VARIETY OF EXOTHECAL COCCOLITHS OF *SYRACOSPHAERA*

Lluïsa Cros

Institut de Ciències del Mar (CSIC), Passeig Joan de Borbó s/n, 08039, Barcelona, Spain

Abstract: Species of the genus *Syracosphaera* produce an outer coccolith layer, the exotheca. The coccoliths of this layer differ considerably from species to species. This study examines the diversity of the exothecal coccoliths of *Syracosphaera* species found in NW Mediterranean waters, presents 11 new records of exothecal coccoliths, and proposes a tentative classification of the exothecal coccoliths of *Syracosphaera*. Within the groups that emerge from this classification, it is possible to recognise common characteristics of the coccospheres that could be relevant for understanding the phylogeny of the genus.

Introduction

Syracosphaera is a diverse genus with a high number of extant species (Kleijne, 1993; Jordan & Green, 1994) but few fossil representatives (Perch-Nielsen, 1985). Due to the small size of the coccoliths of most *Syracosphaera* species and their low preservation potential (Young, 1998), the development of their systematic study has depended upon extant nannoplankton work using electron microscopy. The morphological complexity of this group, especially with regard to the presence or absence of an exotheca, has resulted in very different views regarding the characterisation of the genus (Gaarder & Heimdal, 1977; Okada & McIntyre, 1977; Jordan & Young, 1990). Moreover, representatives of *Syracosphaera* have also been observed as hetero-holococcolithophorid combination coccospheres (Cros *et al.*, 2000).

Most *Syracosphaera* species produce dithecate coccospheres. The inner layer, or endotheca, is composed of murolith-shaped coccoliths with characteristic structural features, normally termed caneoliths (Jordan *et al.*, 1995; Young *et al.*, 1997). All caneoliths have a central area floored by radiating laths, and the rim is rather variable, having one to three flanges on the outer wall; nonetheless the endothecal coccoliths are very similar in many different species. By contrast, the exothecal coccoliths of *Syracosphaera* are much more variable in morphology. But, in spite of their wide variety of shapes, all these exothecal coccoliths are grouped together as ‚cyrtoliths' (Jordan *et al.*, 1995; Young *et al.*, 1997). Arising from the Greek *kyrtós*, curved, the term cyrtolith (Braarud *et al.*, 1955) has undergone a complex evolution of meaning. It was used to designate the heterococcoliths in a calotte-like arrangement, including the calyptroform coccoliths of the family Rhabdosphaeraceae (Heimdal, 1993), but nowadays it only embraces the exothecal coccoliths of *Syracosphaera* species (Kleijne, 1992; Jordan *et al.*, 1995; Young *et al.*, 1997). Some authors have recognised differences in shape and distribution patterns in these exothecal coccoliths (Heimdal & Gaarder, 1981; Jordan *et al.*, 1995; Young *et al.*, 1997) but to date, there have not been any specific studies on this subject.

This study examines the diversity of exothecal coccoliths of *Syracosphaera* species found in the NW Mediterranean and presents a proposal for their classification, based on their morphology.

Material and methods

The material was collected by filtering NW Mediterranean sea-water obtained during several cruises of the Institut de Ciències del Mar (CSIC) carried out in 1995 (MESO-95, from 30th May to 16th June; FRONTS-95, from 17th to 23rd June), 1996 (MESO-96, from 18th June to 3rd July; FRONTS-96, from 16th to 21st September; FANS-1, from 1st to 8th November), 1997 (FANS-2, from 4th to 14th February) and 1999 (Hivern-99, from 20th to 28th February). For each sample, about 200ml of sea-water were filtered, using a vacuum pump, onto polycarbonate Nucleopore filters of 0.8µm pore-size and 25mm diameter. Salt was removed by rinsing the filters with ~2ml of tap-water. An aliquot of the filter was glued, with silver colloidal suspension, onto a SEM stub and coated with gold before examination of the specimens in an Hitachi S-57 SEM.

Tentative classification of the exothecal coccoliths of *Syracosphaera* species

The exothecal coccoliths of the dithecate *Syracosphaera* species found in the NW Mediterranean waters are grouped by morphological affinities to outline the present tentative classification. Some common *Syracosphaera* species not found in the study, but for which the exothecal coccoliths have been illustrated by other workers, are added as ‚other examples' to better illustrate the characteristics of some groups.

Most of the *Syracosphaera* species have flattened, exothecal coccoliths which exhibit a disc-like shape completely differentiated from the endothecal coccoliths. Others present exothecal coccoliths with a distinctly concavo-convex shape, and in some of these it is possible to distinguish as exothecal coccoliths real caneoliths, which sometimes are very similar to the endothecal ones.

Disc-like coccoliths: These coccoliths appear as planoliths; they are commonly flat and present a diversity of outlines and thickness. Usually, they are composed of three parts: (1) a central structure with two plates or an undetermined number of elements; (2) a radial cycle, with narrow elements; and (3) an external cycle, the rim, of broad elements.

Disc coccoliths: Large, circular, plate-like coccoliths with a central, conical protrusion. They cover the endothecal

caneoliths with overlapping disposition and, sometimes, entirely conceal the endotheca. Example: *Syracosphaera anthos* (Plate 1, Figures 3, 4).

Wheel-like coccoliths: Circular and flat coccoliths with characteristic long, narrow laths in the radial cycle and a central-structure of two plates. They cover the endothecal caneoliths with overlapping disposition and, sometimes, entirely conceal the endotheca. Examples: *Syracosphaera nodosa* (Plate 2, Figure 3) and *S.* sp. ,aff. *S. nodosa*' (*S.* cf. *S. nodosa* of Heimdal & Gaarder, 1981) (Plate 2, Figure 4).

Thin, (sub)circular coccoliths: Circular or subcircular sheet-like coccoliths which are very thin and flat. Examples: *Syracosphaera lamina* (Plate 2, Figure 1), *S. tumularis* (Plate 2, Figure 2), *S.* sp. type L of Kleijne (1993) (Plate 2, Figures 5, 7).

Oval coccoliths: Oval to elliptical coccoliths with longitudinal symmetry. They can be flat or have the central elements slightly raised. Examples: *Syracosphaera nana* (Plate 2, Figures 6, 8) and *S.* sp. ,aff. *S. nana*, very small' (Plate 3, Figures 5, 6).

Asymmetrical coccoliths: Asymmetrical, subcircular to subelliptical coccoliths with a rim which varies in width around the coccolith. Often, they appear grouped in an imbricate arrangement forming a ribbon of coccoliths (see Halldal & Markali, 1955), which can surround the endotheca. Examples: *Syracosphaera delicata* (Plate 3, Figures 1, 2), *S. bannockii* (Plate 3, Figures 3, 4), *S.* sp. ,aff. *S. orbiculus,* ovoid' (Plate 4, Figures 1, 3) and *S.* sp. ,aff. *S. orbiculus*, spherical' (Plate 4, Figures 2, 4).

Stratified coccoliths: Thick, multilayered coccoliths, apparently with a construction of stratified laminae. This stratification can be seen in distal view. They present an overlapping pattern around the endotheca. Example: *Syracosphaera* sp. ,with stratified coccoliths' (Plate 1, Figures 5, 6). Other example: *Syracosphaera* sp. type J of Kleijne (1993).

Undulating coccoliths: These are rather irregular, disc-shaped coccoliths, having a broadly convex distal side with an elliptical central depression. There is a distinct division into rim and central area. Individual elements are usually obscure. The central area usually displays parenthesis-shaped slits at the ends of the coccolith; these slits are more visible in proximal view. Based on their structural complexity, two groups can be distinguished:

Simple undulating coccoliths: Symmetrical and of simple elliptical shape. Usually very few coccoliths, only on one side of the coccosphere. Example: *Syracosphaera* sp.I cf. *S. epigrosa* of Kleijne (1993) (Plate 5, Figures 5, 6). Other example: *S. borealis* (see Winter & Siesser, 1994, p.135, fig.105, from C. Samtleben).

Complex, undulating coccoliths or deviating coccoliths: Asymmetrical and ornamented with lateral extensions and wing-like protrusions. These complex, undulating coccoliths are distributed, in an overlapping pattern, only around the apical pole of the cell. Due to their distribution, they have been called deviating coccoliths (Heimdal & Gaarder, 1981; Heimdal, 1993; Jordan *et al.*, 1995). Examples: *Syracosphaera molischii* (Plate 5, Figure 1), *S. ossa* (Plate 5, Figure 2), *S. marginaporata* (Plate 5, Figure 3), and *S.* sp.II cf. *S. epigrosa* of Kleijne (1993) (Plate 5, Figure 4).

Vaulted coccoliths: Exothecal coccoliths with a rounded dome-like structure have been designated as vaulted cyrtoliths (Jordan *et al.*, 1995) or dome-shaped cyrtoliths (Heimdal, 1993). They are distributed over the endotheca in a non-overlapping pattern. Examples: *Syracosphaera pulchra* (Plate 1, Figure 1) and *S. histrica* (Plate 1, Figure 2).

N.B. Studies on *Syracosphaera pulchra* have demonstrated that *S. pulchra* exothecal coccoliths show basically the same structure as the endothecal coccoliths (Inouyé & Pienaar, 1988). So, this group of vaulted exothecal coccoliths might be considered as inverted muroliths and close to the grouping of the caneoliths (see below).

Caneoliths: True exothecal caneoliths with a murolith morphology, a wall that can have laterally extending flanges and a central area floored by radiating laths. (See original descriptions in Braarud *et al.*, 1955; Heimdal, 1993; Jordan *et al.*, 1995.) In the studied samples, three different types were observed:

Elliptical caneoliths with flanges: Elliptical caneoliths with a proximal flange, an almost imperceptible mid-wall flange and a distal flange expanded outwards. These exothecal caneoliths have a delicate appearance and are larger, thinner, with higher walls and weaker central structures than their respective endothecal body caneoliths, with which they can be easily confused. They appear more concentrated near the apical pole. Examples: *Syracosphaera* cf. *S. dilatata* (Plate 6, Figures 1, 2) and *S.* sp. type D of Kleijne (1993) (Plate 6, Figures 3, 4).

(Sub)circular caneoliths with nodes: Rounded caneoliths with a beaded proximal flange, short wall and a very narrow, incipient distal flange. They do not posses a mid-wall flange. These exothecal caneoliths can be found all around the endotheca, but they are usually more frequent near the apical pole. Examples: *Syracosphaera prolongata sensu* Throndsen (1972) (Plate 7, Figures 3, 4) and *S. prolongata sensu* Heimdal & Gaarder (1981) (Plate 7, Figures 5-7). Other example: *S. pirus.*

N.B. Gaarder & Heimdal (1977) suggested, by analogy with *Syracosphaera pulchra,* that these exothecal coccoliths were disposed with their convex side outwards, *i.e.* that they were inverted relative to the endothecal caneoliths. However, careful examination of many specimens reveals that they are usually disposed with the convex side inwards, although they can be found in both positions, convex side outwards and inwards.

Elliptical caneoliths with nodes: Elliptical caneoliths ornamented by a characteristically beaded proximal flange. They have neither mid-wall flange nor distal flange. In

proximal view, they appear delicate and more ornamented than their respective endothecal body caneoliths, due to the more separated laths and the presence of the beads. They can be found all around the endotheca in a non-overlapping pattern. Examples: *Syracosphaera noroitica* (Plate 6, Figures 5, 6) and *S.* sp. type G in Kleijne (1993) (Plate 7, Figures 1, 2).

Syracosphaera rotula

Syracosphaera rotula (Plate 4, Figures 5, 6) has circular exothecal coccoliths which superficially look very like the exothecal coccoliths of *S. nodosa* and *S.* sp. ‚aff. *S. nodosa*'. They have a wide, radial cycle formed of long laths with sinistral obliquity, and a plate-like central area composed of two tiles. However, in *S. rotula* exothecal coccoliths, the outer part of the rim is bent through 90°, forming a real wall, and resembling the exothecal subcircular caneoliths. Nevertheless, the disposition on the coccosphere, with the convex side outwards, is similar to the disposition of the vaulted coccoliths. It can be suggested that *S. rotula* exothecal coccoliths could be a link between disc-like coccoliths and caneoliths.

Relationship between exothecal coccoliths and body caneoliths

The dithecate *Syracosphaera* species display relationships between the exothecal coccolith type and morphologic characters of the endothecal coccoliths (see Table 1). The species which possess vaulted exothecal coccoliths, *S. pulchra* and *S. histrica*, both exhibit circum-flagellar caneoliths with spines that have bifurcate endings. Species which have complex undulating coccoliths (deviating coccoliths) exhibit circum-flagellar caneoliths with spines, which divide into four at the tips; often, these species, also have an antapical spine-bearing caneolith. Species which have (sub)circular exothecal caneoliths with nodes exhibit circum-flagellar caneoliths with spines that have bifurcate endings and have a well-known tendency to form very long coccospheres. The species which possess exothecal elliptical caneoliths with a beaded proximal flange display a high varimorphism in their endothecal caneoliths.

Discussion and conclusions

This article describes, for the first time, 11 instances of exothecal coccoliths not previously recognised: *Syracosphaera* sp.I cf. *S. epigrosa* of Kleijne (1993), *S. marginaporata*, *S.* sp.II cf. *S. epigrosa* of Kleijne (1993), *S. tumularis*, *S.* sp. (aff. *S. orbiculus,* ovoid), *S.* sp. (aff. *S. orbiculus,* spherical), *S.* sp. (aff. *S. nana*, very small), *S.* cf. *S. dilatata*, *S.* sp. type D of Kleijne (1993), *S. noroitica* and *S.* sp. type G of Kleijne (1993). These observations, together with published studies (Gaarder & Heimdal, 1977; Okada & McIntyre, 1977; Winter *et al.*, 1979; Heimdal & Gaarder, 1981; Kleijne, 1993), indicate that exothecal coccoliths in the genus *Syracosphaera* show a great morphological diversity. These exothecal coccoliths are often disc-like, with a planolith morphology, but real caneoliths, with a murolith morphology, can be also found. Other exothecal coccoliths appear highly curved, such as the undulating (simple and complex) and the vaulted coccoliths, which can be modified planoliths and inverted muroliths, respectively. Among the disc-like exothecal coccoliths, we can distinguish the following kinds: disc, wheel-like, thin (sub)circular, oval, asymmetrical and stratified. Among the caneoliths, we can distinguish the following groups: elliptical with flanges, (sub)circular with nodes and elliptical with nodes. The exothecal coccoliths of *S. rotula* are difficult to classify within this scheme because they present intermediate features between the vaulted, wheel-like and the (sub)circular caneoliths.

There is a strong relationship between exothecal coccolith type, distribution pattern around the endotheca, general shape of the coccosphere, and characteristics of the endothecal caneoliths (*e.g.* number and type of flanges, possession and shape of circum-flagellar coccoliths). Because of these connections, the study and classification of exothecal coccoliths may be a useful tool to clarify the

Syracosphaera species	Exothecal coccolith type	Body caneolith flanges	Differentiated apical caneoliths
	DISC-LIKE COCCOLITHS		
S. anthos	disc coccoliths	proximal	yes, with robust spines
S. nodosa , *S.* sp. 'aff. *S. nodosa* '	wheel-like coccoliths	proximal	yes, with robust spines
S. lamina , *S. tumularis* , *S.* sp. type L of Kleijne	thin, (sub)circular coccoliths	proximal	no
S. nana , *S.* sp. 'aff. *S. nana* , very small'	oval coccoliths	proximal	yes, with small spines
S. delicata , *S. bannockii* , other *S.* spp.	asymmetrical coccoliths	proximal	yes, with spines
S. sp. (with stratified cyrtoliths)	stratified coccoliths	proximal	yes, with spines
	UNDULATING COCCOLITHS		
S. sp.I cf. *S. epigrosa* of Kleijne	simple, undulating coccoliths	proximal and distal	no
S. molischii , *S. ossa* , *S. marginaporata*, *S.* sp.	complex, undulating coccoliths	proximal and distal	yes, with four-ended spines
S. pulchra , *S. histrica*	**VAULTED COCCOLITHS**	proximal, mid-wall and distal	yes, with bifurcated spines
	CANEOLITHS		
S. cf. *S. dilatata* , *S.* sp. type D of Kleijne	elliptical caneoliths with flanges	proximal, mid-wall and distal	yes, with robust spines
S. prolongata (two different types)	(sub)circular caneoliths with nodes	proximal, mid-wall and distal	yes, with bifurcated spines
S. noroitica , *S.* sp. type G Kleijne	elliptical caneoliths with nodes	proximal	yes, with bi-ended long spines
	TRANSITIONAL FORM?		
S. rotula	wheel-like coccoliths 'with wall'	proximal and distal	no

Table 1: Relationship between exothecal coccolith type and endothecal caneolith characters.

taxonomic and phylogenetic relationships within the complex *Syracosphaera* genus.

Acknowledgements

I thank R. Margalef and M. Estrada for their direction and assistance. I thank also L. Arin for collecting the samples; J.M. Fortuño for the microphotography and assistance with the SEM; J. Biosca for technical assistance with the photography and D. Blasco for valuable criticisms. The manuscript was highly improved by the comments of the reviewers P.R. Bown and J.R. Young. The research was supported by the CSIC and the projects CODENET (EU-FMRX-CT97-0113), GRQ93-8041(CIRIT) and MAR98-0932 (CICYT). Samples were provided, too, by the project MAS3-CT95-0037.

References

Braarud, T., Deflandre, G., Halldal, P. & Kamptner, E. 1955. Terminology, nomenclature, and systematics of the Coccolithophoridae. *Micropaleontology*, **1**(2): 157-159.

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.

Gaarder, K.R. & Heimdal, B.R. 1977. A revision of the genus *Syracosphaera* Lohmann (Coccolithineae). *„Meteor" Forschungs-Ergebnisse, Reihe D,* **24**: 54-71.

Halldal, P. & Markali, J. 1955. Electron Microscope Studies on Coccolithophorids from the Norwegian Sea, the Gulf Stream and the Mediterranean. *Av. Ut. Av. Det. Norske Videnskaps-Akademi Oslo*, **No.1**: 5-28.

Heimdal, B.R. 1993. Modern Coccolithophorids. *In*: C.R. Tomas (Ed.). *Marine Phytoplankton. A Guide to Naked Flagellates and Coccolithophorids.* Academic Press Limited, London: 147-250.

Heimdal, B.R. & Gaarder, K.R. 1981. Coccolithophorids from the northern part of the eastern central Atlantic. II. Heterococcolithophorids. *„Meteor" Forschungs-Ergebnisse, Reihe D*, **33**: 37-69.

Inouyé, I. & Pienaar, R.N. 1988. Light and Electron Microscope Observations of the Type Species of *Syracosphaera*, *S. pulchra* (Prymnesiophyceae). *British Phycological Journal,* **23**: 205-217.

Jordan, R.W. & Green, J.C. 1994. A check-list of the extant Haptophyta of the world. *Journal of the Marine Biological Association UK*, **74**: 149-174.

Jordan, R.W., Kleijne, A., Heimdal, B.R. & Green, J.C. 1995. A glossary of the extant haptophyta of the world. *Journal of the Marine Biological Association UK*, **75**: 769-814.

Jordan, R.W. & Young, J.R. 1990. Proposed changes to the classification system of living coccolithophorids. *INA Newsletter*, **12**(1): 15-18.

Kleijne, A. 1992. Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Scripta Geologica*, **100**:1-63.

Kleijne, A. 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton).* Unpublished PhD thesis, FEBO, Enschede, The Netherlands, Vrije University, Amsterdam: 321pp.

Okada, H. & McIntyre, A. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, **23**(1): 1-55.

Perch-Nielsen, K. 1985. Cenozoic calcareous nannofossils. *In*: H.M. Bolli, J.B. Saunders & K. Perch-Nielsen (Eds). *Plankton Stratigraphy*. Cambridge University Press: 427-554.

Throndsen, J. 1972. Coccolithophorids from the Caribbean Sea. *Norwegian Journal of Botany*, **19**: 51-60.

Winter, A. & Siesser, W.G. 1994. Atlas of living coccolithophores. *In*: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press.

Winter, A., Reiss, Z. & Luz, B. 1979. Distribution of living coccolithophore assemblages in the Gulf of Eilat (Aqaba). *Marine Micropaleontology*, **4**: 197-223.

Young, J.R. 1998. Neogene. *In*: P.R. Bown (Ed.). *Calcareous Nannofossil Biostratigraphy*. British Micropalaeontological Society Publications Series/Chapman & Hall/Kluwer Academic Publishers: 225-265.

Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., van Niel, B.E., Romein, A.J.T. & von Salis, K. 1997. Guidelines for coccolith and calcareous nannofossil terminology. *Palaeontology,* **40**(4): 875-912.

Taxonomic appendix

Syracosphaera anthos (Lohmann, 1912) Janin, 1987
Syracosphaera bannockii (Borsetti & Cati, 1976) Cros *et al.*, 2000 (aff. *S.* sp. type K of Kleijne, 1993)
Syracosphaera borealis Okada & McIntyre, 1977
Syracosphaera delicata Cros *et al.*, 2000
Syracosphaera dilatata Jordan *et al.*, 1993
Syracosphaera histrica Kamptner, 1941
Syracosphaera lamina Lecal-Schlauder, 1951
Syracosphaera marginaporata Knappertsbusch, 1993 (*S.* sp. type H of Kleijne, 1993)
Syracosphaera molischii Schiller, 1925
Syracosphaera nana (Kamptner, 1941) Okada & McIntyre, 1977 (*S.* sp. type A of Kleijne, 1993)
Syracosphaera nodosa Kamptner, 1941
Syracosphaera noroitica Knappertsbusch, 1993 (orthog. emend. Jordan & Green, 1994) (*S.* sp. type E of Kleijne, 1993)
Syracosphaera orbiculus Okada & McIntyre, 1977
Syracosphaera ossa (Lecal, 1966) Loeblich & Tappan, 1968
Syracosphaera pirus Halldal & Markali, 1955
Syracosphaera prolongata Gran *ex* Lohmann, 1913
Syracosphaera pulchra Lohmann, 1902
Syracosphaera rotula Okada & McIntyre, 1977
Syracosphaera tumularis Sánchez-Suárez, 1990 (*S.* sp. type C of Kleijne, 1993)

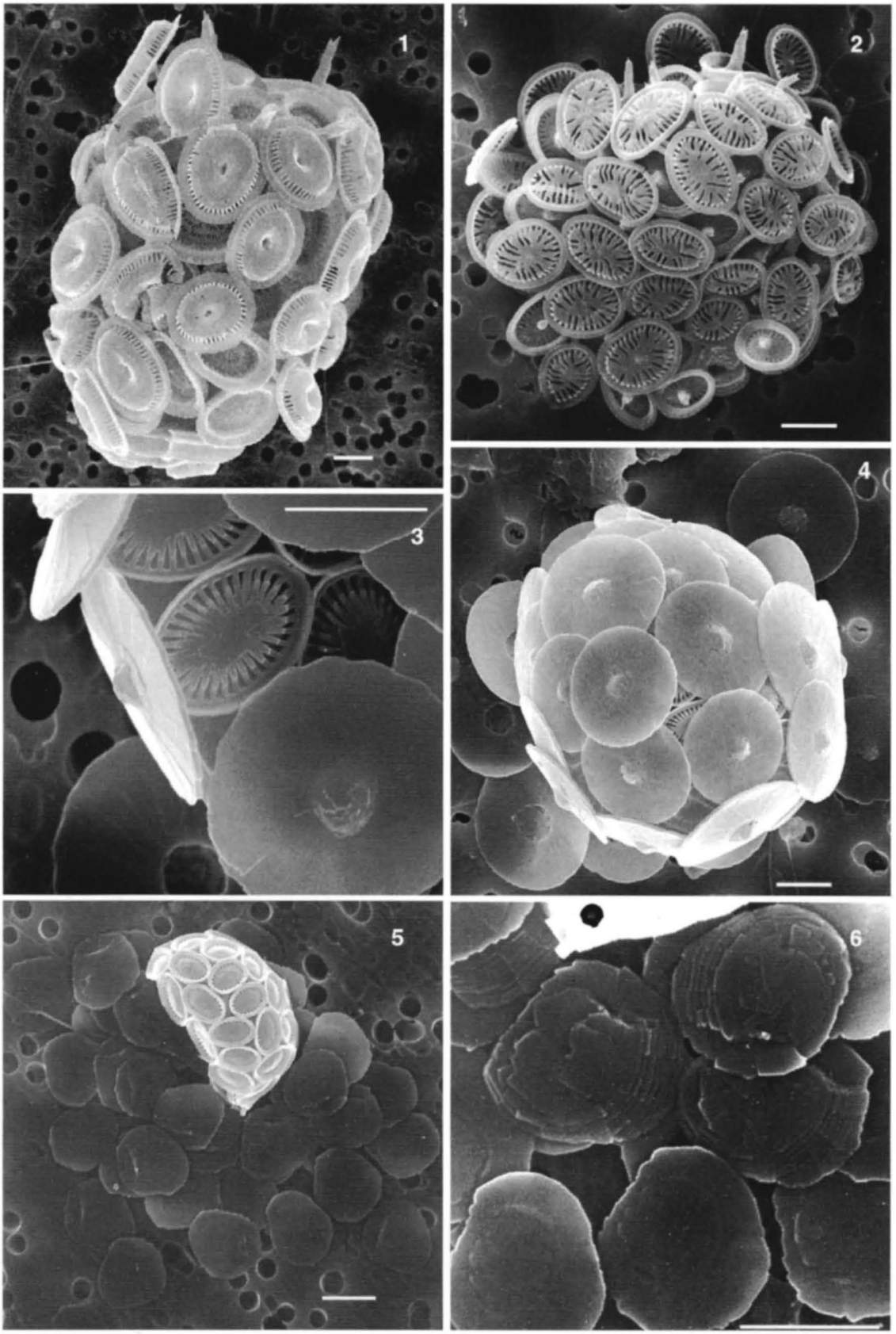

Plate 1: *Syracosphaera* exothecal coccoliths. Scale bars = 2µm. **Figs 1, 2: Vaulted coccoliths: Fig.1**: *S. pulchra* with exothecal coccoliths all around the coccosphere. FRONTS-96, St. 038 (41°51'N, 3°12'E), 15m. **Fig.2**: *S. histrica* with exothecal coccoliths all around the coccosphere. MESO-95, St. 161 (38°59'N, 0°16'E), surface. **Figs 3-5, 6: Disc-like coccoliths: Figs 3, 4: Disc coccoliths: Fig.3**: Detail of *S. anthos* coccoliths. In the middle (left) a disc coccolith in latero-distal view exhibiting the central, hollow, conical protrusion. MESO-96, St. G2 (41°21'N, 2°34'E), 70m. **Fig.4**: *S. anthos* covered by the exothecal coccoliths in overlapping position. FRONTS-96, St. 013 (41°18'N, 3°51'E), 66m. **Figs 5, 6: Stratified coccoliths: Fig.5**: *Syracosphaera* sp. ,with stratified coccoliths'. The exothecal coccoliths are figured in detached position. MESO-96, St. D8 (41°02'N, 3°49'E), 70m. **Fig.6**: Detail of the stratified coccoliths of Fig.5.

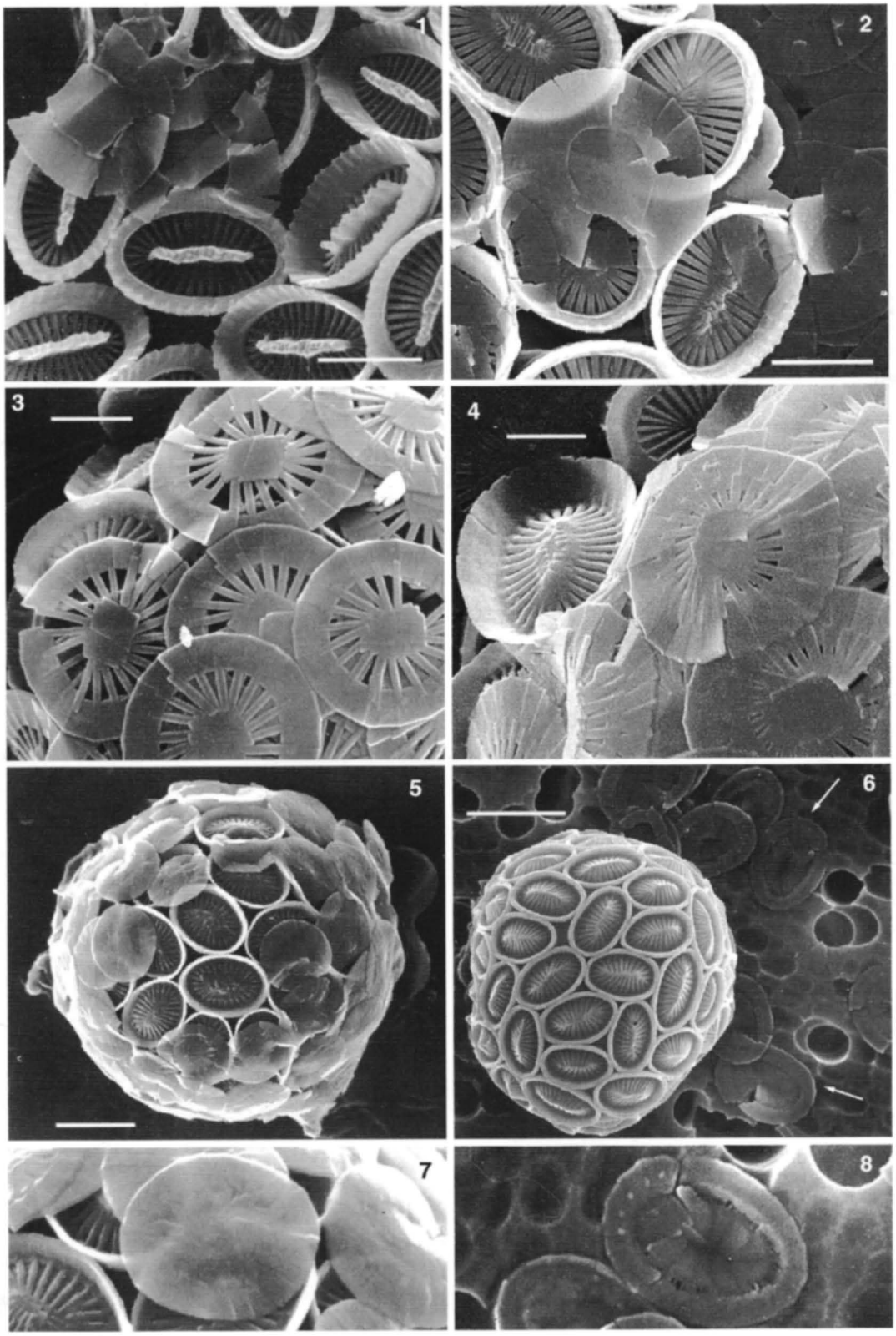

Plate 2: *Syracosphaera* exothecal disc-like coccoliths. Scale bars = 2µm (Figs 1, 2, 5, 6), 1µm (Figs 3, 4). **Figs 1, 2, 5, 7: Thin, (sub)circular coccoliths: Fig. 1**: Detail of *S. lamina* coccosphere exhibiting very thin, (sub)circular exothecal coccoliths (top left). FRONTS-95, St. 23D (40°40'N, 2°52'E), 70m. **Fig.2**: Detail of *S. tumularis* coccosphere exhibiting very thin, (sub)circular exothecal coccoliths; note the well-formed example in central position. Notice that Figs 1 and 2 are at the same scale. FRONTS-96, St. 019 (41°19'N, 3°33'E), 57m. **Fig.5**: *Syracosphaera* sp. type L of Kleijne (1993) exhibiting small, thin, (sub)circular exothecal coccoliths. MESO-95, St. 023 (40°12'N, 3°18'E), surface. **Fig.7**: Detail of Fig.5 showing the thin, (sub)circular exothecal coccoliths. **Figs 3, 4: Wheel-like coccoliths: Fig.3**: Detail of *S. nodosa* coccosphere exhibiting wheel-like exothecal coccoliths with large slits between the radial laths. FRONTS-95, St. 23D (40°40'N, 2°52'E), 50m. **Fig.4**: Detail of *Syracosphaera* sp. ‚aff. *S. nodosa*' coccosphere exhibiting wheel-like exothecal coccoliths clearly similar to those of *S. nodosa* but having a wider rim and a greater number of radial laths. Note that Figs 3 and 4 are at the same scale. Hivern-99, St. 25 (40°49'N, 2°44'E), 60m. **Figs 6, 8**: **Oval coccoliths: Fig.6**: Egg-shaped coccosphere of *S. nana* with detached oval exothecal coccoliths on the filter (see arrows). MESO-96, St. I3 (41°07'N, 2°26'E), 70m. **Fig.8**: Detail of the oval exothecal coccoliths from Fig.6.

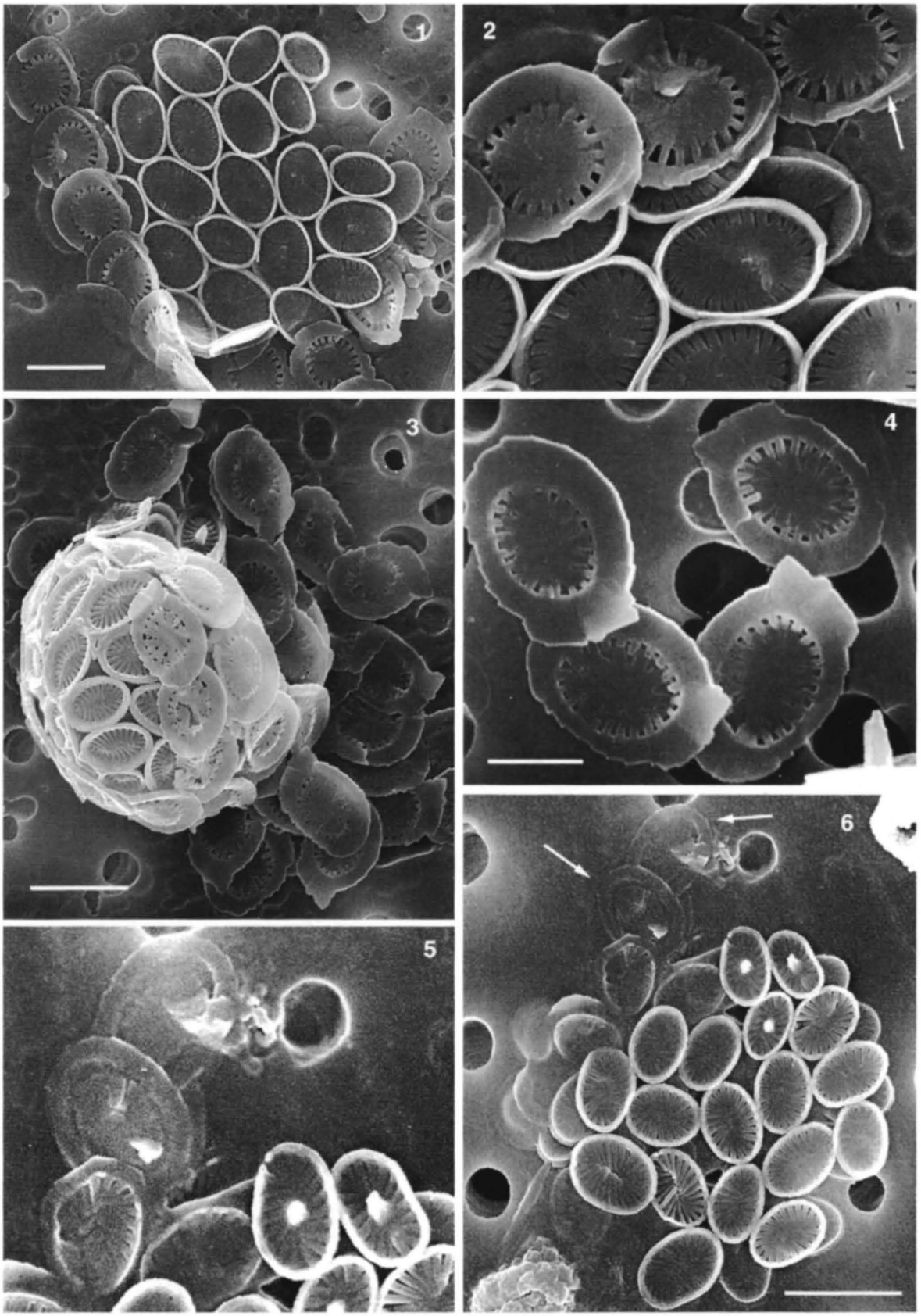

Plate 3: *Syracosphaera* exothecal disc-like coccoliths. Scale bars = 2µm (Figs 1, 3, 5, 6), 1µm (Fig.4). **Figs 1-4: Asymmetrical coccoliths: Fig.1**: *S. delicata* exhibiting a ribbon of asymmetrical exothecal coccoliths on the coccosphere (left side of figure). FANS-2, St. N7 (39°55'N, 0°52'E), 10m. **Fig.2**: Detail of Fig.1 showing the asymmetrical exothecal coccoliths in distal view at the top of the figure. Notice the ridge along part of the rim (arrow). **Fig.3**: Coccosphere of *S. bannockii* exhibiting asymmetrical exothecal coccoliths forming ribbons on the endotheca and other detached asymmetrical coccoliths around the coccosphere, on the filter. MESO-96, St. G2 (41°21'N, 2°34'E), 50m. **Fig.4**: Asymmetrical exothecal coccoliths of *S. bannockii*. MESO-96, St. E3-4 (41°23'N, 3°10'E), 40m. **Figs 5, 6: Oval coccoliths: Fig.5**: Detail of Fig.6 with the detached oval exothecal coccoliths at the top of the figure. **Fig.6**: *Syracosphaera* sp. ‚aff. *S. nana*' with oval exothecal coccoliths at the top of the figure (see arrows). FRONTS-96, St. 013 (41°18'N, 3°51'E), 60m.

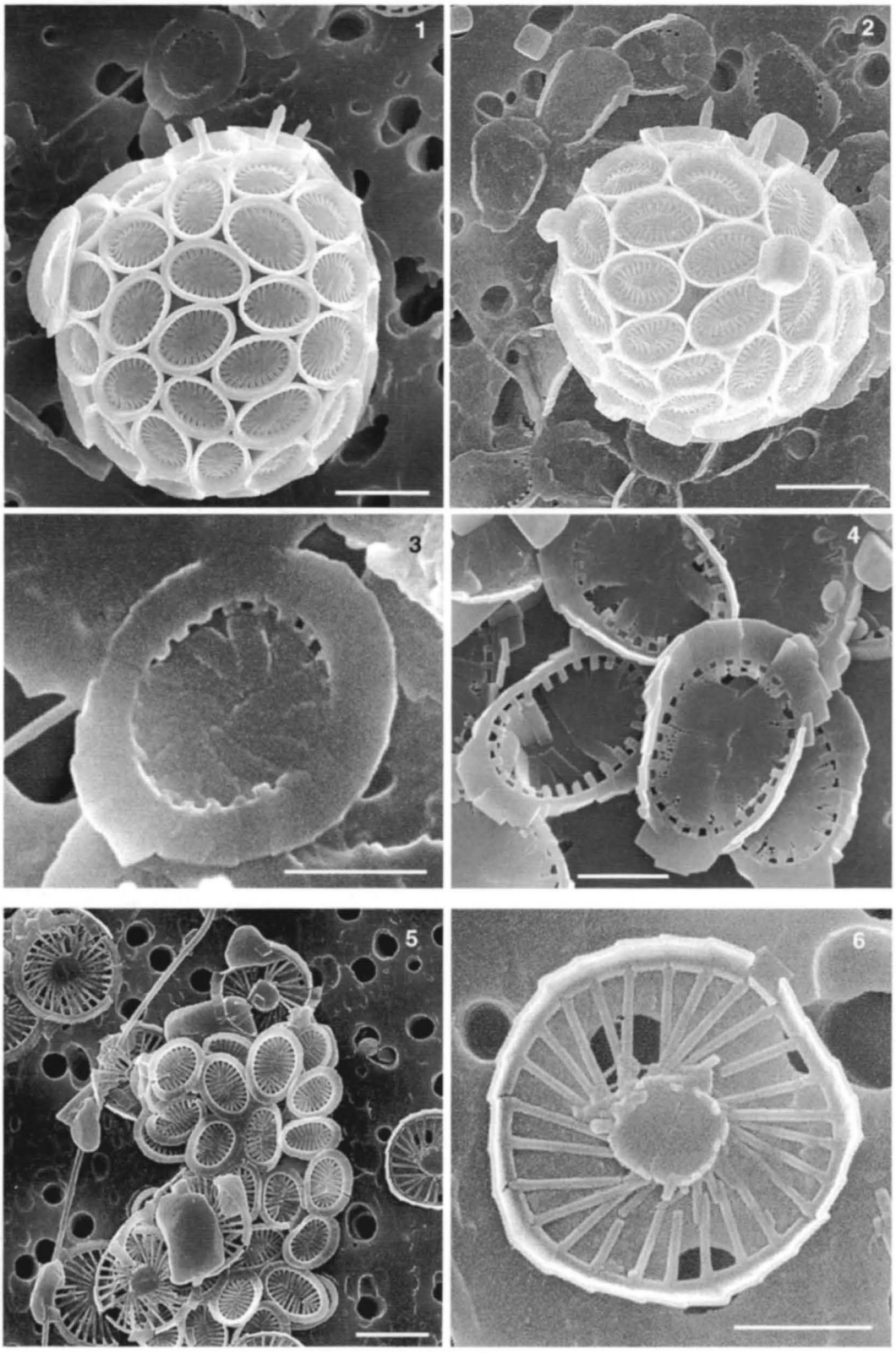

Plate 4: *Syracosphaera* exothecal coccoliths. Scale bars = 2µm (Figs 1, 2, 5), 1µm (Figs 3, 4, 6). **Figs 1-4: *Syracosphaera* asymmetrical coccoliths: Fig.1**: *Syracosphaera* sp. ‚aff. *S. orbiculus*, ovoid' exhibiting an asymmetrical exothecal coccolith on the coccosphere and another detached on the filter (top of the figure). FANS-2, St. M3 (40°11'N, 0°37'E), 10m. **Fig.2**: *Syracosphaera* sp. ‚aff. *S. orbiculus*, spherical' exhibiting asymmetrical exothecal coccoliths, detached, on the filter. Hivern-99, St. 25 (40°49'N, 2°44'E), 40m. **Fig.3**: Detail of the detached asymmetrical coccolith of Fig.1, in proximal view. Note the anticlockwise direction of the central elements. **Fig.4**: Different views of asymmetrical coccoliths of *Syracosphaera* sp. ‚aff. *S. orbiculus*, spherical'. Notice that longitudinal parts of the rim are bent, presumably in a distal direction (compare with specimens of *S. delicata* in Pl.3, Fig.2). Hivern-99, St. 25 (40°49'N, 2°44'E), 20m. **Figs 5, 6: *Syracosphaera rotula* exothecal coccoliths: Fig.5**: Collapsed coccosphere of *S. rotula* exhibiting endothecal and exothecal coccoliths. Hivern-99, St. 25 (40°49'N, 2°44'E), 20m. **Fig.6**: Detail, in proximal view, of one detached exothecal coccolith from the figured coccosphere of Fig.5. Notice the angular elements of the rim which form a wall all around the coccolith.

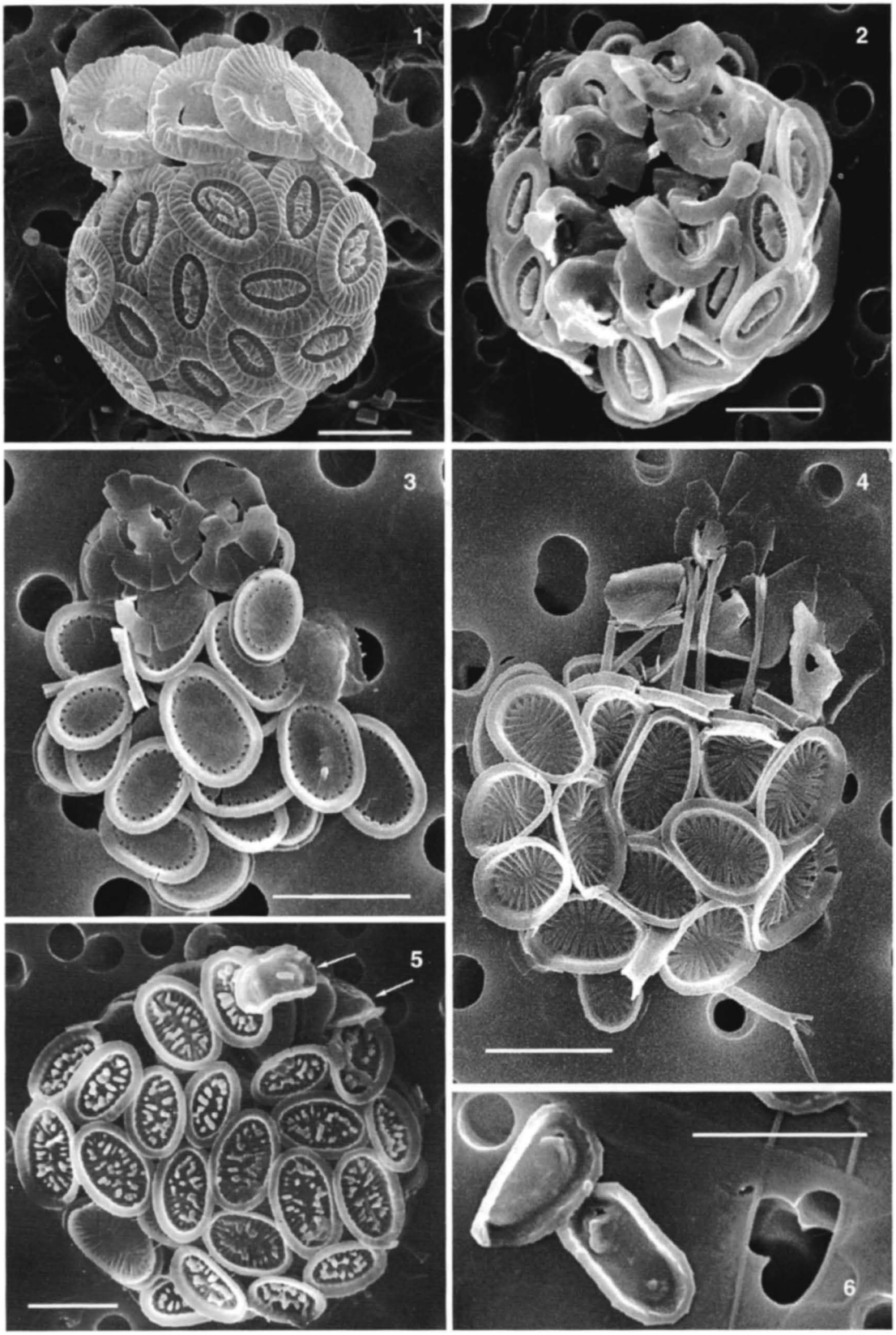

Plate 5: *Syracosphaera* exothecal undulating coccoliths. Scale bars = 2µm.. **Figs 1-4: Complex, undulating coccoliths (deviating coccoliths): Fig.1**: Coccosphere of *S. molischii* with the complex undulating coccoliths in apical position. Note antapical spine-bearing coccolith. MESO-96, St. I6 (40°49'N, 2°43'E), 70m. **Fig.2**: Coccosphere of *S. ossa* in apical view exhibiting complex undulating coccoliths around the apical pole. FRONTS-96, St. 027 (41°46'N, 3°03'E), 5m. **Fig.3**: Collapsed coccosphere of *S. marginaporata* exhibiting complex undulating coccoliths at the top. FRONTS-96, St. 013 (41°18'N, 3°51'E), 60m. **Fig.4**: Coccosphere of *Syracosphaera* sp.II cf. *S epigrosa* of Kleijne (1993) exhibiting complex, undulating coccoliths in apical position, next to the spine-bearing circum-flagellar caneoliths. Notice the characteristic caneolith with spine in antapical position. FRONTS-96, St. 013 (41°18'N, 3°51'E), 60m. **Figs 5, 6: Simple, undulating coccoliths: Fig.5**: Coccosphere of *Syracosphaera* sp.I cf. *S epigrosa* of Kleijne (1993) with simple, undulating coccoliths (top right, see arrows). MESO-96, St. E8 (40°55'N, 3°37'E), 40m. **Fig.6**: Two simple, undulating exothecal coccoliths. FANS-1, St. 100-113 (40°17'N, 0°55'E), 40m.

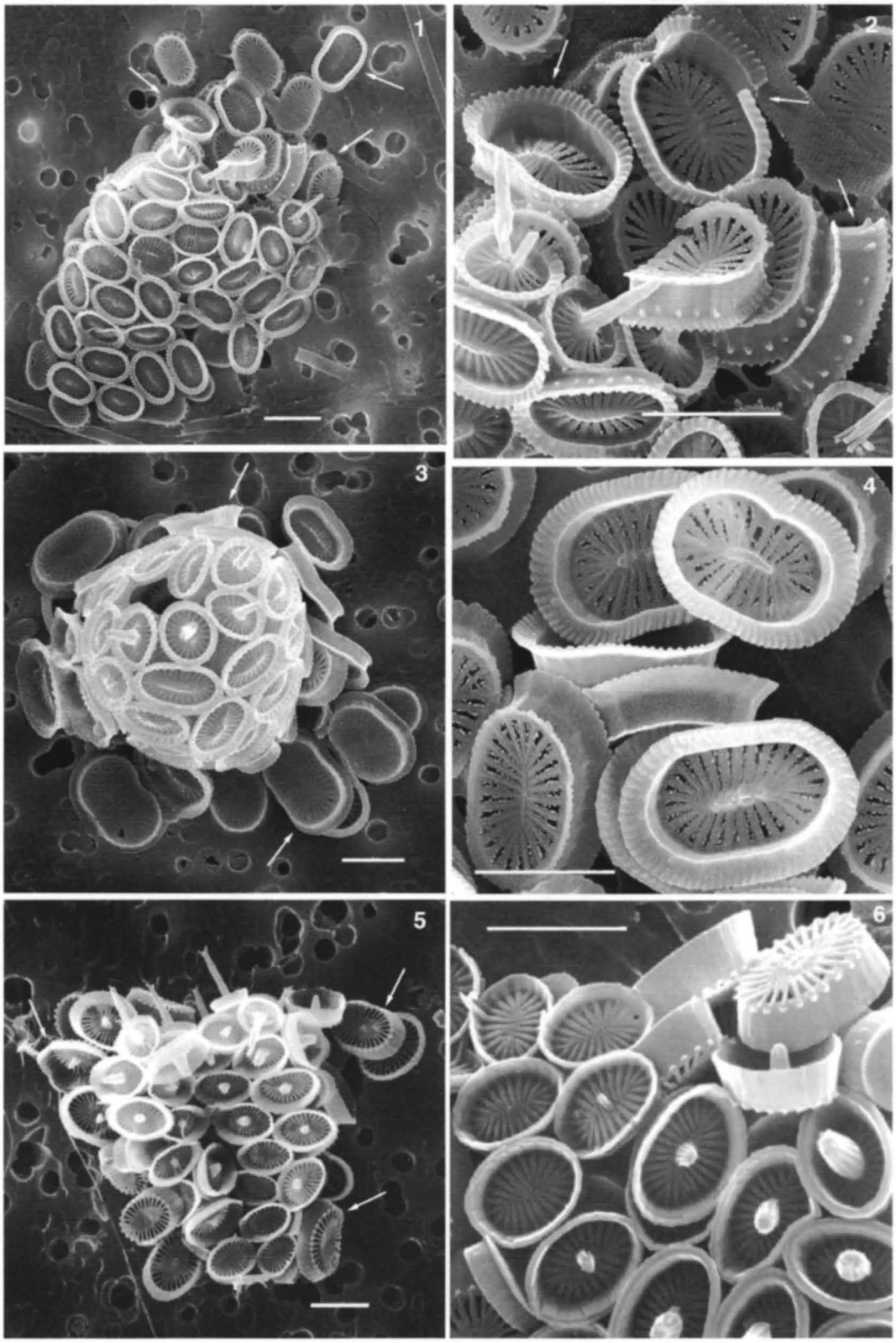

Plate 6: *Syracosphaera* exothecal caneoliths. Scale bars = 2µm. **Figs 1-4: Elliptical caneoliths with flanges: Fig.1**: Coccosphere of *S.* cf. *S. dilatata* with exothecal caneoliths in the apical area and in detached position (top of figure, see arrows). MESO-96, St. I2 (41°13'N, 2°20'E), 40m. **Fig.2**: Detail of Fig.1 with the exothecal caneoliths at top right. Notice the larger exothecal caneoliths (see arrows) in front of the endothecal ones (bottom left corner). **Fig.3**: Coccosphere of *Syracosphaera* sp. type D of Kleijne (1993) exhibiting the exothecal caneoliths (see arrows) around it (some of them in detached position). Hivern-99, St. 25 (40°49'N, 2°44'E), 60m. **Fig.4**: Exothecal caneoliths of *Syracosphaera* sp. type D of Kleijne (1993). FRONTS-96, St. 013 (41°18'N, 3°51'E), 66m. **Figs 5, 6: Elliptical caneoliths with nodes: Fig.5**: Coccosphere of *S. noroitica* exhibiting some detached exothecal caneoliths with nodes forming a proximal flange (see arrows). MESO-96, St. E3-4 (41°23'N, 3°10'E), 70m. **Fig.6**: Detail of *S. noroitica* caneoliths. Notice (top right) some exothecal caneoliths exhibiting nodes in place of the proximal flange of the endothecal caneoliths. At bottom left corner there is an endothecal caneolith, in side-view, exhibiting the usual proximal flange. MESO-96, St. I8 (40°37'N, 2°55'E), 70m.

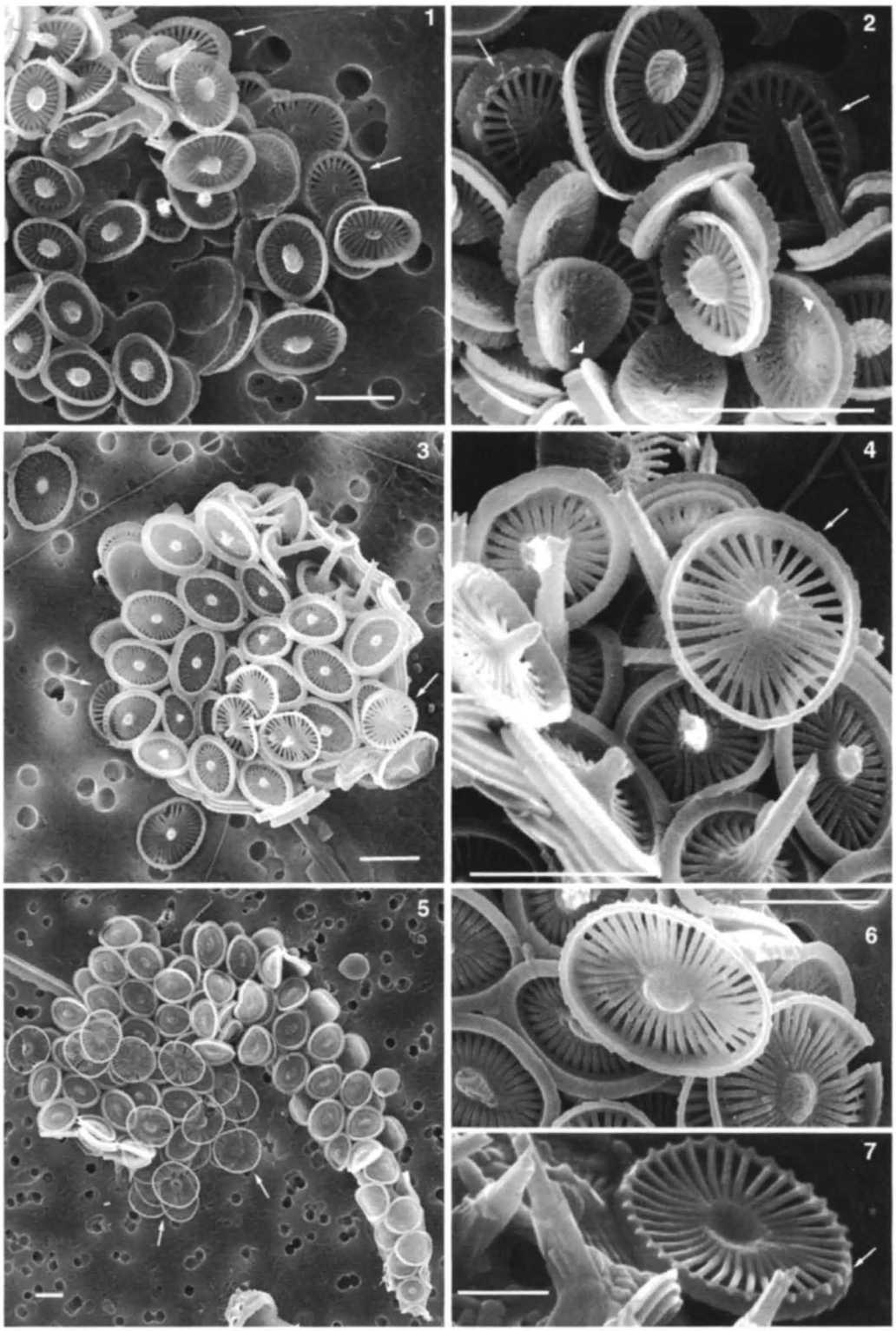

Plate 7: *Syracosphaera* exothecal caneoliths. Scale bars = 2μm (Figs 1, 3-6), 1μm (Fig.7). **Figs 1, 2: Elliptical caneoliths with nodes: Fig.1:** Collapsed coccosphere of *Syracosphaera* sp. type G of Kleijne (1993) with both, endothecal and exothecal caneoliths. The exothecal caneoliths possess nodes instead of the usual proximal flange (see arrows). MESO-96, St. G4 (41°08'N, 2°45'E), 70m. **Fig.2:** Endothecal and exothecal caneoliths of *Syracosphaera* sp. type G of Kleijne (1993). Notice the nodes of the exothecal caneoliths (arrows) and the usual proximal flange in the endothecal coccoliths (arrowheads). MESO-96, St. A5 (41°48'N, 3°57'E). **Figs 3-7: (Sub)circular caneoliths with nodes: Figs 3, 4**: *S. prolongata sensu* Throndsen (1972). **Fig.3**: Coccosphere exhibiting some slender exothecal coccoliths in their normal position on the coccosphere, and others, detached, showing the proximal nodes (arrows). FRONTS-96, St. 039 (41°35'N, 3°16'E), 10m. **Fig.4**: Detail of the three kinds of caneoliths: body caneoliths with their three flanges; circum-flagellar caneoliths with bifurcate spines; and exothecal caneoliths, in distal view, exhibiting an incipient distal flange (see arrow). FRONTS-96, St. 013 (41°18'N, 3°51'E), 10m. **Figs 5-7**: *S. prolongata sensu* Heimdal & Gaarder (1981). **Fig.5**: Coccosphere with several large, (sub)circular exothecal caneoliths near the apical area (see arrows). MESO-96, St. G4 (41°08'N, 2°45'E), 70m. **Fig.6**: Distal view of two slender exothecal caneoliths exhibiting the twisted central structure. FRONTS-96, St. 021 (41°12'N, 3°42'E), 68m. **Fig.7**: Exothecal caneolith in proximal view exhibiting the nodes (arrow) and the hollow central structure. FRONTS- 95, St. 23D (40°40'N, 2°52'E), 60m.