



ATLAS OF HOLOCENE ORGANIC-WALLED DINOFLAGELLATE CYSTS OF THE MAR PICCOLO (TARANTO, SOUTHERN ITALY)

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Abstract: Dinoflagellates are one of the major components of modern plankton. Some of them produce a preservable organic-walled resting cyst, known as a dinocyst, which represents a direct link between the organism, its environment, and the sedimentary record. Dinocysts provide a unique window into key palaeoecological and palaeoenvironmental factors, such as past sea-surface conditions. Analyzing dinocyst assemblages, essential for deciphering such factors, requires a robust taxonomy and consistent nomenclature for accurate taxa identification. Here, 60 dinoflagellate cyst taxa have been identified in the frame of palynological analyses of Holocene sedimentary archives (S05B core and surface sediments) from Mar Piccolo, a semi-enclosed basin of the Mediterranean Sea. Taxa have been briefly described, and 251 micrographs have been collected in 21 plates. The Atlas offers comprehensive iconographic documentation that is also valuable for comparing dinocyst assemblages from open and semi-enclosed seas of the Mediterranean.

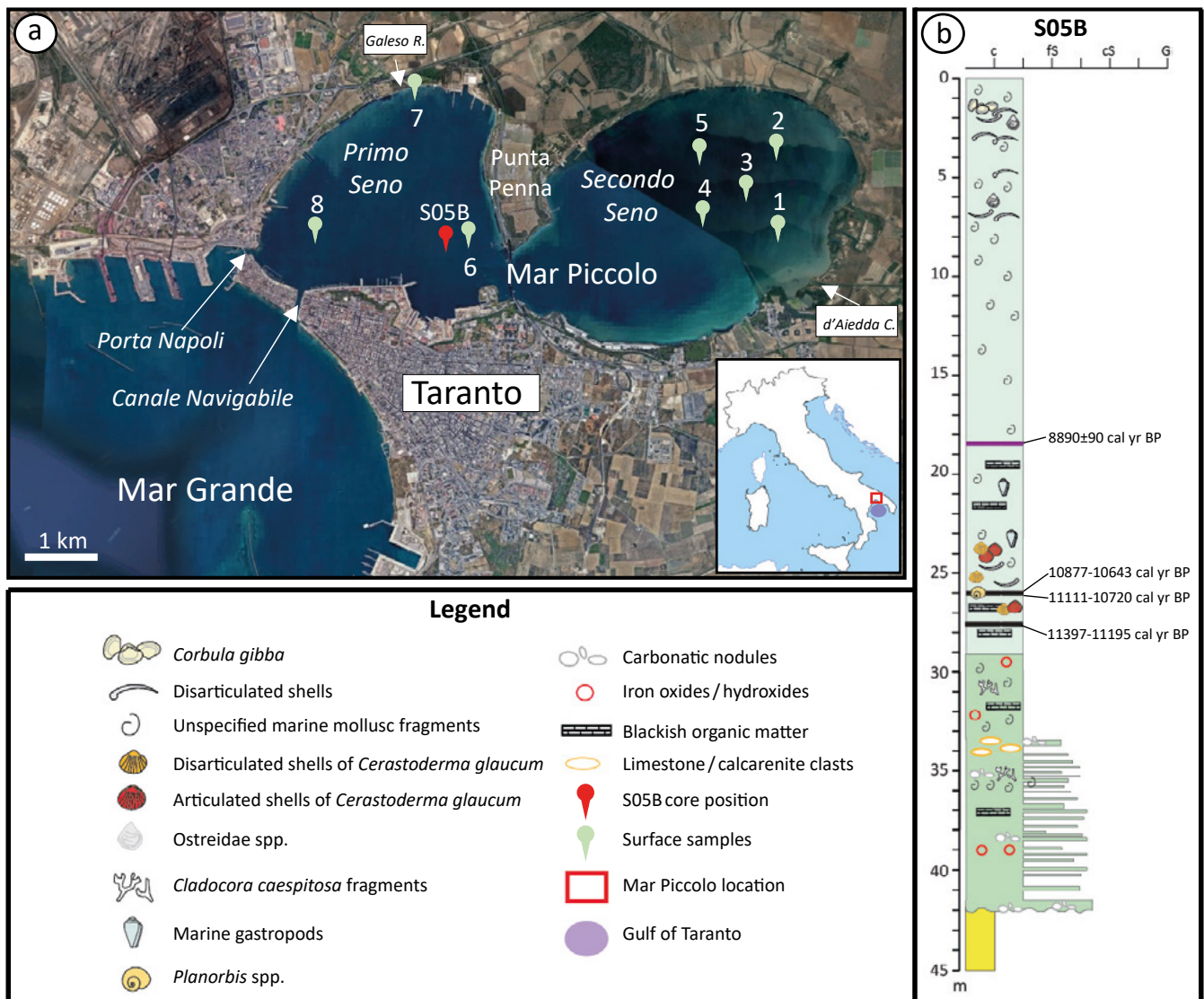
Key words: resting cysts, sedimentary core, surface sediments, semi-enclosed marine basin, Late Quaternary, Mediterranean Sea

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Introduction

Dinoflagellates are microscopic unicellular protists (division Dinoflagellata; Fensome et al. 1993). They inhabit a wide range of aquatic environments, from lakes to open oceans, across all latitudes, from the equator to the polar regions. They are significant primary producers, along with diatoms and coccolithophorids. About half of the present dinoflagellate taxa are phototrophic; others are heterotrophic, mixotrophic, parasitic, or symbiotic. Some dinoflagellates, such as *Symbiodinium* (LaJeunesse et al. 2018), are symbionts of several organisms, notably corals but also radiolarians, and foraminifera (Pawlowski et al. 2001, Pochon et al. 2004). They have a complex life cycle involving several stages: asexual and sexual, motile and non-motile (Dale 1983). The motile cell of dinoflagellates does not fossilize; however, during their life cycle, some species produce resistant organic-walled cysts composed of dinosporin, which protects the diploid cells after fusion of the gametes. The cyst permits survival of the organism during a dormancy period of variable length, from the season to decades (e.g., Wall and Dale 1968, Fensome et al. 1993). About 10–20 % of the species produce organic-walled cysts (e.g., Dale 1977, Head 1996), also known as “dinocysts”, ranging from ca. 15 to 100 µm. They are routinely observed in palynological slides under an optical

microscope at magnifications ranging from 250× to 1,000×. Their extraction from sediments is according to the same laboratory procedures used for pollen analyses, including treatments with hydrofluoric and hydrochloric acids. A few dinoflagellate taxa produce calcareous (e.g., Gómez 2020) or siliceous cysts (e.g., Harding 2020). Organic-walled dinocysts are generally well preserved in most sediments, unlike calcareous or siliceous biological remains that can be affected by dissolution. Moreover, unlike many biological tracers that are stenohaline and thus restricted to the open ocean (Zonneveld et al. 2013), dinoflagellates are euryhaline and can tolerate a wide range of salinities, which allows for investigations in near-shore environments, epicontinental seas, or estuaries, in addition to full oceanic environments. Nonetheless, the concentration of dinocysts in sediment falls notably offshore, particularly in low-productivity ocean gyre areas (e.g., de Vernal et al. 1994, Marret 1994, Vink et al. 2000). Dinocysts are largely used in biostratigraphy, palaeoceanography, and palaeoecology throughout Mesozoic and Cenozoic sediments. Continuous revisions in dinocyst taxonomy have been made, with tabulation serving as the primary morphological connection between living dinoflagellates and their fossilized cysts (e.g., Zonneveld and Pospelova 2015, Riding et al. 2022). Relationships between modern assemblages and present-day environmental factors allow for dinocyst-based quantitative



Text-fig. 1. (A) Location map of Mar Grande and Mar Piccolo near Taranto (Mediterranean area); position of both S05B core and surface samples in Mar Piccolo also indicated. **(B)** Lithostratigraphic log of S05B core (modified from Valenzano et al. 2018).

reconstructions derived from transfer function calculations, especially applied for the study of Quaternary sedimentary successions (Hohmann et al. 2020 and references therein).

Despite the growing interest in Quaternary dinocysts, a comprehensive atlas has yet to be developed to systematically document and illustrate dinocyst assemblages in Southern Italy. To address this gap, the present study focuses on Holocene dinocysts from Mar Piccolo (MP), a shallow semi-enclosed marine basin of the Mediterranean located in Southern Italy (Text-fig. 1). Ongoing palynological research in MP includes studies on pollen (Niccolini and Bertini 2023), dinocysts, and non-pollen palynomorphs (NPPs) (Degl'Innocenti, PhD thesis 2025; Niccolini et al. 2026). As part of this research, we present a curated collection of micrographs from both the Holocene sedimentary core S05B and surface sediment samples, organized into an atlas based on morphological and taxonomic criteria. Additionally, this atlas will serve as a valuable reference for researchers studying phytoplankton biodiversity and ecological dynamics of semi-isolated marine environments, and their relationship with adjacent open-sea ecosystems.

Study area

Environmental setting

The MP of Taranto is a shallow, semi-enclosed marine basin of nearly 20 km², situated in the central Mediterranean region, at the northern end of the Ionian Sea (Text-fig. 1a). Together with Mar Grande (maximum depth of ca. 35 m and mean salinity of 37.8), it is part of a coastal marine ecosystem heavily impacted by human activities, especially the industry settlement (e.g., Cardellicchio et al. 2007, 2016, Kralj et al. 2016). As a result, the Taranto area has been classified as a Site of National Interest under National Law no. 426 (1998) and included in the National Environmental Remediation and Restoration Projects.

The *Punta Penna* promontory divides the MP into two sub-basins named *Primo Seno* and *Secondo Seno* (Text-fig. 1a). The *Primo Seno*, the western sub-basin, has a maximum depth of 13 m; here, the annual mean salinity of the water column is around 37, while the annual mean temperature is

around 18.5 °C (Pascalis et al. 2016). The *Secondo Seno*, the eastern sub-basin, has a maximum depth of 9 m and shows an annual mean salinity of water column of around 37 (36 during the winter and fall seasons), while the annual mean temperatures reach 19 °C, especially near the shoreline (Pascalis et al. 2016). The water circulation of the MP is weak, without significant tidal excursions (< 30–40 cm). The seawater exchanges with the larger semi-enclosed bay of the Mar Grande take place from *Primo Seno* through two channels, the *Canale Navigabile* and the *Porta Napoli* (Text-fig. 1a). The *Canale Navigabile* is an artificial, navigable channel with a depth of 12 m and a width of 58 m, while *Porta Napoli*, of natural origin, has a depth of 2.5 m and a width of 48 m. The low hydrodynamism and the reduced water exchange with the nearby Mar Grande (Umgiesser et al. 2007) are particularly evident in the *Secondo Seno* (current velocity close to 0 cm/s, Pascalis et al. 2016), as attested by both water stratification (especially in summer) and the stabilization of wetlands along its coasts (Scroccaro et al. 2004). The weak water circulation (De Serio et al. 2007) promotes organic matter sedimentation and the accumulation of pollutants in sediments. For many decades, this area has been impacted by the effects of the largest steelwork complex in Europe (ILVA), the main Italian Navy shipyard and arsenal, an oil refinery, and shipbuilding activities. Moreover, the discharge of urban wastewater and the freshwater draining from the nearby agricultural soil (e.g., Caroppo et al. 2012) are responsible for eutrophication. The unique hydrological characteristics of MP, including limited water circulation, low water exchange, and shallow depth have encouraged extensive mussel farming. MP currently boasts the largest mussel farm in Italy, with widespread installations in the northern areas of both sub-basins (e.g., Cardellicchio et al. 2016). In the two MP sub-basins, water salinity and temperature values are influenced by seasonal freshwater flows from several submarine springs, locally called “*Citri*” (Valenzano et al. 2020 and reference therein), and small surface watercourses, e.g., “*Galeso*” (the most important with a mean flow of 50,000 m³ day⁻¹) in the *Primo Seno*. Submarine springs dispense uniform 18 °C freshwater (salinity of 2–5) with a maximum total flow of 0.01 km³ week⁻¹ into the basin (total water volume ca. 0.15 km³). In the north of the two sub-basins, these springs favor the occurrence of a thin, brackish surface water layer (< 10 cm), whereas the remaining water column is usually homogeneous and not stratified. Sediments in the basin primarily comprise grain sizes ranging from silt to clay (Rubino et al. 2016); sand size grains only occur near the connection to the Mar Grande and the northern coast of *Secondo Seno*. Sedimentation rates were calculated to be 0.15 ± 0.01 g cm⁻² y⁻¹, in *Primo Seno*, and 0.17 ± 0.04 g cm⁻² y⁻¹ in *Secondo Seno* (Dominik et al. 2023). The main geomorphological changes during the latest Quaternary were analysed and discussed in several works (e.g., Pagliarulo and Bruno 1990, Mastronuzzi and Sansò 1998, 2003, Guerricchio and Simeone 2013, Mastronuzzi et al. 2013). According to the most recent interpretation by Valenzano et al. (2018), the formation of MP involved a sequence of events, starting with fluvial incision, followed by the development of a lacustrine environment until the Middle Holocene. It was during this

time that a marine transgression occurred, ultimately leading to the establishment of the semi-closed marine basin that persists today (Niccolini et al. 2025).

Modern dinoflagellate communities and their resting stages in the Mar Piccolo

Several studies have investigated the composition of planktonic communities in the Taranto seas; here we especially focus on those based on samples collected during sampling campaigns conducted in 2010–2011 (Rubino and Belmonte 2021), December 2011 (Ferraro et al. 2017), June 2013 and April 2014 (Rubino et al. 2016), December 2016 (Francescangeli et al. 2024). Research on dinoflagellate cyst communities has revealed significant differences between the two sub-basins (*Primo Seno* and *Secondo Seno*), despite their close geographic proximity (Text-fig. 1a).

Rubino and Belmonte (2021) provided valuable data from the 2010–2011 campaign in the *Primo Seno*. The use of multiple devices for integrated sampling of both benthic and pelagic stages enabled the identification among Dinophyta of 48 taxa as motile forms and 59 taxa as resting stages. With reference to the motile stages in the water column, they include: *Akashiwo sanguinea*, two species of *Alexandrium*, five species of *Ceratium*, *Cochlodinium polykrikoides*, four species of *Dinophysis*, *Diplopsalis lenticula*, *Goniodoma polyedricum*, three species of *Gonyaulax*, two species of *Gymnodinium*, *Lingulodinium polyedrum*, *Nematodinium* sp., *Neoceratium furca*, *Oblea rotunda*, *Ornithocercus* sp., *Oxytoxum* sp., *Polykrikos schwartzii*, three species of *Prorocentrum*, *Protoceratium* sp., twelve species of *Protoperidinium*, *Pyrophacus steinii*, and four species of *Scrippsiella* (for a complete list of taxa, see Rubino and Belmonte 2021: tab. 3).

Ferraro et al. (2017) identified 66 dinoflagellates cysts in the samples retrieved during the December 2011 campaign (for a complete list of taxa, see Ferraro et al. 2017: tab. 3). *Scrippsiella* spp. constitute 30 % of the assemblage in both sub-basins, with *S. acuminata* being the most abundant taxon in MP. Notably, *Calciodinellum albatrosianum* was the species most characteristic of *Primo Seno*, while *Gymnodinium impudicum* dominated in *Secondo Seno*.

Rubino et al. (2016) identified 49 taxa from four samples retrieved during the two campaigns in June 2013 and April 2014. In their analyses, the resting stage of the dinoflagellate *Scrippsiella trochoidea* was by far the most abundant species, accounting for 67 % of the total abundance in June and 49 % in April. Other abundant taxa included the resting stage of *Calciodinellum operosum*, *Pentaparsodinium tyrrhenicum*, *Posoniella tricarinelloides*, *Gonyaulax* group, *Gymnodinium impudicum*, and *Lingulodinium polyedrum* (for a complete list of taxa, see Rubino et al. 2016: tab. 4). Moreover, Rubino et al. (2016) revealed variations in resting stage assemblages between the two sub-basins. The *Primo Seno* exhibited higher species richness and ecological diversity, while the *Secondo Seno* had a greater abundance of resting stages. This shows not only how the dinophyta assemblages have changed over time in the same study location, but also how the environmental differences between the *Primo* and *Secondo Seno* have a direct impact

on the assemblages, activity, and production of both the active community and the resting biodiversity.

Francescangeli et al. (2024), studying the samples collected during the campaign of December 2016, recognised a total of 51 taxa. The dinoflagellate cyst assemblage was dominated by *S. acuminata* in both sub-basins (63.7 % and 65.5 % in the *Primo Seno* and *Secondo Seno*, respectively), along with *S. erinaceus* and *P. tyrrhenicum* (for a complete list of taxa, see Francescangeli et al. 2024: tab. S1). Interestingly, Francescangeli et al. (2024) discovered overall density (cyst/g) results higher than in 2011, while the species diversity follows an opposite trend, i.e., it was higher in 2011. To explain these patterns, the authors examined a number of factors potentially influencing cyst communities in the sediments, including seasonality variations in encystment rates (between 2011 and 2016), chemical contamination, sedimentation rates, horizontal transport, bioturbation, reworking of the sediments, and degradation due to oxidative conditions in the sediments.

Materials and methods

Palynological samples

In the MP, palynological samples were collected from both the surface sediments and sedimentary core S05B (Text-fig. 1a, b).

Sedimentary core

The S05B core (Text-fig. 1b) was recovered during seismic and drilling campaigns in 2013 and 2015 (Valenzano et al. 2018) from the deepest part of the *Primo Seno* (40° 28.853' N, 17° 15.801' E, 13 m b.s.l., Text-fig. 1a, Tab. 1), and stored in the laboratory of the Department of Earth and Geoenvironmental Sciences (DISTEGEO), in Taranto. The S05B core is approximately 45 m long, but for this study, here only the Holocene interval (according to Valenzano et al. 2018, Niccolini et al. 2025), from 29 m to the top, was analysed (Text-fig. 1b). From 29 m to 24 m, the sedimentary core consists of continuous organic-rich silts with abundant plant remains and malacofauna (e.g., gastropods and bivalves); two peat layers rich in vegetal remains (seeds and wood fragments) are present between 27.50 m and 25.95 m. The peat stratum at 25.95 m was dated to 10,336 ± 87 cal yr BP (Valenzano et al. 2018). Recently, new AMS ¹⁴C datings were performed in peat strata retrieved at 27.61, 26.05, and 25.76 m (Niccolini et al. 2025), respectively calibrated at 11,397–11,195, 11,111–10,720, and 10,877–10,643 cal yr BP. From 24 m to the top, there are prevalent grey silts with occasional organic matter content. At 18.50 meters, the *Pomici di Mercato* tephra was identified; it was dated to 8,890 ± 90 cal yr BP (Aulinas et al. 2008, Mele et al. 2011).

Palynological sub-samples were collected every 3 cm, resulting in a total of 971 samples, 473 of which were processed at the Palynological Laboratory of the Department of Earth Sciences in Florence.

Table 1. List of sedimentary archives and their respective geographical coordinates, locations in Mar Piccolo, and depths (below sea level, b.s.l.).

Type of sedimentary archive	Sedimentary archive name/ number	North	Est	Location	Depth (b.s.l.)
Surface samples	1	40°28.792'	17°18.860'	<i>Secondo Seno</i>	2.8 m
	2	40°29.474'	17°18.818'	<i>Secondo Seno</i>	7.2 m
	3	40°29.180'	17°18.460'	<i>Secondo Seno</i>	7.3 m
	4	40°28.965'	17°18.182'	<i>Secondo Seno</i>	8.1 m
	5	40°29.547'	17°17.990'	<i>Secondo Seno</i>	6.7 m
	6	40°28.853'	17°15.801'	<i>Primo Seno</i>	13 m
	7	40°29.985'	17°15.255'	<i>Primo Seno</i>	2.4 m
	8	40°28.889'	17°14.368'	<i>Primo Seno</i>	12 m
Marine Core	S05B	40°28.853'	17°15.801'	<i>Primo Seno</i>	13 m

Surface sediments

In November 2023, eight surface samples (1 to 8) were collected in the MP basin from different basin depths and environmental contexts (Text-fig. 1a, Tab. 1) using Van Veen grab sampler with a 3-litre capacity. Surface samples 1 to 5 were retrieved in the *Secondo Seno* along two perpendicular transects; in particular, surface samples 1 and 2 were retrieved in proximity to submerged springs. Surface samples 6 to 8 were collected in the *Primo Seno*; near the S05B core site (surface sample 6), the *Galeso* river mouth (surface sample 7), and at ca. 800 m from *Canale Navigabile* (surface sample 8).

Laboratory procedure

A total of 473 sediment core samples and eight surface sediment samples underwent the same palynological chemical-physical treatment. The procedure consists of the following main steps: i. Cleaning and weighing (maximum 14 g – minimum 5 g); ii. Adding a tablet containing a known quantity of *Lycopodium* spores according to the marker-grains methods (Matthews 1969); iii. Acid treatment (HCl 20%, HF 38%, HCl 20%); iv. Addition of sodium hexametaphosphate (NaPO₃)₆; v. Sieving through a 10 µm mesh in an ultrasound bath; vi. Dilution at 1 : 10 ratio with glycerol and mounting of mobile slides.

Microscope analysis

All slides were analysed under a light-transmitted microscope (Nikon ECLIPSE 80i) at a magnification of 400× and 1000× (oil immersion). Image acquisition was performed with a Nikon Digital Sight camera mounted on a trinocular tube and the software NIS element F. LO analysis (Erdtman 1959, 1969) was employed when necessary to enhance taxonomic identification. Images and plates processing was carried out using Adobe Illustrator (2014).

Cyst identification

Taxonomic identification of dinocysts is based on numerous studies (e.g., Head 2002, Pospelova and Head 2002, Matsuoka et al. 2009, Zonneveld et al. 2013, Mertens et al. 2015, 2017, 2020, Mudie et al. 2017, Gurdebeke et al. 2018, Limoges et al. 2018, 2020, Marret and Mertens 2018, Potvin et al. 2018, Van Nieuwenhove et al. 2018, 2020, Head et al. 2020, Head and Mantilla-Duran 2020). The morphological terminology for dinocysts follows Zonneveld and Pospelova (2015), and Matsuoka and Fukuyo (2000). Specimen measurements were performed using ImageJ software.

Dual nomenclature in organic-walled dinoflagellate cysts

In recent years, the scientific community has engaged in an active discussion regarding the dual nomenclature system in organic-walled dinoflagellate cysts. This system allows for the use of distinct names for the fossilized cyst

stage and the corresponding motile stage, even when these stages are demonstrated to belong to the same organism through incubation studies and other methodologies (Mertens et al. 2017; Head et al. 2024). The rationale for this dual system stems from the fact that cyst-based and motile-based taxonomies rely on different morphological criteria and life cycle stages, which are difficult to reconcile under a single taxonomic framework (Head et al., 2024). The recent XX International Botanical Congress (Madrid 2024) has officially recognized this practice by amending the International Code of Nomenclature for algae, fungi, and plants (ICN), formally distinguishing between synonymy (different names for the same taxon) and taxonomic equivalence (different names for cyst and motile stages of the same organism). In this atlas, in Tab. 2, we adopt a dual nomenclatural approach by reporting both the cyst morphotypes and their known motile equivalents, in alignment with these recent advancements, thereby providing a comprehensive reference for future taxonomic and ecological research.

Table 2. List of dinocyst species from Mar Piccolo in fossil record (S05B core) and/or sub-recent archives (surface sediments). On right, Plates and Figures numbers, trophic habits of corresponding motile stage (P = Phototrophic; H = Heterotrophic; M = Mixotrophic; ? indicates uncertainty). Temperature preferences: W = warm dinocysts, C = cold dinocysts. Taxa marked with asterisk also reported in Rubino et al. (2016), Ferraro et al. (2017), Rubino and Belmonte (2021), and Francescangeli et al. (2024).

CYST NAME	Pl.	Figs	S05B CORE	SURFACE SEDIMENTS	TROPHISM	MOTILE STAGE NAME
Cyst of <i>Gymnodinium microreticulatum</i>	1	1–3	X		P	<i>G. microreticulatum</i>
Cyst of <i>Polykrikos kofoidii</i> *	1	4–9	X		H	<i>Polykrikos kofoidii</i>
Cyst of <i>Alexandrium</i> spp.	1	10–12	X	X	P	<i>Alexandrium</i> spp.
<i>Tuberculodinium vancampoe</i>	2	1–6	X		P	<i>Pyrophacus steinii</i>
<i>Polysphaeridium zoharyi</i> *	2	7–8	X	X	P	<i>Pyrodinium bahamense</i>
<i>Lingulodinium machaerophorum</i> *	2 ; 3	9–12 ; 1–6	X	X	P	<i>Lingulodinium polyedra</i>
<i>Operculodinium centrocarpum</i>	3	7–12	X	X	P	<i>Protoceratium reticulatum</i>
<i>Operculodinium israelianum</i> ^W	4	1–3	X	X	P	Unknown
<i>Ataxiodinium choane</i>	4	4–5	X		P	<i>Gonyaulax</i> sp.
<i>Bitectatodinium spongium</i>	4	6–7	X		P	<i>Gonyaulax</i> sp.
<i>Bitectatodinium tepikiense</i> ^C	4	8–12	X		P	<i>Gonyaulax</i> sp.
<i>Impagidinium aculeatum</i> ^W	5	1–6	X		P	Unknown
<i>Impagidinium paradoxum</i>	5	7–12	X		P	<i>Gonyaulax</i> sp.
<i>Impagidinium patulum</i> ^W	6	1–6	X	X	P	<i>Gonyaulax</i> sp.
<i>Impagidinium plicatum</i>	6	7–12	X		P	Unknown
<i>Impagidinium sphaericum</i>	7	1–3	X		P	Unknown
<i>Impagidinium striolatum</i> ^W	7	4–9	X		P	Unknown
<i>Impagidinium velorum</i>	7	10–12	X		P	Unknown
<i>Impagidinium japonicum</i>	8	1–3	X		P	Unknown
<i>Nematosphaeropsis labyrinthus</i> ^C	8	4–9	X		P	<i>Gonyaulax spinifera</i> complex
<i>Spiniferites belerius</i>	8 ; 9	10–12 ; 1–3	X	X	P	<i>Gonyaulax scrippsae</i>
<i>Spiniferites bentorii</i>	9	4–12	X	X	P	<i>Gonyaulax digitale</i>
<i>Spiniferites bulloideus</i>	10	1–3	X		P	<i>Gonyaulax scrippsae</i>

Table 2. continued

<i>Spiniferites delicatus</i>	10	4–9	X	X	P	<i>Gonyaulax</i> sp.
<i>Spiniferites elongatus</i> ^C	10	10–12	X		P	<i>Gonyaulax elongata</i>
<i>Spiniferites hyperacanthus</i> ^W	11	1–2	X	X	P	<i>Gonyaulax</i> sp.
<i>Spiniferites lazus</i>	11	3–11	X		P	Unknown
<i>Spiniferites membranaceus</i>	12	1–6	X		P	<i>Gonyaulax membranacea</i>
<i>Spiniferites mirabilis</i> ^W	12	7–9	X	X	P	<i>Gonyaulax spinifera</i>
<i>Spiniferites mirabilis</i> subsp. <i>serratus</i>	12	10–12	X		P	Unknown
<i>Spiniferites pachydermus</i> ^W	13	1–6	X	X	P	<i>Gonyaulax ellegaardiae</i>
<i>Spiniferites ramosus</i>	13	7–12	X	X	P	<i>Gonyaulax spinifera</i>
<i>Peridinium ponticum</i>	14	1–12	X	X	H	<i>Protoperidinium</i> sp. indet.
Cyst of <i>Diplopelta symmetrica</i>	15	1–6	X		H	<i>Diplopelta symmetrica</i>
<i>Dubridinium caperatum</i>	15	7–12	X		H	<i>Preperidinium meunieri</i>
<i>Dubridinium ulsterum</i>	16	1–3		X	H	Unknown
Cyst of <i>Archaeperidinium minutum</i> sensu Wall and Dale 1968	16	4–6		X	H?	<i>Archaeperidinium minutum</i>
<i>Brigantedinium asymmetricum</i>	16	7–9		X	H	Unknown
<i>Brigantedinium auranteum</i>	16	10–12	X		H	Unknown
<i>Brigantedinium cariacense</i>	17	1–2	X		H	<i>Protoperidinium avellana</i>
<i>Brigantedinium simplex</i>	17	3	X	X	H	<i>Protoperidinium conicoides</i>
<i>Islandinium?</i> <i>cezare</i>	17	4–6	X		H	Unknown
<i>Lejeunecysta oliva</i>	17	7–9	X	X	H	<i>Protoperidinium</i> sp.
Cyst of <i>Protoperidinium denticulatum</i>	17	10	X		H	<i>Protoperidinium denticulatum</i>
Cyst of <i>Protoperidinium nudum</i>	17	11–12	X		H	<i>Protoperidinium nudum</i>
Cyst of <i>Protoperidinium stellatum</i> *	18	1–3	X	X	H	<i>Protoperidinium stellatum</i>
Cyst of <i>Protoperidinium thulesense</i>	18	4	X		H	<i>Protoperidinium thulesense</i>
Cyst of <i>Protoperidinium tricingulatum</i>	18	5–7	X	X	H	<i>Protoperidinium tricingulatum</i>
<i>Quinquecuspis concreta</i> *	18	8–9	X	X	H	<i>Protoperidinium leonis</i>
<i>Selenopemphix nephroides</i> *	18	10–12	X		H	<i>Protoperidinium subinermis</i>
<i>Selenopemphix quanta</i> *	19	1–3	X	X	H	<i>Protoperidinium conicum</i>
<i>Selenopemphix undulata</i>	19	4–9	X		H	Unknown
<i>Trinovantedinium applanatum</i> *	19	10–12	X		H	<i>Protoperidinium shanghaiense</i>
<i>Votadinium calvum</i> *	20	1–3	X	X	H	<i>Protoperidinium oblongum</i>
<i>Votadinium spinosum</i>	20	4–5	X	X	H	<i>Protoperidinium claudicans</i>
<i>Xandarodinium xanthum</i> *	20	6–12	X	X	H	<i>Protoperidinium divaricatum</i>
<i>Echinidinium granulatum</i>	21	1–3	X	X	H	Unknown
Cyst of <i>Pentapharsodinium dalei</i> *	21	4–7	X	X	P	<i>Pentapharsodinium dalei</i>
Cyst of <i>Scrippsiella</i> cf. <i>trifida</i>	21	8–9	X		P	<i>Scrippsiella trifida</i>
Cyst of <i>Scrippsiella</i> cf. <i>trochoidea</i>	21	10–12		X	M	<i>Scrippsiella trochoidea</i>

Result

Palynological analyses of the S05B core (473 samples) and surface sediments (eight samples) allow taxonomic identification of a total of 60 dinoflagellate cyst taxa. Among these, two belong to the order of Gymnodiniales, 30 to Gonyaulacales, and 28 to Peridinales, comprising 34 phototrophs and 26

heterotrophs (Tab. 2). As shown in Tab. 2, of the 60 dinoflagellate cyst taxa detected, 25 are common to both sedimentary archives, 31 are exclusive to the core sediments (S05B), and four were found only in the surface samples. Excluding two barren surface samples, i.e., 1 and 7, all the other surface samples yield quite rich assemblages, exhibiting some differences in the dominant components, depending on their

location within the basin. Surface sample 6, located near the S05B core site in the *Primo Seno*, has the greatest number of species and is the only one to include heterotrophic dinocysts, i.e., *Brigantidium asymmetricum*, cyst of *Archaeoperidinium minutum* (sensu Wall and Dale 1968), and *Dubridinium ulsterum*. Sample 8 (Text-fig. 1a) is the only surface sample in which an *Impagidinium* species (i.e., *I. patulum*) was recorded. On the other hand, several *Impagidinium* species were found in the S05B core, i.e., *I. aculeatum*, *I. paradoxum*, *I. patulum*, *I. plicatum*, *I. sphaericum*, *I. striatum*, *I. velorum*, and *I. japonicum* (Tab. 2).

Secondo Seno surface samples 2 through 5 are especially characterized by *Lingulodinium machaerophorum*, *Spiniferites belerius*, and *S. ramosus*.

The good to excellent preservation of dinoflagellate cysts facilitated their identification and ensured that good micrographs could be obtained. The 251 micrographs were organized into twenty-one plates (Pls 1–21).

Dinocyst description

Each cyst is identified based on its generic description, drawing from previous studies focused on morphological and systematic identification. The description of dinoflagellate cysts is organized according to the systematic order, as reported in more recent similar studies (e.g., Limoges et al. 2020, Mertens et al. 2020, Van Nieuwenhove et al. 2020).

For each taxon, there is a descriptive section (“Descriptions”) that outlines the morphological features essential for identifying the cyst. If any distinctive characteristics mentioned in the literature are not observed, they are reported at the end of the descriptive section, crediting the original authors and providing additional context. In the “Remarks” section, we emphasize the sedimentary archive in which the dinocyst is documented, noting how frequently a dinocyst was observed along the S05B core. In this section, we also highlight and discuss any morphological variations observed within the same taxa.

Systematic palaeontology

Division Dinoflagellata (BUETSCHLI, 1885) FENSOME et al., 1993

Class Dinophyceae PASCHER, 1914

Subclass Gymnodiniphyceae FENSOME et al., 1993

Order Gymnodinales APSTEIN, 1909

Suborder Gymnodiniineae (Autonym)

Family Gymnodiniaceae (BERGH, 1881) LANKESTER, 1885

Genus *Gymnodinium* F.STEIN, 1878

Cyst of *Gymnodinium microreticulatum*

BOLCH et al., 1999

Pl. 1, Figs 1–3

Description. Small, brown and spherical cyst (30–32 µm) with distinct microreticulate surface ornamentation comprising numerous polygons of different sizes. Archeopyle stretches over much of the cysts as a cut, is chasmic, usually

forming from the apex to the antapex, and commonly oriented along the sulcus. According to Bolch et al. (1999) and Bolch and Reynolds (2002), the archeopyle area extends from the acrobasis towards antapex, commonly oriented along the sulcus and marked by rows of smaller polygons.

Remarks. Only a few cysts of *Gymnodinium microreticulatum* are present in the core sediments (S05B).

Family Polykrikaceae KOF. et SWEZY, 1921

Genus *Polykrikos* BUETSCHLI, 1873

Cyst of *Polykrikos kofoidii* CHATTON, 1914

Pl. 1, Figs 4–9

Description. Large proximochoate cyst (89–90 µm length and 53–63 µm width) with elongate central body. It is characterized by a coarsely reticulate ornamentation with solid, thin and smooth endophragm overlaid by a thin periphragm. High and fibrous crests (height of 10–15 µm) cover the entire cyst, forming an irregular and variable reticulation. According to Chatton (1914) and Matsuoka et al. (2009), the archeopyle is tremic, occurs at one end of the central body, and has a roundly polygonal outline with a zigzag margin.

Remarks. Cysts of *Polykrikos kofoidii* are found in the core sediments (S05B), but their occurrence is infrequent.

Subclass Peridiniphyceae FENSOME et al., 1993

Order Gonyaulacales F.J.R.TAYLOR, 1980

Genus *Alexandrium* HALIM, 1960

Cyst of *Alexandrium* spp. (BRAVO et al., 2006)

Pl. 1, Figs 10–12

Description. Transparent cyst, spherical (32–44 µm), with rounded ends, thick walls, and a thin mucilaginous membrane covering it. No tabulation can be seen. According to Bravo et al. (2006), this cyst can show an elongate central body shape too.

Remarks. Cysts of *Alexandrium* spp. are present in sediment surface samples 2, 3, 4, and 6, as well as in the core sediments (S05B), although they are rarely observed in the latter.

Suborder Goniodomineae FENSOME et al., 1993

Family Pyrophacaceae ER. LINDEM., 1928

Subfamily Helgolandinioidae FENSOME et al., 1993

Genus *Tuberculodinium* D.WALL, 1967

Tuberculodinium vancampoae

(M.ROSSIGNOL, 1962) D.WALL, 1967

Pl. 2, Figs 1–6

Description. Large, flattened and discoidal cyst (83–92 µm diameter). The wall layers show light brown to yellowish

pigment, and the wall is characterized by numerous hollows, barrel-shaped processes (13–20 µm length) that appear circular in surface view. The processes can have flaring distal extremities that merge with the outer wall layer. According to Wall (1967) and Matsuoka et al. (1998), the compound archeopyle is polygonal and epicystal, but not clearly related to the epithecal tabulation.

Remarks. *Tuberculodinium vancampoe* is present in core sediments (S05B), but only a few cysts are observed.

Subfamily Pyrodinioideae FENSOME et al., 1993

Genus *Polysphaeridium* R.J.DAVEY et G.L.WILLIAMS, 1966 emend. J.P.BUJAK et al. 1980

***Polysphaeridium zoharyi* (M.ROSSIGNOL, 1962) J.P.BUJAK et al., 1980**
Pl. 2, Figs 7, 8

Description. Proximochorate and spherical cyst (36–44 µm diameter), with a smooth to microgranulate surface wall. Processes are hollow and opened distally (8–15 µm in length). Some processes can be fused together and are distally bifurcate. Archeopyle is epicystal and splits the cyst into two parts. According to Wall (1967) and Limoges et al. (2020), under light microscopy, before excystment, *P. zoharyi* cysts are superficially similar to ungerminated specimens of *O. centrocarpum*. However, after opening, *P. zoharyi* differs in having a large hemispherical epicystal archeopyle.

Remarks. *Polysphaeridium zoharyi* is present in sediment surface samples 2, 6, and 8, as well as in core sediments (S05B), where it is infrequently observed.

Suborder Gonyaulacinae (Autonym)

Family Gonyaulacaceae ER. LINDEM., 1928

Subfamily Cribroperidinioideae FENSOME et al., 1993

Genus *Lingulodinium* D.WALL, 1967
emend. J.D.Dodge 1989

***Lingulodinium machaerophorum* (DEFLANDRE et COOKSON, 1955) D.WALL, 1967**
Pl. 2, Figs 9–12; Pl. 3, Figs 1–6

Description. Chorate and spherical cyst (35–58 µm diameter) with a finely granulate surface. Processes are randomly distributed, with lengths ranging from a few micrometers to > 25 µm, and are characterized by a circular base. They are hollow and usually have a smooth surface over most of their length. Small spinules may be present on processes tips. The processes distal ends are closed, some show thinning (Pl. 2, Figs 9, 10) towards distal ends while others maintain a uniform thickness (Pl. 2, Figs 11, 12). This difference is observed predominantly on longer processes. The processes terminations are usually ornamented with pointed or blunt tip. Slight bifurcations were observed on shorter processes (Pl. 3, Figs 1–3). The archeopyle is precingular and shows a variable morphology in relation to the loss of one to five precingular plates.

Remarks. Cysts of *Lingulodinium machaerophorum* are present in sediment samples 2, 3, 4, 5, 6 and 8, as well as in the core sediments (S05B), where they are commonly observed. Cysts with different process lengths were observed both in core sediments (S05B) and surface samples. Cysts with truncated processes were observed only in core sediments (S05B; Pl. 3, Figs 5, 6).

Genus *Operculodinium* D.WALL, 1967
emend. Matsuoka et al. 1997

***Operculodinium centrocarpum* sensu**
D.Wall and B.Dale (1966)
Pl. 3, Figs 7–12

Description. Spherical cyst (33–41 µm diameter) with a microgranular and thin wall. Processes are slender, circular in cross-section, numerous and uniformly dispersed across the cyst. They are non-tabular and hollow, with lengths varying from long (8 µm – Pl. 3, Figs 7–9) to short (0.7 µm – Pl. 3, 10–12), and show capitate or slightly furcated terminations. The shorter the processes, the less bifurcation of the terminations occurs (Pl. 3, Figs 10–12).

Remarks. *Operculodinium centrocarpum* is present in surface samples 1, 2, 3, 5, and 8, as well as in core sediments (S05B), where it is commonly observed. Cysts with short processes have been observed only in S05B core samples.

Operculodinium israelianum
(ROSSIGNOL, 1962) D.WALL, 1967
Pl. 4, Figs 1–3

Description. Chorate, spherical to ovoidal cyst (47–51 µm diameter) with relatively thick granular to fibro-pitted cyst wall. The processes (6–10 µm) are nontabular, hollow, solid, and fibrous, with acuminate to minutely expanded tips. They widen toward the base, where striations are also present. The archeopyle is precingular with rounded angles. According to Rossignol (1964) and Head (1993), the archeopyle is formed by loss of plate 3''.

Remarks. Cysts of *Operculodinium israelianum* are present in sediment surface sample 8, as well as in core sediments (S05B), where they are infrequently observed.

Subfamily Gonyaulacoideae (Autonym)

Genus *Ataxiodinium* P.C.REID, 1974

***Ataxiodinium choane* P.C.REID, 1974**
Pl. 4, Figs 4, 5

Description. Spherical to egg-shaped cyst (33–37 µm diameter), surrounded by an outer layer of transparent and crenulate membrane, which is connected to the thin inner wall by funnel-shaped depressions. Including the outer membrane, this cyst reaches dimensions of 45–48 µm. The archeopyle margin has well-developed angles; according to Reid (1974), Rochon et al. (1999), and Head (2007), the archeopyle is formed by loss of the third precingular plate (3''').

Remarks. *Ataxiodinium choane* is sporadically found in the core sediments (S05B).

Genus *Bitectatodinium* G.J.WILSON, 1973

***Bitectatodinium spongium* (ZONNEVELD, 1997) ZONNEVELD et JURKSCH., 1999**

Pl. 4, Figs 6, 7

Description. Proximate and spherical cyst (42–51 µm diameter). The cyst wall is characterized by a thin pedium and a spongy, thicker, fibrous, and distally open luxuria (wall thickness, including fibrous layer, of 3–6 µm). Solid fibers (5–7 µm) with acuminate tips densely cover the entire cyst. Archeopyle is precingular; according to Wilson (1973) and Zonneveld (1997), it appears to be formed by often-incomplete loss of one or two precingular plates.

Remarks. *Bitectatodinium spongium* is sporadically found in the core sediments (S05B).

***Bitectatodinium tepikiense* G.J.WILSON, 1973**

Pl. 4, Figs 8–12

Description. Proximate spherical cyst (35–40 µm) with a smooth wall (thickness of 2–4 µm) characterized by microreticulate layer with erected or suberect lamellae. The bases of these lamellae appear long and sinuous, sometimes branching into two. The overall pattern often appears densely vermiculate. The archeopyle is precingular and very large, formed by loss of two almost equal-sized third and fourth precingular plates. Based on Lewis et al. (2001), a small apical protuberance (1–4 µm) may be present.

Remarks. *Bitectatodinium tepikiense* is sporadically found in the core sediments (S05B).

Genus *Impagidinium* STOVER et EVITT, 1978

***Impagidinium aculeatum* (D.WALL, 1967)**

LENTIN et G.L.WILLIAMS, 1981

Pl. 5, Figs 1–6

Description. Proximochorate ovoid cyst (35–37 µm length and 26–28 µm width) with finely granulate surface. Cyst body is characterized by small apical protuberance and sutural septa which express the tabulation of the cyst. The height of the septa increases at the plate junctions (8–10 µm height), forming a conspicuous point where they merge. According to Wall (1967), and Stover and Evitt (1978), the archeopyle is precingular by loss of plate 3'' or plate 5''.

Remarks. *Impagidinium aculeatum* is sporadically present in core sediments (S05B).

***Impagidinium paradoxum* (D.WALL, 1967) STOVER et EVITT, 1978**

Pl. 5, Figs 7–12

Description. Proximochorate cyst with ovoidal shape body (25–30 µm length and 28–31 µm width) and finely

granulate surface. The sutural septa, which have crests that are roughly consistent in height (4–6 µm), effectively express the tabulation over the majority of the cyst body. According to Wall (1967), and Stover and Evitt (1978), an apical protuberance is often present and archeopyle is precingular by loss of plate 3''.

Remarks. *Impagidinium paradoxum* is sporadically present in core sediments (S05B).

***Impagidinium patulum* (D.WALL, 1967) STOVER et EVITT, 1978**

Pl. 6, Figs 1–6

Description. Large cyst with a proximochorate ovoidal central body (50–60 µm length and 45–53 µm width), and a smooth to weakly and finely granulate surface. Sutural septa well express the tabulation of the cyst. Sutural septa crests (3–7 µm height) are well visible, and clearly define the cyst tabulation. The archeopyle is precingular. An apical protuberance can be present. According to Wall (1967), and Stover and Evitt (1978), the sutural septa are reduced in the sulcal area. Sutures are absent between plate 5'' and the sulcus. Archeopyle is formed by loss of plate 3''.

Remarks. *Impagidinium patulum* is present in sediment surface sample 8 as well as in core sediments (S05B), where it is commonly observed. Cysts observed in the sediment surface sample show a well-developed apical protuberance (Pl. 6, Figs 4–6).

***Impagidinium plicatum* VERSTEEGH et ZEVENBOOM, 1995**

Pl. 6, Figs 7–12

Description. Ovoidal to elongate proximochorate cyst (28–30 µm length and 23–25 µm width). Tabulation is well expressed by low crenulate septa of uniform height. According to the original description of Versteeghet and Zevenboom (1995), the sutural septum between plate 1'' and the sulcus is absent. Septa between 1'/4', sulcus/1p, sulcus/6'', 1''/1c, 1c/2'', and 6c/6''' can be lacking as well. Archeopyle formed by loss of precingular plate 3''.

Remarks. Only a few cysts of *Impagidinium plicatum* are present in core sediments (S05B).

***Impagidinium sphaericum* (D.WALL, 1967)**

LENTIN et G.L.WILLIAMS, 1981

Pl. 7, Figs 1–3

Description. Proximochorate, spherical to ovoidal cyst (40–46 µm length and 33–36 µm width) with apical protuberance and microgranulate wall surface. Undulate and low sutural septa (2–3 µm height) well express the tabulation all over the cyst. Archeopyle is precingular; according to Wall (1967) and Lentin and Williams (1981), it is formed by loss of precingular plate 3''.

Remarks. Only a few cysts of *Impagidinium sphaericum* are present in core sediments (S05B).

***Impagidinium striatum* (D.WALL,
1967) STOVER et EVITT, 1978**
Pl. 7, Figs 4–9

Description. Proximochorate and ovoidal cyst (27–30 µm diameter), with microgranulate wall surface. Tabulation is expressed by relatively high radiant sutural septa, with roughly constant height (5–7 µm) all over the cyst, except in the ventral area. Archeopyle is precingular. According to Wall (1967), and Stover and Evitt (1978), the tabulation is incomplete in the dorsal and sulcal regions, and the archeopyle is formed by loss of plate 3”.

Remarks. Cysts of *Impagidinium striatum* are rarely observed in core sediments (S05B).

***Impagidinium velorum* J.P.BUJAK 1984**
Pl. 7, Figs 10–12

Description. Proximochorate, pale, and ovoidal cyst (37–44 µm length and 30–34 µm width), with a smooth surface. Sutureal septa are characterized by expressed high membranous crest (16–20 µm height) with smooth distal margins. However, tabulation is difficult to determine. According to Bujak (1984), the archeopyle is precingular, formed by loss of plate 3”.

Remarks. Only a few cysts of *Impagidinium velorum* are present in core sediments (S05B).

***Impagidinium japonicum* MATSUOKA, 1983**
Pl. 8, Figs 1–3

Description. Chorate, transparent and spherical to ellipsoidal cyst (55–60 µm length and 47–48 µm width), with a finely granulate surface. Septa are granulated and well-developed, with uniform crest (13–15 µm height). They represent the tabulation but are not well defined. According to Matsuoka (1983), the archeopyle is precingular, formed by loss of plate 3”.

Remarks. Only two cysts of *Impagidinium japonicum* are present in core sediments (S05B).

**Genus *Nematosphaeropsis* DEFLANDRE et
COOKSON, 1955 emend. Wrenn 1988**

***Nematosphaeropsis labyrinthus*
(OSTENF., 1903) P.C.REID, 1974**
Pl. 8, Figs 4–9

Description. Chorate and ovoidal cyst (28–44 µm diameter) with smooth surface. Processes are gonial, slender, and tall (15–20 µm length) with trifurcate tips. Bifurcation also present in the processes’ distal tips, with parallel pairs of ribbon-like trabeculae (about 1.0 to 1.5 µm wide) that connect with adjacent processes. According to Ostensfeld (1903), Reid (1974), and Mudie et al. (2017), the cyst wall surface can be faintly granulated, and a small apical protuberance may be present. Archeopyle is precingular, formed by loss of plate 3.

Remarks. *Nematosphaeropsis labyrinthus* is present in core sediments (S05B), although its presence is infrequent.

**Genus *Spiniferites* MANTELL, 1850
emend. Sarjeant 1970**

***Spiniferites belerius* P.C.REID, 1974**
Pl. 8, Figs 10–12; Pl. 9, Figs 1–3

Description. Ovoidal cyst (28–34 µm length and 28–30 µm width) with a smooth to very finely granulate wall and apical protuberance. The processes (7–11 µm length) are irregularly shaped, gonial, short, distally trifurcate with recurved bifurcate tips, or simple or branched conical structures. These show a box-like or trumpet shape. Some cysts showed one or a few occasional intergonal processes (Pl. 9, Fig. 3). Archeopyle is precingular. According to Reid (1974) and Rochon et al. (1999), the archeopyle is formed by loss of plate 3”.

Remarks. *Spiniferites belerius* is present in all surface sediment samples as well as in core sediments (S05B), where it is commonly observed.

***Spiniferites bentorii* (M.ROSSIGNOL,
1964) D.WALL et B.DALE, 1970**
Pl. 9, Figs 4–12

Description. Proximochorate and ovoidal to pear-shape cyst (58–62 µm length and 47–53 µm width) with a smooth to microgranulate surface. The central body is characterized by an apical protuberance, which can be pronounced and characterized by the presence of a developed crest. Processes are gonial and occasionally intergonal. They show trifurcate and tips are also bifurcate with V-shaped. They are highly variable in shape, ranging from slender to conical and tapering with a wide and curved base, as well as in length, with the longest processes occurring at the antapex. Tabulation is expressed by sutures, which are marked by low septa. Some cysts show reduced dimension (Pl. 9, Figs 10–12), with shorter and conical processes (*Spiniferites bentorii* subsp. *truncatus* ROSSIGNOL, 1964; Lentin 1976). Archeopyle is precingular. According to Reid (1974) and Rochon et al. (1999), process bases may occasionally show fenestrate texture. Archeopyle is formed by loss of plate 3”.

Remarks. *Spiniferites bentorii* is present in sediment surface samples 3, 4, 6, and 8, as well as in core sediments (S05B), where it is commonly observed. Specimens with reduced processes, corresponding to *Spiniferites bentorii* subsp. *truncatus* (ROSSIGNOL, 1964; Lentin 1976), are present in core sediments (S05B).

***Spiniferites bulloideus* (DEFLANDRE et COOKSON,
1955) SARJEANT, 1970 sensu stricto**
Pl. 10, Figs 1–3

Description. Spherical cyst (28–30 µm diameter) with smooth surface. Processes are relatively long (8–10 µm),

trifurcate with bifurcate tips, gonial and slender and delicate. Archeopyle is precingular with low sutural crest along the border. On the rest of the cyst body there are no crests. According to Deflandre and Cookson (1955), archeopyle is formed by loss of plate 3''.

Remarks. *Spiniferites bulloideus* is present in sediment surface samples 3, 4, 5, and 8, as well as in core sediments (S05B), where it is infrequently observed.

***Spiniferites delicatus* P.C.REID, 1974**

Pl. 10, Figs 4–9

Description. Proximochorate and ovoidal cyst (44–51 µm length and 36–38 µm width), with a thick wall, probably bilayered, characterized by radial columellae and microreticulate body surface. Processes are gonial (12–16 µm length) and connected by high and well developed granulate membranes. These incorporate the processes, giving the impression of “skeletal rods”. Archeopyle is precingular. According to Reid (1974) and Rochon et al. (1999), archeopyle is formed by loss of plate 3''.

Remarks. *Spiniferites delicatus* is present in sediment surface samples 2, 3, 4, 5, and 8, as well as in core sediments (S05B), where it is infrequently observed.

***Spiniferites elongatus* P.C.REID, 1974**

emend. Van Nieuwenhove et al. 2018

Pl. 10, Figs 10–12

Description. Proximochorate and cylindriciform elongate cyst with smooth wall. Processes are gonial (7–11 µm length), tapering, and connected by proximally hollow septa. According to Reid (1974) and Van Nieuwenhove et al. (2018), septa height can vary from discrete ridges to well-developed membranes, and are usually higher at the apex and notably toward the antapex. The archeopyle is precingular, formed by loss of plate 3''.

Remarks. Only a few cysts of *Spiniferites elongatus* are present in core sediments (S05B).

***Spiniferites hyperacanthus* (DEFLANDRE et COOKSON, 1955) COOKSON et EISENACK, 1974**

Pl. 11, Figs 1, 2

Description. Proximochorate spherical to subspherical cyst (47–51 µm diameter) with smooth to microgranulate cyst wall. Gonial and intergonal processes are present (9–15 µm length). Typically, they are slender and distally furcate with recurved bifurcate tips. Tabulation is expressed by very low sutural septa. Archeopyle is precingular. According to Deflandre and Cookson (1955), archeopyle is formed by loss of plate 3''.

Remarks. *Spiniferites hyperacanthus* is present in surface sediment samples 3, 4, and 6, as well as in core sediments (S05B), where it is commonly observed.

***Spiniferites lazus* P.C.REID, 1974**

Pl. 11, Figs 3–11

Description. Elongate ovoidal cyst (44–48 µm length and 31–38 µm width) with a moderately thick wall and a finely granulate to microreticulate surface. The processes are gonial (11–16 µm length), trifurcate with fenestrate bases, and bifid recurved tips. Some cysts show membranes on the apical processes (Pl. 11, Figs 3–5). A small apical protuberance can be present (Pl. 11, Figs 6–8). In some cases, very low septa weakly highlight the tabulation, especially of the cingulum (Pl. 11, Figs 3, 4). Archeopyle is precingular; according to Reid (1974), it is formed by loss of plate 3''.

Remarks. *Spiniferites lazus* is present in core sediments (S05B), although it is rarely observed.

***Spiniferites membranaceus* (M.ROSSIGNOL,**

1964) SARJEANT, 1970

Pl. 12, Figs 1–6

Description. Proximochorate and ovoidal cyst (38–43 µm length and 34–40 µm width), with smooth to microrugulate surface wall. Processes are exclusively gonial (7–16 µm length) and distally furcate with recurved bifurcate tips. Tabulation is expressed by sutural septa, with low sutural crests over the cyst body, which increase near the processes. In the apical portion, the crest may form a crown-like structure (Pl. 12, Figs 1–3). In the antapex portion, a conspicuous granular flange is present (11–21 µm length). Tabulation is expressed by sutural septa. Archeopyle is precingular. According to Wall (1967) and Reid (1974), the antapex flange develops along the 4'''/1''' suture connecting the two slender dorso-antapical processes. The archeopyle is formed by loss of plate 3''.

Remarks. *Spiniferites membranaceus* is present in sediment surface samples 3 and 4, as well as in core sediments (S05B) but it is rarely observed.

***Spiniferites mirabilis* (M.ROSSIGNOL, 1964)**

SARJEANT, 1970 emend. Limoges et al. 2018

Pl. 12, Figs 7–9

Description. Proximochorate and broadly ovoidal to spheroidal cyst (54–61 µm length and 49–53 µm width), with smooth to finely granulate surface. Processes are wide, both gonial and intergonal (13–20 µm length), and distally furcate with recurved bifid tips. Suture crests are nearly absent, except at the antapical area, where a well-expressed sutural flange runs along the dorsal portion (19–22 µm length). Archeopyle is precingular. According to Reid (1974) and Rochon et al. (1999), the antapex flange runs along the dorsal suture of antapical plate. Suture crests, except the antapical flange, may show greater heights. The archeopyle is formed by loss of plate 3''.

Remarks. *Spiniferites mirabilis* is present in sediment surface samples 3, 4, 5, and 8, as well as in core sediments (S05B) where it is commonly observed.

***Spiniferites mirabilis* subsp. *serratus* (MATSUOKA, 1983)**

Pl. 12, Figs 10–12

Description. Ovoidal to spheroidal cyst (42–45 µm length and 43–47 µm width). Processes are conical to subconical (7–9 µm length). Sutural crests are generally low, except at the antapex, where they form a flange (9–13 µm length). The archeopyle is precingular. According to Matsuoka (1983) and Limoges et al. (2018), the archeopyle is formed by loss of plate 3”.

Remarks. *Spiniferites mirabilis* subsp. *serratus* is present in core sediments (S05B), but only a few cysts are observed.

***Spiniferites pachydermus* (M.ROSSIGNOL, 1964) P.C.REID, 1974**

Pl. 13, Figs 1–6

Description. Proximochorate spherical to subspherical cyst (43–50 µm length and 40–46 µm width) with a thick and granulate wall. Processes are gonial (16–18 µm length) and long, distally trifurcate with bifurcate tips. Some cysts show reduced size with shorter processes (8–10 µm length). Archeopyle is precingular; according to Reid (1974) and Mertens et al. (2015), it is formed by loss of plate 3”.

Remarks. *Spiniferites pachydermus* is present in surface sample 8 and in core sediments (S05B), where it is rarely observed. In the S05B core, some cysts with shorter processes are present (Pl. 13, Figs 4–6).

***Spiniferites ramosus* (EHRENB., 1838) MANTELL, 1854**

Pl. 13, Figs 7–12

Description. Ovoidal cyst (36–45 µm length and 29–35 µm width) with smooth to microgranulate wall surface. Processes are gonial (13–25 µm length), hollow, slender, and have long distal furcations with bifurcate tips. Very low sutural septa rise slightly towards the processes. Archeopyle is precingular. According to Davey et al. (1966), and Marret and Zonneveld (2003), occasionally narrow thread-like trabeculae are present between adjacent process tips. The archeopyle is formed by loss of plate 3”.

Remarks. *Spiniferites ramosus* is present in sediment surface samples 2, 3, 4, 5, 6, and 8, as well as in core sediments (S05B), where it is infrequently observed.

**Order Peridiniales HAECKEL, 1894
Suborder Peridiniineae (Autonym)
Family Peridiniaceae EHRENB., 1832**

Genus *Peridinium* EHRENB., 1832

***Peridinium ponticum* D.WALL et B.DALE, 1973**

Pl. 14, Figs 1–12

Description. Light to dark brown cyst (40–47 µm length and 40–44 µm width) with moderately pointed to subrounded apex and broadly rounded antapex. Archeopyle shows

a hexagonal, pentagonal or subspherical form. The body wall is ornamented by non-tabular submicron-sized tubercles and numerous very short, transparent spines, sometimes curved, sometimes straight. The intercalary archeopyle is large and hexagonal. The archeopyle can be offset towards the left (Pl. 14, Figs 4–9).

Remarks. Cysts of *Peridinium ponticum* are present in surface samples 4 and 6, as well as in core sediments (S05B), where they are infrequently observed.

**Family Protoperidiniaceae BALECH, 1988
Subfamily Diplopsalioideae ABE, 1981**

Genus *Diplopelta* F.STEIN, 1883 ex JÖRG., 1912

Cyst of *Diplopelta symmetrica* PAVILL., 1913

Pl. 15, Figs 1–6

Description. Brown to dark brown and spherical to sub-spherical cyst (40–45 µm), with a moderately thick wall, and densely covered with hair-like processes (length of 2–4 µm). Based on Dale et al. (1993), the archeopyle follows a zigzag pattern, which probably represents the tabulation, following the boundaries of 1a/2”, 1a/2’, 2/2a, 3’/2a, and 3’/5”.

Remarks. Only a few cysts of *Diplopelta symmetrica* are present in the core sediments (S05B). The cysts are always folded or broken along the directions of the cracks, with a similar zig-zag pattern (Pl. 15, 4–6), which could be due to the presence of the archeopyle, as reported by Dale et al. (1993).

Genus *Dubridinium* P.C.REID, 1978

***Dubridinium caperatum* P.C.REID, 1978**

Pl. 15, Figs 7–12

Description. Brown to light-brown, lenticular shape and cavate cyst with polar compression (41–45 µm diameter). The archeopyle is theropylic, with a long-split aperture following the cingulum.

Remarks. Only a few cysts of *Dubridinium caperatum* are present in core sediments (S05B).

***Dubridinium ulsterum* P.C.REID, 1978**

Pl. 16, Figs 1–3

Description. Spherical to subspherical brown cysts with polar compression (40–41 µm diameter). The wall is thin, with lines of verrucae ornamentation. Archeopyle theropylic, with a long-split aperture following the cingulum. According to Reid (1978), lines of verrucae may also distinguish the cingulum, and a flagellar scar can be observed.

Remarks. Cysts of *Dubridinium ulsterum* are present in sediment surface sample 6.

Subfamily Protoperidinioideae BALECH, 1988

**Genus *Archaeperidinium* JÖRG.,
1912 emend. YAMAGUCHI et al., 2011**

**Cyst of *Archaeperidinium minutum* (KOFOLD,
1907) JÖRG., 1912 sensu D.WALL et B.DALE 1968**
Pl. 16, Figs 4–6

Description. Brown to dark brown and spherical cysts (38–42 µm). The central body wall is characterized by hollow processes (length of 6–8 µm) with circular bases and flat-topped distal extremities. The outer extremities of these processes bear spinules that may be minutely expanded distally. According to Wall and Dale (1968), the archeopyle is intercalary, rarely clearly discernible, and the cell contents are often dense and include numerous plastids.

Remarks. Cysts of *Archaeperidinium minutum* sensu Wall and Dale (1968) are present in sediment surface sample 2.

**Genus *Brigantedinium* P.C.REID, 1978
ex LENTIN et G.L.WILLIAMS, 1993**

***Brigantedinium asymmetricum* MATSUOKA
et al., 1987 ex HEAD, 1996**
Pl. 16, Figs 7–9

Description. Small, spherical, and brown to light brown cyst (30–33 µm), with smooth to microgranular surface wall. Archeopyle intercalary, relatively large, and comprising one long, two intermediate, two short, and one convex side.

Remarks. *Brigantedinium asymmetricum* is present in sediment surface sample 6.

***Brigantedinium auranteum* P.C.REID, 1978
ex LENTIN et G.L.WILLIAMS, 1993**
Pl. 16, Figs 10–12

Description. Brown and spherical cyst (51–54 µm) with smooth to microgranulate surface wall. Archeopyle is large (38 µm length and 36 µm width), subhexagonal, with the longest axis up to three fifths of the cyst diameter.

Remarks. Only a few cysts of *Brigantedinium auranteum* are present in the core sediment (S05B). The cysts identified in this record have a larger archeopyle with respect to that described by Reid (1978) (26–30 µm length and 26–30 µm width).

***Brigantedinium cariacense* (D.WALL,
1967) LENTIN et G.L.WILLIAMS, 1993**
Pl. 17, Figs 1, 2

Description. Spherical light brown to dark brown cyst (40–43 µm diameter) with a smooth surface wall. The archeopyle is intercalary and hexagonal (21 µm length and

13 µm width); according to Wall (1965), Reid (1978), and Matsuoka et al. (1987), the archeopyle is formed by loss of plate 2a with a length almost twice its width. There may be folds or splits in the archeopyle area, but no other indications of tabulation are present.

Remarks. Only a few cysts of *Brigantedinium cariacense* are present in the core sediment (S05B).

***Brigantedinium simplex* D.WALL, 1965
ex LENTIN et G.L.WILLIAMS, 1993**
Pl. 17, Fig 3

Description. Spherical light brown to dark brown cyst (34–47 µm diameter) with smooth surface wall. The archeopyle is intercalary (28–30 µm length and 20–23 µm width). According to Wall (1965), Reid (1978), and Matsuoka et al. (1987), the surface wall can show light ornamentation, and the archeopyle is formed by loss of plate 2a.

Remarks. Only a few cysts of *Brigantedinium simplex* are present in the core sediment (S05B).

**Genus *Islandinium* M.J.HEAD et al.,
2001 emend. Potvin et al. 2013**

***Islandinium? cezare* (ex DE VERNAL in ROCHON
et al., 1999) M.J.HEAD et al., 2001**
Pl. 17, Figs 4–6

Description. Spherical and brown cyst (33–35 µm diameter) with a finely granulated wall. Processes are numerous (6–8 µm length), solid and hollow at the basis, separated from one another by about 2 to 3 µm. Process tips are expanded into platforms and margins appear recurved. In longitudinal section, process tips appear mushroom-like. Archeopyle is apical.

Remarks. Cysts of *Islandinium? cezare* are present in core sediments (S05B), although their presence is infrequent.

**Genus *Lejeunecysta* ARTZNER et DÖRHÖFER,
1978 emend. Lentin et G.L.Williams 1976**

***Lejeunecysta oliva* (P.C.REID, 1978)
TURON et LONDEIX, 1988**
Pl. 17, Figs 7–9

Description. Light brown and dorso-ventrally compressed cyst with a typical peridinioid outline (65–71 µm length). The cyst wall is thin with a smooth surface. The antapical portion is characterized by two symmetrical horns separated by a shallow antapical depression. Along the cingulum margin there are low, thickened ridges, marking a narrow, excavated, circular cingulum. Archeopyle is intercalary and shows a bell-like shape.

Remarks. Cysts of *Lejeunecysta oliva* are present in core sediments (S05B), although their presence is infrequent.

Genus *Protoperidinium* BERGH, 1881

**Cyst of *Protoperidinium denticulatum*
(GRAN et BRAARUD, 1935) BALECH, 1974
Pl. 17, Fig 10**

Description. Spherical dark brown cyst (39–44 µm) with smooth wall. The archeopyle is equatorially elongate and hexagonal (36 µm length and 21 µm width).

Remarks. Cysts of *Protoperidinium denticulatum* are found in the core sediments (S05B), where their occurrence is infrequent.

**Cyst of *Protoperidinium nudum*
(MEUNIER, 1919) BALECH, 1974
Pl. 17, Figs 11, 12**

Description. Brown-pigmented subspherical/oval cysts with a weak polar compression (35–37 µm width), ornamented by relatively long and conical processes (10–12 µm length). These processes are simple, without particular ornamentation. According to Wall and Dale (1968), the archeopyle is intercalary (2a), and the cingulum is marked by two parallel rows of processes.

Remarks. Only a few cysts of *Protoperidinium nudum* are present in core sediments (S05B).

**Cyst of *Protoperidinium stellatum* (D.WALL
et B.DALE, 1968) ROCHON et al., 1999
Pl. 18, Figs 1–3**

Description. Proximate and brown cyst, with dorso-ventral compression and pentagonal body (32–37 µm length) with smooth wall. The cyst is affected by five distinct horns of approximately equal length (10–16 µm length). They are positioned at each of the angles of the pentagonal body, they are simple and have no ornamentation. The archeopyle is identified by a split positioned in the center of the cyst body. According to Rochon et al. (1999), archeopyle is large and intercalary, formed by an opening along the margins of plates 1a and 2a. Supplementary horns can be present around the cingular zone.

Remarks. Cysts of *Protoperidinium stellatum* are present in sediment surface samples 2, 3, 4, and 6, as well as in the core sediments (S05B), where their occurrence is infrequent.

**Cyst of *Protoperidinium thulesense*
(BALECH, 1958) BALECH, 1973
Pl. 18, Fig 4**

Description. Spherical and brown cyst with a smooth wall (37–40 µm diameter). The theropylic archeopyle is a large slit. It is located equatorially and encircles approximately two-thirds to three-quarters of the circumference of the cell.

Remarks. Only a few cysts of *Protoperidinium thulesense* are present in core sediments (S05B).

**Cyst of *Protoperidinium tricingulatum*
KAWAMI et al., 2009
Pl. 18, Figs 5–7**

Description. Spherical brown cysts with a smooth to finely granulate wall (27–30 µm diameter). Processes (6–7 µm length) are randomly distributed and solid, with the exception of a hollow basis that is circular in cross section. They are capitate or cauliflorate, and no branching is observed at the distal tips. The archeopyle is theropylic, probably along plate boundaries. According to Kawami et al. (2009), the archeopyle is formed by loss of plates 2'/1a, 2'/2a, 3'/2a, 4'/2a, 4'/6'' and 4'/7'. The number of processes is ~15 per 10 µm².

Remarks. Cysts of *Protoperidinium tricingulatum* are present in sediment surface sample 6, as well as in core sediments (S05B), where only a few cysts are observed.

**Genus *Quinquecuspis* HARLAND, 1977
Quinquecuspis concreta (P.C.REID, 1978) HARLAND, 1977
Pl. 18, Figs 8, 9**

Description. Brown and large cyst (60–71 µm length) with dorso-ventrally compressed and pentagonal body. The apical zone is characterized by prominent apical horn. Two distinct rounded antapical horns are present in the antapical zone. According to Harland (1977) and Rochon et al. (1999), the cingulum is well delimited and slightly excavated. The archeopyle is intercalary.

Remarks. Cysts of *Quinquecuspis concreta* are present in sediment surface sample 6 as well as in core sediments (S05B), where only a few cysts are observed.

**Genus *Selenopemphix* P.N.BENEDEK,
1972 emend. M.J.Head 1993**

***Selenopemphix nephroides* P.N.BENEDEK, 1972 emend.
J.P.Bujak in Bujak et al. 1980, nom. cons.
Pl. 18, Figs 10–12**

Description. Brownish-pigmented and large cyst (48–57 µm diameter), with polar compression and ovoidal to reniform outline in polar view. The wall is single-layered with a smooth surface. Low apical and antapical horns are present with rounded terminations. The cingulum is well defined by deep indentation. The sulcus is wide and short and may show two small depressions that reflect the flagellar pores. The archeopyle is large and intercalary, with rounded angles.

Remarks. *Selenopemphix nephroides* is rare in core sediments (S05B).

***Selenopemphix quanta* (M.R.BRADFORD,
1975) MATSUOKA, 1985
Pl. 19, Figs 1–3**

Description. Brown peridinioid cyst (54–70 µm width and 35 µm depth) with polar compression. The cyst wall is smooth and ornamented with numerous simple and rigid

processes (11–14 µm length) with sharp or blunt terminations that become solid distally. According to Rochon et al. (1999) and Matsuoka (1985), processes occur along the cingular margins with variable density on the epi- and hypocyst, but not in the sulcus. Archeopyle is 2a intercalary plate with rounded angles.

Remarks. *Selenopemphix quanta* is present in sediment surface sample 6 as well as in core sediments (S05B), where it is infrequently observed.

***Selenopemphix undulata* VERLEYE et al., 2011**
Pl. 19, Figs 4–9

Description. Pale brown and large cyst (60–71 µm width). The cingulum is well developed and formed by two parallel ridges with slightly thickened and undulating margins. The apical portion is conical, and the antapical carries distally two weakly-developed, rounded horns. Archeopyle is large and intercalary (28–32 µm width and 12 µm height).

Remarks. Only a few cysts of *Selenopemphix undulata* are present in core sediments (S05B).

Genus *Trinovantedinium* P.C.REID, 1978
emend. de Verteuil and G.Norris 1992

***Trinovantedinium applanatum* (M.R.BRADFORD, 1977) J.P.BUJAK ET E.H.DAVIES, 1983**
Pl. 19, Figs 10–12

Description. Large and pentagonal cyst (68–73 µm length), dorso-ventrally compressed with an apical horn, and two antapical lobes separated by a shallow antapical sulcus. Processes are short (5–6 µm length) and solid, with acuminate or expanded tips, with irregular intratabulation distribution. They are aligned along the cingular margins. Archeopyle is intercalary and hexagonal; according to Bradford (1977) and Reid (1978) it is formed by loss of plate 2a.

Remarks. *Trinovantedinium applanatum* is present in core sediments (S05B), although rarely observed.

Genus *Votadinium* P.C.REID, 1978
emend. Gurdebeke et al. 2020

***Votadinium calvum* P.C.REID, 1978**
Pl. 20, Figs 1–3

Description. Light to dark brown dorso-ventrally compressed cyst (54–61 µm length) with a smooth to microgranulate surface. This cyst is characterized by two rounded antapical horns separated by a shallow depression in dorso-ventral view. Archeopyle is intercalary, often truncating the apex obliquely; according to Reid (1978), Rochon et al. (1999), and Sarai et al. (2013), it is formed by loss of plate 2a.

Remarks. *Votadinium calvum* is present in sediment surface samples 4, 6, and 8, as well as in core sediments (S05B), where it is infrequently observed.

***Votadinium spinosum* P.C.REID, 1978**
Pl. 20, Figs 4–5

Description. Brown dorso-ventrally compressed cyst (51–53 µm length), with two rounded antapical horns and a rounded apex. The central body wall is thin with a smooth surface, and covered by numerous short, solid spines (3–7 µm). The archeopyle is intercalary; according to Wall and Dale (1968), and Reid (1978), it is formed by loss of intercalary plate 2a.

Remarks. *Votadinium spinosum* is present in sediment surface sample 6 and in core sediments (S05B), where it is infrequently observed.

Genus *Xandarodinium* P.C.REID, 1978

***Xandarodinium xanthum* P.C.REID, 1978**
Pl. 20, Figs 6–12

Description. Light brown cyst (44–47 µm length and 35–41 µm width) with a thin and smooth surface, concave ventral area, and convex dorsal area. Processes form as extensions from the surface wall with spines or multifurcate extensions (9–16 µm) that have elliptical, circular, or elongate bases.

Remarks. Cysts of *Xandarodinium xanthum* are present in sediment surface sample 6 and in core sediments (S05B), where they are rarely observed.

Subfamily Uncertain

Genus *Echinidinium* ZONNEVELD, 1997 ex M.J.HEAD et al., 2001

***Echinidinium granulatatum* ZONNEVELD, 1997 ex M.J.HEAD et al., 2001**
Pl. 21, Figs 1–3

Description. Spherical brown cyst (26–46 µm diameter) with a granular to microgranular surface wall. Processes are numerous (5–7 µm length), hollow and acuminate, and bear small solid spinules at the distal ends. Process bases are sub-circular (2–3 µm diameter). According to Zonneveld (1997), some larger processes may have longitudinal striations extending from the base. The theropylic archeopyle consists of a single split along one or two sutures.

Remarks. Cysts of *Echinidinium granulatatum* are present in sediment surface sample 6, as well as in the core sediments (S05B), where only a few cysts are observed.

Family Thoracosphaeraceae J.SCHILLER, 1930
emend. TANGEN in TANGEN et al., 1982

Genus *Pentapharsodinium* INDEL. et A.R.LOEBL., 1986 emend. Montresor et al. 1993

Cyst of *Pentapharsodinium dalei*

INDEL. et A.R.LOEBL., 1986

Pl. 21, Figs 4–7

Description. Small chorate and colorless cyst with sub-spherical central body (18–22 μm). The processes (length of 4–6 μm) are straight or may branch at any point along their length, with different types often present on a single cyst. Some process bases may be expanded, and some may be joined to adjacent bases by low septa. Archeopyle is represented by a slit-like rupture, as also evidenced by Dale (1977), Lewis (1991), and Rochon et al. (1999).

Remarks. Cysts of *Pentapharsodinium dalei* are present in all sediment surface samples, as well as in core sediments (S05B), where they are commonly observed.

Genus *Scrippsiella* BALECH, 1959 ex A.R.LOEBL., 1965

Cyst of *Scrippsiella* cf. *trifida* JANE

LEWIS, 1991 ex M.J.HEAD, 1996

Pl. 21, Figs 8, 9

Description. Ovoidal cyst (36–38 μm length and 25–33 μm width) with an inner smooth organic layer and an outer undulating organic layer. According to Head et al. (2006), in some places, the organic walls are perforated. The zigzag-shaped chasmic archeopyle includes three apical plates and the 1a–3a intercalary plates.

Remarks. Only a few cysts of *Scrippsiella* cf. *trifida* are present in core sediments (S05B).

Cyst of *Scrippsiella* cf. *trochoidea*

(F.STEIN, 1883) A.R.LOEBL., 1976

Pl. 21, Figs 10–12

Description. Small sub-spherical to ovoidal cyst (33–35 μm length and 26–30 μm width). Processes show sub-triangular bases from which hair-like processes come out. According to Lewis (1991), the archeopyle is apical, about 25 % of the cyst width, with the operculum remaining attached by one-third of the cyst circumference.

Remarks. Cysts of *Scrippsiella* cf. *trochoidea* are present in sediment surface samples 4 and 6.

Discussion and conclusions

The MP, together with the adjacent Mar Grande and the open area of the Gulf of Taranto, is aligned along a transect (Text-fig. 1A) characterized by a progressive degree of confinement (towards the MP). This confinement gradient significantly influences both the structure of biological communities and physical features (e.g., Matarrese et al. 2004, Mastrototaro et al. 2008, Belmonte et al. 2013). In the MP, ecological communities are further affected by various stressors, including anthropogenic activities in the surrounding urban area. These activities encompass mussel-farming systems as well as industrial and shipping activities in the Mar Grande basin. The

resulting environmental conditions promote the proliferation of opportunistic species characterized by a relatively short life cycle, small body sizes, and the capacity to reach high population densities (e.g., Cardellicchio et al. 2016). The predominant economic activities, characterized by intense maritime trade with non-Mediterranean countries, have also contributed to the introduction of non-native species in the seas of Taranto, including the MP basin (e.g., Mastrototaro et al. 2004, Giangrande et al. 2021). Previous environmental pressures have had a substantial impact on phytoplankton communities, leading to consequences for both the marine ecosystem and human health, including the contamination of cultures resulting from algal blooms.

The combined data from the two natural archives, which includes the list of all dinoflagellate cyst taxa identified in 473 samples obtained from the 29-meter-thick Holocene sedimentary core (S05B) retrieved from *Primo Seno*, along with the eight surface sediments collected at various stations in both *Primo* and *Secondo Seno*, allow for their integration and comparison. Surface sediment samples are particularly informative in revealing recent environmental changes in the MP and elucidating the impact of local factors. For instance, surface sediment samples closest to both river inputs, such as samples 1 (near the *d'Aiedda* channel) and 7 (near the *Galeso* river), both at depths of less than 3 meters b.s.l. (Tab. 1), were barren in dinocysts. This could be attributed to the relatively high freshwater discharge from the *d'Aiedda* channel (0.52 m^3/s) and *Galeso* river (0.70 m^3/s) (Pascalis et al. 2016). These discharges, combined with extensive mixing in the shallow water column, create an unfavorable environment for the production and preservation of resting cysts. Conversely, surface sediment sample 6, situated near the SB05 sedimentary core, exhibits a comparatively rich diversity of heterotrophic taxa (e.g., *Lejeunecysta oliva*). This sample is located near the mussel farming palisades; an area characterized by significant organic matter enrichments. These conditions impact both biochemical processes and nutrient levels in the ecosystem, promoting increased phytoplankton activity. The proliferation of other life forms, including diatoms, ciliated protozoa, and bacteria, all of which serve as nutritional sources for heterotrophic dinoflagellates (e.g., Gaines and Taylor 1984; Lessard and Swift 1985, Jacobson and Anderson 1986, 1996), contributes to the diversity of heterotrophic taxa. In surface sediment sample 8, taken approximately 800 meters from *Canale Navigabile* and near *Porta Napoli* (Text-fig. 1A), we find the presence of *L. machaerophorum*, *O. centrocarpum*, and *O. israelianum*, with *Impagidinium patulum* uniquely occurring in the MP in this location. Both the previously mentioned *Operculodinium* species, characteristic of outer neritic environments, and *I. patulum*, a typical full-oceanic taxon, suggest the influence of oxygenated and oligotrophic surface water inflow (e.g., Pospelova et al. 2008, de Vernal et al. 2020, Coussin et al. 2022) from the nearby Mar Grande. Surface sediment samples 2 to 5 exhibit low diversity and a prevalence of cosmopolitan taxa, such as *S. belerius* and *S. ramosus*. This dominance can be attributed to their location in the *Secondo Seno* (Text-fig. 1A), which is the most confined part of the MP. This area is characterized by limited hydrodynamics and heavily stressed surface water conditions.

In summary, the dinocyst species and their compositions reaffirm the distinct environmental conditions between the

Primo and *Secondo Seno*, as previously indicated in prior studies on surface sediments (Rubino et al. 1996, 2009, 2016, Belmonte et al. 1997). Additionally, our ongoing palaeoecological and palaeoenvironmental investigation of the S05B sedimentary core allows us to extend our understanding of the present changes affecting dinophyta assemblages (Caroppo et al. 2016, Rubino et al. 2016, Ferraro et al. 2017, Rubino and Belmonte 2019, 2021) back to the beginning of the Holocene, approximately 12,000 years ago according to Niccolini et al. (2025). In the S05B samples, we find a variety of dinocyst taxa representing different ecological niches, including estuarine/lagoonal (e.g., *Lingulodinium machaerophorum*), neritic (e.g., *Spiniferites* spp.), and full oceanic (e.g., *Impagidinium* spp.) taxa (Tab. 2). Furthermore, the presence of eutrophic (e.g., *Pentapharsodinium dalei*) to oligotrophic (e.g., *Operculodinium centrocarpum*) taxa as well as heterotrophic (e.g., *Lejeunecysta oliva*, *Selenopemphix quanta*) taxa provides insights into the occurrence of various trophic levels. Additionally, dinocysts offer valuable information on fluctuations in sea surface temperature that are characteristic of warmer (e.g., *Spiniferites mirabilis*) and cooler (e.g., *Nematosphaeropsis labyrinthus*) conditions. This extensive iconographic documentation from the MP significantly expands the regional database of dinocyst taxa found in the Mediterranean Sea, particularly within shallow and semi-enclosed environments, over the last 12,000 years. Notably, this record reveals a greater number of taxa, identified in both core and surface sediment samples, in comparison to the plankton list (Dinoflagellates) described in numerous studies focusing on the water column of the MP (e.g., Ferraro et al. 2017, Rubino and Belmonte 2019, 2021, Francescangeli et al. 2024). This evidence plays a crucial role in advancing our comprehension of the intricate relationship between organisms and their resting cysts, as introduced by Rubino and Belmonte (2021), thus contributing to the exploration of benthic-pelagic coupling. Furthermore, it significantly enhances the reliability of ongoing palaeontological and palaeoenvironmental reconstructions within the MP basin.

In conclusion, our study, based on a morphological approach, provides detailed and systematic documentation of dinoflagellate cysts in the Mar Piccolo, serving as a fundamental reference for future research on biodiversity, ecological dynamics, and benthic-pelagic interactions in this unique, semi-enclosed marine environment. These baseline data will contribute to the development of more refined environmental quality assessments and enhance our understanding of past and present ecological changes. Furthermore, they offer essential information to guide necessary conservation and management strategies aimed at improving future environmental quality, while also providing valuable insights into pre-human environmental transformations.

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Data availability

Additional data will be available on request

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Explanations of the plates

PLATE 1

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.
 1.–3. Cyst of *Gymnodinium microreticulatum*.
 4.–9. Cyst of *Polykrikos kofoidii*.
 10.–12. Cyst of *Alexandrium* spp.

PLATE 2

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.
 1.–6. *Tuberculodinium vancampoeae*.
 7.–8. *Polysphaeridium zoharyi*.
 7. Black arrow indicates two fused processes connected by membrane.
 9.–12. *Lingulodinium machaerophorum*, specimen with long processes (> 10 µm).

PLATE 3

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.
 1.–6. *Lingulodinium machaerophorum*, specimen with short processes (< 10 µm).
 7.–10. *Operculodinium centrocarpum*, specimen with long processes.
 11.–12. *Operculodinium centrocarpum*, specimen with short processes.

PLATE 4

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.
 1.–3. *Operculodinium israelianum*.
 4.–5. *Ataxiodinium choane*.
 6.–7. *Bitectatodinium spongium*.
 8.–12. *Bitectatodinium tepikiense*.

PLATE 5

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.
 1.–6. *Impagidinium aculeatum*.
 7.–12. *Impagidinium paradoxum*.

PLATE 6

Dinoflagellate cysts from Mar Piccolo basin. Black numbers indicate dinocyst micrographs from surface samples. Scale bars 20 µm.
 1.–6. *Impagidinium patulum*. Black arrow in Fig. 6 indicates well-developed apical protuberance.
 7.–12. *Impagidinium plicatum*.

PLATE 7

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.
 1.–3. *Impagidinium sphaericum*.
 4.–9. *Impagidinium striatum*.
 10.–12. *Impagidinium velorum*.

PLATE 8

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–3. *Impagidinium japonicum*.
4.–9. *Nematosphaeropsis labyrinthus*.
10.–12. *Spiniferites belerius*.

PLATE 9

Dinoflagellate cysts from Mar Piccolo basin. Black numbers indicate dinocyst micrographs from surface samples. Scale bars 20 µm.

- 1.–3. *Spiniferites belerius*.
4.–9. *Spiniferites bentorii*. Black arrow in Fig. 8 highlights margin of archeopyle, emphasizing its well-developed suture crest.
10.–12. *Spiniferites bentorii*, specimen with reduced processes (*Spiniferites bentorii* subsp. *truncatus*).

PLATE 10

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–3. *Spiniferites bulloideus*.
4.–9. *Spiniferites delicatus*.
10.–12. *Spiniferites elongatus*.

PLATE 11

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–2. *Spiniferites hyperacanthus*.
1. Black arrows highlight bifurcate intergonal processes with bifid tips
3.–11. *Spiniferites lazus*.

PLATE 12

Dinoflagellate cysts from Mar Piccolo basin. Black numbers indicate dinocyst micrographs from surface samples. Scale bars 20 µm.

- 1.–6. *Spiniferites membranaceus*.
7.–9. *Spiniferites mirabilis*.
7. Black arrow indicates trifurcate gonial process with recurved, bifid tips.
8. Black arrow highlights bifurcate intergonal process with bifid tips.
10.–12. *Spiniferites mirabilis* subsp. *serratus*.
10. Black arrow indicates archeopyle opening, showing shape and position.

PLATE 13

Dinoflagellate cysts from Mar Piccolo basin. Black numbers indicate dinocyst micrographs from surface samples. Scale bars 20 µm.

- 1.–3. *Spiniferites pachydermus*.
2. Black arrow indicates archeopyle opening
4.–6. *Spiniferites pachydermus*, specimen with short processes.
7.–12. *Spiniferites ramosus*.

PLATE 14

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–12. *Peridinium ponticum*.
1. Black arrow indicates hexagonal archeopyle opening.

PLATE 15

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–6. Cyst of *Diplopetta symmetrica*.
7.–12. *Dubridinium caperatum*.

PLATE 16

Dinoflagellate cysts from Mar Piccolo basin. Black numbers indicate dinocyst micrographs from surface samples. Scale bars 20 µm.

- 1.–3. *Dubridinium ulsterum*.
4.–6. Cyst of *Archaeoperidinium minutum*.
5. Black arrow indicates large circular base of process, highlighting well-defined shape and attachment to cyst wall.
6. Black arrow points to spinules developing from process.
7.–9. *Brigantedinium asymmetricum*.
10.–12. *Brigantedinium auranteum*.

PLATE 17

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–2. *Brigantedinium cariacense*.
3. *Brigantedinium simplex*.
4.–6. *Islandinium?* *cezare*.
7.–9. *Lejeunecysta oliva*.
7. Black arrow indicates cingulum, highlighting narrow and excavated structure.
9. Black arrows indicate two well-developed antapical horns.
10. Cyst of *Protoperidinium denticulatum*.
11.–12. Cyst of *Protoperidinium nudum*.

PLATE 18

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–3. Cyst of *Protoperidinium stellatum*.
4. Cyst of *Protoperidinium thulesense*.
5.–7. Cyst of *Protoperidinium tricingulatum*.
8.–9. *Quinquecuspis concreta*.
10.–12. *Selenopemphix nephroides*.

PLATE 19

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 µm.

- 1.–3. *Selenopemphix quanta*.
4.–9. *Selenopemphix undulata*.
10.–12. *Trinovantedinium applanatum*.

PLATE 20

Dinoflagellate cysts from Mar Piccolo basin. Scale bars 20 μm .

1.–3. *Votadinium calvum*.

4.–5. *Votadinium spinosum*.

6.–12. *Xandarodinium xanthum*.

PLATE 21

Dinoflagellate cysts from Mar Piccolo basin. Black numbers indicate dinocyst micrographs from surface samples. Scale bars 20 μm .

1.–3. *Echinidinium granulatum*.

4.–7. Cyst of *Pentapharsodinium dalei*.

8.–9. Cyst of *Scrippsiella* cf. *trifida*.

10.–12. Cyst of *Scrippsiella* cf. *trochoidea*.

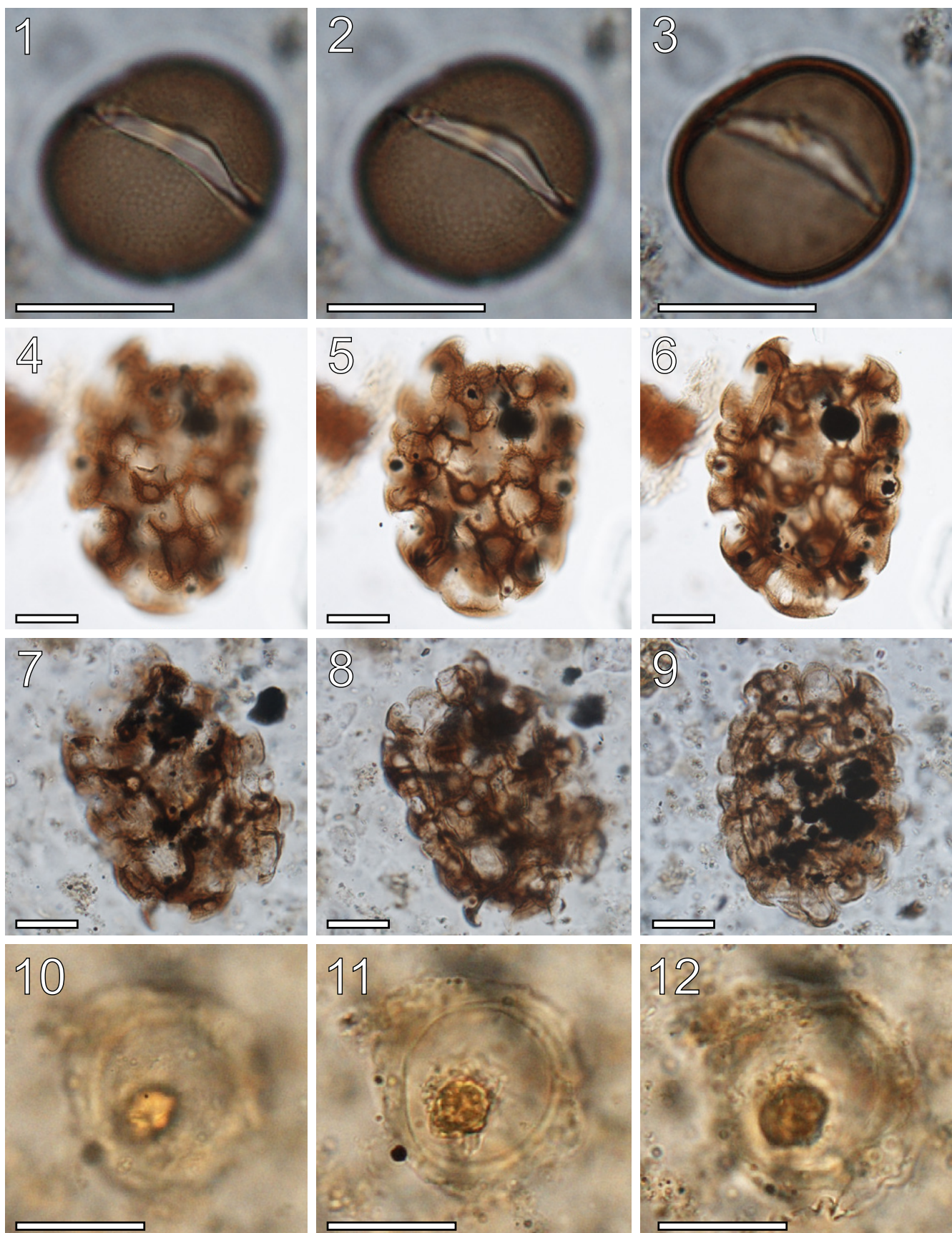
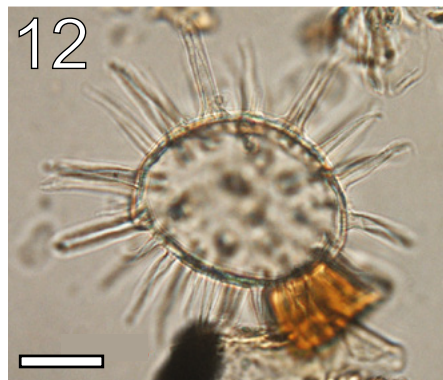
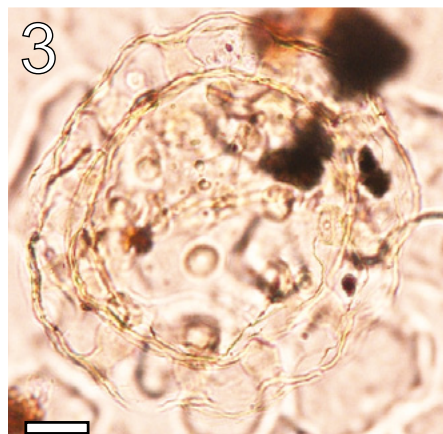
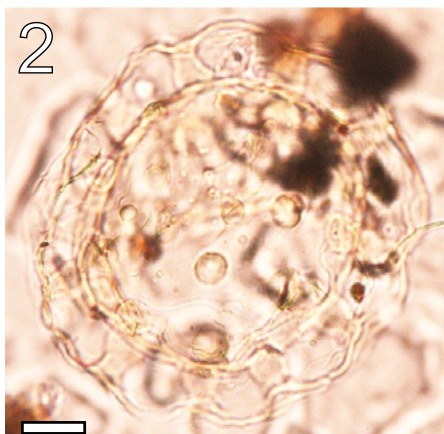
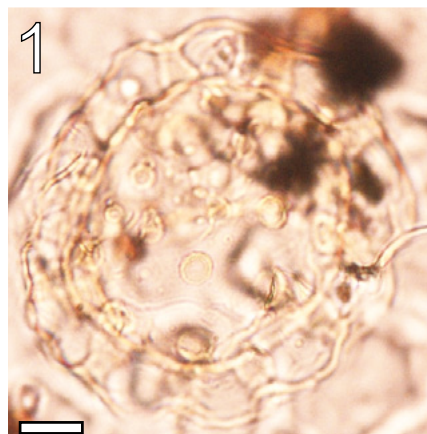


PLATE 2



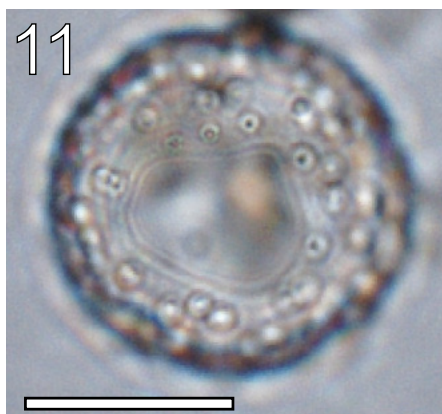
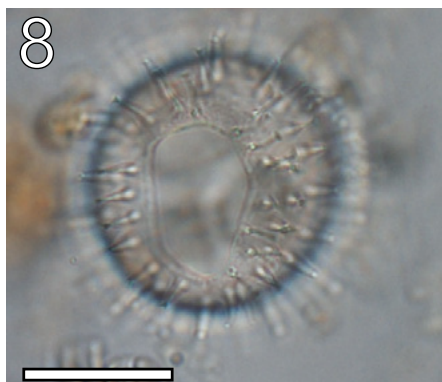
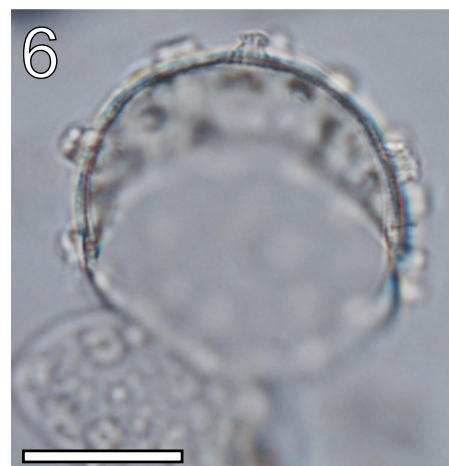
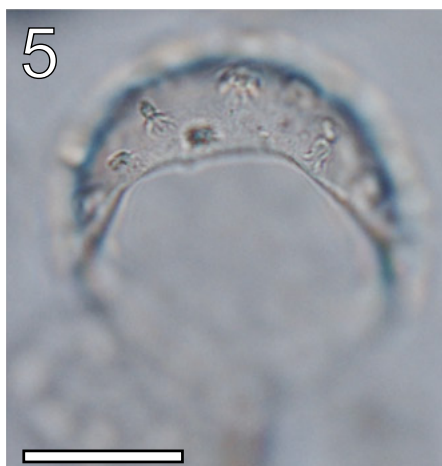
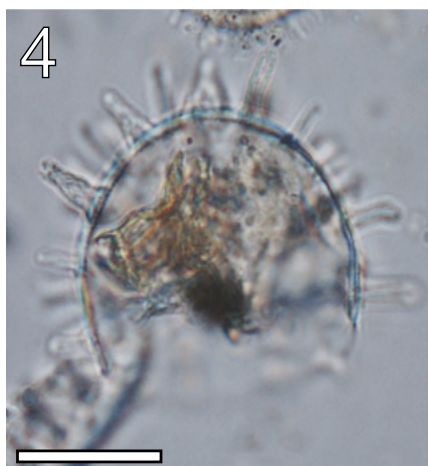
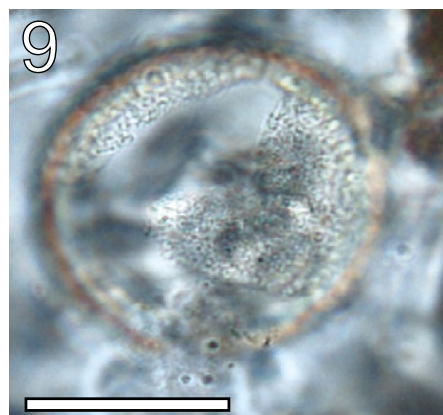
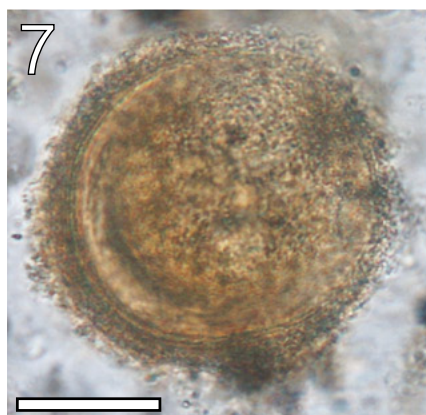
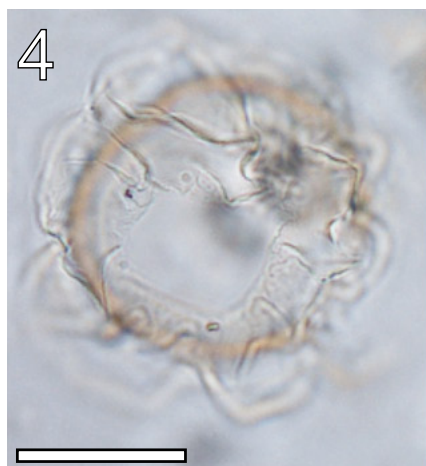
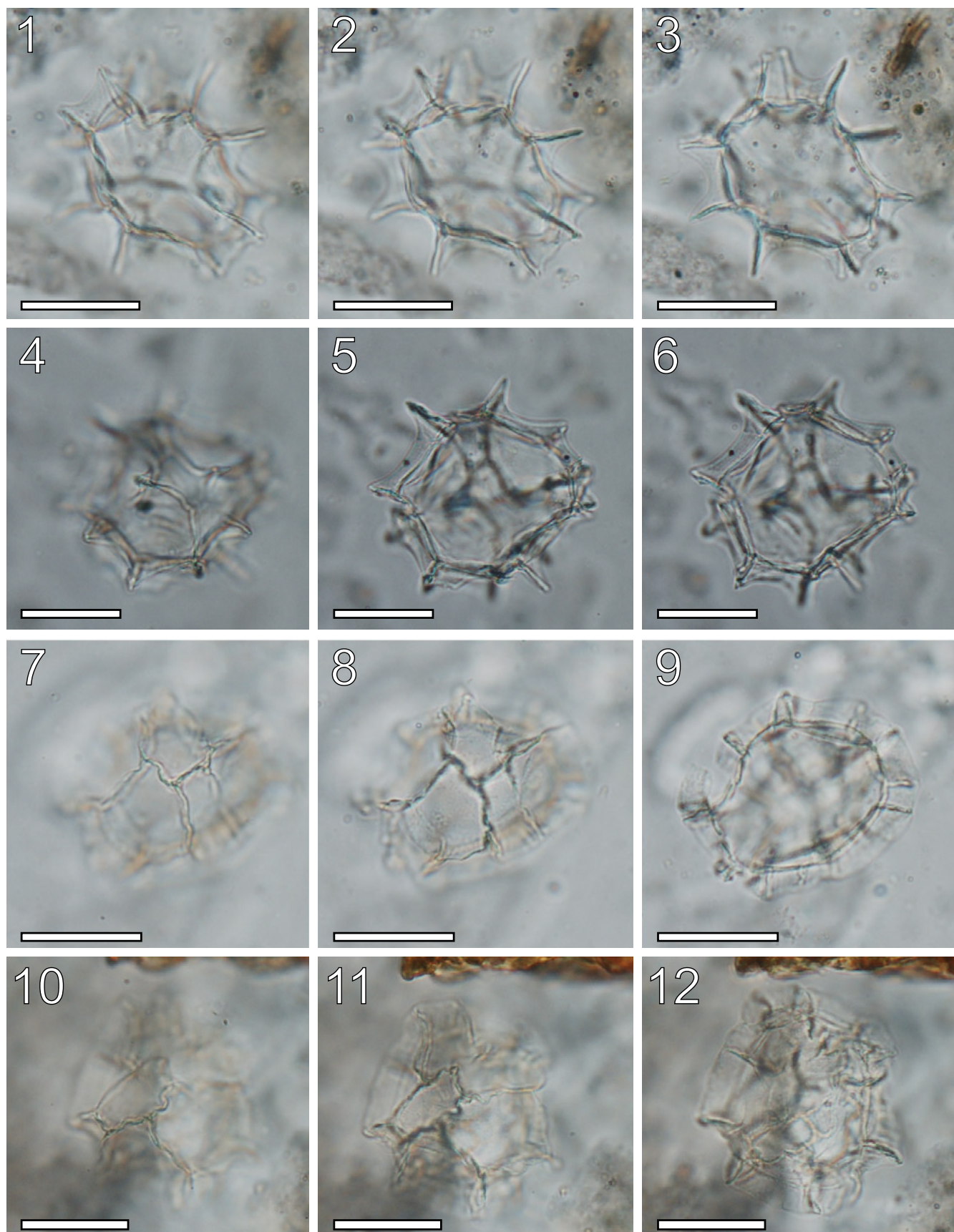
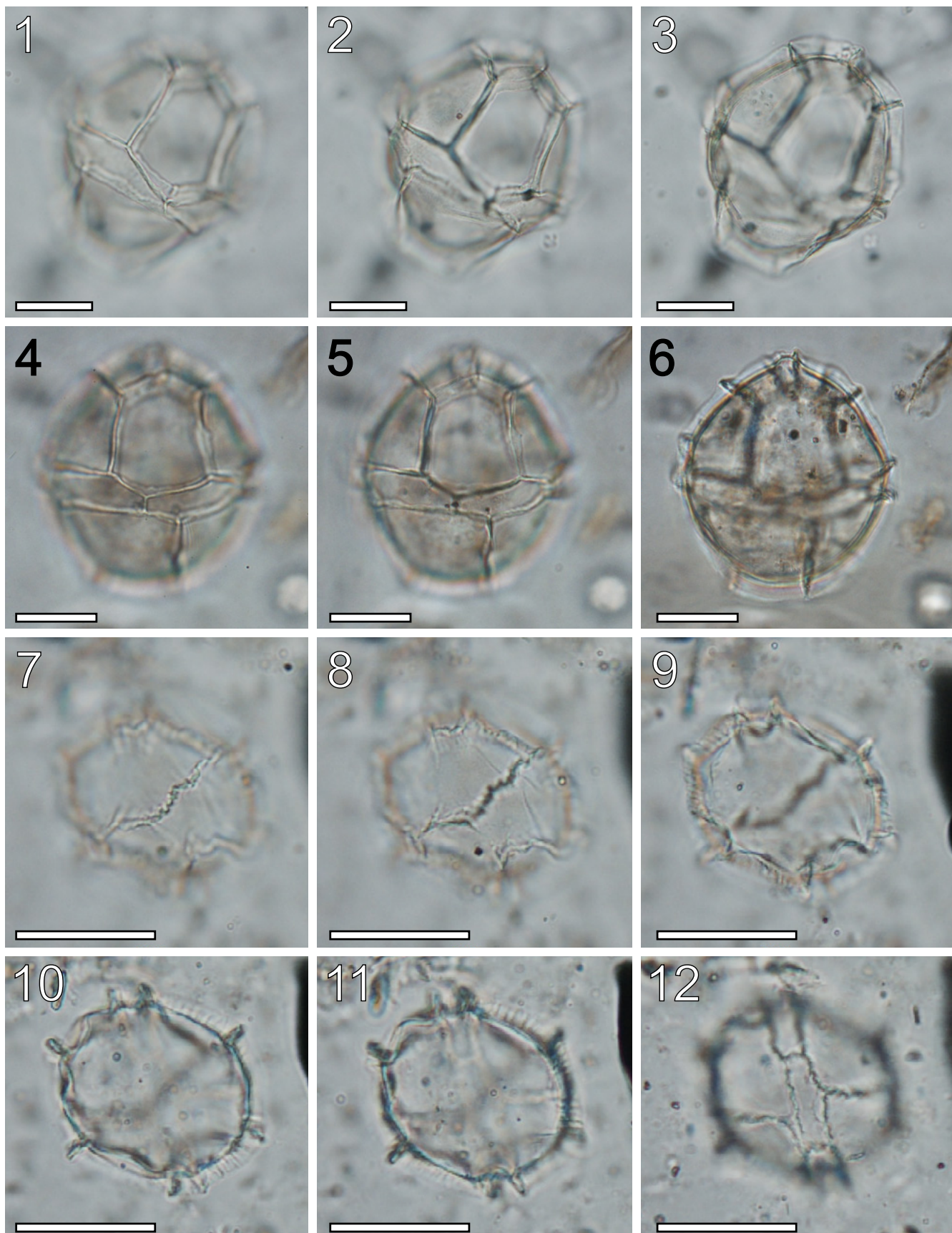


PLATE 4







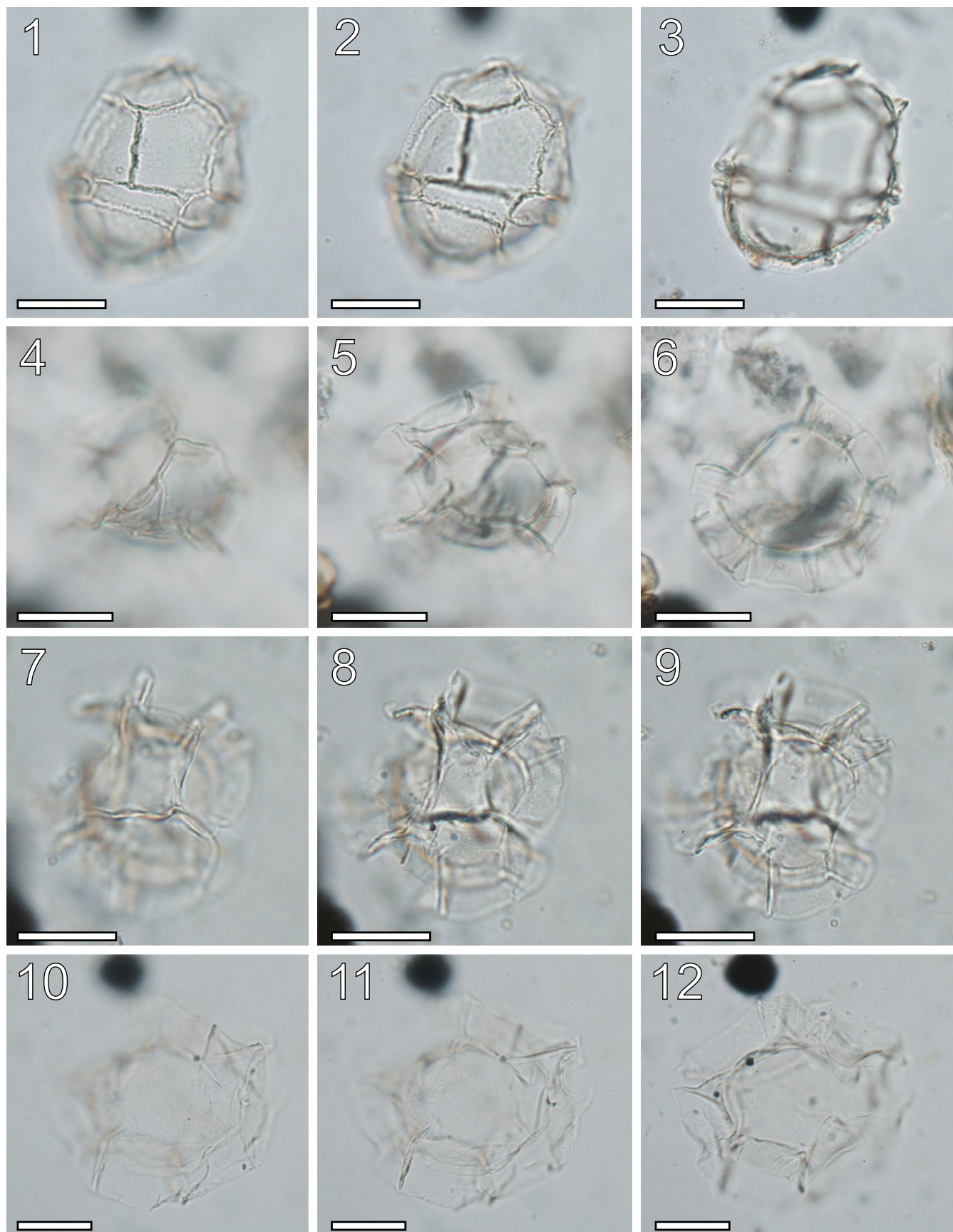


PLATE 8

