ORIGINAL ARTICLE

A review of bipolarity concepts: History and examples from Radiolaria and Medusozoa (Cnidaria)

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Abstract
Bipolarity, its history and general interpretation are investigated and discussed herein. Apart from the classical view, namely that a bipolar distribution is a peculiar biogeographical phenomenon, we propose that it is ecologically controlled too. This approach was used for bipolarity assessment within the following groups: Phaeodaria, Nassellaria, Spumellaria (Radiolaria) and Medusozoa (Cnidaria). We recognize 46 bipolar radiolarian species and three radiolarian genera. However, although species concepts in radiolarians are relatively stable and well known, the high-rank taxonomy of radiolarians is still not well defined. Caution should therefore be taken in the interpretation of distribution data at a taxonomic level higher than the species. In the Medusozoa, bipolarity is observed for 23 species and 32 genera. The different ways in which bipolarity can develop are discussed under the different groups, but preference has been given to the recent and most probable routes of migration. In our investigation of the bipolarity phenomenon, we reviewed more than 400 articles dealing with taxonomy, ecology and biogeography of the modern fauna in both groups.

Key words: *Biogeography, bipolarity, Medusozoa, Radiolaria*

Introduction

The bipolarity phenomenon is herein investigated using examples from the exclusively pelagic classes Euradiolaria and Medusozoa (phylum Cnidaria), the latter having both pelagic and benthic stages. In both groups, the phenomenon of bipolarity is very clearly represented: as Radiolaria (Bjørklund, Cortese, Kruglikova) and Cnidaria (Stepanjants) specialists we concentrated on these two groups of organisms, and therefore hope that this paper will be of interest to colleagues studying other living taxa, and thus stimulate debate on the bipolarity problem within other taxonomic groups.

As the term "bipolarity" has different interpretations and meanings, we will first cite the classical definition and then, after a short and critical analysis of the history of this problem, we will offer our own views on this phenomenon.

Bipolarity is an interrupted distribution of identical or closely related species (or higher taxa level) of flora or fauna in polar, temperate or subtropical zones of both hemispheres, characterized by their absence in the tropics (Bergh 1947; Stepanjants et al. 1996, 1997a).

Many publications have been dedicated to different aspects of the bipolarity phenomenon, including some (Stepanjants et al. 1996, 1997a) concentrating on the bipolar distribution of Medusozoa (Cnidaria). The representatives of this group display, during their ontogeny, both benthic and pelagic stages, inhabit all depth horizons, and are distributed in all oceanic provinces. The study of bipolarity in Cnidaria is limited to their Recent representatives, as relict forms and fossils are extremely rare. Stepanjants et al. (1996, 1997a) reported 38 bipolar species and 30 bipolar genera of Hydrozoa and Siphono-

phora, but the number of bipolar species is adjusted to 23 herein.

Our interest in analysing the bipolar distribution of Radiolaria is connected with Petrushevskaya (1986), who was the first to question the bipolar distribution of some radiolarian species, and with our own knowledge of the geographical distribution of cold-water radiolarian species in the northern and southern hemispheres. Radiolarian skeletal remains are preserved in sediments and, for some species, we are able to provide evidence about the time of their origin and, accordingly, outline how and where their bipolar distribution developed. New data, however, persuaded us that earlier estimates of the bipolarity phenomenon are different from that proposed by classical authors.

The bipolarity concept and its history: From Captain J. C. Ross until today

James Clark Ross participated on many expeditions in the Arctic and the Antarctic. He was by no means a biologist, but he personally collected and investigated several zoological collections, which made it possible for him to compare faunistic peculiarities from northern and southern polar regions. The results from these observations, based on the collections taken during the H.M.S. *Erebus* and H.M.S. *Terror* expeditions from 1839 to 1843, led by Captain J. C. Ross, have been summarized and published in two volumes. In the first of these volumes (Ross 1847), the idea of a bipolar distribution of some marine organisms was expressed for the first time. Captain Ross traced the deep-water connection between populations of the same, cold-water species from the northern to the southern hemispheres. This means that he was the first author to present the hypothesis that the bipolar distribution of some taxa of marine organisms was due to deep-water migration (Andriashev 1978).

J. Hooker (1847), a member of Ross's expedition, investigated the plants that were collected during this expedition to the Antarctic, and he supported Ross's hypothesis by discovering some plant species in Patagonia, which were also known from Great Britain, but unknown in the tropics. Candolle (1855), in his *Botanical Geography*, also touched upon "des espèces disjointes" (species with disjunct distribution), referring to 32 species that were known from the temperate zones of both hemispheres. Dana (1854) pointed out the similarity, between New Zealand and Great Britain, in genera composition of Decapoda (Crustacea). In his opinion, the closeness (propinquity) effect of faunas in the temperate zones creates morphologically similar

("convergent appearance") species in areas with similar ecological conditions.

We emphasize that all pioneering investigations of bipolarity analysed the same species, or closely related species, from the temperate or subtropical zones of both hemispheres. These species had an interruption in their distribution pattern in the tropics. This, without doubt, allowed earlier biogeographers to equate the meaning of the notions "bipolar" and "antitropical" distribution, as also suggested by Kafanov & Kudrjashov (2000).

Bergh (1920, 1936, 1947) devoted three research papers to this question and paid special attention to *On the Origin of Species* (Darwin 1859). Darwin showed that the same plant species (or subspecies) were found in Europe, southern Australia and New Zealand as in high-mountain areas of the tropics. These plants were typical for the temperate zones of both hemispheres, and were absent in the lowlands of the tropics. This conclusion of Darwin's was adopted as a fact by Bergh.

Bergh (1947: 128, 129) concluded that it should be possible to characterize the presence and distribution of "temperate forms" in the deep cold water of the tropical and subtropical zones as bipolar species. If it is possible to conclude that, from a biogeographer's point of view, bipolar and antitropical species distributions are quite different, then the bipolar distribution probably has an ecological–biogeographical significance, and the two concepts have different meanings. Bergh analysed all data known at his time about closely related species of the same genus that were known from the cold waters off New Zealand, South Africa and South America from the southern hemisphere (and from England, Norway and Kamchatka from the northern hemisphere), but which were absent in the shallow, warm-water areas of the tropical zone. He wrote: "this distinctive and enigmatic peculiarity of the geographic distribution was named bipolarity" (Bergh 1947: 128). This opinion by Bergh (1947: 131) applies mostly to "identical forms or subspecies, or close species" of water mammals or marine fishes, common for "the temperate latitudes of the North and South".

Derjugin (1915), in his *Fauna of the Kola Bay and Conditions of its Life*, included a chapter on "The theory of cosmopolitism and bipolarity", where the faunistic similarities of the "Arctic–Subarctic–boreal" and "Antarctic–Subantarctic–notal" zones were analysed. Here "the same or closely related species" were also found, but these were absent in the "tropical–subtropical waters". This chapter is rich in examples, many of which are without supporting data. However, with respect to some species, e.g. some hydroids, their status as "bipolar" is still valid (see below).

The existence of bipolar species distributions is practically accepted by all biogeographers. Nevertheless, after more than 150 years, the bipolarity question continues to be discussed, and there are both supporters and opponents to whether this phenomenon is real or not. We will try to discuss the available points of view that we have come across concerning the explanation of the causes of this phenomenon.

The idea of bipolarity is discussed, argued and categorically rejected, due to either of the following two reasons:

1. Species are insufficiently identified (Thompson 1897–1898; Knudsen 1970; Pasternak 1973);
2. The comparison of faunas from different zones showed totally different assemblages (Ortmann 1896, partly; Dollo 1904; Stiasny 1934).

The idea of bipolarity is supported (only selected publications on taxonomy, faunistics and biogeography cited) by Ross (1847), Dana (1854), Theel (1886), Pfeffer (1891), Murray (1896), partly Ortmann (1897), Derjugin (1915), Bergh (1920, 1933, 1936, 1947), Zenkevitch (1948, 1960), Hubbs (1952, "antitropical", "bi-temperate" distribution), Ekman (1953), Hubbs et al. (1953), Vinogradova (1955, 1969, 1977), Vinogradov (1959, 1965), Birstein (1960, 1963), Andriashev (1964, 1965, 1987), Darlington (1965), Kussakin (1967), Petrushevskaya (1967, 1969a), Stepanjants (1967, 1979), Kruglikova (1969b, 1999), Stepanjants et al. (1996, 1997a), Beklemishev (1969), Mead (1970), Averintsev (1972), Brundin (1975), Hasle (1976), Dunbar (1979), Pierrot-Bults & Van der Spoel (1979), Rass (1980), Semenov (1982), Es'kov (1984), Gruzov (1985), Briggs (1987), Van der Spoel (1991), Voronov et al. (2002) and others.

Below we have cited the most popular explanations of the bipolarity phenomenon (see also Table I). The definitions of these concepts are by no means accepted by all authors.

Polytopic origin

One of the first ideas on the independent origin of some identical species, "original local creations", was provided by Dana (1854), who pointed out the close environmental similarity, i.e. the cold or temperate conditions of oceanic waters on both hemispheres. Dana noted the presence of some genera within Decapoda (Crustacea), such as *Cancer, Palaemon* and others, and very similar species, such as *Palaemon squilla* (in Great Britain) and *Palaemon affinis* (in New Zealand) in both hemispheres. This allowed him to speak about identi-

cal species of undetermined/independent origin (Stepanjants et al. 1996, 1997a).

Convergent origin

This hypothesis explains the independent origin of identical or closely related species in the temperate zones of both hemispheres as having evolved from warm-water or even tropical forms. The founder of this theory on the origin of bipolarity was Hesse (1924). He examined the distribution of the foraminifer genus *Globigerina* (*Neogloboquadrina*) and proposed *Globigerina pachyderma* as an example of a bipolar species. In his opinion there are in reality two identical species, both originating from the warm-water species *Globigerina dutertrei* under the temperate condition of both hemispheres, and both of these species are named *Globigerina pachyderma*. Darling et al. (2004) concluded, by molecular dating, that the northern *Neogloboquadrina pachyderma* (sin) small subunit (SSU) ribosomal genotype and the southern *N. pachyderma* (sin) SSU genotype separated about 1.8–1.5 Ma ago. This hypothesis has something in common with the opinions of Brinton (1962) and Beklemishev (1969): "the rule of homologous biotopes". This was defined earlier in connection with the mapping of medusae distribution (Maas 1897, 1906, 1909; Vanhöffen 1906), and is also discussed below in connection with the theory of bionomic bipolarity.

Relict theory

The earliest and most widely accepted theory among bipolarity supporters may be named the "relict theory". The founders of this theory were Theel (1886), Pfeffer (1891) and Murray (1896), who developed it from the concept of a universal distribution of marine fauna during the Tertiary. At this time, the climate was sufficiently warm and uniform all over the Earth, and species had a close to global distribution (Steuer 1910; Derjugin 1915; Bergh 1947). During later cold periods, the fauna living close to the poles either died or adapted to the cold waters on both hemispheres, and may be characterized as relict faunas (species). On the contrary, in the tropics, where intensive competition had developed, relict species did not adapt, and disappeared, while a new fauna evolved. Bergh (1947) categorically rejected this possibility. He argued that even before the Tertiary periods there were already strongly pronounced and clearly marked faunistic zones. However, the near-polar fauna had evolved as a result of changes in these environments, whereas the tropical fauna remained almost unchanged. Moreover, Bergh accepted the view by Derjugin (1915)

Table I. Concepts of the origin of the bipolarity phenomenon.

	Hypothesis	Author	Points of concepts
1.	Polytopic origin	Dana 1854	The independent origin of some identical species, "original local creations", where the environments are very similar, i.e. low temperature conditions of the water masses in both hemispheres.
2.	Convergent origin	Hesse 1924	Independent origin of identical, or closely related species in the temperate zones of both hemispheres as having evolved from warm-water or even tropical forms.
3.	Relict theory	Theel 1886 Pfeffer 1891 Murray 1896 Derjugin 1915 Briggs 1987	This concept developed from the idea of the universal distribution of marine fauna during the Tertiary, when the climate was sufficiently warm and uniform all over the Earth, and species had an almost global distribution. During the later colder (glacial) periods, the fauna living close to the poles either died, or became adapted to the cold waters in both hemispheres, and may be characterized as relict fauna (species). In contrast, in the tropics, where intensive competition had developed, the relict species did not adapt and disappeared and new fauna evolved.
3a.	The replaced relict theory, a modification of the relict theory	Gepthner 1936 Darlington 1965 Es'kov 1984	Concentrations of relict forms in extratropical areas are interpreted as specific relict reservations. The tropical zone, therefore, is interpreted as the area where relatively young biota are formed.
4.	Contemporate migrations	Ortmann 1897	This phenomenon was explained as a result of modern migration by coastal or deep-water cold currents. The origin of bipolarity by the migration theory now has wide support among classical faunists and modern biogeographers.
4a.	Anthropogenic transfer	Theel 1911 Derjugin 1915 Mileykovsky 1977	Epibiotic fouling species are drifting along with macrophytes (see discussion below). This theory is applicable to numerous planktonic organisms, including medusae, whose polyps are being distributed as foulings by drifting substratum or ships. The same dispersal mechanism is also possible for species with a pelagic larvae stage.
4b.	Deep-water migrations	Ross 1847 Bergh 1947 Birstein 1963 Vinogradov 1968	Migration of pelagic cold-water species from one hemisphere to the other through meridional deep- and cold-water currents.
5.	Glacial theory	Bergh 1947	Not only the Arctic and the temperate latitudes were affected by the Quaternary cooling during the glacial periods, but the tropics too. During this time, some northern species penetrated into equatorial waters, and then finally inhabited the southern hemisphere. When the temperature in the tropical regions rose again during post-glacial times, cold-water species here either died or were forced to migrate northwards or southwards.
6.	Bionomic bipolarity concept	Andriashev 1986, 1987	The combined influence of closely related environmental factors creates conditions for the parallel development of similar characters in unrelated species. These factors include low water temperature, sea-ice conditions, short insolation periods for the hydrobionts, limited vegetative periods, all of which have a general influence on the character of the reproductive processes, the prolonged embryogenesis, and low food specialization of the hydrobionts. This concept showed independently that the origin of identical conditions, not only accounted for unrelated and morphologically similar species, but for the development of the whole coenosis on both poles of the Earth.

who explained that bipolarity originated from cosmopolitism. It is appropriate to underline that hydroids (Cnidaria, Hydrozoa), based on their flexibility and their accordingly wide distribution, were presented by Derjugin as a group that is very suitable for the investigation of the bipolarity phenomenon. The examples given by Derjugin are convincing, as the species *Filellum serpens*, *Lafoea dumosa*, *Halecium beani*, *Sertularella polyzonia* f. *gigantea* (and others) are, according to Stepanjants et al. (1996)Stepanjants et al. (1997a)), transitional between cosmopolitan and bipolar species. Many of the radiolarian species listed in Appendix 1 seem to confirm the idea of bipolarity arising as a biogeography-/ecology-related phenomenon, and can be interpreted as having a transitional character between cosmopolitan and bipolar species. Examples of these species are, among others, *Lithomitra lineata clevei*, *Lithomitra lineata arachnea*, *Cycladophora davisiana* and *Artostrobus annulatus* (Petrushevskaya 1986; Kruglikova 1999).

Among twentieth-century biogeographers, the relict theory was supported by Briggs (1987), who analysed the latest views on the interrupted distribution of organisms ("antitropical disjunction"), such as "vicarianism", "hologenesis", "island integrations", and so on. He considered that the relict theory is defined and explained by the mechanism of "antitropical disjunction". Similar views were also expressed by Jarms & Mühlenhardt-Siegl (1998), and their precursors (Crame 1974, 1996; Van der Spoel 1991; Dayton et al. 1997). However, Geptner (1936), Darlington (1965) and Es'kov (1984) had a slightly different explanation of this phenomenon. According to their theory, climatically stable tropical faunas migrated to the north and south of the tropics as a consequence of climatic changes, and these relict biotas outside the tropical regions are serving as "reservations" of extinct tropical faunas.

Contemporary migrations

Ortmann (1896) rejected the numerous examples in favour of the existence of the bipolarity phenomenon. However, he analysed the distribution of Decapoda (Crustacea) and found no bipolar species among them. He argued for the genera *Crangon*, *Pandalus* and *Ponthophilus* to be considered as bipolar.

Note here that a bipolar genus does not exclusively include bipolar species. Often a bipolar genus includes cold-water species distributed only in the northern hemisphere, and other cold-water species that are typical for the southern hemisphere, but with no other species having whatever other geographical distribution. As an example of this, the bipolar genus *Gymnogonos* (Cnidaria, Hydrozoa) includes *Gymnogonos crassicornis* from the deep Arctic and *Gymnogonos ameriensis* from the Antarctic regions, and no other species are included in this genus (Stepanjants and Svoboda, 2001).

Ortmann (1897: 581) found some species of *Ponthophilus* "... auf der nördlichen als auch auf der südlichen Halbkugel in den gemässigten und kalten Gegenden" ("... in the northern and southern hemisphere in temperate and cold regions"), whereas the other species of this genus inhabit the great depths in the tropical regions, and representatives of the genus *Ponthophilus* are not known from the shallow waters of the tropics (Ortmann 1897). These arguments allow us to define *Pontophilus* as a bipolar genus, if we follow Darwin's reasoning. Ortmann (1897) offers his own interpretation of the origin of bipolarity, and explains the phenomenon as a result of modern migration by coastal or deep-water cold currents. The origin of bipolarity by the migration theory has now a wide support among classical faunists and modern biogeographers. The distribution of different pelagic organisms, and their bipolar distribution, was confirmed for radiolarians (Popofsky 1908; Haecker 1908), pteropods (Meisenheimer 1905), and other groups, such as medusae, chaetognaths and many others (Chun 1897; Steuer 1910).

Anthropogenic transfer. Among hydroids, the migration theory is convincingly confirmed by the examples of epibiotic-attached species, which are drifting along with macrophytes (see discussion below). This theory is applicable to numerous planktonic organisms, including medusae, whose polyps are being distributed by attachment on drifting substrata, or in ballast tank water on ships. The same distribution mechanism is also possible for species with a pelagic larvae stage (Derjugin 1915; Mileykovsky 1977). According to Derjugin (1915), migrations by way of the larval stage are unlikely, as the larvae are very short lived (a few hours to some months). However, the displacement of suspended particles via the Gulf Stream from the Norwegian Sognefjord estuary to the Lofoten Islands takes only about a year (Helland-Hansen & Nansen 1909). The warm Atlantic current (a branch of the Gulf Stream) needs about 1 year to pass through the Barents Sea (Rudels et al. 1994), giving room for about 12 radiolaria generations, each lasting about 36 days (Casey et al. 1971). Bjørklund & Kruglikova (2003) concluded that the Arctic radiolarians are recruited from the Norwegian Sea, either through the Barents Sea or the Fram Strait. The warm Atlantic water takes about 11 years to reach the Lomonosov Ridge from the Fram Strait (Rudels et al. 1994), and as

radiolarians are found in the Arctic Basins, they must live and reproduce in these water masses. Radiolarians were first introduced to the Arctic Basins not earlier than about 12,400 years bp (Bjørklund & Kruglikova 2003). The self-sustaining Arctic Ocean radiolarian fauna originates from the Norwegian Sea. However, the Arctic Ocean radiolarian population is constantly being recruited from the inflowing Atlantic (Norwegian Sea) water, thus contributing to a renewal of genetic material for the species that can survive the harsh Arctic environments. Similarly, recent data on the settling time for the planulae of some hydroid species (Orlov 1994, 1996) show that it is impossible to exclude the possibility of migration through surface currents.

Deep-water migrations. The migration through deep-water currents is another way to explain a bipolar distribution whose origin can be considered as a self-sustaining system. This theory was first proposed, as an assumption, by Ross (1847), whereas Bergh (1947: 146) did not, in his discussion, exclude it as a possible mechanism. He proposed the typical example of the anglerfish (*Lophius piscatorius*), which is distributed in the North Atlantic to the south of the Azores and Cap Verde Islands, and in the South Atlantic to the north of Cape of Good Hope, living down to about 700 m depth. Bergh supposed that this species may be found at depth in the tropical zone of the Atlantic Ocean. However, in opposition to Ortmann (1897), he supposed that its migration would be from the northern to the southern hemisphere. Bergh (1947: 155), in an idiomatic style, wrote that "… the northerners are more active". The idea of a deep-water migration route was later supported by Birstein (1963). He wrote that the bipolar distribution, typical for some relict shallow-water species, remained after they disappeared from the surface waters, as deep-water progenies (offspring). Andriashev (1964, 1987) supposed that the distribution of some fish species in the families Zoarcidae and Liparidae had, without doubt, a Pacific origin. They migrated, according to his opinion, across deep-water masses along the western districts of North and South America to the Antarctic regions. Here they created a secondary centre of speciation, with a large number of not only species, but also genera. According to Andriashev's (1964, 1987) opinion, the bipolar species distribution of these fish families originated even earlier than the glacial Quaternary. This results in a specific shallow-water fauna into the notal and polar waters of the Southern Ocean. Vinogradov (1968) instead explained the penetration of pelagic cold-water species from one hemisphere to the other through meridional deep- and cold-water currents, the latter being intensified during periods of increased cold-water formation. Some other examples from other fossil groups are available in Boltovskoy (1994) and Boltovskoy et al. (1996).

Glacial theory

Bergh was one of the most prominent supporters of the bipolarity phenomenon. Most of the named theories were only partly accepted when Bergh (1933, 1947) developed his own general theory, the so-called "glacial theory". According to it, not only were the Arctic and temperate latitudes affected by the Quaternary cooling during the glacial periods, but the tropics too. During this time, some northern species penetrated into equatorial waters, and then finally inhabited the southern hemisphere. When the temperature in the tropical regions rose again during post-glacial times, the cold-water species there either died or were forced to migrate northwards or southwards. These species had also the possibility of occupying abyssal depths, just as the terrestrial plants of the high latitudes, as pointed out by Darwin, managed to penetrate the tropical highlands. As already stated, Bergh supposed that the distribution of species, as a rule, took place from north to south. The opposite penetration route (from south to north), however, applies for some fish species in the family Clupeidae (Svetovidov 1949) and Liparidae, genus *Psednos* (Andriashev 1993); most species of the families Trachymedusae and Narcomedusae (Van der Spoel & Heyman 1983; Van der Spoel 1991); several hydroid species of the genus *Monobrachium* (Jarms & Muhlenhardt-Siegl 1998), for some holothurian species of the genus *Elpidia* (Beljaev 1989), some radiolarian species, such as *Lychnocanium grande* (Campbell et Clark) *rugosum* Riedel, *Artostrobus praetabulatus* Petrushevskaya, *Saturnalis circularis* Haeckel, *Pterocanium trilobum* Haeckel and others (KrasheninNIkov et al. 1983; Kruglikova 1989b), and some diatom species such as *Coscinodiscus marginatus* Ehrenberg, *Rhizosolenia barboi* (Brun) and others (A. P. Jouse, pers. comm.).

A variant of this "glacial theory" is probably represented by the earlier named "theory of the shrinking relicts" (Es'kov 1984). According to this theory, some biota remained at their taxonomic and coenotic level as they followed the migrating water masses they were inhabiting, ending up to the north and south of an initial, climatically stable area. These water mass movements were induced by the major Quaternary climatic shifts from glacial to interglacial conditions and back again, and normally implied a north–south migration. The best example of this is in the North Atlantic, where the CLIMAP (Climate/Long Range Investigation Mapping and

Predictions) (1976) project demonstrated that the polar front migrated from its present interglacial position in the Norwegian Sea to a position at about 45°N during the last glacial maximum. Since the establishment of a glaciated northern hemisphere (last 2.7 Ma), there have been at least 40 glacial periods (Mangerud 1992), indicating that major oceanic frontal systems have migrated, in a north–south direction, more than 80 times. The CLIMAP project (1976) demonstrated that the Arctic faunal province drastically expanded during glacial periods, whereas the Subarctic and transitional faunal provinces shrank. The tropical faunal province also became restricted, but remained fairly stable. McIntyre (1967) pointed out that coccoliths showed that surface temperatures in the tropics during the last glaciation did not drop below 20°C, which was also confirmed by the CLIMAP project (1976) results. This indicates that the temperature did not drop to a level permitting cold-water species to cross the tropics through surface currents, but a crossing via subsurface currents still remained possible. It is, however, still not known whether some radiolarian species established themselves as bipolar after the last glacial period, or in any earlier glacial periods. However, after the establishment of the northern hemisphere glaciation there are several examples of radiolarians with a bipolar distribution, as will be discussed later.

The term "bipolarity" ethymologically supposes a comparison of polar flora or fauna. However, the classical understanding of the phenomenon in question applies to polar, temperate and even subtropical areas, as far as distribution patterns are concerned. Bergh (1936: 35) wrote that some biogeographers affirm that …"bipolarity consists in supposed similarity of Arctic and Antarctic faunas. As a rule there is no such similarity and there can't be, but there is similarity between faunistic or floristic elements of temperate latitudes of both hemispheres …". Nevertheless, some investigators have the opinion that the "bipolarity" concept is only valid for Arctic and Antarctic biotas, and only seldom does anybody include boreal and notal distribution patterns in this definition. Hubbs (1952) suggested not using the term bipolar, and using antitropical instead, as most species described as bipolar are usually found at low and moderate latitudes, but not in the tropics, rather than at high latitudes. This kind of limitation is probably a result of ignorance, by many faunists and taxonomists, of the enormous body of literature devoted to this question. Apart from the above-mentioned works, it is sufficient to mention the following monographs on radiolarians (Petrushevskaya 1967), hydroids (Stepanjants 1979), polychaetes (Averintsev 1972) and isopods (Kussakin

1967). General questions of marine biogeography were approached by Semenov (1982: 193), who proposed an original scheme of the latitudinal/zonal nomenclature of species distribution, and named as bipolar a "… distribution in the cold waters of the Arctic and Antarctic". This was largely accepted by several contemporary faunists (Pierrot-Bults & Van der Spoel 1979; Jarms & Mühlenhardt-Siegl 1998) and biogeographers (Dunbar 1979: 116). The last author considered bipolarity as "the presence in the Arctic and the Antarctic of apparently identical species without their presence in the intervening temperate and tropical regions".

During the second half of the twentieth century, "bionomic bipolarity", a new aspect of the bipolarity concept, was developed and defined by Andriashev (1986, 1987). Only true polar biotas were investigated in his analysis. Andriashev (1987: 65) considered himself as the follower of Zenkevitch on this question. In his opinion, the "bionomic bipolarity" is a particular case of Zenkevitch's concept of "longitudinal symmetry of the biologic structure in the Ocean" (Zenkevitch 1948). Nevertheless, Andriashev's "bionomic bipolarity" concept is based on the interpretation of Bergh (1977), suggesting that the geographical landscape has a transforming and selecting influence on the organisms. As a matter of fact, the question is centred on the similarity of abiotic factors in different environments. In this sense, the close environmental characters of the polar regions are especially significant. The combined influence of closely related environmental factors creates conditions for the parallel development of similar characters in unrelated species. These factors include low water temperature, sea-ice conditions, short isolation period for the hydrobionts, and limited vegetative period, all of which have a general influence on the character of the reproductive processes, the prolonged embryogenesis, and low food specialization of the hydrobionts. Andriashev (1987) developed the concept proposed by Bergh (1977) and showed independently that the origin of identical conditions, accounted not only for unrelated and morphologically similar species, but for the development of the whole biocoenosis on both poles of the Earth.

The origin of the cryopelagic communities, taxocoenosis and some species with similar morphological characters (Andriashev 1967, 1970, 1978) is more illustrative in this sense. Some adaptive biological characters were found for the first time in Arctic (Rass 1941; Andriashev et al. 1980) and Antarctic fishes (Andriashev 1964; White 1977; White & North 1985). A specific organic substance having antifreeze properties was found in their blood, a fact of special significance (DeVries 1970; DeVries & Lin

1977; Schneppenheim & Theede 1982; Andriashev 1986, 1987). This specific morpho-ecological category of fishes, characterized by active swimming, a permanent life in water temperatures close to freezing, and a permanent contact with pack ice, was named "cryopelagic" (Eastman & De Vries 1985; Andriashev 1987). In the Arctic, this phenomenon occurs mainly in codfish (family Gadidae), whereas in the Antarctic it has been observed in the genus *Pagothenia* (family Nototheniidae). Apart from the cryopelagic fish species already mentioned, cryopelagic ichthyocoenosis and biocoenosis of fishes and invertebrates were described and investigated in both the Arctic (McGinitie 1955; Barnard 1959; Golikov & Averintsev 1977; Mel'nikov 1980, 1989) and the Antarctic (Gruzov et al. 1967; Andriashev 1967). The similarity of the species composition, as well as the biocoenosis composition, in the two polar regions has been studied previously (Ushakov 1958; Andriashev 1987; Svoboda et al. 1995; Stepanjants et al. 2004).

It is interesting to analyse the origin of bionomic bipolarity, due to its implications for the epigenetic theory of evolution. This theory assumes that in some isolated ecosystems, such as islands, lakes, and other very special ecological niches (e.g. cryopelagic biocoenoses), evolution proceeds quicker than usual, and in this way new forms arise by speciation (Schwarz 1980; Levushkin 1982; Rasnitzin 1987).

According to the position of "adaptive compromise" (Rasnitzin 2002), there is some contradiction in these systems between the environmental situation and the necessity of some organisms to adapt to these environments. If these organisms do not adapt quickly (compromise) to their new environments, they are simply eliminated (extinct). We may therefore conclude that in this situation of an "adaptive compromise" new forms (species) may develop. Moreover, these forms may be similar (although not obviously related) in similar environments.

The current view on the peculiar bipolar distribution for some foraminifera species is that it is caused by genetic exchange of the same subpolar Arctic and Antarctic species (Darling et al. 2000; Norris & De Vargas 2000).

After having concluded the historical survey of the bipolarity concept and its evolution, in addition to the different opinions and approaches to the problem, it is now possible for us to offer a new definition of bipolarity.

New definition of the bipolarity phenomenon

Bipolarity is the wide distribution of either the same, or closely related, or even unrelated taxa at the species and higher taxonomic levels, of flora and fauna having similar morphological characters, and inhabiting similar environments of the cold zones or cold waters of both hemispheres.

We have two distribution patterns that we can describe as being bipolar. The first includes representatives of bipolar taxa that are found in the polar and temperate zones of the World Ocean only, but are missing in the tropics, being characterized by a complexity of environmental conditions (bipolarity type 1, Figure 1). However, some bipolar species may also be found in subtropical and even in tropical zones, but then at greater depths. These migrating species follow the paths of water masses of polar origin with low temperatures and other adequate and closely similar environmental conditions. These marine organisms that are supposed to be "bipolar", but are also found at greater depths in the tropical zones, are described as "bipolar species with an equatorial submergence" (bipolarity type 2, Figure 1). In other words, "bipolarity" is not a clear biogeographical concept based on distribution only, but it is better treated as a biogeographical–ecological phenomenon. We believe that the terms "antitropical" and "bipolar" distribution are different, as the former is a typical biogeographical term, applied to species that are totally absent in the tropics, i.e. a synonym of "interrupted" or "disjunct" distribution. Contrary to an antitropical distribution, a species' bipolar (type 2) distribution would, if plotted on a map, include points in the tropics too, and their occurrence in this zone would be proof of their transport to the tropics by water of supbolar origin (Bogorov 1946). According to Beklemishev (1969), the centre of distribution of these species is situated in Arctic, high-boreal, notal and Antarctic waters, whereas their "expatriation zone" (the periphery of their distribution) is located in the deep cold waters of the tropics. We stress once again how this means that bipolarity (regardless of type) is not only a biogeographical term, but at the same time an ecological phenomenon. The distribution of the type 2 species on a map seems to be cosmopolitan, and therefore, from a biogeographical/ecological point of view, we may classify them as "species with bipolar/cosmopolitan distribution".

Peculiarities of the bipolar distribution of radiolarians

In this paper we consider the protist group "Radiolaria", which has the following higher taxonomic ranking: class Euradiolaria Lameere, 1931, which includes the superorder Phaeodaria Haeckel, 1879 and the superorder Polycystina Ehrenberg, 1838.
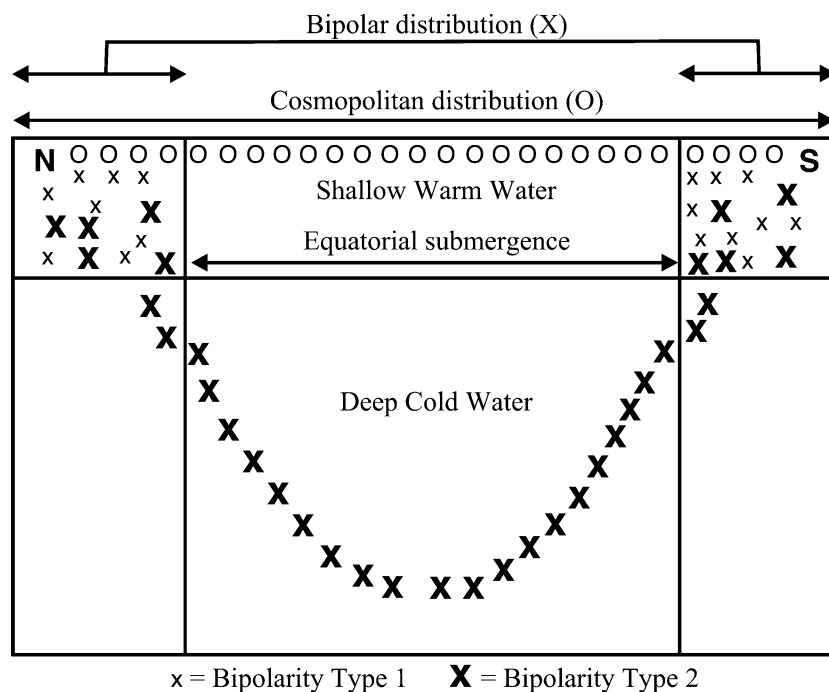
Figure 1. Schematic illustration of cosmopolitan and bipolar distribution types.

Within the latter, the orders Spumellaria and Nassellaria are found, as proposed by Ehrenberg (1875) and later supported by Petrushevskaya (1984, 1986), Petrushevskaya et al. (1976) and Cachon et al. (1990). Herein we do not discuss the protist group Acantharia Müller, 1855, as many taxonomists regard it to be a separate group, at the same taxonomic level as Euradiolaria (Levine et al. 1980; Reshetnjak 1981; Page 1984).

Investigations of peculiar radiolarian distribution patterns have now become possible due to a higher accuracy in the identification of species by contemporary taxonomists. Goll & Merinfeld (1979) calculated the number of described species of living and fossil radiolarians, and proposed species counts of more than 600 for the Phaeodaria, and a far higher but uncertain number, perhaps more than 1500, for present and extinct Polycystina. Recently De Wever et al. (2001) wrote that probably more than 8000 species of polycystine radiolarians, grouped into nearly 2500 genera, are distributed throughout the fossil record. They also surveyed all available sediment trap and haul studies, reporting a total of 269 nassellarian and 210 spumellarian species known from the Arctic, tropical, and Antarctic domains. The number of radiolarian species may be slightly lower, not only due to unwarranted splitting, but most importantly by the limited knowledge we have of both the ontogeny and the geographical distribution of most radiolarian species. The absence of knowledge of the juvenile stages of radiolarians, and of their geographical variability both lead to unjus-

tified descriptions of a multitude of new species. This particularly applies to authors who only investigated restricted areas, and did not pay attention to the distribution and morphological similarities or differences in species from different regions.

Today we have knowledge about radiolarian faunas from practically all regions of the World Ocean. The presence of large collections of radiolarians personally allows authors to ascertain the validity of the species that are included in published species lists. It should be emphasized that in standard plankton samples (plankton net with a mesh size of 125 μm or larger) the representatives of the Polycystina are very rare or even missing, and therefore seldom identified and presented in faunal lists. Phaeodaria tests are considerably larger and, as a rule, almost all phaeodarian species are reported in plankton samples, even if some particularly fragile taxa may be present only as fragments. During the last decades, sediment trap studies have provided important information on radiolarian species composition and living depths, but so far such results are only available from a few scattered points in the World Ocean. Another, and probably more reliable, way to study the polycystine radiolarian fauna, is to investigate the large collections of bottom sediments from the World Ocean. Sedimentary material (box, gravity and piston cores, as well as grab samples) from the deep ocean bottom from a large number of stations began to accumulate during the 1950s in different core libraries in many countries. Since the late 1960s, geological investigations based on drilling

of the deep oceans (Deep Sea Drilling Project, Ocean Drilling Program, Integrated Ocean Drilling Program) regularly recovered complete sedimentary sections, from the oceanic basement to the sediment surface, from different regions of the World Ocean. This allows us to study the distribution of radiolarians in both time and space.

For the work on bipolarity of radiolarians we have used a large number of taxonomic and faunistic publications, from the old classical to the most recent (Bailey 1856; Ehrenberg 1862, 1872; Haeckel 1862, 1881, 1887; Brandt 1895; Cleve 1899, 1900, 1901; Jørgensen 1900, 1905; Borgert 1901; Popofsky 1904, 1908, 1913; Haecker 1908; Dogiel & Reshetnjak 1952; Reshetnjak 1955, 1966, 1981; Riedel 1958, 1971; Hülsemann 1963; Hays 1965; Petrushevskaya 1966, 1969a,b, 1971, 1972, 1977, 1979, 1981, 1986; Nigrini 1967, 1970, 1971; Kruglikova 1969a,b, 1975, 1977, 1988, 1989a,b, 1995, 1999; Riedel & Sanfilippo 1970, 1971; Beers & Steward 1971; Casey et al. 1971; Ling et al. 1971; Kling 1973, 1976, 1977; Ling 1974; Bjørklund 1974, 1976, 1984; Chen 1975; Renz 1976; Weaver 1976; Johnson & Nigrini 1980, 1982; Takahashi & Honjo 1981; Stanley 1981; Nakaseko & Nishimura 1982; Blueford 1983; Bjørklund & Goll 1984; Riedel et al. 1985; Matul 1989, 1990, 1991, 1997; Takahashi 1991; Abelmann 1992a,b; Boltovskoy et al. 1993, 1996; Cortese & Bjørklund 1996; Abelmann & Gowing 1997; Nishimura et al. 1997; Bjørklund & Kruglikova 1998, 2003; Bjørklund et al. 1998; Dolven & Bjørklund 2001; Kruglikova & Bjørklund 2001; Matul et al. 2002; Cortese unpublished).

At the beginning of these investigations on the (palaeo)biogeography of radiolarians, the authors had many hundreds of samples of recent plankton available, as well as a great amount of Palaeocene to Holocene bottom sediment cores from different regions of the World Ocean. These included the Greenland and Norwegian Seas, the shallow waters north of Iceland, the Norwegian fjords, the shallow Eurasian Arctic seas, the high-latitude basins of the Arctic Ocean, different regions of the Atlantic, Indian and Pacific Oceans, including the tropical (equatorial) zone, the Russian Far East seas, and finally the Atlantic, Indian and Pacific sectors of the Antarctic.

By summarizing the available literature and including our own original data, it is now possible to evaluate and estimate the number of radiolarian species inhabiting the different areas (zones) of the World Ocean. The cold-water provinces, i.e. waters with temperatures from −2 to +13°C based on data from Petrushevskaya (1971, 1986), are of special interest to us.

Our data suggest that about 70 polycystine radiolarian species are distributed in the Arctic Basin (Bjørklund & Kruglikova 2003), and about 100 species are known from the Okhotsk Sea (Kruglikova 1975, 1999). A little more than 80 species were identified in the Bering Sea (Blueford 1983) and about 200 species are present in the Arctic–boreal zone of the Pacific Ocean (Kruglikova 1999). In the Norwegian Sea, including the Iceland and Greenland Seas, 105 species have been identified (Bjørklund et al. 1998), whereas more than 100 species comprise the radiolarian assemblage in the Antarctic (Petrushevskaya 1966; Abelmann, pers. comm.). According to Petrushevskaya (1986: 82), radiolarians originated in the tropics, and therefore most of the species are found in warm waters, inhabiting the subsurface levels from 50 to 500 m of the tropical zone. Although it is still unclear whether this theory of a low-latitude origin for radiolarians is true, it is evident that this group is more diversified in the tropics than at the poles. Obviously all these species have not been analysed in the scope of this article.

The list of radiolarian species in Appendix 1 includes those taxa whose geographical distribution, according to our understanding, may be classified as bipolar. To understand the rationale behind the classification of each species as displaying a bipolar distribution, we provide information on the distribution of each species in the northern and southern hemispheres. From this list it appears that 46 species of Phaeodaria, Spumellaria and Nassellaria are in accordance with our definition of bipolar species. The reader should notice that at present we may suggest a bipolar distribution pattern within radiolarians at the species level mostly. However, bipolarity may also occur in three radiolarian genera (i.e. some, but not necessarily all, of the species belonging to each genus have a bipolar distribution), as Petrushevskaya (1981) proposed that the genera *Dumetum* Popofsky, 1913 and *Protoscenium* Jørgensen, 1905 have bipolar distributions, and we propose herein the same for the genus *Botryocampe* Ehrenberg, 1860 emended Petrushevskaya (1975). So far we have not observed any bipolarity at family or higher levels because the taxonomy of these higher rank Radiolaria/Polycystina has not yet been satisfactorily revised. Synonymy issues at the genus level can occasionally cause the grouping of up to eight previous genera. As an example, in the works of Petrushevskaya (arguably the best present-day taxonomist) *Cycladophora davisiana* has been reported as: *Theocalyptra*, *Cycladophora*, *Eucecryphalus*, *Diplocyclas*, and in other works it has also been assigned to *Eucyrtidium*, *Stichopilium*, *Pterocodon* and *Pterocanium*. Bjørklund (1976) combined the genera *Echinomma*, *Actinomma*, *Cromyomma* and *Cromyechinus*

in the single genus *Actinomma*. Thus, at this stage we limit our discussion to the bipolarity of radiolarian species whose taxonomy is more or less confidently known to us.

The species *Sethopilium meunieri* Schröder, 1914 (Appendix 1, 27; Figure 2) has a distribution that fully satisfies the original meaning of the word "bipolarity", as this species is known from the highest Arctic (Meunier 1910; Schröder 1914; Bjørklund & Kruglikova 2003), and from the glacial Antarctic zone (Petrushevskaya 1977). Single occurrences of this species are reported from the Kara Sea and in the central polar basin. Here conditions are similar to "the glacial subregion" of the southern hemisphere (Antarctic Atlas 1966), indicating the possibility that similar species appear in special (extreme) ice conditions (see discussions above and below).

At present, distribution data are available for the following species in the Arctic and high-boreal waters of the Atlantic and Pacific Oceans, or only in the Pacific:

Phaeodaria: *Aulacantha laevissima* Haeckel, 1887 (Appendix 1, 1); *Aulastrum spinosum* Borgert, 1901 (Appendix 1, 5) (Figure 2); *Sagenoscena irmingeriana* Borgert, 1901 (Appendix 1, 8, absent in the Arctic); *Coelographis antarcticus* Haecker, 1908 (Appendix 1, 9).

Spumellaria: *Actinomma boreale* Cleve, 1899 (Appendix 1, 10); *Actinomma l. leptoderma* (Jørgensen, 1900) (Appendix 1, 11); *Actinomma l. longispina* Cortese & Bjørklund, 1998 (Appendix 1, 12); *Rhizoplegma boreale* (Cleve, 1899) (Appendix 1, 15); *Prunopyle? antarctica* Dreyer, 1889 (Appendix 1, 16); *Spongurus pylomaticus* Riedel, 1958 (Appendix 1, 19); *Stylodictya aculeata* Jørgensen, 1905 (Appendix 1, 21); *Stylochlamydium venustum* (Bailey, 1856) (Appendix 1, 22).

Nassellaria: *Protoscenium simplex* (Cleve, 1899) (Appendix 1, 26), *Pseudodictyophimus gracilipes* (Bailey, 1856) *bicornis* (Ehrenberg, 1861) (Appendix 1, 29), *Lophophaena clevei* Petrushevskaya, 1971 (Appendix 1, 31); *Phormacantha hystrix* Jørgensen, 1905 (Appendix 1, 32), *Plectacantha oikiskos* Jørgensen, 1900 (Appendix 1, 33); *Mitrocalpsis araneafera* Popofsky, 1908 (Appendix 1, 34); *Sethoconus tabulatus* Ehrenberg, 1872 (Appendix 1, 35); *Androcyclas gamphonycha* (Jørgensen, 1900) (Appendix 1, 44) and *Botryocampe inflata* (Bailey, 1856) (Appendix 1, 46). These species are found similarly in the "glacial subregion" of the Antarctic. This distribution pattern is referred to as bipolarity type 1 (Figure 1).

The distribution of five additional phaeodarian species can also be considered bipolar, but with some restrictions, as no conclusive data about their vertical distribution are available. So far they have
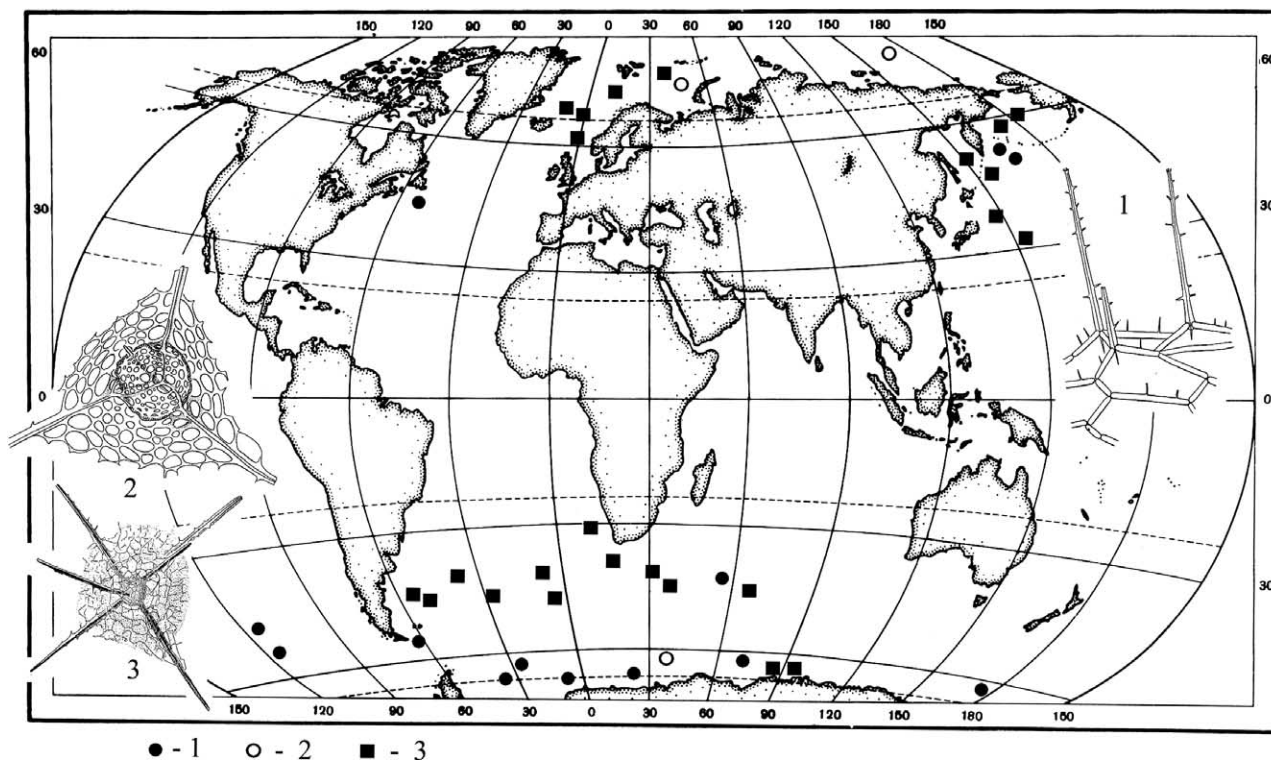

Figure 2. The bipolar distribution of three radiolarian species. The numbers in parentheses refer to the species numbers in Appendix 1. 1, *Aulastrum spinosum* Borgert, 1901 (no. 5); 2, *Sethopylium meunieri* Schroeder, 1914 (no. 27); 3, *Rhizoplegma boreale* (Cleve, 1899) (no. 15).

only been found at subsurface, bathyal and even abyssal depths of the ocean, and there are no data indicating whether these species also exist in surface waters. These species are: *Aulodendron verticillatum* Haecker, 1908 (Appendix 1, 2; 500–3420 m); *Auloceros arborescens irregularis* (Appendix 1, 3; 0– 8500 m); *Aulographonium antarcticum* Haecker, 1908 (Appendix 1, 4; 0–8500 m); *Castanidium inclinatum* Reshetnjak, 1952 (Appendix 1, 7; 0– 4000 m). The distribution of *Castanura primitiva* Reshetnjak, 1952 (Appendix 1, 6; 4000–8000 m) is particularly interesting, as this species has only been found at abyssal depths in the boreal Pacific and in the "glacial" subregion of the Antarctic. In spite of the opinion that no characteristic radiolarians could be found at depths >4000 m (Vinogradov 1968: 175), data by Dogiel & Reshetnjak (1952) indicate that *Castanura primitiva* occurs only at depths >4000 m, and may be considered, probably only in the Pacific, as a typical deep-water bipolar species.

Representatives of *Spongurus pylomaticus* (Riedel, 1958) (Appendix 1, 19) and *Stylochlamydium venustum* (Bailey, 1856) (Appendix 1, 22) are remarkably different morphologically in the northern and southern hemispheres (Kruglikova 1969b, 1974, 1977). The former was described from the Antarctic. Its test has an upper loose layer ("mantle") that grows on a massive spongy part, and covers the test completely. In the Arctic–boreal province of the Pacific, juvenile stages of *Spongurus pylomaticus* resemble a solid, spongy bow-tie. The mantle begins to grow from the middle, and gradually moves towards the ends of the test. During the earliest juvenile stages, the mantle looks like a narrow belt around a "waist". The species from the North Pacific was described as *Spongurus pylomaticus borealis* (Kruglikova 1974, 1977). *Stylochlamidium venustum* from the North Pacific differs from the Antarctic species by its more convex and lenticular shape. Plates covering the spiral central part of the skeleton are more easily seen on it compared with the Antarctic forms (Petrushevskaya 1967; Kruglikova 1969a,b, 1974, 1977). Nevertheless, each of them is regarded as the same species in both hemispheres. This case of bionomical or ecological bipolarity represents an example of closely related species with very similar characters, as they originated independently under the influence of very special conditions. The stratigraphic and regional distribution of a few species was studied by Stanley (1981). On the basis of her data, *Actinomma delicatulum* (Dogiel, 1952) (Appendix 1, 14) and *Spongurus pylomaticus* had a northern and southern population that separated before the glacial onset. No specimens of these taxa have been found at equatorial and low latitudes since the Late Miocene and the timing of their separation is unknown.

The following six Spumellaria species are bipolar: *Actinomma popofskii* (Petrushevskaya, 1967) (Appendix 1, 13), *Actinomma delicatulum* (Dogiel, 1952) (Appendix 1, 14), *Prunopyle? tetrapila* Hays, 1965 (Appendix 1, 17), *Stylatractus pyriformis* (Bailey, 1856) (Appendix 1, 18), *Stylodictya stellata* Bailey, 1856 *validispina* Jørgensen, 1905 (Appendix 1, 20), *Spongotrochus glacialis* Popofsky, 1908 (Appendix 1, 23; Figure 3).

The following 13 Nassellaria species are also bipolar: *Enneaphormis rotula* Haeckel, 1881 (Appendix 1, 24), *Enneaphormis enneastrum* Haeckel, 1887 (Appendix 1, 25); *Pseudodictyophimus gracilipes gracilipes* (Bailey, 1856) (Appendix 1, 28); *Ceratocyrtis histricosa* (Jørgensen, 1905) (Appendix 1, 30); *Artostrobus annulatus* (Bailey, 1856) (Appendix 1, 36); *Artostrobus joergenseni* Petrushevskaya, 1967 (Appendix 1, 37); *Lithomitra lineata clevei* Petrushevskaya, 1974 (Appendix 1, 38); *Lithomitra lineata arachnea* (Ehrenberg, 1862) (Appendix 1, 39; Figure 3); *Cycladophora davisiana davisiana* Ehrenberg, 1862 (Appendix 1, 40); *Cycladophora d. cornutoides* (Petrushevskaya, 1967) (Appendix 1, 41); *Dictyocephalus hirundo* (Haeckel, 1887) (Appendix 1, 42); *Corocalyptra craspedota* (Jørgensen, 1900) (Appendix 1, 43); and *Artobotrys borealis* (Cleve, 1899) (Appendix 1, 45).

The species listed in the two paragraphs above have a very wide distribution area and the borders between them are limited by similar ecological parameters. Distribution plots for these species reveal that they are found in practically all zones of the World Ocean, including the tropics. Due to their ecological requirements, their distribution depths in different oceanic zones are also different. In other words, these migrating species follow the paths of water masses having low temperatures and other adequate environmental conditions (see the concept of latitudinal vertical submergence: Haecker 1908; Reshetnjak 1965), and they are therefore good examples of the above-defined bipolar distribution (bipolarity type 2, Figure 1).

At present we do not know the reasons and time for the development of bipolar species distribution. Stanley (1981), in her thesis, discussed several very interesting aspects of bipolarity in the genera *Prunopyle* and *Sphaeropyle*. There is a series of taxonomic problems that would have been worth discussing in greater detail here, but this is outside the scope of this paper. However, the four species in question are namely: *Prunopyle antarctica* Dreyer, 1889 (Appendix 1, 16) and *Prunopyle tetrapila* Hays, 1965 (Appendix 1, 17), both of which are common in the southern hemisphere in the Pacific, Atlantic and
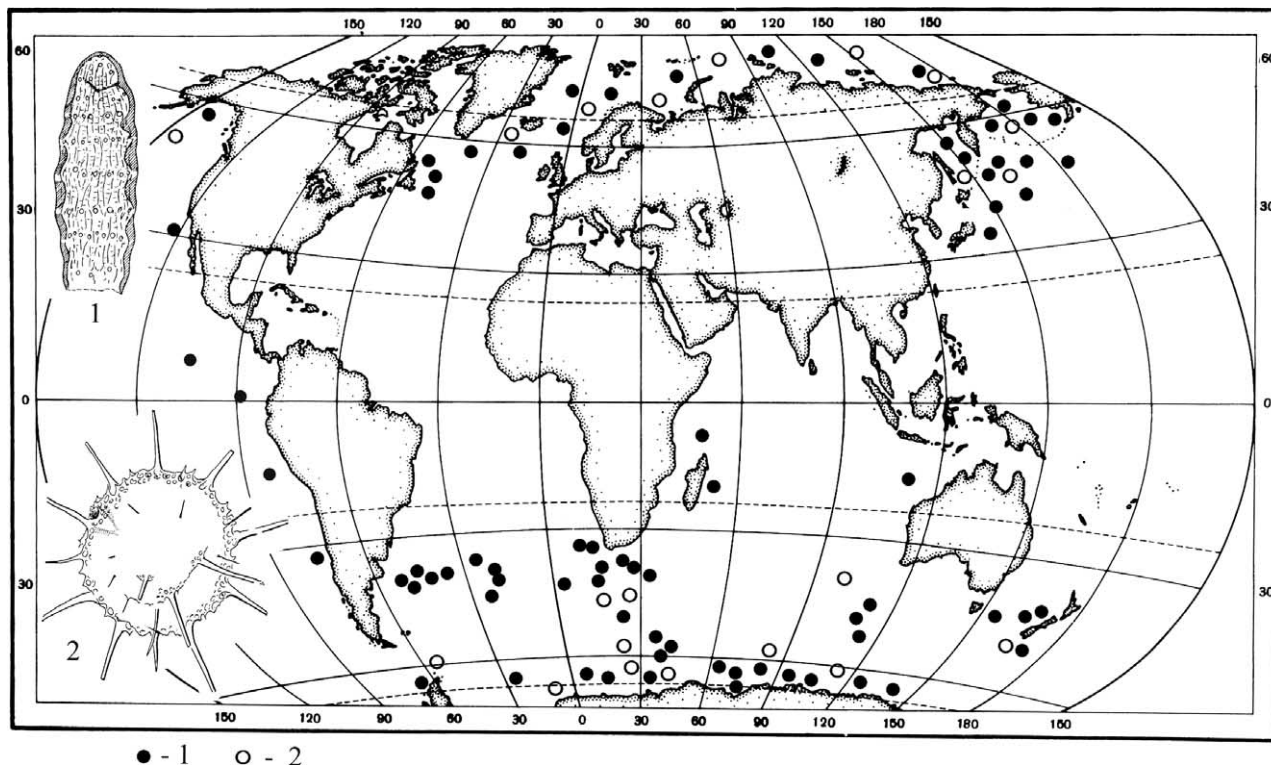
Figure 3. The bipolar distribution of two radiolarian species. The numbers in parentheses refer to the species numbers in Appendix 1. 1, *Lithomitra lineata arachnea* (Ehrenberg, 1862) (no. 39); 2, *Spongotrochus glacialis* Popofsky, 1908 (no. 23).

Indian sectors of the Southern Ocean, and *Sphaeropyle langii* Dreyer, 1889 and *Sphaeropyle robusta* Kling, 1973 are both common in the northern hemisphere in the Pacific Ocean. But Stanley (1981) found *Prunopyle tetrapila* in drilling material in the tropics (at DSDP Site 77) and concluded that this is a cosmopolitan form. Kling (1973) kept *Prunopyle antarctica* as a synonym of *Sphaeropyle langii* and preferred to use *Sphaeropyle langii*. The same taxonomic interpretation was made by Stanley (1981), who synonymized *Sphaeropyle langii* with *Prunopyle antarctica*. Petrushevskaya (1975) pointed out the possibility that *Prunopyle tetrapila* and *Sphaeropyle robusta* are conspecific, and Stanley (1981) also synonymized *Sphaeropyle robusta* with *Prunopyle tetrapila*.

We agree with Petrushevskaya (1975) and Stanley (1981) that *Prunopyle tetrapila* and *Sphaeropyle robusta* are conspecific. However, we do not fully agree with the conclusion of Kling (1973), Petrushevskaya (1975) and Stanley (1981) that *Prunopyle antarctica* and *Sphaeropyle langii* should be synonymized. We think these two forms are different and can be identified and recognized as species or subspecies in both hemispheres and therefore exhibit a bipolar distribution. For the time being we recognize the following three morphotypes: *Prunopyle? langii*, *Prunopyle? tetrapila* and *Prunopyle? antarctica*, the first one with only a northern

distribution, whereas the two latter ones have both a northern (Subarctic) and southern (Antarctic) distribution, i.e. the same species at both hemispheres. At this stage we have some doubt about which genus these species belong in but they should definitely be in the same genus. We include all these forms within the genus *Prunopyle(?)*. In fact, the genus *Sphaeropyle* is artificial, as any form with an incomplete outer sphere (the so-called pylome) can fit its definition. Dreyer (1889), who first proposed the genus, included species with two, three and four spheres, which is a highly artificial practice, and has nothing to do with natural relationships. But we have now arrived at a slightly different interpretation and understanding of their relationship to other actinommids. Petrushevskaya (1967) placed *Sphaeropyle antarctica* in the genus *Cromyechinus* and later transferred this species to the genus *Actinomma* (Petrushevskaya, 1975) (a move that we strongly support). This is beyond the scope of this paper, but we will point out the fact that *Actinomma boreale* Cleve, *Actinomma leptoderma* (Jørgensen), and *Prunopyle(?) antarctica* (our Appendix 1) are three species with very similar skeletal morphology, but all three show a bipolar distribution. This is based on the new material that is now available to us (study in progress). A revision of these genera and species is needed to fully understand their relationship.

Our attempt was to answer the question: what were the reasons for, and when did the bipolar species obtain their present disjunct distribution? We may get some answers from palaeontological data. *Prunopyle tetrapila* was reported by Kling (1973) to be extinct in the Pliocene (ca. 1.85 Ma), close to the Pleistocene boundary, but Stanley (1981) extended the extinction to close to 1 Ma. In the Antarctic, Hays (1965) reported *Prunopyle tetrapila* to be extinct in the lower Pleistocene at ca. 0.7 Ma. Stanley (1981) found *Prunopyle tetrapila* to be extinct at ca. 1.6 Ma in the tropics, at DSDP Site 77, and concluded that it was a cosmopolitan form prior to 1.6 Ma, but had a disjunct or bipolar distribution after 1.6 Ma.

Motoyama's (1997) data can also be used to explain this phenomenon. *Cycladophora davisiana davisiana* first occurred in the Northwest Pacific at 4.2 Ma, and rapidly increased in abundance at 2.7 Ma. This is the time when the northern hemisphere glaciation started, a timing that is well documented in the North Atlantic (Jansen et al. 1989) and in the North Pacific (Haug et al. 2005). During the Early Pleistocene, *Cycladophora davisiana davisiana* had a cosmopolitan distribution, but at about 1 Ma it became common at high latitudes in both hemispheres, whereas at low latitudes it only occurred in low numbers, as is also the case today.

Cycladophora davisiana davisiana is the only species, for the time being, that we can demonstrate having a distribution pattern associated with glacial events, as this taxon had an abundance increase at the onset of northern hemisphere glaciation at 2.7 Ma and became common at high latitudes in the time interval (1.2–0.9 Ma) when Pleistocene glaciations were changing from a 41 to a 100 ka cycle. *Cycladophora davisiana davisiana* evolved first in the northern hemisphere and then, as suggested by Motoyama (1997), it migrated from the north to other oceans, again an example supporting the glacial theory of Bergh (1947).

In summary, radiolarians do not provide conclusive evidence of which theory better explains the mechanism behind the present-day bipolar distribution of some taxa. Another aspect relevant to the interpretation of the proposed evolutionary changes and, more generally, the contribution of radiolarians to bipolarity theories, concerns the chronology used in Stanley (1981). This was based on Berggren's timescale (Berggren 1972; Haq et al. 1977), where the Pliocene/Pleistocene boundary is dated at 1.6 Ma, and is supposed to represent the onset of rapid glacial/interglacial oscillations (Keany & Kennett 1972). This is not correct as oxygen isotope stratigraphy and ice rafted detritus records from the North Atlantic suggest that the strengthening of

the northern hemisphere glaciation took place at about 2.7 Ma (Jansen et al. 1989). Between 2.7 and ca. 1.2 Ma, glacial oscillations had a period of 41 ka (short-lasting glacials of small amplitude), but since ca. 0.9 Ma the well-known 100 ka oscillations (long glacials of large amplitude) became established. One could speculate that the onset of glaciations on both poles and the shift from short and small to long and extensive glacial intervals at 0.9 Ma could represent events having a strong ecological impact, and could have caused the appearance of a disjunct bipolar distribution in some species. However, only the *Prunopyle antarctica* event seems to match the time interval (1.2–0.9 Ma), at the time when Pleistocene glaciations changed from a 41 to a 100 ka cycle. The stratigraphic range of *Prunopyle tetrapila* clearly indicates how this species was most common in the northern hemisphere and in the tropics. *Prunopyle antarctica* evolved in the lowermost Lower Pleistocene and, according to the chronology used by Stanley (1981), this transition occurred slightly later in the Antarctic. This would indicate a transport from north to south, which is in agreement with the theory of bipolarity proposed by Bergh (1947).

An indication of the importance of glacial cycles for the establishment of a bipolar distribution in Protozoa also comes from molecular biology investigations on planktonic foraminifera. Darling et al. (2004) discussed the genetic variation in *Neogloboquadrina pachyderma* from the Atlantic Arctic and the Antarctic. They obtained, by molecular dating, an estimate of 1.8–1.5 Ma for the divergence of the northern hemisphere left-coiling *Neogloboquadrina pachyderma* SSU genotype from the southern hemisphere left-coiling *Neogloboquadrina pachyderma* SSU genotype. They further concluded that the northern and southern SSU genotypes are mutually exclusive and remained genetically and geographically isolated until today. The two populations, after their initial isolation, were unable to maintain a genetic exchange across the tropics and have therefore been geographically and genetically isolated until today. In the southern hemisphere there are four SSU genotypes, and their diversification seems to be linked to glacial/interglacial climate dynamics. The left-coiling *Neogloboquadrina pachyderma* type IV separated from the other SSU genotypes around 1.1–0.5 Ma (i.e. during the climate system transition to 100 ka glacial cycles).

All of the above-mentioned species assumed to be bipolar are typical representatives of the recent radiolarian fauna. Petrushevskaya (1986) mentioned two nassellarian species, *Enneaphormis rotula* Haeckel, 1881 (Appendix 1, 24) and *Cycladophora davisiana davisiana* (Ehrenberg, 1862) (Appendix 1, 40) as possible species of relict genera of Palaeogene

or Cretaceous origin. These species presently inhabit subsurface waters in the geographical area bordering the centre of their origin (see Appendix 1), and never occur at the surface in the tropical zone. There are, in fact, indications that a bipolar geographical distribution was also characteristic for some components of ancient radiolarian faunas too, and bipolarity in radiolarians would then not necessarily be a very recent development. Species having a bipolar distribution were rather numerous in the post-Miocene deposits from the Norwegian–Greenland Seas and the South Atlantic Ocean (Lazarus 2002). Additionally, the Early Palaeogene associations of the New Zealand area (Hollis 2002) are very similar to the associations found on the Russian Platform and in west Siberia (Kozlova 1999; Afanasieva et al. 2005). Amon (2000, 2003) suggested a bipolar distribution for some members of the Late Cretaceous genus *Prunobrachium*, whereas Vishnevskaya (1991, 2001) pointed to a possible bipolar distribution for several of the Jurassic and Cretaceous species recovered from the boreal province in Russia. Other authors noted the similarity of Triassic associations between east Siberia and New Zealand (Aita & Bragin 1999). All this body of evidence, and several other reports from different areas of the world, seem to indicate that bipolarity in radiolarians is a rather ancient phenomenon.

We do not know when the present bipolar radiolarian species established themselves, but it is probably a relatively recent feature. Although it is still uncertain whether they established themselves as such after the last glaciation or after the development of northern hemisphere glaciation. In the latter case, they have also survived earlier glaciations. Geological and palaeontological evidence does not support vicariance as a process to create bipolar distributions (Lindberg 1991), but it instead favours biotic interchange, both southward and northward, between the hemispheres. These events are probably related to a plurality of mechanisms (i.e. regional tectonic events and Pleistocene glaciations), rather than a single event. This is in good agreement with our radiolarian events that indicate that the separation of species took place both before and during the northern hemisphere glacial onset.

The following conclusions can be drawn on the bipolarity of radiolarian taxa:

- All of the species of Phaeodaria, Spumellaria and Nassellaria having a bipolar distribution belong to the recent fauna, except for *Prunopyle? tetrapila* (extinct in the Pliocene). No Phaeodaria have any analogues in the fossil record, whereas in Spumellaria and Nassellaria we have several examples.
- Of the 46 recent species discussed here, only one is restricted to the polar areas, 26 have bipolarity type 1 (disjuncted areal distribution), of which two are examples of bionomical bipolarity, and 19 species are of bipolarity type 2 (equatorial submergence).
- At present, we know of only two bipolar Nassellaria species that are presumably relicts of Palaeogene and Cretaceous radiolarian genera, although additional examples may be found in the Miocene.
- Some bipolar species developed their bipolar distribution in Late Miocene, a time interval that is not associated with any northern glaciation events.
- Some bipolar species became disjunct in the Early Pleistocene (onset of the 100 ka glacial cycles) and seem to have evolved from species with a cosmopolitan distribution.
- As bipolarity within polycystine radiolarian species arose at different times, the causes were probably active over a long time interval, and separation by temperature changes in the Pleistocene is only one of the possible reasons.
- The origin of the bipolar distribution of some radiolarian species can be explained by their deep-water migration through the cold meridional currents.
- Within the euradiolarians there are three bipolar genera, and no families or higher taxa.

Peculiarities of the bipolar distribution of Medusozoa

As noted earlier, Stepanjants et al. (1996, 1997a) discussed the bipolar distribution of Cnidaria: Medusozoa (Hydrozoa, Siphonophora and Scyphozoa; Anthozoa not discussed) based on numerous publications by taxonomists and faunists who have been working with these groups of invertebrates (Chun 1897; Vanhöffen 1902, 1906; Maas 1906, 1909; Broch 1910; Stepanjants 1967, 1979, 1989; Antsulevitch 1987; Margulis 1989; Van der Spoel 1991; Svoboda et al. 1995; Stepanjants et al. 1997a, 2004; Sheiko & Stepanjants 1997a,b; Jarms & Mühlenhardt-Siegl 1998; Stepanjants & Svoboda 2001; Svoboda & Stepanjants 2001). General faunistic and biogeographical investigations were carried out by Derjugin (1915), Bergh (1947) and Ushakov (1958). However, it is clear from these publications that these authors did not clearly understand the concept of "bipolar distribution", and they presented different explanations of this concept. The identification of species that were previously

assumed to be bipolar is no longer trustworthy. For example, the Hydrozoa species *Campanularia verticillata* (Linnaeus, 1758), mentioned by Derjugin (1915) and Bergh (1947) as a "classically bipolar" species, in reality has another areal distribution, and it now belongs to the family Campanulariidae and is named *Rhizocaulus verticillatus* (Linnaeus, 1758) (Stechow 1919; Cornelius 1982, 1995a; Stepanjants 1989). Its distribution may be classified as Arctic–boreal, and is only restricted to the northern hemisphere. *Rhizocaulus verticillatus* does not exist at all in the southern hemisphere, where another pan-Antarctic species of the family Campanulinidae (Stechow 1919; Stepanjants 1979), *Stegella grandis* (Hickson et Gravely, 1907), occurs. The vertical hydrothecae distribution on the polysiphonic stem and branches is very similar to that on the colonies of *Rhizocaulus verticillatus*, which is the only character common to both species.

At present, the reliability and accuracy of species identification within Medusozoa has significantly improved. There are now a significant number of well-qualified articles on the systematics of Cnidaria based on material obtained from the surface to abyssal depths from different regions and zoogeographical provinces of the World Ocean, from the Arctic to the Antarctic. A species list of Medusozoa based on the material in the large collections of the Zoological Institute of the Russian Academy of Sciences is now available in our database, along with a list of publications that are relevant to our bipolarity discussion (Briggs 1928, 1938; Hyman 1929, 1930, 1931a,b; Fraser 1940, 1941, 1943a,b, 1944, 1946; Manton 1940; Kramp 1942, 1943a,b, 1961, 1963, 1965, 1968; Russel 1953, 1970; Hirai & Kakimura 1957; Vervoort 1959, 1966, 1967, 1968, 1972, 1985, 1993a,b; Naumov 1960, 1961, 1971; Brinckman 1962, 1965; Blanko 1963, 1967, 1969, 1977, 1978, 1980, 1982, 1991; Yamada 1964; Hirai & Yamada 1965; Brinckmann-Voss 1966, 1970, 1989; Stepanjants 1967, 1975, 1979, 1980, 1988, 1989, 1994, 1998, 1999, 2001; Calder 1970, 1971, 1972a,b, 1975, 1983, 1984, 1986a,b, 1988, 1991, 1993a,b, 1996, 1997; Uchida 1970; Alvarino 1971; Christiansen 1972; Edwards 1972, 1973, 1983; Robins 1972; Bouillon 1975, 1978a,b,c, 1984, 1985, 1995a,b; Cornelius 1975a,b, 1979, 1982, 1987, 1990, 1992, 1995a,b, 1998, 1999; Millard 1975, 1977, 1978, 1979; Hirohito 1977, 1984, 1988, 1995; Vervoort & Vasseur 1977; Kubota 1978, 1987, 1989, 1991, 1992a,b, 1993, 1999; Svoboda 1979; Margulis & Karlsen 1980, 1985; Chapligina 1980, 1992, 1993; Arai & Brinckmann-Voss 1980; Larson 1980, 1988, 1990; Boero 1981; Kubota & Yamada 1982, 1992; Antsulevitch & Stepanjants 1985; Watson 1985, 1992, 1998; Calder

& Vervoort 1986, 1998; Antsulevitch 1987; Campbell 1987, 1989; Rees & Vervoort 1987; Jarms 1988, 1990, 1991, 1994, 1997; Larson & Fautin 1989; Margulis 1989; Stepanjants & Lobanov 1989; Brinckmann-Voss et al. 1989; Gibbons & Riland 1989; Stepanjants et al. 1990, 1996, 1997a,b, 1998, 1999a, b; Namikawa et al. 1990, 1992; Beshbeeshy 1991; Larson et al. 1991; Namikawa 1991; Ryland & Gibbons 1991; Svoboda & Cornelius 1991; Yamada & Kubota 1991; Boero & Hewitt 1992; Kubota & Takashima 1992; Pages et al. 1992; Ramil & Vervoort 1992; Antsulevitch & Vervoort 1993; Boero & Bouillon 1993a,b; Pugh & Pages 1993; Pages & Kurbjeweit 1994; Boero et al. 1995; Medel & Vervoort 1995, 2000; Segonzac & Vervoort 1995; Svoboda et al. 1995, 1997; Marques 1996; Migotto 1996; Peña Cantero et al. 1996, 1997a, b; Schuchert 1996, 1997, 2001a,b, 2004; Stepanjants & Dianov 1997; Pages 1997; Brinckmann-Voss & Arai 1998; Gravier-Bonnet 1998, 1999; Jarms & Mühlenhardt-Siegl 1998; Mapstone 1998; Marques & Migotto 1998; Medel & Lopez-Gonzalez 1998; Migotto & Calder 1998; Peña Cantero 1998; Ramil et al. 1998; Stübing & Piepenburg 1998; Panteleeva 1999; Panteleeva et al. 1999; Bouillon & Boero 2000; Marques & Calder 2000; Marques et al. 2000; Ansin Agis et al. 2001; Hewitt & Goddard 2001; Stepanjants & Svoboda 2001; Svoboda & Stepanjants 2001; Watson & Vervoort 2001; Bouillon et al. 2002; among others).

In most cases, the reliability of species identification does not give rise to any doubt. The conclusions below are based on a database that includes more than 800 species of Hydrozoa, Siphonophora, Scyphozoa and Cubozoa (Siphonophora are treated here as an independent class). This database includes information concerning species found in nine areas of the North Pacific [Pacific shores of Alaska, Aleutian Islands, Commander Islands, eastern shores of Kamchatka, Bering Sea, Okhotsk Sea, North Kurile Islands, South Kurile Islands (separated by the Friza Strait, between Urup and Iturup Islands), the northern part of the Sea of Japan, to about 40°N]; 12 regions in the Arctic Basin (eastern Greenland, western Greenland, Canadian Arctic archipelago and Labrador shore, northern shore of Norway, Barents Sea, White Sea, Kara Sea, Laptev Sea, East Siberian Sea, Chukchi Sea and Beaufort Sea); 21 areas of the Southern Ocean (Ross Sea, Bellingshausen Sea, Weddell Sea, Sodruzestva Sea, Mousson Sea, Riiser-Larsen Sea, Cosmonaut Sea, Davis Sea, Dumont D'Urville Sea, Graham Land, Macquaire Island, South Georgia Island, the west Antarctic Islands; the open parts of the Indian, Atlantic, and Pacific Oceans, Patagonian shelf,

South Africa, South Australia with Tasmania, southern part of New Zealand with adjoining islands).

The Medusozoa taxa that have a northern and southern hemisphere distribution, and that can be considered as bipolar according to our definition, are listed in Appendix 2. Within Medusozoa there are not only bipolar species, but also genera and families, in contrast to Radiolaria, where so far we have only found bipolarity within three genera, and otherwise mostly at the species level. According to newly published data, and new material that only recently became available, the previous list of bipolar Medusozoa taxa (Stepanjants et al. 1996, 1997a) is herein revised and updated (Appendix 2). The number of bipolar species is reduced by one third (23 species instead of 38) and we conclude that 32 genera and five families are bipolar. If the list of bipolar Medusozoa taxa (Appendix 2) is analysed further, it is possible to reach another four important conclusions:

- There are almost no fossil records of Medusozoa (except hydrocorals and Conulata) and whether these fossil Medusozoa are really Cnidaria or not is still debated and is very problematic.
- The group Medusozoa is highly plastic with respect to environments, which explains the high number of bipolar species, genera, and even families.
- The Medusozoa are organisms that are either completely pelagic or bottom dwellers having pelagic stages.
- A considerable part of the representatives of Hydrozoa is epibiotic (i.e. attachment on living organisms), a life cycle that allows for easy transportation of these species.

We would like to stress here that our concept of bipolarity has a wider definition than previously. Without doubt, it must be taken into consideration that about half of the bipolar Medusozoa species (11) are pelagic organisms. The remarkable part is that eight species have no bottom polyp stage at all, or that this stage has not been recognized: *Paragotoea bathybia* Kramp, 1942; *Rhabdoon reesi* (Shirley et Leung, 1970) (= *Yakovia polinae* Margulis, 1989); *Botrynema brucei* Browne, 1908; *Ptychogastria polaris* Allman, 1878; *Dimophyes arctica* (Chun, 1897) (Figures 4 and 5); *Muggiaea bargmannae* Totton, 1954; *Atolla wyvillei* Haeckel, 1876; *Periphylla periphylla* (Peron et Lessueur, 1809). Of these pelagic species, four are restricted mainly to deep waters.

The bipolar distribution of these four species probably appears because of the presence of deep-water meridional polar and subpolar currents (Vino-gradov 1968). This does not contradict classical theories, and is also close to the interpretations of Ross (1847), Ortmann (1896) and Chun (1897), and to some modern opinions, such as Birstein (1963), Andriashev (1987) and others (see above). All the cases cited are preferably interpreted as a result of modern deep-water migrations. It is possible that *Voragonema profundicola (pendunculata?)* Naumov, 1971 will in the future be placed in the same group. In our opinion, this species is the only representative of the genus *Voragonema*. Nevertheless, three known species of this genus are reported in the literature, and the last one, *Voragonema laciniata*, was described from the Weddell Sea from a depth of 1583 m (Bouillon, 2002).

The other 13 bipolar species have polyp with epibiotic stages: *Obelia longissima* (Pallas, 1766); *Staurophora mertensii* Brandt, 1835; *Filellum serpens* (Hassal, 1848); *Monobrachium parasitum* Mereschkowsky, 1877; or are found as attachments: *Sertularella polyzonias* (Linnaeus, 1758); *Sertularella gayi* (Lamouroux, 1821); *Symplectoscyphus tricuspidatus* (Alder, 1856); *Abietinaria abietina* (Linnaeus, 1758); *Grammaria abietina* (Sars, 1851); *Acryptolaria conferta* (Allman, 1877); *Kirchenpaueria pinnata* (Linnaeus, 1758); *Kirchenpaueria bonneviae* (Billard, 1906); *Halopteris catharina* (Johnston, 1833). The distribution of these species is connected with fouling on ships, drifting algae and other swimming organisms. Their plasticity to the environment has given them the ability to adapt and tolerate rather uncomfortable conditions, for example the high temperatures in the tropics. They penetrate these water masses and adapt to new territories in the two hemispheres having adequate environments because stable populations of these species are absent in the tropics.

Let us now analyse in detail the bipolar distribution of some species. Within pelagic Medusozoa, the characters of the siphonophora *Dimophyes arctica* (Chun, 1897) are well known. This species was first found in the Arctic only, then, based on investigations from all zones of the World Ocean, it was also found in the Antarctic, as well as in the Caribbean Sea and other tropical regions (Stepanjants 1975). For a long time it was presumed to be a cosmopolite, whereas later it was shown that cold-water masses and currents limited its distribution. The use of statistical methods (Stepanjants & Lobanov 1989), including a computer visualization method (Stepanjants & Dianov 1997), allows us to show how this species spawns in waters of polar origin. It was found in the Caribbean Sea, at depths between 500 and 200 m and at temperatures below 10°C and salinity <35 psu. This indicates penetration of Subantarctic water masses to this region (Figure 5).
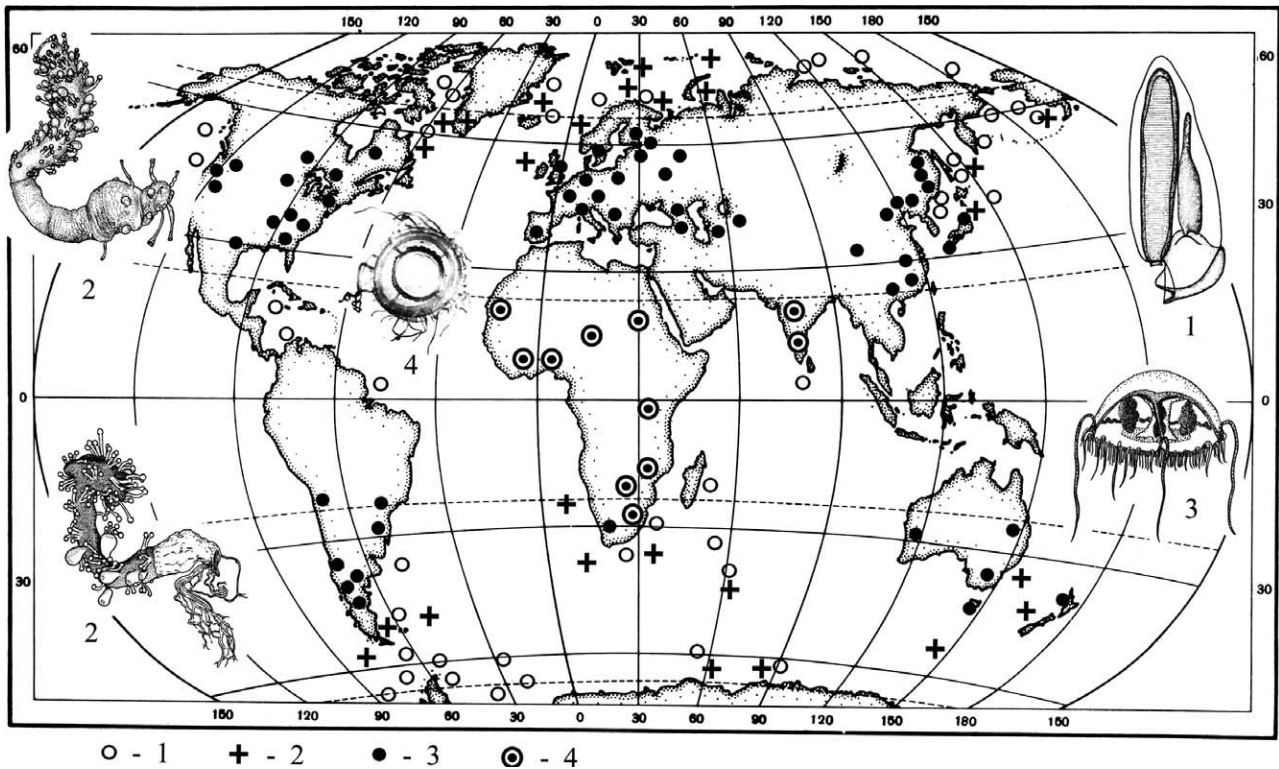
Figure 4. The bipolar distribution of some Medusozoa (Cnidaria) taxa. The numbers in parentheses refer to the species numbers in Appendix 2. 1, *Dimophyes arctica* (Chun, 1897) (no. 20); 2, family Candelabridae, represented by genus *Monocoryne* with *M. giganthea* (northern hemisphere, upper left) and *M. minor* (southern hemisphere, lower left); 3, *Craspedacusta* sp., showing a bipolar distribution; 4, *Limnocnida* sp., showing a tropical distribution only.

Some reports of *Dimophyes arctica* are also from the tropical zone, at depths of about 1000 m. It is possible to interpret the *Dimophyes arctica* appearance in the tropics as a result of cold-water masses penetrating into the tropical zone. The distribution of the siphonophora *Muggiaea bargmannae* can be explained by the same mechanism as for *Dimophyes arctica*. The species *Muggiaea bargmannae* is practically always accompanied by *Dimophyes arctica* in the Arctic and in the North Pacific, and it is known that *Muggiaea bargmannae* inhabits waters with temperatures between −1.45 and +4°C (Stepanjants 1967).

There is no pelagic stage in *Filellum serpens* (Hassal, 1848). This is an epibiotic organism, whose colonies cover other organisms, preferably other hydroid species, but without any preference to settle on specific hydroid species. Previously, most taxonomists and faunists assumed *Filellum serpens* to be cosmopolitan. Derjugin (1915) was the first who suggested this species to be bipolar, later supported by Stepanjants (1980). However, until now there has been no clear understanding of which characters are important in the distribution of *Filellum serpens*. It has been found in the Arctic and Antarctic, in cold and temperate waters of the Pacific and Atlantic Oceans, mainly at depths from 9–300 to 3500 m.

The fact that this species was found near the western shore of tropical Africa excludes the possibility of an antitropical distribution. However, an ecological approach to the interpretation of bipolarity allows us, following Darwin and Bergh (see above), to classify this species distribution as bipolar. In other words, the penetration of *Filellum serpens* into the tropics must be connected to the cold-water masses along the west African shore.

Monobrachium parasitum Mereschkowsky, 1877 is epibiotic, living on the shells of various bivalves. New data by Jarms & Mühlenhardt-Siegl (1998) show that this species is widely represented in the Arctic. It also settles substantially in the Antarctic and in areas around the Falkland Islands. It inhabits shells of four to five species of bivalves in the Arctic and North Atlantic, six species in the Antarctic and about 10 species in the North Pacific. In each of the mentioned areas, the bivalve species are different and the hydroid distribution is most probably independent from the substratum. According to Jarms & Mühlenhardt-Siegl (1998), the bipolar distribution of *Monobrachium parasitum* is connected with its migration from the Southern Ocean during the Mesozoic, in accordance with Crame (1974, 1996) and Van der Spoel (1991). We, on the other hand, would conclude that there are clear differences
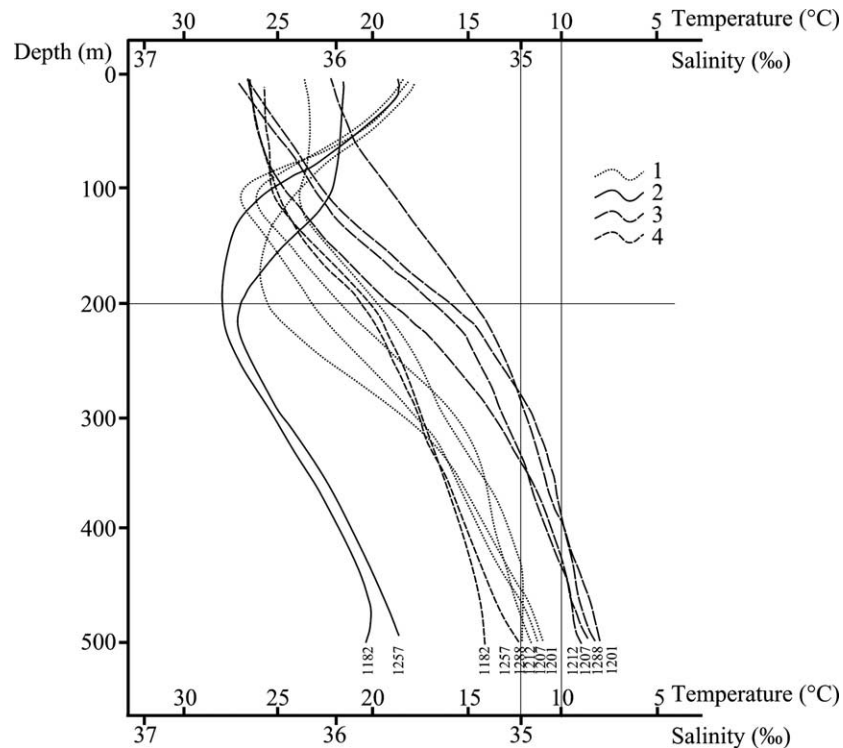
Figure 5. Temperature and salinity profiles at the Caribbean Sea stations with and without *Dimophyes arctica* (Chun, 1897), according to Stepanjants (1975). Station numbers are given below each curve. 1, Stations with *D. arctica*, salinity profile; 2, stations without *D. arctica*, salinity profile; 3, stations with *D. arctica*, temperature profile; 4, stations without *D. arctica*, temperature profile.

in the northern and southern populations of *Monobrachium parasitum* in some characters (Jarms & Mühlenhardt-Siegl 1998). This allows us to conclude that these two forms are different but closely related cold-water species. These two species are in turn closely related to the third Antarctic species of this genus, namely *Monobrachium antarcticum* (Robins, 1972). The morphological similarity between these three species can be explained as a result of inhabiting the same biotope, i.e. settling on bivalve shells.

The other 10 species (see above) are found in high numbers and have a wide distribution, usually in temperate, but also in cold waters of both hemispheres. Their general distribution patterns have two explanations: (1) recruitment is most probably from the north to the south through deep-water currents; (2) recruitment occurs via attachment on drifting substrata.

Finally, *Craspedacusta sowerbyi* (Lankester, 1880) is a typical inhabitant of freshwater basins. This species has a free-living medusae stage and its polyps are minute organisms without tentacles. In the northern hemisphere, this species is known from freshwater lakes in Europe, continental Asia, Japan and North America, whereas in the southern hemisphere it is reported from South America and Australia (Figure 4, *Craspedacusta* sp. is shown).

Representatives of the closely related genus *Limnocnida* (in the same family) inhabit the tropical zone of India and central Africa, as well as in South Africa, according to Bouillon (1956–1957) (Figure 4). At present, the genus *Craspedacusta* includes six species (Bouillon & Boero 2000). These authors erroneously placed a seventh species, *Craspedacusta vovasi*, in it, which has now been re-named *Eperetmus typus vovasi* (Naumov & Stepanjants 1971; Stepanjants 1988). The validity of the five other species is also doubtful, and they are only found in Asia. The origin of the bipolar distribution of *Craspedacusta sowerbii* is explicable by transport of algae attached to birds. This transport takes place from the Asian continent (Figure 4) westwards (Eurasia and Europe) and southwards (Australia and South America). The discovery of the limnomedusa *Kirklandia* in Germany and America in Jurassic–Cretaceous sediments supports the idea of an ancient origin for this group, as proposed by Harrington & Moore (1956).

Among the 32 bipolar genera of Medusozoa, some deserve special attention. Two of these genera are monotypical: *Paragotoea* and *Dimophyes*. The third monotypical genus, *Yakovia*, is reported to be a synonym of *Rhabdoon* with two species (one from the northern hemisphere and the other from both the northern and southern hemispheres; Stepanjants

and Kosobokova, in press). The species placed in *Paragotoea* is from the Arctic and from temperate waters of the southern hemisphere (*Paragotoea bathybia* Kramp, 1942). Later Margulis (1989), probably erroneously, described another species from the Arctic and Antarctic as *Paragotoea elegans*. We support the opinion of Brinckmann-Voss & Arai (1998) and Bouillon & Boero (2000) who designated *P. elegans* a junior synonym of *Paragotoea bathybia*. As mentioned earlier, the genus *Voragonema* is also monotypical, with the species *Voragonema profundicola*, and accordingly is also a bipolar genus. This means that only monotypic genera are known among pelagic Medusozoa having a bipolar distribution. As stated, the distribution of these genera and species takes place via the mechanism that is typical for deep-water pelagic forms, namely through cold-water meridional currents, as also stated by Vinogradov (1968).

Twelve bipolar genera of Medusozoa are represented by a rather large number of species (two to five or more). As a rule these species are closely related, but they are different in the northern and southern hemispheres and are absent from the tropical zone. They are epibionts, whereas other species are either distributed via the actinula-like larval stage or are pelagic. According to the present status of knowledge, this is the number of species for these genera: *Gymnogonos* – five; *Monocaulus* – four; *Bouillonia* – three; *Monocoryne* – five; *Candelabrum* – 15; *Rosalinda* – four; *Monobrachium* – three; *Margellopsis* – five; *Staurophora* – two; *Ptychogastria* – three; *Voragonema* – three; *Craspedacusta* – five(?). The species from the northern and southern hemispheres are very similar and it is often difficult to distinguish between them. Examples of such species are: *Gymnogonos crassicornis* Bonnevie, 1898 from the Arctic and *Gymnogonos ameriensis* (Stepanjants, 1979) from the Antarctic (Stepanjants & Svoboda 2001); *Monocaulus groenlandicus* Allman, 1876 from the Arctic and *Monocaulus parvula* (Hickson & Gravely, 1907) from the Antarctic (Svoboda & Stepanjants 2001) (Figure 6).

The species *Monocaulus groenlandica* (Arctic) and *Monocaulus parvula* (Antarctic), in the family Corymorphidae, are not only morphologically and anatomically similar, but some fine structures in the polyps of both species have orange-brown colouring that is still preserved after more than 100 years of fixation. This coloration is ensured by pigment granules in cells of the epiderm and gastroderm, after applying the thyrosin–tryptophan group of the carbolic acid as a tissue dye. The coloration is a character typical for these species and distinguishes them from other Corymorphidae species (Svoboda & Stepanjants 2001). The genus *Corymorpha* contains 11 species that are distributed mainly in the tropical and subtropical zones of the World Ocean, which represent possible centres of origin for these family and genera. From these zones *Corymorpha (Steenstrupia) nutans* (Sars, 1835) penetrates to the north, and the monotypic genus *Paragotoea (with Paragotoea bathybia)* penetrates to the south. A neothenic origin of the cold-water *Gymnogonos* and *Monocaulus* is more probable. Although there are no fossils that are close to the present Corymorphidae representatives, it is nevertheless possible that this group is relict.

The species in the genus *Candelabrum* were recently revised in great detail (Segonzac & Vervoort 1995; Hewitt & Goddard 2001), and their cold-water nature is well documented. Most of the 15 known species inhabit the temperature interval 2.4–11°C, and are restricted to significant depths. Stepanjants (1989) reported that *Candelabrum phrygium* (Fabricius, 1780) inhabits and reproduces in the northern hemisphere at temperatures between –1 and 7°C. The other species of this genus are restricted to the southern hemisphere, where they inhabit mainly Subantarctic waters with temperatures between 0.5 and 5°C. The closely related species of the genus *Monocoryne* (the other genus belonging to the family Candelabridae) are also cold-water inhabitants in the Arctic, in the boreal Atlantic and Pacific, and in the southern hemisphere near South Africa (Stepanjants et al. 2004). As a result there are basic data supporting our conclusion that the family Candelabridae is also bipolar (Figure 4). In spite of the absence of fossil data, we propose that the representatives of this family are relict. We suggest that their distribution, most probably from the northern to the southern hemisphere, took place during the last 65 million years, and at great depths, as also suggested by the fact that the present forms also have a tendency to inhabit considerable depths. The fact that the Candelabridae fauna of the southern hemisphere is noticeably richer than the one of the northern hemisphere (nine against six species for *Candelabrum* and three against two for *Monocoryne*, respectively), may indicate that a second centre of speciation appeared in the southern hemisphere. The presence of Candelabridae species at the Antarctic shelf, where temperatures are between 0.5 and 1.9°C, displays similarities to their distribution in the northern hemisphere, where *Candelabrum phrygium* and *Monocoryne gigantea* also inhabit the shallow waters of the high Arctic.

Within the two other families closest to Candelabridae, such as Rosalindiidae and Fabulosiidae (it is considered that this is a valid family with *Fabulosus* as a type genus; see Stepanjants et al. 1990), it is known that Rosalindiidae display a tendency to
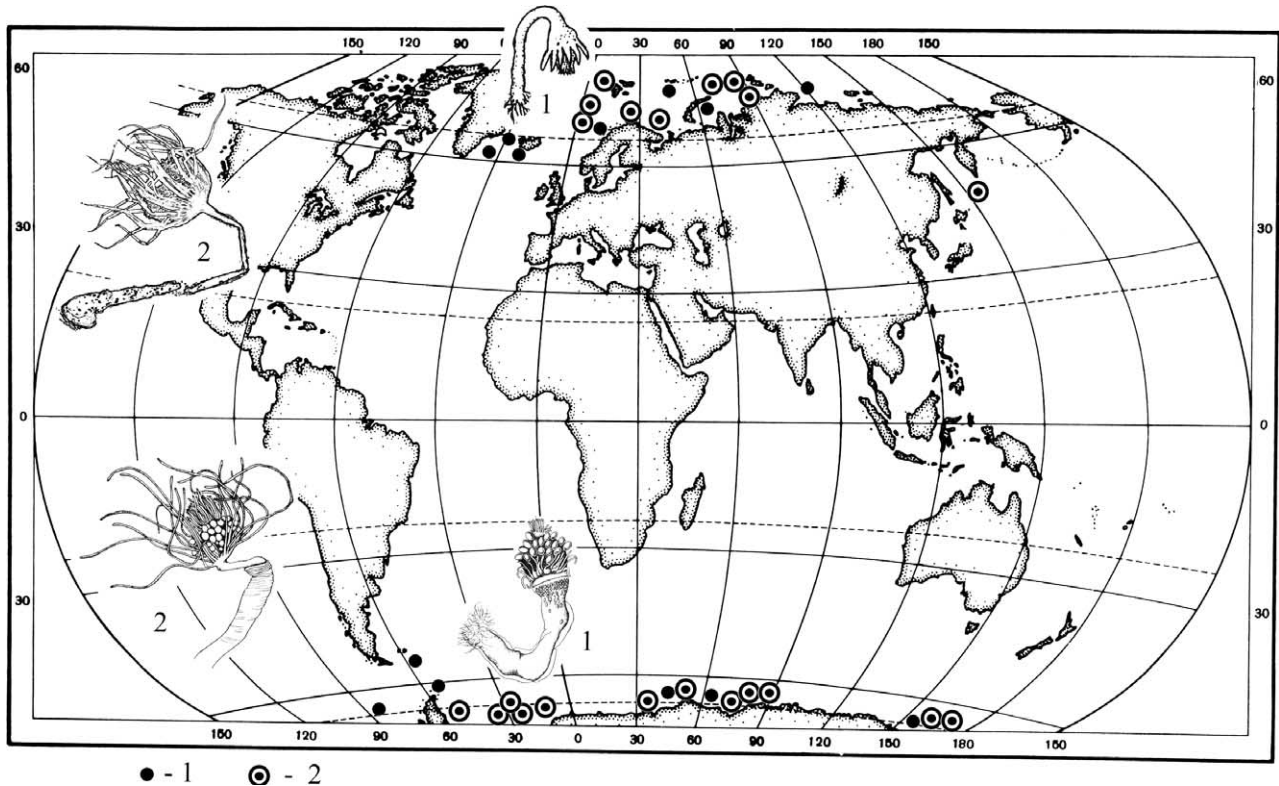
Figure 6. The bipolar distribution of the genera *Gymnogonos* and *Monocaulus* (Hydrozoa, Athecata, Corymorphidae) (Appendix 2). 1, Genus *Gymnogonos* here includes *G. crassicornis* Bonnevie, 1898 (1 upper centre) and *G. obvolutus* (Kramp, 1933) in the northern hemisphere and *G. ameriensis* (Stepanjants, 1979) (1 lower centre) in the southern hemisphere. 2, Genus *Monocaulus* here includes *M. groenlandica* Allman, 1876 (2 upper left) and *M. parvula* (Hickson & Gravely, 1907) (2 lower left).

bipolarity (only the genus *Rosalinda* is bipolar, with four species), whereas the Fabulosiidae include only the northern Pacific species *Fabulosus kurilensis* Stepanjants, 1990. However, as the latter family is strongly related to the family Candelabridae, possibly having a bipolar distribution, it is not unlikely that *Fabulosus kurilensis* can also be found in the southern hemisphere.

Some genera include many species, such as *Rhizogeton* (six), *Zygophylax* (53), *Ptychogena* (seven), *Staurotheca* (20), *Kirchenpaueria* (six) and *Schizotricha* (10), of which many may be considered as bipolar. The genus *Rhizogeton* undoubtedly includes cold-water species, but the number of species included in this genus is yet not settled. For example, the species *Rhizogeton nudum* Broch, 1910 was described from the Arctic, but Millard (1975) also found it in cold waters on the shores of South Africa (Agulhas Bank). However, in our opinion the species identified by Millard (1975) as *Rhizogeton nudum* probably belongs to another cold-water species of the same genus.

We recognize here Zygophylacidae as the valid name of a family that includes three genera: *Abietinella*, *Cryptolaria* and *Zygophylax*. The species of the genus *Abietinella* are not found in the northern hemisphere, whereas the species of the genus *Cryptolaria* inhabit subtropical and tropical shallow waters. The last revision of the genus *Zygophylax* (Rees & Vervoort 1987) led to about 53 species being included in this genus. These species inhabit the subtropical waters of the northern and southern hemispheres, usually deeper than 100 m. Only one species is known from the Arctic, *Zygophylax pinnata* (Sars, 1874) and one from Subantarctic, *Zygophylax armata* (Ritchie, 1907). The fact that 12 species of the genus *Zygophylax* have been found in the tropical zone, but at depths between 200 and 1600 m, clearly proves this genus to be bipolar, and indicates a deep-water origin of these species. Their migration possibly took place northwards and southwards via deep waters along North and South America, where an independent cold-water (polar shelf) fauna developed on both hemispheres. It is possible that these migrations took place before the onset of the northern hemisphere glaciation.

The family Kirchenpaueriidae evolved from the warm-water superfamily Plumularioidea (Plumulariidae, Aglaopheniidae, and Halopteridae). Genera and species of Halopteridae are represented in high numbers in the tropics and subtropics, whereas species of Kirchenpaueriidae belonging to the genera

Kirchenpaueria, *Oswaldella*, *Ophinella*, *Ventromma*, *Naumovia* and *Wimveria* are usually typical for cold waters (Stepanjants et al. 1996, 1997a, 1998), as is also true for *Schizotricha* (Halopteridae). The genera *Pycnotheca* and *Halicornopsis* (family Kirchenpaueriidae) display some typical morphological characters exclusive to these colonies and are found in warm water on the shores around Australia and New Zealand. We suppose that the genera *Pycnotheca* and *Halicornopsis* must be investigated in greater detail in order to erect a new family for them. If this can be done, it will be possible to conclude that the family Kirchenpaueriidae is bipolar.

There are no bipolar species among the very large family Sertulariidae (more than 400 species). Among genera of this family, however, the genus *Papillionella* may be regarded as bipolar (Antsulevitch &Vervoort 1993) (Appendix 2).

The genus *Sertularia*, with more than 20 species in the northern hemisphere (mainly with two rows of hydrothecae on the branches), and the genus *Thuiaria*, with more than 50 species (with many rows of hydrothecae on the branches, as a result of polymerization of the row numbers), are both absent in the Southern Ocean. The closely related genus *Staurotheca* includes 19 species (Peña Cantero et al. 1997b; with four to many rows of hydrothecae), and is distributed in the Southern Ocean. If we take into account that the hydrothecae distribution has a staurotheca form on the branches of some *Sertularia* and *Thuiaria* (in two rows that are perpendicular to each other), or that, on the contrary, some *Staurotheca* hydrothecae are distributed similarly on the branches as on the northern *Sertularia* and *Thuiaria*, we may be able to propose a close relationship between these genera. Similarly, we can discuss the Southern Ocean species group as having originated from the northern *Sertularia* genus (and possibly also from the *Thuiaria* genus), from which the *Staurotheca* genus in the south evolved.

Among the Medusozoa species investigated are undoubtedly some species whose distributions could be used as examples of ecological (bionomical) bipolarity, in spite of the fact that until now some species from both hemispheres were considered to be one taxonomical species, or two closely related species, belonging to the same genus. Another interesting case can be added to these examples: two obviously very different species of the family Hydractiniidae, *Stylactaria (Hydractinia?) ingolfi* Kramp, 1932 from the Arctic and *Hydractinia vallini* Jaederholm, 1926 from the Antarctic, are both attached as epibiotic organisms on different *Ophiura* species that belong to the family Ophyolepididae. This would represent a textbook example of ecological (bionomical) bipolarity. In spite of small differences, there are great morphological similarities between colonies and zooids of these species (Svoboda et al. 1995, 1997), which is also supported by very similar environments.

Ushakov (1958) compared faunas from shallow waters in the Subantarctic and North Pacific islands, and showed their bionomical similarity. Sheiko & Stepanjants (1997a,b) studied peculiarities in the hydroid taxacoenoses of the Commander Islands, and demonstrated that the families Sertulariidae (45%), Campanulariidae (20%), Haleciidae (10%) and Lafoeidae (10%) were dominant. Our analysis of the taxocoenoses on the Subantarctic islands has produced very homogenous results, and the families Sertulariidae (20%), Campanulariidae (11.6%) and Haleciidae (8.7%) are the most dominant, based on species number. This can be used as evidence of bionomic similarity of polar faunas.

It is possible to summarize our data on the bipolar distribution of Medusozoa as follows:

- All the 23 species of Medusozoa (Cnidaria) whose distribution may be defined as bipolar are contemporary. There are very few analogues of closely related species in the fossil record, represented by imprints or skeletal remains.
- Among 32 bipolar Medusozoa genera there are some, such as *Gymnogonos*, *Candelabrum*, *Monocoryne* and *Rosalinda*, which we assume to be relict, in spite of the absence of fossil remains.
- The origin of the bipolar distribution of the Medusozoa, mostly at the species and genus level, is a result of the high plasticity of this group, due to the modern migration via cold deep-water currents, either at the larval stage, or as a result of attachment on drifting organisms and objects.
- The distribution of relict forms during the Recent, together with the modern migrations, resulted in the formation of a sufficiently rich cold-water Medusozoa fauna, which is well represented today by bipolar taxa at the species, genus and even at the family level.
- Among the representatives of the cold-water Medusozoa fauna there are examples of well-defined ecological (bionomical) bipolarity at both the generic and coenotic levels, which developed in both polar regions.

Conclusions

1. In this paper, bipolarity is interpreted as the wide distribution of the same, closely related, or even not closely related taxa (at the species,

genus or family level) of the flora and fauna, which are characterized by very similar characters and linked to similar environments in the cold and temperate zones and cold waters of both hemispheres.

2. The bipolarity phenomenon is herein investigated using examples from the exclusively pelagic classes Euradiolaria and Medusozoa (phylum Cnidaria), the latter having both pelagic and benthic stages. In both groups, the phenomenon of bipolarity is very clearly represented.

3. In Radiolaria, bipolarity becomes apparent mostly at the species level. Only three genera, as we suggest, are bipolar in their distribution. This is probably explained as a result of the fauna of Radiolaria–Polycystina being most diverse and abundant in the equatorial–tropical area. The Recent Arctic fauna only migrated into the Arctic Ocean in Holocene time, and some family and genera are absent or can be recognized only from the Pliocene–Pleistocene in typical faunas of cold-water areas of the World Ocean.

4. The Medusozoa display a rich and typical cold-water fauna. Bipolar distribution is recognized at the species, genus and even family levels.

5. In both of the investigated groups, bionomical bipolarity is well developed at high and low latitudes, both at the taxonomic as well as the coenotic level.

6. In spite of their presence in both groups, relict forms are not common in either of the faunas. The origin of a bipolar distribution is generally interpreted herein as a result of recent (Holocene) migrations (after the last glaciation, the Weichselian). Although this is true for most of the examined species, we also present several examples of Pliocene and Pleistocene taxa that developed a bipolar distribution that predates the last glaciation.

Acknowledgements

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Appendix 1. Bipolar radiolarians

Taxa	Distribution in hemispheres Northern	Southern	References
Superorder Phaeodaria			
Family Aulacanthidae			
1. *Aulacantha laevissima* Haeckel	Ar, Bor A P	An	Reshetnjak 1965, 1966
2. *Aulodendron verticillatum* Haecker	H Bor P	An	Reshetnjak 1965, 1966
3. *Auloceros arborescens irregularis* Haecker	H Bor P	An	Reshetnjak 1965, 1966
4 *Aulagraphonium antarcticum* Haecker	H Bor P	An	Reshetnjak 1965, 1966
Family Aulosphaeridae			
5. *Aulastrum spinosum* Borgert	H Bor A P	An	Haecker 1904, 1908; Schröder 1913; Dogiel & Reshetnjak 1952; Hülsemann 1963; Reshetnjak 1965, 1966
Family Castanellidae			
6. *Castanura primitiva* Reshetnjak	H Bor P	An	Reshetnjak 1965, 1966
7. *Castanidium inclinatum* Reshetnjak	H Bor P	An	Reshetnjak 1965, 1966
Family Sagosphaeridae			
8. *Sagenoscena irmingeriana* Borgert	H Bor A P	An	Dogiel & Reshetnjak 1952; Reshetnjak 1965, 1966
Family Coelodendridae			
9. *Coelographis antarcticus* Haecker	H Bor P	An	Jørgensen 1905; Dogiel & Reshetnjak 1952; Hülsemann 1963; Reshetnjak 1952, 1965, 1966
Superorder Polycystina			
Order Spumellaria			
Family Actinommidae			
10. *Actinomma boreale* Cleve	H Bor A P	An SubAn	Cleve 1899; Jørgensen 1905; Hülsemann 1963; Tibbs 1967; Bjørklund 1973, 1976; Kruglikova 1977; Cortese & Bjørklund 1998; Stanley 1981; Nishimura & Yamauchi 1984a; Nakaseko & Nishimura 1982; Itaki 2004; Cortese (unpubl.)
11. *A. leptoderma leptoderma* (Jørgensen)	Ar Bor A P	An SubAn	Jørgensen 1900, 1905; Schröder 1909; Bernstein 1934; Bogorov 1946; Hülsemann 1963; Tibbs 1967; Bjørklund 1973, 1974, 1976; Kruglikova 1989a; Abelmann 1992a,b; Abelmann & Gowing 1997; Nishimura et al. 1997; Bjørklund et al. 1998; Cortese & Bjørklund 1998; Bjørklund & Kruglikova 2003
12. *A. leptoderma longispina* Cortese & Bjørklund	H Bor A P	An SubAn	Cortese & Bjørklund 1998; Nishimura & Yamauchi 1984a,b; Cortese (unpubl.); Kruglikova (unpubl.)
13. *A. popofskii* (=*Echinomma popofskii)* Petrushevskaya	H Bor A P Tr	An	Cortese & Bjørklund 1998; Petrushevskaya 1967; Kruglikova 1969a, b; Matul 1997; Cortese et al. 2003; Cortese (unpubl.)
14. *A. delicatulum* (=*Echinomma delicatulum*) (Dogiel, Reshetnjak)	H Bor A P Tr	An SubAn	Dogiel & Reshetnjak 1952; Riedel 1958; Petrushevskaya 1967, 1969; Kruglikova 1969a,b; Ling et al. 1971; Nakaseko & Nishimura 1982; Matul 1989, 1990, 1991, 1997; Nishimura et al. 1997; Bjørklund (unpubl.).
15. *Rhizoplegma boreale* (Cleve)	Ar Bor A P	An SubAn	Petrushevskaya 1969; Ling et al. 1971; Kruglikova 1975, 1977; Kling 1977; Ling et al. 1971; Nishimura et al. 1997; Dolven & Bjørklund 2001; Nimmergut 2001; Bjørklund & Kruglikova 2003; Cortese (unpubl.)

Taxa	Distribution in hemispheres Northern	Southern	References
16. *Prunopyle (?) antarctica* Dreyer	Ar Bor A P	An SubAn	Dreyer 1889; Riedel 1958; Petrushevskaya 1967, 1975; Kling 1973; Petrushevskaya 1975; Chen 1975; Kruglikova 1977; Stanley 1981; Benson (unpubl.); Nakaseko & Nishimura 1982; Bjørklund (unpubl.).
17. *P.(?) tetrapila* Hays (=*P. (?) robusta* Kling)	Bor P Tr	SubAn	Hays 1965; Kling 1973; Petrushevskaya 1975; Chen 1975, Stanley 1981
Family Druppulidae			
18. *Stylatractus pyriformis* (*S. neptunus* =*Dorydruppa bensoni*) (*Bailey*)	Bor A P Tr P	An SubAn	Bailey 1856; Kruglikova 1977; Petrushevskaya 1967, 1977; Takahashi 1991; Benson 1966; Bjørklund (unpubl.).
Family Sponguridae			
19. *Spongurus pylomaticus* (*Riedel*)	NP	An SubAn	Riedel 1958; Petrushevskaya 1967, 1975; Kruglikova 1969a, b, 1977; Ling et al. 1971; Stanley 1981; Nishimura et al. 1997; Matul 1997
Family Trematodiscidae			
20. *Stylodictya validispina* Jørgensen (= *S. stellata* Bailey)	Ar Bor A P Subtr	An SubAn	Jørgensen 1905; Petrushevskaya 1967; Kruglikova 1969b, 1977; Matul 1989, 1990, 1991, 1997; Schröder-Ritzrau 1995; Bjørklund et al. 1998; Cortese (unpubl.)
21. *S. aculeata* Jørgensen	Bor A P	An SubAn	Jørgensen 1905; Petrushevskaya 1967; Kruglikova 1969b; Matul 1997; Cortese & Bjørklund 1998
22. *Stylochlamydium venustum* (Bailey)	Bor A P Subtr?	An SubAn	Bailey 1856; Petrushevskaya 1967, 1969; Kruglikova 1969a, b, 1975, 1977, 1999; Ling et al. 1971; Nigrini & Moore 1979; Blueford 1983; Matul 1989, 1990, 1991, 1997; Nimmergut 2001; Cortese (unpubl.)
Family Spongodiscidae			
23. *Spongotrochus glacialis* Popofsky	Ar Bor A P Tr	An SubAn	Popofsky 1908; Riedel 1958; Hülsemann 1963; Tibbs 1967; Petrushevskaya 1967, 1975; Kling 1973; Chen 1975; Kruglikova 1975, 1977; Blueford 1983; Matul 1989, 1990, 1991, 1997; Bjørklund & Kruglikova 2003
Superorder Polycystina Order Nassellaria			
Family Sethophormididae			
24. *Enneaphormis rotula* Haeckel	Ar Bor A P Tr?	An SubAn	Tibbs 1967; Kruglikova 1977; Nakaseko & Nishimura 1982; Takahashi 1981; Petrushevskaya 1981, 1986; Matul 1989, 1990, 1991, 1997; Schröder-Ritzrau 1995; Bjørklund & Kruglikova 2003
25. *E. enneastrum* Haeckel	Ar Bor A P Tr	An SubAn	Cleve 1900; Jørgensen 1905; Popofsky 1908; Hülsemann 1963; Petrushevskaya 1971; Nakaseko & Nishimura 1982; Nishimura & Yamauchi 1984a,b; Bjørklund & Kruglikova 2003; Cortese (unpubl.)
26. *Protoscenium simplex* (Cleve)	Ar Bor A P	An SubAn	Cleve 1899; Jørgensen 1905; Petrushevskaya 1971; Bjørklund & Kruglikova 2003
Family Plagiacanthidae			
27. *Sethophylium meunieri* Schroeder	Ar	An	Meunier 1910; Schröder 1914; Petrushevskaya 1977; Bjørklund & Kruglikova 2003
28. *Pseudodictyophimus gracilipes gracilipes* (Bailey)	Ar Bor A P Tr	LAn SubAn	Bailey 1856; Petrushevskaya 1967, 1971; Petrushevskaya & Bjørklund 1974; Takahashi 1981; Schroder-Ritzrau 1995; Kruglikova 1975, 1999; Bjorklund et al. 1998; Nimmergut 2001; Bjorklund & Kruglikova 2003

Taxa	Distribution in hemispheres Northern	Southern	References
29. *P.gracilipes* Bailey *bicornis* Ehrenberg	Ar Bor A P	An SubAn	Schröder 1914; Petrushevskaya 1967, 1971; Kruglikova 1975; Bjorklund & Kruglikova 2003
30. *Ceratocyrtis histricosa* Jørgensen	Ar Bor A P Subtr	An SubAn?	Jørgensen 1905; Hays 1965; Kruglikova 1977; Petrushevskaya 1967, 1977; Matul 1989, 1990, 1991, 1997; Schröder-Ritzrau 1995; Bjørklund & Kruglikova 2003; Cortese (unpubl.)
31. *Lophophaena clevei* Petrushevskaya	Ar Bor A P	An	Cleve 1899; Hülsemann 1963; Petrushevskaya 1971; Matul 1997; Bjørklund & Kruglikova 2003
32. *Phormacantha hystrix* Joergensen	Ar Bor A P	An SubAn	Hülsemann 1963; Benson 1966, 1983; Tibbs 1967; Petrushevskaya 1969, 1971, 1986; Matul 1997; Boltovskoy 1998; Abelmann 1992; Schröder-Ritzrau 1995; Nishimura et al. 1997; Nimmergut 2001; Bjørklund et al. 1998; Bjørklund & Kruglikova 2003; Cortese (unpubl.)
33. *Plectacantha oikiskos* Jørgensen	Ar Bor A P	An	Jørgensen 1900, 1905; Hülsemann 1963; Tibbs 1967; Petrushevskaya 1971; Kruglikova 1977; Abelmann 1992; Matul 1997; Bjørklund et al. 1998; Bjørklund & Kruglikova 2003
Genus *Mitrocalpis*			
34. *Mitrocalpis araneafera* Popofsky	Ar Bor P	An	Popofsky 1908; Riedel 1958; Petrushevskaya 1971; Ling et al. 1971; Nakaseko & Nishimura 1982; Matul 1997; Lazarus 2002; Bjørklund & Kruglikova 2003
Family Eucyrtidiidae			
35. *Sethoconus tabulatus* (Ehrenberg)	Bor A P	An SubAn	Ehrenberg 1872; Haeckel 1887; Cleve 1899; Hülsemann 1963; Petrushevskaya 1967, 1971; Ling 1974; Kruglikova 1969b, 1975, 1977; Bjøklund et al. 1998; Boltovskoy 1987; Matul 1989, 1990, 1991, 1997; Nimmergut 2001; Bjørklund & Kruglikova 2003; Cortese (unpubl.)
36. *Artostrobus annulatus* (Bailey)	Ar Bor A P Tr	An SubAn	Bailey 1856; Petrushevskaya 1967, 1971; Kruglikova 1969, 1975, 1977; Bjørklund 1976; Takahashi 1981; Abelmann 1992; Bjørklund et al. 1998; Nimmergut 2001; Bjørklund & Kruglikova 2003
37. *A. joergenseni* Petrushevskaya	Ar Bor A P Tr	An SubAn	Petrushevskaya 1967, 1971; Bjørklund 1976; Schröder-Ritzrau 1995; Molina-Cruz & Bernal-Remirez 1996; Nimmergut 2001; Bjørklund & Kruglikova 2003; Cortese (unpubl.); Kruglikova (unpubl.)
38. *Lithomitra lineata clevei* Petrushevskaya	Ar Bor A P Tr	An SubAn	Riedel 1958; Petrushevskaya 1969, 1972, 1986; Kruglikova 1969b, 1975, 1977, 1999; Krasheninkov et al. 1983; Petrushevskaya & Bjørklund 1974; Schröder-Ritzrau 1995; Matul 1989, 1990, 1991, 1997; Bjørklund et al. 1998; Bjørklund & Kruglikova 2003
39. *L. lineata arachnea* (Ehrenberg)	Bor A P Tr	An	Riedel 1958; Kruglikova 1969a, b, 1977; Petrushevskaya 1967, 1969, 1977; Petrushevskaya & Bjørklund 1974; Matul 1989, 1990, 1991, 1997; Nimmergut 2001

Taxa	Distribution in hemispheres Northern	Southern	References
40. *Cycladophora davisiana* (Ehrenberg) *davisiana* (Petrushevskaya)	Ar Bor A P Subtr Tr	An SubAn	Ehrenberg 1862; Cleve 1899, 1901; Riedel 1958; Hülsemann 1963; Petrushevskaya 1967, 1971, 1986; Petrushevskaya & Bjørklund 1974; Chen 1975; Kruglikova 1969b, 1977; Kling 1977; Nigrini & Moore 1979; Stanley 1981; Krasheninkov et al. 1983; Nishimura & Yamauchi 1984; Bjørklund & Ciesielski 1994; Schröder-Ritzrau 1995; Matul 1989, 1990, 1991, 1997; Bjørklund & Kruglikova 2003; Cortese (unpubl.)
41. *C. davisiana* (Ehrenberg,) *cornutiodes* (Petrushevskaya) (= *Halycaliptra cornuta* Bailey = *Cycladophora cosma cosma* Lombari & Lasarus)	Ar Bor A P Subtr Tr P	An SubAn	Petrushevskaya 1967, 1979; Kruglikova 1969b, 1977; Kling 1973; Stanley 1981; Takahashi 1981; Nakaseko & Nishimura 1982; Krasheninkov et al. 1983; Lombari & Lazarus 1988; Schröder-Ritzrau 1995; Morley & Nigrini 1995; Matul 1997; Bjørklund et al. 1998; Matul et al. 2002; Cortese (unpubl.)
42. *Dictyocephalus hirundo* (Haeckel)	Bor A P Tr	An SubAn	Riedel 1958; Petrushevskaya 1967, 1971; Kruglikova 1975, 1977; Takahashi 1981; Abelmann 1992; Nimmergut 2001
43. *Corocalyptra craspedota* (Joergensen)	Ar Bor A P Tr	An Suban	Jørgensen 1900, 1905; Schröder 1914; Petrushevskaya 1971, 1977, 1986; Krasheninkov et al. 1983; Bjørklund 1976; Matul 1989, 1990, 1991; Schröder-Ritzrau 1995; Bjøklund et al. 1998; Bjørklund & Kruglikova 2003
44. *Androcyclas gamphonycha* (Jørgensen)	Bor A P	SubAn P	Jørgensen 1900, 1905; Schröder 1914; Hays 1965; Bjørklund 1976; Nigrini & Moore 1979; Bjørklund et al. 1998; Petrushevskaya 1971, 1977, 1986; Matul 1989, 1990, 1991; Schröder-Ritzrau 1995
Family Cannobotryidae			
45. *Artobotys borealis* (Cleve)	Ar, Bor A P Tr	An SubAn	Cleve 1899; Petrushevskaya 1971; Petrushevskaya & Bjørklund 1974; Bjørklund 1976; Takahashi 1981; Molina-Cruz & Bernal-Ramires 1996; Bjørklund et al. 1998; Nimmergut 2001; Bjørklund & Kruglikova 2003; Cortese (unpubl.)
46 . *Botryocampe inflata* (Bailey)	Bor AP	An	Bailey 1856; Kruglikova 1969b, 1974, 1975, 1977; Petrushevskaya 1971, 1975, 1981; Ling et al. 1971; Matul 1989, 1990, 1991, 1997; Nimmergut 2001; Bjørklund (unpubl.); Cortese (unpubl.).

A, Atlantic; Am, American; An, Antarctic; Ar, Arctic; As, Asiatic; B, bipolar; Bd, bipolar deep water; Bl, Black Sea; Bor, boreal; GlAn, "Glacial Antarctic" subregion; H, high; Haw Isl, Hawaiian Islands; Mc, Macquaire; NZ, New Zealand; P, Pacific; NP, northern Pacific; Pat, Patagonian Shelf; SAf, South Africa; SAm, South America; SAu, South Australia; SG, South Georgia; SNZ, South New Zealand Island; Subtr, subtropical; SubAnIsl, Subantarctic islands; Tr, tropical; ?, doubt.

Appendix 2. Bipolar Medusozoa

Taxa	Type of bipolar distribution	Distribution in hemispheres		References
		Northern	Southern	
Class Hydrozoa				
Order Anthoathecata				
Genus *Rhizogeton* (6)★	B	Ar Bor A P	SAf, SNZ	Millard 1975; Bouillon 1985; Schuchert 1996, 2004
Genus Rhizorhagium *(3)* ★	B	Ar Bor A P	GlAn SubAnIsl SNZ	Bouillon 1985; Schuchert 1996
Family Monobrachiidae★	B	Ar Bor A P	GlAn SubAnIsl	
Genus *Monobrachium* (3)★	B	Ar Bor A P	GlAn SubAnIsl	Robins 1972; Bouillon 1975; Jarms & Mühlenhardt-Siegel 1998
1. *M. parasitum* Mereschk	B	Ar Bor A P	GlAn SubAnisl	Jarms & Mühlenhardt-Siegel 1998
Genus *Paragotoea* (1?)★	Bd	HAr Bor-Subtr d A	GlAn d	Kramp 1942; Bouillon 1985; Margulis 1989; Pages & Bouillon 1997
2. *P. bathybia* Kramp	Bd	HAr Bor-Subtr d A	GlAn d	Margulis 1989; Pages & Bouillon 1997
Genus *Rhabdoon?* (2)★	Bd	HAr d? Subtr	SubAn	Margulis 1989; Bouillon & Boero 2000
Genus *Gymnogonos* (5?)★	B	HAr	GlAn	Stepanjants & Svoboda 2001
Genus *Monocaulus* (4)★	B	Har HP	GlAn	Svoboda & Stepanjants 2001
Genus Bouillonia (3?)★	B	HAr HA BorA SubtrA	GlAn SubAnIsl	Svoboda et al. in press
Family Candelabridae★	B	Ar Bor A P	GlAn SubAnIsl SAf	Bouillon 1985; Hewitt & Goddard 2001
Genus *Candelabrum* (15?)★	B	Ar Bor A P	GlAn SubAnIsl SAf	Millard 1975; Segonzac & Vervoort 1995; Hewitt & Goddart 2001
Genus Monocoryne (5?)★	B	Ar Bor A P	GlAn SAf	Calder 1972a; Stepanjants et al. 2003
Genus *Margelopsis* (5)★	B	Bor Subtr A P Ind?	GlAn ubAnIsl	Kramp 1961; Bouillon 1985
Family Rosalindidae★	B?	Bor Subtr A P	SAust	Bouillon 1985
Genus Rosalinda (4?)★	B	Bor Subtr A P	SAust	Antsulevitch & Stepanjants 1985
Order Thacaphora				
Genus *Obelia* (5?)				
3. *O. longissima* (Pallas)	B	Ar Bor Subtr A P Bl	GlAn SubAnIsl Pat, SNZ	Cornelius 1995b; Stepanjants 1998, 1999
Genus *Tulpa* (3)★	B	Ar Bor Subtr A P	SubAnIsl Pat SAf SNZ	Vervoort 1972; Millard 1977; Stepanjants 1979
Genus *Filellum* (6?)				
4. *F. serpens* (Hassal)	B	Ar Bor Subtr A P HawIsl?	GlAn Pat SAf TrAf d	Vervoort 1972; Millard 1975; Sheiko & Stepanjants 1997a,b
Genus *Grammaria* (5?)★	B	Ar Bor Subtr A P	SubAnIsl Pat SG	Cornelius 1995; Hirohito 1995
5. *G. abietina* (Sars)	B	Ar Bor Subtr A P	SubAnIsl Pat SG	Sheiko & Stepanjants 1997a, b; Schuchert 2001
Genus *Acryptolaria* (4★)				
6. *A. conferta* (Allman)	B	WAr Bor Subtr A P	Pat NZ SAf Tr d	Stepanjants 1989; Schuchert 2001
Genus *Zygophylax* (53?)★	B?	Ar Bor Subtr Tr A P	SubAnIsl Pat Tr P?	Rees & Vervoort 1987
Genus Calycella (4)★	B?	Ar Bor A P	Pat SAf	Millard 1975; Bouillon 1985
Genus *Staurophora* (2?)★	B	Ar Bor A P	SubAnIsl Pat	Kramp 1961; Bouillon & Boero 2000
7. *St. mertensi* Brandt	B	Ar Bor A P	SubAnIsl Pat	Arai & Brinckmann-Voss 1980

Taxa	Type of bipolar distribution	Distribution in hemispheres		References
		Northern	Southern	
Genus *Ptychogena* (7?)★	B	Ar Bor Subtr A P	GlAn SubAnIsl	Arai & Brinckmann-Voss 1980
Genus *Halopsis* (2?)★	B	WAr Bor A	Pat	Bouillon & Boero 2000
8. *H. ocellata* Agassiz	B	WAr Bor A	Pat	Kramp 1961
Genus *Parascyphus* (2?)★	B	WAr Bor A	SubAnIsl SAf SNZ SAust	Stepanjants 1979; Bouillon 1985
Genus *Sertularella* (150?)				
9. *S. gayi* (Lamouroux, 1821)	B?	Ar Bor Subtr A P Tr d	Pat SNZ	Stepanjants 1979; Calder & Vervoort 1998; Schuchert 2001a
10. *S. polyzonias* (Linnaeus)	B?	Ar Bor Subtr A P	SunAnIsl SAf Pat	Vervoort 1972; Stepanjants 1979; Cornelius 1995b; Schuchert 2001
Genus *Symplectoscyphus* (110?)				
11. *S. tricuspidatus* (Alder)	B	Ar Bor A P	Pat	Stepanjants 1979; Hirohito 1995; Cornelius 1995; Schuchert 2001
Genus *Staurotheca* (20?)★	B	Bor P	GlAn SubAnIsl	Stepanjants 1979; Peña Cantero et al. 1997b
Genus *Abietinaria* (40?)				
12. *A. abietina* (Linnaeus)	B?	Ar Bor Subtr A P	SAf Pat	Stepanjants 1979; Hirohito 1995; Sheiko & Stepanjants 1997
Genus *Papilionella* (4)★	B	Bor P	Pat SNZ	Antsulevitch & Vervoort 1993
Family Kirchenpaueriidae★	B?	Ar Bor Subtr A P Tr? d	GlAn SubAnIsl Pat SAf	
			SNZ	Cornelius 1995; Ramil et al. 1998; Schuchert 2001
Genus *Kirchenpaueria* (6?)★	B?	Ar Bor Subtr AP Tr?	SAf SNZ SAust	Stepanjants et al. 1997, 1998; Schuchert 2001
13. *K. pinnata* (Linnaeus)	Ba	Ar Bor A P	SAf	Millard 1975; Hirohito 1995
14. *K. bonnevieae* (Billard)	B	Ar Bor Subtr A P	SAf SNZ	Schuchert 2001
Genus *Schizotricha* (10?)★	B	Ar Bor Subtr A P	GlAn SubAnIsl SAf Pat	Peña Cantero et al. 1996; Schuchert 1997, 2001
Genus *Halopteris* (30?)				
15. *H. catharina* (Johnston)	Ba	Bor Subtr A	Pat	Schuchert 1997, 2001
Genus *Nemertesia* (6?)				
16. *N. antennina* (Linnaeu)	B	Ar Bor Subtr A P	SAf	Millard 1975; Schuchert 2001
Order Trachymedusa				
Genus *Botrynema* (2)★	B	Ar Bor Subtr A B d	GlAn SubAn d	Kramp 1961; Bouillon & Boero 2000
17. *B. brucei* Browne	Bd	Ar Bor A P d	GlAn SubAn d	Kramp 1961; Bouillon & Boero 2000
Genus *Voragonema* (3?)★	Bd	Bor P d	GlAn d	Naumov 1971; Bouillon et al. 2002
Family Ptychogastriidae★	Bd	Ar Bor Subtr A P d	GlAn SubAn d	Kramp 1961; Sübing & Piepenburg 1998; Panteleeva et al. 1999
Genus *Ptychogastria* (3?)★	Bd	Ar Bor Subtr A P d	GlAn SubAn d	Panteleeva et al. 1998
18. *P. polaris* Allman	Bd	Ar Bor Subtr A P d	GlAn SubAn d	Panteleeva et al. 1999
Order Limnomedusa				
Genus *Craspedacusta* (6?)★	B	Bor Subtr As Eu Am	Aust SAm	Kramp 1961; Bouillon & Boero 2000
19. *C. sowerbyi* Lancester	B	Bor Subtr As Eu Am	Aust SAm	Kramp 1961

Taxa	Type of bipolar distribution	Distribution in hemispheres		References
		Northern	Southern	
Class Siphonophora				
Order Physophorae				
Genus *Marrus* (3)★	B	Ar Bor A P d	GlAn SubAn SAf SNZ d	Stepanjants 1967; Alvarino 1971
Order Calycophorae				
Genus *Dimophyes* (1)★	B	Ar Bor Subtr APTr d	GlAn SubAn Tr d	Stepanjants 1967; Pages et al. 1992
20. *D. arctica* (Chun)	B	Ar Bor Subtr APTr d	GlAn SubAn Tr d	Stepanjants 1975; Pages et al. 1992
Genus *Muggiaea* (4?)				
21. *M. bargmannae* Totton	B	Ar Bor Subtr A P	GlAn SubAn	Stepanjants 1967; Alvarino 1971
Class Scyphozoa, Order Coronatae				
Genus *Atolla* (2?)★?	Bd			
22. *A. wyvillei* Haeckel	Bd	Subtr Ar Bor A P Tr	An SubAn	Kramp 1942, 1961
Genus *Periphylla* (1?)★?	Bd			
23. *P. periphylla* (Peron et Lesueur)	Bd?	Ar Bor A P Subtr Tr	An SubAn	Kramp 1942, 1961

★Bipolar taxa at above the species level.
The number in parentheses is the total number of species in the genus.