

## Evidence for a possible life-cycle association between *Syracosphaera protrudens* (heterococcolithophore) and *Syracosphaera pulchra* HOL *pirus*-type (holococcolithophore)

M. V. TRIANTAPHYLLOU<sup>1</sup>, M. D. DIMIZA<sup>1</sup>, E. MALINVERNO<sup>2</sup> & J. R. YOUNG<sup>3</sup>

<sup>1</sup>Department of Historical Geology-Paleontology, Faculty of Geology & Geoenvironment, University of Athens, Panepistimiopolis, Athens 157 84, Greece (e-mail: mtriant@geol.uoa.gr)

<sup>2</sup>Department of Geological Sciences and Geotechnologies, University of Milano-Bicocca, 4 - 20126 Milano, Italy

<sup>3</sup>Palaeontology Department, Natural History Museum, Cromwell Road, London SW7 5BD, UK

**ABSTRACT** – An apparently unambiguous combination coccosphere from the Eastern Mediterranean (Aegean Sea, Greece) is documented involving *Syracosphaera protrudens* Okada & McIntyre, 1977 and *Syracosphaera pulchra* Lohmann, 1902 HOL *pirus*-type. This finding is difficult to interpret in terms of the current understanding of *Syracosphaera* taxonomy and adds evidence to the hypothesis of a distinctly complex *Syracosphaera pulchra* life cycle. *J. Micropalaeontol.* 28(1): 1–6, May 2009.

**KEYWORDS:** *living coccolithophores, combination coccospheres, Syracosphaera, taxonomy, life cycle*

### INTRODUCTION

Coccolithophores form a major component of the marine nanoplankton and, at least at some stage in their life cycle, produce minute calcium carbonate plates called coccoliths. Two types of coccoliths, heterococcoliths and holococcoliths, the products of different biomineralization modes, are recognizable (Young *et al.*, 1999, 2004; Young & Henriksen, 2003). In culture studies several coccolithophores have been shown to have complex life cycles involving an alternation between a haploid holococcolith-producing phase and diploid heterococcolith-producing phase (Parke & Adams, 1960; Houdan *et al.*, 2004). The limited data available from culture studies have been supplemented greatly by the observation of combination coccospheres, representing the moment of life-cycle transition, in field samples (Kamptner, 1941; Lecal-Schlauder, 1961; Kleijne, 1991; Thomsen *et al.*, 1991; Alcober & Jordan, 1997; Young *et al.*, 1998; Cortés, 2000; Cros *et al.*, 2000; Cortés & Bollmann, 2002; Cros & Fortuño, 2002; Geisen *et al.*, 2002, 2004; Triantaphyllou & Dimiza, 2003; Triantaphyllou *et al.*, 2004). None the less, for the vast majority of extant coccolithophores their life cycle is still unknown, and new observations are much needed (Young *et al.*, 2003; Jordan *et al.*, 2004).

This paper presents the first description of a combination coccosphere between the heterococcolithophore species *Syracosphaera protrudens* Okada & McIntyre, 1977 and holococcolithophore species *S. pulchra* HOL *pirus*-type [= *Dakylethrapirus* (Kamptner, 1937) Norris, 1985].

### MATERIALS AND METHODS

The *S. protrudens*–*S. pulchra* HOL *pirus*-type combination coccosphere evidenced in this study comes from water samples collected off Andros Island (middle Aegean Sea). The samples were collected on 21 August 2001, from eight stations at selected depths (Fig. 1, Table 1), between 0 m and 120 m, using a single oceanographic Hydro-bios bottle. Additional samplings were performed in the same area during April 2002 and September 2004. For each sampling depth, 1.5 l of sea water was filtered through Millipore cellulose nitrate filters (47 mm diameter, 0.45 µm pore size), using a vacuum filtration system. Salt was removed by washing the filters with about 2 ml of bottled

drinking water. The filters were oven dried and stored in plastic Petri dishes. A piece of each filter approximately 8 × 8 mm<sup>2</sup> was attached to a copper stub using double-sided adhesive tape, and gold-coated. The filters were examined in a JEOL JSM 5600 Scanning Electron Microscope (SEM) and all coccolithophore specimens occurring on the examined filter piece were identified and counted. The working magnification was 1200 × throughout the counting procedure. The absolute abundances of coccolithophores (cells l<sup>-1</sup>) were calculated following the methodology of Jordan & Winter (2000).

### RESULTS

Coccolithophore biocommunities constitute a significant part of the flora in the upper photic zone of the coastal waters of Andros Island, showing quite diverse assemblages. The complete nanoflora recorded during the present study is described in Triantaphyllou *et al.* (2002) and Dimiza *et al.* (2008).

A single well-developed combination coccosphere (Pl. 1, figs 1–2), consisting of numerous body coccoliths of *Syracosphaera protrudens* (heterococcoliths) and characteristic body holococcoliths of *Syracosphaera pulchra* HOL *pirus*-type (holococcoliths), was found in sample T3-5 at 45 m water depth (37° 47.93' N, 24° 59.33' E). The heterococcoliths (caneoliths) of *Syracosphaera protrudens* have a high, almost vertical, wall with two flanges, and a variable number of teeth protruding centripetally from the distal flange. Both *Syracosphaera protrudens* (Pl. 1, fig. 4) and *Syracosphaera pulchra* HOL *pirus*-type (Pl. 1, fig. 7) were minor components in the assemblages (less than 3% – included in *S. halldalii* abundance – and 6% of the coccosphere standing stock, respectively, Table 1). The filter sample and the SEM micrograph are in the collections of the Museum of Paleontology and Geology in the University of Athens.

### DISCUSSION

*Syracosphaera protrudens* is known from the Red Sea, Mediterranean Sea and North Atlantic (Kleijne, 1993). This form was described by Okada & McIntyre (1977) but has often been included in *Syracosphaera halldalii* Gaarder in Gaarder & Hasle, 1971. Recently, Young *et al.* (2003) and Jordan *et al.*

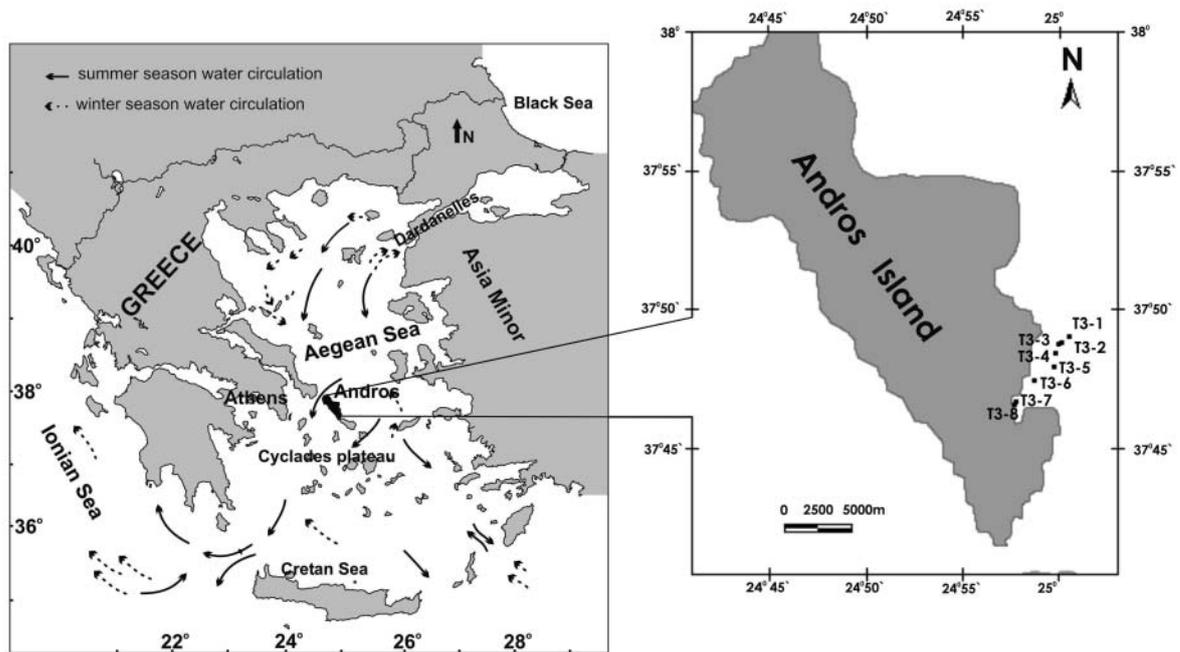


Fig. 1. Map of Andros Island and location of the sampled stations.

(2004) reinstated *S. protrudens* as a separate species, but closely related to *S. halldalii*. Triantaphyllou *et al.* (2004) illustrated an unambiguous combination coccosphere of *S. halldalii* heterococcoliths and holococcoliths of *Calyptrorolithina divergens* var. *tuberosa* (Heimdal in Heimdal & Gaarder, 1980) Heimdal, 1982. This strongly suggested that these two 'species' are alternate life-cycle stages and they recommended that *C. divergens* var. *tuberosa* should be regarded as a junior synonym of *S. halldalii*.

As illustrated in Figure 2, *pirus*-type holococcoliths (= *S. pulchra* HOL *pirus*-type) and *tuberosa*-type holococcoliths (= *S. halldalii* HOL) are similar in shape. They both have moderately flaring tubes with a distal cover that is slightly recessed in the tube then rises to form a central dome. They differ primarily in that *tuberosa*-type holococcoliths have numerous small pores in the distal cover, whilst *pirus*-type holococcoliths have a few large pores. So in this respect the associations *halldalii*-*tuberosa* and *protrudens*-*pirus* appear unproblematic. However, *pirus*-type holococcoliths are also known to be formed by the very different species *S. pulchra*. As has been well documented (Lecal-Schlauder, 1961; Cros *et al.*, 2000; Geisen *et al.*, 2002, 2004; Saugestad & Heimdal, 2002), the heterococcolithophore *Syracosphaera pulchra* Lohmann, 1902 forms life-cycle associations with two holococcolithophore coccosphere-types previously assigned to different genera: *Calyptrorolithina oblonga* Lohmann, 1902 and *Daktylolethra pirus* (Kamptner, 1937) Norris, 1985. Geisen *et al.* (2002) documented both the *S. pulchra*-*C. oblonga* and *S. pulchra*-*D. pirus* associations from a mix of culture observations (one strain showing alternations between *S. pulchra* and *C. oblonga*) and multiple plankton observations of combination coccospheres. They gave an extended discussion on the similarities and differences between *pirus*-type and *oblonga*-type holococcoliths and demonstrated a clear affinity in their

coccolith morphology and structure, despite the consistent differences in morphology (Geisen *et al.*, 2002; Young *et al.*, 2003). Geisen *et al.* (2002) also discussed various possible interpretations of these data and concluded that this was most likely a case of pseudo-cryptic speciation, inferring that *S. pulchra* probably comprises two biological species, which are almost impossible to separate in the heterococcolith phase, but which produce quite distinct holococcoliths. Based on these data, Geisen *et al.* (2002) synonymized *C. oblonga* and *D. pirus* with *S. pulchra*; this opinion was followed in the recent taxonomic syntheses of Young *et al.* (2003) and Jordan *et al.* (2004).

The set of relationships suggested by the various combination coccospheres, as summarized in Figure 2, is clearly rather problematic. A number of different hypotheses can be suggested as possible explanations.

1. *Syracosphaera pulchra* and *S. protrudens* are sibling species that have evolved different heterococcolith morphologies but retained similar holococcolith morphologies. The problem with this hypothesis is that the heterococcolith morphologies are totally dissimilar, differing in numerous ways, including: exothecal coccolith form (dome-shaped in *S. pulchra*, absent in *S. protrudens*); body coccolith rim structure (complex in *S. pulchra* with three flanges (Young *et al.*, 2004), simple in *S. protrudens* with two flanges); circum-flagellar coccolith spine type (bifurcate in *S. pulchra*, simple in *S. protrudens*). These characters have been inferred to be significant indicators of phylogenetic relationships between the numerous *Syracosphaera* species and so *S. protrudens* and *S. pulchra* have been included in disparate groups in the syntheses of Young *et al.* (2003) and Cros & Fortuño (2002), with the implication that they are related only distantly. So, this interpretation would imply that heterococcolith

Stations	Sea bottom depth (m)	Longitude	Latitude	Water depth (m)	Total standing crop ( $\times 10^3$ cells $l^{-1}$ )	<i>Syracosphaera halldalii</i> (cells $l^{-1}$ )	<i>Syracosphaera pulchra</i> (cells $l^{-1}$ )	<i>Syracosphaera pulchra</i> HOL <i>pirus</i> (cells $l^{-1}$ )	<i>Syracosphaera pulchra</i> HOL <i>oblonga</i> (cells $l^{-1}$ )
T3-1	130	37°49'01" 25°00'31"		0	4.05		96		
				5	13.43	220	440		330
				15	12.72	25	330		165
				45	14.7	652	119	237	889
				90	6.75		147	220	
T3-2	120	37°48'48" 25°00'02"		0	8.70	330	220		110
				5	12.64	144	361		72
				15	11.08	48	96		530
				45	5.93	57	114	114	57
				90	3.36			60	60
T3-3	124	37°48'46" 24°59'58"		0	3.08				220
				5	6.70	94	188		283
				15	13.64	116	116		694
				45	7.40	132		198	330
				90	3.72			83	330
T3-4	110	37°48'28" 24°59'41"		0	3.70				264
				5	8.48		308		617
				15	10.28		385		257
				45	11.34	110	110	661	550
				60	5.94			220	220
T3-5	75	37°47'56" 24°59'20"		0	2.48				
				5	7.30	53	158		368
				15	5.97	48			193
				45	13.58	367	73	734	587
T3-6	50	37°47'24" 24°58'45"		0	8.38	385	96		193
				5	10.38	189	283	94	283
				15	11.17	64	128		257
				45	1.99		171		
T3-7	30	37°46'40" 24°57'44"		0	4.24		96		
				5	8.26	413	83		330
				15	8.92	165	330		1321
				25	7.93	377	189		1227
T3-8	15	37°46'34" 24°57'23"		0	7.80	96	193		96
				5	11.95		289		193
				7	8.32	370	185		370

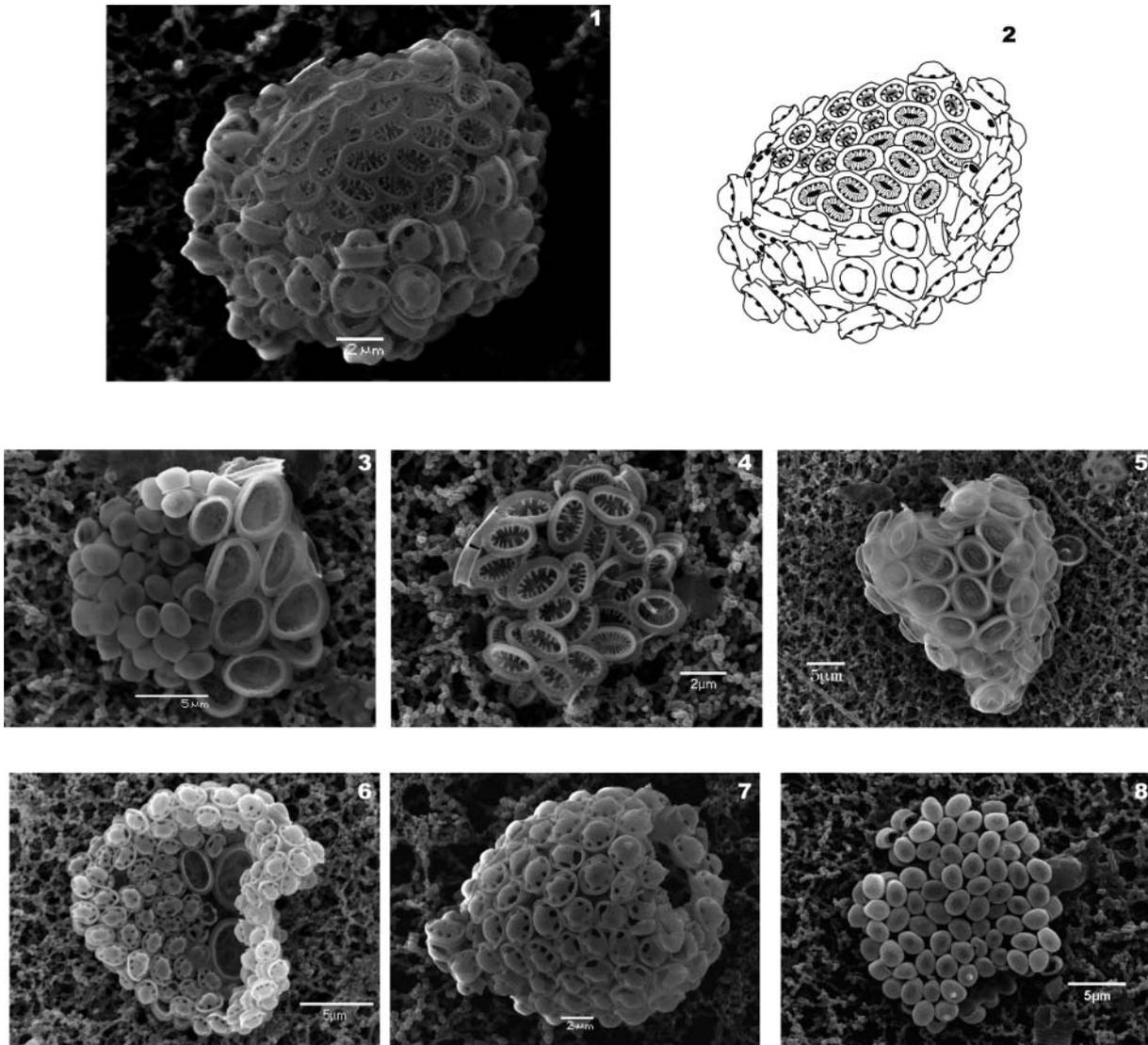
**Table 1.** Local position of samples collected on 21 August 2001, heterococcolithophore and holococcolithophore total standing crop and *S. protrudens* (counted together with *S. halldalii*), *S. pulchra*, *S. pulchra* HOL *pirus*-type, *S. pulchra* HOL *oblonga*-type abundances at all depths

morphology is much more plastic and less reliable as an indicator of evolutionary relationships than has been assumed.

- Syracosphaera pulchra* and *S. protrudens* are related only distantly but have evolved similar holococcolith morphologies as a result of convergent evolution. The problem with this hypothesis is that the *pirus*-type holococcoliths are rather distinctive and the holococcoliths on the *protrudens-pirus* combination coccosphere show the typical morphology. So, if it is an example of convergent evolution it is rather extraordinary.
- S. pulchra* and *S. protrudens* are, in fact, not discrete species but rather one species with a very complex life cycle capable of producing multiple coccolith types. Thus, *pulchra*-type and *protrudens*-type heterococcoliths and *pirus*-type and *oblonga*-type holococcoliths may actually all be formed by one polymorphic species. An ambiguous specimen showing coccoliths of both *Syracosphaera pulchra* HOL *oblonga*-type and *Syracosphaera pulchra* HOL *pirus*-type has been

reported by Malinverno *et al.* (2008). The problem with this hypothesis is that culture studies have provided no evidence of this type of polymorphism. So, this interpretation would imply much more complexity in coccolithophore life cycles than has been observed previously.

- The *S. protrudens-pirus* combination coccosphere may be a xenosphere (*sensu* Young *et al.*, 1997; Young & Geisen, 2002), i.e. an artefact produced by accidental agglomeration of coccoliths, inclusion of coccoliths from the water column onto a coccosphere or agglutination of coccoliths into the wall of a non-coccolithophore. The problems with this hypothesis are that the two coccolith types are rather rare in the water column, they are separated into different areas on the coccosphere, no other coccolith types are included in the coccosphere and the coccolith arrangement on the coccosphere is rather regular. So, this interpretation implies that combination coccospheres are less reliable indicators of life-cycle associations than has been assumed and perhaps can be produced by mechanisms not considered previously.



#### Explanation of Plate 1.

**figs 1, 2.** *Syracosphaera protrudens*–*Syracosphaera pulchra* HOL *pirus*-type combination: **1**, a single well-developed coccosphere consisting of numerous body caneloliths of *Syracosphaera protrudens* bearing a high and almost vertical wall with two flanges and with a variable number of teeth that protrude centripetally from the distal flange, and characteristic ordinary areoliths of *Syracosphaera pulchra* HOL *pirus*-type, sample T3-5 at 45 m; **2**, index sketch of fig. 1. **fig. 3.** *Syracosphaera pulchra*–*Syracosphaera pulchra* HOL *oblonga*-type combination coccosphere (T1-100, 15 m, September 2004). Numerous elliptical cap-shaped *oblonga*-type holococcoliths associated with *Syracosphaera pulchra* body coccoliths. **fig. 4.** *Syracosphaera protrudens* (T1-2, 60 m, August 2001). Body coccoliths are elliptic with relatively high vertical wall with basal and distal flange; several distinct well-separated long teeth protrude toward the central area, which is spanned by thin radial laths leaving slits in between, with a very small axial structure. **fig. 5.** *Syracosphaera pulchra* (T3-1, 45 m, April 2002). Body coccoliths are elliptical with three well-developed flanges; central area is closed by three concentric cycles of small radial laths, leaving small slits in between. Apical coccoliths are similar, but with more elevated central area and robust bifurcated spine. The exothecal coccoliths are formed by a basal flat rim and an elevated dome-shaped central area, built of laths, which – in the basal part – leave slits in between, and with a central conical depression. **fig. 6.** *Syracosphaera pulchra*–*Syracosphaera pulchra* HOL *pirus*-type combination coccosphere (T3-1, 45 m, April 2002). Numerous elliptical cap-shaped with areolate interior *pirus*-type holococcoliths associated with *Syracosphaera pulchra* body coccoliths. **fig. 7.** *Syracosphaera pulchra* HOL *pirus*-type (T3-4, 45 m, August 2001). Holococcoliths are elliptical cap-shaped with areolate interior (areoliths), formed by a tube, a vaulted central area and a proximal ring forming a basal flange. Apical holococcoliths are similar but more elevated and with a well-developed pyramidal spine extending distally. **fig. 8.** *Syracosphaera pulchra* HOL *oblonga*-type (T1-6, 10 m, August 2001). Holococcoliths are elliptical cap-shaped calyptroliths with proximal ring forming a basal flange. Apical holococcoliths are similar, with a well-developed pyramidal spine extending distally.

#### CONCLUSIONS

The coccosphere illustrated here, involving *protrudens*-type heterococcoliths and *pirus*-type holococcoliths, looks like an unambiguous example of a combination coccosphere, indicating a life-cycle association between these two coccosphere-types.

However, all possible interpretations of the coccosphere pose difficult problems for our understanding of coccolithophore biology or evolutionary relationships. From the available evidence it is not possible to reach a simple conclusion. More significantly, any possible interpretation raises significant

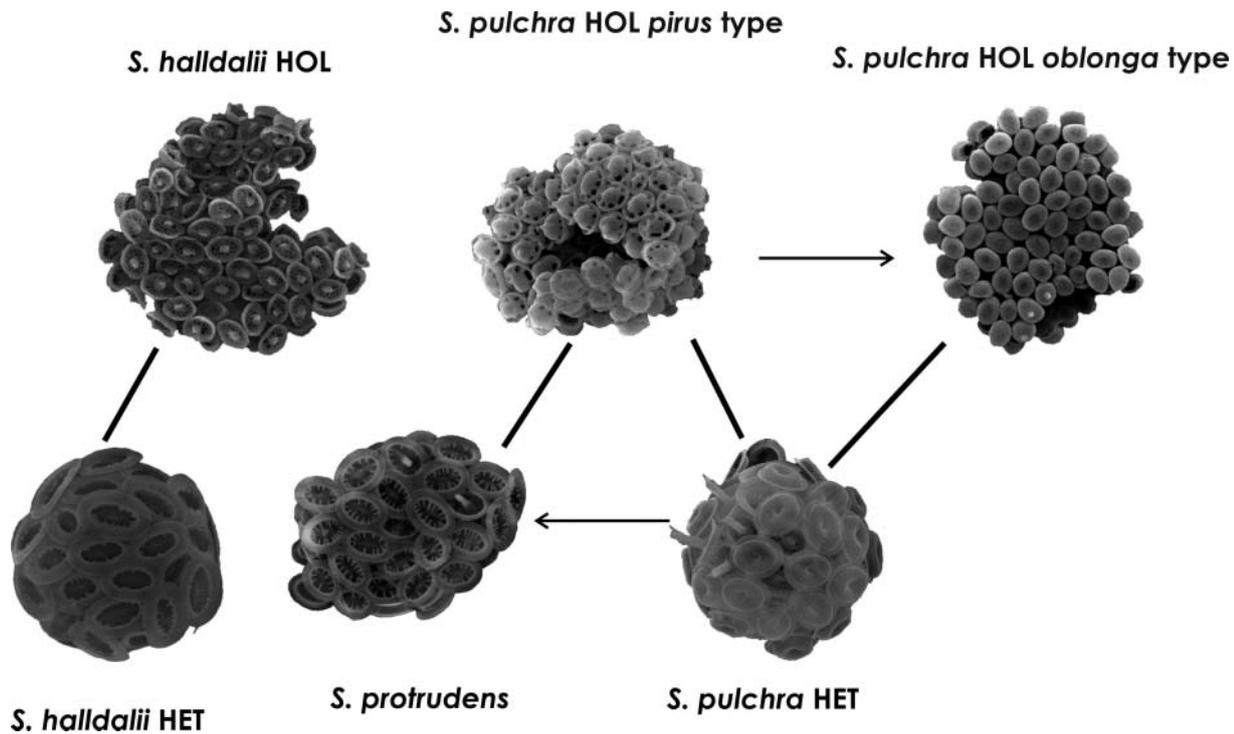


Fig. 2. Verified life-cycle associations of the heterococcolithophore species *Syracosphaera pulchra*, *S. halldalii* and *S. protrudens*.

problems with our current understanding of coccolithophore evolution, coccolithophore life cycles or the significance of combination coccospheres. Evidently, more research is needed in this field and, in particular, more observations from both culture studies and field observations of combination coccospheres.

#### ACKNOWLEDGEMENTS

Financial support for this study was provided by Research Project 70/4/3385 of the University of Athens, 01ED100/PENED Project and 04EP59/ENTER Project of the European Union, the General Secretariat for Research and Technology / Greek Ministry of Development. The valuable criticisms of Dr Ric Jordan are acknowledged warmly.

Manuscript received 26 October 2007

Manuscript accepted 20 July 2008

#### REFERENCES

Alcober, J. & Jordan, R.W. 1997. An interesting association between *Neosphaera coccolithomorpha* and *Ceratolithus cristatus* (Haptophyta). *European Journal of Phycology*, **32**: 91–93.

Cortés, M.Y. 2000. Further evidence for the heterococcolith–holococcolith combination *Calcidiscus leptopus*–*Crystallolithus rigidus*. *Marine Micropaleontology*, **39**: 35–37.

Cortés, M.Y. & Bollmann, J. 2002. A new combination coccosphere of the heterococcolith species *Coronosphaera mediterranea* and the holococcolith species *Calyptrolithophora hasleana*. *European Journal of Phycology*, **37**: 145–146.

Cros, L. & Fortuño, J.-M. 2002. Atlas of Northwestern Mediterranean Coccolithophores. *Scientia Marina*, **66** (Suppl. 1): 186pp.

Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J.R. 2000. New examples of holococcolith–heterococcolith combination coccospheres

and their implications for coccolithophorid biology. *Marine Micropaleontology*, **39**: 1–34.

Dimiza, M.V., Triantaphyllou, M.V. & Dermitzakis, M.D. 2008. Seasonality and ecology of living coccolithophores in E. Mediterranean coastal environments (Andros Island, Middle Aegean Sea). *Micropaleontology*, **52**: 159–175.

Gaarder, K.R. & Hasle, G.R. 1971. Coccolithophorids from the Gulf of Mexico. *Bulletin of Marine Science*, **21**: 519–544.

Geisen, M., Billard, C., Broerse, A.T.C., Cros, L., Probert, I. & Young, J.R. 2002. Life-cycle associations involving pairs of holococcolithophorid species: intraspecific variation or cryptic speciation? *European Journal of Phycology*, **37**: 531–550.

Geisen, M., Young, J.R., Probert, I., Saez, A., Baumann, K.-H., Bollmann, J., Cros, L., de Vargas, C., Medlin, L. & Sprengel, C. 2004. Species level variation in coccolithophores. In: Thierstein, H.R. & Young, J.R. (Eds), *Coccolithophores. From Molecular Processes to Global Impact*. Springer-Verlag, Berlin, 327–365.

Heimdal, B.R. 1982. Validation of the names of some species of *Zygospaera* Kamptner. *International Nanoplankton Association Newsletter*, **4**: 52–56.

Heimdal, B.R. & Gaarder, K.R. 1980. Coccolithophorids from the northern part of the eastern central Atlantic, I. Holococcolithophorids. 'Meteor' *Forschungsergebnisse. Reihe D, Biologie*, **32**: 1–14.

Houdan, A., Billard, C., Marie, D., Not, F., Sáez, A.G., Young, J.R. & Probert, I. 2004. Flow cytometric analysis of relative ploidy levels in holococcolithophore–heterococcolithophore (Haptophyta) life cycles. *Systematics and Biodiversity*, **1**: 453–465.

Jordan, R.W. & Winter, A. 2000. Living microplankton assemblages off the coast of Puerto Rico during January–May 1995. *Marine Micropaleontology*, **39**: 113–130.

Jordan, R.W., Cros, L. & Young, J.R. 2004. A revised classification scheme for living haptophytes. *Micropaleontology*, **50**: 55–79.

Kamptner, E. 1937. Neue und bemerkenswerte Coccolithineen aus dem Mittelmeer. *Archiv für Protistenkunde*, **89** (3): 279–316.

Kamptner, E. 1941. Die Coccolithineen der Sudwestküste von Istrien. *Annalen des Naturhistorischen Museums in Wien*, **51**: 54–149.

- Kleijne, A. 1991. Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Marine Micropaleontology*, **17**: 1–76.
- Kleijne, A. 1993. *Morphology, Taxonomy and Distribution of Extant Coccolithophorids (Calcareous Nannoplankton)*, Enschede: FEBO. Vrije Universiteit, Amsterdam, 320pp.
- Lecal-Schlauder, J. 1961. Anomalies dans la composition des coques de flagelles calcaires. *Bulletin de la Societe d' Histoire Naturelle de l' Afrique du Nord*, **52**: 63–66.
- Lohmann, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntniss des Mittelmeerauftriebs. *Archiv fur Protistenkunde*, **1**: 89–165.
- Malinverno, E., Triantaphyllou, M.V., Dimiza, M. & Young, J.R. 2008. New possible hetero– holococcolithophore combinations within the genus *Syracosphaera*. *Journal of Nannoplankton Research*, **30**: 1–8.
- Norris, R.E. 1985. Indian Ocean nannoplankton, II. Holococcolithophorids (Calyptosphaeraceae, Prymnesiophyceae) with a review of extant genera. *Journal of Phycology*, **21**: 619–641.
- Okada, H. & McIntyre, A. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, **23**: 1–55.
- Parke, M. & Adams, I. 1960. The motile (*Crystallolithus hyalinus* Gaarder and Markali) and non-motile phases in the life history of *Coccolithus pelagicus* (Wallich) Schiller. *Journal of the Marine Biological Association of the United Kingdom*, **39**: 263–274.
- Saugestad, A.H. & Heimdal, B.R. 2002. Light microscope studies on coccolithophorids from the western Mediterranean Sea, with notes on combination cells of *Daktylethra pirus* and *Syracosphaera pulchra*. *Plant Biosystems*, **136**: 3–28.
- Thomsen, H.A., Østergaard, J.B. & Hansen, L.E. 1991. Heteromorphic life histories in Arctic coccolithophorids (Prymnesiophyceae). *Journal of Phycology*, **27**: 634–642.
- Triantaphyllou, M.V. & Dimiza, M.D. 2003. Verification of the *Algirosphaera robusta*–*Sphaerocalyptra quadridentata* (coccolithophores) life-cycle association. *Journal of Micropaleontology*, **22**: 107–111.
- Triantaphyllou, M.V., Dermitzakis, M.D. & Dimiza, M.D. 2002. Holoand heterococcolithophorids (calcareous nannoplankton) in the gulf of Korthi (Andros island, Aegean Sea, Greece) during late summer 2001. *Revue de Paleobiologie*, **21** (1): 353–369.
- Triantaphyllou, M.V., Dimiza, M.D. & Dermitzakis, M.D. 2004. *Syracosphaera halldalii* and *Calyptrolithina divergens* var. *tuberosa* life-cycle association and relevant taxonomic remarks. In: Triantaphyllou, M.V. (Ed.), *Advances in the biology, ecology and taphonomy of extant calcareous nannoplankton*. *Micropaleontology*, **50** (suppl. 1): 121–126.
- Young, J. & Geisen, M. 2002. Xenospheres – Associations of coccoliths resembling coccospheres. *Journal of Nannoplankton Research*, **24**: 27–35.
- Young, J.R. & Henriksen, K. 2003. Biomineralization within vesicles: the calcite of coccoliths. *Reviews in Mineralogy and Geochemistry*, **54**: 189–215.
- Young, J.R., Bergen, J.A., Bown, P.R. *et al.* 1997. Guidelines for coccolith and calcareous nannofossil terminology. *Palaeontology*, **40**: 875–912.
- Young, J.R., Jordan, R.W. & Cros, L. 1998. Notes on nannoplankton systematics and life-cycles – *Ceratolithus cristatus*, *Neosphaera coccolithomorpha* and *Umbilicosphaera sibogae*. *Journal of Nannoplankton Research*, **20**: 89–99.
- Young, J.R., Davis, S.A., Bown, P.R. & Mann, S. 1999. Coccolith ultrastructure and biomineralisation. *Journal of Structural Biology*, **126**: 195–215.
- Young, J., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I. & Østergaard, J. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue*, **1**: 125pp.
- Young, J.R., Henriksen, K. & Probert, I. 2004. Structure and morphogenesis of the coccoliths of CODENET species. In: Thierstein, H.R. & Young, J.R. (Eds), *Coccolithophores. From Molecular Processes to Global Impact*. Springer-Verlag, Berlin, 327–365.