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# Possible affinities between the holococcolithophores *Syracosphaera pulchra* HOL *oblonga*-type and *Calyptrolithophora papillifera*

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**Abstract** Several coccospheres, composed of typical *Syracosphaera pulchra* HOL *oblonga*-type body and apical coccoliths and a varying number of flat-topped coccoliths that resemble *Calyptrolithophora papillifera*, have been observed in samples from the Aegean Sea. The observed coccospheres indicate that the morphology of these two holococcolithophores may be less distinct than has been previously assumed.

**Keywords** Living coccolithophores, life-cycle, holococcoliths

## 1. Introduction

Coccolithophores, the most productive calcifying organisms on Earth, have been shown, from a number of culture studies, to have life-cycles typically involving alternation between a haploid holococcolith-producing phase and a diploid heterococcolith-producing phase (*e.g.* Parke & Adams, 1960; Houdan *et al.*, 2004). A significant number of field studies have revealed the existence of spectacular combination coccospheres that represent the moment of life-cycle transition (Kamptner, 1941; Lecal-Schlauder, 1961; Kleijne, 1991; Thomsen, 1991; Alcober & Jordan, 1997; Young *et al.*, 1998; Cros *et al.*, 2000; Cortes, 2000; Cortes & Bollmann, 2002; Geisen *et al.*, 2002; Cros & Fortuño, 2002; Triantaphyllou & Dimiza, 2003; Triantaphyllou *et al.*, 2004, 2009; Geisen *et al.*, 2004; Malinverno *et al.*, 2008a; Frada *et al.*, 2009). In many cases, a single holococcolith type is associated with a single heterococcolith type. In several other cases, however, one heterococcolith is associated with two or more holococcolith types. These more complex associations have been inferred to indicate either intraspecific varation in holococcolith morphology (*e.g. Helicosphaera carteri*) or sets of sibling species, in which the discrete species can only be distinguished in the holococcolith stage (*e.g. Syracosphaera pulchra*: Cros *et al.*, 2000; Geisen *et al.*, 2002; Saugestad & Heimdal, 2002; Malinverno *et al.*, 2008a; Dimiza *et al.*, 2008; Triantaphyllou *et al.*, 2009).

The main objective of the present study is to further our understanding of coccolithophore life-cycles by describing an unusual holococcolith morphotype that seems to have characteristics in common with both *Calyptrolithophora papillifera* and *Syracosphaera pulchra* HOL *oblonga*-type (the former *Calyptrosphaera oblonga*).

## 2. Material and methods

In total, 13 water samples were analysed during the present study. Five samples were collected on April 18th, 2006 from three stations in the Evoikos Gulf (western continental shelf of the Aegean Sea), using a single oceanographic Hydro-bios bottle. In addition, eight samples were collected on February 2nd, 2007 from one station in the Skyros Basin (northern Aegean Sea) during the *Meteor* M71-3 cruise (Emeis, 2007). The locations of the samples, water-depth, temperature and salinity data are presented in Figure 1 and Table 1.

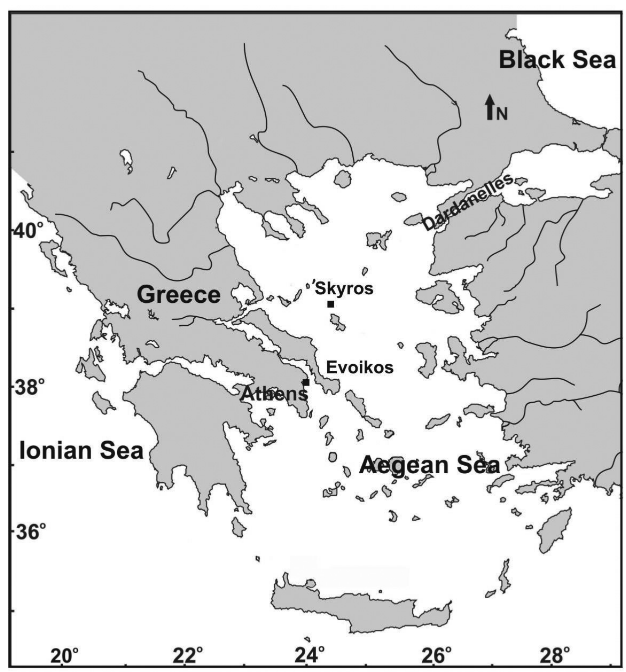



**Figure 1**: Location of the sampled stations in the Aegean Sea. Water samples Ev-2, Ev-3, Ev-4 from Evoikos Gulf, Sk-1 from northern Skyros Basin

For each sampling depth, 2l of sea-water was filtered through a Whatman cellulose nitrate filter (47mm diameter, 0.45$\mu$m pore-size), using a vacuum filtration system. Salt was removed by washing the filters with about 2ml of mineral water. The filters were oven dried and stored in plastic Petri dishes. A piece of each filter, approximately 8 x

8mm², was attached to a copper electron microscope stub using double-sided adhesive tape, and coated with gold. The filters were examined in a Jeol JSM 6360 Scanning Electron Microscope (SEM) and all the individual coccolithophore specimens occurring on the examined filter piece were identified and counted. A working magnification of x1200 was used throughout the counting.

| Station | Date | Latitude | Longitude | Water depth (m) | Temperature (°C) | Salinity (psu) |
|---|---|---|---|---|---|---|
| Ev- 2 | 18/4/06 | 38°09.32'N | 24°03.00'E | 5 | 15.40 | 37.00 |
| Ev- 3 | | 38°06.28'N | 24°00.70'E | 5 | 14.80 | 37.00 |
| | | | | 15 | 14.70 | 37.00 |
| Ev- 4 | | 38°07.08'N | 24°02.49'E | 5 | 15.30 | 37.00 |
| | | | | 15 | 14.90 | 37.10 |
| | | | | 30 | 14.70 | 37.10 |
| Sk-1 | 2/2/07 | 39°33.36'N | 23°48.00'E | 5 | 13.65 | 38.12 |
| | | | | 20 | 13.66 | 38.12 |
| | | | | 43 | 14.84 | 38.66 |
| | | | | 50 | 15.00 | 38.75 |
| | | | | 80 | 14.93 | 38.91 |
| | | | | 100 | 14.67 | 38.89 |
| | | | | 200 | 14.09 | 38.89 |

**Table 1**: Locations of the studied samples and environmental parameters

Coccolithophore cell density (number of cells/l) was calculated following the methodology of Jordan & Winter (2000), by scaling up the raw counts from a known scanned area, using the equation,

$$A = N \, x \, S/V$$

where $N$ is the number of cells of a species on the whole piece of filter, $S$ the scaling factor (area of the whole filter/area of scanned filter piece), $V$ the volume of the seawater filtered (in l), and $A$ the absolute abundance of the species in cells/l. All the filter samples and the SEM micrographs are kept in the collections of the Museum of Palaeontology & Geology at the University of Athens.

## 3. Results

The observed spring coccolithophore assemblages from Evoikos Gulf comprise 14 heterococcolithophore and nine holococcolithophore species (Table 2). The total cell density varied between 6.4x10$^3$ and 11.7x10$^3$ cells/l. The highest species richness (13 taxa) was observed at Stations Evoikos-2 at 5m and Evoikos-4 at 30m, and the lowest (eight taxa) at Station Evoikos-4 at 5m. *Emiliania huxleyi* was the major heterococcolithophore component of the communities (up to 5.2x10$^3$ cells/l), followed by *Syracosphaera pulchra* (up to 2.8x10$^3$ cells/l) and *Syracosphaera nodosa* (up to 0.8x10$^3$ cells/l). Holococcolithophores showed relatively high absolute abundances (up to 5.7x10$^3$ cells/l), being represented mostly by *S. pulchra* HOL *oblonga*-type (up to 4.2x10$^3$ cells/l) and *Calyptrolithina wettsteinii* (up to 1.2x10$^3$ cells/l).

In the winter coccolithophore assemblages from the northern Skyros Basin, 20 heterococcolithophore and only two holococcolithophore species were present (Table 2). The total cell density ranged from 1.3x10$^3$ to 31.4x10$^3$ cells/l, whereas species richness ranged between two and 11 species. *E. huxleyi* was the dominant species (up to 15.8x10$^3$ cells/l). *Rhabdosphaera clavigera* preferred the upper photic zone (up to 3.1x10$^3$ cells/l), whereas in the lower photic zone, *Algirosphaera robusta* became a significant component of the nannoflora (up to 1.3x10$^3$ cells/l). Holococcolithophores were represented only by *S. pulchra* HOL *oblonga*-type and *C. wettsteinii*. In general, they were present in few samples and occurred in low abundances (<0.5x10$^3$ cells/l).

*Calyptrolithophora papillifera* was found in the spring assemblages of the Evoikos Gulf, only at 5m water-depth. In contrast, *S. pulchra* HOL *oblonga*-type was relatively very abundant throughout the upper 30m of the water-column in the spring assemblages, whereas it was found only at 20m water-depth in the winter assemblages of the northern Skyros Basin.

Thirty-four coccospheres were observed in the Evoikos samples, and an additional one in the Skyros samples, bearing coccoliths which have characteristics somewhat in common with *C. papillifera* and *S. pulchra* HOL *oblonga*-type (Plates 1, 2). In detail, the observed coccospheres feature '*C. oblonga*' body and apical coccoliths and also a varying number of flat-topped coccoliths that look like *C. papillifera*.

## 4. Discussion and conclusions

*Syracosphaera pulchra* HOL *oblonga*-type ('*C. oblonga*') and *Calyptrolithophora papillifera* have body coccoliths of similar shape and size, which show hexagonal-mesh wall-fabrics. They are, however, usually clearly separated by a number of differences. Coccospheres of '*C. oblonga*' have spherical to subspherical shape, with >100 elliptical, cap-shaped calyptroliths, formed by hexagonal crystallites. A proximal ring with three to four rows of crystallites, one crystallite thick, forms a basal flange. The apical coccoliths are similar, with a well developed pyramidal spine extending distally (Young *et al*., 2003; Malinverno *et al*., 2008b).

*C. papillifera* has a dimorphic, spherical to elongated coccosphere made of 100-150 coccoliths. The body coccoliths are elliptical, built of hexagonal crystallites. The tube is eight to nine crystallites high, one crystallite wide, with a single-crystallite-wide basal flange. The distal surface is flat, with a perforated hexagonal mesh and no larger perforations. Apical coccoliths are highly vaulted, with flat sides and a central elevated area and with parallel strings of crystallites (Young *et al.*, 2003; Malinverno *et al.*, 2008b). Comparison between '*C. oblonga*' and *C. papillifera* reveals that ordinary calyptroliths in the former species are slightly higher and possess a convex distal surface, while in the latter they have a flat distal surface. Additionally, the basal ring is present in *C. papillifera*, but more developed in '*C. oblonga*', and the apical coccoliths of '*C. oblonga*' show characteristics well-separated from those of *C. papillifera*.

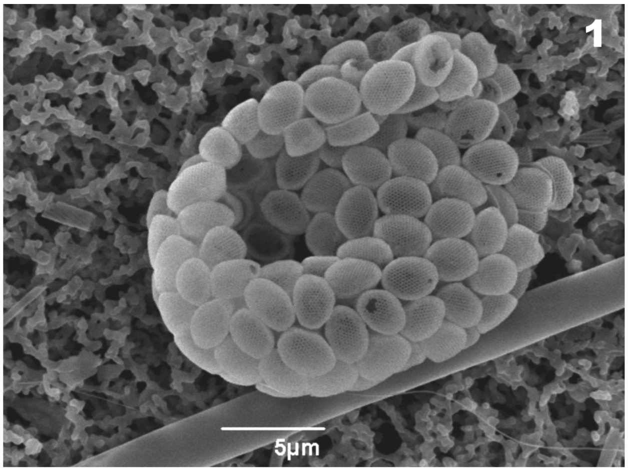
Both holococcolithophore types have been shown to form combination coccospheres with heterococcoliths. In particular, '*C. oblonga*' has been found with *S. pulchra* (Lohmann, 1902; Kamptner, 1941; Cros *et al.*, 2000; Geisen *et al.*, 2002), which also forms combinations with *S. pulchra* HOL *pirus*-type (the former *Daktylethra pirus*: Geisen *et al.*, 2002; Saugestad & Heimdal, 2002). '*D. pirus*' has also been observed forming a combination coccosphere with the heterococcolithophore *Syracosphaera protrudens* (Triantaphyllou *et al.*, 2009). This rather confusing coccolithophore suite has been further added to by observations of a collapsed possible-combination coccosphere of *Syracosphaera histrica* with *C. papillifera* (Cros *et al.*, 2000), and possible combinations between *S. pulchra* HOL *oblonga*-type and *S. pulchra* HOL *pirus*-type, and also of *S. histrica* with *S. pulchra* HOL *oblonga*-type (Malinverno *et al.*, 2008a).

The documented specimens of the present study have coccoliths with mixed characteristics, seemingly intermediate between '*C. oblonga*' and *C. papillifera* (*e.g.* Plates 1, 2), however the numerous flat-topped coccoliths observed in the coccospheres do not really look like *C. papillifera* as, when seen in side view, they have well-developed basal flanges (Pl.2, fig.3), typical of '*C. oblonga*' (Pl.1, fig.1), but not of *C. papillifera* (Pl.1, fig.2), and there is no obvi-

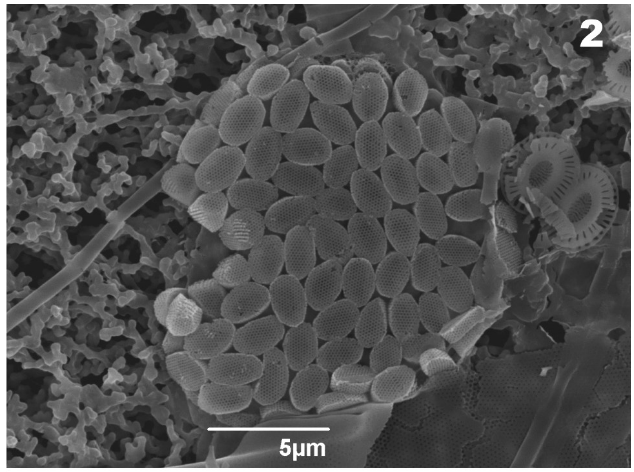
| Stations | Ev-2 5 | Ev-3 5 | Ev-3 15 | Ev-4 5 | Ev-4 15 | Ev-4 30 | Sk-1 5 | Sk-1 20 |
|---|---|---|---|---|---|---|---|---|
| **Number of specimens/sample** | 100 | 98 | 100 | 134 | 121 | 139 | 199 | 110 |
| **Total standing crop (cells/l)** | 6421 | 8095 | 9632 | 8606 | 11752 | 12408 | 12650 | 21389 |
| *Acanthoica acanthifera* | | | | | | | 64 | 193 |
| *A. quattrospina* | 64 | | | | | | | |
| *Algirosphaera robusta* | | | | | | | | |
| *Alisphaera gaudii* | | | | | | | | |
| *Calciosolenia murrayi* | | | | | | | | |
| *Canistrolithus* sp.1 POL | | | | | | 89 | | |
| *Cyrtosphaera lecaliae* | | | | | | | 128 | 193 |
| *Emiliania huxleyi* | 1798 | 3468 | 3179 | 2762 | 5106 | 5178 | 10597 | 15799 |
| *Florisphaera profunda* | | | | | | | | |
| *Gephyrocapsa oceanica* | | | | | | | | |
| *Gladiolithus flabellatus* | | | | | | | | |
| *Ophiaster hydroideus* | 64 | | | | | | | |
| *Rhabdosphaera clavigera* | | | 96 | | | 268 | 1220 | 3083 |
| *Syracosphaera corolla* | 193 | | | | | 89 | 64 | |
| *S. histrica* | | | | | | | 64 | 193 |
| *S. lamina* | | | | | | | | |
| *S. molischii* | | 165 | | | | 89 | 128 | 771 |
| *S. nodosa* | 193 | 661 | 771 | 450 | 482 | 268 | | 193 |
| *S. ossa* | 64 | 83 | 96 | 128 | 96 | | 257 | 385 |
| *S. protrudens* | 64 | | 193 | 128 | 289 | | | |
| *S. pulchra* | 385 | 2808 | 289 | 2184 | 2216 | 625 | 64 | |
| *Syracosphaera* sp. type L | | | | | | 89 | | |
| *Syracosphaera* sp. | | | | | | | | |
| *Umbellosphaera tenuis* | | 83 | 96 | | 96 | | | 193 |
| *Calcidiscus quadriperforatus* HOL | | | | | 96 | | | |
| *Calyptrolithophora papillifera* | 128 | 578 | | | | | | |
| *C. wettsteinii* | 1028 | 83 | 1156 | 642 | 674 | 803 | 64 | 193 |
| *Helicosphaera carteri* HOL | 128 | 83 | 96 | 64 | 289 | | | |
| *Homozygosphaera arethusae* | 64 | | | | | | | |
| *H. vercellii* | | | | | | 446 | | |
| *Syracosphaera anthos* HOL | | | | | | 179 | | |
| *S. pulchra* HOL *oblonga* type | 2248 | 83 | 3564 | 2248 | 2312 | 4196 | | 193 |
| *S. pulchra* HOL *pirus* type | | | 96 | | | 89 | | |
| *Zygosphaera hellenica* | | | | | 96 | | | |

**Table 2**: Species cell densities (cells/l) in the studied samples

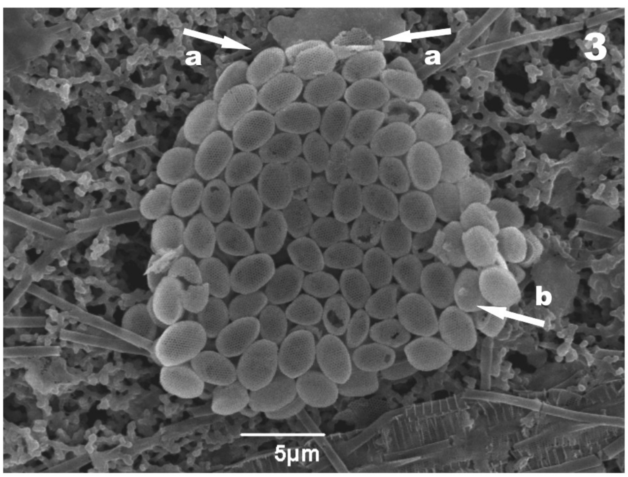
# Plate 1

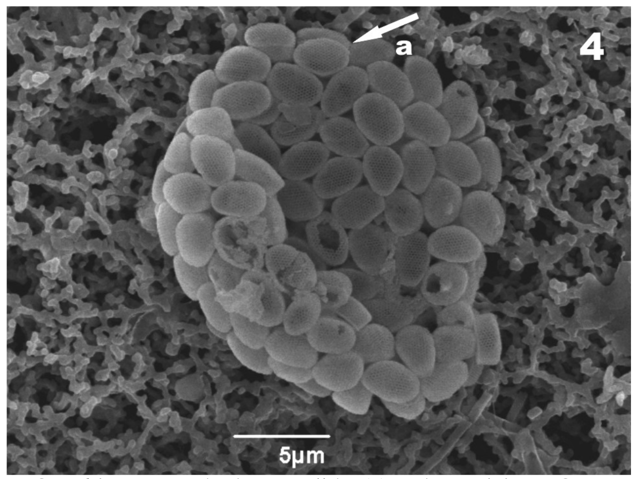



Coccosphere of *S. pulchra* HOL *oblonga*-type
Ev-2, 5m

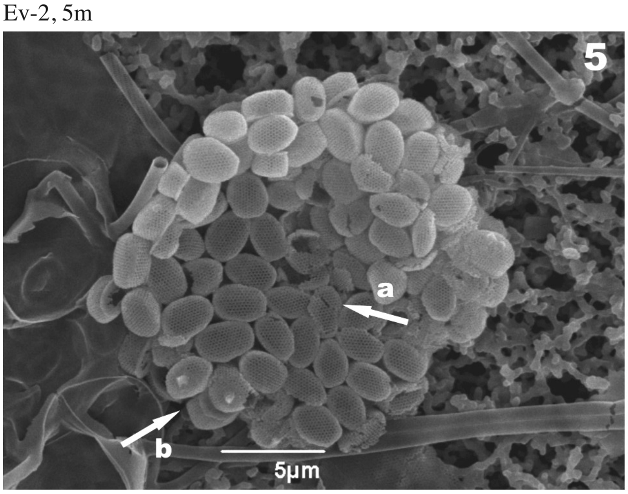


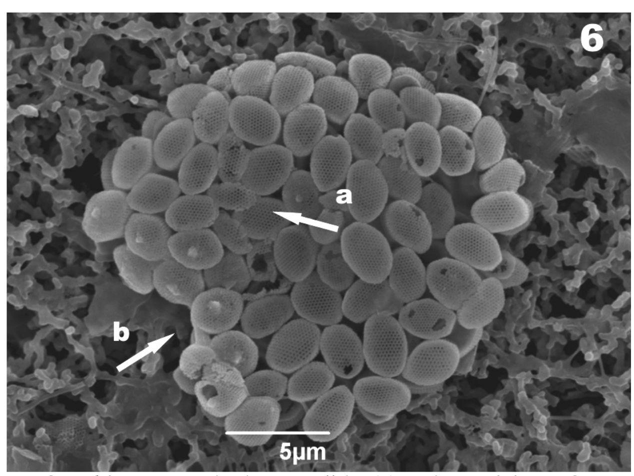

Coccosphere of *C. papillifera*
Ev-2, 5m



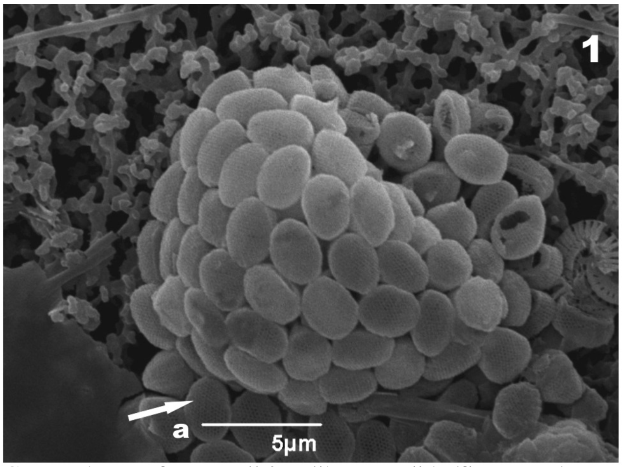

Coccosphere of *C. papillifera*-like coccoliths/flat-topped *S. pulchra* HOL *oblonga*-type body coccoliths (a) and *S. pulchra* HOL *oblonga*-type body and apical coccoliths (b)
Ev-2, 5m

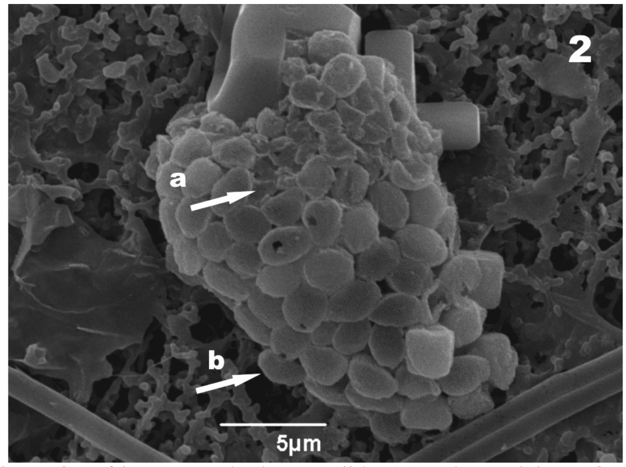


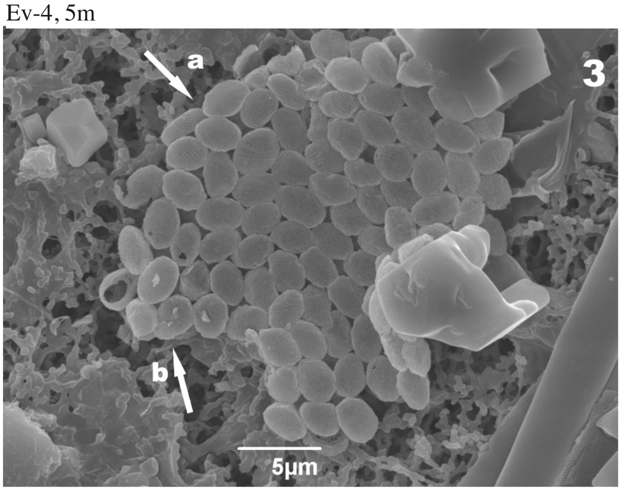

Coccospheres of *C. papillifera*-like coccoliths/flat-topped *S. pulchra* HOL *oblonga*-type body coccoliths (a) and *S. pulchra* HOL *oblonga*-type body and apical coccoliths (b)
Ev-2, 5m

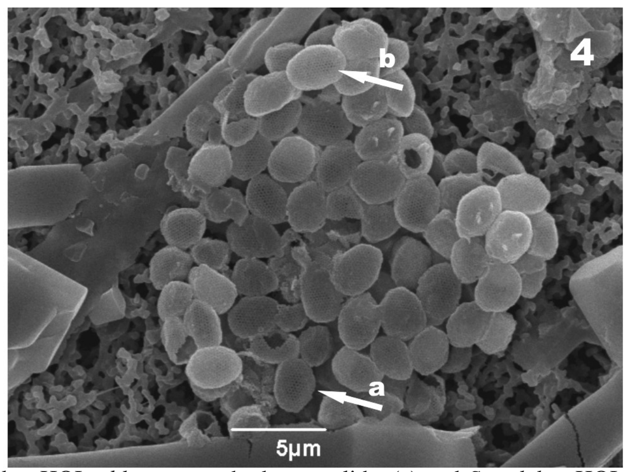
# Plate 2



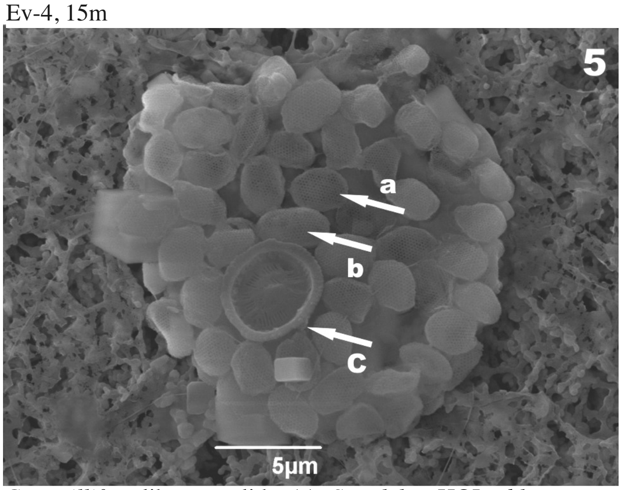



Coccospheres of *C. papillifera*-like coccoliths/flat-topped *S. pulchra* HOL *oblonga*-type body coccoliths (a) and *S. pulchra* HOL *oblonga*-type body and apical coccoliths (b)
Ev-4, 5m

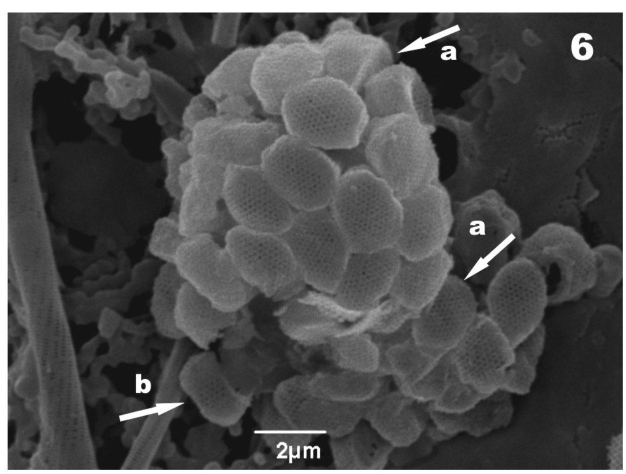





Coccospheres of *C. papillifera*-like coccoliths/flat-topped *S. pulchra* HOL *oblonga*-type body coccoliths (a) and *S. pulchra* HOL *oblonga*-type body and apical coccoliths (b)
Ev-4, 15m




*C. papillifera*-like coccoliths (a), *S. pulchra* HOL *oblonga*-type body coccoliths (b) and *S. pulchra* HET (c)
Sk-1, 20m




*C. papillifera*-like coccoliths (a), *S. pulchra* HOL *oblonga*-type body coccoliths (b)
Ev-4, 5m

ous sign of *papillifera*-type apical coccoliths (Pl.2, fig.6). However, there are examples where a difference can be seen between '*C. oblonga*' body and apical coccoliths and very thin, almost transparent (Pl.2, fig.2), flat coccoliths that resemble *C. papillifera*. An interesting example is presented in Plate 2, fig.5, where a coccosphere with *C. papillifera*-like coccoliths and *S. pulchra* HOL *oblonga*- type coccoliths includes one body coccolith of *S. pulchra* HET.

It is possible that the observed *C. papillifera*-like/flat-topped '*C. oblonga*' body coccoliths may be malformed or damaged specimens, or may even represent a variant of '*C. oblonga*' with slightly atypical morphology. However, although not being true combination coccospheres, the documented specimens may suggest a link between '*C. oblonga*' and *C. papillifera* that supports previous observations documenting combination coccospheres of both '*C. oblonga*' and *C. papillifera* with the same heterococcolithophore species, *S. histrica* (Cros *et al*., 2000; Malinverno *et al*., 2008a). The suggested affinities between '*C. oblonga*' and *C. papillifera*, in combination with the relationship proposed between '*C. oblonga*' and '*D. pirus*' (Malinverno *et al*., 2008a), adds to the implications concerning the *Syracosphaera pulchra-S. histrica-S. protrudens* plexus being associated with three holococcolithore types ('*D. pirus*', '*C. oblonga*' and *C. papillifera*), as these were tentatively incorporated into a possible evolutionary scheme (Malinverno *et al*., 2008a).

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