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Homology of Bacteria Proteins, Diatoms and Sponges Participating in Biomineralization, and Human Proteins, and other Animals

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Abstract : *In this paper computer research data of silicateins (50), silicases (1), silaffins (5), silicon transporters and magnetosome proteins (97) are presented. The research was carried out with the use of biological processing servers UniProt (www.uniprot.org) and Blast (www.ncbi.nlm.nih.gov). It is shown that the proteins which have the biomineralization mechanism and homological to them are widely spread in the tree of life and could be met in different organisms starting with protozoa to humans.*

Keywords : *silicateins, silicases, silaffins, magnetosome proteins, biomineralization, bioinformatics..*

INTRODUCTION

According to the theory of matrix synthesis organic world appeared on the basis of inorganic crystals. At present between minerals and living organisms we can see a lot of interrelations [1]. There is an opinion that on the Earth, at first, "mineral" organisms appeared [2-9], and then during long evolution on their basis, protobiological structures arose which then helped the first protocells to come into the world. Several scientists [2; 10-19; 21-31] think that living organisms appeared because of keystone biomolecules and biostructures matrix synthesis based on inorganic matrix. Minerals in this case were the first catalysts [17; 32]. In this case we can suppose the first part of minerals participated in matrix synthesis, the second was as ion-exchange reactor; the third part could be catalyst or fulfill other functions. This whole mineral ensemble carried out the main function on the Earth – created life. In spite of different theories of evolution whatever we studied, one thing is evident – organic and inorganic world co-evolve.

Today we know approximately 300 sorts of biominerals and nearly 50 of them are in human organism [31].

We can suppose the first biomolecules which were synthesized on inorganic matrix spontaneously must have maximum affinity to some mineral lattices. Therefore, we consider some biopolymers which were modified and still exist in living organisms must be among specific enzymes and transporters working with minerals.

There are a number of enzymes which use crystal lattices as substratum (silicic minerals, apatite and some others). For instance, silicateins, silicases, silaffins – the proteins which are able to form and destroy inorganic structures on the basis of silicon, such as silica (SiO_2). It was shown that forming silica in sponges is enzymatic process opposite from forming silica in diatoms, which took place together with polyamines [33] and/or polycationic peptide – silaffins where the remains of lysine are modified by methilpropylamine units [34; 35].

Continuing this theme definite interest so called magnetosomes discovered in some bacteria represents. Synthesis of these natural nanoparticles is regulated with the help of special genes (Mam, Mms etc.). Biomineralization in magnetosomes is considered to be similar to the processes of crystallization in other biominerals. With the help of these organelles bacteria react the magnetic field and orientate in the space [13; 36-39].

Now the perspective of using proteins which take part in biomineralization attracts great interest because of their application in the sphere of nanobiotechnology, both theoretically and in practice it is possible to have direct synthesis of nanostructures with a given form and characteristics [40; 41].

SILICATEINS

The first silicatein was discovered in the coring of sponge spicules and named silicatein-α [42]. At present we know nearly 50 silicateins which are got from fluvial and marine sponges. Typical specimen of these enzymes are given in Table 1. The chemical nature of silicateins is similar to protheolytic enzymes – cathepcins [42-44]. Cathepcins are wide family of cysteine peptidases class enzymes which do not form silica.

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Instead of cysteine there is serine in catalytic centre of silicateins [45]. Phylogenetic analysis allows us to suppose all silicateins are originated from cathepsins in particular from marine sponge cathepsin L [46].

Table 1. Silicateins of fluvial and marine sponges

Protein name	Gene name	Organism	Quantity AA*
Silicatein alpha	silicaa	Geodia cydonium (Sponge)	334
Silicatein A1	SilA1	Latrunculia oparinae (Sponge)	329
Cathepsin L 1		Pheronema raphanus	328
Silicatein-like protein		Aulosaccus sp. GV-2009	352
Silicatein alpha		Tethya aurantium	330
Silicatein a2	silicaa2	Lubomirskia baicalensis	326
Silicatein alpha		Hymeniacidon perleve	331
Silicatein alpha	silicaa-g	Suberites domuncula (Sponge)	330
Silicatein	Ef silicatein	Ephydatia fluviatilis	326
Silicatein		Petrosia ficiformis	339

*AA – amino-acid residue

In sponges silicateins catalyze forming of amorphous silica and its monomeric compounds – silicic acid ethers [46]. The process consists of two stages: 1) hydrolysis (rate-limiting) of silicon ether with silanol formation; 2) polymerization of silanol molecules with amorphous silica formation [47].

Computer research showed that highly-homologous proteins to silicateins could be met in a lot of animals including amoeba (Acanthamoeba castellanii, Acanthamoeba healyi), trichoplax (Trichoplax adhaerens), sea anemone (Nematostella vectensis), hydra (Hydra attenuata), trepang (Stichopus japonicus), mollusk (Haliotis diversicolor supertexta), rotifer (Adineta vaga), worms (Rotylenchulus reniformis, Meloidogyne incognita, Theromyzon tessulatum), beetles (Dermestes frischii, Tenebrio molitor, Diaprepes abbreviatus), ticks (Dermacentor variabilis, Boophilus microplus, Haemaphysalis longicornis, Ixodes ricinus, Rhipicephalus appendiculatus), shrimps (Metapenaeus ensis, Artemia parthenogenetica, Litopenaeus vannamei, Artemia salina, Artemia sanfranciscana, Pandalus borealis), lobsters (Nephrops norvegicus, Homarus americanus), fly (Sarcophaga peregrina), fruit fly (Drosophila mojavensis, Drosophila erecta, Drosophila sechellia, Drosophila melanogaster, Drosophila simulans, Drosophila grimshawi, Drosophila yakuba, Drosophila persimilis, Drosophila pseudoobscura, Drosophila virilis, Drosophila willistoni), mosquitoes (Aedes aegypti, Anopheles gambiae, Culex quinquefasciatus), aphides (Toxoptera citricida, Aphis gossypii, Myzus persicae), weevils (Sitophilus zeamais, Diaprepes abbreviatus), lancelets (Branchiostoma floridae, Branchiostoma lanceolatum), fishes (Ictalurus punctatus, Danio rerio, Myxine glutinosa, Fundulus heteroclitus, Oryzias latipes, Osmerus mordax, Tetraodon nigroviridis, Salmo salar, Hippoglossus hippoglossus, Engraulis japonicus, Misgurnus mizolepis), frogs (Xenopus tropicalis, Xenopus laevis), mouse (Mus musculus), rat (Rattus norvegicus), hamster (Mesocricetus auratus), rabbit (Oryctolagus cuniculus), dog (Canis familiaris), pig (Sus scrofa), bovine (Bos taurus), chicken (Gallus gallus), human (Homo sapiens) and other. For instance, typical representatives of silicateins are silicatein α (334 AA; Geodia cydonium), silicatein A1 (329 AA; Latrunculia oparinae) and silicatein A2 (329 AA; Latrunculia oparinae), they have rather high identity level with cathepsin L1 (44%, 45%, 44%), CTSK protein (40%, 44%, 44%), cathepsin S (44%, 43%, 44%), cathepsin K (40%, 44%, 45%), cathepsin L2 (41%, 44%, 43%), which are human cathepsins. Homologous degree between silicateins themselves is 40-72%.

SILICASE

Silicase, enzyme which provides silica depol ymerization, was discovered in marine sponge [46]. The expression of silicase gene increases sharply when there is concentration of silicon extension [43]. Silicase belongs to the family of carbonic anhydrases [45], which are the class of zink-dependable metalloenzymes [48]. The mechanism of silicase sponge work is similar to the mechanism of zinc-dependable metalloenzymes hydrolyzing ethers [46]. In literature we did not see information about sponge silicase analogues. It is supposed in silicase bacteria there are enzymes – silicases which are responsible for destroying ties Si-O in crystal lattices of clay minerals, and also ties Si-C in silicon organic compounds [49], however pure enzymes are not given off [50].

Comparison of sponge silicase and carbonic anhydrase II sequences shows (Fig. 1), that amino acids which are more typical for 10 carbonic anhydrases eukaryote also exist in sponge silicase [46; 51].

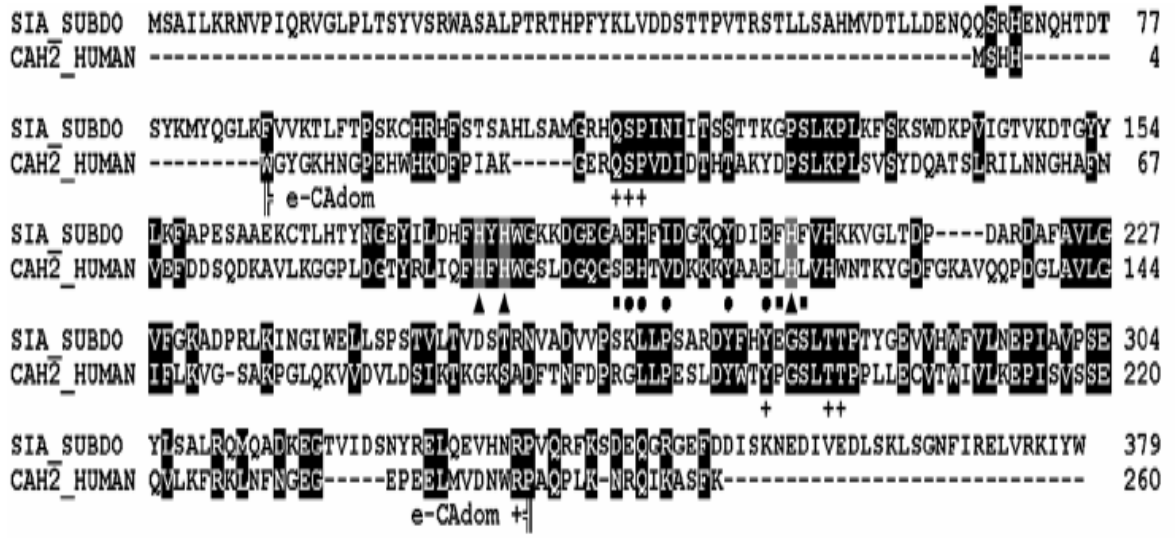

Fig. 1. Align of silicase from S. domuncula (SIA_SUBDO) of human carbonic anhydrase II (CAH2_HUMAN). Carbonic anhydrase domain sphere (╠ e-CAdom +╣). Similar amino acid remains in both sequences are shown white on black. Three zinc-connected remains of histidine (▲), typical for amino acid carbonic anhydrases eukaryote (●, discovered in both sequences; ■, which are situated only in carbonic anhydrases, but not in silicase) [70].

It is known carbonic anhydrases (CAs, EC 4.2.1.1) are widely spread in phylogenetic tree (diatoms, eubacteria, archaea) [52]. The search of homologues (UniProt, Blast) showed practically all proteins identical to sponge silicase by 29-40% are carbon anhydrases found in the organisms of sponges (Astrosclera willeyana, Amphimedon queenslandica), nematodes (Brugia malayi, Caenorhabditis elegans), flies (Drosophila willistoni, Drosophila persimilis, Drosophila ananassae, Drosophila pseudoobscura pseudoobscura, Drosophila grimshawi, Drosophila sechellia, Drosophila mojavensis, Drosophila yakuba, Drosophila erecta, Drosophila simulans, Drosophila melanogaster, Drosophila virilis), sea lamprey (Petromyzon marinus), lancelet (Branchiostoma floridae), fishes (Danio rerio, Chionodraco hamatus, Eptatretus stoutii, Tribolodon hakonensis, Oreochromis mossambicus, Salmo salar), frogs (Xenopus laevis, Xenopus tropicalis), chicken (Gallus gallus), mouse (Mus musculus), rat (Rattus norvegicus), rabbit (Oryctolagus cuniculus), sheep (Ovis aries), pig (Sus scrofa), horse (Equus caballus), bovine (Bos taurus), chimpanzee (Pan troglodytes), human (Homo sapiens) and other animals. Most likely, in all the organisms there are proteins and necessary genes which are typical in structure and functions to marine sponge silicase.

SILAFFINS

Silaffins are peptide origin substances rich with lysine. These polypeptides were first discovered in diatoms, which cell walls form amorphous silica “shell”. Typical silaffin representatives were evolved from Cylindrotheca fusiformis (Marine diatom): silaffin-1A (4 kDa), silaffin-1B (8 kDa) and silaffin-2 (17 kDa) [33]. Sillafines, according to [34] are widely spread though they do not exist in all algae.

They are considered to be the participants of biosilification process and are able to form silica in vitro, when it is neutral pH and room temperature [53]. It is determined in vitro silaffins are able to form different nanostructure silica, but such diatom biosilica structures were not discovered [33; 35]. Some researchers, in particular [54], utter an opinion if silaffins, indeed, play the role of organic matrix on a definite stage of silica morphogenesis, in this case silica must copy the structure of silaffin matrix. Silica with less spores (till 100 nm) may be directly connected with the sizes of set units formed by natSil-2, and big silica structures with their sizes 100-1000 nm may be generated by different amount of natSil-2 и natSil-1A combinations, electrostatically connected between each other. More over the authors of these researches pay attention to silaffins can catalyze different structure silica formation (for instance porous) in definite stoichiometric relations.

In UniProt electronic database of proteins we found amino acid sequences of five silaffins discovered in two types of diatoms (Cylindrotheca fusiformis and Thalassiosira pseudonana). Homology between these five silaffins is 90-95%. Comparison of these silaffine representatives with the sequences which are in electronic database of proteins showed the proteins identical to silaffins by 29-40% are widely spread in animal world. These proteins are discovered in amoeba (Acanthamoeba polyphaga mimivirus), infusorium (Paramecium tetraurelia), plasmodium (Plasmodium falciparum, Plasmodium yoelii yoelii), bacteria (Bacteroides sp.), fungi (Coprinopsis cinerea), yeasts (Candida albicans, Pichia stipitis, Schizosaccharomyces pombe), worm (Phragmatopoma californica), fruit flies (Drosophila persimilis, Drosophila melanogaster, Drosophila pseudoobscura pseudoobscura, Drosophila grimshawi, Drosophila erecta, Drosophila yakuba), mouse (Mus musculus), pig (Sus scrofa), human (Homo sapiens) and in organisms of other animals. Biological functions of these proteins are different (binding proteins, binding metal ions, transferase activity, proteolysis etc.) and biomineralization. For instance, sialophosphoproteins participate in tooth tissue forming.

SILICON TRANSPORTERS

Typical representatives of silicon transporters are SIT1 (548 AA; 60,572 Da), evolved from diatom Cylindrotheca fusiformis and aquaporine NIP2-1, or low silicon protein 1 (298 AA; 31,978 Da), got from Oryza sativa. Aquaporine NIP2-1, SIT1 and proteins similar to them are united in silicon transporters family (SIT – **Si**licon **T**ransporter, silicic acid transporters). Today we know more then 100 different proteins which are able to transport silicon ions and acids. The representatives of these enzymes were found in approximately a hundred types of algae and plants. Their main part is discovered in diatoms, others in plants of Magnoliophyta section, such as Hordeum vulgare, Zea mays L., Ricinus communis L., Oryza sativa etc. The researches of these proteins do not have common opinion about transmembrane transferring mechanism of ions and silicon acids by silicon transporters [55; 56; 57; 58].

Computer search SIT-similar proteins showed the proteins homologous to silicon transporters (homology was till 40%) exist in a lot of plants and animals from unicellular to higher organism including human. In particular, aquaporine NIP2-1 is homologous to human protein NIP2-1 (271 AA; 28,837 Da) almost by 40%. Homologous degree in silicon transporters family fluctuates within the limits of 45-99%.

MAGNETOSOME PROTEINS

In magnetotactic bacteria which are able to collect iron ions from water there is a number of proteins which fulfill intracellular synthesis of nano- and microparticles (from 10 to 200 nm) of magnetite, greyhite, maghemite and other different ferrites (FeO, Fe_2O_3, Fe_3O_4, Fe_3S_4) with their different forms (cubic, elongated, prismatic, arrow-like). Magnetite particles are accumulated in the intracellular base in magnetosomes which form chain ordered accumulation consisting of several dozens of sections (sometimes in literature magnetosomes are understood as accumulation of magnetite crystals particles). Magnetosomes were discovered by Blakemore in 1975 [59]. These are bubble nucleations having unique biochemical compound and membrane appeared from cytoplasmic membrane [39]. Presumably with the help of acidic protein magnetosome chains build into the structure of cytoskeleton formed by actine-like proteins [39]. In vitro experiences actin-like protein MamK is determined to be able to polymerize with the formation of fiber [60]. Magnetosome biosynthesis mechanisms are determined to regulate by genetic apparatus but they are not well studied [38; 39]. Today we know nearly twenty magnetosome-specific proteins participating in magnetosome forming, direct iron transporting, crystallization and intracellular ordering of magnetide particles in different magnetotactic bacteria [39; 61]. The proteins participating in magnetotaxis are supposed to be much more[62].

In Uniport base data we discovered sequences of 97 magnetosome peptides and proteins evolved from Magnetospirillum gryphiswaldense, Magnetite-containing magnetic vibrio, Desulfovibrio magneticus and other uncultivated bacteria. These peptides and proteins are combined into 27 group (MamA – tetratricopeptide recurrent proteins, MamB – mediators of cation diffusion, MamE – HtrA- similar serine proteases, MamC, MamD, MamS, MamJ, MamO, MamQ, MamM, MamN, MamH, MamF, MamR, MamK, MamP, MamU, MamX, MamI, MamL, MamT, MamW, MamY, MamG, Mms6, MmsF, MmeA). The proteins of some groups, probably, are specific only for magnetotactic bacteria [61]. Computer analyses points out typical representative of most part of the groups have homologues (proteins with the homologous degree less then 20% were not considered) only from the proteins of different bacteria. Proteins from the other groups (MamD, MamJ, MamL, MamT, MamG, MamW, MmeA, Mms6 etc.) has homologous of plant and animal origin, represented in too much little degree then homologous of silicateins, silaffins, silicase and silicon transporters.

For more detailed analyses using the method of sequences align magnetosome proteins of the most

studied magnetotaxic bacterium Magnetospirillum gryphiswaldense were chosen. For instance, it is determined protein **MamD** (314 AA; 30,227 Da) is homologous to nematode protein CBR-SSQ-2 (431 AA; 36,092 Da; Caenorhabditis briggsae) by 29%, fibroin light chain of bee-moth fibroin (267 AA; 27,079 Da; Galleria mellonella) by 31%, protein GK10816 of drosophila (427 AA; 36,893 Da; Drosophila willistoni) by 27%, spider silk protein MiSp2 (157 AA; 12,484 Da; Nephila clavipes) by 40%, sialophosphoprotein C of human dentine (763 AA; 71,481 Da; Homo sapiens) by 26%, human domain of mucin-19 (6,254 AA; 598,155 Da; Homo sapiens) by 24%. Protein **MamJ** (426 AA; 44,317 Da) is homologous with protein TESTI2004215 of human (718 AA; 77,060 Da; Homo sapiens) by 28%, with aspartate beta-hydroxylase Danio Rerio (472 AA; 52,729 Da) by 34%, with GD20599 drosophila (908 AA; 88,013 Da; Drosophila simulans) by 24%, with bovine fibrous sheath CABYR-binding protein (818 AA; 87,760 Da; Bos taurus) by 27%. Protein **MamL** (123 AA; 13,391 Da) is similar to proteins like claudin 32a of fish (211 AA; 21,970 Da; Takifugu rubripes) and AGAP000824-PA mosquito (437 AA; 49,603 Da; Anopheles gambiae) by 30%. With proteins Sox3 of mouse (fragment from 448 AA; 45,157 Da; Mus musculus), transcription factor SOX-3 of human (446 AA; 45,210 Da; Homo sapiens) and Sb07g023610 sorghum grain (791 AA; 87,923 Da; Sorghum bicolor) magnetosome protein **MamT** (174 AA; 18,884 Da) has homology 35%, 32% and 27%, accordingly. **MamG** (84 AA; 7,715 Da) has similarity with human elastin (757 AA; 66,106 Da; Homo sapiens) in 39%, protein domain GL13332 of drosophila (3,445 AA; 367,711 Da; Drosophila persimilis) in 46%, protein Wu:fb15e04 of Danio Rerio (fragment from 597 AA; 60,326 Da) in 45%. Homology of **MamW** (138 AA; 15,088 Da) and histone H1 of corn (246 AA; 25,348 Da; Zea mays) is 45%, **MmeA** (364 AA; 38,413 Da) and human myosin-10 domain (1,976 AA; 228,999 Da; Homo sapiens) – 24%. Homologous degree of **Mms6** (136 AA; 12,755 Da) with fibroin-like rice protein (239 AA; 19,434 Da; Oryza sativa subsp. japonica) reaches 45%, 1b fibroin of spider (fragment from 494 AA; 39,918 Da; Deinopis spinosa) – 42%, mussel precollagen-NG (960 AA; 82,969 Da; Mytilus californianus) – 37%.

Earlier on a high similarity of some magnetosome proteins sequences other scientists pointed out. Proteins MamS and MamG of magnetotactic bacteria have high homologous percentage with the fibroin silk sequences [63], elastins, proteins of cartilaginous tissue [64], mollusk proteins [65], for which self-aggregation is typical [61]. The works of different authors showing magnetogenesis in different organisms point out the existence of magnetosome protein analogues in higher organisms including human. In particular, in coast rainbow trout (Oncorhynchus mykiss) the cells-receptors of magnet field containing single-domain magnetite crystals connected in chain with the length nearly 1 mkm were discovered [37; 39; 60-62; 66-76;]. Also other scientists report about higher organisms ability to feel magnet field of the Earth [77-79]. More than 15 years ago in human brain magnetosomes were first discovered (accumulation of 50-100 magnetite crystals, size 10-70 nm – 90%, and 90-200 nm – 10%) [80].

Magnetosome protein homologies found in mollusks, single-celled algae (coccolithophorids) and other organisms take part in the processes of biomineralization [61; 81; 82].

Biological functions of homologues found with the help of bioinformational approach are not studied well but we know some of them take part in biominerals formation.

CONCLUSIONS

Silicateins, silicase, silaffins, silicon transporters, magnetosome proteins and their homologues are met in a great deal of life forms. Probably a lot of organisms lost the ability to utilize such compounds as silica and ferrites, and genes codifying special proteins for this “keep silence” or they changed. It is evident that appearing and developing of living organisms always exist in constant interrelations with mineral environment.

We can suppose the problem of life origin and evolution on the Earth will be solved after decoding biomineralization mechanisms and phylogenetic ties of proteins taking part in this processes.

REFERENCES

[1] Naymark, E.B. et al. "Interaction of clay minerals with microorganisms: a review of experimental data," *Journal of General Biology*, 70 (2): 155-167, 2009. (in russian)

[2] Bernal, J.D. "Phase determination in the x-ray diffraction patterns of complex crystals and its application to protein structure," *Nature,* 169 (4311): 1007–1008, 1952.

[3] Bernal, J.D. "The origin of life. London," *Weidenfel and Nicholson.* 345, 1967.

[4] Cairns-Smith, A.G. "Ambiguity in the interpretation of abiotic syntheses" *Origins of Life,* 6: 265-267, 1975.

[5] Cairns-Smith, A.G. "Chemistry and the missing era of evolution," *Chemistry*, 14 (13): 3830-3839, 2008.

[6]Cairns-Smith, A.G. "Organisms of the first kind," *Chemistry in Britain*, 15: 576-579, 1979.

[7] Cairns-Smith, A.G. "The first organisms," *Scientific American*, 253: 90-98, 1985.

[8]. Cairns-Smith, A.G. "The origin of life and the nature of the primitive gene," *Journal of Theoretical Biology*, 10: 53-88, 1966.

[9]. Cairns-Smith, A.G. "The origin of life: clays" *Frontiers of life*, 1: 169-192, 2001.

[10] Bachmann, P.A. et al. "Autocatalytic self-replication micelles as modes for prebiotic structures," *Science,* 357: 57-58, 1992.

[11] Cherkasov, R.F. "On the geology and mineralogy primordial life," *Proceedings of the IV Intern. Seminar on Mineralogy and Life: The Origin of the biosphere and coevolution of mineral and biological worlds, biomineralogiya"*, Syktyvkar, Komi Republic, May 22-25: 29-30, 2007. (in russian)

[12] Cockell, C.S. "The origin and emergence of life under impact bombardment," *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 361(1474): 1845–1856, 2006.

[13] Deamer, D.W., Pashley R.M. "Amphiphilic com ponents of the Murchison carbonaceious chondrite: surface properties and membrane formation," *Origin of Life and Evolution of the Bioshpere*, 19: 21-38, 1989.

[14]. Ertem, G., Ferris, J.P. "Formation of RNA oligomers on montmorillonite: site of catalysis," *Origins of Life and Evolution of the Biosphere*, 28: 485-499, 1998.

[15] Ferris, J.P. "Montmorillonite catalysis of RNA oligomer formation in aqueous solution. A model for the prebiotic formation of RNA," *Journal of the American Chemical Society*, 155: 12270- 12275, 1993.

[16]. Ferris, J.P. et al. "Synthesis of long prebiotic oligomers on mineral surfaces," *Nature*, 381: 59-61, 1996.

[17] Ferris, J.P., Kawamura, K. "Clay catalysis of oligonucleotide formation: kinetics of the reactionof the 5'-phosphorimidazolides of nucleotides with the non-basic heterocycles uracil and hypoxanthine," *Origins Life Evol. Biosphere*, 29: 563-591, 1999.

[18] Ferris, J.P. "Prebiotic synthesis on minerals: bridging the prebiotic and RNA worlds," *Biol. Bull.*, 196: 311- 314, 1999.

[19] Franchi, M., Gallori, E. "Clay mineral as a resting-place of genetic material in primeval habitats," *Origins of Life and Evolution of the Biosphere*, 30: 322, 2000.

[20] Franchia, M., Gallori, E. "A surface-mediated origin of the RNA world: biogenic activities of clay-adsorbed RNA molecules," *Gene*, 346: 205-214, 2005.

[21] Kostetsky, E.Ya., Aleksakov, S.A. "On the possibility of synthesis of nucleoproteins at the matrix apatite," *Reports of USSR Academy of Sciences*, 260 (4): 1013-1018, 1981. (in russian)

[22] Kostetsky, E.Ya. "On the origin of life and the possibility of forming protokletok and their structural elements in the apatite crystals," *Journal of Evolutionary Biochemistry and Physiology*, 35: 249-256, 1999. (in russian)

[23] Kostetsky, E.Ya. "The possibility of the formation of protocells and their structural components on the basis of the apatite matrix and cocrystallizing minerals," *Journal of Biological Physics*, 31 (3-4): 607-638, 2005.

[24] McClendon, J.H. "The origin of life," *Earth-Science Reviews*, 47 (1-2): 71-93, 1999.

[25] Nisbet, E.G. "RNA, hydrothermal systems, zeolites and the origin of life," *Episodes*, 9: 83–90, 1986.

[26] Nisbet, E.G., Sleep, N.H. "The habitat and nature of early life," *Nature*, 409: 1083-1091, 2001.

[27] Parsons, I. et al. "Biochemical evolution II: Origin of life in tubular microstructures on weathered feldspar surfaces," *PNAS*, 95(26): 15173–15176, 1998.

[28] Schoonen M. et al. "A perspective on the role of minerals in prebiotic synthesis," *AMBIO: A Journal of the Human Environment*, 33(8): 539-551, 2004.

[29] Smith, J.V. "Biochemical evolution. I. Polym erization on internal, organophilic silica surfaces of dealuminated zeolites and feldspars (biological evolutiony/volcanic emissions)," *PNAS*, 95: 3370–3375, 1998.

[30] Weber, B.H. "Emergence of life and biological selection from the perspective of complex systems dynamics" Evolutionary Systems: Biological and Epistemological Perspectives on Selection and Self-Organization, Dordrecth: Kluwer, 59-66, 1998.

[31] Yushkin, N.P. et al. "The origin of the biosphere and the coevolution of mineral and biological worlds" Syktyvkar: Publ. "IG Komi Science Center", 202, 2007.

[32] Pestunova, O.P. et al. "Natural minerals as catalysts for prebiotic synthesis of biologically important compounds," Proceedings of IV Intern. Seminar on Mineralogy and Life: The origin of the biosphere and the co-evolution of mineral and biological worlds, biomineralogiya", Syktyvkar, Komi Republic, May 22-25, 25, 2007. (in russian)

[33] Kröger, N. et al. "Species-specific polyamines from diatoms control silica morphology," *PNAS,* 97(26): 14133-14138, 2000

[34] Kröger, N. et al. "Polycationic peptides from diatom biosilica that direct silica nanosphere formation," *Science,* 286: 1129–1132, 1999..

[35] Kröger, N. et al. "Self-assembly of highly ph osphorylated silaffins and their function in biosilica morphogenesis," *Science*, 298: 584–586, 2002.

[36] Chubukov, V.F. "Microbes stockpile metals," *Chemistry and Life,* 11: 53-55, 1982. (in russian)

[37] Jogler, C., Schüler, D. "Genomics, genetics, and cell biology of magnetosome formation," *Annu. Rev. Microbiol.*, 63: 501-521, 2009.

[38] Nakazawa, H. et al. "Whole genome sequence of Desulfovibrio magneticus strain RS-1 revealed common gene clusters in magnetotactic bacteria," *Genome Res*., 19 (10): 1801-1808, 2009.

[39] Schüler, D. "Genetics and cell biology of mag netosome formation in magnetotactic bacteria," *FEMS Microbiol Rev.*, 32 (4): 654-672, 2008.

[40] Amemiya, Y. et al. "Controlled formation of ma gnetite crystal by partial oxidation of ferrous hydroxide in the presence of recombinant magnetotactic bacterial protein mms6," *Biomaterials*, 28 (35): 5381-5389, 2007.

[41] Prozorov, T. et al. "Cobalt ferrite nanocrystals: out-performing magnetotactic bacteria," *ACS Nano*, 1 (3): 228–233, 2007.

[42] Shimizu, K. et al. "Silicatein alpha: cathepsin L-like protein in sponge biosilica," *PNAS*, 95: 6234-6238, 1998.

[43] Krasko, A. et al. "Expression of silicatein and collagen genes in the marine sponge Suberites domuncula is controlled by silicate and myotrophin," *Eur. J. Biochem.*, 267: 4878-4887, 2000.

[44] Müller, W.E.G. et al. "Molecular mechanism of spicule formation in the demosponge Suberites domuncula: silicatein - collagen – myotrophin," *Prog. Mol. Subcell. Biol.*, 33: 195-221, 2003.

[45] Müller, W.E.G. et al. "The unique skeleton of siliceous sponges (Porifera; Hexactinellida and Demospongiae) that evolved first from the Urmetazoa during the Proterozoic: a Review," *Biogeosciences Discuss.*, 4: 385–416, 2007.

[46] Schrüder, H.C. et al. "Silicateins, silicase and spicule-associated proteins: synthesis of demosponge silica skeleton and nanobiotechnological applications," *Biodiversity, innovation and Sustainability*, 581-592, 2007.

[47] Cha, J.N. et al. "Silicatein filaments and subunits from a marine sponge direct the polymerization of silica and silicones in vitro" *PNAS*, 96: 361-365, 1999.

[48] Sly, W.S., Hu, P.Y. "Human carbonic anhydrases and carbonic anhydrase deficiencies," *Annu. Rev. Biochem.*, 64: 375-401, 1995.

[49] Samsonova, N.E. "Role of silicon in the formation of the phosphate regime of sod-podzolic soils," *Agrochemistry*, 8: 11-18, 2005. (in russian)

[50] Kolesnikov, M.P. "Forms of silicon in plants," *Successes of Biological Chemistry*, 41: 301-332, 2001. (in russian)

[51] Schrüder, H.C. et al. "Silicase, an enzyme which degrades biogenous amorphous silica: contribution to the metabolism of silica deposition in the demosponge Suberites domuncula," Prog. Mol. Subcell. Biol., 33: 250-268, 2003.

[52]. Supuran, C.T. "Carbonic anhydrases - an overview," *Curr. Pharm. Des.*, 14(7): 603-14, 2008.

[53] Wesley, D. et al. "Morphology of artificial silica matrices formed via autosilification of a silaffin/protein polymer chimera," *Biomacromolecules*, 9 (1): 1–5, 2008.

[54] Poulsen, N. et al. "Biosilica formation in diatoms: Characterization of native silaffin-2 and its role in silica morphogenesis," *PNAS*, 100 (21): 12075–12080, 2003.

[55] Grachev, M.A. et al. "Elements of the active center of protein transport of silicic acid in diatoms," *Molecular Biology*, 36 (4): 1-3, 2002. (in russian)

[56] Hildebrand, M. et al. "A gene family of silicon transporters," *Nature*, 385: 688—689, 1997.

[57] Hildebrand, M. et al. "Characterization of a silicon transporter gene family in Cylindrotheca fusiformis: sequences, expression analysis, and identification of homologs in other diatoms," *Mol. Gen. Genet.*, 260: 480-486, 1998.

[58] Thamatrakoln, K., Hildebrand, M. "Approaches for functional characterization of diatom silicic acid transporters," *J. Nanosci. Nanotechnol.*, 5: 158-166, 2005.

[59] Blakemore, P.R. "Magnetotactic bacteria" *Science*, 190 (4212): 377–379, 1975.

[60] Taoka, A. et al. "Polymerization of the actin-like protein MamK, which is associated with magnetosomes," *J. Bacteriol*., 189 (23): 8737-8740, 2007.

[61] Grünberg, K. et al. "Biochemical and proteomic analysis of the magnetosome membrane in Magnetospirillum gryphiswaldense," *Appl. Environ. Microbiol.*, 70 (2): 1040-1050, 2004.

[62] Richter M. et al. "Comparative genome analysis of four magnetotactic bacteria reveals a complex set of group-specific genes implicated in magnetosome biomineralization and function," *J. Bacteriol*., 189 (13): 4899-4910, 2007.

[63] Zurovec, M., Sehnal, F. "Unique molecular architecture of silk fibroin in the waxmoth, *Galleria mellonella," J. Biol. Chem.,* 277: 22639–22647, 2002.

[64] Sudo, S. et al. "Structures of mollusc shell framework proteins," *Nature*, 387: 563–564, 1997.

[65] Bochicchio, B. et al. "On (GGLGY) synthetic repeating sequences of lamprin and analogous sequences," *Matrix Biol.,* 20: 243–250, 2001.

[66] Bingi, V.N., Chernavskii, D.S. "Stochastic resonance magnetoresistance enshrined in the cytoskeleton" *Biophysics*, 50 (4): 684-688, 2005. (in russian)

[67] Ford, K.H. et al. "Data report: Preservation of bacterial magnetosomes at Sites 1225 and 1227," *Proc. ODP, Sci. Results*, 201: 1–17, 2006.

[68] Frankel, R.B., Blakemore, R.P. "Magnetite and magnetotaxis in microorganisms," *Bioelectromagnetics*, 10: 223–237, 1989.

[69] Komeili, A. "Molecular mechanisms of mag netosome formation," Annual Review of *Bioc hemistry*, 76: 351-366, 2007.

[70] Kundu, S. et al. "On the change in bacterial size and magnetosome features for Magnetospirillum magnetotacticum (MS-1) under high concentrations of zinc and nickel," *Biomaterials*, 30 (25): 4211-4218, 2009.

[71] Lang, C., Schüler, D. "Biogenic nanoparticles: production, characterization, and application of bacterial magnetosomes," *J. Phys.: Condens. Matter*, 18: 2815-2828, 2006.

[72] Li, F. et al. "Cloning and functional analysis of the sequences flanking mini-Tn5 in the magnetosome-deleted mutant NM21 of Magnetospirillum gryphiswaldense MSR-1," *Chinese Science Bulletin*, 54 (9): 1522-1528, 2009.

[73] Scheffel, A., Schuler, D. "The acidic repetitive domain of the Magnetospirillum gryphiswaldense MamJ protein displays hypervariability but is not required for magnetosome chain assembly," *J. Bacteriol.*, 189: 6437-6446, 2007.

[74] Scheffel, A. et al. "The major magnetosome proteins MamGFDC are not essential for magnetite bio mineralization in Magnetospirillum gryphis waldense but regulate the size of magnetosome crystals," *J. Bacteriol.*, 190(1): 377-386, 2008.

[75] Schüler, D., Frankel, R.B. "Bacterial mag netosomes: microbiology, biomineralization and biotechnological applications," *Appl. Microbiol. Biotechnol.*, 52(4): 464-473, 1999.

[76] Stephens, C. "Bacterial cell biology: managing magnetosomes," *Current Biology*, 16 (10): 363-365, 2006.

[77] Ferreira de Oliveira, J. et al. "Ant antennae: are they sites for magnetoreception?" *J. R. Soc. Interface*, 7: 143-152, 2010.

[78] Pósfai, M., Dunin-Borkowski, R.E. "Magnetic nanocrystals in organisms," *Elements*, 5: 235-240, 2009.

[79] Safarik, I., Safarikova, M. "Magnetic nanoparticles and biosciences," *Monatshefte für Chemie*, 133: 737–759, 2002.

[80] Kirschvink, J.L. et al. "Magnetite biomineralization n the human brain," *PNAS*, 89 (16): 7683-7687, 1992.

[81] Bäuerlein, E. "Biomineralization of unicellular organisms: an unusual membrane biochemistry for the production of inorganic nano- and micro structures," *Angew. Chem. Int. Ed. Eng*., 10 (42): 614-641, 2003.

[82] Gotliv, B.A. et al. "Mollusk shell acidic proteins: in search of individual functions," *Chem. Biochem.*, 4: 522–529, 2003.