Macroevolution and the major boundaries in the Phanerozoic[1])

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ABSTRACT

The three main stages of the biotic evolution are analyzed in term of environmental changes, the main factor being the oxygene appearance and increase in atmosphere. The largest boundaries in Phanerozoic time, the Permo-Triassic and the Cretaceous–Tertiary differ considerably one from the other. Attention is given to the Permo-Triassic boundary, the time of the maximum destruction of the global ecosystem.

RÉSUMÉ

Les trois grandes étapes de l'évolution de la vie sont analysées. Ces étapes reflètent les niveaux de diversification des êtres vivants et ont été contrôlées en partie par l'apparition et l'augmentation de la quantité d'oxygène disponible dans l'atmosphère. Les autres facteurs environnementaux tels que le climat, la salinité des eaux océaniques, les grandes transgressions et régressions ainsi que les variations du champs géomagnétique ont également joué un rôle important.

Parmi les grandes extinctions et renouvellements des flores et faunes du Phanérozoïque, une attention particulière est portée sur la limite Permien–Trias, période du plus fort bouleversement de l'écosystème mondial.

This paper, which was written as report for the 27th International Geological Congress contains the information on some global environment factors and the analysis of changes in biotic diversity.

Oxygenic compounds in the atmosphere

There are three stages in biotic evolution reflecting the limit level of diversification (ZAKHAROV 1984) – depending apparently on oxygenic compound in the atmosphere. The first stage is the time of formation of the kingdoms, origin and initial development of life (supposedly the Latest Catarchean–Middle Riphean); during the second stage (supposedly the Latest Riphean–Latest Ordovician or Silurian) the highest possible diversification occurred at lower (type) level; during the third (the Silurian or Devonian–Recent) the maximum diversification fell to class–order level (Fig. 1).

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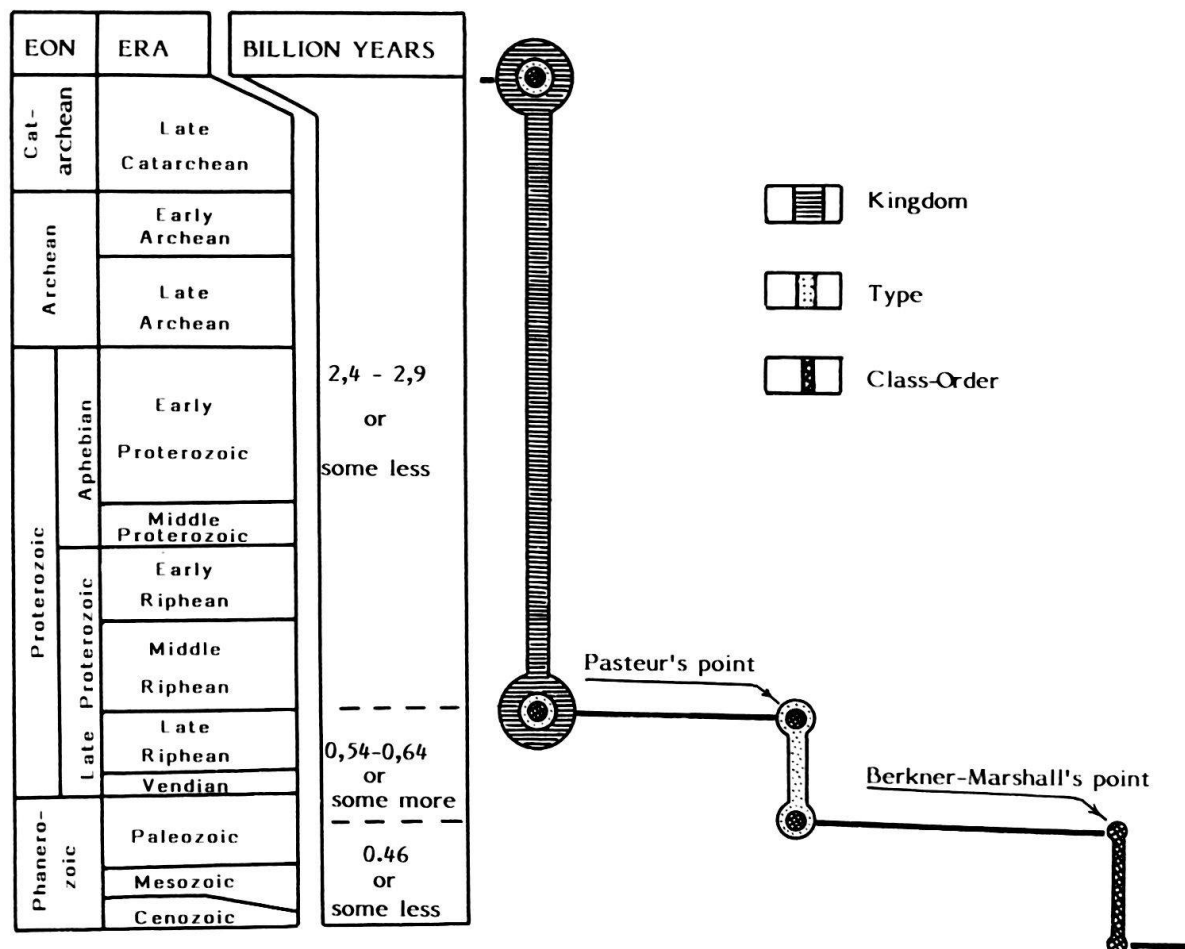
Fig. 1. Stages in macroevolution (reflected the limit level of diversification).

The first stage was formed in non-oxygenous or little oxygenous environment (OPARIN 1963). An evidence of such conditions in that time may be the following facts: abundance of iron-stone formations within the Archean and Lower Proterozoic and finds of uraninite in the Lower Proterozoic (RUTTEN 1973, SCHOPF 1981). The presence of red beds within the Lower Riphean seems to be an evidence of the gradual rise of oxygenic concentration in the atmosphere during the first stage.

The beginning of the second stage seems to be highly approximately 1–1.1 billion years ago, or somewhat more. A reduction of the limit level of diversification is connected with the rise of oxygenic concentration in the atmosphere to 1% of its present level. One of the most important aromorphosis during the end of the first stage and the beginning of the second one is the origin of the organisms that were capable to live through breathing.

The third stage began approximately 460 m.y. ago or some less and goes on now. The next reduction of the limit level of diversification is connected with the rise of oxygenic concentration in the atmosphere to 10% of its present level at the beginning of the stage (the dates of the Pasteur point and the Berkner-Marshall point are induced according to SOKOLOV (1975, 1980). The process of fluctuation of oxygenic concentration in the atmosphere during the Phanerozoic was extremely irregular (BUDYKO 1981). The formation of the oxygen-ozonic screen made conditions possible for land population.

Climate

Periodical climatic fluctuations that are caused by different factors (BARRON & WASHINGTON 1984, NAIDIN et al. 1984) undoubtedly influence the evolution of the biosphere. The signs of a series of large glaciations are known, but none of them was timed to the boundary between Erathems. This confirms the idea about climate to be not the only factor that is responsible for biotic evolution during major stratigraphic boundaries.

Geomagnetic field

The reversals of the geomagnetic field are connected with a change of the speed of earth rotation. The frequent reversals coincide with the most important boundaries in the Phanerozoic and adjacent stages (DAVYDOV et al. 1982, IRVING & PULLAIAH 1976, KHRAMOV 1963, KHRAMOV et al. 1974, KOTLJAR et al. 1984, MOLOSTOVSKIJ & KHRAMOV 1984, ZANINETTI 1978).

Transgressions and regressions

Periodically repeated transgressions and regressions lead to variation of the shelf area that cause the break in the trophic interactions of marine biota. One of the largest regressions during the Phanerozoic coincides with the Paleozoic–Mesozoic boundary (RUZHENCEV 1965, SCHOPF 1974).

Salinity of seawater

Irregularity of evaporite precipitation seem to be one of evidences of salinity changes in the sea basins in the geological past. The Permian period has no equal in intensity of halite precipitation (HOLSER 1977, STEVENS 1977). The Iranian–Japanese Research Group (1981) consider the low contents of boron and lithium in the Dorashamian sediments of Central Iran to be a result of the freshwaters influence of the restricted lagoons in West Tethys. But this is not confirmed by data on carbon isotopic composition of the Midian and Dzhulfian brachiopod shells of Trans-Caucasus (ZAKHAROV et al. 1984). The analysis of isotopic composition of mollusk shells from the Mesozoic of Arctic Siberia (ZAKHAROV et al. 1975) permits at the same time to conclude on freshening of Boreal basin water during the Early Mesozoic.

Some authors have suggested a sharp change of concentration of carbon isotopes in carbonate sediments and invertebrate shells at the Permian–Triassic boundary (CHEN JING-SHI et al. 1984, HOLSER 1984, SUN YIYIN et al. 1984b, ZAKHAROV 1983, ZAKHAROV, in press; ZAKHAROV et al. 1984b).

Cosmic phenomena

Events happening on the Earth that is a cosmic body are connected largely with cosmic phenomena. In STEINER & GRILLMAIR'S (1973) opinion, the largest glaciations coincide with galactic winters of cosmic years (the duration of cosmic years is assumed to have gradually decreased). Possible results of collision of the Earth and large cosmic bodies are investigated now (ALEXEEV et al. 1983, GANAPATHY 1980, NAZAROV et al. 1983, SUN et al. 1984a, b, XU et al., in press, and many others).

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Biotic factors

In GOULD's (1977) opinion, situations favouring the r-selection might include large
and frequent catastrophic mortality, superabundant resources and lack of 'crowding',
which provokes a significant competition.

The pattern of taxonomic diversity change

The most detailed data on this problem were obtained on the basis of study of the last
biotic evolution stage. VALENTINE (1969) has shown some regularities in the evolution of
marine invertebrates during the Phanerozoic. It was ascertained that in the Middle–Late
Paleozoic the tendency to specialization within this group had developed (in connection
with increase in the number of species belonging to limited number of higher taxa). But
these regularities do not reflect completely peculiarities of biotic evolution. It should be
emphasized that, during the Middle Paleozoic, reduction of invertebrate diversification
on the high level was compensated partially or completely by increase in the number of
plant, Tracheata and Chordata higher taxa (Fig. 2). As a result, the degree of di-
versification in Devonian–Carboniferous time has reached the Early Paleozoic level. The
compensation was realized on the whole at the expense of land plants and groups of
animals which led an active life. In addition, great evolutionary changes occurred within
invertebrates that time: their most active representatives (Bactritoidea, Ammonoidea and
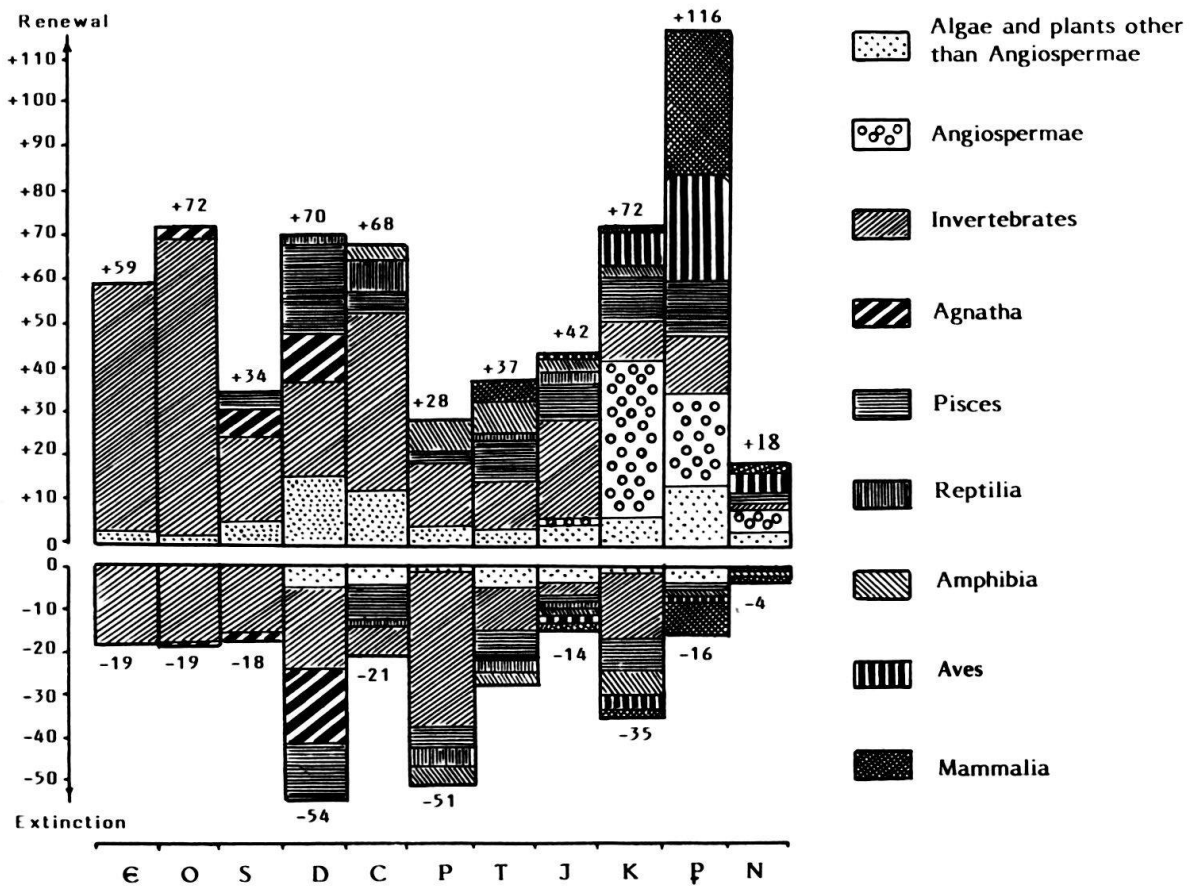

Fig. 2. Macroevolution on order level during the Phanerozoic.

apparently Endocochlia) appear for the first time. The active life is associated with use of a large amount of oxygen. Therefore, these data testify in favour of BUDYKO's (1981) idea according to which the higher oxygen concentration in the Paleozoic atmosphere was attained in Late Devonian–Early Carboniferous time.

During the very late Paleozoic (Permian), the formation of higher invertebrate taxa reduced very sharply. Reduction in diversification on a high level at that time concerned plants and animals also, with the exception of amphibia.

Valentine's assertion that after the Permian–Triassic boundary extinction, the following Mesozoic diversification was limited to a lower level (in comparison with the Early and Middle Paleozoic) is acceptable only with respect to invertebrates. A sharp drop in diversification of the Meso-Cainozoic invertebrates in comparison with the Paleozoic ones was compensated by more drastic rise in diversification of land plants (first of all the Angiospermae) and some animal groups leading an active life (fish, birds and probably mammals). Plant and animal diversification on the order level is believed to be at its zenith during the Cretaceous and the Paleogene respectively. These data also conform to BUDYKO's (1981) hypothesis according to which the time of highest oxygen concentration in atmosphere during all the Earth history falls within the Late Mesozoic. The Cretaceous–Paleogene time is in contrast with Silurian, Permian and Neogene periods characterized by comparatively poorly expressed diversification; among these periods, only the Permian is distinguished by well pronounced elimination of higher taxa.

The major boundaries in Phanerozoic time

The most incisive boundaries in Phanerozoic time were accompanied by the marked reconstruction of biocenotic correlations, exemplified by the Permo-Triassic and Cretaceous–Paleogene successions of marine communities (KOTLJAR et al. 1983, ZAKHAROV 1983, 1984, ZAKHAROV et al. 1984a).

The Paleozoic–Mesozoic boundary was the time for a cardinal change in the structure of marine communities of Trans-Caucasus.

By the end of the Midian, Trans-Caucasian foraminifera were represented by 88 species, including 34 fusulinid species. In the Early Dzhulfian, the number of foraminifer species was reduced by four times (fusulinid ones – 17 times). The last fusulinids is known to occur within the Upper Dzhulfian in Trans-Causasus and Upper Changxing formation in Southeast China. A sharp reduction in taxonomic diversity of other groups inhabiting the Trans-Caucasian basin had happened during the Dorashamian, but this process did not proceed in a strictly descending line. Near the close of the Permian succession a comparatively short-term Megaclimax phase[3]) (*Paratirolites kittli* zone) was recognized (ZAKHAROV 1983). It is characterized by a comparatively high diversity of some community elements. This phase was more pronounced in Southeast China (ZHAO et al. 1978). To judge by new data, the difference in degree of diversification of marine and land organisms during the Late Permian was less expressed than it was considered so far. At

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[3]) The phases, in the course of which many or basic community elements acquire a high diversity, were proposed to be named as Megaclimax, whereas phases dividing Megaclimaxes as Confinis (ZAKHAROV 1983, 1984; ZAKHAROV et al. 1984a).

the same time, it should be emphasized that only some few remains of brachiopods (*Haydenella* sp. – Kotljar's determination) and cephalopods (*Lopingoceras* sp., *Pleuronodoceras* sp.n.) have been found within the uppermost beds of the Dorashamian (*Pleuronodoceras* sp.n. zone that seems to be equivalent to the upper part of *Rotodiscoceras-Pseudotirolites-Pleuronodoceras* zone in Southeast China; ZAKHAROV 1985). Hence, the short-term *Confinis* phase completing the Permian succession is assumed to exist too.

The succession between marine Permian and Triassic faunae is realized at the family and generic levels on the whole. Toward the end of the Dorashamian, fusulinids, rugose corrals, productids, goniatites and trilobites, most of which were abundant in tropical seas during the Paleozoic, became completely extinct.

During the Late Permian, a frequent alteration of humid and arid climates took place, which was apparently accompanied by temperature change. It seems highly likely that the indicators of uniform of humid and variable humid climate of some ages and seasons within Tethys are the Late Midian and Late Dzhulfian coals in Southeast China (ZHAO et al. 1978), the Late Midian coaly argillites and Late Dorashamian bauxites in Trans-Caucasus (GULIEV et al. 1972), the Late Permian siallites in Pamirs (NOVIKOV 1978); the indicators of arid climate seem to be red carbonates from *Vedioceras ventrosulcatum* zone (Dzhulfian) and *Paratirolites kittli* zone (Dorashamian) in Trans-Caucasus and Iran, pink limestones from Changxing formation in Southeast China, evaporites from the Upper Permian in Eurasia and North America.

There are evidences for the existence of more or less pronounced climatic zonation during the time of the Permian–Triassic boundary. Temperature may be presumed to decrease during that time (ZAKHAROV 1980, 1983).

In Early Triassic time, the production of coals and bauxites had completely ceased, which was connected apparently with a sharp aridization of the climate. The Early Induan invasion of cephalopod faunae in high-latitude regions in both hemispheres can be explained only by a visible rise of temperature of the subpolar waters.

As mentioned above, the greatest eustatic fluctuation of sea level and an important inversion of magnetic field also coincide with the Permian–Triassic boundary. Frequent inversions of the magnetic field began in Midian time and went on during the Dzhulfian, Dorashamian and Early Triassic – *Illawara* hyperzone (DAVYDOV et al. 1982, KOTLJAR et al. 1984).

The scheme on cephalopod succession during the Aptian–Albian and Late Cretaceous in the South Sakhalin illustrates the alteration of species diversity and quantity of late Mesozoic ammonoids (ZAKHAROV et al. 1984a). During the last stage of the Megaclimax phase, that falls within the Late Campanian, the abundance of ammonoids was noticeably reduced; during the next *Confinis* phase (Maastrichtian), a very sharp reduction both in species abundance and diversity took place, that finally led to a full extinction of ammonoid to the end of the Maastrichtian. At the Cretaceous–Paleogene boundary, inocerams also became extinct; the species composition of other mollusks practically completely changed.

Data on the alteration of species diversity of the Cretaceous–Paleogene mollusk fauna of South Sakhalin and some material on isotopic thermometry (ZAKHAROV et al. 1984) allow to picture the hypothetical temperature curve with maximum of temperature fall during the time of the Maastrichtian–Danian boundary, but with some warming in the Middle Maastrichtian. A considerable influence of freshwaters on the taxonomic compo-

sition of the Late Mesozoic–Early Paleogene fauna in South Sakhalin is impossible (the Late Cretaceous and Early Paleogene mollusk shells of this region are characterized by a comparatively high content of the heavy carbon isotope).

Frequent inversions of the magnetic field fall within the Campanian–Maastrichtian and Early Paleogene (IRVING & PULLAIAH 1976).

The major boundaries within the Phanerozoic considerably differ from each other. During the Paleozoic–Mesozoic boundary time, the extinction of taxa on the order level was expressed more intensively than during the Mesozoic–Cainozoic one (1.5 times), on the contrary, the order diversification during the same time was expressed considerably more weakly (three times). This confirms the idea about the Permian–Triassic boundary to be the time of maximum destruction of global ecosystems.

Conclusion

The fact of kingdom formation in the pre-Cambrian testifies that changes on the highest level seem to be possible only during the early stage of biotic evolution. Abundance of food resources in non-oxygenous or little oxygenous environment during the major part of the pre-Cambrian and some other factors allow to assume that there was an unexampled pressure (in intensity and duration) of r-selection that time. Reduction of the limit level of diversification in Late Proterozoic and Early Phanerozoic time is connected with the irreversible evolution of the environment and the first apparently with the derected increase of oxygen concentration in atmosphere.

There are evidences of the prolonged formation of higher taxa features (KRASSILOV 1977, TATARINOV 1976). Taking into account the lack of clear correlative connections between the intensity of diversification on high level and the rank of stratigraphic boundary it may be said that the macroevolutional transformation could occur during the different variations of surrounding conditions. Extreme conditions of the major boundaries within the Phanerozoic characterized by the weakened K-selection pressure, are not believed to be a sine qua non for the appearance of new higher taxa.

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