

Changes in Terrestrial Biota before the Permian–Triassic Ecological Crisis

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Abstract—The period around the Permian–Triassic boundary was marked by one of the most important and interesting events in the evolution of life. The diversity of both marine and continental biotas decreased. The changes were global and led to the establishment of the new Mesozoic World. Transformations of the organic world constituted a single process with changes in the inorganic components of the biosphere. The preceding glacial period had ended and the “cool,” zonal, and markedly seasonal climate was replaced by a “warm,” “equable,” virtually non-seasonal and azonal climate. The new climatic organization remained on Earth for more than two hundred million years. The biotic crisis was global: it involved the sea, the land, and inland waters. The changes on land began earlier and more superficial. The principal events were in the Kazanian and Vyatkian, before the end of the Permian. The crisis was caused to a greater extent by biospheric processes than by momentary external influences, the latter at most triggering the crisis.

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INTRODUCTION

Studying the evolution of the biosphere one should concentrate especially on the transitions from one great epoch to another, the times of maximum change in ecosystem organization. One of these was from the end of the Permian to the beginning of the Triassic. The changes were global and affected everything, not only the biota; landscapes and climate were changing radically as well. Transformations of the organic world constituted a single process with changes in the inorganic components of the biosphere. The preceding glacial period had ended; the “cool,” zonal, and markedly seasonal climate was replaced with a “warm,” “equable,” virtually non-seasonal and azonal climate. The new climatic organization remained on Earth for more than two hundred million years. It would be very useful for us, living in conditions of the “cool” biosphere, to understand how this transition took place. It would aid in elucidating the question of whether we live in an interstadial or an interglacial and what is the probability that we are observing the end of a glacial period. First of all, such knowledge would sharply reduce the extent of scientific-political speculations about “global warming” and help to save the resources of humanity from the struggle against imaginary threats. The relatively low cost of detailed scientific studies of these problems would be repaid many times over.

The transition from the Permian to the Triassic was marked by the greatest decline in biodiversity in the Phanerozoic, termed the Permo-Triassic crisis. This process is usually referred to as a mass extinction,

although a considerable decrease in the origination rate of new forms, rather than actual extinction, took place. The study of ecological crises of the past is essential for understanding the behavior of living things during the anthropogenic ecological crisis.

Up to now, the study of the Permian raises more new questions than it answers, but while looking for these answers we can get comparative data on the present-day natural situation. Climatic patterns of the preceding, Carboniferous–Permian glaciation and of the subsequent transition to “warm” biosphere still remain far from complete, despite recent special investigations (Zharkov and Chumakov, 2001; Chumakov and Zharkov, 2002, 2003). However, these papers show the same fundamental flaws as most others. They do not examine how biotic changes affected the landscape, and what are the particularities of the Permian erosion and sedimentogenesis which took place in a biosphere that was distinct both from modern and more ancient ones. How they proceeded in the nearly complete absence of annual and herbaceous plants, which inevitably impeded the early stages of ecogenetic succession? Re-vegetation of drying alluvium and burnt areas must have been much slower and coastal erosion much stronger; therefore, closed lake basins and vast valleys of “wandering” rivers were much more likely to appear than in the same landscape and climatic conditions today. An important question is, how were these processes affected by the dominance shift from spore plants to gymnosperms, with their totally different type of crown and root system? Naturally, at the present state

of knowledge these are pure speculations, but we will need to start with that, if we would indeed like to develop Vladimir Vernadsky's ideas. Now we know that changes of landscape and sedimentation environment sometimes cause such changes of corresponding biotic assemblages that these latter may be interpreted as belonging to different biochoria. When the megafloora of the Tavun-Tolgoi locality, southern Mongolia was studied only from the productive coal-bearing facies of the Tavun-Tolgoi Formation, it was unequivocally interpreted as Siberian due to the complete dominance of cordaites (Durante, 1971, 1976; Ziegler, 1990); however, a markedly different floral assemblage with Cathaysian and Gondwanan relationships was discovered in the coal-less Tsanhi Formation (Uranvileg, 2001). At the same time, several plant and insect species common for both formations indicate that these strata cannot be of essentially different age or climatic origin. Changes in biota and in sedimentation environment are intimately connected and should be interpreted together.

Another flaw in the papers discussed is similarly widespread, although undoubted progress has been made compared to some previous papers (Ziegler, 1990; Kutzbach and Ziegler, 1993). This is, too low temporal resolution. Of course, discussing the "Late Kazanian–Tatarian climate" instead of "Permian climate" is progress, but it is still insufficient to understand the correlation of biotic transformations with changes of climate and landscape. During the Tatarian there are no less than four important stages in the evolution of terrestrial biota, and the maximal changes of both tetrapods and insects occurred within the Vyatkian. Unfortunately, attempts to analyze the changes in more detail meet considerable difficulties. One of major obstacles is insufficient and geographically uneven knowledge of the plant and animal distribution. Another obstacle is that stratigraphic correlation between different terrains is not precise enough. To judge the character and causes of the changes, one should know what events were synchronous in different parts of the Earth, for example in Angaria and Gondwana, in the seas and on the land, but an integrated "calendar of events" for the whole Earth is too far from perfection. Nevertheless, we can conclude that the preceding and recent glacial periods seem to be essentially different.

The preceding "cool" biosphere existed for several ten million years in the Late Carboniferous and Early Permian. This time may be termed "cool" only with reservation. In every textbook one can read about tropical forests in the Carboniferous. They existed under the conditions of "cool" biosphere and were hot only because they grew in the tropical zone near the equator. In the present-day glacial period it is hot in the tropics as well. These forests shared some features with modern tropical ones. So, their inhabitants were very diverse for that time and distinctive in "architectural extravagances." Among Carboniferous insects there are

many large, decoratively colored forms with characteristic outgrowths and spines. Having collected one hundred insect specimens from a locality of this zone, we find nearly one hundred species. At the same time in subpolar regions a biome existed that was named "Carboniferous tundra" by Sergey Meyen. Almost the only plants there were 1-m-long rods with scant foliage on top, and for every hundred insect specimens collected here we find only a few species. Therefore, not a global coolness but a sharp contrast between very warm tropics and very cold polar regions is a characteristic of the "cool" biosphere. The climate was strictly zonal and the general climatic organization was similar to the modern one. However, detailed analysis reveals several differences. The glaciation was sharply asymmetrical, existing on the southern supercontinent Gondwana and often extending into quite low latitudes, while in the Northern Hemisphere no land glaciation is known and only glacial marine deposits are found. Desert zones between about 30° and 40° latitude, so characteristic of modern zonality, were also missing. The distribution of land animals was likewise markedly asymmetrical. So, the distinctive pareiasaurian fauna of South Africa is very similar to that of eastern Europe, but, according to the latest plate tectonic reconstructions, they existed in totally dissimilar zones (Ziegler, 1990), their distance from the equator differing by almost 30 degrees. In the second half of the Permian cockroaches disappear from fossil faunas in two temperate zones, Angaria and Gondwana. It seems natural to explain this with the climate being too cool for these thermophilic insects. However, the climate in fact turned considerably warmer at that time, whereas in the much more contrasting climate of the end-Carboniferous glacial maximum, fossil entomofaunas of Angarian localities consist almost exclusively of cockroaches! These facts raise doubts as to whether the modern type of heat transportation from the tropics to the poles, with three convective cells in each hemisphere and powerful diagonal currents ("heat conveyer belts") such as the Gulf Stream, operated during the Carboniferous–Permian glaciation. For those times there is no reliable evidence of the psychrosphere, a cold-water bottom layer appearing in the modern oceans due to powerful deep currents, which transport the oxygen-rich cold water from the polar regions to low latitudes and thus support quite diverse life in the abyssal zone. Computer models of the Middle–Late Permian climates match considerably with the actual distribution of the main plant biomes (Kutzbach and Ziegler, 1993), but these results should be taken with caution. The parameter values used to model this climate differ little from those of the Late Carboniferous–Early Permian, but climates of these periods differ strikingly, being more zonal and glacial.

Possibly these controversies can at least partly be explained by the different global geographical situation. Towards the end of the Permian all land masses became united into the single supercontinent Pangaea,

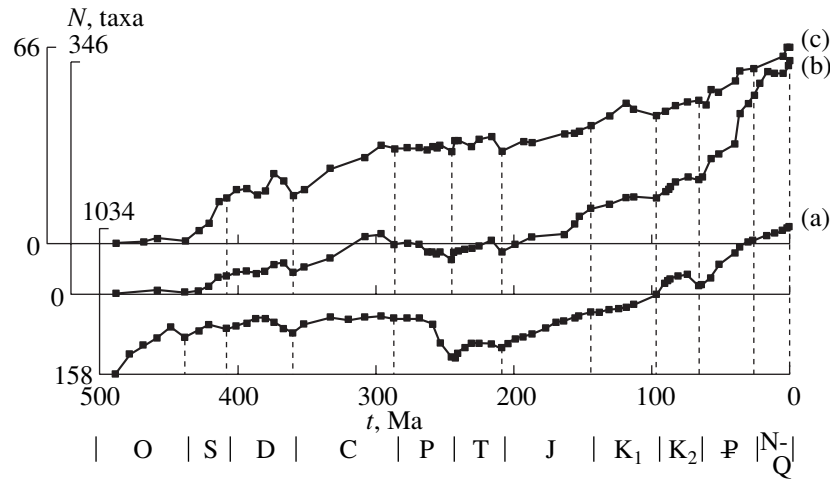


Fig. 1. Diversity dynamics of marine (a) and freshwater (b, c) biota: (a, b) families, (c) orders; (N) number of taxa crossing the boundary between stages (from Alekseev et al., 2001).

which stretched nearly from one pole to the other. However, even its widest part, Gondwana, was narrower than modern Eurasia. This should result in an essentially dissimilar global climatic organization: a winter anticyclone considerably weaker than now, a higher mean temperature, and a decrease in the snow-covered area in winter lessening the albedo and further increasing the mean temperature and reducing zonality (but these seemingly reasonable conclusions are not confirmed by the distribution of pareiasaurian faunas).

Plants represent the best studied group of terrestrial organisms and are most often used for paleoclimatic reconstructions, but the results obtained are still equivocal as can be seen from a recent review of floristic changes about the Permian–Triassic boundary (Gomankov, 2005). Why at the maximal zonality in the Late Carboniferous and Early Permian lycopsid floras of both hemispheres were much more similar than the Permian temperate floras, the northern one dominated by cordaites and the southern by glossopterids? The Late Permian faunas in both hemispheres did not differ considerably and most probably show parallel homotaxal changes, including both easily migrating insects and poorly dispersing tetrapods. In the Tatarian, cordaites in Subangaria were also replaced with pteridosperms, but belonging not to glossopterids but to a different group, peltasperms. It is unlikely to be associated with dispersal barriers: glossopterids were present but rare in Amuria and Western Subangaria.

The idea about mass extinction at the Permian–Triassic boundary was based on the study of marine biota and became universally accepted after papers by Sepkoski (1978, 1979, 1984) that represented a stage in the studies of taxonomic diversity evolution. On the other hand, the changes that occurred at the same time on the land remain insufficiently studied. First of all this is due to a much less complete terrestrial fossil record, but even the data available were not analyzed in detail.

Nevertheless we can conclude that changes in the terrestrial biota and decline in its diversity were quite significant, but without a sudden extinction at the Permian–Triassic boundary. This decline spanned for a considerable period and was probably due to restructuring of ecosystems rather than momentary extraterrestrial or extrabiospheric causes. Diversity decreased in the Middle and early Late Permian and increased somewhat just before the terminal Permian. It is necessary to mention that the global diversity pattern shows a more abrupt decline than some regional patterns. In the general pattern a taxon is present as long as its last species is living, whereas other species of the taxon in most regions become extinct much earlier (different species in different regions) and respective regional diversities are decreasing while the integrative global diversity is still preserved.

The extinction started much before the P/T boundary, the turning point in the rate of diversity decrease is about the middle of Tatarian, the decline is mainly due to a lower rate of origination of new taxa rather than a higher rate of extinction of existing ones, arguing for intrabiospheric causes of the great extinction.

The diversity dynamics of freshwater organisms was discussed earlier (Dmitriev et al., 1995; Alekseev et al., 2001), so only the general pattern and some additions are given below. The extinction in fresh waters proceeded gradually; the number of families decreased since the Carboniferous; at the ordinal level there is nearly no extinction at the P/T boundary (Fig. 1). The diversity of arthropods declined likewise since the Carboniferous, there is a broad depression of diversity about the P/T boundary. A peculiar pattern shows the number of ostracode species recorded in eastern Europe about the P/T boundary: highest in the Kazanian, decreasing to the beginning of the Tatarian, then increasing again, continuing to increase in the basal Triassic; ostracodes are unusually diverse in the Vyat-

kian (15 species compared to a maximum of 11 before). Ostracodes characteristic of the Triassic appear already in the terminal Permian (Vyazniki locality). Only a few ostracode and conchostracan species went extinct at the P/T boundary. The possible occurrence in the Late Permian of the living notostracan species *Apus cancriformis* is interesting. The familial diversity of freshwater mollusks remained practically unchanged at the boundary. In eastern Europe the mollusks analyzed at lower taxonomic levels show no diversity decrease in the Permian, but became exceedingly rare in the basal Triassic.

Among freshwater algae only Charophyta are well represented in the record, but interpretation of these data is highly disputable: some authors state that all families were replaced at the boundary, others declare that all three Late Permian genera crossed the boundary.

Characteristic of the beds near the P/T boundary is so-called “fungal spike,” an unusually high content (up to 95%) in palynoprobes of the microfossils interpreted as aquatic lower fungi (Visscher et al., 1996). In some localities the spike coincided with the mass presence of fragmented plant detritus, so it was concluded that this peak development of fungi is associated with processing the mortmass after the mass death of woody plants in the crisis. It is quite a common mistake in interpreting the results of mass mortality, which decreases rather than increases the mortmass: all organisms are mortal, and mass mortality results in decline of average biomass and therefore of the mortmass. So far as palynoprobes are counted in relative units, dominance of certain microfossils (fungal spores or detritus) may not be due to their abundance but just to the scarcity of other spores and pollen. Recently these microfossils were reinterpreted as green algae of the order Zygnematales (Afonin et al., 2001) and reported as abundant not only in relative but also in absolute dimension (S.A. Afonin, pers. comm.). This “algal bloom” is rather difficult to explain, more so because it is observed in both marine and freshwater deposits. Such a bloom should be associated with an increased input of nutrients into the water bodies, but it is unclear what processes may release nutrients into the sea and lakes at the same time.

The diversity of freshwater fishes decreased from the beginning of the Late Permian and considerably dropped at the boundary. The number of fish species in eastern Europe changed similarly to the familial diversity: gradually decreasing towards the boundary and minimal at the very beginning of the Triassic, then increasing quite rapidly. The diversity of amphibians and aquatic reptiles was declining since the Early Permian, but in the basal Triassic nearly all known tetrapods were aquatic forms. Amphibians dominated among tetrapods in the Carboniferous and Early Permian; in the Late Permian reptiles are almost five times as diverse as amphibians, four-fifths of reptiles belonging to Synapsida, but in the Early Triassic the number of families in Amphibia, Synapsida, and remaining Reptilia became subequal. By the Late Triassic the

number of families decreased in Amphibia and Synapsida + Mammalia, and doubled in the remaining Reptilia. About the P/T boundary many tetrapods, especially synapsids, went extinct; Microsauria and Seymouriamorpha did not survive into the Mesozoic. More than 80 tetrapod families are recorded in all the Middle and Late Permian (Fig. 2), and less than 40 in the Early Triassic when large Parareptilia died out and Diapsida diversified. Tetrapod diversity was quite high in the earliest Permian (such high diversity was only regained after the mid-Jurassic), minimal in the late Early Permian, then increasing somewhat, and declining again after the Kazanian (but in the Early Triassic still somewhat higher than in the late Early Permian). In the Middle and Late Permian tetrapods demonstrate high origination and especially extinction levels. Subsequent Kazanian and Tatarian assemblages share 5 or 6 of 10 to 13 families, very rarely dominating ones; the P/T boundary is crossed by four families, the difference seems not to be significant; 14 families survived from the Early to Middle Triassic. The popular impression of unusually high reptilian diversity in the Late Permian is due to rapid changes in tetrapod assemblages during that period rather than the actual coexistence of very diverse reptiles. Most of animals portrayed together in illustrations can never have actually seen each other, as they lived at different times.

Despite considerable similarity in the changes of tetrapods in South Africa and eastern Europe, one can see some differences. Proterosuchia are known in South Africa only from the Triassic, whereas they already appear in eastern Europe at the end of the Permian. *Lystrosaurus* was numerous and lived for a long time in South Africa, while in eastern Europe their isolated finds are known only in the oldest Triassic beds represented. A similar situation occurs with lydekeriid labyrinthodonts. Analogous differences are recorded in China: in Xinjiang *Lystrosaurus* already appeared by the end of the Permian and one of the dicynodonts is found in the Lower Triassic, whereas in all other regions dicynodonts are known only from the Permian. Therefore, changes of tetrapods about the Permian–Triassic boundary were not catastrophic and significantly dissimilar in different regions (of course, if the boundary positions identified for these regions are essentially synchronous). In general, therapsids are replaced by sauropsids with transition from the Permian to the Triassic, but the change at the P/T boundary itself seems ordinary.

Arthropods and especially insects are, as today, the most diverse animal group in the Permian. Many Paleozoic arthropod localities yield groups that are not recorded from the Mesozoic and Cenozoic as compression fossils, but are abundant in the modern fauna, such as mites or spiders. Arachnids, diplopods, and apterygotes (represented by Monura) are common in the Carboniferous and Lower Permian, occasionally found in the Upper Permian, and then virtually disappear from the record, although their actual abundance and diver-

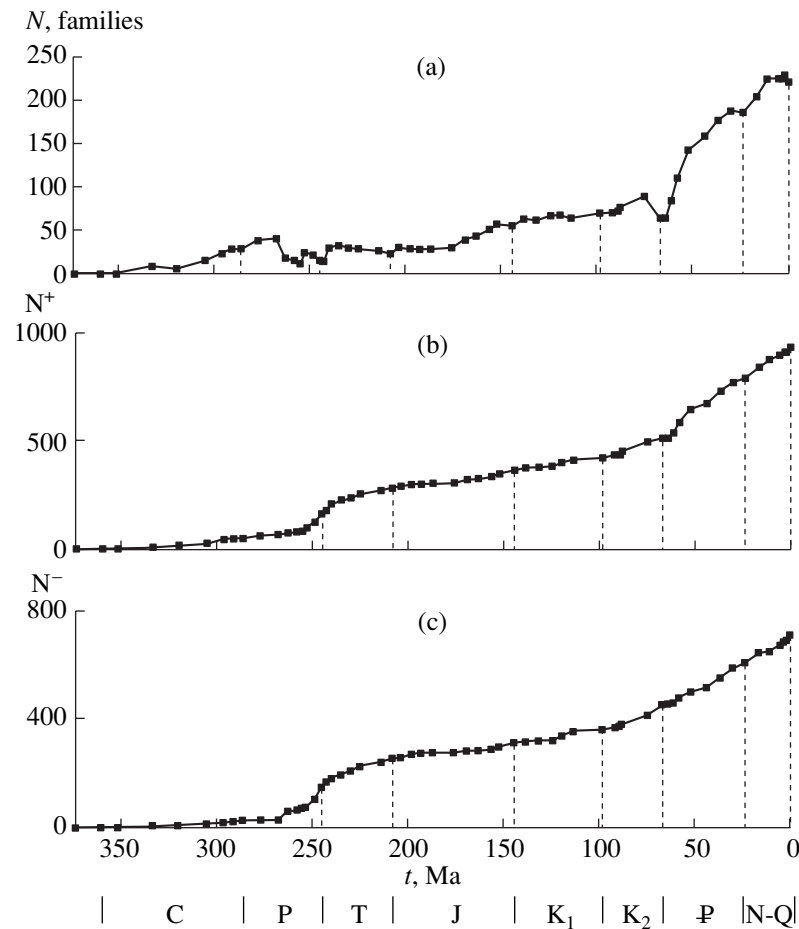


Fig. 2. Tetrapod diversity dynamics: (a) number of families crossing the boundary between stages; (b) number of originating families; (c) number of families going extinct (from Alekseev et al., 2001).

sity hardly decreased. Instead we should assume another life mode for these groups in the Paleozoic, which made their burial more likely. In water bodies insect burial usually takes place rather far from the shore. Surface currents were scarcely able to transport easily sinking apterygotes and especially large, heavy myriapods; therefore, some large floating objects performing such transportation should be in existence. An interesting peculiarity of these apterygotes is that they are similar to the larvae rather than the adults of their nearest relatives. Virtually nothing is known about the Late Permian chelicerates and myriapods (few, mostly undescribed finds), the Carboniferous ones are much better represented in the record. There are few eurypterids in the Permian (until the Kazanian), and all lived in fresh water.

In the Late Permian insects were changing extremely fast (Fig. 3), but nevertheless the insect faunas on the continents situated in different hemispheres were quite similar (Ponomarenko and Shcherbakov, 2005). Due to flight, insects disperse very rapidly, even reaching quite remote areas immediately in terms of geological time. The data available indicate that the

changes of insect faunas on different continents were homotaxal and most probably synchronous. The Permian Period constitutes a rather well marked stage in insect evolution. Most Carboniferous insects belong to extinct orders, whereas in the Permian most are representatives of extant orders. Of 25 insect orders known in the Permian, only eight are extinct, and none are restricted to this period. On the other hand, all the families, genera, and species described from the Permian are extinct (but we cannot rule out the possibility that several localities yielding extant beetle families are Upper Permian rather than Lower Triassic). Insects most characteristic of the Permian are Odonata, Blattinopseida, Hypoperlida, Auchenorrhyncha, Miomoptera, Blattida and especially Mecoptera and Grylloblattida; Auchenorrhyncha originated in the Permian, the remaining are of Carboniferous age. Seven insect orders went extinct during the Permian, and only three more during all the subsequent time. The Permian became a turning point in insect history, when many still-extant orders originated, and most groups characteristic of the Carboniferous died out. The insect diversity at the family level was dropping throughout the

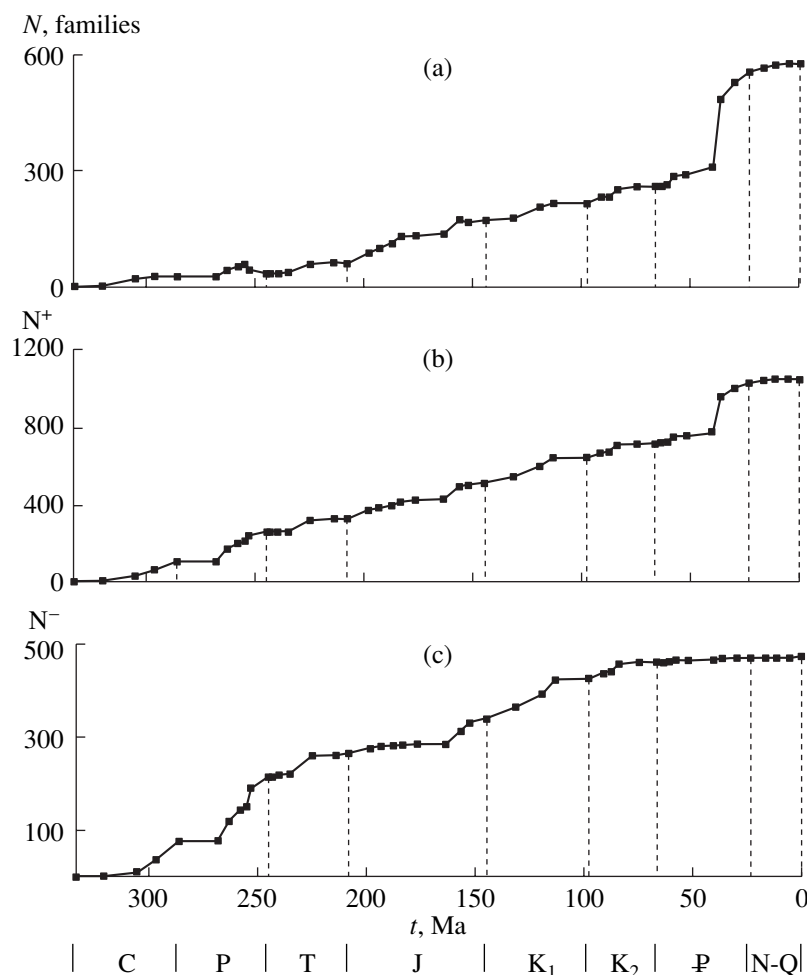


Fig. 3. Insect diversity dynamics: (a) number of families crossing the boundary between stages; (b) number of originating families; (c) number of families going extinct (from Alekseev et al., 2001).

Late Permian (Fig. 3), in many groups the extinction increasing at the mid-Kazanian; the diversity decline about the P/T boundary is relatively small, the extinction being compensated for by a considerable origination of new families in some groups. In this short paper only two orders are considered in detail, Grylloblattida and Coleoptera.

Beetles are not diverse before the Late Permian (Ponomarenko, 2004). Starting from a single family in the Cisuralian, they became somewhat more diverse (with one dominating family) in the Middle Permian. They fed almost exclusively on rotting wood, and few aquatic and terrestrial detritophages and zoophages appeared. In the Tatarian the xylophages became rare (and disappear from the record in the Upper Vyatkian, their direct descendants appearing only in the Middle Triassic); the average size of the beetles nearly halved, and their diversity increased to six families. Possibly, extant beetle families appeared at the very end of the Permian. Beetle families and genera had broad ranges, and species from Brazil and European Russia show

only slight differences. Therefore, the principal changes in the beetles occurred within the Permian, not due to some catastrophe at the P/T boundary; the character of these changes implies that they resulted from inner biotic causes. The disappearance of xylophagous beetles followed the nearly complete disappearance of woody plants from the Lower Triassic localities and to the global pause in coal formation (“coal gap”).

Grylloblattids, although surviving as relicts to the present day, played an important role only in the Paleozoic, their peak diversity being recorded in the late Early Permian (24 families; Aristov, 2005). These were stonefly-like insects, but most of their nymphs apparently lived on land. They were still diverse in the Early Kazanian (20 families), but their diversity decreased (to 8 families) in the Late Kazanian. Until the Middle Tatarian their diversity remained very low (usually only three families found, with Liomopteridae absolutely dominating), but their abundance in the insect faunas increased somewhat. Then the diversity was restored to 11 families, and the families characteristic of the Trias-

sis appeared. Grylloblattids occurred on all continents of that time, being found in South Africa, Europe, Siberia, Central Asia and Mongolia. Eight grylloblattid families had crossed the P/T boundary (and three died out), this extinction being inferior to most extinctions within the Permian. One interesting family is Chaulioditidae (=Tomiidae), most common in the faunas around the P/T boundary. Members of this family, which are known from rare finds since the Tatarian, were an important component of ecosystems in the Early Triassic, and their latest records are from the Middle Triassic. Therefore, again we see no abrupt extinction at the P/T boundary and no resulting renewal of the taxonomic composition.

CONCLUSIONS

Summing up the above considerations on the nature, duration, and extent of the crisis of terrestrial ecosystems about the Paleozoic/Mesozoic boundary, we can state that

(1) the crisis was global in coverage, manifested in the sea, in fresh water and on the land, in the two latter cases more superficial;

(2) the time frame of the crisis phenomena was quite broad, in fact embracing no less than half of the Permian and of the Triassic; the timing of the main events in dissimilar environments and different basins and terrains was chiefly the same; on land, the principal events occurred in the Kazanian and Vyatkian;

(3) the pattern of crisis phenomena implies their inner biospheric rather than momentary external (e.g., Supernova or impact) or abiotic (e.g., traps, 1992) causes, the latter at most triggering the crisis.

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