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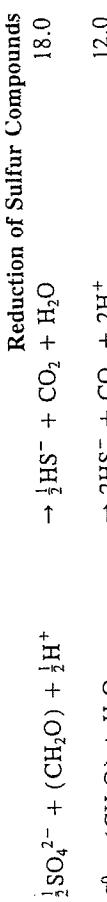
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TABLE 1.5 Anaerobic fermentation and respiration processes

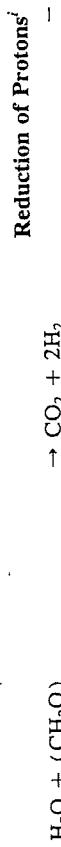
Reaction ^a	Transformations of Carbon Compounds ^c	$-\Delta G^\circ$ per mol of Electrons Exchanged at pH 7 (kJ/mol)	Organisms Catalyzing These Reactions ^b
$n(\text{CH}_2\text{O})^d$	$\rightarrow \text{CO}_2 + \text{C}_2\text{H}_6\text{O}$ $\rightarrow m\text{CO}_2$ and/or fatty acids and/or alcohols and/or hydrogen $\rightarrow \text{CH}_4 + \text{CO}_2$	23.4 5-60 28 ^e	e.g., yeasts, <i>Sarcina ventriculi</i> , <i>Zymonas</i> , <i>Leuconostoc</i> sp., clostridia, <i>Thermoanaerobium</i> <i>brockii</i> , etc. e.g., yeasts, clostridia, enterobacteria, lactobacilli, streptococci, propionibacteria, and many others Some methane bacteria (<i>M. barkeri</i> , <i>M. mazei</i> , <i>M. schragenii</i>) Most methane bacteria e.g., <i>Aerobacterium woodii</i> , <i>Clostridium aceticum</i> e.g., <i>Buoyribacterium</i> <i>methylotrophicum</i>
$\text{CO}_2 + 4\text{H}_2$	$\rightarrow \text{CH}_4 + 2\text{H}_2\text{O}$ $\rightarrow \text{CH}_3\text{COOH} + 2\text{H}_2\text{O}$	17.4 14.4	
$m\text{CO}_2 + n\text{H}_2$	\rightarrow fatty acids and/or alcohols	12-20	
$2\text{NO}_3^- + (\text{CH}_2\text{O})$	$\rightarrow 2\text{NO}_2^- + \text{CO}_2 + \text{H}_2\text{O}$	82.2	e.g., members of the genus <i>Enterobacter</i> , <i>E. coli</i> , and many others
$\frac{4}{3}\text{NO}_3^- + (\text{CH}_2\text{O}) + \frac{4}{3}\text{H}^+$	$\rightarrow \frac{2}{3}\text{N}_2 + \text{CO}_2 + \frac{7}{3}\text{H}_2\text{O}$	112.0	e.g., members of the genus <i>Pseudomonas</i> , <i>Bacillus licheniformis</i> , <i>Paracoccus denitrificans</i> , etc.
$\frac{1}{2}\text{NO}_3^- + (\text{CH}_2\text{O}) + \text{H}^+$	$\rightarrow \frac{1}{2}\text{NH}_4^+ + \text{CO}_2 + \frac{1}{2}\text{H}_2\text{O}$	74.0	Members of the genus <i>Clostridium</i>
$\frac{6}{5}\text{NO}_3^- + \text{S}^0 + \frac{3}{2}\text{H}_2\text{O}$	$\rightarrow \frac{3}{5}\text{N}_2 + \text{SO}_4^{2-} + \frac{4}{3}\text{H}^+$	91.3	Members of the genus <i>Thiobacillus</i>
$\frac{8}{3}\text{NO}_3^- + \text{HS}^- + \frac{3}{2}\text{H}^+$	$\rightarrow \frac{4}{3}\text{N}_2 + \text{SO}_4^{2-} + \frac{5}{3}\text{H}_2\text{O}$	93.0	<i>Thiosphaera pantotropha</i> and members of the genus <i>Thiobacillus</i> ^f

TABLE 1.5 (Continued)

Reaction ^a	$-\Delta G^\circ$ per mol of Electrons Exchanged at pH 7 (kJ / mol)	Organisms Catalyzing These Reactions ^b
$2\text{MnO}_2 + (\text{CH}_2\text{O}) + 2\text{H}^+$	$\rightarrow \text{MnCO}_3 + \text{Mn}^{2+} + 2\text{H}_2\text{O}$ 94.5	Members of the genus <i>Bacillus</i> , <i>Micrococcus</i> , and <i>Pseudomonas</i>
$4\text{FeOOH} + (\text{CH}_2\text{O}) + 6\text{H}^+$	$\rightarrow \text{FeCO}_3 + 3\text{Fe}^{2+} + 6\text{H}_2\text{O}$ 24.3	Members of the genus <i>Bacillus</i>
$\frac{1}{2}\text{SO}_4^{2-} + (\text{CH}_2\text{O}) + \frac{1}{2}\text{H}^+$	$\rightarrow \frac{1}{2}\text{HS}^- + \text{CO}_2 + \text{H}_2\text{O}$ 18.0	<i>Desulfovibrio</i> sp., <i>Desulfovibrio</i> sp., <i>Desulfonema</i> sp., etc.
$\text{S}^0 + (\text{CH}_2\text{O}) + \text{H}_2\text{O}$	$\rightarrow 2\text{HS}^- + \text{CO}_2 + 2\text{H}^+$ 12.0	<i>Desulfovibrio</i> sp., <i>Thermoproteus</i> <i>acetoxidans</i> , <i>Campylobacter</i> sp., <i>Thermoproteus</i> <i>tenax</i> , <i>Pyrobaculum islandicum</i>
$\text{S}^0 + \text{H}_2$	$\rightarrow \text{HS}^- + \text{H}^+$ 14.0	<i>Thermoproteus</i> sp., <i>Thermodesmus</i> sp., <i>Pyrodictium</i> sp., various bacteria, etc.
$\text{H}_2\text{O} + (\text{CH}_2\text{O})$	$\rightarrow \text{CO}_2 + 2\text{H}_2$ —	Obligate proton reducers such as <i>Syntrophomonas</i> sp., <i>Syntrophobacter</i> sp., <i>Syntrophus</i> sp., etc. ^j
		Enrichment culture no pure culture yet
		Reductive Dechlorination ^k



Desulfobacter sp., *Desulfovibrio* sp.,
Desulfomonas acetoxidans,
Desulfonema sp., etc.
Campylobacter sp., *Thermoproteus tenax*, *Pyrobaculum islandicum*
Thermoproteus sp., *Thermodiscus* sp.,
Pyrodictium sp., various bacteria,
etc.



Obligate proton reducers such as
Synriphomonas sp.,
Synriphobacter sp., *Syntrophus* sp., etc.^j



Enrichment culture, no pure culture yet known

^aSome of the more important overall reactions are given.

^bThis list is not complete. Only some of the best known bacteria are indicated.

^cOnly a limited number of reactions are given.

^dThe standard free energy of formation of (CH_2O) was chosen to be one-sixth of glucose (i.e., -153 kJ mol⁻¹) and not that of formaldehyde as in the previous tables.

^eThis is an intramolecular redox reaction and not, as the rest of the listed reactions, an intermolecular redox reaction; 28 kJ mol⁻¹ is the energy released by transforming 1 mol of acetate.

^f HS^- can be replaced by thiosulfate. *Thiomicrospira* sp. can reduce nitrate only with thiosulfate as electron donor.

^gIn the absence of oxygen, FeOOH can also be reduced abiotically at considerable rates.

^hOnly acetate is entirely oxidized to CO_2 and hydrogen. With other fatty acids ($C > 2$), acetate, as well as hydrogen, is an obligate end product.

^jThese bacteria can be grown only in a co-culture with hydrogen-scavenging microorganisms.

^kWhether this chlorinated compound is reduced with electrons from hydrogen and/or from organic substrate is not yet known.

these two metal oxides are reduced chemically, their transformation is strictly dependent on the availability of reduced biogenic compounds and therefore on biological activities. However, it must not be forgotten that manganese and iron oxides can, in certain environments, be reduced by agents (e.g., hydrogen, sulfur compounds) originating from volcanic or anthropogenic activities. Recently, it was shown (31) that synthetic, halogenated compounds can reductively be dechlorinated by biologically mediated reactions and thus act as electron acceptors. The reductive dehalogenation is (fortunately!) not of importance for global cycles but can locally be of considerable interest for the treatment of polluted air, water, and soils.

In relatively stable environments such as lake and ocean sediments, stagnant water bodies, and groundwater systems, a clear, predictable redox sequence will be established (see Section 1.3), which according to the availability of electron acceptors, is colonized by a succession of microorganisms catalyzing the respective redox reaction (51). Some environments are exposed to strong fluctuating conditions: for example, the top of the marine sediments is constantly turned up by large animals (bioturbation), intertidal sediments are subjected to water erosion and alluvial depositions which continuously disturb the creation of a stable environment, shallow water sediments at their water-sediment interface are strongly influenced by diurnal light-dark cycles, and in soil environments the constantly changing water content often limits the access to electron donors and acceptors. Because of the continuously changing conditions, all these unstable environments contain a large diversity of organisms and therefore for microbiologists represent a storehouse for new, often exotic microorganisms.

The effect of bioturbation on biogeochemical processes has been extensively investigated experimentally and theoretically by a variety of researchers (1). Since bioturbation does not result in complete homogenization but rather in random mixing, various redox conditions can exist close together in microniches. The continuous plowing of animals exposes bacteria constantly to new environmental conditions but also brings them in contact with fresh substrates. To survive as a bacterial species in such an ever-changing environment, one must, in addition to escaping from predators, be very versatile (able to use various substrates and/or electron acceptors) or be capable of surviving adverse conditions and/of growing very fast when circumstances improve (9). A very interesting habitat is the water-sediment interface, especially in shallow waters. Advances in microelectrode developments have provided better access to these habitats (27). At the first few millimeters of the marine water-sediment interface which receives sunlight, principally six groups of microorganisms can be found close together: (a) photoautotrophic oxygen producers (e.g., algae), (b) heterotrophic oxygen consumers, (c) "autotrophic" sulfide oxidizing oxygen consumers (e.g., *Beggiatoa*), (d) photoautotrophic sulfide oxidizers (e.g., *Chromatium*), (e) fermenting organisms, and (f) sulfate reducers. A habitat at the water-sediment interface has been studied extensively by Jørgensen and co-workers (15) with special attention given to organisms belonging to groups a, c, and d. During a diurnal cycle, the chemical gradients changed constantly and the microorganisms searched continuously for

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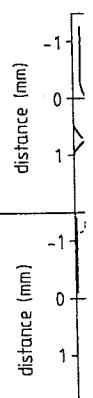


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1.5 PRINCIPLES OF SYNTROPHIC RELATIONSHIPS

ANAEROBIC HABITATS

formation is strictly defined and therefore on biomanganese and iron oxides (e.g., hydrogen, sulfur) reactivities. Recently, it was reductively be dechlorinated electron acceptors. The ice for global cycles but polluted air, water, and

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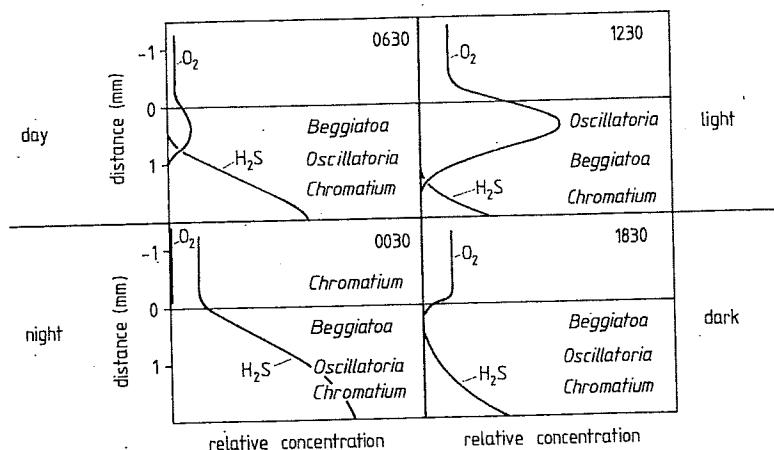


Figure 1.10 Diurnal cycle of oxygen and sulfide distribution and of microbial zonation in a marine sulfureum. Redrawn from Jørgensen (15).

their most optimal place with respect to the physical, chemical, and biological (proximity of other microorganisms) environment (Fig. 1.10).

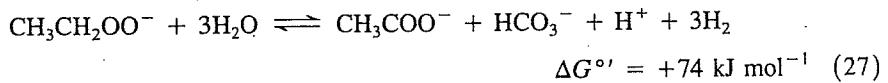
In soils the aeration status is a continuum from virtually completely aerobic conditions in well-drained sands to permanently anaerobic conditions in marshes and swamps. Within this range there are classes of soils with intermediate drainage and aeration characteristics, which result in temporary periods of anoxia or the presence of anaerobic microsites (mostly in an aggregate) within a generally aerobic matrix. Tiedje et al. (41) postulated that the anaerobic zone in an aggregate expands and contracts in response to the velocity of oxygen consumption. During anaerobiosis in this kind of habitat, denitrification and manganese and iron reduction, especially, will occur. At high inputs of organic carbon compounds into soil, fermentation processes have been observed (21) as well as sulfate reduction and methanogenesis.

Fermenting bacteria (Svensson, unpublished) and methanogens (Zehnder, unpublished) can readily be isolated from topsoil, and some sulfide is formed when soils become flooded for an extended period. It is therefore probable that the strict anaerobic bacteria can survive in anaerobic microsites in soil aggregates within an aerobic environment. However, it is not known if they contribute significantly to the overall mineralization processes in soil. With microelectrodes the chemodynamics within a soil aggregate can now be measured (16), but satisfactory techniques are not yet available that allow us to follow the microbial dynamics at the same time. A further development of Perfil'ev's pedoscope or peloscope (24) might be useful for this purpose in both soil and sediments.

1.5 PRINCIPLES OF SYNTROPHIC RELATIONSHIPS

Methane bacteria have an extremely limited substrate spectrum (53). Their main substrates are acetate or carbon dioxide and hydrogen. Molecules with more than

two carbon atoms [except isopropanol (44)] are neither converted to methane nor can their electrons be used to reduce carbon dioxide to methane in methane bacteria. In case only carbon dioxide and protons are present as terminal electron acceptors, other bacteria first have to convert complex organic carbon compounds to acetate or hydrogen and carbon dioxide before methane bacteria can finally produce methane. Fermentation of various compounds leads to the production of these two methanogenic substrates; however, there are other reactions during which fatty acids such as propionate, butyrate, and/or amino acids (alanine, leucine, etc.) are formed (10). The further conversion of these products to hydrogen and carbon dioxide and acetate is, under standard conditions, an endergonic process; thus organisms should not be able to grow in this reaction. In the case of propionate oxidation, the following equation can be written:



However, standard conditions do not describe the conditions prevailing in the environment. Therefore, the actual $\Delta G'$ should be calculated rather than the ΔG° :

$$\Delta G' = \Delta G^\circ + 2.3RT \log \frac{\{\text{CH}_3\text{COO}^-\}\{\text{HCO}_3^-\}\{\text{H}_2\}^3}{\{\text{CH}_3\text{CH}_2\text{OO}^-\}} \quad (28)$$

If we assume that the concentrations of acetate and propionate are about equal and the bicarbonate concentration constant, the only factor that is variable and influences ΔG is the hydrogen concentration. In natural systems, steady-state hydrogen concentrations are very low. Values between 3×10^{-6} and $4.4 \times 10^{-8} \text{ mol}^{-1}$ have been measured (53), which corresponds to a hydrogen partial pressure of 4×10^{-3} to $6 \times 10^{-5} \text{ atm}$. At a hydrogen partial pressure of about 10^{-4} atm , the oxidation of propionate becomes exergonic (Table 1.6) and organisms can grow at the expense of this reaction. The partial pressure of hydrogen is kept low by methane-producing bacteria or other hydrogen oxidizers (e.g., acetogens, or sulfate reducers). The coupling or syntrophic relationship of hydrogen producers and hydrogen consumers is called *interspecies hydrogen transfer* (49). A unique example of interspecies hydrogen transfer is described by Zinder and Koch (56). They found that acetate can be oxidized in a thermophilic syntrophic association to hydrogen and carbon dioxide, and that these two gases are further converted to methane. This reaction (i.e., first oxidation of acetate and subsequent oxidation of hydrogen) can only proceed within very narrow boundaries, at 60°C between 10^{-4} and $2.5 \times 10^{-3} \text{ atm}$ of hydrogen (Fig. 1.11). Although there was doubt 10 years ago that one bacterium could obtain enough energy for growth from the conversion of acetate to methane (55), this example shows that not only one but two bacteria can live from this very small amount of energy. If the energy is distributed equally

AEROBIC HABITATS

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$$+74 \text{ kJ mol}^{-1} \quad (27)$$

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$$\frac{\{ \text{H}_2 \}}{\{ \text{O}_2 \}}^3 \quad (28)$$

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TABLE I.6 Influence of hydrogen partial pressure on the free energy of some typical hydrogen-producing reactions catalyzed by syntrophic microbial associations under methanogenic conditions

Reaction Description	Reactants	Products	Free energy ^a (kJ / reaction)	
			ΔG°	$\Delta G'$
Fatty acid oxidation	Propionate + 3H ₂ O	→ Acetate + HCO ₃ ⁻ + H ⁺ + 3H ₂	+74	-1
	Ethanol + H ₂ O	→ Acetate + H ⁺ + 2H ₂	+2	-44
Alcohol oxidation	Alanine + 3H ₂ O	→ Acetate + HCO ₃ ⁻ + H ⁺ + NH ₄ ⁺ + 2H ₂	+8	-38
Amino acid oxidation	Benzoate + 7H ₂ O	→ 3 Acetate + HCO ₃ ⁻ + 3H ⁺ + 3H ₂	+53	-16
Oxidation of aromatic compounds				

^a ΔG° , standard conditions, pH 7, 25°C; $\Delta G'$, same as ΔG° with the exception that p_{H_2} was 10^{-4} atm.

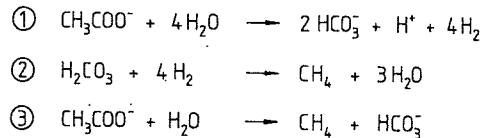
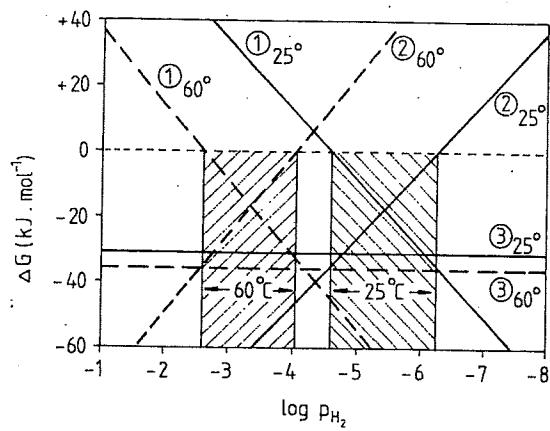


Figure 1.11 Free energy from the oxidation and decarboxylation of acetate and methane formation at different hydrogen partial pressures at 60°C and 25°C. The slopes were calculated for pH 7, 20 mM acetate and bicarbonate, and 1 atm of methane. Temperature corrections have been made using the van't Hoff equation (23).

between the two organisms, each will obtain 17 kJ mol⁻¹, which translates into 4.25 kJ or 44.2 mV per pair of electrons [for the calculation, see equation (13)]. For our present apprehension, this is not enough energy to explain chemiosmotic coupling via vectorial protons with both $a \rightarrow \text{H}^+/2e^-$ and $a \rightarrow 3\text{H}^+/1 \text{ATP}$ stoichiometry (38). However, the entire 17 kJ mol⁻¹ would just be enough to bring one proton across the membrane. It remains to future research to elucidate this intriguing question. Further examples of syntrophic associations and their thermodynamics are discussed in Chapter 9.

Depending on the presence or absence of certain electron acceptors and microorganisms, as well as the nature of the substrate, there are three different possibilities for the oxidation of organic carbon compounds (Fig. 1.12). (a) The first is oxidation of the substrate and concomitant reduction of an inorganic electron acceptor in the same organism (Fig. 1.12A). (b) In the absence of inorganic electron acceptors (except protons and carbon dioxide), the organisms are obliged to use part of the carbon substrate as electron acceptors (Fig. 1.12B). This process is called fermentation. (c) A third possibility is a combination of processes a and b in which the substrate is oxidized in one organism and the electrons liberated are transferred to a second microorganism in the form of hydrogen. There, the hydro-

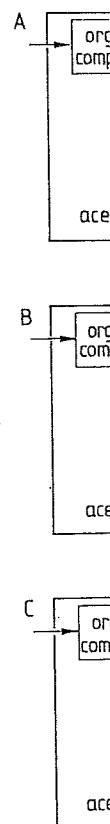
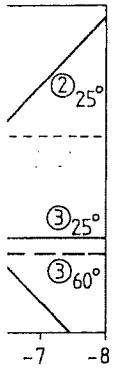


Figure 1.12 Substrate f of both where interspecie berg (52).

gen is oxidized in gen mechanism acts essentially a tions for catabolic rea ones known so far. On change catabolites othe tats.

In most natural eco formed according to F tations take place only are used by a host (e.g ditions in which respir washed out.

1.5 PRINCIPLES OF SYNTROPHIC RELATIONSHIPS



dition of acetate and methane at 25°C. The slopes were calculated from the rate of methane. Temperature

$^{-1}$, which translates into a rate of 1.3 mmol/mg dry weight/h [see equation (13)]. This is enough to explain chemiosmotic coupling between the oxidation of acetate and methane. The energy yield of 1 ATP/mol H₂ would just be enough to bring the energy of the electrons to the level required to elucidate this association and their thermal stability.

Iron acceptors and microorganisms are three different possibilities (Fig. 1.12). (a) The first is an inorganic electron acceptor. The absence of inorganic electron acceptors in some microorganisms is obliged to use organic electron acceptors (Fig. 1.12B). This process is called syntrophy. The electrons of processes a and b are transferred to the same electron acceptor, i.e., hydrogen. There, the hydro-

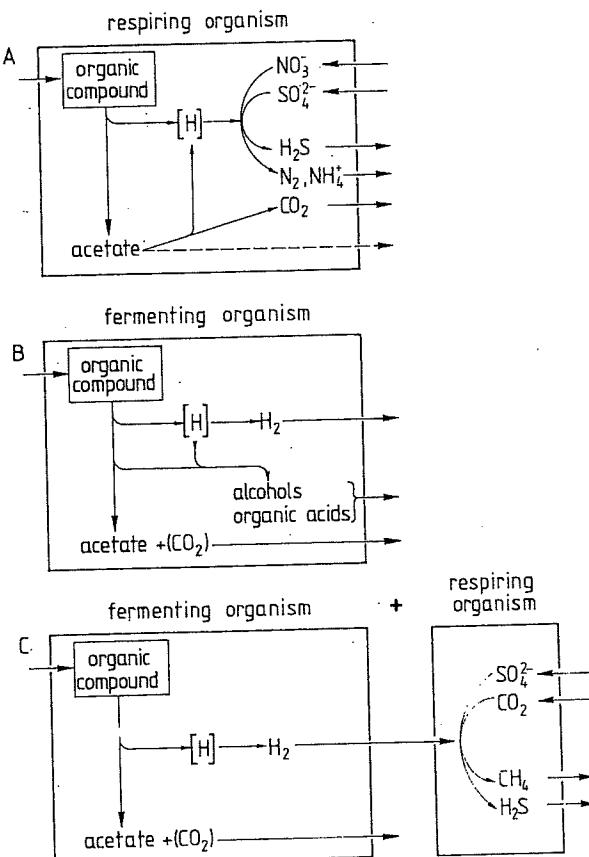


Figure 1.12 Substrate flow in respiring and fermenting organisms and in a combination of both where interspecies hydrogen transfer takes place. Modified from Zehnder and Coleberg (52).

gen is oxidized in general with an inorganic electron acceptor. The second organism acts essentially as a terminal electron sink (Fig. 1.12C). Syntrophic associations for catabolic reactions based on interspecies hydrogen transfer are the only ones known so far. One can hypothesize that syntrophic associations which exchange catabolites other than hydrogen may also be important in anaerobic habitats.

In most natural ecosystems, monomeric organic carbon compounds are transformed according to Fig. 1.12A or C or a combination of A and C. Pure fermentations take place only in pure cultures, in habitats where fermentation products are used by a host (e.g., rumen and other gastrointestinal systems), or under conditions in which respiring organisms are either inhibited (e.g., low or high pH) or washed out.

1.6 EVOLUTION OF ANAEROBIC MICROORGANISMS

Since 16S rRNA was chosen for measuring phylogenetic relationships among bacteria (46), discussion of the evolution of life has been given a considerable boost (7). It goes beyond the scope of this chapter to summarize existing knowledge on the evolution of anaerobes. The interested reader should refer to the respective literature. In the following we simply indicate the place of anaerobes in evolution and their traces in ancient rocks and sediments.

From the pioneering work of Woese and co-workers (47), we know that living organisms cluster in three separate kingdoms (Fig. 1.13) and that all three kingdoms contain anaerobic microorganism (48). However, this does not mean that the three branches were essentially developed before the atmosphere became oxygenated. In fact, eukaryotes seem to have evolved about 1500 million years ago when oxygen was already present in the atmosphere (8). The ability of some of them to grow anaerobically might just be a remainder of their ancestors. It is interesting to note that most eukaryotic cells are still able to function for a limited time in the absence of oxygen (54). The other two kingdoms originated in anaerobic periods, and it is therefore not surprising to find anaerobes (which are probably the majority) in both clusters.

Some bacteria produce molecules which are very specific and difficult to degrade. They can therefore serve as markers in geological formations. Archaeabacteria, especially methanogens, form some very specific isoprenoid hydrocarbons and ethers (19). Based on the analysis of these compounds, methanogens could be traced back 3 billion years, possibly as far back as 3.8 to 4 billion years (11). In addition to organic markers, stable isotope ratios can be employed to obtain an idea of biological activities in the past. Based on $^{34}\text{S}/^{32}\text{S}$ ratios from sedimentary

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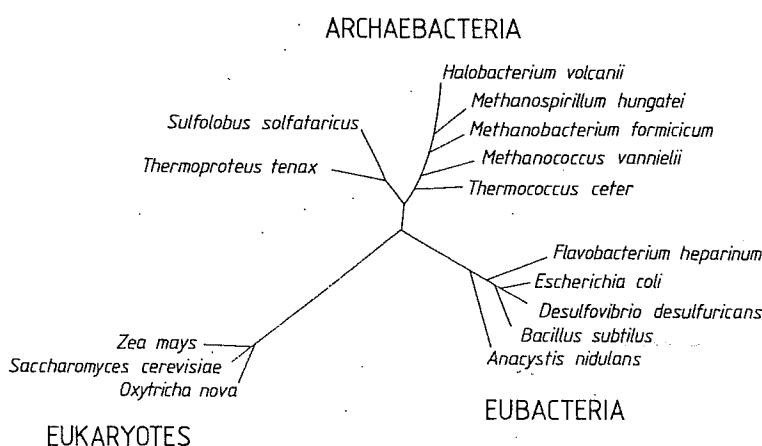


Figure 1.13 Unrooted phylogenetic tree for the three domains, showing some selected organisms. Modified from Woese and Olsen (48).

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pyrites, it can be concluded that sulfate-reducing bacteria existed as early as 3.2 billion years ago (25). The widespread occurrence of barite in Archean sediments suggests that sulfate was present in the ocean 3.5 billion years ago. This first large-scale introduction of sulfate into the environment was probably caused by the activity of photosynthetic sulfur bacteria (25, 42). Carbon isotope ratios from the 3.8-billion-year-old Isua carbonaceous matter shows the signature of autotrophic carbon fixation (30). Thus it can be concluded that life on earth is considerably older than the oldest known rocks (11, 25) and that anaerobes just as billions of years ago still contribute in essential ways to the state of the environment on our planet (20).

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MICROBI AND EC PHOTOT

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