Spatio-temporal patterns of the Callovian-Oxfordian ammonite generic diversity in the transgressing Caucasian Sea (northern Neo-Tethys)

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Abstract
Possible influences of transgressions and regressions on marine invertebrates remain questionable. Data on distribution of 25 ammonite genera in the Caucasian Sea, a typical marginal sea on the northern active margin of the Neo-Tethys Ocean, permits to evaluate an effect of the regional Callovian-Oxfordian transgression on the diversity of their assemblages. Both temporal and spatial patterns of the latter are examined. The total number of genera accelerated significantly during the Early-Middle Callovian together with a strong transgression. However, diversity declined throughout the Late Callovian-Late Oxfordian interval with its biggest losses at the Late Callovian-Early Oxfordian and the Early-Middle Oxfordian transitions, when assemblages impoverished by 40 % and 50 % respectively. This occurred despite of an ongoing transgression. Mapping assemblage diversity for 7 time slices (beginning of the Callovian, Early, Middle, Late Callovian, and Early, Middle, Late Oxfordian) permits to document that ammonites inhabited only the northern part of the Caucasian Sea, which remained shallow. The Early Callovian sea ingressed and opened new dispersal routes for ammonites, which, thus, inhabited the sea from the northwest and the northeast, i.e., from marginal seas of the Mediterranean sector of the Neo-Tethys and interior seas of the Russian Platform. Further transgression strengthened these faunal exchange and, consequently, enhanced the Middle Callovian generic diversity. Slowing of the transgression since the Late Callovian made other factors of diversity dynamics more important. Either global decrease in ammonite taxa number or shrinkage of dispersal routes due to tectonic activity in the Alpine-Carpathian domain led to the gradual demise of ammonites occurred in the study region. Ammonites became unable to inhabit the deeper southern part of the Caucasian Sea during the entire Callovian-Oxfordian interval. This study suggests an absence of any simple relationship between ammonite generic diversity and transgressions/regressions.

Keywords
ammonites, generic diversity, transgression, Callovian, Oxfordian, Caucasian Sea, Neo-Tethys Ocean.

1. INTRODUCTION
Changes in the global marine biodiversity were at least partly controlled by the sea-level fluctuations (PURDY, 2008). However, some evidences do not confirm this rule as for the entire biota (STANLEY, 2007) as for particular fossil groups (MCROBERTS & ABERHAN, 1997; RUBAN, 2007). NEIGE et al. (1997), O’DOHERTY et al. (2000), and SANDOVAL et al. (2001a,b) documented relationships between ammonite diversity and regional sea-level changes. RUBAN (2007) reported that ammonites, in contrast to belemnites, bivalves, and brachiopods were probably the only group enforced significantly by regional transgressions and regressions. Detailed data from the Greater Caucasus, a large region on the northern Neo-Tethyan margin (Fig. 1), can be used to test these observations.

The Caucasian Sea transgressed progressively throughout the Callovian-Oxfordian time interval. When low-resolution analysis indicated a gradual landward shift of the shoreline (RUBAN, 2006b), the more detailed study permitted to recognize a stepwise transgression, which started already in the earliest Callovian (RUBAN, 2007, 2008a). Previous analysis of ammonite diversity responses to this transgression (RUBAN, 2007) was very provisional. It concerned the entire Caucasus and the only species diversity. Moreover, only temporal relationships were examined. The present study has a different purpose. It concerns ammonite genera strictly from the Caucasian Sea, providing a high-resolution analysis of both temporal and spatial diversity patterns and their possible correspondence with the registered sea transgression. It appears results from this study may become useful to enlarge our general knowledge on ammonite diversity responses to shoreline shifts.

II. GEOLOGIC SETTING
The study region is the Greater Caucasus, which lies at the border of Russia, Georgia, and Azerbaijan. It stretches presently as a mountain chain between the Black Sea
and the Caspian Sea (Fig. 1). The Jurassic stratigraphy, tectonics, and palaeogeography of this region were reviewed by JasamAnov (1978), lordKiPanidZe et al. (1984), GamKreLiDze (1986), Rostovtsev et al. (1992), KuznEtsov (1993), Ershov et al. (2003), KazaMin & Tikhonova (2006), Ruban (2006a, 2007), Saintot et al. (2006), and TawadroS et al. (2006). The Caucasian Sea existed since the Early Jurassic. It embraced a large territory between the land of the Russian Platform in the north and the Transcaucasian island arc in the south (Ruban, 2006a). This was a northern marginal sea of the Neo-Tethys Ocean. Tectonics of the northern Neo-Tethys was active and characterized by interactions between numerous terranes (DerCourT et al., 2000; StaMPlfi & BoReL, 2002; GolonkA, 2004; ScoTese, 2004). The Caucasian Sea embraced the Greater Caucasus Basin (Fig. 1). This back-arc basin had a very gentle northern slope and a very steep southern slope. During the Late Jurassic, the Greater Caucasus Basin extended (lordKiPanidZe et al., 1984; Ershov et al., 2003; KazaMin & Tikhonova, 2006) after an enigmatic contractional phase, which occurred in the Bathonian (Ershov et al., 2003; Ruban, 2006a). The Callovian-Oxfordian litho- and biostratigraphic frameworks of the Greater Caucasus Basin were established by Rostovtsev et al. (1992). The regional ammonite-based biozonation was further verified by Ruban (2006a, 2007) according to the current developments in European regions (Cariou & Hantzpergue, 1997), whereas lithologic data were examined and summarized by Ruban (2007). The Lower-Middle Callovian deposits are dominated by siliciclastics with a total thickness up to 600 m (Fig. 2). The Upper Callovian-Oxfordian strata are dominated by carbonates in the northern part of the basin and carbonate-siliciclastic flysch in its southern part. Their total thickness reaches 900 m. Carbonate complexes were formed on a large carbonate platform, which evolved in the study region since the Late Callovian (KuznEtsov, 1993; Ruban, 2005, 2006b). In the Callovian-Oxfordian time interval, the Caucasian Sea was warm (JasamAnov, 1978), which permitted reefal communities to flourish (KuznEtsov, 1993; Martin-GariN et al., 2002; Ruban, 2005, 2006a,b). Both coral and sponge-algal buildups are reported from the Greater Caucasus (Rostovtsev et al., 1992).

The Caucasian Sea was located at an intersection of two seaways. One connected boreal seas and interior seas of the Russian Platform with the Neo-Tethys Ocean, whereas another linked European and Asiatic marginal seas (Ruban, 2006a). Both seaways might have served as potential migration routes for invertebrates. The marine life was very abundant and diverse in the Callovian-Oxfordian Caucasian Sea, which was populated by ammonites, belemnites, bivalves, brachiopods, corals, sponges, echinoids, etc. (Rostovtsev et al., 1992; Ruban, 2007). Palaeobiographically, the study region belonged to the Mediterran-Caucasian Subrealm (WeStermann, 2000).

### III. MATERIALS AND METHODS

Stratigraphic distribution of Callovian-Oxfordian ammonite genera was established precisely in each of 13 particular areas of the Greater Caucasus Basin. Comprehensive data presented by Rostovtsev et al. (1992) were extracted and compiled for this purpose. Some taxonomic corrections were made where necessary. *Dichotomosphinctes* and *Kranaosphinctes* are considered by Rostovtsev et al. (1992) as particular genera, although they are subgenera of *Perisphinctes* (Cariou & Hantzpergue, 1997; Gygi, 2001). In general, 25 ammonite genera populated the Caucasian Sea during the Callovian-Oxfordian. These include *Brightia, Cadoceras,*...
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Cardioceras, Creniceras, Ermmoceras, Euaspidoceras, Grossouvria, Hecticeras, Kepperlites, Kosmoceras, Lunuloceras, Macrocephalites, Ochotoceras, Peltoceras, Perispinctes, “Perispinctes”, Proplanulites, Puteolicaeas, Quenstedtoceras, Reineckelites, Rollierites, Sigaloceras, Sivajiceras, Trimarginites, and Vertumniceras. A total of 15 assemblages can be delineated (Table 1). Each of them corresponds to a particular substage in a given area.

The total generic diversity of ammonites was calculated for each of Callovian and Oxfordian substage. This was plotted against the regional transgressive-regressive curve constrained by RUBAN (2008a) to conclude about possible relationships. Then, an accurate spatial analysis of data was attempted. A distribution of ammonite assemblages and their relative diversity were mapped for 7 time slices, which corresponded to 1) the beginning of the Callovian, 2) the Early Callovian, 3) the Middle Callovian, 4) the...
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Table 1: Callovian-Oxfordian ammonite assemblages of the Greater Caucasus Basin (0 - lack of ammonites, X - lack of deposits). Illustrations of some characteristic taxa can be found in Stankevitch (1964) and Lominadze (1967, 1975, 1982).
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Late Callovian, 5) the Early Oxfordian, 6) the Middle Oxfordian, and 7) the Late Oxfordian. An approximate position of the shoreline was also depicted on these maps. It was evaluated with an account of sedimentary hiatuses (Fig. 2), lithological indicators like basal conglomerate units or cross-bedding (ROSTOVTEV et al., 1992), facies distribution in adjacent Caucasian areas (RUBAN, 2007), and also previous palaeogeographic reconstructions by JASAMANOV (1978). The author’s field observations in the Western Caucasus helped to justify these spatial constraints. Shoreline shifts, which can be registered with the noted maps, indicate a direction of transgression, which can be brought in correspondence with a spatial distribution of ammonite assemblages.

IV. TOTAL AMMONITE DIVERSITY DYNAMICS AND SHORELINE SHIFTS

The dynamics of ammonite generic diversity in the Caucasian Sea during the Callovian-Oxfordian can be described as a unique cycle (Fig. 3). The number of genera accelerated rapidly already in the Early Callovian. The total diversity peaked in the Middle Callovian to be followed by a gradual, but prominent decrease towards the end of the Oxfordian. The Late Oxfordian generic diversity was minimal; just 2 genera, namely Perisphinctes and Euaspidoceras, are known from this time interval. It appears that the biggest losses in the total number of taxa occurred at the Late Callovian-Early Oxfordian transition, when the generic diversity decreased by 40%, and the Early-Middle Oxfordian transition, when the generic diversity decreased by 50%. Euaspidoceras, Peltoceras, and Perisphinctes were the only genera, which crossed the Callovian/Oxfordian boundary.

The documented diversity dynamics did not correspond well to the shifts in the shoreline. When the Early-Middle Callovian ammonite radiation occurred together with a very strong and rapid transgression, further transgressive trend coincided with a decline of ammonite assemblages (Fig. 3). The Early-Middle Oxfordian decrease in the taxa number occurred at a time of weak transgressive pulse in the Caucasian Sea. It is sensible to note that the regional landward shoreline shift of the Caucasian Sea throughout the Callovian-Oxfordian time interval coincided generally with the global eustatic rise, indicated by both available alternative curves despite of some inconsistencies between them (Fig. 3). However, the strong Early Callovian transgressive pulse is ambiguous in the light of global constraints (Fig. 3).

V. SPATIAL RELATIONSHIPS BETWEEN DIVERSITY AND SHORELINE SHIFTS

The Caucasian Sea was very narrow at the beginning of the Callovian (Fig. 4A). A large Ciscaucasian plain lay to the north, whereas a chain of islands situated to the south. The sea looked like a strait, and it was not inhabited by ammonites (at least, previous detailed studies (see overview in ROSTOVTEV et al., 1992) didn’t provide an evidence about the latters and deposits of this age do not seem infavourable for ammonite preservation). However, the situation changed significantly already in the Early Callovian. The sea ingressed to the north to form large bays from both sides of the Ciscaucasian peninsula of the Don landmass existed within the Russian Platform (JASAMANOV, 1978). Available information on the Jurassic deposits of the Ciscauscasus (JASAMANOV, 1978; LETAVIN et al., 1987; ROSTOVTEV et al., 1992) permits to conclude that an ingestion to the northwest was very strong and the bay, formed there initially, soon connected with the interior seas of the Russian Platform in the north and the other Neo-Tethyan marginal seas in the west. Another connection might have appeared in the northeast. This new water spaces were populated by low-to moderately-diverse ammonite assemblages (Fig. 4B) with a different taxonomic composition (Table 1). These assemblages included one common genera, namely Kepplerites. Transgression continued in the Middle Callovian. Ammonite assemblages, which inhabited the sea around the Ciscaucasic Peninsula, diversified again (Fig. 4C). Moreover, a new low-diverse assemblage populated the drowned area in the eastern part of the sea. However, ammonites did not appear in the southern part of the latter. Equally high diversity of assemblages from the Labinskaja and Kabardino-Dagestanskaja areas permits to calculate their similarity with the so-called JACCARD’s index (JACCARD, 1901; RUBAN, 2006b). These assemblages contained 7 common genera (Erymnoceras, Kosmoceras, Putealiceras, Reineckeia, “Perisphinctes”, Hecticoceas, and Lunuloceras), and each had a diversity...
of 10 genera (Table 1). Thus, their similarity was as large as 0.54. The assemblage from the Jugo-Vostotchnyj Dagestan area consisted of taxa common for two other assemblages. Thus, one can imply a regional homogeneity of ammonite fauna. Further transgression led to the drowning of the Ciscaucasian Peninsula. This territory was inhabited by ammonites, which, thus, persisted along the entire northern part of the Caucasian Sea in the Late Callovian (Fig. 4D). A simultaneous transgression over the Caucasian Island did not correspond to the migration of ammonites in this direction. Assemblages of that time differed from one another stronger than in the Middle Callovian. The JACCARD’s similarity between the Labinskaja and Kabardino-Dagestansksja areas was 0.33, and just 3 common taxa (Peltoceras, Kosmoceras, and Quenstedtoceras) were found (Table 1). Ammonite assemblage, which populated the Malkinskaja area, contained 2 genera (Quenstedtoceras and Kosmoceras) common for two other areas mentioned above.

The situation did not change in the Early Oxfordian (Fig. 4E). The Caucasian Sea transgressed over the islands in the Middle Oxfordian (Fig. 4F) and then in the Late Oxfordian (Fig. 4G), which, however, did not result any change in the spatial distribution of ammonite assemblages. The only northern part of the basin remained populated by this fossil group. Moreover, assemblages impoverished...
even there. In the Late Oxfordian, ammonites quit the Labinskaja area. An absence of significant changes in the distribution of ammonites in the Caucasian Sea during the Oxfordian can be explained by a stability of basin geometry. The Oxfordian assemblages shared common genera in each analyzed time slice (Table 1). An exception is the Middle Oxfordian time, when Ochetoceras, the only genus known from the Labinskaja area, did not exist in the Kabardino-Dagestanskaja area. This was probably linked with a decline of ammonites in the Labinskaja area until a shrinkage in their distribution in the Late Oxfordian (Fig. 4G, Table 1) or with a slight difference in age between the assemblages of the Labinskaja and Kabardino-Dagestanskaja areas.

An attempted spatial analysis permits to make three general considerations. First, distribution of ammonites followed a direction of transgression. These fossils rapidly populated the northern margin of the Caucasian sea in the Early Callovian and the drowned land in the Middle-Late Callovian. Second, ammonite assemblages tended to persist for a long time in already inhabited areas. They appeared in the Labinskaja and Kabardino-Dagestanskaja areas in the Early Callovian and remained there during the most part of the studied time interval. Moreover, these were those assemblages, which experienced the total diversity acceleration in the Middle Callovian. Third, ammonites were unable to spread to the southern part of the Caucasian Sea, which remained open for faunal invasion since the beginning of the Callovian. A tentative explanation of these and other observations is given below.

VI. DISCUSSION

The observed spatio-temporal patterns of ammonite diversity in the Caucasian Sea during the Callovian-Oxfordian and their complicated relationship with the regional transgression require a proper explanation. It is very clear that ammonite diversity was transgression-driven during the Early-Middle Callovian, whereas it was not so during the Late Callovian-Oxfordian. Both temporal and spatial analyses suggest that the post-Middle Callovian transgression was weak in comparison to the dramatic landward shoreline shift occurred in the Early-Middle Callovian. Thus, a relative importance of transgressive control over the regional ammonite generic diversity diminished since the Late Callovian. This could permit other factors of prevail and to drive the changes in taxa number. In other words, transgressive environments were favourable for the ammonite radiation, but ammonites were unable to support their diversity at a certain level.

An important task is to find a trigger of the ammonite diversity decline since the Late Callovian. The first reasonable explanation would involve any global-scale factor(s) linked with the evolution of the entire fossil group. An analysis of ammonite subfamilies diversity by TINTANT (1988) permitted to document a very strong radiation among this fossil group in the Callovian to be followed by a strong decline in the Oxfordian. However, detailed constraints of the ammonite diversity dynamics in the Betic Cordillera by SANDOVAL et al. (2001a) did not provide an evidence of a crisis in the Oxfordian. In this region, the number of genera increased in the Early Callovian, which was followed by a profound decline. A recovery began just in the Oxfordian. Diversity accelerated rapidly and reached its peak in the Late Oxfordian, although a minor decline occurred at the end of this age. Such a dynamics does not resemble that observed in the Greater Caucasus (Fig. 3). The Early Callovian radiation is the only common event. Perturbations of ammonites at the Middle-Late Jurassic transition recorded in Europe could be linked with the regional tectonic activity (MARCHAND, 1984), and, thus, it appears questionable whether they reflected any global pattern or whether the same tectonically-enforced biotic changes could also occur in the Greater Caucasus. WESTERMANN (1993) depicted some major-scale changes in the ammonite evolution at the Callovian/Oxfordian boundary and within the Oxfordian. These can be related with perturbations of ammonite assemblages in the Caucasian Sea, which are documented at the Late Callovian-Early Oxfordian and Early-Middle Oxfordian transitions (see above). On the basis of these considerations, a control of global-scale processes on the biotic evolution within the Caucasian Sea cannot be fully excluded.

Some environmental regional causes of the Late Callovian-Oxfordian ammonite decline in the Caucasian Sea should be addressed specially. Changes in the regional sea-water temperature should be rejected as a possible trigger of the ammonite diversity loss. No cooling, but, in contrast, significant warming occurred in the Caucasian Sea in the Oxfordian as recorded by the regional palaeotemperature studies (JASAMANOVIĆ, 1978; RUBAN, 2006b). Thus, palaeoenvironments remained favourable for the ammonite evolution. There is no consensus on global palaeoenvironmental changes across the Callovian-Oxfordian transition. When some specialists argue a glaciation and cooling (DROMART et al., 2003), the others indicate a palaeoenvironmental stability (WIERZBOWSKI et al., 2009). Therefore, it remains unclear whether there was a climatic trigger of faunal change at this transition. The regional growth of a carbonate platform rimmed by reefs since the Late Callovian (KUZNETSOV, 1993; RUBAN, 2005, 2006b, 2008b) also cannot be considered as a cause of the generic diversity decline. Ammonites are known from the same areas, where carbonate deposition occurred. Moreover, these fossils are found together with carbonate buildups (Fig. 4E-G). Evidently, reefs did not serve as barriers for ammonite distribution in the northern part of the Caucasian Sea.
A special attention needs to be paid to the dispersal routes of ammonites through seaways. Although some taxa might have arrived potentially from the south, i.e., from the Neo-Tethys Ocean, we need to exclude this possibility because of lack of ammonites in the southern part of the Caucasian Sea (Fig. 4). However, some taxa might have inhabited its northern part from the northwest and the northeast (Fig. 5), where connections with interior seas of the Russian Platform and marginal seas of the Mediterranean sector of the Neo-Tethys established since already the Early Callovian. These directions of ammonite dispersal to the Caucasian Sea is confirmed by the results of spatial analysis. The Middle Callovian generic diversity accelerated in those areas, which lay first on the possible dispersal routes (Fig. 4C). Faunal exchanges through the western and eastern edges of the Caucasian Sea seem quite improbable. No ammonites are known from its westernmost part, whereas the Early Callovian assemblage populated its eastern part (proximal to the large island mass) was poor and included *Parthsicheras*, which is not known from the other areas of the study territory (Table 1). These considerations provide an explanation of the Early-Middle Callovian radiation of ammonites, but not their further decline. The sea transgressed in the Late Callovian-Oxfordian and, therefore, made migration routes potentially more efficient, whereas diversity declined in fact. If the transgression, which occurred in the Greater Caucasus, was only a regional event, a basinward migration of shoreline in the adjacent basins would explain a shrinkage of ammonite dispersal routes. However, the documented transgression corresponds quite well to the global eustatic rise (Fig. 3) documented by both alternative curves proposed by HALLAM (1988, 2001) and HAQ & AL-QAHTANI (2005), who updated the earlier curve by HAQ et al. (1987). Thus, the regional shoreline shift took place in the course of global eustasy and, thus, no shrinkage of dispersal routes can be assumed. It is also possible to hypothesize that plate tectonic forces could be responsible for a shrinkage of faunal exchange between the Caucasian and adjacent marginal seas of the Neo-Tethys Ocean and the Alpine Tethys Ocean. Collisions in the Alpine-Carpathian sector (GOLONKA, 2004) might have strengthened a separation between these oceans, which persisted through the entire Jurassic (STAMPFLI & BOREL, 2002).

Results of our spatial analysis question a lack of ammonites in the southern part of the Caucasian Sea throughout the entire Callovian-Oxfordian. A consideration of facies distribution in the study region (RUBAN, 2007) suggests that ammonites were absent in those areas, dominated by the deep-marine environments.
This means ammonites preferred more or less shallow-marine environments both to migrate and to radiate. As soon as such favourable conditions appeared in the northern part of the sea during the Early-Middle Callovian, those areas were rapidly colonized.

VII. CONCLUSIONS

The spatio-temporal analysis of the Callovian-Oxfordian ammonite generic diversity in the Caucasian Sea permits to make a number of conclusions.

1) Generic diversity accelerated rapidly during the Early-Middle Callovian together with a strong transgression, which opened new dispersal routes at the northwest and the northeast of the Caucasian Sea.

2) Generic diversity declined gradually during the Late Callovian-Late Oxfordian despite of an ongoing transgression.

3) Global ammonite diversity decrease or shrinkage of dispersal routes due to the tectonic activity in the Alpine-Carpathian sector might have been responsible for an impoverishment of ammonite assemblages during the Late Callovian-Oxfordian.

4) Ammonite assemblages flourished in the areas, which lay on the dispersal routes appeared thanks to the transgression.

5) During the entire studied time interval, ammonites were able to inhabit just the northern shallow part of the Caucasian Sea, but not its deep southern part.

This study suggests that relationships between the ammonite diversity and transgressions/regressions should never be simplified. Shoreline shifts could be more important controls of taxa number during some time intervals, but less important during others. The spatio-temporal patterns of the Callovian-Oxfordian ammonite generic diversity established in the Caucasian Sea can be used as a reference for further diversity modelling in the other marginal seas of the Neo-Tethys Ocean and the Alpine Tethys Ocean.

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