



Evolution of the biosphere

Symptoms of Ecological Crises

N. N. Kalandadze and A. S. Rautian

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117868 Russia

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Abstract – A list of ecological crisis symptoms, empirically observed from the paleontological record and reconstructed, is presented. The symptoms are founded in the results of a study of the global crisis of continental biocenoses in the mid-Cretaceous time and of the largest paleontologically documented crisis in the assemblage of the terrestrial tetrapods in the Early-Middle Jurassic.

We live in an epoch of a progressively evolving anthropo-stimulated ecological crisis, which threatens not only the Earth's biosphere but civilization as well. The single experience that humanity has at its disposal is that of history (Blok, 1986). Therefore, the reconstructions of the biosphere history on the basis of the geological record and, in particular, the study of the preconditions, natures, and consequences of the ecological crises of the Earth's geological past play an important role (Sokolov, 1983, 1988). Based on that knowledge, we can predict the character of the negative consequences of recent crises and can elaborate an adequate strategy of behavior in the conditions of its progressive development.

Furthermore, already obtained results, mainly in the Paleontological Institute of the Russian Academy of Sciences, testify unequivocally that the crisis epochs are of short duration only in the geological time scale. As to "the ripening" of the preconditions of the ecological crises and their relaxation, these processes prove to be even geologically long. Therefore, referring to geological history seems to be an absolute necessity in correctly estimating the scale of the duration of the crisis with which humanity has collided. The research of the ecological crises of the rather distant past, although only indirectly acquainted with their long-term consequences, acquires, therefore, a particular role.

The formulation of the symptoms of the ecological crises is an important step in that direction. The symptoms are essentially a syndrome (Fedonkin, 1991), which expresses, in a very general form, the regularities of the crisis processes in the Earth's biosphere. The following list of symptoms summarizes the results of two large ecological crises with different characteristics from the geological past.

The first of them is the global crisis of the land and freshwater basin biocenoses in the mid-Cretaceous time, studied in the Laboratory of Arthropods of the Paleontological Institute of the Russian Academy of Sciences

(Rasnitsyn, 1972, 1988, 1989, 1990; Zherikhin and Sukacheva, 1973; Kalugina, 1974, 1977; Rodendorf and Zherikhin, 1974; Kalugina and Zherikhin, 1975; Zherikhin, 1978, 1979, 1980, 1987; Zherikhin and Kalugina, 1980; Zherikhin and Rasnitsyn, 1980; Dmitriev and Zherikhin, 1988). This crisis was studied most carefully from the fossil insect records, but participation of other components of the biota were revealed as well: higher plants (Meyen, 1987; Vakhrameev, 1988), some other groups of terrestrial invertebrates (bivalves, gastropods, ostracods, chelicerats, and others), and vertebrates (fishes, amphibians, reptiles, birds, and mammals). For insects and higher plants at least, this crisis was the largest in the history of the biosphere. Vertebrates reacted to it considerably less strongly (Kalandadze and Rautian, 1983, 1993a). Data on this crisis allowed V.V. Zherikhin to formulate the concept of the biocenotic regulation of phylogenesis. The main attention in this concept is given to the regulatory influence of the structure of the adaptive zones and ecological niches of the shaped biocenosis, historically formed in the course of a long phylogenesis (Vakhrushev, 1988) and constantly reproduced (Rautian, 1993), on the processes of the phylogenesis of taxa, which are the constituents of a biota. According to this concept, the disruption of the structure of the biocenosis provokes an ecological crisis. This idea can be considered an important step in the formulation of the theory of the evolution of biocenoses (and not only of the reconstruction of the particular phylogenesis). The absence and necessity of such a theory have been emphasized by many authors (Zavadskii, 1968; Timofeev-Resovskii *et al.*, 1969; Duvin'e, 1979; Shvarts, 1980; Kolchinskii, 1990; Margalef, 1992).

The second crisis was discovered and studied by us (Kalandadze and Rautian, 1983, 1984, 1993a). This was the greatest paleontologically documented global crisis in the assemblage of terrestrial (non-marine) tetrapods of the Early-Middle Jurassic time. It was not accompanied by marked crisis phenomena in other components of

land biota or, most of all, in flora, and the duration of its apogee exceeded noticeably that of the biocenotic crisis in the mid-Cretaceous. Independently of us, M. Benton (1985, 1987, 1988) discovered the same crisis but, however, did not try to interpret it substantially. Data on this crisis allowed us to formulate the following:

(1) We put forth the concept of a considerable autonomy of the terrestrial tetrapod assemblages, which were not so much components of the concrete biocenosis but rather a community of harvest collectors, produced usually by several, sometimes by very many biocenoses. These considerations are consistent with the already-mentioned absence of the synchronous reaction of other components of the biota in the course of the Jurassic crisis and with the relatively weak reaction of vertebrates to the crisis in continental biocenoses of the mid-Cretaceous. Human beings, who historically came from the community of terrestrial tetrapods, demonstrate the same principal ecological strategy but in a monstrously hypertrophical manner: they are transformed into a kind of super-consumer of every resource, including unrenewable mineral resources of the Earth. The exact ecological strategy of the consumer, who is not very interested in the preservation of each separate producer that is, ultimately, the biocenosis, along with a rather weak dependence on the condition of each concrete biocenosis, has caused the confrontation of man with nature.

(2) We constructed a heuristic model of the conjugate evolution of the community and of its forming biota, with its taxonomical and ecological diversities. The model adds to the ideas of Zherikhin by the feed back mechanism, demonstrating the role of the phylogenesis processes in the formation, disruption during crisis, and reconstruction of the community structure, of its adaptive zones, and of ecological niches after the crisis.

The essential differences between these large ecological crises are evident. The first crisis embraces the biocenoses of the land as a whole, although not all of their components in equal degree. The second one concerns selectively all components of only a separate although large group of the organisms, which possess a considerable autonomy and specific function in the economy of the environment. The practically complete coincidence of the symptoms of these crises seems to be all the more significant. However, we must note, to avoid misunderstandings, that we consider only the qualitative coincidence of the symptoms. Some formal quantitative methods of analysis of the taxonomic and ecological diversity dynamics, which were applied to the fossil insect and tetrapod records, prove to be mutually inapplicable because of the phylogenetic, biocenotic, and taphonomic specifications of the above groups and the different degrees to which they are understood.

The interest in the study of the historical preconditions of the Jurassic crisis forces us, in particular, to analyze the previous smaller and essentially more transient ecological crisis in the terrestrial tetrapod assemblage, which took place at the very end of the Late Permian (Olson, 1989; Sennikov, 1991). The prelimi-

nary results of that work (Kalandadze and Rautian, 1992b, 1993c) testify that at least the larger part of the revealed symptoms are fulfilled in that case as well.

The first attempt at compiling the list of seven symptoms for the mid-Cretaceous crisis was caused by the necessity to compare them with those of the recently discovered Jurassic crisis. The qualitative coincidence proved to be perfect (Kalandadze and Rautian, 1983). For a more detailed analysis of the Jurassic crisis, the list of symptoms was doubled as a result of the works of both paleoentomologists and us. The coincidence was practically complete, as before; only the single symptom (1.5) dealing with the zoogeographical situation on the eve of the crisis is excepted (Kalandadze and Rautian, 1993a). The exception is conditioned by the absence of global zoogeographical reconstructions on insects for the Early Cretaceous. We made such reconstructions on terrestrial (non-marine and non-flying) tetrapods for the whole interval from the Carboniferous to the Pleistocene (Kalandadze and Rautian, 1980, 1981, 1983, 1991, 1992a).

The interest that the enlarged list of the ecological crisis symptoms caused before its publication revealed a number of shortcomings in our list. The poor organization of the symptoms within the list produced a false impression of their independence; in actuality, they showed properties of an integrated syndrome (Fedonkin, 1991). The above-mentioned models, proposed by Zherikhin and us, were devoted to the demonstration of that circumstance as well. In the following list, we attempt to systematize more strictly and formulate more exactly the symptoms, though this cannot replace the arguments that are contained in the models.

In our previous versions of the list, we aspired to use when possible more empirical characteristics of the ecological crisis and to avoid those that were the results of reconstruction and could not be considered as direct evidence from the paleontological materials. It was apparent that the symptoms, empirical for paleontologists, are not applicable to recent ecological material because of the high specificity of the methods used in the study of the community evolution of the paleontological material. On the contrary, a matter that is the result of reconstruction for the paleontologist often can be the subject of direct observation for the neontologist.

This was the case when A.A. Vakhrushev (1988) tried to employ our models, which in fact are reconstructions of the processes known only by their traces in the paleontological record, to an analysis of the initial stages of development of communities of city birds. The city is known to be principally a new type of landscape, having no specific historically developed associations of organisms (Klausnitzer, 1990). Therefore, the first steps of the formation of such associations adequately model the initial stages of the recovery of the biocenosis structure after destruction in the course of an ecological crisis. In spite of the huge differences of the spatial, temporal, and taxonomic scales between the processes, reconstructed from the paleontological models and observed in the city's environments, Vakhrushev succeeded in confirm-

ing, with the recent material, a number of essential conclusions that follow from these models.

Taking into account the necessity of such "cross-traffic" in the ecological studies of the paleontological and neontological materials and trying to satisfy the demands of our colleague-neontologists, we included in the list the symptoms resulting from paleontological reconstruction, which can be the subject of direct observation or mediated research by the ecologist dealing with recent communities. The basis for these reconstructed symptoms is contained in cited publications devoted to the formulation of the models and their indirect control of the paleontological record. In this new form, the list of symptoms represents essentially the code of common characteristics (reconstructed and observed empirically from the paleontological record) revealed for the global crisis of the continental biocenoses in the mid-Cretaceous time and simultaneously for the largest paleontologically documented crisis of the terrestrial tetrapod assemblage in the Early-Middle Jurassic.

Thus, we submit for the reader's verdict a list of the symptoms of the ecological crisis, renewed strongly not only by form but by essence as well.

(1) The ecological crisis is preceded (the preparatory phase according to A.P. Rasnitsyn, 1988, 1989) by:

(1.1) An increase of the rate of taxa formation (cf. symptoms: 2.2.1, 2.2.2, 2.2.5, 3.2, and 4.2).

(1.2) An increase in the rate of extinction (first of all, of eurybiontic and less specialized cenophiles¹ at a rate surpassing that of taxa formation.

In consequence, an increase in the number of accumulated taxa is preserved (cf. synonyms: 2.1, 3.1, and 4.1).

(1.3) The appearance of interzonal lacunas² on the boundaries of the adaptive zones. A considerable portion of the lacunas either remain unclosed for a long time or are used by the predecessors of future active destroyers of the former community structure (cf. symptoms: 2.2.4 and 2.2.5).

(1.4) A decrease in the stability (an increase of the vulnerability) of formed communities to endogenic indignations and exogenic influences (cf. symptoms: 1.1 - 1.3, 1.6, 3.5, and 4.4).

(1.5) A relative continuum of the biota of all regions subject to the crisis. The historical-biogeographical "Pangea" precedes the global crisis.

(1.6) A large ecological crisis is preceded by a crisis of a smaller scale (cf. symptom: 4.4).

(2) The characteristics for the time environs of the ecological crisis are as follows (the preparatory, paradoxical, dramatic, and calming phases, according to Rasnitsyn, 1988, 1989):

(2.1) The extinction of a large number of taxa formerly widespread, including those of higher ranks (cf. symptoms: 1.2, 3.1, and 4.1).

(2.2) The appearance:

(2.2.1) of a large number of taxa, including those of higher ranks (cf. symptoms: 1.1., 3.3, and 4.2);

(2.2.2) of a large number of short-ranged taxa (reported in the paleontological record), including those of the comparatively higher ranks, (mainly, of a family level during a large crisis (cf. symptoms: 1.1, 3.2, and 4.2);

(2.2.3) of taxa reported regularly in the paleontological record only in the time environs of the crisis (cf. symptoms: 3.4 - 3.8);

(2.2.4) of large ecological innovations that had essential consequences in the further history of the biosphere, in the case of the large crisis (cf. symptoms: 1.3 and 2.2.5);

(2.2.5) of the majority of the future ecological dominants either before or after the crisis (cf. symptoms: 1.1., 3.2, and 4.2).

(2.3) An increase in a share of taxa reaching the present and a decrease in their taxonomic rank (cf. symptoms: 2.4 and 2.6.).

¹ The terms *cenophiles* and *cenophobes* were introduced by S.M. Razumovskii (1981) to designate plant species, respectively, included in the succession system and not included in it. The property of being a cenophile or cenophobe refers not to the species on the whole, but to the living form, in this case, to the role of the cenopopulation of the species in the phytocenosis of the present botanic-geographical area. The species can be a cenophile in one botanic-geographical area and a cenophobe in a neighbouring area, and vice versa. We use these terms in a wider sense (Kalandadze and Rautian, 1993a), keeping the spirit of the first definition but not its letter.

Cenophiles are the living forms of the organisms, specialized during the preceding coevolution to a life in the conditions of quite definite biotic and abiotic settings (environment). They constitute the community of organisms formed during the preceding phylogenesis. The structure of the adaptive zones and ecological niches of the community is stable, reproduced by self-assembly from taxa of the characteristic biota (the flora and fauna) in the historically typical conditions (Shmal'gauzen, 1968) of the environment, called an ecotope (Rautian, 1993). The cenophiles are more competitive, but only in conditions historically typical of their community. The motto of the adaptive strategy of the cenophiles is, "our power is in the coordination of our actions."

The cenophobes are the living forms of organisms surviving successfully in various (poorly predicted) conditions of rather unstable (uncertain) abiotic and biotic environments. In contrast to complex communities, they form groups of organisms, indefinite both in composition of the biota and in structure of the adaptive zones and ecological niches. The groups are characteristic of environments disturbed or newly arisen as the results of geological processes and have not been captured or are unfit for the life of the formed community. The wide spectrum of the different habitations but low level of specialization and competitive ability in a particular biotope, which they can occupy only in the absence of competitive pressure from the specialized cenophiles, is characteristic of cenophobes. The motto of the adaptive strategy of the cenophobe is "every life form for itself."

² Interzonal ecological lacunas are the boundary regions of the adaptive zones, extremely poorly defend their highly specialized stenobiotic owners and, are therefore, accessible to the less specialized forms from ecotones because of their euvrybiontity, but inaccessible to specialized stenobiotic cenophiles. Interzonal lacunas arise as a result of a mutually stipulated increase in the stenobiontity and competitive ability of the owners of the adaptive zones in the process of their phylogenetic specialization and of the competitive ouster of less specialized and, therefore, less competitive eurybiontic cenophiles (Kalandadze and Rautian, 1984, 1993a).

(2.4) A vicarious replacement of a number of ancient taxa of high rank by phylogenetically successive taxa of the same rank (cf. symptom: 2.6).

(2.5) An increase in the share of the phylogenetic relicts leading to the obsolescence of some the biota, which is particularly characteristic for the climax of the crisis (cf. symptoms: 3.4 - 3.8).

(2.6) A change in the ecological dominants, which is expressed in the transformation of a number of taxa from the category of the rare and the rarest to the category of those regularly reported in the paleontological record and vice versa (cf. symptom: 3.5).

(2.7) A sharp change in the taxonomic composition of the biota (moreover, even sharper for a large crisis) and in the composition of the living forms of the dominant types of communities during the relatively short interval of the geological time (cf. symptoms: 1.1, 1.2, 2.1 - 2.6, 3.2, 3.3, 4.1, and 4.2). This symptom is an exceptional expression of the principle of threshold reaction of W.R. Ashby (1959, 1962) and testifies indirectly to the stability of the communities of organisms in the geologically long intercrisis epochs.

(3) The characteristics for the climax of the ecological crisis are as follows (the paradoxical phase according to Rasnitsyn, 1988, 1989):

(3.1) Some decrease in the rate of extinction due to symptom 3.4 (cf. symptoms: 1.2 and 4.1).

(3.2) A sharp decrease in the rate of taxa formation, surpassing the decrease in the rate of extinction and leading to a reduction in the number of accumulated taxa (not only species and genera, but also families in a large crisis; cf. symptoms: 1.1, 2.2.5, and 4.2).

(3.3) A sharp decrease in biota diversity, which is connected not so much with an increase in the rate of extinction of the taxons as with a decrease in the rate of their appearance (cf. symptom: 3.2).

(3.4) A decrease in the intensity of the factors in the struggle for existence, depending on the population density (cf. symptoms: 2.2.3, 2.5, and 3.1).

(3.5) A destruction of the former structure of the communities: the succession system (if it is present in a given type of community) and the structure of the adaptive zones and ecological niches (cf. symptoms: 1.4 and 4.4). Thus, the cenotic limitations of the phylogenesis³ are

³ The cenotic limitations of the phylogenesis are the limitations of the phylogenesis of taxa, connected with the presence of: (1) a definite ecological niche or adaptive zone, which appeared during the preceding phylogenesis and (2) a community with the definite structure of a succession system, adaptive zones, and ecological niches, which appeared during the preceding phylogenesis in its biotic surrounding (environment). The destruction of the community structure during the ecological crisis, which affects the inner structure of the adaptive zones and ecological niches of taxa that make up the community, removes at least a part of the cenotic restriction of the phylogenesis of the last ones. V.A. Krasilov (1969) called the evolution (phylogenesis) occurring under the hard cenotic restriction of the formed community (Vakhru-shev, 1988) a coherent evolution. He named the evolution occurring without such a control, incoherent evolution. (Rodendorf and Zherikhin, 1974; Zherikhin, 1978 - 1987; Zherikhin and Rasnitsyn, 1980; Rasnitsyn, 1988 - 1990).

removed in proportion to the degree of the destruction of the community structure.

(3.6) A loss of the conformity of the phylogenetic and ecological specialization of a number of taxa due to symptom 3.5 (a great many of taxa in the course of a large crisis).

(3.7) A decrease in the ecological valence and an increase in the probability of extinction of the highly specialized cenophiles due to symptoms 3.5 and 3.6 (especially in the next stage of phylogenesis because of symptom 4.3).

(3.8) An increase in the ecological valence and a decrease in the probability of the less specialized and eurybiontic forms of ecotones, first of all, cenophobes, due to symptoms 3.5 - 3.7 (especially in the next stage of the phylogenesis because of symptom 4.3).

(3.9) A falling out of a number of taxa, remaining without any significant changes during the crisis, from the geological record due to symptoms 3.5 - 3.7.

(3.10) An active approach of ecotones to the preserved areas of the formed communities due to symptoms 3.5 - 3.8.

(3.11) A variegated mosaic of the areas, which preserved, to some degree, the former biota and the community organization, and of the spacious ecotones, which have an indefinite biota composition. The biota includes the ancestors of the future ecological dominants of the postcrisis communities (cf. symptoms: 3.5 and 3.10).

(3.12) A wide geographical representation of the localities, which is accompanied by a low diversity of their biotas and weak biogeographical connections between the taxa because of the rarity of their repeated finds in various sites (cf. symptoms: 3.3 and 3.11).

(4) The ecological crisis is completed by (the dramatic and calming phases, according to Rasnitsyn, 1988, 1989):

(4.1) An increase in the rate of extinction due to symptom 4.3.

(4.2) A sharp decrease in the rate of formation of taxa, which outstrips that of extinction. In consequence, an increase in the accumulation of the number of taxa is restored (cf. symptoms: 1.1 and 3.2).

(4.3) An increase in the intensity of the factors in the struggle for existence, which are dependent on the population density (cf. symptom: 3.4).

(4.4) The appearance of a new biota (a new type community), which, if it was preceded by a large crisis, would be short-lived and would be affected by a new crisis but of smaller scale shortly (in the geological sense) after its appearance (cf. symptom: 1.6).

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