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Permian–Triassic Biotic Crisis and Foraminifers

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Abstract—Two phases can be distinguished in development of foraminifers during the Late Permian crisis. The first phase was marked by extinction of 40% of total foraminiferal genera. The crisis affected particularly fusulinids, which lost 76% of genera and 70% of families. At the end of the Permian, all foraminifers became extinct. Moreover, fusulinids die off completely, whereas some smaller foraminifers (Lazarus-taxa) appear again in the *I. isarcica* conodont zone. At the beginning, they were represented by archaic Paleozoic forms. The renewal of assemblages owing to development of Mesozoic forms commenced at the end of the Induan Age and significantly accelerated in the Anisian Age.

Key words: Permian, Triassic, foraminifers, crisis.

INTRODUCTION

Biotic changes at the Paleozoic–Mesozoic boundary attracted attention of researchers for a long period, and different aspects of the problem were discussed in many papers. In most publications, authors share the views of Schindewolf (1954) who believed that these changes were catastrophic. However, other researchers argued that the Late Paleozoic extinction was gradual (Ruzhentsev and Sarycheva, 1965; Reitlinger, 1965; and others). This work represents an attempt to solve the problem tracing dynamics in development of foraminiferal assemblages in the terminal Permian–initial Triassic. Although many researchers paid a sufficient attention to foraminifers when they considered biotic changes during this period of the geological history, most publications are dedicated to individual problems being restricted to the analysis of their distribution in particular sections. To the contrary, summarizing works were too generalized to notice all important regularities.

This paper presents the results of generalization of all available published data on foraminifers from the Upper Permian and Lower Triassic Tethyan sequences and of original materials from sequences of the Transcaucasia, Pamirs, and Afghanistan. Distribution of foraminifers through the indicated stratigraphic interval was analyzed, using, where possible, their zonal scales, and foraminifers proper were considered at the genus and family levels, although changes at the species level were also analyzed. The taxonomic revision was beyond the scope of this work, and published lists of foraminiferal species are used therefore without any corrections. Revision of lists would, probably, slightly change the estimated numbers of extinct and newly appeared genera at certain historical boundaries, but this could hardly affect the essence of conclusions. As for higher-rank taxons, their classification follows that

in the recently published reference books on Paleozoic foraminifers (*Spravochnik...*, 1993, 1996).

The trustworthiness of inferences concerning the problems under consideration depends, to a large extent, on stratification resolution attained in the examined sections and on accuracy in determination of stratigraphic position of foraminiferal assemblages. Unfortunately, a number of sections, which would comply with these requirements and which we consider as reference sections, is limited, and this compels us to analyze other sections rich in foraminifers, but poorly characterized by conodonts and ammonoids. Correlation of such sections with the reference ones is often ambiguous. Nevertheless, stratigraphic levels we are interested in, such as the Middle–Upper Permian and Permian–Triassic boundaries, are sufficiently distinct in them, and we believe that changes in fossil foraminiferal assemblages across these boundaries are close to the true ones.

STRATIGRAPHY OF THE PERMIAN–TRIASSIC BOUNDARY SEQUENCES

Before going to an essence of the considered problem, we should define a stratigraphic scheme, which will serve as the basis for our interpretations. This is necessary because there is no unified view on the position and definition criteria of the Permian–Triassic boundary. In addition, existing opinions on stage subdivisions and biozonation of boundary strata and on their correlation are also controversial. Relationships between zonations based on different faunal groups, such as fusulinids, conodonts, and ammonoids, are not always interpreted unambiguously.

Inasmuch as thorough consideration of all these problems is beyond the scope of our work, we will just outline and specify variants of our decision.

The Permian–Triassic boundary is accepted to correspond to the base of the *Hindeodus parvus* Zone in line with latest recommendations of the International Working Group on the Permian–Triassic boundary (Yin, 1997). This boundary is of a highest correlation potential, which makes it preferable. However, it is not an event-based boundary. Main events, which are believed to mark the Paleozoic–Mesozoic boundary (regression, facies changes, mass extinctions, geochemical anomalies, and others) occurred slightly earlier and were not synchronous (Wang, 1997).

In line with recommendations of the International Subcommittee on the Permian System (SCPS) approved by the International Geological Congress in Beijing in 1997 (Jin *et al.*, 1997), we accept the three-member division of the Permian System, according to which the Lopingian Series is divided into the Wuchiapingian and Changhsingian stages. As for the middle, Guadalupian Series, the SCPS variant of its subdivision into the Roadian, Wordian, and Capitanian stages is unambiguously appropriate only for the North American sequences. Inasmuch as all sections we would like to consider here are located within the Tethyan realm, we prefer to operate thus far with the Kubergandian, Murgabian, and Midian stages of the Mediterranean scale (Leven, 1980, 1981) for the middle series, the more so as the upper boundary of the Midian Stage coincides with the Guadalupian–Lopingian boundary recommended by the SCPS.

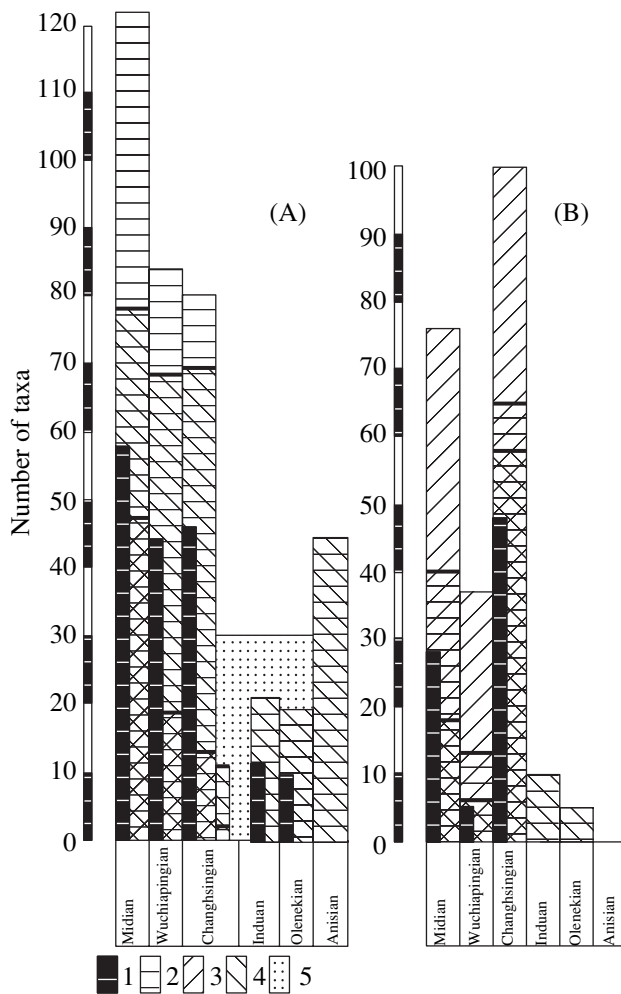
Having no universally accepted zonal subdivisions for stages of the upper Permian Series, we take for the basis the conodont zonation proposed by Jin *et al.* (1997). In addition, we refer to cephalopod zones defined in the Transcaucasian and South China sections (Ruzhentsev and Sarycheva, 1965, Yin *et al.*, 1996). To correlate the Permian–Triassic boundary sequences, we use the conodont zones established in the Meishan section of South China (Zhang *et al.*, 1996; Yin *et al.*, 1996). It should be noted however that opinions about paleontological substantiation of these units and their age interpretation are controversial (Mei, 1996). The zonal scheme proposed by Matsuda (1985) was accepted for the Triassic.

Different viewpoints on classification of conodonts and relatively limited number of sections, where their stratigraphic successions are continuous, restrict the correlation accuracy even in case of reference sections. Only several levels can be traced, more or less certainly, in most reference and some supplementary sections. Among these is the boundary between Midian and Wuchiapingian stages placed at the base of the conodont *C. postbitteri* Zone. In the Transcaucasian region, this level corresponds to the base of the Chankhchi or *Codonofusiella–Reichelina* Beds (Reitlinger, 1965; Kotlyar *et al.*, 1989). In the Abadeh section, the considered level coincides with the lower boundary of Bed 5 (*Iranian–Japanese...*, 1981), and in sections of South China, it corresponds to the boundary separating the

Maokou and Loping groups (Jin *et al.*, 1994). The next level is the lower boundary of the conodont *C. leveni* Zone, which is defined at the base of the Akhura Formation of the Transcaucasian region (Kozur *et al.*, 1978), in the upper part of Bed 6 of the Abadeh section (*Iranian–Japanese...*, 1981), and inside the Wuchiaping Formation of South China (Jin *et al.*, 1994). Well traceable is also the Wuchiapingian–Changhsingian boundary or the base of the conodont *C. subcarinata* Zone recognizable in Transcaucasian and South China sections (Kozur *et al.*, 1978; Jin *et al.*, 1994). The high correlation potential is characteristic of lower boundaries of the *H. parvus* and *I. isarcica* conodont zones distinguished in section of the Transcaucasian region, Central Iran, Southern Alps, Kashmir, South China, and Tibet (Kozur, 1980; Kozur *et al.*, 1995). As for easily correlative levels in higher parts of the Lower Triassic succession, which yield foraminifers (usually assemblages of the *Meandrosira pusilla* Zone), these are *Parachirognathus turnishies* (= *Neospathodus waageni*) and *Neospathodus triangularis–Neospathodus homeri* conodont zones established in the Guchevo section of Inner Dinarides (Sudar, 1986). It is thought that stratigraphic position of the *Meandrosira pusilla* and *Meandrosira cheni* foraminiferal zones in the biostratigraphic scheme of Balkan Mts. is substantiated by finds of the ammonoid species *Tirolites* sp. (Salaj *et al.*, 1988).

FORAMINIFERS FROM THE PERMIAN– TRIASSIC BOUNDARY LAYERS IN BEST-STUDIED AND WELL-DATED SECTIONS

In our opinion, the Dzulfa section of the Transcaucasian region (Leven, 1975, Kozur *et al.*, 1978; Kotlyar *et al.*, 1989; Zakharov, 1988), Abadeh section of Central Iran (*Iranian–Japanese...*, 1981, and Meishan section of South China (Yin *et al.*, 1996) are most important among the well-dated Permian–Triassic boundary successions. Owing to occurrence of conodonts and ammonoids, the Permian part of these sections is subdivided into easily correlative zones. We regard data on these sections as reference ones for solving problems of stratigraphic ranges of Permian foraminifers. Supplementary materials are from sections of the Salt Range (*Pakistan–Japanese...*, 1985; Wardlaw and Pogue, 1995), Alps (Broglia-Loriga *et al.*, 1986; Buggish and Noe, 1986), Taurus (Lys and Marcoux, 1978; Zaninetti and Dager, 1978; Zaninetti *et al.*, 1981; Altiner, 1981, 1984; Köyüglü and Altiner, 1989), northern Caucasus (K. Miklukho-Maclay, 1954; Kotlyar *et al.*, 1983, 1989), southeastern Pamirs (Leven, 1967; Kotlyar *et al.*, 1983, 1989), and Primor'e (Burago *et al.*, 1974; Sosnina and Nikitina, 1977; Kotlyar *et al.*, 1983, 1989; Vuks and Chediya, 1986). These materials were used with the accuracy required for their correlation with reference successions. When possible, data on other



Changes of the Permian–Triassic boundary time in abundance of foraminiferal taxa by the end of each age (A) and percentage of extinct taxa by this moment (B): (1) families; (2) all foraminifers; (3) fusulinids; (4) smaller foraminifers; (5) genera of smaller foraminifers that became extinct at the Permian–Triassic boundary and appeared again (Lazarus-taxa).

Tethyan and North American sections were also considered.

Because of the rare occurrence of Triassic (particularly Lower Triassic) foraminifers, it is difficult to characterize adequately the taxonomic composition and stratigraphic distribution of their assemblages considering only the above-mentioned sections. Therefore, some other sections, where stratigraphic position of foraminiferal assemblages is sufficiently well substantiated, were involved into the analysis. Such sections are known in the following areas: Kuh-e-Ali-Bashi in northwestern Iran (Baud *et al.*, 1974), central and eastern Alborz localities (Brönnimann *et al.*, 1972a, 1972b; Stampfli *et al.*, 1976), Tabas (Brönnimann *et al.*, 1973), eastern Taurus (Dagger and Zaninetti, 1976; Altiner and Zaninetti, 1981), Inner Dinarides (Sudar, 1986), Southern Alps (Jenny-Deshuesses, 1991), Carpathians (Salaj

and Borza, 1983), South China (He, 1988; Zhang *et al.*, 1989), northern Caucasus and Ciscaucasia (Efimova, 1974). Generalized data on foraminifers from some of the mentioned sections can be found in the monograph by Zaninetti (1976).

It is reasonable to consider distribution of fusulinid and smaller foraminifer assemblages separately.

Fusulinids. Beginning from the Middle Carboniferous to the terminal Middle Permian, fusulinids were one of the most abundant and diverse groups of benthic organisms populating warm seas. In the Permian, their peak diversity and specialization were in the Midian Age, probably in response to the world-wide transgression (Leven, 1993). The number of families and genera amounted to 20 and 46, respectively, at that time. Prevalent were representatives of orders Schwagerinida and Neoschwagerinida.

By the end of the Midian Age, both these orders became extinct. Significant changes occurred also in the order Schubertellina. For instance, the previously abundant family Yanchienidae completely disappeared, whereas the family Paleofusulinidae experienced essential renewal owing to appearance of its new genera *Ogbinella*, *Paradunbarula*, *Pseudodunbarula*, and *Paleofusulina* appeared. They all appeared immediately after extinction of last schwagerinids and neoschwagerinids in the lower part of the Wuchiapingian Stage of South China and in the correlative Chankhchi beds of the Transcaucasian region. Until recently, it was believed that the genus *Paleofusulina* appeared later. A few years ago however, it was found in the lower zone of the Wuchiapingian Stage of China (Zhu, 1996). Two new genera of the Boultoniidae family (*Gallowainella*, *Tewoella*), which were previously considered as occurring in the Changhsingian Stage, also appeared at this level. Nothing substantial happened at this level in the relatively scarce orders Ozawainellida and Staffellida.

The above distribution patterns characterizing the reference sections are also typical of many Tethyan successions, although synchronism of events that are recorded at the Midian–Wuchiapingian boundary cannot be always reliably proved. In addition, we do not exclude that some of typical Midian genera characteristic of the *Lepidolina kumaensis* Zone continue to occur in the Wuchiapingian Stage (Toriyama, 1973). No clear evidence is available so far.

Quantitative changes in fusulinid assemblages at the Midian–Wuchiapingian boundary can be exemplified by the following facts (Figure). Of 20 families and 46 genera of Midian fusulinids, 14 families (70%) and 35 genera (76%) became extinct at this level. Seven of 11 remained genera pass into the Changhsingian Stage. The Wuchiapingian Age was marked by appearance of 8 genera, 5 of which continued to exist in the Changhsingian Age. In fact, the Changhsingian Age was a time of gradual extinction of earlier genera. The only genus *Parananlingella* is unknown from older layers,

but it is not inconceivable that even this genus appeared in the Wuchiapingian Age.

In total, 5 families and 13 genera are registered in the Changhsingian Stage. By the beginning of the Triassic, all of them disappeared. This happened slightly prior to the first occurrence of *Hindeodus parvus*, and this event is believed to mark the Permian–Triassic boundary. In the Meishan section, that is recommended to represent the stratotype boundary succession, last fusulinids are recorded in Bed 20 of the scheme by Zhao *et al.* (1981), which is correlative to Beds 23 and 24 of the scheme by Yin *et al.* (1996). A slightly higher level of last fusulinid occurrence is established in the succession of the Dolomitic Alps where the basal part (1.5–2.0 m) of the Tesero Horizon of the Werfen Formation contains *Nankinella* and *Staffella* forms (Broglia-Loriga *et al.*, 1986). Passini (1984) mentioned also a find of *Paleofusulina* specimens in this section, although the validity of their stratigraphic position is doubtful. Conodont species *Hindeodus latidentatus* ancestral to *H. parvus* is also registered at the considered level. In the Meishan section, this species appears in white clays of Bed 25 (Kozur, 1995; Yin *et al.*, 1996) lacking fusulinids.

According to dynamics of changes in fusulinid assemblages during the period from the Midian to the Changhsingian Age, the two crises in fusulinid evolution are usually recognized (Jin, 1993; Stanley and Yang, 1994). The first one most distinct occurred at the Midian–Wuchiapingian boundary time, when 76% of fusulinid genera, 70% of their families, and all representatives of the Schwagerinida and Neoschwagerinida orders became extinct. The second crisis terminated with the complete disappearance of fusulinids at the end of the Changhsingian Age. Beside the appearance of several genera in the Wuchiapingian Age and one genus in the Changhsingian Age, nothing else significant happened with composition of fusulinid assemblages between these two crises. In fact, there was a belief that the Changhsingian transgression resulted in a significant renewal of foraminiferal assemblages, namely in appearance and flourish of the *Paleofusulina* genus in association with close *Nanlingella* and *Parananligella* genera, and one more genus *Gallowaiinella*. However, three of these genera were found in the Wuchiapingian Stage, as is mentioned above, and the idea of the Changhsingian renewal lost its validity. In addition, the increased abundance and diversity of Changhsingian fusulinids is recorded only in South China and Indochina sections. In all other Tethyan regions, this event is undetectable.

Smaller foraminifers. Similarly to fusulinids, the peak diversity of smaller foraminifers was in the Midian Age. We know 38 families and 78 genera of that age. Dominant were representatives of orders Nodosariida and Cornuspirida. According to G.P. Pronina who studied in detail foraminifers from Transcaucasian sections, species of the first order prevail in the lower part

of the stage and representatives of the second order in its upper part (Kotlyar *et al.*, 1989). In her opinion, these distribution patterns are also characteristic of all sections outside the Transcaucasian region (Pronina, 1995). Most common amid nodosariids are representatives of genera *Pachyphloia*, *Geinitzina*, *Pseudolanigella*, and some others. Families Hemigordiidae and Hemigordiopsidae are most abundant and characteristic representatives of cornuspirids. Sufficiently diverse is the order Palaeotextulariida, particularly its families Palaeotextulariidae (genera *Palaeotextularia*, *Climacammina*, *Cribrogenerina*), Biserimminidae (genus *Globivalvulina*), and Dagmaritidae (genus *Dagmarita*). Characteristic, though supplementary, are genera *Sphairionia* (family Lagenidae), *Abadehella* and *Neoendothyra* (families Valvulinellidae and Endothyranopsidae, respectively).

In contrast to fusulinid case, the Guadalupian–Lopingian boundary in successions of smaller foraminifers is less distinct, marked mostly by changes in dominant taxons. Many Midian genera passed into the Wuchiapingian Stage, and their total number in that stage of reference sections is as high as 48. When the data on smaller foraminifers from the Pamirs, Salt Range, Taurus, and Alps are taken into consideration in addition to those from reference sections, the total number of their Wuchiapingian genera would be close to 68, i.e., they became by 14% less diverse than Midian genera (76% in the fusulinids case). Moreover, only several genera can be considered extinct at the end of the Midian Age. These are genera *Shanita*, *Sphairionia*, and others characteristic of the Midian Stage. The Wuchiapingian Age was probably marked by an appearance of several new genera, among which *Louissetta*, *Paradagmarita*, *Pseudocolaniella*, and *Colaniella* can be mentioned. In general, the main difference between the Midian and Wuchiapingian foraminiferal assemblages is that the dominant taxons changed, since the abundance and diversity of genera belonging to families Hemidordiidae, Hemigordiopsidae, and Baisalidae (order Cornuspirida) decreased, and the leading role of nodosariids was restored to be high until the end of the Permian.

We should emphasize that the above characteristic of foraminiferal assemblages of the Wuchiapingian Stage is averaged. It varies in concrete sections depending on facies enclosing the assemblages. This is also true for the outlined differences between foraminiferal assemblages of the Midian and Wuchiapingian stages. For instance, the depositional settings in many Tethyan areas considerably changed at the beginning of the Wuchiapingian Age, before which there was a regression and short-term break in sedimentation. Shallow-water carbonate facies favorable for benthos development were replaced by pelagic clayey and pelitomorphic limy facies. Correspondingly, abundance of planktonic and nektonic organisms increased in contrast to benthic forms, and this impoverished foraminiferal assemblages, which mostly consisted of benthic forms at that time. This is best manifested in South China sec-

tions, where differences between the Midian and Wuchiapingian foraminiferal assemblages are rather substantial. In Transcaucasian sections, the facies change is confined to the base of the *C. leveni* Zone that is slightly above the base of the Wuchiapingian Stage. Beginning from this level, foraminiferal assemblages are highly impoverished, which was noted earlier by Reitlinger (1965) and Pronina (Kotlyar *et al.*, 1983). Simultaneously, the Midian–Wuchiapingian boundary indistinct in lithological aspect is marked only by a change of some dominant taxons. It is noteworthy that schwagerinids and neoschwagerinids become extinct precisely at this boundary. Even lesser changes are observed in foraminiferal assemblages from the Taurus sections where facies did not change at least until the end of the Wuchiapingian Age.

Similarly to fusulinids, the Wuchiapingian and Changhsingian assemblages of smaller foraminifer are just slightly different in composition and diversity. Prevalent in them are nodosariids, and almost all genera known from the Wuchiapingian Stage continue to occur in overlying beds. The only genus *Meandrospira* (family Meandrospiridae), very characteristic of foraminiferal assemblages from the upper part of the Induan Stage and existing now, appeared at that time. The total number of genera discovered in reference sections is 49 (48 genera occur in the Wuchiapingian Stage). When data on other sections (North Caucasus, Pamirs, Primor'e, Taurus, Southern Alps) are taken into consideration, the number of genera increases to 69 (68 Wuchiapingian genera therewith).

Keeping in mind the problem we deal with, it is interesting to reconstruct dynamics of changes in foraminiferal assemblages throughout the entire Changhsingian Age. In every particular section, their diversity depends on rock facies and significantly varies up to the complete disappearance of foraminifers. The Meishan section more or less uniform in lithology shows the gradual increase of foraminiferal diversity from 6 genera and 9 species at the base of the stage to 20 genera and 52 species at its top (Zhao *et al.*, 1981). The diversity increases also in the Transcaucasia and Southern Alps, where this is related, however, to the lack of favorable facies in the lower part of the stage.

In all studied sections, foraminifers completely disappear near the Permian–Triassic boundary, but this event was diachronous. Leaving aside those sections where the Permian–Triassic boundary cannot be confidently recognized because of probable hiatuses or data deficiency (North Caucasus, Primor'e, Taurus, Central Iran, Salt Range, and some others), we can establish precisely the level of foraminifer extinction only in three regions: the Transcaucasia, South China (Meishan), and Southern Alps.

In the Transcaucasian region, foraminifers are recorded in the *Paratirolites kittli* Zone, where they are represented by 19 genera and 37 species (Pronina, 1989). The overlying layers are completely barren of

foraminifers. In the Meishan section, foraminifers occur in the uppermost part of the *Pleuronodoceras–Rotodiscoceras* Zone, where 20 foraminiferal genera and 52 species are registered near the top of the Changshing Limestones (Zhao *et al.*). As was mentioned, the uppermost layers of the Bellerophon Formation in Southern Alps correspond to the same zone. These layers enclose 33 genera and 43 species of smaller foraminifers (Broglia-Loriga *et al.*, 1986; Buggish and Noe, 1986).

The diversity of foraminiferal assemblage in overlying strata of both the Meishan and South Alpine sections is sharply reduced. In the first locality, single representatives of nine genera belonging to seven families are registered in white clays of Bed 25, i.e., several centimeters below the Permian–Triassic boundary (Yin *et al.*, 1996; Zhao *et al.*, 1981). These several centimeters of the section (Beds 26, 27a, and 27b) are barren of foraminifers like the basal layers of the Triassic. In Southern Alps, the basal part of the Tesero Horizon of oolitic limestone is correlative with Bed 25 of the Meishan section, as it yields *H. latidentatus*, the conodont species ancestral to *H. parvus* (Broglia-Loriga *et al.*, 1986). Similarly to Bed 25, these layers also yield occasional smaller foraminifers of 20 species belonging to 12 genera (Broglia-Loriga *et al.*, 1986; Buggish and Noe, 1986). The upper part of the horizon is barren of foraminifers like the basal part of the overlying Masin Formation below the *H. parvus* Beds.

Foraminifers are unknown so far in the basal Triassic *H. parvus* Zone of either studied sections. They appear again in the *I. isarcica* Zone (Himalayas, northwestern Iran, Eastern Taurus). Their finds are scarce and represented by archaic primitive genera belonging to families Ammodiscidae and Earlnadiidae. Occasionally occurring are the Nodosariidae, Ichthyolariidae, and Cornuspiridae forms whose first representatives appeared in the Permian. In total, 11 genera and slightly more species are discovered at this level in different localities (Altiner *et al.*, 1980; Altiner, 1981; Altiner and Zaninetti, 1981; Kapoor, 1996). The foraminifer-bearing *Otoceras–Ophiceras* Beds from the base of the Kumoan section in Himalayas are probably coeval with the *I. isarcica* Zone (Kristan-Tollman, 1984). If this is true, the foraminiferal list from this zone should include 20 genera.

In the uppermost layers of the Induan Stage and in basal layers of the Olenekian Stage, foraminifers are significantly more abundant. Like in underlying deposits, these boundary interval yields the foraminiferal assemblage dominated by Paleozoic genera belonging mainly to the Ammodiscidae and Nodosariidae families. They are accompanied by first representatives of Mesozoic foraminiferal genera *Arenovidalina*, *Rectoglomospira*, *Lenticulina*, *Gaudryina*, and *Triadodiscus* belonging to four families, one of which (Involutinidae) is newly-appeared (Efimova, 1974; Gazdzicki, 1974; Sudar, 1986; Salaj *et al.*, 1988). Single representatives

of the *Meandrospira* genus registered in the uppermost Permian also appeared approximately at the same level. Slightly higher in the sections (*Parachirognathus tur-nishies* and *Neospathodus triangularis*–*N. homeri* conodont zones), they are more frequent and characterize the *M. pusilla* Zone traceable from the Alps in the west to South China in the east. The average diversity remains the same as in the earlier assemblage (18–20 genera), but the number of Mesozoic genera slightly increases. The substantial renewal of foraminiferal assemblages begins from the Anisian Age (the conodont *Neogondolella regale* Zone), being remarkable in its middle part (the conodont *Paragondolella bul-garica* Zone and ammonoid *Balatonites* Beds), where over 10 new genera and 5 families appear almost simultane-ously. The total number of genera amounts here to 45 (Gaetani *et al.*, 1970; Efimova, 1974; Gazdzicki, 1974, 1983; Salaj *et al.*, 1983; Sudar, 1986). Thus, since that time, elements of Mesozoic assemblages become dominant.

Summing up the data on development of smaller foraminifers during the Late Permian–Early Triassic, we can state the following:

(1) The maximum diversity of foraminiferal assem- blages was characteristic of the terminal Midian Age, when representatives of the Cornuspirida order were prevalent.

(2) At the Midian–Wuchiapingian boundary, the Nodosariida order becomes dominant. The generic and species composition of foraminiferal assemblages becomes impoverished, but less noticeably than that of fusulinids.

(3) Similarly to fusulinids, foraminiferal assem- blages did not substantially change during the Wuchi- apingian and Changhsingian ages and retained the same generic composition.

(4) The diversity of foraminiferal assemblages became sharply reduced at the base of the *H. latidentat- us* Zone or slightly earlier, simultaneously with the sharp and universal facies change.

(5) The Permian–Triassic boundary layers are bar- ren of foraminifers, and all the sections are character- ized by this foraminifer-free interval. They appear again in the *I. isarcica* Zone being represented by scarce, mainly archaic forms known since the Paleozoic (Lazarus-taxa). Near the Permian–Triassic boundary, 40 genera (58%) and 17 families (43%) become extinct. This boundary is crossed by 29 genera, 20 of which are recorded in the Induan Stage, whereas other genera appear higher in the section.

(6) New foraminiferal genera and families typical of the Mesozoic time appear in the uppermost layers of the Induan Stage and become prevalent in assemblages only in the Anisian Stage.

CONCLUSIONS

The analysis of considered materials clearly indi- cates that the Permian–Triassic boundary marks a crisis in development of foraminifers, as well as in evolution of other sea dwellers of that time. The available data suggest that the terminal Permian extinction marks the crisis peak, first distinct signs of which are seen as early as at the Guadalupian–Lopingian boundary time. Cor- respondingly, two phases, *initial* and *terminal*, can be distinguished in the Late Permian foraminiferal crisis. The first of them decreased diversity of smaller for- aminifers and resulted in extinction of schwagerinids and neoschwagerinids. The next one was responsible for complete disappearance of all fusulinids and smaller foraminifers, but the latter, dissimilarly to fusulinids, recovered after a short-term period. A simi- lar conclusion is inferable from distribution patterns of many other fossil groups (Jin *et al.*, 1994; Stanley and Yang, 1994).

When trying to understand causes of the Permian extinction, one should pay attention to the fact that both the initial and terminal phases of the crisis were pre- ceded by the extensive Midian and Changhsingian transgressions. This fact was noted first by Kauffman (1986), when he analyzed peculiarities of Late Creta- ceous extinction. He considered it important, believing that extensive transgressions are responsible for rising and leveling of water temperature and increase diver- sity of stenothermal organisms. As a result, the system appears to be “prepared for the death” that happens by sudden environmental changes. This conclusion is also true for the first phase of the Late Permian extinction. Indeed, foraminifers are most diverse in the Midian sediments. The Midian–Wuchiapingian boundary is marked by sharp environmental changes. In the Lopin- gian, environments substantially differed from those of the preceding transgression period. The post-Midian regression resulted in expansion of land areas and in appearance of more or less isolated basins, which accu- mulated mainly clayey and micritic limy sediments. The extremely low admixture of the terrigenous com- ponent in the sediments indicates peneplanation of land topography, which, in turn, suggests a calm tectonic regime that prevailed uniformly after the epoch of active Hercynian orogeny. Such a rapid paleo- geographic transformation should influence the climate, chemistry of seawater, and other environmental factors, which undoubtedly also changed, although the type and degree of these changes are to be clarified. The unique character of the considered time in the geological his- tory is also evident from a rapid decrease of oxygen content in the atmosphere, which dropped, by the beginning of the Triassic, down to the value lowest for the entire Phanerozoic history (Budyko *et al.*, 1985). This was probably responsible for the onset of anoxic conditions in the World Ocean (Isozaki, 1997). All this was sufficient for destabilization and destruction of ecosystems that formed during the Midian transgres-

sion. Only groups of organisms highly resistant to the ecological stress continued to exist. Smaller foraminifers represented such a relatively eurybiontic group. To the contrary, fusulinids, particularly the larger and highly specialized schwagerinids and neoschwagerinids, became mostly extinct.

Thus, the initiation of the Late Permian extinction was most likely caused by many factors, most important of which was probably the post-Midian regression that triggered all subsequent environmental reorganizations.

This is less apparent when only the terminal phase of extinction coinciding with the Permian–Triassic boundary is considered. This boundary is marked, in addition to paleontological data, by the absolute minimum of the organic carbon content in sediments (Baud *et al.*, 1989). As compared with the post-Midian event, the terminal Permian extinction is much more prominent. Fusulinids become completely extinct. Smaller foraminifers also disappear, although for a short-term period. Recovering, they are initially scarce and dwarfish. Their diversity was more or less restored only in the Middle Triassic. Of interest is the fact that similar distribution patterns are characteristic of radiolarians—an absolutely different group of microorganisms with planktonic way of living in contrast to Paleozoic benthic foraminifers (Kukawa, 1996; Isozaki, 1997). The fact that disappearance of foraminifers and radiolarians was concurrent to the global ceasing of coal accumulation owing to extinction of turf-forming plants (Retallack *et al.*, 1996) means that the terminal Permian crisis was universal and affected both the marine and terrestrial biota. Such a conclusion suggests that factors responsible for this crisis were also more universal than local transgressions and regressions with all their consequences, and their impact was manifested all over the planet (Jin *et al.*, 1994; Hallam, 1994). Inasmuch as biotic reorganizations at the Permian–Triassic boundary happened suddenly, in a catastrophic manner, geological events responsible for destructive effects in the entire biosphere should be equally tremendous. Most probable of them was a catastrophic greenhouse effect related to the outburst of volcanic activity or to an extraordinary meteorite impact (Budyko, 1980; Budyko *et al.*, 1986; Alvarez *et al.*, 1982; Renne and Basu, 1991; Renne *et al.*, 1995; Campbell *et al.*, 1992; Kozur, 1994). The destructive effect of possible catastrophe could be aggravated by the stress state of biota in response to the post-Midian extinction and oxygen deficiency.

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