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# THE ARCTIC SEAS

## Climatology, Oceanography, Geology, and Biology

*Edited by*

Yvonne Herman



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# 14: Arctic Ocean Bryozoa

Valentina I. Gontar and  
Nina V. Denisenko

## INTRODUCTION

Bryozoans (Bryozoa, Polyzoa, Ectoprocta) are aquatic colonial animals. A few kinds live in fresh water (class Phylactolaemata) while the majority are marine (class Gymnolaemata and Stenolaemata). The phylum contains over 4,000 living species and about 15,000 extinct species. The colonies are formed by asexual reproduction from one individual, the ancestrula, that arises through metamorphosis of the larva developed by sexual reproduction. The bryozoan colony, the zoarium, is almost always firmly attached to the substratum and can be ramified, lobed, fan-shaped, and very frequently have the appearance of crusts covering the substratum. The size of colonies vary from several millimeters to several decimeters. The colonies consist of individuals, the zooids. Bryozoans are bilaterally symmetrical, coelomic, protostomian animals. As a result of their sessile and colonial way of life, their organization

has undergone profound changes in different subclasses.

The structure of bryozoans is as follows: Every zooid bears a circlet of tentacles. The mouth is surrounded by tentacles. The anus is located near the mouth, but outside the crown of tentacles. In marine bryozoans, the lophophore, a fleshy structure that surrounds the mouth, is ring-shaped. When the anterior part of the body is withdrawn, the tentacles are also retracted into the body known as the tentacle sheath.

Marine bryozoans have neither heart nor vascular system. The inner zooidal cavity is a coelom that is separated from the lophophore cavity by an incomplete partition. The nervous system comprises a nerve ganglion that lies between the mouth and the anus and a plexus in the body wall. From the nerve ganglion, nerves radiate to the tentacles and other organs. The muscular system consists of circular and longitudinal muscles, namely, circular sphincter muscles, transverse parietal muscles, and strong retractor muscles. Reproduction can be both asexual and sexual; colonies are formed mainly by asexual

*Note:* This chapter has been reviewed, edited, and rewritten by the Editor, Yvonne Herman.

reproduction. Most bryozoans are hermaphrodites.

The zooidal body cavity contains gonads of both sexes that develop simultaneously, although some species show a tendency for protandry (functional male gonad maturation precedes female gonad maturation). Spermatozoa are released from the zooidal cavity either through the terminal pores of tentacles, or through the supraneural pore coelomopore situated at the vertex of the funnel between tentacles. In some species, the coelomopore is transformed into an intertentacular organ in which fertilization occurs. Fertilized eggs can be discharged into the sea, although in many marine taxa their development up to larval stage occurs either in the coelom or the zooid in a special brooding chamber (ovicell). The larvae are close to the trochophore and according to some authors may be significant as a dispersal mechanism. After being set free, the larvae swim for a few hours and eventually settle on a suitable substratum, producing through metamorphosis and budding a primary zooid, the ancestrula, which subsequently initiates a colony.

The above-described complex of organs is termed the polypide; it is encased in the exoskeleton of various shapes, called the zoecium or cystid. It is secreted by the body wall, which consists of cellular layers. The zooidal skeleton can be separated, but its walls are usually in touch with other zoecia or zoecia may have common proximal and distal walls. Connection between separate zooids is through single pores or more complex structures (porous lamellae or septa, porous chamber or diatalia) in the cystid walls. The zoecium bears an orifice through which the anterior end of the polypide is protruded. It can be provided with an operculum. The space between the tips of tentacles withdrawn into the tentacle sheath and the orifice is the atrium or vestibulum. The zoecium can be chitinous, jellylike (other polymer of chitin of Insecta), or calcareous.

In bryozoan colonies the zooids are usually polymorphic, that is, there are in addition to the zooids' typical structures: the autozooids, morphologically modified and physiologically specialized zooids such as the heterozooids, including gonozoids (where maturation of sperm and oocyst occurs), the kenozooids (performing supporting function), the avicularia (defense function), the vibracula (apparently providing water current beneath the colony), and other structures (*Treatise on Invertebrate Paleontology*, 1983). The phylum Bryozoa is divided into three classes.

Class Stenolaemata with 6 orders:

- Order Cyclostomata (Paleozoic–Recent)
- Order Trepostomata (Paleozoic–Triassic)
- Order Cystoporata (Paleozoic)
- Order Rhabdomesonata (Paleozoic)
- Order Cryptostomata (Paleozoic)
- Order Fenestrata (Paleozoic)

Class Gymnolaemata with 2 orders:

- Order Ctenostomata (Paleozoic–Recent)
- Order Cheilostomata (Jurassic–Recent)

Class Phylactolaemata (Carboniferous–Recent)

Bryozoa are known to have been widespread in the Paleozoic seas (7 orders) and are valuable in stratigraphy; their ancestry and early evolutionary relationships are difficult to infer. Skeleton-bearing bryozoans are believed to have evolved during the lower Ordovician (Baltic province), although the high level of organization of the early Ordovician bryozoans suggests that they might have evolved during the early Cambrian. The evolutionary development of skeleton-bearing Bryozoa is divided into large stages, their boundaries corresponding to boundaries of geologic epochs defined by major evolutionary changes that led to a change in the rank of orders (Morosova and Viskova, 1977). The first stage encompasses the period from

early Ordovician up to late Permian; the second stage occurred during the Mesozoic-Cenozoic. During the first stage, 7 orders evolved simultaneously with an abrupt change of genera and families at three boundaries: The first boundary corresponds to the end of the Silurian; the second, to the end of the Devonian; and the third, to the end of the Permian. The second stage covers the Mesozoic-Cenozoic eras. It is noteworthy that the currently accepted systematics of the Bryozoa is far from being adequate, as the paleontological classification is based only on the morphology of skeletal elements.

The Permian is the final period of evolution of Paleozoic bryozoans. Permian taxa were widespread in the World Ocean. However, the Arctic region was rich in bryozoans between the Ordovician and Permian (Astrova, 1965; Morosova, 1981; Morosova and Kruchinina, 1986; Nekchorosheva, 1965, 1966, 1970, 1976). About 300 species described by these authors are used for the stratigraphic division of Paleozoic deposits of this region as well as for dividing the Paleozoic Arctic seas into biogeographic regions.

During the Dzhulphinian and Dorosham times, the bryozoan faunas were declining. They survived only in the Tethys Sea. Nearly all bryozoans had disappeared by the end of the Permian. Only 4 genera (*Discritella*, *Reptonodicava*, *Paralioclema*, and *Pseudobatostomella*) with few species characterized by simple morphological organization continued to evolve in the Triassic seas (known from the Primorsky Territory and the northeastern USSR) together with a small number of Cyclostomata. The Mesozoic-Cenozoic stage commences in Triassic and is characterized by a different type of bryozoans, which must have given rise to all the younger taxa. Favorable environmental conditions in the Middle Jurassic seas, where the Cyclostomata were probably the only bryozoans, may have triggered their rapid speciation. During the Late Jurassic and throughout

the entire Cretaceous period, the Cyclostomata, which were the dominant bryozoans, became ubiquitous in the World Ocean. The penetration of the Cyclostomata to relatively great depths in Campanian and Maestrichtian seas must have been related not only to extensive marine transgressions but also to the rapid development of the Cheilostomata that had evolved in early Jurassic time (*Pyriporopsis portlandensis*). The Cyclostomata are represented today by relicts of Mesozoic seas.

Another order of recent bryozoans is the Ctenostomata. The fossil record of this group is very scanty because they lack calcareous skeleton; to date 55 genera have been described. They belong to 23 families, 3 of which are Paleozoic while 15 are recent. Most recent species belong to the order Cheilostomata (80 percent of the total number of recent species). In the Early Cretaceous, only the *Anasca* suborder was represented. Two other suborders, *Ascophora* and *Cribrimorpha*, evolved at the beginning of the Late Cretaceous. The end of the Late Cretaceous and the beginning of the Cenozoic are characterized by the extinction of most cribrimorphs and by the diversification of the *Anasca* and *Ascophora*. The evolution of bryozoans suggests a parallel evolution of colonies of different phylogenetic branches of the phylum owing to polymorphism. This provided bryozoans with a high degree of adaptation to environmental factors with evolutionary plasticity and led to their flourishing in modern oceans and seas.

Bryozoans, represented by three orders in the World Ocean—the Cyclostomata, Ctenostomata, and Cheilostomata—are a ubiquitous group of aquatic invertebrates. They occur in every climatic zone and inhabit depths ranging from the littoral to the abyssal zones. Bryozoans constitute a part of many marine bottom biocenoses and play an important role in the total economy of the sea. Colonies live on rocks, algae, hydroids, worm tubes, mollusk shells, crab tests, ascidians, corals,



colonies of other bryozoans, fragments of sea urchins' skeletons, and also on various sunken objects such as buoys and nets.

## ARCTIC BRYOZOA

The distributional pattern of various biogeographic groups shows that all Arctic seas are dominated by boreal-Arctic\* species. The western part of the Barents Sea and areas of the Atlantic Ocean adjoining the Arctic Basin are dominated by Atlantic boreal† species. Boreal species‡ are replaced by the Arctic taxa§ in the eastern Barents, Kara, Laptev, and East Siberian seas. Arctic species¶ are replaced by boreal Pacific taxa in the eastern Chukchi Sea and adjoining part of the Bering Sea. North American Arctic waters are dominated by Arctic species. Most species are confined to the Eurasian and Amerasian subbasins with the boundary in the area of the New Siberian Islands. Eurybathyal species are predominant in the western Barents, and the Chukchi Sea fauna exhibits the lowest degree of similarity with the fauna of Siberian seas and the Arctic-American waters.

The majority of bryozoans inhabit rocky substrates. They comprise many marine benthic biocenoses and play an important part in the overall trophic relations of the sea. They are well preserved in sediments of different geological age and are very im-

portant in biostratigraphic zonation. There are numerous reviews dealing with the bryozoan fauna of the Arctic Basin (Packard, 1867; Smitt, 1878, 1879; Vigelius, 1882, 1884; Waters, 1900, 1904; Nordgaard, 1906, 1912, 1918, 1923, 1929; Norman, 1906; Osburn, 1913, 1932, 1936; Kluge, 1962; Gostilovskayja, 1978). While the faunal composition in this region has been adequately studied, knowledge of their ecology remains incomplete. Nevertheless, the literature and material collected during the last 250 years and deposited at the Zoological Institute of the USSR Academy of Sciences allows us to summarize their distribution in the Arctic Ocean.

Here we follow the classification of Kluge (1962) with several additions based on recent investigations of Soviet and foreign scientists. In the Arctic Ocean, the phylum is represented by 3 orders, 11 suborders, 41 families, 89 genera, 340 species including 40 varieties and 1 form.

Variations in species composition in different seas of the Arctic Ocean have been analyzed using cluster analysis and estimating the degree of similarity according to Jaccard (1901),

$$j = \frac{c \times 100\%}{D_1 + D_2 - c}$$

and with the inclusion method

$$j = \frac{c \times 100\%}{D_{\min}}$$

Results are presented in Tables 14-1 and 14-2 (see pages 349-363) and Figure 14-1. As shown in Table 14-1, the decline in number of species occurs from boreal Atlantic waters to the Arctic proper. There is a significant difference between the bryozoan fauna of the western Barents Sea of boreal character, and faunas of eastern Barents Sea and adjoining seas. The groups showing the closest affinity are from the eastern Barents, Kara, and Lap-

\*Boreal-Arctic species (for their boundaries see map) occur in the boreal and Arctic biogeographic regions.

†Boreal species including amphiboreal, widespread boreal, low boreal, and high boreal taxa are distributed within the boreal biogeographic regions.

‡Arctic species include Eurasian species distributed in the Arctic Ocean off the European and Asian coasts; Euroamerican or Ameroeuropean species distributed in the Arctic Ocean off the Asian and North American coasts. Circumpolar species are distributed in the Arctic Ocean off the coasts of Europe, Asia, North America, Greenland, Iceland, and Arctic Ocean islands. Amerasian species are distributed in the Arctic Ocean off the Asian and North American coasts. American species are distributed in the Arctic Ocean off the North American coasts.

tev seas. The fauna of these seas contain a larger proportion of Atlantic taxa than of Pacific elements. There is a significant difference in composition between the fauna of the East Siberian Sea, comprising species of Atlantic and Pacific origin, and the fauna of the Eurasian sector of the Arctic and Chukchi seas.

D <sub>I</sub>	D <sub>2</sub>	D <sub>3</sub>	D <sub>4</sub>	D <sub>5</sub>	D <sub>6</sub>
193	66	63	60	64	62
47	211	93	80	76	84
45	78	186	90	65	94
30	40	55	119	72	68
31	35	46	53	110	56
25	35	45	53	34	93

Correlation of different biogeographic groups in the Arctic seas (Fig. 14-2) shows that the boreal-Arctic species are the most abundant group in all seas. Boreal species predominate in the North Atlantic and western Barents Sea as well as in the eastern Chukchi Sea. The number of Arctic species exceeds that of boreal species in the eastern Barents Sea and western Chukchi Sea, delineating the boundaries of the Arctic region. Major faunal differences exist between the Eurasian and the American sectors of the Arctic Basin; the boundary between the two regions is the New Siberian shoals. Boreal-Arctic species are predominant here; however, there is a decline in species numbers in this region. The western part of the Barents and eastern part of the Chukchi seas may be considered a transitional zone between the Atlantic and the Pacific boreal biogeographic regions and the Arctic region (Fig. 14-3).

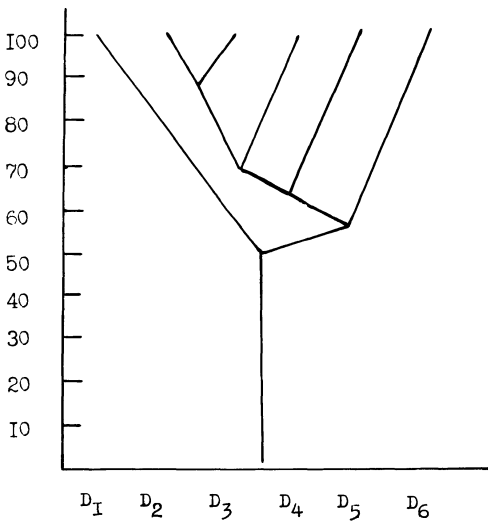


Figure 14-1. Dendrogram expressing similarities; similarities (bottom) and degree of inclusion (top) of bryozoan fauna (%) in Arctic seas. D<sub>1</sub>, western part of the Barents Sea; D<sub>2</sub>, eastern part of the Barents Sea; D<sub>3</sub>, Kara Sea; D<sub>4</sub>, Laptev Sea; D<sub>5</sub>, Eastern Siberian Sea; D<sub>6</sub>, Chukchi Sea.

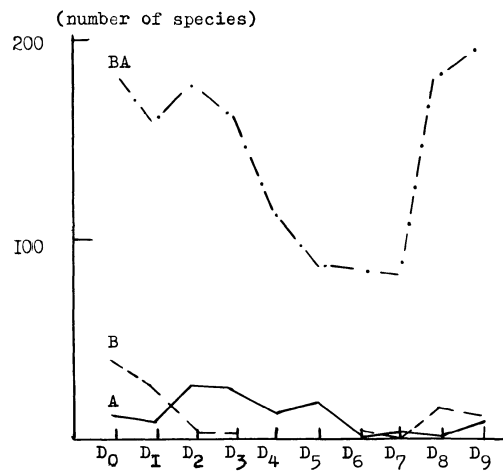


Figure 14-2. Depth distribution of different biogeographic groups of bryozoan species in the Arctic Seas. Legend as in Figure 14-1. D<sub>0</sub>, northern part of the Atlantic Ocean; D<sub>6</sub>, eastern part of the Chukchi Sea; D<sub>7</sub>, western part of the Chukchi Sea; D<sub>8</sub>, northern part of the Pacific Ocean; D<sub>9</sub>, Arctic coastal waters of North America; BA, boreal-Arctic species; B, boreal species; A, Arctic species.

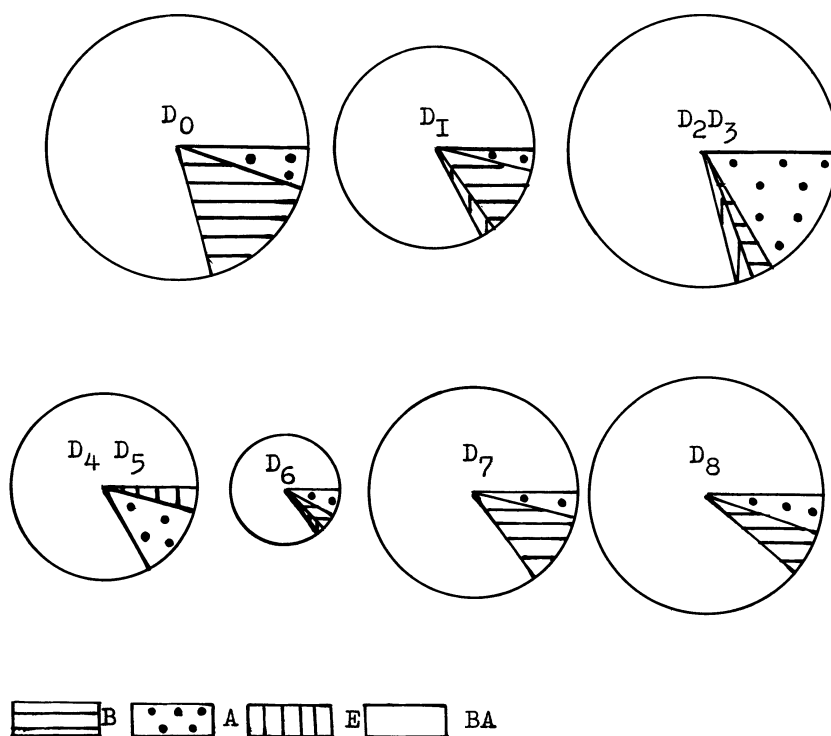


Figure 14-3. Biogeographic distribution of the bryozoan fauna in the Arctic Seas. Legend as in Figures 14-1 and 14-2 except D<sub>7</sub>, northern part of the Pacific Ocean; D<sub>8</sub>, Arctic coastal waters of North America; E, endemic species.

The distribution of bryozoans in the Arctic region (Fig. 14-4) indicates that species number is highest between 50 m and 100 m depths. Valuable information concerning the vertical distribution of water masses is provided by analyses of various biogeographic groups (Fig. 14-5). Boreal-Arctic species are predominant to a depth of 500 m with a maximum at 50–100 m depths. The number of boreal species gradually declines with increasing depth, increasing slightly at 50–100 m depths. Species endemic to the Arctic region occur between 0 m and 250 m depths, reaching maximum diversity between 50 m and 100 m depths. The number of Arctic species

exceeds that of boreal taxa between 40 m and 450 m depths.

Bryozoa colonies live on a variety of substrates (Fig. 14-6). It should be emphasized that although the number of Bryozoa in different facies depends on various factors, including temperature and currents, generally the most important factor is believed to be the substrate (Hayward and Ryland, 1979). In our opinion, the low number of species on rocky substrates and their relatively high number on sandy and argillaceous facies is principally due to the total area occupied by these types of facies in the Arctic seas.

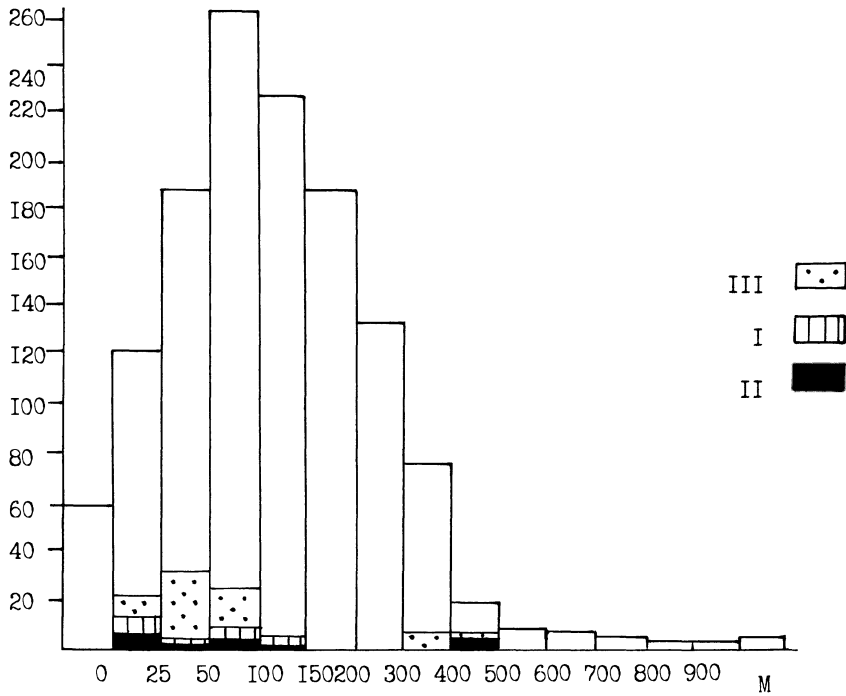


Figure 14-4. Depth distribution of species. Patterns indicate species confined to certain depth ranges. I, Barents Sea; II, western part of the Barents Sea; III, other Arctic seas. Ordinate: number of species; abscissa: water depth in meters.

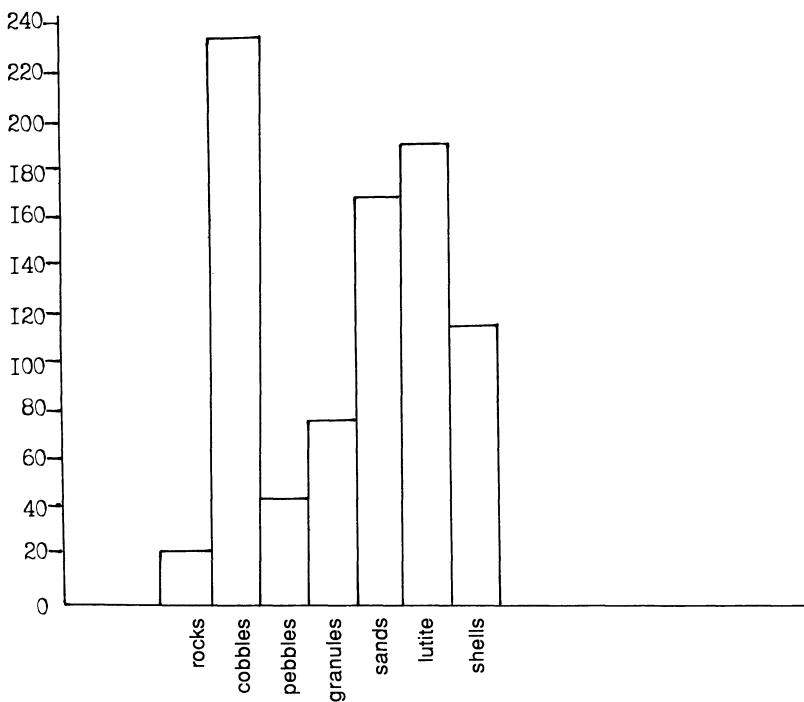


Figure 14-5. Distribution of bryozoans on various substrates. Ordinate: number of species.

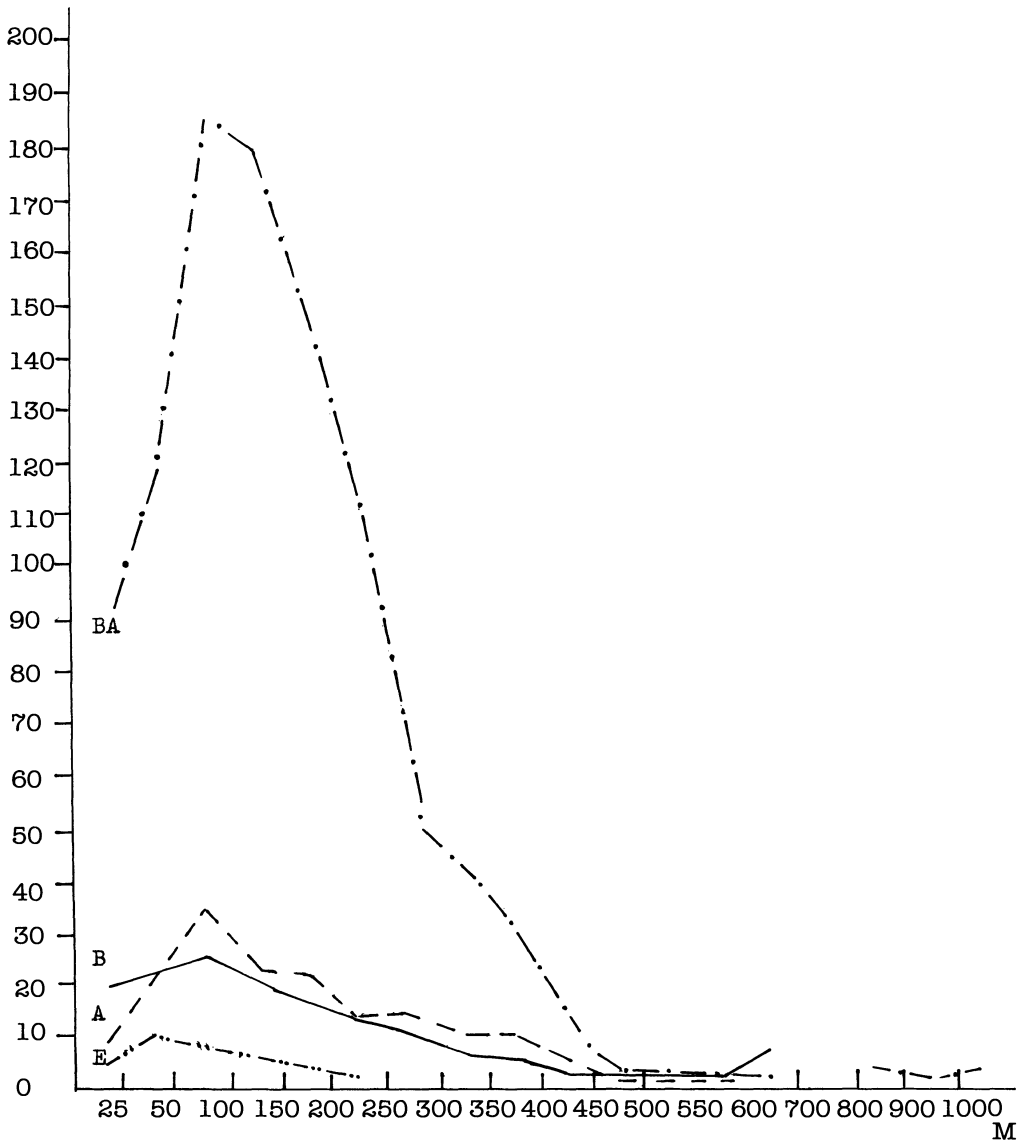


Figure 14-6. Depth distribution of species belonging to different biogeographic groups. Ordinate: number of species. Legend as in Figure 14-2.

Table 14-1. Distribution of Bryozoa in the Arctic Ocean

Species	Biogeography	Species Presence																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Parasmittina trispinosa</i> (Johnston)	sub.-b.						+		+										+						+
<i>Schizomavella auriculata</i> (Hassall)	sub.-b.			+			+		+			+						+							
<i>Proboscina major</i> (Johnston)	atl.sub.-b.				+															+					
<i>Tubulipora dilatans</i> (Johnston)	atl.sub.-b.							+						+						+					+
<i>Tubulipora iliacea</i> (Pallas)	atl.sub.-b.						+			+										+					+
<i>Crisidia cornuta</i> (Linnaeus)	atl.sub.-b.							+		+			+							+					+
<i>Diplosolen obelia</i> (Johnston)	atl.sub.-b.			+				+		+										+					+
<i>Stegohornera violacea</i> (M. Sars)	atl.sub.-b.								+								+								+
<i>Boverbankia pustulosa</i> (Ellis et Solander)	atl.sub.-b.																+								+
<i>Boverbankia imbricata</i> (Adams)	atl.sub.-b.																	+							+
<i>Callopora aurita</i> (Hincks)	atl.sub.-b.																			+					+
<i>Tessarodoma boreale</i> (Busk)	atl.sub.-b.																			+					+
<i>Tubulipora penicillata</i> (Fabricius)	atl.b.																								+
<i>Boverbankia gracilis</i> Leidy	atl.b.																								+
<i>Valkeria uva</i> (Linnaeus)	atl.b.																								+
<i>Amphiblestrum flemingii</i> (Busk)	atl.b.																								+
<i>Amphiblestrum solidum</i> (Packard)	atl.b.																								+
<i>Charitella barleei</i> (Busk)	atl.b.																								+

Note: sub.-b., subtropical boreal; atl.b., Atlantic boreal widespread; atl.sub.-b., Atlantic subtropical boreal; atl.h.-b., Atlantic high boreal; amph.b., amphiboreal; b.-a., boreal-Arctic widespread; b.-a.atl.circ.-p., boreal-Arctic Atlantic circumpolar; b.-a.atl.eurasian, boreal-Arctic Atlantic Eurasian; b.-a.atl.am.-eur., boreal-Arctic Atlantic American-European; b.-a.pac.circ.-p., boreal-arctic Pacific circumpolar; b.-a.pac.amer.-as, boreal-Arctic Pacific American; b.-a.pac.eur.-as., boreal-Arctic Pacific Eurasian; arc.circ.-p., Arctic circumpolar; arc.eur.-as., Arctic Eurasian; arc.amer.-as., Arctic American; arc.eur.-am., Arctic Euroamerican; arc.amer., Arctic American; pac.b., Pacific boreal.

+ = species in: 1, northwestern coast of Alaska; 2, northern coast of North America; 3, the Archipelago of Canadian Islands; 4, Baffin Bay; 5, Davis Strait; 6, Hudson Bay; 7, Gulf of Labrador; 8, Newfoundland; 9, St. Lawrence Gulf; 10, western Greenland; 11, eastern Greenland; 12, Greenland Sea; 13, Iceland; 14, Jan Mayen; 15, Norwegian Sea; 16, North Sea; 17, northern Norway; 18, White Sea; 19, Barents Sea; 20, Kara Sea; 21, Laptev Sea; 22, East Siberian Sea; 23, Chukchi Sea; 24, Bering Strait.

This table is based on the authors' present data and the literature listed.



<i>Reussina impressa</i> (Reuss)	atl.h.-b.									+
<i>Dendrobeatia murmanica</i> Kluge	atl.h.-b.									+
<i>Bicellarina alderi</i> (Busk)	atl.h.-b.									+
<i>Notopites jeffreysii</i> Norman	atl.h.-b.			+						+
<i>Scrupocellaria intermedia</i> Norman	atl.h.-b.									+
<i>Gephyrotes nitidopunctata</i> (Smitt)	atl.h.-b.			+						+
<i>Escharella octodentata</i> Hincks	atl.h.-b.									+
<i>Escharella latodonta</i> Kluge	atl.h.-b.									+
<i>Schizoporella hexagona</i> Nordgaard	atl.h.-b.									+
<i>Schizoporella smithi</i> Kluge	atl.h.-b.									+
<i>Schizoporella thompsoni</i> Kluge	atl.h.-b.			+						+
<i>Turbicellepora smithi</i> Kluge	atl.h.-b.			+						+
<i>Berenicea meandrina</i> (S. Wood)	amph.-b.			+						+
<i>Filicristia geniculata</i> (Milne- Edwards)	amph.b.									+
<i>Lichenopora radiata</i> (Audouin)	amph.b.									+
<i>Flustrellidra hispida</i> (Fabricius)	amph.b.									+
<i>Bowerbankia composita</i> (Kluge)	amph.b.									+
<i>Triticella pedicellata</i> (Alder)	amph.b.									+
<i>Membranipora membranacea</i> (Linnaeus)	amph.b.									+
<i>Tegella unicornis</i> (Fleming)	amph.b.			+						+
<i>Cauloramphus spiniferum</i> (Johnston)	amph.b.									+
<i>Flustra foliacea</i> (Linnaeus)	amph.b.									+
<i>Corynoperella tenuis</i> Hincks	amph.b.									+
<i>Tricellaria peachii</i> var. <i>beringia</i> Kluge	amph.b.			+						+

Note: sub.-b., subtropical boreal; atl.b., Atlantic boreal widespread; atl.sub.-b., Atlantic subtropical boreal; atl.h.-b., Atlantic high boreal; amph.b., amphiboreal; b.-a., boreal-Arctic widespread; b.-a.atl.circ.-p., boreal-Arctic Atlantic circumpolar; b.-a.atl.eurasian, boreal-Arctic Atlantic Eurasian; b.-a.atl.am.-eur., boreal-Arctic Atlantic American-European; b.-a.pac.circ.-p., boreal-arctic Pacific circumpolar; b.-a.pac.amer.-as, boreal-Arctic Pacific American; b.-a.pac.eur.-as., boreal-Arctic Pacific Eurasian; arc.circ.-p., Arctic circumpolar; arc.eur.-as., Arctic Eurasian; arc.amer.-as., Arctic American; arc.eur.-am., Arctic Euroamerican; arc.amer., Arctic American; pac.b., Pacific boreal.

+ = species in: 1, northwestern coast of Alaska; 2, northern coast of North America; 3, the Archipelago of Canadian Islands; 4, Baffin Bay; 5, Davis Strait; 6, Hudson Bay; 7, Gulf of Labrador; 8, Newfoundland; 9, St. Lawrence Gulf; 10, western Greenland; 11, eastern Greenland; 12, Greenland Sea; 13, Iceland; 14, Jan Mayen; 15, Norwegian Sea; 16, North Sea; 17, northern Norway; 18, White Sea; 19, Barents Sea; 20, Kara Sea; 21, Laptev Sea; 22, East Siberian Sea; 23, Chukchi Sea; 24, Bering Strait.

This table is based on the authors' present data and the literature listed.



Table 14-1. (continued)

Species	Biogeography	Species Presence																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Smittioidea reticulata</i> (Mac Gillivray)	amph.b.																			+						
<i>Stomachetosella magniporata</i> (Nordgaard)	amph.b.	+																		+						
<i>Microporella ciliata</i> (Pallas)	amph.b.	+	+			+				+	+									+						+
<i>Retepora beaniana</i> King	amph.b.									+	+									+						
<i>Tubulipora lobulifera</i> Hastings	amph.b.								+																	
<i>Tubulipora flabellaris</i> (Fabricius)	b.-a.	+	+	+																+	+	+	+	+	+	+
<i>Diptosolen obelia</i> var. <i>arctica</i> (Waters)	b.-a.									+	+			+						+	+	+	+	+	+	+
<i>Crisia eburnea</i> (Linnaeus)	b.-a.									+	+									+						+
<i>Crisia Klugei</i> (Ryland)	b.-a.									+	+									+						+
<i>Lichenopora verrucaria</i> (Fabricius)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Lichenopora hispida</i> (Fleming)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Alcyonidium gelatinosum</i> (Linnaeus)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Alcyonidium mytili</i> Dalyell	b.-a.										+									+	+	+	+	+	+	+
<i>Buskia nitens</i> Alder	b.-a.																			+	+	+	+	+	+	+
<i>Eucratea loricata</i> (Linnaeus)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Electra arctica</i> (Borg)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Tegella armifera</i> (Hincks)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Tegella spitzbergensis</i> (Bidenkap)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Tegella arctica</i> (d'Orbigny)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Tegella nigrans</i> (Hincks)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Callopora lineata</i> (Linnaeus)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Callopora craticula</i> (Alder)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Cauloramphus cymbaeformis</i> (Hincks)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Doryporella spatulifera</i> (Smitt)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Caribaea caribaea</i> (Ellis et Solander)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Terminoflustra membranaceotruncata</i> (Smitt)	b.-a.									+	+									+	+	+	+	+	+	+
<i>Dendrobeatia murrayana</i> (Bean in Johnston)	b.-a.									+	+									+	+	+	+	+	+	+

<i>Dendrobeatia pseudomurrayana</i> Kluge	b.-a.				+							+		+						+				
<i>Dendrobeatia pseudomurrayana</i> var. <i>fessa</i> Kluge	b.-a.			+																		+		
<i>Dendrobeatia fruticosa</i> (Packard)	b.-a.																						+	
<i>Dendrobeatia fruticosa</i> var. <i>quadridentata</i> (Lowen)	b.-a.																							+
<i>Tricellaria psachii</i> (Busk)	b.-a.					+																		+
<i>Tricellaria ternata</i> (Ellis et Solander)	b.-a.					+																		+
<i>Tricellaria gracilis</i> (Van Beneden)	b.-a.					+																		+
<i>Scrupocellaria scabra</i> (Van Beneden)	b.-a.					+																		+
<i>Scrupocellaria scabra</i> var. <i>paenulata</i> (Van Beneden)	b.-a.					+																		+
<i>Scrupocellaria elongata</i> (Smitt)	b.-a.					+																		+
<i>Caberea ellisii</i> (Fleming)	b.-a.					+																		+
<i>Cribrilinea annulata</i> (Fabricius)	b.-a.					+																		+
<i>Escharella immersa</i> (Fleming)	b.-a.					+																		+
<i>Escharella ventricosa</i> (Hassall)	b.-a.					+																		+
<i>Smittina majuscula</i> (Smitt)	b.-a.					+																		+
<i>Smittina bella</i> (Busk)	b.-a.					+																		+
<i>Smittina minuscula</i> (Smitt)	b.-a.					+																		+
<i>Smittina rigida</i> Lorenz	b.-a.					+																		+
<i>Porella concinna</i> (Busk)	b.-a.					+																		+
<i>Porella concinna</i> var. <i>belli</i> (Dawson)	b.-a.					+																		+
<i>Parasmittina jeffreysii</i> (Norman)						+																		+
<i>Porella compressa</i> (Sowerby)	b.-a.					+																		+
<i>Porella acutirostris</i> Smitt	b.-a.					+																		+
<i>Porella smitti</i> Kluge						+																		+

Note: sub.-b., subtropical boreal; atl.b., Atlantic boreal widespread; atl.sub.-b., Atlantic subtropical boreal; atl.h.-b., Atlantic high boreal; amph.b., amphiboreal; b.-a., boreal-Arctic widespread; b.-a.atl.circ.-p., boreal-Arctic Atlantic circumpolar; b.-a.atl.eurasian, boreal-Arctic Atlantic Eurasian; b.-a.atl.am.-eur., boreal-Arctic Atlantic American-European; b.-a.pac.circ.-p., boreal-arctic Pacific circumpolar; b.-a.pac.amer.-as, boreal-Arctic Pacific Amerasian; b.-a.pac.eur.-as., boreal-Arctic Pacific Eurasian; arc.circ.-p., Arctic circumpolar; arc.eur.-as., Arctic Eurasian; arc.amer.-as., Arctic Amerasian; arc.eur.-am., Arctic Euroamerican; arc.amer., Arctic American; pac.b., Pacific boreal.

+ = species in: 1, northwestern coast of Alaska; 2, northern coast of North America; 3, the Archipelago of Canadian Islands; 4, Baffin Bay; 5, Davis Strait; 6, Hudson Bay; 7, Gulf of Labrador; 8, Newfoundland; 9, St. Lawrence Gulf; 10, western Greenland; 11, eastern Greenland; 12, Greenland Sea; 13, Iceland; 14, Jan Mayen; 15, Norwegian Sea; 16, North Sea; 17, northern Norway; 18, White Sea; 19, Barents Sea; 20, Kara Sea; 21, Laptev Sea; 22, East Siberian Sea; 23, Chukchi Sea; 24, Bering Strait.

This table is based on the authors' present data and the literature listed.

Table 14-1. (continued)

Species	Biogeography	Species Presence																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Cystisella saccata</i> (Busk)	b.-a.	+	+	+	+		+	+	+	+	+	+														+
<i>Umbonula patens</i> (Smitt)	b.-a.									+	+															+
<i>Buffonellaria biapertura</i> Michelin	b.-a.	+	+	+	+					+	+	+														+
<i>Myrzoella crustacea</i> (Smitt)	b.-a.	+	+	+	+	+	+			+	+	+	+													+
<i>Schizomacella auriculata</i> var. <i>lineata</i> (Nordgaard)	b.-a.									+	+	+	+													+
<i>Schizomacella porifera</i> (Smitt)	b.-a.	+	+	+	+	+	+			+	+	+	+													+
<i>Stomachetosella incerta</i> (Kluge)	b.-a.									+	+	+	+													+
<i>Stomachetosella sinuosa</i> (Busk)	b.-a.	+			+					+	+	+	+													+
<i>Stomachetosella cruenta</i> (Busk)	b.-a.	+	+		+					+	+	+	+													+
<i>Hippoporina propinqua</i> (Smitt)	b.-a.							+		+	+	+	+													+
<i>Myriapora coarctata</i> (M. Sars)	b.-a.					+		+	+	+	+	+	+													+
<i>Hippothoa divaricata</i> var. <i>arctica</i> Kluge	b.-a.				+			+	+	+	+	+	+													+
<i>Hippothoa hyatina</i> (Linnaeus)	b.-a.	+	+	+	+	+	+	+	+	+	+	+	+													+
<i>Hippomonella hippopus</i> (Smitt)	b.-a.	+	+	+	+	+	+	+	+	+	+	+	+													+
<i>Rhamphostomella scabra</i> (Fabricius)	b.-a.					+		+	+	+	+	+	+													+
<i>Rhamphostomella costata</i> Lorenz	b.-a.					+		+	+	+	+	+	+													+
<i>Rhamphostomella ovata</i> (Smitt)	b.-a.	+	+	+	+	+	+	+	+	+	+	+	+													+
<i>Rhamphostomella radiatula</i> (Hincks)	b.-a.	+	+							+	+	+	+													+
<i>Ragonula rosacea</i> (Busk)	b.-a.									+																+
<i>Stomatopora granulata</i> (Milne-Edwards)	b.-a. atl. circ.-p.																									+
<i>Proboscina incrassata</i> (Smitt)	b.-a. atl. circ.-p.							+		+																+
<i>Oncoscoecia diastoporoidea</i> (Norman)	b.-a. atl. circ.-p.									+																+
<i>Tubulipora ventricosa</i> Busk	b.-a. atl. circ.-p.									+	+	+	+													+
<i>Idmonaea atlantica</i> Forbes MSS	b.-a. atl. circ.-p.	+	+	+	+	+	+	+	+	+	+	+	+													+
<i>Entalophora clavata</i> (Busk)	b.-a. atl. circ.-p.	+	+							+	+	+	+													+
<i>Entalophora harmeri</i> (Osburn)	b.-a. atl. circ.-p.	+	+							+	+	+	+													+
<i>Defrancia lucernaria</i> M. Sars	b.-a. atl. circ.-p.									+	+	+	+													+
<i>Fasciculiporoidea americana</i> (d'Orbigny)	b.-a. atl. circ.-p.								+	+	+	+	+													+

<i>Stegohomera lichenoides</i> (Linnaeus)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Alcyonium mammillatum</i> Alder	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Notella dilatata</i> (Hincks)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Electra pilosa</i> (Linnaeus)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Amphiblestrum septentrionalis</i> (Kluge)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Amphiblestrum trifolium</i> var. <i>quadrata</i> (Hincks)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Securiflustra securifrons</i> (Pallas)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sarsiflustra abyssicola</i> (G.O. Sars)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Bugula elongata</i> (Nordgaard)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Kinetoskias arborensis</i> Danielsen	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Kinetoskias smitti</i> Danielsen	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lepralioides nordlandica</i> (Nordgaard)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pachyegis groenlandica</i> Norman	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Retepora cellulosa</i> (Linnaeus)	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Idmonea atlantica</i> var. <i>gracillima</i> Busk	b.-a.atl.circ-p.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Alcyonium hirsutum</i> (Fleming)	b.-a.atl.eur-as.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Alcyonium gelatinosum</i> var. <i>diaphanum</i> (Farre)	b.-a.atl.eur-as.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Alcyonium albidum</i> Alder	b.-a.atl.eur-as.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Arachnidium clavatum</i> Hincks	b.-a.atl.eur-as.	+	+	+	+	+	+	+	+	+	+	+	+
<i>Arachnidium hippothoides</i> Hincks	b.-a.atl.eur-as.	+	+	+	+	+	+	+	+	+	+	+	+

Note: sub-b., subtropical boreal; atl.b., Atlantic boreal widespread; atl.sub.-b., Atlantic subtropical boreal; atl.h.-b., Atlantic high boreal; amph.b., amphiboreal; b.-a., boreal-Arctic widespread; b.-a.atl.circ-p., boreal-Arctic Atlantic circumpolar; b.-a.atl.eurasian, boreal-Arctic Atlantic Eurasian; b.-a.atl.am.-eur., boreal-Arctic Atlantic American-European; b.-a.pac.circ-p., boreal-arctic Pacific circumpolar; b.-a-pac.amer.-as, boreal-Arctic Pacific Amerasian; b.-a.pac.eur.-as., boreal-Arctic Pacific Eurasian; arc.circ-p., Arctic circumpolar; arc.eur.-as., Arctic Eurasian; arc.amer.-as., Arctic Amerasian; arc.eur.-am., Arctic Euroamerican; arc.amer., Arctic American; pac.b., Pacific boreal.

+ = species in: 1, northwestern coast of Alaska; 2, northern coast of North America; 3, the Archipelago of Canadian Islands; 4, Baffin Bay; 5, Davis Strait; 6, Hudson Bay; 7, Gulf of Labrador; 8, Newfoundland; 9, St. Lawrence Gulf; 10, western Greenland; 11, eastern Greenland; 12, Greenland Sea; 13, Iceland; 14, Jan Mayen; 15, Norwegian Sea; 16, North Sea; 17, northern Norway; 18, White Sea; 19, Barents Sea; 20, Kara Sea; 21, Laptev Sea; 22, East Siberian Sea; 23, Chukchi Sea; 24, Bering Strait.

This table is based on the authors' present data and the literature listed.

Table 14-1. (continued)

Species	Biogeography	Species Presence																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Electra pilosa</i> var. <i>dentata</i> Ellis et Solander	b.-a.atl.eur.-as.																		+	+	+				
<i>Electra pilosa</i> var. <i>baltica</i> Borg	b.-a.atl.eur.-as.															+									
<i>Bugula purpurotincta</i> Norman	b.-a.atl.eur.-as.											+													
<i>Smittina peristomata</i> (Nordgaard)	b.-a.atl.eur.-as.											+													
<i>Smittina pseudoacutirostris</i> Gostilovskaja	b.-a.atl.eur.-as.																		+						
<i>Haplopora impressum</i> (Audouin)	b.-a.atl.eur.-as.																			+					
<i>Bicellariella ciliata</i> (Linnaeus)	b.-a.atl.am.-eur.	+							+																
<i>Cribrella watersi</i> Andersson	b.-a.atl.am.-eur.											+													
<i>Escharella microstoma</i> (Norman)	b.-a.atl.am.-eur.			+								+													
<i>Phylactella labiata</i> (Boeck in MS, Smitt)	b.-a.atl.am.-eur.																								
<i>Porellodes struma</i> (Norman)	b.-a.atl.am.-eur.																								
<i>Porellodes laevis</i> (Fleming)	b.-a.atl.am.-eur.	+																							
<i>Porella minuta</i> (Norman)	b.-a.atl.am.-eur.	+																							
<i>Palmicellaria skenei</i> (Ellis et Solander)	b.-a.atl.am.-eur.	+																							
<i>Palmicellaria skenei</i> var. <i>bicorris</i> (Busk)	b.-a.atl.am.-as.																								
<i>Escharina alderi</i> (Busk)	b.-a.atl.am.-eur.																								
<i>Schizoporella pachystega</i> Kluge	b.-a.atl.am.-eur.																								
<i>Microporina articulata</i> (Fabricius)	b.-a.pac.circ.-p.	+																							
<i>Smittina mucronata</i> (Smitt)	b.-a.pac.circ.-p.																								
<i>Umbonula arctica</i> (M. Sars)	b.-a.pac.circ.-p.	+																							
<i>Porella fragilis</i> Levensen	b.-a.pac.circ.-p.																								
<i>Stomachetosella limbata</i> (Lorenz)	b.-a.pac.circ.-p.																								
<i>Schizobrachiella stylifera</i> (Levensen)	b.-a.pac.circ.-p.	+																							
<i>Hippoporina reticulatopunctata</i> (Hincks)	b.-a.pac.circ.-p.	+																							



Table 14-1. (continued)

Species	Species Presence																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Semibugula birulai</i> Kluge																									
<i>Scrupocellaria scabra</i> var. <i>paenulata</i> forma <i>orientalis</i> Kluge																									
<i>Schizoporella costata</i> Kluge																									
<i>Hippoporina ussoui</i> (Kluge)																									
<i>Stomachetosella hincski</i> Powell																									
<i>Rhaphostomella bilaminata</i> var. <i>sibirica</i> Kluge																									
<i>Celleporina nordenskjoldi</i> (Kluge)																									
<i>Cheloporina inermis</i> (Busk)																									
<i>Oncosocia canadensis</i> (Osburn)																									
<i>Oncosocia polygonalis</i> (Kluge)																									
<i>Diplosolen intricarius</i> (Smitt)																									
<i>Crisia eburneodenticulata</i> Smitt																									
<i>Crisia denticulata</i> var. <i>borgi</i> Kluge																									
<i>Lichenopora crassiuscula</i> (Smitt)																									
<i>Crisia denticulata</i> var. <i>arctica</i> M. Sars																									
<i>Alcyonidium mammillatum</i> var. <i>erectum</i> Andersson																									
<i>Alcyonidium disciforme</i> Smitt																									
<i>Flustrellidra corniculata</i> (Smitt)																									
<i>Bowerbankia arctica</i> Busk																									
<i>Eucratea loricata</i> var. <i>cornuta</i> (Osburn)																									
<i>Eucratea loricata</i> var. <i>arctica</i> (Kluge)																									
<i>Callopora smitti</i> Kluge																									
<i>Callopora whiteavesi</i> Norman																									
<i>Callopora lata</i> (Kluge)																									
<i>Flustra serrulata</i> Busk																									





Table 14-1. (continued)

Species	Species Presence																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Tubulipora eminentis</i> Kluge																									+
<i>Tubulipora borgi</i> Kluge																		+							+
<i>Tubulipora soluta</i> Kluge																			+						+
<i>Tubulipora nordgaardii</i> Kluge																		+							+
<i>Tubulipora fruticosa</i> Kluge																		+							+
<i>Idmonaea tumida</i> (Smitt)																		+							+
<i>Idmonaea bidenkapi</i> Kluge																		+							+
<i>Idmonocoides arctoflabellaris</i> (Kluge)																		+							+
<i>Idmonocoides simplex</i> Kluge																		+							+
<i>Berenicea arctica</i> Kluge																		+							+
<i>Berenicea oblonga</i> Kluge																		+							+
<i>Cristella diversa</i> (Kluge)																		+							+
<i>Cristella complecta</i> (Kluge)																		+							+
<i>Crisis aculeata</i> var. <i>bathyalis</i> Kluge																		+							+
<i>Crisia constans</i> Kluge																		+							+
<i>Stegohornera arctica</i> (Kluge)																		+							+
<i>Lichenopora multicestra</i> Kluge																		+							+
<i>Lichenopora sibirica</i> Kluge																		+							+
<i>Fungella dali</i> Kluge																		+							+
<i>Alcyonidium gelatinosum</i> var. <i>anderssonii</i> Abrikosov																		+							+
<i>Alcyonidium gelatinosum</i> var. <i>pachydermatum</i> Kluge																		+							+
<i>Alcyonidium radiceatum</i> Kluge																		+							+
<i>Tegella armiferoides</i> Kluge																		+							+
<i>Callopora craticula</i> var. <i>sedovi</i> Kluge																		+							+
<i>Rhamphonotus gorbunovi</i> Kluge																		+							+
<i>Dendrobeania fruticosa</i> var. <i>frigida</i> (Waters)																		+							+
<i>Bugula tricusps</i> Kluge																		+							+
<i>Utschakovia gorbunovi</i> Kluge																		+							+
<i>Notoplites sibirica</i> (Kluge)																		+							+







## APPENDIX

### Plate 14-I

1. *Proboscina* sp., × 21, Barents Sea, incrusting kelp.
2. *Tubulipora* sp., × 35, Barents Sea, incrusting kelp.
3. *Tubulipora* sp., × 21, Barents Sea, incrusting kelp.
4. *Tubulipora soluta* Kluge, × 21, Barents Sea, incrusting kelp.
5. *Idmoneoides* sp., × 5, Barents Sea, on polychaetes tubes.
- 5a. *Idmoneoides* sp., fragment of zoarium with oecistome.
6. *Entalophora clavata* (Busk), × 3.5, Barents Sea, on rock.
7. *Tubulipora* sp., × 14, Barents Sea, incrusting kelp.
8. *Tubulipora eminens* Kluge, × 3.5, East Siberian Sea, on rock and argillaceous sand.

### Plate 14-II

1. *Berenicea* sp., × 10.5, Chukchi Sea, on rocks.
2. *Fasciculiporoides* sp., × 10.5, East Siberian Sea, on a hydrozoa.
3. *Berenicea* sp., × 7, Barents Sea, on polychaetes tubes.
4. *Lichenopora multicestra* Kluge, solitary zoarium, × 3.5, substratum: argillaceous sand with rocks, Laptev Sea.
5. *Lichenopora multicestra* Kluge, compound zoarium, × 6, Laptev Sea, on the legs of sea spiders.
6. *Lichenopora sibirica* Kluge, × 6, Laptev Sea, on hydrozoa, on argillaceous substratum.

### Plate 14-III

1. *Eucratea loricata* var. *arctica* (Kluge), × 17.5, Kara Sea, on rocks; argillaceous rocky substratum.
2. *Notoplires smitti* (Norman), × 14, Barents Sea, on shells; on argillaceous rocky substratum.
3. *Semibugula birulai* Kluge, × 28, Barents Sea, on rocks; on argillaceous rocky substratum.
4. *Dendrobeatia fruticosa* (Packard), × 17.5, Barents Sea, on rocks; substratum: rocks, shells, clays.
  - a. marginal avicularium side view, × 42.
  - b, c. middle avicularium view from above, × 52.5.
5. *Dendrobeatia levinseni* (Kluge), × 17.5, Kara Sea, on rocks.
  - a. marginal avicularium side view, × 28.
  - b. middle avicularium side view, × 28.
  - c. middle avicularium frontal view, × 28.
6. *Flustra serrulata* Busk, Chukchi Sea, × 17.5, on hydrozoa; on argillaceous rocky substratum.

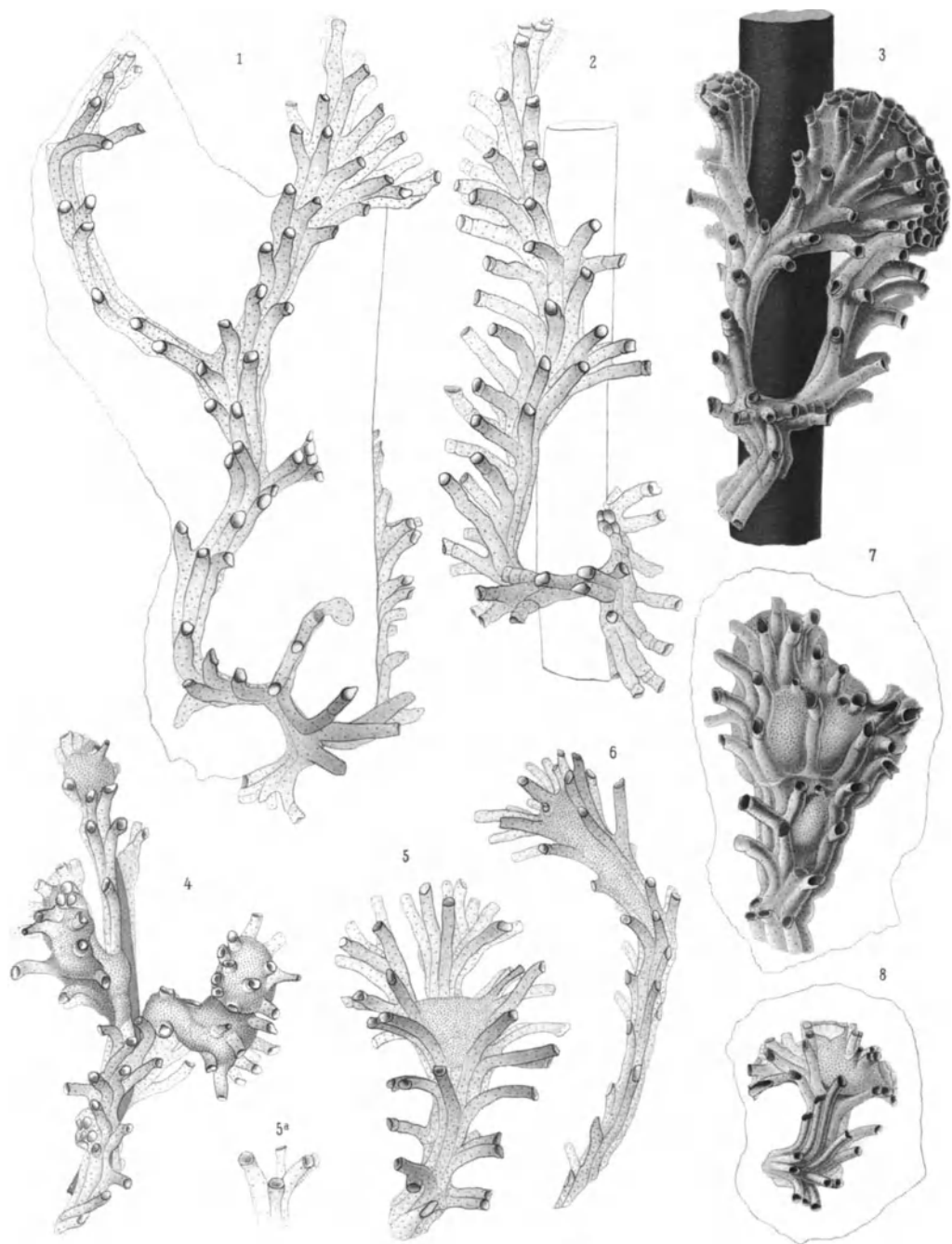


PLATE 14-I

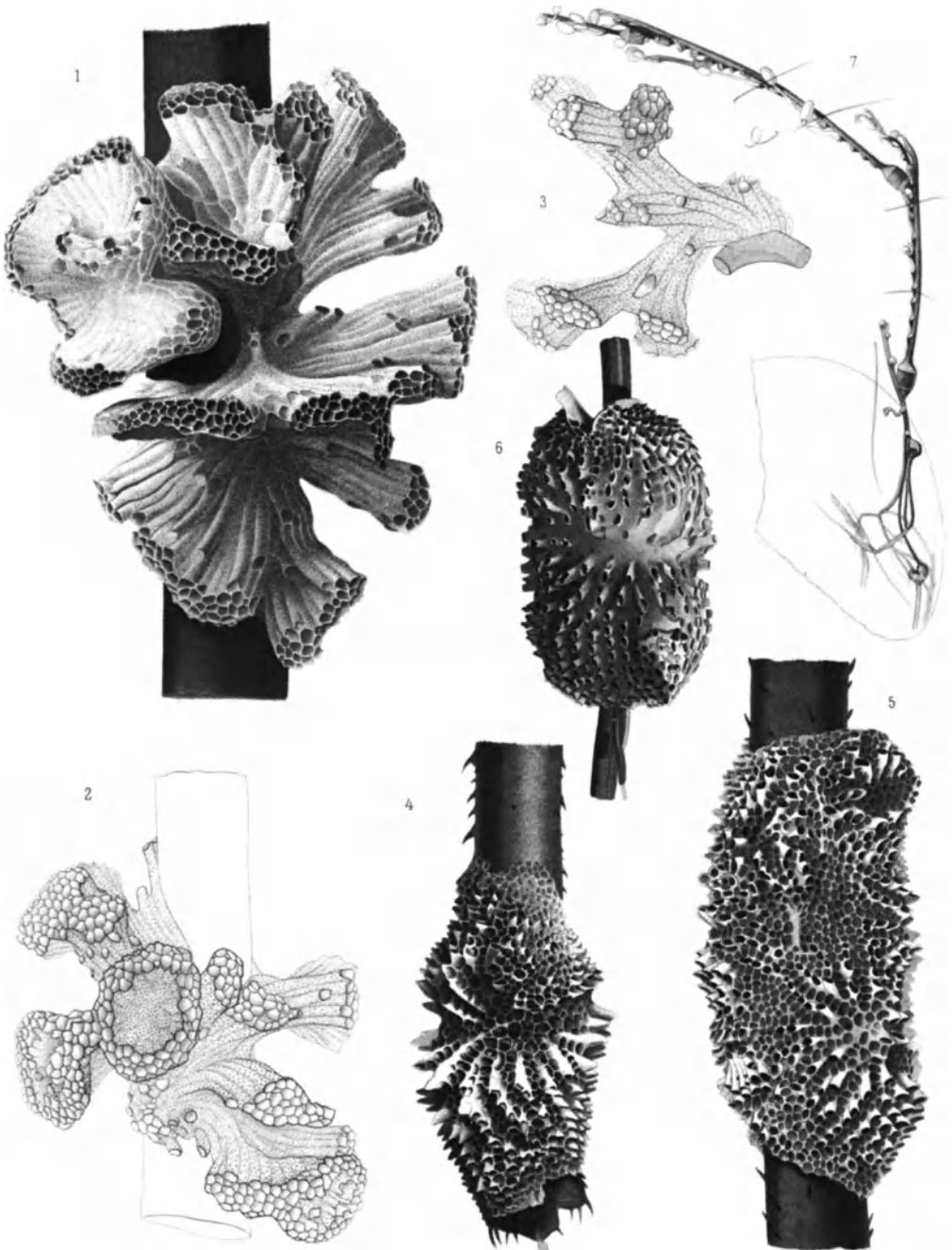


PLATE 14-II

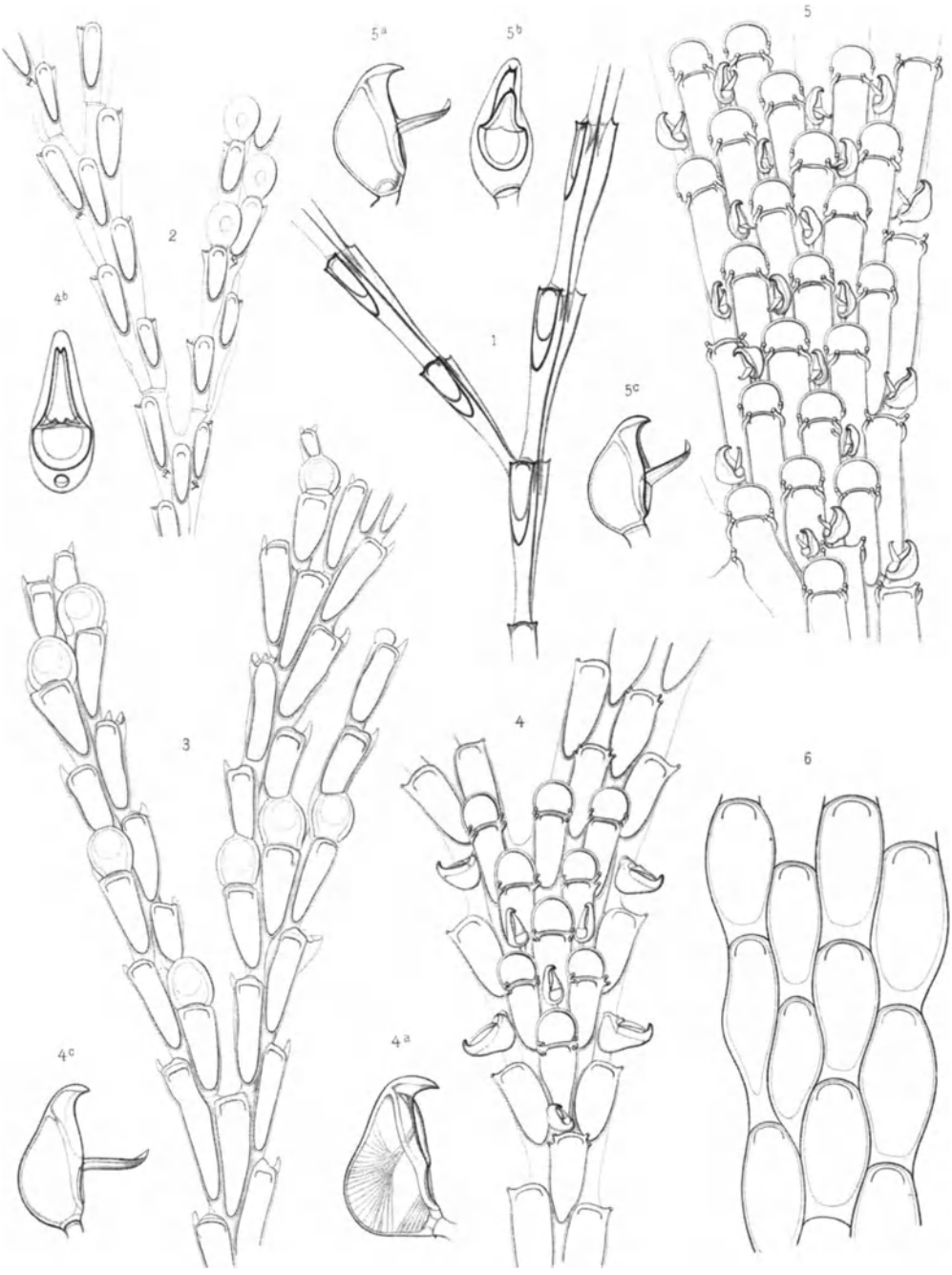


PLATE 14-III



### Plate 14-IV

1. *Callopora smitti* (Kluge), × 21, Kara Sea, on shells; on argillaceous-rocky-sandy substratum.
2. *Stomachetosella incerta* (Kluge), × 21, Barents Sea, on rocks.
3. *Schizoporella pachystega* (Kluge), × 21, Barents Sea, on shells, on argillaceous-rocky-sandy substratum.
4. *Pseudoflustra solida* (Stimpson), × 21, Laptev Sea, on rocks.
5. *Pseudoflustra birulai* (Kluge), × 21, Barents Sea, on rocks, on argillaceous rocky substratum.
6. *Rhamphostomella bilaminata* var. *sibirica* (Kluge), × 21, on shells, Chukchi Sea, on rocky argillaceous substratum.
7. *Rhamphostomella ovata* (Smitt), × 21, Barents Sea, on algae, on rocky argillaceous substratum.
8. *Cellepora canaliculata* Busk, × 28, on shells, Kara Sea.
9. *Celleporina nordenskjoldi* (Kluge), × 17.5, East Siberian Sea, on algae.

All illustrations were drawn by Kluge in 1916 but were never published.

### Map 14-1

Map of the seas of the Northern Hemisphere divided into biogeographic regions, subregions, and provinces.

- I. Arctic subregion, Arc-Atlantic region.
- II-IV. Atlantic boreal subregion, Arc-Atlantic region.
- II. Celtic high boreal province.
- III. Delaware low boreal province.
- IV. Scandinavian low boreal province.
- V. Aleutian high boreal subregion, Pacific boreal region.
- VI. Ainian low boreal subregion, Pacific boreal region.
- VII. Oregonian low boreal subregion, Pacific boreal region.

### Map 14-2

Distribution of the three Arctic species:

- *Dendrobeatia fruticosa* (Packard)
- *Semibugula birulai* Kluge
- ▲ *Rhamphostomella ovata* (Smitt)

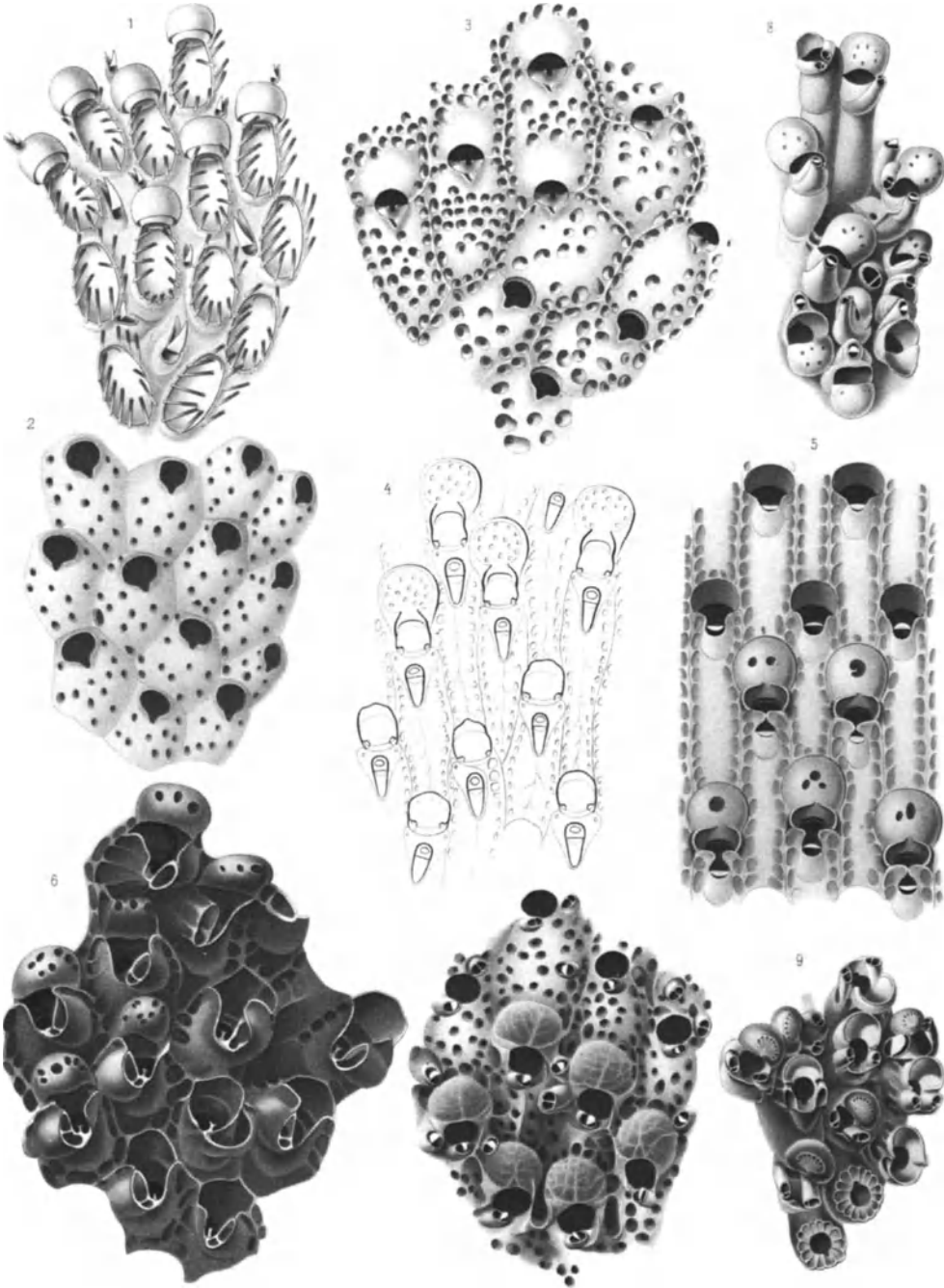
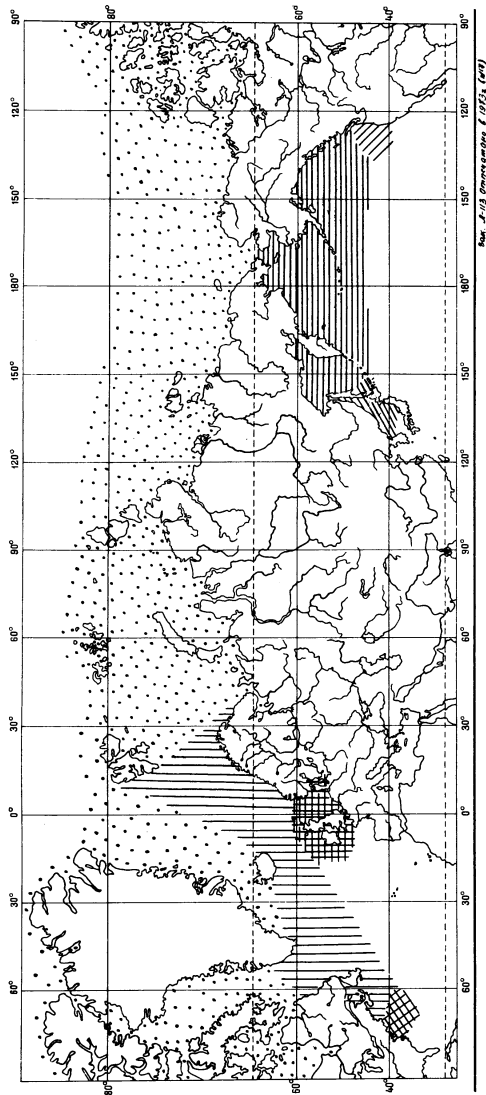
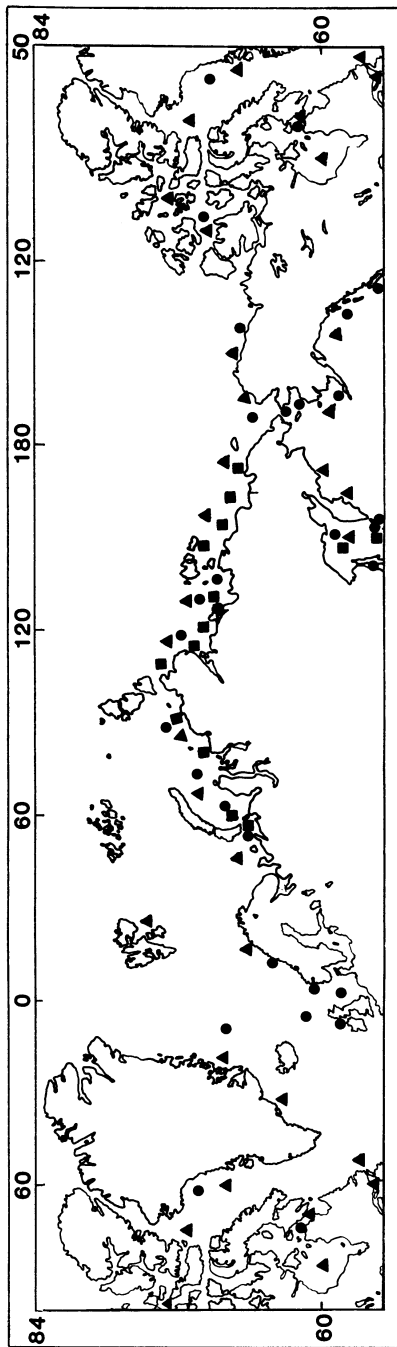


PLATE 14-IV



MAP 14-1



MAP 14-2

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