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Polycystine radiolarians vertical distribution in the subtropical Northwest Pacific during Spring 2015 (KS15-4)

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Abstract.

Polycystine radiolarian remains were collected during Expedition KS15-4 in plankton tow sample from 0 to 3000 m of water depth at station (Sta.) 1 (30°28.8537N; 132°24.9532E). Obtained data from this site provide precious information about radiolarian assemblages living at deep-water depth. Based on R-mode cluster analysis, the surface water is characterized by well-known subtropical species such as *Tetrapyle circularis/fruticosa* group and *Didymocyrtis tetrathalamus*. The subsurface water depths (200–500 m) are characterized by species such as *Siphonosphaera abyssi*. The intermediate-water depths (500–1000 m) are characterized by relatively high abundances of *Larcopyle weddellium* and *Actinomma boreale*, while species such as *Cycladophora davisiana* inhabits mainly water depths below 2000 m

and *Carpocanarium papillosum* group inhabits the deep-water depths between 1000 and 2000 m.

Keywords: Living radiolarians, Subtropical Northwest Pacific, vertical distributions

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Introduction

Polycystine radiolarians are marine Protista bearing opaline skeletons. They are widely distributed in the World Ocean and inhabit shallow to deep-water depths (e.g. Suzuki and Aita, 2011; Suzuki and Not, 2015). Numerous studies have clarified the geographic distribution of radiolarian species in the North Pacific in order to promote their suitability as paleoceanographic proxies (e.g. Boltovskoy *et al.*, 2010; Kamikuri *et al.*, 2008; Lombardi and Boden, 1985; Matsuzaki and Itaki, 2017; Motoyama and Nishimura, 2005; Motoyama *et al.*, 2016). The distributions of radiolarians in the water column have been also investigated in numerous areas of the North Pacific: the Japan Island surrounding seas (e.g. Itaki *et al.*, 2010; Matsuzaki *et al.*, 2016); northern Japan Sea (Itaki, 2003); Sea of Okhotsk (Nimmergut and Abelmann, 2002; Okazaki *et al.*, 2004); Northwestern Pacific Oyashio area (Okazaki *et al.*, 2004); Subarctic North Pacific near Bering Sea (Tanaka and Takahashi, 2008), Central North Pacific (Renz, 1976; Kling, 1979) and the western and central Equatorial Pacific (Yamashita *et al.*, 2002). Therefore, the vertical distribution of radiolarians in the North Pacific is well understood and commonly used for biostratigraphic and paleoceanographic studies in the North Pacific (e.g. Kamikuri and Moore, 2017; Kamikuri *et al.*, 2017, 2019; Matsuzaki *et al.*, 2015a, 2018). As an example, shallow waters of the subtropical area of the North Pacific are characterized by warm-saline conditions, and their radiolarian assemblages are dominated by species such as *Didymocyrtis tetrathalamus* (Haeckel), *Dictyocoryne profunda* Ehrenberg and *Tetrapyle circularis/fruticosa* group (see taxonomic remark). On the other hand, subarctic species such as *Cycladophora davisiana* (Ehrenberg) and *Larcopyle weddellium* (Lazarus, Faust and Popova-Goll) are abundant at intermediate water depth because these waters are cold and less saline (Matsuzaki *et al.*, 2016). Lastly, species such as *Carpocanistrum papillosum* (Ehrenberg) and *Cornutella profunda* Ehrenberg are thought to be exclusively related to deep-water of the North Pacific (>500 m) (Takahashi, 1991), although there is a

lack of plankton studies aiming to clarify the occurrence of radiolarian species assemblages at deep-water depths. This is an important concern, which has so far hampered the reconstruction of ecological conditions in past deep-water. To resolve such issue, in this report we document radiolarian assemblage changes in shallow to deep-water depths based on plankton tow samples collected from 0 to 3000 m water depths in the Kyushu-Palau Ridge area, an area directly under the influence of the Kuroshio Current and the North Pacific Subtropical Mode Water in the Northwest Pacific.

Oceanographic setting

The low-mid latitudes of the Northwestern Pacific are strongly influenced by the Kuroshio Current (KC), which carries warm-oligotrophic water from the tropics to the higher latitudes (Tomczak and Godfrey, 1994) (Figure 1). Based on the World Ocean Atlas 2013 of Locarnini *et al.* (2013), the Sea Surface Temperatures (SSTs) in the tropics reach maximum values between 27 and 30°C during summer. The mid to high latitudes of the Northwest Pacific are influenced by the Oyashio Current, which is circulating counterclockwise (Tomczak and Godfrey, 1994) (Figure 1). This Current transports cold water and causes drops in SSTs (between 20 and 25°C in summer based on Locarnini *et al.* (2013)). The sub-surface of this area (about 200 m water depth) is characterized by the North Pacific Subtropical Mode Water (Masuzawa, 1969). In the Northwest Pacific, the Mode Water is originated by the Kuroshio Extension and is characterized by temperature ranges between 16 to 18°C, and the salinity is 34.8‰ at the core (Hanawa and Talley, 2001). In East China Sea, the Mode Water is likely located at 50–200 m water depth (Matsuzaki *et al.*, 2016). The northwestern Pacific is also known as being influenced by the North Pacific Intermediate Water (NPIW), which is characterized by low salinity (33.9–34.16‰) and low oxygen concentrations (50–150 µmol

kg⁻¹) (e.g. Bostock *et al.*, 2010, Kaneko *et al.*, 2001). In the low to mid latitude of the Northwest Pacific, the NPIW is recorded at water depths between 300 and 800 m (e.g. Yasuda, 1997).

Material and methods

Plankton samples were obtained from the Kyushu-Palau Ridge at mid latitudes in the Northwest Pacific. In late May 2015 at Sta. 1, (30°28.8537N; 132°24.9532E), vertical tows were carried out with a closing net having a 63 µm mesh using a Vertical Multiple-opening Plankton Sampler (VMPS). At Sta. 1, Samples from 0–50 m, 50–200 m, 200–500 m, 500–1000 m, 1000–2000 m and 2000–3000 m were collected. The filtered volume of sea-water was initially measured using a flow meter, however, the flowmeter could not work properly during the survey. Therefore, in this study we could not convert the obtained radiolarian data into standing stocks and thus we just show relative abundances of each species at the sampled water depths. We have followed the method used in Itaki (2003) and Matsuzaki *et al.* (2016) for the treatment of the collected samples. All collected materials were preserved in 100% ethanol during the survey. At the National Institute of Advanced Industrial Science and Technology (AIST), the samples were stained with Rose Bengal solution for later identification of living and dead specimens. The sample processing involved the use of a sieve with meshes larger than 1 mm, in order to exclude the large-sized zooplankton. Then the material was washed again using a 45 µm mesh-size sieve for radiolarian analysis. The residual materials (45 µm–1 mm) were divided into equal parts using a plankton splitter, providing aliquots of 1/4 and 1/8 of the original volume of the plankton samples. These aliquots were mounted onto a glass slide with Canada balsam, and covered with a 24×36 mm cover glass. All radiolarians on slides were identified with a light microscope Nikon Eclipse at the University of Tokyo, Graduate School of Science and we followed the nomenclature of

Matsuzaki *et al.* (2015b) and Zhang and Suzuki (2017). Only well preserved specimens with more than 50% of their skeletons present were counted as an entire specimen (i.e. fragments were not considered in the counting). Only specimens with protoplasm clearly stained with Rose Bengal were considered as living. Counts of radiolarians were converted to percentage (%) and as mentioned above standing stocks (number of radiolarians in m^{-3} of filtered sea water) could not be estimated because the flowmeter did not work properly. Temperatures and salinity could be however measured from 0 to 3000 m of water depths using a CTD profilers set on the VMPS during the survey.

In order to have a better understanding of how radiolarian assemblages change with water depths, temperature and salinity we have performed a R-mode cluster analysis on a sub dataset composed of species having a relative abundance higher than 2% at one water depth at least. Before the run of the R-mode cluster analysis, the data have been log transformed to normalize the dataset ($N_{xa}=\log(x_a+1)$), where N is the log normalized percentage and x is the relative abundance of the corresponding species at water depth a . R-mode cluster analysis has been performed using the PAST software version 2.17 of Hammer *et al.* (2001). We used a Wards-method clustering algorithm and a Euclidean distance, the number of boots is $N=10$.

Results and discussion

At Sta.1, we have identified 133 distinct polycystine radiolarian species and/or species groups (see Table 1). We thus identified 63 Nassellarians, 63 Spumellarians and 8 Collodarians. These species are illustrated from Figure 2 to Figure 7.

Deep-water assemblages (Cluster A: 2000–3000 m)

This cluster is composed of *Cycladophora davisiana* (Ehrenberg), *Arachnocorallium calvata* Haeckel, *Pseudodictyophimus gracilipes* (Bailey), *Actinomma leptodermum* (Jørgensen) and *Lithelius minor* Jørgensen group (Figure 8). The species belonging to this cluster inhabit the water depth between 200 and 3000 m (Figure 9). However, a maximum in the relative abundance (80%) of cluster A species is observed between 2000 and 3000 m water depth (Figure 9). Thus, we assume that species belonging to this cluster are representative of the deep-water depths between 2000 and 3000 m in the subtropical Northwest Pacific, with possibly a secondary sub-surface peak between 200 and 500 m water depth. Comparison with temperatures and salinity profiles obtained during the survey showed that except for the water depths between 200 and 500 m, the relative abundances of species belonging to cluster A tend to increase with a decreasing temperature, while salinity likely does not influence the vertical distribution of cluster A species at our site (Figure 9). This can be easily explained by the fact that *C. davisiana* is the principal component of this cluster with relative abundance between 26 and 52% (Figure 10).

Cycladophora davisiana dominates the radiolarian assemblage of the Sea of Okhotsk and is known to be an indicator of the Okhotsk Sea Intermediate water (OSIW), a water mass which is cold and oxygen rich (e.g. Abelman and Nimmergut, 2005; Hays and Morley, 2004; Itaki and Ikehara, 2004; Matul, 2011; Okazaki *et al.*, 2003, 2004). In the North Pacific, *C. davisiana* is also abundant in the freshly formed NPIW around the northern Japan Oyashio area because the OSIW directly influences the formation of NPIW in this area (e.g. Abelman and Nimmergut, 2005; Itaki and Ikehara, 2004; Matul, 2011; Matsuzaki and Itaki, 2017; Matsuzaki *et al.*, 2014; Okazaki *et al.*, 2003; Yasuda, 1997, 2004). In other areas of the North Pacific, although still *C. davisiana* inhabits the water depth corresponding to the NPIW (Matsuzaki *et al.*, 2014), our data show for the first time that in subtropical areas, *C. davisiana* inhabits water depths below 1000 m and dominates the radiolarian assemblage at

water depths between 2000 and 3000 m, where the temperature is about 3–4°C (Figure 10). In the subtropical Pacific, the NPIW is characterized by a salinity between 33.9 and 34.16‰ and oxygen concentrations between 50 and 150 $\mu\text{mol kg}^{-1}$ (e.g. Kaneko *et al.*, 2001; Bostock *et al.*, 2010). In this survey, although we did not measure dissolved oxygen concentration, based on the salinity profiles obtained during the survey, it is likely that at our site the water depth between 500–1000 m corresponds to the NPIW because salinity is about 34.1‰ (Figure 10). At these water depths, although *C. davisiana* is present, its abundances are much lower than those recorded from water depths below 1000 m. Therefore, our data demonstrate that in the Subtropical area of the North Pacific, *C. davisiana* is likely not a marker of NPIW. Instead, it seems that the principal factor controlling *C. davisiana* spatial distribution is likely temperature because the maximum of *C. davisiana* is recorded at water depths between 2000 and 3000 m and the temperature at those depths is about 3–4°C. This temperature roughly corresponds to the temperature of the freshly-formed NPIW and the OSIW, where *C. davisiana* is abundant (Abelmann and Nimmergut, 2005; Itaki and Ikehara, 2004; Matul, 2011; Matsuzaki and Itaki, 2017; Matsuzaki *et al.*, 2014; Okazaki *et al.*, 2003; Talley, 1993; Yasuda, 1997, 2004).

Intermediate to deep-water assemblages (Cluster B: 1000–2000 m)

Cluster B is composed of *Arachnocorallium* spp., *Carpocanistrum diadema* Haeckel, *Periphyramis murrayana* (Haeckel), *Carpocanistrum papillosum* (Ehrenberg) group, *Cornutella profunda* Ehrenberg group, *Lithelius* spp., *Clathrocanium* spp., *Lithocampana jorgenseni* Popofsky s.l. and *Stylosphaera pyriformis* (Bailey) (Figure 8). Species belonging to this cluster inhabit the water depth between 500 and 3000 m (Figure 9). However, a maximum of 30% is recorded between 1000 and 2000 m water depth. Among the species

listed above, *Clathrocanium coarctatum* Ehrenberg (included in *Clathrocanium* spp. during the R-mode cluster analysis), *C. papillosum* and *C. profunda* are the most representative species of this cluster and thus we assume that these species are likely markers of water depths between 1000 and 2000 m in the subtropical Northwest Pacific (Figure 10).

In the North Pacific, the spatial distribution of *Clathrocanium coarctatum*, *Carpocanistrum papillosum* and *Cornutella profunda* is still poorly understood because of a lack of plankton studies including samples collected from the deep-water depths. Most of the records of these species were obtained from analysis of surface sediments, thus it was not possible to assign a water depth to these species (Kling, 1979; Motoyama and Nishimura, 2005; Nishimura and Yamauchi, 1984; Kamikuri *et al.*, 2008; Matsuzaki and Itaki, 2017). In this study we could assign for the first time a tentative water depth to these species, which is likely between 1000 and 2000 m (Figure 10). Comparisons with temperature and salinity profiles do not show any plausible linkage between the species belonging to this cluster and neither temperature, nor salinity (Figure 9). Therefore, a parameter other than temperature and salinity might control the distribution of these species. Based on measurements taken during oceanographic surveys conducted in the North Pacific between latitude 25° and 40° (excluding the Japan Sea), the water depth between ca. 900 and 2000 m is characterized by a minimum in the concentration of dissolved oxygen, which implies that this water depth range is poorer in oxygen (e.g. Gamo *et al.*, 2014; Ozawa *et al.*, 2007). Therefore, considering the specific vertical distribution of *C. coarctatum*, *C. papillosum* and *C. profunda* it is likely that these species are related to oxygen poorer intermediate to deep-water in the mid latitude Northwest Pacific. In particular, *C. papillosum* is likely restricted to the water depths between 1000 and 2000 m, which correspond to the oxygen poorer water masses. Therefore, based on our data and on the findings reported by other studies it is likely that *C. papillosum* is related to oxygen-poor water masses at intermediate to deep-water depth.

Intermediate water assemblage (Cluster C: 500–1000 m)

This cluster is composed of *Archiperidium* cf. *triclavigera* (Tan and Tchang), *Larcopyle weddellium* Lazarus, Faust and Popova-Goll, *Dictyophimus crisiae* Ehrenberg, *Siphonosphaera socialis* Haeckel, *Flustrella* spp. and *Spongopyle osculosa* Dreyer (Figure 8). Species of this group inhabits water depths between 500 and 2000 m and a maximum of 24% is recorded at water depths between 500 and 1000 m (Figure 9), thus we assume that this assemblage is representative of these water depths in the subtropical Northwest Pacific.

These water depths correspond to the interval where we record a salinity minimum of 34.1‰ (Figure 9). Considering that in the subtropical Northwest Pacific the NPIW is defined by a salinity between 33.9 and 34.16‰ (e.g. Kaneko *et al.*, 2001; Bostock *et al.*, 2010), we assume that these water depths correspond to the NPIW in the subtropical Northwest Pacific. Thus, we infer that *Archiperidium triclavigera*, *Larcopyle weddellium*, *Dictyophimus crisiae*, *Siphonosphaera socialis* and *Spongopyle osculosa* are representative of the NPIW in the subtropical area. At this time, little is known about *Siphonosphaera socialis* and our data is the first clarifying its ecology in the North Pacific. However, previous studies have shown that *Larcopyle weddellium*, *Dictyophimus crisiae*, and *Spongopyle osculosa* are common in the subsurface water depth of the subarctic area of the North Pacific and in the Bering Sea (Kamikuri *et al.*, 2008; Kling and Boltovskoy, 1995; Matsuzaki and Itaki 2017; Okazaki *et al.*, 2004; Tanaka and Takahashi, 2008). These areas are characterized by relatively low temperature and salinity (e.g. Tomczak and Godfrey, 1994; Locarnini *et al.*, 2013). Considering that at our site, the species cited above are abundant at the water depth with the lowest salinity, it is likely that *Larcopyle weddellium*, *Dictyophimus crisiae*, and *Spongopyle osculosa* are more salinity, rather than temperature, dependent. The case of *A. triclavigera* is more complicated as this species is not reported from subarctic areas of the North Pacific

(Nishimura and Motoyama, 2005; Kamikuri *et al.*, 2008; Kling and Boltovskoy, 1995; Matsuzaki and Itaki 2017; Okazaki *et al.*, 2004; Tanaka and Takahashi, 2008). However, in the northern East China Sea this species occurred between 100 and 200 m water depth and these depths were characterized by relatively low and variable salinity (Matsuzaki *et al.*, 2016). Therefore, it is also likely that *A. triclavigera* is related to low salinity.

Subsurface water assemblage (Cluster D: 200–500 m)

This cluster is composed of *Eucyrtidium hexagonatum* Haeckel, *Hexacantium enthacanthum* Jørgensen, *Cycladophora bicornis* (Popofsky), *Litharacnium tentorium* Haeckel, *Flustrella orbiculata* (Haeckel), *Drupptractus irregularis* Popofsky, *Larcopyle* cf. *buetschlii* Dreyer, *Siphonosphaera abyssi* (Ehrenberg), *Spongodiscus* cf. *resurgens* Ehrenberg, *Thecosphaera multispinula* (Su) and *Thecosphaera bulbosa* Hollande and Enjument (Figure 8). Species belonging to this cluster inhabit water depth between 0 and 1000 m and a maximum of 40% is recorded between 200 and 500 m water depth and thus it is likely that species belonging to this group are characteristic of the subsurface and upper intermediate water depths of the subtropical North Pacific (Figure 9).

The temperature profile indicates that between 200 and 500 m water depth, the temperature is about 16 to 18°C (Figure 9). In the northwestern Pacific, it is known that a few hundred meters thick water mass characterized by a temperature range between 16 and 18°C is formed at subsurface depths by the cooling of the Kuroshio Extension eastward (Hanawa and Talley, 2001; Suga and Hanawa, 1990). This water mass is called the North Pacific Subtropical Mode Water (NPSTMW) (Masuzawa, 1969). Therefore, it is likely that the water depths between 200 and 500 m at our site correspond to the NPSTMW and cluster D is the assemblage characterizing the NPSTMW in the subtropical Northwest Pacific. However, in

the East China Sea previous studies suggested that the NPSTMW is located at about 100 to 200 m of water depth and the assemblages of radiolarians differed from those at our site (Matsuzaki *et al.*, 2016). Indeed, only *Druppatractus irregularis* and *Cycladophora bicornis* occurred at both locations. One of the plausible explanations is that in the northern East China Sea the local hydrography is likely altered by regional factors. Indeed, the northern East China Sea is known to be not only under the influence of the Kuroshio Current but also to be influenced by the nutrient-rich Taiwan Warm Current and freshwater discharge from the Yangtze River, whose hydrographic regime is largely influenced by the intensity of the East Asian summer monsoon (Chen *et al.*, 1994; Ichikawa and Beardsley, 2002; Sagawa *et al.*, 2018; Matsuzaki *et al.*, 2019; Tada *et al.*, 2016). Therefore, it would be wiser to consider as typical for NPSTMW conditions the assemblages obtained at Sta. 1, rather than those reported in the East China Sea, which have mixed influences. Matsuzaki *et al.* (2016) also highlighted this possibility.

Shallow water assemblage (Cluster E: 0–200 m)

This cluster is composed of *Lampromitra erosa* Cleve, *Peromelissa phalacra* Haeckel, *Theocorys turgidula* (Ehrenberg), *Botryocyrtilis scutum* (Harting), *Phortidium pylonium* Haeckel, *Zygocircus piscicaudatus* Popofsky, *Acanthodesmia vinculata* (Müller), *Pylodiscus triangularis* Haeckel, *Collosphaera tuberosa* Haeckel, *Spongosphaera streptacantha* Haeckel, *Lophophaena hispida* (Ehrenberg), *Lophophaena variabilis* (Popofsky), *Pterocorys sabae* (Ehrenberg), *Pterocanium praetextum praetextum* (Ehrenberg), *Spongaster tetras tetras* (Ehrenberg), *Dictyocoryne muelleri* (Haeckel), *Pterocorys zancleum* (Haeckel), *Didymocyrtilis tetrathalamus* (Haeckel) and *Tetrapyle circularis/fruticosa* group (Figure 8). The species belonging to cluster E inhabit water depths between 0 and 200 m and an abundance maximum of 76% is recorded between 0 and 50 m water depth. Therefore, we assume that the species

mentioned above are shallow water species in the subtropical North Pacific (Figure 9). The temperature profile shows highest values (25°C) at the surface, and thus it is likely that species belonging to this cluster are related to warm and shallow water depths.

In fact, previous studies already suggested that most species belonging to this cluster are related to warm and shallow water in the whole North Pacific, therefore this result is in agreement with previous studies (Ishitani and Takahashi, 2007; Kamikuri *et al.*, 2008; Matsuzaki *et al.*, 2016; Matsuzaki and Itaki, 2017; Motoyama and Nishimura, 2005; Okazaki *et al.*, 2008; Yamashita *et al.*, 2002). However, for the first time, we could clearly define the living depths of species such as *Theocorys turgidula*, *Botryocytis scutum* and *Pterocorys sabae*, which were recorded in a few surface sediment surveys of the subtropical area of the North Pacific, but whose living depth range remained unknown (e.g. Nishimura and Yamauchi, 1984; Matsuzaki and Itaki, 2017). In addition, recently Zhang *et al.* (2018) analysed symbiotic associations of modern radiolarians and most of the species belonging to this cluster likely harbor algal symbionts. Such as *Acanthodesmia vinculata*, *Botryocytis scutum*, *Lophophaena hispida*, *Pterocanium praetextum*, *Pterocorys clausus*, *Didymocyrtis tetrathalamus*, *Dictyocoryne muelleri*, *Phorticium pylonium*, *Spongospaera streptacantha* and *Tetrapyle circularis/fruticosa* group. This observation highlights how the fact that shallow-water radiolarians are closely related to ocean primary productivity and have the potential to be used as an index of biological productivity in warm oceanic regions such as the equatorial and subtropical areas.

Conclusion

We have investigated samples collected from the subtropical Northwest Pacific during the cruise KS15-4 onboard the R/V Shinsei-maru during spring 2015. Our observations

showed that shallow water radiolarian assemblages are similar to those recorded in other subtropical areas of the Northwest Pacific, while subsurface water assemblages differ from those recorded in other areas such as the East China Sea. This difference might be caused by regional factors such as the monsoon influence (This study, Matsuzaki *et al.*, 2016). For the first time we could clarify accurately living depth range of radiolarians inhabiting intermediate to deep-water depths: our data show that *Cycladophora davisiana* is clearly not inhabiting NPIW in the subtropical northwest Pacific, but much deeper water masses (2000–3000 m) whose temperatures are around 4°C and thus this species is not related to salinity minima but rather to low temperatures. In addition, we clearly showed that the species *Carpocanarium papillosum* exclusively inhabits the water depths between 1000 and 2000 m, which are characterized by lower dissolved oxygen content in the mid latitude Northwest Pacific (e.g. Gamo *et al.*, 2014; Ozawa *et al.*, 2007) and we thus infer that *C. papillosum* is related to oxygen poorer intermediate to deep-water.

Taxonomic remarks

Tetrapyle circularis/fruticosa group (Figure 5.2-5.4): According to Zhang and Suzuki (2017), *T. circularis* Haeckel, 1887 differ from *T. fruticosa* (Tan and Chen, 1990) by a straighter outline on both joint and by a more pronounced circular shape. However, except those two minor characteristics the taxonomic base of both species present similarities such as the presence of a pyloniid central combination, the presence of three to four roundish pores on the periphery of the girdle and absences of portal-spines (Zhang and Suzuki, 2017). In most studies, both species were usually grouped into *T. octacantha* Müller group because of their similarities (e.g. Itaki *et al.*, 2010; Matsuzaki *et al.*, 2015). However, as argued Zhang and Suzuki (2017), both species must be separated from *T. octacantha* Müller, 1859 because they

drastically differ from the latter by the absence of portal spines. Thus, considering the findings of Zhang and Suzuki (2017) and the taxonomic similarities between *T. circularis* Haeckel, 1887 and *T. fruticosa* (Tan and Chen, 1990), we proposed to group both species as *T. circularis/fruticosa* group in the context of this study. This grouping is suitable for paleoceanographic studies in the North Pacific as both species inhabited shallow water of the tropical to subtropical North Pacific (e.g. Matsuzaki *et al.*, 2016; Matsuzaki and Itaki, 2017).

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Captions

Table 1. Counts of the species at KS-15-4 Sta.1.

Figure 1. Location of the studied site in the Northwest Pacific KS15-4 Sta.1 (30°28.8537N; 132°24.9532E).

Figure 2.

1, *Polysolenia* cf. *lappacea* (Haeckel) (KS15-4-V2-2-300-200-1/4d); **2–4**, *Polysolenia lappacea* (Haeckel) (sample KS15-4-V3-2-3000-2000-1/4b); **5–6, 9**, *Disolenia* spp. (5, KS15-4-V2-2-300-200-1/4d; 6, sample KS15-4-V3-2-2000-1000-1/4d); **7, 8**, *Polysolenia spinosa* (Haeckel) (sample KS15-4-V3-2-3000-2000-1/4b); **10, 11**, *Siphonosphaera abyssii* (Ehrenberg) (sample KS15-4-V3-2-3000-2000-1/4b); **12**, *Collosphaera tuberosa* Haeckel (sample KS15-4-V3-3-50-0-1/4a).

Figure 3.

1, *Hexacontium pachydermum* Jørgensen (sample KS15-4-V3-2-2000-1000-1/4b); **2, 8**, *Hexacontium enthacanthum* Jørgensen (2, sample KS15-4-V3-2-2000-1000-1/4d; 8, sample KS15-4-V3-2-3000-2000-1/4b); **3**, *Thecosphaera multispinula* (Su) (sample KS15-4-V3-2-2000-1000-1/4b); **4**, *Hexacontium hostile* Cleve (sample KS15-4-V3-2-2000-1000-1/4b); **5**, *Thecosphaera inermis* (Haeckel) (sample KS15-4-V3-2-3000-2000-1/4b); **6, 7**, *Thecosphaera bulbosa* Hollande and Enjumet (sample KS15-4-V3-2-1000-500-1/4d); **9**, *Cladococcus* spp. (sample KS15-4-V3-2-2000-1000-1/4b); **10**, *Haliometta miocenica* (Campbell and Clark) (sample KS15-4-V3-2-2000-1000-1/4d); **11**, *Actinomma boreale* Cleve (sample KS15-4-V3-2-2000-1000-1/4d); **12**, *Actinomma leptodermum* (Jørgensen) (sample KS15-4-V3-2-3000-2000-1/4b).

Figure 4.

1, *Spongaster tetras tetras* Ehrenberg (sample KS15-4-V3-2-2000-1000-1/4b); **2**, *Spongopyle osculosa* Dreyer (sample KS15-4-V3-2-1000-500-1/4d); **3, 4**, *Dictyocoryne muelleri* (Haeckel) (3, sample

KS15-4-V2-2-300-200-1/4d; 4, sample KS15-4-V3-2-3000-2000-1/4b); **5**, *Spongurus cylindricus* Haeckel (sample KS15-4-V3-2-2000-1000-1/4b); **6, 7**, *Spongodiscus* cf. *resurgens* Ehrenberg (sample KS15-4-V3-2-3000-2000-1/4b); **8**, *Spongosphaera streptacantha* Haeckel (sample KS15-4-V3-2-2000-1000-1/4d); **9**, *Flustrella orbiculata* (Haeckel) (sample KS15-4-V2-2-300-200-1/4d); **10**, *Stylodictya* sp. (sample KS15-4-V3-2-3000-2000-1/4b); **11**, *Amphirhopalum* cf. *ypsilon* Haeckel, (sample KS15-4-V3-2-1000-500-1/4d); **12**, *Flustrella* cf. *perispira* Haeckel (sample KS15-4-V2-2-300-200-1/4d); **13, 14**, *Flustrella* spp. (sample KS15-4-V3-2-3000-2000-1/4b); **15**, *Stylochlamydidium asteriscus* Haeckel (sample KS15-4-V3-2-2000-1000-1/4b).

Figure 5.

1, *Phorticium pylonium* Haeckel (sample KS15-4-V2-2-300-200-1/4d); **2–4**, *Tetrapyle circularis/fruticosa* group (2-3, sample KS15-4-V2-2-300-200-1/4d; 4, sample KS15-4-V3-2-3000-2000-1/4b); **5, 6**, *Lithelius* cf. *hayesi* (Chen) (5, sample KS15-4-V3-2-1000-500-1/4d; 6, sample KS15-4-V3-2-2000-1000-1/4b); **7, 8**, *Larcopyle* cf. *buetschlii* Dreyer (sample KS15-4-V3-2-2000-1000-1/4b); **9–11**, *Didymocyrtis tetrathalamus* (Haeckel) (9, sample KS15-4-V3-2-1000-500-1/4d ; 10-11, sample KS15-4-V3-2-2000-1000-1/4d); **12**, *Lithelius* spp. (sample KS15-4-V3-2-1000-500-1/4d); **13, 15**, *Lithelius minor* Jørgensen group (sample KS15-4-V3-2-1000-500-1/4d); **14**, *Lithelius nautiloides* Popofsky (sample KS15-4-V2-2-300-200-1/4d); **16**, *Larcopyle weddellium* Lazarus, Faust and Popova-Goll (sample KS15-4-V3-2-2000-1000-1/4b); **17, 21**, *Stylosphaera pyriformis* (Bailey) (sample KS15-4-V3-2-2000-1000-1/4b); **18, 19**, *Drupptractus irregularis* Popofsky (sample KS15-4-V3-2-2000-1000-1/4b); **20**, *Amphisphaera* cf. *tanzhiyuani* Matsuzaki and Suzuki (sample KS15-4-V3-2-2000-1000-1/4b).

Figure 6.

1, 2, *Tricyclidium* spp. (1, sample KS15-4-V3-2-3000-2000-1/4b; 2, sample KS15-4-V3-2-2000-1000-1/4d); **3**, *Lithocircus* spp. (sample KS15-4-V3-3-50-0-1/4a); **4, 5**, *Dimelissa thoracites* (Haeckel) (4, sample KS15-4-V3-2-1000-500-1/4d; 5, sample KS15-4-V3-2-2000-1000-1/4b); **6–10**, *Arachnocorallium calvata* Haeckel group (6, KS15-4-V2-2-300-200-1/4d; 7-10, sample KS15-4-V3-

2-3000-2000-1/4b); **11**, *Pseudodictyophimus* sp. (sample KS15-4-V3-2-1000-500-1/4d); **12–13**, *Clathrocanium* spp. (sample KS15-4-V3-2-2000-1000-1/4b); **14**, *Pseudocubus obeliscus* Haeckel (sample KS15-4-V3-2-2000-1000-1/4b); **15, 16**, *Carpocanistrum diadema* Haeckel (sample KS15-4-V3-2-2000-1000-1/4b); **17–20**, *Carpocanistrum papillosum* (Ehrenberg) (17, 18, sample KS15-4-V3-2-2000-1000-1/4b; 19, sample KS15-4-V3-2-2000-1000-1/4d, 20, sample KS15-4-V3-2-1000-500-1/4d); **21, 22**, *Cornutella profunda* Ehrenberg group (sample KS15-4-V3-2-3000-2000-1/4b); **23**, *Peripyramis murrayana* (Haeckel) (sample KS15-4-V3-2-2000-1000-1/4b); **24**, *Pterocorys zancleum* (Haeckel) sensu lato (sample KS15-4-V3-3-50-0-1/4a); **25**, *Pterocorys sabae* (Ehrenberg) (sample KS15-4-V3-3-50-0-1/4a); **26**, *Pterocorys clausus* (Popofsky) sensu lato (sample KS15-4-V2-2-300-200-1/4d); **27**, *Pterocanium praetextum praetextum* (Ehrenberg) (sample KS15-4-V3-3-50-0-1/4a); **28**, *Pterocanium praetextum eucolpum* (Haeckel) (sample KS15-4-V3-3-50-0-1/4a).

Figure 7.

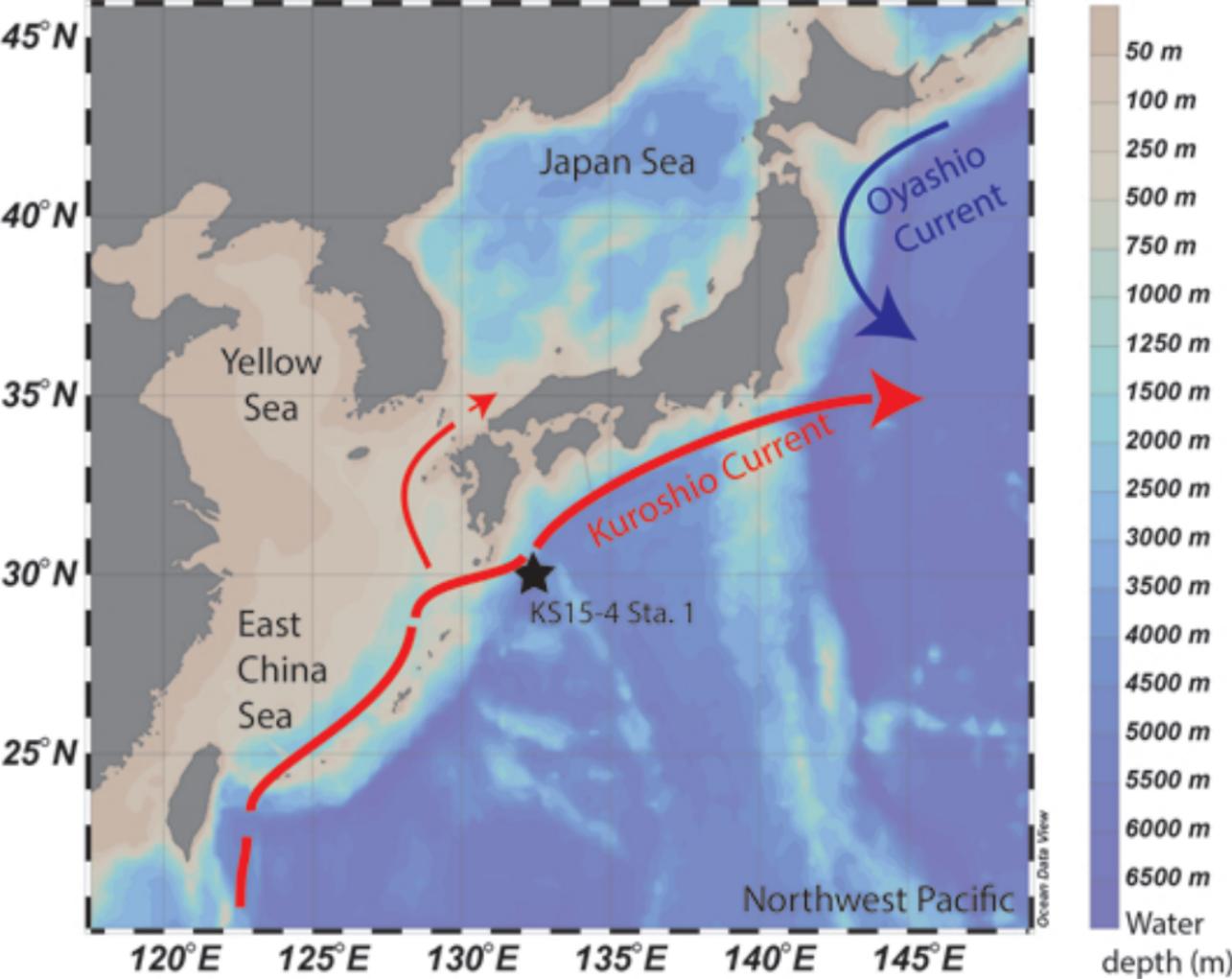
1, *Gondwanaria dogieli* (Petrushevskaya) (sample KS15-4-V3-2-2000-1000-1/4b); **2, 3**, *Cycladophora* cf. *davisiana* Ehrenberg (2, sample KS15-4-V3-2-2000-1000-1/4b; 3, sample KS15-4-V3-2-3000-2000-1/4b); **4–11**, *Cycladophora davisiana* Ehrenberg (4-7, 10, sample KS15-4-V3-2-2000-1000-1/4b; 8-9,11, sample KS15-4-V3-2-3000-2000-1/4b); **12**, *Spirocyrtis scalaris* Haeckel (sample KS15-4-V3-2-2000-1000-1/4b); **13, 14**, *Stichocorys seriata* (Jørgensen) (13, sample KS15-4-V3-2-2000-1000-1/4b; 14, sample KS15-4-V3-2-3000-2000-1/4b); **15–18**, *Eucyrtidium hexagonatum* Haeckel (15,17, sample KS15-4-V3-2-3000-2000-1/4b, 16, KS15-4-V2-2-300-200-1/4d; 18, sample KS15-4-V3-2-1000-500-1/4d); **19**, *Botryostrobos auritus* (Ehrenberg) group (sample KS15-4-V3-2-3000-2000-1/4b); **20**, *Cycladophora bicornis* (Popofsky) (sample KS15-4-V3-2-2000-1000-1/4b); **21**, *Lophophaena hispida* (Ehrenberg) (sample KS15-4-V3-3-50-0-1/4a); **22, 23**, *Artostrobos jorgenseni* Popofsky sensu lato (sample KS15-4-V3-2-2000-1000-1/4b); **24**, *Botryocyrtis scutum* (Harting) (sample KS15-4-V3-2-3000-2000-1/4b); **25, 26**, *Cannostrobos* spp. (sample KS15-4-V3-2-2000-1000-1/4b); **27**, *Acanthodesmia vinculata* (Müller) (sample KS15-4-V3-3-50-0-1/4a); **28**, *Zygocircus piscicaudatus* Popofsky (sample KS15-4-V3-2-2000-1000-1/4b); **29**, *Siphocampe arachnea* (Ehrenberg) sensu lato (sample KS15-4-V3-2-2000-1000-1/4b).

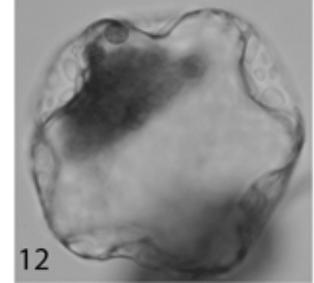
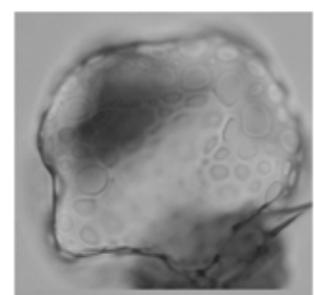
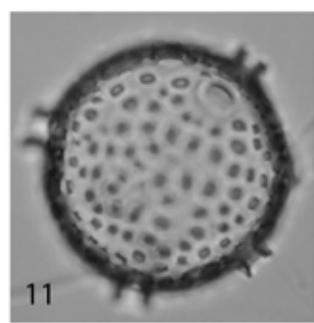
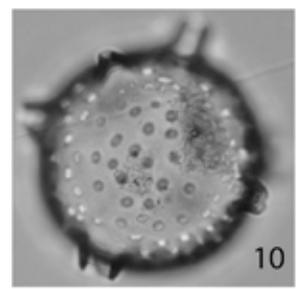
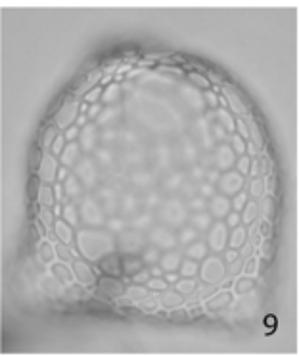
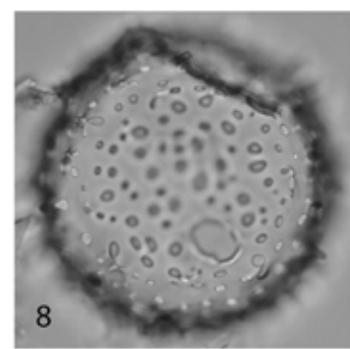
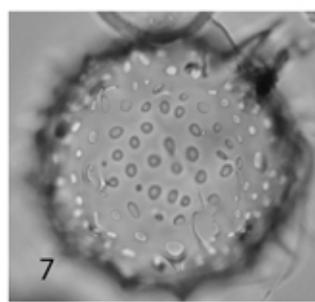
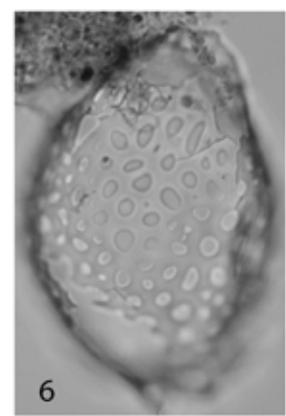
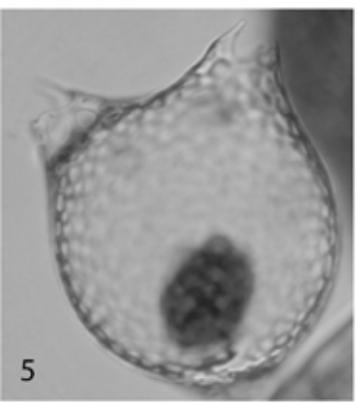
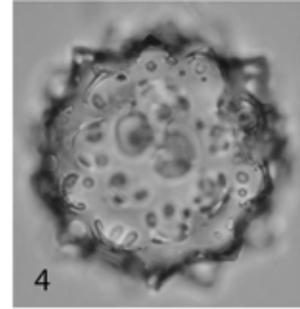
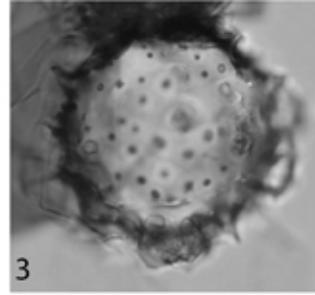
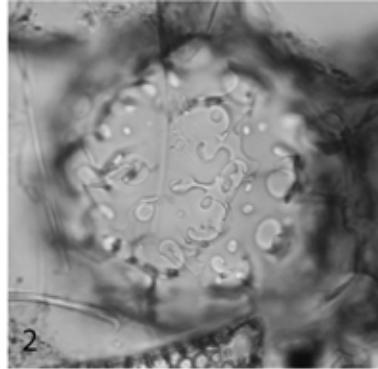
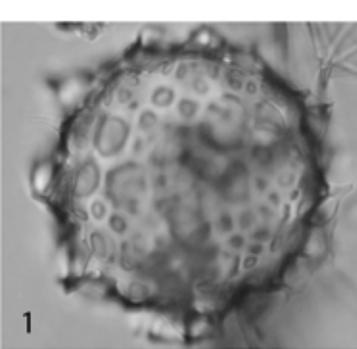
Figure 8. Results of the R-mode cluster analysis conducted on radiolarian assemblages obtained at Sta. 1 of KS15-4.

Figure 9. Vertical distribution of species clusters depending on temperature and salinity profile at Sta. 1 of KS15-4.

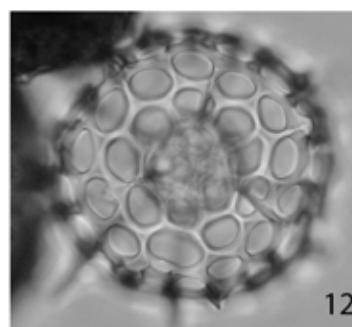
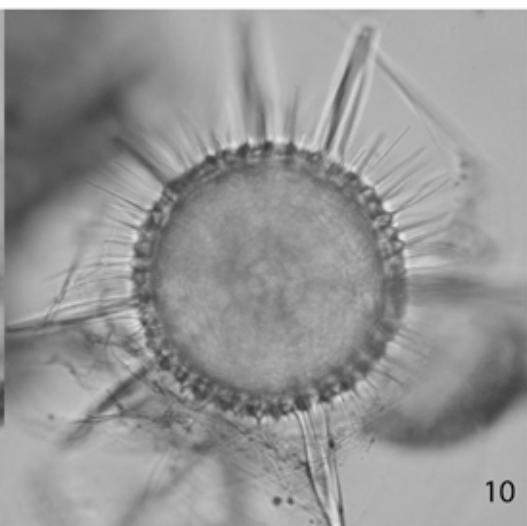
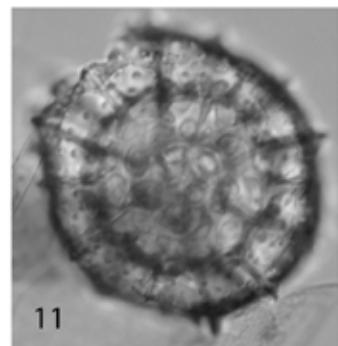
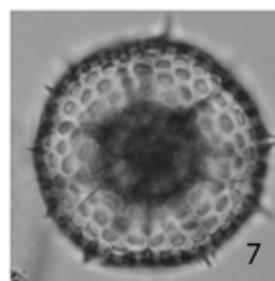
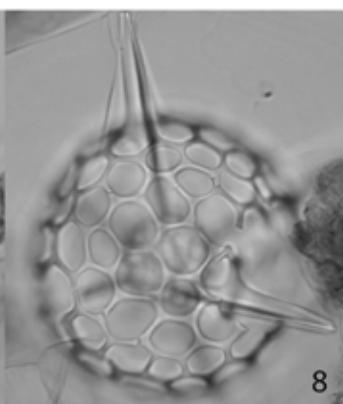
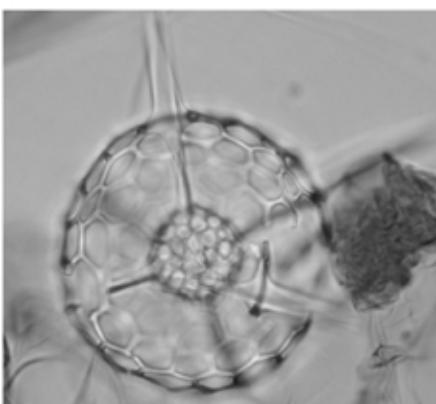
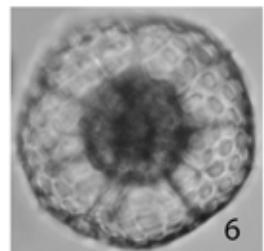
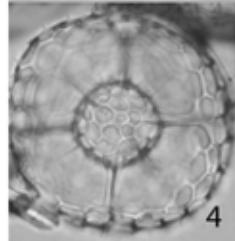
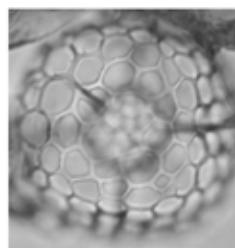
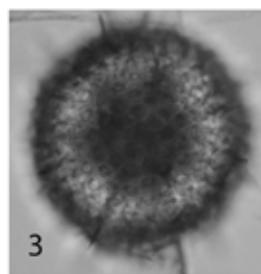
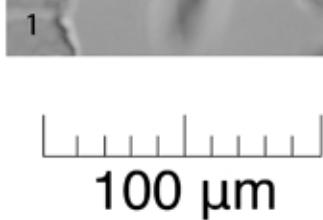
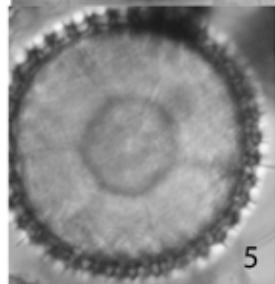
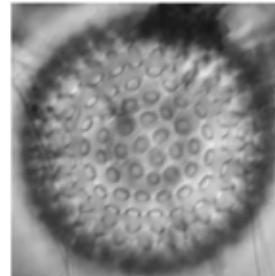
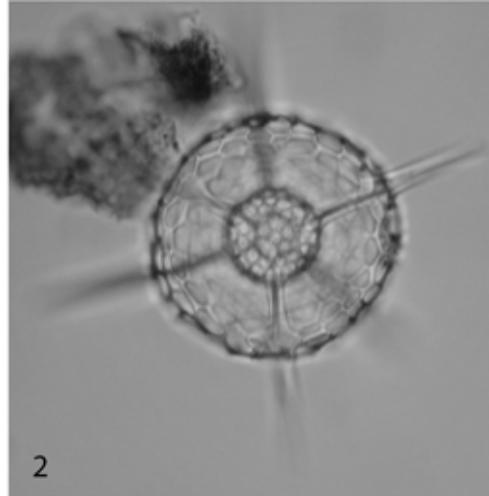
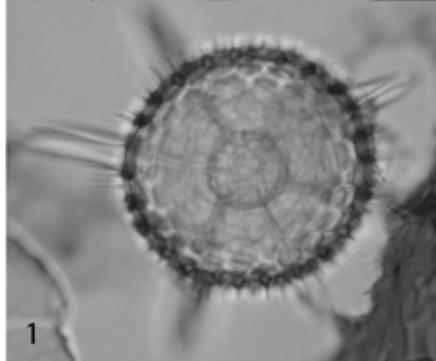
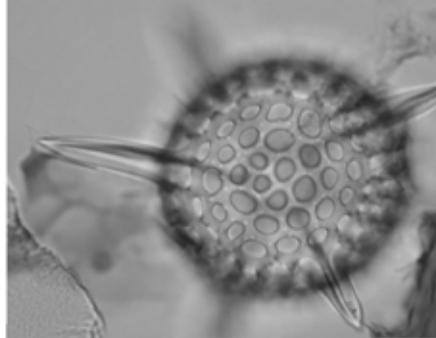
Figure 10. Key species vertical distribution profiles depending on temperatures and salinity.

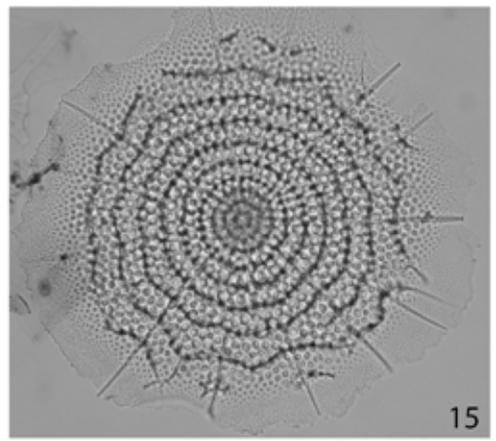
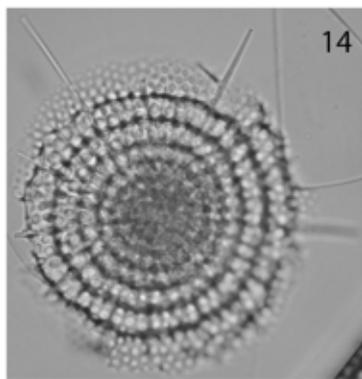
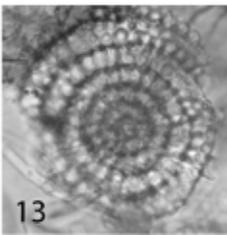
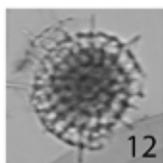
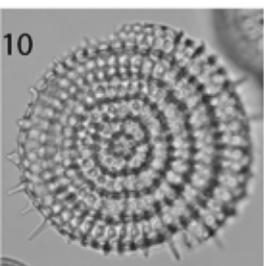
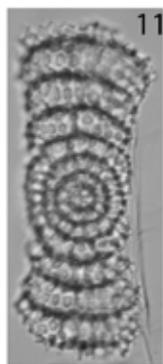
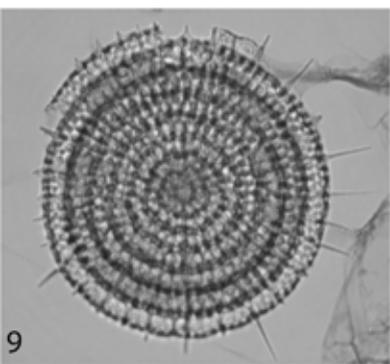
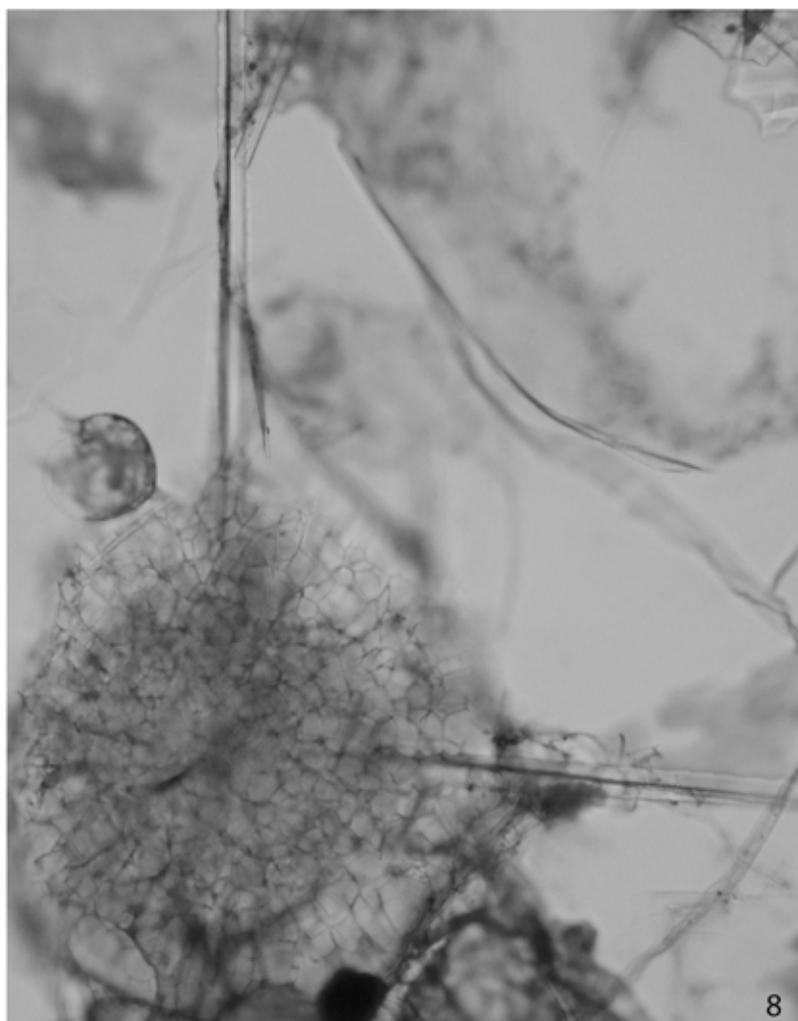
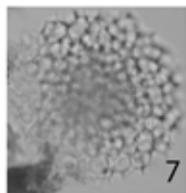
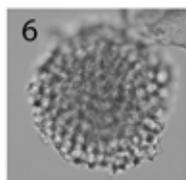
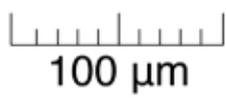
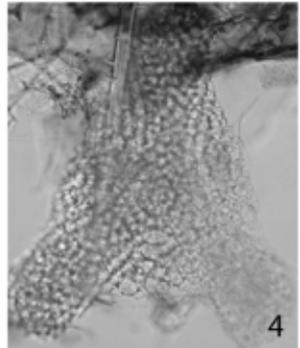
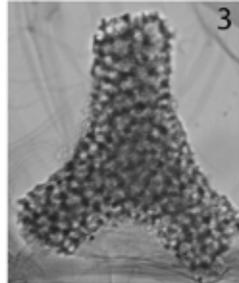
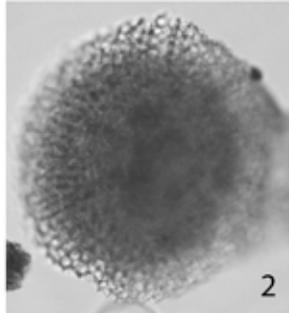
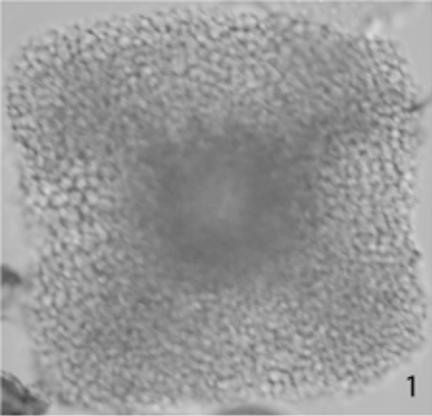
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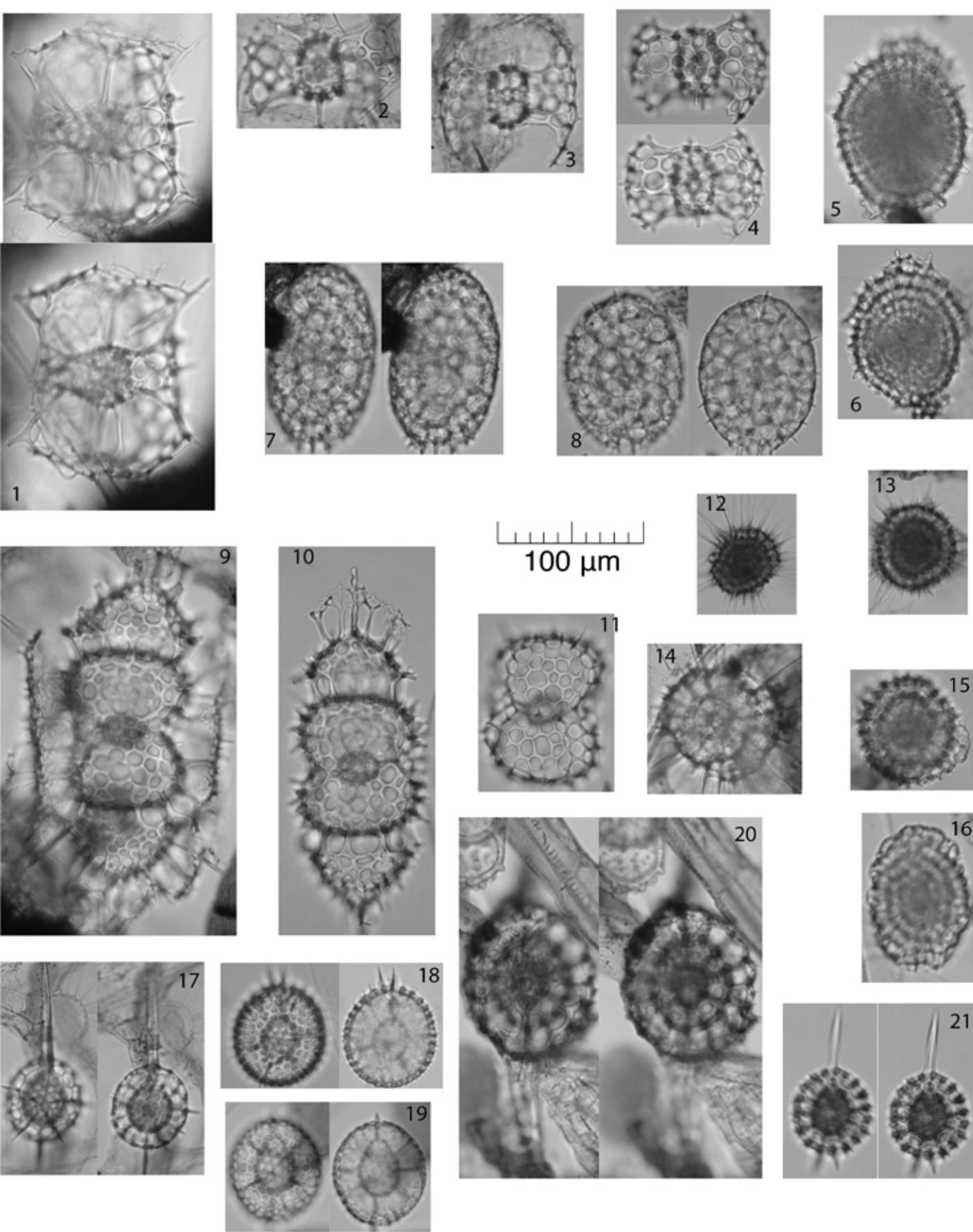


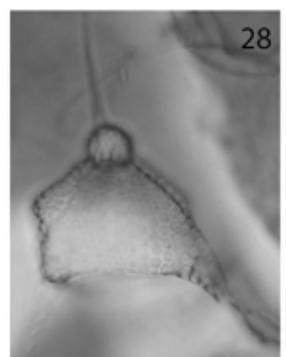
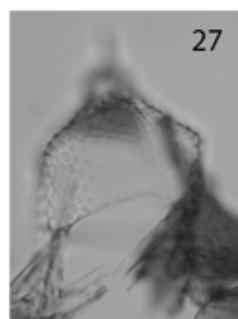
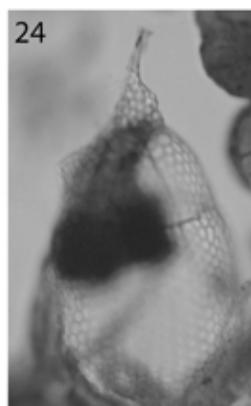
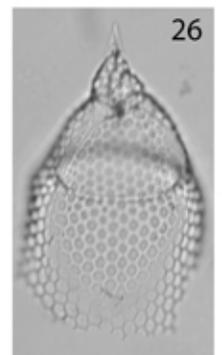
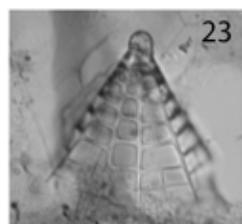
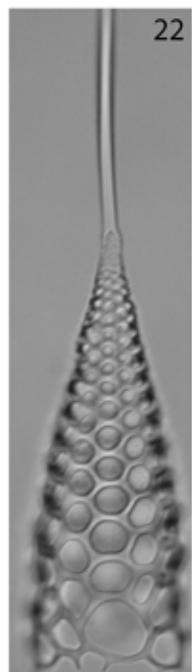
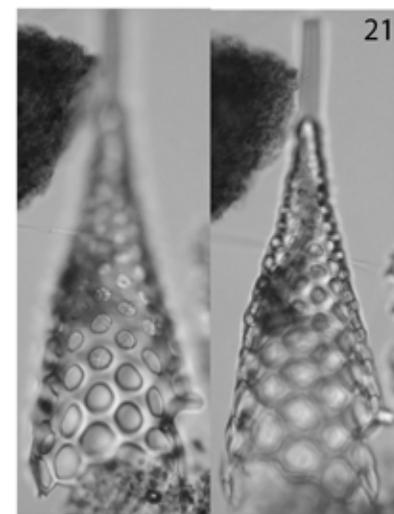
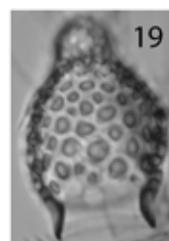
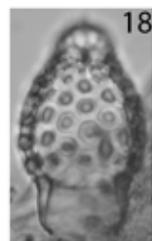
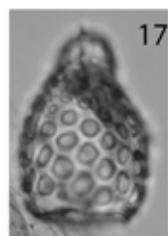
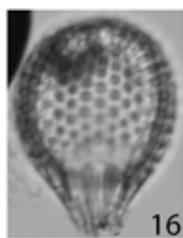
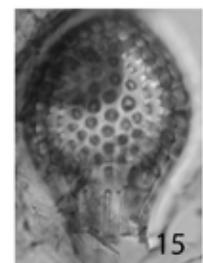
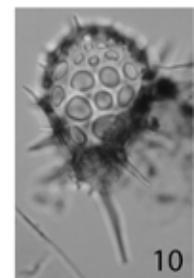
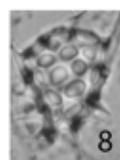
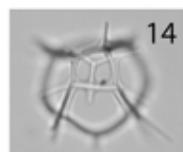
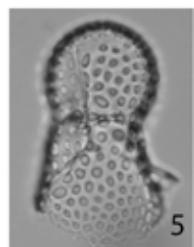
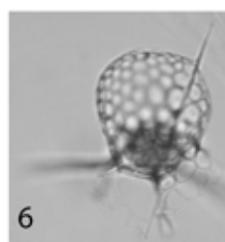
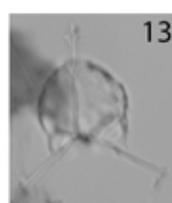
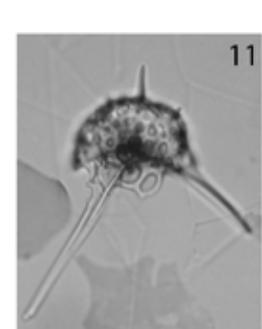
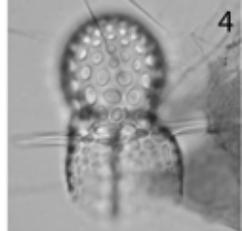
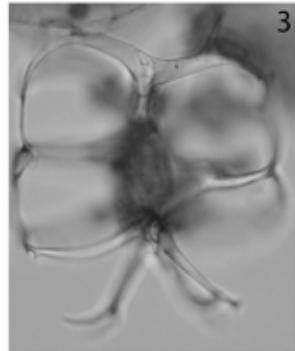
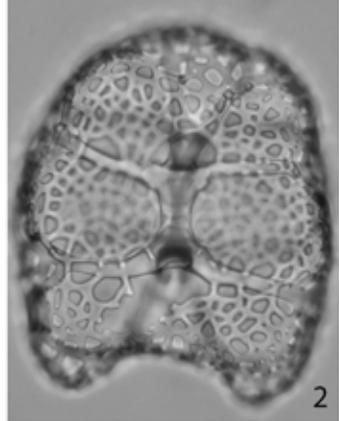
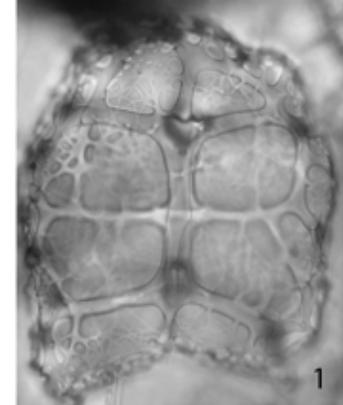


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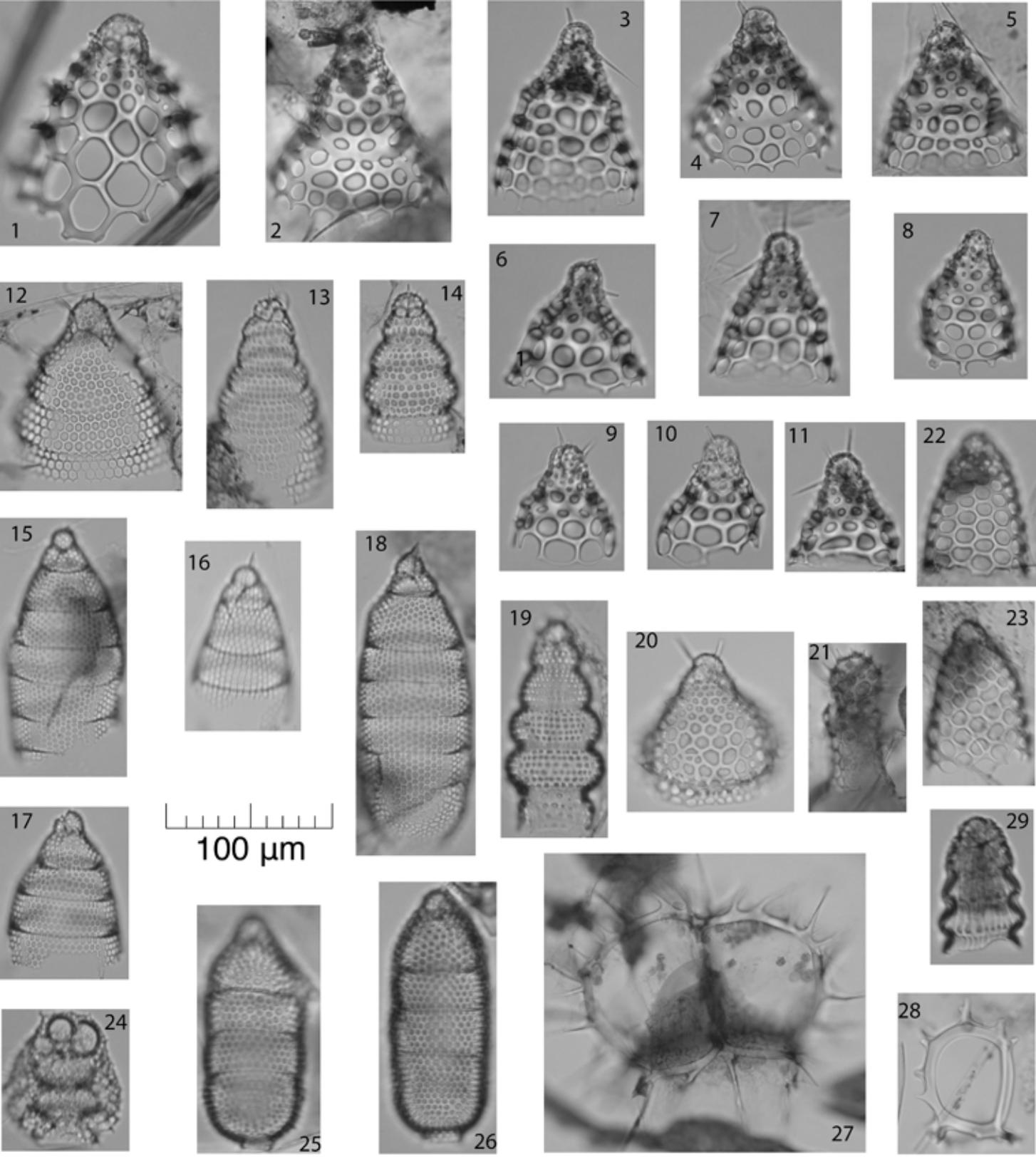






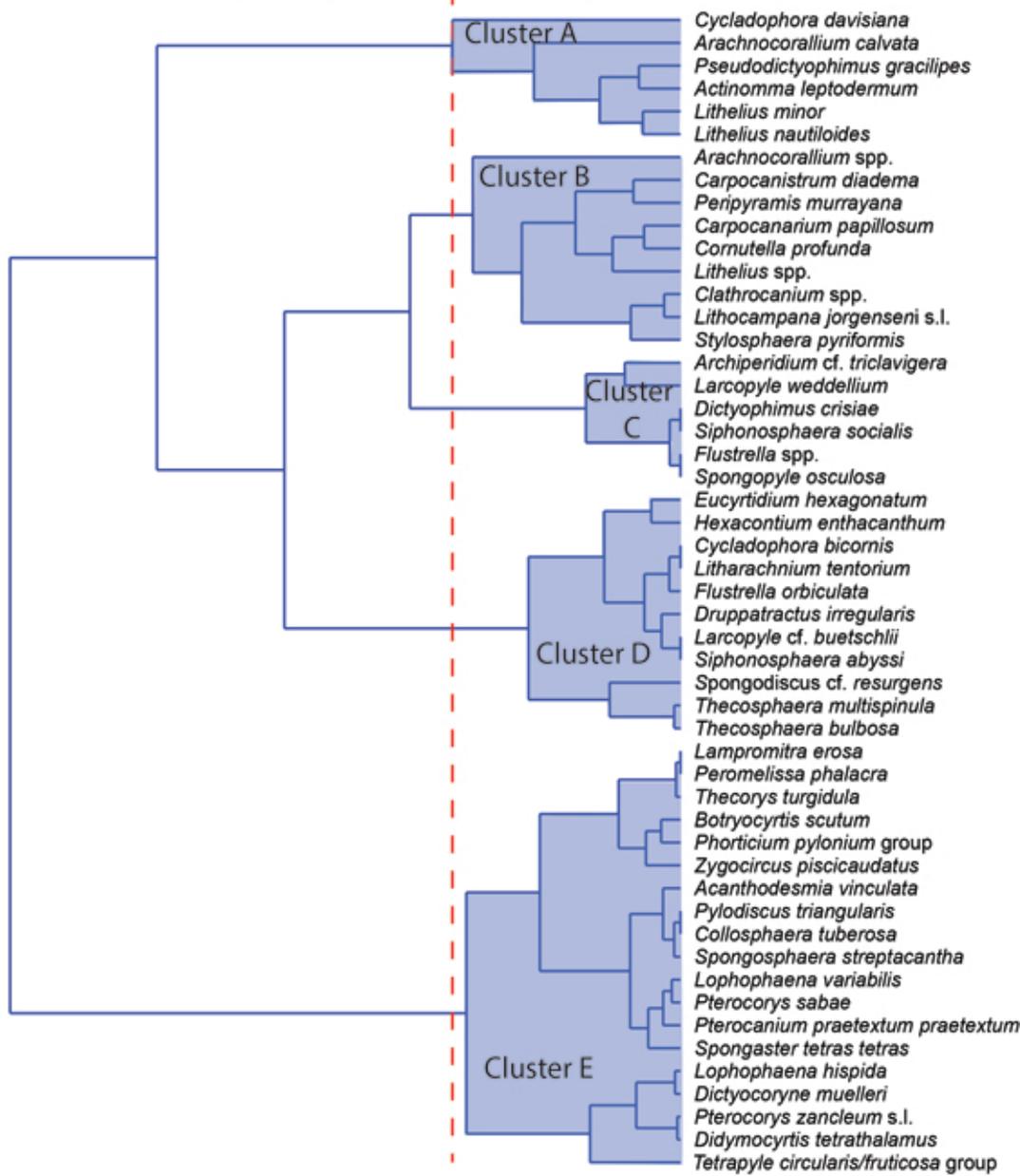


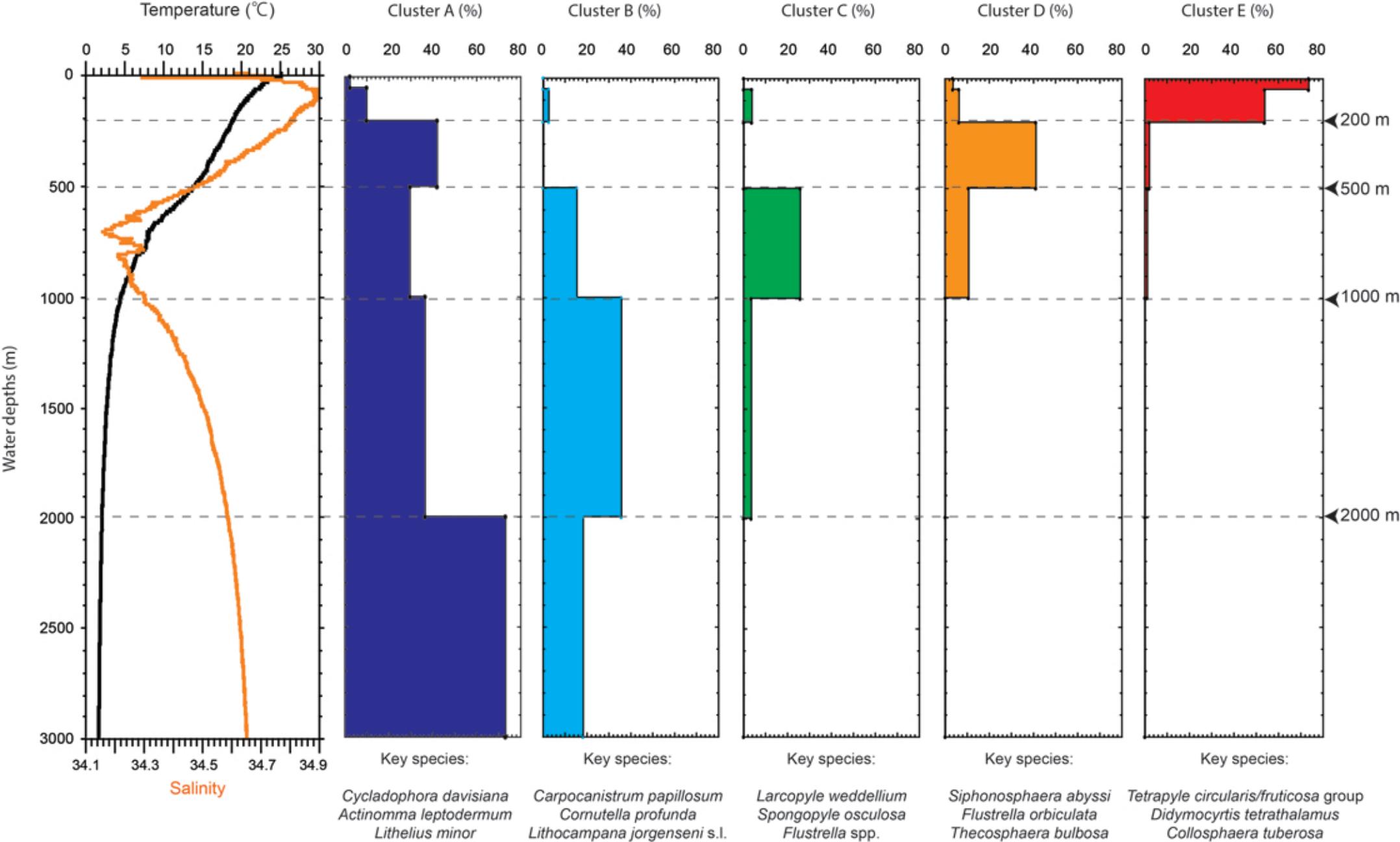
100 μm



Euclidean distance

6.4 5.6 4.8 4.0 3.2 2.4 1.6 0.8 0.0





<i>Litharachnium tentorium</i> Haeckel 1861b					3			1				2
<i>Lithocampana jorgenseni</i> Popofsky, 1908 sensu lato								3		12	6	
<i>Lophophaena hispida</i> (Ehrenberg, 1862)	9	2	6	1	6						3	
<i>Lophophaena variabilis</i> (Popofsky, 1913)	8		2	5							4	
<i>Lophophaena</i> cf. <i>witjazii</i> (Petrushevskaya, 1971)							2					1
<i>Lophophaena</i> cf. <i>laticeps</i> (Jørgensen, 1905)											1	
<i>Lophophaena</i> spp.	1		3	3	3		1	5				5
<i>Tricyclidium</i> spp.					1						3	2
<i>Peripyramis murrayana</i> (Haeckel, 1879)							3		3			2
<i>Peromelissa phalacra</i> Haeckel 1887	2											
<i>Phormospyris stabilis</i> (Goll) <i>scaphipes</i> (Haeckel, 1887) sensu lato						2					2	
<i>Phormacantha hystrix</i> (Jørgensen, 1899)					1	1						1
<i>Peromelissa phalacra</i> Haeckel, 1887			7	8								
<i>Pseudocubus obeliscus</i> Haeckel, 1887											3	
<i>Pseudodictyophimus gracilipes</i> (Bailey, 1856)			3	2	3		4	2	3			4
<i>Pterocanium praetextum</i> <i>praetextum</i> (Ehrenberg, 1873)	10		3	3	4			3			1	4
<i>Pterocanium praetextum</i> <i>eucolpum</i> (Haeckel, 1887)	2		2	1								
<i>Pterocanium korotnevi</i> (Dogiel and Reshetnyak, 1952)						1						
<i>Pterocanium trilobum</i> (Haeckel, 1860)			1									
<i>Pterocorys clausus</i> (Popofsky, 1913) sensu lato									2		7	14
<i>Pterocorys zancleum</i> (Müller, 1855) sensu lato	11		17	4	16			2			7	14
<i>Pterocorys minithorax</i> (Nigrini, 1968)			1	2								
<i>Pterocorys sabae</i> (Ehrenberg, 1873)	8		1	3	10			2				2
<i>Siphocampe arachnea</i> (Ehrenberg, 1839) sensu lato										2		
<i>Spirocyrtis scalaris</i> Haeckel, 1887						2				1	1	
<i>Semanthis gracilis</i> Popofsky, 1908			2			1						
<i>Theocorythium trachelium</i> Ehrenberg, 1873			2			1					1	1
<i>Theocorys turgidula</i> (Ehrenberg, 1873)			6			3						2
<i>Zygocircus piscicaudatus</i> Popofsky, 1913	2		5	3			1					
<i>Zygocircus productus</i> (Hertwig, 1879)	3	1			1	5	1	1			3	3
Unidentified Nassellarians			5	1		13						4
Spumellarians												
<i>Acanthosphaera</i> spp.	1											
<i>Actinomma boreale</i> Cleve, 1899									2			1

<i>Actinomma leptodermum</i> (Jørgensen, 1899)					5		7		1		5	3	
Actinommidae			1										
<i>Rhizosphaera mediana</i> (Nigrini, 1967)									1				
<i>Actinomma langii</i> (Dreyer, 1889)									1	1			
<i>Axoprunum bispiculum</i> Popofsky, 1912						1							
<i>Amphirhopalum ypsilon</i> Haeckel, 1887									2				
<i>Cenosphaera</i> spp.											3		
<i>Cladococcus</i> spp.				1							1		
<i>Circodiscus microporus</i> (Stöhr, 1880)						1							
<i>Dictyocoryne elegans</i> (Ehrenberg, 1873)	1						10		7				
<i>Dictyocoryne muelleri</i> (Haeckel, 1862)	8		5	2		1			10		3	16	
<i>Dictyocoryne profunda</i> Ehrenberg, 1873	1						2		2			3	
<i>Dictyocoryne truncatum</i> Haeckel, 1862											3	1	
<i>Didymocyrtilis tetrathalamus</i> (Haeckel, 1887)	12	1	16	6		28			19		18	21	
<i>Drupptractus irregularis</i> Popofsky, 1912						6	4		3		2	3	
<i>Flustrella orbiculata</i> (Haeckel, 1861b)						2	2		2		6	8	
<i>Flustrella</i> cf. <i>perispira</i> Haeckel, 1887	2						1	1					
<i>Flustrella</i> spp.							1	3	3			8	
<i>Flustrella subtilis</i> Ehrenberg, 1854	1												
<i>Haliometta miocenica</i> (Campbell and Clark, 1944)						1							
<i>Heliodiscus asteriscus</i> Haeckel, 1887									2				
<i>Hexacantium hostile</i> Cleve, 1900						1							
<i>Hexacantium enthacanthum</i> Jørgensen, 1899			3	2	3	13					2	4	
<i>Hexacantium pachydermum</i> Jørgensen, 1899								2	2		3	1	
<i>Pylodiscus triangularis</i> Haeckel, 1887											2		
<i>Hexastylus</i> spp.	2	1				9			5		6	1	
<i>Pylodiscus triangularis</i> Haeckel, 1887	4		2								6		
<i>Larcopyle</i> cf. <i>buetschlii</i> Dreyer, 1889			1	4	4	14			15			9	
<i>Larcopyle weddellium</i> Lazarus, Faust and Popova-Goll, 2005			1	1				10	5	3	12		
<i>Larcopyle cervicorne</i> (Haeckel, 1887)												1	3
<i>Larcospira quadrangula</i> Haeckel, 1887			2										
<i>Larcopyle</i> spp.	3											2	
<i>Lithelius</i> sp. A										1	4	1	
<i>Lithelius</i> spp.			6			1			6	4			
<i>Lithelius alveolina</i> (Haeckel, 1862)			2										
<i>Lithelius minor</i> Jørgensen, 1899 group						7	2	10	3	5	5	1	10
<i>Lithelius nautiloides</i> Popofsky, 1908						12	3	5	7	3	17	3	10

<i>Phorticium pylonium</i> Haeckel, 1887	2		5			8		9		10		19	
<i>Saturnalis circularis</i> Haeckel, 1887									1				
<i>Schizodiscus</i> spp.								1		7			
<i>Spongaster tetras tetras</i> Ehrenberg, 1862	6			1		2		1		3		4	
<i>Spongoliva ellipsoides</i> Popofsky, 1912	1												
<i>Spongaster froudum</i> Tan and Su, 1982	1		1										
<i>Spongurus cylindricus</i> Haeckel, 1861b								2		1			
<i>Spongodiscus biconcavus</i> Haeckel, 1887	2		1	1		1							
<i>Spongopyle osculosa</i> Dreyer, 1889								3	2	5		4	
<i>Spongodiscus</i> cf. <i>resurgens</i> Ehrenberg, 1854	6	2	2	3	6	2	2	19		8		17	
<i>Spongodiscus</i> spp.	1					4		3		2		3	
<i>Spongodiscus</i> aff. <i>cauletti</i> Kamikuri, 2010									1				
<i>Spongosphaera streptacantha</i> Haeckel, 1861a	5		2	4						2		4	
<i>Spongurus cylindricus</i> Haeckel, 1860					1								
<i>Stylosphaera pyriformis</i> (Bailey, 1856)								6	3	16	3	2	4
<i>Stylosphaera melpomene</i> Haeckel, 1887	1												
<i>Stylochlamydium asteriscus</i> Haeckel, 1887					1			2		5		2	
<i>Stylodictya</i> sp.	1	1											
<i>Stylodictya arachnia</i> (Popofsky, 1912)	3		4	1									
<i>Tetrapyle circularis/fruticosa</i> group sensu this study	33		31	24	2	83		23		64		67	
<i>Thecosphaera multispinula</i> (Su, 1982)					3		4	1		2			
<i>Thecosphaera inerme</i> (Haeckel, 1860)								1					
<i>Thecosphaera bulbosa</i> Hollande and Enjumet, 1960					3		4	1		3			
Unidentified spumellarians			4	4	2	8			3	6	3	12	
Collodarians													
<i>Collosphaera tuberosa</i> Haeckel, 1887	4	1	2					4					
<i>Collosphaeridea</i> spp.			1									4	
<i>Collosphaera invaginata</i> (Haeckel, 1887)	1												
<i>Disolenia</i> spp.			6	1		18		8		5		1	
<i>Polysolenia lappacea</i> (Haeckel, 1887)						1	1	3					
<i>Polysolenia spinosa</i> (Haeckel, 1861b)	1									11		5	
<i>Siphonosphaera abyssii</i> (Ehrenberg, 1873)			1	1	4	8		5		5		5	
<i>Siphonosphaera socialis</i> Haeckel, 1887								4					
