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THE BOREAL-TETHYAN BIOGEOGRAPHICAL MOLLUSC ECOTONE IN EUROPE DURING THE JURASSIC-CRETACEOUS TRANSITION

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Abstract. Late Jurassic and earliest Cretaceous molluscs of the northern hemisphere were distinctly differentiated geographically into Boreal taxa, usually north of 50° N, and Tethyan taxa, usually south of 45° N. Between these latitudes certain areas were displaced from time to time, although the biogeographical ecotone was stable. The magnitude of the ecotone and the migration of molluscs inside the ecotone varied in time and space, in direction (unidirectional and bidirectional) and intensity (expansion and "isolate straying"). The frequency of the Boreal-Tethyan migrations of molluscs is explained by eustacy and by geographical barriers existing between the Northern Caucasus and Middle-Russian basins.

Riassunto. I molluschi marini del Giurassico superiore e del primo Cretaceo dell'emisfero settentrionale erano nettamente differenziati dal punto di vista geografico in taxa boreali, di solito a Nord dei 50° N, e taxa tetidei, di solito a Sud dei 45° N. Tra queste latitudini certe aree venivano di volta in volta spostate, sebbene l'ecotono biogeografico fosse stabile. L'ampiezza dell'ecotono e la migrazione dei molluschi al suo interno è variata nel tempo e nello spazio, in direzione (unidirezionale e bidirezionale) ed intensità (espansione e "dispersione isolata"). La frequenza delle migrazioni boreali-tetidee dei molluschi è spiegata dall'eustasia e dall'esistenza di una barriera geografica tra i bacini del Caucaso settentrionale e della Russia centrale.

Introduction

The Boreal-Tethyan biogeographical ecotone existed in Europe during the late Jurassic-earliest Cretaceous represented by a co-occurrence of Boreal and Tethyan forms. During the Mesozoic it was located in the Northern Hemisphere along the Tethys-Pantalassa / Panboreal Super-realms boundary. The ecotone was established by the molluscs in the Triassic, Jurassic and Early Cretaceous in the Boreal-Pacific Realm (Zakharov et al. 1996). The position of the Boreal-Tethyan ecotone in the Boreal-Atlantic Realm from Late Volgian to Early Neocomian is assumed on the basis of ammonites (Zakharov & Bogomolov 1998). It is very important to investigate the Boreal-Tethyan migrations inside the ecotone at the Jurassic/Cretaceous transition to make a precise correlation between the Tithonian-Volgian and the Berriasian-Boreal Berriasian.

Material and methods

Data on ammonite, belemnite and bivalve migrations across the south margin of the Boreal-Atlantic Realm from Late Jurassic (Kimmeridgian and Volgian) to Early Neocomian (Boreal Berriasian -Valanginian) were reviewed. The migrations were considered at substage intervals. The latitudes of 45° and 50° N were accepted as the northern margin of the Tethys-Pantalassa Super-realm, and as the southern margin of the Panboreal Super-realm, respectively. A taxon "advancing" from north to south and crossing 50° N was considered a boreal influence, and the limit of Tethyan influence was set at the crossing of 45° N for taxa "moving" from south to north.

New molluscan data collected over the last few decades, mainly from Upper Jurassic and Lower Neocomian sequences of Europe, have improved our knowledge of the Boreal-Tethyan ecotone, of the position of the southern margin of the Boreal-Atlantic Realm (Sachs et al. 1971; Fig. 1), and of the migration of Tethyan mollusc associations and taxa into and from the Boreal basins (Fig. 2). Migrations with different intensities and direction from the Kimmeridgian to the Valanginian, considered in this paper, were restricted to the Boreal-Atlantic Realm (West European and East European Provinces). The molluscs, such as ammonoids, belemnites and bivalves, were divided into 3 groups: Tethyan, Boreal and Sub-boreal (mostly with Tethyan affinities typical for the ecotones). It is impossible to attribute some ammonoids, such as Phylloceratida and Lytoceratida, to either the Tethyan or Boreal Realm. Their distribution was probably controlled by water depth.

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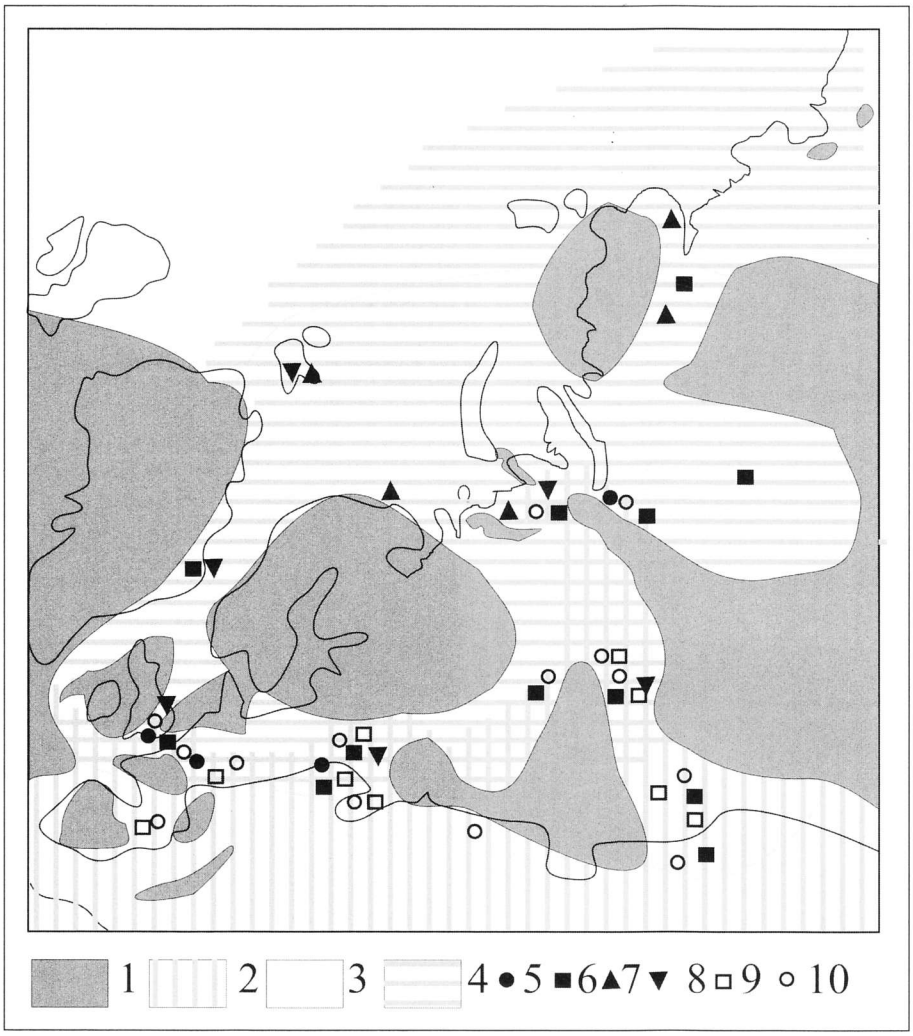

Fig. 1 - Boreal-Tethyan ecotone in the Upper Kimmeridgian (Autissiodorensis Chron) of Europe. 1 - land; 2 - Tethyan ammonites, 3 – Subboreal ammonites, 4 - Boreal ammonites; 5-10. Finds of the selected ammonite genera: Sub-boreal: 5 - *Gravesia*, 6 – *Aulacostephanus;* Boreal: 7 - *Suboxydiscites*, 8- *Amoeboceras;* Tethyan: 9 – *Metahaploceras/ Neochetoceras*, 10 – *Aspidoceras.*

Results

It is interesting to note that in Europe an ammonite ecotone was either absent for a rather long time (from the Latest Volgian to the beginning of the Valanginian) or quite restricted (during the Late Boreal Berriasian). Subboreal ammonites are either unknown or they occupied a small area (e.g. *Garniericeras*). At the beginning of the Valanginian, *Platylenticeras* appeared, presumably from Boreal ancestors, but its geographical distribution was typically Sub-boreal. During the Berriasian and Valanginian, the bivalve *Buchia* extended to the South, up to 48° N in the West-European Province of the Boreal-Atlantic Realm, and reached 42 - 40° N in the East-European Province (Zakharov 1981; Kelly 1990). Tethyan trigoniid bivalves penetrated up to 55° N into the East-European Province during the Volgian (Gerasimov 1955). The most northern penetration of Tethyan ammonoids known was made by *Aspidoceras* (Late Kimmeridgian, East-European Province, 65° N; Bogomolov & Dzyuba 1998; Fig.1).

Based on intensity, migrations are subdivided into expansions (mass migrations) and influences (isolated «straying», after Rawson 1973). Expansions are characterized by the moving of mollusc associations (e.g., migrations of the Mediterranean ammonoids into the East-European Province during the Latest Kimmeridgian and Early Volgian), while influences refer to the moving of separate taxa, usually with an insignificant number of specimens (e.g., penetration of *Aspidoceras* northward into West Siberia). Expansions quite often lead to the starting of endemic clades (e.g. *Riasanites* in Central Russia, Late Valanginian Neocomitidae of Western Europe), but they may be restricted to short intervals without new taxa. The most indicative example of such migrations was the penetration of numerous *Anaspidoceras neoburgense* into the East-European Province during the Early Volgian (Pseudoscythica Chron, *neoburgense* hemera) (Rogov 2002). *Buchia* bivalves also illustrate the intensity of migrations. The migration-influences in the Boreal-Atlantic Realm took place during the Late Jurassic - Early Neocomian in the West-European Province (Fig. 2a), and during the Berriasian - Valanginian in the East-European Province (Fig. 2b).

Two kinds of migrations were determined based on the direction of penetration: bidirectional (e.g., Volgian- Early Berriasian) and unidirectional (e.g., latest Valanginian of West-European Province). Bidirectional Boreal-Tethyan migrations are explained by a reduction of

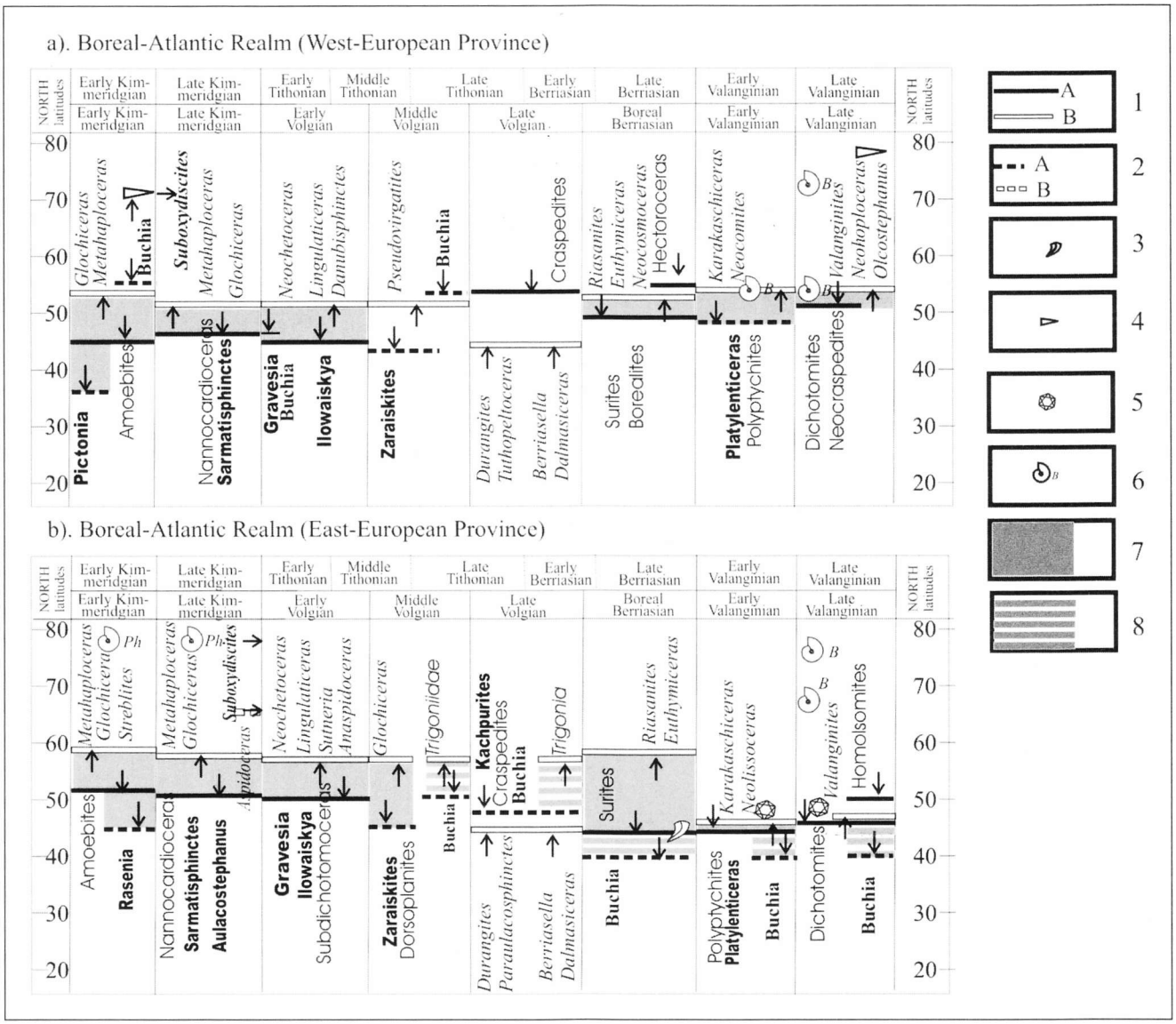

Fig. 2 - Setting of the Boreal-Tethyan ecotone and boundary between Boreal and Tethys-Pantalassa Super-realms from Kimmeridgian to Valanginian. 1-2 – Boreal (A) and Tethyan (B) expansions (1) and isolated straying (2); 3 – finds of Rudista together with Boreal ammonites; 4 – finds of Tethyan belemnites (*Hibolithes*) together with boreal ammonites; 5 – finds of hermatypic corals together with boreal ammonites; 6 – oceanic ammonites in the high latitudes (Ph – Phylloceratida; L – Lytoceratida; B – *Bochianites*); 7 – ecotone based on ammonoids; 8 – ecotone based on ammonites and bivalves or only on bivalves.
Affiliations of ammonites and bivalves noted by different fonts.
Ammonites: Tethyan *Glochiceras*, Boreal with Tethyan affinities ***Suboxydiscites***, Sub-boreal **Zaraiskites**, Boreal Surites. Bivalves: Boreal **Buchia**, Tethyan *Trigoniidae*.

the temperature gradient between zoochorems (the influence of this factor is felt if geographical barriers impeding migrations are absent). As a rule, at this time the ecotone widens. Quite often unidirectional migrations are accompanied by displacement of the high-rank zoochorems boundaries. They are characterized by a sharp change of ammonoid associations. In the West-European and East-European Provinces of the Boreal-Atlantic Realm, despite their proximity, mollusc migrations are not always mutually correlated (Fig. 2, 3). This may be explained by the influence of currents and the presence of geographical barriers. Thus, a significant northward displacement of the Tethys-Panthalassa/Panboreal Super-realms boundary developed in the latest Valanginian of the West-European Province. Nevertheless, only Boreal ammonoids occur in the East-European Province during this interval. The Boreal-Tethyan ecotone in Europe was not always delineated clearly. The increasing Boreal influence can be seen in the Northern Hemisphere at the beginning of the Cretaceous: the Super-realms boundary, in particular in the Early Valanginian, is displaced to the south (Fig. 2). This obviously indicates the development of the Boreal

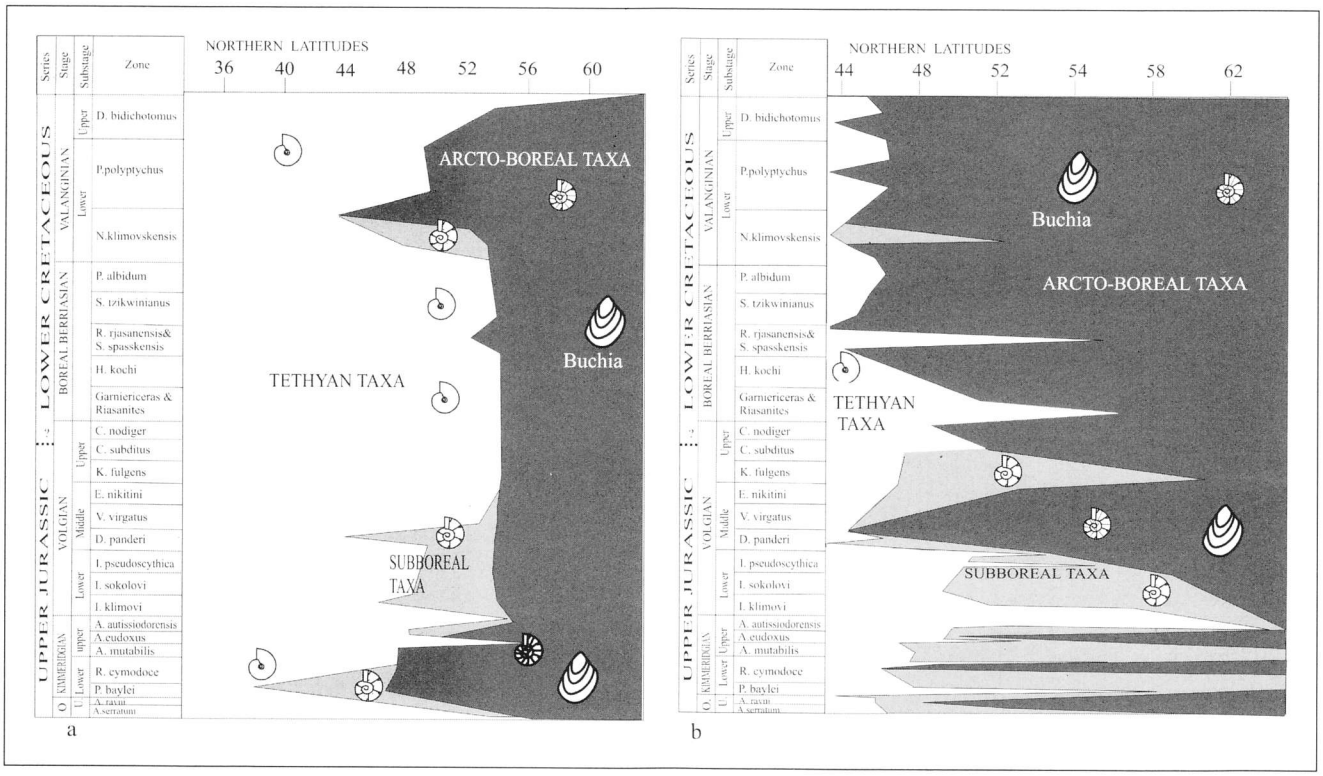

Fig. 3 - Molluscs migration restricted by the ecotone in the Boreal-Atlantic Realm from Kimmeridgian to Valanginian. a) West-European Province; b) East-European Province.

transgression. The Tethyan influence in the Kimmeridgian and earliest Volgian is appreciable only within the limits of the Boreal-Atlantic Realm, where «migration waves» are observed (Fig. 3b).

The examples considered and illustrated above give the average pattern of migrations (for the substage level) and positions of the ecotone. However, in reality the character and direction of migrations might strongly vary during this insignificant time interval. The change of the Boreal-Tethyan migrations during the latest Early Volgian to the earliest Middle Volgian (in the Tethyan scale this time spans the interval from the base of the Middle Tithonian up to the Calpionella Zone A of the Upper Tithonian) is discussed as an example.

In the *neoburgense* hemera (corresponding approximately to the Semiforme Chron) mass penetration of the Tethyan molluscs into the Central Russia was observed. The ammonites *Anaspidoceras* and *Sutneria* were more common, the Tethyan *Hibolithes* superseded the Boreal Cylindroteuthinae in the Volga region, and among bivalves both Tethyan (*Myophorella*) and Boreal (*Buchia*) taxa were present (Rogov 2004). Apparently, this was a mass unilateral migration from the North Caucasian Sea. However, this event is unknown in the Timan-Pechora Province and in Sub-polar Ural. At the same time, it is possible that some Boreal ammonites penetrated into Southern Germany (Scherzinger & Schweigert 1999) during the *neoburgense* hemera , though the identification of these ammonites is doubtful.

During the *puschi* hemera in the Central Russian Sea the ammonoids were essentially comparable to those in Poland. Only Tethyan *Danubisphinctes* are rarer in Russia. Associations of Bivalves (largely *Buchia*) and belemnites (only *Cylindroteuthis*) became extreme Boreal, which indicates a strengthening of the influence of the Arctic Basin. Sub-boreal influences were marked also in Western Europe. Rare Sub-boreal *Pseudovirgatites (?) tenuicostatum* was present in Austria (Zeiss 1977). In the Panderi Chron all migrations of molluscs were characterized by individual penetrations (isolated straying), but were variable in direction. Connections between Central Russian and North Caucasian Seas were somewhat amplified. *Sutneria*, *Lingulaticeras*, and *Pseudolissoceras* penetrated into the Volga region from the south, and rare *Dorsoplanites* extended into Caucasus from the north (Douvillé 1910; Khimshiashvili 1989). At the same time, individual *Zaraiskites regularis* penetrated into the Balkan-Carpathian region through the Polish Basin.

Discussion

What factors influenced mollusc Boreal-Tethyan migrations and the adjustment of the bio-geographical ecotone? A primary factor, accepted by a majority of researchers, was cooler water temperature in the north. However, only a few Boreal and Tethyan molluscs were involved. Some typical Tethyan molluscs reached 60° N

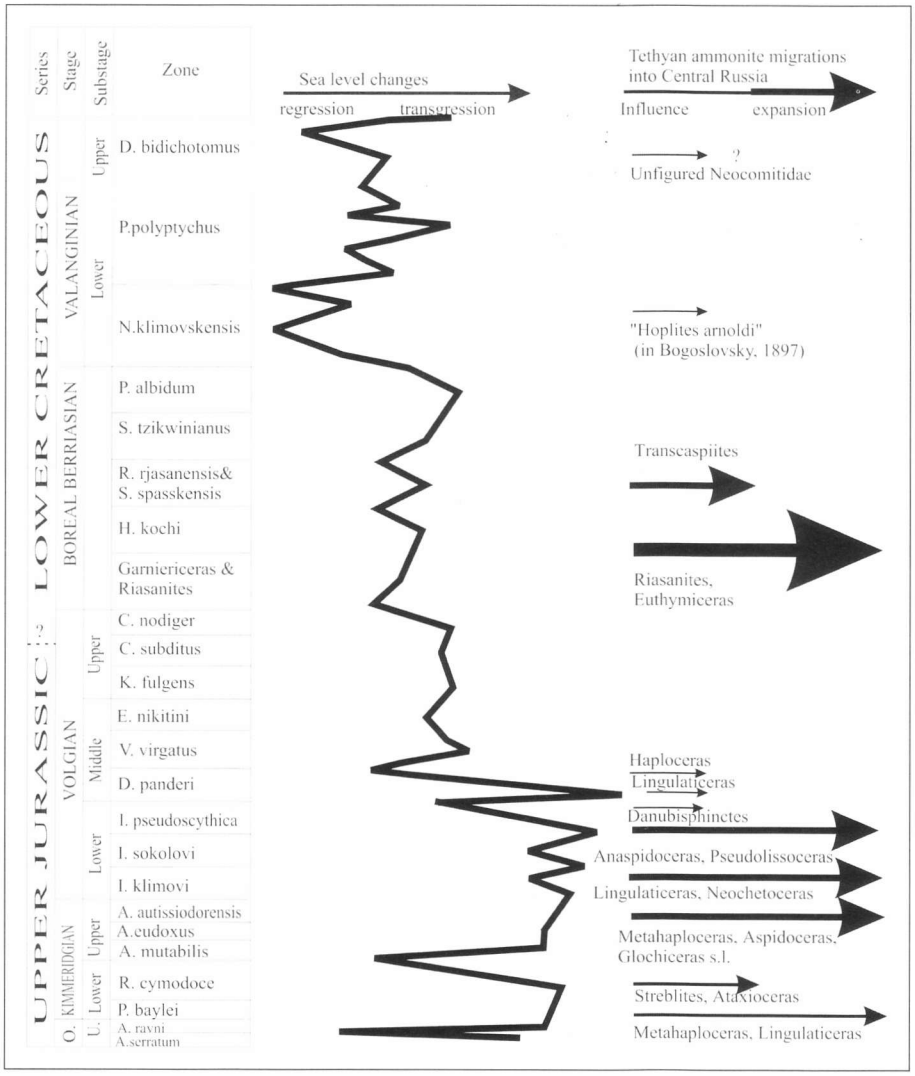

Fig. 4 - Transgressive-regressive curve (from Sahagian et al. 1996) and ammonite migrations via the Middle Russian Sea during the Kimmeridgian-Valanginian.

and even 65°N, i.e. moved away from the Tethys-Panthalassa margin (45°N) to 2.000-2.500 km to the north. Among «Boreal wanderers» are the cephalopods, which penetrated southward beyond 38°N, but covered a lesser distance, since they moved away from the margin of the Panboreal Super-realm no more than 700 km. It is likely that only a few Tethyan molluscs had temperature tolerances wider than the Boreal forms. This could be considered as a possible explanation for the mainly southern origin of the majority of Boreal taxa. The high frequency of the Boreal-Tethyan migrations is explained by eustacy: during a rise of sea-level migration pathways were opened, and during sea-level falls migration pathways were closed (Kemper et al. 1981). In addition, it is supposed that rises of sea-level eliminated temperature barriers between water masses. A most suitable area to check these hypotheses is the central part of the East-European Province of the Boreal-Atlantic Realm (Middle-Russian sea). As seen in Fig. 4, the coincidence of transgression peaks with episodes of ammonoid migrations is observed only for the Kimmeridgian -Middle Volgian interval, while in the Berriasian a correlation is absent. Obviously, the migration-expansion of berriasellids during the Boreal Berriasian is not connected with a eustatic rise (Fig.4). This event may be related to the destruction of a geographical barrier between the Northern Caucasus and Middle-Russian basins. Apparently, the influence of Tethyan over Boreal water masses prevailed, when connections between the Middle-Russian Sea and the Arctic basin were restricted to the north.

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