

## Gaia: The Planet Holobiont

Rainer MATYSSEK (München) and Ulrich LÜTTGE ML (Darmstadt)

With 1 Figure

*Dedicated to Prof. Dr. Otto L. LANGE on the occasion of his 85<sup>th</sup> anniversary.*

### Abstract

The strict definition of holobiont is that it is a host organism (plant or animal) in interaction with all associated microorganisms as an entity for selection in evolution. This definition can be generalized when not only microorganisms internal of or endogenous to a host organism are concerned but any regular organisms which strongly interact between each other also externally. Such latter associations may altogether function as co-evolutionary entities at the community level, as can be concluded from their evolutionary history. A thorough inspection of habitats and ecosystems shows that such kinds of mutualistic associations prevail. Therefore, we can scale up examples of endogenous symbioses to ecosystems, biomes and the entire biosphere as holobionts, where the planet holobiont is Gaia. James LOVELOCK defines Gaia as the biosphere being a self-regulating entity that ensures the planet's capacity for harboring life by controlling the chemical and physical environment in conducive ways. Thus, the question is of whether Gaia manages a global equilibrium which sustains life on Earth. Possibly this holds for life as such but not for any specific forms of life as illustrated by several extinction waves of organisms during geological history. Such events were typically followed by the emergence of innovative new forms as arising from adaptive radiation into abandoned ecological niches. Will man be subject of the next extinction wave? Such a possibility raises ethical imperatives for man to sustain the biosphere *sensu* Gaia on which he not only depends, but also is part of. Holobiont research must aim at gaining advanced understanding, both in mechanistic and holistic terms, by extending the holobiont concept across the spatio-temporal scales of ecological organization. This implies to delineate the humble position of man in the biosphere and to explore conditions for man's sustained survival on Earth.

### Zusammenfassung

In ihrer strengsten Form besagt die Definition von Holobiont, dass er ein Wirtsorganismus (Pflanze oder Tier) in Wechselwirkung mit allen assoziierten Mikroorganismen als eine Einheit für Selektion und Evolution ist. Es liegt nahe, die Definition so zu verallgemeinern, dass nicht nur interne oder endogene Mikroorganismen in einem Wirt gemeint sind, sondern generell typische Organismen, die auch extern intensiv miteinander interagieren. Assoziationen dieses Typs können zusammengenommen als in Co-Evolution geformte Einheiten auf der Ebene der Organismengesellschaften angesehen werden. Dies folgt auch aus der evolutionären Geschichte. Sorgfältige Beobachtungen in Standorten und Ökosystemen zeigen, dass solche mutualistischen Assoziationen sogar die Regel sind. Wir können deshalb von Beispielen endogener Symbiosen zu den Skalierungsebenen der Ökosysteme, Biome und der ganzen Biosphäre als Holobionten aufsteigen, wo die ganze Erde als Holobiont dann als Gaia identifiziert wird. JAMES LOVELOCK definiert Gaia als die selbst-regulierende Einheit Biosphäre. Danach soll durch ihr Vermögen, unseren Planeten durch die Regulation der chemischen und physikalischen Umwelt gesund und lebensfähig zu erhalten, die Biosphäre *sensu* Gaia die Kapazität unseres Planeten sichern, Leben zu beherbergen. Die Frage, die also gestellt werden muss, ist, ob Gaia wirklich ein globales Gleichgewicht gewährleistet, das das Leben auf der Erde dauerhaft trägt. Dies trifft vermutlich auf das Leben als solches zu, aber nicht auf ganz konkrete Formen des Lebens. Der Gedanke wird durch die verschiedenen Aussterbewellen von Organismen in geologischer Zeit veranschaulicht. Auf solche Ereignisse folgten typischerweise immer Innovationen und das Auftreten neuer Formen von Organismen durch adaptive Radiation in verlassene ökologische Nischen. Wird der Mensch, die Art *Homo sapiens*, von der nächsten Aussterbewelle mit erfasst sein? Diese Möglichkeit stellt dem Menschen den ethischen Imperativ, die Biosphäre *sensu* Gaia zu erhal-

ten, von der er nicht nur abhängig, sondern deren Bestandteil er auch ist. Die Holobiont-Forschung muss nach einem vertieften Verständnis der Mechanismen und holistischen Zusammenhänge trachten, indem das Holobiont-Konzept über die verschiedenen Skalierungsebenen ökologischer Organisation verfolgt wird. Die schließt ein, des Menschen bescheidene Position in der ganzen großen Biosphäre und als Teil von Gaia zu erkennen und zu lernen, welche Bedingungen unumstößlich sind, um das nachhaltige Überleben des Menschen auf der Erde zu gewährleisten.

## 1. The Concepts of Gaia and Holobiont

In ancient Greek mythology Gaia is the mystical goddess of the Earth. Broad-breasted Gaia is Mother Earth. The contemporary Gaia concept was advanced by the famous environmentalist James LOVELOCK in the 1960s to 1970s (LOVELOCK 1979). He defines Gaia as “a complex entity involving the Earth’s biosphere, atmosphere, oceans and soil”, where Gaia is “a shorthand for the hypothesis [...] that the biosphere is a self-regulating entity with the capacity to keep our planet healthy by controlling the chemical and physical environment”. Keeping the planet healthy means sustaining the planet’s capacity for harboring life. With “biosphere” we refer in this essay comprising all life harbored by lithosphere, hydrosphere and atmosphere at the surface of our planet. Thus, providing conditions supportive of life, the biosphere arrives at being a self-regulating living organism. The biosphere is a dynamic system, stabilized *via* feedback coupling mechanisms so that our entire planet is considered to be one single living being, a supra-organism. By using another term we may say that Gaia, i.e. the biosphere, is the ultimate case of a holobiont. This facilitates our approach because we can first ask what is a holobiont? Then we can look for examples of holobionts which allow extrapolation to Gaia.

The basic and strict definition of holobiont is that it is a host organism (plant or animal) in interaction with all associated microorganisms as an entity for selection in evolution.

One of the best examples for this is man himself. Man is the host of innumerable bacteria on his skin, in his mouth, in his intestine and elsewhere in the body. In our digestive system each of us carries a good kilogram of bacteria with him. This amounts to 10 to 100 bacterial cells per human body cell. It comprises several hundred different species of bacteria. The number of genes of the bacteria in our body is about 100 to 150 fold the number of genes in our own genome. Taken together we can name the integral of the genetic information provided by the host and its associated microorganisms the hologenome of the holobiont. Without these bacteria, not only our digestion would not function. They have many other beneficial effects. For example without these bacteria our immune system could not be established and attain functional maturation. Biologically man can only live and survive as a holobiont with all these bacteria (LA RECHERCHE 2010b).

If we underline the term *interaction* in the above definition and if we generalize from microorganisms to organisms in general – of the same or another species – we do not substantially modify the definition in reaching higher spatio-temporal scales of biological organization. However, with respect to man this already leads us to perform a step of enormous consequences. With the extension to man’s cultural means of interaction and globalization, arising from his biological evolution, the entire mankind as an abstraction may be considered as a holobiont.

Before we pursue this to eventually arrive at the entire biosphere and Gaia it is worth mentioning that there is a wealth of other examples when briefly viewing the animal kingdom. Among the mammals we can name the ruminants with their rich internal fauna of ciliates mediating digestion of cellulose, and other herbivores, such as horses or rabbits with bacteria in their intestinal appendices. These are examples of symbioses.

Let us take the term symbiosis very general as it was used originally by DE BARY (1879) and as it is frequently done again now, i.e. meaning the association of different organisms closely living together. Thus, there are symbioses either with advantage to the partners (mutualistic relations) or with exploitation of one partner by another (parasitism) or with mutualistic and parasitic interactions of different partners at the same time. This evidently implies that symbiotic systems are holobionts. A holobiont already is a supra-organism with interactions and synergism of its parts (including parasitism and food chains in view of co-evolutions of host-parasite and predator-prey systems, respectively).

Resuming the above introduced generalized holobiont definition or concept, in addition to endogenous symbioses also biotic interactions between separate organisms in the same environment may be envisaged, e.g. systems which have been subject to very intimate co-evolution. The best examples are obligate mutualistic pollinator systems, such as bees and flowers. This generalization of the definition of holobiont is quite logical. Co-evolved systems produce competition and facilitation. Although for competition this may not be intuitively evident, in fact both may increase fitness of the organisms involved, which generalizes rather than widens the holobiont definition. Nevertheless, the reached scope of consideration paves the avenue for a gradual approach to the entire biosphere as the supra-organism Gaia. We shall explore this in Section 2.

When James LOVELOCK introduced the Gaia hypothesis he faced controversy from two angles, namely (i) from the scientific point of view that the history of life on Earth has shown that the biosphere is not that stable that one might be able to talk of stabilization or equilibrium, and (ii) the philosophical point of view that referencing Gaia as the mystical goddess of the Earth might imply moving from science to metaphysics. The first one is a matter of interpretation as we shall view it in Section 3. Regarding the second one LOVELOCK considers the concept purely scientific. When in his book (LOVELOCK 1979) there is conjecture, such speculations are clearly scientific, i.e. open to investigation and experimental examination. LOVELOCK explicitly refrains from any metaphysical implications. However, as we shall see in Section 4, notably on the one hand man is biologically part of the biosphere and hence of the Gaia holobiont, and on the other hand, given his cultural evolution as a spin-off from biological evolution, man is performing as if he were the master of nature. Such a specificity of man is conducive to developing metaphysical projections, particularly in an ethical perspective.

## **2. Scaling Holobionts from Organisms to Biosphere**

We can explore nature for examples of holobionts on different levels of scaling from microscopic organisms up to the biosphere and try in this way to advance from the holobiont concept in its original strict sense (see above) to the Gaia concept. The following examples will be chosen from plant life.

### *2.1 The Endosymbiosis Theory of the Eukaryotic Cell*

The endosymbiosis theory of the evolution of eukaryotic cells was first conceived by A. F. W. SCHIMPER (1883) and then elaborated in detail in 1905 by the Russian scholar K. MERESHKOWSKI. A serial ingression is claimed to have occurred *via* phagocytosis by non-compartmented ancestral cells of prokaryotes capable of respiration and of cyanobacte-

ria-like prokaryotes performing photosynthesis, respectively. As failure of digestion proved beneficial, the phagocytized cells were kept as endosymbionts, evolving to mitochondria and chloroplasts, respectively, during the further course of symbiogenesis. Originally, it was a daring hypothesis up to the 1960s when new cytological techniques, especially the advent of electron microscopy, opened new breakthroughs. The eucyte concept developed by Eberhard SCHNEPF (SCHNEPF 1966) with among others studying the extant endosymbiosis of *Geosiphon* (see Section 2.5), and subsequently modern developments of cytology, biochemistry, genetics and molecular biology made the endosymbiotic origin of eukaryotic cells a widely accepted theory (see Chapters 1.6.2 and 1.6.3 of LÜTTGE et al. 2010). Symbiogenesis and evolution make eukaryotic cells the best examples of holobionts in the strictest sense of the original definition, where a holobiont is a host organism constituting in interaction with all associated microorganisms an entity for selection in evolution. As a consequence actually all eukaryotic organisms from the very beginning of their evolution carry the holobiont syndrome along with them.

## 2.2 Virus-Infected Unicellular Organisms

Many photosynthesizing prokaryotic cyanobacteria and eukaryotic microalgae are infected by viruses. For example it is estimated that about 20% of all such organisms in the marine phytoplankton have a virus (SUTTLE 1994). The scalar level of these associations is from fractions of micrometers (viruses) to several tens of micrometers (algae). The associations of cells and viruses are most interesting within a perspective of holosymbiont evolution. Viruses of the unicellular eukaryotic green algae of *Chlorella* contain a mosaic of prokaryotic and eukaryotic genes. They may be related to the last common ancestor. Algal viruses and their genes have a long evolutionary history (VAN ETTEN 2003).

## 2.3 Symbioses between Unicellular Organisms

Some *Chlorella* species live as hereditary endosymbionts with freshwater or marine organisms (REISSER 1992). They are also called *Zoochlorella*. An interesting example is the symbiosis of two unicellular eukaryotic organisms with the ciliate *Paramecium bursaria* being the host of endosymbiotic *Chlorella* (KARAKASHIAN 1975, SMITH and DOUGLAS 1987). Inside the cells of *Paramecium Chlorella* is protected from virus infection. The scalar level is 90 to 150 µm.

## 2.4 Lichens

Lichens are ecto-symbioses. They are holobionts of a fungus (mykobiont) and photosynthetically active symbiotic prokaryotic cyanobacteria (cyano-lichens) or eukaryotic green algae (chloro-lichens) as the phycobionts, living in very close extracellular association. Some lichens have both types of green phycobionts (and photobionts), i.e. green algae as well as cyanobacteria. The morphological appearance of lichens is determined by the mykobiont. It is noteworthy that the lichen holobionts attain a very characteristic gestalt. It is so specific that one can distinguish lichen “species” and perform lichen taxonomy, where the mykobionts are determining the names of the various lichens. The scalar level is in the range of centimeters to decimeters.

## 2.5 *Geosiphon*

*Geosiphon pyriformis* is an endosymbiosis of a fungus and cyanobacteria of the genus *Nostoc*. Again there is formation of specific gestalt. When the hyphae of the fungus get in contact with the appropriate strains of *Nostoc* they ingest the *Nostoc* cells phagocytotically and form characteristic bladders where they retain their *Nostoc* phyto- and photobionts. This is the characteristic gestalt of the *Geosiphon* holobiont which is only formed when the cyanobacteria are present. Beyond this, *Geosiphon* is also part of higher holobiotic integration. In addition to the cyanobacteria there are also bacteria of yet unknown phylogenetic affiliation in the bladders. In the field *Geosiphon* is closely related with bryophytes, such as *Anthoceros* and *Blasia*, which house the same *Nostoc* as exosymbionts and which may exchange *Nostoc* with *Geosiphon* and among each other. Moreover, all three of them are interconnected and may even be connected to grasses by mycorrhiza. The fungus of *Geosiphon* belongs to the phylum Glomeromycota and is closely related to the fungi which form vesicular-arbuscular mycorrhizas. With *Geosiphon pyriformis* itself we are at the scale of several hundred micrometers, but with the higher holobiont integration we arrive at the scale of mini-ecosystems of centimeters to decimeters (KLUGE et al. 2002, Chapter 29.2.1.4 in LÜTTGE et al. 2010).

## 2.6 *Endosymbioses and the Evolution of the Various Lineages of the Algae*

An establishment of holobionts related to evolution of species and associated with the formation of very characteristic gestalt is most impressively seen among the algae. The endosymbiosis theory of the evolution of compartmentalized eukaryotic cells states that mitochondria and chloroplasts originated from prokaryotic endosymbionts initially acquired by phagocytosis (see Section 2.1). Thus, eukaryotic cells can be considered as holobionts. Among the algae such holobionts were established frequently and polyphyletically as it is revealed by the structure of chloroplast envelopes. Chloroplasts with a double membrane envelope originated from primary endosymbiosis, where endosymbionts were prokaryotic green cells. Chloroplasts with a triple membrane envelope resulted from secondary endosymbiosis, where endosymbionts were eukaryotic green cells and the external membrane of the phagocytotically acquired symbionts was degraded. Chloroplast with a quadruple membrane envelope are due to tertiary endosymbiosis, where the endosymbionts obtained carried already chloroplasts with a triple membrane envelope. We can see that the staggered formation of endosymbioses or holobionts led to different divisions of the alga with the specific gestalt of their species ranging from microscopic scales to meters and even many tens of meters (see LÜTTGE et al. 2010), e.g.:

- double membrane envelope: rhodophyta, heterokontophyta and chlorophyta;
- triple membrane envelope: dinophyta, euglenophyta;
- quadruple membrane envelope: cryptophyta.

## 2.7 *Cuscuta Linking Different Host Plants*

The holoparasites of the Convolvulaceae genus *Cuscuta* (see Chapter of Ralf KALDENHOFF, this volume) form long thread-like pale shoots which wind around their host plants. For parasitism they form haustoria penetrating into the shoots of the host and making contact to both phloem and xylem. Individual *Cuscuta* plants can grow simultaneously on different host plants of different species. In this way they can interconnect host species between each other.

It is observed that even viruses can move along these connections from plant to plant. The consortium as a whole can be regarded as a holobiont. The scalar level is that of whole plants in the order of magnitude of meters.

## 2.8 Quorum Sensing and the Formation of Bacterial Biofilms

Many surfaces are covered with biofilms, which are mucilaginous excretions of bacteria embedding their colonies as a joint medium that provides protection and enables for metabolic communication. Biofilms occur on surfaces of and within other organisms, in some cases becoming pathogenic, e.g. *Pseudomonas aeruginosa* infecting the lung. In addition, biofilms are found on surfaces of buildings and other objects around human settlements.

Bacteria can sense their local cell density. This is called quorum sensing (WATERS and BASSLER 2005). Originally the term quorum comes from the times of the Roman Empire where it referred to a fixed minimum number of members to make the proceedings of an assembly or society valid. Bacteria use a variety of different molecules, named autoinducers (AI) or pheromones, as signals of cell density in a bacterial population. In Gram-negative bacteria the most common AI is acyl-homoserine lactone (AHL) (review: MATHESIUS and WATT 2010). The AIs act as transcriptional regulators once they reach a threshold concentration. Thus, quorum sensing is used by the bacteria to coordinate their gene expression and their behavior including the formation of aggregates and biofilms as their density increases. Quorum sensing can occur within a single bacterial species as well as between different species. Biofilms are often made up of a variety of interacting microorganisms.

Plants have evolved strategies to modulate bacterial biofilms and to defend themselves. They can interfere with the quorum sensing signals of bacteria by producing compounds which mimic quorum sensing signals. Such compounds either block or stimulate AHL-regulated quorum sensing in bacteria (review: MATHESIUS and WATT 2010).

Quorum sensing and the formation of bacterial biofilms are very illustrative with respect to the definition of holobiont. Individual bacterial cells are parts of a decentralized system which with its self-organizing communication networks can create a new supra-organism, i.e. the biofilm, with completely new properties and behavior. For example *P. aeruginosa* does not become aggressive as long as its cell density is too low to avoid the risk of being destroyed by the host's immune system. However, the population becomes pathogenic if the bacterial density is high enough to form a biofilm. Similarly, pathogenic bacteria on the surface of plants, e.g. in the rhizosphere, may escape the plant's defense before they can overwhelm it. Through signaling within biofilms, bacterial communities perform like multicellular organisms (MATHESIUS and WATT 2010) – i.e. in this way become holobionts.

## 2.9 Soil Crusts

Similar to biofilms are the globally important but more complex soil crusts (BELNAP and LANGE 2001), which represent layers of soil particles that adhere to each other *via* contacts with (micro-)organisms and/or their excretions. Such layers have a thickness of a few millimeters up to centimeters but can extend over quite large surfaces. They are found especially on apparently bare surfaces of the sand of dunes, in savannas and deserts and other dry sites where larger vegetation cannot get established or forms gaps. They constitute a complex community of organisms with cyanobacteria, eukaryotic algae, fungi, lichens and

bryophytes and small animals (non-vertebrates). Also associations of such kinds may be considered as holobionts.

### 2.10 Rhizosphere and Forests

In the tropics plants of the genus *Ficus* may begin their life as epiphytes on trees. Subsequently they form aerial roots which gain ground-contact. With secondary growth the aerial roots supporting and carrying their crown can look like stems. Often many such pseudostems of one individual may appear like a forest. The most famous example is a tree of *Ficus bengalensis* described by WALTER and BRECKLE (1984), which was only 26 m tall but had an average crown diameter of 170 m, a crown circumference of 530 m and a crown area of 22,000 m<sup>2</sup>. However, such a pseudostem forest really is still one individual and therefore not a supra-organism or holobiont.

It may be a different matter with clones. In herbaceous plants they often originate in nature from ramet networks of rhizomes or stolons. The largest clones of vascular plants are found among trees of the genus *Populus*. In the Qira Oasis of the Taklimakan desert (Hotan Province, Chinese Xinjiang Uygur Autonomous Region, China) a clone of *Populus euphratica* Oliv. of a size of at least 4 ha has been identified by molecular fingerprinting using amplified fragment length polymorphism (AFLP) (BRUELHEIDE et al. 2004). The largest clones known in the world are of *Populus tremuloides* Michx., i.e. in the Wasatch Mountains in Utah, North America, with 42.9 ha (GRANT 1993) or even larger elsewhere (81 ha: KEMPERMAN and BARNES 1976). When we consider genetically identical members of such clones as individuals these clones are evidently supra-organisms or holobionts.

Still more closely covered by the holobiont-concept appear to be root symphyses between different tree individuals of same species. Such structures are direct anastomoses which result from intergrowth between roots and may form stand-level networks. They may compare in function with clonal rhizome systems, however, with the exception of being hetero-vegetative structures. Such networks evidently also represent holobionts, although their ecological meaning is poorly understood.

Viewing entire forests as holobionts certainly climaxes when we realize the intensive tree-microbe interactions and mycorrhiza in the rhizosphere. The roots of plants in the soil are surrounded by a myriad of microorganisms, some of which have evolved to form mutualistic or pathogenic relations. Others are helper bacteria for the establishment of the fungi/tree symbiosis of mycorrhiza. This is a network with complex rhizosphere signaling systems (review: MATHESIUS and WATT 2010). There is quorum sensing and microbes build up biofilms (see Section 2.8). The complexities of quorum sensing in structured microbial communities growing in the rhizosphere are quite sophisticated so that the concept of “efficiency sensing” has been developed (HENSE et al. 2007). It combines (i) the functions of quorum sensing by regulating gene expression and coordinating group behavior in response to population density (see Section 2.8) with (ii) sensing distance by incorporating the sensing of diffusion by regulating gene expression in response to mass flow in the surrounding medium. Efficiency sensing takes into account that the AI concentration sensed by bacteria is a combination of AI synthesis, chemical and biological turnover and diffusion characteristics in the environment (review: MATHESIUS and WATT 2010).

The hyphae of the mycorrhiza fungi create extended networks with the fungi, bacterial biofilms and tree roots connected among each other in the soil. In the ectotrophic mycorrhiza

with trees fungal hyphae grow around the fine roots creating a coat of hyphae which also penetrate into the apoplast of the cortex of the roots forming the so called HARTIG net which serves the exchange of metabolites and mineral nutrients. Hyphae of individual fungi can interconnect different trees. In this way entire forests can become holobionts, where the scalar level may be up to square kilometers (Chapter 29.2.2 in LÜTTGE et al. 2010). This led to the association of “www = wood-wide web” to stress the capacity of hyphal networks to reach largely extending spatial scales.

### *2.11 Ecosystems*

Ecosystems in general may be considered as holobionts. The living organisms in ecosystems develop a plethora of interactions, such as competition and facilitation including competition for space (GRAMS and LÜTTGE 2010), predation, symbiosis with both mutualism and parasitism, and many others. Life itself is always affecting its environment. Organisms occupy niches and have niche specialization. Their activity may create new niches. Thus, ecosystems are highly dynamic systems the conditions of whose existence can be stabilized by the complex interactions of all organisms present. Ecosystems are self-regulating to the extent that external perturbations do not become too severe. The scale of ecosystems in special cases may be quite small, e.g. in the cases of biofilms or soil crusts (see above), or may reach many square kilometers. At this stage, we are approaching the scale and concept of Gaia.

### *2.12 Biomes*

After WALTER and BRECKLE (1991, 1999) we globally distinguish nine zonobiomes from the equator to the Arctic and Antarctic. In addition, azonal orobiomes and pedobiomes exist as well as extrazonal local biomes. Biomes are composed of ecosystems and on such higher integrated level we may also consider them as holobionts. The zonobiomes attain global dimensions scaling at thousands of square kilometers.

### *2.13 Biosphere*

Moving up the various scalar levels with integrations of increasingly complex subsystems, we systematically approach the biosphere globally integrating all life on the planet. Its immediate subsystems are the biomes. Interdependence of the biomes is vividly recognized and realized by the current global climate debate. The biosphere as the boundary on Earth between the atmosphere and the lithosphere organically is Gaia. Some forms of life are found almost everywhere on the Earth's outer surface including land and oceans so that its  $510 \cdot 10^6$  square kilometers are the scalar level attained by the holobiont Gaia.

## **3. Gaia: a Global Equilibrium**

We have seen that the central argument of the Gaia hypothesis is that the biosphere is a dynamic system with self-organization through feedback stabilization. The critique concerns the question if therefore equilibrium and steady state are to be presumed. In a strict thermodynamic sense only closed systems can approach equilibrium with the establishment of



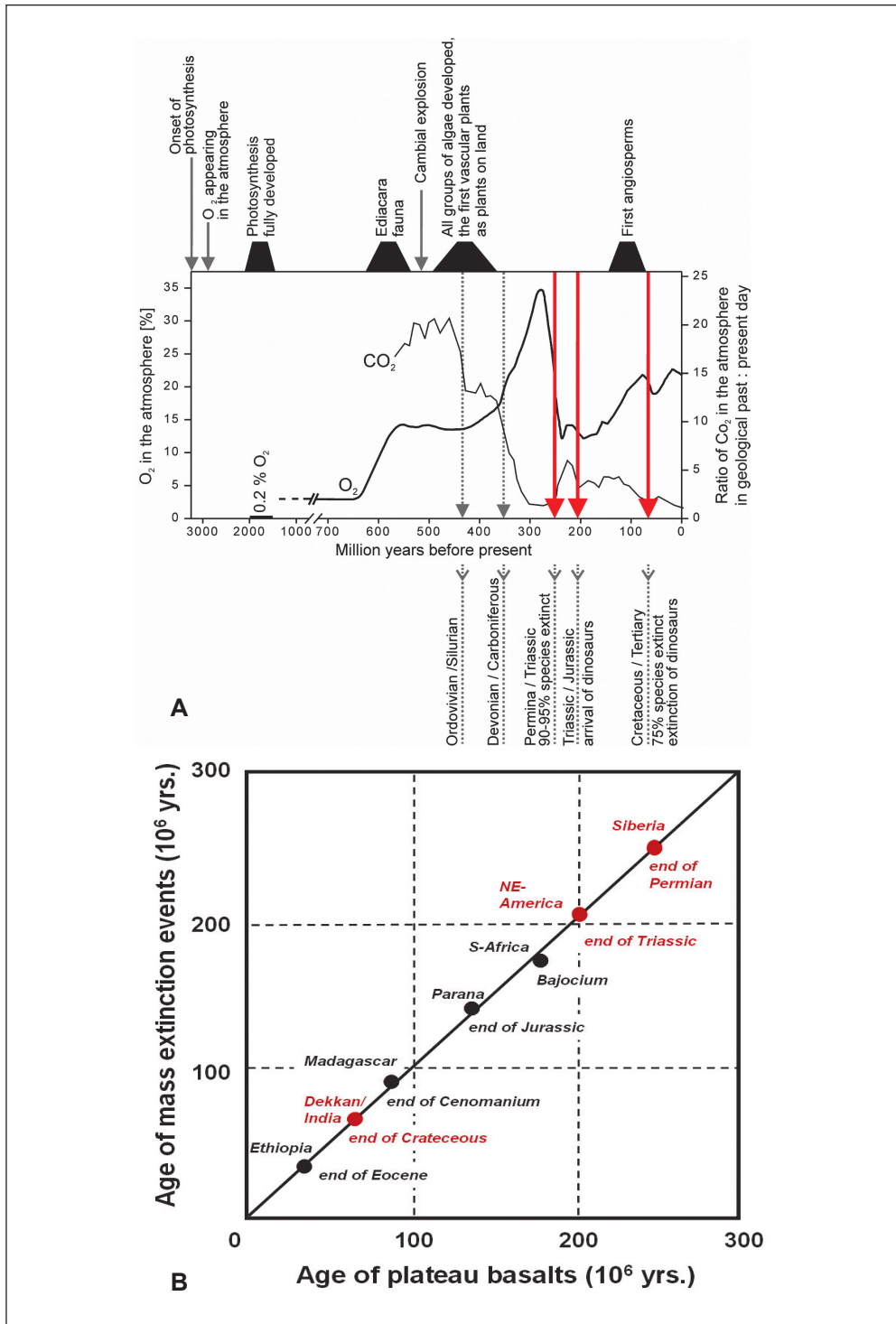
steady state. Conversely, all living organisms are open systems through which there is a continuous flow of matter and energy. This includes ecosystems and holobionts. They can at best approach some kind of dynamic equilibrium which is also termed pseudo steady state. A simple cybernetic technical example of an open system is a water reservoir with an inflow and outflow and a control device that should maintain the water table of the reservoir at a constant level. The control device is operated *via* a sensor which can check the actual level of the water table against the set desired constant level. Regulation by the control device occurs *via* taking into account the feed-forward of inflow and the feed-back of outflow. All feed-back and/or feed-forward systems intrinsically bear non-linear dynamics. Our reservoir, therefore, is also a system with non-linear dynamics. During its regulation oscillations of the water table to be regulated are occurring. When regulation fails the system may get chaotic. As long as this is not the case, the permitted amplitudinal size of oscillations around the pseudo steady state to still talk of acceptable regulation is only an arbitrary issue. However, it is implicit in these considerations that all living systems as open systems are governed by non-linear dynamics.

Evidently the biosphere as a whole also is such an open system. The consideration of oscillations in cybernetic regulation systems is highly pertinent to the Gaia concept. LOVELOCK actually takes the occurrence of such a mechanism as a proof for the possible existence of Gaia: “The discovery of such a system, operating on a global scale and having as its goal the establishment and maintenance of optimum physical and chemical conditions for life, would surely provide us with convincing evidence of Gaia’s existence.”<sup>1</sup> The goal here can be taken as meaning the set point of the cybernetic system. The critical question to be asked is whether the observed fluctuations of the conditions for and of the forms of expression of life itself in the biosphere are so large that we cannot accept the hypothesis that life stabilizes itself on our planet? Should we question stabilization of special forms of life, and if so which kind of forms? Or should we rather talk of stabilization of life as such in whatever form it may be expressed?

Indeed there were very large fluctuations of the conditions for life during the more than  $3.5 \cdot 10^9$  years of the history of life on our planet (Fig. 1). Most important for the conditions of life are the atmospheric gases oxygen and carbon dioxide (BERNER 1994). In LOVELOCK’s (1979) concept of Gaia’s self-regulation of environmental conditions favorable for life, the atmosphere plays a predominant role. He views the atmosphere as “an extension of the biosphere”, i.e. *sensu stricto*, the part supportive of life. The accumulation of oxygen in the atmosphere is thought to be mainly due to the activity of life itself, i.e. as a consequence of photosynthesis. Presumably after the onset of oxygenic photosynthesis on Earth the O<sub>2</sub> evolved was first bound by oxidation of iron in the Earth crust and gypsum formation (SCHLESINGER 1997) before accumulating in the atmosphere. About  $2 \cdot 10^9$  years ago atmospheric O<sub>2</sub> concentration was about 0.2%. Then it began to rise with considerable fluctuations over the times (Fig. 1). Atmospheric CO<sub>2</sub> is consumed by photosynthesis and – across geological time scales – by sedimentation, from which CO<sub>2</sub> is currently released intensively back into the atmosphere by industrial activity of man. Also fluctuations in CO<sub>2</sub> were quite high during Earth history. Atmospheric CO<sub>2</sub> concentrations in the Earth’s atmosphere were more than 20-times higher in the Ordovician and still 10-times higher at the beginning of the Carboniferous period than today (Fig. 1). Still, the climate stayed supportive of life, as the solar constant was lower at that time than today by about 5%. Hence, one needs to consider atmospheric and solar fluctuations in concert to understand impacts on the biosphere. Perhaps, changes in the

---

1 LOVELOCK 1979, pp. 49–50.



atmospheric CO<sub>2</sub> level in response to the solar energy supply provide one strong argument in favor of the Gaia hypothesis. Conversely, major fluctuations in CO<sub>2</sub> are produced by geo-dynamical processes. On the one hand, volcanism liberates CO<sub>2</sub> from the Earth interior, while on the other hand, CO<sub>2</sub> is removed from the atmosphere upon crust formation (carbonates) and transport into the Earth interior *via* the process of subduction (as Earth tectonics force some continental plates to be submerged underneath others). Such geodynamic carbon cycling has time scales of around 10<sup>5</sup> years. It is unlikely, however, that changes in the solar constant and in geodynamics are intrinsically linked to each other.

Nevertheless, atmospheric temperature during early Earth history at times was that low so that the entire planet must have been covered by a thick layer of ice (snow ball Earth hypothesis: KIRSCHVINK 1992, ETIENNE 2008). Such situations prevailed during the Proterozoic 750 to 575 · 10<sup>6</sup> years ago. Also, solar constant was lower at that time than today, promoting glaciation (SCHRÖDER et al. 2008). Probably, glaciation was reinforced by subduction in the absence of high volcanic activity, draining the atmospheric CO<sub>2</sub> concentration to a rather low level, and hence, cooling the global climate. Given that complete glaciation for millions of years would have disrupted all photosynthesis-driven life in the oceans due to darkness underneath the mighty ice shell, a snow slush rather than snow ball stage is to be assumed, with incomplete or missing glaciation in the tropics (cf. NIELD 2007). Apparently, not even massive and prolonged planetary glaciation did eradicate life on Earth until eventually warming was re-introduced through huge global volcanic activity with an enormous release of CO<sub>2</sub> into the atmosphere. While the oldest known fossils of multi-cellular organisms discovered in Africa may date back 2.1 · 10<sup>9</sup> years (EL ALBANI et al. 2010, DONOGHUE and ANTCLIFFE 2010), this then led to an outburst of multi-cellular life, the Australian Ediacara fauna 630 – 542 · 10<sup>6</sup> years ago, followed by the Cambrian explosion of metazoic life 535–525 · 10<sup>6</sup> years ago (Fig. 1).

Due to the pronounced global fluctuations of climate there were also pronounced changes in the expression of forms of life (Fig. 1). We know of five large waves of massive species extinction during the last 450 million years occurring at intervals of 45 to 140 million years (100 million years on average), i.e.

- 444 million years ago at the change from the Ordovician to the Silurian,
- 364 million years ago at the change from the Devonian to the Carbonic,
- 251 million years ago at the change from the Permian to the Triassic, when 90–95 % of all existing species were extinct including the well-known trilobites,
- 206 million years ago at the change from the Triassic to the Jurassic, when extinction was associated with the appearance of the dinosaurs,
- 65 million years ago at the change from the Cretaceous to the Tertiary when 75 % of all existing species were extinct and with them the ammonites and also the dinosaurs, which led to the tremendous proliferation of the mammals on Earth.

Some of these waves of extinction appear to be correlated with changes of the atmosphere, i.e. the first one with increasing O<sub>2</sub> and decreasing CO<sub>2</sub>, the second one with an acceleration of

---

Fig. 1 (A) Changes of atmospheric levels of O<sub>2</sub> and CO<sub>2</sub> during the history of life on Earth, major forms and activities of life and important waves of extinction of species. (B) Correlation between events of mass extinction and outbursts of trapp volcanoes (along with their geographic locations), driven through “mantle plumes” in Earth magma (COURTILLOT 1995). Red color exemplifies major extinction events at the end of Permian, Triassic and Cretaceous each.

these changes especially that of increasing O<sub>2</sub>, the third one with decreasing O<sub>2</sub> and increasing CO<sub>2</sub>, the fourth one with a dip of both gases (Fig. 1). Particularly the high O<sub>2</sub> concentrations are intriguing causes of the massive species extinctions of up to 95%, in particular, hitting all those life forms during the early extinction waves adapted to an anaerobic world. LOVELOCK (1979) considers O<sub>2</sub> concentrations above 25% as disastrous for life (leading to spontaneous self-ignition with open flame even of moist organic matter; SCHLESINGER 1997).

The atmosphere fluctuations most likely were predominantly due to volcanism. Thus, specific periodic activities in volcanism are regarded to be one probable cause of the extinction waves, i.e. the outburst of so-called trapp volcanoes. These originate from a number of "hot-spots" in the mantle layer of the Earth's interior (not related to the edges of tectonic plates as in the case of other volcanoes), inducing "mantle plumes" (in German "Manteldiapire"), which carry upward streams of huge amounts of magma (COURTILLOT 1995). Upon breaking through the Earth's surface in cracks of hundreds of kilometers in length, in the case of "super-plumes" areas of hundreds to thousands of kilometers in diameter can be covered through a continuous lava outflow over some hundred thousands of years. During such periods, the planetary environment is changed dramatically. Decisive events are (i) reduction of irradiance and initial cooling of the global climate through particulate accumulation in the atmosphere, (ii) as a consequence of exhausts destruction of stratospheric ozone with increase of UV radiation at the Earth's surface, (iii) alkalization of the upper oceanic water layer upon volcanic particulate deposition, (iv) long-term warming through atmospheric CO<sub>2</sub> accumulation, and (v) acidification of precipitation upon intense SO<sub>2</sub> release by the continuous and massive volcanic activity. Evidently, such changes represent tremendous impacts on terrestrial and aquatic ecosystems with fundamental effects on primary producers and food chains so that massive species extinction is the consequence. Ten of such "super-plume" eruptions are known since life has conquered land, occurring on average by 30 to 40-million-year intervals. Seven of these events synchronize conspicuously with mass extinctions (as compared to those three other events that occurred on the ocean floor), including the most prominent ones at the transitions from Permian to Triassic and Cretaceous to Tertiary. The initiation of such "super-plumes" appear to relate to marked re-polarizations in Earth magnetism, mediated through periodic processes in 2000 km depth at the boundary between the Earth's mantle and the magnetic core. It is believed, therefore, that the last mass extinction of Cretaceous/Tertiary (ending the era of dinosaurs) at 65 million years ago was not solely caused by an asteroid impact, rather this impact was coincidental and only accelerated the species break-down after preceding weakening by volcanism (COURTILLOT 1995). It also appears that in geological terms the next "super-plume" eruption is overdue.

Regarding the questions asked above with respect to special forms of the expression of life on Earth, the answer clearly is: No, Gaia does not stabilize the existence of particular forms of life. On the other hand life as such was maintained. Innovations always accompanied extinctions. The most notable innovation was the evolution of respiration in response to the formation of O<sub>2</sub> by the early green prokaryotes performing oxygenic photosynthesis. This O<sub>2</sub> production as the waste product of photosynthesis was the first dramatic global pollution because the O<sub>2</sub> was highly poisonous for the originally evolved anaerobic organisms. Evolution of respiration first served detoxification of the O<sub>2</sub> and then proved to be the most profitable choice for maintaining energy metabolism in the vast majority of extant organisms. Much more recent innovations were the appearance of dinosaurs 206 million years ago and with the extinction of the dinosaurs the proliferation of mammals 65 million years ago.

An interesting example of biochemical innovations are the metabolic CO<sub>2</sub>-concentrating mechanisms for photosynthesis which began to evolve in the period of very low atmospheric CO<sub>2</sub> about 300 million years ago, towards the end of the Carboniferous period. (see Chapter 28.9 in LÜTTGE et al. 2010). Isoenzymes of the CO<sub>2</sub>-fixing phosphoenolpyruvate carboxylase (PEPC) emerged. This enzyme leads to the formation of the C-4 dicarboxylic malic acid, where the carbon atom 4 comes from fixed CO<sub>2</sub>, hence the term C<sub>4</sub> fixation. This supported the innovation the CO<sub>2</sub>-concentrating photosynthetic modes of crassulacean acid metabolism (CAM) and later C<sub>4</sub> photosynthesis. Between 300 and 150 million years ago the C<sub>4</sub>-PEPC isoenzyme of monocotyledons was separated, between 200 and 100 million years ago the divergence of monocotyledons and dicotyledons occurred and the C<sub>4</sub>-PEPC isoenzymes of dicotyledons and the CAM-PEPC were separated (Fig. 1; TOH et al. 1994, LAWS et al. 2002). CAM is rather old dating back to the Carboniferous. Extant relicts are succulent tropical ferns performing CAM. About 250 million years ago the genus *Isoëtes* with extant CAM-species branched off the other pteridophytes (LÜTTGE 2005). C<sub>4</sub> photosynthesis in single cells dates back 100 to 70 million years. C<sub>4</sub> grasses with a complex anatomical basis of C<sub>4</sub> photosynthesis evolved 25 to 12 million years ago and spread out about 8 to 6 million years ago while atmospheric CO<sub>2</sub> concentration declined continuously (Fig. 1). In the case of C<sub>4</sub> grasses, the high enzymatic CO<sub>2</sub> affinity was an ideal pre-adaptation to drought conditions, allowing for carbon gains similar to those of C<sub>3</sub> plants, but at reduced stomatal opening, and hence, transpiration.

From the point of view of biological evolution there is also no reason to assume a stable (pseudo-) steady state of the forms of life. Evolution of life is a vector in time. Species are not stable but subject to continuous change during Darwinian natural selection. This is independent of whether we accept DARWIN's gradualism, i.e. gradual evolution of new species by transformation of parent populations, or the punctualism of ELDREDGE and GOULD (GOULD 2002), i.e. rapid appearance of new species after longer periods of stasis. Terminating stasis new species arise from splitting of lineages and a small sub-population of the original parent population is the origin of the new species. Termination of stasis among other reasons may be induced by preceding mass extinctions (see above). In such latter terms, one may speak about the "survival of the luckiest", possessing the right features at the right time, rather than the "survival of the fittest", the specialized adaptations of which may become worthless through – in geological terms – "sudden" environmental discontinuities. It is exaptation *sensu* GOULD (2002) which then comes into play. Non-adaptive, i.e. effectively or nearly neutral features not directly built as adaptations for a current function, which persist the pressures of natural selection, can suddenly reveal evolutionary importance of a dormant cooption for utility in occupying new niches or *spandrels* in GOULD's metaphor.

The waves of extinctions and innovations and the time vector of evolution, both show that Gaia proved to be capable of stabilizing conditions such that they remained basically suitable for the existence of life on Earth. In this sense, the core of the Gaia hypothesis of LOVELOCK evidently is acceptable. So far! In a recent book LOVELOCK (2009) himself develops a more pessimistic view. Therefore, the next question is if life is imperative on Earth. This question leads to a consideration of the so called anthropic principle and touches the metaphysical domain as we shall see in the next section.

#### 4. Imperative Life on Earth

The concept of the anthropic principle arose out of physics because precisely the very given values of physical constants of nature in our universe permitted the evolution and the persistence of life. The basic principal physical PLANCK constants of time, length, mass, energy and temperature which  $10^{-43}$  s after the Big Bang began to determine causality describing the parameters for the velocity of light in the vacuum, the energy of photons and gravitation should not be even tiny bits different from what they are. The way they are allows the existence of life on our planet as we know it and possibly elsewhere in the universe. The weak anthropic principle says that our universe is built in a way making life possible. The strong anthropic principle says that its construction makes life unavoidable including the existence of thinking self-conscious beings such as man. GIERER (1998) calls it a meta-law of nature. The manifestation of the principle towards the initiation of life might be conceived then through the intrinsic capacities of carbon for building complex long-chained or cyclic molecular skeletons, readily reacting with O, N, P, and S as other elements of paramount importance for life, and most importantly, of interacting with liquid water in manifold ways. Of course, such characteristics are also subject to prevalent physico-chemical conditions allowing carbon to unfold its potential. The position taken by EIGEN (1992) differs, in that life *per se* may not be an inherent property of matter (although being associated with it), but that specific conditions are required for life to express itself. EIGEN does not claim a general physical theory to explain the origin of life – or, in other terms, if such a theory existed, then it should be able to mechanistically explain life to form reproducibly in its complexity (a pre-requisite currently not met). Being aware of the gradual transition between philosophy and natural science reflected by the above excursus, nevertheless, attempts to detect any traces of life in the universe might be associated with the search for carbon and liquid water in a physico-chemical environment similar to that on Earth (probably including appreciable amounts of molecular oxygen of photosynthetic origin in the atmosphere in view of the energy demand of life; SCHLESINGER 1997). In such a case, even encountering a self-regulated biosphere *sensu* Gaia would not appear to be *a priori* impossible.

One of the great virtues and the most sympathetic aspects of the Gaia concept is that it makes man part of the holobiont biosphere: “[...] if Gaia does exist, then we may find ourselves and all other living things to be parts and partners of a vast being who in her entirety has the power to maintain our planet as a fit and comfortable habitat for life”; “... from its origin the human species has been as much a part of Gaia as have all other species and ... like them it has acted unconsciously in the process of planetary homeostasis.”<sup>2</sup> Man arose from evolution within the biosphere, including his capacity of a cultural evolution. Apparently, it must have been an evolutionary advantage that his survival was not based exclusively on the development of specific anatomical structures or metabolic functions, but of intellectual capacities. Nevertheless, man depends on the biosphere. Most of its time, the biosphere was without man. Life on Earth began about  $4 \cdot 10^9$  years ago. The oldest fossils of green organisms available are the  $3.5 \cdot 10^9$  years old Australian stromatolites of cyanobacteria-like cells or biofilms. Man did not appear earlier than  $2 \cdot 10^6$  years ago. There were several species of man some of which lived simultaneously, but now only one species, *Homo sapiens*, is remaining (La Recherche 2008, 2010a):

---

2 Quotations from LOVELOCK 1979, pp. 1 and 128.

- *Homo rudolfensis* 1.9 million years ago,
- *Homo habilis* 1.9 to 1.44 million years ago,
- *Homo erectus* 1.9 to 0.5 million years ago,
- *Homo heidelbergensis* 0.8 to 0.3 million years ago,
- *Homo neanderthalensis* 0.2 to 0.03 million years ago,
- *Homo sapiens* since 0.2 million years until present.

Perhaps, it is not surprising that eventually just one species of man has survived – given his evolutionary history as a tribal carnivore driven by territorial instincts in combination with his intellectual capacities (HESCHL 2009). It appears that the encounter of two similarly evolved species inevitably would have led (or would lead) to the aggressive elimination of one of them – not permitting the co-existence of an almost identical and similarly capable competitor. Such a consideration is speculative if previous companion species within the genus *Homo* became extinct due to other reasons (as the pre-history cannot be unveiled to the full extent). However, the evolutionary heredity and related tribal behavior of man may bear intrinsically his eventual failure and disappearance as a species, because of three reasons: (i) being highly evolved, i.e. specialized, but decoupled from natural selection so that further biological adaptation cannot occur, representing an evolutionary “dead end”; (ii) being caught in his inherited tribal behavior, which limits further cultural evolution; so that (iii) exploitation of the biosphere will continue to far beyond the ecological capacities, under which man’s biological evolution had originally taken place.

Metaphysically JONAS (2003) has expressed the categorical imperative that man must exist on Earth – if evolution lasts long enough, given all the coincidences necessary, to eventually reach the required stage of highly complex biological organization. GIERER (1998) also thinks that the self-conscious man is an essential part of the nature of our universe. MORRIS (2003) much uses the phenomenon of convergence of the selective formation of structures and functions of organisms in phylogenetically separated lineages, e.g. the evolution of large brains in whales and dolphins and in man, to arrive at the conclusion that the evolution of man-like self-conscious thinking beings can occur repeatedly in a convergent way. It must not be overlooked, however, that the success of man does not only relate to his brain capacity, but also his ability to develop strategies of joint action with his conspecifics in highly abstracted ways (LOVELOCK 2009). MORRIS (2003) is convinced that if man would disappear from our planet new evolution would generate again thinking self-conscious beings. Moreover, he postulates that self-conscious beings like man must also have originated elsewhere in the universe. Notwithstanding such scientific reflections it appears that the quality of the argument that man must exist is metaphysical (JONAS 2003). From a purely scientific point of view we can easily imagine that life on our planet after a possible extinction of man might continue without man just as life on Earth was before man appeared. DIXON (1981) makes projections on a world after man into a future at about 50 million years from now, assuming man’s extinction upon degeneration due to the suspended natural selection. In parallel, DIXON accounts for principles in evolution which are derivable from the past in combination with the predictable continental drift and its global consequences for climate.<sup>3</sup> His approach, therefore, is not science fiction, but solidly anchored in our current knowledge on evolutionary processes. Winners in evolution after the loss of ecologically dominant species would be – as was the case

---

<sup>3</sup> DIXON 1981, p. 124.

in the past – either species with exadaptive features *sensu* GOULD (2002) or species with low specialization in their adaptations, being modest and generalists in their ecological demands. Such species possess best pre-requisites for subsequent adaptive radiation into abandoned ecological niches. In the past, this was the case, as we know, e.g. for the early mammals after the extinction of the dinosaurs. Again exemplifying mammals, in the future winners might be e.g. rats or rabbits, which currently are lowly specialized generalists, so that they appear to be ideal candidates for a potentially upcoming adaptive radiation. They might be able to newly conquer manifold ecological niches by diversely differentiating into the broad range of herbivores, carnivores and omnivores across all climate zones. Such evolutionary trends in the future do not invalidate the Gaia-hypothesis as it promises stabilization of the conditions of life as such and not of specific life forms as we have seen above.

If a particularly catastrophic extinction wave were to comprise all forms of life with higher complexity including man evolution of new innovations may start again from the bacterial prokaryotes. In fact evolution of prokaryotes at the origin of life on Earth was subject to a severity of selective forces beyond comparison with what we have today. For example UV-radiation was extreme. Radioactivity was also high. As we can calculate from the radioactive half life of uranium-235 and a current stock of 0.72 %  $^{235}\text{U}$  in the Earth's crust, the level of the radioactive element must have been 15 %  $^{235}\text{U}$   $4 \cdot 10^9$  years ago (LOVELOCK 1979). By contrast to the suggestion by Paul CRUTZEN to call our era the "Anthropocene", Stephen Jay GOULD demonstrates that notwithstanding the evolution of high complexity, even to date the prokaryotic bacterial organization still is the most successful mode of life on Earth, considering "persistence in place and constant growth in height"<sup>4</sup>: "We do not live in [...] 'the age of man' (1 species), or 'the age of mammals' (4000 species among more than a million for the animal kingdom alone), or even in 'the age of arthropods' (a proper designation if we restrict our focus to the Metazoa, but surely not appropriate if we include all life on Earth). We live, if we must designate an exemplar at all, in a persisting 'age of bacteria' – the organisms that were in the beginning, are now, and probably ever shall be [...] the dominant creatures on Earth by any standard evolutionary criterion of biochemical diversity, range of habitats, resistance to extinction, and perhaps [...] even in biomass." Again bacterial biofilms may become the first holobionts leading to evolution of more highly complex supra-organisms.

Nevertheless, it must be clear that the existence of life on Earth is not infinite in time. When will life cease on this planet? With the Gaia concept discussed in this essay we restrict ourselves to life on Earth. So, the question of when life is ceasing on our planet Earth is identical with the question of 'when is the holobiont Gaia dying'? The age of the universe is  $13.7 \cdot 10^9$  years. In  $5 \cdot 10^9$  years the Sun will become a so-called red giant, heat the surface of the Earth to over 1000 K and absorb the Earth's orbit before eventually ceasing to give energy. However, the conditions favorable for life may be lost earlier than that – probably already in  $10^9$  years from now. At that time, during the long process of becoming the red giant and eventually swallowing Earth, the Sun will begin to significantly increase its energy load to Earth, so that the planet will gradually dry out, losing all its liquid water (SCHRÖDER and SMITH 2004). Another scenario are subduction processes of geodynamics removing  $\text{CO}_2$  from the atmosphere towards the Earth interior within  $0.5 \cdot 10^9$  years which may lead to insufficient  $\text{CO}_2$  levels for photosynthesis as the basis of life (BOUNAMA et al. 2009). Thus, as life on Earth appeared  $4 \cdot 10^9$  years ago it may already have consumed, in the worst case, about 90 % of its total avail-

---

<sup>4</sup> GOULD 2002, Fig. 9–29, pp. 897 – 898.



able time of evolution. The much more recent *Homo sapiens* only used 0.05% of his possible time. However, subduction as the “killer” of Gaia appears to be less likely than the warming up of the Sun towards becoming the red giant. Earth appears to have stayed “juvenile” as compared to the companion planets Mars and Venus, given by the still intense tectonics on Earth as manifested by the ongoing continental drift, of which subduction is one facet. However, subduction is hardly imaginable without volcanism, releasing CO<sub>2</sub> back into the atmosphere. In fact, subduction and volcanism are two sides of the same medal (NIELD 2007). In this context, the active “conventional” volcanoes along the “seams” of continental plates are crucial, and there is no indication that tectonics may cease in the geologically near future.

Man is not only biologically part of and dependent on the Gaia/biosphere but from his cultural position he also influences it. Man assumes he “is the possessor of the planet, if not the owner” rather than “the tenant”. Conversely, “the Gaia hypothesis implies that the stable state of our planet includes man as a part of, or partner in, a very democratic entity”.<sup>5</sup> Does man really perform like a partner? Human exploitation of nature is enormous and progressive, for reasons of man’s evolutionary history (see above). There is pollution affecting the climate globally. The danger of wars with dreadful globally destructive nuclear weapons is not eliminated. Extinction through nuclear disaster, by purpose or accidentally, might even be an inherent part of man’s evolution, which enabled him to discover nuclear fission (NIELD 2007). Perhaps, Gaia is naturally doomed even to terminate itself as a stringent consequence of having been able to evolve man. Such a risk is high, as Gaia over time, i.e. during its own process of ageing, has become highly differentiated, which increases vulnerability as compared to early developmental stages (LOVELOCK 2009). However, as pointed out above, bacterial life is tough, perhaps even in the worst case withstanding nuclear contamination.

One major immediate risk for man, however, arises from the continued unbroken increase of the global human population. Man behaves like an “r-strategist” in population dynamics due to his cultural evolution reflecting exponential growth progressively in exploiting the biosphere, although he did biologically evolve as a “K-strategist”, adapted to make sustainable use of environmental resources by not exceeding a maximum population density. Catastrophic failure of population growth, however, is the ultimate fate of any “r-strategist” upon exhaustion of the available resources (some insect species are suitable examples). Until 1990 the arable land increased proportionally with the human population. Since then it stagnates at about  $230 \cdot 10^6$  hectares while population continues to increase to a predicted  $9 \cdot 10^9$  people by the year 2050. Arable land and resources, such as water and nutrients particularly phosphorus. For feeding them will become limiting. Will there be a sixth wave of extinction, a man made one in this case?

Evidently Gaia teaches us that we must further develop ethics. As biological part of the biosphere man shares many genes and evolution with the other organisms. Does that not create a strong ethical demand of protecting them? Due to man’s activities extinction of species is rapidly progressing, each of which is an invaluable and irreplaceable treasure and living natural heritage. Gaia comprises world-wide mankind. We need global world ethics (KÜNG and KUSCHEL 1989) for maintaining the dynamic equilibrium of Gaia. This is essential for sustaining and not destroying the very basis of our own existence. Science and metaphysics merge with the holobiont biosphere being the nurturing Earth-mother identified as Gaia. In the quest of harmony, what appears to be more appropriate than ending this essay with the

---

<sup>5</sup> Quotations from LOVELOCK 1979, p. 145.

words of James LOVELOCK, founder of the modern Gaia-concept: “It may be that the destiny of mankind is to become tamed, so that the fierce, destructive, and greedy forces of tribalism and nationalism are fused into a compulsive urge to belong to the commonwealth of all creatures which constitutes Gaia. It might seem to be a surrender, but I suspect that the rewards, in the form of an increased sense of well-being and fulfillment, in knowing ourselves to be a dynamic part of a far greater entity, would be worth the loss of tribal freedom.”<sup>6</sup> In his most recent book, however, LOVELOCK (2009) begins to become doubtful, if man will succeed, given his strong ties in behavior as a species, as imposed by his evolutionary heredity.

## 5. Outlook

Evidently the generalized holobiont concept with supra-organisms at increasing hierarchical levels with the climax of biosphere or Gaia as developed in this essay is intriguing. It bears enormous challenges for research both theoretically on conceptions and empirically on observations. Concepts of such kind bear the fascinations of the web of life on Earth, even at the scope of Gaia (regardless of liking or disliking in terminology the allusion to a goddess). Future research must aim to unravel the background of these fascinations (*i*) to advance man’s information and knowledge towards an understanding, (*ii*) to delineate man’s humble position in the biosphere, and (*iii*) to explore the conditions of man’s sustained survival on Earth, i.e. to give him a chance at least.

## Acknowledgements

We are much adepted to young members of the DFG-Sonderforschungsbereich SFB 607 for stimulating suggestions and thought-provoking ideas on the concept of holobiont and Gaia, namely Drs. W. ZU CASTELL, F. FLEISCHMANN, S. GAYLER, T. GRAMS, K. PRITSCH, T. RÖTZER and B. WINKLER.

## References

- BARY, A. DE: Die Erscheinung der Symbiose. S. 1–30. Straßburg: K. J. Trübner Verlag 1879
- BELNAP, J., and LANGE, O. L. (Eds.): Biological soil crusts: structure, function, and management. *Ecol. Stud.* 150, 1–503 (2001)
- BERNER, R. A.: Geocarb II: a revised model of atmospheric CO<sub>2</sub> over Phanerozoic time. *Amer. J. Sci.* 294, 56–91 (1994)
- BOUNAMA, C., BLOH, W. VON, und FRANCK, S.: Auf der Suche nach einer zweiten Erde. In: BÜHRKE, T., und WENGENMAYR, R. (Eds.): Geheimnisvoller Kosmos: Astrophysik und Kosmologie im 21. Jahrhundert. S. 52–59. Weinheim: Wiley-VCH 2009
- BRUELHEIDE, H., MANEGOLD, M., and JANDT, U.: The genetical structure of *Populus euphratica* and *Alhagi sparsifolia* stands in the Taklimakan desert. In: RUNGE, M., and ZHANG, X. (Eds.): *Ecophysiology and Habitat Requirements of Perennial Plant Species in the Taklimakan Desert*; pp. 153–160. Aachen: Shaker Verlag 2004
- COURTILLOT, V.: La vie en catastrophes – Du hasard dans l’évolution des espèces. Paris: Librairie Arthème Fayard 1995
- DIXON, D.: *After Man – A Zoology of the Future*. New York: St. Martin’s Press 1981
- DONOGHUE, P. C. J., and ANTCLIFFE, J. B.: Early life: Origins of multi-cellularity. *Nature* 466, 41–42 (2010)
- EIGEN, M.: *Steps Toward Life*. Oxford, UK: Oxford University Press 1992

---

<sup>6</sup> LOVELOCK 1979, p. 148.

- EL ALBANI, A., BENGTSON, S., CANFIELD, D. E., BEKKER, A., MACCHIARELLI, R., MAZURIER, A., HAMMARLUND, E. U., BOULVAIS, P., DUPUY, J. J., FONTAINE, C., FÜRSICH, F. T., GAUTHIER-LAFAYE, F., JANVIER, P., JAVAUX, E., OSSA, F. O., PIERSON-WICKMANN, A. C., RIBOULLEAU, A., SARDINI, P., VACHARD, D., WHITEHOUSE, M., and MEUNIER, A.: Large colonial organisms with coordinated growth in oxygenated environments 2.1 Gyr ago. *Nature* 466, 100–104 (2010)
- ETIENNE, J.: Sedimentary challenge to snowball earth. *Nature Geoscience* 1, 817–825 (2008)
- GIERER, A.: Im Spiegel der Natur erkennen wir uns selbst. Wissenschaft und Menschenbild. Reinbek: Rowohlt 1998
- GOULD, J. G.: The Structure of Evolutionary Theory. Cambridge, Massachusetts: Harvard University Press 2002
- GRAMS, T. E. E., and LÜTTGE, U.: Space as a resource. *Progr. Bot.* 72, 349–370 (2010)
- GRANT, M. C.: The trembling giant. *Discover* (Los Angeles) 84, 82–89 (1993)
- HENSE, B. A., KUTTLER, C., MÜLLER, J., ROTHBALLER, M., HARTMANN, A., and KREFT, J. U.: Opinion – does efficiency sensing unify diffusion and quorum sensing? *Nature Rev. Microbiol.* 5, 230–239 (2007)
- HESCHL, A.: Darwins Traum. Die Entstehung des menschlichen Bewusstseins. Weinheim: Wiley-VCH 2009
- JONAS, H.: Das Prinzip Verantwortung. Versuch einer Ethik für die technologische Zivilisation. Frankfurt (Main): Suhrkamp 2003
- KARAKASHIAN, M. W.: Symbiosis in *Paramecium bursaria*. *Symp. Soc. Exp. Biol.* 29, 145–173 (1975)
- KEMPERMAN, J. A., and BARNES, B. V.: Clone size in American aspens. *Can. J. Bot.* 54, 2603–2607 (1976)
- KIRSCHVINK, J. L.: Late Proterozoic low-latitude glaciations: the snowball earth. In: SCHOPF, J. W., and KLEIN, C. (Eds.): The Proterozoic Biosphere; pp. 51–52. Cambridge: Cambridge University Press 1992
- KLUGE, M., MOLLENHAUER, D., WOLF, E., and SCHÜSSLER, A.: The *Geosiphon/Nostoc* endosymbiosis. In: RAI, A. N., BERGENMANN, D., and RASMUSSEN, D. (Eds.): Cyanobacteria in Symbiosis; pp. 19–30. Dordrecht: Kluwer Academic Publishers 2002
- KÜNG, H., und KUSCHEL, K. J.: Wissenschaft und Weltethos. München: Piper 1989
- La Recherche*: Les Dossiers de la Recherche No. 32, August 2008
- La Recherche*: Les Dossiers de la Recherche No. 438, February 2010a
- La Recherche*: Les Dossiers de la Recherche No. 41, November 2010b
- LAWS, E. A., POPP, B. N., CASSAR, N., and TANIMOTO, J.: <sup>13</sup>C discrimination patterns in oceanic phytoplankton: likely influence of CO<sub>2</sub> concentrating mechanisms, and implications for palaeoreconstructions. *Funct. Plant Biol.* 29, 323–333 (2002)
- LOVELOCK, J.: Gaia. A New Look at Life on Earth. Oxford: Oxford University Press 1979
- LOVELOCK, J.: The Vanishing Face of Gaia – A Final Warning. New York: Basic Books 2009
- LÜTTGE, U.: Genotypes – phenotypes – ecotypes: Relations to crassulacean acid metabolism. *From Plant Taxonomy to Evolutionary Biology. Nova Acta Leopoldina N. F. Bd. 92, Nr. 342, 177–193* (2005)
- LÜTTGE, U., KLUGE, M., and THIEL, G.: Botanik. Die umfassende Biologie der Pflanzen. Weinheim: Wiley-VCH 2010
- MATHESIUS, U., and WATT, M.: Rhizosphere signals for plant – microbe interactions: Implications for field grown plants. *Progr. Bot.* 72, 125–161 (2010)
- MORRIS, S. K.: Life's Solution. Inevitable Humans in a Lonely Universe. New York: Cambridge University Press 2003
- NIELD, T.: Supercontinent: Ten Billion Years in the Life of Our Planet. London: Granta 2007
- REISSER, W. (Ed.): Algae and Symbioses. Bristol (UK): Biopress 1992
- TOH, H., KAWAMURA, T., and IZUI, K.: Molecular evolution of phosphoenolpyruvate carboxylase. *Plant Cell Environ.* 17, 31–43 (1994)
- SCHIMPER, A. F. W.: Über die Entwicklung der Chlorophyllkörner und Farbkörper. *Bot. Ztg.* 41, 105–120 (1883)
- SCHLESINGER, W. H.: Biogeochemistry – An Analysis of Global Change. San Diego (USA): Academic Press 1997
- SCHNEFF, E.: Organellen Reduplikation und Zellkompartimentierung. In: SITTE, P. (Ed.): Probleme der biologischen Reduplikation. S. 372–393. Berlin, Heidelberg, New York: Springer 1966
- SCHRÖDER, K.-P., and SMITH, R. C.: Distant future of the Sun and Earth revisited. *Month. Not. Roy. Astronom. Soc.* 386/1, 155–163 (2008)
- SMITH, D. C., and DOUGLAS, A. E.: The Biology of Symbiosis. London: Edward Arnold Ltd. 1987
- SUTTLE, C. A.: The significance of viruses to mortality in aquatic microbial communities. *Microbiol. Ecol.* 28, 237–243 (1994)
- VAN ETEN, J. L.: Unusual life style of giant *Chlorella* viruses. *Annu. Rev. Genet.* 37, 153–195 (2003)
- WALTER, H., und BRECKLE, S. W.: Ökologie der Erde. Bd. 2: Spezielle Ökologie der tropischen und subtropischen Zonen. Stuttgart: G. Fischer 1984
- WALTER, H., und BRECKLE, S. W.: Ökologie der Erde. Bd. 1: Ökologische Grundlagen in globaler Sicht. 2. Aufl. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung 1991

*Rainer Matyssek and Ulrich Lüttge*

WALTER, H., und BRECKLE, S. W.: Vegetation und Klimazonen. 7. Aufl. Stuttgart: Ulmer 1999

WATERS, C. M., and BASSLER, B. L.: Quorum sensing: Cell-to-cell communication in bacteria. *Annu. Rev. Cell Dev. Biol.* 21, 319–346 (2005)

Prof. Dr. Rainer MATYSSEK  
Technische Universität München  
Lehrstuhl Ökophysiologie der Pflanzen  
Hans-Carl-von-Carlowitz-Platz 2  
85354 Freising  
Germany  
Phone: +49 8161 714575  
Fax: +49 8161 714576  
E-Mail: matyssek@wzw.tum.de

Prof. Dr. Ulrich LÜTTGE  
Technische Universität Darmstadt  
Institut für Botanik  
Schnittspahnstraße 3–5  
64278 Darmstadt  
Germany  
Phone: +49 6151 147052  
Fax: +49 6151 164630  
E-Mail: luetgge@bio.tu-darmstadt.de