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Diversity changes of the Brachiopods in the Northern Caucasus: a brief overview

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The diversity of the brachiopods in the Northern Caucasus significantly fluctuated throughout the Paleozoic-Mesozoic. Weak diversifications occurred in the Middle Cambrian, Late Silurian – Early Devonian, and Late Devonian – Early Carboniferous. Since the Late Permian brachiopod assemblages became quite diverse. The maximum number of species was reached in the Rhaetian. The Permian/Triassic mass extinction and enigmatic Ladinian crisis, on the other hand, led to regional brachiopod demises. In the Jurassic – Early Cretaceous interval the diversity of brachiopods generally decreased. The strongest drops of species numbers occurred in the Toarcian and Berriasian following the Pliensbachian–Toarcian and end-Jurassic global mass extinctions, and in the Kimmeridgian due to the regional salinity crisis. It is evident that some of the regional brachiopod diversifications coincided with the development of rimmed shelves.

Key words: brachiopods, diversity, mass extinctions, reefs, Paleozoic, Mesozoic, Caucasus

Introduction

Global and regional diversity changes of the brachiopods have been discussed in numerous publications (Hallam 1987; Vörös 1995; Sulser 1996; Racki 1998; Alvarez and Modzalevskaya 2001; Harper and Rong 2001; Rong and Shen 2002). This fossil group has developed in high diversity during the Phanerozoic overall and seems to be one of the most important in the paleontological record.

This article is devoted to the brachiopods known from the Paleozoic and Mesozoic deposits of the Northern Caucasus (Fig. 1). Their diversity changes

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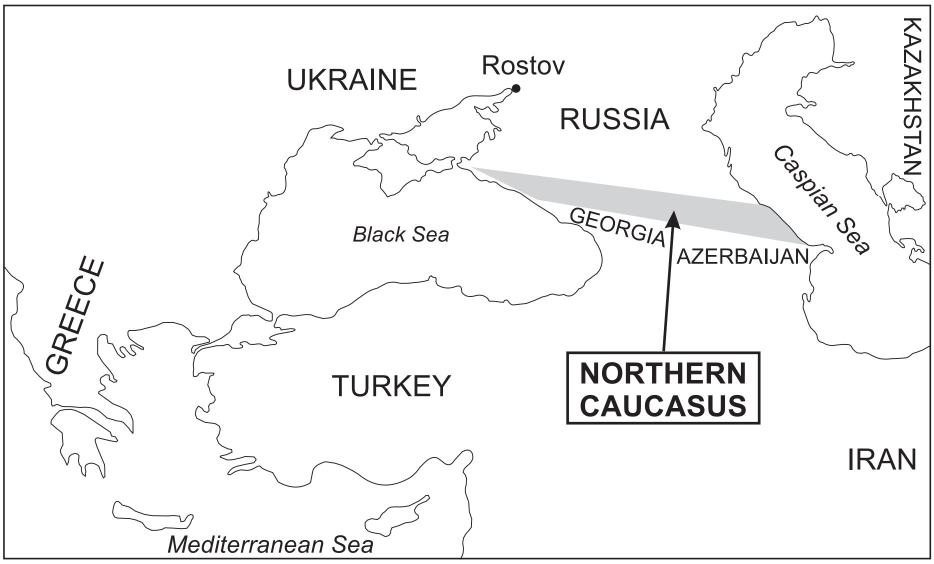

Fig. 1
Geographical location of the Northern Caucasus

have never been discussed before, except for the Jurassic as reviewed by Ruban (2003, 2004a). A comparison between the global and local Caucasian events shows some interesting results.

Stratigraphic setting

According to the paleotectonic reconstructions by Stampfli and Borel (2002) and Scotese (2004), the Northern Caucasus was located on the active northern Paleotethyan and then Neotethyan margin. A thick sedimentary succession was accumulated there during the Paleozoic–Mesozoic (Fig. 2). The Paleozoic deposits are exposed in the central part of the studied region, while the Triassic strata crop out in its western part. The Jurassic–Cretaceous sediments are distributed widely within the entire Northern Caucasus.

During the Early–Middle Paleozoic, deposition of clastics and shale occurred. A major regional hiatus embraced the Ordovician. Episodes of carbonate sedimentation took place in the Middle Cambrian, late Silurian and Late Devonian. Volcanics and volcanoclastics are common in the sedimentary succession, especially in the Devonian. Non-marine deposition dominated in the Pennsylvanian–Middle Permian. Carbonates were accumulated in the end-Permian, and an episode of reef growth is known from the Late Changhsingian.

During the Early Triassic–Anisian interval, carbonate deposition dominated, while accumulation of clastics and shale prevailed in the Ladinian–Carnian. Carbonate deposition and reef growth characterized the Norian–Early Rhaetian.

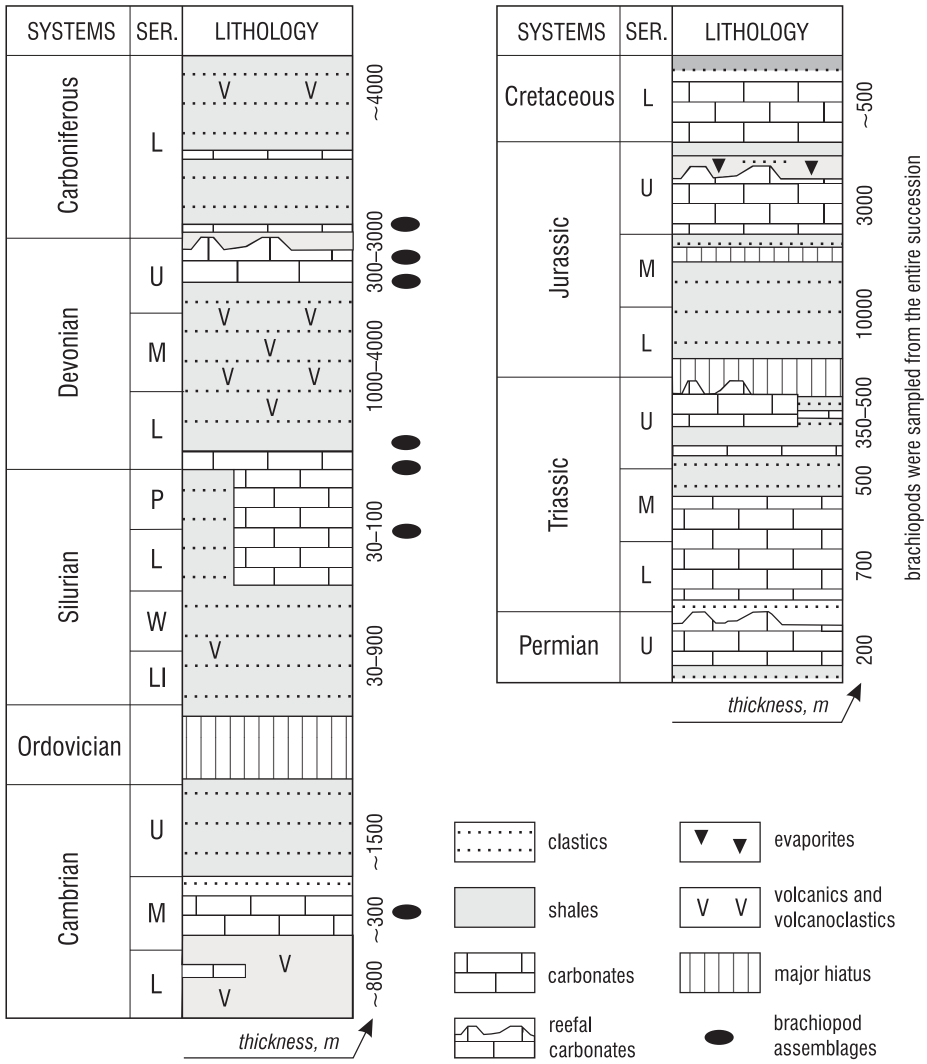

Fig. 2
A generalized lithologic section of the Paleozoic–Mesozoic of the Northern Caucasus

A major regional hiatus spans the latest Triassic–earliest Jurassic. Until the Bathonian, deposition of clastics and shale was common in the Northern Caucasus, while after the Bathonian hiatus, ie., in the Callovian, a large carbonate platform appeared (Kuznetsov 1993; Ruban 2005). The regional salinity crisis, introduced by Ruban (2006), led to the deposition of evaporites together with "color-beds" and red-beds in the Late Jurassic. Carbonate sedimentation was restored in the latest Jurassic and dominated during the Early Cretaceous. In the Aptian-Albian clastics and shale were deposited.

Materials and methods

To obtain as much information on stratigraphic distribution of the brachiopods as possible a data compilation from different sources was attempted. These sources are cited below.

Cambrian: Paffengol'ts (1959, 1965), Tchernysheva (1968); Silurian: Obut et al. (1988); Devonian: Rzhosnitskaja (1968), Kizeval'ter and Robinson (1973), Zanina and Likharev (1975), Obut et al. (1988); Carboniferous: Kotlyar (1977); Permian: A.D. and K.V. Miklukho-Maklaj (1966), Likharev (1968), Kotlyar (1977), Kotlyar et al. (1999, 2004); Triassic: Dagis (1963, 1974), Dagis and Robinson (1973), Rostovtsev et al. (1979); Jurassic: Makridin and Kamyshan (1964), Rostovtsev et al. (1992), Prosorovskaya (1993a, b), Ruban (2004a); Early Cretaceous: Smirnova (1972).

Brachiopods were sampled in numerous sections and small outcrops located within the Northern Caucasus.

Finally, data of two distinct kinds have been collected. The brachiopod assemblages of the Paleozoic are poorly studied and they show little diversity (except for the Permian). The data on them are incomplete, i.e. further sampling is necessary. In some sources only the presence of the brachiopods is stated without indication of the specific taxa. Thus only a general appreciation of their diversity changes in this interval is possible, without quantitative estimates of diversity. However, to take these data into consideration seems to be useful, particularly to simplify further comparisons between the Northern Caucasus and other regions. As for the Permian, numerous brachiopod taxa were collected in the Northern Caucasus, but published sources do not contain their full lists and should be further normalized. Therefore the available data is not sufficient to estimate the Permian diversity quantitatively.

On the other hand the compiled data on the Mesozoic interval is more complete and detailed (see Appendix). Those assemblages have been well studied. This allows quantitative estimations of the diversity changes per stage to be made.

Paleozoic brachiopods

The Cambrian–Carboniferous diversity of brachiopods species in the Northern Caucasus is characterized by very low numbers. Most known brachiopod finds are restricted to the carbonate facies (Fig. 2).

Three weak diversifications have been documented in the Cambrian–Carboniferous history of brachiopods in the Northern Caucasus (Fig. 3). The first one took place in the Middle Cambrian, when *Acrotreta gerassimovi* Lermontova appeared. The global "explosion" of biodiversity occurred at the same time interval (Geyer 1998).

For the second time, brachiopods appeared in the Northern Caucasus in the Ludlow–Přidoli. Poor assemblages existed in the Lochkovian (*Cingulodermus* ex gr. *superstes* (Barrande), *Clorinda pseudolinguifera* (Kozlowski) and *Janius* ex gr.

irbitensis (Tschernyshova)) and Pragian (*Ivdelina* (*Procerulina*) ex gr. *procerula* (Barrande)) before brachiopods disappeared.

The Frasnian assemblage was also very poor. It included *Atrypa posturalica* Markowskii, *Gypidula comis* Owen, *Hypothyridina cuboides* Sowerby and *Spinatrypa* ex gr. *bifidaeformis* Tschernyshova. A radiation strengthened in the Famennian, when 11 species appeared. They are *Cyrtospirifer verneuili* (Murchison), *Cyrtospirifer* cf. *calcaratus* Sowerby, *Cyrtospirifer* cf. *archiaci* Murchison, *Cyrtospirifer* cf. *postarchiaci* Nalivkin, *Isopoma brachyptycta* (Schnur), *Productus* sp., *Productella* ex gr. *subaculeata* (Murchison), *Productella calva* var. *multispinosa* Sokolskaya, *Productella calva* var. *koscharica* Nalivkin, *Pugnax janischevskii* Rozman and *Rhipidiorhynchus* ex gr. *livonicus* Buch. The Frasnian/Famennian transition coincided with a significant change in the taxonomic composition of assemblages. In contrast to the Frasnian, assemblages with *Cyrtospirifer* and *Productella* dominated in the Famennian. In some other regions, e.g. in South China, the Famennian assemblages were also characterized by diverse cyrtospiriferids (Ma et al. 2001). In the East European Platform area, however, cyrtospiriferid-dominated communities appeared earlier – in the Late Frasnian (Sokiran 2001). One of the biggest mass extinctions, the Frasnian–Famennian event, strongly stressed brachiopods (McGhee 1996; Hallam and Wignall 1997; Racki 1998; House 2002); but in the Northern Caucasus we cannot document the patterns of this event due to the low-resolution data. In the Early Carboniferous, the poorest assemblage with a unique *Spirifer* cf. *distans* Sowerby existed. Probably the poverty of those faunas may be explained by the mass extinction that occurred at the Devonian/Carboniferous boundary (Hallam and Wignall 1997). Such a hypothetical conclusion, however, should be further verified.

After a long period of non-marine deposition in the Late Carboniferous–Middle Permian, the sea transgressed into the Northern Caucasus in the Late Permian, which reached its maximum in the Changhsingian. At the same time a strong diversification of brachiopods began. Dozens of species appeared (Kotlyar et al. 1999, 2004). However, at the Permian–Triassic transition, a significant crisis occurred. It led to the short-term but total disappearance of the brachiopods. They are absent in the deposits of the Abagskaja Formation, the age of which is established as the latermost Permian–earliermost Triassic. This event is evidently connected with the global mass extinction, which took place at this time (Hallam and Wignall 1997; Harper and Rong 2001; Erwin et al. 2002; Shen and Shi 2002).

Mesozoic diversity changes

In the Early Triassic brachiopod assemblages were of extremely low diversity. The presence of ?*Crurithyris extima* Grant 1970 (Rostovtsev et al. 1979), which is a characteristic taxon of the lowermost Triassic (Grant 1970), suggests that the repopulation of this group was initiated just after the mass extinction. A major diversification occurred in the Anisian, when a recovery after the Permian/

Triassic crisis was completed (Fig. 3). The Anisian is an important stage in the evolution of shelly benthos, when its diversity rose extraordinarily (e.g. Komatsu et al. 2004).

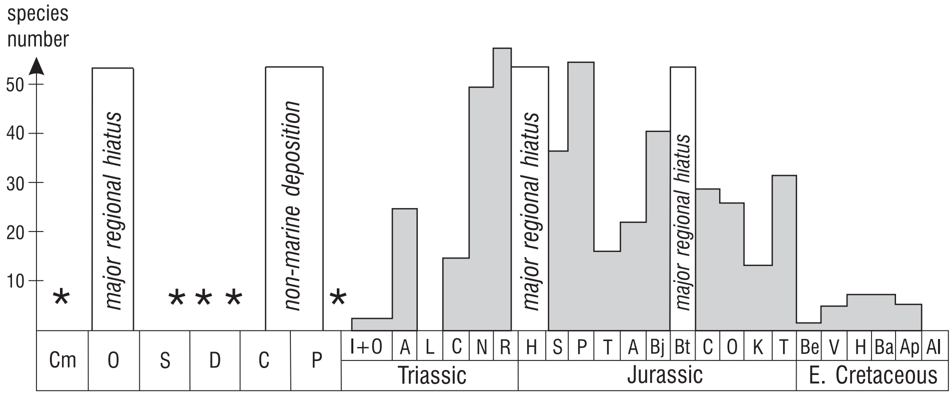

Fig. 3
Total species diversity of the Paleozoic–Mesozoic brachiopods of the Northern Caucasus. Asterisks mark quantitatively unestimated diversifications

However, brachiopods abruptly disappeared already in the Ladinian (Fig. 3). All pre-Ladinian taxa became extinct. As for other fossil groups, i.e. bivalves, ammonoids, foraminifers, they are well represented in strata of this age (Rostovtsev et al. 1979). Moreover, there are no strong differences between the Ladinian and Carnian intervals in the sedimentary succession, although the brachiopod diversity in the Carnian was high enough (Fig. 3). This suggests that differences in the diversity between the mentioned stages cannot be explained by the differences in preservation potential. The existing paleoenvironmental studies (Gaetani et al. 2005) also do not provide clear evidence about the possible causes of the enigmatic Ladinian crisis among brachiopods. In the other regions, particularly in the Alps and Jura Mountains, the Ladinian brachiopods were also not diverse, but their species number is comparable with that in the Anisian (Sulser 1999).

In the Carnian to Rhaetian, a new radiation of brachiopods took place, and by the end of this interval the diversity in the region reached its Phanerozoic high point. The most significant changes took place in the Norian, when the species quantity increased more than threefold.

After a depositional hiatus, which embraced Late Rhaetian, Hettangian and Early Sinemurian, the repopulation of brachiopods began once again. The maximum of diversity was rapidly reached in the Pliensbachian (Fig. 3). But a significant extinction occurred in the Toarcian, which corresponded to the a global event (Hallam 1986, 1987; Vörös 1995). This event was already documented in the studied region (Ruban 2004a, 2006; Ruban and Tyszka 2005).

A new increase of the species quantity continued during the Aalenian–Bajocian. The Bathonian sediments are missing due to a major regional hiatus. In the Callovian, the diversity of brachiopods was relatively high. It decreased slowly in the Oxfordian, but in the Kimmeridgian it dropped abruptly. This is possibly explained by unfavorable conditions due to increasing aridity, shalloving, and a salinity crisis in the Caucasus (Jasamanov 1978; Ruban 2006). However, brachiopods survived this crisis and rapidly recovered after it, in contrast to bivalves (Ruban 2003, 2006). Prosorovskaya (1996) stated the ability of brachiopods to radiate rapidly even during short time intervals with favorable environments.

The last significant diversification of brachiopods in the Northern Caucasus is documented in the Tithonian. A major drop in species number after this age seems to correspond with another global mass extinction, although the last one is sometimes considered to be doubtful (Hallam 1986; Hallam and Wignall 1997; Wignall 2001; Ruban 2004b).

The Early Cretaceous assemblages were very poor. A slight diversity increase is observed during the Berriasian–Hauterivian. Thereafter a similarly weak decreasing trend was established. In the Albian the brachiopod record terminates.

Discussion

The diversity changes of brachiopods in the Northern Caucasus was controlled by several factors.

The regional sea-level fluctuations have been reconstructed only for the Jurassic (Ruban 2006). A comparison between the regional sea-level changes and the brachiopod diversity during this time interval suggests that there are no direct links between them (Fig. 4). The diversity rises in the Pliensbachian and Bajocian corresponded to transgressions, while the maximum of species number in the Tithonian coincided with a regression. The Toarcian and Kimmeridgian diversity drops occurred during transgressions. Undoubtedly sea-level changes were able to influence the brachiopod diversity, while other regional factors (such as salinity crises or anoxia) were superposed on them.

It is very interesting to note that diversity maxima in the Famennian, Changhsingian, Norian-Rhaetian, and Callovian–Oxfordian corresponded to the regional development of rimmed shelves (term after Ginsburg and James, 1974; Read 1985), i.e. carbonate platforms bounded by reefs (Khain 1962; Dagis and Robinson 1973; Kuznetsov 1993; Ruban 2005). Thus, the absence of reefs in the Frasnian may explain why brachiopods were not so diverse in the Northern Caucasus as in the other regions, where Frasnian reefs were abundant (Copper 1994, 2002; Webb 1996; Droser et al. 2000; Baliński et al. 2002). Just after the appearance of reefs in the Famennian in the central part of the studied region (Fig. 2), brachiopod diversity accelerated significantly. The recent observation

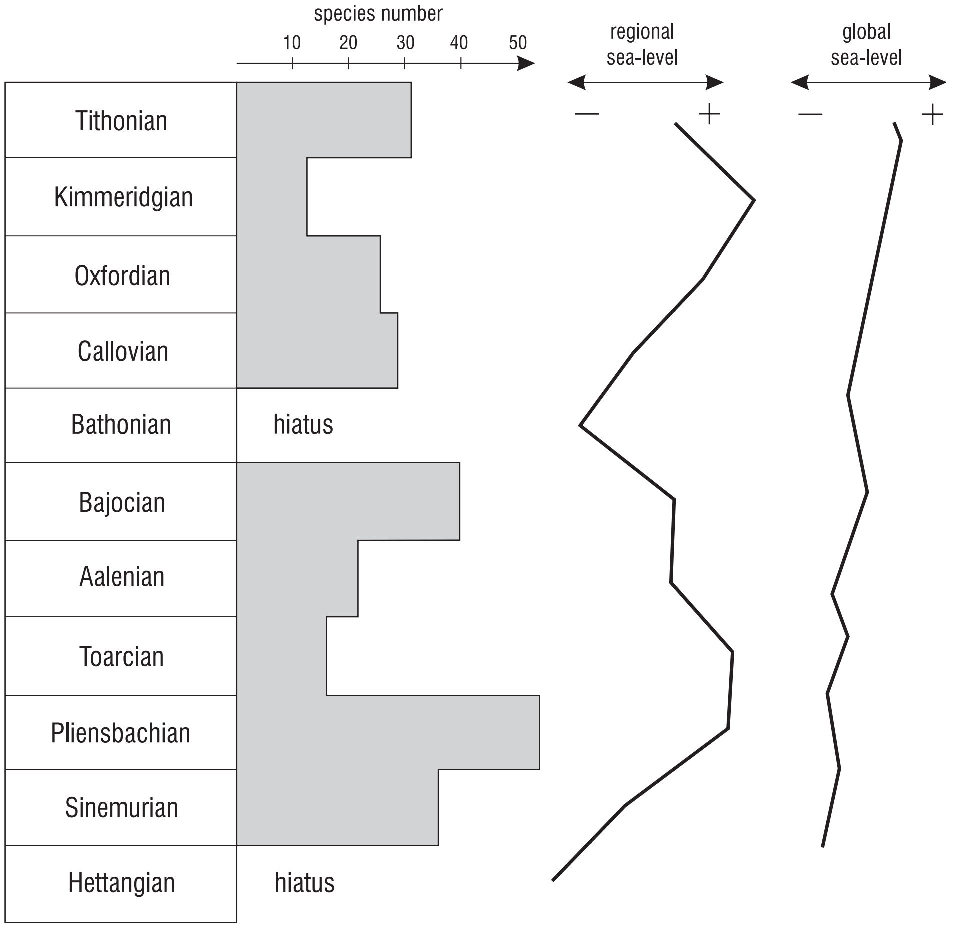

Fig. 4
Jurassic sea-level changes (after Ruban 2006) and brachiopod diversity. The global sea-level fluctuations, given for general reference, are simplified from Haq et al. (1987)

that the Famennian reefs grew spectacularly (Webb 2001, 2002; Shen and Webb 2004) may lead to significant changes in how we visualize the Late Devonian biotic crises.

Two interesting kinds of paleoenvironmental events strongly influenced the regional diversity of the brachiopods. The first is the above-mentioned regional salinity crisis, which occurred in the Kimmeridgian–Tithonian (Jasamanov 1978; Ruban 2006) and diminished the species quantity. Another phenomenon is that of oxygen-depleted conditions. Zakharov et al. (1999) explained the regional faunal crisis at the Permian–Triassic transition by anoxia. Efendiyeva and Ruban (2005) reconstructed the regional chronology of the Jurassic dysoxic and anoxic events. Dysoxic environments dominated during the entire Late Pliensbachian–Middle Aalenian, as well as the Bajocian. When oxygen depletion strengthened in the Toarcian (when anoxia occurred) brachiopod diversity dropped. Ruban (2004a, 2006) and Ruban and Tyszka (2005) also commented on the influences of the Toarcian anoxia on the Caucasian marine biota.

The regional preservation potential might have heightened our estimations of the brachiopod diversity. This is especially significant for the Paleozoic because brachiopods of that age are restricted to the carbonate facies (Fig. 4). As for the Mesozoic, it is difficult to speculate about this because of distinct facies in the each stratigraphic interval. However, high diversity, documented in the Anisian, Norian–Rhaetian and Oxfordian, corresponds to the intervals of the carbonate sedimentation. It is also very interesting to note a high diversity in the Callovian, although those deposits are strongly condensed (Ruban 2004c).

Conclusions

Summarizing the material presented above it is possible to conclude that the diversity of brachiopods in the Northern Caucasus fluctuated strongly through Cambrian–Early Cretaceous times (Fig. 3). The key points in the regional brachiopod diversity changes are located in the Famennian (first significant diversification), Late Permian (the beginning of rapid species number acceleration, followed by mass extinction), Rhaetian (the highest diversity), and in the end-Liassic (the initiation of gradual extinction).

The data should be further updated, and other diversity patterns (e.g. origination, extinction rates, etc.) need to be taken into consideration. It will be necessary to discuss the problem of the relationship of the brachiopod diversity dynamics to regional paleoenvironmental changes (not yet well established, and not dicussed completely in this paper), as well as rates of faunal immigrations/emigrations during the Paleozoic and Mesozoic. Special attention should be paid to the explanation of the Ladinian crisis among this fossil group.

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Appendix

Stratigraphic distribution of the Mesozoic brachiopods in the Northern Caucasus (see text for literature sources). Number of species of each genera in the Triassic–Lower Cretaceous stages is indicated

TRIASSIC

GENERA	Induan+ Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian
"Rhynchonella"		1				
Abrekia	1					
Adygella				1	1	1
Adygelloides						1
Amphiclina					1	2
Ampliclinodonta					1	
Angustothyris		1				
Aulacothyropsis				1		4
Austriella					1	
Austrirhynchia						2
Balatonospira				1		
Bobukella				1	1	
Caucasorhynchia					1	1
Caucasothyris					1	
Coenothyris		2				
Costirhynchia		1		1		
Costispiriferina		1				
Crurirhynchia					1	
Crurithyris	1					
Cubanothyris					2	2
Decurtella		2				
Dinarispira		2				
Dioristella		1		1		
Euxinella					3	6
Fissirhynchia					1	1
Guseriplia						2
Holcorhynchella		1				
Koeveskallina		1				
Koninckina				1	1	
Laballa					2	3
Lepismatina						1
Lobothyris					2	
Majkopella						3
Mentzelia		1		2	1	2
Moisseievia					3	
Neoretzia						3
Neowelerella	1					
Norella		1				
Oxycolpella					3	2
Pexidella		1			1	
Piarorhynchella		1				
Pseudocyrtina					1	
Pseudorugitella					2	2
Punctospirella		1				
Rhaetina				1	6	4
Rhimirhynchopsis					1	1
Robinsonella						1
Sinucosta		1			1	1
Spinolepismatina					1	
Sulcatinella		2				
Sulcatothyris				1		
Tetractinella		1				
Thecospira					1	
Thecospiropsis					1	
Triadithyris					2	1
Trigonirhynchella					1	2
Volirhynchia		2				
Wittenburgella					1	1
Worobievella					1	1
Zeilleria					3	6
Zugmayerella						1

JURASSIC

GENERA	Si	Pl	To	Aa	Bj	Bt	Cl	Ox	Km	Tt
"Rhynchonella"	2	1	2	2	2					
"Spiriferina"	1	1								
"Terebratula"							1	1		2
Acanthorhynchia								1		
Acanthothyris				1	3					
Aromasithyris							1	2	1	
Aulacothyris		2	1				2			
Bodrakella		1								
Calcirhynchia	1	1								
Calvirhynchia					1					
Capillirhynchia				1			1			
Cardinirhynchia							1			
Caucasella							1			
Caucasorhynchia		1								
Cererithyris					1					
Cheirothyris										1
Cincta		2								
Cirpa		1								
Colosia								2	1	
Cryptorhynchia					1					
Cuersithyris		1								
Cuneirhynchia		4								
Curtirhynchia			1							
Digonella		1						1		
Disculina		1								
Dorsoplicathyris							2			
Ferrythyris							1			
Flabellirhynchia		1	1							
Furcirhynchia	1			1	1					
Gibbirhynchia	1	2	1							
Goniothyris							1		1	1
Grandirhynchia			1	1	1					
Gusarella							1			
Heimia					1					
Homoeorhynchia	1	2	1							
Ismenia										2
Ivanoviella							3	1		
Juralina								5	1	2
Lacunosella							1	3	2	1
Linguithyris	1				1					
Liospiriferina	2	4	1							
Loboidothyris					1			1		
Lobothyris		3	1	2	2					
Lophothyris									1	
Monsardithyris					1					
Monticlarella									1	2
Morrisithyris					1		1			
Nucleata								2	1	1
Paruirhynchia				1						
Piarorhynchia	1	4	1							
Postepithyris									1	
Praemonticlarella			1							
Prionorhynchia	1	1	1							
Pseudogibbirhynchia			2	2	2					
Ptyctorhynchia			1							
Ptyctothyris					1		3			
Quadratirhynchia					2					
Rhactorhynchia					3					
Rhynchonelloidea				1						
Rhynchonelloidella							1			
Rimirhynchia		1								
Rudirhynchia	2									
Rugitela					1					
Scalpellirhynchia	1									
Securina	1	1								
Sellithyris								1	1	
Septaliphoria							2	2		6
Somalirhynchia								1		
Sphaeroidothyris					2					
Spiriferina	4	3								
Squamirhynchia		1								
Stolmorhynchia				4	2		1			
Striirhynchia					1					
Stroudithyris				1						
Tchegemithyris							2			
Terebratula								1		

LOWER CRETACEOUS

GENERA	Be	Va	Ha	Ba	Ap	Al
Belbekella	1		1	4	1	
Belothyris			1	2	2	
Orbirhynchia				1	1	
Peregrinella			1			
Praelongithyris					1	
Psilothyris		2				
Sellithyris		1	3			
Sulcirhynchia	1					
Symphythyris			1			
Terebrataliopsis		1				
Weberithyris		1				

stage abbreviations: Be – Berriasian, Va – Valangianian, Ha – Hauterivian, Ba – Barremian, Ap – Aptian, Al – Albian

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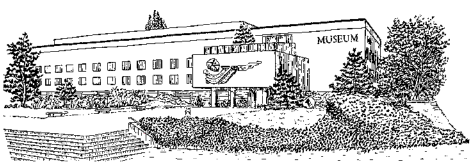

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Diversity dynamics of the Triassic marine biota in the Western Caucasus (Russia) : A quantitative estimation and a comparison with the global patterns

Dmitry A. RUBAN[1]

Abstract

Diversity dynamics of discovered Triassic marine biota in the Western Caucasus (Russia) have been studied quantitatively. The stratigraphic distribution of 422 species was taken into account. Foraminifers and brachiopods, followed by ammonoids, were the most diverse groups in comparison with bivalves, corals, algae and sponges. Total diversity, relatively low in the Early Triassic, strongly increased in the Anisian. Diversity decreased significantly in the Ladinian. Repopulation began in the Carnian, and the Norian is characterized by a new «explosion» of diversity. Weak diversification continued in the Early Rhaetian. The faunal diversity documented in the Western Caucasus generally reflected both the influences of the regional palaeoenvironmental changes and the global evolutionary patterns of the Triassic marine biota.

Keywords

Diversity, marine biota, ammonoids, bivalves, brachiopods, foraminifers, Triassic, Western Caucasus.

1. INTRODUCTION

The present knowledge on the Phanerozoic diversity dynamics of the marine biota on a global scale is summarized in the well-known articles of Benton (1995), Peters & Foote (2001) and Sepkoski (1993). But it is always important to evaluate the fossil diversity for the particular territory to test the regional appearance of the global patterns.

All Triassic stages (Induan to Rhaetian) are represented within the Western Caucasus – a region located on the northern periphery of the Neotethys Ocean (Golonka, 2004 ; Gaetani *et al.*, 2005 ; Stampfli & Borel, 2002). Its palaeontologic record is characterized by numerous taxa of ammonoids, brachiopods, bivalves, foraminifers, corals, algae and sponges. The study of the diversity dynamics (i.e., changes of the total number of taxa) of Triassic marine biota in the Western Caucasus and its comparison with the global record is attempted in this article.

2. GEOLOGIC SETTING

In the Triassic, the Western Caucasus was situated on the northern periphery of the Neotethys Ocean (Gaetani *et al.*, 2005 ; Golonka, 2004 ; Stampfli & Borel, 2002) (Fig. 1). Triassic strata and fossils of this region have been described by Dagis (1963, 1974), Dagis & Robinson (1973), Diakonov *et al.* (1962), Efimova (1991), Gaetani *et al.* (2005), Jaroshenko (1978), Paffengoltz (1959), Popov (1962), Prozorovskaja (1979), Rostovtsev *et al.* (1979), Shevyrjov (1990) and Vuks (2000).

The Triassic deposits of the Western Caucasus unconformably overlie the Paleozoic strata and are subdivided into four groups (Fig. 2). The most ancient is the Tkhatchskaja Group (~700 m) that consists of dominated carbonate deposits. The Sakhrajskaja Group (~500 m) consists of shales with clastic beds ; its lower and upper contacts are marked by unconformities. The upper groups were deposited in the same time and they are named as the Khodzinskaja Group, composed of carbonates including reefs (the total thickness is ~500 m), and the Khadzhokhskaja Group, embracing shales with clastic and carbonate beds (total thickness is ~350 m). The Upper Rhaetian-Lower Liassic interval corresponds to a major regional hiatus.

3. MATERIALS AND METHODS

The compilation of all available palaeontologic information provided a database of the Western Caucasus marine biota (see Appendix). The principal sources are monographs and articles of Dagis (1963, 1974), Dagis & Robinson (1973), Diakonov *et al.* (1962), Efimova (1991), Gaetani *et al.* (2005), Jaroshenko (1978), Paffengoltz (1959), Prozorovskaja (1979), Rostovtsev *et al.* (1979), Shevyrjov (1968) and Vuks (2000).

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Fig. 1 : Geographical and palaeogeographical location of the studied region (global palaeogeography at 210 Ma after SCOTESE, 2004, position of the Western Caucasus is marked by black circle).

In its final version the database contains the distribution per stage of 422 taxa. When possible, taxonomic revisions of taxa were made to avoid under- or overestimation of the diversity due to the synonymy errors. Species identified has "sp." only were excluded, because it is difficult to understand their relation to the completely identified species mentioned in other papers. Species defined with "cf." and "aff." were considered as concrete species to avoid underestimation of the diversity. Similarly suggestions were made by ALBA *et al.* (2001).

The analysis of the diversity dynamics of the Triassic marine biota of the Western Caucasus attempted herein is based on the simple procedure of calculation the total number of species in each stage.

4. DIVERSITY DYNAMICS OF THE MARINE BIOTA

The total number of analyzed species of the Triassic marine biota in the Western Caucasus is 422. In decreasing order, foraminifers (175 species), brachiopods (122 species), ammonoids (69 species), bivalves (31 species), corals (17 species), algae (5 species) and sponges (3 species) were registered. The evaluated faunal diversity dynamics is presented in Fig. 3. Diversity changes within the particular fossil groups partly differ from that observed within the total biotic dynamics (Fig. 4).

The Early Triassic diversity remained relatively low. However, the palaeoenvironments, characterized by the dominated low energy carbonate sedimentation below wave base (GAETANI *et al.,* 2005), were favourable enough for the rapid recovery of the marine biota after the crisis, which occurred at the Permian/Triassic boundary. Such assumption is supported by the presence of 35 Early Triassic species, known in the Western Caucasus, which number is not so little. During the Anisian, a strong diversification, recognized in ammonoids, brachiopods, foraminifers and to a lesser scale in bivalves, reached a total species number exceeding 100. The palaeoenvironments were the same as in the Early Triassic (GAETANI *et al.*, 2005). This diversification is especially an interesting event, because the distribution of the Anisian deposits became restricted in comparison with the preceding time intervals (ROSTOVTSEV *et al.*, 1979).

In the Ladinian, diversity decreased significantly in most groups, although less pronounced in bivalves and foraminifers. Species numbers declined strongly in ammonoids, while brachiopods disappeared entirely. The total absence of the last ones is enigmatic. At least, it cannot be explained by the sampling errors, because palaeontological data were collected randomly from the entire Triassic succession (see above mentioned data sources). A repopulation began in the Carnian, with renewed radiation of the brachiopods, bivalves and foraminifers, while the diversity of ammonoids decreased. The Ladinian and Carnian palaeoenvironments were the same. Shales with clastic beds are interpreted by GAETANI *et al.* (2005) as turbidites, which were accumulated in the deep basin. Such conclusion is supported by my own field observations. Thus, abrupt deepening occurred in the Early Ladinian. It was resulted in the dominance of the palaeoenvironments, unfavourable for the pre-existed shallow-water Anisian fauna. In the Carnian, brachiopods, bivalves and foraminifers might have adopted to such environments, in contrast to ammonoids. Alternatively, the Carnian basin might have been shallower, which is documented by the appearance of carbonate rocks in the upper part of the Sakhrajskaja Group (GAETANI *et al.*, 2005). In this case, palaeoenvironments became more favourable to initiate the faunal diversification.

The Norian "explosion" of total marine biota resides in the diversification of brachiopods, though less ammonoids. The number of the Norian bivalves species was the same as in the Carnian. Corals, sponges and algae also appeared in the Norian, while a decline in the foraminiferal diversity is observed. This Late Triassic "explosion" may be directly linked to the dominance of the favourable palaeoenvironments of the carbonate platform and appearance of the diverse reefal communities (GAETANI *et al.*, 2005 ; RUBAN, 2005).

In the Early Rhaetian, slight diversification of brachiopods

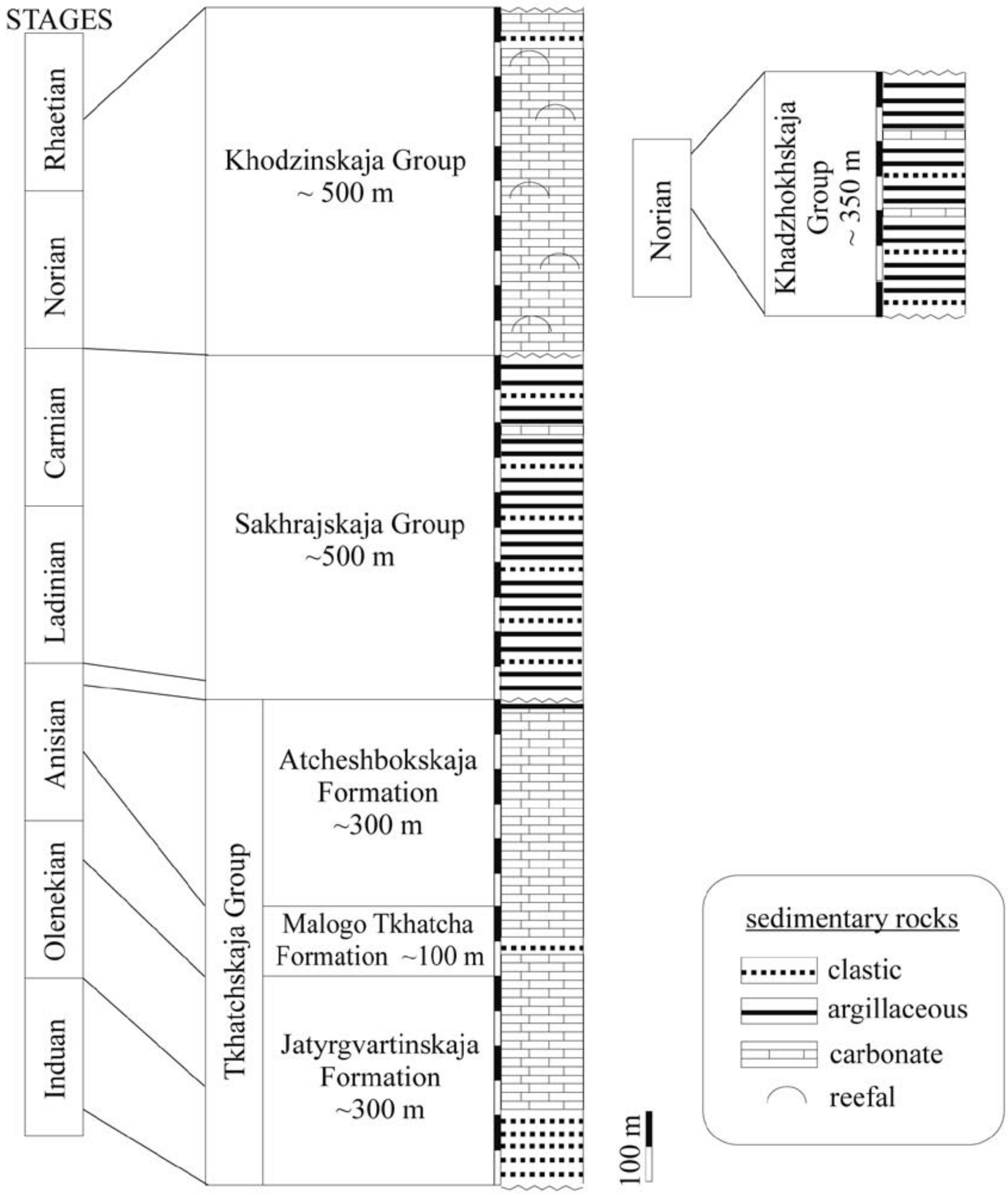

Fig. 2: The Triassic lithostratigraphy of the Western Caucasus (after DAGIS & ROBINSON, 1973; GAETANI *et al.*, 2005; PROZOROVSKAJA, 1979; ROSTOVTSEV *et al.*, 1979 with corrections).

and ammonoids went on and foraminifers recovered, while bivalves disappeared entirely. The Late Rhaetian-Early Sinemurian phase of tectonic activity resulted a major hiatus, which embraced the mentioned time interval.

5. DISCUSSION

These regionally documented diversity patterns (Fig. 3) are somewhat similar to the global trends (BENTON, 1995; PETERS & FOOTE, 2001; SEPKOSKI, 1993). The globally-known recovery after the Permian/Triassic mass extinction is evidently observed in the regional record. The diversity acceleration is documented globally in the Middle Triassic. The present studies (KOMATSU *et al.*, 2004) bring the evidences for the similar diversity rise in the Anisian. BONUSO & BOTTJER (2005) suggested the improvement of the environmental conditions after the Permian/Triassic mass extinction in the Middle Triassic, which may be considered as the main cause, which provoked diversification at this time. However,

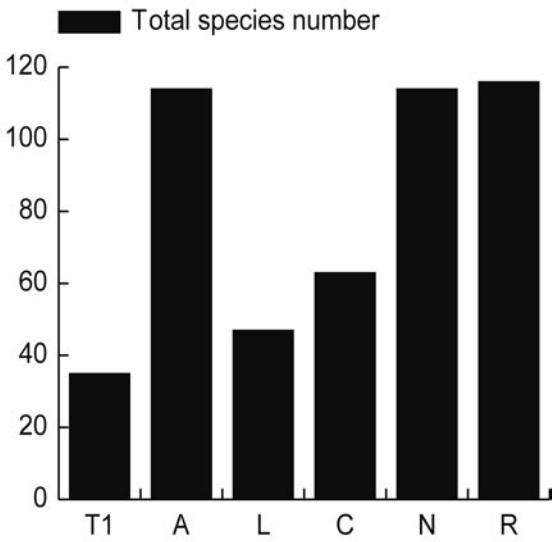

Fig. 3: The total diversity dynamics of the Triassic marine biota in the Western Caucasus. Time intervals: T1 - Lower Triassic (Induan+Olenekian), A - Anisian, L - Ladinian, C - Carnian, N - Norian, R - Rhaetian.

the Ladinian diminishing of the taxa quantity is not well documented by the data of the above mentionned global compilations. This may be explained by their low resolution

The Norian diversity «explosion» corresponded with the global patterns (BENTON, 1995; PETERS & FOOTE, 2001; SEPKOSKI, 1993). Although the decrease in the bivalve diversity is evident (Fig. 4), the globally known end-Triassic interval of the mass extinction (HALLAM, 2002) cannot be observed in the Western Caucasus due to the major Late Rhaetian-Early Sinemurian hiatus.

6. CONCLUSIONS

The analysis of the diversity dynamics of the Triassic marine biota in the Western Caucasus permits to make some main conclusions:

1. Diversity increase in the Early Triassic strengthened in the Anisian; it was followed by the decline in the Ladinian. Diversity began to rise in the Carnian. The Norian is characterized by a new diversity "explosion",

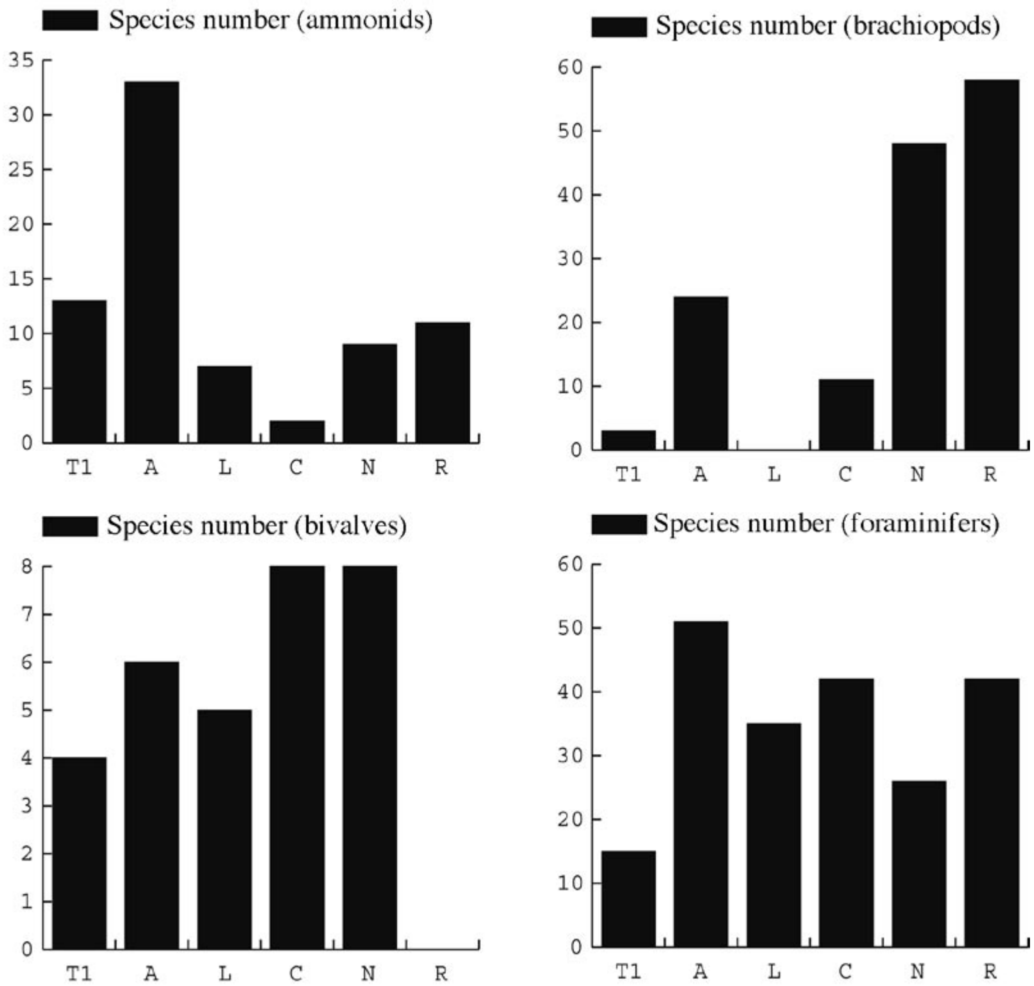

Fig. 4: Changes of the total species number of the Triassic ammonoids, brachiopods, bivalves and foraminifers of the Western Caucasus. For abbreviation of time intervals see Fig. 3.

and the Early Rhaetian is characterized by the very diverse marine biota.

2. Diversity dynamics within the principal fossil groups (ammonoids, brachiopods, bivalves, foraminifers) differ rather strongly.

3. Documented diversity changes may be explained by the changes of the regional palaeoenvironments.

4. The regional diversity dynamics reflected some global tendencies.

It seems that sharp diversity changes of the marine biota may be effectively used to correlate the Triassic strata of far-located regions.

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APPENDIX. Compiled list of genera of the Triassic marine biota of the Western Caucasus. Number of species in each genus in the Triassic stages is indicated.

Genera	Induan + Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian
AMMONOIDS						
Acrochordiceras		3				
Aegeiceras		1				
Arcestes			1			3
Arpadites		1				
Badiotites			1			
Beyrichites		1				
Caucasites		2				
Cladiscites					2	2
Dieneroceras	1					
Flemingites	1					
Flexoptychites		1		1		
Gymnites		1				
Hollandites		3				
Japonites		1				
Joannites				1		
Juvavites					1	
Laboceras		3				
Leyophyllites		4				
Lobites					1	
Longobardites		1				
Megaphyllites		1			2	1
Mesocladiscites		1				
Monophyllites		1	3			
Nannites	1					
Owenites	3					
Paracladiscites						2
Paradanubites		2				
Paragoceras	1					
Parasageceras		1				
Parussuria	1					
Phyllocladiscites		2				
Pinacoceras					1	1
Placites					1	1
Proptychites	1					
Pseudosageceras	1					
Rhacophyllites					1	1
Smithoceras		1				

Genera	Induan + Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian
Sturia		2	1			
Subowenites	1					
Subvishnuites	1					
Wyomingites	1					
Xenodiscus			1			
ALGAE						
Lithotamnidium					1	
Spongiomorpha					4	
BRACHIOPODS						
«Rhynchonella»		1				
Abrekia	1					
Adygella				1	1	1
Adygelloides						1
Amphiclina					1	2
Ampliclinodonta					1	
Angustothyris		1				
Aulacothyropsis				1		4
Austriella					1	
Austrirhynchia						2
Balatonospira				1		
Bobukella				1	1	
Caucasorhynchia					1	1
Caucasothyris					1	
Coenothyris		2				
Costirhynchia		1		1		
Costispiriferina		1				
Crurirhynchia					1	
Crurithyris	1					
Cubanothyris					2	2
Decurtella		2				
Dinarispira		2				
Dioristella		1		1		
Euxinella					3	6
Fissirhynchia					1	1
Guseriplia						2
Holcorhynchella		1				
Koeveskallina		1				
Koninckina				1	1	
Laballa					2	3
Lepismatina						1
Lobothyris					2	

Genera	Induan + Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian
Majkopella						3
Mentzelia		1		2	1	2
Moisseievia					2	1
Neoretzia						3
Neowelerella	1					
Norella		1				
Oxycolpella					3	2
Pexidella		1			1	
Piarorhynchella		1				
Pseudocyrtina					1	
Pseudorugitella					2	2
Punctospirella		1				
Rhaetina				1	6	4
Rhimirhynchopsis					1	1
Robinsonella						1
Sinucosta		1			1	1
Spinolepismatina					1	
Sulcatinella		2				
Sulcatothyris				1		
Tetractinella		1				
Thecospira					1	
Thecospiropsis					1	
Triadithyris					2	1
Trigonirhynchella					1	2
Volirhynchia		2				
Wittenburgella					1	1
Worobievella					1	1
Zeilleria					3	6
Zugmayerella						1
BIVALVES						
Cassianella					1	
Claraia	4					
Daonella			2			
Halobia			1	5		
Hoernesia		1				
Indopecten					1	
Leda			1			
Limea		1				
Lyssochlamys				2		
Monotis					3	
Myophoria					1	

Genera	Induan + Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian
Mytilus		1				
Paleocardita					1	
Posidonia		1	1			
Pseudomonotis					1	
Schafhaeutlia		1				
Velopecten		1		1		
CORALS						
Astraeomorpha					2	1
Montlivaultia					1	
Rhabdophyllia					1	
Stephanocoenia					1	
Stylophyllopsis					2	
Thamnastraea					2	2
Thecosmilia					6	2
FORAMINIFERS						
«Frondicularia»						2
«Orthovertella»	1					
«Protonodosaria»	1					
«Tetrataxis»					1	1
Agathaminina					1	1
Ammobaculites		2		1	1	
Ammodiscus	1		2	1	1	
Angulodiscus					1	1
Arenovidalina		4				
Astacolus		2	1	3		
Auloconus					1	1
Aulotortus					3	3
Calcitornella		1	1			
Cornuloculina		1		1	1	1
Cornuspira				1		
Coronipora						1
Dentalina	3	5	6	4		
Diplotremmina		1		1		
Duostomina		1	1			
Duotaxis						1
Earlandia		1				
Galeanella					1	2
Gandinella	1					
Gaudryina				2		1
Gaudryinella						1
Glomospira		2				

Genera	Induan + Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian
Glomospirella		3				1
Hoyenella	1	1				2
Hyperammina		2		1		
Ichtyolaria				2		
Involutina					2	2
Labalina				1		
Lagena		1				
Lenticulina			4	3		2
Lingulina		2	4	1		
Marginulinopsis				1		
Meandrospira	2	3				
Miliolipora					1	1
Nodosaria	5	2		6		2
Nodosinella		1				
Ophthalmidium			1	2	3	4
Pachyphloides			1	2		
Pilammina		3				
Planiinvoluta					1	4
Pseudonodosaria		7	9	5		
Quinqueloculina			1			
Reophax			2			
Saccammina		1				
Semiinvoluta					1	1
Spiroplectammina		1		1		
Tetrataxis					1	
Tolypammina		3				
Triasina					1	
Trochammina		1		2	2	3
Trocholina				1	3	4
Turrispirillina						1
Vaginulina			1			
Vaginulinopsis			1			
SPONGES						
Hodsia					1	
Molengraffia					1	
Sahraja					1	