Pliensbachian–Toarcian Biotic Turnover in North Siberia and the Arctic Region

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Abstract—The biotic turnover in the Pliensbachian–Toarcian transition and changes in assemblages of bivalves, ostracodes, foraminifers, dinocysts, spores, and pollen are described. Only five of 24 bivalve genera and two of four ostracode genera cross the Pliensbachian–Toarcian boundary so that composition of genera and families to be entirely renewed at the base of the *Harpoceras falciferum* Zone. In the interval of three ammonite zones, diversity of foraminifers is reducing from 27 genera in the *Amaltheus margaritatus* Zone (upper Pliensbachian) to 17 and then to 15 genera in the *Tiltoniceras antiquum* (lower Toarcian) and *Harpoceras falciferum* zones, respectively. Single dinocysts of the Pliensbachian are replaced by their abundant specimens at the base of the Toarcian, and substantial changes in composition of palynological assemblages are simultaneously established. Factors responsible for "mass extinctions" of marine invertebrates are suggested to be the paleogeographic reorganization, anoxic events, eustatic sea-level changes, and climatic fluctuations. The biotic turnover in the Arctic region is interrelated mainly with thermal changes, which caused the southward displacements of taxa distribution areas during a rapid cooling and their gradual return to former habitat areas in the period of warming, rather than with extinction events.

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Key words: Pliensbachian, Toarcian, biotic turnover, North Siberia, bivalves, foraminifers, ostracodes, dinocysts, spores, pollen, paleoclimate, eustatic fluctuations, anoxia.

INTRODUCTION

Raup and Sepkoski (1982, 1984; Sepkoski and Roup, 1986) were first to establish a global biotic turnover across the Pliensbachian–Toarcian transition (183 Ma ago) based on changes in taxonomic diversity of marine invertebrate families during the Phanerozoic. According to Sepkowski, 10 of 12 extinction peaks in the Phanerozoic took place in the last 250 Ma. The Pliensbachian–Toarcian extinction that followed the terminal Permian and terminal Triassic events was the third one during this period. Despite a substantially lower magnitude as compared with preceding extinctions, the extinction peak at the Pliensbachian–Toarcian boundary was permanently noted in all the subsequent works. Little and Benton (1995) established five extinction levels for ammonite families during the late Pliensbachian–early Toarcian period 7.5 m.y. long and demonstrated that these levels were diachronic in the Boreal, Tethyan, and Austral realms. Behavior of invertebrate macrofauna was studied most carefully in complete sedimentary successions of northwestern Europe, where is established that most extinction events of species took place in the early Toarcian due to the regional anoxic event. Contrary to assumption of Sepkoski (1990), no evidence of simultaneous extinction of families at the end of the Pliensbachian has been found here. Actually, five zonal phases of extinction have been established in the period from the late Pliensbachian to early Toarcian.

At the regional extent (marine sections in northern West Europe), the biotic turnover was first described by Hallam (1986) first based on bivalves and then on other groups of marine invertebrates: ammonites, brachiopods, foraminifers, ostracodes (Hallam, 1987). Later on, Zakharov, Shurygin, Il'ina, and Nikitenko presented evidence for a substantial biotic turnover among bivalves, ostracodes, foraminifers, dinocysts, spores, and pollen in northern Siberia at the same stratigraphic level (Zakharov et al., 1993, 1994; Il'ina et al., 1994; Nikitenko and Shurygin, 1994; Zakharov, 1994). Recently, Aberhan and Fürsich (1997) discovered reorganization in communities of marine bivalves from the Andean basin (South America). They claimed that discovery of the second region provides grounds to conclude that the biotic turnover at the Pliensbachian–Toarcian transition is of the global scale. References to Russian publications appeared in their later work (Aberhan and Fürsich, 2000).
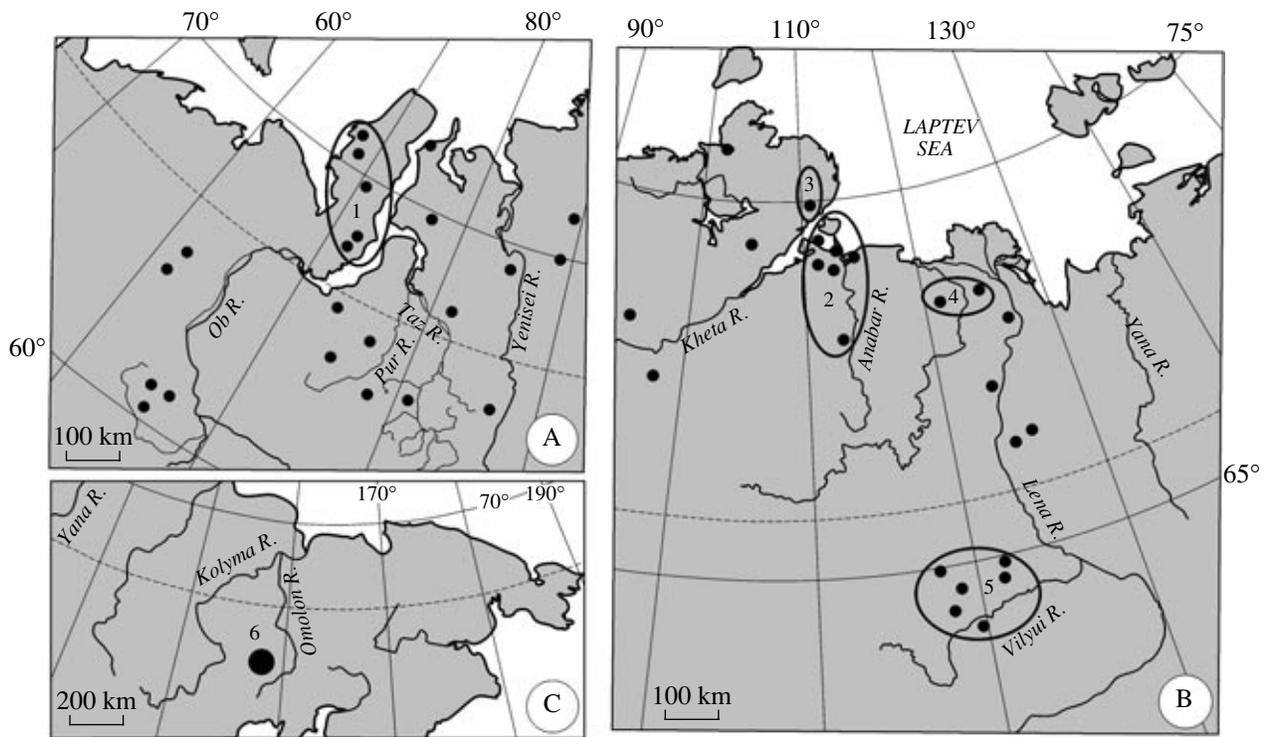
Fig. 1. Localities of the main Lower Jurassic sections (dots) examined in (A) West Siberia, (B) East Siberia, and (C) Northeastern Russia; ovals with numbers denote areas of standard Lower Jurassic sections: (1) northern West Siberia (boreholes Novoportovskaya, Bovanenkovskaya, Kharasaveiskaya, Arkticheskaya, and others fields), (2) Anabar–Nodvik area (outcrops, Suolem and Vostochnaya boreholes), (3) eastern Taimyr, (4) Olenek–Elimyar area, (5) Vilyui syneclise (sections and boreholes along the Tyung, Markha, and Vilyui rivers), (6) Northeastern Russia (Levyi Kedon River basin).

STRATIGRAPHY AND PALEOGEOGRAPHIC SITUATION

The lower Toarcian clays occupy in Siberia an area sized several millions square kilometers. These sediments overlie the upper Pliensbachian sandy and silty rocks with sedimentary unconformity, though usually without biostratigraphic hiatus. These sediments of a relatively uniform lithology and geochemical characteristics span the interval of the *Tiltoniceras antiquum* and *Harpoceras falciferum* zones coupled with a lower part of the *Dactylioceras commune* Zone (Knyazev et al., 1991). The interval corresponds to the Kiterbyut Horizon in northern East Siberia, Kiterbyut and Togur formations in the Vilyui hemicyneclise, and to Suntar Formation (lower part) in the Verkhoyansk region. The total area occupied by lower Toarcian clayey–silty sequences is over 10^6 km², and their thickness is remarkably persistent in general (20–40 m). Owing to the well-coordinated biostratigraphic zonations, all the Toarcian marine sequences are confidently correlated between each other at the level of ammonite, bivalve, and ostracode zones (Shurygin et al., 2000). Based on the parallel biostratigraphic scales, the Pliensbachian–Toarcian transition defined in North Siberia is reliably correlated with coeval sequences through the entire Arctic region, Northeastern Asia, and northern East Europe. That is why instead of a particular section, we

consider in this work the materials on many localities of Pliensbachian–Toarcian boundary layers in North Siberia and the Arctic region, including Svalbard and Frantz Josef Land and North Alaska (Fig. 1).

The upper Pliensbachian and lower Toarcian sections of North Siberia are substantially variable with respect of lithology. In sections of the Ust-Yenisei area, Yenisei–Khatanga trough (Figs. 1A, 1B), eastern Taimyr Peninsula (Fig. 1, 3B), and the Anabar River (Fig. 1, 2B), the upper Pliensbachian base corresponds to the widespread Zimnyaya Formation (Hettangian–basal upper Pliensbachian) composed of marine to coastal-marine sandstones with argillite and siltstone intercalations and with gravelstone and conglomerate interbeds at different levels (Fig. 2). In northeastern East Siberia (Olenek River basin) (Fig. 1, 4B), the Zimnyaya Formation is correlated with a lower part of the marine Kyra Formation (Hettangian–Pliensbachian) composed of clays with silty and sandy interbeds. In the Ust'-Yenisei area and western Yenisei–Khatanga trough, the Zimnyaya Formation is conformably overlain by marine dark gray argillites and siltstones of the Levinskii Formation (middle part of the upper Pliensbachian), sediments of which contain scattered pebbles of quartz, cherts, and volcanics (Fig. 2). In northern West Siberia, the Levinskii Formation (Fig. 1, 1A) rests upon Paleozoic rocks. In sections of the eastern Taimyr
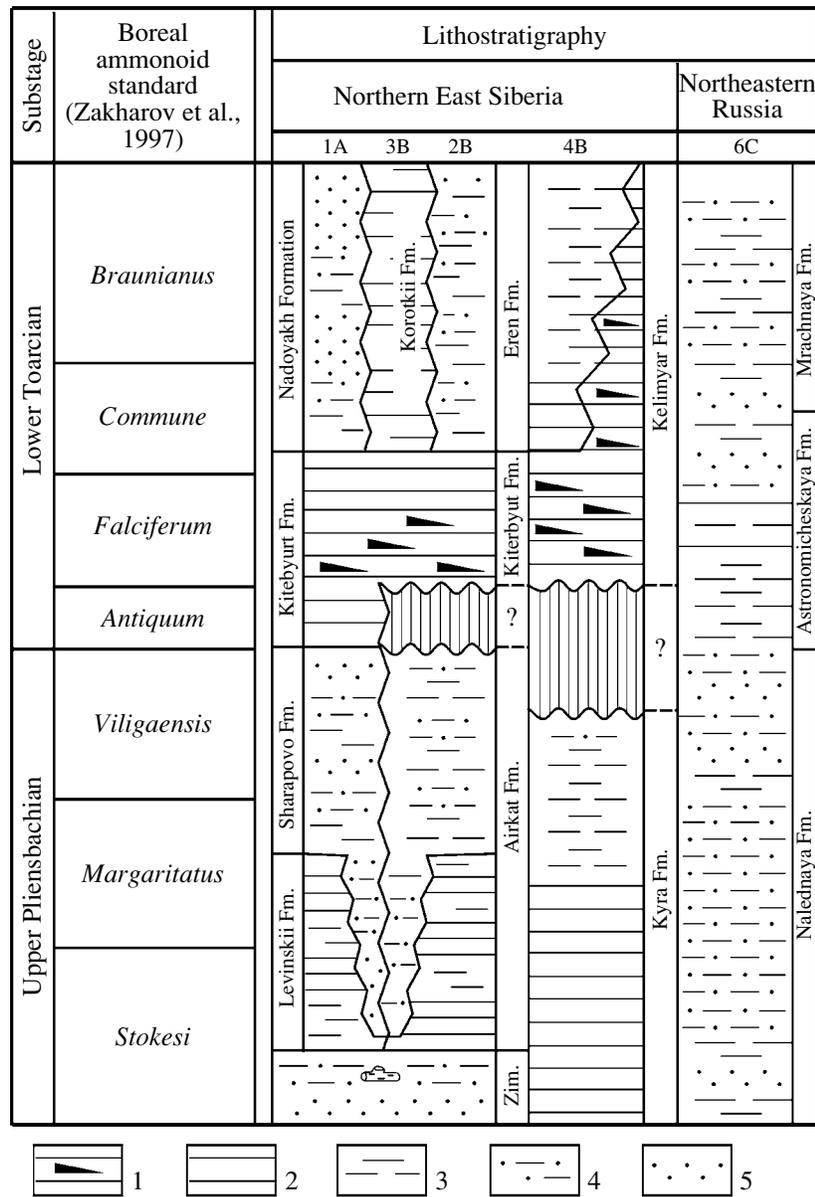
Fig. 2. Lithostratigraphic columns of the upper Pliensbachian–lower Toarcian deposits in North Asia: (1) high-carbonaceous clays and siltstones; (2) clays and argillites; (3) sands and sandstones; (4) sandy silts and siltstones; (5) sands and sandstones; (Zim) Zimnyaya Formation (other symbols as in Fig. 1).

Peninsula (Fig. 1, 3B) and Anabar River (Fig. 1, 2B), the Levinskii Formation corresponds to the lower part of the Airkat Formation (middle part of the upper Pliensbachian) composed largely of clays and argillites with siltstone interbeds and rare scattered pebbles. Higher layers of the Airkat Formation (upper half of the upper Pliensbachian) are represented by cyclic members of coarse-grained siltstones with clay and fine-grained sandstone interbeds. In northern West Siberia and western Yenisei–Khatanga trough, this level corresponds to the Sharapovo Formation of shallow-water to coastal-marine siltstones, argillites, and sandstones with thin conglomerate and gravelstone interbeds (Fig. 2).

In northeastern Russia (Omolon massif), the upper Pliensbachian siltstones and sandy siltstones with sandstone and clay interbeds are discriminated into the Naledaya Formation (Fig. 2).

The Toarcian sediments are readily distinguishable in sections owing to a uniform lithology of the lower part composed of fine clay that is enriched in organic matter, being bituminous sometimes. In western and central areas of East Siberia (Figs. 1, A, 2B, 3B), the basal portion of the Toarcian section corresponds to the Kiterbyut Formation (lower part of the lower Toarcian) of uniform argillites and fine clays with bituminous interlayers (Fig. 2). Eastward (Fig. 1, 4B), the Kiterbyut

Fig. 3. Stratigraphic ranges of bivalve mollusks in the Pliensbachian–Toarcian boundary beds of North Siberia and Northeastern Russia; abbreviations denote the Aalenian Stage (Aa) and its lower Substage (l.).

Ammonite zones: A.s. – *Amaltheus stokesi*, A.m. – *A. margaritatus*, A.v. – *A. viligaensis*, T.a. – *Tiltoniceras antiquum*, H.f. – *Harposeras falciferum*, D.c. – *Dactylioceras commune*, Z.b. – *Zugodactylites brauianus*, P.c. – *Pseudolioceras compactile*, P.w. – *P. wurttenbergeri*, P.f. – *P. falcodiscus*, P.m. – *P. maclintocki*.

Formation is replaced by fine clays of the lower Kelim-yar Formation (Toarcian–basal Bathonian) that includes the thin Kurung Member (lower–basal upper Toarcian) with black foliated bituminous clays at the base. In sections of Northeastern Russia (Fig. 1, 6B), the Kiterbyut clays correspond approximately to the Astronomicheskaya Formation of fine clays with silt-stone interbeds (Fig. 2). In northern West Siberia, the Ust'-Yenisei region, and western Yenisei–Khatanga trough, the Kiterbyut Formation is overlain by alternating sandstones, siltstones, and rare argillites of the Nadoyakh Formation lower part (upper lower Toarcian–basal lower Aalenian). In eastern Taimyr sections (Fig. 1, 3B), coeval layers are composed of clays and argillites of the Korotkii Formation (Fig. 2). In the Anabar River sections (Fig. 1, 2B), this part of the Toarcian is represented by the Eren Formation of cyclic sandy–silty deposits (terminal lower–basal upper Toarcian). In the Vilyui syncline (Fig. 1, 5B), sediments of the lower Toarcian are represented by fine, locally, bituminous clays in the lower part of the section and by silty clays with siltstone and sandstone interbeds of the Suntar Formation (Toarcian–basal lower Aalenian). In Northeastern Russia (Fig. 1, 6B), the upper part of the lower Toarcian is composed of sandy–silty deposits of the Mrachnaya Formation (upper lower–upper Toarcian) (Fig. 2).

Thus, the upper portion of the Pliensbachian succession is composed in East Siberia of sandy–silty rocks locally with conglomerates at the base, while its lower part is of clayey to silty–clayey lithology (Fig. 2). It is possible to suggest therefore a substantial paleogeographic rearrangement across the Pliensbachian–Toarcian transition. Most likely, the coastal landscapes of Pliensbachian seas were mountainous and hilly in the north (upper Pliensbachian conglomerates are known in the northeastern Taimyr Peninsula and Lena River mouth area) and in the south, from the side of Central Siberian land. The facies analysis implies development of a low land (peneplain) in the initial Toarcian time (*Paleogeography of the Northern…*, 1983).

MATERIALS AND METHODS

Main sections, which yielded materials for this study (observation results and collections of fossils), are located in northern East Siberia (Fig. 1). In addition to East Siberian section, we also considered data on sections of Northeast Asia, numerous boreholes drilled in West Siberia, and original materials and collections from boreholes in northern Alaska. The extent and trend of the Pliensbachian–Toarcian biotic turnover have been estimated based on the following fossil groups: bivalves, foraminifers, ostracodes, dinocysts, and spore–pollen assemblages. These fossils are most abundant and diverse. The other, less common fossils taken into consideration are ammonites, belemnites, gastropods, and scaphopods.
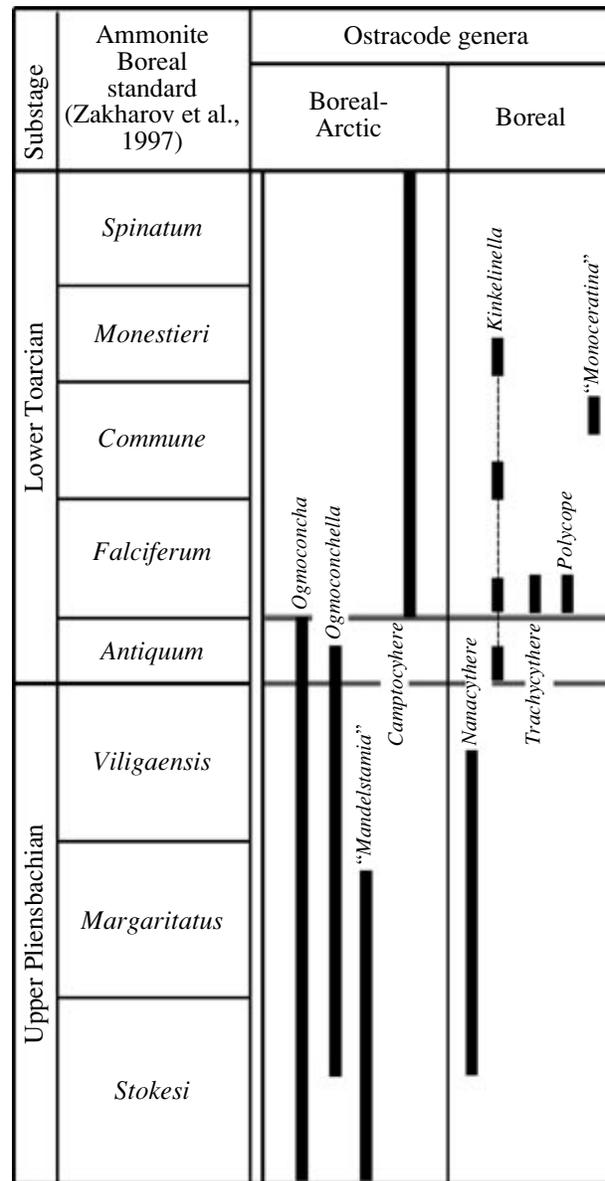

Fig. 4. Stratigraphic ranges of ostracodes in the Pliensbachian–Toarcian boundary beds of North Siberia and Northeastern Russia.

A genus is considered as a main taxonomic unit, when composition and distribution of mollusks, foraminifers, and ostracodes have been analyzed. The choice is made to avoid, as far as possible, subjectivism in understanding an elementary operative taxonomic unit. A species is used as a main operative taxonomic unit by palynological analysis. In order to determine the dominant genera of benthic bivalve communities, the occurrence frequency of each genus is estimated in three relative categories: rare, common, and abundant. The occurrence frequency of palynological taxa is estimated in four relative categories: rare, few, common, abundant. To assess the biogeographic selectivity of taxa in the course of biotic reorganization, all the fossil
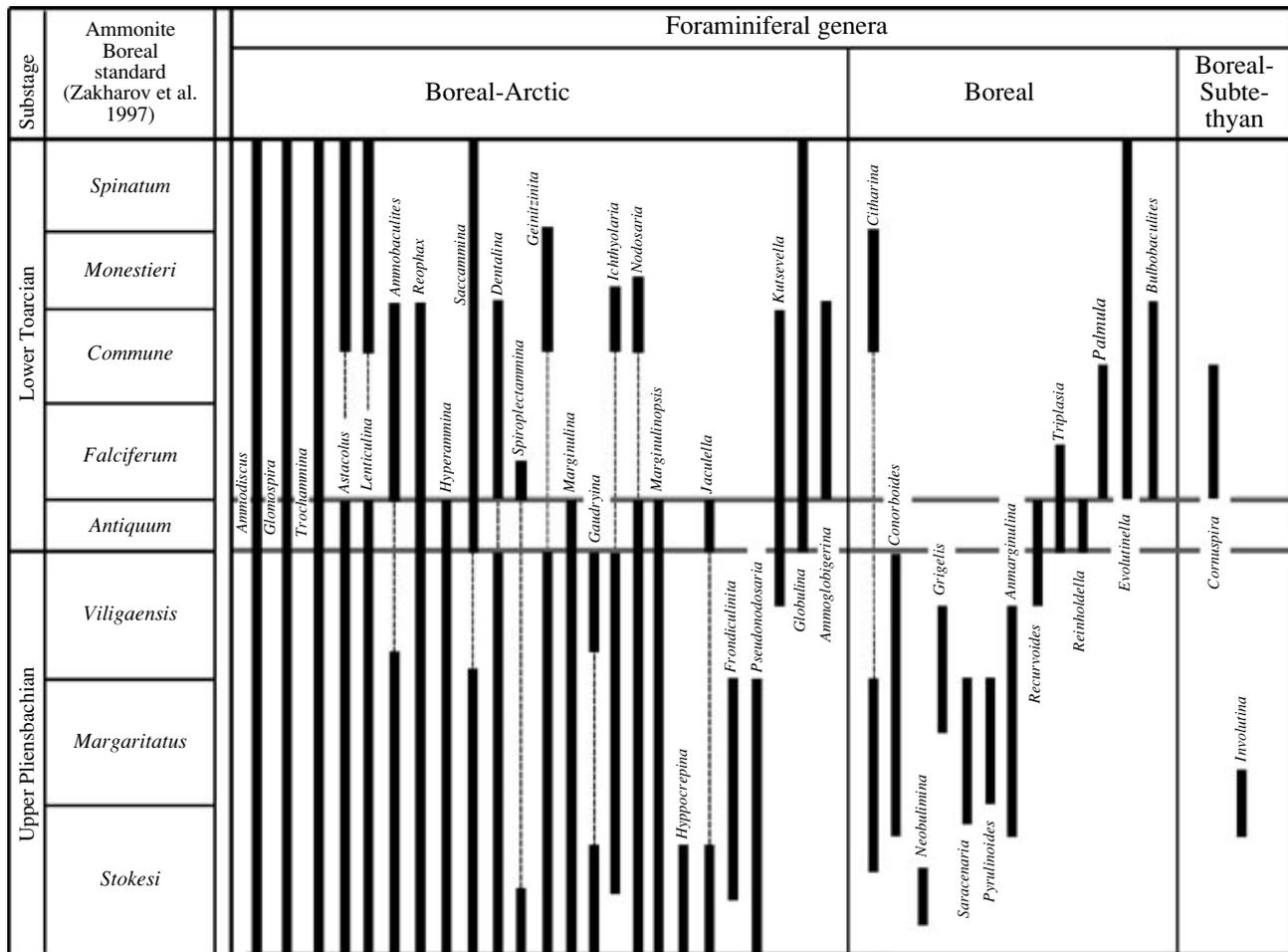
Fig. 5. Stratigraphic ranges of foraminifers in the Pliensbachian–Toarcian boundary beds of North Siberia and Northeastern Russia.

groups are classed in terms of their affiliation with particular biogeographic zone or biochore that presumably determines their tolerance to different thermal regimes. Bivalves are divided into Boreal–Arctic (or High Boreal), Low Boreal, and Subtethyan genera; foraminifers into the Boreal–Arctic, Boreal, and Boreal–Subtethyan genera; ostracodes into the Boreal–Arctic and Boreal genera; dinoflagellates into the Boreal–Arctic and Boreal–Atlantic species; spores and pollen into predominantly Siberian, cosmopolitan, and Euro-Sinian taxa.

EVIDENCE OF BIOTIC TURNOVER

The dynamics of turnover (crisis) in geological time is usually analyzed based on taxonomic diversity, sometimes, on the ecological structure of biotic communities (a change of dominants, taxonomic homogenization, destruction of former nutrition chains). The biogeographic structure of communities is a rare case of analysis, but precisely this issue is of particular interest in this work.

Judging from taxonomic reorganizations recorded in the examined fossil groups (bivalves, ostracodes, foraminifers, dinoflagellates, spores and pollen), principal events in the sea and on land took place in northern Siberia at the beginning of the Toarcian, in the *Tiltoniceras antiquum* phase. Biota experienced the main "impact" at the very beginning of the Toarcian Age. Subsequently, dynamics of reorganizations progressed slower, being largely reduced to restoration of taxa positions lost at the early stage.

As is mentioned, we consider primarily data on the North Siberian sections. with attraction of materials on the other, mostly Arctic regions, e.g., on the King Karl Land, Frantz Josef Land, Pechora River basin, and northern Alaska, which are considered in some specified cases, when they are necessary for inferences.

Taxonomic diversity. The taxonomic diversity decrease in the Pliensbachian–Toarcian transition is observable in all the examined groups of marine invertebrates. A sharp reduction of diversity among bivalve mollusks is registered at the base of the Toarcian, in the *Tiltoniceras antiquum* Zone (Fig. 3). In North Siberia,
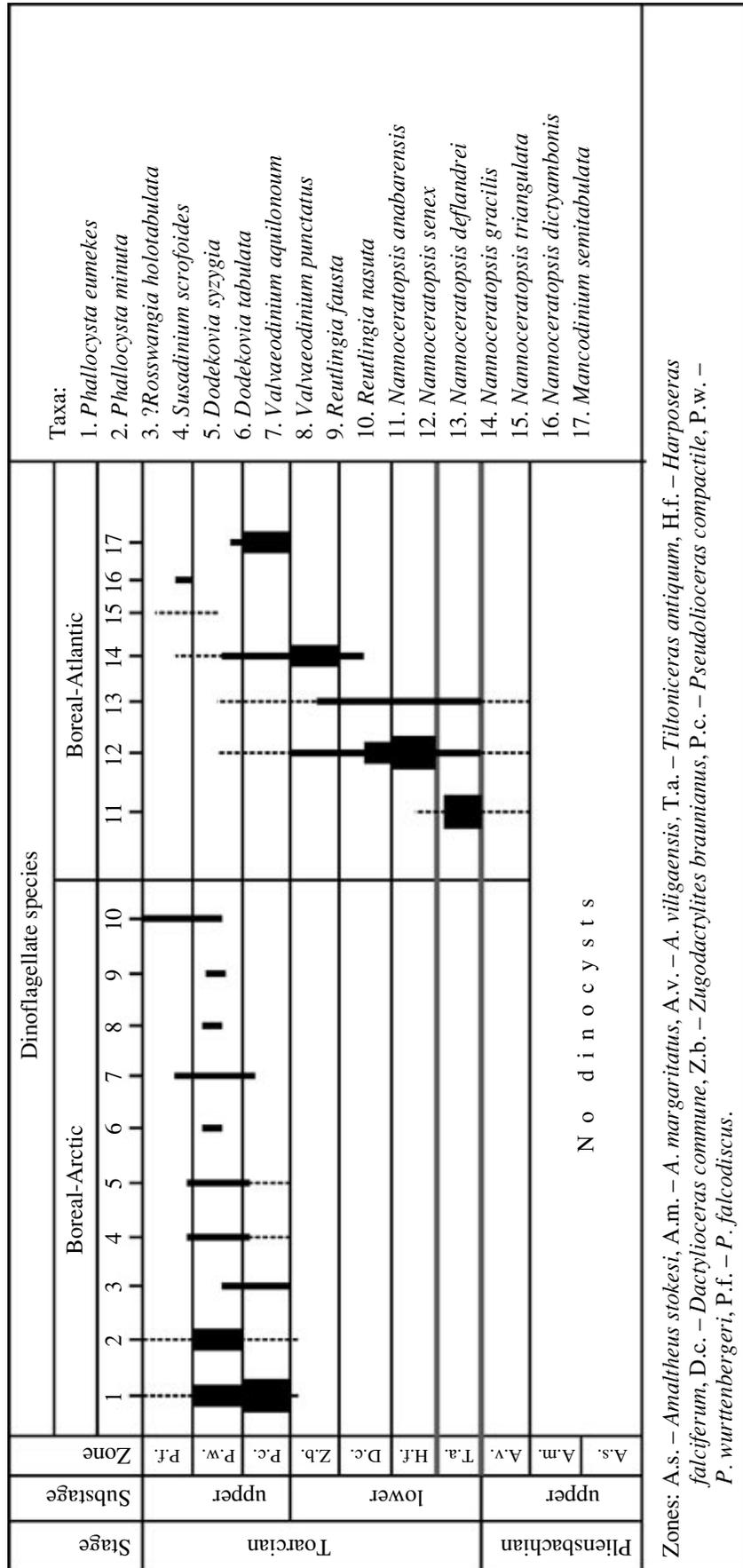
Fig. 6. Stratigraphic ranges of dinoflagellates in the upper Pliensbachian–Toarcian sediments of North Siberia.

Zones: A.s. – *Amaltheus stokesi*, A.m. – *A. margaritatus*, A.v. – *A. viligaensis*, T.a. – *Tiltoniceras antiquum*, H.f. – *Harposeras falciferum*, D.c. – *Dactylioceras commune*, Z.b. – *Zugodactylites braunianus*, P.c. – *Pseudolioceras compactile*, P.w. – *P. wurttenbergeri*, P.f. – *P. falcodiscus*.

only four of 35 bivalve genera typical of the upper Pliensbachian and two of four ostracode genera cross the Pliensbachian–Toarcian boundary; both fossil groups experienced a complete renewal in their generic and family composition at the base of the *Harpoceras falciferum* Zone (Fig. 4). Diversity of foraminifers decrease substantially within the interval of three ammonite zones from 27 genera in the *Amaltheus margaritatus* Zone to 17 and then to 15 genera in the *Tiltoniceras antiquum* and *Harpoceras falciferum* zones respectively (Fig. 5). Occasional species of Pliensbachian dinocysts give place to abundant assemblages of these fossils at the base of the Toarcian (Fig. 6), and substantial simultaneous reorganizations (*Classopolis* fluctuations, Fig. 7) are established in spore–pollen assemblages (SPA).

Structure of benthic communities. Above the Pliensbachian–Toarcian boundary, benthic bivalve communities differ sharply from their older counterparts by dominant genera, feeding chains, food capturing, feeding levels, homogenization level, and population density of taxa. Changes in structure of benthic communities are evident primarily from taxonomic diversity, which decreased by almost an order of magnitude. At the onset of the Toarcian, the communities became less homogeneous due to disappearance of dominant taxa. The communities became completely deprived of high-level detritovore genera *Malletia* and *Taimyrodon*, the subdominants of some former assemblages. Although high-level sestonophages constitute 50% of all genera preserved in biocoenoses, they can hardly be attributed to most viable, being represented only by scarce finds of two genera only. The only genus *Tancredia* is a low-level sestonophage. This genus was a dominant taxon in the late Pliensbachian and retained this position in the Toarcian as well. The high-level detritovore genus *Dacryomya* that was rare in the Pliensbachian and survived the boundary crisis becomes again dominant soon after the survival (*Harpoceras falciferum* Zone). During the early Toarcian, bivalves regenerated gradually to be, nevertheless, more than twice less diverse at the generic level in the late Toarcian as compared with the late Pliensbachian.

Analysis of microfossils from the Pliensbachian–Toarcian boundary sediments of North Siberia implies a discontinuity in development of Pliensbachian–Toarcian foraminiferal and ostracode communities. The early Toarcian crisis resulted in a sharply reduced differentiation of benthic communities in affiliation to bionomic zones (two- or three-member catenas instead of three- to four-member catenas of the late Pliensbachian), and diversity of viable forms in individual catena links decreased. Habitat conditions that existed at the beginning of the Kiterbyut time (the *Falciferum*–initial *Commune* phases) were unfavorable for microbenthos. Geochemical data indicate that sedimentation in the shallow coastal part of the North Siberian sea at the beginning of the *Falciferum* phase progressed in settings with unstable salinity (Levchuk, 1985). Fora-

miniferal tests in all the bionomic zones of the Siberian paleosea were dwarfish and thin-walled, suggesting unfavorable environments (stagnation) in the basin at the beginning of the Toarcian. It should be noted that the section interval under consideration is characterized by alternation of sedimentary laminae enriched in either foraminifers or ostracodes that is indicative of unstable bottom-water environments.

Biogeographic selectivity of taxa elimination from marine communities and spore–pollen complexes. Among bivalves divided according to their biogeographic affinity into three the Boreal–Arctic or High Boreal (26 genera), Low Boreal (16), and Subtethyan (7) groups, only 20% of High Boreal genera survived the boundary crisis, while representatives of the Low Boreal and Subtethyan groups disappeared from benthic communities (Fig. 3). Thus, bivalves illustrate the dramatic history of the Pliensbachian–Toarcian crisis most clearly. Of three Boreal–Arctic ostracode genera (four in total), only the genus *"Mandelstamia"* disappeared at the end of the Pliensbachian, while two other genera (*Ogmoconcha, Ogmoconchella*) crossed the boundary, although being unknown above the *Antiquum* Zone. The genus *Nanacythere* the only one of four Boreal taxa known in the Pliensbachian disappeared at the end of this age, and the genus *Kinkinella* appeared immediately above the Pliensbachian–Toarcian boundary (Fig. 4). Thus, changes in ostracode community took place in a short interval of the *Antiquum* phase. The Boreal–Arctic group of foraminifers consisted of 24 genera, and 13 of them crossed the Pliensbachian–Toarcian boundary. Only five genera disappeared for some time immediately at the boundary or near it. Six of 13 Boreal genera become extinct at various levels of the upper Pliensbachian, while five genera appear at the base of the Toarcian. One genus (*Citharina*), which disappeared in the Pliensbachian, appeared three phases later in the Toarcian, and only genus *Recurvoides* crossed the boundary between stages. The Boreal–Subtethyan foraminifers are represented by two genera: *Involutina* in the Pliensbachian and *Cornuspira* in the Toarcian (Fig. 5). Thus, the most significant reorganization in biogeographic structure of the foraminiferal community affected the relatively thermophilic taxa. Dinocysts of the Boreal–Arctic (10 species) and Boreal–Atlantic (7 species) groups are practically unknown in the Pliensbachian: only three *Nannoceratopsis* species have been found in uppermost layers of this stage. One of these species (*N. anabarensis*) becomes abundant and two others common immediately above the boundary under consideration (Fig. 6). It is remarkable that precisely the Boreal–Atlantic, not Boreal–Arctic, species appeared in abundance in the early Toarcian. In the interval of the *Amaltheus viligaensis–Tiltoniceras antiquum* boundary zones, spore–pollen assemblages (divided into Siberian, cosmopolitan, and Euro-Sinian types) lost 16 of 18 Siberian taxa (Fig. 7). All the cosmopolitan taxa (four species) crossed the boundary and several of 14 Euro-Sinian
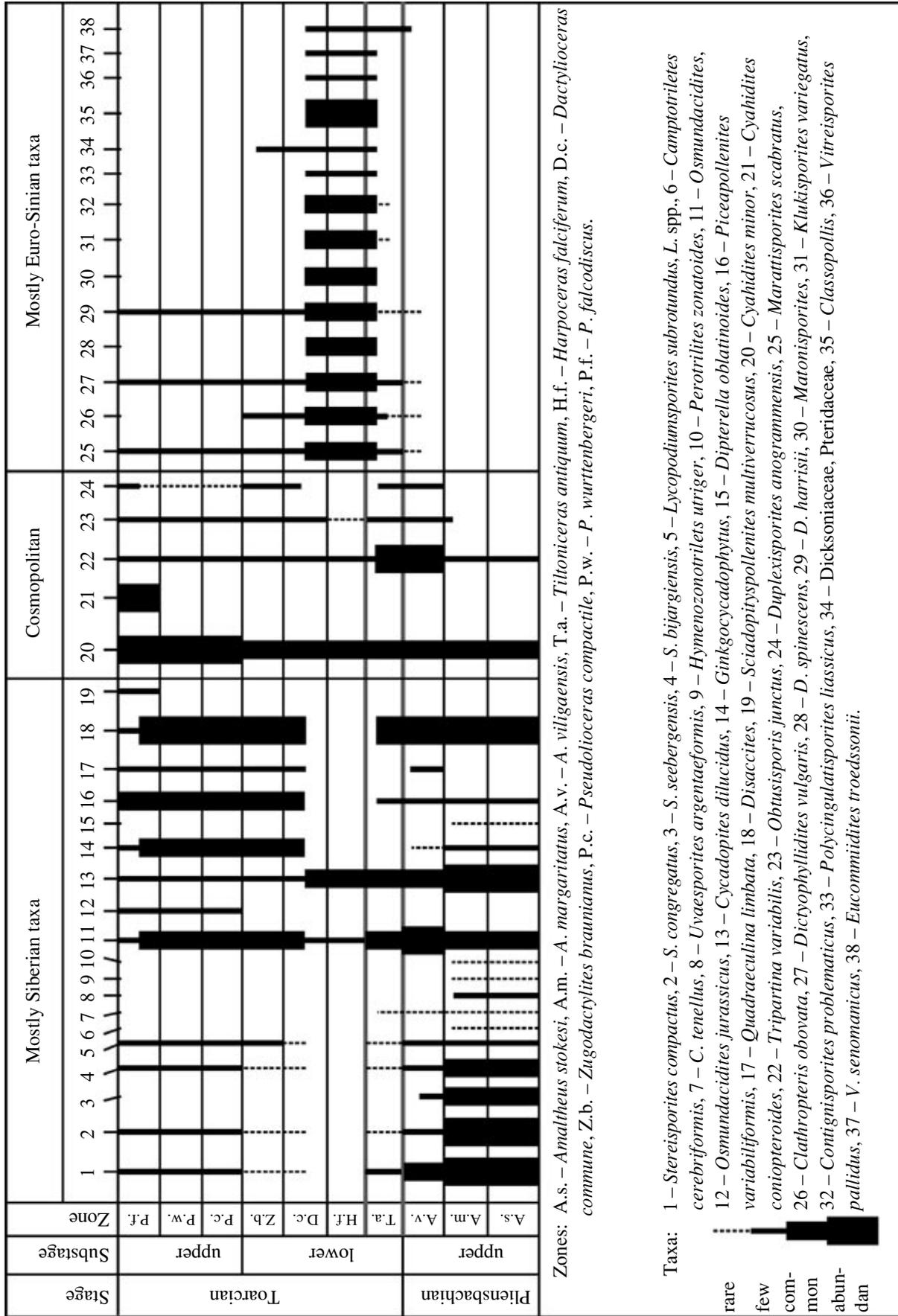
Fig. 7. Stratigraphic ranges of spore and pollen taxa in the upper Pliensbachian–Toarcian sediments of northern Siberia.

Zones: A.s. – *Amaltheus stokesi*, A.m. – *A. margaritatus*, A.v. – *A. viligaensis*, T.a. – *Tiltoniceras antiquum*, H.f. – *Harpoceras falciferum*, D.c. – *Dactylioceras commune*, Z.b. – *Zugodactylites braunianus*, P.c. – *Pseudolioceras compactile*, P.w. – *P. wurttenbergeri*, P.f. – *P. falcodiscus*.

Taxa: 1 – *Stereisporites compactus*, 2 – *S. congregatus*, 3 – *S. seebergensis*, 4 – *S. bijargiensis*, 5 – *Lycopodiumsporites subrotundus*, L. spp., 6 – *Camptotriletes cerebriformis*, 7 – *C. tenellus*, 8 – *Uvaesporites argentaeformis*, 9 – *Hymenozonotrilets utriger*, 10 – *Perotrilites zonatoides*, 11 – *Osmundacidites*, 12 – *Osmundacidites jurassicus*, 13 – *Cycadopites dilucidus*, 14 – *Ginkgocycadophytus*, 15 – *Dipterella oblatinoides*, 16 – *Piceapollenites variabiliformis*, 17 – *Quadraeculina limbata*, 18 – *Disaccites*, 19 – *Sciadopityspollenites multiverrucosus*, 20 – *Cyahidites minor*, 21 – *Cyahidites coniopteroides*, 22 – *Tripartina variabilis*, 23 – *Obtusisporis junctus*, 24 – *Duplexisporites anogrammensis*, 25 – *Marattisporites scabratus*, 26 – *Clathropteris obovata*, 27 – *Dictyophyllidites vulgaris*, 28 – *D. spinescens*, 29 – *D. harrisii*, 30 – *Matonisporites*, 31 – *Klukisporites variegatus*, 32 – *Contignisporites problematicus*, 33 – *Polycingulatisporites liassicus*, 34 – *Dicksoniaceae, Pteridaceae*, 35 – *Classopollis*, 36 – *Vitreisporites pallidus*, 37 – *V. senomanicus*, 38 – *Eucommiidites troedssonii*.

species appeared at the very base of the Toarcian (or, probably, in the uppermost Pliensbachian), where they are found in abundance at the *Antiquum* Zone top and in the *Falciferum* Zone. Thus, main events in the terrestrial vegetation happened during the *Antiquum* phase of the initial Toarcian.

BIOTA RESTORATION AFTER CRISIS

Almost all taxa of fauna and flora experienced reorganization in the *Antiquum* phase of the initial Toarcian. In all the groups, the crisis was accompanied by more or less essential reduction of taxonomic diversity and by destruction of community structures. The restoration of benthic communities begins usually with return of thermophobic taxa (the Lazarus effect). For example, the Boreal–Arctic taxa that became extinct in the Pliensbachian appear gradually in the lower Toarcian. Five Boreal–Arctic genera appear in benthic communities one phase later (0.5 to 1.0 m.y.) to become completely restored during the subsequent 2–3 m.y. (the same genera and majority of former species). At the same time, different dominant genera appeared in communities (Fig. 3). The Low Boreal bivalves became restored only in the late Toarcian largely owing to immigrants. None of nine Low Boreal bivalve taxa (the same genera and many species) has been found immediately above the Pliensbachian–Toarcian boundary. The genus *Chlamys* appeared in benthic communities only 3 m.y. after the crisis, and 5–6 m.y. later newcomers occupied almost all the Arctic biotopes. A similar situation is also characteristic of Subtethyan bivalve taxa: all of them disappeared below the Toarcian, and only one genus (*Goniomya*) returned. Two new genera appeared only after three and six phases (i.e., 3 and 6 m.y. later). Thus, the extinction of bivalves was much faster as compared with their restoration.

Except for the genus *Camptocythere*, all the Arctic ostracodes disappeared from the early Toarcian benthic community, being replaced here by more thermophilic Boreal genera (Fig. 4). The thermophilic foraminiferal community experienced substantial renewal above the Pliensbachian–Toarcian boundary. During the late Pliensbachian–early Toarcian, the renewal rate among Boreal foraminiferal taxa was higher as compared with that in their Boreal–Arctic communities (Fig. 5). As was mentioned, the Boreal–Atlantic (i.e., thermophilic) dinoflagellate species dominated in the pelagic zone of the Early Toarcian seas of North Siberia (Fig. 6). The event of reorganization was immediately followed by outburst of the thermophilic genus *Classapolis* (dominant of the SPA). Eleven of 18 Siberian taxa appear again in the *Dactylioceras commune* Zone, while the SPA of underlying *Tiltoniceras antiquum* and *Harpoceras falciferum* zones consists of 14 Euro-Sinian species, most of which occur in abundance (Fig. 7).

SCENARIO OF BIOTIC TURNOVER

According to materials discussed above, the following, most reasonable scenario can be proposed for biotic turnover recorded in the Pliensbachian–Toarcian transition of North Siberia:

—late Pliensbachian (late *Stokesi*–initial *Margaritatus* phase) ⟶ transgression ⟶ warming ⟶ immigration of Low Boreal and Perithethyan invertebrate taxa to the Arctic basin;

—late Pliensbachian (late *Margaritatus*–early *Viligaensis* phase) to early Toarcian (early *Antiquum* phase) ⟶ regression ⟶ formation of geographic barriers ⟶ changes in bottom topography and circulation system in the second half of the *Viligaensis* phase ⟶ rapid cooling ⟶ decline of the taxonomic diversity of marine invertebrates (?reduction of northern distribution areas);

—early Toarcian (terminal *Antiquum* phase) ⟶ commencement of eustatic sea-level rise ⟶ warming ⟶ slight freshening of surface waters ⟶ onset of the phytoplankton bloom and immigration of terrestrial Euro-Sinian plant taxa ⟶ development of first disoxic settings ⟶ extinction of marine invertebrates;

—early Toarcian (*Falciferum* phase) ⟶ further sea-level rise with the maximum in the terminal *Falciferum* phase ⟶ changes in bottom topography and circulation system ⟶ substantial warming on land and in seas ⟶ intermittent immigrations of Low Boreal invertebrate taxa to the Arctic basin ⟶ migration of *Arcto-Boreal* microbenthos to Low Boreal seas (*Falciferum*–initial *Commune* phases) ⟶ sharp increase in diversity of Euro-Sinian terrestrial vegetation (abundance of *Classopolis*) ⟶ phytoplankton bloom ⟶ development of disoxic to, locally, anoxic environments in the entire water column ⟶ termination of the invertebrate extinction at the beginning of the *Falciferum* phase;

—early Toarcian (*Commune* phase) ⟶ high sea-level stand ⟶ reduction of disoxic settings ⟶ warm water masses and atmosphere ⟶ immigration of Low Boreal and Perithethyan taxa and increased diversity of Boreal–Arctic marine invertebrate genera ⟶ increase in diversity of phytoplankton and terrestrial plants owing to invasion of Siberian forms;

—early Toarcian (*Braunianus* phase) ⟶ sea-level fall ⟶ stability of taxonomic diversity among marine invertebrates ⟶ onset of cooling ⟶ sharply decreased species diversity of Euro-Sinian terrestrial vegetation (disappearance of *Classopolis*) ⟶ decreased abundance of phytoplankton.

FACTORS RESPONSIBLE
FOR BIOTIC TURNOVER

Paleogeography. It is reasonable to assume that significant paleogeographic events that resulted in substantial renewal of marine settings could cause perturbations in biotic communities as well. In connection

with the Pliensbachian–Toarcian biotic crisis, worth of mentioning is large paleogeographic reorganization in the North Atlantic that coincides with the transition between these ages. The paleobiogeographic analysis of marine invertebrates reveals that the southern boundary of the Tethys–Panthalassa superbiochore was located at the latitude of southern England and northwestern France in the late Pliensbachian. The paleogeographic reorganization that occurred in the North Atlantic at the beginning of the Toarcian strengthened the influence of cold water masses that triggered southward migration of thermophilic mollusks and simultaneous northward displacement of boundary between the Tethys–Panthalassa and Panboreal superbiochores for several hundreds kilometers (Damborenea, 2002, fig. 7).

Macchioni and Cecca (2002) defined in sections of northwestern and southern Europe and northwestern Africa two distinct levels of the ammonite diversity fall at the beginning of the Toarcian (*Dactylioceras tenuicostatum* Zone). The first of these events coincides with the base of the *Dactylioceras mirabile* Subzone and reflects destruction of the Boreal–Tethyan provinciality due to rapid extinction of the Boreal endemic family Amaltheidae, which populated seas of northwestern Europe, on the one hand, and disappearance of the late Domerian endemic ammonites in the Mediterranean realm, on the other. The second drastic fall of the ammonoid diversity in the upper part of the *Dactylioceras semicelatum* Subzone corresponds to the anoxia (OAE) attack. This is reflected in epioceanic ammonoid clades Phylloceratacea and Lytoceratacea. We consider both extinctions as autonomous, not representing episodes of a single stepwise extinction event.

It can be thought that influence of the above paleogeographic reorganizations should be restricted to areas adjacent to the North Atlantic having distant relation to biotic events in the Andean and North Siberian basins located many thousands kilometers away. Nevertheless, this is not the case. According to recent data, the early Toarcian intensification of water exchange between North Atlantic and Arctic seas via the so-called Viking Corridor was accompanied by enhanced water and biota exchange between the western Pacific and Central Atlantic via Hispanic Corridor (Zakharov, 2005 and references therein). The widened seaways activated the faunal exchange between paleobasins. Aberhan (2002) assumed that extinction in South America can be partly explained by immigration of bivalves via the Hispanic Corridor and their subsequent selective migration. Although the calculated rates of molluscan migrations from the Atlantic to the Pacific and back demonstrated their insignificant mutual influence, the effect of this factor cannot be ruled out completely. The North Siberian biota appeared to be dependent of the North Atlantic biota more than of the Andean one. For example, extinction of the late Pliensbachian ammonite family Amaltheidae in the Arctic region (and globally as well) was synchronous with the enhanced water exchange

between the Arctic and North Atlantic basins. Subsequent colonization of Siberian and North Asian basins by ammonites of the family Dactylioceratidae, the immigrants from North Atlantic seas, occurred at the beginning of the Toarcian so quickly that this event cannot be estimated by the traditional biochronostratigraphic method. Thus, the principal renewal of ammonite communities in North Siberia at the time of Pliensbachian–Toarcian transition and in the initial Toarcian was caused by paleogeographic reorganization in the North Atlantic. The related influence of Atlantic water masses stimulated invasion of West European Toarcian ammonites from the family Dactylioceratidae and belemnites from the family Passaloteuthide in the Arctic basin (Saks et al., 1971).

Eustatic factors and anoxia. A wide development of anoxic environments in response to sea-level rise during the Early Toarcian transgression (Hallam, 1987; Hallam and Wignall, 1999; Aberhan and Baumiller, 2003) is most popular explanation for the mass extinctions of bivalve mollusks. As is assumed this transgression of eustatic origin most likely stimulated formation of black shale facies. Shales and clays of the early Toarcian age are known in many regions of the Northern Hemisphere, i.e., in northwestern Europe, Alpine–Mediterranean domain, Canada, Arctic region, and Japan. These sediments have been deposited in different paleooceanographic settings, but the common viewpoint of researchers, who studied these facies and relevant fossils, is that the lower Toarcian high-carbonaceous black shales have been deposited in basins with oxygen-deficient bottom waters. The worldwide distribution of these sediments impelled Jenkins (1988) to assume the oceanic anoxic event (OAE) that took place in the initial early Toarcian (*Falciferum* phase). The oxygen-deficient environments in deep basins and on shoals (Tremto Plateau in the Southern Alps) are inferred from sedimentological and geochemical data (Jenkins et al., 1985; Jenkins and Clayton, 1997). Bellanca et al., (1999) who studied productivity of Toarcian black shales in the Belluno basin of northern Italy concluded that shales enriched in organic carbon and rhythmically alternating with bioturbated limestones and gray marls were deposited in anoxic settings of the Tethys during the early Toarcian. The negative $\delta^{13}C$ excursion established in the middle of the examined interval is correlative with the peak content of total organic carbon (TOC) and high V/Rb and Ba/Rb values are indicators, as they believe, of the Toarcian anoxic event, i.e., of the near-bottom anoxia coupled with a high productivity of surface waters. In this respect, the lower Toarcian Posidonia shales of southwestern Germany can be considered as a classical standard of high-carbonaceous black shale sequences. In opinion of most researchers who studied them, these facies formed in a shallow semiclosed sea basin. Röhl et al. (2001) who investigated Posidonia shales in sections of the Schwäbische (in southwest) to Franconian Alb (in the northeast) arrived at the conclusion that anoxic condi-

tions in bottom waters of the Posidonia basin existed permanently during its development. Moreover, the maximal oxygen deficiency and extreme negative excursion of $\delta^{13}C_{org}$ value (–34‰) corresponds to the initial *Falciferum* phase. It should be noted also that some researchers (Aberhan, 2002; Aberhan and Für-sich, 1997) consider the high sea-level stand and wide development of anoxic environments as factors respon-sible, among others, for reorganization in bivalve com-munities of the Andean basin (Chile) at the time of Pliensbachian–Toarcian transition. The cited examples show that anoxic conditions in the bottom water layer were characteristic of different-type basins in the Northern and Southern hemispheres.

Thus, anoxia is referred to as one of principal factors responsible for the taxonomic diversity reduction in marine benthic groups. In the oceanographic scenario, the expansion of anoxic settings is explained by sea-level changes viewed as main factors. The triggering factor of a rapid, instant in fact from geological stand-point (one phase shorter than 1 m.y.), global sea-level rise used to be omitted in that scenario.

The North Siberian sections spaced for hundreds and even thousands kilometers from each other demon-strate a rapid (sometimes, within the interval several decimeters thick) replacement of sandy–silty–clayey sediments by clayey and clayey–silty facies locally enriched in C_{org}. This is accompanied by a sharp decline in the taxonomic diversity of macro- and microfossils. Several bivalve genera belonging to three trophic groups continue to exist however: sestonophages of low (*Tancredia*) and high (*Kolymonectes, Oxytoma*) levels, and gathering detritovore genus *Dacryomya*. They all dwelt in oxygen-enriched bottom settings and, natu-rally, could not survive even disoxic environment, leav-ing aside the anoxic one. Moreover, *Dacryomya* fed below the water/sediments interface, and consequently not only H_2S contamination, but even a significant oxy-gen deficiency is inadmissible below this level. Rela-tively diverse benthic foraminifers (17 genera), which required aerated environments, populated the bottom during the initial Toarcian *Antiquum* phase as well. Nat-urally, it cannot be ruled out that necessary conditions existed in the entire spacious epicontinental sea of North Siberia between the Yamal and Chukotka penin-sulas. Undoubtedly, oxygen deficiency of bottom waters could be characteristic of some areas. By logic, a wide distribution of lower Toarcian fine-grained sedi-ments, which are locally enriched in organic matter, can be explained by a high sea-level stand and relatively leveled low-mountainous relief around the relevant basins (Jenkins, 1988). In opinion of some experts, the highest sea-level stand during the entire early Jurassic and initial Middle Jurassic was characteristic precisely of the early Toarcian (Hallam, 1992, figs. 4, 5).

Climate. All the aforesaid is correct, but many researchers relate episodes of general climatic warming with eustatic transgressions. As for biota, it was directly influenced by climate changes precisely. As is demon-strated below, it is more logical to explain many dynamic events in transformation of invertebrate and vegetation communities by climatic fluctuations. We consider this factor as principal one for the biota reor-ganization in North Siberia, where warm environments of the late Pliensbachian were followed by cooling at the stage termination (at the end of the *Viligaensis* phase) and in the initial Toarcian (the beginning of the *Antiquum* phase), and then by a gradual warming (see scenario). This inference is based on disappearance of marine thermophilic fossils from the Pliensbachian–Toarcian boundary beds, and this event was followed in the North Siberian seas by gradual return first of High Boreal and then of thermophilic fauna and floral taxa. Moreover, some of the former thermophilic genera were replaced by newcomers. Such dynamics in biota restoration points to a gradual warming. It should be noted however that a relatively early outburst of Euro-Sinian taxa in vegetation and abundance of *Classopolis* in the SPA imply a relatively rapid warming on land. This inference is consistent with the phytoplankton bloom against the background of highly impoverished benthic invertebrate communities. The taxonomic impoverishment of filtering organisms can be explained by substantial changes in the nutritional chain, because outburst of dinoflagellates changed it qualitatively. Indeed, prior to the Toarcian, dinoflagellates were prac-tically missing from the diet of filtering organisms. It is conceivable that precisely a long adaptation to new food explains the fact that the post-crisis period of col-onization of North Siberian seas by the early Toarcian bivalves lasted several millions years. Nevertheless, the temperature should be considered as a principal factor. Actually, the Subtethyan and Low Boreal bivalves, which populated the epicontinental seas northward of latitude 68° N in the terminal Pliensbachian, migrated southward to the latitude 55° N (to the Boreal–Tethyan ecotone in northern Primor'e) at the beginning of the Toarcian (*Antiquum* and *Falciferum* phases); they returned back to North Siberia only in the late Toarcian (Fig. 8). To some extent, this inference is consistent with data on foraminifers and ostracodes. During the greater part of the late Pliensbachian, microfauna dwelt at the latitude 73° N. At the end of the *Viligaensis* phase, foraminifers and ostracodes migrated almost down to 55° N. Later on at the beginning of the Toar-cian, both groups of fauna returned relatively soon from lower to higher latitudes and adapted to new environ-ments during a relatively short period, probably, shorter than 1 m.y. (Fig. 9). A similar climatic regime is recon-structed for northern Siberia based on palynological data. The early Toarcian warming was maximal one through the entire Jurassic (Fig. 10). In opinion of Il'ina et al. (1994), the peak warming corresponds to the *Fal-ciferum* phase. The terminal Pliensbachian was a time of cooling that probably progressed in the initial Toar-cian as well, although the exact period of cooling is unknown because of the boundary sediments are dated
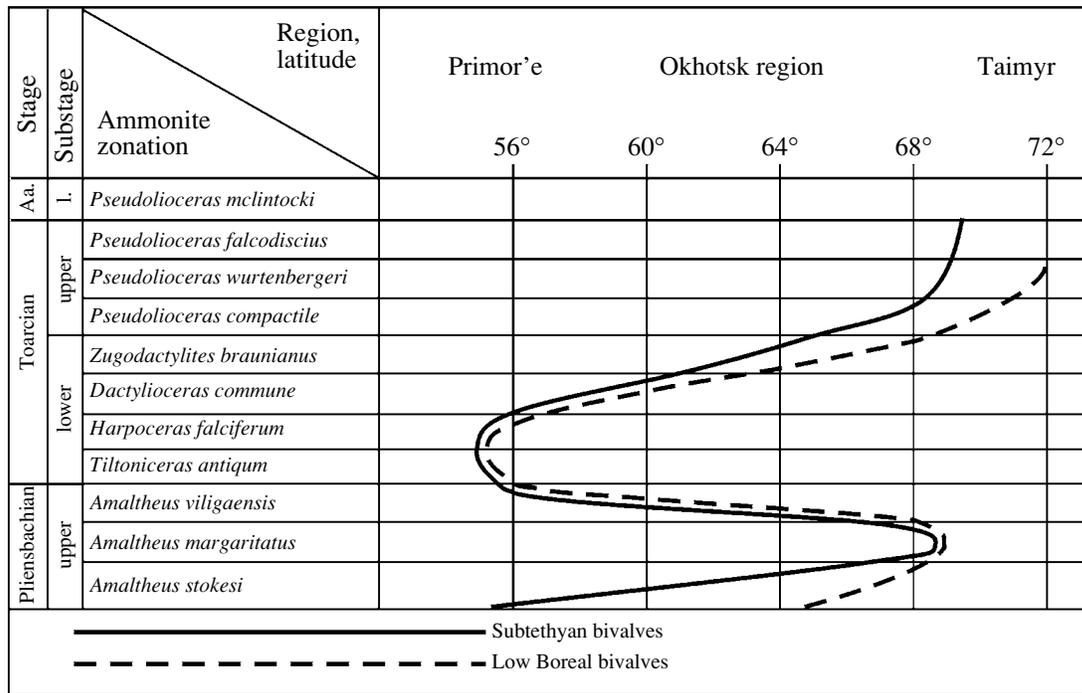
Stage	Substage	Ammonite zonation	Region, latitude	Primor'e	Okhotsk region		Taimyr
				56°	60° 64°	68°	72°
Aa.	l.	*Pseudolioceras mclintocki*					
Toarcian	upper	*Pseudolioceras falcodiscius*					
		Pseudolioceras wurtenbergeri					
		Pseudolioceras compactile					
	lower	*Zugodactylites braunianus*					
		Dactylioceras commune					
		Harpoceras falciferum					
		Tiltoniceras antiqum					
Pliensbachian	upper	*Amaltheus viligaensis*					
		Amaltheus margaritatus					
		Amaltheus stokesi					

——————— Subtethyan bivalves

– – – – – – Low Boreal bivalves

Fig. 8. Migration of Subtethyan and Low Boreal marine bivalve genera in the Arctic paleobiogeographic region during the late Pliensbachian and early Toarcian from high to low latitudes and backward, a principal model; abbreviations denote Aalenian Stage (Aa) and its lower substage (l.).

uncertainty to some extent (at the subzone level). It is conceivable that the terminal Pliensbachian–(?)initial Toarcian cooling was induced by growing humidity of North Siberian climate. Geochemical signals (Levchuk, 1985) and specific composition of microfossil assemblages point to water freshening in the southeastern North Siberian sea. The Toarcian Age of enhancing climate aridity explains absence of coarse-grained sediments even in coastal shallow-water Toarcian successins in North and West Siberia (*Paleogeography of the Northern…*, 1983).

DYNAMICS OF BIOTIC REORGANIZATIONS

The first quantitative curve illustrating the extinction dynamics of marine invertebrate families during the Phanerozoic (Raup and Sepkoski, 1982, 1984; Sepkoski and Raup, 1986) gives an impression that peaks of taxonomic diversity decline coincide with boundaries between stages and substages. Subsequent, more precise data showed however that critical events of biota reorganization do not coincide frequently with boundaries of stratigraphic units. For example, Sepkoski estimated that 22 and 11 ammonite families became extinct in the world during the Pliensbachian and Toarcian, respectively. According to Little and Benton (1995), 28 ammonite families became extinct in the Northern and Southern hemispheres in the Early Jurassic beginning from the late Pliensbachian *Margaritatus* phase to the early Toarcian *Bifrons* phase (from 191.51

to 184.00 Ma) that was a period of most intense ammonoid extinction: as they estimated 8, 7, 4, 8, and 6 families disappeared respectively during the *Margaritatus, Spinatum, Teniocostatum, Falciferum,* and *Bifrons* phases. Two maximums of extinct families corresponded to the terminal Pliensbachian (*Spinatum* phase) and initial Toarcian (*Tenuicostatum* phase).

Based on distribution of eight fossil groups (bivalves, gastropods, scaphopods, ammonites, belemnites, brachiopods, serpulids, crinoids) in the northern Yorkshire section (England) of the Pliensbachian–Toarcian transition, it was established that the highest rate of species extinction was characteristic of the *Semicelatum* Subzone, the uppermost one of four subzones of the *Dactylioceras tenuicostatum* Zone (Little and Benton, 1995). Hallam (1987) demonstrated that taxonomic diversity of ammonite genera and species of bivalves, brachiopods, foraminifers, and ostracodes increased progressively in the Early Jurassic seas of northwestern Europe during the Hettangian, Sinemurian, and Pliensbachian to drop at the Pliensbachian–Toarcian boundary (except for foraminifers in northwestern France), especially in bivalve communities. In all these groups, except for foraminifers and ostracodes in England, the peak appearance of newcomers corresponds to the uppermost Pliensbachian zone, and exactly these taxa "new" for the Northwest European sea disappeared in majority during the biota turnover. The gradual growth of taxonomic diversity is observable practically in all the invertebrate groups, but
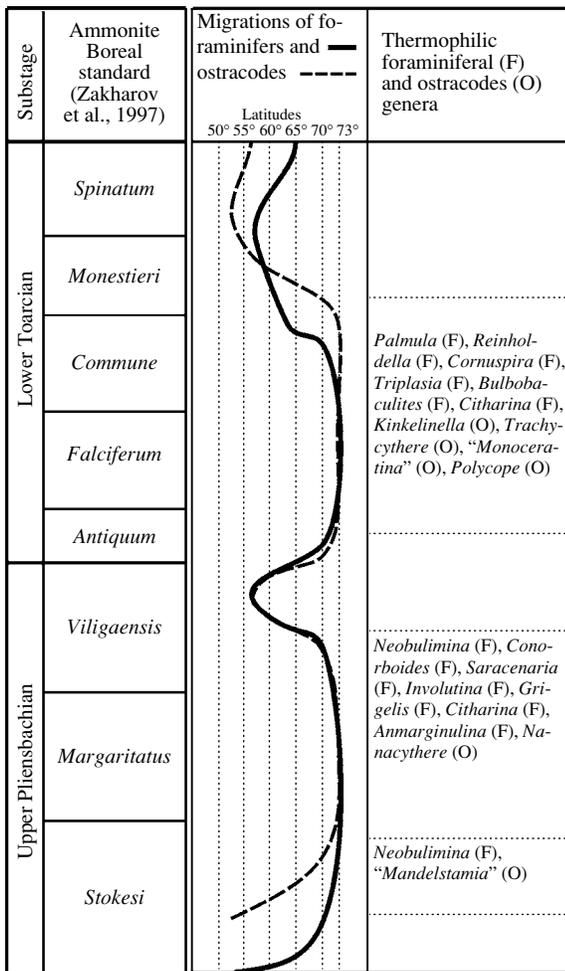
Substage	Ammonite Boreal standard (Zakharov et al., 1997)	Migrations of foraminifers and ostracodes - - - - Latitudes 50° 55° 60° 65° 70° 73°	Thermophilic foraminiferal (F) and ostracodes (O) genera
Lower Toarcian	Spinatum		
	Monestieri		
	Commune		Palmula (F), Reinholdella (F), Cornuspira (F), Triplasia (F), Bulbobaculites (F), Citharina (F), Kinkelinella (O), Trachycythere (O), "Monoceratina" (O), Polycope (O)
	Falciferum		
	Antiquum		
Upper Pliensbachian	Viligaensis		Neobulimina (F), Conorboides (F), Saracenaria (F), Involutina (F), Grigelis (F), Citharina (F), Anmarginulina (F), Nanacythere (O)
	Margaritatus		
	Stokesi		Neobulimina (F), "Mandelstamia" (O)

Fig. 9. Migration of Subtethyan and Low Boreal foraminiferal and ostracode genera in the Arctic paleobiogeographic region during the late Pliensbachian and early Toarcian (a principal model).

it has never reached the diversity level of the terminal Pliensbachian even near the Aalenian base.

Dynamics of biota reorganizations was not identical in different paleobiochores in terms of rate, succession of events, and time, as is evident from correlation of sections at the zonal (subzonal) level. For example, two extinction levels of ammonoids are defined in the Tethyan and Boreal superbiochores at the base and in the upper part of the *Tenuicostatum* Zone (Macchioni and Cecca, 2002). Little and Benton (1995) demonstrated however that a minimal number of extinct families corresponds to this zone in northwestern Europe. Consequently, the extinction peaks in question are determined by Mediterranean ammonoids.

The maximal taxonomic diversity of benthic macrofossils (bivalves and brachiopods) is confined in the West European Boreal province to the *Falciferum* Zone (*Exaratum* Subzone). In the Andean basin, where zonation has not been described, the extinction interval corresponds to the terminal Pliensbachian–Early Toarcian,

as is evident from diagrams published by Aberhan and Fürsich (1997, 2000). Hallam (1987), who considers anoxia as the main factor responsible for extinction, believes that this phenomenon suppresses nekton and benthos but not plankton. As it follows from analysis of extinctions in particular zones, diversity of ammonites in the northern West European basin dropped significantly earlier than that of benthic fossils (Hallam, 1987, fig. 1). This event coincided with the onset of formation of high-carbonaceous black shales close to the *Falciferum* phase, the initial part of which is marked by the oxygen deficiency maximum and anomalous negative $\delta^{13}C_{org}$ (−34‰) excursion established in the South German basin (Röhl et al., 2001). Bailey et al. (2003) confirmed this inference based on the data from the Yorkshire basin, where they registered the OAE signals at the base of the *Falciferum* Zone (*Exaratum* Subzone).

The extinction rates detectable in different fossil groups are of particular interest. It is well known that diversification rate of Mesozoic ammonoids was higher than of other marine invertebrates. The relative biochronological scale based on the ammonite succession is unsuitable however for an accurate assessment of rates characterizing their morphogenesis. On the other hand, the absolute dates characterizing intervals even of the Mesozoic ages, not to mention the zonal phases, are still far from being estimated precisely (Gradstein et al., 1994). Nevertheless, the dates estimated by interpolation of $^{87}Sr/^{86}Sr$ values for the upper Pliensbachian–lower Toarcian boundary subzones (McArthur et al., 2000) deserve attention. The mentioned authors calculated time spans of the lower Toarcian ammonite subzones and demonstrated that one can be 30 times longer than the other one, e.g., the *Clevelandicum* Subzone 0.036 m.y. long versus the *Exaratum* Subzone 1.08 m.y. long. The early Toarcian OAE lasted 0.52 m.y. If equal relative deviations (systematic calculation errors) but not the above absolute values are taken into consideration, one can figure out the transformation rate of ammonite community was at least an order of magnitude higher than the transformation of benthic communities. In fact, the integral duration of four subzones of the *Tenuicostatum* Zone is 0.302 m.y. (reorganization period of ammonite assemblages), while that of the *Exaratum* Subzone (reorganization period of benthic communities) is 1.080 m.y. It should be noted once again that reorganization in ammonite communities of the Boreal and Tethyan basins commenced prior to the anoxic event.

The scenario proposed above for the Pliensbachian–Toarcian turnover in benthic communities of the Arctic basin is similar in many respects to that peculiar of Northwest European and even Andean basins. On the other hand, there were substantial differences in dynamics of taxa extinction. First, the Late Pliensbachian nekton was represented in the Arctic basin by the genus *Amaltheus* only. This genus was sole representative of the ammonite family Amaltheidae that became extinct worldwide, in the Arctic basin as well, at the
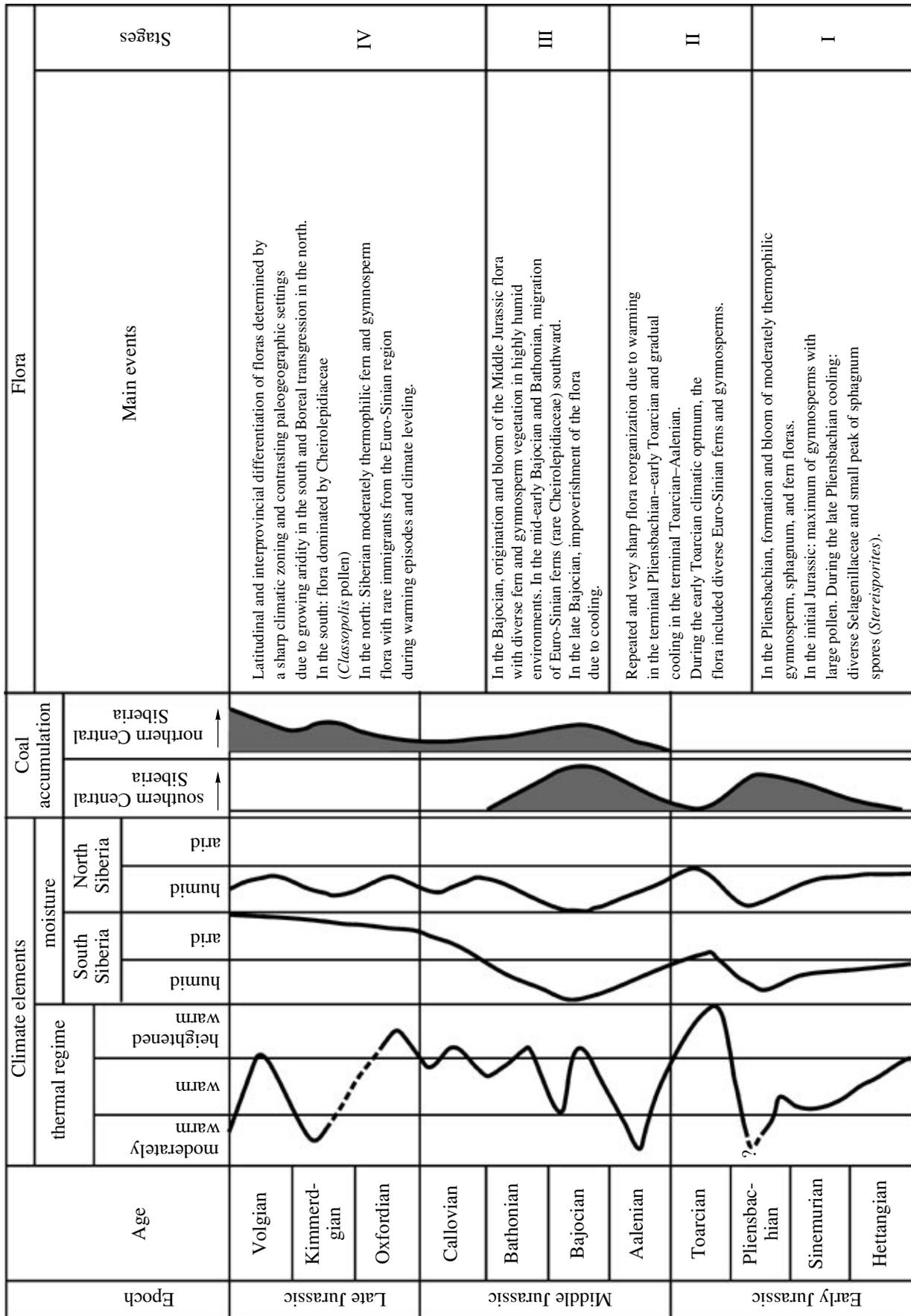
Stages

IV

III

II

I

Flora — Main events

Latitudinal and interprovincial differentiation of floras determined by a sharp climatic zoning and contrasting paleogeographic settings due to growing aridity in the south and Boreal transgression in the north. In the south: flora dominated by Cheirolepidiaceae (*Classopolis* pollen) In the north: Siberian moderately thermophilic fern and gymnosperm flora with rare immigrants from the Euro-Sinian region during warming episodes and climate leveling.

In the Bajocian, origination and bloom of the Middle Jurassic flora with diverse fern and gymnosperm vegetation in highly humid environments. In the mid-early Bajocian and Bathonian, migration of Euro-Sinian ferns (rare Cheirolepidiaceae) southward. In the late Bajocian, impoverishment of the flora due to cooling.

Repeated and very sharp flora reorganization due to warming in the terminal Pliensbachian–early Toarcian and gradual cooling in the terminal Toarcian–Aalenian. During the early Toarcian climatic optmum, the flora included diverse Euro-Sinian ferns and gymnosperms.

In the Pliensbachian, formation and bloom of moderately thermophilic gymnosperm, sphagnum, and fern floras. In the initial Jurassic: maximum of gymnosperms with large pollen. During the late Pliensbachian cooling: diverse Selagenillaceae and small peak of sphagnum spores (*Stereisporites*).

Coal accumulation
- northern Central Siberia ↑
- southern Central Siberia ↑

Climate elements

moisture — North Siberia: arid / humid; South Siberia: arid / humid

thermal regime — heightened warm / warm / moderately warm

Age / Epoch

Epoch	Age
Late Jurassic	Volgian
	Kimmerdgian
	Oxfordian
Middle Jurassic	Callovian
	Bathonian
	Bajocian
	Aalenian
Early Jurassic	Toarcian
	Pliensbachian
	Sinemurian
	Hettangian

Fig. 10. Fluctuations of climate (temperature and humidity), coal-accumulation epochs, and main on-land events of the Jurassic in Siberia .

time of Pliensbachian–Toarcian transition. Almost all the Toarcian ammonites of the Arctic region originate from the North Atlantic. Evolution of these forms in Arctic seas was identical to their development in original habitats, i.e., in West European seas. Second, in contrast to the England–Parisian and Andean basins the share of extinct taxa among benthic groups was negligible in the Arctic region. Dynamics of taxonomic diversity was controlled here largely by changes in boundaries of distribution areas rather than by extinction and diversification (Figs. 7, 8). At the end of the Pliensbachian, the only genus *Harpax* became extinct among Arctic bivalves. Most of the Boreal–Arctic genera migrated at the beginning of the Toarcian southward to return subsequently to their former biotopes (Fig. 8). More thermophilic genera left the Arctic seas, not died off. Microfauna followed in general the scenario suggested for bivalves (Fig. 9). Thus, there was no mass extinction of marine invertebrates in the Arctic basins at the time of Pliensbachian–Toarcian transition. The biotic crisis was mostly connected here with a rapid southward migration of Arctic marine invertebrates during a sharp climatic cooling, which gradually returned afterward to former biotopes under conditions of subsequent warming (the Lazarus effect).

CORRELATION OF EVENTS IN DIFFERENT REGIONS

Two regions, where a sharp decrease in species diversity of bivalves is established in the Pliensbachian–Toarcian transition, are the southern England (Yorkshire) to southern Germany (epicontinental seas of northwestern Europe) and South America (Andean basin). Hallam (1986, 1987) considered this phenomenon as regional, but after discovery of turnover in bivalve community of the Andean basin (Aberhan and Fürsich, 1997, 2000), the event gained a global status. The inferred global character of biotic crisis at the time of Pliensbachian–Toarcian transition is consistent with data obtained in North Siberia and Arctic regions as a whole (Shurygin and Nikitenko, 1996; Nikitenko and Mickey, 2004). Dynamics of taxonomic diversity in three remote regions (northwestern Europe, Andean basin, Arctic region) is similar: the diversity growing rapidly in the Sinemurian and Pliensbachian decreased sharply afterward, in particular at the beginning of the Toarcian, and was increasing gradually again up to the former (pre-crisis) level during the terminal Toarcian or in the Aalenian. Like in epicontinental seas of northwestern Europe and in the Andean basin, the period of biota decline in the North Siberian basin was several times shorter than the restoration period. The Arctic benthic communities acquired former diversity in the late Toarcian, while in West Europe and the Andean basin the bivalve communities reached their pre-crisis state in the Aalenian only. This is thought to be a consequence of bivalve larvae migration via the Hispanic Corridor. As was suggested, the diversity decline dur-

ing the crisis is related to immigration of taxa from the Andean basin to West European seas in the terminal Pliensbachian–initial Toarcian, while the restoration of biota is caused by their backward migration from West European to East Pacific basins, because bivalves acquired their pre-crisis diversity already in the Toarcian. Calculations by Aberhan (2002) show, however, that the migration rate was low in both regions during the early Pliensbachian–Aalenian, and this fact disproves both hypotheses. On the contrary, diversification was much more important than the immigration, controlling the divergence in both regions. Aberhan argued that the global Pliensbachian–Toarcian crisis in biota evolution is better explainable by a combination of physicochemical (intense volcanism, high sea-level stand, widespread anoxia environments) and biological factors. The mass extinction was followed by restoration, when generation rate of new taxa increased again during the Aalenian in the Andean basin and during the late Toarcian in West European basins.

A group of West European researchers who studied geochemistry and isotopic composition calcitic belemnite rostra from the Pliensbachian and Toarcian sections of the Yorkshire coast in the United Kingdom and southern Germany arrived at some important conclusions (Bailey et al., 2003). Owing to confident bio- and chemostratigraphic correlation of sections, these researchers demonstrated that geochemical trends established for belemnite successions of both regions are correlative to each other. The Mg/Ca, Sr/Ca, and Na/Ca ratios in calcitic material of belemnites increase from 1.7 to 2.0 within the interval of negative (by 3‰) $\delta^{18}O$ excursion between the middle of the *Tenuicostatum* Zone and the lower part of the *Falciferum* Zone (time span 0.6 to 0.7 m.y. long) of the ammonite zonation determined in England. These data support the assumption that dramatic environmental changes were synchronous to the Toarcian OAE. The Mg/Ca and $\delta^{18}O$ values imply a sharp warming (by 6–7°C) and substantial water freshening at that time. The global warming accompanied by increased hydrological cycles and runoff has been assumed responsible for these changes. Data on the lower part of the Yorkshire section suggest that these events were preceded by cooling and synchronous growth of water salinity during the period from the late Pliensbachian *Margaritarius* phase to the initial *Tenuicostatum* phase of the early Toarcian.

Thus, the succession of the terminal Pliensbachian to initial Toarcian events in the Northwest European epicontinental sea and Andean basin is well consistent with scenario proposed for concurrent biota reorganizations in North Siberian seas and the Arctic basin as a whole, although the dynamics of reorganization had specific features in different regions.

CONCLUSIONS

In North Siberia and the Arctic as a whole, there is recorded a biotic turnover in the Pliensbachian–Toarcian transition. The event is evidenced by sharp reduction of taxonomic diversity at the generic level of marine invertebrates (bivalves, ostracodes, foraminifers) in the uppermost Pliensbachian(?)–basal Toarcian boundary layers (*Tiltoniceras antiquum* Zone). Concurrent spore–pollen assemblages show disappearance or substantial decrease in abundance of many species characteristic of Siberian paleoflora. Restoration of biota was gradual and asynchronous in different groups of marine and terrestrial organisms. The Boreal–Arctic bivalves and Boreal foraminifers were first (*Harpoceras falciferum* Zone) to appear in benthic communities of North Siberian seas; the Low Boreal and Subtethyan bivalves and Boreal ostracodes appeared here in the late Toarcian only. The Boreal–Atlantic dinoflagellates, which are represented in the terminal Pliensbachian by single specimens of the genus *Nannoceratopsis*, demonstrate an outburst at the very beginning of the Toarcian, being flourishing throughout the early Toarcian. Abundant Boreal–Arctic dinoflagellate taxa (10 species of 6 genera) appear only in the late Toarcian. In the basal Toarcian (*Tiltoniceras antiquum* Zone), spore–pollen assemblages become diverse largely owing to the Euro-Sinian taxa (14 species of 12 genera). Siberian taxa appear in abundance in the *Dactylioceras commune* Zone at the stratigraphic level, where abundance of Euro-Sinian forms is sharply declined.

Based on bivalves, microfossils, and spore–pollen assemblages, the biotic turnover can be logically explained by climate changes: warm conditions of the terminal Pliensbachian were followed by a sharp cooling at the time of Pliensbachian–Toarcian transition and then by warming in North Siberia. This warming might be related to the sea-level rise that explains a wide occurrence of clayey, locally high-carbonaceous sediments in the Arctic region, West and East Siberia included. The sea-level rise coupled with the water temperature increase was likely responsible for the outburst of thermophilic phytoplankton in the initial Toarcian. This could reduce oxygen concentration in the water column ("red tide" phenomenon) and, locally, in bottom waters or beneath the sediment/water interface. The same event destroyed the former nutritional chains and caused a sharp reduction of diversity of filtering bivalves.

The gradually grown diversity of macrofossils (bivalves, ammonites, belemnites) and, partly, of microfauna indicates that warming in northern Siberia was gradual. At the same time, the outburst of thermophilic terrestrial vegetation and thermophilic marine microscopic algae points to a rapid warming at the time of two the terminal *Antiquum–Falciferum* and initial *Commune* ammonite phases. The exact duration of this warming episode is unknown, approximately estimated to be 2 m.y. long. Paleobotanical data suggest the onset of the next cold period in northern Siberia already at the early–late Toarcian transition. This event was concurrent to appearance of abundant and diverse Boreal–Arctic dinoflagellates in North Siberian seas and to prosperity of taxa, which dominated in on-land vegetation of the Siberian phytogeographic region. This climatic scenario is weakly consistent with data on bivalves and ostracodes whose communities included relatively thermophilic genera in the terminal Toarcian–initial Aalenian. Should we assume different responses of bivalves and microscopic algae to changes in basin water temperature? The question remains without answer.

It should be noted that climatic changes represented probably a decisive factor that caused reduction of distribution areas of some taxa doomed to extinction in the Mesozoic. For example, last conodonts disappeared in the Tethyan realm in the Rhaetian, while their last representatives are found in Norian sediments of the Arctic region. The last remains (vertebrae) of marine dinosaurs are known in North Siberia from the mid-Maastrichtian. In the tropical zone, large dinosaurs existed up to the terminal Maastrichtian and, probably, to the Danian. Cephalopods became extinct in Tethyan seas in the terminal Cretaceous–initial Paleogene, while in the Arctic paleobiogeographic region, their extinction is recorded in the mid-Maastrichtian. Bivalves of the family Inoceramidae are even more illustrative. Their last representatives in the Arctic region are known from the lowermost Campanian, while in the western Tethys they occur in the Cretaceous–Danian (Paleogene) boundary layers. Thus, the additional evidence for climate-induced extinctions is obtained by analysis of distribution areas of doomed-to-extinction taxa: extinction of particular groups in the Mesozoic was usually preceded by reduction of their distribution areas and subsequent disappearance from the Boreal realm.

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