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Detailed vertical distribution of radiolarian assemblage (0-3000 m, fifteen layers) in the central subarctic Pacific, June 2006

Seiji Tanaka* and Kozo Takahashi*

Abstract

The vertical distribution of radiolarians was investigated by using plankton nets with 63 μm mesh in the central subarctic Pacific (Station OS06-SA) from the surface down to 3000 m depth, which were divided into fifteen sample layers. These samples were obtained in June 2006. Radiolarian standing stocks were high in the 0-250 m interval, and they generally decreased with increasing depth. The maximum standing stocks of living radiolarians occurred in the 75-100 m depth interval. The radiolarian production is likely to be associated with temperature and dissolved oxygen. A total of 80 taxa were encountered: 33 Spumellaria, 32 Nassellaria, and 15 Phaeodaria. Six radiolarian groups were identified based on R-mode cluster analysis: Group 1: surface dwellers (0-250 m), Group 2: the taxa with pronounced abundance peaks in the 75-150 m, Group 3: subsurface to upper intermediate dwellers (750-500 m), Group 4: lower intermediate dwellers (500-1000 m), Group 5: the taxa with relatively high abundance in the 1000-2000 m; and Group 6: lower deep dwellers (2000-3000 m).

Keywords: Radiolaria; vertical distribution; standing stocks; the subarctic Pacific; vertical multiple plankton sampler (VMPS)

1. Introduction

Radiolarians represent as one of the common pelagic microzooplankton groups with siliceous skeletons. Their main dwelling habitats range from the pelagic to hemipelagic oceans with a wide vertical distribution. Their neritic distribution is also known, though it is rare (e.g., Bjørklund, 1974; Boltovskoy et al., 2003). They inhabit virtually wide depths of pelagic water column and their abundance reflects various environmental conditions. Hence, they can provide useful information as environmental tracers, especially for water mass changes (e.g., Pisias et al., 1997; Okazaki et al., 2003a). Most radiolarians are heterotrophs, preying other particles such as phytoplankton, detritus, and bacteria, while some species harbor endosymbionts (Casey, 1977). Taxonomically Radiolaria are divided into Polycystina and Phaeodaria at the highest level (Anderson et al., 2002). Phaeodaria are characterized by specific skeletal morphology and structures (Takahashi et al., 1983; Takahashi and Anderson, 2002;

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Takahashi and Hurd, 2007). Polycystina are further subdivided into two suborders, Spumellaria and Nassellaria, based on the morphology of their shell structures (Anderson et al., 2002).

Many studies using plankton-tow samples have been performed to characterize radiolarian vertical distributions all over the world (e.g., Okhotsk Sea: Okazaki et al., 2004; Equatorial Pacific: Yamashita et al., 2002; Southern Ocean: Abelson and Gowing, 1996; California Current region: Kling and Boltovskoy, 1995; eastern equatorial Atlantic: Dworetzky and Morley, 1987; Greenland Sea: Swanberg and Eide, 1992; Norwegian fjords: Swanberg and Bjørklund, 1992; Japan Sea: Ishitani and Takahashi, 2007). In the central part of the North Pacific, Kling (1979) reported on the vertical distribution of polycystine radiolarians at two stations in July 1977. They reported that the maximum polycystine radiolarian standing stocks generally occurred at intermediate depths (200-500 m). In the equatorial Pacific, Petrushevskaya (1971) showed the radiolarian standing stock values were much higher (ca. 18,000 radiolarians m^{-3} at Station 5117: 0°, 154°W; ca. 7,000 radiolarians m^{-3} at Station 5124: 8°N, 154°W) than those at the high latitude stations in Kling (1979). However, almost all studies were limited to relatively shallow depths such as <1000m due to the technical difficulty for deep plankton-net sampling. Dogiel and Reshetnyak (1952) reported their significant work on radiolarian taxon vertical distribution in the northwestern North Pacific down to 4000 m. Furthermore, Reshetnyak (1966) also reported on the taxonomy of phaeodarians from the northwestern North Pacific. Nevertheless, these studies were qualitative and mainly devoted to radiolarian taxonomy. Therefore, there is little quantitative information available on radiolarian vertical distribution greater than 1000 m depths in the North Pacific and the Bering Sea.

Earlier, we reported on the vertical distribution of radiolarians in the Bering Sea (Stations OS03-AB and OS04-AB) and in the subarctic Pacific (Stations OS03-SA and OS04-SA), as determined from plankton-tow samples, collected from six depth intervals (Tanaka et al., submitted). The followings are high lights of the paper:

- (1) Total radiolarian standing stocks were primarily concentrated in the 0-250 m depth interval both at Stations AB and SA;
- (2) The major factors governing radiolarian standing stocks are temperature (approximately >4°C), dissolved oxygen (>1 $\text{m} \ell^{-1}$), and dissolved silicon concentration;
- (3) A total of 79 taxa were encountered in the study: 25 Spumellaria, 41 Nassellaria, and 13 Phaeodaria;
- (4) The radiolarian assemblages in the 0-250 m interval were dominated by two surface dwellers (*Spongotrochus glacialis* and Spongodiscidae juvenile form) and eight subsurface dwellers (*Stylochlamydidium venustum*, *Tholospira cervicornis*, *Tholospira* sp., *Ceratospyrus borealis*, *Pseudodictyophimus glacilipes*, *Zygocircus productus* group, *Pterocanium korotnevi*, and *Rhizoplegma boreale*);
- (5) *Rhizoplegma boreale* occurred as a major subsurface species at Station AB but not at Station SA;
- (6) *Botryostrobus aquilonaris* showed different distribution patterns between Station AB (50-250 m) and Station SA (250-500m);
- (7) Five radiolarian taxa showed significant population maxima below 1000 m: *Actinomma leptoderma*, *Carpocanarium papillosum*, *Dorydruppa bensoni*, *Cycladophora cornutoides*, and *Cycladophora davisiana*;
- (8) The favorable conditions of *Cycladophora davisiana* are low temperature and high dissolved oxygen contents; and
- (9) The standing stock of *C. davisiana* is governed by transported food (particles such as phytoplankton, detritus) and/or bacteria biomass in the deep waters.

In our present study, we report on a further detailed vertical distribution of radiolarians in the central subarctic Pacific. The purpose of this study is to characterize the radiolarian vertical distribution and

compare with the ambient environmental conditions of the water column. A significant focus is given to the important depth range from the surface to subsurface layers with fifteen discrete detailed plankton tow sampling.

2. Oceanographic setting

The subarctic Pacific is characterized by low salinity in the surface layer. Together with a wide-range of the sea surface temperature (SST) variability, a significant seasonal variability of the near surface water conditions (e.g., occurrence of dichothermal layer) is the characteristic of the region. In summer, high solar radiation heats the sea surface waters to 10-12°C (Reynolds and Smith, 1994), leading to well-developed thermoclines at 15 m depth around the central subarctic Pacific (Levitus and Boyer, 1994). Such a seasonally well-developed thermocline obstructs the convective supply of nutrients from the subsurface waters. In winter, on the other hand, the surface water is cooled off, deepening the thermocline to 90 m (Levitus and Boyer, 1994). This change in the mixed layer depth mainly controls the supply of nutrients to the surface. The Alaskan Stream, which has a deep baroclinic velocity structure, is the dominant surface current around the subarctic Pacific Ocean, and is the westward flow originating from the Alaskan Gyre in the Gulf of Alaska. Volume transport of the Alaskan Stream based on deep observations in the central North Pacific was estimated to be $28 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ by geostrophic calculation with current meter measurements (Warren and Owens, 1988).

In general, the subarctic Pacific can be vertically divided into four water masses present during summer: the warm surface layer from 0 to 50 m, the cold subsurface layer (dichothermal layer) from 50 to 200 m, the warm intermediate layer from 200 to 800 m, and the deep water below 800 m (e.g., Natarov, 1963; Luchin et al., 1999). It is well known that seasonal variations of the water temperature and solar radiation in the subarctic ocean are larger than those in the tropical oceans, where they remain nearly the same level throughout the year.

3. Materials and Methods

Plankton net samples were collected at Station OS06-SA (SA: subarctic: 49°00'N, 174°00'W, 16 June 2006) in the subarctic Pacific during Cruise OS06 of T/S Oshoro-maru, the Hokkaido University (Table 1; Fig. 1). Plankton nets were towed in the depth intervals of 0-25, 25-50, 50-75, 75-100, 100-150, 150-250, 250-350, 350-500, 500-750, 750-1000, 1000-1250, 1250-1500, 1500-2000, 2000-2500, and 2500-3000 m. The net samples were obtained with a vertical multiple plankton sampler (VMPS: mouth diameter 1 m; mesh size 63 µm: Terazaki and Tomatsu, 1997), and immediately stained with Rose Bengal on board in order to distinguish between living and dead cells, and preserved in 5% buffered formalin. Hydrographic data (temperature, salinity, and dissolved oxygen) down to 3000 m water depth were obtained by a conductivity temperature and depth (CTD) survey at the same time with this plankton sampling.

In the shore-based laboratory, the samples were sieved through a stainless screen with 1 mm mesh to remove large zooplankton such as copepods, and then split to an appropriate aliquot size (1/8). The split samples were sieved through two stainless screens with 63 µm and 500 µm mesh sizes, respectively. Remains on the screens were filtered through Gelman® membrane filters with a nominal pore size of 0.45 µm. The filtered samples were desalted with distilled water and dried, then permanently mounted with Canada Balsam on microslides.

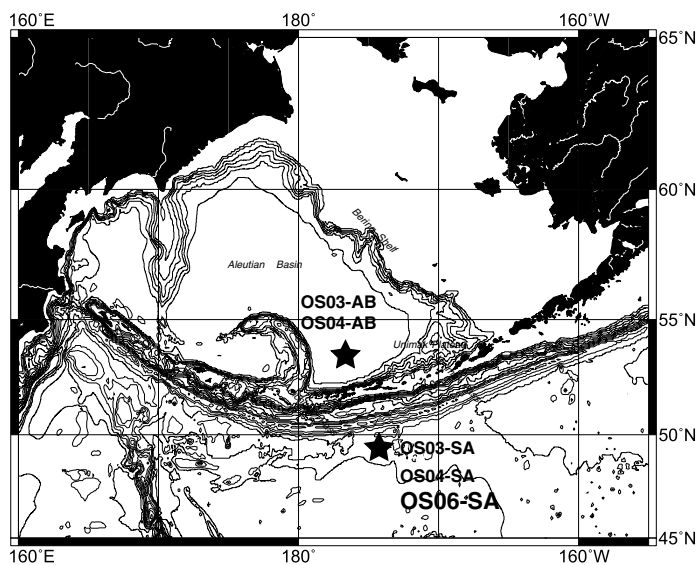


Fig. 1. Map showing the locations of plankton stations (this study; Station OS06-SA and those in the previous study) in the Bering Sea and the central subarctic Pacific.

Table 1. The fifteen sampled intervals and logistics of the VMPS plankton tows conducted at Station OS06-SA in 2006.

Station	Sampled			Sampled	Water	Aliquot	Total
Latitude	date			interval	filtered	size	count
Longitude				(m)	(m ³)		(Number)
OS06-SA 49°00'N 174°00'W	16	June	2006	0-25	2.9	1/8	25
				25-50	7.9	1/8	104
				50-75	4.9	1/8	88
				75-100	3.2	1/8	106
				100-150	13.5	1/8	301
				150-250	21.0	1/8	304
				250-350	17.2	(1/8) x2	181
				350-500	38.8	1/8	133
				500-750	53.5	(1/8) x2	254
				750-1000	56.1	(1/8) x2	227
				1000-1250	50.9	(1/8) x2	338
				1250-1500	52.2	(1/8) x2	320
				1500-2000	113.8	(1/8) x2	630
				2000-2500	104.0	(1/8) x2	364
				2500-3000	102.5	(1/8) x2	273

(1/8) x2: Two microslides of the aliquot size 1/8 were subjected to the microscopic counts.

All radiolarians on slides were counted at x100-400 magnification with an Olympus® compound light microscope. Only specimens that were clearly identifiable, with over 50% of their skeletons present, were counted as a whole specimen. Stained specimens were counted as “Live”, and empty skeletons were counted as “Dead”. We determined that specimens were “Live”, if their protoplasm was stained clearly, to avoid false staining by other organisms. Counts of radiolarians were converted to standing stocks (No. radiolarians m^{-3} of sea water). Species identification of radiolarians follows the taxonomy of Nigrini (1970), Renz (1976), Bjørklund (1976), Nigrini and Moore (1979), Boltovskoy and Riedel (1987), Takahashi (1991), Abelman (1992), Welling (1996), Bjørklund et al. (1998), and Nimmergut and Abelman (2002).

We performed R-mode cluster analysis using Morisita's index (C'_λ ; Morisita, 1971) and the average linkage method with the PAST (Paleontological Statistics, ver. 1.06) software package (Hammer et al., 2001). Thirty two taxa with a 3% relative abundance in at least one sample were selected for the cluster analysis.

4. Results

4.1. Hydrographic profiles

Profiles of temperature, salinity, and dissolved oxygen (DO) down to 3000 m depth are shown in Fig. 2. The observed SST was 7.8°C. The temperature profile presents a clear temperature minimum layer (dichothermal layer) around 125 m depth. While the surface salinity value in the 0-100 m depth interval was low (32.8 psu), the value in the 100-150 m depth interval increased significantly, reaching 34.0 psu. The profile of DO content shows high values over 7.0 $\text{m} \ell^{-1}$, whereas those in the 100-150 m interval decreased quickly to 1 $\text{m} \ell^{-1}$. The DO minimum layer with the values of less than 1 $\text{m} \ell^{-1}$ is extended in the 250 to 1000 m interval, and the DO values increased with depth below 1000 m.

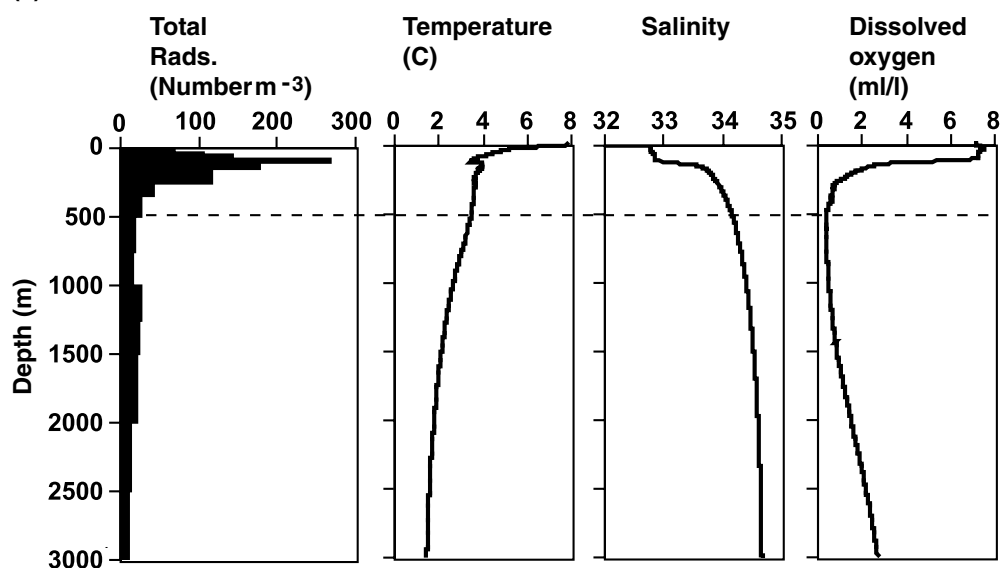
4.2. Living radiolarian standing stock

The vertical distribution patterns of total living radiolarians are shown in Fig. 2. Between 0 to 250 m, the radiolarian standing stocks were high over 50 radiolarians m^{-3} , while they decreased with depth below 250 m. Living radiolarian standing stock maxima were found in the 75-100 m interval reaching 268 radiolarians m^{-3} .

A total of 80 taxa were encountered in this study: 33 Spumellaria, 32 Nassellaria, and 15 Phaeodaria. Table 2 shows all living radiolarian standing stocks in each of the depth intervals. The dominant species whose standing stocks exceeded 10 radiolarians m^{-3} are as follows: Spongodiscidae juvenile form in the 0-25, 25-50, 50-75, 75-100, and 100-150 m intervals; *Spongostochus glacialis* in the 25-50 to 150-250 m intervals; *Actinomma delicatulum* in the 50-75 and 150-250 m intervals; *Stylodictya* sp. in the 50-75 and 75-100 m intervals; *Stylochlamydidium venustum* in the 75-100 m interval; *Ceratospyrus borealis* in the 50-75, 75-100 and 100-150 m intervals; *Pterocanium korotnevi* in the 75-100 and 100-150 m intervals and *Zygocircus productus* group in the 0-25, 75-100, 100-150 and 150-250 m intervals. Other common to abundant species are as follows:

<i>Actinomma leptoderma</i> ,	<i>Botryostrobus aquilonaris</i> ,	<i>Cycladophora cornutoides</i> ,
<i>Cycladophora davisiana</i> ,	<i>Dorydruppa bensoni</i> ,	<i>Lithelius minor</i> ,
<i>Pseudodictyophimus glacilipes</i> ,	<i>Rhizoplegma boreale</i> ,	<i>Spongurus</i> sp.,
<i>Stylodictya validispina</i> ,	<i>Tholospira cervicornis</i> ,	<i>Tholospira</i> sp.,

(a) 0-3000 m



(b) 0-500 m

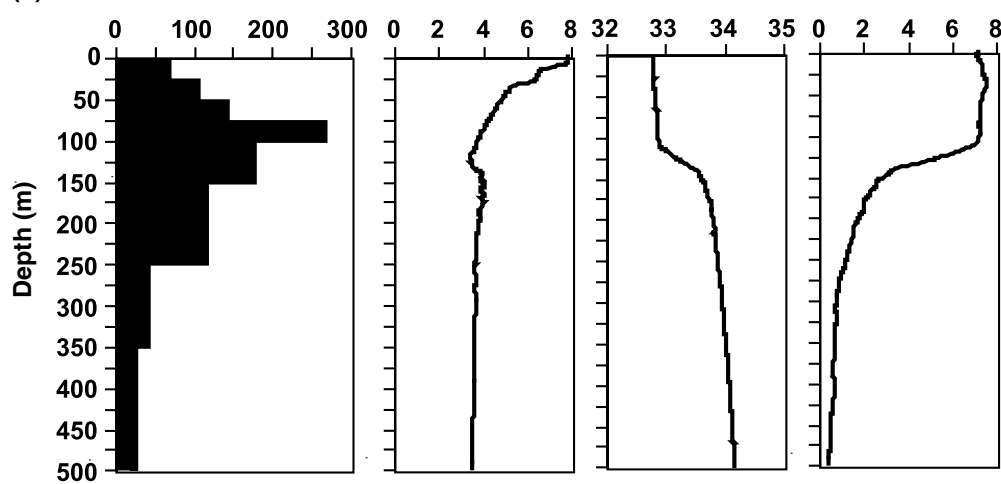


Fig. 2. Vertical profiles of total living radiolarian standing stocks, the observed temperature, salinity and dissolved oxygen from: (a) 0 to 3000 m depth; (b) 0 to 500 m depth (Graduate School of Fisheries Sciences and Faculty of Fisheries, Hokkaido University, 2007).

Table 2. Living radiolarian standing stocks at Station OS06-SA.

Interval: Top(m)	0	25	50	75	100	150	250	350	500	750	1000	1250	1500	2000	2500	2500
Interval: Bottom (m)	25	50	75	100	150	250	350	500	750	1000	1250	1500	2000	2500	3000	
<i>Actinomma delicatulum</i>	8.4	4.0	11.5	5.1	2.4	10.7	5.3	3.5	0.3	0.6	0.6	0.4	0.3	-	0.1	
<i>Actinomma leptoderma</i>					0.6	3.1	1.6	1.0	0.2	0.6	0.8	1.5	0.9	0.2	0.3	
<i>Actinomma</i> sp. C.										0.3						
<i>Actinomma</i> sp. D.			1.6			0.8	0.5	1.4	0.4		1.0	0.8	0.4	0.1	0.1	
<i>Actinomma</i> sp.						5.0	0.2		0.1		2.0	2.6	0.5	-	0.1	
<i>Actinomma boreale</i>												0.1	0.2	-		
? <i>Didimocyrtis</i> group					0.6			0.4	0.2		0.6	0.3	0.1	0.3	0.1	
<i>Dorydoruppa bensoni</i>									1.3				0.1	0.6	0.6	
<i>Druppattractus ostracion</i>			1.6					0.6				0.2		0.1	0.1	
<i>Heliosoma</i> sp.									0.1			0.1				
<i>Larcopyle butschlii</i>					0.6	0.4			0.1	0.1			0.0			
<i>Lithelius minor</i>							0.5	0.2	0.5	0.9	0.7	2.2	0.5	0.3	0.4	
<i>Lithelius nautiloides</i>						0.8	0.2	0.2	0.1	0.4	0.2		0.1			
<i>Lithelius</i> sp.						0.4					0.5			-		
<i>Pylosolenia</i> sp.							0.7		0.1	0.1				0.1		
<i>Rhizoplegma boreale</i>		1.0			8.3											
<i>Sphaeropyle langii</i>									0.1							
Spongodicidae juvenile form	13.9	17.2	13.1	25.3	13.0	8.4	1.9	2.7	0.9	0.2	0.3	0.2				
<i>Spongodiscus</i> sp.						1.5	0.2									
<i>Spongophacus</i> sp.			1.6			1.1				0.1						
<i>Spongopyle osculosa</i>	8.4	1.0	1.6	2.5		1.9	0.2	1.6	0.7	0.3	0.2	0.1	-	0.1		
<i>Spongotrochus glacialis</i>	5.6	26.3	32.8	17.7	7.7	11.4	5.3	2.7	1.0	0.3	0.2	0.1	0.2	0.1	0.1	
<i>Spongurus pylomaticus</i>						0.4	0.2	1.0	0.3	0.2	0.1		-			
<i>Spongurus</i> sp.		4.0				0.8	0.2	0.4	1.0	0.7	2.0	1.5	1.0	0.4	0.1	
<i>Stylatractus</i> spp.									0.2	0.5			0.1		0.2	
<i>Stylatractus</i> sp. A							0.2		0.4	0.5		0.2		-		
<i>Stylodictya aculeata</i>								0.4								
<i>Stylodictya validispina</i>			1.6			1.1	0.2		1.3	0.6	0.5	0.2	0.1		0.1	
<i>Stylodictya</i> sp.		3.0	11.5	10.1	0.6	6.1	1.2	0.4	3.6	1.1	1.2	0.1	0.2	0.6	0.6	
<i>Stylochlamydidium venustum</i>	5.6	1.0	6.6	20.2	0.0		0.2					0.1				
<i>Tetrapyle octacantha</i>												0.1				
<i>Tholospira cervicornis</i>					1.2						0.1					
<i>Tholospira</i> sp.	5.6	7.1	3.3	7.6	5.9	2.3	0.5				0.2					
Other Spumellaria	8.4	2.0	4.9	15.2	3.6	3.4	1.2	1.0	0.2	0.7	1.2	0.7	0.4	0.4	0.2	
<i>Artbotrys borealis</i>							0.2	0.2		0.1					-	

Table 2. (continued)

Interval: Top (m)	0	25	50	75	100	150	250	350	500	750	1000	1250	1500	2000	2500
Interval: Bottom (m)	25	50	75	100	150	250	350	500	750	1000	1250	1500	2000	2500	3000
<i>Pseudodictyophymas gracilipes</i>					4.7	1.1		0.6	0.1	0.2		0.4		0.2	0.2
<i>Pseudodictyophymas</i> sp. A.						1.1		0.2		0.2					
<i>Pseudodictyophymas</i> sp. B.									0.1				-		
<i>Pterocanium korotonevi</i>		8.1	8.2	43.0	32.0	0.4	0.5								
<i>Saccospyris</i> sp.						3.1									
<i>Siphocampe arachnea</i>														0.2	-
<i>Zygocircus productus</i> group	11.1	8.1	9.8	22.8	17.2	14.9	3.2	1.9	0.1		0.2	0.2			
Other Nassellaria		8.1	3.3	2.5	7.7	2.7	1.2	0.2	0.6	0.7	1.0	0.8	0.4	0.2	0.4
<i>Borgertella caudata</i>					0.6		1.2	0.2	0.4	0.3	0.8	0.5	0.2	-	
<i>Challengeron ornithocephala</i>							0.5			0.2	0.2	0.1	0.2		0.2
<i>Challengeron vicina</i>				10.1	3.0		1.6	0.6	0.4	0.4	0.1	0.2		0.1	
<i>Challengerosium avicularia</i>												0.2			
<i>Conchellium tridacna</i>										0.4	0.3	0.1	0.1		-
<i>Conchopsis compressa</i>									0.1	0.1					
<i>Euphysetta elegans</i>							0.5				0.1	1.6	1.7	1.1	0.5
<i>Euphysetta staurocodon</i>								0.4		0.8	1.8	3.1	10.7	4.0	1.2
<i>Lirella melo</i>							0.5		0.2		0.9			0.2	-
<i>Lirella bullata</i>					2.4		0.2		0.1	0.1	0.5	0.5	0.2	0.1	0.1
<i>Lirella tortuosa</i>												0.2			
<i>Porospathis holostoma</i>										0.4	0.6		0.3	0.2	-
<i>Protocystis auriculata</i>											0.1				
<i>Protocystis sloggetti</i>											0.1				
<i>Protocystis thomsoni</i>			1.6				0.9	0.2	0.6	1.1	0.9	0.4	0.1	-	
Other Phaeodaria				15.2	3.0				0.2	0.1	0.4	0.4	0.2	0.4	0.4
Others		3.0	3.3	2.5	1.2	1.1	0.2		0.1					-	-
Total living Radiolaria	69.6	105.3	144.1	268.3	178.2	115.9	42.0	27.4	19.0	16.2	26.6	24.5	22.1	14.0	10.7
Total living Spumellaria	55.7	68.8	91.7	103.8	44.4	59.5	20.6	17.7	13.2	8.2	12.3	11.3	5.3	3.2	3.0
Total living Nassellaria	13.9	33.4	47.5	136.7	123.8	55.3	15.8	8.2	3.7	4.1	7.7	6.1	3.3	4.6	5.0
Total living Paeodaria			1.6	25.3	8.9	0.0	5.3	1.4	2.1	4.0	6.6	7.2	13.6	6.2	2.5

-: Rare (<0.1 radiolarians m⁻³)

4. 3. Vertical distribution patterns of living radiolarians

Based on the results of the cluster analysis, thirty-two radiolarian taxa with 3% or higher relative abundance in at least one sample are classified into six groups (Figs. 3-4). The cumulative contributions of the thirty-two taxa accounted for 80% of the total living radiolarian assemblages. The vertical distribution patterns of radiolarian taxa in each group are shown in Fig. 3.

Group A (Lower intermediate dwellers: 500-1000 m)

The vertical distribution patterns of radiolarian taxa in Group A are characterized by abundant standing stocks in the lower intermediate water (500-1000 m). Six taxa are mainly classified as the lower intermediate water dwellers (Fig. 3a): *Stylatractus* spp., *Stylatractus* sp. A., *Protocystis thomsoni*, *Stylodictya validispina*, *Stylodictya* sp., and *B. aquilonaris*. Among the taxa in Group A, ten times higher standing stock of *Stylodictya* sp. than those of the other taxa in Group A was observed in the 75-150 m.

Group B (Lower subsurface to upper intermediate dwellers: 150-500 m)

The radiolarian taxa belonging to Group B represent high standing stocks in the lower subsurface to the upper intermediate waters (150-500 m). Four taxa are classified as Group B (Fig. 3b): *Lithalacnium tentorium*, *Challengeron vicina*, *Actinomma* sp. A, and *Spongurus pylomaticus*.

Group C (Upper to lower deep dwellers: 1000-3000 m)

Abundant standing stocks of Group C were mainly confined to the 1000-3000 m range, especially high occurrences in the upper deep waters (1000-2000 m). Eight taxa are classified as Group C (Fig. 3c): *Euphysetta elegans*, *Euphysetta staurocodon*, *Actinomma leptoderma*, *Lithelius minor*, *Spongurus* sp., *Cycladophora cornutoides*, *Actinomma* spp., and *Lirella melo*.

Group D (Lower deep dwellers: 2000-3000 m)

The vertical distribution of Group D shows a wide depth range pattern in the intermediate to deep waters, however, only this group dwelled in the lower deep waters with relatively high standing stocks. Two taxa are classified as Group D (Fig. 3d): *Dorydruppa bensoni* and *Cycladophora davisiana*.

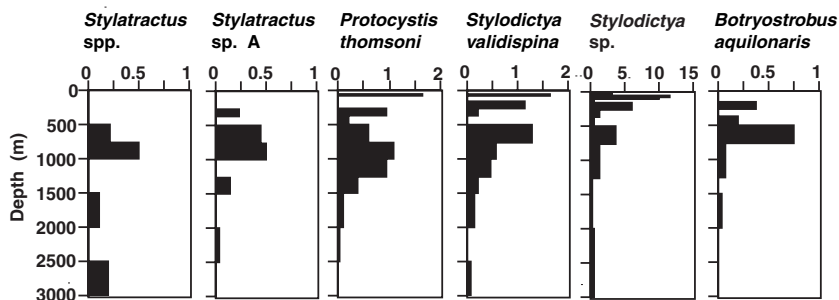
Group E (Subsurface dwellers: 75-150 m)

Radiolarian taxa belonging to Group E showed high standing stocks over 10 radiolarians m⁻³ only in the 75-100 and/or 100-150 m intervals. Four species are classified as Group E (Fig. 3e): *Rhizoplegma boreale*, *Dictyophimus* spp., *Ceratospyris borealis*, and *Pterocanium korotnevi*. Note that *C. borealis* and *P. korotnevi* accounted for 40% of total radiolarians in the 75-100 and 100-150 m intervals.

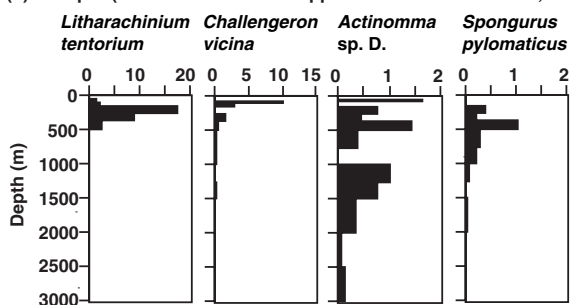
Group F (Surface to subsurface dwellers: 0-250 m)

The vertical distribution patterns of radiolarian taxa in Group F are characterized by abundant standing stocks in the surface waters (0-250 m). Only this group showed high abundance in the 0-25 m interval. Eight taxa are classified as the surface water dwellers (Fig. 3f): *Spongopyle osculosa*, *Lophophaena* spp., *Stylochlamydidium venustum*, Spongodiscidae juvenile form, *Zygocircus productus* group, *Tholospira* sp., *Spongotrochus glacialis*, and *Actinomma delicatulum*.

(a) Group A (Lower intermediate dwellers; 500-1000 m)



(b) Group B (Lower subsurface to upper intermediate dwellers; 150-500 m)



(c) Group C (Upper to lower deep dwellers; 1000-3000 m)

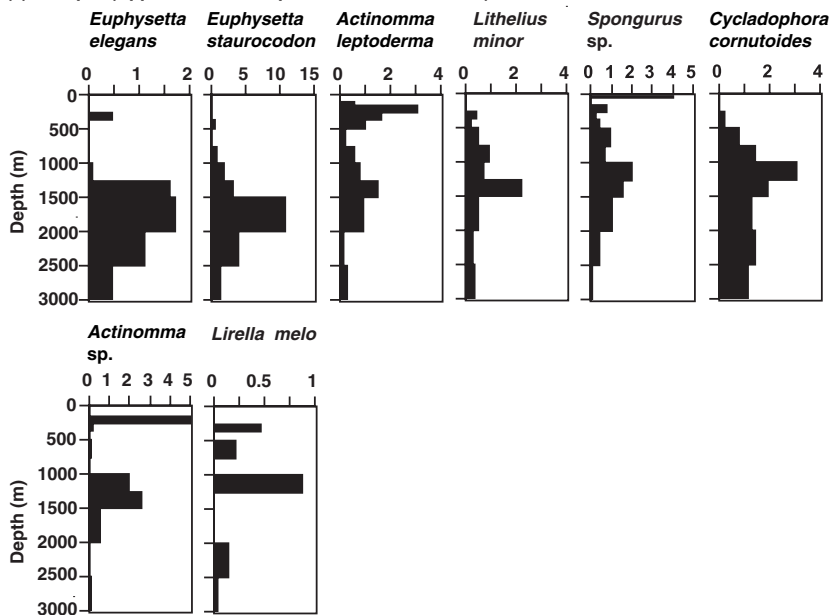


Fig. 3. Depth profiles of living radiolarian standing stocks (radiolarians m^{-3}) for each radiolarian taxon employed in the cluster analysis.

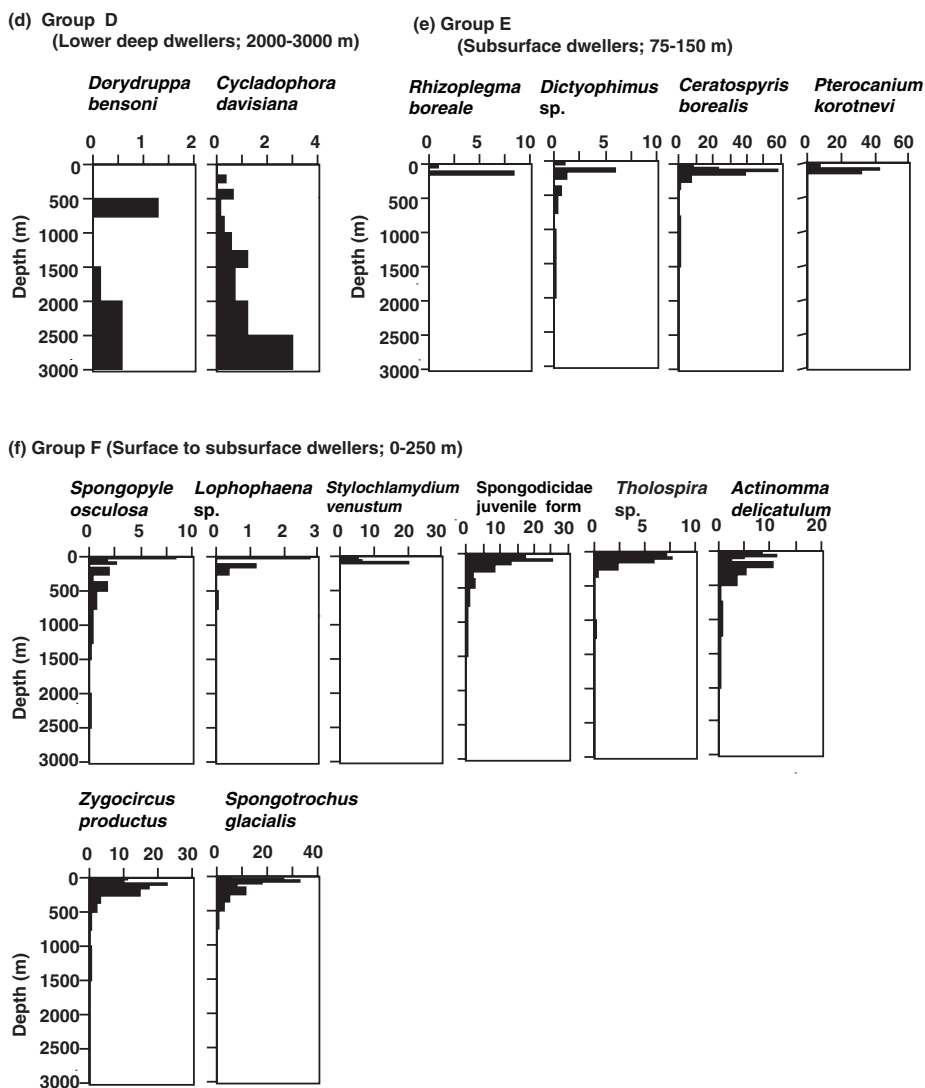


Fig. 3. (continued)

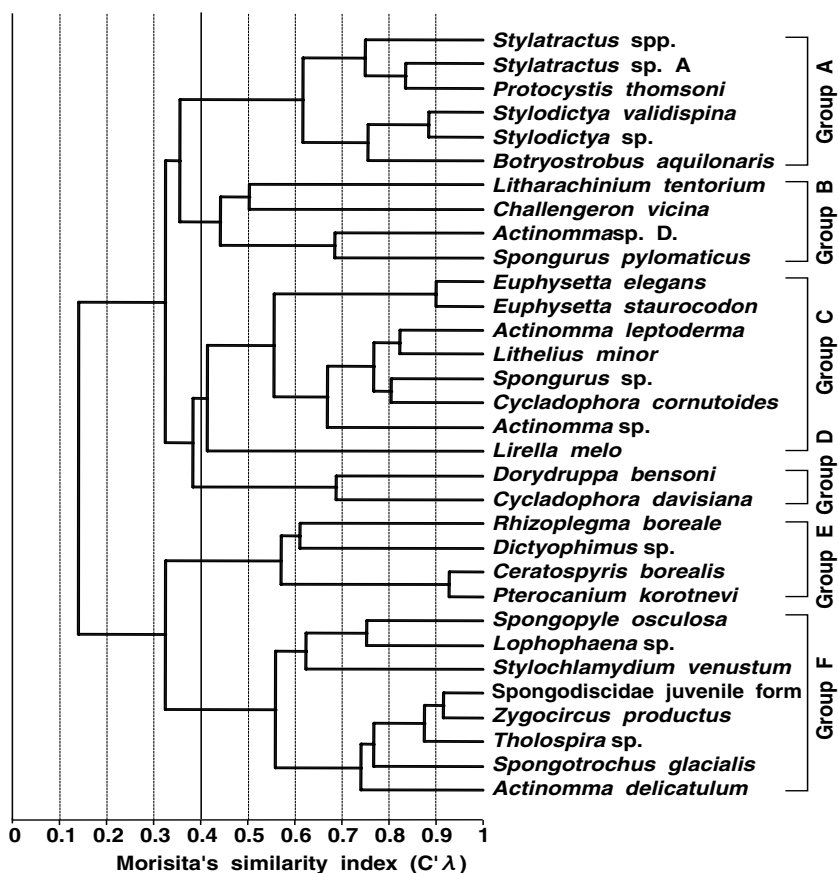


Fig. 4. Dendrogram of average linkage cluster using Morisita's similarity index (Morisita, 1971). The obtained six radiolarian groups are shown.

5. Discussion

5. 1. Vertical distribution of total radiolarians

It is generally reported that radiolarian standing stocks are concentrated in the surface waters (e.g., Petrushevskaya, 1971; Kling, 1979; McMillen and Casey, 1978; Kling and Boltovskoy, 1995; Yamashita et al., 2002). In our study, high radiolarian standing stocks were found from the 0-250 m depth interval, especially the 75-100 m. This is because that the surface waters have more favorable conditions for radiolarian production than the waters below (e.g., abundant foods, adequate dissolved oxygen, and appropriate temperature, respectively). While the SST was 8 °C, the temperature around 250 m depth was 3.8°C (temperature minimum layer). Below 250 m depth, temperature and radiolarian standing stocks decreased with increasing depth. Fukumura (2002ms) indicated that total radiolarian fluxes displayed relatively high spring to autumn values and decreased in winter in the central subarctic Pacific (Station SA: the same location as this study). In our study, total radiolarian standing stocks were concentrated within the high temperature depth interval. These results indicate that radiolarian production occurs in the depth range

of high temperature during the seasons with high temperature in the central subarctic Pacific. Therefore, we suggest that the favorable water temperatures for radiolarian production in summer are higher than approximately 3.8°C in the central subarctic Pacific. Our previous study also showed the high standing stocks in the surface layer where temperature was over 4°C (Tanaka et al., submitted). The results from these two sets of independent data from different years agree very well.

The dissolved oxygen (DO) contents from the 0-250 m depth interval were high reaching over 7 mℓ ℓ⁻¹. These values decreased with increasing depth and reached 1 mℓ ℓ⁻¹ around 250 m depth. The oxygen minimum layer (<1 mℓ ℓ⁻¹) ranged from 200 m to 1000 m depth, and the radiolarian standing stocks were also low with less than 50 radiolarians m⁻³ in this depth interval. Hence we propose that the favorable DO content for radiolarian production is higher than 1 mℓ ℓ⁻¹ in the central subarctic Pacific. Our previous study (Tanaka et al., submitted) also showed similar results with the radiolarian standing stocks decreasing with low DO contents such as <1 mℓ ℓ⁻¹.

5.2. Radiolarian depth zones

Group A (Lower intermediate dwellers: 500-1000 m)

Radiolarian taxa belonging to Group A mainly dwell in the lower intermediate water (500-1000 m depth). These six taxa display a wide range of geographic distribution from the equatorial to subarctic Pacific (e.g., Lombardi and Boden, 1985; Takahashi, 1991; Welling, 1996; Takahashi, 1997). These taxa may be associated with stable hydrographic conditions in the intermediate water throughout the year in comparison with the severe surface condition. Lower intermediate layer between 500 and 1000 m represents the oxygen minimum layer (<1 mℓ ℓ⁻¹; Fig. 2). This suggests that radiolarian taxa belonging to Group A have tolerance for low oxygen. In particular in our previous study (Tanaka et al., submitted), *Stylodictya validispina* also showed a small standing stock maximum only in the lower intermediate layer with low DO contents.

Group B (Subsurface to upper intermediate dwellers: 150-500 m)

The species standing stocks of Group B showed very small values in the surface layer, but they showed relatively high values in the 350-500 m interval compared to other species. The DO contents of this interval decreased rapidly from 100 m and downward, and the values reached approximately 0 mℓ ℓ⁻¹ at 500 m depth. The characteristic of Group B compared to Group A is absent or very few occurrence of the taxa below 500 m. This suggests that radiolarian taxa belonging to Group B do not have tolerance for low oxygen.

Group C (Upper to lower deep dwellers: 1000-3000 m)

In the 1000-2000 m interval, the standing stocks of the species of Group C showed much higher values than those of the other groups. Three phaeodarians belonged in Group C. Among them, *Euphysetta staurocodon* showed significantly high standing stocks greater than 10 radiolarians m⁻³ in the 1500-2000 m interval. In general, the deep water below 1000 m depth represented unfavorable conditions for radiolarian production (less food, low temperature, low DO contents, and low light precluding symbiosis). Why then these deep dwelling phaeodarians were encountered there? The answer can be found in dissolved silica (DSi) distribution. Okazaki et al. (2004) suggested that phaeodarians migrated to deeper water depth where the DSi content was high, when their original dwelling depth zone had low DSi contents. It is possible that in order to build their skeletons phaeodarians like *E. staurocodon* (small and thin skeleton) dwelled in the deep water where the DSi content was high. Although the linkage between DSi content in the ambient waters and phaeodarian skeletal development is not well understood, they may be linked as suggested by their vertical distributions (i.e., high phaeodarian standing stocks vs. high nutrient contents; e.g., Björklund, 1974; Takahashi and Honjo, 1981; Abelson and Gowing, 1996; Nimmergut and Abelson, 2002).

Group D (Lower deep dwellers: 2000-3000 m)

Radiolarian taxa belonging to Group D were *Dorydruppa bensoni* and *Cycladophora davisiana*. Notably, the standing stock of *C. davisiana* showed the highest values in the 2500-3000 m interval. These species also showed high abundances below 1000 m in 2003 and 2004 (Tanaka et al., submitted), although the depth intervals below 1000 m were relatively low resolution with the 1000-2000 and 2000-3000 m intervals. In our present study, the depth intervals have been further divided into 1000-1250, 1250-1500, 1500-2000, 2000-2500, and 2500-3000 m. The standing stocks of *C. davisiana* increased with depth and they appeared to be in proportion to the increase of DO contents. Based on the distribution patterns of *C. davisiana*, Ohkushi et al. (2003) suggested that this species appeared to be a useful tracer of cold, well-oxygenated intermediate-waters in the North Pacific. Furthermore, Okazaki et al. (2003b) reported the temporal fluxes of *Cycladophora davisiana*, the major intermediate dweller (300-500 m) in the Okhotsk Sea, during 1997 to 2000 at five stations in the Okhotsk Sea and the northwestern North Pacific. They suggested that the production of *C. davisiana* was closely related to the microbial production in the intermediate water because the distinct maxima of *C. davisiana* fluxes were found during summer to autumn, when the microbial production reached its maximum. According to Okazaki et al. (2004), standing stocks of *C. davisiana* in the Okhotsk Sea were much higher than those in the Oyashio region especially in the intermediate depth (300-500 m). They suggested the difference in radiolarian standing stocks between the Okhotsk Sea and the Oyashio region appeared at least to partially reflect the differences in bacterial biomass at intermediate depths. In our previous study (Tanaka et al., submitted), we suggested that the favorable conditions for *C. davisiana* were low temperature and high dissolved oxygen contents, and that the standing stocks of *C. davisiana* were governed by transported food (particles such as phytoplankton, detritus) and/or bacteria biomass in the deep waters. The results of the present study further supported these suggestions.

Group E (Subsurface dwellers: 75-150 m)

Four radiolarian taxa showed significant standing stock maxima only in the 75-100 and/or 100-150 m intervals (*Rhizoplegma boreale*, *Dictyophimus* spp., *Ceratospyrus borealis*, and *Pterocanium korotnevi*). The dwelling depth and standing stock maxima of these taxa in our previous study were in the 50-250 m interval. In the present study the dwelling depth zone of these taxa was limited in the 0-250 m. The 75-150 m depth where these significant standing stock maxima coincided with the dichothermal layer. In this interval, the hydrographic conditions also rapidly changed with increasing depth (halocline and the DO contents: Fig. 2). We suggest that the common favorable conditions for four subsurface dwellers are associated with the dichothermal layer (temperature minimum layer), halocline, and the DO contents.

Group F (Surface dwellers: 0-250 m)

Only eight taxa in Group F showed high standing stocks in the 0-25 m interval. Especially the standing stocks of four taxa reached greater than 20 radiolarians m^{-3} (*Stylochlamydidium venustum*, Spongodiscidae juvenile form, *Zygocircus productus* group, and *Spongotrochus glacialis*). Among them, *S. glacialis* and Spongodiscidae juvenile form were the most dominant species also in the 0-50 m intervals in our previous study. Spongodiscidae juvenile form represents juvenile specimens of *Spongotrochus glacialis* and *Stylochlamydidium venustum*. *Stylochlamydidium venustum* showed significant standing stock maxima in the 50-75 and 75-100 m intervals, and this taxon did not occur below 100 m. This species was a typical subsurface dweller (50-250 m) in our previous study. However, we showed that the maximum standing stock of this taxon was limited in the 50-100 m depth interval.

6. Summary

Vertical distribution of radiolarians was investigated by using VMPS with 63 μm mesh from the sea surface down to 3000 m depth, whose range was divided into fifteen layers, in June 2006 at Station OS06-SA in the central subarctic Pacific. High radiolarian standing stocks were found in the 0-250 m depth interval, with their maxima in the 75-100 m interval. The determined favorable water temperatures for radiolarian production are higher than approximately 4 °C, and DO contents higher than 1 $\text{m}\ell\ \ell^{-1}$ in the subarctic Pacific. These results are conformable with those of our previous study (Tanaka et. al., submitted). Based on the results of the cluster analysis, thirty-two radiolarian taxa are classified into six depth zonal groups; Group A: lower intermediate dwellers (500-1000 m), Group B: subsurface to upper intermediate dwellers (150-500 m), Group C: upper to lower deep dwellers (1000-3000 m), Group D: lower deep dwellers (2000-3000 m), Group E: subsurface dwellers (75-150 m); and Group F: surface dwellers (0-250 m). Because that we thoroughly investigated with the finely divided four new intervals (50-75, 75-100, 100-150, and 150-250 m) in the present work, in stead of employing one former 50-250 m interval applied in our previous study, we were able to characterize the detailed dwelling maximum zones of the important subsurface species.

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9. PLATES

- Plate 1.** All scale bars equal 50 μ m. **1.** *Actinomma leptoderma* (Jørgensen), Live. **2.** *Actinomma* sp. A, Live. **3.** *Actinomma* sp. B, Live. **4.** *Actinomma* sp. C, Live. **5.** *Actinomma* sp. D, Live. **6.** *Actinomma delicatulum* (Dogiel and Reshetnyak), Live. **7-8.** *Dorydruppa bensoni* Takahashi, Live. **9.** ?*Didymocyrtis* spp., Live. **10.** *Larcopyle butschlii* Dreyer, Live. **11.** *Larcopyle butschlii* Dreyer, Dead. **12.** *Tholospira* sp. Haeckel, Live. **13.** *Druppatractus ostracion* Haeckel, Live. **14.** *Lithelius minor* Jørgensen, Live.
- Plate 2.** All scale bars equal 50 μ m. **1-2.** *Spongostrochus glacialis* Popofsky, Live. **3.** *Stylochlamydidium venustum* (Baily), Dead. **4.** *Stylatractus* spp., Live. **5-7.** *Spongodiscidae* juvenile form, Live. **8.** *Rhizoplegma boreale* (Cleve), Dead. **9.** *Sphaeropyle langii* Dreyer, Live. **10.** *Spongopyle osculosa* Dreyer, Live. **11.** *Stylodictya aculeate* Jørgensen, Dead. **12.** *Stylodictya validispina* Jørgensen, Dead. **13.** *Spongurus pylomaticus* Riedel, Live. **14.** *Spongurus pylomaticus* Riedel, Dead.
- Plate 3.** All scale bars equal 50 μ m. **1.** *Larcopyle butschlii* Dreyer, Live. **2.** *Lithelius nautiloides* Popofsky, Dead. **3.** *Spongurus* sp., Dead. **4.** *Polysolenia arkios* Haeckel, Live. **5.** *Ceratospyris borealis* Baily, Dead. **6.** *Ceratospyris borealis* Baily, Live. **7-8.** *Cycladophora davisiana* Ehrenberg, Live. **9.** *Cycladophora bicornis* (Popofsky), Live. **10-11.** *Cycladophora cornutoides* Petrushevskaya, Live. **12.** *Conarachnium* sp., Dead. **13.** *Pterocyrtidium dogieli* Petrushevskaya, Live. **14.** *Lamprocyrtis nigrinae* (Caulet), Dead. **15.** *Pterocanium korotnevi* (Dogiel and Reshetnyak), Live. **16-17.** *Pterocanium korotnevi* (Dogiel and Reshetnyak), Dead. **18.** *Peripyraxis circumtexta* Haeckel, Live.
- Plate 4.** All scale bars equal 50 μ m. **1.** ?*Pseudodictyophimus* sp., Dead. **2.** *Conarachnium* sp., Dead. **3.** *Peridium longispina* Jørgensen, Dead. **4.** *Lithomelissa* spp., Dead. **5.** *Cornutella profunda* Ehrenberg, Live. **6.** *Peridium* spp., Live. **7.** *Lophospyris pentagona* Haeckel, Live. **8.** ?*Cornutella* sp., Dead. **9.** *Carpocanarium papillosum* (Ehrenberg), Live. **10.** *Spirocyrtis subscalaris* Nigrini, Dead. **11.** *Cyrtopera languncula* Haeckel, Live. **12.** *Botryostrobus aquilonaris* (Bailey), Live. **13.** *Botryostrobus auritus/australis* (Ehrenberg), Live. **14.** *Cyrtopera languncula* Haeckel, Live. **15.** *Calimitra solocicribrata* Takahashi, Dead.
- Plate 5.** All scale bars equal 50 μ m. **1.** ?*Dictyophimus* sp. **2-4.** *Dictyophimus* spp. **5-7.** *Dictyophimus hirundo* (Haeckel), Live. **8-9.** *Dictyophimus* sp., Live. **10-12.** *Lithalachnium tentorium* Haeckel, Live.
- Plate 6.** All scale bars equal 50 μ m. **1.** *Pseudodictyophimus glacilipes* (Baily), Live. **2.** *Peridium* spp., Dead. **3.** *Peridium* spp., Live. **4.** *Eucyrtidium hexagonalis* Haeckel, Dead. **5-6.** *Challengeron vicina* (Reshetnyak), Live. **7.** *Protocystis auriculata* Takahashi, Live. **8.** *Protocystis aduncicuspis* Takahashi, Live. **9.** *Porospathis holostoma* (Cleve), Live. **10.** *Borgertella caudate* (Wallich), Dead. **11-12.** *Lirella tortuosa* Takahashi, Live. **13-14.** *Euphysetta elegans* (Borgert), Live.

Plate 1

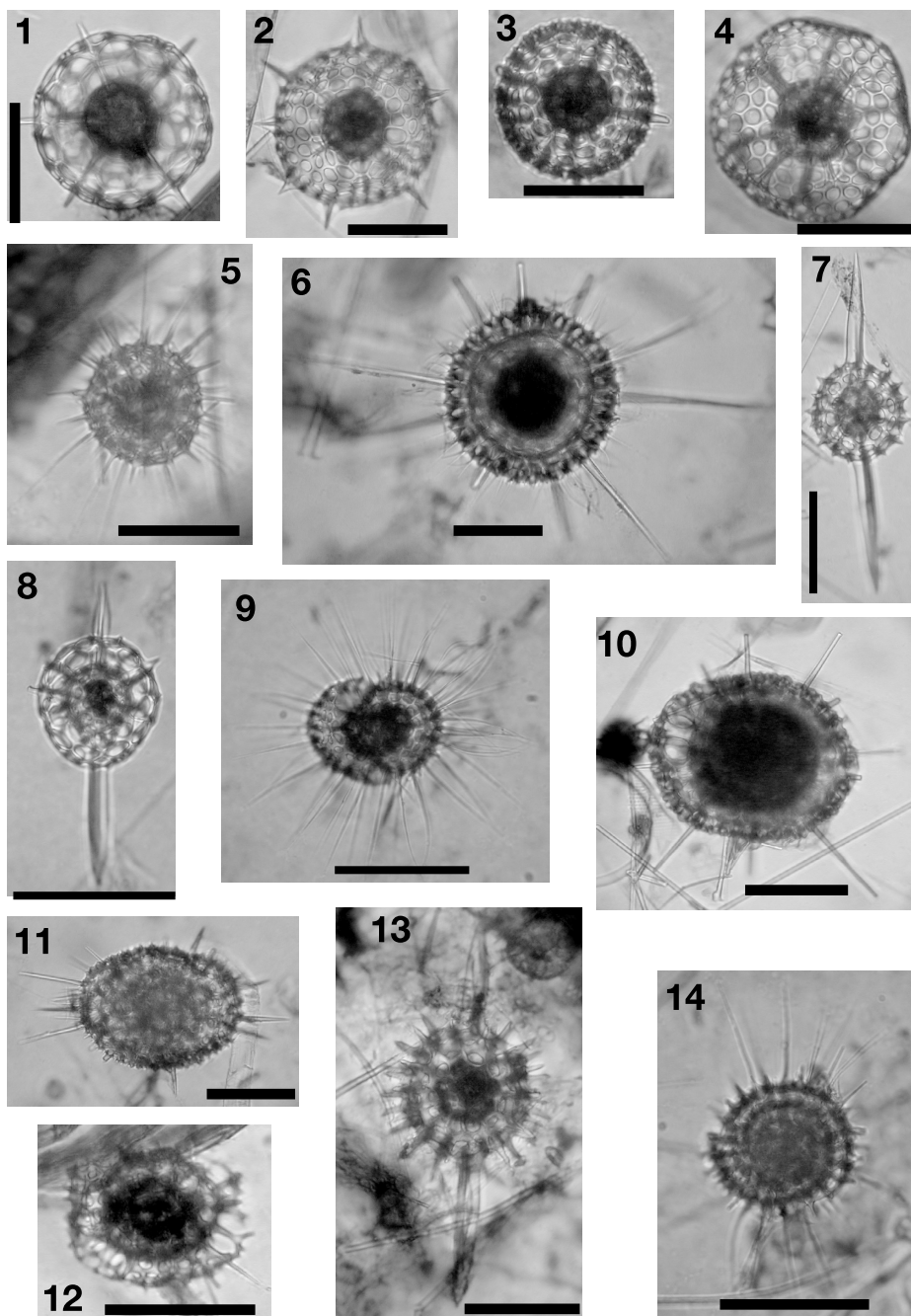


Plate 2

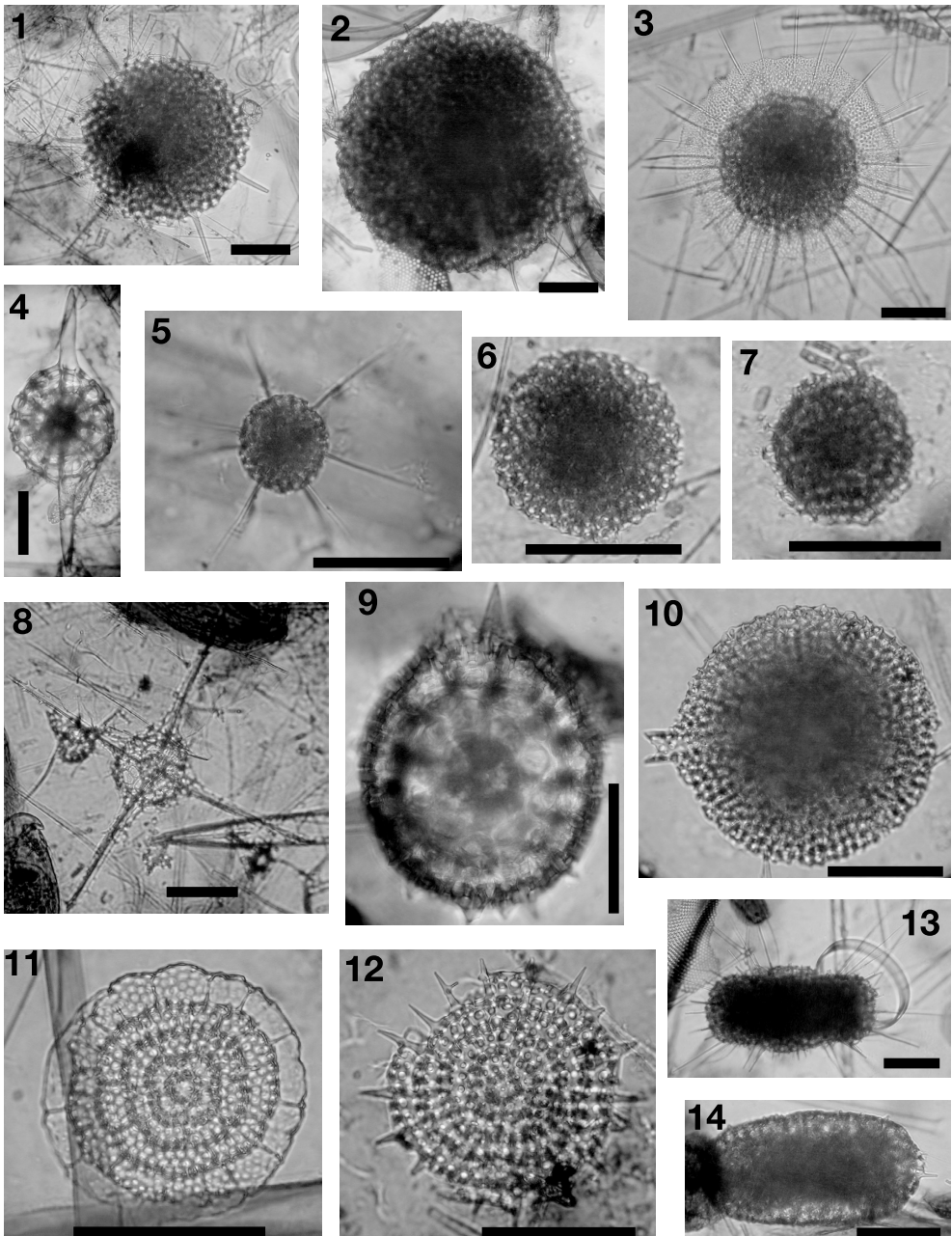


Plate 3

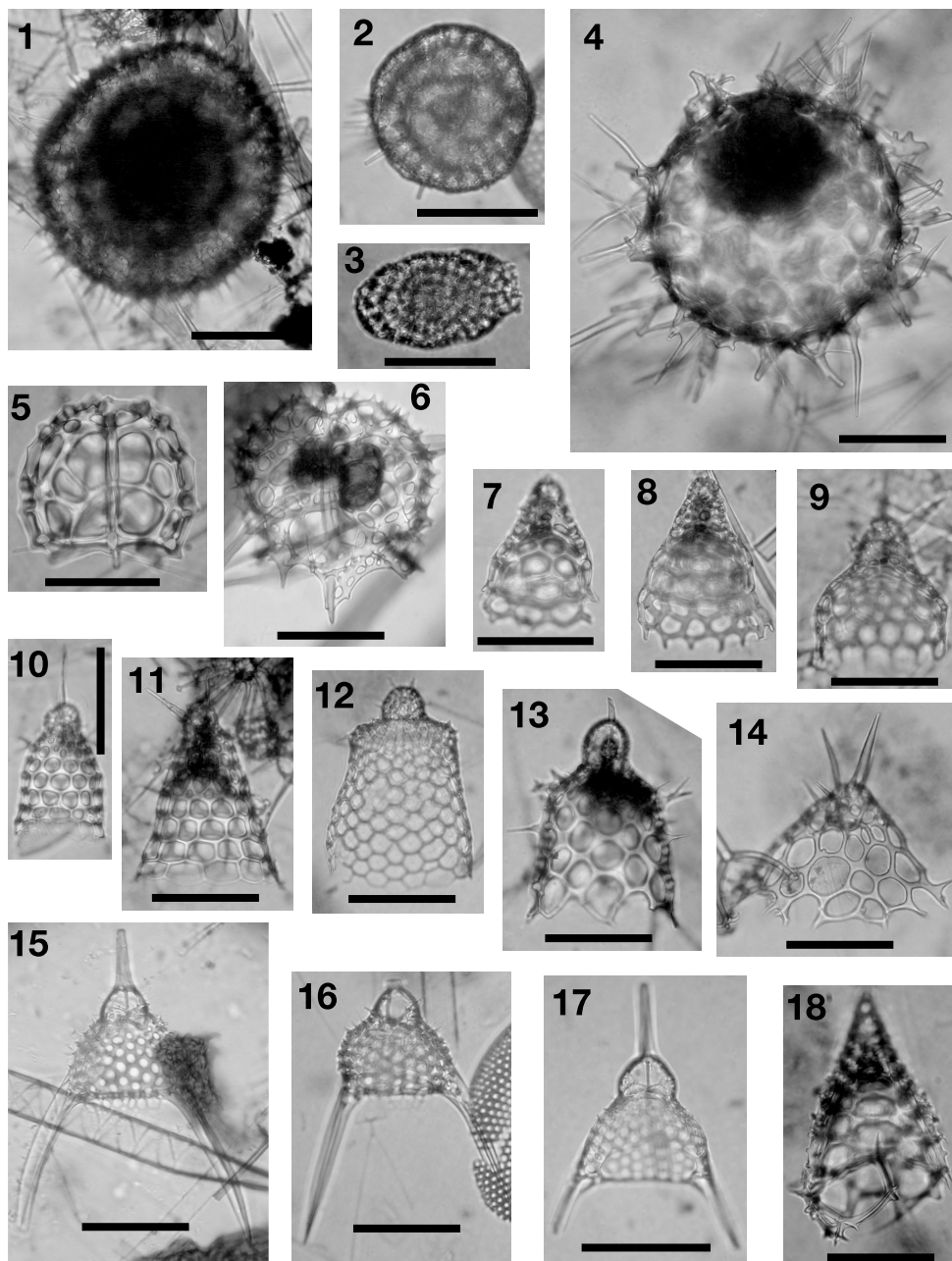


Plate 4

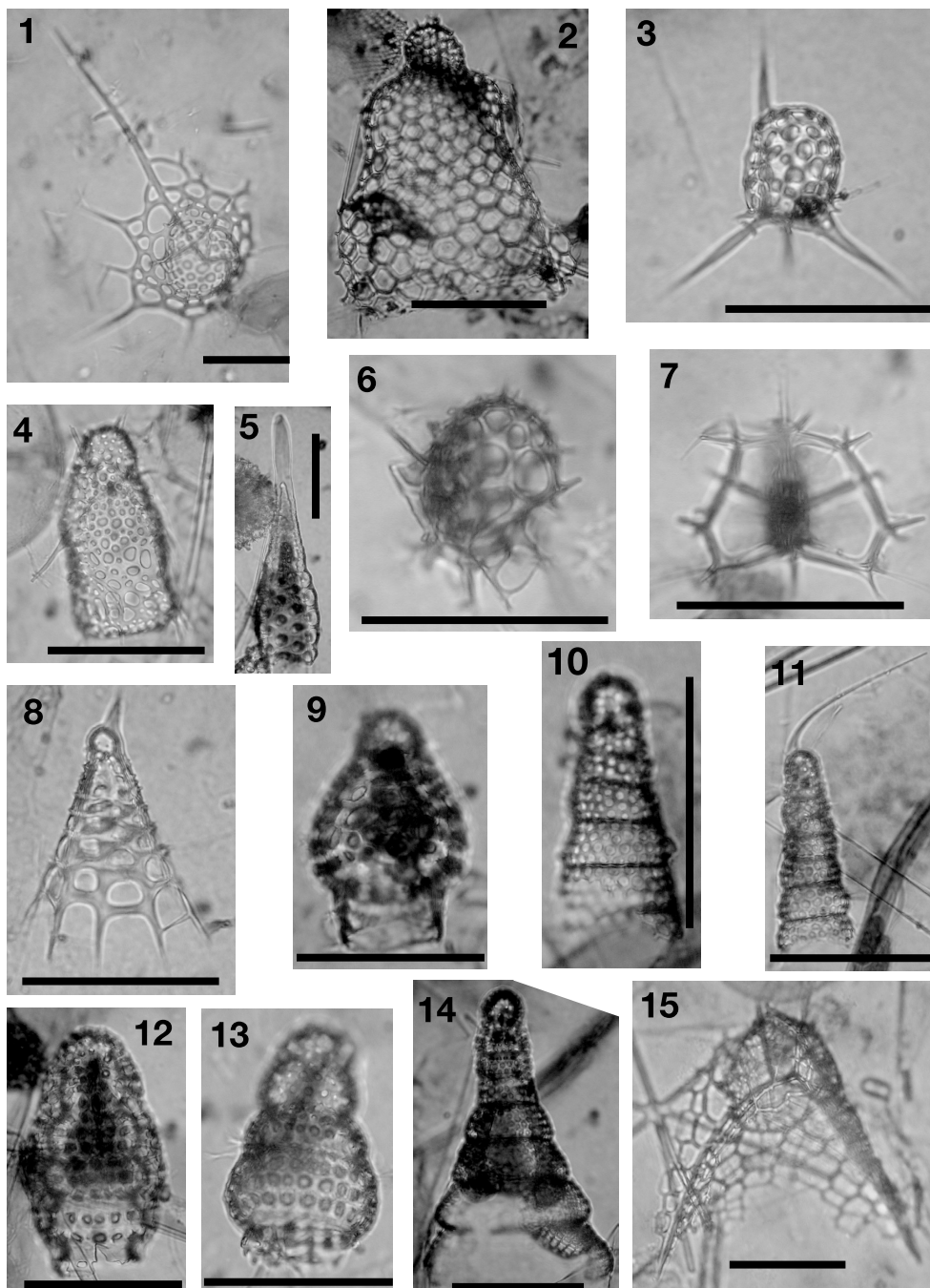


Plate 5

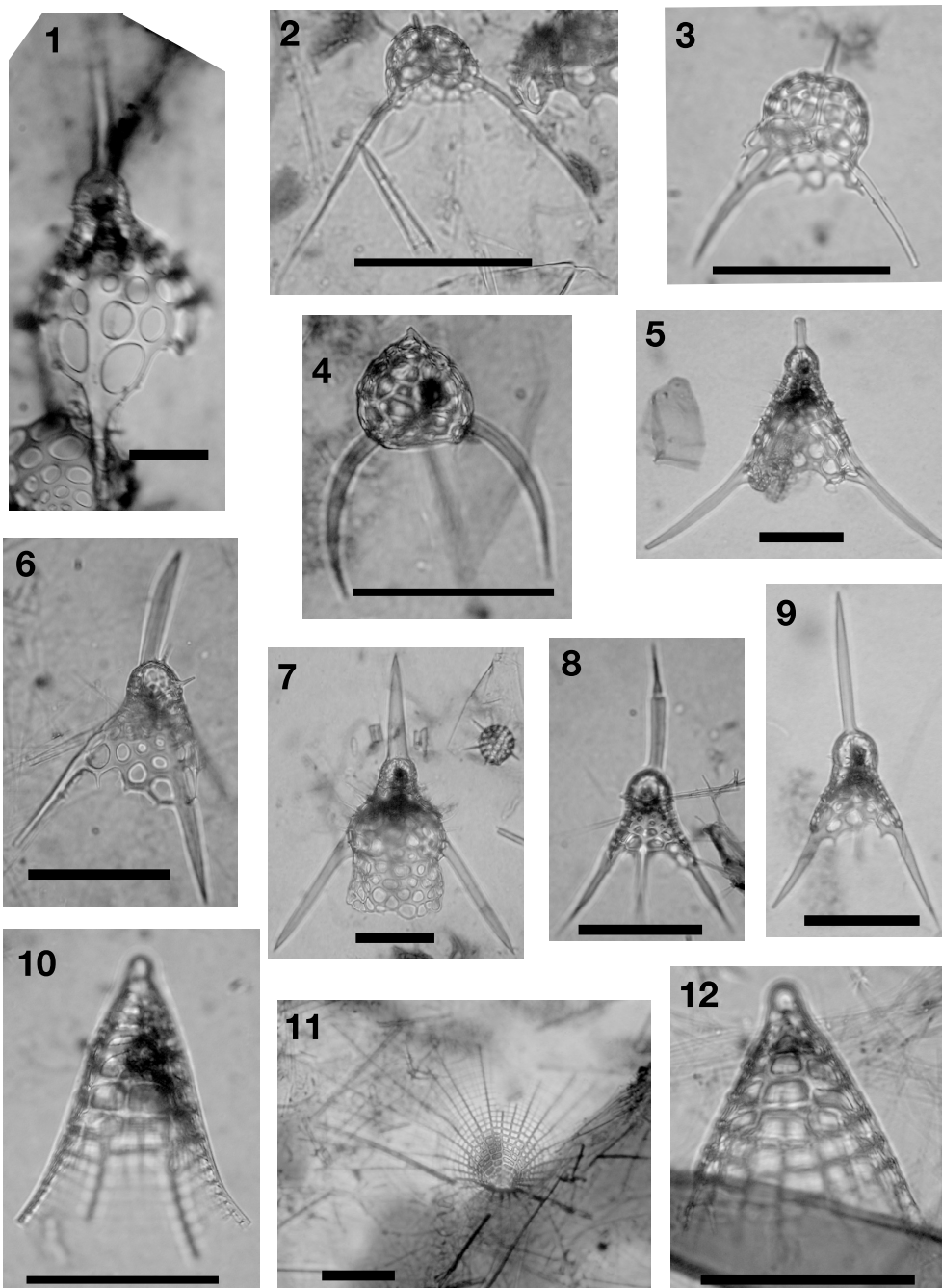


Plate 6

