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DISCUSSIONS

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# Evolution of Paleobiocommunities Is One of the Most Intractable Problems of Biostratigraphy

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**Abstract**—The biostratigraphic data accumulated to date on the subdivision of the Phanerozoic marine sequences make it possible to interpret the evolution features of not only low-ranking biotic taxa but also paleocommunities (assemblages), which can be considered as biotic groupings historically formed under certain conditions. Examples of their evolution stages in various Geomerida marine ecosystems are given. The opinion is stated about the need to intensify the research on this topic with the involvement of both geologists and biologists.

**Keywords:** biocommunities, successions, biostratigraphic zones, structuralism, and paleoecosystems

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## INTRODUCTION

Several years ago, the author of this paper already made attempt to highlight the problem of evolution features of the Phanerozoic communities with the hope of attracting attention of his colleagues to it and discussing this topic (Gladenkov, 2018). But, apparently, the fight against COVID and the resulting limit in contacts lowered the interest in this important problem. Therefore, after a short break, it seems appropriate to return to it in view of new data and new arguments.

The Earth's stratisphere is known to be a "stone repository" of successively recorded biosphere evolution from the origin of the Geomerida on the ancient Earth to the great diversity of present-day biotic communities. Along with that, the taxonomic biodiversity of life was considered as a *biocenotic continuity* in the geological history. Understanding of this fact opened up a new approach to the idea of the phasing of evolution of the organic world obtained owing to a considerable contribution of historical geology and paleontology. Namely, they played before and are currently playing a great role in the study of the formation ways of "former biospheres" (according to Vernadskii (1926)), which underwent a complex multistage history. The identified stages are recorded on multiscale *stratigraphic schemes* taking into account their features in connection with the uniqueness of different ecosystems making up the biosphere. It can be stated that modern stratigraphy, with its focus on studying the stratigraphic units as protocols of stage-by-stage historical changes in the *states* of individual ecosystems and the biosphere as a whole, seems to be a "biosphere" science from the standpoint of geological analysis.

Up to twenty different stratigraphic methods are currently used in the geological practice. They make it possible to distinguish stratigraphic units of different types at different scales. In addition to *basic* comprehensive rationale subdivisions including *general* (systems, series, stages, and chronozones), *regional* (horizons—regional stages and layers with geographic names), and *local* (groups, formations, and members) units, there is a separate block of *special* subdivisions of particular rationale (lithostratigraphic, biostratigraphic, climatostratigraphic, magnetostratigraphic, seismostratigraphic, etc.) (*Stratigraficheskii...*, 2019). Today, the biostratigraphic method is the most important (primarily for the Phanerozoic). The identification of detailed units on the stratigraphic schemes of all Phanerozoic systems, not only stages, but also biozones (with a duration of 0.2–3.0 Ma), can be considered as one of the most notable achievements of geology in recent decades.

## ZONES AS STRATIGRAPHIC UNITS AND THEIR TYPES

Many works, sections of stratigraphic codes, and reference books are devoted to the zone identification method. It would not be an exaggeration to state that obtaining the striking results of using zones in division and correlation of bottom sediments of modern oceans led to a whole era of "zonomania," which has continued to date. Currently, all Phanerozoic systems are provided, to one degree or another, with zonal subdivisions.

However, despite the undoubted achievements of zonal stratigraphy, some problems still remain unresolved. In a number of cases, this method for dividing

of ancient sequences, seemingly becoming familiar to many paleontologists, began to be used not entirely correctly, without full revelation of its capabilities and without trying to understand what scientific questions can be solved on its basis. It is surprising that many micropaleontologists (currently predominant among the zone creators) are occasionally not aware of the types of zones they use: *chronozones* as small units of “basic” subdivisions or various *biostratigraphic zones* related to “special” units. And this happens despite the fact that entire sections of the Stratigraphic Code of Russia (*Stratigraficheskii...*, 2019) and the International Stratigraphic Guide (*International...*, 1999) are devoted to this topic, as well as the chapters of many monographs and special papers.

From analysis of the latter, two types of *special biostratigraphic zones* are used most often in practice—*interval zones and assemblage zones*. Interval zones are a set of layers between two identified biohorizons (*datum levels*). In general, these are levels of appearance or extinction of any one or different taxa in the section. Assemblage zones are bodies of layers characterized by an assemblage of three or more taxa which are different from complexes of underlying and overlying layers. According to the Stratigraphic Code of Russia (*Stratigraficheskii...*, 2019), an assemblage zone should have a stratotype, while a zonal assemblage can contain different fossil groups of the same or different ranks. The assemblage zone is drastically different from the interval zone in this feature.

The zones have become so widely accepted in the geological practice that all current regional and summary works on stratigraphy are simply unconceivable without a zonal component. Although the zones are still not subdivisions of the International Stratigraphic Scale, they are always used to characterize its most detailed units such as stages (for example, *Geologic...*, 2020). According to geological practice, biostratigraphic zones are distinguished, in particular, in the Cenozoic bottom sediments of all oceans (and more than 3000 deep-sea cores have been drilled to date) and make it possible to correlate sedimentary deposits of different basins. On the other hand, zonal categories are often used in the creation of regional stratigraphic schemes in the study of sections of ancient sequences on land. A notable illustration in this regard can be the voluminous summary “Zonal Stratigraphy of the Phanerozoic in Russia” (*Zonal'naya...*, 2006). This summary contains almost all data of recent decades on the zones of the Russian Phanerozoic geological systems with a detailed study of their features.

Three aspects should be taken into account in the study of zones. The first aspect is actually stratigraphic: identifying the succession of layers with different age assemblages accompanied by testing the isochronism of biozonal boundaries and event ranges used as an additional basis for interregional and sub-global stratigraphic correlations. The second aspect is

biological: identifying the evolution trends in different biotic groups and communities. The third aspect concerns paleobiogeographic reconstructions (analysis of timewise changes in the taxa ranges and groups in different sea basins).

In general, the zones are used by paleontologists (primarily micropaleontologists) who study successive *orthostratigraphic* groups of fauna and flora in sections. Many publications are focused on this topic. A striking example in this regard is the Cenozoic zones identified during deep-sea drilling of the ocean floor based on foraminifera, nannoplankton, radiolarians, etc. These parallel zones (subglobal and interregional) have long become an integral part of stratigraphic research. For instance, the foraminifera zones of the tropical belt of the Atlantic, Indian, and Pacific oceans identified in the second half of the last century are used in almost all modern stratigraphic schemes. In the Paleogene, there were 22 zones, and in the Neogene, they numbered about 20. They were assigned the corresponding numbering which has long become familiar to all specialists. In Russia, V.A. Krasheninnikov (1980), who participated in many deep-sea drilling cruises, made a particularly great contribution to the research on this topic.

Meanwhile, it should be noted that the zones are also distinguished based on *parastratigraphic* groups. As is known, the Russian practice often uses the subdivisions such as *horizons* (and regional stages), the basic units of regional stratigraphic schemes. Horizons as sets of rocks formed at certain stages of geological history in the region are usually identified on the basis, on one hand, of lithological features of deposits and, on the other hand, of their paleontological characteristics. In general, *chronozones* identified on the basis of assemblage zones and horizons, taking into account their biostratigraphic base, are similar in terms of methodology. Therefore, back in the 1950s, Stepanov (1958) drew an analogy between *oppelzones* (actually *chronozones*) and horizons and emphasized the similarity of the basis of their identification. Within Russia, many Phanerozoic horizons (and perhaps most of them) were identified in the past based on a shallow-water fauna, primarily from benthic groups. However, if we compare horizons of different sea basins (platform, epicontinental, semi-enclosed, shelf, and open ocean varieties), we will find a certain difference between them. The latter can be observed, for example, as the difference in their formation time (“duration”). This fact can be indicative of different rates of development of bio-assemblages in different provinces; evolution features of bio-assemblages and their individual parts (with gradualistic and catastrophic changes in communities); different numbers of endemic forms in the assemblages; etc.

We can find many examples in this regard in the Russian literature, in particular, the marine Neogene horizons of the Eastern Paratethys identified based on mollusks at the beginning of the last century by

N.I. Andrusov and L.Sh. Davitashvili and used for more than 120 years (Nevesskaya, 1999). Fourteen horizons with an average “duration” of about 1.0–1.5 m.y. were noted in this case. The analysis of mollusk assemblages alternating in the sections led to the identification of speciation outbreaks in the Neogene history of the basin and the appearance of dozens of endemic species and genera in many horizons (Solenovsky, Kotsakhursky, Sarmatsky, Pontichesky, Akchagylsky, and Apsheronky). This phenomenon is related to the isolation period of the Black Sea–Caspian basin or, conversely, its connection to the Mediterranean basin. In this case, a relatively rapid change in ecological and paleogeographical settings led to rapid evolution transformations and changes in mollusk communities under the conditions of lower competition (Popov et al., 2005). Unfortunately, the correlation of these horizons with the International Stratigraphic Scale still remains largely conventional because of the lack of zonal schemes based on plankton (diatoms and calcareous nannofossils were identified only from individual layers). But from a methodological point of view, these data obtained in the “natural” laboratory of the Neogene of the Ponto–Caspian Sea are unique.

The second example is the marine Cenozoic horizons (Neogene and Paleogene) identified in a completely different region, namely, Kamchatka and Sakhalin, which belong to the transition zone from the North Pacific to the Asian continent. The first real attempts to substantiate them using marine mollusks were made by Krishtofovich (1961) in the late 1950s and early 1960s. Over the decades that passed since then, the horizons were relatively completely described and often used in the geological practice (*Resheniya...*, 1998). If we analyze, for example, the Western Kamchatka Neogene horizons (from bottom to top, Kuluvenky, Il’insky, Kakertsky, Etolonsky, Ermanovsky, and Enemtensky), then certain features of their biocommunities will be revealed. First of all, each successive horizon is characterized by a renewed species composition of paleo-assemblages (up to 30–50%), and the latter contain autochthonous and allochthonous elements. The average duration of formation of these horizons can be estimated at about 3 m.y. (within 2–5 m.y.). In these time periods, assemblages of each horizon generally retained their composition and apparently correspond to periods of certain dynamic equilibrium. Along with that, the Neogene horizons were distinguished by a consistent change in the number of living forms: from 10% in the Early Miocene to 40–50% in the Late Miocene, 60–65% in the Pliocene, and 96–98% in the Eopleistocene. It should be emphasized that groupings of mollusk species changed while the trophic zonation common to the Cenozoic in this region remained unchanged (paleobiocenoses of the mainly sublittoral zone are analyzed in this case). Along with that, each horizon is characterized by certain changes in leading and characteristic species and dominants (partially,

perhaps owing to facies changes in the layers). The horizons usually contain their own endemic species reaching 10–40% of the total assemblage. It is noteworthy that communities change without catastrophic extinctions, even at occasional paleotemperature variations in Arctic–Boreal waters.

The list of similar examples of the use of paleocommunities in identifying the regional stratigraphic units can be continued. For instance, Ganelin et al. (2001) identified 9 horizons and 17 assemblage zones based on the succession of brachiopod and bivalve assemblages in the Upper Paleozoic section of the North-eastern region. In particular, these data served as the basis for the creation of regional stratigraphic schemes currently used in geological practice. The data on the Ordovician of Siberia can be viewed in a similar way: according to the succession of brachiopod and trilobite assemblages, up to 14 biozones were identified and used to characterize the horizons. The data on the Ordovician–Devonian in a number of regions (Boucot, 1975) will also be discussed below.

#### TWO POINTS OF VIEW ON BIOCOMMUNITIES AND METHODS OF STUDY

When analyzing zones and horizons, special attention should be paid to their biotic characteristic features. This means in terms of practice that we should study not only individual taxa (species and genera), as is often done by many researchers, but also *biota communities*. As mentioned above, the author made an attempt several years ago to draw attention to certain issues on this topic (Gladnikov, 2018). The communities are often called “assemblages,” “associations,” “groups,” “biocenoses,” etc., in the scientific literature. Taking into account the available interpretations of these terms, we can give the following definition to the concept of community: *community is an assemblage of organisms of one species (population) or a unique set of different species due to ecological conjugation in a certain area of a water body or land*. Owing to the fact that the stratigrapher deals with fossil communities, “paleo” in appropriate terms defines the difference between fossil and present-day assemblages (in terms of duration of their formation, degree of preservation of remains, taxonomic completeness, and representativeness of their elements). In view of the aforesaid, *paleocommunity (or paleobiocenosis) can be defined as a grouping of organisms which historically developed under certain conditions with the smallest competition with each other*. In the literature, the term “succession” is often used when analyzing their sequences in sections. It means changes in communities in a relatively short period of time. In our case, the concept of “paleosuccession” is likely more acceptable. It has a slightly different meaning: a phenomenon of changes in ancient communities against the background of evolution processes of geological time.

This term usually refers to the change of certain *orycto-* or *taphocenoses* noted in the sections. It should be noted that the reasons causing temporary changes in cenoses may be different. In addition, the communities can be studied in different directions: not only in terms of systematic composition but also in terms of dominants or structure (monodominant, oligodominant, and polydominant groups).

On the basis of the analysis of biotic paleoassemblages of horizons and zones, their changes in sedimentary sections of all Phanerozoic systems record changes in *certain conditions of ecosystem development*. Seven regional horizons with a “duration” of about 2–5 m.y. were identified precisely taking into account changes in the Neogene mollusk assemblages in the shelf-type sections of the Kamchatka–Sakhalin region (Gladenkov, 2018). Sedimentary sequences in the aforementioned examples were divided on the same basis.

In general, the communities can be considered as a living element of ecosystems (according to Tansley, 1935) or biogeocenoses (according to Sukachev, 1942). And if ecosystems make up the biosphere, then their “living” components can also be summed up on a global scale, in particular, in a concept called *Geomerida*. This term was first proposed by K.D. Starynkevich in 1918, when he, working at the Taurida University of Crimea, made a report which served as the basis for a future publication on the “structure of life.” It was then that he began to use the concept of “merida” understood as “an organic integral element,” i.e., a part of what we call ecosystems today. These meridas form that integrity on the scale of the biosphere which he called Geomerida (from the word “Gea” meaning the Earth). The ideas by K.D. Starynkevich, who left Russia during the Civil War and died abroad in 1926, were recorded in a brochure which, on the basis of Starynkevich’s manuscript, was later published in Prague by G.V. Vernadskii (Starynkevich, 1931). It should be noted that the Geomerida concept likely known in the 1920s only to some of Starynkevich’s colleagues began to be actively used in the Russia and the Soviet Union from the late 1920s, after well-known publications on this topic by V.N. Beklemishev (1928, 1951, etc.).

The accumulation of data on biocommunities (living and fossil) requires understanding the essence of their development. Therefore, their role in ecosystems and the biosphere has become especially actively discussed recently. Biologists (especially botanists) have written about it for several decades. Recently, Zhirkov (2010) studied two concepts that differently reveal the position of communities in natural systems. (1) The concept of continualism was proposed by L.G. Ramenskii (1971) and H.A. Gleason (1939), Soviet and American geobotanists, in the 1920s. It is based on the following basic principles: (a) species evolve from each other against the background of local

abiotic conditions, (b) random combinations of species gradually transform into one another (continuum), and (c) in fact, there are two life organization levels such as organisms and the biosphere. (2) The *structuralism* concept was proposed somewhat later. This paradigm was developed by American geobotanists F.E. Clements and V.E. Shelford (1939) and Soviet scientist S.M. Razumovskii (1981). It is based on another ideas: (a) the biosphere has an endogenic structure, and discrete structures have boundaries; (b) structures evolve as *a single whole* (it should be emphasized!), and species become ecosystem elements in the course of the evolution; and (c) the ecosystem response to external influences depends on the species composition and the stage of succession.

If we analyze marine fossil bioassemblages of regional horizons from the standpoint of the mentioned concepts, we can come to the conclusion that they are elements of past ecosystems and developed over time as some kind of relatively isolated units (as a “single whole”). In other words, many of us, consciously or unconsciously, are proponents of the structuralism concept. And we have to admit that the central place previously occupied by the individual (species) in reconstructions is already transferring to *communities*. The fact that the existence of a species outside a community is impossible becomes more and more evident, and when we use the term “stable equilibrium,” it characterizes the evolution not of an individual taxon, but of a community.

Apparently, many development features of paleocenoses depend on the *size* of ecosystems and the degree of their *isolation*, the confinement of communities to certain *climatic zones*, specific features of *natural conditions* within *provinces*, characteristic features of the systematic composition of taxa, complexity of the community structure, etc.

Voluminous useful data on the community structure and distribution in sea basins can be found in a number of works published by hydrobiologists. In the early 1960s, R.F. Gekker drew the author’s attention to the new data obtained by Kuznetsov (1963) published at that time on living benthic invertebrates in sea waters off Kamchatka. His works focusing on marine biocenoses (including mollusks) in the shelf zone of Eastern Kamchatka and the Kuril Islands are of particular importance for the analysis of the Cenozoic assemblages in the Kamchatka stratigraphic horizons, because these paleobiocenoses are certainly similar to living cenoses in their generic composition, structural features, and settlement on the seabed. According to the research results obtained by A.P. Kuznetsov, a *vertical* and related *trophic zonation* plays an important role in the formation of specific biocenoses on the shelf. The trophic zonation reflects a number of similar adaptive features owing to a similar way of life in organisms of different systematic groups. The main factor affecting the zonation is animal nutrition conditions. The feeding features depend on food, bottom topography,

water circulation, their saturation with suspended material, sedimentation rate, richness of organic matter in surface bottom sediments, degree of aeration, mechanical composition of the soil, etc. As a result, a certain combination of these factors leads to the zonal distribution of different groups of organisms. There are four such trophic zones within the shelves.

The first zone, represented by *immobile sestonophages*, occupies the areas of mass development of filter feeders capable of passing through large volumes of water to obtain food. Typical mollusk representatives include *Mytilus*, *Modiolus*, *Musculus*, and *Saxicava*. This zone is located in the shallowest areas with a depth of about 0–50 m. Boulder–pebble soils are common in these areas; strong bottom currents and abundant suspended material are noted.

The second zone, represented by *mobile and sedentary sestonophages*, includes areas of distribution of organisms with weak hunting apparatuses. These forms are characteristic for a depth of up to 100 m, where sandy soils are typical and water mobility is sufficient to maintain the organic seston groundmass in suspension in the bottom water layer. Mollusks include different species of *Astarte*, *Cardium*, *Serripes*, etc.

The third zone, represented by *surface deposit detritivores*, is located in the zone of mass development of genera such as *Acila*, *Macoma*, *Yoldia*, and *Tellina*. Their forms have special organs for searching the bottom and collecting organic detritus on its surface. This zone is generally confined to the lower part of the sublittoral and partly to the upper bathyal to depths from 100–200 to 300 m or more, where silty soils are common and calm areas with slow currents are typical.

The fourth zone, represented by *subsurface deposit feeders*, coincides with the bathyal (with clayey soils, slow-moving waters, often with oxygen deficiency). Mollusks are extremely rare in this area. It is evident that this zoning can be complicated. In particular, it can be affected by the steepness of the shelf (it is easier to recognize this zonation on a flat shelf than on a narrow one), features of sedimentation processes, and other factors.

A.P. Kuznetsov not only analyzed biocenoses, having highlighted their characteristic features depending on the trophic and temperature zonation of sea waters, but also made an interesting assumption about characteristic features of relationships between the species. It is assumed that both “positive” (close) and “negative” (interspecific) relationships are observed in the studied biocenoses. The latter relationship is apparently the predominant one, because, according to A.P. Kuznetsov, the species included in the biocenosis, especially the mass ones, are mostly “selected” from organisms with different requirements for the environment and are least dependent on each other. In other words, on the basis of this interpretation, biocenosis is a grouping of organisms developed under certain conditions and almost devoid of any competition with each other.

Many paleontologists have used the data from hydrobiologists on mollusk biocommunities in their research for a long time. For example, they include works on the Paleogene of the Fergana Gulf (Gekker et al., 1962), on the Neogene of Paratethys (Neveskaya, 1999), on the Neogene of Sakhalin (Zhidkova et al., 1974), on the Permian of Northeast Asia (Ganelin et al., 2001), etc. It turns out that it is necessary to pay attention to certain features which distinguish communities in *different types* of past basins: closed, semi-closed, epicontinental, shelf, and oceanic. And these features reveal similar and different characteristics of the geological development of various ecosystems. On the basis of the data studied, when analyzing fossil communities, paleontologists can now use many hydrobiological data which previously escaped attention, in particular, a certain isolation (or “integrity”) of species groupings noted in their commonly cyclical change within individual areas or facies zones of sea basins. It may be worth adding a caveat. This paper is focused on marine biological communities which are actually relatively shallow. But it should be taken into account that geologists made an important discovery about 50 years ago: the widespread occurrence of autolithotrophic communities in the ocean depths, whose trophic basis was bacteria feeding not on solar energy, but on endogenic energy of hydrothermal sources. Recently, a wide distribution of similar ecosystems has been discovered in the Late Paleozoic of both hemispheres (Ganelin, 2022). They are not analyzed below.

#### SOME FEATURES OF FOSSIL COMMUNITIES AND THEIR STRATIGRAPHIC TURNOVER

It is natural to expect that the paleontological data play an extremely important role in solving the problem under discussion. We can somehow imagine the community evolution in geological time from changes in paleontological assemblages in the sections. The paleontologists’ works contain many observations and thoughts which require a substantive discussion. For example, the suggestion that the community evolution can go in the direction of both strengthening the interconnections of organisms and minimizing interspecific relationships, and that an evolution is controlled by the biotic environment. In this regard, we should remember, for example, the ideas proposed by Krasilov (2001) related to the coherent and incoherent evolution of ecosystems. When considering the development features of cenotic systems, it is necessary to take into account, on one hand, the integrity of these systems in certain periods of time supported by a constant species composition and a certain set of niches and, on the other hand, the direction of evolution of cenotic systems related to an increase in the number of niches or in the density of their packing. Each cenotic system can evolve not only in a stable environment through restructuring periods for internal reasons with changes

in species but also in a changing environment (for example, climate variations) also with changes in species. In other words, in all cases, one system is replaced by another with partial changes in the number and composition of species. And it is evident that when analyzing paleosuccessions, it should be taken into account that they differ in occurring changes, in species composition trends, in scale, in time duration, in constancy of the succession process, in origin of communities, etc.

From the standpoint of studying the trends of natural communities, the biotic changes can generally be subdivided into *endogenic* and *exogenic*. The driving force of endogenic changes is the functioning of assemblages. Meanwhile, external influences can also lead to the replacement of one community by another in the same cenotic system with the subsequent development of endogenic succession. In this case, we should distinguish between “paleosuccessions” in the cenotic system and “changes” in groupings of species. The former seem to record historical strictly determined processes, while the latter represent a stochastic process of transformation of one group into another.

As is known, the boundaries of areas of communities are marked by transitional (usually relatively narrow) zones some of which are classified as *ecotones*. Distinctness (clarity) of these boundaries varies. It can be considered that the boundaries between associations of one cenotic system are usually ecological, and those between associations of different cenotic systems are biogeographical. According to the spatial displacement of such boundaries in successive time intervals, it is possible to reconstruct the scale and nature of migration of paleocommunities and find their reasons (changes in the paleoclimate, etc.). By example of mollusks of Tertiary communities in the North Pacific region, the author was able to show that ecotones occasionally (in particular, during global warmings in the Early Eocene, Middle Miocene, and Early Pliocene) moved to the North Pacific region from the south (from Japan) to the north (almost to the Bering Strait) by 2000–3000 km (Gladenkov, 2004, 2015).

Synthesizing all this information, we finally come to the question: How do individual “meridas” evolve? It should be admitted that, in my opinion, a clear idea has not been formed yet. There are probably some things we are not yet prepared for. It may be hard for us to find the place of this phenomenon in the general biosphere evolution process, and we often lack the ability to determine a desired direction of analysis among complicated problems of natural science, because the practical research is usually focused on relatively narrow problems. Therefore, rarely does anyone rise to large generalizations, although serious attempts by individual researchers to highlight various aspects of the problem under consideration, as mentioned above, are already being made. For instance, the latest papers by Zherikhin (2003) raised important

questions related to features of internal structure of biocommunities, confinement of their individual elements to different niches, etc.

As to a range of works related to the study of ancient communities, it is important to note the study by Boucot (1975) devoted to the factors controlling the rate of evolution and extinction of the Silurian–Devonian brachiopod cenoses. According to A.J. Boucot, the development of communities combines the consequences of both *organic* and *biogeographic* evolution, but it is still an independent process. When analyzing the fossil communities, we have to take into account many difficulties and even allow for a certain generalization of data. For example, we often have to combine different ecological groups into one community (in particular, assemblages of various trophic zones related to the vertical seabed zonation are combined into a *shelf community* for purposes of simplicity). In this case, communities of a “flat” (relatively wide) bottom (the simplest for analysis) are a special case.

The evolution of communities, according to A.J. Boucot, can be understood in different ways. In some cases, the evolution of a community coincides with the organic evolution, when related descendants originated from ancestors of the previous community, etc. In other cases, taxa from unrelated communities can co-occur with them owing to their migration and subsequent adaptation to environmental requirements. Cosmopolitan taxa usually evolve more slowly than provincial ones. On the basis of the Silurian–Devonian benthic groups studied, Boucot pays special attention to the *inverse* relationship between the *size* of populations and the *rate* of evolution and extinction. This is his main conclusion. And the struggle for food and living space is obviously not the primary factor affecting the rate of evolution. Meanwhile, the noted pattern (or, in more careful terms, the revealed observation which can turn out to be a special case) does not always find confirmation when studying other groups. For example, a large area of microplankton communities (foraminifera, nannoplankton, etc.) in the Cenozoic (it is a huge warm-water area of three oceans—Atlantic, Pacific, and Indian) apparently did not become an obstacle to reducing the rate of microplankton evolution. This statement is supported by the quite detailed biostratigraphic zonations designed in the oceans.

#### SOME DISPUTABLE ISSUES AND THEIR DISCUSSION

The author of this paper is not a biologist and, therefore, cannot participate in determining the best theory (or hypothesis) of evolution of the organic world on the Earth. But in order to somehow decide on the idea of the development of communities in line with the available hypotheses, he would like to at least outline a direction in which the problem of paleobiocenoses can be considered.

As is known, Darwinism and the synthetic theory of evolution give their well-known interpretation of development of the organic world, in particular, speciation. The main driving factor of evolution is considered to be *natural selection* based on the selection of random and small mutations. Despite the fact that Darwinism was accepted by many biologists and paleontologists as the main idea of development, a number of specialists called into question this theory. And it concerned various aspects.

For example, Vernadskii (1926, 1988) rejected the monophyletic evolution of Charles Darwin with its idea of the origin of life from one or a few ancestors. In his opinion, life from the very beginning could only have existed as a biosphere in a complex of physico-chemical connections of living, inert, and bioinert material in the field of a gigantic planetary geological process. Therefore, the unity of all living organisms, according to V.I. Vernadskii, was related to the common spatiotemporal and material–energy base (Vernadskii, 1988). In general, he contrasted Darwin's principle of “struggle for existence” (with its natural selection) rather with the “principle of solidarity” discussed in Russia by P.A. Kropotkin and K.F. Kestner more than a hundred years ago (Vorontsov, 1999). From this point of view, the presence of separate biocommunities at different stratigraphic levels should not be surprising.

Among those who disagreed with Charles Darwin was, in particular, L.S. Berg, who proposed the concept of *nomogenesis* in the 1920s (Berg, 1922). In his opinion, the selection process does not involve a selection of extreme deviations, but it cuts them off, maintaining the species at the acquired height; in other words, “it keeps the norm.” New organic forms do not occur by chance, but naturally, because the formation of new characteristic features proceeds in a certain direction based on autonomous and choronomic reasons. And this process is accompanied by mass transmutations. In other words, the development of new forms needs the occurrence of new characteristic features over vast areas immediately in a huge number of individuals. In this case, new characteristic features are formed mainly in the process of geographic separation (isolation) of organisms. The development of new forms through the geographic isolation needs a huge number of individuals to be subjected to modifications at once in a large area. Among various and special geographic isolation cases, L.S. Berg points out lake isolation, separation of adjacent regions by isthmuses, and isolation in mountains, in deserts, and on islands. Separately, he relates modifications of species to the influence of environmental changes over time, etc. It follows from these constructions that it is impossible to consider the issues of changes in paleobiocommunities without taking into account the geographic factor. L.S. Berg had many supporters in Russia including Sobolev (1924), Lyubishchev (1973), Meyen (1974, 1989), and others.

Meanwhile, another question arises: What ensures the different-scale stages and periodicity of changes in biocommunities of various biochories of the past? Despite all heterogeneous interpretations of the phasing of biosphere development in the scientific literature, attempts are made more and more often to identify different-scale *biosphere rhythms* recording the direction of its evolution. Mass extinctions of biota that apparently occurred with a certain periodicity can be considered as a particular result of this process (Alekseev, 1989). Of them, four or five are considered “major” and about 15 are considered “minor.” The intervals between them are about 30 m.y. (about 37 m.y. in the Paleozoic, 26 m.y. in the Mesozoic and Cenozoic), although they do not always correspond to these ranges. The duration of global biotic crises is estimated to be up to 10–15 m.y. (they record a simplification of community structure, a reduction in biodiversity, etc.). On the other hand, a number of works (in particular, Shimanskii, 1987) outlined major stages in the evolution of the organic world in the Phanerozoic used to identify geological systems and series. And in one of his latest works devoted to the general problems of development of the biosphere and Geomerida, Sokolov (2010a, 2010b) presented a visual drawing (Fig. 1) that was based on the latest generalized geological materials and recorded certain stages of a long-term evolutionary process, starting from the formation of the Earth, in particular, from the Archean, to the end of the Phanerozoic (Neogene and Quaternary). Figure 1 actually demonstrates a whole worldview in the field of the geological history of our planet (it is given in the author's version of 2010, although now it can be supplemented or corrected by new data obtained).

But our practical work is usually focused on smaller scale phenomena revealed when studying communities of individual paleoecosystems (for example, shelf zones of the boreal or tropical belts, etc.). For this reason, the identification of a smaller periodicity in changes of biotic communities in the sections of ancient sequences seems to be one of the promising areas of biostratigraphic research. In other words, the set objective is to interpret phasing of development of the organic world *at different biosphere organization levels* and in different ecosystems (different in geographic location, size, degree of isolation, etc.). In practice, this means that, against the background of long-term stages (or waves) of evolution, it is necessary to identify smaller phases which are often clear in the sections of ancient sequences in some regions and their parts.

When returning to the specific data which make it possible to move in this direction, we should note several features of paleo-assemblages studied in the Cenozoic of the Sakhalin–Kamchatka region. From the analysis of the aforementioned data, even in the variable paleogeographic environment of the Cenozoic (for almost 65 m.y.), the generally boreal biotic communities sought to preserve their structure as a

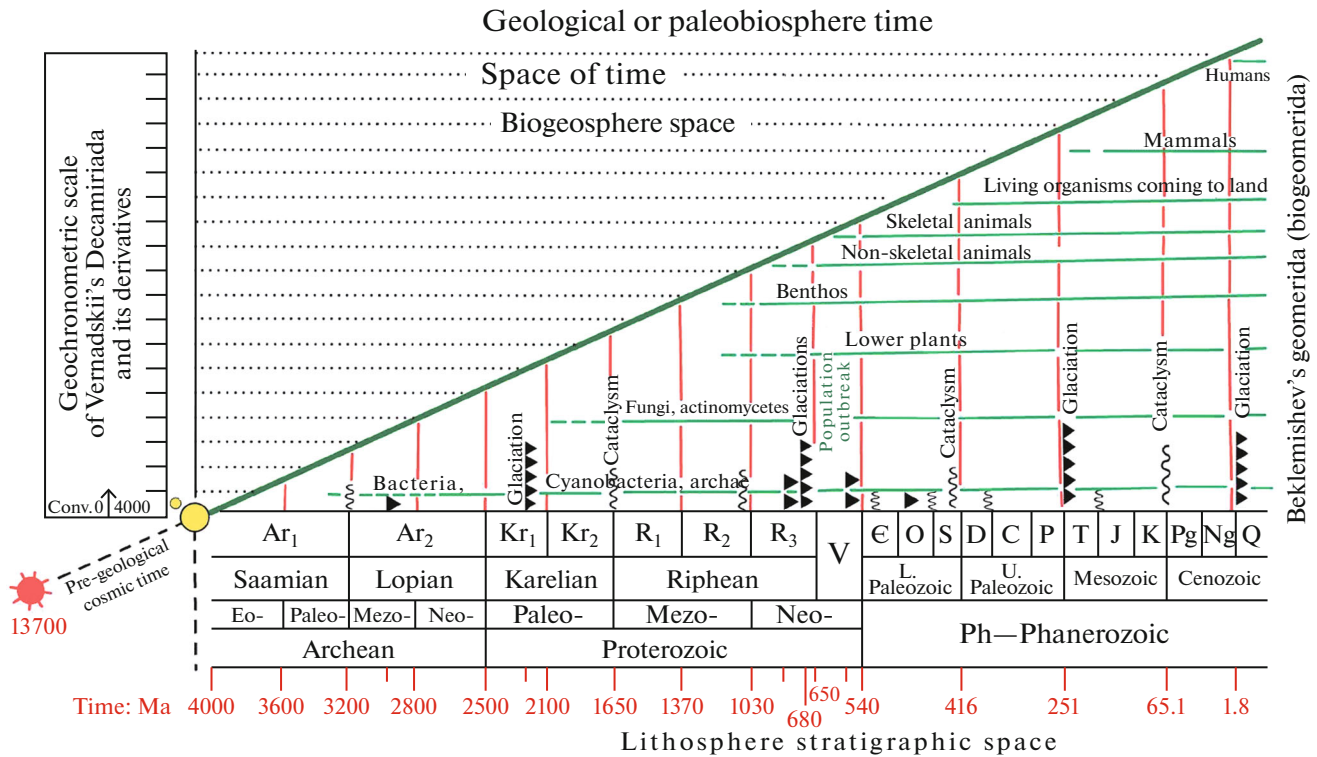


Fig. 1. Time in its uneven event divisions (stages) (according to Sokolov, 2010a, 2010b).

whole (within trophic zonation) and, in this regard, were conservative to some extent. This phenomenon—*community homeostasis*—is apparently accomplished through a well-functioning system of trophic relationships. In particular, mollusks of the biocenoses discussed above are included in the chain of consumers. Their systematic composition is believed to be partially controlled by competitive and nutritional relationships of their forms. Therefore, mollusk biocenoses acquire integrity, stability, and relatively independent elements of development. Along with that, from stage to stage, bioassemblages regenerate, while maintaining a certain continuity. Meanwhile, in some cases, we have to reckon with migrants occurring in them. For example, warm-water “aliens,” namely, taxa of “Japanese origin” (*Arca*, *Ostrea*, and *Glycymeris*), join the Sakhalin and Kamchatka (generally boreal) assemblages in the warming periods, whereas in the climatic cooling periods, arcto-boreal taxa (*Astarte*, *Portlandella*, and *Neptunea*) are observed in Japan. In a number of cases, we can note stages of formation, flourishing, and extinction of certain species and genera, but at the same time, paleocommunities of individual horizons are perceived, first of all, as *integral* assemblages.

In general, the question of direction, rate, and processes of evolution of communities, rather than species, in ecosystems remains, unfortunately, far from being resolved. We can give a long list of famous scien-

tists who addressed this problem to some extent. For example, Simpson (1944) paid special attention to the difficulties of estimating the rates of group evolution. Mayr (1970) noted the need to take into account the population structure of species. Timofeev-Resovsky et al. (1977) proposed the ideas of evolution of biogeocenoses, etc. However, no coherent concept has been proposed yet, and considerations on this topic are limited only to individual general theses. It is no coincidence, given the difficulties of solving these problems, that N.V. Timofeev-Resovsky et al. suggested that it would require the studies of two to three generations. And we should admit that, although one generation has already changed, the ways to solve the problem still remain generally unclear.

Meanwhile, we can already state that, when solving these issues, it is obviously necessary to separately consider and take into account certain features of *different-type ecosystems* (their different size, confinement to certain latitudes, degree of isolation, etc.) where natural processes are characterized by some differences. This paper is limited to the general problem statement. Despite the fact that it follows from the above-mentioned information that a general phasing in development of the biosphere can be considered as identified (with recording in the Geomerida evolution), it can also be stated that, against this background, its individual different-scale ecosystems develop in phases and with their own characteristic



features. And this statement is recorded in the “meridas” of K.D. Starynkevich and in the corresponding stage-by-stage change of biotic communities of these different meridas. In synthesis, this likely testifies in favor of a number of the above-mentioned ideas proposed by L.S. Berg. It is hoped that the identification of specific phasing features of different ecosystems recorded by the stratigraphic change of biocommunities in the sections of ancient sequences and the determination of the corresponding general trends will ultimately make it possible to achieve the objectives set.

## CONCLUSIONS

Biostratigraphers and paleontologists have at their disposal a huge data bank on paleocommunities in the entire marine Phanerozoic. They are the basis for the identification of stratigraphic units: *special* (in particular, biostratigraphic) units including, for example, assemblage zones, and *basic* ones represented by horizons (and oppezone). The latter are actively used in creating the regional stratigraphic schemes. A targeted synthesis of this data could really help solve the problem of *evolution of communities*. But, apparently, the time for this has not yet come. Meanwhile, it becomes evident that we should stop limiting ourselves only to studying the stratigraphic position of individual taxa (species). We should reconstruct the course and direction of changes in *integral biocommunities* recording the evolution of certain ecosystems. The synthesis of these data can make it possible to consider certain features of changes in paleoecosystems in the integral biosphere process. The earlier collected data on the biological structure and biogeocenology of the living and past ocean, recorded to some extent in the generalizations in recent decades by oceanologists, biologists, and paleontologists (Zenkevich, 1947, 1963; Nevesskaya, 1999; Zhirkov 2010, etc.), in view of new ideas of the development of paleosystems, can be interpreted in a new way.

There is an open question with no clear answer yet. To what is the phasing of their development related: to the self-development of biocommunities in the current natural environments or to the controlling influence on Geomerida and the biosphere of cosmic processes whose role is still not entirely clear, but apparently extremely important (for example, Obridko et al., 2013)? Perhaps, we underestimate (or, more precisely, do not know how to directly estimate) the cosmic impact caused by the quasiperiodic interactions of the Sun and Solar System with stars in the jet streams of the Galaxy. Modern stratigraphy, with its focus on studying stratigraphic units as protocols of changes in the *states* of terrestrial paleoecosystems and the biosphere as a whole, can rightfully be called “*biosphere stratigraphy*” (Gladenkov, 2004). After all, on the basis of the study of a layered structure of the Earth’s crust, it is focused on solving the most important general geological problem—*identifying the natural periodicity*

*of the geological development of the Earth*. But in any case, against this general background of global natural processes, the problem of identifying the features of evolution of individual ecosystems (with their biotic communities), primary objects of study for geologists and paleontologists, will always remain unresolved. The solution of the problem will require a more reasonable comparison (correlation) of the stages of development of individual and different ecosystems. This approach is impossible to implement without the use of physical, geochemical, and other methods (palaeomagnetic, isotope, paleoclimatic, etc.) to identify real benchmarks and markers being major additions to interpreting the sequence and course of geological events in certain time intervals. It is precisely this kind of integration which can ensure the control over the reality of the correlations being made.

In conclusion, I would like to say that it might be advisable to unite the scientific forces interested in solving this problem (maybe, create a special project under the auspices of the Russian Academy of Sciences, gather a separate group of researchers, etc.) and to organize an extensive discussion of the issues raised. And maybe then we will solve the problem in the very near future, rather than in several generations, as N.V. Timofeev-Resovsky assumed. As the author of this paper, I am aware of the fact that my reasoning does not really advance the solution of the problem posed, but I still hope that I will be able to attract the attention of other specialists to it.

In conclusion, let us recall the words of I. Newton: “Nature does nothing in vain, and more is in vain when less will serve” (Vorontsov, 1999). It would be great to find this “less.”

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## CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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