10

The Atmosphere as Circulatory System of the Biosphere—The Gaia Hypothesis

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We would like to discuss the Earth's atmosphere from a new point of view—that it is an integral, regulated, and necessary part of the biosphere. In 1664 Sachs von Lewenheimb, a champion of William Harvey, used the analogy shown in Figure 10.1 to illustrate the concept of the circulation of blood. Apparently the idea that water lost to the heavens is eventually returned to Earth was so acceptable in von Lewenheimb's time that Harvey's theory was strengthened by the analogy (Pagel 1951).*

*Pagel quotes Harvey himself as saying: "I began to think whether there might not be a motion as it were in a circle. Now this I afterwards found to be true; . . . which motion we may be allowed to call circular, in the same way as Aristotle says that the air and the rain emulate the circular motion of the superior bodies; for the moist earth, warmed by the sun evaporates; the vapours drawn upwards are condensed, and descending in the form of rain moisten the earth again; and by this arrangement are generations of living things produced . . . And so in all likelihood, does it come to pass in the body, through the motion of the blood; the various parts are nourished, cherished, quickened by the warmer more perfect vaporous spiritous, and, as I may say, alimentive blood; which, on the contrary, in contact with these parts becomes cooled, coagulated, and, so to speak, effete; whence it returns to its sovereign, the heart, as if to its source, or to the inmost home of the body, there to recover its state of excellence of perfection."

FIGURE 10.1. Frontispiece* to Sachs von Lewenheimb, 1664, Oceanus Macro-Microcosmicus. This illustration stresses the analogies between the circulation of the blood and the circulation of water. According to W. Pagel (1951),

> "The subtitle of the dissertation (which addresses itself to the famous anatomist Thomas Bartholinus) explains that it deals with the analogies between the circular motion of the water from and back to the sea, on the one hand, and that of the blood from and back to the heart, on the other. This motion is "circular," not because it describes the geometrical figure of a circle, but because it reverts to its point of departure. The earth resembles the human body in that, like the latter, it is pervaded by canals and harbours an internal fire. The sea lets water rise by evaporation and return in the form of rain whereby the rivers and subterranean waters are nourished and these finally return the same water to the sea. The latter thereby acts not unlike the heart from which the blood goes out to the organs, starting on its way attenuated by the influx of heat and 'perfected' in the 'workshops' of the organs; finally, after its absorption and assimilation by the organs, its residue is drawn back into the heart in order to be attenuated again—just as the waters are diluted by joining the sea."

*From the original treatise in the Wellcome Library, courtesy of the trustees, with permission.

Three hundred and ten or so years later, with the circulation of blood a universally accepted fact, we find it expedient to revive von Lewenheimb's analogy—this time to illustrate our concept of the atmosphere as circulatory system of the biosphere. This new way of viewing the Earth's atmosphere has been called the Gaia hypothesis (Lovelock 1972). The term "Gaia" is from the Greek for "Mother Earth," and it implies that certain aspects of the Earth's atmosphere—temperature, composition, oxidation reduction state, and acidity—form a homeostatic system, and that these properties are themselves products of evolution (Lovelock and Margulis 1974a,b).

From recent articles and books (Rasool 1974; Kellogg and Schneider 1974) one gets the impression that fluid dynamics, radiation chemistry, and industrial pollution are the major factors determining the properties of the atmosphere. The Gaia hypothesis contends that biological gas exchange processes are also major factors, especially processes involving microorganisms. The human impact on the atmosphere may have been overestimated. Humans are only one of some three million species on Earth, all of which exchange gas and most of which exchange gas with the atmosphere. Humans have been around for only a few million years, while microorganisms have existed for thousands of millions of years. The atmosphere is probably not so much the product of humans as of the several billion smaller organisms living in every pail of rich soil or water.

It seems to us that early twentieth-century nonmicrobiological analysis of the Earth's lower atmosphere will one day be considered as ignorant as early nineteenth century nonmicrobiological analysis of fermentation or disease is today. In an excellent introduction to atmospheric science, Goody and Walker (1972) said, "There is a great difference between research in the laboratory and studies of the Earth and planets. In the laboratory the scientist can perform controlled experiments, each carefully designed to answer questions of his own choosing. Except in minor respects, however, the Earth and planets are too large for controlled experimentation. All we can do is observe what happens naturally in terms of the laws of physics and chemistry."

We agree that the laws of physics and chemistry are basic to the understanding of atmospheric phenomena but insist that the laws of biology must be considered as well. It is our contention that the paucity of overall understanding of certain aspects of the atmosphere, especially composition and temperature, is due to too narrow a paradigm: the idea that the

Table 10.1. Reactive gases in the atmosphere (billions of tons/year)

Gas	Concentration in Parts per Million	How much of the Gas Comes from: Inorganic Sources Volcanic, etc.?	Biological Sources: Gaian?	Biological Sources: Human?	Residence Time	Where Does the Gas Come From Principally?
Nitrogen (N_2)	790,000	0.001	1	0	1–10 million years	Bacteria from dissolved nitrate in soil
Oxygen (O_2)	210,000	0.00016	110	0	1000 years	Algae and green plants, given off in photosynthesis
Carbon Dioxide (CO_2)	320	0.01	140	16	2–5 years	Respiration, combustion
Methane (CH_4)	1.5	0	2	0	7 years	Fermenting bacteria
Nitrous oxide (N_2O)	0.3	less than 0.01	0.6	0	10 years	Bacteria and fungi
Carbon monoxide (CO)	0.08	less than 0.001	1.5	0.15	Few months	Methane oxidation (methane from bacteria)
Ammonia (NH_3)	0.006	0	1.5	0	Week	Bacteria and fungi
Hydrocarbons $(CH_2)_n$	0.001	0	0.2	0.2	Hours	Green plants, industry
Methyl iodide (CH_3I)	0.000001	0	0.03	0	Hours	Marine algae
Hydrogen (H_2)	0.0000005	0	?	?	2 years	Bacteria, methane oxidation?
Methyl chloride (CH_3Cl)	0.00000000114	0	?	?	?	Algae?

Gaian = nonhuman biological sources.

atmosphere is an inert part of the inorganic environment and therefore amenable to methods of study that involve only physics and chemistry.

In this chapter we explore what is perhaps a more realistic view—that the atmosphere is a nonliving, actively regulated part of the biosphere. In our model atmospheric temperature and composition are regulated with respect to certain biologically critical substances: hydrogen ions, molecular oxygen, nitrogen and its compounds, sulfur and its compounds, and some others, whose abundance and distribution in the atmosphere are presumed to be under biological control. Biological gas exchange processes, thought to be involved in possible control mechanisms, are discussed elsewhere (Margulis and Lovelock 1974). The purpose of this chapter is simply to present our reasons for believing the atmosphere is actively controlled.

Traditional atmospheric studies have left us with some strange anomalies. The atmosphere is an extremely complex blanket of gas in contact with the oceans, lakes, rivers (the hydrosphere), and the rocky lithosphere. It has a mass of about 5.3×10^{21} grams. (The mass of the oceans—the other major fluid on the surface of the Earth—is almost a thousand times heavier, being about 1.4×10^{24} grams.) Because the atmospheric mass corresponds to less than a millionth of the mass of the Earth as a whole, one would expect small changes in the composition of the solid earth to cause large changes in the composition of the atmosphere. Yet even in the face of a large number of potential perturbations, the atmosphere seems to have remained dynamically constant over long periods of time.

Many facts about the atmosphere are known—its composition, its temperature and pressure profiles, certain interactions with incoming solar radiation, and the like (Goody and Walker 1972). Some of these are shown in Tables 10.1 and 10.2. However, as the efficacy of long-range weather forecasting attests, there is no consistent model of the atmosphere that can be used for the purpose of prediction (Kellogg and Schneider 1974). The Earth's atmosphere defies simple description. From the point of view of chemistry, it sustains such remarkable disequilibrium that Sagan (1970) was prompted to remark that given the temperature, pressure, and amount of oxygen in the atmosphere, "one can calculate what the thermodynamic equilibrium abundance of methane ought to be . . . the answer turns out to be less than 1 part in 10^{36}. This then is a discrepancy of at least 30 orders of magnitude and cannot be dismissed lightly."

Table 10.2 shows that given the quantity of oxygen in the atmosphere, not only the major gases such as nitrogen and methane but also the minor

Table 10.2. Composition of the Atmosphere: Gases in Disequilibrium

Gas	Abundance	Flux (moles/yr $\times 10^{13}$)	Disequilibrium Factor	Oxygen Used up in the Oxidation of these Gases (moles/yr $\times 10^{13}$)	Abiological Processes	Source of Gas % Contribution by Biological Process	
						Human	Gaian*
Nitrogen	78%	3.6	10^{10}	11	0.001	0	>99
Methane	1.5 ppm	6.0	10^{30}	12	0	0	100
Hydrogen	0.5 ppm	4.4	10^{30}	2.2	?	0	?
Nitrous oxide	0.3 ppm	1.4	10^{13}	3.5	0.02	0	>99
Carbon monoxide	0.08 ppm	2.7	10^{30}	1.4	0.001	10	90
Ammonia	0.01 ppm	8.8	10^{30}	3.8	0	0	100

*Gaian = nonanthropogenic biological sources; for details see Table 1; ? = some quantities not known; ppm = parts per million.

atmospheric components are far more abundant than they ought to be according to equilibrium chemistry. Even though the minor constituents differ greatly in relative abundance, they sustain very large fluxes—comparable with those of the major constituents. The Earth's atmosphere is certainly not at all what one would expect from a planet interpolated between Mars and Venus. It has too little CO_2, too much oxygen, and is too warm. We believe the Gaia hypothesis provides the new approach that is needed to account for these deviations.

A new framework for scientific thought is justified if it guarantees new observations and experiments. The recognition that blood in mammals circulates in a closed, regulated system gave rise to meaningful scientific questions such as: How is blood pH kept constant? By what mechanism is the temperature of mammalian blood regulated around its set point? What is the purpose of bicarbonate ion in the blood? What is the role of fibrinogen? If the blood were simply an inert environment (as the atmosphere is presently viewed), such questions would seem irrelevant and never be asked at all.

Let us consider another analogy. Bees have been known to regulate hive temperatures during midwinter at about 31°C, approximately 59°C above ambient (Wilson 1970). Under threat of desiccation they also maintain high humidities. While the air in the hive is not alive, it maintains an enormous disequilibrium due to the expenditure of energy by the living insects—ultimately, of course, solar energy. How is the hive temperature maintained? How does the architecture of the hive aid to reduce desiccation? How does the behavior of the worker bees alter temperature? These are all legitimate scientific questions, generated by the circulatory system concept.

The Gaia hypothesis of the atmosphere as a circulatory system raises comparable and useful scientific questions and suggests experiments that based on the old paradigm would never be asked, for example: How is the pH of the atmosphere kept neutral or slightly alkaline? By what mechanism(s) has the mean midlatitude temperature remained constant (not deviated more than 15°C) for the last 1000 million years? Why are 0.5×10^9 tons nitrous oxide (N_2O) released into the atmosphere by organisms? Why is about 2×10^9 tons of biogenic methane pumped into the atmosphere each year (representing nearly 10% of the total terrestrial photosynthate)? What are the absolute limits on the control mechanisms, that is, how much perturbation (emanations of sulfur oxides, chlorinated compounds, and/or carbon monoxide; alterations in solar luminosity; and so forth) can the atmosphere regulatory system tolerate before all its feedback mechanisms fail?

The Gaia approach to atmospheric homeostasis has also led to a number of observations that otherwise would not have been made, for example, an oceanic search was undertaken for volatile compounds containing

Table 10.3. Critical Biological Elements that May Be Naturally Limiting

Major elements	Use in Biological Systems	Possible Form of Fluid Transport
C (carbon)	All organic compounds	CO_2; food; organic compounds in solution; biological volatiles; carbonate, bicarbonate, etc.; usually not limiting
N (nitrogen)	All proteins and nucleic acids	N_2, N_2O, O_3^-, NO_2^- (often limiting)
O, H (oxygen, hydrogen)	H_2O in high concentration for all organisms	Rivers, oceans, lakes
S (sulfur)	Nearly all proteins (cysteine, methionine, etc.); key coenzymes	Dimethyl sulfide; dimethyl sulfoxide, carbonyl sulfide
P (phosphorus)	All nucleic acids; adenosine triphosphate	Unknown (biological volatiles? spores? birds? migrating salmon?)
Na, Ca, Mg, K (sodium, calcium, magnesium potassium)	Membrane and macromolecular function	Usually not limiting, except in certain terrestrial habitats (Botkin et al. 1973)
Trace Elements		
I (iodine)	Limited to certain animals (e.g., thyroxine)	Methyl iodide
Se (selenium)	Enzymes of fermenting bacteria (production of ammonia, hydrogen; animals (Stadtman 1974)	Unknown (dimethyl selenide?)
Mo (molybdenum)	Nitrogen fixation enzymes of bacteria, including cyanobacteria; carbon dioxide reductase (*Clostridium*)	Unknown

elements that are limiting to life on the land, and large quantities of methyl iodide and dimethyl sulfide were in fact observed (Lovelock, Maggs, and Rasmussen 1972).

Given the Gaia hypothesis, one deduces that all the major biological elements (Table 10.3) must either be not limiting to organisms (in the sense that they are always readily available in some useful chemical form) or must be cycled through the fluids on the surface of the Earth in time periods that are short relative to geological processes. (Attempts to identify volatile forms of these elements are in progress.) The cycling times must be short because biological growth is based on continual cell division, which requires the doubling of cell masses in periods of time that are generally less than months, and typically days or hours. On lifeless planets there is no particular reason to expect this phenomenon of atmospheric cycling, nor on the Earth is it expected that gases of elements that do not enter metabolism as either metabolites or poisons will cycle rapidly; for example, based on the Gaia hypothesis, nickel, chromium, strontium, rubidium, lithium, barium, and titanium will not cycle, but cobalt, vanadium, selenium, molybdenum, iodine and magnesium might (Egami 1974). Because biological solutions to problems tend to be varied, redundant, and complex, it is likely that all of the mechanisms of atmospheric homeostasis will involve complex feedback loops [see Margulis and Lovelock (1974) for discussion.] Because, for example, no volatile form of phosphorus has ever been found in the atmosphere, and because this element is present in the nucleic acids of all organisms, we are considering the possibility that the volatile form of phosphorus at present is totally "biological particulate." Figures 10.2 and 10.3 rather fancifully compare the Earth's atmosphere at present with what it might be if life were suddenly wiped out.

Ironically, it is the past history of the Earth, with its extensive sedimentary record (fraught, as it is, with uncertainties in interpretation), that might provide the most convincing proof for the existence of continued biological modulation. If one accepts the current theories of stellar evolution, the Sun, being a typical star of the main sequence, has substantially increased its output of energy since the Earth was formed some 4500 million years ago. Some estimates for the increase in solar luminosity over the past history of the Earth are as much as 100%; most astronomers apparently accept an increase of at least 25% over 4.5 billion years (Oster 1973). Extrapolating from the current atmosphere, given solar radiation output and radiative surface properties of the planet, it can be concluded that until about 2000 million years ago either the atmosphere was different (for example, contained more ammonia) or the Earth was frozen. The

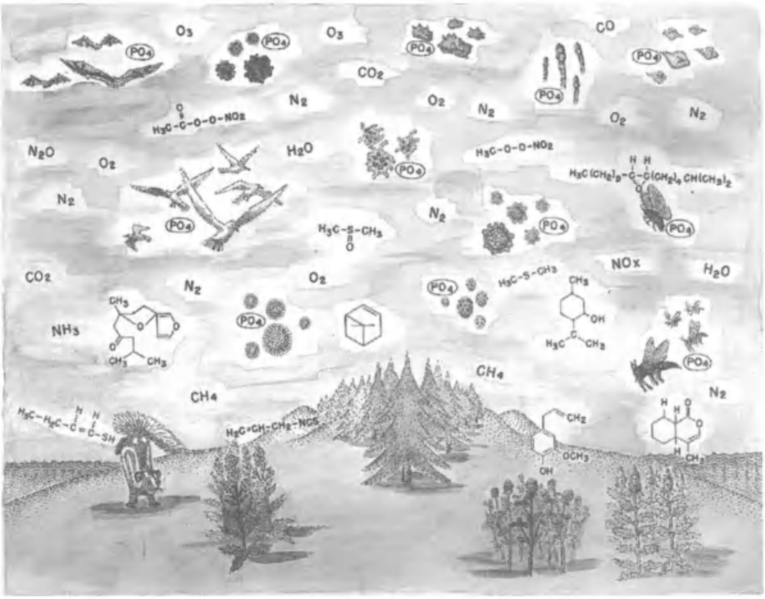

FIGURE 10.2. Earth's atmosphere at present: examples of major volatiles. (Key: the following compounds and spores are depicted. It is left to the reader to identify them. See Gregory, 1973 for many details.) Spores of: ferns, club mosses, zygomycetes, ascomycetes, basidiomycetes, slime molds, bacteria. All contain nucleic acids and other organic phosphates, amino acids and so forth. Animal products: butyl mercaptan, plant products: myoporum, catnip (nepetalactone), eugenol, geraniol, pinene, isothiocyanate (mustard); disparlure; PAN (paroxacetyl nitrate), dimethyl sulfide, dimethyl sulfoxide; gases: nitrogen, oxygen, methane, carbon monoxide, carbon dioxide, ammonia. Painting by Laszlo Meszoly.

most likely hypothesis is that the Earth's atmosphere contained up to about one part in 10^5 ammonia, a good infrared absorber (Sagan and Mullen 1972). Other potential greenhouse gases apparently will not compensate for the expected lowered temperature because they do not have the appropriate absorption spectra or are required in far too large quantity to be considered reasonable (Sagan and Mullen 1972). [There are good arguments for the rapid photodestruction of any atmospheric ammonia (Ferris and Nicodem 1974).] However, it has been argued that ammonia is required for the origin of life (Bada and Miller 1968), and there is good evidence for the presence of fossil microbial life in the earliest sedimentary rocks [3400 million years ago (Barghoorn 1971).] There is no geological evidence that since the beginning of the Earth's stable crust the entire

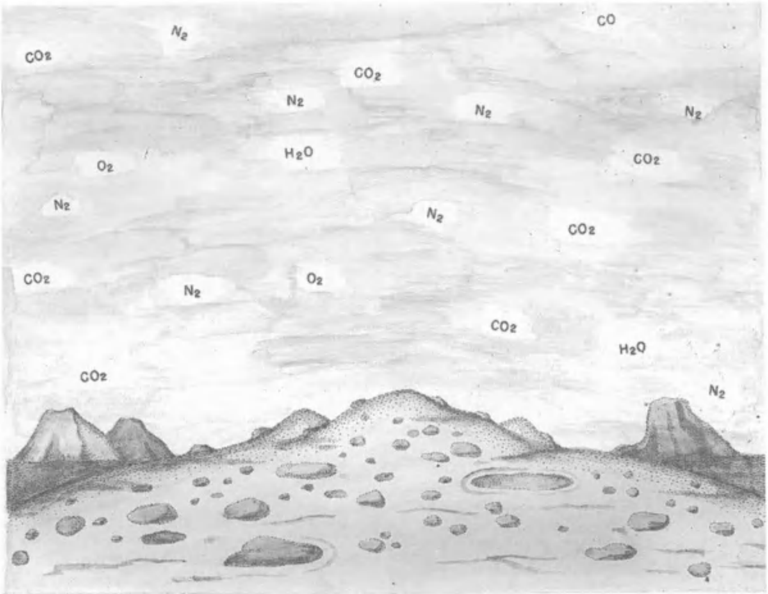

FIGURE 10.3. The present atmosphere were life deleted. Painting by Laszlo Meszoly.

Earth has ever frozen solid or that the oceans were volatilized, suggesting that the temperature at the surface has always been maintained between the freezing and the boiling points of water. The fossil record suggests that, from an astronomical point of view, conditions have been moderate enough for organisms to tolerate, and the biosphere has been in continuous existence for over 3000 million years (Barghoorn 1971; Cloud 1968). At least during the familiar Phanerozoic (the last 600 million years of Earth history for which an extensive fossil record is available), one can argue on paleontological grounds alone that through every era the Earth has maintained tropical temperatures at some place on the surface and that the composition of the atmosphere, at least with respect to molecular oxygen, could not have deviated markedly. That is, there are no documented cases of any metazoa (animals, out of about 3 million species) that can complete their life cycles in the total absence of O_2 (Augenfeld, 1974, personal communication). All animals are composed of cells that divide by mitosis. The mitotic cell division itself requires O_2 (Amoore 1961). Thus it is highly unlikely that current concentrations of oxygen have fallen much below their present values in some hundreds of millions of years. By implication, oxygen and the gases listed in Table 10.2 have been maintained at stable atmospheric concentrations for time periods that are very long relative to their residence times. (Residence time is the time it takes for the concentration of gas to fall to 1/e or 37% its value; it may be thought of as turnover time). Furthermore, because concentrations of atmospheric oxygen only a few percent higher than ambient lead to spontaneous combustion of organic matter, including grasslands and forests, the most reasonable assumption is that the oxygen value of the atmosphere has remained relatively constant for quite long time periods (Lovelock and Lodge 1972).

How can these observations be consistently reconciled? How can we explain the simultaneous presence of gases that are extremely reactive with each other and unstable with respect to minerals in the crust and at the same time note that their residence times in the atmosphere are very short with respect to sediment forming and mountain building geological processes? In this respect Table 10.3 can be instructive. One can see that even though absolute amounts of the gases vary over about three orders of magnitude, the fluxes are remarkably similar. These gases are produced and removed primarily by nonhuman biological processes (see Table 10.1); (Margulis and Lovelock 1974). While the processes involved in atmospheric production and removal of reactive gases are not primarily dependent on human activity, for the most part they are not based on animal or plant processes either. (See Margulis and Lovelock 1974 for a version of the table that lists these.) It is mainly the prokaryote microorganisms that are involved in gas exchange—the rapidly growing and dividing masters of the microbiological world that make up in chemical complexity and metabolic virtuosity what they lack in advanced morphology. These organisms presumably played a similar role in biogeochemical processes in the past as they do today. There is direct fossil evidence for the continued existence of Precambrian microorganisms (Barghoorn 1971). That they have an ancient history can also be deduced from current studies of their physiology. Among hundreds of species of these prokaryotic microorganisms are many obligate anaerobes, that is, organisms poisoned by oxygen. (All organisms are poisoned by oxygen at concentrations above those to which they are adapted.) Hundreds of others are known that are either microaerophils (adapted to concentrations of oxygen less than ambient) or facultative aerobes (can switch their metabolism from oxygen requiring to oxygen nonrequiring).

As a group, the prokaryotic microbes show evidence that the production and release of molecular oxygen into the atmosphere was an extremely important environmental determinant in the evolution of many genera. Prokaryotic microbes (formerly known as the blue-green algae, cyanobacteria) were almost certainly responsible for the original transition to the oxygen-containing atmosphere about 2000 million years ago (Barghoorn 1971; Cloud 1968).

Figure 10.4 and 10.5 present scenes before and after the transition to oxidizing atmosphere, respectively. Figures 10.6 and 10.7 are reconstructions of anaerobic cycles corresponding to Figures 10.4 and 10.5, respectively. Figure 4 attempts to reconstruct the scene as it might have looked 3400 million years ago, admittedly in a rather geothermal area. Although no free oxygen (above that produced by photochemical processes and hydrogen loss) is available in the atmosphere, the scene is teeming with life—microbial life. For example, entire metabolic processes, as shown in Figure 10.6, are available within the group of anaerobic prokaryotic microbes today. Because at the higher taxonomic levels (kingdoms and phyla) once successful patterns evolve they tend not to become extinct (Simpson 1960), it is likely that ancestors of present-day microbes were available to interact with atmospheric gases very early on the primitive Earth. Certainly life was very advanced metabolically by the time the first

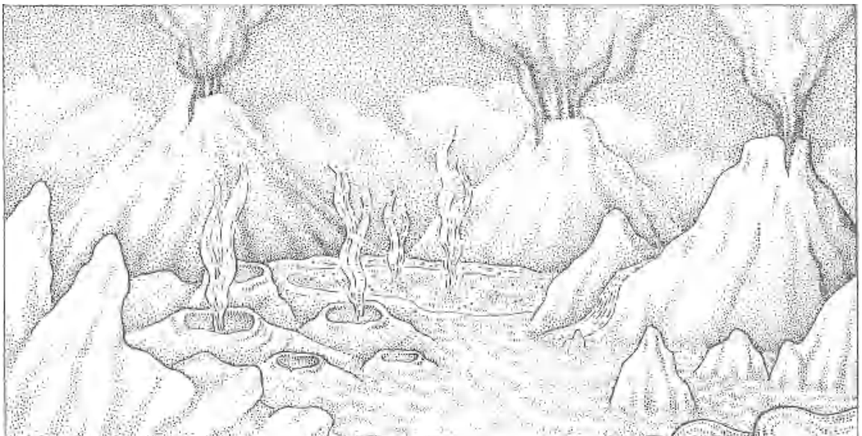

FIGURE 10.4. Scene from a geothermal area in Fig Tree times (about 3400 million years ago). Drawing by Laszlo Meszoly.

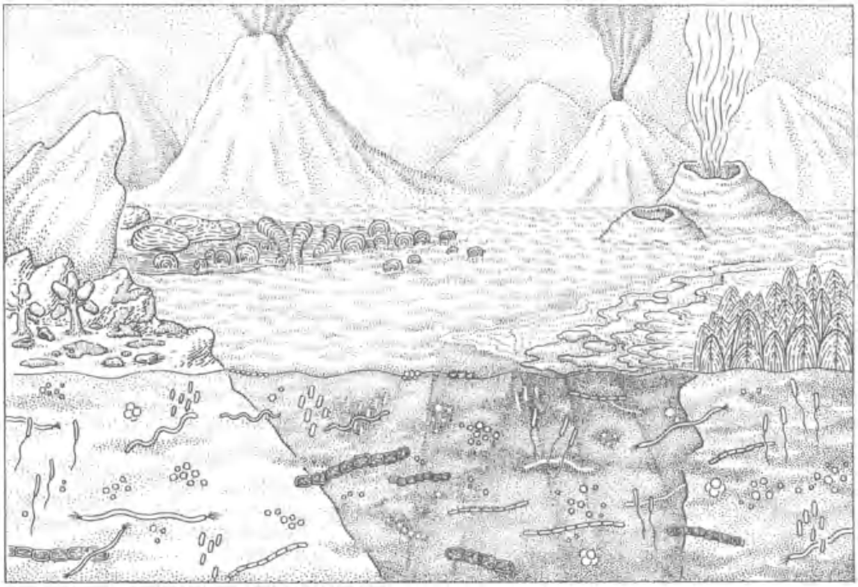

FIGURE 10.5. Scene from a geothermal area in Gunflint times (about 2000 million years ago). Drawing by Laszlo Meszoly.

stromatolitic rocks were deposited. With the evolution of oxygen-releasing metabolism by cyanobacteria came the stromatolites. These layered sediments are extremely common, especially in the late Precambrian (Awramik 1973). With the stromatolites come other Precambrian evidence for the transition to the oxidizing atmosphere. By the middle Precambrian, about 2000 million years ago—the time at which the stromatolites and microfossils become increasingly abundant (Barghoorn and Tyler 1965; Schopf 1970)—the scene might have looked like that in Figure 10.5. The metabolic processes accompanying that scene are shown in Figure 10.7. It is obvious that from among metabolic processes in prokaryotic microbes alone there are many that involve the exchange of atmospheric gases. This figure shows how oxygen-handling metabolism was essentially superimposed on an anaerobic world, a concept that is consistent with the observation that reaction with molecular oxygen tends to be the final step in aerobic respiratory processes. All of the processes shown in Figures 10.6 and 10.7 are known from current microorganisms (and, by definition, those that haven't become extinct are evolutionarily successful).

The fossil evidence, taken together, suggests that the Earth's troposphere has maintained remarkable constancy in the face of several enor-

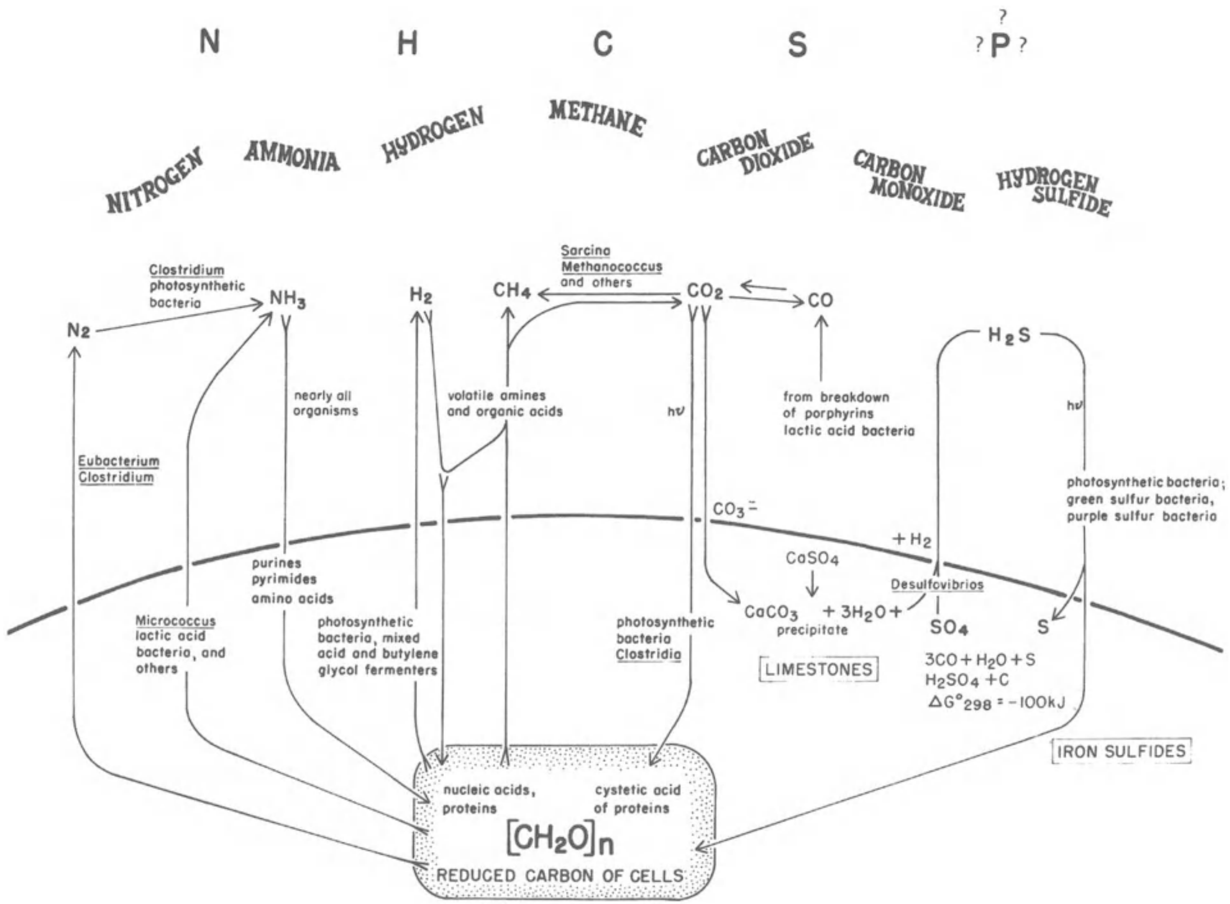

FIGURE 10.6. A reconstruction of possible anaerobic cycles: 3400 million years ago. (Genera of microorganisms catalyzing the reactions are underlined; drawing by Laszlo Meszoly.)

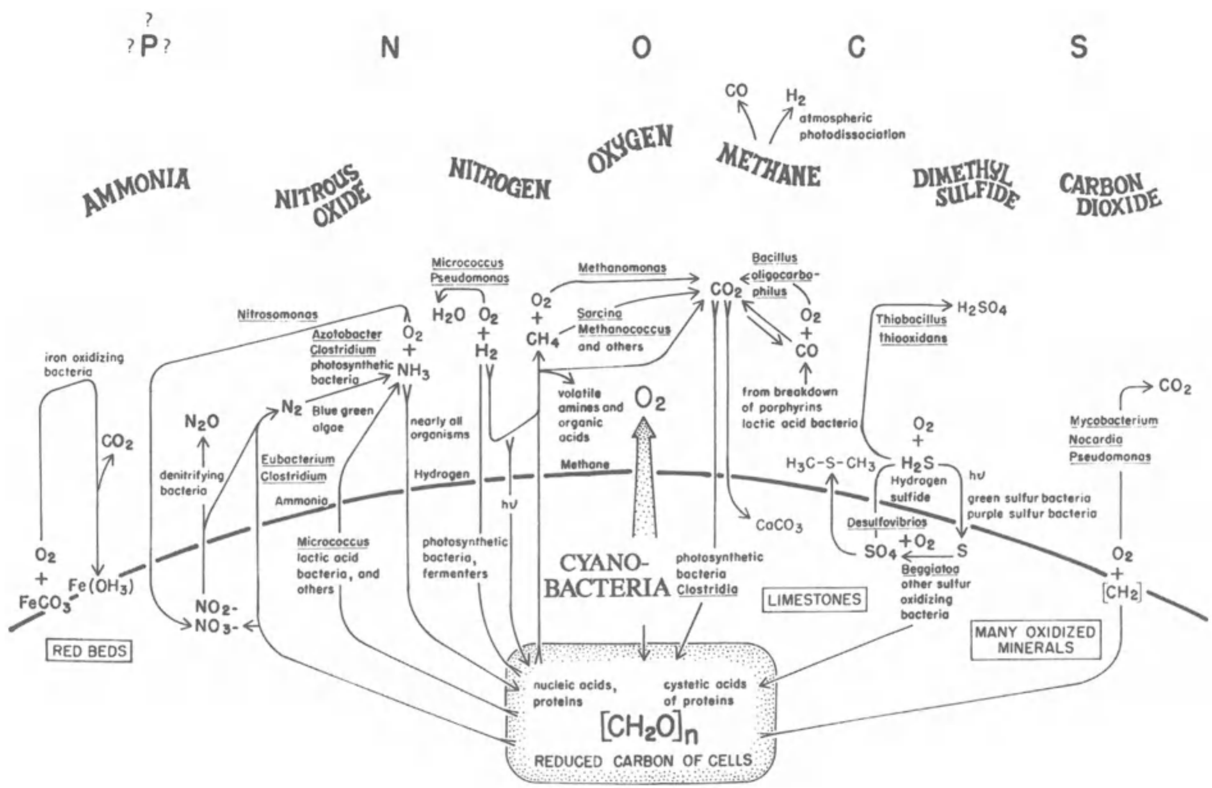

FIGURE 10.7. A reconstruction of possible microbial aerobic cycles: 2000 million years ago. Drawing by Laszlo Meszoly.

mous potential perturbations—at least the increase in solar luminosity and the transition to the oxidizing atmosphere. The Earth atmosphere maintains chemical disequilibria of many orders of magnitude containing rapidly turning over gases produced in prodigious quantities. The temperature and composition seem to be set at values that are optimal for most of the biosphere. Furthermore, the biosphere has many potential methods for altering the temperature and composition of the atmosphere (Margulis and Lovelock 1974). The biosphere has probably had these methods available almost since its inception more than 3000 million years ago. Is it not reasonable to assume that the lower atmosphere is maintained at an optimum by homeostasis and that this maintenance (at the ultimate expense of solar energy, of course) is performed by the party with the vested interest: the biosphere itself?