Molluscan immigrations via biogeographical ecotone of the Middle Russian Sea during the Jurassic

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ABSTRACT: Patterns of molluscan immigration via the biogeographical ecotone zone of the Middle Russian Sea during the Middle – Late Jurassic have been studied in detail. Firstly, the migration routes and ranges of recent molluscs are briefly reviewed, with some comments about their applicability to the Jurassic. Secondly, the migrational events have been classified by their direction, duration and intensivity. We recognize two main types of immigration by their direction (unidirectional and multidirectional) and by their intensity (mass immigrations and isolated strayings). Recent progress in infrazonal ammonite biostratigraphy leads us to the more precise recognition of paleobiogeographical events and to the understanding of the immigration patterns that can produce more precise correlations.

INTRODUCTION

Jurassic molluscs, especially ammonoids, are the only group of fossils which has been traditionally used to elaborate new approaches in biostratigraphy such as the concept of zones by Oppel (1856-58) and the hemerae of Buckman (1893) as well as in paleobiogeography (Neumayr 1878; Uhlig 1911) and, recently, Sachs *et al.* (1971), Westermann (2000).

This paper summarises the results of recent detailed investigations of the biostratigraphy and paleobiogeography of the Middle Russian Sea (Fig. 1) during Middle-Late Jurassic time. This water body was chosen mostly because of its position as an ecotone between two main Superrealms during the Middle-Late Jurassic (Zakharov and Rogov 2004).

The so-called Middle Russian Sea flooded the East-European Platform during Bajocian-Bathonian time. After that for ca. 30 Myr this sea repeatedly changing its configuration, but always remaining connected with Boreal Basin via the Timan-Pechora Sea to the north. The southern connection with Peri-Tethyan (Caucasian) seas was not permanent and sometimes disappeared.

MIGRATION PATTERNS IN MODERN CEPHALOPODS AND BIVALVES AS KEY TO THE PAST

Modern cephalopods are represented by different living forms which inhabit all seas and oceans from tidal areas to the hadal zone. The taxa include both neritic and oceanic species, and both assemblages include pelagic and bottom dwellers,
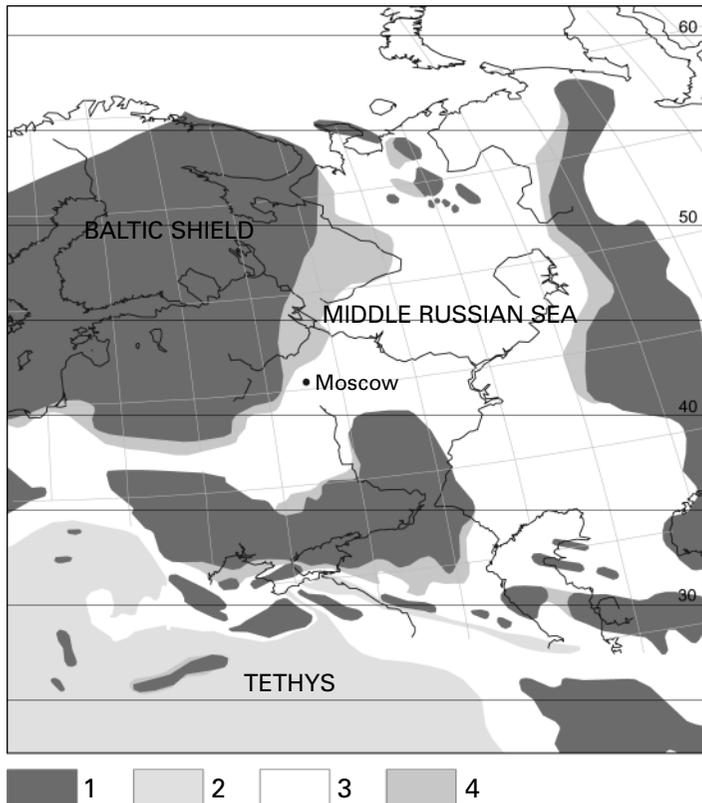
Fig. 1. Middle Russian Sea and adjacent areas during the Late Jurassic (example of Late Kimmeridgian – Early Volgian): 1 – land areas; 2 – oceanic basins; 3 – shallow epicontinental seas; 4 – coastal areas, sometimes flooded by sea. Palaeogeography and paleolatitudes are from Thierry and Barrier (2000), corrected.

(Nesis 2003). Post-mortal drift is common for Sepiidae and Spirulidae shells.

Cephalopods are very prone to expand and to reduce their species ranges quickly. After the opening of Suez Channel more than 200 different hydrobionts penetrated into the Mediterranean Sea, including the Indo-Pacific *Octopus kagoshimensis* (Salman *et al*. 2005) Recent warming of the climate (the so-called "Global warming") has provoked a gradual disappearance of the squid *Loligo forbesi* from Portugal (Chen *et al*. 2006) and, presumably, well before this, in Morocco, where it was recorded in the past but never met during intensive investigations in 1995-1998 (Laptikhovsky, pers. comm). The influence of interspecific competition on the ranges of extant cephalopods is still insufficiently known. Inverse patterns of abundance of two commercial squids *Illex argentinus* and *Loligo gahi* has been suggested as the possible result of interspecific competition (Arkhipkin and Middleton 2002), and the same causal hypothesis was invoked to explain the strong depth segregation in some North African coleoids (Arkhipkin and Laptikhovski 2005). Nevertheless, numerous occasions of the coexistence of morphologically close species are known, amongst commercial taxa (Bonaud *et al*. 1998; Herke and Foltz 2002).

With respect to cephalopods, bivalves are slow-moving when adult, (except when attached to algae or wood) and their migratory ranges are restricted up to several kilometers, such as in *Macoma baltica* (Hiddink 2002). However, many species have planktonic larvae that can be widely dispersed by oceanic currents. The major factor limiting their spreading is water temperature during spawning. Temperature limits for gonad maturation and hatching could be much narrower in comparison with those of adult animals (Scarlato 1981). Another important factor is the presence/absence of a suitable substrate for juvenile settling. Gastropod taxa with pelagic larvae are widely distributed along the west coast of South America, where the necessary rocky substrates are abundant. In contrast to this, the east coast of the continent is represented almost exclusively by sandy substrates, and species with direct development predominate from the subtropics

with the maximum diversity in the tropics and subtropics (Nesis 2003). They occur in water of normal marine salinity, between 27 and 37‰ (Jereb *et al*. 2005) with some rare exclusions. The bulk of modern cephalopods is characterized by very fast growth and short life-cycles with terminal spawning. Cephalopods are voracious, active predators (Nesis 1985; Jereb *et al*. 2005).

The major factors which influence cephalopod distribution are temperature, food and currents. Oceanic species usually undergo daily vertical migrations, occurring at depths of about 200 to 700 m during the day, and ascending into the uppermost 200 m for the night (Jereb *et al*. 2005). Some cephalopods are characterized by ontogenetic and/or seasonal migrations, either active (Ommastrephidae) or passive, through areas with closed circulation (*Spirula*) (Nesis 1985). Some neritic cephalopods have small natural habitats and some of them have very wide distribution, for example *Octopus vulgaris* (Nesis 1987). Oceanic coleoids usually have latitudinal distribution, but also panboreal, bi-subtropical amphi-atlantic ranges occur

to Antarctica (Gallardo and Penchaszadeh 2001). Bivalves probably could suffer the same problem.

The critical temperatures differ between species and populations depending on latitude or seasonal temperature acclimatization. Peck and Conway (after Pörtner 2001) suggested that tropical and temperate species are more eurythermic than polar ones.

The polarbound limit of the species range in summer is determined in bivalves by the minimum temperature suitable for reproduction, and in winter by the minimum survival temperature. The equator-ward limit of the species distribution in winter is determined by the maximum temperature of reproduction whereas the maximum survival temperature restricts this boundary in summer (Scarlato 1981). These adaptive patterns permit the bivalves of high latitudes to inhabit the deep waters of the temperate zone, whereas tropical or subtropical species are able to penetrate far into high latitudes in summer. For example, a Boreal species *Astarte crenata* inhabits shallow areas in both the Barents Sea and the North Sea, and occurs in deep biotopes of the Gulf of Biscay. Some tropical-subtropical (for example, *Solen corneus*) and numerous subtro-pical relatively deepwater bivalves occur in the shallow habitats of Possjet Bay (42° N, Japan Sea) (Golikov and Scarlato 1967; Scarlato 1981).

These biological features controlling the geographical ranges of bivalves in modern seas, were important for bivalve spreading in the past. That is why, in our opinion, the southward spreading of natural habitats of Boreal bivalves (for example, belonging to the genera *Buchia* and *Retroceramus*) and the northward penetration of Tethyan Trigoniidae were caused by movement of larvae by currents. Another explanation of these events is the movement of water masses caused by transgressive-regressive events. In comparison to the situation with ammonites and other active poikilotherm animals, we should suppose more developed eurythermy within bivalves (Scarlato 1981). In spite of the planktonic mode of life of bivalve larvae, sometimes "ecological opportunity" rather than current direction influenced their dispersion (Amano 2005).

DISCUSSION ABOUT THE AMMONITE MODE OF LIFE AND THEIR MIGRATIONAL PATTERNS

The biogeography, life habitat and migrational patterns of ammonites were intensively studied during the last decades (Kennedy and Cobban 1976; Olóriz 1990; Cecca 1992; Westermann 1996; Westermann and Tsujita 1999, among others). In a similar manner to modern cephalopods the ammonoids were possibly animals with different modes of life, from planktonic to quasi-nektonic and nekto-benthic ones. The ammonoids inhabited different biomes, and the oceanic groups of ammonites are usually different from those of neritic areas. Perhaps their penetration from shelf areas to the oceans, in contrast to coleoids, happened to planktonic, non nektonic, forms. It is very possible, that many ammonoids (especially heteromorphs) were vertical migrants (Westermann and Tsujita 1999), while others mostly swam above the bottom. The bulk of ammonoids was restricted to waters with normal oceanic salinity, with some exceptions like *Ceratites* which lived in restricted carbonate platforms surrounded by evaporate basins (Westermann and Tsujita 1999). Ontogenetic migrations leading to spatial segregation of juvenile and adult growth stages are also known in ammonoids (Westermann 1996).

Migrations which are related to long-time changes in the natural habitat, sometimes accompanied by diversification or sharp changes in fossil (ammonite) communities, should be separated from cyclic and repeated vertical, ontogenetic and seasonal migrations. Some of these types of migration in ammonites were recently reviewed by Reyment (2005) with some additions concerning necroplanktonic drift and "spurious migrations", caused by tectonics (continental drift, terrane movement, *etc*). Long-time and non-cyclic migrations we could call "immigrations", following the earlier usage of this term in ammonite biogeography (Westermann 1996; Fernandez-Lopez and Melendez 1996; Schweigert 2000; Navarro *et al.* 2005) and study of recent coleoids (Neige 2003), or "invasions" (Sei and Kalacheva 1983). The term "invasion" usually means a strong event, leading to the alteration of ecological relationships (*i.e.* mass migrations), while "immigration" could be used for all the characters of ammonite range movement. The analysis of ammonite immigrations involves difficulties due to problems in the precise outlining of their natural habitat (Bengtson and Kakabadze 1999). Ammonoids could be assigned to biogeographic categories (eudemic, miodemic and parademic, carrying by currents, and so on (Fernandez-Lopez and Melendez 1996)), but even analyzing modern cephalopod areas we sometimes could
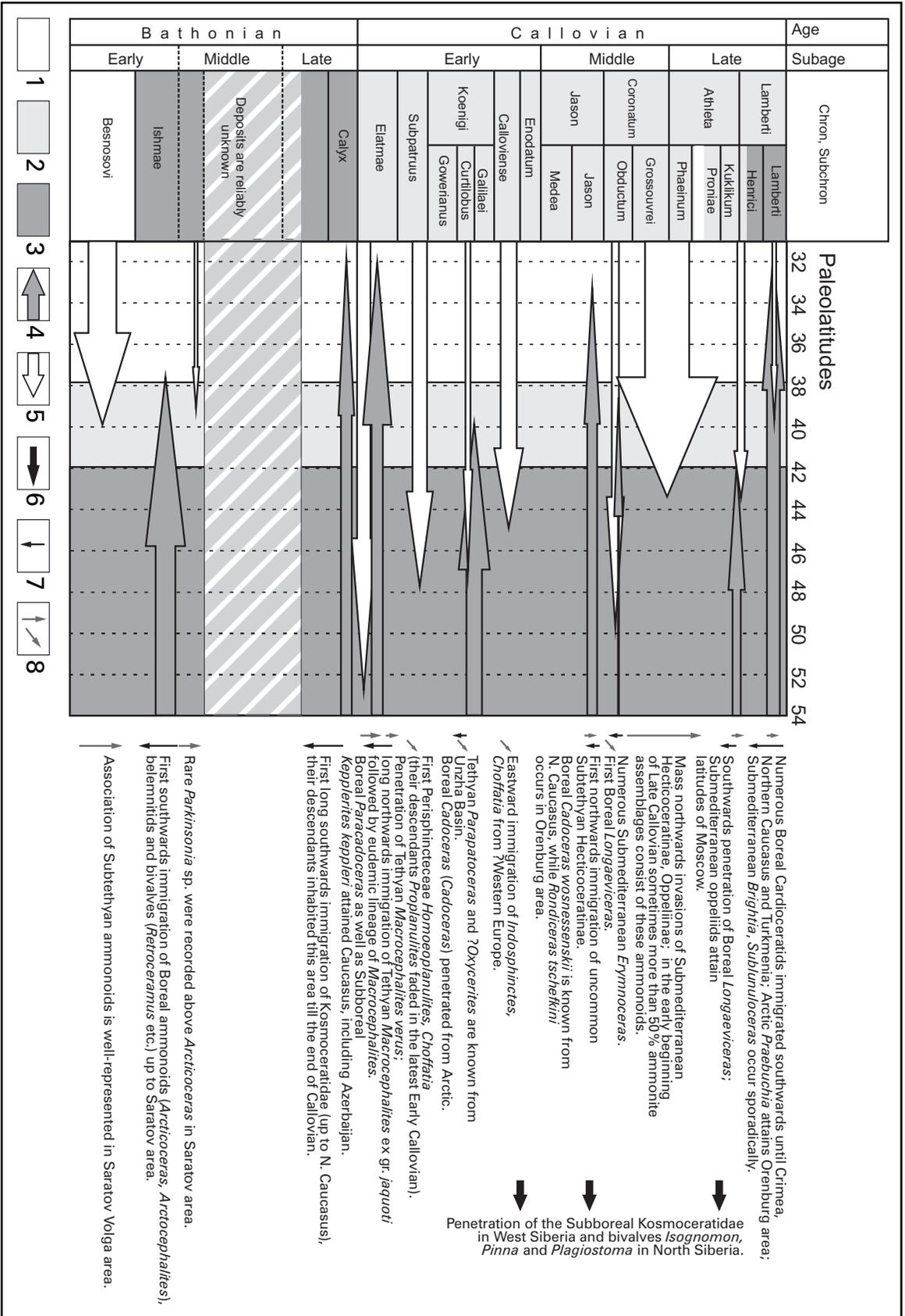
Fig. 2. Latitudinal and most important longitudinal immigrations of Boreal, Subboreal and Submediterranean molluscs during the Middle Jurassic through the Middle Russian Sea. 1-3 – domination of: 1 – Submediterranean, 2 – Subboreal, endemic or mixed, 3 – Boreal taxa (in scale); 4-6 – migrations of: 4 – Boreal, 5 – Submediterranean molluscs, 6 – longitudinal migrations in West Siberian Basin; 7 – southwards immigration of Boreal molluscs; 8 – northwards and eastwards immigration of Submediterranean molluscs. Widths of arrows roundly coincide with event duration. Ecotone zone with mixture of Boreal, Subboreal and Submediterranean mollusks chiefly allocated between 38 and 42 N.

Legend: 1, 2, 3, 4, 5, 6, 7, 8

Age / Subage / Chron, Subchron

Age	Subage	Chron, Subchron
Bathonian	Early	Besnosovi / Ishmae
	Middle	Deposits are reliably unknown
	Late	Calyx
Callovian	Early	Elatmae; Subpatruus; Koenigi (Gowerianus, Curtilobus, Galilaei); Calloviense (Enodatum)
	Middle	Jason (Medea, Jason); Coronatum (Obductum, Grossouvrei)
	Late	Athleta (Phaeinum, Proniae, Kuklikum, Henrici); Lamberti (Lamberti)

Paleolatitudes: 32 34 36 38 40 42 44 46 48 50 52 54

Annotations (right side):

Numerous Boreal Cardioceratids immigrated southwards until Crimea, Northern Caucasus and Turkmenia; Arctic *Praebuchia* attains Orenburg area; Submediterranean *Brightia*, *Sublunuloceras* occur sporadically.

Southwards penetration of Boreal *Longaeviceras*; Submediterranean oppelids attain latitudes of Moscow.

Mass northwards invasions of Submediterranean Hecticoceratinae, Oppeliinae; in the early beginning of Late Callovian sometimes more than 50% ammonite assemblages consist of these ammonoids.

Numerous Submediterranean *Erymnoceras*.

First Boreal *Longaeviceras*.

First northwards immigration of uncommon Subtethyan Hecticoceratinae.

Boreal *Cadoceras wosnessenskii* is known from N. Caucasus, while *Rondiceras tschefkini* occurs in Orenburg area.

Eastward immigration of *Indosphinctes*, *Choffatia* from ?Western Europe.

Tethyan *Parapatoceras* and ?*Oxycerites* are known from Unzha Basin.

Boreal *Cadoceras* (*Cadoceras*) penetrated from Arctic.

First Perisphincteceae *Homoeoplanulites*, *Choffatia* (their descendants *Proplanulites* faded in the latest Early Callovian).

Penetration of Tethyan *Macrocephalites verus*; long northwards immigration of Tethyan *Macrocephalites* ex gr. *jacquoti* followed by eudemic lineage of *Macrocephalites*.

Boreal *Paracadoceras* as well as Subboreal *Kepplerites keppleri* attained Caucasus, including Azerbaijan.

First long southwards immigration of Kosmoceratidae (up to N. Caucasus), their descendants inhabited this area till the end of Callovian.

Rare *Parkinsonia* sp. were recorded above *Arcticoceras* in Saratov area.

First southwards immigration of Boreal ammonoids (*Arcticoceras*, *Arctocephalites*), belemnitids and bivalves (*Retroceramus* etc.) up to Saratov area.

Association of Subtethyan ammonoids is well-represented in Saratov Volga area.

Penetration of the Subboreal Kosmoceratidae in West Siberia and bivalves *Isognomon*, *Pinna* and *Plagiostoma* in North Siberia.

confuse these categories. Examples of post-mortem shell distribution published in the last decades were peculiar to the some groups of ammonoids only (Westermann 1996), especially from the oceanic biome.

In comparison to most of juvenile coleoids, very small ammonite hatchlings with a spherical shell filled by gas perhaps were easily scattered by currents. After growing and maturation, some ammonites remained planktonic while other began near-bottom or demersal life styles. There are different ways to reconstruct the mode of life in ammonites, from morphofunctional studies to facies and stable isotope analysis and to the studying of palaeopathologies and stable isotope signals (Ziegler 1967; Keupp and Ilg 1992; Westermann 1996; Anderson *et al*. 1994; Zakharov *et al*. 2006). We have to admit the high diversity in ecology of different ammonites.

Following Rawson (1973) we have recognized two different types of immigration according to intensivity: 1) mass immigrations (or expansions) which lead to the movement of high-ranked biogeographic boundaries and alter the charactistics of ammonite communities, and 2) isolate straying, when immigrants are scarce and didn't give rise to new stocks. These types sometimes could be similar both spatially and temporally. One of the most unusual examples of the considerable distance travelled by small ammonite populations is shown by the aspidoceratids of latest Kimmeridgian age. Already living in the Subboreal seas of Poland and central areas of the Russian Platform, aspidoceratids of the late Autissiodorensis Chron are extremely rare (Kutek and Zeiss 1997; Rogov 2004). But some representatives of this group travelled as far as the Pechora River Basin and even the Subpolar Ural (Mesezhnikov 1984; Zakharov *et al*. 2005).

There are also two main types of immigrations which differ in their direction.

Unidirectional immigrations that usually coincide with movements of the biochore boundaries and drastically change ammonite communities.

Multidirectional (bidirectional) immigrations reflecting the simultaneous southward penetration of the Boreal taxa and the northward of Tethyan taxa. Perhaps, bidirectional immigrations occur rarely and reflect mainly a high sea-level stand. The biogeographical ecotone is usually enlarged at this time (Zakharov and Rogov 2004).

The ranges of ammonite species were influenced (with the exception of evolution) by the following major factors: climate, geographical barriers and currents. Climate and geographical barriers often were interrelated, because an appearance or a disappearance of a barrier usually lead to a change in the water mass circulation and hence to climate change. The effect of currents was expressed mostly in the differences between fossil assemblages within different parts of a single basin with constant paleolatitude and sedimentation. A good example of sign of a cold paleocurrent via the Middle Russian Sea along the Urals during the Middle-Late Jurassic has been suggested by Kiselev (2004) due to the strong prevalence of Boreal ammonites. The same current also persisted during the Volgian (Rogov 2004).

MOLLUSCAN IMMIGRATIONS THROUGH THE MIDDLE RUSSIAN SEA

Any paleobiogeographical reconstruction, in contrast to modern biogeography, needs preliminary correlation and the revealing of the bio-events. It could be carried out accurately through the faunal horizons and their temporal equivalents, so-called hemerae (~ca. 0.08-0.2 My, after Page 1995). Only sometimes important changes in relative abundance of taxa were widely traced within the smaller part of faunal horizons.

The Middle Russian Sea existed on the boundary zone of two climatic belts, Boreal and Tethyan. Analysis of the biogeographical distribution of mollusks shows a permanent location of the biogeographical ecotone in this region (Zakharov and Rogov 2004). This is shown by the contemporaneous existence of the mixed Boreal, Subboreal and Submediterranean taxa in the bulk of the Middle-Upper Jurassic zonal assemblages (Hantzpergue *et al*. 1998; Mitta and Seltzer 2002; Rogov 2004). The Middle Russian Sea was influenced by Arctic and Peri-Tethyan water masses. This is demonstrated by the temporal dynamics of the Boreal and Tethyan elements in molluscan faunas (Figs 2-3).

Boreal taxa were dominant and widely distributed at the end of the Early (?) and the Late Bathonian, the earliest Callovian (when multidirectional migrations were important), in the latest Callovian and beginning of the Oxfordian, in the Late Oxfordian, in the beginning of the Middle Volgian and near to the Jurassic-Cretaceous boundary. Prolonged Tethyan influences occurred in the earliest Bathonian, in the beginning of
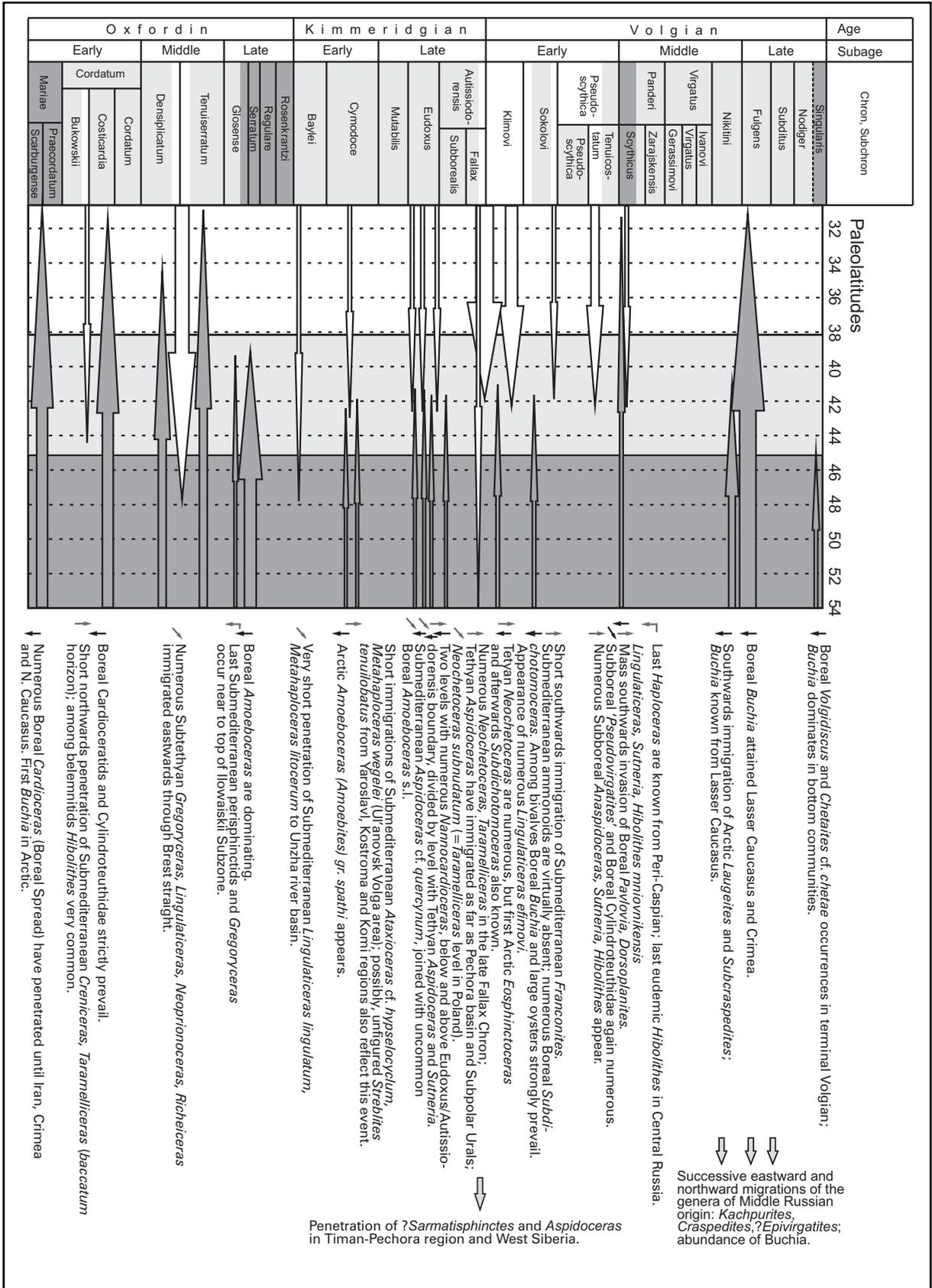
Fig. 3. Latitudinal and most important longitudinal imigrations of Boreal, Subboreal and Submediterranean molluscs during the Late Jurassic through Middle Russian Sea (see Fig. 2 for explanation).

Age / Subage / Chron, Subchron

Oxfordin — Early: Mariae (Scarburgense, Praecordatum), Cordatum (Bukowskii, Costicardia, Cordatum); Middle: Densiplicatum, Tenuiserratum, Glosense, Serratum, Regulare, Rosenkrantzi; Late.

Kimmeridgian — Early: Baylei, Cymodoce; Late: Mutabilis, Eudoxus, Autissiodorensis (Subborealis, Fallax).

Volgian — Early: Klimovi, Sokolovi, Pseudoscythica (Pseudoscythica, Tenuicostatum, Scythicus); Middle: Panderi (Zarajskensis, Gerassimovi), Virgatus (Virgatus, Ivanovi), Nikitini, Fulgens; Late: Subditus, Nodiger, Singularis.

Paleolatitudes: 32 34 36 38 40 42 44 46 48 50 52 54

Right-side annotations (top to bottom):

- Boreal *Volgidiscus* and *Chetaites* cf. *chetae* occurrences in terminal Volgian; *Buchia* dominates in bottom communities.
- Southwards immigration of Arctic *Laugeites* and *Subcraspedites*; *Buchia* known from Lasser Caucasus.
- Boreal *Buchia* attained Lasser Caucasus and Crimea.
- Last *Haploceras* are known from Peri-Caspian; last eudemic *Hibolithes* in Central Russia.
- *Lingulaticeras*, *Sutneria*, *Hibolithes mniovnikensis*
- Mass southwards invasion of Boreal *Pavlovia*, *Dorsoplanites*.
- Subboreal *Pseudovirgatites*. and Boreal Cylindroteuthidae again numerous. Numerous Subboreal *Anaspidoceras*, *Sutneria*, *Hibolithes* appear.
- Short southwards immigration of Submediterranean *Franconites*. Submediterranean ammonoids are virtually absent; numerous Boreal *Subdichotomoceras*. Among bivalves Boreal *Buchia* and large oysters strongly prevail. Appearance of numerous *Lingulaticeras efimovi*. Tetyan *Neochetoceras* are numerous, but first Arctic *Eosphinctoceras* and afterwards *Subdichotomoceras* also known. Numerous *Neochetoceras*, *Taramelliceras* in the late Fallax Chron; Tethyan *Aspidoceras* immigrated as far as Pechora basin and Subpolar Urals; Two levels with numerous *Nannocardioceras*, below and above Eudoxus/Autissiodorensis boundary, divided by level with Tethyan *Aspidoceras* and *Sutneria*. Submediterranean *Aspidoceras* cf. *quercynum*, joined with uncommon Boreal *Amoeboceras* s.l.
- *Neochetoceras subnudatum* (= *Taramelliceras* level in Poland). Short immigrations of Submediterranean *Ataxioceras* cf. *hypselocyclum*, *Metahaploceras wegelei* (Ul'anovsk Volga areal); possibly, unfigured *Streblites teruilobatus* from Yaroslavl, Kostroma and Komi regions also reflect this event.
- Arctic *Amoeboceras* (*Amoebites*) gr. *spathi* appears.
- Very short penetration of Submediterranean *Lingulaticeras lingulatum*, *Metahaploceras litocerum* to Unzha river basin.
- Boreal *Amoeboceras* are dominating. Last Submediterranean perisphinctids and *Gregoryceras* occur near to top of Ilowaiskii Subzone.
- Numerous Subtethyan *Gregoryceras*, *Lingulaticeras*, *Neoprionoceras*, *Richeiceras* immigrated eastwards.
- Numerous Subtethyan *Gregoryceras*, *Lingulaticeras*, *Neoprionoceras*, *Richeiceras*
- Numerous Subtethyan *Gregoryceras*, *Lingulaticeras*, *Neoprionoceras*, *Richeiceras* immigrated eastwards through Brest straight.
- Boreal Cardioceratids and Cylindroteuthidae strictly prevail. Short northwards penetration of Submediterranean *Creniceras*, *Taramelliceras* (*baccatum* horizon); among belemnitids *Hibolithes* very common.
- Numerous Boreal *Cardioceras* (Boreal Spread) have penetrated until Iran, Crimea and N. Caucasus. First *Buchia* in Arctic.

Bottom annotations:

- Penetration of ?*Sarmatisphinctes* and *Aspidoceras* in Timan-Pechora region and West Siberia.
- Successive eastward and northward migrations of the genera of Middle Russian origin: *Kachpurites*, *Craspedites*,?*Epivirgatites*; abundance of Buchia.

the Late Callovian and during the Late Kimmeridgian – Early Volgian. Also two short but strong Tethyan events were restricted to the Oxfordian: in the Early Oxfordian (Cordatum Chron, *baccatum* hemera) and the Middle Oxfordian (Densiplicatum-Tenuiserratum chrons). The Late Kimmeridgian – Early Volgian penetration of the Peri-Tethyan ammonoids, such as the Oppeliidae and the Aspidoceratidae were mostly long termed in comparison with other Middle – Late Jurassic invasions. But even during this time the predominance of Peri-Tethyan taxa was combined with the presence of numerous Boreal genera (Fig. 3). In summary, the analysis of the fossil assemblages shows strong Boreal influence during the Middle-Late Jurassic. In spite of the mixed character of the faunas, Boreal taxa prevailed during the Callovian, Oxfordian, Early Kimmeridgian and Middle-Late Volgian. Nevertheless, by detailed investigation of the outcrops situated in the East-European Platform, representatives of both Peri-Tethyan and Boreal taxa are encountered within nearly all the ammonite zones.

Among the most important discoveries of the last few years influencing our paleobiogeographic knowledge, were the finding of true Boreal molluscs of Early Bathonian age in the Saratov Volga area (~37° N in paleolatitudes). These are the cardioceratid ammonites *Arcticoceras* and *Arctocephalites* and also the bivalve *Retroceramus* (Mitta *et al.* 2004). During the Late Bathonian the first signs of Boreal influence appeared in West Europe and, at the same time, in the Northern Caucasus, where recently some Bathonian *Kepplerites* have been discovered (Mitta 2003). The beginning of the Callovian coincides with the opening of the long-term Boreal-Tethyan connection of the Arctic and Tethys seas through the Middle Russian Sea perhaps caused by sea-level rise. Simultaneously Boreal *Paracadoceras* penetrated to the Northern Caucasus (and even its south slope, in Azerbaijan), while the Tethyan Macrocephalitidae (*M. jaquoti*) travelled as far as the Pechora region (Gulyaev 2005). During the Callovian some oscillations in the predominance of the Boreal, Subboreal and (scarcely) Submediterranean ammonites occured. Major events of Tethyan ammonite immigration were observed in the late Early Callovian, when *Oxycerites* and *Parapatoceras* penetrated northwards to the Unzha River Basin (~46° N in paleolatitudes; Gulyaev 2002; Mitta 2004b), and in the beginning of the Late Callovian. The turn of the Callovian and Oxfordian has been marked by the vast Boreal transgression connected with the southward migration of Boreal ammonites, especially cardioceratids (Boreal Spread of Arkell, 1956). These ammonoids mostly predominated during the Oxfordian, but during short warming episodes Tethyan cephalopods also inhabited the Middle Russian Sea (Fig. 3). The Tenuiserratum Chron could be listed among the strongest Tethyan faunistic influence intervals, when oppeliids (*Richeiceras, Creniceras, Glochiceras, Neoprionoceras*) have penetrated to the Unzha River. The Early Kimmeridgian also was characterized by a few short events of the penetration of Submediterranean ammonites (Zakharov and Rogov 2004), while the Late Kimmeridgian shows even a predominance of these ammonites (aspidoceratids are common in the Eudoxus and earliest Autissiodorensis Chron, whereas oppeliids became numerous during the Autissiodorensis Chron and persist till the Early Volgian). Nevertheless, some strata in the Upper Kimmeridgian and Lower Volgian are characterized still by numerous Boreal fossils (*volgae* horizon of the basal Autissiodorensis Zone; *pavida* horizon of the Sokolovi Zone). At the beginning of the Middle Volgian numerous Boreal *Pavlovia* penetrated to the Orenburg area (~36° N in paleolatitudes) and possibly even to the Northern Caucasus (Rogov 2004). The *Regularis* hemera of the Middle Volgian shows a wide spreading of *Zaraiskites*, from the Pechora area to the Peri-Caspian region. During the Middle-Late Volgian (Virgatus Chron and later) Submediterranean mollusks were very rare; only the bivalve family Trigoniidae is known. At that time Boreal bivalves (*Buchia*) penetrated very far south. Recently some Middle-Upper Volgian *Buchia* have been recorded from the Minor Caucasus (~28° N in paleolatitudes; Zakharov and Kasumzadeh 2005). Latitudinal immigrations of Boreal ammonites also were common, especially around the Middle-Late Volgian transition. The latest Volgian deposits are characterized by the appearance of the Arctic *Volgidiscus* in the Yaroslavl region (Kiselev 2003). Significant Boreal influence also persisted through to the earliest Ryazanian, where ammonites of the genus *Praetollia* are known (Mitta 2004a).

CONCLUSION

The precise study of molluscan immigration leads to the more accurate recognition of paleogeography, while contemporaneous records of

fossils with different paleogeographic affinities permits the correlation of different biostratigraphic schemes. The European part of Russia seems to be one of the most suitable areas for the recognition of both the Boreal and Tethyan influences in the Middle-Late Jurassic due to its unique position between the Arctic Basin, Tethys and the West-European shallow seas.

Acknowledgements

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