

Diversity and Stages in Evolution of Conodontophorids and Bivalve Mollusks in Triassic Seas of Siberia and the Far East

T. V. Klets

Novosibirsk State University, Novosibirsk, Russia

Received November 15, 2004; in final form, March 23, 2005

Abstract—Comparative analysis of taxonomic diversity dynamics of conodontophorids from Boreal (Arctic regions of Russia) and Tethyan (Northwest Pacific) paleobasins showed that they had most favorable habitat environments in tropical seas. In the Boreal realm, conodontophorids went through three stages of evolution comprising probably four substages and four phases, whereas three stages with six substages and twelve phases are distinguished in the Tethyan realm. The most important abiotic factors that controlled development of conodontophorids are paleotemperature of seawater and paleogeographic settings. Renewals in taxonomic composition conodontophorids and diversification of their assemblages have been confined to moments of paleotemperature and/or sea level rise. The comparative analysis of stages in evolution of conodontophorid and bivalve assemblages has been carried out. As is established, the peak taxonomic diversity of bivalves in Boreal seas was in the Late Triassic after the diversity minimum of the Early Triassic time. In contrast, conodontophorids were most diverse in the Olenekian Age.

DOI: 10.1134/S0869593806020055

Key words: conodontophorids, bivalve mollusks, Triassic, evolution, Russian Arctic, Northwest Pacific.

Triassic period is one of most interesting in Phanerozoic history of marine biotas. Considerable changes in taxonomic composition of many groups of marine fossils depict tendency of their diversification in that period and, concurrently, a higher degree of geographic differentiation of faunas in lower and high latitudes (Dagys et al., 1979; Kurushin, 1998, 2000; Afanas'eva et al., 2004). Conodontophorids were important components of Triassic marine biota. Possessing a high rate of evolution, they left fossil remains weakly dependent in distribution on sedimentary facies that is important in terms of geological practice. It would be incorrect to state that evolutionary transformations of conodontophorids progressed in a steady-state manner beginning from the Late Cambrian to Triassic inclusive, i.e., during more than 300 m.y. In contrast, it is clear that periods of their prosperity and intense diversification (Ordovician, Devonian, Early Carboniferous) alternated with stasis periods of organic development, when diversification rate decreased (Silurian, Permian).

Being inadequately studied, the Triassic period in evolution of conodontophorids is of special interest, because it terminates development of this fauna. According to investigation results obtained in North-eastern Asia, their northern and southern assemblages differed considerably during this interval of geological time (Klets, 2005). Taxonomic composition of conodontophorid communities depended on their development in that or other paleoclimatic zone. In seas of the Northwest Pacific, these organisms have been abun-

dant, diverse, and highly endemic beginning since the Middle Triassic. In Arctic regions of Russia, conodont assemblages of the Middle and Late Triassic are of a low taxonomic diversity (Fig. 1).

On the other hand, bivalve mollusks have been very widespread in Triassic sea basins. In shelf facies, this group of taxonomically diverse benthic organisms is represented by more than 100 genera. Pelagic pseudoplanktonic bivalve mollusks of six genera are known in addition from deposits of pseudoabyssal zone (Kurushin, 1998, 2000). To get a deeper insight into evolution history of Triassic marine biota, stages in evolution of conodontophorid assemblages are compared in this work with development stages of bivalve communities.

The studied assemblages of conodonts and benthic to pelagic bivalve mollusks from Boreal seas (Arctic regions of Russia), as well as conodontophorids from Tethyan seas (Northwest Pacific), reveal three stages in evolution of Triassic marine biota, which correspond respectively to the Early, Middle, and Late Triassic epochs. At the same time, it is established that dissimilar evolutionary trends are characteristic of ecologically different groups of organisms within one biochore, on the one hand, or of one group in different paleoclimatic zones, on the other (Fig. 2). To understand better what factors controlled evolution of conodontophorids, dynamics of their diversification is studied in this work based on conodont assemblages from the Boreal (Russian Arctic) and Tethyan (Northwest Pacific) paleobasins.

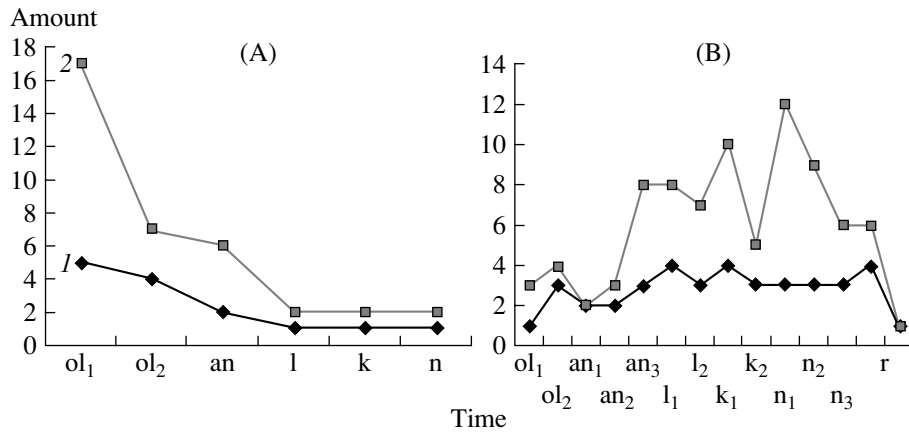


Fig. 1. Diversity dynamics of genera (I) and species (2) of Triassic conodontophorids in Boreal (A) and Tethyan (B) sea basins.

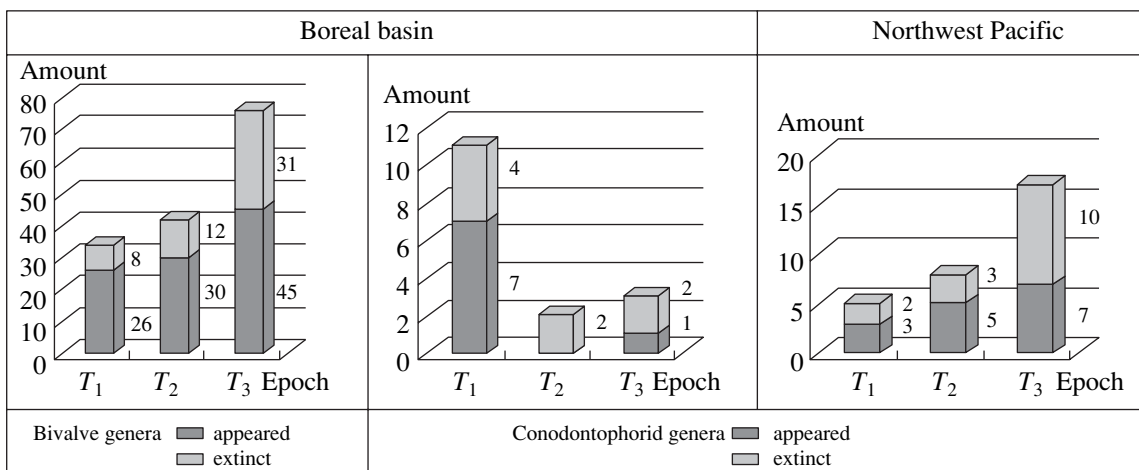


Fig. 2. Amount of bivalve and conodontophorid genera appeared and extinct in the Early, Middle, and Late Triassic epochs.

Materials for this study have been obtained in the course of comprehensive investigation of conodonts in a series of sections examined in the Arctic and Far East regions of Russia (Klets, 1995, 1998, 2000; Klets and Yadrenkin, 2001; Klets and Kopylova, 2005). Comparative data on bivalve mollusks are cited from works by Kurushin (1998, 2000), and the other data used are from several other publications (Igo and Koike, 1983; Dags, 1984; Burii, 1989; Igo, 1989; Bragin, 1991).

INVESTIGATION RESULTS

Early Triassic Stage

Boreal realm

Conodontophorids. Confident finds of Induan conodonts are unknown in Arctic regions of Russia. Their migration into northern seas was concurrent to the eustatic sea-level rise of the early Olenekian time, the maximum one in the Triassic.

Olenekian substage. The most characteristic feature of this substage is the highest taxonomic diversity of conodontophorids as compared to other substages and stages in evolution of marine biota throughout the Triassic period. Seas of this substage have been inhabited by 24 species of 7 genera, dominant *Neospathodus* and *Neogondolella* included (Figs. 3 and 4). The Olenekian substage is divided in two phases. Characteristic of the first *Neospathodus waageni* phase (with subphases *Scythogondolella mosheri*, *Neospathodus bicuspidatus*, and *Scythogondolella milleri*) were 17 species of five genera *Clarkina*, *Neospathodus*, *Scythogondolella*, *Pseudogondolella*, and *Neogondolella*. In the next *Neogondolella jubata* and *Paragondolella paragondolellaeformis* phases of the early Olenekian, number of species decreased sharply down to 7, although amount of genera (4) remained almost the same. Genera *Clarkina*, *Scythogondolella*, and *Pseudogondolella* do not occur at this level that is marked by appearance of genera *Paragondolella* and *Chiosella*.

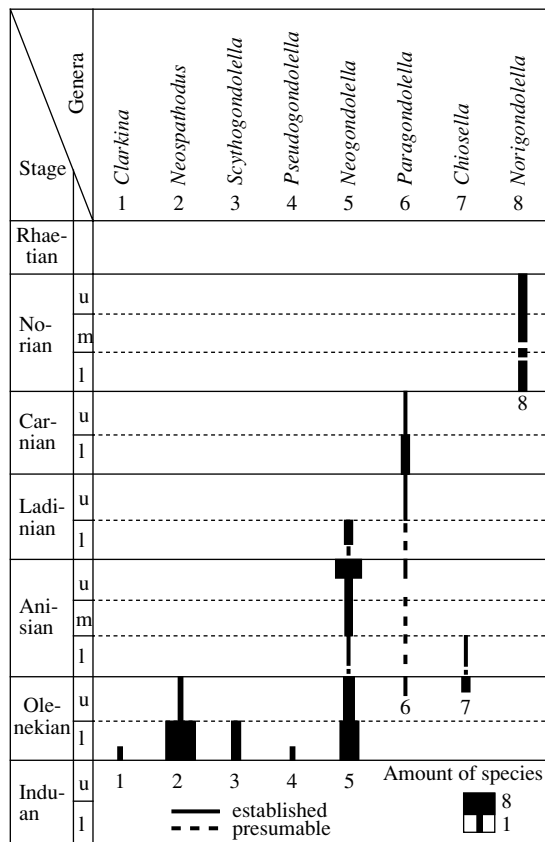


Fig. 3. Diversity dynamics of Triassic conodontophorid genera in Boreal basin: (l) lower, (m) middle, and (u) upper substages.

Bivalve mollusks. In distinction from conodontophorids, Early Triassic bivalves are relatively impoverished in taxonomic aspect: only 33 of 110 Boreal genera known in the Triassic dwelt in early epoch. They belong to 21 families and 16 superfamilies; 26 genera appeared in this time and 8 genera became extinct (Fig. 2). The Early Triassic stage is divisible into the Induan and Olenekian substages (Kurushin, 1998, 2000).

Induan substage is characterized by the minimal taxonomic diversity of bivalves represented by species of 20 genera and 17 families. Dominant among them were myalinids, nuculids, and pachycardiids. The Induan Age is marked by appearance of 15 genera and 7 families. Also characteristic is appearance of first representatives of the Boreal endemic family Streblopteroideidae. The substage includes two phases: 12 genera appeared in the first one (early Induan), while only three genera *Malletia*, *Taimyrodon*, and *Pseudocorbula* appeared in the second phase (late Induan).

Olenekian substage is characterized by 31 genera of 19 families. Two families (Pectiniidae, Chlamydidae) and 12 genera occur at this level for the first time. One family and two genera appeared in the first phase (early

Olenekian). Newcomers of the second phase (late Olenekian) are 10 genera of three families.

Concurrent stages, substages and phases in evolution of conodontophorids and bivalves are well correlative with abiotic events, which took place in Boreal basins of Siberia during the Olenekian Age (Fig. 5). The first conodont phase coincides in time with eustatic sea-level rise that was maximal one in the Triassic, associated with increase of seawater temperature up to 26°–29°C (Kurushin and Zakharov, 1995). Communities of bivalve mollusks were dominated at that time by species of genera *Periboisitria* and *Bakevellia* whose dense numerous populations are buried in deep-water shelf facies of bituminous limestones (Chekanov and Tuor-Yuryakh formations). The high sea-level stand and favorable abiotic factors led to equalization of conodontophorid assemblages and to cosmopolitan dispersal of *Neospathodus waageni*, *Ne. dieneri*, and *Ne. curtus*. The second phase (late Olenekian) corresponded to development of regression and to decrease of seawater temperature down to 24°C (Kurushin and Zakharov, 1995). Only *Neogondolella jubata* was of a broad Boreal–Tethyan distribution. By the phase termination, endemic species appeared in both groups of fossils.

Tethyan realm

Induan conodontophorids are unknown so far from deep-water siliciclastic–cherty deposits in Japan, Sakhalin, and the Far East of Russia.

Olenekian substage. Conodontophorid assemblages of this substage are relatively impoverished in taxonomic aspect: only 3 of 15 known genera and 7 of 51 known species dwelt at this time in basins of the Northwest Pacific (Figs. 6 and 7). The Olenekian substage is divided in two phases concurrent to their counterparts in Boreal province. The first *Neospathodus waageni* phase (early Olenekian) is characterized by three species belonging to one genus *Neospathodus*. The next *Neospathodus homeri*–*Neospathodus triangularis* and *Chiosella timorensis* phases (late Olenekian) are marked by changes in taxonomic composition of assemblages: genus *Neospathodus* is represented now by two species *Ne. homeri* and *Ne. triangularis*. Species *Icriospathodus collinsoni* appears at the beginning of the early phase; *Chiosella timorensis* in the late phase (Fig. 7).

Sea-level rise of the early Olenekian time stimulated migration of species *Neospathodus waageni*, *Ne. dieneri*, and *Ne. curtus* from the Tethys in northern sea basins (Fig. 8). By the end of the late Olenekian phase, endemic genus (*Icriospathodus*) and species (*Ne. homeri*, *Ne. triangularis*) appeared in conodontophorid assemblages.

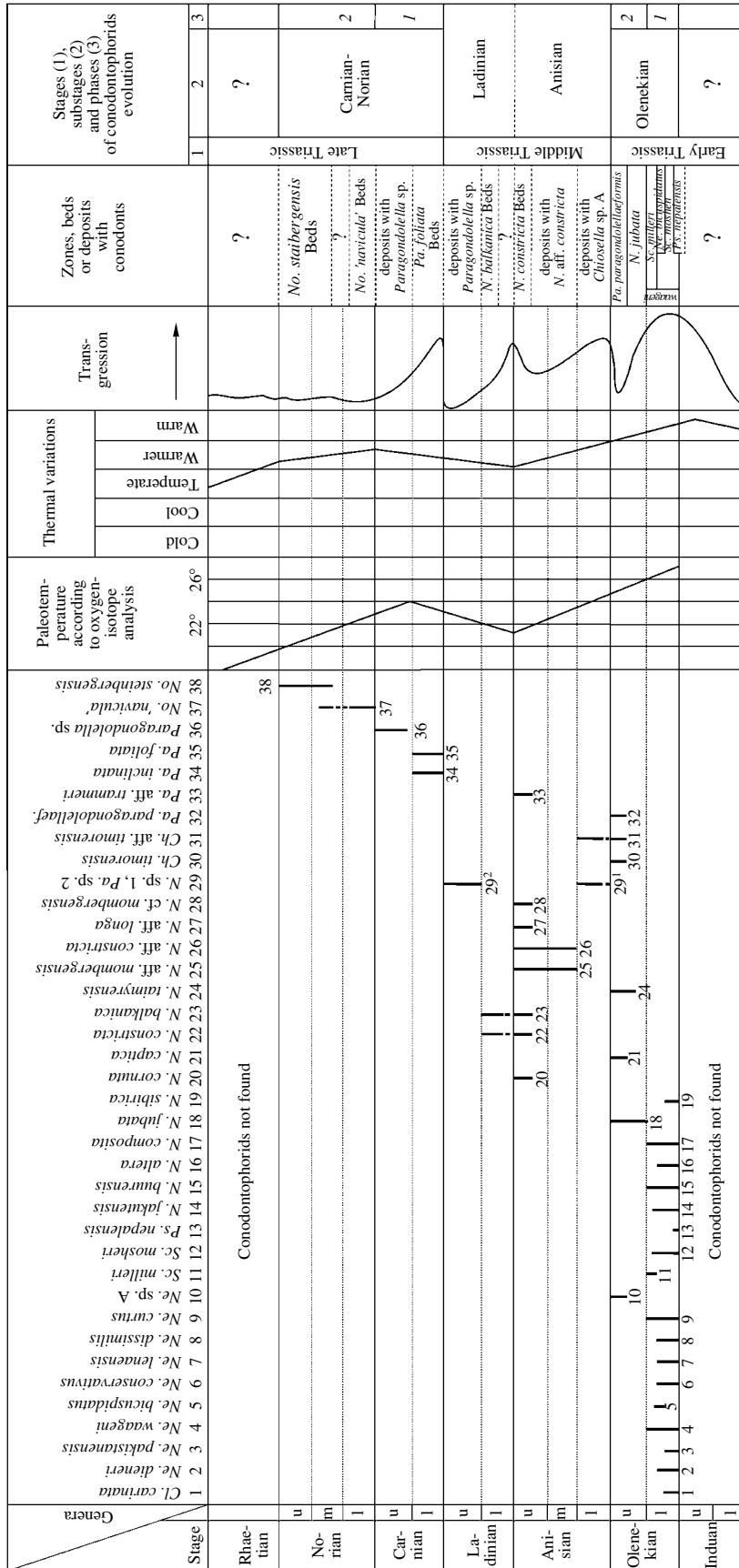


Fig. 4. Stages in evolution of conodontophorids and main events in Boreal basin (after Kurushin and Zakharov, 1995) during the Triassic period (abbreviations as in Fig. 3).

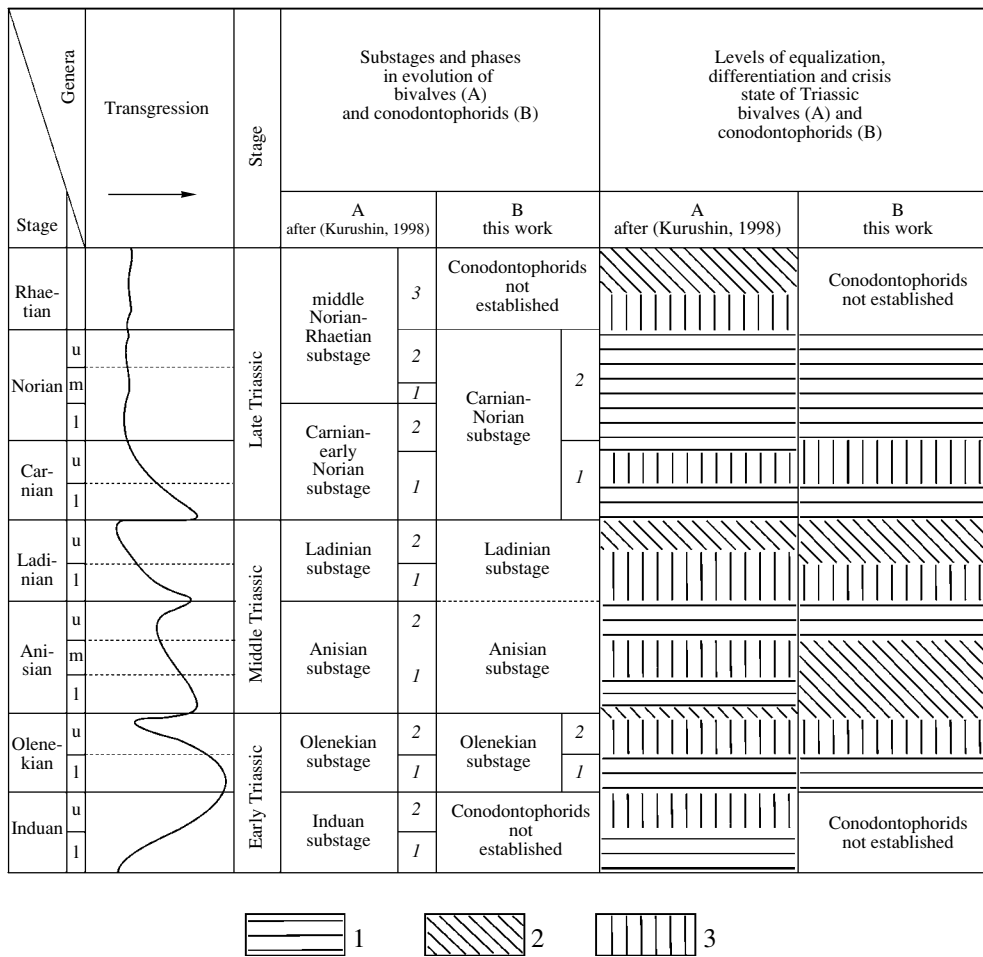


Fig. 5. Evolution of bivalves and conodontophorids, main events in Boreal basin, and datum levels of (1) equalization, (2) differentiation, and (3) crisis state of biota; (1, 2) evolution phases (abbreviations as in Fig. 3).

Middle Triassic Stage

Boreal realm

Conodontophorids. A certain decrease of conodont diversity is characteristic of the stage under consideration, because two genera become extinct and appearance of new genera is not established (Figs. 2 and 3). Three genera *Neogondolella*, *Paragondolella*, and *Chiosella* together with 11 species belonging to them, which are inherited from the Early Triassic and especially characteristic of the Anisian Age, existed at this stage (Figs. 3 and 4). Deposits with *Chiosella* sp. A and *Neogondolella* aff. *constricta*, the *Neogondolella constricta* and *N. balkanica* beds, and deposits with *Paragondolella* sp. have been formed during this stage. By subsequent paleontological and stratigraphic research, the stage can be probably divided in two Anisian and Ladinian substages.

Bivalve mollusks. In distinction from conodontophorids, bivalve mollusks retained tendency to diversify further in taxonomic aspect. Typical of the stage are 17 superfamilies, 29 families, and 54 genera; 30 new genera appeared and 12 genera became extinct

(Fig. 2). Kurushin (1998, 2000) divided the Middle Triassic stage of bivalve evolution into the Anisian and Ladinian substages.

Anisian substage was the existence time of 38 genera and 19 families. Appearing in the substage are 15 genera (*Mytilus*, *Meleagrinnella*, *Daonella*, etc.) and two families (Hiatelliidae, Pleuromyidea). Two phases are distinguishable, and the first one (early-middle Anisian) is characterized by appearance of eight genera and two families. Bivalve assemblages of the first phase are lacking pelagic forms. The second phase (late Anisian) is recognized based on appearance of *Daonella* forms, which migrated from the Tethys into seas of high latitudes. Characteristic of this phase are pelagic posidoniids and a high diversity of genera (32).

Ladinian substage. Known in this substage are 49 genera of 26 families; 15 genera (*Magnolobia*, *Palaeopharas*, *Lima*, *Oxytoma*, etc.) are newcomers. Two phases are recognizable. The first one is marked by appearance of two genera. Benthic bivalve assemblages have been dominated by bakevelliids (*Bakevella*), paleotaxodonts (*Malletia*, *Lapteviella*, *Dacryomya*), pachy-

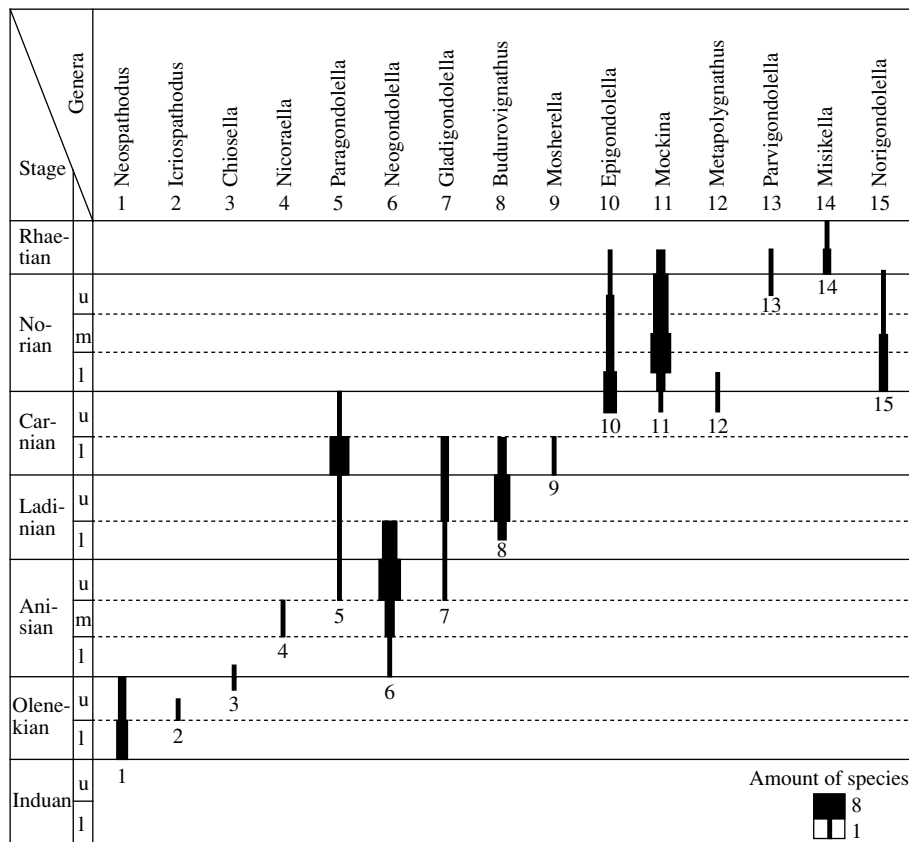


Fig. 6. Diversity dynamics of Triassic conodontophorid genera in Northwest Pacific seas (symbols as in Fig. 3).

cardiids (*Unionites*, *Cardinioides*, *Janaija*), Mytilaceae, Oxytomaceae, and pectinoid forms. Pelagic assemblages have been represented by species of genera *Daonella*, *Magnolobia*, and *Peribositria*. A sharp increase in diversity is characteristic of the second phase, when 13 genera of three families appeared.

Thus, the Middle Triassic stage of diversification of two faunal groups progressed differently in the Boreal basins of Siberia. The diversification rate in bivalve communities was high enough, enabling the stage division in two substages and four phases. Evolutionary changes in conodontophorid communities progressed very slowly, and two substages can be recognized conventionally in this case. Commencement of the Middle Triassic stage has been concurrent to one of the largest transgressions in Boreal seas. The second level of less differentiated bivalve assemblages (second Anisian phase, Fig. 5) is also indicative of a sea-level rise that favored migration of pelagic bivalves from the Tethys (Kurishin, 2000). Conodontophorids, which lost their evolutionary potential in the late Olenekian time, turned out to be unable to restore the former taxonomic diversity in colder Anisian and Ladinian seas, where water temperature dropped down to 16–20°C (Kurushin and Zakharov, 1995). Two long-lived genera *Neogondolella* and *Paragondolella*, which had been inherited from the Early Triassic and represented by a

few species, existed in Boreal seas almost throughout the Middle Triassic epoch. Taxonomic diversification of late Anisian conodont assemblages and appearance of *Neogondolella constricta*, *N. cornuta*, and *N. balkanica* in northern latitudes have been likely interrelated as well with sea-level rise that opened ways for their migration from southern latitudes (Figs. 4 and 5). The crisis state of biota in the terminal Olenekian–initial Anisian (it was longer in conodontophorid than in bivalve communities) and in the terminal Ladinian (this event affected conodontophorids earlier than bivalves) was a consequence of a vast regression and considerable reduction of sea-basin areas (Fig. 5). It was a time of mass extinction in both groups of organisms under consideration.

Tethyan realm

In distinction from the Boreal basin, the Middle Triassic epoch in the Tethyan seas was a time of high diversification rate of conodontophorid assemblages. The seas were populated by 20 species of six conodontophorid genera; three genera became extinct and five genera appeared (Figs. 2 and 6). The stage is divisible in two the Anisian–early Ladinian and late Ladinian substages.

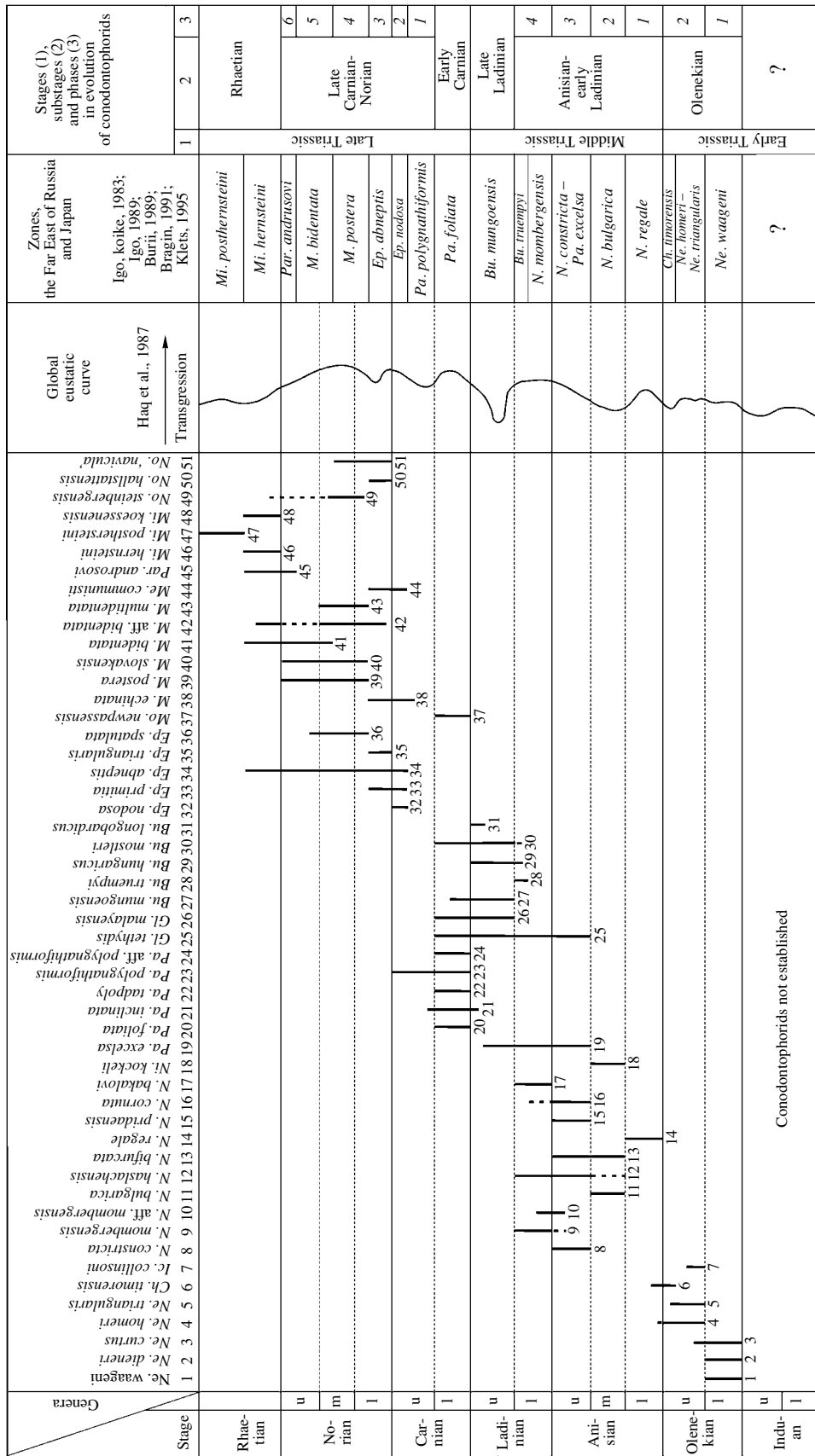


Fig. 7. Stages in evolution of Triassic conodontophorids and sea-level fluctuations in Northwest Pacific seas (1–6) evolution phases; symbols as in Fig. 3).

Stage	Genera	Boreal basin			Northwest Pacific					
		Transgression →	Zones, beds and deposits with conodontophorids	Substages (1) and phases (2) in evolution of conodontophorids		Global eustatic curve	Zones, the Far East of Russia and Japan Igo, Koike, 1983; Igo, 1989; Buri, 1989; Bragin, 1991; Klets, 1995	Substages (1) and phases(2) in evolution of conodontophorids		
				1	2			1	2	
Rhaetian			?	?			<i>Mi. posthernsteini</i>	Rhaetian		
Norian	u		<i>No. steibergensis</i> Beds	Carnian-Norian		Haq et al., 1987 Transgression →	<i>Par. andrusovi</i>	Late Carnian-Norian		
	m	?					<i>M. bidentata</i>			
	l	<i>No. 'navicula'</i> Beds	<i>Ep. abneptis</i>							
Carnian	u		deposits with <i>Paragondolella</i> sp.	1			<i>Ep. nodosa</i>	2		
	l		<i>Pa. foliata</i> Beds			<i>Pa. polygnathiformis</i>	<i>Pa. foliata</i>			Early Carnian
Ladinian	u		deposits with conodontophorids	Ladinian			<i>Bu. mungoensis</i>	Late Ladinian		
			<i>N. balkanica</i> Beds			<i>Bu. truempyi</i>				
	l		?			<i>N. mombergensis</i>	4			
Anisian	u		<i>N. constricta</i> Beds	Anisian			<i>N. constricta</i> – <i>Pa. excelsa</i>	Anisian-early Ladinian		
	m		deposits with <i>N. aff. constricta</i>			<i>N. bulgarica</i>	2			
	l		deposits with conodontophorids			<i>N. regale</i>	1			
Olenekian	u		<i>Pa. paragondolellaeformis</i>	Olenekian			<i>Ch. timorensis</i>	Olenekian		
			<i>N. jubata</i>			2				
	l		<i>Sc. milleri</i> <i>Ne. bicuspidatus</i> <i>Sc. mosheri</i>			1				
			<i>Ps. nepalensis</i>			<i>Ne. waageni</i>	1			
Induan	u		?	?			?	?		
	l					1				

Fig. 8. Datum levels (1) of equalization in Triassic conodontophorid assemblages (abbreviations as in Fig. 3).

Anisian–early Ladinian sibstage. Characteristic of the substage are six genera (*Chiosella*, *Nicoraella*, *Paragondolella*, *Neogondolella*, *Gladigondolella*, *Budurovignathus*) and 14 species; three genera became extinct and five genera appeared (Figs. 2, 6, and 7). The substage can be divided into the early Anisian, middle Anisian, late Anisian, and early Ladinian phases, four in total.

Characteristic of the first *N. regale* phase (early Anisian) were genera *Neogondolella* and *Chiosella*. The latter died out at the beginning of the phase. In the second *N. bulgarica* phase (middle Anisian), genus *Nicoraella* was newcomer, and species diversity of the genus *Neogondolella* was two times greater. The third *N. constricta*–*Pa. excelsa* phase (late Anisian) commenced at the time of sea-level rise (Haq et al., 1987). Neogondolellids whose taxonomic diversity became three times greater dominated at that time in conodon-

tophorid assemblages of the Tethyan sea basins; two genera *Paragondolella* and *Gladigondolella* appeared, and the genus *Nicoraella* died out. The high sea-level stand stimulated migration of *Neogondolella constricta* and *N. cornuta* from the Tethys in northern seas (Fig. 8). The fourth *N. mombergensis*–*Bu. truempyi* phase (early Ladinian) was also characterized by renewals in conodont assemblages. Species *Neogondolella mombergensis* still occurred in assemblages, although general diversity of neogondolellid species was lower. The genus *Budurovignathus* was newcomer of the early Ladinian time, while the long-lived genus *Neogondolella* became extinct by the end of the phase. Neogondolellids, which dominated in conodont assemblages, dwelt most likely in pelagic settings away from coastline, because the high sea-level stand was a characteristic feature of the late Anisian–early Ladinian time.

Late Ladinian substage and corresponding *Bu. mungoensis* phase mark the existence time of seven species belonging to three genera *Budurovignathus*, *Gladigondolella*, and *Paragondolella* (Figs. 6 and 7). Conodont assemblages have been dominated by *Bu. mungoensis*, *Bu. hungaricus*, *Bu. mostleri*, and by *Gladigondolella* species. A quite significant regression of the terminal Ladinian time was likely responsible for extinction of the genus *Neogondolella* that was widespread before (Fig. 7).

Late Triassic Stage

Boreal realm

Conodontophorids. In evolution of conodontophorids, the *Carnian–Norian substage* is terminal one. In Arctic seas of Russia, their taxonomic diversity has been decreasing in general despite some renewals in assemblages: two genera became extinct and only one appeared. Only five species existed at the time of the substage (Figs. 3 and 4). The substage could be divided in two phases. The genus *Paragondolella* still existed in the first phase (Carnian) corresponding to deposition time of the *Paragondolella foliata* Beds, and deposits with *Paragondolella* sp. Species *Pa. foliata* and *Pa. inclinata* appeared at that time. The *Norigondolella* “*navicula*” and *No. steinbergensis* beds accumulated in the second phase (Norian), when genus *Paragondolella* became extinct and genus *Norigondolella* with two species appeared instead.

Deposits with Rhaetian conodonts are unknown at present in Arctic regions of Russia. It is most likely that representatives of conodontophorids died out in Boreal seas during the *Monotis ochotica* phase of the late Norian.

Bivalve mollusks. In contrast to conodontophorids, Late Triassic assemblages of bivalve mollusks are very diverse: in these assemblages, there are known 89 of 110 Triassic genera of Boreal bivalves, which belong to 39 families and 20 superfamilies. In this epoch, 45 genera have appeared and 31 genera became extinct (Fig. 2). The Late Triassic evolutionary stage of bivalves consists of two the Carnian–early Norian and middle Norian–Rhaetian substages (Kurushin, 1998, 2000).

Carnian–early Norian substage was the existence time of 73 genera of 39 families; 31 genera and 9 families have appeared during this substage. Two phases of the substage correspond to the early–late Carnian and latest Carnian–early Norian intervals of geological time. The first phase is marked by invasion of family Halobiidae that resulted in appearance of 17 genera, the genus *Zittelhalobia* included, and six families. During the second phase, the genus *Halobia* migrated from the Tethys, development of the genus *Zittelhalobia* was in progress. Newcomers of this phase are 14 genera and 3 families.

Middle Norian–Rhaetian substage was also the time of high taxonomic diversity in bivalve assemblages (74 genera of 38 families). Bivalves of the substage succeeded the Carnian–early Norian assemblages in general, although 13 genera and one family are newcomers. The substage includes three phases. The first phase has recorded the mass abundance of *Otapiria* forms and origin of five genera. The second phase of the middle (greater part)–late Norian was remarkable because of appearance and prosperity of *Eomonotis* and *Monotis* forms. It was a time, when seven genera appeared, while halobiids died out. One genus appeared in the third phase lacking representatives of the genus *Monotis*.

Consequently, the highest sea-level rise of the initial Late Triassic epoch stimulated synchronous invasion of bivalves and conodontophorids into northern sea basins (Fig. 5). Pelagic mollusks of the family Halobiidae (*Zittelhalobia* and *Halobia* forms) and not numerous conodontophorids of the genus *Norigondolella* migrated using warm currents from the Tethys into Boreal seas. High temperature of seawater (up to 24°C) and climatic warming (Kurushin and Zakharov, 1995) determined a very high diversity of bivalve assemblages, the maximum one in the Triassic (74 of known 110 genera). Despite favorable abiotic factors and innovations, diversity of conodontophorid assemblages was however under decline. Species *Norigondolella* “*navicula*” became extinct, but newcomers *No. steinbergensis* continued evolution of the genus (Fig. 4). Last representatives of this terminal species existed in Boreal seas during the *Monotis ochotica* phase (late Norian). Decreasing areas of sea basins, activation of tectonic processes, and drop of seawater temperature down to 18–20°C caused extinction of many bivalve and all conodontophorid taxa in the terminal Triassic time.

Tethyan realm

A high diversity of Late Triassic conodontophorid genera and species from Tethyan seas differs them from counterparts, which existed in Boreal regions. In the Northwest Pacific areas, there are known 10 of 15 genera and 29 of 50 species of the Late Triassic stage; seven genera are newcomers and ten genera became extinct there (Figs. 2 and 6). The stage includes the early Carnian, late Carnian–Norian, and Rhaetian substages.

Early Carnian substage. In the substage corresponding to the *Paragondolella foliata* phase, there are known four genera and ten species. The essential sea-level rise at the beginning of the Late Triassic has resulted in renewal of conodont assemblages. Species *Paragondolella excelsa* was ancestor of five species *Pa. foliata*, *Pa. inclinata*, *Pa. tadpole*, *Pa. polygnathiformis*, and *Pa. aff. polygnathiformis*, which dominated in pelagic assemblages. Genera *Gladigondolella* and *Budurovignathus* became extinct by the end of the substage. The genus *Mosherella* existed during this evolutionary substage only (Figs. 6 and 7). A high sea-level

stand and favorable temperature of seawater stimulated migration of *Pa. foliata* and *Pa. inclinata* into Arctic seas (Fig. 8).

Late Carnian–Norian substage includes the *Paragondolella polygnathiformis*, *Epigondolella nodosa*, *Ep. abneptis*, *Mockina postera*, *M. bidentata*, and *Parvigondolella andrusovi* phases, six in total. Characteristic of the substage are six genera *Paragondolella*, *Epigondolella*, *Mockina*, *Metapolygnathus*, *Norigondolella*, *Parvigondolella* and 17 species.

The first *Paragondolella polygnathiformis* phase (initial late Carnian) was at the time of insignificant sea-level drop (Haq et al., 1987) that was probably responsible for extinction of genera *Gladigondolella*, *Mosherella*, and *Budurovignathus*. Only species *Paragondolella polygnathiformis* existed later on. The second *E. nodosa* phase (second half of the late Carnian) coincided with development of an insignificant transgression that favored appearance of genera *Epigondolella*, *Metapolygnathus*, and *Mockina*. Conodontophorid assemblages of the third *E. abneptis* phase (earliest Norian) succeeded the previous ones. Epigondolellids *E. abneptis*, *E. triangularis*, and *E. primitia* dominated in sea basins during this phase. In the relevant trend of sea-level rise, there was a minor episode of regression (Haq et al., 1987), and this could mean that most favorable habitat environments for above species were in sea zones adjacent to coastline. Cosmopolitan species of the phase was *No. "navicula"* (Fig. 8). The fourth *M. postera* phase (second half of the early–initial middle Norian) was at the time of the maximum sea-level rise in Tethyan seas, when dominant forms of conodont assemblages were *M. postera*, *M. slovakensis*, *M. multidentata*, and *M. aff. bidentata* associated with rather widespread species of genera *Epigondolella* and *Norigondolella*. The very characteristic late Norian species *M. bidentata* originated at the beginning of the fifth phase (terminal middle–initial late Norian), which coincided in time with a sea-level dropping. Origin of peculiar species *Parvigondolella andrusovi*, the descendant of *M. bidentata*, had been characteristic of the sixth phase, when representatives of the genus *Epigondolella* were much less frequent than in the second and third phases. The general decrease of diversity in conodont assemblages and appearance of species with more simple morphological features took place at the time of a gradual sea-level decline.

Rhaetian substage distinct owing to appearance of characteristic genus *Misikella* whose representatives dominated in conodont assemblages included the *Mi. hernsteini* and *Mi. posthernsteini* phases, when areas of sea basins became considerably reduced. *Norigondolella* forms died out at the beginning of the substage, when conodont assemblages still comprised representatives of genera *Epigondolella*, *Mockina*, and *Parvigondolella*, which were of subordinate signifi-

cance however. The only species *Mi. posthernsteini* was characteristic of the substage terminal time.

CONCLUSION

Results of this work represent a contribution to comprehensive research of marine biota evolution in the Triassic period. Inferences based on comparative analysis of bivalves and conodontophorids, the dissimilar ecologic groups of fossils from different paleoclimatic zones, are as follows:

1. In distinction from Boreal bivalve mollusks whose peak taxonomic diversity is recorded in the Lower Triassic, conodontophorids have been most diverse in the Olenekian Age, when diversity of bivalves was at the minimum.

2. Tropical seas represented most favorable habitat areas of conodontophorids at the terminal stage of their evolution.

3. In Boreal basins, evolution of conodontophorids is divisible into three stages, which consisted probably of four substages and four phases, while three stages with six substages and twelve phases are recognizable in the Tethyan seas.

4. The most important abiotic factors, which controlled evolution of conodontophorids, were paleotemperature of seawater and paleogeographic environments.

5. Renewals of taxonomic composition and diversity peaks of conodont assemblages were confined in Boreal seas to moments of paleotemperature increase and/or sea-level rise, which favored migrations of conodontophorids from the Tethys in northern latitudes.

6. Stratigraphic intervals (reference levels) with relatively equalized taxonomic composition of biota are of particular importance in stratigraphy, as they enhance precision of global Boreal–Tethyan correlations. As for conodontophorids, their assemblages appear to be relatively equalized at several levels (Fig. 8). These are the *waageni* phase of the *early Olenekian*, when *Neospathodus waageni*, *Ne. dieneri*, and *Ne. curtus* had broad geographic range, and the next *constricta* phase of the *late Anisian*, when cosmopolitan behavior was characteristic of *Neogondolella constricta*, *N. cornuta*, and *N. ex gr. mombergensis*. The subsequent *foliata* phase of the *early Carnian* is established based on geographic distribution of *Paragondolella foliata* and *Pa. inclinata*, and the *abneptis* phase of the *early Norian* is remarkable because of *Norigondolella "navicula"* existence in southern and northern seas.

ACKNOWLEDGMENTS

I am grateful to B.N. Shurygin, V.A. Zakharov, and A.V. Kanygin for their valuable advices and comments to this study. The work was supported by the Russian Foundation for Basic Research, project no. 03-05-64737, and granted by Ministry of Education of Russian Federation (grant E02-9.0-20) and by the Integration

Project no. 193 of the Siberian and Far East Divisions of Russian Academy of Sciences.

Reviewers N.Yu. Bragin and A.A. Shevyrev

REFERENCES

1. M. S. Afanas'eva, Yu. V. Agarkov, and E. O. Amon, "Biotic Crises in Evolution of Radiolarians during the Phanerozoic," in *Proceedings of the 50th Session of Paleontological Society* (VSEGEI, St. Petersburg, 2004), pp. 9–11 [in Russian].
2. N. Yu. Bragin, *Radiolarians and Lower Mesozoic Sequences of the Eastern USSR* (Nauka, Moscow, 1991) [in Russian].
3. G. I. Burii, *Conodonts and Triassic Stratigraphy of the Sikhote-Alin* (DVO AN SSSR, Vladivostok, 1989) [in Russian].
4. A. A. Dagys, *Early Triassic Conodonts from the North of Central Siberia* (Nauka, Moscow, 1984) [in Russian].
5. A. S. Dagys, Yu. V. Arkhipov, and Yu. M. Bychkov, *Triassic Stratigraphy of Northeastern Asia* (Nauka, Moscow, 1979) [in Russian].
6. B. U. Haq, J. Hardenbol, and P. R. Vail, "Chronology of Fluctuating Sea Levels Since the Triassic," *Science* **235**, 1156–1167 (1987).
7. H. Igo, "Mixed Conodont Elements from Hachiman Town, Mino Terrane, Central Japan," *Trans. Proc. Palaeontol. Soc. Japan, New Series*, No. 156, 270–285 (1989).
8. H. Igo and T. Koike, "Conodont Biostratigraphy of Cherts in the Japanese Islands," *Trans. Proc. Palaeontol. Soc. Japan, New Series*, No. 36, 65–77 (1983).
9. T. V. Klets, *Triassic Biostratigraphy and Conodonts from the Central Sikhote-Alin* (NGU, Novosibirsk, 1995) [in Russian].
10. T. V. Klets, "New Conodont Species from the Lower Triassic of the Kolyma River Basin," in *News of Paleontology and Stratigraphy* (NITs OIGGM SO RAN, Novosibirsk, 1998), Issue 1, pp. 113–121 [in Russian].
11. T. V. Klets, "Late Triassic Conodonts from Northeastern Asia (Composition, Biostratigraphy, Correlation)," in *Proceedings of the Regional Conference of Geologists from Siberia, the Far East and Northeastern Russia, Vol. 2* (GalaPress, Tomsk, 2000), pp. 328–331 [in Russian].
12. T. V. Klets, "Palaeobiogeographic Zoning of Triassic Seas of Northeastern Asia Based on Conodontophoridae," *Albertiana*, No. 32, 40–50 (2005).
13. T. V. Klets and A. V. Kopylova, "New Triassic Conodontophorids Found in Northeastern Asia," in *News of Paleontology and Stratigraphy* (SO RAN Filial GEO, Novosibirsk, 2005) [in press].
14. T. V. Klets and A. V. Yadrenkin, "Conodonts from the Lower Triassic of the Kotel'nyi Island (Taxonomic Composition, Correlation)," in *News of Paleontology and Stratigraphy* (SO RAN Filial GEO, Novosibirsk, 2001), Issue 4, pp. 14–21 [in Russian].
15. N. I. Kurushin, Extended Abstract of Doctoral Dissertation in Geology and Mineralogy (NITs OIGGM SO RAN, Novosibirsk, 1998).
16. N. I. Kurushin, "Evolutionary Stages of Bivalves in the Boreal Realm," in *Proceedings of the Regional Conference of Geologists from Siberia, the Far East and Northeastern Russia, Vol. 2* (GalaPress, Tomsk, 2000), pp. 325–327 [in Russian].
17. N. I. Kurushin and V. A. Zakharov, "Climate in North Siberia during the Triassic Period," *Byull. Mosk. O-va Ispyt. Prir., Otd. Geol.* **70** (3), 55–60 (1995).