

# Latitudinal Gradient of Taxonomic Richness of Ammonites in the Kimmeridgian–Volgian in the Northern Hemisphere

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**Abstract**—The latitudinal gradient of taxonomic richness (LGTR) of Kimmeridgian and Volgian ammonite genera of the Northern Hemisphere is evaluated, and the LGTR evaluation methods and factors influencing LGTR are discussed. In the Kimmeridgian–Volgian the LGTR values for ammonites were largely influenced by the paleogeography of the Middle Russian Sea, which was directly connected with the Neotethys and, to a lesser extent, by the exchange through the connection between the Arctic and Pacific oceans. The Middle Russian Sea is considered to have been a major source of immigrant taxa to the Arctic basins. The highest latitude ammonite faunas were influenced by the Pacific faunas, and due to the permanent presence of oceanic phylloceratids and lycoceratids, ammonite taxonomic richness was relatively high compared to some mid-latitude sites. The gradual decrease in taxonomic richness that occurred from the end of the Kimmeridgian to the end of the Volgian in all Subboreal basins probably resulted from the eventual isolation from the Neotethys. Subboreal ammonite associations from the ecotone between the two superrealms (Panboreal and Tethys–Panthalassa) were affected by short-term climatic oscillations, which led to rapid changes in the ammonite assemblages.

**Keywords:** latitudinal gradient of taxonomic richness (LGTR), Kimmeridgian, Volgian, Northern Hemisphere, ammonites.

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## INTRODUCTION

The latitudinal gradient of taxonomic richness (LGTR) as an ecological pattern, extensively studied for recent taxa and to a lesser extent for fossils, is now known to have existed throughout the Phanerozoic (Naimark and Markov, 2010). LGTR is a decrease in diversity of animal and plant taxa of various ranks from the tropics to the poles. About 30 hypotheses have been put forward to explain this phenomenon (see Stevens, 1989; Brayard et al., 2005; Escarguel et al., 2008). However, most factors that allegedly produce the gradient such as difference in productivity, temperature, competition level, heterogeneity of the environment and its stability, presence of barriers, different rates of appearance and extinction of taxa near the equator and the poles, etc., primarily affect the shape of the LGTR curve, but are not responsible for the presence or absence of the phenomenon itself. In recent years, the hypothesis of the mid-domain effect has become one of the most widely debatable hypotheses explaining the existence of LGTR. According to this hypothesis, LGTR is geometrically determined, with random distribution of taxon ranges within the geometrical constraints of a bounded domain, which does not lead to an even spatial distribution. Instead, taxa ranges tend to form a peak or plateau more toward

the center of the domain than towards its limits (Colwell et al., 2004; Brayard et al., 2005). Computer simulations taking into account both the mid-domain effect and sea surface temperature in the oceans showed that in contrast to the prevailing views suggesting a regular increase in taxonomic diversity from the poles toward the equator, two peaks rather than one are formed near the equator, being separated by a region with decreased diversity on the equator itself (Brayard et al., 2005; Escarguel et al., 2008). The latitudinal gradient of the surface temperature is the main parameter controlling the shape of the curve and position of the peaks for the oceans (see Roy et al., 1998; etc.). Indeed, the LGTR estimates for most groups of extant marine invertebrates (including cephalopods) show two peaks of diversity near the equator (Macpherson, 2002; Rosa et al., 2008). A variety of local factors considerably influence the shape of the curve. For instance, LGTR at the species level in extant cephalopods is considerably different along the western and eastern Atlantic coasts, with peaks shifted to almost 20° (Rosa et al., 2008). In the Western Atlantic, the main input for the species diversity is contributed by octopuses (60% species), whereas in the Eastern Atlantic, they are considerably less diverse (13% species). At the same time, LGTR in gastropods of the Western Atlantic and Eastern Pacific was shown to be very similar

despite considerable physical and historical differences between the oceans, but correlating significantly to the average sea surface temperature (Roy et al., 1998).

There are still only few LGTR reconstructions for different stratigraphic intervals in the Phanerozoic and different invertebrate groups, but the existing data correlate with the dependence of LGTR from the sea surface temperature (Brayard et al., 2004, 2007). Although the degree of LGTR in some groups correlate with their geological age, and in recently appeared groups of bivalves the curve is steeper (Crame, 2000), in other groups (e.g., Carboniferous brachiopods) LGTR has remained almost unchanged throughout geological time (Leighton, 2005). Often in these cases, the peak of taxonomic diversity, as in the extant faunas, is not centered at the equator (Crame, 2001, 2002; Cecca et al., 2005). For instance, in Jurassic bivalves, the maximum TR is observed in paleolatitude 33°–40° (Crame, 2001).

The LGTR values in the Jurassic and Cretaceous ammonites at the genus level (Cecca et al., 2005; Yacobucci and MacKenzie, 2007), obtained mainly for the low and middle-latitude basins, and the generalized LGTR curve for the Tithonian bivalves (Crame, 2002), correlate significantly with the hypothesis of a relatively low temperature gradient in the Mesozoic. Only for the Early Triassic there are recorded considerable fluctuations of LGTR within relatively short intervals (Brayard et al., 2006). At the same time, preliminary results from LGTR of ammonites in high latitudes (Zakharov and Rogov, 2007a, 2007b) showed that for the shallow water epicontinental Arctic basins the LGTR curve was considerably dependent on local paleogeography, while in the Kimmeridgian the linear changes in LGTR were noticeably disturbed due to the different effect of the subboreal on different Arctic regions.

Although the climate in the Jurassic and the Mesozoic in general was warmer and more uniform than now, all the Jurassic epochs show relatively short, but sharp climatic fluctuations, in some cases possibly connected with brief glaciations (Price, 1999). In the interval considered (Kimmeridgian and Volgian) characters of the high-latitude glaciations are missing, but brief and sharp changes in the ranges of mollusks occur, which in some cases are recorded in distant basins and which probably reflect climatic fluctuations. These changes are also well expressed by changes in ammonite diversity and in dominant taxa throughout time. The boundary between the *Eudoxus* and *Autissiodorensis* chrons is a good example of rapid change in molluscan ranges related to climatic fluctuations. At the end of the *Eudoxus* Chron the Subboreal basins of England, Poland, and Central Russia were dominated by small Boreal cardioceratids *Nannocardioceras*, whereas other ammonites occurred very rarely or were altogether absent. At the beginning of the *Autissiodorensis* Chron these basins show a wide

distribution of the ammonite association with numerous Tethyan aspidoceratids (Rogov, 2010).

In analyzing changes in LGTR (and in biogeographical studies in general) in the geological past, the final results are largely dependent on the existing level of knowledge and that of stratigraphy of localities and regions, correlation of distant sections, evolutionary rates of the groups studied and time-averaging of the composition of faunas. These factors play an especially significant role when analyzing relatively short-term intervals, suggesting considerable fluctuations of climate, prominent in the ecotone regions between the Arctic and Tethys. Below I briefly consider the effects of each of these factors.

Differences in the degree of knowledge on the sections and the extent of their stratigraphic subdivision complicate the synchronization of the ammonoid faunas and the time-averaging over geological time. These factors are particularly important for comparison of natural outcrops rich in fossils with boreholes with poor fossil content. Therefore a more frequent change on the environment in the ecotone regions at biohorizon boundaries of high rank leads to artificially increased TR values even when they are compared with TR in the more southerly and northerly regions at the same chrons (see Fürsich and Aberhan, 1990, text-fig. 3). Differences in the evolutionary rates of different groups have a similar effect. In order to lessen the effect of these factors to LGTR estimates I used taxa co-occurring within the same bed or a series of beds, which mostly correspond to the same biohorizon rather than some generalized ranges. The maximum diversity later spread over the entire zone.

Additional complications in the ammonite distribution patterns may result from dimorphism, polymorphism, and accordingly historically developed differences in taxonomic rank of the supposed dimorphs (which may be considered as members of the same species, different species, different genera, or subgenera). In this paper the supposed dimorphs are considered to belong to the same taxon. Because in a number of cases, microconchs and macroconchs are considerably morphologically different (e.g., *Aspidoceras* and *Sutneria*), the taxonomic diversity is on average somewhat lower than the ecological diversity. TR is also influenced by difference in scientific interpretations of both the diversity of faunas, and identifications of the same taxa. Therefore in this study I primarily used the publications in which the taxa are illustrated, and my own observations.

## MATERIAL AND METHODS

A genus was selected as a taxonomic unit for calculating LGTR. This is because there are considerable differences in the scientific interpretations of lower rank categories, and because of a relatively simple method of bringing all data to a common denominator. The difference also decreases between the epicon-

tinental and epiocceanic assemblages, which mainly differ at the species rather on the generic level and are characterized by different dominant groups. (Olóriz, 2000). However this approach may result in some artificially increased TR values in the lower latitudes, because the species to genera ratio in many taxa changes with latitude. For instance, bivalves in high latitudes are represented by a small number of genera rich in species, whereas in low latitudes there are more genera with fewer species (Krug et al., 2008).

The lack of quantitative data on ammonite assemblages does not in most cases allow the recognition of the role of relative abundances of taxa and changes in the dominant taxa throughout time. Previously, presence or absence of Subboreal and Tethyan ammonites was recorded throughout the zones (Zakharov and Rogov, 2007), which allowed the calculation of a relative Boreal affinity of these faunas. However, the time-averaging and impossibility of detailed correlation in many cases do not permit the precise synchronization of the events. It is possible to consider that the presence of one noticeable level within a zone or a substage, characterized by more thermophilic assemblages in different regions, is an indication of the same event.

Altogether data from 20 regions have been used (Fig. 1), which in the Kimmeridgian and Volgian were located approximately in the interval between 20° to 87° N. In all these regions there are reliable biostratigraphic data for, at least, half of this interval, with the ammonite assemblages differing in each of these regions. For the analysis, the data on the most complete and the best characterized fossiliferous sections were used.<sup>1</sup> The correlation scheme for the Boreal, Subboreal, and Subtethyan scales for the interval under considerations is shown in Fig. 2.

For the analysis, seven levels were chosen that embrace the entire stratigraphic interval from the basal Kimmeridgian to the Upper Volgian. These levels have the best correlation potential across the territory under consideration and are sufficiently characterized by mollusks in most regions included in the study.

## RESULTS AND DISCUSSION

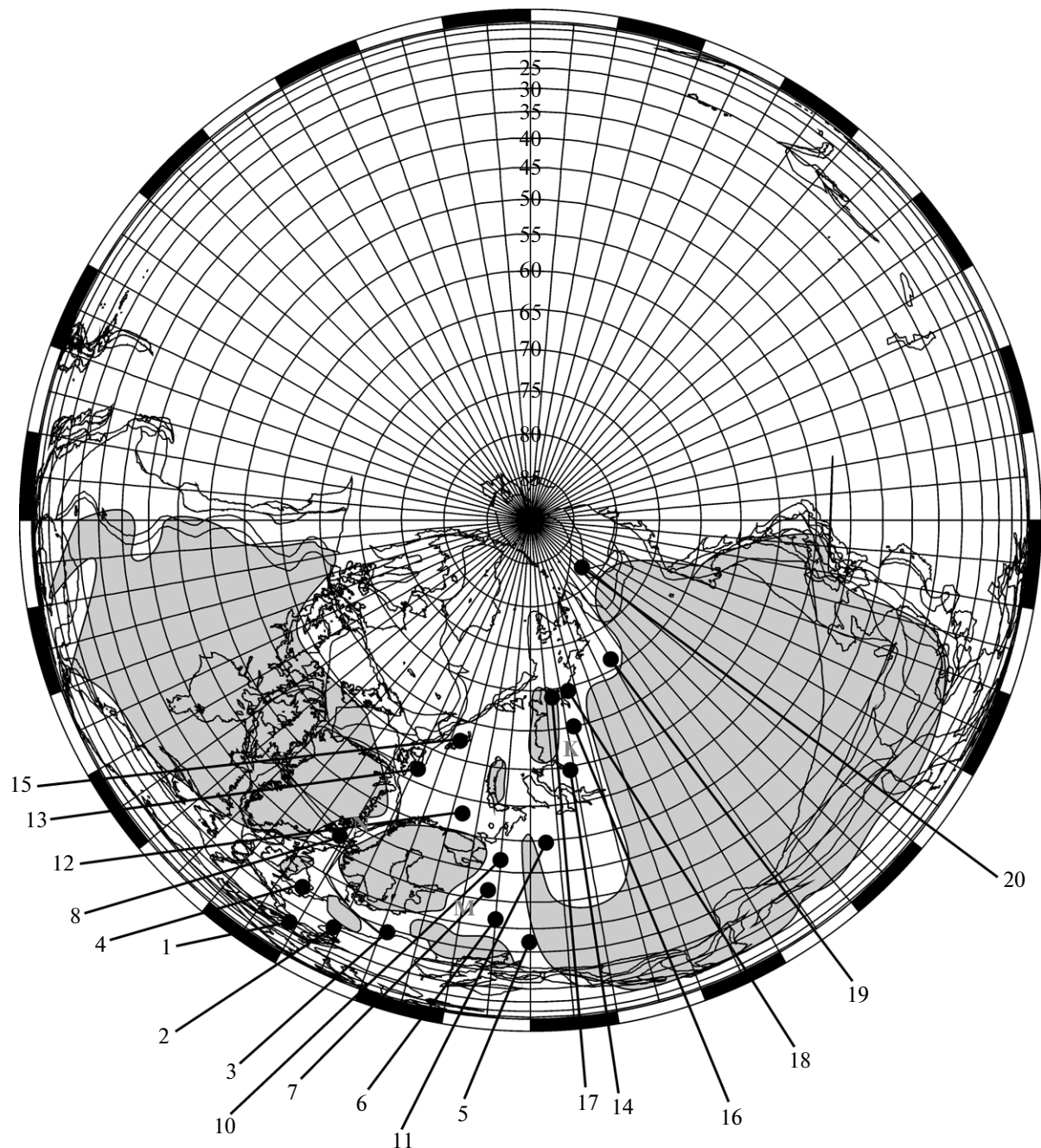
### *LGTR for the Kimmeridgian–Volgian Ammonites in the Northern Hemisphere and Possible Reasons for its Changes in Time*

The entire Kimmeridgian–Volgian interval shows a sharp decrease in diversity between 30° and 40°N, which agrees with the previously published data (Cecca et al., 2005). Although TR regularly decreases towards high latitudes in the entire time interval considered (Fig. 3), a number of specific features charac-

teristic for time levels and regions are apparent. For all levels studied an increase in diversity was recorded for latitude 37°N (Volga Region). Although in the Kimmeridgian and Early Volgian this increase in diversity was primarily connected with the position of this region within the ecotone zone and the region contains taxa of Boreal, Subboreal, and Tethyan origins, this peak in the Middle and Late Volgian reflects diversification of Subboreal and Boreal ammonites. The comparatively small diversity of ammonites in the more southerly Kimmeridgian sections of England was probably related to the restricted possibility for immigration of Subtethyan ammonites, and in the Volgian to a completely sealed connection between that basin and more southerly basins resulting in the presence of exclusively Boreal faunas. As previously noted for the Kimmeridgian, the western Arctic (eastern Greenland, Barents Sea shelf, Svalbard), an extremely low diversity of ammonite faunas was characteristic for the Volgian. In most cases it was considerably lower than the diversity of ammonites that inhabited the Khatanga Strait occurring to the north. In the Kimmeridgian, this was related primarily to the effect of the Middle Russian Sea on the more easterly basins. This is evident from the much less Boreal aspect of the Kimmeridgian faunas of the Khatanga Basin compared to the synchronous faunas of Franz Josef Land and Svalbard. On Franz Josef Land and Svalbard, the Subboreal aulacostephanids are restricted to two narrow intervals within the Kimmeridgian (levels with *Rasenia* ex gr. *cymodoce* and *Zenostephanus*), whereas in the Kheta River basin they existed uninterrupted throughout the Kimmeridgian, except for its terminal *Taimyrensis* Chron. In the Volgian, the influence of the Middle Russian Sea on the more easterly basins decreased: only one genus, *Kachpurites*, reached Western Siberia and the northern regions of Eastern Siberia. A high taxonomic diversity of ammonites in the basin of the Kheta River at the beginning of the Late Volgian was attained because of the increasing influence of the Paleopacific, which was manifested by the appearance of oceanic phylloceratids and lytoceratids. The permanent presence of phylloceratids explains the relatively high taxonomic diversity of the northernmost of the regions under consideration (northeastern Russia). The influence of the Norway–Greenland Seaway at the ammonite migration pathway to the Arctic was low in the Kimmeridgian–Volgian. Apparently this was because it was relatively shallow with many dysoxic environments in the Late Jurassic (Mutterlose et al., 2003).

Changes in TR in time were considerably different in the Boreal and Subtethyan basins compared to the Subboreal basins (Fig. 4). No distinct trends in changes in TR with time are recorded for the Boreal and Subtethyan regions, whereas TR in the Subboreal areas regularly decreases from the Kimmeridgian to

<sup>1</sup> Supplementary data used for LGTR estimations and additional references are available online through the following hyperlink: [http://jurassic.ru/Rogov,2012\\_esupplement.doc](http://jurassic.ru/Rogov,2012_esupplement.doc).



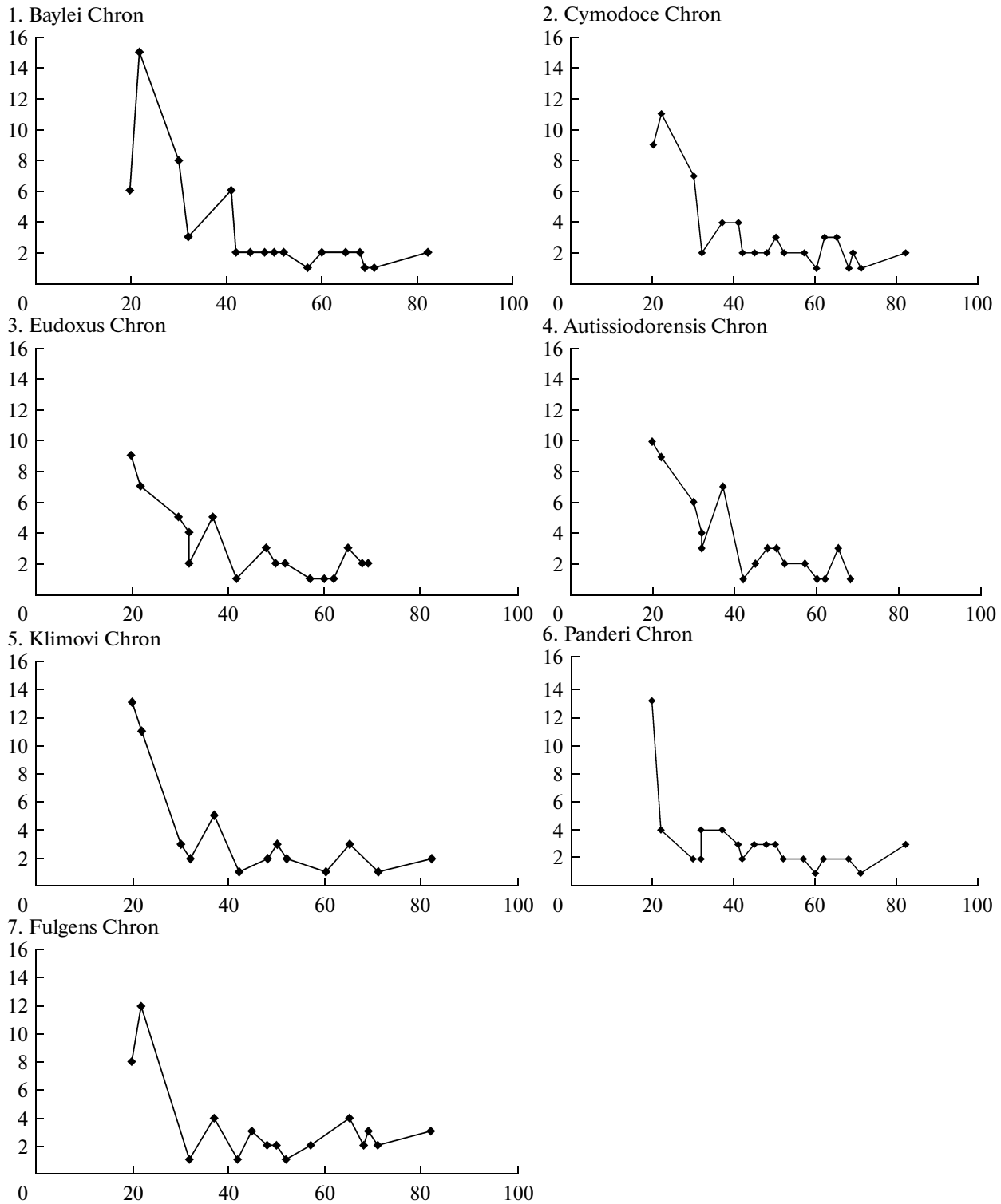
**Fig. 1.** Locations of the regions used for calculations of taxonomic diversity of Kimmeridgian–Volgian ammonites (position of the continental blocks and paleolatitudes are given for the beginning of the Tithonian based on the data from <http://www.odsn.de/>). The figures indicate: (1) southeastern France; (2) southeastern Germany; (3) central Poland; (4) England and Scotland; 5. Orenburg Region; (6) Middle Volga Region; (7) Unzha River basin and Yaroslavl Volga Region; (8) Eastern Greenland; (9) Western Siberia; (10) Pechora River basin; (11) Subpolar Urals; (12) Barents Sea shelf; (13) Svalbard; (14) Yenisei River mouth; (15) Franz Josef Land; (16) Khatanga Basin; (17) Eastern Taimyr; (18) Nordvik; (19) lower reaches of the Lena River; (20) northeastern Russia (Bolshoi Anyui, Korkodon, and other rivers); (N) Norwegian–Greenland Seaway, (M) Middle Russian Sea, (K) Khatanga Strait. Grey color shows land.

the second half of the Volgian. This trend is related to the progressive shallowing and subsequent closure of the seaway connecting the Subboreal basins with the Subtethyan ones, which made the migration of the Subtethyan taxa to the northern regions impossible. In

the west (England) the last episode of the Subtethyan influence is recorded for the beginning of the *Autisiodorensis* Chron (Late Kimmeridgian) (appearance of *Schaireria* and *Sutneria* aff. *rebholzi*), and further east, in Central Poland and Peri-Caspian for the very

Subboreal scale (Russian Platform)		Boreal scale (Eastern Siberia)		Subboreal scale (Western Europe)		Mediterranean scale (Western Europe)		
Sub-stage	Zone	Subzone	Zone, subzone	Zone, subzone	Stage	Zone, subzone	Sub-stage	
UPPER VOLGIAN	NODIGER	Beds with <i>Volgidsiscus singularis</i> <i>Craspedites milkovensis</i> <i>Craspedites mosquensis</i>	<i>Chetaites chetae</i>	<i>Berrisella jacobii</i>	PORTLANDIAN	<i>Berrisella jacobii</i>	UPPER TITHONIAN	Berr.
			<i>Craspedites okensis</i>	<i>Micracanthoceras micracanthum</i>				
						<i>Craspedites subdinus</i>		
	FUGENS	<i>Craspedites nekrassovi</i> <i>Kachpurites fulgens</i>	<i>Craspedites okensis</i>	<i>Craspedites okensis</i>	<i>Subcraspedites primitivus</i> <i>?Paracraspedites oppressus</i>	BOLONIAN	<i>Micracanthoceras ponti</i>	LOWER TITHONIAN
	VIRGATUS	<i>Epivirgates nikitini</i> <i>E. lahuseni</i> <i>E. bipliciformis</i>	<i>Taimyrosphinctes excentricus</i> <i>Dorsoplanites maximus</i>	<i>Virgatopavlovia fittoni</i> <i>Pavlovia rotunda</i> <i>Pavlovia pallasioides</i>				
					MIDDLE VOLGIAN	<i>Epivirgates nikitini</i> <i>E. lahuseni</i> <i>E. bipliciformis</i>	<i>Taimyrosphinctes excentricus</i> <i>Dorsoplanites maximus</i>	<i>Virgatopavlovia fittoni</i> <i>Pavlovia rotunda</i> <i>Pavlovia pallasioides</i>
	PANDERI	<i>Zaraiskites zarajskensis</i> <i>Zaraiskites scythicus</i>	<i>Dorsoplanites ilovaiskii</i> <i>Pavlovia tairiensis</i>	<i>Pectinatites pectinatus</i> <i>Pect. hualesoni</i> <i>Pectinatites wheatleyensis</i> <i>Pectinatites scitulus</i> <i>Pectinatites elegans</i>				
					LOWER VOLGIAN	<i>'P.' tenuicostatum</i> <i>I. pseudocorythica</i>	<i>"Pectinatites pectinatus"</i>	<i>Semiformiceras semiforme</i>
<i>Ilovaiskya sokolovi</i>	<i>Ilovaiskya sokolovi</i>	<i>Sphinctoceras subcrassum</i>	<i>Semiformiceras darwini</i>					
				<i>Ilovaiskya klimovi</i>	<i>Ilovaiskya klimovi</i>	<i>Eosphinctoceras magnum</i>	<i>Hybonitoceras hybonotum</i>	

Fig. 2. Correlation scheme of the Boreal and, Subboreal and Tethyan zonal schemes of the Kimmeridgian and Tithonian stages.



**Fig. 3.** Changes in TR for ammonites with the latitudes in the Kimmeridgian and Volgian Stages. The horizontal axis shows paleolatitude while the vertical axis is number of genera of ammonites.

beginning of the Middle Volgian. Although, judging from the presence of the Boreal bivalves *Buchia* in the Middle–Upper Tithonian of the Lesser Caucasus (Zakharov and Kasumzade, 2005), the connection

between the Middle Russian basin and the northern margin of the Neotethys was not sealed completely, the Subtethyan ammonites reached the Middle Russian Sea only in the mid-Berriasian. Judging from the

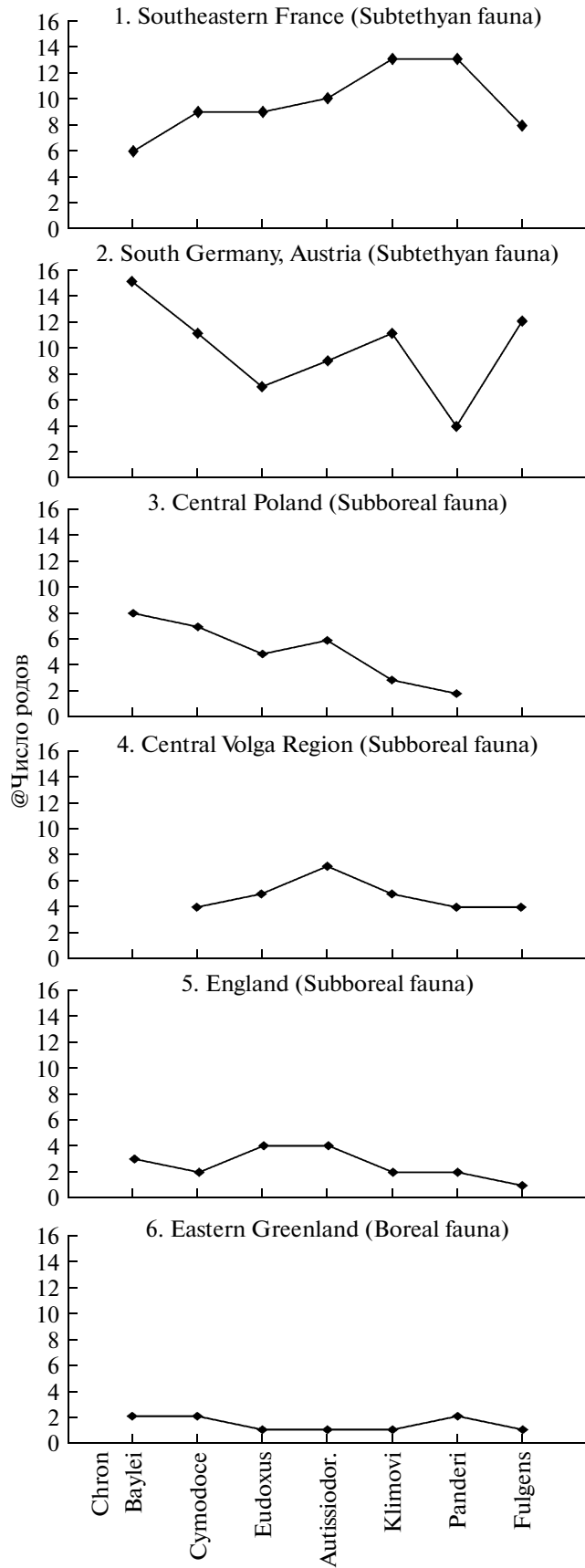


Fig. 4. Changes in TR ammonites in various regions through time.

isotope data, a gradual increase in temperature was recorded during the late Jurassic and in middle and high latitudes of the Northern Hemisphere (see Zakharov et al., 2005; Nunn et al., 2009; Price and Rogov, 2009; Žák et al., 2011), which continue until the end of the Volgian. Nevertheless, due to the sharp reduction of possibilities for molluscan immigrations in the latitudinal direction, all Subboreal basins show a decrease in TR due to the disappearance of taxa of Subtethyan origin.

## CONCLUSIONS

LGTR of ammonites of the Northern Hemisphere at the end of the Jurassic was influenced by various factors, which were dominated by paleogeography (presence/absence of migration pathways and connection with the ocean) and temperature. Increased diversity compared to the adjacent regions was recorded for favorable environment (presence of straits) within the ecotones between the superrealms. In the highest latitude an increased TR was connected to a strong influence of the Paleopacific, which was felt in the Arctic, at least until the end of the Valanginian. Considerable changes in TR are only recorded in the middle latitudes, where the above mentioned changes in paleogeography in the Volgian time considerably decreased compared to the Kimmeridgian.

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