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Terrestrial Ecology around the Permian–Triassic Boundary

A. G. Ponomarenko
Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia
e-mail: aponom@paleo.ru
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Abstract—Permian–Triassic event is usually regarded as the greatest mass extinction in the Earth's history, although detailed studies have shown that it was not very severe. Localities of fossil insects in European Russia, Tunguska and Kuznetsk basins, and Mongolia provide a unique (the best in the world) opportunity to study the preparation, course of the crisis, and restoration of the biota after it. It is generally believed that climatic changes causing the crisis resulted from eruption of the Siberian traps, so that localities of intertrappean deposits were undoubtedly formed during the crisis. Sedimentation conditions of volcanogenic deposits provide the most detailed time resolution, so that the crisis processes can be investigated in detail. The dynamics of insect diversity in the Paleozoic and basal Mesozoic shows that mass extinctions were absent, although many groups disappeared for some time from the taphonomic window. The crisis events in ecosystems appear earlier than events usually considered as the reason for crisis. The analysis of oryctocoenoses from localities of the intertrappean beds has shown that, during the formation of traps on the mountain plateau, rather diverse ecosystems were retained, including those of the forest formations. They are a source of information, allowing restoration of ecosystems at the end of the Early Triassic.

Keywords: Permian–Triassic event, Siberian traps, ecology, lagerstätte
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INTRODUCTION

When studying the evolution of the biosphere, the points of replacement of the greatest epochs, the time of the greatest changes in the organization of ecosystems are especially important. They are usually regarded as biospheric crises and traditionally used for the establishment of the major stratigraphic boundaries. Recently, the importance of investigation of the biospheric has crises increased considerably. They were proposed to be used as the models for the study of the modern anthropogenic ecological crisis.

The evolutionary events around the Permian–Triassic boundary are usually regarded as a mass extinction (end-Permian mass extinction). Changes in oryctocoenoses at this boundary were very profound, so that the boundary between the Paleozoic and Mesozoic was placed at this point. In doing so, the conformity of the composition of investigated fossil remains to the composition of initial ecosystems usually escaped consideration. The changes at this boundary have attracted attention of researchers for a long time; they are considered in a great many of various works. Extensive bibliography was provided by generalizing works, in particular, by Benton (2002) and Erwin (2005). Nevertheless, a generalized revision of ideas concerning this evolutionary crisis, its dating, causes, character of processes, and consequences is still absent.

The Permian–Triassic event is considered in thousands of works by hundreds of authors, who proposed many hypotheses to gain an understanding of it. This raises a question as to why a universally recognized theory explaining what and why occurred 252 Ma has not been proposed. Perhaps, this is caused by a lack of falsifications of these hypotheses, resulting from the liberal foundation of the organization of scientific community. Along with the liberal ideas, competition increased considerably, eventually determining an opportunity of scientific activity. V.A. Krassilov before his death sighed about the absence of monasteries, where Mendel could perform his experiences with pea for a long time. To date, it has become necessary to care only of the rating assisting to compete for grants and programs rather than of scientific results. The place of publications has become more important than the content of works. It is necessary to cite the lists of own publications and publications of supporters and ignore all other opinions. In any event, the opponents should not be criticized, because, for the citation index, it makes no difference whether a statement is praised or abused. Unfortunately, liberal representations control the noosphere and eradicate dissent more efficiently than any tyranny.

Critical analysis of works of predecessors is performed rarely. In a particularly interesting work devoted to conchostracans, Kozur and Weems (2011) provided correlation of continental and marine deposits based mostly on the distribution of the genus *Falsiska*. Another work devoted to boundary conchostracans does not contain information on *Falsiska* (Scholze at al., 2015). And there is no comment why this genus is absent. Perhaps, in the first paper, the conchostracan system was understood incorrectly or correlation was erroneous. Readers have to guess.

It appears that, for gaining an understanding of the Permian–Triassic boundary event, numerous conferences and formally collective works, where everybody merely states his opinion without coordination with the hypotheses of other researchers, make little sense. It is necessary to organize actually collective work, in which an expert on a certain group or method directly indicates results that come in conflict with the results of other coauthors, intending to overcome these contradictions. Inconsistent results should not cause a priori abandonment and, the more so, indignation. They are not only natural, but even desirable. In particular, in insects, the evolutionary stages even in larvae and imago of the same group are not synchronized.

Since the recognition of periodic crises and development of the ideas about their extent (Sepkoski, 1978, 1984), the main attention was paid to the study of events in the marine biota, which is investigated much more thoroughly than others. At present, almost all works are devoted to the continental biota, where a significant growth of the volume of knowledge and interest of researchers are observed. Very substantial reviews also appeared (see, e.g., Sepkoski, 1978, 1984; Benton, 2002; Erwin, 2005; Benton and Newell, 2014) and rather interesting works devoted to the crisis as an ecological event (Knoll et al., 2007). Attempts at detailed correlation of events around the Permian–Triassic boundary (Kozur and Weems, 2011) are of great importance. Nevertheless, a final variant has not been obtained. The present study pursues two goals; first, to draw attention to domestic works, which are only slightly involved in discussion irrespective of the language of publications and, second, to discuss some debatable problems, which can be considered properly based just on extensive paleontological data accumulated in Russian literature. At the same time, note that the best conditions for studying the Permian–Triassic event are available in Russia. In two regions of Russia, there are numerous localities of fossil faunas and floras. These are northern and eastern European Russia and Middle Siberia with the Kuznetsk and Tunguska basins. In both cases, there are rather dense sequences of Middle and Upper Permian and Triassic localities. According to the modern data, substantial gaps close to the Permian–Triassic boundary in these regions are absent. All main groups are represented, including plants, ostracods, conchostracans, insects, fishes, and tetrapods. It is important that basically almost all of these groups and stratigraphical relationships of localities have been investigated; in addition, the data on the absolute age, magnetostratigraphy, and the ratio of carbon and oxygen isotopes have been obtained (Arefiev et al., 2015). Certainly, available data are far from completeness, but it is evident that we deal with a remarkable field for a full-scale study of the Permian–Triassic boundary event.

In the study of events around the Permian–Triassic boundary, significant changes occurred; extensive new data have been obtained, but the general manner of works has not changed according to these changes. At present, the overwhelming majority of researchers believe that extinction at the Permian–Triassic boundary was catastrophic and changes in the biota were caused by climatic changes resulting from eruption of the Siberian (Tunguska) traps. At the beginning, eruption was explosive and ash thrown out into the atmosphere spread globally. In particular, they are found to the west of the point of eruption, whereas prevailing winds should transport ash to the east, so that it came westerly moving around the entire Earth. Subsequently, basalt lavas began to flow, resulting in the formation of a basalt plateau, which was apparently up to 1.7 km high, while the total thickness of basalts was up to 3 km, including the part which later descended into a caldera. The size of the caldera is estimated as 400 thousand km^2 and the total amount of volcanites is 2–40 million km^3. This was one of the greatest volcanic events in Phanerozoic history. It was only inferior to the Deccan traps, but their effect on the biosphere was apparently even greater. At the beginning of eruption, ash and sulfur dioxide emission should result in significant cooling, but then, ascending lavas passing through carbonates and coals of the Tunguska Syneclise should cause warming due to emission of greenhouse gases, carbon dioxide and methane. Methane was particularly important, since it gave rise to a great greenhouse effect. The temperature increased; the greenhouse effect could have been intensified since methane hydrate melted out. The study of the oxygen isotope ratio has provided evidence of considerable warming, but it occurred at the end of the Induan Stage, i.e., much later than extinction of the marine fauna, which approximately coincides with the Permian–Triassic boundary. In addition, it is hardly probable that eruption lasted for millions of years.

It is supposed that acid rains and an increase in temperature above the tolerant level caused the loss of plants, resulting in intensification of erosion, wide distribution of playalike landscapes and wandering rivers. However, acid rains cannot result in such a long effect. Certainly, forests perished from these rains and scorching clouds, but, on the geological time scale, they rapidly restored. This is evidenced by constant presence of forests on the basalt plateau, where hundreds of localities with plant remains have been recorded. In other cases of mass volcanism (both ancient and modern), there are only a few episodes of long oppression of vegetation by volcanic activity. It seems more probable that the desert zones were shifted as a result of a general climatic trend toward a greater equability of the climate. At the same time, forests were preserved in mountains, as they are preserved now on the mountains of deserted zones, if they are not destroyed by people. They were also preserved in the Siberian traps, which are extensive mountain areas. Desertification at the foothills of the Paleourals decreased westward. The flatter territory is considered, the greater desertification developed, with temporal water streams, salt lakes, and badlands. Naturally, searching for traces of ancient life in these territories, we see a decrease in body size of inhabitants, low diversity, and prevalence of aquatic taxa and organisms with rapid development, such as conchostracans.

It should be understood that the recognition of the position of the boundary in particular sections and discussion of the Permian–Triassic event are different questions. "A gold nail" was driven in Meishan and this is generally accepted fact irrespective of agreement or disagreement with it by particular researchers. The proposition of Sadovnikov (2008) to establish a special nail for the Permian–Triassic boundary in continental deposits on the Tunguska River is attractive, because relations of the Permian–Triassic event with traps are rather probable and, hence, the boundary is located somewhere here (but where is it?). Sediments are accumulated here in ecological rather than geological time, that is, very rapidly and, therefore, in the paleosuccession of ecosystems, ecological factors can have a greater significance than evolutionary factors; as a result, it is highly probable that correlations reflect ecologically and taphonomically similar rather than simultaneous localities. In the traps, which were deposited during a geologically short time, Sadovnikov is inclined to recognize six or seven biostratigraphic units in several sequences, some stages of which are correlated rather confidently. However, the similarity in their taphocoenoses may depend on a similar hypsometric position in a rapidly growing basalt plateau rather than on a close position in geological time (all of them are almost synchronous in geological time). Basalts, tuffs, and tuffites are easily eroded, so that the relief of the plateau was always rather dissected; the plateau grew from above and the entire highland area lowered, occupying the place of lavas flowing onto its surface. The lowering below the base level of erosion allowed the preservation of mountain facies, which are not preserved on usual mountains. Note that it is impossible to arrange insect localities in the intertrappean beds in the time order (see Rasnitsyn et al., 2013). My attempts to do this based on beetles show the same result. Recollect that localities of European Russia are easy to arrange in the time order based on both beetles and all insect. Localities of the Asiatic part of Angaraland and Gondwana also fit into this sequence. Insects are a rather promising object for the study of biological diversity. Species diversity of insects was always higher than that of any other group of organisms.

Another reason for the similarity of taphocoenoses from intertrappean localities can be similar phases of ecogenetic successions; similar stages of restoration of vegetation on volcanogenic rocks should have similar floras. Unfortunately, the plant taxocoene of the lava plateau has not been analyzed in this respect. Ferns of the taxocoene are traditionally regarded as a cover, whereas in modern forests of the same type, the majority of ferns are lianas and epiphytes.

The modern ideas concerning the Permian–Triassic event remain contradictory, in spite of substantial growth of available paleontological data. The book devoted to the Permian–Triassic event Benton (2003) entitled *When Life Nearly Died: The Greatest Mass Extinction of All Time* and Rasnitsyn (2012) published a paper considering the same topic "When the life even did not tend to become extinct." The paleobotanist Sadovnikov, who investigated fossil plants from the Tunguska traps for almost half a century, has written in a recent paper that "In the section of the volcanic plateau, the event corresponding to the concept of 'crisis' is not reflected" (Sadovnikov, 2016, p. 87). This is surprising, since in the place where there was an event that gave rise to the crisis, qualified experts do not find it, whereas in remote territories, including the opposite hemisphere, the crisis signs are distinctly manifested. Opinions differ considerably as to the duration and intensity of the crisis, the influence of the lava flow on the climate and landscapes, and other parameters. Unfortunately, at present, there is no reason to hope that the situation will soon change for the better, since the possibility of field geological and paleontological studies is reduced considerably. Nevertheless, it is possible to ascertain that the concept of the apocalyptic character of the Permian–Triassic event is artefact.

Most of the researchers studying the evolution of diversity, apply the method developed by Sepkoski. Operational units in the analysis of the evolution of biodiversity are usually families. The distribution in time of lower-rank taxa is usually very incompletely known and they are frequently represented by endemics. The ideas concerning extinction are based on calculation of taxa found in certain beds, usually within a stage. If evolution is rapid, both diversity and extinction are strongly overestimated. Actually, if ten species existed during an age, replacing each other, and the last had become extinct, both diversity and extinction will be determined as ten species, although in fact each moment only one species existed and one became extinct. The estimated diversity is ten times greater than actually existing one. If one age is represented by a Lagerstätte, while a succeeding age lacks it, we will get a peak of diversity followed by severe extinction. Certainly, the method proposed by Sepkoski was a great achievement, but it is also noteworthy that the newly appeared interesting methods of the analysis are undoubtedly insufficiently used. I prefer the method for the analysis of diversity developed by V.Yu. Dmitriev. In this case, the operational unit is a family that crosses the boundary between ages, i.e., instantaneous diversity is estimated. This method strongly underestimates the existing diversity because of omitting endemic families, but shows much better the character of diversity evolution. It shows that, around the Permian–Triassic boundary, the number of families of insects or terrestrial vertebrates that became extinct was not extremely great.

When estimating the intensity of extinction, it is necessary to count not only organisms that survived a particular boundary (found directly after extinction), but also the so-called *Lazarus taxa* and ancestors of taxa that appeared in the fossil record in the Middle Triassic and later. Otherwise, where have they come from? Extinction of taxa was incomplete; they only significantly decreased in number, so that they temporarily disappeared from the fossil record. In the terminal Permian (Vyatkian), at least ten beetle families are known; in the Lower Triassic, only two genera of one family are recorded; however, beginning from the Middle Triassic, all but one other families gradually appear.

An important point is the time separating the sites studied. Comparing the curves obtained for vertebrates by Kalandadze and Rautian (1993) and Benton (1989), it is evident that they are completely different, although they are based on almost the same material; the only difference in approaches is the fact that, in the first case, the points considered are separated by an epoch, while in the second, by an age. The curve constructed by Dmitriev (Alekseev et al., 2001) differs from them even greater.

The change in the position of taphonomic windows as a result of transformation of macrolandscapes is also rather important. It has been shown that changes taken for the Permian–Triassic boundary are asynchronous even within South Africa (Gastaldo et al., 2009). Changes in the biota began long before the Permian–Triassic boundary. Beetles of the Mesozoic–Recent type appeared as early as the terminal Middle Permian in southern China (at that time, it was a separate microcontinent situated at the equator), but they became abundant in the Late Vyatkian of European Russia. Among terrestrial vertebrates, the terminal Vyatkian (before the Permian–Triassic boundary) is marked here by the appearance of Pseudosuchia, direct ancestors of dinosaurs. In the Angara flora, the Cordaitaceae stopped to dominate; phylladoderms and, then, tatarinovians and lepidopterian pteridospermatophytes appeared in the foreground. The replacement occurs in different time, depending on the paleorelief of a particular region. In Gondwana, the glossopterian flora existed up to the end of Permian, while dicroidian pteridospermatophytes became widespread only in the Triassic. The replacement of biotas does not look as a sharp shift with strong extinction as a result of an external impact; different groups in different territories changed asynchronously. It was sometimes proposed to draw the Permian–Triassic boundary in South Africa between extinction of dicynodonts and emergence of lystrosaurs. Subsequently, it turned out that the beds, in which it was drawn, are not synchronous. On the Russian Platform, archosaurs appeared earlier than lystrosaurs and, in Dalankou (China), lystrosaurs appeared much earlier than the disappearance of dicynodonts (in Dalankou, the Permian–Triassic boundary is drawn between these events). At the same time, the presence of *Tupilakosaurus* in the Nedubrovo locality is regarded as a sufficient basis for the assignment of this locality to the Triassic, although many researchers believe that it should be dated terminal Permian. The prevalence of Permian insects in the Babii Kamen' locality in the Kuznetsk Basin and in the majority of intertrappean localities of the Tunguska Basin should not be regarded as unequivocal evidence of the Permian age of these localities. Thus, we have to admit that such mixed faunas and floras could exist in the beds younger than the Permian–Triassic boundary. Nevertheless, many researchers are inclined to assign to the Triassic any bed that encloses *Lystrosaurus* or *Tupilakosaurus*. Changes in the biota were not extremely catastrophic and lasted for a significant time interval. Miniaturization of beetles characteristic of the event began as early as the Middle Permian; simultaneously, cupedoid beetles, whose larvae inhabited wood, almost completely disappeared. They have not been recorded in Late Vyatkian localities, although Nedubrovo has yielded a strange cupedoid. Their remains are not known in the Lower Triassic, but in the Anisian of Germany and France, they are rather diverse from the very onset of this age. It is evident that many changes that are considered to be characteristic of the Permian–Triassic boundary actually appeared much earlier than eruptions of traps, the beginning of which can be recorded in many sections based on the appearance of characteristic ash and spherulae and also on the change in the ratio of light and heavy carbon isotopes. The above enables us to make two conclusions about the event around the Permian–Triassic boundary:

(1) The event was not an instantaneous response to the influence of one external factor.

(2) The event resulted from modification by an external effect of a rather long-term process of internal transformation of the biosphere. Such a process is usually based on transformation of producers.

It is supposed that:

(1) At the end of the Late Paleozoic, there were three independent, but synergically connected processes developed in the continental biosphere: (1a) changes in the composition of many groups of the biota, in particular, plants, insects, and tetrapods;

(1b) global warming leading to redistribution of landscapes and reaching a maximum at the end of the Early Triassic, with the final transition to equable biosphere; (1c) catastrophic eruption of the Siberian traps, the climatogenic effect of which was sharply intensified by reduction of carbon in coals and carbonates to methane in the Tunguska Basin.

(2) The process of changes in the biota lasted from the Permian to Triassic, being most intensive from the Vyatkian to Middle Triassic. The new biota began to develop before the crisis rather than after and as a result of it.

(3) The change in landscapes and vegetation was climatogenic, connected with gradual transition from zonal to equable biosphere, rather than resulted from volcanogenic acid rains. It is evident that they and scorching clouds caused temporal destruction of vegetation, but on the geological time scale, it was restored. Therefore, on the mountain plateau of the Tunguska River, Sadovnikov has not recognized a crisis and, on the plains, with wide distribution of playa landscapes and "braided river" systems, there was a strong decrease in biodiversity treated as the strongest ecological crisis in Phanerozoic history.

(4) The change in landscapes resulted in redistribution of *taphonomic windows,* many taxa disappeared from the fossil record, although they were retained in the biota as Lazarus taxa.

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