REVUE DE PALÉOBIOLOGIE

Brachiopod decline preceded the Early Toarcian mass extinction in the Northern Caucasus (northern Neo-Tethys Ocean): A palaeogeographical context

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Abstract

Brachiopods were affected strongly by the Early Toarcian mass extinction within the Northern Caucasus, which at that time was a large region on the northern margin of the Neo-Tethys Ocean. However, their decline preceded the mass extinction event, and it took place in the mid-Pliensbachian with only one species survived in the Domerian. To understand the causes of this phenomenon 7 precise palaeogeographical reconstructions have been produced for the Northern Caucasus. It is proposed that a mid-Pliensbachian deepening of the Caucasian Sea and an associated oxygen depletion stressed brachiopod assemblages. Data from some European regions and South America suggest a high diversity in the late Pliensbachian. In contrast, brachiopod diversity decreased in the Bakony Mountains of Hungary in the latest Pliensbachian and on the Pacific margin of North America in the late Pliensbachian. The decline which preceded the Early Toarcian mass extinction was a regional phenomenon unrelated to the mass extinction itself.

Keywords

Taxonomic diversity, mass extinction, brachiopods, transgression, regression, water depth, Pliensbachian, Toarcian, Northern Caucasus, Neo-Tethys Ocean.

I. INTRODUCTION

The Early Toarcian mass extinction stressed most marine communities including brachiopods (HALLAM, 1986; LITTLE & BENTON, 1995; LITTLE, 1996; ABERHAN & FÜRSICH, 1997; HALLAM & WIGNALL, 1997; HARRIES & LITTLE, 1999; PÁLFY *et al*., 2002). A detailed analysis of the taxonomic diversity changes of this fossil group in the Northern Caucasus – a large region on the northern margin of the Neo-Tethys Ocean – highlights a specific feature of their evolution before the mass extinction, namely a sharp decline already in the late Pliensbachian (RUBAN, 2004). The overal demise of brachiopods during the entire Pliensbachian-Toarcian interval differed from the diversity dynamics of other fossil groups (e.g., foraminifera), which were not affected until the Toarcian (RUBAN & TYSZKA, 2005).

A number of possible explanations of this earlier brachiopod decline can be suggested. It appears sensible to begin its discussion within a palaeogeographical context. Regional transgressions/regressions and changes in water depth may be responsible for this peculiar decline among brachiopods. In order to establish the probable cause of the latter, a high-resolution analysis of the Pliensbachian palaeogeography of the Northern Caucasus is presented in this paper.

II. GEOLOGIC SETTING

The Northern Caucasus is a large geographical region, comprising the northern portion of the Caucasus Mountains between the Black Sea and the Caspian Sea (Fig. 1). Tectonically, it corresponds to the northern part of the Greater Caucasus structural domain. During the Early Jurassic, the Northern Caucasus was located on the northern margin of the Neo-Tethys Ocean, where a number of elongated basins and island arcs existed (Fig. 1) (MEISTER & STAMPFLI, 2000; STAMPFLI & BOREL, 2002; ERSHOV *et al.,* 2003; GOLONKA, 2004; KAZMIN & TIKHONOVA, 2006; RUBAN, 2006a; SAINTOT *et al.*, 2006; TAWADROS *et al.*, 2006; RUBAN, 2008a). The Caucasian Sea (a marginal sea of the Neo-Tethys Ocean) encoached over the entire Northern Caucasus from the south (RUBAN, 2006a).

The Pliensbachian deposits spread over the entire Northern Caucasus (ROSTOVTSEV *et al.*, 1992; RUBAN, 2007a, 2008b). They are dominated by siliciclastics and shales, whose thickness varies from 300 up to 5,000 m (Fig. 2). These strata were accumulated in the northern part of the Caucasian Sea, which was warm (JASAMANOV, 1978). The presence of black shales indicates an oxygen depletion, although an evidence for the global early Toarcian anoxia (JENKYNS *et al.*, 2002)

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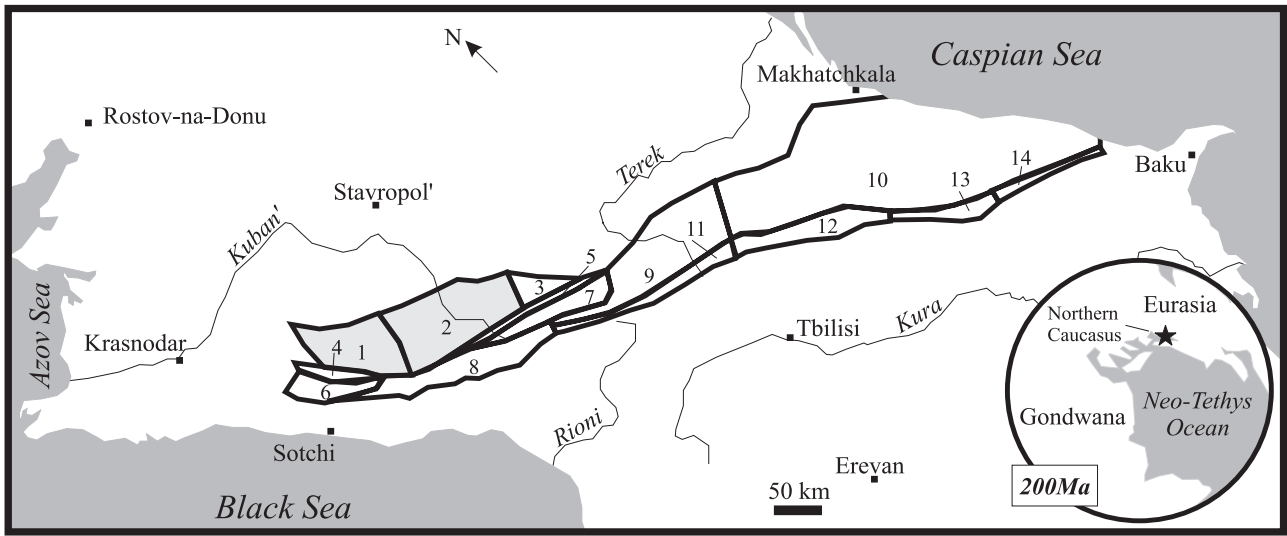   *E-mail: ruban-d@mail.ru, ruban-d@rambler.ru*

Fig. 1: The Northern Caucasus and its particular areas (adapted from ROSTOVTSEV *et al*., 1992; RUBAN, 2007a, 2008b). Areas with especially rich brachiopod assemblages are shaded by light grey. Palaeotectonic map of the Neo-Tethys Ocean is simplified after STAMPFLI & BOREL (2002). Numbers: 1 – Western Labino-Malkinskaja, 2 – Central Labino-Malkinskaja, 3 – Eastern Labino-Malkinskaja, 4 – Western Pshekish-Tyrnyauzskaja, 5 – Eastern Pshekish-Tyrnyauzskaja, 6 – Northern Arkhyz-Guzeripl'skaja, 7 – Eastern Arkhyz-Guzeripl'skaja, 8 – Southern Arkhyz-Guzeripl'skaja, 9 – Digoro-Osetinskaja, 10 – Agvali-Khivskaja, 11 – Western Bokovogo Khrebta, 12 – Central Bokovogo Khrebta, 13 – Eastern Bokovogo Khrebta, 14 – Southeastern Bokovogo Khrebta.
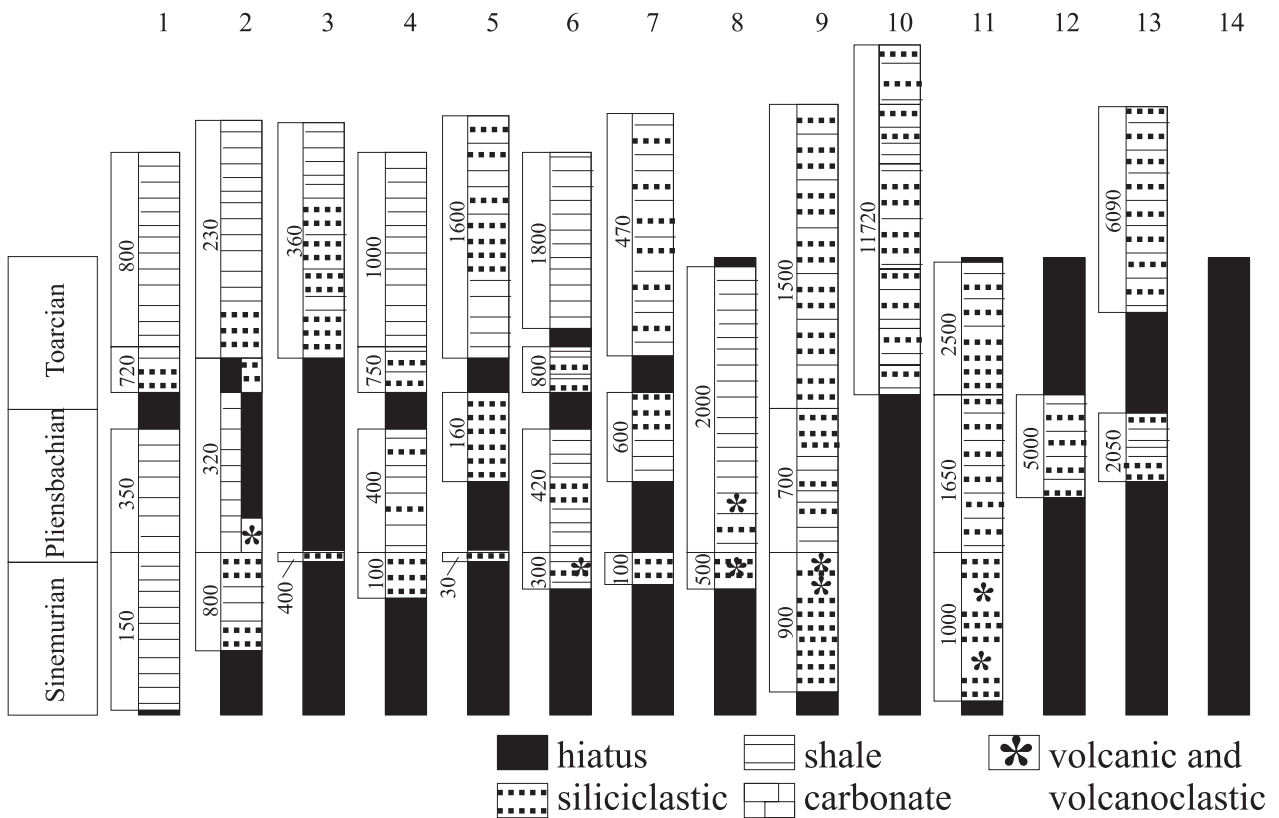

Fig. 2: The Sinemurian-Toarcian deposits of the Northern Caucasus (after ROSTOVTSEV *et al*., 1992; RUBAN, 2007a, 2008b). Numbers above columns indicate particular areas (see Fig. 1) and numbers to the left of columns indicate thickness (m).

is unclear within the study area (RUBAN, 2004; RUBAN & TYSZKA, 2005). The Northern Caucasus was populated by diverse brachiopod assemblages (MOISEEV, 1934; MAKRIDIN & KAMYSHAN, 1964; ROSTOVTSEV et al., 1992; PROSOROVSKAYA, 1993). Previous regional data on this fossil group are presently reviewed by RUBAN (2004, 2006b, 2007b).

III. MATERIAL AND METHODS

This paper makes use of data previously compiled, verified (when possible), and already published by RUBAN (2006b, 2007b). The regional reviews by MOISEEV (1934), MAKRIDIN & KAMYSHAN (1964), ROSTOVTSEV et al. (1992), and PROSOROVSKAYA (1993) were taken into account originally. The data presented by RUBAN (2004) are all considered, but this paper addresses to a geographically larger territory and several taxonomical levels of brachiopods. A total of 83 species, 34 genera, and 11 superfamilies are considered (Table 1), the majority found within the Early Jurassic deposits of the western part of the Northern Caucasus (Fig. 1). The total number of brachiopod taxa is calculated for local Sinemurian-Toarcian substages, which were mentioned by RUBAN (2004). Lower and upper Pliensbachian as defined in the Northern Caucasus correspond generally to the Carixian and the Domerian. There are no brachiopods in the lower Sinemurian and the lower Toarcian deposits. The reconstructions of transgressions/regressions and changes in the water depth are based on an interpretation of facies data from RUBAN (2007a, 2008b). The whole territory of the Northern Caucasus is divided into 14 particular areas (ROSTOVTSEV et al., 1992; RUBAN, 2007a, 2008b) (Fig. 1). An analysis of composite Sinemurian-Toarcian sedimentary successions (Fig. 2) of these areas permitted to recognize continental, shallow-marine, and deep-marine facies (RUBAN, 2007a). These data in conjunction with those from other adjacent areas of the Ciscaucasus (the territory to the north of the Northern Caucasus) and the entire Greater Caucasus (ROSTOVTSEV et al., 1992; RUBAN, 2007a, 2008b) allowed an evaluation of the basin geometry for every time slice. Seven time slices (p1-7) within the Pliensbachian are specified (Fig. 3), and a distribution of facies is depicted for every time slice in order to document the changes in both basin shoreline and water depth. A comparison of diversity patterns with the the mentioned palaeogeographical changes will allow to weigh up their probable relationships.

IV. SINEMURIAN-TOARCIAN TAXONOMIC DIVERSITY OF BRACHIOPODS

Brachiopods appeared in the Northern Caucasus in the late Sinemurian and radiated immediately. Their species
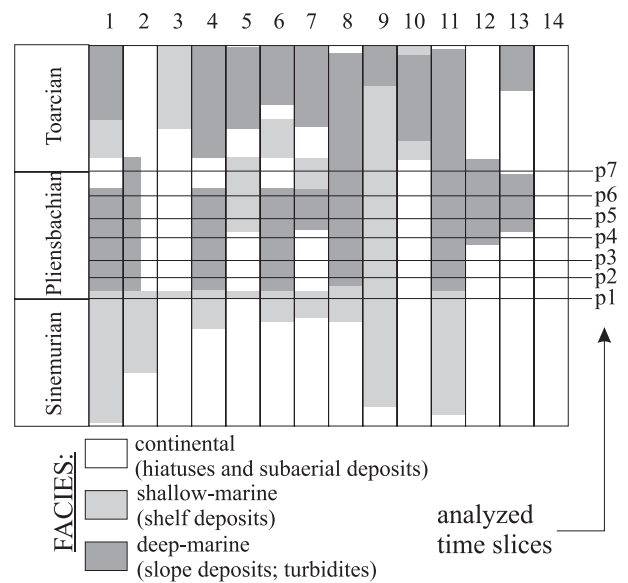
Fig. 3: The Sinemurian-Toarcian facies of the Northern Caucasus (adapted from RUBAN, 2007a) and the analyzed time slices.

and generic diversity rose by 1.5 times already in the early Pliensbachian (Fig. 4). The numer of superfamilies, however, remained the same. An abrupt decline of the total diversity occurred in the late Pliensbachian, where only 1 taxon existed, namely *Lobothyris punctata* (SOWERBY). However, the mass extinction occurred much later (HALLAM, 1986; LITTLE & BENTON, 1995; LITTLE, 1996; ABERHAN & FÜRSICH, 1997; HALLAM & WIGNALL, 1997; HARRIES & LITTLE, 1999; PÁLFY et al., 2002). It was evidently responsible for the entire regional disappearance of brachiopods in the Early Toarcian. Their weak radiation began in the middle Toarcian, when 3 species and 3 genera appeared (Fig. 4). They belong to the superfamilies Rhynchonelloidea and Rhynchotetradoidea. Recovery accelerated in the late Toarcian, when both species and generic diversity increased significantly (by about 4.5 times), whereas the total number of superfamilies returned to the same as in the late Sinemurian-early Pliensbachian. However, not all late Toarcian superfamilies were the same as before the mass extinction. Cancellothyridoidea and Wellerelloidea are not reported from the upper Toarcian of the Northern Caucasus, whereas Pugnacoidea is not found in the Sinemurian-Pliensbachain strata.

The data from the Northern Caucasus presented herein confirms an earlier conclusion (RUBAN, 2004) that the regional decline of brachiopods preceded the Early Toarcian mass extinction. Not only the total number of species, but that of genera and even superfamilies diminished abruptly at the early-late Pliensbachian transition. Taking into account the absolute ages of the lower (189.6 Ma) and upper (183.0 Ma) boundaries of

Table 1: Taxonomy of the Sinemurian-Toarcian brachiopods from the Northern Caucasus used in this study (this follows RUBAN [2007b]).

Superfamily Cancellothyridoidea	*Disculina? liasina* DESLONGCHAMPS
Superfamily Dyscolioidea	*Linguithyris? bimammata* ROTHPLETZ
Superfamily Hemithiridoidea	*Flabellirhynchia lycetti* (DAVIDSON), *Gibbirhynchia curviceps* (QUENSTEDT), *G. gibbosa* BUCKMAN, *G. heiningensis* ROLLIER, *Grandirhynchia capitulata* (TATE), *Rudirhynchia belemnitica* (QUENSTEDT), *R. calcicosta* (QUENSTEDT), *Squamirhynchia squamiplex* (QUENSTEDT), *Tetrarhynchia pontica* MOISSEJEV
Superfamily Loboidothyridoidea	*Cuersithyris radstockensis* (DAVIDSON), *Lobothyris havesfieldensis* ROLLIER, *L.? ovatissima* QUENSTEDT, *L. punctata* (SOWERBY), *L. subpunctata* (DAVIDSON)
Superfamily Norelloidea	*Praemonticlarella schuleri* (OPPEL), *Scalpellirhynchia scalpellum* (QUENSTEDT)
Superfamily Pugnacoidea	*Pseudogibbirhynchia jurensis* (QUENSTEDT), *P. moorei* (DAVIDSON)
Superfamily Rhynchonelloidea	*«Rhynchonella» babala* DUMORTIER, *"R."* ex gr. *fraasi* OPPEL, *"R." latifrons* GEYER, *"R."* ex gr. *obtusiloba* ROLLIER, *"R." reinesi* GEMMELARO, *Cuneirhynchia dalmasi* (DUMORTIER), *C. gussmani* (ROLLIER), *C. persinuata* (RAU), *C. rauei* ROLLIER, *Curtirhynchia* sp., *Furcirhynchia laevigata* (QUENSTEDT), *Homoeorhynchia deffneri* OPPEL, *H.* sp.1, *H.* sp.2, *Piarorhynchia* aff. *albertii* (OPPEL), *P. juvenis* (QUENSTEDT), *P. rostellata* (QUENSTEDT), *P. triplicata* (PHILLIPS), *P. variabilis* DAVIDSON, *Ptyctorhynchia* sp., *Rimirhynchia rimosa* (BUCH)
Superfamily Rhynchotetradoidea	*Prionorhynchia greppini* (OPPEL), *P.? regia* ROTHPLETZ, *P. serrata* (SOWERBY)
Superfamily Spiriferinoidea	*«Spiriferina» moeschi* HAAS, *Liospiriferina alpina* (OPPEL), *L. obtusa* (OPPEL), *L.* cf. *obtusa* (OPPEL), *L. rostrata* (SCHLOTHEIM), *Spiriferina angulata* OPPEL, *S. haasi* MAKRIDIN ET KAMYSHAN, *S. haueri* (SUESS), *S. ilminsteriensis* DAVIDSON, *S. walcotti* (SOWERBY)
Superfamily Wellerelloidea	*Bodrakella* aff. *bodrakensis* MOISSEJEV, *Calcirhynchia plicatissima* (QUENSTEDT), *Caucasorhynchia visnovskii* MOISSEJEV, *Cirpa borissiaki* MOISSEJEV
Superfamily Zeillerioidea	*Aulacothyris griffini* ROLLIER, *A. resupinata* (DOUVILLE), *A. salgirensis* MOISSEJEV, *Cincta leptonumismalis* (ROLLIER), *C.* cf. *numismalis* (VALENCIENNES), *Digonella subdigona* (OPPEL), *Securina partschi* (OPPEL), *Zeilleria cornuta* QUENSTEDT, *Z. davidsoni* MAKRIDIN ET KAMYSHAN, *Z. engelhardii* (OPPEL), *Z. indentata* (SOWERBY), *Z. lunaris* (ZIETEN), *Z. mutabilis* (OPPEL), *Z. ovalis* ROLLIER, *Z. ovimontana* (BOESE), *Z. perforata* (PIETTE), *Z. rehmanni* (ROEMER), *Z. retusa* MARTIN, *Z. roemeri* (SCHLOENBACH), *Z. scalprata* (QUENSTEDT), *Z. stapia* (OPPEL), *Z. subsphaeroidalis* ROLLIER, *Z. thurvieseri* BOESE, *Z. vicinalis* (SCHLOTHEIM), *Z. waterhousi* (DAVIDSON)

Taxa ranges of species are generally the same as outlined by RUBAN (2004) with two modifications listed below:
"R." ex gr. *fraasi* is found in the upper Sinemurian. *Z. waterhousi* is sinonymous to *Aulacothyris waterhousi*

the Pliensbachian as well as an approximate duration of the Domerian (about 4 myr) (GRADSTEIN *et al*., 2004; OGG *et al*., 2008), one can assume that brachiopod communities were stressed regionally at least 4 myr before the mass extinction.

V. TRANSGRESSIONS AND REGRESSIONS

Transgressions had two consequences, which were favourable for brachiopod radiation. They led to the drowning of land to establish a broad continental shelf
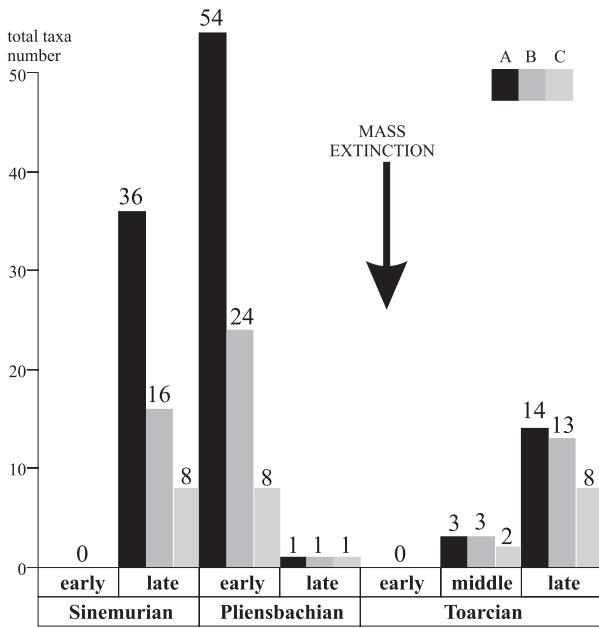
Fig. 4 : The Sinemurian-Toarcian changes in brachiopod total diversity. A - species, B - genera, C - superfamilies. Numbers above columns indicate the total diversity.

Fig. 5 : Pliensbachian facies (see legend on Fig. 3) of the Northern Caucasus for the time slices (p1-7 : see Fig. 3). Bold dashed line indicates the shoreline. Data on the Southern Ciscaucasus (ROSTOVTSEV et al., 1992) are also accounted.

to be colonized by marine shelly benthos ; and they strengthened connections with adjacent basins and oceans (e.g., HALLAM, 1987).

At the onset of the Pliensbachian, the Caucasian Sea embraced the western part of the Northern Caucasus and stretched northwards into the Southern Ciscaucasus (Fig. 5, p1). A regression occurred already in the early Pliensbachian, when the sea abandoned the Ciscaucasus and some areas in the central Northern Caucasus (Fig. 5, p2). The shoreline remained stable for some time (Fig. 5, p3), but a new transgression began in the mid-Pliensbachian, when the Caucasian Sea extended eastwards (Fig. 5, p4). This trangression was followed by the drowning of the central Northern Caucasus (Fig. 5, p5). The transgression maximum occurred during the late Pliensbachian (Fig. 5, p5-6) and was recorded as a relevant surface (RUBAN, 2008b). However, this was followed by an abrupt regression before the end-Pliensbachian. It resulted in the seaward shift of the shoreline both in the western and eastern parts of the Northern Caucasus (Fig. 5, p7).

A comparison of the Pliensbachian transgressions/ regressions with the brachiopod diversity dynamics suggests a coincidence of a major landward shift of shoreline during the mid-Pliensbachian with a sharp brachiopod decline. This unexpected observation contrasts with a hypothesis that marine transgressions commonly favour a regional increase in biodiversity (HALLAM, 1987 ; WIGNALL, 2004). Two areas in the western part of the Northern Caucasus, preferre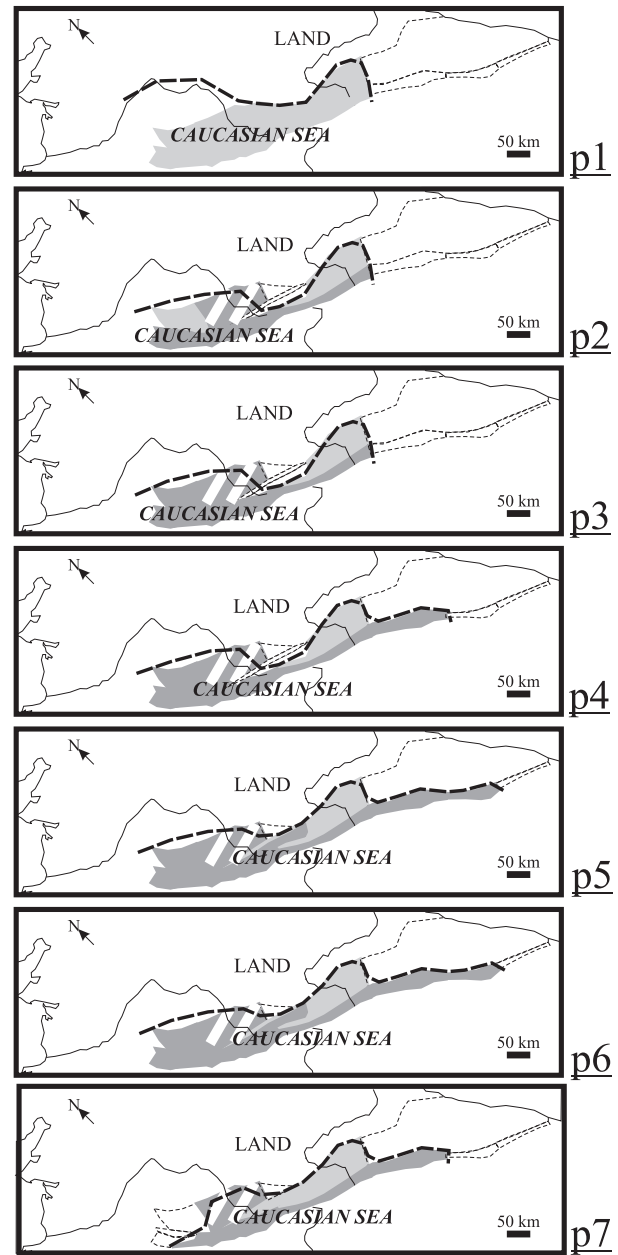d by brachiopods (Fig. 1), were not affected by shifts in the shoreline until the end of the Pliensbachian, when a regressive episode (Fig. 5, p7) was able to produce a bias in a record of brachiopods. However, these fossils are anyway not known from the "pre-regressive" upper Pliensbachian deposits, which persist in the western part of the Northern Caucasus (Figs. 2, 3). Thus, no bias, so significant to explain the lack of brachiopods in the entire late Pliensbachian, can be hypothesized.

VI. CHANGES IN WATER DEPTH

Changes in water depth seem to be another potential control on brachiopod diversity. At the beginning of the Pliensbachian, the Caucasian Sea was shallow-water (Fig. 5, p1), but rapid deepening of the southern periphery of the Northern Caucasus and its large western part began already in the early Pliensbachian (Fig. 5, p2). During the most of the Pliensbachian, the Caucasian Sea remained deep, except a large shallow shelf in its central part (Fig. 5, p3-6). A weak shallowing episode occurred at the end of the Pliensbachian, when shallow-water zone enlarged in the central part of the Northern Caucasus (Fig. 5, p7). However, a significant part of the sea remained deep even at this time.

A comparison of the above-mentioned changes in the water depth with the brachiopod diversity dynamics indicates that the decline of this fossil group coincided with a deepening of the basin. It is possible to envisage a scenario where the persistence of deep-water environments limited the ability of brachiopods to evolve. The same observation was made for the same region in the Ladinian age, when an abrupt deepening terminated the local brachiopod record. The latter subsequently restored either together with the forthcoming shallowing or due to the long-term adaptation (RUBAN, 2006d). ALMÉRAS et al. (1997) also reported that bathymetrical changes forced Pliensbachian brachiopod assemblages in the French basins.

Deepening may have stressed brachiopods both directly and indirectly. The direct influence means impoverishing of shallow-water communities in deeper environments, which might also establish barriers for exchanges with communities in adjacent regions. The indirect influence involves another phenomenon, namely oxygen depletion (HALLAM, 1987; HALLAM & WIGNALL, 1999; WIGNALL, 2004). Dys- to anoxic conditions were typical for the semi-enclosed basin of the Greater Caucasus during the entire Early-Middle Jurassic (RUBAN & TYSZKA, 2005). They are documented easily by the abundance of "black shales" with siderite concretions and pyrite mineralisation (ROSTOVTSEV et al., 1992). Basin deepening led to the water stagnation. The marine transgression, which began in the mid-Pliensbachian, led to the drowning of a densely-vegetated land, which lay to the north of the Caucasian Sea (JASAMANOV, 1978). The Pliensbachian deposits of the Northern Caucasus are quite rich in fossil plant remains (e.g., VAKHRAMEEV & KRASILOV, 1961). This permits to apply (at least in part) the model by GUEX et al. (2001) and MORARD et al. (2003), who linked the oxygen depletion with the massive input of plant remains to the basin at a time of its transgression. Thus, significant water deepening seems to be an appropriate explanation of an earlier onset of the local brachiopod crisis in comparison to the global oceanic anoxia, which took place in the early Toarcian (JENKYNS et al., 2002).

VII. DISCUSSION

The brachiopod decline which preceded the Early Toarcian mass extinction seems to have been a regional phenomenon of the Northern Caucasus, controlled by basin dynamics. Nevertheless, it is sensible to compare brachiopod diversity of this region with that of some other regions. HALLAM (1987) reported the diversity changes of the Pliensbachian rhynchonellid brachiopods in northwest Europe. Despite a strong diversity drop in the beginning of this age, the quantity of species increased during the most of the Pliensbachian with an acceleration at its end. This was followed by a striking extinction event. LITTLE & BENTON (1995), LITTLE (1996) and HARRIES & LITTLE (1999) indicated a persistence of brachiopods in the uppermost Pliensbachian deposits in the localities of the United Kingdom and Germany. Similarly, late Pliensbachian brachiopods were quite diverse in the French basins (ALMÉRAS et al., 1997). Data from the Bakony Mountains of Hungary presented by VÖRÖS (1993, 1995) indicate a considerable diminishing of the brachiopod species diversity during the latest Pliensbachian, already suggested as a similar trend to that of the Caucasus (RUBAN, 2004). However, extinctions in the Bakony Mountains realized within much shorter time A review of the Early Jurassic fossils from the Pacific margin of North America (SMITH et al., 1994) implies that none of the 8 Liassic brachiopod taxa occurs in the upper Pliensbachian deposits of this region, whereas two species are known from the lower Pliensbachian. In contrast, the Pacific margin of South America provides an evidence about brachiopod diversification throughout the Pliensbachian. RICCARDI et al. (1990) mention 13 species from the lower Pliensbachian and 19 species from the upper Pliensbachian. Moreover, 9 of these taxa survived in the earliest Toarcian.

Thus, one can observe a difference between the Pliensbachian record across the globe. Local environmental factors (such as deepening in the Northern Caucasus) created especially unfavourable conditions for brachiopod radiation. Consequently, it is likely that these conditions were not related to those provoked the Early Toarcian mass extinction. In some regional records, the coincidence of global and local environmental effects, responsible for the pre-extinction decline and the mass extinction itself, may have led to confusion and an exaggeration of the catastrophe duration (e.g., RUBAN, 2004). When deepening in the mid-Pliensbachian resulted in almost total demise of brachiopods in the Northern Caucasus, the absence of these fossils in the early Toarcian (Fig. 3) was a result of the mass extinction. However, the influence of the latter on already-diminished brachiopod assemblages could make this mass extinction more devastative. In comparison, foraminifers were not affected until the Toarcian, and their mass extinction-related decline was not so dramatic as that of brachiopods (RUBAN & TYSZKA, 2005).

VIII. CONCLUSIONS

In the Northern Caucasus, brachiopods declined long before the Early Toarcian mass extinction. The diversity of species, genera, and superfamilies dropped during the middle of the Pliensbachian. It is proposed that this regional decline, which preceded the global-scale catastrophe, was a result of a regional water deepening, which initiated oxygen depletion. In some other regions, brachiopods were not impoverished before the end of the Pliensbachian as they did in the Northern Caucasus. Thus, an earlier decline of brachiopods in particular regions was not related genetically to their Early Toarcian extinction. Previous studies suggested that sea-level changes should not be considered as the only triggers of biodiversity and mass extinctions (MCROBERTS & ABERHAN, 1997; RUBAN, 2004a, 2006c, 2007a). The results from this study, however, underline that a clear separation between transgressions/regressions and changes in water depth should be made in order to support such a conclusion. Indirect influences of basin dynamics as well as a composite effect of its patterns need also to be considered.

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REFERENCES

ABERHAN, M. & F.T. FÜRSICH (1997) - Diversity analysis of Lower Jurassic bivalves of the Andean Basin and the Pliensbachian-Toarcian mass extinction. *Lethaia*, 29: 181-195.

ALMÉRAS, Y., A. BOULLIER & B. LAURIN (1997) - Brachiopodes. *In*: CARIOU, E. & P. HANTZPERGUE (Eds.). Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. *Bulletin de le Centre de la Recherche Elf Exploration Production, Mémoire*, 17: 169-195.

ERSHOV, A.V., M.-F. BRUNET, A.M. NIKISHIN, S.N. BOLOTOV, B.P. NAZAREVICH & M.V. KOROTAEV (2003) - Northern Caucasus basin: thermal history and synthesis of subsidence models. *Sedimentary Geology*, 156: 95-118.

GOLONKA, J. (2004) - Plate tectonic evolution of the southern margin of Eurasia in the Mesozoic and Cenozoic. *Tectonophysics*, 381: 235-273.

GRADSTEIN, F.M., J.G. OGG, A.G. SMITH, F.P. AGTERBERG, W. BLEEKER, R.A. COOPER, V. DAVYDOV, P. GIBBARD, L.A. HINNOV, M.R. HOUSE, L. LOURENS, H.P. LUTERBACHER, J. MCARTHUR, M.J. MELCHIN, L.J. ROBB, J. SHERGOLD, M. VILLENEUVE, B.R. WARDLAW, J. ALI, H. BRINKHUIS, F.J. HILGEN, J. HOOKER, R.J. HOWARTH, A.H. KNOLL, J. LASKAR, S. MONECHI, K.A. PLUMB, J. POWELL, I. RAFFI, U. ROHL, P. SADLER, A. SANFILIPPO, B. SCHMITZ, N.J. SHACKLETON, G.A. SHIELDS, H. STRAUSS, J. VAN DAM, T. VAN KOLFSCHOTEN, J. VEIZER & D. WILSON (2004) - *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, 589 pp.

GUEX, J., A. MORARD, A. BARTOLINI & E. MORETTINI (2001) - Découverte d'une importante lacune stratigraphique à la limite Domérien-Toarcien: implications paléo-océanographiques. *Bulletin Société vaudoise des Sciences naturelles*, 87: 277-284.

HALLAM, A. (1986) - The Pliensbachian and Tithonian extinction events. *Nature*, 319: 765-768.

HALLAM, A. (1987) - Radiations and extinctions in relation to environmental change in the marine Lower Jurassic of northwest Europe. *Paleobiology*, 13: 152-168.

HALLAM, A. & P.B. WIGNALL (1997) - *Mass Extinctions and their Aftermath*. Oxford University Press, Oxford, 320 pp.

HALLAM, A. & P.B. WIGNALL (1999) - Mass extinctions and sea-level changes. *Earth-Science Reviews*, 48: 217-250.

HARRIES, P. & C.T.S. LITTLE (1999) - The early Toarcian (Early Jurassic) and the Cenomanian-Turonian (Late Cretaceous) mass extinctions: similarities and contrasts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 154: 39-66.

JASAMANOV, N.A. (1978) - *Landshaftno-klimatitcheskie uslovija jury, mela i paleogena Juga SSSR*. Nedra, Moskva, 224 pp. (in Russian).

JENKYNS, H.C., C.E. JONES, D.R. GROECKE, S.P. HESSELBO & D.N. PARKINSON (2002) - Chemostratigraphy of the Jurassic System: applications, limitations and implications for palaeoceanography. *Journal of the Geological Society, London*, 159: 351-378.

KAZMIN, V.G. & N.F. TIKHONOVA (2006) - Evolution of Early Mesozoic back-arc basins in the Black Sea-Caucasus segment of a Tethyan active margin. *In*: ROBERTSON, A.H.F. & D. MOUNTRAKIS (Eds.). Tectonic Development of the Eastern Mediterranean Region. *Geological Society, London, Special Publications*, 260: 179-200.

LITTLE, C.T.S. (1996) - The Pliensbachian-Toarcian (Lower Jurassic) extinction event. *In*: RYDER, G, D. FASTOVSKY & S. GARTNER (Eds.). The Cretaceous-Tertiary Event and Other Catastrophes in Earth History. *Geological Society of America, Special Paper*, 307: 505-512.

LITTLE, C.T.S. & M.J. BENTON (1995) - Early Jurassic mass extinction: A global long-term event. *Geology*, 23: 495-498.

MAKRIDIN, V.P. & V.P. KAMYSHAN (1964) - Stratigrafitcheskoe raspredelenie brakhiopod v jurskikh otlozhenijakh zapadnoj i tsentral'noj tchastej Severnogo Kavkaza. *In*: ANDRUTSCHUK, V.L. (Ed.). *Trudy po geologii i poleznym iskopaemym Severnogo Kavkaza*, Stavropol'skoe knizhnoe izdatel'stvo, Stavropol', 11: 54-61. (in Russian).

MCROBERTS, C.A. & M. ABERHAN (1997) - Marine diversity and sea-level changes: numerical tests for association using Early Jurassic bivalves. *International Journal of Earth Sciences*, 86: 160-167.

MEISTER, Ch. & G. STAMPFLI (2000) - Les ammonites du Lias moyen (Pliensbachien) de la Néotéthys et de ses confins ; compositions fauniques, affinités paléogéographiques et biodiversité. *Revue de Paléobiologie*, 19 : 227-292.

MOISEEV, A.S. (1934) - *Brakhiopody jurskikh otlozhenij Kryma i Kavkaza*. NKTP Edition, Moskva, 212 pp. (in Russian).

MORARD, A., J. GUEX, A. BARTOLINI, E. MORETTINI & P. DE WEVER (2003) - A new scenario for the Domerian – Toarcian transition. *Bulletin de la Société géologique de France*, 174 : 351-356.

OGG, J.G., G. OGG & F.M. GRADSTEIN (2008) - *The Concise Geologic Time Scale*. Cambridge University Press, Cambridge, 177 pp.

PÁLFY, J., P.L. SMITH & J.K. MORTENSEN (2002) - Dating the end-Triassic and Early Jurassic mass extinctions, correlative large igneous provinces, and isotopic events. *In* : KOEBERL, C. & K. E. MACLEOD (Eds.). Catastrophic Events and Mass Extinctions : Impacts and Beyond, *Geological Society of America Special Paper,* 356 : 523-532.

PROSOROVSKAYA, E.L. (1993) - Brachiopod subdivisions in the Jurassic of the southern ex-USSR. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 100 : 183-188.

RICCARDI, A.C., S.E. DAMBORENEA, M.O. MANCEÑIDO, A. BALDONI, S. BALLENT, Z. GASPARINI, A. VON HILLEBRANDT, M. E. QUATTROCCHIO, W. VOLKHEIMER & A.M. ZAVATTIERI (1990) - Lower Jurassic of South America and Antarctic Peninsula. *Newsletters on stratigraphy,* 21 : 75-103.

ROSTOVTSEV, K.O., V.B. AGAEV, N.R. AZARJAN, R.G. BABAEV, N.V. BEZNOSOV, T.A. GASANOV, V.I. ZESASHVILI, M.G. LOMIZE, T.A. PAITCHADZE, D.I. PANOV, E.L. PROSOROVSKAYA, A.S. SAKHAROV, V.A. TODRIA, M.V. TOPTCHISHVILI, M.R. ABDULKASUMZADE, A.S. AVANESJAN, V.S. BELENKOVA, N.S. BENDUKIDZE, V.Â. VUKS, M.P. DOLUDENKO, A.I. KIRITCHKOVA, V.G. KLIKUSHIN, G.Â. KRYMGOL'TS, G.M. ROMANOV & T.V. SHEVTCHENKO (1992) - *Jura Kavkaza*. Nauka, Sankt-Peterburg, 185 pp. (in Russian)

RUBAN, D.A. (2004) - Diversity dynamics of Early-Middle Jurassic brachiopods of Caucasus, and the Pliensbachian-Toarcian mass extinction. *Acta Palaeontologica Polonica*, 49 : 275-282.

RUBAN, D.A. (2006a) - The Palaeogeographic Outlines of the Caucasus in the Jurassic : The Caucasian Sea and the Neotethys Ocean. *Geolo⬚i anali Balkanskoga poluostrva*, 67 : 1-11.

RUBAN, D.A. (2006b) - Diversity changes of the Brachiopods in the Northern Caucasus : a brief overview. *Acta Geologica Hungarica*, 49 : 57-71.

RUBAN, D.A. (2006c) - Taxonomic diversity dynamics of the Jurassic bivalves in the Caucasus : regional trends and recognition of global patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239 : 63-74.

RUBAN, D.A. (2006d) - Diversity dynamics of the Triassic marine biota in the Western Caucasus (Russia) : A quantitative estimation and a comparison with the global patterns. *Revue de Paléobiologie*, 25 (2) : 699-708.

RUBAN, D.A. (2007a) - Jurassic transgressions and regressions in the Caucasus (northern Neotethys Ocean) and their influences on the marine biodiversity. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 251 : 422-436.

RUBAN, D.A. (2007b) - Taxonomic diversity structure of brachiopod associations at times of the early Mesozoic crises : evidence from the Northern Caucasus, Russia (northern Neotethys Ocean). *Paleontological Research*, 11 : 349-358.

RUBAN, D.A. (2008a) - The Jurassic events in the Greater Caucasus Basin (Northern Neotethys) and the Neuquén Basin (West Gondwana). *Revista de la Asociación Geológica Argentina*, 63 : 766-775.

RUBAN, D.A. (2008b) - Jurassic maximum flooding surfaces in the Greater Caucasus Basin (Northern Neo-Tethys). *Central European Geology*, 51 : 99-112.

RUBAN, D.A. & J. TYSZKA (2005) - Diversity dynamics and mass extinctions of the Early-Middle Jurassic foraminifers : A record from the Northwestern Caucasus. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 222 : 329-343.

SAINTOT, A., M.-F. BRUNET, F. YAKOVLEV, M. SÉBRIER, R. STEPHENSON, A. ERSHOV, F. CHALOT-PRAT & T. MCCANN (2006) - The Mesozoic-Cenozoic tectonic evolution of the Greater Caucasus. *In* : GEE, D.G. & R.A. STEPHENSON (Eds.). European Lithosphere Dynamics. *Geological Society, London, Memoirs*, 32 : 277-289

SMITH, P.L., J.M. BEYERS, E.S. CARTER, G.K. JACOBS, J. PÁLFY, E. PESSAGNO & H.W. TIPPER (1994) - Lower Jurassic. *In* : WESTERMANN, G.E.G. & A.C. RICCARDI (Eds.). Jurassic Taxa Ranges and Correlation Charts for the Circum Pacific. North America. *Newsletters on Stratigraphy*, 5 : 1-38.

STAMPFLI, G.M. & G.D. BOREL (2002) - A plate tectonic model for the Paleozoic and Mesozoic constrained by dynamic plate boundaries and restored synthetic oceanic isochrons. *Earth and Planetary Science Letters*, 196 : 17-33.

TAWADROS, E., D. RUBAN & M. EFENDIYEVA (2006) - Evolution of NE Africa and the Greater Caucasus : Common Patterns and Petroleum Potential. *The Canadian Society of Petroleum Geologists, the Canadian Society of Exploration Geophysicists, the Canadian Well Logging Society Joint Convention. May 15-18, 2006*, Calgary, 531-538.

VAKHRAMEEV, V.A. & V.A. KRASILOV (1961) - Domerskaja flora Severnogo Kavkaza. *Paleontologitcheskij zhurnal*, 3 : 101-108. (in Russian).

VÖRÖS, A. (1993) - Jurassic brachiopods of the Bakony Mts (Hungary) : global and local effectson changing diversity. *In* : PÁLFY, J. & A. VÖRÖS (Eds.). *Mesozoic brachiopods of Alpine Europe*. Hungarian Geological Society, Budapest : 179-187.

VÖRÖS, A. (1995) - Extinctions and survivals in a Mediterranean Early Jurassic Brachiopod fauna (Bakony Mts, Hungary). *Hantkeniana*, 1 : 145-154.

WIGNALL, P.B. (2004) - Causes of mass extinctions. *In* : TAYLOR P.D. (Ed.). *Extinctions in the History of Life*. Cambridge University Press, Cambridge : 119-150.