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Mesozoic marine fossil diversity and mass extinctions: an experience with the middle XIX century paleontological data

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Abstract
The recalculation of the paleontological data of A. d'ORBIGNY on the marine fossils distribution within the Mesozoic stages was attempted. About 18.000 species and 1200 genera were accounted. It was surprisingly found that fossils diversity changes constrained with the 150 years old data seem to be enough similar to ones calculated with the recent data. Most of the Mesozoic mass extinctions might be identified in the middle of the XIX century. That means the leading role in the growth of paleontology belongs not only to the data collecting, but to the analytical approach developments.

Key words
Diversity, mass extinctions, catastrophism, fossil record, completeness, Mesozoic.

1. INTRODUCTION

Thanks to the excellent compilations of SEPKOSKI (1982) and his co-workers (e.g., SEPKOSKI *et al.*, 1981) we obtained a real basis to discuss the fossil diversity changes and particulary such outstanding events in geological history as mass extinctions. Later biodiversity trends were several times updated (BENTON, 1995; PETERS & FOOTE, 2001; SEPKOSKI, 1993; SIGNOR, 1985). Meantime, the data are still incomplete and they will be much enlarged and improved later; e.g., recently only ~10-15% of Paleozoic megafossils were described (BOUCOT, pers. comm.). Therefore, a question arises: what may be changed in our imaginations on the diversity changes and the mass extinctions due to further paleontological studies? One of the possible way to answer it is to compare the estimations of fossil diversity changes based on recent and past data compilations. This also allows to clarify what could do the paleontologists with their data more than a hundred years ago. Such retrospective analyses were already attempted few times with other data (e.g., PADIAN & CLEMENS 1985; SMITH, 2001).

In the middle of the XIX century an "explosion" in the paleontological studies began. The first really comprehensive data compilations were appeared. One of the best attempt was made by Alcide d'ORBIGNY, whose contributions to studies of all principal fossil groups are enormous. His "Prodrome..." (ORBIGNY, 1850a, b, 1852) was a complete reference of the fossil distribution for the 1850s.

The main goal of this article is to analyze the Mesozoic marine fossil total diversity recalculating the data of A. d'ORBIGNY and then to compare results with the present knowledge on the marine biodiversity changes in the Earth's history.

2. MATERIALS AND METHODS

The d'ORBIGNY's "Prodrome..." contains information on about ~18.000 species and ~1200 genera of bivalves, brachiopods, bryozoans, echinoids, foraminifers, etc. Although not all fossil groups were accounted, it is possible to assume these data characterized enough representatively the whole marine biodiversity. The main difficulty to analyze them is connected with the misunderstanding of the time intervals used. Finally it was decided to concentrate the attention only on the Mesozoic (and Danian), which stages may be more evidently attributed to the present subdivisions.

The "database" of d'ORBIGNY allows to analyze total species and genera diversity per stages (TSD and TGD respectively).

3. MARINE FOSSIL DIVERSITY IF ANALYZED IN THE XIX CENTURY

TSD as it might be analyzed by d'ORBIGNY quickly accelerated in the Triassic (Fig. 1). In the average it

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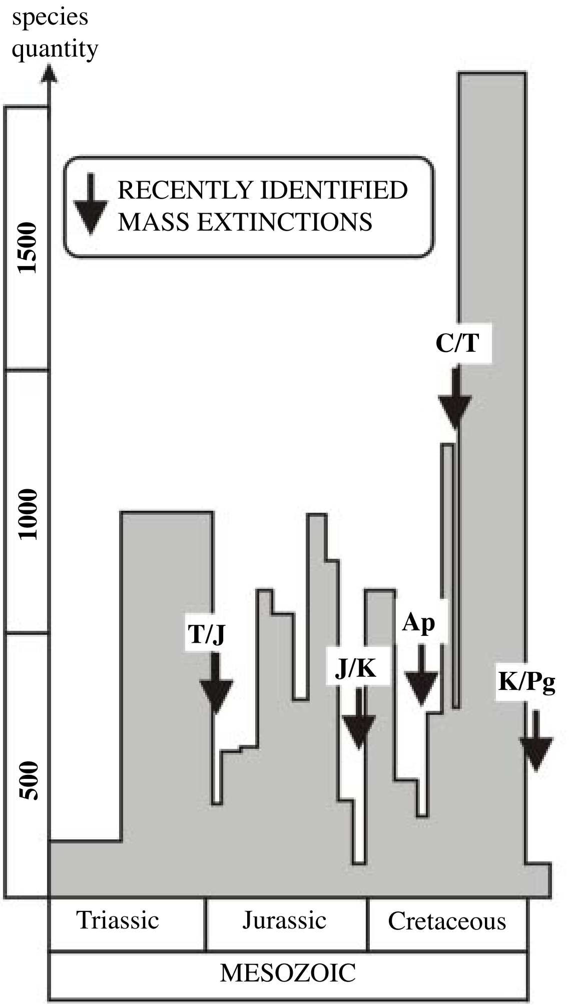

Fig. 1: The total species diversity changes in the Mesozoic calculated with the data of Orbigny (1850a, b, 1852).

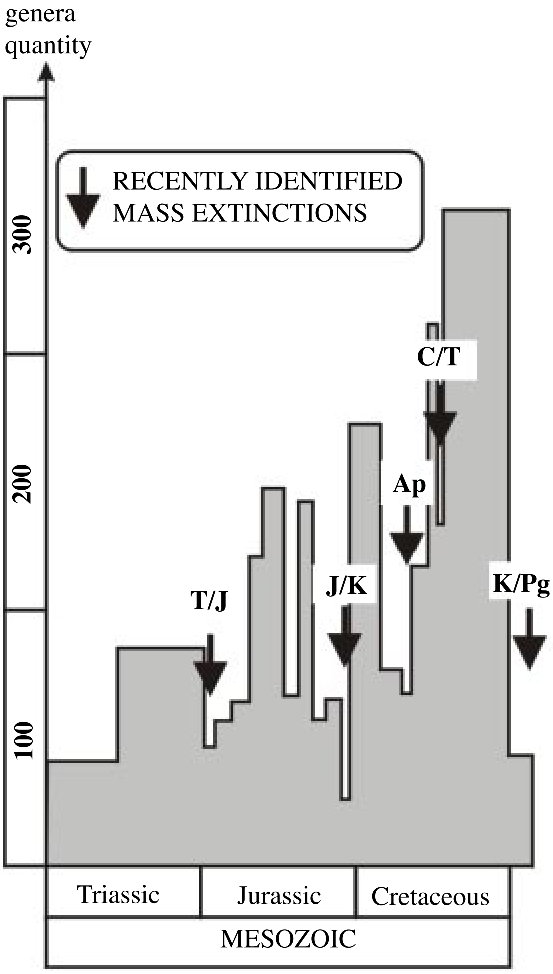

Fig. 2: The total genera diversity changes in the Mesozoic calculated with the data of Orbigny (1850a, b, 1852).

stayed at the same level until the mid-Cretaceous, when a new significant rise began. An abrupt decrease of the species number occured in the Danian. But the taxa quantity significantly fluctuated through the Mesozoic. The most intense TSD drops are documented for the beginning of the Jurassic, in the Callovian, in the end of Late Jurassic, in the Aptian and Turonian. Some long intervals corresponded to the several stages of the recent chronostratigraphical scale were defined by d'Orbigny as unique stages (Conchylian and Saliferian in the Triassic, Neocomian and Senonian in the Cretaceous). Therefore, it is impossible to discuss the TSD changes in detailes at them. Moreover, the diversity peaks observed for some of them should be reduced after their differentiation into the several distinct stages.

TGD changes are comparable with above mentionned patterns of TSD (Fig. 2). Only minor differencies may be documented. All the diversity drops established for species have also been recorded for genera.

4. DISCUSSION

Let's imagine that Alcide d'Orbigny analyzed marine fossils diversity in the middle of the XIX century. Results he received were not surprising for him and his contemporaries. They well coincided with the concept of "catastrophism" wide spread that times. Abrupt changes may easily be attributed to the catastrophic events in the Earth's history, which led to the disappearance of fossils. Just note, in reality the understanding of the Earth's history of d'Orbigny fluctuated between Cuvier and Lamarck (Laurent, 2002), i.e. between "catastrophism" and "evolutionism". But finding intervals of fossils disappearance, he had to chose the first concept without any doubts. This might turn all the further development of paleontology and geology. It is difficult to say was it good or bad, but none of these events mentionned above occurred in real history.

And are results of d'Orbigny's data recalculation surprising for us ? Both negative and positive answers are possible.

As we know enough much on the global fossils diversity (Peters & Foote, 2001 ; Sepkoski, 1993) and on the mass extinctions (Courtillot, 1999 ; Hallam & Wignall, 1997 ; Raup, 1993 ; Raup & Sepkoski, 1982) the results of d'Orbigny 's data recalculation seem not to be surprising for us. The diversity increase in the Triassic may be interpreted as a recovery after the mass extinction at the Permian/Triassic boundary. The diversity drops in the beginning and the end of Jurassic, in the Aptian and Turonian are corresponding well to the Triassic/Jurassic, Jurassic/Cretaceous, Early Aptian and Cenomanian/Turonian mass extinctions. Finally the significant drop of TSD and TGD in the Danian seems to be a result of famous K/T event. The unique unusual event is a diversity drop in the Callovian, which can be explained by the incompleteness of d'Orbigny 's data.

On the other hand, the results of our recalculation are very surprising : all Mesozoic mass extinctions (except one during the Early Toarcian) could be documented 150 years ago – even such short-termed events as recorded in the Early Aptian and at the Cenomanian/Turonian boundary. In fact, the intensity of mass extinctions recorded by the "past" data is uncomparable with estimated at now ; also the relation of strength between distinct extinction events differs from one established today (Peters & Foote, 2001). This is caused by the high degree of d'Orbigny's data incompleteness (absence of many taxa found later, taxonomical errors, restriction to the Western Europe, stratigraphical uncertainties, etc.). But even that fact, many of presently stated events might be recorded in the middle of the XIX century, is too significant itself.

It was pointed out above d'Orbigny accounted ~1200 genera, while Sepkoski - ~36.000 ones. This means the quantity of paleontological data increased in 30 times during the century and a half, although the results of recalculations are somewhat similar. Anyway this seems to be possible, because d'Orbigny evidently collected data on the most common taxa. Further studies led to the relatively uniform increase of the paleontological information for each interval.

It is interesting, Smith (2001), comparing results of Phillips (obtained in 1860s) to ones of Sepkoski (1993) and Benton (1995), also stated enough high similarity between their curves.

Now we can try to answer the question outlined in the beginning (see Introduction). It is possible, that even very significant enlargement and improvement of paleontological data in the future may not lead to the great changes in our principal imaginations on the marine fossil diversity changes and the mass extinctions, although many new detailes will become clear. The development of a science needs something more than a collecting of data, and evidently in the future paleontologists could do much more interesting analyses using even our present data. Perspectives of the fossil record exploration lie mostly in the area of development of the analytical techniques (see also Jablonski, 1999).

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Diversity dynamics and mass extinctions of the Early–Middle Jurassic foraminifers: A record from the Northwestern Caucasus

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Abstract

The Early–Middle Jurassic foraminiferal assemblages of the Northwestern Caucasus, including a total of 315 species and 68 genera, were analysed to establish the principal diversity patterns at substage level of resolution. An overall conclusion is that the number of species varied significantly in contrast to the number of genera. The most diversified were Late Sinemurian–Pliensbachian, Late Toarcian–Early Aalenian, and Late Bajocian assemblages. Significant diversity drops have been documented in the Early Toarcian and in the Middle Aalenian. The first of them corresponds to the well-known mass extinction, which regionally was initiated in the Pliensbachian and terminated when rapid Late Toarcian diversification began. The second event could be considered as a regional evidence of a new mass extinction that appeared in the Middle Aalenian and was most likely associated with the Aalenian/Bajocian regional anoxic event also recorded in the Carpathian part of the Western Tethys. The most intense foraminiferal turnovers took place in the Toarcian, and in the Middle Aalenian–Early Bajocian. The Lazarus-effect in spite of its high value has not much influenced the estimation of principal diversity trends.

Keywords: Foraminifers; Diversity; Origination; Mass extinction; Early–Middle Jurassic; The Caucasus; Tethys

1. Introduction

Evolution of the Early–Middle Jurassic marine biota in response to palaeoenvironments is a significant subject to be studied with the help of microfauna. Foraminifera are especially useful microfossils in such studies due to their relatively high diversity, widespread occurrence, and a high preservation potential. Early–Middle Jurassic

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assemblages dominated by benthic foraminifera of the suborder Lagenina were far from actualistic assemblages known from Late Cretaceous, Tertiary or Recent oceans. At the same time, several new foraminiferal lineages appeared, including planktonic foraminifera, that dominated post-Jurassic assemblages. Our recent knowledge on Jurassic foraminifera from the Western Tethyan and and Boreal realms is already considerable. Nevertheless, data of comparable quality and resolution are still not available that is especially evident in the taxonomic data from Western and Eastern Europe. First attempts summarizing global dynamics of Jurassic foraminifera based on genera and higher taxonomic levels were presented by Tappan and Loeblich (1988), and later by Basov and Kuznetsova (2000). The problem appears when we try to compile data at species level at the species level from different palaeogeographic areas. In this case, the best method is to focus on selected areas and look at dynamics at regional scales. The next step would be to compare different faunal dynamics from all available palaeogeographic areas.

The Caucasus seems to be a promising region for analyzing dynamics of Early–Middle Jurassic foraminiferal assemblages (Figs. 1 and 2). Their record, including over 300 species, in north-west Caucasus is substantial (Antonova, 1958, 1962, 1975; Antonova and Pintchuk, 1991; Alieva et al., 1991; Antonova et al., 2000; Mamontova, 1956, 1957; Rostovtsev et al., 1992). Currently used foraminiferal regional biozonation (Alieva et al., 1991; Antonova and Pintchuk, 1991; Rostovtsev et al., 1992) is characterized by resolution comparable with that of brachiopods or even ammonites (Fig. 2; see Rostovtsev et al., 1992). Moreover, due to the lack of uniform macrofaunal record, it becomes especially significant for both stratigraphical and palaeoenvironmental studies (Ruban, 2002a).

This paper presents an attempt of quantitative analysis of the Early–Middle Jurassic foraminifers from the North-western Caucasus with a view to

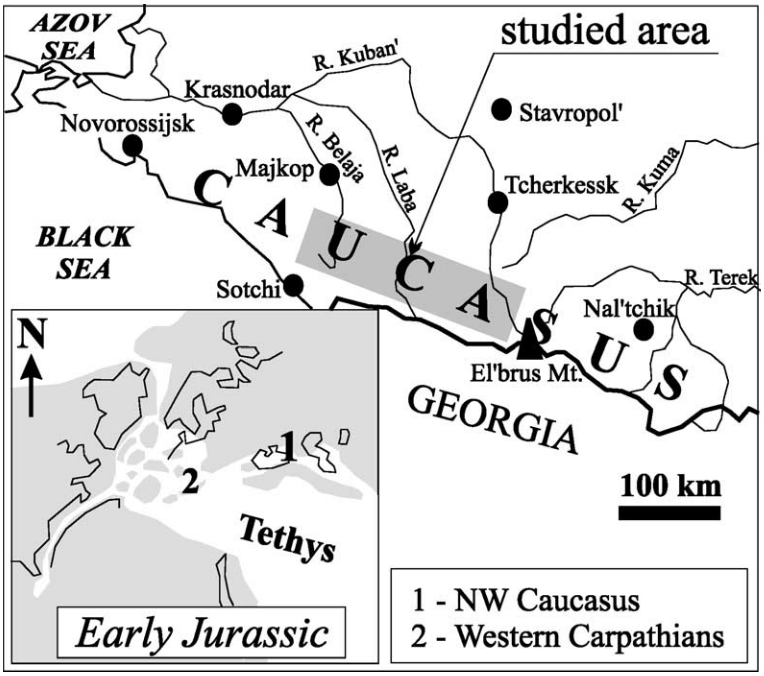

Fig. 1. Geographical location of the NW Caucasus (paleogeographic base map is modified from Owen, 1983; Dommergues et al., 2001). Land areas shaded.

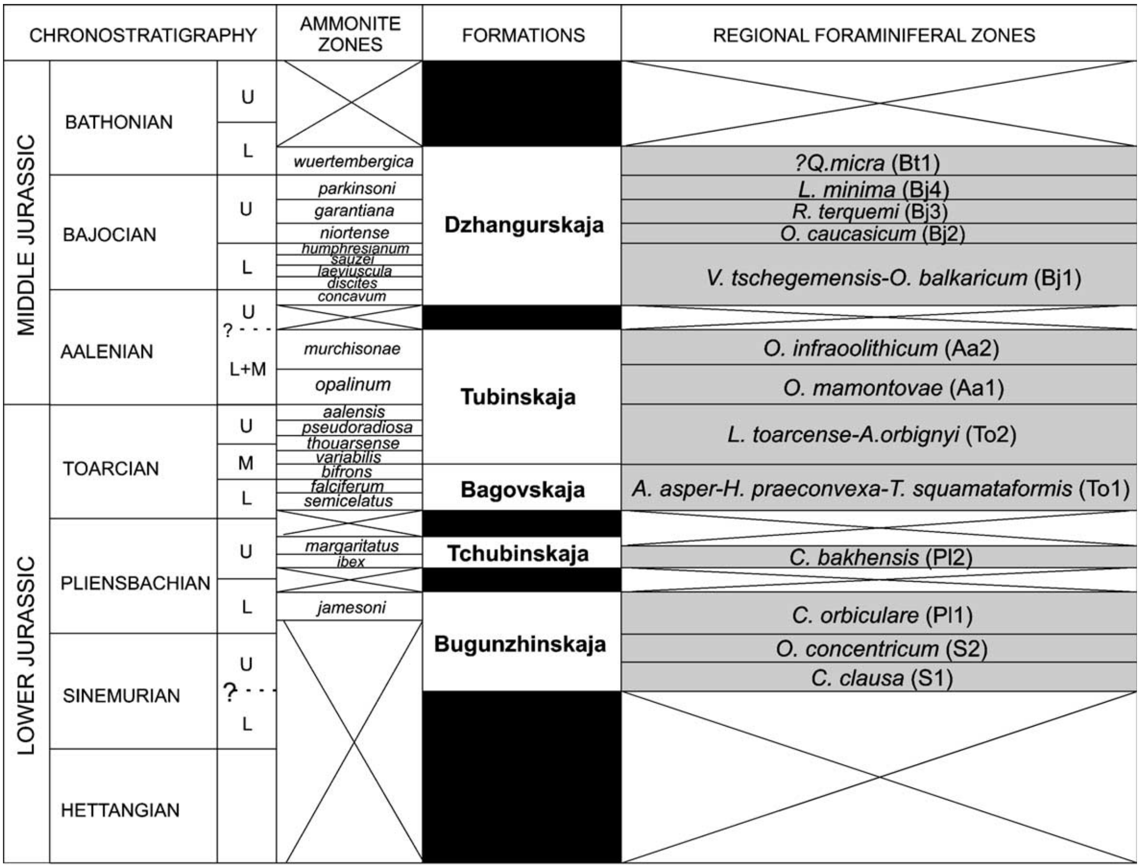

Fig. 2. Stratigraphy of the Lower–Middle Jurassic deposits of the NW Caucasus (zones after Alieva et al., 1991; Antonova and Pintchuk, 1991; Rostovtsev et al., 1992, with slight modifications).

obtain regional trends in taxonomic diversity dynamics and to evaluate possible influences of the global mass extinctions.

2. Geological setting

2.1. Lithostratigraphy

The studied area (Fig. 1) represents the western part of the Labino–Malkinskaja tectonic zone, which was incorporated into the active structures of the Northwestern Caucasus (Lordkipanidze et al., 1984; Meister and Stampfli, 2000).

The deposits of the Early–Middle Jurassic interval have already been investigated (Krymholz, 1972; Prosorovskaja, 1979; Rostovtsev et al., 1992; Granovskij et al., 2001; Ruban, 2002a). They are subdivided into 5 formations (Figs. 2 and 3) (Prosorovskaja, 1979; Rostovtsev et al., 1992). The Bugunzhinskaja Formation (Upper Sinemurian–Lower Pliensbachian) consists of sandstones and dark-grey claystones up to 150 m thick, with calcareous interbeds. A hiatus embraces the middle part of the Pliensbachian. It is overlain by the terrigenous Tchubinskaja Formation (Upper Pliensbachian), 300–350 m thick. A hiatus on the top corresponds to the uppermost Pliensbachian–lowermost Toarcian. Above the hiatus, the Bagovskaja Formation (Lower–Middle Toarcian) starts with conglomerates (mixed grains of different size) and succeeding sandstones with intercalations of claystones, altogether about 700–800 m thick. There follows the Tubinskaja Formation (Middle Toar-

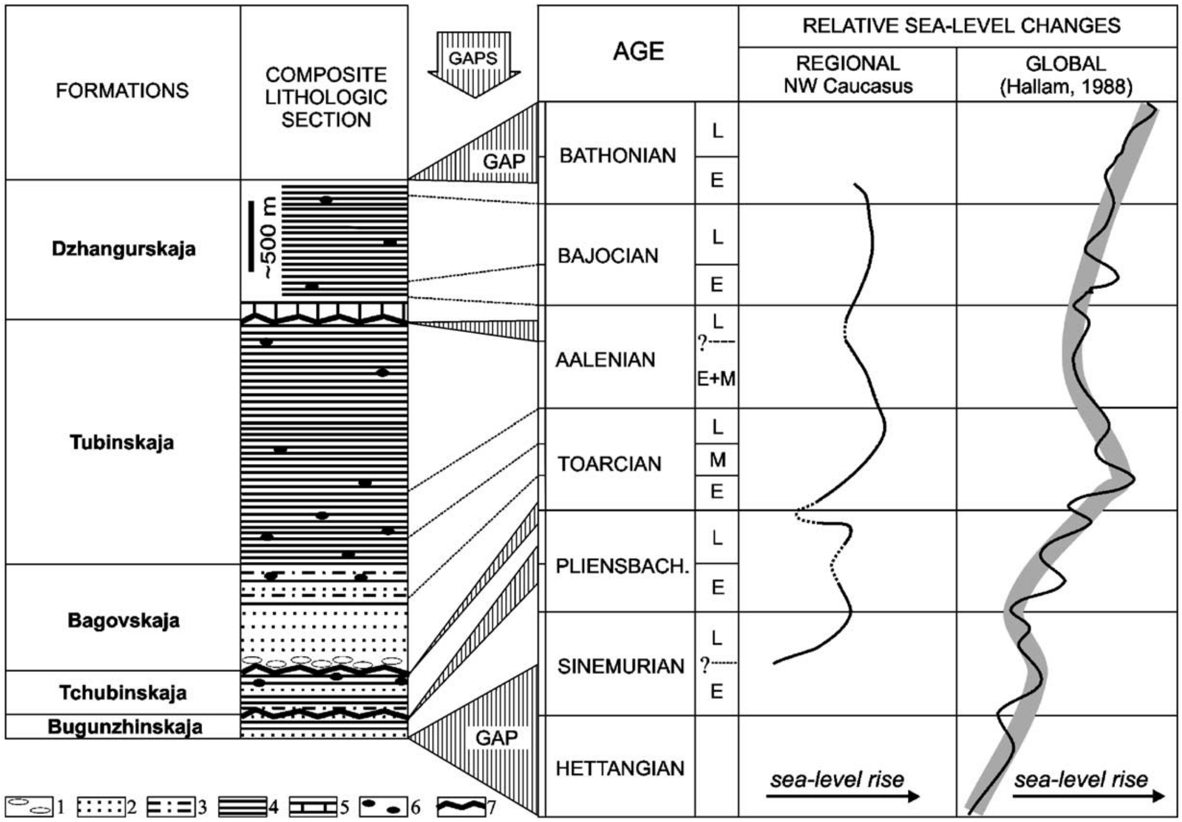

Fig. 3. Composite lithologic section of the Lower–Middle Jurassic and relative sea-level changes in the NW Caucasus compared to the global eustatic curve (after Hallam, 1988). 1—conglomerates, 2—sandstones, 3—siltstones, 4—claystones, 5—limestones, 6—siderite concretions.

cian–Middle Aalenian) consisting of dark grey to black shaly claystones, so-called “black shales”, up to 1800 m thick. A hiatus, probably corresponding to a middle part of Aalenian, separates the deposits of the Tubinskaja Formation from the deposits of the Dzhangurskaja Formation (uppermost Aalenian–lowermost Lower Bathonian). This formation is represented by a 1 m thick pinkish detrital crinoidal limestone, followed by dark claystones and siltstones (altogether up to 1000 m thick). These dark grey to black claystones and siltstones of all levels contain siderite concretions and dispersed pyrite grains (Granovskij et al., 2001; Rostovtsev et al., 1992; Ruban, 2002a). An interval, corresponding to a major regional hiatus, covers a considerable part of the Bathonian. The terrigenous Callovian deposits overly older deposits with the angular unconformity.

2.2. Biostratigraphy

An ammonite zonation was developed for the Caucasus by Rostovtsev et al. (1992). Regional zones are cited below to facilitate the interregional correlation of the units used in this paper. None zones were established in the Sinemurian. This ammonite zonation is quite limited within the Pliensbachian to: *Uptonia jamesoni* (upper part of the Bugunzhinskaja Formation), *Tragophylloceras ibex* and *Amaltheus margaritatus* zones (Tchubinskaja Formation, although foraminifers suggest that relation of its lower part to the *T. ibex* Zone is doubtful) were defined in successive order, but sedimentary gaps exist between them. Further 7 regional zones were defined in the Toarcian: *Dactylioceras semicelatum*, *Harpoceras falciferum*, *Hildoceras bifrons* (Bagovskaja Formation), *Haugia* *variabilis*, *Grammoceras thouarsense*, *Dumortieria pseudoradiosa*, *Pleydellia aalensis* (lower part of Tubinskaja Fm). Aalenian zones include *Leioceras opalinum*, *Ludwigia murchisonae* (upper part of the Tubinskaja Formation) and *Graphoceras concavum* (not well established in NW Caucasus). The following zones were defined in the Bajocian: *Hyperlioceras discites*, *Witchellia laeviuscula*, *Otoites sauzei*, *Stephanoceras humphresianum*, *Strenoceras niortense*, *Garantiana garantiana*, *Parkinsonia parkinsoni*. A single unit represented by the *Parkinsonia würtembergica* Zone was established in the base of Bathonian. Both Bajocian and Bathonian zones are attributed to the Dzhangurskaja Formation. A detailed correlation of ammonites-based zones of the Caucasus and reference regions of Western Europe is in progress now, but a preliminary comparison to Spanish (Sandoval, pers. comm. 2004) and French sections indicate their utility for the chronostratigraphical correlation.

Regional biozonation has been developed based on the studies of foraminiferal assemblages from the Lower and Middle Jurassic of the NW Caucasus (Alieva et al., 1991; Antonova and Pintchuk, 1991; Rostovtsev et al., 1992). All units identified were proposed as “zones” or “beds with”. In fact, they are abundance (acme)-assemblage zones (sensu Salvador, 1994). This zonation is linked to the chronostratigraphy of the Early–Middle Jurassic (Fig. 2). It was finally done by Antonova and Pintchuk (1991), who established correlations between the regional zonation and other, mostly European, regions. This zonation is directly attributed to the formations (Rostovtsev et al., 1992). In this paper, we generally accept proposed stratigraphical framework except for the Aalenian–Bajocian transition. Brachiopods suggest the lowest horizons of the Dzhangurskaja Fm may be related to the Upper Aalenian (Ruban, 2003). Therefore, we extended the lower boundary of the Bj1 foraminiferal zone a little downwards (see Fig. 2).

Foraminifers have a larger potential in the NW Caucasus for the development of the regional Lower–Middle Jurassic biostratigraphy than ammonites (Ruban, 2002a). Additionally their record is more uniform, while ammonites often are restricted to the relatively short intervals within the stratigraphic succession. We would like to stress that the presented regional foraminiferal zonation (Fig. 2; see Rostovtsev et al., 1992) has just local or regional value limited to the NW Caucasus. Foraminifers have been used to correlate a large number of small outcrops presenting several meters thick sections. Comparison of the NW Caucasus to different Tethyan and Boreal areas would be possible after verification of all described foraminiferal taxa.

2.3. Palaeogeography and palaeoenvironment

The studied basin (Fig. 1) was located at the northern Tethyan periphery in the Early–Middle Jurassic (Lordkipanidze et al., 1984; Meister and Stampfli, 2000). The deposits mentioned above accumulated in a marine sedimentary basin, which was relatively warm during the whole Early and Middle Jurassic interval except for the Early Aalenian when palaeotemperatures probably dropped to ~10 °C (Jasamanov, 1978). Marine transgressions occurred during the Sinemurian–Early Pliensbachian, Early–Middle Toarcian and Early Bajocian intervals, while regressions took place at the end of Pliensbachian, in Middle Aalenian, and in Middle–Late Bajocian (Fig. 3). The “black shales” possibly have been accumulated on the shelf margin (Granovskij et al., 2001). Their sedimentologic characteristics, such as coloration, abundant siderite concretions, and synsedimentary and/or early diagenetic pyrite mineralization suggest deposition under dysoxic to anoxic conditions.

We suppose that the silled basin model best describes conditions and sluggish circulation in such a stratified dysoxic basin (see Bernoulli and Jenkyns, 1974; Wignall, 1994) recorded in the Lower–Middle Jurassic of North-west Caucasus. Large terrestrial areas under a wet or at least seasonally wet climate surrounded the basin in Early Jurassic (e.g., Hallam, 1994). Sedimentation of the described above thick deposits took place in a tectonically active basin with a relatively high subsidence. These conditions are probably responsible for a relatively high average sedimentation rate calculated at 10–15 cm/ka.

A general palaeogeographical position of NW Caucasus is still under debate due to the lack of high-quality data on all faunal groups. Dommergues (1987) locates this area within the Euro–Boreal domain, while Westermann (2000) considers it as a part of the Tethyan Realm. It seems, however, that this region shows some transitional features between both realms.

3. Materials and methods

Several reviews of the Early–Middle Jurassic foraminiferal data from the NW Caucasus were presented (Alieva et al., 1991; Antonova and Pintchuk, 1991; Rostovtsev et al., 1992; Antonova et al., 2000). They include both biozonation development, interregional correlations and taxonomic descriptions. This paper is based on the comprehensive information on biostratigraphic ranges of all 315 recorded species within this region, refereeing to the established foraminiferal zones. These data, presented in sources mentioned above, were compiled by Antonova, Zozulja and Pintchuk, and provided with permission by T.N. Pintchuk (see Appendix). The data were obtained from hundreds relatively small sections and available boreholes. Unfortunately, the NW Caucasus lacks extensive continuous sections, thus, the generalized data are used for analysing diversity trends instead of studying them in selected type sections. Most explanatory data on sampled horizons were already presented by Alieva et al. (1991), as well as, Antonova and Pintchuk (1991).

Among different measures of diversity usually chosen to be analysed (see Buzas, 1979), the most significant are: total diversity (total number of species or genera), appearance, disappearance, origination and extinction rates, number of singletons (sensu Foote, 2000), as well as two indices used to estimate rates of association changes (Ruban, 2001, 2002a).

Making a distinction between the terms “appearance” and “origination”, and “disappearance” and “extinction” is necessary because of a high amount of the so-called Lazarus-taxa (Flessa and Jablonski, 1983; Jablonski, 1986; Wignall and Benton, 1999; Fara, 2001). If a break in a taxon range is recognized, this taxon may appear or disappear several times, while only once it can be originated or go extinct forever. To avoid the Lazarus-effect, it is also necessary to recalculate data accounting for possible presence of taxa at intervals corresponding to their temporal absence in the fossil record. This way we document only the highest probable value (HPV) of this effect. If the Lazarus-effect were connected with the real temporal disappearance (regional or global) or migration, and not with the incompleteness or defects of fossil record, the break in a taxon regional range would be real. In this case we would consider disappearances as extinctions and appearances as originations. In fact, we can hardly conclude unequivocally, what is the nature of the Lazarus-effect (especially when analysing regional data). Considering the Early–Middle Jurassic foraminifers from the NW Caucasus, their Lazarus-effect seems to be an effect of incompleteness of the fossil record, so the HPV possibly is not so different from the real effect value.

Evaluation of the number of appearances/originations in the first (lowermost) zone within the succession is not possible because there is no data on the preceding zone to compare. The disappearances/originations in the terminal zone might be an effect of sedimentary hiatus in the Upper Bathonian, when foraminifers might have still existed.

Two indices of associations changes rate proposed by Ruban (2001, 2002b) have been used. The first of them is R, which reflects the Jaccard similarity (Jaccard, 1901; Shi, 1993) of two fossil assemblages, characterized stratigraphic intervals:

$$R = C/[(N_1 + N_2) - C],$$

where C is the number of common taxa for two intervals, and N_1 and N_2 are the taxa quantities in the lower and upper intervals respectively.

Faunal transformation rate (FTR) is estimated as $1/R$. This rate shows how quickly changes in taxonomical composition of assemblages took place through geological time. A similar method, but with Simpson’s coefficient, has been used by Hallam (1983), as well as, Smith and Tipper (1986) to evaluate macrofaunal evolutionary turnovers. Another index is R_{st}, which reflects a similarity of taxonomical structure of diversity in assemblages. It is determined as a simple coefficient of Spearman rank correlation (Kendall, 1975) between two assemblages by presence/absence of the genera, accounting species number in each of genera. The rate of transformation of taxonomic diversity structure (TTDSR) could be estimated as $1/R_{st}$. It shows changes in the generic control of species diversity, i.e., changes in significance of each genus for the determination of species diversity.

4. Species and genera diversity dynamics

The species diversity dynamics of foraminifers in the Early–Late Jurassic of the NW Caucasus is not characterized by any kind of stability (Fig. 4). After a slight diversification in the Late Sinemurian–Pliensbachian (S2–Pl2 zones), a sharp decrease of the total species number occurred in the beginning of Toarcian (To1 zone). It was caused primarily by a high value of extinction rate in the Pliensbachian and less by the decline of origination rate. But just after this Toarcian event a fast recovery took place (To2 zone). The diversity maximum was reached during the Late Toarcian–Early Aalenian (To2, Aa1 zones). Then a new diversity drop occurred (Aa2 zone), which was connected with a high rate of extinction documented in the Aa1 zone. A gradual recovery that began at the end of Aalenian (Bj1, Bj2 zones) did not compensate the previous decrease. A relatively high rate of originations was preserved during the first half of Bajocian (Bj1, Bj2 zones). Then, until the end of the Bajocian the species number did not change much, while the Bathonian foraminiferal assemblages became impoverished due to a major regional regression episode.

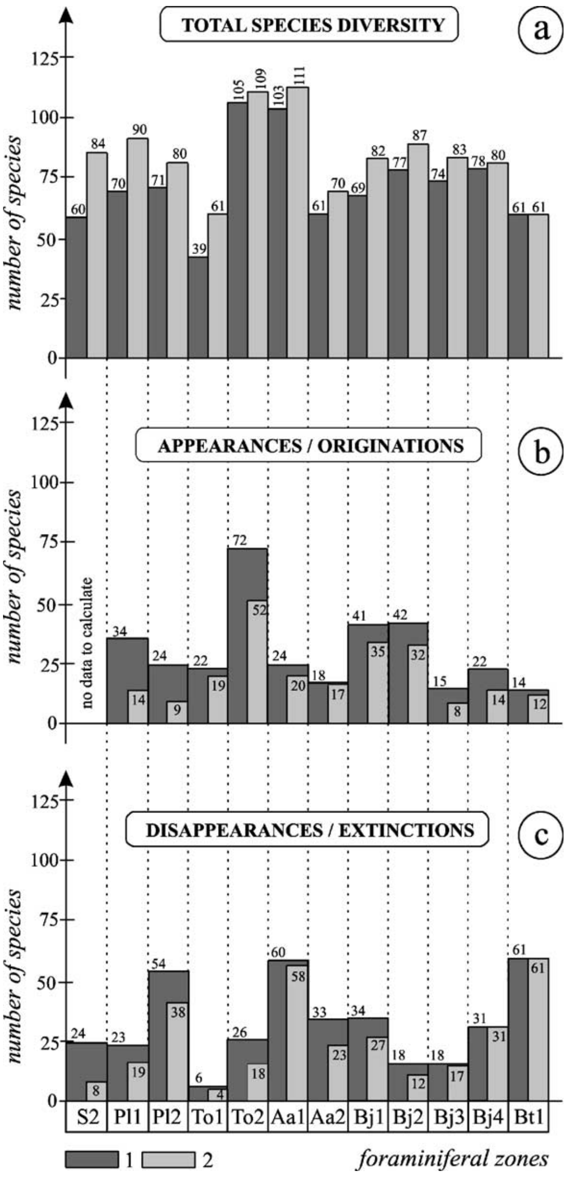

Fig. 4. Species diversity of foraminifers (per zones): total diversity (a), appearances/originations (b), disappearances/extinctions (c). Columns: 1—“original”, 2—accounting for the Lazarus-effect. See Fig. 2 for foraminiferal zones abbreviations.

In contrast, the genera diversity dynamics seems to be rather stable in the Early–Middle Jurassic (Fig. 5). The number of genera did not vary so much as the species number. The most significant event was a decline of diversity in the To1 zone followed by a recompensed diversification documented already in the To2 zone. The diversity drop in the Aa2 zone was not very great. It is evident that overall diversity changes of foraminifers in the NW Caucasus resulted mostly in species (but not generic) turnovers. That means strong variations of average species number within the relatively stable number of genera.

Calculations of R and R_{st} indices changes suggest that the most intense transformations of assemblages took place within the intervals of Pl2–To2 zones and Aa1–Bj2 zones, when both the specific and generic compositions have been renewed (Figs. 6 and 7). It is evident that principal transformations at species level took place earlier than at the level of genera. That could be possibly explained by the above-mentioned higher stability at the generic level. In fact, this shifted turnover at this level resulted from low changes in number of extinctions in contrast to relatively high appearances/originations of new genera just after both extinctions levels, i.e., in To2 and Bj1–2 zones (Figs. 4–6).

The singletons number (i.e., quantity of species appeared, existed and disappeared within the same single interval) changed cyclically during the Early–

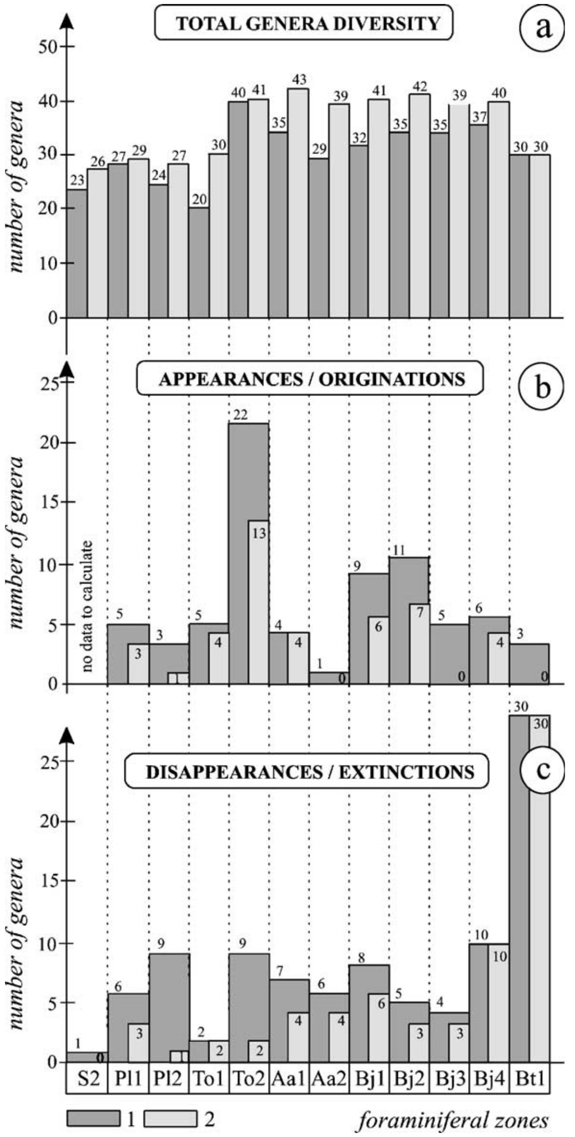

Fig. 5. Generic diversity of foraminifers (per zones): total diversity (a), appearances/occurrences (b), disappearances/ number of species going extinct (c). Columns: 1—"original", 2—accounting for the Lazarus-effect. See Fig. 2 for foraminiferal zones abbreviations.

Middle Jurassic (Fig. 8). The highest values coincided mostly with intervals of significant diversifications. It is necessary to point out that the acceleration of singletons quantity in Bt1 zone is simply explained by the regional termination of development of all taxa, including just-originated ones, due to regression of the sea.

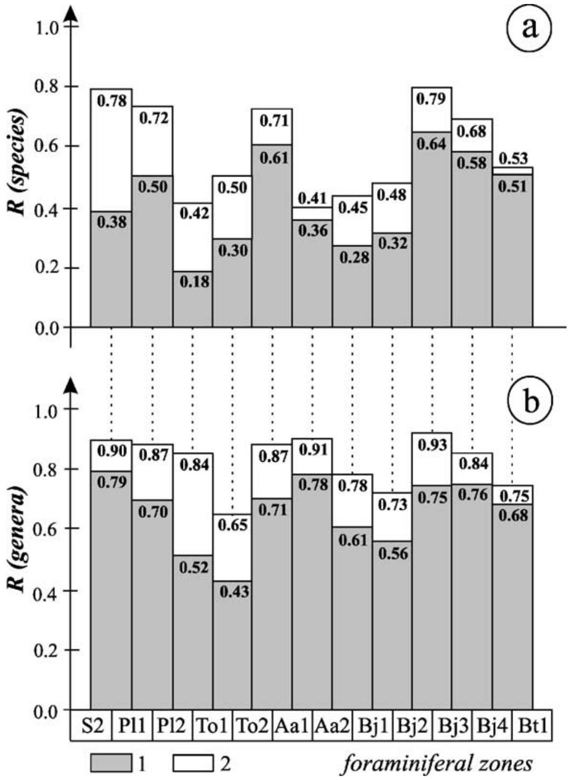

Fig. 6. R index changes (per zones): species (a), genera (b). Columns: 1—"original", 2—accounting for the Lazarus-effect. See Fig. 2 for foraminiferal zones abbreviations.

Analysing all components of foraminiferal diversity, comparisons between curves calculated "as original", and as accounting for the Lazarus-effect were made.

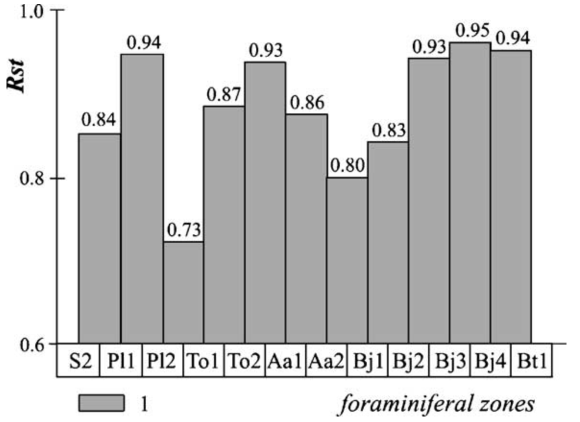

Fig. 7. R_{st} index changes (per zones). Column: 1—"original". See Fig. 2 for foraminiferal zones abbreviations.

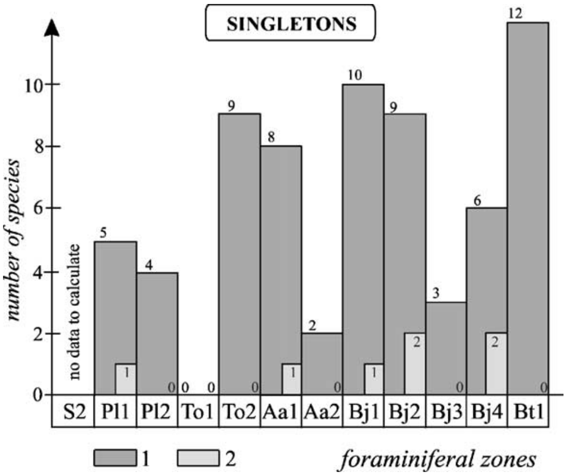

Fig. 8. Number of singletons accounting for the Lazarus-effect (per zones). Columns: 1—species, 2—genera. See Fig. 2 for foraminiferal zones abbreviations.

The result is quite surprising. Although the value of this effect is relatively high, that does not distinctly influence the estimation of diversity trends. The indices of the total diversity and *R* become higher, while, in contrast, rates of appearance/origination and disappearance/extinction decrease. Nevertheless, relative values follow the same trend in the succession of events. Therefore, the Lazarus-effect has not significantly influenced the results of foraminiferal diversity calculations from the Early–Middle Jurassic deposits of the NW Caucasus.

5. Interpretation and discussion

In the Early Jurassic marine biota were subject to a significant mass extinction coincided to major sea-level changes and appearance of anoxia, which led to the diversity drop in the Late Pliensbachian–Early Toarcian (Hallam, 1961, 1987; Jenkyns, 1988; Hori, 1993; Little and Benton, 1995; Aberhan and Fürsich, 1997, 2000; Hallam and Wignall, 1997, 1999; Guex et al., 2001; Harries and Little, 1999; Hylton et al., 2000; Jenkyns et al., 2002; Pálfy et al., 2002; Vőrős, 2002; Wignall, 2001; Ruban, 2004). Unfortunately, the impact of this event on foraminifers, although evidently established (Bassoullet and Baudin, 1994; Bassoullet, 1997), has been less extensively discussed.

The most comprehensive global data also suggest that diversity drop occurred in the Toarcian (Tappan and Loeblich, 1988). Tappan and Loeblich (1988) have reported a slight generic diversification in the Pliensbachian, followed by the relatively low-diversity Toarcian–Aalenian interval. A significant diversification occurred in the Bajocian, while in the Bathonian the number of genera slightly declined. Regional Early–Middle Jurassic trends of the foraminifers diversity dynamics calculated coincided with the global tendencies, except for the Bajocian diversification which has not been evidently documented in the NW Caucasus. Ruget and Nicollin (1997), based on the Western European data suggested diversification in the Sinemurian, which perhaps also took place in the NW Caucasus (S2 zone). They also pointed out two significant renewals of assemblages, which took place in the Early Pliensbachian and Early Toarcian. Data from La Rambla del Salto Section in Spain by Herrero (2001) also allow pointing a significant turnover at the Pliensbachian–Toarcian transition.

The first renewal is enigmatic in the NW Caucasus because in this particular case the Lazarus-effect brings misunderstanding into our results. But another strong intensification of the assemblages transformation (i.e., high values of the faunal transformation rate ‘FTR’ and the rate of transformation of taxonomic diversity structure ‘TTDSR’) is truly documented in the studied area. It was also noted by Ruget and Nicollin (1997) this transformation was taking place gradually. In the NW Caucasus, duration of this event covers a quite long interval represented by the Pl2–To2 zones.

Our results from the NW Caucasus support the idea of the significant mass extinction during the Early Jurassic that strongly influenced foraminiferal assemblages. The total species diversity of foraminifers in the To1 zone decreased to 55% of the level recorded in the Pl2 zone (Fig. 4). Thus, a strong extinction took place after the time representing the Pl2 zone. Taking into account the Lazarus-effect, it is suggested that this extinction was already initiated after the time representing Pl1 zone, but it was not intense (11%). We should nevertheless be aware that exclusion of the Lazarus taxa gives a very stable total species number in both Pl1 and Pl2 zones.

This described Pl2/To1 crisis was not that evident at generic level (disappeared 16.6% of recorded genera). Actually, this bioevent began earlier in the Pliensbachian when at the Pl1/Pl2 disappeared 11% of genera (Fig. 5). A rapid recovery of species and genera took place at the time of To2 zone and it completely compensated the previous demise. As a result, the To2 assemblage was even more diversified than pre-event assemblages at specific and generic levels. Thus, we can document duration of the main mass extinction of foraminifera in the NW Caucasus as the latest Late Pliensbachian to the earliest Middle Toarcian. A slight gradual (or stepwise) decrease has actually been recorded from the uppermost Lower Pliensbachian upwards, considering relations of foraminiferal zones to chronostratigraphic units (Fig. 2). In fact, it is quite likely that the above mentioned major extinction event took place around the *falciferum* ammonite zone, correlated with the middle part of the To1 zone. The pre-*falciferum* foraminiferal assemblage of the To1 zone was probably impoverished due to adverse environmental conditions associated with deposition of coarse-grained transgressive sediments, including conglomerates and sandstones (Fig. 3).

Bassoullet and Baudin (1994) have shown that a crisis affected foraminifers just at the Pliensbachian/Toarcian boundary and lasted during the time interval represented by the *tenuicostatum* ammonite zone; then, a rapid diversification began. Global data on all marine biota suggest the beginning of their decimation at the end of Pliensbachian (Pálfy et al., 2002). In both mentioned cases, the Middle Toarcian diversity acceleration is shown as a rapid event, but not as “overcompensated” as it was documented in the NW Caucasus. Should these differences in appearance of mass extinction be explained by any region-specific palaeoenvironmental changes? The answer depends much on what causes of the Pliensbachian-Middle Toarcian event we chose as principal ones. The most promising causes are major sea-level changes and anoxia (see Hallam and Wignall, 1997, 1999). The first seem to be more doubtful because during the interval of mass extinction sea-level changed cyclically, but crisis continued both during regression and during transgression. On the other hand, the peak of mass extinction in the global record corresponds to the maximum of transgression (Hallam and Wignall, 1999), while the Early Toarcian in the NW Caucasus was a time of beginning of the transgression, which reached its maximum in the Late Toarcian (Fig. 3).

Detailed estimation of influence of anoxia on extinction of foraminifera is not possible in the NW Caucasus due to lack of detailed sedimentological, geochemical and palaeoecological studies. Abundance of siderite concretions, “dispersed” pyrite grains, and dark to black color of shales (Granovskij et al., 2001; Rostovtsev et al., 1992; Ruban, 2002a, 2004) suggest that dysoxic to suboxic conditions could be documented in the whole Sinemurian–Bathonian interval. This might have been resulted from isolation of this marine silled basin from other adjacent Tethyan basins connected via relatively shallow seaways (Lordkipanidze et al., 1984).

The question is whether anoxia was the strongest in the Early Toarcian. We suppose that transgressive coarse-grained deposition took place under better oxygenation conditions associated with higher hydrodynamic conditions. Dysoxic conditions probably developed later, i.e., during successive deepening of the basin in the Middle–Late Toarcian. Surprisingly, these dysoxic conditions did not stop a rapid diversification of foraminifers. Most likely, these latest Middle–Late Toarcian well-diversified assemblages disprove an existence of anoxic, or suboxic bottom water conditions. Thus the factors controlling mass extinction of foraminifera in the regional NW Caucasus aspect is still enigmatic.

The Pliensbachian–Toarcian transition in the NW Caucasus is embraced by a short, but regionally recognized hiatus, which may partly or completely explain decline of the taxa number. We can hypothesize that the latest Pliensbachian regression caused a regional emergence of the basin and inevitable disappearance of all taxa. The successive Early Toarcian transgression brought about colonization of a new assemblage from adjacent basins. This new foraminiferal assemblage recorded in the To1 zone was less diversified (45% drop in total species number) and consisted of 17 “old species” and 22 newcomers. A total of 54 species did not come back, including 38 of those which did extinct (Fig. 4). We can therefore presume the extra-basinal faunal impoverishment took place either during existence the regional emersion level or during deposition of transgressive gravel and sandy facies (Figs. 2 and 3). The latter case is more likely because coarse-grained arenaceous facies were deposited during the time represented by the Early Toarcian *semicelatus* and *falciferum* zones. This is the time iterval, corresponding to *tenuicostatum* and *falciferum* zones, when the global extinction event associated with the rapid sea level rise and development of widespread anoxic conditions occurred (see Hallam, 1987; Little and Benton, 1995; Hallam and Wignall, 1999).

It is worthwhile to look at the recovery and recolonization patterns—diversification coinciding with late stages of the relative sea level rise and even its maximum (Figs. 3 and 4). It seems that a high sea level improved connections (via sills) with adjacent Tethyan and Boreal basins and enabled rapid immigration of new taxa and re-immigration of the Lazarus-taxa into the basin. Furthermore, during that time, adaptive radiation followed the global extinction event (Hallam, 1987; Hallam and Wignall, 1997). Overall deepening of the NW Caucasus basin and a shift from sandy to silt and clay facies during Middle and Late Toarcian also facilitated further colonization. It seems to be clear that moderately dysoxic conditions did not disturb this regional trend.

Another significant bioevent is recorded in the Aalenian. The Aa1 zone records a high total species diversity inherited from the To2 assemblage. A drastic species diversity drop (in about 2 times) is recognized in the Aa2 zone. (Fig. 4). Then a gradual recovery began correlated with the Bj1 and Bj2 zones. The causes of this Aalenian crisis are still enigmatic. Dysoxic conditions hypothesized by “black shales” with siderite concretions in the Early Aalenian, existed also in the Bajocian, but this did not stop the recovery of foraminifers. Major sea-water cooling documented regionally in the Aalenian (Jasamanov, 1978) should also be taken into account as a potential cause of extinction. It is also necessary to consider that the drop of species number in this case might also be explained by the incompleteness of palaeontological record.

Global analysis of the foraminiferal diversity suggests that a crisis took place around the Toarcian/Aalenian boundary, and that the recovery was finished in the Early Bajocian (Basov and Kuznetsova, 2000). Tappan and Loeblich (1988) showed that the total generic diversity decrease covered Toarcian and Aalenian. In the Aalenian a weak acceleration took place. Unfortunately, this low-resolution analysis limited to genera only does not allow making further conclusions. In several Spanish sections some patterns of the Aalenian crisis, including diminishing of the diversity, was also documented (Canales and Herrero, 2000; Canales, 2001).

The present results from the NW Caucasus suggest that the Aalenian–Early Bajocian event is not less pronounced than the preceding one observed in the Pliensbachian–Toarcian. This provides a matter of debate on reality of an additional mass extinction. There are no doubts that the results on foraminifers should be further supported by records from other regions and on different fossil groups. The global data on marine biota (Sepkoski, 1993; Markov, 2001) does not provide clear suggestions on particular events in the Middle Jurassic interval. On the other hand, an idea of new mass extinction has recently been supported by Tethyan brachiopods, which record strongly reduced Aalenian assemblages (Vőrős, 1993, 1995; Sulser, 1999; Ruban, 2003, 2004).

We can compare the NW Caucasus record with that of the Western Carpathians. The Pieniny Klippen Belt basin left a sedimentary record of dysoxic to suboxic facies dated from the Pliensbachian to the Late Bajocian (see Birkenmajer, 1977; Tyszka, 1994a,b). Unfortunately, the Early Toarcian Anoxic Event is not well recognized there due to tectonic gaps and limited availability of outcrops. This event is most likely preserved within the Toarcian–Lower Aalenian succession of dark grey to black flysch deposits with interbeding mudstones and sandstones (Birkenmajer, 1977; Birkenmajer and Tyszka, 1996). In contrast, the Aalenian/Bajocian event is documented much better in the Polish, Slovakian, and Ukrainian sectors of the Pieniny Klippen Belt (see Birkenmajer, 1977). It is represented by a relatively thin and widespread horizon of “black shales” with spherosideritic and phosphoritic concretions. This event has already been described as a “regional anoxic event” (Tyszka, 1994a, 1995). The event is associated with impoverishment of microfauna, including extinctions of several foraminiferal taxa, such as *Lenticulina d’orbignyi* (Roemer) (with *Astacolus*-like morphology), *Falsopalmula tenuistriata* Franke, and *Marginulinopsis dictyodes dictyodes* (Deecke). On the other hand, the same event was associated with first appearances (?originations) of some new taxa of agglutinated foraminifers, such as: *Trochammina globoconica*

Tyszka and Kaminski (Tyszka and Kaminski, 1995), *Verneuilinella pieninica* Tyszka and Kaminski, and *Miliammina gerochi* Tyszka (1997) as the first documented appearance of the genus *Miliammina* and the superfamily Rzehakinacea. The upper (Lower Bajocian) part of the "black shales" shows much higher diversity as a result of improvement of conditions, recovery of populations, and colonization by immigrants. It was connected with the sea-level rise, tectonic reorganization of the basin and, in consequence, deepening of sills and widening of seaways (Tyszka, 1994b, 1995).

The history of the Pieniny Klippen Basin seems to be closely linked to the Aalenian extinction event in the NW Caucasus. It also suggests that it is necessary to conduct detailed palaeoenvironmental studies in this Caucasus basin in comparison to other Tethyan and Boreal areas.

Both events documented in the Early–Middle Jurassic of the NW Caucasus are comparable in their intensity with the greatest crisis which occurred at the K/T boundary. Keller (2001) reported that 2/3 of planktic species were extinct at the K/T boundary. In our case 50–75% species went extinct at the Pl2/To1 zones boundary, and 50–60% at the Aa1/Aa2 zones boundary, i.e., around the *opalinum*/*murchisonae* ammonite zones boundary (?Early/Middle Aalenian). If we assume that less than 10% of the total benthic foraminiferal population was influenced at the K/T boundary (Keller, 2001), the Early–Middle Jurassic events could be regarded as significant in comparison to other mass extinction. However, it should be stressed that direct comparison of Jurassic and K/T events is irrelevant because almost a complete turnover of planktonic foraminifers at the K/T boundary is incomparable (see MacLeod, 1996; Keller, 2001).

6. Conclusions

Quantitative analyses of the Early–Middle Jurassic foraminifers taxonomic diversity performed for the NW Caucasus territory (Fig. 1) allow us to make several main conclusions:

(1) there is no stasis in the diversity dynamics of the Early–Middle Jurassic foraminifera recorded (Figs. 4–8);
(2) the diversity changed strongly at species level while at generic one it was relatively stable (Figs. 4 and 5) that is in agreement with other records of the Early Toarcian extinction event (see Hallam and Wignall, 1999; Hylton et al., 2000);
(3) the most intensive foraminiferal turnovers took place at the Pliensbachian/Toarcian boundary followed by the Toarcian, as well as, from the Middle Aalenian to the Early Bajocian (Fig. 6);
(4) significant diversity drops are documented in the Early Toarcian and in the Middle Aalenian. The first event corresponds to the well-known mass extinction. The second event probably represents a new mass extinction that appeared in the middle of Aalenian, possibly around the opalinum/murchisonae ammonite zones (Figs. 2 and 4);
(5) both extinction events were followed by extensive diversification intervals in the middle–late Toarcian and the latest Aalenian–Early Bajocian (Fig. 4);
(6) in spite of high value of the Lazarus-effect, it has not much influenced the estimation of main diversity components (Figs. 4–6).

Further micropalaeontological, sedimentological, and geochemical studies are necessary to explain the diversity dynamics observed, and to compare global and regional evolutionary and palaeoenvironmental changes.

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Appendix A. Supplementay data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2005.03.021.

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Late Paleozoic – Early Mesozoic Tectonic Activity within the Donbass (Russian Platform)

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Abstract: The Donbass is a large structural domain in the south of the Russian Platform, whose origin and tectonic evolution is still debated. Our new model suggests the Late Paleozoic and Early Mesozoic tectonic activity within the Donbass was controlled by the dynamics of the Northern Palaeotethyan Shear Zone. The Late Paleozoic dextral movements along the latter led to the detachment of the Ukrainian Massif and extension of the Donbass. The change to sinistral strike-slip in the Late Triassic resulted in regional contraction and folding.

Key words: Shear zone. Strike-slip. Contraction. Paleozoic. Mesozoic. Palaeotethys. Donbass.

Resumen: El Donbass es un gran dominio estructural de la Plataforma Rusa cuyo origen y evolución tectónica es objeto de debate. Se propone un nuevo modelo según el cual la actividad tectónica durante el Paleozoico tardío y el Mesozoico temprano fue controlada por la dinámica de la Zona de Cizalla Septentrional del Paleotetis. Los movimientos dextrales de esta Zona en el Paleozoico tardío condujeron al despegue del Macizo Ucraniano y a una extensión en el Donbass. El cambio a un movimiento en dirección sinistral durante el Triásico tardío dio lugar a una contracción y plegamiento.

Key words: Zona de cizalla. Strike-slip. Contracción. Paleozoico. Mesozoico. Paleotetis. Donbass.

Recent advances in global palaeotectonic reconstructions (e.g., Stampfli and Borel, 2002; Scotese, 2004; Torsvik and Cocks, 2004) ask for reconsideration of the traditional models of the tectonic evolution of particular regions. The Donbass (alternatively named Donets Basin or Donbass Fold Belt) is a large structural domain in the southern part of the Russian Platform (Fig. 1). It is located between two stable Precambrian blocks: the Ukrainian and Voronezh massifs, and their marginal structures. The Donbass is the eastern and the most "mature" domain of the elongated structure, which also includes the Dniepr-Donets Basin and the Pripyat Trough.The Donbass contains Carboniferous and Permian coal-bearing deposits several kilometres thick, which are strongly folded and disrupted by numerous faults. Overviews of the tectonic activity of the Donbass are presented by Laz'ko (1975), Stephenson et al., (1996), Maystrenko et al., (2003), Saintot et al., (2003), Stovba et al., (2003), Vai (2003), and Kostjutchenko et al., (2004).

Two significant questions arise about the Donbass: (1) why did intracratonic rifting occur in the Late Devonian-Carboniferous, and (2) what forces led to end-Triassic contraction? We present a new model to answer them.

Northern Palaeotethyan Shear Zone

A major shear zone was active on the northern margin of the Palaeotethys in the Late Paleozoic and Early

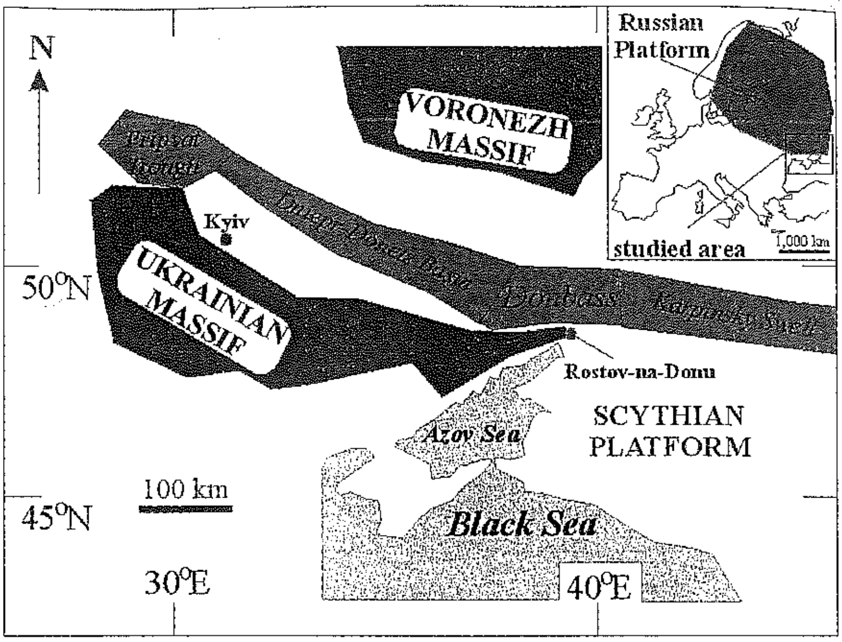
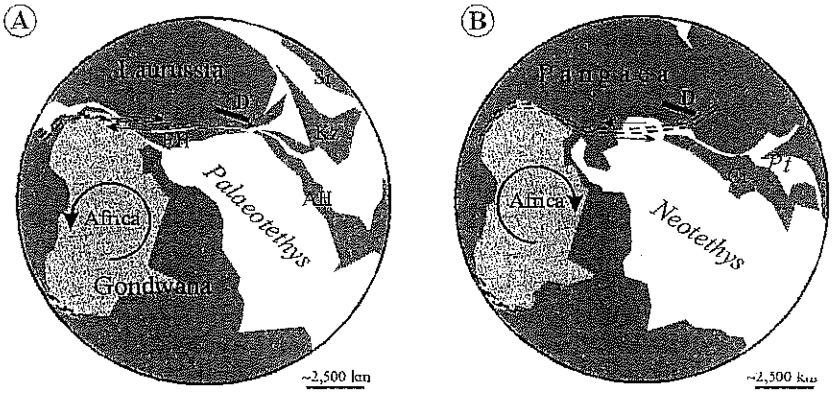


Figure 1. Main tectonic structures in the SW of the Russian Platform (simplified from Maystrenko et al., 2003). Areas of the Precambrian rock exposure are highlighted as black. The Late Paleozoic basins are highlighted as grey. Other areas (white) are covered by the Mesozoic-Quaternary deposits.



Bashkirian (320 Ma)

Norian (220 Ma)

Figure 2. Global palaeotectonic reconstructions for the Bashkirian (Pennsylvanian) (A) and the Norian (Late Triassic) (B); base palaeotectonic maps are strongly simplified from Stampfli and Borel (2002). Double dashed lines trace the shear zones related to the Africa rotation. Abbreviations: D – Donbass, Dniepr-Donets Basin and Pripyat Trough, EH – European Hunic Terranes, AH – Asiatic Hunic Terranes, Kz – Kazakhstan, Si – Siberia, Ci – Cimmerian Terranes, Pt – Palaeotethys.

Mesozoic (Arthaud and Matte, 1977; Swanson, 1982; Rapalini and Vizán, 1993; Lawver et al., 2002; Stampfli and Borel, 2002; Vai 2003; Garfunkel, 2004). Strike-slip movements along this zone were dextral since the Devonian until the Late Triassic (Fig. 2A), and since then it became sinistral (Fig. 2B) (Swanson, 1982; Rapalini and Vizán, 1993; Vai, 2003). These movements stopped in the Middle Jurassic (Rapalini and Vizán, 1993). These displacements were caused by the rotation of Africa (Rapalini and Vizán, 1993). The latter may be explained with the 'global wrench tectonics' (Storetvedt, 2003).

An intriguing question for further studies is connected with the hypothetical relation of motions along the Northern Palaeotethyan Shear Zone in the Late Paleozoic to the strike-slip deformations along the other major shear zone, which was located between the Laurentia and Baltica in the Middle Paleozoic (Lawver et al., 2002).

The global-scale dynamics of the Northern Palaeotethyan Shear Zone could enforce the tectonic evolution of the Donbass.

A tectonic model

Dextral strike-slip movements along the Northern Palaeotethyan Shear Zone occurred since at least the Visean (Lawver et al., 2002; Stampfli and Borel, 2002), but probably began a little earlier, in the Late Devonian,

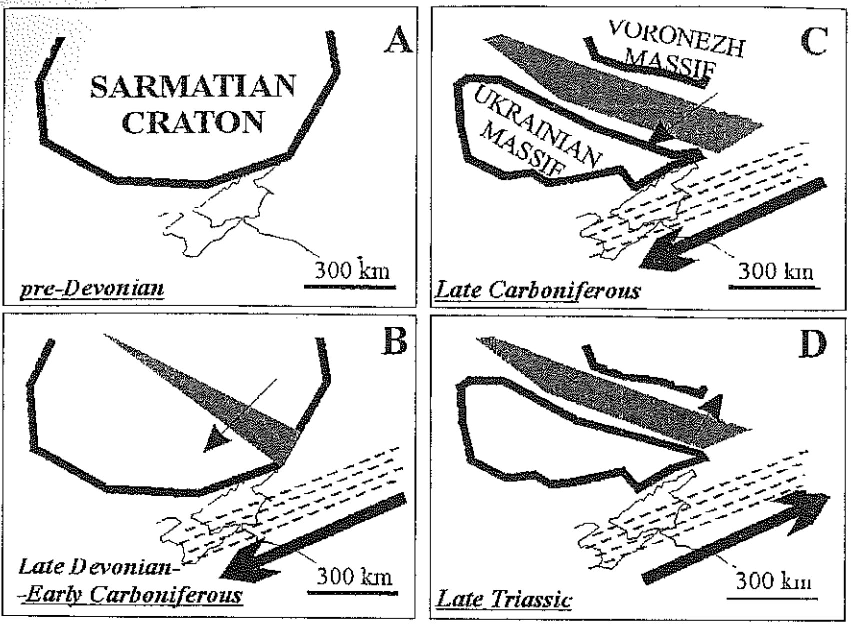


Figure 3. A model of the development of the Donbass from the pre-Devonian (A) to the Late Triassic (D). Dashed lines mark the shear zone. Thick arrows indicate the movements of the land masses in relation to the Russian Platform. Thin arrows indicate direction of the Ukrainian Massif movement. The Pripyat Trough, the Dniepr-Donets Basin and the Donbass are highlighted as grey.

when the European Hunic Terranes just docked to the Laurussia after the partial closure of the Rhenohercynian Ocean (Stampfli and Borel, 2002). These movements influenced intense fault activation and reactivation in European structures (Arthaud and Matte, 1977; Vai, 2003). It seems that dextral strike-slip movements were able to break up the previously stable Sarmatian Craton (Fig. 3A), detaching the Ukrainian Massif (Fig. 3B). This break-up occurred along the tectonically weak zone, which crossed the Sarmatian craton since the Precambrian (Stephenson et al., 1996). Kostjutchenko et al. (2004) estimated that the southeastern part of the Ukraininan Massif was transported 100-150 km off the craton margin. A number of basins (i.e., Pripyat Trough, Dniepr-Donets Basin and Donbass) were formed in this way (Fig. 3C). The regional extension, i.e. between the Ukrainian and Voronezh massifs, in the Carboniferous due to the continued detachment of the Ukrainian Massif seems to be a factor that controlled the deepening of the Donbass and, therefore, provoked deposition of thick sedimentary complexes. The rates of this regional extension, which was also marked by the magmatic activity, are discussed in Stephenson et al., (1996).

The change of movement direction along the shear zone in the Late Triassic caused contraction and folding within the Donbass. Sinistral strike-slip caused the Ukrainian Massif to move back towards the northeast, i.e. towards the Voronezh Massif. Such change of the motion of the Ukrainian Massif in the Triassic was also hypothesized by Kostjutchenko et al., (2004). As the 'mature' structure of the Donbass existed between the massifs, it was contracted (Fig. 3D), with folding of the sedimentary complexes. The main phase of shortening occurred in the Late Triassic (Maystrenko et al., 2003; Saintot et al., 2003; Stovba et al., 2003; Vai, 2003).

Thus, the Donbass evolution was influenced by the African geodynamics because the Northern Palaeotethyan Shear Zone evolution was controlled by the rotations of this continent (Rapalini and Vizán, 1993).

Our model explains the differences between the Pripyat Trough, the Dniepr-Donets Basin and the Donbass. The first is a relatively 'shallow' structure, while the second is deeper, but neither is as deep or deformed as the Donbass (Maystrenko et al., 2003). According to the model presented here, extension at the margin of the Sarmatian Craton increased towards the southeast, i.e., towards the most peripheral part of craton. The latter was especially strongly affected by the strike-slip movements, because shear zone was located along it.

The Donbass tectonic developments has analogues. Similar strike-slip movement along another great shear zone were documented in East Asia during the Mesozoic, particulary in Japan and Korea (Otoh and Yamakita, 1995; Otoh and Yanai, 1996; Yamakita and Otoh, 2000; Sasaki, 2001). The initial dextral movement changed to sinistral in the Early Cretaceous, which influenced the evolution of nearby regions.

Conclusion

Dextral strike-slip movements along the Northern Palaeotethyan Shear Zone detached the Ukrainian Massif from the previousely existed Sarmatian Craton, and the thick Late Paleozoic sedimentary complex was accumulated in the opened basin, i.e. in the Donbass. When these strike-slip movements became sinistral since the Late Triassic, the compression of the Donbass occurred, which was resulted into the strong deformation of the mentionned sedimentary complex.

It is important to note, that the Late Devonian-Triassic movements along the Northern Palaeotethyan Shear Zone also controlled the development of many basins in the North and South America, and Africa (Rapalini and Vizán, 1993).

Further studies are necessary to test deeply the model proposed in this paper.

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