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Cambrian Explosion: A Complex Analysis of Facts

Narima Kazhenovna Ospanova 

Institute of Geology, Earthquake Engineering and Seismology, the National Academy of Tajikistan, 73406, Tajikistan

ABSTRACT

Most researchers attribute the appearance of skeletons to some arbitrarily chosen factors. Many aspects of the phenomenon (the diversity of the composition of the remains, the mass nature of the phenomenon, geological immediacy, the role of geological and biotic factors, etc.) remain unexplained in this case. A comprehensive analysis of facts from different branches of science (lithology, tectonics, chemistry, biology, paleontology) allows us to explain (in addition to the listed) the smallness of Cambrian organisms, the replacement of chemical precipitation by biological, as well as the widespread development of bilaterality, the emergence of new taxa of high rank, and the morphological gap between the Ediacaran and Cambrian faunas. Both abiotic and biotic factors were important: Without the active participation of the living in the precipitation of salts, the formation of skeletons would not have been possible.

Keywords: Biomineragenesis; Skeletonization; Phosphates; Carbonates; Upwelling

1. Introduction

The Vendian-Cambrian boundary is the object of close attention of geologists of various profiles (magmatists, tectonists, metamorphists, geochemists, lithologists, stratigraphers, paleontologists), as well as biologists and astronomers, since one of the greatest events on a biospheric scale is associated with it—the emergence in organisms of the ability to

build skeletons. The author first addressed this topic in 1989^[1,2]. Over the past, a lot of new factual data has appeared, which not only can be used as a more extensive and more evidence base to substantiate our point of view, but also allow us to understand such features of the phenomenon as its geological immediacy, the absence of true bilateral symmetry in the Precambrian and the wide its development since the Cambrian, the emergence of new taxa of high rank,

*CORRESPONDING AUTHOR:

Narima Kazhenovna Ospanova, Institute of Geology, Earthquake Engineering and Seismology, the National Academy of Tajikistan, 734063, Tajikistan; Email: ospanova2005@mail.ru

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and the presence of a morphological gap between the Ediacaran and Cambrian faunas. In addition, the introduction of the term “biominerogenesis”^[3] allows us to consider non-skeletal and skeletal biomineral formation from a broader position—as types of biominerogenesis. Recall that biominerogenesis is *the formation of minerals, carried out in the hydro—and stratisphere with the direct and indirect participation of organisms*. It covers any processes in which mineral compounds are formed because of interaction with the environment of organisms or their metabolic products and decomposition^[3]. Below we display the features of biominerogenesis associated with the formation of organic remains, the most widely represented in the geological record—phosphate, carbonate, siliceous and iron. Examples of both skeletal and non-skeletal mineralization are considered.

2. Methodological foundations of the study

Many processes that took place in the past, we cannot observe in the present. Therefore, in such cases, modeling methods are used, the consequences of these processes are studied for recreating the primary situation, and also numerous indirect data are taken into account. To find out the reasons for the appearance of the skeleton at the Vendian-Cambrian boundary, we used the method of complex analysis of facts: we took into account the data of lithology, chemistry, biology and paleontology; analyzed the geological situation, typical for that period of time; the results of laboratory studies on the precipitation of salts by organisms and data on skeletal and non-skeletal biomineral precipitation are involved. The Karatau phosphorite-bearing basin is considered a model for reconstructing the geological situation. The author believes that only a comprehensive accounting of facts can help in solving this problem, while most researchers focus their attention on any single factor, which is methodologically incorrect.

3. Phosphate residues

The first appearance of organogenic formations

in the form of stromatolitic phosphate buildups is known from the Lower Proterozoic^[4], while the first appearance of skeletons (anabaritids and conodontomorphs) is indicated^[5] from the Vendian (Nemakit–Daldyn time). With the beginning of the Cambrian, the number and diversity of organisms with the phosphate skeleton increased dramatically. This is primarily due to the appearance of free (mobile) phosphorus in the water. Ilyin^[6] points out that in the Precambrian the mechanism of separating phosphorus from iron and carbon in the sedimentary process did not yet function. He considered upwelling as such a mechanism, in the absence of which the transport of dissolved phosphate to the shelf could not be carried out due to the density stratification of seawater. As a result, phosphorites in the Precambrian are irregularly distributed over different geological formations, dispersed chronologically and not differentiated from iron ores of high-carbon rocks.

In addition, Fedonkin^[7] pointed out the stratification of the waters of the Precambrian oceans. He wrote that during most of the Precambrian, the ocean was turbid, the photic zone was narrow, and the thermal gradient was sharp, which contributed to the stratification of the waters. Chaloner and Cocks^[8] believed that the progressive increase in oxygen concentration during the Precambrian contributed to the increase in its consumption for the oxidation of iron and manganese, which entered the ocean from hydrothermal systems and fixed phosphorus. Modern chemogenic co-precipitation of phosphorus with ferruginous suspension entering the water column as a part of high-temperature hydrothermal fluids from rift zones (to which points Baturin^[9]) can probably be considered as an analog of the named process. He also emphasizes the role of upwellings in the accumulation of phosphorus in shallow water (weak upwelling corresponds to weak phosphate accumulation!). Researchers believe that the upwellings were formed, probably, by the Vendian—Early Cambrian^[6], although the first large-scale appearance of upwellings is associated with the Middle Proterozoic—the time of the formation of the continental crust^[10]. Kholodov^[11] also pointed out that in the early

Proterozoic time the phase differentiation of ore material has extremely weakened. However, “at the beginning of the Paleozoic, the vast, but extremely shallow water bodies of the Proterozoic were replaced by much deeper strait-like seas..., the role of the processes of multiple redeposition and “ripening” of sedimentary material noticeably increased”... [11, p. 21]. Many scientists point out the specificity of the ancient seas, which occupied vast areas, but are characterized by exceptional shallow water. It contributed to their colonization by microorganisms, especially cyanobacterial mats, and the areas in which they functioned, could reach thousands of square kilometers [12].

Thus, the deepening of the seas, hydrodynamic (upwellings and repeated washing of sediments) and tectonic activity contributed to the formation of deposits of phosphate ores proper at the end of the Precambrian—the beginning of the Paleozoic.

The effect of these factors can be seen in the example of the Small Karatau basin, which can be considered a model for recreating the situation on the Vendian-Cambrian boundary [3,13]. Here, tectonic processes and the development of sedimentary faults created a system of uplifts and deflections in the Vendian-Tommot time, and a huge area of shallow water was divided by a series of shoals, bay-bars, and cofferdams into shallow baths-depressions that served as sediment traps [14]. These traps periodically received denser waters containing hydrogen sulfide and increased amounts of silica, phosphorus, and manganese, which precipitated after the oxidation of hydrogen sulfide and diffusion of carbon dioxide into the atmosphere. Upwellings played a transporting role. Their depth of conceiving was 100-250 meters [9]. The disruption (at that time) of the Paleopangea (Rodinia) supercontinent could also contribute to the development of upwellings. The deepening of significant areas of the seabed, which, along with the development of sedimentary faults, could have been facilitated by the Vendian transgression, and the development of anoxic environments there, had an adverse effect on the biota adapted to the conditions of well-aerated shallow water (reduction of the ecological niche), and contributed to the concentration

of life in shallow water and increased colonization of shallow areas of the bottom. The indications [15] that the most extensive (Australian-Asian) phosphorite-bearing province was formed in the Vendian-Cambrian epoch can testify to the global nature of the events taking place.

With the advent of organisms with a phosphate skeleton, the latter began to play a leading role in phosphate accumulation. In the accumulation of Vendian-Lower Cambrian phosphorites, bacterial-algal formations still occupy a significant place, but already in the Middle Cambrian phosphorites, grains belong to brachiopods, trilobites, chiolites, and echinoids [6]. Biogenic shell phosphorites of the Ordovician, whose formation epoch was also considered to be global [15], contain shells of lingulids, pteropods, and conodonts [16]. In the Permian Phosphoria Formation, bioclastic varieties are composed mainly of bones, scales, and teeth of fish, as well as foraminifers. In the Cretaceous-Paleogene, there are many grains of foraminifers, coccolithophorids, pteropods, dinoflagellates, and shark teeth are very characteristic. Neogene phosphorites abound in diatom remains [6].

The above review shows that, starting from the end of the Precambrian, organogenic remains played a dominant role in phosphate accumulation. The appearance of phosphate skeletons is associated with the appearance of free (mobile) phosphorus in water, but the onset of phosphatization implies rather high concentrations of it. Upwellings, i.e., flow of deeper waters that rose to the shelf and compensated for the outflow of surface waters caused by offshore winds [17], threw onto the shelf portions of water containing increased amounts of certain elements, and thereby changed the balance of elements in shallow water areas of the seas and contributed to biomineralogenesis.

4. Carbonate residues (magnesium and calcium salts)

Calcium and magnesium have always been brought into seawaters in significant quantities [17];

therefore, the significant scale of their utilization by living organisms is not accidental.

Stromatolites are considered to be the oldest carbonate formations of biogenic origin; they appeared on Earth 2.5-3.0 billion years ago and had a predominantly dolomitic composition^[18]. Stromatolite structures are layered formations of various shapes attached to the substrate and are the waste products of lower algae with the participation of bacteria, that is, not organic remains proper, but organogenic-sedimentary formations^[19]. Thus, the most ancient stromatolites of the Anabar Shield were formed to a large extent by terrigenous material, that is, “mucus films only retained sediment, distributing it in space”^[20, p. 280]. The young buildings are composed of carbonates in the form of peculiar columnar-radiant formations, which is evidence of the assimilation of carbonates from the aquatic environment. In addition, the total amount of carbonates in stromatolites is significantly higher than in the surrounding area^[21], which indicates not only the capture and binding of sediment, but the active participation of organisms in sedimentation. Previously, the dolomite composition of these formations was considered secondary by most researchers, but then it was proved^[20] that dolomite was primary. At present, many researchers are inclined to talk about the purely bacterial nature of stromatolite-forming organisms because blue-greens are classified as bacteria, but others believe^[22] that the question of their status remains open. In most cases, scientists prefer to talk about cyanobacterial communities (mats). When referring to the works of the authors, we will adhere to their views on the nature of the organisms under consideration.

The maximum stromatolite formation is noted in the Proterozoic, at the beginning of the Paleozoic it sharply decreases and, fading, passes to us, remaining in rare super saline lagoons. Although part of the carbonates (carbonate rosettes) in stromatolites could be formed as a result of biomass oxidation^[23], in general, the content of carbon dioxide in the atmosphere and the alkaline reserve of seawater was higher in ancient times, therefore, additional biochemical dolomite formation was developed much

more strongly^[17].

Simple calculations based on the MgO and CaO contents in Precambrian and Paleozoic carbonate rocks given in the work of A.B. Ronov and others^[24] show that the MgO content in the Paleozoic decreased by 2.08 times compared to the Precambrian (the average value is taken for geosynclines and platforms). If we take into account that the CaO content during the same time increased by 1.26 times, then compared with magnesium oxides, it increased by an average of 2.62 times. The decrease in the amount of magnesium is associated both with the decrease in the content of carbon dioxide in the atmosphere, and with a reduction in the areas of development of igneous rocks of the basic composition, considered^[25] as the main sources of income of this element in the sea basins. But it can also be assumed that the duration of the era of stromatolite formation (at least 2.0-2.5 billion years!), in which the deposition of magnesium occupied a prominent place, could affect the subsequent development of the basins.

The decrease in magnesium salts in seawater has led to a decrease in the scale of their utilization by organisms. There are no purely magnesian skeletons, and $MgCO_3$ is present only as an admixture to calcium salts in the skeletons of various representatives of the organic world—echinoderms, brachiopods, decapods, sponges, foraminifers, crimson algae and others; usually its content is 3-5-7%, reaching a maximum in *Octocorallia*—16.90% of the weight of the mineral part of the skeleton^[17].

An even more significant decrease in the content of MgO in carbonate rocks occurred in the Mesozoic, compared with the Paleozoic, it decreased by an average of 4.47 times; against the background of the almost unchanged CaO content (an increase of 1.06 times), the decrease in MgO to CaO is 4.74 times. Fluctuations in the content of Mg/Ca in water even depend on the rate of spreading along the median ridges^[26]. Therefore, the relative increase in the calcium content in the waters of the Mesozoic basins occurred not due to additional input, but due to the sharp decrease in the magnesium content in the water, which immediately affected the chemistry of the

skeletons.

Although the calcium content in the Paleozoic seas increased insignificantly on the whole, a combination of a number of factors led to a significant increase in its concentration in certain areas of water bodies. First, carbonate sedimentation is often concentrated in shallow areas of the bottom, since they are characterized by a higher temperature, and with increasing temperature, the intensification of carbonate sedimentation sharply increases^[17]. Secondly, the observed general decrease in the amount of carbon dioxide in the atmosphere during this period of time^[27] should have contributed to the supersaturation of water with calcium carbonate. The same—and even slightly smaller—amounts of calcium carbonate in water with a low content of CO₂ become, according to the laws of carbonate equilibrium, supersaturate the solution^[17]. Thirdly, against the background of the decrease in the content of magnesium in water and the difficulty of its precipitation, the relative content of calcium increased. All this led to the dominance of calcium salts in shallow areas of the seabed on the Vendian-Cambrian boundary.

5. Ferruginous remnants

Ancient organisms (algae, bacteria) precipitated not only carbonates, but also other chemical compounds that were present in the waters of the Precambrian oceans in high concentrations. This pattern was called the rule of the maximum: *The relationship of the most ancient organisms with their surrounding aquatic environment was such that those chemical compounds were deposited, which were present in the environment at the maximum*^[1,2]. The compounds that could create high concentrations in water also include iron minerals, the biochemogenic precipitation of which occurred in the form of ferruginous quartzites. Balance calculations showed that, if we proceed from the mass of organic carbon in sedimentary rocks, then this mass should correspond not only to the mass of oxygen in the atmosphere, but also to oxygen, which is part of the sulfates of oceanic waters and iron oxide ores in ferruginous quartzites^[28]. Strakhov^[17] wrote about the relative deepness of the

sedimentation of ferruginous quartzites, but other researchers^[11] insist on the extreme shallowness of the conditions for their formation.

Ideas about the shallowness, but the sufficient vastness of the Early Proterozoic seas are well linked with the many kilometers-long rhythmically alternating layers. With a thickness of microlayers of 0.2-2.0 mm, their length can reach almost three hundred kilometers^[11]. Without the participation of living organisms in sedimentation, it is difficult to imagine the mechanism of such a uniform distribution of terrigenous material over the entire area. Surely, both biogenic sedimentation and (along with terrigenous input) halmyrolysis (underwater weathering) took place. Stromatolite structures in the absence of hydrogen sulfide contamination^[14] or “littering” with clastic material also acquire a sheet form and stretch without interruption for tens and hundreds of meters^[19]. The researchers explain the rhythmic structure of ferruginous quartzites by the periodicity of the supply of silica, carbonates, and iron components from the continent and seasonal fluctuations in biogenic phenomena^[11]. Algae (Sokolov^[29]—ferrobacteria) emitted oxygen waves that passed through the water and entered into chemical reactions with the compounds present in the water. Ferruginous quartzites, the formation of which is dated to the interval of 3.0-1.8 billion years ago (Kholodov^[11], 2.6-2.0 billion years), are considered^[30] as evidence of the periodic release of oxygen and precipitation of iron by algae. The scale and duration of the period of deposition of ferruginous quartzites indicate that significant masses of iron entered the ancient seas, like many other elements, from the continents as the result of weathering of rocks.

After the precipitation of iron minerals, the seas became largely saturated with oxygen, and the amount of free oxygen in the atmosphere increased. The formation of the Earth's ozone layer is timed to the interval of 2.0-1.8 billion years^[30]. The enrichment of the atmosphere with free oxygen is confirmed by the deposition immediately after the formation of iron-bearing formations of red rocks,

which indicates that the processes of chemical weathering of iron minerals on the Earth's surface began, and the limitation of their migration ability. This means that never later could there be similar (to ferruginous quartzites) and comparable in scale iron deposits, which have no analogs in their reserves (and genesis). At present, there is no industrial accumulation of iron ores in open water bodies ^[31].

Since eukaryotes need an oxygen-rich environment to function, they could not have appeared before the completion of the oxygen revolution ^[30], that is, earlier than 2.0-1.8 billion years ago. The emergence of eukaryotes after the seas became free of excess iron is consistent with the absence of purely magnetite skeletons, the deposition of which (before the Vendian-Cambrian boundary) occurred mainly by an induced method (with the help of ferrobacteria), and magnetite is usually present in other skeletons only as impurities, for example, in the teeth of some molluscs or in the bones of the temporal region of birds.

Deposits of Precambrian iron ores that arose as a result of biochemogenic sedimentation formed over vast areas (Kursk magnetic anomaly, China, India, Australia, etc.).

6. Siliceous residues

More than 30 deposits of microbiota are known in Precambrian siliceous deposits ^[32], but the first skeletal remains of silicic composition belonging to *Platysolenites* appear from the end of the Vendian in the Nemakit-Daldyn time ^[5]. Approximately to the same time level (about 600 million years ago) the first finds of mineralized spicules of fossil sponges are dated ^[33]. The authors concluded that the first sponges were soft-bodied and probably without spicules. From the beginning of the Cambrian, they become active builders of the siliceous, and in the places of carbonate accumulation, of the carbonate skeleton.

In general, the diversity of siliceous skeletons is relatively small and is significantly inferior in number and variety to calcareous skeletons. The lower prevalence of siliceous skeletons compared to carbonate ones is explained by the maximum diversity

of life in areas of well-heated shallow water—the zone of water saturation with calcium salts. Silica, as emphasized by Strakhov ^[17], is characterized by an “opposite attitude” to temperature conditions and climatic regime compared to calcium carbonate. As the temperature rises, the solubility of SiO₂ increases and the saturation point shifts upward, while the solubility of CaCO₃ decreases and the solution becomes saturated or even supersaturated with calcium salts. But the beginning of biomineral precipitation, as mentioned above, requires sufficiently high solution concentrations. The warm waters of shallow, where the diversity of life is maximum, are always undersaturated with silicic acid, therefore, those (probably few) benthic animals began to build the siliceous skeleton that lived at a somewhat greater depth, where the content of calcium salts falls, and the relative content of silicic acid increases. Being located on the shelf below the zones of carbonate accumulation and to a greater extent exposed to the influence of hydrogen sulfide contamination and anoxicity, which were maximally manifested in depressions and in deeper areas of the bottom, the biotopes confined to the zones of silicic accumulation in the late Vendian—early Cambrian were characterized by a naturally lower taxonomic diversity. Strakhov ^[17] wrote that the majority of siliceous organisms gravitate to high latitudes and cold water, and the majority of calx-producing organisms gravitate to low latitudes and warm water. Modern biogenic silica accumulation is controlled by climatic zonation, circulation of water masses, and upwelling zones ^[34]. It was also shown that bottom-water temperature acts as a primary control that decreases the relative degree of pore-water saturation with biogenic opal while increasing the silica concentration ^[35]. The amount of incoming biogenic silica, the rate of its inflow, dissolution and burial, the chemistry of bottom waters and the mineralogical nature of the sediments are also important ^[35].

A few words should be said about radiolarians, planktonic forms with a siliceous skeleton that appeared at the beginning of the Cambrian and existed throughout the Phanerozoic. The ancestors of

radiolarians led a sedentary lifestyle and had an unstabilized siliceous skeleton. The intensification of the development of pseudopodia contributed to the detachment of radiolarians from the substrate and the transition to free soaring water^[36]. The radiolarian skeleton does not play a direct role in hovering and does not serve as an adaptation that arose for life in plankton, but is a heritage of benthic ancestors^[37]. Representatives of benthic forms of radiolarians are found in marine sediments deposited in different periods of the Phanerozoic time^[34].

The appearance of diatom-like organisms that precipitated silicon is also associated with the beginning of the Cambrian^[38]. Their diversity and the duration of the evolutionary path they had traveled by the beginning of the Cambrian era are emphasized wherein. In addition to radiolarians and foraminifers, benthic ancestors are also known in other pelagic groups—ostracods, trilobites, and graptolites—and are also suggested for conodontophorids and nautiloids^[39].

7. Chemical and biological aspects of biomineral precipitation

Both laboratory studies and observations in natural conditions have shown that the biological precipitation of salts begins earlier than the chemical one and proceeds more completely. Under laboratory conditions, at the same pH (8.0-8.5) in the control vessels and in the vessels with algae, more rapid precipitation of calcite crystals occurred in the vessels with algae^[21]. In the control vessels, precipitation of calcite crystals stopped at pH 8.5-9.0 and there was no subsequent increase in the concentration of hydrogen ions, while in vessels with algae it continued to grow and further precipitation of calcium was noted. Thus, it can be seen that there was a more active and complete precipitation of salts where living organisms were present. It is very important that in vessels with algae, sedimentation began earlier and ended later than the usual precipitation, and subsequent sedimentation required the supply of new portions of the concentrated solution. This explains why the biogenic precipitation of salts accompanies the

chemogenic one, and often, with large accumulations of organic matter, replaces it, leaving no place for the latter. For example, starting from the second half of the Ordovician, the volume of biogenic excretions of calcium carbonate in the skeletons of organisms rapidly increased, and starting from the second half of the Paleozoic, this method of transferring carbonate to sediment became predominant^[27]. Chemogenic sedimentation of phosphorus in the Phanerozoic seas was also practically absent, and the accumulation of phosphates occurred mainly due to organogenic residues^[9].

According to lithological data^[27], at the end of the Vendian—beginning of the Cambrian, there was a general decrease in the content of carbon dioxide in the atmosphere and in water, and some cooling of the climate. These factors contributed to a relative increase in the oxygen content in the water, which made possible the colonization of warm-water seas by cold-loving eukaryotes. As a result, life was concentrated on the shallow shelf. With the accumulation of significant masses of living matter, the factor of collective metabolism came into play, which was expressed in a change in the acid-alkalic balance of the environment. The result was a shift in the timing of salt precipitation. The shift in the timing of sedimentation, the temporary “neutralization” of the environment gave the organisms the opportunity and time to adapt to the long-term adverse effects of the environment—a high concentration of salts delivered to shallow water. As the result, salt precipitation came under increasing biological control. According to paleontological data, each group of organisms solved the problem of controlling salt precipitation in its way. So, without the active participation of organisms in salt precipitation, the formation of skeletons would be impossible.

With similar responses, the methods of “neutralization” of the environment by prokaryotes and eukaryotes could be different to one degree or another. Prokaryotes (and algae that appeared at the end of the Proterozoic, that is, eukaryotes) changed the pH of the solution and accelerated the precipitation, releasing oxygen as a side-product, which led to a

change in the oxidative potential of the environment. Actually, the emergence of eukaryotes (presumably 2.0-1.8 billion years ago) is considered as a reaction of organisms to the toxicity of oxygen, which, being the product of metabolism, at the same time affects living systems ^[7]. The supply of oxygen (to water and the atmosphere) clearly demonstrates the result of the action of collective metabolism. The entry of biogenic oxygen into the hydrosphere at least 3.0 billion years ago is evidenced with sufficient certainty by geochemical studies of sulfur isotopes ^[29]. The accumulation of oxygen has changed the physicochemical conditions of sedimentogenesis and the evolution of the biosphere.

The result of an unprecedented concentration of eukaryotes in the Vendian-Cambrian shallow waters—zones of maximum chemogenic precipitation of a number of chemical compounds—was an increased release of carbon dioxide into the water, which led to a decrease in the pH of the solution and shifted the timing of the precipitation, which gave the organisms a temporary respite and made it possible to adapt to the increased content of these salts in shallow waters. As the result, salt precipitation came under increasing biological control, and adaptation to high salt content became more and more adjusted. As in the case of the “arthropodization of the world” described by Ponomarenko ^[40], this process was characterized by positive feedback: *The change of the forms captured by the process of change causes such shifts in the environment that make the change of the forms more and more adaptable*. According to Ponomarenko, the emerging “chain reaction” gives the process an explosive character. The mechanism of adaptation explains the geological immediacy of the mass appearance of skeleton-building forms and, on the other hand, some prolongation of this process over a given period of time (at least 10 million years).

Thus, it is wrong to associate skeletonization only with external factors (high concentrations of phosphorus and calcium in water), which assign a passive role to the living. Without the active participation of organisms in the precipitation of salts, the

appearance of skeletons in the morphological and functional diversity known to us would hardly have been possible. The massive accumulation of living matter increased the pressure of organisms not only on the environment, but also on each other. As a result, many forms were forced to switch to sedentarity, and the relative proportion of benthos increased, and there was also a general reduction in size, noted by different researchers for different groups of animals. Former studies ^[41] attribute a decrease in the size of invertebrates in the Late Vendian to both the extinction of giant forms of the Vendian and the appearance of ancestors of small-sized Cambrian organisms, which intensively ate plankton and impoverished the diet of the Vendian biota. However, one cannot ignore the biological side of the process: the mass accumulation of organisms in limited spaces commonly leads to the unambiguous result – the general decrease in the size of individuals. The decrease in the size of individuals at large concentrations is a consequence of biocenotic (ecosystem) regulation and is directly related to the intensification of competition in the struggle for limited food resources.

Strakhov ^[42] distinguished four geochemically different groups of elements or substances according to the methods of sedimentation in the final reservoirs of runoff: biogenic, elements of the iron group, microelements, and easily soluble salts (**Figure 1**). In this series, the possibility for chemical precipitation from saturated solutions decreases from left to right; correspondingly, the ability of biological precipitation decreases. Substances of the last group (easily soluble salts) are present only in the form of solutions—they do not precipitate chemically and are not extracted biologically. Thus, those substances were involved in biomineral precipitation, which could give stable chemical components for a certain situation. Simply put, if there is chemical precipitation, then in principle a biological one is also possible.

An important feature of both skeletal and non-skeletal biomineralization is the non-selectivity of sedimentation (lack of initial affinity)—the appearance of calcareous skeletons in places of carbonate accu-

mulation, the confinement of phosphate skeletons to areas with a high content of phosphorus, and siliceous—to areas of siliceous-terrigenous accumulation. In the case of stromatolites (non-skeletal mineralization), there is also a correspondence between the composition of host rocks and the composition of chemical compounds deposited by cyanobacterial communities—dolomite structures were formed in dolomite sequences, limestone structures in rare limestone interlayers, and terrigenous structures in terrigenous sequences [20]. Phosphate buildups formed in areas of phosphate accumulation [4].

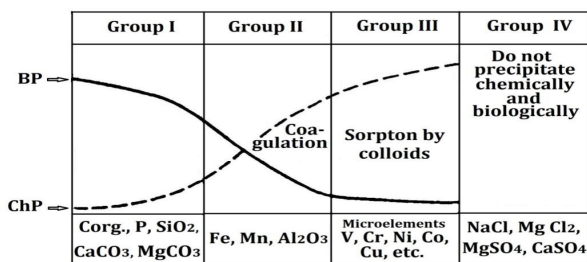


Figure 1. Scheme of sedimentation of dissolved substances in the sea: BP—biological precipitation, ChP—chemical precipitation (Strakhov [42]).

8. Discussion

According to a number of hypotheses, the boundary of the appearance of the skeleton in paleontology can only compete with the problem of the extinction of dinosaurs [43]. It is not necessary to present this extensive material here, not only because of the limited space, but also because it is not the purpose of this work. The maximum possible number of facts related to this topic and allowing to analyze of the problem from different angles objectively is involved. Therefore, we will refer below only to some hypotheses.

One of the hypotheses explains the formation of calcareous skeletons by a significant influx of calcium into the seas due to the erosion of stromatolite structures by the Vendian transgression [44]. This point of view neither takes into account (nor explains) the diversity of the composition of stromatolite structures and the composition of skeletons. For

example, many buildings had a dolomite or phosphate composition. It is permissible to ask: Where did the magnesium disappear during the erosion?

Another hypothesis postulates that the reason for the appearance of the skeleton was the “remember” by organisms of the synthesis of biological structures on matrices of abiogenic minerals [43]. This genetic point of view relies on the complementarity of DNA and collagen with an apatite lattice, and amino acids with the calcite lattice. It remains unclear from this hypothesis, why “remember” took place at the Vendian-Cambrian boundary (3.5 billion years after the formation of the structural units of heredity) although there was a lot of phosphorus in the Precambrian seas. It also does not explain the mechanism of formation of the skeleton based on silicon and celestine, the presence of copper, magnetite, and magnesium salts in the skeletons of organisms, and other points. It is obvious that without taking into account the geological factors and analyzing the geological situation in which the formation of the skeletons took place, it is impossible to answer the question of why the skeleton arose precisely at this interval of geological time.

Sokolov [29] believes that oxygenation of the atmosphere and a number of other factors (temperature regime, partial pressure, pH of the environment) could easily reach the critical point at the end of the Vendian, at which the integumentary protein shells of invertebrates were capable of mineralization in various and completely unrelated phylogenetic branches. Organisms protected by hard covers had an increased survival rate in the conditions of a rapidly populated shelf—a zone of moving shallow water, and selection quite naturally fixed this physiological phenomenon. “The decisive role in the Phanerozoic “explosion” was thus the biochemical mechanisms of the Metazoa and selection itself played, and not the mysterious invasion of cryptogenic faunas” [31]. However, not all organisms had hard covers at that time. For example, radiolarians had a metastable siliceous skeleton [37]. The early representatives of this fauna were characterized by a disorderly interweaving of rod-like elements, and the normal spongy

structure was already formed in the Middle and Upper Cambrian [45]. The biochemical factor, which is put at the forefront here, does not take into account the influence of organisms on the environment and the importance of the increased concentration of life in limited spaces, that is, the criticality of the conditions that forced organisms to seek a way out of the situation.

The hypothesis, based on the galactocentric paradigm [46], states that the main epochs of salt and phosphate deposition, as well as the rapid development of life, are due to the fall of comets of the spiral arms of the Galaxy, which are characterized by an increased content of chemical elements of the “calcium peak” with average atomic weights (Na, Mg, P, S, Cl, K, Ca, etc.). These comets reach their greatest abundance in the galactic arms at a distance from the corotation radius of the galaxy (the radius of the circle within which the rotation speeds of the arms and the matter of the galaxy disk coincide) coinciding with the apogalactia (the part of the galactic year corresponding to the “summer”) of the solar orbit. Therefore, the main epochs of deposition of phosphorus and salts on the Earth (V/C, C/P, and K/p) fall on these parts of the orbit (**Figure 2**).

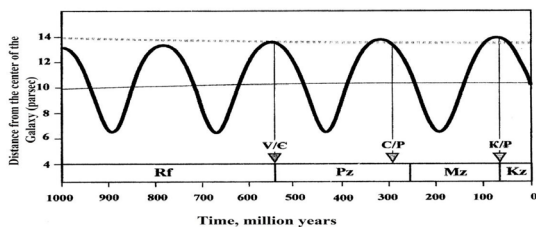


Figure 2. The main periods of accumulation of phosphates and salts [46].

As was shown earlier, the increase in the concentration of calcium salts in the shallow areas of the bottom was due to a combination of climatic and tectonic factors, and not at all to its anomalous supply. At the border of the Paleozoic and Mesozoic, an almost five-fold (in relation to calcium) decrease in the concentration of magnesium occurred, which would hardly have been possible if it had arrived on Earth with a sufficient amount of cometary matter at the beginning of the Permian. The calcium content

practically did not change. As for the third main epoch, the general decrease in the carbonate content of precipitation is noted in the late Cretaceous—early Paleogene. In the areas of the outer shelf and the upper part of the continental slope, predominantly carbonate deposits were replaced by black clays [47]. Numerous data contradict this hypothesis. The influence of cosmic dust or the substance of comets and asteroids on the development of terrestrial life has not yet been studied.

Finally, there is a point of view about the extraterrestrial origin of the skeleton. So Achkasov [48] believes that initially the skeletons could have been brought to the Earth with extraterrestrial life when a planetoid fell on it. He writes: “In the Vendian and Cambrian, out of 90 existing classes, 60 classes of marine multicellular animals suddenly appeared, because life was more developed on the Pacific planet than on Earth”. Further: “The skeletal forms of life appeared on Earth suddenly, they have not found predecessors in the Precambrian, and this is a big mystery. The Cambrian is a period that began shortly after the collision of the Earth with planet A1. Therefore, I assume that there was the life of a skeletal form on planet A1” [48]. Firstly, the question arises: Could highly developed life survive in the catastrophic collision of two planetary bodies? Secondly, the correspondence of the composition of the skeletons to the composition of the salts deposited under those conditions indicates the parallel evolution of inert and living matter on our planet. Thirdly, just as the panspermia hypothesis does not solve the problem of the origin of life in the Universe, so this point of view does not answer the question: Where did the skeletal forms on other planets come from?

Many Vendian animals had glide reflection symmetry, which could have arisen from spiral growth [10], while the beginning of the Cambrian is associated with the massive development of bilaterality. Scientists write [49] that there is a significant morphological gap between the Ediacaran fauna and true bilaterians, which remains fundamentally unexplained, and that Ediacaran taxa could not gradually and without significant complications turn into true Bilateria.

The development of bilaterality can be explained by the following reasons. Mass accumulation of organisms in limited areas of shallow water forced many forms to move to sedentarity. The transition to a benthic way of life contributed to the development of various ways of moving along the bottom of the sediment or in the ground. From the pattern established by Shafranovsky^[50], which we^[51, 52] proposed to call “Shafranovsky’s rule”, as follows: *everything that moves and grows horizontally or obliquely has bilateral symmetry; anything that grows vertically has radial symmetry*. For example, bottom-crawling larvae may be bilaterally symmetrical, while vertically growing polyps that develop from these larvae are radially symmetrical. So, the low mobility of Ediacaran organisms may explain the lack of true bilateral symmetry in them. The transition to sedentarity at the boundary of the Vendian and Cambrian and the development in connection with this of various modes of the movement were carried out evolutionarily quite quickly, which is quite consistent with the explosive nature of the adaptation process at that time. This explains the lack of a gradual transition between the Vendian forms and true bilateria. As for the rest of the morphological characters, the gap between the Ediacarian and Cambrian faunas can be explained by the wide development of the processes of pedomorphosis and neoteny. Earlier, it was said about the small size of the Cambrian organisms. But a decrease in size is achieved, as a rule, due to the reduction of more mature stages of growth, which results in the development of the processes of pedomorphosis and neoteny. The earlier the deviations begin, the greater the difference between the adult stages of the original and derived forms. A radical change in environmental conditions should have contributed to the emergence and development of new phenotypes because the same genotype in different environmental conditions gives different phenotypes.

The few examples given here show that, in principle, any of the factors (both biotic and abiotic), taken in isolation, can be considered as having some potential in trying to explain the causes of skeletal formation. But with this approach, many questions

remain unanswered, and on closer examination, it turns out that these factors conflict with the evidence already available.

9. Conclusions

A review of the organogenic remains that are most widely represented in the fossil record, consideration of skeletal and non-skeletal mineralization as types of biominerogenesis, and a comprehensive accounting of geological-lithological, chemical, and biological-paleontological data allow us to draw the following main conclusions.

1) Skeletal formation cannot be explained by any one arbitrarily chosen (at the discretion of the researcher) factor. This approach is methodologically incorrect, so it is natural that the problem is still considered unresolved. This is evidenced by the continuous growth (as science develops) in the number of hypotheses, with which researchers try to explain the phenomenon of the appearance of the skeleton. Only a complex analysis of all available facts, primarily geological and paleontological ones, can pretend to be a conclusive explanation of the reasons for the appearance of the skeleton at the Vendian-Cambrian boundary.

2) In the formation of minerals that make up skeletal and non-skeletal organogenic remains, the most widely represented in the paleontological record, geochemically mobile compounds took part, which tends to accumulate in the final water bodies (seas and oceans) and are capable of chemical precipitation, that is, to give stable for a given environment, chemical compounds.

3) The scale of the processes of non-skeletal and skeletal biomineral deposition depended on the reserves of these substances in marine basins, accumulated over long epochs of geological time, and the degree of water saturation with them.

4) The onset of non-skeletal and skeletal mineralization was provoked by high substance concentrations in seawater. Skeletal biomineral formation, subject to greater biological control of sedimentation, starting in conditions of saturation and supersaturation of water with salts, could then continue in

conditions far from saturation, which indicates the genetic fixation of the trait. Non-skeletal biomineral formation is more dependent on environmental conditions and proceeds only in the presence of sufficiently high concentrations of substances. This explains, on the one hand, the duration of their sedimentation (billions of years), due to the duration of the entry into water bodies of certain chemical compounds, and, on the other hand, a sharp decrease in the scale of deposition with the disappearance or a sharp reduction in the corresponding environmental conditions.

5) Biological precipitation begins earlier than chemical precipitation and ends later. Therefore, in nature, it often leaves no place for chemical precipitation, as also evidenced by a review of organogenic residues. New portions of the saturated solution are required to renew biological precipitation. Respite is important for organisms because the temporary neutralization of adverse environmental influences allows organisms to adapt to them.

6) Mass skeletonization at the Vendian-Cambrian boundary was due to both abiotic and biotic factors. The differentiation of the seabed in-depth, the development of anoxic conditions in the deeper parts of the basins, and the associated reduction in the ecological niche of organisms adapted to the conditions of well-aerated Precambrian shallow waters contributed to the colonization of shallow areas of the seabed and the concentration of life on the shelf, which increased due to the mass migration of eukaryotes from cool to warm waters. But just in these areas, the concentration of some substances or salts was very high during this period of time, up to supersaturation. If the high concentration was the sufficient condition for the start of bio precipitation, then a significant accumulation of masses of living matter was the necessary condition, when the factor of collective metabolism came into action, changing the environment in the direction of adaptive favoring and significantly accelerating the biological control process over salt precipitation. However, these factors in themselves—both high concentrations of substances in water and the large accumulation of

organisms in confined spaces—are not optimal for the life of organisms. Therefore, we can conclude that the appearance of skeletons was their response to adverse environmental conditions.

7) The appearance of skeletons in response to adverse environmental influences forces us to deny the goal orientation in the evolution of organisms, that is, skeletons appeared in order to protect against predators or to improve bearing-locomotor functions. These functions are secondary and formed in the process of mutual influence of organisms on each other in changing environmental conditions. Statements such as “the appearance of the skeleton were caused by the need to further increase the activity of organisms” cannot be taken seriously, because cause and consequence are reversed here.

8) The high concentration of phosphorus, silicon and calcium salts in the shallow areas of the seas in the Vendian-Tommotian time was not associated with their anomalously high input into the seas during this period of time, but is explained by a combination of a number of factors that is by the change in the conditions of their sedimentogenesis.

9) The massive nature of skeleton formation is explained by the mass accumulation of organisms in shallow water at the end of the Vendian—beginning of the Cambrian, and skeletonization acts as one of the directions in the evolution of the biosphere. The explosive nature of skeletal formation is associated both with the mass accumulation of various groups of organisms and with the mechanism of adaptation to adverse environmental factors (high salt concentration in shallow water and high density of shelf settlements), when the process of interaction between organisms and the environment acquires the character of positive feedback, multiply accelerating the development of adaptations.

10) The concentration of life on the shelf due to the reduction of shallow bottom areas (the intervention of tectonics and the invasion of cryptogenic fauna) had important and far-reaching consequences:

- an increase in the role of the biotic factor, which made it possible to take the precipitation of some substances or salts under biological control;

- a general decrease in the size of the inhabitants of shallow water, which was carried out due to the removal of more mature stages of development;

- widespread development of bilaterality due to the transition of many forms to sedentarity and the forced adaptation to movement along the bottom, in the near-bottom water layer or the upper sediment layers;

- the emergence of high-ranking taxa, the appearance of which is associated with the processes of paedomorphosis and neoteny;

- the formation of new food chains and new forms of co-evolution due to increased predation and competition.

11) The widespread development of bilaterality indicates that the process of searching for new ways to move along the bottom involved many taxa, and bilaterality was not the privilege of some single hypothetical form designed to play the role of LCBA – the Last Common Bilaterian Ancestor. The absence of true bilateral symmetry in Precambrian organisms is due to their low mobility.

12) Being a component dependent on inert matter and representing a natural product of its evolution, living things also had an impact on the environment on a scale comparable to geological processes.

The analysis of a large amount of factual material allows us to explain all the characteristic features of the “Cambrian explosion”. Prior to our studies, the fact that just benthic forms began to build the skeleton was ignored, but scattered data on individual groups, including planktonic ones, confirm this thesis. Benthos is more dependent on external conditions than plankton or nekton, and this also proves the forced transition to the skeletal formation, and not at all the initial readiness of living things to build skeletons. About 98% of the biota in the modern ocean (by a number of the species) is bottom organisms, most of which are inhabitants of the shelf, and only 2% belong to plankton and nekton. Many enzymes and hormones were produced in the Precambrian, and their versatility played a positive role in this critical situation. However, the genetic mechanisms responsible for the formation of the skeleton

have been honed and consolidated in parallel with the changes that organisms have undergone.

Conflict of Interest

There is no conflict of interest.

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