

SEM-LM STUDY OF HOLOCOCOLITHS PRESERVED IN EASTERN MEDITERRANEAN SEDIMENTS (HOLOCENE/LATE PLEISTOCENE)

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Abstract: A short scanning electron microscope and light-microscopy study of holococcoliths and small heterococcoliths preserved in eastern Mediterranean sapropels and associated sediments (Holocene/Late Pleistocene) has been carried out, in order to resolve taxonomic problems encountered in previous studies.

With the scanning electron microscope, nine species have been found: *Syracosphaera pulchra* HO oblonga-type (*Calyptrosphaera oblonga*), *S. pulchra* HO pirus-type (*Daktylethra pirus*), *Helicosphaera carteri* HO-perforate (*Syracolithus confusus*), *H. carteri* HO-solid (*Syracolithus catilliferus*), *Syracolithus ponticuliferus*, *Syracolithus schilleri*, *Calcidiscus leptoporus* ssp. *leptoporus* HO (*Crystallolithus rigidus*), *Calyptrolithophora papillifera* and *Periphyllophora mirabilis*. Observation of optical characters, in conjunction with SEM structure, have allowed identification of *S. pulchra* HO oblonga- and pirus-type, *H. carteri* HO-solid, *S. ponticuliferus* and *S. schilleri*. Discrimination between *H. carteri* HO-perforate and *Syracolithus dalmaticus* is difficult, since they are structurally and morphologically close. In addition, with the light-microscope, we have observed the holococcolith phase of *C. leptoporus* ssp. *quadriperforatus* (*Syracolithus quadriperforatus*), whilst another holococcolith has been tentatively referred to the genus *Corisphaera/Zygospaera*. Other holococcoliths, not assignable to generic/specific level, have been observed by LM from these sediments. Taxonomic revision of the coccoliths reported from the same area by previous authors has revealed the presence of *Poricalyptra aurisinae*.

We have compared the LM relative abundance records of *H. carteri* and its associated holococcolith phases, *H. carteri* HO-solid and *H. carteri* HO-perforate. Our results indicate that the life-cycle alternation *H. carteri*-holococcolithophore phase has been common from at least the Late Pleistocene and seems to confirm that this represents an ecological strategy as suggested by previous studies. Furthermore, we report the presence of *Gladiolithus striatus* in the fossil record of the eastern Mediterranean.

1. Introduction

Using the scanning electron microscope (SEM), Müller *et al.* (1974) found a moderately diverse holococcolith assemblage, and other small coccoliths, in Holocene/Late Pleistocene sediments from the eastern Mediterranean. Numerous authors have subsequently analysed the Holocene/Late Pleistocene calcareous nannofossil assemblages from the eastern Mediterranean, especially for palaeoceanographical-palaeoenvironmental studies (e.g. Violanti *et al.*, 1991; Castradori, 1992, 1993a; Negri *et al.*, 1999; Negri & Giunta, 2001), related to sapropel deposition (de Lange *et al.*, 1999, and references therein), but also for biostratigraphic studies (e.g. Raffi & Rio, 1979; Rio *et al.*, 1990; Castradori, 1993b). These studies usually utilised smear-slide and light-microscope (LM) observation which does not allow easy identification of small coccoliths (<3mm). More generally, holococcoliths are believed not to be preserved in the fossil record because of their low preservation potential (e.g. Tappan, 1980; Siesser & Winter, 1994). Consequently, potentially interesting, small heterococcoliths (e.g. *Algirosphaera*) and holococcoliths have often been disregarded and/or grouped and reported as unclassified holococcoliths (Violanti *et al.*, 1991; Castradori, 1992; Negri *et al.*, 1999; Negri & Giunta, 2001). Since such coccoliths are often abundant (5% to 30% of

the total percentage of the minor species) in the Holocene/Pleistocene Mediterranean fossil record (Crudeli *et al.*, in prep.), accurate identification of these species should be a priority for palaeoenvironmental-palaeoceanographical studies of this area, based on calcareous nannofossils. This is of particular interest since the recent research of Cros *et al.* (2000), Cortés (2000) and Geisen *et al.* (2000) has established holo-heterococcolith pairings for many key taxa and discussed their ecological implications.

The Milan group, working on sapropels, recognised some different holococcolith taxa in the sediments and developed an informal classification for them. Presented here are the results of a short study carried out at the NHM by DC, in order to attempt to replace this informal classification with accurate identifications from the modern nannoplankton taxonomy. Clarification of reticulofenestrid identifications will be dealt with in a separate publication. (Crudeli *et al.*, submitted). This study included detailed SEM and LM examinations of the holococcoliths in eastern Mediterranean sediments (Holocene/Late Pleistocene) and a comparison with modern holococcoliths in plankton samples. This allowed a partial taxonomic revision of the species identified by Müller *et al.* (1974) from core 3MO67, recovered from the eastern Mediterranean (south of Crete, 34°25'5N, 24°50'E, 1950m

water-depth). Moreover, since *Helicosphaera carteri* and *Syracolithus catilliferus* have been shown to form combination coccospheres (Cros *et al.*, 2000), and since Geisen *et al.* (2002) have propounded that *S. catilliferus* and *Syracolithus confusus* represent a case of intraspecific variability in the morphology of these holococcoliths, herein a comparison has been made with their Holocene/Late Pleistocene fossil record from the eastern Mediterranean, previously obtained by DC. Some remarks on the occurrence and classification of various lower photic zone (LPZ) species and some upper photic zone (UPZ) heterococcoliths are also presented.

2. Material and methods

The sediment samples analysed came from boxcore UM42 (34°57.23'N, 17°51.75'E, water-depth 1375m, core-length 35cm), recovered during the *R/V Urania* Cruise 1994 (Paleoflux MAST II) in the Ionian Sea (Medina Rise area), and from boxcore BC3 (33°22.51'N, 24°46.00'E, water-depth 2180m, core-length 86cm), recovered from the Hellenic Ridge, south of Crete, during *Marion Dufresne* Cruise 81 1995 (Paleoflux MAST II) (Figure 1).

In both cores, the total Ba/Al depth-profile has been used to identify the original thickness of sapropel S1 (Freydier *et al.*, 2001, and references therein) (Figure 2). A reworked interval (E. Schefuß, pers. comm., 2002), and a Holocene tephra layer, are present in the upper part of core UM42 (Figure 2a), whereas the ash layer in core BC3 has been identified as tephra Y-5 (Keller *et al.*, 1978) (L. Vezzoli, pers. comm., 2002) (Figure 2b). The post-sapropel interval of core BC3 has not been analysed by LM. Lithological details of these cores, and of other cores mentioned in the text, can be found at www.geo.unimib.it/Conisma/Sapcores.

Samples for this study were initially chosen based on the abundance and diversity of 'unclassified' species observed by cross-polarised LM (Wild Leitz GMBH, 1250x) analysis (Crudeli *et al.*, in prep.). Selected samples from cores UM42 and BC3 were analysed by SEM (Philips XL30, Field Emission SEM) at the NHM (London), and some 60 holococcoliths were imaged. Filter preparation for SEM study was based on the method of Andruseit (1996). Different holococcoliths, and some small heterococcoliths, were observed and photographed by LM, using a Zeiss

Axioplan 1600x connected to a CCD (Charged Couple Device) camera for image capture (Young *et al.* 1996). Selected images are shown in Plates 1-3.

The relative abundances of *Helicosphaera carteri* heterococcoliths and holococcoliths reported in this work (Figure 2) were obtained from LM (1250x) counts of 100 to 150 coccoliths of minor species (*i.e.* excluding the dominant *Emiliania huxleyi*, and associated overgrowth forms (Crudeli *et al.*, submitted), and *Gephyrocapsa*), with the exclusion of LPZ species, following the concepts of Matsuoka & Okada (1989) and Castradori (1992, 1993a). In total, 94 samples have been studied. For the LM study (1250x and 1600x), unprocessed material was permanently mounted on smear-slides using Norland optical adhesive.

3. Results

In general, for each reported species, SEM observation, previous observations from the Mediterranean sedimentary record, surface-sediments or water-samples (see Table 1 for a summary) are remarked on, and suggestions for LM identification made. The terminology used for the description of coccoliths is based on Young *et al.* (1997). The comparison between coccoliths in the fossil record and living nannoplankton is based on Kleijne (1991) and image catalogues of modern coccolithophores available at the NHM. The taxonomy primarily follows Jordan & Kleijne (1994) and Jordan & Green (1994), whereas for selected holococcoliths the revised terminology suggested by Geisen *et al.* (2002) has been used. Abbreviations used for LM observation: XPL (crossed-polars), TL (transmitted light), and PC (phase-contrast).

3.1. Holococcoliths

SEM observations confirmed a significant abundance of well- to moderately-preserved holococcoliths in these samples (Table 1a). Holococcolith fragments, and some holococcoliths difficult to identify to species level, were also observed. In selected samples from sapropel S1, a high specific-diversity of commonly-occurring holococcoliths was qualitatively observed, whereas in non-S1 samples, even if some holococcoliths were found, the overall specific-diversity observed was lower. Although

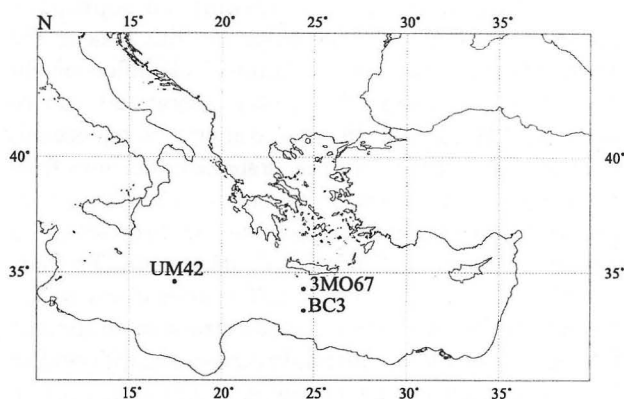


Figure 1: Location of boxcores UM42 and BC3, eastern Mediterranean Sea. Core 3MO67 studied by Müller *et al.* (1974) is also shown. Positions given in the text

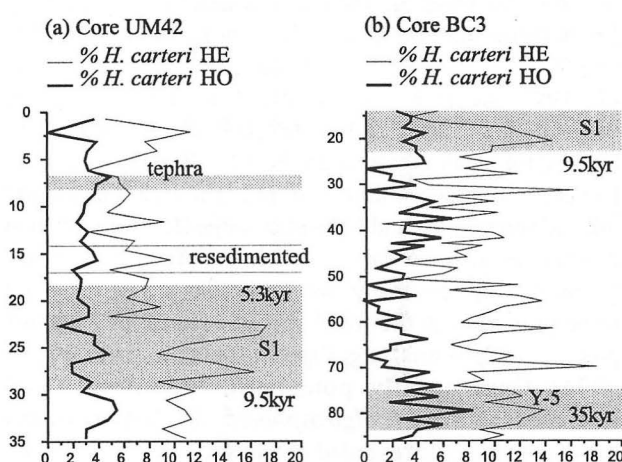


Figure 2: Relative abundance of *Helicosphaera carteri* and *H. carteri* HO in cores UM42 (a) and BC3 (b)

Author	Type of sample	Type of observation	(a) Holococcolithophorids	(b) LPZ Heterococcolith	(c) UPZ Heterococcoliths
			<i>S. pulchra</i> HO oblonga-type (<i>C. oblonga</i>) <i>S. pulchra</i> HO pirus-type (<i>D. pirus</i>) <i>H. carteri</i> HO-perforate (<i>S. confusus</i>) <i>H. carteri</i> HO-solid (<i>S. catilliferus</i>) transitional form <i>H. carteri</i> HO-perforate-solid (+) <i>S. dalmaticus</i> <i>S. ponticuliferus</i> (+) <i>S. schilleri</i> <i>C. leptoporus</i> ssp. <i>quadriperforatus</i> HO (<i>S. quadriperforatus</i>) <i>C. leptoporus</i> ssp. <i>leptoporus</i> HO (<i>C. rigidus</i>) <i>C. papillifera</i> <i>P. mirabilis</i> <i>P. aurisinae</i>	<i>F. profunda</i> var. <i>striata</i> <i>G. striatus</i> <i>A. robusta</i> <i>A. meteora</i> (+)	<i>Acanthoica</i> <i>Alisphaera</i> <i>M. adriaticus</i> <i>M. elegans</i> <i>S. anthos</i> <i>S. nodosa</i> <i>S. ossa</i> <i>S. lamina</i>
This study	#	LM	* * * *	*	
This study	#	SEM	* * * *	* * *	* * * *
Muller <i>et al.</i> (1974)	#	SEM	* † †	†	* *
Knappertsbusch (1993)	##	LM	* *		
Ziveri <i>et al.</i> (2000a)	##	SEM	* *	*	*
Kleijne (1991)	###	SEM	* * * *		
Knappertsbusch (1993)	###	SEM	* * * *	*	* * *
Ziveri <i>et al.</i> (2000a)	###	SEM	* * *	*	*
Cros <i>et al.</i> (2000)	###	SEM	* * *		*
Cros (2002)	###	SEM	* * * *	*	*
Geisen <i>et al.</i> (in press)	###	SEM-LM	* * * *		*
Kleijne (1993)	###	SEM			* *

Table 1: List of (a) holococcolithophores and selected (b) lower (LPZ) and (c) upper photic zone (UPZ) heterococcolithophores observed in this study and/or recorded in the literature in sediment (#), surface sediment (##) and water samples (###). + refers to species observed during a previous low resolution SEM study. † refers to misidentified species. ? refers to names only tentatively assigned (see text for explanation). NB From surface sediments, Knappertsbusch (1993) reported holococcoliths mainly as an ‘unidentified holococcoliths’ group; Kleijne (1991) deals only with holococcolithophores.

about 60 species of extant holococcoliths are known, the specimens found here come from far fewer species and can be divided into three groups, based on their SEM structure, LM appearance and known association with heterococcolith species. Following Cros *et al.* (2000) and Geisen *et al.* (2002), we have used revised taxonomic designations based on the life-cycle associations.

3.1.1. *Syracosphaera pulchra* holococcoliths
The holococcoliths conventionally regarded as discrete species, *Calyptrorphaera oblonga* and *Daktylethra pirus*, are now known to both be produced by *Syracosphaera pulchra* (Cros *et al.*, 2000; Saugestad & Heimdal, 2002; Geisen *et al.*, 2002). The informal terms *S. pulchra* HO oblonga-type and *S. pulchra* HO pirus-type were recommended by Geisen *et al.* (2002) and are used here for these holococcoliths. Geisen *et al.* (2002) noted that the two holococcolith types were well differentiated and inferred that this is a case of recent (sub)speciation in which morphological divergence has only occurred in the

holococcolith phase.
S. pulchra HO oblonga-type (*Calyptrorphaera oblonga*): By SEM, both well-preserved and broken calyptroliths have been observed (Plate 1, Figures 1, 4). It has previously been reported as *C. oblonga* by Müller *et al.* (1974) from the eastern Mediterranean fossil record, whereas Knappertsbusch (1993) and Ziveri *et al.* (2000a) found it in surface sediments. In living assemblages, the form is widely reported from the Mediterranean (Kleijne, 1991; Knappertsbusch, 1993; Ziveri *et al.*, 2000a; Cros *et al.*, 2000; Cros, 2002). *S. pulchra* HO oblonga-type is readily identifiable by LM, both from side and distal views (Plate 1, Figures 2, 3, 5, 6). In side view, these coccoliths are dome-shaped with radial calcite *c*-axes (perpendicular to the coccolith wall). In plan view the rim is birefringent, showing a radial pseudoextinction cross, whilst the crystallites of the distal surface appear as a distinctive dark fill in PC. By LM, with XPL and gypsum-plate, the rim interference colours are yellow in the first and third quadrants (clockwise) and blue in the second and fourth

quadrants, with radial extinction, whereas the central-area shows uniform purple colours.

S. pulchra HO *pirus*-type (*Daktylethra pirus*): SEM analyses have revealed the presence of this species (Plate 1, Figures 7, 10). This form is often overgrown. In Mediterranean sediments, Müller *et al.* (1974, pl.1, figs 5, 6) reported *Homozygosphaera tholifera*. Here, their *H. tholifera* images are interpreted as corresponding to *S. pulchra* HO *pirus*-type. Ziveri *et al.* (2000a) found specimens (reported as *Calyptosphaera pirus*) in surface-sediment samples. The holococcolithophore is common in the living Mediterranean nannoflora (Kleijne, 1991; Knappertsbusch, 1993; Ziveri *et al.*, 2000a; Cros, 2002). Both the side and distal views of the coccoliths are distinctive in the LM (Plate 1, Figures 8, 9, 11, 12). The crystallography is similar to that of *S. pulchra* HO *oblonga*-type but the profile in side view is distinctly different: there is a secondary dome above the tube. In plan view, the distinction can be trickier, but characteristically the wall of the secondary dome forms a second birefringent ring inside the wall. This is commonly better seen in XPL with a gypsum-plate.

3.1.2. *Helicosphaera carteri* HO-solid and -perforate types (*Syracolithus catilliferus*-*Syracolithus confusus*) Cros *et al.* (2000) provided definitive evidence, from combination coccospheres, that the holococcolithophore *S. catilliferus* is, in fact, a life-cycle stage of *H. carteri*. They also showed that *S. catilliferus* and *S. confusus* are not discrete genotypes but intergradational morphotypes, characterised by absence/presence of pits on the distal surface. Geisen *et al.* (2002) provided further evidence for this conclusion. Consequently, they recommended that these morphotypes should only be distinguished informally, as *H. carteri* HO-solid and -perforate types. By SEM, proximal views of *H. carteri* holococcoliths were frequently observed but, in this view, the two morphotypes are indistinguishable. Relatively few distal views were seen, from which both morphotypes could be distinguished, although only good images of the perforate (*S. confusus*) morphotype were captured (Plate 2, Figure 1). Additionally, a coccolith observed during low-resolution SEM in an S1 sample from BC19 was identified as a transitional form between the two morphotypes (Plate 2, Figure 4), similar to that found by Cros (2002, pl.89, fig.1) on a single coccosphere from the western Mediterranean (L. Cros & A. Kleijne, pers. comms, 2002) and also observed by Geisen *et al.* (2002, figs 4, 5).

H. carteri holococcoliths are relatively common in Mediterranean surface-waters and have also been illustrated from Holocene sediments by Müller *et al.* (1974), variously identified as *Sphaerocalyptra papillifera* (their pl.1, fig.14), *S. catilliferus* (their pl.1, fig.13) and *Syracolithus dalmaticus* (their pl.2, fig.1). *H. carteri* HO-solid type was also reported from surface sediments by Knappertsbusch (1993).

H. carteri holococcoliths are unusual in being formed predominantly of a single mass of rhombohedral crystallites with aligned *c*-axes with only a narrow rim of crystallites with radial *c*-axes, which is not usually preserved in fossil specimens. In the LM, this means they appear as

a single, birefringent block, except when oriented N-S or E-W. The perforate and solid types are easily separated in the LM since the pits show much lower birefringence than the main mass. Conversely, the central boss is distinctly brighter than the main mass of the holococcolith (Plate 2, Figures 2, 3, 5). In detail, forms show extinction close to the N-S and E-W direction. When the rim is preserved, it appears as a very thin, birefringent ring difficult to detect in XPL and/or TL. However, the rim is better seen in XPL with a gypsum-plate; within the same quadrant, the crystallographic *c*-axes of microcrystals show opposite yellow-blue colours with radial extinction, whereas the main masses and the central boss have uniform colour (*c*-axis of crystallites have the same orientation). In detail, the central boss has the same orientation of the main mass but is distinguishable in having brighter colour (pale yellow/pale blue) due to its greater thickness with respect to the main mass.

In these sediments, overgrowth has a variable effect on the coccoliths (Crudeli *et al.*, submitted). In XPL, overgrowth of crystallites of *H. carteri* HO-solid results in a very bright figure due to increased thickness of the crystallites (Plate 2, Figure 6). However, marked overgrowth obscures distinction between the central boss and main mass (Plate 2, Figure 7). Similarly, we cannot exclude that overgrowth of HO-perforate gives a similar LM appearance if the perforations are closed. The interference colours of the main mass (XPL) are commonly white-yellow in relation to the thickness of the crystallites. Since overgrowth is an early diagenetic process, the external rim is quite often preserved in overgrown coccoliths (Plate 2, Figures 6, 7).

3.1.3. Other '*Syracolithus*' holococcoliths

From SEM observations, Kleijne (1991) defined laminoliths as a distinctive type of holococcolith with a structure of numerous layers, or laminae, of rhombic crystallites. She noted that species bearing such coccoliths were always monomorphic (*i.e.* lacked differentiated circumflagellar coccoliths) and included them in an emended genus, *Syracolithus*. LM observations herein confirm the distinctive nature of the laminolith structure, and the association with *Helicosphaera* suggests that this is a phylogenetically discrete group.

Of the other species included in *Syracolithus* by Kleijne (1991), *S. dalmaticus* and *S. ponticuliferus* display similar ultrastructure and LM appearance to the *H. carteri* holococcoliths. Two others, however, *S. schilleri* and *S. quadriperforatus*, are rather different; in SEM they resemble typical laminoliths with very large pits, although the microcrystals lack the obvious coalignment of true laminoliths. In the LM, this subtle difference proves highly significant. The entire central mass is dark in XPL, and only the rim is birefringent (*e.g.* Plate 2, Figure 9). This indicates that the crystallites of the central mass have subvertical *c*-axes. This major difference in crystallographic orientation suggests that the two '*Syracolithus*' types are unrelated homoeomorphs and, indeed, *S. quadriperforatus* has now been shown to be the alternate life-cycle stage of a subspecies of *Calcidiscus leptoporus* (Geisen *et al.*, 2002).

All these species have been reported from

Mediterranean nannofloras (e.g. Kleijne, 1991; Knappertsbusch, 1993; Ziveri *et al.*, 2000a; Cros, 2002), and isolated specimens were noted in this study (Plate 2, Figures 8, 11, 12). Most noteworthy is *Syracolithus schilleri*, which is rare in the plankton but distinctly larger than most holococcoliths and is rather more frequent and distinctive in the sediments. Müller *et al.* (1974, pl.1, fig.9) illustrated one such specimen as *Holodiscolithus macroporus*. Similar holococcoliths are sporadically reported, as *H. macroporus*, throughout the Neogene (e.g. Young, 1998).

3.1.4. Other species

Calcidiscus leptoporus ssp. *leptoporus* HO (*Crystallolithus rigidus*): From the western Mediterranean, a coccosphere with a combination of the heterococcolithophore species *Calcidiscus leptoporus* and *Crystallolithus rigidus* was presented by Kleijne (1991), and this life-cycle association has been confirmed by further plankton observations (Renaud & Klaas, 2001) and from culture observations (Geisen *et al.*, 2002). Several *C. leptoporus* ssp. *leptoporus* holococcoliths were observed by SEM (Plate 3, Figure 1). It was not, however, identified by LM. It is likely to be inconspicuous, since the holococcolith is thin and the *c*-axes are oriented vertically.

Calyptrolithophora papillifera: A single coccolith of *C. papillifera* was observed by SEM (Plate 3, Figure 2). In the Mediterranean, the species has been reported from living assemblages by Kleijne (1991), Knappertsbusch (1993), Ziveri *et al.* (2000a) and Cros (2002), and from surface sediments (Ziveri *et al.*, 2000a). Cros *et al.* (2000) reported a coccosphere of *C. papillifera* with *Syracosphaera histrica* at a NW Mediterranean station, but they regarded this association as unconvincing.

Syracosphaera anthos HO (*Periphyllophora mirabilis*): Two combination coccospheres of *P. mirabilis* and *S. anthos* were illustrated by Cros *et al.* (2000), demonstrating a life-cycle association of these species. A single holococcolith was observed by SEM (Plate 3, Figure 3) but it has not been identified by LM, probably because it is rare. *P. mirabilis* was also recorded by Müller *et al.* (1974, pl.1, fig.8) from the Mediterranean fossil record, whereas Kleijne (1991), Knappertsbusch (1993), Cros *et al.* (2000) and Cros (2002) reported the species from living Mediterranean nannofloras.

Unclassified holococcoliths: By LM, a holococcolith tentatively assigned to the genus *Corisphaera/Zygospaera* has been observed (Plate 3, Figure 4). In XPL, the main mass of the holococcolith is birefringent, with two symmetrical, low-birefringence pits and a thin, grey rim at the outer boundary of the pits. In XPL with a gypsum-plate, the main mass shows interference colours (blue first and third quadrants) opposite to those of the microcrystals at the outer boundary of the pits (yellow first and third quadrants). These coccoliths are, thus, clearly separable from *S. ponticuliferus*, which also has two symmetrical, low-birefringence perforations, but which behave as a single block.

Holococcolith type F (?*Poritectolithus*): Small, elliptical holococcoliths, characterised by central-areas

showing a pattern of oblique stripes in XPL and a pseudo-hexagonal figure in TL, have been observed in these sediments and referred to as Holococcolith type F (Plate 3, Figure 5). This holococcolith has a birefringent rim, with a radial extinction cross only on the side of the coccolith. Thus, it is likely that this form is not exactly parallel to the plane of view. The main mass is in extinction when oriented N-S and E-W and birefringent at 45°. A possible identification is *Poritectolithus poritectum*, which displays oblique bands of crystallites covering the central-area, but XPL observations have not been made on modern specimens so this identification is tentative. Other unidentified, elliptical holococcoliths, with a variable number/size/disposition of pores and the absence of a clear, brighter central area have been qualitatively observed by LM.

Species 1 (*sensu* Castradori, 1992), a small, elliptical (holococcolith?) species, often found abundantly in the Mediterranean fossil record (Violanti *et al.*, 1991; Castradori, 1992, 1993a; Negri *et al.*, 1999) has not been positively identified. In plan view and XPL, this coccolith has a birefringent rim with a radial pseudoextinction cross similar to *S. pulchra* HO *oblonga*-type and HO *pirus*-type, whilst the central-area is filled with numerous, small birefringent blocks. Further studies are needed to clarify the taxonomy of this form.

3.1.5. Fossil record of *H. carteri* and associated holococcolith life-cycle stages

This SEM-LM study has allowed identification of the holococcolith stages of *H. carteri* by LM (at 1250x magnification). Since the *H. carteri* holococcoliths are quite common, it is possible to use this data to compare, for the first time, the fossil record of the holococcolith and heterococcolith stages of a single species. For this comparison, the solid and perforate types are combined. These counts may also contain some *Syracolithus dalmaticus* specimens, since this species cannot reliably be differentiated from *H. carteri* HO-perforate by LM. *H. carteri* HO-solid and HO-perforate types, together with *S. dalmaticus*, are here termed *H. carteri* HO (Figure 2a, b).

In the lower part of UM42, *H. carteri* forms up to 10% of the minor species and shows two remarkable peaks (>15%) within the sapropel (Figure 2a). In BC3, *H. carteri* reveals high-amplitude fluctuations in relative abundance (>1%, <18%) from the core-bottom up to 25cm; the species shows abundance values of 10% just below S1 and a peak just near the sapropel base (14.6%) (Figure 2b). In UM42, *H. carteri* HO shows average relative abundance values of 3%, reaching a percentage of >3% within short intervals below, within, and above S1 (Figure 2a). In the other core, *H. carteri* HO reveals high amplitude-fluctuations in relative abundance and has values of >3% in the lower (between 85cm and 70cm from the core-top) and middle (43cm-32cm) parts of the core (Figure 2b). *H. carteri* HO increases in abundance from just before S1's initiation (at about 25cm) throughout the sapropel, where it reaches values of >3% (Figure 2b).

3.1.6. Revision of taxa identified by Müller et al. (1974)
From the Mediterranean record, Müller et al. (1974, pl.1, fig.15) reported the presence of *Helladosphaera aurisinae*, which is now identified as *Poricalyptra aurisinae*. The holococcolith was not found during this study (Table 1a), but it is present in the Mediterranean (Knappertsbusch, 1993) and in NW Mediterranean waters (Cros, 2002). Here it is noted that *Helladosphaera cornifera*, *Helladosphaera strigilis* and *Corisphaera arethusae*, all observed by Müller et al. (1974, pl.1, figs 10-12, respectively) could not be positively identified to species level.

3.2. LPZ species - some remarks

During these SEM-LM analyses, the LPZ species *Florisphaera profunda*, *Algirosphaera robusta*, *Algirosphaera meteora*, *Gladiolithus flabellatus*, and *Gladiolithus striatus* have been observed. Since *F. profunda* and *G. flabellatus* are common in the Mediterranean (e.g. Ziveri et al., 2000a; Castradori, 1993a), Table 1b shows previous authors' observations only for selected LPZ species. Some remarks on occurrence and LM identification are discussed here for *A. robusta*, *G. flabellatus* and *G. striatus*.

***Algirosphaera robusta*:** By SEM and LM, both well-preserved coccoliths and fragments of *A. robusta* (Plate 3, Figures 6-8) were frequently observed. Since fragments of lamellar elements are difficult to recognise with the LM, this results in an underestimation of *A. robusta* coccoliths during LM quantitative analyses, and in counting-method problems during SEM study. This species has previously been reported by Müller et al. (1974, pl.1, fig.3) from the Holocene/Late Pleistocene eastern Mediterranean as *Anthosphaera quadricornu*, and as *Anthosphaera robusta* (their pl.1, fig.4). Knappertsbusch (1993) and Ziveri et al. (2000a) recorded *A. robusta* (the latter authors reported it as *A. oryza*) from Mediterranean water and surface-sediment samples (Ziveri et al., 2000a). As shown by Kleijne (1992), the highly variable outline of the sacculiform protrusion (both in distal and lateral view) explain the difficulties in identification and related synonymy. The Late Quaternary record of *A. robusta* was reported for the first time by Okada & Matsuoka (1996, pl.1, figs 3-6: Indian Ocean), with particularly useful TEM and LM micrographs. Following Kleijne (1992), they assigned all specimens of the genus *Algirosphaera* to *A. robusta*.

***Algirosphaera meteora*:** By SEM, a single coccolith of *A. meteora* was observed (Plate 3, Figure 9) from SL29. The species is rarer than *A. robusta* and has been previously found by Müller et al. (1974, pl.1, figs 1, 2) but has not been reported from surface- or water-samples.

***Gladiolithus flabellatus* and *Gladiolithus striatus*:** Here, for the first time, the presence of the recently described species, *Gladiolithus striatus*, is reported from the eastern Mediterranean. A tabular coccolith, lacking the basal plate, has been observed in one sapropel sample from BC3 (Plate 3, Figure 10). This LPZ species was first observed by Hagino & Okada (1998) in samples from the equatorial and subtropical Pacific Ocean (149m to 199m water-depth). In the LM, the tabular coccoliths, and their disintegrated elements, of *G. striatus* are not easy to

distinguish from *G. flabellatus* elements since they have a similar outline in plan view. The species is likely to be very rare in the Mediterranean. In fact, *G. striatus* was only found in one sample, and so far no living coccospheres have been reported from this basin.

3.3. Other UPZ species

During SEM analysis, some coccoliths were found of well-described, living nannoplankton from the UPZ, some of which have never been observed previously in eastern Mediterranean sediments. Table 1c summarises previous authors' observations on these heterococcoliths. The group includes the genera *Acanthoica* and *Alisphaera*, and the species *Michaelsarsia adriaticus*, *Michaelsarsia elegans*, *Syracosphaera anthos*, *Syracosphaera nodosa* and *Syracosphaera ossa*. One coccolith has been tentatively assigned to *Syracosphaera lamina-Syracosphaera tumularis*. Most of these taxa have been observed in S1 samples from core BC3. From the eastern Mediterranean fossil record, Müller et al. (1974) previously observed *S. anthos*, reported as *Deutschlandia anthos* (their pl.3, fig.2), and *S. lamina* (their pl.3, fig.16).

4. Discussion

4.1. Holococcoliths - SEM-LM observations

In the samples analysed by SEM, nine holococcoliths have been identified, including the species observed during low-resolution SEM study (Table 1a). Four of these have been previously reported by Müller et al. (1974) from the Holocene/Late Pleistocene Mediterranean fossil record. In addition, they reported *Poricalyptra aurisinae*, a holococcolith that has not been observed in this study. By LM, we have identified *Poricalyptra quadriperforatus* (Table 1a), and additional holococcoliths not yet positively identified (Plate 3, Figures 4, 5), so the total diversity in these sediments is probably rather high. However, the species diversity of holococcoliths in the living Mediterranean nannoflora (Kleijne, 1991; Cros, 2002) is still much higher than that observed in the analysed sediments.

Delicate holococcoliths are more prone to dissolution compared to heterococcoliths (e.g. Tappan, 1980), and they are selectively dissolved throughout the water-column (Ziveri et al., 2000b). The Mediterranean basin is carbonate saturated with respect to the ocean, and holococcoliths have a relatively good chance of reaching the sea-floor (Ziveri et al., 2000a) and, consequently, to be preserved in the fossil record (e.g. Castradori, 1992; this work). However, in sediment-trap samples from the eastern Mediterranean (3000m water-depth), 11 species of holococcoliths are present, whereas surface-sediments close to the trap location contain only eight species (Ziveri et al., 2000a, tab.3), suggesting that some dissolution of holococcoliths occurs in the water-column and/or within the sediment. Similarly, the number of living species observed in surface-waters from the NW Mediterranean is higher than in the underlying surface-sediments, suggesting their partial dissolution (Cros, 2002) throughout the water-column and/or within the sediments. In particular, within sapropel S1, the common presence of fragments of *Algirosphaera robusta*, mechanical breakage

and partial detachment of crystallites of selected holococcoliths (observed herein), and the presence of etched *Emiliania huxleyi* coccoliths (Malinverno *et al.*, 2002; Crudeli *et al.*, submitted) indicate the effects of carbonate dissolution on the calcareous nannoflora. Thus, selective dissolution explains the lower specific diversity of holococcoliths observed in the sediments. The fact that only selected holococcoliths have been observed in the sediments indicates that their structure is more favourable to preservation. In the case of syracoliths (*sensu* Kleijne, 1991), the compacted and simple crystal disposition could favour preservation. *Syracosphaera pulchra* holococcoliths have been observed in these sediments, indicating that they are quite resistant to dissolution in comparison to the holococcoliths of other living species. However, *S. pulchra* holococcoliths seem to have a lower preservation potential than syracoliths (Crudeli *et al.*, in prep.). The findings presented here, of moderately diverse and relatively abundant delicate holococcoliths within selected samples, including sapropel samples (Plates 1-3), also suggest variable but moderate effects of carbonate dissolution in the eastern Mediterranean sediments.

4.2. Fossil record of *Helicosphaera carteri* and associated holococcolith life-cycle stages

Whilst the Late Quaternary fossil record of *H. carteri* in the Mediterranean is well known (e.g. Negri *et al.*, 1999; Negri & Giunta, 2001; Corselli *et al.*, 2002), at present almost nothing is known about the spatial and temporal distribution of the holococcolith bearing-phases (Cros *et al.*, 2000; Cros, 2002; Geisen *et al.*, 2002), principally because of uncertainty in their LM identification (e.g. Kleijne, 1991). The occurrence of *H. carteri* with the presence of *H. carteri* HO suggests that their life-cycle alternation has been common for at least the last 35kyr (Figures 2a, b). In discussing the life-cycle alternation of *H. carteri* and related holococcolithophore phases, Cros *et al.* (2000) suggested that this most probably represents an ecological strategy. They indicated that *H. carteri* proliferates in the upper photic zone, near the chlorophyll maximum, whereas *H. carteri* HO-solid lives in the upper 30m of the surface-water. During the sampling time, the water-column was stratified and a well-developed chlorophyll maximum was present between 40 and 70m (Cros *et al.*, 2000).

In core BC3, an increase in relative abundance of *H. carteri* HO associated with a discontinuous trend of *H. carteri* throughout sapropel S1 was observed (Figure 2b). The fact that, in core UM42, *H. carteri* HO are >3% in relative abundance only within a short interval is likely related to more pervasive dissolution effects on holococcoliths at this site. Different studies have suggested the existence of a deep chlorophyll maximum (DCM) during sapropel deposition (Rohling & Gieskes, 1989; Castradori, 1992, 1993a; Kemp *et al.*, 1999; Corselli *et al.*, 2002), whereas an oligotrophic condition of the surface-waters has been suggested on the basis of geochemical proxies (Sachs & Repeta, 1999) and calcareous nannofossil studies (Corselli *et al.*, 2002). The data presented here could suggest that, during S1 deposition, *H. carteri* proliferated near/at the DCM, whereas *H. carteri* HO was present in

the upper, less productive surface-water and that most probably the coccolithophore productivity was strictly confined at this depth. These results seem to confirm the suggestion of Cros *et al.* (2000) that *H. carteri* and associated holococcolithophore phases represent an ecological strategy.

A weak increase in the relative abundance of *H. carteri* HO in the lower and middle parts of core BC3 was also observed (Figure 2b). In particular, the sea-surface temperature curve from the Alboran Sea shows a general increase in values between ~31 and 35kyr BP (Cacho *et al.*, 2000). In addition, the $\delta^{18}\text{O}$ curve from the Arabian Sea provides a continuous record of oxygen isotope minima between ~31 and 35kyr BP (Schulz *et al.*, 1998). It seems likely that this warming trend favoured the proliferation of the holococcolithophore phases of *H. carteri*, whereas during the glacial period the heterococcolith phase dominated.

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Taxonomic appendix

The following list gives full citations for the taxa reported in the text. The taxonomy primarily follows Jordan & Kleijne (1994) and Jordan & Green (1994), and bibliographic references can be found therein. Terminology based on holococcolith-heterococcolith life-cycle associations suggested by Cros *et al.* (2000) and Geisen *et al.* (2002) is followed by the traditional names, given in square brackets.

Holococcoliths

Calcidiscus leptoporus ssp. *leptoporus* (Geisen *et al.*, 2002) HO [*Crystallolithus rigidus* Gaarder in Heimdal & Gaarder, 1980]

Calcidiscus leptoporus ssp. *quadriperforatus* (Geisen *et al.*, 2002) HO [*Syracolithus quadriperforatus* (Kamptner, 1937) Gaarder, 1962]

Calyptrolithophora papillifera (Halldal, 1953) Heimdal in Heimdal & Gaarder, 1980

Corisphaera Kamptner, 1937

Helicosphaera carteri HO-perforate type of Cros *et al.* (2000) [*Syracolithus confusus* Kleijne, 1991]

Helicosphaera carteri HO-solid type of Cros *et al.* (2000) [*Syracolithus catilliferus* (Kamptner, 1937) Deflandre, 1952]

Periphyllophora mirabilis (Schiller, 1925) Kamptner, 1937

Poricalyptra aurisinae (Kamptner, 1941) Kleijne, 1991

Syracolithus dalmaticus (Kamptner, 1927) Loeblich & Tappan, 1966

Syracolithus ponticuliferus (Kamptner, 1941) Kleijne & Jordan, 1990

Syracolithus schilleri (Kamptner, 1927) Loeblich & Tappan, 1963

Syracosphaera anthos (Lohmann, 1912) Janin, 1987 HO [*Periphyllophora mirabilis*]

Syracosphaera pulchra HO *oblonga*-type of Geisen *et al.* (2002) [*Calyptrosphaera oblonga* Lohmann, 1902]

Syracosphaera pulchra HO *pirus*-type of Geisen *et al.* (2002) [*Daktylethra pirus* (Kamptner, 1937) Norris, 1985]

UPZ heterococcoliths

Acanthoica Lohmann, 1903 emend. Schiller, 1913, Kleijne, 1992

Alisphaera Heimdal, 1973 emend. & Chamberlain, 1993, Kleijne *et al.*, 2002

Calcidiscus leptoporus (Murray & Blackman, 1898) Loeblich & Tappan, 1978

Helicosphaera carteri (Wallich, 1978) Kamptner, 1954 var. *carteri*

Michaelsarsia adriaticus (Schiller, 1914) Manton *et al.*, 1984

Michaelsarsia elegans Gran, 1912, emend. Manton *et al.*, 1984

Syracosphaera pulchra Lohmann, 1902

Syracosphaera anthos (Lohmann, 1912) Janin, 1987

Syracosphaera histrica Kamptner, 1941

Syracosphaera lamina Lecal-Schlauder, 1951

Syracosphaera nodosa Kamptner, 1941

Syracosphaera ossa (Lecal, 1966) Loeblich & Tappan, 1968

Syracosphaera tumularis Sanchez-Suarez, 1990

LPZ heterococcoliths

Algirosphaera meteora (Müller, 1972) Norris, 1984

Algirosphaera robusta (Lohmann, 1902) Norris, 1984

Florisphaera profunda Okada & Honjo, 1973

Gladiolithus flabellatus (Halldal & Markali, 1955) Jordan & Chamberlain, 1993

Gladiolithus striatus Hagino & Okada, 1998

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Plate captions

For each image (SEM and LM), the core code, sample code, sample depth from the top of the core, image code and repository location are indicated. SEM scale-bars = 1 µm

Plate 1

Scale-bar for LM images indicated in Figure 2

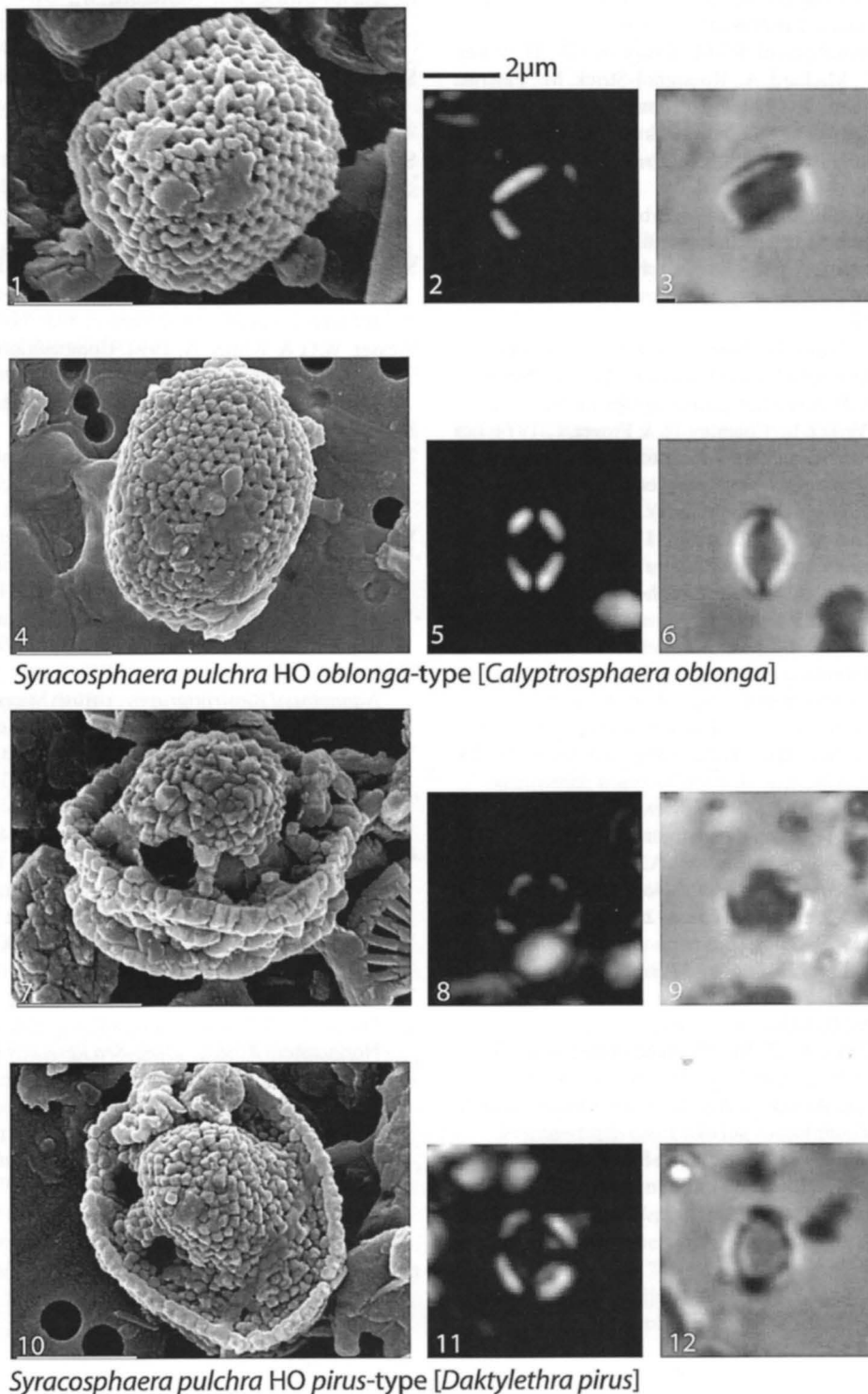


Fig.1: *S. pulchra* HO *oblonga*-type (*C. oblonga*). SEM of calyptrolith in side view; UM42, sample DD01344, 18.65cm; JY158-35, NHM. **Figs 2, 3:** *S. pulchra* HO *oblonga*-type. LM of calyptrolith in side view; UM42, sample DD01364, 28.65cm; 2, XPL, DD01364-1/56, NHM, 3, PC, same specimen, DD01364-1/57, NHM. **Fig.4:** *S. pulchra* HO *oblonga*-type. SEM of calyptrolith in distal view; UM42, sample DD01352, 22.65cm; JY158-12, NHM. **Figs 5, 6:** *S. pulchra* HO *oblonga*-type. LM of calyptrolith in distal view; BC3, sample EE0169, 29cm; 5, XPL, coccosph-EE0169/9, NHM, 6, PC, same specimen, coccosph-EE0169/10, NHM. **Fig.7:** *S. pulchra* HO *pirus*-type (*D. pirus*). SEM of holococcolith in side view; UM42, sample DD01348, 20.65cm; JY159-4, NHM. **Figs 8, 9:** *S. pulchra* HO *pirus*-type. LM of holococcolith in side view; UM42, sample DD01364, 28.65cm; 8, XPL, DD01364-1/3, NHM, 9, PC, same specimen, DD01364-1/4, NHM. **Fig.10:** *S. pulchra* HO *pirus*-type. SEM of holococcolith in distal view; UM42, sample DD01344, 18.65cm; JY158-34, NHM. **Figs 11, 12:** *S. pulchra* HO *pirus*-type. LM of holococcolith in distal view; BC3, sample EE0169, 29cm; 11, XPL, coccosph-EE0169/13, NHM, 12, PC, same specimen, coccosph-EE0169/12, NHM.

Plate 2

Scale-bar for LM images indicated in Figure 12 (shown separately)

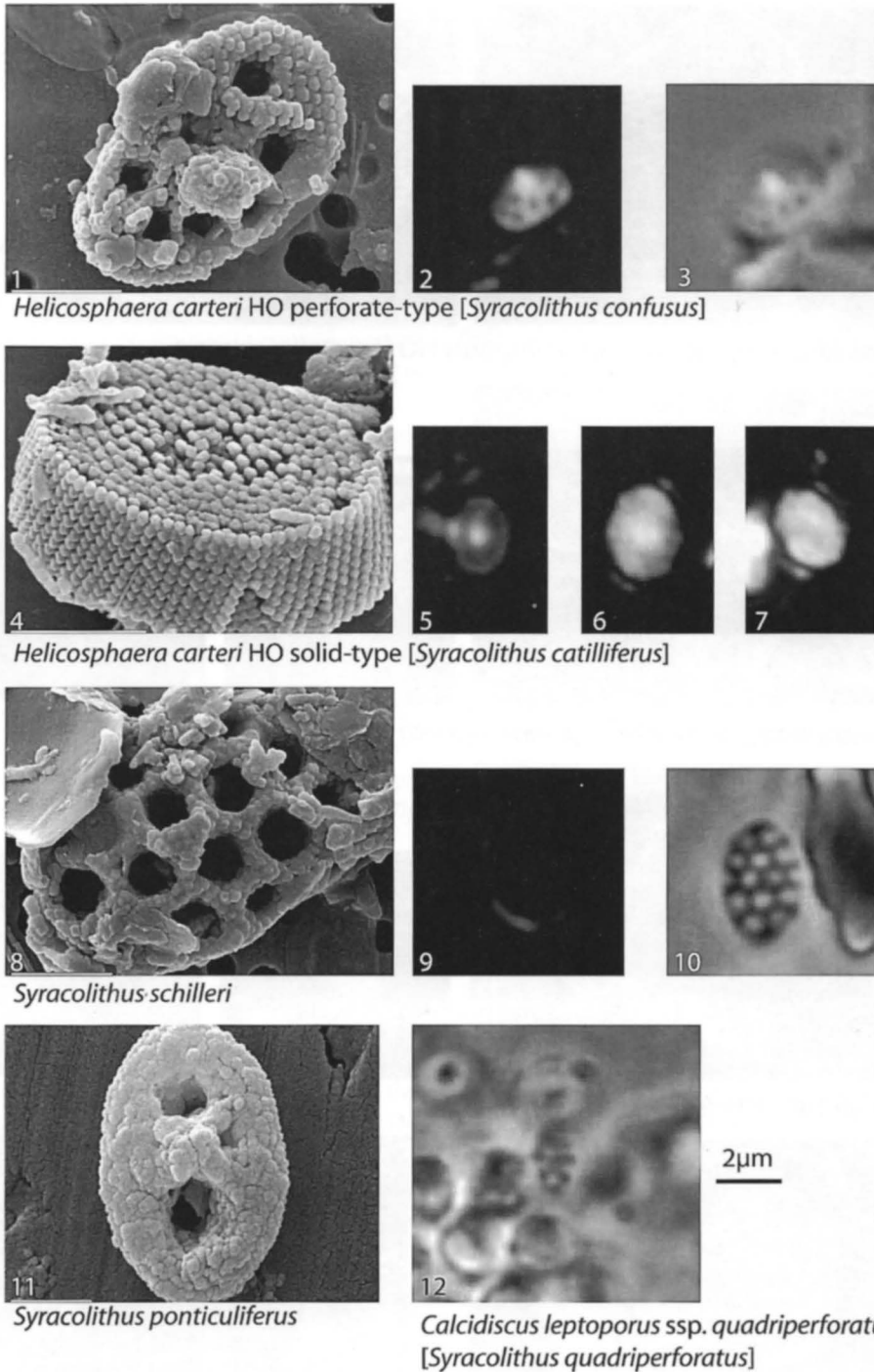


Fig.1: *H. carteri* HO-perforate (*S. confusus*). SEM of holococcolith in distal view; BC3, sample EE0163, 21.8cm; JY163-36, NHM. **Fig.2:** *H. carteri* HO-perforate. LM of holococcolith in distal view, XPL; UM42, sample DD01364, 28.65cm; DD01364-1/9, NHM. **Fig.3:** *S. dalmaticus* or *H. carteri* HO-perforate. LM of holococcolith in distal view, XPL; BC3, sample EE0161, 18.8cm; Ret-EE0161/8, NHM. **Fig.4:** Transitional form of *H. carteri* HO-perforate and *H. carteri* HO-solid (*S. catilliferus*). SEM of holococcolith in distal view; BC19-MD69, sample AA09330, 30cm; original videoprint, Daniela Crudeli (DC). **Fig.5:** *H. carteri* HO-solid (*S. catilliferus*). LM of holococcolith in distal view, XPL; UM42, sample DD01364, 28.65cm; DD01364-1/33, NHM. **Fig.6:** *H. carteri* HO-solid. LM of holococcolith in distal view, XPL - note higher birefringence of main mass and central boss with respect to Pl.2, Fig.5; UM42, sample DD01364, 28.65cm; DD01364-varie/15, NHM. **Fig.7:** Overgrowth on *H. carteri* holococcoliths. XPL; UM42, sample DD01364, 28.65cm; DD01364-varie/2, NHM. **Fig.8:** *S. schilleri*. SEM of holococcolith in distal view; BC3, sample EE0163, 21.8cm; JY163-23, NHM. **Figs 9, 10:** *S. schilleri*. LM of holococcolith in distal view; UM42, sample DD01364, 28.65cm; 9, XPL, DD01364-varie/20, NHM, 10, PC, same specimen, DD01364-varie/19, NHM. **Fig.11:** *S. ponticuliferus*. SEM of holococcolith in distal view; SL29, sample HH01178, 15.5cm; 215-12, Dept. of Geosciences, Milan. **Fig.12:** *C. leptoporus* ssp. *quadriperforatus* HO. LM of holococcolith in distal view, near *S. pulchra* HO *pirus*-type coccosphere, PC; BC3, sample EE0169, 29cm; coccosphere EE0169/2, NHM.

Plate 3

Scale-bar for LM images indicated in Figure 4, except for Figure 5 (shown separately)

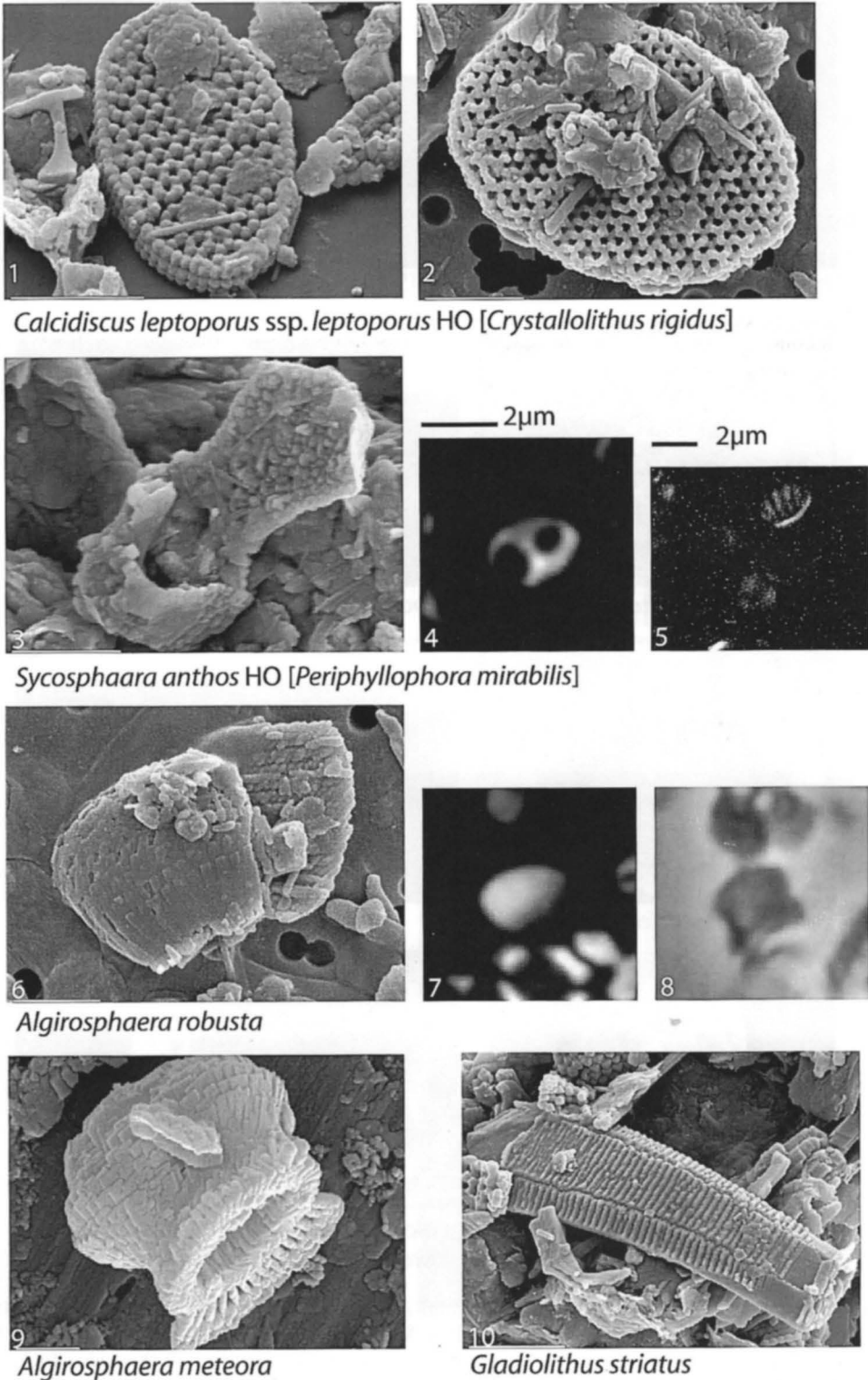


Fig.1: *C. leptoporus* ssp. *leptoporus* HO (*C. rigidus*). SEM of holococcolith in proximal view; BC3, sample EE0146, 0.8cm; JY155-11, NHM. **Fig.2:** *C. papillifera*. SEM of calyptrolith in distal view; BC3, sample EE0163, 21.8cm; JY163-22, NHM. **Fig.3:** *Syracosphaera anthos* HO. SEM of helladolith; PC60, sample HH1040, 206cm; JY173-92, NHM. **Fig.4:** LM of coccolith tentatively assigned to *Corisphaera/Zygosphaera*. XPL; UM42, sample DD01364, 28.65cm; DD01364-1/44, NHM. **Fig.5:** LM of Holococcolith type F - ?*Poritocolithus*. XPL; BC7, sample EE0372, 32.5cm; cocco-372, DC. **Fig.6:** *A. robusta*. SEM, broken into two halves; BC3, sample EE0163, 21.8cm; JY163-32, NHM. **Fig.7:** *A. robusta*. LM of coccolith in side view, XPL; UM42, sample DD01364, 28.65cm; DD01364-1/55, NHM. **Fig.8:** *A. robusta*. LM of coccolith in side view with preserved basal rim, PC; UM42, sample DD01364, 28.65cm; DD01364-1/53, NHM. **Fig.9:** *A. meteora*. SEM of rhabdolite with partially preserved rim; SL29, sample HH01178, 15.5cm; 215-06, Dept. of Geosciences, Milan. **Fig.10:** *G. striatus*. SEM of tabular coccolith in distal view - note inward curve of tabular coccolith covered by fine horizontal grooves; BC3, sample EE0161, 18.8cm; JY157-18, NHM.