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On the Concepts of Biochemical Ecology and Hydrobiology: Ecological Chemomediators

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Abstract—Earlier, the author published two books and some papers, in which he described conceptual foundations of new scientific disciplines — biochemical ecology and biochemical hydrobiology. These trends in research include studies of the role of chemical substances in interorganismal interactions, in communication and regulation of supraorganismal systems. Another part of biochemical ecology concerns studies of the destiny and transformation of external chemical substances when they interact with the organisms. Both natural and man-made compounds are interesting for biochemical ecology. The basic concepts of biochemical ecology include ecological chemomediators and ecological chemoregulators that have already been included in the body of modern conceptions and are used in modern ecological literature. Application of biochemical ecology to aquatic ecosystems creates the basis for development of biochemical hydrobiology.

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The founding concepts of biochemical ecology were formulated in the book "Introduction to biochemical ecology" [1], published in 1986. The author had offered a unified view of many facts on the border between ecology and biochemistry, based on a number of previous works [e.g., 2] and being in agreement with the approach outlined in [3–5]. The further developments in this field [e.g., 6–8] have endorsed the expediency of distinguishing this direction of research, rooted in Vernadsky's doctrine of biosphere [9–12]. The present paper summarizes several in-depth reviews [1, 8, 22] to provide a brief analysis of this interdisciplinary field of science and introduce some key concepts and terms.

The idea of the importance of chemical approaches for studies of ecological and biospheric processes and relationships between organisms and the environment, including the hydrosphere, was thoroughly developed in the works by Vernadsky [9–12] who stated that the ocean in general should be regarded, at its every point, as an unbreakable link between dead inert matter and ever-changing living matter, chemically restructuring the inert environment [9]. Following Vernadsky, the heterogeneous living matter in the ocean, the marine life as a whole, can be viewed as a special mechanism, changing the sea chemistry entirely [11].

According to Vernadsky [11], the Earth's biosphere, in addition to living, biogenic and inert matter, includes bioinert matter, produced at the same time both by living organisms and by inert processes and representing dynamic equilibrium systems of both [9]. In the biosphere, we encounter various forms of biospheric matter: dead inert low-activity matter, alive disperse matter, very active chemically and geologically, and bioinert matter, a natural structure from alive and inert matter. The alive matter is a form of activated matter [9].

The importance of engaging chemical and biochemical approaches for understanding ecosystems and biocenoses has been underscored by many Vernadsky's followers working in ecology and hydrobiology.

The subsequent development of natural sciences brought new questions from the border zone between ecology, chemistry, and biochemistry. Among them, there is a prominent problem of how well integrated is living matter and the biosphere in general and what are molecular mechanisms of regulation of biospheric equilibria ("ecological equilibria" in modern terms, which still need to be defined more precisely) and formation of bodies of organic matter in the biosphere.

Studies of the features of ecological equilibria in the biosphere and the mechanisms of their maintenance and disturbance, including those involving various organic compounds, especially secondary metabolites are currently gaining much importance [13–20]. The main reasons of growing interest to these problems are multifaceted.

First, the advances in ecosystem science have understandably led to the accumulation of a wealth of data regarding the structure and functioning of ecosystems, their dynamics and stability. This information lays the foundation for a new stage in the development of ecology, with an increasing attention given to the factors that regulate the formation of ecosystems' structure, their dynamics and functioning. A deep analysis of the concept of ecologic equilibrium, still insufficiently clear, is urgently needed [7].

Second, improvements in the chemical and biochemical techniques used to study living organisms and their environment reveal new features of biochemical processes and chemical compounds, especially secondary metabolites, mediating and regulating many interactions between organisms [6, 8, 21].

Third, the human impact on the biosphere has risen sharply, including dangerous chemical pollution. This process is understandably worrying because of the growing disturbance of ecological processes and ecological equilibria in many areas of the biosphere [15–20].

Fourth, the intensifying and developing aquaculture and the general rise in the consumption of biological resources pose a problem of engineering artificial ecosystems with sufficient stability and capacity for regulation.

Understanding of the mechanisms of maintenance and disturbance of ecological equilibria (or ecosystem stability) is critically dependent on the rapidly growing information from the borderlines between ecology, biochemistry, chemistry, and physiology.

Some important aspects of these problems are subject of study in the adjacent fields, such as physiology, behavioral science, zoology, toxicology, biochemistry, biophysics, etc. Usually, however, such studies are mainly concerned only with facts from the particular field and neglect general ecological points. These narrowly specialized approaches to the chemical aspects of ecological interactions between organisms are necessary but not sufficient for appreciation of the mechanisms of regulation and destabilization of ecosystems. The vast number of chemically mediated interactions, influences, dependences, and signals in biogeocenoses form a complicated large-scale system. Only painstaking interdisciplinary studies can help us to understand these systems and learn how to manage them.

At this point, it is pertinent to discuss biochemical ecology in general, its subject, object, and methods, and the characteristic features distinguishing it from other scientific disciplines.

The field of science at the interface between ecology, chemistry, and biochemistry is sometimes called chemical ecology. According to Barbier [3], living organisms from both plant and animal kingdom influence their environment through intersecting action of various molecules. These interactions may occur between animals, between plants, between plants and animals, and between animals and plants. The impact of abiotic environment on animals and plants should also be considered. The study of such interactions and their chemical effectors is the subject of chemical ecology.

This definition, analyzed from the ecological point of view, is notable for dividing the interactions between living organisms into two important groups. First, there are interactions involving substances and molecules as sources of energy or building blocks for the organisms that consume them. The second type of interactions engages molecules that serve mainly or exclusively as messengers transmitting certain information or as regulators of such ecological processes as flows of energy and matter through ecosystems.

Biochemical ecology can be appropriately restricted to the compounds of the second group. Furthermore, there is no need to encumber biochemical ecology with many problems of the impact of abiotic environment on animals and plants [3], e.g., uptake of inorganic nutrients by living organisms, etc.

What, then, represents the main subject of study of biochemical ecology? However incomplete and preliminary our answer may be, it is reasonable to define this mainly as ecological interactions between organisms and their high-order systems (populations and communities) mediated by chemical compounds, mostly those that act exclusively or preferentially as information-transmitting messengers or as regulators of ecological processes [1, 8]. Some aspects of anthropogenic impact upon the biosphere, such as chemical pollution, may also be considered a subject of biochemical ecology [13–20].

The main objects of biochemical ecology are biochemically interacting organisms, populations, and communities, the substances that mediate and regulate the wide spectrum of ecological interactions (including both trophic and nontrophic interactions), and biochemical reactions utilizing these compounds. Importantly, biochemical ecology regards chemical compounds and biochemical reactions first of all as components of ecosystems and participants of ecological processes in the biosphere [1, 8]. This conceptually distinguishes biochemical ecology from biochemistry, where the same compounds may be studied as products of intracellular metabolism disregarding the ecological perspective and context.

The set of methods of biochemical ecology includes a wide assortment of techniques from biochemistry, bioorganic chemistry, chemistry of natural compounds, and various bioassays for the substances under study or their mixtures. In addition to traditional toxicological approaches, these assays may address physiological or behavioral reactions to the substances and preparations under study. Carefully done sophisticated bioassays are no less important for biochemical ecology than highly sensitive methods of structural analysis of organic molecules. Finally, the concluding phase of many studies in this field is chemical synthesis of the discovered natural compound following determination of its structure and ecological role. Therefore, the inventory of biochemical ecology also includes methods of organic synthesis.

The compounds studied by biochemical ecology, as a rule, are present in the organisms or excreted by them in much lower amounts than those used mainly as energy sources or building materials. Many of classes to which these compounds belong have long been studied biochemically with respect to their structure and metabolism, most (but not all) of them belonging to the group of secondary metabolites.

Thus, the methods of biochemical ecology include modern techniques of purification and structural analysis of natural compounds, and methods of discovery of ecological functions of organic compounds, many of which were developed or perfected in the past decades [1, 8]. High sensitivity of modern analytical assays is essential for revealing the interactions between organisms.

A very important group of signal or regulatory compounds are pheromones. Many aspects of their role in information transmission, inter-individual communication, and regulation, have been thoroughly reviewed [1]. Since then, many new data have appeared regarding the role of pheromones in the ecology of aquatic and terrestrial organisms. We believe that the canonical definition of pheromones, given in the works of Karlson and Lüscher (reviewed in [1, 8]), needs to be amended. Taking new data and concepts into account, we suggest the following working definition of pheromones:

Pheromones are individual compounds or their mixtures (complexes, sets, or combinations), which are secreted by organisms into their environment (aerial, aquatic, or onto the organisms' outer surface), and which have a function in signaling, information transmission, or influence on the respondents usually of the same biological species; pheromones can cause a defined reaction (behavioral, physiological, or developmental) in the respondents; pheromones can act as stimuli activating or inhibiting some reactions, behaviors, or physiological processes in the respondents [22].

The appropriateness of this particular definition is based on the accumulated body of information on pheromones, discussed in [22].

Various aspects of pheromones and the related compounds have been investigated by many scientists in Russia. V.E. Sokolov initiated studies in this direction at the Severtsov Institute of Ecology and Evolution. The list of authors having actively published in the field of pheromones includes A. S. Isaev, K. V. Lebedeva, V. A. Minyailo, Yu. B. Pyatnova, M. Barbier, S. N. Novikov, E. P. Zinkevich, and many others. Yu. P. Kozlov and colleagues have studied pheromones of fishes from Lake Baikal. A new direction, sensory ecology, is actively developed [21]. The study of pheromones is a very important direction in the field of chemical communication of fishes [6] and other aquatic and terrestrial organisms [1, 22, 23].

In addition to pheromones, other terms can be suggested to facilitate the characterization of roles of chemical compounds in signaling and regulation of interaction between organisms and higher-order systems [1].

The most general term *ecological chemomediators* describes natural chemical compounds acting as mediators in interactions between organisms, transferring information during signaling from one organism to another [1]. They include sex and aggregation pheromones, food attractants, etc.

Ecological chemoregulators are compounds that regulate behavior, physiology, and development of other organisms [1]. This term embraces many pheromones of both aquatic and terrestrial organisms, and plant compounds acting on herbivorous animals (including arthropods) to disturb their development and reproduction (e.g., plant-derived compounds acting as juvenile hormones, molting hormones, phytoestrogens, etc.). Another group of ecological chemoregulators are compounds made by plants (allelopathic agents) and inhibiting other plant species. They act as natural herbicides, used by plants to compete and leading to regulation of population density and species composition in plant communities.

Ecological chemoeffectors is the most common term, denoting all substances, both natural and anthropogenic, influencing the ecology of living organisms to a certain degree [1, 21, 22].

The action of many ecological chemomediators and chemoeffectors is mediated through their activation by enzymatic biochemical reactions. An example is given by a number of substances of plant origin that protect plants against pathogenic fungi or phytophages. On the other hand, biochemical reactions and evolution of the respective enzymes are extremely important for detoxification of potentially harmful compounds produced by the organism's ecological partners; co-evolutional adaptation of fungi or insects and the plants they eat proceeds in this way.

The mechanisms of detoxification and biodegradation of xenobiotics are becoming especially significant because of the large-scale chemical pollution of modern ecosystems. Detoxification and biodegradation of the polluting agents usually employ the same biochemical mechanisms that the cells use to neutralize natural toxic substances or xenobiotics. Importantly, chemical pollution of the environment can disrupt chemical communication between organisms, which involves ecological chemomediators, chemoeffectors, and chemoregulators, as defined above. Therefore, the problems of chemical pollution [13–17] can also be regarded as part of biochemical ecology.

To conclude this brief description of the basic concepts of biochemical ecology, it is worthy to underscore its relations with the field that is increasingly termed chemical ecology [3] or ecological biochemistry [4]. The above discussion shows that biochemical ecology is distinct from and narrower than chemical ecology, if the latter is defined, following M. Barbier, as chemistry applied to ecology. Ecological biochemistry, sometimes placed at the interface between ecology, chemistry, and biochemistry, should encompass biochemical mechanisms of adaptation of organisms to their environment, and purely biochemical aspects of metabolism of ecologically important compounds and mechanisms of detoxification of xenobiotics. Biochemical ecology is closer to ecology, while ecological biochemistry is closer to biochemistry.

It must be reiterated that the above discourse is not an attempt to give some set definitions but rather an invitation to discuss a modern, highly dynamic and not yet finally shaped field at the interface between many traditional scientific disciplines and directions, not limited to those already mentioned. This multitude of science disciplines includes biogeochemistry, toxicology and ecotoxicology, aquatic chemistry, studies of "ecometabolism" and marine biochemistry (e.g., works of Khailov [2]), public health aspects of hydrobiology (see [8]), biochemical pharmacology, biochemical systematics, chemistry of secondary metabolites and natural compounds, etc. It will take time to provide final definitions and draw firm borders between these disciplines; to do so now is premature.

What can biochemical ecology contribute to solving the problems of nature conservation and management, biotechnology, and aquaculture? A brief answer (see chapter 7 in [8] for a detailed discussion) requires consideration of both theoretical and practical aspects. From the theoretical point of view, biochemical ecology brings into view yet another side of the material basis of ecological equilibria in the biosphere. If one compares energy and material flows in the ecosystems to the street traffic, the compounds discussed here will play the role of traffic lights or traffic police. Biochemical ecology only starts to disentangle this complicated system of ecological chemoregulators, which make an important contribution to homeostasis and homeokinesis (stability *sensu lato*) of ecosystems, including aquatic ones.

Theoretical foundations of biotechnology will likely benefit from the ideas of biochemical ecology that explain the *raison d'etre* of secondary metabolites and other biologically active substances, which are among the most important objects of biotechnology despite the lack of conceptual knowledge about their functions. Furthermore, the biochemical-ecological approach seems appropriate in the analysis of principles and mechanisms of formation and functioning of producer cells important in biotechnology.

From the practical point of view, biochemical ecology together with other scientific disciplines can contribute to lowering the pollution of the biosphere. Some ways to achieve this include:

1) Increasing the self-purification capacity of natural and anthropogenic ecosystems, including aquatic ones [13–17]. Biotechnology and genetic engineering can be promising here to construct and manage microorganisms with an enhanced ability to destroy pollutants [1, 8].

2) Development and introduction of compounds and materials with increased capability for destruction in the environment.

3) Lowering the use of pesticides through introduction of alternative ways of population control [1, 8].

Such approaches would play a significant role in decreasing human ecological footprint and lowering the amount of pollutants introduced into the biosphere.

It has been pointed out that one aspect very important for conservation is making consumption of all biospheric resources more "green" [18–20]. This means a significantly higher level of ecological competence both when exploiting natural resources (including marine and freshwater bioresources) and when constructing any new ecosystem, either aquaculture or biogeocenosis designed to processing and treatment of sewage and polluted water. Knowledge of biochemical ecology of the respective organisms and ecosystems allows one to see an important aspect of their self-regulation and maintenance of the stability of these populations and biogeocenoses. Moreover, biochemical ecology provides a key for practical management and fine-tuning of ecological objects and processes, because it reveals regulatory ecological functions of various substances intrinsic for a given population or ecosystem, and these compounds can be made and introduced to biogeocenoses at will, varying time and place of the intervention. Some of these problems have been reviewed in several chapters of [1, 8].

No discussion of problems of biochemical ecology is complete without mentioning biotransformation of xenobiotics (both natural and anthropogenic) in organisms and ecosystems. This topic is given a concise treatment in chapter 6 of the book [8]. A more detailed analysis of these problems is beyond the scope of this brief review.

At this point, it is prudent to bring up several terms of chemical and biochemical ecology often mentioned in the literature.

1. Allelochemical (from the Greek αλληλωυ, or αλληλο — reciprocal, (to) each other) is a substance that has a certain ecological value (but not as an energy source) for organisms belonging to biological species other than the organism producing this substance. This does not exclude the possibility that allelochemicals can ultimately become important for their producers. A wide class of substance can be considered allelochemicals (chapters 2–4 and section 5.2 in [8]). At the same time, they do not include such important substances as pheromones [3, 4, 9, 21, 23] and some autoinhibitory allelopathic agents (chapter 3 in [8]).

2. Exometabolite is a substance excreted to the environment and generally believed to have some ecological significance (not simply a waste product). The etymology of this term is interesting; it is derived from the Greek root βαλλω with two Greek prefixes. The first prefix, εχ (εζ before vowels) means separation or origin, also identifying movement from the inside to the outside. The second prefix, μετα, denotes commonality, joint action, intermediate, sequence in space or

time, change, or movement. The term stems from the word βαλλω, a polysemantic verb meaning "to throw" (as well as to put something on, to expel, to vent, to pour, to sprinkle and even to get pregnant). Exometabolites are a very wide and important class of substances, especially important for understanding aquatic ecosystems [1, 5, 8]. However, this concept is hard or impossible to apply to many ecologically important substances of terrestrial ecosystems, which can act without being excreted to the environment, such as a number of substances important for ecobiochemical interactions of plants with fungi and animals.

3. Semiochemical is a substance that can de defined [8] as a chemical involved in signal, information, or other similar nontrophic interactions between organisms. In practice, however, this term is used more narrowly and applied to pheromones and some other substances, including kairomones and allomones (chapter 5 in [8]); many toxic substances of high ecological importance are not adequately described by this term because of its meaning. The first and fundamental part of this word is derived from Greek σημερου (σημηιου) — characteristics, symbol, sign, token, cue, signal, banner, seal, etc. As such, the term "semiochemical" is used in the cases when a chemical acts as a signal, mark, or carrier of some information. At the same time, many chemicals, e.g., toxins and chemosterilants (chapters 2, 4 and 5 in [8]) and allelochemicals (chapter 3 in [8]) use not as signals but more directly, simply killing or sterilizing other organisms or inhibiting their growth. Thus, the term semiochemical is not universal either and not as widely encompassing as some authors tend to define it.

These important definitions illustrate the point that ecobiochemical interactions are very diverse. They are analyzed in [1, 8], where ecological functions of chemicals are used as a base to systematically explore a great multitude of organisms and substances combined into a single ecobiochemical continuum typical of biosphere and especially of hydrosphere.

The wide diversity of producers of ecological chemomediators and a great number of chemical structural scaffolds of secondary metabolites should not conceal the fact that the variety of the functions of these compounds is limited. The following list of the most important functions is by no means exhaustive [1, 8]:

1) protection from consumers

2) attacking the organisms used as food

3) restricting the competitors for common resources

4) attracting other organisms

5) regulation of interactions within a population, group or kin

6) supplying precursor chemicals (e.g., precursors of hormones or pheromones)

7) conditioning the environment, including aquatic habitats

8) marking the environments and orientating the organisms in time and space.

These functions are discussed in more detail in [1, 8] with many examples of particular substances.

It should be underscored that there are several approaches to classification of substances used in interactions between organisms. One attempt at such classification was undertaken by Whittaker and Feeny in 1971 (discussed in [1]). However, it has a substantial disadvantage because it is based on an essentially anthropomorphic concept of usefulness or benefit that organisms gain from producing a certain chemical.

The concepts of ecological chemoregulators and chemomediators proved useful for development and modern interpretation of basic ideas of ecology [7, 24].

Biochemical ecology and biochemical hydrobiology. Application of the approaches of biochemical ecology to aquatic ecosystems unavoidably leads to the idea of biochemical hydrobiology. This is appropriately validated by the fact that aquatic organisms produce a great variety of biologically active substances [1, 25, 26], many of which play ecologically important roles of pheromones, toxins, repellents, antifeedants, etc. A review of the existing data on the role of chemical signals in the ecology of aquatic organisms is given in [1, 8]. The role of algal exometabolites is analyzed in [5]. Interesting facts about the role of chemicals in the information flow in freshwater ecosystems are covered in [27, 28].

Some of the data forming the basis of biochemical hydrobiology make important difference in comparison with biochemical ecology of terrestrial organisms. At least three groups of such facts can be emphasized.

First, excretion of fatty acids and other lipids with properties of surface-active substances (SAS) into water is of great importance. These natural SAS can be accumulated on the water/air interface and form a surface film. The chemical composition of this biogenic film determines many of its properties, oxygen transfer through it, heat balance of water surface and other important parameters and processes [29]. Thus, biochemical ecology and hydrobiology becomes intertwined with ecological biophysics of aquatic systems and hydrophysical processes of the ecosystem scale [29].

Second, the area of active research is the transport of essential nutrients, including ω3 polyunsaturated fatty acids (PUFA), along food chains. Some available data suggest that, under certain conditions, the composition and amounts of PUFA can significantly influence the functioning of populations and ecosystems. Thus, several papers in this issue considering the problems of formation and transfer of PUFA along side chains (Sushchik and colleagues, Dubovskaya and colleagues) are of great interest.

Third, natural bodies of water contain dissolved vitamins [30]. Water in lakes and ponds have been found to contain vitamin B12 (0.001–0.85 μg/l), thiamine

(0.001–12 μg/l), biotin (0.0001–0.1 μg/l), niacin (up to 3.3 μg/l), pantothenic acid (up to 0.26 μg/l), etc. (reviewed in [30]). The presence of vitamins is due to their production by some hydrobionts. For example, production of vitamins by some cyanobacteria and associated heterotrophic satellite bacteria has been shown [31]. The presence of vitamins in the water can possibly stimulate those organisms that cannot produce these chemicals on their own, providing yet another possibility for interaction between organisms.

The common framework of all new information and conceptual developments in biochemical ecology and adjacent scientific disciplines is an increasingly deeper perception of aquatic ecosystems with a multitude of cooperative interactions between organisms to their direct or indirect mutual benefits. The beneficial character of these interactions is not always evident; sometimes it appears that only one side benefits, although in many cases it can be predicted that further studies will find a mutually advantageous cooperation. In some cases it may be possible to claim that aquatic ecosystems are governed by the principle of synecological cooperativity [32]. I am cautious to attempt any generalization in this complex field; further studies should help us to clarify the role of irreciprocally or mutually beneficial interactions, includiong biochemical ones, in the functioning of aquatic ecosystems.

Practical application of biochemical hydrobiology will likely be in the modeling and prediction of the behavior of aquatic ecosystems, optimization of screening hydrobionts for potential drugs [1, 8, 25, 26], development of aquaculture, deeper understanding of interactions of pollutants with hydrobionts, and understanding of molecular mechanisms and basics of the important role that aquatic organisms play in the processes at the ecosystem and biosphere scale.

CONCLUSIONS

The analysis of facts at the interface between ecology and biochemistry shows the existence of a new field of scientific knowledge, biochemical ecology. The main concepts of biochemical ecology and biochemical hydrobiology, its branch dealing with aquatic ecosystems, are likely concerned with transfer of information and regulatory interactions as chemical compounds. The specific directions of practical applications of advances in biochemical ecology and biochemical hydrobiology encompass many economically important areas, including aquaculture, environmental protection, and prospecting for new drugs among the secondary metabolites produced by hydrobionts. Further studies of ecological chemomediators and ecological chemoregulators will bring a better understanding of the mechanisms of maintaining the ecological equilibrium in the biosphere, which, paraphrasing Maximilian Voloshin, is a world of tangible and steadfast balance.

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