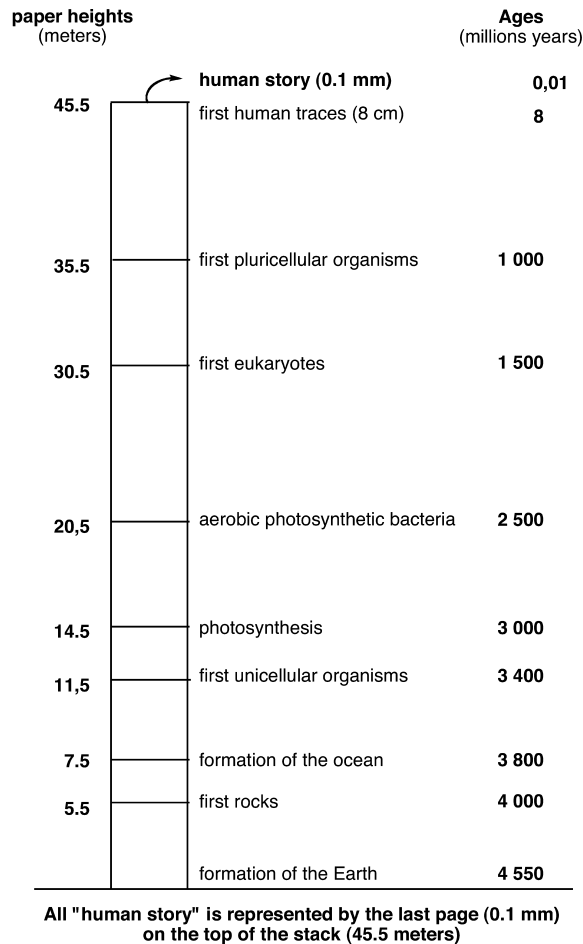
## Main stages of evolution

In a synthetic way, one can distinguish three principal phases of evolution:

- From the formation of the ocean to the first eukaryote cell: *chemical evolution*
- From monocellular eukaryotes to humans: *biological evolution*
- The “human adventure”: *cultural evolution*

The common thread joining these three stages is the progressive control of the environment – from organisms that do not have any means of perceiving the environment in which they live, to human beings who have the ability to modify and, to some extent, control it, ranging from some local improvements to the total destruction of the planet. We illustrate the great stages of chemical and biological evolution by using the visual time scale of the vulcanologist Haroun Tazieff (1914–

<sup>7</sup> The abbreviation UTEX means that the stock comes from the University of Texas; Figure 5 summarizes labelling experiments carried out with <sup>13</sup>C-labelled 1-<sup>13</sup>C-D-glucose, 6,6-<sup>2</sup>H<sub>2</sub>-D-glucose, and 2-<sup>13</sup>C-D-glucose.



(0.1 mm = 10,000 years, 1 million years = 1cm, 1 billion years = 10 meters of paper)

**Fig. 6** Main stages of evolution: scale of time according to H. Tazieff. For more detailed data on the dates, see De Reviere (2002, Vol. 1, p. 105) and Pinti & Marty (2002).

1998), whereby time is represented by imagining a stack of sheets of paper each 0.1 mm thick, where each one represents 10,000 years, i.e. the entirety of human history since the Neolithic Revolution. Using this imagery, the principal stages of evolution are visualized in Figure 6.

Although the theories explaining the appearance of water on Earth are still the subject of debate, the whole of the oceans appeared soon after the formation of our planet and it took even less time – approximately 200 million years – until the first prokaryote cells appeared. These were obviously strict anaerobes, since oxygen did not yet exist in the atmosphere. Approximately 400 million years later, certain prokaryote cells “invented” the process of photosynthesis which, very slowly, produced oxygen, which now seems to have stabilized at about 21% of the atmospheric gases. It is undoubtedly thanks to oxygen that the anaerobic primitive cells evolved into

aerobic prokaryotes, and the Cyanobacteria (which for a long time were called blue-green algae) can be regarded as our true ancestors. The aerobic prokaryotes then evolved into eukaryotes thanks to another spectacular “invention” – the cell nucleus – which nevertheless required 1 billion years. At that stage one can consider that the chemical evolution stage is complete and the biological evolution stage is about to begin. However, nearly two and a half billion years will have been necessary to take us from the first anaerobic prokaryotes to the first pluricellular organisms that are entirely composed of eukaryote cells and are all aerobes. This stage was the longest of all the stages in the history of life, and one of the reasons why it took so long is perhaps related to the fundamental problem of the recognition of self-awareness, or at least the recognition of the distinction between self and non-self.

The biological evolution started in the ocean with the diversification of all the eukaryotes then, gradually, these organisms became adapted to freshwater by means of the estuaries, then rivers, and finally, some organisms “left the water”, adapted to an air-breathing way of life and went on to conquer the terrestrial realm. Despite the immense diversity of multicellular organisms on Earth, the kingdom of the Eukaryotes is, in fact, very recent because they have all appeared in the last billion years, although many of them – like the dinosaurs – have now completely disappeared. On the other hand, a considerable diversity of very primitive organisms, the two Kingdoms of Archaeobacteria and Eubacteria, appeared nearly three and a half billion years ago, are still very much present, and are widely distributed throughout the globe.

## Exceptional resources of marine biodiversity

All forms of life first appeared in the oceans and are still there, from Archaea to mammals, which explains why marine biodiversity is much richer than terrestrial and freshwater biodiversity. This marine biodiversity is examined in more detail in the following chapters but, generally speaking, although it can be observed that there is a greater biodiversity in phyla and genera in the marine environment than in the terrestrial environment, at the species level it is a different story and the biodiversity within species is greater on the ground than in the oceans. The reason usually put forward is that the marine environment is, overall, more constant, and therefore species have evolved very little within the same phylum. On the other hand, on the ground, the

very large variety of biotopes has resulted in a vast amount of adaptation in species belonging to the same order or the same family, or even the same genus.

## Selection of documentary resources

For the first general chapters of this work the references are presented according to the order in which the topics are presented within each chapter. The literature on these various aspects is particularly plentiful and the chosen references, far from being exhaustive, simply reflect the personal preference of the author.

## References

### *Systems of classification of living organisms*

- De Reviere B. (2002). *Biologie et phylogénie des algues*, Belin, Paris, Volume 1, 352 pp.
- Gould S.J. (1977). *Ever since Darwin: Reflections in National History*, Norton and Company, New York. See, in particular, chapter 13.
- Lecointre G., Le Guyader H. (2001). *Classification phylogénétique du vivant*, Belin, Paris, 543 pp. The 3rd edition of this work was published in 2006, 560 pp.
- Le Gal Y. (1991). Diversité des organismes marins, *Biofutur*, November, 12–13.
- Margulis L., Schwartz K.V. (1998). *Five Kingdoms*, 3rd Ed., W.H. Freeman and Co., San Francisco, 520 pp. This book is accompanied by a CD ROM.
- Selosse M.A. (2005). Quelle parenté entre les trois grandes lignées du vivant? *Les Dossiers de La Recherche*, 19: 42–45. This article is a part of a very interesting special issue dedicated to "The History of Life".
- Whittaker R.H. (1959). On the broad classification of organisms, *Quater. Rev. Biol.*, 34: 210–226.
- Woese C.R., Fox G.E. (1977). Phylogenetic structure of the prokaryotic domain: the primary kingdoms, *Proc. Natl. Acad. Sci. USA*, 74: 5088–5090.

### *Archaea (Archaeobacteria)*

- Forterre P. (1990). Rencontre du troisième type: les Archaeobactéries, *Science et Vie*, 173: 30–42.
- Forterre P. (1991). Les origines de la vie, *Biofutur*, November, 14–17.
- Forterre P. (1999). Les hyperthermophiles sont-ils nos ancêtres? *La Recherche*, 317: 36–43.
- Grant W.D., Pinch G., Harris J.E., De Rosa M., Gambacorta A. (1985). Polar lipids in methanogenic taxonomy, *J. Gen. Microbiol.*, 131: 3277–3286.
- Langworthy T.A. (1982). Lipids of bacteria living in extreme environments, *Current Topics in Membranes and Transport*, 17: 45–77.
- Madigan M., Mairs B. (1997). Les organismes de l'extrême, *Pour la Science*, 236: 86–92.
- Mancuso C.A., Odham G., Westerdahl G., Reeve J.N. White D.C. (1985). C15, C20 and C25 isoprenoid homologues in glycerol diether phospholipids of methanogenic archaeobacteria, *J. Lipid Res.*, 26: 1120–1125.

- Martin W. (2005). Archaeobacteria (Archaea) and the origin of the eukaryotic nucleus, *Curr. Opin. Microbiol.*, 8: 630–637.
- Ourisson G., Albrecht P., Rohmer M. (1984). L'origine microbienne des combustibles fossiles, *Pour la Science*, October, 56–66.
- Ourisson G., Nakatani Y., Plobeck N., Brisson A., Schmutz M., Biraault V., Pozzi G., Eifler S. (1994). Comment étaient constituées les membranes les plus primitives?, in: *Les Systèmes moléculaires organisés*, Images de la recherche, 2, CNRS, pp. 83–86. This work also contains many other articles relating to cellular membranes.
- Purves W.K., Heller H.C., Orians G.H., Sadava D. (1998). *Life: The Science of Biology*, 5th Ed., Sinauer Associates, Sunderland MA. See, in particular, chapters 24 (Origins of the life on Earth), 25 (Bacteria and Archaea: domain Prokaryotes) and 26 (Protists and the dawn of Eukaryotes).
- Schleper C. (1999). Les Archaeobactéries sont parmi nous, *La Recherche*, 317: 30–33.
- Woese C.R. (1987). Bacterial evolution, *Microbiol. Rev.*, 51: 221–271.

### *Cell membranes, lipid membranes*

- Barenholz Y. (2002). Cholesterol and other membrane active sterols: from membrane evolution to "rafts", *Prog. Lipid Res.*, 41: 1–5.
- Bretscher M. (1988). Les molécules de la membrane cellulaire, in: *Les molécules de la vie*, Bibliothèque Pour la Science, Diffusion Belin, Paris, pp. 62–71. This work contains a whole series of articles on cellular membranes.
- Duve de C. (1987). La surface cellulaire, avec une introduction aux membranes et aux lipides, in: *Une visite guidée de la cellule vivante*, Bibliothèque Pour la Science, Belin, Paris, pp. 41–52.
- Kates M. (1986). *Techniques of Lipidology*, Elsevier, Amsterdam, Oxford, New York, 464 pp.
- Koga Y., Morii H. (2005). Recent advances in structural research on ether lipids from Archaea including comparative and physiological aspects, *Biosci. Biotechnol. Biochem.*, 69: 2019–2034.
- Moldoveanu N., Kates M., Montero C.G., Ventosa A. (1990). Polar lipids of non-alkaliphilic Halococci, *Biochim. Biophys. Acta*, 1046: 127–135.
- Nelson, D.L., Cox M.M. (2000). *Lehninger Principles of Biochemistry*, Third Ed., Worth Publishers, New York, Chap. 2, p. 29.
- Ohvo-Rekilä H., Ramstedt B., Leppimäki P., Slotte J.P. (2002). Cholesterol interactions with phospholipids in membranes, *Prog. Lipid Res.*, 41: 66–97.
- Ourisson G. (1986). Des pétroles à l'évolution des biomembranes, *L'actualité chimique*, May, 23–30.
- Prasad R. (1996). *Manual on Membrane Lipids*, Springer-Verlag, Heidelberg, Germany, 224 pp.
- Purves W.K., Heller H.C., Orians G.H., Sadava D. (1998). *Life: The Science of Biology*, 5th Ed., Sinauer Associates, Sunderland MA. See, in particular, chapters 4 (Organization of cells) and 5 (Cellular membranes).
- Sargent J.R. (1989). Ether-linked glycerides in marine animals, in: *Marine Biogenic Lipids, Fats, and Oils*, R.G. Ackman, Ed., CRC Press, Boca Raton, Vol. 1, pp. 175–198.
- Van de Vossenbergh J., Driessen A. J.-M., Konings W.N. (1999). La survie à l'abri des membranes, *La Recherche*, 317: 54–56.
- Vigh L., Escribá P.V., Sonnleitner A., Sonnleitner M., Piotto S., Maresc B., Horváth I., Harwood J.L. (2005). The significance of lipid composition for membrane activity: new concepts and ways of assessing function, *Prog. Lipid Res.*, 44: 303–344.

### Hopanoids and biosynthesis pathways of terpenes

- Bochar D.A., Friesen J.A., Stauffacher C.V., Rodwell V.W. (1999). Biosynthesis of mevalonic acid from acetyl-CoA, in: *Comprehensive Natural Products Chemistry*, Sir D.H. Barton, K. Nakanishi, Eds., Elsevier, Amsterdam, Oxford, New York, Vol. 2, pp. 15–44.
- Bode H.B., Dickschat J.S., Kroppenstedt R.M., Schulz S., Müller R. (2005). Biosynthesis of iso-fatty acids in myxobacteria: iso-even fatty acids are derived by  $\alpha$ -oxidation from iso-odd fatty acids, *J. Am. Chem. Soc.*, **127**: 532–533.
- Cassera M.B., Gozzo F.C., D'Alexandri F.L., Merino E.F., del Portillo H.A., Peres V.J., Almeida I.C., Eberlin M.N., Wunderlich G., Wiesner J., Jomaa H., Kimura E.A., Katzin A.M. (2004). The methylerythritol phosphate pathway is functionally active in all intraerythrocytic stages of *Plasmodium falciparum*, *J. Biol. Chem.*, **279**: 51749–51759.
- Dickschat J.S., Bode H.B., Mahmud T., Müller R., Schulz S. (2005). A novel type of geosmin biosynthesis in myxobacteria, *J. Org. Chem.*, **70**: 5174–5182.
- Dubey S., Bhalla R., Luthra R. (2003). An overview of the non-mevalonate pathway for terpenoid biosynthesis in plants, *J. Biosci.*, **28**: 637–646.
- Dudareva N., Andersson S., Orlova I., Gatto N., Reichelt M., Rhodes D., Boland W., Gershenzon J. (2005). The nonmevalonate pathway supports both monoterpene and sesquiterpene formation in snapdragon flowers, *Proc. Natl. Acad. Sci. USA*, **102**: 933–938.
- Eisenreich W., Rohdich F., Bacher A. (2001). Deoxyxylulose phosphate pathway to terpenoids, *Trends Plant Sci.*, **6**: 78–84.
- Fellermeier M., Raschke M., Sagner S., Wungsintaweekul J., Schuhr C.A., Hecht S., Kis K., Radykewicz T., Adam P., Rohdich F., Eisenreich W., Bacher A., Arigoni D., Zenk M.H. (2001). Studies on the non-mevalonate pathway of terpene biosynthesis: the role of 2C-methyl-D-erythritol 2,4-cyclodiphosphate in plants, *Eur. J. Biochem.*, **268**: 6302–6310.
- Ginger M.L., Chance M.L., Sadler I.H., Goad L.J. (2001). The biosynthetic incorporation of the intact leucine skeleton into sterol by the trypanosomatid *Leishmania mexicana*, *J. Biol. Chem.*, **276**: 11674–11682.
- Kashman Y., Rudi A. (2004). On the biogenesis of marine isoprenoids, *Phytochem. Rev.*, **3**: 309–323.
- Kuzuyama T., Seto H. (2003). Diversity of the biosynthesis of the isoprene units, *Nat. Prod. Rep.*, **20**: 171–183.
- Meyer O., Grosdemange-Billiard C., Tritsch D., Rohmer M. (2003). Isoprenoid biosynthesis via the MEP pathway. Synthesis of (3R,4S)-3,4-dihydroxy-5-oxohexylphosphonic acid, an isosteric analogue of 1-deoxy-D-xylulose 5-phosphate, the substrate of the 1-deoxy-D-xylulose 5-phosphate reducto-isomerase, *Org. Biomol. Chem.*, **1**: 4367–4372.
- Ourisson G., Albrecht P. (1992a). Hopanoids. 1. Geohopanoids: the most abundant natural products on earth? *Acc. Chem. Res.*, **25**: 398–402.
- Ourisson G., Albrecht P. (1992b). Hopanoids. 2. Biohopanoids: a novel class of bacterial lipids, *Acc. Chem. Res.*, **25**: 403–408.
- Ourisson G., Rohmer M., Poralla K. (1987). Prokaryotic hopanoids and other polyterpenoid sterol surrogates, *Annu. Rev. Microbiol.*, **41**: 301–333.
- Proteau P.J. (1998). Biosynthesis of phytol in the cyanobacterium *Synechocystis* sp. UTEX 2470: utilization of the non-mevalonate pathway, *J. Nat. Prod.*, **61**: 841–843.
- Rohdich F., Kis K., Bacher A., Eisenreich W. (2001). The non-mevalonate pathway of isoprenoids: genes, enzymes and intermediates, *Curr. Opin. Chem. Biol.*, **5**: 535–540.
- Rohmer M. (1999). A mevalonate-independent route to isopentenyl diphosphate, in: *Comprehensive Natural Products Chemistry*, Sir D.H. Barton, K. Nakanishi, Eds., Elsevier, Amsterdam, Oxford, New York, Vol. 2, pp. 45–67.
- Rohmer M. (2003). Mevalonate-independent methylerythritol phosphate pathway for isoprenoid biosynthesis: elucidation and distribution, *Pure Appl. Chem.*, **75**: 375–387.
- Rohmer M. (2008). From molecular fossils of bacterial hopanoids to the formation of isoprene units: discovery and elucidation of the methylerythritol phosphate pathway, *Lipids*, **43**: 1095–1107.
- Rohmer M., Knani M., Simonin P., Sutter B., Sahn H. (1993). Isoprenoid biosynthesis in bacteria: a novel pathway for the early steps leading to isopentenyl diphosphate, *Biochem J.*, **295**: 517–524.

### The major stages of evolution

- A special issue of *La Recherche*, entitled: "The History of Life: 3 Billion Years of Evolution" (No. 296, March 1997), contains numerous articles concerning the various points touched on in this introductory chapter, and there is also a great deal to be learned from the following books and articles:
- Blandin P., Ed. (1996). *L'Évolution*, Bordas, Muséum National d'Histoire Naturelle, Paris, 96 pp.
- Brack A. (1990). Les premiers signes de vie, in: *L'Évolution, la naissance des espèces*, Sciences et Vie, 173, pp. 22–29.
- Brack A., Raulin F. (1991). *L'évolution chimique et les origines de la vie*, Masson, Paris, 181 pp.
- Cairns-Smith A. (1985). Les premiers organismes vivants, *Pour la Science*, August, 24–33.
- Dejours P. (1982). La vie dans l'eau et dans l'air, in: *La physiologie des animaux*, Bibliothèque Pour la Science, Diffusion Belin, Paris, pp. 18–26.
- De Reviers B. (2002). *Biologie et phylogénie des algues*, Belin, Paris, Volume 1, 352 pp.
- De Ricqlès A. (2005). L'évolution selon Gould, *Les Dossiers de La Recherche: L'histoire de la vie*, **19**: 14–21.
- Dickerson R. (1978). L'évolution chimique et l'origine de la vie, in: *L'Évolution*, Bibliothèque Pour la Science, Diffusion Belin, pp. 17–35.
- Doolittle F. (2000). L'arbre du vivant: un buisson foisonnant, *Pour la Science*, **270**: 84–89.
- Duve de C. (1998). La naissance des cellules complexes, in: *Les sociétés cellulaires*, Dossier pour la Science, 19, pp. 14–21.
- Forterre P. (1997). A la recherche de l'ancêtre de toutes les cellules, in: *L'Évolution*, Dossier Pour la Science, 14, pp. 88–92.
- Gould S.J. (1994). L'évolution de la vie sur la Terre, *Pour la Science*, **206**: 90–98.
- Halstead L.B. (1984). *A la recherche du passé: La vie sur la Terre, des origines aux premiers hommes*, Hachette, Paris, 207 pp.
- Hazen R. (2001). Les minéraux et la naissance de la vie, *Pour la Science*, **284**: 38–44.
- Knoll A. (2000). De la vie primitive aux êtres macroscopiques, in: *La valse des espèces*, Dossier Pour la Science, 28, pp. 28–35.
- Levinton J. (1997). Le Big Bang de l'évolution animale, in: *L'Évolution*, Dossier Pour la Science, pp. 48–55.
- Maurette M. (2002). L'origine cosmique de l'air et des océans, *Pour la Science*, **291**: 36–43.
- Orgel L. (1994). L'origine de la vie sur la Terre, *Pour la Science*, **206**: 80–88.
- Pinti D.L., Marty B. (2002). La mer est tombée du ciel, in: *La Mer*, No. spécial 335, La Recherche, pp. 14–17.
- Purves W.K., Heller H.C., Orians G.H., Sadava D. (1998). *Life: The Science of Biology*, 5th Ed., Sinauer Associates, Sunderland MA. See in particular Parts III (Process of Evolution) and IV (Evolution and Variety).

- Rossello-Mora R., Amann R. (2001). The species concept for prokaryotes, *FEMS Microbiol. Rev.*, 5: 39–67.
- Schopf W. (1978). L'évolution des premières cellules, in: *L'Evolution*, Bibliothèque Pour la Science, Diffusion Belin, pp. 65–83.
- Schwartz A.W. (1981). Chemical evolution: the genesis of the first organic compounds, in: *Marine Organic Chemistry*, E. K. Duursma, R. Dawson, Eds., Elsevier Oceanographic Series, Amsterdam, Oxford, New York, 31, pp. 7–30.
- Valentine J. (1978). L'évolution des plantes et des animaux pluricellulaires, in: *L'Evolution*, Bibliothèque Pour la Science, Diffusion Belin, pp. 84–97.

## Websites

- <http://eaps.mit.edu/geobiology/biomarkers/hopanoids.html>  
About biomarkers. Part of a site of the MIT (Massachusetts Institute of Technology, Boston, MA) dedicated to geobiology.
- [http://www-archbac.u-psud.fr/meetings/lestreilles/treilles\\_frm.html](http://www-archbac.u-psud.fr/meetings/lestreilles/treilles_frm.html)  
A la recherche de LUCA.
- <http://www.ucmp.berkeley.edu/archaea/archaeasy.html>  
Archaea: Systematics.
- <http://library.thinkquest.org/C004367/be.shtml>  
Biological Evolution.
- <http://www.answers.com/topic/carl-woese>  
Carl Woese.
- [http://library.thinkquest.org/C004535/cell\\_membranes.html](http://library.thinkquest.org/C004535/cell_membranes.html)  
Cell Anatomy.
- <http://www.johnkyrk.com/cellmembrane.html>  
Cell Membranes.
- <http://www.biologie.uni-hamburg.de/b-online/library/onlinebio/BioBookCELL1.html>  
Cells: origin.
- <http://www.tutorvista.com/content/biology/biology-iii/modern-classification/five-kingdom-classification.php>  
Five Kingdom Classification.
- <http://www.ibs.fr/>  
Institut de Biologie Structurale Jean-Pierre Ebel (CEA-CNRS). A site that is very rich in diverse information, in particular that concerning extremophile bacteria.
- <http://webiologie.free.fr/cellules/domaines/index.html>  
Les grands types d'organisation cellulaire Part of a more general site entitled *Webiologie* (<http://webiologie.free.fr/index.html>) dedicated to the popularization of biology.
- <http://www.actionbioscience.org/newfrontiers/poolearticle.html>  
LUCA: What is the Last Universal Ancestor?  
<http://www.hort.purdue.edu/rhodcv/hort640c/referen/ipp.htm>  
*Metabolic Plant Physiology*. Set of links on mevalonic and non-mevalonic pathways; see also: <http://wwwsoc.nii.ac.jp/jbiochem/jb/131-3/3fbambrf.htm>
- <http://flipper.diff.org/app/pathways/info/14>  
*Mevalonate pathway*.
- [http://en.wikipedia.org/wiki/Mevalonate\\_pathway](http://en.wikipedia.org/wiki/Mevalonate_pathway)  
*Mevalonate pathway*.
- <http://www.auburn.edu/~duinedu/organism.html>  
*Organisms that contain the non-mevalonate pathway*. List of 70 organisms (often microorganisms) which use the non-mevalonic pathway DXP/MEP.
- <http://www.youtube.com/watch?v=kHiYF15ZlXk>  
*Ocean Origins*.
- <http://www.fossilmuseum.net/PaleobiologyVFM.htm>  
*Paleobiology with Evolutionary Milestones Across Geological Time*.
- <http://users.info.unicaen.fr/~giguuet/java/textes/pigments.html>  
*Rôles et transformations des pigments caroténoïdes dans les réseaux trophiques marins*. Website of the University of Caen, France.
- <http://en.wikipedia.org/wiki/Seawater>  
*Seawater*.
- <http://www.infoplease.com/ipa/A0001822.html>  
*Table of Geological Periods*.
- <http://www.docstoc.com/docs/19485487/1-2-Biosynthesis-of-Natural-Products-Terpene-Biosynthesis-21>  
*Terpene Biosynthesis*.
- <http://www.talkorigins.org/faqs/faq-age-of-earth.html>  
*The Age of the Earth*.
- [http://www.ric.edu/faculty/ptiskus/Six\\_kingdoms/index.htm](http://www.ric.edu/faculty/ptiskus/Six_kingdoms/index.htm)  
*The Six Kingdoms*.
- <http://telstar.ote.cmu.edu/biology/downloads/membranes/index.html>  
*The Structure and Function of the Cell Membrane*.
- <http://tolweb.org/tree/phylogeny.html>  
*The Tree of Life*. Site of the University of Arizona which aspires to build the complete phylogenetic tree of all living organisms.
- <http://www.ucmp.berkeley.edu/help/timeform.html>  
*Web Geological Time machine*.
- <http://www.britannica.com/EBchecked/topic-art/340003/107934/>  
*The-Whittaker-five-kingdom-classification-of-life*  
*Whittaker, Robert H.: five-kingdoms classification of life*.
- <http://home.manhattan.edu/~frances.cardillo/plants/intro/plntlist.html>  
*Whittaker Five Kingdom System – Plant Classification*.
- [http://www.palomar.edu/oceanography/salty\\_ocean.htm](http://www.palomar.edu/oceanography/salty_ocean.htm)  
*Why is the Ocean Salty?*