

# Taxonomic diversity dynamics of the Jurassic bivalves in the Caucasus: Regional trends and recognition of global patterns

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Received 21 April 2005; received in revised form 20 December 2005; accepted 21 December 2005

## Abstract

Jurassic bivalves were quite diverse in the Caucasus—a region located on the northern margin of the Tethys Ocean. Stratigraphic ranges of 513 species were compiled. Total species number, already low, declined during the Early Jurassic, reaching its minimum in the Toarcian (27 species). Although this coincided with the Pliensbachian–Toarcian global mass extinction, the latter is not evident for the Caucasian bivalves. Diversity rises occurred in the Aalenian and then in the Bajocian, when 77 species existed. In the Bathonian species number did not change. A diversity explosion took place in the Callovian, when favourable palaeoenvironmental conditions were established. 163 species are known from deposits of this age. This event is recognized globally as generic diversity significantly rose at this time all over the world. When a rimmed shelf was developed in the Late Callovian–Oxfordian, total species number reached its maximum (166 species). But a regional salinity crisis in the Kimmeridgian–Tithonian led to a final diversity drop, when 86 species existed in the Tithonian. Bivalves could not recover at the end-Jurassic, along with other representatives of shelly benthos. Comparison with the other well-known salinity crisis, which occurred in the Messinian in the Mediterranean, suggests that the Late Jurassic event in the Caucasus was much stronger and stressed bivalve assemblages for a longer time. The influence of the end-Jurassic mass extinction has not been fully documented. Throughout the Jurassic benthic assemblages within the Caucasus changed rapidly. This regional diversity dynamics corresponds quite well to the global trends. Both sea-level and marine palaeotemperature changes may have had an indirect influence on regional bivalve diversity, as they fluctuated strongly during the Jurassic.

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*Keywords:* Bivalves; Diversity; Mass extinction; Jurassic; Caucasus

## 1. Introduction

Bivalves were an important group among the Jurassic marine biota. They have been characterized by a great number of species and genera. Changes in their diversity were analyzed by Hallam (1972, 1986, 1987), Miller and Sepkoski (1988), Johnson (1990), Aberhan (1994), Little and Benton (1995), Aberhan and Fürsich (1997), McRoberts and Aberhan (1997), and Benton (2001).

Most of these studies examined particular patterns of diversity (e.g., extinction rate) or quite short intervals of mass extinctions (i.e., mostly the Pliensbachian–Toarcian event). Therefore, the study of taxonomic diversity dynamics among Jurassic bivalves remains relevant.

Useful evidence of diversity changes among Jurassic bivalves may be obtained from the Caucasus — a large region embracing the territory of Southwestern Russia and the entirety of Georgia, Armenia and Azerbaijan (Fig. 1). During the Jurassic it was located on the northern Neotethyan margin in the “key” position

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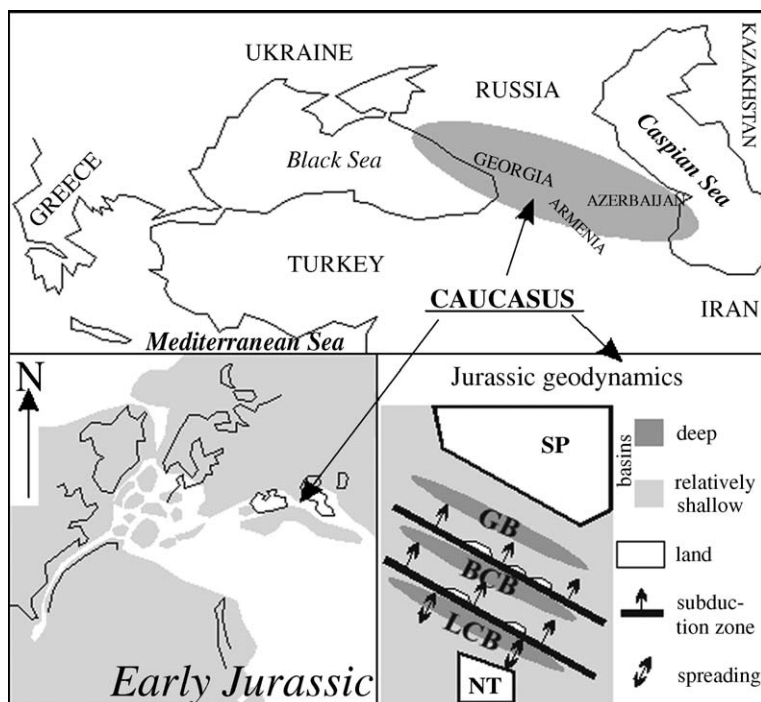


Fig. 1. Geographical and palaeogeographical locations of the Caucasus (Early Jurassic base map simplified after Owen, 1983; geodynamic situation is modified after Lorkipandze et al., 1984). Abbreviations: SP—Scythian Platform, GB—Greater Caucasus basin, BCB—hypothetic Black Sea–Caspian Sea Basin, LCB—Lesser Caucasus Basin, NT—Nakhitchevan' Terrane.

between European and Asiatic areas. In this region Jurassic deposits are widespread and bivalves are common (Rostovtsev et al., 1992). However, the regional diversity of bivalves has yet to be analyzed, except for a preliminary study devoted to the Late Jurassic (Ruban, 2003a), and an intriguing remark by Hallam (1986) on the Tithonian mass extinction, which stressed bivalves in the Caucasus.

A first compilation of all available data on the stratigraphic distribution of Jurassic bivalve species of the Caucasus is presented herein. Several hundred taxa were evaluated. This study provides an excellent basis upon which to evaluate diversity dynamics of this group through the Jurassic.

## 2. Geological setting

In the Jurassic the territory of the Caucasus was occupied by marine basins (Fig. 1). They were well connected to one another as well as to the Neotethys ocean (Owen, 1983; Meister and Stampfli, 2000; Stampfli and Borel, 2002; Brunet and Cloetingh, 2003; Golonka, 2004). These basins had distinct tectonic settings; several spreading and subduction zones were concentrated in a relatively narrow belt

(Lorkipandze et al., 1984; Ershov et al., 2003), where several microplates interacted.

Various sediments accumulated in the Caucasian basins during the Jurassic (Rostovtsev et al., 1992). Most of the typical facies, from continental to deep marine, are represented within the study area. In the Greater Caucasus Basin shales and clastic deposits up to 10000m thick accumulated during the Early–Middle Jurassic, while carbonates and evaporites (up to 3000m) were deposited in the Late Jurassic (Tsejler, 1977; Rostovtsev et al., 1992). The sedimentary succession of the Lesser Caucasus Basin is somewhat similar, although the thickness of the deposits is less; but the main distinctive feature is a great abundance of volcanogenic deposits (Rostovtsev et al., 1985, 1992). During the Jurassic several transgressions occurred within the Caucasus. Their maxima were reached in the Pliensbachian–Toarcian and later in the Oxfordian–Kimmeridgian.

In the Early–Middle Jurassic the Caucasus lay in the subtropical or moderate humid zones. Toarcian palaeotemperatures are estimated as 15–20°C; in the Early Aalenian they dropped to 5–15°C, but already in the Late Aalenian temperatures increased to 20–25°C and stayed at the same level until the end of Jurassic

(Jasamanov, 1978). After the beginning of the Callovian the climate became subtropical to tropical and semi-humid. In the Late Kimmeridgian–Tithonian significant aridization occurred, at which time evaporites accumulated (Jasamanov, 1978; Rostovtsev et al., 1992).

The general palaeogeographical position of the Caucasus is the subject of some discussion. Dommergues (1987) places it in the Euro-Boreal domain for the Early Jurassic. Westermann (2000) mentions it being included in the Tethyan Realm. Perhaps the best interpretation is that region was transitional. This is supported by the taxonomic composition of brachiopod assemblages (Ruban, 2003b). Another significant feature of the palaeogeographical changes in the Caucasus is the drift of this region northward. In the Early Jurassic it was located around 25°N latitude, while at the end of the Jurassic it had moved to 30°N latitude (Lordkipanidze et al., 1984).

### 3. Material and methods

Bivalves were one of the most diverse and abundant groups among the Jurassic marine biota of the Caucasus. They are found in strata of all stages of this system, except the Hettangian, which corresponds to a major regional hiatus (Rostovtsev et al., 1992). Although they have been described in several quite comprehensive papers (Ptchelintsev, 1931; Khimshiashvili, 1957, 1967, 1974; Azarjan, 1983, Romanov, 1985; Rostovtsev et al., 1985, 1992; Ratiani, 1987; Janin, 1989; Romanov and Ksum-Zade, 1991; Ruban, 2005a), a total compilation of Jurassic bivalve data has not yet been made. Therefore, the first stage of the present study was to compile all available information on the stratigraphic distribution of bivalve taxa for the Caucasus. Taxonomic revisions also were conducted to avoid duplication or missing of information on a single taxon. Finally a database of valid species was constructed, where presence and absence of taxa in each stage were tabulated. Unfortunately, the initial resolution of data and various stratigraphic problems do not permit the data to be assessed below stage level. In total, the ranges of 513 valid species were obtained.

A difficulty was encountered with the common reports of underinterpreted taxa, i.e. species defined with “cf.”, “aff.” and “sp.” To avoid overestimation of species numbers it was decided to exclude species identified to “sp.” only, because it is difficult to understand their relation to completely identified species mentioned in other papers, especially where no figures and/or detailed descriptions were available. As for species defined with “cf.” and “aff.”, they were

counted as concrete species, so as to avoid underestimating the diversity. The same assumptions were made in a study of Alba et al. (2001).

A quantitative approach was used to analyze the compiled data, which includes the calculation of *total species number (TSN)*, *appearing species number (ASN)*, *disappearing species number (DSN)*, *number of singletons (SN)*, *R-index* for stages (Sinemurian–Tithonian). Brief explanations of these indices are presented here. *TSN* is the quantity of bivalve species in each stage. All bivalves distributed regionally in the deposits of a particular stage are defined as a single *assemblage*, i.e., each assemblage directly corresponds to the whole stage. *ASN* and *DSN* are indices which show the quantity of species that have appeared or disappeared regionally within a particular stage. It is necessary to distinguish them from number of *originated* or *extinct species* because of the so-called Lazarus-effect (Wignall and Benton, 1999; Fara, 2001). *Appearing species* might have existed earlier and then temporarily have disappeared in the regional fossil record, so that some are not new taxa. *Disappearing species* may appear again in the regional record some time later, i.e., not all of them are extinct. *Singletons* are species that appeared and then disappeared within a single stage (sensu Foote, 2000).

*R-index* establishes Jaccard's (1901) similarity between successive assemblages (Ruban and Tyszk, 2005):

$$R = C / [(N1 + N2 - C)],$$

where *C* is the number of common taxa for two assemblages, and *N1* and *N2* are the taxa numbers in each assemblage. *Assemblage transformation rate (ATR)* essentially is 1/*R*. It shows how rapidly the changes in the taxonomic composition of assemblages are realized through geological time.

It is important to note that lack of data on the Berriasian does not permit a calculation of *DSN* and *SN* values for the Tithonian.

### 4. Regional diversity analysis

Diversity dynamics of Jurassic bivalves in the Caucasus is characterized by significant changes of principal patterns. *TSN* stayed at a relatively low level during the Sinemurian–Aalenian, not exceeding 50 species (Fig. 2). A weak declining trend is observed in the Early Jurassic with a minimum in the Toarcian, when only 27 species existed. A first significant diversification occurred in the Bajocian, when *TSN* reached 77. In

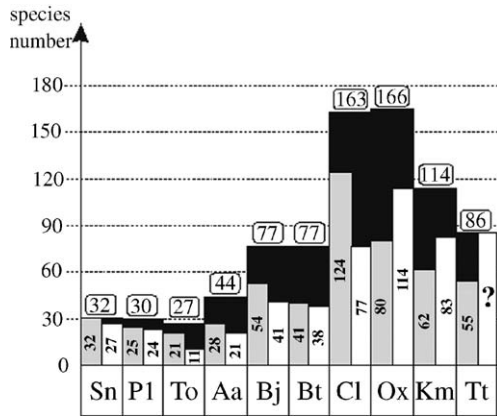


Fig. 2. Principal patterns of taxonomic diversity dynamics of the Jurassic Caucasian bivalves. Columns: black—TSN, gray—ASN, white—DSN. TSN values are indicated above general columns in rectangles, ASN and DSN values are presented in the columns. Stage abbreviations: Sn—Sinemurian, Pl—Pliensbachian, To—Toarcian, Aa—Aalenian, Bj—Bajocian, Bt—Bathonian, Cl—Calloviaian, Ox—Oxfordian, Km—Kimmeridgian, Tt—Tithonian.

the Bathonian the TSN value did not change. An explosion of diversity occurred in the Calloviaian, when TSN value doubled to 163 taxa. Only a minor increase is recorded in the Oxfordian (166 species), but later diversity declined significantly until the end of Jurassic. In the Tithonian only 86 species existed. But the diversity of bivalves did not decrease in the Late Jurassic so much as to reach the Toarcian minimum.

ASN and DSN changed in the same way as the TSN (Fig. 2). However, the number of appearances dropped in the Bathonian and Oxfordian. The number of disappearances, on the contrary, accelerated in the Oxfordian and then stayed at a relatively high level in the Kimmeridgian. A comparison between values of ASN for assemblage of a given stage and DSN of the assemblage of the preceding stage (DSN<sub>p</sub>) may be used to explain the mechanism of TSN changes. During the Early Jurassic the ASN was lower than DSN<sub>p</sub>, which led to the TSN decrease. But TSN decline should be explained mostly by a general ASN decrease. The Aalenian and Bajocian TSN accelerations occurred thanks to an increase in ASN relative to DSN<sub>p</sub>. The Calloviaian diversity explosion took place, when ASN increased to about 3 times greater than DSN<sub>p</sub>. The Late Jurassic diversity decline was realized because ASN was less than DSN<sub>p</sub>. Nonetheless appearances rates were quite stable and total diversity decreased realized thanks to the strength of disappearance rate.

SN values reached maxima in the Sinemurian, Bajocian, and especially in the Calloviaian–Kimmeridgian (Fig. 3). Singletons were the most diverse in the

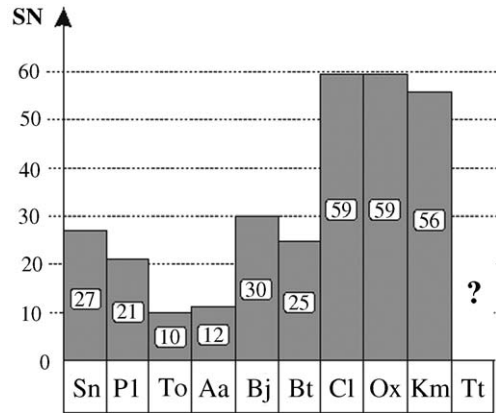


Fig. 3. Singleton quantity among the Jurassic bivalves of the Caucasus. Stage abbreviations—see Fig. 2.

Sinemurian and Pliensbachian, when such taxa composed more than 70% of assemblages. During other intervals of the Jurassic the quantity of singletons in assemblages varied between 25% and 50%.

R-index values fluctuated during the Jurassic (Fig. 4). Maxima in similarity among assemblages were reached for the Toarcian–Aalenian, Bajocian–Bathonian, and Calloviaian–Oxfordian. The turnover of assemblages was quite rapid overall as R-index did not reach even 0.40 at maximum, and was usually below 0.30. In the Early Jurassic the transformation occurred because of turnovers of the assemblages taxonomic composition as TSN is comparable for stages. But in the Middle–Late Jurassic assemblage transformations were realized mostly because of rises or falls of the TSN. At this interval when TSN values for successive assemblages are comparable, the ATR decreased and transformation occurred mostly by turnovers (Bajocian–Bathonian,

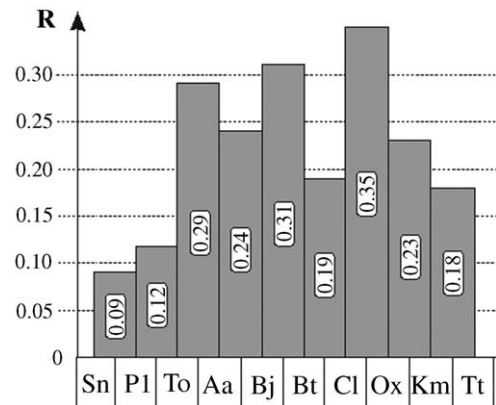


Fig. 4. R-index for assemblages of the Jurassic bivalves of the Caucasus. Stage abbreviations—see Fig. 2.

Callovian–Oxfordian). The most intense assemblage changes took place at the Sinemurian–Pliensbachian, Pliensbachian–Toarcian, Bathonian–Callovian, and Kimmeridgian–Tithonian boundaries.

The most diverse genera were *Cardinia* and *Plagiostoma* (Sinemurian), *Pseudopecten* (Pliensbachian), *Retroceramus* (Toarcian and Aalenian), *Mytiloceramus* (Aalenian), *Pleuromya* (Bajocian), *Camptonectes* (Bathonian, Oxfordian and Kimmeridgian), *Chlamys* and *Plagiostoma* (Bathonian–Tithonian), *Pholadomya* and *Pleuromya* (Callovian), *Astarte* (Callovian and Oxfordian), *Spondylopecten* (Oxfordian), and *Diceras* (Tithonian). These genera are characterized by the highest species numbers in the indicated assemblages. It is necessary to point out they were not always the most abundant taxa. For example, *Radulopecten* and *Entolium* dominated in the Early–Middle Callovian (Rostovtsev et al., 1992; Ruban, 2003a), but they were not the most diverse genera within those assemblages.

## 5. Recognition of global patterns

To explain the observed diversity dynamics of the Caucasian Jurassic bivalves is a significant task. The first step in this direction is to compare the regional versus global records.

An evaluation of the global total diversity changes was attempted by Miller and Sepkoski (1988) and then reconsidered by Benton (2001). Although these studies were aimed at generic diversity (Fig. 5), it seems to be comparable with the species diversity for the general comparison. The total number of bivalve genera was relatively minimal in the beginning of the Jurassic. A weak radiation occurred in the Early Jurassic, which was followed by a short interval when diversity stayed at the same level. In the second part of the Middle Jurassic the number of genera quickly grew. This may be regarded as a “diversity explosion”. Late Jurassic assemblages were the most diverse, but there were no significant variations

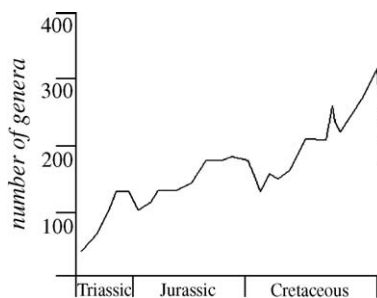


Fig. 5. The global Mesozoic bivalve generic diversity (modified from Miller and Sepkoski, 1988).

in the number of taxa. The Jurassic/Cretaceous transition is marked by an abrupt decline of bivalves on the global scale.

A comparison between regional (Fig. 2) and global (Fig. 5) diversity dynamics of Jurassic bivalves shows they were quite similar. Two differences are different diversity changes in the Early Jurassic and an early decline of the Caucasian bivalves in the Late Jurassic. The first difference may be ignored, because both regional and global trends are too weak to be directly comparable. But more detailed data on the Early Jurassic TSN changes of European (Hallam, 1976, 1986) and Andean (Aberhan and Fürsich, 1997) bivalves also suggest a gradual radiation of the Liassic bivalves. The quantity of Sinemurian bivalves known in North America is also a little lower than that of Pliensbachian bivalves (Smith et al., 1994). Thus a mechanism-driven evolution of Caucasian bivalves was distinct in the Early Jurassic. One of the possible explanations lies in the timing of dysoxic/anoxic events. In the Caucasus dysoxic palaeoenvironments were established beginning in the Pliensbachian, when black shales began to be deposited. This may have negatively influenced the bivalve assemblages because of deteriorating environments. As for the Late Jurassic, palaeoenvironments in the Caucasus were extraordinary at this time, which may have affected the bivalve evolution (see Discussion).

It is important to compare the diversity changes of the Jurassic bivalves between the Caucasus (Fig. 2) and Western Europe (Hallam, 1976). Rapid radiation in the Early Jurassic and decline in the Toarcian, which have been documented in the European record, do not appear in the Caucasus (see also above). However, the diversity acceleration in the Aalenian–Bathonian took place in both regions. A significant difference is the Callovian diversity drop in Western Europe, whereas in the Caucasus the bivalve diversity greatly increased during this time. This may be explained by the onset of the carbonate platform development in the Caucasus in the Callovian (Ruban, 2005b), which resulted in a diversity explosion (see below for details). In Western Europe bivalve diversity rose in the Oxfordian, and in the Caucasus species numbers were high during this age. In the Late Jurassic the diversity trends were similar in both regions, where a decline occurred.

Thus quite strong correspondence is observed between the whole regional and global diversity dynamics of the Jurassic bivalves. This is a significant conclusion, because Caucasian basins were relatively isolated. Such correspondence may be explained by the

high degree of similarity between bivalves of the Caucasus and other regions, i.e. low degree of endemism — at least at the generic level. Many of the Jurassic bivalves found in the Caucasus are known in the other regions of the world, which is suggested by data on their global distribution (Hallam, 1977). For example, more than twenty Caucasian bivalve genera (*Acesta*, *Camptonectes*, *Entolium*, *Meleagrinnella*, *Neocrassina*, *Opis*, *Oxytoma*, *Palaeonucula*, *Pholadomya*, *Pleuromya*, *Trigonia*, etc.) are known even in the far-flung Australasian regions, characterized recently by Grant-Mackie et al. (2000). Hallam (1977) has shown a high proportion of cosmopolitan genera among the Jurassic bivalves. Sha (2003) argued that many Mesozoic bivalves were global colonizers, being characterized by cosmopolitan, anti-tropical or pantropical geographical distributions. Some taxa considered by Sha (2003) (e.g., *Camptonectes*, *Chlamys*, *Gryphaea*) are typical for the Caucasus. Generally, the palaeobiogeographic differentiation in the Jurassic was not so great as later in the Cretaceous and Cenozoic. True superrealms appeared only in the end-Jurassic, and true realms in the Middle Jurassic (Westermann, 2000). Such conclusion is evidently supported by Hallam's (1977) data, which considered only bivalves.

Two globally recognized and remarkable events in the evolution of Jurassic bivalves should be discussed with respect to the data on the Caucasus. They are the Pliensbachian–Toarcian mass extinction and the Callovian diversity explosion.

The Pliensbachian–Toarcian interval is known for a global mass extinction, which particularly stressed bivalves (Hallam, 1972, 1986, 1987; Aberhan, 1994; Little and Benton, 1995; Aberhan and Fürsich, 1997; McRoberts and Aberhan, 1997; Hallam and Wignall, 1997; Harries and Little, 1999; Pálffy et al., 2002). This event was previously recognized in the Northern Caucasus for brachiopods; establishment of anoxic environments seems to be its likely cause (Ruban, 2004a). Our data suggest the TSN of bivalves in the Toarcian was only 3 species lower than in the Pliensbachian (Fig. 2). Although 24 Pliensbachian species disappeared, 21 new species appeared in the Toarcian, which may be explained by both speciation and taxa immigration. Moreover, DSN did not rise in the Pliensbachian. Therefore, although we document a “negative event”, it is not so significant as in the other regions such Northwest Europe or South America (Hallam, 1986, 1987; Little and Benton, 1995; Aberhan and Fürsich, 1997). One possible explanation lies in the area of data resolution. In the Caucasus recovery after the Pliensbachian–Toarcian mass extinction began

already in the Middle Toarcian (Ruban, 2004a). Hence, at the stage level the short-term effect of the shelly benthos collapse during the Toarcian seems to be minimized by the high values of overall diversity in the Middle–Late Toarcian. Thus to recognize a peak mass extinction regionally (if it existed at all) for bivalves should be a task for further detailed studies. But a distinctive feature of the regional record is the relatively low diversity of the Caucasian bivalves in the Pliensbachian, when other marine fossils, e.g., brachiopods, were strongly diversified. In conclusion, the global generic diversity curve does not reflect the influence of the Pliensbachian–Toarcian mass extinction on the bivalves (Miller and Sepkoski, 1988).

The Callovian diversity explosion of bivalves in the Caucasus (Fig. 2) took place along with a radiation in the entire shelly benthos (Ruban, 2003a, 2005a,b). This occurred as favourable environmental conditions were established from the Early Callovian: climate became warmer, and wide shelves were occupied by sands or calcareous silts (Jasamanov, 1978). Moreover, in the studied sections abundant remains of *Chlamys* (*Chlamys*) *viminea* (SOWERBY, 1826), which was one the Callovian dominants, were found as low as in the Lower Callovian basal conglomerates (Ruban, 2005a), i.e. the bivalve radiation was abrupt. In the Late Callovian a great carbonate platform emerged (Fig. 6). It existed until the end of Jurassic (Rostovtsev et al., 1992; Kuznetsov, 1993). This platform was essentially a rimmed shelf (after Ginsburg and James, 1974; Read, 1985), bounded by barrier reefs constructed by corals, which diversified at this time across the entire Tethys (Martin-Garin et al., 2002). In the Oxfordian conditions evidently remained favourable for bivalves. But it is important to note that bivalves were restricted more to shelf, than to reefal facies (Rostovtsev et al., 1992). Generally, the bivalve diversity explosion established in the Caucasus was not a specific regional feature. The similar generic diversity acceleration occurred on the global scale (Miller and Sepkoski, 1988; Benton, 2001). Moreover, the new diversity curves of the whole planetary marine biota (Benton, 2001; Peters and Foote, 2001) indicate an increase of taxa number in the middle of the Jurassic. This suggests that a diversity explosion documented in the Caucasus may be at least partly explained by the influences of the evolutionary mechanism of bivalves overall or even by global factors, enforced in all marine biotas.

A decrease in the total diversity of bivalves in the end-Jurassic occurred globally (Hallam, 1976, 1986; Benton, 2001), which supports the idea of mass extinction. But in the Caucasus its greatest effect is

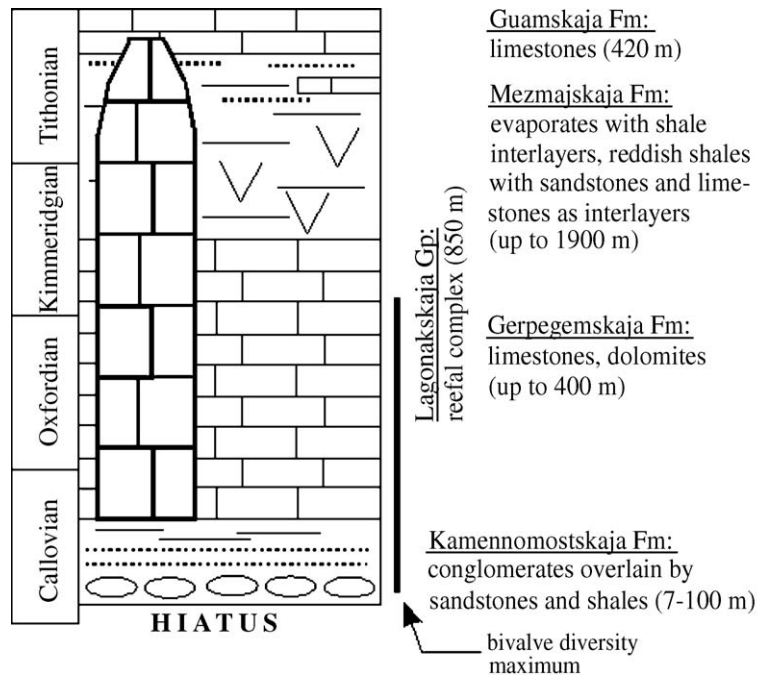


Fig. 6. Stratigraphic extent of the Late Jurassic rimmed shelf in the Western Caucasus (formations and thicknesses after Rostovtsev et al., 1992).

recorded in the Berriasian (Ruban, 2004b), when foraminifers and brachiopods strongly declined. Moreover, in the global record the diversity of bivalves also dropped in the beginning of the Cretaceous (Miller and Sepkoski, 1988). Therefore, it is difficult to discuss how strongly this global event stressed end-Jurassic bivalves regionally. But it is not possible to exclude that the TSN decrease observed in the Tithonian might be explained partially by mass extinction.

## 6. Sea-level changes as a driving force of diversity dynamics

Sea-level fluctuations are often considered as one of the leading factors of diversity changes in bivalves and other marine biota (Newell, 1967; Hallam and Wignall, 1997, 1999; McRoberts and Aberhan, 1997; Smith, 2001). Available data on the Jurassic bivalves of the Caucasus allow a test of this assumption. The first step was an estimation of the regional sea-level changes.

The territory of the Caucasus is subdivided into several dozen areas (traditionally called “zones”, although this is not well appropriated term), distinguished by facies composition of the Jurassic successions (Rostovtsev et al., 1992). A total of 36 “zones” delineate the Hettangian–Bathonian interval, and 26 for the Callovian–Tithonian interval. In the Caucasus the Callovian stage traditionally is attributed to the Upper

Jurassic, which is wrong (see scale of Gradstein et al., 2004). A facies interpretation for each of the hundreds of formations was made herein, based on the information of Rostovtsev et al. (1992) and personal field observations. Three main types of palaeoenvironments were defined: continental, shallow-marine and deep-marine. Then for each stage a total number of “zones” with a particular type of these palaeoenvironments was derived. Stratigraphic patterns between distinct facies types mark transgression/regression and shallowing/deepening episodes (Fig. 7). A somewhat similar approach was used by Hallam and Wignall (1999), who calculated the number of shallow formations to evaluate sea-level highstands and lowstands. Smith (2001) measured the outcrop area of the principal types of sedimentary rocks, and Crampton et al. (2003) calculated the same. Peters and Foote (2001) accounted for the number of marine formations and global rock area.

To reconstruct the sea-level curve a specific index (ISL) was evaluated:

$$ISL = (s + d)/c,$$

where  $s$ ,  $d$ ,  $c$  are the number of “zones” with shallow-marine, deep-marine, and continental palaeoenvironments respectively. The lower values of this index mark regressions, while higher values indicate transgressions. Shallowing is recognized by an increase in  $s$ -number relative to  $d$ -number.

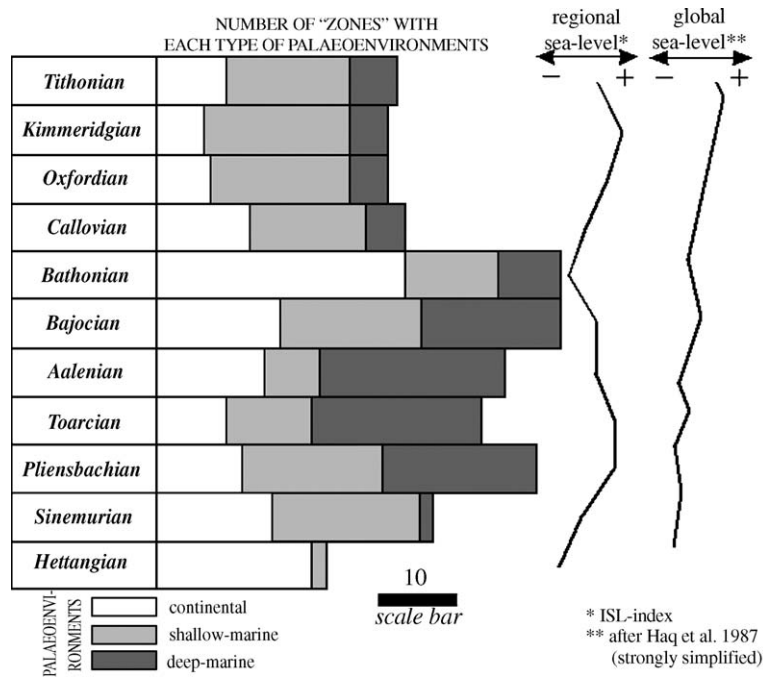


Fig. 7. Changes in the total number of "zones" with interpreted continental, shallow-marine and deep-marine types of palaeoenvironments, regional and global sea-level changes (see text for explanation).

The Hettangian and Bathonian were the time intervals of strong regressions. By contrast, seas transgressed during the Sinemurian–Pliensbachian and later in the Callovian–Kimmeridgian. Deepening reached its maximum in the Toarcian–Aalenian. Therefore, the Early Jurassic transgression is indicated by an increase in depth of the Caucasian basins, while in the Late Jurassic seas were shallow and extensive shelf areas developed.

Comparison between global sea-level changes (Haq et al., 1987; see also Hallam, 2001) and those observed in the Caucasus suggests a regional difference (Fig. 7). This was caused by the regional tectonics. Peaks of transgressions and regressions were not synchronous. The general trends of sea level are somewhat similar, but only in the most generalized view. In the global record a tendency toward transgression is documented for the overall Jurassic, and in the Caucasus, sea-level rise is evident, but it is weak. Globally four transgressive–regressive cycles appeared in the Jurassic, while only two larger ones are recorded within the Caucasus. Sea-level changes recorded in Europe (Jacquin and de Graciansky, 1998; Smith, 2001; Stratigraphische Tabelle von Deutschland, 2002) are a little more similar to those in the Caucasus, but a large difference still exists.

An interesting conclusion may be made. As shown above, the Jurassic bivalves diversity changed globally and in the Caucasus in a similar manner. Therefore, the

differences in sea-level changes imply that they may not be considered as a leading factor of these diversity changes. The same conclusion was reached for Early Jurassic brachiopods in the Caucasus and worldwide (Ruban, 2004a).

The quantitative expression of the regional sea-level changes allows a calculation of the simple index of rank correlation (RS) (Kendall, 1970) between ISL, *s*-, *d*-, *c*-number and the total species number dynamics for the entire Jurassic period. A similar analysis was attempted by McRoberts and Aberhan (1997) for Early Jurassic bivalves of Northwest Europe, and also by Crampton et al. (2003) for Cenozoic molluscs.

Results obtained for the Caucasus are surprising. RS for TSN and ISL is only 0.24. RS values for TSN and *s*-, *d*-, and *c*-number are 0.50, –0.31, and –0.31 respectively. In no case are the correlation values significant. A stronger correlation was observed between number of "zones" with shallow-marine palaeoenvironments and sea-level fluctuations. But even in this case the RS values are low. Therefore, it may be concluded that sea-level changes should not be considered as a driving force of diversity dynamics for Jurassic bivalves of the Caucasus.

The absence of a relationship between diversity of the Early Jurassic bivalve species from the Northwest Europe and sea-level changes was reported by

McRoberts and Aberhan (1997). In another well-known example Hallam and Wignall (1999) showed that transgressions/regressions distinctly enforced mass extinctions among the Phanerozoic marine biota. Undoubtedly, sea-level fluctuations should not be excluded from the list of diversity driving factors, but whether they were direct or indirect factors must be considered in every case. Sea shallowing partially controlled the diversity rises among bivalves of the Caucasus, as inferred from the Sinemurian, Bajocian–Bathonian and Late Jurassic, whereas in the other cases (as in the Aalenian or Kimmeridgian) no direct connections are observed. Regardless, further studies based on global and other regional data are awaited to test this conclusion.

## 7. Discussion

Regional diversity dynamics of Jurassic bivalves from the Caucasus are discussed with respect to the influence of sea-water palaeotemperature changes and the impact of the Late Jurassic salinity crisis.

Sea-water palaeotemperature changes might have controlled the diversity dynamics of Jurassic bivalves within the Caucasus because amplitude changes were significant (Fig. 8). Regional palaeotemperatures of sea-water for each Jurassic stage were established by Jasamanov (1978), who analyzed oxygen isotopic compositions derived from belemnites and other benthic macrofossils. Although such isotopic measurements might lead to wrong interpretations (Longinelli, 1996; Longinelli et al., 2002, 2003; Longinelli, personal communication), results obtained for the Caucasus were compared to palaeoecological studies (Jasamanov, 1978).

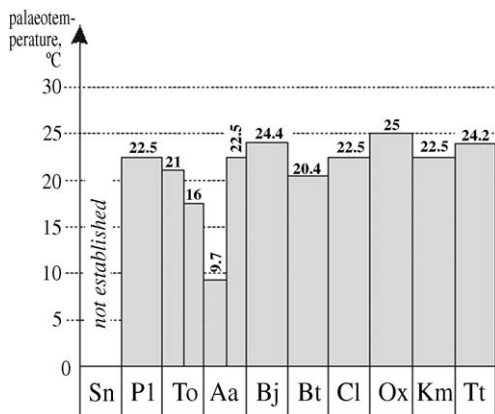


Fig. 8. Jurassic sea-water palaeotemperature changes in the Caucasus (data from Jasamanov, 1978, average values are shown). Stage abbreviations — see Fig. 2.

A comparison between regional bivalve diversity (Fig. 2) and sea-water palaeotemperatures (Fig. 8) suggests there was no direct covariation between them. Even the remarkable Late Toarcian–Early Aalenian cooling did not stress bivalves. Meantime, all Jasamanov’s data and, therefore, our conclusions should be further verified to become trustable. It is important to note, that Late Aalenian–Bajocian and Callovian–Oxfordian episodes of sea-water warming corresponded to the evident radiation of bivalves, i.e. diversity rises. Therefore, there was a partial temperature control of the bivalve diversity changes. On the other hand, changes of sea-water palaeotemperatures might have provoked major changes in the structure of the bivalve assemblages, which were not recorded as diversity events. This is an important matter for further studies.

The Kimmeridgian–Tithonian is characterized by the remarkable decline of bivalves (Fig. 2). The causes of this event are readily apparent in the stratigraphic record. During this time interval in many parts of the Caucasus the deposition of evaporites took place indicating an increase in salinity of sea-water (Jasamanov, 1978; Rostovtsev et al., 1992; Kuznetsov, 1993) (Fig. 6). Also it appears that at least parts of some basins were isolated as lagoons. But complete restriction of the Caucasian basins did not occur as suggested from our facies analysis (Fig. 7). Nonetheless, such “hypersaline” environments were unfavourable for bivalves, which showed a significant diversity drop. In comparison to brachiopods, bivalves had not recovered by the Tithonian (Ruban, 2003a). This can be explained by the ability of brachiopods to radiate more rapidly when favourable conditions appear even for a very short time intervals (Prozorovskaya, 1996). Evidently, the diversification of bivalves needs much more time to accelerate.

In discussing the influence of the regional salinity crisis on bivalves in the Jurassic of the Caucasus, a comparison was made with respect to the effect of the other well-known salinity crisis, which occurred in the Messinian of the Mediterranean Sea (Krijgsman et al., 1999). Comprehensive data are available, including stratigraphic ranges of mollusc species known from the Neogene basins of southeast Spain (Demarcq, 1990). This information allows an evaluation of total numbers of mollusc species (Fig. 9). It is evident that the salinity crisis of the Late Messinian did not lead to the temporal diversity decrease of pectinides. Even if their communities were stressed in the Late Messinian, any recovery seems to have been very rapid and completely compensated for any earlier losses. Data on other molluscs (non-pectinide bivalves and gastropods) support this conclusion (Barrier and Montenat, 1990).

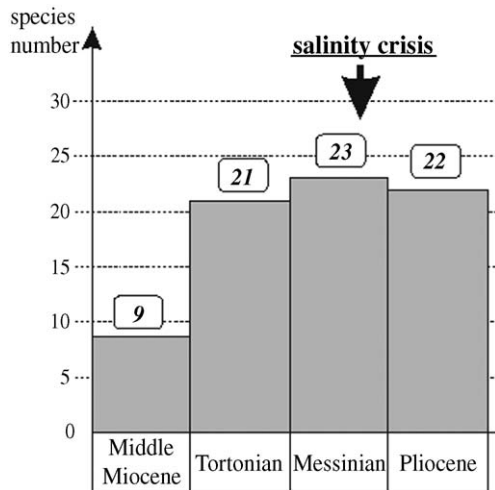


Fig. 9. Total species number of the middle Miocene–Pliocene pectinids in the basins of SE Spain. Initial data extracted from Demarcq (1990).

Therefore, the Late Jurassic salinity crisis in the Caucasus and the much more intense event of the same kind in the late Miocene in the basins of southeastern Spain had different effects on marine faunas. To explain this is a matter for further study.

## 8. Conclusions

A total of 513 species of bivalves are known from the Jurassic deposits of the Caucasus. In the Early Jurassic diversity among bivalves was low and weakly declining. Later in the Aalenian and especially in the Bajocian the total species number significantly increased by 2.5 times. The next radiation took place in the Callovian. It was so intense that it could be called an “explosion”. The Late Jurassic is characterized by a diversity decrease caused by the regional salinity crisis. The most intense assemblage changes took place at the Sinemurian–Pliensbachian, Pliensbachian–Toarcian, Bathonian–Callovian, and Kimmeridgian–Tithonian boundaries. But only in the first two cases were they caused by true turnovers of taxonomic composition. In later two cases they were connected with the significant diversity changes. This study found that regional and global bivalve diversity changes were somewhat similar. A significant conclusion is that the Callovian diversity explosion is a globally recognized event. But Pliensbachian–Toarcian and end-Jurassic mass extinctions evidently have not been recognized within the Caucasus.

Detailed analysis of sea-level changes (both transgressions/regressions and shallowing/deepening) within the Caucasus, realized by facies interpretation, and

marine palaeotemperature changes suggests these factors may not be considered as common direct driving forces of bivalve diversity dynamics. Thus further studies should be aimed at exploring global influences and comparisons with the other regions. This is always important for the estimation of the biodiversity (Alroy, 2003).

An attempted evaluation of principal patterns of the bivalve diversity dynamics and establishment of their correspondence to the global trends of the entire Jurassic make the Caucasus an important region for worldwide comparisons.

## Acknowledgements

The author gratefully acknowledges K.A. Campbell (New Zealand) for her preliminary review of this paper and English corrections, and also T.K. Baumiller (USA) for his useful suggestions on the earlier version of this paper. Very useful improvements made by C.E. Brett (USA) and another anonymous reviewer are highly appreciated, as well as the help of the Editor J. Snelleman (Netherlands). For their help with literature and/or useful comments I thank many colleagues, especially N.M.M. Janssen (Netherlands), and also M. Aberhan (Germany), D.M. Alba (Spain), M. Bécaud (France), M.-F. Brunet (France), A.B. Challinor (New Zealand), S.E. Damborenea (Argentina), E. Fara (France), F.T. Fürsich (Germany), M. Geiger (Germany), B.F. Glenister (USA), S. Jain (USA), A.L.A. Johnson (UK), W. Krijgsman (Netherlands), V.G. Kuznetsov (Russia), C.T.S. Little (UK), A. Longinelli (Italy), B. Martin-Garin (Switzerland), D.A.B. McFarlan (New Zealand), Ch. Meister (Switzerland), M. Menning (Germany), Ch. Montenat (France), Ph. Quereilhac (France), S.E. Peters (USA), E.L. Prossorovskaya (Russia), J.F. Read (USA), J.M. Rouchy (France), B.M. Simonson (USA), A.B. Smith (UK), P. L. Smith (Vancouver, Canada), J. Thierry (France), P.B. Wignall (UK) and H. Zerfass (Brazil). My former colleagues V.D. Kotljar and D.V. Klimov (Russia) are thanked for their assistance in the field. The librarian T. D. Kursheva is specially acknowledged for her help. The hospitality of V.I. Pugatchev (Russia) at a field camp “Belaja Retchka” and his help are highly appreciated. Finally, I would like to thank N.V. and A. F. Ruban for their support of my research.

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