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► To cite this version:

Taniel Danelian, Mathias Meunier, Martin Tetard, Elisavet Skampa, Maria Triantaphyllou, et al.. Diversity of polycystine radiolarians in sediment traps from the Ionian, North Aegean and Cretan Seas: A preliminary account. *Revue de Micropaléontologie*, 2022, 74, pp.100606. 10.1016/j.revmic.2022.100606 . hal-04433496

HAL Id: hal-04433496

<https://hal.science/hal-04433496v1>

Submitted on 4 Feb 2024

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Diversity of polycystine radiolarians in sediment traps from the Ionian, North Aegean and Cretan Seas: a preliminary account

Diversité des radiolaires polycystines dans des pièges à sédiments des mers ionienne, nord-égéenne et de Crète: un rapport préliminaire

Taniel Danelian^{a,*}, Mathias Meunier^a, Martin Tetard^b, Elisavet Skampa^c, Maria Triantaphyllou^c, S. Stavrakakis^d, Alexandra Gogou^d

^a Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France

^b Aix Marseille Univ., CNRS, IRD, Coll France, INRAE, CEREGE, Aix-en-Provence, France

^c National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironments, Panepistimioupols, 15784 Athens, Greece

^d Hellenic Centre for Marine Research, Institute of Oceanography, PO Box 712, 19013, Anavyssos, Greece

* Corresponding author. Email: taniel.danelian@univ-lille.fr

Abstract

The presence and diversity of polycystine radiolarians in the north-eastern Mediterranean Sea is explored for the first time through the analysis of sinking particles obtained from sediment traps moored in three open marine sites. In total, thirty species are identified for which we provide appropriate references and illustrations to clarify the species concept followed in this study; 13 of the identified species are Spumellarians, 16 are Nassellarians and one is an Entactinarian. The highest diversity is recorded in the Ionian site, in which 23 species were observed during November 2014, with approximately as many Nassellarian species as Spumellarians; a large number of species are in common with the fauna reported from the Adriatic Sea, off Dubrovnik, but interestingly, 16 others are not. The lowest levels of radiolarian diversity, with 3 to 4 species at best, were observed in the north Aegean and Cretan Sea sites. Our observations improve also the paleobiogeographic knowledge of two polycystine species, one of which (*Gonosphaera primordialis* Jørgensen) was known previously from the high latitudes of both the northern and southern hemisphere and the other (*Qiuripyrolena chikuchik* Zhang and Suzuki) from the Pacific ocean.

Key-words: Polycystine radiolaria, biodiversity, Eastern Mediterranean, sediment trap, Ionian Sea, Aegean Sea, Cretan Sea

Résumé

La présence et la diversité des radiolaires polycystines sont explorées pour la première fois dans le nord-est de la mer Méditerranée à travers l'analyse de particules récoltées dans des pièges à sédiments amarrés dans trois sites marins ouverts. Au total, trente et une espèces sont déterminées pour lesquelles nous fournissons des références et des illustrations appropriées pour clarifier le concept d'espèce suivi dans cette étude ; 13 des espèces déterminées sont des Spumellaires, 16 sont des Nassellaires et une est un Entactinaire. La plus grande diversité est enregistrée dans le site ionien, dans lequel 23 espèces ont été observées en novembre 2014, avec environ autant d'espèces de Nassellaires que de Spumellaires ; un grand nombre d'entre elles sont communes avec la faune signalée dans la mer Adriatique, au large de Dubrovnik, mais il est intéressant de noter que 16 autres ne le sont pas. Les niveaux les plus faibles en diversité, avec au mieux 3 à 4 espèces de radiolaires, ont été observés dans les sites du nord de la mer Égée et de la mer de Crète. Nos observations améliorent également la connaissance paléobiogéographique de deux espèces de polycystines, dont l'une (*Gonosphaera primordialis* Jørgensen) était connue auparavant des hautes latitudes des hémisphères nord et sud et l'autre (*Qiuripylolena chikuchik* Zhang and Suzuki) de l'océan Pacifique.

Mots-clés: Radiolaires polycystines, biodiversité, Méditerranée orientale, pièges à sédiments, mer ionienne, mer Égée, mer de Crète

1) Introduction

Polycystine radiolarians are holoplanktonic protozoans that secrete a very aesthetic siliceous skeleton; they are omnivorous, feeding on a variety of prey ranging from bacteria to autotrophic/heterotrophic microplankton. Although they are most abundant in surface waters (0 – 100 m), they may live in any depth of the water column, with each individual species being usually restricted to specific depth ranges, reflecting different feeding strategies. Many species are surface dwellers, as they bear photosynthetic endosymbionts (e.g. dinoflagellates, diatoms); others are mainly bacterivores and peak close to the nutricline (ca. 50 – 100m deep); finally deep-dwellers feed essentially on floating organic matter (Casey et al., 1979 a,b; Casey, 1993).

Polycystine radiolarians represent one of the oldest evolutionary lineages amongst Rhizarians (Sierra et al., 2013), with a fossil record stretching back to the early Cambrian (Obut & Iwata, 2000; Pouille et al., 2011). After having survived repeated periods of major extinctions, they are abundant and diverse today, with several hundreds of species living in modern oceans (Anderson, 1983; Lazarus, 2005; Boltovskoy et al., 2010). All living and fossil polycystine species are classified in eight orders, three of which are known exclusively from the fossil record, while five others have both fossil and living representatives (De Wever et al., 2001; Nakamura et al., 2021); these are the Nassellaria, Spumellaria, Entactinaria, Orodaria and Collodaria (colonial species).

The presence of extant polycystine radiolarians in the plankton of the Mediterranean Sea is known since the 19th century; Müller (1859b) and Haeckel (1860, 1862) studied plankton samples collected from near Messina. Sakai et al. (2009) revisited Haeckel's collections from Messina, which are housed currently at the Ernst-Haeckel Haus in Jena (Germany); they were able to find and illustrate 16 amongst the species collected by Haeckel. Other important western Mediterranean sites, where living polycystines were observed in plankton samples, are the gulfs of Alger and Villefranche-sur-mer (Hollande & Enjumet, 1960). The latter site was also important for providing material for cytological studies during the 60s and 70s (e.g. Cachon & Cachon, 1971) and more recently for molecular studies (e.g. Biard et al., 2017; Sandin et al., 2019).

Later, there has been some limited interest for polycystine radiolarians preserved in the surficial and Quaternary sediments of the Mediterranean Sea (Caulet, 1974; Riedel et al., 1985); these studies highlighted the serious dissolution/preservation problems of biogenic silica in modern marine environments, which are particularly important in the super-

oligotrophic Eastern Mediterranean basin. Nevertheless, exquisitely preserved and diverse radiolarian assemblages were described from anoxic sediments south of Crete (Bjorklund & De Ruiter, 1987) and especially from the Sapropel S5, deposited 125,000 years ago (Danelian & Frydas, 1998).

Polycystine radiolarians were also mentioned in a limited number of ecological studies in the Eastern Mediterranean. The study of Kimor and Wood (1975) was based on both phytoplankton and zooplankton distribution data collected with a plankton net during a cruise operated in summer 1965. Abboud-Abi Saab (1988) conducted a quantitative and qualitative ecological study on Acantharian and Polycystine radiolarians along the Lebanese coastal area, while recently, Zakaria et al. (2018) studied plankton populations from six marine sections positioned perpendicularly to the Egyptian coast. Kršinić & Kršinić (2012) reported a large diversity of living polycystine radiolarians from the Adriatic Sea from 4 stations situated at different depths (100 to 1200 m deep) off the Croatian town of Dubrovnik. Observations were based on samples collected with a plankton net equipped with a closing system from different parts of the water column (0-50 m, 50-100 m, ... 800-1,000 m).

Few are the studies on polycystine radiolarians from the Aegean and Cretan seas and none is currently available from the Ionian Sea. Toklu-Aliçli & Balkis (2007) reported the presence of a single polycystine species collected from subsurface water samples of the NE Aegean. One particularly interesting ecological study on living plankton from the Aegean Sea was conducted by Miliou et al. (2012) based on plankton samples collected from 16 shallow water near shore stations (12 – 100 m water depth) of the central and southeastern Aegean Sea; samples were collected with Niskin bottles from surface waters (10 - 30 m deep) during late summer to early autumn 1994.

While exploring the presence of living radiolarians in the Eastern Mediterranean, we discovered the presence of polycystine radiolarians in some sediment trap preparations from the North Aegean, Cretan and Ionian seas used previously for carbonate flux estimates produced by calcareous nannofossils (Skampa et al., 2020). Micropaleontological observations from sediment traps have the potential to provide several insights on important processes related to radiolarian diversity, community structure and biogenic silica accumulation in relation to oceanic currents and nutrient availability (Boltovskoy, 2017). We here report a preliminary account on the diversity of polycystine radiolarians observed in sediment trap samples collected from three different sampling sites of the Eastern Mediterranean; we illustrate each one of the identified species and provide synonymy lists to

clarify the taxon concept used during our identifications; we compare the observed levels of diversity in each site and discuss possible implications.

2) Material and methods

Three PPS3/3 Technicap sediment traps (<https://www.technicap.com/products/sediment-trap>; 0.125m² collecting area, 12 receiving cups, with individual sampling intervals of ~15 days) were deployed at different sites in the North Aegean Sea (Athos Basin, 39°58.16'N, 24°43.48'E), the Cretan (South Aegean) Sea (35°44.76'N, 25°09.29'E) and Ionian Sea (Nestor site; 36°02.96'N, 21°28.93'E) (sites A, B and C, respectively on Fig. 1).

The North Aegean Sea is considered as mesotrophic, the Ionian Sea as oligotrophic and the Cretan Sea as ultra-oligotrophic. Table 1 shows the sampling site for each studied sample, the water depth at which the sediment trap was positioned (respectively 500, 1470 and 2,000 mbsl for the Aegean, Cretan and Ionian seas), the starting date of collection and its duration. As an example, samples M2IIA1 and M2IIA5 were collected from a sediment trap positioned in the North Aegean Sea. Sample M2IIA1 was collected during 1 – 15 of April 2015, while sample M2IIA5 was collected the first fifteen days of August 2015.

Different mooring depths have been chosen in the framework of the research projects Medecos and KRIPIS of the Hellenic Centre for Marine Research in order to study the water column fluxes affected by the various water masses that feature the three studied oceanographic settings.

The North Aegean Sea (1000 m depth) is featured by low-saline (24–28 psu) surface (<70 m depth) Black Sea Water (BSW) flowing through the Dardanelles straits. Warm and salty (>39 psu) Levantine Surface Water (LSW) is present when BSW is absent, whereas Levantine Intermediate Water (LIW; 14–15 °C, 38.8–39.1 psu) extends to a depth of about 400 m below the BSW/LSW.

The Cretan Sea being the largest and deepest basin (2500 m depth) is featured by the warm and saline LSW (>39.3 psu) and the low salinity Modified Atlantic Water (MAW), mostly traced as a surface/subsurface salinity minimum, while the warmer and saline Levantine Intermediate Water mass (LIW) (38.9 < S < 39.1 psu) is located in the intermediate layers of the water column, and the oxygenated Cretan Deep Water (CDW) with S ~39.08 psu occurs in the deep layers.

The Ionian Sea incorporates the deepest basins of the Mediterranean Sea (4600 and 5264 m depth). The structure of the local water masses consists of the MAW (upper 25–100 m), which is characterized by a salinity minimum, the LIW (100–500 m) showing a salinity maximum, the Transitional Waters (TW; layer between 500 and 1200 m) and the Eastern Mediterranean Deep Waters (EMDW: layers below 1200 m).

The recovered trap samples were kept in dark at 4°C, until treated in the laboratory. Large organisms and smaller than 1 mm swimmers were removed and each sample was divided into subsamples by a high-precision peristaltic, microprocessor-controlled dispensing pump.

Each subsample was split into 10 equal fractions by the use of McLane rotary wet splitter, with less than 4% deviation between aliquots. Buffered distilled water (pH > 8) was used in the splitting process. Organic material was oxidized following Bairbakhish et al. (1999) and then each sub-sample was sieved over a 32 µm mesh sieve. Each aliquot was filtered onto Millipore cellulose filters (47 mm diameter, 0.45 µm pore size), using a vacuum pump; each filter was dried in the oven and stored in plastic petri dishes. Approximately 30 mm² of filter was mounted onto a slide for each sample. A selection of slides prepared in Athens University were then imaged at different focal depths in Lille University, using a transmitted light microscope (x 200 magnification) and an image stacking technique (3 to 5 images per stack) and the Helicon Focus software. An image processing step was also used to increase the specimens' contrast on each image using the ImageJ software plugin developed in Tetard et al. (2020).

3) Results

3.1 Polycystine radiolarian systematic classification

This subchapter intends to provide a short synonymy list for each species mentioned herein, with at least one reference that gives appropriate descriptions and illustrations for the species/taxon concept. The higher level classification adopted for this study is based on the most recent and comprehensive radiolarian classification provided by Suzuki et al. (2021). In the case of species already described, the combinations used are derived from O'Dogherty et al. (2021). The identified species/taxa are presented below in detail, under their order and family assignment; they are also listed with an alphabetic order in Table 1. Whenever

possible, we provided for each species details about their designated holotype/lectotype, with the exception of 8 species described by Haeckel (1887) and one by Popofsky (1912). As specified by Aita et al (2009) Haeckel did not designate any holotype and did not deposit his type material in a collection.

Class Polycystinea Ehrenberg, 1839

Order SPUMELLARIA Ehrenberg, 1876

Family HEXACROMYIDAE Haeckel, 1882

Hexacromyum* sp. cf. *H. giganteum (Cortese and Bjørklund)
(Pl. 1, figs. f, g)

cf. *Hexacromyum giganteum* Cortese and Bjørklund, 1998, p. 167, pl. 2, figs. 1-6 [holotype: Cortese and Bjørklund, 1998, pl. 2, figs. 1-4: housed in the Paleontological Museum, University of Oslo, Norway].

Remarks: This large species differs from *H. giganteum* in having lightly silicified cortical shell and larger pores. New combination according to Suzuki et al. (2021).

Hexacromyum* sp. cf. *H. heracliti (Haeckel)
(Pl. 1, fig. i)

cf. *Hexalanche heracliti* Haeckel, 1887, p. 187, pl. 22, fig. 7.

cf. *Hexacromyum heracliti* (Haeckel): Nishimura and Yamauchi, 1984, p. 29, pl. 3, figs. 3, 6; Takahashi, 1991, p. 73, pl. 15, figs. 8, 9.

Hexacromyum sp. cf. *H. heracliti* Benson, 1966, p. 158, pl. 4, figs. 8-10.

Remarks: This species is distinguished from *H. heracliti* by its smaller pores on the cortical shell. New combination following Suzuki et al. (2021).

Family PANARTIDAE Haeckel, 1887

Didymocyrtis tetrathalamus tetrathalamus (Haeckel);
(Pl. 1, fig. d)

Panartus (Panartella) tetrathalamus Haeckel, 1887, p. 378, pl. 40, fig. 3; Nigrini, 1967, p. 30, pl. 2, figs. 4a-4d.

Panartus tetrathalamus tetrathalamus Haeckel: Nigrini, 1970, p. 168, pl. 1, fig. 12.

Ommatartus tetrathalamus (Haeckel): Renz, 1976, p. 107, pl. 1, fig. 6.

Ommatartus tetrathalamus tetrathalamus (Haeckel): Ling, 1972, p. 166, pl. 1, figs. 7-9; Nishimura and Yamauchi, 1984a, p. 36, pl. 16, figs. 1-4, 7-9, pl. 52, fig. 12.

Didymocyrtis tetrathalamus (Haeckel): Sanfilippo and Riedel, 1980, p. 1010, text-fig. 1g; Itaki, 2009, p. 45, pl. 5, figs. 5-8; Kršinić and Kršinić, 2012, pl. III, fig. 31; Matsuzaki et al., 2015, p. 17, pl. 3, fig. 6-8.

Dictyospyris messanensis Müller, 1855, p. 672; Müller, 1859b, p. 46, fig. 8.

Didymocyrtis messanensis (Müller): Van de Paverd, 1995, p. 145, pl. 39, figs. 1-13.

Ommatospyris ? sp. Sakai et al., 2009, pl. 20, figs. 5a, b.

Remarks: The incomplete specimen found in sample M3AVIIIIB8 (Pl. 1, fig. c) is identified only at the species level based on similar identifications by Welling (1997, pl. 4, fig. 6) and Boltovskoy (1998, fig. 15.77B); its distinction between the 2 subspecies (*D. d. tetrathalamus* and *D. d. coronatus*) is not possible.

Family TREMATODISCIDAE Haeckel, 1862

Stylodictya asterisca (Haeckel)

(Pl. 2, fig. j)

Stylochlamyidium asteriscus Haeckel, 1887, 514, pl. 41, fig. 10; Nigrini and Moore, 1979, p. S113, pl. 14, fig. 5; Boltovskoy and Riedel, 1980, p. 118, pl. 4, fig. 2; Kršinić and Kršinić, 2012, pl. III, fig. 29.

Perichlamyidium venustum Bailey, 1856, p. 5, pl. 1, figs. 16-17.

Perichlamyidium venustum Bailey [sic.], Itaki and Bjorklund, 2006, p. 458, pl. 1, figs. 16, 17, pl. 4, figs. 1-4, 7, pl. 5, fig. 1 [lectotype: Itaki and Bjorklund, 2006, pl. 4, fig. 2, slide #656 (E36/0), paralectotype: pl. 4, fig. 4, slide #648 (N34/4), housed in the Farlow Herbarium of Harvard University (Bailey collection), USA].

Porodiscus group B, Danelian and Frydas, 1998, p. 140, pl. 3, figs. 2, 3.

Remarks: New combination following the synonymisation of *Stylochlamyidium* with *Stylodictya* by Suzuki et al. (2021)

Stylodictya multispina Haeckel

(Pl. 1, figs. l, m)

Stylodictya multispina Haeckel, 1860, p. 842; Haeckel, 1862, p. 496, pl. 29, fig. 5; Haeckel, 1887, p. 510; Boltovskoy and Riedel, 1980, p. 118, pl. 4, figs. 4a-b; Takahashi, 1991, p. 81, pl. 20, fig. 10 (*partim.*); Kršinić and Kršinić, 2012, pl. III, fig. 30.

Stylodictya tenuispina Jørgensen, 1905, p. 118, pl. 10, figs. 39a-c; Dolven et al., 2014, p. 39, pl. 3, figs. 6a-c [lectotype: Dolven et al., 2014, p. 39, pl. 3, fig. 6a, specimen number PMO224.465, slide #54 (N37/0), housed in the Zoological Museum (Jørgensen collection), Bergen, Norway].

Stylodictya validispina Jørgensen, 1905, p. 119, pl. 10, fig. 40a-b; Dolven et al., 2014, p. 42, pl. 3, figs. 7a, b [lectotype: Dolven et al., 2014, p. 42, pl. 3, fig. 7a, specimen number PMO224.466, slide #54 (M37/0), housed in the Zoological Museum (Jørgensen collection), Bergen, Norway].

Family HALIOMMIDAE Ehrenberg, 1846, sensu Suzuki et al. (2021)

Haliomma ? sp.

(Pl. 1, fig. a)

Remarks: The state of preservation of the single specimen of this morphotype allows only a tentative assignment to genus *Haliomma*.

Family LITHELIIDAE Haeckel, 1862

Lithelius minor Jørgensen gr.

(Pl. 1, fig. h)

Lithelius minor Jørgensen, 1900, p. 65, pl. 5, fig. 24; Benson, 1966, p. 262, pl. 17, figs. 9-10, pl. 18, figs. 1-4; Nigrini and Moore, 1979, p. S135, pl. 17, figs. 3-4b.

Lithelius minor Jørgensen group ?: Boltovskoy, 1998, p. 26, figs. 16.87a-c.

Larcospira minor (Jørgensen, 1900): Jørgensen, 1905, 121; Dolven et al., 2014, p. 33, pl. 2, figs. 7-10 [lectotype: Dolven et al. (2014), pl. 2, figs. 7a, b, specimen number PMO224.461/1, slide #58 (Q46/3), housed in the Zoological Museum (Jørgensen collection), Bergen, Norway].

Family PHORTICIIDAE Haeckel, 1882 *sensu* Dumitrica (1989)

Phorticum multispinum Popofsky *sensu* Zhang and Suzuki

(Pl. 2, fig. a)

Phorticum multispinum Popofsky, 1912, p. 153, text-fig. 76; Zhang et Suzuki, 2017, p. 42, figs. 24. 1-3.

Qiuripylolena chikuchik Zhang and Suzuki

(Pl. 2, fig. b)

Qiuripylolena chikuchik Zhang and Suzuki, 2017, p. 52, figs. 30.1-10 [holotype: Zhang and Suzuki, 2017, figs. 30.9, 10, housed in the South China Sea Institute of Oceanology, Chinese Academy of Sciences, China]

Family LARCOSPIRIDAE Haeckel, 1887

Larcopyle cervicornis (Haeckel) *sensu* Zhang and Suzuki

(Pl. 2, figs. e, f)

Tholospira (*Tholospirionium*) *cervicornis* Haeckel, 1887, p. 700, pl. 49, fig. 5.

Tholospira cervicornis Haeckel: Popofsky, 1912, p. 152, text-fig. 73.

Larcopyle cervicornis (Haeckel): Zhang and Suzuki, 2017, p. 28, figs. 16, 17.1-6 [topotypic material from the H.M.S. Challenger Station 271: Zhang and Suzuki, 2017, figs. 17.1, 2].

Tholospirionium cervicorne (Haeckel): Van de Paverd, 1995, p. 185, pl. 54, figs. 1-4, 6-12, pl. 58, fig. 7, pl. 59, fig. 6.

Family PYLODISCIDAE Haeckel, 1887

Pylodiscus sp.

(Pl. 1, figs. s-t)

Remarks: The early stage of development of the specimens encountered does not allow an identification at the specific level.

Family ZONARIIDAE Haeckel, 1887

Tetrapyle octacantha Müller group
(Pl. 1, fig. n)

Tetrapyle octacantha Müller, 1859a, p. 154; 1859b, p. 33, pl. 2, figs. 12-13, pl. 3, figs. 1-12; Benson, 1966, p. 245, pl. 15, figs. 3-10, pl. 16, fig. 1, text-fig. 18; Sakai et al., 2009, pl. 3, fig. 7; Kršinić and Kršinić, 2012, pl. III, fig. 33 [lectotype: Müller, 1859b, p. 33, pl. 3, fig. 2; subsequent designation by O'Dogherty et al., 2021].

Pyloniid group, Danelian and Frydas, 1998, p. 140, pl. 1, fig. 7, pl. 3, fig. 14.

Tetrapyle octacantha Müller group, Itaki, 2009, p. 47, pl. 10, figs. 1-10.

Family STYLATRACTIDAE Schröder, 1909 *sensu* Matsuzaki et al. (2015)

Amphisphaera ? sp.
(Pl. 1, fig. b)

Remarks: The skeleton is composed of two spherical latticed shells, with two long, slender three-bladed polar spines. The inner shell is about half the diameter of the cortical shell, and is perforated by large hexagonal pores. Needle-shaped spines are present on the surface of the cortical shell in some specimens.

Order ENTACTINARIA Kozur & Mostler, 1982

Family EXCENTROCONCHIDAE Hollande & Enjumet, 1960
sensu Dumitrica (2014)

Gonosphaera primordialis Jørgensen
(Pl. 2, fig. g)

Gonosphaera primordialis Jørgensen, 1905, p. 133, pl. 14, figs. 64-68; Dumitrica, 2001, p. 196, pl. 1, figs. 1-4, pl. 2, fig. 1; Renaudie, 2014, pl. 2, fig. 3; Dolven et al., 2014, p. 50, pl. 6, figs. 1-2 [lectotype: Dolven et al., 2014, pl. 6, fig. 1, specimen number PMO224.481, slide #35 (H32/0), housed in the Zoological Museum (Jørgensen collection), Bergen, Norway].

Order NASSELLARIA Ehrenberg, 1876

Family EUCYRTIDIIDAE Ehrenberg, 1846

Eucyrtidium acuminatum (Ehrenberg)
(Pl. 1, fig. p)

Lithocampe acuminata Ehrenberg, 1844a, p. 84 ; Suzuki et al., 2009, pl. 14, fig. 12
[lectotype: Suzuki et al., 2009, pl. 14, figs. 13a-c, housed in the Museum für Naturkunde (Ehrenberg collection), Humboldt University, Berlin, Germany; subsequent designation by O'Dogherty et al., 2021].

Eucyrtidium acuminatum (Ehrenberg): Nigrini, 1967, p. 81, pl. 8, figs. 3a-b; Danelian and Frydas, 1998, p. 141, pl. 1, fig. 11, pl. 5, figs. 9-11; Kršinić and Kršinić, 2012, pl. VI, figs. 63-65.

Eucyrtidium acuminatum (Ehrenberg) *tropezianum*: Caulet, 1974, p. 212, pl. XI, figs. 1, 2.

Family PLECTOPYRAMIDIDAE Haecker, 1908

Cornutella profunda Ehrenberg

(Pl. 2, fig. p)

Cornutella clathrata ? *β profunda* Ehrenberg, 1854, p. 241; Suzuki et al., 2009, pl. 35, figs. 4a, b [lectotype: Suzuki et al., 2009, pl. 35, figs. 4a, b, housed in the Museum für Naturkunde (Ehrenberg collection), Humboldt University, Berlin, Germany; subsequent designation by O'Dogherty et al., 2021].

Cornutella profunda Ehrenberg: Riedel, 1958, p. 232, pl. 3, figs. 1-2; Nigrini, 1967, p. 60, pl. 6, figs. 5a-c; Caulet, 1974, p. 244, pl. XII, figs. 1-5; Boltovskoy and Riedel, 1980, p. 123, pl. 5, fig. 6; Danelian and Frydas, 1998, p. 141, pl. 5, figs. 2, 3; Kršinić and Kršinić, 2012, pl. V, figs. 57, 58.

Litharachnium tentorium (Haeckel)

(Pl. 1, fig. j)

Litharachnium tentorium Haeckel, 1860, p. 836; Haeckel, 1862, p. 281, pl. 4, figs. 7-10; Haeckel, 1887, p. 1163; Takahashi, 1991, p. 114, pl. 35, figs. 14-18; Kršinić and Kršinić, 2012, pl. VI, fig. 69.

Litharachnium group, Danelian and Frydas, 1998, p. 141, pl. 5, fig. 12.

Family ARTOSTROBIIDAE Riedel, 1967 *sensu* Sugiyama (1998)

Botryostrobos auritus/australis (Ehrenberg) group

(Pl. 2, fig. h)

Lithocampe aurita Ehrenberg, 1844a, p. 84.

Lithocampe australe Ehrenberg, 1844b, p. 187.

Eucyrtidium australe (Ehrenberg): Ehrenberg, 1847, p. 43.

Eucyrtidium auritum (Ehrenberg): Ehrenberg, 1854b, pl. 22, fig. 25.

Eucyrtidium australe (Ehrenberg): Ehrenberg, 1854b, pl. 35, fig. 18.

Botryostrobos auritus (Ehrenberg) group: Petrushveskaya and Kozlova, 1972, p. 539, pl. 24, figs. 15-18.

Botryostrobos australis (Ehrenberg) group: Petrushevskaya and Kozlova, 1972, p. 539, pl. 24, figs. 12-14.

Botryostrobos auritus/australis (Ehrenberg) gr.: Nigrini, 1977, pl. I, figs. 2-5; Nishimura and Yamauchi, 1984a, p. 64, pl. 40, figs. 2-4, 7; Van de Paverd, 1995, p. 254, pl. 76, figs. 19-22; Kršinić and Kršinić, 2012, pl. VIII, fig. 85.

Family ACANTHODESMIIDAE Haeckel, 1862

Clathrocircus stapedius Haeckel

(Pl. 2, fig. o)

Clathrocircus stapedius Haeckel, 1887, p. 962, pl. 92, fig. 8; Goll, 1972, p. 963, pl. 51, fig. 3; Benson, 1983, p. 501, pl. 7, figs. 5-7; Itaki, 2009, p. 49, pl. 13, figs. 13, 14.
Corythospyris stapedius (Haeckel): Goll, 1978, p. 177.

Remarks. The test is not fully developed.

Family CEPHALOSPYRIDIDAE Haeckel, 1882

Lophospyris pentagona pentagona (Ehrenberg)

(Pl. 1, fig. k)

Ceratospyris pentagona Ehrenberg, 1872a, p. 303; 1872b, pl. 15, fig. 15; Suzuki et al., 2009, pl. 71, figs. 5a-d [lectotype: Suzuki et al., 2009, pl. 71, figs. 5a-d, housed in the Museum für Naturkunde (Ehrenberg collection), Humboldt University, Berlin, Germany; subsequent designation by O'Dogherty et al., 2021].

Dorcadospyrus pentagona (Ehrenberg): Goll, 1969, p. 338, pl. 59, figs. 1-3, 5.

Lophospyris pentagona (Ehrenberg): Caulet, 1974, p. 218, pl. XIV, figs. 1, 2.

Lophospyris pentagona pentagona (Ehrenberg): Goll, 1976, p. 398, pl. 10, figs. 1-7, pl. 11, figs. 1-3, 5; Kršinić and Kršinić, 2012, pl. IV, fig. 37.

Family STEPHANIIDAE Haeckel, 1882

Zygocircus productus (Hertwig) group

(Pl. 1, fig. o)

Lithocircus productus Hertwig, 1879, p. 69, pl. 7, fig. 4.

Zygocircus productus (Hertwig): Petrushevskaya, 1969, p. 644, pl. 3, fig. 3, pl. 6, fig. 11; Petrushevskaya, 1971, p. 281, figs. 16 : II, 145: X, XI; Caulet, 1974, p. 251; Boltovskoy and Riedel, 1980, p. 121, pl. 4, fig. 17.

Zygocircus productus productus (Hertwig): Goll, 1979, p. 382, pl. 2, fig. 3; Danelian and Frydas, 1998, p. 140, pl. 4, figs. 8, 9.

Zygocircus productus (Hertwig) group: Takahashi, 1991, p. 101, pl. 24, figs. 13, 14; Itaki, 2009, p. 49, pl. 14, figs. 1-15.

Family THEOPILIIDAE Haeckel, 1882 *sensu* Caulet *in* Suzuki et al. (2021)

Eucecryphalus ? danaes (Haeckel)

(Pl. 1, fig. e)

Clathrocyclas danaes Haeckel, 1887, p. 1388; Takahashi and Honjo, 1981, p. 152, pl. 8, fig. 13; Dworetzky and Morley, 1987, p. 17, pl. 4, fig. 1.

Lampromitra danaes (Haeckel): Boltovskoy, 1998, p. 65, fig. 15.116; Kršinić and Kršinić, 2012, pl. VI, fig. 67.

? *Eucecryphalus gegenbauri* Haeckel, 1860, p. 836; Haeckel, 1862, p. 308, pl. 5, figs. 12-15; Haeckel, 1887, p. 1222; Takahashi, 1991, p. 111, pl. 33, figs. 13-15.

Remarks: We suggest considering *Eucecryphalus gegenbauri* as a possible synonym for *E. ? danaes*, because the flat discoidal thorax of these two species is very similar. New combination following Suzuki et al. (2021).

Family DICTYOCRYPHALIDAE Suzuki *in* Suzuki et al. (2021)

Lophophaena* sp. cf. *L. witjazii (Petrushevskaya)

(Pl. 2, fig. n)

cf. *Lophophaenoma witjazii* Petrushevskaya, 1971, p. 118, figs. 62,

III-VII [holotype: Petrushevskaya, 1971, slide 269 Q50.0, housed in the Department of Marine Protozoans, ZIN, Academy of Sciences, Russia].

Lophophaena cf. *capito* Ehrenberg: Benson, 1966, pl. 24, figs. 22-23.

Remarks: This large *Lophophaena* species differs from *L. witjazii* in having a more angular cephalis without three-bladed spines.

Lophophaenidae gen et sp. indet.

(Pl. 1, fig. q)

Remarks: All small Lophophaenidae with a rounded cephalis and which cannot be assigned to either the genus *Lophophaena* or *Lithomelissa* are grouped under this name.

Family DIMELISSIDAE Petrushevskaya, 1981 *sensu* Caulet *in* Suzuki et al. (2021)

Lithomelissa setosa Jørgensen

(Pl. 2, fig. i)

Lithomelissa setosa Jørgensen, 1900, p. 81, pl. 4, fig. 21; Jørgensen, 1905, p. 135, pl. 16, figs. 81-83, pl. 18, figs. 108a-b. Boltovskoy and Riedel, 1980, p. 121, pl. 5, fig. 1 ; Dolven et al. 2014, p. 52, pl. 6, figs. 10-17 [lectotype: Dolven et al., 2014, pl. 6, figs. 10a, b, specimen number PMO224.485/1, slide #34 (O39/4 lower right), paralectotype 1: pl. 6, fig. 11, specimen number PMO224.485/2, slide #34 (O39/4 top), paralectotype 2: pl. 6, fig. 12, specimen number PMO224.485/3, slide #34 (O39/3 top), housed in the Zoological Museum (Jørgensen collection), Bergen, Norway].

Remarks: The state of preservation of the illustrated specimen (pl. 2, fig. i) does not allow to be certain of its identification to the species level because it is not possible to know if the four primary spines are absent or broken.

***Arachnocorallium* spp.** (Pl. 1, fig. r)

Arachnocorallium spp. group Kršinić and Kršinić, 2012, pl. IV, fig. 44.

Arachnocorallium group Riedel et al., 1985, p. 508, pl. 3, figs. 13a-c; Danelian and Frydas, 1998, p. 141, pl. 4, figs. 11-15.

Arachnocorallium sp. group Boltovskoy, 2010, p. 213.

Remarks: Are grouped under this name unisegmented Dimelissidae with a latticed cephalis and well-developed A, V, Lr and Ll spines. As outlined in Boltovskoy (2010), this represent an artificial grouping of closely related species which are traditionally assigned to different genera (e.g. *Phormacantha*, *Peridium* or *Arachnocorys*) whose systematics is very complicated.

Family PLAGIACANTHIDAE Hertwig, 1879 *sensu* Dumitrica (2004)

Neosemantis cladophora (Jørgensen)
(Pl. 2, fig. m)

Campylacantha cladophora Jørgensen, 1905, p. 129, pl. 12, figs. 47a-c
; Dolven et al., 2014, p. 45, pl. 4, figs. 7-10 [lectotype: Dolven et al., 2014, pl. 4, fig. 7, specimen number PMO224.471/1, slide #36 (M37/1 upper left), paralectotype 1: pl. 4, fig. 8, specimen number PMO224.471/2, slide #36 (M37/1 middle), paralectotype 2: pl. 4, fig. 9, specimen number PMO224.471/3, slide #36 (M37/1 lower left), housed in the Zoological Museum (Jørgensen collection), Bergen, Norway].

Neosemantis cladophora (Jørgensen): Goll, 1979, p. 385, pl. 4, figs. 16-19.

Tetraplecta pinigera Haeckel
(Pl. 2, fig. c)

Tetraplecta pinigera Haeckel, 1887, p. 924, pl. 91, fig. 8; Takahashi, 1991, p. 93, pl. 24, figs. 1-5.

Family PSEUDODICTYOPHIMIDAE Suzuki *in* Suzuki et al. (2021)

Pseudodictyophimus gracilipes (Bailey)
(Pl. 2, fig. d)

Dictyophimus gracilipes Bailey, 1856, p. 4, pl. 1, fig. 8; Itaki and Bjorklund, 2006, p. 452, pl. 1, figs. 18, 19 [Lectotype: Itaki and Bjorklund, 2006, pl. 1, figs. 19a, b, slide #654 (R37/0), housed in the Farlow Herbarium of Harvard University (Bailey collection), USA].

Pseudodictyophimus gracilipes (Bailey): Petrushevskaya, 1971, p. 93, fig. 48: I, IV, V; Takahashi, 1991, p. 116, pl. 37, figs. 12-14; Kršinić and Kršinić, 2012, pl. VII, fig. 71 ; Matsuzaki et al., 2015, p. 48, figs. 8.6, 8.7.

Dictyophimus tetracanthus Popofsky, 1913, p. 333, text-fig. 42.

Family PTEROCORYTHIDAE Haeckel, 1882

***Pterocorys* sp.**
(Pl. 2, figs. k, l)

Remarks: The studied samples contain specimens on which only the cephalis was preserved.

3.2 Polycystine radiolarian diversity

Thirty species were identified in our material, although some of them are currently left in open nomenclature; they are assigned to 23 families, 10 of which are Spumellarian (13 species), 12 Nassellarian (16 species) and one Entactinarian (1 species).

The highest levels of abundance and diversity are found in the deepest (4,500 m water depth) but oligotrophic Ionian site, collected from a 2,000 m deep sediment trap, in which 23 species were observed during November 2014 (see Table 1), with approximately as many Nassellarian species as Spumellarians. The lowest levels of radiolarian diversity, with 3 to 4 species at best, were observed in the north Aegean and Cretan Sea sites. The diversity of radiolarians collected in summer 2015, from a 500 m deep sediment trap of the mesotrophic North Aegean Sea amounts to only 4 species, mainly Spumellarians. There is a sharp contrast between the Ionian and Cretan sites when we compare the observed diversity recorded during the month of November (even if data are not from the same year). The second highest diversity in the Ionian Sea is recorded in August 2015 with 10 species, which is nearly 3 times more diverse than in the North Aegean and Cretan sites recorded for the same period.

A seasonal pattern may be tentatively recognized while comparing the investigated sites between them. Regarding the North Aegean Sea, a single species was found in June 2015 while three species were found in August of the same year. A similar distribution was observed for the Ionian Sea, with only three species found in June, ten species in August of the same year and up to 23 species in November of the previous year. However, a reverse pattern appears to occur in the Cretan Sea, with the highest diversity observed during August 2015 (four species), while two species were found in October, and only one and two species in the beginning and middle of November, respectively (Table 1).

4) Discussion

Current circulation in the Eastern Mediterranean is influenced by cyclonic and anticyclonic eddies with water masses displaying a considerable spatial variability. Current circulation is even more complex in the North Aegean, Cretan and Ionian seas, as it is also controlled to a great extent by the highly diverse coastal configuration and bathymetry (Skampa et al., 2020).

Living polycystine radiolarians from the Eastern Mediterranean have been integrated in the few ecological studies published so far, but data are difficult to be compared with our findings, as in most cases these only report a species list, without any accompanying

illustration that would allow to understand the adopted species concept. This is for example the case of the study conducted by Kimor and Wood (1975), who reported a list of eleven polycystine radiolarian species (5 nassellarians and 7 spumellarians). In addition, with the exception of the site situated East of the island of Rhodes (see black circle in Fig. 1), it is not clear whether they found polycystine radiolarians in any of the other sites of plankton collection in the Eastern Mediterranean. The same difficulties exist regarding the study of Abboud-Abi Saab (1988), who published a list of 18 spumellarian, 24 nassellarian and 7 collodarian species sampled in the plankton off Lebanon without any illustration and/or explanation of taxonomic concepts used. Interestingly, this author noted that their maximum abundance was recorded during February and June. Finally, Zakaria et al. (2018) reported a list of 6 nassellarian, 6 spumellarian and 3 collodarian species from plankton samples off Egypt; once again without any illustrations and/or taxonomic explanations comparison of their species occurrences with our findings will remain doubtful.

Kršinić & Kršinić (2012) published a particularly interesting account of the diversity of polycystine radiolarians living in the Adriatic Sea, along a transect situated off Dubrovnik (Croatia). They reported 78 polycystine species (32 spumellarians and 46 nassellarians), which are all illustrated and can be therefore compared with our material, especially with the fauna observed in the Ionian Sea site. More particularly, the Ionian Sea radiolarian fauna sampled in November 2014, the one that displays the highest diversity amongst the few studied samples, shares 13 species in common with the polycystine species reported from off Dubrovnik (see Table 1). These authors noticed that the highest diversity and abundance was observed at their deepest station and that “the average number of species in the vertical column ranged from 12 to 20 species” (p. 204). Although they were collecting plankton with a Nansen net, equipped with a closing system, the reported diversity of 12-20 species is fairly comparable with the 23 species collected over a 15 day interval in the sediment trap we studied. Therefore, as a first approximation we may regard the Ionian Sea radiolarian stocks as fairly similar to the ones living in the Adriatic. Interestingly, eight (8) of the species we observed in the Ionian site (*Gonosphaera primordialis*, *Hexacromyum* sp. cf. *H. giganteum*, *Hexacromyum* sp. cf. *H. heracliti*, *Larcopele cervicornis*, *Litharachnium tentorium*, *Lithelius minor*, *Lophophaena* sp. cf. *witjazii* and *Tetraplecta pinigera*.) are not reported from the Adriatic.

Regarding the Aegean and Cretan seas two previous studies are of relevance. Toklu-Aliçli & Balkis (2007) reported the presence of a single nassellarian species (*Clathrocorys*

teuscheri) observed in a subsurface water sample of the NE Aegean, a species that we did not encounter in our samples. The only other study reporting polycystines from the Aegean and Cretan Seas is the plankton ecological study of Miliou et al. (2012). These authors conducted a multivariate analysis of observations on microplankton assemblages from the central and southeastern Aegean Sea. However, since identifications were made at the family level and the authors did not specify the exact dates of their sampling, neither whether (or not) polycystines were observed in all 16 stations, it is difficult to compare usefully their data with our observations. It is noteworthy that these authors found that polycystines were the most abundant in the stations situated in the Sitia bay, just North of eastern Crete. By comparison with the Ionian site (KMSXV) our sediment trap samples collected from north of Heraklion (Crete) do not seem to reflect an abundant radiolarian living stock. However, any conclusions are pre-mature at this stage.

It is possible that one of the reasons of finding a higher diversity in the Ionian Sea site is related to its collection depth (2,000 m, as opposed to 500 m and 1,470 m for the other two sites) and to the total depth of the water column at this site (4,500 m). As reported from previous studies, deeper sediment traps always record a more diverse and abundant radiolarian assemblage (Boltovskoy, 2017), which may reflect to a great extent the fact that deep traps allow to collect both surface and deep dwelling species. As an example, a well-known deep dwelling species, such as *Cornutella profunda*, was only found in the deep sediment trap of the Ionian Sea.

It is also noteworthy that the species *Gonosphaera primordialis* Jørgensen, which was known previously only from the high latitudes of the northern (Jørgensen, 1905; Dumitrica, 2001) and southern (Renaudie, 2014; Trubovitz et al., 2020) hemispheres, is now found for the first time in the Mediterranean Sea. Another interesting case to report is the species *Qiuripyrolena chikuchik* Zhang and Suzuki, which was previously known only from the Pacific Ocean. Thus, this preliminary report allows to improve the paleobiogeographic mapping of these species.

5) Conclusions

In spite of the limited number of studied samples this preliminary account of polycystine radiolarians in 3 different sites of the North-East Mediterranean with different trophic states allows to reach some tentative conclusions, which are in need to be confirmed in the future.

- 1) The oligotrophic Ionian Sea supports the most abundant and diverse radiolarian communities of the north-Eastern Mediterranean, comparable to the ones reported from the Adriatic Sea. The highest numbers are recorded in late fall (late November).
- 2) The highest diversity may be partly explained by the depth of the sediment trap collection and possibly by the important depth of the water column (4,500 m).
- 3) Comparison of the radiolarian record between the Ionian and north Aegean sites shows a seasonal pattern, with 3 times more species in August than in June 2015. Interestingly, radiolarian communities in the oligotrophic Ionian Sea are 3 times more diverse than in the mesotrophic north Aegean site.

Acknowledgements

Sediment trap samples were obtained in the frame of the projects 'KRIPIS integrated observatories in the Greek seas' (MIS 451724), funded by the Greek National Strategic Reference Framework (NSRF) and 'MedEcos (Decadal-Scale Variability of the Mediterranean Ecosystem)', jointly funded by the EU F.P.6 ERA-network MarinERA call and by the Greek General Secretariat of Research and Technology, Ministry of Development. TD acknowledges support from the TelluS Program of CNRS/INSU. MT, SS and AG acknowledge support by the Action 'National Network on Climate Change and its Impacts – CLIMPACT', funded by the Public Investment Program of Greece (GSRT, Ministry of Development and Investments). Constructive remarks by Johan Renaudie (Berlin) and an anonymous reviewer improved the initial manuscript.

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CAPTIONS

Fig. 1 Map of the Mediterranean Sea displaying the sampling/collection points of polycystine radiolarians from water samples (black circles: confirmed presence; dots: possible presence), sediment traps (squares) and Pleistocene sediments (triangles).

Plankton samples: 1) Müller (1859a), Haeckel (1860, 1862); 2) Hollande & Enjumet (1960); 3) Kimor & Wood (1975): note that only for the site situated east of the island of Rhodes there is clear mention of polycystine radiolarians; 4) Abboud-Abi Saab (1988); 5) Kršinić & Kršinić (2012); 6) Toklu-Aliçli & Balkis (2007); 7) Miliou et al. (2012), note that only for the 3 sites situated north of eastern Crete there is clear mention of polycystine radiolarians; 8) Zakaria et al. (2018).

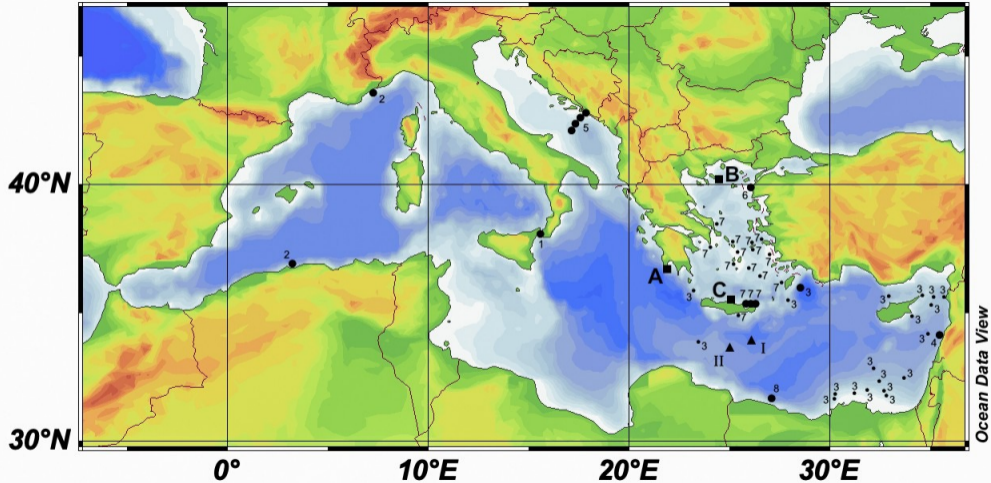
Pleistocene sediment samples: I) Bjørklund & De Ruiter (1987); II) Danelian & Frydas (1998).

Sediment trap samples : A) Ionian Sea; B) North Aegean Sea; C) Cretan Sea.

Plate 1: Microphotographs of polycystine radiolaria found in the sediment trap samples KMSXVC3 (figs. a-b,d-e,g-s) collected from the Ionian Sea, M3AVIII B8 (fig. c) and M3AVIII B6 (fig. t) from the Cretan Sea, and M2IIA5 (fig. f) from the North Aegean Sea. Scale corresponds to 80 µm. **a)** *Haliomma* ? sp.; **b)** *Amphisphaera* ? sp.; **c)-** *Didymocyrtis tetrathalamus* (Haeckel); **d)** *Didymocyrtis tetrathalamus tetrathalamus* (Haeckel); **e)** *Eucecryphalus* ? *danaes* (Haeckel) ; **f -g)** *Hexacromyum* sp. cf. *H. giganteum* (Cortese and Bjørklund); **h)** *Lithelius minor* Jørgensen group; **i)** *Hexacromyum* sp. cf. *H. heracliti* (Haeckel); **j)** *Litharachnium tentorium* (Haeckel); **k)** *Lophospyris pentagona pentagona* (Ehrenberg); **l-m)** *Stylodictya multispina* Haeckel; **n)** *Tetrapyle octacantha* Müller group; **o)** *Zygocircus productus* (Hertwig) group; **p)** *Eucyrtidium acuminatum* (Ehrenberg); **q)** Lophophaenidae, gen et sp. indet.; **r)** *Arachnocorallium* spp.; **s - t)** *Pylodiscus* sp.

Plate 2: Microphotographs of polycystine radiolaria found in the sediment trap samples KMSXVC3 (figs. a-e, l, p), KMSXVIC5 (g, h) and KMSXVIC1 (m - o) from the Ionian Sea, samples M2IIA5 (figs. f, i) and M2IIA1 (fig. j) from the North Aegean Sea, samples M3AVIII B6 (fig. k) and M3AVIII B8 (fig. p) from the Cretan Sea. Scale corresponds to 80 µm for all specimens with the exception of g, h, m, n and for which scale = 50 µm. **a)**

Phorticium multispinum Popofsky *sensu* Zhang and Suzuki; **b**) *Qiuripyrolena chikuchik* Zhang and Suzuki ; **c**) *Tetraplecta pinigera* Haeckel; **d**) *Pseudodictyophimus gracilipes* (Bailey); **e - f**) *Larcopyle cervicornis* (Haeckel) *sensu* Zhang and Suzuki (2017); **g**) *Gonosphaera primordialis* Jørgensen; **h**) *Botryostrobus auritus/australis* (Ehrenberg) gr.; **i**) ? *Lithomelissa setosa* Jørgensen; **j**) *Stylodictya asterisca* (Haeckel); **k - l**) *Pterocorys* sp.; **m**) *Neosemantis cladophora* (Jørgensen); **n**) *Lophophaena* sp. cf. *L. witjazii* (Petrushevskaya); **o**) *Clathrocircus stapedius* Haeckel; **p**) *Cornutella profunda* Ehrenberg.



	North Aegean Sea		Cretan Sea					Ionian Sea			off Dubrovnik
Mooring depth (m)	500		1470					2000			
Water column depth (m)	970		1570					4500			
Coordinates	39° 58.16'N, 24°43.48'E		35° 44.76'N, 25° 09.29'E					36° 2.96'N, 21° 28.93'E			
Sample	M2IIA1	M2IIA5	M3AVIII B1	M3AVIII B6	M3AVIII B7	M3AVIII B8	KMSXVC3	KMSXVIC1	KMSXVIC5		
Start of sampling d	01/06/2015	01/08/2015	01/08/2015	16/10/2015	01/11/2015	16/11/2015	16/11/2014	01/06/2015	01/08/2015		
Taxa \ Sampling duration (day)	15	15	15	16	15	15	15	15	15		
<i>Amphisphaera</i> ? sp.							X				
<i>Arachnocorallium</i> spp.			?				X	X			X
<i>Botryostrobus auritus/australis</i> (Ehrenberg) gr.									X		X
<i>Clathrocircus stapedius</i> Haeckel								X			
<i>Cornutella profunda</i> Ehrenberg							X		X		X
<i>Didymocyrtis tetrathalamus</i> (Haeckel)						X					
<i>Didymocyrtis tetrathalamus tetrathalamus</i> (Haeckel)							X				X
<i>Eucecryphalus</i> ? <i>danaes</i> (Haeckel)							X				X
<i>Eucyrtidium acuminatum</i> (Ehrenberg)							X				X
<i>Gonosphaera primordialis</i> Jørgensen									X		
<i>Haliomma</i> ? sp.							X				
<i>Hexacromyum</i> sp. cf. <i>H. giganteum</i> (Cortese and Boltovskoy)		X					X	X	X		
<i>Hexacromyum</i> sp. cf. <i>H. heracliti</i> (Haeckel)							X				
<i>Larcopele cervicornis</i> (Haeckel) <i>sensu</i> Zhang and Suzuki, 2017		X					X				
<i>Litharachnium tentorium</i> (Haeckel)							X				X
<i>Lithelius minor</i> Jørgensen gr.					X		X				
? <i>Lithomelissa setosa</i> Jørgensen		X									
<i>Lophophaena</i> sp. cf. <i>witjazii</i> (Petrushevskaya)								X			
Lophophaenidae gen et sp. indet.			X				X				
<i>Lophospyris pentagona pentagona</i> (Ehrenberg)							X		X		X
<i>Neosemantis cladophora</i> (Jørgensen)								X			
<i>Phortidium multispinum</i> Popofsky							X				
<i>Pseudodictyophimus gracilipes</i> (Bailey)							X				X
<i>Pterocorys</i> sp.			X	X			X				
<i>Pyrodiscus</i> sp.			X	X			X				
<i>Qiuripylolena chikuchik</i> Zhang and Suzuki							X				
<i>Stylodictya asterisca</i> (Haeckel)	X					X			X		X
<i>Stylodictya multispina</i> Haeckel							X				X
<i>Tetraplecta pinigera</i> Haeckel							X				
<i>Tetrapyle octacantha</i> Müller gr.							X		X		X
<i>Zygocircus productus</i> (Hertwig) gr.							X		X		X