

# The problem of bipolarity, with emphasis on the Medusozoa (Cnidaria: Anthozoa excepted)

S. Stepanjants, A. Svoboda & W. Vervoort

Stepanjants, S., A. Svoboda & W. Vervoort. The problem of bipolarity, with emphasis on the Medusozoa (Cnidaria: Anthozoa excepted).

Proceedings of the 6th International Conference on Coelenterate Biology, 1995: 455-464, table 1.

S. Stepanjants, Zoological Institute Russian Academy of Sciences, Universitetskaya Nab. 1, 199034 St. Petersburg, Russia.

A. Svoboda, Ruhr-Universität, Fakultät für Biologie, Universitätsstrasse 150, D-44780, Bochum, Germany.

W. Vervoort, Nationaal Natuurhistorisch Museum, P.O. Box 9517, 2300 RA Leiden, The Netherlands.

**Key words:** Bipolarity; biogeography; ecology; hydroids; siphonophores.

**Abstract:** The concept of bipolarity in general and possible explanations of this phenomenon are briefly discussed. Some examples relating to bipolar distribution of Medusozoa (Cnidaria with the exception of Anthozoa) are discussed and a table is presented of 38 species and some 30 genera of Medusozoa that according to the opinion of the authors in their pattern of distribution show this type of phenomenon. Generally bipolar distribution can now better be judged owing to better species diagnoses and the presence of a data base listing the geographical distribution of a great number (692) of Medusozoa in 9 regions of the North Pacific, 12 of the Polar basin and 21 in the Southern Ocean.

## Introduction

The authors joined forces in order to summarize their information on bipolarity of the Medusozoa fauna: Arctic, North Pacific, Antarctic (S. Stepanjants); Antarctic and Mediterranean (A. Svoboda). Information on North Atlantic, tropical and Antarctic hydroids was supplied by W. Vervoort. This paper only deals with geographic/eco-logical phenomena of this group of animals.

## The phenomenon of bipolarity

Bipolarity should be taken literally as interrupted distribution of identical or closely related species (or higher taxa) of flora and fauna in polar, temperate, and subtropical regions of both hemispheres and their absence in the tropics. Advocates of bipolarity proceed from "The Origin of species" (Darwin, 1859: chapter XI) where is shown that European plants of the same species, or their subspecies, occur in both hemispheres on plains of temperate regions and on mountain tops of the tropics, but are absent on the tropical plains (Bergh, 1947: 128; Briggs, 1987: 237). Over the last century this problem has been repeatedly discussed, and its opponents (Thompson, 1897-1898: 347-349; Dollo, 1904: 199; Stiasny, 1934: 35-53) brought forward arguments of unreliability in identification or of dissimilarity of the faunae of both hemispheres. However, there are far more supporters of bipolarity (except for those already named: Ross, 1847: 208; Dana, 1854: 36; Pfeffer, 1891: 17; Murray, 1896: 494; Derjugin, 1915: 871; Ekman, 1953: 261; Andriashev, 1964: 335; Beklemishev, 1969: 213; Vinogradova, 1977: 297; Dunbar, 1979: 116, et al.).

Different conceptions concerning the origin of bipolarity are known at present:

1. "Original local creation" of identical species of both hemispheres in similar environments (Dana, 1854: 36).

2. Independent evolution of species living in both hemispheres outside the tropics from warm water species (Hesse, 1924: 293).

3. "Relict theory" (Théel, 1886; Pfeffer, 1891; Murray, 1896) proceeding from the idea of a uniform marine fauna during the Tertiary epoch, when the climate of the earth was warmer and the temperature more uniform. As a result of cooling in polar zones the once homogeneous fauna became extinct or adapted to cold water conditions existing in both hemispheres. Adapted species remained as relicts in temperate or polar faunae; in tropical waters the further evolution of the fauna proceeded. Some present day faunists supported the Relict theory. Briggs analysed many new conceptions: "the island integration hypothesis", "the hypothesis of vicariance", and "the theory of hologenesis", concluding however that "the relict theory appears to provide a mechanism whereby antitropical distributions may be brought about" (1987: 246). Previously Derjugin (1915) derived bipolar distribution from cosmopolitanism and came close to accepting the relict theory. His examples on hydroids are highly convincing: *Filellum serpens* (Hassall, 1848), *Lafaea dumosa* (Fleming, 1820) in their distribution are in between cosmopolitanism and bipolarity (see below) and demonstrate bipolarity "in statu nascendi" (Derjugin, 1915: 873).

4. The migration theory (Ortmann, 1897) was advanced as an objection to the relict theory. Ortmann basically rejected bipolarity. But in spite of this he recorded closely related *Crangon* species in temperate waters of both hemispheres and he discussed the possibility of present day migrations along the West African coast and along American shores with cold currents or in deep waters (Ortmann, 1897: 571). As will be shown below, this view about the secondary origin of bipolarity by means of present day migrations is quite founded. It is demonstrated by epibiotic species on drifting objects and on macroalgae.

5. Berg (1947: 137) advanced his conception of bipolarity. In the Pleistocene Glaciation Epoch not only arctic-temperate zones were touched by cooling, but also the tropics. In this period several cold water species are presumed to have penetrated into the southern hemisphere across the equator. After the glaciation period the temperature in the tropics increased again and cold water species either were lost there or retired to the North or the South.

6. The assumption about the deep water origin of closely related arctic and antarctic species was evolved by Ross (1847: 208), Ortmann (1897: 580); Andriashev (1987: 62); Vinogradov (1968: 166) and others.

7. The origin of bipolar distribution has been hypothesised by means of an Atlantic mountain range, during the Pleistocene c. 2000 m above sea level. Along this mountain range the exchange between both hemispheres of the terrestrial fauna and flora could have taken place during the pleistocene period (Malaise, 1945: 34).

There is no escape from the fact that the concept of bipolarity also concerns the temperate-subtropical fauna, though in the view of some investigators it primarily concerns the polar arctic and antarctic faunas to which it was initially restricted. First of all the term "bipolarity" induces to speak about the polar fauna; subsequently we find records of bipolar arctic and antarctic species of moss, lichens, Foraminifera

(*Globigerina pachyderma* Ehrenberg, cf. Berg, 1947: 135, 153). In the original scheme of latitudinal-zonal nomenclature Semenov (1982: 193) considers bipolarity as "distribution in cold waters of Arctic and Antarctic". More radical interpretations define it as "the presence in the Arctic and the Antarctic of apparently identical species without their presence in the intervening temperate and tropical regions" (Dunbar, 1979: 116). For good reasons many taxonomists and faunists considered bipolar distribution of the groups they studied as antitropical distribution of polar species (Petruševskaya, 1967: 180; Kussakin, 1967: 363; Stepanjants, 1967: 95; 1979: 153; 1989: 406).

A new aspect of the concept of bipolarity is the similarity of biota's of both poles as independent entities and taking into account unrelated forms, taxocenoses and biocenoses. This phenomenon was named "bionomic bipolarity" (Andriashov, 1987: 65). A typical example of bionomic bipolarity is the cryopelagic fauna.

Records of bipolar distribution of bottom living and pelagic Medusozoa are known from many taxonomic and faunistic works. However, the characteristics of the areas of bipolar distribution are not always punctual and identification of bipolar species often does not inspire confidence. *Campanularia verticillata* (Linnaeus, 1758) is often given as classical example of a species with bipolar distribution but actually two species are involved: *Rhizocaulus verticillatus* (Campanulariidae) with arctic-boreal distribution in the northern hemisphere and *Stegella grandis* (Hickson & Gravely, 1907) (Campanulinidae) with panantarctic distribution.

Many taxonomists of high qualification now study Medusozoan material from different regions (from Arctic to Antarctic) which assures species identification as exact as possible. We have analysed more than 100 of their publications to prepare the species list which we have used in this work (table 1).

Main material for our work includes a data base with 692 species of 242 genera and 79 families of Hydrozoa, Siphonophora, Cubozoa and Scyphozoa. The data base includes occurrences of these species in 9 regions of the North Pacific, 12 regions of the Polar Basin and 21 regions of the Southern Ocean.

We now dispose of quite exhaustive information on the species composition of those regions. Moreover, we analysed the species distribution in other regions of the World Ocean (based on more than 30 publications). We now have the possibility to include in this analysis new information on tropical faunae (Gibbons & Ryland, 1989: 377; Ryland & Gibbons, 1991: 525; Vervoort & Vasseur, 1977: 98; Rees & Vervoort, 1987: 209; Ramil & Vervoort, 1992: 262; Vervoort, 1993a: 298; 1993b: 537). All this information allows us to give biogeographical characteristics for every species (table 1). As a result we presume to be allowed to judge to which degree the phenomenon of bipolarity occurs in Medusozoa and explore its occurrence with methods based on the peculiarities observed in this group of animals.

Table 1 presents evidences that there are no bipolar species and genera in Cubozoa and Scyphozoa. Thirty-eight species and 30 genera of Hydrozoa and Siphonophora can be treated as bipolar. This can be explained by the "plasticity" of this group and the wider conception of "bipolarity" we presented above. The majority of bipolar species (28) is found in temperate, subtropical zones and in Arctic and Antarctic waters. It appears that there are no true autochthonous arctic or antarctic species with the exception of three: *Botrynema brucei* Browne, 1908, *Paragotoea elegans* Margulis, 1989, and *Yakovia polinae* Margulis, 1989. The remaining have arctic-boreal,

Table 1. The bipolar Medusozoa (species and genera). A = Atlantic; Am = American; Ar = Arctic; As = Asiatic; B = bipolar; Ba = bipolar Atlantic; Bp = bipolar Pacific; Bd = bipolar deepwater; Bl = Black Sea; Bor = boreal; EAr = east Arctic; Eu = European; Gallsl = Galapagos Islands; GIAn = glacial Antarctic; HAr = high Arctic; Mc = Macquarie Id; Nat = natal zone; NZ = New Zealand; P = Pacific; Pat = Patagonian Shelf; SAf = South Africa; SAm = South America; SAust = South Australia; SG = South Georgia; Sub = subtropical; SubAnisl = subantarctic islands; Tr = tropical; WAr = west Arctic; (\*) = number of bipolar species; if there is no such symbol, the genus is monotypic, "?" = doubtful. Opinions on the classification of higher taxa have not always been considered.

Taxa	General distribution	Distribution N. hemisphere	Distribution S. hemisphere
<b>Subclassis Athecatae/Anthomedusae</b>			
I. Gen. <i>Rhizogeton</i> (*)	B	Ar-Bor A P	SAf
1. <i>R. nudum</i>	B?	Bor A	SAf?
II. Gen. <i>Calycospis</i> (*)?	B?	Bor A P	GIAn SAf
III. Gen. <i>Bythotira</i> (*)	B	Bor-Sub A P	GIAn
IV. Gen. <i>Rhizorhagium</i> (*)	B	Ar-Bor A P	GIAn
V. Gen. <i>Monobrachium</i> (*)?	B	Ar-Bor A P	GIAn SubAnisl
2. <i>Eudendrium rameum</i>	B	Ar-Bor-Sub A P	Pat SubAnisl
3. <i>Tubularia indivisa</i>	B	Ar-Bor-Sub A P	SubAnisl SG
VI. Gen. <i>Paragotoaea</i> (*)?	B	HAr Bor-Sub A	GIAn
4. <i>P. elegans</i>	Bd	HAr	GIAn
VII. Gen. <i>Yakovia</i>	B	HAr	GIAn
5. <i>Y. polinae</i>	Bd	HAr	GIAn
6. <i>Sarsia tubulosa</i>	B	Ar-Bor-Sub A P Bl	GIAn SubAnisl Pat
VIII. Gen. <i>Monocoryne</i> (*)	B	Ar-Bor A P	GIAn SAf
IX. Gen. <i>Candelabrum</i> (*)	B	Ar-Bor A P	GIAn SubAnisl SAf
X. Gen. <i>Margelopis</i> (*)	B?	Bor-Sub A P Ind?	GIAn SubAnisl
XI. Gen. <i>Rosalinda</i> (*)	B?	Bor-Sub P	SAust
<b>Subclassis Thecatae/Leptomedusae</b>			
7. <i>Orthopyxis integra</i>	B	Ar-Bor-Sub A P	Pat SAust
8. <i>Obelia longissima</i>	B	Ar-Bor-Sub A P Bl	GIAnisl SubAnisl Pat NZ
9. <i>O. geniculata</i>	B	WAR-Sub A P	Mac SubAnisl Pat NZ SAust
XII. Gen. <i>Tulpa</i> (*)	B	Ar-Bor-Sub A P	SubAnisl Pat NZ
10. <i>Filidium serpens</i>	B?	Ar-Bor-Sub A P Gallsl?	GIAn Pat SAf Tr Af?
XIII. Gen. <i>Grammaria</i> (*)?	B	Ar-Bor-Sub A P	SubAnisl Pat SG
11. <i>G. abietina</i>	B	Ar-Bor-Sub A P	SubAnisl Pat SG
12. <i>Acryptolaria conferta</i>	B?	WAR-Bor-Sub A P	Pat NZ SAf Tr
XIV. Gen. <i>Zygocephalus</i> (?)	B?	AR-Bor-Sub A P Tr P?	SubAnisl Pat Tr P?
XV. Gen. <i>Lafocina</i> (*)	B?	Ar-Bor-Sub A P	GIAn SubAnisl
XVI. Gen. <i>Calycella</i> (*)	B?	Ar-Bor P Red Sea?	Pat SAf
13. <i>C. syringa</i>	B	Ar-Bor A P	Pat
XVII. Gen. <i>Modeeria</i> (*)?	B	Ar-Bor-Sub A P	SubAnisl Pat SAf NZ SAust
14. <i>M. rotunda</i>	B	WAR-Bor-Sub A P	SubAnisl NZ SAf Pat
XVIII. Gen. <i>Stauromedusa</i>	B	AR-Bor A P	SubAnisl Pat
15. <i>S. mertensi</i>	B	Ar-Bor A P	SubAnisl Pat
XIX. Gen. <i>Ptychogena</i> (*)?	B	Ar-Bor-Sub A P	GIAn SubAnisl
16. <i>Halopsis ocellata</i>	B	WAR-Bor A	Pat
XX. Gen. <i>Parascyphus</i> (*)?	B?	WAR-Bor A	Pat SubAnisl NZ SAf SAust
17. <i>P. simplex</i>	B?	Bor A ?	NZ SAust SAf
18. <i>Sertularella gayi</i>	B?	Bor-Sub A P Tr?	Pat NZ

19. <i>S. reticulata</i>	Bp?	Bor P	SAust?
20. <i>Symplectoscyphus tricuspidatus</i>	B	Ar-Bor A P	Pat
XXI. Gen. <i>Staurotheca</i> (*6?)	B	Bor P	GIA n SubAnIs l
21. <i>Abietinaria abietina</i>	B	Ar-Bor-Sub A P	Pat SAf?
XXII. Gen. <i>Papilionella</i> (*4)	B	Bor P	Pat NZ
22. <i>Thuiaria thuja</i>	B	WA r-Bor A P	Pat
23. <i>Haleci um tenellum</i>	B?	Ar-Bor-Sub A P	GIA n NZ Pat SAf SAust
XXIII. Gen. <i>Kirchenpaueria</i> (*6?)	B?	Ar-Bor-Sub A P	SAf NZ Tr?
24. <i>K. pinnata</i>	Ba	Bor-Sub A	SAf
25. <i>K. bonnevieveae</i>	B	Sub A	SAf NZ
26. <i>Ventromima halecioides</i>	B?	Sub A Bl	SAf?
27. <i>Plumularia filicaulis</i>	B?	Bor-Sub P	SAf? Pat?
XXIV. Gen. <i>Oswaldella</i> (*6?)	B?	Bor P?	GIA n SubAnIs l
XXV. Gen. <i>Schizotrichia</i> (*10?)	B	Ar-Bor-Sub A P	GIA n SubAnIs l SAf Pat
28. <i>Halopteris catharina</i>	Ba?	Bor-Sub	Pat
29. <i>Nemertesia antennina</i>	Ba?	Bor-Sub A P	SAf Tr?
<b>Subclassis Trachymedusae</b>			
XXVI. Gen. <i>Botrynema</i> (*2)	B	Ar-Bor-Sub A P	GIA n
30. <i>B. brucei</i>	Bd	Bor P	EBor A GIA n
XXVII. Gen. <i>Ptychogastria</i> (*2?)	B	Ar-Bor A P Sub A	GIA n SubAnIs l
<b>Subclassis Limnomedusae</b>			
XXVIII. Gen. <i>Craspedacusta</i> (*3)	B	Bor-Sub As Eu Am	Aust SAm
31. <i>C. sowerbyi</i>	B	Bor-Sub As Eu Am	Aust SAm
<b>Subclassis Siphonophorae</b>			
<b>Ordo Physophorida</b>			
XXIX. Gen. <i>Marrus</i> (*3)	B	Ar-Bor A P	GIA n SubAnIs l SAf NZ
32. <i>M. antarcticus</i>	Bd	Bor P	GIA n SubAnIs l SAf NZ
<b>Ordo Calycophorida</b>			
33. <i>Clausophyes galeata</i>	Bd	Bor P	GIA n SAust
34. <i>Lensia achilles</i>	Bd	Bor A P	GIA n SAf
35. <i>L. asymmetrica</i>	Bd	Bor P	GIA n SAf
36. <i>Muggiae a bargmannae</i>	Bp	Bor P	GIA n SubAnIs l SG
37. <i>M. havock</i>	Bd	Bor P	An SubAnIs l SG SAf
XXX. Gen. <i>Dimophyes</i>	B?	Ar-Bor-Sub A P Tr?	GIA n SubAnIs l Nat Tr?
38. <i>D. arctica</i>	B?	Ar-Bor-Sub A P Tr?	GIA n SubAnIs l Nat Tr?

arctic-subtropical, or antarctic-natal distribution. Another important feature: of the 38 bipolar species 27 have a bottom dwelling stage, 14 are true epibionts. The other 13 may also be epibiotic. From the 16 species with free medusae, at least 7 species inhabit coastal plankton and their polyps are also epibionts, in any event inhabit drifting objects, ships hulls and macroalgae, and by their presumed ability to tolerate the high temperatures of tropical seawater may migrate. With respect to those species the Migration theory by Ortmann (see above) is quite appropriate. Such species, as e.g. *Obelia geniculata* (Linnaeus, 1758), are represented in the northern hemisphere by dense populations, but in the southern hemisphere occur mainly isolated, often on drifting macroalgae. Migrations are most probably in the direction from north to south.

The eight characteristic pelagic bipolar species include three species of hydro-medusae and five species of Siphonophora (see table 1). The polyps of these three

species of hydromedusae are unknown. For *Paragotoea elegans* and *Yakovia polinae* they may be of the same type as other Tubulariidae or Corymorphidae. These species have been recorded from depths between 50 and 2000 m. In polar waters they are known to occur closer to the surface: 50-200 m. Their distribution pattern probably results from contemporary migration (Vinogradov, 1968), including migration of larvae (Mileikovsky, 1977: 105). It seems likely that these species will be detected at bathyal depths of the tropics.

Three species: *Tubularia indivisa* Linnaeus, 1758; *Eudendrium rameum* (Pallas, 1766) and *Grammaria abietina* (M. Sars, 1851) have no free medusae. Their robust colonies often occupy rocky bottoms and form rich, dense settlements in the sub-tidal zone of Arctic and temperate waters of the northern hemisphere. Less rich but viable populations are known to occur near subantarctic islands and on the Patagonian shelf. *Tubularia indivisa* is represented in the Southern Ocean by the subspecies *antarctica* Hartlaub, 1905. It is probably possible to see such species as the relics of an ancient fauna of northern-boreal origin.

*Craspedacusta sowerbyi* Lankester, 1880 is represented by polyps and medusae in fresh water of the temperate zone of both hemispheres. In the tropics (India, Africa) there is the closely related genus *Limnocnida*. The conception of distribution of terrestrial species in the pleistocene across the Atlantic range may explain bipolarity of *C. sowerbyi*. The presence of the genus *Kirklandia* in Jurassic and Carboniferous formation of Germany and North America confirms the ancient age of this group.

In spite of difficulties in the identification of species of the genus *Filellum* when the coppinia are absent, it can be stated that only two species are sufficiently well known to state their geographical distribution, viz. *Filellum serpens* (Hassall, 1848), known from cold boreal and warmer subtropical regions, and the subtropical-tropical *Filellum serratum* (Clarke, 1879). For a long time *F. serpens* was accepted by taxonomists as a panoceanic species. It was named as bipolar for the first time by Derjugin (1915: 863). A discussion of the distribution of this species was given later (Stepanjants, 1980: 117). *F. serpens* is known from cold and temperate waters of both hemispheres (9-300 m to 3500 m), was found in the Mediterranean and in tropical waters off West Africa. So formally it is not an antitropical species. But if we bear in mind Darwin's reasoning (see above), it is necessary in this case to use ecological data: the cold water species *F. serpens* may penetrate into deep waters of the tropical regions with the cold water masses along the West African coast.

Similarly the distribution of *Dimophyes arctica* (Chun, 1897) could be assessed. This species was first found in the Arctic and later on in different parts of the World Ocean, in the Caribbean Sea and the tropical zone: consequently it was considered to be cosmopolitan. Investigations in later years testify that the distribution of this species is limited to cold water (Stepanjants, 1975: 96). Moreover, new statistical methods allow us to conclude that *D. arctica* reproduces in water of polar origin, but that the tropics represent a sterile eviction area (Lobanov, Stepanjants & Dianov, in press). The same may hold true for *Muggiae bergmannae* Totton, 1954, the Pacific bipolar siphonophore. Penetration in the tropics of the above named species involves transportation in specific water masses, which is equivalent to Darwin's and Berg's opinions about bipolarity as a phenomenon caused by climatic conditions. It is logical, therefore, to agree with Derjugin's opinion that cosmopolitanism is the predecessor of bipolarity.

Amongst the thirty bipolar genera *Staurophora*, *Yakovia* and *Dimophyes* alone are monotypic; *Paragotoea* has two bipolar species; *Margelopsis*, *Monobrachium*, *Papilionella*, *Tulpa*, *Craspedacusta* and others have two to four closely related species from the northern and southern hemispheres, but not a single one in tropical seas (table 1).

*Monocoryne* and *Candelabrum* constitute the bipolar family *Candelabridae*. *Monocoryne* has three species: *M. gigantea* (Bonnevie, 1898) (Arctic, temperate North Pacific and Atlantic); *M. minor* Millard, 1966 (South Africa) and *M. spec.* (Antarctic). *Candelabrum* includes at least thirteen species: *C. phrygium* (Fabricius, 1780) (Arctic, boreal waters of the North Pacific and Atlantic); *C. cocksii* (Vigurs, 1849) (boreal waters of the eastern Atlantic); *C. giganteum* (Bonnevie, 1898), *C. minutum* (Bonnevie, 1898), *C. mitra* (Bonnevie, 1898) and *C. verrucosum* (Bonnevie, 1898) (northern Atlantic); *C. australis* Briggs, 1928, and *C. harrisoni* Briggs, 1928 (New South Wales); *C. meridianum* Briggs, 1938 (Macquarie Id, Marion Id); *C. austrogeorgiae* Jaederholm, 1904; *C. penola* Manton, 1940 (subantarctic Islands, Antarctic); *C. capensis* Manton, 1940 and *C. tentaculata* Millard, 1966 (South Africa). There is no representative of this family in the tropics. All of these species are very close both morphologically and ecologically: they prefer cold water (-1°C to 7°C), and most likely have a deep water nature. In spite of the absence of paleontological data, this species group could be considered to represent relics of a deep water tertiary fauna. Future representatives of this family are likely to be found in deep waters of the tropics.

The bipolar family *Kirchenpaueriidae* amongst others includes the two genera *Kirchenpaueria* and *Oswaldella*, which like the bipolar genus *Schizotricha* (*Plumulariidae*) occur in cold water. These three genera, with the possible exception of *Oswaldella*, are distributed in cold, temperate and subtropical waters of both hemispheres but presumably originate from warm water *Plumulariidae* inhabiting mainly subtropical and tropical zones. The northern *Plumularia microtheca* Naumov, 1960 (North Pacific), *P. fragilis* Hamann, 1882 (Barents Sea) and *P. haleciooides* Alder, 1859 (Black Sea) actually belong in *Kirchenpaueriidae*, not in *Plumulariidae*, but their present status, in absence of supplementary material, remains uncertain.

There are not many bipolar species in the family *Sertulariidae* (table 1). *Thuiaria* (including *Selaginopsis*) is represented in the northern hemisphere by about 40 species in the North Pacific, 10 species in the Arctic and c. 5 species in the North Atlantic. No *Thuiaria* species occurs in the tropics. There are some species in the Southern Ocean that are quite close to the northern species of *Thuiaria* but differ in the distribution of the number of rows of hydrothecae on stem and branches of the colony. These antarctic species were placed in *Thuiaria* by Stepanjants (1979: 92). However, besides the difference in the number of rows of hydrothecae referred to above, there are also differences in the shape of the gonothecae. This allows us to remove those southern species from the genus *Thuiaria* Fleming, 1820, and place these in the genus *Staurotheca*. The five *Staurotheca* species so far described are considered endemics of the southern hemisphere and several of the species now added to the genus are likely to be such. *Sertularia staurotheca* Naumov, 1960, is known from the North Pacific and may be affiliated to the genus *Staurotheca* by the crosswise pairs of hydrothecae. There are, however, no data on the gonothecae. If those resemble the gonothecae of southern species of *Staurotheca* and if other morphological details also match, the genus could be supposed to be bipolar.

*Zygophylax* is convenient for our analysis as it was recently reviewed (Rees & Vervoort, 1987: 51). To date more than 50 species are known, which inhabit mainly subtropical zones of both Atlantic and Pacific, usually at depths exceeding 100 m depth. One Arctic species and two from the subantarctic are known. Twelve species inhabit the tropics, but at 200-1600 m depth. Only five species are known from tropical shallow water localities. We are inclined to refer to deep-water origin of the largely antitropical *Zygophylax* fauna and migration of its species to the north and south may have taken place along the deep, cold water of the Americas, to give independent cold water polar shelf faunae of both hemispheres. This migration may have taken place in the preglacial period since Cambrian *Archaeocryptolaria* and *Archaeolafoea* are known from Tasmania, Australia and North America.

Representatives of Hydractiniidae epibiotic on the ophiurid family Ophiolepididae occur at Arctic depths (*Hydractinia ingolfi* Kramp, 1932) and in the Antarctic (*Hydractinia vallini* Jaederholm, 1926), they allow us to speculate on bionomic (ecological) bipolarity (Svoboda, Stepanjants & Smirnov, in press). It is possible to demonstrate bionomic bipolarity by comparing the hydrozoan faunae of the Commander and Aleutian Islands (123 species) and Kerguelen Island (69 species). There are six species in common: *Tubularia indivisa*, *Sarsia tubulosa*, *Lafaea dumosa*, *Grammaria abietina*, *Muggiaeae bargmannae* and *Dimophyes arctica*. In both regions the same families are dominant: Sertulariidae (26% and 20%), Haleciidae (5.6% and 7.7%), Campanulariidae (5.6% and 11.5%). In Sertulariidae the composition of genera on the northern hemisphere is: *Abietinaria* (12 species), *Sertularella* (8) and *Thuiaria* (7), and on the southern hemisphere: *Symplectoscyphus* (9 species). Cold water Kirchenpaueriidae and Plumulariidae (*Schizotricha*) are represented at the North Pacific Islands by two species [*Plumularia* (*Kirchenpaueria?*) *microtheca* Naumov, 1960 and *Schizotricha* (= *Kirchenpaueria?*) *divergens* Naumov, 1960], and at Kerguelen by *Oswaldella bifurca* (Hartlaub, 1904) and *Schizotricha unifurcata* Allman, 1883.

### Conclusions

1. Many bipolar species, genera and families of Hydrozoa and Siphonophora are known. There are no bipolar Scyphozoa and Cubozoa.
2. The term "bipolar" = "antitropical", "bitemperate" for these groups means distribution from Arctic to Antarctic with interruption in the tropics.
3. Certain species and genera occur in cold, temperate and subtropical zones as well as in the tropics. In the last case they are known at depths with cold water of polar origin. We also consider these taxons as being bipolar.
4. Bipolar species distribution of Hydrozoa is largely a result of present day migration from the northern to the southern hemisphere.
5. Only some bipolar species are relicts of an old temporeate fauna.
6. Some bipolar genera may be considered relicts of a cold deep water fauna: *Monocoryne*, *Candelabrum* and *Zygophylax*; or originate from warm water families: Kirchenpaueriidae from Plumulariidae. There are also some closely related genera in the northern and southern parts of the oceans: *Thuiaria* in the North Pacific and *Selaginopsis* and *Staurotheca* in antarctic waters.
7. Several examples of bionomic bipolarity, on the level of taxa or taxocenoses, are known.

8. All opinions on the origin of bipolarity advocated in the course of time are suitable for the explanation of bipolarity in Medusozoa. There is evidently no universal way to explain the antitropical fauna distribution.

9. Bipolarity is not a unique phenomenon in biogeography. It is most likely the result of different historical or modern ways of the formation of faunae that are similar in their external manifestation.

### Acknowledgements

The authors wish to express their gratitude to drs. A.P. Andriashev, A.I. Kafanov, O.G. Kussakin, K.N. Nessis, Ya.I. Starobogatov, and I.S. Smirnov for suggestions concerning this manuscript.

### References

- Andriashev, A.P., 1964. [A general review of the antarctic fish fauna]. In: Res. Biol. Issled. SAE.— Issled. Fauny Morei 2 (10): 335-386. (Russian).
- Andriashev, A.P., 1965. A general review of the antarctic fish fauna. In: J. van Mieghem & P. van Oye (eds). Biogeography and ecology in Antarctica.— Monographiae biologicae vol. 15, The Hague: 491-550.
- Andriashev, A.P., 1987. [Development of Berg's concept of bipolarity of marine fauna].— Biologiya morya, Vladivostok, 1987 (2): 60-67. (Russian with English summary).
- Beklemishev, K.V., 1969. [Ecology and biogeography of the ocean].— 'Nauka', Moscow: 1-292. (Russian).
- Berg, L.S., 1947. [Bipolar distribution of organisms and glacial epoch]. In: Climate and Life.— Moscow: 128-155. (Russian).
- Briggs, J.C., 1987. Antitropical distribution and evolution in the Indo-West Pacific Ocean.— Syst. Zool. 36 (3): 237-247.
- Dana, J.D., 1854. On the geographical distribution of Crustacea.— Amer. Journ. Sci. Arts. 15 (2): 1-45.
- Darwin, C., 1859. The origin of the species by means of natural selection: 1-502.— London.
- Derjugin, K.M., 1915. [Cosmopolitanism and the bipolar theory]. In: Fauna of Kolskyi Bay and its environmental condition.— Petrograd: 854-875. (Russian).
- Dollo, L., 1904. Poissons. In: Expédition antarctique belge. Résultats du voyage du S.Y. Belgica en 1897-1898-1899, Zoologie.— Anvers: 1-240.
- Dunbar, M.J., 1979. The relation between oceans. In: S. van der Spoel & A.C. Pierrot-Bults (eds). Zoogeography and diversity in plankton.— Utrecht: 112-125.
- Ekman, S., 1953. Zoogeography of the Sea: 1-417.— London.
- Gibbons, M.J. & J.S. Ryland, 1989. Intertidal and shallow water hydroids from Fiji. I. Athecata to Ser-tulariidae.— Mem. Queensl. Mus. 27: 377-432.
- Hesse, R., 1924. Tiergeographie auf ökologischer Grundlage: 1-613.— Jena.
- Kussakin, O.G., 1967. Isopoda and Tanaidacea from the coastal zones of the Antarctic and Subantarctic. In: Res. Biol. Issled. SAE. 3.— Issled. Fauny Morei 4 (12): 220-380. (Russian).
- Lobanov, A.I., S.D. Stepanjants & M.B. Dianov, in press. *Dimophyes arctica* (Chun, 1897) (Siphonophora). Morphological and biological peculiarities research, area distribution improvement with the computer aided methods.
- Malaise, R., 1945. Tenthredinoidea of south-eastern Asia with a general zoogeographical review.— Opusc. ent., Lund, suppl. 4: 1-288.
- Mileikovsky, S.A., 1977. [The structure of the area distributions of the bottom animals and role of pelagic larvae in formation of area distribution]. In: M.E. Vinogradov (ed.). Ocean Biology. 1. Biological Ocean Structure.— 'Nauka', Moscow: 262-266. (Russian).
- Murray, J., 1896. On the deep and shallow-water marine fauna of the Kerguelen Region of the Great Southern Ocean.— Trans. Roy. Soc. Edinb. 38 (2): 494.

- Ortmann, A.E., 1897. Ueber "Bipolarität" in der Verbreitung mariner Tiere.— Zool. Jahrb., Abt. Syst. 9: 571-595.
- Petrushevskaya, M.G., 1967. [Antarctic spumelline and nasseline radiolarians (in collections of the Soviet Antarctic Expedition)]. In: Res. Biol. Issled. SAE. 3.— Issled. Fauny Morei 4 (12): 5-186. (Russian).
- Pfeffer, G., 1891. Versuch über die erdgeschichtliche Entwicklung der jetzigen Verbreitungsverhältnisse unserer Tierwelt: 1-62.— Hamburg.
- Ramil, F. & W. Vervoort, 1992. Report on the Hydroida collected by the "Balgim" expedition in and around the Strait of Gibraltar.— Zool. Verh. Leiden 277: 1-262.
- Rees, W.J. & W. Vervoort, 1987. Hydroids from the John Murray Expedition to the Indian Ocean, with Revisory notes on *Hydrodendron*, *Abietinella*, *Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa).— Zool. Verh. Leiden 237: 1-209.
- Ross, G.A., 1847. Voyage of discovery and research in the southern and antarctic regions during the years 1839-1843: 1-447.— London.
- Ryland J.S. & M.J. Gibbons, 1991. Intertidal and shallow water hydroids from Fiji. II. Plumulariidae and Aglaophenidae.— Mem. Queensl. Mus. 30 (3): 525-560.
- Semenov, V.N., 1982. [Biogeographic range of the South America Shelf on the classification of the bottom animals species area distributions base]. In: O. Kussakin (ed.). Marine biogeography.— Moscow: 1-312. (Russian).
- Stepanjants, S.D., 1967. [Siphonophora of the USSR seas and the north part of the Pacific Ocean].— Opredelitel po faune SSSR 96: 1-216. (Russian).
- Stepanjants, S.D., 1975. Species composition and distributional pattern of Siphonophora of the Caribbean, Gulf of Mexico and adjacent waters of the Atlantic.— Trudy Inst. Oceanol. 100: 96-126.
- Stepanjants, S.D., 1979. [Hydroids of the antarctic and subantarctic waters]. In: Res. Biol. Issled. SAE. 6.— Issled. Fauny Morei 20 (30): 1-199. (Russian).
- Stepanjants, S.D., 1980. [On the cosmopolitanism in hydroids]. In: D. Naumov & S. Stepanjants (eds). Theoretical and practical importance of the coelenterates: 114-122. (Russian).
- Stepanjants, S.D., 1989. Hydrozoa of the Eurasian arctic seas. In: I. Herman (ed.). The arctic seas. Climatology, oceanography, geology, and biology: 397-430.— Libr. Congr. Cat. Card N 88-33800.
- Stiasny, G., 1934. Das Bipolaritätsproblem.— Arch. néerland. Zool. Leiden 1: 35-53.
- Svoboda A., S.D. Stepanjants & I.S. Smirnov, in press. Two polar *Hydractinia* species (Cnidaria), epibiotic on two closely related brittle stars (Echinodermata): an example for a taxonomic and ecological bipolarity.
- Thompson, A.W., 1897-1898. On a supposed resemblance between the marine faunas of the arctic and antarctic regions.— Proc. Roy. Soc. Edinb. 20 (12): 311-349.
- Théel, H., 1886. Report on the Holothuroidea. Part. 1.— Scient. Res. Voy. H.M.S. Challenger, Zool. 14: 1-290.
- Vervoort, W., 1993a. Report on hydroids (Hydrozoa, Cnidaria) in the collections of the Zoological Museum, University of Tel-Aviv, Israel.— Zool. Meded. Leiden 67 (40): 537-565.
- Vervoort, W., 1993b. Cnidaria, Hydrozoa, Hydroida: Hydroids from the western Pacific (Philippines, Indonesia and New Caledonia). I: Sertulariidae (1). In: Rés. Campagn. Musorstrom 11.— Mém. Mus. nat. Hist. nat. Paris 158: 89-298.
- Vervoort W. & P. Vasseur, 1977. Hydroids from French Polynesia with notes on distribution and ecology.— Zool. Verh. Leiden 159: 1-98.
- Vinogradov, M.E., 1968. Vertical distribution of the oceanic zooplankton.— Moscow: 1-339. (Russian).
- Vinogradova, N.G., 1977. [The abyssal and ultra-abyssal bottom fauna]. In: M.E. Vinogradov (ed.). Biology of the ocean, I. Biological ocean structure.— 'Nauka', Moscow: 281-298. (Russian).