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A guide to extant coccolithophores (Calcihaptophycidae, Haptophyta) using light microscopy

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Abstract We present here a collection of light microscope, and comparative scanning electron microscope, images of extant coccolithophores, sampled from various oceanic locations, and also from cultured strains. This series of images is intended to provide students and researchers interested in extant coccolithophore biology with an accessible means of identifying the common coccolithophore species found in modern assemblages.

Keywords Coccolithophores, extant, diversity, light microscopy, scanning electronic microscopy

1. Introduction

Coccolithophores include all algae from the Phylum Haptophyta that possess calcified scales (coccoliths) covering the cell surface, at least in one phase of their life-cycle. According to the fossil record, the coccolithophores originated in the Late Triassic (Bown, 1998), ~225Ma, since when they have evolved and diversified, today comprising ~200 morphospecies (Jordan & Chamberlain, 1997; Young *et al.*, 2003) within the monophyletic subclass Calcihaptophycidae (de Vargas *et al.*, 2007; Liu *et al.*, 2009).

Coccolithophores constitute a major component of planktonic communities throughout the world's oceans (Okada & McIntyre, 1977). A single freshwater coccolithophore, *Hymenomonas roseola*, has also been documented (Manton & Peterfi, 1969). Coccolithophores are of remarkable interest to a wide range of scientists. For marine biologists and oceanographers, they are among the main primary producers, and play a distinct role in the oceans' ecosystems (Field *et al.*, 1998; Balch, 2004). For biogeochemists, they are significant in the global carbon and sulphur cycles (and therefore climate regulation) through direct involvement in ocean-atmosphere gas exchange, and contribute to the transport of matter to the

ocean floor (Rost *et al.*, 2003; Malin & Steinke, 2004). For palaeontologists and geologists, the remarkably complete and continuous coccolithophore fossil record (*e.g.* Bown *et al.*, 2004) makes them ideal tools for biostratigraphic, evolutionary and palaeoceanographic studies of Mesozoic and Cenozoic sediments.

Coccolithophores are characterised by a life-cycle composed of two phases that are morphologically distinct (heteromorphy) and have different ploidy levels, one being haplontic and the other diplontic (haplo-diploidy; Billard, 1994; Billard & Inouye, 2004; Houdan *et al.*, 2004). This inference is based on limited data from chromosome counts and ploidy-level comparisons made on coccolithophore cultured strains (*e.g.* Gayral & Fresnel, 1983; Green *et al.*, 1996; Houdan *et al.*, 2004) and supplemented through the record of 'combination coccospheres' observed in natural samples, these representing the transition between life-cycle phases, and bearing coccoliths characteristic of each stage (*e.g.* Kleijne, 1991; Thomsen *et al.*, 1991; Cros *et al.*, 2000; Geisen *et al.*, 2002). From these studies, four types of life-cycle associations have been identified in coccolithophores:

1. Diploid phase bearing heterococcoliths (coccoliths com-

posed of cycles of one or more radial arrays of elaborate and variably-shaped crystal-units: Young *et al.*, 1992; Young *et al.*, 2003) associated with a non-calcified haploid phase - Noelaerhabdaceae, Hymenomonadaceae and Pleurochrysidaceae;

2. Diploid phase bearing heterococcoliths associated with a haploid phase bearing holococcoliths (disc- or dome-shaped coccoliths composed of numerous minute, equidimensional, rhombohedral calcite crystallites) - Calcidiscaceae, Coccolithaceae, Helicosphaeraceae, Pontosphaeraceae, Syracosphaeraceae, Rhabdosphaeraceae and Papposphaeraceae (Young *et al.*, 2003; Frada *et al.*, 2009);

3. One phase bearing heterococcoliths (possibly diploid) associated with a phase bearing aragonitic coccoliths (possibly haploid) - Alisphaeraceae (Cros *et al.*, 2000);

4. One phase bearing heterococcoliths (possibly diploid) associated with a phase bearing nannoliths, being possibly the haploid phase - Ceratolithaceae (Alcober & Jordan, 1997; Young *et al.*, 2003).

Cross-polarised light microscopy is extensively used for observing, identifying and describing coccoliths in fossil samples by palaeontologists (Bown, 1998). This powerful method has unfortunately been much less widely adopted by biologists studying living coccolithophores, in opposition to other light or electron microscopy techniques. Calcite is highly birefringent and causes coccoliths to show bright patterns (extinction figures), which allows them to be readily differentiated from non-calcified micro-organisms. Moreover, as a result of their size, composition and structure, different coccoliths generally show very distinct extinction figures, which allow identification of many morphological species or genera, and also life-cycle phases (*e.g.* Bown, 1998; Young *et al.*, 2004).

Here, we present a series of plates combining cross-polarised (XPL), differential-interference-contrast (DIC) and phase-contrast (PC) light microscope (LM) images of a variety of coccolithophore morphospecies (in some cases, both life-cycle phases), collected from various oceanic locations and laboratory cultures. Scanning electron microscopy (SEM) images from the collection produced for the *Plankton*Net* website (<http://planktonnet.sb-roscoff.fr>) were added to each plate, in order to provide a cross-reference for recognition of each morphospecies. Our objective is to provide the community interested in extant coccolithophore ecology with a guide for easy identification and taxonomic assignment of coccolithophores from modern samples. This publication complements the recent monographs of Cros & Fortuño (2002), Young *et al.* (2003) and Malinverno *et al.* (2008), by providing extensive LM documentation of extant coccolithophores. For detailed descriptions of coccolith morphology and taxonomy, the above-mentioned monographs should be consulted.

2. Material and methods

The samples from which the images were taken were collected by several of the co-authors using a variety of meth-

ods. The methodology is presented below according to the sample source.

2.1 Atlantic Meridional Transect (AMT) 16 (May-July, 2005), HOTS station, Hawaii, central Pacific (June, 2005), *Tansei Maru* KT11-06 cruise, Japanese east coast (May-June, 2006), bay of Villefranche-sur-Mer, Mediterranean Sea (September, 2006), *Belgica* cruise, North Atlantic (May-June, 2007)

Samples from these various locations were collected either with a 5 μ m-mesh nannoplankton net from surface-waters or, using Niskin bottles, from water at different depths (for further details on AMT16, see Robinson *et al.*, 2006; Poulton *et al.*, 2007). The samples, prepared for COD-FISH morphogenetic analyses (Frada *et al.*, 2006), were fixed for 1hr at 4°C with 1% paraformaldehyde (pH8), filtered onto 0.2 μ m-pore-sized Whatman Anodisc membrane filters, and dried at room temperature. Later, a representative segment of the filters was soaked in immersion oil (Olympus 04), mounted between a glass slide and a coverslip and observed mainly in XPL, but for some species, PC or DIC were also used (as indicated in the plate captions). Observations were performed with an Olympus BX51 microscope and the images were acquired with an RT-Slider Spot cooled charge coupled device digital camera.

2.2 Azores (May-July, 2008)

These samples were collected offshore of Horta, Faial island, Azores (38°36'N, 28°42'W) from surface-waters using Niskin bottles. Samples were directly filtered onto 0.8 μ m-pore-sized Whatman cellulose nitrate membranes, and dried at room temperature. Slide preparation and observations were performed as described above.

2.3 Gulf of Naples (24th November, 2006)

These samples were collected with 5 μ m-mesh plankton nets from surface-waters at an offshore station in the Tyrrhenian Sea (39°30'N, 13°30'E). Samples were fixed with formaldehyde at a final concentration of 2%. Observations were made with a Zeiss Axiovert microscope, equipped with a Zeiss AxioCam digital camera. For determination of the crystallographic orientation of the holococcolith crystals, an aliquot of the sample was filtered onto a 1 μ m-pore-sized Whatman cellulose acetate filter, permanently mounted using Norland optical adhesive (No.74), and examined under XPL using a Zeiss AxioPlan photomicroscope.

2.4 Sediment samples

Sediment samples were taken from the Saldanha hydrothermal field (Azores), from Core MD95-2040, recovered off the Portuguese margin (40°34.91'N, 09°51.67'W), and from the beach in front of the Station Biologique, Roscoff (France). For sample examination, smear-slides were prepared, and observed under an optical polarising

microscope (Olympus BX40 and BX51), at 1250x magnification. Digital images were taken with either an Olympus DP11 camera or an RT-Slider Spot cooled charge coupled device camera. For further information on the sample collection and preparation see Parente *et al.* (2004) and Narciso *et al.* (2006).

3. The images

All scale-bars are 5µm, except where indicated on the plates. 'NHM' is the Natural History Museum, London; [HET] - heterococcolithophore, [HOL] - holococcolithophore. *NB* Copies of most of the SEM images are available on the Plankton*Net website (<http://planktonnet.sb-roscoff.fr>). All taxonomic references can be found in Bown (1998), Young *et al.* (2003) and/or Malinverno *et al.* (2008).

3.1 Image index

Calcidiscaceae

- Calcidiscus leptoporus* (Murray & Blackman, 1898) Loeblich & Tappan, 1978 - **PI.8**
Calcidiscus quadripereforatus (Kamptner, 1937) Quinn *et al.*, 2004 [HET] (previously *C. leptoporus* large morphotype) - **PI.8**
Calcidiscus quadripereforatus Quinn & Geisen in Saez *et al.*, 2003 [HOL] (previously *Syracolithus quadripereforatus* Kamptner, 1937, combination established by Geisen *et al.*, 2002) - **PI.9**
Oolithothus fragilis (Lohmann, 1912) Martini & Müller, 1972 [HET] - **PI.10**
Umbilicosphaera foliosa (Kamptner, 1963 ex Kleijne, 1993) Geisen in Saez *et al.*, 2003 [HET] - **PI.12**
Umbilicosphaera hulburtiana Gaarder, 1970 [HET] - **PI.12**
Umbilicosphaera sibogae (Weber-van Bosse, 1901) Gaarder, 1970 [HET] - **PI.11**

Calciosoleniaceae

- Calciosolenia brasiliensis* (Lohmann, 1902) Young *et al.*, 2003 [HET] - **PI.35**
Calciosolenia murrayi Gran, 1912 [HET] - **PI.34**

Coccolithaceae

- Coccolithus braarudii* (Gaarder, 1962) Geisen *et al.*, 2002 [HET] & [HOL] - **PIs 4, 5**
Coccolithus pelagicus (Wallich, 1877) Schiller, 1930 [HET] - **PI.6**
Coccolithus pelagicus subsp. *azorinus* Parente & Cachão, 2004 in Parente *et al.*, 2004 - **PI.7**

Helicosphaeraceae

- Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954 [HET] & [HOL] - **PIs 15, 16**
Helicosphaera hyalina Gaarder, 1970 [HET] - **PI.18**
Helicosphaera wallichii (Lohmann, 1902) Okada & McIntyre, 1977 [HET] & [HOL] - **PI.17**

Incertae sedis

- Alisphaera ordinata* (Kamptner, 1941) Heimdal, 1973 [HET] - **PI.40**
Alisphaera sp. [HET] - **PI.40**
Braarudosphaera bigelowii (Gran & Braarud, 1935) Deflandre, 1947 - **PI.41**
Ceratolithus cristatus Kamptner, 1950 [HET] & [CER] - **PIs 44, 45**
Ceratolithus cristatus Kamptner, 1950 *coccolithomorpha*-type [HET] - **PIs 44, 45, 46**
Ceratolithus cristatus Kamptner, 1950 *cristatus*-type [CER] - **PI.45**
Ceratolithus cristatus Kamptner, 1950 *nishidae*-type [HET] - **PIs 44, 45**
Florisphaera profunda Okada & Honjo, 1973 - **PI.43**
Gladiolithus flabellatus (Halldal & Markali, 1955) Jordan & Chamberlain, 1993 - **PI.47**
Umbellosphaera irregularis Paasche in Markali & Paasche, 1955 [HET] - **PI.42**
Umbellosphaera tenuis (Kamptner, 1937) Paasche in Markali & Paasche, 1955 [HET] - **PI.42**
Umbellosphaera tenuis type IV (Kamptner, 1937) Paasche in Markali & Paasche, 1955 - **PI.42**

Noelaerhabdaceae

- Emiliana huxleyi* (Lohmann, 1902) Hay & Mohler in Hay *et al.*, 1967 - **PI.1**
Gephyrocapsa ericsonii McIntyre & Bé, 1967 - **PI.2**
Gephyrocapsa muelleriae Bréhéret, 1978 - **PI.2**
Gephyrocapsa oceanica Kamptner, 1943 - **PI.2**
Reticulofenestra sessilis (Lohmann, 1902) Jordan & Young, 1990 - **PI.3**

Pleurochrysidaceae

- Pleurochrysis carterae* (Braarud & Fagerland, 1946) Christensen, 1978 var. *carterae* - **PI.13**

- Pleurochrysis placolithoides* Fresnel & Billard, 1991 - **PI.14**

Pontosphaeraceae

- Pontosphaera japonica* (Takayama, 1967) Nishida, 1971 [HET] & [HOL] - **PI.26**
Pontosphaera multipora (Kamptner, 1948) Roth, 1970 [HET] - **PI.25**
Pontosphaera syracusana Lohmann, 1902 - **PI.24**
Scyphosphaera apsteinii Lohmann, 1902 [HET] & [HOL] - **PIs 19-22**
Scyphosphaera porosa Kamptner, 1967 [HET] - **PI.23**

Rhabdosphaeraceae

- Acanthoica quattrosolina* Lohmann, 1903 [HET] - **PI.38**
Acanthoica sp. [HET] - **PI.38**
Algirosphaera robusta (Lohmann, 1902) Norris, 1984 [HET] - **PI.39**
Discosphaera tubifera (Murray & Blackman, 1898) Ostenfeld, 1900 [HET] - **PI.36**
Palusphaera sp.1 Cros & Fortuño, 2002 [HET] - **PI.38**
Rhabdosphaera clavigera Murray & Blackman, 1898 [HET] - **PI.37**

Syracosphaeraceae

- Coronosphaera binodata* (Kamptner, 1927) Gaarder, 1977 [HET] - **PI.30**
Coronosphaera mediterranea (Lohmann, 1902) Gaarder in Gaarder & Heimdal, 1977 [HET] - **PI.30**
Michaelsarsia adriaticus (Schiller, 1930) Manton *et al.*, 1984 [HET] - **PIs 31, 32**
Michaelsarsia elegans Gran, 1912 emend. Manton *et al.*, 1984 [HET] - **PI.31**
Ophiaster formosus (Gran, 1912) emend. Manton & Oates, 1983 [HET] - **PI.33**
Ophiaster sp. [HET] - **PI.33**
Syracosphaera anthos (Lohmann, 1912) Janin, 1987 [HET] & [HOL] - **PI.28**
Syracosphaera pulchra Lohmann, 1902 [HET] - **PI.27**
Syracosphaera sp. [HET] - **PI.29**

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Plate 1

1-5, 7-10. *Emiliania huxleyi* diploid phase [HET]

- 50m water-depth; Canary Islands, North Atlantic, 29°41'N, 17°53'W; SEM (image NHM 118-14)
- Surface waters; South Atlantic, 04°S, 25°W; AMT16 cruise, June, 2005; XP
- 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP
- Surface waters; Japan, 40°N, 145°E; *Tansei Maru* KT11-06 cruise, May, 2006; XP
- Culture RCC 1249; DIC
- Detached coccolith; surface waters; South Atlantic, 04°S, 25°W; AMT16 cruise, June 2005; XP
- 8-10. Series of images from different phases of an *E. huxleyi* diploid-phase bloom, English Channel, *Belgica* cruise, May, 2007
- Exponentially-growing phase - healthy cells and a few detached coccoliths; XP
- Stationary phase - increased abundance of detached coccoliths, appearance of clumps of cellular debris; XP
- End of the bloom - cellular debris and detached liths, very few whole coccospheres; XP

6. *E. huxleyi* haploid biflagellated (arrowed) phase

Culture RCC 1249; DIC

Plate 1

Noelaerhabdaceae

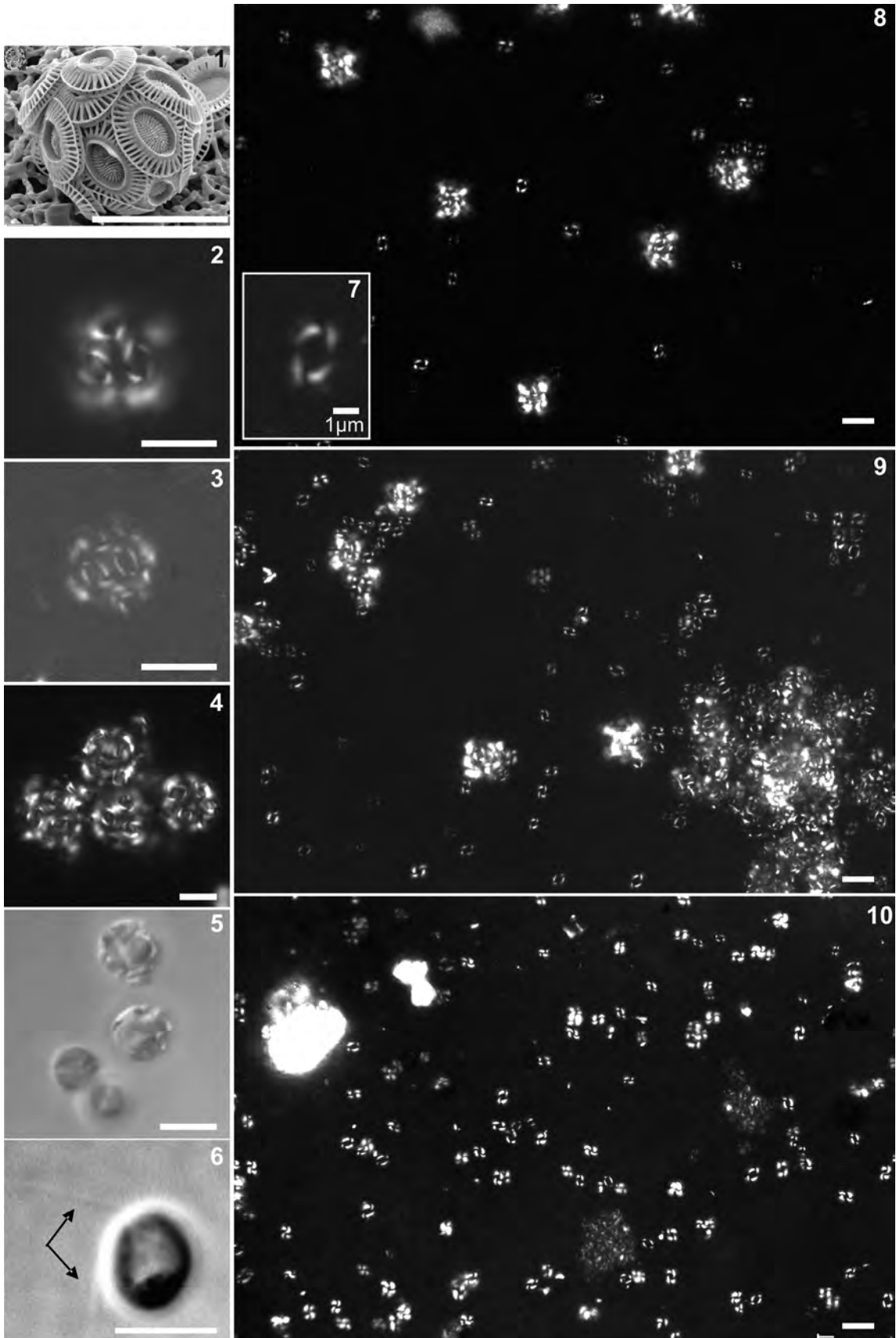


Plate 2

1-7. *Gephyrocapsa oceanica* diploid phase [HET]

1. 5m water-depth; Canary Islands, North Atlantic, 27°33'N, 13°38'W; SEM (image NHM 104-8)
- 2-4. 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP
5. Surface waters; Japan, 34°26'N, 139°E; *Tansei Maru* cruise, May, 2006; XP
- 6, 7. Detached coccoliths; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP

8-12. *G. muelleriae* diploid phase [HET]

8. 37m water-depth; Alboran Sea, western Mediterranean, 37°23'N, 0°56'W; SEM (image NHM 117-19)
- 9, 10, 12. 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP
11. Detached coccolith; Faial, Azores, 30°32'N, 28°33'W; June, 2008; XP

13, 14. *G. ericsonii* diploid phase [HET]

13. 130m water-depth; HOTS station, Hawaii, Pacific Ocean, 22°45'N, 158°E; SEM (image NHM 217-17)
14. Surface water; Faial, Azores, 30°32'N, 28°33'W; June, 2008; XP

Plate 2

Noelaerhabdaceae

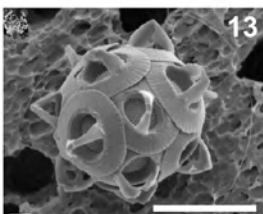
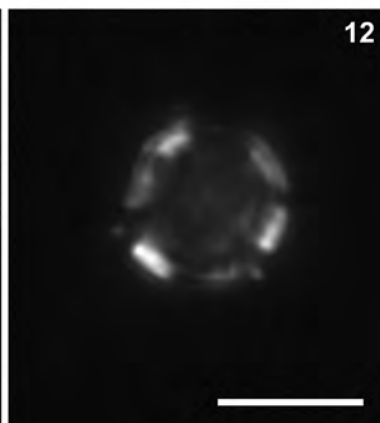
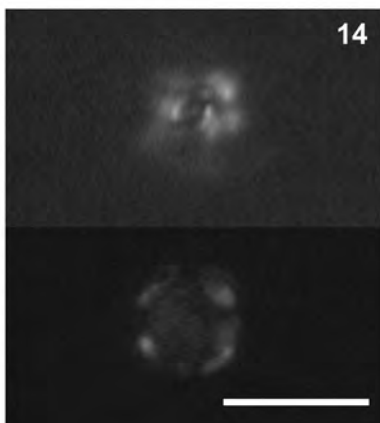
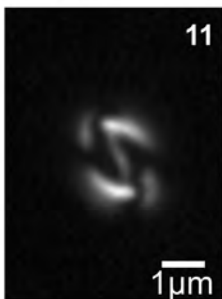
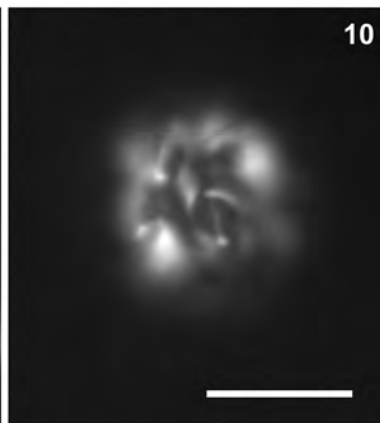
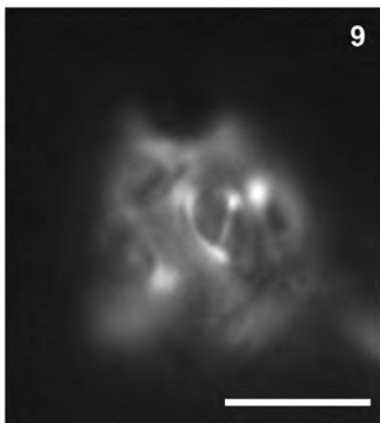
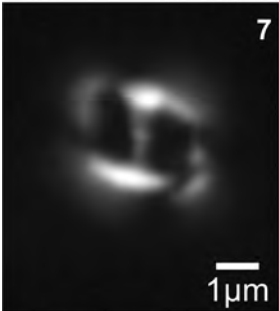
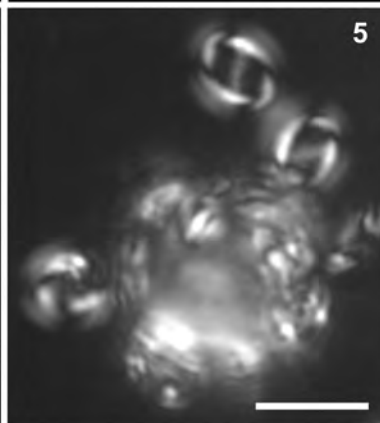
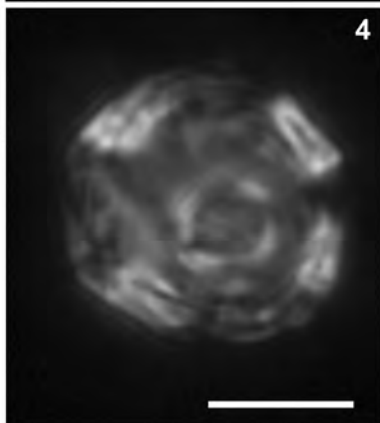
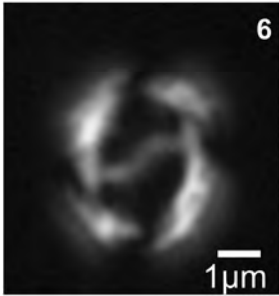
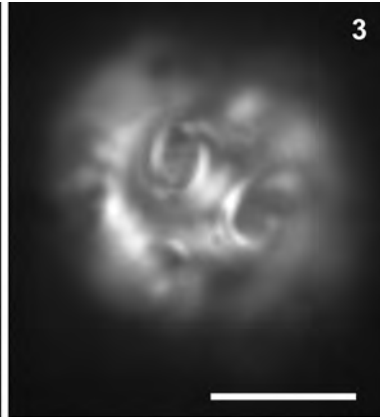
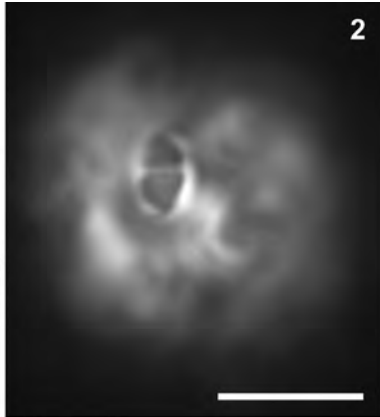
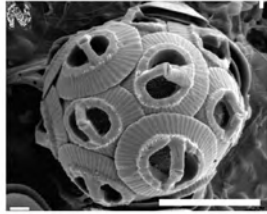


Plate 3

Noelaerhabdaceae

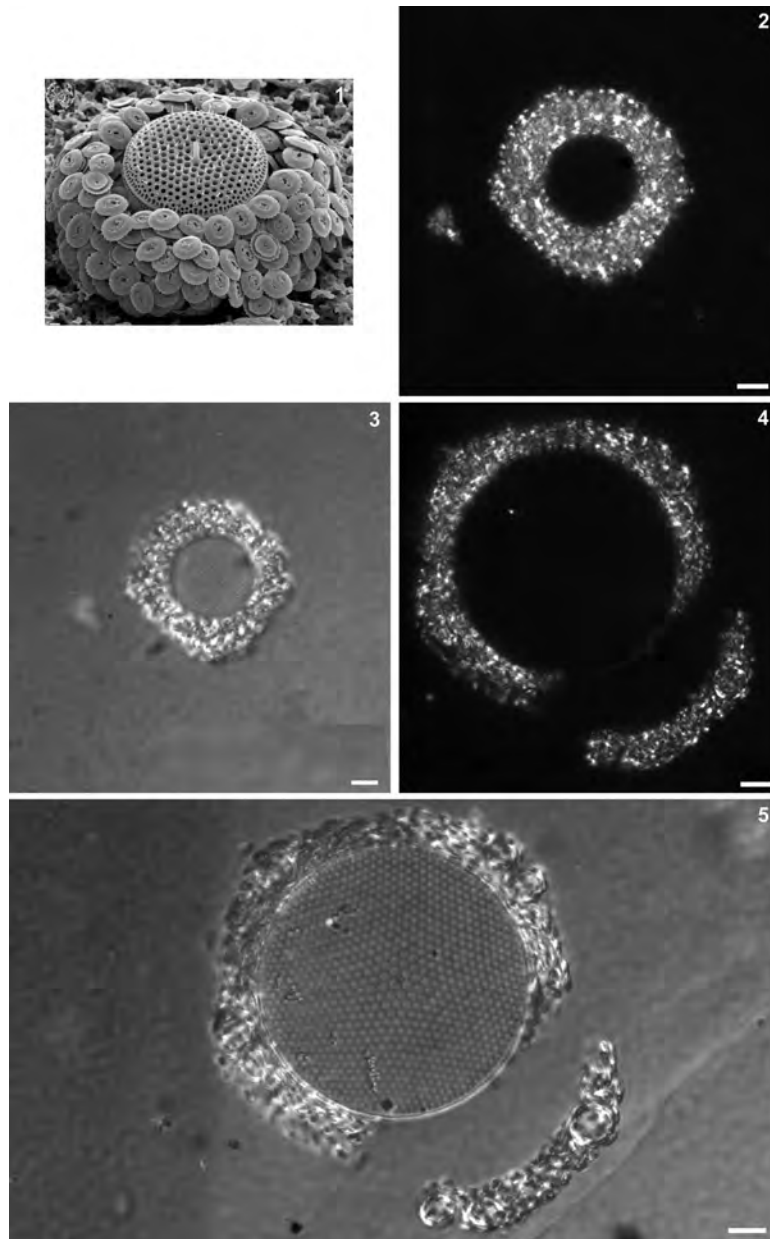


Plate 3

1-5. *Reticulofenestra sessilis* [HET]

1. Cells associated with centric diatom *Thalassiosira* sp.; 175m water-depth; Gulf of Mexico, 26°19'N, 59°38'W; SEM (image NHM 139-47)

2-5. Cells associated with unidentified diatom; surface waters; South Atlantic, 31°49'S, 01°30'W; AMT16 cruise, May, 2005; XP (2, 4), PC (3, 5)

Plate 4

1, 3-5. *Coccolithus braarudii* [HET]

1. 3200m water-depth; North Atlantic, 48°N, 20°W; SEM (image NHM 185-24)

3-5. Culture strain RCC1197; XP

2, 6, 7. *C. braarudii* [HOL] '*Crystallolithus braarudii*' haploid phase

2. Collapsed coccosphere; Alboran Sea, western Mediterranean; SEM (image from L. Cros, CSIC-ICM, Barcelona)

6, 7. Culture strain RCC1197; XP

Plate 4

Coccolithaceae

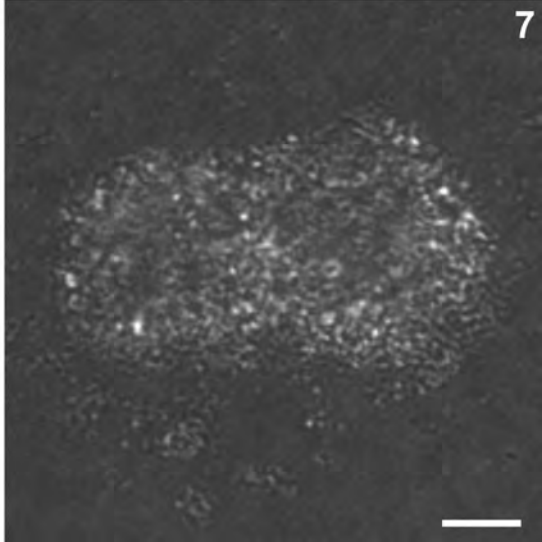
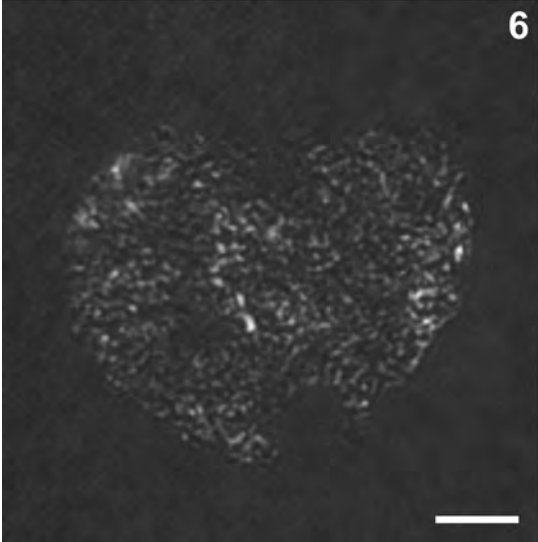
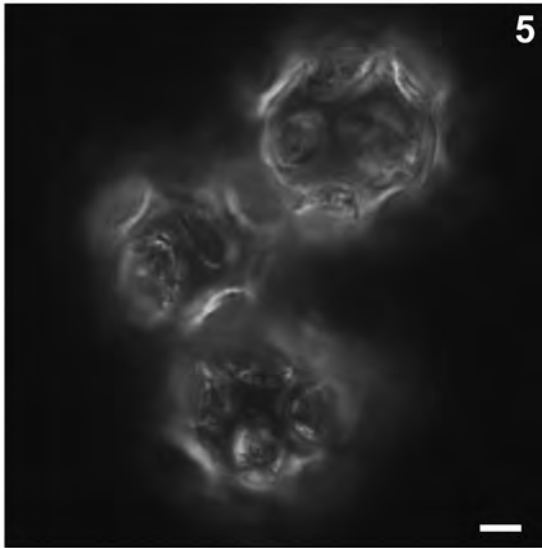
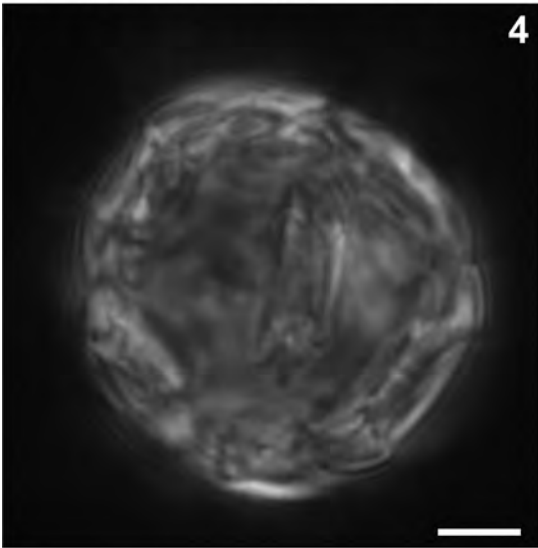
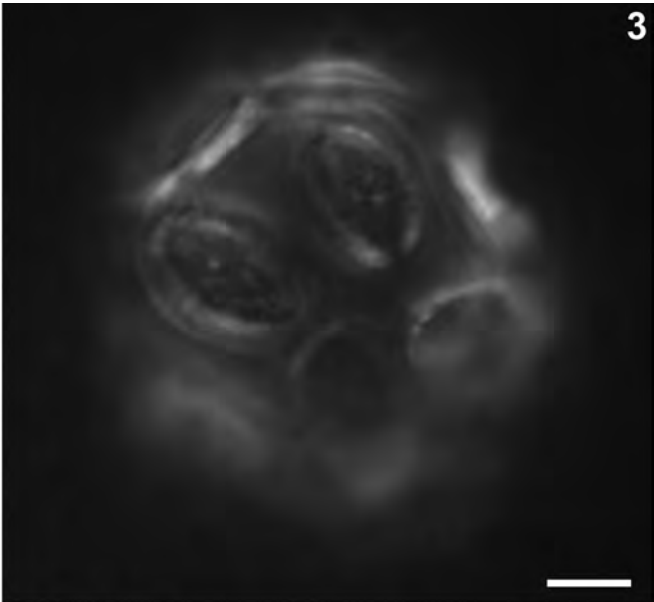
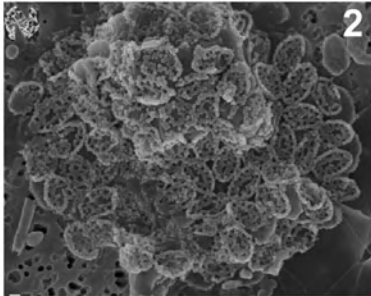
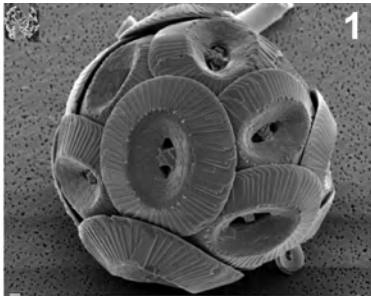
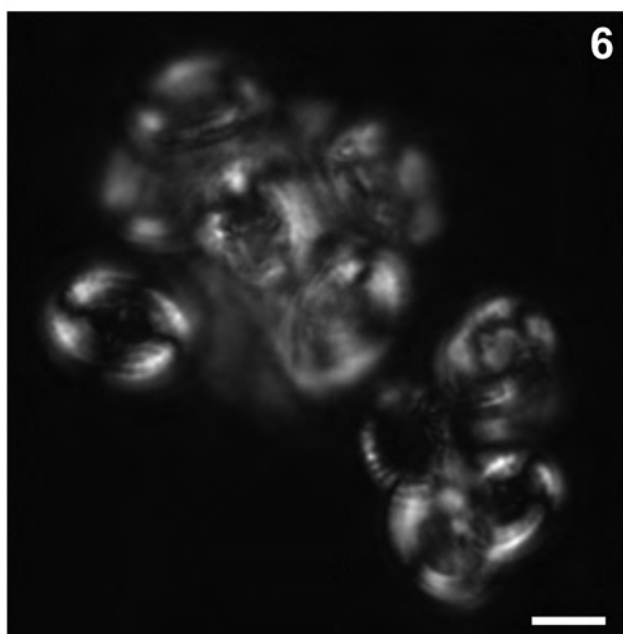
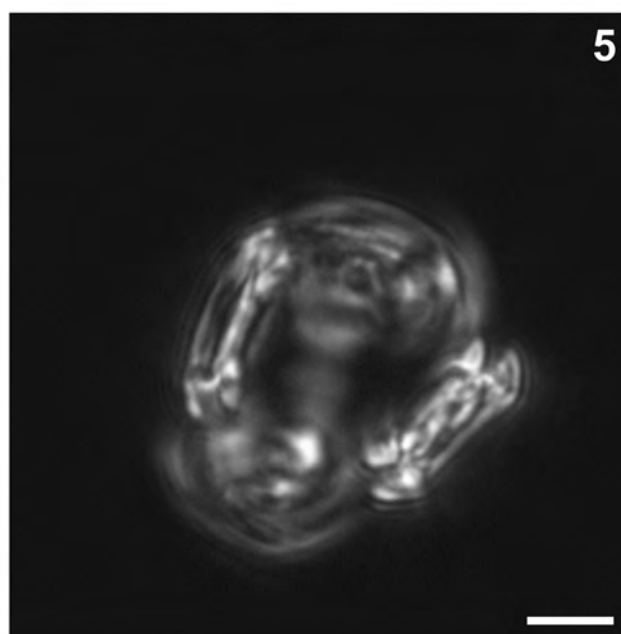
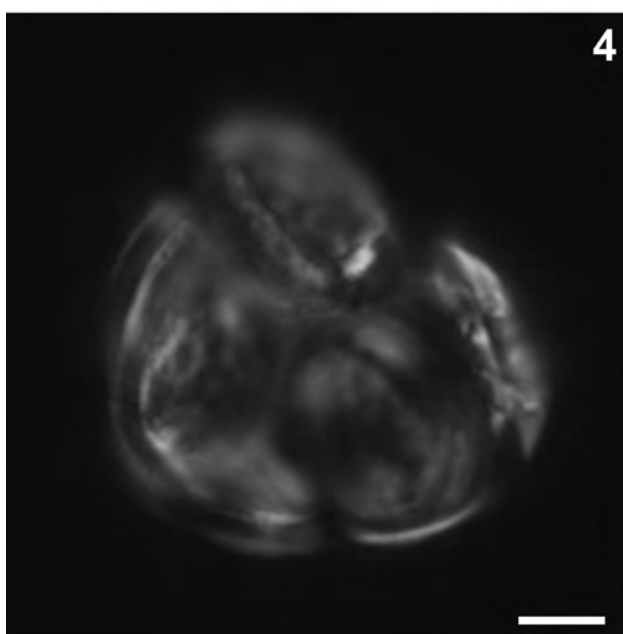
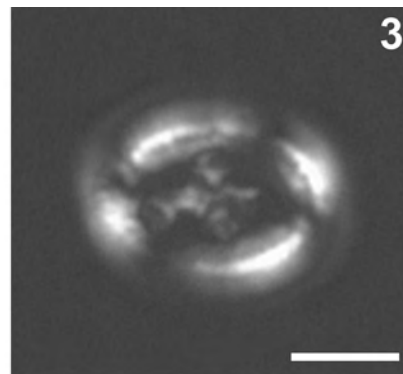
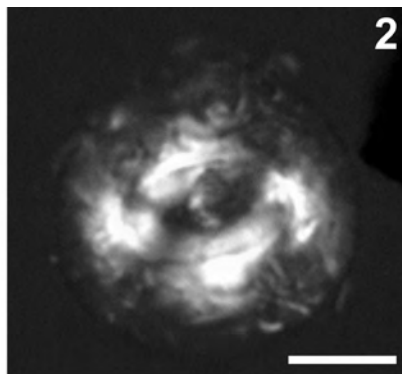
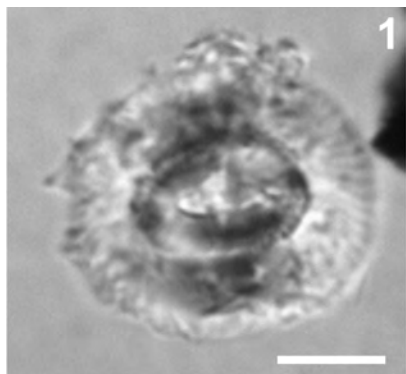


Plate 5

Coccolithaceae

1-6. *Coccolithus braarudii* [HET]

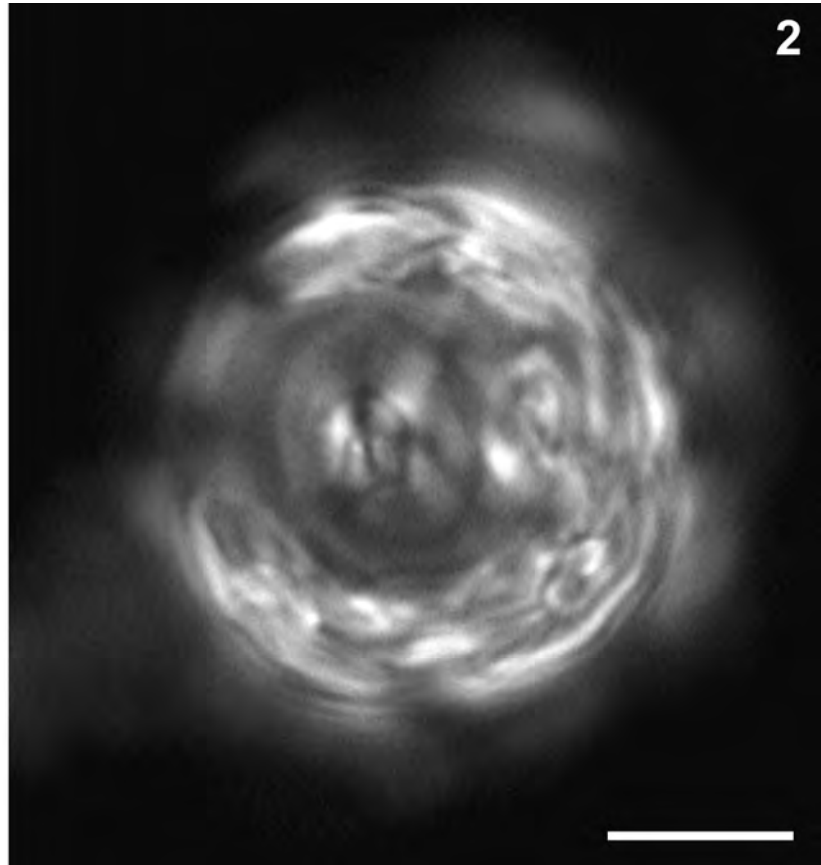
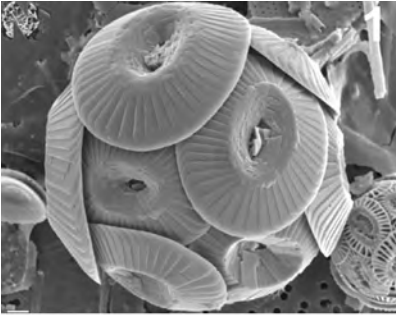
1, 2. Detached coccoliths; sediment sample, Roscoff, France; PC (1), XP (2)

3. Early stage of coccolith formation; sediment sample, Roscoff, France; XP

4-6. Culture RCC1197, dissociated coccospheres; XP

Plate 6

Coccolithaceae



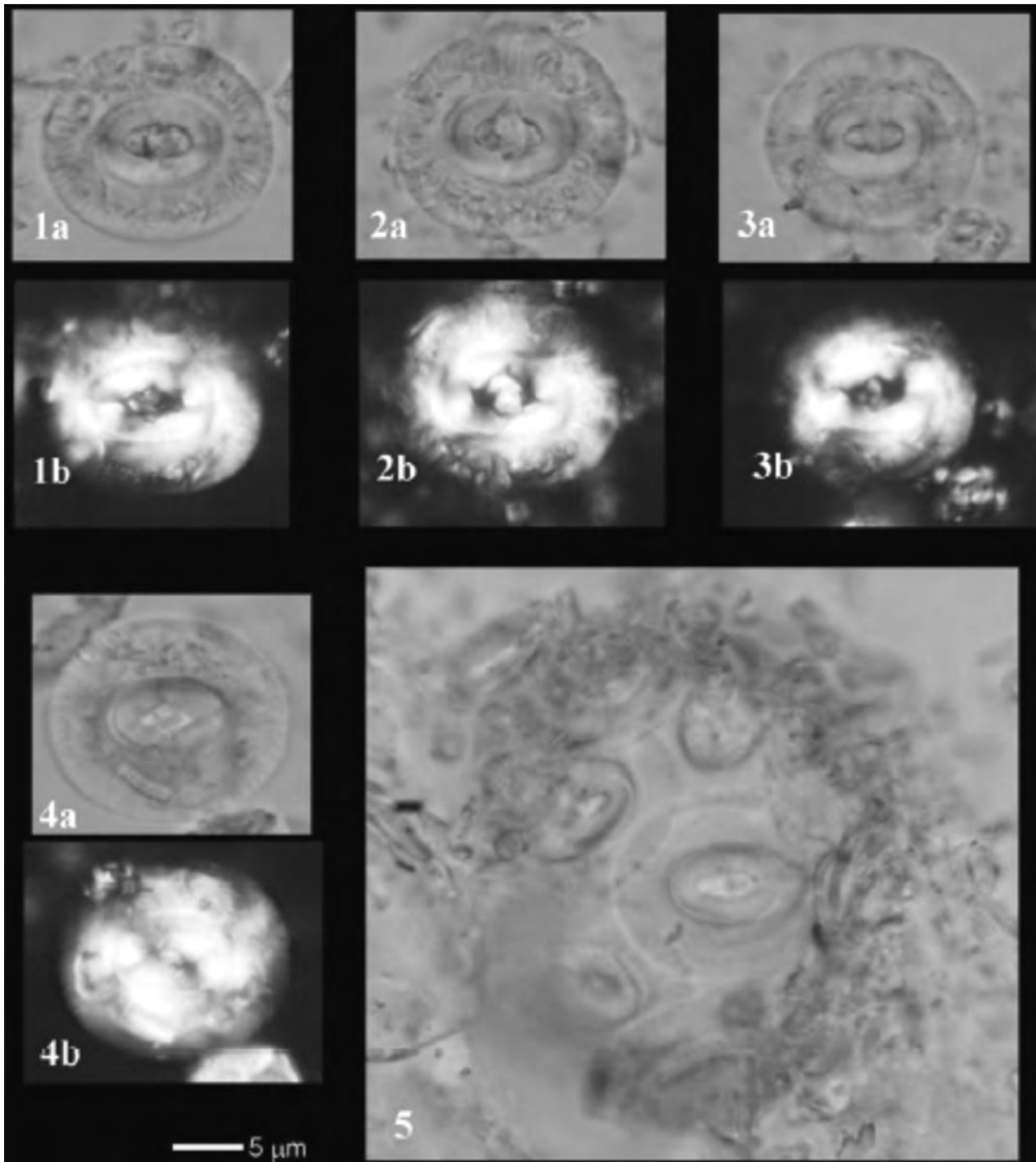
1, 2. *Coccolithus pelagicus* [HET]

1. Surface waters; Iceland, 63°27'N, 20°12'W; SEM (image NHM 111-30)

2. 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP

Plate 7

Coccolithaceae

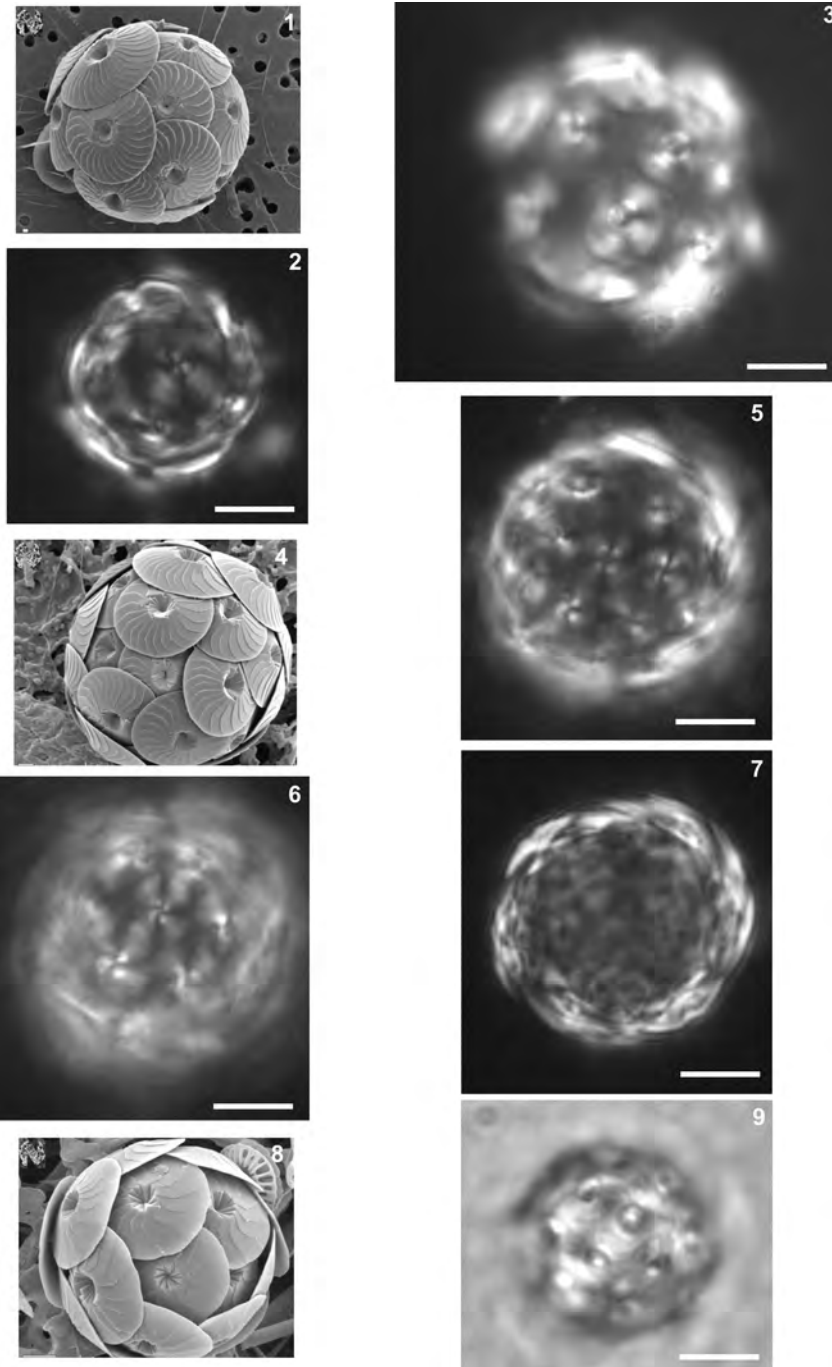
1-5. *Coccolithus pelagicus* subsp. *azorinus*

1-4. Detached coccoliths, distal view; sediment sample; PC (a), XP (b)

5. Coccosphere; sediment sample; PC

Plate 8

Calcidiscaceae

**1-3. *Calcidiscus quadriperforatus* [HET] (previously *C. leptopus* large morphotype)**

1. 20m water-depth; eastern equatorial Atlantic; 18°N, 17°W; SEM (image NHM 240-36)

2. Surface waters; South Atlantic, 01°37'S, 24°59'W; AMT16 cruise, June, 2005; XP

3. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

4-7. *C. leptopus* [HET] intermediate morphotype

4. 5m water-depth; Canary Islands, North Atlantic, 33°27'N, 9°10'W; SEM (image NHM 103-74)

5-7. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, May, 2005; XP

8, 9. *C. leptopus* [HET] small morphotype

8. Off Namibia, South Atlantic; SEM (image NHM 136-03)

9. Possible small morphotype; 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; July, 2008; DIC

Plate 9

Calcidiscaceae

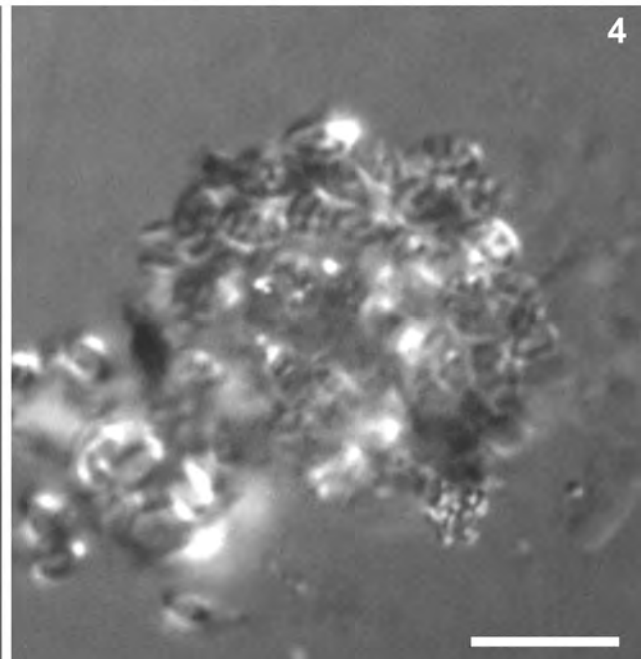
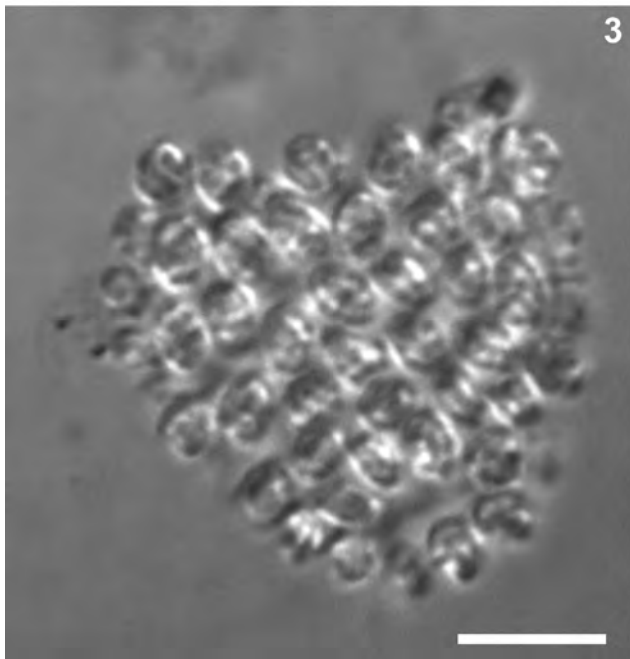
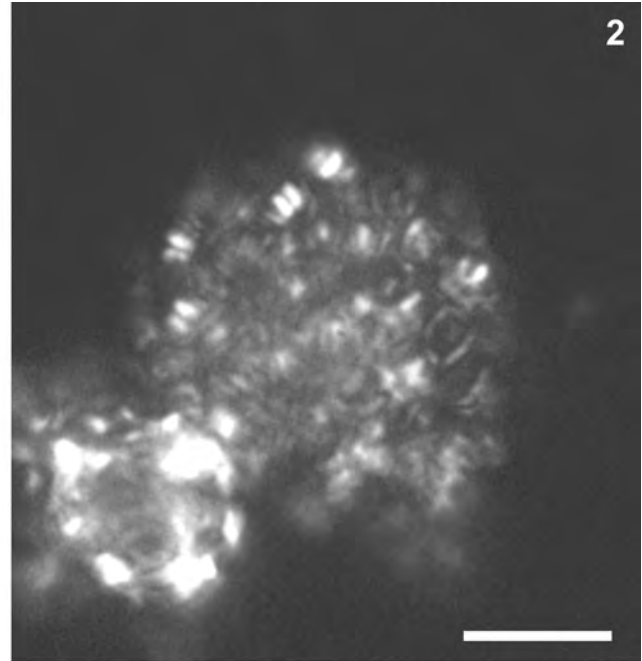
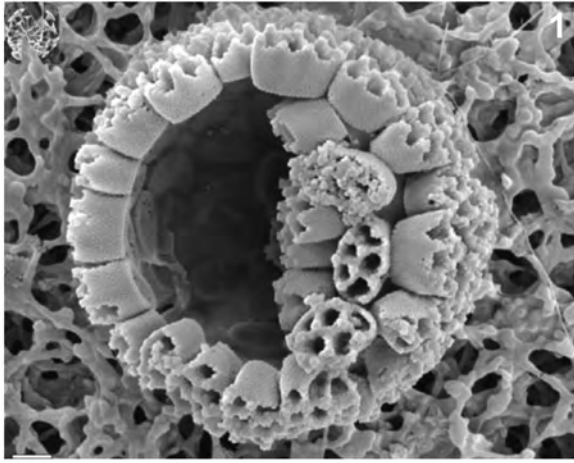


Plate 9

1-4. *Calcidiscus quadriperforatus* [HOL]

1. 25m water-depth; Canary Islands, North Atlantic, 29°45'N, 17°56'W; SEM (image NHM 113-17)

2-4. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP (2), DIC (3, 4)

Plate 10

1-5. *Oolithotus fragilis* [HET]

1. 37m water-depth; Alboran Sea, western Mediterranean, 37°23'N, 0°56'W; SEM (image NHM 119-76)

2, 4. Culture strain RCC 1482; XP

3. Dispersed coccoliths; XP

5. Group of four cells; culture strain RCC 1482; XP

Plate 10

Calcidiscaceae

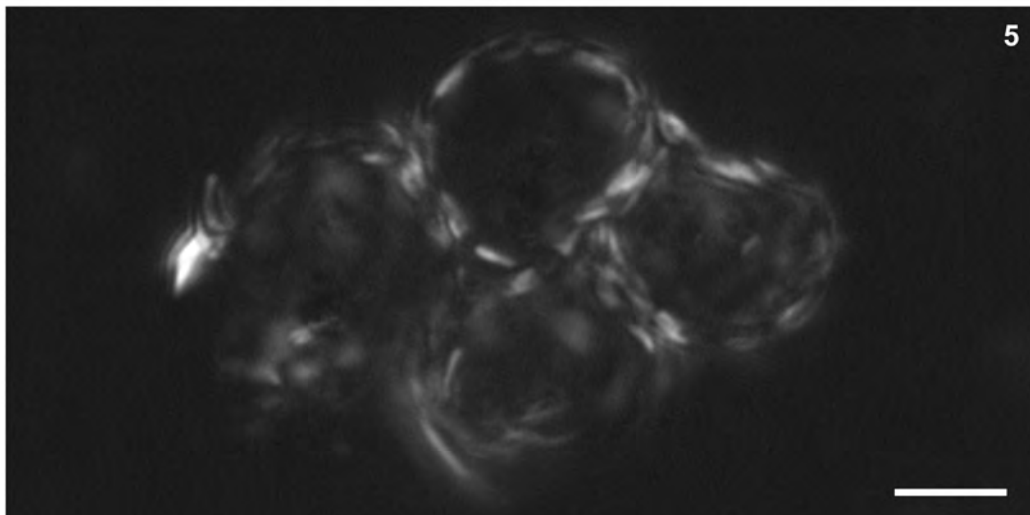
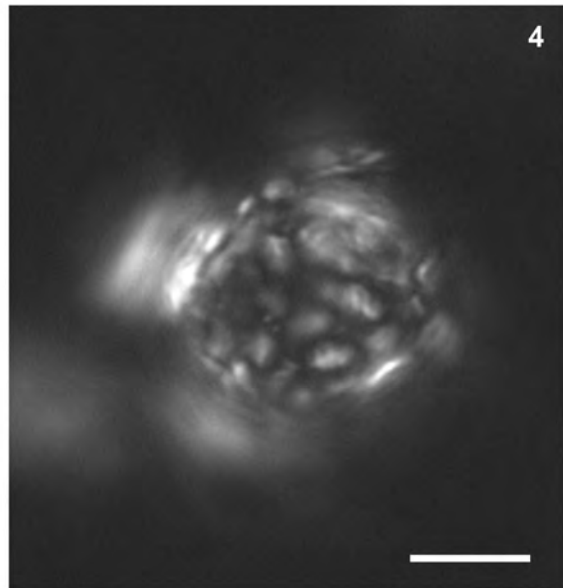
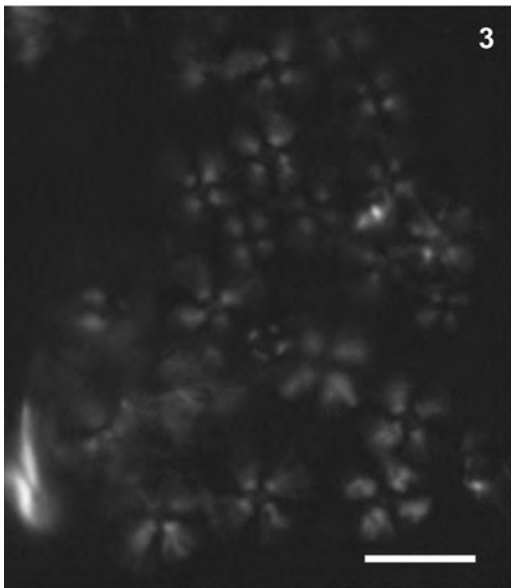
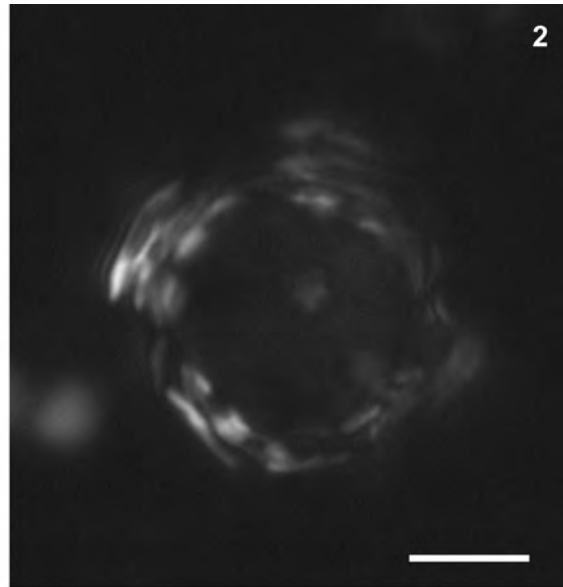
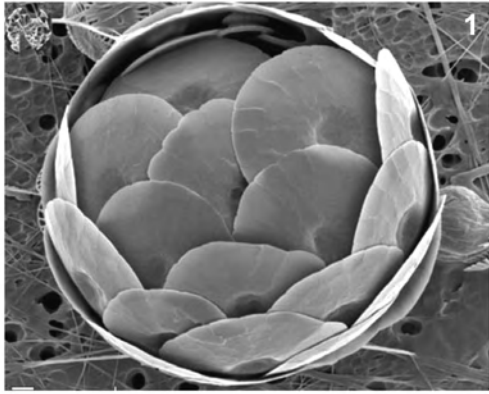
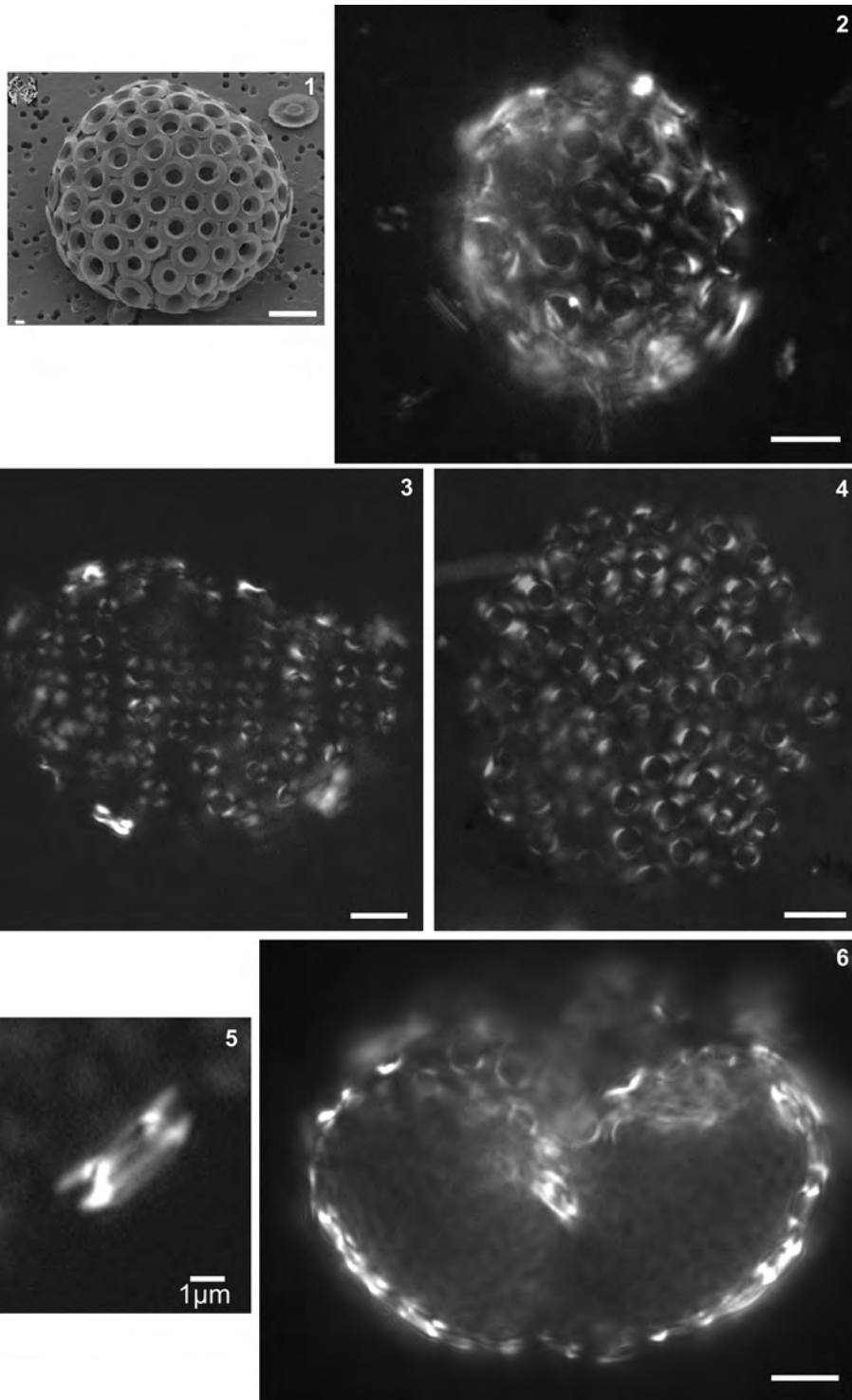


Plate 11

Calcidiscaceae



1-6. *Umbilicosphaera sibogae* [HET]

1. 29m water-depth; eastern equatorial Atlantic, 18°00'N, 26°59'W; SEM (image NHM 240-09)

2-5. Surface waters; AMT16 cruise, June, 2005; XP

2. South Atlantic, 01°37'S, 24°59'W

3. South Atlantic, 20°11'S, 24°59'W

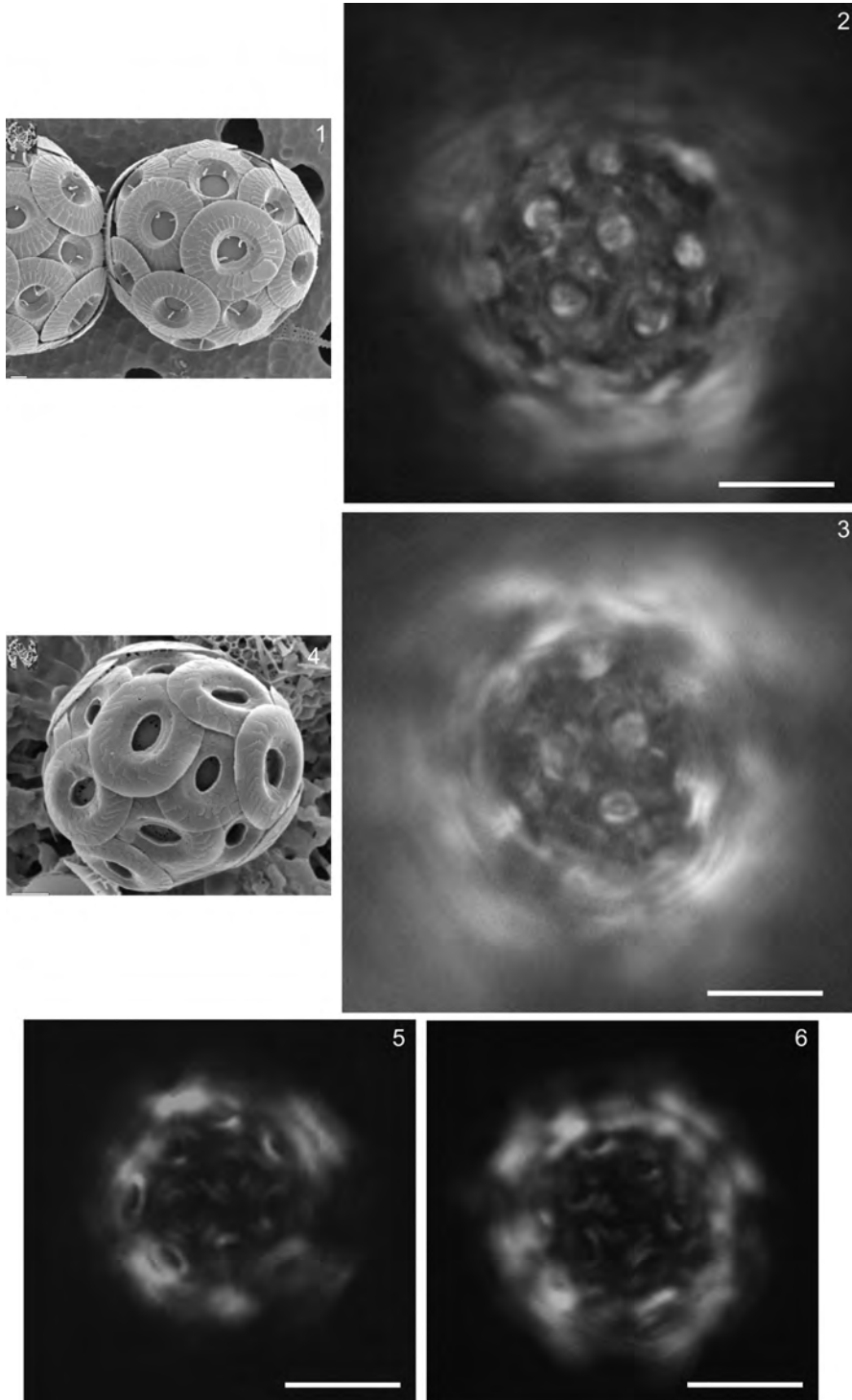
4. North Atlantic, 04°16'N, 27°01'W

5. Detached coccolith, South Atlantic; 20°11'S, 24°59'W

6. 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP

Plate 12

Calcidiscaceae

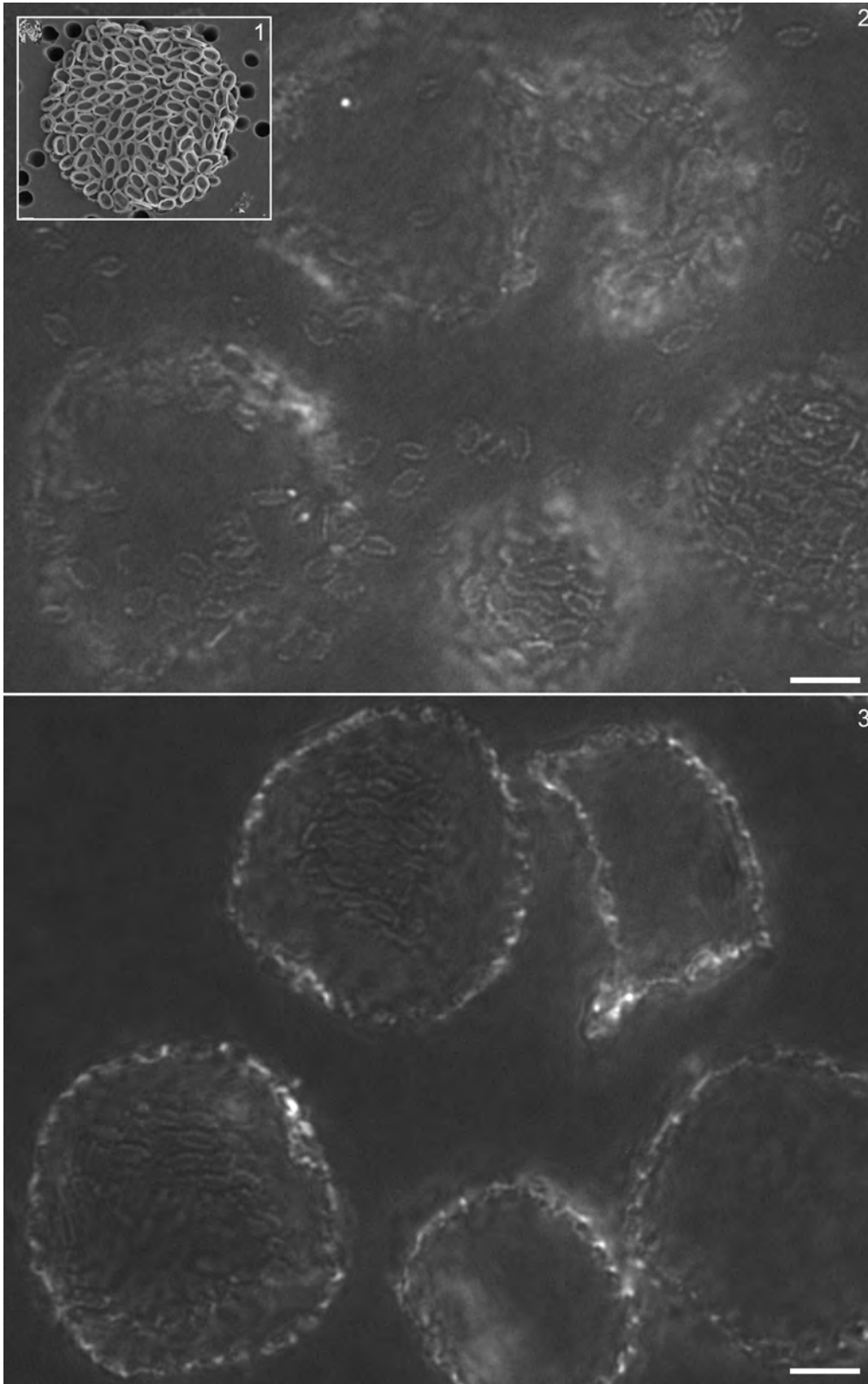


1-3. *Umbilicosphaera foliosa* [HET]

1. Surface waters; Ibo Port, Miyake Island, Japan, 34°06'N, 139°30'E; SEM (image NHM 129-10)
2. Surface waters; South Atlantic, 26°49'S, 10°30'W; AMT16 cruise, May, 2005; XP
3. Surface waters; North Atlantic, 18°57'N, 34°12'W; AMT16 cruise, May, 2005; XP

4-6. *U. hulbertiana* [HET]

4. 5m water-depth; North Atlantic, 21.91°N, -20.29°E; SEM (image NHM 114-34)
5. Surface waters; South Atlantic, 22°52'S, 24°59'W; AMT16 cruise, May, 2005; XP
6. 70m water-depth; South Atlantic, 01°37'S, 24°59'W; AMT16 cruise, May, 2005; XP

Plate 13**Pleurochrysidaceae**

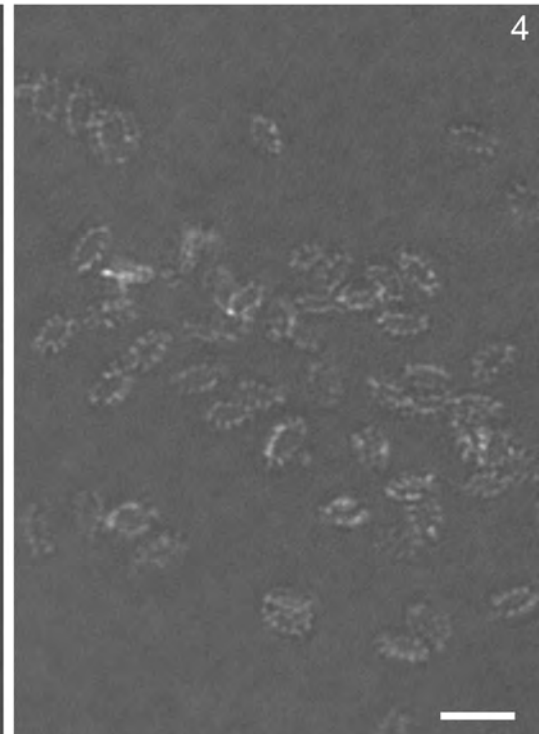
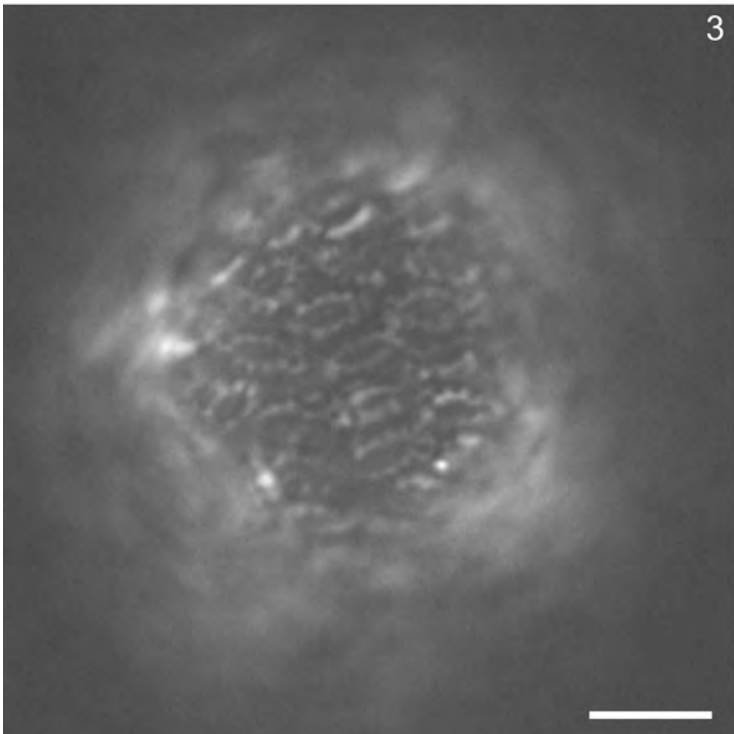
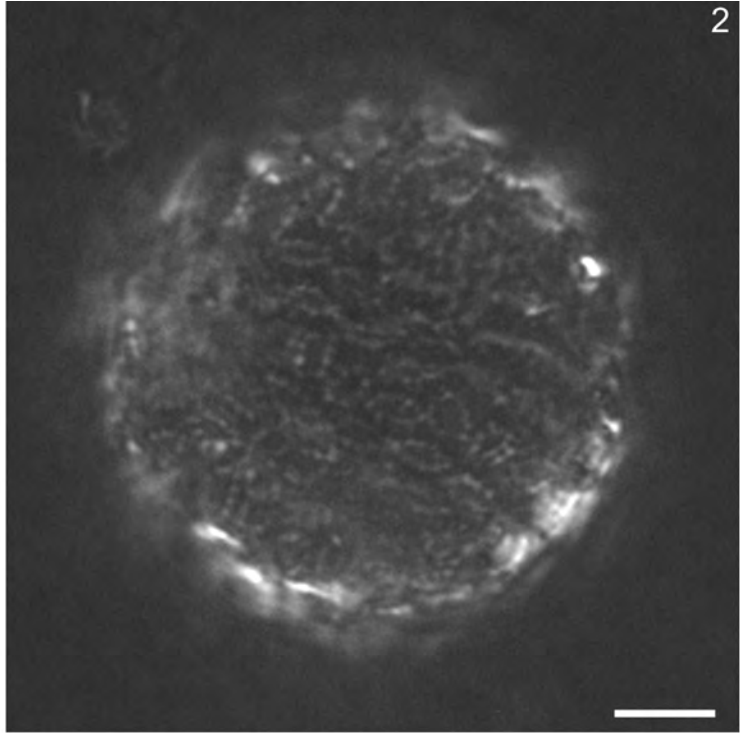
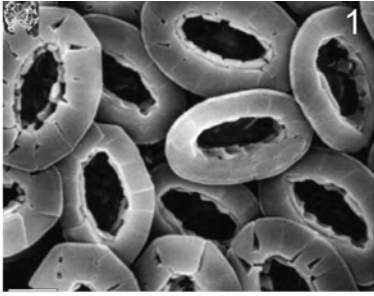
1-3. *Pleurochrysis carterae* var. *carterae*

1. Collapsed coccosphere; SEM (image Fr 99238 from J. Fresnel, University of Caen, France)

2, 3. Cultured strain RCC 1402; XP

Plate 14

Pleurochrysidaceae



1-4. *Pleurochrysis placolithoides*

1. Collapsed coccosphere; culture strain RCC 1401; SEM (image NHM 85-15)

2-4. Cultured strain AC59; XP

Plate 15

1, 4. *Helicosphaera carteri* [HET]

1. 5m water-depth; off Namibia, South Atlantic, 20°S, 09°E; SEM (image NHM 136-37)
4. Surface waters; North Atlantic, 10°00'N, 29°47'W; AMT16 cruise, June, 2005; XP

2, 5. *H. carteri* [HOL solid] (formerly *Syracolithus catilliferus*)

2. 50m water-depth; Canary Islands, North Atlantic, 29°41'N, 17°53'W; SEM (image P233B314 from Claudia Sprengel, University of Bremen)
5. Surface waters; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, June, 2005; XP

3, 7. *H. carteri* [HOL perforate] (formerly *Syracolithus confusus*)

3. 20m water-depth; Villefranche-sur-Mer, Mediterranean; SEM (image NHM 284-24)
7. Surface waters; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, June, 2005; XP

6. *H. carteri* [HET & HOL solid]

- Combination coccosphere bearing both heterococcoliths and holococcoliths; surface waters; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, June, 2005; XP

Plate 15

Helicosphaeraceae

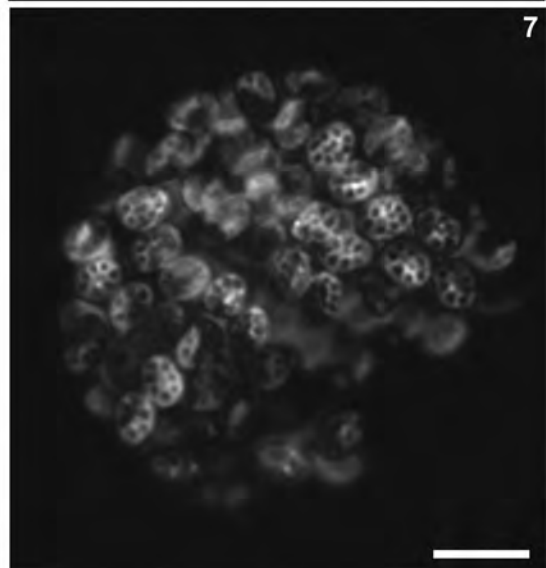
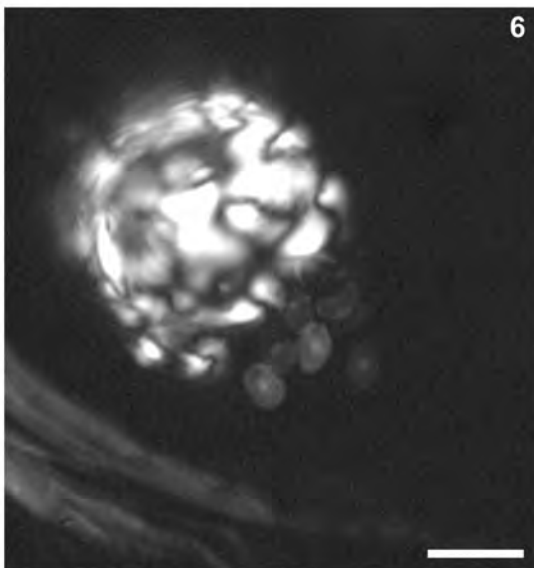
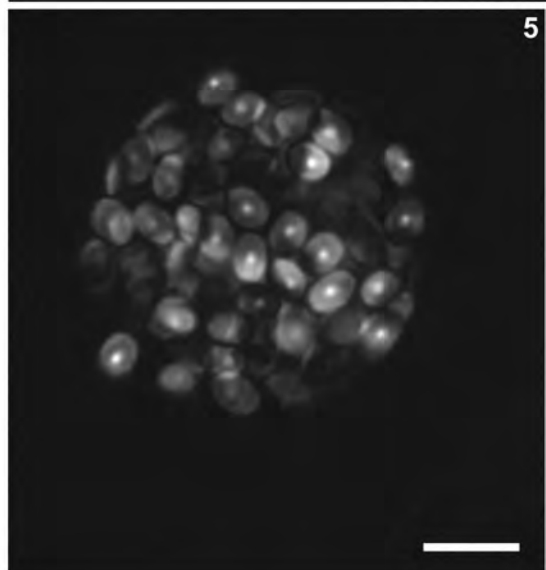
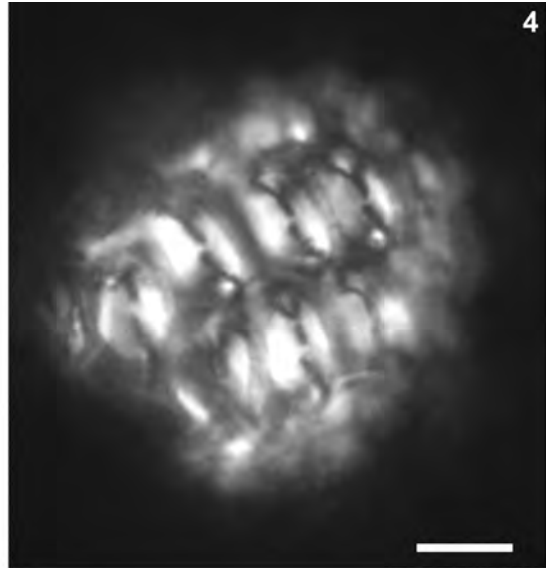
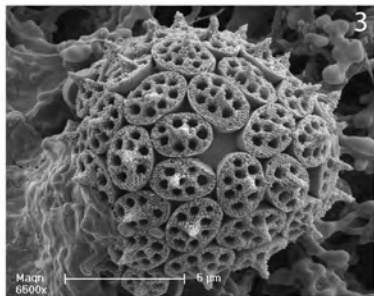
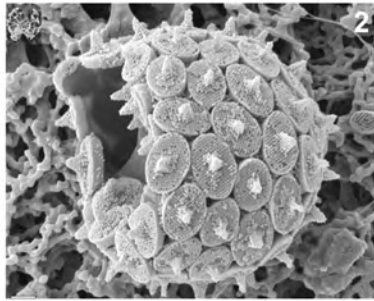


Plate 16**1, 6, 7. *Helicosphaera carteri* [HOL solid]**

1. Distal and side views; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, June, 2005; XP
6. Surface waters; South Atlantic, 20°93'S, 24°59'W; AMT16 cruise, May, 2005; XP
7. Surface waters; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, June, 2005; XP

2, 3, 5. *H. carteri* [HET]

- 2, 3. Detached coccoliths; surface waters; North Atlantic, 10°N, 29°47'W; AMT16 cruise, June, 2005; XP
5. Surface waters; North Atlantic, 10°N, 29°47'W; AMT16 cruise, June, 2005; XP

4, 8. *H. carteri* [HOL perforate]

4. Close-up of coccoliths (see fig.8); North Atlantic, 31°22'N, 42°08'W; AMT16 cruise, June, 2005; XP
8. Surface waters; North Atlantic, 31°22'N, 42°08'W; AMT16 cruise, June, 2005; XP

9. *H. carteri* [HOL solid & HOL perforate]

- Combination coccosphere bearing two types of holococcolith; surface waters; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, June, 2005; XP

Plate 16

Helicosphaeraceae

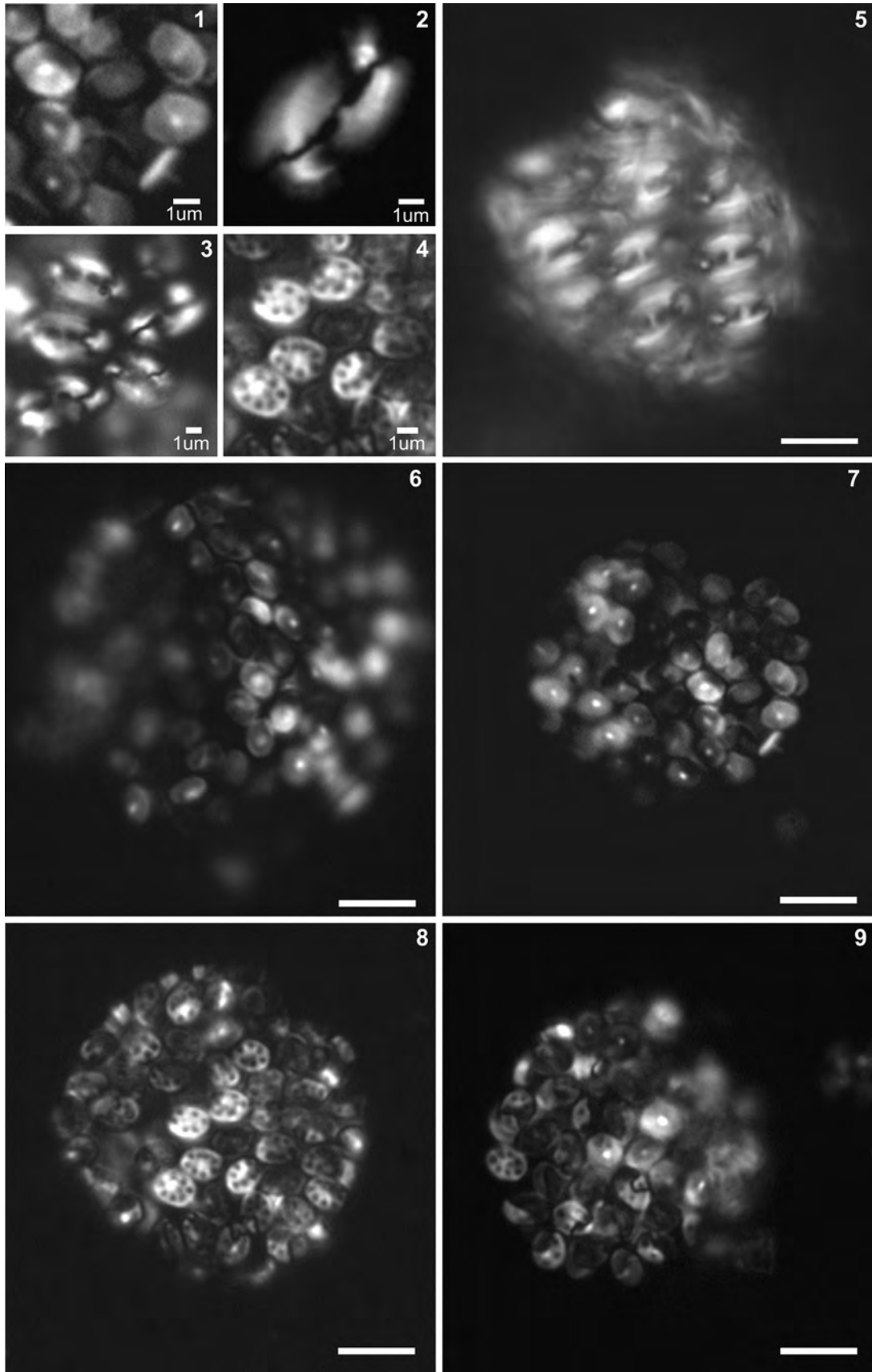
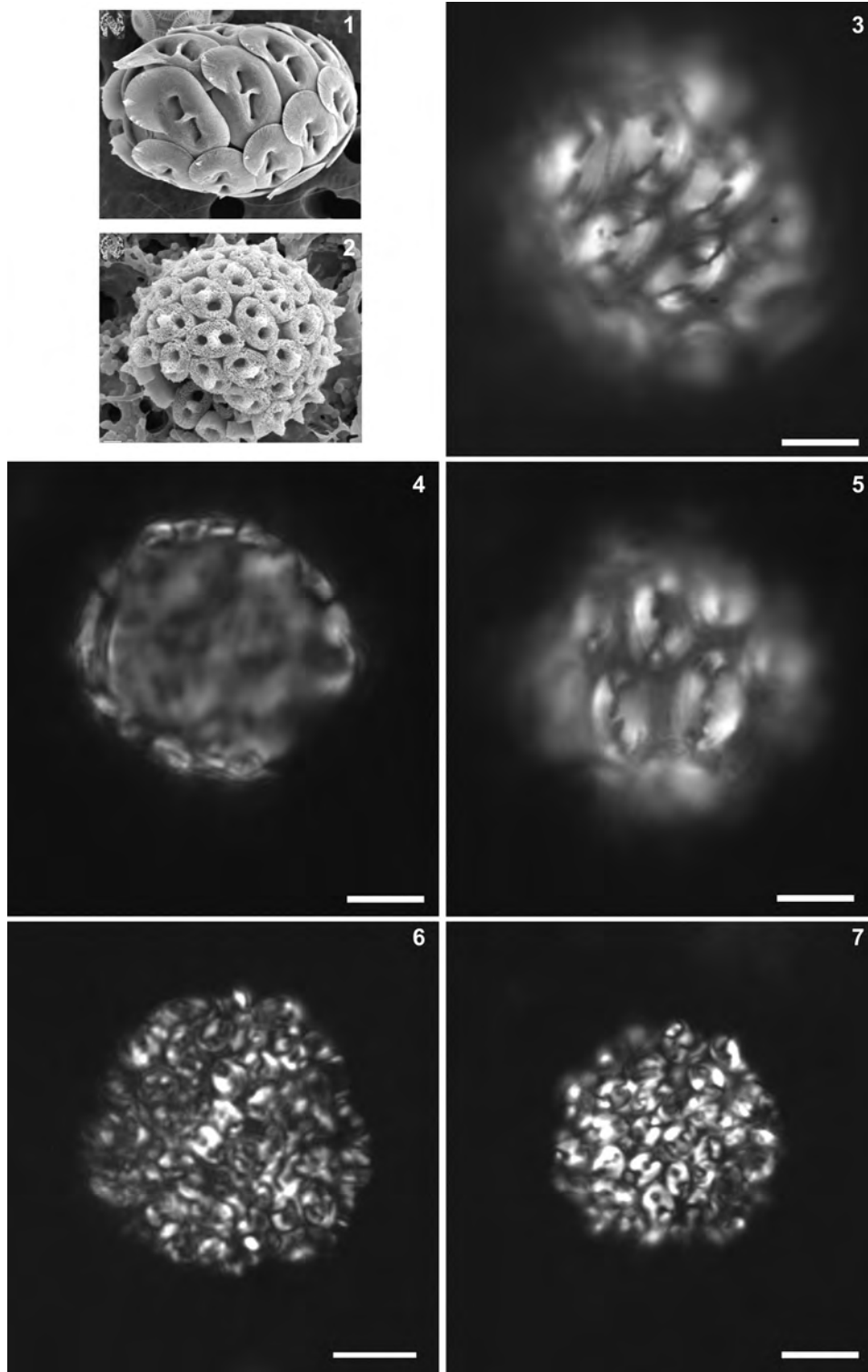


Plate 17

Helicosphaeraceae

**1, 3-5. *Helicosphaera wallichii* [HET]**

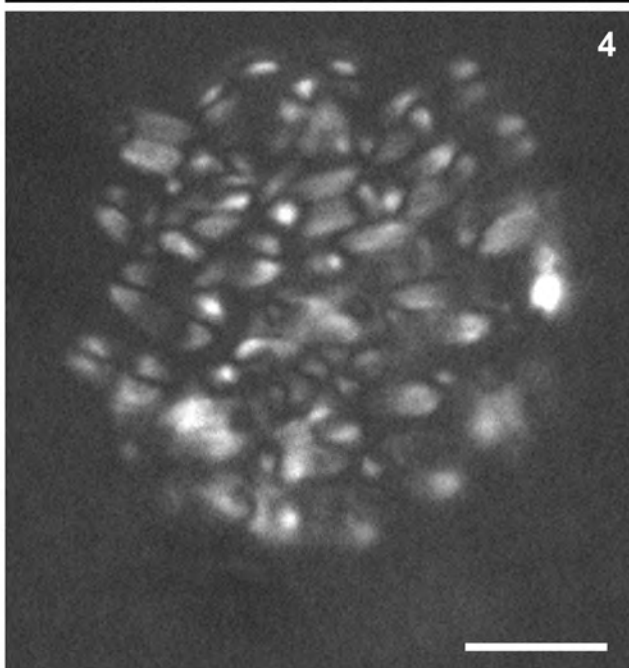
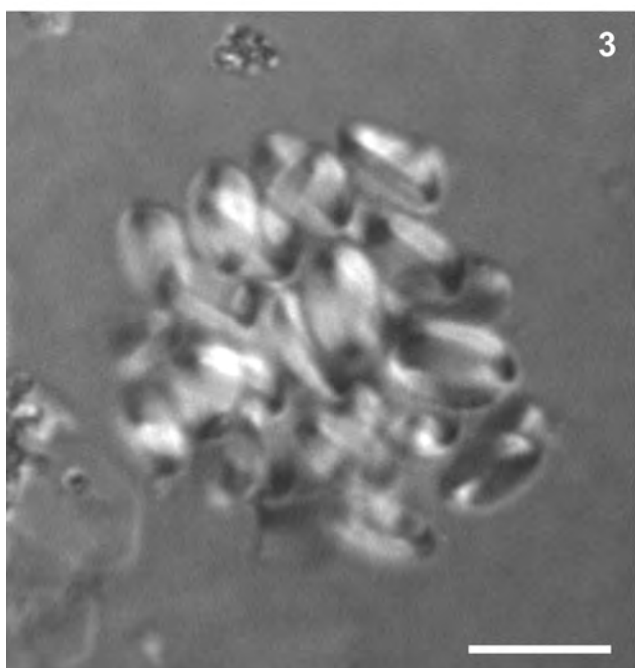
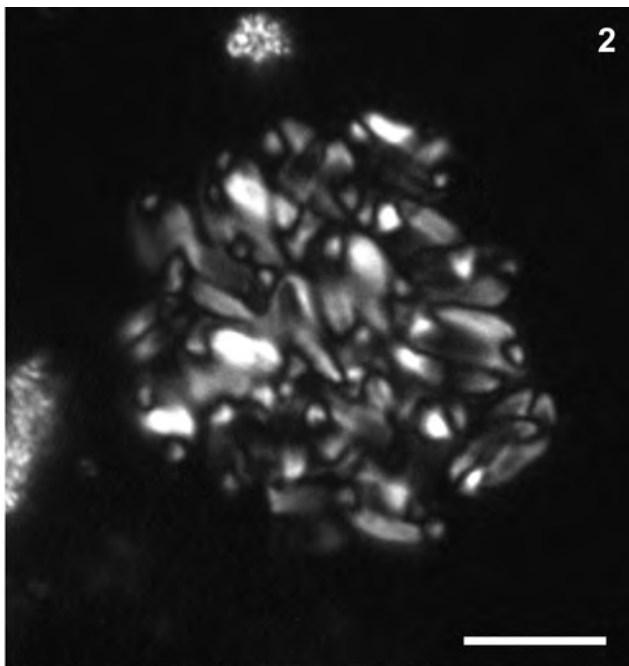
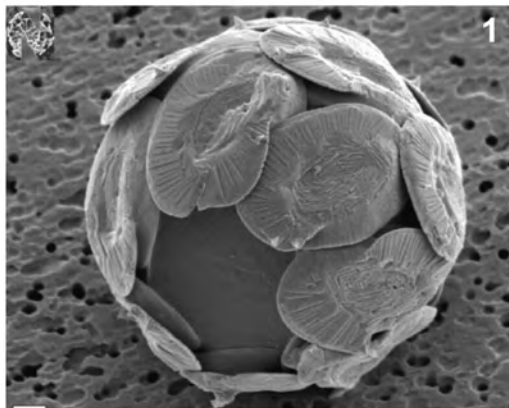
1. Surface waters; Miyake Port, Miyake Island, Japan, 34°01'N, 139°30'E; SEM (image NHM116-74)

3-5. Surface waters; North Atlantic, 04°16'N, 27°01'W; AMT16 cruise, May, 2005; XP

2, 6, 7. *H. wallichii* [HOL] (formerly *Syracolithus ponticuliferus*, combination established by Couapel *et al.*, 2009)

2. 10m water-depth; Gulf of Mexico; SEM (image NHM-CSF0112a)

6, 7. Surface waters; North Atlantic, 25°40'N, 37°40'W; AMT16 cruise, May, 2005; XP

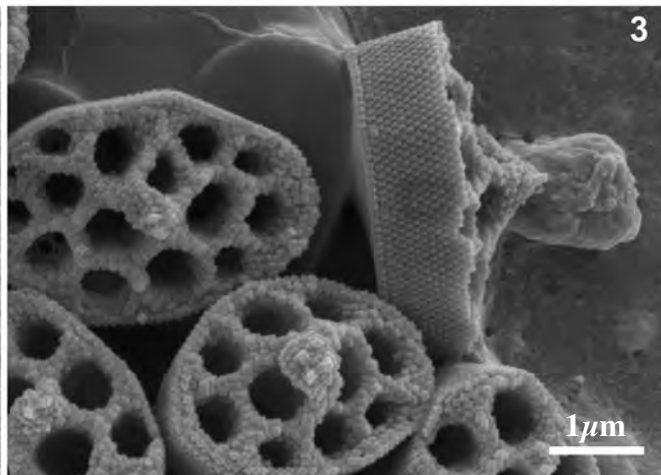
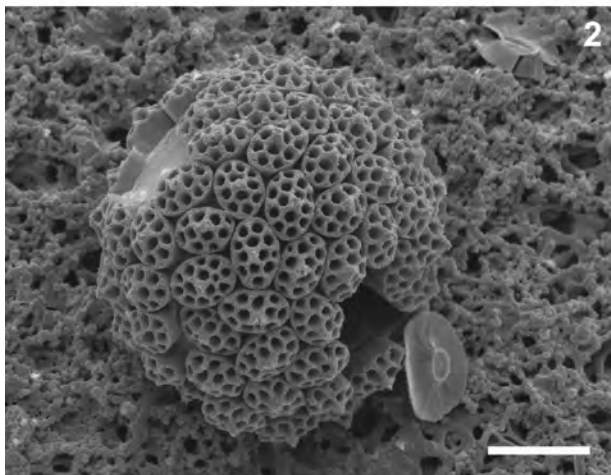
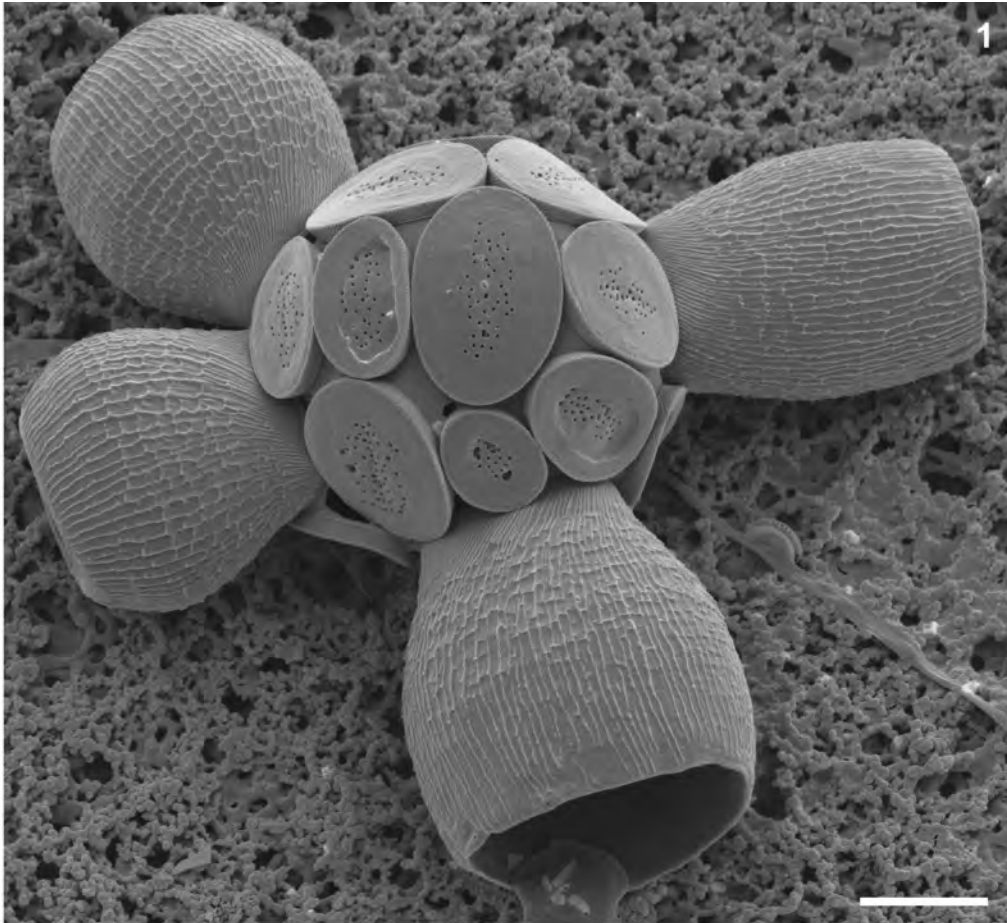
Plate 18**Helicosphaeraceae****1-4. *Helicosphaera hyalina* [HET]**

1. Culture specimen; SEM (image NHM187-51)

2, 3. Surface waters; Faial, Azores, 30°32'N, 28°33'W; XP (2), DIC (3)

4. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

Plate 19
Pontosphaeraceae



1. *Scyphosphaera apsteinii* [HET]

80m water-depth; HOTS station, Hawaii, South Pacific, 22°45'N, 158°E; SEM (image NHM 217-83)

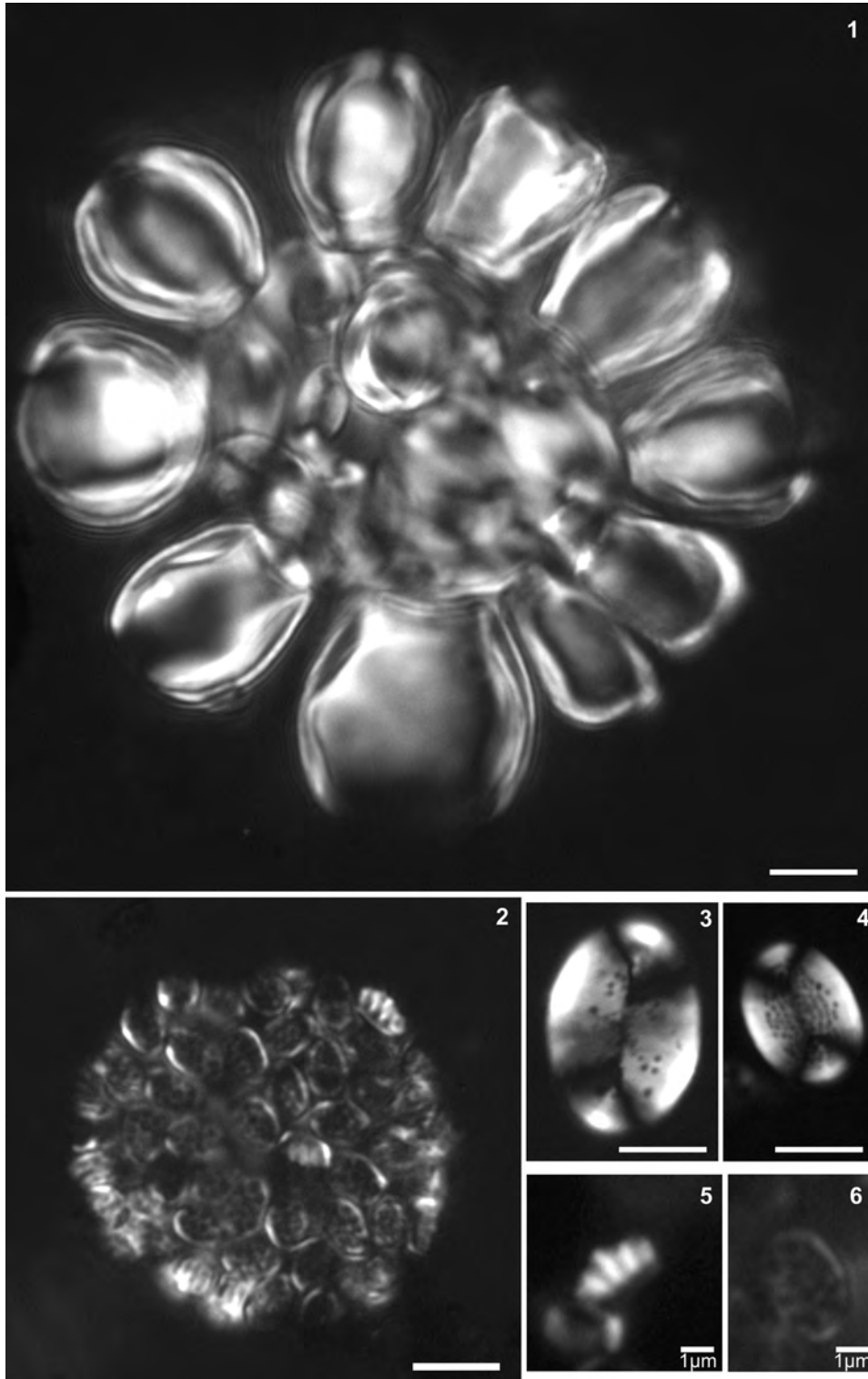
2, 3. *S. apsteinii* [HOL] (formerly *Syracolithus schillerii*, combination established by Frada *et al.*, 2009)

2. 80m water-depth; HOTS station, Hawaii, South Pacific, 22°45'N, 158°E; SEM (image NHM 217-77)

3. Close-up of coccoliths; surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise; SEM (image NHM 271-06)

Plate 20

Pontosphaeraceae

**1, 3, 4. *Scyphosphaera apsteinii* [HET]**

1. Surface waters; South Atlantic, 26°31'S, 17°13'W; May, 2005; XP

3, 4. Detached coccoliths, distal view; North Atlantic, 36°27'N, 36°55'W; AMT16 cruise, June, 2005; XP

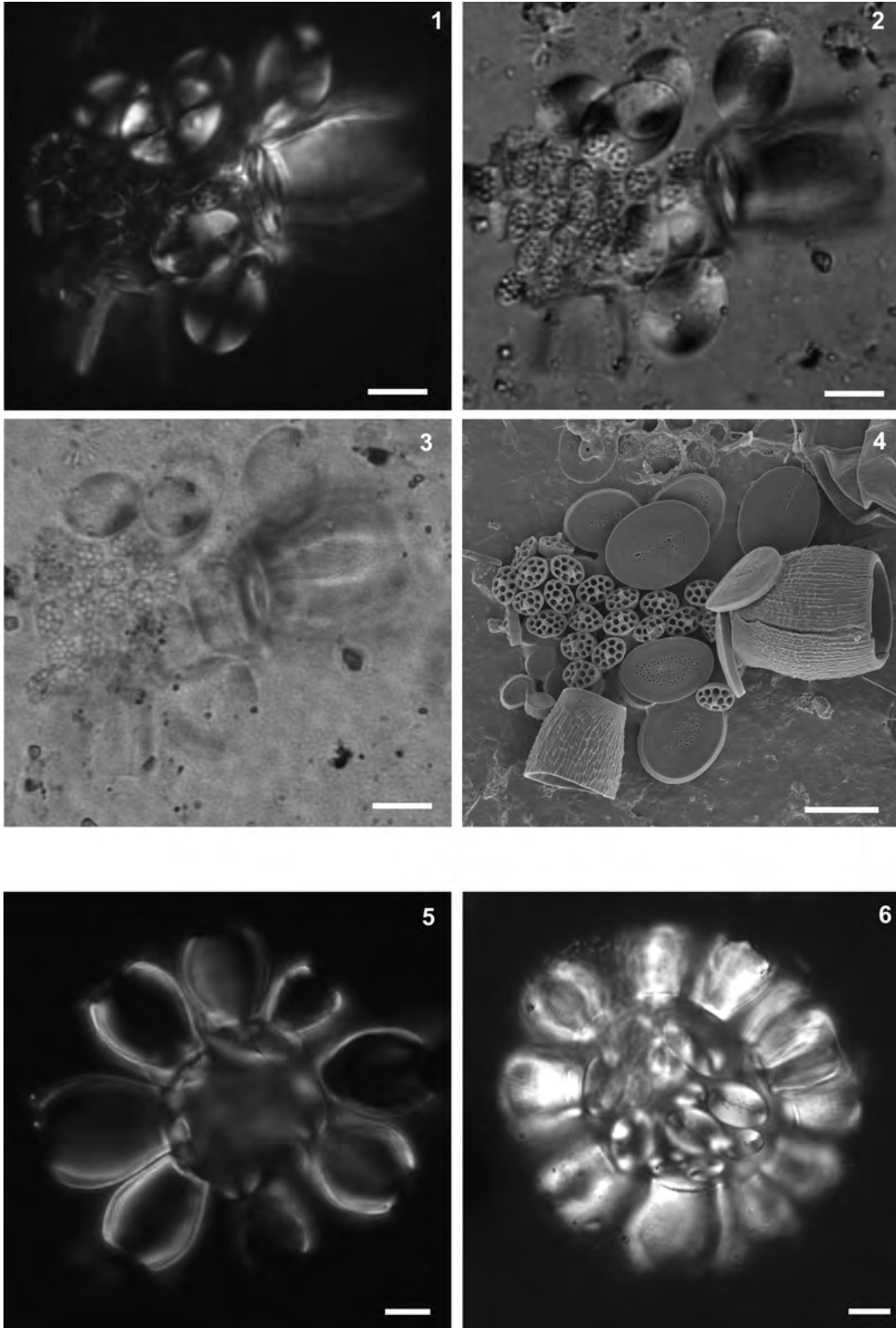
2, 5, 6. *S. apsteinii* [HOL]

2. Surface waters; North Atlantic, 15°45'N, 32°35'W; AMT16 cruise, May, 2005; XP

5-6. Detached holococcoliths, side and distal views; North Atlantic, 15°45'N, 32°35'W; AMT16 cruise, May, 2005; XP

Plate 21

Pontosphaeraceae

**1-4. *Scyphosphaera apsteinii* [HET & HOL]**

Combination coccosphere; 140m water-depth; North Atlantic, 38°18'N, 30°03'W; AMT16 cruise, May, 2005; XP (1), DIC (2), PC (3), SEM (4)

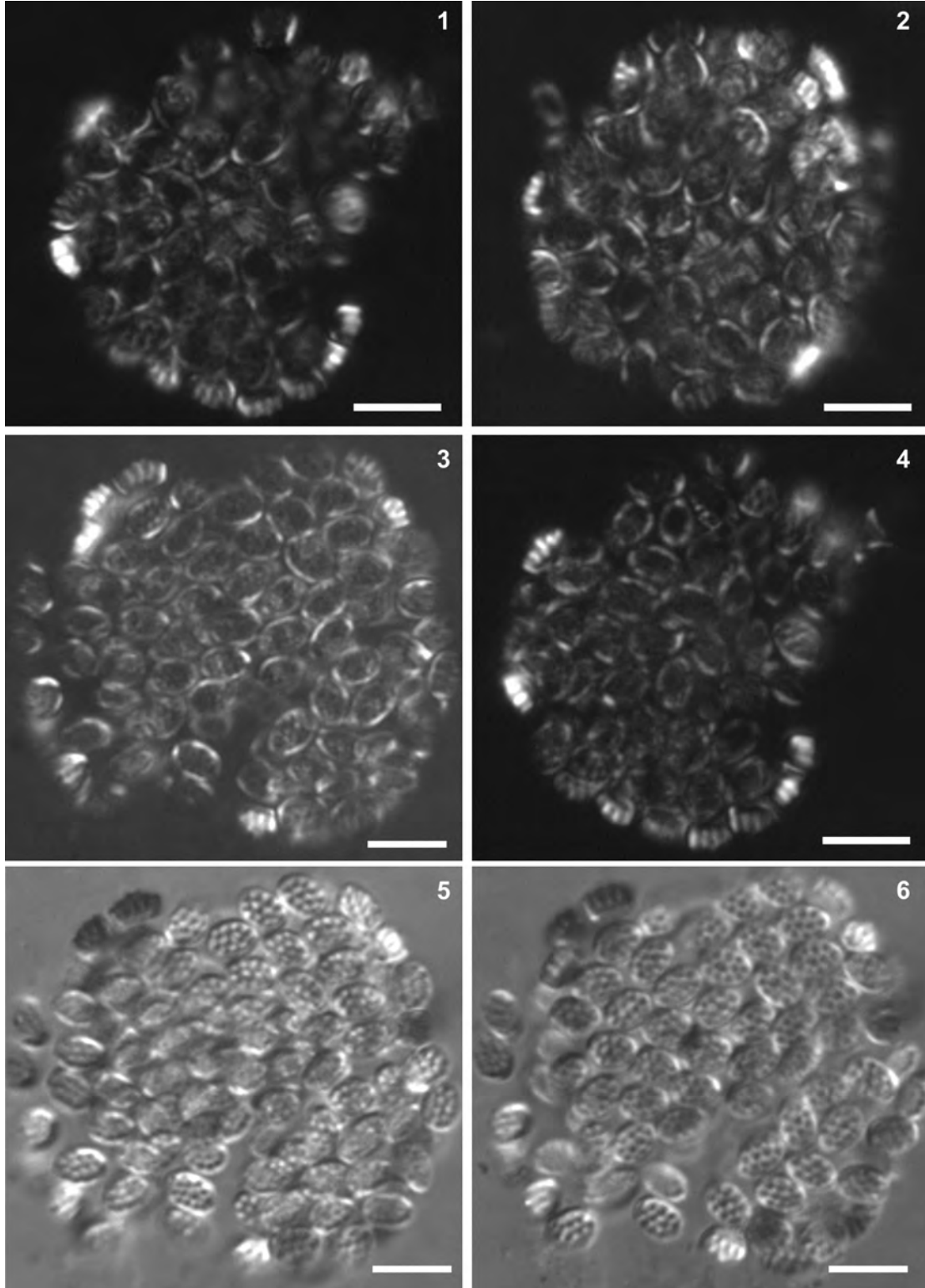
5, 6. *S. apsteinii* [HET]

5. Surface waters; North Atlantic, 36°27'N, 36°55'W; AMT16 cruise, June, 2005; XP

6. Surface waters; South Atlantic, 36°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

Plate 22

Pontosphaeraceae

**1-6. *Scyphosphaera apsteinii* [HOL]**

1, 4. Different focal planes, surface waters; North Atlantic, 15°45'N, 32°35'W; AMT16 cruise, June, 2005; XP

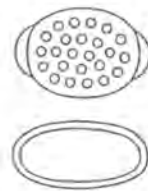
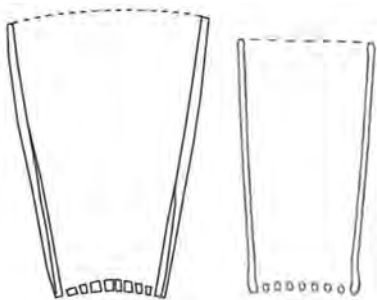
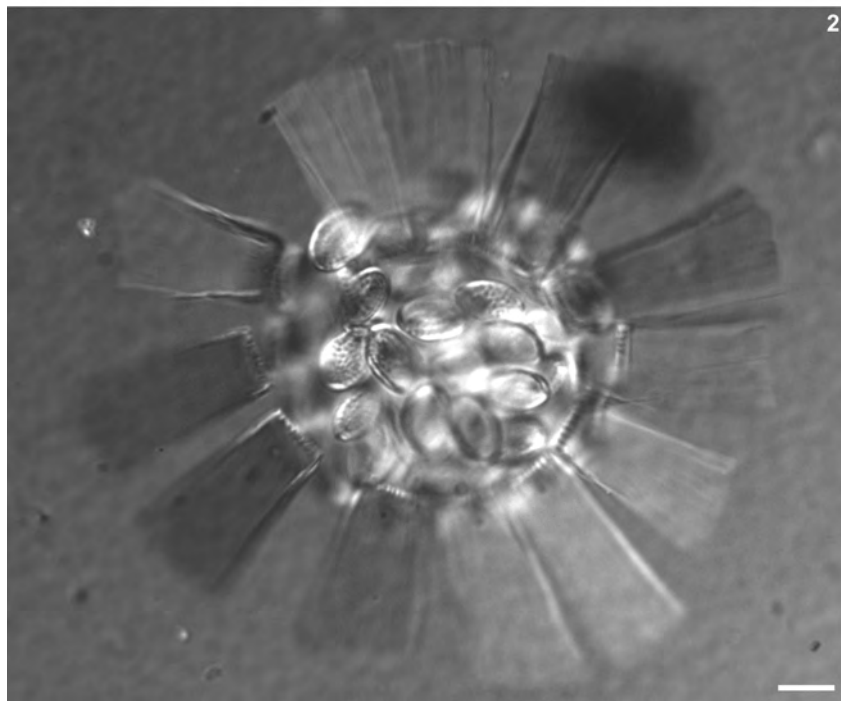
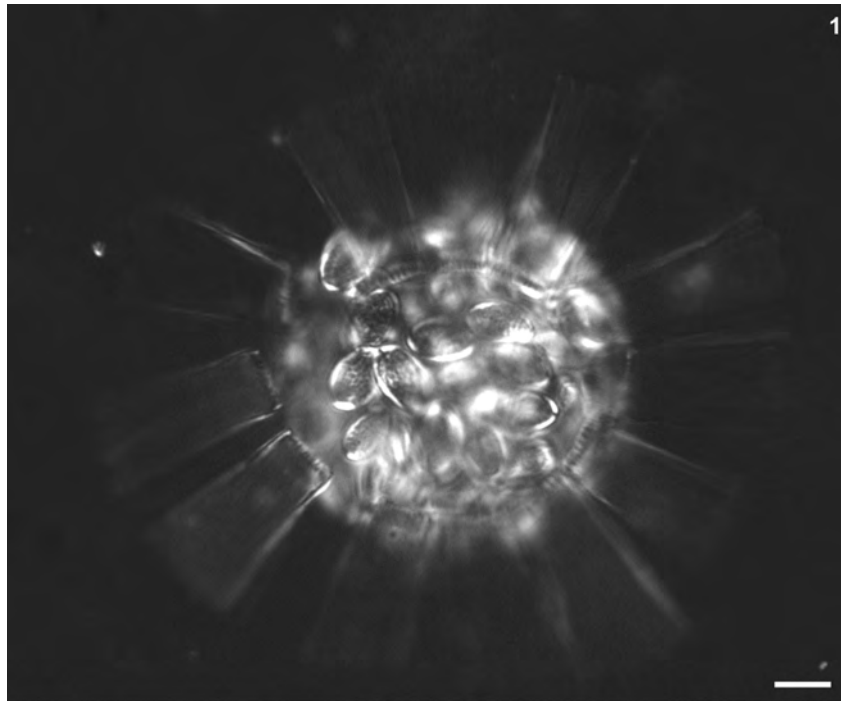
2, 3, 5, 6. Surface waters; AMT16 cruise, May, 2005

2. North Atlantic, 29°09'N, 39°32'W; XP

3, 5, 6. South Atlantic, 36°31'S, 17°13'W; XP (3), DIC (5, 6)

Plate 23

Pontosphaeraceae



3

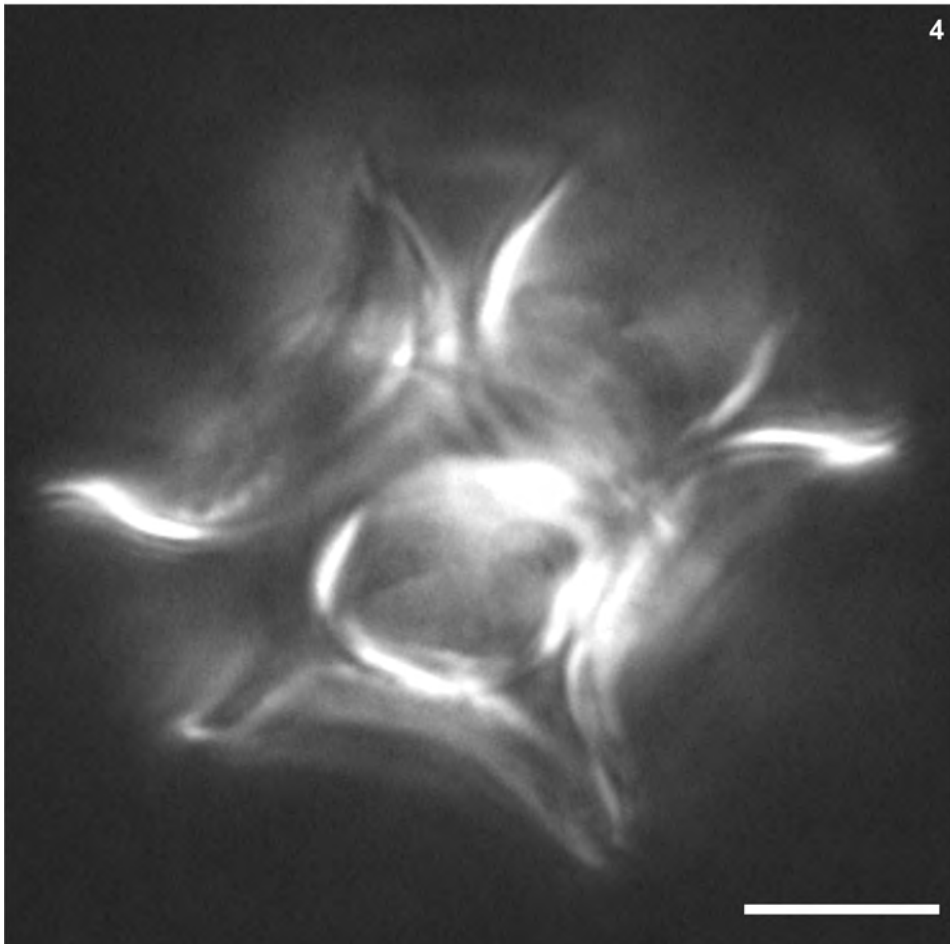
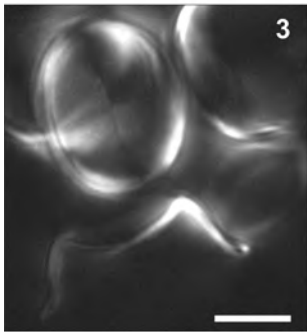
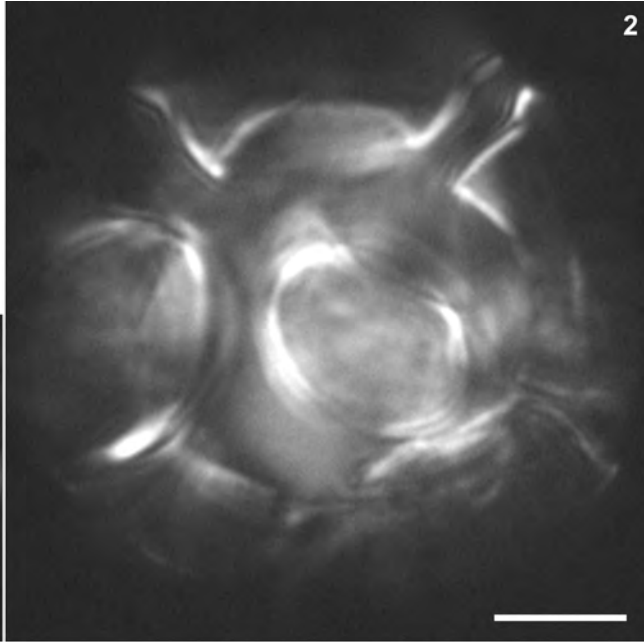
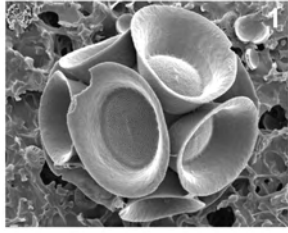
1-3. *Scyphosphaera porosa* [HET]

1, 2. 96m water-depth; South Atlantic, 31°49'S, 10°30'E; AMT16 cruise, May, 2005; XP (1), DIC (2)

3. Line-drawings of holotype (modified from Young, 2008)

Plate 24

Pontosphaeraceae



1-4. *Pontosphaera syracusana*

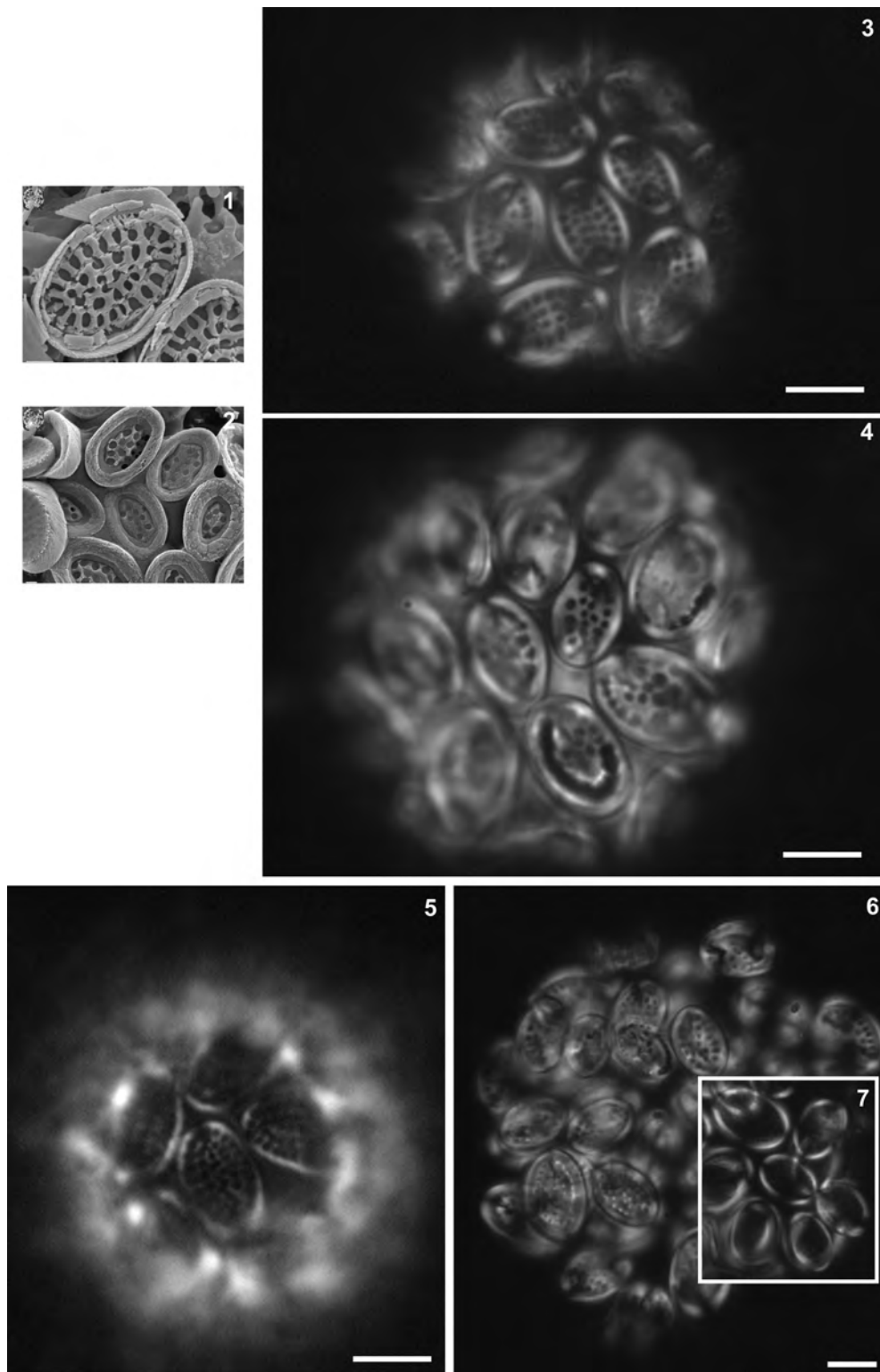
1. 5m water-depth; Alboran Sea, western Mediterranean, 37°27'N, 01°28'W; SEM (image NHM 170-16)

2, 4. Surface waters; South Atlantic, 36°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

3. Detached heterococcoliths; surface waters; South Atlantic, 01°57'S, 24°59'W; AMT16 cruise, June, 2005; XP

Plate 25

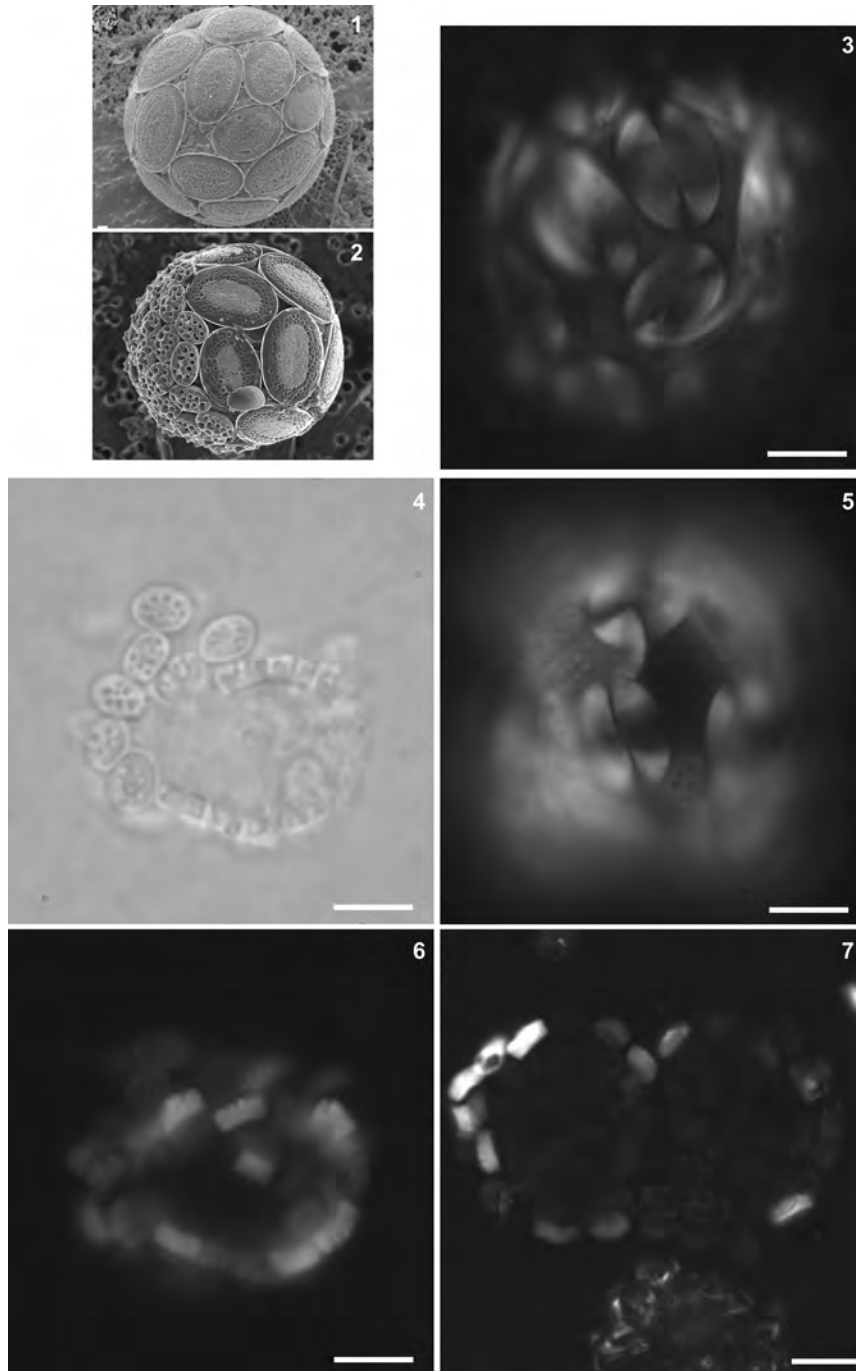
Pontosphaeraceae

**1-7. *Pontosphaera multipora* [HET]**

1. Coccolith, distal view; 120m water-depth; Gulf of Mexico, 26°39'N, 39°50'E; SEM (image NHM 134-06)
2. Coccoliths, distal view; 60m water-depth; Gulf of Mexico, 26°19'N, 59°38'W; SEM (image NHM CSF0103)
3. Surface waters; South Atlantic, 27°49'S, 10°30'W; AMT16 cruise, May, 2005; XP
4. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP
- 5-7. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, May, 2005; XP

Plate 26

Pontosphaeraceae

**1, 3. *Pontosphaera japonica* [HET]**

1. 80m water-depth; HOTS station, Hawaii, North Pacific, 22°45'N, 158°E; SEM (image NHM 217-82)

3. Surface waters; South Atlantic, 01°37'S, 24°59'W; AMT16 cruise, June, 2005; XP

2, 5. *P. japonica* [HET & HOL] ('*Syracolithus*'-like holococcolithophore combination coccospere, see Frada *et al.* (2009) for discussion)

Gulf of Naples; SEM (2, image from Isabella Percopo, SZN Naples), XP (5, image from Jeremy Young, NHM)

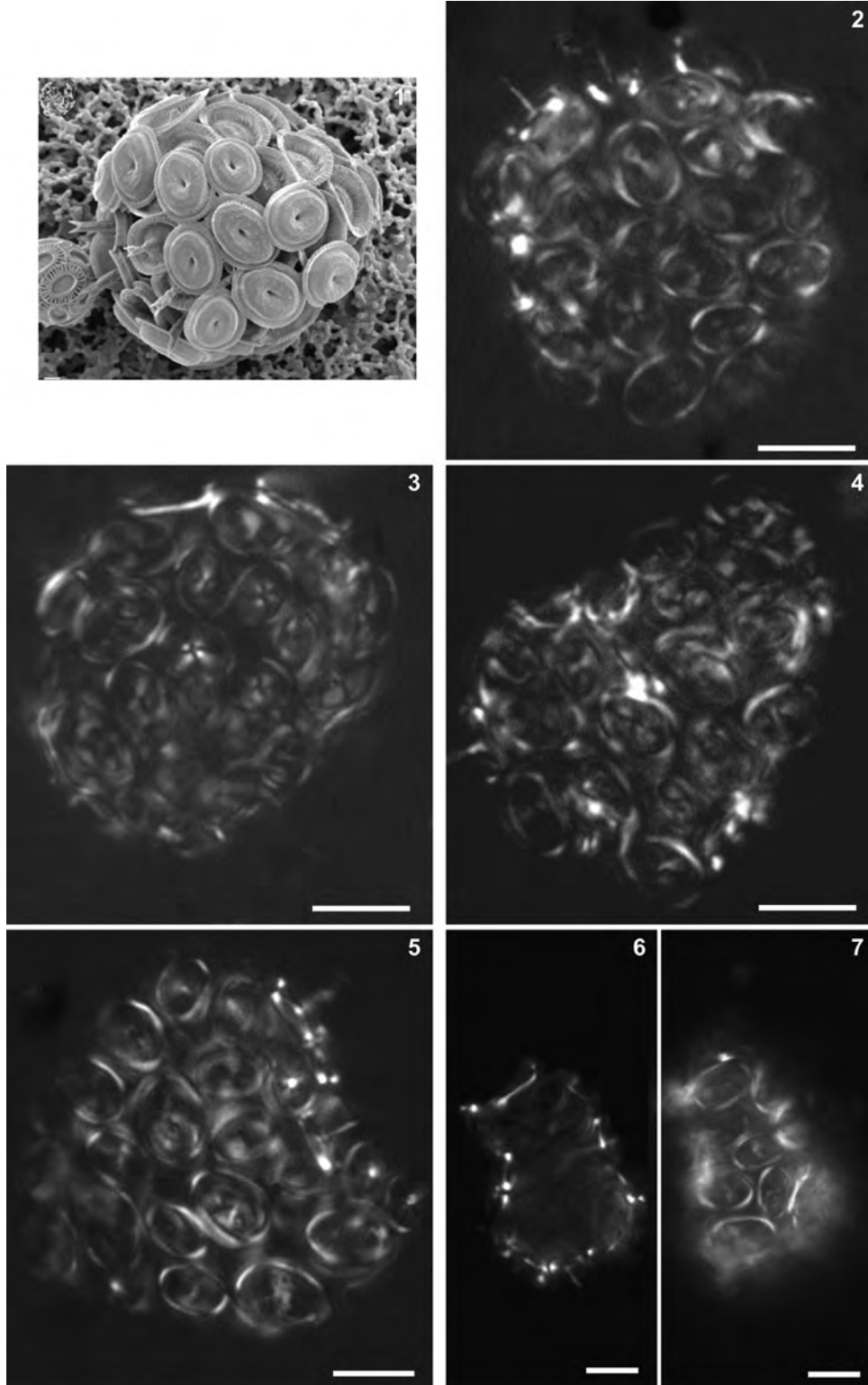
4, 6, 7. *P. japonica* [HOL]

4, 6. Surface waters; eastern Tyrrhenian Sea, 39°30'N, 13°30'E; November, 2006; DIC (4), XP (6) (image from Jeremy Young, NHM)

7. Collapsed coccospere; surface waters; North Atlantic, 18°57'N, 34°12'W; AMT16 cruise, May, 2005; XP

Plate 27

Syracosphaeraceae

1-7. *Syracosphaera pulchra* [HET]

1. 50m water-depth; Canary Islands, North Atlantic, 29°41'N, 17°53'E; SEM (image NHM 166-05)

2, 5. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP

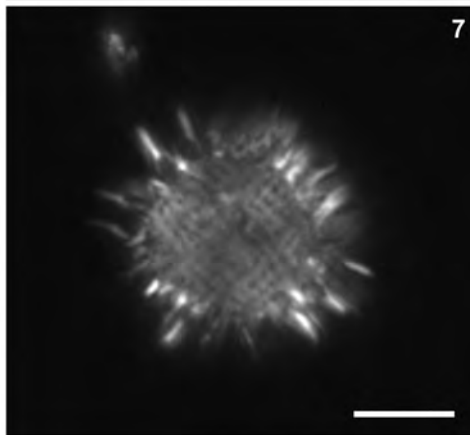
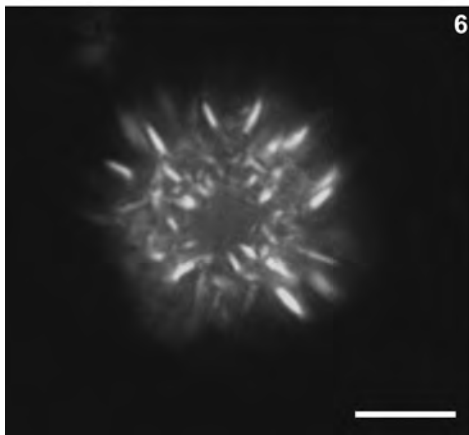
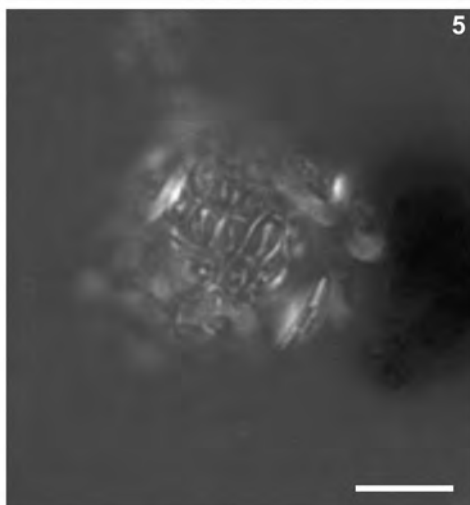
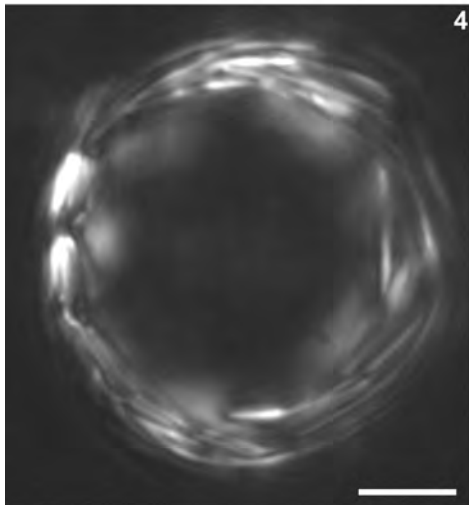
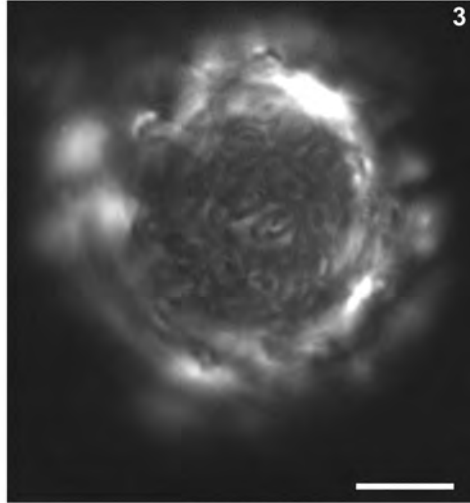
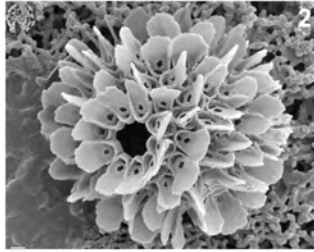
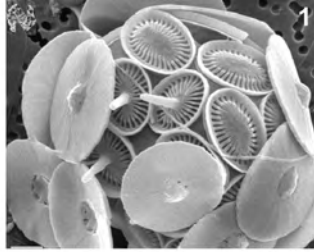
3. Surface waters; North Atlantic, 04°16'N, 27°01'W; AMT16 cruise, June, 2005; XP

4. Surface waters; South Atlantic, 22°52'S, 24°59'W; AMT16 cruise, May, 2005; XP

6, 7. Surface waters; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP

Plate 28

Syracosphaeraceae

**1, 3-5. *Syracosphaera anthos* [HET]**

1. 42.5m water-depth; Alboran Sea, western Mediterranean, 37°25'N, 00°25'W; SEM (image NHM 144-12)

3-5. Surface waters; South Atlantic, 31°49'S, 01°30'E; AMT16 cruise, May, 2005; XP (3, 4), DIC (5)

2, 6, 7. *S. anthos* [HOL] (formerly *Periphyllophora mirabilis*, combination established by Cros *et al.*, 2000)

2. 5m water-depth; Alboran Sea, western Mediterranean, 35°54'N, 01°31'W; SEM (image NHM 133-38)

6. Surface waters; Faial, Azores, 30°32'N, 28°33'W; AMT16 cruise, May, 2005; XP

7. Surface waters; South Atlantic, 26°03'S, 17°13'W; AMT16 cruise, May, 2005; XP

Plate 29

Syracosphaeraceae

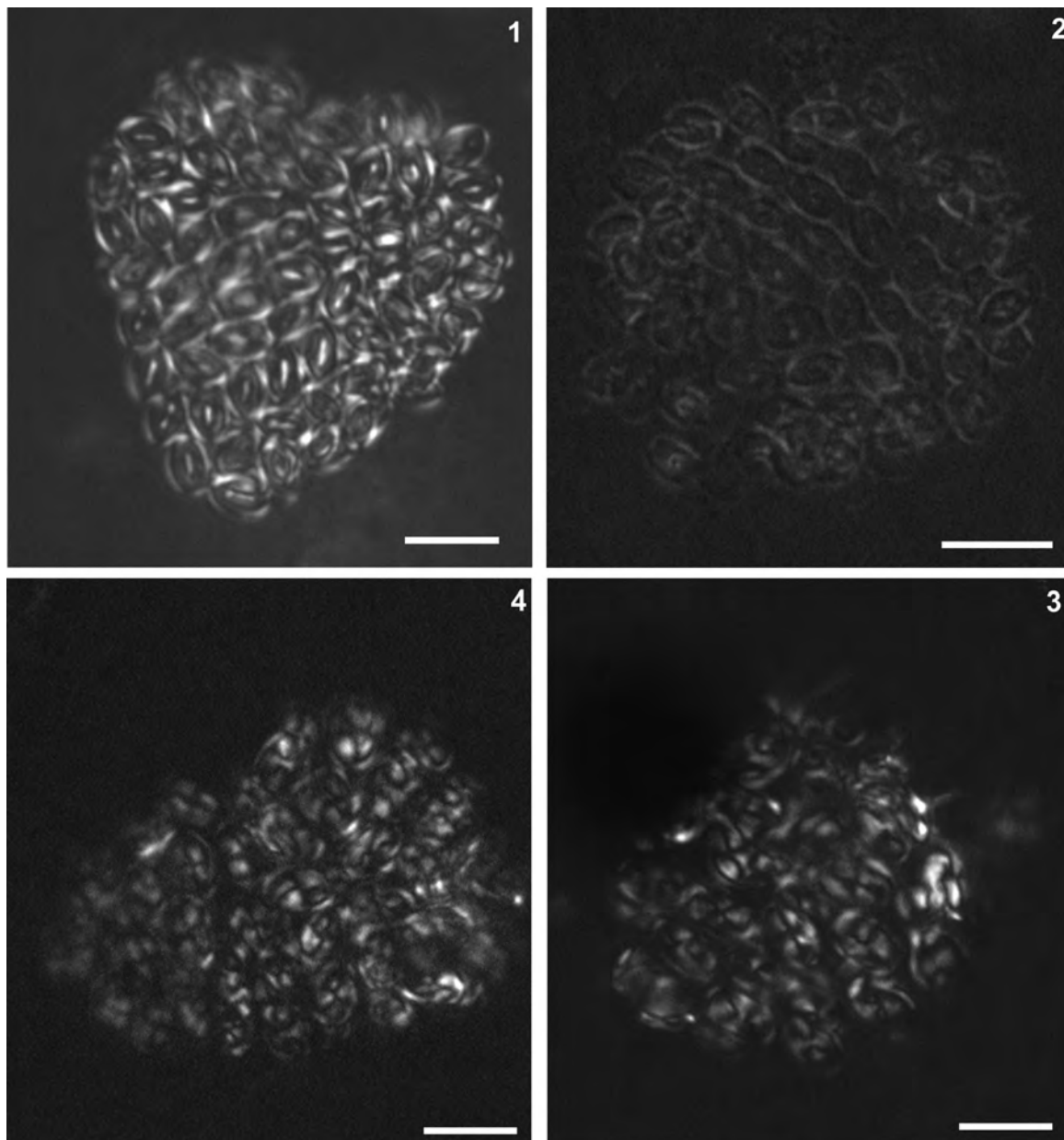


Plate 29

1-4. *Syracosphaera* sp. [HET]

Surface waters; South Atlantic, 31°49'S, 01°30'E; AMT16 cruise, May, 2005; XP

Plate 30

1, 3-6. *Coronosphaera mediterranea* [HET]

- 1. 5m water-depth; North Atlantic, 21°16'N, 20°41'W; SEM (image NHM 114-62)
- 3. Surface waters; North Atlantic, 25°40'N, 37°40'W; AMT16 cruise, June, 2005; XP
- 4, 5. Surface waters; Mediterranean, Villefranche-sur-Mer, France; March, 2007; XP
- 6. Surface waters; Faial, Azores, 30°32'N, 28°33'W; June, 2008; XP

2, 7, 8. *C. binodata* [HET]

- 2. 5m water-depth; Canary Islands, North Atlantic, 33°27'N, 09°10'W; SEM (image NHM 103-33)
- 7. Detached coccoliths, distal view; Canary Islands, North Atlantic, 33°27'N, 09°10'W; SEM (image NHM 103-33)
- 8. Surface waters; South Atlantic, 22°52'S, 24°59'W; AMT16 cruise, June, 2005; XP

Plate 30

Syracosphaeraceae

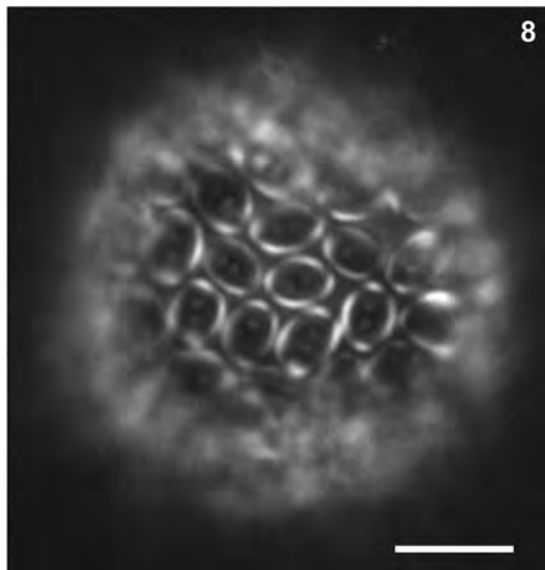
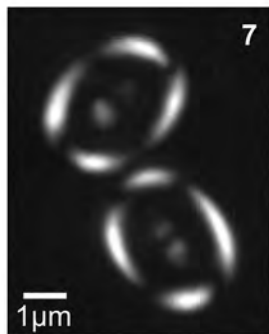
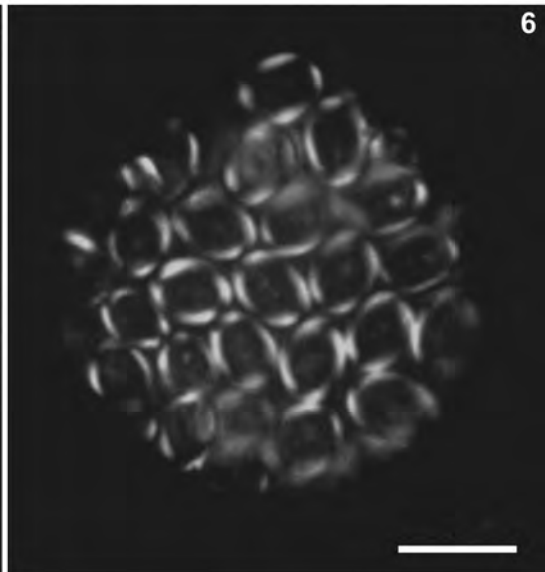
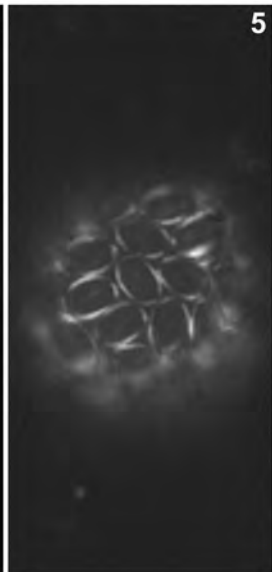
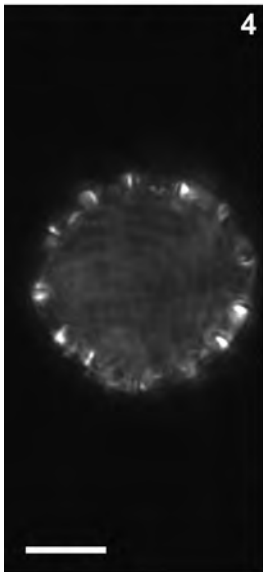
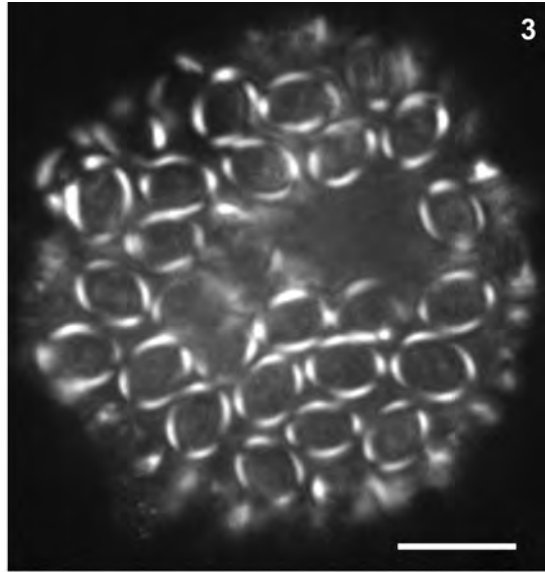
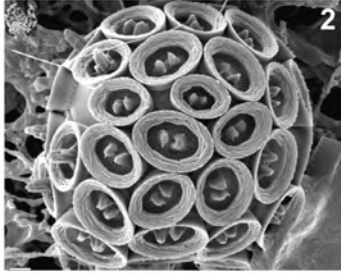
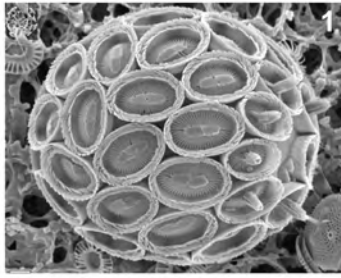
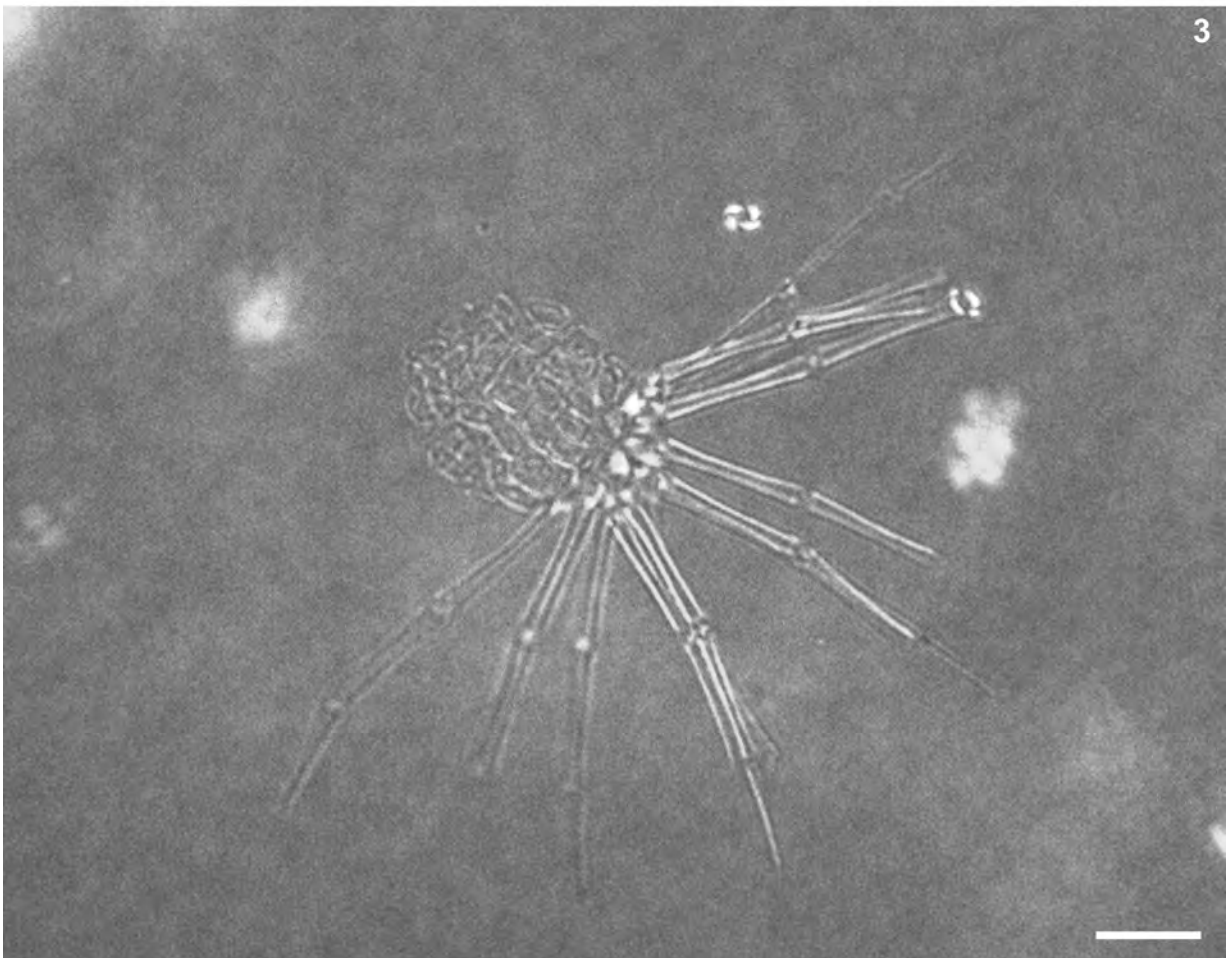
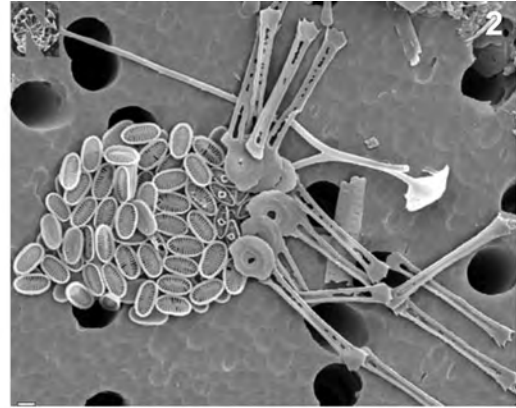
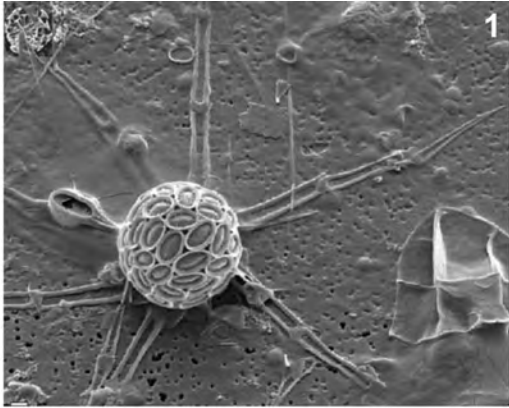


Plate 31

Syracosphaeraceae

**1, 3. *Michaelsarsia elegans* [HET]**

1. 42.5m water-depth; Alboran Sea, western Mediterranean, 37°25'N, 00°25'W; SEM (image NHM 127-23)

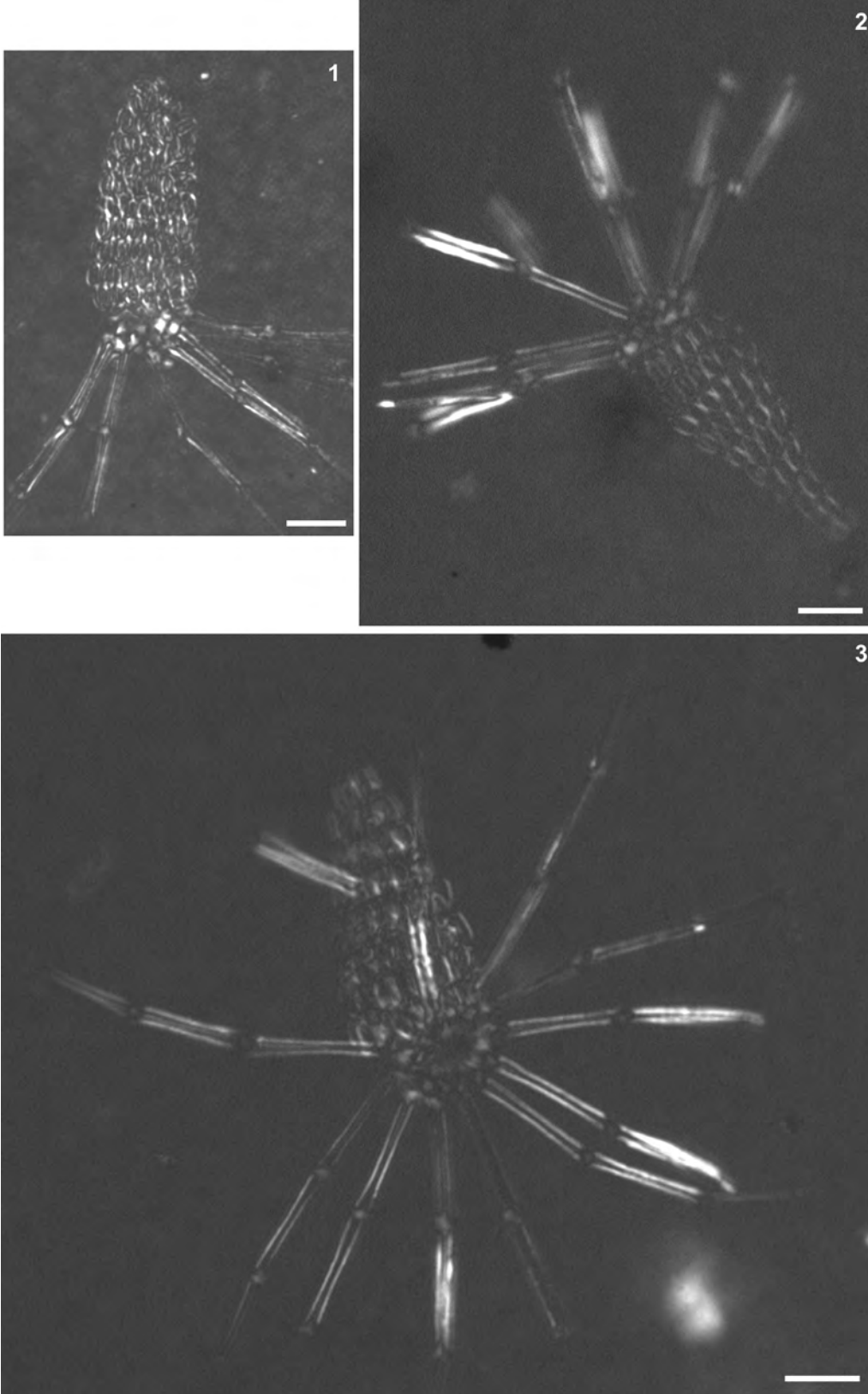
3. 50m water-depth; South Atlantic, 31°04'S, 10°30'E; AMT16 cruise, May, 2005; XP

2. *M. adriaticus* [HET]

Surface waters; Miyake Island, Japan, 34°06'N, 139°30'E; SEM (image NHM 119-61)

Plate 32

Syracosphaeraceae



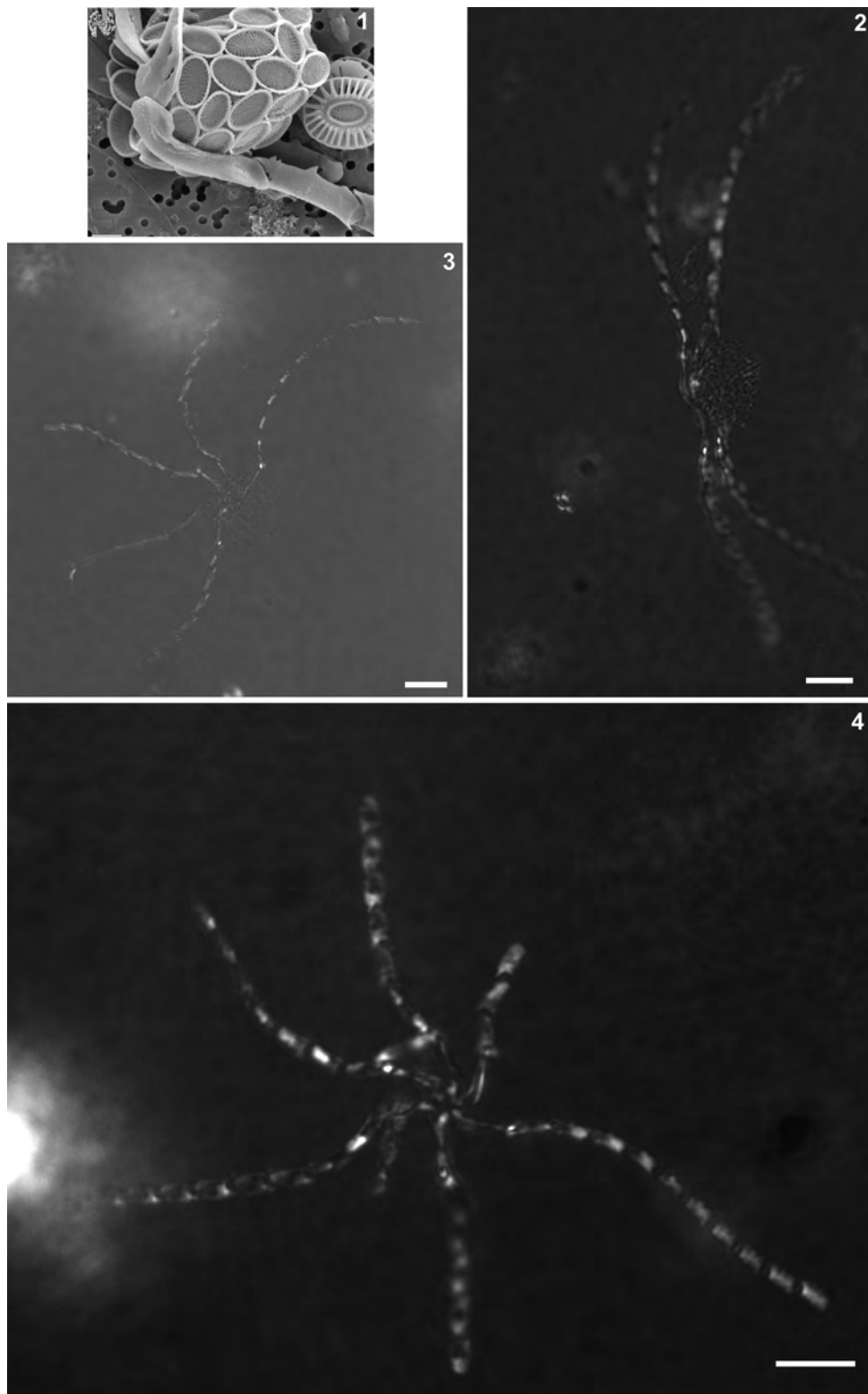
1-3. *Michaelsarsia adriaticus* [HET]

1, 3. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

2. 10m water-depth; Japan, 34°04'N, 140°02'E; *Tansei Maru* cruise, May, 2006; XP

Plate 33

Syracosphaeraceae

**1. *Ophiaster formosus* [HET]**

42.5m water-depth; Alboran Sea, western Mediterranean, 37°25'N, 00°25'W; SEM (image NHM 125-14)

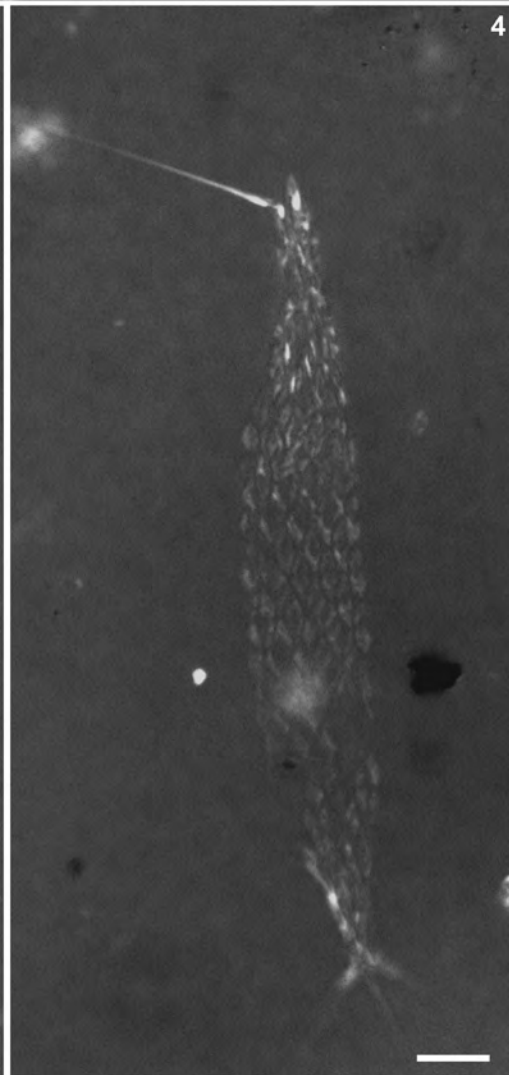
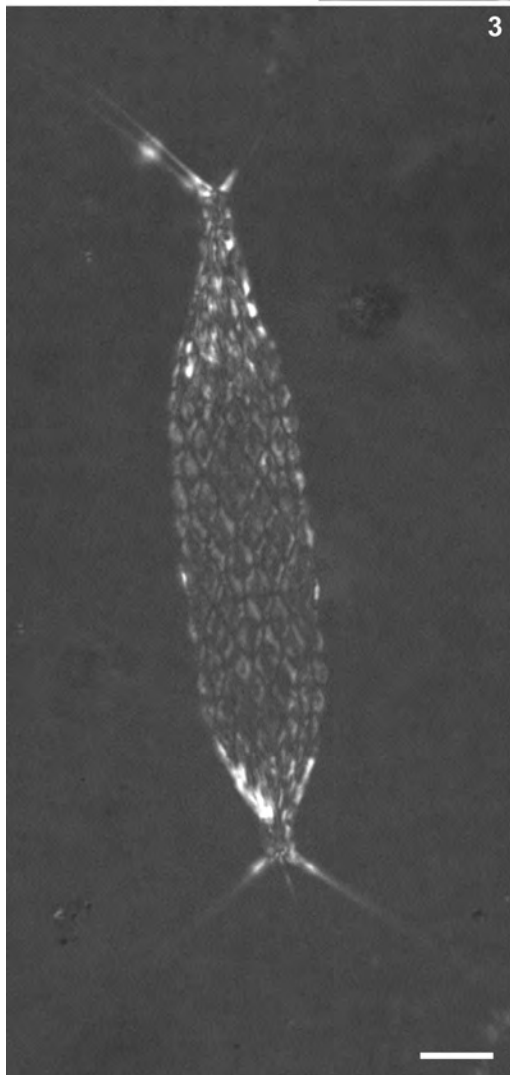
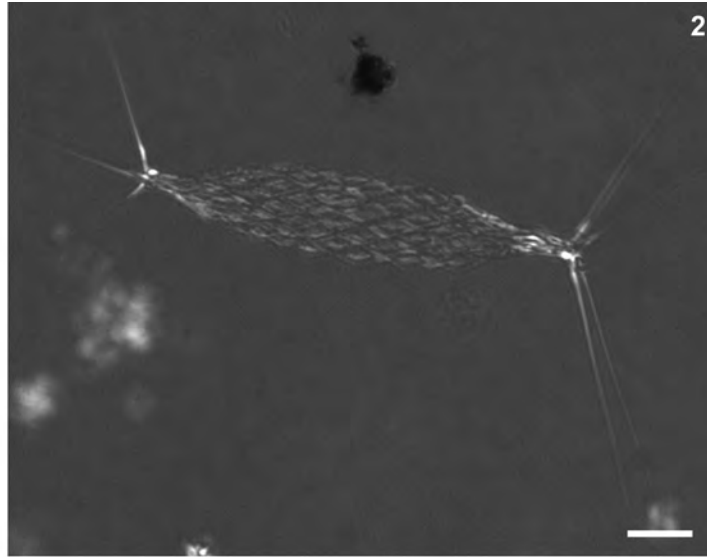
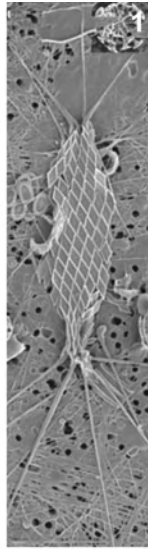
2-4. *Ophiaster* sp. [HET]

2, 3. 96m water-depth; South Atlantic, 31°49'S, 16°28'E; AMT16 cruise, May, 2005; XP

4. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP

Plate 34

Calciosoleniaceae



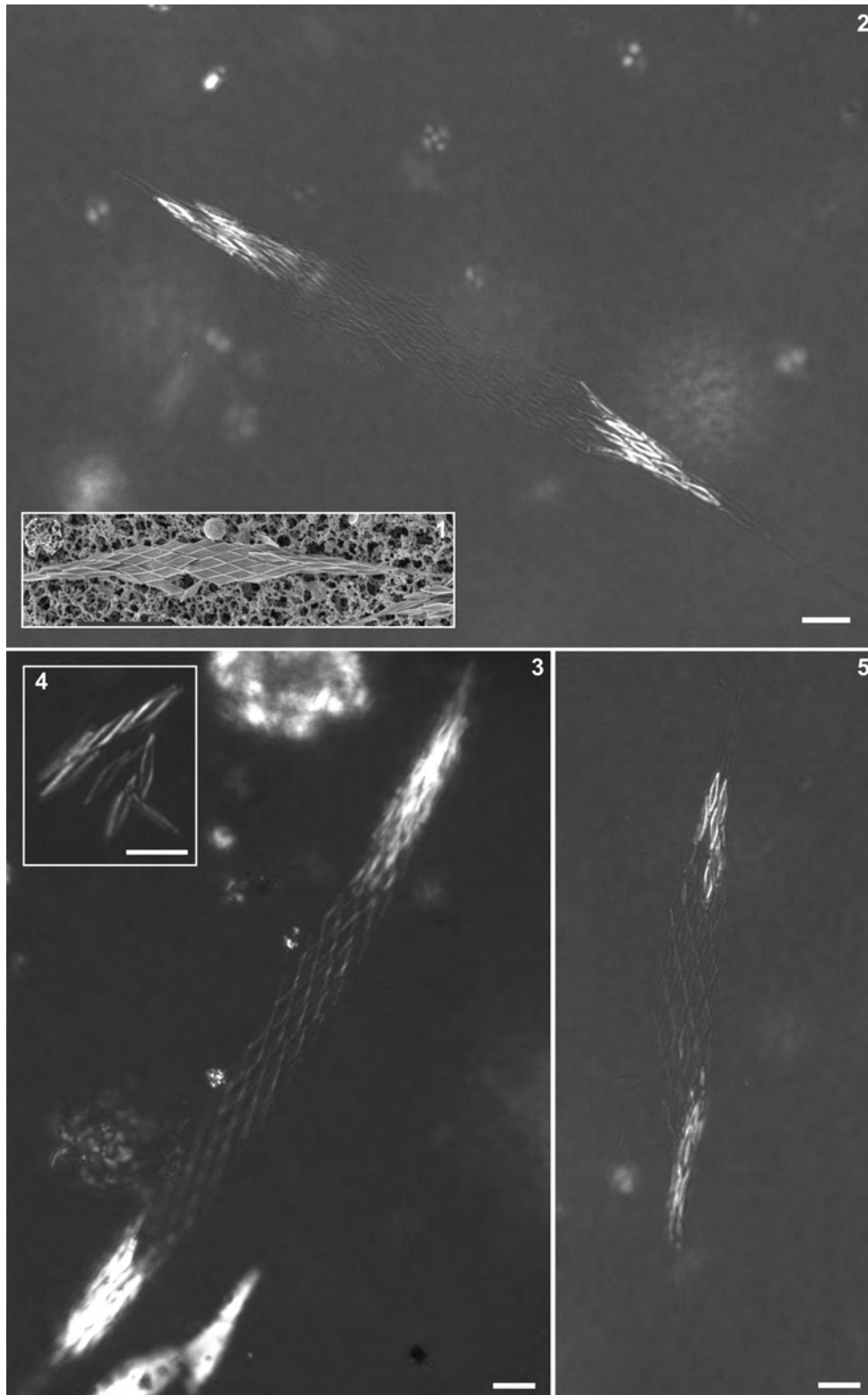
1-4. *Calciosolenia murrayi* [HET]

1. 37m water-depth; Alboran Sea, western Mediterranean, 37°23'N, 00°56'W; SEM (image NHM 117-29)

2-4. Surface waters; South & North Atlantic, 26°31'S, 17°13'W & 38°18'N, 30°03'W; AMT16 cruise, May & June, 2005; XP

Plate 35

Calciosoleniaceae

**1-5. *Calciosolenia brasiliensis* [HET]**

1. 5m water-depth; Alboran Sea, western Mediterranean, 35°54'N, 01°21'E; SEM (image NHM 189-31)

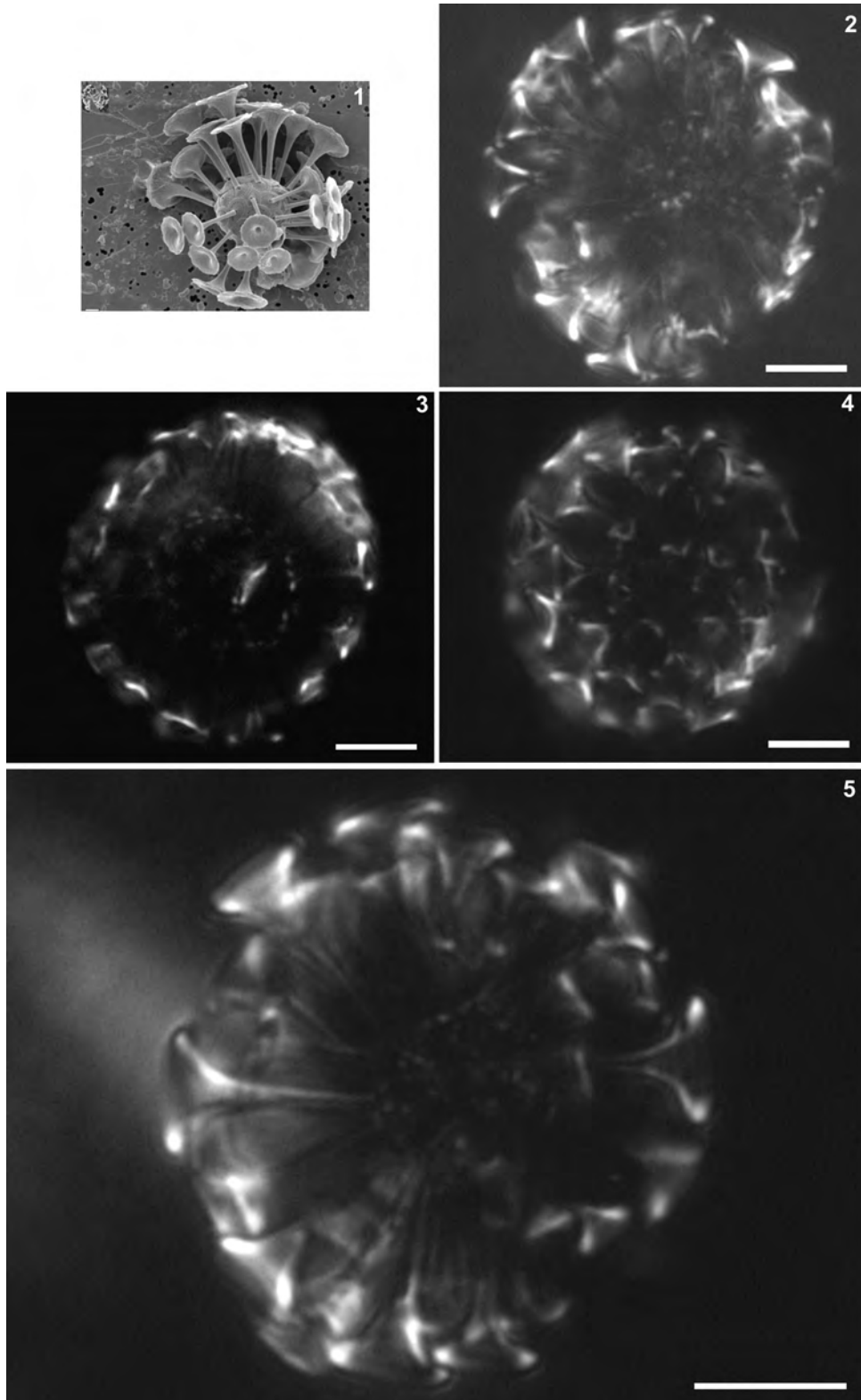
2, 4. 96m water-depth; South Atlantic, 31°49'S, 16°28'E; AMT16 cruise, May, 2005; XP

3. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

5. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP

Plate 36

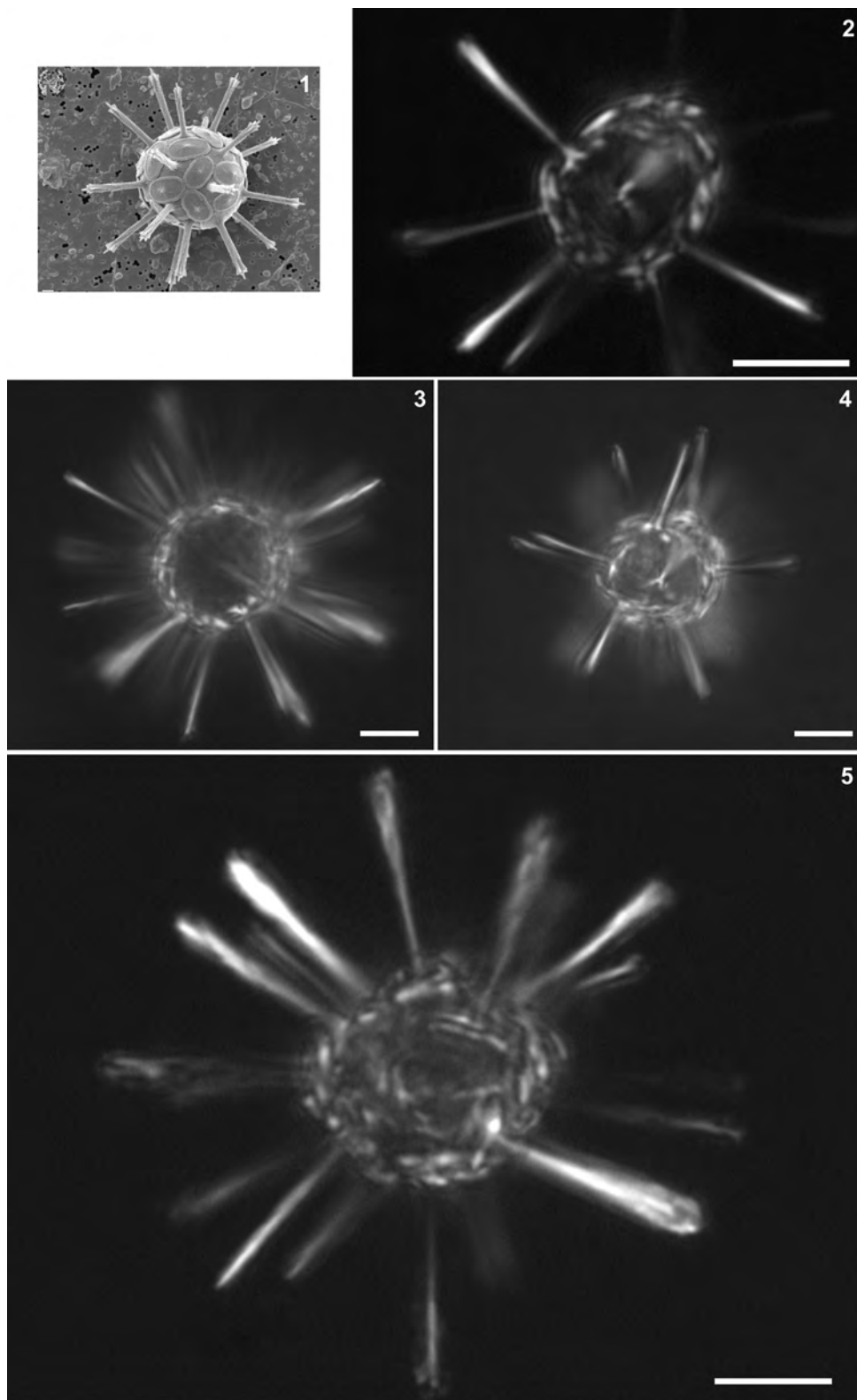
Rhabdosphaeraceae

**1-5. *Discosphaera tubifera* [HET]**

1. 5m water-depth; Alboran Sea, western Mediterranean, 37°25'N, 00°25'E; SEM (image NHM 123-53)
2. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP
- 3, 4. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June 2005; XP
5. Surface waters; North Atlantic, 25°40'N, 37°40'W; AMT16 cruise, June, 2005; XP

Plate 37

Rhabdosphaeraceae

**1-5. *Rhabdosphaera clavigera* [HET]**

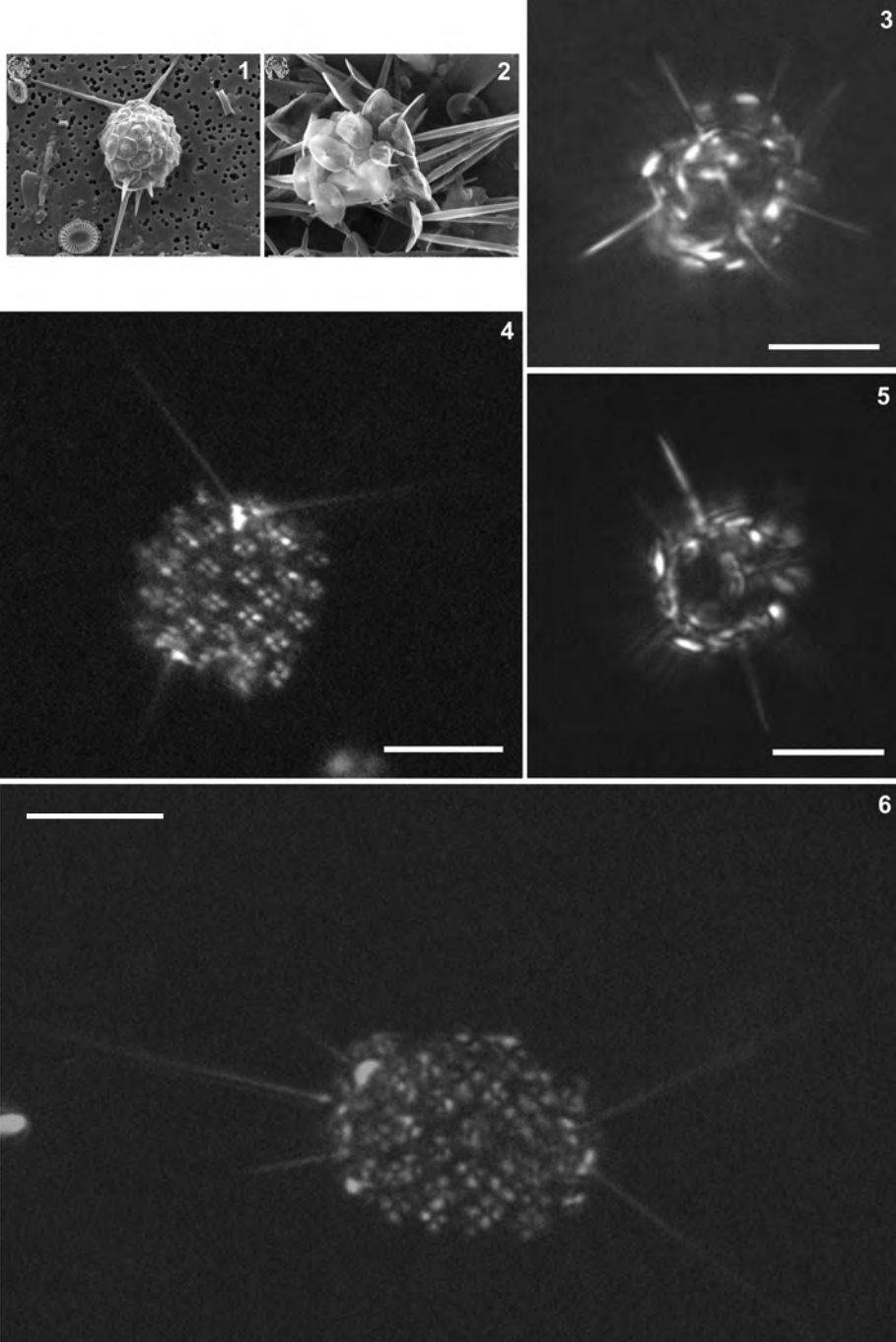
1. 5m water-depth; Alboran Sea, western Mediterranean, 37°25'N, 00°25'E; SEM (image NHM 124-02)

2, 3. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP

4, 5. Surface waters; South Atlantic, 26°31'S, 17°13'W; AMT16 cruise, May, 2005; XP

Plate 38

Rhabdosphaeraceae

**1. *Acanthoica quattrosпина* [HET]**

27m water-depth; Portuguese Shelf, North Atlantic, 38°44'N, 09°46'W; SEM (image NHM 121-22)

2. *Palusphaera* sp.1 [HET]

2. Collapsed coccosphere; 87m water-depth; North Atlantic, 34°17'N, 34°23'W; SEM (image AK81-39 from Annelies Kleijne, VU Amsterdam)

3, 4. *Palusphaera* sp. [HET]

Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP

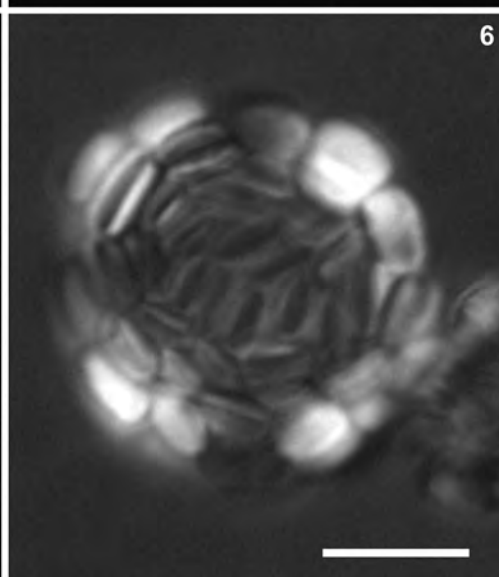
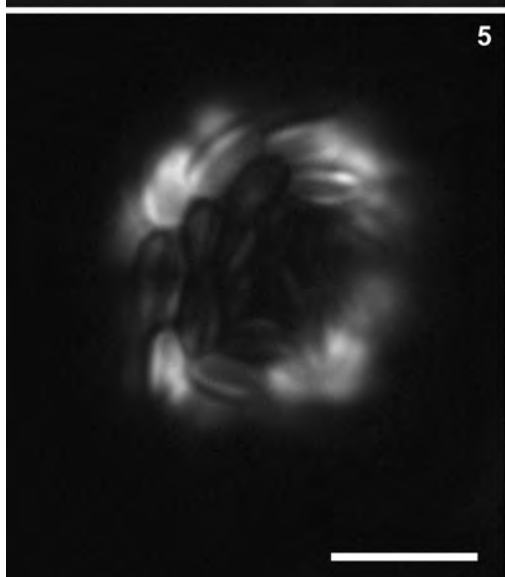
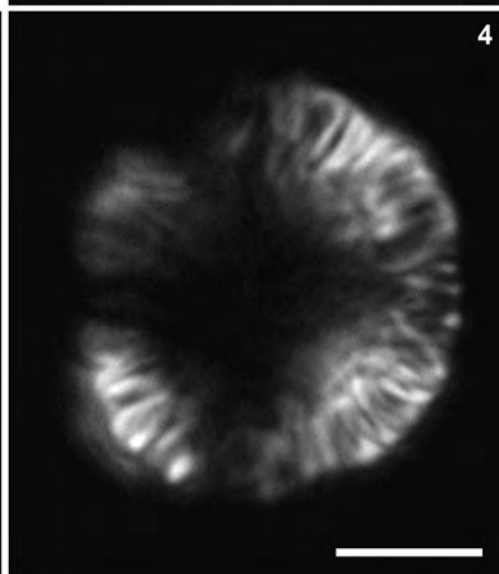
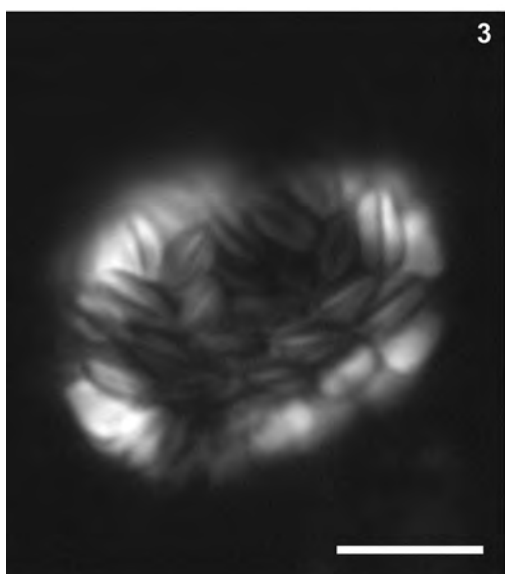
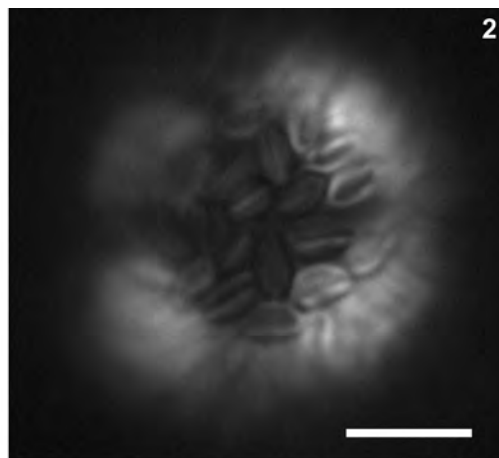
5, 6. *Acanthoica* sp. [HET]

5. Surface waters; South Atlantic, 22°52'S, 24°59'W; AMT16 cruise, May, 2005; XP

6. 67m water-depth; North Atlantic, 36°27'N, 36°55'W; AMT16 cruise, May, 2005; XP

Plate 39

Rhabdosphaeraceae

**1-6. *Algirosphaera robusta* [HET]**

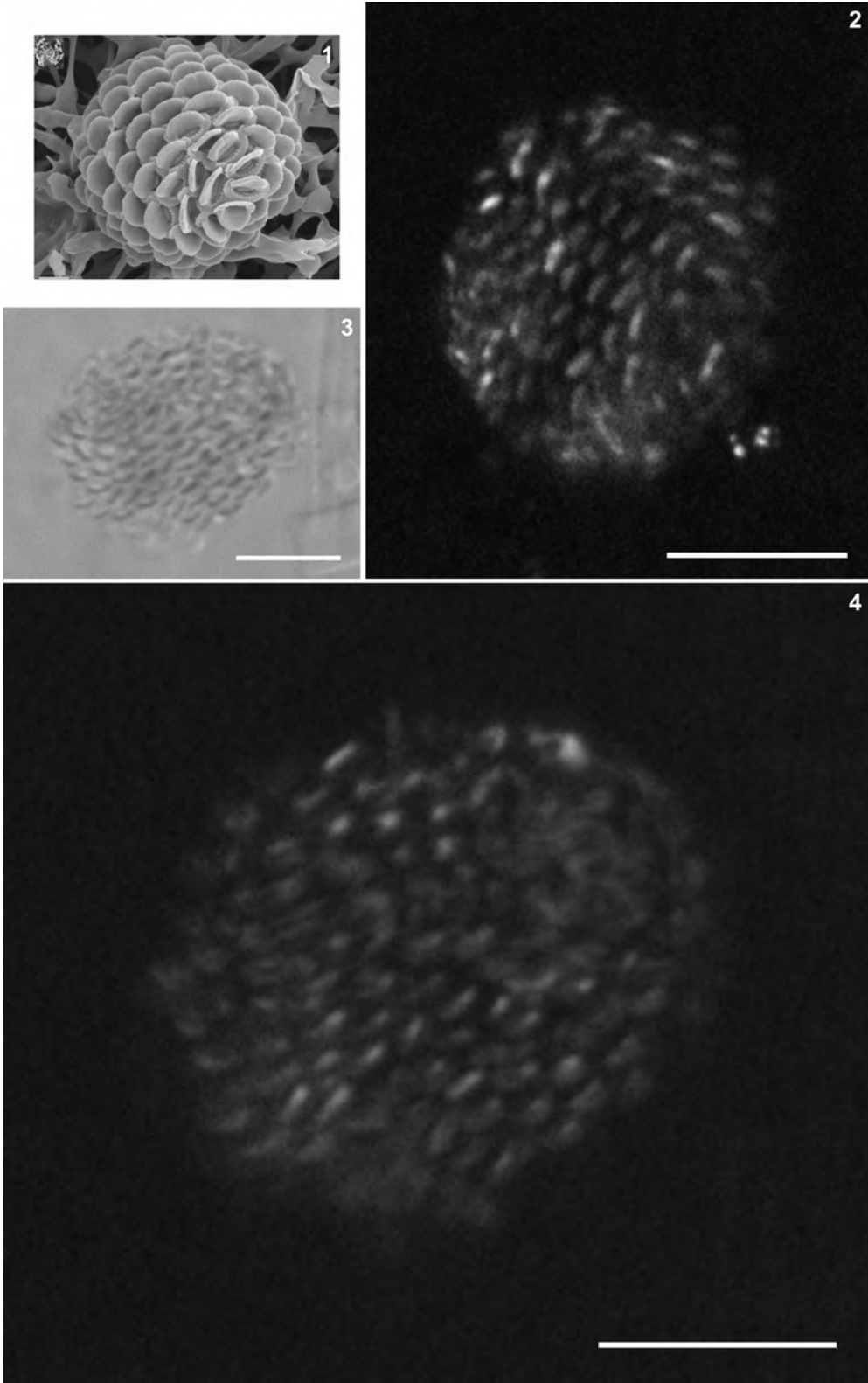
1. Gulf of Mexico; SEM (image from Vita Pariente, Texas A&M University)

2, 4, 5. Surface waters; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP

3, 6. Surface waters; South Atlantic, 01°37'S, 24°59'W; AMT16 cruise, June, 2005; XP

Plate 40

Incertae sedis

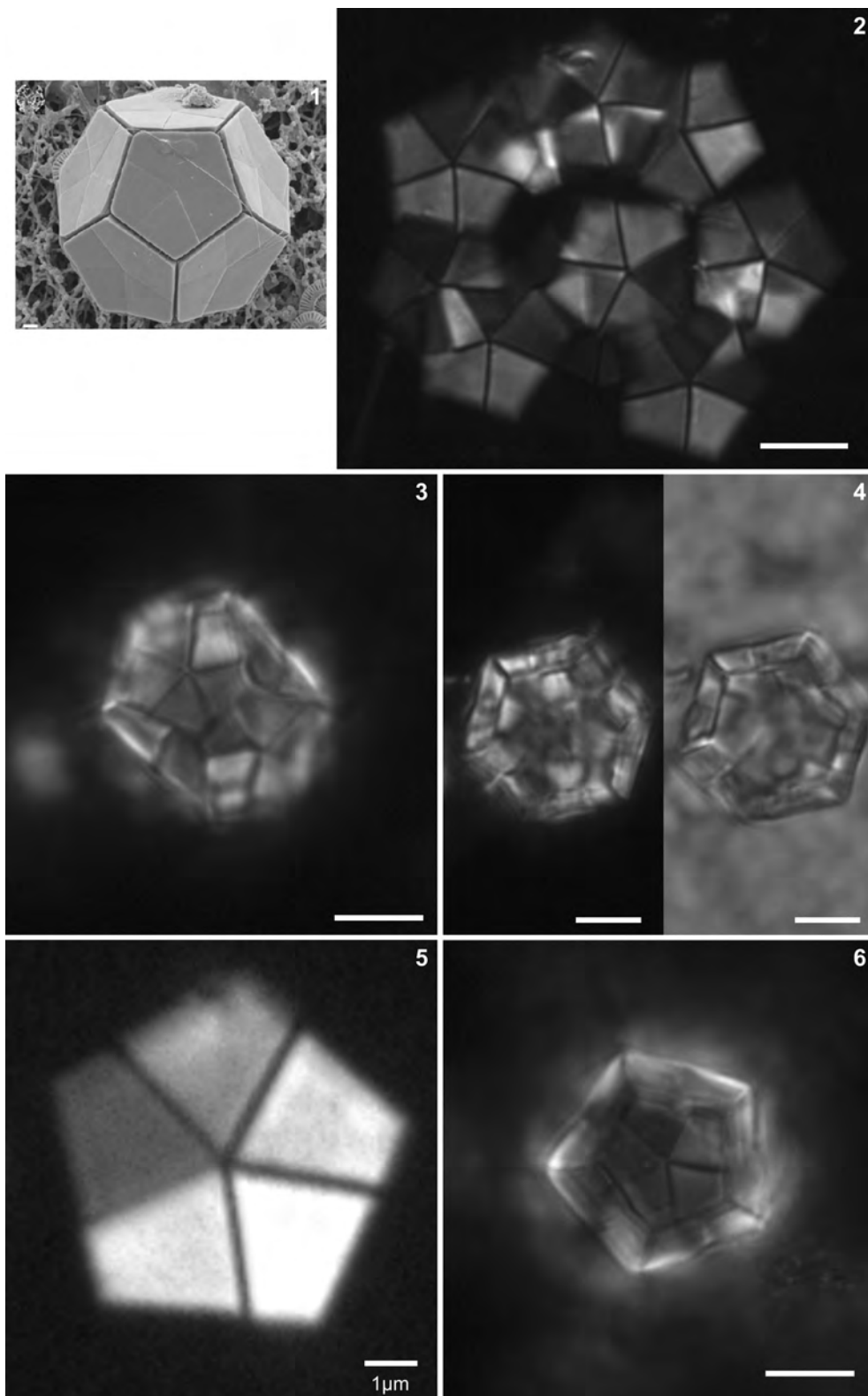


1. *Alisphaera ordinata*
 5m water-depth; off Namibia, South Atlantic, 20°52'S, 06°15'E; SEM (image NHM 136-09)

2-4. *Alisphaera* sp. [HET]
 30m water-depth; Faial, Azores, 30°32'N, 28°33'W; May, 2008; XP (2, 4), DIC (3)

Plate 41

Incertae sedis

**1-6. *Braarudosphaera bigelowii***

1. Surface waters; NE Atlantic, 41°53'N, 09°56'W; SEM (image NHM 209-28)

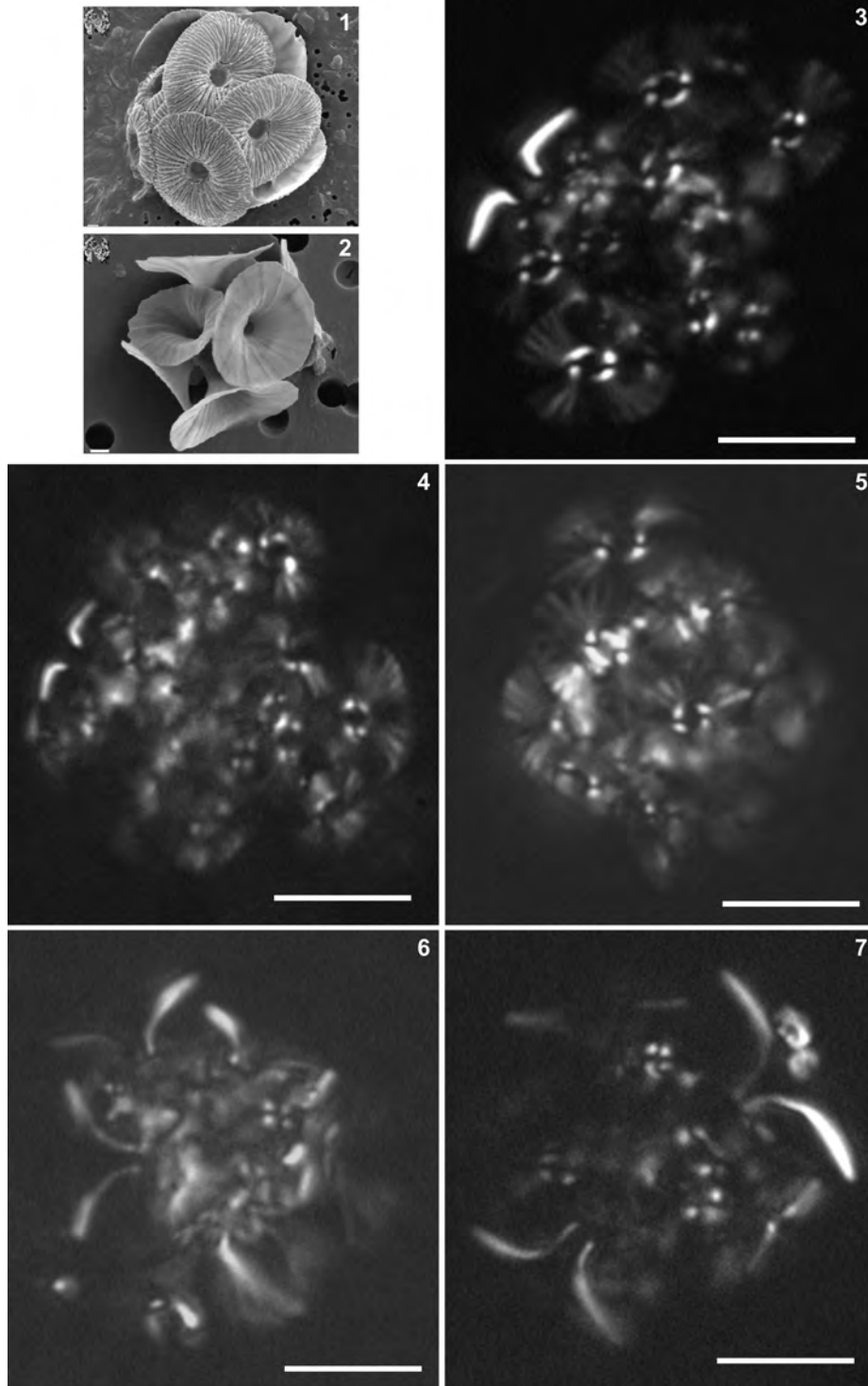
2. Collapsed coccosphere; Faial, Azores, 30°32'N, 28°33'W; June, 2008; XP

3, 4, 6. Surface waters; Faial, Azores, 30°32'N, 28°33'W; July, 2008; XP (3, 4 left, 6), DIC (4 right)

5. Detached nannolith; Faial, Azores, 30°32'N, 28°33'W; July, 2008; XP

Plate 42

Incertae sedis

**1. *Umbellosphaera tenuis* type IV**

5m water-depth; Alboran Sea, western Mediterranean, 37°25'N, 00°25'W; SEM (image NHM 140-11)

2, 6, 7. *U. irregularis* [HET]

2. 50m water-depth; HOTS station, Hawaii, North Pacific; 22°45'N, 158°E; SEM (image NHM 217-12)

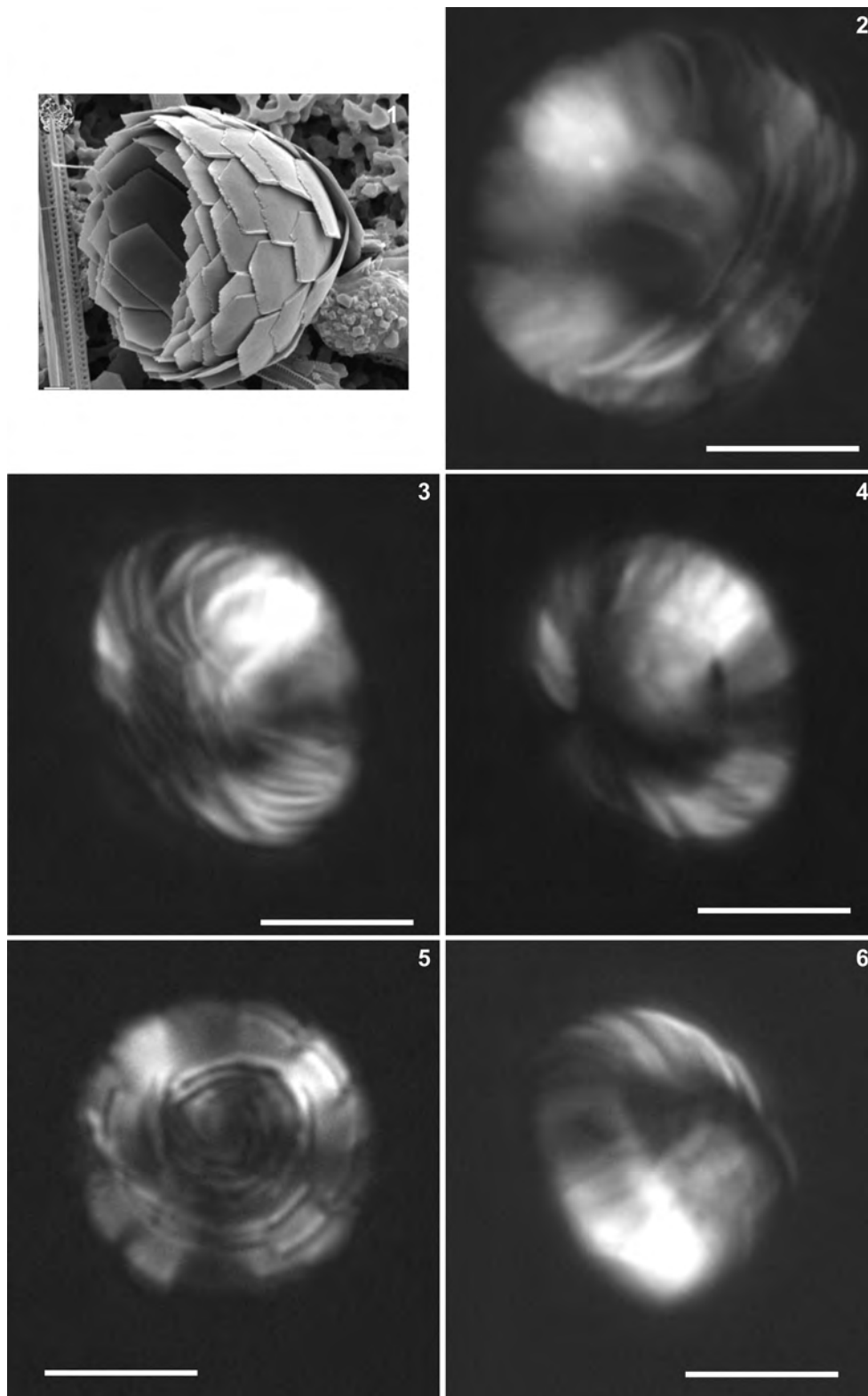
6, 7. Surface waters; South Atlantic, 22°27'S, 24°59'W (6), 20°11'S, 24°59'W (7); AMT16 cruise, June, 2005; XP

3-5. *U. tenuis* [HET]

39m water-depth; North Atlantic, 35°05'N, 41°51'W; AMT16 cruise, June, 2005; XP

Plate 43

Incertae sedis

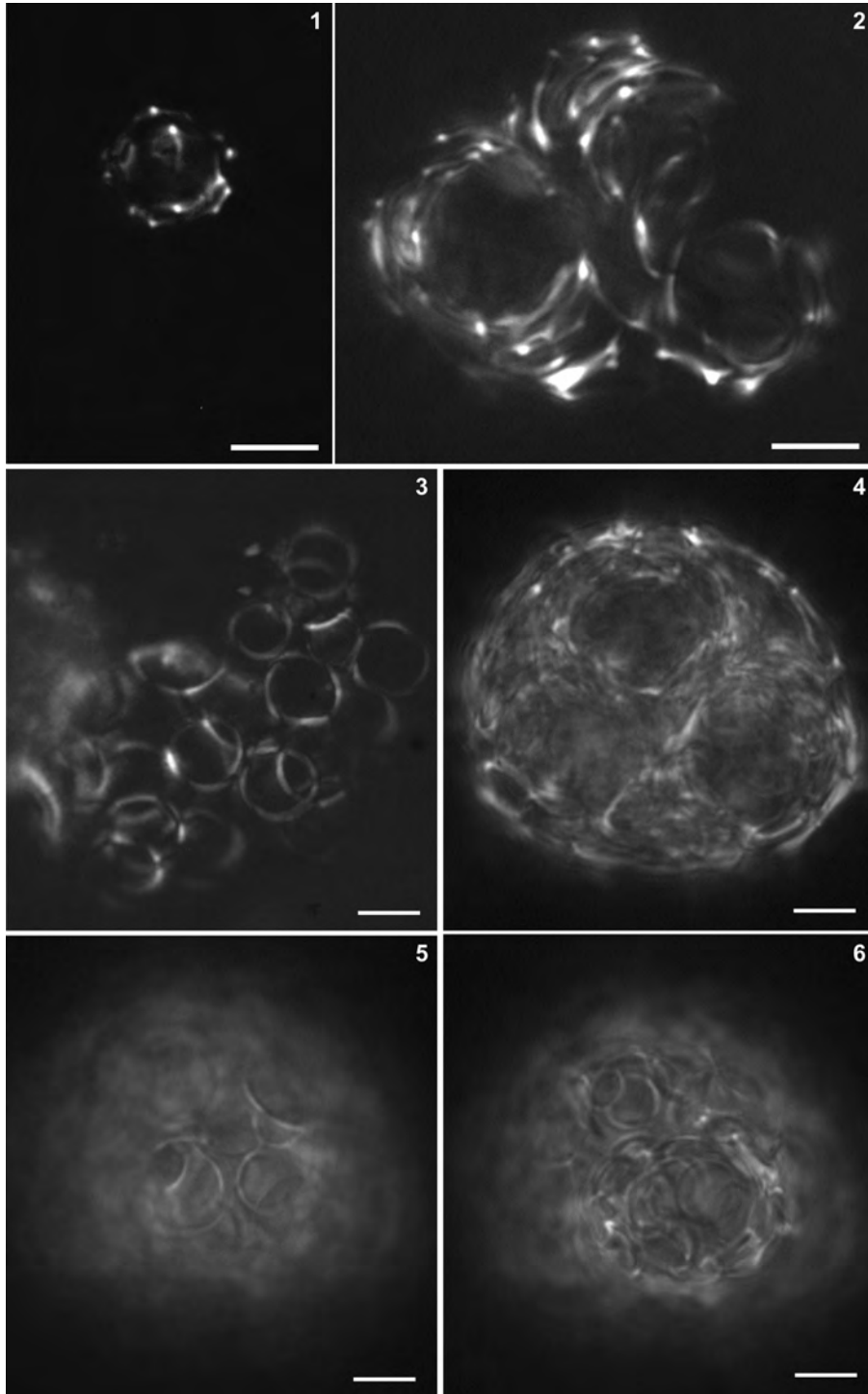


1-6. *Florisphaera profunda*

1. 175m water-depth; Gulf of Mexico, 26°19'N, 59°38'W; SEM (image NHM 132-08)
2. 50m water-depth; South Atlantic, 31°58'S, 16°58'E; AMT16 cruise, June, 2005; XP
- 3, 4. Surface waters, night; South Atlantic, 20°11'S, 24°59'W; AMT16 cruise, June, 2005; XP
- 5, 6. Surface waters, night; South Atlantic, 22°52'S, 24°59'W; AMT16 cruise, June, 2005; XP

Plate 44

Incertae sedis

**1. *Ceratolithus cristatus* [HET]**

50m water-depth; South Atlantic, 31°04'S, 16°28'E; AMT16 cruise, May, 2005; XP

2. *C. cristatus nishidae* type [HET]

50m water-depth; South Atlantic, 31°04'S, 16°28'E; AMT16 cruise, May, 2005; XP

3-6. *C. cristatus coccolithomorpha* type [HET]

3. Collapsed coccosphere?; 10m water-depth; South Atlantic, 31°58'S, 16°58'E; AMT16 cruise, May, 2005; XP

4-6. Same coccosphere viewed in different focal planes; 50m water-depth; South Atlantic, 31°04'S, 16°28'E; AMT16 cruise, May, 2005; XP

Plate 45

1. *Ceratolithus cristatus cristatus* type [CER] (according to Young *et al.*, 2003, it is likely that the ceratolithid stage - CER - is equivalent to the holococcolith stage in other taxa, and is probably thus haploid)

Detached nannolith, proximal view; 10m water-depth; Gulf of Mexico, 50°N, 04°01'W; SEM (image NHM 132-3)

2, 5-9. *C. cristatus* [CER]

2. Detached nannolith, distal view; surface waters; Ibo Port, Miyake Island, Japan, 34°06'N, 139°30'E; SEM (image NHM 129-07)

5. Note presence of two horse-shoe-shaped nannoliths (arrow A) positioned more or less parallel to each other, but on opposite sides, inside a common membrane-like structure (arrow B); 10m water-depth; South Atlantic, 31°49'S, 10°30'E; AMT16 cruise, June, 2005; XP

6. 50m water-depth; South Atlantic, 31°04'S, 16°28'E; AMT16 cruise, May, 2005; XP

7, 8. Surface waters; South Atlantic, 31°34'S, 09°19'E; AMT16 cruise, May, 2005; XP

9. 50m water-depth; South Atlantic, 31°58'S, 16°58'E; AMT16 cruise, June, 2005; XP

3. *C. cristatus coccolithomorpha* type [HET] (= *Neosphaera coccolithomorpha* Lecal-Schlauder, 1950)

60m water-depth; Gulf of Mexico, 27°36'N, 95°E; SEM (image NHM CSF0146)

4. *C. cristatus nishidae* type [HET] (= *Neosphaera coccolithomorpha* var. *nishidae* Kleijne, 1993)

50m water-depth; Canary Islands, North Atlantic, 29°41'N, 17°53'W; SEM (image NHM P233B315)

Plate 45

Incertae sedis

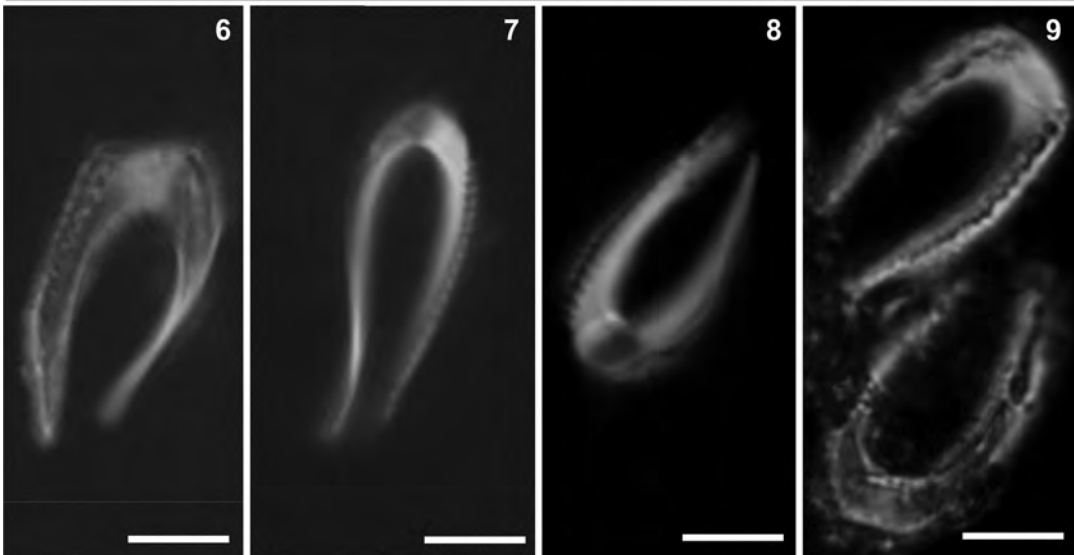
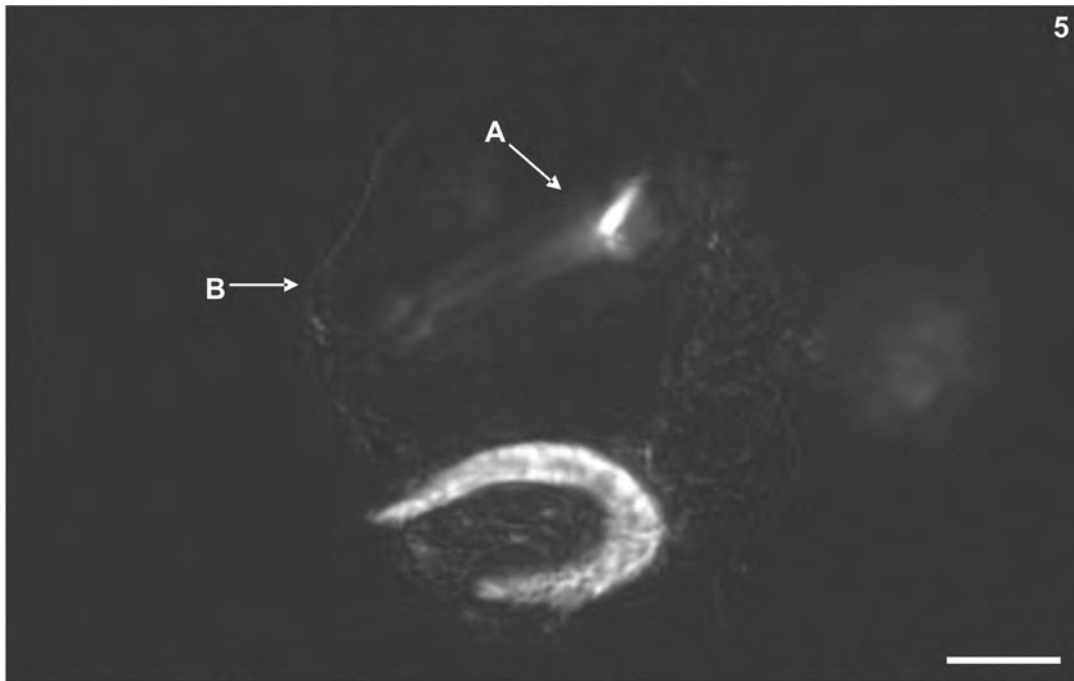
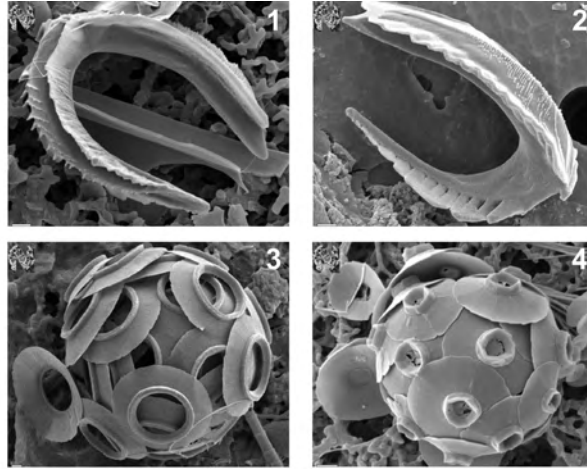
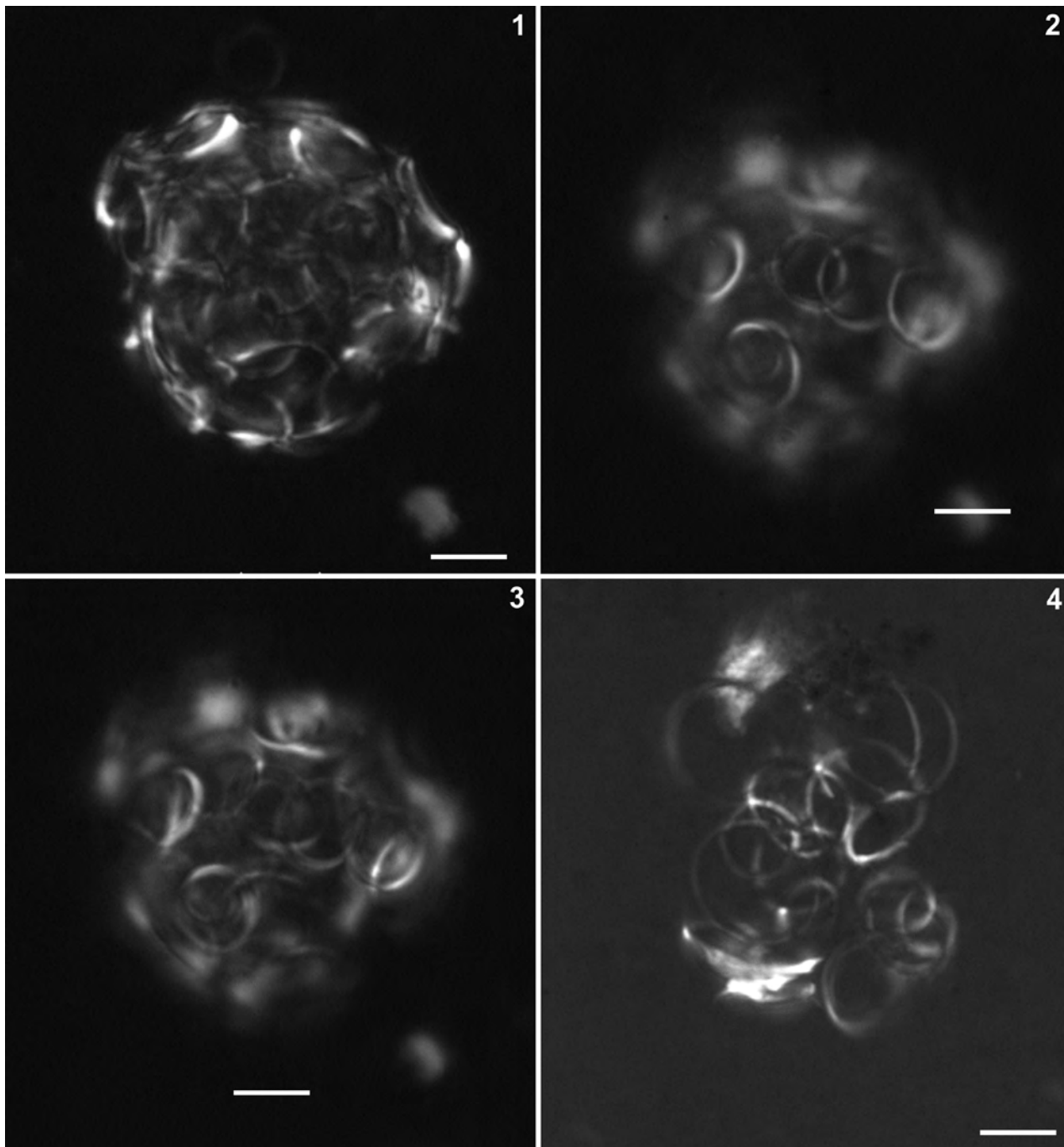


Plate 46
Incertae sedis

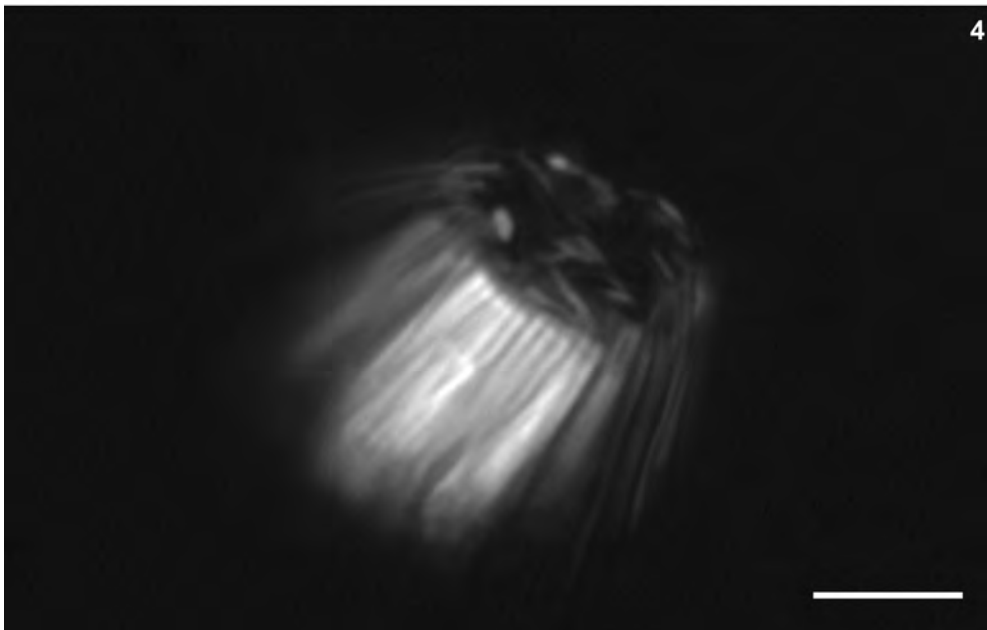
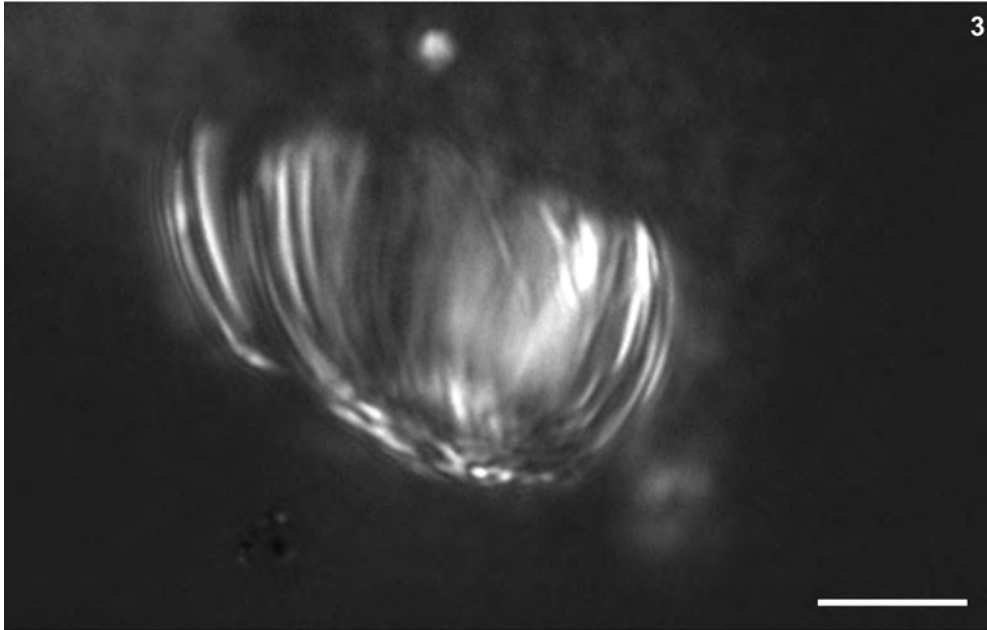
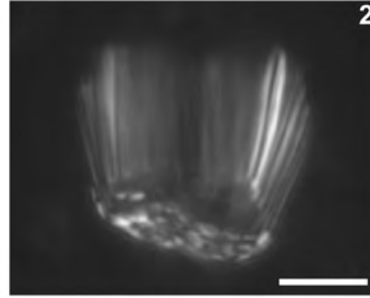
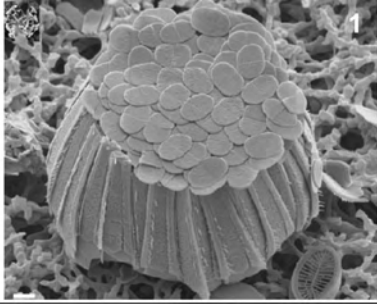


1-4. *Ceratolithus cristatus coccolithomorpha* type [HET]

1-3. 50m water-depth; South Atlantic, 31°04'S, 16°28'E; AMT16 cruise, May, 2005; XP (2, 3 taken in different focal planes)
4. 105m water-depth; South Atlantic, 25°96'S, 21°56'W; AMT16 cruise, May 2005; XP

Plate 47

Incertae sedis

**1-4. *Gladiolithus flabellatus***

1. 180m water-depth; HOTS station, Hawaii, North Pacific, 22°45'N, 158°E; SEM (image NHM 219-25a)
2. 125m water-depth; Mediterranean Sea, Villefranche sur Mer; XP (Plankton*Net, ©Jeremy Young, NHM)
3. 96m water-depth; South Atlantic, 31°49'S, 10°30'E; AMT16 cruise, June, 2005; XP
4. 50m water-depth; South Atlantic, 31°58'S, 16°58'E; AMT16 cruise, June, 2005; XP