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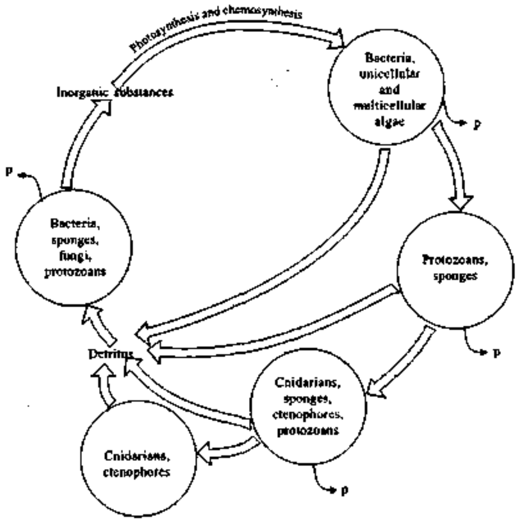
EDMUNDAS LEKEVIČIUS

THE ORIGIN OF ECOSYSTEMS BY MEANS OF NATURAL SELECTION



LITHUANIAN ACADEMY OF SCIENCES

INSTITUTE OF ECOLOGY *VILNIUS, 2002*

CHRONICLE OF EVOLUTION OF LIFE
(Functional aspect)

Million years ago	
4,000	Chemical evolution
	Rise of life and of a primitive nutrient cycle (ecosystems) The first autotrophic ecosystems appear on the basis of anoxygenic photosynthesis and anaerobic decomposition
	Stromatolites emerge. Ecosystems are formed on the basis of oxygenic photosynthesis. Nitrogen fixing organisms originate
	Synthesised by photosynthesisers, oxygen oxidises dissolved in water reduced materials
3,000	Evolution of oxygen-resistance and aerobic respiration takes place
	Reduced hydrosphere gradually turns into an oxidised one. Aerobic respiration, oxic and anoxic zones with their local cycles appear. Stromatolitic form of life becomes predominant
	Aerobic chemolithotrophs emerge to occupy vacant trophic niches resulted in by accumulated in water oxygen. Bacteria form a modern-type ecosystem metabolism (nutrient cycles)
2000	Reduced atmosphere becomes an oxidised one. Oxidation of lithospheric materials starts
	Unicellular algae and the first biophages (protozoans) emerge
	The first production pyramid is formed - at first two and later three trophic levels. Parasites come into existence
1,000	The first multicellular organisms rise - the fourth trophic level is formed
	Diversity of biophages substantially increases in waters. Modern-type production pyramids originate. Life starts to move to land Modern-type nutrient cycles and production pyramids are formed on land
	Competition between terrestrial biophages grows. Their species compete in reducing environmental resistance
0	Modern atmosphere having formed, biosphere biomass ceases growing. Hominids initiate an unprecedented extinction of species

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Vilnius University

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(MONOGRAPH)

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FOREWORD

As it perhaps frequently happens in our life, important solutions are often provoked by, at first sight, absolute trifles. This, seemingly, was the way that time, too. One day some four years ago, I remember, I was leafing the freshest handbooks in English for higher forms of secondary schools and colleges. As usual, I became slightly indignant at chapters on evolution. No, they were not bad. I can say that they were written even better than others that I had read before. And may be because they were not so bad, suddenly I flared up. Yes, it is fine, it is all right, but how long one can demonstrate these old tiresome phylogenetic schemes and cladograms, however freshly tinted and adjusted to time requirements and new facts they are! Again this narrow *genetic* approach to evolution! Cladograms show what has originated from what, what relationship between organisms is, but they do not inform about no less important *functional* aspect, or in what way organisms co-existing at certain time interacted, what a that-time ecosystem and a nutrient cycle were like and what the role of one or another group of organisms in the latter was. Phylogenetic trees and cladograms can not satisfy an insistent and thinking biologist, since they remove organisms from their natural medium, from a net of vitally important connections and place them to a conceptual vacuum where they look no more alive than a mosquito that has been stuck in a piece of amber forty million years ago. In the short run such indignation of mine turned into the resolution to write it myself, better. By the way, I have not meant to write a handbook. Functional approach is so unusual in biology at present that I do not consider my views to be textbook truths. At best I can only hope that my book would provoke some debates and call greater attention to this once urgent issue, which, sooner or later, will undoubtedly get into biologists' outlook again.

The essence of functional approach, I think, could be well expressed by the formula 'only an ecosystem is living'. Here an ecosystem is understood as a nutrient cycle and the accompanying energy flow without which it is really difficult to imagine life. In my consideration, a nutrient cycle is as inseparable attribute of life as are metabolism, growth, reproduction, response to environmental stimuli, variability, inheritance, and adaptation, which are widely advertised in handbooks. Since there is no species, a constituent part of a concrete ecosystem, that by itself is able of nutrient cycling, then there is no species that could be considered autonomous or independent from functional approach. In this sense not a single population isolated from other members of a community is living. The feature to be living originates from the interaction of species forming a community.

This formula having transferred to the sphere of evolution, it is possible to substantially correct our understanding of the evolution of life on Earth and that of evolutionary mechanisms. If it is only an ecosystem that is living, then it means that even primitive life had a shape of a nutrient cycle. Of course, that-time nutrient cycles had to be quite different from modern. Being not independent from the point of view of functioning, individual species indispensably become dependent on one another and while evolving direct the evolution of one another (co-evolve). Natural selection is nothing but functional constraints imposed on genetic variability and formed by species interacting with their living and non-living environment. Evolution is governed not only by struggle for existence, but also by co-operation, which is likely to have been all the time playing a role more important than negative relations. Evolution is not only the development of species towards increasing adaptation, from bacteria to man, but also an improvement of the structure of ecosystems and nutrient cycles leading to the growing biosphere biomass.

Some time ago my monograph was published (Lekevičius 1986) in which for the first time I made an attempt to present this functional or ecological approach to the evolution of life quite in detail. The book was meant for experts of theoretical biology for the most part and it ran mainly about evolutionary mechanisms, just a little part of it being devoted to the evolution of life on Earth. Besides, it was written in Russian, thus its impact on the society of biologists, as it could have been expected, was not very marked. On the other hand, it would be a sin to say that I lacked attention. The book was quite actively discussed throughout the former Soviet Union and, I can say, did not attract any strong criticism. It was especially well accepted by the generation of younger biologists. After eleven years, when I was defending my thesis for habilitation, I felt that the elder generation, too, evaluated my revision of the theory of evolution quite indulgently, even conciliatingly. It appeared to me that at that time, compared to ten or twenty years ago, the idea of the synthesis of the theory of evolution and ecology was possibly becoming more acceptable for the majority.

Still, genetic approach to evolution prevalent until today does not seem to be going to give way. Thus, I had nothing to do but write a new book, that time - in Lithuanian and in English, a book better understandable to a reader not very much educated in theoretical biology. And I have succeeded: in the year 2000 Vilnius University Publishers published a Lithuanian version of the monograph (Lekevicius 2000). The following year, after the edition had been sold out, I made one more at my own expense. The English version is a supplemented and adapted variant of the Lithuanian one.

This book is written in a slightly unusual, at times over-free manner, which is more typical of scientific essays rather than of monographs. I hope this will be acceptable to the reader. I have to confess that I am not very fond of a dry text, so try to avoid it wherever it is possible and whenever this does not contradict my purposes. On the other hand, I wished to break out of the traditional stylistic frame, usually characteristic of monographs, to be free to express my opinion, may be sometimes subjective, on the evolution of life and on the situation of the science of biology in general. Both the text of the book and its style have been determined for the most part by the content of my lectures read to students at Vilnius University, where I give courses in general ecology and ecosystem evolution. I have to say that the content of the book and that of the lectures differ in many aspects, and this is understandable. What is published in a scientific piece of work questioning recognised truths is hardly supposed to be presented to students without certain comments.

In the book, the reader will find comparatively few references to primary sources, i.e. articles in special scientific journals. This is because of two reasons. First, some publications of recent years were, however, inaccessible to me due to certain reasons that did not depend much on me. Second, in this book I, as I think, am presenting an untraditional approach to the course of evolution and evolutionary mechanisms. It is so untraditional that one may consider it an entirely new paradigm of evolution, commonly unaccepted as it is. Thus, naturally, I am interested in stating as wide as possible my *personal* and not somebody else's views. It is already a dozen or more years that I have not noticed researchers who are guided by the purposes like mine and who are using similar methodology. May be this is why the latest literature, which I was able to get acquainted with, principally has not contributed too much in preparing this book. After a long and patient walk along a chosen way you happen to realise that your companions have abandoned you and that the way has come to an end, so you have to tread a path yourself. And there is no use then looking sideways, since this would only take precious time instead of using it efficiently. I understand that these words sound arrogantly, but I can not resist the temptation to be frank and hope that the reader will not object to this wish of mine.

Another thing is that because of insufficient acquaintance with primary sources interpretation of certain data, especially palaeontological, could have deteriorated. It is quite possible that in my text experts will find some subject matter mistakes. I have to put up with this, moreover so that may be in the future there will be a possibility to correct mistakes and inexactitudes. On the other hand, I would not like the reader to notice just secondary importance details paying no attention to substantial moments, which frequently is a case on evaluating my published works.

The first part of this book is describing the evolution of life on Earth from its appearance to nowadays. In it, understandably, functional (ecological) approach prevails. The following subjects are analysed:

1. The appearance of life (and of ecosystems) and the formation of modern nutrient cycles (scenes 1-7);
2. Change in ecosystem structure and the formation of a modern ecosystem structure (scenes 8-14);
3. The evolution of terrestrial organisms - producers and biophages (scenes 15-18);
4. Hydrospheric and atmospheric evolution (the first and the second interludes).

In the second part, I make an attempt to show what connection is between Darwinian evolution (phylogenesis) and ecosystem evolution, which I conditionally call non-Darwinian. There I present a conception of natural selection, a little different from common one, which practically is a simplified narration of my earlier ideas and models (Lekevicius 1986, 1997). By the way, to strengthen my position, this time I have employed not only deductive but also inductive logic: there the reader will find much more factual material than in earlier publications. In addition, in this part I once again turn to my favourite subject - the phenomenon of man - which in the context of ecosystem evolution acquires quite unexpected features, I think.

Like in many of my publications, in this book I am more than once making an excursion into the history and methodology of biology, for it is my favourite subject, too. But it has been inspired not exclusively by liking. I think that during the 20th century the methodology of biology, compared to other fields, lacked attention most of all. On the other hand, those are just methodological gaps that have not allowed us to develop theoretical biology, i.e. a system of conceptions that in its explanatory and predictable force could at least slightly resemble that generated by physicists and chemists. We still have not established an efficient way to simplify life phenomena logically, therefore until today they have seemed to us so extraordinary complicated and insuperable to human understanding. The complexity of the world, however, evidently is merely alleged and subjective and it depends only on how our methods are adequate for an object under investigation.

Now that I have written this book I perceive that I have succeeded to find more or less acceptable answers to some questions essential to our understanding of the evolution of life. Indispensably, this evokes a feeling of satisfaction and vanity. As the reader will see, I do not have answers to some of the questions raised in this piece of work. I think that they will be answered by new generation biologists. To formulate a problem, to look at old truths from another angle often is, however, no easier and sometimes even more difficult than to find solutions to already formulated problems. Therefore, it seems to me that I have a certain right to consider this book a kind of homework for young searching minds. I wish them luck.

ACKNOWLEGEMENTS

I would like to thank most cordially my closest associates who supported and provoked me to finish this book. I must especially mention Acad. Vytautas Kontrimavicius. It is almost twenty years that he has been supporting all my aspirations and helping to find possibilities to realise them in one way or another. The English version of the book would have hardly appeared so soon without Prof. Dr Habil. Juozas Virbickas, Director, and Dr Habil. Mecislovas Zalakevicius, Deputy Director at the Institute of Ecology, who suggested to publish it by financial means of the institute. My thanks are due to Dr Ricardas Paskauskas for his abundant remarks and suggestions. He and doctoral students Dainius Plepys and Asta Audzijonyte kindly assisted me in searching for literature. I am also indebted to experts Dr Habil. Vincas Buda, Dr Ramunas Stepanauskas, Dr Stasys Sinkevicius, Dr Petras Musteikis, and Dr Elena Motiejuniene, who read the Lithuanian manuscript and made their valuable remarks. I am also grateful to translator Aukse Tamosiuniene for her benevolence and hard efforts and hope that the reader will appreciate her work.

Without assistance of my wife Diana, who contributed much in preparing the manuscript, I would have encountered some really great difficulties.

This monograph turns out to be the result of the planned work conducted at the Centre for Environmental Studies of Vilnius University in 1998-2002.I feel obliged to the university administration for providing conditions necessary for the fulfilment of this work.

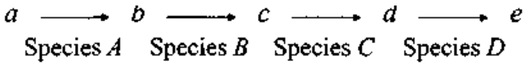
Author

ONLY AN ECOSYSTEM IS LIVING? YES, IN A SENSE

Since, as I have mentioned in the 'Foreword', the feature to be living in the literal sense of the word is characteristic only of an ecosystem, the question about the origin and evolution of life on Earth acquires a completely new, may be somewhat unexpected sense. Knowing that the majority might be shocked by this formula, I hurry up to explain what I mean by it.

The conclusion that life can not exist without detritivores, which bring nutrients back to the cycle, has been arrived at by many outstanding biologists, from L. Pasteur and S.N. Winogradsky to E.P. and H.T. Odum, earlier than by me. I will repeat their argumentation in my own words.

Suppose we have an ecological community formed of species *A, B, C,* and *D.* Species *A* requires compound *a* to convert it into compound *b,* which is used by species *B,* and so on.



As we see, species *B* is dependent on species *A,* species *C* - on species *A* and *B, D -on* species *A, B,* and C. It may seem that species *A* is autonomous, an autotroph. But in fact this happens seldom if at all. The matter is that the whole system works in such a way that the concentration of compound *a* constantly reduces, whereas that of *e* interminably increases. This can not last long and sooner or later the resources of compound *a* will run short and all species will be subjected to death. Perhaps, there is only one way out of this situation: there should emerge one or several more species that will convert *e* into *a.* In other words, there should emerge something what ecologists call a nutrient or biogeochemical cycle (Fig. 1). A nutrient cycle as well as the energy flow accompanying it are major attributes of an ecosystem.

Sure, everything is a little more complicated in reality. Let us go for one abstraction level down and display a natural ecosystem in more detail. We will get a scheme known to every senior form Lithuanian pupil (Fig. 2). It depicts three functional kingdoms of living nature: producers, biophages, and detritivores (decomposers). These kingdoms are not independent: biophages and detritivores depend on producers, which supply them with matter and energy, whereas producers in their turn - on consumers (biophages and detritivores), which supply them with inorganic nutrients.

It is understandable to every ecologist that the presented model reveals just a very approximate picture of the real situation. An expert would miss at least arrows directed from producers and biophages (they also perform decomposition) to inorganic materials and an arrow from detritivores (they also die) to detritus.

Thus, it is possible to construct even 'more real' models, but these will do for us so far. The models, irrespective of some differences between them, testify to the fact that the turnover of nutrients, in other words ecosystem metabolism, tends to acquire a form of a more or less close cycle and just in this form becomes

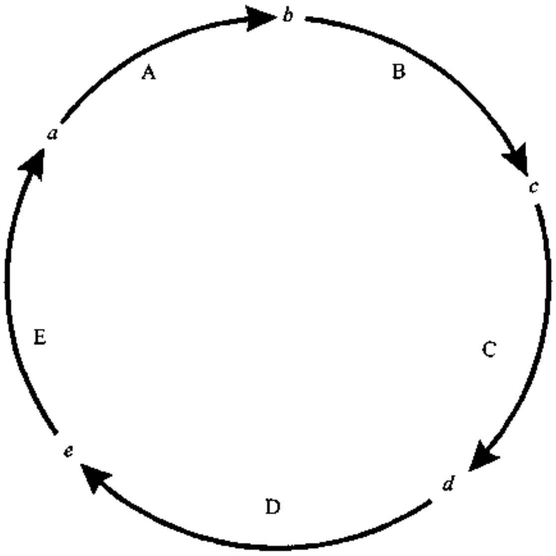


Figure 1. This is how the simplest possible model of an ecosystem could have been looking like. Here *A, B, C, D, E* are species and *a, b, c, d, e* are chemical compounds.

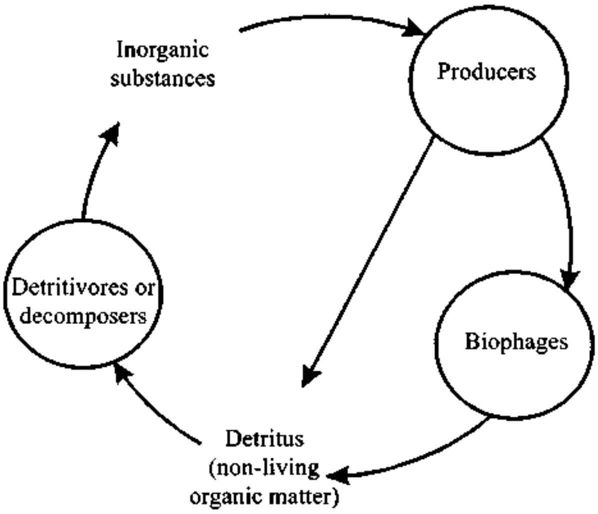


Figure 2. A less abstract and more 'real' model of a natural ecosystem.

self-supporting. A nutrient cycle is an indispensable condition for long-term stability of life. In this sense (and only in this) plants are non-living. We can state with confidence and unmistakably that the reaction of photosynthesis is produced not by them, as a handbook myth says, but by an entire ecosystem, considering that if the activity of detritivores was broken down due to some reason, after a while the supply of nutrients would run short and plants, too, would die.

It should be admitted that all these arguments are a bit deductive and do not refer to any concrete facts. But it is not difficult to find non-discussible inductive arguments, too. Every student of ecology knows well that, let us say, the supply of humus and biogenic materials in the soil of tropical rain forests are comparatively poor. So, if detritivores inhabiting that soil would be exterminated in one way or another, as soon as after a month if not earlier photosynthetic intensity in forest plants would start rapidly reducing. Several more weeks later consumers would feel this, too, and in a year or two life in that locality would cease existing. Similar impact on life would undoubtedly befall other biomes as well, only the period of time from the beginning of the experiment to the catastrophe would be longer.

Even Begon, Harper, and Townsend (Begon *et al.* 1996), who otherwise could hardly be suspected of being E.P. Odum's supporters, being pressed by inexorable empirical evidences admit:

If plants, and their consumers, were not eventually decomposed, the supply of nutrients would become exhausted and life on earth would cease. The activity of heterotrophic organisms is crucial in bringing about nutrient cycling and maintaining productivity.

Strange as it is, such a logical conclusion does not prevent the authors in another part of the book, dealing with mutualism, or reciprocally useful interspecific relations, from not even mentioning a word about interaction between producers and consumers. Instead, much space is devoted to less substantial co-operative connections. Even those ecologists who recognise mutualism as an interaction predominant in the majority of ecosystems usually have in mind only connections between separate species (Herre *et al.* 1999; also see a devoted to the subject Ecology, 1997, vol. 78, N 7). Such or similar inconsistencies are numerous in contemporary ecology.

As recently as a couple of decades ago a question was discussed, to my consideration in a quite well-grounded way, whether viruses are living beings or just 'crystals' of organic molecules. Now seemingly a consensus has been reached: viruses are non-living. Why? The answer is, 'Because viruses can reproduce, thus to be living, only in a host's cell.' A virus is no more living than its host, and if the latter dies the virus also stops showing any signs of life. Applying this essentially quite welcome logic, however, a roe or an elk, too, are no more living than plants on which they feed are. And in general all consumers are living on such a scale that is allowed by producers. Should the latter disappear, all consumers would die. And producers are able to function only until detritivores supply nutrients. Thus, even plants are not independent, or living in a broad sense of this word. 'Stop, stop!', one can say. 'What applies to viruses does not apply to all consumers.' What else one can say I do not know, but if I were in his or her shoes, I would most probably miss consistency here.

If in a natural ecosystem not a single species can be considered independent from the point of view of functioning, if life can not do without a nutrient cycle, then at community level, speaking in terms of systems theory, there is a functional hierarchy. The global community function is divided into a multitude of smaller, narrower functions performed by species forming that particular community. This is a conclusion that is very important to the whole ecology and that should open our eyes and help us to look at Mother Nature in a new way. By the way, by this conclusion I do not mean that each species is vitally indispensable to a community and that any species having withdrawn from a community the whole system would cease functioning. Definitely not. Communities are not superorganisms or, even more, clock mechanism analogies. Community organisation is not rigid. And it is not merely functional inter-dependence that is characteristic of co-existing in the same locality species. Their niches in part coincide. The species not only co-operate, but also compete. Competition gives ecosystems dynamics and plasticity without which they could not resist indeterminacy of environmental conditions. However important is a contribution to the functioning and evolution of natural ecosystems, I am sure that the contribution made by contrary to it interactions - co-operation or mutualism - was and is even more important.

The reader may become interested in why the formulas 'only an ecosystem is living' and 'life is a functional hierarchy' have not become trivial truths in ecology despite their evidence. This question is supposed to be answered, probably, by science historians, but I will express my opinion, too. In science it is a usual case that set, recognised paradigms become a pair of glasses to look at the world through. One puts it on, gets used to it, and coalesces with it. The glasses become a kind of filters, and some facts are allowed to pass through them, whereas other, may be as much important and evident, are stopped. If it is 'well known' that in living nature there are neither ecosystems-superorganisms, nor functional interdependence between producers and consumers or, even more so, the functional hierarchy at ecosystem level, and if the unquestionable opinion prevails among biologists that living beings are always ready for fight *{bellum omnium contra omnes),* then every who will make an attempt to contradict this opinion might be called a retrograde. Would somebody like to lose a good reputation then? The widespread opinion that in science fashion is set by facts and inexorable logic is not quite right. Researchers' subjective outlooks, unrealised ideologies, and personal opinions also play an important role. Not before this backstage of science is comprehended an answer could be found to the question why science sometimes rapidly gallops forward like a restive horse and sometimes makes no headway or moves backwards for no apparent reason.

Since contemporary biologists are disinclined to recognise the formulas 'only an ecosystem is living' and 'life is a functional hierarchy' as right, neither do they recognise that there exists not only species evolution, but also ecosystem evolution. Look, for instance, what an outstanding science historian Golley (1993) writes about this:

> The word 'evolution' was applied to ecosystems in the early 1970s. It was an unfortunate application of the term. There can be no ecosystem evolution.

For the sake of truth there should be stressed something else. 'Ecosystem evolution' has become an unwelcome combination of words not only because the majority of evolutionists do not consider an ecosystem something with its own specific organisation and structure, but also because natural selection, according to them, is nothing but differential survival and differential reproduction *of individuals.* Accordingly, only features of individuals, not those of populations or ecosystems, can evolve. Though this conclusion is also completely ungrounded, I will write about this quite a great deal further.

On the other hand, it would be wrong to claim that each evolutionist and ecologist without exception has abandoned the idea that ecosystems, too, can evolve. As I understand, E.P. Odum is not inclined to renounce his earlier ideas and keeps writing about 'biosphere evolution' (Odum 1997), the mechanism of which he still considers co-evolution and 'group selection'. Enviable persistence in the background of already total disapproval! Such an intentional non-conformist can be only a person who mulls over what he or she does. Apparently, not only E.P. Odum, but also a great many evolutionists and ecologists from the former Soviet Union are not inclined to give up their holistic outlook on the world. This, most likely, is due to the traditional inclination of Russians towards globalism and romanticism. Therefore quite understandable is the surprising respect and popularity in which scientists of that nationality have wrapped the heritage of two great classics of science, microbiologist S.N. Winogradsky and geochemist W.I. Vernadsky. Both of them have suggested that nature is integral and that long-term existence of one or another species is possible only within an ecological community, because biogeochemical cycles are a result of common activities of all community members. Quite possibly, according to Zavarzin (1995), this is why the idea of ecosystem evolution has been popular in Russia until today and, in the author's words, is more likely to become an essential replenishment rather than denial of Darwinism. G.A. Zavarzin calls this point of view on living nature and its evolution the Russian paradigm, an opposition of the Western reductionistic paradigm of molecular biology. I will not judge here whether this respectable scientist is right or wrong, but I think his thoughts are worth attention.

PART 1. THE EVOLUTION OF LIFE ON EARTH: SINCE THE APPEARANCE OF LIFE UNTIL TODAY

ON THE METHODS AND METHODOLOGY USED IN THIS WORK

As somebody has said so aptly, the chronicle of life history used by us is like a novel the first chapters or even as much as two thirds of which are torn out, and the reader can only guess what was going on prior to the described events. We will never learn what the climate was like - cold, moderate, or hot - four milliard years ago. We will hardly ever find out what that-time atmosphere was like. Nor it will be easier for us to conceive how from small inorganic molecules organic ones and later the very first cells originated. However hard we try our efforts will never be crowned with success and our knowledge about the origin of life and the first two milliard years of its history will always be just scientific myths. The picture of that time suggested by me is not an exception in this sense. By the way, in recent decades research on the first two milliard years of life has been enjoying a great revival, and many things have become somewhat clearer.

As I have already mentioned in the 'Foreword', the further presented chronicle of the evolution of life emphasises functional or ecological aspect, rather than that of origin (phylogenetic). Let questions of origin be answered by experts, even more so that I am not very much interested in them. In what follows attention will mostly be paid to what a block structure and a nutrient cycle of ecosystems existing during one or another geological span of time were like and how both of those characteristics of ecosystems changed through time.

In reconstructing past ecosystems, their structure and metabolism, I observed the following order. During the first stage, which conditionally could be called inductive, I studied literature on palaeontology and evolution (e.g. Broda 1975; Cody & Diamond 1975; Cowen 1976; Fairbridge & Jablonski 1979; Windley 1980; Gee & Giller 1987; Boardman *et al.* 1987; Carroll 1988; Fox 1988; Behrensmeyer *et al.* 1992; Schopf 1992a; McMenamin & McMenamin 1994; Smith & Szathmary 1995; Fenchel & Finlay 1995; Margulis & Sagan 1997; Clarkson 1998; Stanley 1999; Margulis *et al.* 2000). I paid special attention to experts' opinion about what metabolism of organisms existing during one or another period and their trophic niche could have been like. In such cases a supposition is usually made that fossil organisms that are morphologically similar or akin to contemporary ones should have fed in a similar way. When experts' opinions differed, I would have chosen the opinion most widespread nowadays, if I did not have my own. The second stage, conditionally called deductive, required a greater expenditure of thinking. Based on the results obtained during the first stage, I had to reproduce a possible block structure of an ecosystem, essential features of a nutrient cycle, and a production pyramid, if there was any then, typical of one or another period. To make that reconstruction, I most often lacked facts. Then argumentation of a deductive character came in handy. I supposed that the functioning laws typical of contemporary ecosystems should have been typical of the former life, too. Thus, conversions of nutrients during one or another span of time tended to become closed cycles, in which metabolism end products of some organisms are primary nutrients to others. Any vacant niche, in this case understood as nutrients that are potentially usable though used by nobody, sooner or later had to be occupied by evolving organisms. The same perhaps was with food chains, trophic levels, and production pyramids in particular: having been influenced by thermodynamic and other kind of constraints the shape of the pyramids must have been tending to become similar to the contemporary one. Nature should not have been too fastidious in that respect: once it came across a handy way of resource distribution, it held on to it.

There is nothing very new in this methodology: it is a partial case of a well-known principle of actualism. It simply suggests that in addition to the ecosystem convergence that takes place in geographical space there should have been an analogous historic convergence, too. One can be surprised, if at all, just at the fact that such an unpretentious principle has been a precondition for the rules soon thereafter turning into the heuristic means cutting the list of alternatives suitable for discussion to minimum. Because vacant niches should have been evolution stimulating and directing factors, there has been even a possibility of forecasting an evolutionary direction of organisms of one or another period and, when needed, verifying that forecast based on palaeontological or other empirical data. This has been even more possible since potential niches are not and have hardly ever been abundant. For instance, it is likely that biophages appeared as early as in the Precambrian, but since they were just small herbivores for some time the production pyramid was of an unusual to us look. It could be easily guessed that that-time herbivores made niches for future primary carnivores, which in their own turn instantly after their appearance had to make vacant niches for secondary carnivores, until finally the pyramid acquired the contemporary shape. According to palaeontological data that scenario should have been realised during the Ordovician.

Let us take another example. Experts tend to think that 1.7 milliard years ago there already existed unicellular algae. It could be supposed with a great probability that by that time there should have been detritus, too, formed of unicellular algae, containing cellulose (a constituent element of the wall of unicellular algae). Then for a certain period of time cellulose must have become a vacant niche - a resource used by nobody. It accumulated since there were no organisms capable of decomposing it. The latter could not appear on the scene of evolution prior to the substrate itself. The nutrient cycle temporary broke down - became wasteful. Thus, algae immediately after their appearance made an enormous selection pressure for that-time detritivores. Of those a new functional group capable of decomposing cellulose had to come out after a while. And not before that the nutrient cycle was restored and the ecosystem returned to a phase of relative peace and stability. Such is the course of events depicted by theory. It suggests no concrete candidates for primary cellulose decomposers, but still it is a really efficient research instrument for a theorist determined to reconstruct past ecosystems. This is even more so since there always is a possibility of verifying hypothetical schemes and forecasts obtained in that way through practice and in case of a negative test to make better schemes, conditionally deductive.

Working in such an obscure sphere as evolution, every synthesis-seeking researcher is inevitably forced to use a great many of statements and concepts often very difficult or even impossible to be verified due to a great lack of empirical material. Commonly some of these doctrines remain merely hypothesis and others are simply forgotten. In order to avoid this and to integrate different researchers' results there could be used a method that I call the principle of a meaningful sentence. If owing to a single sufficiently wide and integral theoretic scheme one succeeds to integrate many various hypothetical doctrines so that they not only do not contradict but also supplement one another, as a result their reliability even increases. The same is with words in a dictionary. Almost each of them has at least several meanings, and we understand one another just because in a sentence a word loses all its meanings but one. Here I mean a meaningful sentence, of course.

In such a case there is no need to verify (or falsify, if you like this better) every single doctrine. It is enough to verify an idea or concept that has served as an integration axis in designing a particular theoretical scheme. One of that kind of ideas is the formula 'only an ecosystem is living' used by me in this work. Another - the principle of actualism and its concrete expression presented above. If these ideas are wrong, the shadow of distrust falls on all my results and conclusions, too. If the sentence itself is meaningless, there is no sense in getting absorbed in the meanings of separate words.

I consider that this methodology has a very important advantage over pure inductive reasoning. Inductive explanation does not refer to unrealised yet theoretically probable possibilities. It does not imply an answer to the question why these and not other possibilities that seemingly are no less probable have been realised. Therefore, despite a possible forecast value the inductive method usually provides no thorough explanation. The explanatory force of the deductive method is greater. I know that just few biologists will agree with this, but all my long-term experience makes me think but this way.

Principally, it is possible to reconstruct past ecosystems by using the inductive method alone. Maisey (1994), for example, has reproduced, very elegantly and successfully enough, trophic relations in fish communities of the Cretaceous using fossil data alone. The fact is that sometimes fossils of these organisms are so well preserved that it is possible to determine even their stomach content and to identify prey. There has been even more of analogous research and it undoubtedly is of a great scientific value. It is apparent, though, that if we trust only direct inductive evidence, it will take a lot of time to reproduce a general picture of ecosystem evolution, and I even doubt whether this is possible at all.

In this work, I am not attempting to reconstruct the metabolism and the structure of ecosystems that existed in a certain location - I would not be able to do this however hard I try. The only thing within my reach is to reconstruct a standard, average, ideal ecosystem that existed during a certain, sometimes even not strictly defined, geological span of time, which I hope could represent quite well a general set of that-time ecosystems. Thus, I have had to content myself with a rather high level of abstraction. To it I have had to adjust a modelling method, too: like in many other publications, in this book I am using qualitative, or conceptual, modelling. This kind of modelling is between verbal and mathematical models. It comes in handy in modelling super-complicated systems (Gigch 1978). Its procedures made properly stricter, it is possible not only to expand its application sphere, but also to markedly increase its heuristic value and to make it possible for models to become verifiable and falsifiable. The greatest merit of the method is in that there is no need of pushing a phenomenon or an object under investigation into a Procrustean mathematical framework by force, so it is possible to obtain models that do not distort the real situation and to describe even those processes for the modelling of which there has been established no mathematical apparatus, and it will hardly ever be.

At least I do not know analogous attempts of other authors to use similar methodology in reconstructing past ecosystems, from the very first ones to contemporary. The subject of ecosystem evolution was quite urgent and popular among ecologists some 20-30 years ago (see e.g. Richardson 1977; May 1978). Past ecosystems, beginning with the very first ones, have been attempted to be reconstructed by Cloud (1974,1978), Walker (1980), Margulis (1981,1982), and some other researchers. Then attention was mostly paid to the development of nutrient cycles, whereas the evolution of ecosystem structure, as far as I know, attracted a far more less interest. Still others have discussed the mechanisms owing to which such complicated structures have evolved (e.g. Lewontin 1970; Wilson 1980; Lekevičius 1980). At that time there was yet no methodology of investigating those processes and, accordingly, achievements were not very great. Besides, the problem also was in that the palaeontological chronicle of that time told little about events more than half a milliard years old. Still results obtained were not null and void. I think that the taken direction was right and, quite possibly, until the end of the century a qualitative change would have taken place resulting in a new attitude towards the evolution of life. However, this has not happened. The collection of articles 'Earth's Earliest Biosphere, Its Origin and Evolution' (Schopf 1983) probably is the last substantial collective work where the old holistic spirit still could be felt. Later interdisciplinary co-operation has declined, works and subjects become more trivial, and an over-analytical way of thinking - firmly established. That new wave has flooded biology and contiguous scientific fields ruthlessly sweeping off starting to shoot seeds of knowledge. The idea of ecosystem evolution has gone out of fashion. Merely fragments of past ecosystems are still calling some attention. Interestingly enough, even the word 'ecosystem' over the recent two decades has acquired an entirely new role its meaning having become absolutely indefinite, it has come to be merely a nice metaphor.

The above presented has allowed me to confine myself to refer to just few authors in this book - they indeed were few. Due to the same reason I have cast aside an idea to present an overview of references in a separate chapter. Yet, in discussing some concrete issues I am referring to some old generation researchers whose works are, in my opinion, still urgent today. Some fresher publications are being referred to as well.

In what has been said I have indicated just the methods I was using in reconstructing the structure and nutrient cycle of past ecosystems. Other methodology regarding search for mechanisms of ecosystem evolution is described further, in 'Part 2'.

It took me a long time to think how to present the evolution of life to the reader. Eventually I have decided that it would be best of all to put it all in a kind of a scenario, with the course of events depicted in 'scenes', a kind of pictures, at the beginning of each of which the period and main characters to be described are introduced, the period itself being characterised merely in laconic strokes with as little text as possible, often using schemes or another kind of visual information. Hydrospheric and atmospheric evolution is discussed in insertions - 'interludes'.

SCENE 1. CHEMICAL EVOLUTION
PERIOD: 4.5 - 4.0 MILLIARD YEARS AGO

One of the versions most widespread in Earth science is the idea of 'fiery cradle'. It provides that immediately after the formation of Earth the temperature of its surface was above 100°C. So, oceans and water bodies were absent for some time, since all the water was in the atmosphere as evaporates. Then the planet gradually cooled and eventually water bodies and the global water circuit originated.

According to this version, 4.5-4.0 milliard years ago volcanic activity was by far more intense as compared with the present. The atmosphere survived huge amounts of different gases and evaporates: H_20, $C0_2$, N_2, CO, CH_4, NH_3, HC1, H_2S, H_2(e.g. Schidlowski 1980; Miller 1992; Margulis & Sagan 1997). Some of these materials are not found in volcanoes, but they may have been resulted in by photochemical reactions. The majority of them easily dissolve in water, so there may have been dissolved materials in primordial water, too. Those materials may have also appeared in water from abundant in those times hydrothermal vents. Precipitation and ocean water may have been much more acid than now, which was due not only to a higher than today atmospheric concentration of $C0_2$ (Kasting 1993), but also to a probable presence of HC1 evaporates.

In the primordial atmosphere, oxygen either was completely absent, or there were merely traces of it, therefore large and small heavenly bodies were reaching the planet's surface unobstructed leaving in its body slowly healing wounds. The UV radiation reaching the planet's surface was far more intense, since in those times there was no ozone screen yet.

It is likely that approximately 4.0 milliard years ago the chemical synthesis of organic materials from inorganic ones (polymerisation) was already very advanced. That kind of synthesis required outer energy sources. They could have been UV, lightning flashes, and radioactivity. Primary inorganic materials, from which organic ones were synthesised, were the majority or at least many of those that emerged as a result of volcanism. It is believed that at first compounds of a comparatively light molecular weight predominated among products of abiotic synthesis. Then due to polymerisation more and more macromolecules gradually appeared.

In recent years, an opinion has been expressed that organic molecules may have been brought to Earth from the cosmos by asteroids, comets, or meteorites. There are suggestions that life itself may have been brought by those heavenly bodies. This opinion strengthened after organic carbon compounds and even some of amino acids had been found in many of heavenly bodies. Particularly famous in that respect were made carbonaceous chondrites - meteorites in the composition of which especially much of organic carbon had been found. I think that the above facts are not very important in the context of this book, so I am not discussing them in what follows.

SCENE 2. LIFE AND ECOSYSTEMS APPEAR AND ALMOST DISAPPEAR

PERIOD: APPROXIMATELY 3.8 MILLIARD YEARS AGO
MAIN CHARACTERS: PROTOBIONTS

This scene is also very hypothetical, but I think that it is somewhat easier deductible from laws known to today's science.

On the scene of evolution the very first living organisms, cells with plasma membrane, emerged. They are called differently, but most often - protobionts. They grew and reproduced, thus metabolised in a primitive way as it was. Most probably protobionts decomposed ketones and aldehydes to organic acids and other small organic and inorganic molecules. Consequently, fermentation without glycolysis occurred (Margulis 1981).

It is most likely that protobionts were strict anaerobes and, based on the feeding character, detritivores. The thing is that they decomposed the organic materials still supplied to them by abiotic synthesis. According to the classification applied in microbiology, all detritivores, protobionts among them, fall under the group of chemoorganoheterotrophs (here 'chemo' means energy source, in this case - chemical materials, 'organo' indicates that a source of hydrogen (electrons) are organic materials and 'hetero' informs that organic materials also are a source of carbon).

On decomposing organic materials, protobionts produced small organic and inorganic compounds and molecules as by-products. The decomposition products could again be utilised for abiotic synthesis. Thus, we may think that already at that time there existed a nutrient cycle, though a very primitive one (Fig. 3). It means then that ecosystems existed, too. As it could be expected, they came into being along with life.

If there was a nutrient cycle, then there must have been an accompanying energy flow, too. The energy of the cosmos and that of the bowels of the earth used for abiotic synthesis converted to chemical energy, which due to catabolism - to heat radiated to the surrounding medium. We obtain the following scheme of the conversions of materials and energy occurring in that-time ecosystems:

inorganic materials → organic materials → inorganic materials
cosmic energy → chemical energy → heat
and that of the
bowels of the earth

One can only speculate where those events developed. According to Darwin, life arose in a little warm pond. During the 20th century the predominant opinion among biologists was that life originated in an ocean, shallow bays rather than in a pond. After organisms living in the vicinity of hydrothermal vents had been found, it was suggested that it was just in those habitats where life could emerge. There also are other opinions, but perhaps there is no use of discussing them all here. It is enough for us to suppose that the event took place in water, most probably seas, at least not on land.

The first ecosystem of Earth, depicted in Fig. 3, had, however, one considerable drawback. The rate of 'soup' production was thousand times lower than that of its 'eating', since protobionts required nutrients and energy not only for the maintenance of vitality, but also

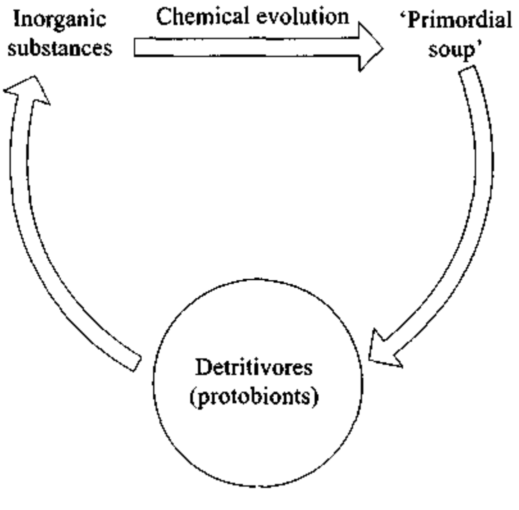


Figure 3. It is thought that life – protobionts – appeared on Earth approximately 3.8 milliard years ago. In my opinion alongside with them there should have appeared the first ecosystem, or the first nutrient cycle, too.

for growth and reproduction. Thus, sooner or later 'soup' resources had to become exhausted, and the newly born life was overtaken by an ecological catastrophe. Mass extinction of protobionts started.

It can be only guessed what happened then. Somebody may think that having converted to detritus (non-living organic substance) protobionts autolysed somehow. Thereby free organic materials may have replenished the running short 'soup' supplies, so that there may have been no mass extinction. Such course of events, however, is hardly in accordance with the second law of thermodynamics. The 'soup' was utilised not only as a fund of building materials, but also as a source of energy. And, due to catabolism, energy sooner or later converted to heat. Therefore, decrease of 'soup' resources was most probably inevitable.

If non-living cells could not autolyse, which also was probable, another scenario came true: most of detritus moved from the cycle, as there were no organisms decomposing it. That could have complicated a complex, as it was, situation even more.

I am not going to analyse other variants of the continuation of the events, the more so that the whole second scene is far too hypothetical. In recent years some experts have been suggesting that the first living organisms were photosynthesisers or even chemosynthesisers rather than decomposers (Maden 1995; McClendon 1999; Wynn-Williams 1999). I do not have my own opinion as to that, though it is more difficult to me to perceive how producers could have appeared prior to detritivores than to visualise the opposite course of the events. I prefer thinking that for the first organisms the 'soup' must have been an easier acceptable and utilisable source of energy and nutrients as compared to other sources existing at that time.

SCENE 3. THE FIRST SEMIAUTOTROPHIC ECOSYSTEMS APPEAR

PERIOD: APPROXIMATELY 3.7 MILLIARD YEARS AGO

MAIN CHARACTERS: GREEN AND PURPLE NON-SULFUR BACTERIA OR THEIR FUNCTIONAL ANALOGUES

Perhaps the only way out of the ecological crisis that befell the first organisms was reaching similarity between catabolism and anabolism rates in ecosystems. Abiotic synthesis of organic materials had to be changed by biotic one. That probably was the case approximately 3.7 milliard years ago - the first photosynthesisers originated. Of contemporary organisms, this role could be suitable to green and purple non-sulfur bacteria. Results obtained by the method of molecular phylogeny show these bacteria to be the oldest photosynthesisers of those currently existing (Xiong *et al.* 2000). Of course, in those old times there may have existed even more primitive functional analogues, too, that disappeared later. This, again, can only be guessed.

Some of green and purple non-sulfur bacteria carry out a very primitive anoxygenic (producing no oxygen) photosynthesis (Kondrat'eva 1974):

$$C0_2 + CH_3\,CH\,OH\,CH_3 \xrightarrow{\text{light}} (CH_20) + CH_3\,CO\,CH_3$$

Quite possibly, such or similar was the way in which the first photosynthesisers on Earth fed. It was merely semiautotrophic or, to put it more exactly, photoorganoautotrophic (energy source - light, hydrogen (electrons) source - organic substance, carbon source - inorganic substance).

In modern times, green and purple non-sulfur bacteria are quite widespread in anaerobic zones of water bodies. The majority of them live in hot streams, thus are thermophilous. All of them contain bacteriochlorophylls and carotenoids.

The first photosynthesisers most probably carried out glycolysis, thus decomposed the glucose synthesised by themselves thereby obtaining energy for the synthesis of different organic compounds. It is hard to say whether they fixed molecular nitrogen or took nitrogen as ammonium ions. Those ions could have been much more abundant in oceans in those times compared to nowadays. On the other hand, quite common is another opinion, too, which suggests that life had established nitrogen fixation quite early, prior to the appearance of oxygenic photosynthesis (Raven & Yin 1998). Given that nitrogen fixation is possible just in an anoxic medium, such a conclusion may be logical.

Undoubtedly, the first photosynthesisers were not one and only living block of that-time ecosystem. Sooner or later cells of photosynthesisers converted to detritus, which resulted in selection pressure promoting the evolution of detritivores. Just after the appearance of photosynthesisers detritus may have been accumulating for a while thereby making a huge vacant niche, but that could have hardly lasted for a long time, especially presuming that the block of detritivores had been originated by evolution prior to that of producers. Even if this is right, most probably coadaptation of producers and detritivores may have been reached not instantaneously, but after a certain period of time, as it is likely that the first photosynthesisers may have been synthesising new compounds hard to decompose under anaerobic conditions. Of them there could be pointed out the above-mentioned bacteriochlorophylls and carotenoids, as well as peptidoglycans - bacteria cell wall fastening compounds. Logically, first of all there must have evolved those hard to decompose compounds and

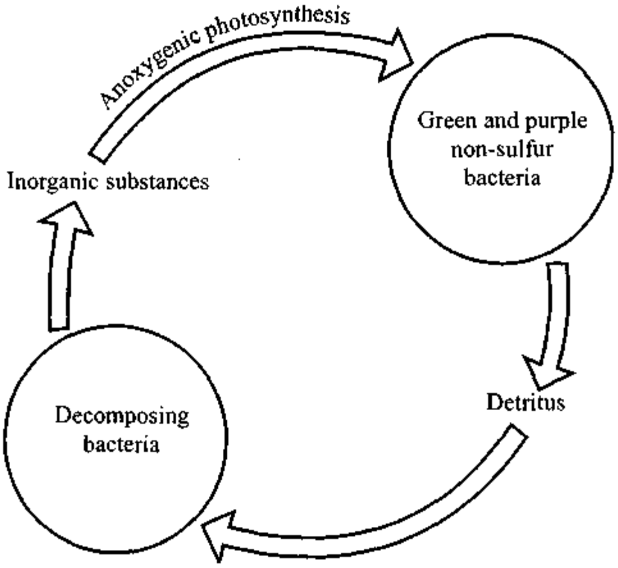


Figure 4. A block scheme of the ecosystem that could have appeared approximately 3.7 milliard years ago. For simplicity, an arrow from detritivores to detritus is not shown here though this kind of an inner loop is likely to have been already existing.

just after a while - organisms decomposing them. Of presently existing anaerobes, this role could probably be quite suitable to the genera *Clostridium, Bacteroides,* and *Ruminococcus* (Schlegel 1985), though it is most likely that in those ancient times there were other genera that had analogous functions.

It is known that under anaerobic conditions and in the presence of a sufficient variety of bacteria the latter are able to decompose practically any organic compound to $C0_2$, NH_3, H_2S, CH_4 and H_2 (Gottschalk 1981). There are reasons to believe that the set of decomposing bacteria should have been existing already 3.7 milliard years ago. Some of those decomposition products may have moved back to the cycle to be utilised for new acts of biosynthesis again.

We obtain a hypothetical block scheme of that-time ecosystem (Fig. 4).

SCENE 4. THE FIRST TRUE AUTOTROPHS APPEAR AND BECOME WIDESPREAD

PERIOD: APPROXIMATELY 3.6 MILLIARD YEARS AGO
MAIN CHARACTERS: GREEN AND PURPLE SULFUR BACTERIA OR THEIR FUNCTIONAL ANALOGUES

The above-described ecosystem, if there existed such at all, also had its shortcomings. The greatest of them was that producers could not do without some of organic compounds, a source of hydrogen and electrons to them. Those compounds may have been produced by detritivores, or there may have been competition for some of them between producers and detritivores. We cannot know. Whatever there was, sooner or later there must have appeared true autotrophs that could do without organic compounds dissolved in water. They could have been green and purple sulfur bacteria or any other of their functional analogues.

Green and purple sulfur bacteria, similarly to their relatives, non-sulfur bacteria, carry out anoxygenic photosynthesis. But they already are true autotrophs, or, to be more exact, photolithoautotrophs (energy source - light, hydrogen (electrons) and carbon source - inorganic materials):

$$C0_2 + 2H_2S \xrightarrow{\text{light}} (CH_20) + 2S + H_20 \quad (1)$$

or

$$C0_2 + 2H_2 \xrightarrow{\text{light}} (CH_20) + H_20 \quad (2)$$

Some of modern bacteria of this group continue the reaction (1) to sulphates. From common photosynthesis, which is performed by cyanobacteria and green plants, this one differs in that the source of hydrogen (electrons) in it is hydrogen sulfide, rather than water. Hydrogen sulfide dissociating, there is produced sulfur rather than oxygen, which is a usual case. In the other reaction (2), the source of hydrogen (electrons) is molecular hydrogen itself.

The materials required for that type photosynthesis - carbon dioxide, hydrogen sulfide, or hydrogen - were most probably quite abundant in the ocean water then. They were outgassed by volcanoes and, apart from that, produced on fermentation.

In nutrient cycling green and purple sulfur bacteria may have been aided by the same groups of anaerobic decomposers that existed during the times of the predominance of non-sulfur bacteria. It is, however, possible that there could have been certain changes. The thing is that along with the new photosynthesisers sulfur and sulphates started accumulating in the environment, thereby making new vacant niches for future detritivores. It did not take long for the latter to emerge. Here I mean sulfur- and sulphate-reducing bacteria, e.g. *Desulfuromonas* and *Desulfovibrio* or other organisms catalysing similar reactions. Then the hydrogen sulfide produced by those bacteria could be utilised for photosynthesis again. The vacant niche became occupied and the nutrient cycle again was free of waste. Here for the first time respiration comes along, yet anaerobic though: those bacteria utilise sulfur and sulphates rather than oxygen as the final acceptor of electrons. This kind of respiration therefore is also called sulfur and sulphate respiration. From the point of view of energy, anaerobic respiration is more effective than fermentation.

That the appearance of sulfur bacteria sooner or later had to evoke the evolution of sulphate reducing bacteria, too, has also been suggested by some experts of this field (e.g. Schidlowski 1989). There is evidence that sulphate reducing bacteria have emerged a very long time ago and they may be even more than three milliard years old (Ohmoto *et al.* 1993; Canfield & Raiswell 1999). Thus, evidently, their appearance just on that scene is advocated not by deductive reasoning only.

We obtain a picture of that-time ecosystem structure (Fig. 5). Unlike the majority of schemes in this book, this one is not original. It was drawn first, though in a little different way, and discussed already by Walker (1980).

After the appearance of photosynthesising sulfur bacteria, non-sulfur bacteria probably did not disappear, though in habitats with low amounts of dissolved organic materials they had to give up their place to rivals.

If the above reasoning is at least slightly grounded, we may suppose that approximately 3.6 milliard years ago there may have been the following yet primitive cycles of carbon, hydrogen, nitrogen, and sulfur:

$$CO_2, NH_3, H_2, H_2S \underset{\text{ecosystem catabolism}}{\overset{\text{ecosystem anabolism}}{\rightleftarrows}} \text{organic compounds}, S^0, SO_4^{2-}$$

Here I mean that ecosystem anabolism is carried out exclusively by producers, whereas catabolism - by all organisms, producers among them. Consumers just utilise materials produced by producers.

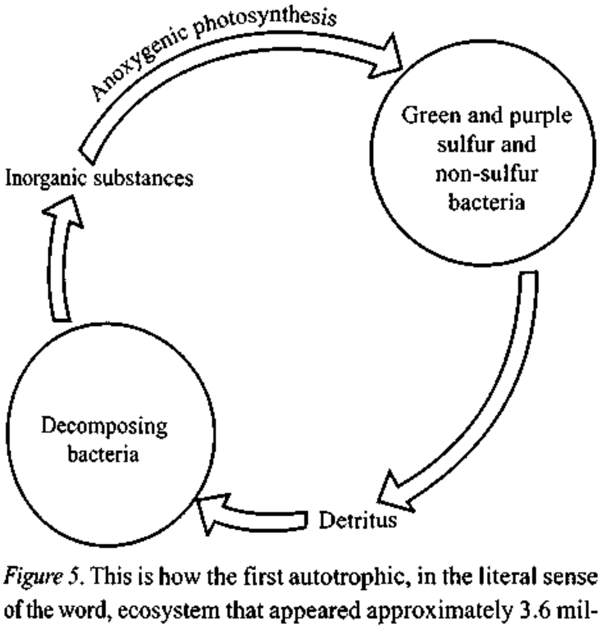


Figure 5. This is how the first autotrophic, in the literal sense of the word, ecosystem that appeared approximately 3.6 milliard years ago could have been looking like.

Except for details, conversions of materials and energy may have become of an entirely modern type:

inorganic materials → organic materials → inorganic materials
light → chemical energy → heat

Here I would like to pay the reader's attention to two very important, as I think, circumstances. First, until nowadays (!) anoxygenic photosynthesisers have been using probably the same materials as nutrients that supposedly were abundant in the atmosphere more than 3.5 milliard years ago and that were major reagents in the abiotic synthesis of organic materials. Besides, the modern anaerobic bacteria *Ruminococcus, Clostridium, Bacteroides* and others somehow are able to decompose detritus to those materials that are used by anoxygenic photosynthesisers as nutrients. I do not think that all this is mere coincidences. Evidently, these supposed coincidences could be explained just through the idea of a nutrient cycle. What was waste for some organisms turned to a potential or real source of materials or energy to other.

Second, of the above presented schemes an erroneous view could be made that in those old times the state of an ecosystem was stationary, i.e. as many inorganic materials were converted to organic ones, as many of them were brought back due to ecosystem catabolism, in the given case - fermentation and anaerobic respiration. This is not an entirely exhaustive picture. It is just more or less right on the scale of ecological time and completely incorrect on that of evolutionary one. Already the very first organisms started to grow and reproduce right after their appearance. The increase of the biomass of ecosystems and that of the entire biosphere was, seemingly, one of the most prominent trends of evolution. This means that life immediately after its appearance began to change its environment reducing the amount of some materials and increasing that of other ones. Just a look at the equations of anoxygenic photosynthesis as well as at those of ecosystem anabolism and catabolism is sufficient to perceive that as the biomass accumulated the amount of nutrients - $C0_2$, NH_3, H_2, H_2S - should have been indispensably reducing in the environment. The same trend must have been enhanced by the accumulation of detritus and fossil fuels, of course, if that accumulation existed at all. On the other hand, it follows from the above equations that as amounts of organic materials increased, sulfur and sulphates, too, should have been increasing in the environment. Later I will explain in a similar way why oxygen level should have been indispensably increasing in the environment.

In the atmosphere of that time, free nitrogen was quite abundant, but it is unknown whether it was utilised by organisms in some way. Modern green and purple sulfur bacteria are fixing molecular nitrogen, but there is no evidence that they also did that in those ancient times. Possibly enough, there were photochemical reactions in that-time atmosphere between the H_2, CO, and N_2 of volcanic origin, thereby producing ammonia and methane (Kasting 1993). That abiotic fixation may have been absolutely sufficient to compensate the loss of nitrogen, resulting in due to its conservation in bottom sediments. In those times, there probably was no way back (denitrification) yet, as there was no nitrification, thus nor sufficient amount of nitrates (for empirical data and discussion, see Beaumont & Robert 1999). Supposedly logical as it is, this view on that time nitrogen cycle is, however, highly speculative. Possible also is another scenario suggesting that it should have been early that ammonia became a primary production limiting factor, thus biological nitrogen fixation, too, could have appeared very early; the resources of atmospheric nitrogen gradually decreased, until quite later, 2.5-2.0 milliard years ago, there emerged nitrification and denitrification, which set the stage for the modern nitrogen cycle.

SCENE 5. CVANOBACTERIA COMPLICATE ECOSYSTEM METABOLISM

PERIOD: 3.5-3.0 MILLIARD YEARS AGO

MAIN CHARACTERS: CYANOBACTERIA OR THEIR FUNCTIONAL ANALOGUES

From that period some fossils have survived to the present, thus this scene compared to the previous ones is much more grounded on facts.

There is an opinion (Schopf 1992b, 1993) that just in that period cyano- and similar to them bacteria originated. Modern cyanobacteria carry out oxygenic photosynthesis, therefore the opinion prevails that the same metabolism was characteristic of them during the described period as well. I will not be much surprised, however, if in the near future it will turn out that in the initial period they, similarly to green and purple sulfur bacteria, carried out anoxygenic photosynthesis. Morphological similarity of fossil microorganisms to modern ones does not necessarily testify to similarity of their metabolism. More or less proved is just the fact that oxygenic photosynthesis existed 2.7 milliard years ago (Summons *et al.* 1999), but indubitable evidence for earlier origin of this process is absent. The question is discussed in more detail by Marais (1997), Nisbet (2000), Nisbet and Sleep (2001).

While there is no definite data grounding one or another opinion, let us consider that just after their appearance cyanobacteria carried out common to us oxygenic photosynthesis:

$$C0_2 + H_20 \xrightarrow{\text{light}} (CH_20) + 0_2$$

So, cyanobacteria, like their antecedents green and purple sulfur bacteria, are photolithoautotrophs, though their source of hydrogen and electrons is not hydrogen sulfide or hydrogen, but water. Therefore, molecular oxygen becomes one of the reaction products. This, oxygenic, synthesis is more advanced than anoxygenic, because from the moment of the appearance of oxygenic photosynthesis primary production could no longer be limited by materials (H_2S, H_2), the amounts of which hardly were very large in that-time ocean. That advantage, too, was immediately made use of - cyanobacteria could reproduce unobstructed even in habitats free of hydrogen sulfide or hydrogen.

However, as a result of the molecular oxygen accumulation in the environment, there arose a new purely ecological problem. Molecular oxygen is known to be toxic to obligate anaerobes. Besides, it converts to even more toxic agents: singlet oxygen, hydrogen peroxide, and superoxide. Accordingly, cyanobacteria through genetic variability and selection were as soon as possible to acquire the enzymes that would make them resistant to oxygen and secondary pollutants of oxygenic origin. Understandably, the same was to be done by decomposers following cyanobacteria.

Thus, during the period discussed the structure of ecosystems changed little, whereas ecosystem metabolism became much more complicated, for in addition to anoxygenic photosynthesis oxygenic one emerged (Fig. 6).

The first photosynthesisers were most probably inhabiting surface water, shoals and were plankton organisms, whereas detritivores were dwelling in both water and bottom, where detritus accumulated. In slightly deeper places, it was probably more difficult for nutrients to reach surface water, like in the present. Therefore there is no wonder that soon after the appearance of photosynthesisers a more effective union between producers and detritivores became established. I have in mind stromatolites, which emerged approximately 3.5 milliard years ago. They are large structures resembling pillows or columns, the first in Earth's history reefs. That-time stromatolites have survived until nowadays in the form of fossils. It is not known so far what organisms the first stromatolites were formed of. Luckily, living samples of stromatolites have survived until nowadays, for example, in the Shark Bay, Australia, which is due to very high salinity that is unfa-

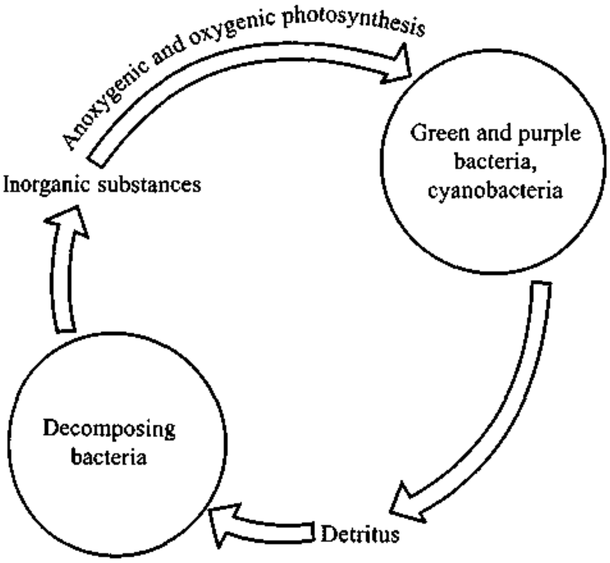


Figure 6. **Oxygenic photosynthesis that probably arose, as some palaeobiologists suppose, 3.5–3.0 milliard years ago complicated ecosystem metabolism for a while.**

vourable for biophages exploiting them.

The structure of modern stromatolites is as follows (Zavarzin 1979; Schopf 1992b; Golubic 2000). The upper layer is formed of cyanobacteria and obligate aerobe detritivores. Cyanobacteria increase the alkalinity of water, thereby precipitating calcium and forming a reef. Detritivores use the non-living organic matter accumulated by cyanobacteria as well as the oxygen produced by latter and return materials to them in the form of nutrients. The middle layer, with some penetrating light, but usually with quite low oxygen concentration, is inhabited by green and purple sulfur bacteria and facultative aerobe detritivores. The sulfur bacteria absorb the light unused by cyanobacteria, another part of its spectrum. A bit deeper, where neither light nor oxygen penetrate, obligate anaerobe detritivores are established. Among them there are sulfur- and sulphate-reducing bacteria, too. Thus, a stromatolite is two relatively independent miniature nutrient cycles, aerobic and anaerobic. Diffusion combines those two cycles into one.

It is quite possible that the stromatolites that appeared 3.5 milliard years ago were formed of just a single layer, comprising anoxygenic photosynthesis performing green and purple bacteria and anaerobic detritivores (Schopf 1992b). Among the latter possibly were sulfur- and sulphate-reducing bacteria, too. Cyanobacteria that emerged later also joined those structures, bringing along the detritivores following them as well. After the vertical gradient of light was joined by the vertical gradient of oxygen, the diversity of organisms in stromatolite increased even more. As it is testified by fossils, stromatolite ecosystems were especially widespread 2.5-0.8 milliard years ago. They were present in seas, lakes, and even in very saline and very hot waters. At that time it was the major form of life existence. Later their gradual extinction started, especially accelerated in the Cambrian, after very aggressive biophages originated.

SCENE 6. THE FORMATION OF AEROBIC NUTRIENT CYCLES STARTS

PERIOD: 3.0-2.5 MILLIARD YEARS AGO
MAIN CHARACTERS: CYANOBACTERIA (STROMATOLITES)

It is hard to say how great was the catastrophe caused in ecosystems by the accumulation of oxygen in water. Two extreme variants are possible. The essence of one of them is that water may have been so polluted with oxygen that mass extinction occurred, followed by the formation of oil reservoirs. The other, less drastic and more probable, provides that there may have been many antitoxins in that-time waters, which prevented the accumulation of oxygen in the environment and accordingly the mass extinction, too. It is thought that the main role of antitoxins was played by ferrous iron abundant in that-time waters. Affected by oxygen, iron oxidised, converted to the ferric form and precipitated. As a result, there appeared the abundant bounded iron formations, magnetites, and hematites, i.e. ores exploited nowadays.

There are other opinions regarding this question, too. Ehrenreich and Widdel (1994) suggest that the formation of those iron ores started already before the appearance of oxygenic photosynthesis, when ecosystems were predominated by purple non-sulfur bacteria. It appears that those bacteria are able of oxidising ferrous iron by using carbon dioxide (Widdel *et al.* 1993). These data slightly contradict the above-presented opinion, expressed already by Cloud and Gibor (1970) and Holland (1984). Hereby I would not like to inquire into this question, the more so that, as it seems to me, there is no ultimate answer to it yet (for discussion, see e.g. Glasby 1998; Canfield & Raiswell 1999).

In addition to ferrous iron, the role of antitoxicants most probably was also played by Mn^{2+} (which upon oxidation converted to Mn^{4+}), S° and H_2S (converted to sulfur acid), CO (converted to $C0_2$), H_2 (converted to H_20), CH_4 (converted to $C0_2$ and H_20), NH_4^+ (converted to nitrogen oxides).

That was an essential turn in the evolution of the atmosphere and hydrosphere - gradually and inevitably a reduced environment becomes an oxidised one with decreasing H_2S, CO, H_2, CH_4 and NH_3, but increasing sulphates, nitrates, and other nitrogen oxides.

Such course of events should have had a drastic effect on green and purple bacteria, which used H_2S, H_2, and NH_3 as nutrients. Thus, cyanobacteria overwhelmed their rivals not only because they started to use water as the source of hydrogen and electrons and polluted the environment with oxygen, but also because they diminished the amount of reduced compounds. From that moment the living space and the biomass of green and purple bacteria started shrinking. That in its turn made a negative effect on the majority of the decomposing anaerobes that followed them. By the way, some of the green and purple bacteria of the described period managed to adapt to living together with cyanobacteria in stromatolite structures, thus escaping extinction. That peaceful co-existence of cyanobacteria and photosynthesising anaerobes continued until the Cambrian and in some specific habitats - as long as until the present.

Anaerobic nutrient cycles have survived in zones of some water bodies until nowadays (Schlegel & Jannasch 1981). Those ecosystems, little changed throughout several milliards of years, are existing and sometimes even flourishing. In those water bodies there is a close relation between the anaerobic cycle and the aerobic one. Converted to detritus, aerobe organisms sink deeper, to anoxic zones, where they are caught by anaerobe detritivores. In their own turn, fermentation products through diffusion or in any other way get to surface layers, which are rich in oxygen, and are involved in aerobic cycles.

But let us go back to 3.0-2.5-milliard-year-old events. The supply of reduced materials in surface waters gradually diminished, thus oxygen level inevitably had to grow there. Therefore, both producers (cyanobacteria) and detritivores that lived in that adaptive zones at first were forced to acquire resistance to oxygen and then, as it usually happens, to become oxygen-dependent. Such course of events is common in many cases, for example, on the adaptation of bacteria to antibiotics or that of plants to heavy metals. This was how aerobic respiration appeared, a completely new and particularly effective form of catabolism that had an essential impact on the later evolution of life. That could have taken place just in that period, 3.0-2.5 milliard years ago.

Saving space I am not presenting a scheme illustrating the structure of the ecosystems predominant during the span of time discussed or major groups of organisms - they should have remained the same as earlier (Fig. 6). The only difference was that in both living blocks - producers and detritivores - aerobes arose in addition to anaerobes.

SCENE 7. MODERN-TYPE ECOSYSTEM METABOLISM IS FORMED

PERIOD: 2.5-2.0 MILLIARD YEARS AGO
MAIN CHARACTERS: CHEMOLITHOTROPHS

As I have already mentioned, the oxygen produced by cyanobacteria reacted with reduced or not completely oxidised materials that were abundant in ocean waters 3.0-2.5 milliard years ago: ferrous iron, bivalent manganese, sulfur, hydrogen sulfide, hydrogen, carbon monoxide, methane, and ammonia. The energy produced during those reactions converted to heat, thus organisms did not use it.

That could not last long. On the appearance of oxygen in the environment, reduced and not completely oxidised inorganic matter made vacant niches, potential energy sources, so that even the slightest inheritable variations enabling to use those resources were immediately grabbed by selection and multiplied. After a while those niches were occupied by newly emerged organisms. That was how the group of chemolithotrophic bacteria, which have survived until modern days, arose:

Iron bacteria: $Fe^{2+} \xrightarrow{O_2} Fe^{3+}$ + energy

Manganese oxidisers: $Mn^{2+} \xrightarrow{O_2} Mn^{4+}$ + energy

Hydrogen oxidisers: $H_2 \xrightarrow{O_2} H_2O$ + energy

Carbon monoxide oxidisers: $CO \xrightarrow{O_2} CO_2$ + energy

Colourless sulfur bacteria: $S^0, H_2S \xrightarrow{O_2} SO_4^{2-}$ + energy

$H_2S \xrightarrow{NO_3^-} SO_4^{2-} + N_2$ + energy

Nitrifying bacteria: $NH_4^+ \xrightarrow{O_2} NO_2^-$ + energy

$NO_2^- \xrightarrow{O_2} NO_3^-$ + energy

Methane oxidisers: $CH_4 \xrightarrow{O_2} CO_2$ + energy

Some of those bacteria use the energy obtained during oxidation for CO_2 assimilation, thereby making primary production. Others are chemolithoheterotrophs.

Thus, the rise of chemolithotrophs was provoked by the environment: at first vacant niches appeared as pairs of oxidants and reductants and only then organisms exploiting those niches did so. It would be very good to compare this version of the appearance of chemotrophs with other authors' opinions, but literature sources on the subject are very scarce. As far as I know, the question has been discussed by Hayes, Kaplan and

Wedeking (1983), and Schidlowski (1989), though in a somewhat narrower context. My opinion principally does not contradict theirs.

Besides, it is quite possible that those chemotrophs appeared on the stage of evolution much earlier, let us say 3.0-2.5 milliard years ago, since oxygen dissolved in water may have been already present at that time (Nisbet 2000). As it is known, some of chemolithotrophs for oxidation use nitrates (some of colourless sulfur bacteria) or carbon dioxide (methanogenic bacteria, the appearance of which is not discussed in this book) and not oxygen. Therefore, it is quite possible that those groups of chemotrophs could have been among the first organisms on Earth (e.g. Reysenbach & Cady 2001; Nisbet & Sleep 2001). For a long time methanogenic bacteria were even thought to be the first autotrophs of our planet (e.g. Walker 1980; Margulis 1981). Whatever the answer to the time of the appearance of those organisms is, there are reasons to believe that all chemolithotrophs were licensed to evolve not before proper vacant niches, certain pairs of inorganic reductants and oxidants, appeared.

But let us return to the main course. We obtain the following scheme of the ecosystems that existed 2.5-2.0 milliard years ago (Fig. 7). As it could be seen, the structure of ecosystems had not undergone any essential changes - again the same two living blocks plus detritus and inorganic compounds. But ecosystem metabolism had changed unrecognisably - nutrient cycles had acquired new features, which have remained practically the same until today.

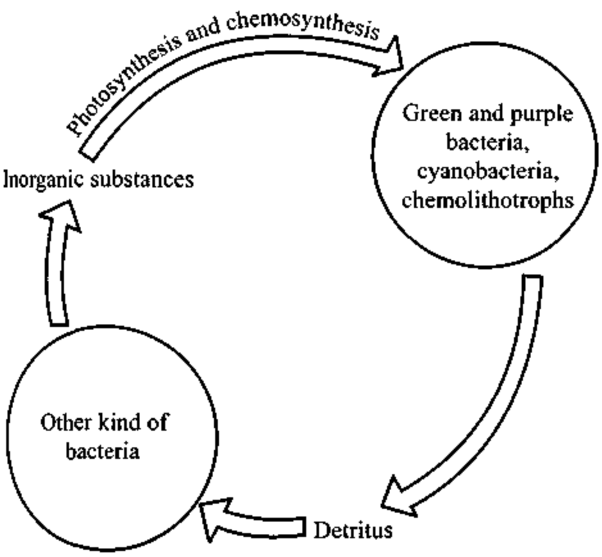


Figure 7. Reconstruction of the ecosystems that existed 2.5–2.0 milliard years ago.

Similarly to nowadays, in those times the main role in the carbon and oxygen cycle was played by oxygenic photosynthesis and aerobic respiration:

$$CO_2 + H_2O \underset{\text{aerobic respiration}}{\overset{\text{oxygenic photosynthesis}}{\rightleftharpoons}} (CH_2O) + O_2$$

In those times direct reaction was carried out by cyanobacteria, whereas back one - by all aerobic organisms of the biosphere, cyanobacteria among them, Probably, stationary state was present already then: ecosystem anabolism was outbalanced by catabolism, which enabled biomass as well as carbon dioxide and oxygen level stabilisation in the environment. However, from the point of view of evolutionary and not ecological time, the biosphere biomass probably was apt to gradually increase. It is likely that on the scale of biosphere the amount of detritus and that of buried organic matter increased as well. Thus, already at that time the carbon and oxygen cycle could have hardly been ideal, for photosynthesis was a bit more intensive than respiration. Therefore, along with the biosphere biomass oxygen level in the environment increased, too, whereas the amount of carbon dioxide had to decrease.

To understand the evolution of the nitrogen cycle is much more complicated. It is hard even to say even when approximately the biological fixation of nitrogen appeared, for instance. The fact itself that oxygen only impedes this fixation and that many of green and purple bacteria as well as cyanobacteria can fix molecular nitrogen in a way indicates that this process is old. On the other hand, at the dawn of life nitrogen compounds, especially ammonia and ammonium ions, might have apparently been much more abundant in the atmosphere and waters. Thus selection pressure, forcing organisms to acquire the ability of nitrogen fixation, might have been absent for a while. Yet there are reasons to believe that later the amount of ammonia and ammonium ions in the environment reduced to minimum, and not only because part of it converted to organic nitrogen, the biomass. The fact was that due to the presence of cyanobacteria, oxygen became accumulating in the environment and, affected by lighting, reacted with ammonia and molecular nitrogen, thereby producing oxides. Besides, as mentioned, soon thereafter originated nitrifying bacteria oxidising ammonia and ammonium ions to nitrates. I think that could have given rise to selection pressure, which induced at least diversification of nitrogen fixing organisms and their spread ever seen, if not their appearance.

Nitrates immediately made a vacant niche that provoked a rise of denitrificators. The latter used nitrates as un-

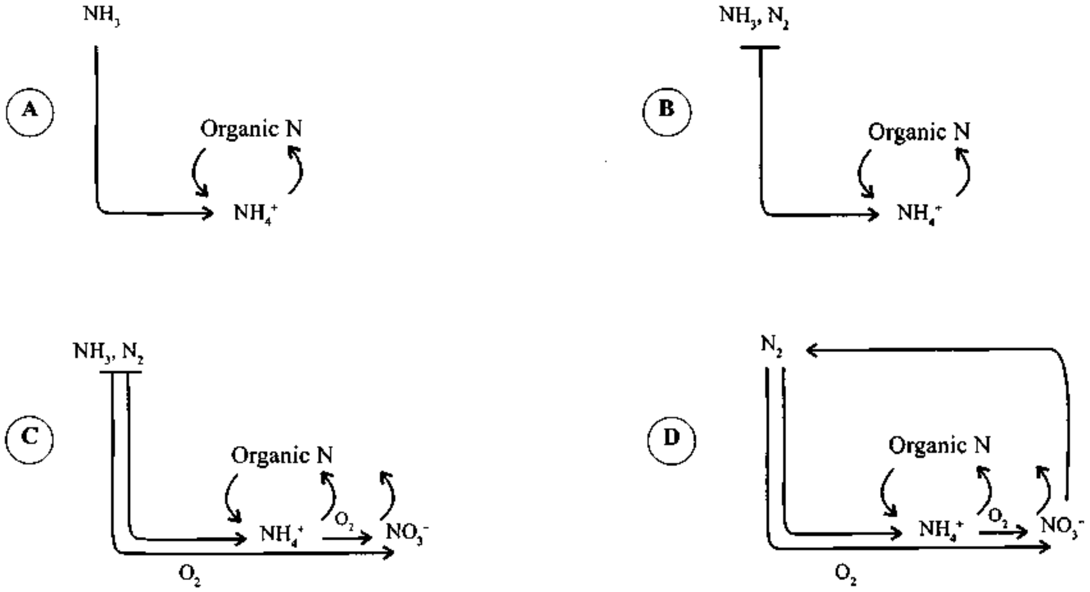


Figure 8. The global nitrogen cycle, the formation of which started along with the appearance of life, should have already acquired the current shape 2 milliard years ago. Stages: A – local cycles are formed; B – biological nitrogen fixation is formed; C – nitrates are formed; D – denitrification arises.

changeable under anaerobic conditions glucose oxidisers, final acceptors of electrons. Due to nitrate respiration nitrates converted to free nitrogen. The global nitrogen cycle became closed.

Accumulating in the environment nitrates might have soon become an additional source of nitrogen to cyanobacteria.

Since in organic molecules nitrogen usually is of a reduced rather than oxidised form, it, however, was not so useful to producers as ammonium ions were.

By the way it is likely that nitrates as a nitrogen source could be used only by cyanobacteria and photosynthesising eukaryotes. Green and purple sulfur bacteria usually assimilate ammonium ions only (Kondrat'eva 1974). Non-sulfur photosynthesisers also use organic nitrogen compounds and not nitrates for the purpose. May be this is another evidence that nitrates have begun accumulating in the environment comparatively recently?

Thus we obtain the following picture of the evolution of the nitrogen cycle (Fig. 8). I understand that this scenario of the change of the nitrogen cycle is far more speculative, though it seemingly is in accordance with the one suggested, based on methodology more inductive than mine, by experts of the field (Falkowski 1997; Raven & Yin 1998; Beaumont & Robert 1999). Difference is merely in some details of secondary importance.

The modern sulfur cycle is not very simple, for it involves not only green, purple, and colourless sulfur bacteria, but also sulfur- and sulphate-reducing bacteria as well as other detritivores and producers, and is modified by the abiotic oxidation of hydrogen sulfide. Despite its complexity, all major chains of the cycle belong to prokaryotes. Thus it is quite possible that cycle to have been existing already during the period discussed.

The phosphorus cycle is the most primitive of all. It appeared probably almost along with life and has undergone almost no changes ever since.

Let me summarise. Two milliard years ago the evolution of ecosystem metabolism must have come to a close - nutrient cycles were completely formed. And they have not essentially changed until present days. Those cycles were formed by prokaryotes alone, with no assistance on the part of eukaryotes. That was a decisive period of evolution, and evolution took another direction.

SCENE 8. ECOSYSTEM STRUCTURE ACQUIRES NEW FEATURES: THE BLOCK OF BIOPHAGES APPEARS

PERIOD: 1.7-1.2 MILLIARD YEARS AGO
MAIN CHARACTERS: UNICELLULAR ALGAE AND PROTOZOANS

As fossils show, the first eukaryotes - unicellular algae and protozoans - could have appeared approximately 1.7 milliard years ago (Schopf 1992b; though see Brocks *et al.* 1999). There is no doubt that 1.5-1.2 milliard years ago they were already very widespread. I am not going to analyse in detail the hypothesis of endosymbiosis suggested by L. Margulis and explaining the origin of eukaryotes. This hypothesis is based on many empirical facts and has become a theory accepted almost by everybody (though see Martin &

Muller 1998). I think the reader knows it quite well. I am just going to remind that based on this theory mitochondrions have emerged from aerobe heterotrophs incorporated into a host's cell, whereas chloroplasts - from photosynthesising bacteria. In the context of my book especially important is that part of the theory which states that relations of symbionts could have hardly been friendly at first and that just after a certain period of co-evolution they could have become such. Predation or parasitism gradually turned into cooperation. Thus, here for the first time we come across evidence about the appearance of a new functional group, biophages.

Since the very formation of eukaryotes their cells should have been constantly increasing (Schopf 1992b). Especially large they were 1.1-0.7 milliard years ago, having reached a diameter of 1 cm. Prokaryote cells, as it is known, are at least ten times smaller. It is a very important difference, since herbivores and predators should have been larger than their prey.

It is very likely that 1.2 milliard years ago there were already three trophic levels: producers, herbivores, and primary carnivores. (In this context the notion 'herbivore' may mislead the reader, therefore I hurry to explain that in those times there were neither plants, nor grasses. Traditionally ecologists use this notion, since they do not have a better one, for primary consumers feeding on producers.) Surely, first protozoans feeding on producers arose through evolution from some antecedents and only then other protozoans feeding on the former ones appeared.

Of currently existing genera, with regard to trophic niches quite close to that-time protozoans are *Euglena, Peranema,* and *Amoeba.* Among them there are herbivores, predators, and even producers. Among that-time protozoans there could have also been detritivores and organisms feeding on detritivores, as it is in the present.

Very possibly, during the period discussed there existed parasites, too. The theory of endosymbiosis allows thinking that both biophagy and parasitism, as a form of biophagy, was already not unusual in those times. It is more difficult to say what were those very first parasites: bacteria, viruses, protozoans, or may be representatives of all those groups.

During the period relations between unicellular algae and detritivores could have been very dramatic. It is likely that along with unicellular algae one more hard to decompose compound - cellulose - appeared approximately 1.7 milliard years ago. It is one of the constituent parts of the algal wall. At present it is the most abundant organic matter on Earth, and detritivores are unlikely to encounter any great difficulties on decomposing it. However, during the period described the situation was different - at first there were no bacteria able to decompose that compound. Therefore, having converted to detritus, cellulose inevitably withdrew from the cycle. This made an enormous selection pressure, and after a while a new functional group - cellulose-decomposing bacteria - separated from detritivores and occupied that niche. It is hard to say how long that evolution lasted, but seemingly not very long. One way or the other the nutrient cycle became non-waste again.

We obtain a block structure of an ecosystem typical of that period (Fig. 9). For picturesqueness, it is presented in a simplified form, ignoring some quite important, though in the context of this book not of primary importance, connections. Nearby the production pyramid of that ecosystem is shown (Fig. 10). I would like to

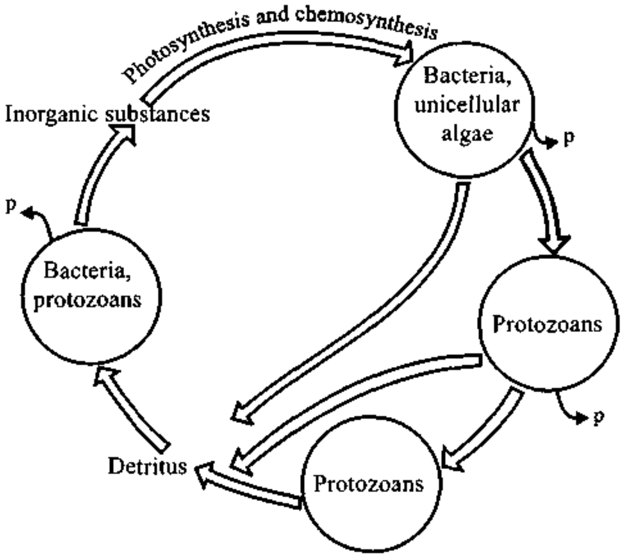


Figure 9. Approximately 1.2 milliard years ago ecosystem structure should have acquired completely new features – a block of biophages with two levels of consumers should have originated. Very possibly, alongside with herbivores and primary predators there existed parasites (p), too.

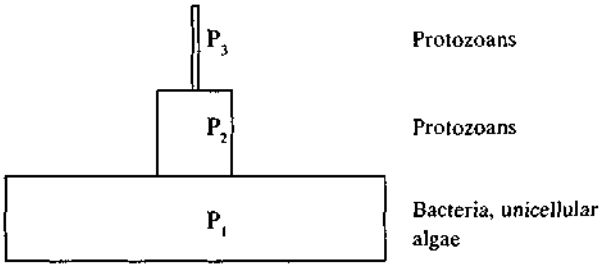


Figure 10. Hopefully, this is exactly how one of the first in the history of life production pyramids looked like. Of course, quantitative proportions of P_1, P_2, and P_3 could not be reconstructed precisely enough.

remind the reader that the production pyramid is particular in that it is made based on biomass increase rates. Here P_1, P_2, and P_3 are production of producers, herbivores, and primary carnivores, respectively. As it is known, the rule of 10% is valid only for this particular type of the ecological pyramid.

SCENE 9. THE ERA OF MULTICELLULAR ORGANISMS STARTS. THE FOURTH TROPHIC LEVEL ORIGINATES

PERIOD: 1,200-650 MILLION YEARS AGO
MAIN CHARACTERS: MULTICELLULAR ALGAE, THE FIRST ANIMALS

Strange as it is, we know less about that period than about some earlier ones. Different authors suggest so different viewpoints that there is nothing to do but wait for some new undisputed empirical data. A more or less real fact is just that multicellular algae emerged about 1 milliard years ago. They most probably were red algae. Animals evidently are far harder traceable, though. Molecular (rRNA) investigation allows a supposition that the first invertebrates - sponges, ctenophores, and cnidarians - arose 1,000-700 million years ago (Runnegar 1992; Wray *et al.* 1996; Knoll & Carroll 1999). There are fossil data supporting this opinion in a way (Schukla *et al.* 1991). Today many experts, however, doubt about that early origin of contemporary animals (e.g. Narbonne 1998). They consider that 1,000-800 million years ago many of animals, if they existed at all, did not belong to any of modern animal groups, but rather made great individual taxons absent today, and do not give any detailed description of those taxons.

There is an impression that during that period, especially during its second part, biodiversity was far greater than that suggested by presently available palaeontological data (Schopf 1992b). It is quite probable that at that time there were some especially unfavourable for fossilisation conditions. Neither could be rejected a possibility that that-time invertebrates were not among easily fossilised ones (Conway Morris 2000).

At such empirical confusion I have nothing to do but use my own methodology. In this scene, I am allowing myself to deduce, may be with too great a confidence, what groups of organisms *might* have existed at that time and what the structure of that-time ecosystems *might* have look like.

A priori it could be expected that the evolution of multicellular organisms could not have been rapid. Started from the colonial way of life, it could have been just after many million years that it converted to mutualism, which is based on cell (tissue) specialisation, obligate interdependence, and strict co-ordination of the activities of the whole organism. Inheritable variability and selection had to invent unprecedented ways of energy, matter, and information transfer from one cell to another. Despite that, during the period described there were many vacant niches - first of all plankton organisms (bacteria, unicellular algae, and protozoans, see the previous scene) - that sooner or later inevitably had to provoke the appearance of large filtrators and multicellular predators exploiting them. That scenario may have come into existence about 700-600 million years ago. Since there is no certainty, I consider them to have been sponges, ctenophores, and cnidarians.

Sponges - filtrators, with a very primitive structure and little advanced cell specialisation. Ctenophores and cnidarians are considered more advanced and more complex animals, with clearly differentiated tissues and organs. Both of these two animal groups are active predators that catch their prey with sticky tentacles or damage it with stinging cells. This allows us to think that at least four trophic levels should have existed as early as 650 million years ago (Figs 11, 12).

SCENE 10. ADAPTIVE RADIATION OF INVERTEBRATE ANIMALS TAKES PLACE. PRODUCTION PYRAMIDS ACQUIRE ALMOST A MODERN SHAPE

PERIOD: 540-500 MILLION YEARS AGO (THE CAMBRIAN)
MAIN CHARACTERS: INVERTEBRATE ANIMALS

At the very beginning of the Cambrian, in so short a period as 10 or several more million years unprecedented biodiversity of invertebrates arose. That already was a typical adaptive radiation. In general, the Cambrian is deservedly regarded a period when nature somewhat experimented one after another throwing forms produced by it into the forge of evolution. The majority of those forms did not survive even until the end of the Cambrian and were replaced by others. This probably testifies to the fact that mechanisms of genetic variability, and especially combinative variability, related to sexual reproduction, were already advanced by that time.

In the Cambrian, molluscs, brachiopods, trilobites, crustaceans, echinoderms, and many other invertebrate groups appeared (Vermeij 1987; Boardman *et al.* 1987; Runnegar 1992; Clarkson 1998). Many of them had a firm outer or inner skeleton. For others than experts, best-known animals of that time undoubtedly are trilobites. And there are grounds for this, since trilobites should have been making a very great part, if not the majority, of the biomass of that-

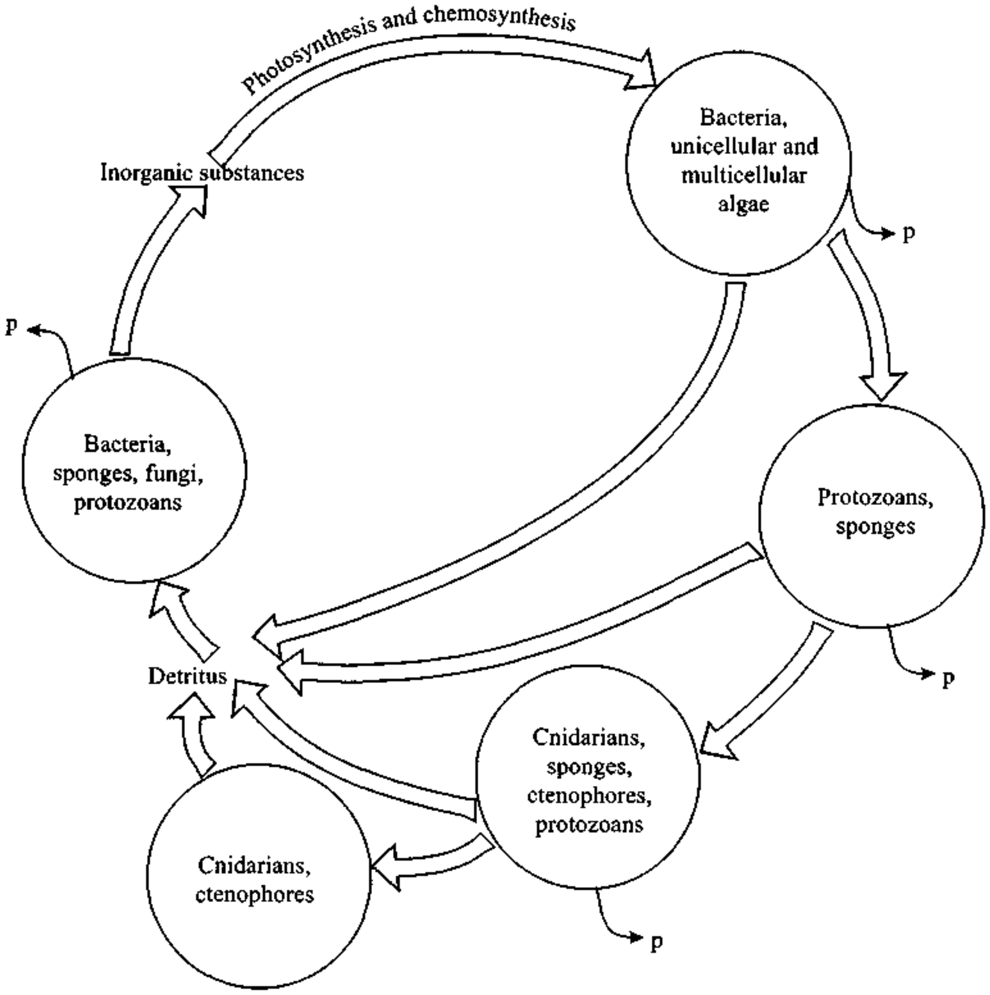


Figure 11. Having come into being more than 1.0 milliard years ago, 650 million years ago multicellular organisms should have already penetrated into all the three blocks – producers, biophages, and detritivores. Ecosystem structure became even more complicated than before.

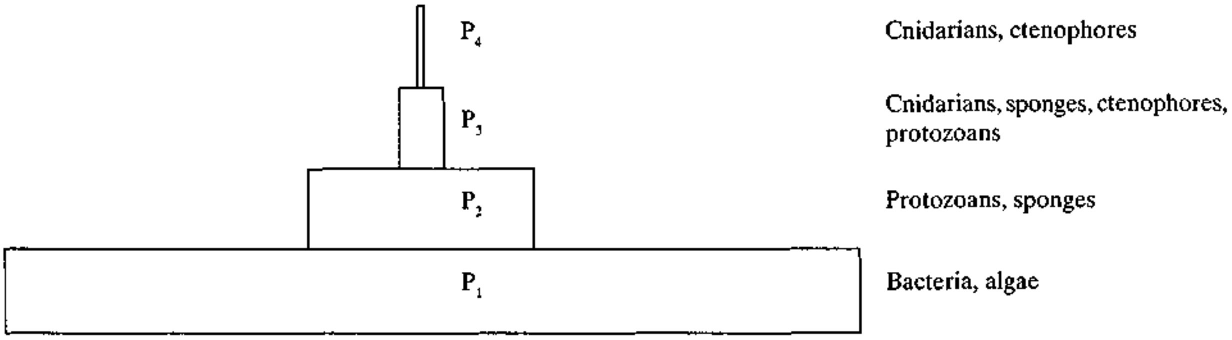


Figure 12. 650 million years ago the production pyramid grew up a little – the fourth trophic level emerged.

time animals. Among the invertebrates originated at the beginning of the Cambrian, few were of large forms. Most of them were merely several millimeters or centimeters long. Trilobites were no exception in this sense. It is likely that they were comparatively peaceful animals, fed on algae, small bottom invertebrates, and detritus (carrion).

At last, in the second part of the Cambrian some quite large invertebrates arose. They were the first chelicerates, to be more precise - their antecedents *(Sidneyia, Anomalocaris, Sanctacaris)*. Some of them could have been as long as 1 m and had powerful claws and a muscular mouth. Other Cambrian invertebrates also should have grown up a little; for instance, some of trilobites and cephalopods should have become 10-20 centimeters long.

The mentioned antecedents of chelicerates were typical predators. Considering their quite large size, it could be stated almost with confidence that by the end of the Cambrian there should have been already five trophic levels and that chelicerates should have become typical top predators (Fig. 13). Thus, by that period the evolution of ecosystem structure should have come nearly to a close. Just still larger predators were lacking, who were to appear in the Ordovician. Naturally, after the appearance of large and strong predators, numbers of animals covered with outer skeleton started increasing, since that was the way they could escape death in predator's mouth, As a response to predation pressure, preys evolved. Some of them covered with the armour made of mineral sclerites, hard shells or sharp spines, whereas others 'learnt' to hide digging themselves in sand or silt.

Certainly, consequent waves of adaptive radiation inevitably resulted in extinction of some previously existed organisms. In the Cambrian, the domain of stromatolites earlier predominant in seas apparently considerably contracted. Experts explain this by the appearance of stronger than stromatolites rivals as well as by abundant and effective biophages who by exploiting unarmed stromatolites aided rivals of the latter. At the end of the Cambrian many other forms that originated at the beginning of the period died out, which was due to some outer interference, too. The extinction experienced in the Cambrian, however, was not so mass compared to some later ones and most probably was related to the fact that that-time ecosystems were far from being saturated with species. As to biodiversity, the Cambrian was much inferior to the Devonian or even more to the Quaternary (Signor 1990). Besides, one should have in mind that in the Cambrian there were many vacant adaptive zones and geographical regions still waiting for life to appear.

The production pyramid typical of the Cambrian is illustrated in Fig. 14.

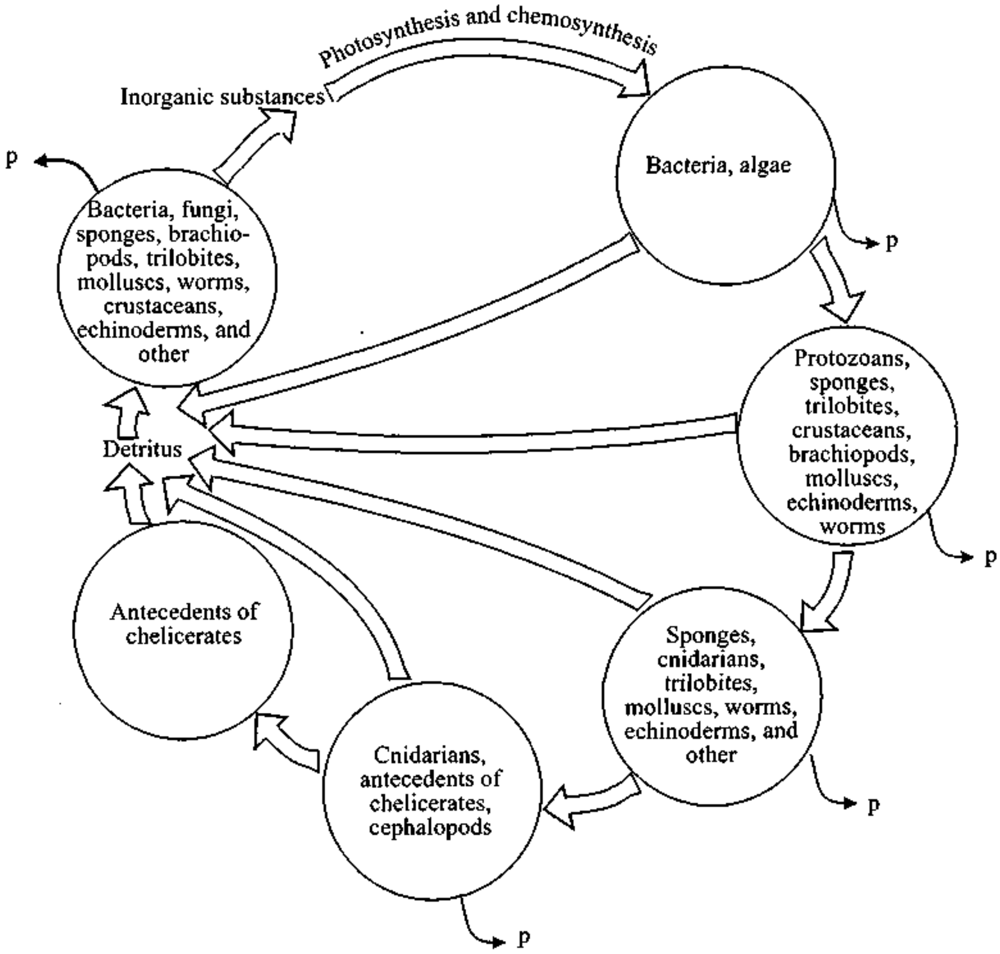


Figure 13. **In the Cambrian, invertebrate diversity extraordinarily increased, old niches were being shared and new ones occupied. Ecosystem structure also changed: at the end of the Cambrian large predators – antecedents of chelicerates – and alongside with them the fifth trophic level saw the light of the day.**

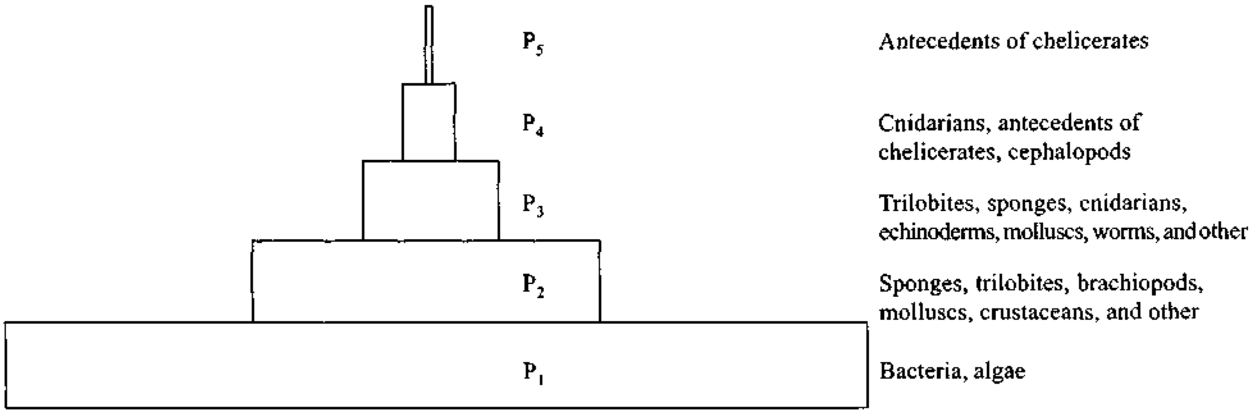


Figure 14. Production pyramids of the end-Cambrian were almost identical in shape to those of the present.

SCENE 11. A GREAT ABUNDANCE OF VERY LARGE AND AGGRESSIVE PREDATORS APPEARS. THE EVOLUTION OF ECOSYSTEM STRUCTURE COMES TO A CLOSE

PERIOD: 500-435 MILLION YEARS AGO (THE ORDOVICIAN)
MAIN CHARACTERS: CEPHALOPODS AND CHELICERATES

The Ordovician, which followed the Cambrian, is famous for its impressive adaptive radiation of the cephalopods from the subclass Nautiloidea. Having been in the background of organisms larger than them in the Cambrian, cephalopods changed and spread so much in the Ordovician that began dictating their own circumstances to the others. Some medium-sized and very large, several meters long, cephalopods emerged. They were already typical top predators. Hardly moving in the Cambrian, in the Ordovician they became pretty quick. Along with species creeping on the bottom there were some swimming, too. Throughout the Ordovician several dozens of new cephalopod families and hundreds of genera arose. By the way, later those genera died out. Non of them was to see the Jurassic.

Another group of predators, chelicerates, became more diverse as well. There appear eurypterids. They were of different sizes: small, average and quite large, almost two meters long. Their claws (chelicerae) could have been strong enough even to crush bones. Contrary to the first chelicerates most of which crept, the majority of eurypterids swam.

The biodiversity of cephalopods and chelicerates having increased at such a scale, other animal groups could not elude suffering from them. At the end of the Ordovician the diversity of trilobites greatly diminished, similarly to that of some other invertebrates that were numerous in the Cambrian. That extinction was almost undoubtedly caused not only by newly appeared large predators, but also by more effective rivals. Trilobites most probably were affected not only by cephalopods, eurypterids, echinoderms, and cnidarians, but also by crustaceans, gastropods, and jawless fishes, all of them still relatively peaceful in the Ordovician.

As a response to the appearance and spread of large predators, trilobites learnt to roll themselves up into a ball the way hedgehogs do, molluscs and brachiopods acquired even harder than in the Cambrian shells, and preys became quicker and their ability to use shelters increased (Vermeij 1987). Every who did not manage to develop some effective tactics to escape predation became extinct.

During the Ordovician bryozoans (Bryozoa), graptolites (Graptolithina), and stromatoporoids (Stromatoporoidea) became widespread. The diversity of echinoderms expanded in particular: sea stars, sea urchins, blastoid echinoderms, and many other forms came into existence. Jawless fishes (Agnatha) dispersed. At the end of the Ordovician they became covered with bone armour in order to protect themselves from more and more aggressive predators (Carroll 1988).

Thus, it is likely that in the Ordovician a modern-type ecosystem structure and modern production pyramids originated at last. Saving space I am not drawing an ecosystem block structure here. The reader could do it as well if he or she feels like it. I am presenting just the production pyramid of the Ordovician (Fig. 15). In it there are six trophic levels, which are typical of modern marine ecosystems, too, the difference being just in the set of organisms making the pyramid.

SCENE 12. FISH AGE BEGINS. COMPETITION INCREASES

PERIOD: 435-355 MILLION YEARS AGO
(THE SILURIAN AND THE DEVONIAN)
MAIN CHARACTERS: FISHES

As already mentioned, jawless fishes became widespread already in the Ordovician. Their role in that-time ecosystems was comparatively insignificant. In

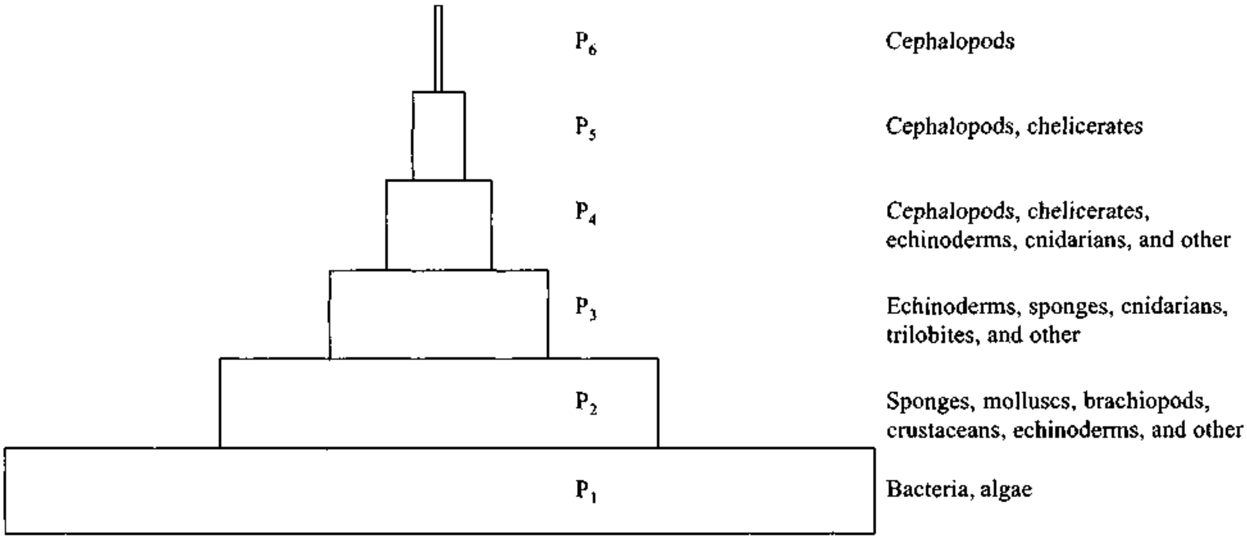


Figure 15. **In the Ordovician, after very large predators appeared, modern-type production pyramids were finally formed. They would no longer change later or if they would that would be just for a while to acquire the common shape again after a certain period of adaptive radiation was over.**

the Silurian, one more fish group - placoderms - emerged. In the mid-Devonian, which followed the Silurian, that group was particularly abundant (Carroll 1988). Along with small forms there existed some medium-sized and extraordinary large, up to 9 meters long, armoured monsters. Some of them fed on bottom organisms, others - on plankton and small fishes, whereas the largest of all became typical top predators. Such a large-scale spread of placoderms had a considerable effect on their rivals. The abundance of jawless fishes markedly reduced. The diversity of eurypterids and cephalopods started to shrink as well, However, things became worse for placoderms themselves after the adaptive radiation of cartilaginous (Chondrichtyes) and cartilaginous ganoid fishes (Chondrostei) began in the second part of the Devonian. At first, those fishes were much inferior to their evolutionary older rivals, armoured fishes, in size. Though size does not seem to be the essential thing in evolution. The ability to manoeuvre rapidly, for example, is far more important. Thus, at the very end of the Devonian there was nothing but remnants left of placoderm diversity. The Devonian having passed, at the beginning of the Carboniferous, armoured fishes were already absent. By the way, during the Carboniferous cartilaginous and cartilaginous ganoid fishes gathered size so that they almost reached their antecedents - placoderms.

Irrespective of the periods of adaptive radiation so abundant in the Silurian and, particularly, Devonian and despite the related elimination of rivals and numerous extinctions, the shape of production pyramid did not undergo a slightest change throughout that almost 100-million-year period. It was just that some species were replaced by others in the same settled niches (Fig. 16). As to species diversity in local ecosystems, it increased just little. Such a strategy of niche occupation has survived in seas until nowadays.

That unusually great diversification of predatory life forms made definite influence upon invertebrates. In the Devonian, many unusual invertebrate groups having been flourishing from as early as the Cambrian became extinct. Eurypterids, still numerous at the beginning of the period, in the late Devonian gave in to their more active rivals. The diversity of cephalopods shrank as well. Of an earlier abundant army of trilobites merely a few species were left.

A voice from behind the scenes:

Here we have to interrupt our story and leave the evolution of aquatic organisms for a while. But this in no way means that in the Devonian the development of aquatic ecosystems ceased. In the Triassic, bony ganoid fishes (Holosteimorpha) and in the Cretaceous teleost ones (Teleostei) are to become unprecedentedly widespread. It will be not without an interference of teleost fishes that at the end of the Jurassic numbers of cartilaginous ganoid ones will diminish to minimum and at the end of the Cretaceous those of bony ganoids will do so. In the Cenozoic, almost all niches meant for fishes are to be shared between cartilaginous and teleost fishes. Similar perturbation will be undergone by the other groups of aquatic organisms, too. Few of Devonian species are to see contemporary times, for devastating periods of mass extinction are awaiting life in the future. New species and genera, orders and classes are to appear, but neither the ecosystem struc-

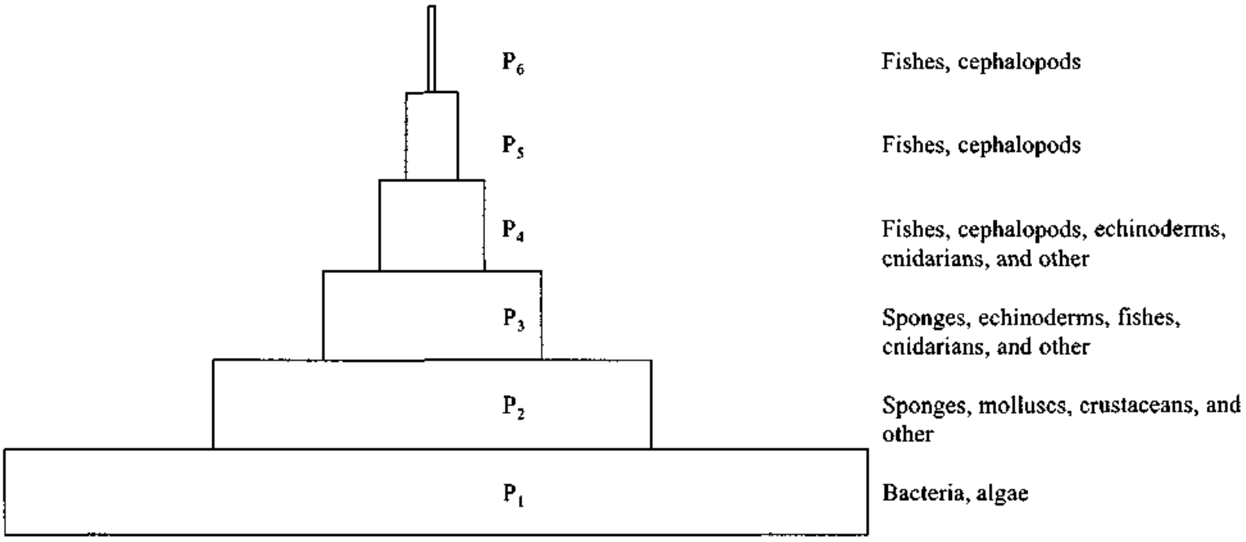


Figure 16. At the end of the Devonian approximately 360 million years ago fishes pushed invertebrates out of many niches of biophages, the pyramid itself remaining changeless.

ture nor the production pyramid (its shape and number of trophic levels) are to undergo any significant changes. New organisms will simply push part of old, less competitive forms out of existing niches, the way it used to be earlier, and things will gradually settle until the next perturbation. Having finished the improvement of the ecosystem structure in the Ordovician, life seemingly was engaged in other activities then, It expanded its domain step by step conquering not only saline, but also brackish as well as fresh waters, ocean depths, water bodies of moderate and cold climatic zones, until in the end it undertook an unprecedented wide-ranging task - to occupy land. As it could have been expected, that conquest of new territories was carried out according to the well-tried scenario. In the beginning territory was occupied by producers to be followed by detritivores, which were followed by the second trophic level, the latter - by the third one, and so on and so forth until common to us nutrient cycles and already traditional production pyramids were formed. Just constituent participants of those cycles and pyramids were new, for they were forced to adapt to abiotic conditions characteristic of each adaptive zone and, certainly, to new biotic surroundings.

THE FIRST INTERLUDE: HYDROSPHERIC EVOLUTION

Somebody may think that there is quite simple unilateral connection between life and non-living environment, i.e. non-living environment changes and alternates, and organisms adapt to those changes and survive or do not adapt and thus die. This point of view is not erroneous, but it has been proved long ago that life changes non-living surroundings. The existence of such a feedback effect is beyond any doubt to a palaeontologist, an ecologist, or an expert investigating ecosystem evolution. Though, strange as it is, the idea of life as a mighty geological force that has essentially changed our planet's face seemingly is being a little forgotten during recent years again. Therefore I would like to remind the reader about something and to relate hydrospheric evolution with the evolution of aquatic ecosystems just discussed, though not to the very end.

First, it should be stressed that at the very dawn of Earth's life the chemical composition of ocean water was determined by processes going on in the lithosphere and atmosphere. Later, after life arose and spread (which is thought to have taken place in water first) the hydrosphere became free from being unconditionally dependent on the other two non-living spheres of Earth. That dependence acquired an opposite direction - the development of life in the hydrosphere decided that of both the atmosphere and lithosphere.

My point of view on how the chemical composition of ocean water changed I have summarized in Table 1. It is based on the same reasoning and logic the reader has already got acquainted with reading about the development of aquatic ecosystems. I would like to let know beforehand that the conclusions presented in the table are mostly hypothetical, thus preliminary, so I expect the reader to consider them a lure of a more serious discussion rather than a steadfast position of the author. Issues of the evolution of the chemical composition of ocean water are so complicated (Schopf 1980; Holland 1984; Dodd & Stanton 1990) that in order to unravel them properly many more efforts of experts of the field will be required.

Table 1. The impact of life on the chemical composition of ocean water in the course of evolution.

Parameter	Decreased or increased	Major mechanisms
Acidity and concentration of dissolved $C0_2$	Decreased	Decreasing volcanism; carbonatisation and calcification; assimilation of $C0_2$ (photosynthesis and chemosynthesis)
Concentration of dissolved 0_2	Increased	Oxygenic photosynthesis
Concentration of dissolved H_2S	Decreased	Decreasing volcanism; anoxygenic photosynthesis; chemosynthesis (colourless sulfur bacteria); abiotic reaction with 0_2
Concentration of Fe^{2+}	Decreased	Abiotic reaction with free 0_2; chemosynthesis (iron bacteria)
Amount of Ca	Increased (during initial stages) then decreased	Washing down from the continents; then calcification
Amount of Si	Increased (during initial stages) then decreased	Washing down from the continents; then biological incrustation
Amount of NH_4^+	Decreased	Decreasing volcanism, biological assimilation; reacting with free 0_2; nitrification
Amount of $P0_4^{3}$~	Increased (during initial stages) then decreased	Washing down from the continents; then biological assimilation and use for skeletons

Of the statements presented in the table, hereby I am going to analyse just those I have not discussed yet previously. One of them deals with water acidity and carbon dioxide levels. A widespread opinion (e.g. Schopf 1980) is, and I share it as well, that some 4-3.5 milliard years ago the acidity of water bodies was far more higher than in epochs to follow. This is explained by higher levels of atmospheric $C0_2$ in water and by the emission of some acidic evaporates (for example HC1) from volcanoes. Later volcanisms diminished, and in the ocean some processes started that might have reduced the $C0_2$ level in the environment. Here I mean the appearance of photosynthesisers. They were taking carbon dioxide from water and assimilating it, thus reducing water acidity. As it is known, medium alkalinity having increased, bicarbonates tend to convert to insoluble carbonates, most often to calcium carbonates, which precipitate. Thus, it was already at the onset of life - more than 3.5 milliard years ago - that two mechanisms for collecting carbon dioxide from the environment existed: the conversion of bicarbonates to carbonates (carbonatisation) resulted in by photosynthesisers and the use of carbon dioxide as a carbon source for the increment of the biomass. We may think that the biosphere biomass increasing, an equivalent amount of carbon dioxide was taken from the environment for good and all. Later, after stromatolites appeared, one more mechanism - calcification, i.e. the use of bicarbonates for the development of a lime skeleton - was created. Organisms with carbonate and phosphate skeletons became especially widespread in the Cambrian. In later times only organisms with carbonate skeleton prevailed. Those skeletons eventually turned into fossils, thus leaving no possibilities for carbon dioxide to get back into the cycle. By the way, having been removed from the cycle, biogenic or abiogenic calcium carbonate because of metamorphism after some time may again free carbon dioxide and emit it into the atmosphere through volcano mouths, thus ending the cycle (Stanley 1999). However, the fact itself that resources of at least biogenic carbonate are quite abundant on Earth indicate that the rate of biogenic carbonate formation for a long time may have been higher than those of its weathering and metamorphic decomposition. It means then that in the course of time both water acidity and the amount of calcium in water reduced.

Similar was the case with silicon. In water it is present as silicic acid and just like this it could be used for skeleton formation, or incrustation. Silicon is known to be accumulated by some sponges, foraminifers, radiolarians, echinoderms, and diatoms. Sometimes due to activities of those organisms the amount of available silicon in water reduces as much as 4-5 times.

Both calcium and silicon, however, hardly ever are major growth-limiting factors, at'least in seas, for these elements are quite abundant. A slightly different situation is with nitrogen and phosphorus. Nitrogen has been a growth-limiting factor in seas since quite long ago in terms of geological time since for quite a while the way of nitrogen from land to seas was, we may say, absent. Thus, as the biomass accumulated, the amount of inorganic nitrogen eventually reduced to minimum. Of course, here I have in mind ocean zones with extensive primary production, namely, surface waters and mostly in continental shelves. Due to understandable reasons, that impact may have been somewhat less in the open ocean. Though, on the other hand, upwellings and water currents made the chemical composition of water quite similar in different geographical zones and water layers.

The history of phosphorus is a little different from that of nitrogen. Phosphates get to the ocean from land because of erosion and runoff. In seas they are involved into the biotic nutrient cycle. However, phosphates easily combine with cations of aluminium, calcium, iron, and magnesium, and the obtained insoluble compounds settle on the bottom. It can seem that there is no way back to fresh waters on land, if not for marine birds that bring back some phosphorus along with food and faeces. This is why in fresh waters phosphorus has been the major growth-limiting factor since very early times, may be already since the Cambrian if not earlier. Besides, one should remember that organisms use phosphorus not only for biosynthesis, but also for phosphorilisation, i.e. skeleton formation. This is typical of molluscs, brachiopods, arthropods, vertebrates, some worms, and protozoans. Because of these reasons phosphate concentration in lake water undergoes great seasonal fluctuations by reducing to minimum as the biomass suddenly increases and by again increasing after the vegetational season is over.

The table should be understood supposing that the rates of photosynthesis, assimilation, and chemosynthesis had for a long time to remain either higher or lower that the ones of contrary to them and not included into the table processes - fermentation and respiration. Otherwise trends of increase or decrease indicated in the third column would be absent. Similar logic is valid for carbonatisation, calcification, and incrustation as well as for contrary to them processes - weathering and metamorphic decomposition.

SCENE 13. **THE** FIRST TERRESTRIAL ECOSYSTEMS APPEAR. **SOIL IS FORMED**

PERIOD: 500-355 MILLION YEARS AGO
(THE ORDOVICIAN, SILURIAN, AND DEVONIAN)
MAIN CHARACTERS: THE FIRST TERRESTRIAL PLANTS AND ANIMALS

It is supposed that for more than 3 milliard years land was merely a barren desert blown by the wind and beaten by the rain. There were plenty of obstacles hindering life from settling on land. First, every living organism on land was killed by UV radiation for a long time. The situation improved after the ozone layer formed one milliard or more years ago. Another difficulty was posed by the metabolism of water and inorganic nutrients. Terrestrial organisms could not do without special tissues and organs storing water in an organism and obtaining it along with nutrients dissolved in it from substrate - weathered rocks in this case. Gravitation-related problems and those caused by mechanical impact of the wind and the rain had to be solved as well. Finally, at that time there was no soil - it still was to be formed.

Two decades ago a widespread opinion was that life on Earth settled not before the Silurian, i.e. a little earlier than 400 million years ago. At present, however, experts undoubtedly suggest that life started occupying land as early as in the Precambrian, about 600 million years ago (DiMichele & Hook 1992) or even earlier (McMenamin & McMenamin 1994; Gutzmer & Beukes 1998; Heckman *et al.* 2001). The first to adapt to living on land were bacteria, cyanobacteria most probably (Richardson 1992). In many humid sites they covered land surface with a thin mat. Apparently, those mats eventually played a very important role: settled on land producers were followed by the detritivores - fungi and bacteria - becoming a constituent part of the mats and thereby of the first terrestrial ecosystems. There is no doubt that those organisms slowly, though inevitably, altered their closest abiotic environment, thus making preconditions for barrel land to turn into soil. That, however, was just the beginning, for soil and turf formation took very long, and the whole matter was finished by other terrestrial organisms.

Thus, we may consider that terrestrial ecosystems existed already in the Cambrian and that they were made just of a couple of blocks - producers and detritivores - like the first aquatic ecosystems were.

In late the Ordovician, i.e. approximately 450 million years ago, yet very primitive liverworts and lichens originated (DiMichele & Hook 1992; Heckman *et al.* 2001). They even promoted rock weathering and soil formation. It is likely that in the Ordovician the diversity of terrestrial plants and lichens was very poor and that continuous plant cover was absent. Just here and there in humid places the earth was covered with a mat of little flabby plants.

In the Silurian, land was swept over by the first wave of adaptive radiation of plants, though yet weak, resulting in quite a great diversity of rhyniophytoids and mosses. Later, already at the beginning of the Devonian, i.e. a bit earlier than 400 million years ago, rhyniophytes appeared and spread and thereafter lycophytes and trimerophytes did so. Lycophytes and trimerophytes most probably already had roots, thus they may have been among the first able to colonise not only humid, but also dryer habitats (DiMichele & Hook 1992). In the second half of the Devonian, the first pterophytes and sphenophytes came into being.

The first terrestrial plants were herbaceous, not woody. It could be supposed, however, that since the very occupation of land there was a strong selection pressure inducing the appearance of lignin, wood, bushes, and trees. Evidently (Richardson 1992), already rhyniophytes synthesised lignin, though the first true bushes and trees appeared on land just in the middle of the Devonian.

The first terrestrial plants were not adapted to living under the new conditions, especially when droughts set in, and experienced mass extinction. Thus, they fertilised barren rocks and for some time preserved humidity, so needed by living organisms. On dead remnants new plants set in, and under them armies of detritivores - bacteria, fungi, protozoans, and worms - worked hard. Of course, those detritivores, too, did not fall from the moon. Similarly to the first terrestrial plants, in the course of 10-20 million years having exchanged life in the water for that on land they adapted to feeding on plant remnants and humus. Given a comparatively short generation time it was not hard to them to co-evolve with producers. Irrespective of that the delay was inevitable. There is no doubt, for instance, that in the beginning lignin - a new hard to decompose compound - should have accumulated in soil and just after a certain period of evolution lignin-decomposing fungi or bacteria could have risen. They occupied the newly-established niche, and the nutrient cycle was restored. But respiration and decomposition rate still were lower than that of primary production all the time, therefore there could accumulate not only the biomass, but also humus. Thus was established food reserve for soil-inhabiting detritivores. Besides, humus performed an important anti-erosion function and gave soil particles a proper mechanic structure.

Soil evolution lasted almost two hundred million years and was terminated with the formation of turf. That most probably might have happened about 390-380 million years ago. Since then there was no threat of either rain, or the wind, because washing out of materials had reduced to minimum.

After soil was formed the first woody plants - progymnosperms, the antecedents of gymnosperms - appeared. They could grow up to several meters high thus obstructing the sun for their rivals. Since that was an indubitable advantage, those trees rapidly spread pushing out trimerophytes and many of pterophytes and lycophytes. Soon thereafter many of lycophytes became woody, and later some of pterophytes and sphenophytes had to do so. At the end of Devonian the first gymnosperms - seed ferns - arose from progymnosperms. Seemingly, they could grow in comparatively dry habitats as well.

Producers and detritivores having emerged and spread, biophages, too, did not drowse, however. For them the first terrestrial plants and soil-inhabiting detritivores were nothing but a huge adaptive zone with plenty of vacant niches.

Evidently, in the late Silurian there already might have been the first terrestrial predators - scorpions, which are attached to chelicerates, i.e. the group to which the already-mentioned eurypterides that lived in water, belong. Later, at the beginning of the Devonian, spiders, which also belong to chelicerates, emerged, and scorpions reached one meter length turning into real monsters. From the late Silurian centipedes have been known, too (DiMichele & Hook 1992).

The existence of predators means that preys should have emerged still earlier. The latter may have been litter- and soil-inhabiting detritivores - some of worms, archipolypodan myriapods, and springtails. It is difficult to talk about herbivores of the Silurian and Devonian, since indubitable herbivore fossils seemingly have not been found so far. Still, I do not reject a possibility that in those times herbivorous niches were occupied by any of the three existent myriapod groups: archipolypods, arthropleurids, or millipedes. Millipedes were particularly abundant. May be all those myriapods were the ones who fed on non-living plant tissues, as it has been suggested by DiMichele and Hook (1992), and by Beerbower (1993). This, however, is hard to believe. Is it possible that throughout the Devonian they managed to resist the temptation of trying shoots? Besides, it is very hard if at all possible to judge from myriapod fossils, even if they are of a good quality, about whether those organisms were herbivores or just crushers of leaves, like some of modern earthworms or millipedes. Thus, contrary to the above authors I think that in Devonian there *should* have existed plenty of herbivorous myriapods. On the other hand, this issue is pretty intricate and vague (McMenamin & McMenamin 1994), but I hope that in the short run new fossil data will give a more definite answer.

From the above a conclusion could be drawn that that-time predators fed most probably on both detritivores and herbivores, though the existence of the latter is doubted.

The following production pyramid of mid-Devonian is obtained (Fig. 17).

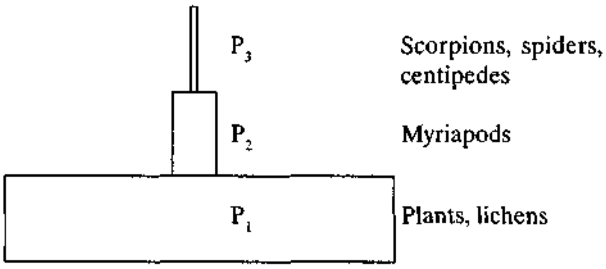


Figure 17. **In the mid-Devonian, approximately 380 million years ago, the block of biophages of terrestrial ecosystems was still rather poor in species. Despite that local nutrient cycles were already formed.**

SCENE 14. TERRESTRIAL ECOSYSTEMS ACQUIRE A MODERN SHAPE

PERIOD: 355-295 MILLION YEARS AGO (THE CARBONIFEROUS)
MAIN CHARACTERS: WOODY PLANTS, MYRIAPODS, INSECTS, AND AMPHIBIANS

At the beginning of the Carboniferous new adaptive radiation of plants took place, which set a stage not only for the majority of herbaceous forms, but also for an unseen abundance of trees and bushes. Layers, lianas, or may be even epiphytes typical of modern forests originated. Woody sphenophytes, pterophytes, lycophytes, and in particular seed ferns spread. In Carboniferous, the first cordaites and conifers saw the light of the day.

Hardly could be there any doubt that in the Carboniferous terrestrial life was already widespread not only in tropics, but also in zones of temperate climate. In that period, myriapods became even more abundant than in the Devonian. Some of arthropleurids reached a length of two meters, and part of archipolypods were in no way shorter. Besides, myriapods acquired firm spines, which could have been for protection against predators. Such course of events probably indicates that in those times in many terrestrial ecosystems there were no vertebrate herbivores yet and that myriapods instantaneously radiated by temporarily occupying those free niches. Part of the myriapods fed not only on living plants, but also on vegetative detritus.

There were other herbivores, too, which were mostly pulmonate gastropods and flying and non-flying insects. The specialisation of insects was quite great, Mouth apparatus of some insects was adapted to chewing, whereas that of others - to sucking or feeding on pollen, spores, or seeds. It is quite possible that that-time insects were the first to try pollinators' niches, thus promoting a spread of seed ferns (DiMichele & Hook 1992).

Still greater changes were induced by the adaptive radiation of amphibians started at the beginning of the Carboniferous with the close of which millions of tailed predatory living beings belonging to hundreds of different species widespread in forests. Most known amphibians of that time were labyrinthodonts. They were generally quite large predators, up to several meters long. Aquatic or semiaquatic at first, part of amphibians became semiterrestrial or even pure terrestrial animals in the second part of the Carboniferous. In addition to predatory forms, there emerged omnivores, too, feeding both on animal and vegetarian food, mostly seeds. Never again were amphibians fated to reach such a high status as at the end of the Carboniferous and the beginning of the Permian when they had occupied the majority of niches meant for biophages (Carroll 1988; DiMichele & Hook 1992).

In the mid-Carboniferous, the first reptilians - cotylosaurs - came into existence, to be followed by pelycosaurs a bit later. From the very appearance reptilians undoubtedly had certain advantages over amphibians dwelling in dryer habitats. Important is also the fact that reptilians were far more mobile than their rivals, amphibians. Because in those times all niches of biophages were occupied by amphibians, insects, and arachnids, reptilians had but the only way out - to push out weaker rivals. But during the second part of the Carboniferous reptilians still were playing a secondary role. And their native element still were vast inlands, where the influence of amphibians was far less.

We obtain a production pyramid typical of the end-Carboniferous (Fig. 18). It probably did not differ essentially from that typical of modern forests in either the number of levels or the shape itself. I am writing 'essentially', because certain differences still could be found. They were inevitable at least for the fact that the Carboniferous pyramid was formed of ectotherms, whereas the structure of modern terrestrial pyramids is known to involve many endotherms, too. Because ectotherms produce more biomass from the energy present in a certain amount of food than endotherms do, ectotherms carry the energy from one trophic level to another more effectively. Therefore, *ceteris paribus*, they are able of forming slightly higher production pyramids, with more trophic levels and a relatively greater biomass of predators compared to that of herbivores.

Thus, the evolution of the structure of terrestrial ecosystems lasted for about 100 million years, supposing that it started with the onset of true terrestrial plants 400 million years ago. In the water, the process continued more than 3 milliard years. Indeed, in the Carboniferous evolution made a really good progress.

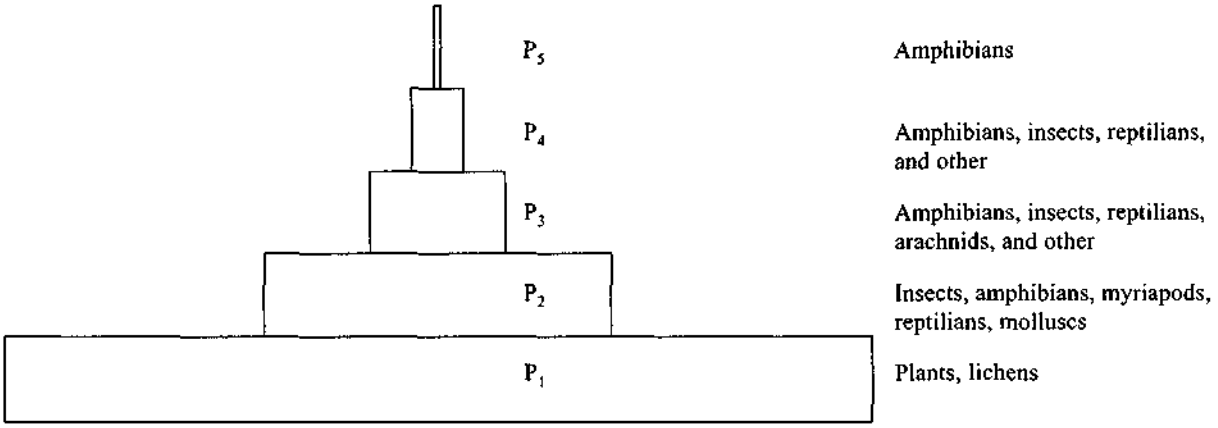


Figure 18. In the Carboniferous, an age of luxuriant humid forests, the production pyramid generally did not differ from that of the present. Species composition, however, was quite different, though small and large amphibians as well as insects and myriapods were predominant. That idyll was at times interrupted but by the first reptilians dropping in from dryer habitats.

SCENE 15. GYMNOSPERMS OUTRIVAL SEEDLESS VASCULAR PLANTS, AND REPTILIANS PUSH OUT AMPHIBIANS

PERIOD: 295-203 MILLION YEARS AGO (THE PERMIAN AND TRIASSIC)
MAIN CHARACTERS: GYMNOSPERMS, REPTILIANS, AND INSECTS

In the Permian, the diversity of sphenophytes, pterophytes, and lycophytes started to decline. Woody forms of those plants suffered most. Cordaites became extinct. On the contrary, in the Permian and especially Triassic conifers and three new groups - cycads, ginkgos, and cycadeoids - began to flourish. From the Permian many xeromorphs have survived like fossils, therefore it is likely that in that period not only wetlands and dryish habitats, but also droughty ones were already inhabited.

Insects, yet comparatively poor in species in the Carboniferous, underwent pretty rapid diversification in the Permian and especially Triassic. In the Triassic, there were already many insect orders that are also found in the modern fauna. Among them both herbivores and primary as well as secondary predators could be found. Many of that-time beetles performed the function of pollination (Wing & Sues 1992).

In the Permian, in addition to the above mentioned cotylosaurs and pelycosaurs new reptilian groups originated and spread: mesosaurs, millerosaurs, and pareiasaurs. Among them there were not only large predators, but also quite large omnivores and herbivores. Fruits and seeds became not only a desired food resource, but also the factors that eventually induced diversification of vertebrate herbivores. At the end of the Permian all those reptilians were replaced by new ones: therapsids, lepidosaurs, and thecodonts. Among them there also were predators, omnivores, and herbivores, and some of them could be even six meters long. In the Triassic, reptilians had occupied not only the majority of terrestrial habitats, but also freshwaters as well as seashores. Aquatic habitats were settled by some of lepidosaurs and thecodonts as well as by notosaurs, placodonts, plesiosaurs, crocodilians, and ichthyosaurs, which emerged in the Triassic. Reptilians became even larger than in the Permian. That evolutionary lineage became especially prominent at the end of the Triassic, after the first dinosaurs appeared (Carroll 1988; DiMichele & Hook 1992).

In the first part of the Permian, amphibians were still abundant, with 40 existing families, more than half of them belonging to terrestrial forms. In the mid-Permian, the majority of those niches were, however, ceded to reptilians. Naturally, amphibians inhabiting terrestrial habitats. were the first to suffer, and then the diversity of semiterrestrial and semiaquatic amphibians, too, reduced to minimum. Amphibians somewhat recovered in the Triassic, but those were only almost purely aquatic forms, Finally, at the end of the Triassic a new wave of the adaptive radiation of reptilians overflowed all water bodies pushing out amphibians of the majority of aquatic habitats. Of the former amphibian diversity merely remnants were left (Carroll 1988; DiMichele & Hook 1992).

Being exterminated by amphibians and predatory reptilians, pressed by ever growing vertebrate herbivores, in the Permian all large myriapods survived from the Carboniferous - arthropleurids and archipolypods - became extinct.

In the Triassic, some 220 million years ago, the first mammalians appeared. It is supposed that they lived nocturnal life, were small, just of a size of a shrew, climbed trees, and caught insects causing no troubles to anybody.

The end-Triassic production pyramid is depicted in Fig. 19.

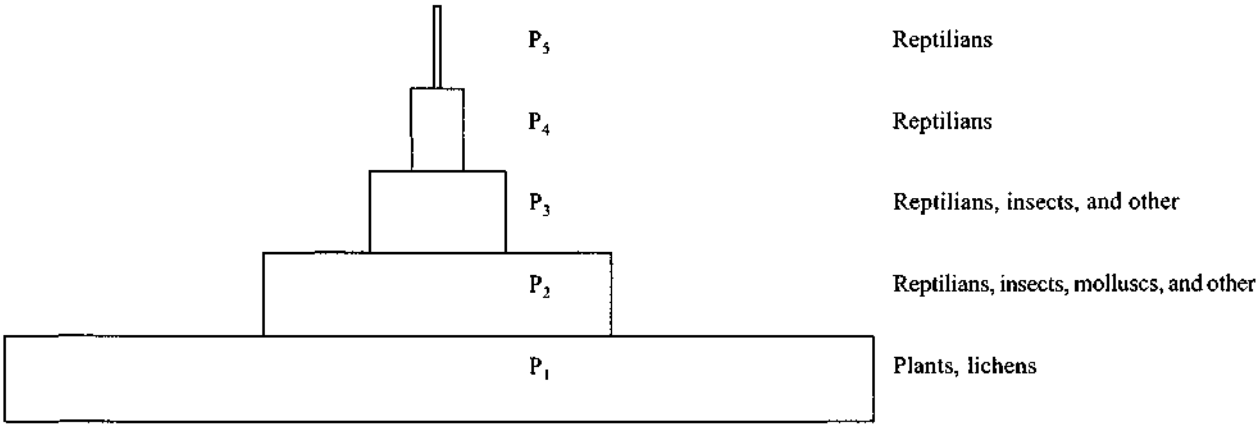


Figure 19. At the end of the Triassic a little more than 200 million years ago reptilians should have already pushed amphibians out of almost all niches suitable for biophages. Insect diversity increased.

SCENE 16. FLOWERING PLANTS EMERGE. LARGE REPTILIANS CONTINUE FLOURISHING AND THEN MYSTERIOUSLY DIE OUT

PERIOD: 203-65 MILLION YEARS AGO (THE JURASSIC AND CRETACEOUS)
MAIN CHARACTERS: FLOWERING PLANTS AND REPTILIANS

From the close of the Triassic dinosaurs predominated on land and pterosaurs - in the air. During the Jurassic and Cretaceous more and more reptilians went over to living and feeding in water bodies, where they played a role of top predators. Here I have in mind crocodilians, plesiosaurs, mosasaurs, and ichthyosaurs. In water bodies, huge herbivorous dinosaurs - sauropods - fed as well. The diversity of reptilians reached maximum approximately in the middle of the Cretaceous period, with already over a thousand of species. Such an incessant spread of dinosaurs and kindred reptilians had a negative effect on older reptilian groups. As early as at the beginning of the Jurassic thecodonts, notosaurs, and placodonts were already missing and in the middle of the Jurassic therapsids became extinct as well, The expansion of reptilians completely ruined amphibians, and of the 40 families that existed at the beginning of the Permian only two were left at the end of the Jurassic (Carroll 1988; Wing & Sues 1992).

During that period, similarly to earlier ones, animal bodies still grew, and smaller forms became even more mobile. Obvious was also the trend of increasing the efficiency of reproduction (per cent of newborns reaching maturity) by usually spending more time and energy for caring for eggs and offspring. Selection kept accumulating the features enabling to stabilise body temperature at a comparatively high level, until part of reptilians finally became endotherms. Individuals associated into increasingly integrating groups, and the rudiments of social life became apparent (Ostrom 1992).

The Jurassic was a period of a great flourishing of gymnosperms. Never again will they be allowed to reach such diversity. Especially abundant were conifers, cycads, and cycadeoids. However, in the Cretaceous period, which followed the Jurassic, over 120 million years ago, the flora underwent quite dramatic changes, Flowering plants began pushing gymnosperms out of many of their habitats. Flowering plants should have emerged in the tropics, where they had been involved into the first wave of adaptive radiation. It was not before several dozen million years later that they reached the temperate zone and yet later - the zone of frigid climate. At the end of the Cretaceous the majority of plant species was already made by flowering plants. But the diversity of cycads and ginkgos inevitably had to shrink, whereas cycadeoids became extinct at all. Conifers suffered somewhat less (Wing & Sues 1992).

That abundance of blossoms and fruits set a stage for the adaptive radiation of insects. Butterflies and moths emerged, and a rapid diversification of pollinators took place. A particular spread was seen by hymenopterans and dipterans (ants, wasps, bees, and flies),

The enriched diversity of flowering plants and insects had a direct connection with the evolution of birds, especially herbivorous and insectivorous ones. Though birds appeared already in the Jurassic, before the rise of flowering plants, their diversity still was very low, they flied badly, somewhat like hens, and were rather small. In the second part of the Cretaceous, after the adaptive radiation of flowering plants, numbers of birds, however, began to grow. Birds seemingly were luckier than mammalians, and this probably was because of the fact that pterosaurs were not so abundant than dinosaurs predominant on land. Besides, pterosaurs were narrow-specialised, fed mostly on fish and other aquatic animals, so that their rivals - birds - could escape competition by settling in other niches. Furthermore, it should not be forgotten that the Cretaceous birds were far better fliers than pterosaurs were.

The birds evolved in three main directions: some of them became large non-flying resembling an ostrich animals, whereas others - quite large wading, swimming, and diving, and still others - comparatively small and pretty well flying birds. According to some experts (Chiappe 1995;Padian&Chiappe 1998), as early as before the extinction of pterosaurs and dinosaurs, at the very end of the Cretaceous, there already existed the majority of modern orders of birds. One way or the other, there is no general conviction yet, but there is no doubt that that period saw a great diversity of birds (Feduccia 1995).

Mammalians dispersed a little as late as in the Cretaceous. In addition to multituberculates, triconodonts, and trituberculates, modern groups - monotremes, marsupials, and placental mammalians - originated. All of them were small, no larger than a cat. According to the feeding character they were both herbivorous and omnivorous. To the very end of the Cretaceous the role of mammalians was merely episodic (Carroll 1988). The pyramid of the second half of the Cretaceous is depicted in Fig. 20.

From the mid-Cretaceous the diversity of reptilians started to decline. Ichthyosaurs were the first to become extinct, and the number of species was diminishing in other groups, too. Finally, during several million years of the end-Cretaceous almost all terrestrial reptilians became extinct, with an exception of but terrestrial turtles and a few of lizard and snake species, That was not without an impact of a cosmic or some other catastrophe, which will be discussed further.

SCENE 17. ESPECIALLY RAPIDLY RADIATING BIOPHAGES RESTORE THE DESTRUCTED PYRAMIDS

PERIOD: 65-23 MILLION YEARS AGO (THE PALEOGENE)

MAIN CHARACTERS: BIRDS AND MAMMALIANS

The extinction of abundant herbivorous reptilians seen at the end of the Cretaceous period had to be responded toby that-time plants. At the beginning of the Paleogene the diversity of plants, seemingly, reduced, resulted in by the spread of the species that were strong rivals and the expansion of which during the Cretaceous was impeded by dinosaurs that fed on them (Wing & Sues 1992). Plants using much energy for protection from already non-existent herbivores became extinct. By the way, the above events did not last too long, and the diversity of plants began gradually increasing. Grasses and composites came into being and started to spread. They were to have the good fortune to reach particular diversity in the following period, the Neogene. Experts relate the rise and spread of those plants to the expansion of open woodlands, grasslands, and deserts, which took place in the Neogene.

After the majority of terrestrial reptilians died out, production pyramids looked rather miserable. Plenty of specialised herbivorous, which used to feed on plant shoots, leaves, fruits, seeds, and bark, were missing, The highly diverse group of small and large predators, which had occupied many niches at the third, fourth, or fifth trophic level, disappeared - the pyramid remained topless, we may say. Since there were so many dinosaurs in the Cretaceous that they had to feed on each other (large predators - on other predators, omnivores, and herbivores, and mature individuals of certain species - on eggs and offspring of other species; Sereno 1999), then after all of them died out entire trophic chains became missing. A great deal of niches became vacant, and later that was the major stimulus for

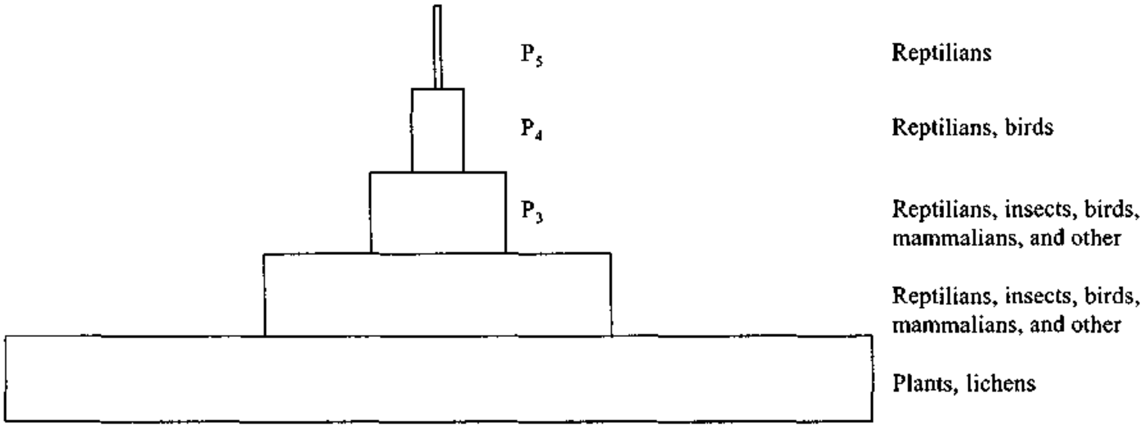


Figure 20. **In the second half of the Cretaceous, reptilians were still predominant on land, but they already had to share part of niches meant for biophages with birds and mammalians.**

the further adaptive radiation of biophages. The dying out of dinosaurs and that of the multitude of other reptilians like a start signal moved every who had at least a slightest, may be even theoretical, possibility to make use of resources used by nobody - there started radiation, and not only that of birds and mammalians, but also of still existent reptilians and amphibians. Surely, most lucky were those closest to the finish line.

Mammalians, apparently, were most successful at occupying the vacant niches previously belonging to herbivorous reptilians. In about 10 million years (65-55 million years ago) the adaptive radiation of placental mammalians produced primitive ungulates, rodents, proboscideans, lagomorphs, and primates. Soon there after those herbivores surpassed the diversity of multituberculates, which fed on vegetary food and had survived from the Cretaceous period, to push them out for good during the second half of the Paleogene. In the beginning, new-generation herbivores were comparatively small animals, but they gradually grew, until in the second half of the Paleogene some of ungulates reached a size of the modern giraffe.

In the Paleogene, herbivores were joined by birds. The radiation of the latter might have been less abrupt and powerful than that of mammalians, though birds, too, achieved quite a great diversity and all the modem bird orders and families emerged. Many of birds fed on seeds, fruits, nectar, or insects, though there were some omnivores as well. There is no doubt that that adaptive radiation would have not occurred without an unprecedented expansion of flowering plants and insects that started already in the Cretaceous period.

Things were different on the attempt to occupy the top of the production pyramid. Niches meant for large predators may have been claimed by all the four groups of vertebrate animals: mammalians, birds, amphibians, and reptilians. The latter two had already been at the top of the pyramid once. By the way, by that time few of amphibian and reptilian species had been left and almost all of them must have been small. Of reptilians, just crocodilians could have been suitable for the role, but at first they had to adapt to hunting on land. Theoretically thinking, the situation was most favourable for birds. Already in the Cretaceous there were quite large predatory birds, so they could easily radiate and occupy niches of terrestrial predators. Contrary to birds, that-time mammalians were far too small for the role of top-predators. Besides, almost all of them were omnivorous or herbivorous. Still, further events testify to a surprising variability and evolutionary adaptability of mammalians, which most probably determined their success. By the way, they were to meet that success later.

Palaeontological records indicate (Carroll 1988; Potts & Behrensmeyer 1992; Marshall 1994) that already in the Paleogene there existed the following groups of terrestrial predators:

1) phorusrhacoids - large non-flying birds;
2) terrestrial crocodilians (the family Sebecidae);
3) creodonts - predatory placental mammalians;
4) predatory marsupials - didelphids and borhyaenids.

The first predatory mammalians were rather primitive and far surpassed by modern predators in both size and mobility and, as it seems, in mental abilities, too (Potts & Behrensmeyer 1992). It is likely that phorusrhacoids fully countervailed part of their rivals' shortcomings - some of them were as high as three meters and had a beak like a wood-cutter's axe raised above a prey. Being non-fliers they could perfectly run. The diet of those birds was made mostly of medium-sized and large reptilians and mammalians. So, seemingly they should have already climbed up the very top of the production pyramid. Experts consider that the diversity of those birds should have been quite rich. The same could be said about that-time crocodilians lounging about plains. Certainly, at the top of terrestrial pyramids were some large flying birds, too.

Creodonts survived until the second part of the Paleogene. They were pushed out by a newly appeared group of placental predators - Carnivora (the first dogs, cats, and mustelides). They were so violent and so well armed that in the short run not only creodonts had to withdraw from many regions, but also marsupial predators and the above-mentioned non-flying predatory birds had to do so. For some period of time representatives of the order Carnivora could not get but to South America and Australia, thus in those regions predatory marsupials and phorusrhacoids existed not only in the Paleogene, but also during almost the whole Neogene. Crocodilians gave up the land to their rivals earlier, already in Paleogene.

After a very long break that lasted from the Permian to Paleogene, amphibians, too, began to recover - quite an intense adaptive radiation of tailless and other amphibians was observed (Carroll 1988). But that time their radiation, contrary to that in the Carboniferous, was rather limited, since the evolution of amphibians was on all sides restricted by other groups - mammalians, birds, and reptilians - that had been the first to have occupied a great number of vacant niches. Thus, there should not be any surprise that that wave produced, in terms of ecology, a poor, dull mass - several thousand species feeding almost entirely just on small invertebrates. Irrespective of that amphibians spread almost throughout the whole biosphere and reached as far as the polar circle.

Lizards and snakes radiated as well. In the Paleogene over a thousand of species of snakes alone emerged. Lizards and snakes, being pressed on all sides by stronger rivals, over millions of years were producing, however, merely small predators feeding on insects and other invertebrates, amphibians and small mammalians. It was just in those habitats where due to different reasons large predatory birds or mammalians were absent that reptilians dared to increase their body mass and to crawl to the top of the pyramid. Here I mean boas, Komodo dragons, and a few of other large predatory reptilians.

The appearance of such a comparatively great diversity of amphibians and reptilians was predetermined by the spread of organisms that served as prey to them; in the Paleogene the abundance of small amphibians and mammalians, especially rodents, easily available to predatory reptilians, particularly increased. The spread of amphibians, on the other hand, should first of all be related to the diversification of insects in the Cretaceous and Paleogene.

Having got a chance to spread, already at the beginning of the Paleogene mammalians and birds proceeded with the evolutionary trends earlier typical of reptilians - their body mass grew, mobility and reproduction efficiency increased, thermoregulation advanced, co-operative connections between individuals strengthened, behaviour improved. Those features developed at such a rate that it may seem that those trends must have not been interrupted by the catastrophe that occurred at the end of the Cretaceous.

Everything what has been written here about the adaptive radiation of mammalians concerns generally Eurasia, Africa, and both Americas. But several words yet should be said about Australia. It separated from other continents comparatively very early, already in the Cretaceous, and never again did it attach to any of them. Perhaps it was due to the isolation from the other continents that Australia has preserved a comparatively great diversity of marsupials. They are known to have inhabited Eurasia and both Americas, but those regions were far too less isolated from one another and they had far better conditions for faunal interchange, so eventually placental animals pushed out many of marsupials there. In the Paleogene, or may be already at the end of the Cretaceous Australian marsupials were involved in adaptive radiation, which produced a variety of species that in terms of ecology were equivalent to the placental species emerged at that time in other continents. Below are presented some of Australian marsupials and their equivalents from other continents (Table 2).

Table 2. Radiation and convergence of marsupials and placental mammalians in the Cenozoic.

Australian marsupials	Placental analogues living in the other continents (occupying the same niches)
Tasmanian wolf	Grey wolf
Majority of bandicoots	Rabbits and hares
Numbats	Anteaters
Gliders	Flying squirrels
Walabies	Some of monkeys
Spotted cuscuses	Lemurs
Marsupial moles	Moles
Wombats	Woodchucks
Large kangaroos	Horses, antelopes, and other ungulates
Tasmanian devils	Wolverines
Koalas	Tree sloths
Dibblers	Mice

The table could be supplemented, but the given list also is suffice to make quite a suggestive impression that Australian marsupials radiated in the same directions as placental mammalians living in other continents did. The formation of pyramids took place according to the same scenario again, which every time led to a very similar final result: analogous sets of niches were formed and then those niches were occupied by unrelated organisms, and not only species occupying the same niches converged, but also entire production pyramids did so.

In the Paleogene, some mammalians became marine animals (whales, dolphins, seals). So, they not only occupied niches that became vacant after ichthyosaurs and plesiosaurs died out, but also discovered additional, little used ones.

Thus, as early as in the second half of the Paleogene terrestrial production pyramids acquired a common to them shape again (Fig. 21).

THE SECOND INTERLUDE: ATMOSPHERIC EVOLUTION

I have already discussed how the evolution of life affected the chemical composition of ocean water. Now I am going to get deep into how life changed the atmosphere. What I am going to survey are just changes in carbon dioxide and oxygen levels in the past, for other issues of atmospheric evolution are rather controversial and require a more detailed discussion, which I by no means can afford in this book.

The whole or almost whole modern oxygen, bound or free, is probably biogenetic. Before the appearance of life, oxygen, perhaps, was completely absent in the at-

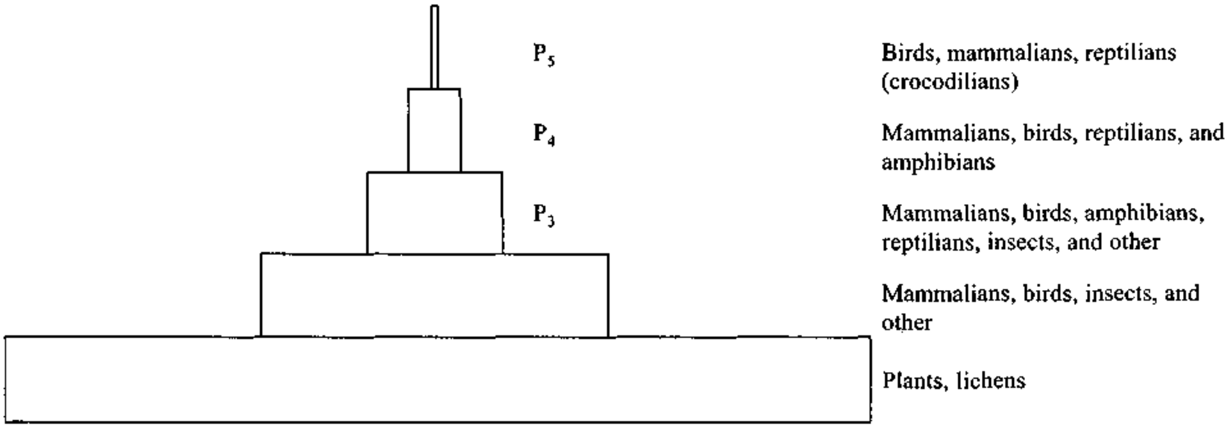


Figure 21. In the first half of the Paleogene, there predominate birds and mammalians, which were the first having occupied niches after the majority of reptilians died out.

mosphere, or there were merely traces of it. This opinion is shared by the majority of experts. Carbon dioxide is quite a different matter. Its level is believed to have been much higher several milliard years ago compared to the present, the difference making several hundred times (Kasting 1993). By the way, in those times or a little earlier Earth's atmosphere could have resembled that of the modern Mars or Venus: approximately 95-96% of $C0_2$ and a few per cent of molecular nitrogen. Indeed, if such a structure is typical of the neighbour 'left' and the one 'right', why it should be different in the planet 'in the middle' (Hunten 1993).

Thus, seemingly, there is an agreement (Berkner & Marshall 1965; Cloud & Gibor 1970; Kasting 1993; Allegre & Schneider 1994; Rye & Holland 1998; though see Kerr 1999) that there should have been inverse correlation between change in carbon dioxide and that in oxygen - the carbon dioxide level continuously reduced whereas that of oxygen increased. Many experts do not doubt those trends to have been determined by the biosphere. But what concrete mechanisms were responsible for those trends is a question still requiring coherent explanation, and therefore it is the one I am going to cast some light on now.

Let us go back to the equations of oxygenic photosyn-

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$$CO_2 + H_2O + \text{energy} \underset{\text{respiration}}{\overset{\text{photosynthesis}}{\rightleftarrows}} (CH_2O) + O_2$$

Let us mark gross production, or assimilation, of the biosphere with $A_{biosph.}$ Let us also mark aerobic respiration of all biospheric organisms with $R_{biosph.}$ For simplicity, let us suppose that we deal exclusively with aerobic organisms. Then in a stationary (climax) state $A_{biosph.} = R_{biosph.}$, $P_{biosph.} = 0$, $B_{biosph.} = \text{const}$. In this case neither environmental concentration of CO_2, nor that of 0_2 is to change, for as much of oxygen is produced, as much of it is consumed per time unit. And here the indispensable condition for the environmental 0_2 concentration to increase becomes clearer - respiration should lag behind photosynthesis (see the equations). In other words, oxygen can accumulate just as the biomass does so $(A_{biosph} > R_{biosph.}, P_{biosph} > 0)$.

Here (CH_20) stands for carbohydrates rather than for the biomass, which in addition to carbohydrates is known to contain other type compounds, too. But for the sake of simplicity we will keep regarding this member of the equation an analogue of the biomass.

It is easy to take in that not only the accumulation of the biomass, but also that of detritus results in similar effect - an increasing amount of free oxygen. Isn't the removal of detritus from the cycle and its conversion to fossil fuels an escape from a reverse reaction with oxygen (respiration) (Schidlowski 1980; Walker 1980)? Reasoning from the other way round we may make an even clearer generalisation. There is so much of biogenic oxygen, bound and free, accumulated in the environment that it would react without remainder with biospheric carbon, present in the biomass, detritus, and fossil fuels. If such a total oxidising occurred, a huge amount of carbon oxides and water would accumulate in the environment and free oxygen would disappear. Quite possibly, after such a global catastrophe the Earth's atmosphere would get back into the state it was in 4.0-3.0 milliard years ago.

As usual, the simplification of the real situation in this case, however, has lead to a somewhat inexact formulation. The thing is that oxygen, possibly, may react without remainder, but whether organic carbon may do so is a more intricate question. We have not taken into account some very important participants of the atmospheric evolution. Oxygenic photosynthesisers are not the only producers of organic matter in the biosphere. There also are anoxygenic photosynthesisers and chemosynthesisers. They assimilate $C0_2$ from the environment, but do not produce 0_2. It could have been even for half a milliard of years that $C0_2$ was assimilated from the environment producing no 0_2. Thus, the above presented reactions of oxygenic photosynthesis and aerobic respiration are not all of those characterising the carbon cycle. Therefore, the above drawn conclusion should be corrected like this: oxygen, possibly, may react with carbon without remainder, however then a certain amount, may be even quite great, of unreacted carbon, assimilated in other than oxygenic photosynthesis way, should be left.

But let us go back to the main line of reasoning. We have cleared up that the amount of oxygen in the environment could have been increasing just with the organic matter accumulating in the biosphere. Is that kind of accumulation probable to have taken place? Experts (Simpson 1969; Wicken 1980) give a positive answer: it is true that the biomass has been increasing, though with some breaks, all the time. There has been taking place both extensive and intensive growth. The latter is related with biomass increase in a unit of area or volume. The amount of detritus and fossil fuels, too, has likely been increasing. This fact is very important in the context being discussed, for calculations show carbon as coal alone to have been accumulated at least several times more than that present in the entire biomass (Falkowski *et al.* 2000). Should these calculations confirm, we would have to change our outlook on the past changes in the atmospheric composition. Coal deposits are known to have formed in the Carboniferous, Permian, Jurassic, Cretaceous, Paleogene, and even Neogene. During the Carboniferous and Permian the biosphere biomass, too, incredibly increased. Thus, during that period oxygen amount in the atmosphere should have increased at least several times, whereas from the appearance of life on land to modern times - may be even a dozen or more times. To find out whether it was so or not is a task for empiricists.

I have emphasised oxygen accumulation, though one should also take into account that at the same time the $C0_2$ level in the environment should have equivalently dropped, as it is suggested by the stoichiometry of the oxygenic photosynthesis reaction. Understandably, this conclusion is right just providing that the amounts of those gases were not affected by other phenomena. For example, it is right just on condition that the rate of atmospheric carbon dioxide replenishment through volcanoes and weathering of carbonate rocks was approximately equal to that of abiogenic carbonatisation and biogenic calcification (Table 1 and comments to it). I do not have any data about whether that condition was fulfilled or not. However, considering that throughout life history on Earth there have accumulated quite great reserves of biogenic carbonates, it is likely that at least calcification could have considerably reduced the $C0_2$ level in the environment. On what scale - is another question, rather to be answered by experts (for discussion see Berner & Kothavala 2001; Rothman 2001).

On summarising what has been said regarding atmospheric evolution the following picture is obtained (Fig. 22).

It is clear from the figure that in the Neogene all the indicators became stabilised. I ground such an opinion of mine on the following arguments. Further growth of the biosphere biomass and an increase in the oxygen level usually following it is impossible, since it would result in ceaseless spontaneous fires. There is powerful negative feedback in this case. Another negative feedback is related with the impact of carbon dioxide. In the Neogene, carbon dioxide became a factor limiting primary production, similarly to phosphorus and nitrogen. It is well known that after the concentration of this gas is artificially increased in the environment with growing plants, photosynthesis intensifies. Thus, current concentrations of both of these gases (0_2 - 21%, CO_2-0.03%) are limiting.

Though it was not in order to satisfy consumers that

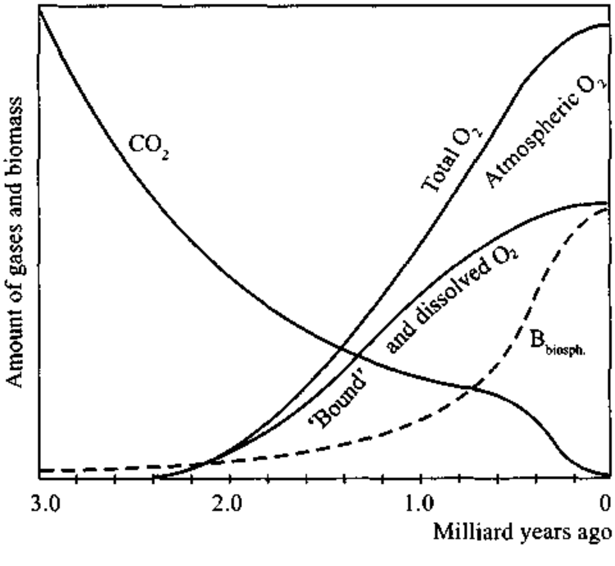

Figure 22. As provided by the reactions of anoxygenic and oxygenic photosynthesis and chemosynthesis, the increase of the biosphere biomass ($B_{biosph.}$) was followed by the decreasing atmospheric level of CO_2 and by the accumulation of O_2 in the environment. For details on quantitative changes see the text. The figure shows neither the dynamics of the accumulation of detritus nor that of fossil fuels, both of them having had quite a great impact on the amount of those gases.

producers increased oxygen amount in the environment, the final result is paradoxical - now producers are even more dependent on consumers than they were, let us say, 2 milliard years ago. If all consumers of the biosphere became extinct today, it would be after several years at the latest that producers, too, would die out CO_2 having run short. The biosphere would return to the heterotrophic way of life. Indeed, all of us Earth's inhabitants - plants, animals, and humans - are tied up with the same rope and share the same destiny...

By the way it is quite probable that the emergence of C_4-plants 15 million years ago was related with the reduced atmospheric level of carbon dioxide in the Paleogene and Neogene (Cerling *et al.* 1998; Jacobs *et al.* 1999). These plants, compared to evolutionary older C_3-ones, are known to use carbon dioxide more effectively and to be less vulnerable to its shortage. This, undoubtedly, is merely a hypothesis, and experts of this field could give a more correct wording of it.

To bring the topic to an end, several words should be said about the wide-known Gaia's hypothesis, suggested already in the 1970s by J. Lovelock and L. Margulis (Lovelock 1979). That hypothesis did not attract proper attention for a while mainly because it lacked empirical grounding. Later the shortcoming having been eliminated scientists' audience was already changed, and experts were no longer interested in it, since it was no longer within the limits of the scientific paradigm of the 1980-1990s. By the way, it was taken great interest in by non-experts and humanitarians then, the circumstance likely to have rescued the authors from sinking into oblivion. Today, seemingly, experts are becoming more and more interested in the hypothesis again - it is being rehabilitated, its status rising. I have been supporting Gaia's hypothesis, with some reservations, from the very day of its appearance. I think I have somewhat contributed to its popularisation in my motherland Lithuania.

Gaia's hypothesis regards interaction of the biosphere and non-living environment and their coevolution. J. Lovelock and L. Margulis suggest that life not only adapted to non-living environment, but also changed it throughout evolution to make it almost optimal for life. Besides, life itself is able of regulating the composition of atmospheric gases and water and the temperature of Earth's surface, not allowing those parameters to decline from the optimum. I consider the part of Gaia's hypothesis dealing with the management of the amount of atmospheric gases to be of a particular value. The authors have discovered a very simple solution. Suppose that due to some reasons atmospheric concentration of oxygen increases and exceeds a usual one. Then the probability of spontaneous fires in the biosphere should inevitably grow, respiration intensify, photosynthesis slow down, thus causing powerful negative feedbacks, which eventually return oxygen amount to its initial state. On the contrary, oxygen amount having dropped below 21 % and carbon dioxide concentration still increasing, reverse processes should occur in the biosphere - the probability of fires should diminish, respiration slow down, whereas photosynthesis intensify. Thus in this case, too, homeostasis is evident.

The main difficulty encountered by the hypothesis has been quite well defined by Lenton (1998):

Evidence indicates that the Earth self-regulates at a state that is tolerated by life, but why should the organisms that leave the most descendants be the ones that contribute to regulating their planetary environment?

It seems that not only the authors of the hypothesis, but also the whole official science of evolution have not found a satisfactory answer to this question so far. In this work of mine I am attempting to find such an answer (Part 2). I am also concerned about what the prehistory of that superorganism (Gaia) was like. The biosphere could not have been so mighty and self-regulating forever, it has acquired these features just owing to a long evolution.

This hypothesis with an exception of some of its parts, probably of a minor importance, does not contradict the ideas I am speaking in support of in my works. In it, most probably, is a kind of a complement rather than contradiction or repetition. Therefore I do not feel like going deep into this question - there is a time and place. It is mentioned here just because it is impossible to be evaded. It is too important to our understanding of the interaction between living and non-living nature. It contains some quite grounded ideas and conceptions.

At the end of the story I would like to point out that my point of view on atmospheric evolution is far too theoretical (I have followed the guideline that *it should be* so, unless there has been some influence of other, not discussed herein, conditions) and, most likely, casts a rather one-sided light on the question. There is no doubt that the composition and change of atmospheric gases were affected by both rock weathering and possible changes of volcanism, as well as by many other factors (Knoll 1991; Berner *et al.* 2000; Berner & Kothavala 2001). I think that right are the authors of a survey recently published in the 'Science' journal (Falkowski *et al.* 2000), who after long-term studies have drawn a conclusion that biogeochemical cycles are being affected not only by biotic, but also abiotic factors, and it will require much of collective attempt to detect, relate and evaluate them all:

'Our knowledge is insufficient to describe the interactions between the components of the Earth system and the relationship between the carbon cycle and other biogeochemical and climatological processes. Overcoming this limitation requires a system approach.'

By the way, this article, as it seems to me, stands out from the rest in that its authors express a collective disappointment at the traditional (analysis-based) methodology, which in their opinion turns out to be not completely suitable for the modelling of particularly complex systems.

SCENE 18. THE BIOSPHERE REACHES THE EARTH'S CARRYING CAPACITY. **ONE** OF **HOMINID** SPECIES BECOMES A SUPERRTVAL

PERIOD: 23-0 MILLION YEARS AGO (THE NEOGENE AND QUATERNARY)

MAIN CHARACTERS: HOMINIDS

In the Neogene, the diversification of mammalians, birds, reptilians, and amphibians proceeds. During that period the latter two groups became almost as diverse (10,500 species in all) as mammalians and birds (13,000 species in all). Then the diversity of insects, too, reached an astronomical loftiness - it is thought that they may have reached at least several million of species. In the Neogene, species of plants, especially grasses and composites, became more numerous as well. In short, at that time the biosphere was enriched by species more than ever (Signor 1990). According to Wilson (1994), the total number of species currently existing on Earth may be as high as several dozen millions.

There are many indications testifying to the fact that the biosphere biomass, too, became particularly great in the Neogene and then, at the very end of that period, became constant. It is likely that during the recent several million years neither the biosphere biomass, nor amounts of oxygen and carbon dioxide in the environment have undergone any greater changes, though there have occurred certain fluctuations. Amounts of these gases have become limiting and, most probably, it is them that influence further growth of the biomass, which has been described in the interlude 'Atmospheric Evolution'. Thus, there are reasons to believe that the biosphere continuously increasing its biomass has finally reached Earth's carrying capacity, i.e. a maximal biomass possible under existing astrophysical conditions.

What does it all mean? May be fate has decided that we should be contemporaries of events that are no longer within the limits of traditional evolution and that point to some revolutionary changes being ripening in the depths of life? But what kind of changes? Is it possible that the answer to this question is right here - in the history of ours? May be the circumstance that the stagnation of ecosystem evolution more or less coincided in time with the emergence and expansion of hominids shows a close causal relationship and not only a meaningless coincidence? There are too many questions and so few clear answers.

Those were hominids themselves that had the honour to realise the ideal of evolution at the species level - to increase reproduction efficiency to almost the maximal possible limit, to accumulate a multitude of other features useful for the species, and to become invincible in the struggle for existence. Let us take a look at how that happened.

Australopithecines, the first hominids, appeared in Africa approximately 5 million years ago. Of them the species *Australopithecus afarensis,* which lived 4-3 million years ago, has been devoted greatest attention. Those hominids walked bipedally already quite well, though still had many features characteristic of modern apes. Living in forest edges and savannahs, australopithecines may have escaped competition with apes and successfully diverged. Two to 1.7 million years ago there may have been coexisting already up to 10 hominid species, of which 9 may have been belonging to australopithecines. The one remaining species was *Homo habilis.* All those hominids already had tools and weapons, which seemingly were used not only when searching for food and defending from predators, but also during wars among themselves. Wars broke out among both individuals of the same species and those from different ones. The thing is that species ranges most probably overlapped.

Some 1.6 million years ago *H. habilis* gave a rise to the upright man - *H. erectus.* Upright men may have already been using fire and, seemingly, were quite good hunters. They lived in herds, built shelters and primitive dwellings. It is likely that they have been using an articulated language. In short, it was a species more advanced than *H. habilis,* so already 1 million years ago all other hominid species were pushed out. The upright man is usually considered to be responsible for a rather sudden decrease in the diversity of large African mammalians, which also started approximately 1 million years ago. It most probably was caused by intensive hunting (Foley 1987; Tobias 1992).

Upright men inhabited not only Africa, but also Eurasia. In times of flourishing, 0.5 million years ago, their population could have been as large as several million individuals. However it was just at that time that the first humans - *H. sapiens neanderthalensis* - originated in Africa. Later they moved to Europe and Asia pushing upright men out of all ranges. But this was just for a while, for about 150,000 years ago there appeared *H. sapiens sapiens,* also called Cro-Magnon, to do the same with its more primitive subspecies. It was 40,000 million years ago that Cro-Magnons became absolute rulers of hominids. The human population of that time could have reached some 10-20 million.

About 13,000 years ago, having passed the isthmus at the place of the modern Bering Strait, humans got to North America. Gradually moving southwards, during several thousand years they conquered South America, too.

After agriculture and cattle breeding appeared, the population began to grow even more rapidly. Only two means of population regulation remained - infectious diseases and intraspecific competition - which also disappeared later the scientific and industrial revolution having started and wars having been restricted, Environmental resistance was broken down, and the population dictated by inborn features started to grow unrestrainedly (Fig. 23). In the year 1850, the global population was as large as one milliard and in 2000 - six milliard. The real rate of growth became close to the biotic potential typical of the species,

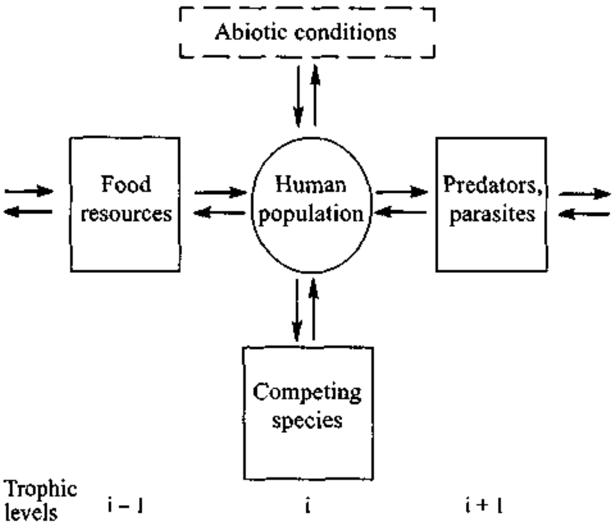

Figure 23. A scheme of the ecological niche of the human population. Like an increase of a population of any species, that of human one is limited by the environmental resistance resulted in by the influence of components of an ecological niche: unfavourable climatic conditions, shortage of food, pressure exerted by predators, parasites, and rivals. Civilisation and culture enabled to lower the death rate caused by the above factors, and thereby having eliminated environmental resistance the human population began to grow uncontrolled. Understandably, that growth is possible just for a short while. Here the arrows indicate a regulatory impact and those directed from the left to the right – the direction of the flow of nutrients and energy, too. By the way, an attitude towards a niche as to an ecosystem segment or its fragment, I think, is useful in constructing ecological or evolutionary models.

Having eliminated or reduced environmental resistance to minimum, a species automatically becomes a superrival and a diversity consumer. That was the case with our species, too. Now dozen thousand species die out in a year due to human activities. This is mainly related with the devastation of rainforests. This negative eneci on oiner species is increasing exponennauy, like the human population. Due to this effect the number of trophic levels in biosphere ecosystems is reducing, food chains are simplifying to minimum, and the flow of nutrients and energy is being increasingly directed to our kitchens and factory shops.

The lights are going out on the stage, the curtain is dropping

A voice from behind the scenes:

Ladies and gentlemen! Some of you may think that this story going from the very appearance of life to nowadays is merely a dream, an imaginary play of shadows in the mist of the sky the day drawing to a close. You may be asking yourself - is it possible that what we have seen and heard is the real history of the Earth and man? Is it the course of events we have expected to see and hear? Indeed, the characters of the play were called by common to us names, and their exterior was not very different from what we have heard so far, but the fabula was strange, little understandable, alien. May be the story has been quite interesting, told in a picturesque, at times even elegant way, but you ask yourself - could it really be the history of *ours?* Doubts torture you, but they torture the author, too. He, like many of you, also thinks that doubt is everything, whereas conviction is equal to death. He even acknowledges that something of what you have seen on the stage he has created by means of his imagination, but still he considers that imagination and fantasy are better than supposed knowledge. By such words he bids farewell for a while.

PART 2. EVOLUTION DIRECTING FORCES

MERITS AND SHORTCOMINGS OF DARWINISM

It is not easy to single out the main principles of a theory formulated rather freely. Such a rather free theory is Darwin's theory of natural selection. In it is a variety of propositions. Emphases are sometimes lacking, and concepts are often defined not exactly. In short, it is not easy for a reader to differentiate between major and minor elements of the theory. Still I will try to do this.

I think that essential in Darwin's theory of natural selection are four propositions. I will formulate them in my own words using terminology more familiar to a modern reader:

1. Organisms have an unlimited reproduction potency;
2. The amount of resources suitable for organisms is limited. Besides, realisation of unlimited reproduction potency is hampered by other unfavourable environmental conditions too - rivals, predators, and parasites, as well as by savage climatic factors;
3. In natural population there exists an accidental (not directional) diversity in the ability to resist unfavourable environmental conditions;
4. This diversity is inheritable.

The logic of Darwin's reasoning is simple. Though organisms have unlimited reproduction potency, this potency is never realised fully, since resources are always limited and nature is unable to feed all offspring. This excess of offspring experienced by each generation is doomed: some of them die of hunger, others are killed by predators and parasites, still others are finished off by cold or droughts or die out due to other reasons. So, according to Darwin, organisms of each generation are involved into a struggle for existence, i.e. into a struggle with an unfavourable for them environment. The third of the above-presented postulates maintains that in natural populations some 'fighters' are better and some are worse. Understandably, those better win, thus survive. Therefore, contrary to diversity, death and survival are rarely accidental. Finally the fourth postulate states that this diversity of individuals is inheritable, which means that the offspring survived transfer their good features to the next generation.

To sum up all the four statements, a general conclusion could be drawn: there is a struggle for existence in each generation, and winners are the fittest offspring; they transfer their inheritable features to individuals of the next generation who in their own turn are involved into the stages of inheritable variability, struggle for existence, and selection, and so on and so forth in every generation. Darwin called this survival of better or the fittest 'fighters' natural selection.

I would like to point out some very important as I think features of this theory. First, Darwin's theory is not tautological, as it is sometimes considered. In it, the notion of the fittest individuals is rather concrete: they are individuals who have better abilities to resist unfavourable environmental factors. According to Darwin, evolution takes place in the direction of decreasing death rate: in every next generation a species adapts to the environment better and better, thus fewer and fewer offspring die of hunger, because of the pressure of rivals, predators, and parasites, or due to unfavourable climatic conditions. An ecologists may say that here we are talking about an increasing reproduction efficiency (it is the ratio r/b, when $r > 0$, and b^{-1} or d^{-1}, when $r = 0$; here r - population increase rate, b - birth rate, d - death rate). Has such an evolutionary trend really existed? What can theorists and empiricists tell about it? It seems that they have given a positive answer long ago (Huxley 1942; Simpson 1949; Thoday 1958; Zavadsky 1958; Rensch 1960): such a trend has really existed and is probably existing now. And this is not only in microevolution, but also in macroevolution. My own rough calculation indicates that reproduction efficiency in fish makes about 0.0001%, amphibians - 0.01%, reptilians - about 1%, birds and mammalians - about *5%*. In the case of the upright man *Homo erectus* this indicator could have been as high as 15—20%. In this respect modern man is the most advanced species indeed. Its reproduction efficiency - approximately 90%o - is highest of all to compare with that of organisms that have ever existed. It is a species fittest of all on Earth, least inclined to feed other species on its zygotes and offspring.

Thus, according to Darwin, it means that all individual features help to survive, maintain and increase reproduction efficiency - this is the main direction of the evolutionary process. This is how I understand Darwinism.

I would not like to agree with Gould's (1994) opinion that 'natural selection is a principle of local adaptation, not of general advance or progress.' Otherwise Darwin's theory should really be declared pure tautology (see Peters 1976). By the way, it is not only S.J. Gould, but also many other evolutionists who until today have been regarding natural selection as having temporary or local trends rather than general direction. I think that the formation of this opinion has been particularly influenced by E. Mayr's works (e.g. Mayr 1961). It has been even included into handbooks for colleges and universities. This is disturbing. Is it a revision of Darwinism or just lack of continuity? I hope for the latter.

As much important is another feature of Darwinism, which most probably is a shortcoming rather than merit. According to Darwin, natural selection is a cleaning and diversity-reducing force releasing population from all less adapted genotypes to leave only one of them - the fittest. The latter geneticists sometimes call wild. As R.C. Lewontin has written in one of his monographs (1974), natural selection could not be understood somehow differently than biodiversity antithesis. The moment a mutant with some particularly good features appears in a population, survival probability of other genotypes of the population automatically reduces to minimum. Therefore all natural populations should inevitably be monomorphic, i.e. with only one predominant genotype. As it is known at present, this theoretical conclusion is not true - natural populations are polymorphic. And this polymorphism is unlikely to be of a temporary character or neutral with respect to selection.

The theory of natural selection maintains that species, too, compete attempting an exclusion of one another. Therefore, it is most probably that in a certain locality predominates one species that is fittest for local conditions and that has excluded other less fit species. Naturally, the fittest species are those that have appeared recently, and evolutionary older ones will be excluded. That merciless is the logic of natural selection.

I think that such quite unexpected conclusions will be arrived at by every reader of Darwin who, like R.C. Lewontin and some other attentive researchers, will try to single out the main principles of the theory of natural selection and to follow them. Such a reader is likely to draw a conclusion that Darwinism quite well explains the phylogenesis of species, their improvement from generation to generation, whereas it is not so good at explaining how polymorphism appears and is maintained and how of one species there can originate two and of the latter - still more, and so on and so forth. In short, in the context of the struggle for existence, a great biodiversity becomes a difficult to understand phenomenon, though the fact itself is beyond any doubt. Hardly could there be a greater reproach to Darwinism than the above.

Darwin must have foreboded this reproach and therefore in addition to the theory of natural selection presented some other ideas, too, which could be regarded a supplement to the theory. In the book 'The Origin of Species' we can find a scheme of species divergence and explanation to it. Darwin suggests that the exclusion resulted in by competition could be escaped just in one way: features should become so divergent that competition would decrease or even disappear. In other words, if inheritable variability is able to create considerably differing genotypes, then the latter, according to Darwin, are to occupy different positions in natural polity. Then an explanation follows allowing a conclusion that such new genotypes are to have a possibility of either migrating to new localities, or turning to somewhat different feeding way. The inherited differences gradually growing, some genotypes may eventually turn into different subspecies and later - into species.

Thus, Darwin yet presents some arguments explaining why many species rather than one are existing in nature. It is hard to expect something more, providing the understanding of connections between organisms of the mid-19th century. Still I think that Darwin has done a lot - given a hint that individuals and species may not only compete, but also complement one another by occupying different positions in the general 'natural polity' thereby solving the problem of long-term co-existence in one locality.

By the way, there we can find an answer to the question why better organised forms have not excluded primitive ones of which, as the theory suggests, the former should have risen. Darwin explains that this is because of the fact that primitive forms should have remained to live and have been living until nowadays under conditions so primitive that high organisation is unnecessary for them for it does not give any merits in the struggle for existence. Besides, in such primitive habitats those forms should have been subjected to a less severe competition. Thus, despite the existence of an unappeasable trend of the exclusion of less-organised forms by more-organised ones, it manifests itself just under complicated living conditions.

And though to a logically thinking reader this answer may also look quite unclear and even contradicting the above presented postulates of the theory, you should agree that Darwin does not close his eyes to the faults of the theory or ran away from them. At least to me it seems that by that explanation he admits that the appearance of biodiversity and the subject of the biological meaning of it is too complex even to him and that it should be answered by biologists of future generations.

I would like the reader to take a look once again at the four main postulates of the theory of natural selection. You can notice that two of them are of an ecological, whereas the remaining two - of a genetic character.

Darwin deduces evolutionary mechanisms from ecological and genetic laws. This methodology is worthy of attention. By the way, Darwin has not described his methodology precisely, i.e. why he has done something in this way and not another. He has followed his intuition rather than a well-considered and well-grounded method. This, however, has not made the final result any worse.

This methodology is worthy an exceptional attention because it gives a key to other researchers who being tortured by doubts may feel like revising the theory of natural selection or creating an analogous new theory. Without this key they would hopelessly wander in the dark, as it was the case in the 20th century, when Darwinians ignored their teacher's experience or simply paid no attention to the methodology used by him, its merits. Darwin kind of says that if you do not like my theory then its shortcomings should probably be searched for in the main principals. And since the latter have been taken from ecology and genetics, let experts of these spheres make corrections, because in my times both ecology and genetics were absent, so you should not expect impossible from me.

Here I have to say several words about the revision of Darwinism, which took place in the 20th century. I have in mind so-called neo-Darwinism or, to be more precise, its theoretical kernel - population genetics. Geneticists have *detailed* the third and the fourth of the main postulates of the theory of natural selection explaining how an inheritable non-directional diversity originates. Population genetics, however, has lent the theory of evolution a quite different, mechanistic-analytic spirit. The fire of mathematical modelling has burnt much of what was especially valuable in Darwinism. First, there has suffered the ecological part of Darwinism or the conception of the struggle for existence, i.e. ecological context has been completely declined. It is not that the struggle for existence has been rejected. This kind of a struggle is taking place, but in population genetics those 'competing' are alleles of the same gene rather than individuals. Then the evolutionary process is inevitably reduced to gene frequency changes occurring in an ecologically indefinite vacuum. It seems to me that such a reduction, which according to its conceivers is useful in making the theory more rigid, could have resulted in but one outcome: in the end the theory should have become very rigid and monosemantic, but absolutely invalid *in situ.* I think that this is exactly what has occurred. By the way, in recent years there has been some sobering, an euphoria caused by the application of mathematical methods has passed, but a clear alternative still is absent.

At first sight the logic of geneticists may seem very simple: if a feature (a protein) is decided by a gene and a phenotype is decided by a genotype, then a population, too, could be and even is useful to be reduced to a gene pool, i.e. a gene set of a population. The matter is that information 'flows' in one direction only - from genes to features. I do not feel like considering the subject in detail, but I have to emphasise that this logic is faulty. My knowledge of genetics allows considering that even individual development is decided not exclusively by genes. The role is also played by a feedback from a forming phenotype to a genotype (see e.g. Lekevicius 1986; Lewontin 2000). Due to such a faulty attitude towards the connections between a genotype and a phenotype many have come to a conclusion that natural selection selects genes, and features just follow them. I think that this is just in opposite - what is selected are features, whereas genes, being non-kinetic elements of a system, are able to do nothing but obey and follow. This attitude of population genetics contradicts Darwinism rather than details and complements it. I do not think that Darwin would have approved of it. Therefore, to call population genetics the quintessence of neo-Darwinism, as it is often the case, is somewhat incorrect with respect to the originator of the theory of natural selection.

Luckily, the modern evolutionary biology is not exclusively the so-called neo-Darwinism, but also great many of publications that are outside the Procrustean framework of this doctrine and therefore could be useful in creating a new, wider and more exhaustive theory. Historians of science, however, know well that it is not easy for new paradigms, usually consolidating new and old ideas and making their selection and evaluation, to come into being. These are just new-paradigms-formulating works that due to subjective reasons are ignored most of all by the 'parliamentary majority' during the initial stage.

Since I have made a more detailed analysis of population genetics and its methodology in other publications, I will not go deeper into the subject. The more so that as the years pass I have become not so violent and criticism is no longer so pleasant an occupation for me.

A LOST SHEEP

I have been interested in evolutionary problems since more than 20 years ago, 1976. By the way, at that time I related all evolutionary problems with the context of theoretical biology. I was obsessed by the idea that a new palace of biology should be built, an unprecedented synthesis made, and something analogous to theoretical physics created. One of my favourite books at that time was 'Towards a Theoretical Biology. Part I. Prolegomena', edited by C.H. Waddington. In my dreams I saw myself successfully creating such a general biological theory - the panacea for all obscurities and fallacies. How could I know that in the short run I would get confused and lost...

I was naive, quite young, and, what is more, pretentious. On the other hand, I understood that my theoretical preparedness was too poor and I would have to learn the whole biology again, on my own, and that in addition to biology I would have to study some spheres of mathematics, general systems theory and cybernetics, thermodynamics, and may be even something else, By the way, I was not only very pretentious, but also persistent.

I remember that at first it seemed to me that it would be enough to properly study mathematics only and that I would find answers to the most important questions of theoretical biology. The thing is that all leading figures in theoretical physics mastered mathematical apparatus quite well. Indeed, I was absorbed in that sphere of science for a while. Luckily, the fate had endowed me with the keenness of wit rather than with the love of mathematical purism, so I recovered from that disease quite soon. I think that so I have escaped from one of the forms of scientific snobbery, which has ruined many theorists. Still, I had to study thermodynamics, general systems theory, and cybernetics seriously and for quite a long period of time.

The first questions that arose to me while reading literature on evolution were the following: What is deciding an evolutionary lineage of an individual species? How free are species in evolving? Finally it was also not known for me precisely why primitive species have not been excluded. I did not found an answer to any of those questions in population genetics, and I was not going to study Darwinism hard, since I thought that I had known that theory since school times and that it was so 'old and primitive'. I remember I appealed to experienced mathematicians and cyberneticists for advice. And I was so surprised when they could not give me any piece of it. Gradually I became convinced that those questions were somehow related with ecology and the conception of an ecosystem in particular and that mathematicians had nothing to do with that. But isn't it an absolute nonsense to search for answers to purely evolutionary questions in ecology? If this is a rational way out, then why it is used by a few? Such thoughts disturbed and disbalanced me. Inspired by doubts I started to study Darwin's works themselves expecting to find out at least some vague hints. And I was so surprised. It turned out that I was not an anti-Darwinian, though I had considered the theory of natural selection somewhat old. Notwithstanding all the novelties I had studied - general systems theory, cybernetics, and thermodynamics - Darwin's theory seemed to me more acceptable than the modern neo-Darwinism with its theoretical kernel, population genetics. It was evident that that already ancient theory is far deeper than it may seem to a person looking from above at such ideas of an honourable age. I was particularly astonished and glad about the fact that Darwin, as it turned out to be, had deduced evolutionary laws from ecological and genetic principies. It means that intuition had not disappointed my hopes and that the answers to the questions I was interested in should really be searched for in ecology and genetics. Neo-Darwinians had ignored ecological aspects of Darwinism thereby turning the theory to an unpractical scheme. Besides, I understood something else, i.e. if we do not find satisfactory answers to certain yet unclear evolutionary questions, we should look over the basic postulates of Darwin's theory first. At need they could be replaced by new ones, which better meet the modern attitude. It is so easy. It was strange that such an elementary idea had not occurred to somebody before. Or at least I did not know that. One way or the other, I was sure that after a long wandering in every nook and cranny and risking to get lost for good, in the end I came across something that I needed most of all - traces of the methodology applied by Darwin and possible to be used by anybody seeking greater clearness in evolutionary biology,

Though I have been impressed by Darwin's methodology, in 'The Origin of Species' I have not found an answer to the subject-matter-related questions that I am interested in. Darwin writes about species divergence and why primitive species have not been eliminated, but his arguments are weak. On the other hand, the whole inner logic of the theory of natural selection itself says that genetic diversity in populations and species diversity in ecosystems are antithesis rather than a logical consequence. Darwin had a feeling that in that case the answers should also be looked for in natural polity, but he could not add something more.

What could be done then? It was possible to supplement the postulates of natural selection with new ecological statements. However, there was another way, less straightforward and far more difficult though more fundamental. Trying to involve in evolutionary biology not only ecological principles, but, let us say, physiological ones, too. It meant that first of all the principles of organisation and functioning of biosystems could be gone into. Ranges of such prospects were breathtaking, and that could be an inveterate optimist only who could have expected that that way of action would bring the giddy joy of discovery and not only bitter disillusionment. I, understandably, could not resist the temptation. Hesitations ceased and the new stage of my search began. By the way, if I had known what difficulties were awaiting me, I would have probably chosen an easier way.

First I tried to replace the conception of the struggle for existence by the idea of a functional hierarchy (an ecosystem is a super-organism) leaving the remaining part of Darwin's theory unchanged with the exception of some details, taken from genetics. Later I understood that I had created nothing but a giant with clay legs - my model did not work, as I have expected. I had to think everything over once again, and it was not before the year 1982 that I found the answer: the functional hierarchy in populations and ecosystems is nonrigid, which makes it possible for competition and the related effects to manifest themselves. Of course, that attitude still had to be made more concrete in order to eliminate multisemantics in the basic statements. Finally I finished that work, too. From then I was no longer disturbed by evolutionary questions, well-grounded answers to which I had been looking so long. I already knew those answers, and not only to the above questions, but also to many those that arose in the course of the work. What was still to be done were merely general conclusions, which eventually were made as well (Lekevicius 1986).

Simultaneously I was engaged in methodological work, too. As mentioned, the methodology used by Darwin seemed to me very advanced, but it had not been described in detail anywhere and, understandably, had no theoretical argumentation, i.e. why something has to be done in such and not another way. There was a definite cry for publicity. So, I set myself that goal, too, and it took me several more years to achieve it. As a result I founded the methodology that I called the concept of a conditionally complete causal explanation (Lekevičius 1985). I consider that it is my greatest achievement throughout my scientific career. Such a conviction is based on the idea that in science method is everything: there are no bad results, there are bad methods (and improper prejudices). If you have a method adequate to the object under investigation, to achieve good results is a matter of technology. In what follows I will attempt to present this methodology of mine as brief as possible.

BIOLOGICAL TIME AND BIOLOGICAL SPACE

When searching for the basis of the methodology used by Darwin I started from the concepts of 'cause' and 'explanation'. The cause is usually regarded a condition or an event that has caused another event, which is called a consequence. The latter always follows the cause. When explaining some phenomenon or event we refer to prior events that have caused it, we deal with causal explanation. In addition to causal explanation, there are suggestions pointing out genetic explanation, too, which simply shows how a certain object changed through time without pointing out the mechanisms that caused the change. So, genetic explanation is considered to be the most primitive and it hardly explains something at all. Unlike physicists and chemists, biologists in addition to genetic and causal explanation use functional explanation. The latter does not refer to temporal connections and involves exclusively spatial ones. For instance, to the question 'Why molecules of this enzyme are here and now?' could be given three quite different answers. If merely antecedents of these molecules, i.e. materials from which they have been synthesised and the gene coding this enzyme are indicated, we deal with genetic explanation. If the description has references to the mechanisms of biosynthesis of these molecules, we deal with causal explanation. Again, functional explanation is quite different: the molecules of the enzyme are here and now because they perform particular functions. To a biochemist or a cytologist such an answer is often quite satisfactory, though sometimes an expert could be interested in the causal explanation of the fact. The stage for functional explanations was set by Darwinism, which maintains that almost each feature of an organism is adaptive, thus helps it to survive and reproduce. On the other hand, this kind of explanation is possible just for the fact that in an organism exists an indubitable functional hierarchy. This does not impress physicists and chemists, since the explanation of the objects investigated by them does not require the hypothesis of a functional hierarchy.

It is natural that the biological spheres related with development problems traditionally are more inclined to use causal explanation, whereas the spheres that describe the structure, organisation, and functioning of biosystems most often manage with functional explanation without going deep into development aspects (here I am greatly generalising, though there is a great deal of truth in these statements). Therefore, on including ecological and genetic principles into the theory of evolution, Darwin simultaneously supplements causal explanation with functional one, thus making a synthesis of these ways of explanation. Obviously, such a methodology enables to obtain a far more thorough explanation compared to the case when exclusively a traditional causal or functional description is used.

When Darwin draws 'trees' of species divergence, he seeks but the genetic explanation, why in the same locality exist a lot of species and not the fittest one having excluded those less fit. However, when he complements this picture with the references to the struggle for existence and the differences in environmental conditions forcing species to diverge, we already deal with causal explanation, even though not thorough. If he had supplemented that verbal model with the explanation why evolving species tend to form that particular kind of species sets, he would have obtained a more-or-less thorough causal explanation. Such an explanation would have been of a particular value. Thus, Darwin's scheme lacks hints of factors directing species evolution. The evolutionary convergence of species and ecosystems is so widespread that there is no doubt that such directing forces have really existed. Now we know that references to these forces should be searched for in the principles of organisation and functioning or, to be more precise, in the conception of an ecosystem.

According to the methods of evolutionary explanation development used by Darwin and described explicitly and supplemented by me, the explanation of any biological object should be searched for in the functional connections involving antecedents of this object. Combining causal and functional explanation is the only way to obtain a more-or-less exhaustive explanation, which can satisfy even the most captious critic. In this way the line dividing the biology of development and that of functioning, biological time and biological space is erased.

How should the latter statement be understood? I will give an example. Suppose, ecologists have carried out a research and established that in *modern* ecosystems species not only compete, but also are involved in the functional hierarchy. This ecological principle could also be used in explaining evolutionary facts. If species *are* dependent on one another from the point of view of functioning, then they also *have been* dependent on one another while evolving, thus they have been constraining the evolution of one another. What kind are these ecosystem constraints of? To answer this question, we do not need to address palaeontologists. The answer is right here, in ecology. We just need to find out what parameters are essential to ecosystems and how they change through ecological succession. All the conclusions obtained are also fit to describe evolution, since there is no gap between evolutionary and ecological time - biological time and space make continuum. It could have been broken just by minds too inclined to analysis, who have made biology a quasi-complicated science, whereas it really isn't such.

An important feature of this methodology is that in this case a theorist deals with huge causal fields causing a particular result rather than with individual causes. Just superficially thinking ones may consider that in biology, like in mechanics, there are single causes and that long causal chains made of several dozen links are merely fiction, a boring *Naturphilosphie,* does not fitting the modern practical mind. My statement that the existence of detritivores is an indispensable precondition for photosynthesis may also be unacceptable to many, and I can understand them: this precondition, or cause, is quite distant from the final consequence (the act of photosynthesis) with regard to both time and space. If soil-inhabiting detritivores disappear, a tree will continue to keep its green head high for quite a long, until eventually it will languish and fade out, though. So, such people may say that the cause of photosynthesis, as you call it, is not evident. I don't know whether there is something that can help them. I can only give them a piece of advice - never go in for theoretical biology.

I think that there will surely be somebody who will not accept such a methodology of constructing theories of general biology. However, I am sure that nobody will be able to negate one thing - just this or similar kind of a methodology could be efficient in those spheres of biology where traditional mathematical modelling, experimental, and observational methods are powerless. In quasi-complicated situations so abundant in living nature, it does not have any more-or-less acceptable alternative, any acceptable way of logical simplification. I think that this book of mine, like some of my previous publications, testifies to this quite clearly.

AN ODIOUS SUBJECT: A FUNCTIONAL HIERARCHY

Darwin is sure that in the inside of each organism there is no struggle for existence, thus there is no competition, too. There co-operation and harmony are reigning. By the way, this attitude towards the character of intraorganismic connections is just supposed, but it is clear from the context that the author uses it intuitively. Supraindividual connections, on the other hand, do not seem so obvious to Darwin, thus he gives much attention to them. At those levels he has found mainly connections of a negative character. How is such an attitude right towards the organisation and functioning of biosystems? As the reader may have already understood, the answer to this question decides our attitude on evolutionary mechanisms: the basic postulates of a theory having changed, explanations suggested by that theory have indispensably to change, too.

The subject of a functional hierarchy is one of those that biologists are not too fond of. They use the notion of a functional hierarchy just when speaking about intraorganismic connections, which happens seldom. As far as I know, ecologists do not use the notion at all. The majority of them are inclined to speak about some mysterious emergent features presumably typical of all ecosystems. Thus, if you want to elucidate something, you have to address not biologists, but rather experts of the general systems theory. The latter characterise a functional hierarchy as a kind of an interdependence of structures, when a function common to the whole system is divided into two or even more functions fulfilled by parts - subsystems - of that system. The more different subsystems are there in a system, the greater usually is their specialisation level in case other conditions are similar.

Any structure comprising a functional hierarchy can not do without control, co-ordination. In this respect life is no exception. Control may be carried out by certain subsystems, the central nervous system or the humoral system, for instance. Control may also be of a diffusive character, when there is no certain structure meant for control and the required co-ordination of action as well as a functional hierarchy are achieved through an interaction among partners more-or-less equal in the sense of control. Understandably, the latter case is fitter for populations and ecosystems. In any case, in the presence of a functional hierarchy control is specific constraints of subsystems activities. Without such freedom restricting forces co-ordinated activities are impossible.

Here I am not going to question the opinion about the existence of a rather rigid functional hierarchy and the absence of competition in a multicellular organism. I do not consider that the case is so simple. But let it be so. The more so that I have written about this quite much in other publications. I would better discuss other two levels, those of a population and an ecosystem. The reader already knows my attitude towards ecosystems - there the existence of a functional hierarchy is beyond any doubt. Since species are not independent in the functional point of view, then living, or independent, in the literal sense of the words, is but an ecosystem or at best but a biosphere. Similar hierarchy could be found in populations of many species. This is indicated by intrapopulational diversity: genetic polymorphism, sexual dimorphism, ranks, and castes. Such a diversity mitigates intrapopulational competition creating complementary and co-operative relations among individuals. For example, a male and a female are closely interrelated, and none of them is able to fulfil the function of reproduction by himself or herself. Even the simplest genetic polymorphism typical of the majority or may be even of all animals and plants as well as microorganisms mitigates intraspecific competition and creates complementary relations (see e.g. Lekevicius & Balciunas 1986). Possibly it is not co-operation, but by no means it is a severe competition causing exclusion of all genotypes but the fittest. The notion of a 'wild' genotype used by geneticists until today is incorrect, for fluctuations of environmental conditions as to time and space make adaptive values of different genotypes similar. A genotype that is good here and now becomes bad in another place and at another time, therefore exclusion is hardly possible.

So, life is a functional hierarchy extending from single macromolecules to global ecosystem functions. There could be different kind of hierarchies, however. One kind of hierarchy is in a multicellular organism and quite another one in populations and ecosystems. At supraindividual levels hierarchy obviously is far less rigid. In addition to complementary and co-operative relations, there also exist competitive ones. In order to exclude the multitude of details and to generalise the relations existing on those two levels, the following summary could be made. At each point in space individuals of the same and different species co-operate and compete simultaneously. In its natural surroundings, an individual is as if mythological Janus, whose one face is turned to higher levels and lights up with submissiveness whereas the other - a face of an egoist and despot - looks down. An individual, like species (a population), simultaneously is both a part of the whole and a relatively independent unit aiming just at its own 'objectives'. It is likely that egoism is of inner origin, whereas submissiveness could come just from the outside.

In general, in living nature are just two mighty contradicting forces, which could be called biotic repulsion and biotic attraction. Competition - intra- and interspecific - is a typical case of the manifestation of biotic repulsion. If you planted several pines side by side so you would be able to observe their behaviour, they would push off one another if they could. However, there exist forces that in a similar situation make organisms to behave in a contrary way - to come together, even if those organisms are situated rather far from one another. Those are forces of biotic attraction. It is known that organisms exist in groups mostly because of the heterogeneity of the environment or due to the presence of co-operation elements in relations among individuals.

In living nature, throughout its evolution the two opposite forces have been in a kind of a dynamic equilibrium. Without the force of co-operation, or biotic attraction, there would not have formed stable ecosystems with the multitude of species comprising them, and without biotic repulsion life would have lost its lability and would have really become a giant with clay legs.

I think that the modern attitude of many ecologists towards interspecific relations is not very different from that which existed in Darwin's times prior to the rise of ecology: negative relations are thought to be widespread and important, whereas positive - rare and insignificant. This is how this attitude and the reasons that have caused it are characterised by Kareiva and Bertness (1997):

'Most ecologists agree that positive species interactions occur, even though they are not typically discussed as important community processes in contemporary textbooks and models. This disparity is interesting historically, because early ecologists such as F. Clements and W.C. Allee initiated modern ecological theory with the notion that communities were the products of a combination of positive and negative processes. The reluctance of community ecologist to incorporate positive interactions into their thinking has, in part, been driven by the focus of MacArthur and his followers on competitive interactions. In addition, the suggestion of mathematical modeller that positive interactions lead to instability and the evolutionary naive idea of biological systems as superorganisms have also contributed to the reluctance of community ecologists to consider the role played by positive interactions in communities. Recently, however, ecologists have begun to realise that positive interactions are pervasive forces in communities.'

I would like to specify the last statement of the authors. Yes, interest in positive relations has been growing in recent years. However, I dare say that those changes have not changed the attitude of ecologists. Until today there has not been accepted that:

1) life can not exist without nutrient cycles;
2) those cycles can be 'rotated' just by an ecological community formed at least of producers and consumers;
3) producers and consumers are interconnected, though not all of those connections are compulsory - life is a functional hierarchy, though not rigid.

I do not doubt that in the future the 'parliamentary' majority of ecologists will have to change their attitude towards relations between plants and herbivores, prey and predators, hosts and parasites. Until today in handbooks those relations have been marked with '-' and '+' marks meaning that one of the partners has only harm from those relations whereas the other - only benefit. I consider it quite a superficial attitude. It may be a result of our inclination towards anthropomorphism and philantrophy: looking from the position of a single individual, and such a point of view is most common to us, being someone's prey is an indubitable evil. However, in the light of the biology of populations and ecosystems a death of a part of individuals is not only inevitable, but also desirable. During the 19th century alone it was commonly considered that all organisms seek to have as large populations as possible, which is wrong. For the most of natural populations optimal density is average and not the greatest possible. Predators, parasites, and herbivores fulfil a stabilising role, thus preventing the most competitive species from excluding those less competitive. Such relations are more likely to maintain biodiversity rather than reduce it. Those may not necessarily be typical cases of interspecific complementation or co-operation, but the above-described relations are not merely unilateral positive ones. I would rather regard them as cases of biotic attraction and not repulsion. Understandably, I have in mind partners that have co-evolved at least for a while. When species migrate and face not co-adapted partners, everything may happen. Sometimes one or another species may become extinct, and biodiversity may reduce.

Imagine what would happen if all biospheric insects occupying niches of herbivores and predators died out. Thinking in a traditional way, it may seem that at least for preys of insects it would be even better. Would it be really so? Sure, insectivores and those the diet of whom includes insectivores would be the first to suffer: many of amphibians, reptilians, birds, and mammalians would become extinct. However, the groups of organisms previously exploited by insects would suffer too. The majority of flowering plants would become extinct, and the survival of tropical rainforests would become problematic, whereas forest of the temperate climate zone would change beyond recognition. Along with the drastic languishing of flowering plants and forests a great many of habitats required for the survival of still existing herbivores and predators would be lost. Still other herbivorous and biophagous groups would be involved into a merciless and weakly controlled competitive fight after which merely some of them would be left. In short, the biosphere would degrade to the state typical of it in the Devonian or even earlier.

There are important evolutionary arguments, too. As it has been described in 'Part 1', the first aquatic and terrestrial ecosystems were made of merely two blocks - producers and detritivores. Later herbivores emerged, then primary predators did so, and so on and so forth. Producers induced the rise of herbivores and the latter - that of primary predators, and so on. If the logic of the minus and plus signs was correct, then the appeared herbivores would have had to negatively affect the diversity of producers in some way, and primary predators soon after their formation would have had to exterminate at least part of herbivores, and so on. Palaeontological chronicle, however, does not support such reasoning. On the contrary, biophages rather than destroying producers made a significant contribution to biodiversity. At present insect species alone make as many as a million or more. It is unlikely that parasites, too, reduced the diversity of their hosts, irrespective of all plant and animal species hosting them.

An attitude towards those interspecific relations as to unilaterally beneficial is groundless because of still easier motives. If plants are damaged by herbivores and the latter - by predators, then according to this logic relations between plants and predators should be marked with two plus signs for those relations are indeed mutually beneficial. In a word, all odd trophic levels, like even ones, rather than smother maintain and stimulate one another. This specific feature of interspecific relations is well known by ecologists, who sometimes make use of it in eliminating eutrophication results: predatory fishes are introduced (or added) into a lake in order to reduce the abundance of planktophagous fishes, which in its turn promotes the growth of zooplankton populations and the decrease of the phytoplankton biomass. A similar role is played by predators with regard to plants in terrestrial ecosystems too - even a secondary school pupil knows that a wolf is a best friend of plants. So, even if the logic of the plus and minus marks is correct, then extrapolated it to the whole food web we obtain an inevitable result that this web is woven from a multitude of mutually beneficial interactions. I have not found a similar conclusion in any of serious articles or handbooks of ecology, though I can not say that relations between plants and the primary predators are not investigated - of the freshest publications see e.g. Terborgh *et al.* 2001. In general, I have an impression that ecologists are not too fond of analysing and particularly of modelling situations with more than two species and the more so with species belonging to several trophic levels. The notions of causal chains and causal fields are out fashion at present.

I hope the reader will understand that I write this just because I am a little sorry for ecology and not because I have pretensions to being a discoverer of new ecological laws. These laws are better known to elder generation ecologists than to me, so if I have discovered something at all, it is just America. It is sad and strange that things elementary even to a school pupil are an unthinkable suggestion to an experienced scientist. How this could be explained? I think that here we face a certain methodological blindness - a pair of glasses given to us by somebody some time ago let pass just a certain kind of information into our consciousness, and we have got used to these glasses so much that we not only do not notice their shortcomings, but even do not feel that we wear them at all. Biological and ecological methodology is the most forgotten island in the ocean of cognition, and therefore we, scientists, have to pay for it so much. Are those just future generations that are fated to perceive this?

NATURAL SELECTION. NEW VARIATIONS OF THE OLD SUBJECT

Though it may seem that the answer to the question 'What is the evolution of life?' has been found long ago and that there is a general agreement about it, it is not right. Most commonly you are given the following explanation: evolution is a gradual conversion of some forms of life into other ones, which takes millions of years. This answer is not wrong. However, if your interlocutor asked whether evolution is a directional process and, if it is, what is then that direction, it would be more difficult to find an answer for there is no general agreement. For Darwin, evolution is a more-or-less directional process. As I have already mentioned, many neo-Darwinians and particularly experts of population genetics do not see any distinct direction and for them evolution is driven by accidental climatic factors and non-directional genetic variability.

As for me, I keep to old views and think that evolution is a directional process. To my mind, treating evolution as a thermal motion of molecules controlled by a merest chance is some misunderstanding. It is quite possible that neo-Darwinism is not inclined to acknowledge any directedness of evolution just because it has rejected any ecological context. If there is no ecological context, then where constraints, which possibly are the only responsible for the directedness of evolution, should be searched for?

The word 'evolution' always arouses the following graph in my head (Fig. 24).

This kind of an attitude raises certain questions. What are those parameters that change directionally through evolution? What are evolving - structures (genes, macromolecules, cells, organs, individuals, populations, ecosystems) or functional parameters of those structures? Finally, what are those forces that give a direction to evolution? I think that evolving are many structures: genes, macromolecules, etc. up to ecosystems and the biosphere. Besides, it is not only structure what changes, but functional parameters, too, for structure is inseparable from a function. However, just few regard evolution this way. Many of orthodox neo-Darwinians maintain that evolving are only genes,

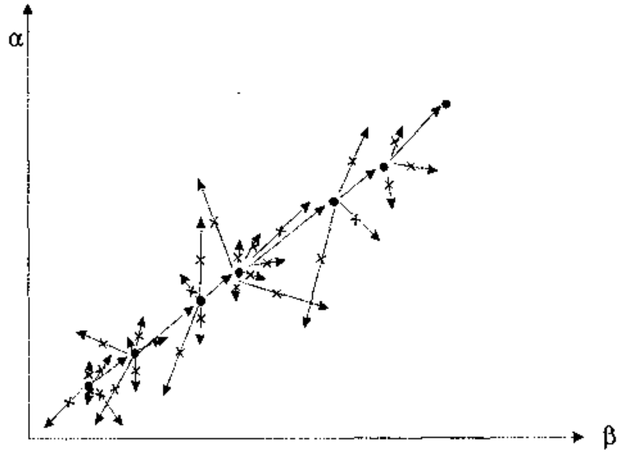

Figure 24. I regard evolution a more or less directional process. Here α and β are certain parameters characterising life and the crossed arrows are inherited variations eliminated by selection (Lekevičius 1986).

genotypes, and gene pools and along with them - features, individuals, and species. And as to ecosystem evolution, it is absent at all according to the attitude widespread now. At the beginning of this book (p. 8) I have quoted an opinion of science historian F.B. Golley that the words 'ecosystem evolution' have no sense. This is also how representatives of neo-Darwinism themselves, for instance Ridley (1996), think:

'A change in the composition of an ecosystem, which is made up of a number of species, would not normally be considered as evolution.'

Luckily, not all evolutionists are of this opinion. At least two or three decades ago this opinion would have attracted strong criticisms. But I think that I have had already enough discussion with real and supposed opponents. So, let us go on with our story about evolution and natural selection. I would like the reader to have a look at Fig. 24 once again. If you do not find any great faults with it, then you will probably accept one more scheme (Fig. 25).

Thus it comes out that natural selection is that 'black box' turning non-directional inheritable variability into a more-or-less directed evolutionary development. This is an essential attribute of selection. Differential survival and that kind of reproduction are merely external and most obvious features of selection. Quite possibly, selection may have another external form, too, but anyway it is the force constraining inheritable variability in a specific way.

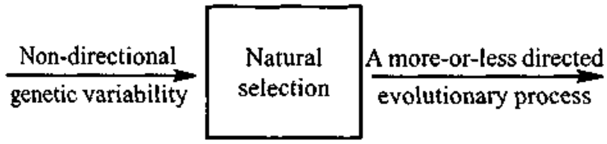

Figure 25. Natural selection turns non-directional genetic variability into a more-or-less directed evolution. In other words, mutations and recombinations create a field of potential evolutionary possibilities, whereas selection constrains it in a specific way. Thus, it is likely that what we call natural selection is nothing but functional constraints (Lekevičius 1986).

Somebody may think that there is no great difference between constraints or differential survival and reproduction. May be the difference is not great, but it is essential: traditional attitude emphasises selection units and cares *what* is selected, whereas I suggest taking an interest in what *is making selection.* When we say 'constraints', a natural wish arises to find out the origin of those constraints and what is constraining and directing what. In other words, I suggest paying attention to the forces inducing differential survival and reproduction (and possibly not only them). Besides, when evolution-directing forces are known, it should not be too difficult to find major directions of the evolutionary process, too, which is no less important.

Life is a functional hierarchy, though, as I have already written, not rigid. I have also mentioned that a functional hierarchy is impossible without co-ordination, i.e. specific constraints arising from either a control centre or an interaction of structures equivalent with regard to control. I would like to relate the earlier ideas with those just presented maintaining that those co-ordinative constraints are mostly what we are used to call natural selection.

I will illustrate a conception of selection, which possibly is new, with an example. Males and females of the same population usually compete and co-operate simultaneously. Co-operation is inevitable, since non of sexual partners can fulfil the function of reproduction without another partner. However, when resources are lacking there might develop a heated fight between former partners. So extraordinarily briefly could be described relations between sexual partners in *modern* species. On the other hand, biological time and biological space are inseparable: functional dependence of partners gives rise to evolutionary dependence (co-evolution). And evolutionary freedom may manifest itself on such a scale on which functional dependence is not rigid. Evolutionary changes in males and females should be mutually co-ordinated, but this does not prevent them from accumulating the genes enhancing competitiveness of each of the partners. So, here we have two kinds of constraints: one of them forbids losing the co-adaptation required for reproduction, whereas the other serves an individual's interest. Non-directional mutations and recombinations do not disappear. They drive sexual partners from generation to generation in hardly predictable directions, with permanently operating functional constraints that do not allow chaos to set in. If there was just competition in populations, there would be no complementation and even more so a functional interdependence, and eventually there would be left but a single 'wild' genotype in each population, and sexual dimorphism would also disappear.

Such kind of logic fits ecosystem level, too. In natural ecosystems, species are functionally dependent on one another, thus they could not be independent in their own evolution. Ecosystem constraints direct the evolution of species in such a way that they should not lose co-adaptation. The main ban at this level is that a nutrient cycle should not be broken. On the other hand, co-existing species have sufficient functioning freedom for the accumulation of features beneficial to them alone.

So, organisms not only adapt, but also are adapted. They are not only a purpose, but also a means. Ulanowicz (1986) expressed his so apt opinion about this some time ago:

'Darwinists are always speaking of fitness for the environment. The biogeochemical cycles in which every living being participates are most assuredly a part of any creature's environment. If it were possible to quantify the autonomous attributes of communities, then one's understanding of fitness would markedly improve.'

What are constraints that may play the role of selection in general? I think there can be various attitudes towards this question based on a researcher's objectives. For simplicity, all constraints could be divided according to organisation levels:

- internal or intraorganismic constraints;
- intrapopulational constraints;
- biocenotic constraints;
- constraints imposed by non-living environment.

This means that constraints of inheritable variability emerge as a result of the interaction of:

- intraorganismic structures (macromolecules, metabolic pathways, cells, organs, and organ systems);
- individuals of the same population;
- species of the same ecosystem;
- organisms and non-living environment.

Of course, we may speak about, let us say, thermodynamic constraints, too, which are not included into this list though they also decide much in the functioning and evolution of life.

Irrespective of such a multitude of constraints, a statement could be made that there must have been just two major evolutionary lineages: species evolution and ecosystem evolution. The thing is that subindividual structures are not free enough with regard to functioning to form independent evolutionary lineages. Likewise an individual can not exist without other representatives of the same species (though this is far from being typical of all species). Individual species or populations, on the other hand, are quite independent structures. Independent at such an extent that they have a possibility due to selection to accumulate features beneficial to them alone. Some time ago I quite voluntary called these features 'selfish', i.e. meeting exclusively a species' interest, whereas for a community they may become even destructive, reducing species diversity and breaking ecosystem stability under certain conditions.

Still another lineage, ecosystem evolution, emerges due to the fact that only ecosystems are independent in the literal sense of the word, and the ecosystem of ecosystems (the biosphere) is absolutely unique in this respect. Such an attitude towards evolutionary lineages is resulted in by an understanding that there are principally just two forces in living nature - biotic repulsion and biotic attraction. Ant it is just in populations and ecosystems that the existence and collisions of these oppositely directed forces is most obvious.

Differences between those two evolutionary lineages would become more distinct if we talked about evolutionary progress and fitness. From the point of view of a phylogeny expert, evolution is a process of species progress from protobionts to humans. Humans are the fittest species on Earth, the top of evolution. From the point of view of an ecosystem evolution expert, all species, even the most primitive ones, co-existing in the same ecosystem are equally well fit, each of them - for its own niche. Such an expert would relate evolutionary progress with an ecosystem biomass or another indicator and by no means to a supposed or real superiority of certain species to other ones. And if he or she would, then the top of evolution would most probably be considered woody plants rather than humans.

I tend to call one of those two evolutionary lineages - coenogenesis (or ecosystem evolution) - a non-Darwinian evolution, too, thus emphasising its difference from phylogenesis or the Darwinian evolution. However, as we will see later, both of those evolutions are driven by the same natural selection and their differences are in to whom the selected features are beneficial - species and the whole community or just species. Thus, the division into Darwinian and non-Darwinian evolution does not mean that there exists one more evolution controlled by absolutely different mechanisms.

Now I will try to describe the way from a single mutation, or recombination, to the appearance of a new ecosystem with new features. It is quite a long and complicated way, but I hope the reader will be attentive and patient enough to hear me out.

As we already know, genetic variability is non-directional or almost non-directional. Mutagenesis and recombinations are probably the only processes in living organisms subjected to non or, to be more precise, almost non of functional constraints. Here there is no 'supreme' co-ordination on the part of phenotype. So that functional constraints would begin to operate, a just established single mutation (recombination) should leave the sphere not subjected to co-ordination, which may happen not before it is activated in some way. The role of activation is played by:

- transcription and translation of the newly emerged variation;
- mitosis of the cells bearing the novelty;
- multiplication of the mutant (recombinant) and increase in its frequency in a population;
- growth of the population containing the novelty and extension of the species ranges;
- rise and spread of new races and species bearing the novelty.

Thus a single mutation (recombination) finds itself in a zygote, which in other respects is the same as milliards of other zygotes, and with a bit of luck may be multiplied, i.e. strengthened to a degree enabling the appearance of a new ecosystem bearing the new features. However, in order to understand how this happens let us keep to the sequence of events and begin with the formation of a mutant (recombinant).

Usually it is a long way from a mutation to a mutant. A mutant is a mutated individual. It has already got through intraorganismic selection. The latter should be understood as biochemical and physiological constraints preventing from the appearance of a functionally non-vital embryo or adult organism. The constraints resulted in by intraorganismic interactions are so strict and abundant that scarcely any mutation or recombination turns into a mutant or a recombinant. It is just mutagenesis, and by no means mutantogenesis, that is a non-directional process. The outer manifestation of internal selection usually is the mortality of embryos and new-borns. However, possible also are more delicate selection effects, too, such as the turning of mutant genes into 'silent' loci.

When a novelty successfully clears the hurdles of internal selection, it becomes a mutant (recombinant). But then it faces new ordeals posed by non-living environment: it should be resistant to cold, heat, droughts, etc. Those unfavourable environmental factors inevitably eliminate some of the new mutants from a population. Nevertheless, some of them live through thanks to their resistance to those factors. Then they are involved into the stage of co-adaptation. Here I mean intrapopulational and biocenotic constraints. The fate of the new mutation is further decided by its contribution to an individual's ability to find food as well as to using it efficiently, competing with individuals of the same and other species for resources, and escaping the pressure of predators and parasites. But even if those constraints, too, did not kill our mutant, this would guarantee just its survival and not reproduction. In order for an individual to reproduce, in many species a compatibility of a male and a female, their co-adaptation, is required. These are new co-ordinative constraints, and this time - populational. Similar co-adaptation occurs in all the species where the 'division of labour' is prominent.

Finally, let us suppose that our mutant has not only began to reproduce successfully spreading its features within the population, but also turned out to have many good 'selfish' features, i.e. those that have not only increased the frequency of the genotype, but also promoted the growth of the population and the expansion of its ranges. Then the stage comes when the novelty becomes a mighty force able to change features of the whole ecosystem. The ecosystem, however, responds to the appearance of the novelty as to an internal stress - prior to this it was in a stationary or almost stationary state, and a new disturbing form has emerged like a bolt from the blue. During this stage, the fitness of the new form for the ecosystem as a whole, which fulfils certain general functions, is tested. Two extremes are possible: either the spread of the new form is stopped, or the form spreads further. In the latter case, the new species may exclude other species or at least contract their ranges. The appeared vacant niches will make conditions for our species to form new ecotypes, races, and a bit later - new species, each of them bearing the mutation (recombination) that has set the stage for the whole course of events. A single mutant protein molecule in the beginning, it may be multiplied millions or milliards of times at the end, to be strengthened to the greatest possible limit. Understandably, in nature in addition to such extraordinary successful genetic variations there originate less successful ones, which are far more numerous and which climbing up the levels of organisation stop halfway thus creating a stock of 'selfish' features. This stock helps the species to evolve.

I have called this course of events cascade selection (Lekevicius 1986; 1987). I consider this term quite good, though I would like to emphasise that principally it means nothing but the same natural selection, just with extended action fields and detailed forces deciding the directedness of the evolutionary process. The above conception of mine is presented in a somewhat simplified form. So, if the reader gets interested in it or has any questions with regard to it, he or she is welcome to get acquainted with primary sources.

Though, as mentioned, the aim of this monograph is to present my own position on evolution and not that of other authors, here I have at least to mention those evolutionists who have thought and written about evolution like me, and the majority of them - earlier than me. The role of biocenotic and ecosystemic constraints in evolution has been described by Shmalhauzen (1968) and Bock (1972, 1979). Some others -Timofeef-Resovsky *et al.* (1977) - have been very close to the idea of cascade selection. There should be also mentioned Riedl (1977), Weill and Reynaud (1980), Alberch and Oster (Alberch 1980; Oster & Alberch 1982) and Godwin and Webster (1981), who have introduced the modern conception of internal selection into biology. Wynne-Edwards (1962) has developed the conception of group selection. Stanley (1975) has described the possibility of species selection. Dunbar (1960) and Lewontin (1970) have developed the conception of ecosystem selection. There have been even more authors and works directly related with my idea of cascade selection (for review, see Lekevicius 1986). Here, however, I would not like to talk about who of us has made the greatest contribution to the formation of this attitude or who should be given priority in one case or another. I consider that almost all conceptions of these authors are undoubtedly fruitful and extend our attitude towards evolution. I have certain reasons to assert that in order to make an integral and exhaustive picture of what, finally, this selection is and how it works, it would be best of all to get acquainted with my concept of cascade selection, since it is synthetic with regard to other conceptions.

I can not ignore the problem of selection units. Extremist neo-Darwinians suggest that a selection unit can be just a gene ('selfish gene'). Still others consider that genotype suits this role better.

There have been evolutionists maintaining that differential survival may involve entire populations (species) and even ecosystems. Thus, there have been attempts not only to discover evolutionary mechanisms of individual features, but also to explain how parameters specific to populations and ecosystems could have evolved. So, there has been a hope finally to find out how nature creates and maintains biodiversity and, based on the latter, societies and nutrient cycles.

Still others suggest to combine all these ideas rejecting the mentality of 'either-or'. Thus the idea of hierarchic, or multilevel, selection has arisen (Williams 1966; Gould 1982; Wilson 1997; Gould & Lloyd 1999; also see Keller 1999). It suggests that differential survival involves all or almost all structures from single genes to entire ecosystems. As far as I understand, those evolutionists do not doubt that evolving are not only individual features, but also populations, ecosystems, and even the biosphere. However, they consider that adaptation at any level requires a process of natural selection operating at that level. I think that here they make an essential mistake for they restrict the problem of selection to the question of what is being selected and are little interested in what is making that selection. Because of that the problem becomes quasi-complicated and, unfortunately, insoluble.

Basing on my model of cascade selection, I am inclined to think that Darwin, however, was right in considering that it is an individual that should be regarded the major selection unit. These are individuals who survive or die and leave offspring, whereas evolve all the structures inheritable variations of which affect the survival or reproduction of an individual - macromolecules, cells, and other intraorganismic structures and functions. Species (populations) and ecosystems evolve selectively affecting the survival and reproduction of individuals forming them. So, in this case, too, a selection unit usually is an individual. It may seem that after all individuals of a certain species become extinct or a certain population becomes widespread to split into two independent species, a qualitative leap occurs. However, from a point of view of a theorist, there is no quantitative leap at all: in the former case selection weakens certain features to a logical minimum, whereas in the latter it strengthens them.

As I understand, the problem of selection units has become so complicated and intricate because it has not been related with functional biology. Researchers are hindered by a wall built between biological time and biological space. If the wall was pulled down, the problem would immediately become quite simple and clear. The greater is the integration of constituent parts of a biosystem, the greater is the possibility that selection will affect the whole system as a unit. And on the contrary, if constituent parts of a system are functionally autonomous, they will be involved into the ever-lasting 'struggle for existence' and each of them will become a selection unit. Even ecosystem selection would be possible, if ecosystems functioned like real superorganisms. However, such a state can not be pretended to by either populations, or ecosystems. By the way, already Rosen (1967) has solved the question of selection units in a similar way, but his point, apparently, has not been seen.

In the context of this book, the conception of group selection is among the most important. Its author Wynne-Edwards (1962) has ascertained that individual, or

Darwinian, selection is unable to make co-operative connections between individuals, though such connections are widespread. Thus, in addition to Darwinian selection, which serves an individual's interests, group selection, i.e. differential survival of entire groups (populations), should manifest itself in nature as well. In the latter case, features favourable for the whole population rather than for single individuals are selected. Later this idea has been extended to cover a differential survival even of entire ecosystems or communities. However, recently, as elder-generation ecologists and evolutionists have become fewer, the above ideas have principally been abandoned for lack of empirical data basing them. For me, too, it is difficult to conceive a differential survival of entire groups and ecosystems and communities. It is no easier to think up how selection can accumulate features beneficial to a group, but harmful to an individual, with an exception of those quite rare cases when that to suffer is a close altruistic relative, thereby enhancing the spread of its genes. Here I have in mind the so-called kin selection. In all other cases non-compromise altruism can hardly be promoted by selection. What is favourable for a group or an ecosystem should first of all be favourable for an individual itself. In a word, I think that for protocooperation or co-operation to appear at the level of both population and society, the extravagant way suggested by V.C. Wynne-Edwards and his adherents is not necessary. For the purpose, individuals of the same and different species should simply interact, which they do all the time. It is this interaction that makes specific constraints deciding the survival of some genotypes and the elimination of other ones. These are individuals that survive and reproduce, whereas those that evolve are populations and ecosystems.

HOW SELECTION HAS MADE ECOSYSTEMS CONVERGE

If there was a possibility of visiting rainforests of South America, Africa, and South East Asia and comparing those ecosystems, our knowledge about them would possibly change in the following order. First, we would most probably see only differences - each of those ecosystems is inhabited by its own species - and we would hardly find a plant or an animal species common to all the three continents. A more detailed research would show not only specific, but also common features. It is likely that soon we would pay attention to the fact that in those ecosystems there are plenty of equivalents - species that live in different continents and are little kindred have become morphologically similar. May be we would find out the causes, too, i.e. that those species have become similar because they have occupied either the same or at least very similar niches. Started to investigate the niches, we would discover that the set of the niches is similar in all the three continents. Finally, we would probably be even more surprised at the fact that all those geographically distant ecosystems have absolutely similar production pyramids. This phenomenon, similarity of geographically distant ecosystems, ecologists call the functional convergence of ecosystems.

The functional convergence of ecosystems has been discovered quite long ago. Already in 1957 P.J. Darlington wrote in his book 'Zoogeography: The Geographical Distribution of Animals':

'Neither the world nor any main part of it has been overfull of animals in one epoch and empty in the next, and no great ecological roles have been long unfilled. There have always been (except perhaps for very short periods of time) herbivores and carnivores, large and small forms, and a variety of different minor adaptations, all in reasonable proportion to each other. Existing faunas show the same balance. Every continent has a fauna reasonably proportionate to its area and climate, and each main fauna has a reasonable proportion of herbivores, carnivores, etc. This cannot be due to chance.'

A bit later similar conclusions have been drawn by other biologists, too: H.A. Mooney, M.L. Cody, J.M. Diamond, J.H. Brown, and some others. Facts of convergence were so impressive and unbelievable that Cody (1974) could not restrain from writing:

'Such a degree of convergence gives reason to believe that there is a single optimal way of dividing up the resources.'

Here I would like to draw the reader's attention to one important, as I think, episode from the history of general ecology. It is known that the conception of an ecosystem was developed based on empirical data in the 1960s of the last century. For the purpose, especially useful were the data obtained by those pursuing the International Biological Programme. Thousands of scientists from different countries investigated local ecosystems according to standard methods. The data obtained were collected at one centre in order to discover some regularities. And it did not take long for those regularities to come out: it turned out that the majority of world's ecosystems have a surprisingly similar structure and, seemingly, similar nutrient cycles. It was discovered, for instance, that neither the number of trophic levels, nor ecosystem structure in general are dependent on primary productivity, which is known to vary within very great limits on a world scale. Luckily for ecologists, in that respect nature turned out to be quite unified. Otherwise, individual conceptions would have had to be developed for individual ecosystems. Thus, ecosystem convergence was a trivial fact for that-time ecologists.

Time passed and elder-generation ecologists retired one after another to be changed by young people interested in other problems. That was possibly due to the fact that in those times it was not easy to explain facts of the functional convergence of ecosystems, since they were hardly within the framework of the neo-Darwinian paradigm. It was difficult, or, according to somebody, impossible to build a bridge between a change in gene frequency in a population and a global phenomenon such as ecosystem convergence. It was 'common knowledge' that each species is affected by a multitude of internal and external factors and that its fate depends not only on an accidental genetic variability, but also on a gene drift, climatic changes that are usually difficult to forecast, the effect of other species, and other difficult to describe events. During millions of years those abundant factors must have probably developed such a chaos of consequences in living nature that non of theorists was able to explain it. In a word, there was an opinion, which by the way exists nowadays as well, that evolution is controlled by accidental forces and that it can not be predicted. This is why the phenomenon of ecosystem convergence was and is out of place in the neo-Darwinian conception. On the contrary, facts of convergence rather than supporting neo-Darwinian experience contradicted it. However, it is known that facts do not necessarily break theories. It is often the other way round - facts contradicting a generally accepted theory are simply ignored. Thus, it is little surprise that in the course of time an interest in that phenomenon gradually decreased. It is difficult to say what the ecologists who first discovered the phenomenon of ecosystem convergence thought, but it is almost beyond any doubt that they were acquainted with neo-Darwinian dogmas and had to obey them. Hence, they refused any attempt to search for the explanation of that phenomenon. Thus, those who had started the game withdrew from it. By the way, at present some non-conformist researchers show up still considering that sphere worth attention and attempt (e.g. Valiente-Banuet *et al.* 1998).

Has it been so or not - this is just my own version. But let us leave facts of recent history in peace and pass to the explanation of convergence itself. First, we have to agree about definitions. In this book, I suggest to use the notion of the functional convergence of ecosystems in a little wider sense than that used by my colleagues some 20-30 years ago. It is becoming similar, but not only with regard to production pyramids, but also to the whole ecosystems structure and nutrient cycles. Sure, I have in mind invariability as to both time and space, which has been described by P.J. Darlington. By this I do not maintain that ecosystems have not been changing through time - we know better than anybody else does that they have, thus their structure and nutrient cycles have been changing. However, I am inclined to consider that approximately 2 milliard years ago ecosystem metabolism finally became settled and since then nutrient cycles have been just replicated. The evolution of ecosystem structure took longer: it was over in the Ordovician in water and in the Carboniferous on land. Since then ecosystems have maintained the invariability of both functions and structure, despite all internal changes followed by adaptive radiation and extinction.

Besides, when we use the notion of the functional convergence of ecosystems, we have to have in mind the convergence at the level of individual species, too, i.e. a great abundance of ecological equivalents - species that are little kindred and live in different locations and that have converged due to living in similar niches. In 'Scene 17', I have pointed out some known Australian marsupials and their placental equivalents from other continents. Here is an example of still less kindred equivalents: sharks, ichthyosaurs, dolphins, and penguins. It is possible to present many analogous examples. There is no doubt that the convergence of entire ecosystems and that of individual species is a result of the manifestation of the same forces and therefore those phenomena should not be separated from one another.

I will try to tell my view about what forces made ecosystems converge. I would like to calm the reader down - for the purposes no additional theoretical doctrines will be required, we have all we need: methodology and the theory itself.

Let us start from the appearance of life. The very first ecosystem, as we already know, most probably were made of one living block - detritivores, represented by protobionts, and non-living surroundings, where the main role was played by 'soup'. If it really was the case, then the evolution of protobionts should have been constrained and directed by the qualitative composition and concentration of the 'soup', in addition to other factors. If protobionts had been using the 'soup', they should have had to provide themselves with the enzymes specific as to the organic matter dissolved in water. The appearance of such enzymes had been promoted by selection also because protobionts, having converted into detritus, obviously replenished the 'soup' with similar materials, which could again be at least a source of materials if not energy to those living. All activities of protobionts on the global scale were restricted by the rate of chemical evolution, which seemingly was far lower than that of 'soup' consumption. In the nearest surroundings of protobionts, products of their activities, inorganic and fine organic compounds and molecules of which the 'soup' had been previously synthesised, became more and more abundant. That disbalance between synthesis and decomposition created a powerful selection pressure that directed the evolution of protobionts towards autotrophy. Any mutation or recombination giving at least the merest possibility to use those products of protobiont activities as a source of materials for synthesis turned into a mutant that had very many chances to reproduce and spread. This is how the first photosynthesisers eventually emerged. One may think that soon after their appearance photosynthesisers had to exclude their antecedents that fulfilled the function of detritivores, but it was not so, because the latter were not competitive with the former. On the contrary, detritivores became allies of photosynthesisers as they maintained photosynthesis by supplying the required inorganic and fine organic substances. However, that alliance could have hardly been without shortcomings, for photosynthesisers synthesised new materials absent in the 'soup' for their own purposes, and protobionts, too, did not synthesise them. At that time, those materials could have been bacteriochlorophylls, carotenoids, and peptidoglycans. The new materials accumulated in the detritus formed of photosynthesisers, thus they made new vacant niches for detritivores. Those niches became evolution-directing factors, so after a while there should have emerged the enzymes catalysing the decomposition of those materials. It is natural to think that that evolution lasted until finally all of the new difficult to decompose compounds were converted into biogenes, i.e. materials no longer useful to something with an exception of photosynthesisers. The cycle became closed, non-waste again.

In this evolutionary episode, hypothetical as it is, it is difficult to make out any preliminary purpose sought by evolving organisms. Everything happened on its own as self-organisation, based on inheritable variability and species interaction directing it, occurred. In that case, like in many others to follow, a very simple rule was in force: vacant niches can not be unoccupied for a long. 'If there is a free lunch to be had, someone (or something) will eat it' (Olsen 1999).

In other words, after new pairs of oxidants and reductants appear, sooner or later there should appear organisms to benefit from this, i.e. use those pairs as a source of energy or energy and materials. I think that this rule of 'the occupation of vacant niches' explains quite well how organisms that, seemingly, are trying to receive benefit for themselves only make combinations of mutually beneficial species on evolving. And there is no *deus ex machina,* no *demiurgos.* When I speak about the specific to ecosystem level functional constraints that perform the role of selection, I mean the interspecific interactions of the just described type - when some species directly or indirectly affect the evolution of other species.

The situation in evolution has not always been such a comparatively simple one like in the example with the first photosynthesisers. There have been more complicated cases, too, for example, when cyanobacteria right after their appearance began producing oxygen. Then everything that had been created for such a long time was under the threat of perdition. Most possibly there should have occurred a mass extinction of anaerobic forms. Oxygen became a mighty selective factor directing the evolution of life towards oxygen resistance. However, other events should be pointed out, too. Being an extraordinary useful oxidant, oxygen along with the multitude of reductants that had existed before made almost an indefinite number of vacant niches, which after a long evolution were occupied by aerobic organisms among which there were both producers (photosynthesisers and chemosynthesisers) and detritivores.

Was it possible or not to predict the rise of oxygen resistance and aerobic respiration? I think it was, though that would have been just a general and not detailed prediction. One may say that it is easy to make *a posteriori* forecast, for this does not require much knowledge. But how lucky would you be in predicting events that still are to happen? We should agree that it is a sound reproof. My excuse is only one: I do not consider the above described episode of oxygen appearance and the evolution of aerobes unique, but rather one of many analogous situations, which have been so numerous through evolution and all of which show that life tends to produce new materials and the latter usually make vacant niches. The niches are to be occupied. And it is just this principle which is a tool of forecast or at least of explanation. Moreover so that it is not difficult to tell what kind of a role was played by inheritable variability in those situations and what constraints of that variability - permissions or prohibitions - were acting.

3-2.5 milliard years ago there should have seemingly been a great deal of both reductants and oxygen. First of all I mean ferrous iron and bivalent manganese, sulfur, hydrogen sulfide, hydrogen, carbon monoxide, methane, and ammonia (see 'Scene 7'). Although it was 'spare food', organisms able to use it appeared just after a while. It is likely that at first the reaction of those reductants with oxygen was carried out by itself without any interference on the part of life, and the energy produced in the form of heat dispersed in space. So, along with abundant prohibitions (to acquire no enzymes that have no substrates in the medium) there were many concrete permissions (to acquire enzymes able to make those oxidation-reduction reactions act to an organism's advantage). Genetic variability should have made a far-reaching field of evolutionary possibilities for organisms seeking those niches, whereas merciless selection gave a licence to live just to those scarce mutants that were able to meet strict requirements made by the environment. There were many of those invited and very few of those selected. Eventually there emerged all known to us groups of aerobic chemolithotrophs exactly corresponding to the set of vacant niches. All other parts of the field of possibilities were blocked by strict prohibitions.

Chemolithotrophs appeared not in order to please that-time detritivores or other autotrophs. They tried to attain just their own purposes, though it is likely that their appearance was a general benefit: they helped to accumulate a greater biomass in ecosystems and form more effective nutrient cycles, which in general have not changed until today.

Why those cycles principally have not changed during the past 2 milliard years? Probably because there were no important factors constraining the growth of the biosphere biomass during that period. The thing is that in the cycles innovations occurred the moment life reached the 'ceiling' of its development or when there were produced waste, which made vacant niches. After life began using carbon dioxide as a carbon source and atmospheric molecular nitrogen as a nitrogen source, after no unused though potentially suitable inorganic compounds were left, after the cycles became non-waste or needed just unimportant corrections to become such, it was absolutely unnecessary for life to change the cycles. Such a need has arisen, if at all, just recently (according to geological scale).

Life conquering the land 600-100 million years ago, nutrient cycles were copied from those that had been existing from long ago in water, or, to be more precise, in the biosphere. Irrespective of external differences, 400 million years ago terrestrial organisms began carrying out principally the same metabolism that had been carried out by their aquatic analogues from more ancient times. And though just few species of those times have survived unchanged until nowadays and the majority of them have been excluded by those that emerged later, the cycles themselves have remained as before. They have not changed through such a long period of time not because genetic variability has possibly been exhausted. The latter worked ceaselessly and thanks to it countless variations were thrown into the forge of evolution, though non of them have left any marked trace in nutrient cycles. It could even be asserted that throughout that period at that global level a stabilising form of selection was in force and it rejected any deviation from the nutrient cycle tested by time. Indeed, as M.L. Cody has suggested, there possibly is the only optimal way of allotting resources and functions, and it has been not without the reason that nature has sacrificed almost two of the first milliards of years in order to find that way.

Let us discuss the mechanisms of the convergence of another feature of ecosystems - community structure. Life having appeared approximately 3.8 milliard years ago, there were just two living blocks for quite a while - producers and detritivores (see Scenes 3-7). The former produced organic matter, which was decomposed to inorganic one by all organisms of ecosystem - producers and detritivores. Detritivores were able to decompose non-living organic matter only, so they had to wait until the organisms carrying out functions of producers would die a natural death. Producers and detritivores in a sense still were vacant niches - in fact those organisms were exploited just after they had been converted into detritus, though as an energy and matter source they could have potentially been used prior to that, before their death. These were just those vacant niches which were occupied by the first biophages that appeared about 1.7 milliard years ago (Scene 8). It is hard to say why they had not appeared earlier. May be because, contrary to detritivores, the first biophages had to learn to overcome the resistance of a still living organism, and, besides, they had to be larger that their prey, so evolution had to 'bring them up'. It probably was not without the reason that biophages emerged just when aerobic respiration had already became almost a common feature - biophagy, quite possibly, needed a way of metabolism more effective than anaerobic one.

The formation of the biophagous block seemingly had certain regularities. Usually the first to arise were herbivores and those who fed on detritivores. (It is quite possible that the first biophages were other organisms, leading a parasitic way of life, but I am not discussing this scenario, though it is also possible). The evolution of all those biophages was directed not only by organisms that were their prey, but also by abiotic conditions. Still the main directing and limiting role in that situation was played by biotic environment. It promoted specialisation as to prey, thus quite soon a great variety of herbivores and organisms feeding on detritivores usually appeared. Then the rise and spread of those organisms promoted the evolution of typical primary predators, i.e. the third trophic level. The matter was that having occupied vacant niches, the very herbivores and organisms feeding on detritivores used to become vacant niches, which had to be occupied. Eventually the fourth and higher trophic levels used to be formed, to be inhabited by large top predators, too. As the pyramid was being formed, the species making it became hosts of parasites. Thereby, evolution created not only a certain species, but also a complex of factors stabilising its population size. After that the block of biophages was completely formed, and then if anything could have happened at all it could have been just a narrowing of niches (specialisation). Such a division of the niches meant for biophages and the final formation of production pyramids in aquatic ecosystems was completed approximately 450 million years ago (Scene 11) and in terrestrial ecosystems - some 300 million years ago (Scene 14). Later, irrespective of various perturbations, the shape of pyramids either did not undergo any changes at all, or, like in the Paleogene, was immediately restored.

Why the formed set of organisms carrying out biophagous functions was of that and not another kind and why was it formed in exactly that and not another sequence? Because the already mentioned biological constraints should have been probably in force: producers and detritivores directed the evolution of the first biophages and the latter - that of the primary predators, and so on and so forth. Surely, there also was a contrary impact, which was made by a higher trophic level on a lower one: organisms that had become prey acquired different means of protection from herbivores and predators, means that were both morphological, or physiological, and behavioural. All of them aided victims in reducing loss due to biophagy, thereby increasing their reproduction efficiency and turning a unilaterally beneficial partnership to co-adaptation. Co-adaptation, on the other hand, is nothing but even more strict inter-constraints. However, throughout the period of life existence, in addition to biological constraints there should have been non-biological ones, too. Species composition of biophages of a particular ecosystem and especially species numbers at different trophic levels as well as their biomass and production were determined by thermodynamic constraints. A typical generally replicated production pyramid could not be of a different shape just because throughout evolution in addition to biotic constraints thermodynamic ones, too, continually were in force. Due to the latter about nine tenths of energy present in food were converted into heat, thus merely one tenth could have pass to a higher trophic level. As it is known, according to that rule there have never been more than five or six trophic levels, and top predators had to feed on different kind of food so as not die of hunger. Sure, those constraints affected not only the evolution of predators, but also that of producers and detritivores. Because the nature of all those constraints is quite simple and clear and, what is more, invariable, it should not be too difficult for an evolutionist to explain the evolution of life and forecast its development. That kind of explanation will never be final and forecast - very exact, for many things on earth have been and will be beyond cognition.

For easier understanding of how co-existing species direct the evolution of one another and finally make standard pyramids, let us analyse examples from a comparatively recent history of life.

In 'Scene 17', which is meant for the Paleogene, I have attempted to describe how, after the majority of reptilians became extinct, production pyramids were devastated and how those pyramids were restored by the adaptive radiation of birds, mammalians, reptilians, and amphibians. The main stimuli of that radiation were niches having become vacant after the mass extinction. In about 10 million of years a great many of mammalians and birds, which performed herbivorous functions, came into existence, and right after their appearance they themselves became vacant niches for future predators. A rapid radiation of predators occurred, which gave a rise to flying and non-flying birds, terrestrial crocodilians, creodonts, and predatory marsupials. Because vacant niches were sufficient, amphibians radiated as well, but they had to content themselves mostly with insectivorous roles, for other niches had been already occupied by others. Lizards and snakes produced hundreds of species, though, similarly to amphibians, just small predators. Why in the Paleogene amphibians and reptilians did not manage to repeat the scenario typical of the Carboniferous (amphibians) and the Triassic (reptilians)? I think that the answer is obvious: in the Paleogene those two groups met stronger than them rivals, which were evolving faster and were more efficient in their niches. The inheritable variability and evolution of amphibians and reptilians were directed in those directions that, we may say, had been left by mammalians and birds. Therefore, after the wave of adaptive radiation settled down we could see a picture, which simultaneously was common and strange: production pyramids were restored and looked very similar to those in the Cretaceous, but at that time the same niches were occupied by absolutely different, little kindred extinct species. This could hardly be accounted for coincidences - in that case invariant biotic and abiotic constraints, including thermodynamic ones, should have been in force. Interestingly enough, in different continents, especially those reliably isolated from one another, similar niches were occupied by different, little kindred organisms, and this is why each continent acquired a unique set of equivalent species already in the Paleogene. Is it possible that in that case, too, according to some modern evolutionists, there was a mere non-directional inheritable variability and no directed selection?

On many of volcanic islands situated thousands of kilometres from continents, in the recent several million years or in such a short period of time as several hundred thousand years uncommon endemic flora and fauna have been formed (I apologise to the reader very much should the further presented facts about the episodes of adaptive radiation on volcanic islands be inexact, for they have been taken mostly from textbooks and surveys: Darlington 1957; Cox *et al.* 1973; Grant 1977; Pianka 1978; Raven *et al.* 1986; Wilson 1994; Paulay 1994). Let us begin with flora. Those distant islands are hardly reached by plant seeds from continents. This is especially difficult for plants of certain families, particularly woody. This is easier for plants of the families Asteraceae and Campanulaceae. Their seeds carried by the wind can spread rapidly and widely. Many of you have possibly seen how easily the wind carries the parachutes of a dandelion - this plant is one of Asteraceae. Plants of those two families are also exceptional for they are very adaptive, likely to play any evolutionary trick. So, an island having emerged of the ocean, in the time being the wind accidentally brings the first seeds of herbaceous plants. Here they come up and facing no rivals become widespread and after a while start producing various herbaceous forms. Still after a while woody plants emerge from herbaceous forms. At first a single mutant or recombinant appears to multiply and spread rapidly within a population later. Woody plants exclude part of herbaceous representatives of the species and begin to expand their ranges by excluding other species. Still later there originate various forms of bushes and trees adapted to different climatic, edaphic, and light conditions. Ecosystem responds to those changes as to an internal disturbance, threat of disbalance. A great reserve of non-living, hard to decompose wood is accumulated, and some time having passed this niche is overwhelmed by detritivores producing new, specialised for wood decomposition, varieties. Thanks to those and other evolutionary rearrangements the balance is restored again. On the islands, evolution once again enters the stage of a relative peace. Thereby, entire forests and shrub stands have been formed on many of volcanic islands from not very common to us antecedents.

A vacant niche is permission, whereas occupied - prohibition to evolve. Probably, the genetic variations that provide herbaceous representatives of those families with the features typical of woody plants of other families appear through mutagenesis not only on islands, but also in continents, though mutants bearing those variations can not survive - they are not allowed to do so by the old species of trees and bushes well-adapted to local conditions.

Of this group of plants, which took part in the above-described evolutionary adventure sometime in the past, group Madiinae inhabiting Hawaii, comprising 28 endemic species, that originated from one herbaceous form of Asteraceae, seems to be best investigated. Among those species there are not only very different herbaceous plants, but also bushes, lianas, and even real trees. Surprisingly, all those dissimilar species still interbreed among themselves, which most probably indicates that the divergence has occurred quite recently and has not been finished until today.

Campanulaceae plants have also got into Hawaii. Having found non of their common rivals, Orchidaceae, common in continents, they radiated producing 150 endemic species and varieties, making nine genera. Among them, there are rather small herbaceous forms, more-or-less close to an ancestral one, and bushes as well as trees. In a word, plants of that family similarly to the Asteraceae co-existing with them, evolved into the woody forms equivalent to various species of other families spread in continents. And though they did not succeed to create such a diversity of woody plants like that from where they have come, in Hawaii they resulted in the appearance of forests, and accordingly the rise of habitats and niches provided by forests, which soon thereafter were made use of by other new-comers.

Insects, too, somehow have got into Hawaii. At present there are at least 10,000 endemic insects that have originated from about 400 immigrant species. Sure, those several hundred new-comers are very few to any tropic location of a continental zone. So, it is not astonishing that those species immediately radiated - niches that could have been occupied by insects were far more numerous than the new-comers themselves. Among the first insects that reached the archipelago there was one species of fruit flies. It has diverged into more than 500 endemic species. It makes one third of the species of that genus known in the world. In Hawaii, they have occupied a great many of trophic niches: some of the species feed on some plants, others - on other plants, some species exploit some parts of a plant, whereas others - other parts of it, larvae of some of them live in rotting tree trunks, still others eat fruits, bark, leaves, roots, or plant juice. Many of local drosophiles so greatly differ in their appearance and behaviour compared to those common to all of us that if you are not an expert you would easily take them for other insects. Another genus of flies very close to drosophiles is *Scaptomyza,* and in Hawaii it is represented by 300 species. Elsewhere in the world there are several more species. That genus and drosophiles are so close that there are suggestions that all those 800 (500 + 300) species have originated from a single species of flies that has got into Hawaii some time in the past.

Though Hawaiian fruit flies have proved to be able to occupy practically any vacant niche, their radiation was most probably stopped by other insects that came into the isles - 400 species in all, as I have already mentioned. Fruit flies succeeded just because they reached the isles prior to many other species. If the first comers were other insect genera rather than those flies, now we would be writing about the latter and not fruit flies. Adaptive radiation, like evolution in general, is a competition where winning is decided by many factors. So, sometimes to an outside observer it may seem that coincidences are so important there and that directional trends are absolutely impossible.

In Hawaii, lack of species was so great that some insect genera have occupied absolutely unusual niches there. For example, nymphs of one of damselflies do not feed in water, which is usual for nymphs of those organisms, but catch insects on land. In Hawaii, caterpillars of some moths do not feed on plant tissues and prefer hiding and staying in foliage waiting for a careless insect to approach - then a caterpillar snatches it swiftly with forefoot and starts devouring. The latter case possibly accounts for lack of insectivores in those ecosystems compared to many 'normal' ecosystems.

Hawaiian birds, especially honeycreepers, have attracted great attention of evolutionists as well. It is an endemic family that is made, or, to be more precise, was made of 22 species not long ago. Among those species there are such that feed similarly to goldfinches, warblers, woodpeckers, and sunbirds of the Old World. The ancestral form of all those species was the first among terrestrial birds to have reached Hawaii many years ago. It seemingly reminded of a goldfinch and fed on seeds and insects. The species came there to find many vacant niches. Particularly lacking were insectivores and animals feeding on seeds and nectar. Thus, after an instant adaptive radiation those birds occupied not only their 'own' niches, but also those that in continents are usually occupied by representatives of absolutely different families or even orders. So, they became in many ways similar to their continental equivalents.

My attitude towards the phenomena of adaptive radiation and the functional convergence of ecosystems differs from the traditional one mostly in that I consider that all evolutionary processes are rather strictly canalised. That canalising role is played by species interaction, which every time and everywhere directs the evolution of species to few invariant directions. The raw material from which evolution sculptures a community may differ and, as it could be seen from the above presented examples, usually very greatly. However, the final result - what the structure and function of that community will be like - is easier predictable for it often recurs with respect to both time and space. God does not dice, so evolution could be predicted. But for this, of course, one should have sufficient information not only about ancestral forms, but also about constraints. However, that kind of information most commonly is lacking, because until today, as I think, evolutionists have not paid great attention to factors constraining the evolution of species. Let us take the case of Hawaii, for instance. The descriptions of radiations of fruit flies and honeycreepers usually lack data on other animal groups that could have had certain influence on those radiations. For example, in Hawaii, in addition to honeycreepers, live thrushes, crows, hawks, owls, flycatchers, and some other birds, and of mammalians - bats. Though many of those vertebrates have reached the Hawaii isles later than ancestors of honeycreepers, they managed to form endemic subspecies, species, and even genera. In the absence of those birds and mammalians the radiation of honeycreepers would have probably been even wider and they would have been given rise to far greater diversity. This could be easily explained: other vertebrates were more suitable for the occupation of the majority of those niches, they were closer to the 'finish' though they had arrived later. On the contrary, later new-comers could have been able to produce a far more greater diversity if they had not been prevented by the already diverged honeycreepers.

In addition to Hawaii, there exist isles and archipelagos of a similar fate. An example of this could be, for instance, Galapagos Islands or the island of St. Helena. However, I will limit myself to Hawaii, for a description of analogous processes that occurred on other islands is of little value in the sense of theory, unless we are interested in the impact of the area of islands, their distance to the nearest continent, or climate on radiation. But since I am somewhat less interested in this, I will end with this. I will present just a couple of short notes to complement the above expressed ideas.

Like in Hawaii, in Galapagos herbaceous plants through adaptive radiation have produced not only herbaceous, but also woody forms, thus compensating lack of the diversity of local plants. However, differently to Hawaii, the climate is much dryer there, and therefore plants do not have so abundant and various blossoms like in more humid Hawaii. On the other hand, Galapagos are rich in cactuses. May be this is why in Galapagos nectar is hardly enough to provide merely one species of finches, which has to feed not only on nectar, whereas in Hawaii several species of honeycreepers feed exclusively on nectar. In Galapagos, on the other hand, there is a species of finches feeding on cactus blossoms and fruits, which is quite understandable. Other interesting facts could be presented as well. Niches of woodpeckers existed in both Galapagos and Hawaii, and birds having arrived to those islands succeeded to occupy those niches after a while. Possibly, that event could have been predicted. But who could have predicted that 'woodpeckers' of one archipelago would differ so greatly from 'woodpeckers' of the other one? The famous woodpecker finch has a beak that is completely not Picidae-like, and it picks insects out of gaps and holes not with a beak or tongue, but with a cactus spine, sometimes broken off beforehand to fit the purpose. Hawaiian 'woodpeckers', on the other hand, the same operations perform with their hooked frail beaks, which do not remind of a beak typical of our woodpeckers at all. Undoubtedly, the 'tools' of real woodpeckers are fitter for those operations, and those birds would easily exclude the amateurish woodpeckers inhabiting those remote islands if they lived together with them.

So, I agree that it is by no means easy to explain everything that has been created by nature. It, probably, is impossible at all. However, it is likely, that we being scared at the complexity of life phenomena, which most often is supposed and depends on the available methodology, tend to consider them generally impossible to be explained.

Oceanic islands usually are poor in mammalians, because the latter, except for bats, can not get so easily over wide oceans. This most likely is why the niches that in continents are usually occupied by mammalians in many of islands are inhabited by endemic birds and even insects.

To close this subject, which is one of the most important in the context of this book, I will present one more case of adaptive radiation to demonstrate once again how strong are those forces that make production pyramids to acquire a particular shape. I have in mind the cichlids of Lake Victoria (East Central Africa). This lake has originated 12,000-20,000 years ago on the formation of the present Rift Valley. Experts suggest that there was no fish at all in the lake for a certain period of time. Later birds brought fish spawn into the lake from an adjacent water body or it got into it otherwise. The fish belonged to one of cichlid species. It is likely to have been small fish feeding on plankton. Having found no serious rivals and predators in its new habitats, the species rapidly diverged producing over 300 endemic cichlids among which in addition to planktophagous there were herbivorous and benthophagous species, those feeding exclusively on molluscs or fish fry, and also large predatory fish (e.g. Sturmbauer 1998; Turner 1999). One group of closely kindred fish occupied almost all fish niches, thus forming almost the entire production pyramid to the very top predators on its own. All those species seem to get on quite well, because each of them exploit their own trophic niche, little different from niches of other species. By the way, the past tense would be more suitable than the present one in this case, for today, after the giant Nile perch was introduced in the lake, many of the cichlids have become extinct.

This example of the cichlids of Lake Victoria reminds me of another story - the restoration of the terrestrial production pyramids, devastated after the extinction of the majority of reptilians, in the Paleogene. But at that time everything happened far more slowly, and animal groups involved into adaptive radiation were quite different.

In the case of Victorian fish, similarly to the previously-described cases of adaptive radiation, a more-or-less grounded explanation of the formation of a particular set of species could be given. Concrete mechanisms, however, are covered with a mist of millenniums. And the more distant are events, the more difficult it is to discover those mechanisms. We will hardly ever find out what kind of mutations, recombinations, geological barriers influenced the adaptive radiation of invertebrates in the Cambrian, that of cephalopods - in the Ordovician, myriapods, spiders, and scorpions - in the Silurian, fish and the first woody plants - in the Devonian, amphibians - in the Carboniferous, reptilians - in the Permian, flowering plants, insects, and birds - in the Cretaceous and Paleogene, mammalians and birds - in the Paleogene, and hominids - in the Neogene. To explain why that waves of radiation produced certain kinds of species sets is, however, easier, since factors directing the evolution of species and ecosystems should be quite well known to ecologists today. Nature has invented few variants of resource allocation among species, which may console not only ecologists, but also evolutionists. We, ecologists and evolutionists, have accumulated quite much experience and may assert - evolution is a peculiar way of the self-organisation of life, which is both similar and dissimilar to other ways of self-organisation, such as ecological succession. But what is common to all those ways is the ability of species by means of interaction to discover those solutions that are more-or-less optimal.

The description of the functional convergence of ecosystems I have presented above is not exhaustive. I have not discussed some quite important factors that could have influenced the convergence as well. For example, there could have been many climatic, edaphic, and other kind of abiotic conditions the invariance of which could have also decided the convergence of species. Fish and ichthyosaurs, penguins and dolphins, for instance, are not very kindred, but habitats selected by them have been so similar that they should have inevitably left no similar traces in their body shapes. Similar examples testifying to the impact made by a habitat are very numerous in literature and it is impossible to describe all of them. It is clear, however, that abiotic factors alone can not account for the formation of a certain set of species in a certain location. The diversity of climatic and edaphic conditions on earth has undoubtedly promoted the specialisation of species with regard to those conditions. Those forces have not played the organising role, though. They have not joined accidental sets of species to make associations able to 'rotate' local and global nutrient cycles or to 'build' production pyramids. That could be carried out exclusively by biotic forces. Probably, this is why ecosystem metabolism and ecosystem structure were so little dependent on geographical latitude and climatic fluctuations during the recent two hundred million years.

THE ROLE OF COMPETITION IN EVOLUTION. THE FATE OF SUPERRIVALS

I have just attempted to show how species interaction, having acquired the form of selection, consolidates species scattered by genetic variability and how those species eventually form nutrient cycles and production pyramids. In living nature, the forces of biotic repulsion, too, have been permanently existing, however, and they rather than increasing have been tending to reduce biodiversity, destroy the set food chains, thus making vacant niches and space for more competitive species.

In earthly life, there is too much of passion for merely peaceful nutrient cycling and pyramid building. From Darwin's times we know that in every species a potency of unrestricted reproduction is lurking, irrespective of a possible impact of the realisation of that potency on other species, and, finally, on the very species bearing it. At community level a functional hierarchy and co-ordination is not so rigid as, let us say, in a multicellular organism, and therefore in ecosystems species have comparatively much freedom. Freedom to function and accordingly freedom to evolve. It is not surprising then that they realise that freedom by constantly accumulating inheritable variations beneficial exclusively to themselves. I call such features 'selfish'. Whenever such a great amount of that kind of features was accumulated that a critical point was reached, which inevitably happened sooner or later, a species that had been hiding in the dark suddenly started its expansion excluding a great number of other species. The period of species extinction began, and sometimes it acquired an incredibly wide scale.

It is considered that throughout the existence of life at least 99% of species have become extinct. So, there have been at least several milliard of them - too many to escape the phenomenon of extinction as if something completely insignificant. There are two types of extinction: phyletic and final. Phyletic extinction is a kind of extinction when one species evolves into another without remainder, thus no ancestral form is left, like no pupa is left after it turns into an adult insect. Final extinction is when a species becomes extinct leaving no evolutionary offspring. Here I will analyse just cases of the latter kind of extinction.

According to the model of cascade selection, mutants having increased their frequency within a population at best may spread further: absolute number of mutants may increase, a mutant population may expand its ranges and later diverge into two or more subspecies and species. That kind of expansion may often result in the exclusion of other species. All species are able to accumulate features beneficial to them only, so an ecological community has no counterpoise to prevent that. However, when a species having accumulated the required selfish features starts excluding other species within a community, such a counterpoise usually evolves. I have attempted to demonstrate that by more than one example. Therefore, sooner or later the expansion and radiation of the superrival is slowed down, it encounters inescapable negative feedback due to a functional dependence of the hotspur. That negative feedback is a demand to co-adapt, i.e. not to destroy nutrient cycles, to maintain a common shape of production pyramid. Often that co-adaptation is impossible without a certain evolutionary reconstruction into which not only the hotspur but also the majority of other community members is involved. And it is not before the balance is restored by common attempt that the disturber finally gets the right to exist. The superrival rums into a common species or a species group, in addition to selfish features having acquired those beneficial to the whole community.

Superrivals may originate and presumably often do that not in an ecological vacuum, but in the very depths of communities saturated with species by emerging from them as if a malignant tumour. Quite possibly it was a common case that communities did not manage to adapt themselves to superrivals for lack of both physiological and evolutionary reactions. Then the disturber itself also died, like cancer cells after the death of their host. Due to their temporality those episodes do not seem to have been included into the palaeontological chronicle we have been using.

Based on the model of cascade selection we can explain quite well many cases of extinction observed throughout the history of life. I will remind about some of them. Some time ago cyanobacteria excluded green and purple bacteria from many adaptive zones, later algae did so with cyanobacteria. Then in the Cambrian algae and the first invertebrates by common attempt excluded stromatolites from many zones, in the Ordovician cephalopods and eurypterids did so with many other invertebrates, in the Devonian fish and woody plants - with many forms of eurypterids, cephalopods, trilobites, and herbaceous forms, in the Permian reptilians and gymnosperms - with amphibians and seedless vascular plants, in the Cretaceous flowering plants - with gymnosperms, in the Quaternary hominids - with large mammalians. The list could be far longer - there are enough of data and I have presented them in Part 1 of this book.

Could cyanobacteria, which have excluded green and purple bacteria from surface waters, be considered superrivals? I think they could. And not only them, but also later appeared algae, many of the Cambrian invertebrates, Ordovician cephalopods and eurypterids, as well as other above-mentioned groups. In all those cases, after an instantaneous expansion and wide radiation of superrivals followed a period of their bridle then changed by a new balance that after a while was disturbed by new superrivals. Common to all those cases was that evolutionary younger groups excluded or did a considerable 'harm' to elder ones. As it is known, not all of elder species have become extinct, and that was due to prohibitions acquired the form of biotic attraction, which, I think, should already not be explained to the reader. In a word, there has been selectivity in species extinction, like in species survival, and causes of that selectivity could be explained just having understood that among species there has been not only competition.

This scenario of species extinction, which attaches the most important role to superrivals and in general to stronger rivals in episodes of extinction, well agrees with Darwinian postulates. It is most suitable when speaking about cases of extinction in assembled ecosystems, i.e. such ecosystems where all niches are already distributed. Since there are no vacant niches, new strong forms can not establish themselves somehow differently than excluding something. On the other hand, in those times when there were vacant niches in ecosystems, speciation rather than extinction prevailed, which has been well described in the previous chapter. There is no greater stimulus for species to split than vacant niches. Later, however, when the majority of niches were occupied (in water this happened in the Ordovician and on land - in the Carboniferous), cases of extinction became a common tool and result of ecosystem evolution. By the way, vacant niches in the form of less favourable for life adaptive zones existed later as well, though not very many of species managed to settle in those peripheral zones.

Though I have already mentioned the forces that have helped 'primitive' forms of life to survive, now this question should be discussed in more detail. A deeper analysis of data presented in literature reveals that:

1) cases of complete phyletic extinction of a species are not so frequent as it could be expected;
2) newly-emerged forms usually excluded not all of elder forms.

I have but one explanation of those facts and it possibly is not exhaustive, though quite suitable so far. Each species usually has not one, but several populations living in different parts of species ranges. Some of those populations evolve more rapidly, whereas others - slower. Some of them evolve in one direction, whereas others - in a slightly different one. Here much depends on its majesty the accident. Let us suppose that genetic variability has endowed one of those populations with an essential innovation and the species has turned into a new subspecies or even species, whereas another population has remained almost unchanged. For simplicity, suppose that that innovation is an ability to use water molecules, and not hydrogen sulfide as before, as a source of hydrogen (electrons) for photosynthesis. As hydrogen sulfide is not too abundant in the environment, whereas water in oceans is suffice, immediately after its appearance the new form starts to spread. It also invades that part of the ranges where the ancestral form is still existing. Two results are possible in such a situation: either the new form excludes the elder one, or both of them survive. The latter case should not be too rare, because the new form has not only acquired, but also lost something - this is an almost general biological principle. So, it was often that both forms peacefully divided niches between themselves. Possibly the new one was superior as to abundance and biomass, but the elder one, too, found some ensured place, modest as it was. It was presumably in this way that species diversity increased in local ecosystems. The more so that superrivals causing death wherever they migrated later compensated that loss in excess by producing even more new species, if not larger taxons. But the entire story would not be exhaustive without the explanation of what happened later with the elder form. I think that the elder (ancestral) forms were usually kind of preserved: they were not allowed to develop in the direction in which daughter species already were successfully evolving. Thus many of elder forms eventually turned into living fossils. They kept mutating and recombinating may be no less intensively than before, but being among others, more advanced forms, they had to yield to the will of stabilising selection, which could have lasted milliards of years. Sometimes they responded in one way or another to changes in living and non-living surroundings, but their look and status in an ecosystem remained principally unchanged. Nobody could exclude such species, for there was no serious rival - species of an ecosystem competed for more prestigious niches.

In that scenario of the spread of some species and extinction of others, there is still one circumstance already mentioned, though not emphasised sufficiently. It is the role of migration and geographical barriers. There is no doubt that the majority of species of any local ecosystem have not been born at the place they are existing now. Born elsewhere, even not being superrivals they usually had a possibility to get into other regions, too. Migration usually occurred in all directions, so was rather chaotic, but ecosystemic constraints had to see that in each location not an accidental combination of species, but a more-or-less coadapted system was formed. Migration enriched ecosystems with species, thereby deciding their evolution. If migration as a phenomenon had been absent, each local ecosystem should have had to content itself with those species that got asleep *in situ*, thus species diversity therein would have been very poor. And finally, without the concept of migration we would hardly explain how in a certain location, which is not divided into sectors by more-or-less effective barriers, thousands of species eventually concentrate, in spite of the fact that it is known that the allopatric way of species formation is widespread.

Too intense migration rather than increasing species diversity is likely to reduce it, though. I am almost sure that if all geographical barriers would disappear, a mass extinction of species of the current biosphere would begin, which possibly would be even more rapid than that induced by man devastating natural habitats. And conversely, there is almost no doubt that geographical barriers, provided they are not too numerous, promote and maintain biodiversity. Our experience obtained from various cases of an intentional and unintentional introduction of species is likely to confirm those propositions. Ecologists and experts of environmental protection know this well, for this has been described by different authors in both scientific and popular literature.

It is well known that every continent isolated from other continents for quite a long time produced its own flora and fauna, and the longer it was isolated, the greater became the differences. Thus, theoretically thinking, continental drift, if it ended with continent merging, had to result in not only bilateral migration, but also cases of mass extinction. The history called by palaeontologists the Great American Interchange is likely to confirm the Tightness of those propositions. Some 60 million years ago South America became isolated from other continents, and just few mammalians, mostly from North America, managed to get there. In their own turn, mammalian species from South America somehow got one after another to the northern continent, where they have survived. That did not prevent both the continents from forming their own mammalian faunas: in the northern continent placental mammalians prevailed, whereas in the southern one, in addition to placental there were many marsupials, which even made the majority among predators. Before the formation of an isthmus, there were 32 families of terrestrial mammalians in South America, whereas in North America - 35 of them. In each continent, 30-31 families were of local origin (Marshall *et al.* 1982). Despite that great differences in faunas, production pyramids of both the continents were similar, with great many of ecological equivalents in each. South America, for example, had many primitive ungulates and marsupials that occupied the niches in other continents usually belonging to placental rodents.

And so, approximately 3 million years ago, after a 57-million-year isolation, both the continents of America merged again to make an isthmus. There started bidirectional migration - the great interchange. It has been going on until the present. However, some conclusions could be drawn already now. In the southern continent, the number of species of local origin has decreased from 30 to 21, though migrants from the north (12 families) have compensated this extinction in excess. After the interchange the number of families in North America has remained almost the same (34) except for 8 families that are already of a southern origin. So, the fauna of the northern continent has not managed to escape extinction (Marshall *et al.* 1982; Potts & Behrensmeyer 1992).

Experts suggest that there should have been certain regularity in those cases of extinction: most to suffer were those local mammalians that encountered the comers occupying similar niches. Accordingly, a wide-scale competitive exclusion should have probably taken place (Marshall 1988). Marsupial predators of South America were particularly unlucky - in the course of time all of them were pushed out by northern comers - placentals belonging to the families of cats, dogs, martens, and bears. Those placentals seemingly excluded the non-flying giant birds prevalent in the southern continent until then. In addition to competitive exclusion, there should presumably have also been extinction of the species that did not manage to adapt to exotic predators exploiting them too efficiently. Just this is how, for instance, the extinction of notoungulates of South America is explained. Despite those perturbations, production pyramids in each of the two continents presumably have not been broken. Hardly this could have done any harm to local ecosystems, for there one set of species has been directly changed by another one similar in both functions and number of species.

In this chapter, I was so involved in emphasising the importance of the forces of biotic repulsion that I almost forgot to mention climatic and cosmic factors, which undoubtedly could have also added to the extinction of some forms and to the spread of other ones. The first thought most probably to occur to the reader regarding those factors is the mass extinction of reptilians in the end-Cretaceous. The thing is that now a popular opinion is that that extinction was caused by a cosmic catastrophe - possibly some large bolide. May be - it is difficult to argue with experts. Having in mind those millions and milliards of years of earthy life, it is difficult to believe that great cosmic cataclysms could have been escaped. As suggested by the modern Earth science, the Earth could have encountered far more serious events than the call of a bolide approximately 66 million years ago. However, I think that a reference to similar events gives little explanation. Why large reptilians must have suffered from a bolide whereas mammalians wandering in forests and grasslands together with those reptilians have escaped any harm? A bolide may possibly account for that extinction unless the latter should not have been so strangely selective. In general, a reference to stochastics could not be a sufficient argument to ground directed processes. In other words, I think that mammalians would have excluded large reptilians all the same, though without the interference of a bolide that should have happened later.

By the way, large reptilians and large organisms in general are more vulnerable, and they have always been the first to become extinct if environmental conditions instantaneously change. This presumably is because their adaptability, or ability to adapt, is less than that of smaller forms. And to blame is the long generation time and small populations typical of large organisms - indicators deciding evolutionary plasticity (see Lekevicius 1986, 1997 for details on features deciding adaptability).

One should ask, however, why it is often that in many evolutionary lineages the trend of producing large forms out of small ones is so marked. I will try to explain this in short, without going into detail. The evolution of large organisms from small ones does not contradict what has been described above. Simply, the appearance of such organisms shows that the environment has been comparatively stable for a long time and there have been no great natural calamities. The second part of the explanation is also related with the above described. Large stature of trees and bushes is an indubitable merit in the struggle for existence. Larger animals have had similar merits: herbivores could have easier escaped predation, whereas predators - overcome their victims and become reachless to other predators. Endothermic animals' becoming larger could be explained by thermodynamics - compared to small animals, large endotherms can do with a lower intensity metabolism, which is useful under cold climatic conditions and during famine.

Yet, it is time to return to the subject of superrivals. What was their further fate like? As I have already described, due to their functional dependence superrivals could not carry on their expansion for a long, for sooner or later mighty negative feedback originated making 'hotspurs' co-adapt. What kind of feedback is it? What concrete mechanisms are involved in this suppression? These questions are also important because they are related with a man's problem, man's present and the near future. So let us try to answer them.

I call superrivals those species that have accumulated more than usual selfish features, i.e. the features that allow reducing to minimum the environmental resistance usually hampering an unrestricted growth of populations. To put it in mathematical language, environmental resistance is a difference between a population's maximum possible growth rate (its biotic potential) and its real growth rate. It reduces as death rate does so. For instance, the current demographic explosion of man is due to the dozen times reduced death rate of the human population. Such little controlled population growth is a feature characteristic to all superrivals. It is the external indication of species' competitive features, its unusual power, and superiority over other species, for it expands its population ranges at the expense of other species. But this is exactly what leads superrivals to their perdition.

First, environmental resistance having reduced to minimum, natural selection, too, reduces very much. From this moment almost all, fittest and unfit, begin to survive. Therefore, mutations and recombinations start to accumulate, for the mechanism eliminating them does not work or works inefficiently. Let us take one more look at Figure 25 - it clearly shows that selection plays a role of specific constraints, so in the absence of selection non-directional inheritable variations should inevitably accumulate in a population. Selection having removed, genetic variability remains.

I think the reader has faced facts demonstrating decreasing natural selection in human populations. Therefore here I will mention just a few figures. In Germany, as recently as 200 years ago half of newborns did not live till 20 years of age. In Lithuania, newborn (babies under one year old) mortality rate has reduced almost 20 times during so short a period as 100 years. A similar decrease in mortality rate is characteristic of the majority of the countries with strong economies, and it is known that this rate is a result of civilisation and culture and mostly of medicine and hygiene achievements. The decreased mortality rate also means reduced natural selection, because, as suggested by modern theory of biology, those to die usually are weaker, less fit individuals. The selection of the genes controlling resistance to infectious diseases has particularly reduced, which is mostly due to hygiene as well as vaccination and the use of antibiotics.

It could be deduced that currently inhabitants of countries of strong economies unusually rapidly, according to evolutionary scale, lose a genetically-predetermined resistance to infectious diseases, cold, and heat, quality of teeth and eye sight, physical strength, and other phenotypic features the absence of which in a civilised society is easily compensated by various innovations born by scientific and technical revolution and therefore does not reduce the fitness off carriers of those features. So, it turns out that not only antibiotics, but also eyeglasses are a mighty factor of evolution.

The research carried out by a well-known German geneticist Vogel (1983) has shown that Afro-Americans are quite rapidly losing some of their genes common until now in populations of black Africans, who live under less comfortable conditions than Americans and therefore are subjected to a much greater pressure of stabilising selection.

Quite possibly, one third of inhabitants, and presumably even more of young people, of countries of strong economies have a rather low genetically-predetermined fitness. All of them should have been eliminated by selection already 100 years ago. So, it is likely that due to gradually reducing selection genetically-predetermined healthiness has also considerably reduced. Despite different inborn defects weaker individuals, however, not only survive, but also successfully reproduce, thereby spreading their genes. There is no unconditional evil in it, rather the other way round - this situation is due to our humane attitude towards our own and other people's sufferings - but any way it is useful for us to know the magnitude of this genetic load.

So, the example of man, one of superrival species, demonstrates that superrival populations, having reduced to minimum environmental resistance, in the course of microevolutionary restructuring tend to become vulnerable to those unfavourable environmental factors that have recently controlled population size. This is one kind of the above-mentioned negative feedback.

Another kind of the negative feedback should materialise due to the fact that superrivals usually extend their population and ranges by doing harm to other species. This means that in the short run superrivals become huge vacant or more-or-less vacant niches. Man, obviously, has achieved most of all in this respect: humans have destroyed not only their main rivals, but also predators and the majority of parasites exploiting their populations, which has caused that unprecedented demographic explosion witnesses of which we are. It is likely, however, that this good luck in the fight with nature is temporary, since our populations have become comparatively easily available (due to the above-mentioned reasons) vacant niches. And that kind of niches, as we already know, never are vacant for a long time, for they themselves provoke the evolution of exploiters. Such course of events seems to be most probable in the case of man, too. Every year new genotypes, strains, subspecies, or even species should develop from wild natural forms by means of evolution and they should be specifically fit to exploit human populations or compete with them. Those new varieties should become more and more abundant until the more-or-less-vacant trophic niche, which we, humans, have been becoming in recent centuries, is filled up. Old chains are broken, but its seems that nature is forging for us new, possibly even much stronger chains to bridle the new 'hotspur'.

It is likely that having come across superrivals nature works very efficiently following the principle of a buffer: every action of superrivals provokes a contra-action against them - they begin to strangle themselves with their own hands. Thus, instantaneously they become just predominant and no longer suppressing species.

Are there any facts testifying in the favour of the foregoing propositions? A physician would give a more precise answer to this question, the more so that I have never collected such facts for the purpose. But I have my own opinion regarding the question. I consider that the number of species, especially parasites, exploiting man lately has been increasing, rather than decreasing. Because the majority of those species have a short generation time and vast populations, it is not too difficult for them to adapt to so abundant new prey by means of microevolutionary restructuring. In this way they play a co-adaptive role by adapting themselves as well as human populations to other species of the biosphere. So it is likely that the fight of mankind with parasites, contrarily to that with predators, will not be a success. Besides we are not in luck with rivals, too. For example, in addition to man potatoes currently have at least two hundred species exploiting them, the number increasing exponentially. And this is not astonishing - to wild nature potato fields are but a more-or-less vacant niche. Farmers seem to be losing rather than winning the fight with pests, like physicians - with parasites. I consider those failures of mankind negative feedback which is inescapable in this situation and with which nature has provided itself for a long. Therefore everything regarded by us as good tends instantaneously to turn into evil. It cuts both ends.

Probably it is quite correct to compare the fate of superrivals with the course of various ecological invasions. Let us take an example of Canadian pondweed *(Elodea canadensis),* also called water plague. Having somehow reached Europe from their native habitats in North America, in the end of the 19th century those plants blocked up channels and rivers at certain places of the old continent so that ships could not sail through. And nothing helped until nature put everything in order. Seemingly, in its new motherland the species eventually 'got encrusted' with new parasites and herbivores exploiting it, which mostly played a co-adaptive function. At present Canadian pondweed is making no trouble. Its populations seemingly are abundant at places, but they are far smaller than during the first stage of their invasion.

I will try to generalise. Everything what has been written about evolutionary mechanisms testify to the fact that species are both elements of an ecosystems and conditionally independent structures enjoying some freedom. Therefore on evolving they have to accumulate features beneficial not only to themselves, but also to their community. They evolve both together with their ecosystems and individually. Having accumulated certain selfish (egoistic) features, species would often become superrivals, which have overcome environmental resistance completely or at least in part. Then they would launch out on a life of adventures - begin to reproduce and spread intensively excluding a great number of other species and sowing death around. Sooner or later communities, however, would take back what belonged to them: space and food resources would be overconsumed, superrivals would start 'got encrusted' with new species that exploited it efficiently, and in due course superrivals would become common, though sometimes quite lucky species. That was quite an often case in evolution. Will this scenario recur in the case *of Homo sapiens,* too, our descendants will learn.

SEVERAL NOTES ON 'ASSEMBLY RULES' AND VACANT NICHES

Having written so much about ecosystem construction by means of evolution, I ought to mention a subject that in modern ecology is called ecological assembly rules. That term was mentioned first in J.M. Diamond's (1975) article from the collection 'Ecology and Evolution of Communities' (Cody & Diamond 1975). By the way, that monograph was written in memory of R. MacArthur, one of the authors of the theory of island biogeography. According to Diamond, ecology should discover the rules explaining why in a certain location a certain set of species is formed. He considered that the solution of that problem should be searched for in the theories of island biogeography and competition:

'Much of the explanation for assembly rules has to do with competition for resources and with harvesting of resources by permitted combinations so as to minimise the unutilised resources available to support potential invaders. Communities are assembled through selection of colonists, adjustment of their abundances, and compression of their niches, in part so as to match the combined resource consumption curve of all the colonists to the resource production curve of the island.'

On forming the theory Diamond based it on his own data obtained while investigating birds of the archipelago of New Guinea.

That article was a kind of spark that set a universal fire. One after another numerous articles poured in exploiting that fruitful, according to many, idea. Hundreds of publications have appeared on the subject and the enthusiasm is not likely to reduce in the near future. However, there are some indications, though yet rather insignificant, predicting a storm. Recently the material of a symposium on assembly rules (Weiher & Keddy 1999) has appeared generalising the way made in almost a quarter of the century. During that period not only the methods suggested by Diamond, but also other mathematical methods investigating the problem were tested. Many combinations of species 'permitted' and 'forbidden' in living nature were discovered. Until present many experts of that field consider that the combinations of species observed in nature are a result of interspecific competition. A unanimous opinion, however, is absent. There are opinions that the combinations of species are mostly decided by accidental factors. Finally, the pleiad includes those who until now are not sure what those assembly rules are, how and where they should be searched for, do they have to cover the whole ecological community or just individual guilds, and so on.

I think that one of the articles from the above-mentioned symposium material (Booth & Larson 1999) is worth particular attention. The authors consider that the history of assembly rules clearly demonstrates what a large wall some researchers sometimes tend to build in order to separate from other researchers, the younger generation - from the elder one:

'It can be argued that if the word constraint is used to substitute for the word rule and the word development is used to substitute for the word assembly, then the current discussion of assembly rules is reduced to a discussion of developmental constraints on community structure: an idea fully explored by Clements, Gleason and many other ecologists.'

F.E. Clements and H.A. Gleason were botanists, whereas the majority of proponents of the idea of assembly rules are zoologists. May be this is why the ideas of the former ones have been ignored, since according to the latter what fits for assembling of plant communities does not fit for that of animal ones. Presumably, the role was also played by the age of those ideas - they were born as far back as the beginning of the 20th century. Since new-generation ecologists have not made any public statement on the subject, it is difficult to judge. An outsider should be even more surprised at the fact that advocates of assembly rules have ignored the concept of an ecosystem as if it were absent at all. The famous E.P. Odum's article 'The strategy of Ecosystem Development' (Odum 1969), for instance, could have been a starting-point or, finally, a critical analysis target seeking to obtain 'better grounded' rules of community assembling. This has not happened, though.

I have my own explanation of those at first glance hardly understandable turns of community ecology. I consider that E.P. Odum and like-minded persons do not please younger-generation ecologists (though I do not think that all of them without exception) first of all because those veterans of science were and are conscious supporters of the systemic method. They see the world as an integral system not divided into independent blocks, whereas science - as a large palace residents of which are recommended as frequently as possible to communicate and share opinions on how to make that palace even more beautiful and cosy. Elder-generation ecologists were firmly convinced that in addition to competition an even more important role in living nature is played by complementary relations (according to Clements' terminology - relations of dominance and subordination) and co-operative connections. I think that to younger experts of community ecology the old methods of ecosystem research (informal and verbal modelling as well as general systems theory), too, were not acceptable. They preferred R. MacArthur's way of thinking and formal ways of modelling suggested by him. So, I think that this time like in many similar situations the wall built by the younger generation to separate from the elder one is made of methodological convictions. And the latter have a great effect, as if they were a religious taboo threatening with death for any communication with those belonging to another confession, even for the mentioning of their name in public.

In the material of the already mentioned symposium, Keddy and Weiher (1999) have presented several propositions that could be regarded typical ecological assembly rules:

'In the absence of predation, a pond in the temperate zone can be expected to have between 5 and 10 amphibian species.'

'The ratio of insectivorous to granivorous birds in deciduous forests is between 0.25 and 0.33, whereas in boreal forests the ratio falls between 0.45 and 0.55.'

'There is a linear relationship between the number of beetles in deciduous forests and the volume of coarse woody debris.'

Such 'rules' do not impress me at all because of two reasons. First, they are too miniature, and in the absence of more general 'rules', similar to those discussed by E.P. Odum, a search for specific rules hardly makes any sense at all - they would simply appear in a conceptual vacuum and it would be difficult to find any explanation for them. Besides, those 'rules' do not have any hints of forces that make communities acquire a certain shape, which greatly reduces their explanatory and predictive value and they become purely empirical propositions, so excessively abundant in biology. In my opinion, single facts have no value at all unless they are related with other facts to make an integral theoretical construction. A fact, like a word, acquires value and becomes synonymously understandable just in a meaningful integral context.

I am interested in assembly rules as well and in this monograph I have paid much attention to the constraints (prohibitions and permissions) that bring together into an organised system species driven by genetic variability. However, I could have not mentioned the problem of 'assembly rules' in ecology if it were not for one essential circumstance: according to my conviction the 'rules' that are in force in an ecological succession principally are the same which evolution, too, obeys. What differ are just mechanisms and thus rates of assembling. In both the cases, we deal with the self-organisation controlled by functional constraints that rise due to the interaction of species among themselves and that with non-living surroundings. It is well known, for example, that the further an island is situated from a continent, the more endemic species could be found in that island in case other conditions are similar. Contrarily, community assembling in islands close to a continent occurs mainly through colonisation. Though assembly mechanisms and rates are different in both the cases, the final result is predictable. Sure, I have in mind the most general characteristics of a community, its functional features, rather than species composition (taxonomic features).

I am so rather critical of those who support the idea of 'assembly rules' also because they, as it seems to me, ignore merits of the experimental method. If I were them, I would solve the problem in the following way. I would take a laboratory cylinder, put some silt into it, pour some water upon it and put the cylinder by a window. A week or two later a model ecosystem would form, called Winogradsky's column. On the top of that column we presumably would find algae, cyanobacteria, and aerobic decomposers, under them - purple non-sulfur bacteria, still lower - purple and green sulfur bacteria, and at the very bottom - sulphate-reducing bacteria and other anaerobic decomposers.

This is how since long ago microbiologists have been investigating the course and mechanisms of the formation of the aquatic ecosystems with characteristic anoxic zones. However, such a way of problem solution is unlikely to be acceptable to advocates of the idea of assembly rules. Seemingly, a wall built between ecologists interested in micro-organisms and those dealing with macro-organisms is as great as that between elder- and younger-generation researchers (Atlas & Bartha 1998). This again is a methodological wall: macro-ecologists usually are involved in *in situ* observation and quantitative surveys of species composition, whereas microbial ecologists, on the other hand, prefer laboratory experiments, often with microcosms, and make theories in their own way - through empirical generalisation.

By the way, may be this is why those schools have different attitudes towards the forces deciding community assembly. Microbial ecologists by no means regard competition the main force in living nature (e.g. Atlas & Bartha 1998; Lengeleref *al.* 1999).

If I had to formulate assembly rules of my own, I would start with the notion of a vacant niche. I use it frequently in this monograph. Especially useful to me has been a rule according to which vacant niches are to be occupied. I have illustrated this principle with numerous examples. I hope that the reader have understood the notion of a vacant niche monosemanticaly, from the context. But I would like to revert to it once again, for in literature are other opinions on the issue, too, which are competent enough.

Unlikely to the issue of assembly rules, a notion of a vacant (free, empty or unoccupied) niche is exploited rather seldom: according to my data, possibly not exhaustive, during the recent ten years that notion was used in as few as twenty articles. Vacant niches most often are interpreted as a circumstance extenuating colonisation (Walther 2000) or, in the theory of evolution, as a strong stimulus for species diversification (Rohde 1991; Yamagishi *et al.* 2001; Kawata 2002).

The popularity of the notion of a vacant niche has been greatly affected by Lewontin's article (1978). He has suggested that evolution should not be restricted to the process when in the beginning vacant niches appear and then - organisms to occupy them. He writes: 'in the absence of organisms in actual relation to the environment, there is an infinity of ways the world can be broken up into arbitrary niches'. The author considers that there is no theory allowing *a priori* describe yet unoccupied niches.

It should be pointed out that Lewontin's conception of the niche is slightly different than that of mine. He writes *(ibidem):* 'The ecological niche is a multidimensional description of the total environment and way of life of an organism.' This definition should most probably be traced back to Hutchinson (1957) and MacArthur (1968). The former is known to have introduced a multidimensional description of the niche and the latter is said to have identified a niche with a phenotype. I think that the multidimensional attitude is really useful in this case, especially as a means of quantitatively describing individual subniches. However, I would not like to agree with MacArthur's position. For me a niche first of all is a place of a population (or an individual) in ecosystem metabolism, i.e. food and other kind of resources exploited by that population, its relations with rivals, predators, parasites, as well as nonliving surroundings (for more details see Fig. 23 and the text to it). This attitude principally agrees with that widespread at present (e.g. Begon *et al.* 1996, p. 89).

A niche being identified with a phenotype or 'way of life', the existence of vacant niches becomes problematic indeed. Then I do not see a means of deducing any truth about a possible number of niches in nature. A vacant niche, on the other hand, could be easily imagined as resources of space, food, and energy temporarily used by nobody though potentially usable. Then this conception may become operational and of a heuristic value.

Understandably, for lucidity the situation when vacant niches are absent in nature should be recounted as precisely as possible. As I see it, it is a case when nutrient cycles are non-waste and the block of biophages contains no unexploited species. By the way, it sometimes may happen and possibly happens that in nature some parasites are not exploited at all, for they have so little of energy reaching them that their parasites have absolutely no chances to originate and establish themselves. Such a situation is most probable at the level of top predators exploiting parasites. Speaking about saturated with species communities, it should be taken into account that all of them may differ as to the degree of specialisation, or, in other words, an average width of a niche, and therefore species diversity could hardly be used as the only indicator of saturation or non-saturation.

So, my understanding is that the conception of a vacant niche has a right to exist and be used like the conceptions of occupied niches and saturated or assembled communities, which supplement it.

By the way, in his new essay Lewontin (2000) again returns to the conception of a vacant niche and quite well-groundedly, in my opinion, suggests that organisms not only adapt to the environment, but also constantly alter it, thereby themselves creating new niches. However, a conclusion, which is not very correct, is made therein too, maintaining that there could be no pre-existent and vacant niches. Further one more conclusion, which is quite unexpected and summarising, is drawn:

'The metaphor of adaptation, while once an important heuristic for building evolutionary theory, is now an impediment to a real understanding of the evolutionary process and needs to be replaced by another. Although all metaphors are dangerous, the actual process of evolution seems best captured by the process of *construction* (italics by R.C.L.).'

If I have understood the course and logic of Lewontin's thoughts right, he asserts that organisms not only adapt to the environment, but also reorganise and adapt it. If it is right, then the idea of construction should most likely be understood as a metaphor describing the process of self-organisation involving the whole community and non-living surroundings. This conclusion, I think, is also suitable to end with my own reasoning regarding assembly rules and vacant niches.

WHERETO LIVING NATURE EVOLVES

The reader could be somewhat surprised at the title of this chapter. Can it be so that the author has not found out yet whereto nature evolves? It has been written so much about how ecosystems changed, what kind of new organisms evolved and what features they had, and again that question 'whereto'. I would like the strict reader to excuse me. Indeed, I have already mentioned alteration of one or another kind of indicators, but this issue is so important that I think it is worth an individual chapter. The more so that I have probably failed to differentiate essential things from not essential ones. First of all I would like to emphasise that in what follows I will describe alteration of indicators characteristic of entire ecosystems. Besides, there will be discussed exclusively functional parameters only: ecosystem biomass, energy efficiency of life, degree of species specialisation, etc. I will make an attempt to recount the connection between those indicators, for, as it seems to me, they are interconnected in an objective sense.

Darwin's theory of natural selection predicts that from generation to generation species should become more and more adapted to the environment - more and more successfully search for food and compete with other species and less and less suffer from predators, parasites, and unfavourable abiotic conditions. This is how Darwin saw the direction of evolution. Later researchers (Huxley 1942; Simpson 1949; Thoday 1958; Zavadsky 1958; Rensch 1960) have made that conception more rigid and demonstrated that while evolving species tend to reduce environmental resistance. In other words, the rate of death and that of birth decrease, whereas reproduction efficiency (the percentage of new-borns survived to maturity) increases. Based on this conception, man undoubtedly is the top of evolution. What can be added to this is just that in an extreme case a species that has reduced environmental resistance to minimum rapidly increases its biomass, becomes a superrival and biodiversity consumer, like it is the case with the human population.

And what about ecosystem evolution? It would be very difficult to answer this question if not for one circumstance: we have quite comprehensive data about alteration of ecosystem parameters during ecological succession. Once upon a time, some twenty years ago, as I was thinking about alteration of ecosystem parameters through evolution I turned my attention to the fact that trends typical of ecological succession principally are very similar to those that ought to be typical of evolution. In both the cases, for instance, ecosystem biomass and species diversity therein constantly increase, whereas metabolism intensity (R/B, here R is respiration rate and B is biomass) decreases mostly because larger and larger organisms emerge. What is it - still another meaningless coincidence, which, according to many experts, are countless in biology? It was quite later that I understood that it is not a simple coincidence, because the ecosystem constraints directing succession also direct ecosystem evolution. There is no gap between biological space and biological time - principles of life functioning and those of its evolution can not be different. So, it turns out that evolutionary laws should not be searched for elsewhere - they could be found right here, in each abandoned field or a burnt down forest.

According to Odum (1969, 1971), in ecological succession to the moment of maturity metabolism intensity continuously reduces, whereas ecosystem biomass and species diversity grows. By the way, there were different opinions regarding the trend as to species diversity, though it is likely that later the existence of that trend has been acknowledged. In addition to those indicators, E.R Odum also writes about some other: as communities mature nutrient cycles become closer and more efficient, organisms - larger, niches occupied by species - narrower (specialisation - greater), and positive interspecific connections - more abundant. If those trends reveal the real situation, and nobody doubted of it during those three decades, then I think that similar trends could be expected in evolution.

There are quite well-grounded data in literature (e.g. Simpson 1969; Wicken 1980) suggesting that through evolution biosphere biomass increased both ways - extensively and intensively (per unit of area or volume) and that growth was presumably related to a more and more efficient use of energy and materials by life in the course of time. There is also no doubt that species diversity in both biosphere and local ecosystems continuously, though with some interruptions, increased (Signor 1990).

To answer the question which of those indicators are major and which are minor is difficult, though much depends upon this answer in biology. I do not have a firm opinion about it, but still I would prefer ecosystem (and biosphere in general) biomass the basic indicator of the evolutionary progress of life. The rest of indicators are subsidiary, related to the basic one, meaning that those are alterations of subsidiary parameters that have decided the growth of biomass through evolution. However, other attitudes are also possible, so I would give up this opinion of mine if serious arguments supporting another point of view appeared.

Theoretically thinking, an intensive accumulation of biomass is impossible otherwise than increasing the efficiency of the use of energy and materials. If not, a supposition would have to be made that biomass has increased due to the increasing energy flow from the Sun that flow having increased at least several dozen times. Possibly, there has existed the latter mechanism of biosphere biomass increase, but the former one should have played a role as well.

A higher efficiency of energy could be obtained in at least two ways: either the energy consumption for the maintenance of a biomass unit should be reduced, or reproduction efficiency should be increased. The first indicator is nothing but metabolism intensity. Has it really reduced through the evolution of life? Not going deep into details, we may undoubtedly say - yes. The lowest metabolism intensity is most probably in woody plants, which make the main part of biosphere biomass. They are known to have appeared on the scene of evolution quite recently. Small organisms usually have far more intensive metabolism and they are more spendthrift in the sense of energy. By the way, this is true not only for plants. On the other hand, metabolism in mammalians and birds, as it could be expected from endotherms, usually is a great deal more intensive than that in ectotherms, i.e. the rest of organisms. Those differences are especially obvious in moderate and cold climatic zones. So, at first sight mammalians and birds may seem to break the direction typical of evolution and be out of general context. This is even more strange taking into account that life is a functional hierarchy, thus lower organisation levels (species) should not break trends typical of the higher level (ecosystem).

The matter is more complicated, though. First, of all taxonomic groups mammalians and birds are least inclined to feed other species on their zygotes and immature offspring. Their reproduction efficiency is extraordinary high, which also is a means of energy saving. However, this supposed deviation from the general evolution demonstrated by mammalians and birds could be even better explained in the following way: a functional hierarchy is not rigid at ecosystem level, therefore there is a possibility for two rather than one evolutionary lineage to exist. One of them is species (or phylogenetic) evolution and the other - ecosystem evolution. Those two lineages often come into conflict, because what is beneficial to a species is not necessarily beneficial to the ecosystem, and vice versa. Mammalians and birds, which use the energy obtained with food comparatively wastefully and radiate more heat into the surrounding space (per mass unit) than ectotherms do, possibly benefit in excess elsewhere, for endothermy helps them in reducing environmental resistance, increasing reproduction efficiency, and therefore becoming invincible in the struggle for existence.

So, man is the top of species evolution, like trees are a realised ideal of ecosystem evolution.

Metabolism intensity is an indicator that is specific not only to community level. Reproduction efficiency, on the other hand, is not at all a parameter of a community. However, there is a specific ecosystemic indicator, which could have had certain effect on the efficiency of the energy, thus on ecosystem biomass, too. I have in mind species diversity. It is likely that in the biosphere species diversity constantly increased, which should have been related in some way to the growth of the biosphere biomass. Experts of the systems theory explain that fact through a very simple formula and they would suggest something like this: it has to be this way, because specialisation always increases efficiency.

I will explain briefly what is meant when speaking about species specialisation. We would have a zero specialisation if an ecosystem nutrient cycle was 'rotated' by a single species. The niche of such a species would be extremely wide, encompassing all the functions usually carried out by thousands of species - all producers, biophages, and detritivores of a certain ecosystem. So, when I speak about species specialisation I have in mind that it is positively related to species diversity, i.e. the greater is the diversity, the greater is the number of the structures that have to carry out the global ecosystem function - 'rotate' the nutrient cycle and accumulate biomass. Because species diversity is likely to have been increasing through evolution in both local ecosystems and the whole biosphere in general, it could be considered that species specialisation has been increasing as well. In other words, there should have been a trend of the narrowing of species niches. According to experts of the systems theory, in such a case an increase in functioning efficiency could also be expected. However, such an effect of specialisation could be obtained not before activities of specialised parts are well co-ordinated. The task natural selection was facing must have been really difficult: selection had not only to produce a great deal of species, but also to find out an optimal way of organising their activities in order to fulfil the general function. And it is likely to have found that way quite easily. Selection did not started to construct communities based on the model of a superorganism - that kind of solution would have been irrational taking into account low adaptability of such communities. Instead, it produced many spatially separate structures, isolated from one another also genetically in any event. Their status as to control was similar, but functions were so definite and comparatively narrow, that the degree of freedom they had was not high. The thing was that the set of vacant niches proposed by selection to new species was always the same. All communities in all geological spans of time were managed this way.

There are two kinds of specialisation - specialisation as to biotic and that as to abiotic factors. The specialisation of parasites as to their host and that of herbivores as to plants are examples of biotic specialisation. Abiotic specialisation is expressed by a response of organisms to abiotic conditions. This specialisation is commonly observed in the geographical zones with the abiotic conditions greatly changeable through time. In the zone of moderate climate, for instance, abundant are different planktonic organisms co-existing within the same water body and differing but in their response to temperature, light, and the amount of biogenes. Since in that climatic zone all of those indicators fluctuate markedly not only in the course of a year, but also during a 24-hour period, better reproduction is demonstrated by all phyto- or zooplankton species in turn, and non of them can exclude the remaining ones, despite trophic niches being very similar. Such tactics enables the stabilisation of the plankton biomass. Some time ago this phenomenon was called a paradox of plankton, because at first it was thought that niches of all those co-existing species are absolutely similar.

In rainforests or coral reefs, abiotic conditions change through time quite less, so there should have been almost ideal conditions for a narrow specialisation of species with respect to biotic surroundings. Evolution has made use of this by producing lots of stenophagous species.

Seemingly, different responses of detritivores to individual types of detritus ant its components should also be attached to abiotic specialisation. Terrestrial detritivores have particularly narrow specialisation, whereas their aquatic analogues are far less fastidious. Undoubtedly, detritivores co-existing in communities of the temperate climatic zone demonstrate quite distinct differences in their response to temperature and other climatic factors. Due to such a great species diversity, the function of detritivores - a more-or-less integral block of a community - little depends upon the change of abiotic conditions through time.

The experience of many famous biologists, from H. Milne-Edwards and Darwin to our contemporaries, shows that species specialisation in an ecosystem, like that of organs and tissues in a multicellular organism, is favourable for life because it increases the efficiency of its activities. I am of the same opinion. I consider that the almost uninterruptible increase in species diversity occurring through evolution may account for narrower specialisation resulting in a greater biomass of ecosystems. Or may be lower fluctuations in biomass with respect to time as well. On the other hand, narrow specialisation becomes a shortcoming when environmental conditions, having been relatively stable for a long geological time, change drastically and suddenly. I would agree with a person who would declare such an explanation teleological, i.e. referring to the final goal rather than causes. In this I see nothing very wrong, though. We, biologists, have always used a causal and functional kind of explanation as supplementing each other, and this practise of thinking is based on the conception of a functional hierarchy of biological structures.

Let me summarise. Evolution, like succession, presumably has the following trends:

1. Major indicator
   $B_{ec.} \rightarrow \max$;
2. Subsidiary indicators
   $R_{ec.} / B_{ec.} \rightarrow \min$;
   Species diversity and specialisation → max;
   Efficiency of the use of materials and energy → max;
   Reproduction efficiency → max.

Here 'ec.' means both a local ecosystem and the biosphere in general.

EPILOGUE: ON THE SITUATION IN EVOLUTIONARY BIOLOGY AND COMMUNITY ECOLOGY

In 1988, in Lithuania a 'singing revolution' started, which swept up into its vortex me, too. I abandoned my scientific activity and devoted myself to politics. I wrote a lot of publicistic articles and was quite an active 'street' politician. After Lithuania regained its independence, I worked within the government for a while and then for six years I was engaged in the reform of natural sciences at comprehensive schools: wrote articles on pedagogics, handbooks, standards, and so on. It was not before 1998, after a ten year's break, that I returned to evolutionary biology again.

What I found after my return saddened me very much. During those past ten years no essential advance occurred either in the theory of ecology or in that of evolution. Scientific scepticism even increased. Publications still demonstrated the previous spirit of scientism disposed of the past heritage. Despite abundant publications essential scientific problems, existent from at least the 1960s of the past century, were either forgotten or still under consideration without any obvious results. Some of those problems are the following.

In evolutionary biology - the methodology of evolutionary research, ecosystem evolution, selection units, evolutionary progress, role of accident and determinism. In ecology - the methodology of community and ecosystem research, functional hierarchy and control at super-individual levels, diversity and stability, mechanisms of adaptation of populations and communities to stressful conditions, the course and mechanisms of ecological succession, laws of self-regulation in populations, classification of interspecific connections and their role.

To describe that situation I could not find a better word than a crisis. What shocked me most was that during the past decade strong nihilistic trends, far stronger than before, originated. First of all I have in mind disillusions related to the very essence of biology - Darwinism and the adaptationist paradigm in general. This is how one of the most authoritative evolutionists has resumed his attitude (Gould 1994):

'Natural selection is a principal of local adaptation, not of general advance or progress.The history of life is not necessarily progressive; it is certainly not predictable. The earth's creatures have evolved through a series of contingent and fortuitous events.'

So, it turns out that Darwinism is suitable for the description of local phenomena of adaptation only. In this context it is worth to remember an earlier article by Gould and Lewontin (1979) where the authors express their doubts regarding the whole adaptationist paradigm. This even strengthens the sense of a crisis, the more so that the authors suggest the constructionist idea as the way out, which (hope the respectable authors will pardon me) at best may serve as a starting point for a more detailed theoretical scheme.

A certain loss has been felt in ecology too. For instance, already in 1992 E.R. Pianka, one of the most outstanding authorities of ecology, wrote (a quote from Keddy & Weiher 1999):

'Community ecology has for too long been perceived as repugnant and intractably complex...The discipline has been neglected and now lags behind the rest of ecology.'

P. Keddy agrees with him *(ibidem):*

'Community ecologists run the risk of becoming more like the humanities than the sciences.'

I am inclined to trace the current situation in biology back to positivism, which sometimes is called a religion of modern times. Positivism is known to have the following characteristics: absolutisation of practical benefit, dissociation of metaphysics from natural sciences, limiting oneself to what is accessible to mind, aspiration to the precision of propositions and conclusions, priority to positive suggesting rather than criticism. Extreme positivism (scientism) has become famous for its urging to apply mathematical methods to history, psychology, and sociology. There have been even promises to present society with the equation of love no less complicated than the famous A. Einstein's formula. This wave has also reached evolutionary biology. Some authorities of that discipline were and possibly still are sure that we do not have to wait for a long - what we need is just a great mathematician and then all the questions regarding the evolution of life will be solved at once. Such rubbish often makes me think that biologists' fascination with mathematical methods is inversely proportional to their mathematical education. Mathematicians themselves are far more sceptical about the application of their methods to biology.

I. Kant's idea suggesting that each natural teaching contains as much science as much mathematics is in it is natural to every physicist or chemist. Therefore they are justly proud of achievements of their disciplines. Biologists, on the other hand, since long ago have been feeling certain inferiority, and are ready to surpass themselves in their attempts to touch physicists and chemists. This sometimes results in haste and lack of a sound mind.

The reader must have already understood that I am sceptical about the application of mathematical methods to evolutionary biology and ecology. Some time ago me, too, expected very much from mathematics. I even was involved in designing together with mathematicians a model of an ecosystem of one of Lithuanian lakes. Now, however, I believe I know that what could be easily transformed into mathematical equations is not essential and what is essential can not be mathematised. Even the genius of a mathematician would not be able to help a researcher attempting to describe the course and mechanisms of ecosystem evolution, with a possible exception when it is required to obtain a more precise definition of a certain notion. In spheres of my interest, mathematical models can be tools of description rather than of explanation at best. If mechanisms are ignored and what is being searched for is just correlation, the same data set, as it is known, could be described in many various ways, and it is impossible to find a criterion of truth to select the best of them. If data basis, which means the aim of a research as well, is adjusted to an available mathematical apparatus and not vice versa, there could be little use of all this. I am inclined to reject scientistic views because of psychological reasons, too: I disapprove of a further depreciation of mind and thinking, entrusting the function of thinking to a computer, being simply afraid of forming courageous and audacious hypothesis that do not result directly from available data. I dare claim that the naked empirism combined with scientism raises monsters - young people who for the sake of solidarity cut their own wings and burden themselves with weights and lead in order to make their thinking as standard as possible. I do not know how the father of empirism F. Bacon would like the scientific society so disposed to standardise, but for me it is not very appealing - it is my civic position if you like. I am for the balance of induction and empirism with deduction and rationalism rather than the counterbalance between them as it is usually the case. I think that the method of hypotheses suggested by K. Popper will be vindicated sooner or later. Biologists should do this as soon as possible. In our science, production of courageous hypotheses instead of being punished should be promoted by all possible means, even if falsification of those hypotheses were hardly possible in the present stage of biology development.

It is beyond the bounds of single person's possibilities to change settled in society ideologies. The more so that usually those ideologies are not declared in public. Despite that or may be just because of that they, being promoted by a conformist spirit, quite effectively control young minds directing their thoughts and solutions. Just few of the younger generation later find out what kind of glasses they have been looking through at the world and what philosophers of science have made that pair of glasses. Even fewer are those who having rejected the conformist spirit try to put another kind of eyeglasses possibly made even by themselves.

Biology would not have been befallen by this crisis if it had found effective ways of logical simplification of complicated situations. In the mid-20^{h} century it was considered, quite well-groundedly as I think, that such kind of ways were already found. Those hopes were related to the general systems theory, thermodynamical point of view, and methods of qualitative (informal) modelling. The beginning was not bad - in evolutionary biology and ecology many things became much clearer than before. A particular contribution was made to ecology. However, minds imbued with the scientistic spirit also were awake and not going to give up. Finally, after approximately a ten-year's fight they won, and everything do not meeting new standards was left on library shelves to get dusted. However, as it has appeared at the turn of the century, the new current has not brought much promised at the beginning. Standards requiring mathematical preciseness in everything cause disillusionment. Though the machine producing theories is operating further, only few believe that it will produce a quality product some day.

What way out do authorities suggest? S.J. Gould and R.C. Lewontin seem to be expecting much from the theories of chaos, catastrophe, and complexity. Ecologists, on the other hand, do not suggest any alternative to the currently applied methodology, as far as I know. My opinion regarding the question is somewhat untraditional: biologists should reconcile themselves to the idea that nobody other will suggest a methodology suitable to describe their objects. A new methodology should originate in the depth of biology itself. It should be impregnated with the sweat and experience of biologists themselves. Non of the theories of chaos, catastrophe, or complexity can and will take root, like dozens of other exotic matters, for they have originated in another medium. If we do not like strange methods to dictate strange to us objectives and world outlooks, we should take up on ourselves the responsibility for the future of biology.

Now that the time has come to say good bye, I would like to end with some words from the bottom of my heart - may be they will help us to understand one another. Those will not be calming words, though. Moreover, many may find them even unpleasant. In such a case, you may think that they are a result of my fatigue - and you will be right in a way.

Some ten or fifteen years ago I believed that biology would recover in the short run and leave the period of stagnation. At present I am not such an inveterate optimist. Sometimes I regret that quite possibly there is much of truth in the rumours asserting that my world is finished and it is not known whether it will resurrect some day at all. By 'my' I mean Ch. Darwin, A. Wallace, Ch. Lyell, T. Huxley, W. Vernadsky, P. Teilhard deChardin, E. Odum, and many others with a similar attitude. It is likely that what has left of that attitude are just regrettable remnants, and for some time we have already been living in a world of other dimensions, in another system of co-ordinates.

I am fond of looking through old handbooks of biology for secondary schools and colleges. Many of them have something what is so very familiar and appealing to me. Not long ago I happened to come across one of such, namely 'Biological Science: An Inquiry into Life' by D.E. Meyer and V.M. Dryden (eds) published in the U.S.A. in 1963. I will cite just a little of what has touched me so much (p. 177):

'We have observed that harmony and co-ordination exist at all levels of organisation. Structure and function are always related. The living system is always in balance with what is outside it and around it - its environment. Individuals of the same species form populations with relationships between young and old, parents and offspring, males and females. Populations exist in communities made up of many interdependent kinds of organisms - plants, animals, and micro-organisms. Consumers live at the expense of producers, and decomposers return the materials of the dead to the reservoirs of the atmosphere, fresh waters, seas, and soil. The biosphere includes all living things on the earth. Each of them affects all the others, directly or indirectly, for all of them are a part of the balance of nature; all take part in the cycles of nature and form the food webs.'

I do not know whether world's mass media has fixed when and under what circumstances we lost that kind of seeing and thinking. But I am sure that in the life of biologists and not only of them that should have been an event really grandiose as to its consequences.

They say that ancient cultures die trodden under the foot of brutal conquerors. May be. However, if human culture is, first of all, what every of us bears deep in his or her own self and believes in, then the greatest threat lies in ourselves.

ABSTRACT

In the first part of the monograph, an attempt was made based on inductive and deductive argumentation to describe how nutrient cycles and ecosystem structure changed from the appearance of life to the present. On reconstructing past ecosystems I was guided by the idea that life can exist just in the form of a nutrient cycle ('only an ecosystem is living') and therefore the very first ecosystems should have appeared together with the very first organisms. Besides, it is quite possible that since the very moment of the appearance of life there should have been quite a simple mechanism by which ecosystems and nutrient cycles were formed - metabolism end products of some organisms became waste, i.e. resources potentially usable though used by nobody. Such vacant niches provoked the evolution of organisms able to exploit those resources. The final result was that metabolism end products of detritivores became primary materials for producers. Similarly ecological pyramids should have been formed: producers provoked the evolution of herbivores, the latter - that of primary predators, and so on and so forth until eventually evolution produced common to us pyramids with large predators at the top.

The first earthly organisms should have probably been heterotrophs. The main shortcoming of the first ecosystem was that decomposition was carried out far more intensively than the chemical synthesis of organic matter. That disbalance might have caused the very first in the history of life ecological crisis, which finished with the rise of the first producers. The latter could have been green and purple non-sulfur bacteria, which carried out anoxygenic photosynthesis. They used organic compounds as a source of hydrogen (electrons). Along with those bacteria, detritus-decomposing ones, too, are likely to have been involved in that-time local nutrient cycles. Their emergence and diversity was decided by the diversity of organic substances present in detritus. Already at that time cycles must have been non-waste, and decomposition was carried out to the very biogenes.

As biomass accumulated, sooner or later aquatic resources of free organic compounds had to come short. That could have caused the rise of true autotrophs (photolithoautotrophs). The latter could have been green and purple sulfur bacteria, which used H_2S and H_2as a source of hydrogen (electrons). Those bacteria accumulated sulfur and sulphates as waste, so after a while evolution should have brought about organisms reducing sulfur and sulphates. The vacant niche was occupied to make the cycle become non-waste again. Some time having passed, however, the resources of H_2S and H_2 had to run out, which should have resulted in the appearance of cyanobacteria carrying out oxygenic photosynthesis. The merit of that kind of photosynthesis is in that it uses water molecules as a source of hydrogen (electrons). However, the oxygen having become waste began to accumulate in water, which should have inevitably caused the evolution of oxygen resistance. Still after a while, presumably some 2.5-2.0 milliard years ago, cyanobacteria and detritivores accompanying them became aerobes. It must have been at that time that all modern aerobic chemolitotrophs came into existence. The motives of their rise were very simple: the oxygen accumulating in the environment reacted by itself with the dissolved in water ferrous iron and manganese, hydrogen, carbon monoxide, sulfur, hydrogen sulfide, ammonia, and methane. The energy produced during oxidation was lost. Naturally, those vacant niches became factors stimulating and directing evolution. Thus, after a while all those niches were occupied.

There are sound reasons to believe that 2 milliard years ago all modern global cycles - carbon, oxygen, nitrogen, sulfur - were already formed. From the point of view of chemistry they have not changed until nowadays.

Of course, all those innovations increased biomass in local ecosystems and in the whole biosphere. The increase of biomass must have presumably been accompanied by the accumulation of detritus and fossil fuels. Thus, atmospheric resources of carbon dioxide reduced, whereas those of oxygen continuously increased. Along with that aquatic resources of inorganic nitrogen, sulfur, calcium, phosphorus, and silicon diminished. Eventually life unrecognisably changed the chemical composition of water, atmosphere, and lithosphere. Being reduced at first, the environment became more and more oxidised in the course of time. Organisms altered the environment to adapt to it later. There is no doubt that the ability of life not only to influence, but also to control non-living surroundings improved all the time.

Two milliard years ago ecosystems were still formed of as few as a couple of 'functional kingdoms' - producers and detritivores. For quite a long some organisms were exploited by other ones not before the former died. Accordingly, there must have been a huge vacant

adaptive zone. Its exploitation started about 1.5 milliard years ago, after the rise of protozoans. At the beginning a group of organisms feeding on detritivores and producers was formed and later the first predators came into being. Along with those the first parasites emerged. Still later, approximately 700 million years ago, multicellular predators formed the fourth trophic level. The formation of ecological pyramids was finished in the Ordovician after the first large predators (cephalopods) appeared on the stage of evolution. Ecosystem structure having become settled, evolution, however, did not stop. New forms increasingly emerged, competition continuously increased, because the new forms could not get established otherwise than excluding part of elder ones.

The conquest of land began about 600 million years ago or even earlier. It followed the aquatic scenario: at the beginning producers got established on land to be followed by detritivores, thereby forming local cycles. There evolved organisms feeding on detritivores along with herbivores the latter making preconditions for primary predators to appear, until finally evolution bore large top predators. Besides, every new species provided itself with its parasites. It is likely that terrestrial ecosystems were completely formed already in the Carboniferous. After that, similarly to the aquatic case, the competitive exclusion became frequent, since it was not very easy to find a vacant niche. During the Permian and Triassic gymnosperms excluded many of seedless vascular plants, whereas reptilians similarly treated amphibians. In the Jurassic and Cretaceous, competition increased even more, and evolutionary priorities at species level - increase of reproduction efficiency and reduction of environmental resistance, improvement of the nervous system as well as forms of communication and intraspecific co-operation - cleared up.

After reptilians became extinct in the end-Cretaceous, entire food chains were broken and production pyramids acquired an unusual shape - a great many of niches became vacant. Then not only birds and mammalians, but also the remained amphibians and reptilians were moved out of evolutionary stagnation. After an adaptive radiation that took approximately 10 million years the pyramids acquired their common shape again. For a while the function of top predators in many ecosystems was fulfilled by flying and non-flying birds and terrestrial crocodilians, but in the end of the Paleogene the majority of them gave up to predatory mammalians. Amphibians and reptilians had to content themselves with niches left unoccupied by stronger rivals. The formation of ecosystems being over, competition increased again. Finally, in the Neogene hominids embodied the ideal of evolution at species level in reality - one of hominid species, having reduced environmental resistance to minimum and improved to perfection the forms of communication and intraspecific co-operation, became a superrival and consumer of biodiversity. In the Neogene, other no less important processes occurred as well: the atmospheric amount of carbon dioxide and that of oxygen reached an extreme level and became stable and therefore biosphere biomass stopped increasing. The biosphere reached the Earth's carrying capacity.

In the second part of the monograph, evolutionary mechanisms are analysed in more detail. I suggest to deduce an attitude towards them from functional biology. This kind of methodology was also followed by Darwin, though he did not describe it in detail. Having elucidated and made it more explicit, in 1985 I developed a conception of a conditionally complete causal explanation. Combining causal and functional explanation, it eliminates the boundaries between developmental biology and functional biology, between biological time and biological space. According to this conception, species in evolution are as independent as they are in functioning. Evolution, like ecological succession, is directed by co-ordinative constraints emerging due to the interaction of organisms among themselves and with non-living surroundings. Both evolution and succession could be treated as self-organisation (self-assembly) of ecological communities controlled by the same forces and therefore leading to a similar final result. So, this conception makes the search for evolutionary mechanisms much easier. The main question to be answered by an evolutionist is the following: are there a functional hierarchy at population and ecological community level, or not. My understanding is that such a hierarchy really exists, though it is apparent not in all species and ecosystems. It is hardly possible that life can exist without nutrient cycling, thus without a common attempt of many species. Then species simply must evolve in a united front. Evolve in such a way that nutrient cycling would be preserved. Evidently, in evolution co-operative connections among species have played a very important role in maintaining and even increasing polymorphism and species diversity. On the other hand, populations and ecosystems are not superorganisms. At supraindividual levels, in addition to co-operative connections an important role is also played by competition. This opposition, or to be more correct - balance, between the forces of biotic attraction and biotic repulsion presumably testify to the fact that individuals and species through selection have a possibility to accumulate two kinds of features. Some of them are devoted to ecosystem maintenance, whereas the rest are useful with regard to their own purposes only. So, from the point of view of functioning, in evolution at least two relatively independent lineages should have been existing: ecosystem evolution and species evolution. The former deals with an increasing biomass of ecosystems and that of the whole biosphere, whereas the latter - with a species ability to increase its own biomass irrespective of how this may affect the whole ecosystem.

I have just mentioned that both ecosystem functioning and their evolution are decided by co-ordinative constraints. As far as I think they carry out not only a function of self-organisation. They are just what we call natural selection. This point of view instead of emphasising what is being selected accentuates what is making that selection, what forces make evolution move in a certain direction. If natural selection is merely a 'black box' turning a non-directional genetic variability into a more-or-less directed evolutionary process, then its essence is in specific constraints of that variability rather than in differential survival and that kind of reproduction. In order selection and evolution to occur, 'struggle for existence' is not necessary. Contrarily, structures related through co-operative connections constrain the evolution of one another even more than in the case of competition.

The way of any feature, however widespread it may be, always starts from a single unimportant mutation or recombination. At first, a new feature has to clear barriers of internal selection. Then a contribution of the new variation into individual's resistance to unfavourable climatic factors, its ability to compete and escape death caused by predators and parasites is tested. In addition to this, mutants (recombinants) often have to pass intrapopulation selection - a test of their ability to maintain sexual and other kind of contacts. Having passed those barriers successfully, the new feature may spread further or even increase competitiveness of its species. Species ranges having extended, there is a possibility to produce new ecotypes, subspecies, and even species based on the new variation. Other species then are forced to co-adapt to alterations made by the new species. All this affects global ecosystem parameters in a certain way. Understandably, in addition to such exclusively successful inheritable variations, in evolution those that either were eliminated or stuck at some intermediate levels should have been incomparably more numerous.

There is an opinion that ecosystem evolution may occur just under condition that ecosystems, too, are involved into differential survival and reproduction. This is valid for species evolution ('group selection', 'species selection') as well. I think that those attitudes do not reflect the real situation quite adequately. In this respect, Darwin regarding an individual the main unit of selection was closer to the truth. What could be added to this is but the fact that those who die or leave fewer offspring are individuals, whereas evolving are all structures from macromolecules to ecosystems. Differ just causes - forces that carry out a certain act of selection.

How natural selection works, what constraints of inheritable variability act in a concrete case could be judged from numerous examples presented in Part 1 of this monograph. I consider that those examples testify to the fact that irrespective of abundant constraints the latter could be easily modelled. The more so that they seem to be quite invariant or at least frequently recurring in space and time (functional convergence of ecosystems). There is no doubt that evolution could be predicted, particularly its trends at ecosystem level.

In the monograph, I more than once discuss why until today biologists have not found answers to many important and, as it seems, not very difficult questions regarding evolutionary biology and community ecology. I think that this situation is a result of methodological difficulties that have been oppressing biology for at least several decades. I believe that this crisis should be traced back to neo-positivistic and, first of all, scientistic ideology. The latter propagates attitudes and methods applicable to modern physics and chemistry. Rather than bringing closer, scientistic ideology diverts us from the solution of primary importance questions year after year. There is no will to rise questions monosemantic answers to which can not be expected to be obtained by means of mathematical modelling or experiment. So, the worst consequence of this situation is that scientistic methodology affects aims of biological research. Wide spheres of biology attract no attention at all, because their objects are not within a Procrustean framework of the new methodology. Modern science absolutely groundlessly ignores methodology existent several decades ago - the general systems theory, qualitative modelling, a hypothetical deduction method.

SANTRAUKA

Pirmajame monografijos skyriuje, remdamasis induktyvia ir deduktyvia argumentacija, bandau aprašyti, kaip keitėsi medžiagų ciklai ir ekosistemų struktūra, pradedant nuo gyvybės atsiradimo ir baigiant dabartiniu laikotarpiu. Rekonstruodamas praeities ekosistemas vadovavausi idėja, jog gyvybė gali egzistuoti tik medžiagų ciklo pavidale ("gyva tik ekosistema"), todėl pačios pirmosios ekosistemos turėjo atsirasti kartu su pačiais pirmaisiais organizmais. Be to, visai galimas dalykas, kad nuo pat gyvybės atsiradimo momento būta ir gana paprasto mechanizmo, kurio dėka susiformuodavo ekosistemos ir medžiagų ciklai. Galutiniai vienų organizmų veiklos produktai tapdavo atlieka, niekieno nenaudojamais, tačiau potencialiai panaudotinais ištekliais. Tokios laisvos nišos išprovokuodavo evoliuciją organizmų, gebančių šiais ištekliais pasinaudoti. Visa tai pasibaigdavo tuo, kad galutiniai skaldytojų veiklos produktai tapdavo pradinėmis medžiagomis gamintojams. Panašiai tikriausiai būdavo komplektuojamos ir ekologinės piramidės: gamintojai išprovokuodavo augalėdžių evoliuciją, pastarieji suteikdavo tokią galimybę pirminiams plėšrūnams ir taip toliau kol ilgainiui evoliucija pagamindavo įprastas mums piramides su stambiais plėšrūnais viršūnėje.

Pirmieji Žemės organizmai tikriausiai buvo heterotrofai, vykdantys skaldytojų funkciją. Pagrindinis pirmosios ekosistemos trūkumas buvo tas, kad skaidymas vyko kur kas intensyviau, nei cheminė organinių medžiagų sintezė. Šis disbalansas galėjo iššaukti pačią pirmąją gyvybės istorijoje ekologinę krizę, kuri pasibaigė tik atsiradus pirmiesiems gamintojams. Jais galėjo būti žaliosios ir purpurinės nesierabakterės, vykdančios anoksigeninę fotosintezę. Kaip vandenilio (elektronų) šaltinį jos naudojo organinius junginius. Kartu su šiomis bakterijomis to meto lokaliuose medžiagų cikluose greičiausiai dalyvavo ir detritą skaidančios bakterijos. Jų atsiradimą ir įvairovę lėmė detrite buvusių organinių medžiagų įvairovė. Ciklai jau tada turbūt buvo beatliekiai ir skaidymas vyko iki pat biogenų.

Kaupiantis biomasei anksčiau ar vėliau turėjo pasibaigti laisvų organinių junginių atsargos vandenyse. Tai galėjo iššaukti tikrų autotrofų (fotolitoautotrofų) atsiradimą. Jais galėjo būti žaliosios ir purpurinės sierabakterės, kaip vandenilio (elektronų) šaltinį naudojančios H_2S ir H_2. Kaip atliekas šios bakterijos kaupė sierą ir sulfatus, tad po kurio laiko evoliucija turėjo pagimdyti sierą ir sulfatus redukuojančius organizmus. Laisva niša buvo užpildyta, o ciklas vėl tapo beatliekis. Tačiau po kurio laiko turėjo išsekti ir H_2S bei H_2 atsargos, kas tikriausiai ir iššaukė melsvabakterių, vykdančių oksigeninę fotosintezę, pasirodymą. Šios fotosintezės privalumas yra tas, kad vandenilio (elektronų) šaltiniu jai yra vandens molekulės. Tačiau atlieka tapęs deguonis pradėjo kauptis vandenyse, kas neišvengiamai turėjo iššaukti atsparumo jam evoliuciją. Dar po kurio laiko, greičiausiai prieš 2,5-2,0 mlrd. m., melsvabakterės bei jas lydintys skaldytojai tampa aerobais. Tuo laiku greičiausiai atsirado ir visi dabartinių laikų sulaukę aerobiniai chemolitotrofai. Jų pasirodymo motyvai labai paprasti: aplinkoje besikaupiantis deguonis savaime reaguodavo su vandenyje ištirpusia dvivalente geležimi ir manganu, vandeniliu, anglies monoksidu, siera, vandenilio sulfidu, amoniaku ir metanu. Oksidacijos metu išsiskyrusi energija būdavo prarandama. Natūralu, kad šios laisvos nišos tapo evoliuciją stimuliuojančiais ir kreipiančiais veiksniais. Tad po kurio laiko visos nišos buvo okupuotos.

Esama gana tvirto pagrindo galvoti, kad prieš 2 mlrd. m. jau buvo susiformavę visi dabartiniai globalūs ciklai: anglies, deguonies, azoto, sieros. Cheminiu požiūriu jie nepasikeitė iki pat šių dienų.

Visos šios inovacijos negalėjo nedidinti biomasės lokaliose ekosistemose ir visoje biosferoje. Biomasės augimą tikriausiai lydėjo detrito ir organinės kilmės naudingųjų iškasenų kaupimasis. Tad anglies dioksido atsargos atmosferoje mažėjo, o deguonis ir toliau kaupėsi. Kartu vandenyse mažėjo neorganinio azoto, sieros, kalcio, fosforo bei silicio. Ilgainiui gyvybė neatpažįstamai pakeitė vandenų cheminę sudėtį, atmosferą ir litosferą. Iš redukuotos aplinka laikui bėgant tampa vis labiau oksiduota. Organizmai keitė aplinką, o vėliau patys turėjo prie jos prisitaikyti. Nėra abejonių dėl to, kad gyvybės sugebėjimas ne tik įtakoti, bet ir reguliuoti negyvą apsuptį visą laiką auga.

Prieš 2 mlrd. m. ekosistemos vis dar buvo sudarytos viso labo iš dviejų "funkcinių karalijų": gamintojų ir skaldytojų. Ilgą laiką vieni organizmai buvo eksploatuojami kitų tik po pirmųjų žūties. Tad būta milžiniškos laisvos adaptyvios zonos. Jos panaudojimas greičiausiai prasidėjo prieš maždaug 1,5 mlrd. m., atsiradus pirmuonims. Pradžioje susiformuoja grupė organizmų, besimaitinančių skaldytojais ir gamintojais, vėliau atsiranda pirminiai plėšrūnai. Kartu pasirodo ir pirmieji parazitai. Dar vėliau, prieš maždaug 700 mln. m., daugialąsčiai plėšrūnai suformuoja ketvirtą mitybos lygmenį. Ekologinių piramidžių statyba pasibaigia ordovike, kai evoliucijos scenoje pasirodo stambūs plėšrūnai (galvakojai moliuskai). Tačiau evoliucija nesustoja nusistovėjus ekosistemų struktūrai. Atsiranda vis naujos ir naujos formos, konkurencija vis stiprėja, nes naujosios formos nuo šiol negali kitaip įsitvirtinti kaip tik išstumdamos dalį senesnių.

Sausumos užkariavimas prasidėjo prieš maždaug 600 mln. m., o gal dar anksčiau. Jis vyko pagal tą scenarijų, kuris prieš tai buvo išbandytas vandenyse: pradžioje sausumoje įsikuria gamintojai, po jų - skaldytojai, taip suformuodami lokalius ciklus. Vėliau užpildomos ir kitos nišos: evoliucionuoja organizmai, besimaitinantys skaldytojais, augalėdžiai, šie sukuria prielaidas išsirutulioti pirminiams plėšrūnams, kol galų gale evoliucija pagimdo stambius viršūninius plėšrūnus. Kartu kiekviena nauja rūšis apsirūpina savais parazitais. Sausumos ekosistemos buvo pilnai sukomplektuotos greičiausiai dar karbone. Po to, panašiai kaip ir anksčiau vandenyse, padažnėja konkurentų išstūmimo atvejų, nes laisvą nišą susirasti nėra lengva. Per permą ir triasą plikasėkliai išstumia daugelį sporinių induočių, o ropliai panašiai pasielgia su varliagyviais. Juroje ir kreidoje konkurencija darosi dar intensyvesnė, išryškėja evoliucijos rūšies lygmenyje prioritetai: dauginimosi efektyvumo didinimas ir aplinkos pasipriešinimo mažinimas, nervų sistemos, komunikacijos ir vidurūšinės kooperacijos formų tobulinimas.

Stambiems ropliams kreidos pabaigoje išnykus, suyra ištisos mitybos grandinės, produkcijos piramidės įgauna neįprastą formą, atsilaisvina daugybė nišų. Tai išjudina iš evoliucinio sąstingio ne tik paukščius ir žinduolius, bet ir užsilikusius varliagyvius ir roplius. Po maždaug 10 mln. m. trukusios adaptyvios radiacijos piramidės vėl įgyja įprastą formą. Kurį laiką viršūninių plėšrūnų funkciją daugelyje sausumos ekosistemų atlieka skraidantys ir neskaidrantys paukščiai bei sausumos krokodilai, tačiau paleogeno antroje pusėje dauguma jų užleidžia pozicijas plėšriems žinduoliams. Varliagyviai ir ropliai pasitenkina nišomis, atlikusiomis nuo stipresnių konkurentų. Ekosistemoms susikomplektavus, konkurencija vėl sustiprėja. Neogene hominidai galop realizuoja evoliucijos rūšies lygmenyje idealą. Viena iš hominidų rūšių, iki minimumo sumažinusi aplinkos pasipriešinimą, ištobulinusi komunikacijos ir vidurūšinės kooperacijos formas, tampa superkonkurente ir bioįvairovės vartotoja. Neogene vyksta ir kiti, ne mažesnės svarbos procesai: anglies dioksido ir deguonies kiekis atmosferoje pasiekia ekstremalų lygį ir stabilizuojasi, kartu nustoja augti ir biosferos biomasė. Biosfera pasiekia Žemės aplinkos talpą.

Antrajame monografijos skyriuje detaliau apsistoju prie evoliucijos mechanizmų. Požiūrį įjuos siūlau dedukuoti iš funkcionavimo biologijos. Savo laiku panašios metodologijos laikėsi ir Darvinas, nors jis jos detaliau ir neaprašinėjo. Išryškinęs ir sugriežtinęs šią metodologiją, 1985 metais parengiau sąlygiškai išsamaus priežastinio aiškinimo sampratą. Apjungdama priežastinio ir funkcinio aiškinimo būdus į vieną, ji panaikina ribą tarp vystymosi ir funkcionavimo biologijos, tarp biologinio laiko ir biologinės erdvės. Pagal šią sampratą, rūšys yra tokiu laipsniu savarankiškos savo evoliucijoje, kiek ir funkcionavime. Evoliucijai, kaip ir ekologinei sukcesijai, kryptį suteikia koordinacinio pobūdžio apribojimai, atsirandantys sąveikaujant organizmams tarpusavyje ir su negyva apsuptimi. Ir evoliuciją, ir sukcesiją galima traktuoti kaip ekologinių bendrijų saviorganizaciją (komplektavimą), kuri yra valdoma tų pačių jėgų ir todėl veda link panašaus galutinio rezultato. Taigi ši samprata gerokai supaprastina evoliucinių mechanizmų paieškas. Pagrindinis klausimas, į kurį privalo atsakyti evoliucionistas, yra toks: esama ar nesama funkcijų hierarchijos populiacijos ir ekologinės bendrijos lygmenyse. Mano supratimu, tokios hierarchijos tikrai esama, nors ji ryški anaiptol ne visose rūšyse ir ekosistemose. Gyvybė vargu ar gali egzistuoti be medžiagų ciklo, taigi - be daugelio rūšių bendrų pastangų. Jeigu taip, tai rūšys tiesiog privalo evoliucionuoti daugmaž vieningu frontu. Taip evoliucionuoti, kad medžiagų ciklas būtų išsaugotas. Akivaizdu, kad evoliucijoje kooperacinio pobūdžio ryšiai tarp rūšių vaidino labai svarbų vaidmenį palaikydami ir netgi didindami polimorfizmą bei rūšių įvairovę. Antra vertus, populiacijos ir ekosistemos nėra superorganizmai. Be kooperacinio pobūdžio santykių supraindividualiuose lygmenyse svarbų vaidmenį atlieka ir konkurencija. Ši priešprieša, o gal teisingiau - balansas, tarp biotinės traukos ir biotinio atostūmio jėgų greičiausiai byloja apie tai, kad individai ir rūšys atrankos būdu turi galimybę kaupti dvejopus požymius. Vieni jų turi tarnauti ekosistemos palaikymui, gi kiti gali būti naudingi vien tik saviems tikslams. Taigi evoliucijoje, jeigu spręsti iš funkcionavimo pozicijų, turėjo egzistuoti mažiausiai dvi sąlygiškai savarankiškos linijos: ekosistemų ir rūšių evoliucijos. Pirmajai būdingas ekosistemų ir visos biosferos biomasės augimas, o antrajai -rūšies sugebėjimas didinti nuosavą biomasę nepriklausomai nuo to, kaip tai gali atsiliepti visai ekosistemai.

Tik ką buvo užsiminta apie tai, kad ir ekosistemų funkcionavimą, ir jų evoliuciją apsprendžia koordinaciniai apribojimai. Mano supratimu, jie atlieka ne tik saviorganizuojančią funkciją, jie ir yra tai, ką mes vadiname gamtine atranka. Šis požiūris perkelia akcentą nuo to, kas atrenkama, prie to, kas atrenka, kokios jėgos suteikia evoliucijai vieną ar kitą kryptį. Jei gamtinė atranka tėra "juoda dėžė", verčianti nekryptingą genetinį kintamumą į daugmaž kryptingą evoliucinį procesą, tai jos esmėje glūdi specifiniai šio kintamumo apribojimai, o ne diferencinis išgyvenimas ir toks pat dauginimasis. Kad atranka ir evoliucija vyktų, nebūtina ir "kova už būvį". Netgi atvirkščiai, kooperaciniais ryšiais susietos struktūros riboja viena kitos evoliuciją netgi daugiau, nei konkurencijos atveju. Bet kokio, netgi labiausiai išplitusio, požymio kelias visada prasideda nuo mažai reikšmingos pavienės mutacijos ar rekombinacijos. Pradžioje naujasis požymis turi praeiti vidinės atrankos barjerus. Po to tikrinamas naujosios variacijos indėlis į individo atsparumą nepalankiems klimato veiksniams, sugebėjimą konkuruoti, išvengti žūties nuo plėšrūnų ir parazitų. Greta to mutantai (rekombinantai) dažnai turi praeiti vidupopuliacinę atranką, kai tikrinamas jų sugebėjimas palaikyti lytinio ar kitokio pobūdžio kontaktus. Jei šie barjerai sėkmingai praeinami, naujasis požymis turi galimybę dar labiau išplisti ir gal net padidinti rūšies konkurencines savybes. Išsiplėtus arealui, atsiras galimybė naujosios variacijos pagrindu produkuoti naujus ekotipus, porūšius ir netgi rūšis. Kitos rūšys bus priverstos koadaptuotis prie naujosios rūšies sukeltų pokyčių. Visa tai vienaip ar kitaip atsilieps globaliems ekosistemos rodikliams. Suprantama, be tokių išskirtinai sėkmingų paveldimų variacijų evoliucijoje būta nepalyginamai daugiau tokių, kurios arba būdavo eliminuojamos, arba įstrigdavo tarpiniuose lygmenyse.

Esama nuomonės, kad ekosistemų evoliucija gali vykti tik su sąlyga, jei jos irgi yra įtraukiamos į diferencinį išgyvenimą ir dauginimąsi. Panaši sąlyga kartais keliama ir rūšių evoliucijai ("grupinė atranka", "rūšių atranka"). Manau, kad šie požiūriai ne visai adekvačiai atspindi realią situaciją. Darvinas šioje srityje buvo arčiau tiesos laikydamas individą pagrindiniu atrankos vienetu. Prie to galima pridėti nebent tai, kad žūva ar mažiau palikuonių palieka individai, o evoliucionuoja visos struktūros, pradedant makromolekulėmis ir baigiant ekosistemomis. Skiriasi tik priežastys arba jėgos, atlikusios tą ar kitą atrankos aktą.

Apie tai, kaip dirba gamtinė atranka, kokie paveldimo kintamumo apribojimai egzistuoja kiekvienu konkrečiu atveju, galima spręsti iš gausių pavyzdžių, pateiktų pirmajame monografijos skyriuje. Jie, mano supratimu, byloja ir apie tai, kad nepaisant apribojimų gausos, jie gali būti nesunkiai modeliuojami. Tuo labiau, kad jie, atrodo, yra gana invariantiški arba bent jau dažnai pasikartojantys erdvėje ir laike (ekosistemų funkcinė konvergencija). Nėra abejonių, kad evoliuciją įmanoma prognozuoti, ypač tendencijas ekosisteminiame lygmenyje.

Monografijoje ne vienoje vietoje aptarinėju, kodėl iki šiol biologai neturi atsakymų į daugelį svarbių ir, rodosi, ne tokių jau sunkių klausimų iš evoliucinės biologijos ir bendrijų ekologijos. Manau, kad ši situacija susiklostė dėl metodologinio pobūdžio sunkumų, kurie slegia biologiją mažiausiai kelis pastaruosius dešimtmečius. Šios krizės šaknys, kaip man atrodo, glūdi neopozityvistinėje ir visų pirma scientistinėje ideologijoje. Ji propaguoja požiūrius ir metodus, taikomus šiuolaikinėje fizikoje ir chemijoje. Deja, ji ne artina, o kasmet tolina mus nuo pirmos svarbos klausimų sprendimo. Nelinkstama kelti klausimus, į kuriuos nesitikima gauti vienareikšmių atsakymų matematinio modeliavimo ar eksperimento pagalba. Taigi pati blogiausia šios situacijos pasekmė yra tai, kad scientistinė metodologija atsiliepia ir biologinių tyrimų tikslams. Plačios biologijos sritys lieka apskritai be dėmesio vien todėl, kad jų objektai nebetelpa į prokrustiškus naujosios metodologijos rėmus. Dabartinis mokslas visai be pagrindo ignoruoja metodologiją, kuri dar buvo gyva prieš kelis dešimtmečius: sisteminį požiūrį, kokybinį modeliavimą, hipotetinį dedukcinį metodą.

REFERENCES

Adoutte, A., Balavoine, G., Lartillot, N., Lespinet, O., Prud'homme, B. and de Rosa, R. 2000. The new animal phylogeny: reliability and implications. *Proceedings of the National Academy of Sciences USA* 97 (9): 4453-4456.

Alberch, P. 1980. Ontogenesis and morphological diversification. *American Zoologist* 20: 653-667.

Allegre, C.J. and Schneider, S.H. 1994. The evolution of the Earth. *Scientific American* 271 (4): 44-51.

Atlas, R.M. and Bartha, R. 1998. *Microbial Ecology: Fundamentals and Applications.* 4th ed. Menlo Park, CA., etc. Addison Wesley Longman.

Beaumont, V. and Robert, F. 1999. Nitrogen isotope ratios of kerogens in Precambrian cherts: a record of the evolution of atmosphere chemistry? *Precambrian Research* 96: 63-82.

Beerbower, R. 1993. Ends and beginnings: early tracheophyte evolution. *Geological Society of America Abstracts with Program* 25: A-82.

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. and Wing, S.L. (eds) 1992. *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals.* Chicago and London: Univ. of Chicago Press.

Begon, M., Harper, J.L. and Townsend, C.R. 1996. *Ecology: Individuals, Populations and Communities.* 3rd ed. Oxford, etc.: Blackwell Sci. Ltd.

Berkner, L.V. and Marshall, L.C. 1965. History of major atmospheric components. *Proceedings of the National Academy of Sciences USA* 53: 1215-1226.

Berner, R.A. and Kothavala, Z. 2001. Geocarb III: a revised model of atmospheric $C0_2$ over Phanerozoic time. *American Journal of Science* 301 (2): 182-204.

Berner, R.A., Petsch, S.T., Lake, J.A., Beerling, D.J., Popp, B.N., Lane, R.S., Laws, E.A., Westley, M.B., Cassar, N., Woodward, F.I. and Quik, WP. 2000. Isotope fractionation and atmospheric oxygen: implications for Phanerozoic 0_2 evolution. *Science* 287 (5458): 1630-1633.

Boardman, R.S., Cheetham, A.H. and Rowell, A.J. (eds) 1987. *Fossil Invertebrates.* Palo Alto, etc.: Blackwell Sci. Publ.

Bock, W.J. 1972. Species interactions and macroevolution. In: Th. Dobzhansky *et al.* (eds) *Evolutionary Biology.* Vol. 5, pp. 1-24. New York: Appleton - Century - Crofts.

Bock, W.J. 1979. The synthetic explanation of macroevolutionary change - a reductionistic approach. *Bulletin of Carnegie Museum of Natural History* 13: 20-69.

Booth, B.D. and Larson, D.W. 1999. Impact of language, history and choice of system on the study of assembly rules. In: E. Weiher and P. Keddy (eds) *Ecological Assembly Rules: Perspectives, Advances, Retreats,* pp. 206-229. Cambridge: Cambridge Univ. Press.

Brocks, J.J., Logan, G.A., Buick, R. and Summons, R.E. 1999. Archean molecular fossils and the early rise of eukaryotes. *Science* 285 (5430): 1033-1036.

Broda, E. 1975. *The Evolution of the Bioenergetic Processes.* Oxford, etc.: Pergamon Press.

Canfield, D.E. and Raiswell, R. 1999. The evolution of the sulfur cycle. *American Journal of Science* 299 (7-9): 697-723.

Carroll, R.L. 1988. *Vertebrate Palaeontology and Evolution.* New York: W.H. Freeman and Co.

Cerling, T.E., Ehleringer, J.R. and Harris, J.M. 1998. Carbon dioxide starvation, the development of C_4 ecosystems, and mammalian evolution. *Philosophical Transactions of the Royal Society of London [Biology]* 353 (1365): 159-170.

Chiappe, L.M. 1995. The first 85 million years of avian evolution. *Nature* 378 (6555): 349-355.

Clarkson, E.N.K. 1998. *Invertebrate Palaeontology and Evolution.* 4th ed. Oxford, etc.: Blackwell Sci. Ltd.

Cloud, P.E., Jr. 1974. Evolution of ecosystems. *American Scientist* 62 (1): 54-66.

Cloud, P.E., Jr. 1978. *Cosmos, Earth and Man: A Short History of the Universe.* New Haven: Yale Univ. Press

Cloud, P. and Gibor, A. 1970. The oxygen cycle. *Scientific American* 223 (3): 111-123.

Cody, M.L. 1974. Optimisation in ecology. *Science* 183: 1156-1184.

Cody, M.L. and Diamond, J.M. (eds) 1975. *Ecology and Evolution of Communities.* Cambridge, MA: Harvard Univ. Press.

Conway Morris, S. 2000. The Cambrian 'explosion': slow - fuse or megatonnage? *Proceedings of the National Academy of Sciences USA* 97 (9): 4426^1429.

Cowen, R. 1976. *History of Life.* New York: McGraw-Hill.

Cox, C.B., Healey, I.N. and Moore, P.D. 1973. *Biogeography: an Ecological and Evolutionary Approach.* Oxford, etc.: Blackwell Sci. Publ.

Darlington, P.J., Jr. 1957. *Zoogeography: The Geographical Distribution of Animals.* New York: Wiley.

Des Marais, D.J. 1997. Isotopic evolution of the biogeochemical carbon cycle during the Proterozoic eon. *Organic Geochemistry* 27: 185-193.

Diamond, J.M. 1975. Assembly of species communities. In: M.L. Cody and J.M. Diamond (eds) *Ecology and Evolution of Communities,* pp. 342-444. Cambridge, MA: Harvard Univ. Press.

DiMichele, W.A. and Hook, R.W. 1992. Paleozoic terrestrial ecocystems. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing (eds) *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals,* pp. 205-325. Chicago and London: Univ. of Chicago Press.

Dodd, J.R. and Stanton, R.J., Jr. 1990.*Paleoecology. Concepts and Applications.* 2nd ed. New York, etc.: Wiley-Interscience Publishers.

Dunbar, H.J. 1960. The evolution of stability in marine environments: natural selection at the level of the ecosystem. *American Naturalist* 94: 129-136.

Ehrenreich, A. and Widdel, F. 1994. Anaerobic oxidation of ferrous ion by purple bacteria, a new type of phototrophic metabolism. *Applied and Environmental Microbiology* 60: 4517-4526.

Fairbridge, R.W. and Jablonski, D. (eds) 1979. *Encyclopedia of Earth Sciences.* Vol. VII. *The Encyclopedia of Paleontology.* Stroudsburg: Dowden, Hutchinson and Ross, Inc.

Falkowski, P.G. 1997. Evolution of the nitrogen cycle and its influence on the biological sequestration of $C0_2$ in the ocean. *Nature* 387 (6630): 272-275.

Falkowski, P., Scholes, R.J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Hogberg, P., Linder, S., Mackenzie, F.T., Moore, B. Ill, Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V. and Steffen, W. 2000. The global carbon cycle: a test of our knowledge of Earth as a system. *Science* 290 (5490): 291-296.

Feduccia, A. 1995. Explosive evolution in Tertiary birds and mammals. *Science* 267 (5198): 637-638.

Fenchel, T. and Finlay, B.J. 1995. *Ecology and Evolution in Anoxic Worlds.* Oxford, etc.: Oxford Univ. Press.

Foley, R. 1987. *Another unique Species: Patterns in Human Evolutionary Ecology.* New York: Longman Group and J. Wiley and Sons.

Fox, R.F. 1988. *Energy and the Evolution of Life.* New York: W.H. Freeman and Co.

Gee, J.H.R. and Giller, PS. (eds) 1987. *Organisation of Communities: Past and Present.* Oxford, etc.: Blackwell Sci. Publ.

Gigch, J. van. 1981. *Applied General Systems Theory.* Book 1. Moscow: Mir Publ. (Russian transl.).

Glasby, G.B. 1998. Earliest life in the Archean: rapid dispersal of $C0_2$ - utilising bacteria from submarine hydrothermal vents. *Episodes* 21 (4): 252-256.

Golley, F.B. 1993. *A History of the Ecosystem Concept in Ecology: More than the Sum of the Parts.* New Haven, London: Yale Univ. Press.

Golubic, S. 2000. Microbial landscapes: Abu Dhabi and Shark Bay. In: L. Margulis, C. Matthews and A. Haselton (eds) *Environmental Evolution: Effects of the Origin and Evolution of Life on Planet Earth.* 2nd ed. Cambridge, MA and London: MIT Press.

Goodwin, B.C. and Webster, G.C. 1981. Rethinking the origin of species by natural selection. *Riv. di Biol.* 74 (1-2): 11-26.

Gottschalk, G. 1981. The anaerobic way of life of prokaryotes. In: M.P. Starr, H. Stolp, A.G. Triiper, A. Balows and H.G. Schlegel (eds) *The Prokaryotes: A Handbook on Habitats, Isolation, and Identification of Bacteria.* Vol. l, pp. 1415-1424. Berlin, etc.: Springer-Verlag.

Gould, S.J. 1982. Darwinism and the expansion of evolutionary theory. *Science* 216 (4544): 380-387.

Gould, S.J. 1994. The evolution of life on the earth. *Scientific American* 271 (4): 63-69.

Gould, S.J. and Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Ser. B* 205: 581-598.

Gould, S.J. and Lloyd, E.A. 1999. Individuality and adaptation across levels of selection: how shall we name and generalise the unit of Darwinism? *Proceedings of the National Academy of Sciences USA* 96 (21): 11904-11909.

Grant, V 1977. *Organismic Evolution.* San Francisco: W.H. Freeman and Co.

Gutzmer, J. and Beukes, N.J. 1998. Earliest laterites and possible evidence for terrestrial vegetation in the Early Proterozoic. *Geology 26* (3): 263-266.

Hayes, J.M., Kaplan, I.R. and Wedeking, K.W. 1983. Precambrian organic geochemistry, preservation of the record. In: J.W. Schopf (ed.) *Earth s Earliest Biosphere, its Origin and Evolution,* pp. 93-134. Princeton: Princeton Univ. Press.

Heckman, D.S., Geiser, D.M., Eidell, B.R., Stauffer, R.L., Kardos, N.L. and Hedges, S.B. 2001. Molecular evidence for the early colonisation of land by fungi and plants. *Science* 293 (5532): 1129-1133.

Herre, E.A., Knowlton, N., Mueller, U.G. and Rehner, S.A. 1999. The evolution of mutualism: exploring the paths between conflict and co-operation. *Trends in Ecology and Evolution* 14 (2): 49-53.

Holland, H.D. 1984. *The Chemical Evolution of the Atmosphere and the Oceans.* Princeton, NJ: Princeton Univ. Press.

Hunten, D.M. 1993. Atmospheric evolution of the terrestrial planets. *Science* 259: 915-920.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415—427.

Huxley, J.S. 1942. *Evolution: The Modern Synthesis.* London: G. Allen and Unwin.

Jacobs, B.F., Kingston, J.D. and Jacobs, L.L. 1999. The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden* 86 (2): 590-643.

Kareiva, P.M. and Bertness, M.D. 1997. Re-examining the role of positive interactions in communities. *Ecology* 78 (7): 1945.

Kasting, J.F. 1993. Earth's early atmosphere. *Science* 259: 920-926.

Kawata, M. 2002. Invasion of vacant niches and subsequent sympatric speciation. *Proceedings of the Royal Society of London. Ser. B* 269 (1486): 55-63.

Keddy, P. and Weiher, E. 1999. Introduction: the scope and goals of research on assembly rules. In: E. Weiher and P. Keddy (eds) *Ecological Assembly Rules: Perspectives, Advances, Retreats,* pp. 1-20. Cambridge: Cambridge Univ. Press.

Keller, L. (ed.) 1999. *Levels of Selection in Evolution.* Princeton, NJ: Princeton Univ. Press.

Kerr, R.A. 1999. Early life thrived despite earthly travails. *Science* 284 (5423): 2111-2113.

Knoll, A.H. 1991. End of the Proterozoic eon. *Scientific American* 265 (4): 42-49.

Knoll, A.H. and Carroll, S.B. 1999. Early animal evolution: emerging views from comparative biology and geology. *Science* 284 (5423): 2129-2137.

Kondrat'eva, E.N. 1974. Phototrophic bacteria. In: A.A. Fedorov (ed.) *Life of plants.* Vol. 1, pp. 323-336. Moscow: Prosveshchenie Publ. (in Russian).

Lekevicius, E. 1980. Multilevel selection as a consequence of functional hierarchy. In: K.L. Paaver, T.J. Sutt (eds) *Micro- and Macroevolution,* pp. 175-179. Tartu: Institute of Zoology and Botany, Tartu University (in Russian).

Lekevičius, E. 1985. Synthesis of functional and evolutionary biology as a problem of uniting two major types of explanation. In: R. Pavilionis (ed.) *Scientific Knowledge: Systemic Aspect,* pp. 119-135. Vilnius: Institute of Philosophy, Sociology and Law (in Russian).

Lekevičius, E. 1986. *Elements of a General Adaptation Theory.* Vilnius: Mokslas Publ. (in Russian).

Lekevičius, E. 1987. The conception of cascade selection: natural selection as functional constraints. In: J. Mlikovsky and VJ.A. Novak (eds) *Towards a New Synthesis in Evolutionary Biology. Proceedings of International Symposium,* pp. 193-195. Praha: Czechosl. Acad. Sci.

Lekevičius, E. 1997. *A Model of Adaptive Rearrangements on Community, Population and Organism Levels.* Thesis for Habilitation. Vilnius: Institute of Ecology.

Lekevičius, E. 2000. *Only an ecosystem is living. Not entirely traditional attitude towards the evolution of life.* Vilnius: Vilnius Univ. Publ. (in Lithuanian).

Lekevičius, E. and Balčiūnas, D. 1986. Polymorphism and complementarity in intraspecific relations: experiments on Daphnia. *Zhurnal obshchej biologii* 47 (2): 259-267 (in Russian).

Lengeler, J.W., Drews, G. and Schlegel, H.G. (eds) 1999. *Biology of the Prokaryotes.* Stuttgart, New York: Blackwell Sci. Publ.

Lenton, T.M. 1998. Gaia and natural selection. *Nature* 394 (6692): 439-447.

Lewontin, R.C. 1970. The units of selection. *Annual Review of Ecology and Systematics* 1: 1-18.

Lewontin, R.C. 1974. *The Genetic Basis of Evolutionary Change.* New York and London: Columbia Univ. Press.

Lewontin, R.C. 1978. Adaptation. *Scientific American* 239 (3): 157-161, 164-169.

Lewontin, R. 2000. *The Triple Helix: Gene, Organism, and Environment.* Cambridge, USA and London: Harvard Univ. Press.

Lovelock, J.E. 1979. *Gaia. A New Look at Life on Earth.* Oxford: Oxford Univ. Press.

MacArthur, R. 1968. The theory of the niche. In: R.C. Lewontin (ed.) *Population Biology and Evolution,* pp. 159-176. Syracuse: Syracuse Univ. Press.

Maden, B.E.H. 1995. No soup for starters? Autotrophy and the origin of metabolism. *Trends in Biochemical Science* 20: 337-341.

Maisey, J.G. 1994. Predator-prey relationships and trophic level reconstruction in a fossil fish community. *Environmental Biology of Fishes* 40: 1-22.

Margulis, L. 1981. *Symbiosis in Cell Evolution. Life and Its Environment on the Early Earth.* San Francisco: W.H. Freeman and Co.

Margulis, L. 1982. *Early Life.* Boston: Jones and Bartlett.

Margulis, L. and Sagan, D. 1997. *Microcosmos. Four Billion Years of Evolution from Our Microbial Ancestors.* Berkeley, etc.: Univ. of California Press.

Margulis, L., Matthews, C. and Haselton, A. (eds) 2000. *Environmental Evolution: Effects of the Origin and Evolution of Life on Planet Earth.* 2nd ed. Cambridge, MA and London: MIT Press.

Marshall, L.G. 1988. Land mammals and the Great American Interchange. *American Scientist* 76 (4): 380-388.

Marshall, L.G. 1994. The terror birds of South America. *Scientific American* 270 (2): 64-69.

Marshall, L.G., Webb, S.D., Sepkoski, J.J., Jr. and Raup, D.M. 1982. Mammalian evolution and the Great American Interchange. *Science* 215 (4538): 1351-1357.

Martin, W. and Muller, M. 1998. The hydrogen hypothesis for the first eukaryote. *Nature* 392: 37-41.

May, R.M. 1978. The evolution of ecological systems. *Scientific American* 239 (3): 161-175.

Mayr, E. 1961. Cause and effect in biology. *Science* 134: 1501-1506.

McClendon, J. 1999. The origin of life. *Earth- Science Reviews* 47: 71-93.

McMenamin, M. and McMenamin, D. 1994. *Hypersea: Life on Land.* New York: Columbia Univ. Press.

Miller, S.L. 1992. The prebiotic synthesis of organic compounds as a step toward the origin of life. In: J.W. Schopf (ed.) *Major Events in the History of Life,* pp. 1-28. Boston: Jones and Bartlett.

Mooney, H.A., Dunn, E.L., Shropshire, F. and Song, L. 1970. Vegetation comparisons between the Mediterranean climatic areas of California and Chile. *Flora* 159:480-496.

Narbonne, G.M. 1998. The Ediacara biota: a terminal Neoproterozoic experiment in the evolution of life. *Geological Society of America Today* 8 (2): 1-6.

Nisbet, E. 2000. The realms of Archaean life. *Nature* 405 (6787): 625-626.

Nisbet, E.G. and Sleep, N.H. 2001. The habitat and nature of early life. *Nature* 409 (6823): 1083-1091.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164: 262-270.

munity evolution. *Brookhaven Symposia in Biology* 22: 162-167.

Smith, J.M. and Szathmary, E. 1995. *The Major Transitions in Evolution.* Oxford, etc.: W.H. Freeman Spektrum.

Stanley, S.M. 1975. A theory of evolution above the species level. *Proceedings of the National Academy of Sciences USA* 72 (2): 646-650.

Stanley, S.M. 1999. *Earth System History.* New York: W.H. Freeman and Co.

Sturmbauer, C. 1998. Explosive speciation in cichlid fishes of the African Great Lakes: a dynamic model of adaptive radiation. *Journal of Fish Biology* 53 (A): 18-36.

Summons, R.E., Jahnke, L.L., Hope, J.M. and Logan, G.A. 1999. 2-Methylhopanoids as biomarkers for cyanobacterial oxygenic photosynthesis. *Nature* 400 (6744): 554-560.

Terborgh, J., Lopez, L., Nunez, V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveras, M., Ascanio, R., Adler, G.H., Lambert, T.D. and Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294 (5548): 1923-1926.

Thoday, J.M. 1958. Natural selection and biological progress. In: S.A. Barnett (ed.); A *Century of Darwin.* London: G. Allen and Unwin.

Timofeef-Resovsky, N.V., Vorontsov, N.N. and Yablokov, A.V. 1977. *A short overview of the theory of evolution.* Moscow: Nauka (in Russian).

Tobias, RV. 1992. Major Events in the History of Mankind. In: J.W. Schopf *(ed.) Major Events in the History of Life*, pp. 141-175. Boston: Jones and Bartlett.

Turner, G.F. 1999. Explosive speciation of African cichlid fishes. In: A.E. Magurran and R.M. May (eds)*Evolution of Biological Diversity,* pp. 113-129. Oxford: Oxford Univ. Press.

Ulanowicz, R.E. 1986. *Growth and Development: Ecosystems Phenomenology.* New York, etc.: Springer-Verlag.

Valiente-Banuet, A., Flores-Hernandez, N., Verdu, M. and Davila, P. 1998. The chaparral vegetation in Mexico under Nonmediterranean climate: the convergence and Madrean-Tethyan hypothesis reconsidered. *American Journal of Botany* 85 (10): 1398-1408.

Vermeij, G.J. 1987. *Evolution and Escalation: An Ecological History of Life.* Princeton, NJ: Princeton Univ. Press.

Vogel, F. 1983. Effect of cultural evolution on biological evolution in man. *Athandlungen derAkademie der Wissenschaften der DDR* 1: 265-277.

Walker, J.C.G. 1980. Atmospheric constraints on the evolution of metabolism. *Origins of Life* 10: 93-104.

Walther, G.R. 2000. Climatic forcing on the dispersal of exotic species. *Phytocoenologia* 30 (3-4): 409-430.

Weiher, E. and Keddy, P. (eds) 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats.* Cambridge: Cambridge Univ. Press.

Weill, J.C. and Reynaud, C.A. 1980. Somatic Darwinism *in vivo. Biosystems* 12 (1-2): 23-25.

Wicken, J.S. 1980. A thermodynamic theory of evolution. *Journal of Theoretical Biology* 87 (1): 9-23.

Widdel, E, Schnell, S., Heising, S., Ehrenreich, A., Assmus, B. and Schink, B. 1993. Ferrous iron oxidation by anoxygenic phototrophic bacteria. *Nature* 362:834-836.

Williams, G.C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought.* Princeton, NJ: Princeton Univ. Press.

Wilson, D.S. 1980. *The natural selection of populations and communities.* Menlo Park, CA: Benjamin/ Cummings.

Wilson, D.S. 1997. Biological communities as functionally organized units. *Ecology* 78 (7): 2018-2024.

Wilson, E.O. 1994. *The Diversity of Life.* London: Penguin Books.

Windley, B.F. (ed.) 1980. *The Early History of the Earth.* Moscow: Mir (Russian transi.).

Wing, S.L. and Sues, H.-D. 1992. Mesozoic and early Cenozoic terrestrial ecosystems. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing (eds) *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals,* pp. 327-416. Chicago and London: Univ. of Chicago Press.

Wray, G.A., Levinton, J.S. and Shapiro, L.H. 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. *Science 274(*5287): 568-573.

Wynne-Edwards, V.C. 1962. *Animal Dispersion in Relation to Social Behaviour.* Edinburgh, London: Oliver and Boyd.

Wynn-Williams, D.D. 1999. Evolution on planet Earth: origins and achievements. *Trends in Ecology and Evolution* 14 (10): 379-381.

Xiong, J, Fischer, W.M., Inoue, K., Nakahara, M. and Bauer, C.E. 2000. Molecular evidence for the early evolution of photosynthesis. *Science* 289: 1724-1730.

Yamagishi, S., Honda, M., Eguchi, K. and Thorstrom, R. 2001. Extreme endemic radiation of the Malagasy vangas (Aves : Passeriformes). *Journal of Molecular Evolution* 53 (1): 39-46.

Zavadsky, K..M. 1958. To the understanding of progress in organic nature. In: B.A. Chagin (ed.) *Development problems in nature and society,* pp. 78-120. Moscow and Leningrad: Academy of Sciences of the USSR (in Russian).

Zavarzin, G.A. 1979. Prokaryotic systems in relation to phylogeny of bacteria. *Zhurnal obshchej biologii* 40 (1): 5-16 (in Russian).

Zavarzin, G.A. 1995. Paradigm change in biology. *Vestnik Rossiiskoi Akademii nauk* 65 (1): 8-23 (in Russian).

Edmundas Lekevicius

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Monograph

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