

Biogeography of the Recent Brachiopods

O. N. Zezina

Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovskii pr. 36, Moscow, 117997 Russia

e-mail: kap@ocean.ru

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Abstract—The vertical, latitudinal, and circumcontinental zonality of the distribution of the species, genera, and families of recent brachiopods is considered. The distortions of the latitudinal and meridional symmetry of the biogeographic structure of the ocean are analyzed in view of the patterns of the global circulation of the surface and intermediate waters. Thus ancient faunas may be reconstructed based on data on the structural characteristics of the taxocene of recent brachiopods. The features of the paedomorphic evolution of brachiopods from the different families in extreme habitats (interstitial, underwater caverns, submarine rises, abyssal depths, hydrothermal areas, and margins of habitats) are discussed. The biogeographic structure of bottom dwellers is shown to simplify with depth as well as with simplification of the hydrological structure of the ocean. The important role of the bathyal oceanic zone (slopes of continents, islands, submarine mountains, ridges, and rises) in the preservation of faunal relicts is shown. The historical change from brachiopods to bivalves that occurred from the Paleozoic to the Mesozoic and Cenozoic is shown to have resulted not from competitive exclusion, but from complex and global changes in the plankton composition, which were unfavorable for articulate brachiopods, which had already developed specialized feeding habits, feeding on food that led to the production of almost no metabolic waste products; they had even partly lost their alimentary canal. The development of shelly plankton and, especially, of diatoms hampered the post-Paleozoic revival of large assemblages of articulate brachiopods in shallow-water habitats. The unfilled ecological niches were colonized by bivalves, which were widely adapted to feeding on live phyto- and zooplankton. Recent articulate brachiopods, which are adapted to feeding on the products of decay of dead plankton, form a belt of densely populated settlements of the organic biofilter outside the photic zone on the seaward edge of shelves and on the upper parts of the slopes of continents, islands, and submarine rises throughout the world.

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INTRODUCTION

Much progress has been achieved in the last four decades in biogeography, a science dealing with the irregular distribution of life on our planet. The same concerns biooceanology. The seas and oceans now occupy twice as much area on the Earth as the land. At the end of the 20th and beginning of the 21st century, people study the seas and oceans in order to find new sources of seafood, as a source of protein for the rapidly growing human population. Marine biogeography, which is useful in the human economy, also became theoretically useful as it allows the reconstruction of the history of the development of ancient marine faunas based on the actualistic approach. Some new concepts of marine biogeography were discussed in the recent literature. In the present paper we shall consider those concepts which are important for paleobiology, and especially for the sections connected with the study of brachiopods.

Brachiopods are marine invertebrates that are represented in the recent seas and oceans by 370 species, 116 genera, and 26 families. Since the late 1960s they were especially carefully studied in detail in the context of modern zoology and biogeography based on the

study of the large collection of the Shirshov Institute of Oceanology, Russian Academy of Sciences. This collection was formed during the expeditions of the research vessels *Vityaz*, *Akademik Kurchatov*, *Dmitrii Mendeleev*, *Professor Shtokman*, and *Akademik Mstislav Keldysh*. The manned submersibles *Paisis* and *Mir* were also used. Some material was collected during scientific exploration expeditions on the ships of the Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), Pacific Fisheries Research Center (TINRO), Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), in the special cruises of the Zoological Institute, Russian Academy of Sciences, and also during incidental collecting on geologically oriented cruises. The author also examined collections gathered during the expeditions on the Danish research vessel *Galathea*, the American research vessels *Atlantis*, *Chain*, and *Panulirus*, international expeditions of the German research vessel *Polarstern*, and also in the course of the French projects BENTHEDI and NORFOLK-2. The results of the treatment of the materials were published in the *Trudy Instituta Okeanologii*, other journals, and monographs. Twenty-six new species, 5 subspecies, 9 genera, 1 sub-

family, and 2 families were described based on the original data. The taxonomic composition of recent brachiopods, their distribution, and dependence of characteristic features of the recent animals on the habitat conditions were specified and clarified based on the treatment of the above-mentioned collections and summarizing of all available literature data.

Here we give an account of the generalized results on the determination of both geographical and vertical distributions of species, genera, and families and consider peculiarities of the symmetry of the latitudinal and altitudinal faunal belts distinguished based on the distribution of modern taxa. The distortions of the latitudinal and meridional symmetry in the biogeographic structure of the ocean are considered in connection with the patterns of global circulation of the surface and intermediate waters. The peculiarities of brachiopod evolution in optimal and extreme habitat conditions are analyzed. The possibility of the paleoreconstruction of ancient faunas accounting for the structural and functional characteristics of the recent brachiopod taxocene is discussed.

The historical change from brachiopods to bivalves that occurred from the Paleozoic to the Mesozoic and Cenozoic is considered to have resulted not from competitive exclusion, but from complex and global changes in the plankton composition, which were unfavorable for articulate brachiopods, which had already developed specialized feeding habits, feeding on food that led to the production of almost no metabolic waste products; they had even partly lost their alimentary canal. The development of shelly plankton and, earlier, of diatoms hampered the post-Paleozoic revival of large assemblages of articulate brachiopods in shallow-water habitats. The unfilled ecological niches were colonized by bivalves, which were widely adapted to feeding on live phyto- and zooplankton. Recent articulate brachiopods, which are adapted to feeding on the products of decay of dead plankton, form a belt of relatively deep-sea organic biofilter outside the photic zone on the seaward edge of shelves and on the upper parts of the slopes of continents, islands, and submarine rises throughout the world.

VERTICAL DISTRIBUTION

Recent brachiopods inhabit all oceanic depths except the deep oceanic trenches, from the tidal (littoral) zone down to ocean floor (abyss). Of inarticulate brachiopods, several lingulid and discinid species inhabit the littoral zone, and the cosmopolitan *Pelagodiscus atlanticus* reaches the maximum depth known for any brachiopod, in the abyssal zone. Of articulate brachiopods, the North Atlantic *Diestothyris frontalis* and *Megerlina davidsoni* from the Indian Ocean inhabit the littoral zone, and the cosmopolitan *Abyssothyris wyvillei* was found in the abyss.

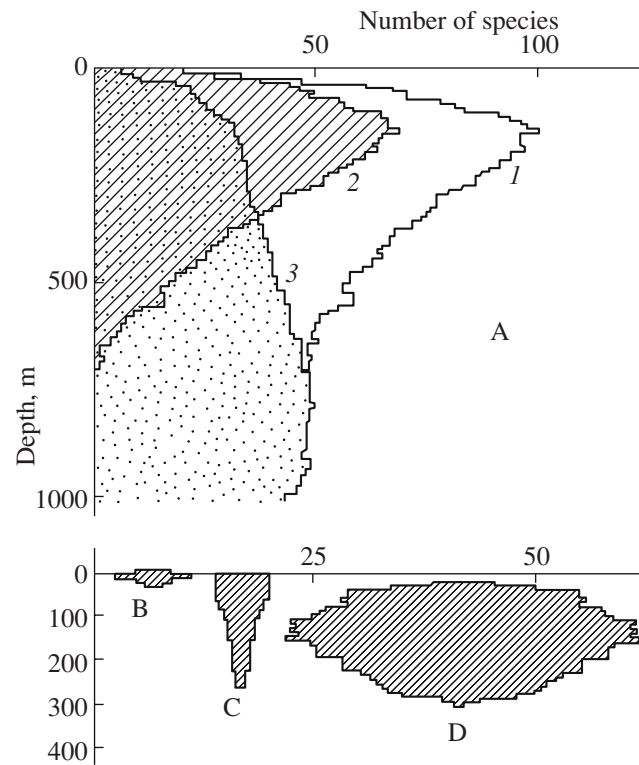


Fig. 1. Change in the number of brachiopod species with depth in the upper horizons of the benthic zone. Designations: (A) total number of species: (1) number of species within each 10 m interval of depth; (2) number of species that do not go deeper than 700 m; (3) number of species that go deeper than 700 m; (B), (C), and (D): distribution of sublittoral species: (B) in the littoral and phytal zones; (C) within the whole sublittoral zone; and (D) in the elit-littoral zone.

The range of the vertical distribution of species varies from a few meters to three or five kilometers. The depth ranges are known not for all species and for many of them only solitary indications of depth were pointed out. Thus the vertical range of distribution has been reliably established for only 200 species.

The general pattern of vertical brachiopod distribution (Fig. 1) shows that the number of species increases with depth from the water line, reaches its maximum between depths of 100 and 150 m, and then decreases. The following points in the vertical change in the species composition of brachiopods are distinguished based on the change in the total number of species within each 50 m depth interval and the curves showing the density of the boundaries between the vertical ranges of species (number of species that appeared and disappeared).

(1) The maximum number of species appears and disappears in the upper horizons of the benthic zone, i.e., it is here that the most intense change of fauna occurs.

Table 1. Endemic species in the vertical zones

Zones, m	Number of species		% of endemics	
	total number	more than once met	total number	more than once met
0–300	184	154	59	51
300–700	114	94	23	6
700–2000	58	56	10	7
deeper than 2000	34	27	35	18

(2) The inflection points of the curve of the total number of species are located below the maximum point at levels of 300 and 700 m and correspond to the maximum rate of disappearance of species in the 200–300 m interval and to the restriction of a considerable number of species to the upper 700 meters.

(3) The appearance of new species is at a maximum in the upper horizons and discontinues at a depth of approximately 1000 m. The deep-water species appear at a depth of more than 1800 m.

The following groups of recent brachiopods may be distinguished based on these points and on the pattern of their vertical distribution: species inhabiting the upper 300 meters; species descending lower than 300 but no deeper than 700 m; species descending lower than 700 m; and species known from depths of more than 2000 m. The upper boundaries of the species distribution vary in each group and are located at different levels (Fig. 1).

Only 43% of all species that were found more than once do not descend lower than 300 m. According to the scheme of the vertical biological zonation of the ocean (Belyaev et al., 1973), these species may be considered as sublittoral. Seventeen of them were found near the water line during the tide or within the upper 10 meters. Among them, nine species (*Lingula anatina*, *L. parva*, *Glottidia audebarti*, *Discina striata*, *Disciniscia lamellosa*, *D. strigata*, *D. cumingi*, and *Megerlina davidsoni*) are unknown from horizons deeper than 30 m. Thus they are distributed within the phytal zone (Fig. 1B). Only some of them (*Lingula anatina*, *Glottidia audebarti*, *Discina striata*, *Megerlina davidsoni*, and *Diestothyris frontalis*) are certainly known in the tidal (littoral) zone. *Pumilus antiquatus* dwells in littoral baths, which are not dry at low tide. Therefore it is not a littoral species in the strict sense. The literature contains no data on the depth range of many species from the families Lingulidae and Discinidae; thus, some of them may also be littoral species.

Most of the sublittoral species, about 82%, do not rise higher than 10 m below sea level. This group of species show an increase in the number of species with depth, a feature typical of brachiopods (Fig. 1D). Forty-one sublittoral species of recent brachiopods occur at depths 300–700 m. Two of these species, *Cancellothy-*

ris cancellata and *Diestothyris frontalis*, are known from the upper horizon (0–10 m). Six species are endemics of depths of 300–700 m below sea level: *Crania patagonica*, *Cryptopora boettgeri*, *Gryphus tokionis*, *Liothyrella winteri*, *Campages asthenia*, and *Magallania* sp. (Thomson, 1918).

One-third of the recent brachiopod species are known from waters deeper than 700 m. Most of the 61 species that were found more than once deeper than 700 m are also known from depths above 700 m. Fourteen species are unknown from depths above 700 m.

The zone of the richest brachiopod fauna corresponds to the depths of the seaward edge of the continental shelf in most regions of the ocean. The seaward edge of the entire oceanic shelf has an average depth of 130 m (Shepard, 1969; Kennett, 1987). The maximum diversity of recent brachiopod species falls between 100 and 150 m. The preference for the shelf edge that the majority of brachiopod species show is well pronounced in a number of regions of the ocean. It is worth noting that the maximum species diversity on the “submerged” shelf of Antarctica is also lowered to 500 m below sea level. The influence of the lowered Antarctic shelf on the vertical distribution of the bottom fauna was repeatedly noted by investigators (Belyaev and Ushakov, 1957; Gusev and Pasternak, 1958) even during the earliest period of hydrobiological studies in Antarctica, and indicates that the vertical distribution of many animals within the shelf and continental slope is more governed by relief and sedimentation patterns than by depth.

The schemes of the vertical trophic zonation of bottom fauna that were elaborated based on materials from the northern Pacific (Sokolova, 1956; Neiman, 1961; Kuznetsov, 1963), demonstrate that on the bends of macrorelief, including the shelf edge and the upper part of the slope, there is a zone where sestonophages dominate in numbers. The majority of recent brachiopod species belongs to this zone, and a considerable number of species are endemic to this zone. The seaward part of the shelf and the upper part of the continental slope or the so-called “shelf-slope break” are possibly the most favorable for the brachiopod existence in the modern ocean (Zezina, 1997, 2005a).

ENDEMISM OF BRACHIOPODS WITHIN VERTICAL ZONES

Thus, the following vertical zones may be distinguished in the benthic zone according to the patterns of distribution of recent brachiopods: 0–300, 300–700, 700–2000, and below 2000 m. The endemism of the fauna of these zones is shown in Tables 1 and 2. The tables show that the fauna of the uppermost zone (0–300 m) exhibits the greatest development of endemism at the species and generic level. The lowest zone (below 2000 m) ranks next in the number of endemic taxa. The intermediate zones contain comparatively

small numbers of endemic species and genera. In what way is the brachiopod fauna of the distinguished zones separated at generic and family levels?

The families Lingulidae, Thaumatosiidae, and Thecididae, and 20 genera from other families were found only within the uppermost zone (300 m). All families, except for Dyscolidae and 12 genera from other families, are known from this zone. Thus this zone differs the presence of five endemic families and a large number of endemic species.

The lower limits of the vertical distribution of 17 genera are located at depths of 300–700 m. The families Cnismatocentridae and Thecidellinidae completely disappear in this zone. Yet the majority of genera unknown in the upper zone dwell at depths of 300–700 m: *Pelagodiscus*, *Comsothyris*, *Hispanirhynchia*, *Chlidonophora*, *Eucalathis*, and *Fallax*. Thus this zone is the transitional horizon between the sublittoral and more deep-water zones. All families except Dyscolidae and all genera except *Dyscolia*, *Neorhynchia*, *Abyssothyris*, *Notorygmia*, and *Leptothyris* are known from the sublittoral and transitional horizons. Five families and 37 genera from other families do not occur deeper than the transitional horizon. The sublittoral and transitional horizon account for 57% of all genera of recent brachiopods.

The brachiopod fauna at depths below 700 m consists of 31 genera, of which 27 also occur at higher levels. The genera *Pelagodiscus*, *Compsothyris*, *Hispanirhynchia*, *Chlidonophora*, and *Eucalathys* are endemic to the bathyal and abyssal zones, including the transitional horizon. All of them, except for *Pelagodiscus*, are distributed above 4600 m and thus may be considered as bathyal–suprabyssal on a scale of all oceanic fauna.

The upper limit of the distribution of the endemically deep-water genera *Neorhynchia*, *Abyssothyris*, *Notorygmia*, and *Leptothyris* is located at depths of about 2000 m. These genera may be regarded as abyssal.

FACTORS DETERMINING THE VERTICAL DISTRIBUTION OF BRACHIOPODS

The vertical distribution of brachiopod species is characterized by an increase in the number of species with depth from the water line to the shelf edge and a decrease below the shelf edge; the bathyal fauna is endemic up to the family level; and the deep-water fauna consists of eurybathic and endemic species. The low diversity of brachiopod species in the littoral and upper sublittoral zones may be explained by two unfavorable factors.

(1) The abundance of suspended large particles both mineral and organic, including phytoplankton. Lingulids and discinids are the most tolerant of this factor and thus form the majority of species in the uppermost benthic zone. Their alimentary canal was completely preserved in the evolution and it is possibly an important peculiarity of their adaptation to life in the upper sublittoral.

Table 2. Endemic genera in the vertical zones

Zones, m	Number of genera			% of endemics
	total number	appears	disappears	
0–300	60	38	–	37
300–700	46	6	17	4
700–2000	28	–	11	4
deeper than 2000	19	–	16	16

toral. Craniids have a similar structure of the alimentary canal but are distributed like the majority of articulate brachiopods, i.e., they do not enter shallow water.

(2) The strongest competition for space occurs in the upper horizons of the sublittoral, which is inhabited by macrophytes along with animals. It is apparently characteristic of the majority of species of recent brachiopods that the upper limit of their distribution is below 30–50 m, i.e., beyond the limits of the phytal zone or in its lower horizons.

The environmental conditions favorable for brachiopods at depths of the shelf edge and shelf-slope break may be formed in the following way. Relatively rapid currents near the seaward edge of the shelf make the sediments coarser, a necessary condition for all brachiopods except for those that burrow. The absence of bottom macrophytes near the seaward edge of the shelf may reduce competition for hard substrate, which is also important for the attaching forms of modern brachiopods. The seaward edge of the shelf and the upper part of the slope correspond to the horizons where the production of phytoplankton is also reduced but the biomass and production of bacterioplankton are high. Suspended material at these depths is not very rich in living cells of planktonic algae but is still rich in slightly transformed organic matter.

The decrease of the number of species with depth below the shelf edge is accompanied by the disappearance of environmental conditions favorable for brachiopods in general. According to the vertical and circumcontinental zonality of sedimentation (Bezrukov, 1964), the areas with hard substrates are reduced with depth; but when they are present in the regions with low sedimentation rates far from the coast in the central regions of the ocean, it combines with feeding conditions that are too severe for brachiopods.

Deterioration of feeding conditions with depth is possibly the most important factor in the natural selection of species. In the open regions of the tropical zone of the Pacific Ocean, the average biomass of bacterioplankton in the upper 600 meters of the water column is on average 15–30 mg/m³ and in the layers of maximum abundance at depths of 70–90 and 400–600 m it reaches 100–300 mg (Sorokin, 1970, 1971). The biomass of bacterioplankton sharply decreases below 700–

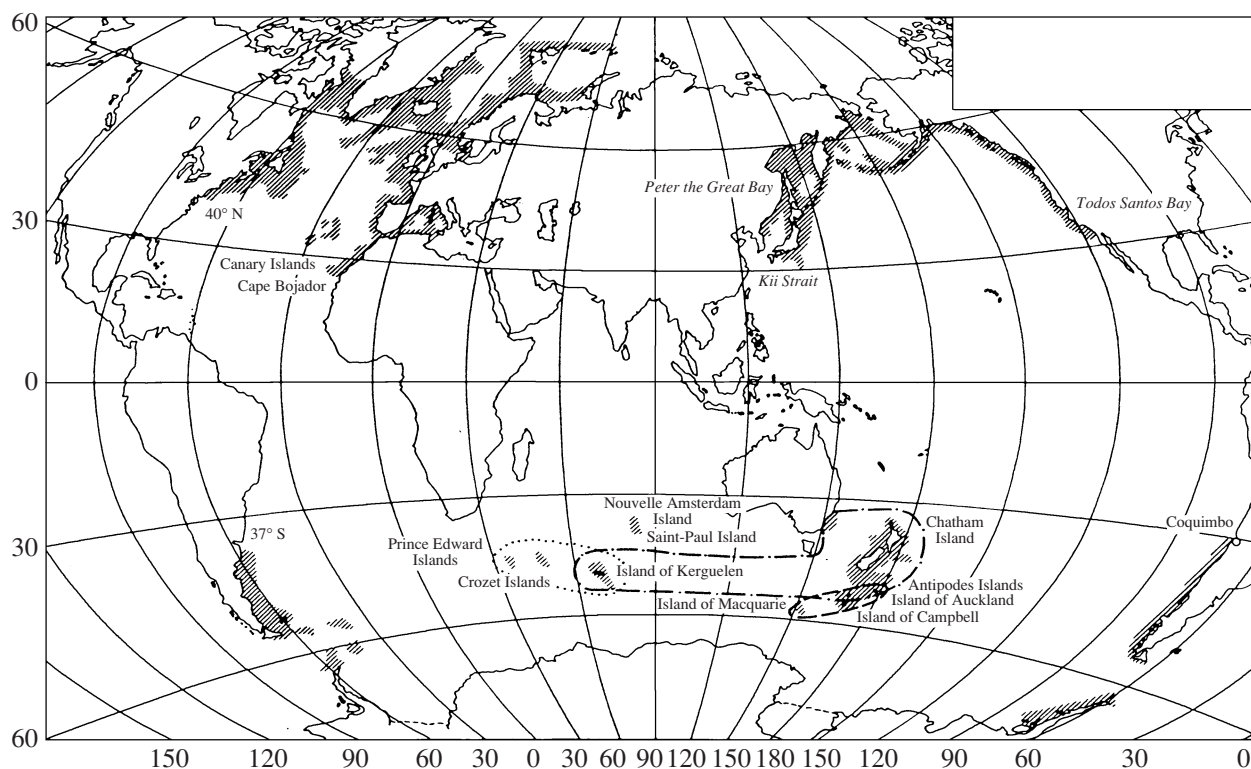


Fig. 2. Distribution of the geographical elements of brachiopod fauna with North Atlantic, North Pacific, South American, Kerguelen, Nouvelle Amsterdam, New Zealand (dot-and-dash line), and Macquarian (dashed line) types of areas in temperate waters in the Southern and Northern Hemispheres.

800 m and constitutes 1–2 mg/m³ in the abyss. This regularity of the vertical distribution of bacterioplankton is also possibly true for the coastal waters, but with larger absolute values.

According to Agatova and Bogdanov (1972), the quantity and quality of suspended organic matter also changes considerably with depth. The feeding conditions for sestonophages sharply deteriorate at depths below 800–1000 m and feeding resources may be considered to be extremely restricted, if the possibility of feeding on organic matter that is dissolved or adsorbed from the solution is excluded.

Therefore, the main factors determining the vertical distribution of recent brachiopods are (1) relief, and the depositional regime, which is governed by the relief; (2) competition for the substrate, which is especially strong in the phytal zone; and (3) deterioration of the feeding conditions with a decrease in depth within the shelf and with an increase in depth within the slope.

It is important that the majority of the brachiopod species, about two-thirds of the total fauna, does not go to the depths where food particles of suspended material sharply decrease in abundance. The species endemic to the bathyal and abyssal zones possibly have special adaptations to life in conditions of limited food resources (Zezina, 1994, 2003).

RANGES AND GEOGRAPHIC ELEMENTS OF FAUNA

Recent brachiopods are known from the seas and oceans of oceanic salinity in all latitudes from the Arctic Ocean to Antarctica. Species of recent brachiopods that dwell on the shelf and on the slope are divided into groups based on similarity in their distribution. These groups are geographical elements of fauna. Here we list the largest groups; each of them is characterized by an array of species that have the largest ranges in the region. Species with narrower ranges are also considered in each group. They may form independent lower-rank elements of fauna. However, there often occur poorly studied ranges with a small number of records; thus, species found in restricted areas are tentatively referred to more widespread elements of fauna, which are conditionally termed here as basic.

The main geographic elements of brachiopod fauna are distinguished here based on the distribution of species with the following ranges.

Novocrania anomala, *Terebratulina retusa*, *Arctosia arctica*, *Macandrevia cranium*, *M. tenera* have **North Atlantic type of ranges** in the fullest sense (Fig. 2). All of them dwell near the western coasts of Iceland and eastern coasts of Greenland and penetrate southwards not farther than New York state (Block Island, latitude 41° N) near the coast of North America

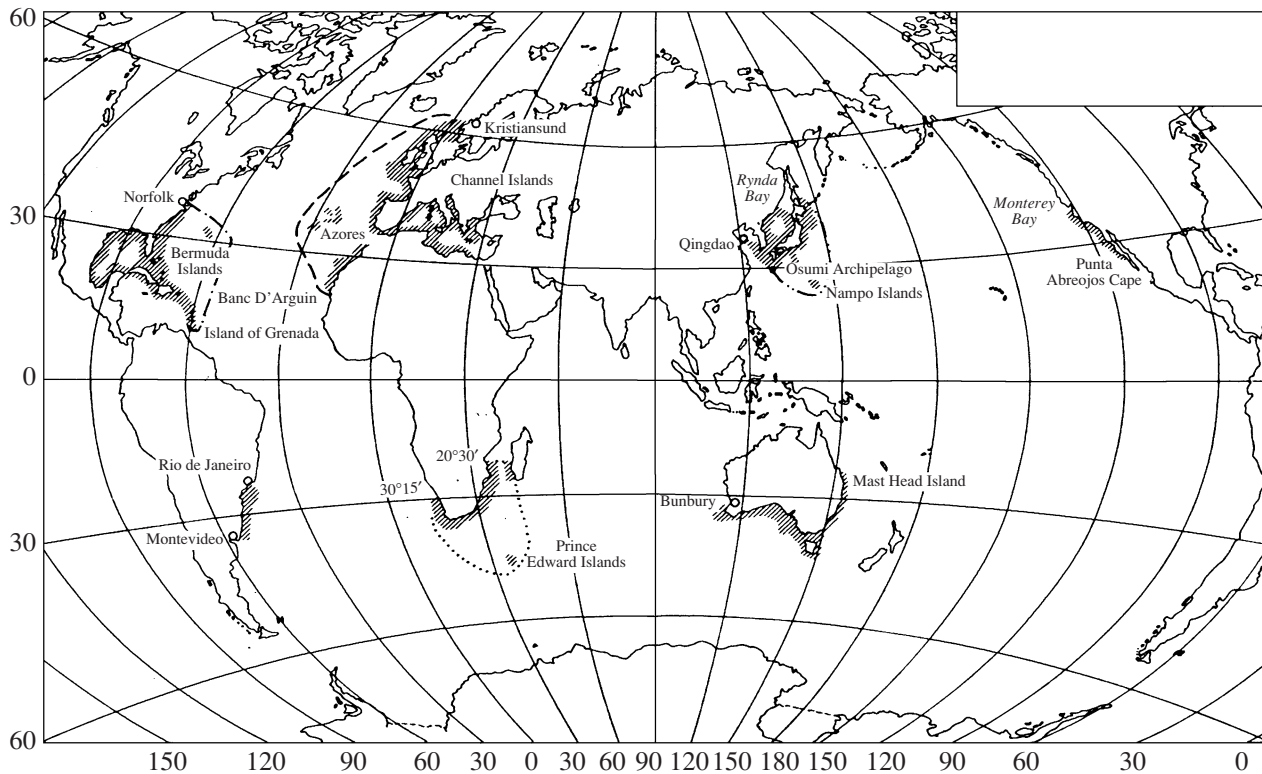


Fig. 3. Distribution of the geographical elements of brachiopod fauna with Lusitanian-Mauritanian-Mediterranean, West Atlantic, South Brazilian-Uruguayan, South African, Japanese, South Australian, and Californian types of ranges.

and Cape Bojador (south of the Canary Islands, latitude $26^{\circ}10' N$) near the coast of Africa. This range stretches north-westward up to Franz Josef Land and the Southern Island of Novaya Zemlya. The North Atlantic species also include species that are restricted to the east or the west of the ocean. The latter include the most warm-water and lower boreal *Dallina septigera*. *N. anomala*, *T. retusa*, and *M. cranium* are considered as widely ranging boreal and *A. arctica* as higher boreal.

Frieleia halli, *Terebratulina unguicula*, *T. crossei*, *T. kiiensis*, and *Diestothyris frontalis* have the most complete **North Pacific type of ranges** (Fig. 2). They were found near Asian and American coasts, up to the Gulf of Anadyr and Point Barrow to the north, and southward up to Peter the Great Bay and the Island of Sado in the Sea of Japan, to the Kii Strait on the oceanic shore of Japan and Todos Santos Bay near the Baja California Peninsula (latitude $32^{\circ} N$). The North Pacific species also include species distributed only near Asian or American coasts. It is difficult to divide the North Pacific species into more or less cold water groups based on the currently accumulated data.

Hemithyris psittacea and *Glaciarcularia spitzbergenensis* have **north circumpolar type of ranges**. These two species dwell in the Arctic basin and northern parts of the Atlantic and Pacific. Their southern boundaries pass in the Atlantic Ocean near the coast of Nova Scotia and near Cape Saint Vincent (Portugal, latitude $37^{\circ} N$); near

the southern coast of the Island of Kyushu (latitude of $32^{\circ} N$) and near the town of Astoria (latitude $46^{\circ} N$, Oregon, United States) in the Pacific Ocean.

Glottidia pyramidata, *Crania pourtalesi*, *Cryptopora rectimarginata*, *Eurysina bartletti*, *Tichosina bartchi*, *T. cubensis*, *Argyrotheca bermudana*, *A. schrammi*, *A. johnsoni*, *Platidia clepsysra*, *Dallina floridana*, and *Thecidellina barretti* have **West Atlantic type of ranges** (Fig. 3). They are known in the Gulf of Mexico, near the Antilles, on the shelves of the Bermuda and Bahamas islands. They do not go farther north than latitude $37^{\circ} N$ (Norfolk, Virginia, United States) and southward farther than the Island of Grenada (Lesser Antilles).

Hispanirhynchia cornea, *Eucalathis ergastica*, and *E. tuberosa* have **East Atlantic type of ranges**. They were found near the coasts of Europe and Africa and pass northwards up to the Bay of Biscay, to the south up to Banc D'Arguin (latitude $20^{\circ} N$); to the west up to the Azores and Canary Islands. *Dyscolia subquadrata*, *Eucalathis trigona*, and *Gwynia capsula* are more locally distributed in this region and were found only near the coast of Western Europe. *Magasella crenulata* is known only from the Canary Islands.

Xenobrochus (?) affinis, *Dyscolia wyvillei*, and *Platidia incerta* have **amphiatlantic type of range**. They are distributed both near American and European-African coasts of the Atlantic Ocean and go to the north up to Cape Finisterre (Spain), Azores and Bermuda

Islands, to the south up to the Grenada Basin in the Caribbean Sea and Banc D'Arguin (latitude 20° N) near the shores of Africa. *Xenobrochus* (?) *affinis* also belongs to the fauna of the Mediterranean Sea.

Megathyris detruncata, *Argyrotheca cistellula*, and *Megerlia truncata* have **Lusitanian–Mauritanian–Mediterranean type of ranges** (Fig. 3). They are known from the Mediterranean Sea and coasts of Western Europe and northern West Africa. They go to north up to Kristiansund in southern Norway and the Channel Islands in the English Channel; to the west up to the Azores Islands; to the south up to the Canary Islands. *Gryphus vitreus* and *Pantellaria monstrosa* were found only in the Mediterranean Sea and near the Atlantic shores of Western Europe. *Crania rostrata* and *Argyrotheca cuneata* are known only from the Mediterranean Sea and the Atlantic shores of Africa. Six endemic species are known from the Mediterranean Sea: *Crania lamellosa*, *C. kermes*, *Tethyrhynchia mediterranea*, *Megathyris barroisi*, *Argyrotheca cordata*, *Megerlia granosa*, and *Lacazella mediterranea*.

Discinisca antillarum, *Terebratulina cailleti*, *Argyrotheca lutea*, *A. barretiana*, and *A. turmanni* have **Caribbean type of ranges**. They were found in the Caribbean Sea and near the coast of South America. These species go to north to Cape Hatteras and south to Rio de Janeiro.

Bouchardia rosea has **southern Brazilian–Uruguayan range** (Fig. 3). It dwells along the Atlantic coast of South America from Rio de Janeiro to Montevideo. This species is the only one of its kind distributed between the boundaries of the Caribbean and South American ranges and constitutes an independent geographical element of the fauna.

Lingula parva, *Discina striata*, and *Kraussina mercatori* have **West African type of ranges**. They go north to the town of Conakry (latitude 8° N) and go to the south up to the delta of the Niger River.

Cryptopora boettgeri, *Terebratulina abyssicola*, *T. meridionalis*, *Agulhasia davidsoni*, *Xenobrochus agulhasensis*, *Gryphus capensis*, *Kraussina rubra*, *K. crassicostata*, *Megerlina capensis*, *M. striata*, and *M. natalensis* have **South African type of ranges** (Fig. 3). They go to the west up to longitude 13°03' E in the Atlantic Ocean and to the east up to longitude 35°43' east in the Mozambique Channel. Their ranges stretch southward up to the Prince Edward Islands (Marion Island). The locally distributed *Crania roseradiata*, *Xenobrochus africanus*, *Eucalathis fasciculate*, *Megathyris capensis*, *Kraussina cognate*, *Terebratella rubiginosa*, and *Nipponithyris afra* are also referred to the South African type. An empty shell of *Terebratulina* sp. aff. *T. meridionalis* was recently found near the coast of Namibia (latitude 25° S) (Zezina, 2006).

The types of ranges in the Indian Ocean are difficult to determine because the fauna of this region is poorly known. Of the eastern part of the ocean, *Thaumatostia*

anomala from the Andaman Sea and *Thecidellina blochmani* from Christmas Island are known. *Cryptopora curiosa*, *Frenulina cruenta*, and *Xenobrochus indianensis* dwell in the western part of the ocean, along the coast of Africa from the Gulf of Aden up to the Mozambique Channel. *Argyrotheca somaliensis* is known only from the shore of Somali; *Compsoria suffusa* is known only from the Mozambique Channel; *Argyrotheca jacksoni*, only from the Red Sea; *Pantellaria gigantea* only from the Persian Gulf and the Mascarene Islands; *Dallithyris cernica*, *Megerlina pisum*, and *Lacasella mauritiana* only from the Mascarene Islands; *Rhytirhynchia sladeni* and *Kraussina gardineri* only from the Saya de Malha Bank; *Dallithyris murray* only from the same bank and the Maldives; *Dyscolia johannisdavisi* only from the Maldives; and *Cryptopora maldiviensis* from the Maldives and possibly from the coast of Africa. The deep-water (740–3490 m) *Chlidonophora chuni* has the widest range in the West Indian Ocean, from the African coast (near Dar es Salaam) to the Chagos Archipelago, the Maldives, and the Laccadive Islands.

Lingula rostrum, *L. tumidula*, *Discinisca stella*, *Craniscus japonicus*, *Basiliola pompholyx*, *B. elongata*, *Acanthobasiliola doderleini*, *Terebratulina callinome*, *T. valdiviae*, *T. photina*, *T. hawaiiensis*, *Campages basilanica*, *Frenulina sanguinolenta*, and *Thecidellina maxilla* have **West Pacific type of ranges**. All these species were found in the central part of the Indo-Malayan Archipelago. They go to the north up to the southern shores of the Korean Peninsula near the Asian continent and outskirts of the town of Hakodate near the Japanese islands, to the south up to the port of Adelaide along the eastern and southeastern shores of Australia; to the west up to the Strait of Malacca; to the east up to the Hawaiian, Society, and Tonga islands. Species distributed more locally near the Marshall, Fiji, and Kermadec islands and near the shore of Queensland also belong to the West Pacific type. A large group is formed by the species found only in the Indo-Malayan Archipelago, near the Philippine Islands and the islands of Borneo and Sulawesi. Four endemic species dwell near the Hawaiian Islands. *Lingula adamsi* has an intermediate between the West Pacific and Japanese independent type of range and is distributed from the Island of Taiwan to the Korean Strait.

Lingula anatina, *L. translucida*, *L. murphiana*, *L. exusta*, *Discinisca indica*, and *Frenulina alcocki* have **Indo–West Pacific type of range**. These species dwell near the coasts of the Indian Ocean and West Pacific Ocean. They go to the north up to the Shandong Bandao (Peninsula); to the east up to the Fiji Islands; to the west up to the Gulf of Aden and town of Durban; to the south up to the Timor Island and Port Jackson in East Australia (latitude 34° S).

Crania suessi, *Cryptopora brazieri*, *Eohemithyris colurnus*, *Dallithyris* (*Epacrosina*) *fulva*, *Cancellothyris cancellata*, *Megerlina lamareckiana*, *Aldingia*

willemoesi, *Campages furcifera*, *Jaffaia jaffaensis*, *Magadina cumingi*, *Pirothyris vercoi*, *Terebratella mayi*, *Magellania flavescens*, and *M. iredalei* have **South Australian type of ranges** (Fig. 3). They are known from the southern and eastern shores of Australia no further west than the town of Bunbury (near Perth on the south of the West Australia), no further north than Mast Head Island near Queensland (latitude 23°30' S); and no further south than the shelf of the island of Tasmania. *Terebratulina cavata*, *T. radula*, *Murravia exarata*, *Argyrotheca australis*, and *Magellania australis* are more locally spread near the Australian shores. Seven Australian species and two endemic species (*Argyrotheca mayi* and *Megerlina atkinsoni*) were found near Tasmania.

Fifty species compose the *Japanese* geographical element of fauna (Fig. 3). All of them are treated here as a single entity, although some isolated groups differ slightly geographically (Hatai, 1940). The classification of Recent Japanese brachiopods is poorly elaborated and it is possible that the species list includes synonyms. This has hampered the detailed zoogeographical analysis and is the reason for uniting all Japanese brachiopod fauna. Species with the Japanese range go north to Rynda Bay (latitude 44°50' N) near the continental coasts and up to the Tsugaru Strait near the island shores in the Sea of Japan, and to the southeastern shores of Sakhalin Island in the Sea of Okhotsk. Southward, the Japanese species reach the Osumi Archipelago (latitude 30° N), and the Nampo Islands (the Izu, Bonin, and Volcano islands; latitude 25° N) and town of Qingdao on the Shandong Bandao (Peninsula).

Crania californica, *Annuloplatidia horni*, and *Dallinella occidentalis* have **Californian type of ranges** (Fig. 3). They reach Monterey Bay (latitude 36°5' N; California, United States) in the north and Punta Abreojos Cape (latitude 27° N; near the western shores of the Baja California Peninsula) in the south.

Glottidia semen, *G. audebarti*, *Discinisca lamellosa*, *D. laevis*, *D. cumingi*, *D. strigata*, *Liothyrella uva*, and *Macandrevia americana* have **Pacifico-Central American type of ranges**. They reach the city of San Diego in the north and the Strait of Magellan in the south. *Discinisca cumingi*, which was previously known from Punta Abreojos Cape to Chiloé Island (latitude 40° S), has now been found near the western coast of the Antarctic Peninsula (latitude 68°13' S) by Russian-German expedition on the research vessel *Akademik Boris Petrov* (Zezina, 2005b).

Liothyrella "uva", *Terebratella dorsata*, *T. submutica*, and *Magellania venosa* have **South American type of ranges** (Fig. 2). They dwell near the Pacific and Atlantic coasts of South America northward up to latitude 30° S (Chile) and latitude 37° S (Argentina); southward up to the South Orkney Islands and Graham Land; and eastward up to South Georgia Island. More locally distributed species from the Birdwood Bank,

Tierra del Fuego, South Shetland Islands, Strait of Magellan, Valparaíso, and South Georgia Island also are referred to the South American type.

Endemic species dwelling near the islands Nouvelle Amsterdam and Saint-Paul in the South Indian Ocean constitute **Nouvelle Amsterdam type of ranges** (Fig. 2). They are *Crania valdiviae*, *Valdiviathyris quenstedti*, *Striarina valdiviae*, *Liothyrella winteri*, and *Megerlina davidsoni*.

Terebratella enzenspergeri, *Magellania kerguelensis*, and *Aerothyris eichleri* belong to **Kerguelen type of ranges** (Fig. 2). Two of them are endemic to Kerguelen Island and *M. kerguelensis* also dwells near the Prince Edward Islands. Although the Crozet Islands are located between Kerguelen and the Prince Edward Islands, the Kerguelen species were not found there but a species endemic to the Crozet Islands, *Tichosina (Eurygina?) moselei*, was discovered. A subspecies of the widespread *Notosaria nigricans* was also found near Kerguelen Island.

Notosaria nigricans, *Pumilus antiquatus*, *Terebratella sanguinea*, *Terebratella inconspicua*, *Neothyris lenticularis*, and *N. ovalis* have **New Zealand type of ranges** (outlined by dot-and-dash line in the Fig. 2). All of them are known from the coast of South Island, New Zealand. Only *N. nigricans*, *T. sanguinea*, and *T. inconspicua* are spread more widely: coast of North Island and the islands of the New Zealand (Campbell) Plateau (Stewart, Chatham, and Auckland islands). *N. nigricans pyxidata* is known from Kerguelen Island. The endemic *Terebratella haurakiensis* dwells near the coast of North Island of New Zealand and is sometimes considered to be a warm-water subspecies of the widely spread New Zealand *Terebratella sanguinea*. *Novocrania huttoni*, *Liothyrella neozelanica*, and *Amphithyris buckmani* were found only in the Cook Strait.

Aerothyris maquariensis and *Gyrothyris mawsoni* have **Macquarie type of range** (outlined by dotted line in Fig. 2). They dwell near Macquarie Island (Bishop and Clark seamounts southeast of the New Zealand Plateau).

Crania patagonica, *Novocrania lecointei*, *Compsothyris racovitzae*, *Liothyrella antarctica*, *Macandrevia vanhoffeni*, *Aerothyris fragilis*, and *A. joubini* have a circumpolar distribution around Antarctica and have **Antarctic type of range**. Species with the Antarctic type of range go north up to latitude 43°30' S near the Pacific coast of South America and latitude 44° S near the Atlantic coast of South America. The species recorded only once such as *Crania joubini*, *Compsothyris antarctica*, *Tichosina (Eurygina?) ovata*, *Macandrevia lata*, and *Stetothyris antarctica* also belong to the Antarctic range. Some of them are not "valid" species and that is why we do not analyze their distribution in the present paper.

A separate group is formed by two species whose areas in the current state of study may be regarded as **bipolar transitional regions**. *Platidia davidsoni* has Lusitanian-Mauritanian-Mediterranean range in the

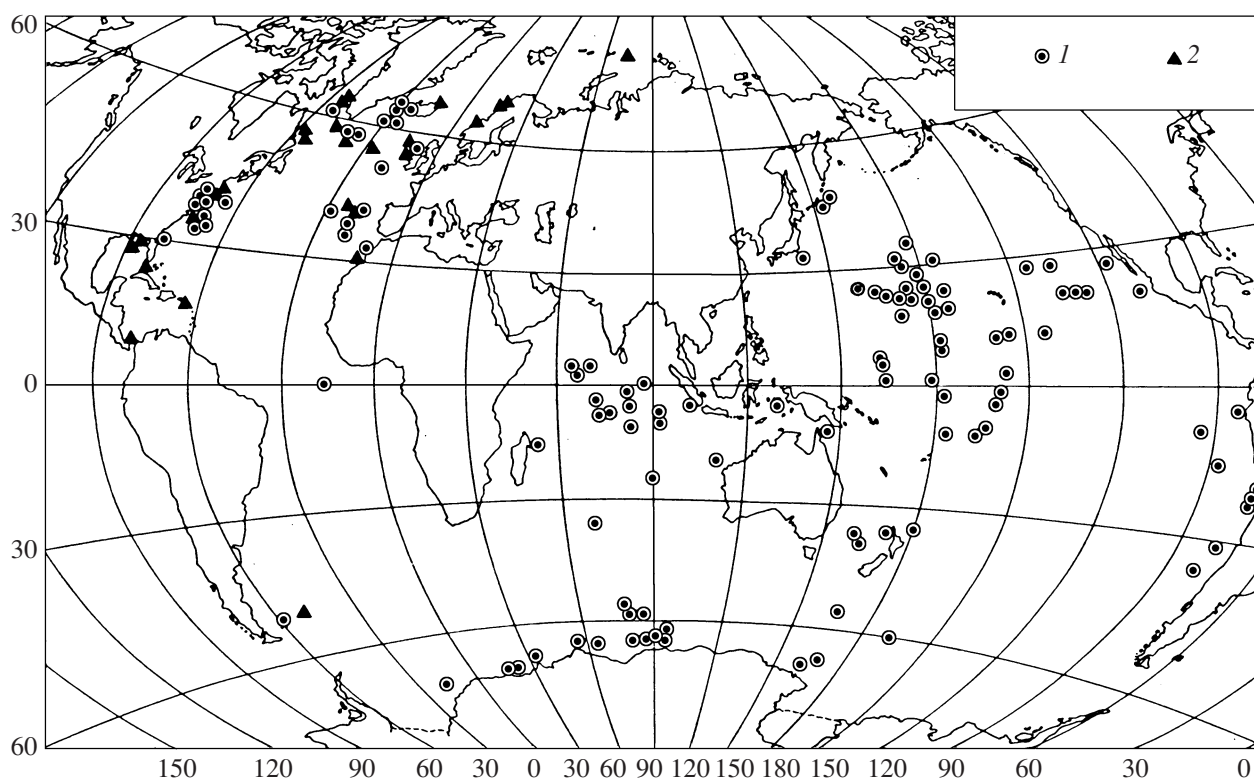


Fig. 4. Distribution of the eurybathic species entering the abyssal zone. Designations: (1) *Pelagodiscus atlanticus*; (2) *Cryptopora gnomon*.

Northern Hemisphere but was also found near the coast of Argentina. *Platidia anomioides* has amphiatlantic type of range in the Northern Hemisphere but was also found on the Agulhas Bank near South Africa and near Marion Island and on the Ob' Tablemount in the Antarctic Ocean.

The range of *Pantellaria echinata* may be considered as **widely tropical**. This species is amphiatlantic in the Northern Hemisphere but was also found near South Africa, in the Red Sea, and on the southern Australian shelf.

The area of *Megerlia truncata* is poorly known and is referred here to the Lusitanian–Mauritanian–Mediterranean type but is also questionably known from the Philippine Islands and South Africa.

The eurybathic species entering the abyss form isolated types of ranges (Fig. 4). Of them, *Pelagodiscus atlanticus* is a **cosmopolitan** and *Cryptopora gnomon* is known from the Atlantic and Arctic oceans, from Franz Josef Land to the Falkland Islands. The range of *C. gnomon* should be considered as **coastal–deep-water** (term used by S. Ekman, 1953).

The types of ranges described for brachiopods dwelling the shelf and slope possibly are typical of benthic invertebrates of many other systematic groups, as they generally correspond to the faunas distinguished by S. Ekman (1935, 1953) within the continental shelf. The brachiopoda differ from other benthic

invertebrates in the narrower ranges of many species. This testifies to the narrow specialization of brachiopods and makes them good indicators of the biotopical changes in the ocean.

The presence of eurybathic and shallow-water species in the same geographical elements of fauna is evidence of the geographical similarity of many eurybathic and sublittoral species.

The geographical elements of fauna distinguished at the species level are poorly separated in higher taxa. No one of them contains endemic families and many of them lack endemic genera (Table 3). The North Atlantic and South American groups of species are very important geographically but they are not distinguished higher than at the species level. North Pacific, Japanese, South Australian, and New Zealand groups are better characterized in the number of endemic genera.

Brachiopod genera and species are usually widespread and are common to several, often remote, geographic elements of fauna. The widespread taxa of higher rank are very interesting for the study of the history of the formation of faunas. Here we shall consider the ranges of genera and families with restricted distribution in order to assess the degree of the systematic isolation of the faunas of separate regions.

The families Lingulidae, Thecideidae, Megathyrididae, and Kraussinidae form a distinctive group as their members do not belong to the cold-water faunas. The

Table 3. Taxonomic isolation of the geographic elements of the brachiopod fauna at generic level

Faunal element	Number of genera		
	total	endemic	% of endemics
North Atlantic	6	—	—
North Pacific	6	2	33
Northern circumpolar	2	—	—
West Atlantic	10	—	—
East Atlantic	6	—	—
Amphiatlantic	4	—	—
Lusitanian–Mauritanian–Mediterranean	8	—	—
Caribbean	4	—	—
South Brazilian–Uruguayan	1	1	100
West African	2	1	50
South African	10	1	10
Indian Oceanic	11	1	9
West Pacific	18	3	17
Indo–West Pacific	3	—	—
South Australian	17	6	35
Japanese	18	4	22
Californian	3	1	33
Pacific–Central American	5	—	—
South American	5	—	—
Nouvelle Amsterdam	5	1	20
Kerguelen	5	—	—
New Zealand	8	3	37
Macquarian	2	1	50
Antarctic	7	1	14

families Discinidae, Cryptoporidae, Basiliolidae, Plati-diidae, and Phaneroporidae have similar occurrence; only solitary eurybathic and deep-water species *Pelagodiscus atlanticus*, *Cryptopora gnomon*, *Neorhynchia strebeli*, *Platidia anomioides*, *Annuloplatidia indopacifica*, *Phaneropora incerta*, and *Leptothyris ignota* can leave warm shallow waters.

Thus the cold-water regions are poor in brachiopod taxa of higher ranks. Recent brachiopods lack families restricted to the cold-water regions, and the fauna of these regions lacks endemics with rank higher than genus.

LATITUDINAL ZONALITY AND SYMMETRY OF FAUNAL ZONES

The geographical elements of the fauna are arranged more or less symmetrically about the equator. The distribution of the amphiocenic and bipolar species aids to specify the order of the arrangement of zones and their homology. The following zones of the geographi-

cal elements of the fauna of recent brachiopods are distinguished:

(1) The zone of the cold-water species of the Northern Hemisphere consists of North Atlantic, North Pacific, and northern circumpolar species. The North Atlantic and North Pacific species form the boreal zone. Arctic brachiopod species are unknown. The distribution of species with northern circumpolar ranges outlines the limits of the unified arctic–boreal zone.

(2) The zone of the cold-water species of the Southern Hemisphere is disjunct and consists of the more cold-water species with Antarctic type of ranges (Antarctic zone) and moderately cold-water species with South American, Kerguelen, Nouvelle Amsterdam, New Zealand, and Macquarie types of ranges (Subantarctic zone). The Antarctic species are possibly homologous to the higher boreal species and subantarctic species may be homologous to the lower boreal species. However, the higher boreal and lower boreal brachiopod species in the Northern Hemisphere are distinguishable only in the Atlantic ocean, while in the Pacific Ocean the low boreal zone is strongly over-

Table 4. Proportions of species in transitional zones

Region	Number of species, %			Total number of species
	cold-water	endemic	warm-water	
Japanese	9	74	17	64
Californian	22	33	44	9
Chilean	43	—	57	7

lapped by the subtropical zone and thus cannot be distinguished. Homologues of the northern circumpolar boreal–Arctic species were found in the Southern Hemisphere only near South America. *Novocrania lecointei* may also be referred to this group. Its area is the widest and stretches from Antarctica to the north up the islands of the Indian Ocean and to the southeastern rises of the Pacific Ocean. The areas of the northern and Southern Hemispheres differ probably because of the disconnection of the shelf waters in the southern cold and moderately cold waters.

(3) Species of Caribbean, West African, and West Pacific types of ranges and the majority of species of the Indian Ocean form the zone of the most warm-water species. In terms of Ekman (1953), this zone must be considered tropical. Two more zones are distinguished between the zones of tropical and cold-water species of the northern and Southern Hemispheres that correspond to the subtropical zones by Ekman (1953) and to the moderately warm-water by Briggs (1974).

(4) The northern subtropical zone consists of the West and East Atlantic, Lusitanian–Mauritanian–Mediterranean, amphiatlantic, Japanese, and Californian species.

(5) The southern subtropical zone consists of the South African and South Australian species. The South Brazilian–Uruguayan *Bouchardia rosea* from the Atlantic coast of South America is referred to the subtropical zone. The Pacific coast of South America lacks subtropical brachiopod fauna.

The distribution of the northern and southern subtropical, lower boreal and subantarctic species corresponds to the transitional areas, where the ranges of the species of the tropical zone meet or superpose the areas of the species of the cold-water zones. The transitional zone is best pronounced in the Northern Hemisphere. In the Pacific Ocean, the areas of the cold-water species are superposed by the areas of the warm-water species

near the coasts of Japan and California. Thus the transitional zones are formed and subtropical species became endemic in these regions. In the northern part of the Atlantic Ocean, the areas of tropical species and northern cold-water zone are not overlapped; subtropical species occupy the northern margin of the tropical zone near the coast of America and the southern margin of the cold-water zone near the coast of Europe and Africa. The range of the lower boreal *Dallina septigera* extends the concept of the transitional zone in the northeastern Atlantic Ocean. The faunal zones of the Southern Hemisphere are isolated. The only exception is the region near the Pacific coast of South America, where the areas of warm-water and cold-water species superpose over a long distance.

The area with endemic faunas of the subtropical and subantarctic zones we tentatively refer to the transitional zone of the Southern Hemisphere. The faunas of the transitional zones are tropical rather than cold-water judging by the proportions of warm-water, cold-water, and endemic species within the limits of the transitional zone (Table 4). Besides, the endemic elements of the fauna of the transitional zones, when present, contain many tropical genera unknown in the temperate and cold waters.

The fauna of the Chilean transitional zone lacks endemic species. The coefficient of biotic similarity (Preston, 1962) of its fauna and faunas of the neighboring regions is 0.38 (to Pacific–Central American) and 0.28 (to South American). The coefficient of biotic similarity of faunas of the transitional zones of the Northern Hemisphere with the faunas of the neighboring regions (Table 5) is close to these values.

Table 6 demonstrates the distribution of brachiopod species between the climatic zones. The northern subtropical and tropical zones are the richest in species. Each of them contains almost one-third of the total brachiopod fauna. The endemic subtropical species of both northern and southern zones together with the endemic species of the subantarctic zone account for 57% of all species of modern brachiopods. As the transitional zones contain both warm-water and cold-water species, these regions are the richest in fauna. The largest number of species was revealed near the shores of Japan, West Europe, Northwest Africa, and Southeast Australia. The subantarctic and Antarctic zones taken together are almost three times as rich as the arctic–boreal zone, possibly because the southern cold-water faunas are

Table 5. Coefficient of biotic similarity of the faunas of the transitional zones of the Northern Hemisphere with the faunas of the neighboring zones

Boreal zone	Coefficient of biotic similarity	Transitional zone	Coefficient of biotic similarity	Tropical zone
Northern Pacific	0.16	Japanese	0.19	West Pacific
Northern Pacific	0.13	Californian	0.34	Pacific–Central America

more geographically isolated in comparison with the northern faunas.

The zones are taxonomically isolated at the level no higher than of the generic rank. Both subtropical and subantarctic zones are almost equal in the percentage of endemic genera (Table 7). The proportion of endemics in the tropics is lower. The boreal-arctic and Antarctic zones are poorest in endemic genera.

The symmetrical arrangement of the geographical elements of the brachiopod fauna in the climate zones corresponds to the modern ideas on the biological structure of the oceans. This symmetry is distorted according to the asymmetry in the arrangement of the continents and in the system of water circulation in the oceans (Zezina, 1975, 1978, 1981a, 2000a, 2001).

BIOGEOGRAPHIC ASYMMETRY AS A RESULT OF THE EFFECT OF PLANETARY-SCALE FEATURES ON THE OCEAN

So, the geographical elements of the fauna of recent brachiopods on the shelves of the ocean constitute seven latitudinal climate zones: arctic–boreal, lower boreal (southern part of the arctic–boreal zone that is considered here as a single whole), northern subtropical, tropical, southern subtropical, subantarctic, and Antarctic. The main features of the biological structure of the ocean are governed by the symmetry of the latitudinal faunal zones relatively to the equator and also by symmetry of the geographical elements of the fauna within one zone on the east and west of each ocean. The violation of this symmetry and the analysis of the reasons of such violations are of special interest.

The violation of the symmetry of the latitudinal brachiopod-based zones about the equator is in the different distances of northern and southern faunas from the equator (Fig. 5). The zones in the Southern Hemisphere are farther drawn apart than in the Northern Hemisphere, where they considerably superpose each other. This distortion of the faunal symmetry is connected with the distortion of the equatorial symmetry of the global circulation of surface waters, which is due to the uneven distribution of land and ocean relatively to the equator.

The violation of the symmetry of the faunal zones about the meridional axis of the Pacific and Atlantic oceans is in the different width and spatial superposition of the latitudinal faunal zones on the west and east of each ocean that is caused by different directions of the global hydrological circulation, which are in turn determined by the Earth's revolution and configuration of land. The different directions of the anticyclonic circulation in the Northern and Southern Hemispheres cause the largest width and less spatial superposition (mixture) of the faunal zones near the eastern coasts of the Pacific and Atlantic oceans than near their western coasts.

Table 6. Distribution of species between the climate zones

Zone	% of the total number of species
Boreal–arctic	7
Northern subtropical	32
Tropical	31
Southern subtropical	12
Subantarctic	13
Antarctic	5

Table 7. Endemism of genera in the climate zones

Zone	% of endemics to the number of genera of the zone
Boreal–arctic	15
Northern subtropical	31
Tropical	28
Southern subtropical	30
Subantarctic	31
Antarctic	12

One of the most significant peculiarities of the violation of the meridional faunal symmetry of the Pacific and Atlantic oceans may be seen in recent brachiopods

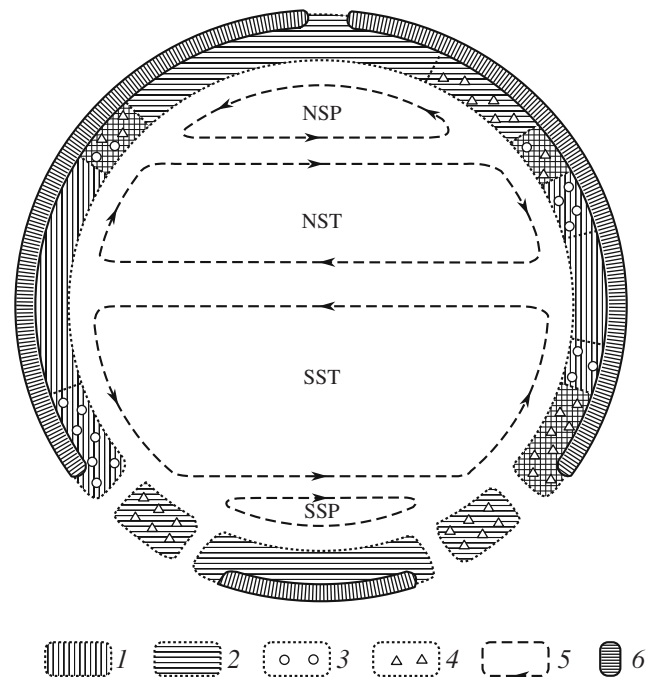


Fig. 5. Scheme of the distortion of the spatial symmetry of the latitudinal faunal zones on the shelves and slopes of the oceanic benthal. Designations: (1) tropical zone; (2) arctic–boreal and subantarctic–Antarctic zones; (3) northern and southern subtropical zones; (4) lower boreal and subantarctic zones; (5) main currents of circulation of surface waters: (NSP) northern subpolar; (NST) northern subtropical; (SST) southern subtropical; and (SSP) southern subpolar; (6) land.

Table 8. Vertical distribution of the geographical elements of the brachiopod fauna (parenthesized figures denote depths for empty shells)

Geographical element	Range of the vertical distribution, m
North Atlantic	0–2652, 3614
North Pacific	0–2393, 4550–4640
Northern circumpolar	2–2450
West Atlantic	2–987, 4920
East Atlantic	0–46, 439–2995
Amphiatlantic	132–4798
Lusitanian–Mauritanian–Mediterranean	2–2679
Caribbean	33–1518
South Brazilian–Uruguayan	24–108
West African	Littoral–20
South African	18–564, 740–960, 1180–1280
Indian Oceanic	10–3490
West Pacific	18–1280, (2021)
Indo–West Pacific	Littoral – 342
South Australian	6–549, (?1097)
Japanese	13–612
Californian	46–399
Pacific–Central American	Littoral – 146, 112–4062
South American	5–1362, 1814–1919
Nouvelle Amsterdam	Littoral – 679
Kerguelen	10–384
New Zealand	0–366
Macquarian	?0, 69–176
Antarctic	75–2273, (2580)
Bipolar of transitional zones	46–1238
Widely tropical	10, 183–782
Coastal–deep-water Atlantic	300–4060
Cosmopolitan	366–5530, (6160, 7460–7600)

as a difference in the quality of the tropical shelf faunas near the west and east coasts of each ocean. There are three reasons for differences between the tropical faunas on both sides of the oceans: (1) waters washing the eastern coasts of the Pacific and Atlantic oceans have higher production compared to the waters washing their western coasts, thus causing differences in the species composition of brachiopods; (2) tropical faunas of the West Pacific and West Atlantic oceans are located in the ancient centers of the brachiopod dispersal, which determines the faunal enrichment of these regions; (3) the spreading of the shelf and bathyal faunas of the tropical zones from west to east is hampered by the oppositely directed currents.

The coefficient of biotic similarity of faunas on the west and east shelves of the Pacific Ocean differs from that of the Atlantic Ocean within one latitudinal zone. The coefficient of biotic similarity of faunas in the Pacific Ocean is less than in the Atlantic because of the longer route for larval interchange between opposite shelves.

SIMPLIFICATION OF THE BIOGEOGRAPHIC STRUCTURE WITH DEPTH

The biogeographic zones of the brachiopod faunas, which are observed on the shelves and slopes and are explained by different climatic conditions, vary at different depths. For instance, the tropical brachiopod species with West African range are represented in the East Atlantic Ocean mainly by Inarticulata and were not found below 20 m. The typical Articulata tier on the seaward edge of the shelf and the upper part of the slope is absent probably because of the unfavorable environmental conditions.

The same is known for the tropical shores of the East Pacific Ocean. Numerous inarticulate brachiopods dwell in the upper sublittoral while the articulate *Macandrevia americana* is known from the depth of the slope only near California and southern Chile; in the equatorial region it descends to the abyssal. The brachiopod tier on the shelf edge and the upper part of the slope here is also absent.

The pelagic zones of the eastern regions of all three oceans are highly productive due to the upwelling of deep-laid waters rich in nutrient elements. The plankton algae are abundant all the year round. For instance, the average monthly quantity of the phytoplankton cells (index of P.I. Usachev) in the Gulf of Panama is almost ten times as much as the same index in the highly productive Kamchatka region (Semina, 1967). The muddy bottom is extremely rich in organic matter at the depths that are usually inhabited by articulate brachiopods. However, such a bottom is not suitable as a substrate for articulates and prevents oxygen formation. These conditions, unfavorable for Articulata, substantially restrict their occurrence in the sublittoral and transitional horizon of the tropical zone.

In the eastern part of the Indian Ocean brachiopods are poorly known but their ability to disperse under these conditions is possibly the same. Anyhow, the Indian–West Pacific element of fauna belongs to shallow waters and consists only of the sublittoral species. In the bathyal zone, the faunas of Indian and Pacific oceans are completely isolated at the species level.

Without the species that dwell only in the sublittoral and transitional horizon, i.e., less than 700 m deep, the brachiopod fauna turns out to be rather poor (Table 8), and the number of its geographical elements decreases considerably. The groups of species with the following types of ranges completely disappear: West African, Indian–West Pacific, Japanese, Californian, South Bra-

zilian–Uruguayan, South Australian, New Zealand, Kerguelen, Nouvelle Amsterdam, and Macquarie.

The biogeographic latitudinal zones also turn to be impoverished in the bathyal. The arctic–boreal zone is represented only by two boreal faunas, North Atlantic and North Pacific.

Of the species of the cold-water zone, only species with Antarctic and South American types of ranges enter the bathyal in the Southern Hemisphere. All other geographical elements of the fauna of the southern cold-water zone including almost all elements of the subantarctic zone (except South American) were not found in the bathyal.

The fauna of the transitional regions undergoes the maximum changes with depth. Of the subtropical and subantarctic zones, only two South African species from the Mozambique Channel and three South American species remain in the bathyal zone in the Southern Hemisphere. In the bathyal zone the transitional zones of the Atlantic and Pacific oceans in the Northern Hemisphere are different. The endemics of the transitional zones are absent in the bathyal near the shores of Japan and California. On the contrary, the fauna of the transitional zones in the Atlantic Ocean is composed of West Atlantic, East Atlantic, amphiatlantic, and Lusitanian–Mauritanian–Mediterranean species and reaches the abyssal zone.

The biogeographic structure of the brachiopod fauna in the bathyal zone is generally simplified compared with the fauna of the sublittoral mainly due to the disappearance of the endemic faunas of transitional zones at depths below 700 m. The exceptions are the North Atlantic Ocean, Mozambique Channel, and slopes of the Southern America.

CORRELATIONS OF THE BIOGEOGRAPHIC AND HYDROLOGICAL STRUCTURES OF THE OCEAN AND POSSIBILITY OF PALEORECONSTRUCTIONS

The brachiopod-based subdivision of the benthic zone on the basis of the distribution of the geographical elements of the fauna within the sublittoral and transitional horizon mainly corresponds to the shelf zoning that is based on the entire fauna (Ekman, 1953; Gur'yanova, 1964, 1972). The most significant distinctive features of the brachiopod distribution are a large coefficient of biotic similarity of subtropical faunas in the west and east of the North Atlantic and a high degree of independence of the faunas of the transitional zones both in the Southern and Northern Hemispheres. In this regard the brachiopod distribution is very similar to the distribution of plankton. It is natural as the brachiopods are benthic filter-feeding animals spreading by dispersing planktonic larvae and thus their vital functions are connected more with the water column than with the substrate.

The brachiopod faunas of the American and European coasts of the Atlantic Ocean are closely related as these coasts are located within a single global large-scale circulation stretched from Central America to the European coast (Fig. 6). That is why the same species of benthic invertebrates from many systematic groups dwell on both sides of the ocean (Mironov et al., 2006).

Many investigators studied recently the possibility of the transatlantic migration of the larvae of benthic invertebrates and concluded that in one way or another it was possible. Probably it is possible also for brachiopods, although their known larval planktonic period is obviously too short to cross the Atlantic. Numerous submarine seamounts produce favorable conditions for amphiatlantic ranges.

In the Pacific Ocean The West Pacific species are distributed from the Asian continent to the Hawaii and Society islands and have the largest gap in ranges. Brachiopods lack amphipacific ranges. The coasts of Asia and America, washed by the currents of the northern subtropical circulation, are possibly inaccessibly far for brachiopods in the Pacific Ocean.

The abundance of brachiopod species in the subtropical regions, which are simultaneously transitional in the Northern Hemisphere, also resembles the peculiarities of the biogeography of the epipelagic zone (Beklemishev, 1967, 1969; Parin, 1968, 1984; Semina, 1974, 2003), where a considerable number of species of the transitional regions is endemic.

The biogeographic division of the benthic zone that is based on brachiopods at bathyal depths resembles the biogeographic division of the abyssal based on the entire bottom fauna due to the decrease in the number of latitudinal (climate) zones with depth (Vinogradova, 1956). Thus the transition from the shelf zoogeography to the zoogeography of the ocean floor is well pronounced in the distribution of brachiopods.

The discreteness of biogeographic division certainly depends on the state of knowledge of fauna and flora and also on the dependence of biogeographic boundaries on the change in various abiotic characteristics, as it was revealed in numerous investigations in this field. The distribution of brachiopods is possibly mainly determined by the complex of factors that change with the change in the water structures. Differences in the structures within the limits of the surface and intermediate waters are more considerable and various than that those in deep waters (Radzikhovskaya and Leont'eva, 1968; Stepanov, 1974). This is determined by the differences in the systems of surface and abyssal ocean circulation. The main currents of the surface oceanic circulation are equally isolated in the intermediate and surface waters (Burkov, 1968). That is why the eurybathic brachiopods dwelling within the surface and intermediate waters, which are subdivided by the main currents of the oceanic circulation, are distributed similarly with the sublittoral species. The number of latitudinal faunal zones distinguished based on the brachio-

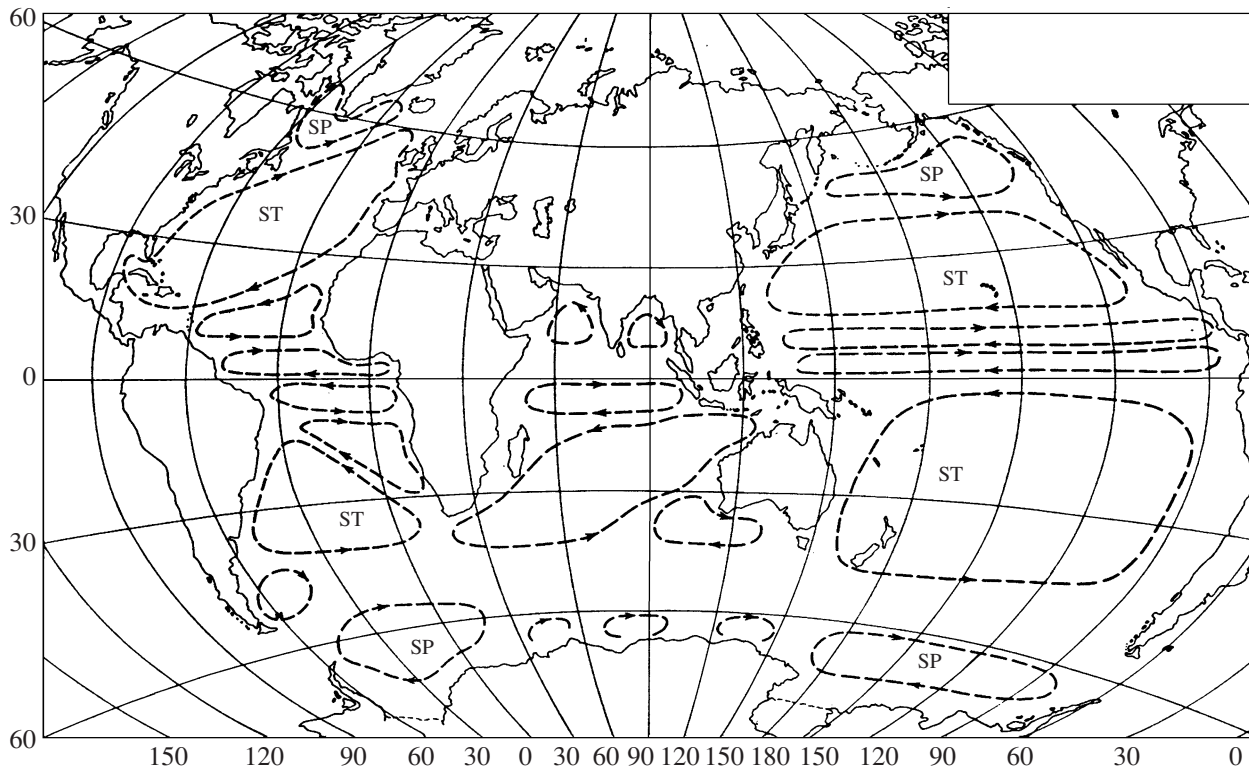


Fig. 6. Arrangement of the main currents of the oceanic circulation of surface and intermediate waters in the modern oceans (after Burkov, 1968, 1980; Bulatov, 1971; Neiman et al., 1997). Designations: (SP) subpolar cyclonic circulation; (ST) subtropical anti-cyclonic circulation.

pod faunas decreases with depth; thus, the hydrological subdivision of the ocean becomes simpler with depth.

The geographical elements of the brachiopod fauna are usually located within the limits of one or several hydrological structures (Zezina, 1976a). The biogeographic boundaries drawn according to the ranges of species coincide with the location of the hydrological frontal zones.

The symmetry in the location of the faunal zones distinguished based on brachiopods depends on the symmetry of the main types of structures of water. The latter depends on the symmetry of the oceanic circulation, which reflects the general climatic processes in the ocean. As the distribution of recent brachiopod species reflects well the modern circulation of waters, the reverse paleoceanic reconstructions based on the brachiopod distribution in the past geological epochs seem to be sufficiently well-founded.

As it is difficult to analyze the distribution of fossil brachiopods at the species level, it is important to reveal the significance of the latitudinal climatic zones for the distribution of supraspecific taxa. As for genera and families, it was shown above that some genera are distributed in comparatively close limits, which correspond to the boundaries of geographical elements of fauna distinguished for species. Other more widespread

taxa are endemic to one or several latitudinal zones: boreal–arctic and subtropical, tropical and subtropical, Antarctic and subantarctic. The distribution of some families coincides with the tropical zone together with the transitional zones. Thus it is quite possible that the borders of the areas of the supraspecific taxa that are used in the paleogeography of brachiopods and some other animals may help to reveal the location of the borders of some paleoclimate zones or anyway to determine the direction of their arrangement.

It is important that the subspecies along with the species may be used both in paleobiogeography and modern biogeography. The following observation was made for the recent brachiopods on this occasion. Species with wide areas located within several hydrological structures are often polytypic and dwell the margins of areas, in the regions of water mixture or behind them, or are represented by local subspecies. *Laqueus californianus erytreus* (Dall, 1920) is the Californian warm-water subspecies of the widespread North Pacific *L. californianus* and differs from the latter only in the deep pink shell. *Dallinella occidentalis obsoleta* (Dall, 1891) from the same region differs from the type subspecies in the smoothed radial ornamentation of the shell. *Terebratella sanguinea haurakiensis* from the coast of North Island of New Zealand is a northern and more warm-water subspecies of the widespread New

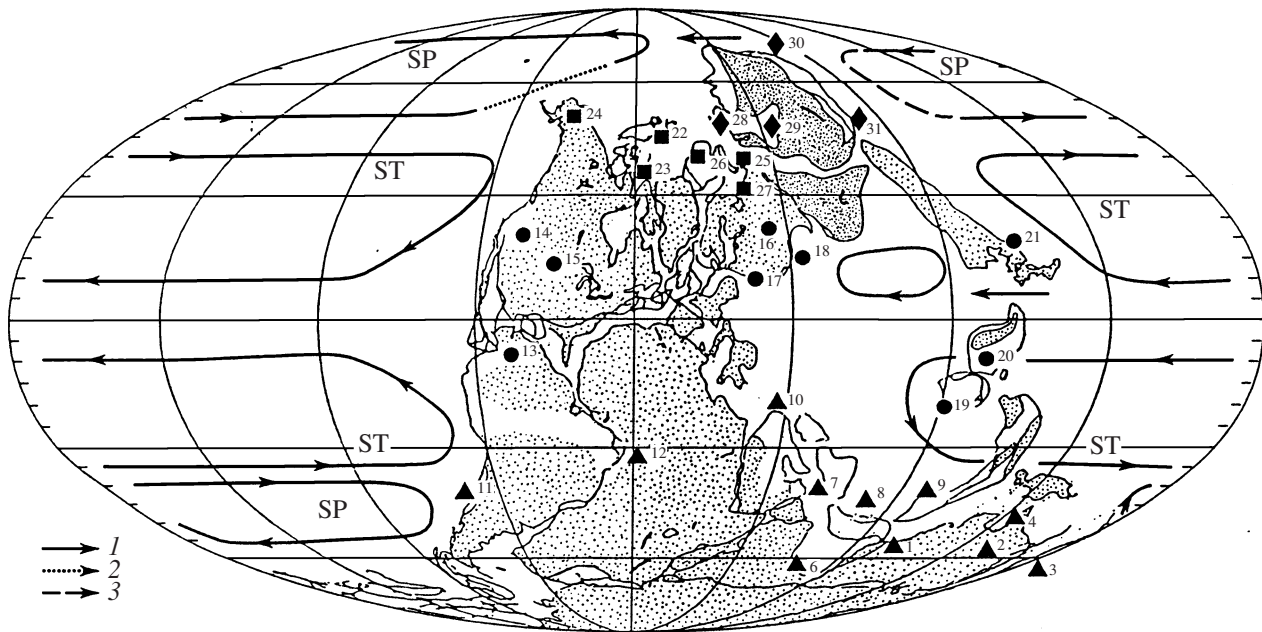


Fig. 7. Scheme of the assumed arrangement of the subtropical (ST) and (SP) subpolar currents of the circulation of surface waters in the Early Permian paleocean and asymmetry of the high-latitude currents near western and eastern shelves (after Grunt and Zezina, 2000). Designations: (1) current directions of the global circulation; (2) warm currents of the northern subpolar circulation; (3) cold currents of the northern subpolar circulation. The arrangement of the lithospheric plates in the second half of the Early Permian (after Scotese and McKerrow, 1990), shelf water areas according to Ziegler et al. (1996). The locations of brachiopod faunas of the subantarctic zone marked with triangles, equatorial–tropical zone by circles, subzones of the temperate latitudes of the boreal zone by squares, subzones of the high latitudes of the boreal zone by rhombs. Designations: paleogeographic elements of fauna: (1) West Australian, (2) East Australian, (3) New Zealand, (4) Irian, (5) Indian–Pakistani, (6) Pamirs–Avgan, (7) Himalayan, (8) South Thailand, (9) Iranian, (10) Andes, (11) Parati, (12) Columbian–Peruvian, (13) Cordilleras, (14) Texan, (15) southern Ural, (16) Alpine, (17) Darwaz–Trans-Alay, (18) Indo–Chinese, (19) South Chinese, (20) Japanese, (21) New Siberian–Wrangelian, (22) Canadian, (23) Yukon, (24) Novaya Zemlya, (25) Greenland–Svalbard, (26) Timan–Pechora, (27) Taimyr–Khatanga, (28) Verkhoyansk, (29) Kolyma–Omolon, and (30) Mongolian–Transbaikalian.

Zealand *Terebratella sanguinea* and differs from *Terebratella sanguinea sanguinea* from South Island both in the pink color and smoothed ornamentation. Some authors suppose *Hemithyris woodwardi* from Japan to be the southern variety of the widespread arctic–boreal circumpolar *H. psittacea* as it differs from the latter only in the smooth and almost black shell. These examples demonstrate a common tendency of widespread cold-water species to form smooth and richly colored forms in the warm-water margins of their ranges.

The above-listed examples prove that the geographical subspecies fit one of the types of ranges of the transitional regions and thus may be used in the biogeographic analysis along with the species. It was known earlier in plankton (Beklemishev, 1969, p. 101).

So the borders of the ranges of brachiopod species and subspecies correspond to the location of frontal hydrological zones near the oceanic shores and are the most sensitive indicators of the biotopic changes; their areas aid to reveal the boundaries between the waters with different physical structure and productive properties. These circumstances make paleoreconstructions possible.

For instance, in the analysis of the brachiopod distribution in the Late Paleozoic seas, the biogeographic paleoreconstruction was produced using data on the meridional asymmetry of the latitudinal faunal zones (Grunt and Zezina, 2000). The analysis was based on the distinguishing of the paleogeographic elements of the brachiopod taxocene at the species level in the same manner as in modern marine biogeography. Then the reasons of the asymmetry of the latitudinal zonality of marine faunas were interpreted using the actualistic approach. The Early Permian benthic faunas were more cold-water in the northeast of the supercontinent Pangaea-2 and less cold-water in the northwest of the same continent. This fact was explained by the oppositely directed coastal currents of the northern subpolar global circulation of the surface waters in the ocean (Fig. 7).

Consequently in the same geographical paleolatitudes within the boreal zone, the coastal waters were colder in the west of the ocean (i.e., near the northeastern shores of the Pangaea) than in the east of the ocean. These paleogeographic concepts could only appear with the usage of mobilistic maps, and thus are a result of progress in the complex development of the modern knowledge of our planet.

ROLE OF THE BATHYAL OCEANIC ZONE IN THE PRESERVATION OF FAUNAL RELICTS

The bathyal zone is a vertical zone of seas and oceans that extends from the edge of the littoral (i.e., the seaward edge of the shelf) down the slope to the ocean floor. The bathyal zone comprises slopes of the continents, islands, underwater mountains and rises, including mid-oceanic ridges. The bathyal zone of the open ocean without shelf was called *thalassobathyal* by Andriyashev (1979), *thalassic modification of the bathyal zone* by Parin (1982, 1984), and *oceanic faunal zone of bathyal* by Mironov (1983, 1985).

Based on the vertical distribution of the bottom fauna, the bathyal zone is divided into the upper subzone (500–1500 m) with transitional horizon (200–1000 m) and lower subzone (1500–3000 m). The bathyal zone is also divided into the mesobenthonic zone (200–1000 m) and bathybenthonic zone (1000–3000 m) based on the distribution of the near-bottom fish fauna. Here we consider the whole range of the bathyal depth from 200 to 3000 m.

Until recently the bathyal remained the most poorly known zones of life. Even the deeper abyssal zone was more attractive for investigators than the bathyal and especially oceanic bathyal. Meanwhile, the slopes of continents, islands, and underwater rises in the above-mentioned range of depths occupy from 12 (without seas) to 18% (with seas) of the total area of the ocean floor. Thus the area of the bathyal zone is 2.4 times (4.2 with seas) as much as the area of the sublittoral zone (*Atlas of Oceans...*, 1980), which is the best studied and used by man.

Historically, a key role of the bathyal zone in the preservation of the marine fauna may be assumed (Zezina, 1979a, 1979b, 1985). This zone is the most available refuge for shallow-water and eurybathic fauna during the considerable sea-level changes in the oceans (about 200 m or more). It is possible that deep-water fauna also finds better conditions and survives in the bathyal zone during periods of major hydrological reconstructions connected with the change in water temperature and gas conditions in the abyss zone. The bathyal zone becomes a source of replenishment both of deep-water and shallow-water biocenoses in the periods between global cataclysms. Due to the property of the bathyal zone to be both a refuge and a source of faunal dispersal, it was called “archibenthal” in the scientific literature. Though this zone is worthy of this name, it was not widely accepted.

The preservation of relicts is one of the more stirring themes in historical biogeography. The term “relict” was first used in the zoological literature in order to explain the records of Mysidacea from freshwater lakes as the remains of the marine fauna after the regression of the sea (Loven, 1862). Strakhov (1932) determined the relict, or vestigial, fauna as differing from the fauna dominating on the Earth at present, but similar to a fauna that dominated some time ago and became

extinct over most of the territory. The detailed analysis of the ecological and geographical criteria of the modern relicts was carried out by Birshtein (1947). According to these criteria, relict taxa are those that changed little over time, i.e., have a slow rate of evolution, and the taxa that according to Darwin “gave up their places” to more improved taxa, but survived under certain conditions up to recently. If the taxa surviving in the modern fauna were initially described on the paleontological material, they are customary called “living fossils.” The problem of relations of relicts and living fossils was multilaterally considered on many concrete examples from different systematic groups of land, freshwater, and marine faunas (Eldredge and Stanley, 1984). We shall not investigate this question more closely but only note that the living fossils are relicts whose history was not reflected or is not enough sufficiently traced in the paleontological chronicle. Anyhow, the fact that, if a taxon was first described on fossil material and only subsequently discovered in the modern fauna, this reflects a wider distribution or larger numbers of individuals in paleocommunities compared to modern ones.

Until recently most of the faunal relicts from the modern high salinity sea waters were found in the sublittoral of low latitudes, where the conditions are supposed to be most stable: inarticulate brachiopods of the family Lingulidae; *Limulus*, or horseshoe crab, from the family Limulidae; reef-building corals *Heliopora coerulea*; gastropods *Neritopsis radula*, *Campanile symbolicum*, *Diastoma melanoides*, and *Gourmya gourmyi*.

These examples are supplemented by the taxa whose ranges include both sublittoral and bathyal zones: bivalves of the family Trigoniidae (six species from the genus *Neotrigonia*, which are distributed from the low water line to a depth of 400 m); cephalopods of the family Nautilidae (a few species from the genus *Nautilus*, which are known from depths of 5–500 m); the bryozoan *Nellia tenella*, which was found from the low water mark down to a depth of 1000 m; primitive crustaceans of the class Cephalocarida (11 species from five genera, mainly sublittoral, but also known to a depth of 1600 m); benthopelagic crustaceans of the family Nebaliidae (15 species of four genera, mainly bathyal but widely vertically spread from sublittoral to abyssal zones). The relict decapods of the family Glypheidae were found at the boundary between the sublittoral and bathyal zones (at depths from 181 to 210 m). This family was considered to have become extinct in the Mesozoic until rediscovered in 1908, and in 1975 the finds of the new modern genus and species *Neoglyphea inopinata* from the Philippine Islands were first published.

The existence of the deep-water (abyssal) relicts is connected with the bottom communities that live on bacterial chemosynthesis in the regions of hydrothermal activity (Laubier, 1986). Barnacles *Neolepas*, bivalves *Bathypecten*, cap-shaped gastropods *Neomphalus* are

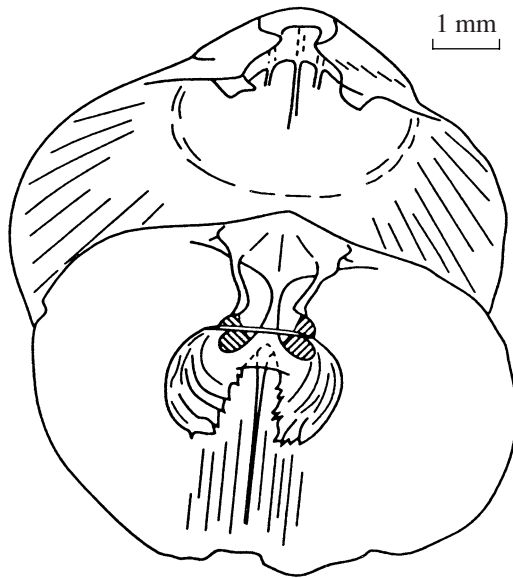


Fig. 8. Modern relict species of articulate brachiopod *Septicollarina oceanica* from the underwater uplift Sala y Gómez Ridge (depth 470–485 m, 18th cruise of the research vessel *Professor Shtokman*).

sometimes regarded as relicts of the ancient shallow warm-water faunas, which took refuge in the conditions of the hydrothermal oases, aberrant for the abyssal zone. The vestimentiferans (Malakhov and Galkin, 1998), or pogonophores (Belyaev, 1989) from the class Aphrenulata are the most populous of the chemotrophic animals. They are not fully deep-water abyssal animals as was previously believed, and they may now be described as bathyal–abyssal. Pogonophores from the

class Phrenulata now are also known from a wider range of depths, 22 to 9735 m. Modern representatives of the ancient mollusks *Monoplacophora* also cannot be considered as abyssal, as *Vema (Laevipilina) hyalina* was found near California coast at a depth of 229–388 m and a number of Russian finds were made at a range of 1600–2000 m, including *Monoplacophorus zenkevitchi* from the underwater mountain in the northern part of the Pacific Ocean (Filatova et al., 1969; Moskaev et al., 1983).

Thus, the distribution of many shallow-water and deep-water relicts and living fossils is more or less connected with the bathyal depths. The bathyal zone was for the first time considered as a zone favorable for the preservation of relicts when living coelacanthid fishes were discovered at depths of the continental slope near South Africa (Smith, 1939). Later they were studied in more detail near the Comoro Islands. The list of bathyal relicts gradually widened. My own interest in the subject grew during the study of the collection of brachiopods that was gathered by the expedition of Thomas Mortensen in 1929 and half a century later was sent for the study from the Zoological Museum of the Copenhagen University to the Shirshov Institute of Oceanology, Russian Academy of Sciences. Then I found and described (Zezina, 1981) two new species of living fossils from a depth of 240 m to the north of the island of Bali, *Sphenarina ezogremena* and *Septicollarina hemiechinata*. Both these species of articulate brachiopods were included into the first International Invertebrate Red Book (*Invertebrate Red Data Book*, 1983). Then the list of bathyal relict brachiopod species was extended (Figs. 8, 9). The articulate *Septicollarina oceanica* was described from the Sala y Gómez Ridge in

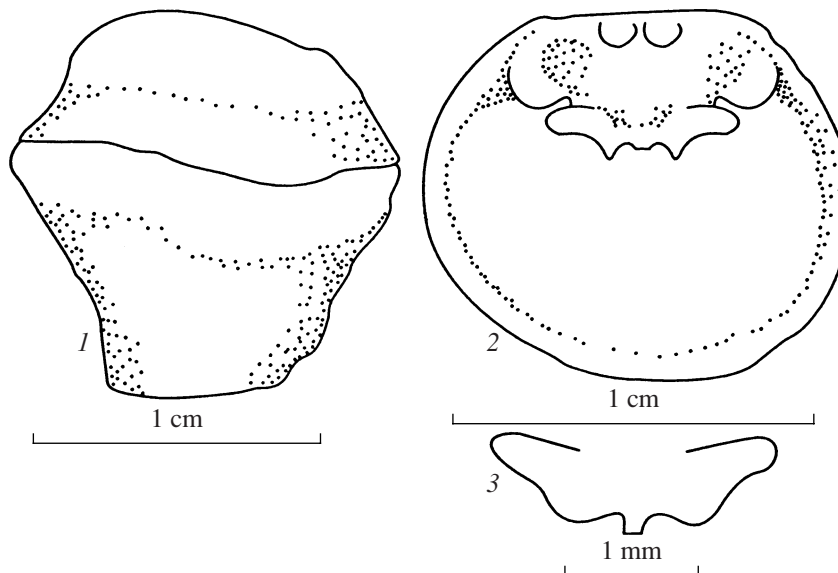


Fig. 9. Modern relict species of inarticulate brachiopod with lophophore supports *Neoancistrocrania norfolki* from the bathyal zone of the Tasman Sea; drawings based on the photographs of Laurin, 1992: (1) lateral view of the holotype shell; (2) interior of the dorsal valve of the holotype; (3) shape of the lophophore supports of the specimen younger than the holotype.

the southeastern part of the Pacific Ocean, depth 470–485 m (Zezina, 1990). *Sphenarina*-like forms were found in the underwater caverns of the Okinawa Islands (Saito et al., 2000; Motchurova-Dekova et al., 2002). Modern inarticulate species *Neoancistrocrania norfolki* with a calcareous shell and lophophore supports was discovered on the underwater ridge dividing the Tasman and Fiji seas (Laurin, 1992, 1997; Zezina, 2005c). Its closest relative must be considered to be the recent *Valdiviathyris quenstedti* known from a single empty shell found near the Saint-Paul Island at a depth of 672 m (Helmke, 1940). Similar fossil inarticulate brachiopods are known only from the Upper Cretaceous of Europe and Middle Asia.

The list of bathyal relicts rapidly widens. Here we shall give a short review, bearing in mind that every one of the discoveries mentioned is as sensational as the find of living coelacanthid fish.

The most numerous are the bathyal finds of relict crinoids. The stalked crinoid *Proisocrinus*, which is similar, according to the French researchers (Roux et al., 1991), to the Jurassic forms, was found near the Loyalty Islands (near New Caledonia) at a depth of 1276 m. The stalked crinoids from the genus *Guillecrinus* resembling Paleozoic forms was found in the same region at a depth of 1276 m. Another species of the same genus was found (Roux, 1985) in the West Indian Ocean near the island of Réunion also in the bathyal zone. The stalked crinoid *Gymnocrinus richeri* described from a depth of 470 m near New Caledonia (Bourseau et al., 1987) is referred to a Jurassic genus, which is united together with genera *Cyrtocrinus* and *Hemicrinus* into the Jurassic–Early Cretaceous family Hemicrinidae. Earlier two modern relict crinoid species *Holopus rangi* from the Caribbean Sea and region of the Bermuda Islands and *Cyathidium foresti* from the bathyal zone of the Azores and Great Meteor Tablemount, at depths 580–850 m, were marked (Arendt, 1974). Both species are referred to the family Holopodidae, order Cyrtocrinida, which is known from the early Jurassic and reached its prime in the Late Jurassic and Early Cretaceous. Later *C. foresti* was also found by the expedition of the Institute of Oceanology, Russian Academy of Sciences (Moskalev et al., 1983) on the slope of the same mountain at a depth of 960–1140 m. The study of the Russian collections of the stalked crinoids from the order Hyocrinida revealed that the family Guillecrinidae, described by researchers from the bathyal zone, at depths of 700–2191 m, is the most primitive among the other families of the order Hyocrinida (Mironov and Sorokina, 1998). This point of view was confirmed by the examination of the French collection of hyocrinids (Roux, 2004), received by the submersible *Nautilé* from the southwestern Pacific and fits the idea of the initial character of the bathyal relict fauna during the secondary settling of great depths by more progressive forms.

Some bathyal relicts are known among gastropods. For instance, the family Pleurotomariidae (Archeogastropoda, Pleurotomariacea) consists of two tens of modern species from several genera from the primitive, mainly Paleozoic group with its prime in the Late Paleozoic. Now these gastropods dwell deeper than 200 m on the tops of underwater banks and on the seaward slopes of the reef islands in the subtropical and tropical waters from East Japan to Taiwan Island and also near South Africa, South America, and Caribbean region. Gastropods from the genus *Cypraeopsis* (Padicularina) until recent were known only from two fossil species from the Miocene of Europe and southeastern Asia and one undescribed species from the Oligocene of France. Modern *C. superstes* was found near New Caledonia and the island of Réunion on 24 stations at a depth range of 435–1005 m (Dolin, 1991).

Under conditions of low seasonal and geographical variations in water temperature, the bathyal zone in the productive valuation is comparable with the sublittoral. The bathyal trophic resources for invertebrates and fishes are considered safe compared with the abyssal ones. In spite of the efforts of biooceanologists, the practical development of the bathyal zone outstrips its scientific research. The bathyal zone, including the oceanic bathyal, is increasingly mastered and is promising for the practical usage as the slopes are more remote than the coast shoal from the exclusive economic zone, or the zone of priority practical usage of the coastal states.

The species dwelling on the tops and slopes of the isolated underwater rises, on the mid-oceanic ridges rising like the underwater mountains, banks, and plateau are the most vulnerable. Trading exploitation of these regions runs the risk of annihilation of rare animals, including relicts and living fossils. The isolated populations of the latter are unrecoverable when the population decreases below a critical level and such species are irreplaceable as biological objects. Anthropogenic exposure may yet destroy taxa that have only just been preserved by nature.

As the majority of species of articulate brachiopods dwell at the depths of the bathyal zone, it seems that this zone was a refuge for a number of taxa of family and even order rank. For animals feeding on the products of decay of pelagic organisms it was easier to survive in this zone, outside the photic layer, even under conditions of the change of the plankton composition at the Paleozoic–Mesozoic boundary.

LARGE DEPTHS, UNDERWATER RISES, UNDERWATER CAVERNS, AND HYDROTHERMAL FIELDS AS REGIONS OF MARGINAL AND EXTREME CONDITIONS FOR BRACHIOPOD EXISTENCE

Ancient and modern brachiopods are the convenient and significant indicators of the temporal and spatial changes in the environment. Phenomena of dwarfism,

paedomorphosis, and homeomorphy testify to the initially unfavorable conditions causing the depression of faunas and restricting complete physical development of the sexually mature individuals. Such faunas were described from the brackish-water (low salinity), small, and more or less isolated basins and regions with elevated concentration of inorganic suspended material (Stepanov, 1937, 1957; Cloud, 1948; Makridin, 1952). Later in the publications of the Paleontological Institute on the change in faunas at the Paleozoic–Mesozoic boundary, the depressed brachiopods and other marine invertebrates were considered as indicators of global reconstruction (Sarycheva et al., 1965).

Despite the fact that brachiopods are relatively scarce in the modern seas in comparison with their abundance in ancient seas, they may be used for the indication of the conditions and processes that may be with certainty checked on zoological objects. The most abundant modern species of articulate brachiopods are studied in detail and therefore it is possible to observe the changes in the modern forms under conditions different from the usual average oceanic conditions. The latter are most favorable for the majority of species of articulate brachiopods in the lower part of the shelf and the upper part of the slopes of the modern seas with high salinity.

Interstitial, Littoral Baths, and Underwater Caverns

The interstitial conditions are highly specific for all invertebrates, including articulate brachiopods. There the life ripples in the limited spaces between the sediment particles, the environmental conditions are unstable and thus the life of the biota is short. The single, but quite impressive, example of a modern interstitial articulate brachiopod is *Gwynia capsula*, which has been known for a long time from the Atlantic coast of Europe. Rudimentary deltidial plates and brachial apparatus and the simplest trocholophe lophophore impart juvenile appearance to adult individuals with a short life cycle and small size (up to 2 mm long).

The littoral baths are another unreliable and short-lived biotope. *Pumilus antiquatus* was found near the coast of South Island, New Zealand. It is simplified form with features of the young kraussinids. They are no longer than 2.5 mm and produce a density of 19000 specimens per square meter of the settled surface (Rickwood, 1968).

The shallow underwater caverns are also an exotic biotope. They are characterized by unstable conditions and low range of food resources. The axolotl *Siredon pisciformis* was found exactly in the underwater caverns of the Mexican lakes at the end of the 18th century and then was brought to Europe by A. de Humboldt and described by G. Cuvier (Nikolskii, 1902). It is a classical example of the neotenic form of the salamander-like amphibian *Ambystoma tygrinum*. As for the brachiopods, the study of marine caverns was begun quite

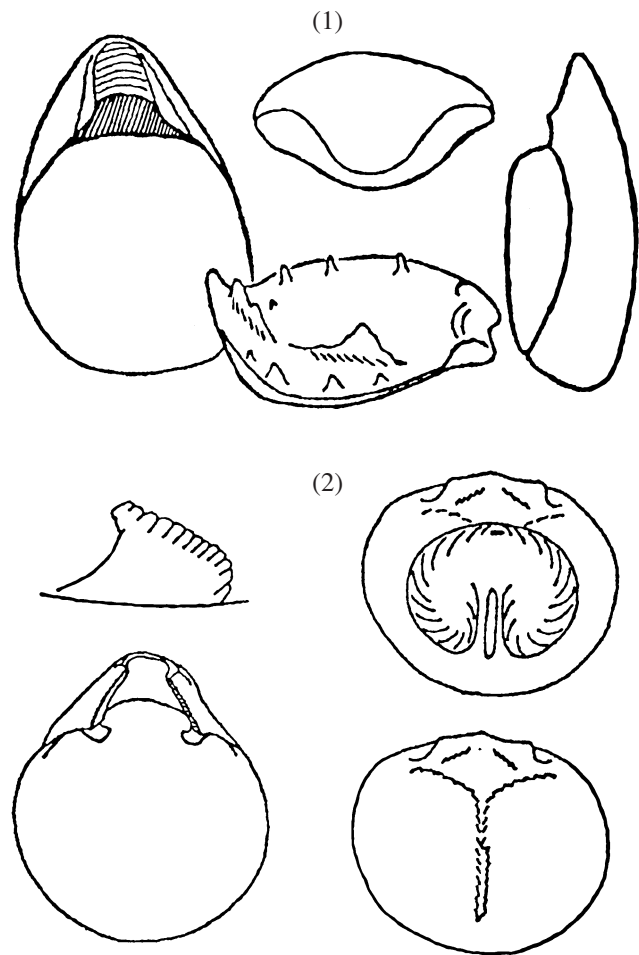


Fig. 10. Simplified forms of the articulated brachiopods: (1) *Pumilus antiquatus* Atkins, 1958, family Kraussinidae, from the littoral baths of the South Island of the New Zealand; (2) *Simplicithyris kurilensis* Zezina, 1976, family Tythothyrididae, from the underwater caverns of the Kuril Islands.

recently as a result of the development, perfection, and wide distribution (also in amateurs and sportsmen) of the lightweight diving equipment and also as a result of the special researches with the usage of manned submersibles. The cavern brachiopods were first found in samples received by scuba divers in the Kuril Islands expeditions of the Zoological Institute, Russian Academy of Sciences; Institute of Marine Biology, Far East Division, Russian Academy of Sciences; and TINRO in 1969–1972. The new genus and species of the terebra-telloid brachiopod *Simplicithyris kurilensis* was described during the systematic examination of these samples (Zezina, 1976b). These brachiopods are small (up to 6 mm long) and have simplified brachial skeleton, which consists of one median septum (Fig. 10). The genus *Simplicithyris* is the simplest form of the family Tythothyrididae, which was described later (Zezina, 1979c), in comparison with the moderately

simplified genus *Tythothyris* and the genus *Diestothyris*, which is the most complicated of them.

The modern articulated brachiopods from the underwater caverns are better studied in the Mediterranean Sea, near the Okinawa Islands (south of the Japanese Islands), near the Maldives (in the Indian Ocean), and on the Osprey Reef in the Coral Sea. Small rhynchonellids from the family Frielleidae with the features of paedomorphic underdevelopment of the brachial skeleton were found in the underwater caverns of Okinawa (Motchurova-Dekova et al., 2002) together with the earlier described West Pacific species. The new genus and species *Tethyrhynchia mediterranea* Logan, 1994, referred by the authors to the new family Tethyrhynchidae was described from the underwater caverns of the Mediterranean Sea near Marseilles and coasts of Tunis (Logan and Zibrovius, 1994). Tethyrhynchids have small (up to 1.2 mm long) smooth shells and a simplified (hypomorphic) brachial skeleton. Of widespread Mediterranean species, very small brachiopods from the genera *Megathyris* and *Argyrotheca* were found in caverns (Simon and Willems, 1999; Ruggiero, 2001). Later small thecideids were also found in caverns (Logan, 2005; Luter et al., 2005). The species composition of the underwater caverns of Croatia was minutely described and the proportions of all discovered species were calculated using the shells that fell from the cavern vaults and became part of the marine coastal sediments (Simon and Willems, 1999). The population changes and growth rates of the brachiopods from the underwater caverns near the Sorrento Peninsula were traced (Ruggiero, 2001). Against the background of the numerous small and short-lived megathyrids, the only species of the comparatively large inarticulate brachiopod *Neocrania anomala* was noted to have slow rates of growth and supposed to have the previously unknown life expectancy of up to 40 years or more.

The Margins of Ranges, Tops of Underwater Rises, and Hydrothermal Fields

The articulate brachiopods with slow rates of growth were found also in the fast currents in the straits of the Aleutian Islands and Kuril Islands arc and in the Sea of Okhotsk near the entrance into the Gulf of Shelikhov. These brachiopods are *Diestothyris frontalis aleutica* (= *Magasella aleutica* Dall, 1872), *Cnismatocentrum parvum*, and *Tythothyris rosemarginata*. *C. parvum* differs from the large related cancellothyrids in the slow rates of growth, considerably smaller sexually mature individuals, and ornamentation consisting of concentric rugae. *M. aleutica* is probably a neotenic variety of the widespread North Pacific *D. frontalis*. *T. rosemarginata* has a features of inherently fixed paedomorphosis. The latter refers to such evolutionary phenomena as juvenilization, progenesis, retrogenesis, and negative anabolism (Iordansky, 2005). The crura and descending branches do not develop in the ontogeny of *Tythothyris*. This evolution-

ary simplification of the brachial skeleton occurs parallel and is distinctly traced in at least three families of terebratuloid brachiopods: Tythothyrididae, Kraussiniidae, and Neothyrididae. The superfamily Cancellothyroidea with short loop is also characterized by the simplification of the brachial skeleton from the genus *Terebratulina* to the genera *Chlidonophora*, *Euclathis*, and *Bathynanus*. The crural processes in this row consecutively shorten and then disappear; the transverse band of the brachial loop also disappears and the lophophore of *Bathynanus* is supported only by crura. There are possibly more examples of paedomorphic evolution in other families of articulate brachiopods that are actually not revealed. According to the New Zealand specialist MacKinnon (2001), the entire Mesozoic–Cenozoic family Megathyrididae (rich in genera and species) is polyphyletic, or according to the author, paraphyletic, as it consists of paedomorphic (secondarily simplified) taxa from at least three superfamilies.

Within the limits of one species, the features of depression are usually observed at the margin of its range. *Hemithyris psittacea* dwells in the White Sea at the limit of permissible salinity of 26.2‰ (Zezina and Semenova, 1979) and at the age of 11 it is smaller than representatives of the same species in the high-salinity seas at the age of 8. Arctic–boreal circumpolar species *H. psittacea* and *Glaciarcula spitzbergensis* live under conditions of sub-zero temperature and desalination up to 32.7‰ in the shallow waters of the Siberian seas. Even in the cases of long life expectancy they are smaller and depressed compared to typical individuals of these species from the southern parts of their ranges (Zezina, 1999). For instance, the circumpolar *G. spitzbergensis* in the boreal waters of the Pacific and Atlantic oceans usually has 13.0-mm-long shells while the largest specimen of this species from the shallow waters north of the New Siberian Islands is 10.2 mm long (according to materials of Russian expeditions and international expeditions of the German research icebreaker *Polarstern*).

Study of the bottom-dwellers of the thalassobathyal zone (slopes and tops of the underwater mountains, rises, and mid-oceanic ridges) became new important area of scientific exploration. Tops and slopes of the underwater rises may be compared in terms of global biogeography with the destination areas of emigration for the species inhabiting continental slopes and thalassobathyal (without considering the endemics of the shelves of islands). Only 18% of the species of the tropical zone of the Pacific Ocean (including the precontinental bathyal) enter the thalassobathyal (Zezina, 1981b). In the northern part of the Atlantic Ocean they constitute 30% (Zezina, 2001a). The number of species of the near-bottom fishes on the underwater rises of the tropical zone of the ocean is about 25% of the entire species composition of mesobenthic and mesobenthopelagic fish fauna (Pakhorukov, 2003). Thus the number of benthic species decreases from three to five times due to the circumpolar geographical zonality (Zezina,

2005a). In the migration to the thalassobathyal, mainly small forms with a wide range of vertical and geographical distribution are selected (Fig. 11). The genera *Cryptopora* (rhynchonellids), *Eucalathis*, *Bathynanus*, *Nanacalathis*, and *Chlidonophora* (cancellothyrids), *Megathyris*, *Argyrotheca*, *Platidia*, and *Phaneropora* are examples in the North Atlantic Ocean. Species with large adult individuals are represented on the underwater rises only by young sexually immature specimens.

The French investigator Legrand-Blain (2000) obtained results similar to ours. She studied Famennian (Upper Devonian) deposits in central France and found that the resettlement of the mountain, which rose over the bottom of an ancient sea and turned from time to time into erupting volcano, occurred periodically by very small spiriferids. But unlike modern dwellers of underwater mountains, the majority of species described by Legrand are known until recent only as endemics of this underwater mountain.

Brachiopods from the regions with underwater volcanic activity (near the hydrothermal springs and cold seeps) are of special interest as many different systematic groups of invertebrate animals inhabit these regions (Gebruk, 2002). Modern brachiopods are still not found immediately near the smokers or seeps but were discovered among the so-called background species on the margins of the hydrothermal fields and fields of cold seeps, in the zones of accumulations of sestonophages, which use one or another unit of the chemotrophic chain based on bacteria. The latter exist on the account of oxidation of the reduced compounds of carbon, sulfur, and iron.

Some brachiopods from the regions with underwater volcanic activity were not determined at the species or even generic level (Hessler and Smithey, 1983; Van Dover et al., 1990; Grassle and Boudrais, 1990; Gregory and Lee, 1995; Lee and Gregory, 2000). The identified species (Zezina, 1990, 1991, 2000b, 2001b, 2002, 2003; Zezina and Pakhnevich, 2000) were found to be small varieties of the genera *Platidia*, *Eucalathis*, *Nanacalathis*, *Abyssothyris*, which are widely distributed both geographically and vertically (eurybathic) and thus highly eurybathic, or species of the local fauna (*Terebratulina kiiensis*, *Laqueus blanfordi*, *Macandrevia americana*, and *Aneboconcha smithi*). Species with large sexually mature individuals (*T. kiiensis*, *L. blanfordi*, *M. americana*) in the studied regions are represented only by young specimens. Dwarfish individuals of *A. smithi* were discovered near the Antarctic Peninsula on the underwater volcano Orca (Zezina and Pakhnevich, 2000). This species was described from other regions using larger specimens. Therefore the trophic and gas conditions near the hydrothermal fields and fields of cold seeps are possibly not favorable for modern articulate brachiopods. The selection of small eurybathic species, presence of dwarfish forms and absence of the sexually mature individuals of the species from

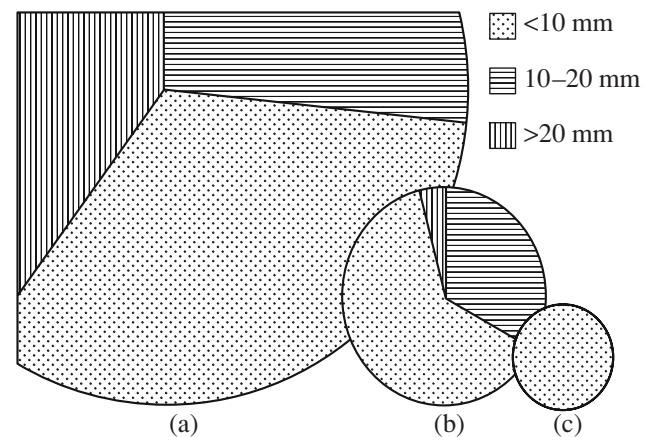


Fig. 11. Ratio of the large to small brachiopods (based on the largest length of adult specimens of each species, mm): (a) all species of recent Articulata; (b) species of Articulata from the open oceanic rises in the North Atlantic; (c) Articulata inhabiting underwater caverns.

the local fauna testify to the marginal conditions for modern terebratulids.

The Mesozoic rhynchonellids (Early Jurassic *Anarhynchia* and Early Cretaceous *Peregrinella*), which are supposed to inhabit paleohydrotherms and paleoseeps, are considered to be eurybathic and capable of living in a broad range of aberrant conditions (Sandy and Campbell, 1994; Sandy, 1995, 2001; Little et al., 1999a).

Large (up to 6 cm in diameter) Silurian lingulats *Pyrodiscus lorraineae* with chitino-phosphate shells were found together with vestimentifers in the paleo-communities of the rift zone of the Southern Urals paleo-ocean (Little et al., 1997, 1998, 1999b). Recently they are the only brachiopods with proven specialization to the conditions of chemotrophic communities in the regions of underwater volcanic activity.

The response of modern brachiopods to the hydrothermal emission and cold seeps may be treated as a response to natural environmental pollution, with the only possible exception being *Dyscolia wyvillei*.

Deep-Water Conditions

Living on the oceanic abyssal, at depths of more than 2000 m is also marginal, or extreme for brachiopods (Zezina, 1989, 1994). The special-purpose deep-water features of the articulate brachiopods include a branched pedicle with long rhizoid-like processes for the attachment to the shells of foraminifers and other hard particles of the deep-water silty sediments. Homeomorphic features also were observed. The classical examples are *Neorhynchia strebeli*, *Abyssothyris wyvillei*, and *Macandrevia (Notorygmia) diamantina* with 1.5-cm-long, thin, and translucent sulcate shells, which are very similar externally but belong to three different families. The morphological similarity of these deep-water species is also in the shell structure

(Zezina and Morozova, 1984). Their fibrous layer is composed of very flattened (lamellar) fibers. Fibers of related shallow-water species are rounded or rhomboidal in cross section. This difference is a result of the economy of the constructional material by the deep-water forms under conditions of high solubility of calcium carbonate under high hydrostatic pressure at a depth of 2000 m or more. Live brachiopods are known up to the depth of 6776 m. The deep-water species of articulated brachiopods also have underdeveloped lophophores with small number of whorls in spire lobes of spirolophore lophophores or with rudimentary median lobe of plectolophore lophophore. Specifically, the lophophore of all deep-water cancellothyridids from the genera *Eucalathis*, *Nanacalathis*, and *Bathynanus* is a variety of the simplified (hypomorphic) so-called "early plectolophore" formed by the underdevelopment of the "complete plectolophore," which is typical of the shallow-water cancellothyridids, for instance, terebratulins.

Thus the main and fairly standard response of brachiopods to the various aberrant conditions (on the oceanic abyssal and underwater rises, near hydrotherms, in the underwater caverns or simply on the margin of a range) is as follows: (1) in all above-mentioned cases except for the latter the small eurybiotic forms are selected; (2) the rate of growth decreases and the sexually mature forms have features of physical depression, that is fixed in the process of pedomorphosis; i.e., the settling of marginal biotopes have important evolutionary consequences for brachiopods and possibly for the other animals.

The process of pedomorphosis in the evolution has a vital importance for many systematic groups including nematodes, echinoderms, and insects. Recently, Plathelminthes, Scolecida, Loricifera, Kinorhyncha, and Kamptozoa were also referred to the groups of "neotenic" origin. A detailed analysis of the correlations of various forms of pedomorphosis in the evolution of vertebrate animals was produced by Iordansky (2005). The hereditary fixation of the neotenic features was also studied in the plant kingdom. Thus the simplification of structure may be considered to be a broadly beaten track, and the example of brachiopods demonstrates that the adaptation to extreme conditions is the starting gun for this type of evolution.

BRACHIOPODS AND MOLLUSKS IN THE BIOLOGICAL FILTER OF MODERN AND ANCIENT SEAS

The history of the development and interrelationship between these two groups of bottom invertebrate animals have always received much consideration of paleontologists (Sarycheva et al., 1965; Stehli et al., 1967; Nevesskaja, 1972, 2004; Stanley, 1977; Afanasjeva and Nevesskaja, 1994; Ciampaglio, 2004).

The aim of this section is to show that the historical change from brachiopods to bivalve mollusks resulted

from the complex changes in the hydrobiological environment in the pelagic and benthic zones of the oceans and seas rather than from competitive replacement.

Bivalve mollusks, which are sestonophages feeding on organic particles suspended in water, occupy a significant place in the natural benthic biological filter of the modern marine water bodies. The primary significance of bivalves, however, is the role they play in the communities of the tidal zone and in the biocenoses of the shelf. A distinctive feature of the filtering activity of bivalve mollusks is the formation of pseudofecal pellets in their mantle cavities that subsequently settle on the bottom and either are used by other aquatic organisms as a food source or are buried in the sediment to enrich it with organic matter rather than to be used for feeding by the mollusks themselves. The role of modern bivalve mollusks as components of the biofilter was thoroughly studied by Voskresenskii (1948) in the White Sea. The Swedish researcher Jansson (1980) made such a study for the Baltic Sea in the late 1970s, when he measured the energy budget in this sea. Sanina (1983) studied the role of bivalves for the northern Caspian Sea. According to data of the American researchers Haven and Morales-Almo (1966), from 3 to 6 kg of sediment (dry weight) is settled by 60 oysters growing on one square meter of the artificial oyster beds in the mouth of the York River (Virginia) from April to October, by these authors' estimate this deposition is seven times as large as that caused by the purely physical process of sedimentation, i.e., without the contribution of bottom-dwelling mollusks.

The modern brachiopods form the largest assemblages in the bathyal zone of the seas and oceans. Under the conditions of rocky substrates and coarse-grained sediment on the upper part of the slopes and, especially, on the seaward edge of shelves and the so-called "shelf break," the population density of articulate brachiopods is up to 410 per square meter and the biomass amounts up to 334 g/m² (Filatova, 1938). A distinctive feature of the filtering activity of brachiopods is that they pick up small, soft food particles, while large, hard particles drop to the bottom from the surface of the lophophore. In articulate brachiopods fecal pellets are expelled one after the other from the gullet, since the process of evolution in articulate brachiopods has resulted in a loss of the hindgut and in the development of a blind-end digestive tract as a result of the adaptation to the feeding on the finest suspended material, which produces almost no metabolic waste products.

According to data of American investigations (McCammon, 1969), the modern articulate brachiopods feed on aggregates that are formed by the adsorption of dissolved organic carbon (DOC) on their surface. The experimental deflocculation of these aggregates, which appear as white flakes and are occasionally considered to be "marine snow," and filtration reveal that the nuclei of the flakes represent pelitic-

size mineral particles. Based on these data the articulate brachiopods are thought to feed predominantly on that part of dissolved organic carbon which was converted from the dissolved to the particulate phase. The brachiopods also assimilate dissolved organic carbon immediately from the solution, as is often the case in marine animals; however, the direct absorption of dissolved organic carbon from the surface of the lophophore meets only a minute fraction of the metabolic energy needs (Doherty, 1981). The main food source of the modern brachiopods is organic suspended material, the nutritional value of which are known to be largely determined by the abundance of bacteria that are present on the surface of flaky particles. The role of bacteria in the feeding of modern articulate brachiopods is clearly shown by the fact that in aquaria brachiopods can live without feeding for months, as long as the water supply does not pass through too fine screens.

Judging from the occurrence of the assemblages of fossil shells, as a component of the biological filter the brachiopods of the Paleozoic epicontinental seas had an importance comparable to that of the bivalve mollusks of modern shelves. In the number of Phanerozoic genera the articulate brachiopods compare well with the bivalve mollusks (Fig. 12a), and it is generally agreed that brachiopods were replaced by mollusks in the process of competition for living space and food.

The comparison of data on the feeding of modern articulate brachiopods with that of bivalve mollusks makes it possible to advance another hypothesis about the interrelationships between these two groups in historical terms. It has been established that the articulate brachiopods and bivalves mollusks feed on different objects: the modern filter-feeding mollusks feed predominantly on living plankton and detritus, and the modern articulate brachiopods feed on suspension that includes products of a more profound transformation of organic matter.

At the Paleozoic–Mesozoic boundary all groups of marine animals suffered the so-called “great extinction event,” which was caused by the decrease in the area of epicontinental seas, and it would appear reasonable that many of the taxa of shallow-water articulate brachiopods that became then extinct disappeared together with their biotopes. Thus, when new seas appeared as a result of the post-Paleozoic transgressions, it was found that they were populated by a new kind of plankton, unknown in the Paleozoic (see Fig. 12b).

In particular, according to Tappan's data (1968, 1971), new components of the Mesozoic–Cenozoic plankton were thick-walled cells of the so-called “shelly” phytoplankton (diatoms, coccolithophorids, and dinoflagellates). The diatom algae, which account for more than half of the Cenozoic plankton both in the number of cells and in biomass, are used for food by many modern benthic animals, but are inedible to articulate brachiopods, which perceive them as unwanted suspended material and respond to the presence of the

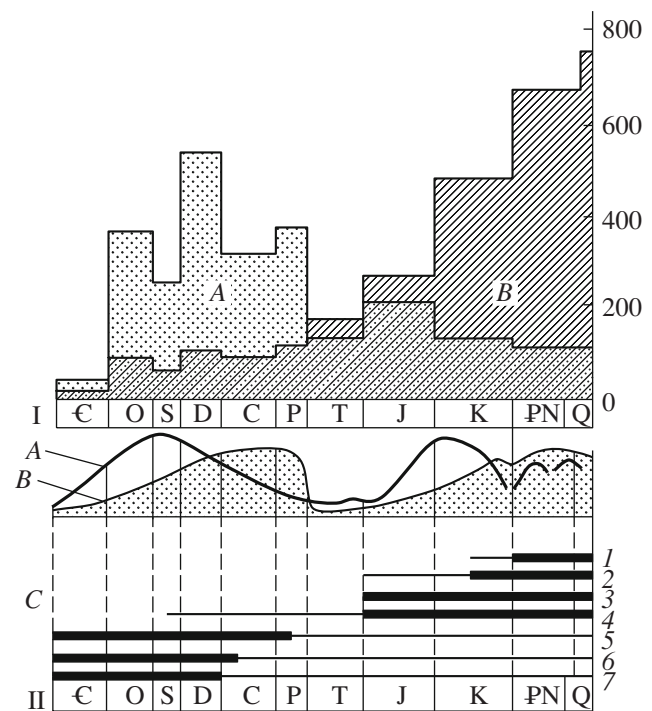


Fig. 12. Changes in benthos and plankton during the Phanerozoic. The time scale of the Paleozoic is reduced by a factor of 1.5. (a) The change in the numbers of genera of (A) articulate brachiopods and (B) bivalve mollusks according to Nevesskaja (1972) and Willams and Hurst (1977) and (b) the change in the (A) production, (B) biomass, and (C) qualitative composition of phytoplankton according to Tappan (1968, 1971) with modifications introduced by Zhuze (1974). (1) silicoflagellates, (2) diatoms, (3) coccolithophorids, (4) dinoflagellates, (5) green algae, (6) blue-green algae (cyanobacteria), (7) and acritarchs.

cells of diatom algae and other “shelly” plankton in much the same manner as to suspended mineral particles: they cease to filter and close the valves, i.e., behave as if in turbid water with suspended inorganic particles.

In the light of these data it would appear reasonable that in the Mesozoic and Cenozoic the brachiopods were far more affected by the emergence of a new kind of plankton, unfit to eat, than by the evolutionary success of bivalve mollusks. The articulate brachiopods adapted to feeding on the products of decomposition of this new plankton and lived under optimal environmental conditions at the continental margin, in the bathyal zone, beyond the photic zone, which is characterized by maximum concentrations of living planktonic organisms. The bivalve mollusks adapted to the new Mesozoic–Cenozoic plankton as a food source because they developed more perfect filtering devices and attained considerable ecological diversity. The rapid increase in the number of siphonal forms among bivalve mollusks (Stanley, 1977) from the Triassic to the Recent indicates that this taxonomic group has met with considerable evolutionary success because the trophic adapta-

tions of this group to the catch and selection of food from the water column allowed it to flourish, especially within the euphotic zone of the seas and oceans.

Thus, the decline of brachiopods at the end of the Paleozoic appears to be a prerequisite rather than the consequence of the flourishing state of bivalve mollusks, since the Early Mesozoic seas were already poor in brachiopods, and this ensured bivalve mollusks (sestonophages) unoccupied ecological niches. A new successful evolutionary radiation of articulate brachiopods on the shelf was delayed by the change in the composition of the plankton; thus, under these conditions bivalve mollusks had a great advantage.

The comparison between the filtering activities of the modern brachiopods and bivalve mollusks shows that the filtration rate of articulate brachiopods is one-third of the filtration rate of mollusks (Hammen, 1971, 1977), whereas the metabolic level of articulate brachiopods is only half of the metabolic level of mollusks. According to some authors (La Barbera, 1981), this suggests that in brachiopods the efficiency of the utilization of the energy expended on the extraction of nutrients from the suspended material is higher than in mollusks. If this is the case, the brachiopods should be in a sense more perfect than mollusks; thus, in the light of these data the competitive replacement of brachiopods by mollusks is extremely improbable. This can be more simply explained by the proposal that throughout their history the suspended material extracted by articulate brachiopods was more nutritious than that extracted by bivalve mollusks (except for those adapted to autochemotrophy under hydrothermal conditions). This explanation is consistent with the hypothesis that was advanced in this section, which is based on the consideration of two different taxonomic groups as components of the benthic biofilter affected by the change in the composition of plankton in oceanic ecosystems during the Phanerozoic.

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