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Boreal-Tethyan Mollusk Migrations at the Jurassic-Cretaceous Boundary Time and Biogeographic Ecotone Position in the Northern Hemisphere

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Abstract—Mollusk migrations of various intensity in the Kimmeridgian to Valanginian time span were established in the Boreal Atlantic (West and East European Provinces), Boreal Pacific (Chukotka-Canadian and Boreal Pacific Provinces), and Arctic Realms of the Panboreal Superrealm. According to intensity degree, the migrations are classified as expansions, i.e., mass migrations, and influence migrations, i.e., penetration of separate taxa. Migrations of the cross- and unidirectional types are distinguished according to directions of taxa exchange. Mollusks (ammonites, belemnites, and bivalves) are subdivided into Tethyan and Boreal forms, which inhabited areas south of 45°N, and north of 50°N, respectively. Low-boreal mollusks distinguished among the latter were characteristic of an ecotone between the Panboreal and Tethy s-Panthalassa Superrealms, and Boreal-Arctic taxa dwelt north of 60°N. The ecotone of the Boreal Atlantic Realm was situated between 50° and 55°N. The ecotone zone persistently existed in the Boreal Pacific Realm. The ammonite ecotone of the Chukotka-Canadian Province (Primor'e) was between 45° and 55°N. In the Boreal Pacific Province (northern California), an ecotone of the Tithonian-Valanginian time was located between 40° and 50°N. Water temperature lower in the north was the major factor that influenced Boreal-Tethyan migrations and positioning of biogeographic ecotones. The coincidence of transgression peaks with the ammonite migration events is characteristic only of the Kimmeridgian-Middle Volgian time, when northward migrations of the Tethyan ammonites coincided with sea level rises. The Berriasian expansion of berriasellids to the Central Russian Sea was not associated with eustatic events. It might be a consequence of a sea way opening between the North Caucasian and Central Russian seas.

Key words: Jurassic, Cretaceous, Boreal, Tethys, ecotone, biogeography, migrations, mollusks.

INTRODUCTION

Elucidation of dynamics of Boreal-Tethyan mollusk migrations at the Jurassic-Cretaceous boundary time, especially of ammonites and buchiids (bivalves), is extremely important for solution of problems associated with zonal correlation between the Tithonian and Volgian stages, and between the Berriasian and Boreal Berriasian. In the Panboreal Superrealm, the migrations occurred, as is established (Saks *et al.,* 1971), between the Boreal Atlantic (North Western and Eastern Europe to the north of 50°N), Arctic (modern Arctic seas and adjacent lands to the south of the Arctic Circle), and Boreal Pacific (Pacific Ocean and surrounding lands to the north of 45°N) Realms (Fig. 1). Many publications are devoted to the analysis of migrations in the Boreal Atlantic (Mesezhnikov *et al,* 1971; Rawson, 1981; Kelly, 1983; Michalík, 1995; Vašíček and Michalík, 1999; Baraboshkin, 2001; and others) and Boreal Pacific (Sey and Kalacheva, 1983, 2000; Zakharov and Bogomolov, 1996; Zakharov *et al.,* 1996) Realms. However, area of the biogeographic ecotone between the Panboreal and Tethys-Panthalassa Superrealms did not attract a considerable attention up to now. In the Boreal Pacific Realm (Chukotka-Canadian Province), its geographical position during the Late Triassic, Jurassic, and Early Cretaceous was established based on mollusk distribution in order to evaluate a conceivable meridional displacement of terranes (Zakharov *et al.,* 1996). In the Boreal Atlantic Realm, positioning of the ecotone area in the late Volgian and early Neocomian was elucidated based on ammonites (Zakharov and Bogomolov, 1996, 1998).

Bearing in mind a lack of the GSSP officially accepted for the Jurassic-Cretaceous boundary (Zakharov *et al.,* 1996) and difficulties in correlation between the Boreal and Tethyan successions, we show in correlation schemes only one of possible levels of that boundary. In our view, the problem of relationship between the Volgian and Tithonian stages is still far from an ultimate solution, and we can discuss only a preliminary correlation. We also believe that there is no strict evidence for the age equivalence of the lower Berriasian and upper Volgian substages.

The undeniable correlation of the uppermost Valanginian top in Siberia, Western Europe, and North America is also impossible in view of incomplete

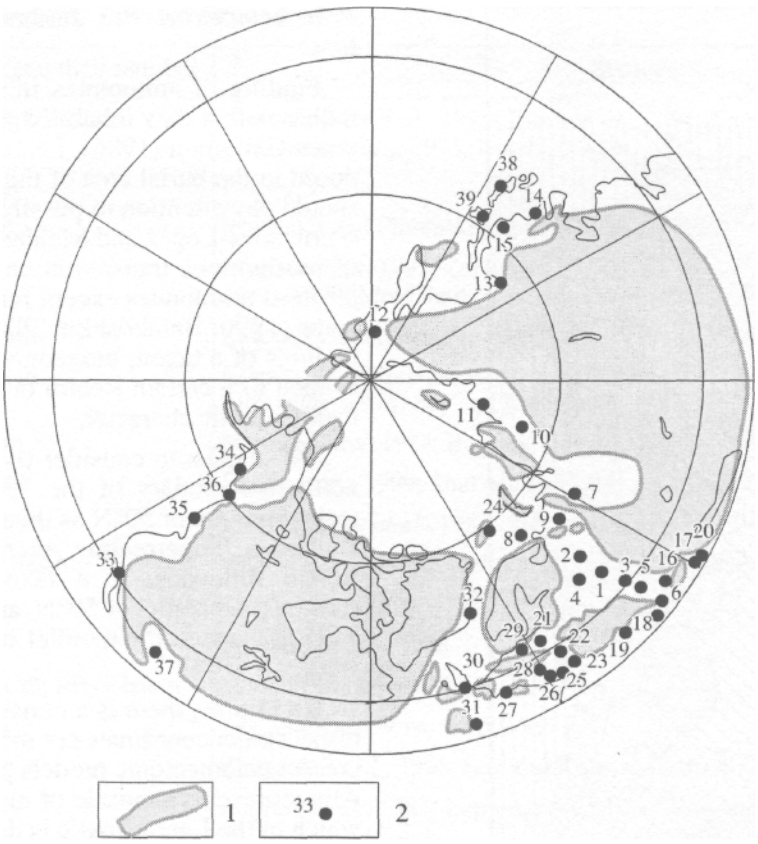

Fig. 1. Major localities of fossils analyzed in this work: (1) land; (2) localities (numbers correspond to those in the table).

records. The position of the *Homolsomites bojarkensis* Zone still remains uncertain. Researchers place it either at the base of the Hauterivian, or in the upper Valanginian (Rawson, 1981; Shul'gina, 1985; Bogomolov, 1989; Marek and Shulgina, 1996). This should be kept in mind when the age is not specified advisedly.

1.1. MATERIALS

We considered data on ammonite, belemnite, and bivalve migrations in the Northern Hemisphere (table, Fig. 2) during the Late Jurassic (Kimmeridgian and Volgian ages) and Early Neocomian (Boreal Berriasian-Valanginian time). Data on migrations within substage time spans were grouped and analyzed. We tried to take into consideration all the data on studied collections and available in the literature. In our work, we encountered traditional difficulties: a common lack of pictures of taxa listed in publications, inaccessibility of collections of fossils presented in low-quality images, and impossibility to identify forms from photographs only. For instance, there are only few images of sub-Mediterranean ammonites encountered in Volgian deposits of the East European Province. We admit that some Tithonian, Berriasian, and Valanginian ammonites from the Far East (Sey and Kalacheva, 1983, 1999) are in the imperfect preservation state. Moreover, there is no way to identify with certainty even the generic affiliation of buchiids and inoceramids from the Tithonian of Cuba (Myczyński, 1999) using their images only. Accordingly, when information is particularly important, we indicate whether or not the corresponding form is pictured, and how precise its identification is. Other things being equal, the preference is given to an illustrated form or to a conclusion based on personal examination of fossils in collections.

In addition to migrations proper, we must take into account the effect of "parallel evolution" implying that the same features appear, sometimes concurrently, in representatives of different groups. Contrary to Oloriz (1990), we do not attach much importance to this factor. Perhaps, the most significant examples of parallel development of similar features in different ammonite groups are the *"Gravesia"* occurrence in Kenya (Verma and Westermann, 1984), an independent development of perisphinctids with virgate branching ribs during the early—middle Volgian in the East and West European Provinces, and bipolar distribution of thin-ribbed perisphinctids *Kossmatia, Virgatosphinctes,* and

[1] Like Bengtson and Kakabadze (1999, p. 227-228), we can mention the major problems of a paleobiogeographic analysis. These are the absence of data on biogeographically important taxa except for their listing, taxonomic uncertainties, contingency of distribution, diverse age interpretations, facies inconsistency, and sampling deficiency.

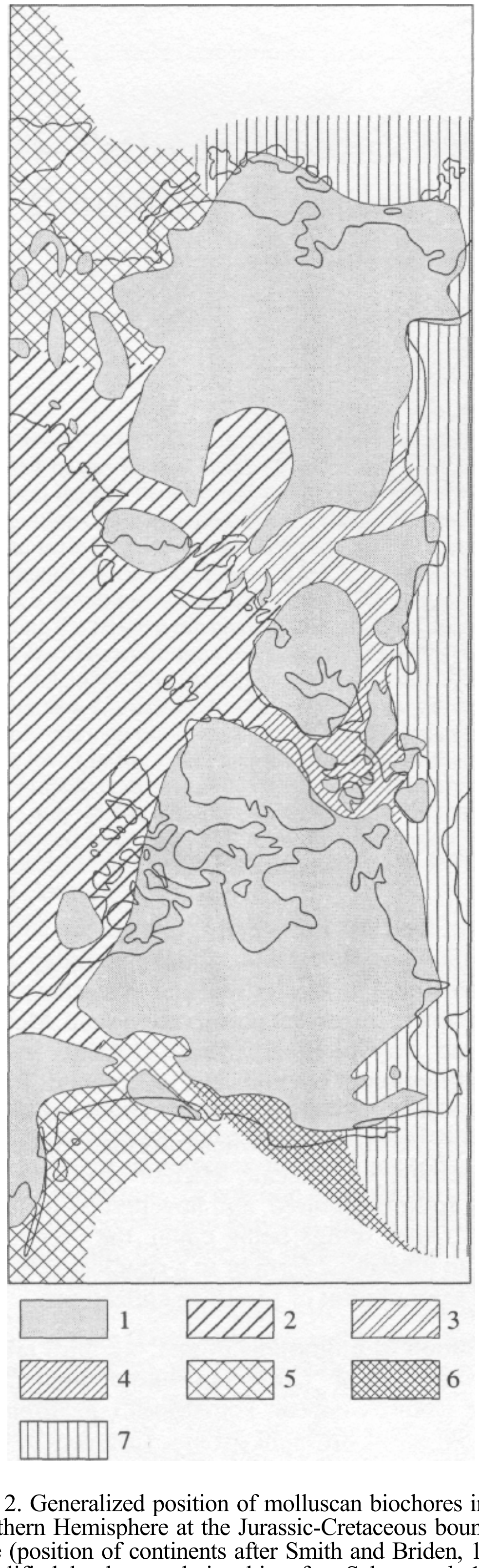

Fig. 2. Generalized position of molluscan biochores in the Northern Hemisphere at the Jurassic-Cretaceous boundary time (position of continents after Smith and Briden, 1977; simplified land-sea relationship after Saks *et al,* 1971; Rawson, 1973; Imlay, 1984; Thierry, 2000; nomenclature of biochores after Saks *et al.,* 1971): (1) land; (2) Arctic Realm; (3) East and (4) West European Provinces of the Boreal Atlantic Realm; (5) Chukotka-Canadian and (6) Boreal Pacific Provinces of the Boreal Pacific Realm; (2-6) Panboreal and (7) Tethys-Panthalassa Superrealms.

Praechetaites at the Jurassic-Cretaceous boundary time.

Finding of ammonites in some Realm not always indicates that they inhabited the area or were eudemic sensu Callomon (1985), i.e., occurred and were reproduced in the burial area of their shells.[2] Therefore, one should pay attention to possible burials of empty shells (Fernándes-López and Meléndez, 1996). The influence of posthumous transportation was likely insignificant for most ammonites except for Phylloceratida (Westermann, 1990; Baraboshkin, 2001). In the case of single findings of a taxon, biogeographic affiliation of which is alien to a certain Realm or Province, one can doubt their eudemic character.

We suggest to consider the parallel of 45°N as the northern boundary of the Tethys-Panthalassa Superrealm and that of 50°N as the southern boundary of the Panboreal Superrealm. Accordingly, we admit the Boreal influence, if a taxon migrating southward crossed the parallel of 50°N, and the Tethyan influence, when it crossed the parallel of 45°N migrating northward.

Up to now, there is a considerable uncertainty with respect paleocoordinates of most terranes. According to present paleotectonic models par example, the Sikhote-Alin represents a mosaic of many terranes, positions of which in the Late Jurassic is defined within a comparatively wide range of paleolatitudes, from 35° to 60°N (Cecca, 1999). Despite the peculiar composition of the Late Jurassic molluscan assemblages, which include Boreal buchiids in association with Tethyan ammonites, they do not indicate an exact paleolatitude. Only the highest latitudes can be excluded in this case. However, the interval between 35° and 50°N appears to be most probable. In this interval exactly, the mixed Boreal-Tethyan molluscan assemblages of the Late Jurassic are encountered. Accordingly, we had to indicate localities of all findings in modern coordinates.

1.2. DISTRIBUTION AREAS OF MOLLUSCAN GENERA AND CONTROLLING FACTORS

Boreal-Tethyan migrations of Kimmeridgian to Valanginian mollusks took place within the Panboreal and Tethys-Panthalassa Superrealms (Westermann, 2000a, 2000b; Zakharov *et al.,* 2003; see Fig. 1). Whereas the Arctic taxa did not commonly penetrate into the Tethyan areas south of 30°N, the Tethyan forms or their descendants migrated as far north as 76°N. The water temperature lowering to the north was the major factor that controlled the dispersal of mollusks and other faunal groups in the Northern Hemisphere during the Late Jurassic-Early Cretaceous period, as it is evident

[2] In addition to eudemic ammonites, Fernándes-López and Meléndez (1996) also recognize their miodemic (inhabitants not reproducing themselves in the habitat), parademic (specimens passively transported alive), and ademic (transported dead shells) forms.

Main localities of molluscan fauna analyzed in this work

Major localities (Realms) and their number		Sources
1	Ul'yanovsk Volga Realm	Mesezhnikov *et al,* 1977; Blom *et al.,* 1984; *Unifitsirovannaya stratigraficheskaya...,* 1993; Rogov, 200la, 2002
2	Kostroma Realm	Rogov, 200la
3	Ural River basin	Ilovaiskii and Florenskii, 1941; Zakharov, 1981
4	Central Russia	Bogoslovskii, 1895; Zonov, 1937; Sazonova, 1971, 1977; Mesezhnikov *etal.,* 1979; Mesezhnikov, 1984; Baraboshkin, 1999
5	Caspian Sea Realm	Sasonova and Sasonov, 1983; Luppov *etal.,* 1986; Mesezhnikov, 1989
6	Northern Caucasus	Renz, 1904; Douville, 1910; Khimshiashvili, 1967; Sazonova, 1971; Khalilov *etal.,* 1974; Sey and Kalacheva, 1993;
7	Polar Ural Realm	Mesezhnikov, 1984; Bogomolov and Dzyuba, 1998
8	Barents Sea shelf	Basov *et al,* 1989; Shul'gina and Burdykina, 1992
9	Pechora River basin	Mesezhnikov *et al,* 1983; Mesezhnikov, 1984; Rogov, 2001a
10	Khatanga River basin	Saks *et al,* 1969; Mesezhnikov, 1984; Shul'gina, 1985; Bogomolov, 1989
11	Paksa Peninsula	Shul'gina, 1985
12	Chukotka	Zakharov *et al,* 1988
13	Tugurskii Bay, Uda River basin	Sey and Kalacheva, 1992
14	Southern Primor'e	Sey and Kalacheva, 1995, 1997
15	Northern Primor'e	Zakharov *et al,* 1996; Sey and Kalacheva, 1999; Markovich *et al,* 2000
16	Mangyshlak	Luppov *et al,* 1983; Luppov *et al,* 1986; Bogdanova *et al,* 1989
17	Southern Karakum	*Nizhniimel..,* 1985
18	Abkhazia	Khimshiashvili, 1989
19	Crimea	Yanin, 1970
20	Central Kopetdag	*Nizhnii mel...,* 1985
21	Kujawy	Kutek, 1994; Marek, Shul'gina, 1996
22	Rogosnik	Zakharov, 1981; Kutek and Wierzbowski, 1986
23	Bulgaria	Kutek, 1994
24	Spitsbergen	Zhirmunskii, 1927; Ershova, 1983; Shul'gina and Burdykina, 1992
25	Western Carpathians	Vašíček, Michalík, 1999
26	Switzerland	Atrops *etal,* 1993
27	Southeastern France	Thieloy, 1973; Kemper *et al,* 1981
28	Southern Germany	Atrops *et al,* 1993; Schweigert, 1993, 1994; Scherzinger, Schweigert, 1999; Schweigert, Jantschke, 2001
29	Northern Germany	Kemper *et al,* 1981; Kemper, 1987
30	Southern England	Casey, 1973; Casey *et al,* 1977; Kemper *et al,* 1981; Kelly, 1990
31	Southern Spain	Geyer, Oloriz Saez, 1983
32	Eastern Greenland, Milne Land	Callomon, Birkelund, 1980; Rawson, 1981
33	Northern California	Imlay, 1961; Johnes *et al,* 1969; Imlay, Johnes, 1970
34	Southern Alaska	Imlay, 1981
35	British Columbia	Frebold, 1964; Jeletzky, 1984; Poulton *et al,* 1988; Hoedemaeker, 1991
36	Western Canada	Jeletzky, 1964
37	Western Mexico	Burckhardt, 1906; Imlay, 1980, 1984; Adatte *et al,* 1994
38	Honshu Island	Sato, 1962, 1985; Takahashi, 1969
39	Hokkaido Island	Zakharov, 1981.

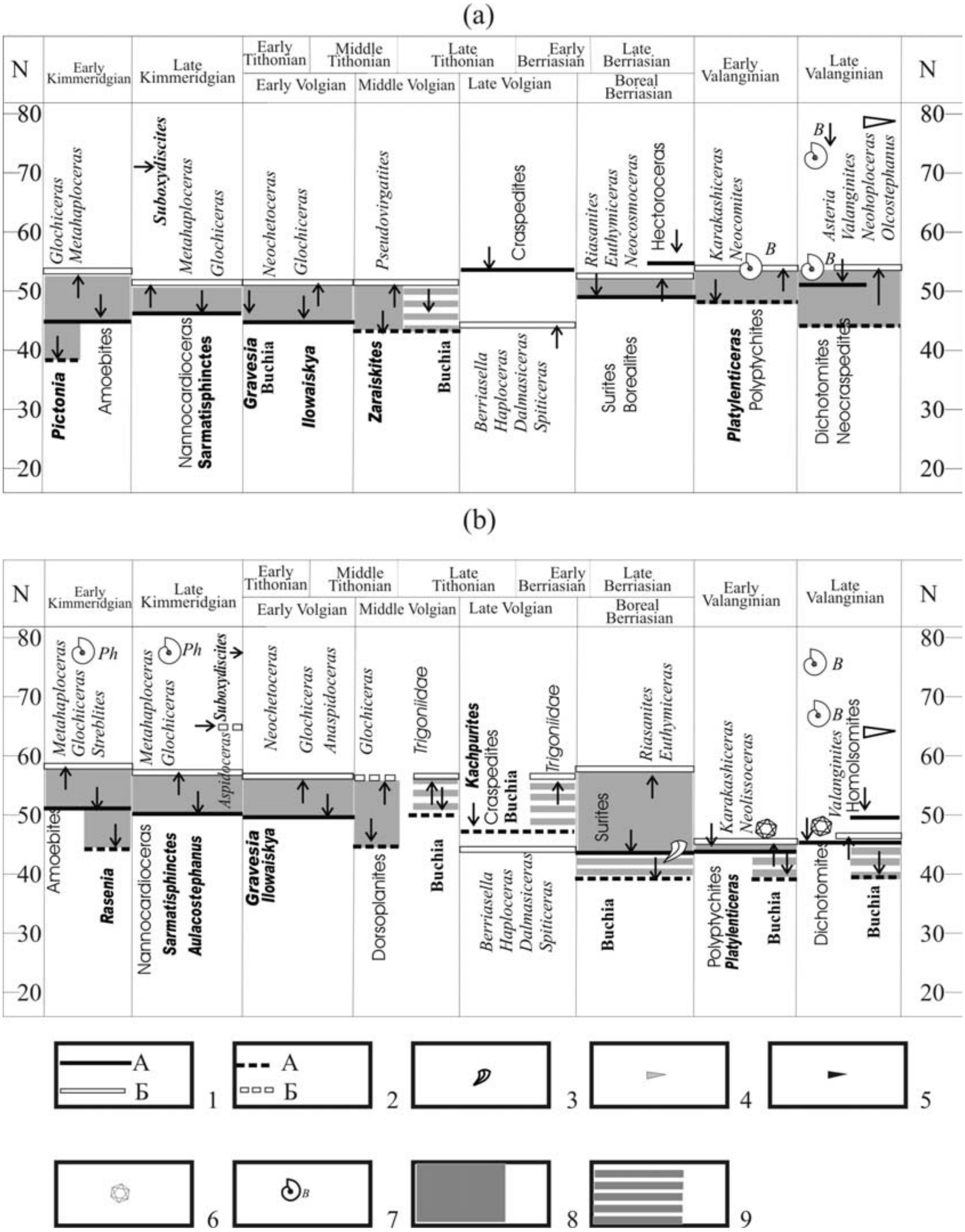

Fig. *3.* Location of the Boreal-Tethyan ecotone and boundaries between the Panboreal and Tethys-Panthalassa Superrealms in the West (a) and East (b) European Provinces of the Boreal Atlantic Realm during the Kimmeridgian-Valanginian: *(1-2)* limits of Boreal (a) and Tethyan (b) expansion (1) or isolated "straying" (2); (3) coexisting rudists and Boreal ammonites; (4) coexisting Tethyan belemnites *(Hibolithes)* and Boreal ammonites; (5) Boreal belemnites Cylindroteutinae from low latitudes; (6) coexisting Hermatypic corals and Boreal ammonites; (7) oceanic high-latitude ammonites Phylloceratida (Ph), Lytoceratida (L) and *Bochianites* (Ammonitida, Perisphinctina) (B); (8) ecotone of ammonite faunas; (9) ecotone of ammonites and bivalve mollusks. Different fonts designate paleobiogeographic affinity of ammonites and bivalves as follows: *Glochiceras* if Tethyan, ***Suboxydiscites*** if Boreal descendant of Tethyan ancestor, ***Zaraiskites*** if low-boreal, and Surites if high-boreal (Arctic) ammonite genus; **Buchia,** if Boreal and Trigoniidae if Tethyan bivalve taxa.

tions within the Boreal Atlantic Realm (Fig. *3). A* significant enlargement of ecotone area was recorded in the East European and especially in the West European Provinces. In the earliest Kimmeridgian *(densicostato/planula* Chrons), numerous Tethyan *Metahaploceras, Lingulaticeras* and, later, *Streblites* penetrated into the northern Poland and Russia (Figs. 3a, b). These taxa constitute a significant part of the ammonite assemblage from the basal Kimmeridgian of the Kostroma Realm (Rogov, 2001 a). The Arctic subgenus *Amoeboceras (Amoebites)* concurrently migrated to the south. In some sequences of Poland, certain beds yield shells of the last taxon representing up to 70% of the total ammonite assemblage. These ammonoids were also encountered further southward (45-47°N), in distribution areas of sub-Tethyan sediments in southern Germany, Switzerland, and southern France (Atrops *et al.,* 1993). An *Amoeboceras (Amoebites)* specimens was also found in northern Iraq (Howarth, 1992), and if its identification is correct (the specimen has not been pictured), we should suggest transportation of empty shells, most likely from the Caspian Realm of the East European Province, but not the taxon migration. At the same time, judging from the geodynamic reconstruction, the last Realm was located near the eastern coast of Africa (Cecca, 1999), and we likely deal with an inadequate identification in this case. Along with other Arctic ammonites and buchiids, first *Suboxydiscites* penetrated into southern Germany at the beginning of the Kimmeridgian (Schweigert and Jantschke, 2001). It is likely, however, that first representatives of the genus were relatively thermophilic, and later on their descendants migrated northward from Germany. The low-boreal *Rasenia* (not figured) is reported from the northern Caucasus, 44°N (Khimshiashvili, 1967), and *Pictonia* findings are known from southern Spain, 37°N (Geyer and Olóriz Sáez, 1983). Few *Rasenia* specimens were also found in Sicily (Pavia and Cresta, 2002). Submediterranean *Hibolithes* occur in eastern Greenland, 71°N (Callomon and Birkelund, 1980), together with first *Suboxydiscites* (Oppeliidae), which appeared here at the beginning of the late Kimmeridgian, earlier than in northern Siberia. In the West European Province, buchiids reached southern Germany, 48°N (Zakharov, 1981; Kelly, 1990), and trigoniids penetrated into the North Siberian Province of the Arctic Realm up to the Khatanga River basin, 72°N (Saks *etal,* 1969).

In contrast, early Kimmeridgian faunas of the Boreal Pacific Realm were more isolated than those of the Oxfordian Age (Figs. 4a, 4b). Only buchiids migrated southward to Mexico, 30°N (Imlay, 1984). Data on *Amoeboceras* forms from western Mexico (Imlay, 1980) are published without their images. Reliable data on early Kimmeridgian mollusks from the Far East are unknown. Along the West Pacific coast, thermophilic ammonite genus *Taramelliceras* and Ataxioceratinae are unknown north of Japan (40°N; Sato, 1962; Takahashi, 1969).

1.3.2. Late Kimmeridgian

In the late Kimmeridgian, the character of ammonite migrations in the Boreal Atlantic Realm remained unchanged, but the Boreal-Atlantic and Boreal-Arctic molluscan assemblages became more contrasting than those of the early Kimmeridgian time (Saks *et al.,* 1971). The southward migration of Boreal Arctic ammonites somewhat weakened, but penetration of sub-Tethyan genera into Arctic seas became more distinct (Fig. 1). Within the West European Province, oppeliids migrated northward into the seas of Poland, and aspidoceratids reached southern England. The Boreal-Arctic *Nannocardioceras* and low-boreal *Gravesia, Aulacostephanus,* and *?Sarmatisphinctes* are known from southern Germany, 48°N (Atrops *et al.,* 1993; Schweigert, 1993, 1994; Fig. 3a). In the above areas, Tethyan ammonites occur together with buchiids (Kelly, 1990). The relatively thermophilic ammonites copiously penetrated into the East European Province up to 56°N (Nizhni Novgorod oblast), and some of them migrated even further northward, especially in the terminal Kimmeridgian *autissiodorensis* Chron (Fig. 3b). The sub-Tethyan genus *Aspidoceras* inhabited the Pechora subprovince. Its remains are encountered in the *autissiodorensis* Zone of the Pechora River basin (65°N). The genus also penetrated eastward in the West Siberian subprovince, where its species and *Sarmatisphinctes fallax* (How.) were found in the Severnaya Sos'va River basin (Mesezhnikov, 1984; Bogomolov and Dzyuba, 1998). The Arctic Realm represented the development site of peculiar oppeliid genus *Suboxydiscites.* The last taxon is characteristic of all upper Kimmeridgian zones of northern Siberia at 76° N (Saks *et al.,* 1969), being known as well from the analogues of the *autissiodorensis* Zone in Spitsbergen (Ershova, 1983), Pechora River basin (Mesezhnikov, 1984), and from boreholes sections of the Barents Sea shelf (Shul'gina and Burdykina, 1992; Fig. 5). Representatives of low-boreal genus *Aulacostephanus* are abundant in the south of the East European Province (Ural River basin and Orenburg oblast) and in the Severnaya Sos'va River basin and Polar Urals of the North Siberian Province (Mesezhnikov, 1984). Scarce *Aulacostephanus* specimens were also found in the northern Caucasus, where they associate with dominating Mediterranean ammonites (Khimshiashvili, 1967).

There are few reliable data on the upper Kimmeridgian sediments in the Boreal Pacific Realm. The joint occurrence of Boreal-Arctic and Tethyan forms is known only from northern California at 38°N, where *Amoeboceras (Amoebites)* and *Richeiceras* forms were found together with *Buchia* species (Imlay, 1961). *Pararasenia* forms occur in Mexico at 30°N (Burckhardt, 1906), but their age cannot be considered as exactly defined. According to Olóriz (1990), these ammonites are most likely not the true aulacostephanids and cannot be used for the Boreal-Tethyan correlation[3]. This conclusion seems to be rightful, as there are no related forms in Canada and Alaska (and in the Chukotka-Canadian Province as well), i.e., in the assumed migration way along the east-

[3] Hypothesis of Olóriz (1990) implying a decisive significance to colonization of epiplatform basins by ammonites whose oceanic ancestors developed in numerous parallel lineages is, in our view, insufficiently proved yet and does not explain all cases of their distribution. We believe that it is necessary to consider both possibilities: the distant migrations and the parallel development of similar features in different ammonite groups.

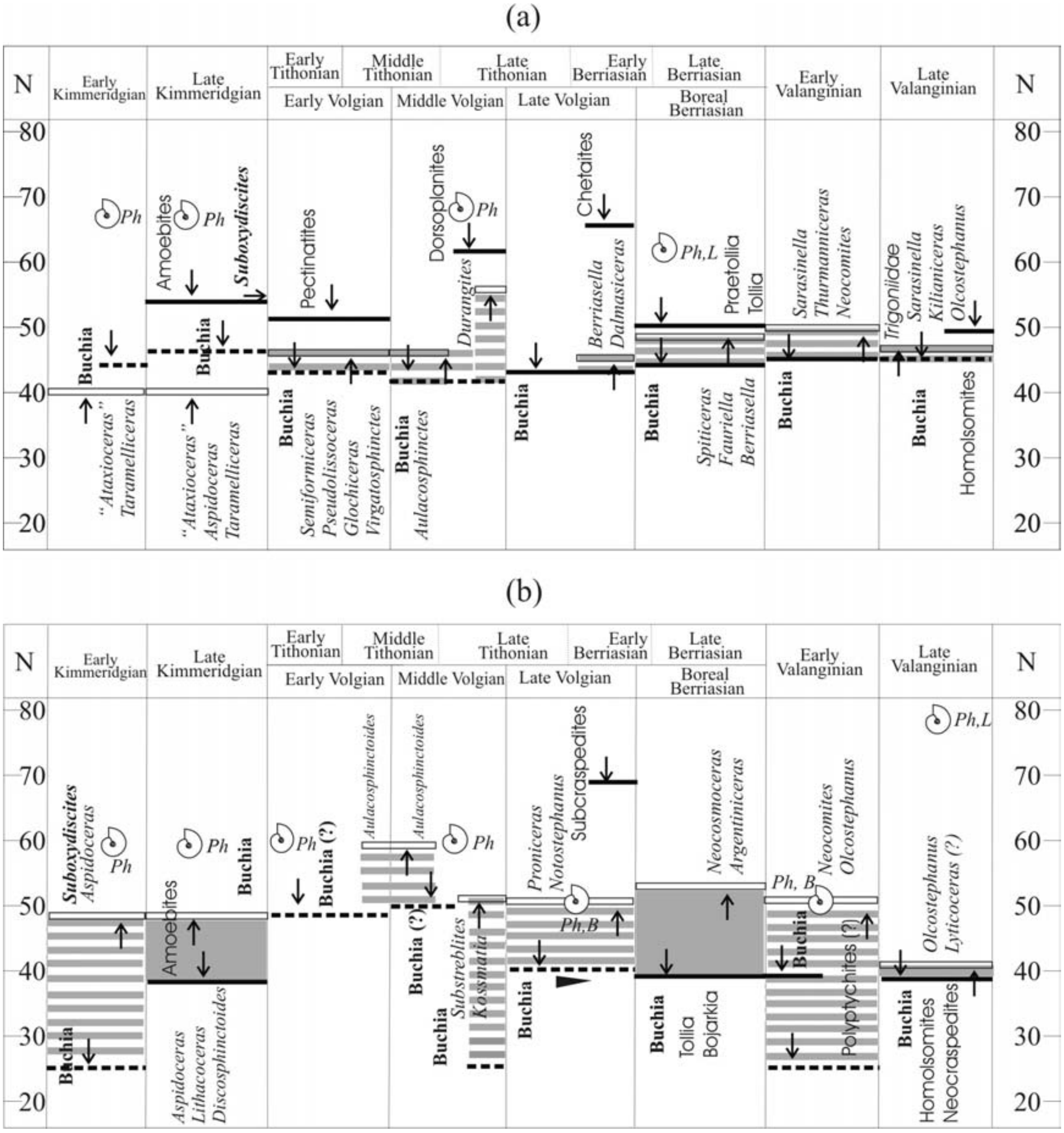

Fig. 4. Location of the Boreal-Tethyan ecotone and boundaries between the Panboreal and Tethys-Panthalassa Superrealms in the Boreal Pacific Realm during the Kimmeridgian-Valanginian (symbols as in Fig. 3).

ern coast of the Paleopacific. A possibility of migration through the Spanish corridor finds no support, because necessary forms are unknown from areas, through which the ammonite dispersal was to come about. It is likely that *Pararasenia* represents a descendant of the Tethyan *Idoceras* whose shells are abundant in older, lower Kimmeridgian sediments of Mexico. At the same time, it is also conceivable that the former genus is descendant of *Pictonia* whose remains are known from southern Spain (Geyer and Olóriz Sáez, 1983). The genus *Pararasenia* is therewith an endemic of the Caribbean Province, whereas the younger "*Pararasenia*" forms from Europe and Siberia can be attributed to the genus *Aulacostephanus.* Findings of *Buchia mosquensis* (von Buch) and *B. concentrica* (Sow.) from Mexico, 30°N (Burckhardt, 1906; Imlay, 1980), are most likely of the late Kimmeridgian age, though their images have not been published. In western Canada (49°N, British Columbia), Submediterranean genera *Lithacoceras, Discosphinctoides, Aspidoceras,* and *Suboxydiscites* occur in association (Fig. 4b) with scarce buchiids (Poulton *et al.,* 1988). The stratigraphic range of the assemblage is not strictly defined, but its late Kimmeridgian age can be assumed based on presence of *Lithacoceras* and *Discosphinctoides.* This is the only assemblage apart from the early Kimmeridgian fauna of southern Germany, where *Suboxydiscites* forms were encountered in association with Tethyan ammonites. The Canadian genus *Suboxydiscites* is likely somewhat older than the uppermost *mutabilis* Zone, during which it coexisted in northern Siberia and eastern Greenland with Arctic taxa. Another possible version is that *Suboxydiscites* migrated in British Columbia via cold bottorn current from the north with associated buchiids and Tethyan ammonites.

Exclusively Tethyan *Taramelliceras,* its species close to that of the lower Tithonian *T. (Fontannesiella)* included, *Aspidoceras* and Ataxioceratinae, all analogous to the West European taxa, are known in Japan at 40°N (Sato, 1962,1985; Takahashi, 1969), but they did not penetrate further northward however. In the Far East only scarce *Amoeboceras (Amoebites)* species, similar to the Californian *A. (A.) dubius* (Hyatt), and buchiids were encountered in the late Kimmeridgian (Sey and Kalacheva, 1992). Arctic descendants of Tethyan *Suboxydiscites* are known from the Uda River basin at 55°N, and buchiids migrated down to 44°N (Fig. 4a). Accordingly, the western marginal ecotone area of the Chukotka-Canadian Province was situated between 45 °N and 55°N in the late Kimmeridgian (Zakharov *et al.,* 1996).

1.3.3. Early Volgian-Early Tithonian and Early Middle Tithonian

Within the Boreal Atlantic Realm, the character of ammonite migrations remained practically the same as in the Kimmeridgian, but boundaries between Provinces were more distinct. In the West European Province, *Ilowaiskya* forms were rare (Fig. 3a). These ammonoids (not figured) were identified in Hungary and southern Germany (Rogov, 2002). However, many of them can likely be referred to the genus *Danubisphinctes* (Scherzinger and Schweigert, 1999). The low-boreal *Gravesia* species are known from the lowest Tithonian of southern Germany (Schweigert, 1993). Arctic buchiids were widespread in northwestern Europe at that time; they are known in southern England, northwestern France, northern and southern Germany, Austria, and Polish Carpathians, and have reached 48°N (Zakharov, 1981; Kelly, 1990; Kutek and Wierzbowski, 1986).

Tethyan *Neochetoceras, Lingulaticeras, Haploceras, Sutneria,* and *Anaspidoceras* are abundant in the Ul'yanovsk Realm of the East European Province (Fig. 3b). Lower Volgian *Neochetoceras, Sutneria,* and *Glochiceras* s.l. are known from central Poland. Low-boreal genus *Ilowaiskya* penetrated southward to 51°N (Orenburg Realm), where its species constitute the major part of the ammonite assemblage. Large accumulations of buchiids were found together with them in marly limestones (Zakharov, 1981).

New findings of supposedly Boreal-Arctic *Wheatleyites* were recently reported from the southern Tibet (Takei *et al.,* 2002). Judging from the reproduced pictures however, these ammonites represent more likely the Berriasian Berriasellidae.

In the Boreal Pacific Realm, the character of ammonite migrations markedly changed in the early Volgian (early Tithonian) as compared to that of the Kimmeridgian time. In circum-Pacific areas, Tethyan ammonites penetrated considerably further northward than in the Kimmeridgian. The ammonite assemblage from the Chukotka-Canadian Province (southern Primor'e)[4] is very similar to that of the South America, however it includes Mediterranean elements as well, especially in upper strata (Sey and Kalacheva, 1995; Fig. 4a). Buchiids represent the dominant benthic group here (Sey and Kalacheva, 1997). Scarce Boreal-Arctic ammonites close to *Pectinatites fedorovi* Mesezhn. were found in northern Primor'e at about 50°N (Sey and Kalacheva, 1999; images unpublished). In Japan at 39°N, only scarce Tethyan *Aulacosphinctoides* (Sato, 1985) and *Hybonoticeras* (Matsuoka *et al.,* 2002) forms are known, and Boreal taxa are missing. A poorer assemblage bearing *Aulacosphinctoides* and unidentified ammonites similar to *Subplanites* was recorded in southern Alaska at 59°N (Imlay, 1981).

In British Columbia, Submediterranean perisphinctids were found at 49°N (Poulton *et al.,* 1988) though the enclosing sediments can be of the Kimmeridgian age. The stratigraphic position of buchiids from central Mexico is undefined so far (Fig. 4b; Zakharov, 1981; images unpublished).

1.3.4. Middle Volgian-Late Middle and Early Late Tithonian

In the middle Volgian time, biogeographic differentiation of mollusks drastically increased in the Panboreal Superrealm. In the West European Province, Tethyan ammonites of the terminal early-initial middle Tithonian are unknown, except for *Danubisphinctes,* north of southeastern France and Polish Carpathians (Fig. 3a). Low-boreal *Zaraiskites regularis* Kutek and associated Tethyan ammonites were encountered in the upper Tithonian of Bulgaria at 43°N and in Poland (Kutek, 1994). In the West European Province, buchiids inhabited northwestern France, southern England, southern Poland, and Czechia (Zakharov, 1981; Kelly, 1990). The westward migrations of East European mollusks can likely be a reaction to stronger influence of the Boreal-Arctic water masses.

In the East European Province, Tethyan and Arctic ammonites coexisted during the *panderi* Chron only (Fig. 3b). *Haploceras, Sutneria,* and *Glochiceras* s.l. still occur, though being extremely scarce, in the lowermost *Panderi* Zone in the Ul'yanovsk Realm (Mesezhnikov *et al.,* 1977). *Haploceras* is also recorded in the uppermost *Panderi* Zone of the northern Caspian Realm (Mesezhnikov, 1989). Like *Anaspidoceras* of the terminal early Volgian time, these ammonites most likely penetrated into the Central Russian Sea from the

4 Since the specific Tithonian-Neocomian ammonite assemblages of Primor'e strongly differ in composition and diversity from those of Chukotka and Arctic Canada, Sey and Kalacheva (personal communication, 2002) distinguished an independent Far East Province. Substantiated characteristic of the province are absent in their paper, and we use here the province name proposed by Saks *et al.* (1971).

south, and the Pripyat' strait was the only way for westward migrations of low-boreal ammonites (Rogov, 2002). Connections between Central Russian and North Caucasian basins are inferable based on of ammonites similar to *Dorsoplanites panderi* (d'Orb.), *D. dorsoplanus* (Vischn.), and *Lomonossovella lomonossovi* (Vischn.) found in the northern Caucasus at 44°N (Renz, 1904; Douvillé, 1910; Khimshiashvili, 1967). Pictures of two latter forms are unpublished. After the *panderi* Chron and up to the terminal early-initial late Berriasian time, Boreal-Arctic and Tethyan ammonites did not occur concurrently in the Boreal Atlantic Realm. Therefore, an ecotone of ammonite fauna was missing in this Realm beginning from the mid-middle Volgian to the late Berriasian.

In the Boreal Pacific Realm (Chukotka-Canadian Province and Primor'e), the ammonite assemblage analogous to that of the lower middle Tithonian supposedly existed to the terminal middle Tithonian or initial middle Volgian time (Fig. 4a). Scarce *Durangites* forms encountered slightly northward, in the Uda River basin at 55°N, were likely characteristic of the terminal middle Volgian as well. *Dorsoplanites* occurred further northward at 66°N (Zakharov *et al,* 1988). *Berriasella* found by Khudolei in the (?) middle Tithonian sediments (Sey and Kalacheva, 1988) were evidently also characteristic of the middle Volgian. In southern Primor'e, buchiids dominated among benthic fauna; their remains were also reported from Hokkaido (Zakharov, 1981). In places, they coexisted with sub-Tethyan trigoniids (Zakharov *et al.,* 1996). As compared to the Kimmeridgian time, the northern boundary of the ecotone was displaced for several degrees northward.

In the eastern part of the Boreal Pacific Realm, i.e., in British Columbia and northern California (Fig. 4b), Tethyan ammonites *Kossmatia, Substeuroceras,* and *?Substreblites* were widespread in the late Tithonian corresponding most likely to the terminal middle Volgian (Zeiss, 1983,1984)[5]. Boreal-Arctic ammonites are represented in British Columbia (Canada, 52°N) by scarce specimens similar to *Titanites* forms (Frebold, 1964). The precise stratigraphic position of Canadian *"Titanites"* is not defined. It is likely that they are actually characteristic of the older, Kimmeridgian sediments (Hillebrandt *et al,* 1992). Buchiids reached northern California to coexist there with Tethyan ammonites (Johnes *et al.,* 1969). The middle Volgian *Buchia mosquensis* (von Buch) and *B. rugosa* (Fischer) were reported (without images) from the beds in Mexico bearing *Durangites* (Imlay, 1980). However, stratigraphic range *of Durangites* in Mexico, as in Primor'e, is yet to be exactly defined in terms of the West European zonal succession, and it would be premature to make any reliable stratigraphic conclusions based on their findings. Imlay (1980) suggested that the *Durangites-Kossmatia* assemblage existed at the very beginning of the late Tithonian. His inference is compatible with data suggesting the terminal Tithonian episode of cooling near the eastern coast of the Paleopacific (Jeletzky, 1984).

1.3.5. Late Volgian-Terminal Late Tithonian and Initial Early Berriasian

Existence of the West European Province practically terminated in the late Volgian owing to a vast regression and associated deposition of the Purbeckian lagoonal-continental facies. Boreal-Tethyan ammonite migrations in Europe almost ceased, and Boreal-Arctic ammonites are unknown south of northern England (Fig. 3a). In the East European Province, *Craspedites* penetrated far southward, down to lower reaches of the Emba River in the Caspian Realm (47°N), where *Craspedites nodiger* (Eichw.) whose images are unpublished was encountered in association with typical early Berriasian *Calpionella alpina* (Lor.) and *Tintinopsella carpathica* (Murg. et Fil.) (Fig. 3b; Sasonova and Sasonov, 1983)[6]. In the Mangyshlak, Boreal-Arctic *Kachpurites fulgens* (Traut.) and *Garniericeras? interjectum* (Nikitin) of the upper Volgian Substage are known, but their photos and descriptions are unfortunately missing in the publication (Luppov *et al.,* 1986).

In view of embarrassing Boreal-Tethyan connections, the identification of "Tethyan" ammonite genera *Aulacosphinctes, Berriasella, Lemencia,* and *"Virgatosphinctes"* (= *Praechetaites* Sasonova, 1979) within the North Siberian Province of the Arctic Realm (Khatanga River basin, Nordvik Peninsula, Fig. 5), seems unexpected. These ammonites occur in beds corresponding to the upper and, to a lesser degree, middle Volgian. Previously they were regarded as Tethyan genera (Shul'gina, 1967, 1985), but actually they most likely represent descendants of low-boreal ammonites (Zeiss, 1984; Kutek and Zeiss, 1988; Sey and Kalacheva, 1993). At least, the Siberian *"Berriasella"* shows the bidichotomous branching of ribs that is untypical of actual berriasellids. The ammonites have not been revised after the initial examination by Shul'gina. The new name *Praechetaites* was proposed only for *"Virgatosphinctes"* (Sasonova and Sasonov, 1979), and other forms of that peculiar ammonite assemblage should be reexamined.

In the Boreal Pacific Realm, the situation was practically unchanged. The association of Tethyan ammonites *Berriasella, Dalmasiceras, Proniceras, Spiticeras,* etc. and Boreal-Arctic buchiids is known in Primor'e, British Columbia, and northern California

[5] It is difficult to establish the exact age of *Kossmatia, Substeuroceras,* and *Parodontoceras* faunas from sections of California and British Columbia (see discussions in Jeletzky, 1984; Zeiss, 1984). In Mexico, representatives of these genera are known from both the upper Tithonian and lower Berriasian (Adatte *et al,* 1994).

[6] The correlation potential of associated Boreal ammonites and calpionellids is moderately high, because diverse ranges of some species, e.g., of zonal *C. elliptica,* have been established in different provinces of the Tethys-Panthalassa Superrealm (Pessagno, written communication).

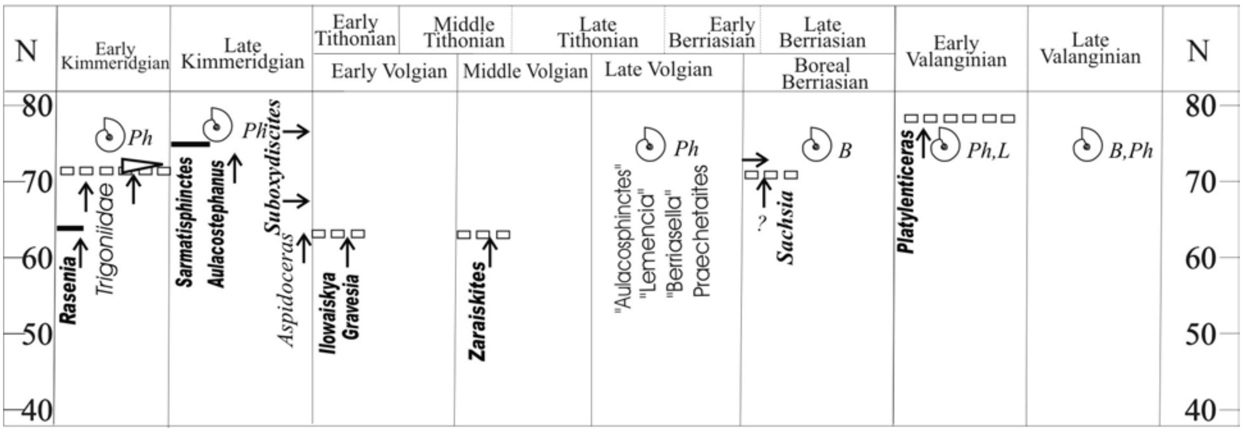

Fig. *5.* Isolated "straying" events of Tethyan, low-boreal, and oceanic mollusks in the Arctic Realm during the Kimmeridgian-Valanginian (symbols as in Fig. 3).

(Fig. 4a; Johnes *et al.,* 1969; Imlay and Johnes, 1970; Sey and Kalacheva, 1999). In the northwestern Pacific coast, findings of ammonites are extremely scarce, and only the Arctic genus *Chetaites* was identified in Chukotka at 66°N (Zakharov *et al.,* 1988). Rare specimens of Arctic *Subcraspedites* were encountered in northern Canada (Jeletzky, 1984).

1.3.6. Boreal Berriasian—Terminal Early (?) and Late Berriasian

At the end of the Berriasian, transgression of Boreal seawaters is again recorded in North Western Europe. Rare findings of buchiids are known in Lincolnshire (England) and in the northern Jutland, Denmark (Kelly, 1990). Numerous Boreal-Arctic ammonites *Borealites, Surites,* etc., also occur in England, being though not associated with Tethyan forms (Casey, 1973). *Euthymiceras* and *Riasanites* penetrated to Poland most likely through the Central Russian sea (Fig. 3a). In Pomerania and Kujawy areas, the Rogozno Formation yields *Riasanites* forms in association with Tethyan ammonites *Himalayites* and *Picteticeras,* whereas *Euthymiceras* is found here together with Boreal-Arctic *Surites* and Tethyan *Neocosmoceras* (Marek and Shulgina, 1996).[7]

At the end of the early Berriasian, or most likely at the beginning of the late substage, Tethyan basins of the North Caucasian and Boreal seas of the East European Provinces were connected anew. The Boreal-Tethyan migrations ways were first opened for mollusks since the middle Volgian time. Tethyan ammonites *Euthymiceras* and *Riasanites* penetrated to the East European Province and Boreal-Arctic buchiids reached the North Caucasian seas (Fig. 3b; Sasonova, 1977; Sey and Kalacheva, 1993). In addition, scarce representatives of Boreal-Arctic *Surites* advanced down to the Belaya River basin in the northern Caucasus (Sasonova, 1971). Boreal-Arctic mollusks are known from 44°N in the Mangyshlak, where rudists and Tethyan *Berriasella, Jabronella,* and *Mazenoticeras* occasionally coexisted with *Surites* and *Buchia* (Luppov *et al.,* 1983; Bogdanova *et al.,* 1989). Buchiids penetrated even further southward, to 39°N in the southern Karakum area *(Nizhnii mel...,* 1985); their single findings are also known in the Crimea (Yanin, 1970). Presence of *"Hoplites* cf. *rjasanensis"* (figures unpublished) has been once detected in Berriasian beds of Spitzbergen (Zhirmunskii, 1927), but this fact was not confirmed later on despite the intense investigations, and Shul'gina and Burdykina (1992) disputed a possibility of distinguishing the "*R. rjasanensis* beds" in Spitzbergen, as was proposed earlier by Ershova (1983). At the same time, some typical Boreal-Arctic ammonites, e.g., *Hectoroceras* and *Chetaites,* penetrated to the central Russian Sea (Sasonova, 1977; Mesezhnikov *et al.,* 1979); the latter has not been figured.

In the terminal Berriasian, cosmopolitan *Bochianites* and descendants of Tethyan *Sachsia sachsi* Schulgina penetrated from the Boreal Pacific to the Arctic Realm (Fig. 5; Shul'gina, 1985; Zakharov and Bogomolov, 1989). These peculiar berriasellids are morphologically similar to *Argentiniceras* cf. *noduliferum* described from the Berriasian of British Columbia (Jeletzky, 1984), and are likely descendants of this taxon[8].

In the late Berriasian, the southern part of the Chukotka-Canadian Province (Primor'e) was inhabited by Tethyan ammonite genera (Fig. 4a). These are *Fauriella, Spiticeras,* and *Berriasella?* occurring in association with buchiids at 49°N (Zakharov *et al.,* 1996; Sey and Kalacheva, 1999; Markovich *et al.,* 2000). In Primor'e, the ecotone was displaced southward. Its northern boundary was at the parallel of 50°N owing to penetration of Boreal-Arctic ammonite genera *Tollia* and *Surites* to the south (Zakharov *et al.,* 1996). Associations of Tethyan ammonite assemblages and

[7] *Riasanites* specimens from Poland somewhat differ from those of central Russia; they are lacking grooves on the ventral side and show a relatively high position of the ribs branching points (Baraboshkin, 1999).

[8] According to Jeletzky (1984), the found *Argentiniceras* approximately correspond in age to the Berriasian *occitanica* Zone of Western Europe.

abundant benthic buchiids with the Boreal-Arctic *Bojarkia* and *Tollia* are also characteristic of the East Pacific coast (Fig. 4b; Johnes *et al.,* 1969; Imlay and Johnes, 1970; Zakharov, 1981; Shul'gina, 1985). *Neocosmoceras* and *Argentiniceras* were found in British Columbia at 51°N (Jeletzky, 1984; Hoedemaeker, 1991), and Boreal-Arctic *Surites* is known here slightly northward at 55°N (Jeletzky, 1964). It is important that the whole Berriasian of the Boreal Pacific Realm is characterized by a low taxonomic diversity and scarcity of Arctic ammonites (Zakharov and Bogomolov, 1989).

1.3.7. Early Valanginian

The early Valanginian marks a significant change in ammonite distribution in all three Realms. Beginning from the Valanginian, the ecotone of Boreal Atlantic Realm that hosted Boreal and Tethyan biotas extended considerably, and cross-migrations resumed (Fig. 3a). Numerous ammonites of the *Pseudogarnieria-Platylenticeras* group are known from northern Germany, Poland, Czechia (western Carpathians), France, England, European Russia, eastern Greenland, Spitzbergen, and Novaya Zemlya (images of fossils from the three latter Realms are unpublished). Boreal or Tethyan origin of these ammonites is disputable. They are interpreted as indicators of the Tethyan influence in northern Realms (Kemper *et al.,* 1981) and of Boreal impact in southern areas (Marek and Shulgina, 1996; Vašíček and Michalík, 1999). Some experts accepted their descent from the Tethyan Spiticeratinae (Kemper *et al.,* 1981; Kemper, 1987). Alternatively, it was suggested that these ammonites descended from craspeditids (Schindewolf, 1966; Shul'gina, 1985) that is confirmed by similar changes in their lobe lines during ontogeny. We prefer the latter standpoint, because the aforementioned character of the geographic distribution of ammonites in question likely indicates their low-boreal origin. Moreover, umbilical tubercles are characteristic not only of *Spiticeras* forms, but also of some late Volgian craspeditids and Valanginian polyptychitids. Thus, *Platylenticeras* forms found in Western Europe may indicate strengthening of Boreal influence at the beginning of the Valanginian. This is supported by joint occurrence *of Platylenticeras* and *Menjaites* in England (Casey *et al.,* 1977). It is strange, but according to Kelly (1990), buchiids are unknown in the Valanginian of Western Europe. In the second half of the early Valanginian the Boreal influence was still strong, and first polyptychitids penetrated into southeastern France exactly at that time (Shul'gina, 1985; Bogomolov, 1989). The Tethyan *Karakaschiceras* and *Neocomites* known from Poland (Marek and Shulgina, 1996) migrated to the north almost simultaneously with the Boreal-Arctic *Polyptychites* and low-boreal *Platylenticeras* (Fig. 3a). Sporadic penetrations of Tethyan *Neocomites* to England were likely associated with the early Valanginian transgression (Kemper *et al.,* 1981). On the other hand, these unique findings may also indicate the posthumous transportation of shells (Baraboshkin, 2001).

In the East European Province, Tethyan influence was almost intangible in the early Valanginian (Fig. 3b). Its only evidence in favor is the neocomitid species *"Hoplites* aff. *arnoldi* Kil." (TsNIGR Museum, no. 71/623) figured by Bogoslovskii (1895, Plate 4, figs. 7a-7c). This specimen is not yet precisely identified however. At the beginning of the Valanginian, low-boreal *Platylenticeras* penetrated from the East European Province to the Northern Caucasus (Khalilov *et al.,* 1974; images unpublished), and *Polyptychites* reached Mangyshlak at the same time. In the Arctic Realm, only Boreal taxa, but rare cosmopolites *Bochianites* and *Phylloceras,* existed in the Valanginian time (Fig. 5; Shul'gina, 1985).

The ecotone of the Chukotka-Canadian Province (Primor'e) was narrowed down to five degrees, being located between 51° and 46°N (Fig. 4a). Boreal-Arctic *Polyptychites* and *Neotollia* coexisted in the ecotone with Tethyan *Thurmanniceras, Neocomites, Olcostephanus, Sarasinella, Kilianella,* and *Neohoploceras* (Zakharov *etal,* 1996; Sey and Kalacheva, 1989, 1999; Markovich *et al.,* 2000). Abundant *Buchia* remains occur in association with Tethyan ammonites in southern Primor'e. In northern California, comparatively diverse and numerous Boreal-Arctic ammonites *Tollia, Neotollia,* and *Polyptychites* are associated with Tethyan *Olcostephanus* and *Thurmanniceras* (Anderson, 1938; Imlay, 1984; Shul'gina, 1985). A single *Polyptychites* specimen was described even in Mexico (Burckhardt, 1906), but it may point to transportation of empty shells.

1.3.8. Late Valanginian

At the beginning of the late Valanginian, sea level rise recorded in the Northern Hemisphere, and influence of Tethyan fauna sharply increased in the West European Province. Abundant *Saynoceras, Bochianites, Valanginites, Olcostephanus, Karakaschiceras, Neohoploceras, Neocomites,* and *Sarasinella* appeared in England, Germany, and Poland (Figs. 3a, 3b).

The southward migrations of Boreal taxa became more intense concurrently with penetration of Tethyan forms into northern Europe at the beginning of the late Valanginian. For instance, Boreal-Arctic *Prodichotomites* are known from the lowermost upper Valanginian of western Carpathians (Vašíček and Michalík, 1997); *Dichotomies, Polyptychites, Prodichotomites,* and *Neocraspedites* are identified in northern and central Poland (Marek and Shulgina, 1996); and scarce *Prodichotomites* and *Dichotomites* occur in the upper Valanginian of France at 45°N (Thieloy, 1973; Besse *etal.,* 1986). Buchiids dwelt in the seas of North Western Europe (Kelly, 1990).

Through the seas of East European Province, polyptychitids penetrated southward down to the northern margin of the Tethys-Panthalassa Superrealm and into the North Caucasian Province and Mangyshlak (44°N), where they coexisted with Tethyan ammonites of the genus *Valanginites* (Fig. 3b; Luppov *et al.,* 1983). The genus *Homolsomites* attributed to craspeditids is known from latitude of 49°N in the Caspian Realm (Shul'gina *et al.,* 1989). Buchiids and associated Tethyan genera *Valanginites, Neocomites,* and *Saynoceras (Nizhnii mel...,* 1985) migrated further to the south, to 38°N in the central Kopetdag. These migrations were triggered most likely by the decreased temperature gradient between the Panboreal and Tethys-Panthalassa biogeographic Superrealms.

In the second half of the late Valanginian, distribution areas of Boreal-Arctic polyptychitids, which were driven away to the north, sharply decreased in the West European Province (Kemper *et al.,* 1981), and Tethyan ammonites markedly enhanced their position. It is likely that we deal in this case with a northward displacement of boundary between the Panboreal and Tethys-Panthalassa Superrealms rather than with migration of certain ammonite group. The impact of warming is recorded not only in northern Europe but also in the Arctic Realm up to the Barents Sea plate, as it is evident from expansion of thermophilic foraminifers and from penetration of Tethyan belemnite genus *Hibolithes* into the Timan-Pechora basin (Mesezhnikov *et al.,* 1983; Basov *et al.,* 1989). The obvious predominance of Arctic ammonites in the East European Province indicates cessation of direct connection between the Central Russian and Polish basins at least in the late Valanginian. The only evidence in favor of strengthened Tethyan influence in the East European Province by the end of the Valanginian is the following statement of Zonov (1937, p. 45): "In the Neocomian sandy beds of the Russian Platform we encountered representatives of *Neocomites, Bochianites,* and other genera, and *Distoloceras* sp. in the Volga River basin." However, images and precise geographic and stratigraphic positions of ammonites remained unpublished, this considerably reduces value of this statement.

In the Boreal Pacific Realm, the ways of late Valanginian ammonite migrations were the same as in the early Valanginian, with the only difference: the Boreal influence slightly strengthened in the West Pacific coast, where dominating Tethyan ammonite genera *Olcostephanus, Sarasinella,* and *Kilianella* occur in association with Boreal-Arctic *Homolsomites* and buchiids (Fig. 4a; Zakharov *et al.,* 1996; Markovich *et al.,* 2000). On the contrary, the Boreal influence was somewhat reduced in the eastern coast (Fig. 4b). The Boreal-Arctic ammonites *Homolsomites, Neocraspedites* and bivalves *Buchia* did not penetrate southward of northern California, where they coexisted with Tethyan *Olcostephanus* and *Lyticoceras* (Johnes *et al.,* 1969; Imlay and Johnes, 1970; Zakharov, 1981; Shul'gina, 1985).

1.4. REGULARITIES IN MIGRATIONS OF KIMMERIDGIAN-VALANGINIAN MOLLUSKS AND POSITION OF BIOGEOGRAPHIC ECOTONE IN THE NORTHERN HEMISPHERE

In the Late Jurassic and Early Cretaceous, mollusks of the Northern Hemisphere were rather distinctly differentiated into Boreal taxa, which inhabited seas north of the 50°N, and Tethyan ones typical of the basins south of 45°N. A biogeographic ecotone existed between these latitudes in certain time spans and its basins experienced with time certain displacements in space.

New data obtained in last decades offer a possibility to establish more exactly the geographic position of boundaries of the Boreal-Tethyan ecotone in the Late Jurassic and early Neocomian, and to define the southern boundary of the Boreal Atlantic and Boreal Pacific Realms (Figs. 3,4). Previously revealed time spans and events of Tethyan-Boreal and reverse migrations of molluscan assemblages or certain taxa are confirmed and new ones are established (Figs. 6, 7).[9] Kimmeridgian to Valanginian migrations of variable intensity are distinguishable in the Boreal Atlantic (West and East European Provinces), Boreal Pacific (Chukotka-Canadian and Boreal Pacific Provinces), and in Arctic (North Siberian Province) Realms. Mollusks, such as ammonites, belemnites, and bivalves, were divided into Tethyan (epicontinental sub-Tethyan forms included) and Boreal taxa. Among the latter, we discriminated more abundant Boreal-Arctic mollusks from low-boreal ones, many of which had Tethyan ancestors and were characteristic of the ecotone. It is interesting that during a considerably long time, from the second half of the late Volgian to the beginning of the Valanginian, when the ecotone ammonite fauna was either missing in Europe, or dwelt in places (in the late Berriasian), the low-boreal ammonites did not exist or occupied small distribution areas like that of the genus *Garniericeras* (Fig. 6b).[10] The genus *Platylenticeras* that descended from Arctic ancestors, though was of low-boreal type according to geographic distribution, appeared only at the beginning of the Valanginian. During the discussed time span, Boreal-Arctic buchiids reached the lowermost latitudes (30°N in the Boreal Pacific Province) only twice: in the early Kimmeridgian and late? Tithonian. In the West European Province they penetrated southward down to 48 °N and reached 42-40°N in the East Europe only in the Berriasian and Valanginian. In the Boreal Pacific Realm, the Kimmeridgian-Valanginian buchiids constantly inhabited basins of the ecotone area down to latitudes of 42°N in the Chukotka-Canadian Province and of 38°N in the Boreal Pacific Province (Figs. 7a, 7b). In the North Siberian Province,

[9] For better clearness of Figs. 6 and 7, the Boreal scale of the East European Province was taken as a basis, and regional scales were preliminarily correlated with it.
[10] This taxon is absolutely unknown in the Boreal Pacific Realm.

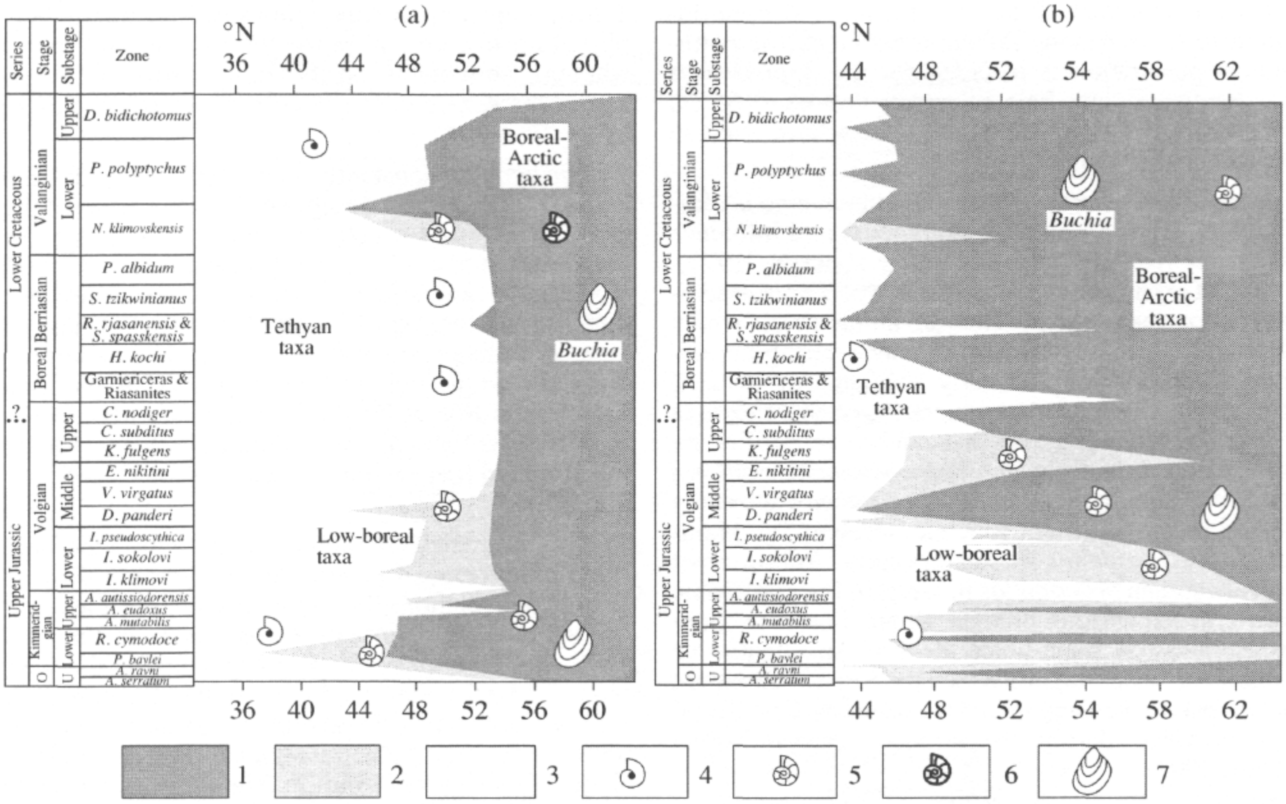

Fig. 6. Mollusk migrations within the Boreal–Tethyan biogeographic ecotone of the Boreal Atlantic Realm during the Kimmeridgian–Valanginian (basic scheme):

(1) Boreal taxa; (2) low-boreal taxa in Fig. 6 and *Buchia* in Fig. 7; (3) Tethyan taxa; (4) Tethyan ammonites; (5) low-boreal ammonites; (6) Boreal ammonites; (7) *Buchia*. Abbreviations in the stratigraphic columns: (u) upper; (O) Oxfordian; (Bor.) Boreal.

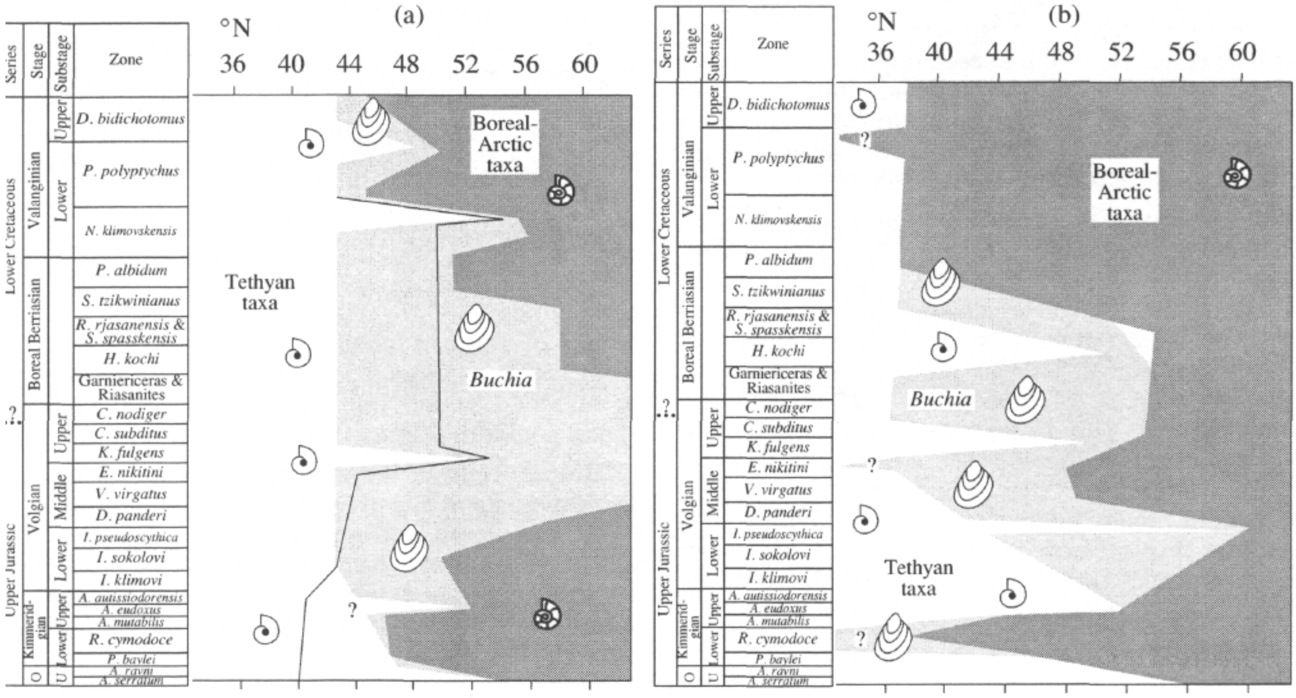

Fig. 7. Mollusk migrations within the Boreal-Tethyan biogeographic ecotone in the Boreal Pacific Realm during the Kimmeridgian-Valanginian (basic scheme; symbols as in Fig. 6).

Tethyan Trigoniidae advanced in the early Kimmeridgian up to 72°N. Among Tethyan ammonites, the northernmost penetration is recorded for the *Aspidoceras* (late Kimmeridgian, East European Province, 65°N) and *Durangites* (late Tithonian, Chukotka-Canadian Province, 54°N) genera.

In degree of intensity, the faunal interchange is classified into expansions (mass migrations) and influence migrations (isolated "straying" after Rawson, 1973). Typical of expansions were migrations of whole assemblages, for instance, of Tethyan ammonites, which migrated in the East European Province during the terminal Kimmeridgian and early Volgian. An isolated "straying" corresponded to penetration of separate taxa or their few representatives that can be exemplified by immigration of the Tethyan *Aspidoceras* to the northern East European Province. Expansions rather commonly resulted in appearance of endemic lineages, for example, of new *Riasanites* species in central Russia or of late Valanginian neocomitids in Western Europe. Some short-term expansions brought about, however, only species invasion their home Realm. An illustrative example of such migration is invasion of abundant *Anaspidoceras neoburgense* (Oppel) in the East European Province during the terminal early Volgian (Rogov, 2002).

Bivalves of the genus *Buchia* are also suitable to demonstrate the intensity of migrations. Their expansions were characteristic of the entire Kimmeridgian-Valanginian in the Boreal Pacific Realm. Beginning from the middle Volgian, the northern boundary of buchiids dispersal was near 43°N within the Chukotka-Canadian Province and at 38°N in the Boreal Pacific Province (Figs. 7a, 7b). Influence migrations in basins of the Boreal Atlantic Realm took place throughout the Late Jurassic-early Neocomian in the West European Province (Fig. 3a) and during the Berriasian-Valanginian in the East European Province (Fig. 3b).

Two migration types are distinguishable based on directions of taxa ways. These are multidirectional-migrations, for instance that in the Volgian-early Berriasian, and unidirectional migrations, like that of the terminal Valanginian in the West European Province. We connect the Boreal-Tethyan multidirectional-migrations with decrease of temperature gradient between paleozoochores. This factor is operative, when geographic barriers to migration are absent, and leads to expansion of ecotone area in corresponding periods. The unidirectional migrations were commonly followed by displacement of boundaries of high-rank paleozoochores. They were characterized by sharp compositional changes in ammonite assemblages.

Despite the close position of West and East European Provinces in the Boreal Atlantic Realm, mollusk migrations within their limits were not always interconnected that may be explained by influence of currents and geographic barriers. In the terminal Valanginian, for example, the boundary between Panboreal and Tethys-Panthalassa Superrealms was significantly displaced northward within the West European Province, whereas ammonites of the East European Province were represented at the same time almost exclusively by Arctic taxa.

The ecotone constantly existed in the Boreal Pacific Realm. Tethyan ammonoids sometimes coexisted there with Boreal-Arctic taxa and almost constantly with buchiids. In the Chukotka-Canadian Province (Primor'e), the ammonite ecotone was positioned from time to time between 45° and 55°N (Fig. 7a). The ecotone of Tethyan ammonites and buchiids extended to 43°N almost throughout the time interval under discussion. In the Boreal Pacific Province (northern California), the ecotone of the Tithonian-Valanginian time was located approximately between 40° and 50°N (Fig. 7b).

The comparison of mollusk migrations in the Boreal Atlantic and Boreal Pacific Realms does not show any distinct correlation. The only perceptible fact is the strengthening influence of Boreal fauna in the whole Northern Hemisphere by the beginning of the Cretaceous, when boundary between the Panboreal and Tethys-Panthalassa Superrealms was displaced to the south, especially in the Valanginian (Figs. 6, 7). This is obviously a sign of evolution. The Tethyan impact during the Kimmeridgian and early Volgian periods was well pronounced only in the Boreal Atlantic Realm, where "migration waves" are recorded (Fig. 6). It was less distinct in the Boreal Pacific Realm (Fig. 7).

What factors influenced the Boreal-Tethyan migrations and position of the ecotone? The major factor was water temperature lowering toward the north. However, migrations involved only separate taxa of Boreal-Arctic and Tethyan mollusks. Some typical Tethyan mollusks reached 60° and even 70°N, i.e., they migrated for 2-3 thousand km northward from the northern Tethys-Panthalassa boundary (45°N). Among Boreal "wanderers," there are no reliably identified (illustrated) genera of cephalopods, which crossed parallel of 38°N, i.e., migrated for more than 700 km southward from southern boundary of the Panboreal Superrealm. Certain groups of Tethyan fauna were likely more tolerant to temperature changes than Boreal forms. This fact can be regarded as substantiating the notion of predominantly southern origin of most Boreal taxa.

Boreal-Tethyan migrations are often explained in terms of eustatic hypothesis: their migration ways must be open or closed in the periods of high or low sea-level stands, respectively (Kemper *et al.,* 1981). In addition, sea level rises are assumed to smooth out the thermal barriers between water masses. Data on the central East European Province (Central Russian sea) are the most suitable to check the hypothesis. As seen in Fig. 8, the coincidence of transgression peaks with alternating ammonite migrations is observable only within the Kimmeridgian-middle Volgian period, when northward migrations of Tethyan ammonites were coeval to

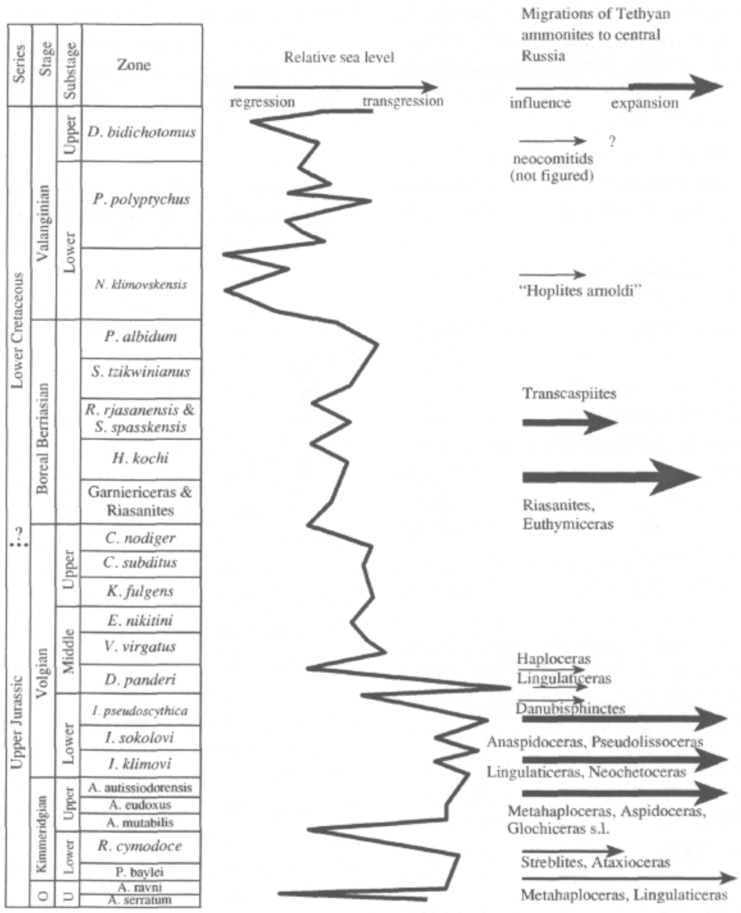

Fig. 8. Correlation between transgression-regression events and migrations of Tethyan ammonites into the Central Russian Sea in the Kimmeridgian-Valanginian period (transgression-regression curve after Sahagian *et al,* (1996) with additions; thickness and length of arrows indicate duration and intensity of migrations, respectively). Abbreviations in the stratigraphic column: (u) upper; (O) Oxfordian; (Bor.) Boreal.

the sea level rises. Higher in the sequence, there is nothing of this kind. The berriasellid expansion during the Berriasian was obviously not associated with the eustatic sea-level rise. This event may be explained by breakage of the geographic barrier that existed between the North Caucasian and Central Russian seas. The influence of Tethyan water masses evidently dominated over that of the Boreal ones, as connections between Central Russian Sea and Arctic basin in the north were limited.

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