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

BY LYNN MARGULIS AND JAMES E. LOVELOCK

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 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 (1).

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 (2). 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 —

The Gaia Hypothesis ("Gaia" is pronounced to rhyme with papaya) treats the anomalous Earth atmosphere as an artifact of life and comprehends the planet itself as a single life.

The two old puzzles — 1) How does the bizarre Earth atmosphere maintain itself? and 2) How does fragile Earth life maintain itself? — solve each other. It took two remarkable scientists — Margulis & Lovelock — meeting outside their specialties to discover that convergence.

Lynn Margulis is a microbiologist at Boston University. Her best-known contribution is the symbiotic theory of the origin of complex cells (her book Origin of Eukaryotic Cells *is reviewed on p. 41). Popularization of that theory in* The Lives of a Cell *won Lewis Thomas a National Book Award last month. He even perpetuated Dr. Margulis' misspelling — "Myxotricha paradoxa" (should be Mixotricha, she notes).*

James Lovelock is the envy of every scientist, a successful free-lancer. Working out of a thatched cottage in the Salisbury Plain, England, this biospheric chemist has accumulated some 69 patents — most of them in what he calls "gas pornography" — chromatographic analysis of gases at the parts-per-billion level. The New Scientist *recently wrote of him, "In some ways, Jim Lovelock — begetter of the Gaia hypothesis — is one of the last of the old-style natural philosophers. A scientist who works from his own home because he believes that lack of security encourages creativity, he has invented — among other things — 'a magnificent Pandora's box', the electron capture detector gas chromatograph. Most sensitive of the analytical chemist's tools, it has been responsible for arousing concern about pesticide residues and Freons in the stratosphere, and may yet help to show that, thanks to Gaia, our fears of pollution-extermination are unfounded."*

It is an honor for The CoEvolution Quarterly *to be the first non-specialist American publication to carry the Gaia Hypothesis. Margulis and Lovelock will doubtless take some flak for appearing in suspect company — condom evaluations, poetry, and such — but both seem comfortable that their science is sound enough to withstand the science-plus context. We are grateful to Carl Sagan, who put us in touch with Lynn Margulis, and to* Natural History *editor Alan Ternes, who will publish an expanded version of this article in his magazine in September or October.*

Gaia is an old idea. She is one of the four primary divine beings of the Ancient Greeks — Chaos (Space), Gaia (Earth), Tartarus (the Abyss), and Eros (Love). But Gaia is still a new hypothesis, containing more questions than answers.

It is too early for proofs, conclusions, or morals, beyond the one increasingly obvious, that as long as human activity works against the self-balancing of biosphere and atmosphere there is no Teilhardian noosphere in evidence, just a damned human cartel.

In Gaia we are — all — Tangled Up In Blue.

— SB

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form a homeostatic system, and that these properties are themselves products of evolution (3, 4).

From recent articles and books (e.g., 5 and 6) 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. Man's impact on the atmosphere may have been overestimated. Man is only one of some three million species on Earth, all of which exchange gas and most of which exchange gas with the atmosphere. Man has been around for only a few million years while microorganisms have existed for thousands of millions of years. It is probably not so much the products of the several billion smaller organisms living in every pail of rich soil or water.

It seems to us that early 20th Century nonmicrobiological analysis of the Earth's lower atmosphere will one day be considered as ignorant as early 19th Century nonmicrobiological analysis of fermentation or disease is today.

In an excellent introduction to atmospheric science Goody and Walker (7) say, "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 atmosphere is an inert part of the inorganic environment and therefor amenable to methods of study that involve only physics and chemistry.

In this paper 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 (8). The purpose of this paper 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.

Lynn Margulis

Gaia

It appeared to us that the Earth's biosphere was able to control at least the temperature of the Earth's surface and the composition of the atmosphere. Prima facie, the atmosphere looked like a contrivance put together co-operatively by the totality of living systems to carry out certain necessary control functions. This led us to the formulation of the proposition that living matter, the air, the oceans, the land surface were parts of a giant system which was able to control temperature, the composition of the air and sea, the pH of the soil and so on so as to be optimum for survival of the biosphere. The system seemed to exhibit the behaviour of a single organism, even a living creature. One having such formidable powers deserved a name to match it; William Golding, the novelist, suggested Gaia – the name given by the ancient Greeks to their Earth goddess . . . .

Man's present activity as a polluter is trivial and he cannot thereby seriously change the present state of Gaia let alone hazard her existence. But there is an aspect of man's activities more disturbing than pollution. If one showed a control engineer the graph of the Earth's mean temperature against time over the past million years, he would no doubt remark that it represented the behaviour of a system in which serious instabilities could develop but which had never gone out of control. One of the laws of system control is that if a system is to maintain stability it must possess adequate variety of response, that is, have at least as many ways of countering outside disturbances as there are outside disturbances to act on it. What is to be feared is that man-the-farmer and man-the-engineer are reducing the total variety of response open to Gaia.

(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.) Since 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 (7). Some of these are shown in Tables 1 and 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 (6). The Earth's atmosphere defies simple description. From the point of view of chemistry it sustains such remarkable disequilibrium that Sagan (9) 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."

[more →]

James Lovelock

TABLE 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	a few months	from methane oxidation (methane from bacteria)
Ammonia (NH_3)	0.006	0	1.5	0	a 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)	0.000000000114	0	?	?	?	algae?

*Gaian = nonhuman biological sources.

The growing human population of the Earth is leading us to use drastic measures to supply this population with resources, of which food has prime importance. Natural distribution of plants and animals are being changed, ecological systems destroyed and whole species altered or deleted. But any species or group of species in an ecological association may contribute just that response to an external threat that is needed to maintain the stability of Gaia. We therefore disturb and eliminate at our peril; long before the world population has grown so large that we consume the entire output from photosynthesisers, instabilities generated by lack of variety of response could intervene to put this level out of reach . . . .

Now for one more speculation. We are sure that man needs Gaia but could Gaia do without man? In man, Gaia has the equivalent of a central nervous system and an awareness of herself and the rest of the Universe. Through man, she has a rudimentary capacity, capable of development, to anticipate and guard against threats to her existence. For example, man can command just about enough capacity to ward off a collision with a planetoid the size of Icarus. Can it then be that in the course of man's evolution within Gaia he has been acquiring the knowledge and skills necessary to ensure her survival?

Excerpted from "The Quest for Gaia",
by James Lovelock & Sydney Epton,
The New Scientist, *6 Feb 75*

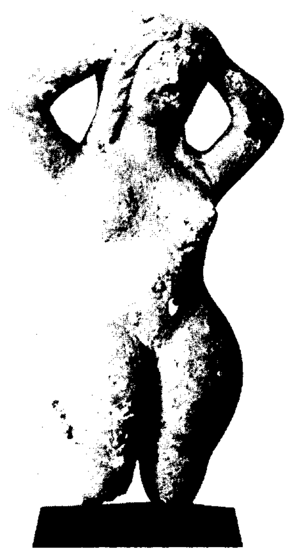
TABLE 2. Composition of the atmosphere: gases in disequilibrium

Gas	Abundance	Flux (moles/yr x 10^{13})	Disequilibrium factor	Oxygen used up in the oxidation of these gases (moles/yr x 10^{13})	Source of gas % contribution by abiological process	Source of gas % contribution by biological process: human	Source of gas % contribution by biological process: gaia*
Nitrogen	78%	3.6	10^{10}	11	.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	.02	0	>99
Carbon monoxide	0.08 ppm	2.7	10^{30}	1.4	.001	10	90
Ammonia	0.01 ppm	8.8	10^{30}	3.8	0	0	100

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

TABLE 3. Some critical biological elements that may be naturally limiting

Element	Use in biological systems	Possible form of fluid transport
MAJOR ELEMENTS		
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, NO_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 (27)
TRACE ELEMENTS		
I (iodine)	limited to certain animals (e.g., thyroxine)	methyl iodide
Se (selenium)	enzymes of fermenting bacteria (production of ammonia, hydrogen; animals (26))	unknown (dimethyl selenide?)
Mo (molybdenum)	nitrogen fixation enzymes of bacteria & blue green algae; carbon dioxide reductase (*Clostridium*)	unknown



Gaia – the Greek personification of Earth as a goddess. Terra cotta statuette from Tanagra; in the Musee Borely, Marseille. From Encyclopedia Britannica.

Table 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 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 to 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.

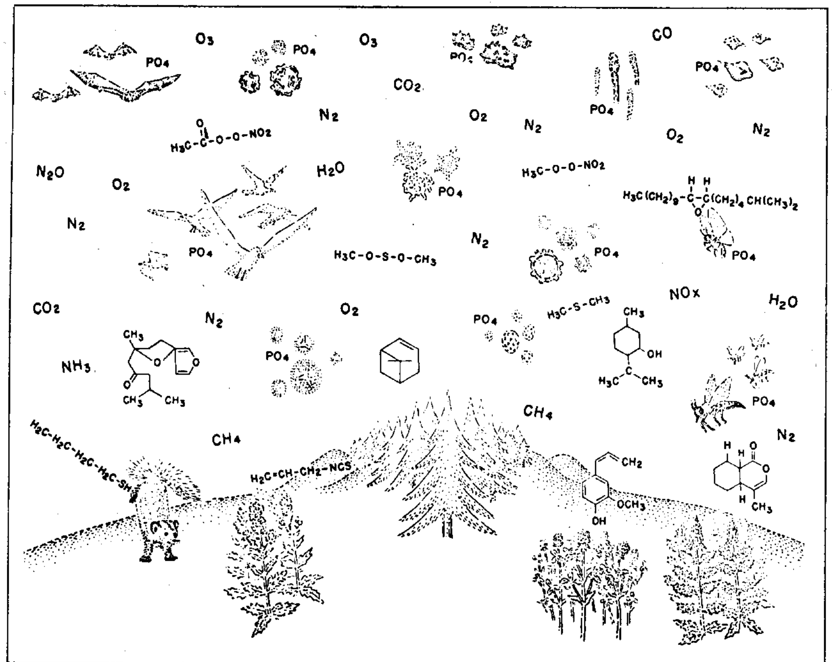


FIGURE 2. Earth's atmosphere at present: examples of major volatiles. (Key: the following compounds and spores are in the picture. It is left to the reader to identify them. See 28 for many details.) Spores of: ferns, club mosses, zygomycetes, ascomycetes, basidiomycetes, slime molds, bacteria. All contain 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); unknown; PAN (paroxacetyl nitrate), dimethyl sulfide, dimethyl sulfoxide; gases: nitrogen, oxygen, methane, carbon monoxide, carbon dioxide, ammonia.

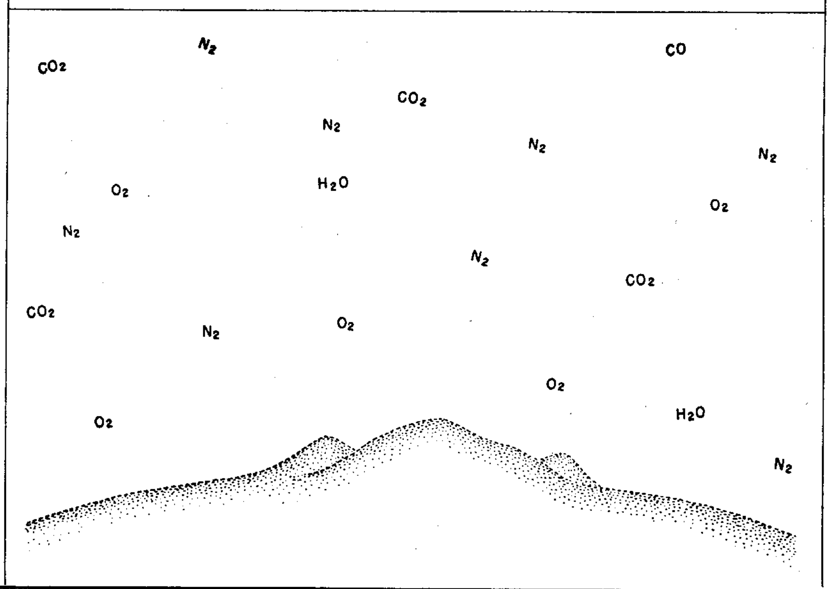


FIGURE 3. The present atmosphere were life deleted. *[Also see CQ cover.]*

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 (10). 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 x 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, i.e., 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 elements that are limiting to life on the land, and large quantities of methyl iodide and dimethyl sulfide were in fact observed (11).

Given the Gaia hypothesis one deduces that all the major biological elements (Table 3) must either be not limiting to organisms (in the sense that they are always readily available in some useful chemical form) or they 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 that 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,

The atmosphere, therefore, is the mysterious link that connects the animal with the vegetable, the vegetable with the animal kingdom.

–Dumas and Boussingault, 1844

nor on the earth is it expected that gases of elements that do not enter metabolism as either metabolites or poisons will cycle rapidly; (e.g., 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 (12).) 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 (8) for discussion.] Since, for example,

Gaia and cybernetics

There is little doubt that living things are elaborate contrivances. Life as a phenomenon might therefore be considered in the context of those applied physical sciences which grew up to explain inventions and contrivances, namely thermodynamics, cybernetics and information theory.

The first cautious approach to a classification of life, reached general agreement as follows 'Life is one member of the class of phenomena which are open or continuous reaction systems able to decrease their entropy at the expense of free energy taken from the environment and subsequently rejected in a degraded form' (Bernal, 1951; Wigner, 1961).

This may also be expressed in the form of the equation of continuity for entropy (Denbigh, 1951).

$$\varrho \frac{dS}{dt} + \operatorname{div} S = \theta$$

Where θ is the rate of internal creation of entropy, ϱ the density and S the entropy; div S is the outflow of entropy and $\varrho(dS/dt)$ the rate of change of entropy in the enclosed region; θ must by second law be zero or positive; the possibility that div S can be large and positive makes possible a negative trend for $\varrho(dS/dt)$.

This classification is broad and includes also phenomena such as vortices and flames and many others. Life differs from such primitive processes of the abiological steady state in the singularity, persistence and size of the entropy reduction it sustains. Although limited, this phenomenological description of the class of process, which includes life, is helpful in our search for proof of the existence of Gaia in two ways. Firstly by serving to define the boundary of the internal region where entropy is reduced and secondly by suggesting that the recognition of a living entity can be based upon the extent of its physical and chemical disequilibrium from the background environment.

On the matter of boundaries, it is obvious that a man, as an example of a living entity, takes in free energy in the form of the chemical potential difference between food and oxygen and sustains a low internal entropy through excretion of waste chemicals and heat. To a man, the environment to which entropy is discarded includes the atmosphere and his boundary is therefore his skin. It might seem pointless therefore on Earth to seek the existence of a general living system, Gaia, in terms of entropy reductions within the atmosphere which clearly for some species is a sink for degraded products and energy but this neglects the fact that photosynthetic life uses premium radiation direct from the sun to sustain a high chemical potential gradient within the atmosphere on a planetary scale. For a tree, the boundary within which entropy is reduced is not its surface in contact with the atmosphere but rather the interface between the sun with the

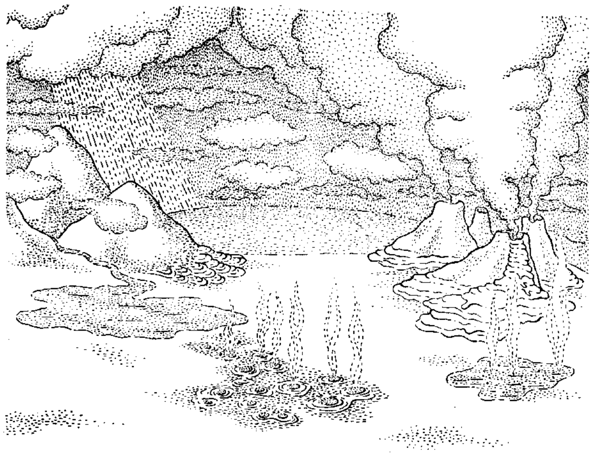


FIGURE 4. Scene from a geothermal area in Fig Tree times (about 3400 million years ago).

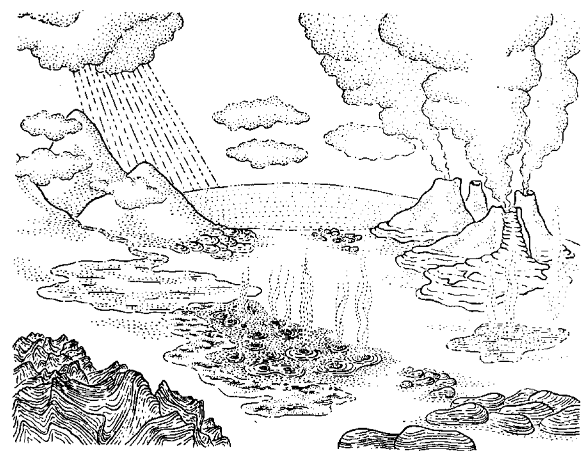


FIGURE 5. Scene from a geothermal area in Gunflint times (about 2000 million years ago). *[Also see* CQ *cover.]*

no volatile form of phosphorus has ever been found in the atmosphere, and since 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 2 and 3 rather fancifully compare the Earth's atmosphere at present to 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

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atmosphere as an extension of the tree. The tree produces not only food for consumers but also the equally important gas, oxygen, which does not accumulate within the tree waiting to be eaten.

When the whole assembly of life is so seen it is clear that the true boundary is space. The outgoing entropy flux from the Earth indeed from Gaia 'if she exists', is long wavelength nfra red radiation to space. This then, is the physical justification for delineating the boundary of life as the outer reaches of the atmosphere. There is also to a lesser extent an inner boundary represented by the interface with those inner parts of the Earth as yet unaffected by surface processes. We may now consider all that is encompassed by the bounds as putative life. Whether or not Gaia is real will depend upon the extent to which the entropy reduction within a compartment uch as the atmosphere is recognisably different from the biological steady state background.

On the matter of recognition a debt is owed to the fertile oncept of information theory, Shannon & Weaver (1963). t has been demonstrated, for example, by Evans (1969) that he classical properties, entropy and free energy, have exact information theoretic equivalents. Thus the information *(I)* f a system can be defined as

$$I = S_0 - S$$

where S_0 is the entropy of the components of the system at thermodynamic equilibrium and S the entropy of the system assembled. This relationship can be transferred directly from information theoretic to classical thermodynamic terms as follows:

$$I = (E + PV - TS - \Sigma N, N_i)/T$$

where the right hand side of the equation expresses information in terms of temperature *(T)*, pressure *(P)*, internal energy *(E)*, volume *(V)*, entropy *(S)*, and the chemical potential *(N)* of the molecules present; it follows that information is a measure of disequilibrium in the classic sense and recognisability in the information theoretic sense.

By examining the extent to which the atmosphere is in chemical and physical disequilibrium both within itself and with the surface of the Earth we have a measure of the extent to which it is recognisable as a separate identity against a neutral background equilibrium state. Whether or not it is seen to be a component part of Gaia will depend upon the size of the disequilibrium revealed.

Excerpted from "Atmospheric Homeostasis by and for the Biosphere: The Gaia Hypothesis", by James Lovelock & Lynn Margulis, Tellus *1974, (1-2).*

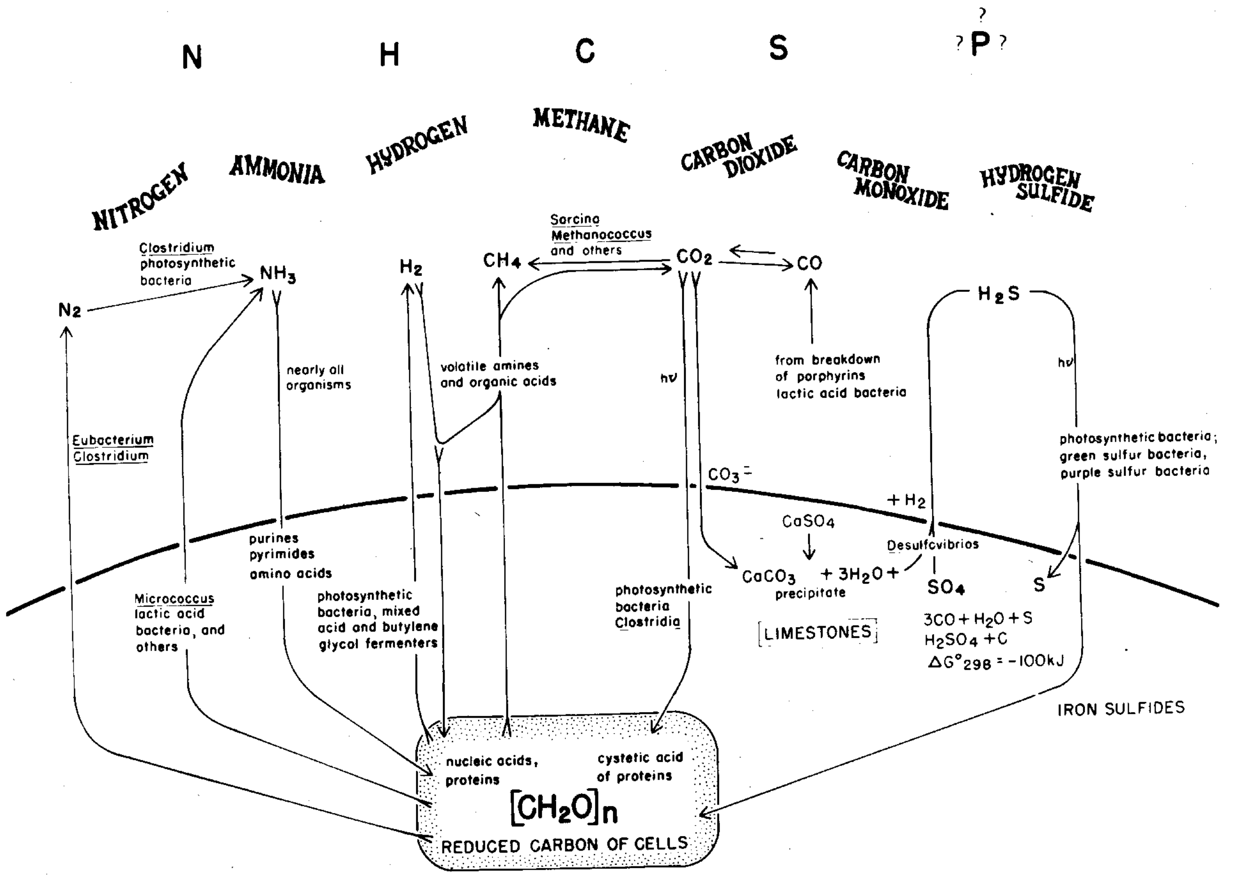

FIGURE 6. A reconstruction of possible anaerobic cycles: 3400 million years ago (genera of microorganisms catalizing the reactions are underlined).

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 (13). 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 (e.g., contained more ammonia) or the earth was frozen. The most likely hypothesis is that the earth's atmosphere contained up to about one part in 10^5 ammonia, a good infrared absorber (14). Other potential "green house" 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 (14). [There are good arguments for the rapid photodestruction of any atmospheric ammonia (15).] However, it has been argued that ammonia is required for the origin of life (16), and there is good evidence for the presence of fossil microbial life in the earliest sedimentary rocks [3400 million years ago (17).] There is no geological evidence that since the beginning of the earth's stable crust the entire 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 (17, 18). 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 metazoan animals (out of about 2 million species) that can complete their life cycles in the total absence of O_2 (19). All animals are composed of cells that divide by mitosis. The mitotic cell division itself requires O_2 (20). 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 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, since concentrations of atmospheric oxygen only a few per cent higher than

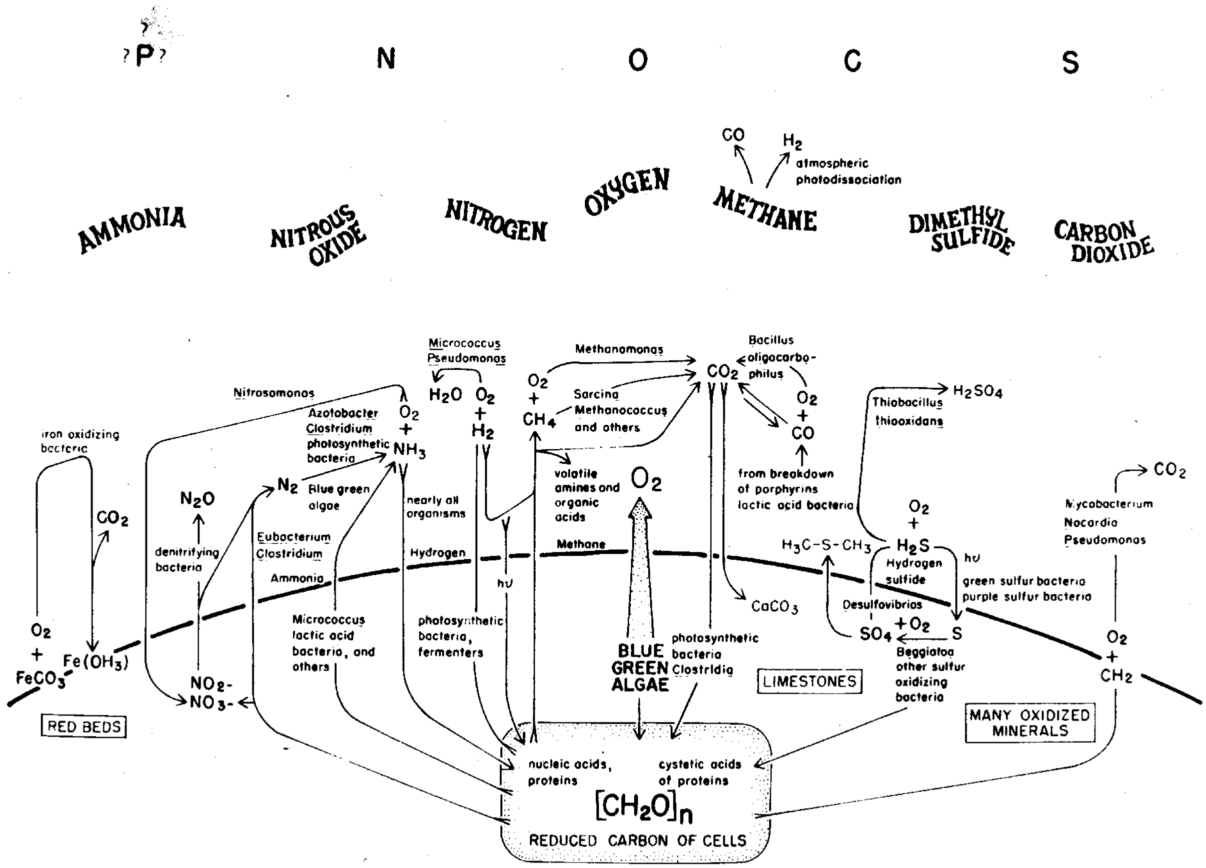

FIGURE 7. A reconstruction of possible microbial aerobic cycles: 2000 million years ago.

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 (21).

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 3 can be instructive. For one can see that even though absolute amounts of the gases vary over about 3 orders of magnitude, the fluxes are remarkably similar. These gases are produced and removed primarily by nonhuman biological processes. [See Table 1 and (8).] 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 (8) 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 (17). 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 (in the form known as the blue green algae, cyanophytes) were almost certainly responsible for the original transition to the oxygen-containing atmosphere about 2000 million years ago (17, 18).

Figures 4 and 5 present scenes before and after the transition to oxidizing atmosphere respectively. Figures 6 and 7 are reconstructions of anaerobic cycles corresponding to Figures 4 and 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 6, are available within the group of anaerobic prokaryotic microbes today. Since at the higher taxonomic levels (kingdoms and phyla) once successful patterns evolve they tend not to become extinct (22) 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 stromatolitic rocks were deposited. With the evolution of oxygen-releasing metabolism by blue-green algae came the stromatolites. These layered sediments are extremely common, especially in the late Precambrian (23). With the stromatolites comes other Precambrian evidence for the transition to the oxidizing atmosphere sphere. By the middle Precambrian, about 2000 million years ago — the time at which the stromatolites and microfossils become increasingly abundant (24, 25) — the scene might have looked like that in Figure 5. The metabolic processes accompanying that scene are shown in Figure 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 6 and 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 enormous 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 (8). 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? ■

ACKNOWLEDGMENTS

We are grateful to J. R. Williams for excellent editorial aid; to Prof. G. E. Hutchinson, E. S. Barghoorn, H. D. Holland, and J. C. G. Walker for critical suggestions; to Laszlo Meszoly for Figures 2-7 and to NASA NGR22-004-025 for research support.

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Origin of Eukaryotic Cells

It would be difficult to decide whether to place Margulis' book on the shelf next to Kropotkin's **Mutual Aid** *or next to* **Of Molecules and Men** *by Francis Crick. The book is no doubt one of the first statements in a revolution that will rock the Sciences and then the Arts and Social Sciences. Despite the difficulty of microbiological terms and concepts, anyone capable of reading* **Origin of Eukaryotic Cells** *should certainly do so. Sometimes Margulis' prose shines like a black gem:*

"In the late Pre-Cambrian, organisms of all descriptions inhabited the seas and lakes, covered the soil, and formed spores in the air. Some resembled free-living spirochetes, some resembled free-living aerobic eubacteria, and some resembled today's mycoplasms."

In the 19th century when microscopes had been sufficiently developed scientists noticed that the organelles in cells resembled free-living organisms and that the cell seemed to be an assemblage of smaller independent organisms evolved together into a unit.

This view was offensive to the new converts to Darwinism and the insight was swept under the rug. Margulis presents in great detail her compilation of information and research proving that the higher cell — any cell of any creature or multicellular being above microbe level — is indeed a combination of symbiotic partners that have evolved together. She demolishes, with facts, the idea that there is an evolutionary step between the primitive prokaryotic cell and the higher nucleated eukaryotic cell. The most apparent difference between the prokaryotic cell and the eukaryotic cell is the absence of a nucleus in the former and the presence of the nucleus in the latter.

Margulis establishes the separation between the prokaryotic and the eukaryotic cell as the major division of life. This theory replaces the traditional split between plant and animal kingdoms. Animal cells are basically symbiotic associations of three partners evolving together and plants are the same symbiotic cluster, but with the addition of a chlorophyll organism similar to the blue-green algae microbe.

Symbiotic associations of prokaryotic cells, in Margulis' assertion, become eukaryotic cells — or are the ancestors of eukaryotic cells.

Our scientists and social scientists have leaned heavily on a crude understanding of Darwin rather than on the subtleties of Darwin's thought. They have seen competition in all things. Margulis' work should force every science to re-examine itself for gross error — such as she has discovered in biology. The social sciences which have always been crudely Darwinistic or Behaviouristic should follow suit — and the same with the Arts. In Margulis' work there is, by inference, a solution to the mechanist/vitalist controversy over the nature of living matter. The simple prokaryotic cell is relatively inert and mechanical. When prokaryotic cells combine in symbiosis there is a "spiritual occasion" and the meat, the cytoplasm of the cell begins to flow — to move with obvious self volition and make complex swirls and streamings. This book is an extraordinary, beautiful new vision for those who can follow it — and a treasure for anyone interested in frontier science.

— Michael McClure

Origin of Eukaryotic Cells
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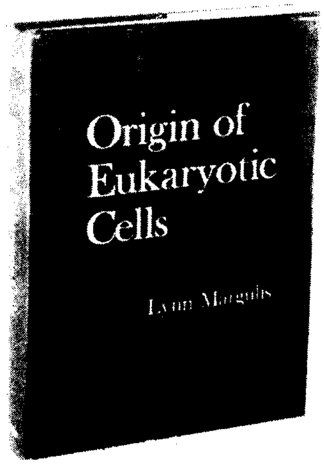
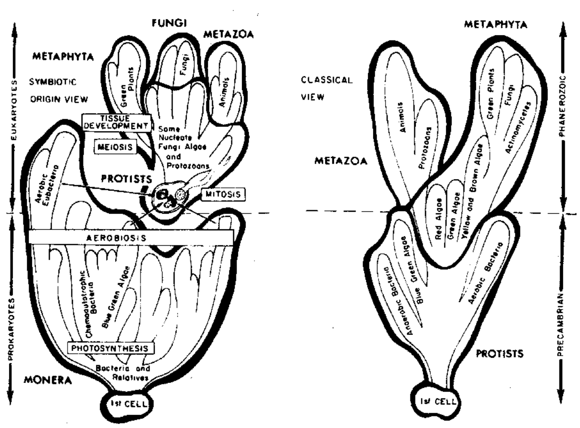
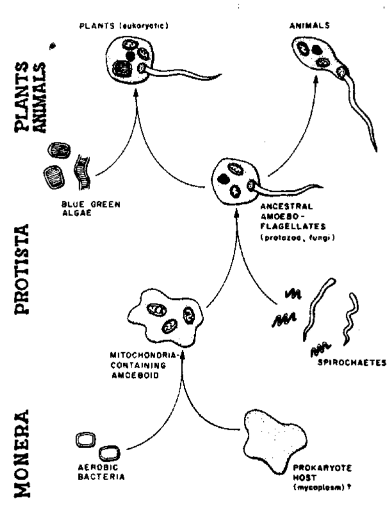




Comparison between the symbiotic and classical phylogenies of the lower organisms.

Evolution of the eukaryotic cell by serial symbioses



As pointed out by Simpson (1967), biology, unlike chemistry and physics, is a historical science.

•

The history of the modern eukaryotic line began when a pleiomorphic microbe, capable only of anaerobic fermentation of glucose to pyruvate, symbiotically harbored a smaller prokaryote. The endosymbiont microbe was an aerobe, a relative of extant aerobic eubacteria, having the biosynthetic ability to form cytochromes and to oxidize all of its foodtuffs completely to CO_2. Flavins, ubiquinone, cytochromes, were intermediate electron carriers in the total oxidation of carbohydrates by the small aerobic symbiont. This association, one of many bizarre and different types, many of which exist today, led to the formation of primitive amoebas. The host became the ground nucleus and cytoplasm, by definition the *protoeukaryote*. It harbored the eubacterial aerobe (by definition, the *protomitochondrion*) that later became mitochondria. From this association amoebas that contained extensive cytoplasmic membrane systems and formed food vacuoles subsequently evolved. Whole-cell predation became common. The aerobic symbiotic bacteria requiring more surface membrane for oxidation-reduction reactions differentiated into the cristae-containing mitochondria of today.