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History of investigations and current state of knowledge of bryozoan species diversity in the Bering Sea

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1. Introduction

The Bryozoa are one of the most abundant and widely distributed groups of macrobenthos in the Bering Sea. Although investigations of the phylum have taken place over a century, knowledge of species diversity in this sea is still very incomplete. The coastal waters of the Bering Sea belong territorially to Russia and the United States of America and, accordingly, study of the bryofauna has been achieved generally by the efforts of the Russian and American bryozoological schools. For a number of reasons, their investigations were conducted independently and, because the investigators identified specimens collected within their “national” sea areas, species occurring in the eastern and southeastern shelves of the sea were generally studied by American scientists and those in western coastal waters by Russians. Therefore the history of bryozoan investigations of the Bering Sea is most usefully presented according to the two lines of research.

2. Investigations of the American bryozoological school

The first reliable data about bryozoans in the Bering Sea were connected with biological investigations of the Alaskan shelf and reported by Alice Robertson.¹ She recorded three species – *Membranipora membranacea* (L.), *Bugula purpurotincta* (later changed to *B.*

pacifica, see below) and *Celleporina incrassata* (Lamarck), collected near the Pribilof Islands by the Harriman Alaska Expedition. Two years later a new ctenostome bryozoan, *Alcyonidium pedunculatum*, was described from the same area.² In further taxonomic work on Eastern Pacific cheilostomes Robertson³ described two new species – *Bugula pacifica* and *Tricellaria pribilofi* (afterwards synonymised with *T. ternata* (Ellis and Solander),⁴ based on new material from coastal waters off the Pribilof Islands. Two other species, *Dendrobeatia murrayana* (Johnston) and *Terminoflustra membranaceotruncata* (Smitt), were newly recorded for the fauna of the Bering archipelago.⁵ After reorganization of the Harriman Alaska Expedition into a division of Smithsonian Institution, the data on the Alaskan bryozoan fauna were formally repeated in the Harriman Alaska Series of the Smithsonian Institution.⁶

More than a decade later, Raymond Osburn⁷ reported finding bryozoan colonies in the stomachs of eider ducks taken from nests in the Pribilof Islands. Fragments of *Crisia* sp. and *Celleporina incrassata* (Lamarck) were taken from the alimentary canals of king and pacific eiders (*Somateria spectabilis* and *S. nigra* respectively), caught near St Paul Island. *Tricellaria pribilofi* and *Myriapora subgracilis* (d'Orbigny) were included in an alimentary bolus of king eider from St George Island. Additionally, several colonies were found in the stomachs of the fishes *Tautoga onitis* and *Tautogolabrus adspersus* taken near the islands.

New data on Beringian bryozoans were published almost thirty years later. Nine anascans were indicated for the American sector of the Bering Sea in the monograph of western North American Bryozoa by Osburn.⁸ Four of them, *Bidenkapia spitzbergensis* (Bidenkap), *Callopora craticula* (Alder), *Tegella arctica* (d'Orbigny), and *T. armifera* (Hincks), were registered near Punuk Island situated in the neighbourhood of St. Lawrence Island. *Callopora lineata* (L.) was found in shallow water off Nunivak Island; *B. pacifica* Robertson and *T. membranaceotruncata* (Smitt) were mentioned with reference to Robertson⁹ for the Pribilof Islands. Disappointingly short inscriptions (“Bering Sea”, without any more details) were on the labels accompanying specimens identified by Osburn as *Dendrobeatia murrayana* (Johnston) and *Microporina articulata* (Fabricius).¹⁰

Seven ascophoran bryozoans were reported from the Bering Sea in the second part of his monograph.¹¹ Five species, *Arctonula arctica* (M. Sars), *Porella concinna* (Busk), *Stomachetosella cruenta* (Busk), *S. sinuosa* (Busk), and *Cylindroporella tubulosa* (Norman), recorded near Punuk Island, and two representatives of the genus *Celleporina* (*C. incrassata* (Lamarck) and *C. ventricosa* (Lorenz)) were recorded in the coastal waters of the Pribilof Islands and Nunivak Island accordingly. The concluding part of Osburn's monograph¹² contains records or indications of five cyclostomes and a single ctenostome bryozoan (*Alcyonidium pedunculatum* Robertson with reference to Robertson),¹³ gathered in the Alaskan shelf of the Bering Sea. The cyclostomes included a new genus and species, *Bathysoecia hastingsae*, from Nunivak Island together with a couple of other cyclostomes,

Diplosolen obelium (Johnston) and *Diaperoecia johnstoni* (Heller), newly recorded for the region.

Taxonomic research on bryozoans of Beringian Alaskan waters was renewed in 1988 when ten species were described among the intertidal bryozoan fauna of the Narrow Strait, Kodiak Islands, Gulf of Alaska.¹⁴ The additional material of *Callopora craticula* (Alder) from Penuk Island and of *Terminoflustra membranaceotruncata* (Smitt) and *Myrionzoella crustacea* (Smitt) from the vicinity of the Pribilof Islands was examined. Material of seven other species was studied from the Beringian marine sector of Unalaska Island (Aleutian Islands). Six of them – *Stomachetosella sienna*, *Microporella germana*, *Celleporella reflexa*, *Hippothoa mawatarii*, *Hippoporidra truculenta*, and *Cryptosula okadai* (later recognized as a junior synonym of *C. zavjalovensis* Kubanin 1976, see Kubanin)^{15,16} – were described as new to science.¹⁷ These species, together with *Dendrobeania exilis*, supplemented the list of the previously known bryozoans of the Bering Sea.

A new species of *Microporella*, *M. speciosa*, has recently been described from the Pacific coast of Alaska, and some additional material of this species has also been examined from the shore of Nanvak Bay, Bering Sea coast of Alaska.¹⁸

Several cyclostome bryozoans, generally identified to genera or to family level and collected in Alaskan waters of the Bering Sea (mainly Unalaska to Cook Inlet) were illustrated in the work of Boardman.¹⁹

Some indications of the importance of bryozoans in the benthic communities of the Alaskan shelf of the Bering Sea are given in a few hydrobiological papers. Thus, in Lower Cook Inlet, Alaska, *Flustrellidra* sp. and *Dendrobeania* spp. were associated with the largest catches of the juvenile red king crab *Paralithodes camtschaticus* (Tilesius).²⁰ Four species common in Cook Inlet were mentioned by Kessler²¹ – *Eucratea loricata* (L.), *Carbasea serrulata* (Busk), *Escharopsis lobata* (Lamouroux), and *Rhamphostomella costata* (Lorenz). A brief account of bryozoan diversity in the Beringian shelf of Alaska has also been given by MacIntosh.²²

3. Investigations of the Russian bryozoological school

Perhaps the first investigator to note the abundance and appreciable role of bryozoans in the benthic communities in the Bering Sea was Evpraksiya F. Gurjanova, who gathered some rich collections from the intertidal zone of Bering Island in the Commander Islands.²³

In the early 1950s, Herman Kluge (Figure 1) described six cheilostome species – *Tegella inermis*, *Callopora obesa*, *C. amissavicularis*, *Hippoconella fastigatoavicularis*, *Porella tumida*, *Smittina beringia* – and single cyclostome bryozoan, *Borgella tumulosa*,

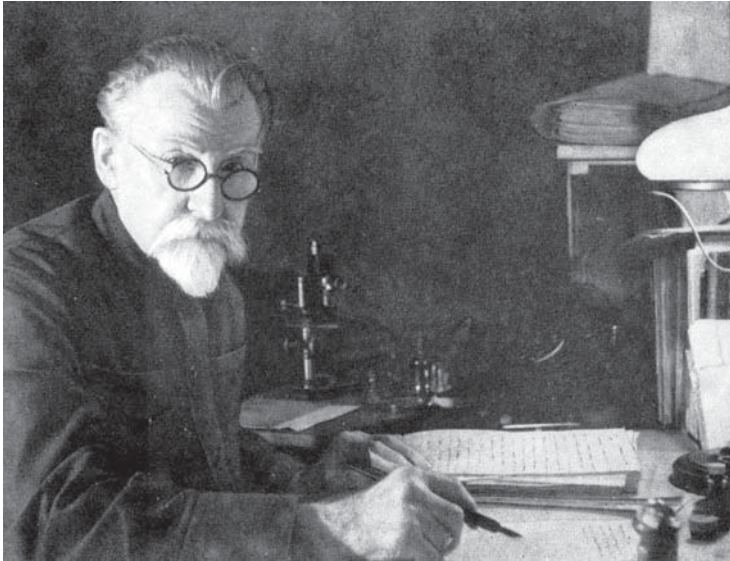


Figure 1. Herman Kluge (photograph of 1949)

from the Bering Strait.²⁴ Shortly after, a representative of the abyssal fauna, *Kinetoskias beringi*, was described from 3812 m in the Commander Valley of the Bering Sea.²⁵ Twenty seven of 35 bryozoans included in the *Atlas of Invertebrates of the Far Eastern Seas of U.S.S.R.* were enumerated for the Bering Sea.²⁶

The most detailed information about 135 Beringian bryozoans (comprising 13 cyclostomes, 14 ctenostomes, and 108 cheilostomes), accompanied by depth and locality data from more than twenty explored areas within the sea, was given in the *List of the species (Bryozoa) of the Far Eastern Seas of S.S.S.R.*, the posthumous work of Kluge.²⁷ In that publication, 74 species, together with newly described *Schizoporella stelloperforata* from the Avacha Gulf, were reported from the shelf zone of Eastern Kamchatka.

One hundred and six species, distributed mainly on the shelves of the Arctic Russian seas, are enumerated for the Bering Sea in the life-work of Kluge.²⁸ Taxonomic descriptions and the text-figures for two of them, the ctenostome bryozoans *Flustrellidra vegae* (Silén) and *F. cervicornis* (Robertson), were based on specimens from the Commander Islands region.

Androsova²⁹ cited *Kinetoskias beringi* Kluge (with reference to the early paper of Kluge)³⁰ for the Bering Sea basin in an account devoted to the abyssal fauna of the Pacific Ocean. In another generalization on cyclostomes of the family Heteroporidae Androsova³¹ has indicated that the Bering sea is an area of distribution for two cerioporines, *Heteropora pelliculata* Waters and *Borgella tumulosa* Kluge.

Preliminary data on the intertidal bryozoan fauna of the western coast of the Bering Sea were published only in the late 1970s.³² Eleven of the 16 species reported for the whole studied area came from the shores of the Commander Islands. Later, the intertidal bryozoan fauna of the Commander archipelago was chosen as the subject of my own investigations.^{33,34} These publications gave ecological data about 65 species, including 59 species of Eurystomata. Results of studies on the intertidal bryozoan fauna of the coast of the Russian Far Eastern seas were summarized recently with more than 70 species recorded within the Bering Sea.³⁵ Eight of them were found along the tidal belt of the Chukchi Peninsula, 18 along Eastern Kamchatka, and about 70 species in the Commander Islands.

Gontar³⁶ provided information about nine rather common bryozoans as a small part of some preliminary results of floral, faunal, and hydrobiological investigations in the Avacha Inlet (Avacha Gulf of Eastern Kamchatka). Seven cheilostomes (including two species new to the fauna of the Bering Sea, *Schizobrachiella perforata* (Kluge) and *Stomachetosella hincksi* Powell), were reported for the Bering Strait in the contemporaneous paper of Gontar and Denisenko³⁷ describing the pattern of biogeographical distribution of Bryozoa in the Arctic basin.

Taxonomic work on Beringian bryozoans was continued by examination of three umbonulomorph species (i. e., having umbonuloid frontal shields), *Desmacystis sandalia* (Robertson), *Rhamphostomella scabra* (Fabricius), and *Umbonula arctica* (M. Sars) using material from the shallow water of the Commander Islands. Zooidal morphology and the distribution of zooidal polymorphs were given as reasons to transfer *U. arctica* to a new genus *Arctonula* gen. nov.³⁸

The results of an inventory of different groups of macrobenthos of the Commander Islands has been published by Nauka Press in 1997 in the volume *Benthic Flora and Fauna of the Shelf Zone of the Commander Islands*. Nine ctenostomes and 132 cheilostome species (103 new to the fauna of the islands) were reported for the shelf zone of the archipelago.³⁹

Some Bering Sea representatives of *Doryporella* – *D. spathulifera* (O'Donoghue and O'Donoghue) and *D. armata* Gontar – were recently used for taxonomic revision of this poorly known cheilostome genus.⁴⁰

The visible role of bryozoans as permanent components of benthic communities of the Bering Sea has been mentioned in the hydrobiological literature. Thus, for example, Kuznetsov⁴¹ has recorded the high frequency of bryozoans in many benthic communities of hard, soft, and mixed substrata of the Eastern Kamchatka shelf, though an overwhelming majority of the species indicated in his monograph were identified only provisionally.

Indications of the relatively high biomass and diversity of bryozoans in some intertidal biocoenoses of the Commander Islands were presented in the work of Tarakanova⁴² for Bering Island and by Kussakin and Ivanova⁴³ for Mednyy Island. Bryozoans were recognized as subdominant forms in at least three benthic communities of hard substrata within the zone of encrusting calcareous red algae in the upper shelf of the Commander Islands.⁴⁴

One or more species of *Alcyonidium* (Ctenostomata) have been cited among the most typical and frequent components of fouling communities on the ships cruising along the eastern coast of the Kamchatka Peninsula.^{45,46} According to Kubanin,⁴⁷ about 19 species of fouling bryozoans have been recorded on anthropogenical substrata within the Bering Sea. Also, at least eight cheilostome species have been introduced via shipping to ports and harbours in the region of Eastern Kamchatka.^{48,49} In some cases, *Alcyonidium* forms particularly dense encrustations in the ports of Avacha Inlet.⁵⁰ Some preliminary data on the role of bryozoans in some fouling shallow-water communities off Bering Island were presented by Oshurkov and Ivanjushina.^{51,52}

Associations between nudibranch molluscs and bryozoans in intertidal pools of rocky shores of Bering Island were described by Roginskaya.⁵³ The special importance of erect bryozoans as food items for the Beringian nudibranchs *Colga pacifica* (Bergh) and *Triopha catalinae* (Cooper) has been indicated in recent publications of Martynov⁵⁴ and Grischenko and Martynov,⁵⁵ and at least five species of decapod crustaceans that preferentially associate with bryozoans in shallow-water assemblages off the Commander Islands have been recorded.⁵⁶

A history of investigations of marine bryozoans in the waters of the Kamchatka Peninsula and an account of taxonomic diversity in the regional fauna has been briefly described by Grischenko.⁵⁷

4. Current knowledge on the bryozoans of the Bering Sea.

4.1 Total diversity

Historically and in recent years several attempts have been made to estimate the total bryozoan diversity of the Russian Far Eastern seas⁵⁸ and also the diversity of the separate seas of the region. Nevertheless, these inventories have only concerned the Sea of Okhotsk^{59,60,61} and the Japan Sea.^{62,63} Although two accounts of the bryozoan fauna of the Bering Sea have been recently published discussing the shelves of both Eastern Kamchatka⁶⁴ and Alaska,⁶⁵ the total taxonomic diversity of the sea – coast, shelves, basin – has not previously been estimated. Based on published data, there are 223 species including 22 cyclostomes, 18 ctenostomes, and 183 cheilostomes (Table 1, Figure 2).

4.2 Regional diversity

It will be appreciated from the above chronicle of historical and recent investigations that bryozoan studies have been ad hoc and piecemeal, so that some areas have been explored more intensively than others.

Eastern and Southeastern Bering Sea: It has been truly mentioned by Dick and Ross⁶⁶ that “bryozoans have been scantily studied in Alaska...”, since only 46 species were reported in previously published papers dealing with the fauna of the Beringian shelf of Alaska (including 7 cyclostomes, 7 ctenostomes, and 32 cheilostomes). Twenty-four species were recorded near Unalaska Island, 24 species in shallow water off the Pribilof Islands, five species near Nunivak Island, and one species, *Carbasa serrulata* (Busk), off St Matthew Island.

Western and Northwestern Bering Sea: Our knowledge of bryozoans in the western and northwestern parts of the Bering Sea is also still rather incomplete. Fifty-eight species are known for the Bering Strait, 62 for the coast of the Chukchi Peninsula, and 89 for the Eastern Kamchatka Peninsula.⁶⁷ The most intensively studied region is the Commander Islands. Thus the known diversity of Bryozoa recorded from the western part of the Sea is about 90 species, from the north/northwestern parts of the Sea about 106 species, and 144 species for the Commander Islands.

5. Discussion

In spite of a long history of investigation, the Bryozoa of the Bering Sea have been studied only irregularly and our knowledge of the diversity and distribution of the total fauna is still incomplete. At the same time, there are several reasons to suspect a very rich bryofauna.

First, the Bering Sea is subdivided topographically into two highly contrasting areas – a shallow north/northeastern shelf (about 43.7% of the bottom area) with depths less than 200 m, and deep-water south/southwestern basins – the Aleutian and Commander Valleys (about 43.3% of the bottom area) – with depths over 2000 m. The boundary between these two main areas is the abrupt continental slope (about 13% of area of the seafloor) with depths 200–2000 m.⁶⁸

Secondly, the Bering Sea is relatively open. The wide north/northeastern shelf of the sea narrowly connects at several places with the North Pacific Ocean via the straits of the Aleutian Islands in the South, with the Chukchi Sea via the Bering Strait in the North, and with the narrow shelf of Eastern Kamchatka in the West. The circulation, transport, and exchange of water mass in the Bering Sea⁶⁹⁻⁷⁴ occurs mainly via the Bering Strait and also via the straits of the Aleutian ridge and along Eastern Kamchatka.

Thirdly, the Bering Sea is connected to some areas with high bryozoan diversity, i.e., to the Kuril Islands in the south-west (where more than 210 species have been recorded – see Gontar⁷⁵⁻⁸⁵ and to the Gulf of Alaska in the south-east (with noticeably rich fauna described by Osburn;^{86, 87, 88} Cuffey and Turner;⁸⁹ Dick and Ross.⁹⁰ The transitional setting of the sea and its general environmental conditions are conducive for an intensive exchange of varied biogeographical elements (of Pacific Asian, American, and Arctic origin) and hence for enrichment of the fauna. Thus, in accordance with some unpublished data (kindly supplied by Ms Nora R. Foster, the Aquatic Collection, University of Alaska, Fairbanks, pers. comm. 1993) there are at least 43 additional unrecorded species of cheilostomes distributed on the Alaskan shelf of the Bering Sea. Thirty-two of them occur along the Aleutian Islands chain, 19 in the Bristol Gulf, 12 in Norton Sound, and eight in other less well-known localities. Taking these figures into account, the total bryozoan diversity in the Beringian shelf of Alaska may be as high as 90 species.⁹¹ Further, preliminary identification of specimens (deposited in the Kamchatka Institute of Ecology and Nature Management, Petropavlovsk-Kamchatsky) collected by RV *Nazarovsk* along the Eastern Kamchatka shelf in 1988 has demonstrated that a diverse bryofauna occurs in the area with a significant number of undescribed taxa. Moreover, 38 cheilostomes (14 anascans and 24 ascophorans) were found recently in the shelf and slope of the Commander Islands (unpublished data of the author). Hence, the cteno-cheilostome fauna of the archipelago comprises more than 175 species. Even taking into consideration both the published and unpublished data mentioned above, the total diversity of Bryozoa in the western part of the Bering Sea is likely to increase significantly, especially if more thorough sampling and detailed analysis are carried out.

Migration of Pacific temperate biogeographical elements of Asian and American origin through the Bering Sea may have been reasonably intensive, during the existence of the Beringia, until the Late Miocene⁹² prior to the opening of the Bering Strait. Current knowledge is inadequate to reconstruct species distributions and the origin of the fauna in the region, though some paleontological data from both Asian^{93, 94} and American⁹⁵ coasts of the North Pacific obliquely suggest a significant “crossroads” role for the Bering Sea in relation to bryozoan diversity. As has been mentioned by many authors,^{96, 97} shelf and slope zones of the Commander-Aleutian Ridge constitute a “bridge” connecting the American and Asian continents, supporting the distribution of both American and Asian faunal elements (including bryozoans) at the present day. For example, at least 15 species previously considered to the Eastern Pacific⁹⁸ – *Callopora nuda* Dick and Ross, *C. decida* Dick and Ross, *Dendrobeatia exilis* (Hincks), *Porella columbiana* (O’Donoghue and O’Donoghue), *Hippoporina vulgaris* Dick and Ross, *Celleporina robertsoniae* (Canu and Bassler), etc. – were recently found in coastal waters of the Commander Islands.⁹⁹

Inadequate sampling of the bryofauna in the Bering Sea does not allow objective comparisons among different parts of the sea. Further, many of the reported species require taxonomic revision and not enough ancillary data are reported in the relatively

little literature to allow environmental and other comparisons. In short, we are still in the discovery phase where the Bering Sea bryofauna is concerned and more work needs to be done. Finally, as is well known, many parts of the Bering Sea are subject to intensive fisheries for teleosts and king crabs. As in many parts of the world, such activities are accompanied by impacts on seafloor habitats and benthic species abundance. It has been pointed out by Nelson and Gordon: “There is no doubt that seafloor habitats are being modified and their species negatively affected faster than we can inventory them”.¹⁰⁰ Thorough inventories of coastal and shelf assemblages everywhere, including the Bering Sea, are desirable in order to make reliable within- and between-assemblage comparisons of bryozoans and other benthos – a worthy goal of the international bryozoological community.

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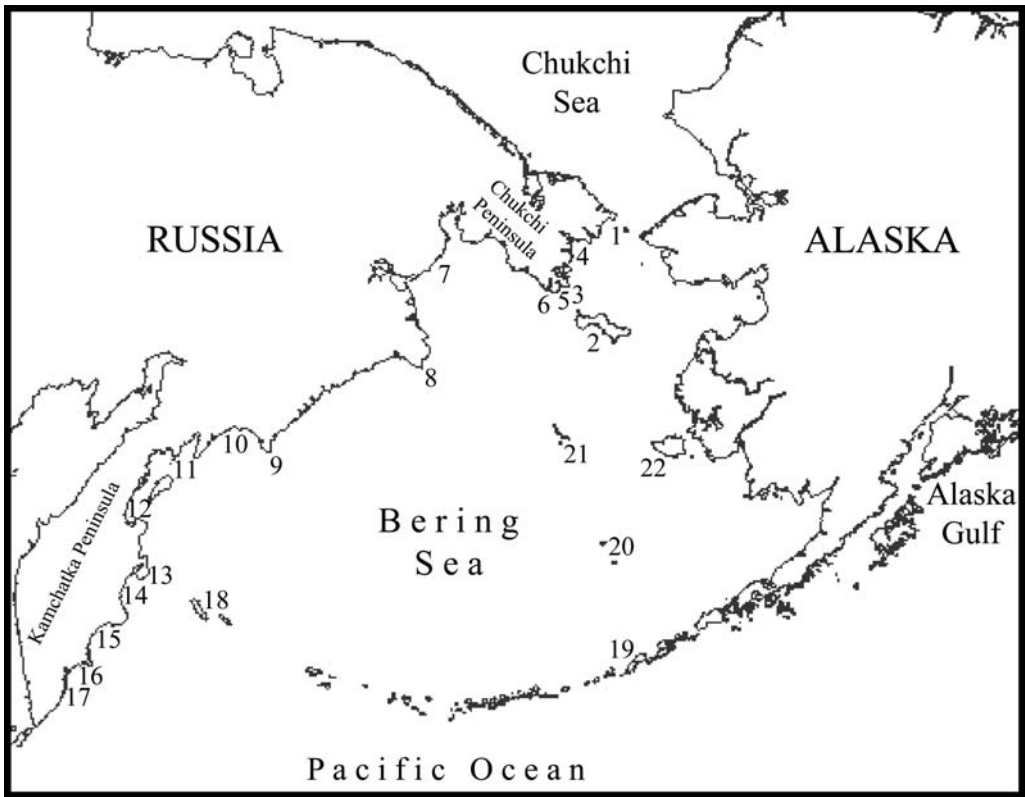


Figure 2. Map showing examined localities within the Bering Sea. The numbers of localities corresponds to Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Microporella neocribroides</i> D & R																		•					
<i>Microporella germana</i> D & R																			•				
<i>Microporella speciosa</i> Suwa, D&M																							•
<i>Fenestrulina malusii</i> (Audouin)																		•					
<i>Cheilopora sincera</i> (Smitt)								•	•														
<i>Cheilopora praelucida</i> (Hincks)	•																	•					
<i>Cheilopora orientalis</i> (Kluge)																	•						
<i>Cheilopora inermis</i> (Busk)																					•		
<i>Hippoporidra trunculenta</i> D & R																		•	•				
<i>Hippoconella hippopus</i> (Smitt)	•	•																			•		
<i>Hippoconella parva</i> Androsova																		•					
<i>Hippoconella fastigatoavicularis</i> K ¹	•																	•					
<i>Retepora imperatii tumescens</i> Ort ¹																							•
<i>Retepora cellulosa</i> (L.)																							•
<i>Phidolopora elongata</i> (Smitt)																		•					
<i>Cellepora nodulosa</i> (von Lorenz)																		•					
<i>Celleporina nordenskjoldi</i> (Kluge)		•				•	•	•	•			•		•	•			•					
<i>Celleporina robertsoniae</i> (C & B)																		•					
<i>Celleporina incrassata</i> (Lamarck)	•	•	•		•			•	•					•				•	•	•			
<i>Celleporina ventricosa</i> (von L)			•	•	•		•	•								•		•				•	
Cyclotomata: 22	3	1	2	0	0	1	1	1	0	0	0	0	0	0	1	4	1	5	4	3	0	3	3
Ctenostomata: 18	8	0	0	1	0	0	4	0	0	1	1	1	0	5	6	6	3	9	5	3	0	0	1
Cheilostomata: 183	47	32	21	10	14	19	35	34	19	7	7	9	24	15	29	48	9	130	15	18	1	2	9
Total diversity: 223	58	33	23	11	14	20	40	35	19	8	8	10	24	20	36	58	13	144	24	24	1	5	13