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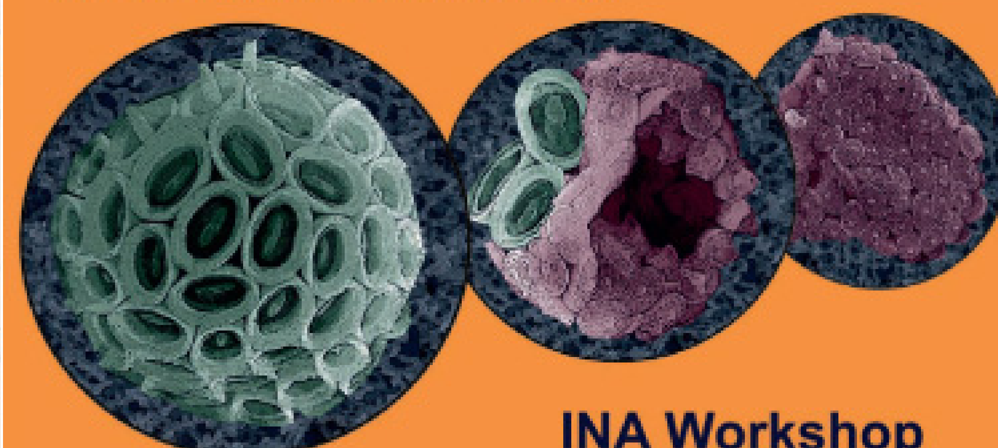

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Adding proofs to *Syracosphaera histrica-Calyptrolithophora papillifera* life-cycle association

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Abstract: Two specimens of the coccolithophore *Calyptrolithophora papillifera* associated with single exothecal and endothecal coccoliths of *Syracosphaera histrica*, collected from the North Aegean Sea (NE Mediterranean), have been verified by Scanning Electron Microscopy. The two specimens strengthen previous reported hints that *Syracosphaera histrica* and *Calyptrolithophora papillifera* represent a life-cycle association, documenting accordingly the relationships between the different phases within the genus *Syracosphaera*.

Keywords: living coccolithophores, combination coccosphere

1. Introduction

Combination coccospheres containing both hetero- and holococcoliths have been recorded from field-samples, most possibly documenting the moment of transition between the two life cycle phases (e.g., Kamptner, 1941; Lecal-Schlauder, 1961; Kleijne, 1991; Thomsen *et al*., 1991; Samtleben & Schröder, 1992; Samtleben in Winter & Siesser, 1994; Alcober & Jordan, 1997; Young *et al*., 1998; Cros *et al*., 2000; Cortés, 2000; Cortés & Bollmann, 2002; Geisen *et al*., 2002; Cros & Fortuño, 2002; Malinverno *et al*., 2008a, b; Triantaphyllou & Dimiza, 2003; Triantaphyllou *et al*., 2004, 2009; Triantaphyllou, 2010). More complex combinations have also been reported, suggesting relationships of one hetero- with two or three holococcolith types (e.g., Cros *et al*., 2000; Geisen *et al*., 2004; Malinverno *et al*., 2008a, b; Triantaphyllou *et al*., 2009). Several mechanisms including complex life-cycles, and cryptic speciation visible only in the holococcolith phase, have been proposed in order to explain these multiple combinations (e.g., Cros *et al*., 2000; Geisen *et al*., 2002).

In this paper, we present two new specimens adding proofs to the hetero-holococcolithophore combination between *Syracosphaera histrica* and *Calyptrolithophora papillifera*. This documentation supports the previously proposed (Malinverno *et al*., 2008b; Triantaphyllou, 2010) evolutionary scheme for the *Syracosphaera pulchra*-*Syracosphaera histrica*-*Syracosphaera protrudens* plexus concerning the independent evolution of the multiple involved HET and HOL phases.

2. Materials and methods

The *Syracosphaera histrica* - *Calyptrolithophora papillifera* potential combination coccospheres evidenced in this study come from water samples collected with a rosette system deployment from the north Aegean Sea (sample M1-100m depth January 2011, sample 2AMT7-2m depth March 2014; for location see Dimiza *et al*., this volume, AMT7=M4), during R/V Aegaeo cruises (Medecos and AegeanMartech projects) respectively. For each sampling depth, 2 liters of seawater were filtered on Whatman cellulose nitrate filters (47 mm diameter, 0.45 mm pore size), using a vacuum filtration system. Salt was removed by washing the filters with about 2 ml of mineral water. The filters were open dried and stored in plastic Petri dishes. A piece of each filter approximately 8x8 mm^2 was attached to a copper electron microscope stub using a double-sided adhesive tape and coated with gold. The filter was then examined with a Jeol JSM 6360 Scanning Electron Microscope (University of Athens, Department of Historical Geology and Palaeontology) and is kept in the collections of the Museum of Paleontology and Geology in the University of Athens. Coccolithophore densities (coccospheres/l) were calculated following the methodology of Jordan and Winter (2000).

3. Results

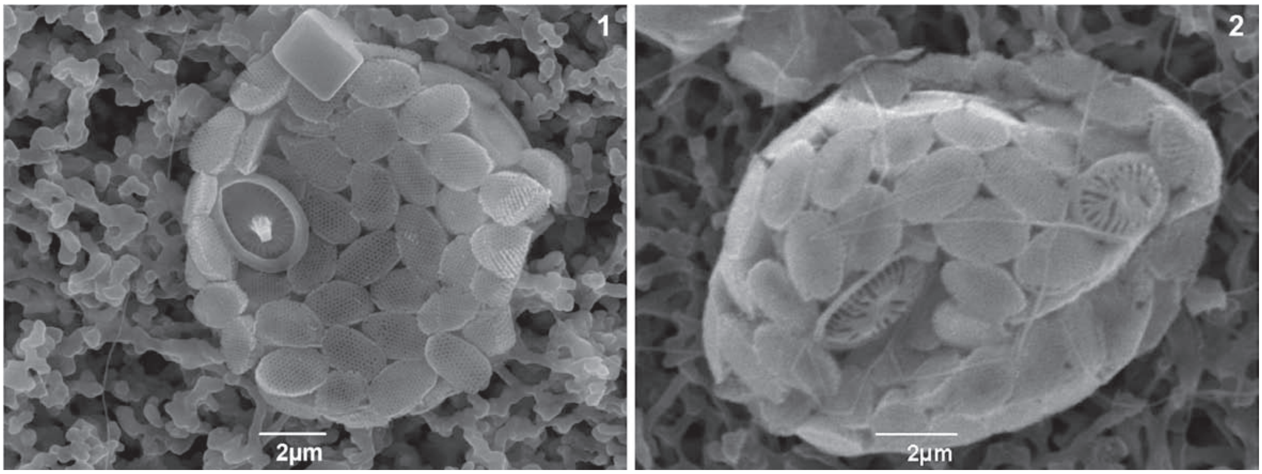
Total coccospheres at sample M1-100m reached 12.6 x 10^3 cells/l, whereas absolute cell densities in sample 2AMT7-2m have been calculated as 28.3 x 10^3 cells/l. The coccolithophore communities in both samples were dominated by *Emiliania huxleyi,* with abundances of 90% (M1-100m) and 70% (2AMT7-2m). *Calyptrolithophora papillifera* was a minor component in both samples (<0.5%), whereas *Syracosphaera histrica* was practically absent in M1-100m and reached 2.5% in sample 2AMT7-2m.

Two likely combination coccospheres were found, one in each of the studied samples (Pl. 1, figs 1–2), consisting of numerous body and circum-flagellar coccoliths of *C. papillifera* (holococcoliths). Both coccospheres show signs of *S. histrica*; one has a body coccolith with a well-developed spine (Pl. 1, fig. 1), the other has two exothecal coccoliths with rib-like slits in the central part (Pl.1, fig. 2).

4. Discussion

Cros *et al*. (2000) showed an SEM image of a possible combination coccosphere of *S. histrica* and *C. papillifera* (their Plate VIII Fig. 2). This was a collapsed coccosphere of *C. papillifera* surrounded by body, circum-flagellar and exothecal coccoliths of *S. histrica*. Later, Malinverno *et al*. (2008b) published a possible combination coccosphere of *S. histrica* and "*Calyptrosphaera oblonga*", discussing in detail the problem of complex evolution or complex (multiple) life-cycles in *Syracosphaera* that might accordingly be raised. Indeed, "*C. oblonga*" is established as one of the holococcolithophore phases of *Syracosphaera pulchra* life-cycle (i.e. *S. pulchra* HOL *oblonga* type;

Plate 1



Well developed coccospheres consisting of numerous body and circum-flagellar coccoliths of *Calyptrolithophora papillifera* (holococcoliths); both coccospheres show signs of *Syracosphaera histrica* **fig. 1.** *C. papillifera* coccosphere with one *S. histrica* body coccolith with well-developed spine (sample M1-100m), **fig. 2.** *C. papillifera* coccosphere with two *S. histrica* exothecal coccoliths with rib-like slits in the central part (sample 2AMT7-2m).

Young *et al*., 2003). The other is "*Daktylethra pirus*" that has also been repeatedly found in association with *S. pulchra* (Lecal-Schlauder, 1961; Saugestad, 1967; Saugestad & Heimdal, 2002; Geisen *et al*., 2002 in SEM), and so has transferred to this species as *S. pulchra* HOL *pirus* type (Geisen *et al*., 2002; Young *et al*., 2003). Based on the morphological affinities between *S. pulchra* and *S. histrica*, Young *et al*. (2003) and Geisen *et al*. (2004) have already considered them to be genetically close. Interestingly, Malinverno *et al*. (2008b) have provided some relatively poor evidence (only LM photograph) of possible "*C. oblonga*"- "*D. pirus*" combination, and Triantaphyllou (2010) argued about a link between '*C. oblonga*' and *C. papillifera*. In addition, Triantaphyllou *et al*. (2009) have also shown a rather unambiguous combination coccosphere of S. *pulchra* HOL *pirus* type with *S. protrudens,* implying close relationship between *S. pulchra* and *S. protrudens*.

Apparently, our new evidence on the *S. histrica-C. papillifera* association supports previous observations of Cros *et al*. (2000). Together with the suggested affinities between '*C. oblonga*' and *C. papillifera* (Triantaphyllou, 2010), in combination with the relationship proposed between '*C. oblonga*' and '*D. pirus*' (Malinverno *et al*., 2008b), our data add 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 have tentatively been incorporated into a possible single coherent evolutionary scheme (Malinverno *et al*., 2008b). Obviously, further well supported data are urgently needed in order to proceed to a thorough taxonomical revision for all involved coccolithophore forms.

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