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Late Cenozoic Interactions between the Arctic and Pacific Oceans Inferred from Sublittoral Molluscan Faunas – a Review

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THEME 11: Cenozoic Sedimentary Archives of the Eurasian Marginal Seas: Sampling, Coring and Drilling Programmes

Summary: The analysis of original and published data on the distribution of modern and fossil molluscs in the Late Cenozoic deposits of the North Pacific and Eastern Arctic allowed to trace variations in the composition of fossil assemblages with time and to reconstruct faunistic exchanges between the two oceans. The first exchange between the Pacific and Atlantic molluscs via the Arctic Ocean probably occurred during the Late Miocene. Recent evidence came from southwestern Alaska showing the strait had opened by at least the Late Miocene or earliest Pliocene (4.8-5.5. Ma). Detailed analysis of the Pliocene formations of Kamchatka gives evidence for immigrations of species of the genera *Elliptica* (4 Ma), *Tridonta, Rictocyma, Nicania* and *Cyrtodaria* (3.5 Ma) from the Arctic into the North Pacific. The most abundant migration of Pacific species into the Arctic and North Atlantic occurred during the Late Pliocene. Transgressive marine deposits of this age containing molluscs of Pacific origin have been found in many localities along the Arctic coast from northern Chukotka to the American coast, Greenland, Iceland and even the Pechora Sea. Age determinations of North American and Canadian shells range from 2.7 to 2.14 Ma, thus suggesting the Bering Strait was opened during this period. Abundance of boreal Pacific molluscs throughout the Arctic shelf, together with other paleofaunistic and paleofloristic data, gives evidence for the existence of seasonally ice-free coastal areas. However, no arctic species, in a biogeographical sense, have been found in the late Pliocene Beringian and Ust-Limimtevayam assemblages of the North Pacific. First traces of the arctic cold water species *Portlandia arctica* in the North Pacific were found in the Eopleistocene deposits of Chukotka (Pinakul beds), Kamchatka (Lower Olkhovaya and Tusatuvayam beds), and Alaska (Anvilian and Middletonian beds). All these mainly boreal assemblages display a unique coexistence of arctic cold water and lower boreal warm water species. Presently such a combination is not observed anywhere. The maximum immigration of arctic molluscs into the North Pacific occurred during the Middle Pleistocene, when boreal-arctic and arctic molluscs of atlantic origin (*Yoldiella fraterna, Y. intermedia, Y. lenticula, Bathyarca glacialis*) appeared in this area for the first time. Late Pleistocene regression isolated faunas of the two oceans for a long time and strongly influenced the modern distribution of sublittoral molluscs: recent assemblages of the Pacific are warmer than Pleistocene ones (due to the absence of arctic species), and the modern high Arctic assemblages are the coldest among Pleistocene ones.

INTRODUCTION

The Late Cenozoic marine beds of the coastal regions of the North Pacific and the Eastern Arctic contain abundant fossil molluscan assemblages (Fig. 1). The latter often serve as the basis for stratigraphical subdivision of the coastal sequences (PETROV 1966, 1982;, GLADENKOV 1988, HOPKINS 1967, BRIGHAM 1985). Variations in species composition of the Late Cenozoic fossil molluscan assemblages allow to reconstruct the interactions between the two oceans. These variations depend upon both, environmental changes (depth, temperature, substrate, salinity, existence of seaways connecting different oceans) and biological controls ruling distribution of species within biocoenoses. Molluscs of the Arctic and North Pacific did not undergo any significant evolutionary changes since the Pliocene epoch. Most species inhabiting the present arctic Ocean appeared in the Late Miocene or Pliocene formations of the North Pacific (mainly) and North Atlantic. That is why migrations of index molluscan species, the coldest arctic and the warmest boreal ones, were the most striking events of the Late Cenozoic history of molluscan faunas giving evidence for considerable environmental changes occurring in this vast region.

MATERIAL AND METHODS

This study was based on thorough analysis of both original and published data on distribution of fossil and recent molluscs in the Late Cenozoic deposits of the North Pacific and Eastern Arctic. In order to compare different assemblages we used several approaches. Firstly, the zoogeographical affinity of most species (except the local north american ones) was considered according to the recent data of SKARLATO (1981) on the modern distribution of bivalves in the North-Western Pacific. Hence, the percentage of species of different zoogeographical groups in fossil assemblages was recalculated (Fig. 2). Besides biogeographical characteristics, a kind of paleoecological description was given for fossil assemblages. The latter was based on the correlations between species dwelling at different depths and on different grounds (Tab. 1, Fig. 2).

LATE NEOGENE EPOCH

Prior to the Late Miocene the studied area represented two isolated oceanic basins with warm water masses inhabited by diverse molluscan assemblages. Separation of these faunas started since the Paleogene (KAFANOV 1978). The North Pacific basin, isolated from the Atlantic-Arctic basin by the Beringian land massif, was mainly inhabited by subtropical and lower boreal molluscs. However, such modern species as *Liocyma fluctuosa, Serripes groenlandicus, Mytilus edulis* appeared in the assemblages of Middle Miocene age against the general warm-water

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Species (1)	Zoographical distribution (2)	(3)	(4)	(5)	(6)	Dwelling temperature Skarlato 1981) (7)	Dwelling depth (8)	(9)	(10)	Preferable grounds Petrov 1966, 1982, Skarlato 1981 (11)	Average areal latitude (12)
	Petrov, 1966	Petrov, 1982	Gladenkov, 1980	Skarlato, 1981	Hopkins, 1972		Skarlato, 1981	Petrov, 1966, 1982	Wagner, 1977		
Acila castrensis (Hinds)							el-b				52
Leionucula tenuis tenuis (Montagui)	ab	ab	ab	wab		-1.7-20	sbl-b	to 200	18-60	mud, sand	60
Nuculana pernula pernula (Muller)	ab	ab	ab	wab		-2-10	sbl-el	to 100		mud, mud-gravel	55
Nuculana lamellosa lamellosa (Leche)	a	a		a	a	-2-3	sbl	15-70		mud, mud-sand	72
Nuculana lamellosa radiata (Krause)	ab			ba		-2-10	sbl	20-200		mud	60
Nuculana minuta minuta (Muller)	ab			wba		-2-10	sbl-el			mud, mud-sand	57
Nuculana fossa (Baird)		ub (p)						90-100		mud	57
Megayoldia thraciaeformis (Storer)	b	wb		amb		-1-20	sbl-el	50-200		mud, mud-sand	52
Portlandia arctica arctica (Gray)		a	a	a	a		sbl-el	10-50	20-100	mud	74
Portlandia arctica siliqua (Reeve)	a			a		-2-3	sbl	10-50	6-66	mud, mud-sand	73
Portlandia aestuariorum (Mossewitsch)				a		-2-3	usbl		2-16	mud, sand	73
Yoldia hyperborea (Loven) Torell	ab			wba		-1.7-20	sbl-el	3-660		mud, mud-sand	60
Yoldia myalis (Couthouy)	amb			amb		-1-10	sbl-el			sand, mud-sand	60
Y.(Cnesterium) excavata Dall		lb (p)		lb (p)			sbl-el			sand, mud	45
Yoldiella fraterna Vereill et Bush	a			ab (atl)	a	-2-10	sbl-el	5-500	4-128	mud-sand	65
Yoldiella intermedia (M.Sars)	a	a	a	ab (atl)	a	-2-10	sbl-el	>50	4-6	mud	65
Yoldiella lenticula (Moller)	a	a	a	ab (atl)	a	-2-10	sbl-el	20-200	13-439	mud, mud-sand	65
Crenella decussata decussata (Montagui)	ab	ab		wba		-1.7-20	sbl-b	10-1100		sand, mud-sand	55
Musculus discors (Linne)	ab	ab		wba		-1.7-20	sbl-el	9-200		mud-sand	57
Musculus corrugatus (Stimpson)	ab			ba		-1.7-20	sbl-el	20-265		mud-sand	55
Musculus niger (Gray)	ab	ab	ab	wba		-1.7-20	sbl-el	<40		mud, mud-sand	57
Mytilus edulis Linne	amb	amb	amb	amb		-1-20	l-usbl	to 20		solid	50
Bathyarca glacialis (Gray)	a				a			5-573	38-174	mud, mud-sand with stones	72
Chlamys islandicus (Muller)	ab			b-la		-1.7-20	sbl-el			pebbles	57
Chlamys beringianus (Middendorff)	b	ub		ub (p)		-1-10	sbl-el	40-90		pebbles	58
Chlamys strategus (Dall)	b(p)			b(p)		-1-12		40-140		pebbles, mud-sand	45
Swiftopecten swifti (Bernard)				lb (p)		-1-25	sbl			sand	45
Pododesmus macroshisma (Deshayes)		wb		wb (p)		-1-20	l-el	0-150		pebbles, sand	45
Lyonsia arenosa arenosa (Moller)	ab			ba		-2-10		sbl		different	65
Pandora glacialis (Leach)	a	ab		wba			sbl-el	30-50		mud, sand	60
Elliptica alaskensis alaskensis (Dall)	ab	wb		wb (p)		-1-10	sbl-b	20-200		mud-sand	55
Tridonta borealis borealis Schumacher	ab	ab	ab	ba		-2-10	sbl-el	<100		mud, sand	50
Tridonta borealis placenta (Morch)	a	a		ba (p)	a	-2-10	sbl	<30		mud, mud-sand	70
Tridonta rollandi (Bernard)	b	ub		ub (p)		-1-10	sbl-el	6-90		sand, gravel	55
Tridonta loxia Dall		ub						sbl		sand, gravel	53
Nicania montagui montagui (Dillwyn)	ab	ab	ab	wba		-2-10	sbl-el	<100		sand, mud-sand	60
Nicania montagui fabula (Reeve)		a		a		-2-3		10-40		mud, sand	70
Nicania montagui warhami (Hancock)		a		a		-2-3		20-60		mud, clay	68
Nicania montagui striata Leach		a		a				sbl		mud-sand	70
Astarte esquimalti Baird					b		12-160				55
Hiatella arctica Linne	ab	ab	ab	wba		-2-10	eurybiontic	0-2000		eurybiontic	50
Hiatella pholadis Linne					wba				0-140		about 40
Cyrtodaria kurriana Dunker	a	ab		ba (p)	a	-2-10	sbl	to 50-60	3-19	sand	70

Panomya ampla Dall		wb (p)		wb (p)		-1-12	sbl	0-180		mud	60
Panomya arctica Lamarck		wba		wba			sbl-b	18-240		mud-sand	53
Thyasira gouldi (Philippi)	ab			wba			sbl	2-50		sand, mud	65
Axinopsida orbiculata orbiculata (G.Sars)	ab	ab		wba		-1.7-20	sbl-b	to 50-70	13-296	mud, sand	58
Mysella planata (Dall in Krause)				ba (p)		-0.6-7	sbl-el			mud-sand	58
Cyclocardia crebricostata (Krause)	b	wb		wb (p)		-1-20	sbl-el	40-45		sand, mud-sand	55
Cyclocardia paucicostata (Krause)	hb			lb		8.9-14.2	sbl-el	43-52		Sand, pebbles	58
Cyclocardia ventricosa (Gould)		wb		wb			sbl	to 450		mud, mud-sand	53
C. ventricosa ovata (Rjabininae)		ba (p)		ba (p)			sbl	13-60		mud, mud-sand	62
Crassicardia crassidens (Broderip et Sowerby)	b	wb		wb (p)		-1-20	sbl-el	20-140		gravel, sand	60
Ciliatocardium ciliatum (Fabricius)	ab	ab	ab	wba			sbl-el	30-180		mud, mud-sand	60
Clinocardium californiense (Deshayes)	b	wb		wb (p)		-1-20	sbl-el	2-70		different	52
Clinocardium nuttallii (Concard)				b		-1-20	sbl			different	50
Serripes groenlandicus (Bruguiere)	ab	ab	ab	wba		-2-10	sbl-el	20-130		mud, mud-sand	63
Diplodonta aleutica Dall		ub		ub (p)		-1-10	sbl	12-140		sand, sand-gravel	60
Peronidia lutea (Wood)		wb (p)		wb (p)		-1-18	sbl	5-100		sand, mud-sand	57
Macoma calcarea (Gmelin)	ab	ab	ab	wba		-2-10	sbl-el	2-500	11-117	mud-sand	55
Macoma balthica (Linne)	amb	wb		amb		-1-20	l-usbl	l-usbl		mud-sand	50
Macoma incongrua (Martens)	b	ub		st-lb			l-usbl	l-usbl		mud, sand	45
Macoma middendorffii Dall		wb (p)		wb (p)		-1-12	sbl	16-59		mud-sand, sand	55
Macoma lama lama Bartsch				wb (p)		-1-10	sbl			sand, mud-sand	58
Macoma moesta (Deshayes)	a	ab		wba		-2-10	sbl-el	30-80		mud, mud-sand	55
Macoma brota Dall	b	ub		ub (p)				20-100		mud, sand	60
Liocyma fluctuosa (Gould)	ab	ab		wba			sbl-el	to 50	7-45	mud-sand	57
Protothaca staminea (Conrad)	b			wb (p)		-1-10		l-usbl		sand-gravel	48
Callithaca adamsi (Reeve)	lb	lb		lb (p)		-1-25	usbl	to 25		mud-sand	45
Siliqua alta (Broderip et Sowerby)	b	wb (p)		wb (p)		-1-20	usbl	12-30		sand, pebbles	60
Spisula (Mactromeris) voyi (Gabb)		wb (p)		wb (p)		-1-20	sbl	8-70		sand, gravel	58
Mya (Mya) truncata Linne	ab	ab	ab	wba		-1.7-20	sbl-el	sbl-el		mud, mud-sand	58
Mya (Mya) pseudoarenaria Schlesch	ab			ba		-1.7-20	l-sbl	l-sbl		mud-sand	60
Mya (Mya) priapus Tiesius		wb		wb		-1-20	l-usbl	l-usbl		gravel, pebbles, mud-sand	55
Mya (Arenomya) arenaria Linne	amb							l-usbl		mud, mud-sand	50
Mya (Arenomya) japonica Jay		wb		wb		-1-20	l-usbl	l-usbl		mud-sand	50
Mya (Arenomya) elegans (Eichwald)		ub		ub (p)		-1-10	usbl	usbl		solid	55
Zirphaea crispata (Linne)		wb	b	amb		-1-20	l-usbl	to 7		soft	50
Penitella penita (Conrad)				wb (p)		-1-20	sbl			soft	45

Tab. 1: Zoogeographical and ecological characteristics of bivalve molluscs according to different authors.
Zoogeographical characteristics: a – arctic; ab – arctic-boreal; ba – boreal-arctic; wba – widely spread boreal-arctic; ab (atl) – arctic-boreal of Atlantic origin; b – boreal; ub – upper boreal; lb – lower boreal; wb – widely spread boreal; amb – amphiboreal; (p) – of Pacific origin; st-lb – subtropical-lower boreal.
Ecological characteristics: l – littoral; usbl – upper sublittoral (down to 10-15 m); sbl – sublittoral (down to 50-70 m); el – elittoral (down to 200 m); b – bathyal (>200 m).

zoogeographical background (Tab. 2). Now these species are referred to as widely distributed boreal and boreal-arctic ones (Tab. 1). These belong to the most ancient bivalves inhabiting the North Pacific at present. The Arctic Ocean during this epoch represented a kind of the high latitudinal bay of the Atlantic Ocean (Kafanov 1979; Hopkins 1967, Danilov 1985). The deep sea fauna of the Arctic Ocean consisted of species common to the Atlantic Ocean. Even now the deep-sea fauna, unlike the sublittoral one, has practically no species of Pacific origin (Gur'yanova 1970) thus indicating the general "shallow" character of the interaction between the two oceans. The sublittoral fauna of the Miocene deposits of northern Alaska and Arctic Canada included only species of Atlantic origin and endemic species (Marincovich et al. 1990).

The Late Miocene deposits of Kamchatka and Sakhalin include such recent widely spread boreal and boreal-arctic species as *Macoma calcarea, Ciliatocardium ciliatum, Leionucula tenuis,*

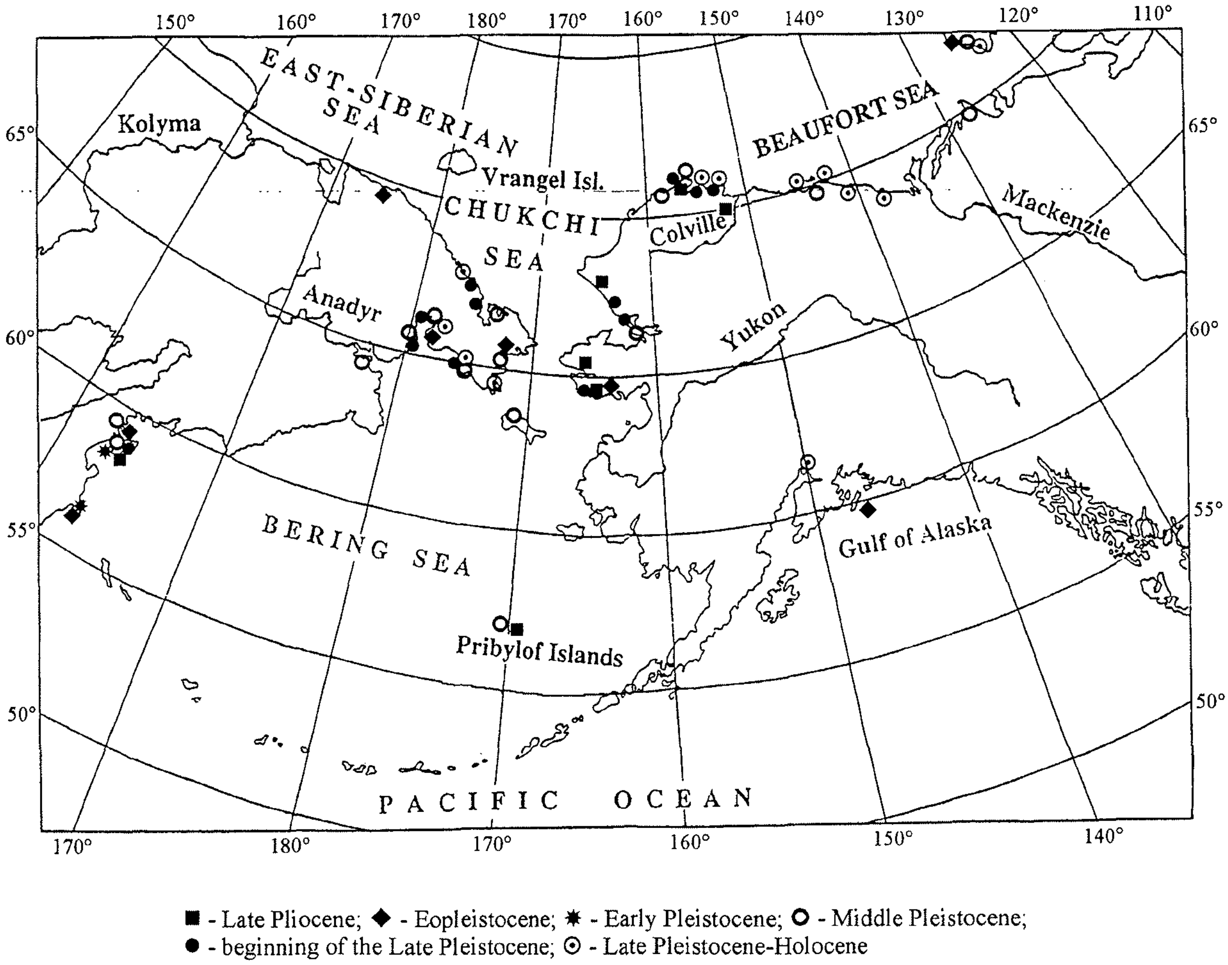

Fig. 1: Distribution of Late Cenozoic marine deposits and fossil molluscan assemblages

Megayoldia thraciaeformis, Pododesmus macroshisma, Cyclocardia crebricostata (Tab. 2). There exists a point of view (KAFANOV 1974, 1978, 1981) that the biogeographical affinity of some of the "old" species, namely the boreal-arctic ones, was gradually changing during the geological history, since the first stages of their existence coincided with environmental conditions considerably different from present ones. Most data on climatic conditions of the North Pacific during the Miocene (GLADENKOV & SINEL'NIKOVA 1990) suggest them to be rather warm, mainly corresponding to the modern lower boreal biogeographic area (SKARLATO 1981). Probably, these young eurybiontic species, unlike old subtropical and lower boreal ones which became extinct in northern regions in the course of cooling, were in the stage of widening their ecological niche, since they were able to adapt to decreasing temperatures, as has been experimentally proven by ZHIRMUNSKII (1974). General cooling favoured decreasing of the lower boundary of temperature tolerance. Extinction or partial migration of "evolutionary adult" subtropical and lower boreal species to the south during the Late Miocene resulted in the destruction of existing biocoenotic links and appearance of new ecological niches for newly formed species. For instance, the modern subtropical to lower boreal species *Chlamys farreri nipponensis* was reported from the Middle Miocene beds of Chukotka, and the Pliocene beds of Kamchatka and Sakhalin, being now restricted to the Peter the Great Gulf. Free niches were occupied by young progressive species from southern regions which were ready for further northward migrations to the Arctic basin.

The Late Miocene was a period of considerable cooling and tectonic activity. The openning of the Bering Strait may have occurred during this period. POLYAKOVA (1997) recognized Miocene diatoms of Pacific origin in the Late Miocene beds of the northern Chukchi lowlands and the Kolyma River basin. Though practically nothing is known about the Late Miocene molluscs of the Arctic ocean, it is believed that the first exchange between the Pacific (*Mytilus edulis, Macoma calcarea*) and Atlantic molluscs via the Arctic Ocean occurred during this epoch. The Late Miocene and Early Pliocene deposits of Iceland (*Tapes* and *Mactra* zones), The Netherlands, England contain the first immigrants from the Pacific belonging to *Mya, Mytilus, Zirphaea, Modiolus, Placopecten* genera (DURHAM & MACNEIL 1967, KAFANOV 1979, GLADENKOV et al. 1980). Detailed analysis of the Pliocene formations of Kamchatka gives evidence for immigrations of the species of *Elliptica* (4 Ma), and *Tridonta, Rictocyma, Nicania, Cyrtodaria* genera (3.5 Ma) into the North Pacific from the Arctic (BARINOV 1994). The findings of *Astarte* shells in the southwestern Alaska (the Bear Lake Formation) were recently dated from microfossils of diatoms found in the same sediment layer (MARINKOVICH & GLADENKOV

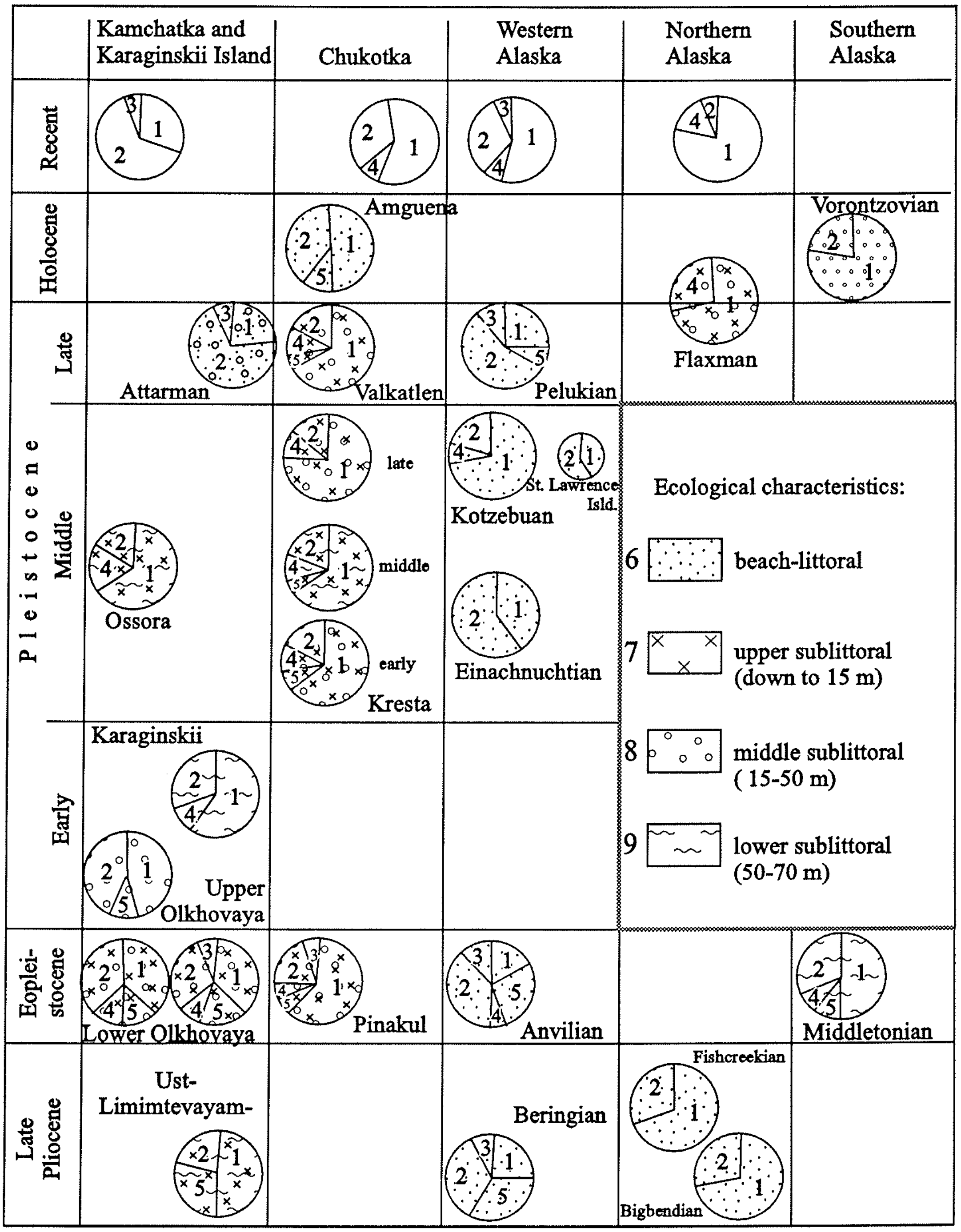

Fig. 2: Biogeographical composition (1-5) and ecological characteristics (6-9) of fossil and recent bivalve assemblages. (1) boreal-arctic species; (2) boreal species; (3) lower boreal species (among boreal ones); (4) arctic species; (5) extinct species; (6) beach littoral; (7) upper sublitoral (down to 15 m); (8) middle sublittoral (15-50 m); (9) lower sublittoral (50-70 m).

1999). Marine diatoms are correlative with the subzone b of the *Neodenticula kamtschatica* zone of the North Pacific diatom biochronology, yielding an age range of 4.8-5.5 Ma. Hence, molluscan and diatom evidence proves the first opening of the Bering Strait to occur somewhere around the Miocene-Pliocene boundary.

The most abundant migration of the Pacific species into the Arctic and North Atlantic occurred during the Late Pliocene. Transgressive marine deposits of this age containing molluscs of Pacific origin have been found in many localities along the Arctic coast (Fig. 1): Enmakai deposits of northern Chukotka; Colvillian, Bigbendian and Fishcreekian deposits of northern Alaska; deposits of the Beaufort Formation on Meighen Island; marine deposits at White Point, Ellesmere Island; marine Pliocene units along the northeastern coast of Baffin Island; Kap Kobenhavn Formation of northern Greenland (Danilov & Polyakova 1989, Brigham-Grette & Carter 1992). Pacific

Species (1)	Miocene of Pacific (2)	Late Pliocene				Eopleistocene						Early Pleistocene		Middle Pleistocene						Late Pleistocene					
		Ust-Limimtevayam (3)	Beringian (4)	Bigbendian (5)	Fishcreekian (6)	Breidavik(Iceland) (7)	Lower Olkhovaya (8)	Tusatuvayam (9)	Pinakul (10)	Anvilian (11)	Middletonian (12)	Upper Olkhovaya (13)	Karaginskii (14)	Ossora (15)	Lower Kresta (16)	Middle Kresta (17)	Upper Kresta (18)	Einachnuchtian (19)	Kotzebuan (20)	Attarman (21)	Valkatlen (22)	Pelukian (23)	Flaxman (24)	Amguema (25)	Vorontzovian (26)
Acila castrensis (Hinds)			+																						
Leionucula tenuis tenuis (Montagui)		+				+	+		+				+		+						+				
Nuculana pernula pernula (Muller)		+				+					+		+	+		+									
Nuculana lamellosa lamellosa (Leche)							+						+			+			+						
Nuculana lamellosa radiata (Krause)					+														+						
Nuculana minuta minuta (Muller)					+				+			+	+						+						
Nuculana fossa (Baird)							+																		+
Megayoldia thraciaeformis (Storer)	+						+																		
Portlandia arctica arctica (Gray)						+	+		+		+		+	+	+	+	+		+		+			+	
Portlandia arctica siliqua (Reeve)									+	+					+	+	+				+				
Portlandia aestuariorum (Mossewitsch)																	+								
Yoldia hyperborea (Loven) Torell		+							+									+							
Yoldia myalis (Couthouy)					+														+		+				
Yoldia (Cnesterium) excavata Dall							+																		
Yoldia (Cnesterium) toporoki Scarlato							+																		
Yoldia (Cnesterium) seminuda Dall		+																							
Yoldiella fraterna Vereill et Bush																+	+								
Yoldiella intermedia (M.Sars)														+		+	+		+						
Yoldiella lenticula (Moller)						+								+		+									
Crenella decussata decussata (Montagui)												+				+			+						
Crenella nomeana (MacNeil) Extinct			+																						
Musculus discors (Linné)							+		+																
Musculus corrugatus (Stimpson)									+						+										
Musculus niger (Gray)		+				+	+	+	+				+	+											
Mytilus edulis Linné	+	+	+			+	+		+	+		+						+	+	+	+	+		+	
Mytilus edulis declivis Petrov ssp.nov. Extinct							+	+																	
Bathyarca glacialis (Gray)																+									
Chlamys islandicus (Muller)										+	+														
Chlamys beringianus (Middendorff)												+													
Chlamys strategus (Dall)									+																
Chlamys hindsi (Carpenter)				+ ?					+ ?																
Chlamys lioicus (Dall) Extinct									+																
Fortipecten hallae (Dall) Extinct		+	+																						
Swiftopecten swifti (Bernard)			+																						
Pododesmus macroshisma (Deshayes)	+		+					+		+			+					+		+		+			
Lyonsia arenosa arenosa (Moller)									+									+							
Pandora glacialis (Leach)							+		+												+				
Elliptica alaskensis alaskensis (Dall)								+	+		+				+	+		+	+		+			+	
Astarte (Elliptica) invocata Merklin et Petrov Extinct									+						+	+					+				
Tridonta borealis borealis Schumacher		+			+		+	+	+			+	+	+	+	+	+		+		+	+	+	+	
Tridonta borealis placenta (Morch)						+	+		+					+	+	+	+				+				
Tridonta rollandi (Bernard)							+				+	+								+					
Tridonta olchovica Petrov sp.nov. Extinct							+																		
Tridonta loxia Dall		+						+																	
Nicania montagui montagui (Dillwyn)						+		+	+		+		+	+		+					+			+	
Nicania montagui fabula (Reeve)							+	+		+								+							
Nicania montagui warhami (Hancock)							+	+																	
Nicania montagui striata Leach							+	+						+											
Astarte esquimalti Baird					+																				
Astarte actis Dall Extinct		+								+															
Astarte diversa Extinct		+	+							+															
Astarte hemicymata Dall Extinct		+	+							+															
Astarte leffingwelli Dall Extinct			+							+															
Astarte nortonensis MacNeil Extinct		+	+							+															
Hiatella arctica Linné	+	+	+	+	+	+	+	+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+
Hiatella pholadis Linné										+	+								+						
Cyrtodaria kurriana Dunker		+		+	+		+	+							+	+	+		+	+	+		+		
Panomya ampla Dall	+	+	+							+	+									+		+			
Panomya arctica Lamarck	+	+					+																		
Thyasira gouldi (Philippi)												+			+										
Axinopsida orbiculata orbiculata (G.Sars)				+	+		+												+		+				

Mysella planata (Dall in Krause)																		+							
Cyclocardia crebricostata (Krause)	+		+		+		+	+	+	+	+		+		+	+	+	+	+	+		+			
Cyclocardia crebricostata nomensis MacNeil Extinct			+																						
Cyclocardia paucicostata (Krause)									+						+	+	+		+						
Cyclocardia ventricosa (Gould)												+													
C. ventricosa ovata (Rjabininae)							+							+											
Crassicardia crassidens (Broderip et Sowerby)		+	+		+			+		+				+		+									
Crassicardia subcrassidens MacNeil Extinct			+							+															
Ciliatocardium ciliatum (Fabricius)	+	+			+	+	+		+		+				+	+			+			+			
Ciliatocardium olchovensis Petrov, sp.nov. Extinct							+																		
Clinocardium californiense (Deshayes)		+	+		+				+	+									+	+		+			
Clinocardium subcostalis Petrov, sp.nov. Extinct		+						+																	
Clinocardium nuttallii (Concard)	+																					+			
Serripes groenlandicus (Bruguiere)	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+		
Diplodonta aleutica Dall								+										+							
Peronidia lutea (Wood)	+					+	+	+		+		+	+							+		+			
Macoma calcarea (Gmelin)	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+
Macoma balthica (Linné)	?				+										+	+	+		+	+	+			+	
Macoma incongrua (Martens)									+	+												+			
Macoma middendorffii Dall										+									+	+		+			
Macoma lama lama Bartsch																			+						
Macoma moesta (Deshayes)	+	+					+	+					+						+						
Macoma brota Dall		+			+				+				+							+					
Liocyma fluctuosa (Gould)	+		+		+				+						+	+	+	+	+		+				
Protothaca staminea (Conrad)	+								+													+			
Callithaca adamsi (Reeve)																				+		+			
Siliqua alta (Broderip et Sowerby)			+				+			+			+		+					+		+			
Spisula (Mactromeris) voyi (Gabb)	+			+				+		+		+						+		+		+			
Spisula polynyma (Stimpson) Extinct																			+						
Mya (Mya) truncata Linné	+	+	+		+	+		+	+	+	+	+			+	+	+	+	+	+	+				
Mya truncata olchovica Petrov ssp.nov. Extinct							+																		
Mya (Mya) pseudoarenaria Schlesch	+	+					+		+			+			+	+	+				+	+		+	+
Mya (Mya) priapus Tiesius	+						+						+						+	+					
Mya (Arenomya) arenaria Linné			+						+																
Mya (Arenomya) japonica Jay	?		+					+		+									+	+		+			
Mya (Arenomya) elegans (Eichwald)	+						+					+							+	+					
Zirphaea crispata (Linné)																				+					
Penitella penita (Conrad)	+									+									+						

Tab. 2: Distribution of bivalve molluscs in the Late Cenozoic deposits of the North Pacific and adjacent Arctic regions.

species were also reported from the deposits of the *Serripes* zone, northern Iceland (GLADENKOV 1978), and even from the Kolva beds of the Pechora Sea coast (ZARKHIDZE 1983). Age determinations of North American and Canadian shells range from 2.7 to 2.14 Ma, thus suggesting prolonged existence of the Bering Strait. Abundance of boreal Pacific molluscs throughout the Arctic shelf (together with other paleofaunistic and paleofloristic data, such as the data on ostracodes, marine mammals, palynological evidence, etc.) gives evidence for the existence of seasonally ice-free coastal areas. However, no arctic species, in a biogeographical sense, have been found in the Late Pliocene Beringian and Ust-Limimtevayam assemblages of the North Pacific. Most authors studying the Late Pliocene migrations of molluscs considered biological reasons (greater taxonomic diversity of the Pacific) to be the ruling factor of the migrations. Species that invaded the Arctic Ocean in the Late Pliocene predominated in the lower boreal assemblages of Kamchatka of Early Pliocene age and upper boreal ones of Kamchatka and Alaska of Late Pliocene age. After penetrating into the Arctic Ocean they became boreal-arctic, i.e. gained their modern zoogeographical affinity (Tab. 1).

PLEISTOCENE EPOCH

By the beginning of the Eopleistocene the modern biogeographical structure of the bivalve fauna of the North Pacific area had been practically formed (Tab. 3). Later, no considerable northward migrations of Pacific molluscs into the Arctic Ocean were recorded. Probably, most of the free ecological niches had already been occupied, and sustainable biocoenoses were formed in the Arctic Ocean. In these biocoenoses new arctic species and subspecies evolved due to gradual cooling (subspecies of *Portlandia arctica, Nicania montagui, Nuculana lamellosa)*. This process has been going on during the whole Pleistocene until recently. FILATOVA (1957) wrote that most newly formed arctic subspecies and morphs of different marine organisms were recorded in the boundary Chukchi and Barents Seas. It seems that rather the evolutionary young species are subjected to these changes, since the oldest ones (like *Liocyma fluctuosa, Serripes groenlandicus, Macoma calcarea*) have never formed arctic subspecies. Migrations of the Arctic fauna during coolings were the most striking events of the Pleistocene history of *Bivalvia* of the North Pacific.

First traces of the cold water arctic species *Portlandia arctica* in the North Pacific were found in the Eopleistocene deposits of Chukotka (Pinakul beds), Kamchatka (Lower Olkhovaya and Tusatuvayam beds), and Alaska (Anvilian and Middletonian beds). It should be mentioned that recent investigations introduced several changes in age determinations of these deposits. According to aminoacid and paleomagnetic evidence the Anvilian deposits are now considered to be of Middle Pleistocene age (about 0.5 Ma) (Kaufmann & Brigham-Grette 1993). On the other hand, the Tusatuvayam beds are now dated as Late Pliocene (DETAL'NOE 1992). However, there are a lot of similarities in the composition of molluscan assemblages of the above mentioned deposits. Firstly, the percentage of extinct species is rather high (Fig. 2) being the greatest in the Anvilian assemblage (29 %). Secondly, they all contain Arctic immigrants (up to 12 % in the Tusatuvayam assemblage, Fig. 2, Tab. 2). And finally, all these mainly boreal assemblages display a unique coexistence of cold water arctic species and warm water lower boreal ones (Tab. 2). Presently such a combination is never observed, neither in the North Pacific nor in the Arctic seas: no subtropical or lower boreal species are found together with arctic ones. Since these assemblages do not resemble any modern molluscan community, paleogeographical reconstructions seem to be rather conventional. It might be supposed that there existed cold bottom waters along with well heated shallow coastal areas which were seasonally ice covered.

The Upper Olkhovaya deposits of Kamchatka, which are probably of Early Pleistocene age contain a typical boreal molluscan assemblage with upper boreal species *Tridonta rollandi, Mya elegans, Nuculana minuta angusticauda, N. sachalinica* being dominant (PETROV 1982). The warm water character of this assemblage, the absence of Arctic immigrants, and the predominance of local "Asian" species give evidence for the absence of the Bering Strait and, hence, relative warming of the coastal waters near Kamchatka (Tabs. 2, 3).

The next appearance of arctic molluscs in the Bering Sea occurred during the second half of the Early Pleistocene (Karaginskii beds) (PETROV 1982, Tabs. 2, 3). This fossil as-

AGE	Ma	DEPOSITS: Chukotka	DEPOSITS: Eastern Kamchatka	DEPOSITS: Karaginskii Island	DEPOSITS: W. and S. Alaska	DEPOSITS: Northern Alaska	FOSSIL MOLLUSCAN ASSEMBLAGES	PHASES IN FORMATION OF THE BIOGEOGRAPHICAL STRUCTURE OF *BIVALVIA*	PALEOGEOGRAPHICAL SITUATION
PLEISTOCENE – HOLOCENE		Amguema			Vorontzovian		Late Pleistocene (northward migration of thermphilic species at the beginning of the epoch, impoverishment and differentiation of the Pacific and Arctic assemblages)	Late Pleistocene – Holocene (gradual formation of the modern patterns in distribution of molluscs)	Intercaltion of transgressive and regressive epochs against the background of maximum cooling observed 18-20 Ka
PLEISTOCENE – LATE	0.01	Valkatlen	Attarman	Attarman	Pelukian	Pelukian			considerable warming of waters
PLEISTOCENE – MIDDLE	0.125	Kresta	Ossora		Kotzebuan; Einachnuchtian	Wainwrightian	Middle Pleistocene (abundance of arctic species, first penetration of the arctic and boreal –arctic species of Atlantic origin)		Cooling of the Bering Sea water, openning of the Bering Strait for a long period, equalizing of water temperatures in the N. Pacific and E. Arctic, tundra and forest tundra on the coasts
PLEISTOCENE – EARLY	0.48			Karaginskii			Karaginskii (quantitative predominance of arctic forms)	Eopleistocene – Late Pleistocene (gradual disappearnce of extinct species, predominance of boreal-arctic assemblages, dispersal of arctic species in the Bering Sea)	Transgression, cooling of coastal waters near Kamchatka
		Pinakul	Upper Olkhovaya	Tusatuvayam	Anvilian		Upper Olkhovaya (absence of arctic species)		Regression, warming of coastal waters near Kamchatka
EOPLEISTOCENE	0.70		Lower Olkhovaya		Middletonian		Eopleistocene (rare extinct species, first apprearance of arctic species, co-existence of "opposite" species – arctic and lower boreal ones		General cooling of waters against the background of increasing contrasts (cold bottom waters and warm shallow ones), modern like vegetation
LATE PLIOCENE	1.80				Beringian	Fishcreekian	Late Pliocene (presence of extinct species, the farthest northward migration of thermophilic species)	Late Pliocene (formation of the boreal-arctic group of species, predominance of boreal assemblages)	Equalisation of water temperatures in the N. Pacific and E. Arctic, seasonal ice cover, predominance of forests on the coasts
						Bigbendian			
	3.50			Ust-Limimtevayam		Colvillian			

Tab. 3: The Late Cenozoic deposits and fossil molluscan assemblages of the North Pacific and Eastern Arctic.

semblage is a typical assemblage of cold-resistant ground feeders (*Nuculana, Portlandia, Macoma*) characterizing relatively deep-water environments (neglectable amounts of shallow-water species and a high percentage of arctic ones) (Tabs. 1-3, Fig. 2).

The maximum dispersal of arctic molluscs in the North Pacific was observed during the transgression of Middle Pleistocene age (Kresta, Ossora, Kotzebuan beds) (Fig. 1, Tab. 2). Besides Arctic species that had immigrated into the Bering Sea during previous epochs, boreal-arctic and arctic molluscs of the Atlantic origin (*Yoldiella fraterna, Y. intermedia, Y. lenticula, Bathyarca glacialis*) appeared in these assemblages for the first time (Tabs. 1, 2). The latter had probably originated in the near-Atlantic sector of the Arctic Ocean. Later they gradually inhabited the Arctic shelves, and reached the Chukchi Sea by the Middle Pleistocene. Like other representatives of the Protobranchia order, all these species are ground feeders dwelling on soft muddy grounds. Their appearance in the Bering Sea allows to assume the long lasting existence of the Bering Strait and the spreading of fine grounds due to ice cover. This was the last considerable dispersal of the arctic species recorded in coastal deposits of the Bering Sea and provides evidence for a considerable climatic cooling.

During the glacioeustatic transgression of the beginning of the Late Pleistocene, several thermophilic lower boreal and subtropic-lower boreal species (*Callithaca adamsi, Macoma incongrua*) migrated far northward compared to their modern limit (Petrov 1982, Hamilton & Brigham-Grette 1991, Brigham-Grette & Hopkins 1995) (Tabs. 1-3). Planktonic larvae of these species were probably brought northward by the strong warm current flowing from Kamchatka to Alaska. Arctic species are absent in deposits of this age in Alaska and Kamchatka (Attarman and Pelukian). However, the Valkatlen assemblage of Chukotka includes arctic species, while thermophilic boreal species are absent in it. Probably, the system of currents did not favour their spreading into this region.

The Late Pleistocene regression isolated faunas of the two oceans for a long time and strongly influenced the modern distribution of sublittoral molluscs. The closing of the Bering Strait and the appearance of a vast land massif with periglacial tundra landscapes terminated for a long time the interaction between arctic and boreal species which had actually existed during the whole Pleistocene. Arctic assemblages seem to become more "closed" and cold-resistant during the coldest glaciation. Since this time arctic species have practically not crossed the Bering Strait; only rare *Portlandia* are found now in the Anadyr Bay and Norton Sound. At the same time, boreal species are practically absent in the eastern Arctic Ocean. Only rare boreal molluscs are found now near Cape Barrow (MacGinitie 1959; Skarlato 1981). Even during the Middle Pleistocene, arctic species co-existed in all fossil assemblages of the Arctic coasts with such boreal species as *Mytilus edulis, Macoma balthica, Cyclocardia crebricostata* (Troitskii 1979). Post-glacial transgression has not considerably influenced the distribution of molluscs that was formed during the regression. Recent assemblages of the Pacific are warmer than Pleistocene ones due to the absence of arctic species, and the modern high Arctic assemblages are the coldest among the Pleistocene ones.

CONCLUSIONS

The following groups of fossil assemblages with different biogeographical and ecological composition were established in the studied area:
- Late Pliocene: abundant extinct species comprising up to 30 % of the total composition, predominance of boreal species;
- Eopleistocene: first appearance of arctic species in the North Pacific, simultaneous co-existence of arctic and lower boreal species;
- Early Pleistocene: transitional without any "typical" features;
- Middle Pleistocene: predominance of boreal-arctic species, abundance of arctic species, first appearance of immigrants of Atlantic origin;
- Late Pleistocene: warm water boreal assemblages in the beginning and
- Late Pleistocene-beginning of Holocene: impoverished assemblages.

The main interactions between molluscs of both oceans occurred during the Late Pliocene, Eopleistocene, Middle Pleistocene, and beginning of the Late Pleistocene.

The analysis of the fossil molluscan assemblages of the Beringian sector of the North Pacific and Eastern Arctic allowed us to establish three main phases during the formation of the biogeographical pattern of *Bivalvia* (Tab. 3). The main events of the first phase (Late Pliocene) were the appearance of all modern biogeographic groups and the active invasion of the species of Pacific origin into the Arctic Ocean. During the second phase (Eopleistocene-Late Pleistocene), the repeated penetration of arctic species into the Bering Sea took place as well as a single invasion of boreal-arctic species of Atlantic origin (during the Middle Pleistocene). Thermophilic boreal and arctic species co-existed in the fossil coastal assemblages of the same age in the Bering Sea. The third Late Pleistocene – Holocene phase is characterized by the formation of the modern distribution of molluscs which was mainly predetermined by the last Late Pleistocene regression.

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