

# New possible hetero-holococcolithophore combinations within the genus *Syracosphaera*

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Manuscript received 12th October, 2007; revised manuscript accepted 7th February, 2008

**Abstract** Two new possible hetero-holococcolithophore combinations are shown: *Syracosphaera histrica* with *S. pulchra* HOL *oblonga* type and *S. molischii* with *Gliscolithus amitakareniae*. In addition, an ambiguous combination of *S. pulchra* HOL *oblonga* type with *S. pulchra* HOL *pirus* type is recorded by light-microscope imaging. Although represented by ambiguous combinations, they potentially document new life-cycle associations within coccolithophores to add to the complexity of haplo-diplontic coccolithophore stages.

**Keywords** Coccolithophore, life-cycle, *Syracosphaera histrica*, *Syracosphaera pulchra* HOL *oblonga* type, *Syracosphaera molischii*, *Gliscolithus amitakareniae*

## 1. Introduction

Coccolithophores are a significant, unicellular phytoplankton group that biomineralise a calcareous skeleton (coccosphere) made of minute plates called coccoliths, the morphology and crystal arrangement of which are the primary basis for coccolithophore identification and classification. Two basic kinds of coccoliths can be distinguished on the basis of crystal type: holococcoliths, which are formed of minute, identical, euhedral crystals, and heterococcoliths, which are made of larger crystals of variable shape. Although heterococcolith- and holococcolith-bearing cells were initially regarded as separate species, culture work (Parke & Adams, 1960; Manton & Leedale, 1969; Rowson *et al.*, 1986; Houdan *et al.*, 2004; Noël *et al.*, 2004) has shown that they can undergo transition from one form to the other (respectively, diploid and haploid), and thus are considered to be a part of the life-cycle of the same species. Furthermore, combination coccospheres containing both hetero- and holococcoliths have been recorded from field-samples (Kamptner, 1941; Lecal-Schlauder, 1961; Kleijne, 1991; Thomsen *et al.*, 1991; Samtleben & Schröder, 1992; Samtleben *in* Winter & Siesser, 1994; Alcobér & Jordan, 1997; Young *et al.*, 1998; Cros *et al.*, 2000; Cortés, 2000; Cortés & Bollmann, 2002; Geisen *et al.*, 2002; Cros & Fortuño, 2002; Triantaphyllou & Dimiza, 2003; Triantaphyllou *et al.*, 2004). They are believed to document the moment of transition between the two life-cycle phases.

The factors causing the transition from one phase to the other are still not well constrained, as both phases are self-reproducing and transitions only rarely occur in culture. Noël *et al.* (2004) demonstrated that, in *Calyptrorpha*

*sphaeroidea*, phase transitions in culture can be initiated by physical or chemical stress, but it is not known if this is a common pattern in coccolithophores.

Several such combinations are now well established, due to repeated observations that statistically confirm their authenticity. As a consequence, changes in the taxonomic nomenclature have been proposed (Cros *et al.*, 2000; Jordan *et al.*, 2004), whereby the two species' names are synonymised and the one having taxonomic priority is adopted as the name for both life-cycle phases. Various additional combinations are still unsubstantiated, with the association of different coccolith types having been documented only once and/or the specimens being uncertain, possibly resulting from accidental incorporation of coccoliths from another species onto a coccosphere during sampling, in a faecal pellet, or in the water-column (*i.e.* xenospheres: Young *et al.*, 1997; Young & Geisen, 2002).

Besides the most common, one-to-one hetero-holococcolith combinations, more complex combinations have been reported, suggesting relationships of one hetero- with two or three holococcolith types, for example, *Helicosphaera carteri* with the former "*Syracolithus confusus*" and "*S. catilliferus*" (Cros *et al.*, 2000; Geisen *et al.*, 2002); *Syracosphaera amoena* with the former "*Zygosphaera bannockii*" and *Corisphaera* type A (Cros *et al.*, 2000), and now also with "*Zygosphaera amoena*" (Dimiza *et al.*, *in press*); *Syracosphaera pulchra* with the former "*Calyptrorpha oblonga*" (Cros *et al.*, 2000; Geisen *et al.*, 2002) and the former "*Daktylethra pirus*" (Geisen *et al.*, 2002; Saugestad & Heimdal, 2002); and *Coronosphaera mediterranea* with the former "*Calyptrolithina wettsteinii*" (Kamptner, 1941; Cros *et al.*, 2000), "*Calyptrolithophora*

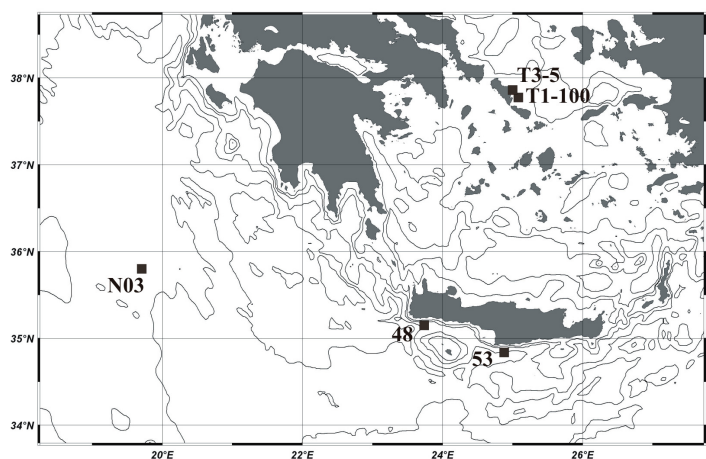
*hasleana*" (Cortés & Bollmann, 2002) and "*Zygosphaera hellenica*" (Geisen *et al.*, 2002). Different mechanisms have been proposed to explain these multiple combinations, involving non-genotypic variation in the degree of calcification in the holococcolith types (Cros *et al.*, 2000, for *H. carteri*), intraspecific variation, sexual dimorphism, hybridisation of two haploid phases, complex life-cycles, and cryptic speciation, visible in the holococcolith phase, but not in the heterococcolith phase (Geisen *et al.*, 2002, for *S. pulchra* and *C. mediterranea*).

In this paper, we document two new possible hetero-holococcolithophore combinations within the genus *Syracosphaera*: *S. histrica* with *S. pulchra* HOL *oblonga* type and *S. molischii* with *Gliscolithus amitakareniae*. Additionally, we provide evidence of an ambiguous combination coccosphere, involving the two holococcolith forms of *S. pulchra*, that is, HOL *oblonga* and HOL *pirus*. These new combinations have the potential to add to the complexity of coccolithophore life-cycles known to date, involving multiple hetero-holococcolithophore combinations.

## 2. Material and methods

### 2.1 Sampling and observations

Water-samples, from which the two new possible hetero-holococcolithophore combinations were observed, were collected at 5m and 25m from Station N03 in the Ionian Sea (eastern Mediterranean; Figure 1) during cruise SIN97 of the R/V *Urania* in December, 1997. Samples were obtained via Niskin bottles mounted on a rosette and controlled by a Seabird 911plus conductivity-temperature-depth (CTD) probe. Water-samples, containing further examples of previously described combinations of *Syracosphaera pulchra* life-cycles, were collected from Stations T3-5 and T1-100, at 45m (April, 2002) and 15m (September, 2004) depth, respectively, off Andros Island in the Aegean Sea (Figure 1), using a single oceanographic Hydro-bios bottle.



**Figure 1:** Sampling site locations in the eastern Mediterranean Sea. Water-sample N03 from the Ionian Sea, sediment-trap samples 48 and 53 from south of Crete and water-samples T3-5 and T1-100 from the Aegean Sea off Andros Island

For all water-samples, 1.5 to 4l of sea-water were filtered through Millipore cellulose nitrate or cellulose acetate filters (0.45 to 0.8µm pore-size) using a vacuum filtration system; for the coastal samples (off Andros), salt was removed by washing the filters with about 2ml of bottled drinking water. The filters were oven dried and stored in plastic Petri dishes.

Coccolithophores were subsequently identified and counted by either light (LM) or scanning electron microscope (SEM). Their abundances and assemblage compositions in the pelagic Ionian and coastal Aegean Seas are described, respectively, in Malinverno *et al.* (2003) and Dimiza *et al.* (in press).

Two specimens, involving a combination of *S. pulchra* HOL *pirus* type and *S. pulchra* HOL *oblonga* type holococcoliths, were found in separate sediment-trap samples, collected at 697m (Station 53) and 995m (Station 48) depth, south of Crete Island (Figure 1). Samples were collected using PPS3/3 Technicap sediment-traps (0.125m<sup>2</sup> collecting area), deployed from June, 2005 to May, 2006. The sampling intervals are September, 2005 (53-IB8) and January, 2006 (48-IIB5). Upon recovery, each sample was split into equal fractions using a rotary splitter (deviation between aliquots 4%); one fraction was subsequently treated for the analysis of coccolithophore fluxes, following the standard preparation techniques for sediment-trap samples (*e.g.* see Broerse, 2000); total coccospheres, coccoliths and calcareous dinoflagellates were identified and counted with the LM at 1250x magnification. The total coccolithophore flux and assemblage composition at the different sites is described in Malinverno *et al.* (2007).

### 2.2 Terminology

For coccolithophore species identification, the classification scheme of Jordan *et al.* (2004) is followed. Following the recommendations of Cros *et al.* (2000) and Young *et al.* (2003), well-established associations of hetero- and holococcolithophores are synonymised, and each phase is defined informally by its hetero- (HET) or holococcolith (HOL) type and by its former specific name (*e.g.* *Syracosphaera pulchra* HOL *oblonga* type). When used, former species names are reported in double quotes (*e.g.* "*Calyptrorphaera oblonga*").

## 3. Results and discussion

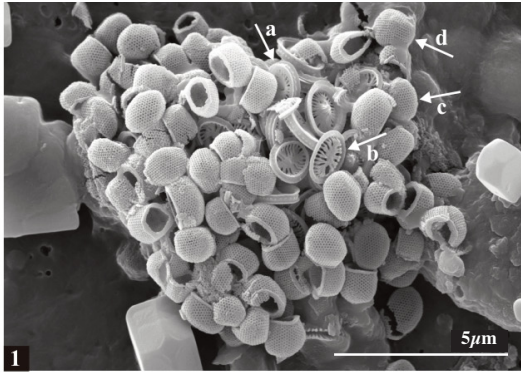
### 3.1 *Syracosphaera histrica* with *S. pulchra* HOL *oblonga* type

A possible combination coccosphere (Pl.1, fig.1) of *Syracosphaera histrica* (heterococcolithophore) and "*Calyptrorphaera oblonga*" (holococcolithophore) was recovered from Station N03 at 5m water-depth. This coccosphere is collapsed and most coccoliths are in random orientations. However, it contains no coccoliths from other species and presents both ordinary and apical (defined by a little protrusion) holococcoliths from *S.*

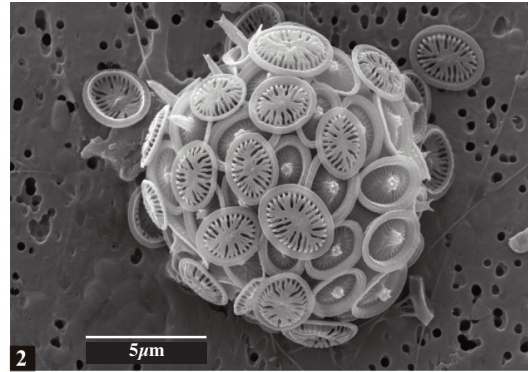


## Plate 1

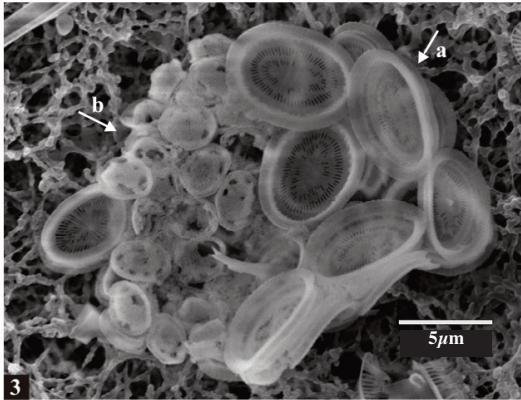
SEM images of simple and combination coccospheres



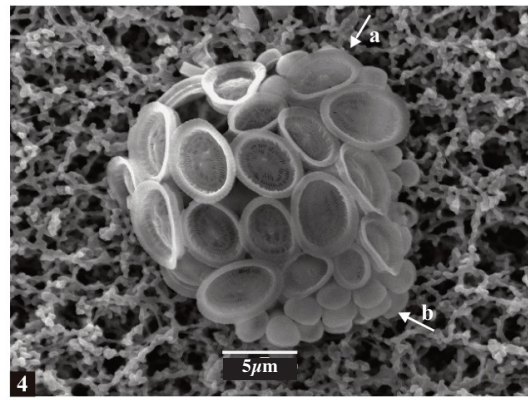
Possible combination coccosphere of *S. histrica* endotheal (a) and exotheal (b) coccoliths with *S. pulchra* HOL *oblonga* type body (c) and apical (d) coccoliths (N03, 5m)



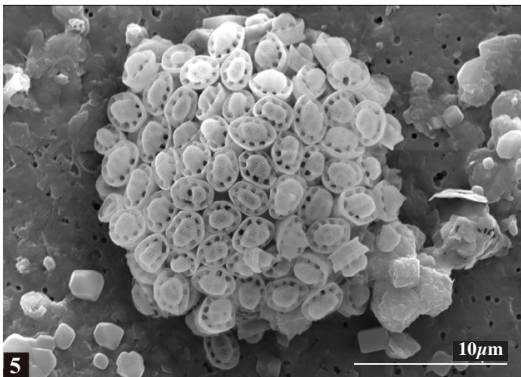
Simple heterococcosphere of *S. histrica* (N03, 10m)



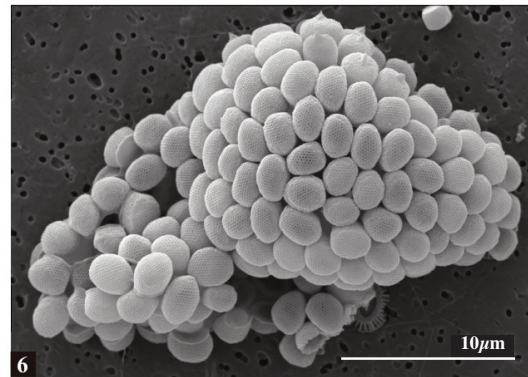
Combination coccosphere of *S. pulchra* HET (a) and *S. pulchra* HOL *pirus* type (b) (T3-5, 45m)



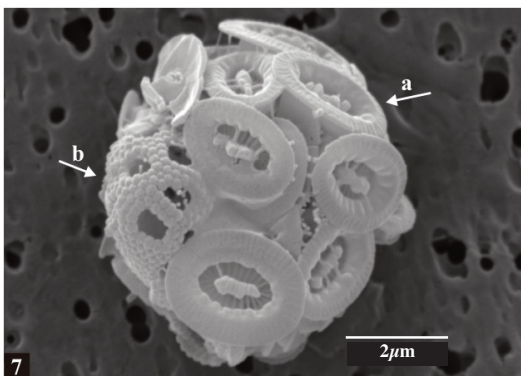
Combination coccosphere of *S. pulchra* HET (a) and *S. pulchra* HOL *oblonga* type (b) (T1-100, 15m)



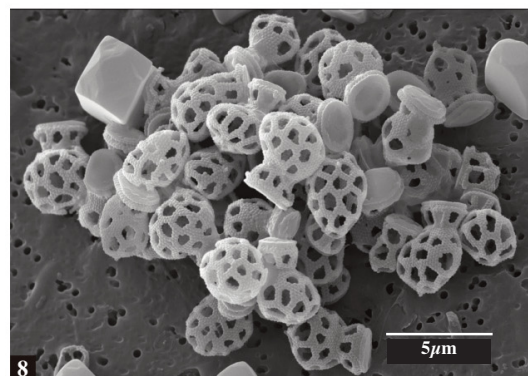
Single holococcosphere of *S. pulchra* HOL *pirus* type (N11, 10m)



Simple holococcosphere of *S. pulchra* HOL *oblonga* type (N03, 10m)



Possible combination coccosphere of *S. molischii* type 3 (formerly *S. corrugis*) (a) and *Gliscolithus amatakareniae* (b) (N03, 25m)



Collapsed holococcosphere of *G. amatakareniae* (N03, 5m)

*pulchra* HOL *oblonga* and both endo- and exothecal coccoliths from *S. histrica*. The specimen could represent a chance collision of two coccospheres at some stage in the sediment-trap sampling process, or a faecal pellet containing two coccospheres, or a real combination coccosphere. From this single specimen, a definitive conclusion cannot be reached.

If we assume this is an authentic combination, however, we face the problem of complex evolution or complex (multiple) life-cycles in *Syracosphaera*. In fact “*C. oblonga*” is now established as the holococcolithophore phase of the life-cycle of *S. pulchra* (Pl.1, fig.4; Figure 2), and it was thus transferred to this species as *S. pulchra* HOL *oblonga* type (Young *et al.*, 2003). However, morphological observations demonstrate strong affinities between *S. pulchra* and *S. histrica*, so that Young *et al.* (2003) and Geisen *et al.* (2004) inferred they should be genetically close. *S. pulchra* is also found in association with “*Dakylethra pirus*” (Pl.1, fig.3; previously documented by SEM in Geisen *et al.*, 2002; LM evidence in Lecal-Schlauder, 1961; Saugestad, 1967; Saugestad & Heimdal, 2002), which was thus transferred to this species as *S. pulchra* HOL *pirus* type (Geisen *et al.*, 2002; Young *et al.*, 2003). Among the various hypotheses to account for such complex associations, Geisen *et al.* (2002) proposed two likely alternative explanations: cryptic speciation, that is, evolution with morphological differentiation occurring only in the holococcolithophore phase and not evident in the heterococcolithophore phase, or complex life-cycles, involving multiple hetero-holococcolithophore combinations. A third possible hypothesis, that this was a case of intraspecific variation within the holococcolithophore phase, was discarded on the grounds that the two holococcolithophore forms have never been found co-occurring on the same coccosphere, and intermediates between them do not occur.

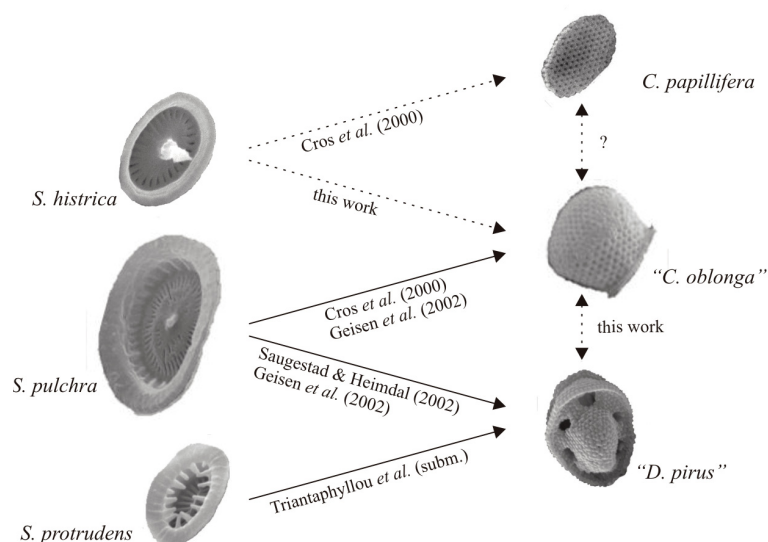
### 3.2 *Syracosphaera pulchra* HOL *oblonga* type with *S. pulchra* HOL *pirus* type

Two possible combination coccospheres of *Syracosphaera pulchra* HOL *pirus* type and *S. pulchra* HOL *oblonga* type (Pl.2, figs 2, 3) were observed by LM in two sediment-trap samples (53-IB8 and 48-IIB5) off Crete. In these two samples, “*C. oblonga*” coccospheres contributed 1.12% and 6.29%, respectively, to the total coccosphere flux, while no “*Dakylethra pirus*” coccospheres were observed (this species was, however, recovered in the samples as loose coccoliths, although with approximately only half the percent abundance of “*C. oblonga*”, that is, 0.5% and 0.9%, respectively). This association is an ambiguous combination, as the coccosphere shape is not regular, it has been documented only by LM, and was recovered from sediment-trap samples, where the possibility of xenosphere formation is higher. Nonetheless, it should be considered as a possibility, as it has been observed in two specimens. In this case, such evidence would suggest that either the two holococcolith types are directly related and represent a simple case of intraspecific variation (although very rarely occurring in association), or that the association coccospheres are due to hybridisation, which could be possible, based on the genetic closeness of the two species.

Recent evidence has also shown a rather unambiguous combination coccosphere of *S. pulchra* HOL *pirus* type with *S. protrudens* (Triantaphyllou *et al.*, in press), which implies that *S. pulchra* and *S. protrudens* should be considered to be closely related (Figure 2). Previous LM observation by Kamptner (1941) recorded (but with no illustration) *S. histrica* in two different combinations with *Calyptrorpha quadridentata* (= *Sphaerocalyptra quadridentata*) and with *Calyptrorpha gracillima* (= *Calyptrolithophora gracillima*), while Cros *et al.* (2000, pl.8, fig.2) showed an SEM image of a possible combination coccosphere of *S. histrica* and *Calyptrolithophora papillifera*.

“*S. quadridentata*” is now considered to be the holococcolithophore phase of *Algyrosphaera robusta*, as they have both been reported to occur in several unambiguous combination coccospheres (Kamptner, 1941; Triantaphyllou & Dimiza, 2003; Malinverno *et al.*, in press). A more uncertain combination with *Rhabdosphaera clavigera* has been documented by Cros & Fortuño (2002).

Although morphological similarity is not a proven measure of taxonomic closeness, observations show that “*S. quadridentata*” and “*C. oblonga*” body coccoliths are relatively alike, as they are built of microcrystals arranged in a similar hexagonal mesh, although the former species displays a more irregular perforate pattern and has slightly smaller and more distinctly conical coccoliths. On the other hand, morphological observations underline a close similarity between “*C.*

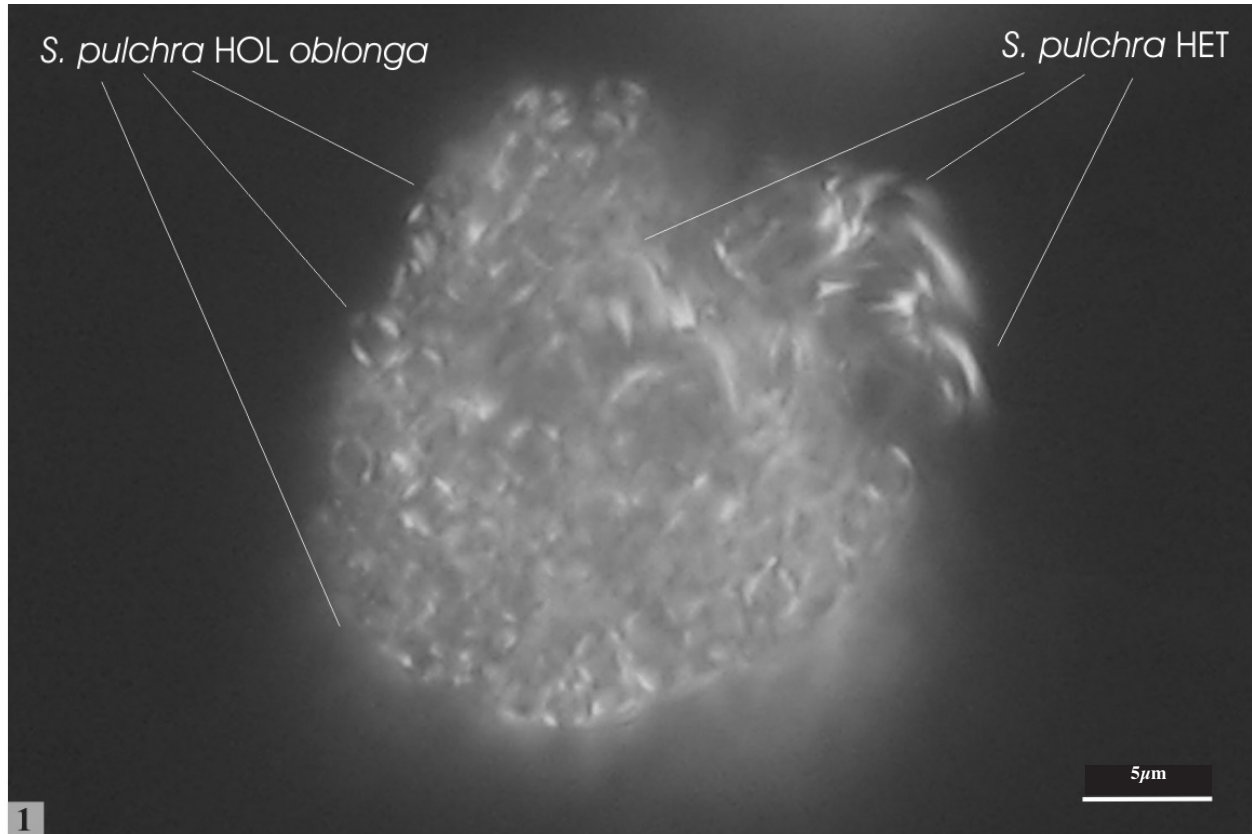


**Figure 2:** Well-established (solid line) and possible (dashed line) syracosphaerid HET-HOL combinations

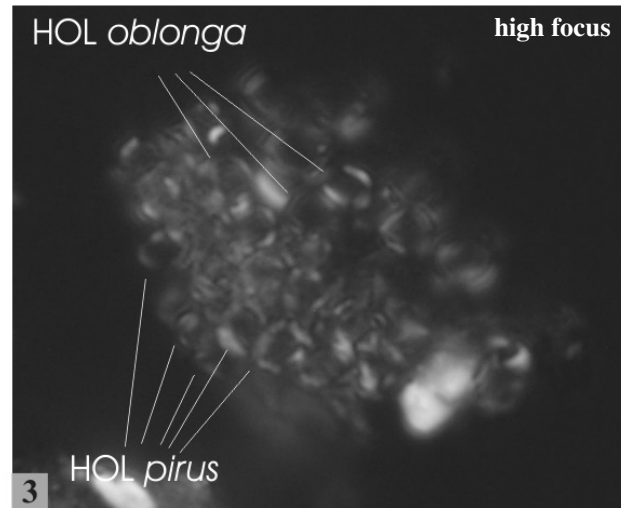
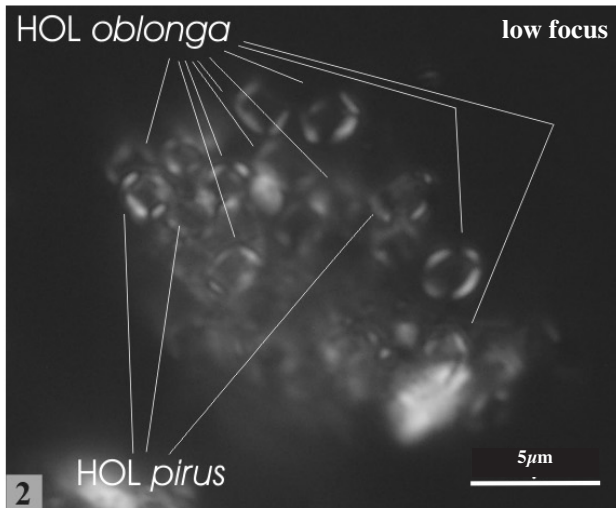


## Plate 2

LM images of established and possible combination coccospheres



LM image of a combination coccosphere of *Syracosphaera pulchra* HET and *S. pulchra* HOL *oblonga* type (Station T1-100, 15m)

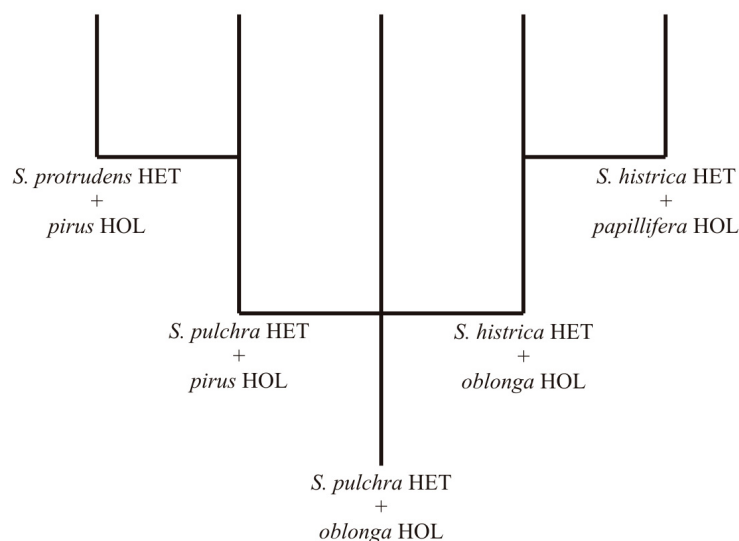


LM images of a possible combination coccosphere of *S. pulchra* HOL *oblonga* type and *S. pulchra* HOL *pirus* type (same specimen, Station 48-IIB5)

*oblonga*” and *C. papillifera*. Ordinary calyptroliths have similar hexagonal mesh construction and overall shape. In the former species, however, they are slightly larger and possess a convex distal surface, while in the latter, they have flat distal surfaces bordered by a ring of crystallites. Additionally, a basal ring, one crystallite thick, is present in

*C. papillifera*, but more developed in “*C. oblonga*”. Apical coccoliths of “*C. oblonga*” are slightly more elevated than ordinary ones, and have a distal, pointed, pyramidal spine; in *C. papillifera*, they are highly vaulted, with flat sides and an elevated central-area with parallel strings of crystals. They show well-separated morphological characteristics,

and thus seem to be distinct species. However, several specimens have coccoliths with mixed characters (MD & MVT, pers. obs., 2007), suggesting these could be a new *Calyptrolithophora* species. If substantiated by further observations, the newly-discovered combination coccosphere found in our samples would imply a complex relationship between three heterococcolithophore types linked with three holococcolithophore types, in combinations of one-to-one or one-to-two (Figure 2). Intriguingly, it is still possible to resolve the rather confusing set of potential associations into a single coherent evolutionary scheme (Figure 3). The evidence for this scheme is weak, but it does highlight the possibility that uncoupled evolution of the haploid and diploid phases may make life-cycle associations of coccolithophore types excellent indicators of phylogenetic relationships.



**Figure 3:** Possible evolutionary scheme for the *Syracosphaera pulchra*-*S. histrica*-*S. protrudens* plexus, involving independent evolution of the HET and HOL phases

### 3.3 *Syracosphaera molischii* with *Gliscolithus amitakareniae*

A single heterococcosphere of *Syracosphaera molischii*, in which is embedded a single holococcolith of *Gliscolithus amitakareniae*, was recovered from Station N03 at 25m water-depth (Pl.1, fig.7). This specimen does not represent an unambiguous combination, as only one coccolith of *G. amitakareniae* is present. It is, however, unlikely that this specimen represents a xenosphere, as the holococcolith appears embedded within the heterococcolith coccosphere.

Previously, Cros & Fortuño (2002, fig.112A) documented a possible combination coccosphere of *S. molischii* and *Anthosphaera fragaria*. The specimen, however, was collapsed and could, therefore, be simply a chance association. Different types of *S. molischii* have been informally distinguished by Young *et al.* (2003), based on the ornamentation of the distal flange and of the central-area. The *S. molischii* species concept includes, in fact, morphologies that were formerly described independently, although

with no clear separation of the diagnostic characters; type 2 of Young *et al.* (2003) corresponds to *S. elatensis* Winter in Winter *et al.*, 1979, while type 3 corresponds to *S. corrugis* Okada & McIntyre, 1977. The combination coccosphere shown by Cros & Fortuño (2002) includes *S. molischii* type 2, with teeth protruding from the inner part of the coccolith's distal flange towards the central-area, and a strongly-calcified central-area structure. In contrast, the coccosphere of our sample includes *S. molischii* type 3, in which coccoliths have no teeth protruding towards the central-area and a less-calcified central-area structure.

None of the two *S. molischii* coccospheres found up to now in combination with holococcoliths represents an unambiguous association. However, if these combinations eventually prove to be real, they would strengthen the argument for separation of *S. molischii* types into separate species.

## 4. Conclusions

Here we have demonstrated two new examples of possible combination coccospheres, *Syracosphaera histrica* with *S. pulchra* HOL *oblonga* type and *S. molischii* with *Gliscolithus amitakareniae*. Additionally, we have documented an ambiguous specimen, showing coccoliths of both *S. pulchra* HOL *oblonga* type and *S. pulchra* HOL *pirus* type. Although all specimens are represented by equivocal combinations, which are not confirmed by multiple examples, they potentially document new life-cycle associations within coccolithophores. If confirmed, these new combinations would imply that the relationships between different phases, at least within the genus *Syracosphaera*, are more complex than explained to date, and they may provide invaluable phylogenetic data. Clearly, there is a need for more observations of combination coccospheres, and other lines of

evidence, in order to elucidate coccolithophore life-cycles, and realise their potential as indicators of evolutionary relationships and keys to understanding coccolithophore ecology.

## Acknowledgements

Financial support for collection and study of samples from the Ionian Sea, Aegean Sea and offshore Crete was provided, respectively, by the Italian Project SINAPSI (Seasonal, INterannual and decadal variability of the atmosphere, ocean and related marine ecosystems), 01ED100/PENED Project and 04EP59/ENTER Project of the European Union and the General Secretariat for Research and Technology/Greek Ministry of Development. This work was carried out within research project ENTER, co-financed by EU-European Social Fund (75%) and the Greek Ministry of Development - GSRT (25%). Dr. Markus Geisen and Dr. Lluïsa Cros are warmly acknowledged for careful review of the manuscript and for suggestions to its improvement.

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