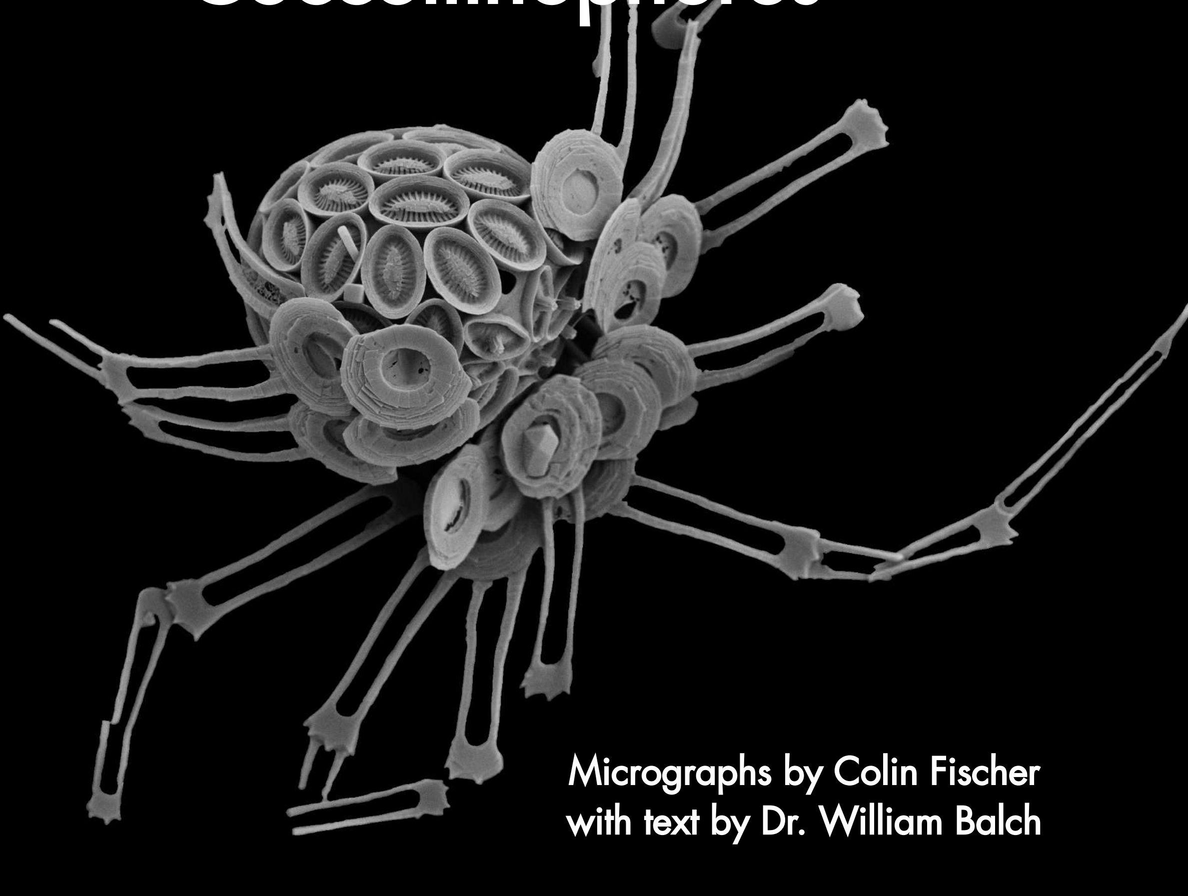
Ultra-Fine Art of Coccolithophores



Micrographs by Colin Fischer
with text by Dr. William Balch

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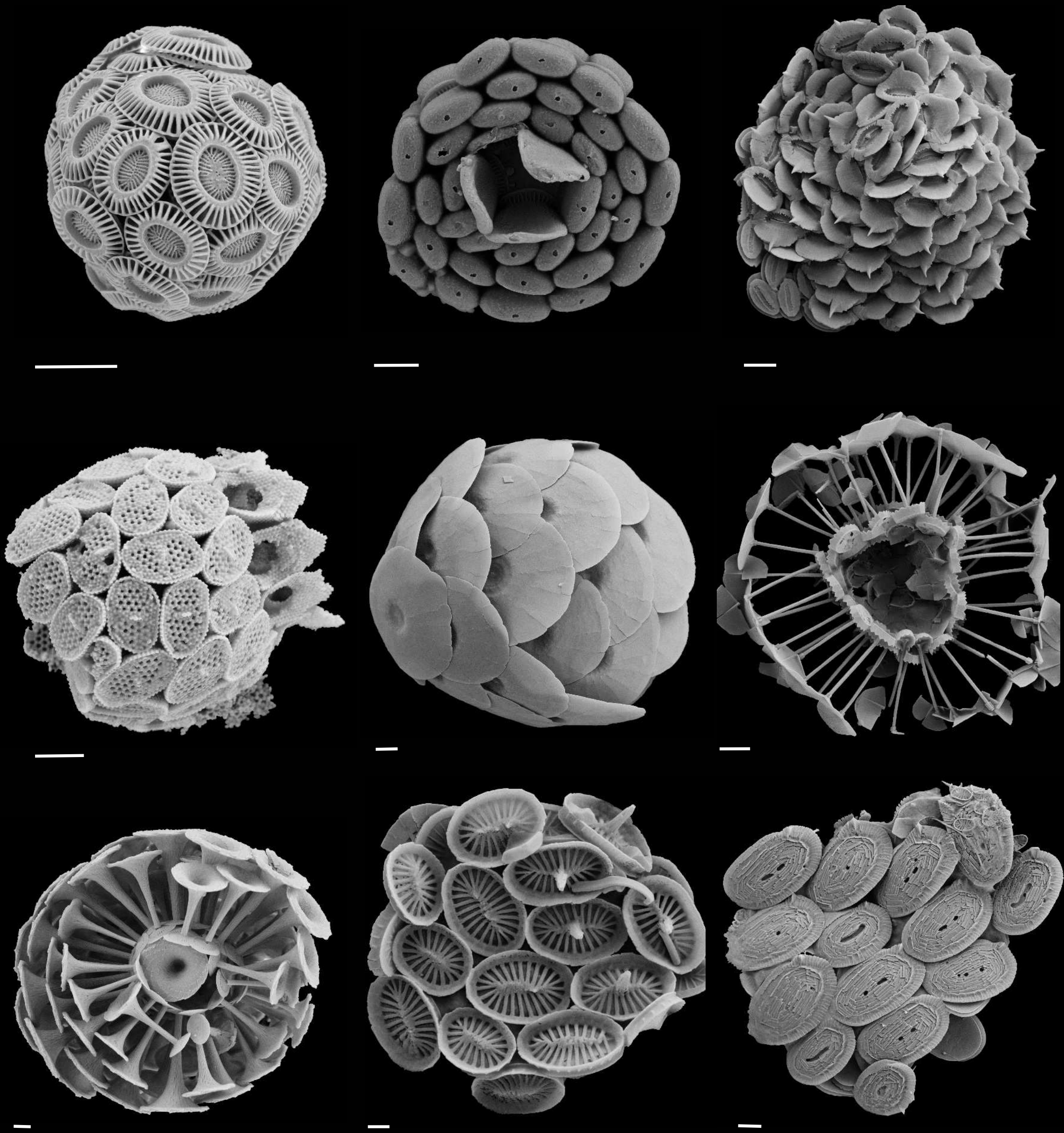
1 Introduction

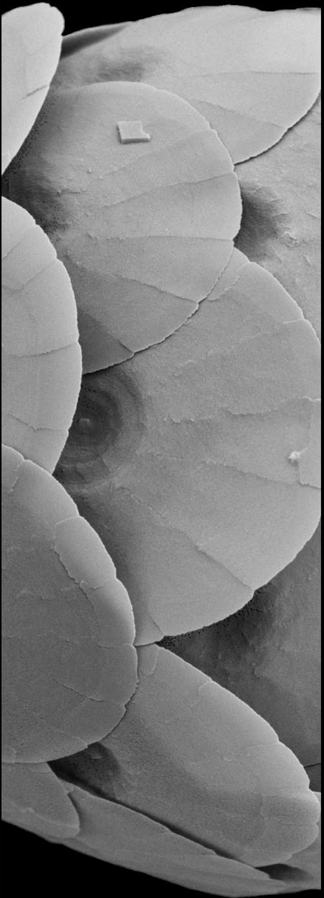
Coccolithophores are grouped in the phylum (or division) Haptophyta, and consist of single-celled, eukaryotic algae that produce scales typically made of calcite, a mineral form of calcium carbonate ($CaCO3$; aka limestone). There is remarkably little known about coccolithophore life cycles, as well as their ecology. Many species of coccolithophores have what is known as a “haplodiplontic” life cycle, that is, a haploid stage (that contains a single complement of DNA) alternating with a diploid stage (with double the complement of DNA). The haploid stage is motile (with flagellae) and is covered with holococcoliths (coccoliths constructed of simple rhombohedral calcite crystals) while the non-motile, diploid stage is covered with heterococcoliths, which are much more elaborately formed calcite scales. Within phytoplankton ecology, this group of unicellular calcifying algae are usually lumped into a single “functional group”, the “calcifiers”, but such a grouping belies the extraordinary diversity in morphology, ecology, physiology and bio-optical properties of this algal group.

The study of coccolithophores sits at the intersection of the major science sub-disciplines of oceanography, ecology, geology, ocean optics, and biogeochemistry. They are relevant to marine ecology because some of their clear preferences for specific types of marine environments. In the most general terms, they typically survive much better in warm, stratified water bodies, than, say, the siliceous diatoms, which prefer well-mixed environments with higher nutrients). Thus, as the ocean warms in the current geological epoch, the Anthropocene, coccolithophores are thought to be better able to compete with other algal species and, indeed, appear to be becoming more abundant (Rivero-Calle et al., 2015).

Image Key (pg 5; note, in this and all subsequent images, scale bars are one micrometer in length):

Upper Left: *Emiliania huxleyi*
Upper Center: *Algirosphaera robusta*
Upper Right: *Alisphaera gaudii*
Middle Left: *Poricalyptra magnaghii*
Middle Center: *Oolithus fragilis*
Middle Right: *Papposphaera lepida*
Lower Left: *Discosphaera tubifera*
Lower Center: *Syracosphaera nodosa*
Lower Right: *Helicosphaera pavimentum*

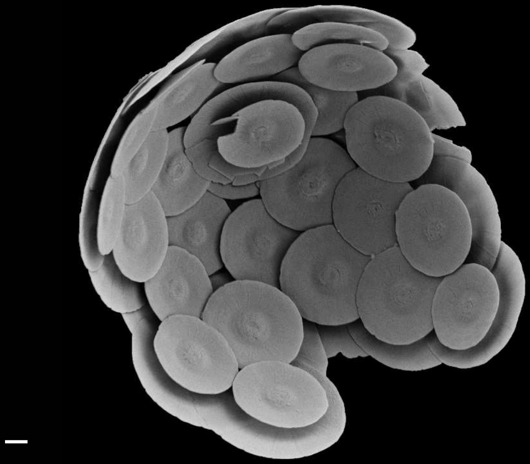




There is accumulating evidence that coccolithophores are mixotrophic, that is, they can fuel their growth from photosynthesis or from the uptake of organic carbon (Godrijan et al., 2020; 2022). Their calcite mineralogy has meant that coccolithophores and their associated coccoliths have been preserved in marine sediments for geological time, thus providing a historical legacy of their abundance in the sea. The first coccolithophores appeared in the late Triassic, some 220 million years ago (Young et al., 2003). Populations have waxed and waned through geological time as global environmental conditions have changed and whole genera died off as they experienced massive events such as the Cretaceous-Tertiary mass extinction event (66 million years ago). In short, coccolithophores provide a remarkable window to the past conditions on Earth. Coccolithophores also provide a window to current environmental conditions due to the fact that they are highly optically active. Coccolithophores, surrounded by their optically-refractive scales made of the mineral calcite, are responsible for significant light scattering in the sea (Balch, 2018). Sunlight penetrating downwards into the ocean is intercepted by these particles, and the interaction of the light with the particles results in the photons changing directions, thus making the light field more diffuse or turbid. Some of this scattered light actually changes direction from downwards to upwards (called backscattering). A fraction of this backscattered light is propagated upwards through the air-sea interface, which is detectable from earth-viewing satellites as higher albedo (Tyrrell et al., 1999).This is especially true in massive blooms of the ubiquitous coccolithophore, *Emiliania huxleyi*, with large swaths of entire ocean basins that have a turquoise color, not the usual navy blue color of seawater (Holligan et al., 1993). To the observer on a boat in the middle of such a coccolithophore bloom, the water takes on the color of seawater found in tropical marine environments over calcium carbonate banks, leaving the impression that one’s boat has run aground in the tropics! While such blooms represent an extreme case, the increased reflectance caused by coccolithophores, even in non-bloom situations with low concentrations, typically accounts for 10-20% of the total light reflected from the sea surface towards outer space. In moderately productive areas of the sea, such as over continental shelves, coccolithophores account for 30-50% of the light reflected from the sea. This point is often overlooked by optical oceanographers who attribute the majority of light coming from the sea being driven by the absorption (light disappearance) by plant chlorophyll. The light scattered by coccolithophores also depends on their shape (Gordon and Du, 2001), an aspect just now being appreciated in models of ocean light scattering, used to estimate the amount of this calcium carbonate suspended in seawater (also called “particulate inorganic carbon” or PIC) (Neukermans and Fournier, 2018).

PIC is much denser than typical phytoplankton and acts as an efficient ballast to sink particles and their aggregates to the sediments, thus being an important driver of the ocean’s biological pump (Francois et al., 2002). That is, the biological pump is the mechanism by which massive amounts of atmospheric CO_2 are fixed by phytoplankton in the surface ocean, which then die and sink, thus “pumping” this carbon to depth where it gets sequestered for thousands of years or even for geological time. Coccolithophores are also associated with the alkalinity pump (Heinze et al., 1991). By virtue of their fixing of two molecules of bicarbonate in the surface ocean, and forming, on average, one molecule of CO_2 and one molecule of calcium carbonate, they lower the surface alkalinity of the sea, and “pump” this alkalinity to depth where some of the calcium carbonate dissolves, thus releasing bicarbonate back into the seawater. Thus, given these two different types of pumps, it is noteworthy that coccolithophores strongly influence the biogeochemistry (indeed the geology) of the sea.

Many fine taxonomic guides have been written about the coccolithophores, for example, Young et al. (2003). The purpose of this e-book is not to replicate such an effort. Instead, this e-book is meant to celebrate the amazing morphological diversity of this group of microalgae, as observed by scanning electron microscopy of samples taken during our many field campaigns around the world. Each image has been painstakingly cropped in order to highlight the beauty of the individual coccolithophores and their coccoliths, free of other marine debris and detritus. The purpose of this book is all about appreciating the beauty of these organisms at the micrometer size scale as well as some of the underlying science that connects them to our planet. Yes, these are organisms that integrate entire sub-disciplines within oceanography but also can be appreciated for the intricate artistry of nature in form and function, as expressed in their coccoliths. These organisms, singularly responsible for producing these elaborate calcium carbonate scales at the micron scale, collectively have an immense impact on the global carbon cycle as well as the optical reflectance of the world ocean. Examining them at different size scales emphasizes that the coccolithophores are an integral part of the ocean ecology and essential part of the biodiversity of the planet. It is for these reasons that we have compiled this ebook of scanning electron microscope images, to communicate not only the scientific importance of this algal class but also their amazing beauty.

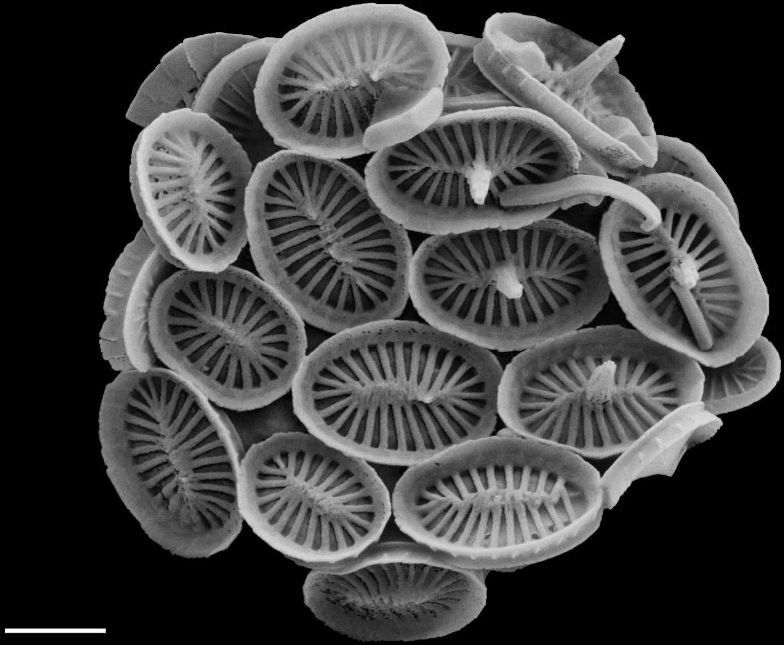


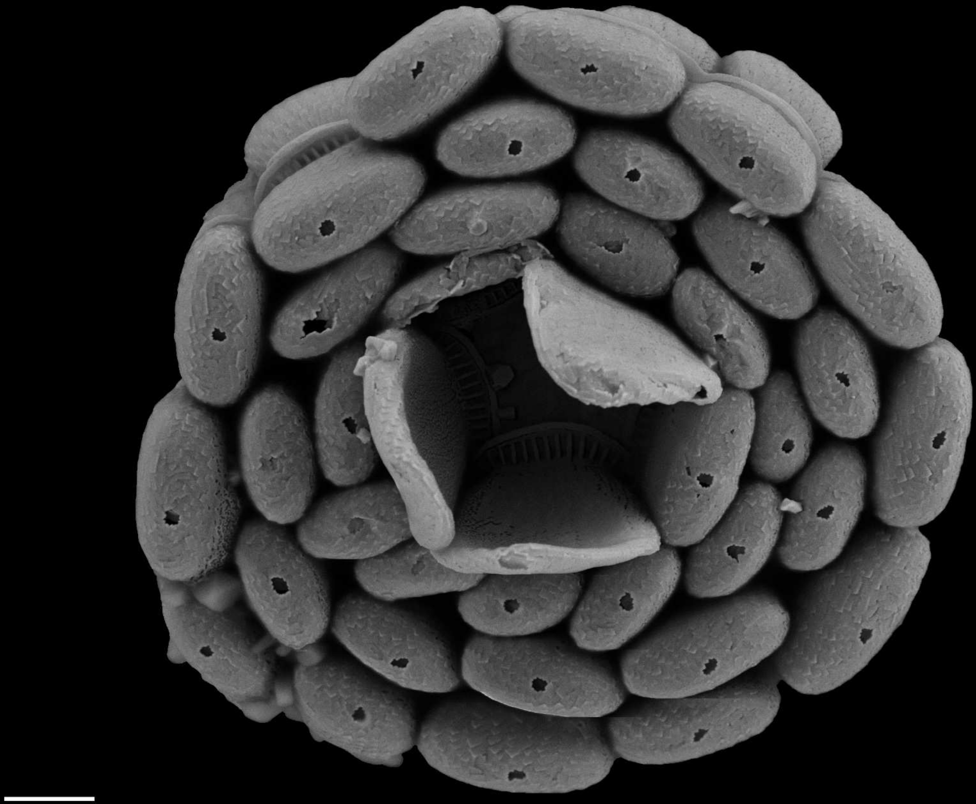
2 Heterococcolithophores

Heterococcolithophores

Heterococcolithophores are haptophytes with intricately shaped coccoliths that consist of beautifully-complex, radially-arranged crystal calcite elements. These are associated with the diploid life stage of coccolithophores (that is, containing twice the genetic complement (2N) of the haploid life stages (1N)) (Taylor et al., 2017). For the coccolithophore species, *Emiliania huxleyi*, the heterococcolith-bearing life stage is the most commonly found morphotype and it is fairly ubiquitous in the global ocean. *E. huxleyi* aside, heterococcolith-forming coccolithophores dominate in lower light environments with higher nutrient concentrations (Cros and Estrada 2013). Moreover, The heterococcolith phase is more abundant during winter months (Šupraha et al., 2016). Ecologically, coccolithophores have traditionally been thought to occupy four general niches within the ocean based on their biogeography (Young 1994): (a) disk-like, placolith-bearing, bloom-forming species in coastal and upwelling waters at low and high latitudes; (b) umbelliform species with "trumpet-shaped" coccoliths in more oligotrophic, blue-water sites, in subtropical latitudes, and in the top 100 m of the sea; (c) floriform species with flower-shaped coccoliths are typically found in deep parts of the euphotic zone (150–200 m), environments that are stratified and in low to middle latitudes; and (d) a group of miscellaneous, rarer species in environmental conditions other than those of the first three groups above (which typically constitute 80% of coccolithophore species but <20% of their abundance).

More details on their large-scale biogeography can be found elsewhere (Balch et al., 2019; Honjo and Okada, 1974; McIntyre and Be, 1967; Poulton et al., 2017; Reid, 1980). In this chapter, we show a variety of heterococcolith-bearing species that suggest a remarkable ecological and genetic diversity in form and function of these amazing plants.





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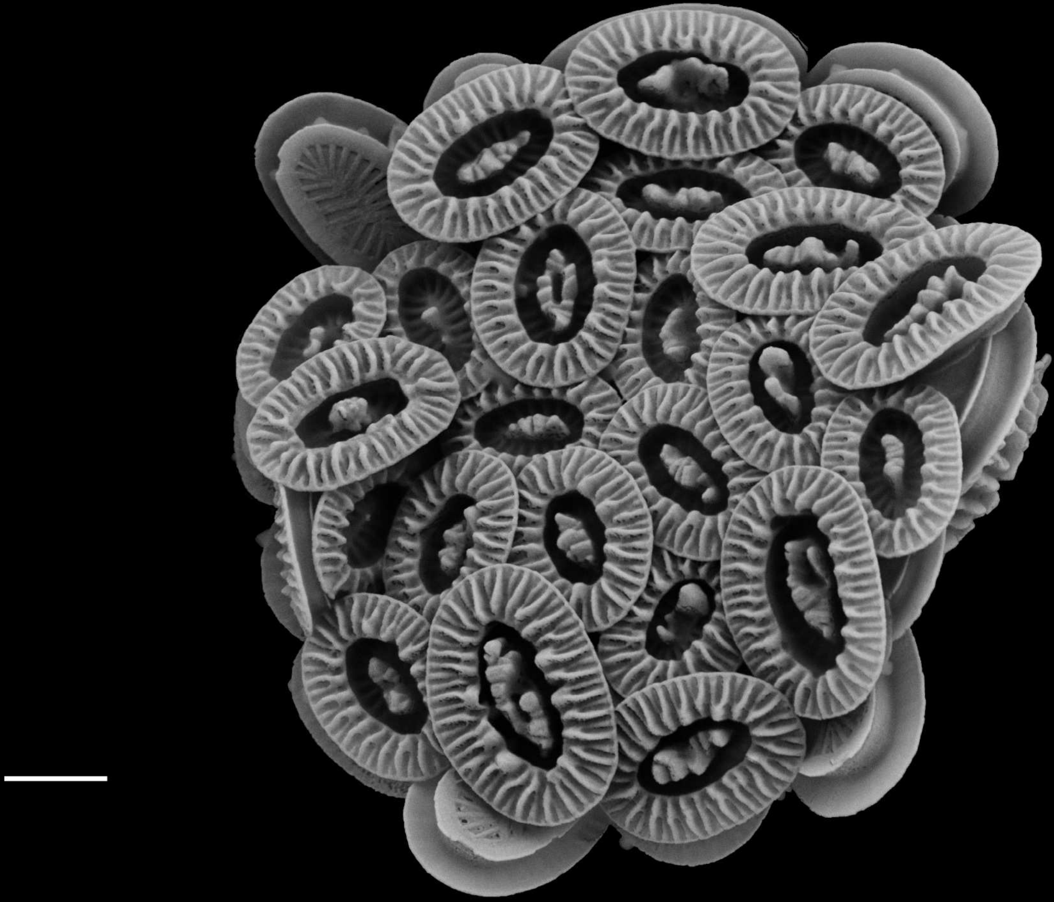

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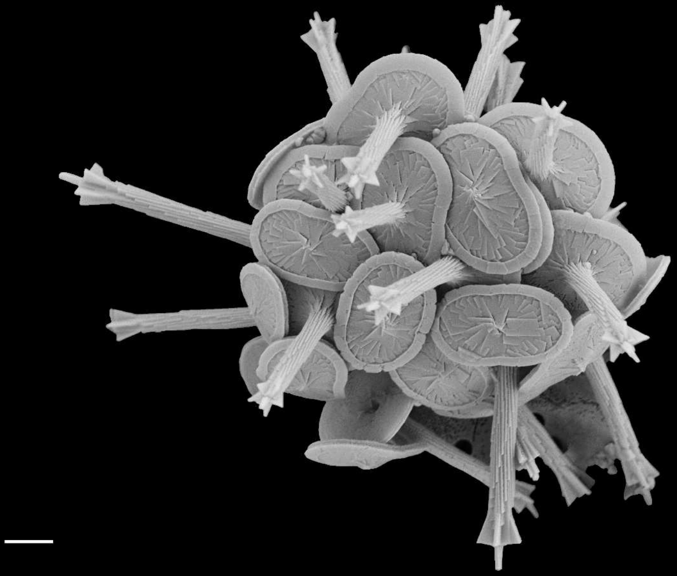

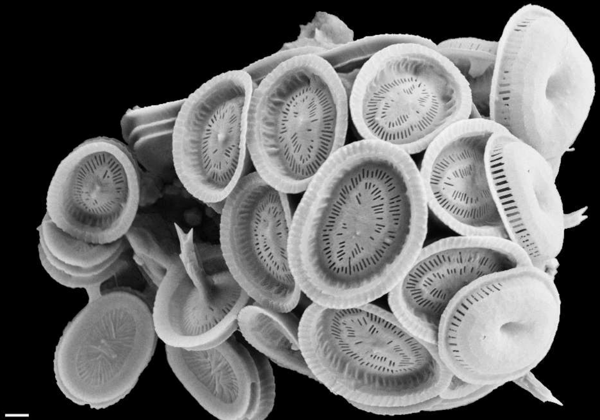

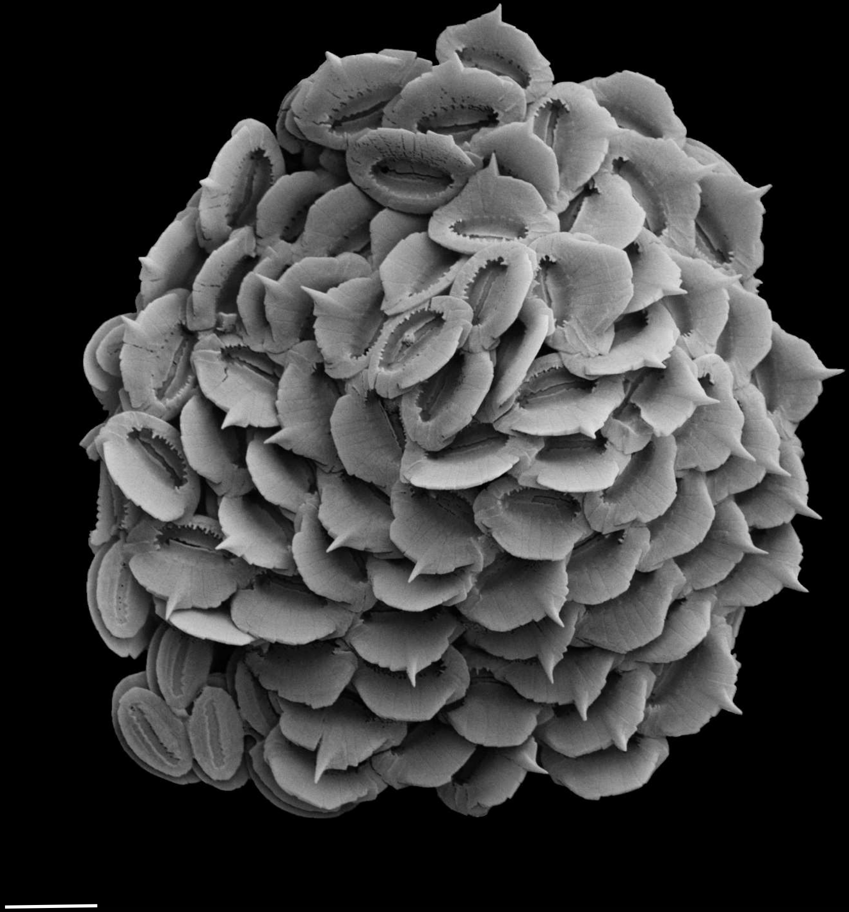

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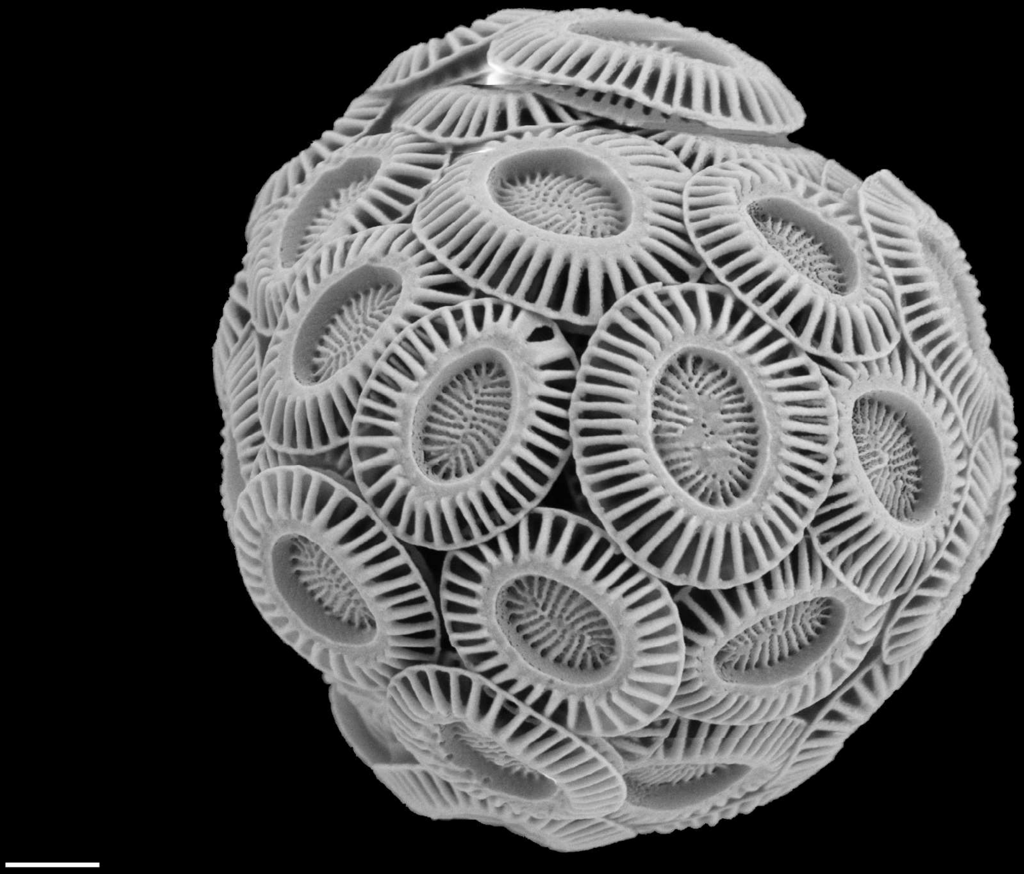

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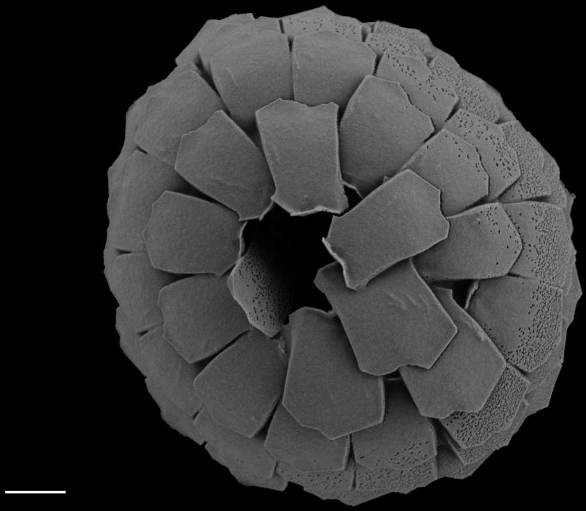

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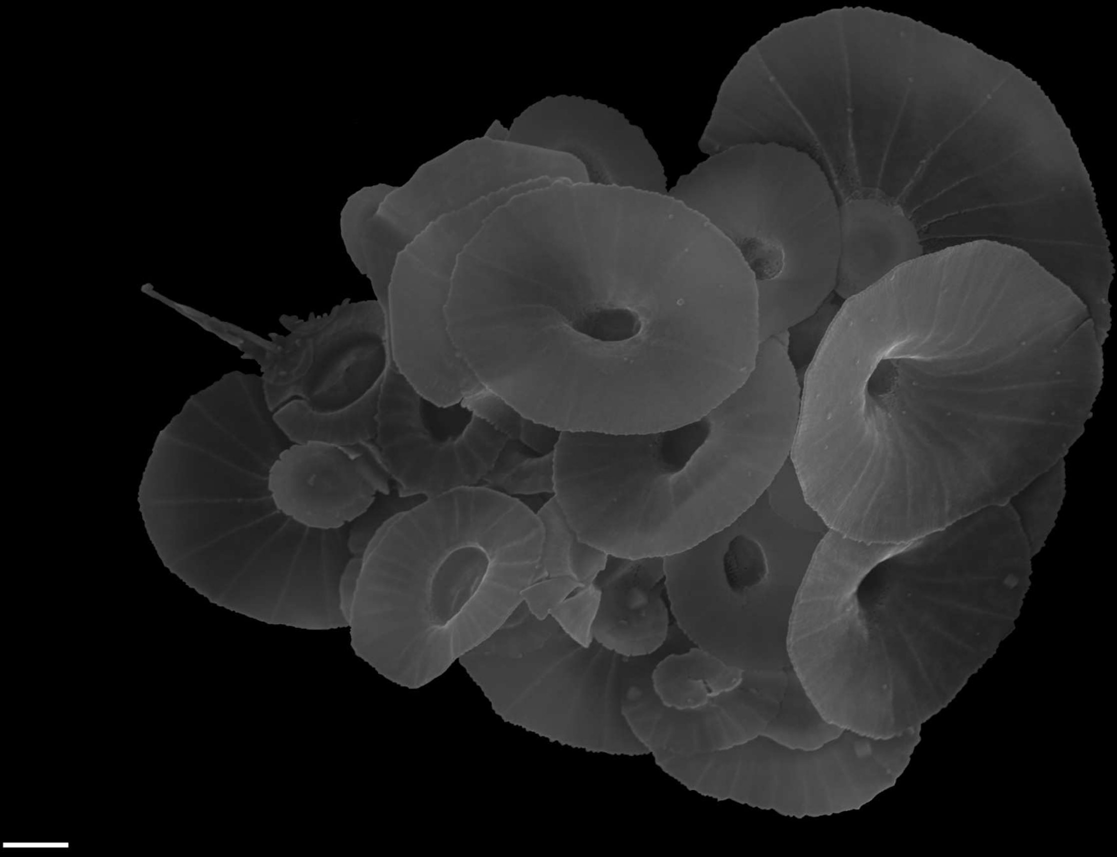

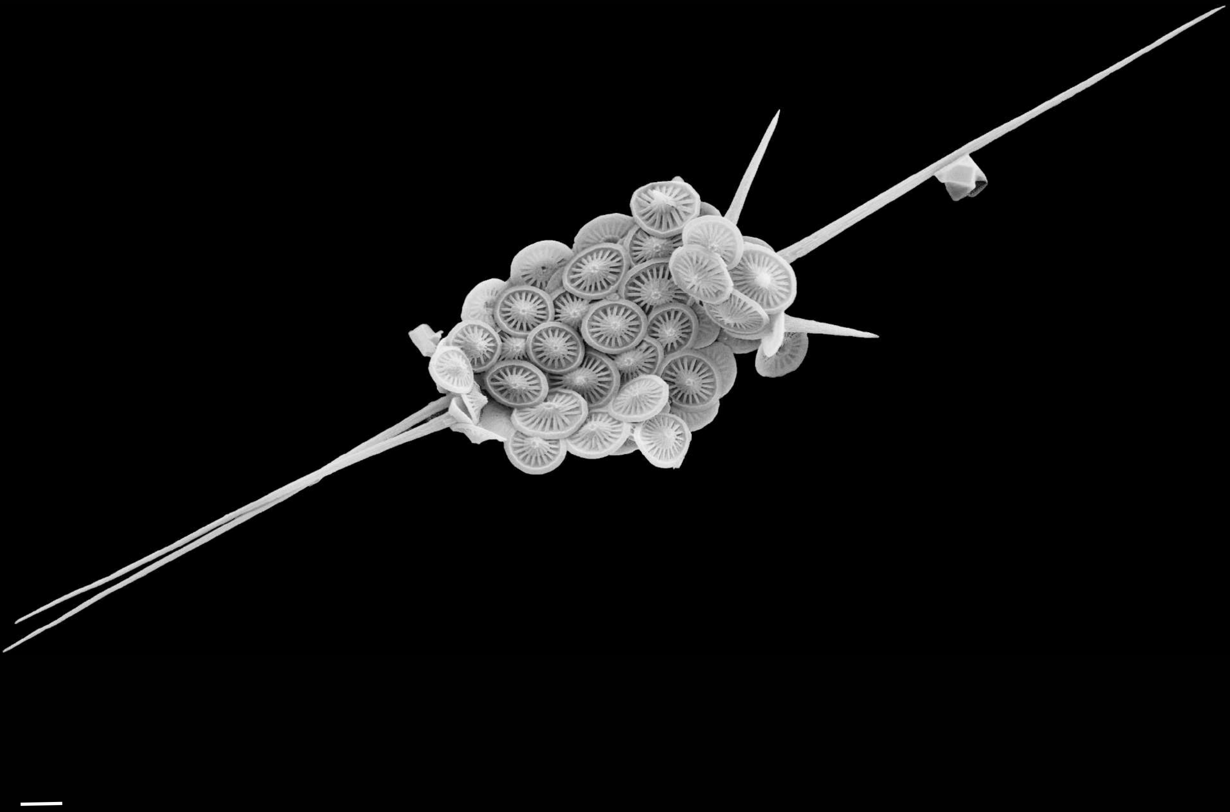

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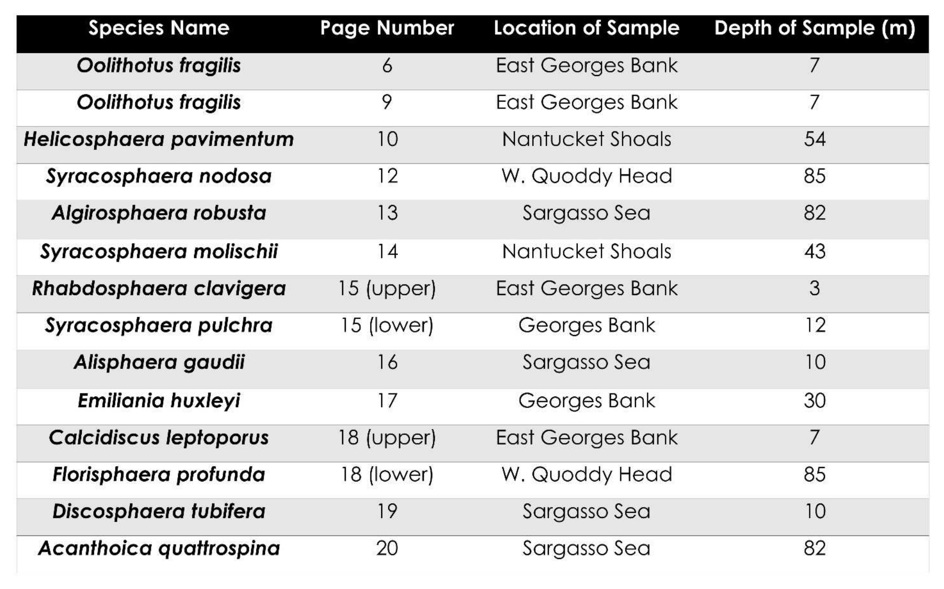
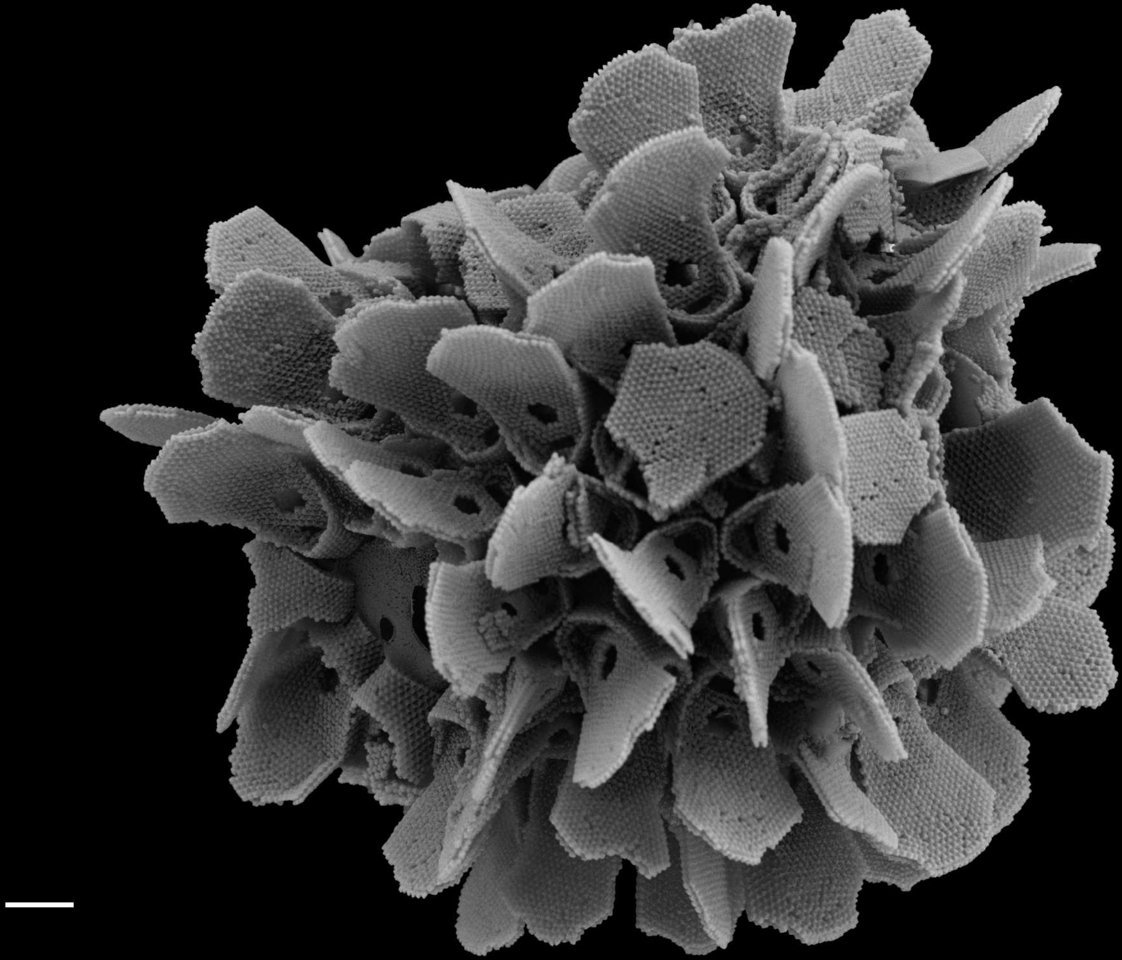
Reference table of heterococcolithophore images. All scale bars are 1 micron in length.



Species Name	Page Number	Location of Sample	Depth of Sample (m)
Oolithotus fragilis	6	East Georges Bank	7
Oolithotus fragilis	9	East Georges Bank	7
Helicosphaera pavimentum	10	Nantucket Shoals	54
Syracosphaera nodosa	12	W. Quoddy Head	85
Algirosphaera robusta	13	Sargasso Sea	82
Syracosphaera molischii	14	Nantucket Shoals	43
Rhabdosphaera clavigera	15 (upper)	East Georges Bank	3
Syracosphaera pulchra	15 (lower)	Georges Bank	12
Alisphaera gaudii	16	Sargasso Sea	10
Emiliania huxleyi	17	Georges Bank	30
Calcidiscus leptoporus	18 (upper)	East Georges Bank	7
Florisphaera profunda	18 (lower)	W. Quoddy Head	85
Discosphaera tubifera	19	Sargasso Sea	10
Acanthoica quattrospina	20	Sargasso Sea	82

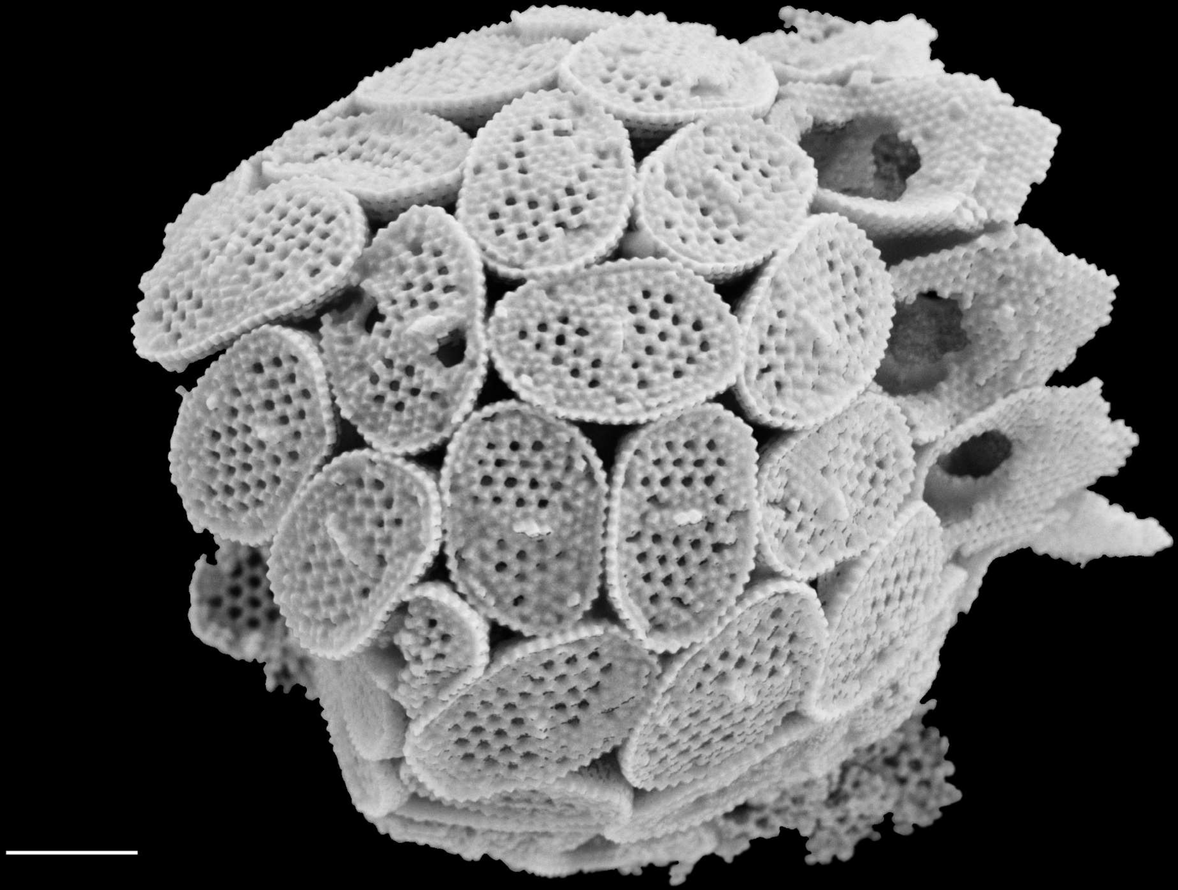
3 Holococcolithophores

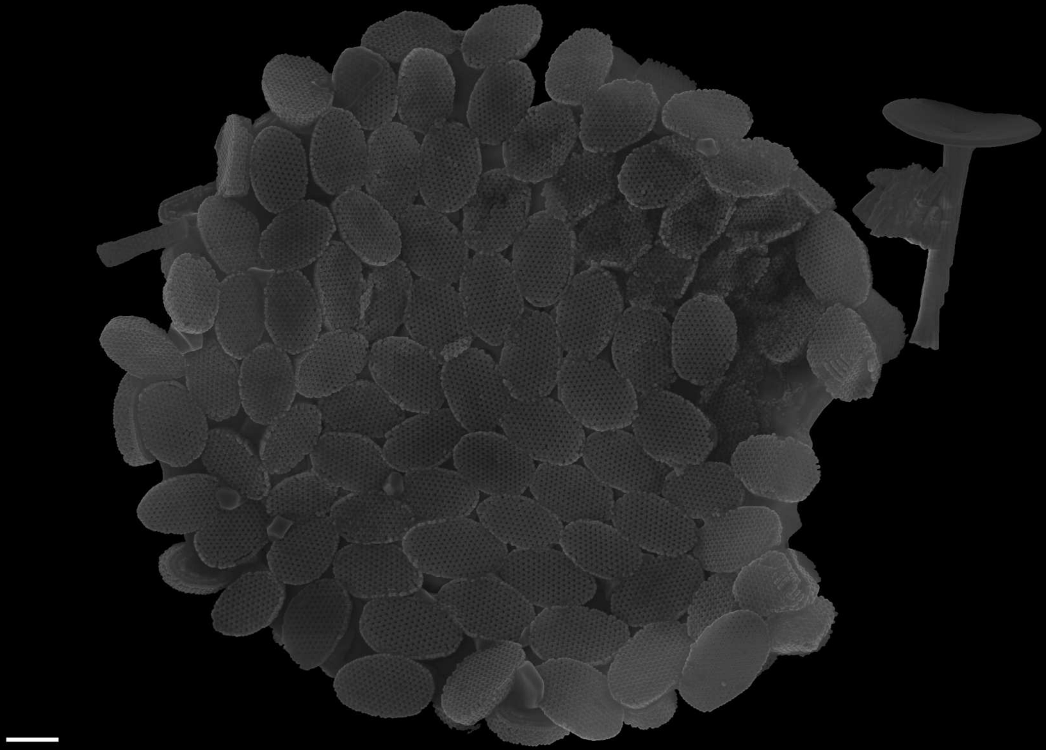


Holococcolithophores

Holococcolithophores are coccolithophores covered by calcite coccoliths, called holococcoliths. These are approximately 0.1-µm in diameter, simply shaped (nowhere as elaborate as the heterococcoliths), composed of calcite rhombohedra organized in a continuous pattern and they are formed by the haploid life stage of coccolithophores (Young et al., 2003). Unlike the heterococcolith-forming coccolithophores, holococcolith forms predominate in more oligotrophic surface waters (Cros and Estrada 2013) and the holococcolith-bearing stage is more abundant during summer months (Šupraha et al. 2016). The transition of the haploid holococcolith stage to the diploid heterococcolith stage has been observed before (Cros and Estrada, 2013; Cros et al., 2000; Geisen et al., 2002) but little is known about the physiological and biochemical changes that occur during this transition.

The evolutionary selective advantage of holococcoliths versus heterococcoliths is not well understood either (Monteiro et al., 2016) presumably since the energetic costs associated with their cellular synthesis are poorly constrained. Similarly, there are no data illustrating that holococcoliths provide better protection from grazing than do heterococcoliths. It might be argued, however, that elaborate-shaped heterococcoliths provide more drag to slow down sinking heterococcolithophores out of the base of the euphotic zone into the sub-euphotic or aphotic zones. Such sinking would spell almost certain death unless the coccolithophores also had mixotrophic or heterotrophic life strategies that would allow them to fix carbon. Meanwhile, in shallow oligotrophic waters with more abundant holococcolithophores, the simple-shaped holococcoliths may provide other unknown selective advantages for these unicellular plants.





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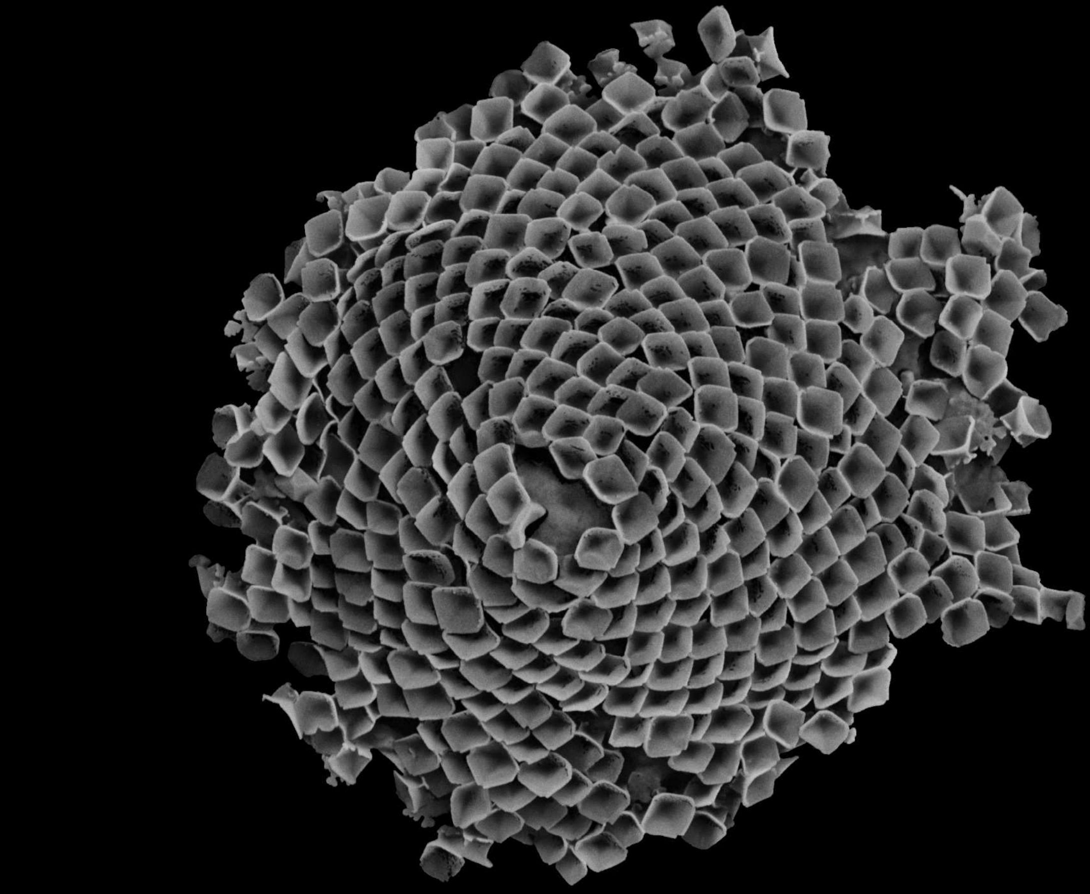

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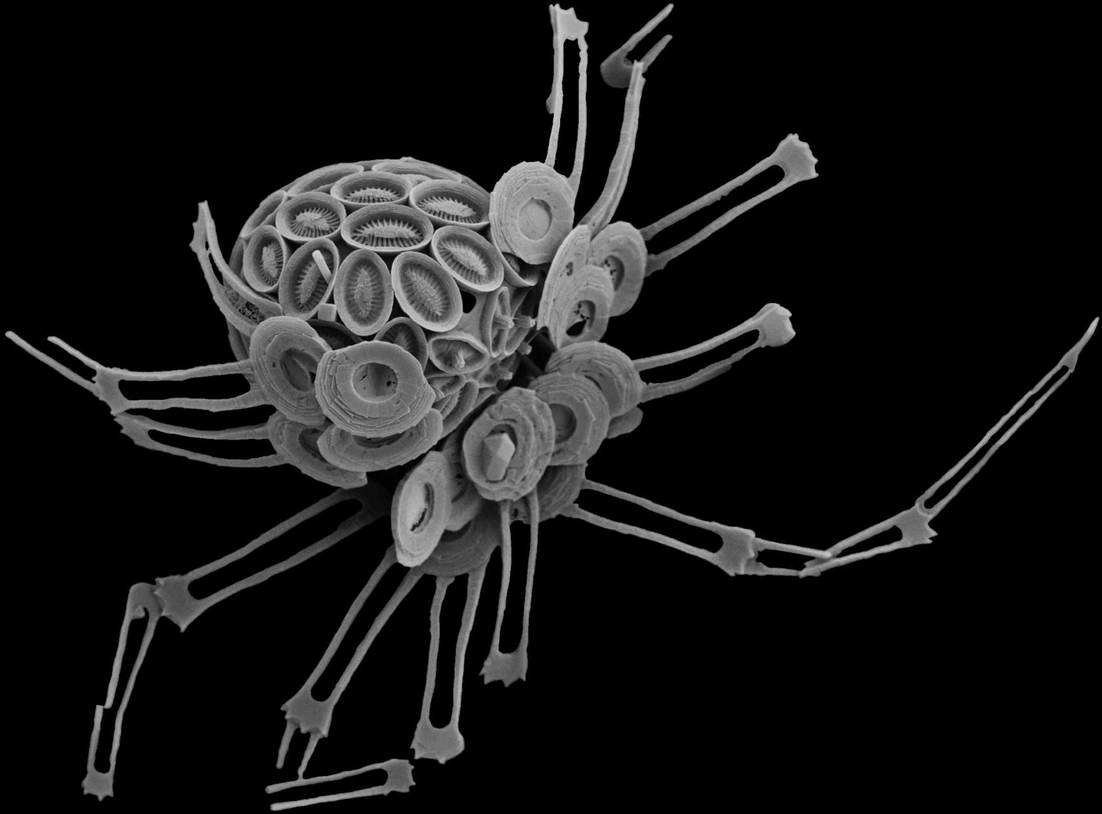
Reference table of holococcolithophore images. All scale bars are 1micron in length.

Species Name	Page Number	Location of Sample	Depth of Sample (m)
Syracosphaera anthos HOL	22	Gulf of Maine	10
Poricalyptra magnaghii	25	Georges Bank	3
Syracosphaera nana HOL	26	Georges Bank	12
Alisphaera gaudii POL	27	Georges Bank	10



4 Heterococcolithophores with Highly Specialized Coccoliths

Heterococcolithophores with Highly Specialized Coccoliths

Deep-dwelling, floriform coccolithophores live mostly in the lower portions of the illuminated ocean (aka photic zone) (Winter et al., 1994; Winter and Siesser, 1994). The deepest species occupy the sub-euphotic zone (Poulton et al., 2017). This is a critical observation, especially when considering whether the species can be considered autotrophic (carbon fixation associated with photosynthesis), heterotrophic (carbon fixation associated with the breakdown of organic carbon molecules), or mixotrophic (carbon fixation associated with both photosynthesis and the breakdown of organic carbon molecules).

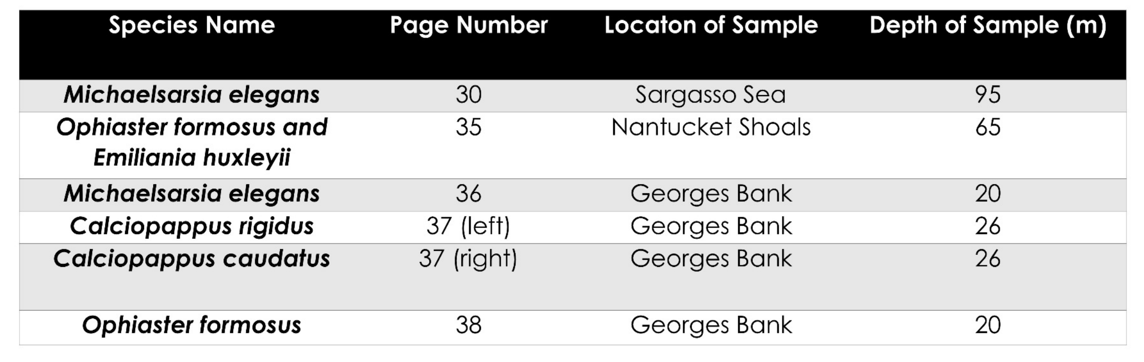
Coccolithophores are typically thought to fix their carbon based on autotrophic processes (i.e. photosynthesis) yet there is a rich historical literature showing that haptophytes can acquire nutrition in a mixotrophic fashion using particle ingestion (see review by Jones et al. (1994)). That said, the significance of mixotrophy for coccolithophore physiology, ecology, and biogeochemistry is barely understood in nature. Phagocytic (engulfing) ingestion of particles has been observed. Haptophytes are unique in that they have a haptonema, a filament-like cellular organelle that appears to be used for adhesion to other particles or substrata (Inouye and Kawachi, 1994). Indeed, the mixotrophic haptophyte species *Chrysochromulina hirta* uses its haptonema for prey capture and appears to have a sensory organelle. Another haptophyte, *Chrysochromulina ericina* (6–10 µm in diameter), can phagocytize a diatom approximately of the same size (9 µm× 3µm) (Parke et al., 1956), and the motile stage of *Coccolithus braarudii* can phagocytize bacteria (Houdan et al., 2006).

Paradigms are shifting, however, regarding the predominance of autotrophy versus mixotrophy in the marine environment. The traditional view of marine protists was that they are either exclusively autotrophic or exclusively heterotrophic, whereas the newer, more nuanced view is that a significant fraction of protists are mixotrophic, able to augment their carbon uptake through either photosynthesis or heterotrophic pathways (Mitra et al., 2014). The changing paradigm has ramifications for the survival of coccolithophores, especially the deep-living floriform species (such as *Florisphaera profunda*), associated with low to middle latitudes (Young, 1994). The presence of deep-dwelling coccolithophores well below the euphotic zone has been taken as evidence that some coccolithophores lead a mixotrophic lifestyle (Poulton et al., 2017). The uptake of dissolved organic carbon (instead of phagocytizing particles) to make a living was noted years ago by Blankley in an unpublished doctoral dissertation (Blankley, 1971) but, more recently, has been documented by Godrijan et al. (2020; 2021).

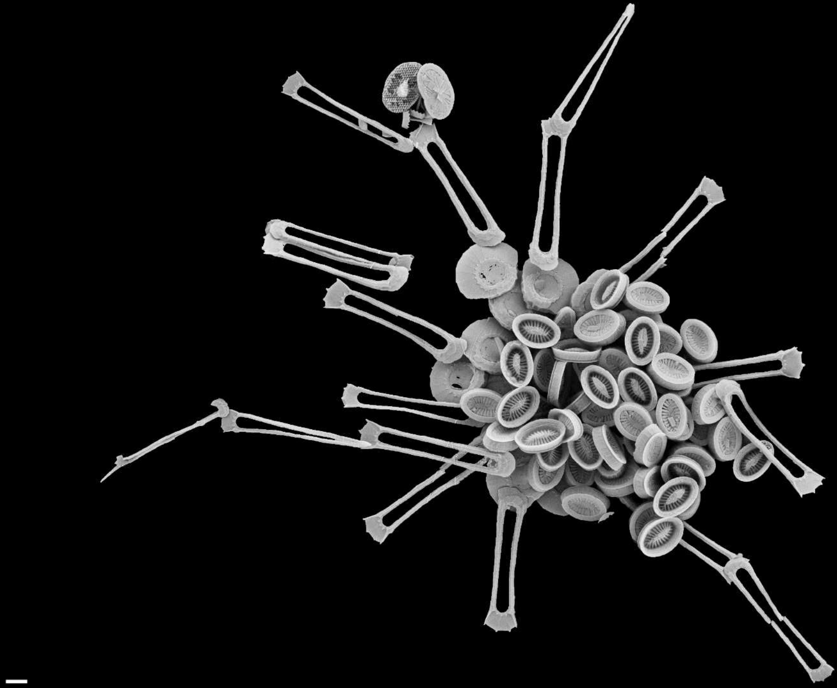
Mixotrophy may have also allowed the coccolithophores to survive through geological time. Indeed, coccolithophores have survived through some profound selective “bottlenecks” when their diversity plummeted. The first coccolithophore species were observed in the late Triassic (220 million years before present). Coccolithophores radiated in the Jurassic and Cretaceous (210-65 million years before present; 18 families; 140spp) with 80% extinction at the Cretaceous/ Tertiary (K/T) boundary (65 million years before present). Only seven families (60spp) survived through the Cretaceous/Tertiary boundary to give rise subsequently to 20 new families of coccolithophores.

Species radiation declined again in the Oligocene (30 million years before present) with the massive increase in global ice volume (only 30 species survived). Now there are 200 coccolithophore species with only 40 known from the Quaternary fossil record over the last 2.6 million years before present. Using molecular clock reconstruction and validation against the fossil record, Medlin et al. (2008) have suggested that mixotrophy played an important role for haptophyte survival after the Cretaceous/Tertiary boundary. They hypothesize that since haptophytes have no known resting stages (unlike diatoms or dinoflagellates), there was strong selection for coccolithophores that used mixotrophic forms of nutrition (including phagotrophy and photoheterotrophy). This allowed for their survival, albeit at reduced growth rates, in low light conditions such as would have been observed following the meteor impact that defined the Cretaceous/Tertiary boundry (Toon et al., 1997) or during the ice-covered Oligocene coccolithophore bottle-neck noted above. Just as all haptophytes have a highly specialized organelle, the haptonema, which appears to facilitate their attaching to particles, some species of deep-living coccolithophores have highly specialized coccoliths, different from the standard heterococcoliths and holococcoliths discussed thus far. These uniquely shaped coccoliths –for example, osteoliths, articulated coccoliths, shaped like bones in a skeleton, some of which even have spikes on their sides that could allow them to more efficiently attach to particles– suggest a highly specialized function that might lead one to hypothesize a heterotrophic or mixotrophic function. In the following section, we present some images of these remarkable species and leave it to the imagination of the reader to hypothesize their function.

Reference table for images of heterococcolithophores with highly specialized coccoliths. All scale bars are 1micron in length.



Species Name	Page Number	Locaton of Sample	Depth of Sample (m)
Michaelsarsia elegans	30	Sargasso Sea	95
Ophiaster formosus and Emiliania huxleyii	35	Nantucket Shoals	65
Michaelsarsia elegans	36	Georges Bank	20
Calciopappus rigidus	37 (left)	Georges Bank	26
Calciopappus caudatus	37 (right)	Georges Bank	26
Ophiaster formosus	38	Georges Bank	20



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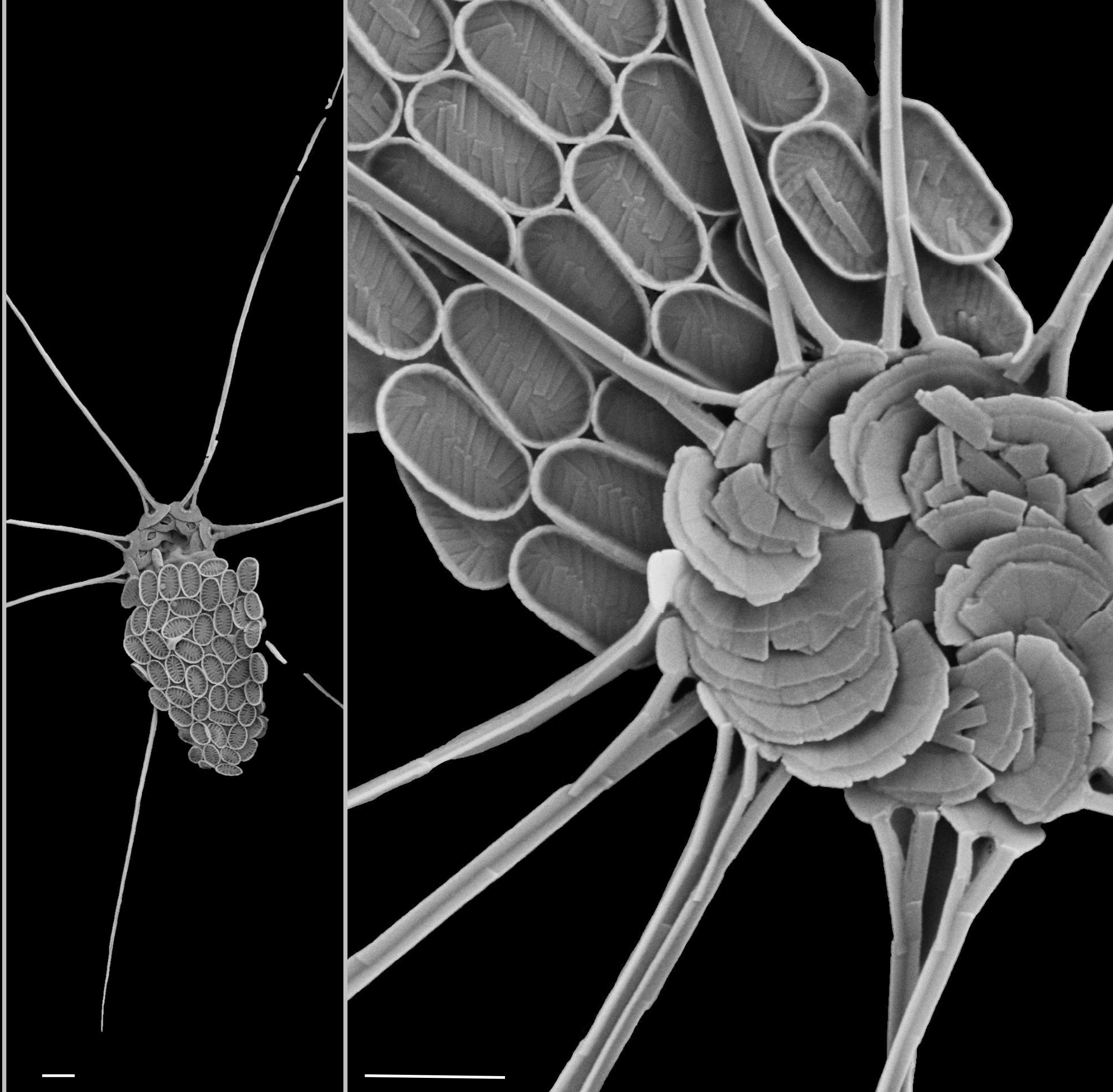

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5 In Closing

We have presented this book about coccolithophores and coccoliths with the goal of sharing the truly remarkable nano-architecture of these amazing organisms, plus some of the science relevant to their role in the environment and the linkages to entire fields of marine science.

We leave you with this thought: the coccolithophores that we observe in the ocean today may live but a few days, but their effect on the environment spans geological millennia. Their size is but a few microns, yet their blooms span entire ocean basins. The broad spatial and temporal impacts of these organisms transcend past the science into natural art forms. Indeed, their beauty has been sculpted by millions of years of selection and evolution, acting on billions of generations of these organisms, from the asteroid that collided with Earth at the Cretaceous/Tertiary boundary which caused massive extinctions, to the microscopic grazers in the the sea that decide whether or not to eat them because of their elaborate limestone armor! We hope that through this work, you can better appreciate the coccolithophore flora of Earth’s ocean garden.

Acknowledgments

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Ultra-Fine Art of Coccolithophores: This book is a collection of images of coccolithophores (microscopic phytoplankton that cover themselves with micro-meter-sized limestone plates called coccoliths). The book is meant to celebrate the amazing morphological diversity of this group of microalgae. These images were prepared from samples taken during our many field campaigns around the world over the last few decades. This book is all about appreciating the beauty of these organisms at the micrometer size scale as well as some of the underlying science that connects them to our planet. Yes, these are organisms that integrate entire sub-disciplines within oceanography but they also can be appreciated for the intricate artistry of nature in form and function, as expressed in their coccoliths. These organisms, singularly responsible for producing these elaborate, calcium carbonate scales, collectively have an immense impact on the global carbon cycle as well as the optical reflectance of the world ocean. Examining them at different size scales emphasizes that coccolithophores are an integral part of the ocean ecology and essential part of the biodiversity of the planet. It is for these reasons that we have compiled this book of scanning electron microscope images, to communicate not only the scientific importance of this algal class but also their amazing beauty.

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