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Late Cretaceous marine biodiversity dynamics in the Eastern Caucasus, northern Neo-Tethys Ocean: regional imprints of global events

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Abstract. During the Late Cretaceous, marine organisms experienced significant changes in their biodiversity. These diversity changes were influenced, particularly, by the Oceanic Anoxic Event 2 near the Cenomanian/Turonian boundary (93.6 Ma). Here, stratigraphic ranges of 80 marine macroinvertebrate genera (cephalopods, brachiopods, gastropods, corals, and echinoids) were employed to assess the Late Cretaceous biodiversity dynamics in the Eastern Caucasus, which covered a large region located in the northern Neo-Tethys Ocean. Our results outline three prominent diversity minima, which occurred in the late Cenomanian–late Turonian, the early Santonian-late Campanian, and the late Maastrichtian. Probably, the latter two were just local. Despite of some differences in trends between the regional and global marine biodiversity dynamics, the late Cenomanian-late Turonian biotic crisis appeared both on the regional and global scales and was probably a long-term consequence of the Oceanic Anoxic Event 2. Oxygen depletion and eustatically-driven shoreline shifts are considered as plausible causes of the observed biodiversity dynamics.

Key words: marine macroinvertebrates, diversity, biotic crisis, OAE2, Eastern Caucasus, Cenomanian/Turonian, Late Cretaceous.

Апстракт. За време горње креде, морски организми доживљавају значајне промене у њиховом биодиверзитету. Ове промене биле су углавном последица океанског аноксицног догађаја 2 на граници ценоман/турон (93,6 Ma). За процену динамике горњокредног биодиверзитета Источног Кавказа, који је покривао пространу област Северног Нео-Тетиског океана, коришћено је стратиграфско распрострањење 80 морских макробескичмењачких родова (цефалопода, брахиопода, гастропода, корала и јежева). Добијени резултати указују на три значајна диверзитетска минимума, који су се десили за време горњи ценоман–горњи турон, доњи сантон–горњи кампан и горњи мастрихт. Највероватније су два последња минимума локалног значаја. Насупрот неких разлика у трендовима између регионалне и глобалне динамике морског биодиверзитета, горње ценоманска–горње туронска биотска криза имала је регионални и глобални значај, вероватно као последица дугог океанског аноксичног догађаја 2. Смањење кисеоника и еустатички контролисане промене обалске линије се могу сматрати као узрочници посматране биодиверзитетске динамике.

Кључне речи: морски макробескичмењаци, биодиверзитет, биотске кризе, OAE2, Источни Кавказ, ценоман/турон, горња креда.

Introduction

The global marine biodiversity changed rapidly during the Late Cretaceous (PURDY 2008). Peculiar events were superposed on the general evolutionary trends. The Cenomanian/Turonian (C/T) boundary (93.6 Ma according to OGG *et al.* 2008), which was suggested tentatively as the upper boundary of the Middle Cretaceous series (GRADSTEIN *et al.* 2008), was a time slice characterized by strong environmental perturbations on a planetary scale. Intense turnovers and some extinctions among the entire range of marine biota (e.g., SEPKOSKI 1986; HALLAM & WIGNALL 1997, 1999; HARRIES & LITTLE 1999; WIGNALL 2001; LECKIE *et al.* 2002; KELLER 2008), an oceanic anoxic event (OAE2; e.g., JENKYNS, 1980,

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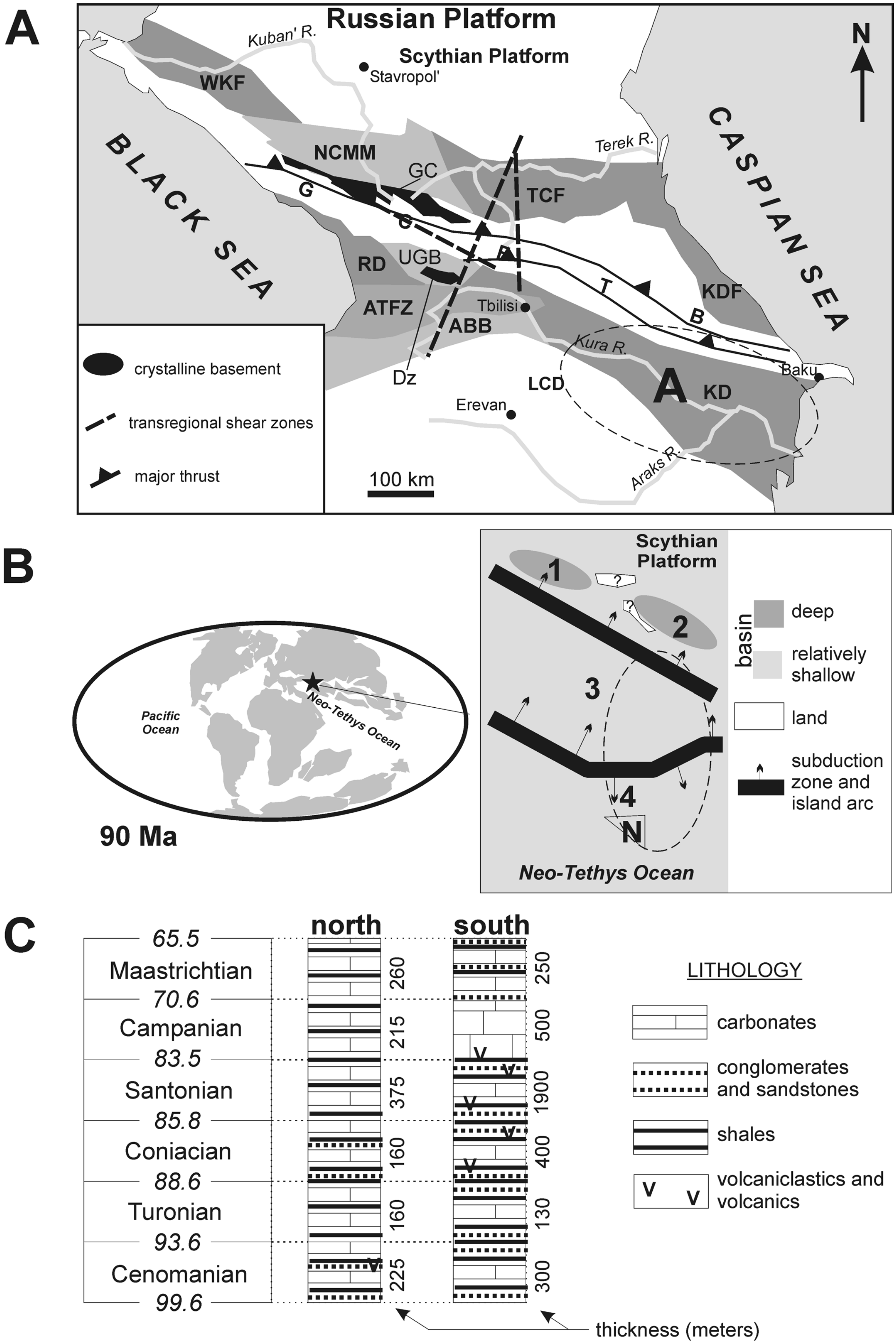
A
Russian Platform
Scythian Platform
Kuban' R.
Stavropol'
WKF
BLACK SEA
CASPIAN SEA
N
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TCF
Terek R.
RD
UGB
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KDF
B
ATFZ
Tbilisi
ABB
Kura R.
Baku
Dz
LCD
A
KD
Erevan
Araks R.
100 km
crystalline basement
transregional shear zones
major thrust
B
Pacific Ocean
Neo-Tethys Ocean
90 Ma
Scythian Platform
1
2
3
4
N
?
?
Neo-Tethys Ocean
basin
deep
relatively shallow
land
subduction zone and island arc
C
north
south
65.5
Maastrichtian
70.6
Campanian
83.5
Santonian
85.8
Coniacian
88.6
Turonian
93.6
Cenomanian
99.6
260
215
375
160
160
225
250
500
1900
400
130
300
LITHOLOGY
carbonates
conglomerates and sandstones
shales
volcaniclastics and volcanics
thickness (meters)

2010; Arthur *et al.* 1987; Schlanger *et al.* 1987; Bralower 1988; Kaiho & Hasegawa 1999; Premoli Silva *et al.* 1999; Wang *et al.* 2001; Desmares *et al.* 2004; Erba 2004; Kuroda *et al.* 2005; Grosheny *et al.* 2006; Jarvis *et al.* 2006; Kuroda & Ohkouchi, 2006; Takashima *et al.* 2006, 2009; Mort *et al.* 2007; Forster *et al.* 2008; Elrick *et al.* 2009; Pearce *et al.* 2009), and increased mantle plume activity (e.g., Larson *et al.* 1991a,b; Wignall 2001; Abbott & Isley 2002; Snow *et al.* 2005; Bralower 2008) left remarkable imprints on the global fossil, sedimentary and geochemical records. However, extent and strength of the biotic crisis near the C/T boundary remain debated. E.g., Gale *et al.* (2000) and Smith *et al.* (2001) argued that the mass extinction related to OAE2 may be an artifact. While more data is available from Mediterranean Europe (e.g., Lamolda & Peryt 1995; Peryt & Lamolda 1996; Coccioni & Luciani 2005), England (e.g., Jarvis *et al.* 1988a,b; Paul *et al.* 1999; Gale *et al.* 2005), and Japan (Toshimitsu & Hirano 2000; Takahashi 2005), palaeontological records of many other potentially important regions are still inadequately explored.

This paper addresses the Eastern Caucasus, which seems to be an important region because of its key palaeoposition on the northern margin of the Neo-Tethys Ocean between the Alpine structures of Europe and the terranes of the Middle East (Fig. 1). This region exhibits a representative Upper Cretaceous succession with the documented distribution of diverse marine macroinvertebrates. A discussion on the regional biotic signature of the C/T event in the northernmost part of the Eastern Caucasus has been attempted by Tur *et al.* (2001) and Ruban (2003a), who considered data on foraminifers. Earlier, Kotetishvili (1999) investigated the diversity of the entire Caucasian ammonites, which also contributed to the noted task. On a broader scope, it is the aim of this paper to examine the regional marine biodiversity dynamics during the Late Cretaceous and, particularly, to evaluate the relative impact of the C/T event in the Eastern Caucasus.

This study is a result of cooperation of specialists in general palaeobiology (DA.R.), geochemistry and palaeoenvironments (A.F.), and micropalaeontology (D.D.). The authors participated equally in writing the manuscript.

Geologic setting

The Eastern Caucasus region encompasses entire Azerbaijan and some adjacent areas (Fig. 1A). Its tectonic structure includes various structural domains of the Greater Caucasus and the Lesser Caucasus (Gamkrelidze 1986, 1997; Ruban *et al.* 2007). The regional geodynamic setting of this region in the Late Cretaceous is revealed on the basis of present models of this region's geologic evolution (Lordkipanidze *et al.* 1984; Ershov *et al.* 2003; Kazmin & Tikhonova 2006; Saintot *et al.* 2006; Tawadros *et al.* 2006) and modern plate tectonic reconstructions (Stampfli & Borel 2002; Golonka 2004; Scotese 2004). During the Late Cretaceous, the Eastern Caucasus lay at the northern active margin of the Neo-Tethys Ocean (Fig. 1B). It included the entire Eastern Greater Caucasus back-arc basin, the eastern part of the Black Sea-Caspian extended – probably rifted – basin, and some parts of the Lesser Caucasus Basin and the Nakhychvan Block (Fig. 1A).

Sedimentation regimes differed within the Eastern Caucasus. Whereas carbonate deposition prevailed in the entire region, the quantity of siliciclastic and volcaniclastic sedimentation increased southwards (Fig. 1C). During the Late Cretaceous, the Eastern Caucasus was embraced by a large marginal sea (Fig. 1B) with normal salinity and relatively high bottom temperatures (Jasamanov 1978). In contrast to the surrounding platform area to the north, the Western and Eastern Greater Caucasus marine basins were relatively deep (Fig. 1B), which is indicated by flysch deposits. Palaeobiogeographically, the study region belonged to the Mediterran-Caucasian Subrealm of the Tethyan Realm (Westermann 2000). Generally,

Fig. 1. Geologic setting of the Eastern Caucasus. **A,** principal structural units of the Caucasus (modified after Gamkrelidze 1986, 1997; Ruban *et al.* 2007). A, Azerbaijan. Areas shown in different shadings of dark grey indicate the here distinguished structural units: ABB, Arthvin-Bolnisi Block; ATFZ, Adjara-Thrialethian Fold Zone; Dz, Dzirula Massif; GC, Greater Caucasian Massif; GCFTB, Greater Caucasian Fold and Thrust Belt; KD, Kura Depression; KDF, Kusar-Divichian Foredeep; LCD, Lesser Caucasus Domain; NCMM, North Caucasian Marginal Massif; RD, Rioni Depression; TCF, Terek-Caspian Foredeep; UGB, Uplifted Georgian Block; WKF, West Kubanian Foredeep. Dashed ellipse indicates the approximate position of the region considered in this study. **B,** location of the Caucasus in the Late Cretaceous. Left: global plate tectonic reconstruction after Scotese (2004). According to Lordkipanidze *et al.* (1984), the Eastern Caucasus lay between 25°N and 35°N. Right: regional palaeotectonic sketch map; modified from Lordkipanidze *et al.* (1984). Basins: 1, Western Greater Caucasus Basin; 2, Eastern Greater Caucasus Basin; 3 Black Sea-Caspian Basin; 4, Lesser Caucasus Basin; N, Nakhychvan Block. Palaeobathymetry of basins is indicated by areas shown in different shadings of grey, white areas represent land. Dashed ellipse indicates the approximate position of the region considered in this study. **C,** composite lithologic sections of Upper Cretaceous deposits of Azerbaijan (on the basis of Ali-zadeh 1988). Absolute ages after Ogg *et al.* (2008).

the abundance and diversity of the Late Cretaceous marine biota in this region were high. Macroinvertebrates included cephalopods, bivalves, brachiopods, gastropods, corals, and echinoids (Ali-zadeh 1988). Coral reef communities with especially high diversity flourished during the Coniacian (Ali-zadeh 1988).

Material and method

Stratigraphic ranges of 80 marine macroinvertebrate genera from the Late Cretaceous deposits of Azerbaijan are compiled here from the most comprehensive source (Ali-zadeh 1988). These data were collected from dozens of localities within the territory of the Republic of Azerbaijan, but they were never used before in order to discuss changes in marine biodiversity. The analyzed fossil groups include (number of genera): cephalopods (11), brachiopods (9), gastropods (21), corals (12), and echinoids (27) (Appendix 1). Bivalves are excluded from the present analysis because of their outdated taxonomy. Sampling biases are unavoidable for studies of individual sections, however, as we here deal with summarized data for the entire study region, probable sampling biases should be minimized. When possible and necessary (as in the case of brachiopods and cephalopods), the original palaeontological data given by Ali-zadeh (1988) were verified with some taxonomic corrections. For few taxa, the stratigraphic ranges are only known with some uncertainty. When the presence of a taxon in the whole stage is indicated without a reference to any particular substage in the original literature, we may hypothesize an equal probability of its occurrence in these substages. To account for this, the presence of such a taxon is recognized for each substage, but as a proportion, e.g., the presence is indicated as 0.5 for each substage if the stage consists of two substages.

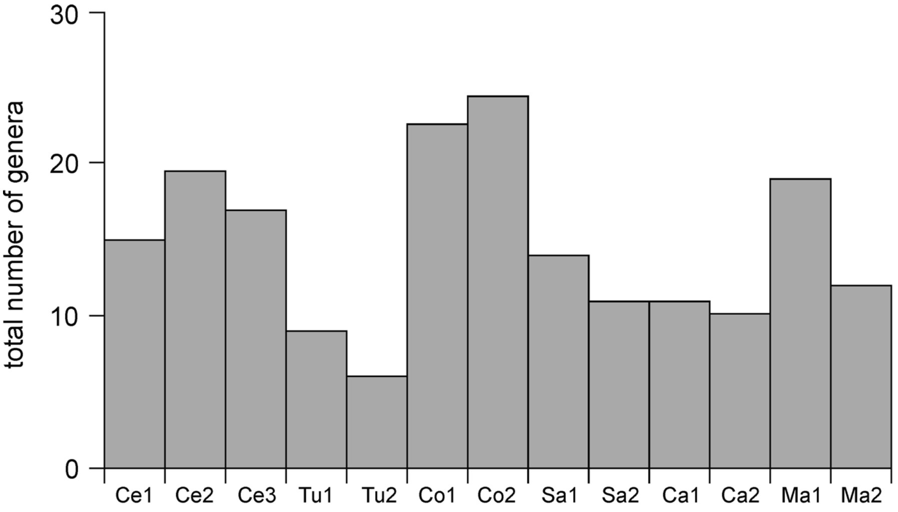

Fig. 2. Dynamics of the Late Cretaceous diversity of marine macroinvertebrates in the Eastern Caucasus (Azerbaijan). Stage abbreviations: Ce, Cenomanian; Tu, Turonian; Co, Coniacian; Sa, Santonian; Ca, Campanian; Ma, Maastrichtian. Stages are additionally subdivided into regional units indicated by numbers (e.g., Ce1; see text for explanation).

The regional stratigraphic framework used here is taken from the original source (Ali-zadeh 1988). The latter study relates the palaeontological data to the Late Cretaceous stages and substages. According to the original data source, all stages are divided into 2 substages, namely early and late, and the Cenomanian into 3 substages (Ce1 to Ce3, as for example shown in Fig. 2). Some minor differences between the regional stratigraphic framework (Ali-zadeh 1988) and the modern chronostratigraphy of the Late Cretaceous (Rawson *et al.* 1996; Ogg *et al.* 2008) may exist, but they seem to be insignificant for the purposes of the present study that is emphasized on long-term patterns. Substages considered in this manuscript (in contrast to stages) are informal time units, which may differ from the conventional substages treated, for example, by Rawson *et al.* (1996). To make a distinction from formal substages, the names of regional substages are not capitalized. A peculiarity of regional substages may explain the documented taxa ranges (Appendix 1); e.g., *Acanthoceras*, which is a Middle Cenomanian taxon, is reported from lower, middle, and upper Cenomanian of the Eastern Caucasus. The informal regionally-restricted substages are useful, nonetheless, for a more precise documentation of the biodiversity patterns. The stratigraphic age of the Late Cretaceous deposits in the Eastern Caucasus was established with an integrated analysis of the entire assemblage of marine invertebrates (Ali-zadeh 1988). Although the regional foraminifer-based biozonation framework is available, foraminifers were not the only group used for relative age determination. Generally, Ali-zadeh (1988) attempted to assign faunistic assemblages to the Upper Cretaceous stages, even if biozonation still needs to be improved. Another study attempted by Ruban (2003b) for the Northern Caucasus confirmed that changes in both standard biozonation and foraminifer taxonomy did not affect significantly the regional chronostratigraphic record and, thus, the earlier-established stages remain generally valid.

The main biodiversity pattern considered in this study is the total number of genera. In order to compare regional and global records, the global marine biodiversity curve proposed by PURDY (2008) is employed herein. The latter curve is based on the well-known compendium by SEPKOSKI (2002) with an exclusion of some stratigraphically-uncertain data. The global marine diversity is measured by PURDY (2008) per stages only. For direct comparison of our regional biodiversity curve with that published by PURDY (2008), the palaeontological data from the Eastern Caucasus were arranged and re-calculated so to show stage-by-stage dynamics. We do not involve the rates of originations and extinctions in this study, because only appearances and disappearances are possible to be established in every regional fossil record. Probabilistic approach, which permits to solve this problem (e.g., RUBAN & VAN LOON 2008), is available, but it does not permit to reveal the true extinction rate, which can be compared with the global rate measured by PURDY (2008).

Although an analysis of marine biodiversity dynamics at the level of species is always informative, the present study focuses on genera because of two main reasons. Firstly, regional dynamics is brought in comparison with global trends, and assessment of the latter is restricted to genera (ALROY *et al.* 2008; PURDY 2008). Secondly, palaeontological data generated in the former USSR are often better justified at the level of genera, which favours an analysis of generic, not species diversity (RUBAN, 2011).

Results

Marine biodiversity dynamics

In the Eastern Caucasus, the generic diversity as monitored by this study (expressed by the total number of genera: cephalopods, brachiopods, gastropods, corals and echinoids; see Appendix 1) fluctuated strongly during the Late Cretaceous (Fig. 2). It rose weakly during the early-middle Cenomanian, then dropped by ~2/3 through the late Cenomanian-late Turonian, but rose again in the early Coniacian. A new abrupt biodiversity decline (by about half) occurred in the early Santonian and then continued gradually, but weakly until the end of the Campanian. A biotic radiation took place in the early Maastrichtian to be followed by a decline in the late Maastrichtian. These results indicate significant diversity disruptions that the regional macroinvertebrate assemblages experienced during the late Cenomanian-late Turonian, the early Santonian-late Campanian and the late Maastrichtian.

Available data (Appendix 1) permit to evaluate the influence of the three above-mentioned diversity minima on the particular fossil groups (Fig. 3). The late Cenomanian–late Turonian event affected corals, cephalopods, and gastropods, whereas echinoids were weakly influenced. The early Santonian–late Campanian event stressed brachiopods, corals, cephalopods, and gastropods. Representing a unique exception, the echinoids even radiated gradually during the entire late Turonian–early Campanian time interval. The late Maastrichtian event affected brachiopods and echinoids. Cephalopods apparently survived this crisis without suffering any stress, i.e., their total diversity didn't change. Conclusively, all three events have in common that they affected several groups of macroinvertebrates, but not necessarily the same groups every time. Each event was characterized by a certain degree of selectivity. Moreover, some groups of fossils declined at different rates through time; e.g., the total diversity of cephalopods dropped gradually already since the middle Cenomanian, whereas demise of corals at the late Cenomanian–early Turonian transition was abrupt. From three noted diversity minima, that early Santonian–late Campanian disruption had especially dramatic consequences on regional marine macroinvertebrates. Two groups, namely corals and gastropods, disappeared completely from the regional Cretaceous record, whereas brachiopods declined strongly to never recover completely.

Regional versus global patterns

The regional changes in the marine biodiversity can be compared to global data shown in Fig. 4. The global marine biodiversity reached a relatively high level in the Cenomanian, but dropped by about 10% in the Turonian and remained diminished until the Santonian, when its gradual, but pronounced acceleration began to reach a diversity peak in the Maastrichtian (PURDY 2008). This biodiversity dynamics differed strongly from that established in the Eastern Caucasus (Fig. 4) with two exceptions. Both regionally and globally, the Turonian appears to be characterized by a diminished marine biodiversity. If so, we need to consider not only short-term (e.g., LECKIE *et al.* 2002), but also possible long-term consequences from the C/T event on both regional and global scales. The other possible exception concerns the Maastrichtian, when marine biodiversity was high both regionally and globally.

Discussion

Interpretations of biodiversity dynamics

Our results (Fig. 3) demonstrate that the changes in total diversity of the studied fossil groups exhibit

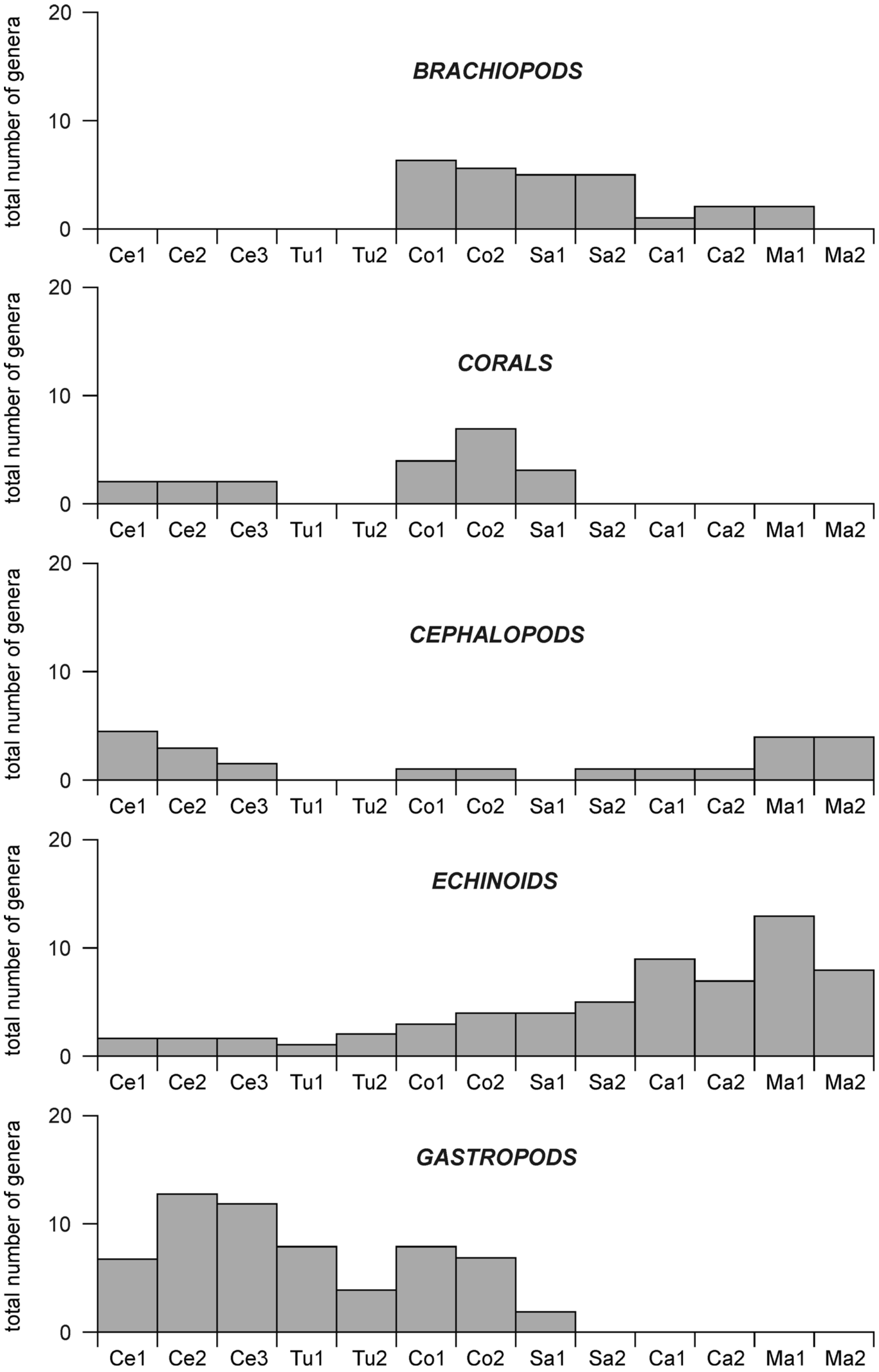

Fig. 3. Changes in the total number of genera of particular fossil groups in the Eastern Caucasus (Azerbaijan) during the Late Cretaceous. See Fig. 2 for stage abbreviations.

some more or less common pattern, which does not permit to judge the cumulative diversity of macroinvertebrates as haphazard (Fig. 2). In contrast, this cumulative diversity reflects the more or less true dynamics of the entire marine ecosystems in the Eastern Caucasus.

The main recognized events are three diversity maxima (middle Cenomanian, late Coniacian and early Maastrichtian) and three minima (late Cenomanian-late Turonian, the early Santonian-late Campanian and the late Maastrichtian). Interestingly, it remains unclear which of these events were unusual, i.e., what of them reflected the "normal" biodiversity and what reflected deviations from this norm. E.g., it is possible that the Coniacian and the early Maastrichtian diversity peaks were unusual events, which were superimposed on the constant and relatively low diversity that persisted during the Turonian–Maastrichtian. If so, the early Santonian–late Campanian and late Maastrichtian minima represent neither diversity disruptions nor biotic crises. In other words, the Late Cretaceous evolution of marine invertebrates in the Eastern Caucasus could have been marked by few spontaneous radiations, not diversity drops.

The biotic signature of the C/T event seems to appear both, globally and regionally as a diversity minimum in the Turonian. The two other events registered in the Eastern Caucasus, namely the early Santonian-late Campanian and the late Maastrichtian diversity minimums (Fig. 2), are not reflected by the global curve (Fig. 4). In the case of the late Maastrichtian, however, this discrepancy can be explained by the low-resolution of the curve given by Purdy (2008). If the Coniacian and early Maastrichtian diversity peaks were regionally-specific unusual events, which can be omitted from comparison, the noted discrepancy between the regional and global records is not something unexpected.

However, analogs of the early Santonian-late Campanian and late Maastrichtian regional biotic crises can be traced with some other geological data, if they cannot be established with the global biodiversity curve of Purdy (2008). The regionally-documented early Santonian-late Campanian biotic crisis might have been linked to the OAE3 event recognized in some other regions (ARTHUR & SCHLANGER 1979; JENKYNS 1980; ARTHUR *et al.* 1990; JENKYNS *et al.* 1994; REY *et al.* 2004; WAGNER *et al.* 2004; TAKASHIMA *et al.* 2006; JONES *et al.* 2007) and left some imprint on marine organisms (e.g., PREMOLI SILVA & SLITER 1999, TOSHIMITSU & HIRANO 2000; TAKAHASHI 2005). But both, duration and global extent of the OAE3 itself remain questionable, which precludes us from drawing any definite conclusion about its signature in the Eastern Caucasus. Similarly, we are not aware of any supporting evidence (either geochemical or lithological) of significant oxygen depletion at the Coniacian-Santonian transition in the study area. On the other hand, if the OAE3 was a global event affecting the marine biota, the biodiversity loss in the Eastern Caucasus was quite likely related to this event. Furthermore, the presence of the Coniacian/Santonian disruption in the marine ecosystems in the Eastern Caucasus region could be interpreted towards a broader extent of the OAE3 event. However, all above-said is valid only, if the early Santonian-late Campanian biotic crisis was a true event. If it was just apparent (see above), none regional evidence of the OAE3 should be hypothesized.

Considering the regionally-reported late Maastrichtian biodiversity minimum, it should be noted that KELLER (2008) suggested the diversity of marine species reached its maximum during the mid-Maastrichtian to be followed by stress started ~ 400 kyr before the end of the Cretaceous. If so, the reduction in macroinvertebrate diversity during the late Maastrichtian (Fig. 2) in fact can be an only regional phenomenon traced in the Eastern Caucasus.

One may hypothesize that the observed biodiversity dynamics, both regional and global, is influenced by the chosen stratigraphic scale. In other words, the stages with longer time duration may exhibit an apparent higher diversity. A comparison of the absolute length of stages with changes in diversity (Fig. 4) does not indicate any dependence. The regional diversity peak occurred in the stage with the shortest duration (Coniacian), whereas the global diversity also peaked in the relatively short stages (e.g., Maastrichtian). Thus, the chosen stratigraphic scale seems not to have a biasing affect on the biodiversity results here.

The documented diversity minima may be interpreted as the true expressions of regional biotic crises. However, it needs to be considered that every set of regional palaeontological data is incomplete because of interruptions of the fossil record (so-called 'Lazarus effect' - see RUBAN & VAN LOON 2008). Temporal disappearance of genera because of migrations, changes in the preservation state, etc. might have caused those total diversity minima mentioned above. Our data (Appendix 1) indicate that ranges of only two genera were temporally interrupted at the time of the late Cenomanian-late Turonian diversity minimum, whereas 6 interruptions were found at a time of the early Santonian-late Campanian diversity minimum. In both cases, however, this incompleteness is not so significant to postulate the minima were just apparent because of pseudoextinctions. We can just point out that the early Santonian-late Campanian biotic crisis was more affected by the state of the regional fossil record than that during the late Cenomanian-late Turonian.

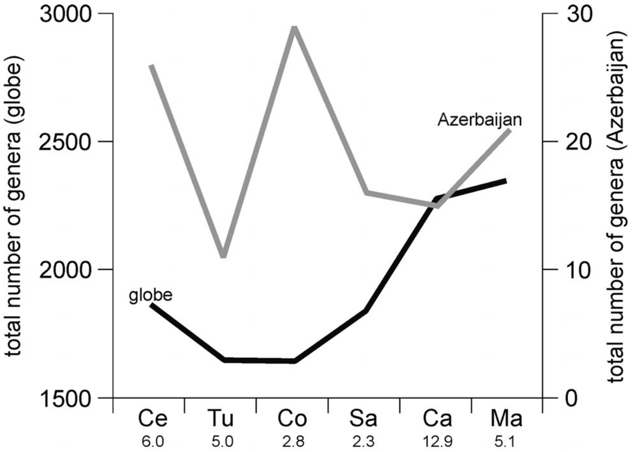

Fig. 4. Dynamics of the Late Cretaceous global (after PURDY 2008) and regional (Azerbaijan, this study) marine biodiversity calculated per stage. See Fig. 2 for stage abbreviations. Numbers given below the stage abbreviations on the horizontal axis indicate the absolute duration (in Ma) of the stages (calculated on the basis of OGG *et al.* 2008).

Possible factors of biodiversity dynamics

Our results raise the question about the factors, which drove the diversity of marine macroinvertebrates in the Eastern Caucasus throughout the Late Cretaceous and triggered the documented biotic events. We consider oceanic anoxia, seawater palaeotemperature changes and shoreline shifts as possible environmental controls on biodiversity dynamics. Regional patterns, which coincide with global ones, may be explained by the possible influence of global mechanisms like oceanic anoxia. This does not mean, however, that only global influences were a driving force. In contrast, they interacted with regional factors such as seawater palaeotemperature changes and shoreline shifts.

Although detailed geochemical studies of the Cenomanian-Turonian transition in Azerbaijan still need to be done, black shales, which bear an evidence of synsedimentary oxygen depletion, are locally reported from this transition (e.g., ALI-ZADEH 1988). Additionally, black organic-rich laminated marlstones that reveal total organic carbon concentrations (TOC) of up to 12% and a stable carbon isotopic excursion with a magnitude of about 5.6 ‰ ($\delta^{13}C_{org}$) are reported from the Cenomanian-Turonian transition of Mountainous Dagestan, i.e., northward of Azerbaijan (Tur *et al.* 2001; Gavrilov *et al.* 2009). At least, the local presence of C/T-black shales in Azerbaijan and Mountainous Dagestan suggests that marine oxygen depletion related to the global OAE2 might have stressed macroinvertebrate communities and triggered their collapse, which resulted in the minimal diversity during the Turonian. A pioneering bottom seawater palaeotemperature study by Jasamanov (1978) employed stable oxygen isotopes ($\delta^{18}O$) and Ca/Mg methods that permit to reconstruct the regional changes in seawater temperature on the basis of benthic organisms during the Late Cretaceous (Fig. 5). It should be noted, however, that any absolute palaeotemperatures reconstructed based on oxygen isotope palaeothermometry face a wide range of uncertainties potentially associated with such techniques (e.g., Longinelli 1996, pers. comm.; Leckie *et al.* 2002; Voigt *et al.* 2004; Wilson *et al.* 2002; Forster *et al.* 2007b). Generally, no definite relationship between the changes in seawater temperatures and macroinvertebrate diversity is observed here for the Eastern Caucasus region. The high total number of genera in the Cenomanian and the Coniacian as well as the low number of genera in the Santonian-Campanian (Fig. 2) corresponded to the relatively cool state of water masses (Fig. 5). The low total number of genera in the Turonian (Fig. 2) occurred at a warmer episode (Fig. 5). This is in some agreement with a suggestion by Keller (2008), who implied that Late Cretaceous biodiversity increased in a cool climate. Although it is self-evident that bottom seawater temperatures might have been more important for benthic organisms, our results on particular fossil groups do not confirm this assumption (Figs. 3 and 5). Diversity of benthic organisms changed with no relations to changes in the bottom seawater temperatures.

Interestingly, both, the global and regional biotic crisis, which followed the C/T boundary, coincided with a warming episode. Acceleration in temperatures at the time of the OAE2 is known not only in the Eastern Caucasus (Jasamanov 1978), but also in the subtropical proto-North Atlantic ocean (e.g., Huber *et al.* 1999; Kuhnt *et al.* 2005; Forster *et al.* 2007a, b), the north European midlatidude shelf seas (e.g., Jenkyns *et al.* 1994; Voigt *et al.* 2004, 2006) and the midlatidudes of the Southern Ocean (e.g., Huber *et al.* 1995; Clarke & Jenkyns 1999). According to various existing long-time Late Cretaceous palaeotemperature records, the relative palaeotemperature maximum corresponds to the Turonian stage (Cretaceous thermal maximum sensu Wilson *et al.* 2002). Nevertheless, evidence for intermittent cooler intervals exists even during this interval of extended global warmth (i.e., during the mid-Turonian: e.g., Clarke & Jenkyns 1999; Forster *et al.* 2007b; Bornemann *et al.* 2008; Sinninghe Damsté *et al.* 2010). Therefore, it appears likely that even the most elevated Cretaceous sea temperatures as recorded during the Turonian stage may not have been prevailing and, thus, these high temperatures were probably not the only underlying cause for the general marine biodiversity decline. More high-resolution palaeotemperature studies in Azerbaijan are necessary to evaluate this consideration on a regional scale.

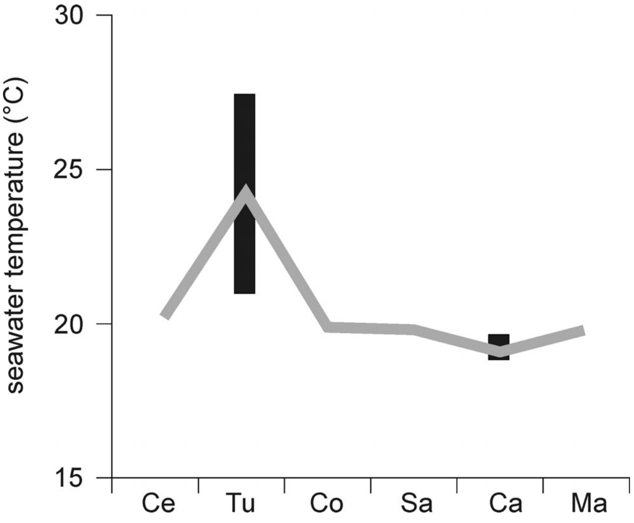

Fig. 5. Changes in the bottom seawater palaeotemperatures in the Eastern Caucasus during the Late Cretaceous. Deduced from Jasamanov (1978). Black bars indicate palaeotemperature ranges observed within the Eastern Caucasus for the Turonian and Campanian stages. See Fig. 2 for stage abbreviations.

When discussing the regional record, shoreline shifts, which are corresponding to transgressions and regressions (sensu Catuneanu 2006), should be separated clearly from changes in basin depth (Ruban 2007). In case of the Eastern Caucasus, the available palaeogeographical reconstructions (e.g., Jasamanov 1978) suggest that both shallow- and deep-marine environments persisted on its territory throughout the Late Cretaceous. Therefore, a similar range of niches remained during the epoch. If so, changes in the basin's depth cannot be considered among main factors of the biodiversity dynamics (although indirectly they may have influenced on some palaeotemperature estimations).

The record of regional transgressions/regression remains scarce. Some information is available for the Turonian and Campanian stages, which are discussed below. The early Turonian regressive episode, which followed the latest Cenomanian transgression, is well-documented in some Peri-Tethyan regions, including the Caucasus (Jasamanov 1978; Baraboshkin *et al.*

2003). In the Lesser Caucasian counterpart of Azerbaijan, the distribution of Turonian deposits is restricted, whereas in the Greater Caucasian counterpart, a transgressive contact between Turonian and underlying upper Albian-Cenomanian deposits is traced (ALI-ZADEH 1988). Globally, the early Late Cretaceous sea level experienced changes, which are now considered as glacioeustatic by some authors (e.g., GALE *et al.* 2002; MILLER *et al.* 2005; KOCH & BRENNER 2009; GALEOTTI *et al.* 2009). The C/T event occurred during a sea-level rise, which is documented across the globe (HAQ *et al.* 1987; HALLAM & WIGNALL 1999; HAQ & AL-QAHTANI 2005; VOIGT *et al.* 2006; GROSHENY *et al.* 2008; PEARCE *et al.* 2009). HAQ & AL-QAHTANI (2005), who updated the earlier eustatic curve proposed by HAQ *et al.* (1987), imply a slight fall of the global sea-level during the Turonian, which followed its C/T highstand. The same is suggested by alternative constraints of MILLER *et al.* (2005), who indicated even a sharper eustatic fall in the Turonian relatively to the Cenomanian. ZORINA *et al.* (2008) report a global concentration of hiatuses within the Turonian sedimentary successions. Thus, there is clear evidence of eustatic lowstand during the Turonian after the latest Cenomanian highstand. This is in line with the sea level history observed in the Eastern Caucasus (see above), and also consistent with the regional and global marine biodiversity dynamics (Fig. 4). The Campanian transgression is another regionally-documented feature (JASAMANOV 1978). The global curves presented by HAQ & AL-QAHTANI (2005) and MILLER *et al.* (2005) propose a different history of the sea level during this stage. The former authors depict a rise followed by a highstand. If so, the eustatic mechanism of the regional transgression in the Eastern Caucasus should be considered. MILLER *et al.* (2005) depict a highstand followed by a stepwise fall. In this case, the regional shoreline shifts would not reflect global influences. Interestingly, the Campanian diversity of marine invertebrates declined in the Eastern Caucasus, but rose globally (Fig. 4). This dissimilarity is in good agreement with the difference between regional shoreline shift and the eustatic change documented by MILLER *et al.* (2005), although this does not clarify the links between diversity and shoreline shifts. Anyway, despite of the above-made observations, it is too early to tell about any direct relationships between marine biodiversity and eustatically-driven shoreline shifts.

Differences between the conventional (PURDY 2008) and modelled (sample-standardized) (ALROY *et al.* 2008) global biodiversity curves indicate a wide range of possible errors in quantitative assessments of the fossil record. GALE *et al.* (2000) and SMITH *et al.* (2001) question the completeness of palaeontological data relevant to the Cenomanian-Turonian transition. It is possible that huge facies shifts as well as hiatuses were able to produce significant biases in the fossil record, both regionally and globally. If this is true, not shoreline motions themselves, but the relevant changes in the habitats and preservation of the fossil organisms should be considered as important controls on the regional biodiversity dynamics.

Comparison with the available foraminiferal record

Foraminiferal assemblages were very sensitive to the C/T event (e.g., JARVIS *et al.* 1988 a,b; KAIHO & HASEGAWA 1994; LAMOLDA & PERYT 1995; PERYT & LAMOLDA 1996; ULIČNY *et al.* 1997; HASEGAWA 1999; PAUL *et al.* 1999; PREMOLI SILVA *et al.* 1999; AGUILERA-FRANCO *et al.* 2001; KELLER *et al.* 2001; DESMARES *et al.* 2004; COCCIONI & LUCIANI 2005; GROSHENY *et al.* 2006; FRIEDRICH *et al.* 2006; KELLER *et al.* 2008). Two regional datasets on foraminiferal distributions in the Upper Cretaceous deposits of the Eastern Caucasus are available. The first one compiled by ALI-ZADEH (1988) permits to outline stratigraphic ranges of 36 genera from Azerbaijan, whereas the other one compiled by SAMYSHKINA (1983) allows to delineate stratigraphic ranges of 73 genera from Mountainous Dagestan. These regional micropalaeontological data are important for this study because of two main reasons. First, the current paper discusses the utility of the available (i.e., published) data for palaeobiodiversity studies. If so, each available dataset should be examined in order to understand its possible importance. Second, even invalid datasets may reveal some interesting patterns, especially with regard to the regional signature of bio-events.

In our view, the foraminiferal data from the Eastern Caucasus require a certain (if not significant) correction. For example, *Rotalipora* and other rotaliporids should not be reported from the Turonian because these taxa were disappearing during the C/T event before the uppermost Cenomanian (CARON 1985; ROBASZYNSKI & CARON 1995). However, it is not excluded that minor inaccuracies exist in the regional biostratigraphic framework (cf. RUBAN, 2003b). This should not affect significantly the stage-by-stage examination of the whole marine biodiversity, but may lead to deviation of particular taxa ranges. Similarly, as documented by SAMYSHKINA (1983), the assemblages of the different species of *Globotruncana* are, at the earlier, characteristics of Santonian (CARON, 1985; ROBASZYNSKI & CARON, 1995), but they should not be identified in Turonian as reported in her study of this region (SAMYSHKINA, 1983). Moreover, *Rugoglobigerina* should not be commonly found prior the Campanian (even if the appearance of some *Rugoglobigerina* yet in the Santonian as suggested by some new unpublished data cannot be fully excluded). This contradiction could be explained here by a taxonomic uncertainty. Indeed, the species of

Rugoglobigerina are described here as intermediate forms between *Archaeoglobigerina* and *Rugoglobigerina*, and the former can be identified in the Turonian. Thus, these, as those which are regrouped in *Globotruncana*, need taxonomic reassignment. As an other example, in the works of Samyshkina (1983) and Ali-zadeh (1988), Turonian species of *Globotruncana* are now classified in *Marginotruncana*. These discrepancies restrict the utility of foraminiferal data from the Eastern Caucasus. Its deep revision, if it is possible, may lead to changes in taxa ranges and, thus, somewhat different diversity patterns. However, as warned above, minor stratigraphic inaccuracies should also be considered.

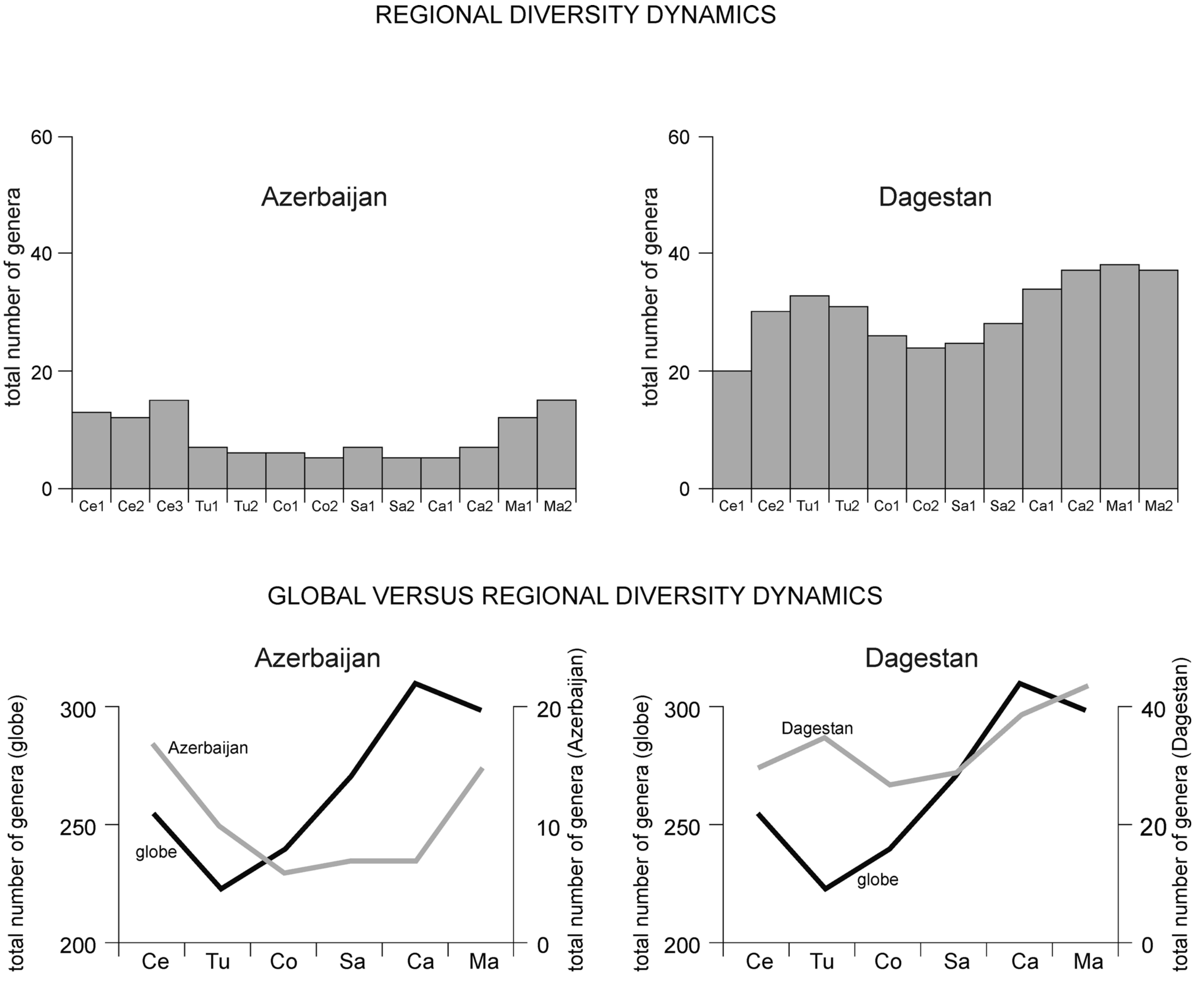

Fig. 6. Regional versus global foraminiferal diversity. Upper graphs: regionally differentiated dynamics of the Late Cretaceous foraminiferal diversity in the Eastern Caucasus. Lower graphs: regional diversity dynamics normalized per stage in comparison with global diversity dynamics (after Tappan & Loeblich 1988). See Fig. 2 for stage abbreviations. Note that only a two-folded subdivision of the Cenomanian stage is implemented in Mountainous Dagestan (upper right: Ce1 and Ce2).

Thus, the micropalaeontological records available from both Azerbaijan and Dagestan are semi-valid, but not invalid. The lack of validity, however, may explain differences in Late Cretaceous diversity dynamics of marine macroinvertebrates and foraminifers (Figs. 4 and 6) as well as differences between regional and global foraminiferal diversity changes (Fig. 6). It is worth to note that global changes in the number of genera of marine invertebrates recorded by Purdy (2008) and foraminifers recorded by Tappan & Loeblich (1988) coincided pretty well (Figs. 4 and 6). Such coherence proves indirectly an idea that deficiencies of micropalaeontological data from the Eastern Caucasus explain the above-mentioned differences. However, the total generic diversity of foraminifers declined both globally and in Azerbaijan.

Conclusions

In the Eastern Caucasus, marine macroinvertebrates experienced losses in the total generic diversity during the late Cenomanian-late Turonian, the early Santonian-late Campanian, and the late Maastrichtian, some of which may be judged regional imprints of global events. There is strong evidence of a regional biotic signature of the C/T event, which stressed corals, cephalopods, and gastropods. With respect to this regionally-documented event, regional and global patterns of long-term marine biodiversity changes match well. The causes of this event may be linked with oxygen depletion (OAE2) and eustatic fluctuations. Available information on foraminifers only provides a very unclear evidence of the C/T event within the study region. The Santonian-Campanian diversity minimum as documented by our study poses another intriguing question about the spatial extent of the palaeoenvironmental perturbations linked to the OAE3 event. It cannot be excluded that impact of the latter event on marine ecosystems still remains underestimated. However, the noted regional minimum can be just apparent and explained by location on the graph (Fig. 2) between short-term radiations in the Coniacian and the early Maastrichtian. Both, the global and regional palaeoenviromenal changes might have been important controls on biodiversity changes. In particular, an importance of the OAE2 for the Turonian diversity decline is recognized both in the Eastern Caucasus and on the global scale.

The results presented in this paper emphasize that regional tracing of signatures of potentially-global events is a powerful tool to test their consistency. This is important, particularly, with regard to the biotic effect of OAE2, whose global extent was recently questioned (WESTERMANN *et al.* 2010). On a regional scale, further geochemical exploration at the C/T boundary interval as well as palaeotemperature and sea-level studies are urgently needed in order to unravel the controls on the regional marine biodiversity dynamics. Another task for future studies is an explanation of the Coniacian and early Maastrichtian diversity peaks. This will permit to realize whether these two were unusual events, and, thus, whether the early Santonian–late Campanian and late Maastrichtian diversity minima do not indicate true crises.

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Appendix 1. Late Cretaceous genera of macroinvertebrates from Azerbaijan (compiled from ALI-ZADEH 1988). See Fig. 2 for stage abbreviations

GENERA	Ce1	Ce2	Ce3	Tu1	Tu2	Co1	Co2	Sa1	Sa2	Ca1	Ca2	Ma1	Ma2
Brachiopods													
Basiliola											×	×	
Bolgarithyris						×	×	×	×				
Concinnithyris						×	×	×	×				
Cretirhynchia						×	×	×	×				
Cyclothyris						×	×	×	×				
Kingena						?	?						
Najdinothyris						×	×			×	×	×	
Orbirhynchia						×							
Ornathothyris								×	×				
Corals													
Actinastraea						×	×						
Agathella								×					
Astrogyra								×					
Aulosmilia						×	×						
Conicosmilotrochus	×	×	×										
Cunnolites							×						
Dimorphastraea							×						
Felixyra	×	×	×										
Fungiastraea							×						
Meandrosmilia								×					
Placocoenia						×	×						
Vallimeandra						×	×						
Cephalopods													
Acanthoceras	?	×	?										
Baculites						×	×						
Belemnella												×	×
Belemnitella									×	×	×		
Diplomoceras												×	×
Neohibolites	×	×											
Pachydiscus													
Parahibolites	×											×	×
Pseudokossmaticeras												×	×
Puzosia	×	×	×										
Schloenbachia	×												
Echinoids													
Cardiaster							×					×	
Catopygus	?	?	?									×	
Conulus	?	?	?	×	×	×	×		×	×		×	×
Coraster										×	×		
Echinocorys						×		×	×	×	×	×	×
Galeaster												×	
Galeola										×			
Galerites												×	×

GENERA	Ce1	Ce2	Ce3	Tu1	Tu2	Co1	Co2	Sa1	Sa2	Ca1	Ca2	Ma1	Ma2
Echinoids													
Guettaria											×	×	
Hemipneustes													×
Holaster	?	?	?										
Holectypus	?	?	?										
Homoeaster												×	×
Isomicraster								×	×	×		×	
Isopneustes													×
Micraster					×	×	×			×	×		
Ornithaster											×		
Peronaster										×			
Phymosoma								×	×				
Plesiocorys							×						
Pseudopyrina								×	×				
Pseudoffaster										×	×	×	
Pygurus	?	?	?										
Rachiosoma												×	
Seunaster										×		×	×
Stegaster												×	×
Turanglaster											×		
Gastropods													
Actaeon	×	×	×										
Actaeonella	×	×	×	×	×	×	×						
Ampullospira		×	×			×	×						
Dalmatea		×	×	×									
Eotrochactaeon	×	×	×										
Glauconiella						×	×						
Gymnentoma		×	×	×	×	×	×						
Haploptyxis						×	×						
Helicaulax					×	×							
Itruvia		×	×	×									
Jaccardiella	×	×											
Neoptyxis	×	×	×										
Nerinella		×	×										
Oligoptyxis		×	×	×									
Omphaloactaonella		×	×	×									
Parasimploptyxis							×	×					
Plesioplocus	×												
Pseudomesalla	×	×	×	×									
Simploptyx													
Trajanella						×							
Trochactaeon				×	×	×	×						

×- presence, ? - possible presence

Резиме

Горњокредна динамика морског биодиверзитета Источног Кавказа, северни Нео-Тетиски океан: регионалне промене узроковане глобалним догађајима

За време горње креде долази до значајне промене у биодиверзитету морских организама. Општи еволуциони трендови били су проузроковани специфичним догадјајима.

Граница ценоман/турон (93,6 Ma), која вероватно указују на горњу границу средњокредне серије, је период који се карактерисао израженим променама средине на читавој планети. Интезивне промене и изумирање појединих морских организама, океански аноксични догађај и повећање вулканске активности значајно се одразило на фосилне, седиментационе и геохемијска податке. Обим и јачина биотских криза близу границе ценоман/турон још увек су дискутабилни. И ако већи део података којима се располаже потиче из подручја Медитерана, Енглеске и Јапана, палеонтолошки подаци, многих потенцијално значајних региона, још увек нису довољно проучени. Источни Кавказ, би могао да буде регион од палеоеколошког значаја због његове специфичне палеопозиције на северној маргини Нео-Тетиског океана, између Алпских структура Европе и терана Средњег Истока, и с обзиром на то да показује репрезентативну горњокредну сукцесију са документованим распрострањењем разноврсне фауне морских макробескичмењака. Овом приликом приказано је стратиграфско распрострањење 80 родова морских макробескичмењака горњокредних седимената Азербејџана. Анализиране фосилне групе укључују (број родова): цефалоподе (11), брахиоподе (9), гастроподе (21), корале (12) и ехиниде (27). За време горње креде у Источном Кавказу разноврсност родова је била јако изражена. Током доњег и средњег ценомана долазо до благог пораста разноврсности која затим опада за 2/3 за време горњег ценомана–горњег турона, да би опет дошло до пораста у горњем конијаку. У доњем сантону долази до следећег наглог опадања у биодиверзиту (за око половину) и овај тренд се постепено наставља све до краја кампана. У доњем мастрихту долази поново до биотске радијације, да би у горњем мастрихту уследило њено опадање. Горњоценомански-доњотуронски догађај утицали су на корале, цефалоподе и гастроподе, док су ехиниди били мање угрожени. Доњосантонски-горњокапмански догађаји били су неповољни за брахиоподе, корале, цефалоподе и гастроподе. Једини изузетак представљају ехиниди чија се разноврсност постепено повећава за време целог горњег турона и доњег кампана. Горњомастрихтски догађај утиче на брахиоподе и ехиниде. Цефалоподи очигледно преживљавају ову кризу без икаквих последица, тј. њихов укупан диверзитет није се променио. Заједничко за поменуте догађаје јесте да су били неповољни за неколико група макробескичмењака, мада то нису биле сваки пут исте групе. Глобална динамика биодиверзитета се разликовала од динамике која се дешавала у Источном Кавказу.

Добијени резултати показују да су промене у укупном диверзитету проучаваних фосилних група одвијале по мање или више заједничким образцима, што указује на то да промене које су довеле до велике разноврсности макробескичмењака нису никако биле случајност. Најзначајнији догађаји су довели до три максимума (средњи ценоман, горњи конијак и доњи мастрихт) и три минимума (горњи ценоман–горњи турон, доњи сантон–горњи кампан и горњи мастрихт) у њиховом диверзитету. Значајни догађаји који су се десили током ценомана и турона довели су до појаве минимума у диверзитету током турона, и то како глобално тако и регионално. Диверзитетски минимум који се догађао током сантона и кампана, а који је документован нашом студијом, указује на суштинско питање које се односи на промене у распореду палеосредина и њихове повезаности са ОАЕ3 догађајем. Међутим, запажени регионални мимимум може бити објашњен краткотрајном радијацијом у конијаку и доњем мастрихту. Смањење диверзитета у оквиру макробескичмењака за време горњег мастрихта може у ствари бити само регионални феномен забележен у Источном Кавказу. Глобалне и регионалне промене палеосредина имале су јак утицај на промене биодиверзитета. Значај океанског аноксичног догађаја 2 за опадање туронског диверзитета је утврђен како у Источном Кавказу као тако и на глобалном нивоу. Резултати рада указују да праћење регионалних промена које су проузроковане потенцијално глобалним догађајима могу бити од изузетног значаја при провери њихове конзистенције.